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Abstract. Habitat fragmentation affects species and their interactions through intertwined mechanisms that include changes to fragment area, shape, connectivity and distance to edge. Disentangling these pathways is a fundamental challenge of landscape ecology and will help identify ecological processes important for management of rare species or restoration of fragmented habitats. In a landscape experiment that manipulated connectivity, fragment shape, and distance to edge while holding fragment area constant, we examined how fragmentation impacts herbivory and growth of nine plant species in longleaf pine savanna. Probability of herbivory in open habitat was strongly dependent on proximity to forest edge for every species, increasing with distance to edge in six species (primarily grasses and annual forbs) and decreasing in three species (perennial forbs and a shrub). In the two species of perennial forbs, these edge effects were dependent on fragment shape; herbivory strongly decreased with distance to edge in fragments of two shapes, but not in a third shape. For most species, however, probability of herbivory was unrelated to connectivity or fragment shape. Growth was generally determined more strongly by leaf herbivory than by distance to edge, fragment shape, or connectivity. Taken together, these results demonstrate consistently strong edge effects on herbivory, one of the most important biotic factors determining plant growth and demography. Our results contrast with the generally inconsistent results of observational studies, likely because our experimental approach enabled us to tease apart landscape processes that are typically confounded.

Key words: connectivity; corridors; edge effects; fragment shape; habitat fragmentation; herbivory; plant growth.

Introduction

Habitat fragmentation is one of the most serious threats to plant and animal populations because it typically leads to decreases in overall amount of habitat, fragment area, connectivity, and distance to edge, all of which impact population dynamics and community structure through multiple, intertwined pathways (Fahrig 2003, Collinge 2009, Didham et al. 2012, Haddad et al. 2015). This complexity of causal links and its repercussions are perhaps best illustrated in fragmentation studies that include habitat corridors: strips of habitat in fragmented landscapes that connect otherwise isolated fragments of similar habitat (Chetkiewicz et al. 2006, Crooks and Sanjayan 2006, Hilty et al. 2006). Although corridors can mitigate negative effects of fragmentation by adding area to a fragment and increasing connectivity, their inherent "edginess" brings many potential costs (Simberloff et al. 1992, Collinge 2000, Gilbert-Norton et al. 2010, Staddon et al. 2010, Astrom and Part 2013, Haddad et al. 2014, Resasco et al. 2014). In particular, corridors might simultaneously benefit some fragmented populations by providing connectivity and threaten the same or other populations by increasing proximity to edge through alteration of fragment shape.

At the center of this uncertainty is the difficulty of teasing apart confounded effects of fragment shape, connectivity, and area (Laurance et al. 2002, Parker et al. 2005, Fletcher et al. 2007, Prugh et al. 2008, Didham et al. 2012, Fahrig 2013, Ibanez et al. 2014). The shape and area of a habitat fragment combine to determine the average distance to the fragment's edges. In particular, many symmetric fragments have greater average distances to edge, more "core" habitat, than do most asymmetrical fragments of equal area, which is relevant in heterogeneous landscapes because connected fragments

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are typically more asymmetrical than unconnected fragments due to their association with a corridor (Laurance and Yensen 1991, Collinge 2009, Didham and Ewers 2012). Given that proximity to edge impacts organisms in many ways (Fagan et al. 1999, Ries et al. 2004), the amount of core habitat in a fragment provides a more ecologically relevant metric of area than does total area (Ewers and Didham 2007, Fletcher et al. 2007). The key point is that edge-associated processes in habitat fragments can be viewed from two complementary perspectives: those determined by distance to the nearest edge and those determined by the edge-to-area ratio of the fragment. We refer to the first as "edge" effects and to the second as "fragment shape" effects. Although intimately related, they can impact individuals, populations, and communities in different ways, making it important to distinguish their effects (Orrock et al. 2011, Evans et al. 2012).

From a management perspective, the interplay between corridors and edges in fragmented landscapes is further complicated by their effects on organisms that interact with species of conservation concern (Harper et al. 2005, Weldon 2006, Staddon et al. 2010). A corridor, for example, might benefit a rare plant by facilitating movement of its pollinators between otherwise isolated populations. But edges associated with the corridor might nullify such a benefit by increasing densities of herbivores or seed predators, a possibility supported by frequent observations of plant–animal interactions responding to connectivity and fragmentation (Tscharntke and Brandl 2004, Orrock and Damschen 2005, Valladares et al. 2006, Garcia and Chacoff 2007, Aguirre and Dirzo 2008, Faveri et al. 2008, Kolb 2008, Collinge 2009, Ibanez et al. 2014). However, the effect size and even direction of such responses are highly variable with respect to fragment area, distance to edge, connectivity, and type of species interaction (Laurance et al. 2002, Ries et al. 2004, Harper et al. 2005, Ruiz-Guerra et al. 2010, Ibanez et al. 2014, Magrach et al. 2014, Mitchell et al. 2014, Haddad et al. 2015). Resolving this variability is key to understanding how connectivity can restore ecosystem processes and functionality in fragmented landscapes (Staddon et al. 2010, Astrom and Part 2013). Focusing on one type of interaction across a wide variety of species under tightly controlled conditions may reveal patterns not detected by the disparate set of existing, often observational, studies.

