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Transient effects of corridors on polygyne fire ants over a decade

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Abstract

1. Although corridors are frequently regarded as a way to mitigate the negative effects of habitat fragmentation, concerns persist that corridors may facilitate the spread of invasive species to the detriment of native species.
2. The invasive fire ant, Solenopsis invicta, has two social forms. The polygyne form has limited dispersal abilities relative to the monogyne form. Our previous work in a large-scale corridor experiment showed that in landscapes dominated by the polygyne form, fire ant density was higher and native ant species richness was lower in habitat patches connected by corridors than in unconnected patches.
3. We expected that these observed corridor effects would be transient, that is, that fire ant density and native ant species richness differences between connected and unconnected patches would diminish over time as fire ants eventually fully established within patches. We tested this prediction by resampling the three landscapes dominated by polygyne fire ants 6 to 11 years after our original study.
4. Differences in fire ant density between connected and unconnected habitat patches in these landscapes decreased, as expected. Differences in native ant species richness were variable but lowest in the last 2 years of sampling.
5. These findings support our prediction of transient corridor effects on this invasive ant and stress the importance of temporal dynamics in assessing population and community impacts of habitat connectivity.

KEYWORDS
connectivity, habitat fragmentation, Solenopsis invicta

INTRODUCTION

As habitat loss and fragmentation continue worldwide, landscape corridors are increasingly considered important for establishing connectivity among fragments to maintain biodiversity (Haddad et al. 2015). Possible negative effects of corridors, proposed decades ago (Simberloff & Cox, 1987), have received relatively little attention in empirical studies (Haddad et al., 2014). The potential for corridors to facilitate the spread of invasive species is particularly troublesome because interactions with invasive species could exacerbate fragmentation's deleterious effects on biodiversity. A review on possible negative effects of corridors found scant evidence that corridors facilitate the spread of invasive species (Haddad et al., 2014). This lack of support could be because invasive species are often strong dispersers such that corridors are unlikely to promote additional spread and impact (Levey et al., 2005). However, our understanding of whether dispersal ability can predict the degree to which invasive species use

