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Spatial arrangement of canopy structure and land-use history alter the effect that herbivores have on plant growth

PHILIP G. HAHN† AND JOHN L. ORROCK

Department of Zoology, University of Wisconsin-Madison, Madison, Wisconsin 53706 USA

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Abstract. The spatial arrangement of past and present human activities could affect the strength of species interactions through changes to environmental conditions. To better understand how land-use history might mediate the effect of insect herbivory on the growth of four herbaceous plant species at the edges between woodlands and open savannas, we coupled large-scale manipulations of canopy structure by thinning overstory trees to create savanna habitat in non-agricultural and post-agricultural longleaf pine woodlands with local-scale herbivore exclosures at two distances from habitat edges. Light availability, grasshopper abundance, and herbaceous plant cover all increased in patches that received overstory tree thinning. Land-use history altered the effect that edges created by the overstory thinning treatments had on grasshopper herbivory for one plant species (*Carphephorus bellidifolius*). The edge between land-use histories also altered herbivore effects on three plant species in thinned patches. These edge effects were driven in part by changes in availability of alternative resources for grasshoppers, shady edges, or grasshopper abundance. Canopy manipulation also had important effects on herbivory that were independent of the habitat edge: grasshopper herbivory reduced plant growth of the smallest species (*C. bellidifolius*) regardless of canopy manipulation, whereas herbivory on two larger species (*Solidago nemoralis* and *So. odora*) reduced plant growth mainly in patches with an intact overstory canopy. Collectively, this work suggests that the species-specific effects of grasshopper herbivory on plant growth were driven by both plant traits (e.g., size or growth rates) and landscape-mediated changes to grasshopper abundance, light availability, or availability of alternative resources for grasshoppers created by land-use history and canopy structure. Furthermore, because the heterogeneity in herbivory revealed by our large-scale experiment is likely linked to plant traits, our results provide a means for understanding the profound, but often idiosyncratic, effects of land-use legacies and edges on plant populations and communities.

Key words: context-dependent; edge effects; grasshoppers; herbivory; landscape experiment; land-use history; plant-insect interaction; species interactions.

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† **E-mail:** pghahn0@gmail.com

INTRODUCTION

Anthropogenic land transformation has created contemporary landscapes with complex configurations of natural, semi-natural, and anthropogenic habitats (Foley et al. 2005). Several recent conceptual frameworks have sought to address this complexity to better understand the effects of landscape configuration on conservation practices (Ries et al. 2004, Fletcher et al. 2007, Driscoll et al. 2013). Central to these frameworks is predicting how edges between habitat patches affect species interactions (e.g., herbivory; Wirth et al. 2008), which are hypothesized to be major factors driving many ecological processes in complex landscapes (Fagan et al. 1999, Ries et al. 2004, Tylianakis et al. 2008). As such, investigating how interactions among species are affected by edges and how edge-mediated changes in interactions might affect persistence of multiple species inherently involves landscape-scale studies. However, large-scale manipulations of both edges and patch types required to explicitly test edge effects on species interactions are rare. Therefore, large-scale manipulations focused on studying the response of species interactions should help fill an important empirical knowledge gap, especially where such studies use manipulations that reflect common large-scale management practices (Driscoll et al. 2013) and where empirical studies are guided by existing conceptual frameworks (Cadenasso et al. 2003, Ries et al. 2004).

Models suggest that edges and the relative quality of the adjacent patch can increase or decrease the intensity of species interactions (Ries and Sisk 2004). In the context of herbivory, negative edge responses occur when herbivory is stronger in the core of the focal habitat and decreases close to the edge of the adjacent habitat. These are predicted to occur when the focal habitat provides high-quality habitat for the consumer, and the adjacent patch is low-quality habitat. Similarly, positive edge responses occur when the strength of herbivory is weaker in the core of the focal habitat and increases close to the edge of the adjacent habitat. These are predicted to occur when the focal patch provides low-quality habitat, and the adjacent patch provides high-quality habitat (Ries and Sisk 2004) or when herbivores build up near edges if they are hesitant to enter the adjacent unsuitable habitat (Haynes and Cronin 2003). These predictions assume that consumer responses map onto resources distributed among the patches. However, more complex edge responses may arise if both consumers and resources are unevenly distributed or respond differently to environmental conditions in the adjacent habitat or at the edge (Ries and Sisk 2004, Wimp et al. 2011). For example, herbivory may respond positively to edges but may not differ between the cores of two adjacent habitat types. Contemporary landscapes that experience a variety of land uses and intensities have the potential to create complex edge responses (Tscharntke et al. 2012, Driscoll et al. 2013). For instance, fire regimes in North America have shifted substantially over the last several decades, resulting in conversion of open habitats to closed canopy forests (Nowacki and Abrams 2008, Ratajczak et al. 2012). Moreover, large tracts of land in North America are also recovering from historical agriculture, which can substantially affect abiotic and biotic properties (Flinn and Vellend 2005, Cramer et al. 2008). Both of these factors likely influence plant-herbivore interactions, but currently few experimental tests appropriately grapple with this complexity at large spatial scales.

Factorial experiments provide a promising means to evaluate edge frameworks and to reconcile the often-contrasting findings of previous studies of herbivory with regards to edges (Wirth et al. 2008). For instance, insect herbivory can be greater in sunny habitats and decline near the (shady) edge of a forest (Agrawal et al. 2012, Evans et al. 2012, Stoepler and Rehill 2012). This effect is presumably because insects are greater in abundance in sunny habitats, despite potentially higher chemical defenses of plants in sunny habitats (Barber and Marquis 2011, Agrawal et al. 2012, Stoepler and Rehill 2012). The opposite pattern can also occur, where herbivory rates are greater in shade habitats (Muth et al. 2008, Hakes and Cronin 2012), presumably because plant defenses are lower than in shady habitats while herbivores are still present (Muth et al. 2008). Alternatively, shady habitats can reduce overall herbaceous cover making the rare herbaceous plants that do persist in a shaded habitat more vulnerable to herbivory (Hakes and Cronin 2012, Hahn and Orrock 2015*a*). The varied results of these studies may be because studies generally only examine a single edge type (but see Wolf and Batzli 2004), include only one or a few focal species, and rarely experimentally manipulate both the edges and the quality of the adjacent patch. Other widespread factors, such as historical agricultural land-use, that can alter plant communities (Flinn and Vellend 2005, Vellend et al. 2007, Baeten et al. 2014), insect communities (Debinski et al. 2011, Hahn and Orrock 2015*b*), and the strength of biotic interactions (Hahn and Orrock 2015*a*) could potentially influence edge responses. However, one important limitation to studying edge effects in existing landscapes is

