Effects of Argentine Ants on Invertebrate Biodiversity in Northern California

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Introduction

Although most biological invasions usually fail (Elton 1958; Simberloff 1981; Lodge 1993), some invasive species can change the composition and function of communities and ecosystems through competition, predation, and habitat alteration (Elton 1958; Simberloff 1981; Mooney & Drake 1986; Drake et al. 1989; Vitousek 1990). The effects of invasive ant species on native ant fauna have been described in many systems (Foster 1908; Crowell 1968; Haskins & Haskins 1965, 1988; Erickson 1971; Tremper 1976; Haines & Haines 1978; Clark et al. 1982; Lubin 1984; Medeiros et al. 1986; Ward 1987; Porter et al. 1988; De Kock 1990; Porter & Savignano 1990; Cole et al. 1992; Holway 1995). Most of these studies have reported striking declines in the abundance and species richness of native ants in areas invaded by exotic ant species, although particular groups of ants occasionally coexist with the invaders (Haskins & Haskins 1965, 1988; Ward 1987).

The effects of invasive ants on non-ant invertebrates have been less extensively studied than effects on other ant species. Invertebrate displacement by invasive species could have cascading effects on ecosystems because many invertebrates play important roles in ecosystem processes. Moreover, understanding how broad classes of organisms are associated with an invasive species can provide insight into the mechanisms of invasion and displacement. We compare the composition of invertebrate communities in areas invaded and uninvaded by the Argentine ant (*Lipepithema humile*). The Argentine ant is native to South America, and it is an increasingly common invasive species world-wide (Ward 1987; Holway 1995; Human & Gordon 1996).

Methods

Study Site

We conducted our study at Jasper Ridge Biological Preserve, a 480-ha reserve in northern California (San Mateo County 122°15′ to 122°12′30″W and 37°25′24″ to 37°25′N, 60–210 m elevation). Vegetation types found at Jasper Ridge include serpentine grassland, annual grassland, redwood forest, chaparral, evergreen forest, oak woodland, wetland, and riparian systems. Argentine ants have invaded approximately 30% of Jasper Ridge, primarily along the edges of the preserve (Human & Gordon 1996). Jasper Ridge is surrounded by residential and agricultural land, most of which has been invaded by Argentine ants.

Invertebrate Surveys

To sample invertebrate communities, we set up a pitfall trapping survey in late September 1994. We chose 20 sites in areas already invaded by the Argentine ant and 20 sites in areas that were not yet invaded and were at least 100 m from the invasion front. Sites with and without *L. humile* were matched by vegetation community. In each area five sampling sites were in grassland, seven in open oak woodland, four in closed canopy oak forest, and four in chaparral. Sites were separated by at least 50 m. We could not match sites according to distance from the edge of the preserve because Argentine ants have invaded from the edges, or according to elevation because at Jasper Ridge, areas invaded by *L. humile* tend to be lower than areas not invaded. Areas without *L. humile* were, on average, 55 m higher than areas invaded (mean ± SE, 104 ± 13 m for non-invaded areas, 160 ± 16 m for invaded areas).

At each of the 40 sites, we set four 40-mL vials (30 mm diameter) filled with 30 mL of a 1:1 mixture of water and ethylene glycol. Soil corers were used to remove a plug of soil with little disturbance to surrounding soil and litter, and traps were set flush with the soil surface. Tuna

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oil was smeared around the inside edges of two of the four traps at each site. Traps were collected after 48 hours.

Invertebrate Identification and Data Analysis

All ants, except for *Formica* spp., were identified to species after Holldobler and Wilson (1990) and Wheeler and Wheeler (1986). Invertebrates were identified at least to order, and more precisely when possible, using Milne and Milne (1980); Powell and Hogue (1979); Disney (1994); and Smith and Carlton (1989). Invertebrates that could not be identified to species were divided into morphological species (sensu Oliver & Beattie 1993). The identities of most specimens were confirmed by comparison to collections at the California Academy of Science. Voucher specimens are deposited in the California Academy of Science.

