Invasive Ants Generate Heterogeneity in Patterns of Seed Survival

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ABSTRACT.—Although studies often focus on the direct effects of invasive species on native taxa, invasive species may also alter interactions among native species. For example *Solenopsis invicta*, the red imported fire ant, may directly alter native seed survival by consuming seeds, but also indirectly alter seed survival, by altering the abundance and/or behavior of native granivores. We tested the effects of invasive *S. invicta* on rodent and arthropod granivory by quantifying seed removal from seed depots that differed in granivore access (arthropods and rodents or arthropods only) and distance from an *S. invicta* mound (0.1 m or 4.0 m). We hypothesized the effect of *S. invicta* on native granivores would be stronger at depots located near (0.1 m) a mound than at depots located 4.0 m from a mound. Use of two different seed species (*Rubus cuneifolius* and *Prunus serotina)* allowed us to evaluate the consequences of *S. invicta* for small-seeded plant species consumed by both arthropods and rodents (*R. cuneifolius*) as well as for large-seeded species that can only be consumed by rodents (*P. serotina*). We found overall removal of *P. serotina* was low, regardless of seed depot location or exclosure type. Near *S. invicta* mounds, the removal of *R. cuneifolius* was also low, with no difference between depots that allowed or excluded rodents. In contrast, removal of *R. cuneifolius* by arthropods 4.0 m from a mound was nearly twice that of removal next to a mound but only when rodents were excluded. Our results indicate *S. invicta* may create hotspots of granivory by native arthropods in the areas between *S. invicta* mounds, but these effects may not extend to large-seeded plants that are consumed by rodents. By influencing seed survival as a function of plant species and proximity to a mound, nonnative *S. invicta* generates heterogeneity in native seed survival, which may affect plant community composition.

INTRODUCTION

Invasive species can have negative direct effects on ecological communities by reducing abundance and diversity of native species and disrupting ecosystem processes (*e.g.*, Elton, 1958; Mooney, 2005; Vilà *et al.*, 2011). Furthermore, invasive species may also have important indirect effects on invaded communities by altering behavior and activity of native species (White *et al.*, 2006). The capacity for invasive organisms to generate both direct and indirect effects is important to understand because these effects may work in concert, leading to strong, often unanticipated effects on native species such as increased apparent competition in addition to direct competition for resources (Orrock *et al.*, 2015). Despite the potential for invasive plants and animals to generate strong direct and indirect effects (Orrock *et al.*, 2010; Vilà *et al.*, 2011; Orrock *et al.*, 2015), few studies have examined how the indirect effects of invasive species affect interactions among native species.

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The invasion of North America by the red imported fire ant, *Solenopsis invicta*, has resulted in substantial ecological impacts, including decreased abundance and diversity of many fauna native to the southeastern United States (Porter *et al.*, 1988; Porter and Savignano, 1990). *Solenopsis invicta* reduces native ant species richness and abundance and alters native ant behavior through competitive displacement (Porter and Savignano, 1990; Morris and Steigman, 1993; Gotelli and Arnett, 2000). *Solenoposis invicta* also affects the survival and distribution of many vertebrate species, including small mammals, birds, and herpetofauna (Killion *et al.*, 1995; Ferris *et al.*, 1998; Allen *et al.*, 2004).

While the effects of *S. invicta* on animals are well documented, *S. invicta* may also play an important role in affecting the distribution and abundance of plants. This role might be especially acute in the context of affecting seed fate. For example, *S. invicta* can directly affect seed survival by consuming seeds that might otherwise be dispersed by native ants (Zettler *et al.*, 2001; Ness and Bronstein, 2004). *Solenopsis invicta* may also alter patterns of seed survival by affecting the behavior or abundance of arthropod and rodent granivores. Small mammals manage the risk of foraging in the presence of *S. invicta* by altering their behavior (Smith *et al.*, 1990; Killion *et al.*, 1995; Ferris *et al.*, 1998) and reducing foraging activity (Holtcamp *et al.*, 1997; Orrock and Danielson, 2004), while abundance and diversity of native ants and other arthropods is decreased by *S. invicta* invasion (Porter and Savignano, 1990; Morris and Steigman, 1993; Gotelli and Arnett, 2000; Allen *et al.*, 2001). Because ants preferentially consume small-seeded species and rodents prefer large-seeded species (Mittelbach and Gross, 1984; Orrock and Damschen, 2005), changes in ant and/or rodent granivory may generate changes in seed survival that lead to shifts in plant abundance and plant community composition (Brown and Heske, 1990; Hulme, 1998; Crawley, 2000; MacMahon *et al.*, 2000; Orrock *et al.*, 2006; Clark *et al.*, 2007) Therefore, understanding how *S. invicta* affect patterns of granivory by native arthropods and rodents may be important for understanding the dynamics of plant species in invaded areas.

