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The influence of habitat fragmentation on multiple plant–animal interactions and plant reproduction

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Abstract. Despite broad recognition that habitat loss represents the greatest threat to the world's biodiversity, a mechanistic understanding of how habitat loss and associated fragmentation affect ecological systems has proven remarkably challenging. The challenge stems from the multiple interdependent ways that landscapes change following fragmentation and the ensuing complex impacts on populations and communities of interacting species. We confronted these challenges by evaluating how fragmentation affects individual plants through interactions with animals, across five herbaceous species native to longleaf pine savannas. We created a replicated landscape experiment that provides controlled tests of three major fragmentation effects (patch isolation, patch shape [i.e., edge-to-area ratio], and distance to edge), established experimental founder populations of the five species to control for spatial distributions and densities of individual plants, and employed structural equation modeling to evaluate the effects of fragmentation on plant reproductive output and the degree to which these impacts are mediated through altered herbivory, pollination, or pre-dispersal seed predation. Across species, the most consistent response to fragmentation was a reduction in herbivory. Herbivory, however, had little impact on plant reproductive output, and thus we found little evidence for any resulting benefit to plants in fragments. In contrast, fragmentation rarely impacted pollination or pre-dispersal seed predation, but both of these interactions had strong and consistent impacts on plant reproductive output. As a result, our models robustly predicted plant reproductive output ($r^2 = 0.52$–0.70), yet due to the weak effects of fragmentation on pollination and pre-dispersal seed predation, coupled with the weak effect of herbivory on plant reproduction, the effects of fragmentation on reproductive output were generally small in magnitude and inconsistent. This work provides mechanistic insight into landscape-scale variation in plant reproductive success, the relative importance of plant–animal interactions for structuring these dynamics, and the nuanced nature of how habitat fragmentation can affect populations and communities of interacting species.

Key words: corridors; edge effects; habitat isolation; herbivory; landscape connectivity; patch shape; pollination; pre-dispersal seed predation.

Introduction

Habitat loss represents the greatest threat to the world's biodiversity (Fischer and Lindenmayer 2007, Collinge 2009, Didham et al. 2012). Despite broad agreement over the ultimate driver, human destruction of natural habitats (Vitousek et al. 1997, Foley et al. 2005), debate persists about the proximate causes of species declines in fragmented landscapes (Fischer and Lindenmayer 2007, Didham et al. 2012, Fahrig 2013, Haddad et al. 2015).

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Resolving this debate is complicated by the myriad ways that fragmented and unfragmented landscapes differ (Haila 2002, Ewers and Didham 2006, Fischer and Lindenmayer 2007, Laurance 2008, Didham et al. 2012). Although loss of habitat in a landscape typically reduces the area of residual habitat fragments, controversy arises because it may simultaneously increase isolation among fragments, increase the prevalence of within-fragment edge effects, and alter the matrix between remaining fragments (Smith et al. 2009, Didham et al. 2012). It is therefore important to disentangle the various impacts of landscape change resulting from habitat loss (Didham et al. 2012, Haddad et al. 2015).

In the same way that landscape features associated with habitat loss are problematic because they are confounded spatially, species interactions are problem-

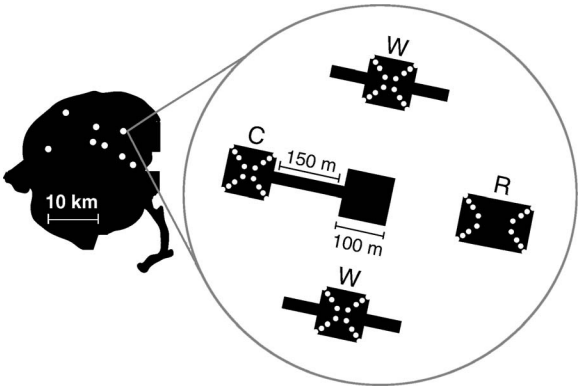

FIG. 1. Locations of experimental landscapes within the Savannah River Site and depiction of experimental patches for one landscape. Patches were either connected (C) to the central patch by a 150 × 25 m corridor or unconnected and rectangular (R) or winged (W), allowing for testing of connectivity (C vs. W or R) and patch shape effects (C or W vs. R). Transplant plot locations (0, 10.25, 19.10, and 36.10 m from edge) within patches are depicted with white dots.