For all analyses we pooled invertebrates from pitfall traps in areas with *L. humile* and separately pooled invertebrates from pitfall traps in areas without *L. humile*. The number of individuals in each family of invertebrates collected in areas with and without *L. humile* were compared with chi-squared tests. When a family was divided into subgoups, individuals in all subgroups were included in the test. Invertebrates not identified to family, such as Collembola, were considered to belong to one family, which may underestimate diversity. We corrected for multiple comparisons using the sequential Bonferoni technique (Rice 1989). The diversity of the non-ant invertebrate families in areas with and without *L. humile* was compared with two diversity indices, Simpson's index D and Shannon and Weaver's H ($D = 1/\sum p_i^2$ and $H = -\sum p_i{*}ln(p_i)$, where p_i is the proportion of the family i in the total sample of individuals).

Non-ant invertebrates caught in pitfall traps were divided into the following four dietary categories: (1) predator; (2) herbivore; (3) parasite; and (4) scavenger, saprophage, or mycophage (Table 1). If individuals could not be identified specifically enough to assign to a dietary category, we excluded them from analysis. The diets of a few organisms fell into two or more categories. In these cases we divided the total number of individuals into the appropriate number of categories. For example, camel crickets (*Ceuthorphilus* sp.) feed on fungi and decaying organic matter as well as some live plant parts. We found 18 camel crickets and 6 (0.33 × 18) were assigned as mycophages, 6 as saprophages, and 6 as herbivores. We used a G test of independence to compare the fraction of non-ant invertebrates collected that fell into these four classes in Argentine ant-invaded and non-invaded areas.

Results

In areas invaded by *L. humile*, there were far fewer native ants (19 in invaded areas versus 1994 in non-invaded areas), and ant communities were less diverse (Tables 1 and 2). When all ants, including *L. humile*, were considered, there were far more individual ants in areas invaded (14,460 in invaded areas versus 1994 in non-invaded areas, Table 1). Total ant biomass was also higher in invaded areas (1.47 g in areas without *L. humile*, 2.22 g in areas with *L. humile*). Sixty-eight percent (13 of 19 individuals) of native ants caught in areas with *L. humile* were hypogaeic ants (*Leptothorax andrei* and *Solenopsis molesta*), which forage below litter or in soil. In areas without *L. humile*, hypogaeic ants represented less than 6% of the native ant individuals collected (113 of 1994 individuals).

Invertebrates sampled from traps with and without tuna oil were pooled before identification. There was no obvious difference between the two types of traps.

Several groups of invertebrates were entirely absent from, or extremely rare in, areas invaded by *L. humile*. There were no muscid flies (Diptera: Muscidae), very few phorid flies (Diptera: Phoridae), and no springtails (Collembola), cynipid wasps (Hymenoptera), ticks (Acarina: Ixodidae), or mites (Acarina: Areneae). In areas invaded by *L. humile*, sowbugs (Crustacea: Isopoda: Armadillidiidae) made up 66% of the total number of non-ant individuals caught in pitfall traps, whereas none were found in areas without *L. humile*. Camel crickets (Orthoptera: Gryllacrididae) and common black ground beetles (Coleoptera: Carabidae) were both more common in areas invaded by *L. humile* (Table 1).

In pitfall traps set in areas invaded by *L. humile*, we found 359 non-ant invertebrates, 237 of which were isopods. In areas without *L. humile*, we found 181 non-ant invertebrates. Twenty-six morphospecies in 19 non-ant invertebrate families were caught in pitfall traps in areas without *L. humile*, but only 14 morphospecies in 12 families were found in areas with *L. humile* (Table 1). In the areas invaded by *L. humile*, over 60% of the individuals caught in pitfall traps were of one family (Armadillididae, Isopoda). In areas not invaded by *L. humile*, five taxa (family or higher) were represented in the first 60% of all individuals caught: Muscidae and Phoridae (Diptera), Vespidae (Hymenoptera), Collembola, and Lepismatidae (Thysanura). Overall, areas without *L. humile* supported a more diverse assemblage of invertebrate families than invaded areas (Table 2).

