

IMPACTS OF FIRE ANT INVASION ON SEED DISPERSAL AND ANT COMMUNITY
COMPOSITION IN THE LONGLEAF PINE ECOSYSTEM

by

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(Under the Direction of L. Katherine Kirkman)

ABSTRACT

The red imported fire ant (*Solenopsis invicta*) has extensively invaded the southeastern United States where it may alter biotic communities. We examined the influence of fire ants on native ant community composition and patterns of seed dispersal of elaiosome-bearing plants using pitfall trapping and observation of ant-seed interactions at experimental seed caches. We found that, while species richness varies independently of fire ant density, native ant abundance is negatively correlated with fire ant density. This inverse relationship may be due, in part, to the ability of native ants to limit fire ant invasion or the preference of native and fire ants for differing abiotic conditions. Fire ants were similar to native ants in quality of seed dispersal as measured by distance of dispersal and destination. Additionally, increasing densities of fire ants resulted in increases in overall rates of seed dispersal without a subsequent decline in dispersal by native ants.

INDEX WORDS: *Solenopsis invicta*, fire ant, myrmecochory, seed dispersal, elaiosome, invasive, community composition

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Project Overview

The red imported fire ant (*Solenopsis invicta*) (Hymenoptera: Formicidae) is an aggressive invader that has spread throughout the southeastern United States as well as along the west coast. Its presence threatens native ecosystems, potentially altering species assemblages, but the effects of fire ants on native ant assemblages and plant communities are not yet understood. Ant communities are believed to be highly structured by competition, making them vulnerable to the addition of a new competitor, and plant communities may suffer the disruption of important mutualisms that have evolved between plants and native ant species for seed dispersal. This study documents the ecological effects of red imported fire ants on native ant communities and on seed dispersal of native ant-dispersed plants in the threatened longleaf pine ecosystem.

The following introduction reviews pertinent literature on the life-history characteristics of the red imported fire ant, the impacts of invasive ant species on native ecosystems, and seed dispersal by ants. Several other species of fire ants are native to the southeastern United States, but they are now uncommon. Here I use the term “fire ant” to refer only to *Solenopsis invicta*, the red imported fire ant.

Literature Review

The Red Imported Fire Ant

The red imported fire ant is native to South America where its range extends through the moist lowlands of southern Peru, Bolivia, Paraguay, Uruguay, northern Argentina, and central

and southern Brazil (Pitts 2002). The species is believed to have been introduced to the United States through shipping ballast released in Mobile, AL in the 1930s (Vinson 1997). Since then, the range of fire ants has spread to include almost all of the southeastern United States (Callcott and Collins 1996) and, more recently, the west coast (Korzukhin et al. 2001). This rapid range extension has been due, at least in part, to human-aided dispersal, particularly through transport of plant materials in the nursery trade (Markin et al. 1971).

Mature fire ant colonies often consist of more than 200,000 workers (Lofgren et al. 1975). Tasks, such as foraging and caring for the brood, are divided among wingless workers according to age and size. Fire ant colonies commonly exist in one of two social forms: the monogyne form, which contains one egg-laying queen, or the polygyne form, which contains multiple queens. Polygyne colonies are spaced more densely than monogyne colonies (Fletcher 1983) and are usually more difficult to suppress, although monogyne queens are likely to disperse more widely than are polygyne queens (Ross and Shoemaker 1997). The social form of the colony is genetically determined (Ross and Keller 1998), and both forms occur in the U.S. (Glancey et al. 1973, Porter et al. 1991, Porter 1992, 1993, Porter et al. 1997), as well as in the native range of the species in South America (Ross et al. 1996, Porter et al. 1997).

Fire ants are omnivorous, feeding on various foods, including invertebrates, seeds, and carbohydrate-rich liquids from both plants and honeydew-producing homopterans (Tennant and Porter 1991, Ness and Bronstein 2004). They are also attracted to many plant and animal lipids (Weeks et al. 2004). In experimental studies, fire ants prefer solid, protein-rich baits over carbohydrates during warmer months when the species is more active and is rearing brood (Stein et al. 1990). Fire ants forage most actively at temperatures ranging from 22 to 36°C during both

day and night (Porter and Tschinkel 1987). In many areas of the United States, foraging is significantly reduced during the colder winter months (Lofgren et al. 1975).

The fire ant invasion has had significant economic repercussions in the United States, including reduced crop yields and damages to livestock and human health, costing an estimated billion dollars annually (Pimentel et al. 2000). These economic and health impacts have driven a commercial market aimed at suppression of fire ants. There is a wide array of chemical control agents ranging from aerosol sprays to granules to baits targeted at control of fire ants. Currently, none of the available agents successfully eradicate fire ants from extensive areas such as pastures, though they do offer some degree of temporary control in smaller areas, such as suburban lawns. Amdro®, one of the more popular control agents on the market, is based on the toxic chemical hydromethylnon. The toxin is dissolved in soybean oil to make it attractive to ants and this liquid is absorbed into grits. The bait is collected by workers and carried into the nest, where it is fed to the queen. Biocontrol agents are another possible means of fire ant control, a major focus of which has been the *Pseudacteon* parasitoid fly. This fly lays its eggs in the body of fire ant workers, which are killed upon emergence of the fly offspring. Presence of these flies can also reduce fire ant foraging (Porter 1998).

Fire Ants and the Natural Environment

Invasive species can dramatically affect native ecosystems, altering both physical and biological parameters in their introduced ranges (Simberloff 1981). Negative interactions between invasive and native species are most commonly studied and include predation and competition (Mack et al. 2000), but invasive species can also facilitate native species through a variety of mechanisms including trophic subsidy, pollination, competitive release, and predatory

release (Rodriguez 2006). Habitat modification is another means through which invasive species influence native species.

Recognition of the broader impacts of fire ants on natural communities is emerging, including their ability to alter the abiotic environment. Active fire ant mounds often exist in high densities, and frequent abandonment of mounds further increases the area of soils altered by fire ants. Fire ant mounds alter moisture levels, chemistry, and the physical structure of soils. Soon after a rain event, fire ant mounds on a range of soil types (from clays to sandy loams) tend to be moister than surrounding areas, but they also drain quickly, making them drier than neighboring soils at longer time periods following rain (Green et al. 1999). Moreover, mounds tend to have higher levels than surrounding soils for a variety of nutrients, including nitrogen, calcium, and potassium, while they may be lower in carbon, phosphorous, magnesium, copper, and zinc (Carroll and Hoffman 1997, Seaman and Marino 2003, Lafleur et al. 2005). Reduced levels of nitrogen may also occur on mounds (Carroll and Hoffman 1997).

Fire ants can dramatically impact biotic communities within their invaded range. One group negatively impacted by fire ants includes vertebrates that nest on or near the ground, especially egg-laying species (Allen et al. 2004). Juveniles seem to be highly vulnerable to fire ant attacks, and fire ants have been shown to cause mortality of chicks in a variety of bird species (Sikes and Arnold 1986, Drees 1994, Lockley 1995, Legare and Eddleman 2001, Allen et al. 2004), including the northern bobwhite (*Colinus virginianus*) (Giuliano et al. 1996, Mueller et al. 1999). Looking more broadly at bird populations, Allen et al. (1995) showed that fire ants reduce the density of northern bobwhites, while suppressing fire ants allowed the birds to increase. In the longleaf pine ecosystem, fire ants are second only to snakes as the most common predator of ground and shrub-nesting birds, and predation by fire ants exceeds levels of nest predation by all

mammals combined in this ecosystem (Conner, personal communication, February 21, 2006). Additionally, the young of numerous herpetofauna are known to be attacked by fire ants (Allen et al. 1997, Moulis 1997, Reagan et al. 2000, Allen et al. 2001, Buhlmann and Coffman 2001, Allen et al. 2004), including gopher tortoises (*Gopherus polyphemus*) (Landers et al. 1980), a keystone species of the longleaf pine ecosystem. Studies have also found negative associations between fire ants and several mammal species (Killion and Grant 1993, Allen et al. 2004).

Arthropods are another group that is influenced by fire ant invasion (Howard and Oliver 1978, Porter and Savignano 1990, Vinson 1991). Fire ants have been found to reduce species richness of native ants by 70% and total native ant abundance by 90%, while at the same time increasing overall ant abundance between 1000 and 3000% (Porter and Savignano 1990). Morris and Steigman (1993) reported that native ant abundance and richness was reduced by a similar magnitude in fire ant-invaded versus uninvaded areas. Fire ants also reduce the abundance of native arboreal ants (Kaspari 2000) and are believed to have displaced two native fire ants, *Solenopsis geminata* and *Solenopsis xyloni*, throughout much of the Southeast (Wilson 1951). Reduction of native ants seems to be due primarily to the ability of fire ants to out-compete natives for food resources (Gibbons and Simberloff 2005), though this competitive asymmetry is likely driven by the disproportionately high abundances of fire ants (Morrison 2000).

Other evidence suggests, however, that native ant communities may be more resilient to fire ant invasions than originally surmised. A follow-up to the Porter and Savignano (1990) study found that, 12 years after a fire ant invasion caused the collapse of the native ant community, species richness and abundance of native ants had returned to pre-invasion levels (Morrison 2002). The capacity of native ants to persist in the presence of fire ants has also been implied by Morrison and Porter (2003), who reported that fire ant density was positively correlated with

native ant species richness. Currently, the response of native ant assemblages faced with invasion of the red imported fire ant remains unresolved.

Ant Dispersal of Seeds

Myrmecochorous plants, which depend on ants for the dispersal of their seeds, may be especially vulnerable to invasion of fire ants. The seeds of myrmecochores bear a lipid-rich fleshy appendage known as an elaiosome that is attractive as a food source to ants. Ants typically carry elaiosome-bearing seeds back to the nest, where the elaiosome is removed and fed to the larvae. The seed is usually discarded unharmed, either within the nest or in middens outside of the nest.

Myrmecochory occurs throughout much of the world (Hölldobler and Wilson 1990) and involves a wide array of both ant and plant species. More than 3,000 plant species worldwide are myrmecochorous, representing diverse families and genera (Beattie 1985). Known temperate zone seed-dispersing ant genera include *Aphaenogaster*, *Formica*, *Lasius*, *Leptothorax*, *Myrmica*, *Pheidole*, and *Tapinoma* (Culver and Beattie 1978, 1980). Ants, however, can also act as seed predators, harvesting and consuming seeds as part of their diet. Many of these ants are in the subfamily Myrmicinae (especially in the genera *Pheidole*, *Pogonomyrmex*, and *Veromessor*), though the subfamilies Ponerinae and Formicinae also contain several seed-harvesting genera (Hölldobler and Wilson 1990). Seed-harvesting ants are responsible for the consumption of many seeds, but they also disperse individual seeds (Levey and Byrne 1993). Seeds may be dropped while being transported or germinate while in the nest if not consumed.

Seed dispersal by ants is considered to be a “diffuse” mutualism, meaning that multiple species of ants disperse the seeds of multiple plant species (Garrido et al. 2002), though it is

frequently skewed toward one particularly important ant species. This type of mutualism is termed an “unevenly diffuse” mutualism and the disproportionately important partner is known as the keystone mutualist. In western Australia, ants of the genus *Rhytidoponera* are keystone mutualists (Gove et al. 2007). Making up less than 2% of ants in the area, *Rhytidoponera* is responsible for the majority of ant-mediated seed dispersal in the region (Gove et al. 2007). In forests of the northeastern United States, *Aphaenogaster rudis* is the primary seed disperser (Ness and Morin 2007).

Seeds dispersed by ants are usually moved short distances, typically less than 2 m, though seeds may occasionally be moved more than 5 m (Berg 1975, Culver and Beattie 1978, Kjellsson 1985, Andersen 1988, Stamp and Lucas 1990). Dispersal distances tend to be related to ant size, with dispersal distance increasing with increasing body length (Ness et al. 2004). Despite short distances of transport, this mode of dispersal provides seeds with several distinct advantages. First, these seeds are subject to lower levels of predation, due to both seed burial and removal of the elaiosome (Culver and Beattie 1978, Heithaus 1981, Bond and Slingsby 1984). Second, the nest environment, where the seeds are deposited, often favors seedling growth due to increased levels of phosphorous and nitrogen (Culver and Beattie 1980). Third, seedlings of ant-dispersed species may experience reduced levels of competition with other plant species as well as with the maternal plant (Handel 1976). Finally, seeds that have been moved inside ant nests may be protected from fire damage (Berg 1975). Through this mutualism, ants can play a major role in structuring plant communities (Hobbs 1985, Risch and Carroll 1986, Rissing 1986, Christian 2001, Peters et al. 2005). Plant communities can be altered not only by movement of seeds to the nest site (Passos and Oliveira 2002), but also by selective removal of seeds from areas surrounding ant nests (Hobbs 1985, Peters et al. 2005).

Invasive Ants and Seed Dispersal

Invasion by non-native ant species threatens to disrupt the seed-dispersal mutualism that has evolved between many species of ants and plants. The detrimental effects of ant invasion have been well studied in the case of the Argentine ant (*Linepithema humile*), which has invaded areas including the western United States and the plant-rich fynbos of South Africa. This invasive ant displaces native ant species (Human and Gordon 1997, Holway 1999) and is an inferior seed disperser compared to the native ant species that it displaces (Carney et al. 2003). *Linepithema humile* finds seeds less quickly and moves them shorter distances than native ants (Bond and Slingsby 1984). Furthermore, *L. humile* neither deposits seeds underground (Bond and Slingsby 1984) nor transports larger seeds, which has resulted in a shift of plant community composition in invaded areas toward small-seeded species (Christian 2001).

The limited research on seed dispersal by fire ants suggests that they, too, may serve as a poor replacement for native ant species with regard to seed dispersal. Ness (2004) found that, in forest edges invaded by fire ants, seeds are dispersed shorter distances and seeds within a single cache are less likely to be dispersed into multiple ant nests. In one study, fire ants ate the seeds of some myrmecochorous plant species, while scarifying others (Zettler et al. 2001), but it is still unclear how scarification by fire ants may ultimately affect survival and germination of these seeds. Factors including seed size, chemical composition, and germination stage can influence the likelihood of a seed being scarified or destroyed by fire ants (Ready and Vinson 1995).

Impacts in the Longleaf Pine Community

The effects of the red imported fire ant on ant assemblages and plant communities are of particular interest in the restoration of the longleaf pine ecosystem as they could potentially alter seed dispersal regimes that are important in reestablishing herbaceous vegetation in disturbed

areas. This ecosystem is one of the most threatened ecosystems in the southeastern United States. It also has extremely high biodiversity, especially of herbaceous plants (Kirkman et al. 2001), including numerous myrmecochorous species (Kirkman et al. 2004). Fire ants typically invade disturbed habitats (Tschinkel 1988, Zettler et al. 2004), but they are also known to dominate ant communities in longleaf pine forests with undisturbed ground cover (Carroll and Hoffman 1997). A recent study performed in such habitat found 24 ant species, with *S. invicta* accounting for 55% of all ants collected (Carroll and Hoffman 1997). This fire ant dominance has the potential to affect patterns of vegetation regeneration in longleaf pine savannas by reducing the abundance of native seed dispersers.

