LAND-USE HISTORY AND FIRE MANAGEMENT DRIVE CONTEXT-DEPENDENT PLANT-HERBIVORE INTERACTIONS

By

Philip G. Hahn

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The dissertation was approved by the following members of the Final Oral Committee:

John L. Orrock, Associate Professor, Zoology
Ellen I. Damschen, Associate Professor, Zoology
Randy L. Jackson, Associate Professor, Agronomy
Anthony R. Ives, Professor, Zoology
Monica G. Turner, Professor, Zoology

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Dedication

To my father.

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Abstract

Land-use legacies often interact with other factors such as fire suppression to generate persistent changes in soil conditions and plant communities in many ecosystems. However, little is known about how these habitat modifications affect higher trophic levels or interactions between plants and herbivores. Working in longleaf pine woodlands, I found that agricultural land-use history altered grasshopper community composition and decoupled positive relationships between plant cover and grasshopper abundance. Herbivory on a palatable plant species was also affected by the interaction between land-use history and fire frequency, and exhibited a hump-shaped response to neighboring plant cover, but herbivore density did not affect herbivory rates. In an experiment that manipulated neighborhood ($10m^2$) plant density and frequency within post-agricultural and non-agricultural habitats, I found that the frequency of neighboring plants determined the amount of herbivore damage received by focal plants. These patterns were driven by herbivore foraging decisions made at the neighborhood scale, highlighting that behavioral decisions are important for generating associational effects. Collectively, these results suggest that the effect of historic agricultural land use extends beyond plants and soils to leave a strong legacy on present-day plant-herbivore interactions.

Using a landscape-scale experiment, I showed that the effect of excluding herbivores on plant growth can be contingent upon canopy structure, historical land-use, and the spatial arrangement of these two factors. Land-use history and canopy structure also affected the degree to which herbivores limit seedling establishment across a suite of plant species. Furthermore, we found strong negative effects of herbivores on the performance of some demographic stages of all four herbaceous plant species we tested, particularly juvenile plant survival, but only in habitats with intact overstory canopies. The exception was the slowest growing plant species, which also suffered reduced juvenile survival due to herbivory in some thinned treatments. Overstory tree thinning substantially increased adult flowering and size for all four species and the effect of thinning on adult performance was often greater in non-agricultural habitats. Collectively, this work experimentally separates the habitat-induced effects from the herbivore-induced effects on plant performance and highlights that context-dependent plant-herbivore interactions depend on plant demographic stages and species traits.

Overview

Background: Historic agricultural land use generates long-lasting changes in plant communities and soil conditions in many ecosystems, but little is known about the effects on higher trophic levels or interactions between plants and herbivores. In the first half of this dissertation, I examine effects of agricultural land-use history on grasshopper community composition (Chapter 1) and herbivory rates by grasshoppers (Chapter 2-3), a dominant insect herbivore in the longleaf pine ecosystem. In Chapters 4-6 I use a landscape-scale experiment that manipulates overstory canopy cover, a common restoration strategy, in post-agricultural and non-agricultural longleaf pine habitats to examine how abiotic and biotic factors interact to affect seedling establishment and plant demography.

Chapter 1: Land-use history alters contemporary insect herbivore assemblages and decouples plant-herbivore relationships (*J Animal Ecol* 2015, 84:745-754): Land-use history altered grasshopper community composition and also decoupled positive relationships between plant cover and grasshopper abundance. Collectively, these results suggest that the effect of historic agricultural land use extends beyond plants and soils to leave a strong legacy on present-day insect herbivore assemblages.

Chapter 2: Land-use legacies and present fire regimes interact to mediate herbivory by altering the neighboring plant community (*Oikos* 2015, 124:497-506): We tested the hypothesis that human activities that alter the plant community lead to subsequent changes in herbivory. Herbivory on a palatable plant species exhibited a hump-shaped response to neighboring plant cover, with low herbivory at low and high levels of plant cover. Herbivore density had a weak negative effect on herbivory. These findings suggest that changes in plant cover related to past and present human activities can modify damage rates on plants by altering foraging behavior rather than density of herbivores. The resulting changes in herbivory may limit natural recovery or restoration efforts by reducing establishment or performance of palatable plants.

Chapter 3: Habitat-level herbivore abundance and neighborhood-level plant frequency affect herbivory on focal plants (manuscript in preparation): We used manipulative field and greenhouse experiments to test the hypothesis that associational effects—where the amount of insect herbivore damage received by a focal plant changes based on the identity of its neighbor—depend on characteristics of the local-scale plant neighborhood (density and frequency of two plant species that differ in palatability), but land-use history at the site-scale will not mediate the associational effects. The findings highlight that foraging decisions are important for generating associational effects and can outweigh the larger-scale environmental context in which these behavioral interactions occur.

Chapter 4: Spatial arrangement of land-use history and canopy structure alter the effect that herbivores have on plant growth (accepted at *Ecosphere*): Using a landscape-scale experiment, we show that the effect of excluding herbivores on plant growth can be contingent upon canopy structure, historical land-use, and the spatial arrangement of these two factors. However, patterns of herbivory differed among the four plant species we tested, with canopy structure having strongly contrasting effects of herbivory on the slowest and fastest growing plant species, and with only two species responding to edges. These results suggest that environmental conditions created by land-use history and canopy structure are important predictors of herbivore effects on some plant species, potentially driven by species-specific ability to tolerate herbivory or availability of alternative resources for consumers.

Chapter 5: Establishment of multiple plant species is contingent upon land-use history, overstory tree thinning, and consumers (in prep for *Glob Change Biol*): Our results show that seedling establishment was affected by interactions between consumer exclosures and land-use history or overstory thinning, and the negative effect of consumers on seedling establishment was strongest in post-agricultural woodlands with intact canopies. Collectively, soil degradation and altered consumer effects on the dynamics of seedling establishment appear to play an underappreciated role in regulating plant community structure in abandoned agricultural fields.

Chapter 6: Stage-specific responses of four plant species to additive and interactive effects of land-use history, canopy structure and herbivory (manuscript in preparation): We found strong negative effects of herbivores on plant performance of some demographic stages of all four plant species we tested, particularly juvenile plant survival, but only in habitats with intact canopies. The exception was for the smallest plant species *Carphephorus bellidifolius*, where juvenile survival was reduced by grasshopper herbivory in thinned post-agricultural patches and unthinned non-agricultural patches. Overstory tree thinning dramatically increased flowering probability and adult size for all four species and the effect of thinning on adult size was greatest in non-agricultural habitats for some species. This work experimentally separates the habitat-induced effects from the herbivore-induced effects on plant performance and highlights that the importance of context-dependent plant-herbivore interactions depend on plant demographic stages and species traits.

Conclusions: My dissertation demonstrates that the legacies of historical agricultural extend beyond soils and plants to affect interactions between plants and insects, including altering herbivore communities, herbivory rates, and plant demography. The results provide new insight into context-dependent plant-herbivore interactions, with implications for the recovery and restoration of the critically endangered longleaf pine ecosystem.

Introduction

Although it is now well established that herbivores can have strong negative effects on plant performance and population dynamics (Crawley 1983), the degree to which herbivores affect plant population dynamics has been historically debated in literature. Some ecologists argue that herbivores may exert only minor influences over plant populations (Hairston et al. 1960), while others have advocated that herbivores can strongly influence plant populations (Crawley 1989). Early insect-exclusion studies provided some of the first convincing evidence that herbivores can affect plant abundance, distributions, and population dynamics (Louda 1982, 1983). Long-term insect-exclusion experiments provide similarly convincing results for the effects that herbivores can have on plant productivity and community structure (Carson and Root 2000, Allan and Crawley 2011). As such, there is now overwhelming evidence that insect herbivores can influence plant performance and that these effects can sometimes scale up to affect plant populations dynamics and even ecosystem functioning (Weisser and Siemann 2004). However, there are certainly examples where herbivores have minimal effects on plant performance, and in certain cases the responses of plants to herbivory can be positive (Maschinski and Whitham 1989, Hawkes and Sullivan 2001, Wise and Abrahamson 2005), suggesting that the effect of herbivores on plant performance or population dynamics is context-dependent (Maron et al. 2014). Understanding when and where herbivores will affect plants (i.e., the context-dependency of plant-herbivore interactions) is an ecologically important, but logistically challenging task because understanding context-dependency inherently necessitates factorial manipulations of both the "context" and of the herbivores. As such, our current knowledge of context-dependent plant-herbivore interactions remains limited by a lack of appropriate experiments (Maron et al. 2014).

The importance of understanding context-dependent plant-herbivore interactions is becoming increasingly important as human activities change the context in which these interactions occur (Thébault et al. 2014). A primary driver of land transformation in contemporary landscapes is habitat destruction for agriculture (Foley et al. 2005, Ramankutty et al. 2008). Abandonment of cultivated agricultural land has increased substantially in certain parts of the globe over the last century, particularly in the eastern portion of North America, allowing natural communities to regenerate on post-agricultural land (Ramankutty and Foley 1999). However, the legacies of historic agriculture can have persisting effects on plant communities by altering composition and eliminating certain species (Foster et al. 2003, Flinn and Vellend 2005, Cramer et al. 2008). Numerous other factors in addition to historic agriculture, such as habitat modification (e.g., canopy closure due to fire suppression; Briggs et al. 2005, Glitzenstein et al. 2012), can also affect plant communities. Furthermore, all of these factors have the potential to interact to affect regeneration trajectories (Suding et al. 2004, Cramer et al. 2008, Hobbs et al. 2009), making predicting recovery outcomes difficult (Cramer et al. 2008, Suding and Hobbs 2009, Brudvig 2011).

After describing how agricultural legacies can affect herbivore community composition in Chapter 1, my dissertation goes on to address two ways that plant-herbivore interactions can be context-dependent: associational effects and resource-plant-herbivore interactions (see Overview). Associational effects occur when a neighboring plant species affects the amount of damage received a focal plant (Barbosa et al. 2009, Underwood et al. 2014). Two types of associational effects can occur: associational resistance (AR) occurs when a neighboring plant reduces damage to a focal plant and associational susceptibility (AS) occurs when neighbors increase damage to a focal plant (Barbosa et al. 2009). Associational resistance generally occurs when the neighboring plant reduces foraging efficiency of insect herbivores, whereas susceptibility generally occurs when insects spillover from the neighboring plant onto the focal plant. Associational effects were originally described regarding specialist insect herbivores in agricultural systems (Tahvanainen and Root 1972, Root 1973). Although the role of generalist herbivores are a key part of associational effect theory (e.g., Atsatt and O'Dowd 1976, Agrawal 2004, Agrawal et al. 2006), empirical studies most often investigate specialist insects or generalist vertebrates (Barbosa et al. 2009, Letourneau et al. 2011). Thus, developing a better understanding of the role of associational effects regarding generalist insect herbivores may help to reconcile predictions regarding the role of neighboring plants in predicting the outcome of associational effects (i.e., AS or AR) (Andow 1991, Agrawal et al. 2006, Barbosa et al. 2009, Underwood et al. 2014). In Chapter 2 and 3 I investigate how agricultural legacies might drive associational effects by altering plant cover and community composition.

In addition to plant performance being negatively affected by herbivores, plant growth is also affected by resources. For example, plants may be susceptible to herbivore attack under low resource conditions, but are able to tolerate herbivore damage, or even overcompenstate, at high resource levels (Maschinski and Whitham 1989, Wise and Abrahamson 2005). Interactions between resources, plants, and herbivores have been shown to be important, although much of this evidence comes from controlled greenhouse studies (Wise and Abrahamson 2007). Few studies have experimentally manipulated both resources and herbivore presence to determine the potentially interactive effects of resources and herbivores on plant growth. In Chapter 4-6 I use a landscape-scale manipulation of overstory tree canopy to investigate how canopy structure (i.e., light availability), land-use legacies, and herbivores affect plant growth, seedling establishment, and demography.

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Chapter 1

Land-use history alters contemporary insect herbivore community composition and decouples plant-herbivore relationships

Philip G. Hahn and John L. Orrock

Hahn, P.G. and J.L. Orrock. 2015. Land-use history alters contemporary insect herbivore community composition and decouples plant-herbivore relationships. *Journal of Animal Ecology* 84: 745-754.

Summary

1. Past land use can create altered soil conditions and plant communities that persist for decades, although the effects of these altered conditions on consumers are rarely investigated.

2. Using a large-scale field study at 36 sites in longleaf pine (*Pinus palustris*) woodlands, we examined whether historic agricultural land use leads to differences in the abundance and community composition of insect herbivores (grasshoppers, Families Acrididae and Tettigoniidae).

3. We measured the cover of six plant functional groups and several environmental variables to determine whether historic agricultural land use affects the relationships between plant cover or environmental conditions and grasshopper assemblages.

4. Land-use history had taxa-specific effects and interacted with herbaceous plant cover to alter grasshopper abundances, leading to significant changes in community composition. Abundance

of most grasshopper taxa increased with herbaceous cover in woodlands with no history of agriculture, but there was no relationship in post-agricultural woodlands. We also found that grasshopper abundance was negatively correlated with leaf litter cover. Soil hardness was greater is post-agricultural sites (i.e., more compacted) and was associated with grasshopper community composition. Both herbaceous cover and leaf litter cover are influenced by fire frequency, suggesting a potential indirect role of fire on grasshopper assemblages.

5. Our results demonstrate that historic land use may create persistent differences in the composition of grasshopper assemblages, while contemporary disturbances (e.g., prescribed fire) may be important for determining the abundance of grasshoppers, largely through the effect of fire on plants and leaf litter. Therefore, our results suggest that changes in the contemporary management regimes (e.g., increasing prescribed fire) may not be sufficient to shift the structure of grasshopper communities in post-agricultural sites towards communities in non-agricultural habitats. Rather, repairing degraded soil conditions and restoring plant communities are likely necessary for restoring grasshopper assemblages in post-agricultural woodlands.

Introduction

The single greatest threat to biodiversity is habitat destruction, with a major source of destruction being land transformation for agriculture (Wilcove *et al.* 1998; Foley *et al.* 2011). Since the 1950’s, more than 200 million hectares of croplands in North America have been abandoned and are regenerating into semi-natural areas, creating potential habitat for diverse taxa (Ramankutty & Foley 1999; Foley *et al.* 2011). However, the legacies of agricultural practices can alter plant community composition for decades to centuries after abandonment (Foster *et al.* 2003; Flinn & Vellend 2005). Many native herbaceous plant species typical of habitats with no history of agriculture fail to reestablish in post-agricultural sites partially because of dispersal limitation (Kirkman *et al.* 2004; Flinn & Vellend 2005; Vellend *et al.* 2007). Tilling also has major effects on soil characteristics (Foster *et al.* 2003), including increasing soil nutrients, particularly phosphorous (Davidson & Ackerman 1993), decreasing soil organic matter (Burke, Lauenroth & Coffin 1995), and compacting soil (Hamza & Anderson 2005; Bassett, Simcock & Mitchell 2005). Altered soil conditions can further affect plant communities by reducing establishment of native plants or promoting establishment of ruderal plants species (Dambrine *et al.* 2007; Baeten *et al.* 2009). Because of the strong legacy effects of historic agriculture on both abiotic and biotic components of ecosystems, recovery trajectories of post-agricultural ecosystems often differ from ecosystems recovering from natural disturbances and can result in alternative stable states (Egler 1954; Cramer, Hobbs & Standish 2008; Kepfer-Rojas *et al.* 2014). Despite these well documented effects of agricultural land-use history on soil conditions and plant communities, less work has examined the effects of land-use legacies on other organisms, such as consumers.

Understanding how anthropogenic drivers alter consumer communities is important, because consumers contribute significantly to ecosystem productivity, biodiversity, and ecosystem functioning (Duffy 2002; Schmitz 2008; Metcalfe *et al.* 2014). Recent evidence suggests that the responses of consumer communities to land-use legacies are highly variable, likely because land-use legacies affect a suite of environmental characteristics (Foster *et al.* 2003). A recent meta-analysis showed that land use affects multiple taxa in tropical systems, but that different land uses had differing effects on biodiversity and that the effects were taxa-specific, with agricultural activities (either current or historic) causing the largest declines in species richness for most taxa (Gibson *et al.* 2011). Debinski et al. (2011) found taxa-specific responses of arthropod communities to land-use legacies (historic agriculture, grazing, or fire regimes) in Midwestern grasslands, with herbivorous taxa responding most strongly to characteristics of the plant community. Furthermore, the effects of land-use legacies were stronger than contemporary management regimes (i.e., burning and grazing). A study in the Argentine pampas found higher densities of pest grasshoppers in disturbed sites dominated by introduced forbs and pasture grasses compared to adjacent natural areas dominated by native vegetation (Torrusio, Cigliano & De Wysiecki 2002). Although these recent studies demonstrate clear contingencies in how land-use legacies affect consumer communities, whether historic agriculture alters relationships between environmental (plant or soil) characteristics and consumer communities remains unresolved.

Grasshoppers are common generalist herbivores in grassland systems worldwide (Otte 1981) and may be particularly sensitive to the effects of historic agriculture through changes to plant community composition, because grasshopper assemblages respond to changes in plant communities from disturbances such as fire and grazing (Joern 2005; Knight & Holt 2005; Branson & Sword 2010). Longleaf pine (*Pinus palustris*) woodlands occur in upland areas of the southeastern United States and are characterized by a patchy overstory of open-grown pines, with a high diversity of herbaceous plants (Walker & Peet 1984) and grasshoppers (Hill & Dakin 2011) in the understory. Historically, longleaf pine woodlands were maintained by low-intensity understory fires ignighted by lightning or native americans as frequently as every two to three years (Frost 1998). Prior to European settlement in the 1700's, longleaf pine woodlands were used for grazing cattle and hogs by early European colonists (White 2004). Throughout the 1700-1800's, longleaf pine woodlands were extensively logged, tapped for turpentine, and tilled for agriculture (Frost 1998; White 2004). Fire suppression was also actively practiced after around 1920, resulting in the conversion of open pine woodlands to closed canopy secondary forests (Frost 1998; White 2004). Over the last several decades, large tracts of agricultural land have been abandoned, allowing longleaf pine woodlands to regenerate and prescribed fire has been reintroduced to many managed areas (Jose, Jokela & Miller 2005). However, the legacies of historic agriculture persist throughout the historic range of the longleaf pine ecosystem through altered soil conditions and altered plant community composition, which generally results in reduced plant diversity and the loss of plant species with a strong affinity for undisturbed longleaf woodlands (Kirkman *et al.* 2004; Brudvig & Damschen 2011; Brudvig *et al.* 2014). Since characteristics of the plant community, such as productivity or composition, are strong regulators of consumer community structure, changes to the plant and soil conditions likely propagate up to consumer communities, although this has not been investigated.

In this paper, we conduct comprehensive sampling of the plant community, environmental variables, and grasshopper communities across 36 separate sites to provide the first large-scale evaluation of how past land use affects the abundance and composition of grasshopper communities. Specifically, we ask: 1) does land-use history affect grasshopper abundance or community composition? and 2) does past land use alter the relationship between plant cover or environmental variables and grasshopper abundance or community composition?

Materials and methods

Site Selection

This study was conducted at 36 upland longleaf pine (*Pinus palustris*) woodlands at the Savannah River Site (SRS), an ~80,000 hectare National Environmental Research Park in South Carolina, USA (Fig. 1). The area around the Savannah River Site was heavily affected by open grazing, logging, turpentining, and agriculture throughout much of the 1700-1800's. However, the most intensive human activites, such as logging and agriculture were restricted to lowland areas near major rivers and tributaries, leaving pine uplands relatively undisturbed by human activites (White 2004). Fertilizers became more common in the southern USA after 1865, allowing for more intensive tilling of upland pine forests, which peaked in the 1920's (White 2004). Tilling for agriculture peaked at SRS around this time, but occurred between about 1865 and 1950 (White & Gaines 2000). Farms were small and dispersed across the landscape, and approximately half of the land remained as untilled woodlands through 1950 (White 2004). Woodlands were used by farmers as timber lots and for grazing, and were fire suppressed starting around 1920 (White 2004), but they have no history of tilling, which is a major destructive force that eliminates all existing vegetation (Foster *et al.* 2003; Cramer *et al.* 2008). Historic agriculture has dramatic effects on contemporary plant community composition, more so than grazing or fire suppression (Brudvig & Damschen 2011; Brudvig *et al.* 2014), and therefore is the focus of our study. We selected sites that varied in land-use history: non-agricultural or post-agricultural woodlands. Land-use histories were determined from aerial photographs taken in 1951, just prior to governmental acquisition of SRS. All agricultural fields were abandoned after governmental acquisition and subsequently planted with pine trees (White & Gaines 2000). Tilled fields in the 1951 aerial photographs were classified as post-agricultural woodlands; non-agricultural sites were mature open woodlands in the 1951 aerial photographs. We examined aerial photographs taken in 1938 to verify that land-use histories were consistent for at least 13 years (Appendix S1). All of our non-agricultural sites were located on mature woodlands in the aerial photographs taken in both 1938 and 1951. One of our 18 post-agricultural sites was mature woodland in 1938 and tilled by 1951, but the rest were located on tilled fields at both time periods. The land-use history types were interspersed across the landscape. All sites were separated by >250 m, covered >1 ha of relatively uniform habitat, and were buffered by >50 m of the same land use history. We also stratified our site selection along a fire frequency gradient. Fire history (number of fires since 1991) was obtained for each site from the USDA-Forest Service.

Grasshopper sampling

We used sweep nets to sample grasshopper assemblages (Acrididae and Tettigoniidae), which is the most common method used to sample grasshopper assemblages (Evans, Rogers & Opfermann1983, Belovsky & Slade 1995, Joern 2005). At each site, we established three 5 m × 5 m plots, separated by >5 m. Plots were vigorously swept for three 3-minute periods, with approximately 15 minute rest periods between sweeps so that any grasshoppers dislodged from the vegetation could crawl back up onto the vegetation. The three sweep samples per plot and the three plots (nine total subsamples) were pooled for each site. Preliminary analyses indicate that, on average the sample from each plot contained more than half the grasshoppers species captured at a site (Appendix S2), suggesting this sampling method captured a representative sample of the grasshoppers present at each site. Sampling was conducted between 23 July and 06 August 2011. Sweeps were restricted to 0900-1500 on sunny days, when grasshoppers are most active at our site (Evans et al. 2012, PGH *personal observation*). Sites were visited in a random order and sampling of the different land-use histories was equally spread across different times of day. Immediately after collection, grasshoppers were frozen and later identified to genus or species using taxonomic guides (Capinera et al. 2004, Eades et al. 2013). Identifications of a subset of the collection were verified by a regional expert (J. Hill, Mississippi Entomology Museum) and these voucher specimens have been deposited in the Insect Research Collection of the Department of Entomology, University of Wisconsin-Madison. Adults and nymphs were included in the analysis.

Vegetation and ground cover

At each 5 m × 5 m plot, vegetation was sampled in four 1 m^2 quadrats (n = 12 quadrats per site) between 19-21 July, 2011. We recorded percent cover of plant functional groups (grasses, forbs, legumes, ferns, woody vegetation, vines) and leaf litter. These functional groups are common at our field site (Parresol, Blake & Thompson 2012) and broad functional groups (grasses and forbs) are commonly used in grasshopper studies because they comprise the dominant food source for grasshoppers (e.g., Behmer & Joern 1993; Belovsky & Slade 1995; Specht *et al.* 2008; Joern, Provin & Behmer 2012). The percent cover of the six plant functional groups and leaf litter were averaged by site for analysis. We also summed grasses, forbs, and legumes into one variable (herbaceous cover) because they were highly correlated.

Environmental data

At each site, we collected environmental data (e.g., canopy cover, substrate temperature) potentially related to grasshopper activity. We calculated the mean proportion of visible sky in photos taken with a hemispherical lens 1 m above the ground in three plots per site following standard protocol (Hemiview Version 2.1, Dynamax Inc., Houston, TX, USA). Temperature of the substrate (bare ground, leaf litter, or vegetation) was recorded in the corner of each 5 m × 5 m plot using an infrared temperature gun (Fluke Corp., Everett, WA, USA) immediately after the sweep netting. We measured soil hardness as the depth at which 2 MPa was attained (max of 72 cm), which is a level of soil compaction that affects plant performance (Bassett, Simcock & Mitchell 2005). Soil hardness measurements were taken at six locations adjacent to the 5 m × 5 m plots and averaged to produce one value per site. Plant and environmental variables are summarized in Table 1 and Appendix S3. Data are available in the Dryad Digital Repository (Hahn & Orrock 2014).

Data analysis

To describe the differences in the cover of plant functional groups and environmental variables between post-agricultural and non-agricultural longleaf pine woodlands, we conducted univariate *t*-tests for each variable.

Prior to analysis, we removed grasshopper taxa that occurred in fewer than three sites of each land-use history. Removing rare taxa was important for our analysis because we are interested in the response of individual taxa to environmental gradients and the resulting consequences for community composition. Therefore, inclusion of rare taxa would mask the response of the community composition to environmental variation (see also the description of the MLM below). We used criterion for rare taxa from McCune and Grace (2002). The resulting dataset contained counts of the six most common grasshopper taxa at 36 sites (Appendix S4). All predictor variables were centered ($\mu = 0$, $\sigma = 1$) before analysis, which allows regression coefficients to be compared among all variables.

We used multilevel models described by Jackson *et al.* (2012) for analysis of community data to evaluate our questions. Multilevel models (MLM) are desirable for our dataset and question for several reasons. First, MLM is similar to other common multivariate techniques (e.g., redundancy analysis or canonical correspondence analysis) but allows for generalized error distributions (e.g., Poisson distribution for counts). Second, we are interested in changes to both grasshopper abundance and community composition. MLM analyze the responses of individual grasshopper species to predictor variables as random effect slopes using a series of Poisson regressions. The standard deviations of these slopes can be interpreted as changes in community composition assuming that two communities with the same relative abundances of species have the same composition, regardless of the total abundances (Jackson *et al.* 2012). Finally, the results can be plotted in an ordination to aid in visual interpretation, if appropriate (Jackson *et al.* 2012). Although MLM are our primary analytical approach, we conducted ancillary univariate Poisson regressions for comparison.

We addressed our two questions (i.e., does land use history affect grasshopper abundance and community composition and does past land use alter the relationship between plant cover or environmental variables and grasshopper abundance or community composition?) using MLM. We followed the general recommendations of Bolker *et al.* (2009) and Grueber *et al.* (2011) for fitting multilevel models that include random intercepts and slopes. We first constructed a global model that included our seven environmental and plant functional predictor variables as continuous fixed effects (Table 1), land-use history as a binary (0 = post-agricultural or 1 = non-agricultural) fixed effect, and an interaction term for land-use history and each of the seven continuous variables. These interaction terms allowed us to formally examine our second question (does past land use alter the relationship between plant cover or soil characteristics and grasshopper abundance or community composition?) because a significant interaction would indicate different relationships (slopes) between land-use histories. We did not include interaction terms among any continuous variables or any three-way interactions to avoid over-fitting our model and to ensure that our global model converged (Bolker *et al.* 2009). We did not include fern cover or soil hardness in these models to avoid multicolinearity with land-use history (see Table 1). Instead we analyze these two variables separately. The global model included random intercepts for site, species, and a unique number for each observation to account for overdispersion. The observation-level random effect models variation beyond the Poisson disruption (i.e., overdispersion) using a Poisson-lognormal distribution (Elston *et al.* 2001). We used a two-step AIC selection approach, a model-reduction step and then a model-selection step. First, we reduced the global model using the dredge function in the MuMIn package in R, which runs all possible models based on the global model and selects the top model(s) based on AIC (Barton 2013). Then we added random slope terms to the top models within 2 AIC units of the best model and selected the best model that included fixed and random effects. The random slope terms (i.e., each fixed effect × taxa) in these models tested for taxon-specific responses to each predictor variable (i.e., changes to community composition). In other words, these random effects test the standard deviation of parameter estimates (slopes) for each taxon in response to an effect, such that a significant random effect can be interpreted as altering community composition because the responses of the different taxa differ in response to the effect (Jackson *et al.* 2012). Furthermore, as in Jackson *et al.* (2012), we consider changes in relative abundances, not absolute abundances, as a change in community composition. Mean relative abundances for two variables following a Poisson distribution is $\lambda_1/\lambda_2 = \exp(a_1\text{-}a_2)$, where a_i are intercepts, such that proportional changes (i.e., both species double in abundance) would not change the relative abundance of the two species (Jackson *et al.* 2012). We avoided model averaging because our top models contained different random effects, which are not able to be incorporated into model averaging procedures (Grueber *et al.* 2011). *P*-values for the random slopes were tested using the rand function in the lmerTest package.

We interpret three products of the final multilevel models: 1) the fixed effect parameter estimates, which report the mean response of all grasshopper taxa to a predictor variable (i.e., changes in abundance), 2) the random effects, calculated as the standard deviations of coefficients, which report the variability in responses of all grasshopper taxa in response to a predictor variable (i.e., changes in community composition), and 3) the random slope parameters, which report the response of individual grasshopper species to a predictor variable.

We used the glmer function in the lme4 package version 1.1-6 for the MLM analysis (Bates, Maechler & Bolker 2013).

Results

Two plant cover variables differed between land-use histories, with greater vine cover in post-agricultural sites and greater fern cover in sites not used for agriculture. Substrate temperature was also lower in woodlands with no history of agricultural use and the depth at which 2 MPa was reached was greater in non-agricultural sites, indicating less soil compaction (Table 1).

We collected 459 individuals representing 18 taxa (species or genera), six of which were abundant enough to include in further analysis (Appendix S4). In the best-supported MLM (Appendix S5), land-use history alone did not affect grasshopper abundance, but there was a significant interaction between land-use history and herbaceous cover (Table 2). Herbaceous cover was not related to grasshopper abundance in post-agricultural woodlands ($z = 1.39$, $P = 0.16$), but the relationship between grasshopper abundance and herbaceous cover was significantly more positive in non-agricultural woodlands ($z = 1.96$, $P = 0.05$). Leaf litter cover was negatively related to grasshopper abundance ($z = -2.34$, $P = 0.019$). The land-use history × grasshopper taxa random term, which allowed each grasshopper taxa to vary with land-use history, was also significant ($\chi^2 = 7.16$, $P = 0.007$, Table 2), suggesting that land-use history altered grasshopper community composition (Fig. 2). Fixed- and random-effect coefficients for the best model are presented in Appendix S5. The two variables that were analyzed separately to avoid multicolinearity with land-use history generally support the results of the best model, with fern cover positively affecting grasshopper abundance and soil hardness associated with altered grasshopper community composition (Appendix S6). Moreover, the grasshopper taxa responses to land-use history and soil hardness were highly correlated between these two models (Fig. S6).

To aid in interpretation of the MLM, we plotted the raw abundance values for each grasshopper taxa to highlight difference in abundances between land-use histories, including best fit Poisson regression lines (Fig. 3, Appendix S6). Three of the six taxa match the results of the MLM in that their abundance was positively related to herbaceous cover in non-agricultural sites, but not in post-agricultural sites. Of the mixed-feeders (i.e., grasshoppers that consume grasses, forbs, and some woody foliage; Ueckert & Hansen 1971, Joern 1983), the two most common *Melanoplus* taxa (subfamily Melanoplinae) both had higher abundances in post-agricultural woodlands (Fig. 2), although only slightly for short-wing species, and only long-winged *Melanoplus* were significantly related to herbaceous cover (Fig. 3C,D). *Schistocerca* (subfamily Cyrtacanthacridinae) had lower abundance in post-agricultural woodlands (Fig. 2) and responded positively to herbaceous cover only in non-agricultural woodlands (Fig. 3F). *Arphia xanthopera* (subfamily Oedipodinae), a banded-winged grasshopper that likely specializes on grasses but may also consume forbs (Ueckert & Hansen 1971, Joern 1983), had similar abundance in both land-use histories (Fig. 2), but increased positively with herbaceous cover only in woodlands without a history of agricultural use (Fig. 3A). *Orphulella pelidna* (subfamily Gomphocerinae), a grass specialist, had higher abundance in post-agricultural woodlands (Fig. 2) and similar (positive) responses to herbaceous cover in both land use histories (Fig. 3E). *Conocephalus* (family Tettigoniidae) had similar mean abundances in both land-use histories (Fig.e 2) but increased positively with herbaceous cover only in non-agricultural woodlands (Fig. 3B). The second best MLM model captured this taxon-specific variation to herbaceous cover via a land-use history × herbaceous cover × grasshopper taxa random effect, although the increase in model parameters did not justify it over the more simple MLM with only the land-use history × grasshopper taxa random effect, based on AIC (Appendix S5).

Discussion

Past agricultural land use generates persistent changes in plant communities and soil conditions in many ecosystems (Flinn & Vellend 2005; Cramer *et al.* 2008). We found a positive relationship between herbaceous plant cover and grasshopper abundance, but only in habitats without a history of agriculture. We also found taxa-specific effects of historic agriculture on grasshopper abundance, which resulted in shifting dominance from *Schistocerca* in sites with no history of agriculture to dominance of *Melanoplus* in sites with a history of agriculture (Fig. 2). Collectively, these results suggest that the effect of historic agricultural land use extends beyond plants and soils to decouple plant-herbivore relationships, leading to a strong legacy of past agriculture on present-day insect herbivore assemblages. Below we discuss the changes in grasshopper assemblages in response to land-use history and environmental drivers, including the potential indirect role of fire, as well as how altered plant community composition and soil conditions resulting from historical agricultural land use may have contributed to the differences in grasshopper assemblages we found. Our results shed light on how human activities can decouple otherwise well-established plant-herbivore relationships and suggest that management efforts should consider the role of historic land use on herbivore assemblages, as well as plant communities.

Plant productivity is often a good predictor of insect abundance and diversity in grasslands around the world (Joern & Laws 2013), but our results suggest that agricultural land-use legacies may decouple this relationship. For instance, we found a strong relationship between herbaceous cover and grasshopper abundance, but only in non-agricultural woodlands for most grasshopper taxa (Fig. 3; Appendix S7). Furthermore, our data suggest that the abundance of certain grasshopper taxa is sensitive to historic agriculture (e.g., *Schistocerca*), whereas other taxa responded positively to historic agriculture (e.g., *Melanoplus*) (Fig. 2). Two other studies conducted within the longleaf pine ecosystem found that grasshopper species that were common in anthropogenic habitats (e.g., old fields, roadsides, power-line right of ways), including *Melanoplus* and some potential pest species, were not common in natural habitats (Squitier & Capinera 2002; Hill 2009). Because of widespread anthropogenic land use, including abandonment of agricultural fields in North America (Ramankutty & Foley 1999), land-use legacies may have underappreciated effects on grasshopper assemblages, and potentially other insects, in grasslands or savannas regenerating from anthropogenic land use.

Agricultural land-use legacies have well documented effects on plant community composition (Flinn & Vellend 2005; Cramer *et al.* 2008), as well as nutrients in the soil and plant tissues (Baeten *et al.* 2011), both of which may provide a potential mechanism altering grasshopper community composition. In the longleaf pine ecosystem, agricultural land-use history is known to reduce plant diversity, alter community composition, and also tends to eliminate long-lived perennial plant species (Kirkman *et al.* 2004; Brudvig & Damschen 2011; Brudvig *et al.* 2014). Although we did not measure plant community composition at the species level, altered plant community composition between post-agricultural and non-agricultural woodlands likely contributed to the different relationships we found between herbaceous cover and grasshopper abundance. For instance, altered or reduced host plant availability in post-agricultural sites could affect grasshopper abundance. Plant diversity can increase grasshopper fitness by providing more diverse nutritional options (Specht *et al.* 2008; Unsicker *et al.* 2010) and differences in plant species richness or community composition among land-use histories may have contributed to altering grasshopper assemblages in our study. Agricultural land-use history also affects soil nutrients, generally resulting in an increase in soil phosphorous and other nutrients (Verheyen *et al.* 1999; Fraterrigo, Turner & Pearson 2006; Brudvig *et al.* 2014) and this can increase nutrients in plant tissues (Baeten *et al.* 2011). Grasshopper assemblages respond to plant phosphorus (Bishop *et al.* 2010) and other nutrients (Joern *et al.* 2012) measured at the plant community level. Thus, it seems likely that land use-mediated changes in plant nutrients may contribute to the changes to grasshopper community composition that we observed. Furthermore, other changes to soil conditions related to agriculture land use, such as compaction or soil organic matter (Burke *et al.* 1995; Hamza & Anderson 2005), could potentially affect grasshopper oviposition preference or egg development in the soil and alter composition (Appendix S6). Studies that incorporate detailed measures of plant community composition, functional traits (e.g., Plas et al. 2012), and plant nutrients (Joern *et al.* 2012), may provide further mechanistic insight into how land-use history alters plant-herbivore relationships.

Fire can affect grasshopper abundance and community composition in grasslands around the world (Joern 2005; Knight & Holt 2005; Branson & Sword 2010; Plas *et al.* 2012) by either killing grasshoppers or eggs directly or by eliminating vegetation, which is their main food source (Evans 1984; Swengel 2001; Branson & Vermeire 2013). Although we found no evidence for direct effects of fire, fire effects on grasshopper assemblages can be subtle and are usually indirectly driven by concurrent changes to the plant community (Evans 1984). Several studies of grasshopper assemblages in tallgrass prairies in Kansas found that the effects of weather or grazing are stronger than the direct effects of fire on regulating grasshopper abundance and community composition (Joern 2004, 2005; Jonas & Joern 2007). Plas et al. (2012) found that the effects of fire and environmental variables on grasshopper assemblages in a

South African savanna were indirect, driven through changes to vegetation structure and plant traits. Although we found no effect of the total number of burns since 1991 on grasshopper abundance or community composition, we did find a negative relationship between leaf litter cover, which decreases with frequent fires in our system (Hiers *et al.* 2007), as well as a positive relationship between herbaceous plant cover (although only significantly in remnant woodlands), which generally increases with frequent fires (Glitzenstein *et al.* 2012), and grasshopper abundance (Table 2, Appendix S5). At our sites, the number of burns was negatively related to leaf litter cover, and was positively, although not significantly, related to herbaceous plant cover (Appendix S3). This suggests that, through its influence on leaf litter, fire may negatively affect grasshopper abundances by reducing microsites suitable for oviposition. The indirect effects of fire on grasshoppers driven through the plant community appears to be weaker in our system compared to herbaceous dominated tallgrass ecosystems (e.g. Joern 2005; Plas *et al.* 2012), possibly because the understory of our sites was composed of woody plants and vines, in addition to herbaceous plants (Table 1). Finally, we reiterate that we only found significant relationships between plant cover and grasshopper abundance in non-agricultural habitat, which might suggest that potential indirect effects of fire on grasshopper assemblages are also decoupled by agricultural land-use history, although this requires future experimental examination.

Grasshoppers contribute significantly to biodiversity (Steck *et al.* 2006; Hill & Dakin 2011; Orrock *et al.* 2011), secondary productivity (Joern & Rudd 1982; Belovsky, Slade & Stockhoff 1990; Champlin, Kilgo & Moorman 2009), and ecosystem processes such as nutrient cycling (Belovsky & Slade 2000; Joern & Laws 2013). Our findings show that land-use history decoupled the relationship between herbaceous plant cover and abundance for most grasshopper species, even over 50 years after agricultural abandonment, could have implications for conservation and management of insect communities. Prescribed fires are common management techniques used in grasslands and savannas to promote plant diversity, insect diversity, and endangered species such as the red cockaded woodpecker in the longleaf pine ecosystem (Panzer 2002; Jose *et al.* 2005; Pyke, Brooks & D'Antonio 2010). Consistent with conclusions from a recent study examining insect diversity in Midwestern grasslands (Debinski *et al.* 2011), our data suggest that current management strategies alone (e.g., prescribed fire) may not shift grasshopper abundance or community composition in post-agricultural woodlands to more resemble assemblages in woodlands without a history of agricultural use and highlight the need to consider the effect of land-use legacies on contemporary biodiversity of primary consumers. Although our study is not able to disentangle agricultural legacies from natural succession processes, the trajectories of plant communities recovering from intensive cultivation have been shown to be drastically altered compared to recovery from less intensive, natural disturbances (Dupouey *et al.* 2002; Kepfer-Rojas *et al.* 2014). Therefore, our results suggest that a comprehensive approach including restoration of the plant community and soil conditions may be required to promote grasshopper assemblages typical of habitats with no agricultural history over disturbance-adapted pest species that are often considered undesirable (Branson, Joern & Sword 2006). Alternatively, focusing conservation and management efforts on less-degraded habitat may have a more desirable effect on conserving both plants and arthropods than trying to reintroduce management practices to highly degraded sites. Because grasshoppers are important herbivores, potential feedbacks between plants and herbivores, and how they are altered by historic agriculture (Hahn & Orrock *in press*), should receive more attention by both land managers and research ecologists.

Data Accessibility

Data available from the Dryad Digital Repository, doi:10.5061/dryad.465t5.

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Supporting Information

Appendix S1. Aerial photographs of select sites at the Savannah River Site, SC, USA in 1938, 1951, and 2010.

Appendix S2. Accumulation of grasshopper species in plots within sites.

Appendix S3. Correlation matrix of predictor variables used in the analysis.

Appendix S4. Information about the grasshopper taxa collected at the Savannah River Site, SC, USA.

Appendix S5. Multilevel model reductions and section results, coefficients, and R code.

Appendix S6. Results of the analysis of fern cover and soil compaction.

Appendix S7. Results of the supplemental Poisson regression analyses.

Table 1. Mean values of environmental variables and plant functional groups in post-agricultural and non-agricultural longleaf pine woodlands.

	Mean (SE)		
Description	Post-Ag	Non-Ag	
Prop visible sky	0.45 (0.02)	0.43 (0.02)	
†Soil Hardness (depth (cm) to 2 Ma)	11.2 (0.73)	22.2 (2.41)	**
Number of burns since 1991	4.28 (0.46)	4.11 (0.50)	
Substrate temperature (°C)	40.2 (1.09)	36.7 (1.08)	*
% leaf litter cover	63.5 (3.46)	63.73 (3.11)	
% herbaceous cover	5.44 (1.32)	3.43 (0.98)	
% woody cover	14.3 (2.04)	18.56 (2.51)	
% vine cover	7.64 (0.51)	3.79 (0.39)	*
†% fern cover	0.00 (0.00)	2.13 (0.85)	*

$*P \leq 0.05$; $**P \leq 0.005$ (Bonferroni correction, alpha = 0.05, 8 corrections, p-value = 0.0055). † indicates variables that were analyzed separately to avoid multicolinearity with land-use history.

Table 2. Analysis of deviance table for the fixed effects, including analysis of random effects, from the best MLM on grasshopper assemblages at the Savannah River Site, South Carolina, USA.

