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LONG-TERM IMPACTS OF AN ARTHROPOD-COMMUNITY INVASION BY THE IMPORTED FIRE ANT, *SOLENOPSIS INVICTA*

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Abstract. Invasive ant species represent a serious threat to the integrity of many ecological communities, often causing decreases in the abundance and species richness of both native ants and other arthropods. One of the most in-depth and well-known studies of this type documented a severe impact of the imported red fire ant, *Solenopsis invicta,* on the **native ant and arthropod fauna** of a **biological field reserve** in central Texas (USA) during the initial invasion in the late 1980s. I sampled the community again in 1999, 12 years later, utilizing the same methodology, to compare the short- and long-term impacts of this invasion. Pitfall traps and baits were used to obtain quantitative measures of the **ant and arthropod community, and hand collecting was additionally employed** to determine the overall ant species composition. Although the abundance and species richness of **native ants and several other arthropod groups decreased precipitously immediately after the S. *invicta* invasion, all measures of native ant and arthropod species diversity had returned to preinvasion levels after** 12 years. *Solenopsis invicta* was still the most abundant ant **species, but not nearly as abundant** as it was during the initial phase of the invasion. The results of this study indicate that the impact of such invasive ants may be greatest during and shortly after the initial phase of an invasion.

Key words: ant abundance; arthropod community; biodiversity; diversity; exotic pests; Formicidae; interspecific competition; invasion; invasive species; Solenopsis invicta; *species coexistence; species richness.*

INTRODUCTION

Invasive ant species represent a serious ecological problem (Williams 1994). Numerous studies have doc**umented the effects of invasive ants on** native ant **and arthropod faunas** (e.g., see Bolger et al. **[2000], Gotelli and Arnett [2000], and Vanderwoude et al.** [2000] and references therein), and invasive ants may also detrimentally impact **vertebrate populations in infested areas (Allen et al. 1994, 1995, Haines et al. 1994, Moulis 1996).** Taken together, these studies generate dire predictions for the native fauna in the path of such an invasion.

Yet most investigations have characterized the impacts of invasive ants at a single point in time, often soon after the initial invasion, and long-term studies of the trajectory of such events are rare. Multiple surveys of the invasive *Pheidole megacephala* and *Linepithema humile* on Bermuda indicated the establishment of a sort of dynamic equilibrium after three decades of coexistence (Haskins and Haskins 1965, 1988, Crowell 1968, Lieberburg et al. 1975), **although the effects on other ant or associated arthropod species were not documented.** Anecdotal evidence indicates that invasive ant species may be naturally "tamed" over time (e.g., *Solenopsis geminata* in the Caribbean [Wilson 1971]). Thus, short-term impacts of invasive ant species may not accurately predict the long-term consequences on **the recipient arthropod community.**

One of the best-documented and frequently cited investigations of the community-level impacts of invasive ants is the work of Porter and Savignano (1990) on the initial invasion of a biological field reserve by *S. invicta* in the late 1980s. **Their study revealed** a 50%o decrease in ant species richness in infested areas, as S. *invicta* occupied >94% of the baits and accounted for >99% of the individual ants caught in pitfall traps. Numerous other arthropod groups were also negatively affected. Here I examine whether such an extreme degree of dominance by an invasive species foreshadows an ominous future for the biodiversity of infested areas. In 1999 1 sampled the ants and invertebrates in the same area by the same methodology, to compare the short-term vs. long-term effects of S. *invicta* on other ant and arthropod species.

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METHODS

This study was conducted at The University of Texas at **Austin's Brackenridge Field Laboratory (BFL) in Travis County,** Texas, USA (30°16' N, 97°43' W). BFL encompasses 32 ha of mixed forests and open grasslands. Pitfall traps and baits were used to assess the diversity and abundance of the ant community. Pitfall traps also provided quantitative evidence of the diversity and abundance of other arthropods. The methodology used by Porter and Savignano (1990) for pitfall traps and baits was replicated as closely as possible. Because baits were biased toward diurnally active ant species that recruited in large numbers, and pitfalls were biased against more sure-footed arboreal ant species, hand-collecting techniques were also employed to assess the overall ant species composition.

Pitfalls

Eight pitfalls were placed at each of 10 sites, for a total of 80 pitfalls. The 10 sites corresponded to Porter and Savignano's (1990) original five paired sites (five in an area that was infested with fire ants and five in a nearby area that was uninfested at the time). Pitfalls were placed 10 m apart along linear transects. The exact placement of the pitfalls was as close as possible to the original placement of Porter and Savignano's (1990) pitfalls, facilitated by a detailed map (see simplified reproduction in Porter and Savignano [1990]) and the use of natural and artificial landmarks (all transects were along roads or trails).