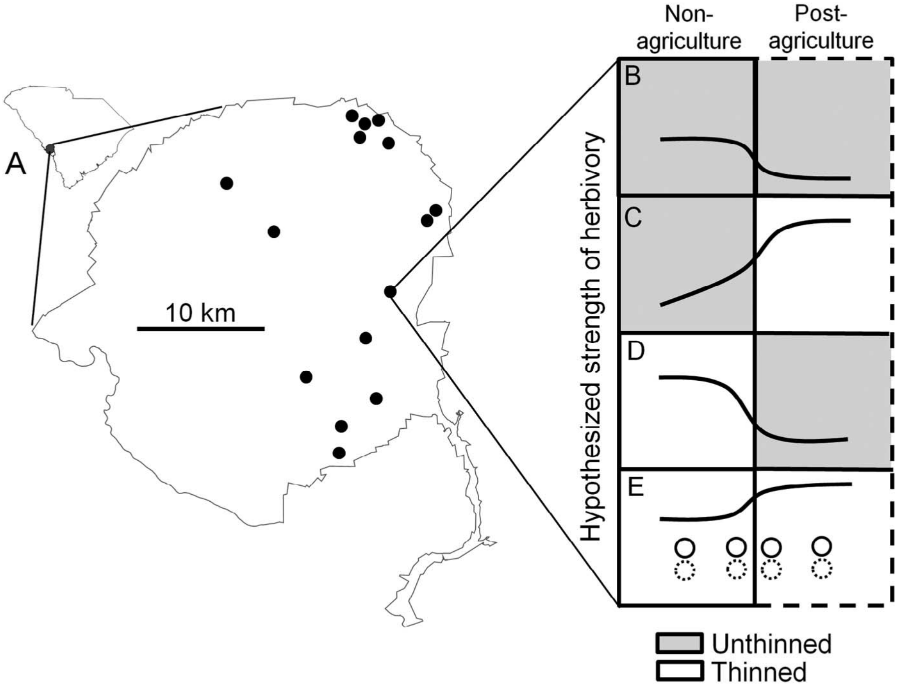

Fig. 1. (A) Overview of the experiment conducted in longleaf pine woodlands at the Savannah River Site, South Carolina, USA, with (B–E) hypothesized edge effects. Diagram on the right shows (B–E) the four experimental configurations (eight 1-ha patches). Circles within these patches (not to scale) represent the paired full herbivore exclosures and pseudo-exclosures (0.125 m^2) that contained two replicate plants of each of the four focal plant species (eight plants per exclosure) located 10 and 50 m from the edge (only one set is shown). Curved lines show hypothesized edge effects.

that patch type and edges are not manipulated experimentally, and thus potentially confounded by non-random land-use practices, limiting robust tests of edge effects in multiple habitat types (Ries et al. 2004).

We used replicated, large-scale experimental landscapes to test the independent and interactive effects of land-use history and overstory canopy structure on the degree to which herbivores suppress plant growth (Fig. 1). Non-agricultural and post-agricultural habitats each support a different assemblage of plants (Flinn and Vellend 2005, Brudvig et al. 2013) and grasshoppers (Hahn and Orrock 2015*b*). In a previous experiment conducted in non-experimental patches with intact canopies we found that herbivory rates were greater in post-agricultural sites and this was driven largely by the amount of alternative resources (plant material) available for herbivores to consume, with the highest rates of herbivory at intermediate levels of plant cover (Hahn and Orrock 2015*a*). Within our experimental landscapes, we use herbivore exclosures to quantify herbivory by grasshoppers on the growth of four species of perennial herbs to evaluate possible changes in herbivory at different distances from the resulting habitat edges (Fig. 1B–E). Grasshoppers are the dominant insect herbivore in this system (Knight and Holt 2005, Evans et al. 2012) and grasshopper abundance and herbivory should respond to the treatments we imposed. Because the plants we selected (Kilgo and Blake 2005) and most grasshopper species (Chapman and Joern 1990) prefer open habitat, overstory tree thinning is expected to increase habitat quality for both plants and grasshoppers. In our experiment, we expected that herbivore exclusion should have greater effects in thinned patches, compared to unthinned patches with an intact canopy (Fig. 1B–E), because herbivore abundance should also be greater in thinned patches. Thus we hypothesized that these habitat-specific effects of herbivory would result in herbivory varying with distance from edges and the nature of the herbivory-edge relationship would differ among the habitat configurations. Specifically, we predicted that herbivory will be highest in thinned post-agricultural patches and this effect will be largely insensitive to the canopy treatment of the adjacent non-agricultural patch (Fig. 1D, E). In non-agricultural patches, herbivory will depend upon the canopy treatment of the adjacent post-agricultural patch, and will be higher at edges where the post-agricultural patch is thinned (Fig. 1C).

METHODS

Study system

The understory of the longleaf pine (*Pinus palustris*) ecosystem is one of the most diverse plant communities in North America, harboring many endemic and federally endangered plant species (Jose et al. 2005). Currently, only about 3% of the original ecosystem remains, and these fragmented remnants are highly threatened by habitat destruction for agriculture and fire suppression (Frost 1998). Over the past century, many agricultural plots that replaced historic longleaf savannas have been abandoned, allowing longleaf woodlands to regenerate (Jose et al. 2005). However, these post-agricultural woodlands tend to have reduced occurrence of many herbaceous species typical of non-agricultural savannas (Kirkman et al. 2004, Brudvig and Damschen 2011, Brudvig et al. 2014). Decreased fire frequency has promoted canopy closure via hardwood encroachment, which also reduces herbaceous cover (Harrington 2011).

Landscape experiment

We established a replicated, landscape-scale experiment at the Savannah River Site (SRS), South Carolina, USA, an 80,125-ha National Environmental Research Park, to test the effects of edges and adjacent patch qualities on herbivory rates. Much of SRS was converted to agriculture between 1865 and 1950, although many pockets of woodland remained untilled (Kilgo and Blake 2005). We determined historical land use by examining aerial photographs taken just prior to governmental acquisition in 1951, at which time all agricultural fields were abandoned. Two-hectare patches were selected that border a non-agricultural/post-agricultural boundary and span a fire frequency gradient, over which we imposed a factorial manipulation of canopy closure (thinned or unthinned). This paired design overcomes potential limitations of non-random agricultural land use by allowing us to block by site (Flinn and Vellend 2005). Sites were relatively homogenous in terms of soil series, slope, canopy closure, and fire frequency. Tree (stem) densities ranged from an average of approximately 550 to 750 trees per hectare (Brudvig et al. 2013). See Brudvig et al. (2013) for a detailed description of the pre-treatment site conditions. Overstory tree thinning increases light availability for understory plants and is a common restoration practice in the southeast (Jose et al. 2005). Patches were thinned to 8–10 mature pine trees per one-hectare patch in early 2012. The experiments described here use 64 one-hectare experimental patches, with eight full replicates of land-use history (non-agricultural or post-agricultural), thinning (thinned or unthinned), and spatial arrangement of these two factors (Fig. 1). Because most sites did not contain large enough patches of each land-use history type to accommodate the full experiment design (eight one-hectare patches), this resulted in an incomplete block design. Thus, the 64 one-hectare patches were distributed among 15 sites (Fig. 1). These 15 sites were randomly selected from the 29 sites used in the Brudvig et al. (2013) study, stratified across a fire frequency gradient.