Fixed effects	**$\chi2$**	***P***
Land-use history	0.32	0.572
Herbaceous cover	8.78	0.003
Leaf litter	5.48	0.019
History × HerbCov	3.84	0.050
Random effects		
Species	40.48	0.000
History × Spp	7.16	0.007
Site	18.60	0.000

Figure legends

Fig. 1. A) Map of the study sites within upland longleaf pine woodlands at the Savannah River Site, South Carolina, USA. “Post-Ag” sites have a history of agriculture (>50 years since abandonment); “Non-Ag” sites have no known history of agriculture. Longleaf pine woodland sites with B) a history of agriculture and C) no history of agriculture. Photo credit: P.G. Hahn.

Fig. 2. Mean abundance (±1 standard error in three 5 × 5m plots per site) of the six most common grasshopper taxa (Acrididae and Tettigoniidae) collected at the Savannah River Site, South Carolina, USA, as a function of land-use history.

Fig. 3. Total number of grasshoppers collected at the Savannah River Site, South Carolina, USA in three 5m × 5m plots per site regressed against herbaceous cover (averaged across the three plots and centered). Fit lines are from Poisson regressions conducted for each land-use history type: post-agricultural or non-agricultural land-use history. R^2 is the proportion of deviance explained by the model (i.e., pseudo-R^2). $^*P \leq 0.05$; $^{**}P \leq 0.01$.

Figure 1

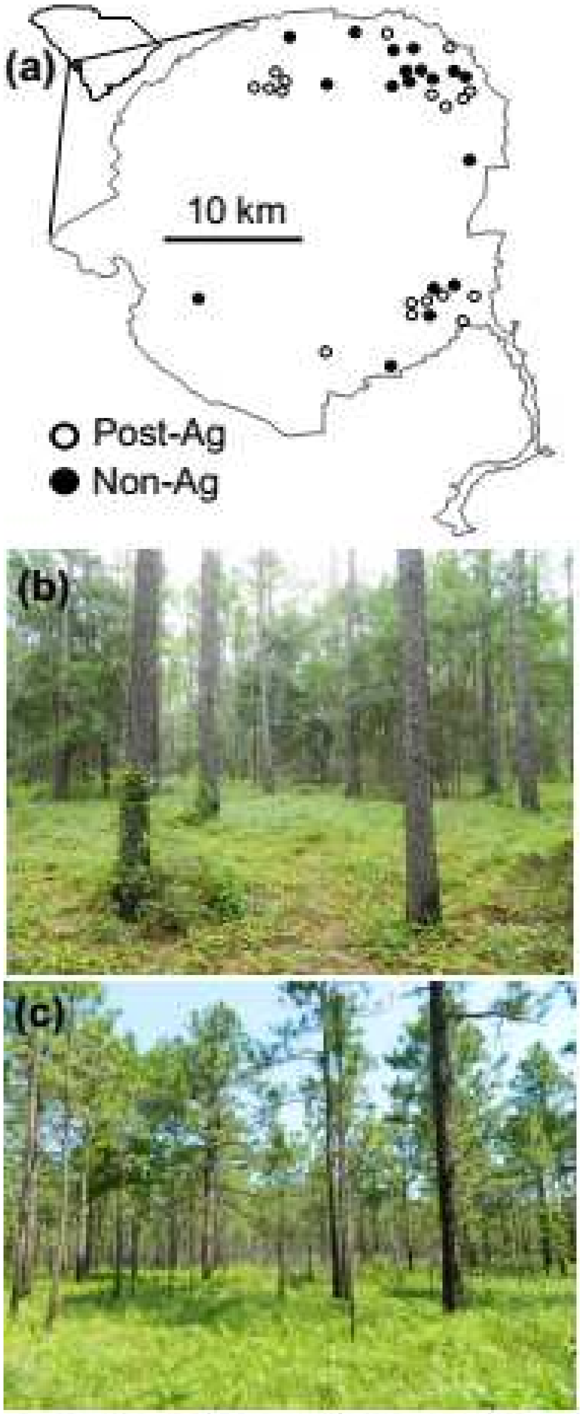


Figure 2

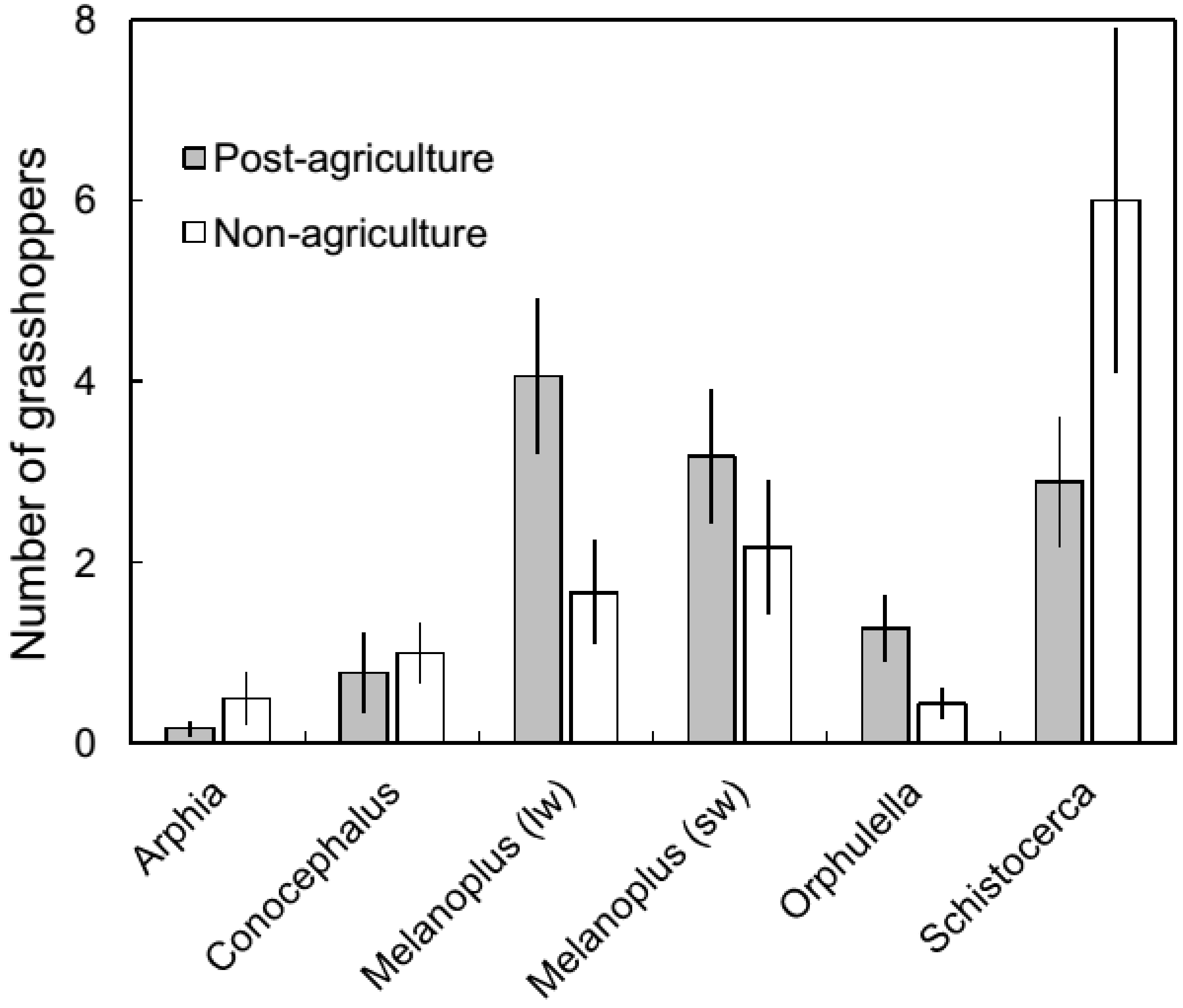
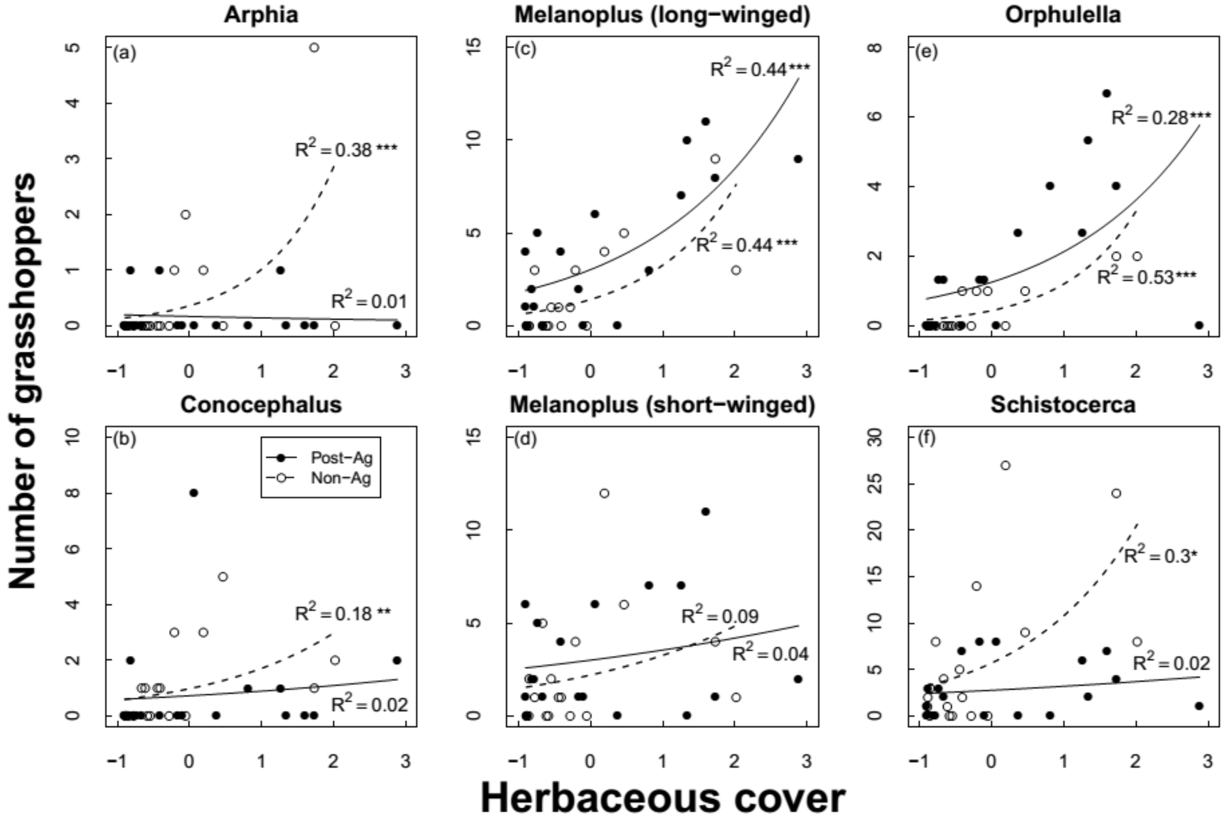
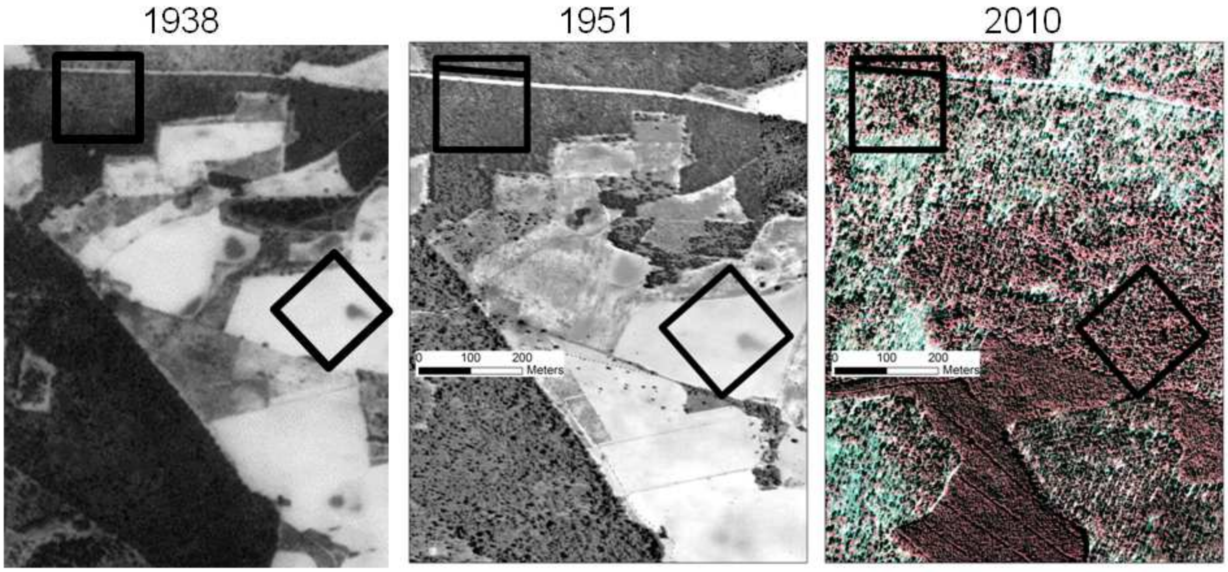

8
6
4
2
0
Number of grasshoppers
Post-agriculture
Non-agriculture
Arphia
Conocephalus
Melanoplus (lw)
Melanoplus (sw)
Orphulella
Schistocerca

Figure 3


Number of grasshoppers
Herbaceous cover
Arphia
(a)
$R^2 = 0.38$ ***
$R^2 = 0.01$
Melanoplus (long−winged)
(c)
$R^2 = 0.44$***
$R^2 = 0.44$ ***
Orphulella
(e)
$R^2 = 0.28$***
$R^2 = 0.53$***
Conocephalus
(b)
Post−Ag
Non−Ag
$R^2 = 0.18$ **
$R^2 = 0.02$
Melanoplus (short−winged)
(d)
$R^2 = 0.09$
$R^2 = 0.04$
Schistocerca
(f)
$R^2 = 0.3$*
$R^2 = 0.02$
−1
0
1
2
3

APPENDIX S1

Aerial photographs of two sites at the Savannah River Site (SRS), SC from 1938, 1951, and 2010 showing one site with a history of agriculture and one site with no history of agriculture. Agriculture was abandoned across all of SRS in 1951. Both sites are now located in mature longleaf pine woodlands. The three 5m × 5m plots used in this study were located near the center of the 175m × 175m site buffers show in the photographs.



APPENDIX S2

Accumulation of grasshopper species in plots

Mean number of grasshopper species collected in one, two, and three plots (subsamples) at each site were calculated using the 'specaccum' function in the vegan package (Oksanen et al. 2012). We used the "random" method, although results were similar based on other methods (e.g., "rarefaction"). In all examples (Fig. A1), more than half of the total species collected at a site were captured in one plot.

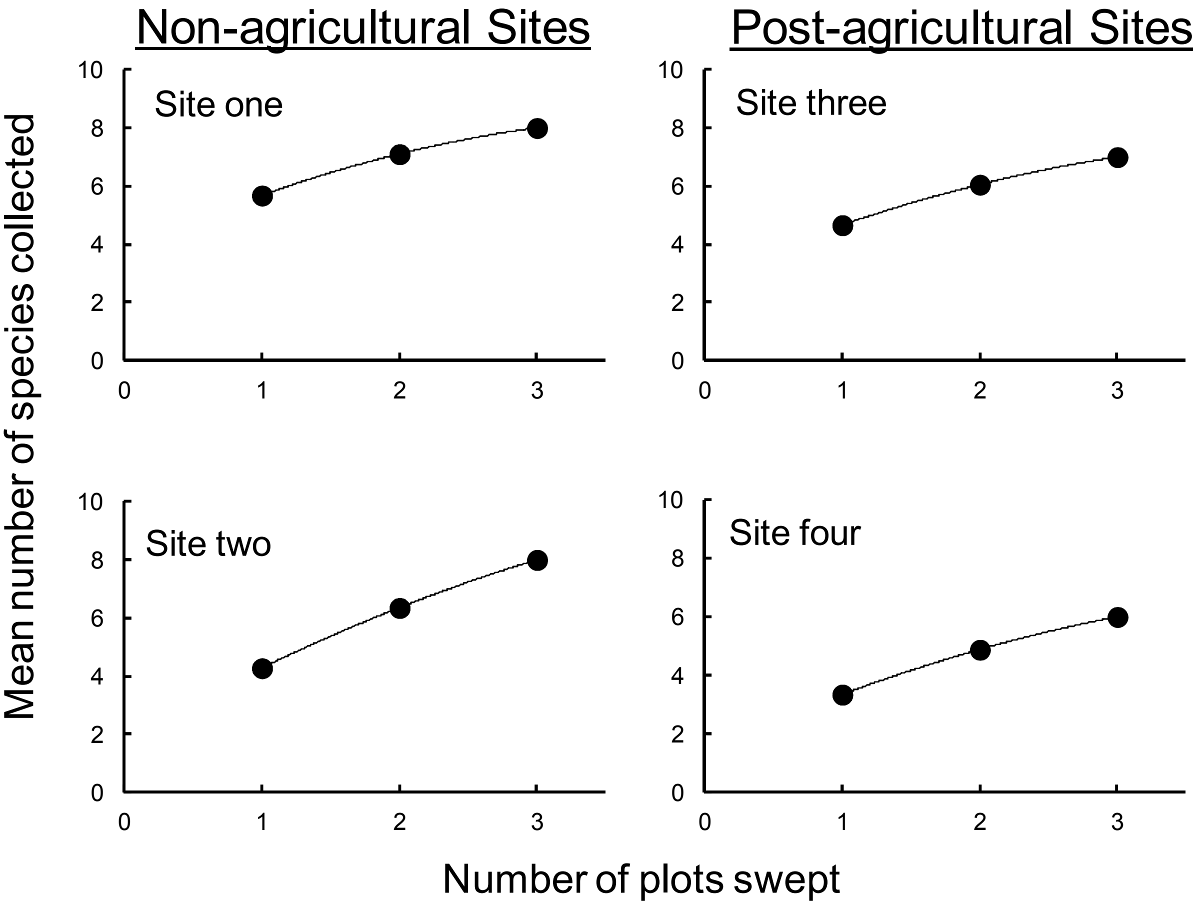


Figure A1. Accumulation of grasshopper species in the two most species-rich non-agricultural (left column) and post-agricultural (right column) sites.

APPENDIX S3

Correlation matrix of predictor variables. Spearman correlation coefficients are on the bottom, p-values are on the top (n = 36). Significant coefficients (α = 0.05) are bolded.

	hist	tot.burn	vis.sky	temp	litter	wood	vine	herb	fern	comp
Land-use history	-	0.975	0.514	0.027	0.926	0.318	0.022	0.514	0.003	0.000
Total burns	0.01	-	0.299	0.951	0.014	0.316	0.529	0.137	0.514	0.640
Visible sky	-0.11	0.18	-	0.000	0.010	0.018	0.131	0.008	0.639	0.908
Substrate temperature	**-0.37**	0.01	**0.57**	-	0.941	0.620	0.301	0.137	0.214	0.065
Leaf litter	0.02	**-0.41**	**-0.42**	-0.01	-	0.000	0.913	0.003	0.134	0.562
Woody cover	0.17	0.17	**0.39**	0.09	**-0.72**	-	0.224	0.298	0.192	0.057
Vine cover	**-0.38**	-0.11	-0.26	-0.18	0.02	-0.21	-	0.687	0.159	0.000
Herbaceous cover	-0.11	0.25	**0.44**	0.25	**-0.48**	0.18	0.07	-	0.257	0.787
Fern Cover	**0.49**	0.11	0.08	-0.21	-0.25	0.22	-0.24	0.19	-	0.046
Soil hardness	**0.64**	0.08	-0.02	-0.31	-0.10	0.32	**-0.56**	-0.05	**0.33**	-

APPENDIX S4

Information about the grasshopper species collected at the Savannah River Site, SC, USA. We collected 459 individuals from 18 taxa (genus or species). Species codes are listed for the six most common taxa, which were used in the analysis. These six taxa also correspond to the dominant feeding guilds at our site. Species that occurred in <3 sites per land-use history were removed from the analysis. Taxa with an "n/a" in the "Taxa Code" column were not used in the analyses. Most *Schistocerca* nymphs are likely *Schistocerca alutacea* based on subsequent rearing observations as part of another study (PGH *personal observation*), although this group could also include *S. damnifica* and *S. americana*.

Species	**Subfamily**	**Feeding Guild**[a]	**Taxon Code**[b]	**Numb. Collected**
Schistocerca alutacea and *Schistocerca* nymphs	Cyrtacanthacridinae	Forbs, woody	Schistocerca	158
Orphulella pelidna	Gomphocerinae	Grasses	Orphulella	31
Melanoplus angustipennis	Melanoplinae	Forbs	Melanoplus (lw)	106
Melanoplus scudderi and sp. *puer* group	Melanoplinae	Forbs	Melanoplus (sw)	96
Arphia xanthoptera	Oedipodinae	Grasses, forbs	Arphia	12
Conocephalus sp.	Conocephalinae	Plant foliage, flowers	Conocephalus	32
Phaneropterinae†	Tettigoniidae‡	Plant foliage, flowers	n/a	3
Scudderia sp.	Phaneropterinae	Plant foliage,	n/a	5

		flowers		
Eotettix pusillus	Melanoplinae	Forbs	n/a	1
Hesperotettix viridis brevipennis	Melanoplinae	Grasses, forbs	n/a	2
Hippiscus ocelote	Oedipodinae	Grasses, forbs	n/a	1
Melanoplus attenuatus	Melanoplinae	Grasses, forbs	n/a	1
Melanoplus impudicus	Melanoplinae	Grasses, forbs	n/a	1
Melanoplus keeleri	Melanoplinae	Grasses, forbs	n/a	1
Melanoplus sp. nigrescens group	Melanoplinae	Grasses, forbs	n/a	1
Mermiria picta	Gomphocerinae	Grasses	n/a	1
Paratylotropidia beutenmuelleri	Melanoplinae	Grasses, forbs	n/a	1
Spharagemon marmorata picta	Oedipodinae	Grasses, forbs	n/a	3
Schistocerca damnifica	Cyrtacanthacridinae	Forbs, woody	n/a	1

† Indicates subfamily.

‡ Indicates family.

[a] Feeding guild is based on Ueckert and Hansen (1971), Joern (1983), Hahn and Orrock (*in press*), and personal observations (PGH).

[b] Melanoplus (lw) and (sw) refer to long-winged and short-winged species, respectively.

APPENDIX S5

Multilevel model reductions and section results, coefficients, and R code.

Table S5a. Model reduction process (i.e., within 2 AIC units of the best model) examining grasshopper assemblages at the Savannah River Site, South Carolina, USA. All models include Site, grasshopper species, and a unique number index (see *Methods*). All other variables are fixed effects. Df is equal to the number of parameters estimated in the model. Variable codes are listed in Table S5b.

Model variables	**df**	**logLik**	**AIC**	**Delta**	**Weight**
1/3	6	-350.84	713.68	0	0.11
1/2/3/9	8	-348.86	713.72	0.04	0.11
1/3/4	7	-350.06	714.12	0.44	0.09
1/3/7	7	-350.2	714.4	0.72	0.08
1/2/3/4/9	9	-348.51	715.02	1.34	0.06
1/2/8/9	8	-349.52	715.04	1.36	0.06
1/2/3/7/9	9	-348.55	715.09	1.41	0.05
1/7	6	-351.58	715.16	1.48	0.05
1/3/5	7	-350.63	715.25	1.57	0.05
1/2/7	7	-350.64	715.29	1.61	0.05
1/2/3/9/10	9	-348.69	715.38	1.7	0.05
1/3/6	7	-350.72	715.44	1.77	0.05
1/2/3/5/9	9	-348.74	715.49	1.81	0.04
1/2/3/8/9	9	-348.77	715.54	1.86	0.04
1/8	6	-351.78	715.56	1.88	0.04
1/3/8	7	-350.83	715.65	1.97	0.04
1/3/4/6	8	-349.83	715.67	1.99	0.04

Table S5b. Codes for the fixed effect variables from the top models in Table S5a.

Variable code	**Variable**	**Prop in top model**
1	**HerbCov**	**1**
2	**Litter**	**0.85**
3	**History**	**0.46**
4	Temp	0.18
5	TotBurn	0.09
6	VineCov	0.09
7	Vis_Sky	0.18
8	WoodCov	0.18
9	**HerbCov** × **History**	**0.41**
10	History × Litter	0.05

Table S5c. Top 10 best models including the addition of random effects that describe community composition (i.e., (0 + “factor”|Spp) in the best model).

Model	**Df**	**AIC**	**ΔAIC**	**BIC**	**logLik**	**deviance**
zzz1.1	9	708.55	0	738.93	-345.28	690.55
zzz1.4	14	713.45	4.9	760.71	-342.73	685.45
zzz1.0	8	713.72	5.17	740.72	-348.86	697.72
zzz1.2	9	713.76	5.21	744.14	-347.88	695.76
zzz1.7	**7**	713.79	5.24	737.42	-349.89	699.79
zzz1.8	8	714.21	5.66	741.21	-349.1	698.21
zzz1.6	7	715.68	7.13	739.31	-350.84	701.68
zzz1.3	9	715.72	7.17	746.1	-348.86	697.72
zzz1.10	8	716.06	7.51	743.06	-350.03	700.06
zzz1.9	8	716.13	7.58	743.13	-350.07	700.13
zzz1.5	14	718.22	9.67	765.47	-345.11	690.22

Description of models. Coding follows lme4 package.
zzz1.1: numb.sum ~ (1 | Spp) + History * HerbCov + Litter + (0 + History |
zzz1.1: Spp) + (1 | index) + (1 | Site)
zzz1.4: numb.sum ~ (1 | Spp) + History * HerbCov + Litter + (0 + History *
zzz1.4: HerbCov | Spp) + (1 | index) + (1 | Site)
zzz1.0: numb.sum ~ (1 | Spp) + History * HerbCov + Litter + (1 | index) +
zzz1.0: (1 | Site)
zzz1.2: numb.sum ~ (1 | Spp) + History * HerbCov + Litter + (0 + HerbCov|
zzz1.2: Spp) + (1 | index) + (1 | Site)
zzz1.7: numb.sum ~ (1 | Spp) + HerbCov + Litter + (0 + HerbCov | Spp) +
zzz1.7: (1 | index) + (1 | Site)
zzz1.8: numb.sum ~ (1 | Spp) + HerbCov + Litter + Temp + (0 + HerbCov |
zzz1.8: Spp) + (1 | index) + (1 | Site)
zzz1.6: numb.sum ~ (1 | Spp) + HerbCov + Litter + (0 + Litter | Spp) +
zzz1.6: (1 | index) + (1 | Site)
zzz1.3: numb.sum ~ (1 | Spp) + History * HerbCov + Litter + (0 + Litter |
zzz1.3: Spp) + (1 | index) + (1 | Site)
zzz1.10: numb.sum ~ (1 | Spp) + HerbCov + Litter + Temp + (0 + Temp |
zzz1.10: Spp) + (1 | index) + (1 | Site)
zzz1.9: numb.sum ~ (1 | Spp) + HerbCov + Litter + Temp + (0 + Litter |
zzz1.9: Spp) + (1 | index) + (1 | Site)
zzz1.5: numb.sum ~ (1 | Spp) + History * HerbCov + Litter + (0 + History *
zzz1.5: Litter | Spp) + (1 | index) +(1|Site)

Table S5d. Parameter estimates (coefficients) from the best MLM for the six most common grasshopper taxa collected at the Savannah River Site, South Carolina, USA.

Taxa coefficients	**(Intercept) Post-Ag**[a]	**(Intercept) Non-Ag**[a]	**HerbCov (Post-Ag)**[b]	**HerbCov (Non-Ag)**[b]	**Leaf litter**[b]
Arphia	0.24	0.26	0.25	0.81	-0.38
Conocephalus	0.56	0.61	0.25	0.81	-0.38
Melanoplus (long-winged)	2.45	1.14	0.25	0.81	-0.38
Melanoplus (short-winged)	2.08	1.42	0.25	0.81	-0.38
Orphulella	0.82	0.38	0.25	0.81	-0.38
Schistocerca	2.04	3.23	0.25	0.81	-0.38

The Poisson model included a land-use history × herbaceous cover fixed-effect interaction term, which produced unique slopes for herbaceous cover in post-agricultural and non-agricultural land-use history sites. The model also included land-use history × taxa random effect, which allows each grasshopper taxon a unique abundance value for each land-use history type (post-agricultural and non-agricultural). Fixed effects are repeated for all six taxa for completeness. Continuous variables were centered ($\mu = 0$, $\sigma = 1$) prior to analysis; intercepts are back-transformed (i.e., exponentiated) so they can be interpreted as mean (counts) at the mean of the (center) covariate. Standard deviations of the untransformed intercepts (i.e., random effect coefficients) for the land-use history × taxa term are 0.60 and 0.92 for post-agricultural and non-agricultural woodlands, respectively.

[a] Random effect (intercept)

[b] Fixed effect (slope)

R code

```
hops <- read.csv(file.choose())  #input data file

hops$index <- c(1:216) #create index of unique numbers

for (i in 5:16){hops[,i] <- (hops[,i] - mean(hops[,i]))/sd(hops[,i])} #center variables

#requires the lme4 package and the car package for the Anova function
z1.1 <- glmer(numb.sum~                                  #structure of the final model
          (1|Spp)+History*HerbCov+Litter+
          (0+History|Spp)+
          (1|index)+(1|Site),
         control=glmerControl(optimizer="bobyqa"),       #control structure for model fitting
         family=poisson, data=hops)
summary(z1.1)          #produces fixed effect coefficient and model fit parameters
Anova(z1.1, type=2)  #conduct chi-square anova for fixed effects
rand(z1.1)             #evaluate significance of the random effects
coef(z1.1)             #extract random effect coefficients
```

APPENDIX S6

Results of the analysis of fern cover and soil compaction.

Table S6a. Model reduction process for the predictor variables that covaried with land-use history examining grasshopper assemblages at the Savannah River Site, South Carolina, USA. All models include Site, grasshopper species, and a unique number index (see *Methods*). Df is equal to the number of parameters estimated in the model. Models with 2 AIC units are bolded.

Model	df	AIC	ΔAIC	BIC	logLik	deviance
c7	**5**	**724.85**	**0**	**741.72**	**-357.42**	**714.85**
c3	**7**	**725.3**	**0.45**	**748.93**	**-355.65**	**711.3**
c5	**6**	**726.49**	**1.64**	**746.74**	**-357.25**	**714.49**
c4	**6**	**726.72**	**1.87**	**746.98**	**-357.36**	**714.72**
c1	8	727.21	2.36	754.21	-355.6	711.21
c2	7	728.37	3.52	752	-357.19	714.37
c6	6	729.51	4.66	749.76	-358.75	717.51
c8	5	730.91	6.06	747.78	-360.45	720.91

Description of models. Coding follows lme4.

c1: numb.sum ~ (1 | Spp) + FernCov + Compact + (0 + FernCov | Spp) + (0 + Compact | Spp) + (1 | index) + (1 | Site)
c2: numb.sum ~ (1 | Spp) + FernCov + Compact + (0 + FernCov | Spp) + (1 | index) + (1 | Site)
c3: numb.sum ~ (1 | Spp) + FernCov + Compact + (0 + Compact | Spp) + (1 | index) + (1 | Site)
c4: numb.sum ~ (1 | Spp) + FernCov + Compact + (1 | index) + (1 |Site)
c5: numb.sum ~ (1 | Spp) + FernCov + (0 + FernCov | Spp) + (1 | index) + (1 | Site)
c6: numb.sum ~ (1 | Spp) + Compact + (0 + Compact | Spp) + (1 | index) + (1 | Site)
c7: numb.sum ~ (1 | Spp) + FernCov + (1 | index) + (1|Site)
c8: numb.sum ~ (1 | Spp) + Compact + (1 | index) + (1 | Site)

Table 6b. Coefficients from the most comprehensive model with 2 AIC units of the best model (model c3 in Table S7a).

Taxon	**Intercept**	**FernCov**	**Compact**
Arphia	-1.44	0.44	-0.15
Conocephalus	-0.64	0.44	0.11
Melanoplus (long-wing)	0.50	0.44	-0.26
Melanoplus (short-wing)	0.48	0.44	-0.12
Orphulella	-0.57	0.44	-0.33
Schistocerca	0.84	0.44	0.14

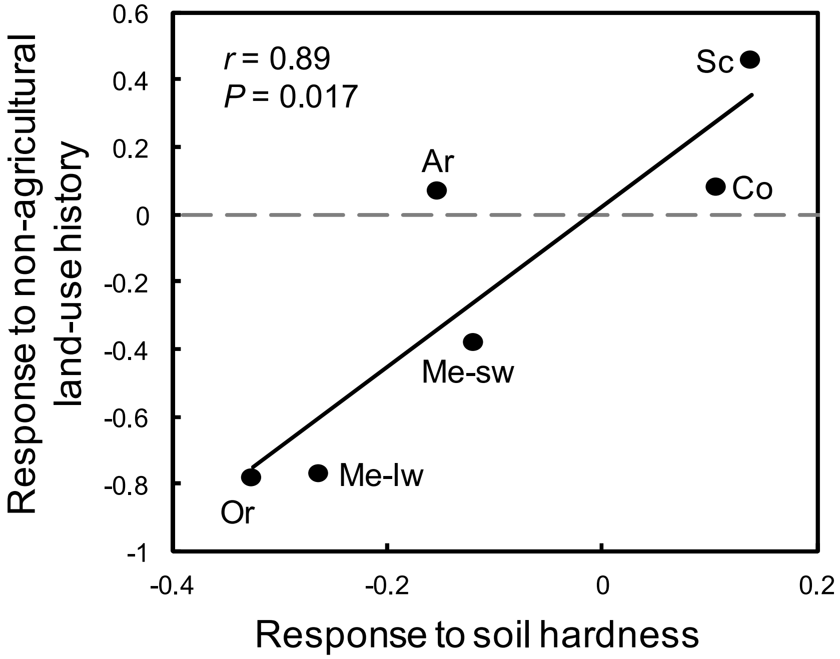


Figure S6. Relationship between grasshopper taxa responses to land-use history (Table S5a) and soil hardness from the ancillary analysis (Table S7c). Codes are the first two letters of the genus. lw = long-winged; sw = short-winged.

APPENDIX S7

Results of the supplemental Poisson regression analyses. Significant relationships are bolded. Models with a quasipoisson distribution to correct for overdispersion are indicated with a “Y”. R^2 is the proportion of deviance explained by the model (i.e., pseudo-R2).

	Post-Agriculture						
Taxon	**Intercept**	**Slope**	**Null Dev**	**Resid Dev**	**R^2**	**p**	**Quasi?**
Arphia	-1.77	-0.17	10.75	10.65	0.01	0.764	N
Conocephalus	-0.32	0.21	45.85	45.04	0.02	0.356	N
Melanoplus (lw)	**1.11**	**0.51**	**66.37**	**36.94**	**0.44**	**0.001**	Y
Melanoplus (sw)	1.10	0.17	54.34	52.20	0.04	0.400	Y
Orphulella	**-0.06**	**0.53**	**34.64**	**24.78**	**0.28**	**0.001**	N
Schistocerca	1.02	0.14	62.02	60.57	0.02	0.513	Y

	Non-Agriculture						
Taxon	**Intercept**	**Slope**	**Null Dev**	**Resid Dev**	**R^2**	**p**	**Quasi?**
Arphia	**-1.02**	**1.03**	**31.34**	**19.55**	**0.38**	**0.001**	N
Conocephalus	**-0.02**	**0.56**	**32.05**	**26.21**	**0.18**	**0.009**	N
Melanoplus (lw)	**0.35**	**0.83**	**55.86**	**31.31**	**0.44**	**0.001**	Y
Melanoplus (sw)	0.79	0.39	64.65	58.99	0.09	0.235	Y
Orphulella	**-1.11**	**1.01**	**18.52**	**8.62**	**0.53**	**0.001**	N
Schistocerca	**1.74**	**0.64**	**162.81**	**114.68**	**0.30**	**0.017**	Y

Chapter 2

Land-use legacies and present fire regimes interact to mediate herbivory by altering the neighboring plant community

Philip G. Hahn and John L. Orrock

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Abstract

Past and present human activities, such as historic agriculture and fire suppression, are widespread and can create depauperate plant communities. Although many studies show that herbivory on focal plants depends on the density of herbivores or the composition of the surrounding plant community, it is unclear whether anthropogenic changes to plant communities alter herbivory. We tested the hypothesis that human activities that alter the plant community lead to subsequent changes in herbivory. At 20 sites distributed across 80,300 hectares, we conducted a field experiment that manipulated insect herbivore access (full exclosures and pseudo-exclosures) to four focal plant species in longleaf pine woodlands with different land-use histories (post-agricultural sites or non-agricultural sites) and degrees of fire frequency (frequent and infrequent). Plant cover, particularly herbaceous cover, was lower in post-agricultural and fire suppressed woodlands. Density of the dominant insect herbivore at our site (grasshoppers) was positively related to plant cover. Herbivore access reduced biomass of the palatable forb

Solidago odora in frequently burned post-agricultural sites and in infrequently burned non-agricultural woodlands and increased mortality of another forb (*Pityopsis graminifolia*), but did not affect two other less palatable species (*Schizachyrium scoparium* and *Tephrosia virginiana*). Herbivory on *S. odora* exhibited a hump-shaped response to plant cover, with low herbivory at low and high levels of plant cover. Herbivore density had a weak negative effect on herbivory. These findings suggest that changes in plant cover related to past and present human activities can modify damage rates on focal *S. odora* plants by altering grasshopper foraging behavior rather than by altering local grasshopper density. The resulting changes in herbivory may have the potential to limit natural recovery or restoration efforts by reducing the establishment or performance of palatable plant species.

Introduction

Human activities affect a large fraction of plant communities across the globe, such as through the introduction of non-native species, habitat fragmentation, historical agriculture, or fire suppression (Wilcove et al. 1998). Herbivores also have important effects on plant population dynamics and community structure in many ecosystems (Crawley 1983). Importantly, the potential exists for human activities to alter the strength of herbivory because human disturbances can directly affect the structure and composition of the plant community, and plant neighbors often alter herbivore attack rates on focal plants (i.e., associational effects, Barbosa et al. 2009). However, although large parts of the biosphere are influenced by both humans and herbivores, it is unclear whether human activities create plant communities that subsequently alter herbivory rates.

Legacies of past agricultural land-use and present fire suppression are two human activities that significantly affect plant communities in ways that could foster changes in herbivory. Agricultural land-use legacies can have persistent effects on plant communities by altering soil conditions and limiting reestablishment of many perennial plant species, resulting in lower diversity and altered community composition for decades to centuries after abandonment (Flinn and Vellend 2005, Vellend et al. 2007). Fire suppression favors growth of woody vegetation relative to herbaceous vegetation and tends to reduce plant diversity (Briggs et al. 2005). Furthermore, many areas that are affected by historic agriculture (Ramankutty and Foley 1999) are in fire-dependent ecosystems that concurrently experience fire suppression (Briggs et al. 2005). Indeed, studies show that both agricultural legacies and fire suppression can interact to alter plant communities (Brudvig and Damschen 2011, Brudvig et al. 2014). Although agricultural legacies and fire suppression cause well-documented, large-scale changes to plant communities, such as changes in productivity or community composition (Briggs et al. 2005, Flinn and Vellend 2005), and these components of plant communities can also mediate herbivore effects (Baraza et al. 2006, Orrock et al. 2008, Caccia et al. 2009), as well as modify herbivore assemblages (Kim and Holt 2012), the degree to which these changes alter the nature of herbivory remains untested.

In this paper, we use a large-scale field study to evaluate how historic and contemporary human disturbances alter the nature of herbivory in longleaf pine (*Pinus palustris*) woodlands of the southeastern, USA. The longleaf pine ecosystem has a history of intensive agriculture followed more recently by large-scale abandonment (Frost et al. 2006). The legacies of historic agriculture tend to eliminate perennial herbaceous plants and reduce overall vegetation cover and diversity in regenerating longleaf woodlands (Kirkman et al. 2004, Brudvig et al. 2014). Fire suppression can exacerbate the effects of historic agriculture on plant communities by promoting woody plants over herbaceous vegetation (Glitzenstein et al. 2012), resulting in even greater changes to plant community composition (Brudvig and Damschen 2011, Brudvig et al. 2014).

Grasshoppers are common generalist herbivores in longleaf pine woodlands (Knight and Holt 2005, Evans et al. 2012) and grasshoppers are capable of exerting strong top-down effects on plant performance, composition, and diversity through selective grazing (Schmitz 2006, Evans et al. 2012, Cease et al. 2012). Furthermore, herbivory by grasshoppers may be altered by past land use or reduced fire frequecy because grasshopper density may be a function of the availability of suitable host plants (Joern and Laws 2013). Alternatively, grasshopper preferences may change as a function of the characteristics of the plant community, such as resource quality (Behmer et al. 2001). Thus, historic agricultural land use and fire suppression could lead to changes in herbivory via two primary mechanisms: 1) changes in total herbivore density or 2) changes in the availability of alternative plant food sources. If agricultural land-use history or fire suppression creates depauperate plant communities that support lower densities of herbivores and if attack rates on palatable focal plants depends on the density of herbivores, this would result in reduced herbivory in habitats that have experienced past agricultural land use or fire suppression (White and Whitham 2000, Rand 2003). On the other hand, herbivory on palatable focal plants could be greater in depauperate plant communities because palatable focal plants are more apparent to herbivores (Atsatt and O'dowd 1976) or because generalist herbivores in depauperate habitats may preferentially target palatable plants to meet particular nutritional needs (Behmer et al. 2001). These changes could lead to herbivores consistently excluding certain species from the plant community, serving to reinforce the maintenance of a particular community state (Parker and Root 1981, Orrock et al. 2010). In the context of the longleaf pine ecosystem, decreased herbivory on focal plants could promote the performance of plants often associated with typical longleaf understory communities. Alternatively, if land-use history and fire suppression increase herbivory on focal plants, herbivory may constrain the re-establishment of plant species of restoration and conservation interest. Increased herbivory rates in depauperate habitats could help to explain the lower cover of herbaceous plants or altered community composition generally found in these habitats (Kirkman et al. 2004, Brudvig and Damschen 2011, Brudvig et al. 2014), although this has not been tested.

