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Habitat fragmentation alters the distance of abiotic seed dispersal through edge effects and direction of dispersal

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Abstract. Habitat loss and fragmentation are leading causes of species declines, driven in part by reduced dispersal. Isolating the effects of fragmentation on dispersal, however, is daunting because the consequences of fragmentation are typically intertwined, such as reduced connectivity and increased prevalence of edge effects. We used a large-scale landscape experiment to separate consequences of fragmentation on seed dispersal, considering both distance and direction of local dispersal. We evaluated seed dispersal for five wind- or gravity-dispersed, herbaceous plant species that were planted at different distances from habitat edges, within fragments that varied in their connectivity and shape (edge-to-area ratio). Dispersal distance was affected by proximity and direction relative to the nearest edge. For four of five species, dispersal distances were greater further from habitat edges and when seeds dispersed in the direction of the nearest edge. Connectivity and patch edge-to-area ratio had minimal effects on local dispersal. Our findings illustrate how some, but not all, landscape changes associated with fragmentation can affect the key population process of seed dispersal.

Key words: *edge effect; habitat fragmentation; landscape corridor; seed dispersal.*

INTRODUCTION

Habitat loss and fragmentation are leading causes of biodiversity decline (Haddad et al. 2015, Newbold et al. 2015), yet the mechanisms linking such landscape changes to biodiversity loss remain unresolved. This uncertainty results from the highly interrelated patterns and processes that accompany habitat loss and fragmentation (Didham et al. 2012). For example, dispersal is a key process impacted by fragmentation, mediating immigration and emigration rates and affecting population persistence in fragmented landscapes (Templeton et al. 2001, Soons et al. 2005). However, fragmentation may influence dispersal through a variety of intertwined landscape changes, such as reductions to patch connectivity and alterations to patch edge-to-area ratios (Levey et al. 2005, Damschen et al. 2014), making it difficult to know how dispersal is affected by fragmentation.

Understanding fragmentation effects on seed dispersal requires consideration of how the processes that mediate seed dispersal are themselves modified by fragmentation (Nathan et al. 2008). For example, habitat fragmentation modifies seed dispersal of wind-dispersed plant species by influencing wind patterns (Soons et al. 2005, Damschen et al. 2014, Herrmann et al. 2016). Broadly, modifications to wind patterns by fragmentation can affect seed dispersal (Nathan and Katul 2005, Bohrer et al. 2008, Damschen et al. 2014). For a given habitat amount, spatial configuration and patch shape can affect important factors like connectivity or edge-to-area ratio; both factors have been found to affect wind speed/direction (Damschen et al. 2014).

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Because the distance of dispersal is often assumed to be the most important aspect of dispersal, the direction of dispersal is rarely considered, especially in the context of fragmentation (van Putten et al. 2012, Rogers et al. 2019). However, fragmentation might influence dispersal directionality through similar mechanisms to effects on dispersal distance. For example, in open habitats surrounded by forest, wind-dispersed seeds may disperse directionally and to greater distances along the long axis of a fragment or toward the edges, due to fragmentation and edges redirecting and accelerating wind in these directions (Detto et al. 2008, Damschen et al. 2014). The direction in which a seed disperses can influence both how far it travels (Nathan and Muller-Landau 2000) and its probability of finding a suitable site to establish and grow (Greene et al. 2008, Horvitz et al. 2014). Directional dispersal is likely to influence where plants occur in fragmented landscapes (Nathan and Muller-Landau 2000, Levine 2003) because seeds that disperse into unsuitable habitat, such as into an inhospitable matrix, result in lower population persistence (Rand 2000, Levine and Murrell 2003).

