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Attachments

Turtle Island Restoration Network Comments on Turkey Point Expansion, NRC-2009-0337, 2009-02417 (SP-MLC)

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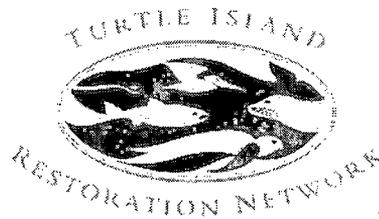
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Add= *A. Williamson (ARW)*



Cindy Bladey
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May 22, 2015

Re: Comments on Turkey Point Expansion, NRC-2009-0337, 2009-02417 (SP-MLC)

Dear Ms. Bladey and Ms. Clouser,

On behalf of the Turtle Island Restoration Network, our over 6,300 members and our over 120,000 activists, we offer the following comments on the Draft Environmental Impact Statement (DEIS) for Combined Licenses (COLs) for Turkey Point Units 6 & 7, released by the Nuclear Regulatory Commission (NRC) under Docket ID NRC-2009-0337 and as publicly noticed by the U.S. Army Corps of Engineers (Corps), 2009-02417 (SP-MLC). We wish to add our support to the comments of the National Parks Conservation Association, Center for Biological Diversity, Miami Waterkeeper, South Florida Wildlands Association, and Tropical Audubon Society and hereby incorporate those comments here. We share these critical concerns regarding the serious environmental impacts of this project.

In addition, we are deeply concerned that the DEIR has not analyzed the full ecological

impacts of development and road construction in increasing the exposure of local ecosystems to invasive species. South Florida is already battling against a wider range of invasive species, and is now particularly vulnerable to impacts of these species. Consequently, the cumulative impacts of this project must be viewed as all the more significant given the dire existing conditions. Roads and development have been demonstrated to increase the susceptibility of ecosystems to invasive species,¹ such as fire ants² and invasive *Melaleuca* trees.³ Not only are disturbed areas uniquely susceptible to establishment of invasive species,⁴ but they also act as corridors to facilitate and accelerate ongoing invasions.⁵ Given the significant ecological impacts of this project in addition to those elaborated upon in our other comment letter, it would be premature to issue any COLs for the proposed project.

Respectfully submitted,



Todd Steiner
Executive Director



Doug Karpa
Legal Program Director

¹ Resasco, J., Haddad, N.M., Orrock, J.L., Shoemaker, D., Brudvig, L., Damnschen, E., Tewksbury, J., Levey, D. (2014) Landscape corridors can increase invasion by an exotic species and reduce diversity of native species. *Ecology* 95:2033-2039.

² *Ibid.*, Forsy, E.A., Allen, C.R., and Wojcik, D. (2002) Influence of the proximity and amount of human development and roads on the occurrence of the red imported fire ant in the lower Florida Keys. *Biological Conservation* 108:27-33.

³ Tsai, F., *et al.* (2005) Remote detection of invasive *Melaleuca* trees (*Melaleuca quinquenervia*) in South Florida with multispectral IKONOS imagery. *International Journal of Remote Sensing* 26: 1057-1063. DOI: 10.1080/01430060512331314119.

⁴ Stiles, J.H., and R.H. Jones (1998) Distribution of the red imported fire ant, *Solenopsis invicta*, in road and powerline habitats. *Landscape Ecology* 335:335-346.

⁵ Wilson, J.R.U., Dormontt, E., Prentiss, P.J., Lowe, A.J., and Richardson, D.M. (2009) Something in the way you move: dispersal pathways affect invasion success. *Trends in Ecology and Evolution* 24: 136-144.



Distribution of the red imported fire ant, *Solenopsis invicta*, in road and powerline habitats

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Key words: ant abundance, corridor, exotic species, invasion, powerline cuts, roads, *Solenopsis invicta*, spatial pattern

Abstract

For early-successional species, road and powerline cuts through forests provide refugia and source populations for invading adjacent forest gaps. Within an 800 km² forest matrix in South Carolina, we determined if width, disturbance frequency or linear features of road and powerline cuts influenced the mound distribution of the red imported fire ant, *Solenopsis invicta* Buren. For each of five linear habitat types, differing in width and disturbance frequency, we mapped all mounds located within ten 500 m segments. Mean mound density was lowest in narrow, infrequently-disturbed closed-canopy dirt road habitats (8.8 mounds/ha). For types with an opening in the forest canopy (i.e., open dirt road, gravel road, paved road and powerline cut), mean mound density was highest in narrow habitats where disturbance was intermediate (open dirt roads, 86.5 mounds/ha). It was lowest in wide habitats where disturbance was infrequent (powerline cuts, 27.6 mounds/ha). Mean mound size was greater in infrequently-disturbed powerline cuts than in frequently-disturbed paved roads. Mounds were located significantly closer to road or forest edges than expected by random. In all types except dirt roads, mounds were more common toward northern edges, and more so as the orientation of the linear habitat changed from north/south to east/west. These data suggest that narrow, disturbed habitats are more suitable for fire ant establishment and success than wider ones, and that the distribution of fire ants in linear habitats is not as uniform as it has been shown to be in pastures. A decrease in roadside disturbance and an increase in shade, especially along the northern edge, may result in lower fire ant mound density in these linear habitats.

Introduction

Linear habitats, such as road and powerline cuts, embedded within a forest matrix may provide suitable habitat for early-successional or disturbance-oriented plants and animals amidst an otherwise uninhabitable landscape (Bennett 1991; Forman 1995; DeMers 1993; Warner 1992). They may also serve as barriers (Merriam et al. 1989; Mader 1984), dispersal corridors (DeMers 1993; Vermeulen 1994; Getz et al. 1978), and invasion routes (Lewis 1991; Amor and Stephens 1976) for many species. For the red imported fire ant, *Solenopsis invicta* Buren, road and powerline cuts may provide not only primary habitat but also a refugia

or source population for dispersal into adjacent forest gaps.

Southeastern U.S. forests are fragmented by a shifting mosaic of early-successional forest gaps caused by logging practices and by a reticulate pattern of linear, early-successional habitat, or corridors (Forman 1995; Rich et al. 1994; Kroodsma 1982), in the form of road and powerline cuts. Unlike forest gaps, these linear habitats are maintained in an early-successional stage by anthropogenic disturbance such as mowing or burning. Additionally, they are typified by higher degrees of edge environments and shading than non-linear gaps (Reed et al. 1996; Kroodsma 1982). *Solenopsis invicta* frequently colonizes both logged gaps and road and powerline habitats. In

logged gaps, populations persist for the first five to ten years of reforestation (personal observations). The prevalence of the more permanent road and powerline habitats ensures that few logged gaps lack nearby refugia or source populations of fire ants. However, if some road and powerline cuts provide better fire ant habitat than others, then the structure of the linear habitat network may determine the rate and degree of fire ant invasion into forest gaps.

Solenopsis invicta is a notorious pest species that has strong effects on other organisms. Native ants are frequently displaced through competition (Tschinkel 1987; Porter and Savignano 1990; Camilo and Phillips 1990; Morris and Steigman 1993; Porter et al. 1988), and total arthropod diversity and abundance are often reduced when *S. invicta* is abundant (Teddars et al. 1990; Reagan 1986). Fire ants are also predators of the young of birds, small mammals, and reptiles (Allen et al. 1994).

The potential impacts of *S. invicta* are exacerbated in areas where mounds are abundant (W.R. Tschinkel, personal communication). Because mound volume is positively related to the number and biomass of ants in a mound (Tschinkel 1993), the impacts are also stronger where mounds are large. Fire ants have been shown to be abundant in open habitats where the soil has been disturbed by agricultural practices, logging, or vehicles (Tschinkel 1986; Porter and Savignano 1990) and where direct sunlight can reach the soil surface (Brown 1980). They are rare in shaded or undisturbed habitats such as forests (Tschinkel 1987; Summerlin 1976; Maxwell 1982).

The objectives of our study were to determine whether the abundance, size, or spatial distribution of *S. invicta* mounds varied among five linear habitat types. We hypothesized that mound density and volume are related to habitat width and to the frequency of direct mound disturbance, and we predicted that mound density and volume would increase with width but would decrease with decreasing disturbance frequency. We also hypothesized that the spatial distribution of mounds is related to linear features of the habitat such as edges and would therefore be less uniform than the mound distribution in pastures.

Wide road and powerline cuts may be preferred by fire ants for two reasons. First, wide habitats have a larger area that is not shaded by the adjacent forest canopy. Secondly, dispersing alates respond to reflectance and vegetation cues from the ground (Maxwell 1982). Therefore, wide habitats may be easier to locate than narrow ones.

Although initial large-scale disturbances such as logging, burning, mowing or tilling often precede fire ant establishment, extremely frequent and direct disturbance to the mound as a result of continued burning or mowing may limit the size and abundance of mounds. For this reason, early-successional habitat with low levels of direct disturbance to the mounds may have higher mound density and volume than those that are mowed or burned more often.

Studies of the spatial distribution of *S. invicta* mounds are few and have been performed mainly in pastures, where mature mounds have an approximately uniform distribution due to intraspecific competition (Adams and Tschinkel 1995; Baroni Urbani and Kanno 1974). Edges, which predominate in linear habitats, are often areas where levels of light, temperature, litter moisture, humidity, and species diversity change abruptly (Matlack 1993; Yahner 1988; Wales 1972). Fire ants may be attracted to or repelled by the edge environment and either target it for mound construction or avoid it. For this reason, the spatial distribution of mounds within linear habitats may be related to the presence or orientation of edges and be less uniform than it is in pastures. Furthermore, like mound density and mound volume, mound distribution may vary with habitat width and disturbance frequency.

Methods

This study was conducted at the Savannah River Site (SRS) in the coastal plain of South Carolina. SRS is an 800 km² national environmental research park forested primarily by longleaf (*Pinus palustris*), slash (*Pinus elliottii*), and loblolly (*Pinus taeda*) pines. The area was probably invaded by *S. invicta* in the early 1970's (Buren et al. 1974; Wojcik 1983). A network of several linear habitat types fragments the forest matrix. In this study, we examined five types distinguished by width and disturbance frequency: powerline cuts, paved roads, gravel roads, open dirt roads (i.e., the forest canopy did not extend into the center of the road), and closed-canopy dirt roads. The roadsides (i.e., the vegetated strip between the road edge and the forest edge) of the paved, gravel and open dirt roads were predominantly grassy. The roadsides of the closed-canopy dirt roads were sparsely vegetated and were covered with pine needles or leaves, and the powerline cuts were vegetated primarily by tall herbaceous species.

Disturbance regimes in each habitat type were obtained from the USDA Forest Service Savannah River Forest Station and verified by observation. In powerline cuts, vegetation was burned or sprayed with herbicide once every five years. Vegetation in the paved roadsides was mowed as needed (usually three or more times per year). Gravel and open dirt roadsides were mowed approximately twice per year. Closed-canopy dirt road habitats were disturbed only by occasional vehicular traffic. Because of the disturbance regimes, the height of the vegetation in October 1996 averaged 12 cm in the paved roadsides, 25 cm in the gravel roadsides, 30 cm in the open dirt and closed-canopy dirt roadsides, and 100 cm in the powerline cuts.