Using experimental herbivore exclosures deployed across a landscape with sites varying in land-use history and fire frequency, we evaluated whether past agricultural land use and fire suppression might affect hebivory on focal plants by altering herbivore density or the cover of preferred herbaceous plants. First, we ask 1) Does agricultural land-use history or fire suppression alter the plant community or grasshopper density? We also asked: 2) Does habitat type (i.e., combinations of land-use history and fire suppression) alter the effect that herbivores have on plant biomass? We then examine the mechanisms whereby land-use history and fire suppression could lead to differences in herbivory by coupling data from our experimental herbivore exclosures with data on grasshopper density and the composition of the neighboring plant community. If herbivory is driven primarily by changes in grasshopper density, we predict herbivory on focal plants will be a function of grasshopper density. If herbivory is primarily affected by changes in herbivore foraging behavior caused by differences in the plants available for consumption, we expect that herbivory will be most strongly explained by the composition of the neighboring plant community, and will not depend upon grasshopper density.

Methods

We conducted this study at the Savannah River Site (SRS), an 80,300 hectare National Environmental Research Park in South Carolina, USA (Fig. 1A). We selected 20 upland longleaf pine (*Pinus palustris*) woodland sites, stratified across land-use histories (“post-agricultural" woodlands that have a history of cultivation or "non-agricultural" woodlands that have never been cultivated) and fire frequencies (frequent and infrequent), resulting in five replicates of four habitat types (Fig. 1A, see Fig. S1 in Supplementary material). The habitat types were on similar soils, interspersed across the landscape and all sites were separated by >500m. See Brudvig et al. (2014) for additional details on about plant diversity and soil conditions at these sites. To avoid edge effects that may arise at the boundary of habitats with different land-use histories or prescribed burn regimes (Knight and Holt 2005), all sites were buffered by >50m of similar habitat (i.e., same land-use and fire history). Tilling for agricultural use occurred at SRS between 1865 and 1950, peaking in the 1920's (Kilgo and Blake 2005). Historic farms were small and dispersed across the landscape, leaving many pockets of longleaf woodlands untilled (Kilgo and Blake 2005). Land-use histories were determined from aerial photographs taken in 1951, just prior to agricultural abandonment that followed the creation of SRS. Non-agricultural sites were open woodlands in 1951, whereas agricultural sites were cultivated fields. Although we could not verify land-use history prior to 1951, it is possible that some of the woodland sites were in agriculture prior to 1951. Historic fire return intervals in this system are estimated to be between 1-6 years (Frost et al. 2006). We determined the number of prescribed fires since 1991 from annual fire records and categorized fire frequencies as frequent (≥5 burns, mean number of fires: 6.3 ±0.79 SE) or infrequent (<5 burns, mean number of fires: 3.2 ±0.57 SE), as was previously determined to separate these sites based on metrics of the plant community (Brudvig et al. 2014). There was no difference in the total number of burns since 1991 between land-use histories (GLM, poisson distribution: $F_{1,16} = 0.01$, $p = 0.94$). To provide time for recolonization of grasshoppers following prescribed burns (Knight and Holt 2005), we did not use sites that had burned, or were near sites that burned (>50 m), during the year of the study.

Site characteristics

We measured vegetation cover in 12 1m^2 quadrats at each site between 07 and 14 July 2011. Quadrats were nested in the corners of three 5×5 m plots, separated by approximately 5m. In each quadrat, we recorded the percent cover of six functional groups – grasses, forbs, legumes, woody plants, vines (woody and herbaceous) and ferns – and averaged the values for each functional group at each site. Maximum vegetation height was recorded in two 1m^2 plots within 1m of the herbivore exclosures (see below) to quantify the potential for light competition. We also collected grasshoppers between 23 July and 06 August 2011 in the three 5×5 m plots. We used a 38 cm diameter sweep net to vigorously sweep through the vegetation for three 3-min periods with approximately15 min rest periods between sweeps, resulting in each plot being swept three times within a one hour period on a single day. All sweeping was conducted between 0900-1500 under sunny conditions on calm days. Sampling under consistent conditions is often used to control for environmental variability when grasshoppers communities are sampled on only one occasion at a site (Squitier and Capinera 2002, Joern 2005). Grasshoppers were stored in a freezer and counted later to get one measure of grasshopper density per site. We averaged the number of grasshopper collected in the three sites to get one number of grasshopper density (25 m^{-2}) per site. We also identified each individual to species, or genus in some cases, in order to determine grasshopper community composition at each site. A formal analysis of the grasshopper community will be presented in a separate manuscript. Voucher specimens have been deposited in the Insect Research Collection of the Department of Entomology, University of Wisconsin-Madison. In order to quantify potential differences in canopy closure related to land-use history and fire frequency, we calculated the mean proportion of canopy closure in photos taken with a hemispherical lens 1m above the ground in three plots per site following standard protocol (Hemiview Version 2.1, Dynamax Inc., Houston, TX, USA). Canopy closure (mean = 58.1%, SD = 8.9%) did not differ with land-use history ($F_{1,16} = 0.98$, $p = 0.34$), fire frequency ($F_{1,16} = 0.15$, $p = 0.70$), or the interaction ($F_{1,16} = 1.59$, $p = 0.23$).

Experimental design

We used four plant species for the field experiment: *Pityopsis graminifolia* (forb), *Schizachyrium scoparium* (grass), *Solidago odora* (forb), and *Tephrosia virginiana* (legume); nomenclature follows the USDA, NRCS (National Plant Data Team, Greensboro, NC, USA). Upland pine savanna is suitable habitat for all four of these species (Kilgo and Blake 2005) and these species were previously found to be indicators of non-agricultural, frequently burned longleaf pine habitat in our study sites at SRS and other locations in the southeast (Brudvig et al. 2014). Plants were selected to represent a variety of functional groups and a range of palatabilities based on the literature (e.g., Knight and Holt 2005, Hakes and Cronin 2012) and field observations; this variation in palatability was confirmed with ancillary feeding trials using *Melanoplus angustipennis* (see Appendix 1 in Supplementary materials), a common grasshopper species at our experimental sites that was most frequently observed feeding on our experimental plants (PGH *personal observation*). Appendix 2 contains additional information on the relative abundance of grasshopper species collected at our site. Rank-order preference to *M. angustipennis* was: *S. odora*, *P. graminifolia*, *T. virginiana* and *S. scoparium*. Seeds were collected from natural populations at the study site and were planted on 27-29 April 2011, germinated indoors (approximately 20°C), moved to a greenhouse after three weeks and then transplanted into 10.8 × 16.2 cm (height × diameter) plastic containers containing a 50:50 mix of potting soil and sand. Each container received one individual of each species, and each container was randomly assigned to a field site with different combinations of land-use histories and fire frequencies (n = 5 replicate sites per habitat type).

On 27-29 June 2011, we deployed the containers to the field and buried them so that the rim of the container was flush with the soil or leaf litter surface. By controlling for soil conditions across sites in our experimental containers (i.e., all plants were in a potting soil/sand mixture), we were able to evaluate herbivory without any potentially confounding effects of differences in plant tissue quality from growing in soils that may differ in nutrients between land-use histories or fire regimes (e.g., Verheyen et al. 1999, Fraterrigo et al. 2005). Containers received one of two experimental treatments: full exclosures or pseudo-exclosures. The full exclosure treatment consisted of an herbivore cage (0.125 m^2 × 90cm height screen cage) and the pseudo-exclosure treatments consisted of the same cages with ten approximately 10 cm diameter holes to permit grasshopper entrance. Exclosures were buried approximately 5 cm into the soil. This experimental design resulted in a split-plot experiment with habitat type (land-use, fire frequency, and the interaction) as the whole plot factors and the herbivore treatments as the split-plot factor.

These exclosures have been successfully deployed in another study focusing on grasshopper herbivory at our field site (Evans et al. 2012). Field observations suggest that exclosures and pseudo-exclosures worked as intended: grasshoppers were occasionally seen feeding on experimental plants inside the pseudo-exclosures but never on plants in the full exclosures (PGH *personal observation*), and very few leaves had evidence of herbivore damage inside the full exclosures. Both exclosure types excluded large vertebrate herbivores but the pseudo-exclosures admitted rodents. However, only a few species of herbivorous rodents occur at our field sites (Cothran et al. 1991) and only two experimental plants showed evidence of rodent grazing (PGH *personal observation*). To determine how the exclosures affected the light and temperature environments, we deployed light and temperature loggers (Onset Computer Corp., Bourne, MA, USA) inside the exclosures (i.e., exclosures and pseudo-exclosures) and adjacent open areas (n = 4 replicates). Data were collected in 10 min intervals between 0700-1900 hours on 01-03 August 2013 and averaged before analysis. Although both exclosures and pseudo-exclosures slightly reduced light relative to open areas (ln-transformed lux, $t_9 = -7.17$, $p < 0.001$ and $t_9 = -7.45$, $p < 0.001$, means ± 1 SE: exclosure = 10.42 ± 0.05, pseudo-exclosure = 10.40 ± 0.05, open = 10.97 ± 0.05), there was no difference in the light environment between the exclosures and pseudo-exclosures that we used for our experiment ($t_9 = 0.28$, $p = 0.78$). Temperature followed similar patterns (data not shown).

Prior to deployment to the field (25-26 June 2011) and after termination of the experiment (2 August 2011), we measured plant height, length of the longest leaf, and counted the number of fully emerged leaves on each plant. We counted the number of damaged (>5% of leaf tissue removed by chewing insects) and total leaves on each plant and harvested aboveground biomass at the end of the experiment. Aboveground biomass was weighed after drying for 48h at 60° C. The duration of this experiment is within the range of other experiments investigating the effects of herbivores on leaf damage and plant performance within a growing season (e.g., White and Whitham 2000; Palmer et al. 2003; Knight and Holt 2005).

Statistical analysis

Question 1: Does agricultural land-use history or fire suppression alter the plant community or grasshopper density?

We evaluated the effect land-use history and fire suppression on plant community composition (i.e., change the relative abundance of plant functional groups) by first conducting a principal component analysis on the correlation matrix of cover of the six plant functional groups. We performed a square root transformation and then centered the data prior to analysis. We then analyzed the two principal component axes using (separate) linear models (ANOVA) with land-use history (post-agriculture or remnant), fire frequency (high or low), and the interaction as predictor variables. We evaluated the effects of land-use history and fire suppression on grasshopper density using a linear model (ANOVA) to compare grasshopper density among the habitat types with land-use history, fire frequency, and the interaction as predictor variables. We used a second linear model to regress grasshopper density against the first principal component axis to aid in interpretation of the ANOVA.

Question 2: Does habitat type (i.e., combinations of land-use history and fire suppression) alter the effect that herbivores have on plant biomass?

We evaluated the effect of agricultural land-use history and fire suppression on herbivory on focal plants by comparing dried aboveground plant biomass between exclosure and pseudo-exclosure treatments across sites that varied in their land-use history and fire frequency. Separate models were conducted for each of the four plant species. These linear mixed models included plant biomass as the response variable, with land-use history, fire frequency, herbivore treatment (exclosure or pseudo-exclosure), and all interactions as fixed effects. Covariates that could affect final plant biomass (stem height measured prior to the experiment, canopy closure, and height of natural vegetation within 1m of the experimental plants, as well as their interactions with main effects) were included in the biomass models when the addition of the covariate reduced the AICc by >2 (Burnham and Anderson 2002). We evaluated each covariate (and interactions) separately to maintain statistical power (i.e., we did not have enough degrees of freedom to run models that included all potential covariates and interaction terms), while still allowing us to detect higher-order interactions among covariates and main effects. When significant herbivore effects (i.e., factor × herbivore treatment) were detected, linear contrasts were conducted to compare the exclosure and pseudo-exclosure herbivore treatments within habitat types. To ensure that there were no differences in biomass among the habitat types, we compared plant biomass within the exclosure treatments among the four habitat types. We conducted similar analyses comparing herbivore damage (number of leaves damaged) on plants exposed to herbivores (i.e., pseudo-exclosure treatment). We also evaluated whether herbivore damage was linked to plant biomass using linear regressions with the proportion of leaves damaged as the predictor variable and plant biomass on surviving plants in the pseudo-exclosure treatments as the response variable. We focus on the biomass results, rather than herbivore damage, because it is more closely linked to fitness than is herbivore damage *per se* (Zangerl et al. 2002) and is often used as a proxy for fitness (e.g., Hakes and Cronin 2012).

Evaluating the mechanisms whereby land-use history and fire suppression could alter herbivory

We evaluated the effects of herbivore density and plant community composition on herbivory rates among sites that vary in land-use history and fire frequency using a linear model with the difference in biomass between the full exclosure and pseudo-exclosure as the response variable. Predictor variables included grasshopper density and the first two principal components from the vegetation analysis (see Question 1 above), as well as quadratic terms for all variables to account for potential non-linear trends. We used a stepwise AIC model selection procedure for model reduction. These analyses were conducted only for plant species significantly affected by herbivores (see Question 2 above). All linear models and multivariate analyses were conducted in R (R version 3.0.1) and linear mixed-models were conducted in SAS (SAS 9.3, Cary, NC, USA). We examined residual plots to ensure that all models adequately fit the data. We conducted analyses similar to ones described above using fire frequency as a continuous variable. These results were not qualitatively different, so we present the results that treat fire as a categorical variable.

Results

Question 1: Does agricultural land-use history or fire suppression alter the plant community or grasshopper density?

The first principal component axis explained 46.8% of the original variance in the cover of the square root-transformed matrix of the six plant functional groups and was a general index of plant cover, except for vines, with forb, grass, and legume cover having the highest loadings (Table 1). This axis differed with land-use history and fire frequency, but not the interaction (Table 1). The second principal component axis explained an additional 19.4% of the original variance and was a contrast between vine cover and woody/fern cover (Table 1). This axis differed between land-use history, but not fire frequency, although the interaction was marginally significant (Table 1).

Grasshopper density did not differ with land-use history (ANOVA: $F_{1,16} = 1.23$, $p = 0.28$), fire frequency (ANOVA: $F_{1,16} = 1.69$, $p = 0.21$), or the interaction (ANOVA: $F_{1,16} = 0.26$, $p = 0.62$). However, grasshopper density increased with the first principal component (i.e., plant cover) (linear regression: $F_{1,18} = 10.03$, $p = 0.005$, $R^2 = 0.36$, Fig. 1C).

Question 2: Does habitat type (i.e., combinations of land-use history and fire suppression) alter the effect that herbivores have on plant biomass?

Details on pre-deployment plant sizes are provided in Appendix 3. Several of the forty initial plants per species died from unknown causes during the experiment: *Pityopsis graminifolia*, n = 11; *Schizachyrium scoparium*, n = 2; *Solidago odora*, n = 1; *Tephrosia* *virginiana*, n = 2. Dead plants were treated as zeros in the biomass analyses, although the results were similar when they were deleted.

Solidago odora biomass was affected by the interaction between land-use history, fire frequency and exclosure treatment, after adjusting for initial plant height (ANCOVA: $F_{1,15}$ = 6.05, p = 0.03, Table 2, Fig. 2C). Including initial plant height and the initial plant height-by-land-use history interaction term improved the model fit (AICc = 88.0 with covariates; AICc = 93.2 without covariates), but canopy closure, height of vegetation within 1m of the exclosures and other interaction terms between initial plant height and main effects did not. Biomass in exclosures was approximately 1.5 times greater than in pseudo-exclosure treatments in high fire post-agricultural sites (linear contrast: mean difference = 0.85 g, SE = 0.4, t = 2.13, p = 0.05) and nearly 2 times greater in low fire remnant woodlands (linear contrast: mean difference = 1.01 g, SE = 0.3, t = 2.97, p = 0.01). We found no differences in *S. odora* biomass across the four habitat types within the exclosure treatment (simple effects of land-use history, fire frequency, and the interaction, given the "exclosure" level of the herbivory treatment: all $p > 0.12$). The proportion of leaves damaged by chewing invertebrates on *S. odora* varied among the land-use history and fire frequency sites (Fig. S2) and was associated with lower final biomass of plants in pseudo-exclosures (linear regression: $F_{1,17}$ = 7.90, p = 0.01, Fig. S3).

Biomass of the other three plant species were not different between the herbivore exclusion treatments, land-use histories, or fire frequencies (Table 2), although several of the species did have lower mean biomass in the pseudo-exclosures than in the exclosures (Fig. 2A,B,D). Three dead *P. graminfolia* had evidence of damage by leaf chewing insects (all in pseudo-exclosures), and mortality for *P. graminifolia* was greater for plants exposed to herbivores (GLMM, binomial response: $F_{1,19}$ = 5.72, p = 0.027; proportion mortality: 0.44±0.12

SE in pseudo-exclosures and 0.09±0.06 in exclosures), but did not differ with land-use history, fire frequency or any interactions (all $p > 0.29$). The proportion of leaves damaged on *P. graminfolia* was negatively related to biomass (linear regression: $F_{1,10} = 20.32$, $p = 0.001$, Fig. S3) of surviving plants damaged by herbivores in pseudo-exclosures. Biomass of *S. scoparium* (linear regression: $F_{1,14} = 0.23$, $p = 0.64$, Figure S3) and *T. virginiana* (linear regression: $F_{1,12} = 0.49$, $p = 0.50$, Fig. S3) was not related to the proportion of leaves damaged.

Evaluating the mechanisms whereby land-use history and fire suppression could alter herbivory

Solidago odora was the only species that had reduced biomass when exposed to herbivores (Fig. 2). The stepwise model selection procedure selected a model (multiple linear regression: $F_{3,15} = 4.90$, $p = 0.01$, $R^2 = 0.48$, Fig. 3) that included the first principal component from the vegetation analysis (slope = 0.22, t = 1.55, p = 0.14), the quadratic term of this principal component (slope = -0.18, t = -3.32, p = 0.004), and grasshopper density (slope = -0.09, t = -2.04, p = 0.058). Because we found a relationship between the first principal component from the vegetation analysis and grasshopper density (Fig. 1C), we tested for collinearity in this model. The variance inflation factors were 1.96, 1.30, and 1.59 respectively, suggesting that collinearity was not problematic. We also conducted the same analysis, but included the density of the three dominant grasshopper species, or grasshopper community composition, instead of overall grasshopper density, to test for the effects of individual grasshopper species or overall community composition. Overall, these models were similar, but worse than when we used overall grasshopper density (Appendix 2).

Discussion

The results from our large-scale study show that agricultural legacies and fire regimes can interact to affect herbivory and suggest that these effects arise because changes in the plant community affect herbivore foraging patterns, rather than through changes in herbivore density. Historic agriculture and reduced fire frequency were associated with altered plant communities, and herbivory exhibited a hump-shaped relationship to plant cover (mainly herbaceous cover), where the difference in plant biomass between the herbivore exclosures increased at low levels of plant cover but leveled off and decreased at higher levels of plant cover, suggesting a saturating effect of neighboring plant cover on herbivory of our focal plants. We also found a weak, negative relationship between the difference in plant biomass between the herbivore exclosures and grasshopper density, suggesting lower per-plant herbivory rates at higher grasshopper density, further supporting the saturating effect of plant cover. Furthermore, these effects were consistent with herbivore feeding preferences, as we found strong herbivore effects on the biomass of one palatable forb species (*Solidago odora*), weak herbivore effects on mortality and biomass of another forb (*Pityopsis graminifolia*), but no effect of herbivores on less preferred plants (*Schizachyrium scoparium*, grass; and *Tephrosia virginiana*, legume). Across a multi-site landscape, our results demonstrate how past and present human disturbance can alter species interactions, which have previously been hypothesized to be potentially important for regulating plant species occurrences in post-agricultural landscapes (Flinn and Vellend 2005, Cramer et al. 2008). Below we discuss how our results may generate the patterns in herbivory we observed in anthropogenically modified habitats by applying a novel perspective to three themes in plant-herbivore interactions: 1) that neighboring plants matter in affecting herbivory (Atsatt and O'dowd 1976, Palmer et al. 2003, Barbosa et al. 2009), 2) that herbivore density is a poor predictor of herbivory in multi-species plant communities (Cronin et al. 2010), and 3) herbivore preference can affect plant-herbivore interactions (Schmitz 2006, Allan and

Crawley 2011).

Neighboring plants matter for affecting herbivory

Herbivore effects on plant communities can depend on herbivore density, foraging behavior, or composition of the herbivore community (Crawley 1983). In our experiment, high herbaceous cover might be satiating herbivores, or making focal plants less apparent, resulting in lower per-plant attack rates on focal plants, more often in frequently burned remnant woodlands. This result is similar to theoretical models (Hambäck et al. 2014) and other field studies that have examined herbivory rates in plots with varying amounts of herbaceous plant cover. For example, Hakes and Cronin (2012) found greater herbivore damage on transplanted *Solidago altissima* in late successional fields, where encroachment of woody plants reduced herbaceous cover, compared to early successional fields, which had greater herbaceous cover. One potential explanation is that the herbaceous cover present in the old fields reduced per-plant herbivory to the focal plants (Hakes and Cronin 2012). Similarly, Underwood and Halpern (2012) found a hump-shaped relationship between neighboring plant density and herbivory rates on focal *Solanum carolinense*, likely due to herbivore satiation at high plant density. In infrequently burned non-agricultural woodlands and frequently burned post-agricultural woodlands, we found that herbivores grazed more intensively on the palatable forb *S. odora* likely because herbaceous plants supply superior nutrition to grasshoppers over the woody foliage (Joern 1983, Behmer et al. 2001) that is common at these sites (Fig. 1B). In other words, herbivores may persist on suboptimal resources, and preferentially consume herbaceous plants when available. Collectively, these results highlight one way in which human activities that alter the structure of the plant community can modify plant-herbivore interactions.

Herbivore density is a poor predictor of herbivory

Although palatable plants might alter herbivory by increasing herbivore density in some systems (e.g., White and Whitham 2000, Rand 2003), we found a weak negative effect of grasshopper density on herbivory. One explanation for this is that grasshoppers may not be able to build up to levels capable of reducing plant cover in the years following fires, relative to post-fire regeneration rates of plant cover (Knight and Holt 2005, Kim and Holt 2012). Thus, it could be expected that grasshoppers would not be able to consume all the available plant material, particularity at sites with high pre-fire plant cover, resulting in a saturating effect of plant cover on overall herbivory rates. Furthermore, this effect should be stronger in non-agricultural sites with high pre-fire vegetation cover, where we documented lower reductions in plant biomass from herbivory. The exception in our study might be at low to medium densities of herbivore densities and plant cover, as we found greater levels of herbivory at low grasshopper densities (Fig. 3B) and herbivory increased with increases at low levels of plant cover (Fig. 3A). In our post-agricultural sites with low to medium levels of plant cover, herbivory may act synergistically with reduced fire frequency by decreasing plant cover and potentially establishment in the short term. However, in the long term, the effect that herbivores have on plant biomass or establishment should diminish as a deepening litter layer (Hiers et al. 2007) and closing canopy (Glitzenstein et al. 2012) cause concurrent reductions in plant cover and establishment, as well as grasshopper density (Fig. 1C).

Changes to grasshopper community composition related to land-use history and fire frequency (Joern 2005) might also contribute to differences in herbivory rates. However, we found no effect, or weak negative effects, of the densities of three dominant species of grasshopper or grasshopper community composition (Appendix 2), suggesting that herbivore community composition probably contributes little to the herbivory rates we documented.

Orthopterans comprised 40.7% of all non-Aranae arthropods collected in our sweep net samples and are the dominant insect herbivore in our system (Knight and Holt 2005, Evans et al. 2012), so the majority of leaf chewing damage was likely from orthoperans. Other insects, such as chrysomelid beetles or other insects associated with *Solidago* species (Root and Cappuccino 1992), likely contributed only a minor amount of chewing damage to our plants and were never observed on our experimental plants (PGH *personal observation*). Although our data point to the important role of herbivore choice in generating different patterns in herbivory, future studies that directly manipulate herbivore communities within human modified landscapes will be necessary to understand whether herbivore choice is changing solely due to vegetative cover, or whether interactions among herbivores and other organisms (i.e., competition or predation) are also important for generating the differential patterns of herbivory we observed.

Herbivore preference can affect plant-herbivore interactions

Feeding preferences of the common grasshopper species at our study site might help explain why the effect of herbivores differed among the four focal species in this study. The grasshoppers *Melanoplus angustipennis*, *M.* sp. (*scudderi* and *puer* group) (both subfamily Melanoplinae) and *Schistocerca* species (subfamily Cyrtacanthacridinae) are abundant at our site and all are classified as mixed feeders that will consume grasses, forbs, and some woody foliage (Joern 1983). In six ancillary feeding trials involving twelve plant species, *M. angustipennis* consumed *S. odora* (Asteraceae) in 50% of the trials, *P. graminifolia* (Asteraceae) in 33%, *T. virginiana* (Fabaceae) in 17%, and *S. scoparium* (Poaceae) in none of the feeding trials (Appendix 1), suggesting a strong preference for forb species used in our experiment. In our field experiment, the biomass of the two most palatable species decreased with increasing herbivore damage (Fig. S3), suggesting that palatable plants receive damage levels that are high enough to reduce plant biomass. Finally, it is notable that *M. angustipennis* consumed several species of woody plants and vines, albeit infrequently, in our feedings trials (Appendix 1), suggesting that grasshoppers may be able to persist in habitats dominated by woody plants and vines, but preferentially feed on herbaceous plants when they are available. This effect could lead to herbivores maintaining the degraded states created by human disturbances if herbivores are having disproportionate effects on plant performance of rare, palatable plants over less preferred, dominant plants.

Future directions for studying species interactions in post-agricultural systems

Because past agricultural use and fire suppression affect a significant fraction of the terrestrial biosphere (Briggs et al. 2005, Flinn and Vellend 2005), our results suggest that plant-herbivore interactions may be modified in many ecosystems. Although our study cannot separate the effects of disturbance from plant community composition *per se*, our results are informative because disturbance and plant community composition are inextricably linked in contemporary landscapes (Flinn and Vellend 2005, Cramer et al. 2008, Brudvig and Damschen 2011). Furthermore, both land-use history and fire can alter other factors that could affect plant-herbivore interactions, such as soil nutrients (Verheyen et al. 1999, Fraterrigo et al. 2005), plant tissue quality (Fraterrigo et al. 2006, Kim and Holt 2012), and herbivore community composition (Kim and Holt 2012, Joern 2005). We avoided any potential effects of soil nutrient differences among land-use histories and fire frequency sites by using standard soil in all experimental plots in order to focus explicitly on differences in herbivory. These topics likely provide profitable avenues for future investigation.

Our results document a link between human modified systems and herbivory, driven in part by altered plant communities related to historical agriculture and contemporary fire regimes.

Importantly, shifts in herbivory we documented were only found for one of the four study species, suggesting that the effect of human disturbance on herbivory is likely to be idiosyncratic. Furthermore, our results suggest a threshold in the relationship between herbivory and plant cover, where herbivore density may be an important driver of herbivory rates at low to medium plant cover, but at higher levels of plant cover herbivores become satiated resulting in lower per-plant herbivory rates on palatable plants. Although our results highlight a link between human activities and altered herbivory rates, invertebrate herbivory can limit plant establishment into new habitats (Parker and Root 1981, Branson and Sword 2009, Hahn and Dornbush 2012) and herbivory may be an important factor limiting plant establishment recently documented in post-agricultural systems (Baeten et al. 2009). Thus, while our results provide a mechanism that may generate differential herbivory on palatable herbaceous plants in post-agricultural habitats (i.e., altered herbivory rates), future studies should evaluate whether these differences in herbivory can limit plant establishment and contribute to the maintenance of degraded plant communities in post-agricultural habitats. In particular, our results suggest that herbivory would be most likely to limit plant establishment in regenerating systems or during ecological restoration where existing plant cover is low. In a broader sense, since many ecological investigations either avoid or ignore historic land-use (Martin et al. 2012), unexplained variation in previous studies may be attributed to legacy effects on ecological interactions.

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Data accessibility

Data available from the Dryad Digital Repository: doi:10.5061/dryad.142m0

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Table 1. Loadings for the first three principal components from the analysis on the plant functional group matrix. % Variance indicates the percent of variance in the original matrix explained by that principal component. Land-use, Fire, and Interaction rows show F-values from univariate ANOVAs.

Variable	PC1	PC2	PC3
Grass	0.48	-0.33	0.07
Forb	0.54	-0.08	-0.10
Legume	0.47	-0.38	0.17
Woody	0.26	0.49	-0.70
Vine	-0.16	-0.60	-0.68
Fern	0.41	0.38	0.03
% Variance	46.8	19.4	15.7
Land-use	4.80*	5.18*	0.00
Fire	6.61*	0.02	0.75
Interaction	1.16	3.73†	1.59

†p<0.1, *p<0.05.

Table 2. ANOVA table for linear mixed models of plant biomass after the herbivory experiment.

	Pityopsis graminifolia		*Schizachyrium scoparium*		*Solidago odora*		*Tephrosia virginiana*	
Effect	F	p	F	p	F	p	F	p
Land use history	0.29	0.60	0.32	0.58	6.41	0.02	0.29	0.60
Fire frequency	0.14	0.72	0.40	0.54	0.64	0.43	0.13	0.73
Land use*Fire	0.32	0.58	1.96	0.18	4.14	0.06	0.10	0.76
Herbivores	0.91	0.35	2.80	0.12	7.74	0.02	1.25	0.28
Herb*Land use	0.51	0.49	1.52	0.24	0.38	0.55	1.29	0.27
Herb*Fire	0.27	0.61	0.68	0.42	0.02	0.89	0.50	0.49
Herb*Land use*Fire	0.09	0.77	0.10	0.75	6.05	0.03	0.77	0.39
Height (cm)	5.63	0.03	42.70	<.001	6.18	0.03	-	-
Height*Land use	-	-	-	-	4.48	0.05	-	-

Figure 1. (A) Map of the study sites within the Savannah River Site, SC. (B) Principal component ordination of sites based on plant functional groups. Axis 1 explained 46.8% of the variability in the cover of six plant functional groups and represents an index of plant cover, particularly forb, grass, and legume cover. Axis 1 differed between land use histories ($p = 0.04$) and fire frequency ($p = 0.02$), but the interaction was not significant ($p = 0.30$). (C) Grasshopper density response to herbaceous cover. The trend line and R^2 are for all treatments pooled. Post-Ag = post-agricultural sites, Non-Ag = sites with no history of agriculture, Low = low fire frequency (<5 burns since 1991), High = high fire frequency (≥5 burns since 1991).

Figure 2. Biomass (g) at the end of the five week field experiment, after adjusting for initial plant height. Plants were protected from herbivores with mesh screen (Exclosure) or mesh screen with holes to allow invertebrate herbivores to enter (Pseudo-exclosure). Post-Ag = post-agricultural sites, Non-Ag = sites with no history of agriculture, Low = low fire frequency (<5 burns since 1991), High = high fire frequency (≥5 burns since 1991). Significant ($p < 0.05$) herbivore effects (i.e. factor*exclosure interactions) are listed on each panel. Asterisks (*) indicate significant ($p < 0.05$) difference between exclosure and pseudo-exclosure treatments. Bars are ±1 standard error. Note the value changes on the y-axis among the different species.

Figure 3. Effect of (A) the first principal component from the analysis of the plant community and its quadratic term and (B) grasshopper density on the (residual) difference in biomass between the full exclosure minus the pseudo-exclosure for *Solidago odora*. The full model included the principal component, the quadratic term of the principal component, and grasshopper density ($F = 4.90$, $p = 0.01$, $R^2 = 0.48$). The graphs show each variable regressed against the residuals from a model containing the other term.

Figure 1:

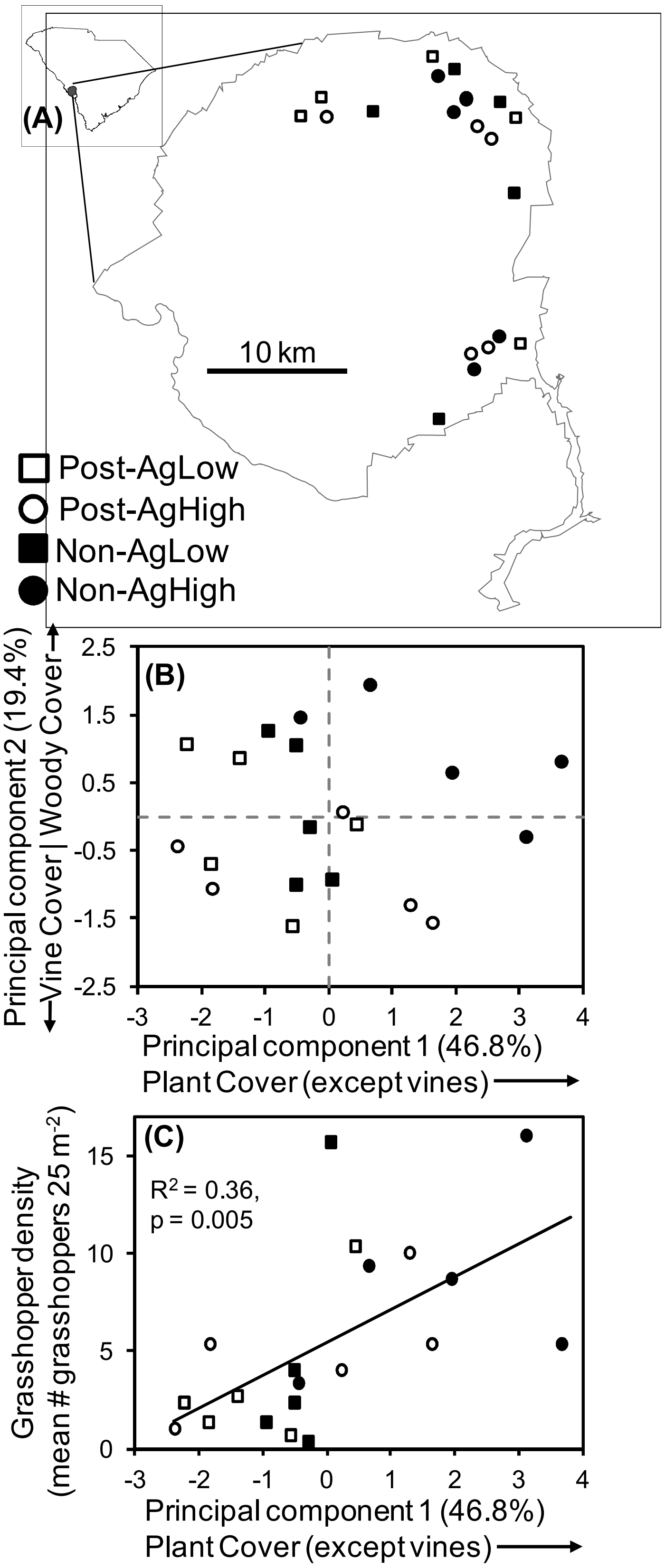

(A)
10 km
□ Post-AgLow
○ Post-AgHigh
■ Non-AgLow
● Non-AgHigh
(B)
Principal component 2 (19.4%)
←Vine Cover | Woody Cover→
2.5
1.5
0.5
-0.5
-1.5
-2.5
-3
-2
-1
0
1
2
3
4
Principal component 1 (46.8%)
Plant Cover (except vines)→
(C)
Grasshopper density
(mean # grasshoppers 25 m⁻²)
R² = 0.36,
p = 0.005
15
10
5
0
-3
-2
-1
0
1
2
3
4
Principal component 1 (46.8%)
Plant Cover (except vines)→

Figure 2:

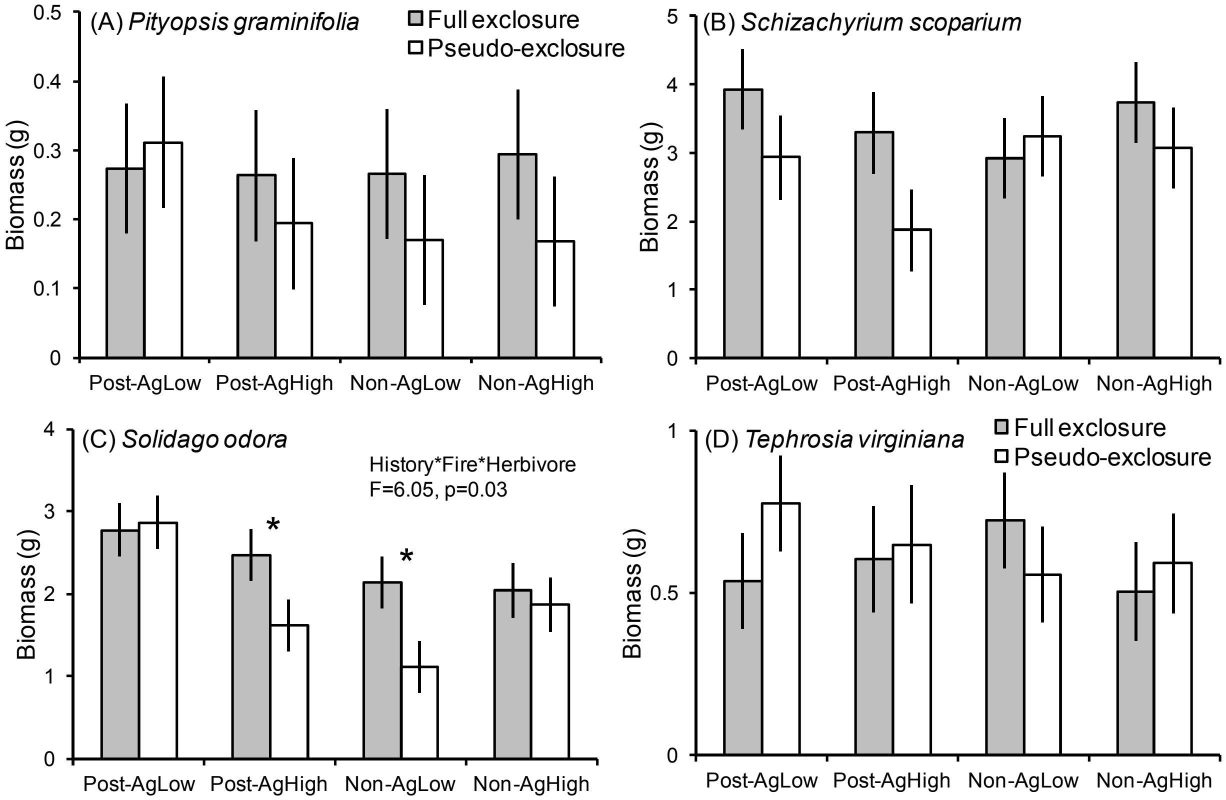
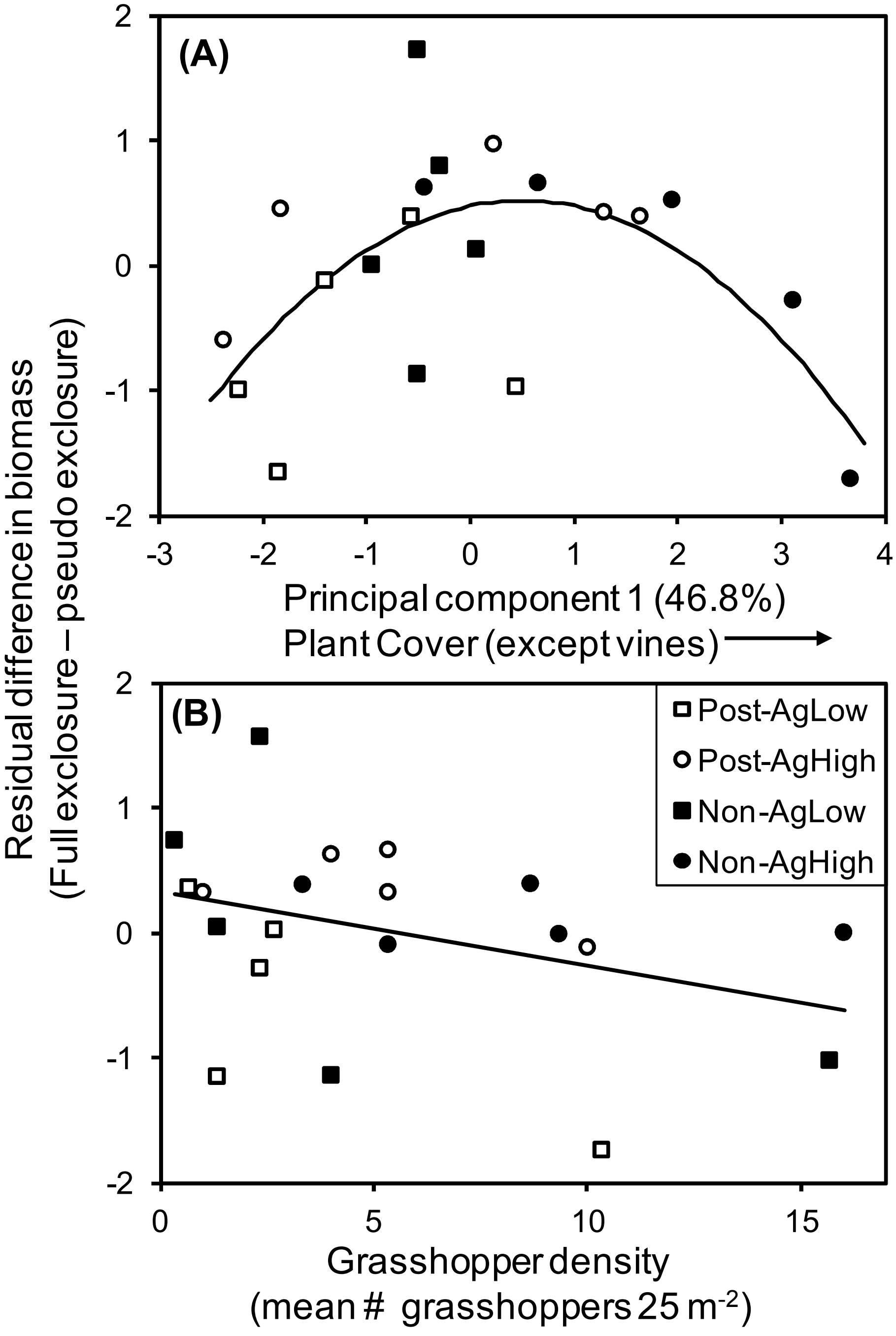

(A) *Pityopsis graminifolia*
Full exclosure
Pseudo-exclosure
Biomass (g)
0
0.1
0.2
0.3
0.4
0.5
Post-AgLow
Post-AgHigh
Non-AgLow
Non-AgHigh
(B) *Schizachyrium scoparium*
Biomass (g)
0
1
2
3
4
5
Post-AgLow
Post-AgHigh
Non-AgLow
Non-AgHigh
(C) *Solidago odora*
History*Fire*Herbivore
F=6.05, p=0.03
*
*
Biomass (g)
0
1
2
3
4
Post-AgLow
Post-AgHigh
Non-AgLow
Non-AgHigh
(D) *Tephrosia virginiana*
Full exclosure
Pseudo-exclosure
Biomass (g)
0
0.5
1
Post-AgLow
Post-AgHigh
Non-AgLow
Non-AgHigh

Figure 3:


(A)
(B)
Residual difference in biomass
(Full exclosure – pseudo exclosure)
Principal component 1 (46.8%)
Plant Cover (except vines)
Grasshopper density
(mean # grasshoppers 25 m-2)
Post-AgLow
Post-AgHigh
Non-AgLow
Non-AgHigh
2
1
0
-1
-2
-3
3
4
5
10
15

Appendix 1. Description of the ancillary feeding trials.

