

INVASION OF POLYGYNE FIRE ANTS DECIMATES NATIVE ANTS AND DISRUPTS ARTHROPOD COMMUNITY¹

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Abstract. The fire ant *Solenopsis invicta* Buren invaded southeastern United States from South America >50 yr ago. Urban and agricultural consequences of this invasion are well documented; however, ecological effects are still poorly understood. Increasing frequencies of "polygyne" or multiple-queen fire ants in Texas and other areas of the Southeast are disturbing because nest densities of this new form are often ten times as great as those of the more familiar monogyne form. We studied the ecological impacts of a polygyne fire ant invasion on ants and other surface-active arthropods at a field station in central Texas. Arthropod abundance and species richness were assessed using a combination of baits, pitfall traps, and litter samples.

This invasion decimated the indigenous ant fauna. Competitive replacement appears to be the primary mechanism behind this effect. Species richness of ants in infested areas dropped by 70%, while the total number of native individuals dropped by 90%. Of 35 species of ants collected in this study, 23 were either significantly less common or absent from infested sites; only *S. invicta* was more common at infested sites. The most dramatic effect of the invasion was a 10–30 fold increase in the total number of ants at infested sites—of which >99% were the imported fire ant *S. invicta*.

The impact of this invasion on other surface-active arthropods was less severe, but still substantial. The abundance of isopods, erythraeid mites, and tumblebug scarabs declined significantly, while the abundance of ground crickets, a brachypterous roach, and a symbiotic scarab increased significantly. Overall, the species richness of non-ant arthropods was 30% lower in infested sites, and individual numbers were 75% lower. Total arthropod species richness (including ants) was 40% less at infested sites. These data indicate that polygyne fire ants pose a substantial threat to the biodiversity of native arthropod communities.

Key words: ant abundance; biodiversity; competition; diversity; exotic pests; foraging intensity; Formicidae; invasion; polygyne ants; polygyny; *Solenopsis invicta*; species richness.

INTRODUCTION

The vast majority of exotic species introduced into new continents either fail or have minor effects on their host communities (Elton 1958, Simberloff 1981). However, a few exotics dramatically alter community structure (Elton 1958, Roots 1976, Mooney and Drake 1986). This paper examines one such exotic, the imported fire ant *Solenopsis invicta* Buren. We demonstrate that an invasion of this species can considerably alter the abundance and diversity of native arthropods.

S. invicta possess many of the characteristics commonly ascribed to successful invaders (Ehrlich 1986). (1) It prefers heavily disturbed habitats associated with human activity (Tschinkel 1988). (2) It tolerates a wide range of climatic conditions and (3) utilizes a wide variety of food resources (Vinson and Greenberg 1986). (4) It is relatively abundant in its homeland (Banks et

al. 1985). (5) Workers are highly variable in size (Porter and Tschinkel 1985), a characteristic that may allow them to utilize a broader feeding niche. (6) Mated queens are capable of establishing new colonies after transport (Vinson and Greenberg 1986). (7) Finally, colonies of this species have a high reproductive capacity; they grow rapidly (Porter 1988) and can produce thousands of reproductives per year (Vinson and Greenberg 1986).

S. invicta was introduced into the United States near Mobile, Alabama, ≈50 yr ago. Since that time it has relentlessly expanded its range, so that today it encompasses almost the entire southeastern United States from Texas to North Carolina. Urban and agricultural consequences of this invasion are reasonably well-documented (Lofgren 1986); however, impacts on natural plant and animal communities are still poorly known. Reports have linked fire ants with changes in the abundance of many arthropods including ticks, spiders, predatory beetles, horn flies, and especially ants (Wilson and Brown 1958, Summerlin et al. 1977, Lofgren 1986, Long et al. 1987). Nevertheless, some studies suggest that fire ants have little or no impact on the arthropod community as a whole (Rhoades 1962, 1963,

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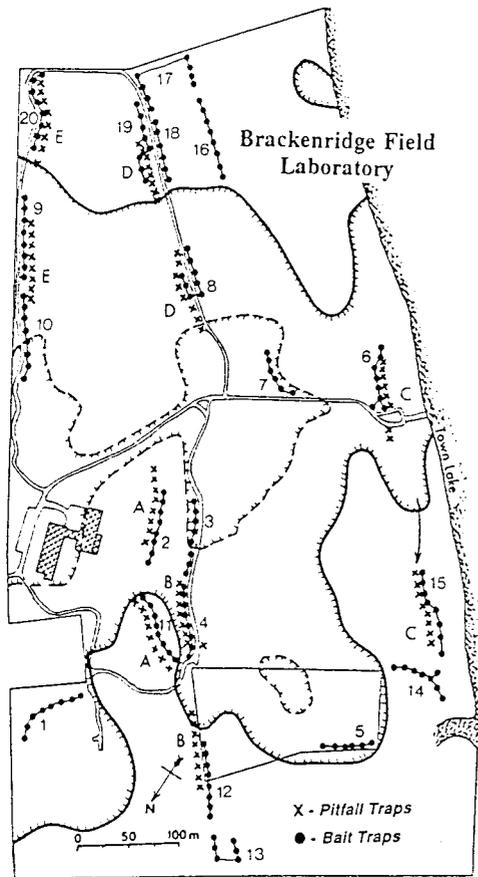


FIG. 1. Distribution of pitfall and bait traps at Brackenridge Field Laboratory, Austin, Texas. The heavy solid lines show the extent of the fire ant (*Solenopsis invicta*) infestation in the fall of 1987, while the inner dashed lines show the distribution three years earlier. Perpendicular tick marks indicate the infested side of the line. Paired lines of pitfall traps are indicated by the letters A-E. Bait-trap lines 1-10 were in the infested area; 11-20 were in the uninfested area.

Howard and Oliver 1978, Sterling et al. 1979), whereas other studies report more substantial effects (Hooper 1976; also see Risch and Carroll 1982).