Pitfalls were set out for 48 h between 29 and 31 May 1999. Porter and Savignano (1990) ran pitfall traps for 48 h in May, July, and October of 1987. I only set out pitfall traps in May because of the great abundance and diversity of arthropods captured (see *Results,* below). As in Porter and Savignano (1990), each pitfall trap consisted of a half-pint canning jar (240 mL) buried up to the rim. A solution of 50% propylene glycol (diluted with water) served as a preservative. Unlike Porter and Savignano (1990), 1 did not use plastic cups as inner liners. I obtained the original data from Porter and Savignano's (1990) study and compared my May 1999 pitfall data with their May 1987 pitfall data.

As in Porter and Savignano (1990), all ants were identified to species. All other arthropods were identified to order and then sorted to morphospecies, except the Acari. Collembolans were not included as no comparative data were available from the 1987 pitfalls. Ant species diversity was calculated by the Shannon index *(H = -1* p; In p;, where p; is the proportion of individuals found in the ith species).

Baits

Baits were set out at 20 sites, corresponding to the 10 infested and 10 uninfested sites in Porter and Savignano (1990). Baits were spaced 10 m apart along linear transects. Sixteen sites had eight baits, while four sites had six baits, for a total of 152 baits, exactly as in Porter and Savignano (1990). As with the pitfalls, it was possible to use a detailed map of prior bait placement along with natural and artificial landmarks to locate the baits very closely to the sites used 12 yr prior. Each bait consisted of a plastic lid 8 cm in diameter that contained a few drops of a 1 mol/L sucrose solution and a freeze-killed cricket *(Acheta domestica L.),* exactly as in Porter and Savignano (1990). Crickets were pinned down so that they could not be carried away.

Baits were set out between 1500 and 1700 on 23 March and on 5 April 1999. I examined the baits 2-3 h after they were set out, and recorded the species of ants present and estimated numbers of individuals by class (1, 2, 5, 10, 20, 50, 100, 200, and 300 individuals), as in Porter and Savignano (1990). I obtained Porter and Savignano's (1990) original data from 13 and 27 March 1987 for comparison. I conducted my baiting trials slightly later in the season than Porter and Savignano (1990) because of cool weather in early March 1999. I waited for soil temperatures >20°C, to better replicate the conditions under which Porter and Savignano (1990) obtained their bait data.

Hand collecting

Hand collecting involved visual searches for foraging workers crawling on the ground and over vegetation. Rocks, leaves, and logs were overturned, woody vegetation was broken into, and leaf litter and soil were examined. Searches for ants were conducted diurnally and nocturnally. Leaf litter was sifted and ants were extracted by Berlese funnels and the Winkler method (see Ward [1987] for a description of this technique). Hand-collecting efforts were carried out between April and August 1999.

Hand collecting of ants has no direct analog with Porter and Savignano's (1990) methodology. The overall *pre-Solenopsis invicta* ant species composition of BFL was relatively well-known, however, as extensive collections had been made by competent myrmecologists. I searched through all available ant specimens collected at BFL and all available records of ant species present before the S. *invicta* invasion. Based on these pre-S. *invicta* records and the 1999 collections (including species discovered by hand collecting, pitfall traps, and baits), I generated a list of species known to be present at BFL before and --12 years after the S. *invicta* invasion.

Statistical analyses

The species richness, native-ant abundance, total ant abundance, and diversity of ants in pitfall traps were analyzed by repeated-measures ANOVAs. The within factor was sample date (1987 or 1999) and the between factor was whether the site was infested or not in the original sampling in 1987. The abundance of ants on baits was analyzed with a similar repeated-measures ANOVA. Ant abundances were log transformed in all analyses to normalize the distributions. Following the ANOVAs, the Bonferroni method of multiple comparisons was employed to generate four contrasts of interest at a family confidence level of a = 0.95 (Neter et al. 1985). These included: (1) a pairwise comparison of uninfested vs. infested sites in 1987, (2) a pairwise comparison of these same groups of sites in 1999 (now all infested), (3) a contrast between all sites in 1999

TABLE 1. Results of statistical analyses for the pitfall trap data.