We present a study of the direct and indirect effects of *S. invicta* on seed survival by examining the relative influence of rodent and arthropod granivores and proximity to *S. invicta* mounds on predation of small and large seeds. Because initial *S. invicta* recruitment to bait decreases with distance from a mound (Hu and Ding, 2009), we expect *S. invicta* activity also decreases with distance from a mound and therefore hypothesize: (1) survival of large seeds (*i.e.*, seeds too large to be consumed by ants) is greater near *S. invicta* mounds where *S. invicta* activity is higher and rodent foraging activity is lower relative to locations further from mounds, and (2) seed removal by native arthropods and rodents differs between locations adjacent to and away from *S. invicta* mounds, increasing spatial heterogeneity in seed survival.

METHODS

STUDY AREA AND DESIGN

Our study was conducted from 4 August to 5 September 2012, at the Savannah River Site (SRS), an 80,000 ha National Environment Research Park near Aiken, SC, U.S.A (33°21′46.3″N, 81°40′58.5″W). The most common forest types at SRS are forests dominated by longleaf pine (*Pinus palustris*) and loblolly pine (*Pinus taeda*) (Kilgo and Blake, 2005). We conducted our study with eight replicated experimental blocks, each consisting of a 15 m^2 plot of forest. We quantified the effect of *S. invicta* on seed removal by deploying four seed depots at each experimental block (n = 32 depots total). Seed depots consisted of plastic storage trays (17 × 11 x 10 cm) with 5.5 cm holes in two adjacent sides

(Orrock and Danielson, 2004). These openings allowed access by all small rodent species common in our study area (most commonly *Peromyscus gossypinus*, the cotton mouse; Golley *et al.*, 1965). Lids were attached to the top of trays in order to prevent loss of seeds via wind and rain. Lids also prevented foraging by avian seed predators, which, within this study area, have a negligible impact on seed predation compared to predation by arthropods and rodents (Orrock *et al.*, 2003). Depots were deployed in pairs at two distances from a single active *S. invicta* mound: 0.1 m and 4.0 m. We expected *S. invicta* activity would be lower at 4.0 m from a mound, given a previous study demonstrated speed and amount of bait removal by *S. invicta* significantly decreases with increasing distance from a mound (after 1 h, removal of bait at 1.08–1.2 m was 10–31% lower than on the mound; Hu and Ding, 2009). We chose mounds that were active based on the appearance of ants when the mound was gently agitated. Within each depot pair, one depot allowed access by only arthropods while the other allowed access by both arthropods and rodents. Arthropod only depots had 1.25 cm^2 wire mesh secured over each entrance, which allowed arthropods to enter while excluding small mammals. Depots allowing both rodents and arthropods had unobstructed entrances.

    Seeds of two native species, both found in our study area, were used in our seed removal study; one small-seeded species, *Rubus cuneifolius* (sand blackberry, 1.83–2.03 mm; 95% CI, n = 10), and one species with much larger seeds, *Prunus serotina* (black cherry, 5.75–5.91 mm; 95% CI, n = 10). Seeds were obtained from commercial suppliers (Sheffield's Seed Co., Locke, New York, U.S.A. and TheSeedman.com, Vancleave, MS, U.S.A). *Prunus serotina* is consumed primarily by rodents, yet ignored by *S. invicta* and other ants due to its large size and hard seed coat (Whelan *et al.*, 1991; Orrock and Damschen, 2005), whereas *Rubus cuneifolius* is consumed by both arthropods and rodents (Orrock and Damschen, 2005). Neither *R. cuneifolius* nor *P. serotina* seeds bear elaiosomes. We scattered ten seeds of each species on the surface of a layer of commercial sand within each depot. Seed depots were left in the field for 20 d, after which, remaining seeds were counted. Seed removal was considered equivalent to seed predation as is supported by observations of signs of predation (seed fragments) in 25% of seed depots from which seeds were removed and by a study conducted at SRS demonstrating the negative relationship between seed removal and seedling recruitment (Orrock *et al.*, 2003).