To date, most studies of *S. invicta* invasions were conducted with "monogyne" or single-queen colonies. The environmental impact of the "polygyne" or multiple-queen form is potentially much greater because nest densities of this form are often 5-10 times as great as the monogyne form (300-1000 mounds/ha vs. 30-100 mounds/ha, Wojcik 1983, Lofgren and Williams 1984, Vinson and Sorensen 1986). The high nest densities characteristic of the polygyne form apparently result from a failure in the nestmate recognition system (Mirenda and Vinson 1982), which allows the formation of interconnected super-colonies and the collapse of territorial boundaries (A. P. Bhatkar and S. B. Vinson, *personal communication*). Polygyne colonies have slightly smaller sizes of workers (Greenberg et al. 1985) and usually contain several dozen egg-laying

queens, but otherwise they are difficult to distinguish from the monogyne form. Current genetic, biochemical, and taxonomic evidence indicates that both forms are the same species (Ross et al. 1987).

Polygyne *S. invicta* colonies were first reported in Mississippi by Glancey et al. (1973). Isolated populations of this form were subsequently reported from locations scattered throughout the Southeast (Ross et al. 1987). For many years, these populations were regarded as minor curiosities. However, recent surveys indicate that the polygyne form either is spreading or is much more common than previously thought (Glancey et al. 1987), especially in Texas where >50% of sampled areas contain polygyne colonies (Porter et al. 1991).

Porter et al. (1988) monitored the microgeography of a polygyne fire ant invasion at Brackenridge Field Laboratory in Austin, Texas, for five years immediately prior to this study. During this period polygyne colonies gradually expanded along an irregular but continuous front (Fig. 1), which resulted from frequent colony budding (Vargo and Porter 1989) and the negligible success of independently founding queens (Porter et al. 1988). The advancing front totally replaced colonies of the native fire ant, *Solenopsis geminata*. In this paper, we describe how this invasion affected the overall ant community and other surface-active arthropods.

MATERIALS AND METHODS

This study was conducted at the Brackenridge Field Laboratory (BFL) of The University of Texas at Austin. BFL is a 32-ha tract that includes a mixture of wooded areas and grassy fields situated on calcareous and loamy soils. Vegetation is characteristic of the Edwards Plateau and the Blackland Prairie of central Texas.

We used pitfall and bait traps to measure ant abundance and diversity. The baits were biased toward species that were diurnal and recruited large numbers of workers. Pitfall traps lacked these limitations, but some species of ants may have been more "slippery-footed" than others. Litter samples were used to provide a supplementary estimate of ant abundance. Overall, the combination of these methods provided a reasonably thorough assessment of the ant community.

Pitfalls.—A total of 80 pitfall traps were set out at five paired sites (A-E, Fig. 1). (A sixth site was dropped from the study after it was overrun by the advancing front.) Sixteen traps were placed at each site, eight in the infested area plus eight more in the uninfested area; traps were spaced 10 m apart. Sites were chosen to include a diversity of habitats. Site A was a heavily wooded area of live oak and juniper situated on the remains of an old limestone quarry. Site B was a rather dry area along the edge of a short-grass clearing and the oak-juniper woods. Site C was a moist grassy area along the riverbottom, bordered by large cottonwood

and pecan trees. Site D was similar to site B except more shrubs were present. Site E was a mixture of small clearings and wooded areas consisting of elms and live oaks. Imported fire ants varied from 60 mounds/ha in wooded areas to 400 mounds/ha in open areas of the station (Porter et al. 1988).

Pitfall traps were set out for 48 h during May, July, and October 1987. Each trap consisted of a standard half-pint canning jar (240 mL) buried in the ground. Plastic cups (200 mL [7 oz.]) were used as inner-liners to hold ≈ 40 mL of dilute ethylene glycol (1:1 with water). These inner-liner cups were trimmed with a razor to fit flush with the top of the canning jar. The inner-liner cups were replaced before each trapping period, but the jars remained permanently implanted in the ground for the duration of the investigation. Eight of the 240 pitfall trap samples collected during this study were not included in the analyses because they were disturbed by large mammals (1 sample), pesticide treatment (5 samples) or the advancing front of *S. invicta* (2 samples). Samples from eight corresponding traps were also eliminated to balance the number of samples in the infested and uninfested areas. Traps in the uninfested area of C were shifted 100 m to the northwest (Fig. 1) after the May sample so that they would not be overrun by the advancing front of *S. invicta*.

Ants were identified to species; most other taxa were identified to order and then visually sorted into morphospecies. This procedure probably resulted in conservative estimates of species numbers because cryptic species may have been lumped. Species diversity was calculated using both the log series α (from nomograph in Southwood [1978]) and the Shannon index ($H = -\sum p_i \ln p_i$, where p_i is the number in the i th category divided by the total for all categories).

Litter samples.—In order to verify estimates of ant abundance obtained from pitfall traps, we collected 16 litter samples from the infested area and another 16 from the uninfested area during June 1989. Half of the samples were collected in the late morning and half in the evening after sunset. Each sample contained ≈ 1 L of material. Ants were separated by sieving and carefully sorting through the residue. Samples from the infested area were collected between bait lines 3 and 7 in Fig. 1, while samples in the uninfested area were collected near lines 16–19.

Bait traps.—The bait traps (152 total) were set out at 10 sites in the infested area and 10 sites in the uninfested area (Fig. 1). Sites were selected to represent a diversity of vegetational types ranging from wooded areas to open fields. Although bait sites were not formally paired, they reflected a similar mix of habitats between infested and uninfested areas. Each site had eight traps spaced 10 m apart (two sites in each area only had six traps). Each trap consisted of an 8 cm diameter plastic lid baited with several drops of 1 mol/L sucrose-water and a freeze-killed cricket (*Acheta do-*

mestica L.). Crickets were pinned to the lids so that ants and other scavengers could not easily drag them away. Traps were set out between 1500 and 1700 on 13 March, 27 March, and 19 September 1987. Baits were examined 2–3 h after they were set out, and the numbers of workers were estimated by class (1, 2, 5, 10, 20, 50, 100, 200, 300 individuals).

Foraging intensity.—Two additional tests were conducted to compare the foraging intensity and recruitment rates in infested and uninfested areas. In the first test, dead crickets were observed continuously to determine when they were first discovered and how quickly afterwards 10 ants recruited to them. Fifteen baits were placed on the ground in each area during early November 1988 and again in August 1989. Baits were set out haphazardly in the same areas used for the litter samples.