We studied impacts of corridors and edges on herbivory in nine understory plant species found in longleaf pine (*Pinus palustris*) savanna. We chose to study herbivory because it is ubiquitous and one of the major determinants of plant growth, reproduction, survival, and competitive ability (Hawkes and Sullivan 2001). We examined herbivory at the community level, recording the total leaf area consumed of focal plant species but not the species identity or impact of particular herbivores. Differences in diet and habitat use among herbivore taxa likely drive the abundance and distribution of herbivores within and among our study sites and underlie spatial patterns of herbivory (see *Methods: Study site and species*).

Our design uniquely addresses concerns about the interdependence of landscape features through application of a large-scale experiment in which we controlled several key features (overall amount of habitat at the landscape scale, fragment area, matrix type, time since fragmentation) while independently manipulating others. In particular, the study design allowed us to separate effects of connectivity, fragment shape, and distance to fragment edges. Because we planted seedlings of the nine species in a stratified random manner and from common seed sources, we also were able to control for effects of plant density, age, size, and genotype. Further, we quantified the relative importance of herbivory and structural features of fragmented landscapes on plant growth. Finally, we sought to assess the degree to which species responses are similar or individualistic (Lindenmayer and Fischer 2007, Didham et al. 2012) by measuring susceptibility to herbivory of species from different taxonomic groups and with different types of leaves and growth forms. Such differences can separate herbivore communities among co-occurring plant species, creating the potential for contrasting responses to landscape features.

For each of the focal plant species in our study, we addressed four questions: (1) Does connectivity (presence or absence of a corridor) affect probability of herbivory? (2) Does distance to the nearest edge affect probability of herbivory within fragments? (3) Does fragment shape (edge-to-area ratio) affect probability of herbivory among fragments? (4) To what extent is plant growth influenced by structural features of fragmented landscapes (connectivity, fragment shape, distance to nearest edge) vs. herbivory? Looking across species, we also asked: (5) Are impacts of landscape structure on herbivory uniform, or do they differ in consistent ways among species with similar growth forms?

METHODS

Study site and species

We worked in a series of eight experimental landscapes (hereafter "experimental blocks") created to test the efficacy of habitat corridors (Tewksbury et al. 2002). The experimental blocks were located within the Savannah River Site (SRS), a National Environmental Research Park in Aiken and Barnwell counties, South Carolina. Each block was composed of five fragments that are maintained as open, longleaf pine savanna and surrounded by a matrix of mature pines (*Pinus palustris* and *P. taeda*). Within an experimental block are three fragment types—connected, winged, and rectangular—arranged with one fragment in the center and four "peripheral" fragments 150 m from each side of the center fragment (Fig. 1). Connected fragments were 100 × 100 m with a 150 × 25 m corridor of the same