Through disruption of the seed-dispersal mutualism, fire ants could influence the recovery of disturbed longleaf pine savannas. For example, several ant-dispersed species are absent or less frequent in long-term recovery areas than in undisturbed sites (Kirkman et al. 2004), though the role of fire ant invasion in this decline is not known. Thus, an understanding of the role of fire ants in the ecology of seed dispersal in this species-rich community would help to determine if seed dispersal as a natural species assemblage process following disturbance has been significantly altered. Identification of the degree of disruption to the recovery process will help to determine if management intervention or direct species reintroductions are important for reestablishment of certain species.

The purpose of this research is to examine the composition of the ant community and to determine how the relative dominance of fire ants affects dispersal of myrmecochorous species in an undisturbed longleaf pine forest.

Objectives:

The overall objective of this study is to determine the impact of fire ants on the composition of the ant community and seed dispersal of native elaiosome-bearing species. Specifically, this study examines the following questions:

- 1) Does the composition and abundance of the native ant community change in response to fire ant density?
- 2) How does the removal of seeds by fire ants differ from native ants in rate and quality of seed dispersal?

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CHAPTER 2

ANT COMMUNITY COMPOSITION IN A FIRE ANT-INVADED LONGLEAF PINE

SAVANNA¹

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Abstract

The red imported fire ant (*Solenopsis invicta*) is frequently associated with a decline in native ants throughout the invaded range, but the causes of these declines are often confounded by the influence of habitat disturbance. Invasion of fire ants into the longleaf pine savanna provides an opportunity to examine the relationship between the red imported fire ant and native ants in the absence of habitat disturbance. Within this context, we addressed the following questions: 1) how does species richness, total ant abundance, and native ant abundance vary relative to fire ant density; 2) how does this relationship vary temporally; and 3) what is the role of soil moisture in structuring this relationship?

We collected ants with monthly pitfall trapping within the longleaf pine savanna between March 2006 and October 2007. We also trapped ants across a naturally occurring soil moisture gradient in plots that had been artificially watered, as well as controls. Results indicate that, although species richness does not vary as a function of fire ant density, there is an inverse relationship between native ant density and fire ant density. This association, however, does not provide evidence of a causal link between fire ant invasion and native ant decline. For individual species, we found that fire ants are negatively correlated with only two native ant species, including *Solenopsis carolinensis*, a native species that potentially limits the invasion of fire ants. We also found that fire ants and native ants respond differently to soil moisture. Native ants prefer drier conditions, whereas fire ants prefer higher levels of soil moisture. The possible exclusion of fire ants by some native ants, as well as the potential for fire ants and native ants to prefer different abiotic conditions, provide support for alternative explanations for the frequently observed negative correlation between fire ants and native ants.

Introduction

Invasive ants threaten ecosystems worldwide (Williams 1994). Due largely to the extremely high densities reached in their invaded ranges, invasive ants alter the composition of terrestrial communities through a variety of mechanisms including competition and predation (Holway et al. 2002, Allen et al. 2004). One of the more conspicuous exotic ants in North America is the red imported fire ant (*Solenopsis invicta* Buren), but the impact of its extensive invasion on native ant assemblages in North America is currently unresolved. There is evidence to suggest that fire ants displace native ants (Porter and Savignano 1990), but there are also suggestions that some native ant communities may be resilient to fire ant invasion (Morrison 2002, Morrison and Porter 2003, Tschinkel 2006). Furthermore, much of the evidence regarding the effects of fire ants on native ant assemblages is confounded by habitat disturbance.

Native to South America, fire ants invaded the United States in the 1930s (Wojcik et al. 2001). The range of the red imported fire ant has since expanded to include the majority of the southeastern United States as well as parts of the west coast (Callcott and Collins 1996, Korzukhin et al. 2001, Tschinkel 2006). Typically, invaded areas are highly disturbed habitats such as lawns, pastures, and agricultural fields, but may also include native habitats, such as the endangered longleaf pine-wiregrass savanna (Carroll and Hoffman 1997).

Fire ants have displaced two species of native fire ants, *Solenopsis geminata* and *Solenopsis invicta* (Wilson 1951), and may also be displacing a wider array of native ant species throughout much of the invaded range (Morris and Steigman 1993, Jusino-Atresino and Phillips 1994). Native ant abundance has been found to drop by 90% and species richness by 70% immediately following invasion of the polygyne form of the red imported fire ant (Porter and Savignano 1990). Further evidence that fire ants may be displacing native ants has been

presented from a regional perspective, where ant species richness along the east coast of the United States was found to peak in Virginia, near the northern range limit of the red imported fire ant, rather than in areas of lower latitude, as was expected (Gotelli and Arnett 2000).

Although these findings could indicate competitive displacement by fire ants, evidence to refute this presumption is emerging. An alternative explanation for the negative association between fire ants and native ants is that fire ants may preferentially invade areas that are highly disturbed (Stiles and Jones 1998). Such sites may have already lost much of their native ant fauna (Zettler et al. 2004, Tschinkel 2006). Thus, rather than depressing levels of native ants, fire ants may simply be capitalizing on the reduction of native ants caused by habitat modification. In forest clear cuts and along roads, native ants have been found to decline dramatically relative to undisturbed areas while fire ant densities increase, despite fire ants remaining virtually absent in adjacent forest interiors (Tschinkel 1988, Zettler et al. 2004). Further support for the view that fire ants respond to reduced levels of native ants, rather than actually reducing levels of native ants themselves, comes from the increase in fire ant densities observed as a result of the application of mirex, a pesticide based on the compound, Perchloropentacyclodecane, used for the suppression of fire ants in the 1960s and 1970s, which killed both fire ants and native ants (Summerlin et al. 1977).

Moreover, some native ant species may be able to persist in the presence of fire ants or to rebound following an initial decline as a result of fire ant invasion. A follow-up to the Porter and Savignano (1990) study resampled the Texas site 12 years after the initial invasion and found that, although fire ants remained the most abundant ant, the community had returned to pre-invasion levels of native ant abundance and species richness (Morrison 2002). Further evidence contradicting the perception that fire ants displace native ants comes from a study in north

central Florida which found that the abundance of fire ants in a pasture was positively correlated with the abundance of co-occurring ants (Morrison and Porter 2003). Similarly, a two-year reduction in fire ant density on pasture land in northern Florida was not associated with a subsequent increase in native ant density, suggesting that fire ants had not been suppressing native ant abundances in the area (King and Tschinkel 2006).

Even less well understood is the ability of fire ants to invade native ecosystems. Tschinkel (1988) found that fire ants occur in longleaf pine uplands, but only in highly disturbed areas or along pond margins. Fire ants have also been reported, however, in low densities in undisturbed longleaf pine flatwoods with abundant herbaceous cover and periodically saturated soils (Lubertazzi and Tschinkel 2003). Nevertheless, Carroll and Hoffman (1997) documented a high relative abundance of fire ants (composing 55% of ants) in an upland longleaf pine-wiregrass savanna, despite the presence of what should have been an intact assemblage of native ants.

Native remnant stands of longleaf pine-wiregrass that lack a history of soil disturbance provide an opportunity to uncouple the impact of fire ants and human-mediated disturbance on native ant declines. The objective of this study is to characterize the composition of the ant community relative to fire ant density in a fire ant-invaded longleaf pine savanna. Specifically, we address the following questions: 1) how does species richness, total ant abundance, and native ant abundance vary relative to fire ant density; 2) how does this relationship vary temporally; and 3) what is the role of soil moisture in structuring this relationship?

Materials and Methods

Study site

This study was conducted on the property of the J.W. Jones Ecological Research Center (Ichauway). The 12,000 ha site, located in southwestern Georgia (Baker County), consists of remnant natural stands of longleaf pine (*Pinus palustris* Miller) with an understory dominated by wiregrass (*Artistida stricta* Michx). This site has been managed for more than 70 years with frequent prescribed fire for game bird management. Currently, prescribed burns are conducted at approximately two-year return intervals. The average daily temperature is 11°C during winter and 27°C during summer with an average annual rainfall of 132 cm/year. These longleaf pine stands have been invaded by fire ants, which probably first appeared in the local area in the 1960s (Callcott and Collins 1996).

Ant community composition

We sampled species richness and abundance of ground-dwelling ants in nine 1 ha plots classified as “somewhat excessively drained upland terraces” based on soil type, vegetation, and landscape position (Goebel et al. 2001). Soils consisted of loamy sands over sandy loams. All sites had an overstory of longleaf pine and an understory dominated by wiregrass. Wiregrass returns very slowly following soil disturbance, so its presence indicates that these sites had not been previously cultivated (Clewel 1989). All plots were burned with prescribed fire in January 2006. Four plots were dropped from the study in 2007 due to unintended habitat disturbance.

Species richness and abundance of ground-dwelling ants were sampled using a standard pitfall trapping technique (Majer 1978). Each pitfall trap consisted of a 15.3 cm long section of 2.1 cm diameter polyvinyl chloride (PVC) pipe that was sunk into the ground. We inserted a test

tube (15 cm long, 2 cm diameter) into the PVC pipe such that the opening of the test tube was flush with the ground. Pitfall traps were arranged in arrays consisting of three pitfall traps positioned to form an equilateral triangle with a distance of 5 m between traps. Arrays of pitfall traps were distributed evenly throughout each plot with nine arrays per plot arranged in a grid composed of three rows of three (27 pitfall traps per plot). Arrays were positioned 20 m from neighboring arrays and the outermost arrays were 30 m from the plot's edge.

Ants were trapped monthly between March 2006 and October 2007. To trap ants, we added a small amount of soapy water to each test tube and left the traps open for 24 hours. Ants retrieved from the traps were stored in 70% ethanol until they could be identified to species. A rubber stopper was used to close the test tubes between sampling periods to prevent them from filling with soil and detritus. We did not sample when rain was predicted during the 24-hour trapping period.

Ant community composition across a soil moisture gradient

We used an on-going water-addition experiment across a natural soil moisture gradient to examine the influence of soil moisture on ant community composition. In this long-term study, eight 0.25 ha (50 m x 50 m) plots have been irrigated with reverse osmosis-treated water to maintain soils at approximately 40% field capacity since 2002, while eight non-watered plots served as controls. Plots were split between opposite ends of a natural moisture gradient, with four plots of each treatment located in xeric conditions in sites classified as “excessively well drained” and the remaining plots located in mesic conditions classified as “somewhat poorly drained” (Goebel et al. 2001).

Ants were trapped in three randomly placed arrays within each of the 16 study plots. Arrays and pitfall traps were set up in the manner described in the ant community composition section above. Trapping was conducted twice in each plot between June and July of 2007.

Analyses

We calculated means and standard errors for number of fire ants, native ants, total ants, and ant species captured per array, both over the course of the study and for the summer season (June through September) (PROC MEANS, SAS version 9.1). We examined the relationship between fire ant density and native ant density and species richness, averaged by plot for each summer, using a multiple linear regression analysis in which we used year as a covariate (PROC REG, SAS version 9.1). We also used regression analysis to examine the density of *Solenopsis carolinensis* as a function of native ant density, using year as a covariate. We used correlation analysis to examine the density of individual native ant species, averaged by plot and summer, in response to fire ant density (PROC CORR, SAS version 9.1). A Spearman rank correlation (PROC CORR, SAS version 9.1) found no correlation among plots between 2006 and 2007 with respect to fire ant, native ant, and total ant densities within plots. Accordingly, data points for 2006 and 2007 within a plot were treated as independent samples in all regression analyses. Finally, we compared ant densities and species richness of the ant community between summer 2006 and summer 2007 (PROC GLM, SAS version 9.1) and calculated the relative abundance of fire ants monthly over the course of the study.

We tested for differences in mean fire ant density, native ant density, total ant density, and species richness in response to irrigation treatment using a general linear model analysis with

water-addition treatment, site type (xeric vs. mesic), and a treatment x site interaction term as independent variables (PROC GLM, SAS version 9.1).

Results

Ant Community Composition

Pitfall-trapping efforts resulted in the capture of 21,380 ants, representing 25 species, from May 2006 to October 2007 (Table 2.1). During this 16-month period, the most common ant collected was *S. invicta*, comprising 44% of the ants captured. *Solenopsis carolinensis* and *Pheidole* spp. were the next two most common ants, making up 18% and 16% of the captured ants, respectively. The relative abundance of fire ants varied seasonally, dropping during the winter months, though it remained relatively constant during the summer (Figure 2.1).

Considering ants trapped between June and September, there was a negative correlation between fire ant and native ant densities ($t = -2.63$; d.f. = 2, 11; $p = 0.02$; $r^2 = 0.4211$) (Figure 2.2). Species richness did not vary as a function of fire ant density ($t = 0.62$; d.f. = 2, 11; $p = 0.55$; $r^2 = 0.0900$) (Figure 2.3).

The mean density of ants trapped per array was lower in the summer of 2007 than 2006 ($t = 2.85$; d.f. = 358; $p < 0.01$). This decline was partially attributable to a decline in fire ant density between 2006 and 2007 ($t = 2.39$; d.f. = 358; $p = 0.02$). The mean relative abundance of fire ants per array declined from 53.9 (+/- 2.7) % in 2006 to 45.8 (+/- 3.0) % in 2007 ($t = 2.04$; d.f. = 349; $p = 0.04$). There was no decline in native ant density ($t = 1.54$; d.f. = 358; $p = 0.12$), but species richness declined from a mean of 3.7 (+/- 0.11) species per array in 2006 to 2.6 (+/- 0.10) species in 2007 ($t = 7.52$; d.f. = 356; $p < 0.0001$).

Fire ant density was positively correlated with the density of four ant species, *Brachymyrmex depilis* ($r = 0.72$; $p < 0.01$), *Camponotus pennsylvanicus* ($r = 0.73$; $p < 0.01$), *Cyphomyrmex rimosus* ($r = 0.66$; $p = 0.01$), and *Proceratium silaceum* ($r = 0.73$; $p < 0.01$). Fire ant density was negatively correlated with *Crematogaster lineolata* ($r = -0.69$; $p < 0.01$) (Figure 2.4) and *Solenopsis carolinensis* ($r = -0.64$; $p = 0.01$) (Figure 2.5). There was a positive relationship between the density of *S. carolinensis* and native ant density ($t = 3.46$; d.f. = 2, 11; $p < 0.01$; $r^2 = 0.5249$).

Ant community composition across a soil moisture gradient

Pitfall trapping in the soil moisture treatment plots resulted in the capture of 2,255 ants, representing 20 species. Fire ants composed 53% of the ants captured in these pitfall traps. Total ant density within plots was independent of treatment status as well as site (xeric vs. mesic) (Table 2.2). The response of native ant density to the water-addition treatment depended on site (Figure 2.6). In the xeric site, greater densities of native ants occurred in the absence of water addition, whereas no differences occurred in response to treatment in the mesic site. The relative and actual abundances of fire ants were greater in the mesic site than in the xeric site and no differences were attributable to treatment, although a trend of increasing fire ant density with water addition was observed at both sites (Figure 2.7). Greater species richness occurred on xeric sites than on mesic sites, and no difference in richness occurred in response to treatment (Figure 2.8).

Discussion

We found the red imported fire ant not only to be present in an intact longleaf pine-wiregrass savanna, but also to be the most common ant in this system. These results are similar to those of Carroll and Hoffman (1997), who also found fire ants to be dominant in the ecosystem. The presence of high densities of fire ants in an undisturbed, fire-maintained longleaf pine savanna interior runs counter to most observations that fire ants are relegated to disturbed areas and virtually absent in forest interiors (Tschinkel 1988, Zettler et al. 2004). One explanation for the prevalence of fire ants within our study area may be the frequent fires used in the management of the land. Fires conducted on a one to two-year return interval maintain an open canopy of pines and reduce the abundance of hardwoods, potentially creating favorable conditions for fire ants.