atic because they are confounded both spatially and temporally (e.g., because one type of interaction usually follows another type; Didham et al. 2012). This complexity is particularly apparent in the study of plant–animal interactions. There is mounting evidence that habitat loss and fragmentation broadly affect plant–animal interactions (e.g., Tewksbury et al. 2002, Faveri et al. 2008, Farwig et al. 2009, Uriarte et al. 2011, Evans et al. 2012, Magrach et al. 2014, Martinson and Fagan 2014) and these effects have implications for plant conservation (Schemske et al. 1994). For example, studies spanning Argentinean dry forest, Australian woodlands, and meta-analyses have shown that declines in pollination rates and concomitant reductions to plant reproduction can occur when ecosystems are fragmented (Aizen and Feinsinger 1994, Cunningham 2000, Aguilar et al. 2006). Fragmentation can also impact antagonistic interactions, including herbivory and seed predation; for example, levels of herbivory can increase with Amazonian forest fragmentation and rates of seed predation can increase with longleaf pine savanna fragmentation (Orrock et al. 2003, Orrock and Damschen 2005, Faveri et al. 2008). Importantly, plant–animal interactions can impact plant populations through positive (e.g., pollination) or negative (e.g., herbivory) effects on fitness or fitness surrogates, yet we know virtually nothing about the demographic consequences of multiple co-occurring interactions in landscape contexts. Moreover, substantial variation exists in how plant species and plant–animal interactions respond to fragmentation (e.g., Aizen and Feinsinger 1994, Orrock et al. 2003, Orrock and Damschen 2005, Faveri et al. 2008) and efforts are needed to understand whether general patterns exist, or if responses are ultimately idiosyncratic (Haila 2002, Fischer and Lindenmayer 2006, Laurance 2008, Didham et al. 2012).

Here, we test how habitat fragmentation impacts plants and their interactions with animals, through effects on patch (i.e., fragment) isolation, alterations to patch shape (i.e., changes to edge-to-area ratio), and greater proximity to patch edges (i.e., within-patch edge effects). To do this, we employ a landscape experiment that manipulates these three factors, while controlling for habitat amount, patch area, and matrix composition. Thus, our experiment either manipulates or controls each type of landscape change that commonly accompanies habitat loss (Haila 2002, Ewers and Didham 2006, Fischer and Lindenmayer 2007, Didham et al. 2012).

We then use structural equation modeling (SEM) to evaluate how landscape changes that accompany fragmentation affect the balance between positive and negative interactions. Specifically, we evaluate how patch isolation, increases in patch edge-to-area ratios, and proximity to edges influence plant reproductive output through impacts on one plant–animal interaction that positively impacts plants (pollination) and two plant–animal interactions with negative impacts for plants (herbivory, pre-dispersal seed predation). We do so across five plant species to understand whether species illustrate consistent or individualistic responses.

METHODS

Experimental system

We conducted this study within a replicated landscape experiment located at the Savannah River Site (SRS), a National Environmental Research Park in Aiken and Barnwell Counties, South Carolina, USA. Eight replicate landscapes were created by harvesting mature pine plantations (six in 2000, two in 2007) to create 1.375-ha open habitat patches that have subsequently been managed for longleaf pine savanna through periodic prescribed fire and clearing of encroaching hardwood and loblolly pine trees. Each landscape consisted of five open patches ($n = 40$ total patches), one central patch and four peripheral patches, and the surrounding pine plantation matrix (~50 ha in total; Fig. 1). Within each landscape, the central 100 × 100 m patch was connected to one peripheral patch (the connected patch) with a 150 × 25 m corridor, also of open habitat. The remaining three peripheral patches were of equal area to the connected patch plus the corridor, but were isolated from the central patch by matrix pine plantation and were of two types: rectangular or winged. Rectangular patches were 100 × 137.5 m (475 m edge, 13 750 m^2 patch area), whereas winged patches had two 75 × 25 m wings, also of open habitat, extending from a 100 × 100 m patch (700 m edge, 13 750 m^2 patch area). Peripheral patch type and corridor orientation were randomly assigned to the extent possible.

This experimental design allows us to test how corridors impact ecological systems through connectivity and changes in patch shape (i.e., edge-to-area ratio). A comparison of connected and winged patches tests for

isolation effects (via presence/absence of a corridor) while controlling for shape, as these two patch types have different connectivity (via the corridor) to the central patch, but roughly equivalent edge-to-area ratios. A comparison of winged and rectangular patches tests for patch shape effects, as these two patch types have the same connectivity to the central patch, but the edge-to-area ratio of the winged patches is ~50% higher than that of the rectangular patches.