ANOVA factor or Bonferroni contrast	Ant species richness	Native-ant abundance	Total ant abundance	Ant species diversitv
ANOVA results				
Sitet	0.11	0.05	0.006	0.003
Date$	<0.0001	0.0002	0.32	0.004
Site x Date	0.0007	0.009	0.0006	0.008
Bonferroni contrasts§				
1) Infested vs. uninfected sites in 1987	Ye	yes	yes	yes
2) Infested (in 1987) and uninfested (in 1987) sites in 1999	s	no	no	no
3) All sites in 1999 vs. uninfested sites in 1987	no	no	yes	no
4) All sites in 1999 vs. infested sites in 1987				

Notes: Numbers represent P values. "Yes" indicates that the contrast was significantly different.

t Infested or uninfested in 1987.

§ Contrasts of treatment means were evaluated by the Bonferroni method of multiple comparisons with a family confidence coefficient of 0.95 (Neter et al. 1985)

and infested sites in 1987, and (4) a contrast between all sites in 1999 and uninfested sites in 1987. Although Porter and Savignano (1990) compared infested and uninfested sites in 1987, the comparison is made here both for completeness and because I used a subset of their data (May sample only).

Because of unequal variances due to the near absence of native species at the 1987 infested sites, nonparametric tests were used to compare species richness and diversity of ants at baits. For both variables, Wilcoxon signed-rank tests were employed to test whether sites that were infested in 1987 were significantly different from sites that were uninfected in 1987, for both years (1987 and 1999). Data from all sites in 1999 were then pooled and a Kruskal-Wallis one-way **ANOVA** by ranks was employed, followed by a multiple-comparison procedure (Daniel 1990).

Mann-Whitney tests were used to compare abundances of individual ant species between years for both the pitfall trap and bait data. Mann-Whitney tests were also used to compare abundances and species richnesses of major taxonomic groups caught in the pitfall traps. When simultaneous Mann-Whitney tests were conducted among multiple taxa, no corrections were made for multiple comparisons. This allows for more direct comparisons with Porter and Savignano's (1990) data, to which no corrections for multiple comparisons were applied. StatView 5.0.1 (BAS Institute 1999) was used for all statistical analyses. Voucher specimens have been placed in the Texas Memorial Museum in Austin, Texas, USA, and retained by the author.

RESULTS

Pitfall *traps*

Comparisons of ant species richness, native-ant abundance, total ant abundance, and ant species diversity all revealed significant interactions between date and whether the site was infested in 1987 (Table 1). Contrasts of treatment-level means revealed the following robust patterns:

1) In 1987, infested sites contained significantly fewer ant species and native-ant individuals compared to uninfected sites. Ant species diversity was significantly lower in infested sites, but total ant abundance was higher, as a result of high densities of *Solenopsis invicta* (Table 1, Fig. 1). These same patterns, analyzed here using only the May 1987 data, are the same as those obtained by Porter and Savignano (1990) after summing pitfall data over three times of year.
2) In 1999 there was no difference between sites infested in 1987 and sites uninfected in 1987, for any of the variables investigated (Table 1, Fig. 1). This finding provides additional evidence that the differences documented by Porter and Savignano (1990) during the invasion were due to the presence of S. *invicta,* rather than habitat variation among the sites.
3) Species richness, native-ant abundance, and species diversity at all sites in 1999 were not significantly different compared to uninfected sites in 1987. Total ant abundance was higher at all sites in 1999 than in uninfected sites in 1987 (Table 1, Fig. 1).
4) Species richness, native-ant abundance, and ant species diversity were all higher, but total ant abundance was lower, at all sites in 1999 than at infested sites in 1987 (Table 1, Fig. I).

Baits

The baiting trials revealed similar results. The interaction between site and date was significant (P = 0.01), and there was a significant effect of site (P = 0.008). The effect of date was not significant (P = 0.09). In 1987 the average abundance of ants at baits was significantly higher at infested sites compared to uninfected sites, but no significant difference was found for these same groups of sites in 1999. Average ant abundances at baits at all sites in 1999 were lower than