The relative density of fire ants varied over the course of the year, but densities were consistently high during the summer. Annual variation in fire ant densities was considerable, with fewer fire ants present in 2007. Variables that could have contributed to this decline include drought and fire. All plots were burned just prior to the beginning of this study and were not burned again in 2007. It is possible that fire ants declined as a result of accumulation of ground cover biomass two years post-burn. Moreover, the second year of study also coincided with a near-record drought (National Oceanic and Atmospheric Administration 2008), and drier soil conditions potentially favored native ants over fire ants.

Our finding that species richness varied independently of fire ant density may indicate resilience of an intact ant assemblage in its native ecosystem to fire ant invasion from the very beginning, or it may reflect the short-term nature of the influence of fire ants on native ants. Fire ants likely arrived in southwest Georgia in the 1960s (Callcott and Collins 1996) and were

abundant in Baker County, Georgia by the 1970s (Baker County Historical Society 1991). We have no data on pre-invasion ant levels at our study site, nor do we know if native ant densities declined immediately following fire ant invasion. Our data do indicate, however, that a negative relationship between fire ant densities and species richness does not exist, at least at the fire ant densities in this study.

Nonetheless, overall abundance of native ants was found to be inversely related to the density of fire ants. Thus, we cannot eliminate the possibility that fire ants may have a long-term effect on the ant assemblage by displacing native ants, nor can we conclude from this evidence that fire ants are the cause of this reduction. Ant communities are highly structured by competition (Hölldobler and Wilson 1990), and fire ants have been shown to be competitively superior to native ants with respect to collecting food resources (Porter and Savignano 1990, Gibbons and Simberloff 2005), providing a mechanism through which fire ants may displace native ants. This apparent competitive asymmetry, however, is probably driven by the disproportionately high abundances of fire ants (Morrison 2000).

Our observation of an inverse relationship between the density of native ants and fire ants might suggest that fire ant density limits native ants, but the opposite could also be the case (Rao and Vinson 2004, Tschinkel 2006). Other studies have suggested that some native ant species, including *S. (Diplorhoptrum)*, may limit fire ants (Tschinkel 1988) through their ability to eliminate small colonies (Tschinkel 1988, Rao and Vinson 2004, Vinson and Rao 2004). The *S. (Diplorhoptrum)* group includes *S. carolinensis*, a native of the longleaf pine ecosystem and one of only two native species we found to be inversely related to fire ant density. This inverse relationship was largely driven by the near absence of fire ants from plots containing high densities of *S. carolinensis*. Further, we observed a positive relationship between *S. carolinensis*

and native ant densities within our study area. Thus, it is possible that the reduced number of fire ants in areas with high densities of native ants may be a result of the ability of members of this group of species to exclude fire ants. We concur with others (Rao and Vinson 2004, Tschinkel 2006) in the suggestion that such interspecific exclusion of fire ants could be an explanation of the frequently observed negative correlation between fire ants and native ants in other studies.

Additionally, the fact that fire ants and native ants responded differently to natural soil moisture variation and water-addition suggests that fire ants and native ants may take advantage of different environmental conditions. Fire ants may thrive in more moist soils, a reasonable conclusion as they are native to the margins of seasonally flooded wetlands in South America (Tschinkel 2006). These results are consistent with the findings of Tschinkel (1988), suggesting that fire ants are more likely to invade areas with wet–mesic soils. This propensity for fire ants and native ants to thrive in differing environmental conditions may be another factor leading to a negative correlation between fire ants and native ants.

The invasion of fire ants into the longleaf pine ecosystem is an important finding and has allowed us to demonstrate that fire ants can be negatively associated with native ant density in the absence of human-mediated habitat disturbance, even 30 years post-invasion. We suggest that the negative relationship may be explained by the ability of particular species of native ants to limit fire ant invasion and/or by differing responses of fire ants and native ants to environmental variables such as soil moisture.

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Table 2.1 Percentage of each species trapped during the summers of 2006 and 2007, combined, and over the course of the experiment.

Species	Summer	All
<i>Solenopsis invicta</i>	45.90	44.15
<i>Solenopsis carolinensis</i>	19.65	17.56
<i>Pheidole</i> spp.	19.25	16.40
<i>Brachymyrmex depilis</i>	3.43	3.68
<i>Crematogaster lineolata</i>	2.59	2.58
<i>Cyphomyrmex rimosus</i>	1.73	1.60
<i>Paratrechina</i> spp.	1.65	1.69
<i>Forelius pruinosus</i>	1.71	2.34
<i>Camponotus floridanus</i>	0.95	0.81
<i>Pheidole dentata</i>	0.85	0.93
<i>Dorymyrmex bureni</i>	0.73	0.72
<i>Trachymyrmex septentrionalis</i>	0.35	0.44
<i>Paratrechina arenivaga</i>	0.21	0.25
<i>Pyramica</i> sp.	0.13	0.13
<i>Crematogaster minutissima</i>	0.05	0.12
<i>Pogonomyrmex badius</i>	0.05	0.05
<i>Hypoponera</i> sp.	0.04	0.03
<i>Aphaenogaster ashmeadi</i>	0.04	0.03
<i>Strumigenys louisianae</i>	0.04	0.03
<i>Formica schaufussi</i>	0.03	0.03
<i>Myrmecina americana</i>	0.02	0.02
<i>Tapinoma sessile</i>	0.02	0.01
<i>Proceratium silaceum</i>	0.01	0.01
<i>Camponotus pennsylvanicus</i>	0.01	0.01
<i>Prenolepis imparis</i>	0.00	5.84
Unknown	0.62	0.54

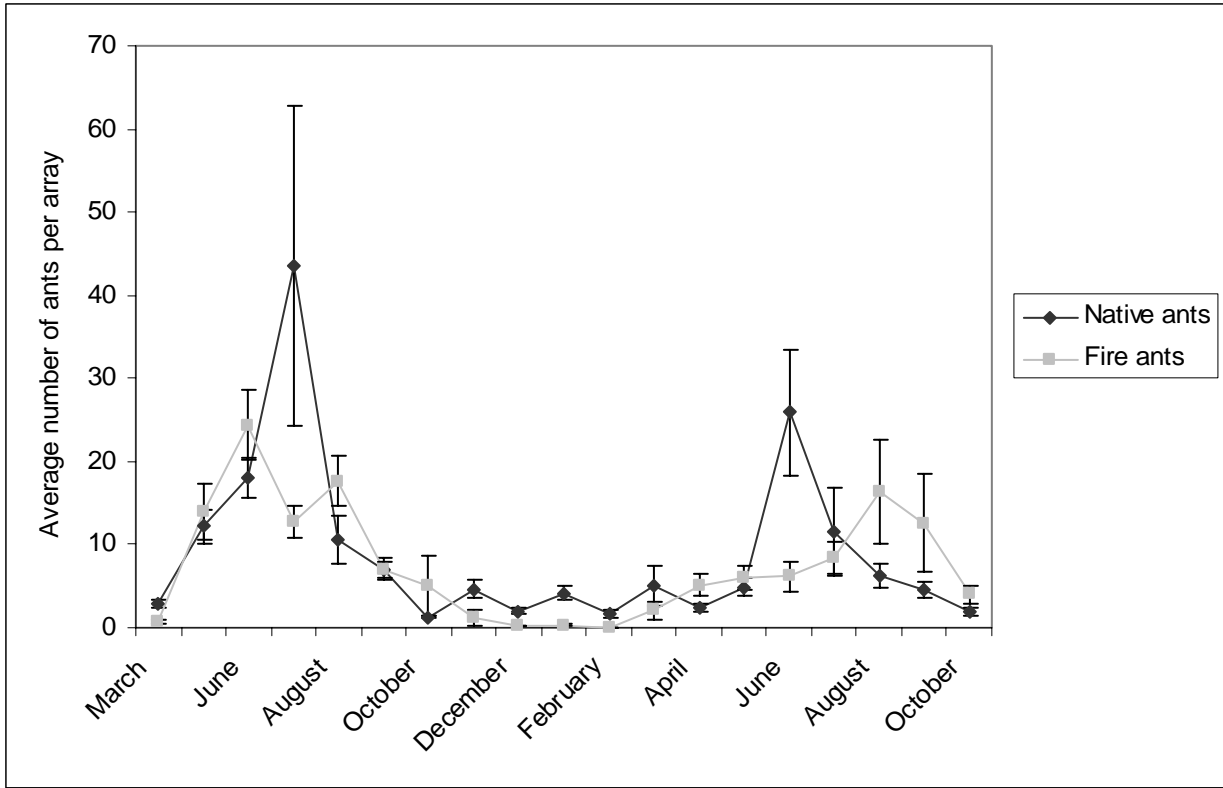


Figure 2.1 Average number of fire ants and native ants per array (+/- SE) by month.

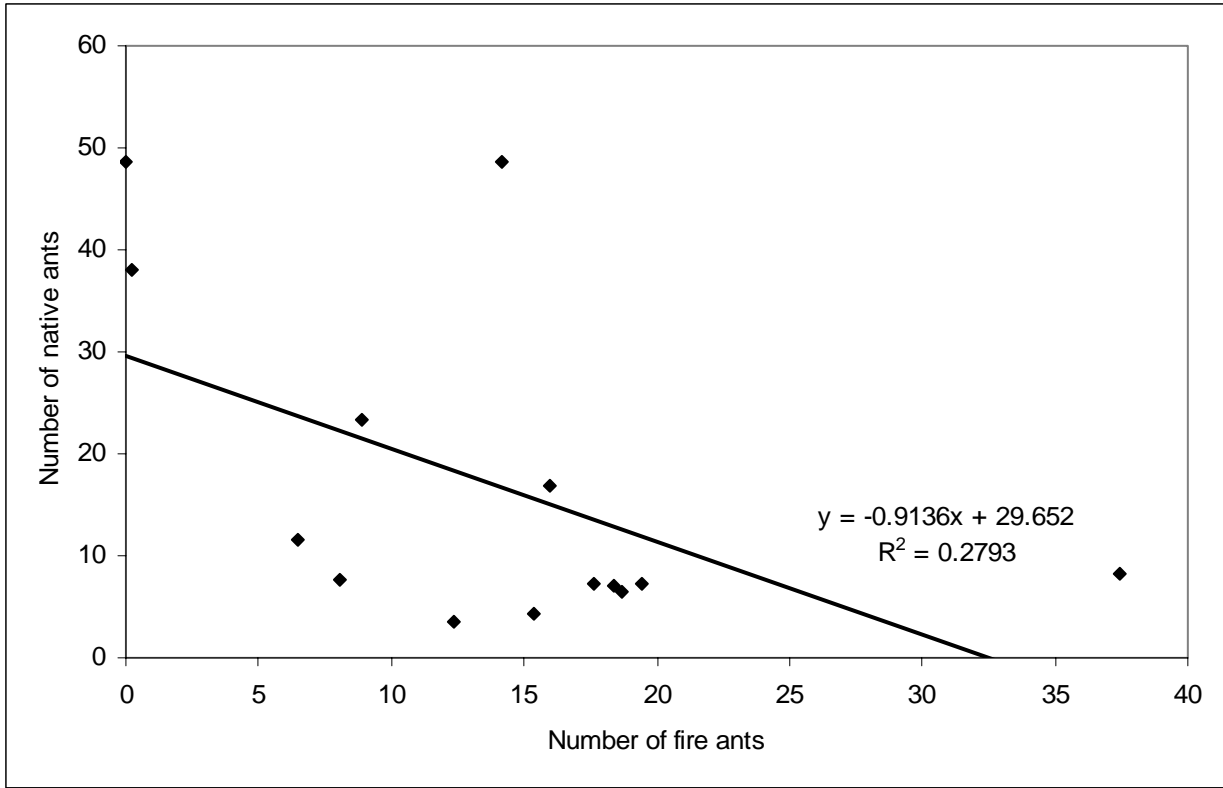


Figure 2.2 Relationship between the density of fire ants and native ants per array, averaged by plot.

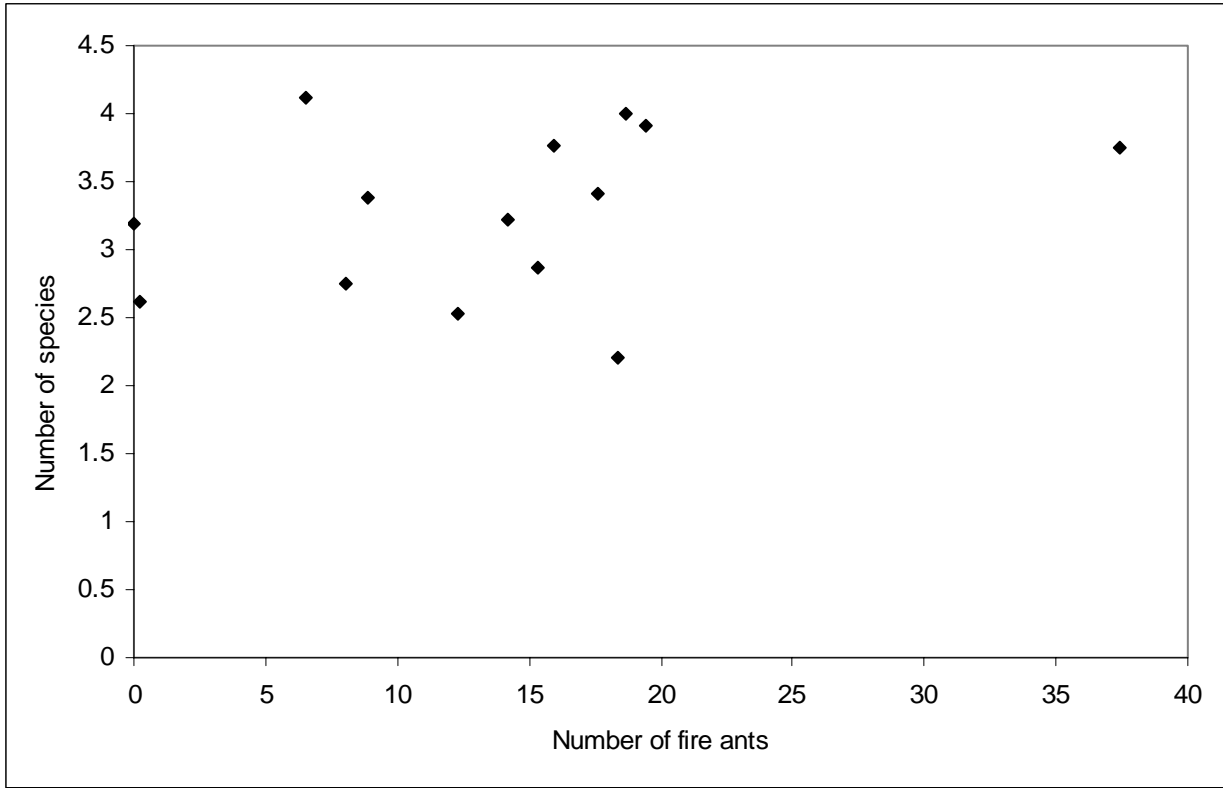


Figure 2.3 Relationship between fire ant density and ant species richness per array, averaged per plot.

