

OPINION

Invasive ants—are fire ants drivers of biodiversity loss?

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Invasive species have long been associated with biodiversity declines (MEA, 2005), and many invasive species that have devastating effects on native faunas are insects (e.g. Majerus *et al.*, 2006; Brown *et al.*, 2011). Whilst there is good evidence that some invasive insects are drivers of declines of native species (e.g. the alien Harlequin ladybird *Harmonia axyridis* in the UK; Brown *et al.*, 2011), there is less consensus for some other invasive insect species.

The red imported fire ant, *Solenopsis invicta* Buren (Hymenoptera: Formicidae) was accidentally introduced into southern USA in the 1930s from South America (Fadamiro *et al.*, 2009). It has subsequently extended its range and is now widespread throughout south-eastern USA. Previous studies have shown that *S. invicta* is associated with declines in native ants (Stuble *et al.*, 2009). However, fire ants are usually associated with habitat disturbance, leading to an area of contention amongst ant researchers, and leading to the alternative suggestion that these invasive species 'are "passengers" of human habitat alteration, rather than "drivers" of biodiversity loss' (King & Tschinkel, 2013a). Untangling these two factors, and understanding whether fire ants are passengers or drivers in native ant declines, is a challenge that merits further research by invasion biologists.

A recent paper (King & Tschinkel, 2013a), reported results from an experimental manipulation of fire ants in an undisturbed pine-savannah ecosystem. The authors report little impact of fire ants on native ants even though there was about five fold difference in fire ant abundance across treatments in the first year of the experiment. Thus the authors conclude that preventing habitat disturbance is the most important way of reducing fire ant impacts. Here we report two responses to the paper.

In the first response, Stuble *et al.* (2013) criticise King & Tschinkel's experiments because there was no treatment where fire ants were completely excluded, there may not have been sufficient time for new species to colonise experimental plots with reduced fire ant abundance, and that threshold effects may result in plots with very low fire ant abundance having detrimental impacts on native ants. Stuble *et al.* (2013) also highlight other studies which have shown negative effects of fire ants in the absence of habitat disturbance. In reply, King and Tschinkel (2013b) defend their experimental design and conclusions, and support their arguments with evidence that

under natural conditions mature colonies of fire ants rarely occur in undisturbed habitats. They agree that there is some evidence showing that where fire ants colonise undisturbed habitats they have a negative effect on native ants, but King and Tschinkel (2013b) argue these examples are of limited importance, especially since these are usually poor quality habitats where overall ant diversity is low. There is clearly more research to be done to determine the importance of habitat disturbance, and whether or not the impacts of fire ants (and indeed, other invasive insect species) are context-specific. Given global climate change and its accompanying range shifts by insects, the present discussion is relevant, timely and highlights the need for considerable further research if we are to successfully assess the potentially complex impacts of invasive insects.

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OPINION

Fire ants are drivers of biodiversity loss: a reply to King and Tschinkel (2013)

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King and Tschinkel (2013) report on a manipulative experiment aimed at assessing the effects of a well-studied invasive ant species (*Solenopsis invicta*) on the species density and worker abundance of native ants in a relatively undisturbed longleaf pine savanna in northern Florida. Admittedly, the experiment was an impressive undertaking in that it examined the responses of native ant assemblages to the addition and removal of colonies of *S. invicta* (the red imported fire ant) with two control treatments, plots with no manipulation (natural levels of fire ant abundance) and soil control plots (soil added) over 3 years. From this experiment, King and Tschinkel concluded that fire ants had minimal impacts on native ant communities. Below, we argue that this experimental manipulation was unsuccessful, leading the authors to make spurious claims about the impact of *S. invicta* on native ant assemblages.

