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Ants disperse seeds farther in habitat patches with corridors

increase plant diversity.

KEYWORDS

Abstract

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INTRODUCTION

Globally, habitat loss and fragmentation are major threats to biodiversity (Haddad et al., 2015; Morreale et al., 2021). In addition to the impacts of habitat loss, habitat fragmentation decreases connectivity among patches and increases potentially negative edge effects (Ries et al., 2004, 2017). These changes to habitat amount, habitat quality, and landscape structure can affect the colonization and extinction dynamics of species, leading to changes in community composition (Damschen et al., 2019). Compositional changes, as well as changes to the behavior of organisms, can transform interactions between species, including predation (Hawn et al., 2018; Martinson & Fagan, 2014; Orrock et al., 2003; Orrock & Damschen, 2005), pollination (Dicks et al., 2021; Hadley & Betts, 2012; Tewksbury et al., 2002; Townsend & Levey, 2005), and seed dispersal (Brudvig et al., 2015; Nield et al., 2020; Ripple et al., 2015). Although there is a large literature on fragmentation effects on seed dispersal by vertebrates (Levey et al., 2005; Ripple et al., 2015; Tewksbury et al., 2002),

1

Habitat fragmentation impacts ecosystems worldwide through habitat loss,

reduced connectivity, and edge effects. Yet, these landscape factors are often

confounded, leaving much to be investigated about their relative effects, espe-

cially on species interactions. In a landscape experiment, we investigated the

consequences of connectivity and edge effects for seed dispersal by ants.

We found that ants dispersed seeds farther in habitat patches connected by

corridors, but only in patch centers. We did not see an effect on the total num-

ber of seeds moved or the rate ants detected seeds. Furthermore, we did not

see any differences in ant community composition across patch types,

suggesting that shifts in ant behavior or other factors increased ant seed dis-

persal in patches connected by corridors. Long-distance seed dispersal by ants

that requires an accumulation of short-distance dispersal events over genera-

tions may be an underappreciated mechanism through which corridors

ants, connectivity, corridors, edge effects, fragmentation, myrmecochory, seed dispersal

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comparatively less is known about the effects of fragmentation on seed dispersal by ants (Bieber et al., 2014; Christianini & Oliveira, 2013; Crist, 2009; Mitchell et al., 2002). Here, we aim to increase the mechanistic understanding of how ant seed dispersal mutualisms respond to fragmentation with an experiment that separates the effects of fragmentation into connectivity and edge amount.

Ants could play an essential role in plant population and community responses to habitat fragmentation. With about 11,000 plant species dispersed by ants, myrmecochory is an important mechanism of seed dispersal structuring plant communities (Giladi, 2006; Lengyel et al., 2010; Penn & Crist, 2018). When ants disperse seeds, the collected seeds may be protected from seed predators, moved to nutrient-rich trash middens in or near the ant's nest that are favorable germination sites, and escape from competition with the parent plant (Culver & Beattie, 1980; Giladi, 2006; Handel, 1978; Lengyel et al., 2010; Penn & Crist, 2018). In return, the ants receive a food resource in the form of a lipid-rich appendage on the seed coat called an elaiosome (Beattie, 2010). However, there is not always evidence that consuming elaiosomes is essential to the ants (Mitchell et al., 2002; Schultz et al., 2022; Warren et al., 2019). The elaiosome may also attract seed predators, but there is evidence that this adaptation has evolved in plants for selecting dispersers over predators or for manipulating the behavior of the dispersers (Giladi, 2006; Levey & Byrne, 1993; Warren & Giladi, 2014). Because ants typically disperse seeds over shorter distances, ant-mediated seed dispersal is especially vulnerable to disruption due to fragmentation.

Unlike prior studies that have focused on the effects of fragment size (Bruna et al., 2005; Mitchell et al., 2002) and dynamics at boundaries across habitat edges (Ness, 2004; Ness & Morin, 2008; Warren et al., 2015), our study focuses on the individual and interactive effects of edge and connectivity. Mitchell et al. (2002) found that the composition of seed-dispersing ant communities differed between large and small forest fragments. Bruna et al. (2005) found no evidence that fragment size affected ant–plant interactions (i.e., plants that ants use for shelter in exchange for protection for the plant) or ant species richness, but found lower densities of ant–plants in smaller fragments.

