

Experimental evidence that dispersal drives ant community assembly in human-altered ecosystems

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Abstract. A key shortcoming in our understanding of exotic species' success is that it is not known how post-introduction dispersal contributes to the success of exotic species and the reassembly of invaded communities. Exotic and native species face poorly understood competition–colonization trade-offs in heterogeneous landscapes of natural and anthropogenic habitats. We conducted three experiments that tested how ant queen behavior during dispersal affects community composition. Using experimental plots, we tested whether (1) different types of habitat disturbance and (2) different sizes of habitat disturbance affected the abundance of newly mated queens landing in the plots. The three most abundant species captured were the exotic fire ant *Solenopsis invicta*, and the native species *Brachymyrmex depilis*, and *S. pergandei*, respectively. When queens were considered collectively, more queens landed in plowed, sand-added, and roadside plots than in control or mow plots, in other words, in the more heavily disturbed plots. We also tested (3) the effect of habitat manipulations on the survival of newly mated fire ant queens (*Solenopsis invicta*). Soil disturbance (tilling), lack of shade, and removal (poisoning) of the ant community resulted in the greatest fire ant colony survivorship. Collectively, experiments revealed that both exotic and native newly mated ant queens select open, human-altered ecosystems for founding new colonies. The selection of such habitats by fire ant queens leads to their successful colony founding and ultimately to their dominance in those habitats. Selection of disturbed habitats is therefore advantageous for exotic species but is an ecological trap for native species because they do not often succeed in founding colonies in these habitats.

Key words: biological invasion; disturbance; fire ant; habitat selection; mass effects; *Solenopsis invicta*; species sorting.

INTRODUCTION

Many exotic ant species are invasive and some achieve ecological dominance in their introduced ranges (Holway et al. 2002). Among exotic, invasive ants, the fire ant, *Solenopsis invicta*, is an especially problematic pest species because in addition to ecological impacts, it is economically costly, a public health concern, and has now been spread by humans to all continents except Antarctica (Tschinkel 2006, Ascunce et al. 2011). Ants are an enormously abundant, keystone arthropod taxon with diverse interactions with plants, animals, and soils (Hölldobler and Wilson 1990, Lach et al. 2010). Thus, when dominant exotic ant invaders change the composition of native ant communities, they likely have far-reaching ecological impacts (Holway et al. 2002). Yet, despite decades of research on the ecology of ants, and nearly a century of study of exotic species like *S. invicta*, we lack a

mechanistic understanding of the interactions that lead to exotic species success, native species failure, and, more generally, ant community assembly in invaded ecosystems (Holway et al. 2002, Tschinkel 2006, Cerda et al. 2013).

Interactive processes in ant assemblages are well studied, especially in invaded ecosystems (Holway et al. 2002). Competition between colonies of dominant invasive species, like fire ants and Argentine ants, and native ants can impact the assembly of local communities, partitioning species in space and time, and driving “incompatible,” less competitive native species to local extinction (Hölldobler and Wilson 1990, Porter and Savignano 1990, Sanders et al. 2003, Parr et al. 2005, Lach et al. 2010). But many exotic species, and especially fire ants, are dominant primarily in anthropogenic ecosystems (King and Tschinkel 2006, 2008, Menke and Holway 2006, Fitzgerald et al. 2012). Other environmental conditions, such as disturbance, abiotic conditions, or time since invasion, are likely mitigating competitive exclusion of natives by dominant invasive ants in unaltered ecosystems (Morrison 2002, Heller

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et al. 2008, Lebrun et al. 2012, Cerda et al. 2013, Tschinkel and King 2013). Noninteractive processes, such as dispersal, could prevent exotic species dominance in undisturbed ecosystems, and thus may determine both ant community structure and exotic, invasive ant species impacts. A majority of ant species disperse through some form of mating flights in which winged males and females depart their parent colonies in synchrony, mate, and then the females depart to found colonies individually or in groups some distance away (Hölldobler and Wilson 1990). However, post-mating recruitment and especially dispersal are key aspects of ant community assembly that are largely unknown.

Andersen (2008) hypothesized that exclusion in ant communities as a result of direct competition between mature colonies is probably limited under most circumstances, because many factors can make such interactions unlikely. Instead, processes acting during the dispersal (queens acting on their own) and recruitment (small, young colonies) phase of a colony life cycle may be much more important in ultimately determining ant community structure (Andersen 2008). It is reasonable to assume that ant communities generally exist as metacommunities, where local communities interact by the dispersal of numerous potentially interacting species (Livingston et al. 2013). For metacommunities, community structure emerges from the interaction of processes like competition within a community and processes like dispersal and colonization that occur across and link multiple communities (Leibold et al. 2004, Holyoak et al. 2005). Generalized community assembly models have been proposed to explain species coexistence (Leibold et al. 2004, Livingston et al. 2013). Dispersal is a key factor determining coexistence in all of these models, but dispersal is generally assumed to be random or undirected dispersal of species into habitat patches where other processes (differential mortality, abiotic conditions, competitors or lack thereof) ultimately determine coexistence (Binckley and Resetarits 2005, Resetarits 2005).

A small number of studies have included study of both interactive and noninteractive processes in the assembly of ants communities living as obligate mutualists on ant-plants (Stanton et al. 2002, Yu et al. 2004, Debout et al. 2009). Specialized ant-plant mutualist communities have competition–colonization trade-offs, generally fitting patch dynamics (Leibold et al. 2004), in which competitive exclusion by superior competitors can be mitigated by other species' dispersal abilities, and dispersal as well as interactions at the recruitment stage ultimately determine community structure (Stanton et al. 2002, Yu et al. 2004, Debout et al. 2009). In the best-studied ant-plant mutualist communities (typically 2–4 species), poor competitors disperse to unoccupied trees to avoid competition with superior competitors (Stanton et al. 2002, Yu et al. 2004). This trade-off plays out primarily among

dispersing queens and through competition among young colonies, rather than mature colonies. It also includes lottery-like replacement (i.e., discovery of and recruitment into unoccupied trees) in addition to strict competition–colonization trade-offs (Chesson and Warner 1981, Debout et al. 2009). The few existing studies of dispersal in ant community assembly not conducted in ant-plant systems showed evidence of fit to both species' sorting models (lack of dispersal limitation and differential adaptation among different species leads to "sorting" of species among different habitats) and mass effects models (a form of species sorting with high dispersal rates creating source and sink habitats for certain species) in the community assembly of tropical coffee agroecosystems (Livingston et al. 2013, Livingston and Jackson 2014). Collectively, these studies provide valuable evidence that ant community assembly is dependent upon dispersal and recruitment that link communities separated in space.

