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Are red imported fire ants facilitators of native seed dispersal?

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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. A total of 14 ant species were observed removing seeds, with fire ants responsible for more than half of all 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, red imported fire ants were similar to native ants with respect to distance of seed movement and frequency of moving seeds back to the nest. Areas of 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.

Keywords Elaiosome · Myrmecochory · *Solenopsis invicta* · Mutualism

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Introduction

Mutualisms are often important in structuring ecosystems (Callaway 1995; Stachowicz 2001), including community composition and overall species richness (Callaway 1995; 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, however, interact negatively with native species, and in some cases they may even facilitate native species (Sax et al. 2005). Facilitation by an introduced species can occur through mechanisms such as trophic subsidy, pollination, competitive release, and predatory release (Rodriguez 2006).

Myrmecochorous plants are those species specifically adapted for seed dispersal by ants. The

elaiosome, a structure characteristic of many myr-mecochorous species, is a lipid-rich fleshy appendage that has evolved numerous 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 the larvae. The seed remains intact and is either discarded within the nest or in aboveground middens (Berg 1975). 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 (Heithaus 1981; Manzaneda et al. 2005) and interspecific competition, higher soil nutrient levels (Culver and Beattie 1978), and protection from fire (Berg 1975).

Myrmecochory is typically considered a diffuse mutualism, with many species of both plants and ants participating. However, there is increasing evidence that this seed dispersal mutualism may frequently be skewed toward one particularly important species of ant (Gove et al. 2007). This type of mutualism is termed an "unevenly diffuse" mutualism and the disproportionately important partner is known as the keystone mutualist. Such a skewed relationship may increase the vulnerability of this relationship to disruption by agents that may alter the composition of the ant community.

Invasive ants can disrupt the seed dispersal mutualism between native ants and plants, a scenario best studied in the case of the Argentine ant (*Linepithema humile*), which reduces populations of native ants in invaded areas (Christian 2001; Gómez et al. 2003; Human and Gordon 1996; Rodriguez-Cabal et al. 2009), while failing to effectively disperse seeds itself (Bond and Slingsby 1984; Carney et al. 2003; Gómez et al. 2003; Rodriguez-Cabal et al. 2009). Through this mechanism, Argentine ants have been found to alter plant community composition (Christian 2001).

The red imported fire ant (*Solenopsis invicta*) is a prolific invader in the southeastern US and is currently extending its range along the west coast of the US, as well as in Australia, New Zealand, and recently China (Xiong et al. 2008), with the potential to alter patterns of seed dispersal. This ant species collects the seeds of numerous plant species, both with and without elaiosomes (Ready and Vinson 1995), but it may serve as a poor disperser of these seeds. Additionally, their potential to alter native ant

assemblages (Gotelli and Arnett 2000; Morris and Steigman 1993; Porter and Savignano 1990) further threatens to disrupt the mutualism that has evolved between plants and native ant species for seed dispersal. Areas invaded by fire ants tend to have the same rate of seed removal 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, evidence of poor dispersal abilities, combined with their extremely high densities in invaded areas, suggest that fire ants may negatively impact ant-mediated seed dispersal. However, the impact of fire ants on seed dispersal has not yet been examined in an intact ecosystem.

The purpose of this study was to compare the dispersal abilities of fire ants with those of native ants in a longleaf pine wiregrass-savanna and to quantify the relationship between the relative density of fire ants and overall 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 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?

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 (Stuble et al. 2009), likely arriving in southwest Georgia in the 1960s (Callcott and Collins 1996). At Ichauway, the longleaf pine forest is currently managed with prescribed burns at approximately 2-year return intervals. The average daily temperature ranges from 5 to 17°C during winter and 21 to 34°C during summer (Goebel et al. 2001) with an average annual rainfall of 131 cm (National Climate Data Center, Asheville, NC).

Seed dispersal ability

We established nine 1-ha plots in areas dominated by wiregrass in the ground cover and longleaf pine in the overstory. The extensive cover of wiregrass indicates that these sites had not been subjected to major soil disturbance (such as cultivation) in the past (Clewell 1989). Plots were positioned at least 30 m from dirt roads and fire breaks and at least 100 m from paved roads (though the distance of most plots from paved roads was substantially farther). All plots were located in areas classified as "somewhat excessively drained upland terraces" based on soil type, vegetation, and landscape position (Goebel et al. 2001). At the outset of this study, the plots ranged from 2 to 55 fire ant mounds per hectare. Within each of 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 h once a month from June through September of 2006 and 2007. Ants were stored in 70% ethanol until they could be identified to species. Voucher specimens are held at the J.W. Jones Ecological Research Center. All nine plots were utilized in 2006, but four of these plots were dropped from the experiment in 2007 after being altered by external disturbance.

