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RESEARCH ARTICLE

Habitat edges decrease plant reproductive output in fragmented landscapes

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Abstract

1. Habitat loss is a major threat to biodiversity, but the effects of habitat fragmentation are less clear. Examining drivers of key demographic processes, such as reproduction, will clarify species-level responses to fragmentation and broader effects on biodiversity. Yet, understanding how fragmentation affects demography has been challenging due to the many ways landscapes are altered by co-occurring habitat loss and fragmentation, coupled with the rarity of experiments to disentangle these effects.
2. In a large, replicated fragmentation experiment with open savanna habitats surrounded by pine plantation forests, we tested the effects of inter-patch connectivity, patch edge-to-area ratio, and within-patch distance from an edge on plant reproductive output. Using five experimentally planted species of restoration interest—three wind-pollinated grass species and two insect-pollinated forb species—we measured plant flowering, pollination rate, and seed production.
3. All plant species were more likely to flower and produce more flowering structures farther from the forest edge. Connectivity and distance from an edge, however, had no effect on the pollination rate (regardless of pollination mode). Despite no influence of fragmentation on pollination, plant seed production increased farther from the edge for four of five species, driven by the increase in flower production.
4. *Synthesis*. Altogether, we demonstrate that plant reproductive output (seed production) is decreased by habitat fragmentation through edge effects on flowering. Our work provides evidence that an important contributor to plant demography, reproductive output, is altered by edge effects in fragmented patches. These species-level impacts of fragmentation may provide insight into the mechanisms of fragmentation effects on community-level changes in biodiversity.

KEYWORDS
demography, edge effects, habitat fragmentation, landscape corridor, pollination, reproductive output, seed production

1 | INTRODUCTION

Habitat loss is a major threat to biodiversity (Dirzo et al., 2014; Newbold et al., 2015; Tilman et al., 2017). Although negative effects of habitat loss on biodiversity are clear, there is more debate about the effects of habitat fragmentation, which is often confounded with habitat loss (Fahrig, 2017; Fahrig et al., 2019; Fletcher et al., 2018; Haddad et al., 2015). To resolve this debate, examining mechanisms of biodiversity change, such as demographic processes within species, may clarify biodiversity trends in fragmented landscapes (Fletcher et al., 2023; Pardini et al., 2017). Population demography determines species persistence, particularly for small populations, and cumulative responses of multiple species may lead to community-level changes in biodiversity (Paniw et al., 2023; Schmidt et al., 2022). Past fragmentation research on demography has primarily focused on the processes of immigration and emigration (Honnay et al., 2005; Jacquemyn et al., 2002). However, other demographic processes, such as reproductive success, may also be impacted by fragmentation (Aguilar et al., 2019). Given that reproduction is a component of population growth (Koons et al., 2017), fragmentation effects on reproductive output may have important consequences for population persistence.

Because fragmentation results in several spatial patterns that arise at multiple spatial scales (Fletcher et al., 2023), experiments that are able to separate out the effects of these spatial patterns are valuable. For example, as a given amount of habitat is broken apart, the number of habitat patches increases at the landscape scale, which decreases habitat structural connectivity at the among-patch scale (Fletcher et al., 2023). At the same time, fragmenting habitat also creates more edge habitat, increasing the edge-to-area ratio at the patch and landscape scale and decreasing the average distance to an edge at the within-patch scale (Fletcher et al., 2023). These multiple components of fragmentation may each influence plant reproductive output (i.e. seed production), through impacts on pollination, growth, seed predation, or herbivory (Brudvig et al., 2015). However, despite broad recognition that effects of habitat loss and fragmentation are often confounded (Ewers & Didham, 2005; Fahrig, 2003; Valente et al., 2023), disentangling their effects remains challenging. Previous research on plant reproductive output has typically focused on patch size to test fragmentation effects (Bruna & Kress, 2002; Portela et al., 2021; Tomimatsu & Ohara, 2010), confounding multiple components of fragmentation with habitat loss. Experiments designed to separate the effects of multiple components of fragmentation from habitat loss will clarify the mechanisms of population demography change in fragmented areas, as we do here using an experimentally fragmented system.