Establishment of founder populations

During 2007–2008, we established founder populations of five longleaf pine savanna understory plant species in each experimental patch. Species were selected based on their high conservation value, absence from our study patches and surrounding matrix, and representation of multiple life-histories. *Aristida beyrichiana*, *Anthaenantia villosa*, and *Sorghastrum secundum* are perennial bunchgrasses (Poaceae) with wind-pollinated flowers, whereas *Carphephorus bellidifolius* and *Liatris earlei* are perennial forbs (Asteraceae) with insect-pollinated flowers. For each species, we propagated seedlings using southeastern U.S. genotype seeds (from SRS, when possible). We transplanted one 2–4 month old seedling into each of 16 1 × 4 m plots in each patch in May 2007 (*A. beyrichiana*, *A. villosa*, *S. secundum*, and *C. bellidifolius*) and May 2008 (*L. earlei*) for a total of 640 individuals per species. Plots were located at 0, 14.5, 27, and 51 m from each of the patch corners, corresponding to 0, 10.25, 19.10, and 36.10 m from the nearest edge, respectively (Fig. 1). Seedlings were randomly assigned to locations spaced 50 cm apart. We removed pre-existing vegetation from each plot by hand 4–6 weeks prior to transplanting and, subsequently, applied glyphosate herbicide to any new or re-sprouting plants 2 weeks prior to transplanting. In cases of transplant mortality, we replanted individuals in June and October 2007, April 2008, and April 2009. To improve transplant survival, we weeded each plot twice annually throughout the duration of this study and, in weeks that did not receive 2.5 cm of rainfall, we applied ~2.5 cm of water to the area of each plant that was transplanted within the previous 12 months.

Data collection

To determine effects of plant–animal interactions on reproductive output of each species, we quantified levels of herbivory, pre-dispersal seed predation, and pollination, as well as plant size (leaf number) and reproductive output during the 2009 field season for each individual. In September, we determined plant size and incidence of herbivory by recording the total number of leaves and, of these, the number of leaves with visual evidence of herbivory. For plants with >100 leaves, we counted and surveyed for herbivory a haphazard subsample of 100 leaves; we then made a visual estimate of the total number of leaves on the plant. Between August and December, we visited plants at approximately weekly intervals to count flowering structures and collect fruit structures for analyses of pollination and pre-dispersal seed predation and to determine the number of developed seeds per structure. We determined plant-level reproductive output by extrapolating the number of developed seeds per floral structure to the entire plant using our counts of total structures. During peak flower production for each individual, we randomly selected and marked one to three flowering structures (culms for Poaceae, inflorescences for Asteraceae), marking all structures if fewer than three were present. We were able to collect developed seeds from ~90% (2592/2911) of structures prior to any dispersal. To correct estimates of reproductive output for plants with seeds that had dispersed prior to collection, we noted the approximate number of dispersed seeds based on culms or floral bracts and corrected our estimates of reproductive output accordingly for structures with ≤60% dispersal; structures with >60% dispersal were excluded from analyses (<3% of total reproductive structures).

For our study species, every flower results in an entity resembling a seed (achene or caryopsis), regardless of successful pollination. This allowed us to assess rates of pollination through collection of seed structures. Following collection, samples were stored in a freezer until they could be inspected; achenes/caryopses were categorized as developed or undeveloped by gently squeezing each with forceps to determine whether each contained a developed seed. We then visually inspected under magnification a random subsample of up to 10 undeveloped achenes/caryopses for signs of damage or insect frass. We quantified pollination as the proportion of achenes/caryopses that developed or were undeveloped but damaged, relative to the total (developed, undeveloped, or damaged). This approach assumes that pre-dispersal seed predators would consume only reproductive structures with developed or developing seeds (i.e., those that had been pollinated). We estimated pre-dispersal seed predation as the proportion of pollinated seeds that were subsequently destroyed by pre-dispersal seed predators.

Structural equation modeling

We developed SEM's in AMOS (Arbuckle 2009) to understand how fragmentation and plant–animal interactions influenced plant-level reproductive output of each species. SEM is a useful framework for investigating the effects of habitat loss and fragmentation (Didham et al. 2012) due to its capacity to evaluate complex systems composed of non-independent variables with direct and indirect relationships (Grace 2006). We developed a separate SEM for each species, based on a common meta-model (Fig. 2). This model contained direct and indirect (mediated through influences on levels of herbivory, pollination, and pre-dispersal seed predation) paths between patch isolation, patch edge-to-area ratio, and proximity to edge (0, 10.25, 19.10, and 36.10 m) to plant-level reproductive output (log-

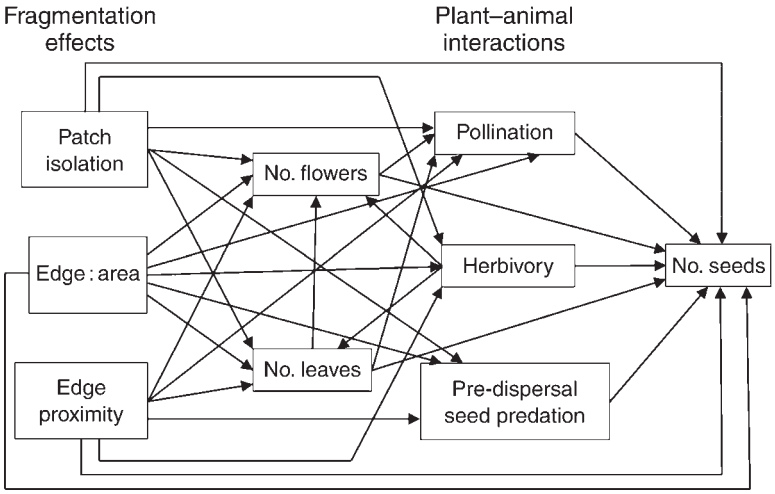

FIG. 2. General structural equation model (SEM) meta-model depicting hypothesized relationships between habitat fragmentation effects (isolation, patch edge-to-area ratio, proximity to edge), plant–animal interactions, and plot-level metrics including reproductive output. The direction of hypothesized relationships is indicated by the direction of each arrow.

