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Effect of Argentine ant invasions on ground-dwelling arthropods in northern California riparian woodlands

Abstract Although the Argentine ant (*Linepithema humile*) is a widespread invasive species that displaces native ants throughout its introduced range, the effects of these invasions on arthropods other than ants remain poorly known. This study documents the consequences of Argentine ant invasions on ants and other ground-dwelling arthropods in northern California riparian woodlands. Baits and unbaited pitfall traps were used to sample different components of the arthropod communities at five pairs of uninvaded and invaded sites. Sites occupied by Argentine ants supported almost no native epigeic ants except for the winter-active *Prenolepis imparis*. Sites with Argentine ants averaged four to ten times more ant workers than did sites with native ants, but ant worker biomass did not differ between uninvaded and invaded sites. Argentine ants recruited to baits in invaded areas, on average, in less than half the time of native ants in uninvaded areas. Despite the loss of epigeic native ants, higher Argentine ant worker abundance, and faster recruitment by Argentine ants at invaded sites, pitfall trap samples from uninvaded and invaded areas contained similar abundances and diversities of non-ant arthropods. These findings suggest that Argentine ants and the native ants they displace interact with the ground-dwelling arthropods of these habitats in a similar manner.

Key words Argentine ants · Biological invasion · Unicoloniality · Pitfall traps · California

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Introduction

Biological invasions are natural experiments useful for testing hypotheses concerning the structure of communities (Diamond and Case 1986; Vitousek et al. 1987; Lodge 1993). For example, the direct and indirect effects of invasions can expose important linkages within food webs (Zaret and Paine 1973; Spencer et al. 1991). Because natural experiments alter communities over temporal and spatial scales rarely attainable in manipulative field studies, they also yield general and realistic results (Diamond 1986). Although natural experiments have shortcomings (Diamond 1986; Underwood 1990), they may be the best way to assess the effects of widespread invasions. In this study, an ongoing invasion is used to assess the changes occurring to a community of ground-dwelling arthropods when native ants are replaced by invasive Argentine ants.

Although native to South America, the Argentine ant (*Linepithema humile*) has spread throughout the world via human commerce. Its introduced range now includes South Africa, Australia, southern North America, Chile, the Mediterranean, Bermuda, Madeira, and Hawaii (Passera 1994). First recorded in California in 1907 (Woodworth 1908), Argentine ants are now widely distributed, firmly established, and spreading in that state (Tremper 1976; Ward 1987; Knight and Rust 1990; Holway 1995; Human and Gordon 1996). In spite of its large introduced range, established populations spread slowly on their own (about 10–100 m year^{-1}; Crowell 1968; Erickson 1971; Holway 1995, in press a) because colony reproduction occurs solely by budding (Newell and Barber 1913). Argentine ant colonies, however, are readily introduced into new areas by humans and flooding (Newell and Barber 1913; Lieberburg et al. 1975).

Throughout their introduced range, Argentine ants competitively displace indigenous ants (Haskins and Haskins 1965; Crowell 1968; Fluker and Beardsley 1970; Bond and Slingsby 1984; Majer 1994; Cammell et al.

1996). In California, *L. humile* replaces numerous species of epigeic (i.e., above-ground-foraging) ants (Michener 1942; Erickson 1971; Tremper 1976; Ward 1987; Human and Gordon 1996), whereas hypogeic (i.e., below-ground- and leaf-litter-foraging) ants and the winter-active *Prenolepis imparis* appear less affected (Ward 1987). Although this pattern of replacement is well known, the degree to which worker abundance, worker biomass, and recruitment patterns change subsequent to invasion remains poorly understood.