The second test was designed to determine if fire ants dominated baits in the vegetation as thoroughly as those on the ground. We compared recruitment rates of foragers to peanut butter baits smeared at four levels of vertical stratification: (1) ground surface; (2) tree trunks, 0.5–1.0 m high and 5–10 cm in diameter; (3) tree branches, 1–2 m high and 0.5–1 m out; and (4) leaves. The trunk, branch, and leaf baits were placed on separate trees to maintain their independence. Infested and uninfested areas were sampled alternately until 10 sites had been done in each area. Eight baits were set out at each site; two at each of the four levels. The numbers and species of ants at the baits were estimated periodically for 30 min. This test was conducted in July 1988 during daylight hours except during the heat of the day (1100–1600). This study was conducted in the same locations as the other foraging-intensity test.

Statistical analyses.—The abundance, species richness, and diversity of arthropods in pitfall traps were analyzed using three-way crossed ANOVAs with infestation and date as fixed variables and site as a random variable. Numbers of ants on baits were analyzed with a similar three-way ANOVA, except that site was nested within infestation. One-way ANOVAs were used for comparing arthropod abundance and species richness in litter samples. We compared numbers of ants in the first foraging-intensity study using a two-way ANOVA with date and infestation as crossed factors. The test of vertical stratification of foraging intensity was analyzed using a four-way ANOVA with infestation, bait stratification, and elapsed time as the three fixed factors. Bait site was the fourth factor; it was random and nested within area. Parametric tests involving numbers of individuals were log-transformed to equalize the variance between samples with low and high means. The species richness and diversity of ants in bait traps and litter samples were analyzed using Wilcoxon rank sum tests because of unequal variance that resulted from a dearth of native ants in infested areas. We similarly used Wilcoxon rank sum tests (sta-

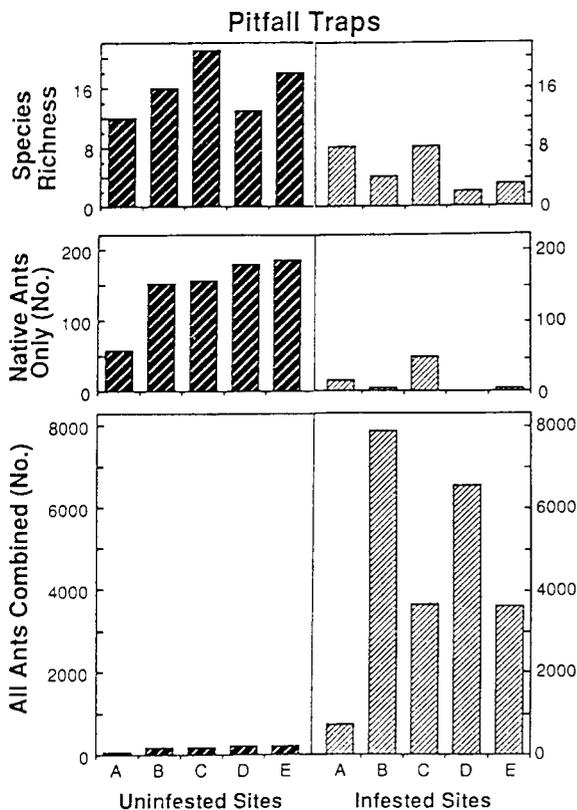


FIG. 2. Impact of the imported fire ant, *Solenopsis invicta*, on ant species richness and the abundance of worker ants collected in pitfall traps. Note the much larger scale on the graph showing numbers of all ants combined. Infested and uninfested sites with the same letter were paired by habitat. Values for each bar were calculated using site trap totals summed across date (May, July, and October 1987).

tistic H) to compare abundance of individual species collected on bait traps. Wilcoxon signed-rank tests were used to analyze paired abundances of individual species in pitfall traps. Means are shown ± 1 SE unless indicated otherwise.

Voucher specimens of ants have been deposited at BFL and the Museum of Comparative Zoology, Harvard University (Cambridge, Massachusetts). Vouchers of other arthropods were deposited at BFL and the Texas Memorial Museum in Austin, Texas. References to "fire ants" refer to the red imported fire ant, *S. invicta*, unless otherwise indicated.

RESULTS

Impact on the native ant community

The invasion of the imported fire ant, *S. invicta*, had a dramatic impact on the abundance, diversity, and species richness of native ants at BFL. Results from pitfall traps, bait traps, and litter samples were consistent.

Pitfall traps.—The average number of ant species trapped in the five uninfested sites was 16.0 ± 1.6

compared to 5.0 ± 1.8 in the infested sites (Fig. 2, $F_{1,4} = 35.6$, $P < .01$). Considering only native ants, the average number of individuals trapped at uninfested sites was 145 ± 23 compared to 14.2 ± 8.7 in the infested sites (Fig. 2, $F_{1,4} = 26.5$, $P < .01$). Even more dramatic, the total number of ants trapped in the infested sites was almost 30 times the number trapped at uninfested sites: 4469 ± 1254 vs. 165 ± 23 (Fig. 2, $F_{1,4} = 205$, $P < .01$). Low numbers of fire ants were captured at site A because this site was completely wooded and contained $\approx 80\%$ fewer *S. invicta* nests than the open sites (Porter et al. 1988). Not surprisingly, species diversity in the infested area was much lower than in the uninfested area. A rank abundance plot of species in the infested area declines precipitously (Fig. 3), with the initial part of the curve approximating a geometric series. The rank abundance of ant species in the uninfested area was much more equitably distributed, with the resulting curve approximating a log series or a log-normal model (Magurran 1988). Diversity calculated by the Shannon index averaged only 0.05 ± 0.02 in the infested area compared to 1.73 ± 0.14 in the uninfested area ($F_{1,4} = 281$, $P < .01$). By way of comparison, the average log series α for infested sites was 0.6 ± 0.2 compared to 4.5 ± 0.6 for uninfested sites ($F_{1,4} = 54.3$, $P < .01$). Neither date of collection nor the interaction between date and infestation were significant in the analyses above.