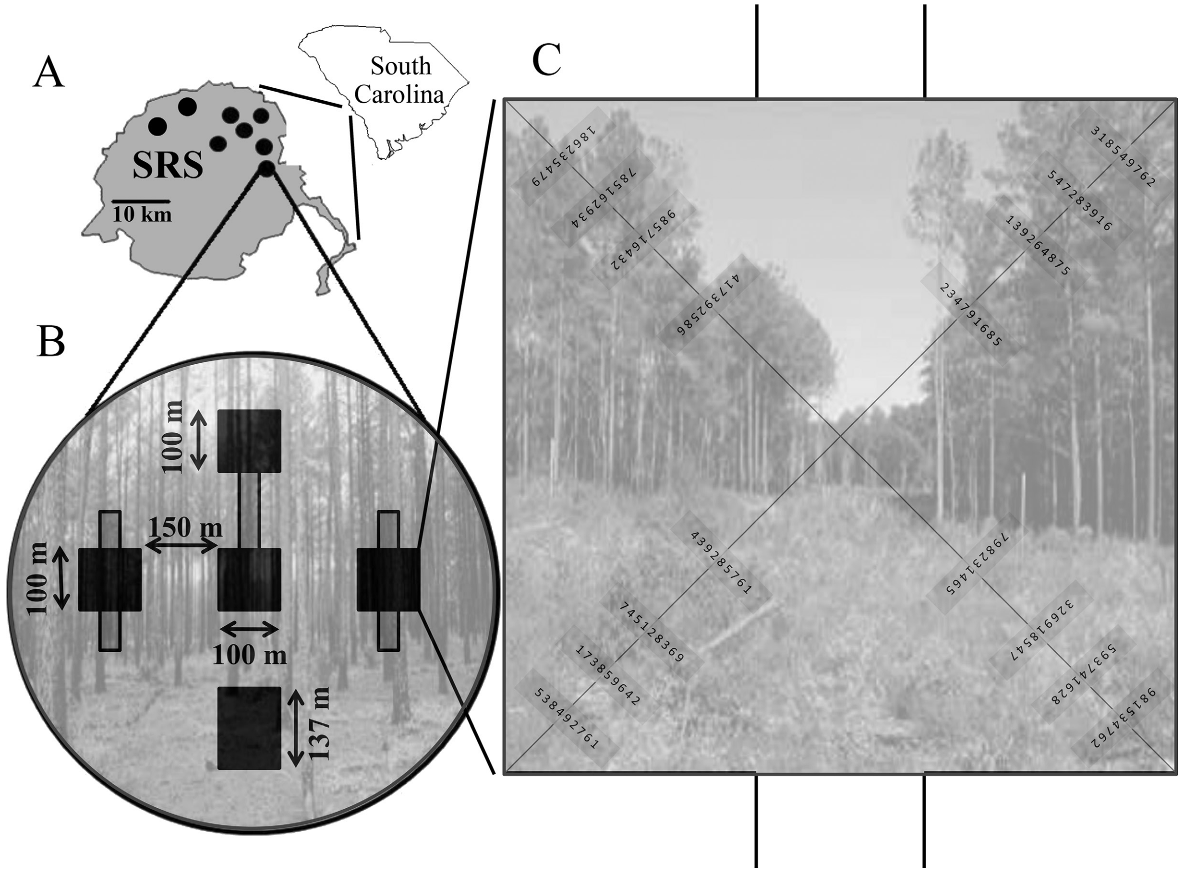

FIG. 1. (A) Location of eight experimental landscapes ("blocks") at the Savannah River Site (SRS) in South Carolina, USA. (B) Diagram of one block, showing its five fragments. Two fragments are connected by a corridor ("connected"), two have blind-end corridors ("winged"), and one is a rectangle. The areas of unconnected fragments are equal. Winged and connected fragments have similar edge-to-area ratios; rectangular fragments have much lower edge-to-area ratios. Gray areas denote corridors, either connecting fragments or blind-ended. Black and gray areas indicate the same habitat, regenerating longleaf pine savanna. Background photograph shows example of pine forest matrix (photo credit: Ellen Damschen). (C) Diagram of plot locations in a fragment; all fragments had the same number of plots arranged as illustrated for this winged fragment. Number strings represent plots (1 × 4 m), which were positioned at distances of 1, 15, 27, and 52 m along each of four transects radiating from fragment corners to the plot center. Numbers represent the nine study species, planted in random order along the central axis of each plot. Background photograph shows open habitat of fragment and corridor, bounded by forested matrix (photo credit: Nick Haddad). Note the distinct edge between fragment and matrix habitats.

habitat joining them to another fragment. Winged and rectangular fragments were identical in area to each other and to a connected fragment plus its corridor (1.375 ha). Winged fragments were 100 × 100 m plus the area of two blind-end corridors (75 × 25 m) extending from opposite sides and parallel to the nearest edge of the center fragment. Rectangular fragments were 100 × 137.5 m. The edge-to-area ratios of winged and connected fragments (including corridor) were similar to each other and averaged 40% greater than the edge-to-area ratio of rectangular fragments (Weldon 2006). Experimental blocks included a buffer area of pine matrix habitat extending ~150 m from the outside edge of all peripheral fragments. Within experimental blocks, fragment type and orientation were randomized. Four blocks consisted of two connected fragments, two winged fragments, and one rectangular fragment. The other four blocks consisted of two connected fragments, one winged fragment, and two rectangular fragments.

We emphasize that our landscapes are composed of open savanna habitat fragments surrounded by a dense pine plantation matrix. Therefore, when we refer to distance from edge in our experimental fragments, the reference point is in open savanna habitat and the distance is to the nearest forest. Longleaf pine savannas were historically the dominant ecosystem type, consisting of a highly diverse herbaceous understory with low numbers of scattered trees. Dense pine plantations are regionally common today, but were historically rare.

Abiotic conditions differ greatly within fragments as a function of distance to edge but are similar among the different types of fragments. Specifically, daytime temperature 0.3 m above soil surface in mid-summer (June and July) of two years (2008 and 2009) averaged approximately 32°C at 1 m from the nearest edge, 33.5°C at 10.5 m, 34.5°C at 20 m, and 35°C at 37 m (Evans et al. 2012). Temperature did not differ among fragment types, nor was there a significant interaction between fragment type and distance to nearest edge. Although we do not have comparable data on light and soil moisture, their spatial variation likely mirrors that of temperature (Chen et al. 1999). We expect light to increase and soil moisture to decrease with distance from edge, with neither greatly impacted by fragment shape.

We selected nine species of understory plants, all native to longleaf pine savanna and most of management interest due to their rare and patchy distributions (Kilgo and Blake 2005). With few exceptions, all populations were restricted to our experimental fragments (i.e., individuals rarely occurred in the matrix) and were planted as founder populations by us (see below). Species were chosen to represent a wide variety of growth forms, leaf textures, and taxonomic affiliations—all factors we suspected might influence their susceptibility to herbivory and their response to edges and connectivity. *Aristida beyrichiana, Sorghastrum secundum,* and *Anthaenantia villosa* are perennial bunch grasses (Poaceae). *Aristida* has stiff, wire-like leaves, whereas *Sorghastrum* and *Anthaenantia* have wider, more flexible leaves. (We use genus names throughout to refer to the species described here.) *Carphephorus bellidifolius* and *Liatris earlei* are perennial forbs (Asteraceae) with basal rosettes of broad, pliable leaves and sparse hairs. *Phytolacca americana* (Phytolaccaceae) and *Solanum americanum* (Solanaceae) are annual, upright forbs that grow quickly in open habitats and have broad, membranous leaves. *Nolina georgiana* (Liliaceae) is a perennial, basal-leaved forb with flat grass-like leaves and stature. *Gaylussacia dumosa* (Ericaceae) is a perennial, short-statured shrub with relatively small, leathery leaves.

