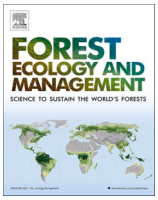
Forest Ecology and Management 541 (2023) 121023

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco



Land-use history, fire regime, and large-mammal herbivory affect deer-preferred plant diversity in longleaf pine woodlands

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ARTICLE INFO

Keywords:
Plant diversity
Prescribed fire
Longleaf forests
Herbivory
Land-use history

ABSTRACT

Since ecological systems often experience multiple disturbances, understanding changes in important ecological interactions, such as plant-herbivore interactions, may require studies capable of disentangling the unique and interactive effects of multiple forms of disturbance. For example, understanding how mammalian herbivores affect plant communities may require understanding how widespread past disturbances, such as agricultural land use, interact with contemporary disturbances, such as prescribed fire. We tested if past agricultural land use and contemporary fire regime modified the effects of mammalian herbivory on focal plant communities by measuring the richness of plant species preferred by deer at 26 longleaf pine woodlands containing paired open and large-mammal exclusion plots. Land-use history significantly affected the community composition of deer-preferred species, and focal species were 8.19 times more likely to be present in post-agricultural sites than non-agricultural sites. Large-mammal herbivory only affected plant species richness in woodlands with low fire frequencies wherein focal species were on average 2.23 times more likely to be present in exclusion plots than open plots. These results suggest that past and present disturbances can mediate contemporary plant-animal interactions and may explain spatial patterns in the intensity of large-mammal herbivory. Our findings also suggest that common management practices, such as use of prescribed burns, may indirectly promote plant species richness by reducing deer herbivory.

1. Introduction

Global environmental change has become so pervasive that many ecological systems typically experience multiple forms of natural and anthropogenic disturbance (Vitousek et al. 1997, Wilcove et al. 1998, Foley et al. 2005, Hobbs et al. 2009, Buma 2015), such as shifts in the occurrence and severity of wildfires and prescribed burns, a history of agricultural land use, and changes in precipitation and storm regime. As a consequence, the way in which ecosystems recover from a past disturbance (e.g., agriculture) may be contingent upon contemporary disturbance regimes, such as fire frequency (Buma 2015, Hansen et al. 2018, Lucash et al. 2018, Kleinman et al. 2019, Brudvig et al. 2021) or herbivory (De Vriendt et al. 2021). However, since ecosystems (and disturbances) are dynamic and ecological systems may take years to respond to disturbance, understanding how multiple disturbances might interact to affect ecological systems requires measuring ecological processes over sufficiently long time periods. For example, long-term studies demonstrate that plant-herbivore interactions shape diversity and function in plant communities over multiple years (Brown and Heske 1990, Huntly 1991, Belsky 1992, Milchunas and Lauenroth 1993, Virtanen et al. 1997, Augustine and McNaughton 1998, Olff and Ritchie 1998, Maron and Crone 2006, Agrawal et al. 2012, Leroux et al. 2020). As a result, long-term studies may be essential for understanding how multiple abiotic disturbances that affect plant-herbivore interactions might ultimately affect plant communities. Moreover, studies are rarely able to experimentally evaluate ecological processes involving large-bodied organisms, which may have large effects on ecological communities (McNaughton 1979, Belsky 1992, Milchunas and Lauenroth 1993, Augustine and McNaughton 1998, Pringle et al. 2007, Ford et al. 2014), due to the challenges of consistently manipulating large-animal presence or activity at sites spanning the overlap of multiple abiotic disturbance regimes over many years.