transformed). We defined isolation as the difference between values in connected and winged patches and edge-to-area as the difference between values in winged and rectangular patches. We defined herbivory as the percentage of leaves with evidence of herbivory, pollination as the percentage of flowers that were pollinated, pre-dispersal seed predation as the percentage of pollinated flowers that were destroyed by pre-dispersal seed predators prior to seed development, and reproductive output as the number of apparently viable seeds produced. To account for variation in plant size and floral production, we included the number of leaves (log-transformed) and the number of flowers (log-transformed) as additional variables in the models. Log transformations were necessary to help meet SEM's assumption of linear relationships between variables. In sum, this resulted in nine measured variables (Fig. 2).

We parameterized models using average values for each patch-by-edge distance for peripheral patches, resulting in a maximum of 128 observations per model. Testing of hierarchical models is not currently supported in AMOS and, thus, our models do not consider variation accounted for by replicate experimental blocks. This may result in our models being conservative, as three of the five species show significant effects of block for seed production (effect of block $P < 0.05$ in blocked/split-plot mixed model); however, this likely does not complicate the interpretation of our main findings, as no species showed block-by-patch type interactions (all $P > 0.1$). Due to our consideration of two plant–arthropod interactions that can only be quantified using reproductive individuals (pollination, pre-dispersal seed predation), we used data only from reproductive individuals ($n = 1588$) in the SEM analyses. We recognize that the likelihood of flowering may also be an important contributing factor in reproductive success. In our experiment, individuals near edges were less likely to flower than those further away from edges for all five species (all $P < 0.05$, based on mixed-effect linear models testing proportion of flowering individuals, with patch type (connected, rectangle, winged), edge distance, and patch type-by-edge distance interaction as fixed effects and experimental block as a random effect). Conversely, the proportion of flowering individuals was never influenced by patch type or the interaction between patch type and edge distance (all $P > 0.05$).

RESULTS

Each of the SEM's fit the data well (minimum $P = 0.1$ for χ^2 goodness of fit; $P > 0.05$ indicates good fit; Grace 2006) and accounted for substantial variation in plant reproductive output ($r^2 = 0.52$–0.7; Figs. 3 and 4). Across models, species illustrated variation in the total influences of patch isolation, increased patch edge-to-area ratio, and edge proximity on reproductive output. Total influences are derived by summing path coefficients across direct and indirect paths connecting two variables and are equivalent to the bivariate correlation between the two variables (e.g., edge distance and seed production; Grace 2006). Values ranged from 0.01 for isolation with *A. villosa* to 0.25 for increased patch edge-to-area ratio with *C. bellidfolius* (Fig. 5). Edge proximity was the only aspect of fragmentation that generally resulted in lower reproductive output, with four of five species showing this response. Surprisingly, even though edge proximity was generally associated with decreased plant reproduction, increased patch edge-to-area ratio consistently increased reproductive output, clearly showing that patch level effects cannot be easily inferred from edge effects. Isolation effects on reproductive output ranged from weakly negative to moderately positive, effects of increasing edge-to-area ratio ranged from weakly to moderately positive, and proximity to edge ranged from moderately negative to weakly