The habitat types varied in their suitability for fire ant establishment. The powerline cuts used in this study did not contain service roads. Therefore, the entire cut was equally available for fire ant colonization. In paved and gravel road habitats, fire ants were not able to colonize the asphalt or gravel and were therefore restricted to the roadsides. The roads in the dirt road habitats consisted of two compacted tire tracks interrupted by a less-compacted, vegetated median. Fire ants could colonize the roadsides and the median but not the tire tracks.

For each habitat type, we randomly chose ten vectors radiating from the center point of the roughly circular SRS and located the 500 m road or powerline segment closest to the end of each vector. Segments that intersected or were adjacent to forest stands younger than fifteen years or other early-successional habitats were disqualified and new segments were chosen. All chosen segments were located in upland, sandy soils dominated by Fuquay and Blanton sands (USDA 1990).

During October 1996, we surveyed each of the fifty segments (ten segments per type) for all active *S. invicta* mounds greater than 10 cm in diameter. We excluded smaller mounds because their size suggested recent establishment. New colonies experience high rates of attrition (Lofgren et al. 1975; W.R. Tschinkel, personal communication), and we chose to exclude mounds that might not persist through the year. Mound activity was determined by observing loose dirt on the mound and by digging into the mound and noting the presence of ants. Temperatures during sampling were moderate (20°–30 °C), and ants were active and near the surface of the mounds. We measured the dimensions of each mound surveyed, and we estimated mound volume using the formula for half of a sphere (Porter et al. 1992, $v=(2/3)(\pi abc)$ where a = length

of the mound's long axis/2, b = length of the mound's short axis/2 and c = mound height). We also measured the distance of each mound (to the nearest 0.1 m) from three points: the forest edge, the road edge, and the starting point of each 500 m segment. Powerline cuts did not contain road edges so distances were measured from the forest edge and from the starting point of the 500 m segment only.

Forest edges were defined as borders where soil disturbance from the original construction of the road or powerline cut ended. In almost all cases, this border was clearly denoted by a small ridge of soil. In cases where a distinct ridge was not present, the forest edge was delineated at the trunks of trees in the treeline. The treeline almost always coincided with a visible shift in vegetation and was easily identified. Some mounds were located just inside the forest, and we included these in our study if their distance into the forest from the forest edge did not exceed two meters. These mounds received insolation similar to mounds opposite the edge, and their proximity suggested a relationship between their presence and that of the adjacent open habitat. Road edges were defined as the border where the vegetation in the roadside abutted the asphalt, gravel or compacted tire track.

The width of each segment was measured at 50 m intervals. In the four road habitat types, we measured the width of the road, the width of each roadside, and the width of the dirt road median. There were no roads in powerline cuts, so we measured the total width only. In addition to width, the orientation of the long axis of each segment was measured using a compass. Some small dirt roads curved moderately, and their orientation was considered the average compass heading.

Analysis. We estimated the area of each site in two ways. The 'total area' was defined as the area of the entire segment, and the 'inhabitable area' was defined as the area assumed to be available for *S. invicta* colonization (i.e., total area minus the area of the asphalt, gravel, or tire tracks). Mound density for each segment was calculated per total area and per inhabitable area before analysis.

Differences in mound density among linear habitat types were compared using a one-way ANOVA and Tukey's HSD (Sokal and Rohlf 1995). Differences in mound volume were analyzed using a nested ANOVA where mounds were nested within segments and Tukey's HSD.

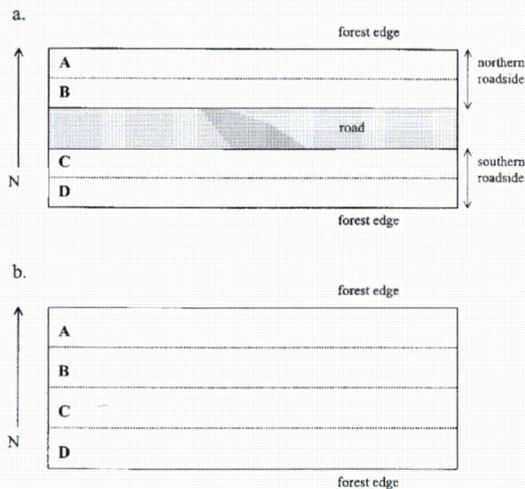


Figure 1. Division of a 500 m segment into linear strips (A, B, C, D) in road (a) and powerline cuts (b).

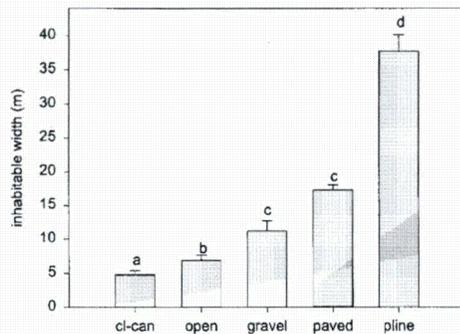


Figure 2. Mean width of closed-canopy (cl-can) and open dirt roadsides+median, gravel and paved roadsides, and powerline (pline) cuts ($n=10$ for each type, + standard errors). Bars with different letters are significantly different ($p < 0.05$) using Tukey's HSD.

We examined the spatial patterns of mounds perpendicular to the long axis of a habitat in two ways. For both these analyses, we excluded all mounds located in the median of the dirt roads. We first determined whether mounds were distributed randomly throughout the inhabitable area by calculating the distance of each mound to the nearest edge (i.e., road edge or forest edge). We compared the distances observed with those expected by a random distribution using a one-sample Kolmogorov-Smirnov test for goodness of fit (Sokal and Rohlf 1995).

Second, we determined whether mound density or volume were greater in some regions than others. We divided each roadside into two linear strips

of equal width parallel to the long axis, for a total of four strips per segment (Figure 1a). In powerline cuts, we divided each segment into four linear strips of equal width parallel to the long axis (Figure 1b). All strips were designated A, B, C and D from north to south respectively. We compared the densities among strips by fitting the data to a Poisson distribution using SAS Proc Genmod with a model for overdispersion since our variances were large (SAS Institute 1996). The number of mounds within most areas was large so we were also able to analyze our results using a one-way ANOVA and Tukey's HSD. These results did not differ greatly from those generated using the Poisson distribution. Since the ANOVA was the more conservative test, we will report only the ANOVA results. We compared mound volume among strips using a nested ANOVA and Tukey's HSD. We determined whether the orientation of the road or powerline cut (i.e., degrees from 0° N) was related to the difference in mound density between the northern and southern roadsides (or halves in powerline cuts) using a weighted regression analysis where segments were weighted according to total mound density.

To examine the spatial patterns parallel to the long axis of a segment, we used the Kolmogorov-Smirnov test to determine whether mounds were distributed randomly along the 500 m length. We divided the 500 m distance into 10 m sections and compared the densities observed in each section with those expected by a random distribution.

Results

Comparison of habitat types

Results of our analyses were similar using either total or inhabitable area; therefore, we report only those for inhabitable area. Habitat types differed significantly in width: powerline cuts were widest, followed by paved and gravel, then open dirt, and closed-canopy dirt roads (Figure 2). Mound density differed among habitat types, but not as predicted. Density was relatively low in the narrowest type (closed-canopy dirt roads) as predicted. However, for the four open canopy types, density was higher in the narrowest type (open dirt roads) than in the widest type (powerline cuts), and there was a trend for decreasing mean density as width increased (Figure 3a). Furthermore, mound density was greater in habitat types with intermediate to frequent disturbance (open dirt and paved roads) than

types with infrequent disturbance (powerline cuts and closed-canopy dirt roads; Figure 3b). Mound density was most variable (i.e., largest standard error) in open dirt road habitats (Figure 3).

Mound volume was not clearly related to habitat width (Figure 3c), but mounds were largest in the unmowed powerline cuts and smallest in the frequently-mowed paved roadsides (Figure 3d). The trend (not significant) in mound volume may indicate an inverse relationship with disturbance frequency. Mound volume was most variable in closed-canopy dirt road habitats (Figure 3).

Spatial distribution within habitats

Distributions perpendicular to the long axis of the habitat. Within four habitat types, mounds were closer to either the forest edge or the road edge than expected by a random distribution (Figure 4). Closed-canopy dirt road habitats were not included in this analysis because the number of mounds ($n=20$) was too low. Most mounds (26%) were located within 2 m of the forest edge in powerline cuts and within 1 m of either edge in paved and gravel roadsides (49% and 64% respectively). Along the road edge, mounds were commonly located so close to the edge that a portion of the mound actually spilled over on to the asphalt or gravel. More mounds were located close to the forest edge than the road edge in gravel (204 vs. 114 mounds), open dirt (206 vs. 80), and closed-canopy dirt (25 vs. 3) roadsides. In paved roadsides, more mounds were located close to the road edge (318 vs. 259).

Solenopsis invicta preferred some linear strips of the habitat for colonization over others. In all fifty segments combined, mound density was greater in strip A than D (Figure 5). This trend was evident in all habitat types except open dirt roads, but the differences were significant in gravel roads only. In all fifty segments combined, mound volume was higher in strip A than in strips B and C (Figure 6). Within each habitat type, however, differences in mound volume among strips were not significant.

A wide and frequently traveled road may act as a barrier to colony movement. If fire ants cannot move the colony across the asphalt or gravel expanse, then each roadside may have a functional northern region (i.e., strips A and C). We combined the mound density in strips A and C and compared it with the combined density in strips B and D. The density in A+C was larger than the density in B+D in paved (74.2

mounds/ha, SE=10.2 vs. 43.9 mounds/ha, SE=7.8, $p<0.05$) and gravel roadsides (66.3, SE=11.6 vs. 29.3, SE=10.4, $p<0.05$). The density in A+C was not different from the density in B+D in powerline cuts (35.2, SE=9.3 vs. 14.8, SE=4.6, $p>0.05$), open dirt (57.3, SE=14.7 vs. 62.4, SE=17.6, $p>0.05$) or closed-canopy dirt roadsides (7.4, SE=2.4 vs. 4.4 mounds/ha, SE=2.4, $p>0.05$).

The difference between the mound density in the northern and southern roadsides (or halves in powerline cuts) was related to the orientation of the habitat (Figure 7). The difference between the mound density in the northern and southern roadsides (or halves) was negative or small in roads or cuts oriented more north/south. This difference increased as the orientation of the road or cut shifted from north/south to east/west ($R^2=0.19$, $p=0.003$). Most of the high-density habitats, however, had orientations within 40° of north (Figure 7).

Distributions parallel to the long axis of the habitat. Along the 500 m axis of the segments, mounds in the roadsides or powerline cuts were not randomly distributed. Mounds in the ten closed-canopy dirt road segments were not analyzed because of low numbers. For the remaining forty segments surveyed, mound density in each of the fifty 10 m sections was similar across the entire 500 m in only four segments: one gravel and three paved road habitats. In the other thirty-six cases, mound density differed more among 10 m sections than would be expected by a random distribution ($p<0.05$).