With fragmentation, the amount of edge relative to interior habitat proportionately increases. This results in potential changes to abiotic and biotic gradients at habitat edges that can have consequences for seed-dispersing ants and their plant mutualists (Crist, 2009). For example, in eastern deciduous forests, habitat edges typically have fewer ant-dispersed plants and mixed effects of edges on the major group of seed-dispersing ants, *Aphaenogaster* spp. (Ness, 2004; Ness & Morin, 2008; Warren et al., 2015). Shorter seed dispersal has been found at distances closer to an edge (Ness, 2004) and ants direct seed dispersal away from the edge toward the habitat interior (Ness, 2004; Warren et al., 2015), suggesting that altered ant behavior plays a role in edge effects on ant-dispersed plant distributions.

In a landscape-scale experiment that manipulated habitat connectivity and edge amount across habitat patches, we investigated the consequences of fragmentation on seed dispersal by ants. Specifically, we asked the following questions: (1) How is seed dispersal by ants impacted by (a) connectivity and edge amount and (b) local-scale proximity to a habitat edge? (2) To what extent might differences in ant-mediated dispersal across patches be driven by (a) changes in ant community composition and (b) changes in the behavior of individual ant species?

METHODS

Experimental landscapes

We conducted this study at the Savannah River Site (SRS), a Department of Energy (DOE) National Environmental Research Park in New Ellenton, SC, USA. Our experimental landscapes are managed by the US Department of Agriculture Forest Service-Savannah River and were established by clearing patches of mature trees within pine plantations in the winter of 1999 and 2000. The habitat patches within our experimental landscapes have been managed as restored longleaf pine savannas. Thus, the habitat patches are relatively open woodlands embedded in more shaded pine plantations. Our experimental design creates patches and corridors of suitable habitat surrounded by a matrix of unsuitable habitat. Previous work on the effects of fragmentation on seed dispersal by ants has largely focused on dynamics within forested fragments (Giladi, 2006; Warren & Giladi, 2014). Given that ants disperse seeds in a wide range of ecosystems (Lengyel et al., 2010), more studies expanding outside forests are needed to determine whether these results apply more generally. Longleaf pine savannas of the southeastern United States are one of the most imperiled ecosystems in North America, with less than 3% of its original range remaining today (Frost, 2006; Noss, 1988, 2013).

To reduce woody shrub encroachment and maintain an open canopy, prescribed burns are implemented every 2–3 years and herbicide and brush-cutting are applied periodically. Each experimental landscape block consists



FIGURE 1 Experimental landscapes (a), focal species (b), and seed depot setup (c). In (a), circles indicate the potential locations of seed dispersal depot observations (four locations per patch type). (b) Photo of *Piriqueta cistoides*. (c) Seed dispersal depot (photo credit: Melissa A. Burt).

of a 1-ha square center patch surrounded by four peripheral patches that are equal in area (\sim 1.4 ha) but differ in the amount of habitat connectivity or edge (Figure 1). One peripheral patch is connected to the center patch by a 150 \times 25-m corridor (hereafter "connected"). The isolated patches are also 150 m from the center patch and vary in their edge amount. The winged patch type (hereafter "isolated high edge") is a 100×100 -m square with two 75×25 -m projections on either side of the patch. The rectangular patch type (hereafter "isolated low edge") consists of a 100×100 -m square with an area equal in size to the corridor added to the part of the patch farthest from the center patch. Each block contains one of each patch type and a duplicate of one of the isolated patch types. To test the effects of connectivity, we compare the high-edge and connected patch types. To test the effects of edge amount, we compare the high-edge and low-edge patch types. We investigated edge effects within the patch as a function of proximity to the matrix. We conducted seed dispersal assays in four experimental blocks because these had preexisting populations of Piriqueta cistoides in each patch type.

Focal plant species

Seed dispersal assays (described below) were conducted with the forb, *P. cistoides* (L.) Griseb. (common name: pitted stripeseed; family: Turneraceae). It can be an annual or perennial and is endemic to the southeastern United States (USDA NRCS, 2020). Populations are distributed across the coastal plain of South Carolina, Georgia, and Florida in sandy soils located along woodland borders. They flower and disperse seeds from May through September (Radford et al., 1964). On average, seed capsules contain 12–20 seeds that are 1.8–2.2 mm long (Ornduff & Perry, 1964; Radford et al., 1964). Each seed has an elaiosome along the entire length of its seed (Radford et al., 1964) and the seeds are dispersed by ants (Cumberland & Kirkman, 2013).