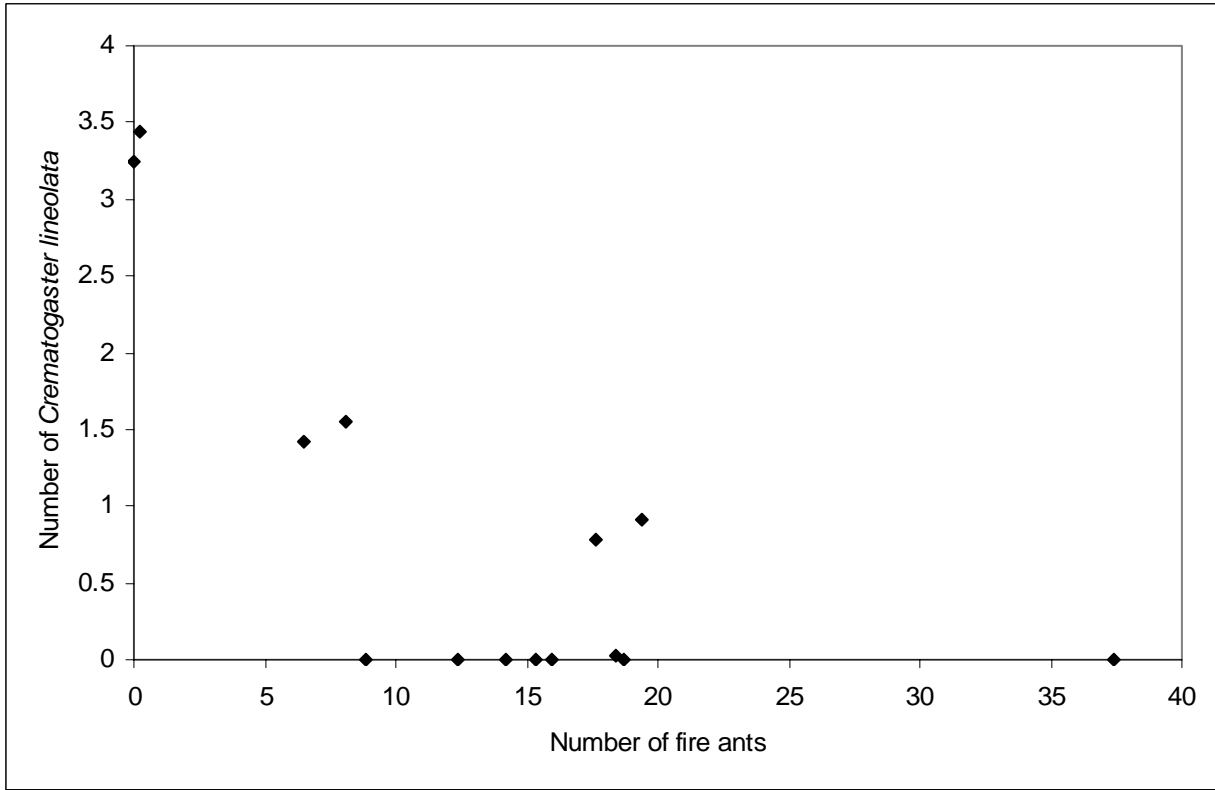


Figure 2.4 Relationship between the density of fire ants and *Crematogaster lineolata* per array, averaged per plot.

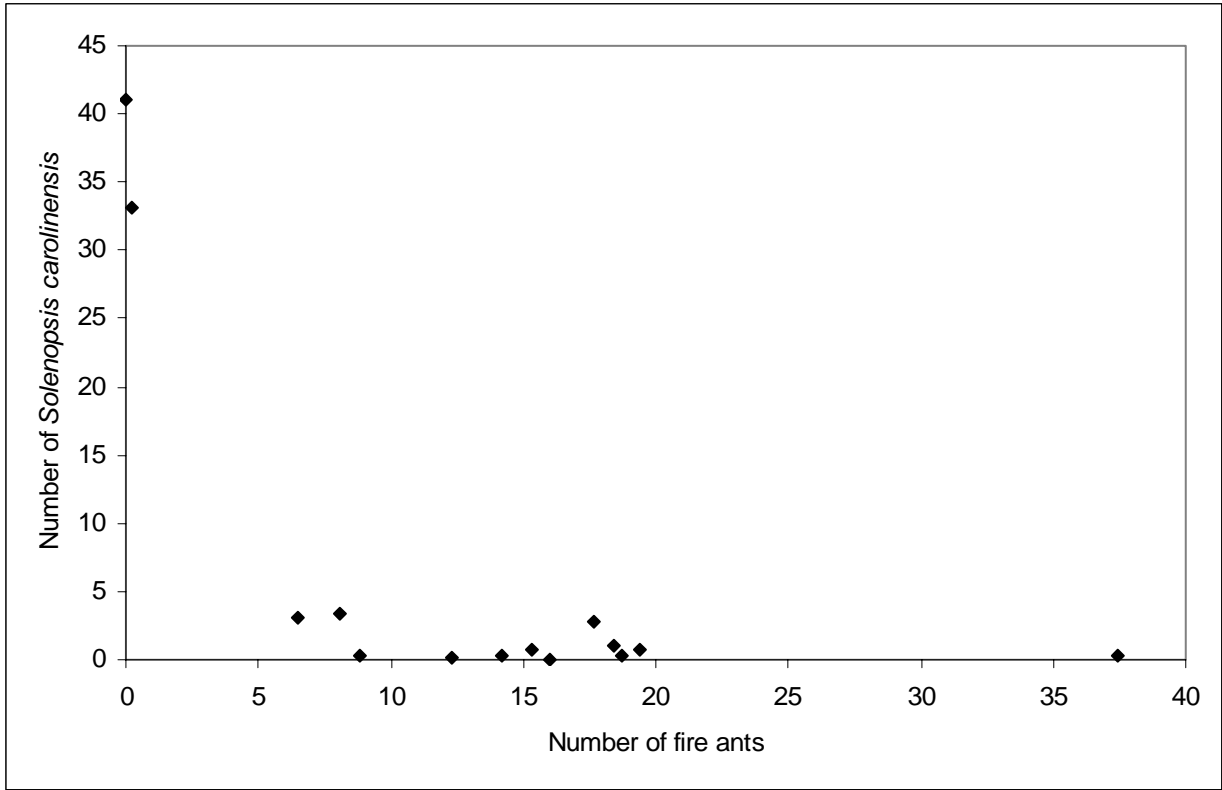


Figure 2.5 Relationship between the density of fire ants and *Solenopsis carolinensis* per array, averaged per plot.

Table 2.2 General linear models evaluating the effects of water-addition treatment and site soil-moisture on ant community composition.

Dependent variable	Independent variable	<i>F</i> statistic	<i>P</i>
Mean ants per array	Site	1.20	0.294
	Treatment	0.39	0.544
	Site x Treatment	1.86	0.198
Mean native ants per array	Site	18.31	0.001
	Treatment	10.66	0.007
	Site x Treatment	9.11	0.011
Mean fire ants per array	Site	4.96	0.046
	Treatment	2.15	0.168
	Site x Treatment	0.58	0.462
Mean species richness per array	Site	19.80	0.001
	Treatment	0.01	0.911
	Site x Treatment	2.55	0.136
Mean percent fire ants per array	Site	52.91	< 0.0001
	Treatment	1.86	0.198
	Site x Treatment	0.03	0.860

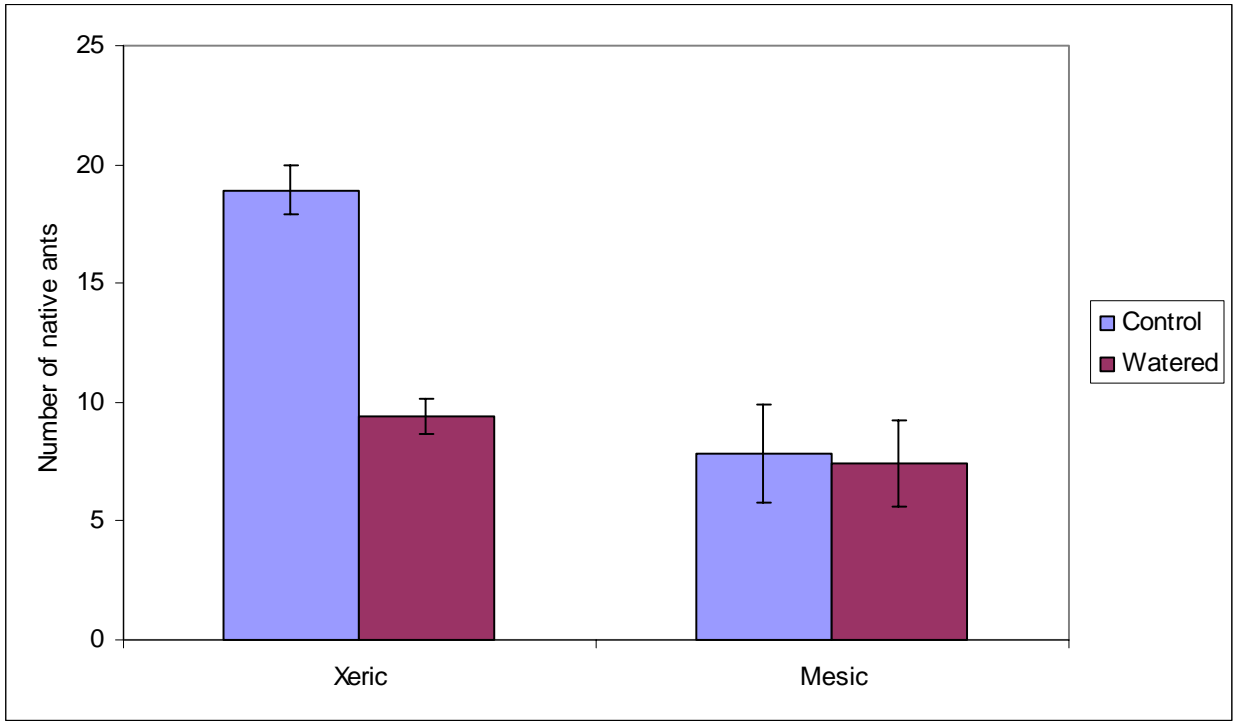


Figure 2.6 Average number of native ants captured per array in watered and control plots within xeric and mesic sites.

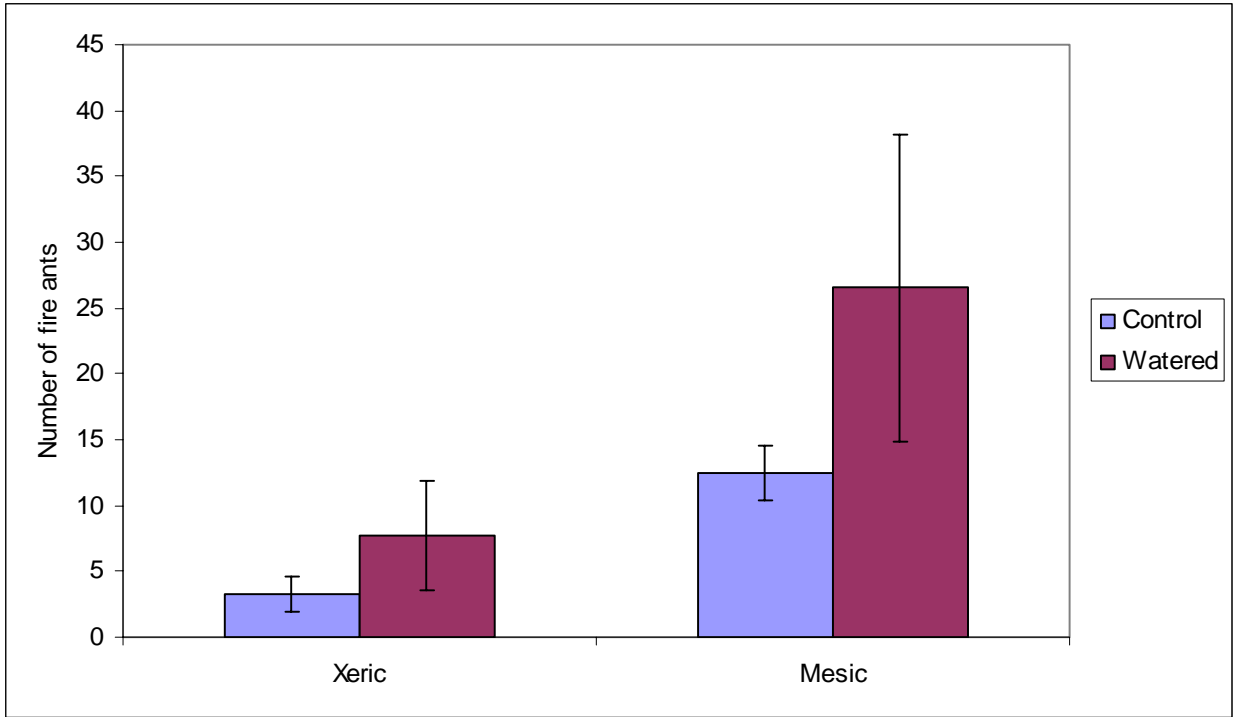


Figure 2.7 Average number of fire ants captured per array in watered and control plots within xeric and mesic sites.

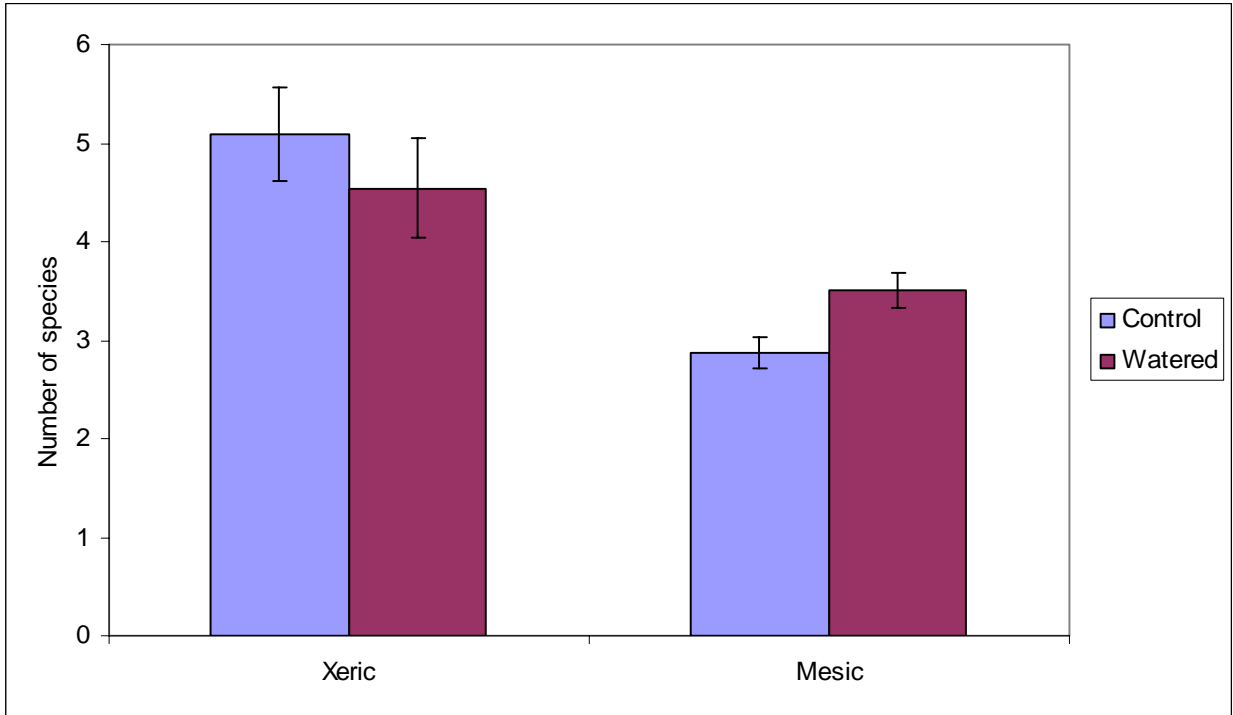


Figure 2.8 Average number of ant species captured per array in watered and control plots within xeric and mesic sites.