Local herbivory experiment

The Asteraceae is one of the dominant plant families in the longleaf pine ecosystem (Kilgo and Blake 2005), representing 10 of the 44 plant species that are significant indicators of non-agricultural habitat in our study plots (Brudvig et al. 2013). We selected four plant species of wind-dispersed, perennial herbs (Asteraceae) that are consumed by grasshoppers (P. G. Hahn, *personal observation*): *Carphephorus bellidifolius* (Michx.) Torr. & A. Gray, *Sericocarpus tortifolius* (Michx.) Nees, *Solidago nemoralis* Aiton, and *Solidago odora* Aiton. Nomenclature follows the USDA, NRCS (National Plant Data Team, Greensboro, North Carolina, USA). All four of these species have a late summer flowering phenology (August–October), emerge as seed in the spring, typically prior to June (Hahn 2015), and do not typically flower in the first year (P. G. Hahn, *unpublished data*). Furthermore, in order to capture the range of species that occur in either non-agricultural habitats, post-agricultural habitats, or both, we selected species that vary widely in their habitat occurrences. *Carphephorus bellidifolius* is an indicator of non-agricultural habitats, *So. nemoralis* is an indicator of post-agricultural plots. *Sericocarpus tortifolius* is found more often in non-agricultural habitats, while *So. odora* is found in nearly equal abundance between both habitat types (Brudvig et al. 2013).

We grew seedlings in a greenhouse at the Savannah River Ecology Laboratory in May 2012, which corresponds to when these species would germinate and establish in the field (Hahn 2015). Plants of similar size were haphazardly matched between a paired set of greenhouse trays (35 × 35 cm) with a large mesh bottom (2 cm mesh) filled with a 50:50 mixture of potting soil and sand. Each tray received two individuals of each species for a total of eight plants per tray (4 species × 2 individuals per species). We established paired insect herbivore exclosures (full exclosures and pseudo-exclosures) in the field within each of the one-hectare patches at two distances (10 and 50 m) in either direction from the edge of the land-use history boundary (n = 264 exclosures). Exclosures were 0.125-m^2 mesh screen cages ("pseudo-exclosures" cages have holes to allow grasshoppers to enter) that have been used to restrict grasshopper access in other experiments at our field site (Evans et al. 2012, Hahn and Orrock 2015*a*). There was no difference in light availability or temperature between the two exclosure types (Hahn and Orrock 2015*a*). We deployed a total of 2,112 seedlings of the four species ($n = 528$ seedlings of each species) into the herbivore exclosures between 2 and 26 July 2012. The trays were randomly assigned to an herbivore exclosure treatment. We added supplemental water during the first three weeks of the experiment. We counted the number of leaves on each plant prior to deployment to the field and again at the end of the growing season between 15 and 25 September 2012. During the final survey, we also counted the number of leaves with greater than 5% of the leaf tissue removed by chewing invertebrates. Plants were approximately two months old when transplanted into the field and had the following number of true leaves (mean ± 1 SD): *C. bellidifolius* (4.9 ± 2.5), *Se. tortifolius* (6.4 ± 3.2), *So. nemoralis* (5.5 ± 3.3), and *So. odora* (10.2 ± 3.8).

Additional environmental data collection

At each herbivore exclosure location, we collected data on additional environmental variables that could affect plant growth or herbivory rates: temperature and light availability, grasshopper abundance, and vegetation cover. We recorded light availability (lux) using Hobo data loggers (Onset Computer Corp., Bourne, Massachesetts, USA). We deployed the loggers ($n = 64$) in two periods; the first between 23 August and 1 September 2012 and the second between 7 and 15 September 2012. We averaged light (lux) data collected in 10 min intervals during daylight hours (06:00–19:00) across the duration for which the loggers were deployed. Data loggers were placed between the paired herbivore exclosures approximately 25 cm off the ground. Lux ($\log_{10}$-transformed) is correlated with canopy closure in unthinned patches measured using a densitometer (Brudvig et al. 2013; $r = -0.56$, $P < 0.001$). Grasshoppers were counted along two 15 m transects in each one-hectare patch during peak grasshopper activity (11:00–17:00) on clear days between 18 and 22 September 2012. Transects were positioned adjacent to the herbivore exclosures and parallel to the edges. We used a modified version of Onsager's (1977) point density counts by walking our 15 m transects and counting grasshoppers as they flushed. This method has been previously employed to quantify grasshopper abundances in our system (Evans et al. 2012). Additionally, we identified the grasshoppers to subfamily as they flushed (katydids were identified to family). If grasshoppers could not be identified to subfamily while in flight, we tracked the grasshopper to its landing position to verify identification. Vegetation cover of six functional groups (grasses, forbs, legumes, vines, woody vegetation, and ferns) was visually estimated in four 1-m^2 quadrats along the 15-m transects where we counted grasshoppers. Vegetation surveys were conducted between 23 and 29 August, 2012 and we recorded all foliage overhanging the plot.

Grasshopper feeding ecology and ancillary feeding trials

The dominant grasshoppers at our site are in the genera *Melanoplus* and *Schistocerca* (Hahn and Orrock 2015*b*). Grasshoppers in the genus *Melanoplus* (subfamily Melanoplinae) are mixed feeders that will consume primarily forbs but also grasses (Ueckert and Hansen 1971, Joern 1985). In previous feeding trials using 12 plant species from five functional groups (grasses, forbs, woody vegetation, and vines), *Melanoplus angustipennis* consumed mainly forbs, but also some foliage of woody vegetation and vines (Hahn and Orrock 2015*a*). Grasshoppers in the genus *Schistocerca* (subfamily Cyrtacanthacridinae) are also mixed feeders that will consume a variety of plant foliage (Capinera et al. 2005). Grasshoppers in the subfamilies Gomphocerinae and Oedipodinae are also present at the study site but are less abundant than the above taxa (Hahn and Orrock 2015*b*) and both subfamilies consume mainly grasses (Ueckert and Hansen 1971, Joern 1985). Thus, grasshoppers in the Melanopinae and Cyrtacanthacridinae are the most likely consumers of the plant species used in our experiment. Finally, we note that grasshopper densities in our system (Hahn and Orrock 2015*b*) are lower than other systems (e.g., tallgrass prairies; Onsager 1977, Joern 2004) probably because understory productivity is lower despite greater evapotranspiration, which is likely because of competition with pine trees (Orrock et al. 2015).