The experimental design in King and Tschinkel (2013) suffers from several flaws. First, there were no plots without fire ants, and therefore no baseline data on the structure of the native ant assemblage in the absence of fire ants. This makes it challenging to know what the impact of fire ants might be. By comparing the number of fire ants in their fig. 1 to the number of co-occurring ants in fig. 2 for 2006, approximately one in every three ants captured in the fire ant-removal plots was a fire ant. Thus, fire ants constituted a substantial component of the ant community in all experimental treatments, limiting the conclusions that might be drawn about their effects. Second, the experiment in King and Tschinkel (2013) failed to effectively alter the abundance of fire ants across treatments. King and Tschinkel (2013) acknowledge that the abundance of *S. invicta* differed among treatments in only the first year of the study and that the number of fire ants did not differ among treatments in subsequent years. However, even in the first year of the study it appears that the abundance of *S. invicta* differed only between the addition and removal treatments (King & Tschinkel, 2013, fig. 1). If the abundance of *S. invicta* did not differ among treatments, there are several

possible interpretations. The first is that, even at relatively low abundances, *S. invicta* alters the structure of native ant assemblage. A second interpretation is that the experimental manipulation was unsuccessful, making it impossible to assess the effects of fire ants on native communities. While we are supporters of experiments that test ecological hypotheses, effective manipulation of the independent variable is key to linking cause and effect.

A second issue arises from the unsubstantiated claims about the relative importance of fire ants and anthropogenic disturbance on native communities. King and Tschinkel (2013) claim that ‘the potential impact of fire ants in uninvaded ecosystems remains an experimental artefact because they colonise many ecosystems only when the ecosystems have first been cleared and ploughed and the native biodiversity has already been reduced’. King and Tschinkel (2013) conclude that fire ants are less important drivers of changes in native ant assemblages than is anthropogenic disturbance. They refer to their previous work (e.g. King & Tschinkel, 2008) in this system (but in a different location) to support their claim that ‘the impact of fire ants on ant assemblages ... appears to be secondary’ to habitat alteration. Their 2008 study (which also manipulated the density of *S. invicta*) was plagued by many of the same shortcomings we have identified in this experiment, including a lack of plots without *S. invicta* despite being conducted in an intact longleaf pine forest. From these studies, we cannot rule out the possibility that, even at these lower densities, fire ants may be negatively affecting native ant diversity and thus may act as drivers of diversity loss, even in the absence of disturbance. Indeed, a growing number of studies indicate that this may be the case (Morris & Steigman, 1993; Gotelli & Arnett, 2000; Cook, 2003; Stuble *et al.*, 2011; LeBrun *et al.*, 2012). However, if nothing else, King and Tschinkel overgeneralise their results. More tellingly, however, the data presented by King and Tschinkel (2008) show that disturbance and invasion cause similar levels of biodiversity loss. From 2004 to 2006, native ant species richness declined by about 18% (from ~29 species to ~24) when *S. invicta* was added to undisturbed plots and by about 16% (from ~27 species to ~23) in disturbed plots to which *S. invicta* was not added. Therefore, if an intact native ant community is invaded

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by *S. invicta* it might lose ~5 species; if that intact native ant community has the top 30 cm of soil ploughed it might lose ~4 species. Based simply on visual inspection, it seems that the effects of disturbance on native biodiversity are roughly equivalent to those of *S. invicta*.

Another issue in King and Tschinkel's 2013 study (and their earlier studies as well) is the scale of the experiment. Such experiments may not detect the effect of removing or adding fire ants on native ant assemblages because fire ants have occurred in these systems for quite some time (Tschinkel, 2006) and may have influenced richness in the regional species pool (Gotelli & Arnett, 2000). Thus, it seems unlikely that the pervasive regional effects of this invasive species on native ant assemblages would be reversed following the removal of fire ants in relatively small plots for 3 years, even if the removal had been successful. Where might new colonists come from to re-seed ant assemblages if fire ants are removed from relatively small plots that occur in a region where fire ants have depressed native species for quite some time? We suggest that such a short-term manipulation would most probably underestimate the effects of fire ants if, for example, the regional richness of native ant species was negatively affected by their presence.

Finally, it appears that the authors have drawn some incorrect conclusions from the recent literature. For example, King and Tschinkel (2013) suggest that the recent work of LeBrun *et al.* (2012) demonstrates that fire ants are passengers of diversity loss when, in fact, the results in LeBrun *et al.* (2012) are more nuanced. LeBrun *et al.* (2012) detected an impact of fire ants on native ant assemblages in undisturbed habitats, indicating that *S. invicta* can be a driver of diversity loss in at least some undisturbed areas.