Litter samples.—Results from the litter samples were consistent with the pitfall trap data. The average number of ant species per sample was 2.1 ± 0.3 in the uninfested area and 1.4 ± 0.1 (including *S. invicta*) in the infested area ($z = -4.19$, $P < .001$). Sixteen species were recovered from uninfested samples compared to six from the infested samples. The average number of

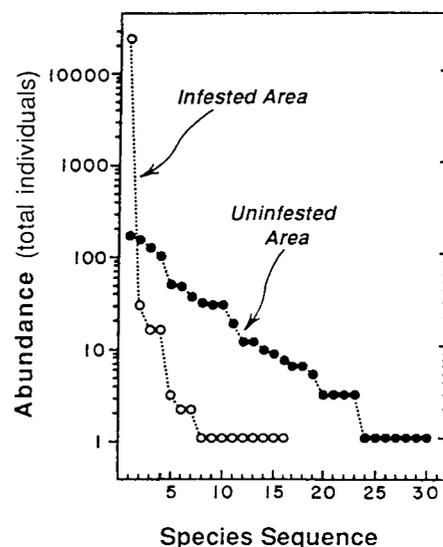


FIG. 3. Rank abundance plot of ant species collected in pitfall traps in infested and uninfested areas of Brackenridge Field Laboratory (see Table 1).

native individuals in infested samples was $\approx 10\%$ of the number in uninfested samples (0.6 ± 0.3 vs. 4.5 ± 0.7 ; $F_{1,29} = 38.5$, $P < .001$). Most importantly, the total number of ants recovered from infested samples was >10 times the total from uninfested samples (47 ± 9 vs. 4.5 ± 0.7 ; $F_{1,29} = 67.3$, $P < .001$); in other words, the 30-fold difference found in the pitfall samples was not merely a result of fire ants being slippery footed.

Bait traps.—Results from the bait traps were similar to those from pitfalls. An average of 7.5 ± 0.4 species were collected at uninfested sites compared to 1.1 ± 0.1 at infested sites (Fig. 4, Wilcoxon's rank sum statistic $W = 155$, $P < .001$; data were summed across date; analyses of individual dates produced equivalent patterns). The average number of ants estimated on bait traps was much higher in the infested area than in the uninfested area (128 ± 40 vs. 54 ± 20 ; $F_{1,18} = 29.3$, $P < .01$); this difference would have been even greater except that numbers of fire ants were frequently limited by both the surface area of the bait and the upper limit of our estimation scale. The number of ants recruited to the baits in both areas increased significantly as the season progressed ($F_{2,36} = 45.2$, $P \ll .01$), probably due to seasonal increases in soil temperatures (Porter and Tschinkel 1987) and rates of brood production. As expected, diversity based on species' occurrence at bait traps was much higher in the uninfested area (Shannon index: 1.75 ± 0.07 vs. 0.05 ± 0.05 , $W = 155$, $P < .001$; Log series α : 4.0 ± 0.4 vs. 0.09 ± 0.13 , $W = 155$, $P < .001$). None of the traps occupied by *S. invicta* were shared with a second species, but $\approx 15\%$ of the occupied traps in the uninfested area contained at least two species, probably a reflection of higher ant diversity in uninfested areas.

Individual species.—During this study, we collected 35 of the 54 species of ants known to occur at BFL. The 19 species not collected were either uncommon, arboreal, or restricted to habitats not sampled. Of the 35 species collected, 10 were significantly more common in the uninfested area than they were in the infested area (Table 1). An additional 13 of the 35 species were only found in the uninfested area, but capture frequencies of these species were too low for the difference to be significant (see 10 species in Table 1 plus three species only collected in uninfested litter samples: *Crematogaster minutissima*, *Proceratium micromatum*, *Strumigenys louisianae*). Slightly $>20\%$ of the pitfall traps in the uninfested area contained *S. invicta* workers (11% of ants trapped). Most of these workers were probably strays or long-distance scouts from the neighboring infested sites because they did not recruit to nearby baits (Table 1).

Only *S. invicta* was significantly more common in the infested sites. Seventeen species of native ants were found in the infested area (see the 16 species listed in Table 1 plus the minute thief ant, *Solenopsis (Diplo-*

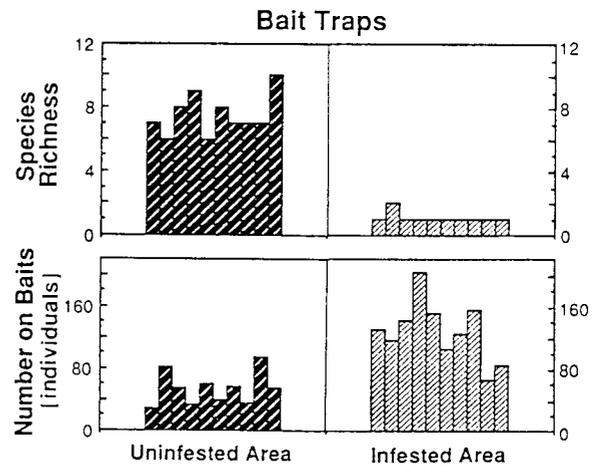


FIG. 4. Ant species richness and numbers of workers attracted to bait traps at 10 uninfested sites and 10 sites infested with the fire ant, *Solenopsis invicta*. Data are from site totals summed across date.

cies were represented by a single individual (Fig. 3), suggesting that some of them may have been strays. *S. invicta* accounted for $>99\%$ of the ants collected in the infested area (Table 1).

The average masses of individual ants in infested and uninfested areas (Table 1) were compared to determine if *S. invicta*'s higher numbers could be attributed to individual workers being much smaller than the native ants. The average *S. invicta* worker weighed $\approx 35\%$ less than the average native ant (0.33 vs. 0.52 mg dry mass). Thus, only a small fraction of the difference in abundance was attributable to smaller worker size.