The trophic structure of invertebrate communities was influenced by the Argentine ant invasion. When grouped by diet, the invertebrate communities sampled from invaded areas contained a larger fraction of scavengers (saprophages and mycophages) than did non-invaded areas (Fig. 1, $p = 0.001$, G test of independence with William's correction), and non-invaded areas contained larger fractions of predators, herbivores, and parasites than invaded areas (Fig. 1, $p = 0.001$, G test of independence with William's correction). The difference between communities in trophic structure is accounted for primarily by the numbers of scavengers in each area (52 individuals in areas not invaded, 253 in areas invaded).

Table 1. Invertebrates sampled in areas with and without Argentine ants.

					Number of individuals where L. humile	
Class	*Order*	*Family*[a]	*Genus/species*[b]	*Trophic class*[c]	*absent*	*present*
Insecta	Anoplura			P (3, 4)	2	
	Coleoptera	Carabidae*	*Pterostichus*	Pr (3)	4	39
		Staphylinidae		Pr (3)	2	8
	Collembola	*		M, S (3)	18	
	Diplura			Pr, V	3	2
	Diptera	Muscidae*	*Musca* sp.	S, V (2, 3)	37	
		Phoridae*	sp. A	Pr (6) (larvae)	9	1
			sp. B	Pr (6) (larvae)	10	2
			sp. C	Pr (6) (larvae)	5	
		Threvidae		(Pr (1, 3)	1	
		?		?		1
	Hemiptera	Lygaeidae	*Geocoris*	Sd, Pr (2)	2	
			sp. A	?	1	
	Hymenoptera	Formicidae*	*Formica* spp.		73	
			Camponotus semitestaceus		92	1
			Crematogaster coarctata		10	
			Leptothorax rudis		30	
			Linepithema humile			14,460
			Messor andrei		420	
			Leptothorax andrei		5	5
			winged male *Leptothorax*		1	
			Pheidole californica		109	4
			Prenolepis imparis		1170	1
			Solenopsis molesta		77	8
			Tapinoma sessile		7	
		Vespidae	*Vespula pennsylvanica*	Pr (2, 3)	31	28
		Cynipidae	sp. A	V (2, 3 larvae)	1	
			sp. B	V (2, 3 larvae)	3	
	Lepidoptera			V (3, 4 larvae)	1	1
	Orthoptera	Acrididae	sp. A	V (3)	1	
			sp. B	V (3)	1	
		Gryllidae	*Myrmecophila*	V, I (2)	1	
		Gryllacrididae*	*Ceuthorophilus*	S, M, V (3)		18
			Stenopelamatus	V (2, 3)		1
	Psocoptera			P (3)	4	
	Thysanura	Lepismatidae		S, M, V (3)	11	4
	Trichoptera			?	1	
Diplopoda				S (1)		1
Isopoda		Armadillidiidae*		M, S (1, 5, 7)		237
Arachnida	Acarina	Ixodidae		P (3)	1	
				P (3)	1	
				P (3)	1	
		Areneae		Pr (3, 4)	29	18

[a] *Asterisks indicate significant effects of* L. humile *invasion on the number of individuals collected in an invertebrate family or order:* $p < 0.05$, *sequential Bonferoni correction for multiple tests. Question mark indicates that the taxonomic group or trophic class could not be determined.*

[b] *Letters distinguish unidentified species of the same family.*

[c] *Trophic classes are coded as follows: Pr, predator; P, parasite; V, feeds on vegetative plant parts and/or plant exudate; M, mycophagic; S, saprophagic; Sd, feeds on seeds; and I, feeds on insect exudate. Numbers next to the trophic class indicate the source of diet information: 1, Essig 1958; 2, Powell & Hogue 1969; 3, Milne & Milne 1980; 4, Arnett & Jacques 1981; 5, Hogue 1993; 6, Disney 1994; 7, Smith & Carlton 1989. "Larvae" indicates that the trophic class refers to larval diet because adults rarely feed.*