Discussion

Effects of linear habitat type

Fire ant mound density differed among habitat types; however, the density was not related to habitat width or disturbance frequency in the ways that we predicted. The narrowest habitat type (closed-canopy dirt roads) did indeed have the fewest mounds, as predicted, but among the four open-canopy types, density was highest in the narrowest type (open dirt roads) and lowest in the widest type (powerline cuts; Figure 3a). Our results suggest that direct sunlight is a requirement for fire ant colonization. Mound densities were non-existent in five of the ten closed-canopy dirt road segments and extremely low in the other five. Thus, our original prediction that greater width

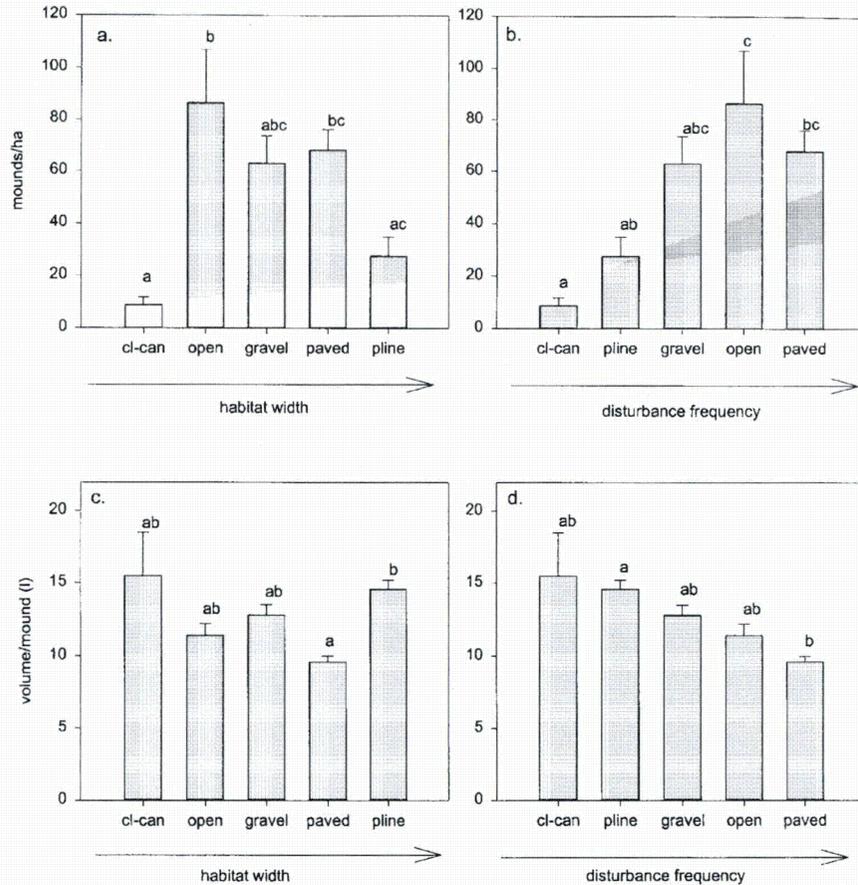


Figure 3. Mean mound density in closed-canopy (cl-can) and open dirt roadsides+median, gravel and paved roadsides, and powerline (pline) cuts ($n=10$ for each type, + standard errors) in order of increasing width (a) and disturbance frequency (b). Mean mound volume per mound by habitat type ($n=10$ for each type, + standard errors) in order of increasing width (c) and disturbance frequency (d). Bars with different letters are significantly different ($p < 0.05$) using Tukey's HSD.

leads to greater density is correct; however, once the habitat exceeds a critical width (i.e., one that allows for some direct sunlight at the soil surface) other factors are more important. Our evidence suggests that disturbance is one of those key factors. Frequent direct disturbance seems to increase rather than decrease fire ant mound density. Mowing or burning decreases vegetative height and exposes or disturbs soil. The increased insolation and soil disturbance may stimulate fire ant colonization or population growth more than the decrease in growth we expected from direct, physical disruption of the existing mounds. Other key factors that may determine differences in mound density among habitat types include the availability of resources and the abundance of predators of fire ant

queens, but our data cannot provide information about these hypotheses.

The differences in fire ant densities suggested by our mound density data may be partly offset by a different trend in mound volume. Mounds were smaller in habitats that were disturbed more frequently, and the difference between the extreme disturbance regimes in open habitats (i.e., powerline cuts vs. paved roadsides) was significant (Figure 3d). Mounds in paved roadsides may be run over by mowing machinery several times a year. Colonies may be forced to move or rebuild each time, and thus, their smaller size may reflect a transition phase. Abandoned mounds, many marked by tire tracks, were often seen within 2–4 m of active mounds. Mean mound volume

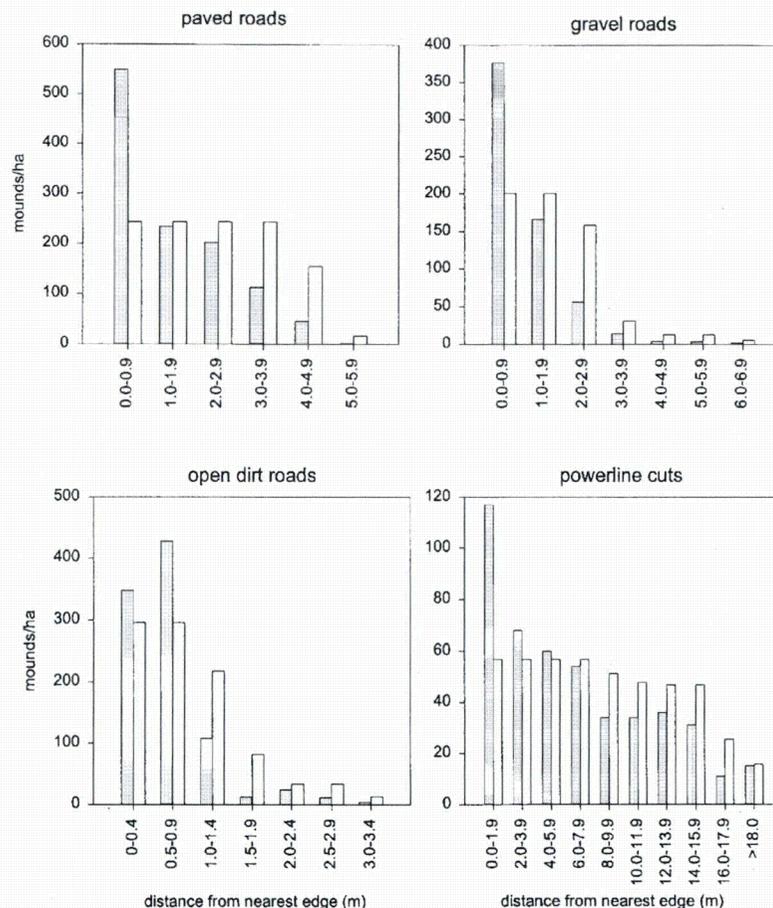


Figure 4. Mound distribution relative to forest or road edges in four linear habitat types. Gray bars represent the observed mound density and white bars represent the density expected by random. All distributions are significantly closer to edges than expected ($p < 0.01$) using a one-sample Kolmogorov-Smirnov test for goodness of fit.

in powerline cuts, however, may have been larger because mounds may escape physical destruction for up to five years. We observed more evidence of mound relocation in paved and gravel roadsides than in powerline cuts. The demonstrated relationship between mound volume and ant abundance (Tschinkel 1993) may not be as strong for frequently-disturbed mounds as it is for infrequently-disturbed mounds; however, our results suggest that powerline cuts have more fire ants per mound than paved roadsides. The impact of fire ants on their community depends on both mound density and volume because both contribute to ant abundance. However, differences in mound volume among habitat types are not nearly as large as differences in mound density. Therefore, it is likely that

mound density plays a larger role in determining the impact of fire ant invasion.

Spatial distribution within habitats

Fire ant mounds were more abundant near the northern side of linear habitats (i.e., strip A), and the disparity between the density in the northern and southern roadsides (or halves) increased in roads or cuts oriented more east/west. Mounds near the northern side may receive more insolation than those near the southern side, especially during winter months. In winter, the area close to the southern edge of a linear habitat (i.e., strip D) is shaded for at least part of the day. Optimal temperatures for colony growth of *S. invicta* are between 24° and 32 °C (Porter 1988, Lof-

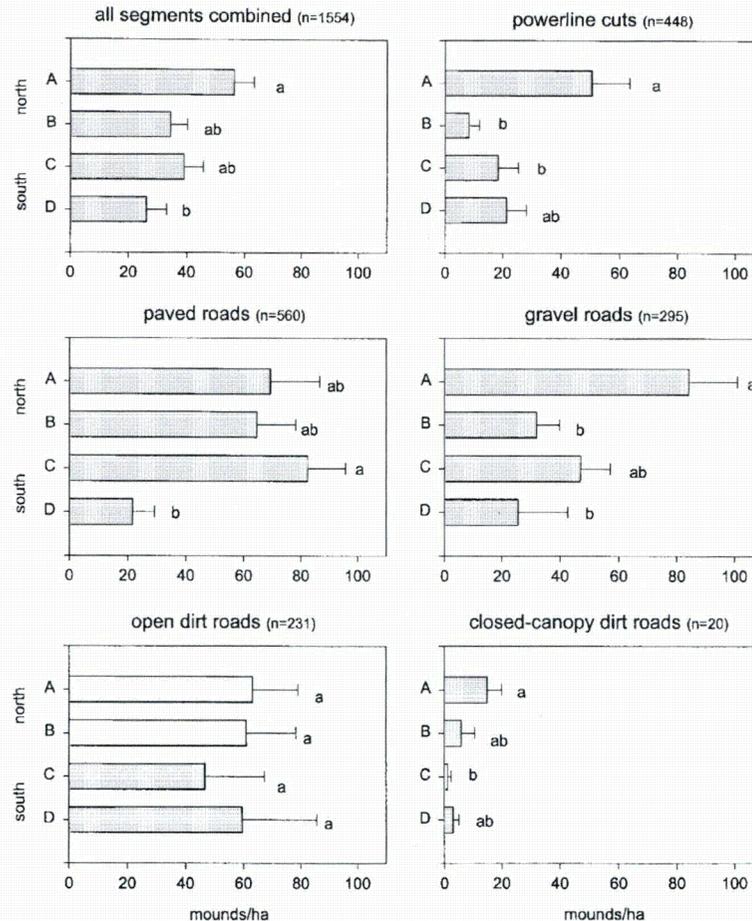


Figure 5. Mound distribution perpendicular to the long axis of the linear habitat by density in all segments combined ($n=50$) and in each habitat type ($n=10$ for each, + standard errors). A, B, C, and D denote linear strips located in the northernmost to southernmost sides of the habitat respectively. Bars with different letters are significantly different ($p < 0.05$) using Tukey's HSD.

gren et al. 1975), and the location of the mound may influence thermoregulation. Individual mounds are often oriented so that the long axis of the mound runs north/south for more effective thermoregulation (Hubbard and Cunningham 1977). It is likely that the location of the mound would serve this same purpose.