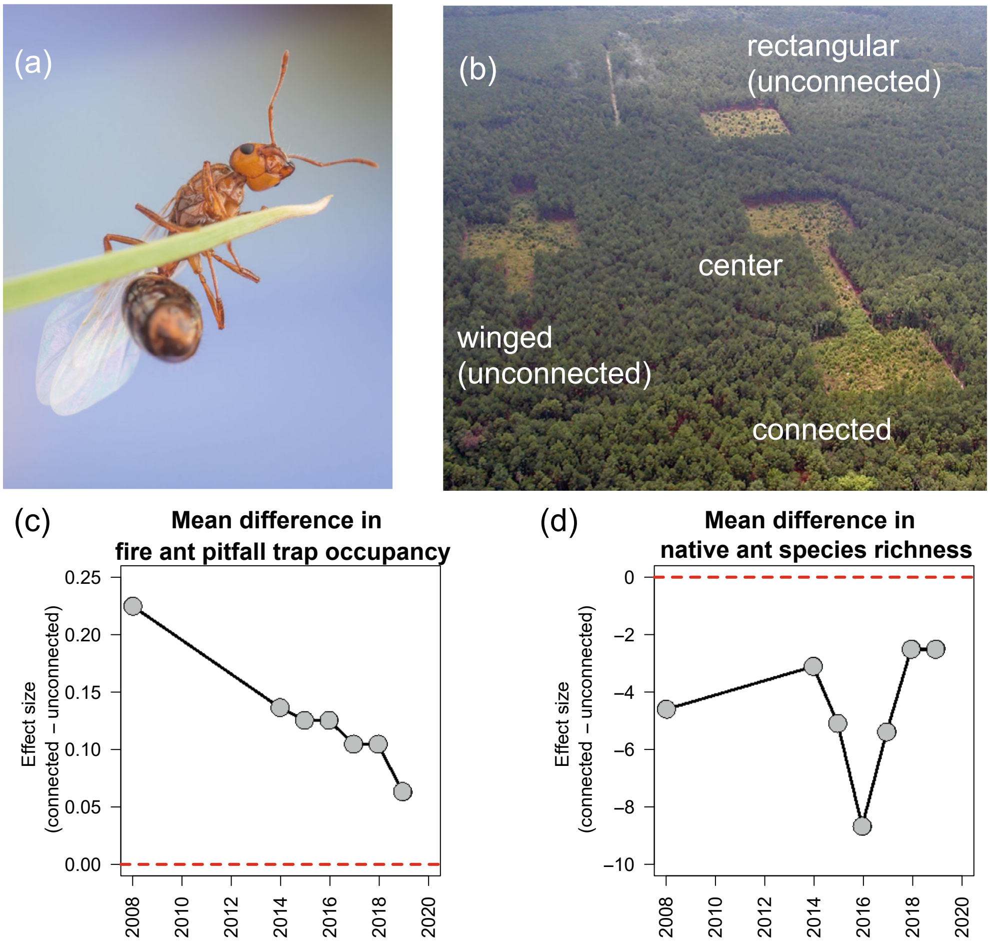

FIGURE 1 (a) A fire ant queen (*Solenopsis invicta*; photo credit: Nash Turley). (b) Aerial photograph of one experimental landscape (block) with patch types indicated (photo credit: Ellen Damschen). (c) Effect sizes of corridors are shown as mean difference in *S. invicta* pitfall trap occupancy between connected and unconnected patches over time. (d) Effect sizes of corridors are shown as mean difference in rarefied native ant species richness between connected and unconnected patches over time.

corridors is limited by a lack of large-scale studies where the effect of corridors is explicitly evaluated in the context of naturally dispersing invasive species. Experiments are needed to further understand the potential role of corridors in population expansion of invasive species and the interplay between dispersal ability and habitat connectivity.

We previously examined the role of corridors in the spread of the invasive fire ant *Solenopsis invicta* (Figure 1a) in a large-scale landscape experiment (Figure 1b; Resasco et al., 2014). We found that trait differences between two discrete fire ant colony social forms were important predictors of the effect of corridors on fire ant population densities and the subsequent impact of fire ants on native ants. Two distinct colony social forms defined primarily by differences in queen number exist in *S. invicta* and several closely related fire ant species. Monogyne colonies contain a single egg-laying queen, whereas polygyne colonies contain multiple egg-laying queens. Social form is determined by a large non-recombining supergene (Sb), which includes hundreds of linked genes that together determine a suite of characteristics that differ between ants of each social form, such as female size, female fecundity, male sperm numbers, and dispersal (Lawson et al., 2012; Wang et al., 2013). Male reproductive fitness and queen polyandry are linked to variation in the supergene Gp-9 in the fire ant *Solenopsis invicta* (Ross & Keller, 1995; Yan et al., 2020). Monogyne queens take part in large aerial mating flights and occur at lower population densities in established areas, whereas polygyne queens are typically limited to local movements at or near ground level and disperse over short distances but establish at higher population densities (DeHeer et al., 1999; Tschinkel, 1998). These differences in queen dispersal provide a link to understanding how corridors affect colonisation dynamics of the two social forms. In landscapes dominated by the polygyne social form, fire ant population densities were higher and native ant species richness was lower in connected than in unconnected habitat patches, likely because of competitive exclusion by fire ants (Resasco et al., 2014; Resasco & Fletcher Jr., 2021; Roeder et al., 2021). However, in landscapes occupied by the monogyne form, connectivity did not influence fire ant population densities and native ant species richness. Fire ant densities and native ant species richness were negatively correlated in both polygyne and monogyne form-dominated landscapes (Resasco et al., 2014).