We collected juvenile grasshoppers (*Melanoplus angustipennis*) from a field near the Savannah River Ecology Laboratory greenhouse at the Savanna River Site (SRS). Grasshoppers were kept individually in 1 gallon cages and acclimated for >3 days before the feeding trials began, during which time they were fed lettuce and greenhouse-grown grass (*Sorgastrum nutans*).

For these feeding trials, we selected twelve species of plants from various functional groups that are common at our experimental sites, including the four plants species used in our experiment. We collected plant material from one site at the SRS. We clipped stems of the twelve test species (one plant per species) containing the same number of similarly sized leaves, placed the stems in water picks, and immediately used them in the feeding trials. Water picks were used to avoid desiccation of the plants. One individual of each of the twelve test plant species was randomly placed in an oval within a ~60x45x45cm cage, which was filled with ~5cm of potting soil. Therefore, all twelve species were available to the grasshopper in a cafeteria-style feeding experiment. Grasshoppers were allowed to feed for 48h, after which we recorded whether each plant was consumed. We considered plants with roughly 0.25cm^2 or more of tissue removed as consumed. We ran six trials total. Each trial used a different grasshopper and different plants. Trials were conducted in July, 2011 in the SREL temperature-controlled greenhouse (~30 °C) on clear days.

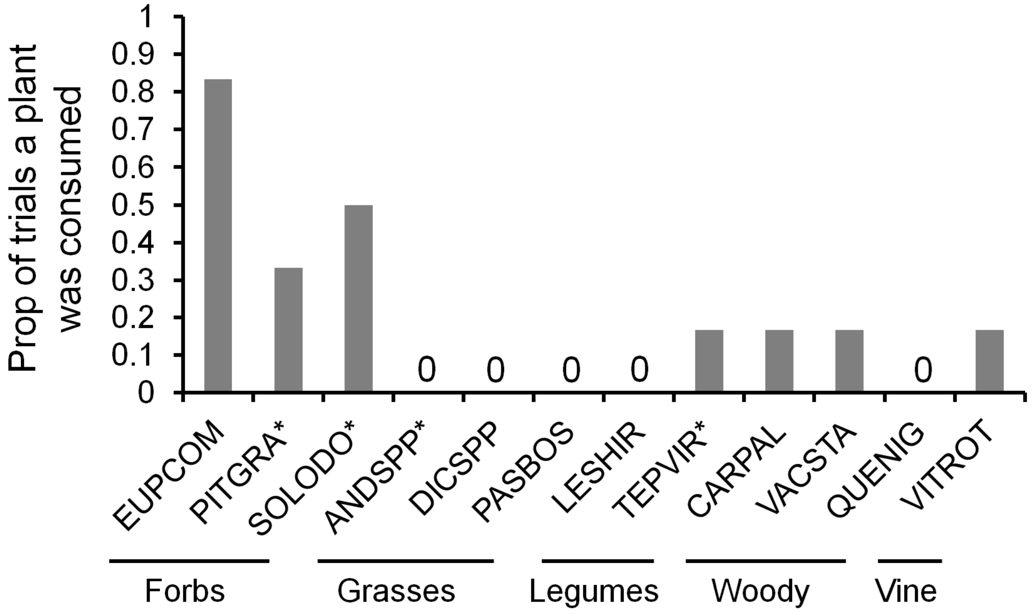


Figure A1. Proportion of times a plant was consumed during cafeteria-style feeding trials conducted in the greenhouse (n = 6 trials) using the grasshopper *Melanoplus angustipennis*. EUPCOM = *Eupatorium compositifolium*, PITGRA = *Pityopsis graminifolia*, SOLODO = *Solidago odora*, ANDSPP = *Andropogon* sp., DICSPP = *Dichanthelium* sp., PASBOS = *Paspalum boscianum*, LESHIR = *Lespedeza hirta*, TEPVIR = *Tephrosia virginana*, CARPAL = *Carya pallida*, QUENIG = *Quercus nigra*, VITROT = *Vitis rotundifolia*. Asterisk (*) indicates that the plant species was used in the field experiment.

Appendix 2. Description of the grasshopper community and relationships between grasshopper community and herbivory. Three grasshopper species (or morphospecies) accounted for greater than 50% of the total grasshopper individuals collected in our sweep net samples. *Schistocerca* nymphs made up 18.2% of all the grasshoppers (Orders Acrididae and Tettigoniidae) collected in the sweep net samples. *Melanoplus angustipennis* made up 15.7% and *M. scudderi* and *puer* group (pooled) made up 17.0% of the collection. These three (morpho)species are all classified as mixed-feeders, which will consume grasses and forbs (Joern 1983). *Melanoplus angustipennis* was seen feeding on our experimental plants on several occasions (PGH *personal observation*). Other grasshoppers collected at our sites include *Arphia xanthoptera*, *Conocephalus* sp., *Orphulella pelidna*, *Schistocerca alutacea*, *Scudderia* sp. and other katydids in the subfamily Phaneropterinae.

We conducted analyses that examined the density of the three most common grasshopper (morpho)species and community composition to determine if individual grasshopper species or the composition of the entire community could predict herbivory better than cumulative grasshopper density (described in the main text). We followed the same model selection procedure used in the main text (see Methods). The global models included the first principal component from the vegetation analysis, the quadratic term of this first principal component, the density of the grasshopper species, and the quadratic term of the grasshopper species' density. The community composition included the two NMDS axes instead of the grasshopper density terms.

We used two axes from a non-metric multidimensional scaling (NMDS) to describe the composition of the grasshopper community. We conducted the NMDS in the vegan package in

R (Oksanen et al., 2012), using a Bray-Curtis distance matrix and a Wisconsin double standardization. The two-dimension solution had a final STRESS of 0.14.

Table A2a. Grasshopper density (*Schistocerca* nymphs) effects on the proportion of *S. odora* leaves damaged.

	Global model	Reduced model
Effect	β	β
Intercept	1.12†	0.86**
PC1	0.17	-
$PC1^2$	-0.16*	-0.16†
PC2	-0.09	-
$PC2^{2}$	0.09	-
Grasshopper density	-0.07	-
Grasshopper $density^2$	0.00	-

†$p < 0.1$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

Table A2b. Grasshopper density (*Melanoplus angustipennis*) effects on the proportion of *S. odora* leaves damaged.

Effect	Global model β	Reduced model β
Intercept	1.41*	1.24**
PC1	0.2	-
$PC1^2$	-0.16*	-0.15*
PC2	-0.15	-
$PC2^{2}$	0.07	-
Grasshopper density	-0.35	-0.32†
Grasshopper $density^2$	0.03	0.03

†$p < 0.1$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

Table A2c. Grasshopper density (*Melanoplus scudderi*) effects on the proportion of *S. odora* leaves damaged.

Effect	Global model β	Reduced model β
Intercept	1.02*	1.14**
PC1	0.07	-
$PC1^2$	-0.17*	-0.17**
PC2	-0.14	-
$PC2^{2}$	0.11	-
Grasshopper density	-0.03	-0.06
Grasshopper $density^2$	-0.01	-0.00

†$p < 0.1$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

Table A2d. Grasshopper community composition, measured as the two axes of a non-metric multidimensional scaling (nmds) conducted on a matrix of the nine most common grasshopper (morpho) species, effects on the proportion of *S. odora* leaves damaged.

	Global model	Reduced model
Effect	β	β
Intercept	0.77	0.87***
PC1	0.01	-
$PC1^2$	-0.16†	-0.16**
PC2	0.04	-
PC2 2	0.04	-
nmds1	0.29	-
$nmds1^2$	0.05	-
nmds2	0.47	0.50
$nmds2^2$	0.13	-

†$p < 0.1$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

Appendix 3. Summary statistics and analysis for pretreatment measures of plant size by habitat type.

Table A3a. Summary statistics (mean ± SD) for pretreatment measures of plant size by habitat type (n = 5 for each group). PITGRA = *Pityopsis graminifolia*, SCHSCO = *Schizachyrium scoparium*, SOLODO = *Solidago odora*, and TEPVIR = *Tephrosia virginiana.*

Species	History	Fire	Herbivore Treatment	Stem Height	Numb. Leaves	Leaf Length
PITGRA	Agricu	Low	Caged	2.18 ± 3.3	7.20 ± 3.2	6.02 ± 1.0
PITGRA	Agricu	Low	Open	1.48 ± 0.6	6.80 ± 2.5	6.36 ± 1.8
PITGRA	Agricu	High	Caged	1.18 ± 0.4	5.60 ± 1.5	6.46 ± 1.3
PITGRA	Agricu	High	Open	1.04 ± 0.3	6.40 ± 0.9	6.10 ± 1.5
PITGRA	Forest	Low	Caged	1.68 ± 1.2	6.80 ± 2.6	5.78 ± 2.4
PITGRA	Forest	Low	Open	1.78 ± 1.1	8.00 ± 1.7	7.40 ± 1.0
PITGRA	Forest	High	Caged	1.28 ± 0.6	7.20 ± 1.9	6.76 ± 0.8
PITGRA	Forest	High	Open	1.76 ± 1.4	6.60 ± 0.9	6.96 ± 0.8
SCHSCO	Agricu	Low	Caged	6.86 ± 3.1	5.40 ± 0.5	16.06 ± 3.5
SCHSCO	Agricu	Low	Open	3.46 ± 1.0	3.60 ± 0.5	9.40 ± 3.6
SCHSCO	Agricu	High	Caged	4.24 ± 1.1	4.80 ± 0.4	11.84 ± 3.6
SCHSCO	Agricu	High	Open	7.10 ± 3.4	5.00 ± 0.7	13.82 ± 3.9
SCHSCO	Forest	Low	Caged	5.52 ± 1.5	5.00 ± 0.7	14.76 ± 2.8
SCHSCO	Forest	Low	Open	6.22 ± 2.2	5.60 ± 0.9	15.26 ± 4.7
SCHSCO	Forest	High	Caged	6.44 ± 4.3	4.80 ± 0.8	13.12 ± 4.1
SCHSCO	Forest	High	Open	6.30 ± 4.6	4.40 ± 1.1	11.92 ± 4.3

SOLODO	Agricu	Low	Caged	14.44 ± 1.4	19.60 ± 1.9	8.02 ± 0.7
SOLODO	Agricu	Low	Open	13.88 ± 2.2	22.60 ± 3.0	8.64 ± 1.4
SOLODO	Agricu	High	Caged	13.18 ± 3.7	20.40 ± 4.4	7.00 ± 0.3
SOLODO	Agricu	High	Open	16.14 ± 1.5	21.80 ± 3.2	7.82 ± 0.9
SOLODO	Forest	Low	Caged	13.32 ± 3.8	20.00 ± 4.1	7.42 ± 0.7
SOLODO	Forest	Low	Open	14.08 ± 1.4	19.40 ± 2.1	8.02 ± 1.5
SOLODO	Forest	High	Caged	11.62 ± 3.6	18.00 ± 2.5	6.44 ± 0.4
SOLODO	Forest	High	Open	11.50 ± 2.8	19.20 ± 2.6	6.92 ± 1.2
TEPVIR	Agricu	Low	Caged	2.38 ± 0.8	5.40 ± 1.3	3.15 ± 0.3
TEPVIR	Agricu	Low	Open	2.56 ± 0.8	5.20 ± 1.6	2.92 ± 2.4
TEPVIR	Agricu	High	Caged	1.58 ± 0.3	4.80 ± 1.3	2.72 ± 1.7
TEPVIR	Agricu	High	Open	4.10 ± 0.8	4.40 ± 1.7	4.64 ± 1.4
TEPVIR	Forest	Low	Caged	2.38 ± 0.9	4.60 ± 1.5	7.85 ± 6.8
TEPVIR	Forest	Low	Open	2.38 ± 0.9	4.80 ± 0.4	7.82 ± 8.0
TEPVIR	Forest	High	Caged	2.16 ± 1.3	4.20 ± 1.1	3.50 ± 1.3
TEPVIR	Forest	High	Open	3.28 ± 0.5	4.80 ± 2.4	6.02 ± 2.3

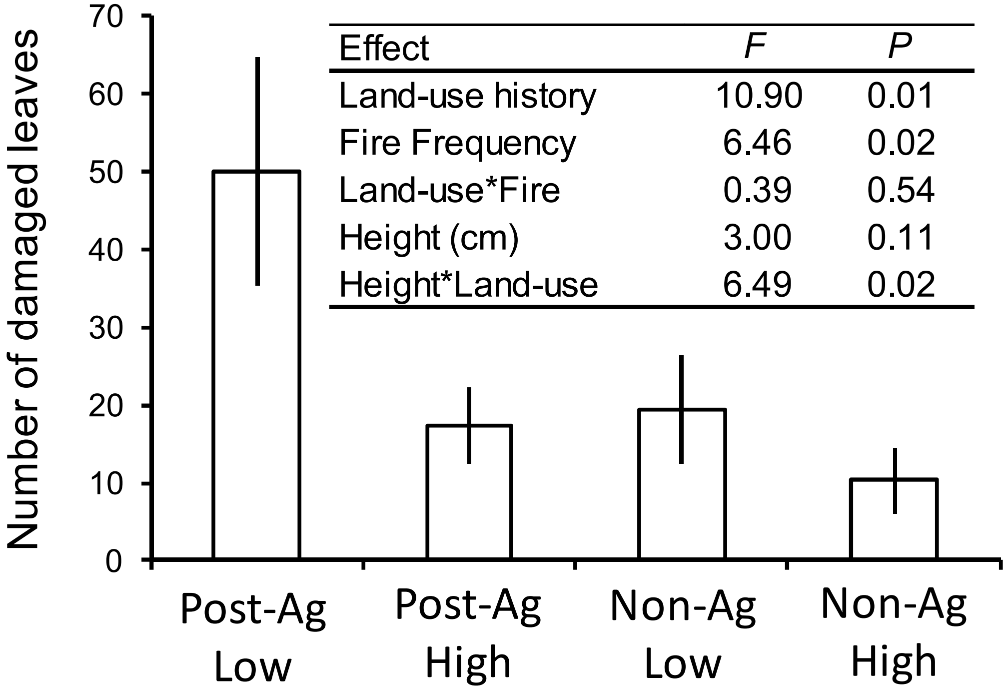
Table A3b. A multivariate analysis of variance (MANOVA) found significant effects of the land-use history treatment and fire treatment in *Solidago odora* plant size, but no difference between the herbivore treatments. Response variables were stem height, number of leaves, and the length of the longest leaf. F-values are calculated from Wilks' Lambda statistic. Because there were differences in pretreatment plant size, we included a measure of plant size as a covariate in most models (see main text). PITGRA = *Pityopsis graminifolia*, SCHSCO = *Schizachyrium scoparium*, SOLODO = *Solidago odora*, and TEPVIR = *Tephrosia virginiana.*

	PITGRA		SOLODO		SCHSCO		TEPVIR	
Effect	F	p	F	p	F	p	F	p
Land-use history	0.57	0.64	3.00	0.05	0.56	0.65	2.04	0.13
Fire frequency	0.75	0.53	3.33	0.03	1.38	0.27	0.72	0.55
Herbivore	0.44	0.72	2.14	0.15	1.32	0.29	3.67	0.02
LU *Fire	0.16	0.92	0.32	0.81	2.16	0.11	0.99	0.41
LU *Herb	0.94	0.43	0.86	0.47	1.28	0.30	1.43	0.25
Fire*Herb	0.85	0.48	0.38	0.77	1.08	0.37	4.12	0.02
LU*Fire*Herb	0.76	0.53	2.35	0.09	4.47	0.01	0.18	0.91

Figure S1. Photographs of the four longleaf pine habitat types.

Figure S1. Longleaf pine woodlands at the Savannah River Site, South Carolina, USA representing a range of site conditions. (Top left) Non-agricultural site with frequent prescribed fires. (Top right) Non-agricultural site with infrequent prescribed fires. (Bottom left) Post-agricultural site with frequent fires. (Bottom right) Post-agricultural site with infrequent prescribed fires. Photo credits: P.G. Hahn.

Figure S2. Number of leaves damaged on *Solidago odora* in the four different habitat types.



Effect	*F*	*P*
Land-use history	10.90	0.01
Fire Frequency	6.46	0.02
Land-use*Fire	0.39	0.54
Height (cm)	3.00	0.11
Height*Land-use	6.49	0.02

Figure S2. Number of leaves damaged on *Solidago odora* in the four different habitat types. All plants are in mesh cages with holes to allow access to invertebrate herbivores (Pseudo-exclosure treatment). Significant covariates and their interactions with main effects were included when they were significant (see also Methods). We included final plant height and the interaction with land-use history in this model. Ag = post-agricultural sites, Non-Ag = sites with no history of agriculture, Low = low fire frequency (<5 burns since 1990), High = high fire frequency (≥5 burns since 1990).

Figure S3. Relationship between proportion of leaves damaged by chewing invertebrates and the final dry biomass of surviving plants.

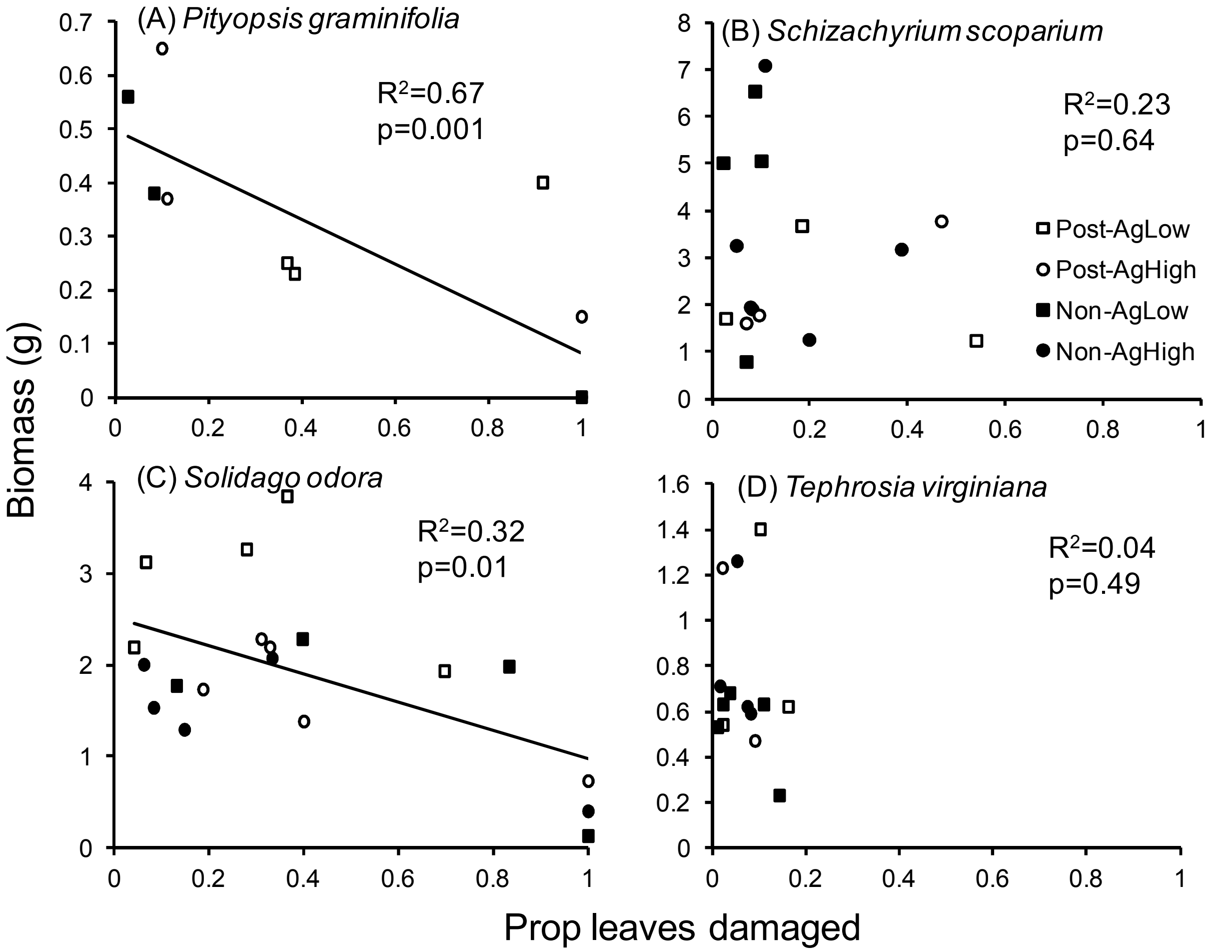


Figure S3. Relationship between proportion of leaves damaged by chewing invertebrates and the final dry biomass of surviving plants that were damaged by herbivores for the four plant species used in the five week experiment. Note the value changes on the y-axis among the different species.

Chapter 3

HABITAT-LEVEL HERBIVORE ABUNDANCE AND NEIGHBORHOOD-LEVEL PLANT FREQUENCY AFFECTS HERBIVORY ON FOCAL PLANTS

Philip G Hahn and John L Orrock

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Address correspondence to: Philip G Hahn, 363 Birge Hall, 430 Lincoln Dr., Madison, WI, 53706, USA. Phone: (608) 262-5868. email: pghahn@wisc.edu

Running head. Habitat- and neighborhood-level predictors of herbivory

Abstract. Associational effects are indirect interactions capable of driving patterns of plant abundance that occur when the amount of herbivore damage received by a focal plant depends on the identity of its neighbors. Moreover, because herbivory can be affected by these neighborhood factors (i.e., associational effects) as well as characteristics of the larger-scale habitat, such as productivity or herbivore abundance, the potential exists for characteristics of habitats at larger spatial scales to modify associational effects at smaller scales. We implemented a factorial manipulation of the neighborhood density and frequency of two plant species (*Solidago nemoralis* and *S. odora*) that differ in palatability in 10 m^2 neighborhoods within two habitat types: post-agricultural and non-agricultural longleaf pine woodlands. Sites (n = 14) spanned a gradient in grasshopper abundance (Order: Orthoptera), which are the dominant insect herbivore in this system. We found that plant frequency at the neighborhood scale was important for determining the amount of herbivore damage received by the more palatable species and that habitat-level environmental context (i.e., land-use history of the site) did not modify these associational effects. Specifically, the more palatable species *S. nemoralis* experienced associational resistance when rare due to frequency-dependent foraging and reduced foraging activity in these neighborhoods. Grasshopper abundance had positive effects on damage to both species at the habitat level likely because of the increased plant apparency within our experimental neighborhoods. To evaluate behavioral decisions of individual grasshoppers, we also conducted foraging trials in experimental arrays where we manipulated frequency of the two plant species used in the field experiment. Foraging experiments with individual grasshoppers partially corroborated the results of the field experiment, confirming the importance of foraging behavior in driving the strength of associational effects. These findings highlight that foraging decisions made at the neighborhood level are important for generating associational effects and can outweigh the larger-scale environmental context in which these behavioral interactions occur.

Key words: associational effects, context-dependent, grasshoppers, herbivory, land-use history, plant-insect interactions.

INTRODUCTION

Herbivory is an important ecological process that can affect plant performance and regulate the abundance and distribution of plants (Crawley 1983, Allan and Crawley 2011). However, the degree to which plants are damaged by herbivores often depends on characteristics of the local environment (e.g. the identity of neighboring plants) as well as larger-scale characteristics of the habitat. At the local scale, the density or frequency of neighboring plants can influence the amount of herbivore damage on a focal plant species (i.e., “associational effects,” Underwood et al. 2014, Kim and Underwood *in press*) by altering local herbivore density (White and Whitham 2000, Palmer et al. 2003, Rand 2003) or foraging behavior (Caccia et al. 2009, Orrock et al. 2010, Hahn and Orrock 2015a). At larger scales, habitat-level factors such as primary productivity (Chase et al. 2000, Maron and Kauffman 2006, Bakker et al. 2006, Hillebrand et al. 2007) or herbivore abundance (Carson and Root 2000, Coupe and Cahill 2003) can dictate herbivory rates. Evidence also suggests that both smaller (i.e., neighborhood) and larger (i.e., habitat or site) spatial scales can be important for regulating herbivore damage received by a focal plant (Baraza et al. 2006, Orrock and Witter 2010, Wang et al. 2010). For instance, generalist herbivores are capable of making habitat-selection decisions at larger scales (i.e., "extent" *sensu* Kotliar and Wiens 1990) and then foraging decisions at the scale of the individual plant (i.e., "grain" *sensu* Kotliar and Wiens 1990) (Holmes and Jepson-Innes 1989, Miller et al. 2009, Castagneyrol et al. 2013). Understanding the mechanisms whereby larger-scale habitat-context may influence neighborhood effects in dictating herbivory rates, however, remains limited by a lack of studies that have explicitly evaluated the mechanisms driving herbivory rates at multiple spatial scales. Experiments conducted in different habitat types that also manipulate neighborhood plant communities across a gradient of primary productivity or herbivore density would be particularly helpful for disentangling herbivore effects at multiple spatial scales.

A variety of anthropogenic activities are altering plant density, productivity, or community composition (i.e., relative abundance or frequency) (Cramer et al. 2008, Thébault et al. 2014), creating the potential for the strength of associational effects to vary among habitats. Abandoned agricultural fields occupy more than 200 million hectares of North American natural areas, and agricultural land-use legacies can have substantial effects on the plant community by altering plant community composition and reducing the number of plant species typical of areas without a history of degradation (Flinn and Vellend 2005, Cramer et al. 2008). We have previously documented altered herbivory rates on adult plants (Hahn and Orrock 2015a) or seeds and seedlings (Hahn and Orrock *in revision*) in post-agricultural longleaf pine woodlands compared to woodlands without a history of agriculture. The mechanism by which land-use history affected herbivory rates in these previous studies appears to be driven through reductions in plant cover, as we found the highest levels of herbivore damage in sites with intermediate levels of herbaceous cover (Hahn and Orrock 2015a). Remnant sites that were maintained by frequent fires had the highest levels of plant cover, but despite higher grasshopper abundance, focal palatable plants experienced low levels of herbivore damage, suggesting that high plant cover diluted herbivory. In contrast, sites that were fire suppressed or historically used for agriculture had reduced plant cover and herbivory rates on the focal palatable plants was elevated (Hahn and Orrock 2015a). Any factor that alters plant cover or community composition, therefore, could potentially change herbivory rates at the scale of the neighboring plants and similar patterns have been documented in other systems (e.g., Underwood and Halpern 2012, Salazar et al. 2013, Stastny and Agrawal 2014). However, the mechanisms that generate these neighborhood-level associational effects, and whether they depend upon the larger-scale habitat context, remain poorly resolved.

In this paper, we evaluated effects of several factors at the habitat and neighborhood scales on predicting insect herbivory rates on focal plants by creating experimental plant neighborhoods (10 m^2) within two habitat types: post-agricultural and non-agricultural (remnant) longleaf pine habitats (n = 14 study sites). At the neighborhood scale, we manipulated plant density (two levels) and frequency (three levels) of two plant species that differ in palatability. The abundance of grasshoppers, the dominant insect herbivore in this system, varies widely among our sites, and plant community composition varies with land-use history, allowing us to examine the role of grasshopper abundance and environmental context on herbivore damage to focal plants. Because behavioral foraging decisions can be an important driver of associational effects, we also used foraging experiments to determine feeding decisions made by the dominant consumer of herbaceous forbs in our system: the grasshopper *Melanoplus angustipennis*. If differences we documented in herbivory rates between post-agricultural and non-agricultural habitats (Hahn and Orrock 2015a) are driven largely by characteristics of the plant neighborhood (i.e., plant density and relative frequency), we expected to find the same results in our experimental plant neighborhoods in both habitat types. However, if herbivory is habitat-dependent, then we expected to find an interaction between land-use history and neighborhood plant composition.

METHODS

Study system

This experiment was conducted in the longleaf pine ecosystem at the Savannah River Site (SRS), South Carolina, USA (Figure 1). The longleaf pine (*Pinus palustris*) ecosystem contains one of the most diverse plant communities in North America and is considered critically endangered (Noss et al. 1995). Over the past century, agricultural plots that replaced historic longleaf woodlands have been abandoned, allowing woodlands to regenerate (Frost 1998). However, these post-agricultural woodlands lack or have reduced cover of many herbaceous plant species typical of longleaf pine woodlands (Kirkman et al. 2004, Brudvig and Damschen 2011, Brudvig et al. 2014). Although many studies have examined the role of abiotic factors and competition on the responses of the plant communities to restoration or management strategies in longleaf ecosystems (Walker and Silletti 2006), there remains a lack of information regarding the effects of other factors, such as herbivory.

Grasshoppers are the dominant invertebrate herbivore in the longleaf pine ecosystem (Knight and Holt 2005, Evans et al. 2012, Hahn and Orrock 2015a). Grasshoppers typically forage at scales of a few meters. One study in western USA grasslands showed that the mean movement distance of several species of rangeland grasshoppers, including several species of *Melanoplus*, was approximately 2 m in a 36 h period. However, some individuals were observed >50m from the release point after 36 h (Narisu et al. 1999). Another study conducted in Midwestern grasslands found that most *Melanoplus femurrubrum* adults studied moved between 3-17 m, although a few moved >50 m over a five week period (Haynes et al. 2007). Thus, grasshoppers are likely mobile enough to move several meters within a site over the course of the experiment, but likely make foraging decisions between neighboring plants. As such, we consider individual plants as the "grain," or the smallest scale at which grasshoppers respond to spatial structure, and habitats (or ~1000 m^2 sites) as the "extent," or the largest scale of heterogeneity to which grasshoppers respond (Kotliar and Wiens 1990).

Experimental design

We conducted a split-plot 2×3×2 factorial experiment (Figure 1) manipulating plant density (two levels; split-plot) and plant frequency (three levels; split-plot), in two habitat types (post-agricultural or non-agricultural land-use histories; whole-plot). We selected 14 sites, seven of each habitat type (post-agricultural and non-agricultural), interspersed across the SRS, resulting in an incomplete block design (Figure 1). Sites encompassed an approximately 1000 m^2 area of relatively homogenous vegetation. Sites received between 3-8 prescribed fires in the last 23 years and were not burned the year of the study. We propagated plants in a greenhouse on SRS (Savannah River Ecology Laboratory) beginning at the end of May 2014. Plants were either a more palatable species (*Solidago nemoralis*) or a less palatable species (*Solidago odora*). Palatabilities were determined via feeding trials conducted in September 2013, with *S. nemoralis* leaf tissue being consumed more than twice as much as *S. odora* (Hahn and Orrock 2015b). In June 2014, we prepared six 10 m^2 plots at each field site by removing existing vegetation using a brush saw followed by an herbicide application (glyphosate, Rodeo, Dow AgroSciences LLC, Indianapolis, IN, USA). Between 07 and 25 July 2014, we created our experimental neighborhoods by transplanting the greenhouse-propagated plants into the prepared field sites at two densities: 8 or 16 plants per 10 m^2 plot. We also manipulated the relative frequency of *S. nemoralis* to *S. odora* at three levels: 3:1 (high *S. nemoralis*), 1:1 (even), and 1:3 (high *S. odora*). Because soil nutrients differ between land-use histories (Verheyen et al. 1999, Fraterrigo et al. 2005, Bizzari et al. 2015), all plants were transplanted in biodegradable 10 cm diameter peat pots (Jiffy International AS, Kristiansand, Norway) containing a 1:1 mixture of potting soil and sand to avoid any confounding effects of soil conditions. The plants were spaced apart to reduce competition for sunlight and transplanting the plants in individual peat pots reduced competition for soil resources. The size of the neighborhood plots (10 m^2) was selected to be large enough for grasshoppers to move or select among the plots but small enough that most foraging decisions were most likely made among plants contained within a plot.

Grasshopper abundance measurements

At 2-3 week intervals, we measured grasshopper abundance at four 10m × 1m transects surrounding each block of plots. We disturbed the vegetation with a long stick and counted the grasshoppers as they flushed (Onsager 1977, Evans et al. 2012). Each site was surveyed 3-4 times during July and August. We averaged the counts along the four transects to get the average number of grasshoppers per $10m^2$ at the site (habitat) level. Since we were not interested in temporal fluctuations in grasshopper abundance, we also averaged across survey periods to get one estimate of grasshopper abundance per site. Grasshopper abundance did not differ between land-use histories ($F_{1,13} = 0.00$, $P = 0.96$).

Herbivory measurements

At the end of the experiment in late August 2014, we recorded the total number of plants with herbivore damage. We used the proportion of plants damaged in each plot as a proxy of feeding activity instead of grasshopper abundance at the neighborhood scale, because grasshoppers usually spend more than 70% of their time in an inactive state (Belovsky and Slade 1986, Joern et al. 1986) and frequently bask on open microsites (e.g., bare soil or litter; Neill and Rolston 2007). Furthermore, grasshoppers are likely mobile enough that they were able to move among our six 10 m^2 plots at each site over the course of the experiment. Thus, the presence of a grasshopper within a plot does not necessarily equate to feeding activity.

We also recorded herbivore damage on three plants of each species within each plot. On each plant, we visually examined five haphazardly selected leaves and estimated the proportion of leaf tissue removed by chewing insects. If five or fewer leaves were present on a plant, we estimated the proportion of leaf tissue removed on all leaves. In cases where an original focal plant died, we randomly selected a neighbor to measure. All measurements were averaged by plant species at the plot level to avoid pseudo-replication.

Grasshopper foraging experiment

During August 2014 we conducted a grasshopper foraging experiment in the greenhouse. Within 30.5 cm^3 rearing cages, we created experimental plant arrays by manipulating the frequency of *S. nemoralis* to *S. odora* at three levels to match the field experiment (3:1, 1:1, and 1:3). Each array contained eight plants. *Melanoplus angustipennis* nymphs (3rd-4th instars) were collected and kept individually in small cages, where they were fed leaf lettuce *ad libatum*. Grasshoppers were starved for a 24-hour period prior to use in the experiments. One *Melanoplus* was added to each array at approximately 09:00 h on the start of the experiment. At ten minute intervals, we recorded the position of each grasshopper within the array and if feeding, the identity of the plant species it was feeding upon. Trials were conducted during daylight hours (approximately 09:00-19:30) for two days. We conducted trials over three periods between 04 August and 12 August 2014, with eight, four, and six replicates respectively. Replicates per treatment are as follows: 3:1 (n=7), 1:1 (n=4), 1:3 (n=7). The trials were conducted on mostly sunny days and the temperature within the greenhouse ranged from approximately 23 to 32°C.

Statistical analysis

To evaluate the total number of plants damaged in each plot, we constructed a generalized linear mixed model using the proportion of plants damaged (a proxy of foraging activity) as the response variable with a binomial error distribution. Fixed-effect predictor variables measured at the habitat scale included land-use history (post-agricultural or non-agricultural) and mean grasshopper abundance (continuous variable). Neighborhood frequency (three levels) and density treatments (high or low) were treated as fixed effects at the neighborhood scale. We also included all possible interactions among these four variables. To account for the incomplete split-plot experimental design, we included site × land-use history as a random effect, which served as the error term for the land-use history, grasshopper abundance, and their interaction. The residual error was the error term for all other effects. We considered effects significant at the $\alpha = 0.05$ level and marginally significant at the $\alpha = 0.1$ level. We used a model simplification protocol where we removed non-significant interaction terms from the model ($P > 0.1$) in order to increase statistical power of the main effects (Crawley 2012). This analysis were conducted in proc glimmix in SAS version 9.4 (SAS Institute Inc., Cary, NC, USA). We included an observation-level random effect to account for potential overdispersion (Harrison 2014) and denominator degree of freedom were estimated using the Kenward-Roger method (Littell et al. 2006). All post-hoc comparisons were made using Tukey-adjusted p-values.

To examine the effects of the experimental treatments on the amount of herbivore damage to the experimental plants across the natural gradient of grasshopper abundance, we constructed linear mixed-models with the proportion of leaf tissue removed by chewing insects, logistically transformed (Warton and Hui 2011), as the response variable. Fixed and random effects were the same as for the proportion of plants damaged described above. We conducted separate analyses for each of the two focal species. We also included all possible interactions among these four variables. As in the analysis above, we accounted for the incomplete split-plot experimental design by including site × land-use history as a random effect, which served as the error term for the land-use history, grasshopper abundance, and their interaction. The residual error was the error term for all other effects. We considered effects significant at the $\alpha = 0.05$

level and marginally significant at the $\alpha = 0.1$ level. We used a model simplification protocol where we removed non-significant interaction terms from the model ($P > 0.1$) in order to increase statistical power of the main effects (Crawley 2012). To compare differences among groups, we used linear contrasts with Tukey-adjusted *P*-values. These analyses were conducted in proc mixed in SAS version 9.4 (SAS Institute Inc., Cary, NC, USA).

To examine the results of the feeding experiment, we used a generalized linear mixed model with the number of plants attacks analyzed as a Poisson distributed response variable. We constructed five models, one for each of the following response variables: 1) the total number of attacks on all plants, 2) the total number of attacks on *Solidago nemoralis*, 3) the total number of attacks on *Solidago odora*, 4) per capita attacks on *So. nemoralis*, and 5) per capita attacks on *So. odora*. Per capita attacks were calculated as the mean number of attacks on each individual plant within an array (i.e., total number of attacks on a given species divided by the number of individuals of that species within an array). The frequency of *S. nemoralis* to *S. odora* (three levels) was the predictor variable for all models. We also included a period term as a random effect to block by the three periods over which we conducted the trials. To compare differences among groups, we used linear contrasts with Tukey-adjusted *P*-values. These analyses were conducted in proc glimmix in SAS version 9.4 (SAS Institute Inc., Cary, NC, USA). We also tested whether the rates of attack differed among the frequency treatments, using the cumulative number of attacks as the response variable. Treatment (categorical), time (continuous), and the interaction were included as fixed-effect predictor variables. The interaction term explicitly tested whether the rate of attack (i.e., slope) differed among the treatments. Grasshopper identity was included as a random effect to account for multiple observations collected on individuals. We removed grasshoppers that had fewer than two total attacks from this analysis. For these analyses, we used considered effects significant at the $\alpha \leq 0.05$ level and marginally significant at the $\alpha \leq 0.1$ level. We included an observation-level random effect to account for potential overdispersion (Harrison 2014) and denominator degree of freedom were estimated using the Kenward-Roger method (Littell et al. 2006). All post-hoc comparisons were made using Tukey-adjusted p-values.

RESULTS

Field experiment: proportion of plants attacked

The total number of plants attacked was affected by the neighborhood plant frequency treatment ($F = 8.39$, $P < 0.001$), with the highest number of plants attacked in the high *S. nemoralis* treatment and the lowest number of plants attacked in the high *S. odora* treatment (Fig. 2A). No other factors or interactions affected the proportion of plants damaged (Appendix A).

Field experiment: proportion leaf tissue removed

The proportion of leaf tissue removed on *S. nemoralis* plants at the end of the experiment was affected (marginally) by grasshopper abundance and the neighborhood frequency treatment (Table 1). Leaf tissue removal increased with increased grasshopper abundance, but *S. nemoralis* plants received less damage when they were rare relative to *S. odora* (Fig. 2B). *Solidago nemoralis* plants in the high *S. odora* treatment (1:3, *S. nemoralis* : *S. odora*) treatment received significantly less damage compared to the even (1:1) treatment (linear contrast: $t = -2.50$, $P = 0.04$) and marginally less damage compared to the high *S. nemoralis* (3:1) treatment ($t = -2.26$, $P = 0.07$). Plants in the even (1:1) and high *S. nemoralis* (3:1) treatments did not differ in the amount of damage they received ($t = 0.23$, $P = 0.97$). The proportion of leaf tissue removed on *S. odora* was positively related to grasshopper abundance (Fig. 2C), although this effect was only marginally significant (Table 1). No interactions affected the amount of damage on either *S. nemoralis* or *S. odora* (Appendix B), so we reduced both models to only contain main effects.

Feeding experiment

In the feeding experiment, the frequency of *S. nemoralis* to *S. odora* did not affect the total number of attacks ($F_{2,13.8} = 2.08$, $P = 0.16$, Fig. 3A), but did affect the number of attacks on *S. nemoralis* ($F_{2,13.8} = 4.61$, $P = 0.03$). *Solidago nemoralis* received fewer attacks in the high *S. odora* treatment (i.e., 1:3 treatment; Fig. 3C) and attacks in this treatment were significantly less than the 1:1 treatment (linear contrast: $t = 2.59$, $P = 0.05$) and the 3:1 treatment ($t = 3.01$, $P = 0.02$). The 3:1 and 1:1 treatments did not differ ($t = 0.41$, $P = 0.91$). Attacks on *Solidago odora* were not affected by the frequency treatment ($F_{2,15} = 0.39$, $P = 0.68$, Fig. 3D). Per capita attacks on *So. nemoralis* were not significantly affected by the frequency treatment ($F_{2,13.9} = 2.4$, $P = 0.128$), although there was a trend towards lower per capita attacks on *So. nemoralis* when it was rare (Fig. 3E). Per capita attacks on *So. odora* were not significantly affected by the frequency treatment ($F_{2,13} = 1.84$, $P = 0.198$, Fig. 3F). We also found a trend towards higher attack rates in the high *S. nemoralis* treatment (Frequency × time: $F_{2,54.7} = 2.3$, $P = 0.11$). Grasshoppers in the high *S. nemoralis* treatment tended to have the highest attack rates, whereas the *S. odora* treatment tended to have the lowest attack rates (Fig. 3B).

DISCUSSION

Our experimental results show a strong role of herbivore foraging behavior at the neighborhood level for predicting herbivore damage (i.e., associational effects) that is largely independent of the larger-scale habitat in which the interaction occurs. Two findings support this result: first, grasshopper abundance measured at the site level predicted herbivory after controlling for neighboring plants. Second, we found that the frequency of the two plant species was important for predicting herbivore damage on the most palatable plant in the field experiment and this trend was evident, although not significant, in the feeding experiment. The more palatable plant experienced associational resistance when it was rare because grasshoppers forage in a frequency-dependent manner leading to increased attack rates on the more frequent but less palatable plant and also reduce foraging activity in these neighborhoods. Understanding associational effects that are driven by foraging behavior rather than abundance, as are occurring in our study system, may be particularly important because behaviorally mediated consumer effects can be disproportionate to consumer abundance and occur more rapidly than abundance-mediated consumer effects (Holt and Kotler 1987, Orrock et al. 2008, Silliman et al. 2013). Moreover, our study suggests that associational effects are one likely explanation for the common finding that herbivory is often context-dependent and varies widely from habitat to habitat (Maron et al. 2014).

