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Experimental evidence for weak effects of fire ants in a naturally invaded pine-savanna ecosystem in north Florida

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Abstract. 1. Fire ants naturally invade some undisturbed ecosystems of high conservation value and may negatively impact co-occurring ants.

2. Over 3 years, fire ants were added and removed from a longleaf pine savanna ecosystem that naturally supports a low density of fire ants. Impacts on co-occurring ants were monitored using pitfall traps.

3. Treatments resulted in significant differences in average fire ant abundance across all plots only in the first year of the experiment. Fire ants had little discernible impact. The abundance and species richness of co-occurring ants in removal plots never differed from unmanipulated control plots. The abundance of co-occurring ants was very slightly lower and ant species richness was slightly higher where *Solenopsis invicta* Buren colonies were added, but neither contrast was significant.

4. The poor conditions in this habitat for many native ants may explain this outcome. More broadly, the impact of fire ants on ant assemblages still appears to be secondary and largely a consequence of human impacts on the environment.

Key words. Ant communities, disturbance, fire, flooding, invasive ants, longleaf pine, *Solenopsis invicta*, wiregrass.

Introduction

Perhaps the most obvious and compelling environmental gradient impacting exotic species distribution is degree of anthropogenic disturbance. Habitat degradation by humans and biological invasion by exotic species clearly have interactive, overwhelmingly negative, impacts on native species and ecosystems (Didham *et al*., 2007). A few general patterns in the distribution and abundance of exotic species have emerged across the wide variety of anthropogenic disturbance that can be found in ecosystems. Typically, exotic species most commonly invade and become most abundant in highly anthropogenically disturbed habitats, such as intensively maintained agricultural lands, roadsides, and urbanized landscapes (Elton, 1958; Orians, 1986; Taylor & Irwin, 2004; Leprieur *et al*., 2008). Exotic species do sometimes invade ecosystems that are apparently free from anthropogenic impacts (Orians, 1986; Martin *et al*., 2009; Hoffmann & Saul, 2010), although many invasive species seem incapable of persisting in intact ecosystems (Christen & Matlack, 2009). Along the spectrum of anthropogenic impacts, in between complete habitat conversion (vegetation clearing and soil turning) and absence of disturbance, lie a wide variety of ecosystems with limited anthropogenic disturbance. These ecosystems are of high conservation value because they retain high levels of native biodiversity, although they are often invaded by a number of exotic species but not to the degree that the exotic species become dominant (King & Porter, 2007; Fisher *et al*., 2009).

Invaded yet intact ecosystems may represent the limits of habitat conditions or sites where biotic resistance of natives (via competitive exclusion) is reduced, or some combination of the two. A current working hypothesis is that many invasive exotic species are ‘passengers’ of human habitat alteration, rather than ‘drivers’ of biodiversity loss, especially in the most altered ecosystems (Seabloom *et al*., 2003; MacDougall & Turkington, 2005; King & Tschinkel, 2008). In reality, most invasive species can probably be either ‘passengers’ of habitat alteration or ‘drivers’ of biodiversity loss, depending on limiting conditions (Firn *et al*., 2011). Therefore, conducting experiments in these invaded, yet largely

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intact, ecosystems may lead to a better understanding of the conditions that determine the impacts of an invasion and the habitat requirements of the invaders.

The invasion of the south-eastern United States by the fire ant, *Solenopsis invicta* Buren, is one of the most studied exotic insect invasions (Tschinkel, 2006). The invasion began when a small number of colonies were established in Mobile, Alabama, in approximately 1935 and subsequently spread throughout the south-eastern USA from approximately 1950 to the late 1970s eventually spreading to other parts of the USA and around the globe (Tschinkel, 2006; Ascunce *et al*., 2011). Fire ants have long been described by some as a major agricultural pest (Wilson & Eads, 1949) and considered a serious ecological threat to native biodiversity (Porter & Savignano, 1990; Wojcik *et al*., 2001).