CHAPTER 3

FIRE ANTS AS FACILITATORS OF SEED DISPERSAL¹

¹ K.L. Stuble. To be submitted to *Oecologia*.

Abstract

Invasive ants threaten native communities, in part, through their potential to disrupt mutualisms, yet invasive species may also facilitate native species. The red imported fire ant (*Solenopsis invicta*) is one of the most conspicuous invasive ants in North America and its high densities, combined with its potential to displace native ants, have led to concerns that it may disrupt ant-plant seed dispersal mutualisms. We examined the potential of fire ants to disperse seeds in the longleaf pine ecosystem by comparing the removal of elaiosome-bearing seeds by fire ants versus native ants. We determined rate and distance of seed removal, as well as likelihood of dispersal to the nest, for 180 experimental caches of *Piriqueta cistoides* and *Polygala grandiflora*. We also used monthly pitfall trapping to determine the relative abundance of fire ants and native ants.

A total of 14 ant species were observed removing seeds, with fire ants responsible for half of all seed removals. While fire ants were the dominant seed remover in this system, they did not remove significantly more seeds than would be expected based on their population density (46% of ground-dwelling ants). Moreover, fire ants were similar to native ants with respect to the quality of the seed dispersal service provided, with no differences in distance moved or frequency of moving seeds back to the nest. Areas with naturally higher fire ant densities were found to have greater rates of seed removal by ants without a subsequent drop in seed dispersal by native ants, suggesting that fire ant-invaded areas may experience overall higher levels of seed dispersal. Thus, fire ants may actually facilitate dispersal of elaiosome-bearing plant species in the longleaf pine ecosystem. Further study is necessary, however, to determine the ultimate fate of these seeds.

Introduction

Interspecific mutualisms are often important in structuring ecosystems (Stachowicz 2001), including community composition and overall species richness (Hacker and Gaines 1997). Disruption of such mutualisms in native ecosystems can occur when invasive species are introduced, potentially resulting in alteration of native communities (Lach 2003). Not all invasive species interact negatively with native species, and in some cases they may facilitate native species (Sax et al. 2005). Invasive species can facilitate native species through a variety of mechanisms including trophic subsidy, pollination, competitive release, and predatory release (Rodriguez 2006).

The red imported fire ant (*Solenopsis invicta*) (Hymenoptera: Formicidae) is an aggressive invader that has spread throughout the southeastern United States, as well as along the western U.S. coast. Due to their high densities (Porter et al. 1988) and potential to alter native ant assemblages (Porter and Savignano 1990, Morris and Steigman 1993, Gotelli and Arnett 2000), fire ants threaten to disrupt an important mutualism that has evolved between plants and native ant species for seed dispersal. Severance of this relationship may result in altered patterns of seed dispersal, potentially changing the composition of native plant communities. However, the actual effect of the fire ant invasion on North American plant communities is currently unknown, and the ability of fire ants to facilitate seed dispersal in native ecosystems has not been explored.

Myrmecochory, or the dispersal of seeds by ants, is a diffuse mutualism with many species of both plants and ants participating. The elaiosome, a structure characteristic of many myrmecochorous species, is a lipid-rich fleshy appendage that has evolved many times as a mechanism for seeds to attract ants as a means of dispersal. Typically, after carrying seeds to the

nest, ants remove the elaiosome and feed it to their larvae, while the seed remains intact and is either discarded within the nest or in aboveground middens (Berg 1975).

Elaiosomes provide ants with a source of food, potentially including essential nutrients that ants cannot synthesize themselves (Gammans et al. 2005). This may allow colonies to produce more and larger larvae (Gammans et al. 2005) and make them more likely to produce gynes (reproductive females) (Morales and Heithaus 1998). The deposition of seeds in the ant nest provides a short-distance dispersal service to the plant (Andersen 1988). It also places the seed in potential regeneration sites with lower predation and interspecific competition, higher soil nutrient levels (Culver and Beattie 1978), and protection from fire (Berg 1975). Through this mutualism, ants may influence the structure of plant communities by altering species densities (Rissing 1986, Peters et al. 2005) and ultimately plant community composition (Mull and MacMahon 1996, Peters et al. 2005).

Myrmecochory may play a role in maintaining the high levels of biodiversity found in the ground cover of the longleaf pine-wiregrass savanna, which includes numerous elaiosome-bearing species (Kirkman et al. 2004). This exceptionally diverse ecosystem is one of the most endangered in North America, with less than 3% of its original extent remaining (Noss 1989). The invasion of the red imported fire ant into this ecosystem (Carroll and Hoffman 1997) may alter natural ant-plant seed dispersal mutualisms and thereby change plant community composition (Lubertazzi and Tschinkel 2003, Kirkman et al. 2004).

This conjecture is well founded, as the presence of invasive ants seems to be particularly detrimental to ant-dispersed plants in native ecosystems (Ness and Bronstein 2004). The deleterious effects of invasive ants on this mutualism are best studied in the case of the Argentine ant (*Linepithema humile*). The Argentine ant reduces populations of native ants in invaded areas

(Human and Gordon 1996, Christian 2001, Gomez et al. 2003) while failing to effectively disperse seeds itself (Bond and Slingsby 1984, Carney et al. 2003, Gomez et al. 2003). Through this mechanism, Argentine ants have been found to alter plant community composition (Christian 2001).

The red imported fire ant collects the seeds of numerous plant species, both with and without elaiosomes (Ready and Vinson 1995), but may serve as a poor disperser of these seeds. Areas invaded by fire ants tend to have the same number of experimentally placed seeds removed by ants as uninvaded areas, but fire ants tend to carry seeds shorter distances than native ant species and are less likely to carry seeds back to the nest (Ness 2004). They also eat the seeds of some elaiosome-bearing species while scarifying others (Zettler et al. 2001). Thus, poor dispersal abilities, combined with their extremely high densities in invaded areas, suggest that the presence of fire ants in the longleaf pine-wiregrass savanna may negatively impact ant-mediated seed dispersal.

The purpose of this study is to compare the dispersal abilities of fire ants with those of native ants in an undisturbed longleaf pine wiregrass-savanna and to quantify the relationship between the relative density of fire ants and rate of seed dispersal. Specifically, we addressed the following questions: 1) Does dispersal distance, the likelihood of a seed being taken to the nest, and the likelihood of an ant species to share a cache with another species differ among native ants and fire ants? 2) How does the rate of dispersal vary with fire ant and native ant densities? 3) Does the soil seedbank associated with fire ant mounds differ from neighboring areas?

Materials and Methods

Study site

This study was conducted on the property of the J.W. Jones Ecological Research Center (Ichauway), a 12,000 ha site, located in southwestern Georgia (Baker County). Ichauway consists of remnant natural stands of longleaf pine (*Pinus palustris* Miller) with an understory dominated by wiregrass (*Artistida stricta* Michx.). The red imported fire ant is present in this longleaf pine savanna, likely arriving in southwest Georgia in the 1960s (Callcott and Collins 1996). At Ichauway, the forest is currently managed with prescribed burns at approximately two-year return intervals. The average daily temperature is 11°C during winter and 27°C during summer with an average annual rainfall of 132 cm/year.

Ant Community Composition

To examine ant community composition, we established nine 1 ha plots on sites dominated by wiregrass in the understory and longleaf pine in the overstory. The presence of wiregrass indicates that these sites had not been subjected to major soil disturbance (such as cultivation) in the past (Clewell 1989). All sites were classified as “somewhat excessively drained upland terraces” based on soil type, vegetation, and landscape position (Goebel et al. 2001). On these plots, we established nine pitfall trapping arrays, each composed of three pitfall traps arranged to form an equilateral triangle with a distance of 5 m between traps. Pitfall traps consisted of a 15.3 cm long section of 2.1 cm diameter polyvinyl chloride (PVC) pipe that was sunk into the ground. We inserted a test tube (15 cm long, 2 cm diameter) into the PVC pipe such that the opening of the test tube was flush with the ground (Majer 1978). Within the plots, we positioned the nine pitfall arrays in a three-by-three grid, with a distance of 20 m between

arrays and a 30 m buffer between the outermost arrays and the boundary of the plot. Ants were trapped for 24 hr once a month from June through September of 2006 and 2007. Ants were stored in 70% ethanol until they could be identified to species. All nine plots were utilized in 2006, but four of these plots were dropped from the experiment in 2007 after alteration by external disturbance.

Seed dispersal

To determine the effectiveness of fire ants as dispersers of myrmecochorous species, we compared the dispersal of two elaiosome-bearing plant species, *Piriqueta cistoides* (L.) Griseb. (Turneraceae) and *Polygala grandiflora* Walt. (Polygalaceae), by fire ants and native ants. Both species were common in the study area and readily removed by ants. For each observation period, we placed 10 seeds of one of the species in a shallow, open Petri dish for presentation to ants. On the rim of each plastic Petri dish, we burned four holes to facilitate movement of ants into and out of the dish. Seed presentations (n = 151) were conducted in the center of randomly selected pitfall trapping arrays within the sampling plots described above. An additional 24 observations were conducted within the longleaf pine savanna outside of these plots. Each seed cache was observed for 1 hr, or until all of the seeds were removed, whichever came first. For each seed removed, we recorded the time to removal, distance moved, destination, and species of ant involved. Seed presentations were made between 0800 hr and 1200 hr, when cooler temperatures allow higher levels of ant activity. We conducted a total of 175 seed presentations between June and October of 2006 and 2007.

Fire ant mound seed bank

We used a seedling emergence technique to examine the soil seed bank associated with fire ant mounds. In January 2007, we collected soil samples from active fire ant mounds that had been identified as also having been active in spring 2006. At each mound, we collected two 0.25 L soil samples (2 cm in depth by 8 cm in diameter) from three points: the center of the mound, the edge of the mound, and 2 m north of the mound (control). For each sample location, we combined the two samples to create a single 0.5 L sample.

Following refrigeration for 5 - 7 days, soil samples were spread over 2.5 cm of potting mix (0.7 m³ of Miracle Grow® Potting Mix to 22.5 kg of sand) in a pot (20.3 cm in diameter by 10.2 cm tall). All samples were treated with Amdro® (0.73% hydramethylnon by weight) and the insecticide Sevin® (22.5% Carbaryl 1-naphthyl N-methylcarbamate, by weight) to kill any fire ants. Soil samples were kept in a greenhouse for 9 months and monitored for seedling emergence. All seedlings were identified to species and removed.

Statistical analyses

Combining data from both years, we examined differences in the mean number of seeds removed from a cache, number of ant species sharing a cache, proportion of seeds moved to the nest, and distance seeds were transported by fire ants versus native ants, as well as among the six ant species most commonly observed removing seeds, using ANOVA (PROC GLM, SAS version 9.1). Count and proportional data were rank transformed.

We used chi-square analysis to compare the proportional composition by species (from June through September) in the ant community with the proportion of seeds removed by that species (PROC FREQ, SAS version 9.1). We defined measures of seed dispersal quality as:

number of seeds removed per cache, mean cache discovery time, and seed removal distance, averaged per plot. We examined the relationship of each of the dispersal quality variables with the mean number of species, and mean densities of fire ants, native ants, and total ants per array per plot (PROC REG, SAS version 9.1). Plots ranked by mean fire ant, native ant, and total ant densities were not correlated between 2006 and 2007 according to a Spearman rank correlation (PROC CORR, SAS version 9.1). Thus, data for both years were treated as independent samples in these regression analyses.

Differences in mean species richness and number of emergent seedlings between treatments were analyzed using ANOVA (PROC GLM, SAS version 9.1).

Results

Seed Dispersal Trials

Of the 175 seed cache observations, 80% of the caches had at least one seed removed from the Petri dish by ants and 64% of all seeds presented (n=1,750) were removed. We observed 14 ant species that removed seeds from caches (Table 3.1), with more than 50% of the removals attributable to *S. invicta*. *Pheidole* spp. was responsible for an additional 23%.

Considering only seed presentations conducted within the pitfall trapping arrays, fire ants were responsible for 52% of all seed removals while representing 46% of the ants captured at the sites, indicating that seed collection rates by fire ants are proportional to their density in the ant community ($p = 0.10$) (Table 3.2). For other species, however, the rate of seed dispersal did not necessarily coincide with their respective relative density. For example, *Solenopsis carolinensis*, the second most common ant in the summer community (relative density of 20%), collected a disproportionately low 3% of seeds ($p < 0.0001$). On the other hand, *Pheidole* spp. was

overrepresented as a seed disperser (26% of seed) based on its relative density (19% of collected ants) ($p < 0.01$). *Crematogaster lineolata* and *Dorymyrmex bureni* also collected a disproportionately high number of seeds ($p < 0.0001$ and $p < 0.01$, respectively).

The mean (\pm SE) number of seeds per cache removed by fire ants (7.37 \pm 0.36) exceeded that dispersed by native ants as a group (5.92 \pm 0.35) ($F = 7.68$; d.f. = 1, 165; $p = 0.0062$). By species, the mean rate of removal of seeds by fire ants was similar to that of native ant species, except for *Dorymyrmex bureni* and *Paratrechina* spp., both of which removed fewer seeds per cache than fire ants ($F = 56.63$; d.f. = 16, 277; $p < 0.0001$) (Figure 3.1).

For all species, mean (\pm SE) seed dispersal distance was 36.47 (\pm 4.35) cm, and no differences in mean dispersal distance were detected between native ant and fire ant-dispersed seeds ($F = 0.96$; d.f. = 1, 164; $p = 0.33$). Mean dispersal distance did vary by species ($F = 14.98$; d.f. = 15, 167; $p < 0.0001$) (Figure 3.2). In particular, the mean (\pm SE) distance of seed dispersal by *Dorymyrmex bureni* was 168.54 (\pm 33.39) cm, notably exceeding that of all other species.

When caches were visited by ants, the mean (\pm SE) number of visiting species was 1.35 (\pm 0.05). There was a significant difference in the likelihood of a given species to share a cache with other species ($F = 2.93$; d.f. = 15, 182; $p < 0.001$) (Figure 3.3). A mean (\pm SE) of 0.43 (\pm 0.07) additional ant species visited a seed cache if that cache was also visited by *S. invicta*. This was significantly lower than the mean (\pm SE) of 1.05 (\pm 0.15) species sharing caches with *Paratrechina* spp. Fire ants did not differ from the other seed-dispersing species with respect to cache-sharing.

Fire ants moved more seeds back to their nests than did native ants as a group ($F = 18.12$; d.f. = 1, 165; $p < 0.0001$). Of seeds removed by fire ants, a mean of 47.6% (\pm 3.72) of these seeds were taken to the nest, whereas native ants took a mean of 31.0% (\pm 3.8) to the nest.