Foraging behavior at the level of the plant neighborhood appears to be important for determining the amount of damage received by focal plants based on results of both our field and greenhouse-feeding experiments. Our results generally support other studies that have found that small-scale herbivore foraging decisions are dependent on the resources available within the larger habitat for both mammals (Hjältén et al. 1993, Miller et al. 2009) and generalist insects (Holmes and Jepson-Innes 1989, Castagneyrol et al. 2013). Grasshoppers consume a variety of food sources to meet their nutritional requirements (Behmer and Joern 1993, Unsicker et al. 2008), but will preferentially consume the optimal food source even when it is rare relative to a suboptimal food source (Behmer et al. 2001). This was not necessarily the case in our study, as we found that the more palatable plant *Solidago nemoralis* received less damage in the field and was attacked less frequently in the feeding experiments when it was rare, relative to the less palatable *Solidago odora* (Fig. 2B, Fig. 3C). Grasshoppers exhibit frequency-dependent foraging where they consume the most common food resource when available options are of similar nutritional quality (Cottam 1985). The two *Solidago* species are likely nutritionally similar and grasshopper preferences may be based on other plant traits, such as leaf toughness or plant chemistry. In the field, we found that reduced herbivory on *S. nemoralis* seemed to be driven by reduced foraging activity in the neighborhoods with high frequency of the less palatable *S. odora* (Fig. 2A). Furthermore, the behavioral observations from our greenhouse-feeding experiment generally support the finding of lower feeding activity in the high *S. odora* treatments (Fig. 3B) and also suggest that grasshopper foraging is in part frequency-dependent (Fig. 3C-D). In other words, grasshoppers foraged more frequently on the less-preferred plant *S. odora* when it was more common, thereby providing associational resistance to the more preferred plant *S. nemoralis*. Thus, associational resistance provided to *S. nemoralis* in high *S. odora* neighborhoods appears to be driven by both frequency-dependent foraging as well as reduced feeding activity in these neighborhoods.

Herbivore abundance is sometimes, but not always (Cronin et al. 2010, Hakes and Cronin 2012), a good predictor of herbivore damage. In some cases, very high levels of standing plant biomass or plant cover can dilute herbivory, resulting in a hump-shaped relationship between herbivore abundance and herbivore damage (Underwood and Halpern 2012, Hambäck et al. 2014). We previously found that herbivory exhibited a hump-shaped response to plant cover and that grasshopper abundance was a poor predictor of herbivory in the same system as the present study (Hahn and Orrock 2015a). In the present study we found positive but weak associations between herbivore abundance and herbivore damage on both plant species (Fig. 2), but the neighboring plant cover was manipulated. Plant cover in the experimental neighborhoods was low in this study, likely increasing the apparency of the focal plants, which may have increased attack rates on the experimental plants relative to the surrounding vegetation (Castagneyrol et al. 2013). We expected a dilution effect to occur in the high-density plots, especially the plots with high density and high frequency of the more palatable plant. However, it seemed that the density of plants used in our experiment was not high enough to create a dilution effect even in the high density treatment. Collectively, these findings corroborate the importance of the relative frequency of neighboring plants for predicting herbivory rates and potentially obscuring relationships between herbivore abundance and herbivore damage.

Associational effects are likely of broad relevance to basic and applied ecology, because a variety of anthropogenic activities are altering plant community composition (i.e., relative frequency of plant occurrence), such as through the introduction of invasive species, agricultural land-use history, fire suppression, and nutrient enrichment, among others (Thébault et al. 2014). Thus, the potential for altering generalist foraging behavior through changes to the plant community is extremely widespread in contemporary landscapes. Our results suggest that associational effects generated by foraging behavior are one factor driving context-dependent plant-herbivore interactions potentially in many systems (Bradley et al. 2003, Maron et al. 2014). Finally, when consumer-effects on resources are driven by behavioral traits, the consequences cannot be predicted based on the abundance of the consumer (Schmitz 2003, Orrock et al. 2008, Peckarsky et al. 2008), making management decisions related to consumer-resource interactions more nuanced.

By combining field experiments with behavioral feeding trials, our results provide strong evidence that the relative frequency of plant occurrence alters the foraging behavior of generalist insect herbivores and ultimately affects the amount of damaged received by the plants. Although many observational studies and experiments demonstrated that associational effects are widespread in many natural and agro-ecosystems (Barbosa et al. 2009, Letourneau et al. 2011, Underwood et al. 2014), the mechanisms driving these patterns have been more elusive. Search behavior of specialist insects has been shown to drive associational effects in some systems (Hambäck et al. 2000, Finch et al. 2003, Castagneyrol et al. 2013). However, foraging of generalist herbivores can be more complex than that of specialists (Bernays 1998) and we currently lack a comprehensive framework for predicting how generalist foraging behavior might generate associational effects. Our study provides some of the first experimental evidence from complementary field and greenhouse studies that relative plant frequency affects the foraging behavior of generalist insects and that this can drive associational effects. Although beyond the scope of this study, it is plausible that the functional response of the foragers changes with regards to relative plant frequency (and likely also density), which could drive the observed associational effects. Most theoretical models of plant-herbivore interactions assume a type I or II functional response (linear or decelerating gain, respectively), although theoretical models that use an adaptive consumer behavior approach have demonstrated that consumer functional response can be more complex (Schmitz et al. 1997). The shape of the functional response (decelerating or accelerating) is important because decelerating and accelerating functional responses can have the opposite effect on patch residency time in response to resource enrichment (i.e., increase patch residency time for a decelerating functional response, but decrease patch residency time for an increasing functional response; Calcagno et al. 2014). Thus, it is plausible that the mechanism whereby relative plant frequency (and density) generates associational effects is by altering the consumer functional response. If so, we now have a predictive framework for understanding how associational effects are generated. Furthermore, because plant-herbivore interactions are reciprocal (Stastny and Agrawal 2014), both functional responses in the short-term and numerical responses (aggregation in the short-term and population dynamics in the long-term) are likely important for driving associational effects (Underwood et al. 2014).

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Table 1. ANOVA table for the results of the proportion of leaf tissue removed on the two focal plant species.

	Solidago nemoralis			*Solidago odora*		
Effect	***df***	***F***	***P***	***df***	***F***	***P***
Land-use history	1, 10.8	0.79	0.3934	1, 10.5	0.20	0.6644
grasshopper abundance	1, 10.7	4.27	0.0638	1, 15.8	3.25	0.0905
Relative plant frequency	2, 64.3	3.75	0.0287	2, 57.7	2.05	0.1381
Plant density	1, 64.7	0.00	0.9729	1, 57.9	0.37	0.5466

Figure 1

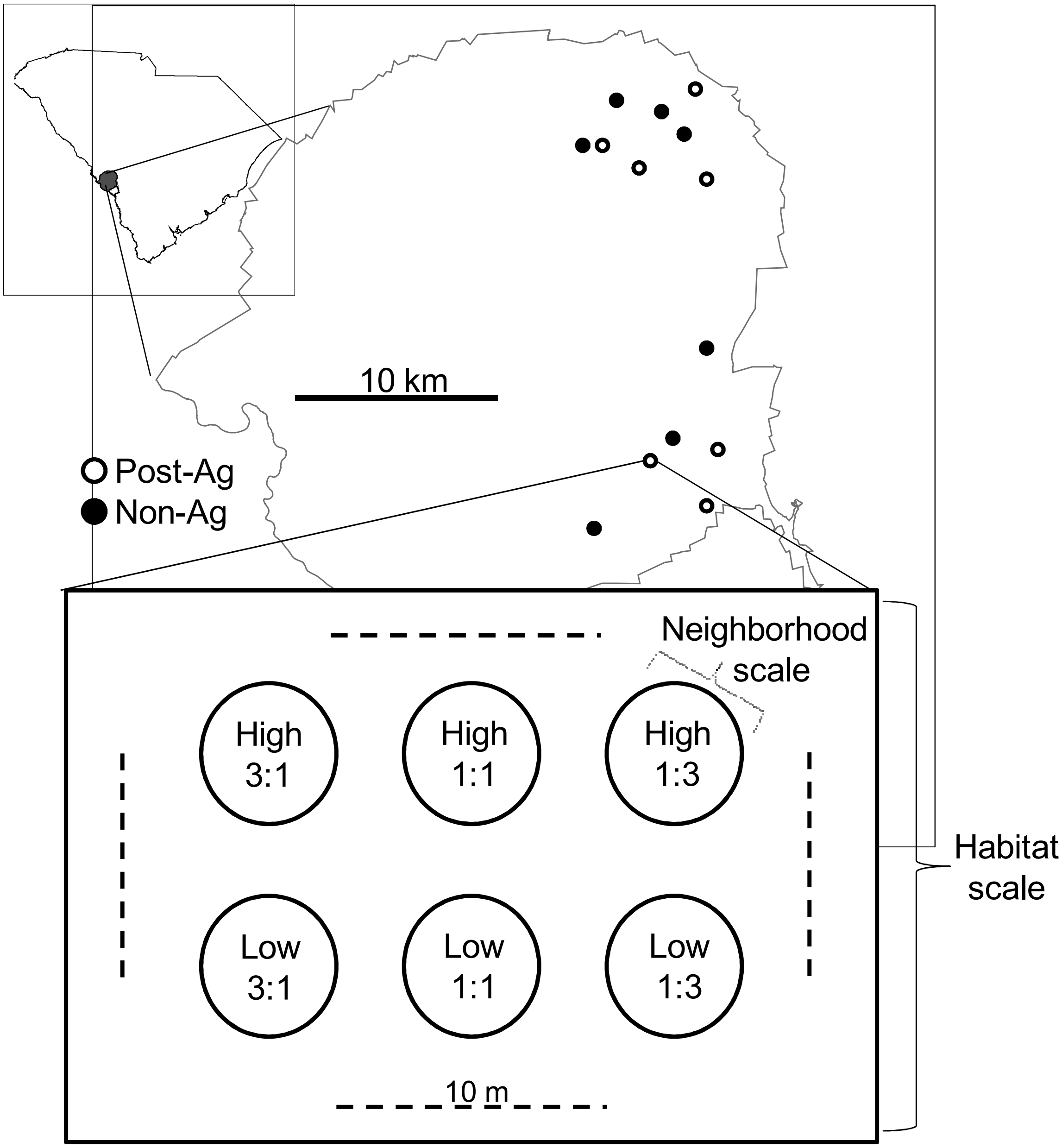

Figure 1. Study sites within the Savannah River Site, SC, USA. We manipulated plant density (low=8 and high=16 plants) and the frequency of *S. nemoralis* to *S. odora* (3:1, 1:1, or 1:3) in 10m^2 neighborhoods within two habitat types: post-agricultural and non-agricultural (remnant) longleaf pine woodlands. We also measured grasshopper abundance at four 10m transects at each site.

Figure 2

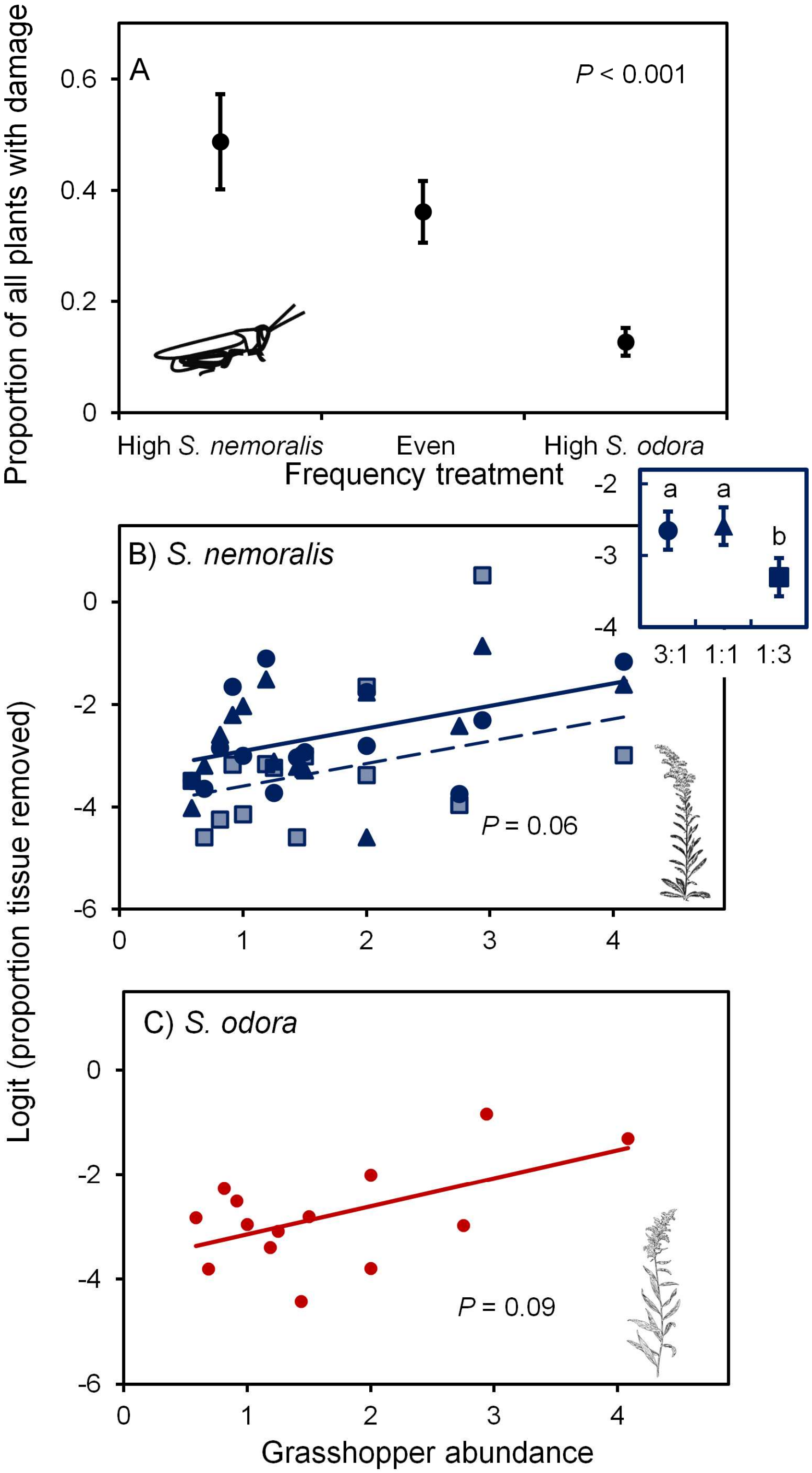
Proportion of all plants with damage
0
0.2
0.4
0.6
A
P < 0.001
High S. nemoralis
Even
High S. odora
Frequency treatment
-2
-3
-4
a
a
b
3:1
1:1
1:3
B) S. nemoralis
0
-2
-4
-6
P = 0.06
0
1
2
3
4
Logit (proportion tissue removed)
C) S. odora
0
-2
-4
-6
P = 0.09
0
1
2
3
4
Grasshopper abundance

Figure 2. Results from the field experiment. A) mean proportion of plants with herbivore damage (±1 SE), a proxy for foraging activity, by frequency treatment. B) Proportion of leaf tissue removed on *Solidago nemoralis* in the three frequency treatments plotted against grasshopper abundance measured at the habitat (site) level. Lines are fit for the high *So. nemorlis* treatment (3:1; dashed line) and the even and high *So. odora* pooled (1:1 and 1:3 pooled; solid line). Inset are the means for the frequency treatment; letters indicate differences based on Tukey-adjusted p-values. C) Proportion of leaf tissue removed on *Solidago odora* plotted against grasshopper abundance measure at the habitat (site) level.

Figure 3

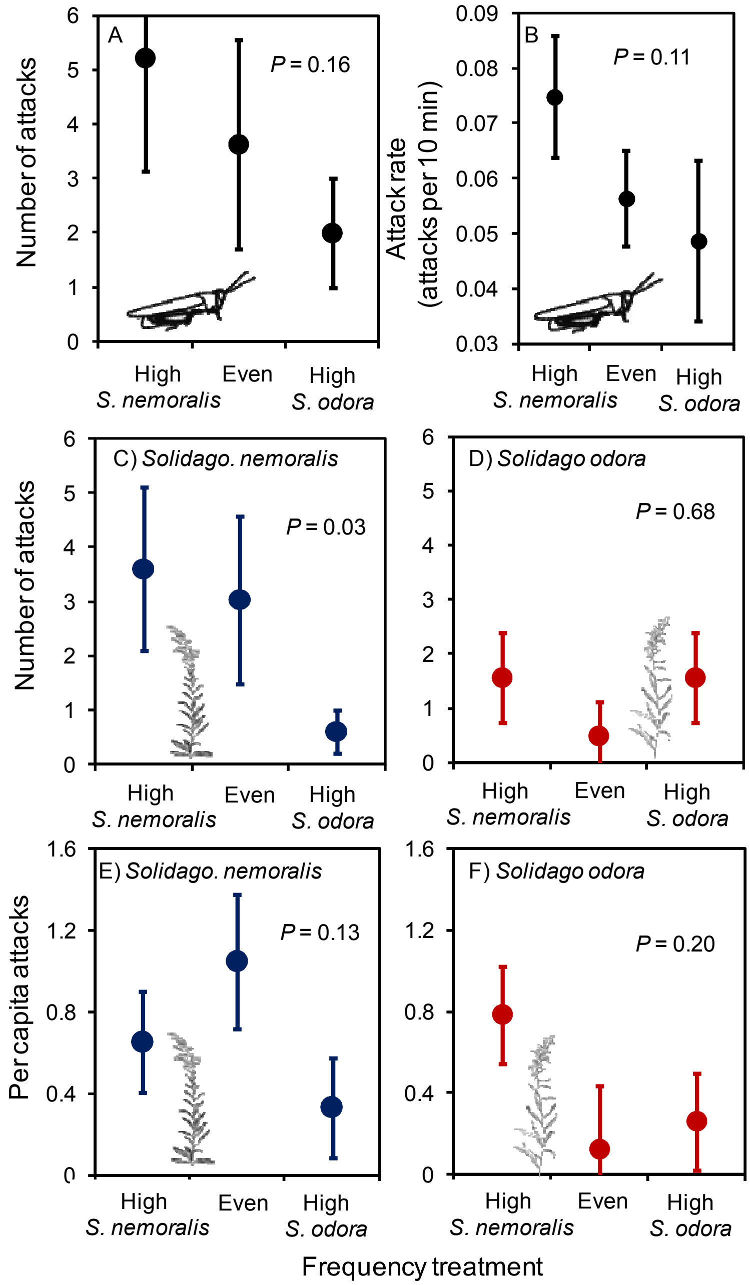

Figure 3. Results from the feeding experiment. A) Total number of plants attacked by herbivores and B) attack rate in the three frequency treatments. Number of C) *Solidago nemoralis* and D) *Solidago odora* plants that were attacked during the experiment. Per capita number of plants on E) *So. nemoralis* and F) *So. odora*. Bars are ±1 SE.

APPENDIX A. Full ANOVA table for the analysis of the total number of plants damaged in the field experiment.

Effect	**Num DF**	**Den DF**	**F Value**	**Pr > F**
History	1	23.04	0.07	0.7986
Frequency	2	44.61	8.39	0.0008
History* Frequency	2	44.61	0.44	0.6492
Density	1	43.86	1.73	0.1949
History* Density	1	43.86	0.03	0.8750
Frequency * Density	2	44.41	1.75	0.1856
History* Freq * Density	2	44.41	0.75	0.4778
Grasshopper abundance	1	34.02	0.94	0.3391
Ghop abundance * History	1	34.02	0.23	0.6337
Ghop abund * Frequency	2	45.88	2.39	0.1026
Ghop *History* Frequency	2	45.88	0.96	0.3904
Ghop * Density	1	44.73	1.78	0.1891
Ghop *History* Density	1	44.73	0.00	0.9703
Ghop * Frequency* Density	2	44.82	2.10	0.1346
Ghop *History* Freq* Den	2	44.82	1.76	0.1833

APPENDIX B. ANOVA tables for the full models examining the proportion of leaf tissue removed by herbivores on the two focal species.

	Solidago nemoralis			*Solidago odora*		
Effect	***ddf***	***F***	***P***	***ddf***	***F***	***P***
History	10.3	0.31	0.5899	11.0	0.86	0.3739
Frequency	47.8	2.77	0.0730	41.8	0.48	0.6252
History* Frequency	47.8	0.86	0.4292	41.8	0.48	0.6237
Density	47.8	0.54	0.4680	43.9	0.32	0.5752
History* Density	47.8	0.04	0.8414	43.9	0.00	0.9456
Frequency * Density	47.9	0.71	0.4967	44.7	0.21	0.8094
History* Freq * Density	47.9	0.01	0.9943	44.7	1.28	0.2876
Grasshopper abundance	11.3	5.72	0.0352	13.6	2.23	0.1580
Ghop abundance * History	11.3	1.19	0.2988	13.6	0.62	0.4450
Ghop abund * Frequency	48.5	1.05	0.3578	41.6	0.03	0.9744
Ghop *History* Frequency	48.5	1.23	0.2999	41.6	0.28	0.7580
Ghop * Density	48.4	0.76	0.3880	45.8	0.80	0.3750
Ghop *History* Density	48.4	0.14	0.7080	45.8	0.02	0.8809
Ghop * Frequency* Density	48.7	1.18	0.3147	45.6	0.20	0.8163
Ghop *History* Freq* Den	48.7	0.00	0.9961	45.6	0.30	0.7443

Chapter 4

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

Philip G. Hahn and John L. Orrock

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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.

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

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 et al. 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 (Evans et al. 2012, Agrawal 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 2015a). 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 2015b), and the strength of biotic interactions (Hahn and Orrock 2015a) could potentially influence edge responses. However, one important limitation to studying edge effects in existing landscapes is 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 2015b). 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 2015a). 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 (Walker and Peet 1984), 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 550-750 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 (PGH *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, NC, 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 and Orrock *unpublished manuscript*), and do not typically flower in the first year (PGH *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 and Orrock *unpublished manuscript*). Plants of similar sizes were haphazardly matched between a paired set of greenhouse trays (35 cm × 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 2015a). There was no difference in light availability or temperature between the two exclosure types (Hahn and Orrock 2015a). We deployed a total of 2,112 seedlings of the four species (n = 528 seedlings of each species) into the herbivore exclosures between 02 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, MA, USA). We deployed the loggers (n = 64) in two periods; the first between 23 August and 01 September 2012 and the second between 07 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 23-29 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 2015b). 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 2015a). 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 study site but are less abundant than the above taxa (Hahn and Orrock 2015b) 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 2015b) are lower than other systems (e.g., tallgrass prairies; Onsager 1977, Joern 2005) 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 2015b). 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 (# leaves at the end of the growing season - # 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 (# new leaves in full exclosures - # 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 Inc., Cary, NC, 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 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., 50m 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 10m 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 10m from the boundary of the thinned post-agricultural patches (Fig. 2D). Notably, the growth of two of the three other plant species was also affected by herbivores in thinned non-agricultural patches 10m from the boundary of thinned post-agricultural patches (Fig. 2D,2H).

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 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 three thinning, thinning in the adjacent patch, and distance from the edge (Table 2). Herbaceous cover increased in thinned patches and was greater near at the edges of unthinned post-agricultural patches near thinned non-agricultural patches (Fig. 3E-H). Grasshopper abundance was only affected by the canopy thinning treatment (Table 2), with about a seven-fold 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. *in press*). 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. *in press*). 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 2015a). 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 (Ballaré 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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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 m 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 bolded.

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

Table 1

	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	**0.056**	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
Landuse × 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
Landuse × Adjacent	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 × Adjacent	29.0	5.98	**0.0208**	82.5	0.15	0.6953	60.0	0.00	0.9568	95.3	0.75	0.3887
Landuse × Thinning × Adjacent	30.1	2.51	0.1234	82.5	4.42	**0.0385**	57.5	0.14	0.7058	95.3	3.90	**0.051**
Dist	63.8	3.48	**0.0667**	82.5	1.62	0.2066	72.4	2.18	0.1442	95.3	0.02	0.8778
Landuse × Distance from edge	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 × Distance	63.8	0.15	0.6997	82.5	4.52	**0.0364**	72.4	6.02	**0.017**	95.3	1.36	0.2461
Landuse × 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
Adjacent × 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
Landuse × Adjacent × 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 × Adjacent × 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
Landuse × Thin × 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

Table 2

	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	**<.0001**	23.0	32.50	**<.0001**	47.0	63.95	**<.0001**
Landuse × 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
Landuse × Adjacent	23.5	0.84	0.3682	14.0	2.10	0.1691	70.4	0.10	0.7495
Thinning × Adjacent	37.8	0.17	0.6825	23.0	2.80	0.1077	47.1	0.34	0.5638
Landuse × Thinning × Adjacent	38.1	1.26	0.2693	23.6	0.01	0.9167	48.7	0.10	0.7583
Dist	54.0	0.22	0.6420	56.1	0.31	0.5769	112.0	1.42	0.2364
Landuse × Distance from edge	54.0	3.38	0.0715	56.1	1.85	0.1787	112.0	0.19	0.6632
Thinning × Distance	54.0	1.61	0.2105	56.1	0.15	0.6998	112.0	0.23	0.6347
Landuse × Thinning × Dist	54.0	5.10	**0.0280**	56.1	0.65	0.4224	112.0	0.08	0.7820
Adjacent × Dist	54.0	5.26	**0.0257**	56.1	1.01	0.3192	112.0	0.00	0.9964
Landuse × Adjacent × Dist	54.0	0.29	0.5896	56.1	0.13	0.7244	112.0	0.21	0.6454
Thinning × Adjacent × Dist	54.0	6.84	**0.0115**	56.1	7.86	**0.0069**	112.0	0.52	0.4740
Landuse × 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.

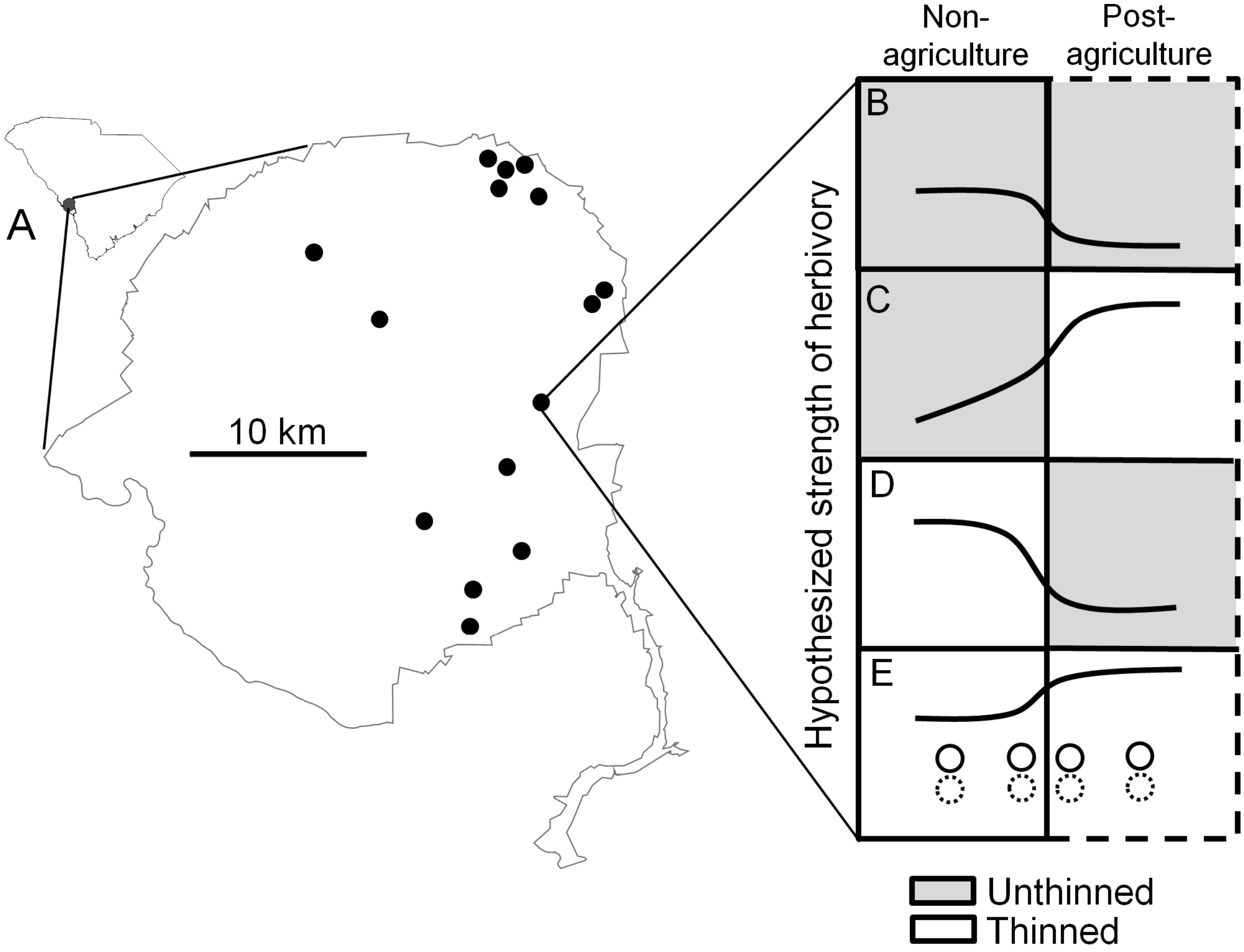

Figure 1. A) Overview of the experiment conducted in longleaf pine woodlands at the Savannah River Site, South Carolina, USA, with (B-E) hypothesized edge effects. Diagram on the right shows (B-E) the four experimental configurations (eight 1 ha patches). Circles within these patches (not to scale) represent 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 50m from the edge (only one set is shown). Curved lines show hypothesized edge effects.

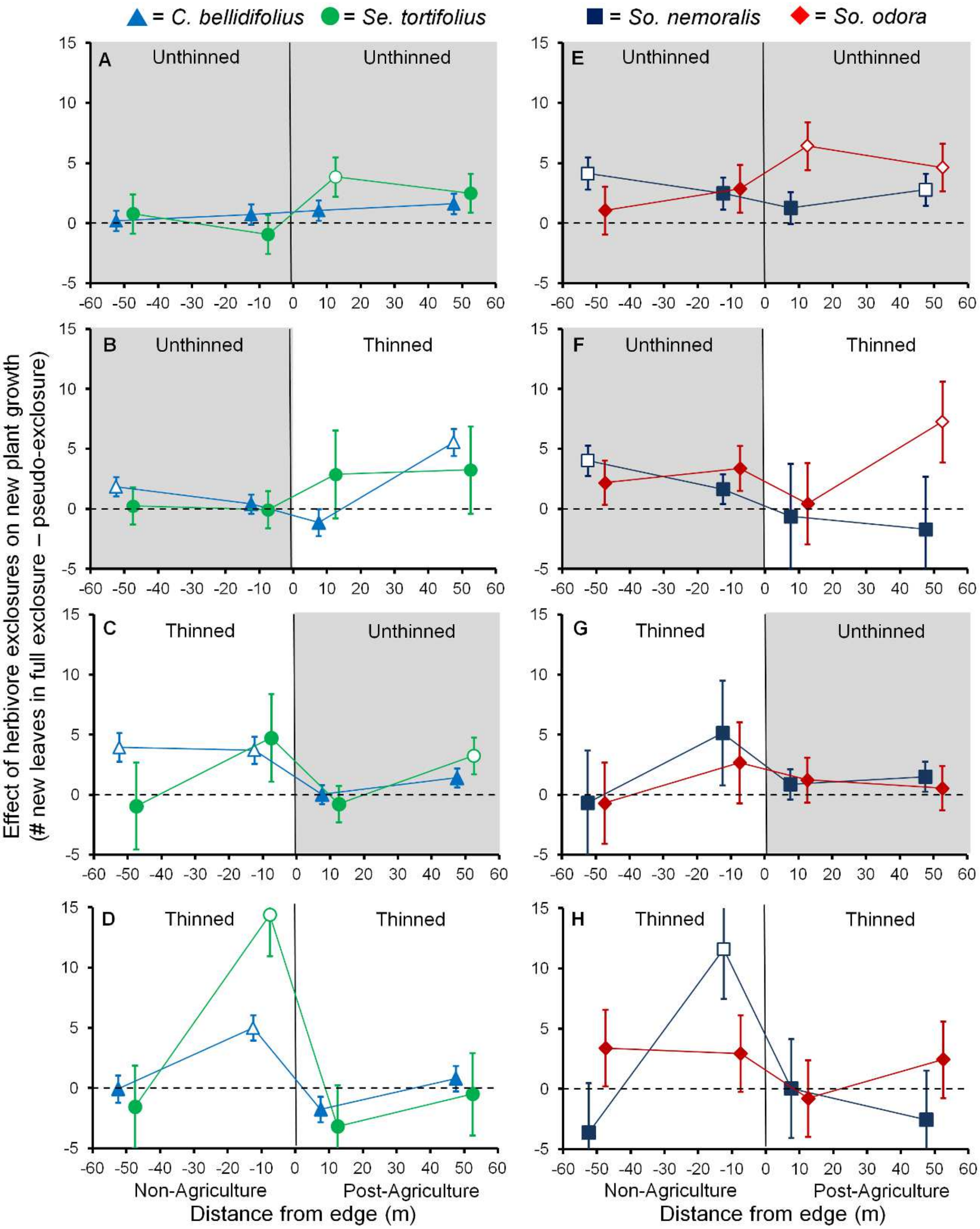

Figure 2. Effect of herbivores on plant growth in relation to habitat edges created by land use history (non- or post-agricultural) and overstory tree thinning (thinned or unthinned) in upland

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.

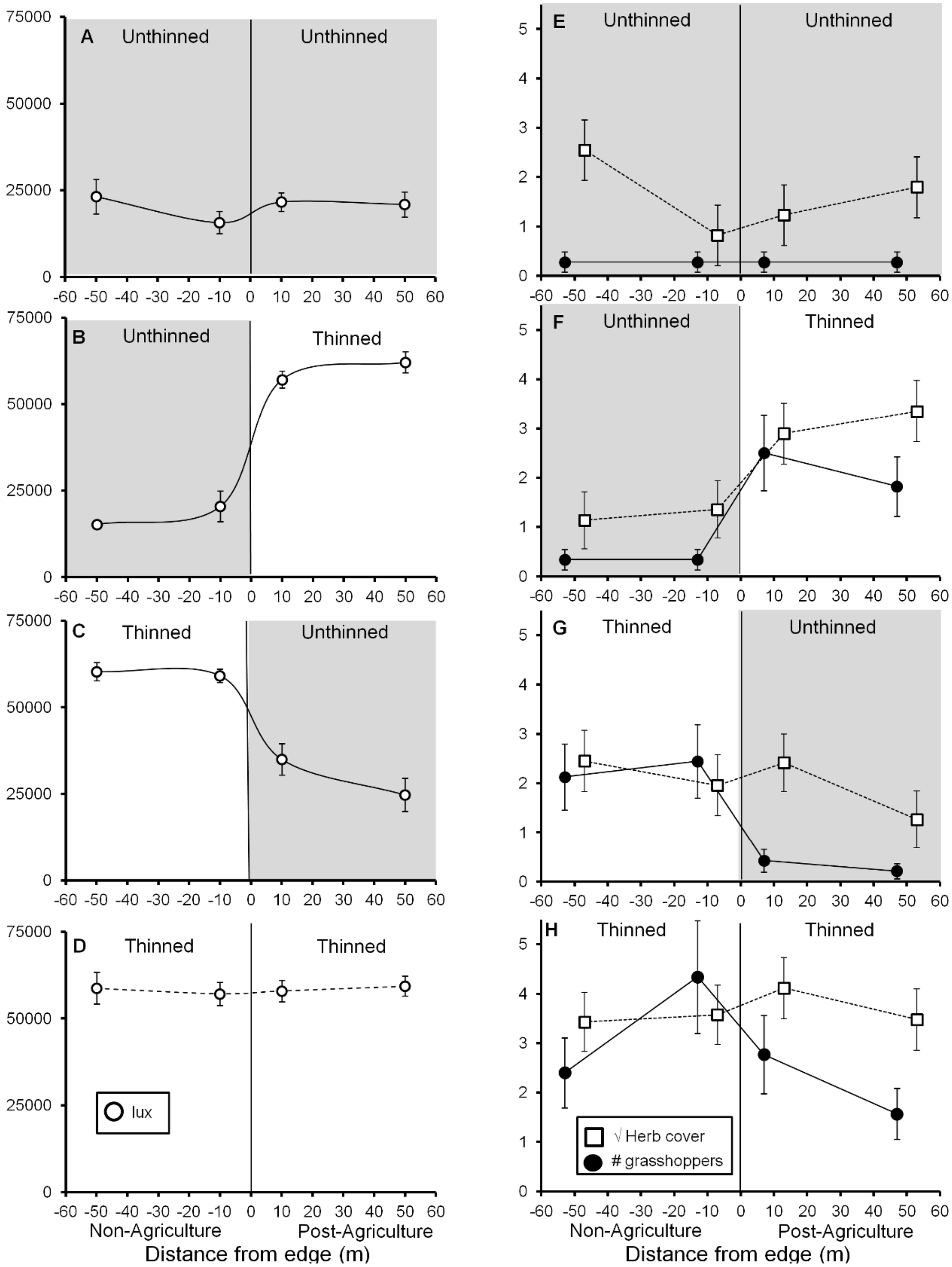

Figure 3. A-D) Changes in light levels (lux), E-H) herbaceous cover (square root transformed),

and grasshopper abundance (mean number per 15m 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 log10 transformed for analysis, but are presented on the original scale in this figure to show actual effect sizes.

Appendix A. Grasshopper feeding preferences.

We conducted cafeteria-style feeding trials between 04 September and 11 September 2013 using the two most common species of grasshopper present at our site: *Melanoplus angustipennis* and *Schistocera alutacea* (Hahn and Orrock 2015b). Grasshoppers were collected from the SRS and kept in small (1 gallon) ventilated plastic containers for at least 5 days prior to the feeding trials. Grasshoppers were fed leafy lettuce *ad libatum*. Test leaves were collected from mature plants in the field. The stem was clipped, immediately placed in a water pick, and returned to the greenhouse. One similarly sized leaf (~6-10 cm^2) attached to the stem in the waterpick of each of the four plant species (*Carphephorus bellidifolius*, *Sericocarpus tortifolius, Solidago nemoralis* and *Solidago odora*) were placed in a 60×45×45cm ventilated plastic cage filled with ~5cm of potting soil. Grasshopper were then introduced into the cages and allowed to feed for 48 hours. After 48 hours, we visually estimated the percent of each leaf that was consumed, to the nearest 5%. Trials were conducted in a greenhouse under sunny conditions at ambient air temperature.

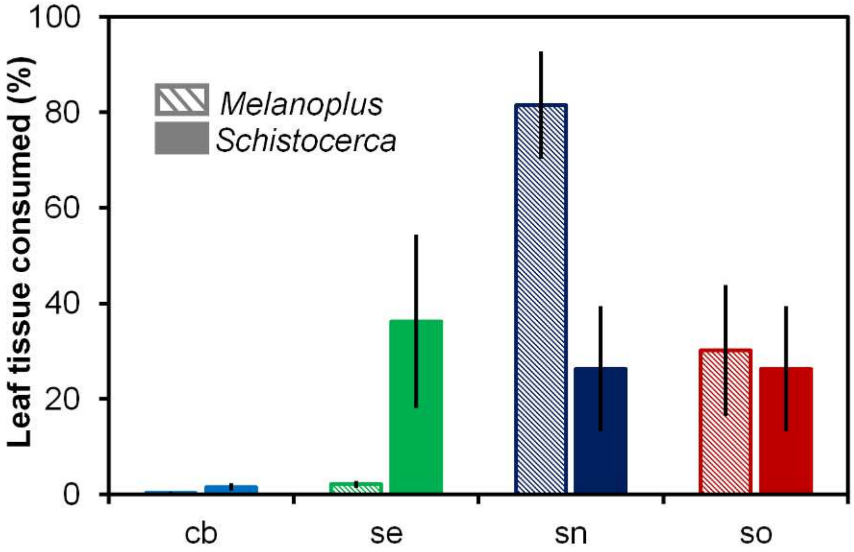

Figure A1. Mean percent leaf tissue consumed after 48 hours in cafeteria style feeding trials for two grasshopper species (*Melanoplus angustipennis* and *Schistocerca alutacea*). Plant species are: cb = *Carphephorus bellidifolius*, se = *Sericocarpus tortifolius*, sn = *Solidago nemoralis*, and so = *Solidago odora*. Error bars are ±1 SE.

Appendix B. Analysis of the growth of plants within full exclosures.

Table B1. ANOVA table for the analysis of plants grown within full herbivore exclosures. Values are *F*-values. We used a four-way mixed-model ANOVA with land-use history, overstory tree thinning, thinning in the adjacent patch, and distance from the edge as fixed effects. We used a four-way ANOVA in order to focus on potential main effects of land-use history and canopy structure, in addition to potential edges effects.

Effect	**Den DF**	***C. bellidifolius***	***Se. tortifolius***	***So. nemoralis***	***So. odora***
Land-use history	14	0.07	1.45	0.91	0.32
Overstory tree thinning	26	44.35*	31.64*	52.18*	19.83*
Landuse×Thinning	26	8.27*	11.12*	2.46	1.36
Adjacent patch thinning	26	0.25	0.77	1.09	0
Land-use×Adj	26	2.12	1.79	1.16	1.01
Thinning×Adj	26	0	2.4	0.64	0.34
Landuse×Thin×Adj	26	0	0.04	0.05	0.53
Distance from edge	58	0.87	0.82	1.56	0.04
Landuse×Dist	58	4.54	0.63	0.01	1.91
Thinning×Dist	58	0.08	3.5	1.43	0.08
Landuse×Thinning×Dist	58	2.94	1.76	0.25	2.08
Adj×Dist	58	1.95	0.25	0.86	0.14
Landuse×Adj×Dist	58	0.05	0.46	0.33	3.07
Thinning×Adj×Dist	58	3.18	0.46	0.67	0.31
Lduse×Thin×Adj×Dist	58	0.43	0.13	0.44	1.09

*$P \leq 0.05$.