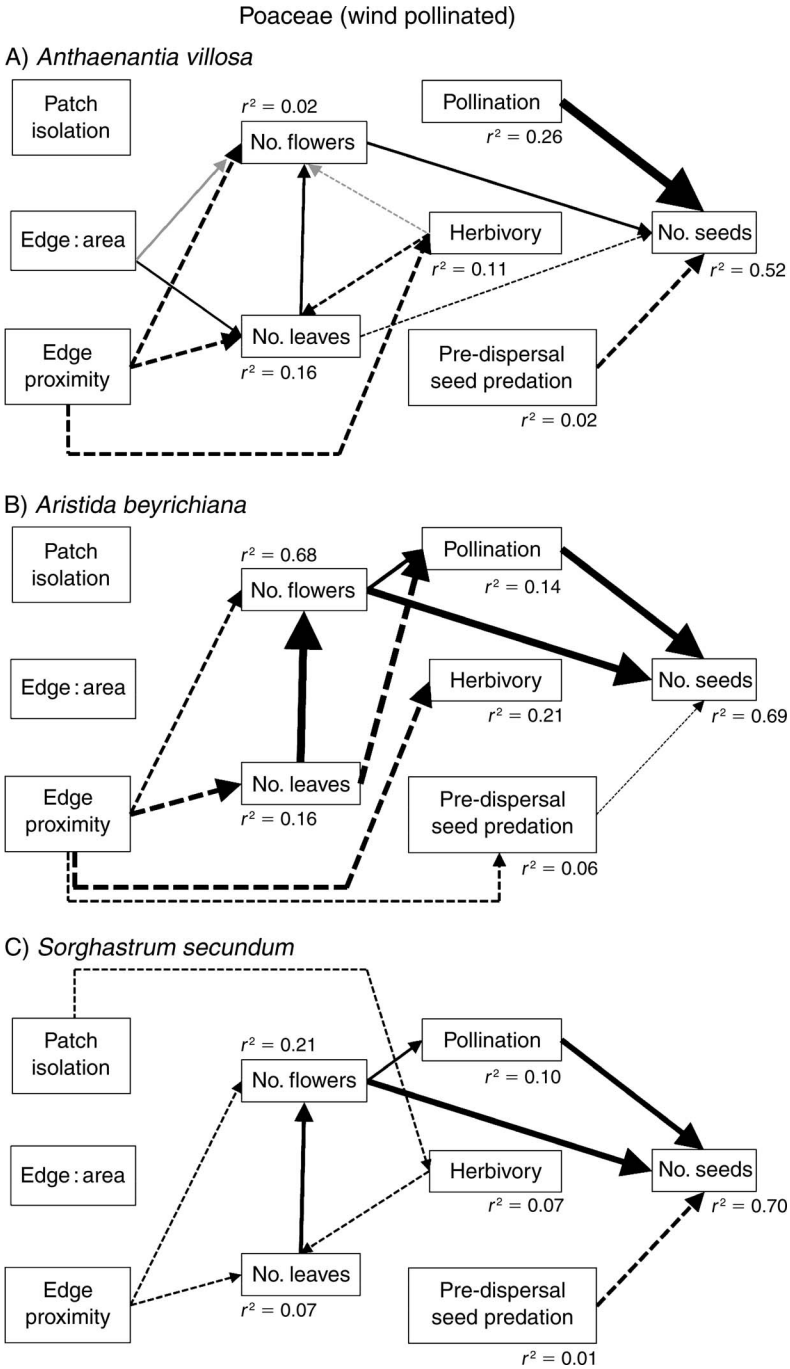

FIG. 3. Structural equation model for wind-pollinated species in the Poaceae: (A) *Anthaenantia villosa*, (B) *Aristida beyrichiana*, and (C) *Sorghastrum secundum*. Significant paths ($P < 0.05$) are shown in black and marginally significant paths ($P < 0.10$) are shown in gray. For simplicity, nonsignificant paths are not shown; however, all paths from Fig. 2 were tested. Positive correlations are indicated by solid lines and negative correlations by dashed lines.

positive. Additional details of plant reproduction responses to fragmentation effects are provided in Appendix: Figs. A1 and A2. Across species, we found strong positive influences of pollination and moderate to strongly-negative influences of pre-dispersal seed predation on reproductive output, whereas influences of herbivory were generally weaker and variable, ranging from −0.09 (*S. secundum*) to 0.15 (*C. bellidifolius*) (Fig. 5).

In the SEMs, we found the most evidence for effects of fragmentation on levels of herbivory, with six total effects across species (Table 1). Levels of herbivory