Virtually all fragmentation research has focused on long-distance dispersal (e.g., Rodríguez-Cabala et al. 2007, Uriarte et al. 2011), yet, it remains unclear if or how habitat fragmentation alters dispersal patterns at a local scale (i.e., short-distance dispersal). Resolving these effects is important because the vast majority of seeds disperse short distances, with consequences for population and community dynamics; for example, by altering neighborhood densities and the arrival to suitable microsites in heterogeneous environments (Nathan and Muller-Landau 2000, Law et al. 2003, Caughlin et al. 2014).

To understand how fragmentation affects local seed dispersal, we studied dispersal distances of five wind and gravity-dispersed herbaceous species. We did so within a replicated, large-scale fragmentation experiment that overcomes the confounding effects of observational fragmentation studies by experimentally disentangling patch connectivity, patch edge-to-area ratio (patch shape), and edge proximity, while controlling for habitat amount, matrix type, and patch area (Tewksbury et al. 2002). Our study system is comprised of open savanna fragments, surrounded by a matrix of pine plantations. We frame hypotheses based on how wind is affected by the landscape structure of our experiment (Damschen et al. 2014). We studied local-scale seed dispersal (to 5 m; hereafter "seed dispersal") and asked five questions:

1) How does patch connectivity affect seed dispersal distance? We hypothesized that patch connectivity would increase dispersal distances, due to higher wind speeds in connected patches.
2) How does patch edge-to-area ratio affect seed dispersal distance? We hypothesized that patches with higher edge-to-area ratios would have greater dispersal distances, due to relatively higher windspeeds in those patches.
3) How does distance to a habitat edge influence seed dispersal distance? We hypothesized that individuals farther from an edge would have greater dispersal distances, due to higher wind speeds at the center of habitat patches.
4) How does the direction of dispersal influence dispersal distance? We hypothesized that seeds would disperse further along the long axis of patches, due to higher wind speeds in that direction.
5) How are relationships between seed dispersal direction and distance affected by proximity to edge? We had two non-mutually exclusive hypotheses. First, the effect of dispersal direction may be stronger near open patch centers, because wind speeds are higher and winds are more directional away from forested edges (Damschen et al. 2014). Alternately, the effect of dispersal direction may be stronger near edges, due to winds eddying back toward the edge after entering a patch from above the adjacent tree canopy (Detto et al. 2008).

METHODS

Site and species

We conducted this experiment within eight experimentally fragmented landscapes, designed to test effects of patch connectivity and differences in edge-to-area ratio. These experimental landscapes (hereafter "blocks") are located at the Savannah River Site (SRS), a National Environmental Research Park in Aiken and Barnwell Counties, South Carolina, USA. SRS is U.S. Department of Energy land that is managed under agreement by the U.S. Forest Service. Each block contains five open-habitat patches, created by clearing mature pine plantation, that differ in their edge-to-area ratio and connectivity (Fig. 1). All blocks have a 100 × 100 m center patch and a connected patch, which is 100 × 100 m and connected to the center patch via a 150 × 25 m corridor. Additionally, all blocks have two types of isolated patches, rectangular and winged, which are not connected to the center patch, but are of equivalent area to the connected patch plus the corridor. The rectangular patch is 100 × 137.5 m and the winged patch is 100 × 100 m plus two 75 × 25 m "wings," which extend from opposite sides of the patch. Winged patches have similar edge-to-area ratio as the connected patch plus the corridor and have a higher edge-to-area ratio than the rectangular patch. Four blocks have two rectangular patches and four have two winged patches. All patch types were randomly assigned. Following initial clearing in the winter of 1999–2000, each patch is being restored to longleaf pine savanna, the historically dominant ecosystem of our study area (Jose et al. 2006). Surrounding and between each patch of open habitat is a matrix of mature pine plantation.

We planted populations of five herbaceous plant species into each patch, at four distances from edge (Fig. 1).

