

Experimental evidence that the introduced fire ant, *Solenopsis invicta*, does not competitively suppress co-occurring ants in a disturbed habitat

JOSHUA R. KING and WALTER R. TSCHINKEL

Florida State University, Department of Biological Science, Unit 1, Tallahassee, Florida, 32306, USA

Summary

1. The fire ant, *Solenopsis invicta*, is a globally distributed invasive ant that is largely restricted to disturbed habitats in its introduced range. For more than half a century, biologists have believed its success results from superior competitive abilities relative to native ant species, as well as an escape from their natural enemies.

2. We used large volumes of hot water to kill fire ant colonies, and only fire ant colonies, on experimental plots in pastures, and found that populations and diversity of co-occurring ants did not subsequently increase.

3. These results are contrary to classical predictions and indicate that *S. invicta* is not a superior competitor that suppresses native ants, and that the low diversity and abundance of native ants in degraded ecosystems does not result from interaction with fire ants. Instead, other factors such as prior disturbance and recruitment limitation may be the primary limiting factors for native species in these habitats.

Key-words: fire ants, Formicidae, interspecific competition, invasive species, removal experiment.

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Introduction

Understanding the factors that govern the spread and success of invasive species is a critical step toward reducing their impact (Williamson 1996). Numerous factors, such as superior competitive abilities, resource pre-emption, release from natural enemies or anthropogenic disturbance, may permit an invasive species to become dominant. However, the success of many invasive species is believed to result primarily from their superior competitive abilities relative to native species (Bruno *et al.* 2005). Often, introduced species first become established in human-altered landscapes and achieve their greatest abundance and diversity there (Oriens 1986; Deyrup, Davis & Cover 2000). Additionally, few invaded habitats are free from anthropogenic effects. When altered habitats are colonized by invasive species, it is uncertain whether the invasive species are driving community change or if they are simply the beneficiaries of community change driven by previous habitat alteration or other factors (MacDougall & Turkington 2005). Direct study of

dominant invasive species in these habitats can provide a deeper understanding of the impact and spread of invasive species, why some species become dominant and how dominant species impact other species. In particular, experimentally manipulating the abundance of invasive species in recently assembled communities may reveal more clearly the importance of contemporary interspecific interactions in driving community structure because many of the species have no historical geographical overlap (and thus, no shared evolutionary history, Bruno *et al.* 2005).

For plants, there is experimental evidence that the success of many dominant invaders cannot be explained solely by superior competitive abilities relative to native species (Seabloom *et al.* 2003). Habitat disturbance plays a significant role in the establishment and persistence of many dominant invasive plant species because it limits the abundance and recruitment of native species (Seabloom *et al.* 2003; MacDougall & Turkington 2005). For animals, interspecific competition has long been considered one of the primary factors affecting community assembly (Elton 1946; Schoener 1974; Chase & Leibold 2003). Because the mechanisms governing community assembly and biotic invasions are conceptually similar (Tilman 2004), it is reasonable to test whether superior competitive ability is the primary

mechanism by which some invasive animals become dominant and, in turn, reduce the abundance and species richness of native species (Holway *et al.* 2002; Bruno *et al.* 2005).

Among animals, ants are an appropriate group to test whether superior competitive abilities are responsible for the success of dominant invasives. Generally, ant communities are thought to be highly interactive, with behaviourally dominant species with large colonies better able to gain access to limiting resources and thereby to suppress or exclude subordinates (Vepsäläinen & Pisarski 1982; Cole 1983; Savolainen & Vepsäläinen 1988; Hölldobler & Wilson 1990; Andersen & Patel 1994). Similarly, the success of many invasive ant species is also thought to result primarily from behavioural dominance and release from natural enemies that allows them to attain numerical superiority and competitively suppress co-occurring species (Porter & Savignano 1990; Porter *et al.* 1997; Holway 1999; Holway *et al.* 2002; Sanders *et al.* 2003). Globally, invasive ants are important – five invasive ant species have been listed among the 100 worst invasive species in the world – as they are significant pests and may disrupt native arthropod communities (Lowe *et al.* 2004).