Among the many types of global change that affect plant communities, changes in fire regime and past agricultural land use are two of the most globally pervasive disturbances. For example, changes in the frequency, size, and severity of fires have been documented across the

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https://doi.org/10.1016/j.foreco.2023.121023
Received 4 February 2023; Received in revised form 4 April 2023; Accepted 12 April 2023
Available online 9 May 2023

globe both in temperate and tropical regions (Cochrane et al. 1999, Flannigan et al. 2009, Harvey et al. 2016, Prichard et al. 2017), and the global area burned was estimated to have increased from 500 Mha year^{-1} to 608 Mha year^{-1} over the second half of the 20th century (Mouillot and Field 2005, Flannigan et al. 2009). Legacies of past agricultural land-use are also widespread: 10 to 44 million km^2 of global land cover is recovering from agricultural land use since 1700 (Hurtt et al. 2006). Fire and agricultural legacies are two types of abiotic disturbance that have profound impacts on plant communities. Changes in fire regime can lead to regeneration failure of forest trees (Harvey et al. 2016) and declines in plant diversity (Prichard et al. 2017). Agricultural legacies can have persistent effects on plant community structure and diversity for decades and sometimes centuries following agricultural land abandonment (Foster 1993, Flinn and Vellend 2005, Kopecký and Vojta 2009, Mattingly et al. 2015, Culbert et al. 2017). Moreover, while it is known that agricultural legacies can interact with contemporary fire regime to determine plant community structure in restored habitats (Brudvig and Damschen 2011, Veldman et al. 2014, Mattingly et al. 2015), the degree to which these differences in plant communities reflect underlying changes in plant-consumer interactions remains unclear. This is an important gap in our knowledge because community composition and optimal approaches for conservation and restoration may be fundamentally different for plant communities limited by consumers compared to those limited by other processes (e.g., dispersal limitation).

Large-mammal herbivores have the potential to generate large-scale and long-term impacts on habitats through top-down control of plant communities (Rooney and Waller 2003, Côté et al. 2004, 2014, Holdo et al. 2009, Winnie 2012, Daskin et al. 2016, Goheen et al. 2018, Leroux et al. 2020), which can affect the trajectory of succession within plant communities following a disturbance (e.g., forest clearcutting; Hidding et al. 2013, Côté et al. 2014, De Vriendt et al. 2021, Beguin et al. 2022). Many studies show that the effects of large-mammal herbivory can vary across environmental gradients (e.g., elevation or large-mammal density; (Schütz et al. 2003, Hidding et al. 2013; Speed et al., 2013a, 2013b 2013c, Côté et al. 2014, Prendeville et al. 2015, Loughnan and Williams 2019, De Vriendt et al. 2021) and recent history of a single disturbance (e.g., fire or clearcutting; Speed et al. 2014, Burkepile et al. 2016). Recently, a study that manipulated moose (*Alces alces)* access, fire, and timber harvest formation in boreal forests (Hardenbol et al. 2021) and another study that manipulated white-tailed deer (*Odocoileus virginianus)* access, fire, and canopy gaps in temperate deciduous forests (Nuttle et al. 2013) revealed that the overlap of multiple contemporary disturbances may interactively alter the impacts of large-mammal herbivory on plant communities. However, it remains unclear how the overlap of recent disturbances and disturbances that occurred in previous decades affects contemporary large-mammal herbivory.

The overlap of agricultural legacies and contemporary fire regime modify large-mammal foraging behavior (Bartel and Orrock 2021). As a result, these two past and present disturbances could interact to generate significant spatial variation in the impact of large-mammal herbivory on plant species. Moreover, agricultural legacies and fire may alter soil nutrient availability (Brudvig et al. 2013), and soil nutrient availability can mediate the effects of herbivory on vegetation (Connolly et al. 2016, Borer et al. 2020). While agricultural legacies and contemporary disturbances have been shown to modify arthropod herbivory in multiple ecosystems (Donihue et al. 2013, Hahn and Orrock 2015a, 2015b), no research has investigated if the overlap of agricultural legacies and contemporary disturbances interactively modifies large-mammal herbivory.