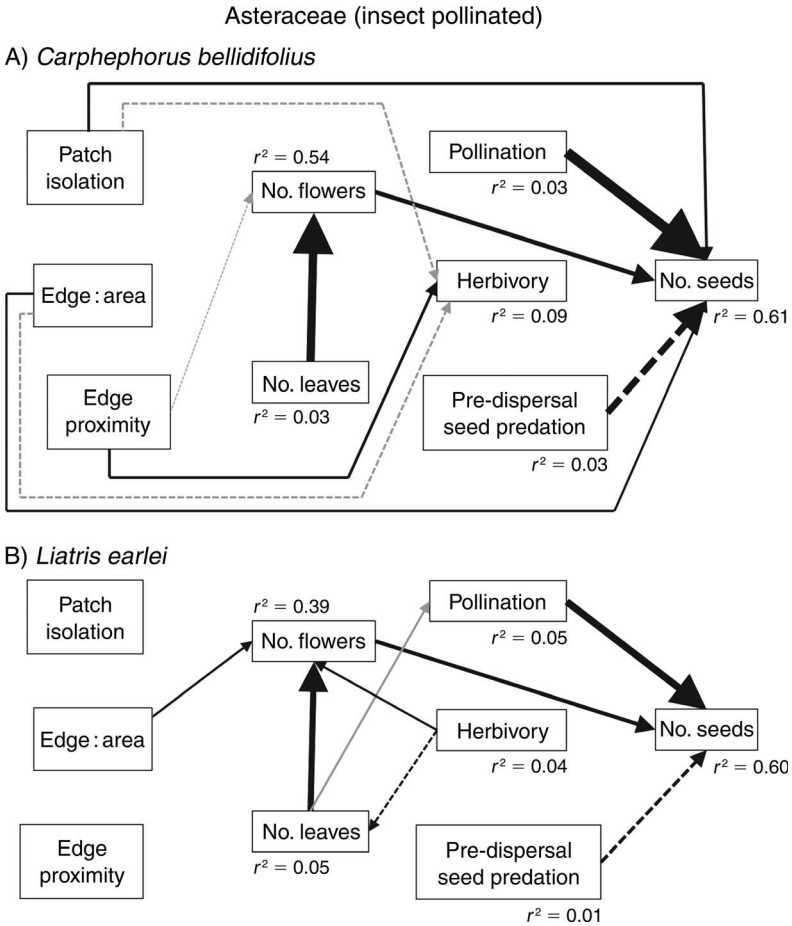

FIG. 4. Structural equation models for insect-pollinated species in the Asteraceae: (A) *Carpheporus bellidifolius* and (B) *Liatris earlei*. Significant paths ($P < 0.05$) are shown in black and marginally significant paths ($P < 0.10$) are shown in gray. For simplicity, nonsignificant paths are not shown; however, all paths from Fig. 2 were tested. Positive correlations are indicated by solid lines and negative correlations by dashed lines.

decreased with patch isolation for *S. secundum* ($P = 0.03$) and trended toward a decrease in *C. bellidifolius* ($P = 0.08$). Levels of herbivory trended toward a decrease with increasing patch edge-to-area ratio for *C. bellidifolius* ($P = 0.09$). Herbivory decreased with edge proximity for two grass species (*A. beyrichiana*, $P < 0.001$; *A. villosa*, $P < 0.001$), but increased for one forb (*C. bellidifolius*; $P = 0.02$). We found little evidence for significant direct effects of fragmentation on pollination and pre-dispersal seed predation, with pre-dispersal seed predation decreasing with edge proximity for *A. villosa* ($P = 0.01$) and no instances of fragmentation effects on pollination rates.

DISCUSSION

We evaluated how reproduction of five herbaceous plant species is affected by three landscape changes that accompany habitat loss and fragmentation—patch isolation, increased edge-to-area ratio, and increased proximity to edge—and by three plant–animal interactions—herbivory, pollination, and pre-dispersal seed predation, which may themselves be affected by isolation, edge-to-area ratio, and proximity to edge. We found that herbivory is most frequently affected by fragmentation, yet this interaction only weakly affected plant reproduction. Conversely, pre-dispersal seed predation and pollination (see Plate 1) strongly and consistently impacted plant reproduction, but these interactions were rarely or never influenced by fragmentation. As a result, species interactions more strongly structured landscape-scale variation in plant reproduction than did habitat fragmentation, and what effects of fragmentation we did observe were inconsistent among species.

Understanding how ecological systems are affected by habitat loss and fragmentation has been challenging due to the numerous non-independent ways that landscapes change following habitat loss, coupled with the resulting complexity of changes to ecological communities. Our work represents, to our knowledge, the first coupling of two general approaches that have been advocated for surmounting these challenges: landscape experiments