DATA ANALYSIS

    Our design is a split-plot design, with distance to the *S. invicta* mound (0.1 m or 4.0 m) as the whole-plot treatment and depot access type as the split-plot treatment (*i.e.*, one depot in the pair allowed access to arthropods, whereas the other depot in a pair allowed both rodents and arthropods). For our analyses of the proportion of seeds removed from seed depots, we used generalized linear mixed models, which treated exclosure type and distance from mound as fixed effects. We treated each site and each pair of depots within a distance from the mound as random effects to appropriately capture the split-plot nature of our design. For analysis of *R. cuneifolius* seed removal, we used a generalized linear mixed model with a binomial response distribution to evaluate the proportion of *R. cuneifolius* seeds removed. The analysis for *R. cuneifolius* fit a fully factorial model that included the interaction of depot access type and distance from a mound. For analysis of *P. serotina*, we did not evaluate the two-factor model because inspection of the data indicated the vast majority of *P. serotina* removal occurred within depots that allowed access to both arthropods and rodents. We conducted follow up analysis to evaluate *P. serotina* removal from only depots allowing both rodents and arthropods, in which we utilized a general linear mixed model with a Gaussian response distribution after transforming the dependent variable (the

proportion of *P. serotina* seeds removed) using the logit transformation (Warton and Hui, 2011). Observations from four seed depots were excluded from analysis due to disturbance by wildlife (n = 3) and failure of rodent exclosure (n = 1). All analyses were performed in SAS version 9.3 (SAS Insitute Inc., 2012); for all analyses, we evaluated residual plots to see that model assumptions were not violated.

<div align="center">RESULTS</div>

Averaged across all treatments, the proportion of *R. cuneifolius* removed from trays allowing access by both rodents and arthropods (0.49 ± 0.09 SE) was higher than the proportion of *P. serotina* removed (0.22 ± 0.10 SE; $t_{27.0} = -2.02$, P = 0.053).

Prunus serotina removal was low across both exclosure treatments and locations relative to *S. invicta* mounds. The *P. serotina* removal that did occur was predominantly from depots that allowed access to both arthropod and rodent granivores (97% of seeds removed were taken from depots allowing both rodents and arthropods). When depots that allowed access by only arthropods were excluded from analysis, the proportion of *P. serotina* did not differ significantly between seed depot locations ($F_{1,6.0} = 1.14$, P = 0.327, Fig. 1).

Removal of *R. cuneifolius* seeds was affected by the interaction between exclosure treatment and seed depot location ($F_{1,24} = 8.73$, P = 0.007, Fig. 1) as well as the main effect of exclosure treatment ($F_{1,24} = 7.24$, P = 0.013). Across both seed depot locations, *R. cuneifolius* removal was 30% higher in depots that excluded rodents, compared to depots that admitted both rodents and arthropods (pairwise comparison, $t_{24} = -2.69$, P = 0.013, Fig. 1). When rodents were excluded from depots, nearly twice the proportion of *R. cuneifolius* was removed at a distance of 4.0 m from a mound compared to the proportion removed 1.0 m from the mound (pairwise comparison, $t_{12.2} = -2.50$, P = 0.028, Fig. 1). At 4.0 m from the mound, 40% more *R. cuneifolius* was removed from depots that excluded rodents compared to depots at 4.0 m which allowed both rodents and arthropods (pairwise comparison, $t_{24} = -3.54$, P = 0.002, Fig. 1).

<div align="center">DISCUSSION</div>

Our results suggest invasive ants generate spatial variation in seed survival, and this variation may be predictable based upon the size of the seed: small-seeded *R. cuneifolius* experienced nearly twice as much removal by arthropods when located far from a *S. invicta* mound than when located near a *S. invicta* mound, whereas the removal of large-seeded *P. serotina* was not affected by proximity to *S. invicta* mounds. The patterns of seed removal observed in our study are likely the outcome of either shifts in abundance or changes in foraging behavior of native arthropods near *S. invicta* mounds in combination with the effects of rodent presence on the availability of small seeds to foraging arthropods. A potential implication of our findings is that, by altering spatial patterns of seed survival (Fig. 1), *S. invicta* may lead to changes in spatial patterns in the recruitment of plant species, just as granivores have done in other systems (Brown and Heske, 1990; MacMahon *et al.*, 2000; Crooks, 2002).