Among these five species, the fire ant, *Solenopsis invicta* Buren has received by far the most attention [a search of FORMIS (Wojcik & Porter 2003), the comprehensive bibliography for ant literature revealed c. 2000 citations, greater than 1000 more citations than any other species of ant] and has been credited with displacing native ant and arthropod species, negatively affecting vertebrate populations, and disrupting mutualisms (Holway *et al.* 2002; Tschinkel 2006). The suppression of native ants by fire ants has been a strongly held and oft-repeated belief for over half a century (Tschinkel 2006). However, at the community level the evidence for the competitive suppression of native ants by *S. invicta* rests solely on correlations (Porter & Savignano 1990), and has not been validated with properly designed experiments (Tschinkel 2006). Additionally, *S. invicta* is largely restricted to human-modified habitats throughout its introduced and native ranges and achieves its greatest abundance in these areas (Tschinkel 2006; references therein). Thus, this species is an excellent invasive animal for testing whether competitive superiority is the principle mechanism for its dominance in disturbed habitats or if other factors are more important. To test the impact of this introduced species on the ant community in disturbed habitat, we used removal experiments to manipulate the density of *S. invicta* in a pasture.

Materials and methods

STUDY SITE

The study was conducted at Southwood Plantation about 8 km east of Tallahassee, Florida, USA. The estimated arrival of fire ants in the Tallahassee area is

prior to 1957 (Tschinkel 2006). The area has never been treated to control fire ants, so the population of fire ants on the study site had been relatively undisturbed for nearly 50 years prior to this study. During this time the land has been privately owned and used for agriculture. The soil is a poorly drained mix of sand and red clay. Plots were maintained in a 10 hectare tract of previously improved pasture used for grazing cattle with a large population of the single queen, or monogyne, social form of *S. invicta*. This is a homogenous habitat with a moderate to dense herbaceous ground cover, but no trees. The ground cover was consistent across all plots and composed of introduced grass species, native grasses, and a few, scattered shrubs. During the course of the study cattle were excluded from the tract. The pasture tract is surrounded on three sides by a mixed oak and pine forest fragment. In November 2003, we established 10 40 m × 40 m plots. Plots were separated by at least 40 m from one another and an adjacent forest fragment. Five of the plots were assigned randomly as treatment plots for removal of *S. invicta* and the other five plots were left as unmanipulated controls.

FIRE ANT REMOVAL

Throughout 2004 and 2005, *S. invicta* colonies in treatment plots were killed regularly with hot water. We developed a high-volume water heating system that we could transport on the back of a pick-up truck to facilitate treatment of many colonies over a large area [see Tschinkel & King (in press), for a full description of the system]. We used 70–85 °C water to kill colonies. Water was carried to colonies using 20-L (5-gallon) buckets. The nest was opened by driving a stick downwards through the subterranean nest chambers, and the hot water was poured rapidly into the resulting hole until the nest was full. The large number of interconnected chambers and vertical shafts assured that the complete nest was filled quickly with hot water, killing all the ants contacted. The remaining hot water was used to collapse the mound. Very large colonies sometimes required two or even three buckets of water, but small colonies could be killed with a quarter- to a half-bucket. The absence of fire ants from pasture is not a stable situation. Every year, colonies moved in from the plot perimeter, and mated queens founded new colonies. Therefore, we treated plots several times annually to keep plots almost free of fire ants for most of each year.

ANT SAMPLING

Ants were censused once per year using pitfall traps in early August during the peak of annual ant activity. Pitfall traps are the best method for estimating the presence and relative abundance of ground-dwelling species in this region and habitat type (King & Porter 2005). Although baits are often used to assess competitive ability of invasive ant species (e.g. Holway 1999; Gibbons & Simberloff 2005), we did not use baits as

this method has been shown to be a biased method of assessing the relative importance of mass recruiting species, such as *S. invicta* (King & Porter 2005). Pitfall traps were 85-mm-long plastic vials with 30 mm internal diameter. Traps were filled to a depth of approximately 15 mm with propylene-glycol antifreeze, inserted flush with the surface of the ground, and operated for 7 days. We sampled from July 29 to August 6 in 2004 and 2005. This sampling period was chosen because it typically includes the warmest and wettest months of the year, and thus is the period of maximum ant activity in Florida. Seasonal variation of ant activity was not addressed. Pitfall traps were arrayed within the central 25 × 25 m area of each 40 × 40 m plot in a 6 × 6 grid for a total of 36 traps spaced 5 m apart. A 7.5-m buffer was left between the plot margin and the sampling grid. Traps were installed with a hand-held, battery-powered drill using an auger bit. Fire ants (*S. invicta*) were also censused three times per year in each plot by counting colony mounds. During censuses, colonies were classified as either small or large by visually estimating mound volume. Large colonies were those that exceeded approximately 5–7 L in volume, which corresponds to a colony of approximately 50 000–70 000 workers (Tschinkel 2006). Peripheral pitfalls on removal plots typically captured more fire ants than interior ones. When colonies die (or are removed), adjacent colonies quickly expand their foraging territory (Tschinkel, Adams & Macom 1995). By removing a large majority of colonies within plots, the colonies near to, but outside, the removal plots almost certainly expanded their foraging territories.