Longleaf pine woodlands can contain some of the most diverse understory plant communities in North America and are ecosystems characterized by contemporary fire as well as past agricultural land use (Frost 2006, Brudvig et al. 2014). Historically, longleaf pine woodlands were maintained by lightning and human-ignited surface fires that occurred at an interval of every-one to six years (Frost 2006, Oswalt et al. 2012), but contemporary fire suppression is currently widespread (Frost 2006). Contemporary fires in longleaf pine woodlands are typically implemented through prescribed burning (Kilgo and Blake 2005, Frost 2006, Oswalt et al. 2012). White-tailed deer are common in these ecosystems, and fire (Cherry et al. 2017) as well as the overlap of fire and land-use history, can affect deer foraging behavior (Cherry et al. 2017, Bartel and Orrock 2021). An accumulating body of evidence across multiple study areas suggests that fire mediates deer perceptions of predation risk, leading to predictable patterns in deer foraging behavior. Specifically, deer spend less time foraging and allocate more time to vigilance when frequent fire removes vegetative cover that protects deer from predators (Cherry et al. 2016, 2017). Moreover, a recent study found that deer vigilance increased with fire frequency in post-agricultural sites and found that deer used a more proactive antipredator behavior (avoiding risky high-fire sites at risky times) in non-agricultural woodlands, suggesting that deer may be most fearful of encountering a predator in frequently burned non-agricultural woodlands (Bartel and Orrock 2021). While recent work in longleaf pine woodlands suggests that strong shifts in deer foraging behavior may lead to significant changes in deer herbivory and its effects on plant species richness in systems without a known history of agricultural use (Cherry et al. 2016), it is not known whether past agricultural land use modifies the role of fire in affecting deer herbivory or if this results in long-term changes in plant species occurrences.

We used a large-scale, long-term herbivore-exclusion experiment to evaluate the effects of past agricultural land use and contemporary fire regime on herbivory by deer. We quantified herbivore effects by measuring the presence or absence of 12 plant species preferred by deer at 26 sites in longleaf pine woodlands. Past research has also indicated that these deer-preferred plant species may respond strongly to changes in deer foraging behavior (Cherry et al. 2016). We hypothesized that herbivory would have the strongest effect in woodlands with infrequent fires because these are habitats with thicker woody shrub layers that provide more protective concealment for deer (i.e., safe foraging habitat; see Bartel & Orrock 2021), leading to greater deer herbivory. We also hypothesized that herbivory would have a stronger effect on the presence of plant species in post-agricultural woodlands than in non-agricultural woodlands because past work indicates that deer may be more fearful of predation in non-agricultural woodlands (see Bartel and Orrock 2021), suggesting that deer herbivory may be less intense in non-agricultural woodlands.

2. Materials and methods

2.1. Study area and design

This study was conducted at the Department of Energy (DOE) Savannah River Site (SRS; Aiken, SC), an 80,125-ha National Environmental Research Park (NERP). Established by the DOE in 1951, SRS is a United States Department of Energy site that is managed by the United States Department of Agriculture Forest Service. SRS is within the historical range of the longleaf-pine woodland ecosystem, much of which was converted to tillage agriculture from 1856 to 1950 (Frost 2006). Since these agricultural lands were small and dispersed, heterogeneous landscapes resulted containing patches of tilled farmland and intact forests (Kilgo and Blake 2005). Agricultural fields were abandoned in 1951 and have henceforth been under management as longleaf and loblolly pine plantations (Kilgo and Blake 2005). We selected 26 sites, spanning an 807-km^2 area, that differed in land-use history and fire frequency. Land-use history classification was based on aerial photography taken prior to land abandonment in 1951. Sites that were farmland in 1951 were classified as “post-agricultural woodlands,” and sites that were forested were classified as “non-agricultural woodlands.” The number of fires since 1991 was determined from annual fire records and sites were characterized as high (five or more burns) or low (fewer than five burns) fire frequency, a metric previously used to classify these sites

based on plant-community characteristics (Brudvig et al. 2014). Sites that were burned five or more times over the course of the past 27 years were characterized as high fire frequency because these sites had an average fire interval of less than 5 years. This fire interval is representative of the historic fire intervals that maintained longleaf pine woodlands prior to European settlement (Van Lear et al. 2005, Frost 2006). Sites that were burned fewer than five times over the course of the past 27 years were characterized as low fire frequency because these sites had an average fire interval of more than 5 years. This fire interval is representative of the frequency at which woodlands would have been burned following European settlement, including during the 20th century when the US Forest Service implemented a fire exclusion policy (Van Lear et al. 2005, Frost 2006). While it is recommended that land managers burn longleaf pine woodlands every 2 – 3 years to restore the historic fire regime in this ecosystem, the variation in fire frequency in woodlands at SRS is representative of contemporary variation in fire frequency across the southeast (Kilgo and Blake 2005, Van Lear et al. 2005, Frost 2006, Oswalt et al. 2012, Veldman et al. 2014). This classification system was previously used in past research evaluating the effects of fire frequency on deer behavior in this study area (Bartel and Orrock 2021). The resulting site classification by land-use history and fire frequency generated four distinct habitat types distributed across the study area (Fig. 1).