There are two social forms of *S. invicta*: monogyne (single queen) and polygyne (multiple queen). Both occur in man-made habitats and are spread equally well by human transport (Tschinkel, 2006; King *et al*., 2009). Generally, invasive ants that are of the multiple queen or polygyne form, including polygyne *S. invicta* [also, for example, the Argentine ant *Linepithema humile* (Mayr)], are considered more of an ecological threat than monogyne populations (Porter & Savignano, 1990; Holway *et al*., 2002), but this is probably an overly broad, anecdotal statement (Deyrup *et al*., 2000). It is probably not true for *S. invicta*, as long-term studies of polygyne *S. invicta* invasions have shown no greater effect on co-occurring ants and arthropods (Morrison, 2002) than the monogyne form (King & Tschinkel, 2006) in man-made habitats. The monogyne form may have the greater potential for impacts in natural areas due to their greater dispersal potential (King & Tschinkel, 2008). More relevant to the local and regional-scale invasion biology of fire ants is the fact that natural spread of polygyne *S. invicta* populations is slow, by colony budding alone, whereas monogyne populations spread through mating flights by queens, which may disperse many metres or even kilometres from their parent colonies (Tschinkel, 2006). Thus, throughout this paper we focus on the monogyne form, which has a much greater potential for local and regional spread, which represents a majority of the Florida and worldwide populations, and whose populations are actually necessary to maintain existing polygyne populations (for polygyne populations to persist, polygyne females must mate with monogyne males; Ross & Keller, 1995).

Recently, long-term observational studies (Morrison, 2002), careful habitat gradient studies (Stuble *et al*., 2009; Lebrun *et al*., 2012), and large-scale addition and removal experiments (King & Tschinkel, 2006, 2008; Stuble *et al*., 2011) have provided a more nuanced understanding of fire ant invasion ecology and the potential impacts on native biodiversity. Fire ants are by far the most abundant ants in the most altered ecosystems, especially pastures and roadsides (Porter *et al*., 1992; Tschinkel, 2006). In a majority of intact habitats, fire ants are absent or rare – present only in association with small-scale soil disturbances (Tschinkel, 2006; King & Porter, 2007; King & Tschinkel, 2008; Lebrun *et al*., 2012). Removal experiments suggest that fire ants do not competitively suppress the largely exotic co-occurring ant fauna in man-made ecosystems (e.g. improved pastures, King & Tschinkel, 2006). Experiments combining fire ant additions with habitat alteration treatments (mowing and plowing) in intact habitats naturally free of fire ants revealed a significantly negative impact of fire ants on native ants, roughly equivalent to major soil disturbance (ploughing), although this impact appeared to be sustainable only through continued addition of fire ant colonies over 3 years (King & Tschinkel, 2008). More specifically, habitat colonization and population growth by fire ants in Florida pine flatwoods occurred naturally (without experimental supplementation) primarily in ploughed sites (King & Tschinkel, 2008). The negative impact of fire ants is not pervasive across the ant fauna in intact natural areas and appears to have the greatest effect on a few species in the genus *Pheidole* and native fire ants, especially *Solenopsis geminata* Fabricius (Morrison, 2002; King & Tschinkel, 2008; Lebrun *et al*., 2012). In sum, the collective research on fire ant invasion ecology suggests that fire ants are dependent upon human habitat alteration, especially soil disturbance, to colonize most ecosystems, and their impacts on the fauna of those ecosystems is limited because much of the native biodiversity is reduced by the initial alteration event(s) (King & Tschinkel, 2006, 2008).