Ant community of longleaf pine savannas

The open habitats of the SRS are home to a diverse ant community dominated by Solenopsis invicta, Dorymyrmex bureni, Crematogaster lineolata, and Pheidole species (Resasco et al., 2014; Resasco & Fletcher, 2021), which have each been documented as seed dispersers in longleaf pine savanna (Stuble et al., 2010). The most common species in our study site, S. invicta, is an invasive non-native species (Tschinkel, 2006). S. invicta has been shown to both disperse and predate seeds in their invaded range, potentially disrupting seed dispersal mutualisms with native ant seed dispersers (Ness, 2004; Stuble et al., 2010; Zettler et al., 2001). Although S. invicta outcompetes native ants foraging for myrmecochorous seeds, in longleaf pine savanna they move seeds to distances commensurate with native ant seed dispersers (Stuble et al., 2010). Additionally, a large proportion of seeds moved to S. invicta trash middens were not damaged (Cumberland & Kirkman, 2013).

Seed dispersal assays

We conducted seed dispersal assays in July-August of 2018 during peak seed production in *P. cistoides*

(M. A. Burt, personal observation). In each patch type within each block, we conducted observations of seed removal at four seed depots, two located at the center of each patch (\sim 37.5 m from the nearest edge) and two located at the edge of each patch ($\sim 12.5 \text{ m}$ from the nearest edge) (4 blocks \times 3 patch types \times 2 edge distances \times 2 replicates = 48 depots total; Figure 1). Each seed depot was made with an open 10-cm petri dish in which we melted four approximately 1-cm openings around the edge to facilitate movement of ants carrying seeds into and out of the depot. The largest ants, major workers of Pogonomyrmex badius, are 7-9 mm long (Deyrup, 2016). This method has been used in previous studies and facilitates observing the seeds on sandy soil during the observation (e.g., Stuble et al., 2010). We also conducted a pilot experiment in 2016 where we observed that even the smaller ants visiting seed caches were able to climb up and over the sides of the petri dishes while holding a seed in their mandibles (Methods and Results in Appendix S1). In each depot, we placed 10 P. cistoides seeds that we collected from local populations at SRS during the same growing season. We chose to use consistently 10 seeds in depots to limit density-dependent variance across observations. Additionally, while seed capsules typically contain between 12 and 20 seeds (Ornduff & Perry, 1964), the seeds gradually fall away from the capsule when it open, which would decrease the total number of seeds on the ground at any given time. We observed each depot individually until all seeds were removed or up to 60 min, whichever occurred first. During each observation, we recorded the amount of time it took for ants to discover seed depots (i.e., when ants first entered the depot and interacted with seeds), the time when ants removed each seed, the distance ants dispersed seeds, and the ant species that dispersed the seeds. We collected voucher specimens of ants visiting depots for later confirmation of identity with a microscope. Because temperature change associated with time of day impacts ant activity, we randomized the order in which we conducted observations within a block and only conducted observations when ants were active (~800-1200 h). Observations for individual blocks were done over two days.

Statistical analyses

To test how patch type and edge proximity affected ant seed dispersal (Q1), we used linear mixed models (LMMs) and generalized linear mixed models (GLMMs) for four response variables: time to discovery, the count of seeds dispersed from a depot, ant species richness visiting seed depots, and seed dispersal distance. We averaged the seed dispersal distance across seeds within a seed depot and treated each depot as a replicate. If assumptions of normality and homoscedasticity were met, we used LMMs. When assumptions were not met, we either transformed the response variable or we used GLMMs with an appropriate error distribution (see Appendix S1: Table S4 for more details). For each model, we checked relevant assumptions to that test including testing for overdispersion in the GLMMs. For each mixed effects model, we specified patch type, edge proximity, and the interaction between patch type and edge proximity as fixed effects and patch nested within block as a random effect. We used Wald χ^2 tests to assess fixed effects using type III tests when the interaction between patch type and edge proximity was at least marginally supported (p < 0.10) and type II tests when it was not. If the interaction between patch type and edge proximity was a significant predictor, we split the analysis into two separate models analyzing the data from seed depots located along the edge and within the center of patches separately. When fixed effects were significant predictors of the response variable, we used a Tukey post hoc test to assess differences between levels.

