

OPINION

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

KATHARINE L. STUBLE,¹LACY D. CHICK,¹MARIANO A. RODRIGUEZ-CABAL,²JEAN-PHILIPPE LESSARD³ and NATHAN J. SANDERS¹ ¹Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, Tennessee, U.S.A., ²Department of Zoology, University of British Columbia, Vancouver, Canada and ³Quebec Centre for Biodiversity Science, Department of Biology, McGill University, Montreal, Canada

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

Correspondence: Katharine L. Stuble, Department of Ecology and Evolutionary Biology, University of Tennessee, 569 Dabney Hall, Knoxville, TN 37996, U.S.A. E-mail: kstuble@utk.edu

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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