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D. M. Epperson

Clemson University, epperson@mms.gov

C. R. Allen

Clemson University, callen3@unl.edu

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Red Imported Fire Ant Impacts on Upland Arthropods in Southern Mississippi

D. M. EPPERSON¹

South Carolina Cooperative Fish and Wildlife Research Unit, Clemson University, Clemson 29634

AND

C. R. ALLEN²

USGS—South Carolina Cooperative Fish and Wildlife Research Unit, Clemson University, Clemson 29634

ABSTRACT.—Red imported fire ants (*Solenopsis invicta*) have negative impacts on a broad array of invertebrate species. We investigated the impacts of fire ants on the upland arthropod community on 20–40 ha study sites in southern Mississippi. Study sites were sampled from 1997–2000 before, during, and after fire ant bait treatments to reduce fire ant populations. Fire ant abundance was assessed with bait transects on all sites, and fire ant population indices were estimated on a subset of study sites. Species richness and diversity of other ant species was also assessed from bait transects. Insect biomass and diversity was determined from light trap samples. Following treatments, fire ant abundance and population indices were significantly reduced, and ant species diversity and richness were greater on treated sites. Arthropod biomass, species diversity and species richness estimated from light trap samples were negatively correlated with fire ant abundance, but there were no observable treatment effects. *Solenopsis invicta* has the potential to negatively impact native arthropod communities resulting in a potential loss of both species and function.

INTRODUCTION

The invasion of non-native species into new habitats has been aided by anthropogenic transformation of land cover and land use, as well as the increasing extent and volume of global trade (Hobbs, 2000). Introductions of new species may be deliberate or accidental (McNeely, 2000), but regardless of the introduction mechanism, non-native species often have negative impacts on native biota and economic and ecological systems. Introduced species may outcompete or prey on native species, resulting in disruption to ecological communities and processes (Jenkins, 1996). Generalist invasive species may become ecological dominants, leading to trophic simplification (Vinson, 1994). In addition to ecological costs, economic costs associated with non-indigenous species are considerable. Pimentel *et al.* (2001), for example, estimated that the economic costs of non-indigenous species for the United States, the United Kingdom, Australia, South Africa, India and Brazil exceeded US \$314 billion per year.

Invertebrates comprise approximately 94% of all animal species and are an integral component of most food webs either directly as prey, or indirectly through nutrient cycling (Wilson, 1988). Invertebrates also perform other vital ecosystem functions including seed dispersal, decomposition and pollination (Vinson, 1994). The introduction of non-indigenous species can decimate native invertebrate communities resulting in a loss of

¹Corresponding author present address: DOI—Minerals Management Service, 1201 Elmwood Park Blvd., New Orleans, Louisiana; Telephone: (504) 736-3257, FAX: (504) 736-2901, e-mail: deborah.epperson@mms.gov

²Present address: USGS—Nebraska Cooperative Fish and Wildlife Research Unit, University of Nebraska, Lincoln

native species diversity, and a disruption of valuable ecosystem processes (Porter and Savignano, 1990).