We agree with King and Tschinkel (2013) that stemming the tide of habitat alteration is an important first step in preserving native ant biodiversity and that *S. invicta*, and some (though not all) invasive ant species are more likely to become established in disturbed sites than in undisturbed sites (Tschinkel, 1988). A critical element of King and Tschinkel's argument here, though, is that *S. invicta* cannot easily invade undisturbed habitats. However, their own study site provides an example of an undisturbed habitat in which *S. invicta* (and seven additional exotic species) has successfully invaded (also see Stuble *et al.*, 2009). Moreover, many other invasive ants have spread into undisturbed sites: *Linepithema humile* (Holway, 1995; Sanders *et al.*, 2001; Krushelnicky *et al.*, 2005; Lach, 2007), *Anoplolepis gracilipes* (O'Dowd *et al.*, 2003), *Pheidole megacephala* (Hoffmann *et al.*, 1999; Vanderwoude *et al.*, 2000), *Pachycondyla chinensis* (Guénard & Dunn, 2010) and *Wasmannia auropunctata* (Clark *et al.*, 1982; Walker, 2006). Indeed, this is true for *S. invicta* as well (Morris & Steigman, 1993; Cook, 2003; Stuble *et al.*, 2009). While disturbance in all of its forms (including ploughing up the top 30 cm of soil) might promote establishment by some invasive species and reduce the diversity and abundance of native species, disturbance is not a prerequisite for invasion, even for *S. invicta*.

King and Tschinkel (2013) could lend support to a pervasive movement (Slobodkin, 2001; Brown & Sax, 2004; Gurevitch & Padilla, 2004; Davis *et al.*, 2011) claiming that threats posed by invasive species are exaggerated. However, such a claim

may be dangerous when based on incorrect interpretations of data as it is abundantly clear that invasive species are a leading cause of population- and species-level extinctions (Clavero & Garcia-Berthou, 2005; Simberloff, 2011), and that invasive species can dramatically alter the structure and function of ecosystems (Wardle *et al.*, 2011). The misinterpretation of King and Tschinkel's (2013) experiment may lead to the spurious conclusion that fire ants are not important drivers of the loss of native species and the services and functions they provide.

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OPINION

Fire ants are not drivers of biodiversity change: a response to Stuble *et al.* (2013)

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Habitat alteration of the environment and biological invasion are intertwined, critically important topics deserving our attention as leading causes for global biodiversity losses as well as drivers of community assembly. Given human impacts on the biosphere (Millenium Ecosystem Assessment, 2005), if ecologists are to explain biodiversity loss and community assembly, then experiments are necessary to separate the effects of habitat alteration, biological invasions, and other potential factors.

We have published a set of experimental studies that collectively tested the effects of the exotic fire ant, *Solenopsis invicta* Buren and habitat disturbance on co-occurring ant abundance and species richness (King & Tschinkel, 2006, 2008, 2013). These experiments were carried out along a fire ant density and anthropogenic disturbance gradient ranging from zero-density, undisturbed well-drained pine flatwoods (King & Tschinkel, 2008), through a midpoint with low-density, poorly drained pine flatwoods (King & Tschinkel, 2013), to high-density improved pasture (King & Tschinkel, 2006). We concluded that anthropogenic disturbance, not *S. invicta*, has the greatest impact on ant communities in these habitats. Other studies support these conclusions.

In its entirety, our work in Florida (Tschinkel, 1988; Lubertazzi & Tschinkel, 2003; Tschinkel, 2006; King & Porter, 2007; King & Tschinkel, 2006, 2008, 2013) has found little evidence that fire ants compete with co-occurring ants, whether native or not. Rather, we have shown through transparent, repeatable, well-replicated, statistically significant and easily understood experiments, as well as large scale survey work and thorough review and critique of the fire ant ecology literature, that the primary factor depressing native ant populations is land-use change. Our experiments show that habitat is the central component of ant community assembly in the southeastern US, and for fire ants, disturbance is the most obvious feature of the habitat in which they enjoy maximal success. We part ways with some other ant community ecologists concerning the role of inter-specific competition in structuring early-succession ant communities, a divergence that we base on having done some of the very few field experiments testing habitat and

competition hypotheses over time spans greater than a few months.