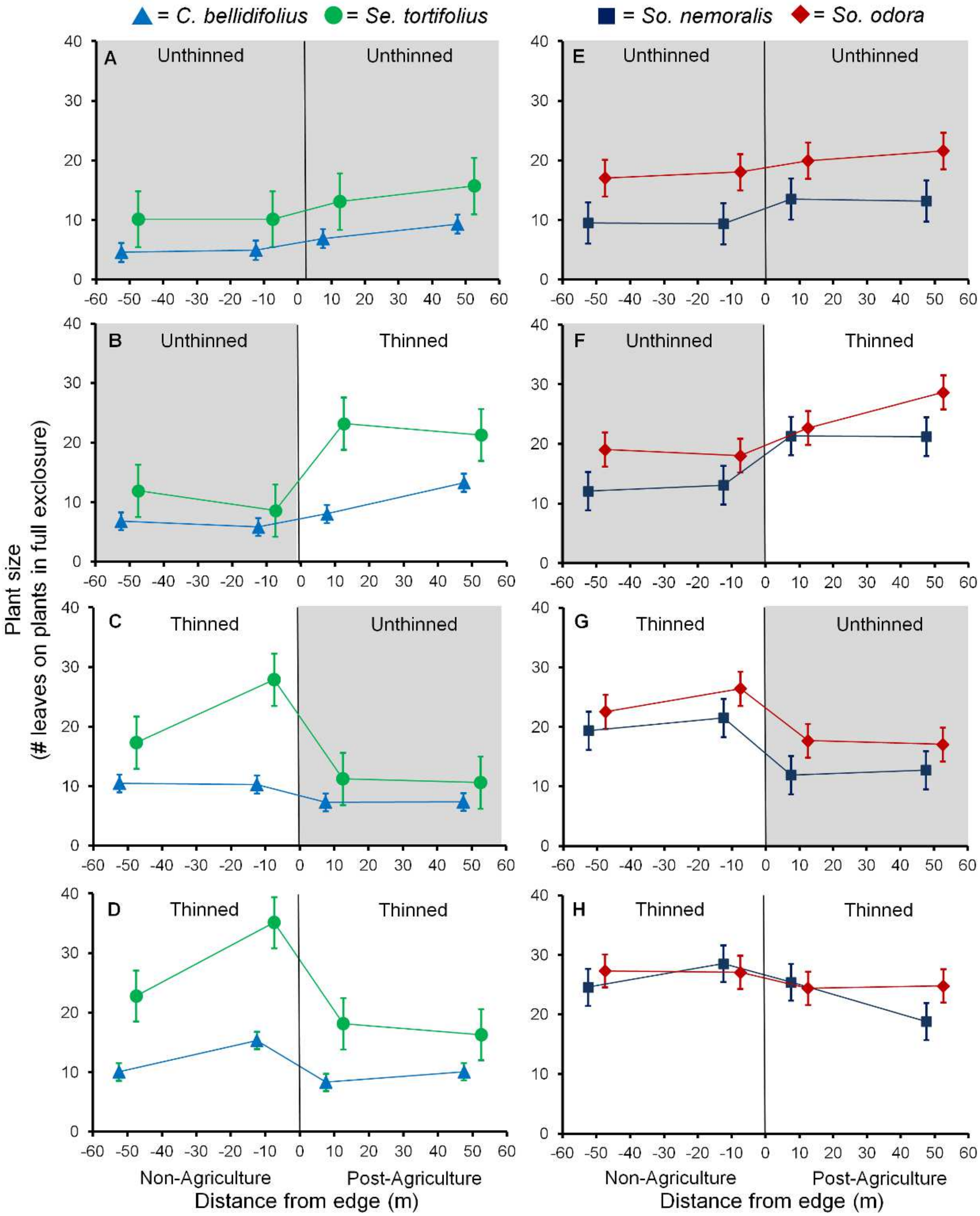

Figure B1. Total number of leaves produced in one growing season on plants protected from herbivores. Data are jittered around distance for clarity. Error bars are ±1 SE.

Appendix C. Effectiveness of herbivore exclosures and additional measures of herbivory.

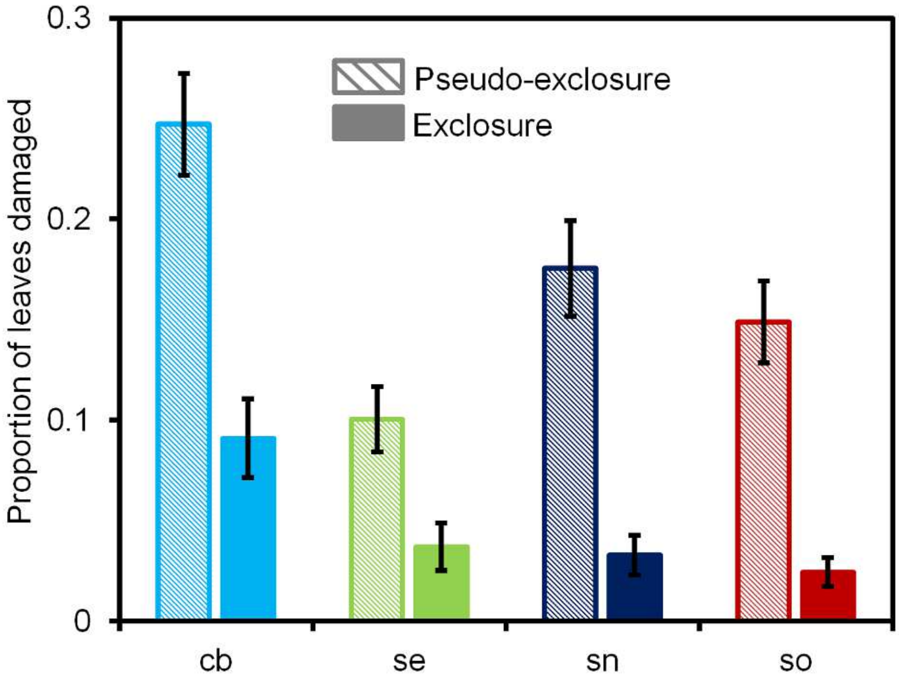

Figure C1. Proportion of leaves damaged in pseudo-exclosures and full exclosures. Plant species are: cb = *Carphephorus bellidifolius*, se = *Sericocarpus tortifolius*, sn = *Solidago nemoralis*, and so = *Solidago odora*. Error bars are ±1 SE. All comparisons between exclosures types are significant ($P < 0.01$) within a species.

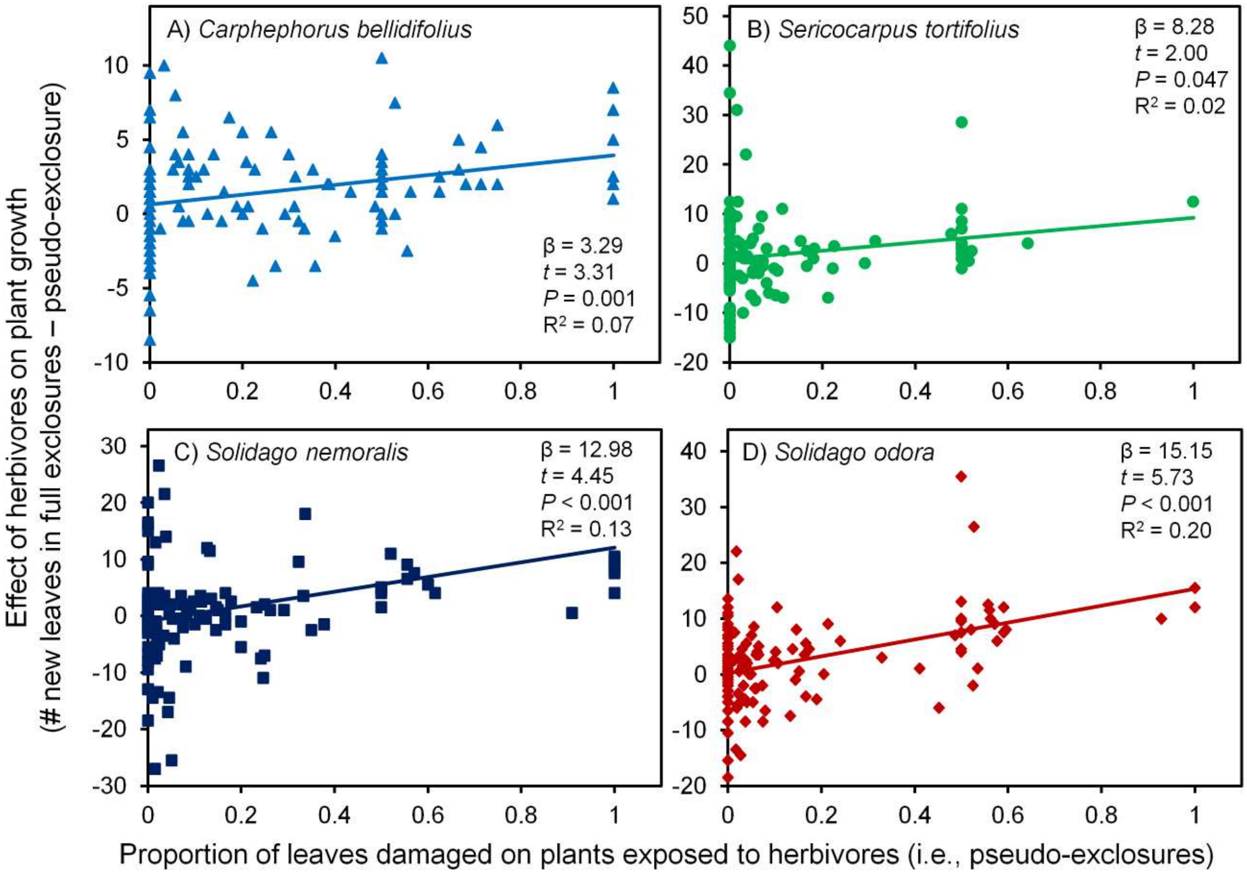

Figure C2. Relationship between the proportion of leaves damaged on plants exposed to herbivores (i.e., inside pseudo-exclosures) and the effect of herbivores on plant growth, measured as the difference in new leaves produced by plants in the full exclosures minus the pseudo-exclosures.

Appendix D. Abundance of grasshopper taxa between overstory tree thinning treatments.

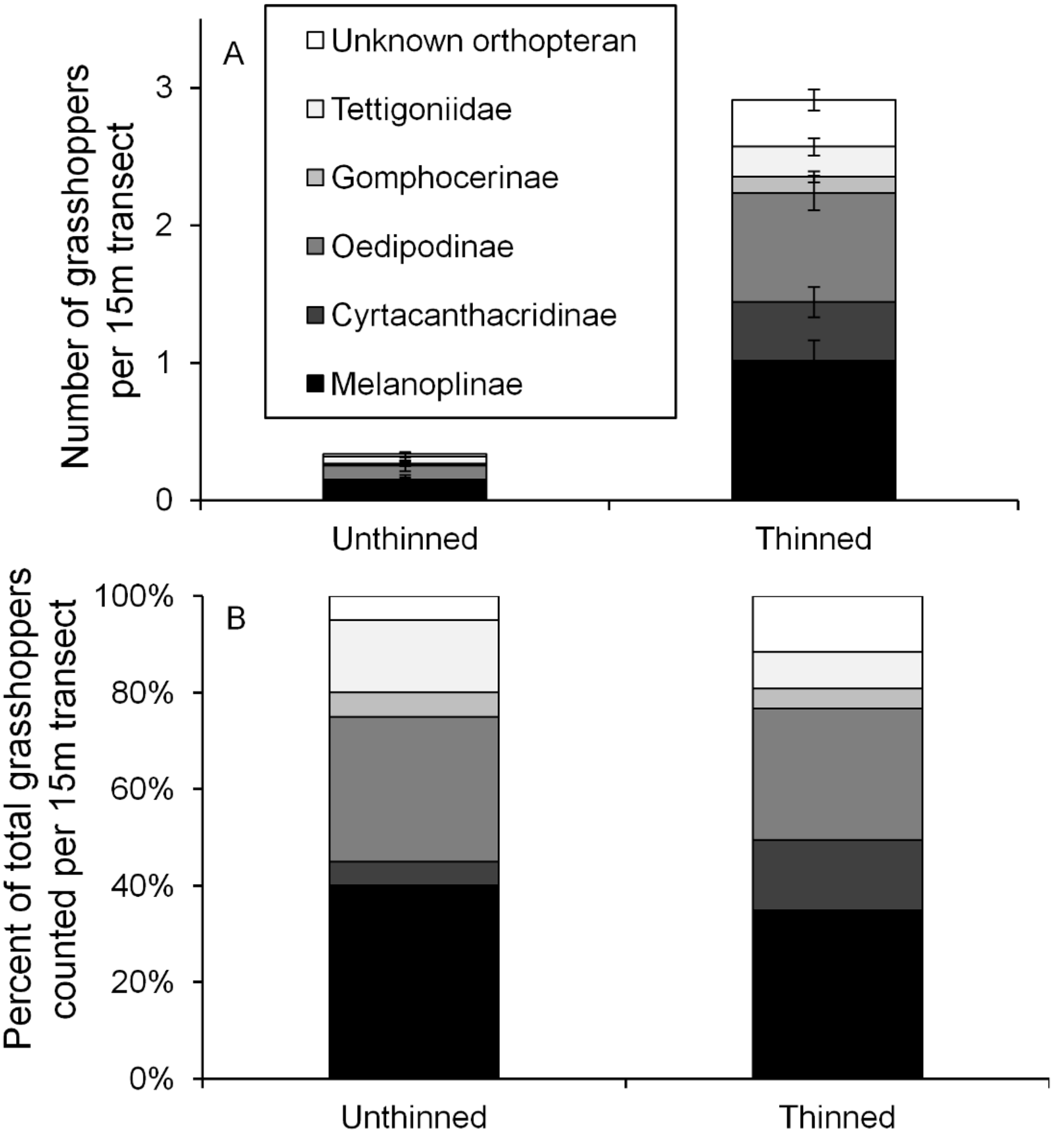

Figure D1. A) Mean abundance of grasshoppers by taxa in unthinned and thinned patches. B) Proportion of taxa present in unthinned and thinned patches. Melanoplinae, Cyrtacanthacridinae, Oedipodinae, and Gomphocerinae are subfamilies within the family Acrididae. Tettigoniidae is the katydid family. We were not able to confirm the identity of the "unknown orthopterans" during our visual surveys. Feeding preferences of the most common species within the Melanoplinae and Cytacanthacridinae are presented in Appendix A.

Chapter 5

Establishment of multiple plant species is contingent upon land-use history, overstory tree thinning, and consumers

Philip G. Hahn and John L. Orrock

[Manuscript to be submitted to *Global Change Biology*]

Summary

1. Despite the importance of seedling recruitment in affecting plant abundance and community structure, our ability to predict seedling dynamics, and hence plant population persistence and community composition, is limited by a lack of understanding of how multiple, interacting factors affect seedling establishment. Agricultural land-use history and canopy closure related to fire suppression are two factors that are both globally implemented and likely have interactive effects on plant community composition. Few studies, however, have evaluated how these factors modify biotic filters of seedling recruitment (i.e., consumers).

2. Using a landscape-level experiment that manipulated canopy structure in paired habitats of non-agricultural and post-agricultural longleaf pine woodlands, we experimentally added seeds and excluded consumers to examine the role of land-use history (non-agricultural or post-agricultural), overstory tree thinning (thinned or unthinned), and consumers (exclosures or pseudo-exclosures) on seedling establishment of four species of Asteraceae in longleaf pine woodlands.

3. Seedling establishment of all four species was affected by interactions between consumer exclosures and land-use history or overstory thinning, and the negative effect of consumers on seedling establishment was strongest in post-agricultural woodlands with intact canopies.

4. Establishment of one species responded positively to soil organic properties and one species responded negatively to soil phosphorus, but only in non-agricultural habitats. Although we found some qualitative differences among species, three of the four species had the greatest establishment in the non-agricultural, thinned, full consumer exclosure treatment combination.

5. *Synthesis.* By combining landscape-scale experiments with local manipulation of consumers and seed availability, our work provides insight into understanding contingency in seedling

establishment across contemporary landscapes. Our results suggest that consumers reduce seedling establishment across a suite of species in post-agricultural woodlands and demonstrate that the effect of consumers on seedling establishment depends on both past and present features of contemporary landscapes (i.e., land-use history or canopy structure). Collectively, soil degradation and altered consumer effects on the dynamics of seedling establishment appear to play an underappreciated role in regulating plant community structure in abandoned agricultural fields over a half century after abandonment.

Key-words. Canopy structure, context-dependent interactions, grasshoppers, herbivory, longleaf pine ecosystem, plant-herbivore interactions.

Introduction

Numerous anthropogenic activities are causing widespread alterations to abiotic and biotic components of ecosystems, with pervasive consequences for many ecological processes. For instance, more than 200 million hectares of agricultural land have been abandoned in North America over the last century (Ramankutty & Foley 1999). Despite the potential of agricultural abandonment to provide new habitat for native plants (Cramer, Hobbs & Standish 2008), this potential is rarely realized; that is, the legacies of historic agriculture generally result in altered soil properties and plant community composition characterized by a lack of native, remnant plant species occurring in post-agricultural forests (Flinn & Vellend 2005; Cramer, Hobbs & Standish 2008). Two explanations are commonly cited for driving patterns of altered community composition in post-agricultural landscapes: 1) dispersal limitation or low seed arrival and 2) establishment limitation or recruitment failure. Results from surveys of reestablished plant communities suggest that dispersal limitation is a primary factor driving patterns of reestablishment in recovering forests (Kirkman *et al.* 2004; Vellend *et al.* 2007; Brudvig &

Damschen 2011), particularity when little remnant (source) habitat remains in the surrounding landscape (Vellend 2003; Matlack 2005; Verheyen *et al.* 2006). However, many species typical of non-agricultural remnant habitat fail to recolonize post-agricultural sites even when in close proximity to remnant seed sources (Baeten *et al.* 2010; Grman, Bassett & Brudvig 2013; Kepfer-Rojas *et al.* 2014), suggesting strong filters on establishment in post-agricultural sites. While some sowing experiments find similar recruitment rates between non-agricultural and post-agricultural forests (Verheyen & Hermy 2004; Jackson, Pearson & Turner 2013), other experiments find that recruitment is more limited in post-agricultural forests compared to non-agricultural forests (Flinn 2007; Baeten *et al.* 2009; Mattingly & Orrock 2013). These experimental results also suggest a stronger filter at the establishment stage, possibly in addition to dispersal limitation. A recent meta-analysis found strong phylogenic clustering among species in their ability to colonize post-agricultural forests with only a weak relationship to dispersal traits (Baeten *et al*. 2015). As such, mounting evidence suggests a stronger filter on establishment than dispersal in terms of species' ability to colonize post-agricultural sites (Flinn 2007; Baeten *et al.* 2009; Mattingly & Orrock 2013; Baeten *et al.* 2015). However, the mechanistic filters at the establishment stage remain unresolved.

Lower seedling recruitment in post-agricultural forests could be due to plant traits, such as small seed size or low seed output, or limited establishment success related to altered soil properties (Cramer, Hobbs & Standish 2008). Furthermore, agricultural abandonment often occurs in conjunction with other management activities, such as altered fire regimes (Brudvig & Damschen 2011; Thébault *et al.* 2014), which could potentially affect recruitment by reducing light availability related to canopy closure (Briggs *et al.* 2005; Ratajczak, Nippert & Collins 2012). Consumers are also important agents regulating seedling recruitment (Moles & Westoby

2004; Barton & Hanley 2013) and because canopy structure can also affect consumer abundance (Bieringer & Zulka 2003; Mabry, Dreelin & Barrett 2003), land-use history and canopy closure have the potential to further interact with biotic factors by affecting the abundance of consumers. While land-use history (Baeten *et al.* 2009; Mattingly & Orrock 2013), light environment (Smith 1982), and consumers (Hulme 1998; Barton & Hanley 2013; Germain *et al.* 2013) can independently affect seedling recruitment and have the potential to interact, studies that evaluate the interaction of these three factors are rare, likely because of the logistical difficulty of conducting fully crossed experiments at spatial scales relevant to large-scale processes such as human land use. As such, the challenge of understanding contingency in seedling establishment remains a central gap in our knowledge that likely affects our ability to understand large-scale patterns in plant persistence and community structure (Grman, Bassett & Brudvig 2013; Maron, Baer & Angert 2014).

We combine landscape and local experiments in the longleaf pine (*Pinus palustris*) ecosystem to address whether agricultural history, canopy structure, and consumers interact to affect the establishment of plants that vary in seed size and natural occurrence in post-agricultural habitat. The longleaf pine ecosystem is characterized by a sparse, open canopy of longleaf pine trees with a floristically diverse herbaceous understory that is maintained by frequent fires (Walker & Peet 1984; Peet 2006). The current range of the longleaf pine ecosystem includes many areas that have experienced decreases in fire frequency over the past century and that are also recovering from historical agriculture (Walker & Silletti 2006; Noss 2013). Reductions in fire frequency promote the encroachment of hardwood trees into the overstory, which dramatically reduces light availability and herbaceous plant diversity in the understory (Gilliam & Platt 1999; Glitzenstein *et al.* 2012). Similarly, agricultural legacies tend to reduce the abundance of plant species that are typical of reference longleaf pine communities (Kirkman *et al.* 2004; Brudvig & Damschen 2011). Collectively, agricultural land-use history and reduced fire frequency can alter plant community composition and reduce the abundance of herbaceous plants typical of the longleaf pine understory (Brudvig & Damschen 2011; Brudvig *et al.* 2014). Seedling recruitment can be limited by seed availability, resource availability, microsite availability, and consumers in this system (Orrock *et al.* 2003, 2006; Myers & Harms 2009, 2011; Iacona, Kirkman & Bruna 2010), although the mechanisms driving altered plant community composition in post-agricultural woodlands are not well understood.

We evaluated the relative roles of land-use history, canopy structure, and consumers in regulating establishment success among species that differ in seed mass and their occurrence in post-agricultural and non-agricultural woodlands. Specifically we addressed the question: do consumers differentially filter seedling recruitment among habitats that vary in land-use history and canopy structure? We selected four Asteraceae species that vary in over an order of magnitude in seed mass (see Appendix S1 in Supporting Information), a key functional trait related to recruitment success and that is also correlated with other functional traits, such as seed output, growth rates (Westoby *et al.* 2002; Verheyen *et al.* 2003), and suseptability to consumers (Orrock *et al.* 2003; Maron *et al.* 2012). In general, heavier seeded species tend to occur more often in non-agricultural woodlands compared to post-agricultural woodlands and lighter seeded species occur more often in post-agricultural woodlands than in non-agricultural woodlands (Verheyen *et al.* 2003; Kirkman *et al.* 2004). The four plant species in our experiment also followed this variation in their occurrence in non-agricultural vs. post-agricultural woodlands measured prior to this experiment (Brudvig *et al.* 2013). We predicted that, if dispersal limitation drives patterns of plant recruitment, experimental seed additions should yield equivalent levels of seedling recruitment in both habitats and establishment of introduced seeds should not differ between non-agricultural and post-agricultural sites. However, if seeds are able to reach the site (i.e., no dispersal limitation), but are subsequently limited by establishment success, we predicted that species should establish in higher proportions in the land-use histories where they most commonly occur, as we assume that their common occurrence indicates suitability for establishing in that particular habitat. We also expected these general patterns to depend on canopy structure and consumers. Since many seeds use light cues to germinate and subsequently enjoy increased growth (Smith 1982), we predicted that overstory tree thinning would increase establishment rates across both land-use histories. Similarly, we predicted consumers would more strongly filter seedling recruitment in thinned habitats because the two dominant consumers of seeds and seedlings, rodents and grasshoppers respectively, should increase in abundance in thinned patches (Bieringer & Zulka 2003; Mabry, Dreelin & Barrett 2003). We also predicted that consumers would more strongly filter recruitment where alternative resources are rare, which occurs more frequently in fire suppressed and post-agricultural sites (Hahn & Orrock *in press-a*). Thus, we expected unique recruitment rates among the combinations of land-use history, canopy structure, and consumer exclosures. We explicitly evaluate the relative roles of the factors that may generate large-scale contingency in recruitment success among species that differ in seed mass by sowing seeds into experimental patches with different land-use histories and canopy structures where we also manipulate consumer access.

Methods and materials

This study was conducted at the Savannah River Site (SRS), near Aiken, South Carolina, USA (Fig. 1a). SRS is an 80,125 ha National Environmental Research Park within the historic extent of the longleaf pine ecosystem (Kilgo & Blake 2005). Much of SRS was converted to agriculture between 1865 and 1950, although farms were small, dispersed across the landscape, and contained many pockets of untilled woodlands (Kilgo & Blake 2005). Agricultural activities included tilling for crop production and use as pasture land (White & Gaines 2000). Agricultural fields were abandoned in 1951 following governmental acquisition of SRS and subsequently planted with pine trees (Kilgo & Blake 2005).

LANDSCAPE EXPERIMENT

We established a large-scale experiment at SRS (Fig. 1). We determined historic land use by examining aerial photographs taken in 1951, just prior to governmental acquisition of SRS. Cultivated fields in 1951 that showed clear signs of plowing (i.e., bare soil was visible in the aerial photographs) were classified as “post-agricultural woodlands” and mature woodlands in 1951 were classified as “non-agricultural woodlands.” Based on a previous analysis of land-use change between 1938 and 1951 (Hahn & Orrock *in press-b*), it is unlikely the non-agricultural woodlands were ever plowed, although they were likely used as timber lots and for grazing prior to 1951 (White & Gaines 2000). The post-agricultural woodlands were subsequently replanted with longleaf, loblolly (*Pinus taeda*), or slash (*P. elliottii*) pine trees in the 1950-60’s (Kilgo & Blake 2005). We selected 4-hectare sites that encompassed a non-agricultural/post-agricultural boundary. Blocking sites that contained both types of land-use history minimizes the potentially confounding issue of non-random site selection of the original agricultural fields because it allows for environmental variation of the site to be accounted for using a blocking term in statistical analyses (Flinn & Vellend 2005). The non-agricultural woodlands experienced fire suppression throughout much of the latter half of the 1900’s, resulting in hardwood encroachment and canopy closure (White & Gaines 2000). All sites experienced low fire frequency between 1951 and 1991, although there were a few prescribed burns during this time (Kilgo & Blake 2005). After 1991, the frequency of prescribed fires increased (Kilgo & Blake 2005). The number of fires between 1991 and 2011 at our sites ranged from two to seven. In 2010, prior to this study, post-agricultural and non-agricultural woodlands supported similar basal area (approximately 20 m^2 ha^{-1}), although the canopy of remnant woodlands was mixed pine and broadleaf deciduous trees (e.g., *Quercus* sp., *Carya* sp.), whereas post-agricultural woodlands were dominated by pines. This resulted in non-agricultural woodlands having slightly greater canopy closure (approximately 77% closure) than post-agricultural woodlands (approximately 66%; see Brudvig *et al*. 2013).

Within this general design, we conducted a factorial manipulation of canopy closure (thinned or unthinned post-agricultural and non-agricultural patches). Overstory tree thinning occurred in early 2012 and 1 ha patches were thinned to 8-10 pine trees per hectare. The overstory thinning was designed as a restoration treatment to increase understory plant diversity, which increases with light availability in the longleaf pine ecosystem (Platt *et al.* 2006). While densities in mature longleaf pine savannas vary considerably (e.g., ~5 to >40 trees ha^{-1}), tree density in our experiment is at the lower end of the natural variability in longleaf pine savannas (Platt, Evans & Rathbun 1988; Kirkman *et al.* 2007). Broad-spectrum herbicide was spot-applied to woody vegetation in the thinned patches in September 2012 to control regenerating broadleaf woody plants (Harrington 2011).

SEED ADDITION EXPERIMENT

We selected four plant species of wind-dispersed Asteraceae: *Carphephorus bellidifolius* (Michx.) Torr. & A. Gray, *Sericocarpus tortifolius* (Michx.) Nees, *Solidago nemoralis* Aiton, and *Solidago odora* Aiton. The Asteraceae is one of the dominant plant families in the longleaf pine ecosystem (Kilgo & Blake 2005), representing 10 of the 44 plant species that were significant indicators of remnant habitat in our study plots prior to the canopy thinning treatment (Brudvig *et al.* 2013). The plant species we selected varied in their habitat occurrences based on a survey of 1300 10m × 10m plots in 29 longleaf pine woodland sites at SRS (Brudvig *et al.* 2013). *Carphephorus bellidifolius* and *Se. tortifolius* were more often present in non-agricultural compared to post-agricultural sites. *Solidago nemoralis* was present more often in post-agricultural sites compared to non-agricultural sites, whereas *So. odora* occurred in a similar number of plots between non-agricultural and post-agricultural plots. Occurrence in non-agricultural and post-agricultural plots was as follows: *C. bellidifolius*: 6.21% and 0.61%; *Se. tortifolius* 17.58% and 7.12%; *So. nemoralis*: 8.79% and 18.48%; and *So. odora*: 49.55% and 55.30%. The seeds also vary in over an order of magnitude in mass, but were similar in the proportion germinating in a laboratory trial (Appendix S1). Seeds are readily consumed by the dominant granivores (e.g., ants and rodents; Orrock & Damschen 2005; Craig, Orrock & Brudvig 2011) and plant foliage is consumed by grasshoppers (Family: Acrididae), the dominant insect herbivores in our system (Evans *et al.* 2012; Hahn & Orrock *in press-a*).

We established study plots near the center of each 1-ha experimental patch (combinations of land-use history and overstory tree thinning). We selected areas with little or no vegetation cover and cleared vegetation, when necessary, to ensure there was no established vegetation inside the study plots. We added 100 seeds to 17.5 cm diameter sub-plots. Each sub-plot was seeded with only one species. Seeding densities (≈4158 m^{-2}) are similar to other seed addition studies conducted in the longleaf pine ecosystem (e.g., Myers & Harms 2009; Iacona *et al.* 2010). We surrounded the sub-plots with 4.5 cm tall plastic barriers, buried approximately 1 cm into the ground, to prevent seeds from being washed out. We then covered the groups of four barriers with a consumer exclosure, either a full exclosure to exclude consumers (i.e., rodents and grasshoppers) or pseudo-exclosure with approximately eight 20 cm diameter holes to allow consumers to enter. Exclosures (0.125 m^2 × 1 m tall cages) were made of wire insect screen (2.7 mm mesh), which is small enough to exclude grasshoppers and rodents but likely allowed ants to enter. Exclosures reduced sunlight by about 5%, but there was no difference in light availability between exclosures (Hahn & Orrock *in press-a*). In order to install the exclosures and barriers, we removed the leaf litter and then replaced leaf litter (~2 cm) back into the barriers before we added the seeds, so the seeds were added on top of the leaf litter. The overstory tree thinning treatment also reduced litter cover through the process of extracting trees, so litter cover was lower in these treatments. Plots were watered immediately after adding seeds. We note that the installation process disturbed the top few cm of soil (~2-3 cm), but this effect was equal across all treatments. Seed additions occurred between 21-26 March 2013. The experiments described here use 32 one-hectare experimental patches, with eight full replicates of land-use history (non-agriculture or post-agriculture), overstory tree thinning (thinned or unthinned), and consumer exclosures (full exclosures or pseudo-exclosures).

We counted the number of plants that established in the plots in early June and late August 2013. Each plant we counted was either marked with a uniquely colored pin or pulled. When we encountered more than 5-10 plants per sub-plot, we would haphazardly select 5-10 plants to pin and pulled the rest to avoid self thinning. The marked plants allowed us to quantify newly established plants between the surveys. All the plants we encountered were juveniles (i.e., the plants had no cotyledons; Hanley *et al.* 2004) and none flowered by the end of the growing season in early October. Over 90% of the plants alive in August survived through the end of the growing season in October and very few seedlings germinated after August (*unpublished data*), so the August survey is representative of the seedling establishment phase. We recognize that seeds may have germinated and died between our surveys, which would have gone uncounted. Therefore, our experiment captured the seedling establishment stage (i.e., seed to established juvenile plant), and not necessarily germination. Few seedlings, including none of our target species, emerged from paired no-seed addition control plots (PGH *unpublished data*) and most species in the longleaf pine ecosystem do not form persistent seed banks (Coffey & Kirkman 2006; Andreu *et al.* 2009).

We also measured several soil variables from three soil samples collected within approximately 20m of the seed addition plots. Percent organic matter, cation exchange capacity, and phosphorus were estimated via by Brookside Laboratories, Inc. (New Knoxville, OH). Percent organic matter was estimated via loss on ignition; cation exchange capacity was estimated by summation; phosphorous was estimated via the Mehlich III extraction method (Brookside Laboratories, Inc., New Knoxville, OH). Soil water moisture holding capacity was estimated following the protocol described in Brudvig & Damschen (2011). The values from three samples were averaged by patch and then we conducted a principal components analysis to collapse the number of soil variables into two axes. The first principal component axis described 41% of the original variation and was a general index of organic matter, water holding capacity, and cation exchange capacity (Appendix S2). The second principal component described 27% of the original variation and was a general index of soil phosphorus and cation exchange capacity (Appendix S2). Note that we inverted this axis for subsequent analyses so that positive values represent higher values of soil phosphorus and cation exchange capacity. These soil properties have been previously shown to be associated with plant community composition in our system (Brudvig *et al.* 2013; Veldman *et al.* 2014). We estimated grasshopper densities in each patch along three 15m transects within 25m of the seed addition plots using walking flush counts (Evans *et al.* 2012). Grasshopper density surveys were conducted between 18 September and 02 October, 2013 on sunny days between 1000 and 1600 hours.

STATISTICAL ANALYSIS

Based on high among-species variation observed in the field, we analyzed seedling establishment of each of the four species separately. We used generalized linear mixed models (GLMM) with a Poisson error distribution and a log link function to analyze the total number of established seedlings combined over the June and August surveys. Land-use history, overstory tree thinning, consumer exclosures, and all interactions were treated as fixed effects. The models included site as a random effect to account for within-site variability and site × land-use history × canopy thinning as a random effect to account for the exclosures being nested within the patches. We conducted linear contrasts to compare full exclosure vs. pseudo-exclosure within different combinations of land-use history and/or overstory tree thinning.

To examine abiotic and biotic drivers of seedling establishment and if these relationships differ between land-use histories, we used Poisson multiple regressions to evaluate the relationships between seedling establishment (response variable) and the first two principal component axes from the soil analysis and grasshopper density (predictor variables). Grasshopper density showed weak predictive power in a preliminary analysis, so we did not include this variable in subsequent analyses (Appendix S3). We then constructed models with seedling establishment as the response variable, soil properties (PC1), soil nutrients (PC2), land-use history, and the interaction between each soil axis and land-use history as fixed effects. Site was included as a random (blocking) effect. We use only data from the pseudo-exclosures for this analysis, which represents the control treatment, and each species was analyzed separately.

We conducted all analyses in PROC GLIMMIX in SAS (version 9.4, SAS Institute., Cary, NC, USA). Denominator degrees of freedom were estimated using the Kenward-Roger approximation (Littell *et al.* 2006). We evaluated all models for overdispersion by examining the ratio of the χ^2-value (i.e., goodness-of-fit) to the residual degrees of freedom (Littell *et al.* 2006). We corrected problematic overdispersion using a negative binomial distribution (Littell *et al.* 2006). In all cases, we report means, back-transformed to the original measurement scale (i.e., counts).

Results

The main effect of land-use history had a marginally significant negative effect on establishment on *C. bellidifolius* and *So. nemoralis* (Table 1). The main effect of overstory tree thinning did not significantly affect the establishment of any of the four species (Table 1). The main effect of the consumer exclosure was significant for all species except *So. odora* (Table 1). Seedling establishment of three of the four species was affected by the three-way interaction of land-use history, overstory tree thinning, and consumer exclosures, although the effect for *C. bellidifolius* was only marginally significant (Table 1). The forth species, *So. nemoralis*, was affected by the interaction between land-use history and consumer exclosures (Table 1).

Establishment of all four species was reduced by consumers in at least some habitats with intact canopy (i.e., unthinned treatments; Fig. 2). The two species that naturally occur more commonly in non-agricultural habitats were affected by consumers in unthinned post-agricultural habitats (Fig. 2). For *C. bellidifolius*, consumers reduced establishment by over ten-fold to nearly zero establishment in unthinned post-agricultural sites (linear contrast: $F_{1,56} = 10.54$, $P = 0.002$). In this same treatment, consumers reduced establishment of *Se. tortifolius* by about half ($F_{1,56} = 6.66$, $P = 0.013$), although establishment was still high relative to other species (Fig. 2).

Establishment of *So. odora* was reduced by consumers in unthinned non-agricultural habitats. *Solidago nemoralis* establishment was reduced by consumers in only post-agricultural habitats, pooled across the thinning treatments ($F_{1,56} = 12.93$, $P < 0.001$). Consumers also reduced establishment of *Sericocarpus tortifolius* by about half in thinned non-agricultural habitats ($F_{1,56} = 12.75$, $P < 0.001$), although establishment was still high in this treatment (Fig. 2).

Soil properties (i.e., the principal component describing soil organic matter, water holding capacity, and cation exchange capacity) had a positive relationship with the establishment of *C. bellidifolius* regardless of land-use history (Table 2; Fig. 3). The interaction between land-use history and soil nutrients (i.e., the principal component describing soil phosphorus and cation exchange capacity) was significant for *Se. tortifolius* (Table 2). There was a significant negative relationship in non-agricultural sites ($t_{26} = -2.43$, $P = 0.031$) and no relationship in post-agricultural sites ($t_{26} = 1.81$, $P = 0.13$; Fig. 3).

Discussion

Agricultural land-use history and canopy closure related to fire suppression are pervasive anthropogenic activities with the potential to interact with biotic factors to affect plant recruitment. Our results from a landscape-scale experiment support the primacy of establishment limitation, in addition to dispersal limitation, in driving plant recruitment in post-agricultural habitats, especially in post-agricultural sites with intact overstory canopies, through three major findings. First, consumer exclosures increased seedling establishment for all four species we tested and this effect was generally strongest in post-agricultural woodlands with intact canopies. This finding helps to explain the low recolonization of plants documented in post-agricultural lands (Vellend *et al.* 2007; Baeten *et al.*2015) and demonstrates that consumers are an important agent reducing establishment in post-agricultural sites with intact canopies.

Second, we found that canopy closure alone, which decreases understory plant diversity and vigor (Platt *et al.* 2006; Harrington 2011), does not necessarily affect seedling establishment, but did increase consumer pressure on most species (Fig. 2). Increased consumer pressure in canopy (unthinned) patches might be driven by the availability of alternative resources for consumers rather than by consumer abundance, because rodent and grasshopper consumers occur in much greater abundance in the thinned patches and grasshopper abundance was not a good predictor of seedling establishment (Appendix S3). Finally, seedling establishment in non-agricultural woodlands for two species was partially driven by abiotic components of these habitats (i.e., soil properties or nutrients), although these relationships were weak. Two of the four species we tested had marginally higher establishment in non-agricultural habitats, suggesting that plant recruitment in post-agricultural habitats may be more strongly limited at the establishment stage than in non-agricultural habitats that are otherwise similar in terms of canopy structure, soil order, and fire history. Collectively, these results show that anthropogenic land transformation interacts with consumers to create contingencies in seedling establishment and that landscape-scale experiments are an important step towards understanding substantial variation observed in seedling establishment across complex landscapes.

Establishment limitation plays a clear role in regulating patterns of diversity in grasslands (Clark *et al.* 2007), including longleaf pine ecosystems (Myers & Harms 2009, 2011; Iacona *et al.* 2010). Our results extend recent findings that establishment is more limited in post-agricultural habitats (Baeten *et al.* 2009; Mattingly & Orrock 2013) by showing that consumers can more strongly filter seedling establishment in post-agricultural habitats compared to remnant habitats. We found that consumers limited seedling establishment under canopy in post-agricultural habitats for three of our four species. Consumer access reduced seedling establishment to nearly zero new recruits for both *C. bellidifolius* and *So. nemoralis*. For *C. bellidifolius*, a species that is typical of remnant longleaf pine understories but rarely occurs in post-agricultural woodlands, consumers could be an agent restricting reestablishment in post-agricultural habitats. Interestingly, the consumer filter was lifted when the overstory canopy was thinned, except for *So. nemoralis* (Fig. 2). We have previously documented greater folivory rates on focal plants in habitats with sparse understory vegetation cover, particularly in post-agricultural longleaf pine woodlands and fire suppressed non-agricultural woodlands (Hahn & Orrock *in press-a*). Similarly, we have also documented greater granivory rates under canopy compared to adjacent open habitats (Craig, Orrock & Brudvig 2011). Another study found that seed removal was greater for *C. bellidifolius* than for larger-seeded species in sites with intact overstory canopies (Craig, Orrock & Brudvig 2011). Our finding that consumer pressure was usually greater under canopy (unthinned patches) generally concurs with these previous results (Craig, Orrock & Brudvig 2011; Hahn & Orrock *in press-a*) and suggests that consumer pressure may contribute more to reducing seedling establishment when alternative resources for consumers are sparse (i.e., seeds and plant material), as is the case in closed canopy woodlands (Gilliam & Platt 1999; Harrington 2011). Furthermore, abundance of grasshoppers, a dominant herbivore in this ecosystem (Knight & Holt 2005; Evans *et al.* 2012), was nearly seven times greater in thinned patches and was a poor predictor of seedling establishment (Appendix S3). Similarly, rodent abundance in this study system also tends to be much higher within thinned habitats compared to mature woodlands (Danielson & Hubbard 2000; Mabry *et al.* 2003) and in our sites (JLO *unpub. data*). Therefore, background resource availability for consumers (seeds or herbaceous plant material) may be a better predictor of consumer pressure than consumer abundance alone, suggesting that consumers may exert stronger influences over population and community dynamics in less productive habitats (Maron & Kauffman 2006; Bakker *et al.* 2006).

Overall, we show that post-agricultural habitats may be important for reducing seedling establishment of plant species regardless of seed size and for species that are characteristic of typical longleaf pine habitats as well as species that occur largely in degraded, post-agricultural sites. The combined effects of consumers, overstory canopy, and agricultural land-use history resulted in the lowest seedling establishment for the largest (*C. bellidifolius*) and smallest (*So. nemoralis*) seeded species in post-agricultural sites. These strong interactive effects resulted in the main effect of land-use history having marginally significant negative effects on establishment of these two species. This finding suggests that species distributions across complex landscapes are likely driven by both seed output and establishment limitation. For instance, *So. nemoralis*, which is significantly more abundant in post-agricultural than non-agricultural habitats (Brudvig *et al.* 2013), had lower establishment in post-agricultural habitats, suggesting that smaller seeds (Appendix S1) and greater seed output likely contributes to its success in post-agricultural habitats. More importantly though, seedling establishment with regards to land-use history was also contingent on other factors, specifically canopy structure and consumers, as we did find high seedling establishment under certain treatment combinations in post-agricultural woodlands (Fig. 2).

