Research Note

Relative Effects of Disturbance on Red Imported Fire Ants and Native Ant Species in a Longleaf Pine Ecosystem

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Abstract: *The degree to which changes in community composition mediate the probability of colonization and spread of non-native species is not well understood, especially in animal communities. High species richness may hinder the establishment of non-native species. Distinguishing between this scenario and cases in which non-native species become established in intact (lacking extensive anthropogenic soil disturbance) communities and subsequently diminish the abundance and richness of native species is challenging on the basis of observation alone. The red imported fire ant (*Solenopsis invicta*), an invasive species that occurs throughout much of the southeastern United States, is such an example. Rather than competitively displacing native species, fire ants may become established only in disturbed areas in which native species richness and abundance are already reduced. We used insecticide to reduce the abundance of native ants and fire ants in four experimental plots. We then observed the reassembly and reestablishment of the ants in these plots for 1 year after treatment. The abundance of fire ants in treated plots did not differ from abundance in control plots 1 year after treatment. Likewise, the abundance of native ants increased to levels comparable to those in control plots after 1 year. Our findings suggest that factors other than large reductions in ant abundance and species density (number of species per unit area) may affect the establishment of fire ants and that the response of native ants and fire ants to disturbance can be comparable.*

Keywords: diversity, fire ant, invasion, *Solenopsis invicta*

Efectos Relativos de la Perturbación sobre Especies de Hormigas de Fuego Importadas y Nativas en un Ecosistema de Pinos

Resumen: *El grado en que los cambios en una comunidad median la probabilidad de colonización y dispersión de especies no nativas no está bien comprendido, especialmente en comunidades animales. Alta riqueza de especies puede impedir el establecimiento de especies no nativas. La distinción entre este escenario y casos en los que especies no nativas se establecen en comunidades intactas (carentes de perturbación antropogénica de suelo) y subsecuentemente disminuye la abundancia y riqueza de especies nativas es un reto basándose solo en observaciones. La hormiga de fuego importada (*Solenopsis invicta*), una especie invasora que ocurre extensivamente en el sureste de Estados Unidos, es un ejemplo de lo anterior. En lugar de desplazar competitivamente a especies nativas, las hormigas de fuego pueden establecerse solo en áreas perturbadas donde la riqueza y abundancia de especies nativas ya están reducidas. Utilizamos insecticida para reducir*

la abundancia de hormigas nativas y hormigas de fuego en 4 parcelas experimentales. Posteriormente obser-
vamos la reagrupación y restablecimiento de las hormigas en estas parcelas 1 año después del tratamiento.
Asimismo, la abundancia de hormigas nativas incrementó a niveles comparables a los de las parcelas control
después de un año. Nuestros hallazgos sugieren que factores distintos a las reducciones en la abundancia de
hormigas y la densidad de especies (número de especies por unidad de área) pueden afectar el establecimiento
de hormigas de fuego y que la respuesta de hormigas nativas y hormigas de fuego a la perturbación pueden
ser comparables.

Introduction

Species-rich communities may be more resistant to establishment of non-native species than species-poor communities (Elton 1958; Fridley et al. 2007), especially at small spatial extents (Levine 2000). Nevertheless, most studies that show species-rich communities are more resistant to non-native species have been nonexperimental, correlational studies, which makes it difficult to discern whether invasive species cause reductions in species richness or instead become established in communities in which richness has already been reduced by some other factor (MacDougall & Turkington 2005; King & Tschinkel 2008). Field experiments in which the species richness of native plants is reduced and then the establishment of non-native plant species is monitored are common (Kennedy et al. 2002; Fargione & Tilman 2005; Fridley et al. 2007). Such experiments with ants, however, are rare (but see Menke et al. 2007). One limitation is that some non-native ants, such as the red imported fire ants (*Solenopsis invicta*) (hereafter fire ants), seldom become established in intact ecosystems (lacking extensive anthropogenic soil disturbance) (Tschinkel 2006), which makes it difficult to decouple the effects of anthropogenic disturbance from the effects of native species richness on colonization success.

One exception to this limitation is fire ant colonization of some intact longleaf pine (*Pinus palustris*) savannas in the southeastern United States (Carroll & Hoffman 1997; Stuble et al. 2009). Results of research in this ecosystem show a negative correlation between the abundance of fire ants and native ants (Stuble et al. 2009). Nevertheless, these studies could not determine whether fire ants became established because native ant abundances were low or whether abundances of native ants were low because fire ants were established. In longleaf pine stands with wiregrass (*Aristida stricta*)-dominated ground cover, soil disturbance does not affect the negative correlation between fire ant and native ant abundances because wiregrass is associated with frequently burned sites that have not been cultivated or disturbed. Consequently, this ecosystem is a good system in which to test whether native species density (species per unit area [sensu Gotelli & Colwell 2001]) and abundance of

worker ants confer resistance to fire ants to an area, irrespective of anthropogenic disturbance.