Habitat fragmentation creates disconnected populations in isolated patches, which may reduce reproductive output for plants through disruption of pollen movement (Betts et al., 2019). Pollination is a key process for the vast majority of plant species' reproductive success (Friedman & Barrett, 2009; Ollerton et al., 2011), meaning that disruptions to pollination under landscape change can have negative consequences for plant reproductive output. Spatial isolation of populations by fragmentation may reduce pollen movement (Hadley & Betts, 2012), subsequently reducing gene flow and leading to a higher probability of inbreeding (Aguilar et al., 2019; Rosas et al., 2011). Both wind-pollination and insect-pollination may be decreased by fragmentation but through different mechanisms. Pollination for species dependent on plant–pollinator mutualisms is directly tied to fragmentation effects on their pollinators, with pollen movement corresponding to pollinator response (Kormann et al., 2016). Connectivity between patches facilitates movement for pollinators (Tewksbury et al., 2002), increasing pollen movement for insect-pollinated species (Townsend & Levey, 2005). However, for wind-pollinated species, abiotic conditions created by fragmentation such as increased edge and isolation may be the limiting cause of pollination through changing wind dynamics (Aguilar et al., 2019; Damschen et al., 2014). Structural connectivity of open habitats increases wind movement between patches, especially when aligned with predominant winds (Damschen et al., 2014), which may facilitate the movement of pollen between discrete populations (Provan et al., 2008). However, because of variation in species responses to fragmentation (Ewers & Didham, 2005; Fischer & Lindenmayer, 2007), more work is needed to understand whether patterns of pollination are consistent among pollination modes, as well as to disentangle the impacts of multiple fragmentation components on pollination that may confound fragmentation effects (Brudvig et al., 2015; Heinken & Weber, 2013; Newman et al., 2013).

Although pollen movement is often considered in the context of fragmentation, fragmentation may also affect plant reproductive output through population-level shifts in flowering and phenology. Edge habitat often hosts unique microclimate conditions, changing abiotic conditions, such as temperature, moisture, and light availability (Tuff et al., 2016). Because plant growth and flowering are highly determined by abiotic conditions, these abiotic changes could impact plant flowering and seed production (Galloway & Burgess, 2012; Müller et al., 2021; Suzán-Azpiri et al., 2017). Additionally, plant fitness can be affected indirectly through edge effects on insect visitors. Pollinators and insect herbivores may be affected by abiotic edge conditions, further impacting seed set and plant growth (Andrieu et al., 2018; Levey et al., 2016; Ren et al., 2023). As demographic structure (e.g. proportion of flowering individuals) and reproductive output can contribute to population growth (Caughlin et al., 2019), edge effects on plant flowering and seed production may impact plant population dynamics (Bruna & Kress, 2002; Suzán-Azpiri et al., 2017).

Plant population growth is determined by several demographic rates, including fecundity, establishment, survival, and growth (Sibly & Hone, 2002), which all may be affected by habitat fragmentation (Bruna & Oli, 2005; Honnay et al., 2005). However, the relative importance of these demographic rates for population dynamics may vary depending on the species' life history, local abiotic environment, and biotic interactions, among other factors (Crone, 2001; de Kroon et al., 1986). As such, seed production may be highly important for population growth and persistence if a species is seed limited, but less important if habitat conditions constrain survival or growth instead (Clark et al., 2007). Within our experimental system of longleaf pine savanna habitat, previous work has found that for two long-lived perennial species, seed production was the most important demographic parameter for predicting population growth (Caughlin et al., 2019). However, for an early-successional species, microsite conditions and seed predation were more significant than seed abundance (Orrock et al., 2006), highlighting the variability of demographic driver significance, even within a system. As a whole, although the relative importance of seed production for plant population persistence may vary, measuring reproductive output provides insight into how one component of demography may be impacted by landscape alterations (Bruna & Kress, 2002; Caughlin et al., 2019; Suzán-Azpiri et al., 2017).

Here, we test how fragmentation affects plant reproductive output, looking at fragmentation effects on plant flowering, pollination, and seed production. We worked in a large-scale, replicated fragmentation experiment designed to manipulate three aspects of fragmentation: among-patch connectivity, patch-scale edge-to-area ratio, and within-patch distance from an edge. We experimentally planted three wind-pollinated and two insect-pollinated plant species to ask (1) Do connectivity, edge-to-area ratio, and distance from an edge affect the likelihood of a plant flowering and flower abundance? (2) If a plant flowers, do connectivity, edge-to-area ratio, and distance from an edge affect pollination rate and seed production? We expected a reduction in plant reproductive output (seed production) near habitat edges and in unconnected patches. Specifically, in our system with open-habitat patches and forested matrix, we expected abiotic effects of canopy shading from the edge to decrease flowering, decreasing plant reproductive output near edges. Additionally, we expected pollination to be reduced in unconnected patches due to a disruption of pollen movement for both wind-pollinated and insect-pollinated species.