Our results also revealed some positive associations between seedling establishment and soil properties (organic matter and water holding capacity), but only for the one species that occur more commonly in non-agricultural sites. The soil organic matter content in our study, a main proxy of soil quality in our system, was in the lower range of other values reported in the longleaf pine savanna (Veldman *et al.* 2014), possibly weakening a potential relationship between soil organic matter and seedling establishment in our study. We also a found negative relationship in non-agricultural habitats and no relationship in post-agricultural habitats between seedling establishment and soil phosphorus for *Se. tortifolius* (Fig. 3). Historic agriculture has persistent positive effects on soil phosphorus (Brudvig *et al.* 2013), as well as variable effects on other soil properties, such as soil microbial communities (i.e., pathogens or mycorrhizae) (Kulmatiski & Beard 2008, Fierer *et al*. 2013) and soil compaction (Bassett, Simcock & Mitchell 2005; Mattingly & Orrock 2013). Therefore, interactions among soil phosphorus and other soil properties, such as microbial communities or compaction, could have further contributed to the different relationship between seedling establishment and phosphorus in post-agricultural and non-agricultural habitats.

Understanding context-dependent plant-herbivore interactions is critical for predicting plant abundance and distributions across broad spatial scales (Maron, Baer & Angert 2014). Our study contributes to a small, but growing body of multi-factor experiments that highlight contingencies in how plant-herbivore interactions regulate plant communities, specifically at the critical seedling establishment stage. Determining the responses of entire plant communities, however, will require studies that examine the establishment of multiple plant families (e.g., grasses, legumes and other forbs) that vary in key traits related to establishment, such as seed output and size (Westoby *et al.* 2002) and across multiple years. Future studies that examine longer-term effects of land-use history, canopy structure, and consumers on plant performance, as well as the role of productivity or neighboring plants in regulating herbivory rates, will provide fruitful information to begin to disentangle the complex factors that generate contingency in plant community structure.

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DATA ACCESSIBILITY

The authors will deposit the data related to this manuscript in Dryad at the time of publication.

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Appendix S1. Additional information on plant species and seed collection.

Appendix S2. Details from the soil analysis.

Appendix S3. Details from the grasshopper analysis.

Table 1. Analysis of variance table from the generalized linear mixed models examining seedling establishment for each of the four plant species.

	C. bellidifolius			*Se. tortifolius*		
Effect	***df***	***F***	***P***	***df***	***F***	***P***
Land-use history	1, 29.1	3.43	0.074	1, 17.8	0.15	0.703
Overstory thinning	1, 29.5	1.05	0.315	1, 17.8	0	0.957
Landuse × thinning	1, 29.3	0.01	0.942	1, 17.9	3.07	0.097
Consumer exclosure	1, 56	14.38	0	1, 56	6.38	0.014
Exclosure × landuse	1, 56	2.37	0.129	1, 56	1.49	0.228
Exclosure × thinning	1, 56	4.68	0.035	1, 56	0.13	0.725
Excl × landuse × thinning	**1, 56**	**3.68**	**0.06**	**1, 56**	**8.43**	**0.005**

Table 1. (con't)

	So. nemoralis			*So. odora*		
Effect	***df***	***F***	***P***	***df***	***F***	***P***
Land-use history	1, 29.4	3.83	0.06	1, 18.5	0.07	0.789
Overstory thinning	1, 30.2	1.5	0.23	1, 18.1	0.06	0.802
Landuse × thinning	1, 30.8	0.62	0.438	1, 17.8	4.64	0.045
Consumer exclosure	1, 56	14.3	0	1, 56	1.43	0.236
Exclosure × landuse	**1, 56**	**5.75**	**0.02**	1, 56	2.87	0.096
Exclosure × thinning	1, 56	0.3	0.587	1, 56	5.43	0.023
Excl × landuse × thinning	1, 56	0.91	0.346	**1, 56**	**11.26**	**0.001**

Table 2. Analysis of variance table examining the relationship between soil properties and soil nutrients on seedling establishment of four plant species in sites with and without an agricultural land-use history.

	C. bellidifolius		*Se. tortifolius*		*So. nemoralis*		*So. odora*	
Effect	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Soil properties[a]	**8.53**	**0.007**	1.38	0.255	1.96	0.173	1.11	0.303
Soil nutrients[b]	1.14	0.295	2.73	0.110	0.97	0.334	0.02	0.889
Land-use history	0.12	0.727	3.04	0.156	1.43	0.243	0.16	0.695
Soil prop × Landuse	1.68	0.206	3.04	0.105	2.51	0.125	0.11	0.744
Soil nut × Landuse	**2.96**	**0.097**	**7.85**	**0.010**	1.21	0.281	0.63	0.435

a The first principal component axis was a general index of soil organic matter, soil water holding capacity and soil cation exchange capacity.

b The second principal component axis was an index of soil phosphorus and soil cation exchange capacity.

Figure 1:

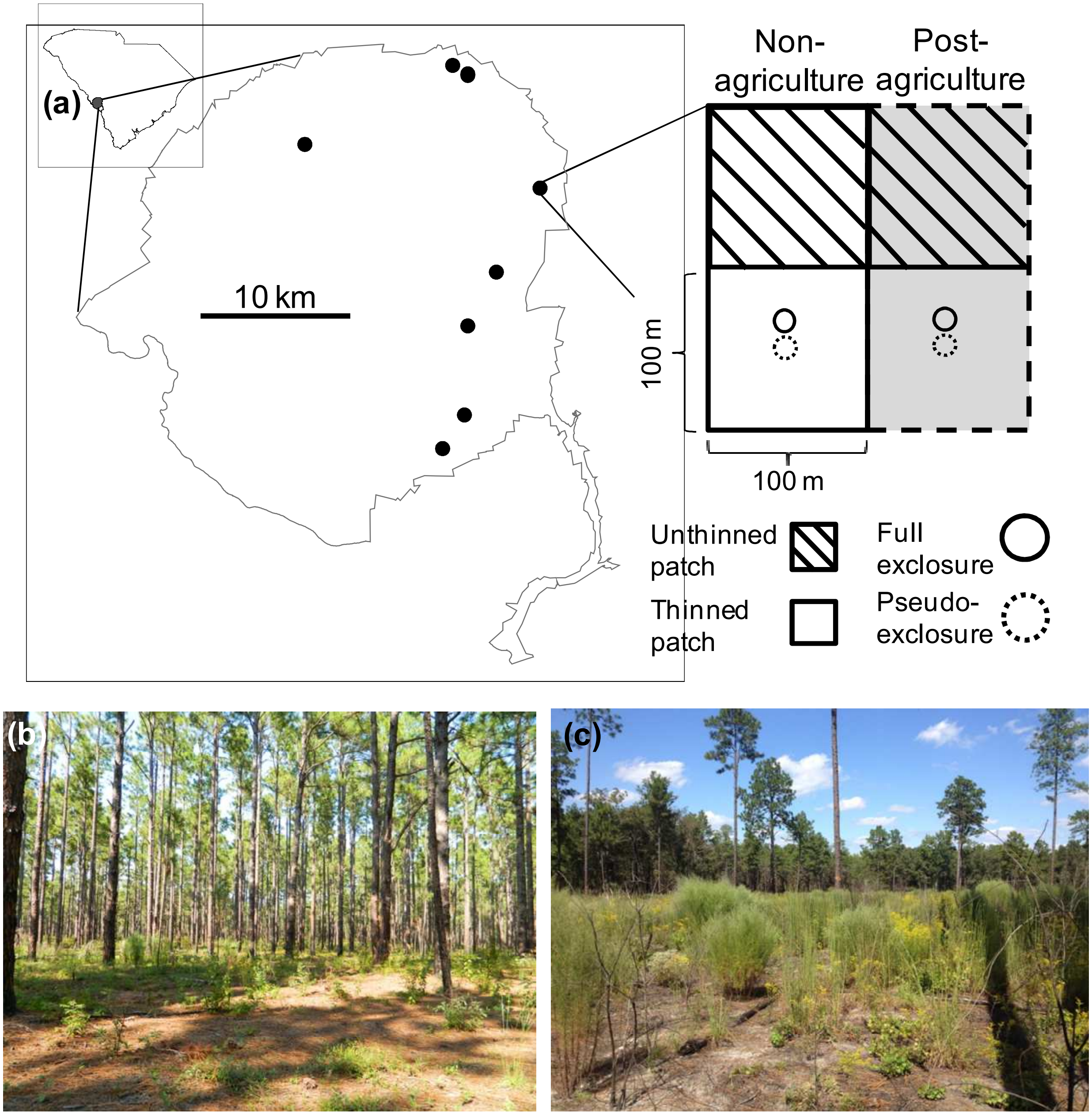

Fig. 1. A) Experimental longleaf pine woodlands at the Savannah River Site, South Carolina, USA. Overstory trees were thinned or left intact (unthinned). Consumer exclosures (not to scale) were located 50m from the boundary between post-agricultural and non-agricultural woodlands to avoid edge effects. View from B) a post-agricultural pine plantation and C) a thinned patch.

Figure 2:

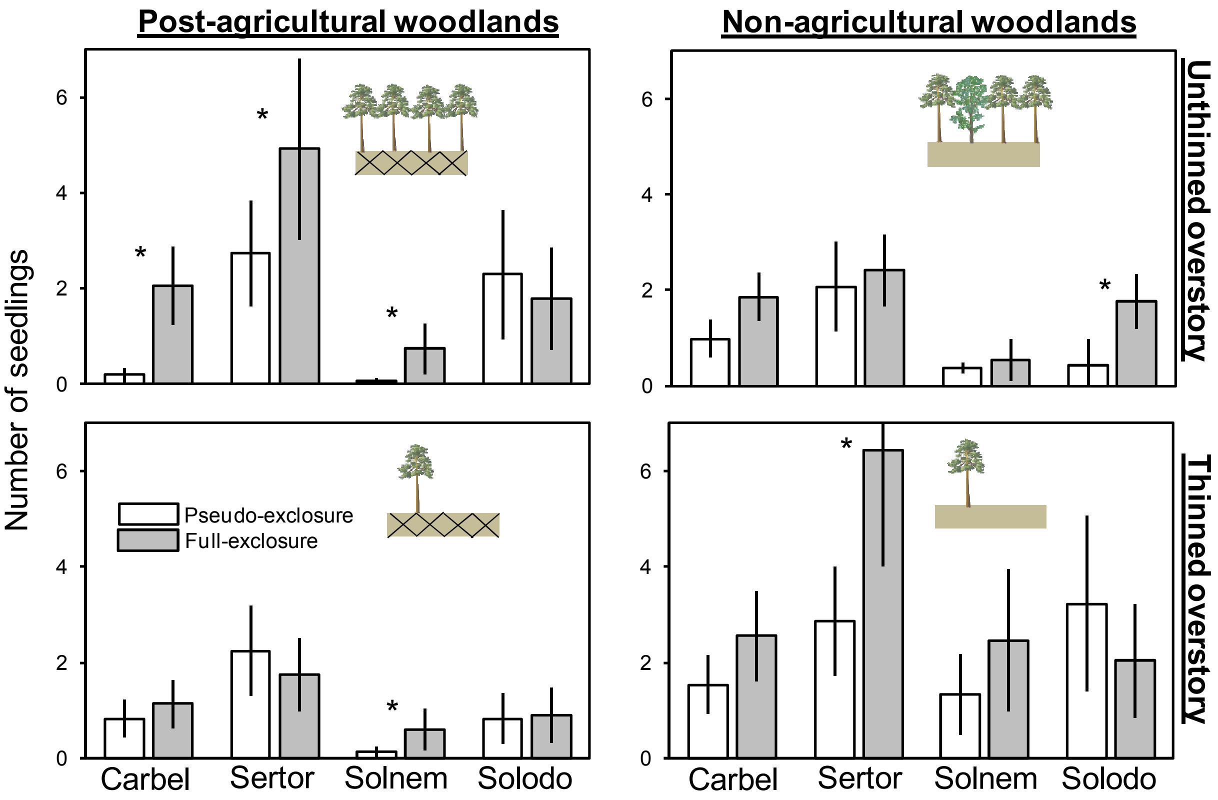

Fig. 2. Number of seedlings establishing in the consumer exclosures within each of the four habitat combinations for the four plant species used in a seed addition experiment conducted in longleaf pine woodlands at the Savannah River Site, South Carolina, USA. Values are back-transformed least-square means from generalized linear mixed models using a Poisson error distribution. Codes on the x-axis are the first three letters of the genus and species. Error bars are standard errors. Presence of an asterisk (*) indicates a significant difference (*P*<0.05) between exclosure treatments within a species.

Figure 3:

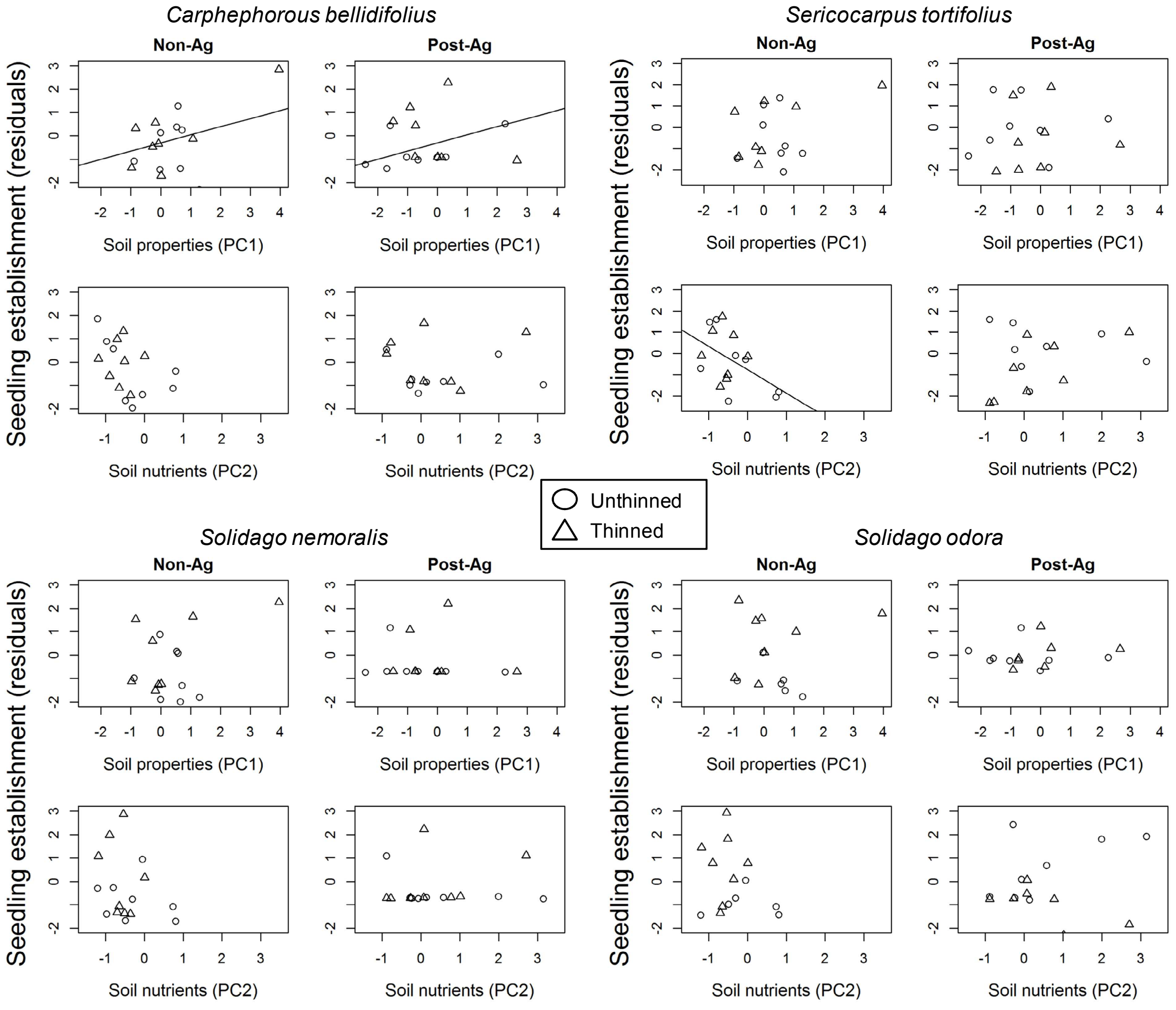

Fig. 3. Relationships between seedling establishment and the first two principal components from the soil analysis. Trend lines are shown for significant ($P \leq 0.05$) (see Table 1 & Table S2c). Points are the residuals after accounting for the other principal component axis. Note that the PC1 trend lines for *C. bellidifolius* are based on the pooled land-use history data, although we present the data in separate panels for clarity. Data are from pseudo-exclosure plots.

SUPPORTING INFORMATION

Establishment of multiple plant species is contingent upon land-use history, overstory tree thinning and consumers

Philip G. Hahn* and John L. Orrock

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

*Corresponding author: Philip G Hahn, 430 Lincoln Dr., Madison WI, 53706. Phone: (608) 262-5868, email: pghahn@wisc.edu

APPENDIX S1. Additional information on plant species and seed collection

Seeds were collected from natural populations on SRS in December 2012. Prior to deployment to the field, we conducted germination trials in a climate controlled growth chamber at 13.5 h light cycle at 29.5°C and 10.5 h dark cycle at 14.2°C, which represent climate norms in South Carolina in May. 25 seeds were placed on a moist filter paper in a 5.5 cm diameter petri dish. We had 10 replicates per species. Germinating seeds (i.e., emergence of a radicle) were counted and removed every 1-3 days for two weeks. Germination was 26.0% (±0.007 SE) for *Carphephorus bellidifolius*, 18.8% (±0.010 SE) for *Sericocarpus tortifolius*, 17.7% (±0.006 SE) for *Solidago nemoralis*, and 18.4% (±0.012 SE) for *Solidago odora*. We continued to monitor germination for an additional two weeks, although a mechanical error interrupted the day/night and temperature cycle (24 h light cycle at 24° C). However, additional germination was low (< 2%) for all species except *C. bellidifolius*, which increased to 46.0%.

Table S1. Plant species used in the seed addition experiment.

Plant species	Seed mass[1] (mg)
Carphephorus bellidifolius	1.00 ± 0.44
Sericocarpus tortifolius	0.59 ± 0.23
Solidago nemoralis	0.08 ± 0.02
Solidago odora	0.20 ± 0.07

1. Seed mass is the mean (± 1 SE) of 10 seeds (including pappus), except for *So. nemoralis* which was weighed in 10 batches of 10 seeds.

APPENDIX S2. Details from the soil analysis.

Table S2a. Results from the principal component analysis on soil organic matter, soil water holding capacity, and soil phosphorus. Variables were scaled prior to analysis and the correlation matrix was used for the principal component analysis.

	PC1	PC2	PC3	PC4
Std dev	1.27	1.03	0.86	0.75
Var explained	0.41	0.27	0.19	0.14

Table S2b. Loadings for the first two axes from the principal component analysis. Note that we inverted PC2 for subsequent analyses so that higher values of PC2 indicate higher values of soil phosphorus and cation exchange capacity.

Loadings	PC1	PC2
Organic matter (%)	0.62	0.01
Water holding capacity (%)	0.62	0.15
Cation exchange capacity	0.45	-0.48
Mehlich phosphorus (µg g^{-1})	-0.14	-0.86

Table S2c. Parameter estimates from Poisson multiple regressions for seedling establishment of four plant species in non-agricultural and post-agricultural habitats.

Species	**Effect**	**Non-agriculture**				**Post-agriculture**		
Carphephorus bellidifolius		β	se	*P*	θ	β	se	*P*
	Intercept	-0.73	0.53	0.170		-0.61	0.68	0.421
	Soil properties (PC1)^{a}	0.69	0.19	0.005		0.45	0.4	0.289
	Soil nutrients (PC2)^{b}	-1.10	0.62	0.101		0.05	0.5	0.924
Sericocarpus tortifolius								
	Intercept	0.15	0.44	0.731		0.91	0.37	0.065
	Soil properties (PC1) ^{a}	0.52	0.18	0.014		0.25	0.19	0.210
	Soil nutrients (PC2) ^{b}	-1.15	0.47	0.031		0.49	0.27	0.131
Solidago nemoralis								
	Intercept	-0.44	0.64	0.508	o	-1.49	0.77	0.112
	Soil properties (PC1) ^{a}	0.55	0.33	0.142	o	0.13	0.49	0.789
	Soil nutrients (PC2) ^{b}	-0.8	0.81	0.341	o	0.04	0.54	0.946
Solidago odora								
	Intercept	0.77	0.58	0.206	o	-1.31	1.45	0.400
	Soil properties (PC1) ^{a}	0.35	0.37	0.367	o	0.33	0.30	0.299
	Soil nutrients (PC2) ^{b}	-0.43	0.76	0.580	o	2.40	0.59	0.001

a The first principal component axis was a general index of soil organic matter, soil water holding capacity and soil cation exchange capacity.

b The second principal component axis was an index of soil phosphorus and soil cation exchange capacity.

θ Column with ‘o’ indicates the model was corrected for overdispersion using a negative binomial distribution (Littell et al. 2006).

APPENDIX S3. Supplementary grasshopper analysis.

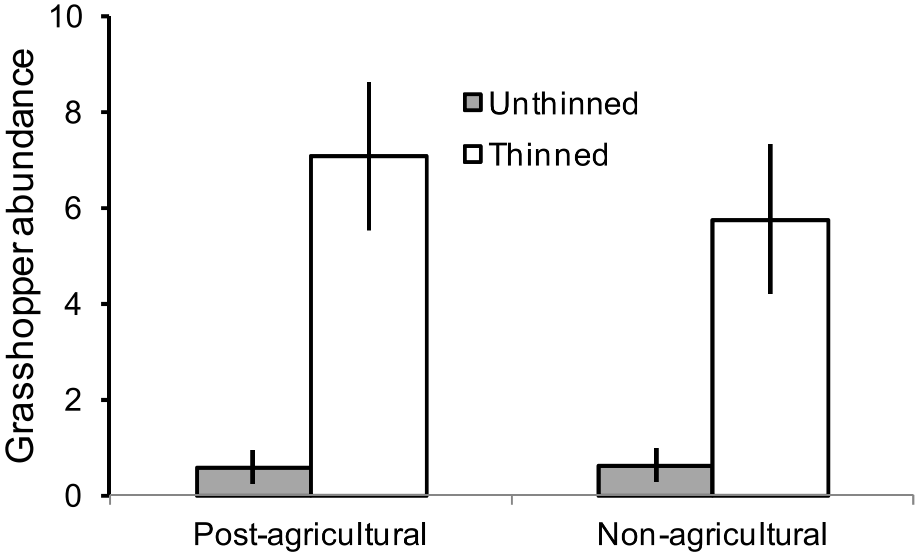

Figure S3. Grasshopper abundance averaged across the three 15m transects in each 1 ha patch. Thinning had a significant effect on grasshopper abundance ($F = 26.7$, $P < 0.001$), although land-use history ($F = 0.33$, $P = 0.57$), and the interaction between thinning and land-use history ($F = 0.37$, $P = 0.55$) did not affect grasshopper abundance. Statistics are based on a linear mixed model conducted in proc mixed in SAS (v 9.4, SAS Inc., Cary, NC, USA) that included site as a random effect and allowed for unequal variance among thinning treatments by including an R-side random effect (Littell *et al.* 2006).

Littell, R.C., Milliken, G.A., Stroup, W.W., Wolfinger, R.D. & Schabenberger, O. (2006) *SAS for Mixed Models*. 2nd Edition. SAS Institute Inc., Cary, NC.

Table S3. Results of preliminary analysis of the effects of soil properties (PC1), soil nutrients (PC2), and grasshopper abundance on seedling emergence in pseudo-exclosure plots.

Species	**Effect**	**Non-agriculture**			**Post-agriculture**		
Carphephorus bellidifolius		β	se	*P*	β	se	*P*
	Intercept	-0.86	0.60	0.149	-1.58	0.81	0.051
	Soil properties (PC1)	0.65	0.17	0.000	-0.30	0.42	0.473
	Soil nutrients (PC2)	-1.09	0.59	0.065	0.10	0.26	0.685
	Grasshopper abundance	0.04	0.07	0.556	0.17	0.12	0.143
Sericocarpus tortifolius							
	Intercept	-0.04	0.51	0.942	1.03	0.42	0.014
	Soil properties (PC1)	0.48	0.17	0.004	0.31	0.35	0.375
	Soil nutrients (PC2)	-1.19	0.47	0.012	0.43	0.23	0.064
	Grasshopper abundance	0.04	0.05	0.402	-0.03	0.05	0.550
Solidago nemoralis							
	Intercept	-1.40	0.72	0.053	-3.44	1.76	0.051
	Soil properties (PC1)	0.60	0.15	0.000	-0.83	0.71	0.245
	Soil nutrients (PC2)	-8.65	0.65	0.182	0.05	0.38	0.904
	Grasshopper abundance	0.19	0.07	0.006	0.30	0.20	0.134
Solidago odora							
	Intercept	-0.12	0.55	0.831	-3.15	2.44	0.196
	Soil properties (PC1)	0.00	0.23	0.988	0.07	0.47	0.882
	Soil nutrients (PC2)	0.14	0.41	0.732	3.24	1.16	0.005
	Grasshopper abundance	0.20	0.20	0.000	0.08	0.09	0.409

Chapter 6

STAGE-SPECIFIC RESPONSES OF FOUR PLANT SPECIES TO ADDITIVE AND INTERACTIVE EFFECTS OF LAND-USE HISTORY, CANOPY STRUCTURE AND HERBIVORY

Philip G. Hahn (pghahn@wisc.edu) and John L. Orrock (jorrock@wisc.edu)

[Manuscript in preparation for *Ecology*]

Abstract. The effect that herbivores have on plant performance often depends on characteristics of the environment, although a major challenge to understanding context-dependent herbivory lies in disentangling the habitat-induced effects on plant performance from the herbivore-induced effects on plant performance. We conducted a landscape-scale manipulation of overstory canopy in longleaf pine woodlands with either a history of agricultural or no agricultural history and coupled this with local-scale grasshopper exclosures. We measured performance of three demographic stages on four perennial herbaceous species (*Carphephorus bellidifolius*, *Sericocarpus tortifolius*, *Solidago nemoralis*, and *So. odora*; n = 1,024 plants) over a two year period at sites spread across an 80,000 hectare landscape. Performance metrics of the four focal plant species were affected by overstory tree thinning, land-use history, and herbivores although to different degrees. Grasshopper herbivory affected juvenile plant survival for all four species we tested regardless of land-use history, but only in woodlands with an intact canopy. The exception was for the smallest plant species *Carphephorus bellidifolius*, where juvenile survival was reduced by grasshopper herbivory in thinned post-agricultural patches and unthinned non-agricultural patches. Performance of adults (flowering and biomass production) was not affected by grasshopper herbivory but increased in thinned patches and for two species more so in thinned non-agricultural patches compared to thinned post-agricultural patches. Damage by all insects, including non-orthopteran insects, was an important agent reducing plant biomass of adult plants but only in thinned patches, likely corresponding to greater abundance of insect herbivores in these patches. Land-use history patches were similar in light availability and herbivory rates, but differ in soil properties, suggesting that altered soil conditions in post-agricultural sites reduce growth and flowering. Collectively, this work experimentally separates the habitat-induced effects from the herbivore-induced effects on plant performance and highlights that the importance of context-dependent plant-herbivore interactions depend on plant demographic stages and species traits.

Key-words: context-dependent, grasshoppers, herbivory, light availability, old-field, plant demography, plant-herbivore interactions.

INTRODUCTION

Mounting evidence suggests that herbivores can exert strong negative effects on plant performance and survival (Crawley 1989). Moreover, the effect that herbivory has on plant performance is often context-dependent, depending on ontogeny of the plant (Massad 2012, Barton and Hanley 2013) or characteristics of the habitat (Maschinski and Whitham 1989, Bakker et al. 2006, Hahn and Orrock 2015a). Disentangling how environmental context may affect herbivory is becoming increasingly important when considering the myriad of human activities that alter existing or create novel environmental conditions (Vitousek et al. 1997). For instance, a large fraction of the terrestrial land surface is undergoing succession on abandoned agricultural lands, the legacies of which can have persistent effects on plant communities by altering soil properties and reducing reestablishment of certain species (Foster et al. 2003, Flinn and Vellend 2005, Cramer et al. 2008). Agricultural legacies can also affect plant performance directly through changes in soil nutrients (Fraterrigo et al. 2006, 2009, Baeten et al. 2011) or indirectly through increased herbivory rates on palatable plants by reducing alternative vegetation available for consumption (Hahn and Orrock 2015a).

Many post-agricultural systems are further modified by concurrent human activities, such as fire suppression (Briggs et al. 2005, Nowacki and Abrams 2008, Ratajczak et al. 2012). Canopy closure and associated reductions in light availability due to fire suppression can also have substantial effects on plant performance (Smith 1982, Harrington et al. 2003, Harrington

2011) and community structure by shifting composition from herbaceous to woody plants (Hartnett and Bazzaz 1985, Meiners 2007, Rogers et al. 2008). Light environment can subsequently affect herbivory rates by altering herbivore abundance (Evans et al. 2012, Stoepler and Rehill 2012) or mediating plant tolerance to herbivory (Salgado-Luarte and Gianoli 2010, 2011, Baraza et al. 2010). Despite what is known about land-use history and light availability individually, the combined effects of multiple anthropogenic disturbances on biotic interactions such as herbivory are only beginning to be recognized (Tylianakis et al. 2008, Thébault et al. 2014, Hahn and Orrock 2015a). Thus, because plant growth can be affected directly by land-use history and canopy structure, or indirectly by increased herbivore abundances and herbivory rates, a major challenge lies in disentangling the habitat-induced responses from the herbivore-induced responses of plant performance in different habitats. An explicit consideration of how historic forces interact with the contemporary abiotic environment to alter the effect of herbivores on different plant life stages is essential for understanding the recovery and plant performance in modified habitats. However, answers to these questions necessitate multi-year factorial herbivore-exclosure experiments conducted across appropriate large-scale variation in land-use history and canopy structure.

In this paper, we combine local herbivory experiments with landscape-scale habitat manipulations to disentangle the effect of habitat-context and herbivores on the performance of multiple plant demographic stages within different environmental contexts at spatial scales relevant to conservation and management. We manipulated canopy structure in 64 1-ha longleaf pine woodland stands that were historically used for agriculture (>60 years since abandonment) and sites that were never used for agriculture. Within these experimental landscapes, we measured herbivore damage and performance on transplanted seedlings exposed to or protected from herbivores. Because context-dependent effects of herbivory on plant performance could potentially be due to traits of different plant species in addition to habitat conditions (Hahn and Orrock 2015a), we selected four species in the Asteraceae that vary in growth rate and occurrence in post-agricultural and non-agricultural habitats. We hypothesized that 1) the effects of herbivory on plant performance would be greatest on earlier life stages (i.e., juvenile survival; Barton and Hanley 2013). We also hypothesized that 2) plant performance would be less affected by herbivory in thinned patches because of increased light availability, particularly for faster-growing species (Hahn and Orrock 2015b). Based on previous findings (Hahn and Orrock 2015a), we predicted that 3) herbivory would have greater effects where alternative plant resources are low, particularly in post-agricultural sites. Collectively, we expected herbivory to have the greatest effect on juvenile plant survival in unthinned, post-agricultural habitats. By combining experimental manipulation of abiotic (habitat) conditions with measurements on multiple demographic stages on a suite of plant species with and without herbivores, we provide a comprehensive overview of the context-dependent effects of herbivores on plant performance.

METHODS

Study site and landscape experiment

We conducted this study at the Savannah River Site (SRS) (Fig. 1A), an 80,125 ha National Environmental Research Park near Aiken, South Carolina, USA located within the historical range of the longleaf pine ecosystem. Much of SRS was converted to agriculture between 1865 and 1950, although farms were small, dispersed across the landscape, and contained many pockets of untilled woodlands (White and Gaines 2000). Agricultural fields were abandoned in 1951 following government acquisition of SRS (Kilgo and Blake 2005). We determined historic land use by examining aerial photographs taken in 1951, just prior to governmental acquisition of SRS. As in Brudvig et al. (2013), cultivated fields in 1951 were classified as "post-agricultural woodlands" and mature woodlands in 1951 were classified as "non-agricultural woodlands." The post-agricultural woodlands were subsequently replanted with longleaf (*Pinus palustris*), loblolly (*P. taeda*), or slash (*P. elliottii*) pine trees in the 1950-70's (Kilgo and Blake 2005). We selected 15 4-hectare sites and one 8-hectare site that encompass a non-agricultural/post-agricultural boundary (Fig. 1). Blocking by sites that contained both types of land-use history reduces the potentially confounding issue of non-random selection of agricultural fields by statistically accounting for environmental variation of the site (Flinn and Vellend 2005). Soil series, slope, fire frequency, and overstory tree basal area were relatively homogenous within sites (Brudvig et al. 2013). Within this general design, we conducted a randomized, factorial manipulation of canopy closure (thinned or unthinned). Overstory tree thinning occurred in early 2012 and 1-ha patches were thinned to 8-10 longleaf pine trees per hectare. Control patches had an average tree density of 550-750 trees per hectare and the canopy in non-agricultural was slightly more dense due to hardwood encroachment compared to the post-agricultural pine plantations (approximately 77% and 66% canopy closure, respectively; Brudvig et al. 2013). A broad-spectrum herbicide was spot-applied to woody vegetation in the understory of the thinned patches in September 2012 to control regenerating broadleaf plants (Harrington 2011), but the herbicide was not applied to study areas where the experimental plants were located.

Local herbivory experiment

The Asteraceae is a dominant plant family in the longleaf pine ecosystem (Walker and Silletti 2006), representing 60 of the 312 species found in our study plots (Brudvig et al. 2013). We selected four plant species of Asteraceae: *Carphephorus bellidifolius* (Michx.) Torr. & A.

Gray, *Sericocarpus tortifolius* (Michx.) Nees, *Solidago nemoralis* Aiton, and *Solidago odora* Aiton. These four species vary widely in their habitat occurrences, with *C. bellidifolius* and *Se. tortifolius* occurring more frequently in non-agricultural habitats, *So. nemoralis* occurring more frequently in post-agricultural habitats, and *So. odora* occurring frequently in both habitat types, based on surveys conducted in the year prior to this experiment (Brudvig et al. 2013). Grasshoppers are common invertebrate herbivores in our system (Evans et al. 2012, Hahn and Orrock 2015a) and include the most likely insect consumers of the focal plant species. The two most common species of grasshoppers at our site are *Melanoplus angustipennis* (subfamily: Melanoplinae) and *Schistocerca alutacea* (subfamily: Cyrtacanthacridiae) (Hahn and Orrock 2015c), both species are mixed-feeders that can eat a variety of grasses and forbs (Joern 1985). Grasshoppers in the subfamilies Gomphocerinae and Oedipodinae are also present at our site (Hahn and Orrock 2015c), although both of these subfamilies consume mainly grasses (Joern 1985) and thus were not likely to eat our experimental plants. We previously measured preference of the plant species to two of the dominant grasshopper species at our site using cafeteria-style (choice) feeding experiments (Hahn and Orrock 2015b). *Schistocerca* grasshoppers consumed similar amounts of *Se. tortifolius, So. nemoralis,* and *So. odora*, but consumed lower amounts of *C. bellidifolius*. *Melanoplus* grasshoppers preferred *So. nemoralis* and to a less degree *So. odora*, and consumed low amounts of *C. bellidifolius* and *Se. tortifolius*.

Plants were obtained by germinating seeds collected on SRS and grown for 30-45 days in a greenhouse at the Savannah River Ecology Laboratory prior to deployment into the field. Seedlings were grown in a 1:1 mixture of potting soil and sand and then transplanted into mesh-bottom greenhouse trays (35 cm × 35 cm, 2 cm mesh) filled with approximately 5 cm of the potting soil and sand mixture. Plants of similar sizes were paired and haphazardly transplanted into each tray. Each tray received a total of eight plants, consisting of two individuals of each of the four study species.

We established paired grasshopper exclosures (full-exclosures and pseudo-exclosures) near the center of each of the one-hectare patches (n = 132 exclosures). Exclosures were 0.125 m^2 × 1 m tall mesh (2.7 mm mesh) screen cages (pseudo-exclosures have holes to allow grasshoppers to enter) and have been previously used to reduce herbivory by grasshoppers (Families Acrididae and Tettigoniidae). Temperature and light availability do not differ between the two exclosure types (Hahn and Orrock 2015a). For this experiment, we transplanted a total of 1,024 seedlings of the four species (n = 264 seedlings of each species) into the grasshopper exclosures between 02 and 26 July 2012. 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). The trays were buried so that the top of the tray was flush with the soil surface. The open-mesh bottom of the trays were directly exposed to the mineral soil so that the plants could root into the native soil at each site allowing us to directly test whether plant performance differ between land-use histories. Observations upon extracting the plants at the end of the experiment confirmed that the plants rooted in the native soil in all treatment combinations (PGH *pers. obs.*). The grasshopper exclosures were installed immediately after the trays were transplanted into the field and were applied as split-plots, with the one-hectare landscape manipulations (combinations of land-use history and canopy thinning) as the whole-plots. Exclosures were buried approximately 3 cm below the soil surface and kept in place using landscape staples. We supplemented water during the first three weeks after transplanting into the field.

Quantifying herbivore damage and plant performance

We measured herbivore damage and plant performance at three time points: September 2012, June 2013, and September 2013. In September 2012 and June 2013, we estimated plant-level herbivory as the proportion of leaves with >5% leaf tissue removed by chewing insects. This is a non-destructive sampling technique that estimates the relative, not absolute, damage to plants (Root 1996). We recorded plant survival in June 2013, after one year. To reduce shading from overcrowding, we thinned each plot to one randomly selected individual plant per species in June 2013. In September 2013, we recorded whether or not a plant flowered and then destructively sampled the plants by collecting 3-6 leaves at regular intervals along the tallest stem and scanned these leaves using a portable scanner (VuPoint Solutions, City of Industry, CA, USA). We then calculated the area removed by leaf chewing insects using ImageJ (National Institutes of Health, Bethesda, MD, USA) and converted this to the proportion of leaf tissue removed. During this last survey, many of the plants became prohibitively large to count all the leaves. We harvested all above-ground plant material in September 2013 and measured dried above-ground biomass production. All four of the species are able to reproduce clonally and all of our measures were at the genet level. In sum, we quantified plant performance of three demographic stages over the two year study: first year survival, proportion of plant flowering in year two, and above-ground biomass production after the second year.

Evaluating the effectiveness of the herbivore exclosures

Herbivore exclosure cages effectively reduced the proportion of leaves damaged in September 2012, but not at subsequent surveys (Appendix A). During both surveys in 2013, we observed a more diverse assemblage of insects on the experimental plants in both exclosures types, including aphids, stem-galling insects, leaf-rolling insects, lepidopteran larvae, and leaf beetles. Grasshoppers were frequently observed on plants in the pseudo-exclosures but rarely observed on the plants in the full exclosures (PGH *pers. obs.*).

Statistical analyses

We used linear mixed models to separately analyze each of the three measures of plant performance for each of the four species. In these models, the response variable was the metric of performance for the three demographic stages (i.e., survival after one year, flowering in year two, and above-ground biomass production in year two). Land-use history, overstory tree thinning, herbivory (caged or open), and all interactions were fixed effects. We included site as a random (blocking) effect and site × land-use history × overstory tree thinning as a random effect to account for the grasshopper exclosures being applied as a split-plot design. We used linear mixed effects models (LMM) for probability of surviving and flowering instead of generalized linear mixed models (GLMM) with binary distributions for survival and flowering, because some species had 100% survival or flowering in one or more treatment combinations, and the GLMMs failed to converge. However, the GLMMs that converged were qualitatively similar to the LMM. Thus, for consistency, we only present the results of the LMM for all models.

To evaluate the effects of herbivore damage by chewing insects in the second year of the study (i.e., the year when the plants were also attacked by non-orthoperan insects) on final plant biomass and whether this relationship varied among habitat types we constructed linear mixed models with the proportion of leaves damaged in June 2013, land-use history, overstory tree thinning, and all interactions as fixed effect predictor variables. The response variable was the final biomass (g). We pooled plants from both exclosure treatments for this analysis. Site was included as a random effect. We conducted similar analyses using the proportion of leaf tissue removed measured in September 2013. However, this measure of herbivore damage was not related to final plant biomass (data not shown).

We natural log-transformed above-ground biomass (+1) for all species to meet the assumptions of normality and homogeneous variance, but did not transform any of the other response variables. We examined the residuals of all models to ensure they did not violate the assumptions of normality and homogeneity of variance. All statistical analyses were conducted using the the lmer function in the lme4 package (Bates et al. 2013) in R (v. 2.1).

RESULTS

Juvenile survival

Grasshopper exclosures affected juvenile survival of all four plant species and also interacted with other factors (Table 1). *Carphephorus bellidifolius* was affected by the three-way interaction between exclosures, land-use history, and overstory thinning (Table 1), with the greatest reductions in survival due to grasshopper herbivory in the thinned, post-agricultural treatment and the unthinned non-agricultural treatment (Fig. 2A). *Sericocarpus tortifolius*, *Solidago nemoralis*, and *So. odora* were all affected by the interaction between grasshopper exclosures and thinning, although the effect was only marginally significant for *So. odora* (Table 1). For all three of these species, grasshopper herbivory significantly reduced survival in unthinned patches, but not in thinned patches (Fig. 2B-D).

Adult flowering

The proportion of plants that survived year one and flowered in the second year was significantly greater in thinned patches compared to unthinned patches for all four plant species (Fig. 3; Table 1). Nearly twice as many *C. bellidifolius* flowered in thinned non-agricultural sites compared to thinned post-agricultural sites, although this effect was only marginally significant ($P = 0.07$; Table 1). No other treatments affected adult flowering for any of the plant species

(Table 1).