Fire ants usually move their mounds at least once per year for reasons that are not apparent (Hays et al. 1982). We sampled all segments in October and did not replicate our study in other seasons. Therefore, we do not know whether ants move their mounds northward as the southern roadside becomes more shaded or whether colonies that initially established near the northern side experience lower attrition.

The structure of the linear habitat type affects the north/south mound distribution (Figure 5). In paved and gravel roadsides, mound density was higher in strips A+C than strips B+D. For fire ants, the road constitutes a wide, uninhabitable expanse. Colonies in the southern roadside may not be able to establish mounds further northward than strip C. The mound densities in strips A and B were different in gravel roadsides, but they were the same in paved roadsides. Since paved road habitats are wider, a larger area may receive more sunlight. Colonies in the northern roadside may not need to be close to the northern edge to receive sufficient insolation. Open dirt road habitats, which had the same mound density in all strips, may not be wide enough to provide insolation along any

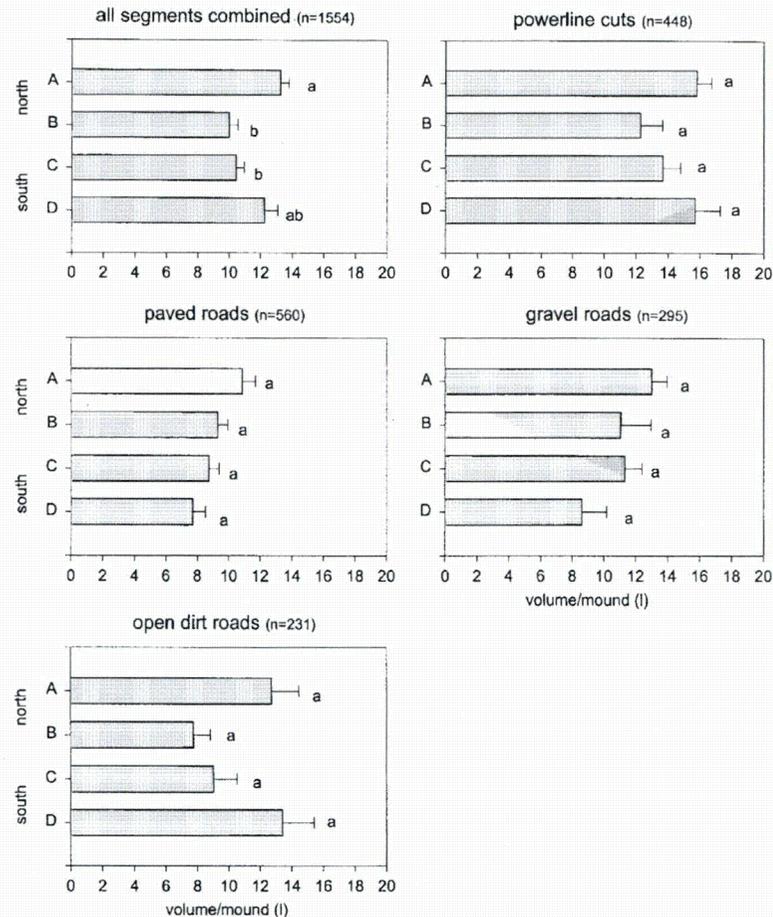


Figure 6. Mound distribution perpendicular to the long axis of the linear habitat by volume in all segments combined ($n=50$) and in each habitat type ($n=10$ for each, + standard errors). A, B, C, and D denote linear strips located in the northernmost to southernmost sides of the habitat respectively. Bars with different letters are significantly different ($p < 0.05$) using Tukey's HSD.

consistent edge. This does not help explain the high mound density in this habitat type, but it may help explain the high variability in mound density among segments. In powerline cuts, fire ants favored the strips near the forest edges (i.e., A and D). Mound density was low in strips B and C even though the adjacent forest never shades these regions.

Mounds were largest towards the northern side of the linear habitats (Figure 6). However, they were not significantly different from those near the opposite forest edge (i.e., strip D). Colonies in strip A may grow larger as a result of more effective thermoregulation, or when close to edges, or both. Additionally, mounds near the forest may escape direct physical disturbance from mowing machinery.

Our results suggest that ants prefer edges in general regardless of orientation and that the spatial distribution of mounds cannot be explained primarily in terms of thermoregulation (Figure 4). Mounds located in any strip were frequently built close to the road or forest edge. Several hypotheses may explain this distribution. For example, fire ants may be responding to the distribution of other species, or the soil structure near edges may be important. Soil near forest edges contains more tree roots and decomposing wood; soil near paved and gravel roads contains more gravel. Both edge soils may be easier to excavate. Banks et al. (1990) documented numerous potholes resulting from the tunneling of *S. invicta* under highways in Florida and North Carolina. Edges may also provide

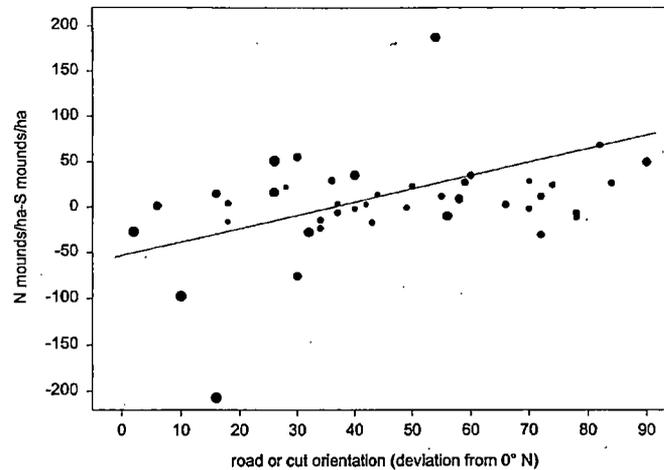


Figure 7. Difference between the mound density in the northern (N) and southern (S) roadsides (or halves in powerline cuts) as a function of road or cut orientation ($R^2 = 0.19$, $p=0.003$) using a weighted regression. Larger symbols denote segments with greater total mound density.

microsites where humidity, temperature, foraging efficiency, vegetative cover, or the frequency of direct disturbance changes.

The spatial distributions of mounds differ between linear and non-linear early-successional patches. Mature mounds in pastures with high mound density are regularly distributed (Adams and Tschinkel 1995). Baroni Urbani and Kanno (1974) found that mounds were somewhat aggregated at a small scale, but over an entire pasture, mounds were roughly uniform. Similarly, we have observed that mounds in forest gaps are not associated with edges. The spatial distribution of mounds within pastures, agricultural fields, and forest gaps may reflect a response to small-scale environmental heterogeneity such as tree stumps, fence posts (Hays et al. 1982), slight variation in topography (Maxwell 1982), or other mounds (Adams and Tschinkel, 1995). In contrast, the spatial distribution of mounds within linear habitats (Figures 4 and 5) may reflect a response to large-scale environmental heterogeneity such as the level of insolation, soil compaction, or temperature found along a consistent edge.

Solenopsis invicta is an exotic species whose effects on native ants and other arthropods are detrimental. Furthermore, its abundance and distribution throughout the southeastern U.S. is growing (Vinson 1994, Porter et al. 1988). In order to prevent or slow further invasion into newly-disturbed areas, the spatial distributions of mounds and the use of different linear habitat types by *S. invicta* need to be considered. To

limit the suitability of road and powerline cuts as primary habitat for the red imported fire ant, our study suggests that a reduction in roadside disturbance (i.e., less mowing) and an increase in the amount of forest canopy allowed to shade roadsides, especially towards northern edges, may result in lower fire ant mound density.

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Influence of the proximity and amount of human development and roads on the occurrence of the red imported fire ant in the lower Florida Keys

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Abstract

We examined the influence of both the proximity and extent of human developments and paved roads on the presence of the predatory, non-indigenous, red imported fire ant (*Solenopsis invicta*). This species was inadvertently introduced into the United States at the port of Mobile, Alabama, around 1930 and rapidly spread to many southeastern states, including Florida. More recently, *S. invicta* colonized the Florida Keys, an area with a high proportion of rare and endemic vertebrate and invertebrate species. We placed bait transects in transitional salt-marsh, pineland, and hardwood hammocks on 13 of the lower Florida Keys and compared habitat type, the shortest distance of the bait transect to a development or road, and area of development and roads 50, 70, 100, and 150 m around each bait transect for areas with and without red imported fire ants. Red imported fire ants were detected on 21 of the 80 transects and were equally abundant in all habitat types. While all of the development and road variables differed significantly between bait transects with and without red imported fire ants, transects that were closest to roads and that had the largest amount of development within a 150 m radii had the highest probability of presence of red imported fire ants. Recovery efforts for endangered species in areas invaded by red imported fire ants should include analyses of the cumulative impacts of roads and developments in areas near protected lands. © 2002 Elsevier Science Ltd. All rights reserved.

Keywords: Red imported fire ant; *Solenopsis invicta*; Lower Keys of Florida; Invasion biology; Non-indigenous species; Fragmentation

1. Introduction

Habitat destruction is the primary cause for the extinction of most terrestrial species (Baillie and Groombridge, 1996), but the impact of a human development or roads may be far greater than the immediate area of the destruction. One potential negative effect that roads and developments can have on native ecosystems is the increase in invasive, non-indigenous species in the surrounding area (Elton, 1958; Simberloff, 1981; Rejmánek, 1989). Human disturbance can increase non-indigenous species in two general ways: it can provide habitat with reduced native predators and competitors for a species that is a human commensal or

an early succession species (Diamond and Veitch, 1981; Williamson, 1996) and/or the disturbance can act as a dispersal corridor, increasing the rate of invasion into undisturbed ecosystems (Tyser and Worley, 1992; Forman, 1995). Once established, some non-indigenous species have a dramatic negative influence on communities (Simberloff, 1981) and ecosystems (Vitousek, 1990; Vitousek et al., 1996).

One of the most destructive non-indigenous species is the red imported fire ant (*Solenopsis invicta*). Red imported fire ants were inadvertently introduced into the United States at the port of Mobile, Alabama, around 1930 from South America and rapidly spread to many southeastern states, including Florida (Vinson and Sorensen, 1986). All counties in Florida were infested by 1976 (Callcott and Collins, 1996). The climate in the southeastern United States is similar to the climate in parts of Africa, Asia, and Australia, indicating that if

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an introduction were to occur in these areas that it might be successful.

Solenopsis invicta is known to prey on or compete with a wide range of invertebrates (Porter and Savignano, 1990) and vertebrates (Allen et al., 1994). *Solenopsis invicta* is attracted to mucous (Vinson and Sorensen, 1986), making newborn mammals, recently pipped birds and herpetofauna, and species that leave mucous trails particularly vulnerable to predation. The larval and pupal stages of invertebrates are at risk because of their inability to escape from fire ant attacks. Vertebrate species that have been predated on by red imported fire ants include gopher tortoises (*Gopherus polyphemus*, Landers et al., 1980), loggerhead turtles (*Caretta caretta*, Moulis, 1997), eastern cottontails (*Sylvilagus floridanus*, Hill, 1970), small mammals (Smith et al., 1990; Killion and Grant, 1993), and white-tailed deer (*Odocoileus virginianus*, Allen et al., 1997). In addition, *Solenopsis invicta* outcompetes native ants and reduces diversity in many insect communities (Porter and Savignano, 1990).