Within each site, four 7 × 7 m plots were established to factorially manipulate large-herbivore access in 2010, and the experimental treatments were implemented in 2011. Large-mammal herbivore access was manipulated by building exclosure fences (~2.4 m tall) around 2 of the four plots. Similar experimental designs using exclosure fences to manipulate large-mamml access at paired plots has been utilized to measure deer herbivory in other past studies (Côté et al. 2004, 2014).

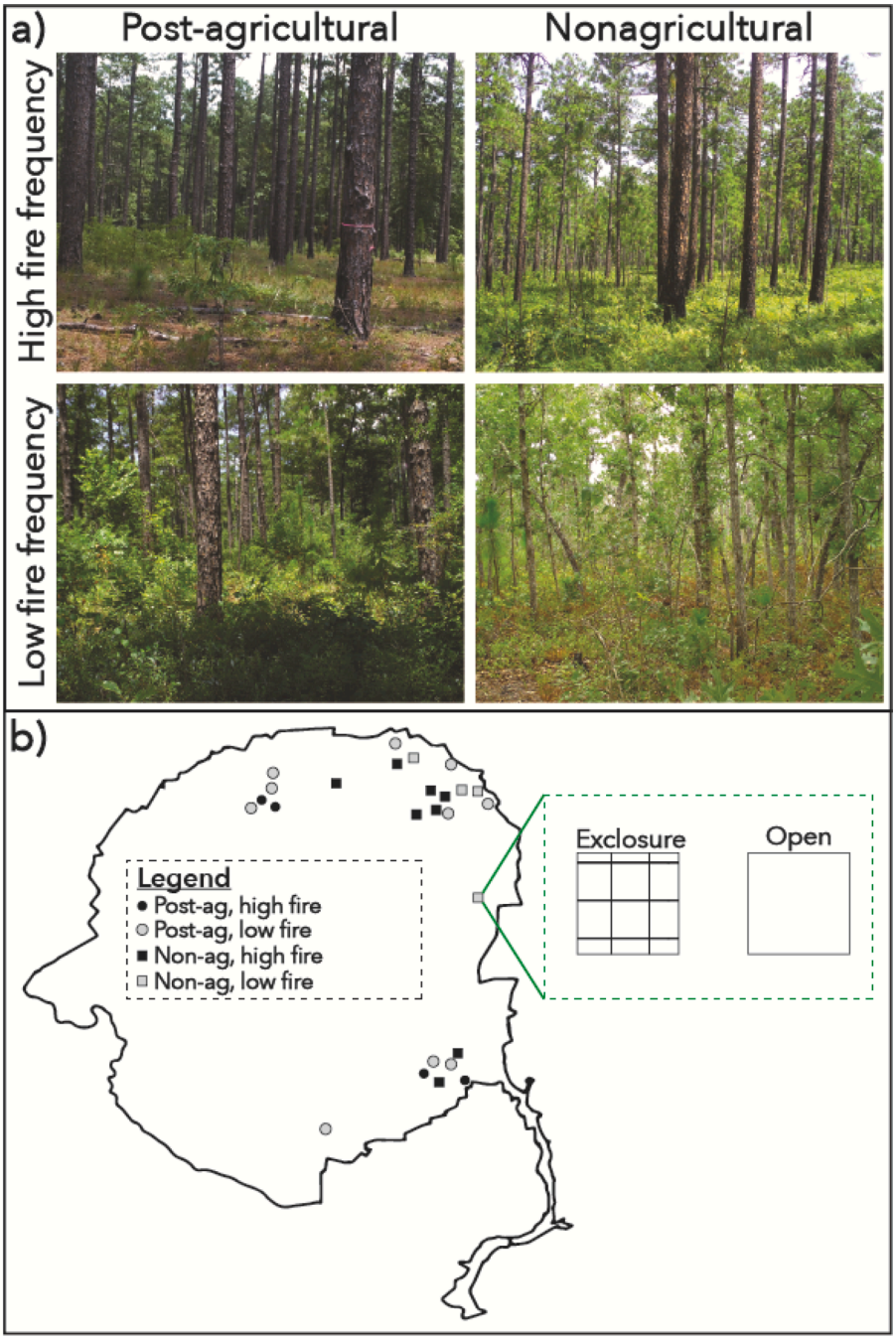

Fig. 1. We conducted our experiment at 26 longleaf pine woodlands within the Savannah River Site (SRS) near Aiken, SC, USA. **a)** Woodlands were classified by past land use and contemporary fire frequency. The images above were captured within our sites during the experimental period and are representative of the variation in habitat across the different disturbance contexts. **b)** SRS is an ~ 80,000-ha area, and sites were stratified across SRS. At each site, paired plots were established to manipulate large-mammal herbivore access.

The fences had two sections that were each 4 feet tall, amounting to a total fence height of 8 feet. For the bottom section, we used 4-foot wide 'field fence' with 8 × 7 in. openings. For the top panel, we used 4-foot wide chicken wire with 1 × 1 in. openings. Fences allow access for all small-mammal and invertebrate consumers, so paired plots within a site can be assumed to experience equal herbivory and granivory pressure from these groups. White-tailed deer are the primary large-mammal herbivores at SRS (Cothran et al. 1991); however, feral hogs (*Sus scrofa*) are common large-mammal omnivores at SRS that can cause significant destruction to plants through rooting behavior (Barrios-Garcia and Ballari 2012). Damage of vegetation by feral hogs (via rooting and trampling of vegetation) is visibly apparent, and we never observed it within our plots. Moreover, we only measured the presence and absence of plant species commonly consumed by deer, and hog damage would not be expected to be directed at deer-preferred species. Since feral hog destruction of plant species is likely to be random while deer herbivory is expected to be greatest on palatable plant species (Edwards et al. 1961, Lashley et al. 2015), we increase the odds that our pattern was driven by deer herbivory and not a different group of consumers by focusing on deer-preferred species. Coyotes (*Canis latrans*) are the primary predators of deer in the southeastern US, including at SRS (Kilgo et al. 2010, 2012, 2014, Chitwood et al. 2015, Gulsby et al. 2017). Past work has shown that predation by coyotes affects both deer population dynamics and foraging behavior in the southeastern US (Kilgo et al. 2010, 2014; Cherry et al. 2015, 2016, 2017, Chitwood et al. 2015, Gulsby et al. 2017).