Apart from displacing native ants, Argentine ants may disrupt communities in other ways as well. First, because they are omnivores (Newell and Barber 1913; Markin 1970a), Argentine ants might affect a variety of arthropod taxa through both predation and competition. For example, Cole et al. (1992) found that of the numerous endemic Hawaiian arthropods affected by Argentine ants, some were potential competitors (e.g., spiders and carabid beetles), and some were potential prey (e.g., collembolans, lepidopteran larvae, bee larvae, flies). Second, the Argentine ant is a unicolonial species forming supercolonies in which numerous queens and abundant workers mix freely among spatially separated nests (Newell and Barber 1913; Markin 1970b; Hölldobler and Wilson 1990). Perhaps due to this lack of intraspecific aggression, worker populations of unicolonial ants commonly reach high densities. If these densities exceed those attained by native ants, then Argentine ants may discover and recruit to resources more quickly and in higher numbers than do native ants, and might, in turn, impact arthropod populations through competition and predation. Third, Argentine ants lack important natural enemies in their introduced range. In South America, by contrast, phorid fly parasitoids may prevent Argentine ants from attaining the ecological dominance they exhibit in their introduced range (M. Orr and D.H. Feener, personal communication). Lastly, Argentine ants displace native ants. Given the importance of ants in many ecosystems (Hölldobler and Wilson 1990), the loss of native ants associated with Argentine ant invasions may give rise to a complex array of indirect effects (Bond and Slingsby 1984; Cole et al. 1992).

Using baits and pitfall traps, I sampled different components of the ground-dwelling arthropod community of northern California riparian woodlands to address the following questions. (1) How do ant species richness, abundance, biomass, and recruitment patterns compare between invaded and uninvaded areas? (2) Are non-ant arthropods less common or less diverse in areas with Argentine ants than in areas with native ants?

Materials and methods

Study area

This study was conducted in 1994–1996 along a 5-km stretch of Putah Creek (38°30′N, 122°00′W) between Lake Solano and Lake Berryessa in Yolo and Solano Counties, Calif., USA. This area experiences a Mediterranean climate with a cool wet season (November–April) and a hot dry season (May–October). The stretch of Putah Creek included in this study is low in elevation (50–150 m), flows perennially, and supports a continuous riparian corridor. The corridor is 15–50 m wide and consists primarily of *Populus fremontii, Juglans hindsii, Quercus lobata, Q. wislizenii, Aesculus californica,* and *Salix* spp. Surrounding habitats include grassland, *Q. douglasii* woodland, and chaparral. In this watershed, Argentine ants thrive in riparian woodland, but fail to occur in arid habitats such as grassland, oak woodland, or chaparral (Ward 1987). Argentine ants occur patchily in riparian woodlands along Putah Creek (Ward 1987), but are actively spreading in these habitats, displacing native ants as they advance (Holway 1995, in press a).

Ground-dwelling arthropods were sampled from five replicate blocks of sites along Putah Creek. Each block included one uninvaded site and one invaded site. Sites within each block were matched qualitatively for spatial proximity, perennial vegetation, and soil type. All sites were relatively undisturbed and ungrazed by livestock. Uninvaded and invaded sites were approximately spatially interspersed along the 5-km stretch of the creek used in this study. Although Argentine ants are spreading at all five invaded sites, the well-delineated nature of Argentine ant invasion fronts permits the unambiguous identification of invaded and uninvaded areas. Rates of diffusion of Argentine ants along Putah Creek suggest that the five invaded sites have supported Argentine ants for at least 5 years (Holway, in press a).

Pitfall trapping

Pitfall traps are commonly used to sample ants and other ground-dwelling arthropods (Porter and Savignano 1990; Cole et al. 1992). I used unbaited pitfall traps consisting of test tubes (18 mm inner diameter × 150 mm long) about 1/3 filled with a 1:1 solution of water and antifreeze (mostly ethylene glycol) (Majer 1978). The ethylene glycol solution killed and preserved entrapped arthropods. Each test tube was protected by a sleeve (an 18-cm piece of polyvinyl chloride tubing) inserted into the ground (Majer 1978). The openings of the sleeves were blocked between sampling periods. Twenty pitfall traps were placed (± 4 m apart) at each site for 2 weeks during each of four sampling periods (May, July, and September 1995, and January 1996). Thus, a total of 800 pitfall trap samples were collected in this study; 16 of these were discarded because the traps appeared disturbed by mammals. After removal from the field, the contents of each trap were rinsed with water and stored in 90% ethanol. All ants were sorted from non-ant arthropods and identified to species (identifications confirmed by P.S. Ward). Voucher specimens of ants have been deposited at the Bohart Museum of Entomology, University of California, Davis (UCDC). All non-ant arthropods were sorted to order and then to morphospecies. Isopods were sorted to genus using Smith and Carlton (1980). The number of morphospecies was used as a surrogate for the number of taxonomic species (as in Oliver and Beattie 1996). The biomass of ant samples was estimated using dry weight; all samples were oven dried at 60°C for 48 h (Tschinkel 1993).