We subjected the ant communities at four sites to insecticide and established four control sites to determine whether large decreases in the density and abundance of native ants, in the absence of land use, affect colonization by fire ants. We predicted that if fire ants principally invade areas with low species density and abundance of native ants, then fire ant abundance in insecticide-treated plots would be higher at the end of the study relative to control plots.

Methods

We conducted our study at the J.W. Jones Ecological Research Center (Ichauway) in southwestern Georgia (31° 13′ 16.88″ N, 84° 28′ 37.81″ W). Ichauway is a 12,000-ha site with large natural stands of longleaf pine savanna and an intact herbaceous groundcover dominated by wiregrass). Prescribed burns are conducted on a 2-year return interval. Burns are low intensity and typically cover an area of around 40 ha. Temperatures range from an average of 11 °C in winter to 27 °C in summer. Rainfall average is 132 cm/year. Monogyne colonies of fire ants are common at the site (with many areas containing upwards of 50 colonies/ha), and first appeared in the 1960s (Callcott & Collins 1996).

To examine ant community composition, we established eight, 1-ha plots. Each plot was at least 50 m from its neighbor and 100 m from paved roads; most plots were >500 m from paved roads. All plots were burned in January of 2006. We used standard pitfall-trapping techniques to sample species density and worker abundance of ground-dwelling ants (Majer 1978). Each pitfall trap consisted of a 15.3-cm-long section of 2.1-cm-diameter polyvinyl chloride (PVC) pipe sunk into the ground. We inserted a glass test tube (15 cm long, 2 cm diameter) into each pipe so that the opening of the test tube was flush with the ground. We arranged traps in groups of three (an array) to form an equilateral triangle; traps were 5 m apart (Supporting Information). We distributed nine arrays evenly throughout each plot in a 3 × 3 grid (27 pitfall

traps per plot). Each array was 20 m from its neighbor, and outer arrays were 30 m from the edge of the plot. We added soapy water to each test tube and left the traps open for 24 hours in July of 2006, 2007, and 2008. We identified all specimens to species.

In 2007 we randomly selected four of the eight 1-ha plots for broadcast treatment of hydramethylnon (Amdro, Atlanta, Georgia), a fire ant insecticide. We applied hydramethylnon three times between 21 May and 21 June 2007. At each application, we distributed 0.68 kg of hydramethylnon/plot, which is the manufacturer's recommendation.

Statistical Analyses

For each plot we tallied the number of fire ant and native ant workers and species density of native ants (number of native ant species per hectare) before (2006) and after (2007 and 2008) treatment. We used two-way multivariate analysis of variance (MANOVA) to examine the effects of treatment and year on the number of native ants, number of fire ants, and species density of native ants. Because the results of the MANOVA indicated a treatment effect, we followed the MANOVA with t tests within each year to examine the effects of treatment on the number of fire ants, number of native ants, and species density of native ants. We also estimated species richness with the Chao2 species-richness estimator, which estimates the asymptotic species richness had sampling gone to completion (Gotelli & Colwell 2001). We then used t tests to examine the influence of treatment on the estimated species richness within each year. We used JMP 8.0 (SAS Institute, Cary, North Carolina) for all analyses. We also created rank-abundance plots, plotting log-transformed worker abundance against species rank (ranked by abundance) (including fire ants) for control and insecticide-treated plots in 2008. We calculated Kendall's tau to determine rank correlation among the two groups to test whether the relative abundances of species changed.

Results

We captured 5972 workers of 21 species (Supporting Information). The response of native ant abundance, fire ant abundance, and species density to the insecticide differed among years (year: $p < 0.01$; treatment: $p = 0.05$; year × treatment: $p = 0.04$). Prior to treatment (2006), neither the number of fire ants nor the number of native ants differed between the control and treated plots (Table 1). One month after insecticide application, mean fire ant abundance was 98% lower in the treated plots (mean [SE] = 2 workers/ha [0.6]) than in control plots (92 workers/ha [22]) (Fig. 1a) and mean abundance of native ants was 84% lower in treated plots (6 workers/ha [3]) than in control plots (37 workers/ha [6]) (Fig. 1b). In 2008 (the year following insecticide application) there was no statistically significant difference in the number of fire ants or native ants between treatments.