We conducted ancillary feeding trials to determine the preference of our experimental plants to two of most common grasshopper genera at our field site: *Melanoplus* and *Schistocerca* (Hahn and Orrock 2015*b*). In the present study, *Melanoplus angustipennis* nymphs had a clear preference for *Solidago* species in the cafeteria feeding trials, consuming approximately 80% of the available leaf tissue of *Solidago nemoralis* and about 30% of *So. odora*. Consumption of *Sericocarpus tortifolius* and *Carphephorus bellidifolius* was low (Appendix A). *Schistocerca alutacea* nymphs consumed approximate 25–35% of the available leaf tissue of all species except *C. bellidifolius*, of which they consumed low amounts (Appendix A).

Statistical analysis

To estimate the potential growth of each species in each habitat type when herbivores were excluded, we analyzed the number of leaves at the end of the growing season for plants grown inside the herbivore exclosures in response to experimental treatments. The number of leaves was averaged for the two plants of each species within an exclosure to avoid pseudo-replication. We used a four-way factorial mixed-model analysis of variance for each plant species using the number of leaves on plants within the full exclosures as the response variable. Land-use history (non-agricultural or post-agricultural), canopy thinning (thinned or unthinned), type of adjacent patch (thinned or unthinned), and distance from the edge (10 m or 50 m), and all interactions were included as fixed effects. Site, site × land-use history, and site × land-use history × canopy thinning × adjacent patch type were included as random effects to account for the split-plot experimental design.

We estimated the effect of excluding herbivores on the growth of each of the four plant species by first calculating the number of new leaves produced during the growing season (no. leaves at the end of the growing season – no. leaves prior to deployment). We averaged the number of leaves on the two plants of each species in each exclosure to avoid pseudo-replication. Then we subtracted the average number of new leaves produced by plants exposed to herbivores from the average number of new leaves produced by plants protected from herbivores (no. new leaves in full exclosures – no. new leaves in pseudo-exclosures) for each pair of herbivore exclosures. This value, the difference in new leaves produced between the herbivore exclosures, was used as the response variable in all analyses. We selected this metric as our response variable because plant growth could respond to land-use history or overstory tree thinning independent of herbivory. Since our hypothesis focuses on the consequence of herbivory in these different habitats, our metric isolates the effect that herbivores have on plant growth in the different habitats. See below for further justification of this metric and its relationship to chewing damage (Results: *Effectiveness of herbivore exclosures and estimated effect of herbivory on plant growth*). Because these plants were part of a multi-year demographic study, we did not destructively sample the plants to measure biomass production. However, based on previous and subsequent experiments, the number of leaves on a plant correlates fairly strongly with dried above-ground biomass (correlation coefficients > 0.50; *unpublished data*). We removed one full set of exclosures because seven of the eight plants inside the full exclosure desiccated within the first few weeks of the experiment. We also removed two plants because a caterpillar had breached the exclosure and consumed the majority of two of the plants within the full exclosure.

We conducted a four-way factorial mixed-model analysis of variance for each plant species using the difference in new leaves between the exclosures as the response variable to test our general hypothesis that land-use history modifies the response of herbivory to canopy edges. Land-use history (non-agricultural or post-agricultural), canopy thinning (thinned or unthinned), type of adjacent patch (thinned or unthinned), distance from the edge (10 m or 50 m), and all interactions were included as fixed effects. Site, site × land-use history, and site × land-use history × canopy thinning × adjacent patch type were included as random effects to account for the split-plot experimental design. We also conducted one sample *t*-tests, which compared the mean difference in new leaves between the two exclosure types to zero. A positive value that differs significantly from zero would indicate that the plants inside the full herbivore exclosures produce significantly more new leaves than plants inside the pseudo-exclosure. This ancillary analysis was included to aid in the interpretation of the treatments in which herbivores reduce plant growth. Denominator degrees of freedom were estimated using the Kenward-Roger approximation (Littell et al. 2006). We examined residual plots to ensure that all models met the assumptions of normality and equal variance. We corrected for unequal variances in herbivory between the overstory tree thinning treatments by adding an R-side covariance matrix using the group command in the repeated statement of proc mixed (SAS version 9.4, SAS Institute, Cary, North Carolina, USA; Littell et al. 2006). Some of the random effects for the nested term explained low variance and resulted in negative variance components, so we used the nobound statement to allow the variance components to be negative (Littell et al. 2006). However, in some cases, these models did not converge (i.e., models containing R-side covariance matrices that were not bounded to positive values), so we did not unbind these variance components. This resulted in some of the random effects for the nested terms to not be estimated and altered the denominator degree of freedom estimates for some of the main effects. However, this never affected the significance of the main effects and therefore does not change any of the conclusions.

To illustrate the variables that could influence plant growth and herbivory rates among the experimental treatments (light, herbaceous cover, and grasshopper abundance), we used mixed model ANOVAs as described above. Light, measured in lux, was $\log_{10}$ transformed and herbaceous cover (total cover of grasses, forbs, and legumes) was square-root transformed before analysis. We used a generalized linear mixed model with a Poisson distribution for the analysis of grasshopper counts. We analyze these variables separately from the main analysis because they responded to our experimental treatments and thus are confounded with the experimental treatments, making formal statistical analyses with these factors as covariates difficult to interpret.

RESULTS

Growth of plants protected from herbivores

For plants that were protected from grasshopper herbivores, all species produced significantly more leaves in the thinned patches (Appendix B). Within the thinned treatments, *C. bellidifolius* and *Se. tortifolius* produced significantly more leaves in non-agricultural woodlands than post-agricultural woodlands (Appendix B).

Effectiveness of herbivore exclosures and estimated effect of herbivory on plant growth

The proportion of leaves damaged by chewing insects on plants inside full exclosures was near zero and significantly reduced compared to pseudo-exclosures for all four plant species (Appendix C). The proportion of leaves damaged on plants inside the pseudo-exclosure was positively related to our estimate of the effect of

Table 1. Results of mixed-model ANOVAs examining the response of the effect of herbivore exclosures on plant growth (number of new leaves produced in full exclosure, number of new leaves produced in pseudo-exclosure), measured on four plant species (Asteraceae), to land-use history (remnant or post-agriculture), canopy thinning (thinned or unthinned), type of adjacent patch (thinned or unthinned), and distance from the edge (10 or 50 m) in a large-scale experiment conducted in upland longleaf pine woodlands at the Savannah River Site, South Carolina, USA. Significant ($P \leq 0.05$) and marginally significant ($P \leq 0.10$) P values are in bold.