To help identify potential patterns of herbivory among sets of species with similar growth forms, we categorized these species into four groups: grass and grass-like (*Aristida, Sorghastrum, Anthaenantia, Nolina*), perennial forbs (*Carphephorus, Liatris*), annual forbs (*Phytolacca, Solanum*), and shrub (*Gaylussacia*). We grouped *Nolina* with the grasses, due to matching basal-leaved growth forms and similar narrow, coriaceous, leaf morphology. We did not have a priori expectations of differences among these groups, and we recognize the limitations of any comparisons with such a small and taxonomically narrow set of species.

All plants except *Gaylussacia* were planted as seedlings into the experimental landscapes in the growing seasons of 2007 and 2008. *Gaylussacia* was transplanted from nearby populations. For all other species, seeds were collected from naturally occurring populations in the southeastern United States and then propagated in greenhouse conditions until planting. By mixing seeds prior to germination, any maternal effects were randomly distributed across treatments. *Solanum* was replanted in 2008 and 2009, since individuals did not survive the winters. During establishment, water was provided whenever weekly rainfall failed to reach the growing season weekly mean for the region (2.5 cm). Individuals that died during establishment were replaced.

One seedling of every species was transplanted into each of 16, 1 × 4 m plots in each of the 40 fragments (8 blocks × 5 fragments/block; $N = 5{,}760$ seedlings, total). In each fragment, plots were arranged in four transects of four plots each (Fig. 1). Transects originated at fragment corners and extended diagonally, at equal distance from the nearest edges, toward the center. Plots were positioned at 1, 15, 27, and 52 m from the patch corner along all transects, representing distances of ~1, 10, 19, and 36 m, respectively, from each of the two nearest edges. Within plots, seedlings were planted 0.5 m apart in a line perpendicular to and centered on the transect. The location of species along this line was randomized separately for each plot.

Grasshoppers (Orthoptera) are major herbivores in the fragments, accounting for >99% of observed herbivory on at least one of our study species, *Solanum americanum,* and are frequently flushed from many other species when walking between plots (Evans et al. 2012, Hahn and Orrock 2015*b*). Common genera include *Hippiscus, Melanoplus, Pardalophora, Psinidia,* and *Schistocerca, Trimerotropis*; *Melanoplus* and *Schistocerca* are most abundant and both are mainly composed of dietary generalists (Orrock et al. 2011, Evans et al. 2012, Hahn and Orrock 2015*b*). Grasshopper abundance increases with distance to edge and is highest in rectangular fragments, presumably because rectangular fragments contain more area far from edge than winged and connected fragments (Evans et al. 2012).

Herbivory and growth

In 2009, all plants were surveyed for herbivory three times: 30 May–13 June, 30 June–11 July, and 8–23 September, with the exception of *Solanum*, which was surveyed twice (27–31 August and 16–20 September) in only two of the transects in each fragment. On every plant, we counted the total number of leaves and all of the leaves with any sign of herbivory. Because the vast majority of herbivory was by insects that partially consumed leaves, assessment at the scale of individual leaves was appropriate. For individuals with more than 300 leaves, we extrapolated the total leaf number and number of leaves damaged by herbivores from a subsample of 100 leaves. To quantify growth, we recorded plant size by measuring maximum height, length (parallel to long axis of plot) and width (parallel to short axis of plot). Plant size was estimated by calculating volume (height × length × width) and relative growth rate was determined by subtracting the log volume of a given plant in June-July from its log volume in September. Results were qualitatively similar regardless of whether we used height, area (length × width), or volume as a metric of plant size (Appendix S1). We did not collect size data for *Solanum* and therefore excluded this species from analysis of growth.

Statistical analyses

All analyses were conducted in R (R Development Core Team 2012). We analyzed herbivory data with generalized linear mixed models (GLMMs), fitted separately for each species, using the lme4 package with maximum likelihood. The response variable was presence or absence of herbivory on individual leaves. Fixed effects were fragment shape (winged, connected, rectangular) and distance to edge, which was treated as a continuous variable (results are qualitatively unchanged if distance is treated as a factor), and the interaction between fragment shape and distance to edge. Random effects were individual plant (n = 4 plants/transect), transect (n = 4 transects/fragment; 2 transects/fragment for *Solanum*), fragment (n = 5 fragments/block), experimental block (n = 8), and census number (n = 3; 2 for *Solanum*). Census number provided a random slope, whereas plant, transect, fragment, and experimental blocks were random intercepts and hierarchically nested from plant to experimental block. These nested random effects controlled for spatial dependence due to environmental heterogeneity at different scales. We assessed the significance of main effects using Wald Z tests. Finally, we checked for evidence of spatial autocorrelation by creating semivariograms of the residuals from the growth regressions; we found no pattern for any species.

