

ARTICLE

Habitat fragmentation alters post-dispersal more than pre-dispersal seed predation through edge effects

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Abstract

In addition to causing loss of biodiversity, habitat fragmentation can alter species interactions. Relative to well-studied effects of fragmentation on mutualistic interactions like pollination, effects on antagonistic interactions remain poorly understood. One such interaction, seed predation, may be particularly important because it can alter plant demographics and trigger cascading changes to both plant and seed predator communities. Previous studies have failed to find consistent effects of fragmentation on seed predation, possibly because seed predation occurs at two distinct stages relative to seed dispersal (pre- and post-dispersal). Working within a large-scale fragmentation experiment, we tested effects of three consequences of fragmentation—edge-to-area ratio, distance to edge, and connectivity (via habitat corridors)—for pre-dispersal seed predation and post-dispersal seed removal of eight plant species of conservation interest. We found that fragmentation effects, especially distance to edge, were more likely significant for post-dispersal seed removal (assumed to positively correlate with seed predation) than for pre-dispersal seed predation, although the significant patterns differed across species. Post-dispersal seed predation declined sharply with seed mass, and this decline was greater at the patch edge. This led to larger seeded species having less predation nearest to the edge compared to patch interiors. This experiment highlights how fragmentation can alter seed predation by generating edge effects and how species traits can predict consequences across a community.

KEYWORDS

edge effects, habitat fragmentation, landscape connectivity, seed predation, species interactions

INTRODUCTION

Habitat loss is the major driver of biodiversity loss (Jaureguiberry et al., 2022; Maxwell et al., 2016). However, the effects of habitat fragmentation that accompany habitat loss are debated (Miller-Rushing et al., 2019), with arguments for both negative (Fletcher et al., 2018; Gonçalves-Souza et al., 2025; Püttker et al., 2020) and positive effects (Fahrig, 2017; Riva & Fahrig, 2023) on species in fragmented landscapes. The focus for these arguments has been on how changes in patch size or isolation impact species richness. However, fragmentation has the potential to alter species interactions (Sandor et al., 2022; Siegel et al., 2024), which may explain the large variation in species' responses to fragmentation.

Fragmentation can affect various types of interactions (Brudvig et al., 2015). Species interactions may have positive effects on demography, for example, in the case of mutualisms like pollination (Hadley et al., 2014; Townsend & Levey, 2005) or frugivory/seed dispersal (Levey et al., 2005; Razafindratsima et al., 2021). In these cases, increases (or decreases) in the abundance of one mutualistic partner could lead to corresponding increases (or decreases) in another. On the other hand, fragmentation may also affect the abundance or activity of antagonistic species such as predators (Hawn et al., 2018; Orrock & Damschen, 2005), herbivores (Pereyra et al., 2015; Pinho et al., 2017), or parasites (Anderson et al., 2019; Froeschke et al., 2013), in which case a positive effect of fragmentation on one species may lead to negative effects on another (Haddad et al., 2014; Siegel et al., 2024).

The best characterized effects of habitat fragmentation on species interactions are those related to edge effects. Edges can alter how species interact by changing the dispersal, demography, or types of interacting species (Ewers & Didham, 2006). Understanding species interactions near habitat edges is essential for developing a mechanistic understanding of edge effects (Ruffell & Didham, 2016). In addition to distance to edge effects, differences in edge-to-area ratio caused by changes in patch shape can be important drivers of species occurrence or abundance at the patch scale (Shake et al., 2012) and can alter community structure (Orrock et al., 2003), further providing a mechanism by which species interactions may be altered by fragmentation.

Fragmentation also influences species interactions through altered connectivity between habitat patches. For instance, increasing landscape connectivity increases dispersal (Fletcher et al., 2016), including for antagonistic species such as herbivores or predators (Haddad et al., 2014), which can reduce populations of other species (Baggio et al., 2011). Most work on connectivity

effects on species interactions has used comparisons of diversity or abundance of interacting species (Fletcher et al., 2016) rather than direct measures of their interactions. Studies that have directly tested connectivity effects on species interactions promoted via habitat corridors have shown that connectivity can increase predation (Hawn et al., 2018; Orrock et al., 2003), herbivory (Maguire et al., 2016), and the spread of parasites (Sullivan et al., 2011). However, connectivity effects can also decrease species interactions or be absent altogether (Brudvig et al., 2015).