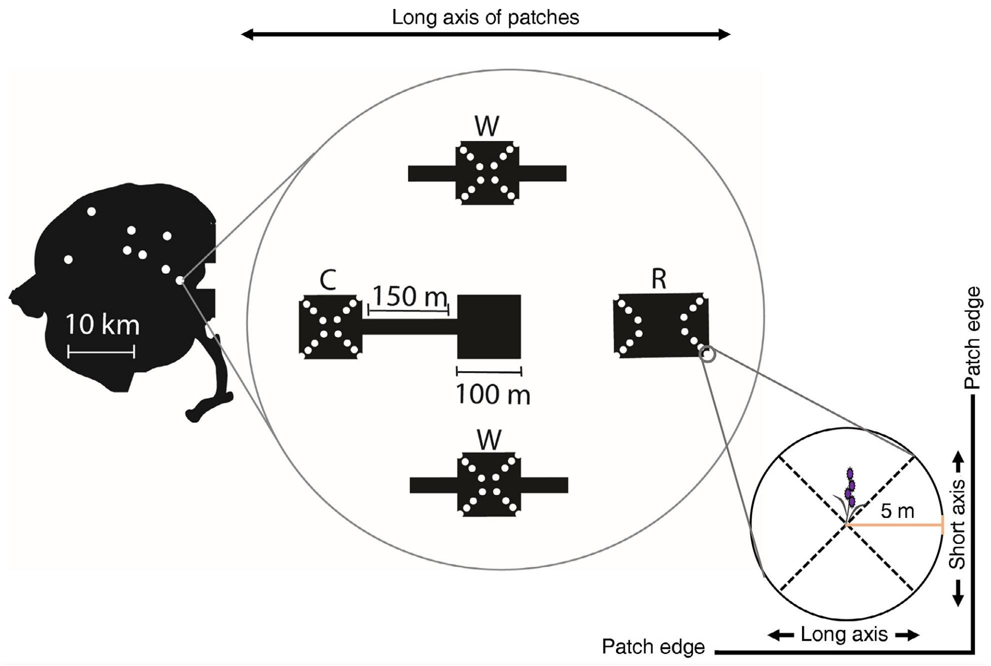

Fig. 1. Experimental design, showing the location of eight experimental blocks within the Savannah River Site, South Carolina, USA (left). Each block (center) has five patches: a connected patch (C) that is connected to a center patch by a 150-m corridor and isolated patches that are either winged (high edge-to-area ratio; W) or rectangular (low edge-to-area ratio; R). Each patch has 16 plots, arranged from edge to center along each of four transects. Each plot contained one individual of each of five study species (with an example individual shown in the right panel), around which dispersed seeds were recovered to 5#x2009;= m in four directional bins (toward edge/short axis, toward edge/long axis, away from edge/short axis, away from edge/long axis). The long and short axes are in reference to the overall habitat patch, in the context of the example individual.

These wind and gravity-dispersed perennial species did not previously occur within our experimental landscapes, but are native components of longleaf pine savannas. Two were forbs in the Asteraceae: *Carphephorus bellidifolius* (Michx.) Torr. & A. Gray and *Liatris squarrulosa* Michx. Three were grasses in the Poaceae: *Aristida beyrichiana* Trin. & Rupr., *Sorghastrum secundum* (Elliott) Nash, and *Anthaenantia villosa* (Michx.) P. Beauv. We hereafter refer to all species by their genus name. Mean seed masses based on 5–15 individuals/species were *Anthaenantia* (22 mg), *Aristida* (7 mg), *Carphephorus* (21 mg), *Liatris* (20 mg), and *Sorghastrum* (28 mg) (E. I. Damschen, *unpublished data*). All five of these species flower and fruit in the fall, from October to December. We started founder populations from seed gathered from SRS, with the exception of *Aristida*, which we sourced as plugs from north Florida. Seeds were mixed within species to avoid maternal effects and were propagated into seedlings in greenhouses.