Mean species density of native ants did not differ between control and treated plots prior to insecticide application. Immediately following treatment species density was 59% lower in the treated plots (mean [SE] = 3 species/ha [0.7]) than the control plots (7.3 species/ha [0.6]) (Fig. 1c). Species density did not differ between treatments 1 year after treatment. The Chao2 estimate of species richness did not differ between treatment groups prior to application of insecticide or immediately following insecticide application. Nevertheless, we observed a roughly 80% increase in Chao 2 estimated species richness in the treated plots relative to the control plots 1 year after treatment ($p = 0.05$) (Fig. 1d). Rank-abundance curves of ants in treated and control plots were similar 1 year after treatment (tau = 0.67; $p < 0.01$) (Fig. 2). Furthermore, the rank of fire ants within these plots was similar for control and treated plots; fire ants were the most abundant species in the control plots and the second-most abundant species in the treated plots.

Table 1. Results of t tests comparing abundance of fire ants and native ants, species density (ant workers per hectare), and Chao2 estimated richness of native species between control plots and plots treated with the insecticide hydramethylnon for each year of the study.

| Response variable	Year	Control (SE)	Hydramethylnon (SE)	t	p
Number of fire ant workers	2006	195.25 (50.96)	63.25 (20.58)	−2.40	0.08
	2007	92.00 (22.05)	1.50 (0.65)	−4.10	0.03
	2008	6.75 (2.69)	34.50 (14.66)	1.86	0.15
Number of native ant workers	2006	158.50 (82.11)	587.50 (354.18)	0.39	0.72
	2007	36.50 (5.68)	6.25 (2.53)	−4.87	0.01
	2008	20.75 (2.21)	37.75 (11.64)	1.44	0.24
Species density	2006	11.75 (1.21)	11.25 (0.63)	−0.36	0.74
	2007	7.25 (0.63)	3.00 (0.71)	−4.49	0.00
	2008	7.00 (1.47)	10.00 (0.91)	1.73	0.14
Chao2 estimate of native species richness	2006	20.42 (4.74)	13.85 (1.24)	−1.34	0.26
	2007	8.25 (3.20)	3.55 (0.99)	−2.50	0.06
	2008	3.55 (0.99)	18.06 (3.09)	2.62	0.05
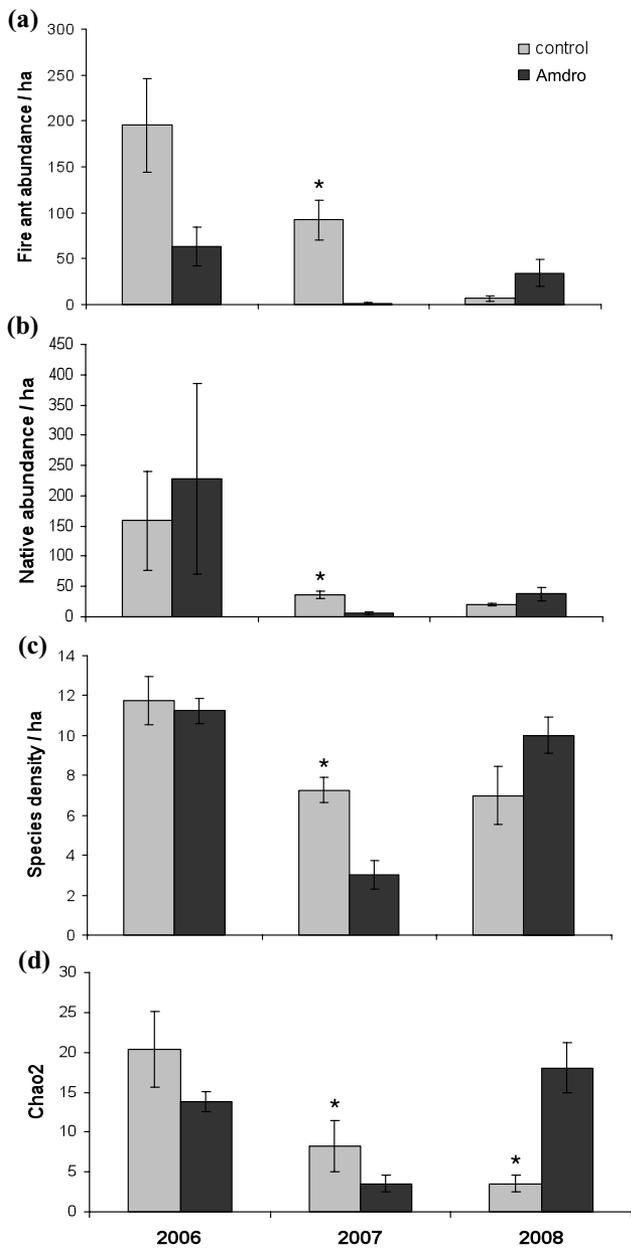
Figure 1. Mean (SE) (a) number of fire ants, (b) number of native ants, (c) species richness, and (d) estimated species richness per plot in insecticide-treated (hydramethylnon) and control plots (*p < 0.05).
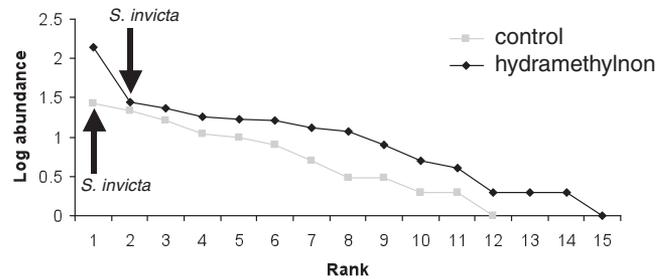