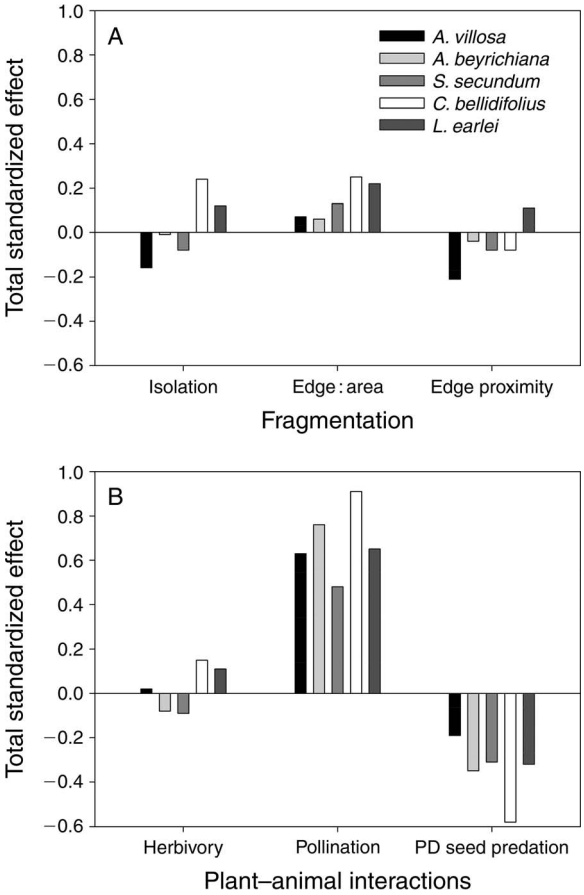

FIG. 5. Total standardized effects from structural equation models, summarizing how reproductive output of five species of longleaf pine understory herbs is affected by (A) habitat fragmentation and (B) plant–animal interactions. Total standardized effects range from −1 to 1 and describe the effect of each variable on reproductive output, summed across all direct and indirect pathways in the model. See Fig. 2 for description of paths tested and Figs. 3–7 for models of each species. *A. villosa*, *A. beyrichiana*, and *S. secundum* are species of Poaceae, whereas *C. bellidifolius* and *L. earlei* are species of Asteraceae. PD, pre-dispersal.

and SEM (Didham et al. 2012, Haddad et al. 2015). This coupling allowed us to link the experimentally generated understanding of fragmentation effects (e.g., predominant effects on herbivory) with how co-occurring positive and negative plant–animal interactions affect plant reproduction. All this was facilitated by the ecological realism permitted by the scale of our experimental landscapes (Gilbert-Norton et al. 2010).

There is mounting evidence that species interactions are impacted by habitat loss and fragmentation (Ewers and Didham 2006, Hadley and Betts 2012, Magrach et al. 2014) and that interactions can be affected, at least in part, through the promotion of landscape connectivity (Gilbert-Norton et al. 2010). Our findings provide four key advances to this body of work.

First, while the influence of spatial scale in ecological interactions has long been argued to be critical (Wiens 1989, Levin 1995, Leibold et al. 2004), few studies have been able to clearly show the scale dependencies of plant animal interactions in the context of fragmentation. By experimentally disentangling the influences of isolation, patch edge-to-area ratios, and edge proximity on species interactions, we show that these impacts of fragmentation have scale-dependent impacts on plant–animal interactions and plant reproduction. In four of the five species we studied, plants closer to edges (increased edge proximity) showed lower plant reproduction, but in patches with higher edge-to-area ratio (more edge habitat with the same patch size) all species showed higher reproduction. These qualitatively different results suggest that processes taking place across smaller-scale edge gradients, such as how arthropods behaviorally track abiotic conditions, can be functionally uncoupled from processes that take place at the larger scale of the patch, such as arthropod population sizes (e.g., Evans et al. 2012).

Second, although fragmentation may affect species interactions through multiple mechanisms (Hadley and Betts 2012, Magrach et al. 2014), rarely are these effects considered in the same study, making it difficult to gauge their relative importance (Didham et al. 2012). Our approach overcomes this limitation, and shows that herbivory is more consistently affected by fragmentation than are pollination and pre-dispersal seed predation, contrasting with previous suggestions that mutualisms may be more affected than antagonisms by fragmentation (Magrach et al. 2014).

Third, despite the long history of literature on fragmentation, little is known about how fragmentation affects key plant demographic rates (Bruna et al. 2009, Ibáñez et al. 2014) and rarely are species interactions and aspects of plant demography coupled at landscape scales (through see plant–pollinator examples; e.g., Aizen and Feinsinger 1994, Cunningham 2000; reviewed by Aguilar et al. 2006, Hadley and Betts 2012). Our approach allows us to link species interactions with plant reproduction in a landscape context. For example, in the context of our study, it is surprising that fragmentation only weakly affects plant reproductive output; the interactions that most strongly structured

TABLE 1. Summary of fragmentation effects on plant–animal interactions.

	Plant–animal interaction		
Effect	Herbivory	Pollination	Pre-dispersal seed predation
Patch isolation	2(−)	0	0
Patch edge : area	1(−)	0	0
Edge proximity	1(+), 2(−)	0	1(−)

Note: Values are the number of significant paths across species, with direction of impact (positive or negative) in parentheses.

PLATE 1. Gulf Fritillary (*Agraulis vanillae*) butterfly visiting a *Carphephorus bellidifolius* inflorescence. Photo cedit: E. I. Damschen.

seed production, pollination and pre-dispersal seed predation, were largely unaffected by fragmentation.

Fourth, we are able to explore co-occurring positive and negative interactions within a single landscape. Species interactions may have varying influences on plant reproduction and path analyses, such as SEM, provide the ability to disentangle these impacts (e.g., Schemske and Horvitz 1988). Our work is among the first attempts to do so at landscape scales, or in context of habitat fragmentation and, thus, provides an important advance to a literature that has typically considered only pair-wise species interactions (Gilbert-Norton et al. 2010, Magrach et al. 2014).