We planted one individual seedling of each species into each of 16 plots/patch in spring 2007 (N = 3,200 plants). In fall 2007/spring 2008, we replaced individuals that had died following initial planting. Prior to transplanting, we prepared plots by removing all vegetation and, afterward, we weeded plots through the duration of this study. We arranged these plots along transects (Fig. 1), with plots at four distances from each corner of each patch (1, 10.5, 20, and 37 m from the nearest edge). In each plot, we planted one seedling of each species at least 0.5 m from any other transplant (Fig. 1). For more details on plot setup, see Levey et al. (2016).

Seed dispersal

In fall 2009, we visited each reproductive plant (796 individuals across the five species; Appendix S1: Table S1). On each individual, we airbrushed fluorescent paint onto the seeds while the seeds were on the plant. This procedure minimally affects seed dispersal (Lemke et al. 2009). Following seed dispersal, we visited each parent plant a single time (after most or all seeds had dispersed), relocated the marked seeds within 5 m of each parent plant with a blacklight at night, and flagged all marked seeds (see Appendix S1: Table S1 for the number of seeds). We then determined the distance that each seed dispersed from its parent (in cm), as well as the direction in which the seed dispersed within four 90° directional bins, with the bins representing each of the four factorial combinations of being in line or out of line with the long axis of the patch and toward or away from the edge (see Fig. 1). We measured seeds within 5 m of the parent plant because 7.5 m is the halfway point between plots and we wanted to minimize ambiguity as to the parentage of a given seed. Across species, 94–98%