The red imported fire ant (*Solenopsis invicta* Buren) is a successful invader into many habitats in the United States primarily due to the absence of predators, effective competitors and disease in their introduced range (Vinson, 1994; Callcott and Collins, 1996). *Solenopsis invicta* was introduced into the United States in the early 1930s, and now occupies much of the southeast, as well as parts of California (Callcott and Collins, 1996). Globally, the species is now invasive in the United States, Australia, China, Taiwan and many Caribbean nations (Morrison *et al.*, 2004; Sutherst and Maywald, 2005). Imported fire ants are often characterized as being associated with disturbed habitat, but may be found in most habitats, including woodlands and savannas, with an open canopy. Polygyny, reduced intraspecific aggression and general dietary requirements are additional characteristics of *S. invicta* that contribute to their dominance in many systems (Tsutsui and Suarez, 2003). Native ant populations are reduced both in abundance and diversity primarily through exploitative and interference competition with *S. invicta* (Porter and Savignano, 1990). Fire ants are documented to negatively impact native arthropod communities (Porter and Savignano, 1990; Wojcik *et al.*, 2001). Invasion by red imported fire ants may impact native invertebrates directly through predation or indirectly through exploitative competition for food resources (Holway *et al.*, 2002). Porter and Savignano (1990) found that fire ant invasion into habitats in central Texas resulted in a 30% reduction in non-ant arthropod species richness, and a 75% reduction in non-ant arthropod abundance. They suggested that the decimation of the native ant fauna was due to competition with *S. invicta*, either for food or for nesting sites. However, Morrison (2002) resampled the same plots 12 y later and found that native ant and arthropod species diversity had returned to pre-invasion levels. He suggested that the impacts of *S. invicta* on native arthropods may be most severe during and shortly after the initial invasion; however, his findings may not be representative of more disturbed areas (Morrison, 2002). Unfortunately, little pre-invasion arthropod information exists for most sites. Most of the evidence accumulated concerning *S. invicta* impacts on native arthropods has come from manipulative studies (Burns and Melancon, 1977; Callcott *et al.*, 2000; Allen *et al.*, 2001) of infested sites. Studies that sample arthropods in infested and uninfested areas typically find fewer species in areas infested with *S. invicta* (Nichols and Sites, 1989; Morris and Steigman, 1993; Jusino-Atresino and Philips, Jr., 1994). Jusino-Atresino and Phillips, Jr. (1994) found significant differences in ant community diversity and native ant foraging activity between infested and uninfested sites. They suggested that native ants may be changing their foraging activities to avoid competition with *S. invicta*. Although King and Tshinkel (2006) documented no changes in co-occurring species abundance following reductions in *S. invicta* densities, their sites had been invaded more than 50 y prior to their study, and the arthropod species composition was already heavily impacted by *S. invicta*. Morris and Steigman (1993) found that species richness of native ant communities in north central Texas declined by 66%, and native ant abundance declined by 99% in sites infested with *S. invicta*.

Solenopsis invicta is a generalist predator and will consume a variety of arthropods including a number of pest arthropod species, for example sugarcane borers (*Diatraea saccharalis* Fabricius), boll weevils (*Anthonomus grandis grandis* Boheman) and lone star ticks (*Amblyomma americanum* Linnaeus) (Negm and Hensley, 1969; Harris and Burns, 1972; Burns and Melancon, 1977; Adams *et al.*, 1981; Fillman and Sterling, 1983; Vogt *et al.*, 2001). Fire ants may also prey on beneficial native arthropods, decreasing native arthropod abundance as well as diversity (Allen *et al.*, 1998). Soil temperature determines fire ant

foraging activity; however, fire ants may forage throughout the year making native arthropods vulnerable during all seasons (Markin *et al.*, 1974; Porter and Tschinkel, 1987). Most foraging occurs on the ground, but ants have been found foraging up to ten meters in the tree canopy potentially impacting canopy arthropods (Kaspari, 2000).

Red imported fire ants can reduce species diversity and become the dominant species in a habitat, but they may fail to replace native species' functions (Peterson *et al.*, 1998; Holway *et al.*, 2002). Native arthropods may act as pollinators, seed dispersers or decomposers and rarely does *Solenopsis invicta* replace these functions (Vinson, 1991; Zettler *et al.*, 2001). In the longleaf pine (*Pinus palustris*) ecosystem, herbivores and detritivores play an important role in ecosystem function and more than 75% of the plants are entomophilous based on flower structure and observation (Folkerts *et al.*, 1993). Effects of *S. invicta* on native arthropod communities within longleaf pine habitat of the southeastern coastal plain are poorly known, although such effects may have critical impacts on the function and structure of these habitats. Lubertazzi and Tschinkel (2003) found that *S. invicta* was the dominant ground-foraging ant species in the pine flatwood community and that fire ants likely have a negative impact on some co-occurring ant species.

To evaluate the potential impacts of *Solenopsis invicta* on arthropods of the longleaf pine ecosystem, we experimentally manipulated fire ant densities on replicated large plots. Our objectives were to document changes in the arthropod community when fire ant populations were reduced and compare arthropod communities on reference sites and sites with reduced fire ant densities.

STUDY AREA

Camp Shelby Training Site (CSTS) in southern Mississippi, USA, is the nation's largest Army National Guard training site. It encompasses approximately 54,471 ha; 47,561 ha of which are within the DeSoto National Forest. The United States Forest Service, DeSoto National Forest, allows the military to use this land under the auspices of a Special Use Permit.