Discussion

At our study site native ants have all but disappeared from areas invaded by *L. humile*. The disruption of native ant communities by invasive ants has been documented for a variety of invasive ants in many habitats. Some authors have speculated that predation and/or competition might help explain the displacement of na-

Table 2. Diversity of invertebrates in areas with and without Argentine ants.

Diversity of	L. humile*	*Diversity indices*	
		Simpson's (D)	*Shannon-H Weaver (e)*
All invertebrates			
	−	1.19	1.51
	+	1.05	1.17
Non-ant invertebrates			
	−	8.79	11.98
	+	2.21	3.76
Ants (Formicidae)	−		
		2.52	3.73
	+	1.00	1.01

**Areas without (−) and with (+)* L. humile *respectively.*

tive ants by invasive ones. At our site competition with the invasive Argentine ant is apparently important in the displacement of several native ant species (Human & Gordon 1996), and the role of predation is unclear.

Most of the native ant individuals collected in areas with *L. humile* were of hypogaeic species, whereas hypogaeic ants represent less than 6% of the native ant individuals collected from non-invaded areas. Ward (1987) found that below-ground foragers are less likely to be displaced than ants that forage above ground, presumably because they are less likely to interact with *L. humile*. Our results are consistent with his.

Although there are far fewer native ants in areas invaded by *L. humile*, there are almost 10 times more ants overall, and ant biomass is greater. Similar differences in the numbers of ants collected in areas invaded by invasive ants and areas not invaded have been reported elsewhere for other invasive ant species (Porter & Savignano 1990; Cole et al. 1992). Ants of many invasive species may be more numerous than native ants for several reasons, including the lack of territorial boundaries and intraspecific competition (Porter & Savignano 1990). There is no evidence that the high numbers of *L. humile* in the traps were mainly due to recruitment. There were more than 16,000 ants in the traps, which indicates that the ants could not escape the traps easily. Once an ant fell into a trap, it could not return to its nest to recruit nestmates.

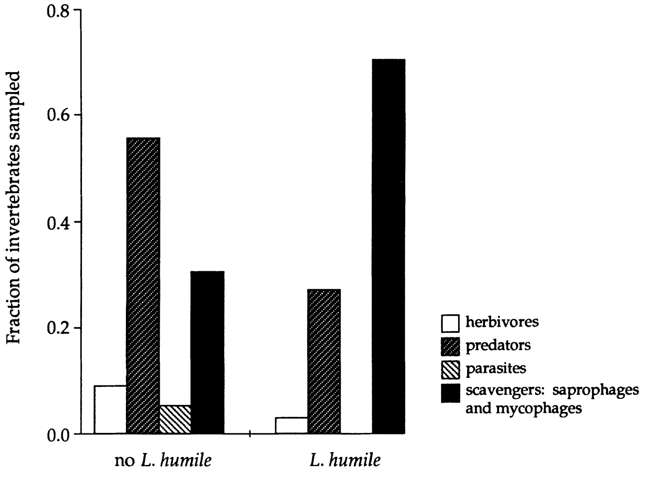

Figure 1. Trophic structure of invertebrates sampled in areas with and without L. humile. *When grouped by diet, the non-ant invertebrates sampled in areas with and without* L. humile *differed from each other. Invaded areas contained a larger fraction of scavengers (saprophages and mycophages) than non-invaded areas (overall* $p < 0.001$, *G test of independence).*

Non-ant invertebrate communities sampled from areas invaded by *L. humile* were, like native ant communities, less diverse than communities in non-invaded areas. Invertebrates belonging to several groups (Collembola, Diptera, Arachnida), were not found at all or were poorly represented in invaded areas, and a few groups were overrepresented (Carabidae, Isopoda, Gryllacrididae). This result may reflect seasonal activity patterns.