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, co-occur with fire ants throughout the local area, and produce seeds that are readily removed by ants. For each observation period, we placed 10 seeds of one of the species (selected at random) in a shallow, open 47 mm Petri dish for presentation to ants. On the rim of each plastic Petri dish, we burned four 0.5 cm holes to facilitate movement of ants into and out of the

dish. Seed presentations ($n = 151$ Petri dishes) 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 Petri dish was observed for 1 h, 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 (*Pheidole* and *Paratrechina* species were pooled by genus as these ants are difficult to identify in the field). Fire ants were commonly observed moving seeds into underground foraging tunnels. We counted these seeds as having been moved to the nest. We conducted a total of 175 seed presentations between June and October of 2006 and 2007. Seed presentations were made between 0800 and 1200 hours, when cooler temperatures allow high levels of ant activity.

Statistical analyses

Combining data from both years of observation, we tested for differences in 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 a one-way ANOVA (PROC GLM, SAS version 9.1). Count and proportional data were rank transformed prior to analyses.

We used χ^2 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 as determined by pitfall trapping (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.

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 remove seeds from caches (Table 1), with more than 50% of the removals attributable to *S. invicta*.

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 2). For other species, however, the rate of seed dispersal did not consistently 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 remover (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 ± 0.36) exceeded that dispersed by native ants as a group (5.92 ± 0.35) by 14.5% ($F = 7.68$; df $= 1$, 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 ($F = 56.63$; df $= 16$, 277; $P < 0.0001$) (Fig. 1).

Table 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
Solenopsis invicta	75	42.9	553	50.3
Pheidole spp.	40	22.9	250	22.7
Paratrechina spp.	20	11.4	67	6.1
Crematogaster lineolata	14	8	71	6.5
Dorymyrmex bureni	14	8	53	4.8
Solenopsis carolinensis	6	3.4	33	3
Pheidole dentata	4	2.3	20	1.8
Brachymyrmex depilis	3	1.7	9	0.8
Forelius pruinosus	3	1.7	18	1.6
Paratrechina arenavega	2	1.1	7	0.6
Cyphomyrmex rimosus	1	0.6	7	0.6
Monomorium sp.	1	0.6	7	0.6
Solenopsis truncorum	1	0.6	4	0.4
Tapinoma sessile	1	0.6	1	0.1

Table 2 Comparison of ant community composition to proportion of elaiosome-bearing seed removed using χ^2 analysis

	Relative abundance in ant community	Percentage of seed removed	P
Crematogaster lineolata	2.6	7.0	<0.0001
Dorymyrmex bureni	0.7	2.5	0.0030
Paratrechina spp.	1.7	3.1	0.0577
Pheidole spp.	19.3	25.5	0.0079
Solenopsis carolinensis	19.7	3.5	<0.0001
Solenopsis invicta	45.9	52.1	0.1034

Fig. 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* ($P < 0.05$)
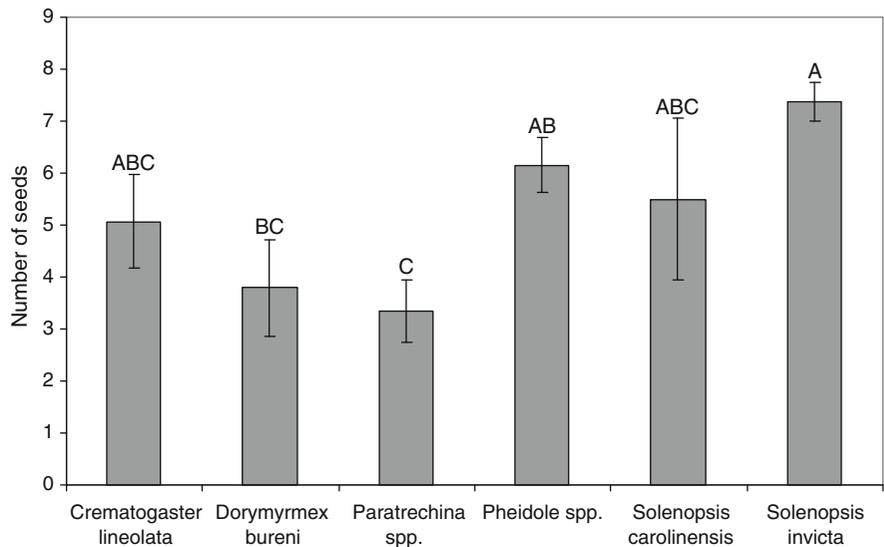
For all species, mean (±SE) seed dispersal distance was 36.47 (±4.35) cm, and no differences in mean dispersal distance occurred between native ant and fire ant-dispersed seeds ($F = 0.96$; df = 1, 164; $P = 0.33$). However, mean dispersal distance did vary by species ($F = 14.98$; df = 15, 167; $P < 0.0001$) (Fig. 2). In particular, the mean (±SE) distance of seed dispersal by *Dorymyrmex bureni* was 168.54 (±33.39) cm, notably exceeding that of all other species.