Baiting

Baits were used to compare the recruitment behavior of Argentine ants and native ants. Baiting took place during three time periods (May, July, and September 1994) at three pairs of sites along Putah Creek. Each pair of sites included an uninvaded and an invaded area matched using the same criteria as in the pitfall trap design. All baiting was conducted on successive days and over narrow intervals of temperature (20–25°C) and time (0700–1000 hours). For each baiting experiment, 20 baits were placed 3–4 m apart in an approximately linear transect on bare ground and away from dense vegetation or deep leaf litter. Baits were canned tuna (≈2.5 g) and apple jelly (≈2.5 g) placed together on numbered index cards

(6.5 cm × 7.5 cm). Baits contained proteins, lipids, and carbohydrates and were highly attractive to the common, epigeic ants in these study areas (Holway, in press b). Recruitment was defined as ten workers of one species present simultaneously at a bait, except for the poorly recruiting *Formica* spp., for which the presence of five workers was considered sufficient.

Statistical analyses

The number of ant species, ant worker abundance, ant worker biomass, recruitment time, number of non-ant arthropod morphospecies, and non-ant arthropod abundance were compared between invaded and uninvaded sites using split-plot analysis of variance (ANOVA). There were two main effects for each split-plot ANOVA: (1) status (invaded or uninvaded), and (2) season (May, July, September, and January). Status was a whole-plot effect; season was a split-plot effect. Blocks of sites were random effects; status and season were fixed effects. For each ANOVA, data were pooled within a site and season. The ANOVAs with number of species (or morphospecies) as the dependent variable used the total number of species (or morphospecies) present within a site and season as data points. The ANOVAs with abundance, biomass, or recruitment time as the dependent variable used means (within a site and season) as data points. Worker abundance, worker biomass, recruitment times, and non-ant arthropod abundance data were $\log_{10}$-transformed prior to analysis to homogenize the variances. Cochran's test for homogeneity of variances verified that the variances within each ANOVA did not differ statistically from one another after transformation. Linear and quadratic contrasts (Kirby 1993) were used to describe seasonal trends in diversity, abundance, and biomass. All statistical analyses were performed in SYSTAT for Windows, version 5.03 (SYSTAT 1992).

Results

Effects on ants

Native epigeic ants failed to coexist with *L. humile* (Table 1); only 1.4% of the ant workers captured at invaded sites were native species. The only clear exception was *P. imparis*. Despite the large sampling effort ($\approx$400 pitfall trap samples), only a few other epigeic ants were recorded in areas occupied by Argentine ants, and these, given their low numbers, were probably strays (Table 1). Hypogeic ants, in contrast, appeared less affected (Table 1). Most of the native ants (58% of species, 70% of individuals) captured at invaded sites were hypogeic species. Of the 26 species of ants captured in this study (Table 1), all were native except for *L. humile* and the non-invasive pavement ant *Tetramorium caespitum* (present at one site only). The ants listed in Table 1 were similar to those found by Ward (1987) who, using different sampling techniques, found 28 species of ants at 12 uninvaded riparian sites located in the same general area as this study.

Sites invaded by Argentine ants supported, on average, less than half the number of ant species present at uninvaded sites (Fig. 1A; split-plot ANOVA: $F_{1,4} = 36.5$, $P = 0.004$). At uninvaded sites, the number of ant species captured remained constant between May and September (linear contrast: $F_{1,16} = 1.0$,

Table 1 Species of ants captured in pitfall traps in this study. Each table entry is the numerical abundance of each species in each sampling period summed across five sites