2 | MATERIALS AND METHODS

We conducted this study in eight experimentally fragmented landscapes, designed to test two components of habitat fragmentation: patch connectivity and edge-to-area ratio (Tewksbury et al., 2002). These landscapes are maintained by the USDA Forest Service at the Savannah River Site (SRS), a National Environmental Research Park in Aiken and Barnwell counties, South Carolina, USA. Each experimental landscape (hereafter, 'block') contains five patches, created by clearing mature pine plantations and restoring the resulting openings to longleaf pine savanna, surrounded by the remaining pine plantation. Blocks were initially created in winter 2000 ($n=6$) or 2007 ($n=2$). Within each block, one central 100 m × 100 m patch is surrounded by four 1.375 ha peripheral patches that are each 150 m from the centre patch and vary in connectivity and edge-to-area ratio (Figure 1). One peripheral patch (connected patch) is connected to the centre patch by a 150 m × 25 m corridor, also of the same open savanna habitat. The other three peripheral patches are isolated from the centre patch by 150 m of pine plantation and are either rectangular or winged. Rectangular patches are 100 m × 137.5 m. Winged patches are 100 m × 100 m with two 75 m × 75 m wings (blind-end corridors) extending from opposite sides. Comparisons between winged and connected patches test for connectivity effects because these patch types have similar edge-to-area ratios but differ in structural connectivity to the centre patch. Comparisons between winged and rectangular patches test for edge-to-area ratio effects, as winged patches have about 50% higher edge perimeter than rectangular patches.

Experimental plots within these patch types allow us to test for edge effects and their potential interactions with the edge-to-area ratio and connectivity of patches. As such, they allow for multiple scales of fragmentation to be evaluated. We established populations of five herbaceous plant species in each patch at four distances from the edge in 2007–2008 (Brudvig et al., 2015). We chose species that are native to longleaf pine savanna, represent multiple pollination modes, and are long-lived perennials of conservation value that did not previously occur in our experimental landscapes (Brudvig et al., 2015). It was important to select species not already occurring in our experimental sites because we wished to standardize the initial population size. Three species are wind-pollinated perennial bunch grasses in the Poaceae family: *Anthaenantia villosa*, *Aristida beyrichiana*, and *Sorghastrum secundum*. Two species are insect-pollinated perennial forbs in the Asteraceae family: *Carphephorus bellidifolius* and *Liatris earlei* (hereafter, species are referred to by their genus name). Based on personal observations, *Carphephorus* and *Liatris* are visited by a wide variety of insect pollinators. *Carphephorus* is generally not self-compatible, while *Liatris* has limited self-compatibility (Burt & Brudvig, 2019). Each population was started from seeds sourced from SRS and propagated in greenhouses, except for *Aristida*, which was started as plugs sourced from northern Florida. In spring 2007, we planted one seedling of each species into 16 plots per patch, located at four distances from each patch corner (0, 10.25, 19.10, 36.10 m from the nearest two edges; Figure 1). Each seedling was planted at least 0.5 m from other transplants in the plots. We removed all preexisting vegetation in the plot prior to transplanting and continued to hand-weed around each transplant throughout this study. In fall 2007 and spring 2008 and 2009, we replaced individuals who had died when transplanted. To improve the survival of individuals planted within the previous 12 months, we watered in weeks that did not receive at least 2.5 cm of rainfall (long-term average rainfall in the region).