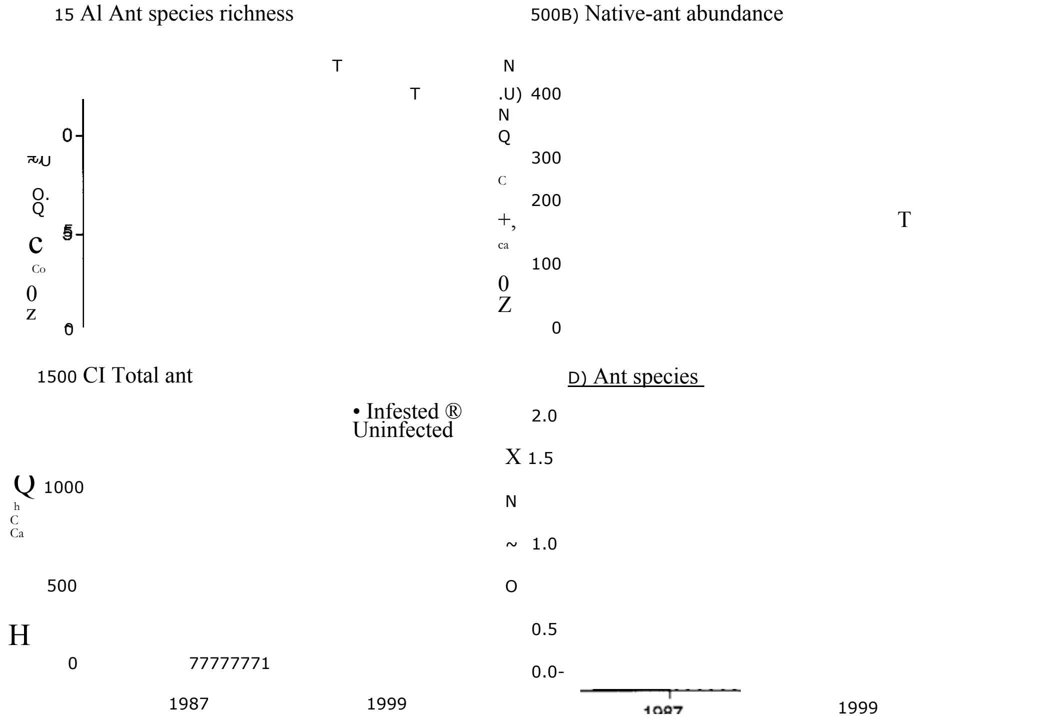

FIG. 1. Histograms of pitfall trap catches in 1987 and 1999. Values were calculated by summing over all pitfalls at each site. "Infested" refers to sites that were infested by *Solenopsis invicta* in 1987; "Uninfected" refers to sites that were not infested in 1987. Bars represent the mean of the five sites ±1 SE.

infested sites in 1987, but not significantly different than uninfected sites in 1987 (Fig. 2A).

Wilcoxon signed-ranks tests revealed both ant species richness and diversity were significantly lower in infested compared to uninfested areas in 1987 ($P = 0.005$ for both ant species richness and diversity). No significant differences were found for the same two groups of sites in 1999 ($P > 0.05$ for both). Thus all sites sampled in 1999 were combined for the KruskalWallis procedure, which compared infested sites in 1987, uninfested sites in 1987, and all sites in 1999. For both ant species richness and diversity, a significant difference was found (P G 0.0001 for both). Multiple comparisons with an experimentwise error rate of a = 0.05 revealed that: (1) both ant species richness and diversity were significantly lower in infested sites in 1987 compared to all sites grouped together in 1999, and (2) there was no significant difference, for either species richness or diversity, between uninfected areas in 1987 and all sites grouped together in 1999 (Fig. 213 and C).

Individual species

A total of 49 ant species were found at Brackenridge Field Laboratory (BFL; Austin, Texas, USA) in the spring and summer of 1999, from pitfall traps, baiting trials, and hand collecting. A compilation of all collections and records of ant species at BFL before 1989 yielded a total of 57 ant species (Appendix A). This includes 42 species recorded both before 1989 and in 1999, 15 species recorded before 1989 but not in 1999, and 7 species found in 1999 that had not been collected previously.

All seven species that had not been collected at BFL before 1999 were rare or cryptic, and could have been present earlier at BFL but not noticed. Several of the species recorded before 1989 but not in 1999 are also often rare or cryptic and may have been present but escaped notice in 1999 (e.g., Proceratium micrommatum, Cerapachys augustae, and Oligomyrmex longii).

Twenty-eight of the forty-nine ant species found in 1999 were captured in pitfall traps (Appendix B). At sites that were uninfected in 1987, 10 ant species revealed significant changes in abundance as measured by the pitfall traps between 1987 and 1999. Six species increased in abundance, while four species decreased in abundance. The most dramatic increase was for S. invicta (from 14 to 354 individuals). At sites that were infested in 1987, seven species increased in abundance. Only one species, S. invicta, decreased in abundance, by an order of magnitude (from 4577 to 499 individuals).