Species	Uninvaded				Invaded			
	May	Jul	Sep	Jan	May	Jul	Sep	Jan
Epigeic:								
Linepithema humile	–	–	–	–	4 422	15 146	7 553	774
Neivamyrmex cf. *nigrescens*	–	9	3	–	–	–	–	–
Crematogaster hespera	11	125	51	1	–	–	–	–
Messor andrei	1	–	–	–	–	–	–	–
Pheidole californica	–	–	–	–	–	1	–	–
Monomorium ergatogyna	141	692	131	–	–	4	5	3
Solenopsis xyloni	12	36	5	1	–	–	–	–
Tetramorium caespitum	12	57	2	–	–	–	–	–
Liometopum luctuosum	152	30	–	–	–	–	–	–
Liometopum occidentale	111	969	47	21	–	–	–	–
Dorymyrmex insanus	–	6	6	–	–	–	–	–
Tapinoma sessile	153	442	70	10	–	–	–	–
Camponotus essigi	–	1	–	–	–	–	–	–
Camponotus semitestaceus	1	13	8	–	–	–	–	–
Camponotus quercicola	–	1	2	–	–	–	–	–
Lasius alienus	49	157	10	–	–	–	–	–
Prenolepis imparis	27	–	1	58	18	–	–	82
Formica aerata	86	150	19	–	1	–	–	–
Formica moki	100	295	148	–	–	1	–	–
Hypogeic:								
Hypoponera opacior	2	14	12	7	5	13	11	1
Stenamma californicum	4	2	–	–	15	2	–	–
Stenamma diecki	7	1	–	8	4	6	2	2
Stenamma punctatoventre	5	–	–	–	9	–	–	–
Solenopsis molesta	15	136	44	–	17	51	29	–
Leptothorax andrei	–	9	3	–	–	11	2	–
Leptothorax nitens	12	118	26	–	10	61	21	–
Totals	901	3 263	588	106	4 501	15 296	7 623	862

$P = 0.340$). Native ants (with the exception of *P. imparis*), however, reduced their foraging in mid-winter (Table 1); this drop in wintertime activity brought the species richness of uninvaded sites down to levels typical of invaded sites and contributed strongly to the significant status × season interaction in the ANOVA (Fig. 1A; split-plot ANOVA: $F_{3,24} = 10.3$, $P < 0.001$). As at uninvaded sites, the number of ant species captured at invaded sites was constant from May to September (linear contrast: $F_{1,16} = 2.7$, $P = 0.120$).

Compared to traps in uninvaded areas, traps in invaded areas captured, on average, from four to ten times more workers (Fig. 1B; split-plot ANOVA: $F_{1,4} = 16.3$, $P = 0.016$) but contained similar worker biomass (Fig. 1C; split-plot ANOVA: $F_{1,4} = 2.0$, $P = 0.163$). Worker activity peaked in July for both uninvaded sites (quadratic contrast: $F_{1,24} = 19.3$, $P < 0.001$) and invaded sites (quadratic contrast: $F_{1,24} = 9.3$, $P = 0.005$). Worker biomass also peaked in July for both uninvaded (quadratic contrast: $F_{1,24} = 11.4$,

$P = 0.002$) and invaded sites (quadratic contrast: $F_{1,24} = 6.5$, $P = 0.017$). The biomass estimates at uninvaded and invaded sites were especially comparable in May and July when ants were most active (Fig. 1C). The discrepancy between worker number and worker biomass (Fig. 1B, C) resulted from the small size of *L. humile* workers relative to the larger epigeic ants they displace. (Only *Monomorium ergatogyna* and *Pheidole californica* minors are smaller than *L. humile*.) In addition to their higher numerical abundance in pitfall traps, Argentine ants were recovered from more traps in invaded areas than were the most common species of native ants in uninvaded areas (Table 2). When native ants are pooled, however, the numbers of pitfall traps containing Argentine ants in invaded areas and native ants in uninvaded areas differed only in January (Table 2).

Argentine ants recruited to baits, on average, in less than half the time it took native ants (taken collectively) to recruit (Fig. 1D; split-plot ANOVA: $F_{1,4} = 20.9$, $P = 0.045$). This disparity was most pronounced in September (Fig. 1D). The Argentine ant was the only species present at baits in invaded areas ($n = 180$) except for one bait at one site in May which attracted *P. imparis*.