However, there are some habitats within ecosystems that fire ants invade naturally, apparently without previous anthropogenic disturbance. Frequently, moist habitats with high water tables, little or no canopy, and especially sandy or loamy soils with underlying clay, such as prairies and wetland margins, are commonly invaded in the absence of human-caused soil disturbance or land clearing (Tschinkel, 1988; Helms & Vinson, 2001; Lubertazzi & Tschinkel, 2003; Stuble *et al*., 2009, 2011; Lebrun *et al*., 2012), although at lower densities than, for example, pastures or roadsides (Porter *et al*., 1992; King & Tschinkel, 2006, 2008; Stuble *et al*., 2009, 2011; Lebrun *et al*., 2012). Carrying out experiments to understand the impacts of fire ants in these sites is important, because it allows comparisons along the spectrum of habitats (and densities) that fire ants colonize or are found nearby. The spectrum includes the intact, uninvaded, drier pine flatwoods present throughout the south-eastern USA, the intact but invaded wet prairies and savannas of Texas and the south-eastern coastal plain, and the ubiquitous man-made ecosystems that are dominated by fire ants throughout its introduced range. Previously we have conducted experiments in uninvaded pine flatwoods (King & Tschinkel, 2008) and fire ant-dominated pastures (King & Tschinkel, 2006). Here, we examine the impact of fire ants on co-occurring ants by manipulating the abundance of fire ants in an intact longleaf pine-savanna ecosystem in north Florida that has been colonized by fire ants (Lubertazzi & Tschinkel, 2003). Specifically, we tested whether changing fire ant abundance affects the diversity and abundance of co-occurring ants.

Materials and methods

Study site

The study was conducted in the pine flatwoods on the western edge of the Apalachicola National Forest (ANF) in Florida from early spring (March) 2004–late summer (August)

2006. This forest is the largest remaining intact longleaf pine forest in the world and a recognized biodiversity hotspot ranking among the highest in terms of floral diversity for any temperate zone plant community (Myers & Ewel, 1990). These forests are generally associated with mildly rolling topography, and moderately to well-drained, acidic, sandy soil. They are structurally characterized by an open overstorey of pines (*Pinus palustris* Mill. and *Pinus elliottii* Engelm.), no understorey, and a dense ground cover that is a mix of shrubby and herbaceous species (Myers & Ewel, 1990).

The western side of the ANF where this study was conducted has two important habitat characteristics that affect the ant assemblage (Lubertazzi & Tschinkel, 2003). First, the ground cover is primarily herbaceous (i.e. wiregrass) rather than the mix of herbaceous and shrubby ground cover that is more dominant elsewhere in the forest (Lubertazzi & Tschinkel, 2003; King & Tschinkel, 2008). The dominant ground-cover species in this location was wiregrass, *Aristida beyrichiana* Trin. and Rupr., although palmetto [*Serenoa repens* (W. Bartram) Small], gallberry [*Ilex glabra* (L.) A. Gray], and fetterbush [*Lyonia lucida* (Lam.) K. Koch] were also common. This is probably a consequence of a lack of anthropogenic fire suppression and limited soil disturbance (which severely impacts wiregrass regeneration) on the western side of the forest for at least several decades (C. Hess, pers. comm.). Secondly, this site is within the floodplain of the Apalachicola River and thus has loamy surface soils and clayey subsoil as opposed to the mostly pure sand or sand with organic layers (e.g. spodosols) present throughout the rest of the ANF and Florida. Specifically, this site is characterized by Brickyard soils which are fine, smectitic, nonacid, thermic typic Endoaquept Inceptisols (USDA Soil Survey, 2003). The site is nearly level and very poorly drained with an apparent water table that is no greater than 30 cm from the surface for much of the year and frequently flooded throughout the spring and summer (May–August). The soil type and flooding frequency of this site are very unusual for Florida pine flatwoods forests generally (Lubertazzi & Tschinkel, 2003). It is one of a few, intact pine-savanna ecosystems that are fully invaded by fire ants in Florida (J. R. King and S. D. Porter, pers. obs.; King & Porter, 2005).