	Carphephorus bellidifolius			*Sericocarpus tortifolius*			*Solidago nemoralis*			*Solidago odora*		
Effect	df	F	P	df	F	P	df	F	P	df	F	P
Land-use history	13.6	3.25	**0.0937**	82.5	0.24	0.6243	55.4	3.80	**0.0560**	95.3	0.17	0.6824
Overstory thinning	29.0	7.07	**0.0126**	82.5	0.87	0.3535	60.0	0.87	0.3534	95.3	0.19	0.6639
Land use × thinning	30.0	9.60	**0.0042**	82.5	4.42	**0.0385**	57.5	0.95	0.3326	95.3	0.05	0.8259
Adjacent canopy	26.6	3.60	**0.0688**	82.5	0.06	0.8016	69.0	0.18	0.6714	95.3	0.30	0.5821
Land use × adjac	26.9	0.00	0.9848	82.5	1.79	0.1847	57.1	0.06	0.7999	95.3	0.00	0.9602
Thinning × adjac	29.0	5.98	**0.0208**	82.5	0.15	0.6953	60.0	0.00	0.9568	95.3	0.75	0.3887
Land use × thinning × adjac	30.1	2.51	0.1234	82.5	4.42	**0.0385**	57.5	0.14	0.7058	95.3	3.90	**0.0510**
Distance from edge	63.8	3.48	**0.0667**	82.5	1.62	0.2066	72.4	2.18	0.1442	95.3	0.02	0.8778
Land use × dist	63.8	14.97	**0.0003**	82.5	5.35	**0.0232**	72.4	1.51	0.2227	95.3	1.57	0.2136
Thinning × dist	63.8	0.15	0.6997	82.5	4.52	**0.0364**	72.4	6.02	**0.017**	95.3	1.36	0.2461
Land use × thinning × dist	63.8	11.24	**0.0014**	82.5	4.84	**0.0306**	72.4	2.34	0.1301	95.3	1.34	0.2493
Adjac × dist	63.8	9.74	**0.0027**	82.5	1.19	0.2788	72.4	0.74	0.3926	95.3	0.02	0.8918
Land use × adjac × dist	63.8	0.35	0.5563	82.5	0.28	0.5979	72.4	0.57	0.4539	95.3	0.54	0.4638
Thinning × adjac × dist	63.8	2.95	**0.0910**	82.5	0.13	0.7148	72.4	0.78	0.3803	95.3	0.03	0.8583
Land use × thinning × adjac × dist	63.8	0.00	0.9918	82.5	3.12	**0.0811**	72.4	0.25	0.6205	95.3	0.41	0.5221

herbivory on plant growth (i.e., the difference in the number of new leaves produced in the full exclosures minus pseudo-exclosures) for all four species (Appendix C). Although there were large portions of unexplained variability in these relationships, this analysis suggests that our estimate of the effect of herbivory on plant growth is capturing some of the natural variability in the negative effect of herbivores on plant growth. Our metric fully leverages the strength of our paired experimental exclosures and likely captures effects that visual estimates of herbivory (e.g., proportion of leaves damaged or the amount of leaf tissue removed) do not. Furthermore, because our metric is focused on plant growth, it measures the effect of damage beyond what is due to tissue removal (Zangerl et al. 2002) and what may be missed through visual examination of a leave (i.e., leaves being damaged and subsequently senescing or entire leaves being consumed). In other words, our metric captures plant growth actually experienced in the field.

Effects of herbivore exclosures on plant growth

The difference in new leaf production between the full and pseudo-exclosures for *Carphephorus bellidifolius* depended on the interaction among land-use history, overstory tree thinning, and distance from the edge (ANOVA: $F_{1,63.8} = 11.2$, $P = 0.001$). The interaction among overstory thinning, thinning in the adjacent patch, and distance from the edge was also marginally significant ($F_{1,63.8} = 3.0$, $P = 0.091$). The marginally significant effect appeared to be driven by several significant two-way interactions involving these three factors (Table 1). Herbivore exclosures mostly affected plant growth of *C. bellidifolius* in thinned patches (Fig. 2A–D). Also, the canopy structure of the adjacent patch had the opposite effect between the two land-use history treatments. The unthinned edge of non-agricultural patches reduced the effect that herbivores had on plant growth in the adjacent post-agricultural, because exclosures only had a significant effect on plant growth in the core (i.e., 50 m from the edge) of these patches (Fig. 2B). The opposite pattern occurred where plant growth was significantly reduced by herbivores in unthinned non-agricultural patches 10 m from edge of post-agricultural patches (Fig. 2C). There was a large reduction in plant growth when exposed to herbivores for *C. bellidifolius* in thinned non-agricultural patches 10 m from the boundary of the thinned post-agricultural patches (Fig. 2D).