Different location and colonization strategies (random, philopatry, habitat selection) during dispersal impact colonization rates of specific habitats as well as linkages (i.e., species interactions) among different habitats (Binckley and Resetarits 2005, 2007) and have been reviewed elsewhere (Resetarits et al. 2005). Here we focus on habitat selection as a potential mechanism structuring ant communities in anthropogenic habitat patches. If habitat selection is prevalent, very different ecological outcomes can be expected when compared with random dispersal followed by differential mortality (i.e., species sorting), because species distributions result from individual choices rather than mortality, and on perceived rather than actual fitness (Binckley and Resetarits 2005, 2007, Resetarits 2005, Resetarits et al. 2005). Events in a species' evolutionary past are assumed to shape a species' perception of fitness and therefore their choices during habitat selection (Resetarits and Wilbur 1989, Binckley and Resetarits 2005).

Redistribution of individuals by directed dispersal, as opposed to differential mortality, have important implications for hypotheses of community assembly because changes in abundance across habitats are not likely to fit classic ecological explanations (Binckley and Resetarits 2005). For example, if immigration and extinction are determined primarily by attractive or repellent habitat characteristics, causing variation in population sizes, factors such as patch size and distance may not be particularly important (Binckley and Resetarits 2005, Resetarits 2005). Thus, habitat selection may also have important implications for exotic species success and native species failure in anthropogenic habitats. The focus of this study is to understand how ant queens distribute themselves among experimentally created habitat patches that mimic either natural ecosystem conditions or different forms of anthropogenic disturbance. Understanding dispersal and colonization patterns among native and exotic

species in anthropogenic habitats has implications for better understanding why exotic species so often dominate human-altered ecosystems while so many native species fail (Seabloom et al. 2003, MacDougall and Turkington 2005, King and Tschinkel 2008). This is a key line of global change research, as human alteration of terrestrial environments for agricultural, silvicultural, and urban infrastructural development now affects >50% of the total land surface of the earth (Steffen et al. 2011, Hooke et al. 2012) while invasive species are simultaneously being translocated at an unprecedented rate (Ricciardi 2007).

The ground-dwelling ant communities of anthropogenic and natural areas in Florida provide a unique opportunity to study habitat selection in natural and anthropogenic ecosystems invaded by a dominant exotic species: in this case the fire ant (*S. invicta*). Previous research has shown that *S. invicta* is absent to rare in unaltered ecosystems with high native ant diversity, but is the dominant species in anthropogenic ecosystems in which native ant diversity is very low (King and Tschinkel 2006, 2008, 2013, King and Porter 2007). The majority of other common exotic ant species show a similar trend but are never as abundant as fire ants (Deyrup et al. 2000, King and Porter 2007). Fire ants compete with some native species, especially *Pheidole morrisi*, commonly the most abundant native species in unaltered ecosystems, but experiments have shown that these two species rarely co-occur because habitat alteration causes local extinction of native species (especially *P. morrisi*), followed by rapid recruitment of fire ants (King and Tschinkel 2008). Thus, competitive exclusion does not explain their distribution. Fire ants decline in abundance as time since habitat disturbance increases, also suggesting that dispersal and recruitment into some early-successional habitats, but not into late-successional habitats, play a key role in fire ant dominance (Tschinkel and King 2013). Collectively, these patterns suggest that habitat selection by queens may play a key role in determining ant community structure in anthropogenic vs. natural areas in this region.

To determine whether habitat selection plays a role in assembling ant communities in longleaf pine (*Pinus palustris*) savannas of northern Florida, we conducted three experiments on how ant queen behavior affects community composition, addressing the following particular questions: (1) Do newly mated queens of native and exotic species choose undisturbed or disturbed habitats? (2) Does the size of a habitat disturbance affect queen habitat selection? (3) What is the ability of newly mated fire ant queens to found colonies and survive in different types of undisturbed and disturbed habitats? (4) What is the effect of an intact native ant community on founding success by fire ant queens? Collectively, these experiments provide a framework for understanding how colonization and recruitment shapes community structure and contributes to trade-offs of species coexistence among ants.

MATERIALS AND METHODS

Study sites

We conducted this study on the eastern side of the Apalachicola National Forest (ANF) in northern Florida ~30 km southwest of the city of Tallahassee. The ANF is the largest intact longleaf pine savanna in the world and a temperate floral biodiversity hotspot (Myers and Ewel 1990). The longleaf pine flatwoods ecosystem where we conducted this study has a slightly undulating topography, and poorly drained, sandy soil (primarily spodosols) (Myers and Ewel 1990). These savanna-like grassland ecosystems have an open overstory of pines (*Pinus palustris* Mill. and *P. elliottii* Engelm.), no understory, and a dense ground cover layer (the dominant species include *Serenoa repens* (W. Bartram) Small, *Ilex glabra* (L.) A. Gray, *Lyonia lucida* (Lam.) K. Koch, *Aristida beyrichiana* Trin. and Rupr., and other herbs [Myers and Ewel 1990, Noss 2013]). In the absence of anthropogenic disturbance or recent fire, ground coverage is often near 80% and is composed of vegetation or pine and grass litter (Lubertazzi and Tschinkel 2003). Bare soil is typically ~20% of ground surface. The sampling area was burned regularly (approximately once every 3 yr), but the experimental plots where our queens were reared (below) were burned 2 yr prior to the experiment and were not burned during the experiments.

Experimental variables

The basis of these experiments was a set of plots that tested two independent variables, habitat manipulation and plot size. Habitat manipulations consisted of mowing, tilling, covering with sand, undisturbed control, and roadside (selected, not manipulated) (Figs 1 and 2). Plot sizes were 100, 10, and 1 m². The dependent measure in all plots was the number of newly mated queens (NMQ) trapped in pitfalls during the 6 months in which the vast majority of local ant species have mating flights and attempt colony founding (J. R. King and W. R. Tschinkel, *personal observation*). This trapping was carried out between May and October in both 2010 and 2011.

Habitat treatments

All habitat treatment plots (except roadsides) were 10 × 10 m in area and were first established in March 2010. Five types of habitat alteration were created as follows: (1) unaltered control plots; (2) mow plots, in which all vegetation was cut at ground level using a gasoline-powered line-trimmer; (3) tilled plots, in which vegetation was first cleared with a line-trimmer and then plowed with a walk-behind rototiller to create loose, turned soil to a depth of ~30–50 cm; (4) sand plots, for which we collected pure sand free of ants and vegetation along forest roadsides and fire breaks