Connectivity effects (Question 1) were tested by comparing probability of herbivory in connected vs. winged fragments because they differ in connectivity but are identical in area and similar in edge-to-area ratio. Edge effects (Question 2) were assessed for all fragment types by comparing distances to edge within each fragment. Fragment shape effects (Question 3) were tested by comparing winged and rectangular fragments because they differ in edge-to-area ratio but are otherwise identical in area and connectivity.

To compare effects of herbivory and structural features of the landscape on plant growth (Question 4), we constructed linear mixed effects models for the relative growth rate of plants, with normally-distributed errors, proportion of leaves damaged (a plant-level index of herbivory), distance to edge and fragment shape as fixed effects, and the same random effects as herbivory (except without the random effect of individual plant). We assessed the relative importance of variables by standardizing the predictors. We first divided by the predictor's standard deviation and then centered the predictor variable around its mean (Gelman 2008), which allows a direct comparison of predictor variable coefficients estimated by the model for each plant species. Differences in herbivory among species with different growth forms (Question 5) were assessed qualitatively, based on GLMM outputs.

RESULTS

Averaging across all plants, transects, and fragments, the probability of herbivory occurring on a given leaf varied among species by a factor of 14 (Table 1). With the exception of *Anthaenantia,* probability of herbivory was much lower on grass and grass-like species than on both types of forbs and the shrub. Results are presented in the same order as the questions they address; all results are applicable to Question 5.

Connectivity

For seven of nine species, probability of herbivory did not differ between winged and connected fragments (Appendix S2), indicating no impact of connectivity on herbivory. For the two remaining species, *Carphephorus*

TABLE 1. Study species, growth forms, and effect of distance to edge on herbivory.

		Herbivory			Edge effect		
Species	Growth form	Probability	SE	Intercept	Estimate	SE	P
Aristida beyrichiana	grass and grass-like	0.04	0.11	0.007	0.006	0.002	0.0009
Sorghastrum secundum	grass and grass-like	0.09	0.13	0.040	0.004	0.001	0.004
Anthaenantia villosa	grass and grass-like	0.21	0.24	0.066	0.003	0.001	0.006
Nolina georgiana	grass and grass-like	0.06	0.12	0.022	0.022	0.002	0.055
Carphephorus bellidifolius	perennial forb	0.17	0.18	0.162	−0.006	0.001	1.00×10^{-8}
Liatris earlei	perennial forb	0.25	0.24	0.175	−0.006	0.002	0.0055
Solanum americanum	annual forb	0.16	0.17	0.121	0.002	0.001	0.0112
Phytolacca americana	annual forb	0.57	0.29	0.467	0.005	0.001	2.58×10^{-9}
Gaylussacia dumosa	shrub	0.15	0.17	0.056	−0.003	0.001	0.048

Notes: Probability of herbivory is calculated at the leaf level (i.e., probability that a given leaf will have any amount of herbivore damage). Intercept represents the probability of an individual leaf having insect herbivory in connected fragments, 1 m from the edge. The edge effect estimate represents the maximum change in the probability of leaf herbivory with an increase of 1 m in edge. The P value is the significance of the edge effect.

and *Liatris*, there was a significant interaction between fragment shape and distance to edge, with relatively strong negative effects of distance to edge for connected and rectangular fragments but not winged fragments (Fig. 2, Table 2). Both of these species are perennial forbs. For *Carphephorus*, probability of herbivory was much higher in connected than in winged fragments for plants near the forest edge but nearly equal far from the edge (Fig. 2). For *Liatris*, probability of herbivory slightly increased with distance from forest edge in winged fragments and decreased with distance from edge in connected fragments.