Results

EFFECTIVENESS OF FIRE ANT REMOVAL

Using hot water, we were able to reduce fire ant density on treatment plots to levels similar to or lower than the level of reduction reported using poison baits (e.g. Cook 2003). We stress that this level of control is specific *only* to fire ants, which cannot be said of experiments using poison baits that have general effects on the arthropod community. Killing fire ant colonies with hot water decreased the abundance of *S. invicta* in pitfalls by 60%, relative to the control plots (treatment, $F_{1,20} = 12.59$, $P = 0.003$; year $F_{1,20} = 4.54$, $P = 0.049$) (Fig. 1). Prior to the first hot water treatments, the total number of *S. invicta* colonies in treatment plots ranged from 25 to 40, with a mean of 31. Of these, 14–26 (mean = 21) were large, fully mature colonies. In treatment plots, the total number of colonies was reduced by 70% (treatment, $F_{1,23} = 19.37$, $P < 0.001$) and the total number of large colonies by 93% (treatment, $F_{1,23} = 202.19$, $P < 0.001$) over 2 years (Fig. 2). We report (Fig. 2) the average number of colonies over the entire 2 years in removal plots, but it is noteworthy that the number of colonies fluctuated over the course of each year. For example, in the winter months (December–February) there were often more small colonies per plot (ranging

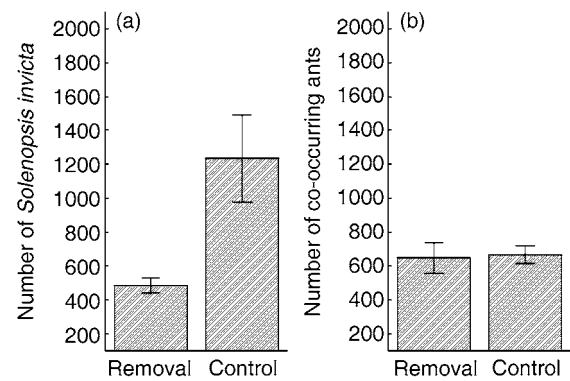


Fig. 1. (a) Total abundance of *Solenopsis invicta* workers in pitfall traps averaged over 2 years. There was a significant difference between experimental treatments and sampling period (treatment, $F_{1,20} = 12.59$, $P = 0.003$; year $F_{1,20} = 4.54$, $P = 0.049$). (b) Total abundance of co-occurring ants averaged over 2 years. There was no significant difference between experimental treatments or sampling period (treatment, $F_{1,20} = 0.05$, $P = 0.827$; year $F_{1,20} = 2.43$, $P = 0.138$). Error bars = mean ± 1 SE.

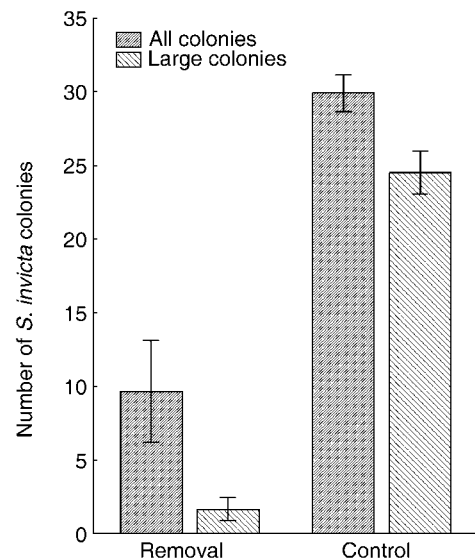


Fig. 2. Average total number of *Solenopsis invicta* colonies and large colonies only in removal and control plots over 2 years. There was a significant difference between experimental treatments for both measures of colony abundance (all colonies, $F_{1,23} = 19.37$, $P < 0.001$; large colonies, $F_{1,23} = 202.19$, $P < 0.001$). Error bars = mean ± 1 SE.

from 0 to 10 in most plots) than in the spring and summer (ranging from 0 to 2 in most plots). The most probable reason for this was that many of the smallest colonies (incipients) that were established during the late spring and summer were not visible until they had grown large enough to build a mound during the following winter. By late spring, several (ranging from 2 to 10 in most plots) large colonies moved within the outer boundary of removal plots as well. As soon as colonies were visible or within the margin of removal plots, however, they were killed. We saw less fluctuation in control plots where the number of colonies remained stable.