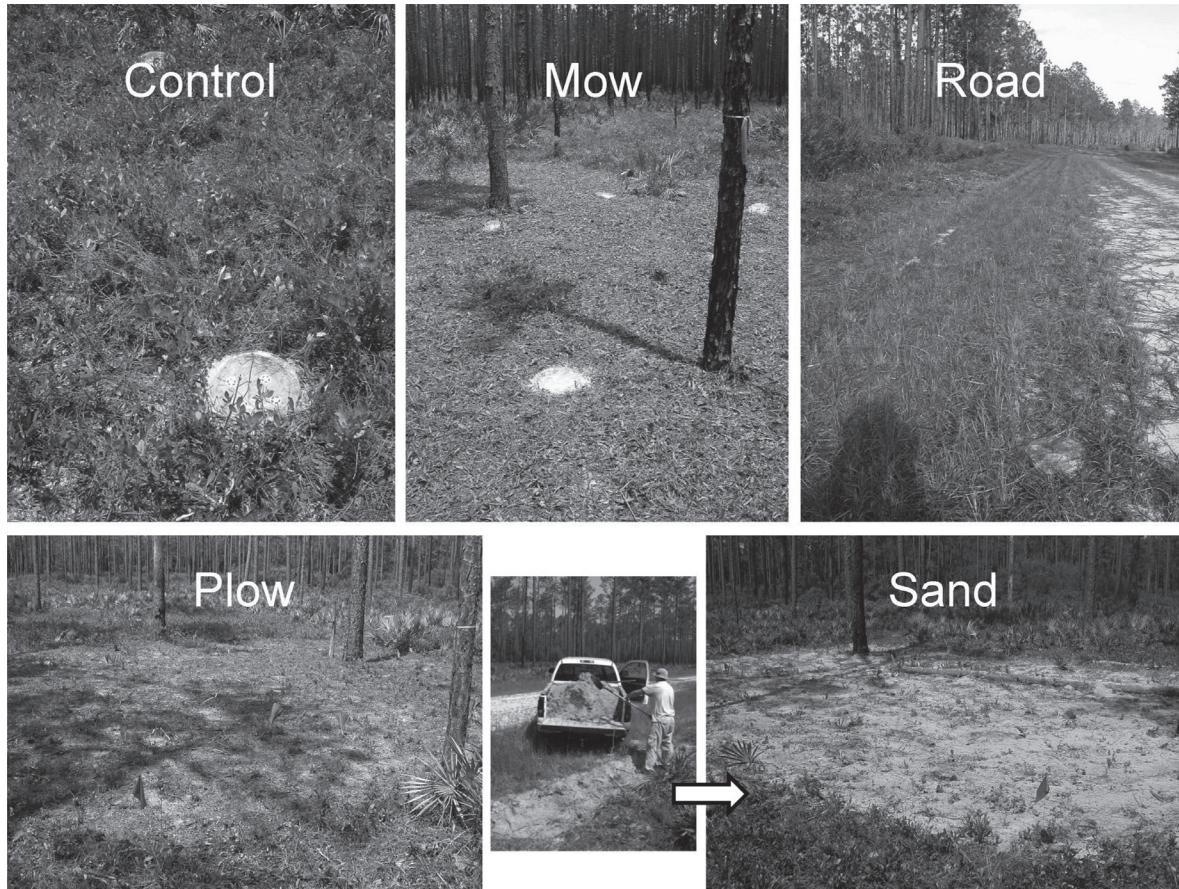


FIG. 1. Five types of habitat alterations used to capture queens in the pine flatwoods ecosystem of the Apalachicola National Forest in north Florida. Control plots were unaltered pine flatwoods. Mow plots were made by cutting all vegetation at ground level using a gas-powered line-trimmer (a weed whacker). Plow plots were made by first clearing vegetation using a line-trimmer and then using a walk-behind rototiller to create loose, turned soil to a depth of ~30–50 cm. Sand plots were made by collecting pure sand free of ants and vegetation along roadsides and fire breaks in the forest, and spreading it to a depth of ~10 cm. In sand plots we carefully raked off much of the debris without disturbing the soil prior to applying sand. Roadside plots were installed along unaltered roadsides on dirt forest roads, which are typically nearly devoid of all vegetation except for a thin ground cover of exotic grasses.

and spread this sand to a depth of ~5–10 cm on plots that we had previously mowed with a line-trimmer and carefully raked free of debris without disturbing the soil (Fig. 1). These plots differed from the mowed plots in that the ground surface appeared as smooth, bare sand, entirely free of ground cover; and (5) roadside plots, which consisted of unaltered, elongated roadside plots along forest dirt roads. These are mowed annually by Forest Service contractors and typically support only a thin ground cover of exotic grasses, or are bare.

All treatment plots except roadside plots were established within the forest at least 50 m from roadsides (Fig. 2). All plots were well within the flight range of queens originating from the dense roadside populations of fire ants (Tschinkel 2006, Tschinkel and King 2013).

This five-treatment design was replicated at five sites separated by 0.1–5 km. Collectively, these treatments

represent a variety of habitat conditions that approximate the broad range of natural and anthropogenic habitats available to queens for post-mating colony founding in this ecosystem.

Size of disturbance treatments

To determine whether the size of a disturbance affects queen site selection we created sand addition plots as in the habitat manipulation experiment previously described, but of two smaller sizes: 1×1 m (1 m^2) and 3.16×3.16 m ($\sim 10 \text{ m}^2$). The 100-m^2 plots served both the habitat manipulation experiment and this plot-size experiment (Fig. 2). At each of the five replicate sites, we installed 20 1-m^2 plots, 5 10-m^2 plots, and 1 100-m^2 plot, with a summed area, respectively, of 20, 50, and 100. Summed over all five replicate sites, there were 100 1-m^2 plots, 50 10-m^2 plots, and

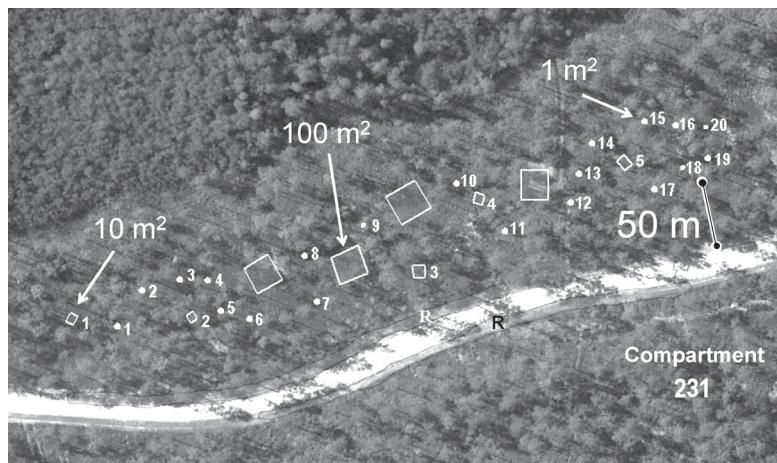


FIG. 2. Typical layout of habitat alteration plots and size of disturbance plots for queen-trapping experiments in the pine flatwoods ecosystems of the Apalachicola National Forest. Plots labeled “R” represent the dirt roadside plots, 1-m² plots are numbered 1–20, and 10-m² plots (small, open squares/rectangles) are labeled 1–5. All plots are well within the known flight dispersal distances of the species present in the fauna.

5 100-m² plots. These sized plots were only created and trapped in 2011.

Queen trapping

Pitfalls are an established and tested method for monitoring the activity and relative abundance of ground-dwelling ants (Bestelmeyer et al. 2000), and can also be used to determine habitat preferences of queens of ground-dwelling ants (Brian et al. 1966, Punttila et al. 1991, 1994, Dekoninck et al. 2008). Whereas worker ants are the usual target of pitfall trapping studies, in our experience queen ants landing upon and moving around on the ground are also clearly trappable (Punttila et al. 1991, 1994). Because such queens are much less abundant than workers, their frequency in traps is also lower, requiring higher trap densities for larger samples.