Effects on non-ant arthropods

As assessed by pitfall traps, invaded areas and uninvaded areas supported similar numbers of ground-
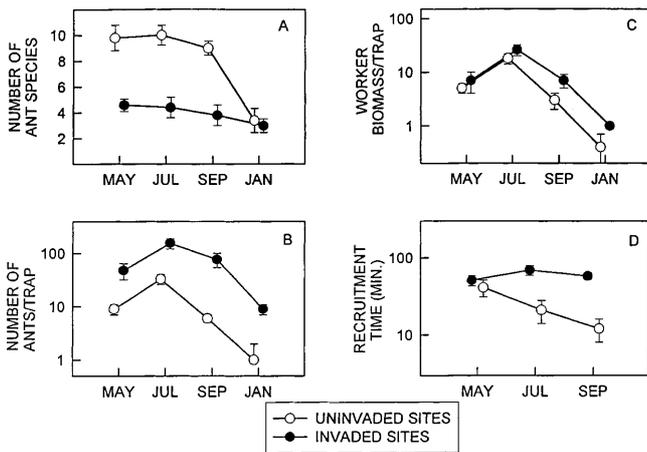
Fig. 1 A The number (mean ± 1 SE) of ant species at five uninvaded and invaded sites during four seasons. B The average number (±1 SE) of ant workers per pitfall trap at five uninvaded and invaded sites during four seasons. C The average biomass (mean dry weight in mg ± 1 SE) of ant workers per pitfall trap at five uninvaded and invaded sites during four seasons. D The average (±1 SE) recruitment time (to baits) at three uninvaded and invaded sites during three seasons
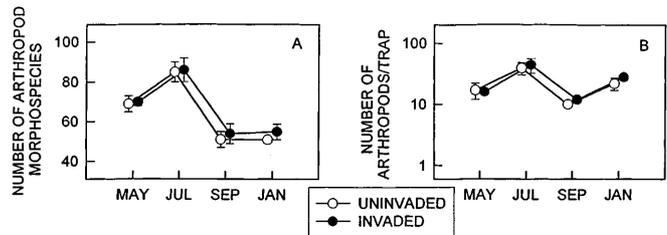
Fig. 2 A The number of (mean ± 1 SE) non-ant arthropod morphospecies at five uninvaded and invaded sites during four seasons. B The average (±1 SE) number of non-ant arthropods (excluding isopods) per pitfall trap at five uninvaded and invaded sites during four seasons

Table 2 The mean (±1 SE) proportion of pitfall traps that captured *Linepithema humile* at five invaded sites and all native ants, *Tapinoma sessile, Formica moki + Formica aerata, Liometopum occidentale + Liometopum luctuosum* at five uninvaded sites during each of four seasons. *Asterisks* indicate significant differences (Mann-Whitney *U*-tests; $P < 0.05$) between *L. humile* and each of the four native ant categories within each season. Because multiple comparisons were involved, α-values were adjusted (for four comparisons within each season) using the sequential Bonferroni procedure to keep α = 0.05 (Rice 1989)

Species	Season			
	May	July	September	January
L. humile	0.97 ± 0.03	1.0 ± 0.00	1.0 ± 0.00	0.92 ± 0.04
All native ants	0.87 ± 0.06	0.97 ± 0.02	0.86 ± 0.06	0.37 ± 0.13*
T. sessile	0.44 ± 0.15*	0.57 ± 0.15*	0.32 ± 0.28*	0.09 ± 0.03*
Formica spp.	0.43 ± 0.17*	0.60 ± 0.14*	0.44 ± 0.10*	0.00 ± 0.00*
Liometopum spp.	0.25 ± 0.05*	0.32 ± 0.07*	0.18 ± 0.07*	0.05 ± 0.03*

dwelling non-ant arthropod morphospecies (Fig. 2A; split-plot ANOVA: $F_{1,4} = 0.4$, $P = 0.59$). The number of non-ant arthropod morphospecies peaked in July for both uninvaded sites (quadratic contrast: $F_{1,24} = 28.2$, $P < 0.001$) and invaded sites (quadratic contrast: $F_{1,24} = 27.3$, $P < 0.001$). Uninvaded and invaded areas also supported similar abundances of non-ant, non-isopod arthropods (Fig. 2B; split-plot ANOVA: $F_{1,4} = 1.5$, $P = 0.28$). Data for isopods were analyzed separately because isopods were numerically dominant in pitfall trap samples (63% of all non-ant arthropods captured). Most ($\approx 90\%$) of the isopods captured were exotic species (*Armadillidium vulgare* and *Porcellio* spp.). Both the number of isopod morphospecies and isopod abundance were not significantly different between uninvaded and invaded sites (Table 3; split-plot ANOVAs: $P > 0.05$).