More recently, *Solenopsis invicta* colonized the lower Florida Keys, a subtropical area with a high proportion of rare and endemic vertebrate and invertebrate species. *Solenopsis invicta* is a voracious predator that could have a large negative impact on many of the species in the lower Keys, as well as overall biodiversity. The lower Florida Keys are the terminal portion of an archipelago of islands extending westward from the

mainland of Florida (Fig. 1). The lower Keys also are a place where substantial habitat destruction and fragmentation have recently occurred (Davis and Odgen, 1994). Primarily due to this habitat destruction, much of the lower Keys' fauna is endangered (Humphrey, 1992). In an attempt to preserve the diversity of the lower Keys, much of this land has been purchased by federal, state, and private conservation organizations. Despite this protection, populations of several species remain low (Humphrey, 1992; Moler, 1992). One possible contributing factor to the low abundances of some of these species may be mortality caused by *Solenopsis invicta*.

Previous studies have shown that *Solenopsis invicta* favors open and semi-open habitats (including disturbed areas), and generally forages when soil temperatures are between 22 and 36 °C at a depth of 2 cm (Porter and Tschinkel, 1987); these conditions are found throughout the Lower Keys. Despite this, *Solenopsis invicta* was not found in Wilson's 1958 collecting trip to Key West and Big Pine Key (Wilson, 1964). Deyrup and colleagues only found *Solenopsis invicta* in highly disturbed areas (e.g. parking lots, roadsides) on two of the main lower Keys (Key West, Saddlebunch) despite numerous collecting trips from 1982 to 1987 (Deyrup et al., 1988). Porter (1992) surveyed the roadsides of seven of the lower Keys and only found *Solenopsis invicta* on one key (Stock Island). While red imported fire ants appear to be able to invade and establish populations in disturbed habitats in the Florida Keys (e.g. developments

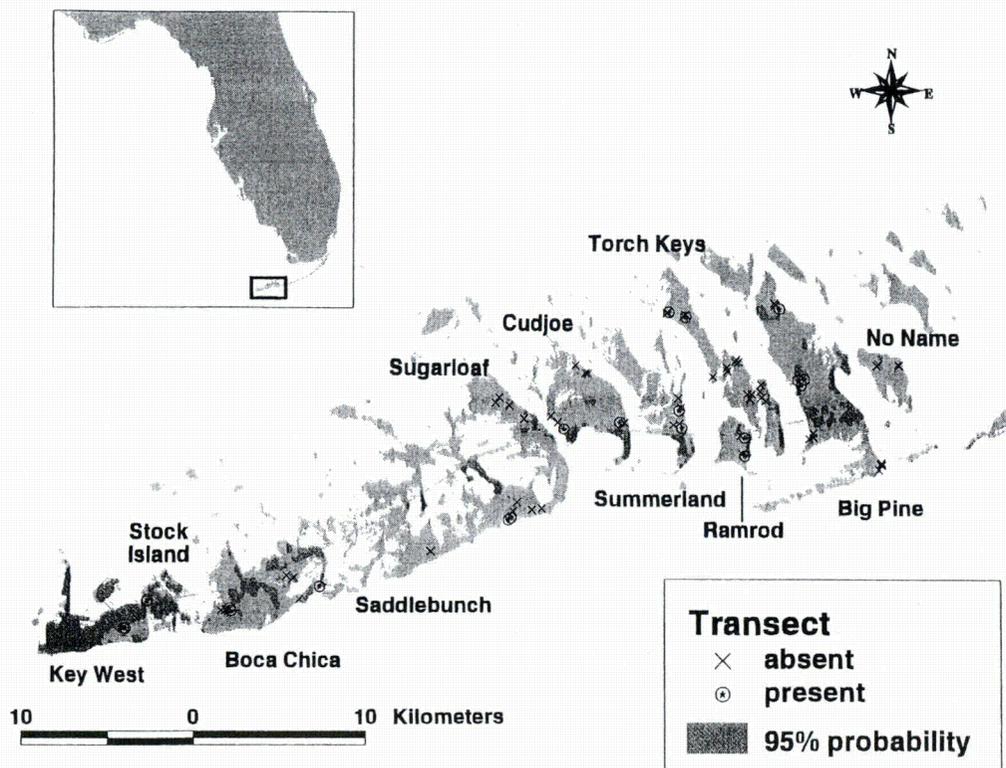


Fig. 1. Location of the lower Florida Keys, bait transect locations, and the predicted distribution of *Solenopsis invicta* (95% probability).

and roadsides), it is not known if the species has the ability to invade undisturbed habitat. In addition, the effects of additional developments and roads on presence of *Solenopsis invicta* in the vicinity of protected lands has never been explored.

The purpose of this study was to examine the influence of development and roads on the presence of *Solenopsis invicta* in undisturbed preserved habitat in the Florida Keys. Specifically, we examined both the proximity of roads and development and the amount of area disturbed by roads or development on presence of *Solenopsis invicta*.

2. Methods

2.1. Distribution and abundance of red imported fire ants

We collected data on the presence of *Solenopsis invicta* on all of the lower Keys that are reachable by road and have some development. Publicly owned habitat patches of pinelands, hardwood hammocks, and transitional salt-marsh that were >0.10 ha were sampled. Some of the smaller, lower-elevation keys lacked these three habitat types, so as many habitats were surveyed as possible. Pinelands are dominated by south Florida slash pine (*Pinus elliottii* var. *densa*) overstory and saw palmetto (*Serenoa repens*) understory. Hardwood hammocks are closed-canopy broad-leaved forests that have a high diversity (>150 species) of both evergreen and semi-evergreen tropical tree species. Transitional salt-marsh typically occurs at 3–5 m above sea-level between mangroves and the upland hardwood hammocks. The dominant tree species is buttonwood (*Conocarpus erectus*) and the understory is comprised of marsh grasses and sedges.

Ant bait transects were placed on preserved lands using randomly chosen Universal Transverse Mercator coordinates within the habitat patch as the starting point and a random number table to determine the orientation of the transect. While ant mound counting is an acceptable method of estimating fire ant presence and abundance in central Florida and north to Virginia, in the Florida Keys red imported fire ants colonies often do not form mounds, but exist in cracks and fissures in the limestone substrate.

Thirty-five of the transects were placed in hardwood hammocks, 34 were placed in transitional salt-marsh and 10 were in pinelands. Each transect was 90 m long and consisted of 10 stations of paired baits (one honey, one meat 45–60 cm apart) placed on the ground, spaced 10 m apart (Wojcik, 1994). Each bait transect was sampled once during a 2-week period from 15 to 31 July 1996 in the morning (07:00–10:00 hours) or the afternoon (16:00–19:00 hours) when temperatures were favorable for fire ant foraging. After placement, baits

were left out for 1.5 h to attract ants and then were collected and placed in cups, frozen, and transported to the USDA, ARS, Imported Fire Ant Laboratory (Gainesville, FL). In the laboratory ants were picked from the bait, placed in alcohol, and identified to species.

2.2. Data analyses

A logistic analysis (a logistic regression that incorporates class variables, SYSTAT, 1992) was conducted using the presence or absence of red imported fire ants at a transect as the dependent variable and the following as independent variables:

- habitat type;
- the euclidean (shortest) distance of the closest portion of the bait transect to a development;
- area of development 50, 75, 100, 150 m around each bait transect;
- the euclidean (shortest) distance of the closest portion of the bait transect to a paved road; and
- area of roads 50, 75, 100, 150 m around each bait transect.

We measured independent variables using habitat and road data sets analyzed using geographic information system (GIS) software (ARC/INFO, 1990). Habitat data (including types of human developments) came from the Advanced Identification project mapping coverages (ARC/INFO data sets) provided by the Environmental Protection Agency (EPA, Region IV, Atlanta). These vector-based coverages were created by digitizing habitats based on photo interpretation and ground-truthing. The minimum resolution was approximately 0.10 ha. To estimate the influence of human development, we selected all areas in the habitat coverage that had been classified as being “developed” by the habitat map. Developed areas included buildings, parking lots, and highly disturbed yards >0.10 ha. In ARC/INFO we created coverages that estimated the euclidean (shortest) distance of a transect to a development. We also used GRID to calculate the sum of development within an oval-sized neighborhood of 50, 75, 100, 150 m radii around each transect in the lower Keys and to produce a raster-based coverage of these values. We did not examine neighborhoods >150 m because many of these would include a large proportion of water. We repeated this process for the roads coverage. Road data came from Florida Department of Transportation vector-based coverages. To prepare these vector-based map coverages for analysis we converted them to raster-based maps using the GRID module of ARC/INFO. We used a 10×10 m sized cell for all raster maps.

Our dependent variable was the presence or absence of *Solenopsis invicta* at the bait stations on a linear

transect. We classified a transect as having *Solenopsis invicta* if it was detected at one of the 10 bait stations. All transects were mapped using a GPS (global positioning system) and the locations were converted to a GIS data layer.

We reduced the inter-correlated variables prior to multivariate analyses. The variable with the highest between-group significance was retained and used in the model. The best model was used to create a grid of predicted values for the dependent variable at each cell throughout the lower Keys. If a variable was not normally distributed we used a logarithmic transformation. The retained and transformed variables were entered into a stepwise logistic analysis to derive a multivariate model that would predict the presence or absence of red imported fire ants. The resulting models were evaluated using goodness-of-fit tests based on maximum likelihood estimates and how accurately they classified red imported fire ant presence or absence. All of the variables were compared using a *t*-test if the data was normally distributed and the variances were equal and a Mann–Whitney rank sum test if otherwise.

3. Results

We identified *Solenopsis invicta* from 21 of 80 transects on 9 of the 13 lower Keys. On the transects where *Solenopsis invicta* was detected, the average number of bait stations with *Solenopsis invicta* was 5.4 (SD=2.4) and the range was from 3 to 10 (out of 10 stations total). We identified 48 species of ants and a total of 287,180 individuals from the 80 transects. *Solenopsis invicta* was the seventh most abundant species, comprising nearly 8% (22,775) of the total ants counted.

Solenopsis invicta was present at 29% of the transects in the transitional salt-marsh, 30% of the pinelands transects, and 23% of the hardwood hammock transects. The proportion of transects with *S. invicta* did not vary significantly by habitat type ($\chi^2=0.262$, $P<0.88$, $df=2$).