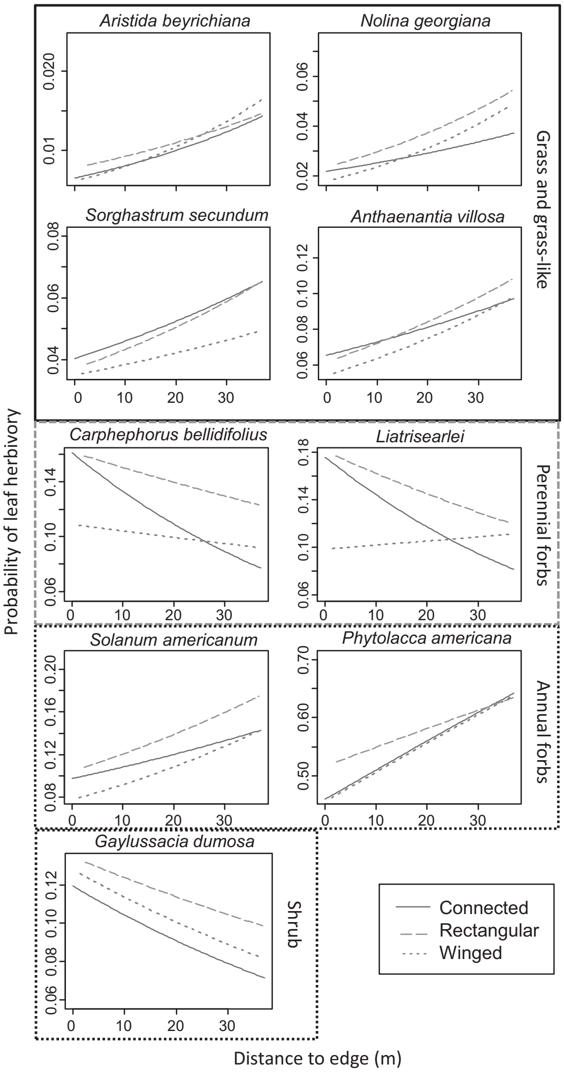

FIG. 2. Probability of leaf herbivory as a function of distance to edge for nine species in three fragment types. Each panel represents the probability of leaf herbivory, predicted using the coefficients from the binomial GLMM, for our nine study species. Lines show the relationship between probability of leaf herbivory and distance to edge, from 0–52 m, in connected fragments (solid line), winged fragments (dotted line), and rectangular fragments (dashed line). Species are grouped in boxes by growth form.

TABLE 2. Model estimates for the effect of fragment type and edge on herbivory for the two species with significant effects of fragment type.

Variable	Estimate	SE	P
Carphephorus bellidifolius			
Connected	−1.634	0.130	$<2 \times 10^{-16}$
Rectangular	0.006	0.181	0.974
Winged	−0.452	0.191	0.018
Connected × Edge	−0.022	0.004	9.97×10^{-8}
Rectangular × Edge	0.014	0.191	0.027
Winged × Edge	0.017	0.007	0.009
Liatris earlei			
Connected	−1.551	0.221	2.54×10^{-12}
Rectangular	0.045	0.304	0.883
Winged	−0.661	0.322	0.040
Connected × Edge	−0.024	0.008	0.0054
Rectangular × Edge	0.01	0.012	0.420
Winged × Edge	0.027	0.013	0.0435

Note: All other species had nonsignificant effects of fragment type.

Distance to edge

Distance between plant locations in the open habitat of fragments and the nearest edge of the forested matrix had a strong effect on the probability of herbivory for all species (all $P \leq 0.055$; Table 1; Appendix S2), despite the large variation in probability of herbivory among species. Six species experienced higher herbivory further from the edge (i.e., had positive slope estimates; Fig. 2). Again, the two perennial forbs, *Carphephorus* and *Liatris,* differed in response from most other species; they had lower probability of herbivory further from the edge, as did *Gaylussacia* (Fig. 2). Edge effects for *Carphephorus* and *Liatris* were dependent on fragment shape (i.e., significant interaction terms), as described in *Connectivity*. For *Gaylussacia*, edge effects were consistent across fragment shapes.

Fragment shape

Differences among patch types in probability of herbivory were indistinguishable for most species (Appendix S2). Herbivory in the two species of perennial forbs, *Carphephorus* and *Liatris*, was significantly higher in rectangular than winged fragments (Fig. 2), indicating that individuals of those species in less edgy fragments are at greater risk of herbivory. Regardless, herbivory effect sizes for all species were smaller and had larger confidence intervals than effect sizes for distance to edge (Appendix S3).

Growth

For all species, relative growth was significantly affected by herbivory and/or distance to forest edge (Fig. 3). In three species (*Aristida*, *Gaylussacia*, and *Nolina*), individuals further from edge grew more slowly than those close to edge; no species showed the opposite pattern. In five species, both perennial forbs and three of four grass and grass-like species (*Carphephorus Liatris, Aristida*, *Sorghastrum*, and *Anthaenantia*), relative growth was significantly negatively associated with herbivory. Association between relative growth and herbivory was positive for one species (*Phytolacca*) and nonsignificant for the remaining two species (*Gaylussacia* and *Nolina*). Not only were herbivory effects on growth more common among species than was distance to edge, but effect sizes within species (the ratio of slope coefficients for each panel of Fig. 3) were greater for herbivory than for distance to edge in six of eight species (*Aristida*, *Sorghastrum*, *Anthaenantia*, *Carphephorus*, *Liatris*, and *Phytolacca*).

Discussion

We found that distance to forest edge significantly impacts probability of herbivory in a wide variety of plants in longleaf pine savannas, a conclusion that contradicts the prevailing view that edge effects on herbivory are often neutral or idiosyncratic (Murcia 1995, Cadenasso and Pickett 2000, Laurance et al. 2002, Ries and Sisk 2004, 2010, Benitez-Malvido and Lemus-Albor 2005, Ibanez et al. 2014). All nine species displayed strong edge effects, either directly or in combination with fragment shape.