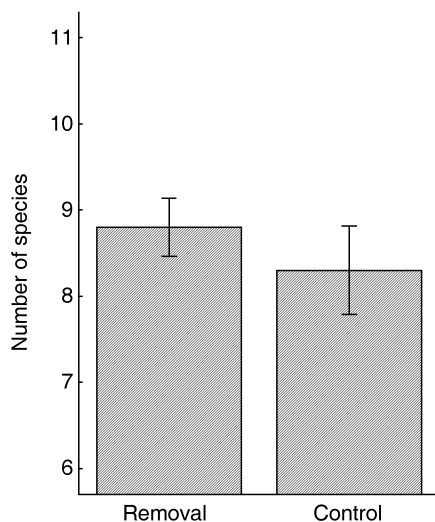


Fig. 3. Total species richness of ants (excluding *S. invicta*) in pitfall traps averaged over 2 years. There was no significant difference between experimental treatments or sampling period (treatment, $F_{1,20} = 0.33$, $P = 0.571$; year, $F_{1,20} = 0.60$, $P = 0.451$). Error bars = mean \pm 1 SE.

EFFECT OF FIRE ANT REMOVAL ON ABUNDANCE AND DIVERSITY OF ANTS

At no level did *S. invicta* competitively suppress co-occurring ants. If competitive interactions are shaping this ant community, effects should depend upon population densities, but removing *S. invicta* had no significant effect on either the abundance (Fig. 1) or species richness (Fig. 3) of co-occurring ant species over 2 years. In treatment plots, the abundance of *S. invicta* was actually lower (Fig. 1a) than the abundance of co-occurring ants (Fig. 1b). This low level is particularly important because population size can be important in determining the outcome of competitive interactions, particularly exploitative competition. When species richness was examined using rarefaction curves to adjust for differing sample sizes, there was still no obvious effect of the removal treatments (Fig. 4). The rarefaction curves show a stabilizing accumulation of species and no differences between treatments and controls in the shape of the accumulation curves (that is, the curves do not cross; see Fig. 4), whether species richness was based on total abundance or species occurrence in samples.

EFFECT OF FIRE ANT REMOVAL ON COMMUNITY COMPOSITION

A species-by-species analysis also shows that greatly reducing the density of *S. invicta* had no impact on the ant fauna. No co-occurring species, whether introduced or native, changed significantly in abundance following reduction of the density of *S. invicta* over 2 years (Table 1).

In this disturbed habitat, the ant fauna is largely composed of introduced species. A total of 27 species from four subfamilies and 14 genera were captured, including seven species that are not native to North

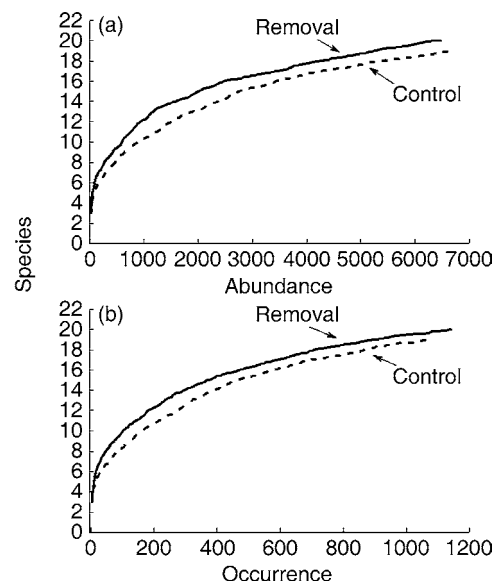


Fig. 4. (a) Species richness (excluding *S. invicta*) as a function of the abundance of worker ants in samples. (b) Species richness as a function of the incidence of worker ant species in samples in removal and control plots. Curves are sample based rarefaction curves generated from 50 randomizations of sample order.