All of the primary criticisms raised by Stuble *et al.* (2013) have been addressed in detail in King and Tschinkel (2006, 2008, 2013) and we would urge readers to consult those papers. Stuble *et al.*'s (2013) primary criticism is that our experimental work is flawed in either design or execution. They make much of the fact that we did not have zero fire ant population plots for comparison in the 2013 study and that our plowed plots in the 2008 paper had significant (self-founded) fire ants in the last year of our experiment. Their critique, however, is built upon two flawed assumptions: that fire ant effects are density independent or exhibit a threshold response, and that there are no zero fire ant density areas nearby for comparison (or to act as source populations for native species). Both of these assumptions are demonstrably false.

To require that fire ants be completely absent in removal plots to validate our conclusions fails to acknowledge that such population effects are *density dependent* (Hölldobler & Wilson, 1990; Morrison, 2000; Tschinkel, 2006). We are unaware of evidence that they are not, or that a threshold effect exists (e.g. Porter & Savignano, 1990; Morrison, 2002).

Therefore, in our King and Tschinkel (2006) pasture study, a large reduction (65%) of fire ants should have been followed by a significant increase in co-occurring species, but was not. In our forest experiment (King & Tschinkel, 2008), there were control plots with zero densities, although we reported only averages, so it is simply not true that we had no fire-ant-free plots for comparison. Even using averages in our forest experiment (King & Tschinkel, 2008), by 2006, 55–75% of the ants captured in plots in which we planted fire ant colonies were fire ants, in contrast to 13% in our plowed, 'fire ant free' plots in King and Tschinkel (2008; whose population arose from newly-mated queens choosing to settle there). According to density dependence, this low population of self-founded fire ants can be expected to have low effects on native ants, approaching that of a disturbed, fire ant free treatment. Moreover, in the previous 2 years, fewer than 5% of the ants on these same plots were fire ants.

In King and Tschinkel (2013), Fig. 1 clearly shows a similar level of reduction of fire ants in years 1 and 2 in removal plots, although it was significantly different from the other

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plots only in year 1. The addition-plot densities of fire ants were also highest in year 3. Clearly we did not have the same level of control over fire ant densities that we managed in the King and Tschinkel (2008) study (as we clearly acknowledge and explain in King & Tschinkel, 2013); however, one cannot dismiss the differences in fire ant densities among plots in King and Tschinkel's (2013) Fig. 1 (an average of ~80 fire ants per plot in removals versus nearly 1000 in addition plots), when the differences in co-occurring ant abundance appear entirely unaffected by the differences, especially in the addition plots (Fig. 2).

Stuble *et al.* (2013) also state that the King and Tschinkel (2008) paper shows that 'disturbance and (fire ant) invasion cause similar levels of biodiversity loss'. They base this claim on the fact that when mature fire ant colonies were transplanted into undisturbed habitat, they reduced abundance and species richness of native ants about the same as did disturbance without fire ants (King & Tschinkel, 2008, Fig. 2a,b). This outcome is clearly reported both quantitatively and verbally in our paper. Indeed, we include an emphatic warning that our result is an experimental artifact, not the result of natural process, and can be easily misinterpreted in exactly the way these authors have. Here is the relevant paragraph from our paper:

Although these results demonstrate a negative effect of fire ants, it is important to dispel a potential misunderstanding. By moving entire colonies, we were able to establish populations of fire ants in undisturbed habitats at ~60–70% of the high forager and colony densities they achieve under natural conditions in highly disturbed habitats, such as pasture. However, we cannot emphasize enough that the suppression of native ants by fire ants in the undisturbed plots of our experiment occurred only because we planted hundreds of mature colonies into native habitat, a habitat that they neither recruit into nor persist in on their own.

To put this situation into proper perspective, the habitat in which the King and Tschinkel (2008) experiments were carried out (the eastern side of the Apalachicola National Forest—a forest about the size of the state of Rhode Island) has been home to *S. invicta* since the early 1960s. Every kilometre of the 1600 km of maintained roadside in this forest bears linear populations of monogyne colonies that emit thousands of sexuals per colony 5–10 times a year, and have done so for almost 50 years. The mated female alates are capable of flying up to 5 km, and with the help of wind, even more (Tschinkel, 2006). No point in this section of the national forest is more than 1–4 km from a maintained road, and yet, the undisturbed native habitat has very low densities of *S. invicta*. Colonies can occasionally be found outside of road margins, but only associated with local soil disturbance resulting from heavy equipment operation or off-road vehicles. Thus, under natural conditions, mature colonies (70 000–200 000 workers) do not appear in undisturbed habitat, as they did in our colony addition treatments. This local distribution of fire ants at high densities along roadsides and other human modified habitats is a common pattern throughout the southeastern US (J. R. King and W. R. Tschinkel, pers. obs.).