Pitfall traps were 85 mm long snap-top plastic vials with 30 mm internal diameter inserted flush with the surface of the ground. Traps were installed with a hand-held, battery-powered drill fitted with an auger bit. Traps were covered with a clear plastic rain shield suspended ~10 cm above the ground surface. The vials were capped with a snap-on lid perforated with several 1 cm diameter circular holes (Appendix: Fig. S1) and contained ~15 mm of the preservative propylene glycol antifreeze. The traps were operated for 3–4 weeks, after which they were emptied, refilled with propylene glycol, and reset into the ground. In this way, traps were run continuously for 6 months in both years.

In 2010, pitfall traps were set out in the 100-m² plots in nine arrays of four traps each (36 traps total) per plot. In 2011, the plot-size experiment was added, and the trapping effort was increased to 1 trap/m². However, these were not uniformly distributed, but

were arranged in 25 regularly spaced arrays of four pitfall traps each in the 100-m² plots. The 10-m² plots had 10 pitfall traps arranged in two 4-trap arrays and one 2-trap array placed haphazardly in the plot, and the 1-m² plots had a single pitfall trap (rather than an array of 4) placed in the center of the plot. For each of the five sites of the plot-size experiment, this translated into 20 traps in 1-m² plots, 50 in 10-m² plots and 100 in 100-m² plots, for a sum of 100, 250, and 500 overall replicates. Because the number of traps and the area of each treatment in the plot-size experiment were different, queen captures were converted to queens per square meter for analysis. These plots were sampled from May to October 2011, as previously described.

Pitfalls also captured large numbers of worker ants, and these were used to verify that the trapping method was capturing queens representative of the surrounding ant fauna (Appendix: Table S1). Approximately one-quarter (by mass) of the workers in pooled pitfall samples from August 2011 were haphazardly subsampled, identified to species, and counted. These counts provided a representative snapshot of the ant community present in 2011 (King and Tschinkel 2008).

Soil temperature monitoring

For ground-dwelling ant colonies that begin life as a small, shallow nest, the soil temperature may be one of the most important factors determining how rapidly, or whether, colonies can grow (Hölldobler and Wilson 1990, Tschinkel 2006). To determine the impact of experimental habitat alterations on belowground temperatures, we monitored soil temperatures from 2 May to 26 October 2011, using thermochrons (iButton data loggers by Dallas Semiconductor; Maxim

Integrated Products, San Jose, California, USA) planted at depths of 5, 15, and 30 cm in the center of each 100-m² habitat treatment. One plot of each plot-size treatment was monitored in three of the five site replicates (three sites were too close to warrant sampling separately). These thermochrons logged hourly temperature measurements. The depths included the range of depths that most queens dig to when starting a colony (e.g., fire ants queens dig to an average of ~7 cm depth to found colonies [Tschinkel 1998]).

Fire ant colony survival

Previous observations (Tschinkel 2006, King and Tschinkel 2008) suggested that lack of shading, soil disturbance, and associated removal of ground-covering vegetation, and elimination of the resident ant community, were all factors that favored fire ant populations (Tschinkel 2006, King and Tschinkel 2008). To test the effect of our habitat manipulations on the survival of newly mated queens (NMQs), in May 2012 we established a three-way factorial “ant gardening” experiment in which we planted monogyne (single queen social form) NMQ’s of the fire ant, *Solenopsis invicta*, in 3 × 3 m plots subjected to plowing, shading, and removal of the ant community in all eight combinations. The eight plots were arranged in 4 × 2 arrays with 3-m spacing between all plots in the array, and the arrays were replicated five times (Appendix: Fig. S2). All plots were within the same 3-km² area of the ANF as the queen-trapping plots (described previously), but were ~300 m from the nearest set of queen-trapping plots. The area had been burned in the late spring 2 yr prior to the start of the experiment.

Plots were plowed as previously described for habitat treatment experiments. A 50% shade treatment was created using a lightweight, green-colored, plastic snow fencing with regularly spaced square openings, supported on 3 × 3 m PVC pipe frames (1.27 cm diameter piping) standing 0.5 m above the surface of the ground. The ant community was reduced by treating plots with poison in a granulated bait form (Amdro; Central Garden and Pet Company, Walnut Creek, California, USA) in the early morning and evening of 1 d, 2 weeks prior to planting newly mated queens.

Approximately 1200 NMQs were collected from monogyne (single-queen) fire ant populations in the Tallahassee area along margins of parking lots and roadsides on 28 June 2012 during the first large mating flights of the year. The following day (~24 h after collection) 27 queens were planted in each of the 40 experimental plots (980 NMQs total). In each plot, nine queen pairs were planted together (18 total; fire ant queens often found colonies together) and nine queens were planted individually. Soil was moist due to rain ~48 h earlier and queens were planted in the evening (~1500–1700) to avoid potential overheating due to daytime temperatures and sunlight. Queens were

planted by making a small ~0.5 cm diameter hole to a depth of ~7–10 cm in the soil and placing a fluted PVC ring (tetrafluorethylene, 15-cm diameter, 10-cm height) around the hole to prevent queens from moving. The rings were removed after ~48 h once it was obvious that the queens had entered the hole and closed it, and the site of each founding nest was marked with a small circle of latex paint so that the nests could rapidly be located during subsequent monitoring.

Beginning 2 weeks after planting (queens do not move during the period before their first round of brood becomes workers), these planted nests were regularly checked and monitored approximately every 28–30 days for 120 days. Checks were both visual and by baiting using pieces of Spam (processed meat) in small glass test tubes. Colonies were verified as those that we planted by location and small worker size (mature colonies would have larger workers). The experiment was terminated after 120 days.

Statistical analysis

For the queen-trapping experiments (habitat alteration and plot size), the primary data consisted of the identity and abundance of alate (winged) and dealate (wingless) queens captured in pitfall traps (Appendix: Table S1). The study design was a randomized complete block design with repeated measures because full replicate sets of the habitat and plot-size treatments were located in five different forest compartments (blocks), and each plot was sampled on a monthly basis (repeated measure). Data were analyzed in SAS version 9.4 (SAS Institute 2013) using PROC GLIMMIX. PROC GLIMMIX allows for error terms that are not normally distributed and allows for random effects in models. As data were counts, the response variables (species richness, abundance of queens, and number of colonies) were fit to generalized linear mixed models using normal, Poisson, or negative binomial distribution as best fit the data and checked for overdispersion (Littell et al. 2006). Type III *F* statistics for fixed effects were calculated, which we report here as *F* statistics and associated *P* values (Appendix: Tables S2 and S3). We examined the result of multiple comparisons here as *P* values after Tukey-Kramer adjustment (Appendix: Tables S2 and S3). When analyzing species individually, we viewed any significant treatment effects for sample sizes less than ~10–30 individuals with caution, as very small sample sizes can be problematic for mixed-model designs (Littell et al. 2006). We discuss and consider coefficients with *P* ≤ 0.1 as “marginally significant” (Hurlbert and Lombardi 2009), as this may suggest ecologically meaningful relationships among these variables.