America (Table 1). Excluding *S. invicta*, six introduced species accounted for 89% of the total abundance of ants. Native species comprised a small minority (11%) of the total abundance of ants but accounted for a majority of the species (74%). The majority of both the native and the introduced species are either habitat generalists or disturbed habitat specialists in the region (J.R.K., unpublished data). Some species were sampled in the second year but not the first, but these occurred in such low numbers (one or a few workers) that it is not clear whether these species were newly recruited or if they were simply missed (a sampling effect).

Previous correlative studies have shown a strong, negative relationship between the abundance of *S. invicta* and the abundance co-occurring ants (e.g. Porter & Savignano 1990). If competitive suppression is the mechanism underlying these patterns, then by removing *S. invicta* we would expect to see an increase in the abundance of co-occurring ants; that is, there should be a negative correlation between fire ant and other ant abundance. In contrast, on control plots in this study, the abundance of other ants was *positively* related to the abundance of *S. invicta* (Fig. 5). Surprisingly, that relationship disappeared in removal plots (Fig. 5). This non-intuitive pattern was a result of co-occurring species abundance remaining relatively constant while *S. invicta* was significantly decreased. Again, these results strongly suggest that factors other than interspecific competition with *S. invicta* are probably regulating the recruitment and density of co-occurring native and introduced species. Put another way, factors that increase fire ant populations also increase the populations of other, co-occurring ants.

Table 1. Species list and total abundance of ant species

Species‡	Removal		Control	
	Year 1	Year 2	Year 1	Year 2
Dolichoderinae				
<i>Dorymyrmex bureni</i> (Trager)	0	0	0	2
<i>Forelius pruinosus</i> (Roger)	2	0	0	0
Formicinae				
<i>Brachymyrmex musculus</i> Forel	499	157	777	174
<i>Camponotus floridanus</i> (Buckley)	0	0	1	4
<i>Camponotus socius</i> Roger	1	0	0	0
<i>Paratrechina concinna</i> Trager	4	4	2	1
<i>Paratrechina parvula</i> (Mayr)	1	0	0	0
<i>Paratrechina vividula</i> (Nylander)	0	0	1	0
Myrmicinae				
<i>Cardiocondyla nuda</i> (Mayr)	31	5	3	4
<i>Crematogaster minutissima</i> Mayr	0	0	0	1
<i>Cyphomyrmex rimosus</i> (Spinola)	815	598	1648	521
<i>Pheidole dentata</i> Mayr	2	0	9	1
<i>Pheidole lamia</i> Wheeler	5	11	0	0
<i>Pheidole metallescens</i> Emery	12	2	0	0
<i>Pheidole moerens</i> Wheeler	1127	1778	1243	1466
<i>Pheidole obscurithorax</i> Naves	303	126	258	142
<i>Pyramica membranifera</i> (Emery)	14	31	12	12
<i>Solenopsis invicta</i> Buren	2907	1932	7467	4876
<i>Solenopsis pergandei</i> Forel	2	15	0	0
<i>Solenopsis</i> sp. nr. <i>abdita</i> Thompson	0	0	1	0
<i>Solenopsis</i> sp. nr. <i>carolinensis</i> Forel	505	381	191	153
<i>Solenopsis tennesseensis</i> M.R. Smith	0	1	0	12
<i>Solenopsis tonsa</i> Thompson	1	2	0	1
<i>Strumigenys louisianae</i> (Roger)	0	0	1	1
Ponerinae				
<i>Hypoponera opaciceps</i> (Mayr)	18	16	3	19
<i>Hypoponera opacior</i> (Forel)	0	5	2	0
<i>Odontomachus brunneus</i> (Patton)	0	2	0	0

‡Introduced species names in bold type.

Discussion

FIRE ANT REMOVAL

We used hot water instead of other control methods, such as insecticidal baits or mound treatments, because our variables of interest (species richness and abundance of co-occurring ants) are affected by non-specific poisons (Summerlin, Hung & Vinson 1977; Seagraves, McPherson & Ruberson 2004). Regardless of the manner (or caution, for example mound drenches) of application, insecticides persist and enter the arthropod food chain. For example, many ants collect and consume dead fire ants that contain insecticidal residue after application of poisons (Tschinkel 2006; references therein). Poison application is also a specific community disturbance that actually favours the establishment and population expansion of *S. invicta* over less than 2 years (Stimac & Alves 1994; Summerlin *et al.* 1977). Because our method of removal was specific to fire ants, and only to fire ants, our study is not comparable to previous experimental manipulations of fire ants (e.g. Cook 2003; Gibbons & Simberloff 2005) or other ants (e.g. Brown & Munger

1985) that used poisons to attempt community-level competition experiments. Given the specificity of our removals to fire ants alone, and our reduction of fire ants by at least as much as in studies that used poisons (Markin, O'Neal & Collins 1974; Cook 2003; Gibbons & Simberloff 2005), it is particularly significant that there was no change in the abundance or diversity of any of the co-occurring ant species. Thus, we found no evidence whatsoever that fire ants suppress populations of co-occurring ants.