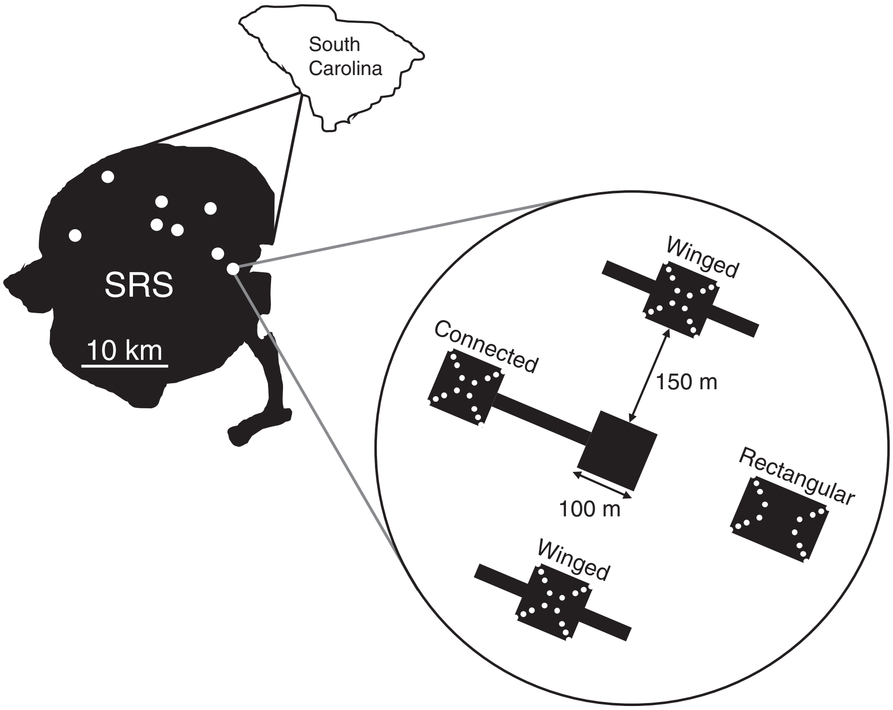

FIGURE 1 Locations of experimental blocks at the Savannah River Site (SRS), South Carolina. Longleaf pine savanna patches were connected to the centre patch by a 150 × 25 m corridor, unconnected with a high edge-to-area ratio (winged), or unconnected with low edge-to-area ratio (rectangular). Each patch contains 16 plots, denoted with white dots, where one individual of each of the five focal species was transplanted. Plots are arranged along four transects in each patch, located at 0, 10.25, 19.10 and 36.10 m from the nearest two edges.

2.1 | Data collection

We measured the plant reproductive output of each transplanted individual in fall 2009, the third growing season since transplanting. If an individual was flowering, we counted the number of flowering structures (culms or inflorescences) and marked three randomly selected flowering structures during peak flowering season (marking all structures if only one or two were present). We collected marked structures just before seed dispersal, collecting ~90% (2584/2897) of structures prior to seed dispersal. We excluded structures with >50% dispersal of seeds from analysis (~2.5% of structures). Collected structures were stored in a freezer until inspection. Because each flower results in a seed structure (achene or caryopsis) regardless of pollination for each of these study species (Brudvig et al., 2015; Burt & Brudvig, 2019), we were able to estimate pollination rates through the collected structures. We gently squeezed each achene/caryopsis to determine if it contained a developed seed, and visually inspected a random subsample of up to 10 underdeveloped achenes/caryopses on one flowering structure per plant for signs of pre-dispersal seed predation or damage. We assumed that seed predators would only consume structures that contained developed seeds and used this rate of pre-dispersal seed predation to correct for developed seeds damaged or consumed by seed predators (Brudvig et al., 2015). We calculated the pollination rate as the proportion of developed achenes/caryopses (corrected for pre-dispersal seed predation) to the total number of achenes/caryopses (developed and underdeveloped) across the collected structures, for each reproductive individual. We then averaged the resulting estimated pollination rate of the 1–3 collected seed structures to obtain one measure of pollination per individual plant. Lastly, we calculated total plant seed production as the average number of developed seeds per structure (culms or inflorescences) multiplied by the total number of structures on the plant.

Because the size of a plant could impact plant reproductive output, we measured plant size to account for potential effects on flowering, pollination, and seed production. During the peak flowering season in the fall 2009, we measured the height, length (longest axis), and width (perpendicular to length measurement) of each plant. We calculated plant size as volume (length × width × height) following Levey et al. (2016). Although we only measured plant reproductive output in the third growing season, the percentage of plants that were flowering was comparable to subsequent years (2009 = 60% flowering, 2012 = 78% flowering, 2015 = 72% flowering, 2019 = 59% flowering), which suggests that our measures of reproductive output in the third growing season may be representative of other growing seasons across the plants' lifespan.

2.2 | Statistical analysis

We tested the effects of connectivity, edge-to-are ratio, and distance from an edge on plant flowering (flowering likelihood and number produced), pollination rate, and total seed production per plant. We analysed fragmentation effects on each species individually, as our primary goal was to understand fragmentation effects within, not among, species.

First, for each focal species, we used a two-part hurdle generalized linear mixed-effects model (GLMM) to analyse two components of flowering: the likelihood of an individual plant flowering and the number of flowering structures produced. We chose to use a hurdle model due to the high number of non-flowering plants (40% not flowering) and because we hypothesized that the ecological processes driving the probability that a plant flower may differ from the processes driving the number of flowering structures produced. We used a binomial distribution to model the likelihood of a plant flowering (zero-component, 1 = flowering, 0 = vegetative). Due to overdispersion in our count data, we used a zero-truncated negative binomial distribution to model the number of flowering structures produced (non-zero conditional component). For both components of the model, we included plant size (log-transformed), patch type (connected, rectangular, winged), distance from edge (0, 10.25, 19.10, 36.10 m), and the interaction between patch type and distance from edge as fixed effects. Random intercepts for both model components were patch corner (4 corners/patch) nested within patch (4 patches/block) nested within block (8 blocks).

Next, we tested how fragmentation affects pollination rate. For each species, we fit a single GLMM with plant size (log-transformed), patch type, distance from an edge, and the interaction between patch type and distance from an edge as fixed effects. Random intercepts were patch corner (4 corners/patch) nested within the patch (4 patches/block) nested within the block (8 blocks). We used a beta-binomial distribution (weighted by the average number of flowers per structure) due to overdispersion in our pollination rate data (proportion data). Non-reproductive plants were excluded from the pollination rate analysis.