Seed predation is an important species interaction that can be altered by fragmentation and directly affects plant species' recruitment, population growth rate, abundance, distribution, and evolution (Kolb et al., 2007). Previous studies have shown that habitat edges and connectivity may increase (Kollmann & Buschor, 2003; Magrach et al., 2011; Orrock & Damschen, 2005) or decrease (Chen et al., 2017; Craig et al., 2011; Orrock et al., 2003) rates of seed predation. However, meta-analyses of forest fragmentation effects on antagonistic species interactions have failed to find a consistent, directional effect (Magrach et al., 2014; Siegel et al., 2024). Seed predation's response to fragmentation is further complicated by the fact that plant species may be habitat specialists, whereas seed predators may be generalists who are able to utilize both patches and surrounding matrix (Larios et al., 2017). Previous fragmentation studies on seed predation have occurred at a single stage, either after the seed has dispersed (post-dispersal) or while the seed is still on the parent plant (pre-dispersal), which may miss the full effects of seed predation on plant populations. Understanding how these two stages combine to alter success across the life of the seed, the subject of our study, is necessary to fully understand the effects of fragmentation on seed predation.

It is unclear from previous studies how habitat fragmentation affects species interactions differently across a community of species. How species respond to fragmentation can depend on the particular traits they possess (Keinath et al., 2017; Tremlová & Münzbergová, 2007), and those traits can influence species interactions (Hagen et al., 2012; Laigle et al., 2018). Seed size, for example, has been directly linked to seed predation rates (Dylewski et al., 2020). In this study, we used a large-scale fragmentation experiment with eight plant species that are targets of restoration and that vary in seed size to address the following questions: (1) Do distance to edge and patch edge-to-area ratio affect pre-dispersal seed predation and/or post-dispersal seed predation? (2) Does landscape connectivity affect seed predation (pre- and/or post-dispersal)? (3) Do fragmentation effects on seed predation vary with seed size?

METHODS

Experimental landscapes

We conducted our study in the Corridor Experiment at the Savannah River Site (SRS), an 80,000-ha National Environmental Research Park located in Aiken and Barnwell Counties, South Carolina, USA, that is owned and operated by the U.S. Department of Energy (Figure 1). The experiment was created in 2000 by clearing openings within pine plantation forests composed of longleaf (*Pinus palustris*), slash (*Pinus elliottii*), or loblolly pine (*Pinus taeda*). Each of eight experimental landscapes (hereafter, blocks) consists of five patches, each approximately 1 ha in size. Each block contains a center patch, 100 m $\times$ 100 m, connected to one peripheral patch by a 150-m long and 25-m wide corridor of the same habitat type. The other three peripheral patches are 150 m from the center patch, isolated, and of two types: rectangular and winged. Each block contains at least one rectangular and winged peripheral patch, with one type chosen at random to be duplicated for the third. The orientation and position of these patches within a block were randomized. The isolated patches are equal in area to the connected patch including the corridor (1.375 ha), which controls for effects of patch area. Rectangular patches are 100 m $\times$ 137.5 m and winged patches are

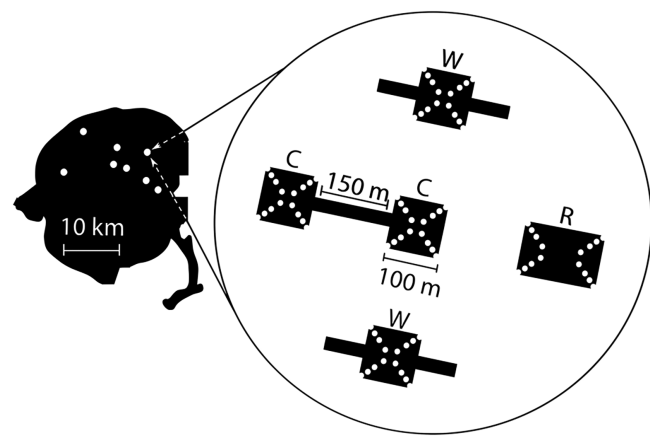


FIGURE 1 Diagram of experiment and sampling scheme: an outline of the Savannah River Site National Environmental Research Park with the distribution of eight experimental landscapes (blocks) and an enlarged depiction of the five patches in each block. Within each patch are the locations of the planted plots ($n = 16$) of species for the pre-dispersal seed predation study and seed trays for the post-dispersal seed predation study. C indicates patches connected by habitat corridors, W indicates patches with habitat “wings” equaling the same total area of corridors, and R indicates patches with the same total area as C and W but contained within a single rectangular patch shape.

100 m $\times$ 100 m with two 75 m $\times$ 25 m projections on opposite sides of the patch (Figure 1). Winged patches control for both the added area and the change in patch shape that accompany the addition of a corridor. From this design, comparisons between winged and rectangular patches are used to test patch-scale edge amount effects, while comparisons between patches connected by a corridor and winged patches are used to test patch-scale connectivity effects. More details on the experimental design and its rationale are provided in Tewksbury et al. (2002).