Like poisons, however, our removals did not completely eliminate fire ants, nor was the suppression long-lasting – removals were conducted throughout the year. What might have been the source of the fire ants that we captured in our removal plots? The territorial biology of the fire ant (reviewed in Tschinkel 2006), combined with the size of our plots (40 m × 40 m, large enough to contain the territories of 25–30 mature colonies), indicates that most of the foragers in removal plots came from colonies outside the plots that had expanded their foraging territory into the plots, while the remainder probably originated in newly founded colonies that were not detected during censuses. This contrasts with

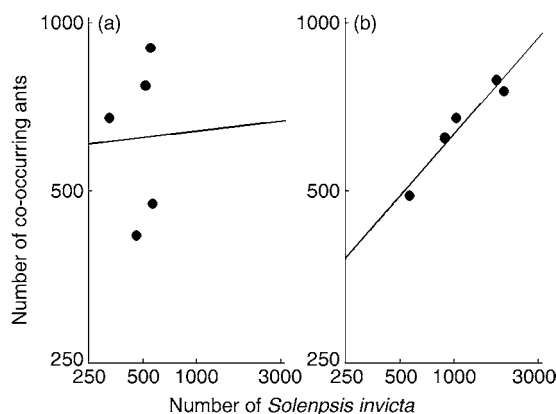


Fig. 5. The relationship between the total abundance of *S. invicta* and co-occurring ants averaged over 2 years. (a) In removal plots there was no significant relationship ($P = 0.97$) between *S. invicta* and co-occurring ant abundance (the relationship was very weakly positive, however; $R^2 < 0.001$). (b) In control plots there was a strong, positive relationship ($P = 0.008$; $R^2 = 0.93$) between *S. invicta* and co-occurring ant abundance.

the control plots, where most of the foragers came from colonies inside the plots (Tschinkel *et al.* 1995).

LACK OF EVIDENCE FOR COMPETITIVE SUPPRESSION

An important question is whether the duration of this experiment (2 years) was sufficient to allow the reduction of competitive suppression by fire ants to produce a response. Among species sharing resources, high population density should convey an advantage in both exploitative and interference competition because more abundant species find more resources, find them more quickly and take them by force more effectively, if necessary (Miller 1967). Among ants, an aggressive, territorial species that saturates the environment should be a superior competitor that affects the density and distribution of co-occurring species, possibly sitting atop a linear dominance hierarchy (Vepsäläinen & Pisarski 1982; Cole 1983; Savolainen & Vepsäläinen 1988; Hölldobler & Wilson 1990; Porter & Savignano 1990; Andersen & Patel 1994; Morrison 1996; Holway 1999). For example, if interference competition (and perhaps predation of co-occurring foundresses and colonies) is the primary manner in which *S. invicta* suppresses other species, then removal of *S. invicta* should result in a relatively rapid recovery of the co-occurring fauna. Within a year, numerous additional colonies should be founded and survival of existing colonies improved in the absence of *S. invicta*. If exploitative competition (resource pre-emption and/or reduction) is the primary manner of competitive interaction, then more time may be needed for the community to recover if *S. invicta* has greatly reduced resources or if *S. invicta* remained abundant enough to continue reducing resources. However, the lack of response from the entire co-occurring ant fauna we observed in this study suggests that it is unlikely that either form of competition explains the

high abundance of *S. invicta* relative to co-occurring ants in disturbed habitats.

Population regulation in *S. invicta* is strongly density-dependent (Adams & Tschinkel 1995, 2001; Tschinkel 2006), with large, mature colonies having the greatest impact on the distribution of territories. Our success in removing large, mature colonies (Fig. 2) is particularly important because these colonies maintain the largest foraging areas, biomass and colony size, and have the greatest population-level effects (Tschinkel 2006). The presence of even a dozen or two small colonies in plots occupied previously by 30 large colonies means that the number of foragers in the plot has been greatly reduced (60% according to our pitfalls). If interaction and competition between species is important in regulating this assemblage of ants, then we would expect that eliminating mature *S. invicta* colonies, or even simply reducing fire ant density, would have a significant positive effect on the community. Nevertheless, there was no evidence that the removal of *S. invicta* had any impact on any individual species or on the community as a whole (Table 1 and Fig. 3).