Last, we tested how fragmentation affects seed production using a hurdle GLMM for each focal species. We chose to use a hurdle model to model seed production to model the probability of producing seeds separately from the number of seeds produced, because many reproductive plants in our experiment did not produce any developed seeds (16% of plants). The zero-component of this model tested the likelihood of a reproductive plant producing seeds (1 = seeds produced, 0 = no seeds produced) using a binomial distribution. The non-zero conditional component of this model evaluated the number of seeds produced using a zero-truncated negative binomial distribution (due to overdispersion in count data). Fixed effects in both model components were plant size (log-transformed), patch type, distance from an edge, and the interaction between patch type and distance from an edge. For *Liatris* and *Anthaenantia*, we dropped plant size as a fixed effect in the zero-component of the hurdle model due to convergence issues. For both model components, we included patch corner (4 corners/patch) nested within patch (4 patches/block) nested within block (8 blocks) as random intercepts.

In all models, distance from an edge was treated as a continuous variable as results were qualitatively unchanged whether it was treated as a factor or not. Because the interaction term between patch type and distance from an edge was not significant ($p > 0.05$) in any model, we dropped the interaction to evaluate the main effects. We tested for significance of fixed effects using Wald χ^2-type III tests, and if patch type was a significant predictor, we used Tukey post hoc tests to evaluate significance levels between pairwise patch comparisons.

All analyses were conducted in R v. 4.2.3 (R Core Team, 2023) and all figures were created with ggplot2 v. 3.4.2 (Wickham, 2016) and ggeffects v. 1.2.1 (Lüdecke, 2018). We used graphs of residuals and Q–Q plots from the DHARMa package v. 0.4.6 to evaluate models for suitability (Hartig, 2022) and checked for overdispersion using the performance package v. 0.10.3 (Lüdecke et al., 2021). We used the glmmTMB package v. 1.1.7 to fit GLMMs (Brooks et al., 2017), the car package v. 3.1–2 for Wald χ^2-tests (Fox & Weisberg, 2019), and the emmeans package v. 1.8.5 for Tukey post hoc tests (*emmeans* function; Lenth, 2023).

3 | RESULTS

3.1 | Flowering

Within patches, individuals were more likely to flower farther from the edge, regardless of species (Figure 2a, Table S1). For all species, individuals were also more likely to produce more flowering structures farther from the edge, even when accounting for plant size (Figure 2b, Table S1; percent increase in flowering structure abundance from 0 to 36.10 m: *Anthaenantia* = 172%, *Aristida* = 229%, *Sorghastrum* = 117%, *Carphephorus* = 84%, *Liatris* = 363%). Patch-level connectivity or edge-to-area ratio did not affect plant flowering likelihood for any species (Tables S1 and S2). However, patch-level connectivity and edge-to-area ratio did affect the number of flowering structures that *Aristida* and *Liatris* produced, though inconsistently among species. *Aristida* produced more flowering structures in winged patches compared with connected patches, indicating a negative connectivity effect (Table S2). *Liatris* produced marginally significantly more flowering structures in winged patches compared with rectangular patches, indicating a positive effect of increased edge-to-area ratio (Table S2).

3.2 | Pollination rate

The average pollination rate varied among species (average number of pollinated seeds per flowering structure: *Anthaenantia* = 47%, *Aristida* = 23%, *Sorghastrum* = 33%, *Carphephorus* = 15%, *Liatris* = 24%). We found no within-patch effects of distance from an edge nor patch-level effects of connectivity or edge-to-area ratio on pollination rate for any species (Figure S1, Table S3). Larger plant sizes increased pollination rates for two wind-pollinated grasses (*Aristida* and *Sorghastrum*), but not for any other species (Table S3).

3.3 | Seed production

The likelihood of a reproductive plant producing seeds (zero-component) was not affected by within-patch distance from an edge, patch-level connectivity, or edge-to-area ratio (Table S4). Larger plants were more likely to produce seeds for *Sorghastrum*, but seed production likelihood was not affected by any factor for other species (Table S4).