Stuble *et al.* (2013) speculate that fire ants may have depressed the 'regional pool' of ant species available for recolonising our experimental plots. Lubertazzi and Tschinkel (2003) reported widespread fire ant free sites in the eastern Apalachicola National Forest where we carried out the King and Tschinkel (2008) study, and our own observations confirm this. Van Pelt's (1947, 1956) work prior to the arrival of the fire ant and King and Porter's (2007) more recent work suggest minor changes in the local and regional species pool of most of the upland ecosystems that occur in north and central Florida since the arrival of the fire ant and no evidence that fire ants have limited recolonisation. In contrast, it is abundantly clear that habitat is a barrier to native ant recolonisation (King & Tschinkel, 2006, 2008).

We acknowledge (and have always done so) that fire ants are capable of colonising some kinds of undisturbed ecosystems (Lubertazzi & Tschinkel, 2003; Stuble *et al.*, 2009; LeBrun *et al.*, 2012), and that their impact on co-occurring ants there may be negative (LeBrun *et al.*, 2012). However, other than the King and Tschinkel (2013) paper, this question has been addressed experimentally in the US only by Stuble *et al.* (2011) whose results do not conflict with ours. In the King and Tschinkel (2013) paper, we wrote that fire ants ... 'in ecosystems ... (colonized) 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)'. LeBrun *et al.*'s (2012) recent paper provides an example of such negative impacts, although this conclusion was based on correlation, not experimental manipulation.

Finally, Stuble *et al.* (2013) contend that fire ants suppress native ants through competition and/or predation, and that 'it is abundantly clear that invasive species are a leading cause of population- and species-level extinctions'. Yet, there is currently no compelling evidence that fire ants are permanently displacing native 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* (Tschinkel, 1988; Morrison, 2002). Furthermore, Morrison and Porter's work (2003), that demonstrates a positive association between fire ant density, co-occurring ant density, and generalised arthropod density, also suggest that common factors, unrelated to inter-specific competition, are more important in shaping ant communities. Most of the previous studies that have credited exotic ants with displacing native ant species, 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). Until the underlying mechanisms are clarified through experiments, invasive ants as drivers of diversity loss will remain a hypothesis awaiting experimental support.

Stuble *et al.* (2013) end their essay with the suggestion that 'King and Tschinkel (2013) could lend support to a pervasive movement ... claiming that threats posed by invasive species are exaggerated'. We are not aware of such a movement

and, like Stuble *et al.* (2013), we would strongly reject any science that made exaggerated claims about invasive species. Only through fully-reported, well-designed experiments and observations can we hope to reveal reality and put invasive species into their proper perspective. If scientists or others take a stance based on exaggerated claims, in the face of conflicting results, then it will only diminish the likelihood of a deeper understanding of exotic ant ecology, exotic ant impacts, and actual solutions to the problems exotic ants pose. Our results, which suggest that competition among colonies is not the primary driver of ant community assembly, are compatible with alternative forms of major negative impacts of exotics ants on native species. For example, predation by exotic species on native species queens during dispersal and colony founding of colonies by exotic species could reinforce the initial loss of native species diversity in disturbed habitats that occurs with anthropogenic disturbance. There may also be widespread impacts on ground-nesting vertebrates, where fire ants act as predators (Tschinkel, 2006).

Exploring these kinds of alternative negative impacts seems the only constructive way forward. We have contributed some of the few experiments testing assumptions about one 'invasive' species, the fire ant, and continue to hope that this work will serve as a springboard for further, rigorous hypothesis testing and pursuit of results that move the science forward. If authors disagree with our conclusions, we urge them to do the necessary experiments and thus to contribute positively to the scientific discourse. Otherwise, it will be difficult to pursue an objective, hypothesis-testing approach to the study of the ecology of exotic ants. Any alternative approach might render the ecological study of exotic ants, and especially fire ants, a stagnant backwater in the broader scientific ebb-and-flow of invasion biology and ecology.

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