Biomass

Biomass production varied widely among the four species, with maximum above-ground biomass production of the largest species *So. nemoralis* being over 10-fold greater than the smallest species *C. bellidifolius*. *Sericocarpus tortifolius* produced the second highest levels of above-ground biomass and *So. odora* produced the third highest values (Fig. 4). Biomass production of all four species was at least five times greater in thinned patches compared to unthinned patches (Fig. 4; Table 1). For *Se. tortifolius* and *So. nemoralis*, the thinning effect was greater in non-agricultural sites compared to post-agricultural sites, although only significantly for *So. nemoralis* and marginally significantly for *Se. tortifolius*. *Carphephorus bellidifolius* biomass production was also marginally affected by herbivory (Fig. 4A; Table 1).

Biomass production was negatively related to the proportion of leaves damaged in June 2013 for three plant species. This effect was only significant in thinned patches for *Se. tortifolius* and *So. nemoralis*, whereas the relationship was marginally significant pooled across thinning treatments for *So. odora* (Table 1; Fig. 5). Biomass production of *C. bellidifolius* was not related to the proportion of damaged leaves in June 2013 (Table 1; Fig. 5). Land-use history did not affect the relationship between biomass and leaf damage for any species (Table 1).

DISCUSSION

By linking local herbivore exclosures with experimental manipulations of large-scale habitat factors, our work provides several insights regarding the role of herbivores and environmental context in shaping performance of multiple demographic stages on four plant species. First, as predicted, grasshopper herbivory caused the greatest reduction in plant performance on earlier demographic stages, particularly under canopy where light was also limited. Grasshopper herbivory did not affect the growth of any of the four plant species in the second year. However, damage by all insects did reduce biomass and this effect was only evident in thinned patches where insects are more abundant. We also found that overstory tree thinning increased the probability of flowering and biomass production of all four plant species and for these species the effect of overstory tree thinning was greater in non-agricultural land-use history sites compared to post-agricultural sites. Collectively, this work provides new insight into the context-dependency of plant-herbivore interactions, as well as the legacy effects of land-use history on plant performance.

Context-dependent effects of herbivory on plant performance

Generalist herbivores often inflict lethal damage to seedlings and thus mortality of seedlings or juvenile plants due to invertebrate herbivores can exert strong pressures on patterns of plant recruitment (Hulme 1994, Hanley et al. 1995, Moles and Westoby 2004, Allan and Crawley 2011, Barton and Hanley 2013). We found strong negative effects of grasshopper herbivory on some demographic stages of all four plant species, particularly juvenile plant survival in habitats with intact canopies (Fig. 2). In the second year of the study we found no effects of grasshopper exclosures on flowering or biomass production. However, we did find that the proportion of leaves damaged in June 2013 reduced plant biomass at the end of the growing season for three of the four species (Fig. 5). For two species, *Se. tortifolius* and *So. nemoralis*, the negative relationship between the proportion of leaves damaged was only evident in thinned patches.

The patterns described above are potentially explained by the switch in the dominant herbivore taxa that we found between the first and second year of the study. In the second year, we observed higher frequencies of lepidoperans, coleopterans, and hemipterans in thinned patches (PGH *pers. obs.*), all of which are taxa that can be more specialized than orthopterans, which are often generalist herbivores (Joern 1983). Furthermore, because larva of these insect taxa require oviposition on or near a host plant, these taxa are perhaps less likely to colonize seedlings and juvenile plants (Feeny 1976, Price and Wilson 1979). Specialists also tend to be more efficient foragers than generalists (Bernays 2001) and their foraging behavior was perhaps were less sensitive to differences in plant community composition between land-use histories than the foraging behavior of generalists. Another non-mutually exclusive explanation is that sun and shade plants differentially allocate resources. Higher allocation to belowground resources in shade plants may allow them to better compensate for herbivore damage (Hakes and Cronin 2012), despite having lower above-ground biomass production (Fig. 5). Interestingly, we found the opposite patterns on these plants during the first year of growth, where plants exposed to grasshopper damage were significantly smaller compared to plants in grasshopper exclosures mostly often in the unthinned treatments (Hahn and Orrock 2015b). Thus, first year plants may not have accumulated enough belowground carbon storage to be able to compensate for herbivore damage, resulting in reduced growth (Hahn and Orrock 2015b) and survival (Salgado-Luarte and Gianoli 2010, Fig. 2) under shade. Finally, the fastest growing plants species, *Se. tortifolius* and *So. nemoralis*, were most able to compensate in biomass production for herbivore damage in shade (Fig. 5), which is potentially related to faster-growing species' ability to accumulate carbon after tissue removal (Atkinson et al. 2014).

In addition to affecting growth and flowering, we found that land-use history can alter the effect that herbivores have on the performance of some plant species (i.e., the most palatable or small, vulnerable plant species). In the present study, survival of juvenile *Carphephorus bellidifolius* plants was reduced by grasshopper herbivory in unthinned non-agricultural patches and thinned post-agricultural patches (Fig. 2). A potential explanation for this pattern is that land-use history can alter the alternative food sources available to herbivores by changing the abundance and composition of the neighboring plant community (Hahn and Orrock 2015a). The dominant grasshopper species also differ between land-use histories (Hahn and Orrock 2015c) and these species may have slightly different dietary preferences (Hahn and Orrock 2015b), but this does not appear to drive differential herbivory between land-use histories (Hahn and Orrock 2015a). Collectively, these results demonstrate that habitat-specific negative effects of herbivory on juvenile plant survival may negatively affect recruitment under certain environmental conditions, specifically low-light environments and for certain plant species, most likely smaller species.

Interaction of land-use history and canopy structure on plant performance

The interaction between land-use history and canopy structure affected flowering probability and adult size (biomass) and these effects were largely independent of herbivory. As expected, overstory tree thinning dramatically increased flowering probability and adult size for all four species (Smith 1982, Harrington et al. 2003, Harrington 2011). Similarly, land-use history can also affect plant growth (Fraterrigo et al. 2006, Baeten et al. 2011). Our study found that the effect of overstory tree thinning on adult size was greater in non-agricultural habitats for *Se. tortifolius* and *So. nemoralis*. Similarly, *C. bellidifolius* flowered in higher proportion in thinned non-agricultural habitats compared to thinned post-agricultural habitats. Interestingly, there were no differences in light conditions (Hahn and Orrock 2015b) or herbivory among these two habitat types but soil properties, such as organic matter, nutrients, and microbial communities differ among land-use histories (McLauchlan 2006, Fierer et al. 2013, Bizzari et al. 2015). This finding suggests that altered soil conditions in post-agricultural sites reduce growth and flowering even after implementing overstory tree thinning, which is a common tool used to restore longleaf pine savannas throughout the historical range (Gilliam and Platt 2006, Walker and Silletti 2006).

Implications for recovery of post-agricultural ecosystems

The longleaf pine ecosystem is one of the most critically endangered ecosystems, with less than 3% of the original extent remaining (Noss 2013). This work provides insight into the recovery of post-agricultural ecosystems, including the role of herbivory and overstory tree thinning, which is a common restoration technique in fire-suppressed longleaf pine woodlands (Harrington 2011). Our works corroborates the findings that overstory tree thinning can improve plant performance (Harrington and Edwards 1999, Harrington et al. 2003, Harrington 2011) and suggests that these effects depend on the demographic stage of the plant. Moreover, the positive effect of overstory tree thinning was greater in sites with no history of agriculture, suggesting that soil legacies in post-agricultural systems (McLauchlan 2006) negatively affect plant performance of our focal plants. Successful restoration of post-agricultural longleaf pine woodlands may thus require techniques that approximate historic soil conditions, such as through soil carbon amendments (Blumenthal et al. 2003). Overall, our results suggesting that small, slow growing plant species will be most affected by grasshopper herbivory, whereas faster-growing species will be able to better tolerate herbivory and also respond more strongly to overstory tree thinning in longleaf pine woodlands with no agricultural legacies.

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Appendix A. Effectiveness of the herbivore exclosures.

Table 1. ANOVA tables for the effects of grasshopper exclosures, land-use history, and overstory tree thinning on juvenile survival, proportion flowering, and total biomass production for four species of Asteraceae.

Juvenile survival	*Carphephorus bellidifolius*		*Sericocarpus tortifolius*		*Solidago nemoralis*		*Solidago odora*	
Effect	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Exclosure	13.2	0.000	9.4	0.002	24.1	0.000	8.9	0.003
Land-use history	3.9	0.056	0.0	0.901	0.9	0.361	1.6	0.218
Overstory thinning	0.1	0.732	8.6	0.005	13.8	0.001	0.6	0.449
Excl x LU	1.9	0.170	1.6	0.201	2.2	0.140	1.9	0.172
Excl x Thin	0.2	0.661	7.0	0.009	15.8	0.000	3.4	0.067
LU x Thin	0.0	0.923	0.0	0.962	0.0	0.917	0.3	0.590
Ex x LU x Thin	4.1	0.045	0.0	0.969	2.2	0.140	0.1	0.813

Flowering	*Carphephorus bellidifolius*		*Sericocarpus tortifolius*		*Solidago nemoralis*		*Solidago odora*	
Effect	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Exclosure	0.9	0.350	0.4	0.546	1.2	0.283	0.0	0.888
Land-use history	1.7	0.210	0.0	0.931	1	0.319	0.0	0.859
Overstory thinning	11.3	0.005	160.9	0.000	101.5	0.000	24.3	0.000
Excl x LU	0.0	0.943	0.0	0.889	2.9	0.094	0.4	0.512
Excl x Thin	0.1	0.787	2.5	0.115	0.3	0.606	0.4	0.537
LU x Thin	3.5	0.074	0.7	0.415	0.1	0.739	0.0	0.932
Ex x LU x Thin	0.4	0.532	0.1	0.726	0.0	0.923	0.8	0.376

Biomass[1]	*Carphephorus bellidifolius*		*Sericocarpus tortifolius*		*Solidago nemoralis*		*Solidago odora*	
Effect	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Exclosure	3.32	0.073	0.3	0.616	0.1	0.805	0.6	0.428
Land-use history	0.31	0.582	0.9	0.354	0.0	0.90	0.4	0.531
Overstory thinning	26.11	0.000	95.5	0.000	161.7	0.000	50.5	0.000
Excl x LU	0.73	0.395	0.1	0.776	1.5	0.222	0.0	0.920
Excl x Thin	0.12	0.734	0.5	0.482	1.5	0.223	0.6	0.459
LU x Thin	2.58	0.123	3.4	0.073	6.6	0.014	0.1	0.740
Ex x LU x Thin	0.04	0.839	0	0.923	0.0	0.872	0.0	0.944

Table 1. (con't)

Biomass^{2}	*Carphephorus bellidifolius*		*Sericocarpus tortifolius*		*Solidago nemoralis*		*Solidago odora*	
Effect	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Herbivore damage	0.01	0.905	13.39	0.001	3.72	0.059	3.33	0.074
Land-use history	0.09	0.768	0.29	0.592	2.48	0.12	0.06	0.815
Overstory thinning	20.87	0	168.22	0	81.84	0	13.6	0.001
Damage x LU	0.53	0.468	0.47	0.496	0.26	0.615	0.01	0.941
Damage x Thin	0.86	0.359	15.15	0	7.63	0.007	0.26	0.61
LU x Thin	0.58	0.448	0.27	0.603	5.61	0.021	0.01	0.938
Dmg x LU x Thin	2.61	0.113	0.07	0.796	1.52	0.223	0.14	0.706

1. Results from the effects of grasshopper exclosures on biomass production.

2. Results from the effects of herbivore damage on biomass production.

Figure 1

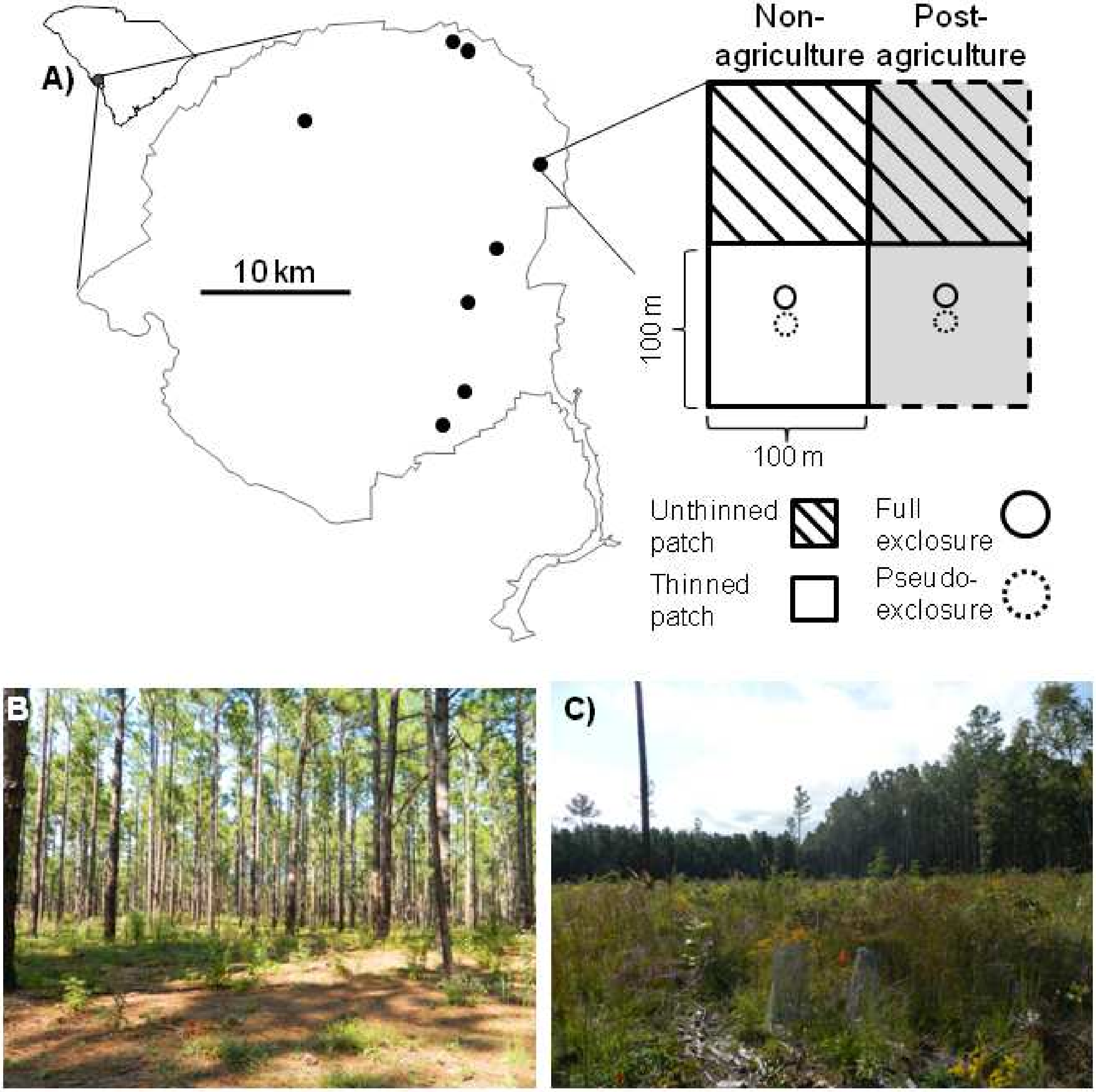

Figure 1. A) Experimental longleaf pine woodlands at the Savannah River Site, South Carolina, USA. Overstory trees were thinned or left intact (unthinned). Consumer exclosures (not to scale) were located 50m from the boundary between post-agricultural and non-agricultural woodlands to avoid edge effects. View from B) a post-agricultural pine plantation and C) a thinned patch.

Figure 2

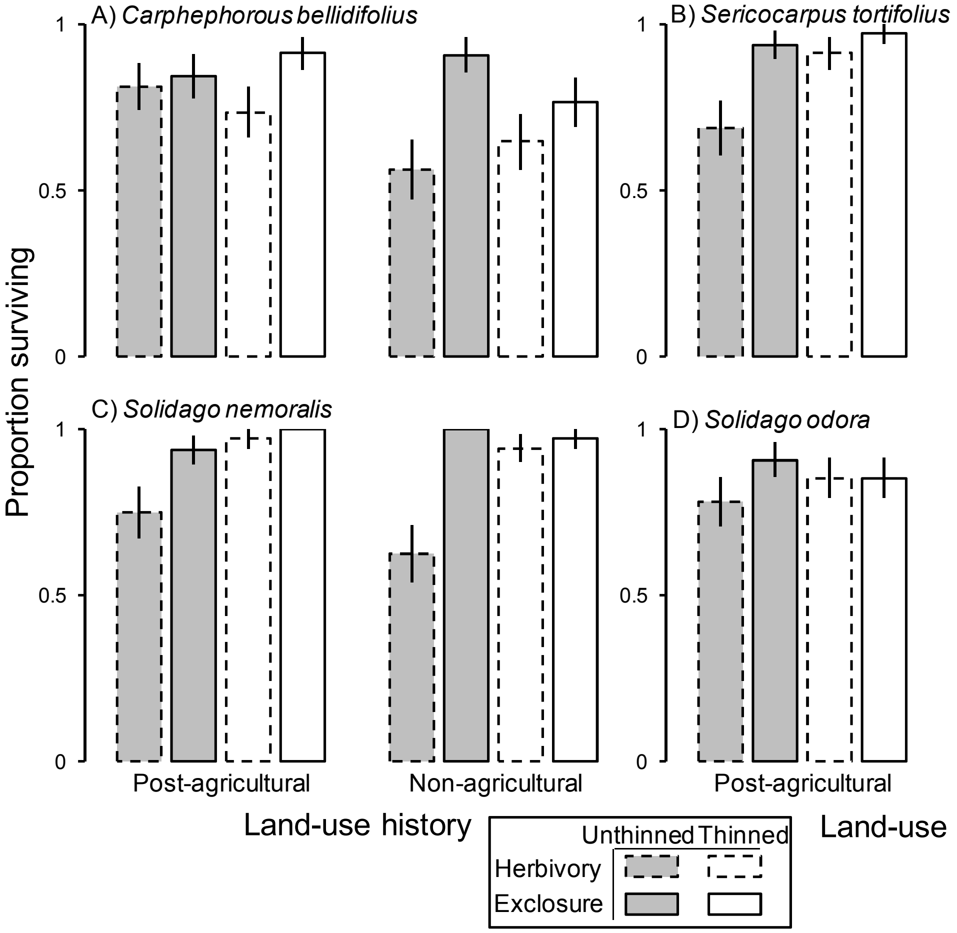

Figure 2. Proportion of juvenile plants surviving after one year for four species of perennial herbs (A-D). The experiment, conducted at the Savannah River Site, South Carolina USA, manipulated overstory tree canopy (unthinned or thinned) and access to grasshopper herbivores (open or exclosures) in post-agriculture (>60 years since abandonment) and non-agricultural (no history of agriculture) habitats.

Figure 3

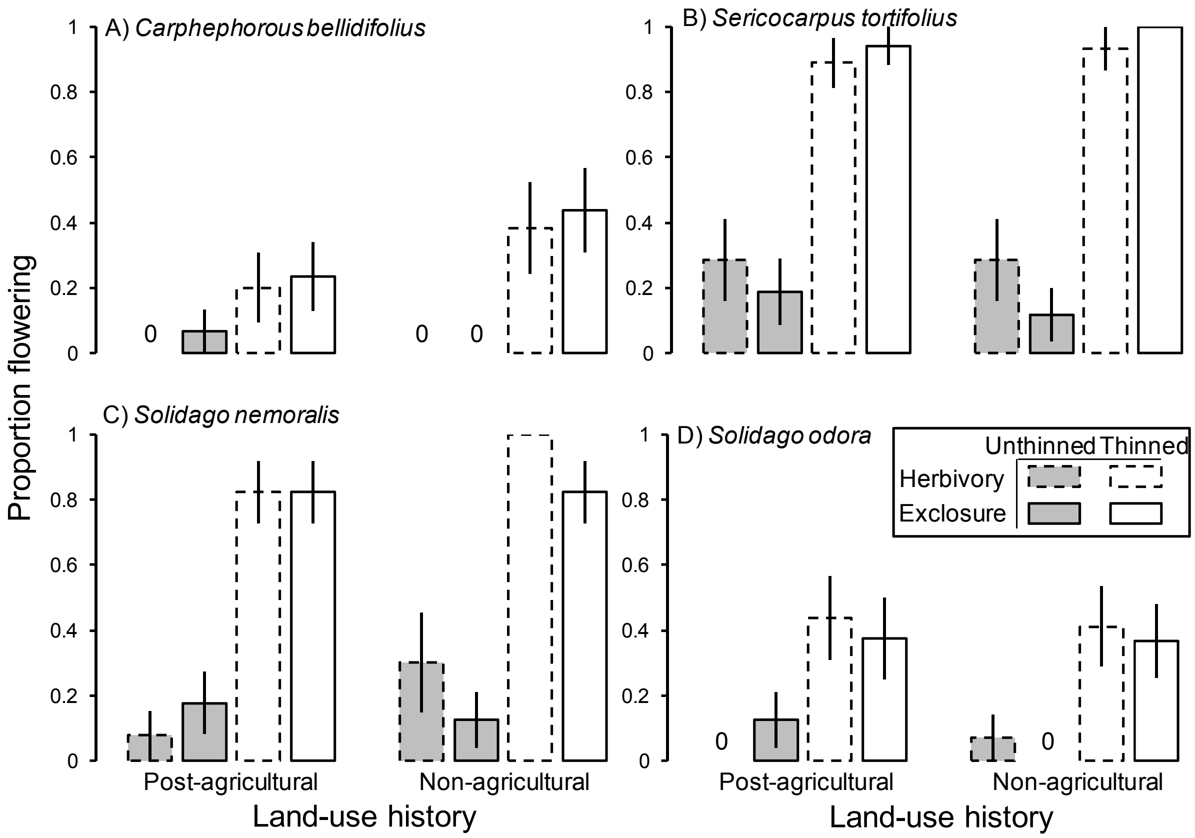

Figure 3. Proportion of plants that survived one year and flowered in the second year for four species of perennial herbs (A-D). The experiment, conducted at the Savannah River Site, South Carolina USA, manipulated overstory tree canopy (unthinned or thinned) and access to grasshopper herbivores (open or exclosures) in post-agriculture (>60 years since abandonment) and non-agricultural (no history of agriculture) habitats.

Figure 4

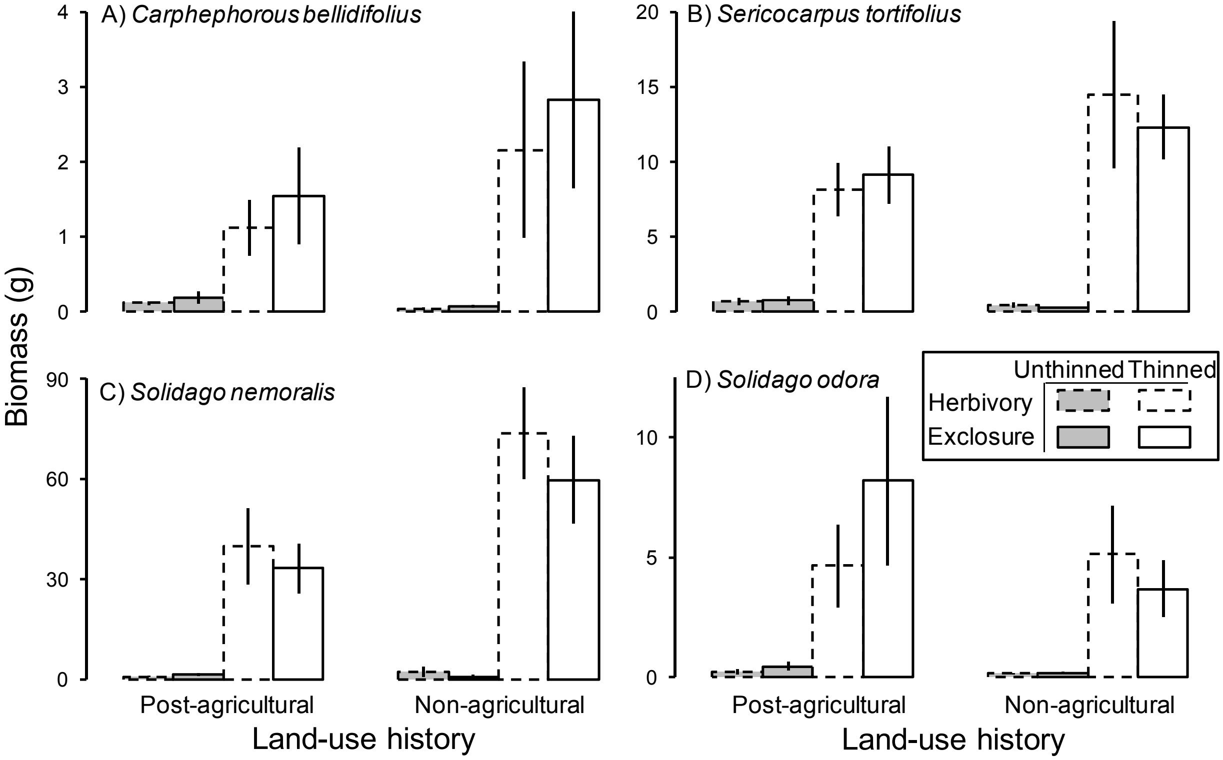

Figure 4. Biomass (g) of four species of perennial herbs (A-D) that survived two years. The experiment, conducted at the Savannah River Site, South Carolina USA, manipulated overstory tree canopy (unthinned or thinned) and access to grasshopper herbivores (open or exclosures) in post-agriculture (>60 years since abandonment) and non-agricultural (no history of agriculture) habitats. Note that the y-axis changes among species.

Figure 5

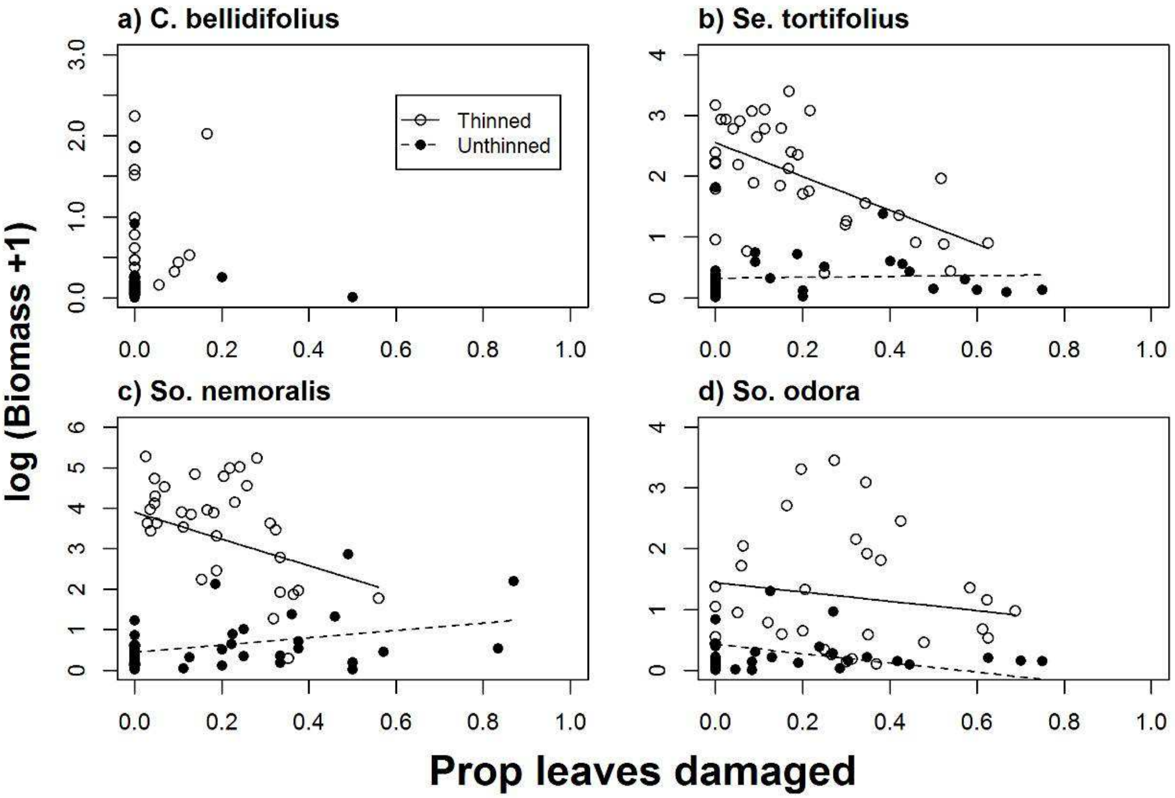

Figure 5. Relationship between the proportion of leaves damaged by chewing insects in June 2013 and final aboveground biomass of two-year old plants harvested in September 2013 from thinned (open dots) or unthinned (closed dots) longleaf pine woodlands. These relationships did not differ among land-use histories (Table 1), so for clarity only the relationships within the overstory thinning treatments are shown. Note that the y-axis changes among species.

APPENDIX A. Effectiveness of herbivore cages.

Table A1. ANOVA table for the comparison of the proportion of leaves damaged by chewing invertebrates between exclosure types (pooled across other treatments) measured in September 2012.

Carphephorus bellidifolius

Effect	**Sum Sq**	**Mean Sq**	**NumDF**	**DenDF**	***F***	***P***
Herbivory	0.29636	0.29636	1	71.049	25.003	3.98E-06

Sericocarpus tortifolius

Effect	**Sum Sq**	**Mean Sq**	**NumDF**	**DenDF**	***F***	***P***
Herbivory	99.933	99.933	1	99.063	32.828	1.09E-07

Solidago nemoralis

Effect	**Sum Sq**	**Mean Sq**	**NumDF**	**DenDF**	***F***	***P***
Herbivory	96.069	96.069	1	100.61	30.529	2.59E-07

Solidago odora

Effect	**Sum Sq**	**Mean Sq**	**NumDF**	**DenDF**	***F***	***P***
Herbivory	119.52	119.52	1	100.49	41.979	3.46E-09

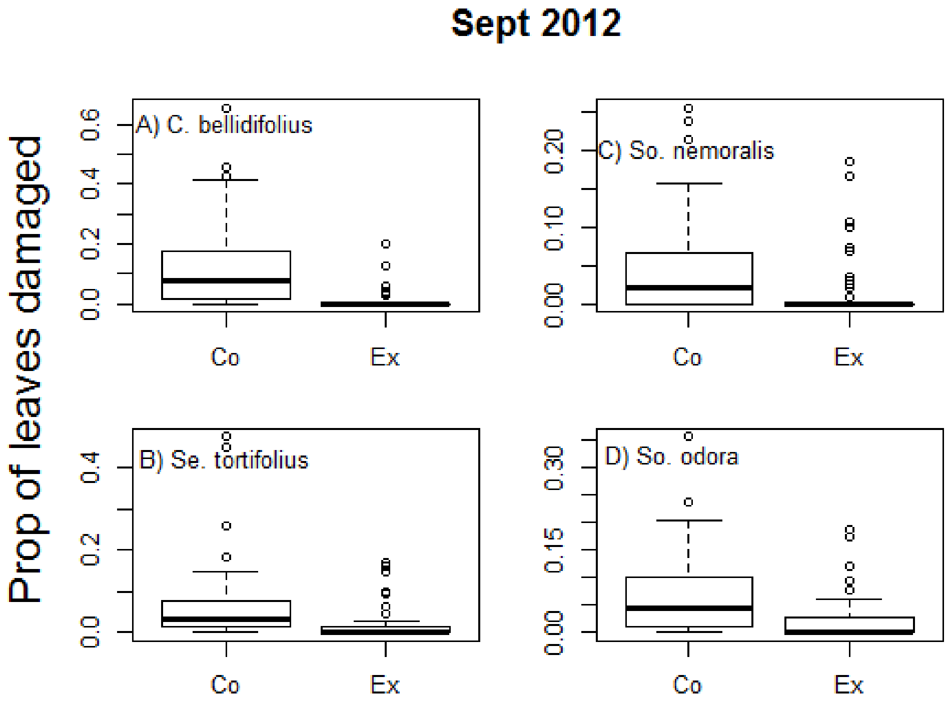

Figure A1. Proportion of leaves with >5% leaf tissue removed by chewing insects between control (open) cages (Co) and full exclosures (Ex), measured in September, 2012.

Table A2. ANOVA table for the comparison of the proportion of leaves damaged by chewing invertebrates between exclosure types (pooled across other treatments) measured in June 2013.

Carphephorus bellidifolius

Effect	**Sum Sq**	**Mean Sq**	**NumDF**	**DenDF**	***F***	***P***
Exclosure	1.719	1.719	1	36.941	0.33574	0.5658

Sericocarpus tortifolius

Effect	**Sum Sq**	**Mean Sq**	**NumDF**	**DenDF**	***F***	***P***
Exclosure	6.6819	6.6819	1	67.034	2.6254	0.1099

Solidago nemoralis

Effect	**Sum Sq**	**Mean Sq**	**NumDF**	**DenDF**	***F***	***P***
Exclosure	1.6449	1.6449	1	76.804	1.4848	0.2268

Solidago odora

Effect	**Sum Sq**	**Mean Sq**	**NumDF**	**DenDF**	***F***	***P***
Exclosure	0.16959	0.16959	1	65.477	0.08772	0.768

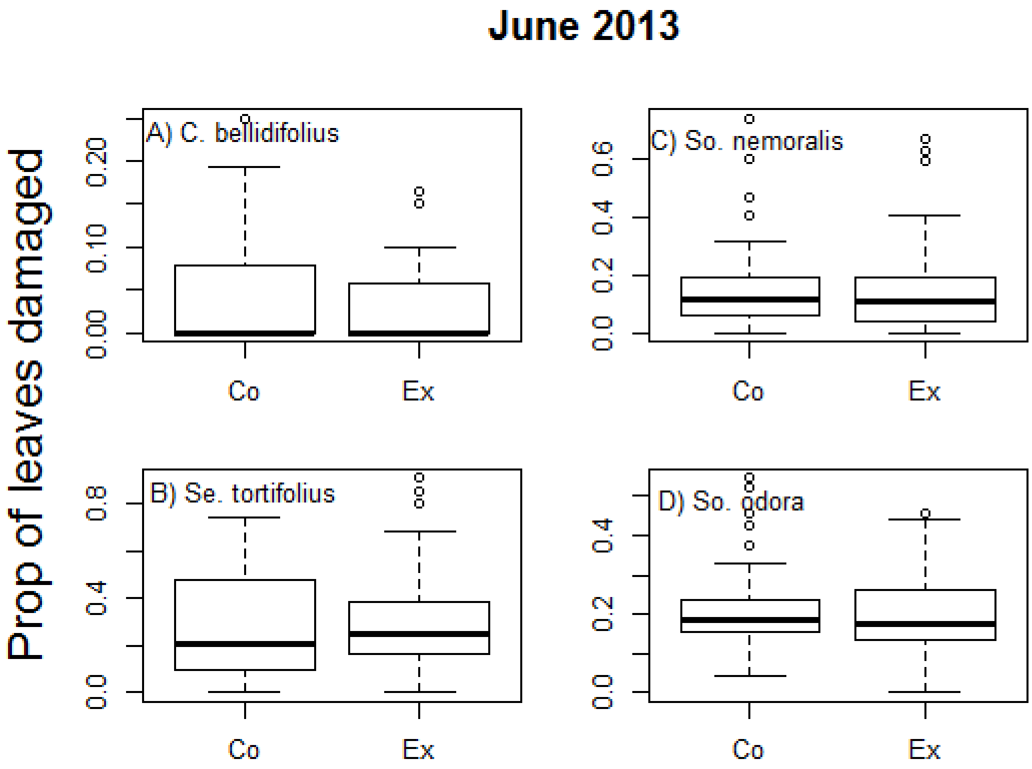

Figure A2. Proportion of leaves with >5% leaf tissue removed by chewing insects between control (open) cages (Co) and full exclosures (Ex), measured in June, 2013.

Table A3. ANOVA table for the comparison of the proportion of leaf removed by chewing invertebrates between exclosure types (pooled across other treatments) measured in September 2013.

Carphephorus bellidifolius

Effect	**Sum Sq**	**Mean Sq**	**NumDF**	**DenDF**	***F***	***P***
Exclosure	0.32846	0.32846	1	66.842	0.18825	0.6658

Sericocarpus tortifolius

Effect	**Sum Sq**	**Mean Sq**	**NumDF**	**DenDF**	***F***	***P***
Exclosure	3.5872	3.5872	1	71.848	1.1979	0.2774

Solidago nemoralis

Effect	**Sum Sq**	**Mean Sq**	**NumDF**	**DenDF**	***F***	***P***
Exclosure	6.8385	6.8385	1	72.946	1.7908	0.185

Solidago odora

Effect	**Sum Sq**	**Mean Sq**	**NumDF**	**DenDF**	***F***	***P***
Exclosure	3.6244	3.6244	1	77.54	0.79486	0.3754

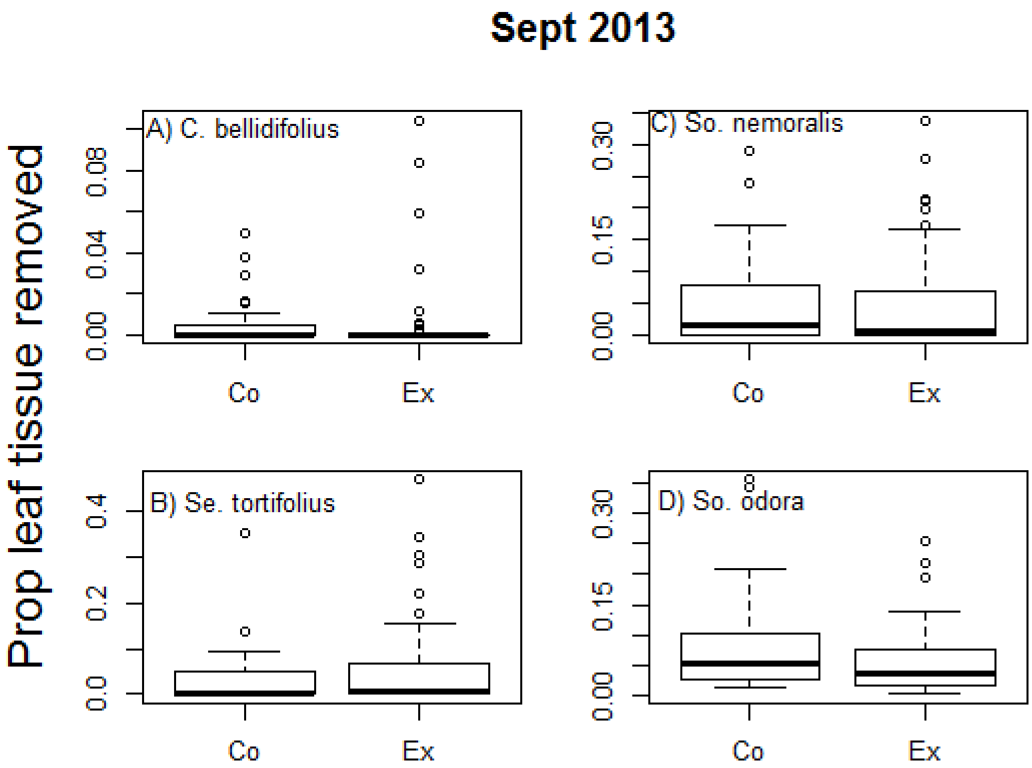

Figure A3. Proportion of leaf tissue removed between control (open) cages (Co) and full exclosures (Ex), measured in September 2013.

Conclusions

My dissertation coupled large-scale observational and experimental studies with laboratory or greenhouse experiments to uncover how behavioral choices and feeding preferences scale up to regulate large-scale patterns in the abundance and distributions of plants. Beyond improving basic understanding of the context-dependency of plant-herbivore interactions, my research has applications to managing and restoring degraded ecosystems and has provided insight into three areas:

1. Relationships between plant communities and insect assemblages: Past agricultural land use generates persistent changes in plant communities and soil conditions in many ecosystems. In a study comparing grasshopper assemblages in post-agricultural sites to non-agricultural remnant longleaf pine woodlands, I found a positive relationship between herbaceous plant cover and grasshopper abundance, but only in habitats without a history of agriculture. There were also taxa-specific effects of historic agriculture on grasshopper abundance, which resulted in shifting dominance from *Schistocerca* in sites with no history of agriculture to dominance of *Melanoplus* in sites with a history of agriculture. Collectively, these results suggest that the effect of historic agricultural land use extends beyond plants and soils to decouple plant-herbivore relationships, leading to a strong legacy of past agriculture on present-day organization of insect herbivore assemblages.

2. The role of associational effects in driving the strength and outcome of plant-herbivore interactions: Associational effects are indirect interactions capable of driving patterns of plant abundance that occur when the amount of herbivore damage received by a focal plant depends on the identity of its neighbors and have the potential to explain how patterns of herbivory scale up to regulate the abundance of plants. However, the relative roles of herbivore abundance and foraging behavior in generating associational effects are not well understood. My work has shown that herbivory on a palatable plant species was greater in habitats with degraded understory vegetation cover and that herbivory exhibited a hump-shaped response to neighboring plant cover, with low herbivory at low and high levels of plant cover. Herbivore abundance had a weak negative effect on herbivory. These findings suggest that changes in plant cover related to past and present human activities can modify damage rates on plants by altering foraging behavior rather than abundance of herbivores. Results from experimental plant neighborhoods created within habitats that vary in herbivore abundance highlight the importance of relative plant frequency in generating associational effects by altering insect herbivore foraging behavior. Collectively, these results suggest that herbivore foraging behavior, rather than herbivore density, is a primary mechanism generating associational effects.

3. Resource availability and landscape factors drive context-dependent plant-herbivore interactions: The effect that herbivores have on the abundance and distribution of plants often depends on environmental factors of the landscape. My research addressed this contingency by conducting experiments at scales rarely achieved in ecological studies to investigate the role of historic agricultural land use, overstory canopy thinning, and herbivores on plant establishment, performance, and demography in the critically endangered longleaf pine ecosystem. Working in experimental landscapes, my research has lead to several key findings. First, I demonstrated that herbivore pressure plays an important role in shaping the distribution of plants at large spatial scales by limiting seedling establishment, and that these consumer effects are themselves contingent on historical land-use and contemporary habitat management. Second, plant growth rate may be a key explanatory trait for predicting when and where herbivory will limit plant growth. I found 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). Herbivores can also have important effects on plant demography that are contingent upon anthropogenic management activities. These contingent plant-herbivore interactions appear to be most evident on younger plant life stages but weaker at adult stages, suggesting that herbivore effects are more important on younger plants. Incorporating life history traits, such as size and growth rates, into plant defense theory may thus add a necessary dimension to understanding the complex defensive strategies employed by plants.