Three native species appeared to be somewhat resistant to the invasion (Table 1). The small formicine *Paratrechina terricola* was relatively unaffected by *S. invicta*, judging from the frequency of captures in pitfall traps. This "snatch and run" species was probably not collected on baits in the infested area because it was easily displaced by more aggressive ants. The little black ant *Monomorium minimum* also persisted in the infested area, although at dramatically reduced levels (Table 1). Several other authors have also reported that small numbers of *M. minimum* or *P. terricola* coexist with *S. invicta* (Baroni Urbani and Kanno 1974, Stein and Thorvilson 1989, Camilo and Phillips 1990). The third species was the harvester ant *Pogonomyrmex barbatus*. Colonies of this species often persisted in the infested area for 2–3 yr before disappearing. At least five *P. barbatus* colonies were directly attacked and destroyed by fire ants during this study (Hook and Porter, *in press*). Several cryptic or subterranean ants (e.g., *Strumigenys*, *Hypoconer*, *Brachymyrmex*) may also be somewhat resistant (Ward 1987), but these species were collected too infrequently in our study to be certain.

Foraging intensity.—The intensity of ant foraging in

TABLE 1. Abundance of ant species collected in pitfall or bait traps in uninfested and infested areas of Brackenridge Field Laboratory, Texas. An asterisk indicates values that were significantly larger in one area than in the other ($P \leq .062$, Wilcoxon signed-rank and rank sum tests; see *Materials and methods: Statistical analyses*). Ellipses (...) indicate species not found at bait traps.

Subfamily Species (\bar{X} dry biomass, mg)	Pitfall traps (total individuals)		Bait traps (percent of traps)	
	Uninfested	Infested	Uninfested	Infested
Ponerinae				
<i>Hypoponera opaciceps</i> †	1	0
<i>Hypoponera opacior</i> †	0	1
<i>Pachycondyla harpax</i> (6.5)	8	1	0.8	0
<i>Leptogenys elongata</i> † (1.6)	44*	0
Ecitoninae				
<i>Neivamyrmex texana</i> †	7	0
Myrmicinae				
<i>Pogonomyrmex barbatus</i> † (4.7)	28	28
<i>Aphaenogaster texana</i> (0.7)	1	1
<i>Pheidole bicarinata</i> (0.04)	29	0	3.2	0
<i>Pheidole constipata</i> (0.05)	46*	0	4.4*	0
<i>Pheidole dentata</i> (0.18)	160*	0	12.9*	0
<i>Pheidole hyatti</i> (0.14)	3	0	2.8	0
<i>Pheidole lamia</i> (0.04)	11*	1	3.6*	0
<i>Pheidole metallescens</i> (0.04)	6	0	0.8	0
<i>Pheidole</i> sp. (near <i>casta</i>)	1	0
<i>Crematogaster laeviuscula</i> (0.91)	9	0	10.0*	0
<i>Crematogaster punctulata</i> (0.33)	6	0	2.0	0
<i>Monomorium minimum</i> (0.05)	114*	15	25.3*	1.8
<i>Solenopsis geminata</i> (0.34)	146*	0	13.7*	0
<i>Solenopsis invicta</i> (0.33)	94	22 300*	0	94.5*
<i>Solenopsis (Diplorhoptrum)</i> sp. (0.02)	28*	0	1.6	0
<i>Myrmecina americana</i> (0.14)	5	2	0.8	0
<i>Strumigenys silvestrii</i> †	1	1
<i>Cyphomyrmex rimosus</i> †	3	0
<i>Trachymyrmex turrifex</i> † (0.50)	11	1
<i>Atta texana</i> † (0.90)	1	0
Dolichoderinae				
<i>Forelius foetida</i> (0.16)	34*	2	2.0	0
<i>Conomyrma flava</i> (0.32)	3	1	3.2	0
Formicinae				
<i>Brachymyrmex depilis</i> (0.01)	0	1
<i>Camponotus americanus</i> (3.3)	1	3
<i>Camponotus texanus</i> (4.1)	3	1
<i>Paratrechina terricola</i> (0.09)	18	15	6.0*	0
<i>Formica pallidefulva</i> (2.4)	1	0

† Species not normally attracted to baits.

infested and uninfested areas was measured by assessing rates of bait discovery and recruitment. In the first test the mean time to discovery of a ground bait in the infested area was 0.9 min (54 s) in November and 0.3 min (18 s) in August—these discovery rates were 20 and 30 times faster than discovery rates in the uninfested area (Table 2, $F_{1,56} = 86.6$, $P < .0001$). These differences approximate the 10- to 30-fold differences in ant densities obtained from pitfall traps (Fig. 2) and litter samples. After bait discovery the mean time to

recruitment of 10 ants $\approx 1/4$ as long in the infested area as in the uninfested area ($F_{1,45} = 43.6$, $P < .0001$). In other words, *S. invicta* was not only faster in finding food items, but also considerably faster in recruiting to them, perhaps because their nests were closer. All baits in the infested area were recruited to after 60 min, compared to only 19 of 30 baits in the uninfested area. We observed 13 species of ants at baits in the uninfested area, but only *S. invicta* was observed in the infested area.

TABLE 2. Time to discovery of a dead cricket and subsequent recruitment of 10 ants ($\bar{X} \pm$ SD). Values for infested and uninfested areas were all significantly different ($P < .001$).

	Discovery time (min)		Recruitment time (min)	
	Uninfested	Infested	Uninfested	Infested
November	18.5 \pm 21.3	0.9 \pm 0.7	24.0 \pm 12.6	6.1 \pm 6.6
August	9.8 \pm 13.4	0.3 \pm 0.4	17.1 \pm 16.0	2.8 \pm 0.7

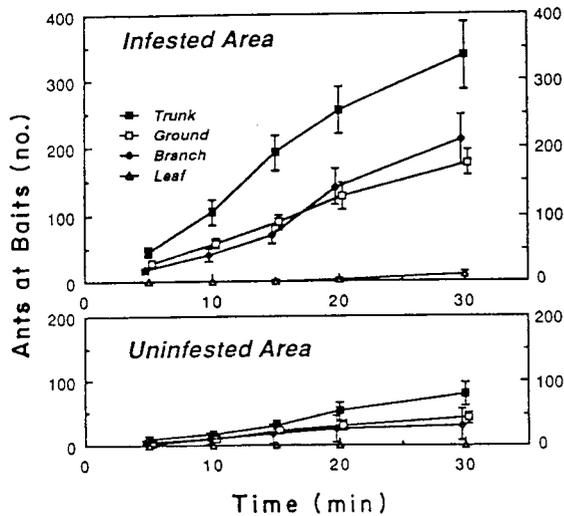


FIG. 5. Recruitment rates of ants to baits in infested and uninfested areas as a function of vertical stratification from the ground into the vegetation. Each point shows the mean (\pm SE) of 10 sites.