Transplant plots and focal species

We tested for effects of fragmentation on seed predation of eight plant species (three grasses, four forbs, and one short-statured shrub) that we experimentally introduced into our patches. The grasses were *Anthenantia villosa* (Michx.) P. Beauv., *Aristida beyrichiana* Trin. & Rupr., and *Sorghastrum secundum* (Elliott) Nash. The forbs were *Carphephorus bellidifolius* (Michx.) Torr. & A. Gray, *Liatrus squarrulosa* Michx., *Nolina georgiana* Michx., and *Phytolacca americana* L. The shrub was *Gaylussacia dumosa* (Andrews) Torr. & A. Gray. Seven are of conservation interest, while *P. americana* is a widespread native species. Species were chosen so that there was variation among species’ seed mass (Appendix S1: Table S1) on which fragmentation could act to affect pre- or post-dispersal predation (Dylewski et al., 2020; Moles et al., 2003).

Seedlings of *A. villosa*, *A. beyrichiana*, *C. bellidifolius*, *N. georgiana*, and *S. secundum* were grown in greenhouses and planted in the spring of 2007. Seedlings of *L. squarrulosa* and *P. americana* were grown in greenhouses and planted in the spring of 2008. *Gaylussacia dumosa* was transplanted from other areas where it occurs on the SRS in 2007. During the first growing season after planting, we hand-watered seedlings and transplants regularly, up to twice per week when the weekly rainfall was below average (<2.5 cm/week). We replaced individual plants that died through the spring of 2009.

We planted seedlings in 1 m $\times$ 5 m plots with 0.5-m spacing between plants, with the location of each plant species randomly assigned within each plot. We established these plots along four transects, bisecting the four corners of each patch. Plots were located 1.5, 14, 27, and 51 m from the corner (see Figure 1). This resulted in 16 plots in every patch ($n = 40$), each containing a single individual of each species. In total, we planted 640 individuals per species and 5120 individuals overall. Plots were maintained free of other vegetation by hand weeding over the course of the present study, as our goal

was to get restoration plants established and reproductive.

Pre-dispersal seed predation

In the fall of 2009, we collected data on pre-dispersal seed predation of five of the plant species; three grasses, *A. villosa*, *A. beyrichiana*, *S. secundum*; and two forbs *C. bellidifolius*, *L. squarrolosa*. These were the species with individuals that were reproductive for at least 40% of transplant locations. To determine pre-dispersal seed predation, we collected up to three reproductive structures (infructescences or culms) from each plant that was reproductive. Reproductive structures were collected after flowering, when seeds (achenes or caryopses) were developing, but before they began to disperse. For each seed, we determined apparent viability based on the presence of intact endosperm and embryo (Borza et al., 2007). We counted all viable and nonviable seeds for each plant from the collected reproductive structures. Of the nonviable (undeveloped) achenes/caryopses, we chose 10 from one of the three fruiting structures from each plant at random and dissected them under a microscope for evidence of pre-dispersal seed predation, which included presence of granivores, frass, or entrance and exit holes. We estimated pre-dispersal seed predation as the proportion of potentially viable seeds (viable seeds plus those unviable due to predation) that were destroyed by pre-dispersal seed predators.

Post-dispersal seed predation

To test fragmentation effects on post-dispersal seed predation, we used seed-removal depots to quantify seed predation. We assume seed predation is reflected by seed removal, a common assumption in seed predation experiments (Moles et al., 2003), since removal is strongly related to recruitment of plants at a location in this system (Orrock et al., 2003) and evidence of depredated seed hulls in depots is common (38%–56% of observations in previous studies in this study system: Craig et al., 2011; Orrock & Damschen, 2005).

For each seed-removal depot, we placed 20 seeds on top of 0.5 cm of sand (similar to the natural sandy soils of the area) within a 19 × 14 × 10 cm plastic container fitted with a tight cover. Lids protected seeds from wind or water while excluding avian predators; our focus on post-dispersal seed predation by arthropods and small mammals is based on previous work demonstrating their importance as post-dispersal seed predators in this system (Craig et al., 2011; Orrock et al., 2003; Orrock &

Damschen, 2005). Two common small mammal predators are old field mice (*Peromyscus polionotus*) and cotton mice (*P. gossypinus*), while invertebrate predators consist of various ant (e.g., Harvester Ants, *Pogonomyrmex badius*) and beetle (e.g., Carabid ground beetles) species (Craig et al., 2011; Orrock et al., 2003). Two 2.5-cm diameter holes were cut on adjacent sides of the container to allow insect and mammalian seed predators to enter freely. These depots and the general approach have been used to quantify seed removal in several previous studies in this system (e.g., Craig et al., 2011).