None of the development variables was significantly correlated with the road variables ($r<0.4$, $P>0.05$), but all of the development variables and all of the road variables were significantly inter-correlated with each other ($r>0.4$, $P<0.05$). None of the independent variables were normally distributed, therefore a Mann–Whitney rank sum test was conducted comparing the median values for transects that had *Solenopsis invicta* present to transects where *Solenopsis invicta* was absent. All of the road and development variables significantly ($P<0.05$) differed between transects with *Solenopsis invicta* absent and present (Table 1). The euclidean distance to roads was the most significant roads-related variable. Transects closest to roads were the most likely to have *Solenopsis invicta*. The amount of development

at the largest scale analyzed (150 m around a bait transect) was the most significant development-related variable. The more development, the more likely red imported fire ants were collected in the bait transect.

These two variables (euclidean distance to roads and development 150 m around the transect) were transformed and used as independent variables for our logistic analysis. The model converged on one significant model based on the function:

$$\text{logit}(P) = 2.543 - 0.034R + 0.044D$$

where P is the probability of presence of *Solenopsis invicta*, R is the euclidean distance to a road, and D is the amount of development 150 m around a transect (Fig. 1). The goodness-of-fit test that compared the two variable model with a model with just the constant was significant ($\chi^2=28.88$, $P<0.0001$, $df=2$). Classification accuracy of the model was high when predicting which bait transects would not have red imported fire ants (51 correct, eight incorrect). The classification accuracy of transects with red imported fire ants was not as high (11 correct, 10 incorrect).

4. Discussion

4.1. Distribution of *Solenopsis invicta*

During the past 10 years, *Solenopsis invicta* has dramatically expanded its distribution in the lower Florida Keys from only highly disturbed areas on a few of the most urbanized keys (Deyrup et al., 1988; Porter, 1992) to all of the major habitat types on most of the lower Keys. The colonization of native habitats by *Solenopsis invicta* appears to be facilitated the greatest by close proximity of roads and by large developments. However, the low classification accuracy of the logistic analysis indicates that there may be additional factors that determine presence or absence of red imported fire ants. In addition, the invasion of red imported fire ants appears to be ongoing and the model only predicts the current distribution.

Previous studies of aggressive, non-indigenous ants have found that roads and developments increase non-native ants, but these studies were conducted on smaller spatial scales. Stiles and Jones (1998) determined that *Solenopsis invicta* mound density was higher in open dirt and paved roads than powerline cuts and closed-canopy dirt roads in coastal South Carolina. They also noted that within the closed-canopy forest, there were more mounds closer to the edge of the roads than 20 m into the forest. Development was not examined in their study.

Studies of the Argentine ant (*Linepithema humile*), an aggressive non-indigenous ant, in southern California

Table 1.

Comparison of the median values (not transformed) of independent variables used to determine *Solenopsis invicta* presence or absence on transects in the Lower Keys of Florida^a

Variable	<i>Solenopsis invicta</i> absent	<i>Solenopsis invicta</i> present
Euclidean distance to development	1273 m	300 m**
Development in a 50 m neighborhood	0	1900 m ² *
Development in a 75 m neighborhood	0	4500 m ² **
Development in a 100 m neighborhood	0	8900 m ² ***
Development in a 150 m neighborhood	2000 m ²	19,400 m ² ****
Euclidean distance to roads	2240 m	900 m****
Roads in a 50 m neighborhood	0	900 m ² *
Roads in a 75 m neighborhood	0	1400 m ² *
Roads in a 100 m neighborhood	900 m ²	4600 m ² **
Roads in a 150 m neighborhood	3000 m ²	8900 m ² ***

^a Mann–Whitney *U* test were performed.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

**** $P < 0.0001$.

(Suarez et al., 1998) and northern California (Human et al., 1998) found that these ants were more likely to be present near the edges of preserves. Preserve edges were apparently closer to both roads and development.

Road construction was found to have a profound effect on the long-term alpha diversity of ants in Western Australia (Majer and Beeston, 1996) and on the ecologically dominant ant species in South Africa (Samways et al., 1997). Samways et al. (1997) hypothesized that aggressive ant species such as *Pheidole megacephala* may have had a competitive advantage on roadsides because of the availability of road kills for food.

In the Florida Keys, it appears that roads and development facilitate colonization both by providing optimal *Solenopsis invicta* habitat and by providing corridors into native habitat. *Solenopsis invicta* probably invade disturbed areas (developed areas and roads) in several ways: (1) natural mating flights which may occur throughout the year in southern Florida, (2) movement of colonies with mated queens in nursery stock or construction fill, and (3) transportation of newly mated queens that land in vehicles and are transported to new areas (Vinson and Sorensen, 1986). Invasion of areas lacking native cover, and thus fauna, is probably facilitated by the lack of competitors and predators. Such areas exhibit higher reflectivity and are thought to be more attractive to newly mated queens.

While close proximity of an undisturbed area to a development did appear to increase the probability of invasion, the amount of development at the largest scale investigated (150 m around the transect) was the most significant variable. Twenty-seven percent (16) of the transects in undisturbed areas that were ≤ 10 m from a development did not have *Solenopsis invicta*, but these areas had significantly less development 150 m around their transects than the 10 transects that had *Solenopsis*

invicta ($t = -2.25$, $P = 0.03$, $df = 24.0$) and were ≤ 10 m from a development.

The shortest distance from a transect to a road was the most significant roads-related variable. Several of the transects with *Solenopsis invicta* were surrounded by relatively little development but were relatively close to a single road. While *Solenopsis invicta* may forage up to 50 m from a colony that exists on the road-side, fire ants at these transects were found at baits > 50 m from the road indicating they came from a colony within the intact habitat.

4.2. Conservation implications

Even a single road traversing through preserved land or the expansion of an existing development near a refuge may increase the probability of invasion by *Solenopsis invicta*. In the lower Florida Keys there are at least nine federally endangered endemics which occur in upland habitats such as transitional salt-marsh, pine-lands, and hardwood hammocks and may be negatively impacted by red imported fire ants. All of these species may be negatively effected by *Solenopsis invicta* either through direct predation or indirect effects. Indirect effects include reduction in survival and weight gain resulting from envenomization, behavioral changes in the impacted species, changes in foraging patterns, changes in habitat use and reduce food availability. Indirect effects may be more important than direct predation, but are more difficult to study (Allen et al., 1998). These nine species include two mammals [Lower Keys marsh rabbit (*Sylvilagus palustris hefneri*), Key deer (*Odocoileus virginianus clavium*)], four reptiles [striped mud turtle (*Kinosternon baurii*), Big Pine Key ringneck snake (*Diadophis punctatus acricus*), Florida brown snake (*Storeria dekayi victa*), red rat snake (*Elaphe guttata guttata*)], and three invertebrates

[Florida tree snail (*Liguus fasciatus*), Florida Keys tree snail (*Orthalicus reses nesodryas*), Stock Island tree snail (*Orthalicus reses reses*)].

Current recovery efforts for these species have been aimed at protecting the habitat where these species currently occur (US Fish and Wildlife Service, 1999). Little effort has been made to reduce new roads and development in surrounding areas. Recovery goals for these species should include research to examine the effect of red imported fire ants. If the direct and indirect effects of red imported fire ants are found to be significant, the cumulative impacts of roads and development in the vicinity of endangered species habitat should be considered when permits are being evaluated.

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Landscape corridors can increase invasion by an exotic species and reduce diversity of native species

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Abstract. Landscape corridors are commonly used to mitigate negative effects of habitat fragmentation, but concerns persist that they may facilitate the spread of invasive species. In a replicated landscape experiment of open habitat, we measured effects of corridors on the invasive fire ant, *Solenopsis invicta*, and native ants. Fire ants have two social forms: polygyne, which tend to disperse poorly but establish at high densities, and monogyne, which disperse widely but establish at lower densities. In landscapes dominated by polygyne fire ants, fire ant abundance was higher and native ant diversity was lower in habitat patches connected by corridors than in unconnected patches. Conversely, in landscapes dominated by monogyne fire ants, connectivity had no influence on fire ant abundance and native ant diversity. Polygyne fire ants dominated recently created landscapes, suggesting that these corridor effects may be transient. Our results suggest that corridors can facilitate invasion and they highlight the importance of considering species' traits when assessing corridor utility.

Key words: ants; biodiversity; biological invasion; connectivity; corridor experiment; fire ant; habitat fragmentation; invasive ants; monogyne vs. polygyne ants; Savannah River Site, South Carolina, USA; *Solenopsis invicta*; species richness.

INTRODUCTION

Corridors, strips of habitat that connect otherwise isolated patches of the same habitat, are an increasingly common strategy to conserve biodiversity in fragmented landscapes. Although evidence for positive effects of corridors has been amassed from many studies (Tewksbury et al. 2002, Damschen et al. 2006, Gilbert-Norton et al. 2010), concerns remain about potential negative effects (Simberloff and Cox 1987, Weldon 2006, Wilkerson 2013; Haddad et al., *in press*). In particular,

corridors may facilitate the spread of invasive species, which commonly threaten biodiversity and disrupt ecological processes (Simberloff and Cox 1987, Wilcove et al. 1998, Mack et al. 2000, Procheş et al. 2005). Ultimately, higher rates of dispersal by invasive species into connected patches could increase their spread, population densities, and ecological impacts. This potential drawback of corridors is critical to evaluate because the same principles that support corridor establishment for threatened species in habitat fragments suggest that corridors could simultaneously jeopardize entire communities through spread of invasive species.

Positive effects have been the focus of most corridor studies (Gilbert-Norton et al. 2010), whereas negative effects have received much less attention (Haddad et al., *in press*). Specifically, there is no evidence of corridors spreading invasive species (Haddad et al., *in press*). Perhaps corridors have not been found to spread invasive species because invasive species are typically

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good dispersers (Bufford and Daehler 2011) and therefore do not need corridors to spread through fragmented landscapes. Yet, invasive species are not uniformly strong dispersers and it is possible that corridors may differentially affect their spread, depending on the capacity of each species for movement. Recent work suggests that species traits and behaviors related to movement are important for predicting species responses to altered landscape configuration, including the presence of corridors (Damschen et al. 2008, Minor et al. 2009, Sullivan et al. 2011). We examine how differences in dispersal behavior of two social forms of invasive fire ants influence their use of corridors and their subsequent impacts on native ant diversity.

We focused on *Solenopsis invicta* (henceforth, fire ant) because it is one of the most noxious invasive species in the United States, its distribution is spreading globally (Ascunce et al. 2011), and it is responsible for displacement of native ants and a wide variety of other taxa (reviewed in Holway et al. 2002, Tschinkel 2006; but see King and Tschinkel 2006, 2008). Of central importance for our study, fire ants have two ecologically distinct social forms, monogyne and polygyne, defined by the number of reproductive queens per colony (Ross and Keller 1998). Monogyne colonies contain a single egg-laying queen, whereas polygyne colonies contain multiple egg-laying queens. The two social forms also differ in two ways highly relevant to conservation. First, ecological impacts of the polygyne social form are more severe than those of the monogyne form. In particular, polygyne invasions result in very high population densities (Macom and Porter 1996) that can devastate native ant communities (Porter and Savignano 1990), whereas the impact of monogyne invasions is comparatively more benign (King and Tschinkel 2006, Tschinkel 2006, LeBrun et al. 2012). Second, monogyne queens participate in mating flights at heights >100 m, dispersing up to several kilometers to establish new, spatially independent colonies (Markin et al. 1971). In contrast, polygyne queens are more limited in their dispersal abilities, typically establishing new colonies within several meters of their natal colony, often through budding (Tschinkel 1998, DeHeer et al. 1999). This fundamental difference in queen dispersal behavior suggests that the two social forms will respond differently to corridors, with the more dispersal-limited and ecologically damaging polygyne form benefiting most from the connectivity provided by corridors. Given how the two social forms differentially impact native species, the overall balance of negative and positive effects of corridors on ant communities may hinge on the difference in movement behavior of the two forms.