For fire ant colony survival experiments the primary data consisted of the number of colonies surviving

from month to month. We used a nonparametric product-limit (Kaplan-Meier) estimate to compare month by month survival of colonies among different treatments using PROC LIFETEST in SAS. This program tests for differences in survivorship among treatments against a null hypothesis that all groups have the same population survivorship over time. Two tests for homogeneity among survivorship curves for each treatment were applied. The log-rank analysis uses the cumulative difference between observed and expected, while the Wilcoxon test uses the sum of differences between observed and expected events, weighted by sample size (SAS Institute, Cary, North Carolina, USA). Survivorship of colonies was analyzed using colony survivorship measured at 35, 82, and 120 days after “planting” NMQs as described previously.

RESULTS

Over both years of the study, queen trapping captured 1335 queens from 48 species of newly mated queens (NMQs), of which nine were exotic (Appendix: Table S1). Fire ant NMQs were the most abundant exotic species, followed by the predatory species *Strumigenys eggersi* and *S. membranifera* (Appendix: Table S1). *Brachymyrmex depilis* was the most abundant native NMQ followed by *Solenopsis pergandei* and the big-headed ant, *Pheidole morrisi* (Appendix: Table S1). In 2010, 28 species were captured, six of which were exotic. In 2011, 38 species were captured, six of which were exotic. The three most abundant species in both years were *S. invicta*, *B. depilis*, and *S. pergandei*, respectively. In 2010, six species were only captured once

(singletons), and in 2011 14 species were only captured once. In total, the number of queens was dominated by a few species in each year (hundreds of individuals captured, e.g., *S. invicta*, *B. depilis*), several species were moderately abundant (tens of individuals captured, e.g., *P. morrisi*, *S. pergandei*, *C. rimosus*), and most species were rare (fewer than 10 individuals captured; Appendix: Tables S1 and S2).

Habitat

We hypothesized that some species of queens would prefer certain habitat treatments over others, considered against a null hypothesis that species would show no preference for any of the available habitats. In 2010 and 2011, when queens were considered collectively, more queens landed in plowed, sand-added, and roadside plots than in control or mow plots (ANOVA, $P < 0.001$; Appendix: Table S2), in other words, in the more heavily disturbed plots. When grouped, exotic species queens were significantly more abundant in roadside and plow plots in both years, while native species were more abundant in control, sand-added, and plow plots in 2010 but showed no preference in 2011 (ANOVA, $P < 0.001$; Fig. 3; Appendix: Table S2).

When the 28 species captured in 2010 were considered individually, there were treatment effects for four native species and one exotic species (ANOVA, $P < 0.05$) and another two native species and one exotic species were marginally significant (ANOVA, $P \leq 0.1$; Appendix: Table S2). Of 38 species captured in 2011 there were treatment effects for 10 native species and five exotic species (ANOVA, $P \leq 0.05$), and

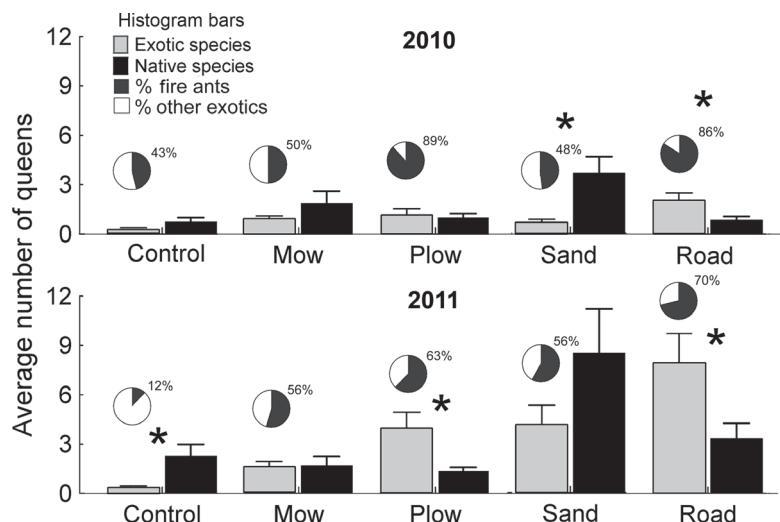


FIG. 3. The average abundance of native and exotic queens landing in 10×10 m plots from May to October in 2010 and 2011. Pie charts and percentages above exotic species box plots represent the percentage of total exotic queens that were fire ants. Significant differences between exotic and native queen abundance ($P \leq 0.05$, Wilcoxon signed-rank test) in each habitat type are indicated by an asterisk. Error bars = +SE.

another two native species were marginally significant (ANOVA, $P \leq 0.1$). For the two exotic species with significant effects of habitat in both years, they were most abundant in road and plow plots (*S. invicta*, *C. rimosus*, *B. patagonicus*; Appendix: Table S2). For most native species that had significant habitat preferences, they preferred plowed, road, or sand sites (e.g., *B. depilis*, *Pheidole morrisi*, *Hypoponera opacior*, *P. dentata*, *P. floridana*, *S. carolinensis*, *Dorymyrmex bossutus*, *Aphaenogaster treatae*; Appendix: Table S2), but three native species were most abundant in undisturbed control plots (*B. depilis*, *S. pergandei*, *Nylanderia parvula*; Appendix: Table S2). Among rare species (<10 individuals captured) there were few significant treatment effects (Appendix: Table S2); however, collectively, 84% of rare species in 2010 and 86% in 2011 landed in disturbed sites (mow, sand-added, plow, and roadside).

There were several significant habitat \times month interactions in these analyses because mating flights of most species were limited to some months in the early to midsummer period, and queens were simply not present in other months. Thus treatment effects could be significant only in the months in which queens flew (Fig. 4; Appendix: Table S2). Inspection of interaction plots confirmed that

treatment effects were therefore valid, but only in months in which queens were abundant (J. R. King, unpublished data).

As a group, exotic species appeared to fly and found earlier in the year than native species (Fig. 4). Inspection of individual species peak abundance times suggest that the pattern was driven primarily by *S. invicta*, which was always most abundant in May and June (Appendix: Table S2). Other exotic species showed no clear preference for flying earlier or later (Appendix: Table S2). Collectively, the abundance of exotic NMQ's peaked in late spring and early summer, whereas the abundance of native NMQ's peaked in mid- to late summer (Fig. 4; Appendix: Table S2).

The experimental habitat alterations affected below-ground temperatures. Open plots with less vegetative cover (roadsides and plowed plots) had much higher daily maximum temperatures than control plots (Fig. 5). The more densely vegetated control plots consistently had the lowest daily maximum and minimum temperatures. Interestingly, sand addition plots, although appearing bare, were cooler than plowed or roadside plots, probably because of their higher albedo. In all cases, daily temperature variation was greater at shallower depths (Fig. 5).