Colony founding is not the only manner by which population size can increase in ants. Colonies can also increase in size, and mature colonies can move into new areas. Presumably, if *S. invicta* were regulating co-occurring species by competition, removing them would allow co-occurring ants to increase by any of the three modes above. At the very least, it seems probable that species that were already present in the removal plots would grow in abundance by increasing colony size. By removing fire ants (the most abundant species) we have reduced the fire ants' ability to exclude other species from food resources. More food for co-occurring species should, over 2 years, certainly result in larger colonies and increased numbers of foragers (which would appear in our traps). We saw no such increase (Table 1, Figs 1 and 3). Many of these species also move their colonies readily from place to place (e.g. *Pheidole moerens*; J.R.K., unpublished data). When neighbours are killed in fire ant populations, surviving colonies expand their foraging into the territorial void within days or weeks, eventually moving the colony as well (Tschinkel 2006). We would expect a similar response in co-occurring ants, if they were limited by interspecific competition. Our results indicate that they did not (over 2 years).

Removal experiments that show a lack of evidence for competitive suppression by a behaviourally dominant species have been conducted before, but not with invasive species. In an Australian study similar to ours, Gibb & Hochuli (2004) removed a dominant *Iridomyrmex*, and examined its impact over only 1 year. As in our study, they also found little overall impact of the removal, although they did see that ecological equivalents (other *Iridomyrmex* species) did better in the absence of the species they removed. We document a similar pattern, but our sites probably lack an ecological equivalent to fire ants we removed (the native fire ant, *S. geminata* would have been one, were it still present).

CO-OCCURRING ANT FAUNA

The fire ant and most of the more abundant co-occurring species in our study (both exotic and native) are disturbed habitat specialists, occurring most frequently and abundantly in highly disturbed ecosystems throughout the region. One common adaptation for this habitat is the capacity for very rapid population increase. Consequently, these species would seem to have the greatest potential for annual increase, and to be most responsive to removal of competition. Additionally, the recruitment of the species would not seem to be in any way limited because they already exist in large numbers in these habitats outside the treatment plots. All of the species occurring in this habitat produce alates at least once a year, and many produce them throughout the year and in very large numbers. For example, *Brachymyrmex musculus* (see Table 1 for species authorities) and *Solenopsis pergandei* have numerous spring and summer mating flights with hundreds if not thousands of alates.

We have some information on the capacity for population increase and niche overlap for two of these co-occurring species, *P. moerens* and *P. obscurithorax*. Both are relatively recent invaders (Deyrup 2003) currently undergoing range expansion in the region (Deyrup *et al.* 2000; Storz & Tschinkel 2004; J.R.K., unpublished data). Both species are most abundant in disturbed habitats, frequently co-occur with *S. invicta*, and thus are potential competitors with *S. invicta*. Both species are dimorphic (major and minor worker subcastes). *P. moerens* workers are small and similar in size to the smallest workers of (polymorphic) *S. invicta*, while workers of *P. obscurithorax* are large and similar in size or larger (in the case of majors) to large workers of *S. invicta* (J.R.K., unpublished data). Colonies of *P. obscurithorax* are also large (> 10 000 workers; W.R.T., unpublished data). Both species nest near – or occasionally on – *S. invicta* colonies, are aggressive towards heterospecifics, and can occupy and dominate baits in the presence of *S. invicta* (J.R.K., unpublished data). Both species also produce large numbers of sexuals throughout the spring and summer and are capable of rapid population increases (Storz & Tschinkel 2004; J.R.K. unpublished data). *P. obscurithorax* increased its nest density by 6.4-fold (Storz & Tschinkel 2004), and *P. moerens* by almost twofold (J.R.K., unpublished data) in similar habitats in this region over 2 years. Yet, in spite of the greatly decreased abundance of *S. invicta* in the removal plots, there was no significant change in the abundance of either species over 2 years (*P. moerens*: treatment, $F_{1,20} = 0.02$, $P = 0.90$; *P. obscurithorax*: treatment, $F_{1,20} = 1.73$, $P = 0.215$). These data suggest strongly that there should be little time lag in population increases for these species if competitive suppression were operating.