We tested the effects of open-habitat corridors on fire ant abundance and impact through a landscape-scale randomized-block experiment (Tewksbury et al. 2002). Specifically, we tested the predictions that (1) corridors increase the population densities of polygyne fire ants, and (2) higher population densities of polygyne fire ants

in connected patches negatively affect native ant diversity. The first prediction is based on expectation from theory that corridors increase population densities of species with high population growth rates and limited dispersal (such as polygyne fire ants), in short time scales (Hudgens and Haddad 2003). In our study system, there are two mechanisms by which corridors could increase population densities of fire ants. The first is that corridors promote the initial spread of fire ants, in our case from their initial and limited distribution within the matrix where our experimental patches were created. Our patches were created by harvesting plantation pine forest, where fire ants occurred at very low densities (Appendix A). In contrast, the disturbed, open patches are preferred habitat for fire ants (Stiles and Jones 1998, Tschinkel 2006). Given that the area of two patches connected by a corridor is approximately double the area of an unconnected patch, it was much more likely that connected patches would have been created in the location of an already existing polygyne colony. This would lead to higher densities in connected than unconnected patches simply because population growth and spread could start immediately after patch creation in connected patches. The second mechanism is that corridors promote a rescue effect (Brown and Kodric-Brown 1977), increasing population persistence and thus size.

Two key features of our experiment permitted an unusually direct test of corridor effects on ant distribution. First, we controlled for typically confounding effects of patch area and length of habitat edges (Didham et al. 2012) by comparing connected and unconnected patches of equal area and equivalent shape (Fig. 1; see *Methods*). Second, five of our experimental landscapes were naturally colonized by monogyne fire ants and three by polygyne fire ants, providing a unique opportunity to compare entire landscapes dominated by each social form.

METHODS

Study area

We conducted this study at the Savannah River Site, South Carolina, USA (33.20° N, 81.40° W) in eight experimental landscapes (henceforth, blocks), designed to examine effects of corridors and patch shape on movement of plants and animals (Tewksbury et al. 2002). The blocks were created in 1999–2000 ($n = 6$) and 2007 ($n = 2$). Each block contained an array of open patches of early-successional longleaf pine (*Pinus palustris*) savanna embedded in a dense plantation forest matrix of loblolly (*Pinus taeda*), slash (*Pinus elliotii*), and longleaf pine, with scattered hardwoods (Fig. 1). Longleaf pine savanna is an endangered habitat of high conservation interest (Jose et al. 2006) and high ant diversity (Lubertazzi and Tschinkel 2003). All blocks were assisted in restoration toward longleaf pine savanna and were kept open by prescribed burns every 2–3 years, removal of hardwoods, and planting of native

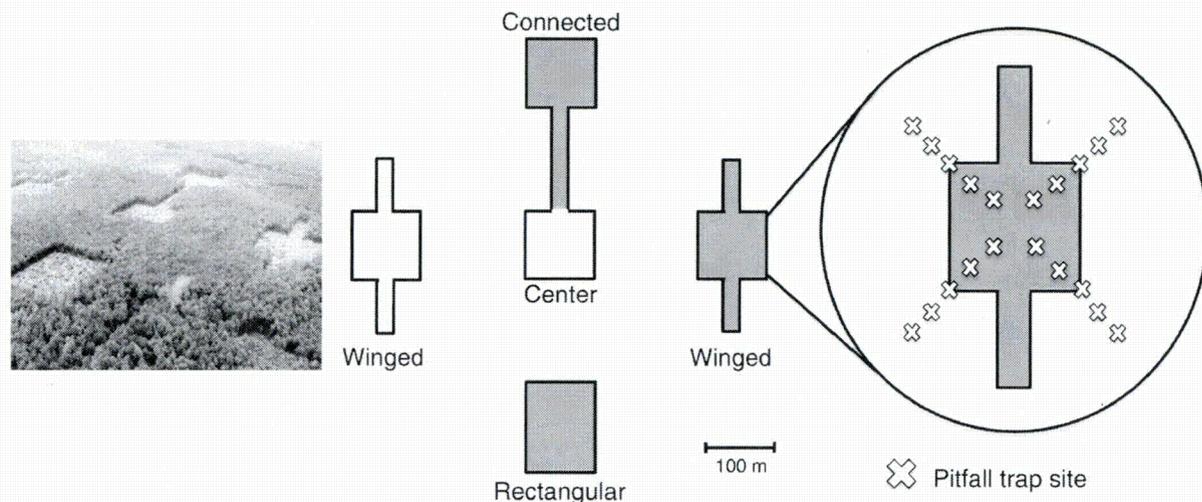


FIG. 1. Aerial photograph (credit: Ellen Damschen) and layout of one block for sampling invasive fire ants, *Solenopsis invicta*, and native ants ($n = 8$ blocks). Shaded patches (connected, winged, and rectangular) were sampled with pitfall traps. One patch is enlarged to show pitfall trap sites, which were positioned 0, 21.5, and 50 m from patch corners toward the center and 21.5 m and 50 m into the matrix.

species in an equal fashion across patch types and blocks.

Each block consists of a square, central patch (100×100 m) surrounded by four peripheral patches of the same habitat (Fig. 1). Each peripheral patch is 150 m from the central patch and is one of three randomly assigned patch types: "connected," "rectangular," or "winged." The connected patch is 100×100 m, with a 150×25 m corridor that connects to the center patch (1.375 ha total). Winged patches are also 100×100 m, but have two 75×25 m dead-end corridors ("wings") extending from opposite sides. Rectangular patches are 100×137.5 m; the additional area (100×37.5 m) that makes these patches rectangular is equivalent to the area of the corridor of connected patches or to the wings of the winged patches. Thus, all peripheral patches have the same area. Furthermore, all patches in each block were created simultaneously from the same matrix plantations. Each block has one duplicate winged or rectangular patch (Fig. 1). In this study, we used only one, randomly selected duplicate patch from each block.

Ant sampling and identification

Within connected, rectangular, and winged patches, we sampled ants in July 2008 using pitfall traps, a standard method for measuring abundance and species composition of ground-dwelling ants (Bestelmeyer et al. 2000). We deployed 12 pitfall traps per patch. Traps were placed at 0, 21.5, and 50 m along transects that extended diagonally from the four corners of a given patch into the patch center (Fig. 1). Each trap consisted of a 15-dram (28.6 mm inner diameter) plastic vial, one-third full of 50% propylene glycol, inserted flush with the soil surface. To reduce "digging-in effects," we left traps capped for 48 h (Greenslade 1973). Once uncapped, traps were open for 48 h. Using the same methodology,

we also collected ants in the pine matrix (details in Appendix A). All trapped ants were counted and identified to species, except for ants within the *Aphaenogaster rudis* species complex and the *Solenopsis* (*Diploporhtrum*) *molesta* group, species of which are morphologically similar and taxonomically uncertain. Voucher specimens were deposited in the California Academy of Sciences (data available online).¹⁰ As a second measure of fire ant abundance, we counted the number of active, mature fire ant nests (see details in Appendix B).

We determined the social form of fire ants using established genetic methods (Valles and Porter 2003; details in Appendix B). In all cases, one social form dominated each block. In blocks designated as monogyne blocks ($n = 5$), 99% of samples were homozygous, indicating monogyny. In blocks designated as polygyne blocks ($n = 3$), 87% of samples were heterozygous, indicating polygyny; two patches in these blocks had both social forms present. Because we could not randomly assign fire ant social form to blocks, we were concerned that factors unrelated to corridors might underlie any pattern in ant distribution that we observed among blocks. We tested two such factors that we considered especially important: land use history and block orientation; neither differed systematically between monogyne and polygyne blocks (Appendix B).

Statistical analyses

To determine differences in fire ant pitfall trap incidence and number of workers in pitfall traps between polygyne and monogyne blocks, we used Mann-Whitney *U* tests. To determine effects of corridors on abundance of fire ants, we tested for an interaction between the

¹⁰ <http://www.antweb.org>

dominant fire ant social form in a given block and patch type on fire ant pitfall trap incidence, with block identity as a random effect, using a generalized linear mixed-effect model with a binomial response distribution and the Kenward-Roger approximation for hypothesis tests (Littell et al. 2006). In the main test, we restricted our analysis to the comparison of connected and winged patches; it provides the most direct test of connectivity because it simultaneously controls for edge and patch shape effects (Damschen et al. 2008). Results for analyses that include rectangular patches are provided in Appendix C. We evaluated overdispersion using the Pearson residuals generated from our analysis and found that the overdispersion parameter was close to 1.0 (± 1.8), indicating an absence of overdispersion (Littell et al. 2006). For pitfall data, incidence is preferable to counts of individuals when estimating density of ants because individuals are highly aggregated in space (Gotelli et al. 2011). We employed a similar generalized linear mixed-effect model for nest counts, using a quasi-Poisson distribution to adjust for overdispersion. Results for nest data are in Appendix C.

To determine effects of corridors on native ants at the community level, we estimated species richness and evenness, using Hurlbert's (1971) probability of interspecific encounter ("PIE") for connected, rectangular, and winged patches. We estimated these metrics with sample-based rarefaction on incidence data from pitfalls, using EcoSim v. 7.71 (Gotelli and Entsminger 2004) with 1000 iterations. We used the resulting 95% confidence intervals for each patch type to assess differences among patch types, rarified to the number of samples in the patch type with the fewest samples. We ran analyses separately for polygyne and monogyne blocks. We calculated a nonparametric estimate of asymptotic species richness, first-order jackknife (Jack1), and corresponding confidence intervals (Jack1 ± 2 SE) for each patch type using the vegan package (R package v. 2.0-2; Oksanen et al. 2013). We selected Jack1 as a richness estimator because it is appropriate for incidence data and is among the most accurate species richness estimators for intermediate-to-high sample coverage (Brose et al. 2003); evaluation of our data showed that Jack1 was highly correlated with observed species richness ($r^2 = 0.98$).

RESULTS

We collected and identified 10 775 ants of 49 species in pitfall traps in the patches (Appendix C: Table C1). Fire ants comprised 99.8% of nonnative ants and 68% of all ants. Genetic assessment of the spatial distribution of fire ant social forms revealed that one social form dominated each block (see *Methods*). Similar to previous studies (Macom and Porter 1996, reviewed in Tschinkel 2006), social form had a strong effect on fire ant density. Pitfall traps from polygyne blocks contained more than 10 times as many individual fire ants and 1.6 times the pitfall trap incidence of fire ants as those from

monogyne blocks (all $P < 0.001$). The number of fire ant nests was likewise higher in polygyne blocks (Appendix C: Fig. C1).