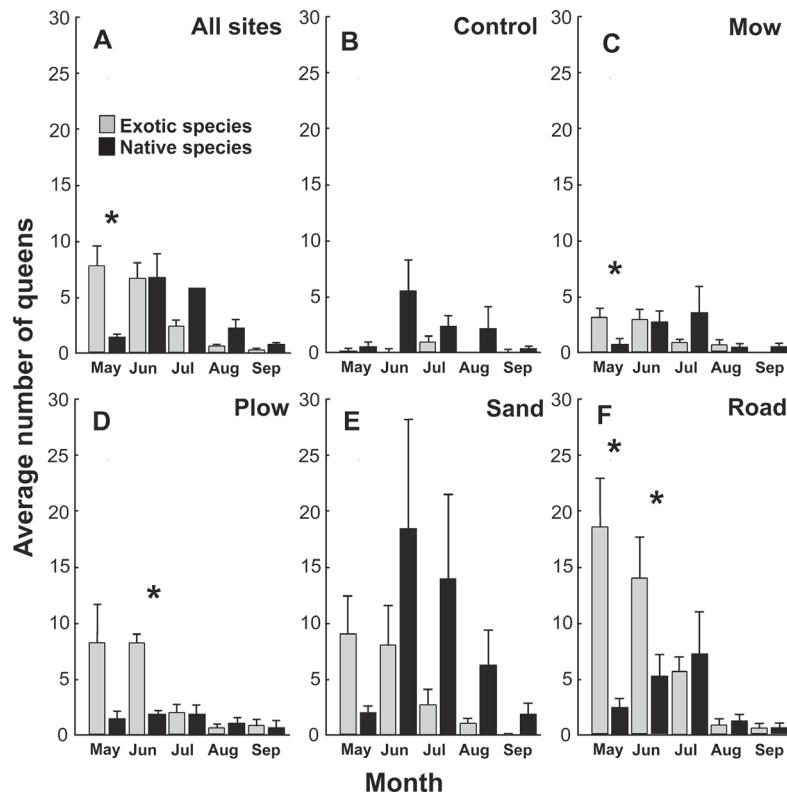


FIG. 4. The average abundance of native and exotic queens trapped per month in 10×10 m plots from May to October in 2011. Significant differences between exotic and native queen abundance ($P \leq 0.05$, Wilcoxon signed-rank test) in each habitat type are indicated by an asterisk. Error bars = +SE.

Size of disturbance

We hypothesized that larger habitat disturbances would be more apparent and therefore more attractive, and would receive more queens per unit area than smaller ones, and that this might vary by species. When queens were considered collectively, there was no effect of plot size on the mean number of queens per unit area, and this was also true when grouped as native and exotic (Fig. 6; Appendix: Table S3). When species were considered individually, a few species were affected by plot size (Appendix: Table S3). Among natives, *D. bossutus* most frequently landed in 10-m² and 100-m² plots, while *D. bureni* landed most frequently in 10-m² plots (ANOVA, $P \leq 0.05$; Appendix: Table S3). There were five species that showed marginally significant preference for plots of different sizes (ANOVA, $P \leq 0.1$; Appendix: Table S3). Of these, one species, the native *Polyergus lucidus* was most abundant in the 1-m² plots, while the native *B. depilis* landed most in 1-m² and 100-m² plots

(Appendix: Table S3). Among the other three marginally significant species, the exotic *S. invicta* was most abundant in 100-m² plots, while the natives *S. pergandei* and *Temnothorax pergandei* both landed most frequently in 10-m² and 100-m² plots (Appendix: Table S3).

Fire ant colony survival

In the third experiment, we hypothesized that newly mated fire ant queens would be more successful founding colonies in disturbed habitats and/or with the ant community removed, considered against a null hypothesis that disturbance and co-occurring ants would not affect colony founding success. Survival of fire ant NMQs over 120 days was greatest in plots that were tilled, without shade, and treated with insecticide (Fig. 7; test for homogeneity of survival curves, log-rank test, $P = 0.002$, Wilcoxon test, $P < 0.001$; Appendix: Table S4). Almost all queens died within the first 120 days: only five out of 980 colonies planted, or 0.51%, survived (Fig. 7).

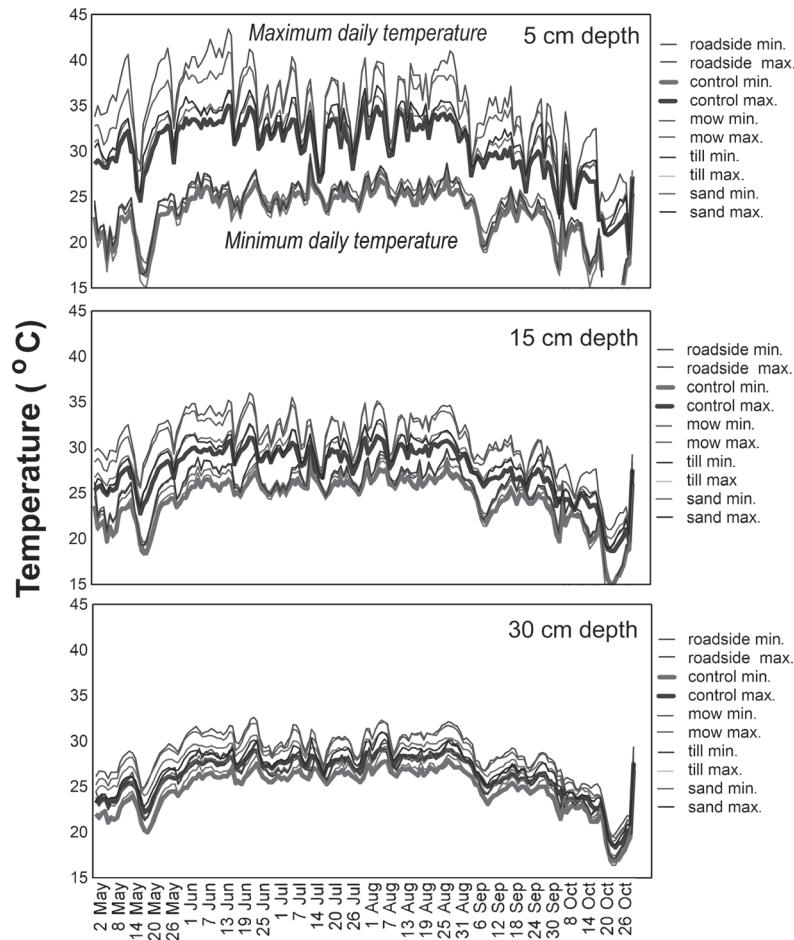


FIG. 5. Average daily maximum and minimum temperatures at 5, 15, and 30 cm depth in experimental queen-trapping plots during 2011.