In the vertical stratification test, recruitment rates in the infested area were significantly higher than in the uninfested area (Fig. 5, $F_{1,18} = 67.5, P < .001$). Differences were significant in the infested area at any specific time or stratification level ($P < .01$, Duncan's new multiple range test), except that recruitment to baits on leaves was not significantly higher in the infested area until 30 min. The pattern of recruitment was similar between infested and uninfested areas. Tree

trunks had the highest rates of recruitment, followed about equally by branches and ground baits, with recruitment to leaf baits being by far the lowest in both areas ($F_{3,54} = 73.0, P < .001$). Six species of ants visited baits in the uninfested area, but only *S. invicta* was found in the infested area.

Impact on the arthropod community

The fire ant invasion also affected the abundance and species richness of other arthropods (Table 3). Pitfall traps in the infested area contained five times as many individuals as those in the uninfested area, but this difference was entirely due to large numbers of imported fire ants. If imported fire ants are excluded, the abundance of other arthropods was actually 75% lower in the infested area than in the uninfested area. This difference was principally a result of fewer isopods and native ants in the infested area (Table 3, Fig. 2).

A total of 13 individual species were significantly less abundant at infested sites (Table 1, Table 3) compared to four that were more abundant (including *S. invicta* and its symbiotic scarab). Only two or three species seemed unaffected by the invasion. Most species were simply not abundant enough to make comparisons. Species richness of arthropods at infested sites was 40% less than at uninfested sites (Table 3). This difference was attributable to a 70% decline in the number of ant species (Fig. 2) and a 30% decline in the number of non-ant species (Table 3). The difference for non-ant species was not quite significant ($F_{1,4} = 7.54, P = .053$) because traps in the infested area of

TABLE 3. Impact of fire ants on the terrestrial arthropods collected in pitfall traps. Numbers are means (\pm SE) of five sample sites summed across date and trap.

	Number of individuals		Number of species	
	Uninfested	Infested	Uninfested	Infested
Total Arthropods	839 \pm 411	4666 \pm 1241*	57 \pm 6*	35 \pm 3
Without <i>S. invicta</i>	*818 \pm 413*	210 \pm 120	56 \pm 5*	34 \pm 3
Without ants and isopods	105 \pm 32	104 \pm 26	40 \pm 4	28 \pm 3
Major Taxonomic Groups				
Aranea	17.8 \pm 1.5	12.4 \pm 2.9	11.2 \pm 1.1	8.0 \pm 1.7
Isopoda	568.0 \pm 376.0*	92.0 \pm 87.0	1.0	0.8
Chilopoda	0.8 \pm 0.3	2.6 \pm 1.2	0.8	0.8
Diplopoda	28.4 \pm 25.6	11.6 \pm 8.0	1.4 \pm 0.2	0.8 \pm 0.4
Orthoptera	6.2 \pm 2.7	45.2 \pm 20.1*	2.4 \pm 0.6	3.2 \pm 0.4
Hemiptera	3.4 \pm 0.7	5.8 \pm 2.6	1.8 \pm 0.4	2.8 \pm 1.1
Dermaptera	2.4 \pm 1.7	0.8 \pm 0.4	0.6	0.6
Coleoptera	15.4 \pm 2.6	16.0 \pm 7.8	8.6 \pm 1.6	4.8 \pm 1.4
Diptera	9.6 \pm 3.3	4.6 \pm 1.2	5.4 \pm 1.4	3.6 \pm 0.7
Hymenoptera (no ants)	3.8 \pm 1.5	4.6 \pm 1.2	2.8 \pm 1.0	2.4 \pm 0.8
Formicidae	165.0 \pm 23.0	4649.0 \pm 1254.0*	16.0 \pm 1.6*	5.0 \pm 1.8
Other	17.4 \pm 4.7	3.4 \pm 1.2	5.4 \pm 0.6*	3.4 \pm 0.9
Individual Taxa				
Mites (Erythraeidae)	11.4 \pm 5.4*	0
Tumblebug scarab (<i>Canthon</i>)	3.4 \pm 3.6*	0
Ground cricket (Nemobiinae)	2.6 \pm 2.1	35.2 \pm 21.3*
Brachypterous roach	0.2 \pm 0.2	7.0 \pm 2.5*
Scarab symbiotic with <i>S. invicta</i>	0	10.0 \pm 3.3*

* Members of pairs of values that were significantly larger (two-way ANOVA for Total Arthropods and Major Taxonomic Groups, $P < .05$; Wilcoxon signed-ranks tests for individual taxa, $P \leq .061$).

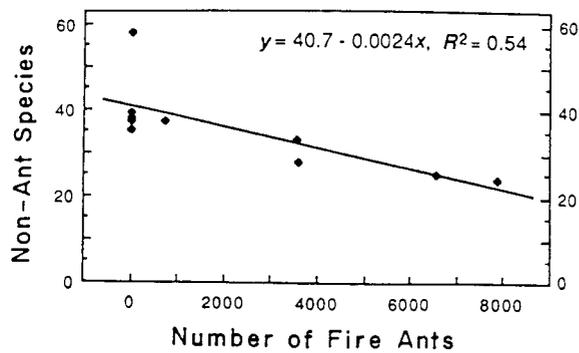


FIG. 6. Relationship between the number of fire ants (*Solenopsis invicta*) and the number of non-ant species collected in pitfall traps at 10 sample sites ($P = .015$).

site A had slightly more species than their counterparts in the uninfested area of the same site (37 vs. 35). It is important to note that site A was heavily wooded, and the pitfalls on the infested side of site A contained only one-seventh as many imported fire ants as the other four infested sites on average. When the number of non-ant species at each site was plotted against the number of *S. invicta* collected at each site, a significant negative correlation resulted (Fig. 6). Litter sampling was not as extensive as the pitfall traps, but samples from the infested area also contained fewer non-ant species (3.6 ± 0.5 compared to 9.4 ± 1.1 ; $F_{1,29} = 23.1$, $P < .001$). Approximately 176 non-ant species were collected in pitfall traps during this study. Fifty of these species (30%) were found in both the infested and uninfested areas. Of the remaining 126 species, 45 were only found in the infested area compared to 81 that were only found in the uninfested area ($\chi^2 = 10.3$; $df = 1$; $P < .005$); in other words, sparsely distributed species were more likely to be collected in the uninfested area.