In the spring of 1997, ten study sites (20–40 ha each) within CSTS were selected for this study. Sites were chosen and paired based on habitat similarities and military activity (disturbance) levels. Four of the sites selected are National Guard firing points. Firing points are cleared, ruderal areas that are maintained with a herbaceous groundcover for military training. One firing point is surrounded by slash pine forest (*Pinus elliottii*); other sites are surrounded by longleaf pine forest. Four sites are in Training Area 44 (T-44) and are predominantly longleaf pine forest with a minimal hardwood understory and groundcover dominated by native grasses. Remaining sites are located in a longleaf plantation (planted 1986) and an adjacent, more mature longleaf stand. The majority of upland soils within the sites were sandy loams (United States Department of Agriculture [USDA] Soil Conservation Service and Forest Service, 1979; USDA Natural Resources Conservation Service, 1999).

Sites are managed in a variety of ways. The firing points are mowed between Nov. and Mar. by the National Guard. The forested areas surrounding the firing points and the other forested study sites are managed by the U.S. Forest Service. Prescribed fire is the preferred management tool. However, intervals between prescribed fires are highly variable and the majority of prescribed fires occur during the dormant season. Military use of these sites also varies, and firing points are the most heavily impacted by military use. Firing points are used for tank maneuvers and firing heavy artillery. Military activity in T-44 is restricted to foot traffic and some limited firing on the firing points within the area. The two remaining sites have no military use.

METHODS

One randomly chosen member of each pair of sites was treated with LOGIC[®] fire ant bait in the spring of 1998, spring and fall of 1999 and the spring of 2000. Broadcast applications were completed with both manual hand spreaders and mechanized ground equipment (4-wheeler and tractor) at the rate of approximately 1.67 kg/ha.

Bait transects.—On each site, two 200 m transects were permanently marked and sampled to determine abundance of *Solenopsis invicta* as well as other ant species. A multi-species ant bait station consisting of five cm diameter petri dishes with filter paper infused with a multi-species ant attractant (MSAA; United States Patent 5939061) was placed at 10 m intervals along the transect (20/transect) and collected after 1 h. The MSAA was a mixture of de-ionized water, confectionary sugar and sodium hydroxide. After collection, samples were then placed into ziploc bags and frozen until they could be transported to the USDA-ARS laboratory in Gainesville, Florida, USA for identification. All samples were sorted, and ants identified to species when possible. Bait transects were sampled in Jul. 1997, and May and Aug. of 1998, 1999 and 2000. Two surveys occurred prior to treatment and five surveys post-treatment.

Fire ant abundance, species richness and species diversity were determined for each site for each sampling period. Mean fire ant abundance for a site was calculated for each sampling period by summing the number of fire ants from both transects on a site and dividing by two (the number of transects). Ant species richness (excluding *Solenopsis invicta*) was determined, and diversity (excluding *S. invicta*) was calculated using the Shannon Diversity Index (Magurran, 1988). Pre-treatment (spring 1997/1998) fire ant abundance and species richness and diversity (excluding *S. invicta*) were compared between treated and untreated sites using a randomized block design analysis of variance. Due to missing data for two time periods for one site, post-treatment fire ant abundance, species richness and species diversity data were compared using PROC MIXED (SAS Institute Inc., 1999). All data were tested for normality using the Shapiro-Wilk test. A probability level of 0.10 was considered “significant” to minimize the chance of making a Type II error (Johnson, 1999).

Mound counts.—In addition to the bait transects, fire ant abundance was monitored using active mound counts at four non-forested sites (firing points). In each of these open sites, three permanently marked 0.10 ha circular plots were established and mound counts were completed three times per year (spring/summer/fall) in 1998, 1999 and 2000. All active mounds within the plot were located and assigned a population index based on the number of ants present in the mound and the presence or absence of worker brood (Lofgren and Williams, 1982). Indices from the three plots at each site were averaged for a single index value for each sampling period.

Light traps.—A fixed location within each study site was selected and light traps were used to sample flying invertebrates. Locations selected for light traps were >100 m from study area boundaries to increase the likelihood that invertebrates collected within the traps originated within the study site. Light traps consisted of 13.3 L capacity UV light traps (Universal Black Light Trap 2851A, BioQuip Products, Gardena, California). Light traps were placed at ground level within the study area approximately 1–2 h before sunset and collected approximately 1–2 h after sunrise the following morning. Paired sites were sampled concurrently to minimize variability resulting from weather. Light trapping was conducted in the spring and fall 1998, 1999 and 2000, resulting in one survey prior to treatment and five surveys post-treatment. Samples collected were transferred to graduated cylinders to obtain an estimated volume (cm³ of arthropods per trap), and then all samples were sorted and arthropods identified to species when possible. Species richness was