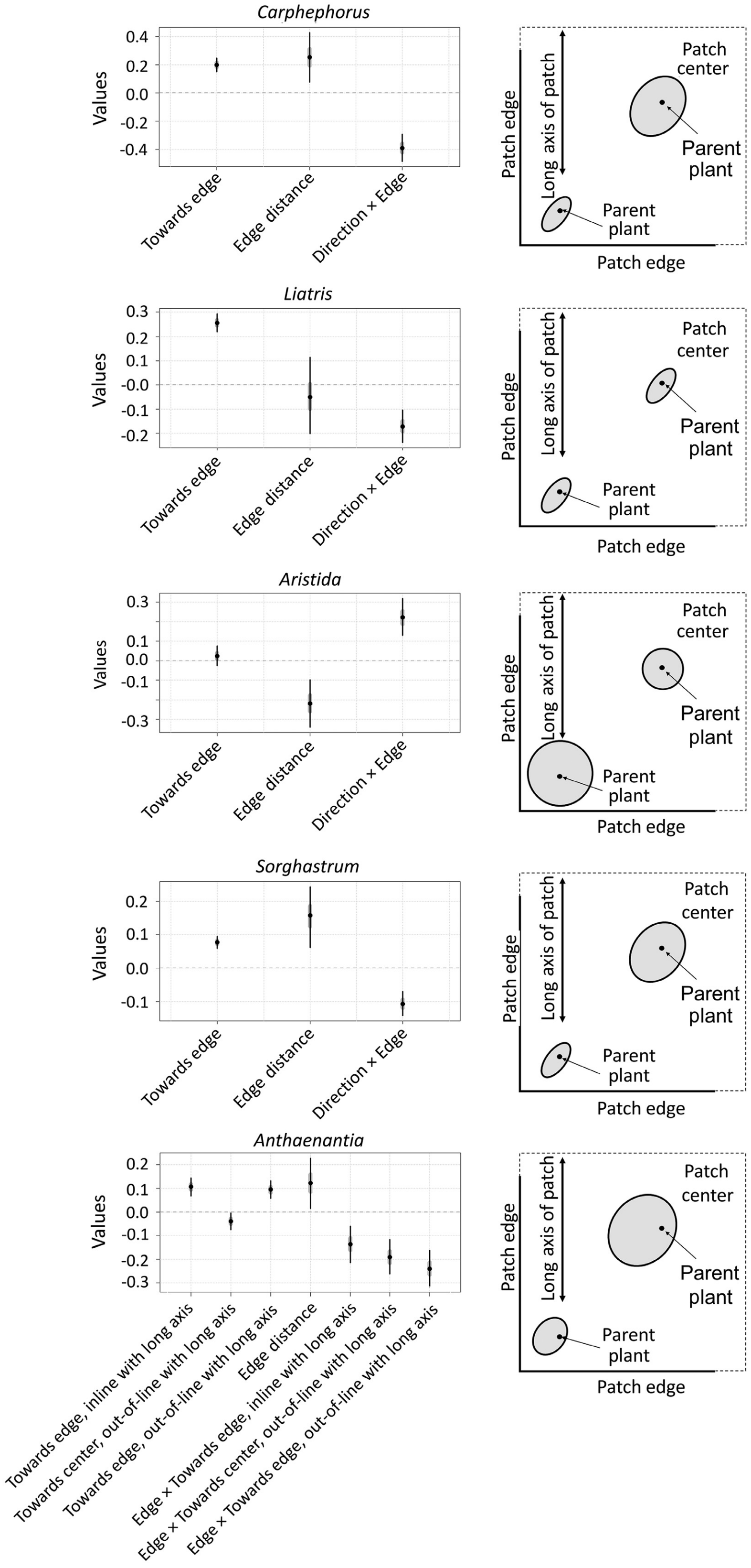

FIG. 2. Left panels show standardized model coefficients with 50% credible intervals (the light gray lines) and 95% credible

(Fig. 2. *Continued*)

intervals (the dark black lines) for five herbaceous plant species in a fragmentation experiment. Values above the 0 line mean greater dispersal than the intercept, while values below mean less dispersal than the intercept. For instance, an effect of edge distance below the zero line would indicate that areas closer to edges have shorter dispersal distances. For the *x*-axis of the *Anthaenantia* panel, the labels correspond to the analogous label on the other panels as follows: The first three labels correspond to directionality (analogous to “toward edge”). The “edge distance” is exactly the same for this species as the others. The remaining three labels correspond to the direction × edge interaction term, as this term is more complicated for *Anthaenantia* (see *Methods*). Right panels are a stylized representation of our interpretation of these results. The gray zone surrounding each parent plant is a stylized representation of mean seed dispersal patterns.

of recovered seeds were within 2 m of a conspecific adult, which we assumed to be the parent plant. We also measured the height of all seed dispersal structures and averaged for each individual, as height is known to be important in seed dispersal patterns (Thomson et al. 2011). Our data are available through the Environmental Data Initiative (Warneke et al. 2021).

Analysis

Our analysis had three stages. In step 1, we performed model selection to identify the set of fixed and random effects and interactions to include in our final models. To facilitate interspecific comparisons and because our goal was inference rather than prediction, our model selection objective was to develop a single model for all species, rather than to identify the best-fit model for each species. We were able to find a common model for all species, with the exception of a directionality term for one species (see step 2). In step 2, within the random effects structure identified in step 1, we conducted a second phase of model selection to determine which set of seed dispersal directions (either four directions or two) to include in our final models. In step 3, to conduct statistical inference on the effects of directionality, patch type, and distance from edge on seed dispersal distances, we compared parameter estimates between our final models for each species. We conducted all statistical analyses in R version 3.1.3 (R Core Team 2020). We did not use a single model with species identity as a fixed or random effect because our goal was not to make comparisons between species, but rather to see how the landscape influenced our different focal species. For additional details, please see the Appendix S1.

At the conclusion of step 1, our model used the distance to which a seed dispersed as the response variable and the direction of dispersal, patch type (categorical; testing connectivity [connected vs. winged] and edge-to-area ratio [winged vs. rectangle]), distance from nearest edge (continuous, in m), plant height, and the interaction of direction and distance from edge as predictor variables. During model selection (step 1), we selected the parent plant as a random effect; we dropped other random effects (e.g., experimental block), as they did not improve predictive fit of models.