Experiments

Two treatments and two controls were assigned: addition plots had fire ants added, removal plots had fire ants removed, control plots were not manipulated and thus represent natural levels of fire ant abundance, and soil control plots had soil added, without fire ants. Each treatment and control was replicated five times for a total of 20 plots. Replicate plots were 40 m × 40 m, including a 7.5 m buffer that was treated in removal and addition plots but not sampled with pitfall traps. All plots were separated by 40 m from one another and at least 40 m from ecotones and roadsides. Monogyne (the single-queen social form) *S. invicta* colonies were visually counted three times per year on all plots. This study took advantage of the natural, relatively low abundance of fire ants (approximately, on average, one-sixth the abundance of fire ants in pastures within the region), which served as a control for fire ant addition and removal treatments (King & Tschinkel, 2006).

In 2004, 25 colonies were added to each addition plot during the spring (April) and again in the fall. After the first year, additions were based on the census, and 10–30 mature colony fragments (depending on how many colonies were established with brood) were added twice annually from 2005 to 2006 to all fire ant addition plots. Colony fragments were collected using a shovel to take most of the above-ground soil mound and all of the ants and brood and were put into a heavy plastic bag. Colonies could then be moved and ‘planted’ into plots by digging a small hole and dumping the bag’s contents into them. Colonies were collected along roadsides during cool winter months (December to February) on sunny mornings to increase the likelihood of capturing queenright colony fragments. A similar number of soil ‘plugs’ (without any ants) was added to soil control plots, functioning as a sham control for the fire ant additions.

Fire ant colonies in removal treatment plots were regularly killed 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 (Tschinkel & King, 2007). We used 70–85 °C water to kill the colonies. Water was carried to colonies using 20-litre buckets. The nest was opened by driving a stick downwards through the subterranean nest chambers, and the hot water was rapidly poured into the resulting hole until the nest was full. The remaining hot water was used to collapse the mound. We treated removal plots at least three times annually.

We operated 36 pitfall traps arrayed in a 6 × 6 grid with 5-m spacing within the central 25 m × 25 m of each plot once per year in July to early August during the peak of annual ant activity to assess the diversity and abundance of ants. 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). Pitfall traps were 85-mm-long plastic vials of internal diameter 30 mm. 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. Traps were installed with a hand-held, battery-powered drill using an auger bit and then covered with a clear plastic rain shield suspended approximately 10 cm above the ground surface. The authors identified all species, and voucher specimens have been deposited at the Museum of Comparative Zoology, Harvard University, Archbold Biological Station and in J. R. King’s personal collection.

Statistical analyses

The primary data consisted of the richness and abundance of all ant species collected by pitfall trapping. All summary data per plot (species richness, total fire ants, total non-fire ants) were $\log_{10}$-transformed and all individual ant species data (abundance per plot) were square root + 0.5 transformed throughout to satisfy parametric assumptions. Data were analysed with SAS version 9 using a mixed-model, repeated-measures design with plots as 'subjects' and year and fire ant treatment as classification variables. As PROC MIXED uses restricted maximum likelihood to estimate unknown covariance parameters, it was necessary to select the best-fitting covariance structure model for the data (Khattree & Naik, 1999). The data in all cases were best fitted by the most general form possible, an unstructured covariance matrix structure, which was then used to construct the tests for fixed effects.

Approximate type III F-statistics for fixed effects were calculated in PROC MIXED using a general Wald-type quadratic form (described in detail in Khattree & Naik, 1999, and refer to SAS Institute, 2008, for determinations of degrees of freedom) which we report here as F-statistics and associated P-values for years, plot treatments, and year × treatment interaction. P-values ≤ 0.05 typically indicate significance (SAS Institute, 2008). Inferences for fixed effects in PROC MIXED allows for comparisons across repeated measures while simultaneously accounting for the underlying covariance structure using differences of least squares means. We examined the result of multiple comparisons here as P-values from Tukey–Kramer's tests among all possible pairwise comparisons of treatments and years. Relationships among variables were also analysed using simple and multiple linear regressions.