TABLE 1.—Mean red imported fire ant abundance (± 1 SE) (average number of ants per transect), mean ant species richness (excluding *Solenopsis invicta*) (± 1 SE), and mean ant species Shannon diversity indices (excluding *S. invicta*) (± 1 SE) collected from bait transects collected from bait transects at five pairs of treated and untreated study areas at Camp Shelby Training Site, 1997–2000. Pre-treatment data are in bold type

Date	Fire ant abundance treated	Fire ant abundance untreated	Ant species richness treated	Ant species richness untreated	Ant diversity treated	Ant diversity untreated
	$\bar{X} \pm SE$	$\bar{X} \pm SE$	$\bar{X} \pm SE$	$\bar{X} \pm SE$	$\bar{X} \pm SE$	$\bar{X} \pm SE$
May 1997	910 \pm 162	1050 \pm 262	5.4 \pm 0.80	3.7 \pm 0.92	1.24 \pm 0.12	0.75 \pm 0.16
May 1998	479 \pm 74	819 \pm 270	3.1 \pm 0.29	2.4 \pm 0.53	0.50 \pm 0.15	0.34 \pm 0.12
Oct 1998	2 \pm 1	1029 \pm 220	4.8 \pm 0.43	3.5 \pm 1.07	0.84 \pm 0.18	0.62 \pm 0.25
May 1999	227 \pm 146	389 \pm 78	3.0 \pm 0.22	1.8 \pm 0.25	0.59 \pm 0.09	0.30 \pm 0.08
Oct 1999	645 \pm 410	3004 \pm 684	3.8 \pm 0.85	2.6 \pm 0.83	0.84 \pm 0.22	0.38 \pm 0.18
May 2000	84 \pm 63	730 \pm 161	2.3 \pm 0.34	1.8 \pm 0.43	0.55 \pm 0.16	0.39 \pm 0.13
Oct 2000	140 \pm 61	1028 \pm 354	3.4 \pm 0.24	2.8 \pm 0.56	0.84 \pm 0.89	0.60 \pm 0.18

determined, and diversity was calculated using the Shannon Diversity Index (Magurran, 1988). Pre- and post-treatment species richness, diversity and biomass were compared between sites using a randomized block design analysis of variance. Each sampling period was treated as an independent observation as species turnover was high between sampling periods. A relationship between post-treatment light trap data (biomass, species richness and diversity) and fire ant abundance from bait transects was tested using Pearson correlations. All data were tested for normality using the Shapiro-Wilk test (SAS Institute, Inc., 1999). If data were not normal, Spearman rank order correlation coefficients were used. A significance level of 0.10 was used to minimize the chance of making a Type II error (Johnson, 1999).

RESULTS

Bait transects.—Pre-treatment analyses of fire ant abundance in both 1997 and 1998 revealed no significant differences in pre-treatment fire ant abundance (1997: $F = 0.5$, $df = 4$, $P = 0.504$; 1998: $F = 1.2$, $df = 4$, $P = 0.323$; Table 1) between treated and untreated sites. Pre-treatment ant species richness and diversity data were significantly different between treated and untreated sites in 1997 ($F = 20.6$, $df = 4$, $P = 0.01$; $F = 33.4$, $df = 4$, $P = 0.004$; Table 1), but were not significantly different immediately prior to treatment in 1998 ($F = 1.4$, $df = 4$, $P = 0.296$; $F = 1.05$, $df = 4$, $P = 0.364$; Table 1). Post-treatment fire ant abundance data were not normally distributed and were log 10 transformed prior to analysis. Fire ant abundance was significantly reduced following treatments ($F_{1,8} = 32.97$, $P = 0.004$; Table 1).

Post-treatment ant species diversity and richness data were normally distributed. Both ant species richness ($F_{1,8} = 3.91$, $P = 0.083$; Table 1) and species diversity ($F_{1,8} = 4.57$, $P = 0.064$; Table 1) were greater on treated sites. Thirty-four species of ants were collected using bait transects (Table 2); of these five species were found only on treated sites (*Crematogaster atkinsoni* was collected only following treatments), while three species were found only on untreated sites.