Although this previous work shows the potential for corridors to facilitate the population establishment of an invasive species, there are reasons to expect only a temporary impact of corridors on the distribution of the polygyne form. Population simulations from a theoretical study (Hudgens & Haddad, 2003) suggest that characteristics of the fire ant system we studied (i.e., the limited dispersal and high population growth rate of the polygyne social form) result in positive, but transient, corridor effects. The only apparent difference between landscapes dominated by monogyne or polygyne fire ants was the time since patch creation. Two of the eight landscapes were created more recently than the others. Polygyne fire ants were found in both of these landscapes that were 1 year old at the time of sampling. They were also found in a 7- to 8-year-old landscape. Polygyne fire ants likely were present in these landscapes in low densities before patch creation.

We predicted that corridor effects on polygyne fire ants and, subsequently, on native ants would be transient, as, eventually, fire ants would establish at high densities in all patches (Resasco et al., 2014). Here, we test this prediction. We resampled experimental landscapes 6–11 years after the sampling in Resasco et al. (2014) to determine whether the effect of corridors on fire ant density and native ant species richness was transient.

METHODS

Our study site is the Savannah River Site in South Carolina, United States (3315^{0}N, 8138^{0}W), a National Environmental Research Park. In our previous study, we sampled fire ants in 2008. In this study, we resampled ants at the same time of year in 2014, 2015, 2016, 2017, 2018, and 2019 in the three experimental landscapes (blocks) that had been dominated by polygyne fire ants (Resasco et al., 2014). These blocks were created in 1999–2000 (n = 1) and 2007 (n = 2).

Each block is comprised of patches that were created by clearing a plantation forest of predominantly pines (Figure 1b). These open patches are much better habitat for fire ants than the closed pine plantation (Resasco et al., 2014). The patches are undergoing restoration to native longleaf pine savanna, an open, diverse, and endangered ecosystem (Noss, 2013). All blocks have a central patch (100 100 m) surrounded by four other patches 150 m away. Each surrounding patch is one of three randomly assigned types: connected, rectangular, or winged (Figure 1b). The connected patch is 100 100 m, with a 25-m-wide cleared corridor that connects it to the centre patch (1.375 ha total). Winged patches are also 100 100 m, but have two 75 25 m half corridors (“wings”) extending from opposite sides. Rectangular patches are 100 137.5 m. The additional area that makes these patches rectangular or winged is equal to the area of the corridor. Each block has one duplicate winged or rectangular patch. We sampled connected, rectangular, and winged patches using only one duplicate patch from each block that was randomly selected in the original study. In this study, we treat winged and rectangular patches as “unconnected patches” because we previously found that these patch types did not differ in fire ant density or native ant species richness (i.e., we found no evidence of patch-shape effects; Resasco et al., 2014).

In July 2014, we collected workers from each of six fire ant colonies interspersed over each patch to determine whether the polygyne social form was still the dominant social form in the resampled blocks. We placed sampled workers in 95% alcohol. We extracted DNA and used the informative gene Gp-9 to determine the colony social form. Procedures followed those described in Resasco et al. (2014). Information on colony social form determination by the Gp-9 gene is found in Valles and Porter (2003), Shoemaker and Ascunce (2010), and Yang et al. (2012).

We used pitfall traps to estimate fire ant density (prevalence per patch area) and native ant diversity. Pitfall sampling methodology slightly differed between 2014 and 2015–2019. We included eight pitfall traps from each patch across all time periods in our analysis (Figure S1). In 2014, we deployed 12 pitfall traps per patch in connected, winged, and rectangular patches, following the original sampling design used in 2008 (Resasco et al., 2014). These traps were placed along transects that extended diagonally from all corners of each sampled patch into the patch centre at 0, 21.5, and 50 m from the corner. Pitfall traps used in 2014 were 15-dram (55.5 ml, 28.6-mm inner diameter) plastic vials, while pitfall traps used in 2015–2019 were made with Corning 50 ml plastic conical centrifuge tubes (28.2-mm inner diameter). Pitfall traps were filled to approximately one-third of their volume with 50% propylene glycol and inserted flush with the soil surface. Pitfall traps were capped for at least 48 h to reduce “digging-in effects” (Greenslade, 1973). Once uncapped, traps were left open for 48 h. In 2015–2019, we distributed pitfall traps in a grid pattern for each patch for greater spatial coverage for a monitoring study. To align the traps with previous years, we selected traps located near the transects used to sample in 2008 and 2014 (Figure S1). Pitfall trap samples were sorted, and ants were identified according to species in the laboratory. We quantified the extent of fire ant invasion as pitfall trap occurrence across each patch.