Results

A total of 49 species, including eight exotic species, were captured in pitfall traps over 3 years (Table 1). Fire ants were, by far, the most abundant ants in plots, with more than twice the abundance of any other species (Table 1). Exotic ants, including fire ants, accounted for nearly 49% of all ants captured but only 16% of total species richness. After fire ants, the most abundant exotic species was *Pheidole moerens* (Table 1). The most abundant native species were *Monomorium viride* and *Solenopsis carolinensis*. The fauna appears to be similar, although lower in diversity, to fauna found elsewhere in the ANF and north Florida (Lubertazzi & Tschinkel, 2003; King & Porter, 2005; King & Tschinkel, 2008).

Overall, fire ant abundance was significantly different among years ($F = 55.50$, $P < 0.001$), treatments ($F = 4.55$, $P = 0.017$), and year × treatment interactions ($F = 2.76$, $P = 0.049$). Fire ant abundance was greatest in addition plots and lowest in removal plots. Within each year, average fire ant abundance was lower in control and removal plots than in addition plots, although the difference was only significant in 2004 (Tukey–Kramer, $P = 0.01$; Fig. 1). Additionally, removal plots and control plots were similar within each year, as were soil addition plots and fire ant addition plots (Fig. 1). Fire ant abundance decreased in fire ant addition plots during the second year of the study (2005), probably as a consequence of a drought, which had an impact on all ants (Fig. 2). However, by the third year, fire ant abundance had increased to the highest levels in fire ant addition plots (Fig. 1).

Co-occurring ant abundance differed significantly among years ($F = 25.04$, $P < 0.001$) but not among treatments

Table 1. Ant species listed alphabetically by subfamily and their total abundance in pitfall traps over 3 years.

Species	Total individuals
Dolichoderinae	
Dorymyrmex bureni (Trager)	3703
Forelius pruinosus (Roger)	5679
Tapinoma sessile (Say)	837
Ecitoninae	
Neivamyrmex opacithorax (Emery)	7
Neivamyrmex texanus Watkins	14
Formicinae	
Brachymyrmex depilis Emery	72
Brachymyrmex obscurior Forel	567
***Brachymyrmex patagonicus* Mayr**	579
Camponotus castaneus (Latreille)	101
Camponotus floridanus (Buckley)	363
Camponotus socius Roger	11
Formica archboldi M.R. Smith	3
Formica dolosa Buren	753
Formica pallidefulva Latreille	381
Nylanderia arenivaga (Wheeler)	67
Nylanderia concinna (Trager)	87
Nylanderia faisonensis (Forel)	1737
Nylanderia parvula (Mayr)	19
Nylanderia wojciki (Trager)	175
Polyergus longicornis Smith	1
Myrmicinae	
Aphaenogaster flemingi Smith	553
Aphaenogaster treatae Forel	735
***Cardiocondyla minutior* Forel**	12
***Cardiocondyla wroughtonii* (Forel)**	21
Crematogaster cerasi (Fitch)	650
Crematogaster lineolata (Say)	1062
Crematogaster minutissima Mayr	204
Crematogaster missuriensis Emery	12
***Cyphomyrmex rimosus* (Spinola)**	3580
Monomorium viride Brown	3786
Pheidole adrianoi Naves	4
Pheidole dentata Mayr	2051
Pheidole dentigula M.R. Smith	376
Pheidole floridana Emery	472
Pheidole metallescens Emery	1578
***Pheidole moerens* Wheeler**	8375
Pheidole morrisi Forel	1263
Pyramica bunki (Brown)	2
***Pyramica margaritae* (Forel)**	67
***Pyramica membranifera* (Emery)**	13
Solenopsis carolinensis Forel	6000
***Solenopsis invicta* Buren**	20 132
Solenopsis nickersoni Thompson	3
Solenopsis pergandei Forel	26
Strumigenys louisianae Roger	125
Temnothorax pergandei (Emery)	17
Trachymyrmex septentrionalis (McCook)	45
Ponerinae	
Hyponera opaciceps (Mayr)	726
Hypoponera opacior (Forel)	73

These data were generated from annual summer pitfall trapping of 36 pitfall traps in 20 40 × 40 m plots. The 2160 samples contained 67 119 ants of 49 species. Exotic species (eight total) are in bold.