A tally of the major taxonomic groups collected in pitfall traps revealed that orthopterans and ants (i.e., *S. invicta*) were significantly more abundant in infested sites (Table 3). Conversely, the introduced isopod *Armadillidium vulgare* was significantly more abundant in uninfested sites. Ants showed a significant decline in species richness; other major taxonomic groups were collected too sporadically to provide significant differences in either abundance or species richness. Arthropods were also tallied according to trophic groups, but observed effects were mostly attributable to changes in isopods and ants.

Two scavengers, a brachypterous roach (Blattellidae) and a ground cricket (Gryllidae: *Neonemobius mormonius* (Scudder)) were significantly more common at infested sites (Table 3). Perhaps these two species fed on dead fire ants that commonly accumulated in large piles in the infested area. Their increased abundance might also be related to less competition from isopods in the infested area. The scarab beetle, *Martinezia du-*

tertrei Chalumeau (formerly *Myrmecaphodius excavaticollis*), was only found at infested sites, a correlation which is not surprising because this beetle lives as a symbiont in fire ant colonies (Wojcik et al. 1977). Two other species, a large long-legged mite (Erythraeidae), and a metallic green tumblebug (Scarabaeidae: *Canthon*) were only found at uninfested sites.

DISCUSSION

Ant community

The invasion of polygyne fire ants (*S. invicta*) at BFL produced major changes in the abundance and diversity of ants and other surface-active arthropods. The impact of this invasion was especially severe on the native ant community: worker abundance declined by 90% and species richness by 70% (Figs. 2–4, Table 1). The species rank abundance plot from the infested area approximated a geometric series (Fig. 3), a pattern typical of highly disturbed habitats with low species diversity (Magurran 1988). In contrast, the plot from the uninfested area was much more equitably distributed, with a full range of common, intermediate, and uncommon species.

The consequences of this invasion appear to be long-lasting. Mound densities in the core of the infestation have remained consistently high for the last seven years (Porter et al. 1988: Fig. 1); furthermore, native ants in these areas show no signs of resurgence (see litter samples). These effects, however, will probably not be permanent on an evolutionary scale. Eventually, ants and other organisms may counteradapt and restore a more balanced community. Such a process appears to have occurred in the Caribbean after invasions of *S. geminata* ≈ 200 –500 yr ago (Wilson 1971).

The severity of *S. invicta*'s impact on native ants at BFL is attributable to polygyny or, more specifically, the high nest densities associated with this form. Monogyne fire ants dominate and simplify native ant communities, but the effects are usually more mild (Wilson and Brown 1958, Glancey et al. 1976, Summerlin et al. 1977, Wojcik 1983, Apperson and Powell 1984, Phillips et al. 1987). Our results are similar to observations of Camilo and Phillips (1990) with polygyne ants in west-central Texas. These authors reported that two polygyne sites had high numbers of fire ants and very few native ants. Similarly, Stein and Thorvilson (1989) reported that imported fire ants accounted for almost 99% of ants collected at four probable polygyne sites in an area of east-central Texas which has been infested for >20 yr.

Other species of polygyne ants also have severe impacts on their host communities (Hölldobler and Wilson 1977). When polygyne Argentine ants (*Iridomyrmex humilis*) occupied riparian habitats in north-central California, species richness declined from 8.7 species/site to 3.1 species/site (Ward 1987). Similarly, Argentine ants totally displaced three native ants in southern

California (Erickson 1971). In the Galápagos Islands, polygyne colonies of the little red fire ant, *Wasmannia auropunctata*, are "devastating all sympatric ants" (Clark et al. 1982). In Australia the occurrence of *Pheidole megacephala* at rehabilitated mine sites was correlated with a 50–80% drop in ant species richness (Majer 1985). In Colombia the polygyne ant *Paratrechina fulva* can reach densities of > 16 000 nests/ha (Zenner de Polanía and Ruíz-Bolaños 1985, Zenner-Polanía 1990). At these densities, *P. fulva* eliminates almost all other ants and apparently causes substantial problems with livestock and wildlife.

As discussed, the invasion at BFL substantially reduced the biodiversity of native ants; however, the most dramatic consequence of this invasion was a tremendous increase in the total number of ants inhabiting infested sites. Results from the pitfall traps and litter samples indicate that fire ants were 10–30 times more abundant after the invasion than all of the native ants had been before the invasion. How did fire ants at BFL manage to reach such high densities? Several possibilities exist: (1) The average size of a fire ant worker could have been much smaller than the average size of the native ants that they replaced. This difference could have allowed more individuals to be supported on the same energy base. In fact, *S. invicta* workers averaged 30% smaller than native ants, but this difference in size would only account for a small percentage of the difference in abundance, especially considering that smaller ants have slightly higher metabolic requirements (Jensen and Nielsen 1975, Calabi and Porter 1989). (2) The fire ants could be using previously untapped food resources. This possibility cannot be eliminated; nevertheless, the diet of *S. invicta* at BFL is similar to that of *S. geminata* (L. E. Tennant and S. D. Porter, unpublished manuscript). (3) Alternatively, individual workers may forage more efficiently than those of other ants. Imported fire ant workers discovered and recruited to baits much more quickly than other species (Table 2), both on the ground and in the vegetation (Fig. 5); nevertheless, high foraging intensity is likely to be the result of high nest densities and not necessarily the actual cause of these densities. (4) Ecological release is another possibility. *S. invicta* colonies in the United States have very few pathogens (Jouvenaz et al. 1977) and parasites (D. P. Wojcik, personal communication). The absence of these natural control factors in the United States may have allowed *S. invicta* to outcompete the native ant fauna. Indeed, a recent survey indicates that fire ants are much less common in Brazil than they are in the United States (S. D. Porter, H. G. Fowler, and W. P. MacKay, unpublished manuscript). (5) A fifth and equally important possibility is that polygyny has led to the collapse of territorial boundaries and the elimination of intraspecific competition. Presumably, this has allowed fire ants to make more thorough use of available food resources. Other possibilities also exist, and several may

have contributed synergistically to the high nest densities observed at BFL following the invasion.