Our work also provides insight into how fragmentation and plant–animal interactions structure plant reproductive output within our landscape-scale study system. Herbivory was most frequently affected by fragmentation and this occurred through effects of isolation, patch edge-to-area ratio, and proximity to edge (Table 1). Fragmented ecosystems may have increased or decreased rates of herbivory relative to unfragmented ecosystems (e.g., Valladares et al. 2006, Faveri et al. 2008), with edge effects as potentially important contributing factors (e.g., Meiners et al. 2000, McKone et al. 2001). Indeed, past work within our system illustrated prominent effects of edge proximity, as well as some effects of patch edge-to-area ratio, on herbivory (Evans et al. 2012, 2013). We speculate that edge proximity effects could be due to common responses of grasshoppers to abiotic gradients, as grasshoppers are major herbivores in our study sites (Evans et al. 2012). We were surprised to find no evidence for fragmentation effects on pollination, given reduced pollination rates observed in other fragmented ecosystems (Aguilar et al. 2006), the relatively small number (16) of individuals per species planted into each patch in our experiment, and the enhancement of inter-patch pollen movement and pollinator abundances by corridors in our system (Haddad and Baum 1999, Tewksbury et al. 2002, Townsend and Levey 2005). Self-incompatible plants are typically most strongly impacted by fragmentation effects on pollination (Aguilar et al. 2006), making our results particularly remarkable for the two largely self-incompatible species of Asteraceae, but perhaps less surprising for self-compatible species like the grass *A. beyrichiana* (M. Burt and L. A. Brudvig, *unpublished data*). Moreover, we found very little evidence for fragmentation affecting pre-dispersal seed predation (Table 1), which contrasts with past studies from our system showing how connectivity, patch edge-to-area ratio, and edge proximity can affect post-dispersal seed predation (e.g., Orrock et al. 2003). Given the prominent and opposing influences of pollination and pre-dispersal seed preda-

tion on plant reproduction (Fig. 5), more work is needed to elucidate the factors controlling variation in these co-occurring processes, at landscape scales.

Island Biogeography Theory (MacArthur and Wilson 1967) remains a dominant theory for understanding effects of habitat fragmentation but makes an outdated assumption that species respond uniformly to changes in area and isolation (Haila 2002, Fischer and Lindenmayer 2006, Laurance 2008, Didham et al. 2012, Mendenhall et al. 2014, Haddad et al. 2015). Although variation in species responses is widely accepted, it remains unclear whether species show largely individualistic responses (Haila 2002, Fischer and Lindenmayer 2006) or whether species may illustrate a set of common responses to fragmentation (Didham et al. 2012). We see some evidence for common responses to patch isolation and edge-to-area ratio, whereas responses to edge proximity appeared more idiosyncratic. Both species of Asteraceae showed increased seed set in isolated patches, whereas the three species of Poaceae showed decreased seed set or no effect of isolation. Asteraceae species illustrated more strongly increased seed set in high edge-to-area patches than did Poaceae. Our SEM's show how these common responses can arise through different mechanisms. For example, the effects of patch shape for *L. earlei* resulted from greater floral production in patches with lower edge-to-area ratio, whereas those of *C. bellidifolius* were manifest through a direct effect, which may have been related to an unmeasured variable or interaction, such as florivory. Although our sample size of species is small, the utility of phylogeny for understanding common responses to fragmentation is intriguing.

In our experiment, landscape connectivity by corridors has increased plant species richness (Damschen et al. 2006). Corridors might promote species richness through higher rates of dispersal, facilitating colonization and rescue effects, or through increased population persistence due to altered within-patch population dynamics. Our finding of relatively weak and inconsistent connectivity effects (Fig. 5), coupled with past work showing elevated rates of seed dispersal among corridor-connected patches (e.g., Tewksbury et al. 2002), support the role of among-patch seed dispersal and not within-patch population dynamics in structuring the increase in species richness. We caution, however, that more work is needed to understand plant reproduction and demography beyond seed production, given the potential importance of other demographic processes such as adult plant density and growth, or the presence of safe sites for recruitment (e.g., Bruna et al. 2002, Bruna and Kress 2002, Uriarte et al. 2010).

Understanding the mechanisms by which habitat fragmentation impacts populations and communities will be critical to resolving questions in landscape ecology and formulating strategies for biodiversity conservation in fragmented landscapes (Didham et al. 2012, Gregory and Beier 2014). We show how patch isolation, edge-to-area ratio, and edge proximity can each affect reproduction of herbaceous plant species, that some general patterns emerge (e.g., prominent role of fragmentation on herbivory), but that many idiosyncrasies exist. Moreover, while we were able to explain the majority of landscape-scale variation in plant reproductive output, much of the variation was unrelated to fragmentation. Resolving the ways that positive and negative interactions jointly structure population dynamics will play an important role in further progress in habitat fragmentation research.

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Supplemental Material

Ecological Archives

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