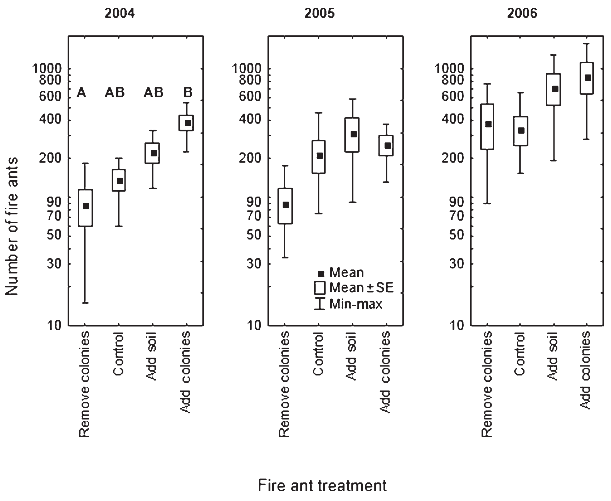

Fig. 1. Average fire ant abundance in treatment plots per year. Letter grouping in 2004 indicate significant differences between removal plots and addition plots in the first year of experiments. Note the y-axis is $\log_{10}$-scaled.

($F = 1.75$, $P = 0.20$) or year × treatment interactions ($F = 1.09$, $P = 0.41$). Co-occurring ant species richness did not significantly differ among years ($F = 2.14$, $P = 0.15$), treatments ($F = 1.58$, $P = 0.23$), or year × treatment interactions ($F = 1.01$, $P = 0.45$). Within years, there were no significant differences among treatments for either the abundance (Fig. 2) and species richness (Fig. 3) of co-occurring ants. Likewise, no significant effects on abundance were detected when each species was analysed individually across treatments within each year. The average abundance and species richness of co-occurring ants were lowest in soil addition plots (Figs 2 and 3). The mean abundances of co-occurring ants on fire ant removal plots and control plots were very similar each year, while the fire ant addition plots had a very slight, but not significant, increase in mean co-occurring ant abundance by the third year (2006; Fig. 2). Average co-occurring ant species richness was greater in addition plots by the third year (2006, Fig. 3), but not significantly so.

Linear regressions revealed no significant relationships among fire ant abundance, species richness and co-occurring ant abundance. Fire ant abundance was negatively related to co-occurring ant abundance ($P = 0.17$, $R^2 = 0.03$). This result was the same for both the overall model and within treatments. In sum, the fire ants had little discernible impact on co-occurring ants (Figs 2 and 3).

Discussion

This study completes a series of large-scale experiments we conducted along a fire ant density and anthropogenic disturbance gradient that ranges from zero-density, undisturbed well-drained pine flatwoods (King & Tschinkel, 2008) to high-density, improved pasture (King & Tschinkel, 2006) with the results of this study in low-density, poorly drained pine flatwoods serving as a midpoint. King and Tschinkel (2006)

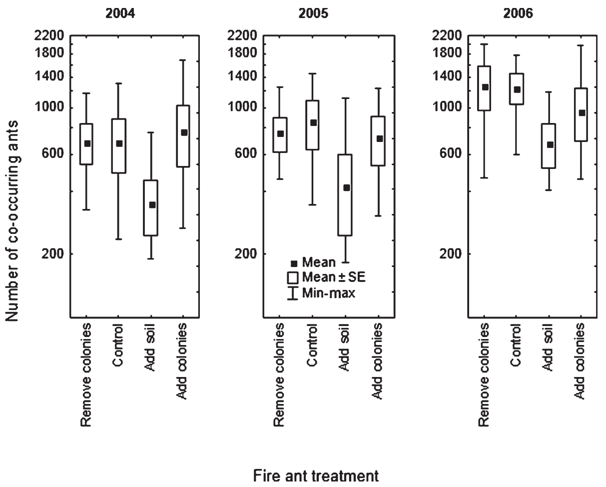

Fig. 2. The average number of co-occurring ants in treatment plots per year. There were no significant differences among treatments for any year. Note the y-axis is $\log_{10}$-scaled.