Among species, fire ants moved significantly more seeds into nests than did *Solenopsis carolinensis*, which moved 0% of seeds to the nest, and *Pheidole* spp., which moved a mean of 18.2% (+/- 4.6) of collected seeds to the nest. ($F = 3.85$; d.f. = 14, 170; $p < 0.0001$) (Figure 3.4).

Seed Dispersal Rates and Ant Densities

The total number of seeds removed from a seed cache was positively related to fire ant density ($t = 3.96$; d.f. = 12; $p < 0.01$; $r^2 = 0.5768$) (Figure 3.5), whereas total ant density ($t = 0.87$; d.f. = 12; $p = 0.40$; $r^2 = 0.0591$) (Figure 3.6) and native ant density ($t = -0.81$; d.f. = 12; $p = 0.43$; $r^2 = 0.0523$) (Figure 3.7) were not related to total seed removal. The total number of seeds removed by native ants from a seed cache was not correlated with fire ant density (Figure 3.8), native ant density, or total ant density ($p > 0.05$). Neither dispersal distance nor time to removal of the first seed was correlated with fire ant, native ant, or total ant densities ($p > 0.05$).

Seedbank Study

A total of 672 seedlings of 64 plant species emerged from soil collected on and adjacent to fire ant mounds (Appendix 3.1). There was no difference in the number of seedlings emerging from soil originating from the three locations ($F = 1.13$; d.f. = 2, 105, $p = 0.33$) (Figure 3.9) or in the number of species originating from the three locations ($F = 1.33$; d.f. = 2, 105, $p = 0.27$) (Figure 3.10). A total of only six seedlings of three elaiosome-bearing species emerged.

Discussion

Elaiosome-bearing seeds are quickly discovered and removed by ants in the longleaf pine ecosystem. The fact that a large proportion of this seed movement is conducted by fire ants is

significant because it establishes the potential of this invasive ant to change dispersal dynamics of myrmecochorous plant species dramatically in the endangered longleaf pine ecosystem.

The superior seed dispersal rate by fire ants is likely a result of their high densities, a circumstance which tends to provide invasive ants a competitive advantage over native ants in their invaded range (Holway 1999, Holway and Suarez 1999, Morrison 2000). Nevertheless, we did not find that fire ants removed a disproportionately large number of seeds based on their abundance in the ant community. On the other hand, several species of native ants, including *Pheidole* spp., *Crematogaster lineolata*, and *Dorymyrmex bureni*, did collect a disproportionately large number of seeds. This suggests that while fire ants may dominate seed dispersal through sheer numbers of foraging ants, their inherent ability to exploit resources does not necessarily exceed that of native ants. This finding is similar to Morrison's (2000) report that although fire ants are often superior competitors against native ants at the colony level, they are not necessarily better at exploiting resources when density is controlled for.

Our finding of high quality seed dispersal by fire ants, in terms of distance and destination, is in striking contrast to a similar study by Ness (2004), who found that fire ants dispersed seeds short distances and rarely took them to nests. Reasons for these discrepancies are unclear, but differences in deciduous leaf litter on the forest floor, or differences in composition of native ant species may be factors. Additionally, fire ants tended to share caches with the same number of additional ant species as did native ants, suggesting that fire ants do not limit dispersion of seeds from a single cache to fewer nest sites by eliminating dispersion of those seeds by other ant species. This, too, diverges from previous findings that seeds from a single cache in fire ant-invaded areas are more likely to be dispersed to a single nest than seeds in uninvaded areas (Ness 2004). The fact that cache discovery time (time to removal of the first

seed) and dispersal distance by native species were independent of fire ant density indicates that increasing fire ant densities do not cause a reduction of seed dispersal quality, at least at the densities of fire ants in this study.

The overall rate of seed dispersal was positively correlated with fire ant density without a subsequent decline in seed dispersal by native ants. Combined with the apparent ability of fire ants to disperse seeds as effectively as native ants, this positive relationship makes it clear that fire ants play a major role in the movement of elaiosome-bearing seeds in this ecosystem. Nevertheless, it is still unclear whether they are seed predators. Fire ants have been observed to disperse some species (removing the elaiosome and ejecting the seed from the nest), while depredating others (Zettler et al. 2001, personal observation). Of course, seed predators can also serve as important dispersers of seeds through failure to consume all seeds that are moved to the nest (Hughes and Westoby 1992, Levey and Byrne 1993). An additional complexity resides in food source differences between the red imported fire ant and the tropical fire ant (*Solenopsis geminata*) and southern fire ant (*Solenopsis xyloni*), both of which have largely been displaced by fire ants throughout much of the Southeast (Wilson and Brown 1958, Buren 1972) and may also be seed predators. Based on a study of food items moved into mounds of *S. invicta* and *S. geminata*, Tennant and Porter (1991) reported that seeds make up fewer than 4% of the *S. invicta* diet, but comprise 30% of the diet of *S. geminata*. Furthermore, *S. geminata* has also been shown to alter plant communities through its harvesting of seeds (Risch and Carroll 1986). Such a shift in the magnitude of interactions between these species and seeds, and probable differences in seed fate, further complicates attempts to quantify the impact of the fire ant invasion on this ecosystem. With respect to the current ant community, seed predation is common. The second most common seed remover in the system is *Pheidole* spp., a seed predator (Hölldobler and

Wilson 1990). Furthermore, we did not find evidence to link seed removal and patterns of seed distribution in the mound.

Based on our results, it is reasonable to consider the possibility that fire ants may be removing seeds that otherwise might not be removed by ants. These seeds would be more vulnerable to predation (Heithaus 1981), and those not depredated would be subjected to higher levels of competition with the maternal plant as well as closely related individuals (Kalisz et al. 1999). Frequent fires in this system may pose further risk to those seeds that are not moved underground. In contrast to expectations, our study demonstrates that a facilitative relationship exists between invasive fire ants and dispersal of elaiosome-bearing plants in the longleaf pine ecosystem. The degree to which this additive effect of an invasive species determines plant community composition requires further study.

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Table 3.1 Seed caches visited and seeds removed per ant species.

Species	Number of trials	Percent trials present	Number of seeds removed	Percentage of seeds removed
<i>Brachymyrmex depilis</i>	3	1.7	9	0.8
<i>Crematogaster lineolata</i>	14	8.0	71	6.5
<i>Cyphomyrmex rimosus</i>	1	0.6	7	0.6
<i>Dorymyrmex bureni</i>	14	8.0	53	4.8
<i>Forelius pruinosus</i>	3	1.7	18	1.6
<i>Monomorium</i> sp.	1	0.6	7	0.6
<i>Paratrechina</i> spp.	20	11.4	67	6.1
<i>Paratrechina arenavega</i>	2	1.1	7	0.6
<i>Pheidole</i> spp.	40	22.9	250	22.7
<i>Pheidole dentata</i>	4	2.3	20	1.8
<i>Solenopsis carolinensis</i>	6	3.4	33	3.0
<i>Solenopsis invicta</i>	75	42.9	553	50.3
<i>Solenopsis truncorum</i>	1	0.6	4	0.4
<i>Tapinoma sessile</i>	1	0.6	1	0.1

Table 3.2 Comparison of ant community composition to proportion of elaiosome-bearing seed removed.

	Community Percent	Seed Percent	p
<i>Crematogaster lineolata</i>	2.6	7.0	< 0.0001
<i>Dorymyrmex bureni</i>	0.7	2.5	0.0030
<i>Paratrechina</i> spp.	1.7	3.1	0.0577
<i>Pheidole</i> spp.	19.3	25.5	0.0079
<i>Solenopsis carolinensis</i>	19.7	3.5	< 0.0001
<i>Solenopsis invicta</i>	45.9	52.1	0.1034

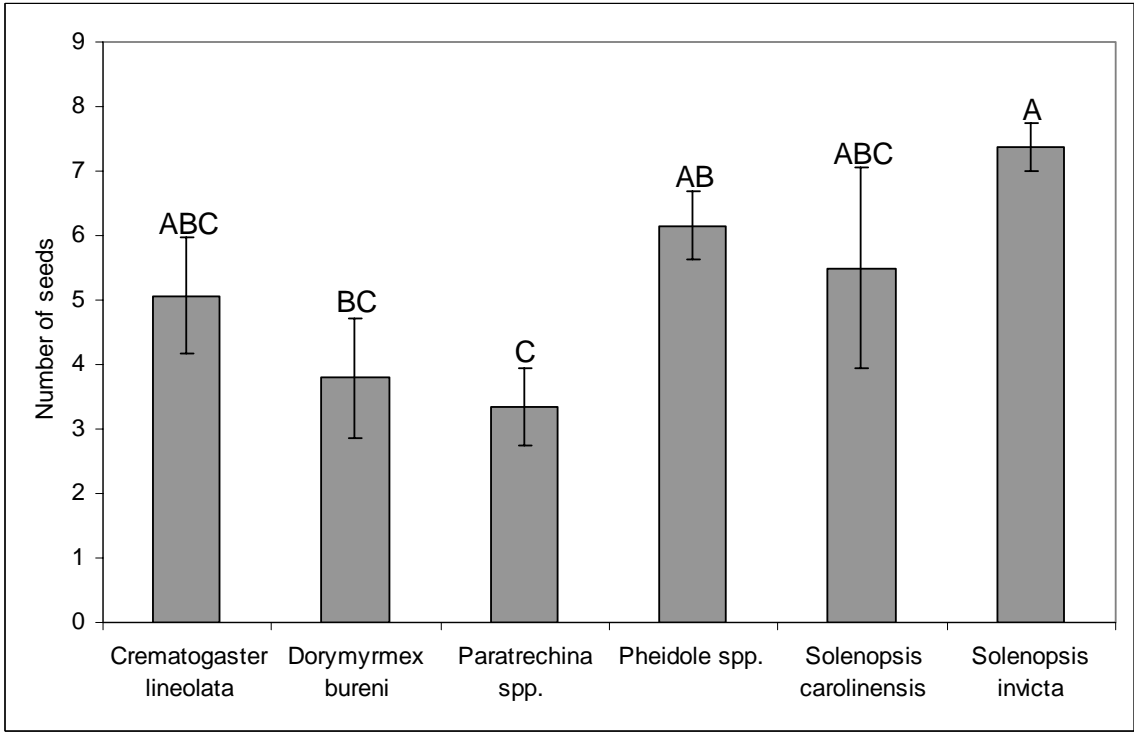


Figure 3.1 Number of elaiosome-bearing seeds removed per cache (mean +/- SE), by ant species, if that species recruited to the cache. Differences between species are indicated by differing letters ($p < 0.05$).

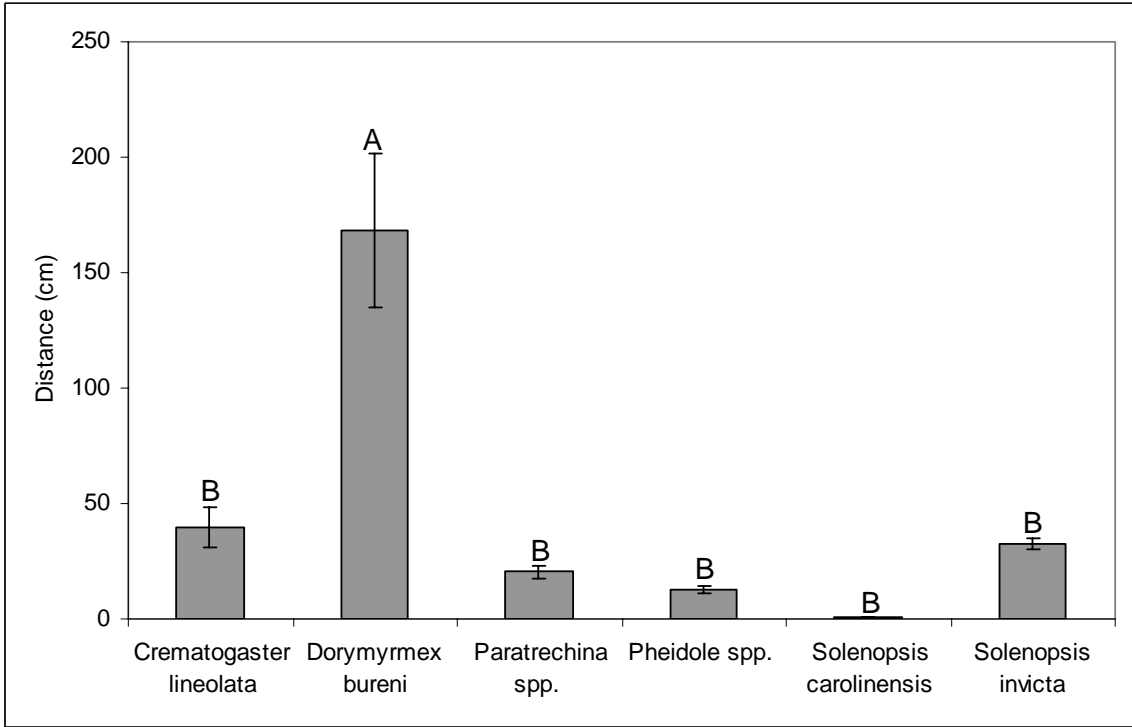


Figure 3.2 Distance of elaiosome-bearing seed removal (mean +/- SE), by ant species. Differences between ant species are indicated by differing letters ($p < 0.05$).

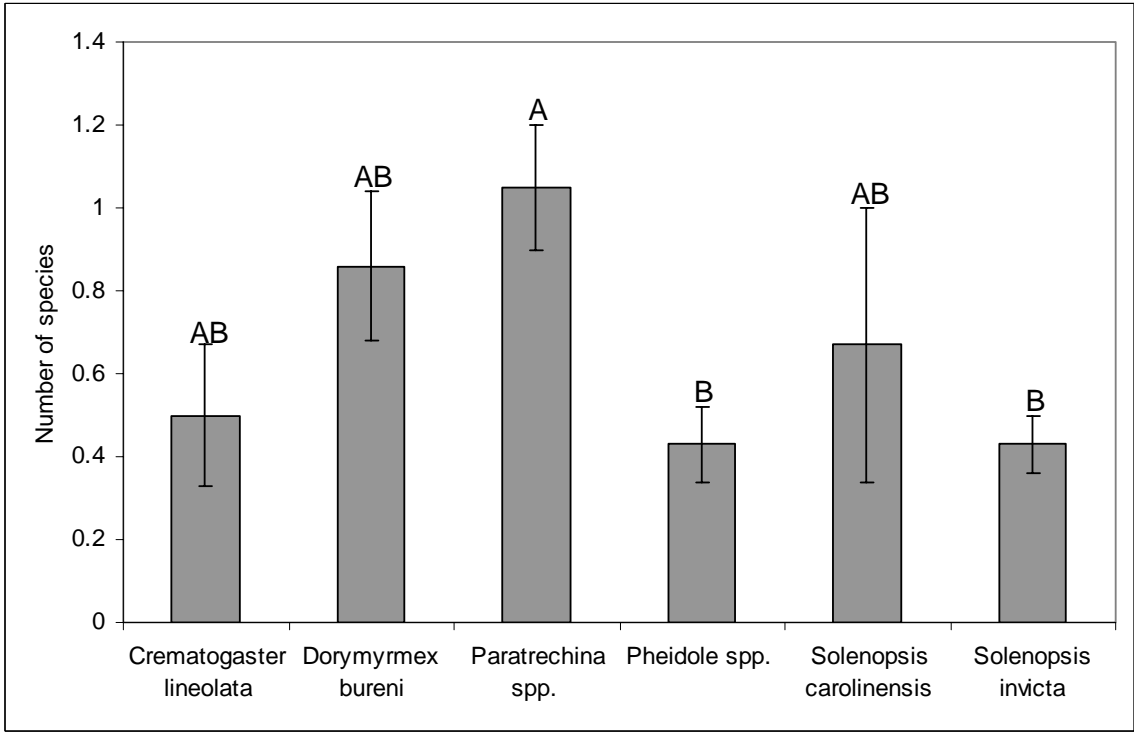


Figure 3.3 Number of additional species sharing cache (mean +/- SE), if a given ant species is present at the cache. Differences between species are indicated by differing letters ($p < 0.05$).