Corridors significantly increased the abundance of polygyne but not monogyne fire ants, as reflected by a significant interaction between the dominant social form present in a given block and patch type (with or without a corridor) on fire ant pitfall trap incidence (generalized linear mixed model; for interaction, $F_{1,12} = 7.48$, $P = 0.02$; for patch type, $F_{1,12} = 3.49$, $P = 0.09$; for block social form, $F_{1,6,9} = 5.64$, $P = 0.05$). Corridors had a positive effect on pitfall trap incidence in polygyne blocks, averaging 36% higher incidence compared to unconnected patches ($F_{1,12} = 6.67$, $P = 0.02$; Fig. 2A and Appendix C: Fig. C1). In contrast, corridors had no effect on pitfall trap incidence in monogyne blocks ($F_{1,12} = 0.91$, $P = 0.36$; Fig. 2A and Appendix C: Fig. C1).

Native ant species diversity in polygyne blocks was lower in connected patches than unconnected patches (Fig. 2B, Appendix C: Table C2, and Fig. C2). In polygyne blocks, connected patches had 23% lower species richness and 11% lower evenness than unconnected patches (Fig. 2B and Appendix C: Fig. C2, and Table C2). In monogyne blocks, however, there was no corridor effect on species richness or evenness (Fig. 2B and Appendix C: Fig. C2).

The lower species diversity in connected patches of polygyne blocks is most likely due to the higher abundance of fire ants in those patches (Fig. 2). Consistent with other studies (reviewed in Holway et al. 2002), fire ant pitfall incidence was negatively correlated with native ant species richness (Fig. 2C; overall: $r^2 = 0.65$, $P < 0.001$; from monogyne blocks: $r^2 = 0.56$, $P = 0.001$; from polygyne blocks: $r^2 = 0.70$, $P = 0.004$). Patches in which fire ants were absent from all pitfall traps had approximately six times as many native species as patches in which fire ants were present in every trap.

DISCUSSION

Our results reveal how the effect of corridors on ant communities can hinge on variation in dispersal ability and population density associated with colony social form of an invasive ant species. The different dispersal behaviors of monogyne and polygyne fire ant queens probably determined their response to corridors, and differences in colony density of the two forms in turn determined effects on native ant communities. Habitat patches connected by corridors are expected to harbor higher, not lower, species richness than unconnected patches of the same area (Gonzalez et al. 1998, Damschen et al. 2006, Gilbert-Norton et al. 2010). Yet, in blocks dominated by polygyne fire ants, we found negative net effects of corridors at the community level; species richness and evenness were both lower in connected than in unconnected patches. By increasing abundance of polygyne fire ants, patch connectivity via corridors apparently negated any potential benefit of corridors to other ant species. This finding provides a possible

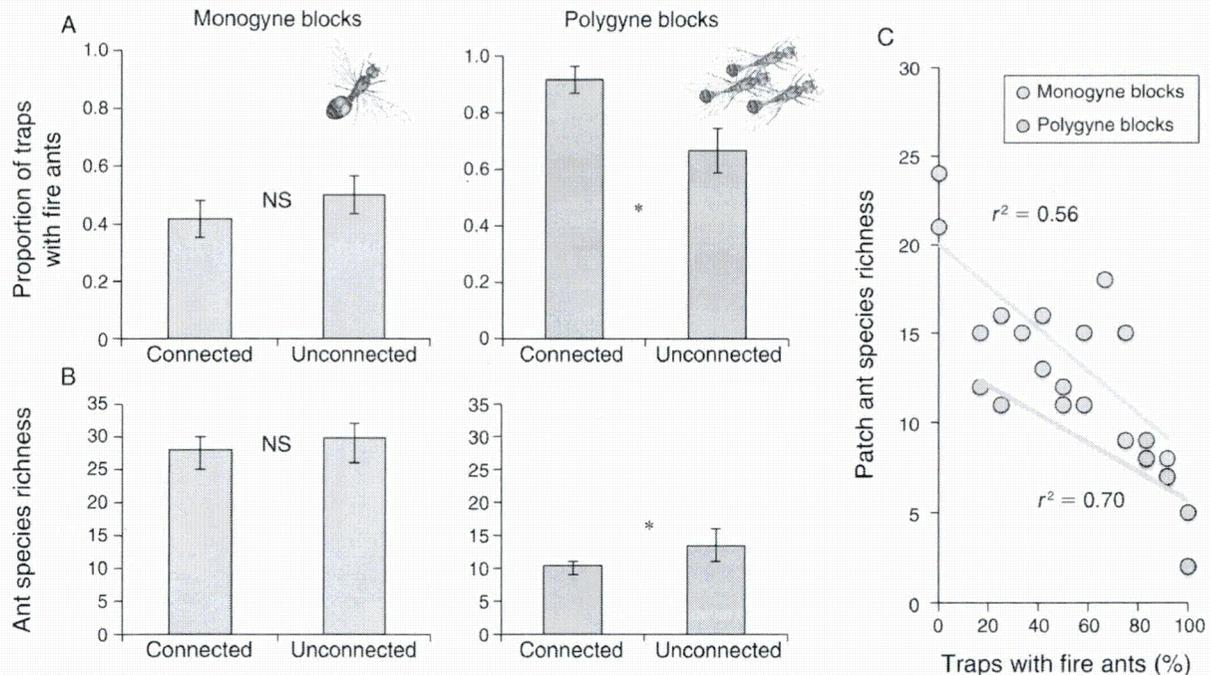


FIG. 2. (A) Effect of corridors on fire ant abundance, measured as proportion of traps with fire ants (mean \pm SE) in connected and unconnected patches (unconnected patches are represented by winged patches, which are equal in area and nearly equivalent in edge: area ratio to connected patches). Fire ants have two social forms: monogyne, which disperse widely but establish at lower densities, and polygyne, which tend to disperse poorly but establish at high densities. Blue bars indicate monogyne blocks ($n = 5$) and orange bars indicate polygyne blocks ($n = 3$). (B) Effect of corridors on native ant species richness, rarefied to lowest number of samples per patch type across blocks. Error bars indicate rarefaction 95% confidence intervals. Asterisks indicate statistical significance ($P < 0.05$) for the polygyne blocks (A, B). (C) Negative correlation of fire ant abundance and species richness of native ants in both monogyne and polygyne blocks. Points represent patches.

explanation for patterns from a previous study in a subset of our blocks that found lower evenness among ant genera in connected patches (Orrock et al. 2011), although that study did not provide data on ant species or social form.

Our results support the prediction that corridors promote spread of polygyne fire ants, increasing their densities in connected patches. Previous studies have also concluded that corridors increase population densities (Haddad and Baum 1999, Collinge 2000, Baum et al. 2004, Gilbert-Norton et al. 2010). In our study, fire ants occurred at low densities in the matrix habitat before patch creation (Appendix A; see also Tschinkel 2006). Because fire ants thrive in open and disturbed habitats (Stiles and Jones 1998, Tschinkel 2006), their populations increased in all patches upon creation. This increase was pronounced for polygyne fire ants in connected patches. We suggest two interrelated reasons. First, polygyne fire ants benefited from connectivity more than monogyne fire ants because they are more dispersal limited. Second, the high growth rate potential of polygyne colonies and the relatively short time scale of our study are conditions that favor large population size in connected patches (Hudgens and Haddad 2003).

The spread of polygyne fire ants via corridors may be a transient phenomenon. Indeed, two of the three polygyne blocks were created more recently (although patches within each block were created at the same time)

than the monogyne blocks and only those two blocks showed higher fire ant abundance in connected patches. Other studies in our system have found that that time mediates community dynamics (Damschen et al. 2008, Damschen and Brudvig 2012). However, the low number of newly created blocks in our study prevents us from teasing apart effects of patch age, social form, and corridors on fire ant abundance. In spite of potential transience, the ecological impacts of fire ant invasion on native ant communities can be dramatic during the initial phase of invasion. Porter and Savignano (1990) documented that during the initial phase of invasion, polygyne fire ants caused extreme declines in native ants. Morrison (2002) resampled the same sites as Porter and Savignano (1990) 12 years later and found that fire ant abundances had declined and native ants had partially recovered. This pattern may be common in invasions (Strayer et al. 2006, Dostál et al. 2013). Future work will be needed to assess the potentially transient nature of the role of corridors on invasions and the specific roles that corridors play in the long-term abundances of both invasive and native species.

Our interpretation of why connected patches in polygyne blocks had higher densities of fire ants than unconnected patches in the same blocks is tempered by the caveat that we did not observe the establishment or spread of fire ants between patches. Although we tested

and rejected alternative hypotheses (corridor orientation and land use history) that might account for the distribution of polygyne fire ants (Appendix B), the only unambiguous way to show that polygyne fire ants benefit from corridors would be to eliminate all fire ants from all patches, reintroduce the polygyne social form into the center patch of each block, and monitor their spread. Ethical considerations and logistical constraints prevented us from doing so.

Despite the detrimental effects of corridors presented here, the weight of empirical evidence still favors beneficial effects of corridors in conservation (Haddad et al. 2011). Many more studies have shown beneficial rather than detrimental effects of corridors on dispersal and diversity (Gilbert-Norton et al. 2010). In situations where corridors are likely to facilitate dispersal of invasive species, efforts should be made to mitigate their impacts, for example, by reducing the abundance or impact of the invasive species or by taking steps to reduce its spread.

Considering that concerns about corridors facilitating the spread of invasive species were raised almost 30 years ago (Simberloff and Cox 1987), it is perhaps surprising that empirical examples of the phenomenon have not been reported previously (Haddad et al., *in press*). This may be because invasive species often have high dispersal capabilities (Bufford and Daehler 2011), as is the case with the monogyne form of fire ants. Given that species with strong movement capacities are typically not dispersal limited, corridors are unlikely to facilitate their spread; indeed, landscape connectivity appears generally more important for native than for invasive species (Damschen et al. 2006, Minor et al. 2009). Some invasive species, however, have inherently poor dispersal abilities but spread well through accidental human transport (Mack and Lonsdale 2001; e.g., polygyne fire ants [Tschinkel 2006, King et al. 2009] and Argentine ants [*Linepithema humile*; Suarez et al. 2001]). In such cases with invasive species that are dispersal limited (but successful by other measures), corridors are likely to facilitate spread and could result in a net negative impact on native species. More studies on species with various dispersal abilities and with different habitats and types of corridors would provide further guidance on when corridors are most likely to spread invasive species across conservation lands.

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SUPPLEMENTAL MATERIAL

Appendix A

Pine matrix sampling and patch–matrix comparisons (*Ecological Archives* E095-179-A1).

Appendix B

Information on nest counts, social form determination, land use, and block orientation (*Ecological Archives* E095-179-A2).

Appendix C

Rectangular patch and nest results, rarefaction curves, species list, and diversity measures (*Ecological Archives* E095-179-A3).