We found little evidence that landscape connectivity influenced herbivory (Question 1). In comparisons of herbivory in winged and connected fragments, no species showed a direct effect of connectivity and only two showed any type of connectivity effect: in both cases, an interaction between fragment connectivity and distance to edge. The consistency of this negative result is surprising, considering that four recent reviews of herbivory in fragmented landscapes have concluded that reduced connectivity and increased fragmentation are associated with decreased herbivory (Ruiz-Guerra et al. 2010, Ibanez et al. 2014, Martinson and Fagan 2014, Haddad et al. 2015). Although all of these studies reveal large variation in response, including situations in which the relationship is reversed (see also Magrach et al. 2014), it is puzzling that the relatively large number of ecologically different study species yielded no clear cases of herbivory being impacted by connectivity. This may be due to the "inverse" nature of our study system: fragments of open habitat in a matrix of forest rather than fragments of forest in a non-forested matrix, which is more typical. We suggest that many of the patterns of herbivory attributed to connectivity in previous reviews are actually caused by confounding factors (e.g., edge effects) because most of the studies included in those reviews did not experimentally manipulate connectivity or isolate its potential effects from other factors (Harrison and Bruna 1999, Fletcher et al. 2007, Didham et al. 2012). Our study design controlled confounding factors.

Indeed, a widely recognized confounding factor, distance to nearest edge (Question 2), underlies much of the spatial variation in herbivory in our system; we found strong correlations between probability of herbivory and distance to edge in all nine study species (Table 1, Fig. 2). This degree of consistency is again surprising because the relationship between herbivory and distance to edge is highly idiosyncratic and often neutral (Meiners et al. 2000, Cadenasso and Pickett 2001, Meiners and Martinkovic 2002, Bach and Kelly 2004, Tscharntke and Brandl 2004, Benitez-Malvido and Lemus-Albor 2005, del-Val et al. 2007, Wirth et al. 2008, Collinge 2009, Evans et al. 2013). A higher abundance of grasshoppers

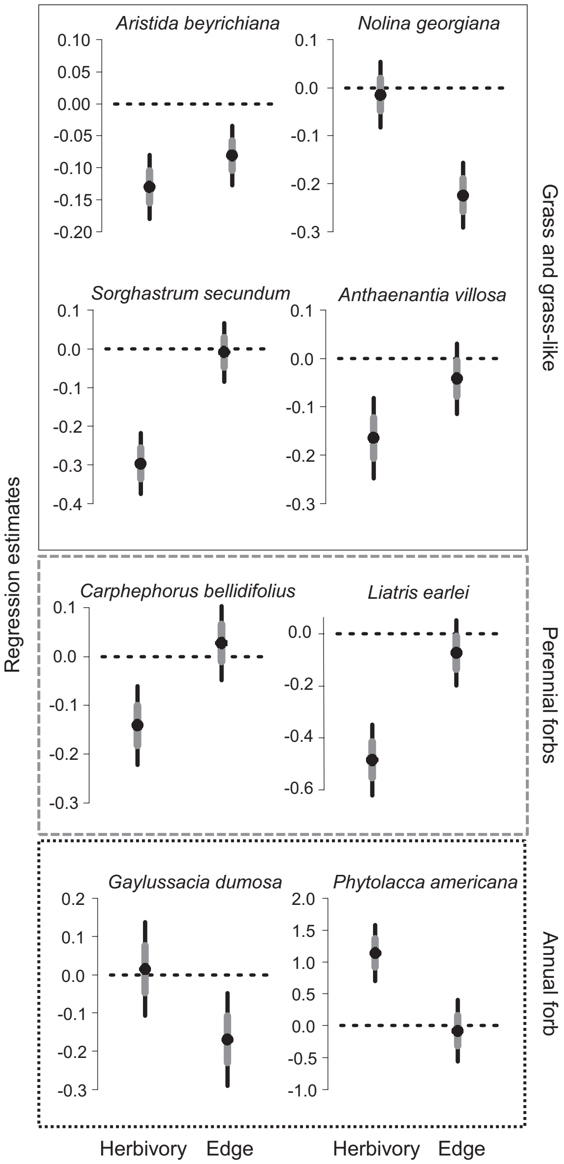

FIG. 3. Regression coefficients for herbivory and distance to edge from Linear Mixed-Effects (LME) for growth of eight plant species. Each panel shows the point estimate (black dot), 50% CI (thick line), and 95% CI (thin line) for regression coefficients for distance to edge and herbivory. The horizontal dashed line represents zero. Coefficients with 95% CI not crossing zero can be considered statistically significant. Because predictor variables in the model were standardized, the magnitude of regression coefficients for edge and herbivory is directly comparable.

far from edge (Evans et al. 2012) likely contributed to the positive correlation between herbivory and distance to edge that we observed in six of our species (Fig. 2). However, it does not explain the negative correlation between herbivory and distance to edge in the three remaining species.

The simplest explanation for opposite patterns of herbivory relative to distance to edge is that the herbivore community varied among our study species, perhaps due to land-use history (Hahn and Orrock 2015*a*, *b*), and that different types of herbivores (e.g., habitat generalists and specialists) responded to edges in opposite ways (Cadenasso and Pickett 2000, Davies et al. 2000, Laurance et al. 2002, Bach and Kelly 2004, Martinson and Fagan 2014). Because herbivore communities are most likely to differ between dissimilar types of plants, this interpretation is supported by the strongly consistent patterns we observed among species of a given growth form (Fig. 2); grass and grass-like species responded alike, as did the annual forbs. The two species of perennial forbs, on the other hand, showed nearly identical patterns in the opposite direction. Species-specific data on abundance and behavior of all herbivores would be necessary to test potential explanations for such differences. At the community level, however, differences in ground-dwelling arthropods among fragment types (Orrock et al. 2011) indeed suggest disparate effects of edge, patch shape, and connectivity among arthropod taxa (Ries et al. 2004).