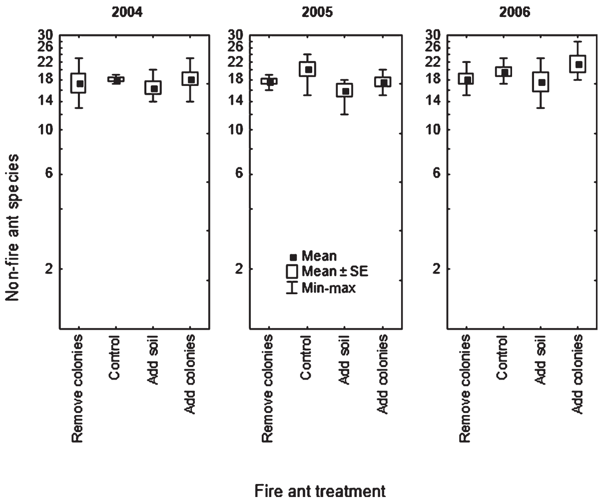

Fig. 3. The average number of species of co-occurring ants in treatment plots per year. There were no significant differences among treatments for any year. Note the y-axis is $\log_{10}$-scaled.

demonstrated empirically that there was no impact of reductions of fire ants in the completely altered pasture habitats. King and Tschinkel (2008) demonstrated strong impacts of fire ant additions, comparable to ploughing – a major habitat disturbance – in intact, uninvaded habitats. However, it seems likely that the potential impact of fire ants in uninvaded ecosystems remains an experimental artifact because they colonize many ecosystems only when the ecosystems have first been cleared and ploughed and the native biodiversity has already been reduced (Tschinkel, 2006; King & Tschinkel, 2008). Finally, in ecosystems that are invaded by fire ants in the absence of human impacts, the results we present here suggest that the impacts of fire ants on native ant biodiversity are potentially negative, but very limited, especially if the habitat is of low quality for most ant species (Gibb, 2011). Impacts on other animals (e.g. vertebrates) in these ecosystems are quite possible but this requires further investigation (Tschinkel, 2006).

The addition and removal of fire ants did not change their abundance as much as it did in our previous studies (King & Tschinkel, 2006, 2008). In particular, the removal method resulted in little change in fire ant abundance (Fig. 1). This is probably a result of applying the hot water method to clayey soils. Unlike very sandy or sand and loam soils (Tschinkel & King, 2007), clay prevents infiltration of water into many chambers within nests. Nest survival appeared reduced during surveys, but this may only have been because colonies we had treated remained alive, but inconspicuous, while colonization by new colonies was limited or negligible (J. R. King, pers. obs.). Additions did increase fire ant abundance, although drought conditions in the second year (2005) appeared to have prevented year-on-year increases for the duration of the study (Fig. 1).

Given that the method and effort were nearly identical to our previous additions (King & Tschinkel, 2008), it seems likely that the peculiarities of this habitat may also have had an impact on the establishment success of the colonies we added. Many colonies could have failed because the habitat was poor and perhaps already mostly ‘saturated’ by other fire ant colonies. We noted little or no evidence for new colony founding in any plots, and the natural density of fire ants in these habitats is low. More broadly, in the south-eastern USA and Texas, the results of other studies lend support to this hypothesis. The results of Helms and Vinson (2001), Lubertazzi and Tschinkel (2003), King and Porter (2005), and Stuble *et al*. (2009, 2011) all showed that ant assemblages in savannas with ground cover dominated by grasses and moderately to poorly drained loamy or clayey soils are relatively species-poor and have lower ant abundance when compared with similar ecosystems (e.g. longleaf – pine savannas) with well-drained soils and shrubby ground cover (King & Porter, 2005; King & Tschinkel, 2008). Thus, while fire ants can invade these ecosystems, they are less productive (lower in quality) for fire ants (Stuble *et al*., 2011) and for ants in general. Furthermore, these ecosystems may be especially prone to negative impact from soil disturbance. The soil additions in this experiment (Figs 2 and 3) reinforce this, as even small soil disturbances (such as turning soil with a shovel) appeared to have decreased ant abundance.