To investigate the extent that differences in ant-mediated dispersal were driven by changes in ant community composition and ant behavior (Q2), we conducted additional analyses. First, to determine whether the relative frequency that different ant species were observed moving seeds from seed depots was different across patch types and edge proximity, we performed Fisher's exact tests on contingency tables. Second, to test whether differences across patch types were driven by shifts in behavior of individual ant species, we used mixed effects models similar in structure to those described above for analyses across species for the seed depot data in which we dropped individual species one at a time from the models. If the behavior of an individual species was driving the overall pattern, we predict that dropping that species would qualitatively change the pattern relative to the pooled dataset.

All analyses were conducted in R version 4.1.1 (R Development Core Team, 2011). We used the lme4 package for mixed effects models, the car package for Wald χ^2 tests, and the emmeans package for Tukey multiple comparison post hoc tests (Bates et al., 2015; Fox & Weisberg, 2019; Lenth, 2020).

RESULTS

Approximately 84% of our seed dispersal depots were visited by ants. We observed 11 ant species dispersing seeds (Figure 2; Appendix S1: Table S3). Isolated Low Edge

Isolated High Edge

Connected

(a)



Isolated High Edge Isolated Low Edge Connected



FIGURE 2 Mosaic plots showing the frequency of seed depots visited by each seed-dispersing ant species across patch types and edge proximities. Horizontal widths of the bars indicate the relative abundance of each ant species, and the vertical height of the bars indicates the relative abundance across patch type (a) and edge proximities (b). Single lines indicate patch types and edge proximities where the species was not observed visiting seed dispersal depots.

The most common species were *S. invicta* (visited 36% of seed depots) and *C. lineolata* (visited 20% of seed depots). We found no effects of patch type, edge proximity, or their interaction on the amount of time it took

for ants to discover seed depots, the number of seeds removed from seed depots, or the number of ant species that removed seeds from seed depots (all p > 0.05; Appendix S1: Table S4).

Table S4).

p = 0.95; Figure 2b).

On average, ants dispersed seeds approximately 96 cm

in connected patches versus approximately 48 cm in isolated high-edge patch types, and this apparent difference

was caused by even higher differences in dispersal in the

centers of connected patches. In analyses pooled across

species, we found a marginally significant interaction

between patch type and edge proximity such that seed dis-

persal distance was positively affected by connectivity, but

only in patch centers (Figure 3; Appendix S1: Table S4).

When considered separately, ants dispersed seeds about

four times as far in the center of connected patches than

in the center of isolated patches (connected centers:

mean: \sim 125 cm, median: 67.7 cm; isolated centers: mean:

~32 cm, median: 31.0; $\chi^2 = 11.14$, p = 0.004; Figure 3;

Appendix S1: Table S4), but there was no difference in

seed dispersal among patch types for seed dispersal depots

at patch edges ($\gamma^2 = 0.56$, p = 0.76; Figure 3; Appendix S1:

removed, the overall pattern of longer seed dispersal dis-

tances in the center of connected patches generally holds

(see Appendix S1 for full details). This is despite mixed

results when different species were lost. We also found

no association between the relative abundance of species

visiting seed depots and patch type (Fisher's exact test:

p = 0.24; Figure 2a) or edge proximity (Fisher's exact test:

When we conducted analyses with individual species

DISCUSSION

Our results show that connecting fragmented habitat patches via corridors may have important effects on ant-mediated seed dispersal. We found ants dispersed seeds farther in habitat patches with corridors, an effect that depended on within-patch proximity to an edge. Variation in seed dispersal distance across habitat patches was not explained by fragmentation-mediated changes to ant community composition, but instead seemingly resulted from changes in behavior across multiple individual species in the ant community. The differences we observed in dispersal distances suggest fragmentation likely has important consequences for plant colonization dynamics.