The increase in the removal of small-seeded *R. cuneifoius* away from *S. invicta* mounds may result from an increase in native arthropod abundance and activity in response to decreased risk of *S. invicta* encounter. The speed and amount of bait removal by *S. invicta* decreases as distance from a mound increases (Hu and Ding, 2009) and the boundary between *S. invicta* colonies is often not occupied by *S. invicta*, but instead occupied by native ant species (Tschinkel, 2011). When colony size is controlled for, *S. invicta* possesses inferior foraging
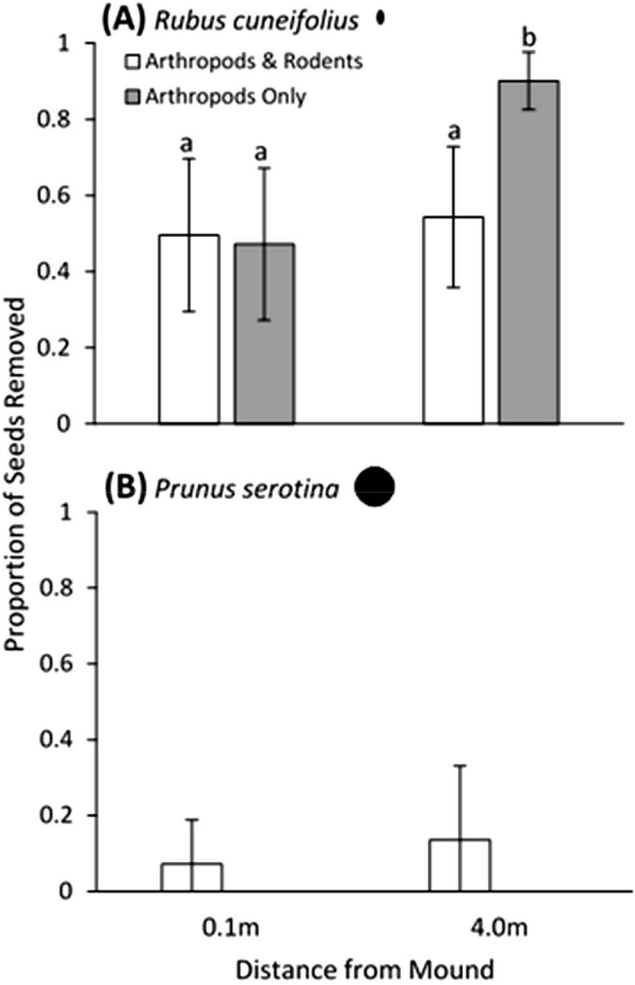
FIG. 1.—The proportion of (**A**) *Rubus cuneifolius* removed by arthropods only or arthropods and rodents from seed depots 0.1 m and 4.0 m from *Solenopsis invicta* mounds and (**B**) the proportion of *Prunus serotina* removed by arthropods and rodents from seed depots 0.1 m and 4.0 m from *S. invicta* mounds. Removal of *P. serotina* from arthropod only trays was excluded from analysis. Error bars represent one standard error above and below the mean. Black shapes next to species names represent the approximate size and shape of a seed of that species. Lowercase letters above bars indicate statistically significant differences in *R. cuneifolius* removal (pairwise comparisons, $\alpha = 0.05$). Logit-transformed values were used in the analysis of *P. serotina* removal, and nontransformed values are presented

ability compared to two native ant species that employ similar foraging strategies (*i.e.*, are omnivorous and use mass recruitment to a food resource), including *Pheidole dentata*, a species found in our study site: *S. invicta* is inferior to *P. dentata* in both foraging distance traveled and number of individuals recruited to bait (Jones and Phillips, 1990). Furthermore, research conducted within our study area found *S. invicta* abundance to be