Data for spiders and carabid beetles were analyzed independently (in addition to being included in the non-ant analysis above) since these taxa were diverse and, as predators of arthropods, might compete with Argentine ants for food. The diversities and abundances of both spiders and carabids did not differ between uninvaded and invaded sites (Table 3; split-plot ANOVAs: $P > 0.05$). Moreover, the spider and carabid faunas of uninvaded and invaded sites were similar in their morphospecies composition. The abundances of spider and carabid morphospecies were highly correlated between invaded and uninvaded sites (spiders: $r = 0.94$, $n = 33$, $P < 0.001$; carabids: $r = 0.98$, $n = 32$, $P < 0.001$).

Discussion

Effects on ants

Although Argentine ants largely replaced epigeic ants, some native ants persisted in invaded areas. *P. imparis* stands out as the only epigeic ant that coexisted with the Argentine ant (Table 1; Tremper 1976; Ward 1987). The persistence of *P. imparis* in areas with *L. humile* may in part stem from the nearly non-overlapping phenologies of these two species. In California, *P. imparis* is most active in winter and early spring (Table 1; P.S. Ward, unpublished data), whereas Argentine ants are most active in summer and early fall (Table 1, Fig. 1B; Markin 1970b). Like *P. imparis*, hypogeic ants appear to coexist with Argentine ants (Table 1; Ward 1987). The mechanisms underlying this coexistence are unknown and deserve study.

As revealed by this study, the abundance and distribution of the Argentine ant along Putah Creek were in agreement with several features of its unique ecology. First, Argentine ants were only recorded from invaded areas (Table 1), evidence consistent with the hypothesis that colony reproduction in this species occurs only through budding and not through independent founding by queens that participated in mating flights. Second, high worker abundance (Fig. 1B) and saturation of the invaded habitat (Table 2) might be typical of unicolonial ants, which lack colony boundaries and occupy extensive networks of physically separated nests. Lastly, rapid recruitment to baits (Fig. 1D) is consistent with the strong competitive ability of this species (Human and Gordon 1996; Holway, in press b). Both large colony size and occupation of spatially separated nests presumably contribute to the Argentine ant's ability to locate and recruit to resources quickly.

Possible biases of pitfall trapping

Pitfall traps may provide biased estimates of ant abundance and biomass due to interspecific differences in recruitment behavior and susceptibility to capture (Adis 1979; Marsh 1985). These biases are probably small relative to the comparisons reported here (Fig. 1B, C, Tables 1, 2) for the following reasons. First, all common species of ants in this study could walk up and down the vertical glass walls of the test tubes; in this respect, their vulnerability to capture was similar. Second, the proportion of pitfall traps capturing each species was significantly correlated with the total number of workers captured ($r_s = 0.97$, $n = 26$, $P < 0.001$). This is evidence that pitfall traps sampled ants in proportion to their abundance. Third, ants probably did not recruit to

Table 3 Number of morphospecies and abundance per pitfall trap for isopods, spiders, and carabid beetles at uninvaded (*U*) and invaded (*I*) sites during four seasons. Table entries are means (± 1 SE) for five sites each. For each taxa, comparisons between uninvaded and invaded sites were not significantly different (split-plot ANOVA: $P < 0.05$)