We used generalised linear models (GLM) with a binomial response distribution to compare the corridor effect on fire ants in the polygyne-dominated blocks in the years following the previous study. Corridor presence (connected vs. unconnected), year (2014, 2015, 2016, 2017, 2018, 2019), and block (1–3) were the predictor variables, and fire ant pitfall trap occurrence (1 or 0 for presence or absence) was the response variable. We included an interaction term between corridor effect and year. We fitted the model using bias-reduced GLM, applying the “brglmFit” function on the brglm2 package (version 0.7.1) to accommodate the high levels of occupancy observed in several patches (Kosmidis 2021)

We estimated species richness for connected and unconnected patches for each year to determine the effects of corridors on native ant diversity. We estimated species richness with sample-based rarefaction on incidence data from pitfalls using the “specaccum” function in the “vegan” R package (Oksanen et al., 2013). To assess statistical significance in differences between connected and unconnected

TABLE 1 Fire ant pitfall trap occurrence (means, SDs, model estimates, and 95% CIs) and species richness (estimated species richness, standard deviations, 95% CIs, and rarefied sample sizes).

Year	Type	Mean occurrence	SD	Estimated occurrence	95% CIs	Species richness	SD	95% CIs	Samples
2008	Connected	0.96	0.07			6.7	0.45	7.6–5.82	13
	Unconnected	0.73	0.46			11.3	1.6	14.44–8.16	13
2014	Connected	0.83	0.07	0.92	0.85–1.00	10.7	1.0	12.66–8.74	15
	Unconnected	0.70	0.21	0.67	0.54–0.81	13.8	1.6	16.94–10.66	15
2015	Connected	1.0	0	0.98	0.96–1.00	5.7	0.8	7.27–4.13	12
	Unconnected	0.88	0.17	0.90	0.82–0.98	10.8	1.6	13.94–7.66	12
2016	Connected	1	0	0.98	0.96–1.00	4.6	0.6	5.78–3.42	15
	Unconnected	0.88	0.13	0.90	0.82–0.98	13.3	1.7	16.63–9.97	15
2017	Connected	1	0	0.98	0.96–1.00	7.3	0.8	8.87–5.73	16
	Unconnected	0.90	0.10	0.91	0.84–0.99	12.7	1.1	14.86–10.54	16
2018	Connected	1	0	0.98	0.96–1.00	9.3	1.5	12.24–6.36	16
	Unconnected	0.90	0.10	0.91	0.84–0.99	11.8	1.3	14.35–9.25	16
2019	Connected	1	0	0.99	0.98–1.00	9.3	1.5	12.24–6.36	16
	Unconnected	0.94	0	0.95	0.89–1.00	11.8	1.3	14.35–9.25	16

patches, we used the resulting 95% confidence intervals rarified to equivalent numbers of samples.

RESULTS

Blocks dominated by polygyne fire ant colonies sampled in 2008 for the original study remained dominated by the polygyne social form (87% of samples in 2008 and 81% in 2014). Fire ants were the most common ant species in all time periods. Fire ants comprised 95% of the ants we collected in 2008, 54% in 2014, 81% in 2015, 88% in 2016, 91% in 2017, 84% in 2018, and 81% in 2019. The number of individual fire ants per trap in polygyne fire ant-dominated blocks was much higher in 2008 than in any subsequent year (2008 [average SD]: 104 159, 2014: 5 5, 2015: 21 20, 2016: 37 64, 2017: 58 106, 2018: 38 44, 2019: 38 49). Non-native species other than fire ants were few, and rare: Brachymyrmex patagonicus, Cyphomyrmex rimosus, and Strumigenys membranifera.