negatively correlated with native ant abundance and diversity in pitfall traps (Resasco *et al.*, 2014; Orrock, unpublished data). As such, the increase in the removal of small-seeded *R. cuneifolius* that we observed away from *S. invicta* mounds was likely a result of increased abundance and/or foraging activity of native arthropods in the areas between *S. invicta* mounds. In a study of seed removal by *S. invicta*, Seaman and Marino (2003) found where *S. invicta* was the only granivorous ant species present, removal of seeds of pigweed (*Amaranthus retroflexus*) did not differ with distance from a mound (up to 4.0 m). In our study sites, where 45 additional species of ants were present, including many granivorous species (although note that harvester ants, *Pogonomyrmex badius,* were not found in any of our sites during our study; Resasco, unpublished data), we observed increased removal of small-seeded *R. cuneifolius* away from mounds. This further supports the conclusion that increased seed removal away from mounds may be a consequence of competitive displacement of native ants by *S. invicta* (Porter and Savignano, 1990; Morris and Steigman, 1993; Gotelli and Arnett, 2000), or a result of a shift in native ant foraging away from *S. invicta* mounds in order to avoid agonistic interactions. This shift in foraging activity may lead to altered composition and increased heterogeneity in the structure of the plant community. Although further research is needed to test whether the increased heterogeneity in seed survival observed results in heterogeneity in seedling recruitment, previous experimental manipulation of granivore activity has been linked to significant changes in plant community composition (Brown *et al.*, 1979; Brown and Heske, 1990; MacMahon *et al.*, 2000; Orrock *et al.*, 2006).

Our finding of increased seed removal away from *S. invicta* mounds is in contrast with results from studies of removal of elaiosome-bearing seeds by *S. invicta*. Stuble *et al.* (2010) found increased removal of elaiosome-bearing seeds in areas with high *S. invicta* density, without a reduction in seed removal by native ants, and Ness (2004) found no difference in seed removal of elaiosome-bearing seeds between invaded and uninvaded areas. The difference in findings between our study, which evaluated seed species without elaiosomes, and studies of removal of elaiosome-bearing seeds may be because elaiosome-bearing seeds are removed faster and in greater amounts by *S. invicta* compared to nonelaiosome-bearing seeds (Cumberland and Kirkman, 2013). If this is the case, species with elaiosome-bearing seeds may benefit from *S. invicta* (Stuble *et al.*, 2010), whereas the fate of species that produce seeds without elaiosomes may depend upon seed size and the distance to the nearest *S. invicta* mound. However, future study of the effect of distance to the nearest *S. invicta* mound using both seeds with and without elaiosomes would elucidate this potentially elaiosome-dependent pattern in seed survival.

Despite the well-documented negative effects of *S. invicta* on rodent behavior (Smith *et al.*, 1990; Killion *et al.*, 1995; Holtcamp *et al.*, 1997; Ferris *et al.*, 1998; Orrock and Danielson, 2004), we did not observe removal of *P. serotina* varying as a function of location relative to mounds. This may be an indication that rodent foraging is not affected by *S. invicta*, that the density of *S. invicta* is too low in our study site to affect rodent foraging, or that a more preferred seed species was abundant and available to rodents at the time of our study; however, this may alternatively be a result of generally low densities of granivorous rodents in the study area, perhaps because rodent densities within intact longleaf and loblolly forests can be low (Golley *et al.*, 1965). The generally low rates of *P. serotina* removal provide support for the latter explanation, as removal of *P. serotina* by rodents has been much higher (>50%) in studies done in oldfield habitats in our study area (Orrock and Damschen, 2005) where rodent abundance is typically higher (Golley *et al.*, 1965).

The observed increase in seed removal when rodents were excluded from seed depots away from *S. invicta* mounds suggests the potential occurrence of an interspecific interaction between rodents and native arthropods that reduces availability of small seeds to arthropods (*e.g.*, interference competition, rodent burial of seeds). Rodents in our study area may consume arthropods (Gentry and Smith, 1968; Wolfe and Linzey, 1977) that would otherwise consume small-seeded *R. cuneifolius*. Alternatively, rodent foraging activity may displace sand, burying small seeds and protecting them from predation by arthropods, resulting in an inadvertent mutualism between rodents and small seeds; arthropods primarily forage for seeds on the soil surface (Reichman, 1979; Hulme, 1994) and burial has been shown to significantly decrease the probability that a seed will be removed by arthropods (Orrock and Damschen, 2007). Therefore, abiotic and biotic factors that lead to low rodent abundance, such as fire or increased predator abundance, may result in increased indirect effects of *S. invicta* on survival of small seeds.

Through its impact on native species interactions, *S. invicta* creates differences in seed survival that vary with proximity to a mound, increasing spatial heterogeneity. Because the effects of *S. invicta* on seed survival are species-specific, changes in seed survival mediated by *S. invicta* may lead to shifts in plant community composition. While our results indicate rodent presence leads to decreased removal of small seeds by arthropods, our study also highlights the need for future studies that focus on understanding the influence of seed morphology on seed predation by invasive and native arthropods, as well as the mechanisms through which rodent-arthropod interactions lead to changes in seed survival.

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