Invasions can affect host communities via competition, predation, parasitism, and/or disease (Diamond and Case 1986). Of these possibilities, competition is the most likely explanation for *S. invicta*'s impact on BFL's native ant fauna. The dynamic nature of the advancing front (Fig. 1) strongly suggests that physical factors are not limiting. The observations of Porter et al. (1988) demonstrate that distribution patterns are mutually exclusive across time for *S. invicta* and *S. geminata*. In this paper we show that *S. invicta* also displaces most of the other native ants as well. Pathogens and parasites are unlikely mediators because of host specificity and their paucity in North American fire ant populations. Predation is another possibility; however, fire ants rarely kill and eat other ants except occasionally when attacking nests or founding queens, situations that are usually considered aggressive interference. Overall, competition appears to offer the most consistent explanation for *S. invicta*'s impact on native ants (see Simberloff 1981). Both exploitation and aggressive interference are probable mechanisms. Fire ants and native ants have similar diets and nesting requirements (Vinson and Greenberg 1986, Tschinkel 1988); consequently, huge numbers of *S. invicta* almost certainly usurp vital resources. Aggressive interference is also likely. Highly aggressive interactions have been observed between *S. invicta* and many other species of ants both in the laboratory and in the field (Bhatkar 1988, Banks and Williams 1989).

Clearly, the elimination of other ants has allowed fire ants to monopolize the food base of an entire feeding guild. Yet domination of these food resources alone is not enough to account for their huge numbers. If their sole impact was on native ant species, then the native ant community should be replaced by a metabolically equivalent amount of fire ants—not 10 or 30 times as many. Additional food needed to support the large populations of *S. invicta* may have two sources. First, polygyne fire ants may be diverting food from other scavengers in the food web. Second, they may be tapping into food resources previously unused by scavenging arthropods. These two possibilities are not mutually exclusive, especially considering the magnitude of the impact.

Arthropod community

As expected, the more fire ants at a site, the fewer species of other arthropods that were collected (Fig. 6, Table 3). Pitfall traps indicated substantial changes in the scavenger community. In particular, isopod abundance was greatly reduced in the infested area, although this was slightly offset by increases in numbers of ground crickets and roaches. Hooper (1976) likewise reported that isopod densities were reduced by the presence of fire ants, but crickets (*Gryllus* sp.) were unaffected. One would expect that fire ants might reduce numbers of

predators either by competing for prey or by attacking them directly. Infested areas had fewer spiders, but the difference was not significant.

The ecological impact of fire ants should be proportional to worker abundance—the more fire ants, the greater their impact (Fig. 6). Thus, polygyne fire ants should have a greater impact than the monogyne form. Indeed, available studies seem to support this proposition, at least in agroecosystems: Rhoades (1962, 1963) found that monogyne fire ants in a north Florida pasture (40–50 mounds/ha) did not affect the abundance of almost 30 selected arthropod taxa collected in pitfalls, sweep nets, light traps, and litter samples. Howard and Oliver (1978) reported that excluding fire ants (20–60 mounds/ha) from unimproved pastures in Louisiana resulted in five arthropod species becoming more abundant and six less abundant, but there were no clear changes in community structure. Sterling et al. (1979) reported that fire ants failed to affect either the abundance or species composition of predacious arthropods in Texas cotton fields.

While these studies indicate that monogyne fire ants have minimal effects on arthropod communities, it should be noted that these studies had several limitations. The first study (Rhoades 1962, 1963) was not replicated because it was primarily designed to test the impact of heptachlor. The other two studies (Howard and Oliver 1978, Sterling et al. 1979) relied on excluding the fire ants with poison baits. While this is a useful technique, these baits also kill a broad range of scavengers. Also, sensitive taxa may require many years to reinvade after fire ants are eliminated. Finally, all three studies dealt with highly disturbed agricultural communities, and none of them specifically looked at species richness or diversity.

Information concerning impacts of the fire ants on natural communities is surprisingly scarce. Hooper (1976) reported that fire ants in early successional fields substantially lowered the standing biomass of herbivores and predators; unfortunately, his study sites were not properly replicated and it is unknown whether he was dealing with polygyne or monogyne fire ants. Polygyne colonies clearly reduced the biodiversity of surface-active arthropods at BFL. Further studies are needed to determine if this impact extends to the entire arthropod community and whether our results are representative of other habitats and regions. Circumstantial evidence suggests that fire ant infestations may also reduce the abundance and diversity of terrestrial vertebrates (Lofgren 1986). Ideally, future studies would involve controlled introductions of fire ants to relatively homogeneous test sites. Unfortunately, controlled introductions are usually impractical because landowners are reluctant to permit establishment of this pest on uninfested land. The impact of this invasion could also be determined by sampling a series of sites before and after the invasion. This approach, while feasible, has been difficult because the main in-

vasion front is usually diffuse and advances erratically; consequently, this procedure would require monitoring a large number of sample sites over a period of 5 yr or more.

In summary, we found that an invasion of polygyne fire ants decimated the native ant community at BFL, apparently by the process of competitive exclusion. A 40% decline in arthropod species richness (Table 3) suggests that polygyne fire ants pose a significant threat to arthropod biodiversity. A 10–30 fold increase in total ant abundance also indicates profound changes in community structure (Fig. 2). Invasions of exotic species such as *S. invicta* can provide insight into forces structuring natural communities in a manner rarely achieved by more conventional experimental methods (Diamond and Case 1986). Hopefully, future studies of fire ant invasions will further define their impact on community structure and the ecological mechanisms involved.

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