Changes in population sizes may be attributed to several factors: predation by the invasive ants, competition with them, dependence upon organisms displaced by invasive ants, or release from competition with organisms displaced by invasive ants. Although the majority of the Argentine ant diet is made up of exudate from phloem-feeding insects and the body fluids of dead organisms, Argentine ants occasionally preyed upon live invertebrates at our sites. Certain types of organisms, such as those that move slowly or cannot fly, may be more vulnerable than others to direct predation by *L. humile*. On several occasions we observed *L. humile* workers swarming around dying caterpillars, for example. Argentine ants have been reported to prey upon the eggs of some invertebrate families, including Neuroptera and Coleoptera (Driestadt et al. 1986; Way et al. 1992). Predation of Diptera eggs or larvae could explain lower numbers of flies in areas invaded by *L. humile*, and it is possible that juveniles or larvae of other groups may be vulnerable as well. Interference with the foraging activity of native ant species appears to be important in the displacement of native ant species (Human & Gordon 1996). Argentine ants may also interfere with the foraging activity of other organisms, such as spiders, decreasing foraging success and survival or encouraging emigration.

Organisms that thrive in areas with invasive ants may do so for many reasons. One reason is that an organism may resist displacement while its competitors or predators are displaced. Another reason is that protection by hard exoskeletons, chemical defenses, or habitats that do not overlap with those of *L. humile* might protect some invertebrates from predation or interference by invasive ants (Cole et al. 1992; Porter & Savignano 1990). For example, hard exoskeletons may afford some protection to the Coleoptera we found in abundance in areas invaded by *L. humile*.

Population sizes of various invertebrate species could also differ between invaded and non-invaded areas because of the disturbance history of the area and not because of invasive ants per se. To our knowledge there have been no published reports on the experimental introduction of any invasive ant species, so many studies, the present one included, potentially confound the effects of ant invasion with the disturbance history of an area. For example, it is possible that the isopods that we found in areas with *L. humile* were there because their distribution tracks disturbance, and not because of any relationship to the invasive ants or to changes in the invertebrate community caused by invasion. Collembola, which have been shown to be particularly vulnerable to disturbance (Springett 1976; Deharveng 1996), are less numerous in areas invaded by *L. humile*.

The trophic structures of invertebrate communities differed in invaded and uninvaded areas. Scavengers, in particular, were overrepresented relative to uninvaded areas, at the expense of herbivores, predators, and parasites. Scavengers, such as sowbugs (Isopoda: Armadillididae) and camel crickets (Orthoptera: Gryllacrididae), made up 70% of the insect communities sampled in invaded areas. Some researchers have suggested that numbers of scavengers could increase in the presence of invasive ants because significantly larger ant populations of invasive species lead to increased numbers of dead ants (Porter & Savignano 1990; Cole et al. 1992). Here, the higher ant numbers and ant biomass might account for the high proportion of scavengers in invaded areas.

Few studies have explored the relationship between the presence of invasive ants and diversity of the invertebrate community as a whole. Our results are compared with those of four similar studies in Table 3. The invasive ants studied, *Linepithema humile*, *Solenopsis wagneri*, *Anoplolepis gracilipes*, and *Wasmannia auropunctata*, are similar to each other in several respects: all feed on insect exudate of one type or another but

Table 3. Results from this study and four others on the effects of invasive ants on invertebrate communities.*