Eleven ant species were found at bait traps in 1999 (Appendix C). At sites that were uninfested in 1987, six species revealed significant decreases in abundance as measured by the baits whereas only one species, S. invicta, significantly increased. At sites that were in-

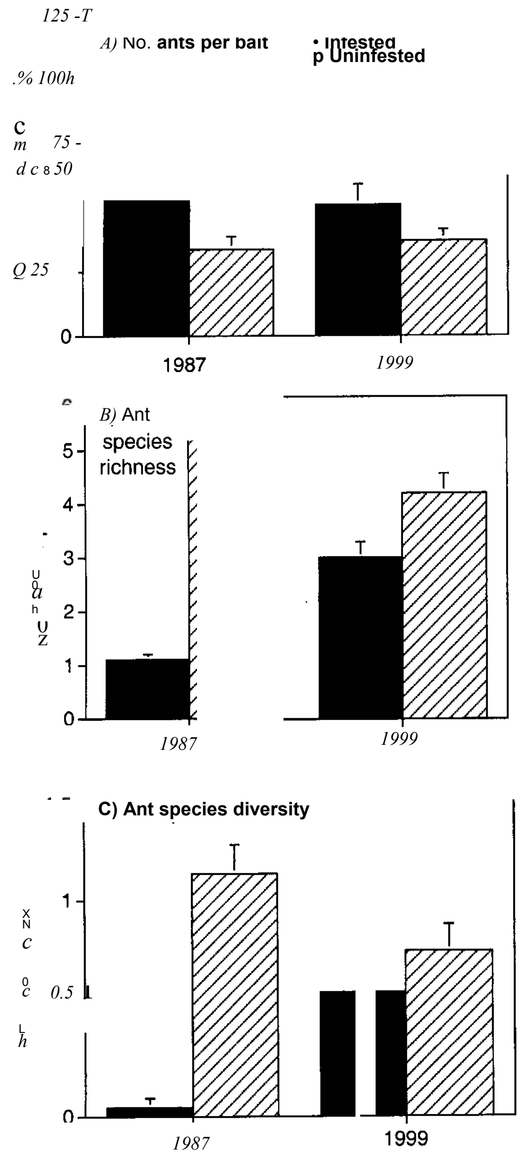

FIG. 2. Histograms of results of baiting trials in *1987* and *1999:* (A) average number of ants per bait (mean across all baits at each site); (B) ant species richness; (C) ant species diversity. Values for (B) and (C) were obtained by summing over all baits at each site. All data are means of the five sites +1 se. "Infested" refers to sites that were infested by *So*lenopsis Invicta in *1987*; "Uninfected" refers to sites that were not

fested in 1987, four species increased in abundance while only *S. invicta* decreased.

Overall arthropod community

As quantified by the pitfall traps, all major arthropod groups were either unchanged or increased in species richness or abundance between 1987 and 1999. This was true both for sites that were infested and those that were uninfected in 1987 (Tables 2 and 3). Remarkably, abundances of most arthropod groups were greater in the May 1999 sample than in the May, July, and October 1987 samples combined (compare Table 2 with Porter and Savignano [1990: Table 3]). Species richness for several arthropod groups (notably Coleoptera, Diptera, Hemiptera, and Hymenoptera) were also greater in the May 1999 sample than in the May, July, and October 1987 samples combined (compare Table 3 with Porter and Savignano [1990: Table 3]).

DISCUSSION

Long-term effects of the Solenopsis invicta *invasion*

The imported fire ant S. *invicta* first appeared at Brackenridge Field Laboratory (BFL; University of Texas, Austin, Texas, USA) about 1980, and detailed surveys from 1983 to 1986 revealed that the species spread at a rate of 18 to 35 m/yr, in wooded and sunny areas, respectively (Porter et al. 1988). By 1991 only a few small patches of forest were reported to be uninfested (Kaspari 2000). Because *S. invicta* usually nests in sunny areas for purposes of brood thermoregulation (Porter and Tschinkel 1993), it is usually not abundant in densely wooded areas.

During the *S. invicta* invasion of BFL, Porter and Savignano (1990) found that infested sites contained much lower ant species richnesses, diversities, and native-ant abundances than nearby uninfected sites. Total ant abundances were much higher (over an order of magnitude) at infested sites, because of a superabundance of *S. invicta.* Using the same pitfall trap and baiting methodologies in 1999, I found that both ant species richness and diversity had rebounded to preinvasion levels. Native-ant abundance as determined by pitfall traps and abundance of all ants at baits were also not different from preinvasion levels. Total ant abundance as determined by pitfalls was at an intermediate level between infested and uninfected areas in 1987. *Solenopsis invicta* was very abundant at BFL in 1999, but not nearly as abundant as it was in infested areas in 1987.

Using pitfalls, baits, and sifting of leaf litter, Porter and Savignano (1990) found 32 species of ants (excluding S. *invicta)* in "uninfected" areas, compared to only 16 species of ants (including *S. invicta)* in "infested" areas. Equal sampling effort was expended, and a diversity of habitats sampled, in both uninfested and infested areas. An extrapolation of these results leads to the prediction of a 50% decrease in ant species richness due to the S. *invicta* invasion.