Given that all nine species showed strong responses of herbivory to edge at relatively small scales, one might expect concordant responses at the scale of fragments (Question 3). In particular, those species with higher herbivory further from edges would presumably experience higher herbivory in fragments with more core area (i.e., rectangular fragments because they have more area far from edges). Likewise, those species with higher herbivory closer to edges would likely experience higher herbivory in fragments with less core area (i.e., winged fragments because they have less area far from edges). These types of fragment shape effects are commonly reported across a wide diversity of habitats, organisms, and species interactions, especially in fragmented landscapes (Fagan et al. 1999, Ewers and Didham 2007, Urbas et al. 2007, Haynes and Crist 2009). Indeed, they have been previously documented for both herbivores and granivores in our experimental landscapes (Haddad and Baum 1999, Orrock et al. 2003, 2011, Evans et al. 2012, Brudvig et al. 2015). In all such cases, consumer abundance and/or rates of herbivory and granivory were highest in rectangular fragments, as would be expected from the positive correlation we frequently observe between rates of herbivory and granivory and distance to the nearest edge. Despite this high level of consistency among previous studies in the same system, results for species in our current study were internally inconsistent. No species with higher herbivory far from edge also had higher herbivory in rectangular fragments, and no species with higher herbivory close to edge had lower herbivory in rectangular fragments. To the contrary, two species with higher herbivory close to edge (*Liatris* and *Carphephorus*), had significantly higher rates of herbivory in rectangular fragments than in winged fragments, which have proportionately more edge habitat.

Reconciling these results is difficult because edges influence different organisms and processes in different ways and on different scales, often due to interspecific variation in natural history (Ostfeld et al. 1997, Laurance et al. 2002, Ries and Sisk 2004, 2010, Cook and Holt 2006). We chose study species representing a wide variety of growth forms and life histories, with the expectation that at least some of the differences in herbivory we might observe among species would correspond to that variation in growth form and life history (Question 5). The strong, consistent patterns related to taxonomy and growth form are remarkable, almost certainly reflecting ecological differences among the plants and herbivores. All grasses and grass-like species (n = 4) showed very similar, positive relationships between probability of herbivory and distance to edge, as did both annual forbs (Fig. 2). The only species with negative relationships were the two perennial forbs (both Asteraceae), which also shared a unique and identical interaction between distance to edge and fragment shape. Together, these results suggest an important influence of growth form and phylogeny on species' response to edges.

Although some of our results differ slightly from those of previous herbivory studies in the same landscapes, all discrepancies can be attributed to different time scales (Evans et al. 2013), methods of quantifying herbivory (Evans et al. 2012), and statistical approaches (structural equation models) that considered more variables with fewer species (five), and that addressed different questions (Brudvig et al. 2015).

Effects on plant growth

To assess effects of landscape structure on plant performance (Question 4), we measured growth under different conditions of distance to edge and connectivity. Because our study species are typical of relatively open habitat (longleaf pine savanna), one might expect decreased competition for light and moisture to result in increased growth further from forest edge (Harrington et al. 2003). Alternatively, the higher herbivory that we observed further from edge for most species might lead to decreased growth further from edge (Strauss and Zangerl 2002).

Overall, our analyses revealed that herbivory is more important than distance to edge in determining growth rates. No species grew more quickly further from edge and three grew more quickly close to edge. Conversely, growth of most species (five of eight) was negatively impacted by herbivory. Of the remaining species, growth of one (*Phytolacca*) was positively impacted by herbivory, and growth of two (*Gaylussacia* and *Nolina*) was uninfluenced by herbivory. The positive response of

Phytolacca suggests overcompensation, which tends to occur in herbaceous species growing in low resource environments (Hawkes and Sullivan 2001); *Phytolacca* at our site meets those criteria. Growth of the other two species, *Gaylussacia* and *Nolina*, was significantly higher near edge, where herbivory was highest for *Gaylussacia* and lowest for *Nolina*. Taken together, these results indicate that distance to edge alone is generally a poor predictor of growth and that observed patterns of growth as a function of edge are often driven by herbivory, likely through herbivores' responses to edge.

Conclusion

Distance to edge was overwhelmingly important in determining the probably of herbivory in a wide variety of longleaf pine savanna understory plants. In contrast, fragment shape and connectivity had little or no influence on herbivory, even though they contributed to the edginess of our fragments. This counterintuitive result underscores the importance of study designs that can disentangle the complex set of interacting factors that drive community responses to habitat loss and fragmentation (Ewers et al. 2007, Fahrig 2013, Haddad et al. 2015, Hahn and Orrock 2015*b*).

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