	This study Linepithema humile	*Cole et al. 1992* L. humile	*Porter and Savignano 1990* Solenopsis invicta	*Lubin 1984* Wasmannia auropunctata	*Haines and Haines 1978* Anoplolepis gracilipes (= A. longipes)
Ant, location	California	Hawaii	Texas	Galapagos	Seychelles
Capture technique	Pitfall traps	Pitfall traps, under rock surveys	Pitfall traps, baits	Under rocks, Sticky traps	Pitfall, visual
Taxa					
Coleoptera	++cara 0 staph	−−cara	0 −−scar		−
Dermaptera		−−	0		
Dictyoptera			++roach		++
Diptera	−−phor −−musc	0 phor, −native, ++non native	0		−
Hemiptera	−	−lyd	0		+
Homoptera				++cocc	++cocc
Hymenoptera (native ants)	−−		−−	−−	−−
Hymenoptera (other)	0 vp −cyn	−hyl	0		
Lepidoptera	0	−agros			+
Orthoptera	0, ++ceu		+		0
Thysanura	0	0			
Annelida		+			
Collembola	−−	−−			++
Chilopoda			0		
Diplopoda		++dimer	0		0
Gastropoda		−oxych			
Isopoda	++	+	−−		+
Mites/Ticks	−		−−eryth		
Arenea	−	−−	0	−−	−−
Scorpions				−−	

**The + indicates a slightly positive association reported between the invasive ant and the indicated taxon; ++ a significantly positive association; − a slightly negative association; −− a significantly negative association, and 0 indicates no difference between areas with and without invasive ants. Abbreviations indicate taxa that showed significant patterns: cara = Carabidae, staph = Staphyllinidae, phor = Phoridae, musc = Muscidae, vp =* Vespula pennsylvanica*, cyn = Cynipidae, ceu =* Ceuthorphilus*, lyd = Lydaeidae, hyl =* Hylaeus *sp., agros =* Agrostis *sp., dimer = native* Dimerogonus *sp., oxych =* Oxychilus *sp., scar = scarab beetles, eryth = Erythraeidae, cocc = Coccoidea. Cole et al. (1992) reported numbers of individuals caught per trap and numbers of traps or rocks in which particular taxa were found; Porter and Savignano (1990) reported species numbers and number of individuals; Haines and Haines (1978) reported the number of pitfall traps in which invertebrates of given taxa were found, and Lubin (1984) presents data on numbers of individuals only.*

also scavenge for food; all have diets and habitat requirements that are quite catholic; all are polygynous; and all may have relaxed or non-existent nestmate discrimination.

All of the three studies that measured changes in Collembola reported significant declines in their population sizes. The ubiquity of this response across several studies that all attempted to control for disturbance implies that there is an important interaction between Collembola and invasive ants that cannot be attributed to disturbance alone. Predation by the invasive ants, especially on immature Collembola, could be important, and further research is warranted.

In three of five studies, spiders, which are predators, were significantly more rare in areas invaded by exotic ants. The remaining two studies found non-significant declines in numbers of spiders in areas with Argentine ants. Competition for prey, and especially interference by *L. humile*, could be important in the displacement of spiders. Three of the four studies that considered native Diptera found them in significantly lower abundance in areas with invasive ants, and one found increased abundance of non-native flies in areas invaded by *L. humile*. Results for most of the other taxa were mixed. For example, we found an extremely strong positive association between Argentine ants and isopods, as did Cole et al. (1992) and Haines and Haines (1978), but Porter and Savignano (1990) report a strong decrease in the numbers of isopods in invaded areas. They speculated that some scavengers, such as roaches and a ground cricket that were over-represented in invaded areas, might thrive by feeding on dead ants; it is interesting that isopods, which are scavengers, responded in the opposite manner in their study (Porter & Savignano 1990). We have observed isopods inside the nests of Argentine ants that have been dug up for collection, but the relationship between the two species has not been studied. Several cases are known of isopods living as commensals in the nests of other ant species (review in Holldobler & Wilson 1990).

Broad surveys such as ours can be used to focus research programs on taxa that show interesting distribution patterns relative to invasive species or taxa representative of displaced organisms. Further studies are needed that consider the effects of invasion on organisms grouped by trophic class or habitat type. Such work may help explain how invasive species alter the ecology of native communities.

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