A list of plant species preferred by deer in the southeastern US was constructed referencing both understory plant identification manuals (Edwards et al. 1961, Miller and Miller 2005, Norden and Kirkman 2006) and published literature of past research on plant preferences by deer (Lashley et al. 2015, Cherry et al. 2016; Supplement 1). We present only the species on this list that were found in our plots and used in our analyses (Table 1). At each site, one of the two paired plots was given a seed-addition treatment at the center 5 × 5 m of each plot as part of a separate experiment (Orrock et al. 2015). Of the 22 seed species added, only two (*Tephrosia virginiana* and *Lespedeza hirta*) are preferred by deer, and these two species were not included our analyses (Table 1). While past work has shown that plant species richness is positively correlated with plant abundance in this experimental system (Orrock et al. 2015), we also verified that this positive correlation existed for plant species preferred by deer that we examined using pre-treatment data on plant communities at our 26 sites (Supplement 2). We therefore assume that species richness of plants preferred by deer provides a reliable metric for the cover of these species at our study sites. Agricultural legacies and fire may alter soil nutrient availability (Brudvig et al. 2013), and soil nutrient availability can mediate the effects of herbivory on vegetation (Connolly et al. 2016, Borer et al. 2020). In order to account for the potential that soil nutrient conditions may moderate the effects of herbivory, we measured phosphorus and nitrogen from soil samples taken at each site in spring 2011. We collected soil cores (2.5 cm diameter by 15 cm deep) at 10 m intervals along the center line of each plot. Soil was composited by site and analyzed by Brookside Laboratories, Inc. (New Knoxville, OH) for Mehlich III-extractable phosphorus (Mehlich 2008) and inorganic nitrogen (N; sum of 1 N KCl cadmium reduction NO3 and NH4; (Dahnke and Johnson 2018). In July 2018, we measured presence or absence of the deer-preferred plant species within each plot at the 7 × 7 m plot level. Thirteen of our 26 sites only had 1 intact herbivore exclosure (totaling 18 intact seed-addition paired plots, 21 intact no-addition paired plots) due to random fence damage that occurred across all fire-frequency and land-use history treatments. As a result, we measured the presence of 12 deer-preferred plant species within a total of 72 plots.