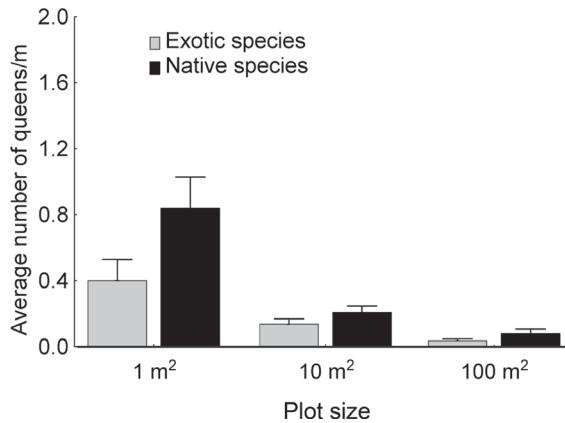


FIG. 6. The average abundance of native and exotic queens/ m^2 landing in different-sized disturbance plots from May to October 2011. Plots were created by spreading loose sand to a depth of ~ 10 cm on plots where we had previously trimmed vegetation and carefully raked off much of the debris without disturbing the soil. Error bars are $+1$ SE.

DISCUSSION

Dispersal ability may be the most important biological trait determining species success under current and future land use and climate change scenarios (Zarnetske et al. 2012, Urban et al. 2013). Understanding how species dispersal shapes community structure in intact and human-altered ecosystems is therefore critical. In sum, these experiments showed

that dispersal, particularly directed dispersal or habitat selection by both exotic and native ant species, is a mechanism underlying ant community assembly. Consequently, it plays a key role in establishing the dominance of the fire ant, *S. invicta*, in anthropogenic ecosystems.

Because exotic species are so often associated with disturbed habitats, we hypothesized that exotic species would more often select disturbed plots than native species. Roadsides, plowing, and mowing were selected as landscape disturbance treatments because they approximate the first steps in the process of land use change, i.e., road-building, vegetation clearing, and soil excavation, associated with human activity. These land use changes are an effective measure of the human activities that positively correlate real estate development with the establishment, dispersal, and spread of many exotic and invasive species, including many ant species (Taylor and Irwin 2004, King and Tschinkel 2008). There were individual species that actively selected habitat and others that showed no preference (Appendix: Table S2). Both exotic and native ant species, specifically the most common species, showed strong evidence of habitat selection (Fig. 3; Appendix: Table S2). For fire ants, human-altered sites are the likely source for the small number of queens that disperse into natural areas (where fire ant populations are very small) as well as the source for dispersal into other human-altered sites (where fire ant populations are large [King and Tschinkel 2008]). For common native species, natural areas are the likely source for queens (where their populations are large) and human-altered sites are the sink (where their populations are small, but where a majority of their queens disperse) (Appendix: Table S2 and King and Tschinkel 2008).

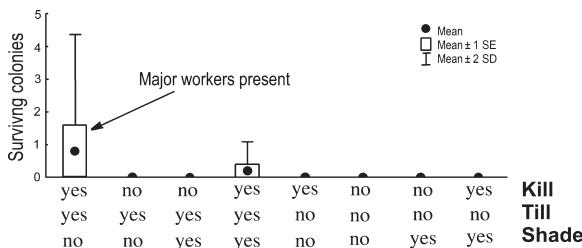


FIG. 7. The average number of surviving fire ant (*S. invicta*) colonies 120 days after establishing newly mated queens (NMJs) in 3×3 m experimental plots. Plots were set out in arrays that contained a full replicate set of all combinations of plowing (Till), shading (Shade), and ant community removal (Kill). Treatments affected the survival of NMJs (test for homogeneity of survival curves: log-rank test, $P = 0.002$, Wilcoxon test, $P < 0.001$, Appendix: Table S4). Removing the ant community using pesticide and a lack of artificial shading resulted in the highest survivorship over 120 days, while tilling without shade and the ant community removed resulted in the greatest fire ant colony survivorship (nonzero results). Major fire ant workers only appeared in plots with the soil plowed, the ant community removed, and with no shading. In the final check of colonies at 120 days, a large, mature *S. invicta* colony was located some distance (~ 5 m) from one of the kill, till, no shade plots. In this plot we had multiple bait cards occupied, including by large major workers. As we had previously detected four colonies on that plot and could not determine with certainty the source colonies of all of the foraging workers (although we did confirm one small colony), we counted four colonies on the plot again.

Only three native species, *B. depilis*, *S. pergandei*, and *N. parvula*, showed preference for founding in undisturbed, control plots (Appendix: Table S2). In contrast, all of the remaining most abundant species in both years (tens to hundreds of individuals) showed preference for some level of habitat disturbance. The lack of evidence for habitat selection by rarer species (fewer than 10 individuals sampled), was probably a consequence of very small sample sizes (Littell et al. 2006). For rare species producing few queens, it is possible that species sorting is occurring (random dispersal followed by differential mortality) or that low sample sizes prevent detection of habitat selection. Nevertheless, even if many rare species are landing in plots in proportion to their availability rather than their habitat types, we would expect 80% of rare species to choose disturbed plots, because these make up 80% of the total plot area. We found that collectively rare species landed in the four types of disturbed plots (as opposed to control plots) 85% of the time. It follows that in a landscape dominated by human-altered ecosystems, the majority of nonselective species queens

are dispersing into disturbed habitats. In combination with species that are actively selecting human-altered ecosystems, this leads to a majority of the queens produced in a community dispersing into human-altered, disturbed habitats (Figs 3 and 4).

Mating and colony founding comprise two of the most challenging phases of the ant colony life cycle. For independently founding ants, this is a period of great vulnerability and high mortality, and this stage likely intensively selects queen behavior for successful founding. Selection operating at this stage likely shapes the “perceived” value of habitat resulting from evolutionary history for ant species (i.e., fitness consequences), and has resulted in habitat selection behavior by queens (Binckley and Resetarits 2005). In spite of the importance of the founding stage, it has rarely been studied for most ant species (Hölldobler and Wilson 1990), although more is known about colony founding in *S. invicta* and some other species (Kannowski 1959, Johnson 2000, Tschinkel 2006). In one of the few studies of habitat selection by queens, Wilson and Hunt (1966) visually directly observed very obvious instances of habitat selection (open fields vs. woodland) by dispersing queens of *Lasius neoniger* and *Solenopsis molesta* after mating flights. These species thus showed strong fidelity to the man-made and naturally open habitats (early-successional fields) in which they are normally found in the northeastern United States. This pattern of queens selecting early-successional habitats may be common in temperate ant assemblages (Pontin 1960, Brian et al. 1966, Puntila et al. 1991, 1994), and has even been shown in subtropical species (*Atta laevigata* [Vasconcelos et al. 2006]). The selection of open habitats by dispersing species may generally confer an advantage for growth and development of any poikilothermic species (experimentally demonstrated now for frogs, beetles, and ants), and thus abiotic conditions may be one of the primary driving forces selecting for habitat selection (Resetarits et al. 2005). This may be especially important for thermophilic social insect species, like ants, whose life history strategy depends upon rapid colony growth in the early stages of the colony life cycle (Andersen 1997).