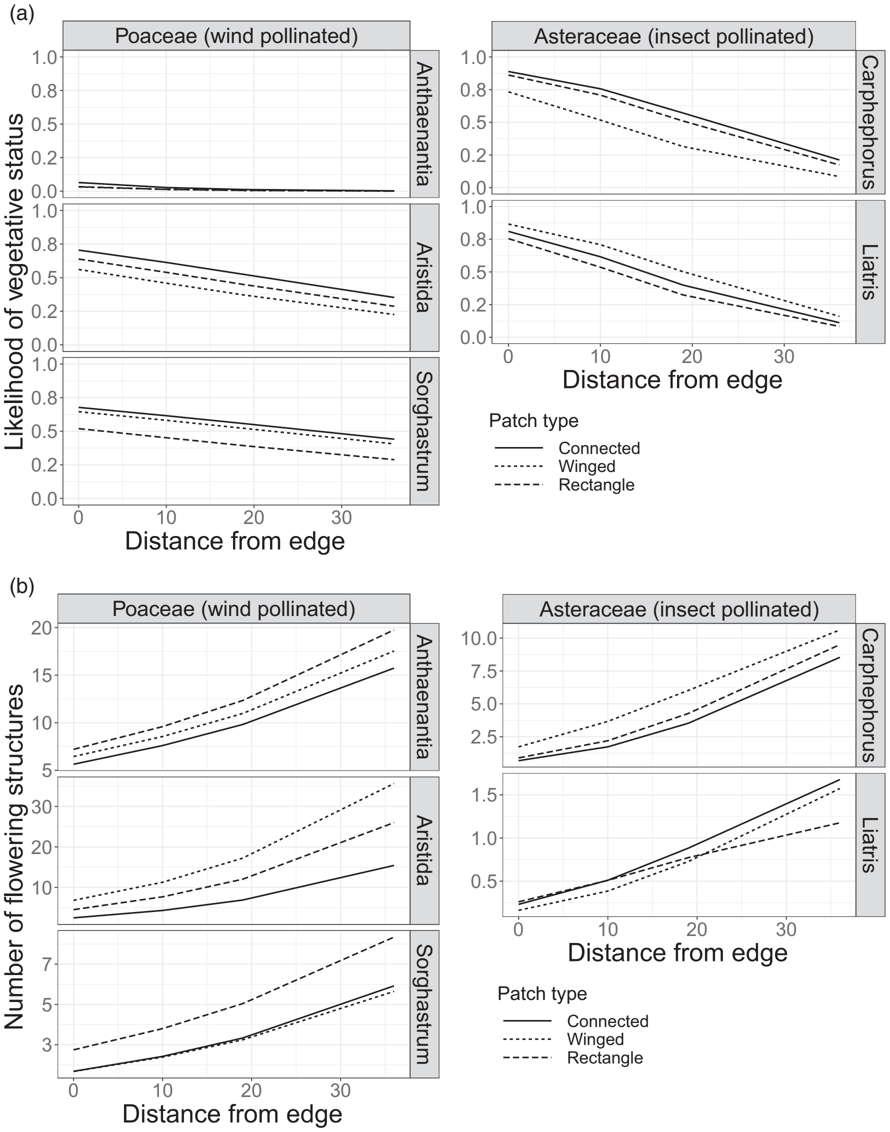

FIGURE 2 Effects of distance from an edge and patch type on flowering for five longleaf pine understory species. (a) Plants were less likely to be vegetative farther from the edge (i.e. more likely to flower). (b) Plants that did flower produce more flowering structures farther from the edge. Patch-type trends are significant for *Aristida* and *Liatris* (Table S2). Lines represent model predictions from hurdle GLMMs.

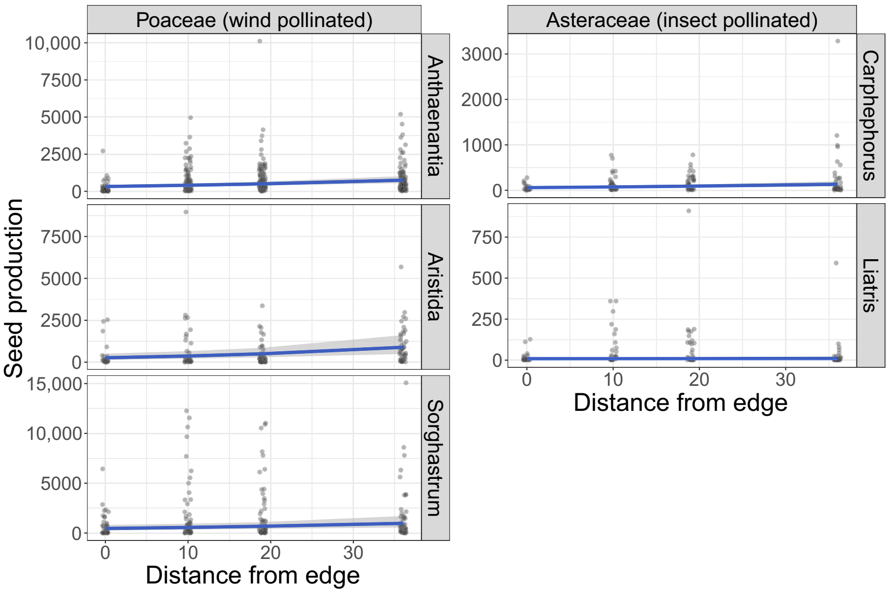

FIGURE 3 Effects of distance from an edge on the number of seeds produced by five longleaf pine understory species. The line represents model predictions from non-zero conditional components of hurdle GLMMs and the shaded region represents 95% confidence intervals. Plants produced significantly more seeds farther from the edge for all species except for *Liatris* (Table S4).