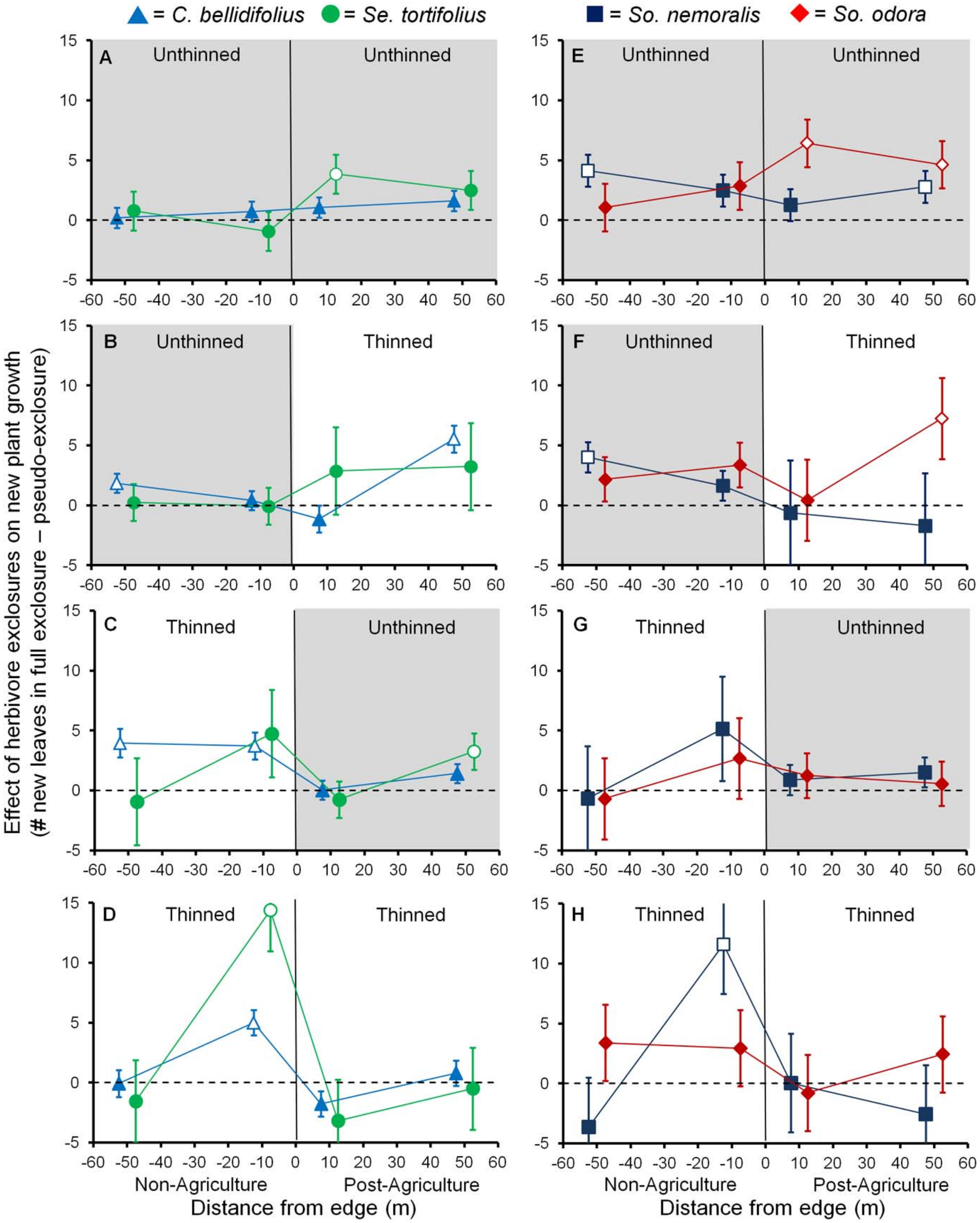

Fig. 2. Effect of herbivores on plant growth in relation to habitat edges created by land-use history (non- or post-agricultural) and overstory tree thinning (thinned or unthinned) in upland longleaf pine woodlands at the Savannah River Site, South Carolina, USA. The effect of herbivores on plant growth is measured as the difference between the number of new leaves produced by plants inside grasshopper exclosures and the number of new leaves produced by plants in pseudo-exclosures that allow grasshopper access. Data are jittered around distance for clarity. Open dots indicate that the exclosures significantly increased new plant growth ($P < 0.05$). Error bars are ±1 SE.

Table 2. ANOVA table for environmental variables. Significant ($P \leq 0.05$) and marginally significant ($P \leq 0.10$) P values are in bold.

	lux†			Herbaceous cover‡			Grasshopper abundance§		
Effect	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*
Land-use history	15.6	3.92	**0.0658**	8.0	1.40	0.2709	35.4	0.15	0.7037
Overstory thinning	37.8	180.31	**<0.0001**	23.0	32.50	**<0.0001**	47.0	63.95	**<0.0001**
Land use × thinning	38.1	4.01	**0.0523**	23.6	0.49	0.4907	48.6	0.16	0.6902
Adjacent canopy	37.1	1.40	0.2443	28.1	1.29	0.2649	53.0	0.12	0.7305
Land use × adjac	23.5	0.84	0.3682	14.0	2.10	0.1691	70.4	0.10	0.7495
Thinning × adjac	37.8	0.17	0.6825	23.0	2.80	0.1077	47.1	0.34	0.5638
Land use × thinning × adjac	38.1	1.26	0.2693	23.6	0.01	0.9167	48.7	0.10	0.7583
Distance from edge	54.0	0.22	0.6420	56.1	0.31	0.5769	112.0	1.42	0.2364
Land use × dist	54.0	3.38	**0.0715**	56.1	1.85	0.1787	112.0	0.19	0.6632
Thinning × dist	54.0	1.61	0.2105	56.1	0.15	0.6998	112.0	0.23	0.6347
Land use × thinning × dist	54.0	5.10	**0.0280**	56.1	0.65	0.4224	112.0	0.08	0.7820
Adjac × dist	54.0	5.26	**0.0257**	56.1	1.01	0.3192	112.0	0.00	0.9964
Land use × adjac × dist	54.0	0.29	0.5896	56.1	0.13	0.7244	112.0	0.21	0.6454
Thinning × adjac × dist	54.0	6.84	**0.0115**	56.1	7.86	**0.0069**	112.0	0.52	0.4740
Land use × thin × adjac × dist	54.0	0.05	0.8295	56.1	0.01	0.9103	112.0	0.06	0.8011

† Log_{10} transformed.
‡ Square-root transformed.
§ Grasshopper abundance (counts) was analyzed using a Poisson error distribution.

Notably, the growth of two of the three other plant species was also affected by herbivores in thinned non-agricultural patches 10 m from the boundary of thinned post-agricultural patches (Fig. 2D, H).

The degree to which herbivore exclusion affected new leaf growth of *Sericocarpus tortifolius* was marginally affected by the four-way interaction among land-use history, overstory tree thinning, thinning in the adjacent patch, and distance from the edge (ANOVA: $F_{1,82.5} = 3.12$, $P = 0.081$). Although this interaction was only marginally significant, we interpret it for conciseness because several lower-order interactions were also significant or marginally significant (Table 1). The four-way interaction appeared to be driven by a large reduction in plant growth when exposed to herbivores in thinned non-agricultural patches 10m from the boundary of thinned post-agricultural patches (Fig. 2D).

The main effect of land-use history ($F_{1,55.4} = 3.8$, $P = 0.056$) and the interaction between overstory tree thinning and distance from the edge ($F_{1,72.4} = 6.0$, $P = 0.017$) influenced the degree to which herbivore exclusion affected *Solidago nemoralis* new leaf growth (Table 1, Fig. 2E–H). The effect of excluding herbivores on new leaf growth trended higher in non-agricultural sites with intact canopies (Fig. 2E–G), but this effect was particularly pronounced in thinned non-agricultural patches 10m from the boundary of a thinned post-agricultural patch (Fig. 2H).

The interaction among land-use history, overstory tree thinning, and thinning in the adjacent patch affected the difference in new growth between the exclosures for *So. odora* (ANOVA: $F_{1,95.3} = 3.9$, $P = 0.051$; Table 1). Herbivore exclosures reduced new growth of *So. odora* in three treatment combinations, but only in post-agricultural habitats and most often under canopy (Fig. 2E–H).