We collected seeds for this experiment from naturally occurring populations in the study region. Seeds were air-dried, stored at room temperature, and deployed within the same season. For fleshy-fruited plants (*G. dumosa* and *P. americana*), seeds were presented after washing the pulp from the seed, mimicking their presentation to predators after passing through an animal's gut. Seeds of other species were presented with their hulls and dispersal structures (e.g., awns, pappus) intact, as they would be when dispersed naturally. For each species, we conducted removal trials to coincide with natural seed production and dispersal. At each transplant plot ($n = 640$, 16 per patch, 40 patches), we placed one depot with seeds of a single species next to the corresponding transplant of the same species. The containers were placed 1 m away from the plant to be outside the cleared plot and within undisturbed surrounding vegetation. For each seed predation trial, seed containers were placed in the field for 20 days, after which the remaining seeds and sand were collected in plastic bags. Later, seeds were separated from the sand and counted. To adequately capture post-dispersal predation across the entire period of natural dispersal, we conducted two separate removal trials for each species, with the first trial occurring during the first half of that species' dispersal window and the second occurring during the latter half of the dispersal window (Appendix S1: Table S1). Because species differ in the timing of dispersal, this led to a staggered timing of trials across species. Overall, we conducted 10,240 total trials for the eight species, omitting from analysis those trials with damaged or disturbed depots. We quantified predation as the number of seeds from the original 20 that were absent or destroyed after the 20-day period.

Analyses

For pre-dispersal seed predation, we fit a generalized linear mixed model (GLMM) with a binomial distribution for each plant species ($n = 5$) to model the number of predated seeds out of the total potential viable seeds per plant. All models included block, patch, transect, and

individual plant as random effects. Fixed effects were patch type (connected, rectangular, winged), distance to edge, and their interaction. Pairwise comparisons of patch type were used to assess the effect of connectivity (connected vs. unconnected patches) and edge-to-area ratio (winged vs. rectangular). The significance of all fixed effects was evaluated using p -values with all nonsignificant interaction terms ($p > 0.05$) dropped from final models. We did not include a model combining all species and using species as a fixed or random effect due to poor fit with high dispersion and non-normality of residuals.

For post-dispersal seed predation, we again fit GLMMs with a binomial distribution. The proportion of seeds removed after 20 days was the response variable for each of the plant species ($n = 8$). The same fixed and random effects from the pre-dispersal models were included with the same post hoc comparisons conducted to assess connectivity and edge effects. However, because there were two post-dispersal trials per species, we included an additional random effect for each trial in these models. We assessed the effect of seed mass on post-dispersal seed predation by combining trials from the eight species and included species identity as a random effect to control for nonindependence of trials among species. We used a beta-binomial distribution to account for overdispersion in model residuals. Models included the interaction of all

fixed effects (seed mass, patch type, and distance to edge) as well as all pairwise interactions, with nonsignificant interactions dropped from the final model.

All GLMMs were fit using the package `glmmTMB` (Brooks et al., 2017) in program R v. 4.4.1 (R Core Team, 2024). Model fit was assessed via residuals using the package `DHARMA` (Hartig, 2018), and the significance of fixed effects was determined using Type II Wald χ^2 using the function `Anova()` in the package `car` (Fox & Weisberg, 2018). Post hoc comparisons were conducted in package `emmeans` (Lenth, 2024).

RESULTS

Pre-dispersal seed predation

We assessed pre-dispersal seed predation for 40,808 seeds from 1277 individual plants. The number of plants analyzed per species ranged from 166 for *L. squarrosa* to 456 for *A. villosa* (Appendix S1: Table S1). An estimated 6394 seeds showed signs of predation for an overall rate of 15.67%, ranging from 8.5% in *L. squarrosa* to 35.4% in *C. bellidifolius*. For *A. villosa*, pre-dispersal seed predation was higher at greater distances from the edge ($\chi^2 = 14.31$, $df = 3$, $p = 0.002$; Figure 2b); other species were not significantly affected by distance (all $p > 0.36$;