For the non-zero count of seeds produced, within patches, seed production increased farther from the edge for the three focal grass species (percent increase from 0 m to 36.10 m: *Anthaenantia* = 135%, *Aristida* = 240%, and *Sorghastrum* = 113%) and one forb species (percent increase from 0 to 36.10 m: *Carphephorus* = 128%; Figure 3, Table S4). Among patch types, connectivity, and edge-to-area ratio did not impact the number of seeds produced (Table S4). Across all species, larger plants produced more seeds per plant (Table S4).

4 | DISCUSSION

Our results demonstrate that habitat fragmentation consistently decreases plant reproductive output through edge effects. We show that within open-habitat patches, plants were more likely to flower, produced more flowering structures, and produced greater numbers of seeds farther from the edge. However, contrary to our expectations, the pollination rate was not affected by connectivity or distance from an edge for neither wind-pollinated nor insect-pollinated species. Connectivity and the edge-to-area ratio of patches affected flower production for two species, but infrequently and inconsistently among species. Altogether, our results suggest that one component of plant population demography, reproductive output, may be affected by edge proximity in fragmented landscapes.

Given that habitat edges have unique microclimate conditions, plant flowering, and seed production may have been driven by abiotic edge effects. In our system, with open-habitat patches and forest matrix, the edges are cooler and shadier than the interior of patches (Evans et al., 2012). These structural changes to canopy cover due to edge impact abiotic conditions that contribute to plant reproductive output, such as temperature and light which largely influence plant flowering and seed production (Qin et al., 2022; Srikanth & Schmid, 2011; Turley et al., 2017). Previous research in longleaf pine savanna habitat found that increased canopy cover decreased flowering (Turley et al., 2017), suggesting that our observed decrease in flowering near edges may have been driven by increased canopy cover at edges. Additionally, because edge proximity did not impact pollination, the decrease in plant-level seed production near edges for four species was also driven by edge effects on the number of flowering structures produced. Our analysis accounted for the effect of plant size on flowering and seed production, indicating that edge proximity decreased the number of flowering structures and seed production independent of plant size. As a result, edge proximity decreased plant reproductive output by decreasing flowering likelihood and the number of flowering structures produced, which decreased seed production.

For our two long-lived perennial forb species (*Carphephorus* and *Liatris*), previous research in our system found that seed production was the most important demographic predictor for population growth (Caughlin et al., 2019), indicating that this reduction in flowering and seed production near habitat edges may have large impacts on population growth for these species. Although the relative importance of seed production for population growth of our three perennial grass species (*Aristida*, *Anthaenantia*, *Sorghastrum*) has not been assessed in our system, our results indicate that at least one demographic parameter, reproductive output, is affected by fragmentation through edge effects. Future research should evaluate the significance of this reduction in reproductive output for the population growth and persistence of these species.

Although the distance from an edge affected the proportion of flowering individuals for all species, the edge-to-area ratio and connectivity of a patch only affected flowering structure abundance for two species, *Aristida* and *Liatris*. Because within-patch edge proximity decreased flowering likelihood and the number of flowering structures produced, we predicted that patch types with higher proportions of edge (connected and winged patches) would also show reduced flowering due to increased amounts of edge at the patch scale that impact abiotic conditions. In our experimental landscapes, connectivity and edge-to-area ratio change several abiotic conditions that may influence plant flowering, such as fire patterns (Brudvig et al., 2012), air temperature (Evans et al., 2012), and wind dynamics (Damschen et al., 2014) that may alter moisture availability. However, despite fewer reproductive individuals closer to the edge for all five species, no species had lower proportions of flowering individuals in patches with high edge-to-area ratio (Figure 2). Instead, connectivity and edge-to-area ratio did not affect plant flowering, except for two species that had a higher number of flowering structures in winged patches (high edge-to-area ratio) compared with rectangular patches (*Aristida*) or connected patches (*Liatris*). Although patch-scale connectivity and edge-to-area ratio affect abiotic conditions that may influence flowering, the strong within-patch abiotic effects of canopy cover due to edge proximity appear to have outweighed any patch-scale abiotic effects on flowering.