For seed caches that were visited by ants, the mean (±SE) number of visiting species was 1.35 (±0.05). Differences among species occurred in the likelihood

of an ant species to share a cache with other species ($F = 2.93$; df = 15, 182; $P < 0.001$) (Fig. 3). However, fire ants did not differ from the other seed-dispersing species with respect to cache-sharing with the exception of *Paratrechina* spp., which was more likely to share the seed cache with other species.

Fire ants moved more seeds back to their nests than did native ants as a group ($F = 18.12$; df = 1, 165; $P < 0.0001$). Of seeds removed by fire ants, a mean of 47.6% (±3.72) were taken to the nest, whereas native ants took a mean of 31.0% (±3.8) to the nest. Among species, fire ants moved significantly more seeds into nests than did *Solenopsis*

Fig. 2 Distance of elaiosome-bearing seed removal (mean ± SE), by ant species. Differences between ant species are indicated by *differing letters* ($P < 0.05$)
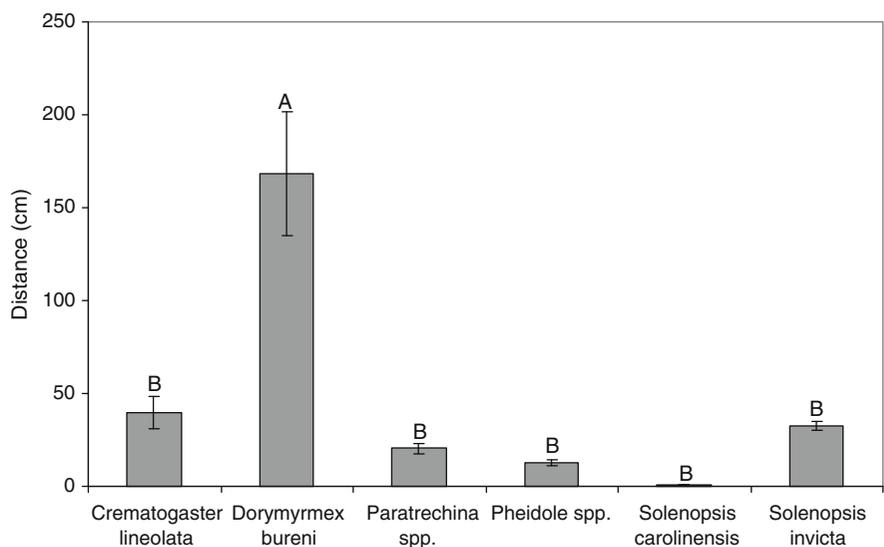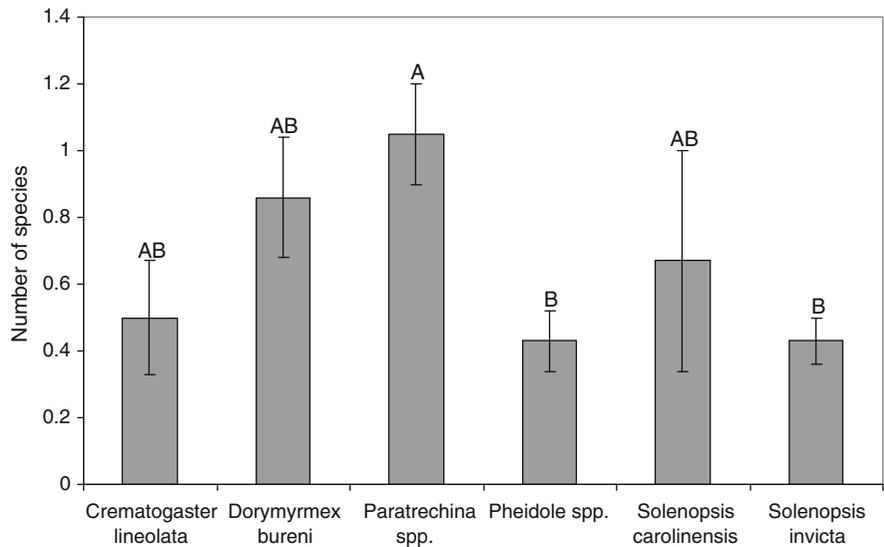
Fig. 3 Number of additional species sharing cache (mean ± SE), if a given ant species is present at the cache. Differences between species are indicated by *differing letters* ($P < 0.05$)


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 ($F = 3.85$; df = 14, 170; $P < 0.0001$) (Fig. 4).