Yet the overall ant species richness at BFL in 1999 (49 species) was 86% of the cumulative ant species richness known before the *S. invicta* invasion (57 species). Moreover, greater collecting effort was expended by more investigators over a longer period of time in obtaining the pre-S. *invicta* records. Thus, the 57 species known from BFL before the *S. invicta* invasion is likely to slightly overestimate the actual species richness at the time of the invasion, because some of the

TABLE 2. Number of individuals captured in pitfall traps per site for major taxonomic groups of arthropods (means ± 1 SE).

Taxa	Uninfested sites (in 1987)			Infested sites (in 1987)		
	1987	1999	P	1987	1999	P
Acari	4.8±3.6	180.6±31.6	*	0±0	325.4±52.9	
Araneae	4.2 ± 0.9	42.2 ± 14.2	*	4.6 ± 1.7	38.2 ± 8.3	
Chilopoda	4.8 ± 3.5	1.6 ± 0.9		2.4 ± 1.1	1.4 ± 0.7	
Coleoptera	4.4 ± 1.4	44.4 ± 8.6	*	3.0 ± 1.4	50.4 ± 10.1	
Dermaptera	0 ± 0	2.6 ± 2.1		0 ± 0	2.2 ± 0.8	
Diplopoda	2.0 ± 0.8	1.2 ± 0.5		1.4 ± 0.6	3.0 ± 1.0	
Diptera	4.0 ± 1.8	18.0 ± 3.4	*	2.4 ± 0.7	21.2 ± 1.2	
Hemiptera	0.4 ± 0.2	17.0 ± 9.8		1.0 ± 0.6	13.6 ± 7.1	
Homoptera	0.6 ± 0.4	22.8 ± 4.8	*	0.6 ± 0.4	25.2 ± 7.6	
Hymenoptera (no ants)	1.2 ± 0.9	16.4 ± 5.4	*	2.0 ± 0.9	22.6 ± 5.1	
Isopoda	226.0 ± 124.6	879.2 ± 537.5		89.2 ± 86.0	449.0 ± 205.8	
Orthoptera	0.8 ± 0.4	15.4 ± 5.1	*	2.8 ± 1.6	20.8 ± 4.7	
Thysanoptera	0 ± 0	3.8 ± 1.7	*	0 ± 0	3.2 ± 1.6	
Other	2.0 ± 1.0	21.4 ± 5.2	*	0.2 ± 0.2	15.2 ± 1.2	

Note: Abundances from 1987 include May data only.
* $P < 0.05$. P values are from Mann-Whitney tests, used to compare abundance between years for each category of sites.

pre-1989 records could reflect species that were at one time present at BFL but had already gone extinct before *S. invicta* arrived. For example, *Tetramorium bicarinatum is* a fairly large, diurnally active species that has been recorded at BFL, but was not found by Porter and Savignano (1990) in 1987-1989. It is also likely that some of the rare or cryptic species found either before 1989 or in 1999 may have been present continuously and simply overlooked during one period or the other. This type of sampling error in theory would not bias species richness one way or another, except that it would probably be less for the pre-1989 records, which represent greater sampling effort.

It is quite likely that S. *invicta* did contribute directly or indirectly to the disappearance or reduction in number of some species. For example, *Pheidole lamia* was sampled by Porter and Savignano (1990) in both pitfalls and at baits, but was not found in 1999. Both T. *bicarittatum* and P. *lamia* are fairly common elsewhere in the Austin area, however, and have not been regionally excluded by S. *invicta.* Overall, a comparison of species lists before and after the S. *invicta* invasion reveals no strong evidence that S. *invicta* has completely excluded many ant species from BFL. The 50% decrease in ant species richness extrapolated from the initial trajectory of the invasion has certainly not materialized (see also Wojcik 1994).

One species that has definitely decreased in abundance as a result of the S. *invicta* invasion is its congener S. *geminata.* As S. *invicta* spread across BFL, it competitively replaced S. *geminata* (Porter et al. 1988). The exclusion of S. *geminata* by S. *invicta* has continued in a similar manner as that documented in the initial stages of the invasion, and in 1999 S. *geminata* was present at BFL in only one isolated area containing --12 colonies. The harvester ant, *Pogonomyrmex barbatus,* was also documented to be aggressively attacked by S. *invicta,* and many colonies of P. *barbatus* were

TABLE 3. Number of species caught in pitfall traps per sit o for major taxonomic groups of arthropods.