Furthermore, there are several species in this fauna that are polygynous and could reproduce steadily by budding throughout most of the 2-year period. Native examples include most of the *Diplophoptrum* (*Solenopsis*),

Crematogaster minutissima, and both *Hypoponera* species (see Table 1 abundance details). Exotic examples include *Brachymyrmex musculus* and *Cardiocondyla nuda*. These species are established exotics that have expanded their populations throughout Florida (Deyrup *et al.* 2000), yet they showed no significant increase upon the removal of fire ants.

The historical record of the ant fauna of disturbed habitat in this region also suggests that there is not likely to be any sort of 'recovery' of the local fauna upon removal of fire ants. Van Pelt (1947, 1956) studied the ant fauna of north and central Florida prior to the *S. invicta* invasion. While his collection methods were different (he used hand collecting), he did estimate the relative abundance of species in several kinds of disturbed habitats. In these disturbed habitats he found an ant fauna very similar to what we report, both in its composition, and in the low abundance of most native species but, of course, without *S. invicta*. This suggests that the faunal composition of native ant species is unrelated to the presence (or absence, as we report) of *S. invicta*.

FACTORS AFFECTING COMMUNITY ASSEMBLY
IN DISTURBED HABITAT

The lack of any demonstrable impact of *S. invicta* on the abundance and species richness of co-occurring ant species is surprising, given the previous (albeit non-experimental) accounts of the impact of fire ants on co-occurring ants (Porter & Savignano 1990; Holway *et al.* 2002). *S. invicta* has been established in this region for greater than 50 years, so perhaps the impact of the initial invasion has faded (Morrison 2002); but if competition were still affecting the assembly of this ant community we would have expected a fire ant removal experiment to positively affect at least some of the co-occurring ants. The lack of any effect of fire ant removal on the remaining ant fauna suggests that many other factors are more important than competition in determining the composition and relative abundance of ants in disturbed habitats. On our control plots, the abundance of other ants was related positively to the abundance of *S. invicta* (Fig. 5), a pattern that has also been documented for *S. invicta* in a correlative study over a larger area (Morrison & Porter 2003). Our experimental results suggest that neither superior competitive ability nor resource pre-emption is responsible for the dominance of *S. invicta* in this habitat.

Across the region, the diversity and abundance of native species is much lower in highly degraded sites than in undisturbed habitats (Lubertazzi & Tschinkel 2003; King & Porter 2005; Tschinkel 2006). For example, both Lubertazzi & Tschinkel (2003) and King & Porter (2005) pitfall-sampled 40–50 species of ants in similarly sized plots in undisturbed native ecosystems in north Florida. In contrast, these authors reported 16–20 species in disturbed habitats suggesting that disturbance impacts the diversity of native species. Factors such as climatic fluctuations (periodic drought) are unlikely to

have affected our results because there was no difference from normal seasonal temperature or rainfall during the experiments (W.R.T., unpublished data). Other factors such as the trophic biology of the ants and ecosystem productivity can also influence the composition of the fauna (Kaspari 2001). However, because a forest fragment adjacent to our study site was a potential source of diverse ant species, the lack of competitive suppression by *S. invicta* of native species in these plots suggests that, instead, prior habitat disturbance and perhaps recruitment limitation are probably responsible for the low abundance and diversity of native species in disturbed habitats in this region.

Conclusions

While our results call into question the legitimacy of linear dominance hierarchies (Vepsäläinen & Pisarski 1982; Cole 1983; Savolainen & Vepsäläinen 1988; Hölldobler & Wilson 1990; Porter & Savignano 1990; Andersen & Patel 1994; Morrison 1996; Holway 1999) as the force governing ant community assembly (and invasion dynamics) in this habitat, they do not change the fact that invasive ants are a significant problem and remain major pest species. For example, there is strong evidence that *S. invicta* has replaced its native ecological equivalent *S. geminata* in a majority of disturbed habitats in the southern United States (Porter, Van Eimeren & Gilbert 1988). What is most troubling is that habitat disturbance may be the apparent underlying cause for the dominance of *S. invicta*. If the dominance and spread of invasive animal species is dependent primarily upon prior habitat disturbance, and not superior competitive abilities, then the impact of invasive species is likely to be largely dependent on the intensity of human-caused disturbance. Furthermore, restoring native populations will not simply be a matter of reducing the density of the invader. Rather, the success of conservation and restoration efforts will probably be more dependent on the difficult task of preservation and restoration of undisturbed habitat.

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