Table 1
Species list and characteristics of the 12 deer-preferred plant species that were found in our plots and used in our analyses.

Forage species	Family	Form	Life cycle	Dispersal Mode
Centrosema virginianum	Fabacaea	Forb, legume	Perennial	Gravity
Chamaechrista fasciculata	Fabacaea	Forb, legume	Annual	Gravity
Chamaechrista nictitans	Fabacaea	Forb, legume	Annual	Gravity
Cnidoscolus stimulosus	Euphorbiacea	Forb, nettle	Perennial	Gravity, animal (external)
Desmodium spp.	Fabacaea	Forb, legume	Perennial	Animal (external)
Galactia spp.	Fabacaea	Forb, legume	Perennial	Gravity
Prunus spp.	Rosaceae	Hardwood, fleshy fruit	Perennial	Animal (internal)
Quercus spp.	Fagaceae	Hardwood, hard mast	Perennial	Animal (external)
Rhyncosia reniformis	Fabacaea	Forb, legume	Perennial	Gravity
Rubus spp.	Rosaceae	Shrub, fleshy fruit	Perennial	Gravity
Smilax spp.	Smilacaceae	Vine	Perennial	Animal (internal)
Vitis spp.	Vitaceae	Vine	Perennial	Animal (internal)

2.2. Data analysis

We used a multilevel model (MLM) described by Jackson et al. (2012) for analyses of focal plant species (i.e., the plants in the community preferred by deer) to estimate both species-level and community-level responses to land-use history, fire frequency, and herbivore access. MLMs allow us to estimate both changes in focal plant species richness and community composition. MLMs analyze the presence/absence of individual plant species in response to predictor variables as random-effect slopes. Significant variation in species-specific responses to land-use history, fire frequency, and herbivore access implies shifts in the composition of the focal plant community (Jackson et al. 2012). The fixed-effect parameter estimates report the mean response of all plant species to a predictor variable and can be interpreted as the mean probability of plant species presence (i.e., higher mean probability indicates higher number of species present). We constructed this model using the *glmer* function in the "lme4" package (Bates et al. 2015) in R ver. 3.6.1.

To test how land-use history, fire frequency, herbivore access, soil N, and soil P affected species richness and community composition for focal deer-preferred plant species, we constructed an MLM with a binomial distribution including species presence/absence as the response variable; land-use history, fire frequency, herbivore access, soil N, soil P, the interaction of soil N and herbivore access, the interaction of soil P and herbivore access, and the interaction of land-use history × fire × herbivore access as fixed effects; random intercepts for site and species; and random slope terms (i.e., fixed effect × species) for land-use history, fire frequency, and herbivore access. We also evaluated if land-use history and fire regime affected soil N or soil P in follow-up analyses (see Supplement 3 for methods and results). To measure the effects of land-use history, fire frequency, and herbivore access on the composition of the focal plant community, we used likelihood ratio tests (LRTs) comparing the full model to models without the random effects of a land-use history, fire frequency, or herbivore access slope wherein a significant random effect of the slope indicates that species vary significantly in their responses to land-use history or fire frequency (Jackson et al. 2012, McCormick et al. 2019).