Mound counts.—Pre-treatment *Solenopsis invicta* population indices averaged 234 per 0.10 ha plot on sites to be treated, and 169 per 0.10 ha plot on untreated sites. This pattern corresponded to a mound density of approximately 131 and 92 mounds per ha, respectively,

TABLE 2.—Ant (Hymenoptera: Formicidae) species found using bait transects at all study sites at Camp Shelby Training Site from 1997–2000. “Treated” refers to species found only on sites treated to reduce fire ant populations, “control” refers to species found only on untreated sites, and “both” refers to species found on both treated and control sites

Genus species	Site
<i>Aphenogaster ashmeadi</i>	both
<i>Aphenogaster flemingi</i>	both
<i>Aphenogaster near rudis</i>	both
<i>Brachymyrmex depilis</i>	both
<i>Brachymyrmex obscurior</i>	both
<i>Camponotus americanus</i>	control
<i>Camponotus floridanus</i>	treated
<i>Camponotus tortuganus</i>	treated
<i>Crematogaster atkinsoni</i>	treated
<i>Crematogaster pilosa</i>	both
<i>Cyphomyrmex rimosus</i>	both
<i>Dorymyrmex bureni</i>	both
<i>Dorymyrmex melanocephalum</i>	both
<i>Forelius mccooki</i>	both
<i>Forelius pruinosus</i>	both
<i>Formica pallidefulva</i>	both
<i>Monomorium floricola</i>	control
<i>Monomorium viridulum</i>	both
<i>Paratrechina arenivaga</i>	control
<i>Paratrechina concinna</i>	both
<i>Paratrechina faisonensis</i>	both
<i>Paratrechina longicornis</i>	both
<i>Paratrechina parvula</i>	both
<i>Paratrechina phantasma</i>	both
<i>Pheidole dentata</i>	both
<i>Pheidole dentigula</i>	both
<i>Pheidole floridana</i>	both
<i>Pheidole metallescens</i>	both
<i>Pheidole moerens</i>	both
<i>Pheidole morrissi</i>	treated
<i>Solenopsis sp.</i>	both
<i>Solenopsis invicta</i>	both
<i>Tapinoma melanocephalum</i>	both
<i>Tapinoma sessile</i>	treated

prior to treatment. After the treatments, fire ant population indices at treated sites were consistently lower, averaging 13% of pre-treatment indices whereas indices at untreated sites averaged 78% of pre-treatment values (Table 3).

Light traps.—Prior to treatment, there were no differences in arthropod biomass ($F = 0.1$, $df = 4$, $P = 0.634$), species richness ($F = 0.1$, $df = 4$, $P = 0.733$) or species diversity ($F = 0.8$, $df = 4$, $P = 0.433$) between treated and untreated sites. Although differences in arthropod volume between treated and untreated sites were detected in one sampling period (May 2000) (Table 4), overall there was no treatment effect ($F_{1,7} = 0.01$, $P = 0.936$). There was no observable treatment effect in species richness and diversity post-treatment ($F_{1,7} = 0.51$, $P = 0.497$; $F_{1,7} = 0.75$, $P = 0.414$) (Table 4). Fire ant abundance from the bait transects was

TABLE 3.—Mean red imported fire ant indices (± 1 SE) calculated from six 0.10-ha circle mound counts (3 per study area \times 2 per treatment) on four ruderal sites. Mound counts were completed on 2 of 5 pairs of study sites at Camp Shelby Training Site. Pre-treatment data are in bold type

Date	Treated	Untreated
	$\bar{X} \pm SE$	$\bar{X} \pm SE$
May 1998	234 \pm 23	169 \pm 22
Aug. 1998	0 \pm 0	65 \pm 13
Oct. 1998	2 \pm 2	145 \pm 30
May 1999	20 \pm 9	192 \pm 35
Jul. 1999	2.0 \pm 2	44 \pm 9
Oct. 1999	141 \pm 49	178 \pm 32
May 2000	73 \pm 35	290 \pm 54
Jul. 2000	0 \pm 0	76 \pm 14
Oct. 2000	5 \pm 2	70 \pm 17

negatively correlated with arthropod volume ($r^2 = 0.12$, $df = 9$, $P = 0.009$), species diversity ($r^2 = 0.04$, $df = 9$, $P = 0.131$), and species richness ($r^2 = 0.04$, $df = 9$, $P = 0.109$) across all sites.