*Figure 2. Rank-abundance curves of fire ants (*S. invicta*) in insecticide-treated (hydramethylnon) and untreated plots in 2008, 1 year after treatment (rank is rank by abundance).*

Discussion

The species richness and abundance of native ants is often lower in areas where fire ants are established than in areas where fire ants are not established (Porter & Savignano 1990; Gotelli & Arnett 2000; Holway et al. 2002), but it is unknown whether fire ants competitively exclude native ants or are limited to invading areas where the abundances of native ants have already been reduced

by some other factor (Tschinkel 2006; King & Tschinkel 2008). The application of dechlorane across much of the southeastern United States as a means of fire ant control in the 1960s and 1970s may have increased the rate of spread of fire ants by also reducing abundances of native ants (Summerlin et al. 1977; Stimac & Alves 1994), given their ability to rapidly recolonize. Similarly, the application of hydramethylnon to areas grazed by domestic livestock substantially increases the relative abundance of fire ants (Stimac & Alves 1994).

In contrast, we found that reductions in ant abundance and species density did not result in differences in the degree of fire ant reestablishment. This suggests that human disturbance resulting in declines in native ants may not promote establishment of fire ants. In fact, the invasion of fire ants in the longleaf pine system we studied suggests that fire ants do not invade only those areas in which native ant abundances are already decreased. Species richness of ants in this ecosystem is among the highest in North America (Lubertazzi & Tschinkel 2003), which makes it unlikely that low species richness increased the probability of invasion in this system. Relative recovery rates of fire ant and native ant abundances were qualitatively similar. Furthermore, estimated species richness of native ants in treated relative to control plots increased. Again, if fire ant invasions are primarily due to the disruption of native ant communities, we should have seen an increase in the abundance of fire ants in the treated plots relative to the control plots following the treatment and a greater increase in abundance of fire ants in response to disturbance than native ants, but we did not. Our results suggest that a large change in the ant community is not necessarily a prerequisite for invasion by fire ants. This suggestion is consistent with the finding that Argentine ants (*Linepithema humile*) are able to invade in the presence or absence of native ants (Menke et al. 2007).

Longleaf pine ecosystems are fire dependent. At our study site prescribed fire (already established) serves as a regular source of disturbance (reduced vegetative biomass and increased solar radiation). It is possible that the effects of fire on abiotic conditions make the area

susceptible to fire ant colonization. Much of the native range of fire ants is seasonally flooded wetlands (Tschinkel 2006), which may increase the species' ability to establish successfully in frequently disturbed areas in their introduced range. This ability to colonize disturbed areas and our results suggest that fire ant colonization may be a result of frequent disturbance rather than a response to niche availability associated with the reduction in abundance of native ants. There is evidence that frequent fire increases the abundance of fire ants. For example, fire ant nests tend to be larger when fire-return intervals are short (C.R.C., unpublished data).

The decline in total ant abundance over the course of this experiment is perplexing. We speculate that differences in annual rainfall could be a factor. The final year of the study was exceptionally wet relative to the 2 prior years (which were drought years), and many native ant species tend to be more abundant in xeric areas (Stuble et al. 2009). We cannot be sure how precipitation may have altered the outcome of the experiment, but because abundances of both native ants and fire ants were reduced, we believe that confounding effects were minimal. We conclude that in a fire-maintained ecosystem, the abundance of fire ants does not increase in response to a large reduction in ant abundance and species density at small spatial extents.

Our results indicate that in a fire-maintained ecosystem, fire ants do not respond to a drastic reduction in ant abundance and ant species density at small spatial extents by increasing population size. To confirm unequivocally whether native ants limit fire ant invasion, the experimental removal of native ant species and introduction of fire ants would be necessary, but logistically challenging. In the study of invasive species more generally, there is a larger debate as to whether invasive species drive declines in the abundance and richness of native species or simply respond to these reductions. Our study provides evidence that invasive species do not always respond to even large reductions in native species richness and abundances.

Acknowledgments

Supporting Information

A plot-layout diagram (Appendix S1) and species list (Appendix S2) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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