3. Results

Across our 26 sites, the average species richness of deer-preferred plant species in plots with herbivore access (i.e., open plots) was 3.82

± 0.32, and the average species richness of deer-preferred plants in exclosure plots was 4.67 ± 0.34. In the MLM model, community composition was significantly affected by land-use history (LRT: X^2 = 42.16, p < 0.001) but not fire frequency (LRT: X^2 = 3.72, p = 0.054) or herbivore access (LRT: X^2 = 0.00, p = 1.00; Table 2). Land-use history had a significant effect on the average probability of species presence (β = -2.62, SE = 0.87, X^2 = 9.06, p = 0.003; Table 3). On average, focal species were 8.19 times more likely to be present in post-agricultural sites than non-agricultural sites (Fig. 2).The average probability of species presence was also positively affected by soil N (β = 0.05, SE = 0.02, X^2 = 4.36, p = 0.037) and negatively affected by soil P (β = -0.07, SE = 0.02, X^2 = 8.01, p = 0.005; Table 3). The interaction of fire and herbivore access significantly affected the average probability of species presence (β = -1.15, SE = 0.56, X^2 = 4.19, p = 0.041; Table 3) such that herbivore exclosures only increased species presence when fire frequency was low, particularly in post-agricultural woodlands (Fig. 2). When fire frequency was low, focal species were on average 2.23 times more likely to be present in exclusion plots than open plots (Fig. 2). The interaction of soil N and access, the interaction of soil P and access, and the interaction of land-use history, fire, and access had no effect on average focal species presence (Table 3).

4. Discussion

In this study, we found that deer-preferred plant species were impacted by both land-use history and herbivory, and the effects of herbivory on these focal plant species were contingent upon contemporary fire regime and land-use history. These findings have two broad implications for our understanding of trophic dynamics in the context of disturbance in woodland habitats. First, our results demonstrate that agricultural legacies can lead to lasting patterns in the occurrence of deer-preferred plant species in woodlands. Second, contemporary disturbances, such as fire, can mediate the impacts of deer herbivory on deer-preferred plant species richness in woodland habitats. Finally, deer foraging behavior may provide a profitable means to understand large-scale variation in the effects of large-mammal herbivory on plant species.

4.1. Deer-preferred plant species richness is greater in woodlands with agricultural legacies

We found that post-agricultural woodlands had more deer-preferred plant species present (i.e., greater species richness) than non-agricultural woodlands, regardless of fire frequency (Fig. 2). Land-use history also had a significant effect on focal plant community composition (Table 2). Long-term herbivore exclosures suggest that the effects of past land use on focal species richness in frequently burned woodlands were not due to deer herbivory (Fig. 2). The importance of

Table 3
Results from the MLM evaluating the effects of land-use history, fire frequency, herbivore access, soil N, and soil P on focal species presence. Significant fixed effects (p < 0.05) are marked with asterisks.

	β	SE	X^2	P-value
Land-use history	−2.62	0.87	9.06	0.003*
Fire frequency	0.52	0.58	0.82	0.365
Herbivore access	0.90	1.66	0.29	0.590
N	0.05	0.02	4.36	0.037*
P	−0.07	0.02	8.01	0.005*
Land-use × fire	0.09	0.78	0.01	0.911
Land-use × access	−0.26	0.63	0.18	0.675
Fire × access	−1.15	0.56	4.19	0.041*
Access × N	−0.02	0.03	0.65	0.419
Access × P	0.03	0.03	1.22	0.270
Land-use × fire × access	0.08	0.90	0.01	0.929