DISCUSSION

To evaluate potential impacts of fire ants on the arthropod community, fire ant densities were reduced using an insect growth regulator (IGR; fenoxycarb). Fenoxycarb has minimal impacts on non-target species, and its application has resulted in increased densities of native ants (Zakharov and Thompson, 1998). Red imported fire ants are efficient foragers and in trials evaluating bait removal, approximately 82% of the bait was removed in the first 24 h by *Solenopsis invicta*, leaving very little available for native species (Ferguson *et al.*, 1996). In this study, fire ant densities were effectively reduced using multiple treatments of fenoxycarb. Efficacy of treatments, using both mound counts and bait transects, indicated an average 87% decline in pre-treatment fire ant population indices from mound count data and a 71% decline in pre-treatment fire ant abundance from bait transects on treated sites, while population indices on untreated sites remained essentially unchanged. Ant species richness and diversity assessed using bait transects were significantly higher on

TABLE 4.—Mean arthropod volume (cm^3) (± 1 SE), mean arthropod species richness (± 1 SE), and mean arthropod species Shannon diversity indices (± 1 SE) collected from light traps at five pairs of treated and untreated study areas at Camp Shelby Training Site, 1998–2000. Pre-treatment data are in bold type

Date	Volume treated	Volume untreated	Richness treated	Richness untreated	Diversity treated	Diversity untreated
	$\bar{X} \pm SE$	$\bar{X} \pm SE$	$\bar{X} \pm SE$	$\bar{X} \pm SE$	$\bar{X} \pm SE$	$\bar{X} \pm SE$
May 1998	38 \pm 19	55 \pm 17	17 \pm 5	20 \pm 5	0.41 \pm 0.17	0.48 \pm 0.22
Oct. 1998	63 \pm 13	52 \pm 8	15 \pm 2	16 \pm 2	1.47 \pm 0.13	1.50 \pm 0.09
May 1999	47 \pm 13	71 \pm 10	11 \pm 2	13 \pm 1	1.53 \pm 0.26	1.45 \pm 0.11
Oct. 1999	2 \pm 1	5 \pm 3	5 \pm 2	7 \pm 3	0.98 \pm 0.41	1.17 \pm 0.39
May 2000	33 \pm 3	21 \pm 5	18 \pm 2	17 \pm 2	1.48 \pm 0.34	1.89 \pm 0.14
Oct. 2000	15 \pm 3	14 \pm 4	10 \pm 1	12 \pm 2	1.58 \pm 0.14	1.87 \pm 0.15

treated sites. The diurnal, terrestrial ant community was diverse, with 34 species representing thirteen genera. Five of the 34 species were found only on treated sites. Three species were unique to untreated sites but none of the genera was unique.

Arthropod volume, diversity and richness, as assessed with light traps, was not significantly different between treated and untreated areas with one exception, arthropod volume during one sampling period (May 2000). A weak negative correlation was detected between fire ant densities (from transects) and light trap biomass, species diversity and species richness. Although the relationships were significant or nearly significant, the variability explained by the correlation coefficients was low (<12%).

The ability of red imported fire ants to monopolize resources as well as prey upon potential competitors enables them to dominate arthropod communities (Vinson, 1991). Negative impacts to decomposers, seed dispersers and herbivores may result in decreased community function and ecosystem resilience, thus increasing vulnerability of fire ant infested habitats to subsequent invasions (Summerlin *et al.*, 1984; Vinson, 1991; Stoker *et al.*, 1995; Hu and Frank, 1996; Allen *et al.*, 1998; Peterson *et al.*, 1998; Calvert, 1999; Zettler *et al.*, 2001). Changes in the relative species composition by invasion of *Solenopsis invicta* may result in a community of arthropods that little resembles the pre-invasion community both in species and function.

This study demonstrates that fire ants negatively impact arthropod communities in southern Mississippi. Ant species diversity and richness were greater in sites treated with an insect growth regulator; however, the long-term benefits to arthropod communities from chemical treatments are short-lived. Calixto *et al.* (2007) noted that some native ant species can respond to reductions in *Solenopsis invicta* densities with a selective use of poison baits, though more data are needed to further investigate this issue and fire ant populations will likely rebound to pre-treatment levels (or higher) in 1–2 y after treatment (Markin *et al.* 1974). Chemical treatments are expensive, and the feasibility of using them at large spatial and temporal scales is low. However, treatments may be useful to increase survivorship of some endangered invertebrate species (*e.g.*, Schaus Swallowtail, *Papilio aristodemus ponceanus*, Stock Island tree snail, *Orthalicus reses reses*) (Forys *et al.*, 2001a; Forys *et al.*, 2001b). Morrison (2002) suggests that some arthropod communities may be able to “rebound” after invasion by *S. invicta*, but the mechanisms responsible have not been identified and for some species (*e.g.*, endangered species) it may be impossible.

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