Taxa	Uninfested sites (in 1987)			Infested sites (in 1987)		
	1987	1999	P	1987	1999	n
Araneae	3.2 ± 0.2 (10)	8.8 ± 1.7 (21)	*	3.0 ± 0.8 (13)	8.0 ± 1.5 (15)	
Chilopoda	0.6 ± 0.3 (1)	0.6 ± 0.3 (2)		0.8 ± 0.2 (1)	0.8 ± 0.4 (2)	
Coleoptera	2.6 ± 0.9 (8)	15.8 ± 3.7 (45)	*	1.8 ± 0.6 (8)	16.8 ± 4.1 (49)	
Dermaptera	0.0 ± 0.0 (0)	0.6 ± 0.4 (2)		0.0 ± 0.0 (0)	1.2 ± 0.4 (2)	
Diplopoda	1.2 ± 0.2 (1)	0.8 ± 0.4 (3)		0.6 ± 0.3 (2)	1.4 ± 0.5 (3)	
Diptera	2.6 ± 0.8 (8)	9.2 ± 2.6 (27)	*	1.8 ± 0.4 (9)	10.2 ± 1.9 (27)	
Hemiptera	0.4 ± 0.3 (2)	3.0 ± 0.6 (8)	*	0.4 ± 0.3 (2)	3.4 ± 0.7 (I1)	
Homoptera	0.4 ± 0.3 (2)	2.6 ± 0.7 (9)	*	0.6 ± 0.4 (2)	2.8 ± 0.8 (12)	
Hymenoptera (no ants)	0.6 ± 0.4 (2)	9.4 ± 2.8 (31)	*	0.6 ± 0.3 (2)	10.4 ± 2.9 (32)	
Isopoda	1.0 ± 0.0 (1)	0.8 ± 0.2 (1)		0.6 ± 0.3 (1)	1.0 ± 0.2 (I)	
Orthoptera	0.6 ± 0.3 (4)	2.0 ± 0.7 (8)		1.4 ± 0.5 (2)	2.4 ± 0.5 (7)	
Thysanoptera	0.0 ± 0.0 (0)	1.8 ± 0.5 (5)	*	0.0 ± 0.0 (0)	1.2 ± 0.5 (4)	
Other	0.8 ± 0.4 (4)	2.6 ± 0.6 (8)	*	0.0 ± 0.0 (0)	1.8 ± 0.4 (7)	

Notes: Data are means ± 1 SE; numbers in parentheses are the cumulative number of unique species of each group found at the five sites within each category and year. Abundances from 1987 include May data only.

* $P < 0.05$. The P values are from Mann-Whitney tests, used to compare species richnesses between years for each category of sites.

eradicated in the early stages of the invasion (Hook and Porter 1990). Like S. *geminata,* however, harvester ants were still present at BFL in 1999, although were not common.

Sources of error

Habitat change, whether artificial or human induced, can affect species distributions and abundances over time. Although BFL has been managed as a biological field laboratory since 1967 and has changed relatively little, nevertheless three factors may have influenced fire ant populations over the past 12 yr. (1) Nonnative plant species have been selectively removed at BFL, potentially affecting *Solenopsis* fire ants, which prefer to nest in open, sunny areas (Porter and Tschinkel 1993). Examination of aerial photos of BFL taken between 1987 and 1999, however, revealed no obvious differences in overall vegetation cover, and over this period open grasslands were mown on a regular basis. (2) The pesticide Logic (fenoxycarb; Novartis, Greensboro, North Carolina, USA) was applied at BFLin 1988 (but not thereafter) in an attempt to control S. *invicta.* Fire ant populations often rebound (sometimes to higher levels) in one to two years after pesticide application, however (e.g., Markin et al. 1974, Summerlin et al. 1977, Buren et al. 1978). Thus, even if pesticide use in 1988 significantly decreased S. *invicta* abundance, *S. invicta* has had ample time to rebound and to reinvade from surrounding areas. (3) Colonies of fire ants have been excavated from the grounds of BFL for use in laboratory studies. Colonies were chosen selectively, however, from areas that were not near the baiting or pitfall transects.

It is of interest that the pitfall traps caught many more arthropod species, and in greater abundance, in 1999 compared to both infested and uninfested sites in 1987. Many factors are known to determine the catch of pitfall traps (summarized by Adis [1979]). Although the diameter and mouth of the traps were exactly the same, the absence of an inner liner in 1999 could have potentially affected the catch.