Effects of landscape treatments on environmental variables

Light levels ($\log_{10}$ lux) were strongly affected by the three-way interaction among land-use history, thinning, and distance from the edge as well as the three-way interaction among overstory three thinning, thinning in the adjacent patch, and distance from the edge (Table 2). Thinning increased light levels by over three-fold and light levels in unthinned patches near the edges of thinned patches had slightly higher light levels compared to the core of these patches (Fig. 3A–D). Herbaceous cover was affected by the three-way interaction among overstory tree thinning, thinning in the adjacent patch, and distance from the edge (Table 2). Herbaceous cover increased in thinned patches and was greater at the edges of unthinned post-agricultural patches near thinned non-agricultural patches (Fig. 3E–H). Grasshopper abundance was only affected by the canopy

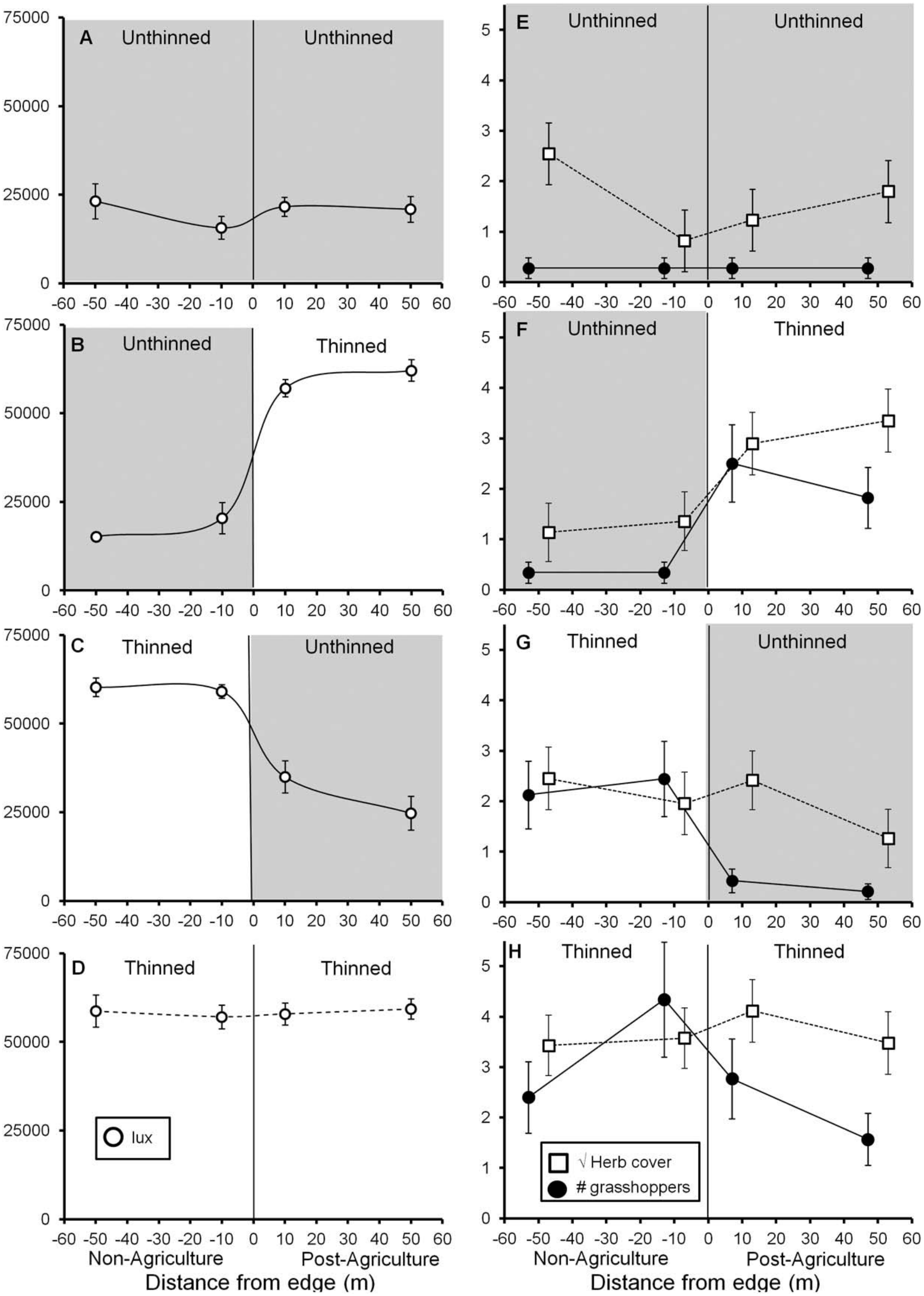

Fig. 3. (A–D) Changes in light levels (lux), (E–H) herbaceous cover (square root transformed), and grasshopper abundance (mean number per 15-m transect) in relation to edges created by the four configurations of overstory tree thinning and land-use history in longleaf pine woodlands at the Savannah River Site, South Carolina, USA. Y-axes are defined in the legend. Error bars are ±1 SE. Note that lux values were $\log_{10}$ transformed for analysis, but are presented on the original scale in this figure to show actual effect sizes.

thinning treatment (Table 2), with about a sevenfold increase in grasshopper abundance in thinned treatments (Fig. 3E–H) and these increases were fairly consistent across the dominant subfamilies (Appendix D).

DISCUSSION

Edges are ubiquitous features of contemporary landscapes that are capable of changing both the nature and strength of ecological interactions (Ries et al. 2004), but the effects of edges on herbivory have proven difficult to predict (Wirth et al. 2008). Using a landscape-scale experiment that explicitly incorporates land-use legacies, we show that the effect of excluding herbivores on plant growth can be contingent upon canopy structure (thinned or unthinned overstory), historic agricultural land use, and the spatial arrangement of these two factors. Herbivory on *C. bellidifolius* qualitatively matched our initial predications that the effects of herbivory on plant growth should be greater in thinned patches and would be dependent upon edges, although herbivory in post-agricultural patches was not necessarily independent of the adjacent edge, as predicted (Fig. 1B–E). However, the effect of herbivory on plant growth of two of the other three species only responded to one edge type, which corresponded to high grasshopper abundance. The lack of responses of plant growth to herbivory in the other treatments suggests that edge-responses may not arise when the strength of species interactions are weak. Canopy structure also created strongly contrasting effects of herbivory on the slowest and fastest growing plant species (Table 1, Fig. 2). Grasshopper herbivory reduced growth of the smallest plant species (*C. bellidifolius*, measured as the total number of leaves produced by plants protected from herbivores) under both canopy treatments, whereas growth of two larger species (*So. nemoralis* and *So. odora*) was mainly suppressed by herbivory under canopy. Light availability, herbaceous plant cover, and grasshopper abundance were all higher in thinned patches. Collectively, these results suggest that environmental conditions created by land-use history and canopy structure are important predictors of the degree to which herbivory suppresses plant growth. Finally, the degree to which herbivory suppresses plant growth was species-specific, suggesting a likely strong role of plant traits (i.e., growth rates, size, or the ability to tolerate herbivory) in determining the outcome of plant-herbivore interactions (Agrawal 2011).