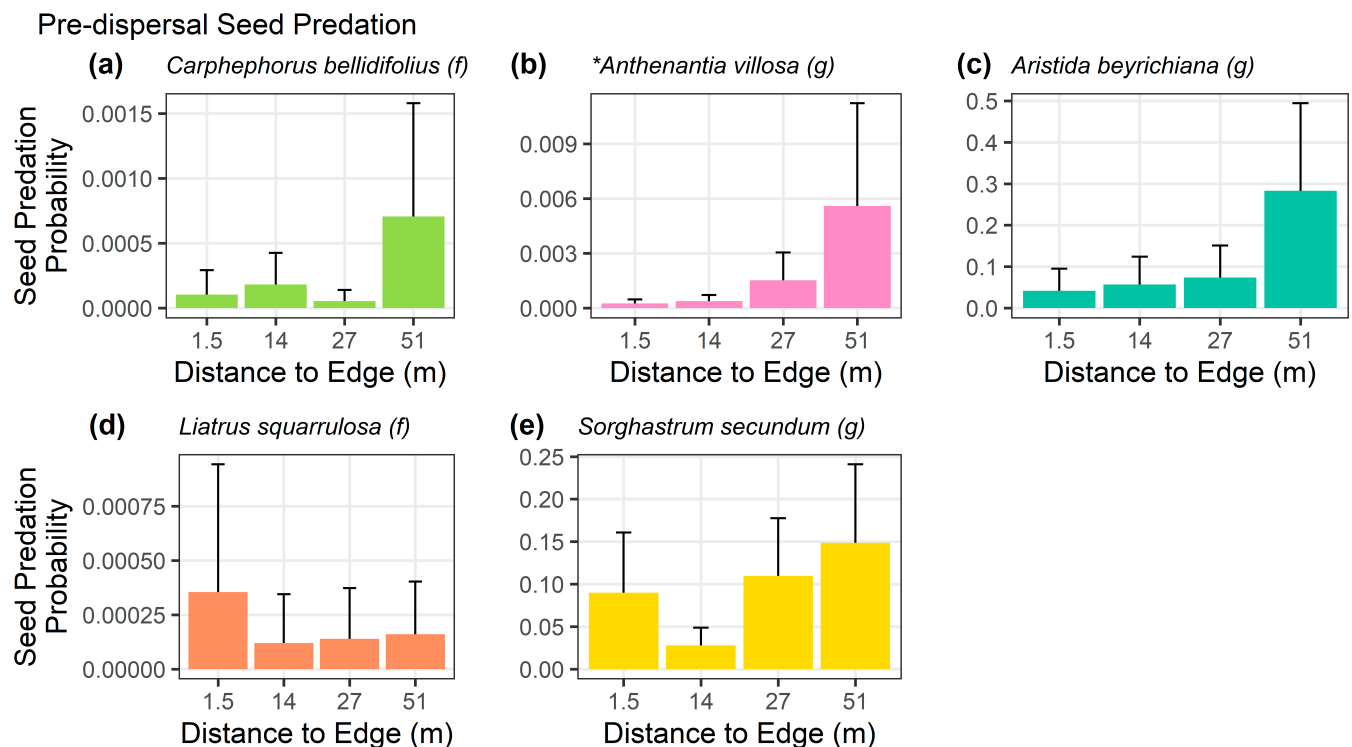


FIGURE 2 Pre-dispersal seed predation in relation to distance to edge. Letters in parentheses describe growth form of each species: (g) for grasses and (f) for forbs. Error bars show SE. An asterisk indicates a significant effect of distance to edge.

Figure 2; Appendix S1: Table S2). Neither connectivity nor patch shape significantly influenced pre-dispersal seed predation for any species (all $p > 0.33$; Appendix S1: Table S2).

Post-dispersal seed predation

Across 190,160 seeds deployed in 9508 intact post-dispersal trials, 31.5% were removed (59,875 seeds). Individual removal rates for species ranged from 5.5% for *N. georgiana* to 44.3% for *C. bellidifolius* (Appendix S1: Table S1). Within-patch effects of fragmentation were common, with the distance to edge significantly affecting

post-dispersal seed predation for five of the eight species (Figure 3g,h). Specific effects of edge proximity varied across species, but the relationship never significantly depended on connectivity or patch shape ($p > 0.07$ for all interactions; Appendix S1: Table S3). For *A. beyrichiana* ($\chi^2 = 8.38$, $p = 0.039$), *L. squarrulosa* ($\chi^2 = 9.14$, $p = 0.027$), and *C. bellidifolius* ($\chi^2 = 26.7$, $p < 0.001$), post-dispersal seed predation was highest closest to and furthest from the edge (Figure 3a–c). For *A. villosa* ($\chi^2 = 4.29$, $p = 0.23$), *G. dumosa* ($\chi^2 = 2.81$, $p = 0.42$), and *S. secundum* ($\chi^2 = 2.19$, $p = 0.53$), there were no significant effects of distance to edge on post-dispersal seed predation (Figure 3d–f). For *P. americana* ($\chi^2 = 51.1$, $p < 0.001$) and *N. georgiana*