The differences in proportion of fire ant pitfall trap occurrences between unconnected and connected patches declined over time (Figure 1c). The mean difference in fire ant pitfall trap occurrence between connected patches and unconnected patches was higher in the original study (approximately 32% higher in connected patches than unconnected patches) than in subsequent years, which decreased approximately linearly (19%, 12%, 12%, 10%, 10%, and 6% higher in connected patches than unconnected patches in 2014–2019, respectively, Table 1, Figure 1c). We did not detect a significant interaction between corridor presence and year ($F_{5,416}$, $p = 0.90$) and subsequently dropped the interaction from the model. We found significant overall effects of block ($F_{2,421}$, $p < 0.001$), year ($F_{5,423}$, $p = 0.001$), and corridor presence ($F_{1,428}$, $p = 0.0001$) on fire ant pitfall trap occurrence. However, contrasts of fire ant pitfall trap occurrence between connected and unconnected patches within years did not statistically differ ($p >$ or $= 0.17$). Across years, estimates of pitfall trap occupancy by fire ants for connected patches overlapped or nearly overlapped with 95% CIs of unconnected patches, and vice versa (Table 1). In the original study, species richness of native ants was lower in connected patches than in unconnected patches (Resasco et al., 2014; Table 1). This effect persisted in the first four of the six resampled years (2014–2017), although the magnitude was quite variable (Table 1 and Figure 1d). However, in the last two resampled years, the magnitude of the effect was the lowest, and species richness estimates did not significantly differ between connected and unconnected patches (means of estimates overlapped with 95% CIs; Table 1, Figure 1d).

DISCUSSION

Conservation corridors are inherently long-term investments, yet few studies evaluate their long-term dynamics in connected and unconnected landscapes. Our results suggest the need to consider temporal dynamics when evaluating corridor effects on invasive species and the impact of those species on native communities. Specifically, we show that the positive effect of corridors on invasive polygyne fire ants and the resulting negative effect on native ants diminish over time. These results are consistent with those of previous studies that have shown that temporal dynamics can play an important role in the context of how corridors affect plant communities (Damschen et al., 2019, Haddad et al., 2015; see also Gibb et al., 2022).

We predicted in an earlier study that the observed effect of corridors on polygyne fire ants may be a transient phenomenon (Resasco et al., 2014). In agreement with that prediction, we found that differences in fire ant pitfall trap occurrence between connected and unconnected patches declined in polygyne fire ant-dominated blocks over the intervening decade. This was likely due to the eventual spread of polygyne fire ants throughout unconnected patches. Morrison (2002) resampled sites in Texas 12 years after the initial invasion of the polygyne social form and documented declines in polygyne fire ants and recovery in native ant species richness. In our study system; however, there was an apparent lagged response of native ant diversity in connected patches relative to unconnected patches; species richness remained lower in connected patches compared to unconnected patches, but in the final 2 years of resampling the effect was small and nonsignificant. This suggests a legacy effect of high densities of polygyne fire ants, which may have been more severe when habitat patches were newly created and initial fire ant populations expanded in two of three blocks.

Our prior findings (Resasco et al., 2014) as well as a meta-analysis (Haddad et al., 2014) suggest that corridors are most likely to affect the dynamics of those few invasive species that are inherently constrained by weak dispersal. Because invasive species are often strong dispersers, we expect corridors to have weak effects on invasive species, with exceptions being species that have relatively limited dispersal capabilities (e.g., the polygyne social form of fire ants). Our findings here suggest that, even in these cases, effects may be transient. More generally, our results imply that understanding the community-level consequences of corridors will require understanding the nature of local interactions between native and invasive species and the degree to which those interactions change over time.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Supporting Information.

Figure S1. Sampling layout of pitfall traps used in this study. Filled circles represent 2008 and 2014 pitfall traps and open circles represent 2015–2019 pitfall traps included in the analyses.

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