The lack of obvious reductions in co-occurring ant species richness or abundance on fire ant addition plots also suggests that fire ants are not competitively suppressing co-occurring ants. This result is similar to the outcome of removal experiments reported by King and Tschinkel (2006). While perhaps surprising, results from King and Tschinkel (2008), Gibb (2011), and Lebrun *et al*. (2012) suggest that this outcome is probably a result of a lack of competitors in the fauna. Medium-sized *Pheidole*, such as *Pheidole morrisi*, and native fire ants such as *S. geminata* appear to be species that are typically displaced by *S. invicta*, especially in moist habitats and when fire ant numbers are extremely high (i.e. addition treatments by King & Tschinkel, 2008). When these species are rare or absent from the fauna, for example due to poor habitat quality for many species (Gibb, 2011), it may be difficult to detect any impacts from fire ants even when their numbers are experimentally increased.

Our previous experiments (King & Tschinkel, 2006, 2008) and this study have allowed us to identify some of the most important factors shaping the abundance and distribution of fire ants. First, human impacts remain the most important factor in first reducing native ant biodiversity and then promoting the spread and enormous abundance of fire ants in converted landscapes. Thus, fire ants are largely ‘passengers’ of human activity throughout the southern USA (King & Tschinkel, 2006, 2008; Lebrun *et al*., 2012). Secondly, fire ants are capable of invading a variety of relatively undisturbed, savanna-like or prairie habitats (Helms & Vinson, 2001; Lubertazzi & Tschinkel, 2003; Stuble *et al*., 2009, 2011). However, these habitats appear to be relatively poor for some native ant species and fire ants, and the impact of fire ants is relatively minor. Thirdly, fire ants can ‘drive’ reductions in diversity of native ants, but their impact appears to be limited to medium-sized *Pheidole* species, including *Pheidole dentata* and *P. morrisi* and native fire ants (*S. geminata* and *Solenopsis xyloni*). Whether or not these species are common in habitats that fire ants invade is questionable. For example, *P. morrisi* is common only in pine forest habitats with well-drained sandy soils, even north of the range of fire ants (J. R. King, pers. obs.). Finally, the impact of an initial ‘invasion front’ of fire ants can fade rapidly over a matter of several years (Morrison, 2002). Unfortunately, fire ant ecology has historically been poorly understood and thus of little benefit for management of this important invasive insect (Tschinkel, 2006). Specifically, there is currently no compelling evidence that fire ants are permanently displacing native North American ant species, regardless of social form (Helms & Vinson, 2001; Morrison, 2002; Lubertazzi & Tschinkel, 2003; King & Tschinkel, 2006), with the possible exception of the native congeners *S. geminata* and *S. xyloni* in some localities (Tschinkel, 1988; Morrison, 2002).

There are many examples on islands and continents other than North America where invasive ant species have become established in natural areas. On other continents and islands, site characteristics, including natural and human-caused disturbance, remain poorly described and invasive ants may or may not be the sole drivers of diversity loss (e.g. Hoffmann *et al*., 1999; Krushelnycky *et al*., 2005), although it is likely that their impacts are negative. In the case of fire ants in North America, anthropogenic land alteration is the most important factor shaping their distribution and abundance. Thus, preventing or mitigating habitat alteration, especially the creation of roads or fire-breaks, remains the single most important step in preventing impacts from fire ants, and probably other exotic ants and invasive weeds (King *et al*., 2009). A priority is to integrate this understanding into future management approaches and to replicate our addition and removal experiments in habitats beyond north Florida with different conditions and different co-occurring species.

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