Seasonally, earlier colony founding in open habitats could confer an advantage in attaining larger colony sizes within the first year of growth due to higher soil temperatures (Fig. 5). In the specific case of *S. invicta*, NMQs were always most abundant in May and June (Fig. 4; Appendix: Table S2), earlier than other species. Monogyne (single-queen social form) fire ant queens found colonies by digging to a depth of ~7 cm (Tschinkel 1998), a depth that would provide temperatures at or above 30°C for much of the day in roadside and plow plots from June to October. This temperature is noteworthy because fire ant brood development rate is maximal at ~32°C under laboratory

conditions (Porter and Tschinkel 1993). Even daily minimum temperatures in these plots were near 30°C, in contrast to the lower minima in sand and control plots (Fig. 5).

We hypothesized that larger habitat disturbances would be more detectable and thus more attractive to queens. Overall, results were equivocal, as most species showed no evidence for selection of larger or smaller plots (Fig. 6). There was only weak evidence that the size of the disturbed habitat matters for species that landed in those plots (Fig. 6; Appendix: Table S3) as long as it was at least 1 m² or greater in size. Thus, even 1 m²-sized plots are not too small to be detected by queens that prefer disturbed sites (e.g., fire ants), and those species also do not discriminate between large or small disturbances at 1 m² or larger in size (Fig. 6; Appendix: Table S3). The ability to detect favorable habitat even at the scale of 1 m² is not particularly surprising, as other ant species have shown preference for habitat features at that size scale, or smaller (e.g., stumps [Brian 1952]).

Fire ant queens clearly preferred founding colonies in roadside, plowed, and sand-added plots (Appendix: Table S2). It could be argued that this outcome is a consequence of queens dispersing only very short distances, thus recruiting into their natal habitats (philopatry) and maintaining already large populations (for example, fire ants along roadsides). However, given that the distances between likely source populations of fire ants (roadsides) and experimental plots (Fig. 2) are well within known dispersal distances of fire ants (Tschinkel 2006), habitat selection seems the more likely cause for fire ant preference for disturbed plots and consequently a major contributor to their dominance in altered habitats. Further support can be found in the queen-rearing experiments. We hypothesized that newly mated fire ant queens would be more successful founding colonies in disturbed habitats with the ant community removed. This is a specific version of a general hypothesis that exotic species are more common in human-modified ecosystems because they are better adapted to conditions that distinguish those habitats from other native habitats. Results suggest that first, the vast majority of NMQs fail to start colonies, even under conditions of warm temperature and moist soil, and second, failure is almost certain for those NMQs in sites with shade and an intact ground cover and ant community (i.e., intact ecosystems) (Fig. 7; Appendix: Table S4). Only queens that found under a reduced ant community and no shading have a chance at survival (Fig. 7). In addition to abiotic conditions, predation of queens by the resident ant community cannot be ruled out as a factor affecting survival (Hölldobler and Wilson 1990). However, predation of founding queens by established colonies may only eliminate ~10% of founding queens (Billick et al. 2001), and even if there are higher rates of predation

by ants and other arthropod predators in early-successional habitats, they are unlikely to offset the high colonization rates for species selecting this habitat (Vasconcelos et al. 2006). Therefore, for this invasive species, we favor the hypothesis that selection of human-altered ecosystems by fire ants is an example of ecological fitting (Janzen 1985) driven primarily by favorable abiotic conditions. This conclusion is further supported by long-term observations in this study area showing the decline of fire ant colonies during habitat succession from mowed and plowed back to pine savanna, but persistence in maintained human-altered ecosystems (roadsides [Tschinkel and King 2013]).

Some of the most abundant native species NMQs such as *P. morrisi*, *D. bossutus*, and *B. depilis* showed preference for anthropogenic sites but have relatively low abundance of colonies (small populations) in those sites (King and Tschinkel 2008 and Appendix: Table S2). To illustrate the discrepancy, consider that fire ants (*S. invicta*) comprise ~75% or more of total ant abundance (as measured by worker abundance in pitfall traps) in anthropogenic habitats in this region, but only ~1% in undisturbed sites, whereas *P. morrisi* comprises ~40% of the ants in undisturbed sites and ~10% or less in anthropogenic habitats (King and Tschinkel 2008). For fire ants there is a close match between queen site choice and overall worker abundance in the site type, while the opposite is true for the native *P. morrisi*, which is typically the most common and abundant native ant in pine savannas in Florida (King and Porter 2005, King and Tschinkel 2008). Given their dispersal patterns, a key question then becomes, is the inability of some native species to increase population size in disturbed habitats driven more by habitat conditions for founding queens (e.g., Fig. 3) or competition with fire ants after founding?

Previous work by King and Tschinkel suggests that experimental removal of fire ants from ecosystems in which they are dominant does not result in recruitment of most native species into those sites (King and Tschinkel 2006, 2013). Furthermore, in the absence of fire ants, native species like *P. morrisi* decrease in population sizes in sites that were experimentally plowed or mowed (King and Tschinkel 2008). This suggests that the effect of human disturbance on the assembly of native ant communities is not driven primarily by the mere presence or absence of fire ants (King and Tschinkel 2006, 2008, 2013). In contrast, the overwhelming success of fire ants in disturbed habitats can be attributed to attraction to these habitats during dispersal, followed by successful colony founding in the absence of native species (Figs 1 and 2). In contrast, many native species remain dominant in unaltered ecosystems, but despite preferring some kinds of disturbed sites, seem unable to increase in abundance there, even in the absence of fire ants (Figs 3 and 5 [King and Tschinkel 2008]).

To put this into perspective, the ANF (a forest approximately the size of Rhode Island) has ~1600 km of unpaved roads. Fire ants have occurred at high densities along most road margins for >50 yr. Despite the presence of this enormous source population, they are largely absent in the native ground cover, even very near the roadsides (Tschinkel and King 2013). Conversely, native species occur in low abundance along the same roadsides, but are abundant within undisturbed habitats (King and Tschinkel 2008, Tschinkel and King 2013) and have been so in this region even prior to the arrival of fire ants (Van Pelt 1947, 1956). Thus, the inability of many of the most abundant native species to persist in human-altered ecosystems (King and Tschinkel 2006, 2008), despite NMQs preferring to found colonies in them, suggests that these ecosystems are acting as a widespread ecological trap (Gates and Gysel 1978, Schlaepfer et al. 2002) for native ant species (Fig. 4).

More broadly, results contribute to our understanding of community assembly by showing that behavior during dispersal can generate patterns of distribution and abundance at multiples scales (Resetarits 2005) and that same behavior is contributing to success of exotic species (Holway and Suarez 1999). Selection of anthropogenic habitats by exotic species can explain their success in those habitats and provides a critical link between the dynamics of exotic species populations at the local scale and their impacts at regional scales. For ant communities, results suggest that community assembly is driven by dispersal by queens and recruitment of young colonies (Andersen 2008, Debout et al. 2009), and these same processes likely underlie ant metacommunity dynamics at the landscape scale.

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