Seed dispersal rates and ant densities

The total number of seeds removed from a seed cache was positively related to fire ant density ($t = 3.96$;

df = 12; $P < 0.01$; $r^2 = 0.577$) (Fig. 5), whereas total ant density ($t = 0.87$; df = 12; $P = 0.40$; $r^2 = 0.059$) and native ant density ($t = -0.81$; df = 12; $P = 0.43$; $r^2 = 0.052$) 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 (Fig. 5), native ant density, or total ant density ($P > 0.05$). Neither dispersal distance nor time to removal of the first

Fig. 4 Percentage of elaiosome-bearing seeds moved to each destination, by ant species. Lost seeds are those that the researcher lost track of before they reached their final destination. *Error bars* are provided for likelihood of a species taking a seed to the nest and differences among species are indicated by *differing letters* ($P < 0.05$)
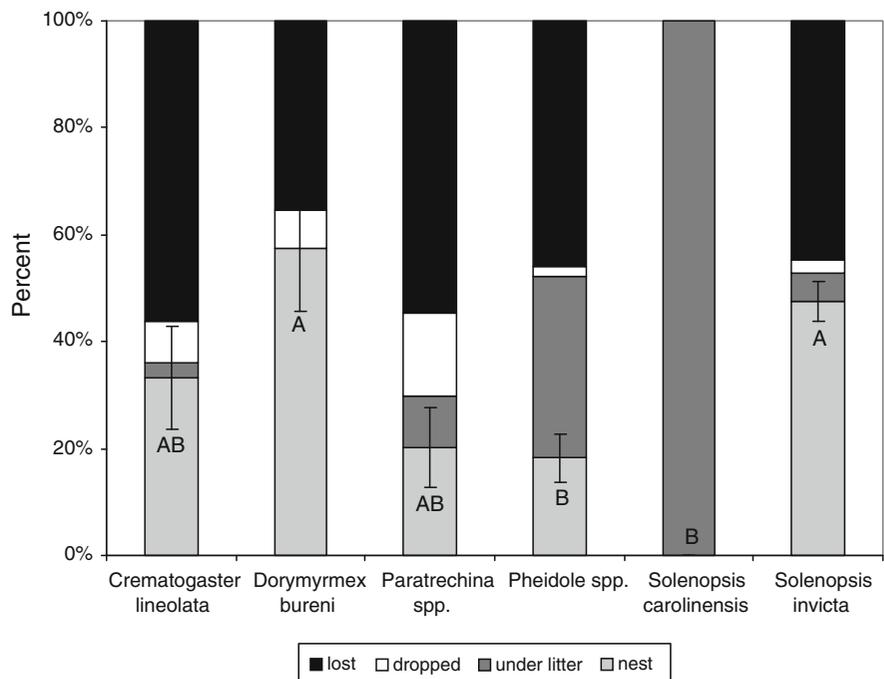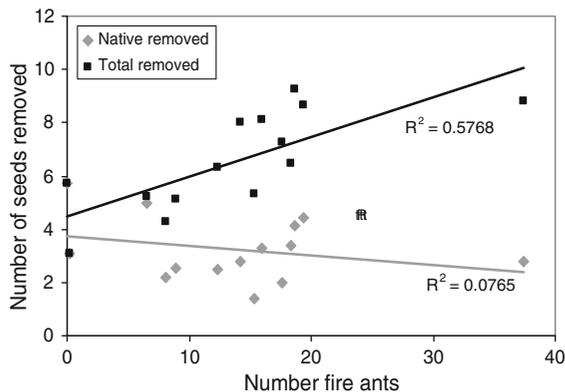
Fig. 5 Relationship between the number of fire ants per pitfall trapping array, averaged by *plot*, and the number of seeds removed per cache overall and by native ants

seed was correlated with fire ant, native ant, or total ant densities ($P > 0.05$).

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 dramatically change dispersal dynamics of myrmecochorous plant species 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 larger number of seeds than would be expected based on relative abundance. 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) conducted along an eastern deciduous forest edge, which 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 or the large differences in composition of native ant communities in these two systems may be factors. Likewise, differences among the species of seeds used [Ness (2004) used *Sanguinaria canadensis*] for these studies may have resulted in differing handling behavior by ants. Additionally, in our study, 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 striking differences in dispersal quality between this study conducted in the longleaf pine ecosystem and the Ness (2004) study conducted in an eastern deciduous ecosystem point to the need to conduct similar studies in a variety of habitats.

The overall rate of removal of elaiosome-bearing seed 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 as a group 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 to what degree fire ants serve as 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). 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 (Buren 1972; Wilson and Brown 1958) 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*. 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.

Based on our results, it is reasonable to consider the possibility that fire ants may be removing elaiosome-bearing seeds that otherwise might not be removed by ants. Seeds not removed 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 potentially facilitative relationship exists between invasive fire ants and dispersal of elaiosome-bearing plants in the longleaf pine ecosystem. However, the degree to which this additive effect of an invasive species ultimately influences plant community composition requires further study into the ultimate fate of seeds removed by fire ants and native ants.

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