Variation in climatic conditions preceding and during the trapping periods of 1987 and 1999 may have affected the abundance and activity of arthropods in general. Cumulative rainfall totals were similar, however, for the 3, 6, 12, and 24 mo preceding each sampling period (13.08, 52.60, 96.93, and 171.12 cm for 1987, compared to 10.97, 56.67, 87.45, and 212.45 cm for 1999, respectively [National Climatic Data Center, Asheville, North Carolina, USA]). Populations of S. *invicta* and other arthropods may fluctuate over time and it is possible that S. *invicta* populations were depressed during 1999 due to some unrecognized variable, and may increase in the future. Yet the data indicate no long-term reduction in overall arthropod species richness or abundance has occurred due to the S. *invicta* invasion, and suggest native ecosystems are re- silient enough to recover from such a perturbation, if the abundance of the invader is reduced.

Potential mechanisms

What has caused the decrease in S. *invicta* densities in infested areas since 1987 and allowed other species to rebound? Porter and Savignano (1990) hypothesized that S. *invicta* managed to reach high densities after the initial invasion by, among other possibilities, using untapped food resources and foraging more efficiently, as a result of the elimination of territorial boundaries due to polygyny. *Solenopsis invicta* may have been so efficient at foraging, however, that it depleted its resource base to a lower level. In an analogous situation, the disappearance of the pest ant *Anoplolepis longipes* from previously infested areas in the Seychelles is thought to be due to a diminished source of protein (Haines and Haines 1978). The social form of S. *invicta* has apparently not changed over time, as the polygyne form was predominant, if not present exclusively, at BFL in 1999.

Another factor is the acquisition of natural enemies. In general, S. *invicta* is 5-8 times more abundant in the United States than in its native South America, and an escape from natural enemies has been posited as a main factor for this difference (Porter et al. 1992, 1997). A superabundance of any species, however, represents a conspicuous potential (or real) host, prey, or competitor for any other species that can adapt appropriately. Adaptations of, or spread by, natural enemies of S. *invicta* may be partly responsible for decreases in some S. *invicta* populations. For example, *Thelohania solenopsae,* a microsporidian that infects *Sole*nopsis species, is known to limit fire ant colonies (Briano et al. *1995a, b,* Williams et al. *1999).* Previously thought only to exist in South America, T. *solenopsae* is now known to infect S. *invicta* in the United States (Williams et al. *1998),* and was present at BFL in the fall of 2000 (D. E Williams and L. E. Gilbert, *unpublished data).*

Conclusions and implications

Although some beneficial effects have been attributed to S. *invicta* (Reagan *1986),* the negative impacts of this invader far outweigh the benefits, due to high densities of this species in the southeastern United States (Porter et al. *1988, 1992, 1997).* Numerous studies have documented the detrimental effects of this ferocious invader on other ants, invertebrates, and vertebrates (Camilo and Phillips *1990,* Savignano and Porter *1990,* Allen et al. *1994, 1995,* Jusino-Atresino and Phillips *1994,* Vinson *1994).* Although S. *invicta* nests in the soil, it forages arboreally as well as terrestrially, and may also detrimentally affect canopy arthropods (Kaspari 2000). *Solenopsis invicta* was the most abundant ant species at BFL in *1999,* occurring at *-v40%* of the baits and accounting for almost a third of the individual ants in pitfall traps.

Yet the overall abundance of S. invicta in 1999 was much less than in infested sites in the early stages of the invasion, when it was present at 94.5% of baits and accounted for 99.6% of the individual ants caught in pitfall traps (Porter and Savignano 1990). Thus it appears the initial ferocity of the S. invicta invasion has been tempered over the past decade.

The results of this study should not be interpreted as an indication that detrimental effects of invasive ants will simply disappear with time. Solenopsis invicta is a serious pest throughout much of its introduced range in the United States and is spreading (Callcott and Collins 1996). My findings may not be representative of other, more disturbed areas invaded by S. invicta. Yet these results do indicate that the impact of invasive ants may be greatest during and shortly after the initial invasion. The mechanisms underlying the decrease in S. invicta abundance and the rebound of other ants and arthropods are not yet apparent, and additional investigations of the long-term trajectory of such invasions are needed.

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APPENDIX A

A list of ant species records from Brackenridge Field Laboratory (University of Texas, Austin, Texas, USA) both before and --12 yr after the *Solenopsis invicta* invasion is available in ESA's Electronic Data Archive: *Ecological Archives* E083045-A 1.

APPENDIX B

The numbers of ants captured in pitfall traps are available in ESA's Electronic Data Archive: *Ecological Archives* E083045-A2.

APPENDIX C

The percentages of baits occupied by ant species are available in ESA's Electronic Data Archive: *Ecological Archives* E083-045-A3.