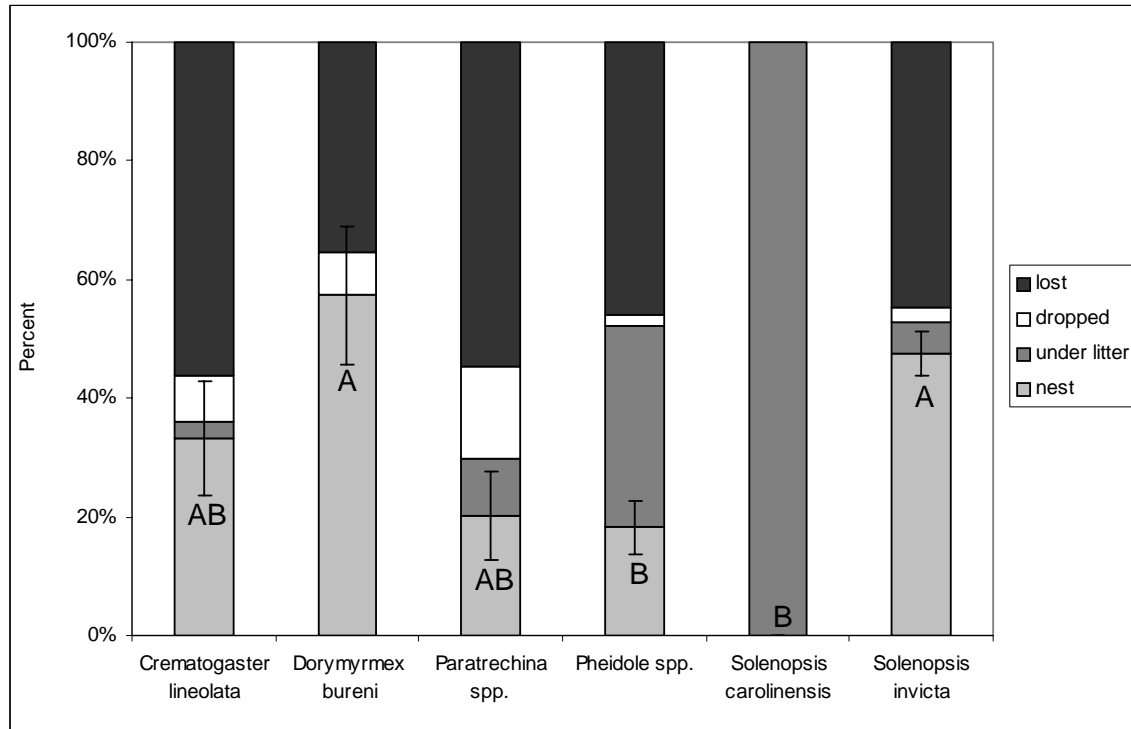


Figure 3.4 Percentage of elaiosome-bearing seeds moved to each destination, by ant species. Error bars are provided for likelihood of a species taking a seed to the nest and differences among species are indicated by differing letters ($p < 0.05$).

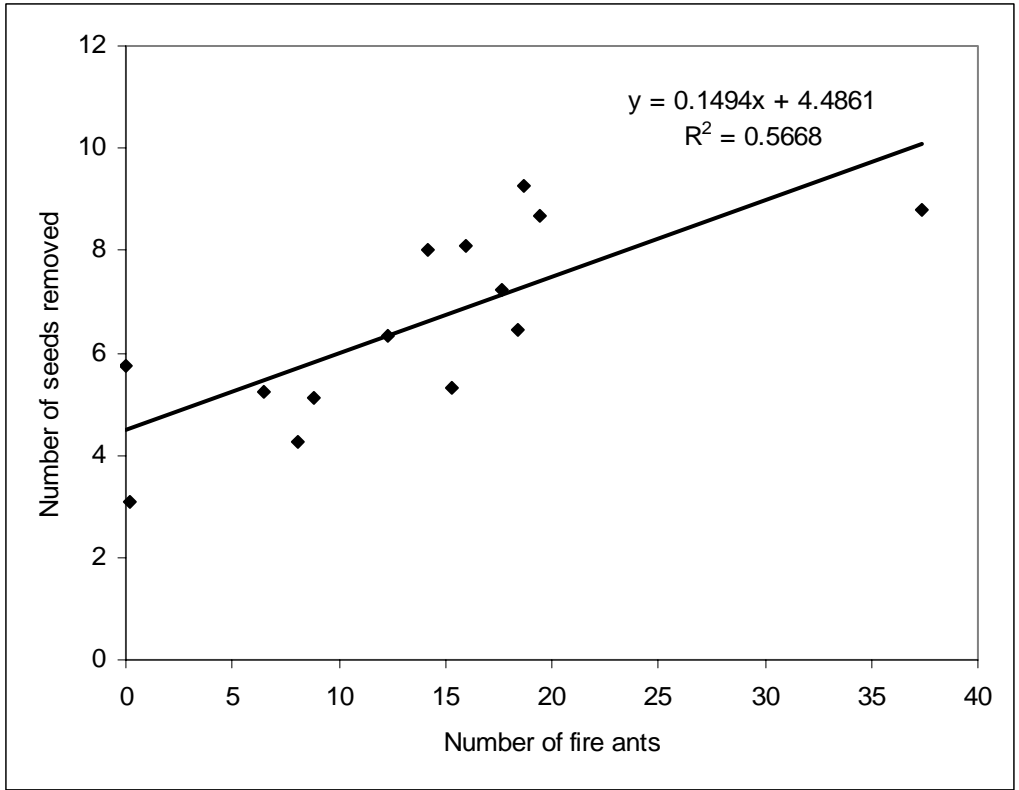


Figure 3.5 Relationship between fire ant density and the average number of seeds removed per cache.

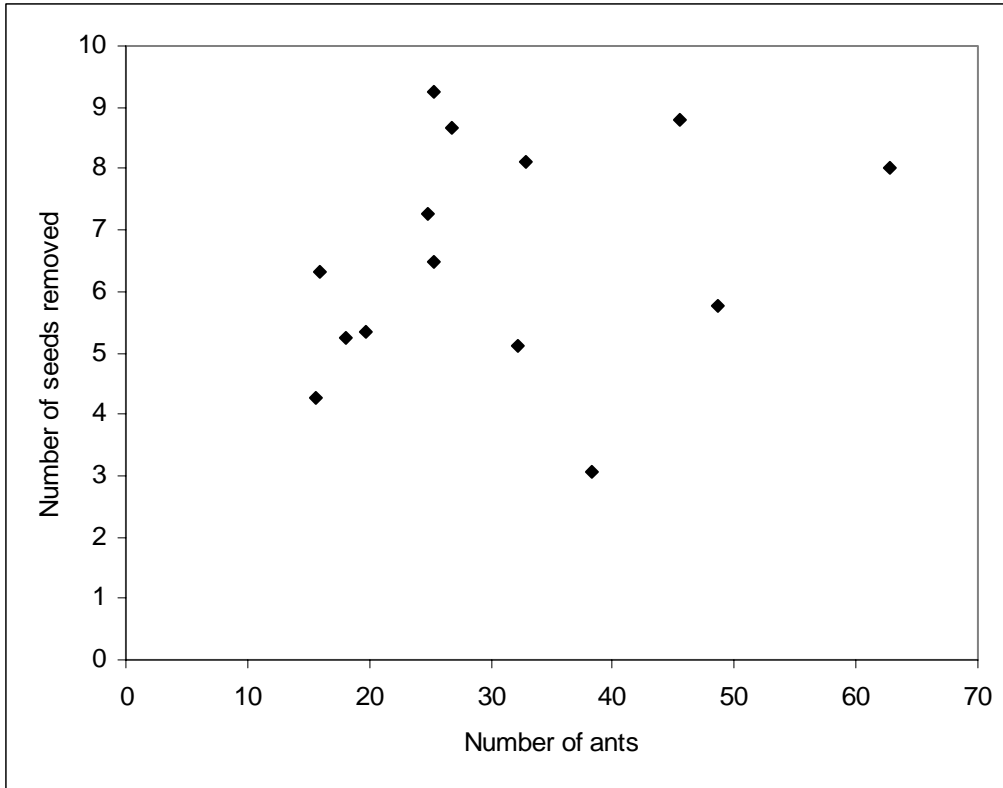


Figure 3.6 Relationship between total ant density and the average number of seeds removed per cache.

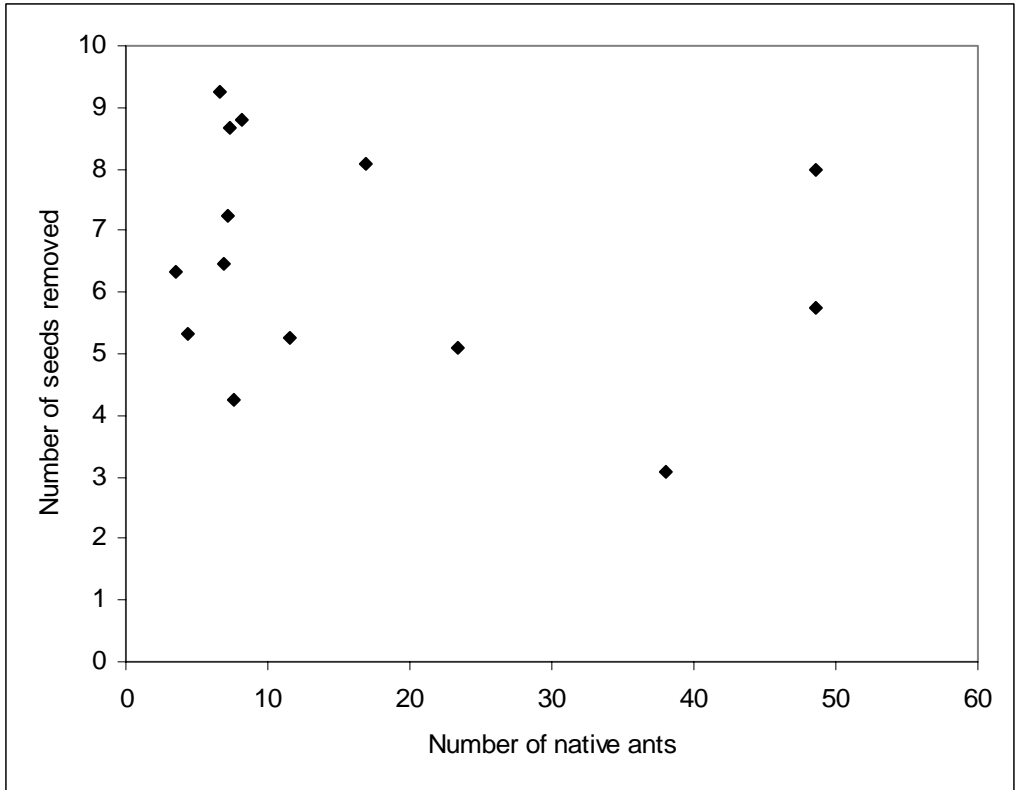


Figure 3.7 Relationship between native ant density and the average number of seeds removed per cache.

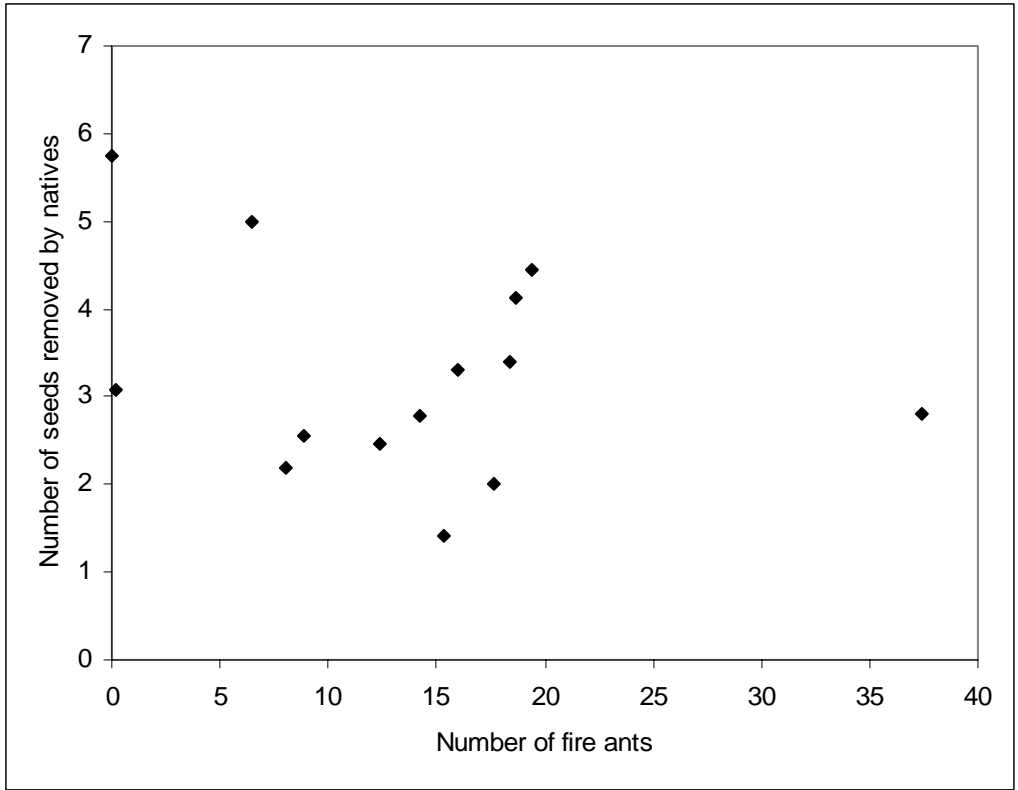


Figure 3.8 Relationship between fire ant density and the average number of seeds removed by native ants per cache.