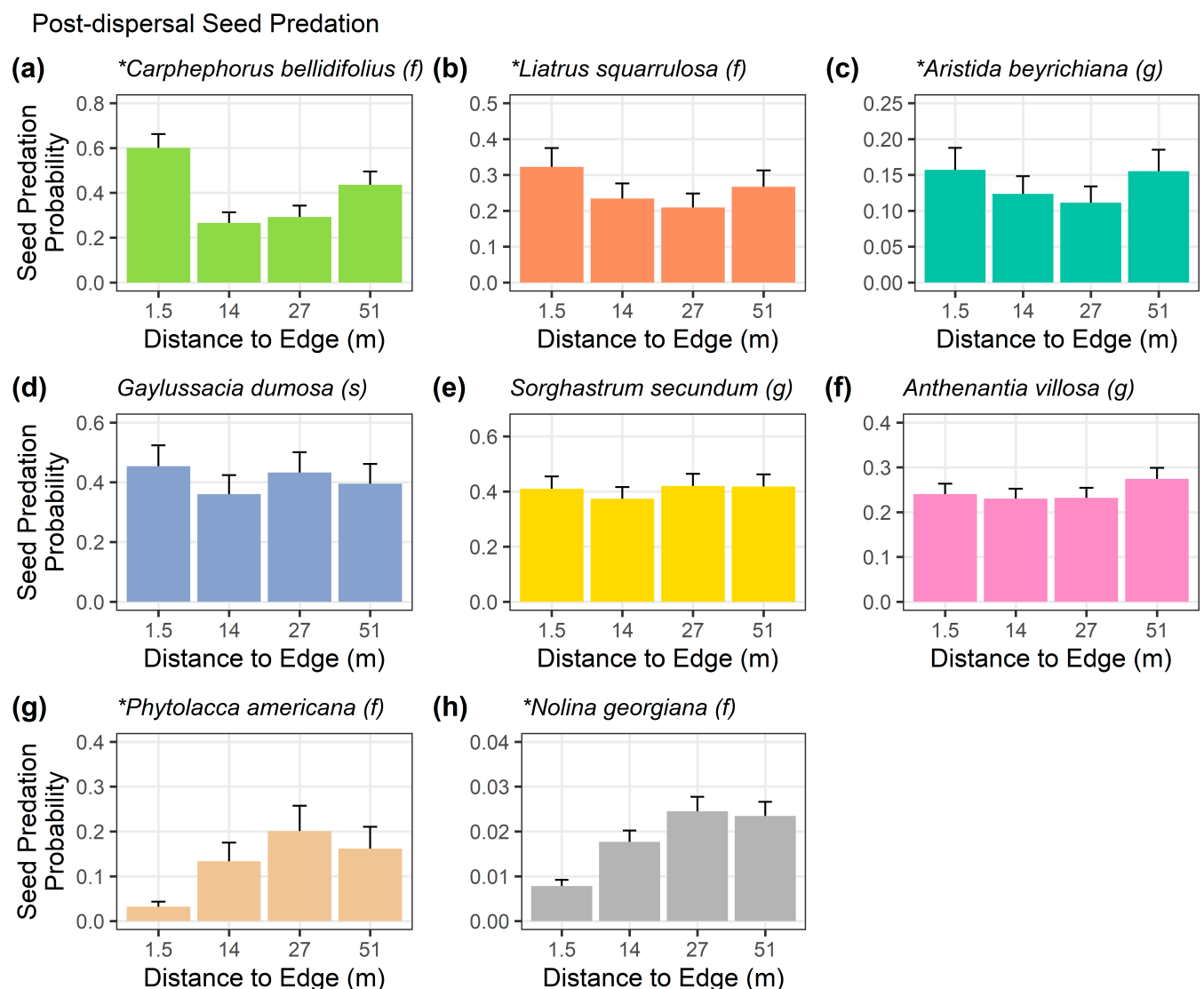


FIGURE 3 Post-dispersal seed predation probabilities based on distance to edge across all eight species. Letters in parentheses describe growth form of each species: (g) for grasses, (f) for forbs, and (s) for shrub. (a–c) Those species with highest predation near and far from patch edges. (d–f) Species with no significant differences based on distance to edge. (g,h) Increased seed predation away from patch edges. Error bars show SE. An asterisk indicates significant effects of distance to edge.

($\chi^2 = 38.5$, $p < 0.001$), post-dispersal seed predation was higher at greater distances from the edge (Figure 3g,h).

Only two species showed patch-scale effects of fragmentation. For *P. americana* and *N. georgiana*, both forbs, predation increased in patches with lower edge-to-area ratios (rectangular/winged: odds ratio = 3.27 ± 1.17 [mean $\pm$ SE], $p = 0.003$; rectangular/winged: odds ratio = 1.52 ± 0.26 , $p = 0.034$; respectively). Predation rates were unaffected by connectivity for both of these species. For the other six species, there were no significant effects of connectivity or edge-to-area ratio on seed predation (Appendix S1: Table S3).

Seed mass affected post-dispersal seed predation with larger seeded species having lower predation ($\beta = -0.17 \pm 0.03$, $p < 0.001$; Figure 4; Appendix S1: Table S4). Seed mass interacted with distance to edge (interaction: $\chi^2 = 330.6$, $p < 0.001$), whereby species with smaller seeds (e.g., *Aristida beyrichiana*, *L. squarrolosa*) experienced higher predation close to the edge and those with larger seeds (e.g., *N. georgiana*, *P. americana*) experienced higher relative predation farther from the edge (Figure 4).

DISCUSSION

Despite the increasing prevalence of habitat fragmentation and the need to understand how patch geometry and connectivity affect species interactions, our knowledge of how fragmentation affects pre- and post-dispersal seed predation remains incomplete. We found significant effects of fragmentation on post-dispersal seed predation due to edge effects (distance to edge and edge-to-area ratios) for some species, but not others. Effects of fragmentation on pre-dispersal seed predation were significant in only a single species responding to distance to edge. Finally, seed mass was strongly related to edge responses for post-dispersal seed predation across species, leading to more variable predation rates closer to patch edges because larger seeded species were removed at greater rates in the patch interior. Taken together, the effects of fragmentation on seed predation are driven by the creation of patch edges and occur after seeds have dispersed from parent plants. The variability in effects across a plant community might lead to different plant community composition due to this important species interaction.