We next determined which direction of dispersal to model for each species, maintaining the random effects and interactions from our selected model (step 2). We retained one dispersal direction factor, selecting either the two-directional factor (in which we collapsed the original four directions to two, which were “away from edge” and “toward edge”) or the original four-directional factor. The models using the two-directional factor had a better fit than the models with four-directional factor for all species, except for *Anthaenantia* (for which we used the four-directional model).

Finally, we ran selected models in a Bayesian framework (step 3), though the rstanarm package, version 2.19.3 (Goodrich et al. 2020). We checked model convergence through visual examination of chains, by checking that *R*-hat values were <1.1, and by ensuring models provided a reasonable number of effective samples. The Bayesian framework facilitated propagation of parameter uncertainty, including random effects, to model predictions.

RESULTS

Connectivity and edge-to-area ratio

Connectivity had no effect on dispersal distance for any species, although for *Liatris*, there was a trend of greater dispersal distance in isolated patches, compared to connected patches (Appendix S1: Fig. S1). Patch edge-to-area ratio affected dispersal distance only of *Liatris*, with greater dispersal distances in high edge-to-area ratio (winged) patches, compared to low edge-to-area (rectangle) patches (Appendix S1: Fig.S1).

Distance from habitat edge

Distance from edge affected seed dispersal distance in four of five species (Fig. 2, Appendix S1: Fig. S2; Appendix S1: Table S2). For *Carphephorus*, *Anthaenantia*, and *Sorghastrum*, seed dispersal distance was greater away from edge, while for *Aristida*, seed dispersal distance was greater when close to edge. For *Liatris*, there was no effect of distance from edge.

Directionality

Seed dispersal direction was correlated with the distance of dispersal for four of five species (Fig. 2, Appendix S1: Table S2). For *Carphephorus*, *Liatris*, and *Sorghastrum*, seeds that dispersed toward the center of the patch dispersed shorter distances than seeds that dispersed toward the edge of the patch. For *Aristida*, there was no effect of directionality on distance of seed dispersal. For *Anthaenantia*, for which the model supported four-directional bins (the bins noted in Fig. 1), seeds in the two bins oriented toward the edge dispersed further than seeds in the two bins oriented toward the center. However, for *Anthaenantia*, in the two bins with seeds that dispersed toward the center of patches, dispersal distances were greater in the direction in-line with the long axis of the patch (Fig. 2).

Relationship between distance from edge and directionality

Dispersal was less directional at locations closer to the center of the patch for all species except *Aristida* (Fig. 2, Appendix S1: Table S2). So, for most species, the pattern of greater dispersal distances toward the edge was stronger for plants located nearer to patch edges. For *Aristida*, seed dispersal was less directional closer to patch edges.

Discussion

We found that habitat fragmentation affects local seed dispersal primarily through the creation of edges. Dispersal distance was generally greater in patch centers and in the direction of an edge, with this directionality pattern typically stronger closer to patch edges. Our consideration of directionality afforded key insights about how fragmentation affects seed dispersal, which would have been missed under the common approach of assuming seed dispersal is equal in all directions. The effect of directionality on seed dispersal was also affected by edges. Our results illustrate consequences of fragmentation on dispersal that may have ramifications for plant population dynamics (Levine and Murrell 2003).

Two mechanisms might explain the observed edge effects on dispersal distance. First, wind is stronger away from edges in open habitats (Damschen et al. 2014), likely resulting in greater seed dispersal distances away from edge for three species. Second, as wind travels over forest canopy into a clearing, it can eddy backward (Detto et al. 2008), likely resulting in three species dispersing to greater distances toward edges, particularly at close proximity to edges.

Conversely, we saw little effect of patch connectivity or edge-to-area ratio on seed dispersal, in spite of our expectations. This may be related to differences in dispersal patterns at different levels above the ground (Bohrer et al. 2008, Detto et al. 2008); patterns of connectivity and edge-to-area ratio may be more apparent at higher altitudes, likely leading to long-distance dispersal for seeds that are lofted upward to those altitudes (thus missed in our data set).