Contrary to our expectations, we found no effect of connectivity or distance from an edge on the pollination rate. Because our two insect-pollinated focal species (*Carphephorus* and *Liatris*) are self-incompatible (Burt & Brudvig, 2019), we expected fragmentation to decrease pollination success for these species. Previous research has found that connectivity increases pollen movement for both insect and wind-pollinated species (Jump & Peñuelas, 2006; Townsend & Levey, 2005); however, other factors such as pollen quality and the timing of pollen deposition may also be significant for pollination success (Aizen & Harder, 2007; Bruckman & Campbell, 2016; Ne'eman et al., 2010). Because we measured pollination rate as the proportion of developed seeds, our measure of pollination accounts for multiple factors that influence successful pollination in addition to pollen movement. Moreover, given that multiple individuals of each focal species were flowering in each patch, there may have been sufficient intra-patch pollen movement to maintain a similar pollination rate among connected and unconnected patches. Connectivity may be more important for habitat patches containing a lower density of individuals, as pollination success may depend more on pollen dispersal between patches.

Species with different life history traits may differ in responses to fragmentation; however, we found no consistent differences between our wind-pollinated (*Anthaenantia*, *Aristida*, *Sorghastrum*) and insect-pollinated (*Carphephorus*, *Liatris*) species. Despite highly different modes of pollen transport, connectivity and edge-to-area ratio did not affect pollination for any of these insect-pollinated or wind-pollinated species. In contrast, edge proximity had strong negative effects on flowering likelihood for all species, despite major life history differences in flowering structures. However, all our focal species are longleaf pine savanna understory species, which are adapted to high light environments without large amounts of accumulated leaf litter on the ground (Hiers et al., 2007; Turley et al., 2017). In our open-habitat system, a negative response to dense canopy cover at edge habitat may explain the ubiquitous response of these species' flowering to habitat edges. Therefore, the habitat requirements of these longleaf pine savanna focal species may have outweighed life history differences in pollination mode and flowering structures in response to fragmentation.

Understanding the mechanisms of biodiversity change in fragmented areas will further efforts to conserve biodiversity and help resolve debates surrounding the effects of fragmentation (Didham et al., 2012; Valente et al., 2023). Using a large-scale fragmentation experiment, we demonstrate that within-patch proximity to the edge can decrease plant reproductive output through effects on flowering, both through decreasing the likelihood of a plant flowering and decreasing the number of flowering structures. In landscapes where fragmentation decreases the average distance to an edge (Fletcher et al., 2023), edge effects may have a significant role in shaping demographic drivers of plant population persistence in fragments. Given that the five species we investigated are of conservation interest for longleaf pine savanna habitat, our results highlight the importance of landscape structure in restoration efforts for plant populations. Increased edge habitat due to fragmentation may reduce the restoration success of plant populations by altering demographic processes such as reproductive output. As a result, although dispersal and migration are often considered in fragmentation research, incorporating other demographic processes, such as reproduction, will strengthen conservation planning in fragmented areas.

AUTHOR CONTRIBUTIONS

Nick M. Haddad and Douglas J. Levey created, and Lars A. Brudvig, Ellen I. Damschen, Douglas J. Levey, Julian Resasco, Joshua J. Tewksbury, and Nick M. Haddad maintained the experimental landscapes. Lars A. Brudvig, Ellen I. Damschen, Douglas J. Levey, Joshua J. Tewksbury, and Nick M. Haddad designed methodology. Lars A. Brudvig, Ellen I. Damschen, Douglas J. Levey, Joshua J. Tewksbury, Julian Resasco, and Nick M. Haddad collected the data. Katherine A. Hulting analysed the data and led the writing of the manuscript, with contributions from all other authors.

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CONFLICT OF INTEREST STATEMENT

No conflicts of interest.

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DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.bnzs7h4mb (Hulting et al., 2024).

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SUPPORTING INFORMATION

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

Table S1. Anova type III results of the hurdle mixed model testing the effects of patch type (connected, winged, rectangular), distance from an edge, and plant size on (a) the likelihood of a plant being in the vegetative stage (zero model, 1 = flowering, 0 = vegetative) and (b) the number of flowering structures produced (zero-truncated conditional model).

Table S2. *Emmeans* pairwise comparisons of the effects of patch type on (a) the likelihood of a plant being in the vegetative stage (zero model, 1 = flowering, 0 = vegetative) and (b) the number of flowering structures produced (zero-truncated conditional model).

Table S3. Anova type III results of generalized linear mixed effects models testing the effects of patch type (connected, winged, rectangular), distance from an edge, and plant size on pollination rate.

Table S4. Anova type III results of the hurdle mixed model testing the effects of patch type (connected, winged, rectangular), distance from an edge, and plant size on (a) the likelihood of a plant producing seeds (zero model, 1 = seeds produced, 0 = no seeds produces) and (b) the number of seeds produced (zero-truncated conditional model).

Figure S1. Effects of distance from an edge and patch type on pollination rate for five longleaf pine understory species.

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