The presence of edge effects on post-dispersal seed predation across the majority of species demonstrates the influence that fragmentation can have on antagonistic species interactions. However, the pattern and significance of these relationships varied across species:

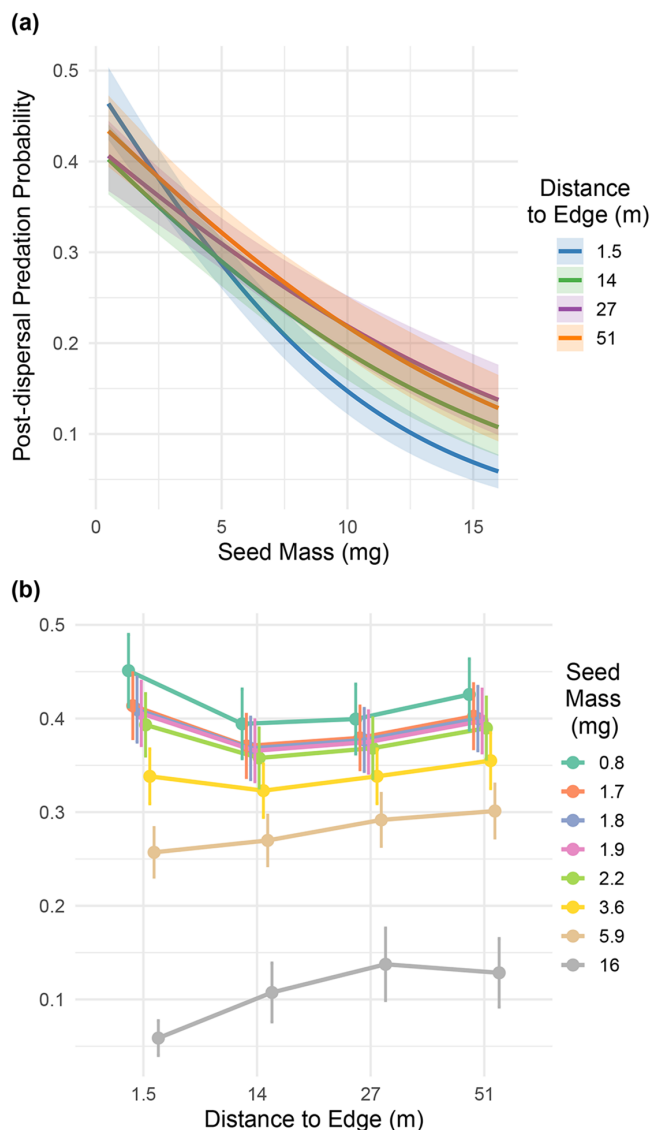


FIGURE 4 Graphs visualizing the interaction between a species' average seed mass and distance to edge for post-dispersal seed predation: (a) Post-dispersal seed predation probabilities by seed mass from the GLMM with lines for each distance to edge. Shaded region indicates SE. (b) Post-dispersal seed predation probabilities by distance to edge from the GLMM with lines for each individual species colored (see Figure 3) by seed mass. Error bars show SE.

predation rates could be highest furthest from the edge, bimodal with peaks close and far from the edge, or not significantly related to distance to the edge. Two of the bimodal species (*A. beyrichiana* and *L. squarrolosa*) had significant distance effects that, after accounting for the large number of statistical tests, might be considered a strong trend. These patterns reflect strong species-specific patterns of seed predation found in other studies in this system (Craig et al., 2011; Orrock & Damschen, 2005), and may be explained by how fragmentation may affect

the different types of seed predators (Siegel et al., 2024). For example, the abundance and community composition of ground-dwelling arthropods sampled with pitfall traps differs as a function of patch geometry and connectivity (Orrock et al., 2011), while movement of seeds by ants is reduced by patch edges and isolation (Burt et al., 2022). Studies of arthropod movement and abundance show effects of connectivity and patch geometry (Fried et al., 2005; Haddad & Baum, 1999), which have been linked to changes in another antagonistic species-interaction, herbivory (Evans et al., 2012). While ants are a major source of seed predation in pine savanna ecosystems (Golley & Gentry, 1964), the predation pressure of other seed predators such as rodents can also be altered by habitat edges (Chen et al., 2017; Kollmann & Buschor, 2003). Differences in the phenology of these seed predators and how this aligns with the timing of seed dispersal in these plant species may also contribute to the varied response to edges. In this study, there was an overlap in the species that showed strong increases in predation away from the edge and species that experienced greater predation in patches with a higher ratio of core to edge area (rectangular patches), suggesting similar fragmentation effects on post-dispersal seed predation operating at both within- and between-patch scales for these species.