An important consequence of our findings is that fragmentation may influence seed dispersal differently at long-distance and local scales. Most previous work has focused on only one scale, without considering differences between them (Nathan and Muller-Landau 2000, Rogers et al. 2019). While we find that local seed dispersal is influenced by edge proximity, past work in our system has illustrated how larger-scale fragmentation effects, such as patch connectivity and edge-to-area ratio, modify long-distance seed dispersal for both biotically and abiotically dispersed species, albeit of different species (Levey et al. 2005, Damschen et al. 2014, Herrmann et al. 2016). Together, these findings suggest that edge proximity may affect seeds dispersing locally, with patch connectivity and edge-to-area ratio influencing only those seeds that reach above-boundary layer heights (e.g., >5 m above the ground surface).

In spite of their different adaptations to dispersal by wind, our study species showed remarkably similar dispersal responses to fragmentation. Two of our species (*Carphephorus* and *Liatris*) have clear morphological adaptations to wind dispersal (the pappus), while the three grasses do not. Adaptations to dispersal could vary with scale of dispersal (Murrell et al. 2002, Muller-Landau et al. 2003). The presence of a pappus almost certainly facilitates long-distance dispersal in *Liatris* and *Carphephorus* and the presence of awns may facilitate short-distance dispersal in *Sorghastrum* and *Aristida*. Local dispersal by wind may even occur without any obvious morphological adaptations, as we see in *Anthaenantia* (Murrell et al. 2002, Riba et al. 2009). How traits affect dispersal patterns at different scales is an avenue for future research.

Creation of edges through fragmentation affected seed dispersal distance, which in turn may influence plant population dynamics in several ways. First, plants close to edges typically dispersed shorter distances than plants away from edges. As a consequence, seedlings closer to edges may experience higher levels of intraspecific competition with other seedlings originating from the same parent plant (Comita et al. 2014). Shorter dispersal distances near edges may also lead to negative demographic consequences through Janzen-Connell effects (Janzen 1970, Hovanes et al. 2018) on seedlings close to their parent plants, which may reduce population growth rates near patch edges. Second, near patch edges, dispersal was more strongly directed toward the edge, which could exacerbate negative density-dependent processes caused by shorter dispersal distances. Third, in our longleaf pine study system, edge proximity is associated with increased leaf litter and shading, which are detrimental to longleaf pine understory herbs (Hiers et al. 2007, Veldman et al. 2013), such as our study species.

We show that the relationship between the distance and direction of dispersal can be important for abiotically dispersed species, even at local scales. Many terrestrial plants are abiotically dispersed (e.g., wind, gravity), and may disperse in a directional manner (Nathan et al. 2002, van Putten et al. 2012). Despite this, relatively few studies have examined directional seed dispersal for abiotically dispersed species, with past work focusing on riparian systems and for long-distance dispersal by wind (Levine 2003, Wright et al. 2008, Damschen et al. 2014, Horvitz et al. 2014). We show how novel insights can emerge through consideration of seed dispersal directionality, in ways that may influence plant populations.

In summary, we show how fragmentation affects seed dispersal at local scales. Our experimental design allowed us to tease apart influences of patch isolation, edge-to-area ratio, and edge effects, factors that are often conflated in observational studies of habitat fragmentation (Didham et al. 2012, Fletcher et al. 2018). Our finding that edges are most important for local seed dispersal while the large-scale factors of connectivity and edge-to-area ratio matter less for this process illustrate how experiments can parse out the scale-dependent influence of fragmentation on key ecological processes, such as seed dispersal.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.3586/suppinfo

OPEN RESEARCH

Data (Warneke et al. 2021) are available from the Environmental Data Initiative: https://doi.org/10.6073/pasta/83dcd48a0d7351acc55b795f307b6f38