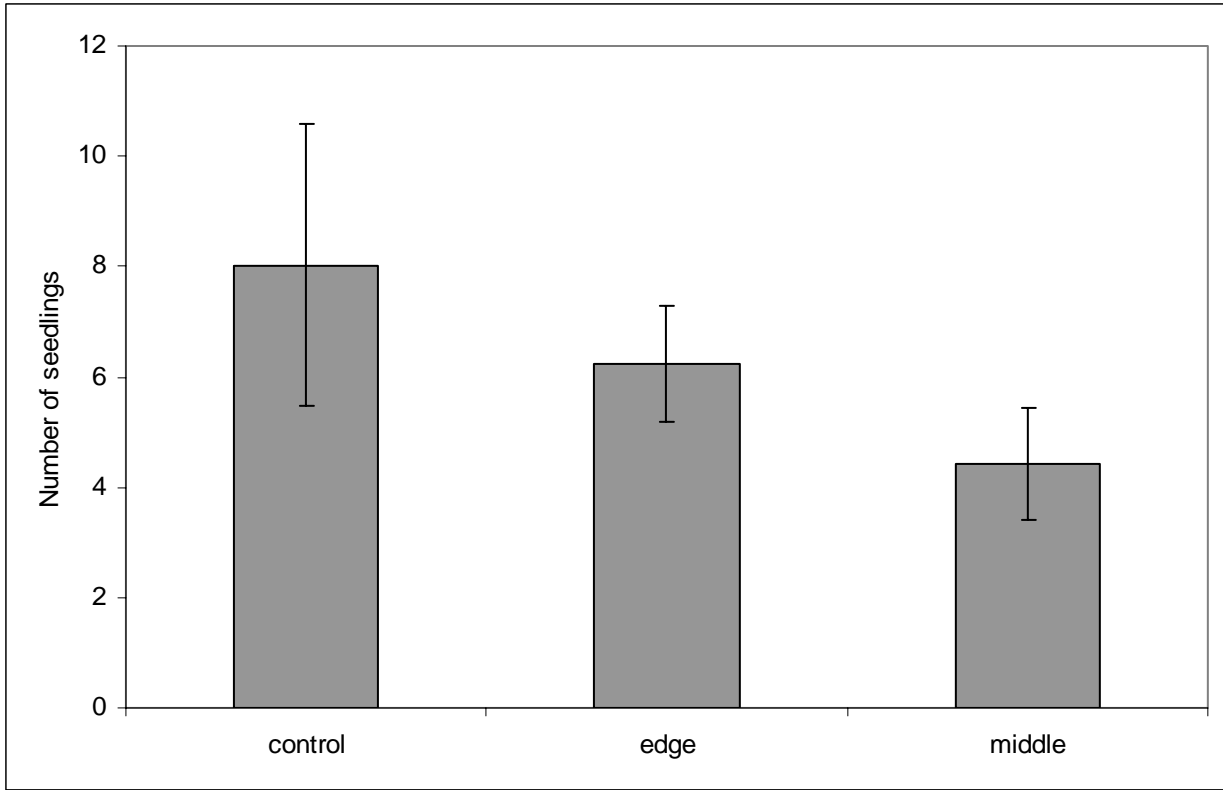


Figure 3.9 Average number of seedlings emerging from soil collected from the center of fire ant mounds, from the edge of mounds, and from control sites.

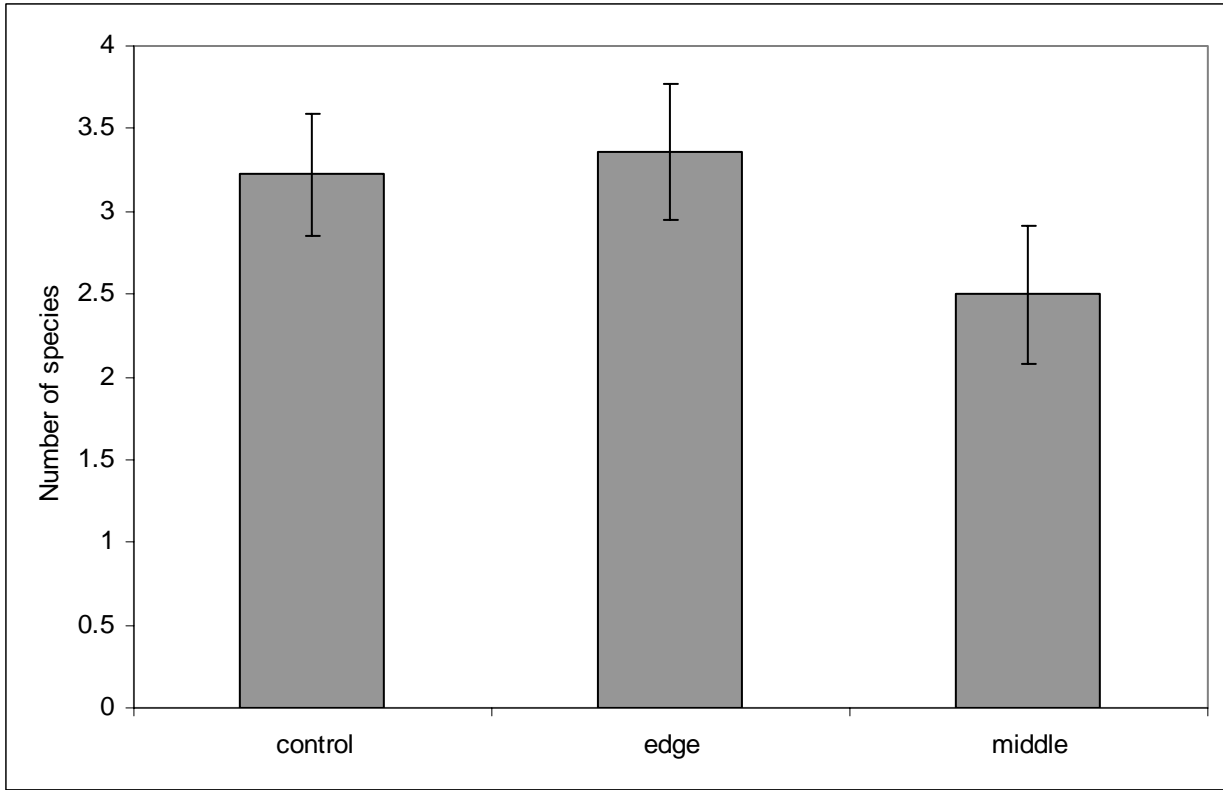


Figure 3.10 Average number of plant species emerging from soil collected from the center of fire ant mounds, from the edge of mounds, and from control sites.

Appendix 3.1 Seedbank species list.

Species	Middle	Edge	Control
<i>Acalypha gracilens</i>	x	x	x
<i>Andropogon</i> spp.	x	x	x
<i>Baccharis halimifolia</i>			x
<i>Bulbostylis ciliatifolia</i>	x	x	
<i>Centrosema virginianum</i>		x	
<i>Chamaecrista nictitans</i>	x	x	x
<i>Chamaesyce cordifolia</i>			x
<i>Commelina erecta</i>	x		
<i>Conyza canadensis</i>	x		x
<i>Crotalaria rotundifolia</i>	x	x	
<i>Croton glandulosus</i>			x
<i>Cynodon dactylon</i>		x	
<i>Cyperus filiculmis</i>			x
<i>Cyperus retrorsus</i>	x	x	x
<i>Desmodium floridanum</i>		x	
<i>Desmodium lineatum</i>	x		
<i>Desmodium strictum</i>			x
<i>Dichanthelium aciculare</i>	x	x	x
<i>Dichanthelium acuminatum</i>	x	x	x
<i>Dichanthelium boscii</i>			x
<i>Dichanthelium commutatum</i>			x
<i>Dichanthelium ovale</i>	x	x	x
<i>Dichanthelium sphaerocarpon</i>	x	x	x
<i>Dichanthelium strigosum</i>	x	x	
<i>Dichanthelium tenue</i>		x	
<i>Diodia teres</i>			x
<i>Dyschoriste oblongifolia</i>		x	x
<i>Eupatorium capillifolium</i>	x	x	x
<i>Eupatorium compositifolium</i>	x		x
<i>Galactia erecta</i>	x	x	
<i>Gamochaeta falcata</i>			x
<i>Gamochaeta purpurea</i>	x	x	x
<i>Hypericum harperi</i>		x	
<i>Hypericum suffruticosum</i>	x	x	
<i>Hypoxis wrightii</i>	x	x	x
<i>Lamium amplexicaule</i>			x
<i>Lactuca</i> sp.			x
<i>Lechea minor</i>	x		
<i>Lespedeza repens</i>			x
<i>Linaria texana</i>		x	x
<i>Lygodium japonicum</i>		x	x
<i>Mollugo verticillata</i>			x
<i>Oxalis</i> sp.			x
<i>Paronychia baldwinii</i>			x

Species	Middle	Edge	Control
<i>Paspalum setaceum</i>	x	x	x
<i>Paspalum urvillei</i>	x		
<i>Physalis walteri</i>			x
<i>Piriqueta cistoides</i>		x	x
<i>Polygala grandiflora</i>	x		
<i>Polypremum procumbens</i>	x	x	x
<i>Rhynchosia reniformis</i>			x
<i>Richardia scabra</i>	x	x	
<i>Rubus cuneifolius</i>	x	x	x
<i>Rudbeckia hirta</i>		x	
<i>Sagina decumbens</i>			x
<i>Scleria ciliata</i>			x
<i>Scleria georgiana</i>		x	x
<i>Stylisma patens</i>	x		
<i>Stylosanthes biflora</i>	x		
<i>Symphyotrichum concolor</i>	x		
<i>Symphyotrichum dumosum</i>	x	x	x
<i>Veronica arvensis</i>	x	x	x
<i>Wahlenbergia marginata</i>	x	x	x
Unknown grass	x	x	x

CHAPTER 4

CONCLUSIONS

We used the invasion of native longleaf pine-wiregrass savannas of the southeastern United States by the red imported fire ant as an opportunity to examine the impacts of fire ants on native ant assemblages and ant-seed dispersal mutualisms. Fire ants are commonly believed to cause declines in the abundance and species richness of native ants. Because fire ant invasion is usually concurrent with habitat disturbance, however, decoupling the two as explanatory factors in the decline of native ants is often difficult. Thus, the longleaf pine habitat, which has been invaded by fire ants, provides a context in which to examine the effects of fire ants on native ant assemblages and ant-plant relationships in the absence of human-mediated soil or vegetation disturbance.

Invasion of the longleaf pine ecosystem by fire ants is not yet understood, but fire may play a large role. The frequent fire return interval in this system reduces oak encroachment in the system and maintains an open overstory dominated by pines, a condition that likely favors fire ants.

Unlike many other studies, we did not find an inverse relationship between fire ants and native ant species richness. We did observe a negative relationship between densities of fire ants and native ants, but we suggest that factors other than direct competition with fire ants are causative agents. Potentially, native ants may limit invasion of fire ants based, in part, on their ability to eliminate small fire ant colonies (e.g. *Solenopsis carolinensis*). Alternatively, fire ants may invade less preferred habitats of native species, particularly sites with wet-mesic soils (Figure 4.1).

We also examined the potential impact of the fire ant invasion on dispersal of elaiosome-bearing species, specifically their influence on seed movement processes prior to deposition inside the nest (Figure 4.2). Contrary to expectations, we did not find evidence to suggest that fire ants are detrimental to ant-plant seed dispersal mutualisms, even though they dominate seed removal events. Observations of aboveground seed movement by ants indicate that fire ants behave similarly to native ants with respect to distance, destination, and number of seeds removed. Furthermore, because fire ant density was positively correlated with seed dispersal rate without a subsequent decline in seed removal by native ants, we suggest that the invasion of the longleaf pine ecosystem by fire ants has served to increase the overall magnitude of seed movement by ants in this system. This additive movement of seeds by ants to nest sites could alter fates of seeds in a fire-dependent ecosystem by providing safe sites for establishment and may have implications for seedling recruitment rates. We found no differences in seedbank composition on and off fire ant mounds, but it is possible that differences would be evident with increased intensity of sampling.

Consequently, our current understanding of the dynamics between fire ants and elaiosome-bearing seeds is largely limited to aboveground interactions. We still do not have a clear understanding of how fire ants manipulate seeds once they have been carried into the nest, although there is evidence to suggest the fire ants can act as seed predators and that their propensity to consume seeds may be plant species-specific (Zettler et al. 2001, personal observation). Further study of the fates of seeds dispersed by fire ants is necessary to determine their effective role in plant community dynamics.

The proliferation of fire ant mounds may also be of importance to overall vegetation dynamics through the alteration of soil properties that influence seedling regeneration niches

(Green et al. 1999, Seaman and Marino 2003, Lafleur et al. 2005). Future work to determine how soil texture, moisture holding capacity, and nutrient levels associated with abandoned fire ant mounds influence seedling establishment is also suggested.

We conclude that the high density of fire ants in the longleaf pine savanna will probably have an impact on the biotic community in this system. Not only are fire ants likely to mediate the recruitment dynamics of elaiosome-bearing species, they may also have large impacts on seed or seedling predation of species that are not ant-dispersed. Furthermore, fire ants may influence the re-establishment of native vegetation in disturbed sites, particularly if these areas harbor high fire ant densities. Thus, the role of fire ants in the restoration of the diverse ground cover of the longleaf pine ecosystem deserves further attention.

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Figure 4.1 Conceptual model showing the potential biotic and abiotic factors regulating total native ant and fire ant density. Solid lines represent direct interactions while dashed lines indicate a correlation between groups.

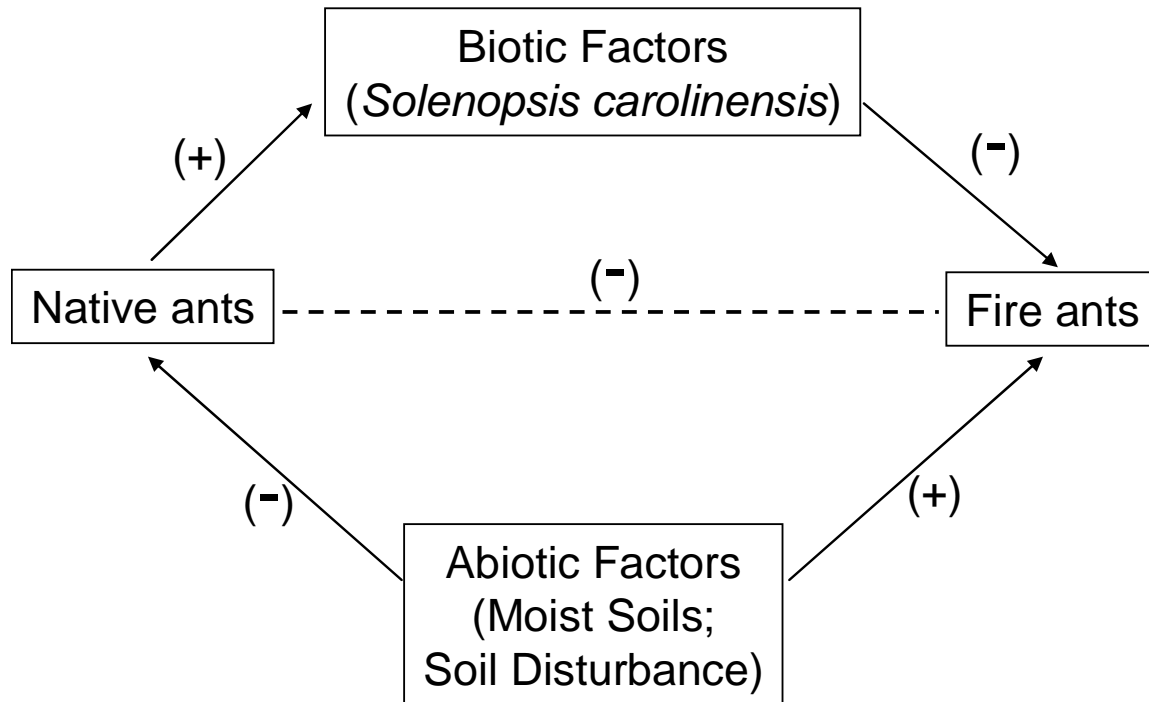


Figure 4.2 Conceptual model of the pathway from seed to seedling establishment and the influences of fire ants and native ants.