The lack of significant fragmentation effects for pre-dispersal seed predation in all but one of the species suggests that pre-dispersal seed predation is primarily driven by other factors. One reason why we may have observed the single effect on pre-dispersal seed predation could be from the presence of a specialist seed predator showing similar responses as specialist insect herbivores (De Carvalho Guimarães et al., 2014). The absence of fragmentation effects on pre-dispersal seed predation has been found elsewhere (Burgos et al., 2008), and when found, these effects are often small in comparison to other drivers of seed predation (Moncalvillo et al., 2021). While we did not find edge effects to be common, strong spatial heterogeneity in pre-dispersal seed predation in southeastern systems can result from other processes such as differences in disturbance regimes (Hiers et al., 2000).

Despite connectivity loss being an important driver of fragmentation effects, we found that connectivity was not a significant driver of seed predation rates. Prior work in this experimental system showed offsetting effects of connectivity for rodent and insect seed predation, resulting in an absence of an overall connectivity effect (Orrock et al., 2003). Also in this study system, seed predation was higher in connected patches (Orrock & Damschen, 2005), but not so for seed predation in the matrix surrounding these patches, which differed due to seed

species and distance from the patch edge (Craig et al., 2011). Elsewhere, seed predation has also been shown to be unrelated to connectivity (Gaytán et al., 2024). This lack of a clear connectivity effect for seed predation mirrors that seen in meta-analyses of antagonistic species interactions (Magrath et al., 2014; Siegel et al., 2024). Connectivity effects may be less common due to replacement of seed predators in unconnected patches since antagonistic interactions are less specialized and interdependent than mutualistic interactions (Kawakita et al., 2010), are more stable due to higher connectedness of species interaction networks (Baumgartner, 2020), and are less vulnerable to habitat disturbance (Kiers et al., 2010).

While fragmentation effects on species interactions can be variable, our results indicate the potential of using seed mass as a predictor of post-dispersal seed predation. On its own, seed mass had a similar negative relationship with seed predation as in Moles et al. (2003), but this contrasts with a recent global meta-analysis showing predation rates are highest at intermediate seed sizes, which are comparable to the largest seeds in our study (Dylewski et al., 2020). It is unclear if the contrasting relationships to seed mass are due to differences in seed predation in pine savanna communities compared to the grassland systems included in Dylewski et al. (2020). In our experiment, the interaction of seed mass with edge distance led to stronger effects of seed mass on predation rates closest to the edge (Figure 4). A potential explanation is that increasing seed mass can correlate with investment in seed coat size and other defenses against seed predation (Linkies et al., 2010; Moles et al., 2003), which may be particularly important at patch edges where there may be more variable seed predators. Future work should explore whether other seed traits such as plant growth habit (grass, forb, etc.) or dispersal mode are also predictors of seed predation responses to fragmentation and whether these also interact with seed mass. Importantly, seed traits can be important predictors of which species may be impacted most by altered seed predation rates due to habitat fragmentation.

The consequences of fragmentation altering seed predation rates for the plant community may interface with other important demographic stages that matter for plant populations such as reproduction, establishment, and dispersal. The variable seed predation responses we observed could lead to changes in the seed community that remains at the patch edge (Appendix S1: Figure S1). It is unclear how these changes would interact with these other demographic stages. Others have found that pre-dispersal seed predation can alter plant reproductive output (Brudvig et al., 2015), while post-dispersal seed predation can lead to changes in species establishment

(Dylewski et al., 2020; Orrock et al., 2006). Therefore, altered community composition of seeds near edges may influence the resulting plant community. All three of these processes—reproduction, establishment, and dispersal—are altered by fragmentation (Hulting et al., 2025; Uriarte et al., 2010; Warneke et al., 2022), and further investigation into how the effects of fragmentation interact across all these processes is needed to understand how plant communities respond to habitat fragmentation.

Understanding the dynamics of species interactions will help predict how plant populations respond to increasing habitat fragmentation and inform conservation. While previous research has highlighted the nuanced effects of habitat fragmentation on species interactions, our results further emphasize the significant role that edge effects can play in shaping post-dispersal seed predation (e.g., Craig et al., 2011; Orrock & Damschen, 2005), which in turn can give insight into how fragmentation might alter plant population demography and resulting plant communities (Brudvig et al., 2015). We show that information about species traits known to alter species interactions can help explain species responses to fragmentation, highlighting the importance of the different mechanisms through which fragmentation operates. Future studies that explore the role of edge effects and seed traits in light of other important aspects of landscape context (e.g., proximity to urban environments and latitudinal gradients in seed predation; Hargreaves et al., 2024) will be important for expanding our understanding of the predictability of plant–granivore interactions in contemporary landscapes.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Smith et al., 2026) are available from Dryad: <https://doi.org/10.5061/dryad.0p2ngf2g6>.

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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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