We found that ants dispersed seeds about twice as far in connected patches, a result caused by dispersal in patch centers that was four times farther than in isolated patches. This difference of approximately 48 cm at the patch scale and approximately 93 cm in patch centers represents quite a large difference relative to total ant seed dispersal. Previous studies found that ants usually disperse seeds approximately 75–200 cm on average (Culver & Beattie, 1980; Gómez & Espadaler, 2013; Stuble et al., 2010). Thus, in unconnected patches, dispersal is lower than average, suggesting that isolation reduces dispersal distance. These seemingly short-distance dispersal



FIGURE 3 Distance seeds dispersed from dispersal depots. Patch type is designated by color and point shape: purple circles for connected, black triangles for isolated high edge, and gray squares for isolated low edge. Significant differences among patch types within edge proximity categories are indicated by different letters.

events by ants accrue over generations, yielding more rapid colonization of distant patches over time. Previous work has shown that the dispersal of seeds by ants results in less clumped distributions of offspring (Mitchell et al., 2002; Pudlo et al., 1980; Zelikova et al., 2011), potentially because of less intraspecific competition (Culver & Beattie, 1980). Therefore, our finding that greater dispersal distances in connected patches suggests that greater connectivity between habitat patches could lead to plant communities in which intraspecific competition would be less limiting for ant-dispersed plants. Future work should follow seedlings germinating from myrmecochorous seeds to determine whether this connectivity effect produces cascading consequences for populations of myrmecochorous plants.

Our results help resolve two unexplained long-term dynamics of plant communities also observed in this experiment. Previous work shows plant species richness continues to increase through time through the positive effects of connectivity on colonization (Damschen et al., 2006, 2008, 2019). Additionally, plants with no obvious long-distance dispersal mechanism, such as P. cistoides, colonize new areas at a similar rate as birdand wind-dispersed species (Damschen et al., 2008, 2019). The results of our ant seed dispersal experiment suggest seed dispersal by ants as one potential mechanism that would result in a higher chance of colonization. Although S. invicta, the most prevalent seed-dispersing ant in our experiment, may damage seeds of other myrmecochorous plant species (Zettler et al., 2001), Cumberland and Kirkman (2013) found little damage to P. cistoides seeds in their aboveground trash middens. This suggests that S. invicta may not limit the accumulation of species in connected patches.

How does greater connectivity via corridors lead to greater dispersal distances? We hypothesized that patch isolation or edge effects would affect seed dispersal through effects on ant community composition or ant behavior. In our experiment, however, we did not detect evidence of an effect of patch connectivity on ant community compositional changes. Conversely, we found that patch type and edge proximity did not affect the composition of ant species visiting seed dispersal depots, suggesting that differences in seed dispersal distance are not mediated by ant community compositional differences. Further, the robustness of our seed dispersal patterns to dropping individual ant species suggests that the changes in seed dispersal difference are not mediated by the seed dispersal abilities of any one species alone. Instead, changes to seed dispersal behavior seem to be occurring across the community as a whole. While not measured in this study, it is possible that changes to worker or colony density in the center of connected

patches could cause workers to travel farther from their nest to forage for resources. A higher nest density may result in workers having to travel further to forage if resources are limited and a lower nest density may mean that colonies were more likely to be further away from our seed depots.

Our finding that seeds were dispersed at similar distances along the edges of both connected and isolated patches suggests that corridors are not enough to overcome the negative effect of being close to an edge. Our experimental habitat patches are fragments of restored longleaf pine savanna surrounded by a timber plantation matrix. Thus, plant and ant communities and their mutualisms are affected by shading caused by the densely spaced trees at patch edges. Past observational studies have also found strong effects of edges on the direction of seed dispersal and the distribution of surviving adult plants after dispersal (Ness, 2004; Ness & Morin, 2008), with areas in close proximity to an edge typically having fewer ant-dispersed plants than interior sites (Ness & Morin, 2008; Warren et al., 2015).

Taken together, our results demonstrate that increasing connectivity via corridors can positively impact seed dispersal by ants. It has long been known that corridors increase seed dispersal by birds at the patch scale (Levey et al., 2005; Tewksbury et al., 2002), and this work now demonstrates that this connectivity even impacts short-distance seed dispersal events by ants. Given that ant-dispersed plants are globally widespread, the implications of this result suggest that seed-dispersing ants and myrmecochorous plants will benefit from restoring connectivity.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Burt et al., 2022) are available from Zenodo: https://doi.org/10.5281/zenodo.7150123.

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SUPPORTING INFORMATION

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

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