Interplay of canopy structure and land-use history in generating spatial contingency in herbivory

Our findings show that past land-use and contemporary patch characteristics can interact to affect the degree to which herbivores suppress plant growth and that the strength of this interaction varies widely among plant species. For *C. bellidifolius* we found that herbivory was highest in the core of thinned, post-agricultural patches but was reduced near the edge of non-agricultural woodlands with intact canopies (Fig. 2B). The opposite pattern emerged when non-agricultural patches were thinned adjacent to post-agricultural sites with intact canopies (Fig. 2C). This result suggests that *C. bellidifolius* may be more susceptible to herbivory in post-agricultural woodlands, where it occurs in low abundance (Brudvig et al. 2013), and that non-agricultural woodland edges may reduce herbivory rates at least 10 m outside the patch. These findings qualitatively match our hypothesis (Fig. 1) and are potentially explained by underlying patterns in plant community composition. Patterns of plant community composition measured prior to thinning indicate that post-agricultural sites had more within-site variability in plant community composition than non-agricultural sites caused partially by the spillover of remnant plant species into post-agricultural sites, but not vice versa (Grman et al. 2015). The spillover of non-agricultural plant species into post-agricultural sites created more starkly contrasting patterns of plant community composition in the non-agricultural side of the boundary and more gradual change in the post-agricultural side of the boundary (Grman et al. 2015). Thus, underlying differences in plant community composition between non-agricultural and post-agricultural sites (Kirkman et al. 2004, Brudvig and Damschen 2011, Brudvig et al. 2013) could subsequently alter herbivore foraging patterns via associational effects (Root 1973, Salazar et al. 2013, Underwood et al. 2014). We previously found similar results in non-experimental plots where the effect of herbivory on plant growth differed among land-use histories and was greatest at sites with intermediate levels of plant cover (Hahn and Orrock 2015*a*). Another possible explanation for the pattern that the herbivore effect on plant growth was low in thinned patches adjacent to unthinned non-agricultural patches is that the denser canopy of unthinned non-agricultural woodlands (Brudvig et al. 2013) may cast deeper shade into adjacent thinned post-agricultural woodlands (Fig. 3B, C), potentially contributing to reducing herbivore effects at these shadier edges (Evans et al. 2012).

We found different patterns in patch combinations that had thinning in both land-use histories, where herbivory was low in the core of non-agricultural patches and increased near the edge of post-agricultural patches for *C. bellidifolius*, *Se. tortifolius*, and *So. nemoralis* (Fig. 2D, H). High effects of herbivores on plant growth in these instances was likely related to the high grasshopper densities at these locations (Fig. 3H), which could result from grasshoppers being able to exploit the higher diversity of food resources (Unsicker et al. 2008) or complimentary food and oviposition sites between the two habitat types (Haynes et al. 2007). Although future studies will be essential for distinguishing between associational effects, shady edges, and consumer densities in driving the strength of herbivory, a key point from our study is that the influence of past land use and edge configuration on herbivory can generate unappreciated, species-specific contingencies in plant performance at large scales.

Growth rate and contingency of herbivory in sun vs. shade habitats

As predicted, the effect of herbivores on plant growth of *C. bellidifolius* was high in most thinned patches (Fig. 2B–D). In contrast, the growth of both *Solidago* species was mainly (although not always) affected by herbivory in unthinned patches (Fig. 2E–G). The differences in plant size or growth rates among the plant species we selected may help to rectify some differences in herbivory between sun and shade habitats. *Carphephorus bellidifolius* is a small, slow-growing plant that exhibited only moderate increases in growth in the overstory tree thinning treatment (Appendix B), suggesting that its slow intrinsic growth rate may make it particularly susceptible to herbivory where herbivores are abundant despite the potential for greater investment in defenses in thinned patches (Ballare 2014). In contrast, we found the opposite patterns of new leaf growth for *So. nemoralis* and *So. odora*, which are larger plants (i.e., more total leaves produced; Appendix B). For these two species, herbivory suppressed plant growth in unthinned woodlands (i.e., low light), at least in some treatment combinations, and herbivory did not affect new leaf growth in thinned woodlands (except for one treatment combination for *So. odora* and *So. nemoralis*; Fig. 2F, H). Plants may also differ in their ability to allocate to defenses in sun vs. shade habitats (Salgado-Luarte and Gianoli 2010, Hakes and Cronin 2011, Agrawal et al. 2012), and thus the differences in preferences among the plant species to grasshoppers could vary between sun and shade habitats. Greater effects of herbivory on plant growth in shaded environments could be caused by the lower ability to tolerate herbivory due to slower growth rates, lower investment in defense, or both (Salgado-Luarte and Gianoli 2010, Hakes and Cronin 2011, Ballaré 2014). Collectively, our results suggest that plants with a slow growth rate may be susceptible to herbivores where herbivores are abundant, whereas plants with a fast growth rate may only be susceptible under conditions where their growth is suppressed by other factors (i.e., low light conditions). Incorporating intraspecific variation in life history traits, such as size and growth rates, into plant defense theory or to understanding the response of plant growth to resource availability and herbivory may thus add a necessary dimension to understanding the complex defensive strategies and growth responses to herbivores employed by plants (Hawkes and Sullivan 2001, Agrawal 2011, Ballaré 2014).

Conclusions and future directions

With increasing habitat fragmentation and intensification of anthropogenic land use (Foley et al. 2005, Kareiva et al. 2007), studying anthropogenic factors that change the environmental conditions in which interactions among species occur is becoming increasingly relevant for understanding the distribution and abundance of organisms (Agrawal et al. 2007, Maron et al. 2014). Our work highlights several areas for future research in edge studies. First, because all edge types are not equal (Wolf and Batzli 2004), studies should incorporate historical or contemporary management activities when examining the response of species interactions at ecological edges. Second, because patch and edge type affected the performance, abundance, and likely community composition of both the resource organisms as well as the consumers, our study suggests that there is tremendous potential for species interactions to be dependent on the local composition of plant and animal communities near edges. As such, future studies should incorporate the potential role of associational effects into experimental designs, ideally with manipulations at two spatial scales (e.g., patch-level manipulations of overstory canopy coupled with local manipulations of neighborhood plant community composition). Finally, research should aim to identify how patch and edge types that affect resource availability differentially affect species based on life history traits. For instance, our results suggest that plant growth rate may be an important predictor of a plants' ability to capitalize on available resources, potentially allowing faster-growing species to better compensate for herbivory in high resource environments. Incorporating growth rates into compensation or tolerance studies could help to reconcile the often contradictory results reported in past experiments (Hawkes and Sullivan 2001). This also has implications for understanding the outcome of certain restoration practices (e.g., overstory tree thinning), which may have unintended consequences by promoting generalist plant species that are able to grow fast and tolerate herbivory (e.g., *So. nemoralis*), over slower-growing species that are typically found in remnant habitats (e.g., *C. bellidifolius* in our study). More generally, our study underscores the point that many landscape factors can interact to influence how edges alter the interactions among species.

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SUPPLEMENTAL MATERIAL

ECOLOGICAL ARCHIVES

Appendices A–D are available online: http://dx.doi.org/10.1890/ES15-00036.1.sm