Taxa	May		July		September		January	
	U	I	U	I	U	I	U	I
Number of morphospecies								
Isopods	3.4 ± 0.4	3.8 ± 0.2	3.0 ± 0.5	3.4 ± 0.4	2.2 ± 0.2	3.0 ± 0.3	3.2 ± 0.2	3.2 ± 0.4
Spiders	7.6 ± 1.0	7.8 ± 0.7	8.2 ± 1.5	8.6 ± 1.1	6.6 ± 0.8	6.8 ± 1.0	5.0 ± 0.8	6.0 ± 1.0
Carabids	6.6 ± 1.6	6.0 ± 0.8	7.4 ± 0.8	8.4 ± 0.5	4.8 ± 1.2	4.8 ± 0.9	4.8 ± 1.2	6.8 ± 0.8
Average number per pitfall trap								
Isopods	27.2 ± 9.8	34.6 ± 14.7	43.8 ± 23.2	90.7 ± 28.0	35.2 ± 13.6	58.2 ± 28.2	3.9 ± 1.2	3.9 ± 2.2
Spiders	2.5 ± 0.8	1.7 ± 0.4	5.1 ± 0.9	6.8 ± 0.9	1.7 ± 0.5	2.6 ± 0.2	1.9 ± 0.9	1.9 ± 0.4
Carabids	4.3 ± 1.0	2.8 ± 0.6	5.3 ± 1.5	5.3 ± 1.7	1.6 ± 0.2	4.0 ± 1.3	5.7 ± 1.8	9.6 ± 1.3

the unbaited pitfall traps used in this study. The high numbers of Argentine ants occasionally captured (e.g., >300/trap) probably reflect high levels of activity, since native ants with mass recruitment (e.g., *Solenopsis xyloni*, *M. ergatogyna*, *Tapinoma sessile*, and *Liometopum occidentale*) rarely occurred in high numbers in individual pitfall traps. Moreover, Argentine ants never occurred in high numbers in individual traps during the January sampling period despite being active (Table 1) and recruiting in large numbers to food resources during this period (D.A. Holway, personal observation). Nonetheless, the measures of abundance and biomass reported here should be interpreted as measures of activity and not absolute abundance or total biomass.

Effects on non-ant arthropods

As estimated using pitfall traps, the diversity and abundance of ground-dwelling arthropods at uninvaded and invaded sites were strikingly similar (Fig. 2). These results were unanticipated given the precedent for invasive ants to disrupt arthropod communities (Lubin 1984; Porter and Savignano 1990; Cole et al. 1992). The impacts on native arthropods reported by Porter and Savignano (1990) may have resulted partly from the much higher biomass of imported fire ants in invaded areas compared to that of native ants in uninvaded areas. This finding suggests that fire ants preyed on or competed with arthropods differently than did native ants (Porter and Savignano 1990). The impacts reported by Cole et al. (1992) on native arthropods might be attributed to the lack of native ants in the Hawaiian archipelago. Hawaiian arthropods might be especially vulnerable to predation and competition by introduced ants by virtue of this evolutionary naivité (sensu Diamond and Case 1986). The similar non-ant arthropod faunas of uninvaded and invaded sites reported in this study suggest that Argentine ants and native ants interact with the ground-dwelling arthropods captured by pitfall traps in a similar manner.

Although Argentine ants appeared not to disrupt present-day communities of ground-dwelling arthropods, the effects of Argentine ant invasions along Putah Creek and in other areas probably extend beyond the displacement of the native ant fauna. Such effects might have been difficult to detect in this study for several reasons. First, pitfall traps largely fail to capture highly sedentary arthropods (e.g., larvae of flies and beetles) or those that rarely occur on the ground. Although Argentine ants perhaps most often encounter ground-dwelling arthropods, *L. humile* also forages in trees where it frequently tends Homoptera (Newell and Barber 1913; Way 1963). The effects of Argentine ant invasions on Homoptera in natural communities are unknown, but the presence of Argentine ants in agricultural systems commonly results in irruptions of Homoptera (Newell and Barber 1913; Way 1963). Second, although community-based surveys such as this one

have numerous advantages, the effects of Argentine ants on rare taxa would evade detection with the methods used here. Third, the arthropod communities of Putah Creek experienced changes prior to invasion by Argentine ants, and species sensitive to these disturbances may have already been lost. For example, because more than half of the non-ant arthropod specimens captured in this study were introduced terrestrial isopods, native detritivores and species that interacted with them may have declined long before Argentine ants invaded these habitats. For this reason, the effects of Argentine ant invasions in more intact ecosystems in California (e.g., chaparral, serpentine grassland) might be different than those reported here. Lastly, immigration of arthropods from uninvaded to invaded sites could maintain populations of arthropods in invaded areas even if Argentine ants prevent such species from reproducing successfully (Pulliam 1988).

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