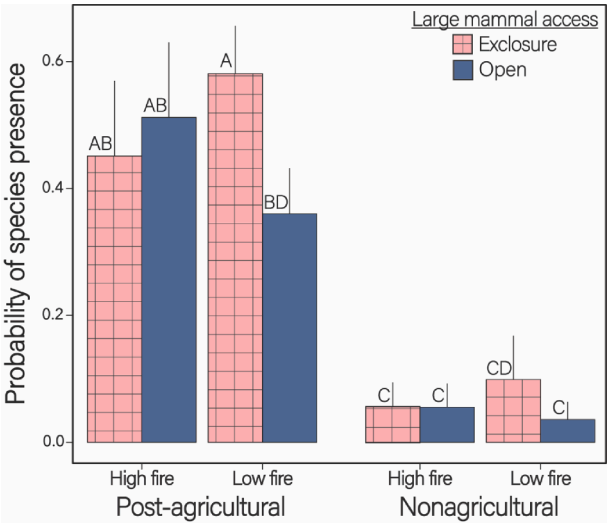

Fig. 2. Land-use history and the interaction of fire frequency and herbivore exclusion had significant effects on the mean probability of deer-preferred species presence. The probability of species presence was greater in post-agricultural woodlands than in nonagricultural woodlands. Large-mammal herbivore access only significantly decreased the probability of species presence in post-agricultural woodlands with low fire frequencies. There was no effect of herbivore access in woodlands with high fire frequencies. Different letters represent group means that are significantly different (p < 0.05 using sequential Benjamini-Hochberg correction; Benjamini & Hochberg 1995). Error bars represent standard error.

Table 2
Random effect coefficients by plant species from the MLM. Coefficients are the random effect plus the fixed effect estimate in order to account for the mean slope. For each species, the predictor variable with the largest effect is bolded.

	Fire frequency		Land-use history		Herbivore access	
Forage species	High	Low	Post-ag	Non-ag	Exclosure	Open
Centrosema virginianum	0.62343	−0.26463	0.39609	**−2.10535**	0.00067	−0.00068
Chamaechrista fasciculata	0.05010	−0.02127	0.17728	**−0.94227**	0.00001	−0.00001
Chamaechrista nictitans	−0.36446	0.15470	0.15981	**−0.84945**	−0.00028	0.00028
Cnidoscolus stimulosus	0.19312	−0.08198	−0.16051	**0.85317**	0.00006	−0.00006
Desmodium spp.	0.54577	−0.23167	0.43252	**−2.29898**	−0.00069	0.00071
Galactia spp.	0.33721	−0.14314	−0.21604	**1.14829**	−0.00026	0.00027
Prunus spp.	−0.01597	0.00678	−0.32864	**1.74683**	0.00107	−0.00109
Quercus spp.	−0.75538	0.32064	−0.62381	**3.31569**	0.00003	−0.00003
Rhyncosia reniformis	−0.12137	0.05152	0.16340	**−0.86853**	−0.00011	0.00012
Rubus spp.	0.14661	−0.06223	0.15975	**−0.84910**	0.00019	−0.00019
Smilax spp.	**−0.35267**	0.14970	−0.04603	0.24465	−0.00033	0.00033
Vitis spp.	−0.28638	0.12156	−0.11384	**0.60507**	−0.00035	0.00035

resource availability in modifying southeastern plant communities in post-agricultural woodlands is evidenced in past structural equation modeling (Veldman et al. 2014), and we found a significantly positive effect of soil N and P on focal plant species richness. We also found that soil P, but not soil N, was greater in post-agricultural woodlands (Supplement 3), indicating that soil P availability may mediate the effects of past land use on deer-preferred plant species. Past work in our study system has also shown that dispersal limitation is an important process contributing to differences in plant communities among post-agricultural and nonagricultural woodlands (Turley et al. 2017). We therefore suggest that the effects of land-use history on the richness and composition of deer-preferred plant species are a result of other mechanisms, such as nutrient availability and dispersal limitation.

While we found increased deer-preferred species richness in post-agricultural woodlands, overall plant richness (Veldman et al. 2014), phylogenetic diversity (Turley and Brudvig 2016), and beta diversity (Grman et al. 2015) are all generally lower in post-agricultural woodlands in the southeast. These contrasting results in diversity likely arise due to our focus on deer-preferred plant species, many of which (e.g., *Desmodium* spp. and *Prunus* spp.) are associated with past agricultural land use (Turley and Brudvig 2016). Past work has found that *Centrosema virginianum* and *Desmodium* spp. are indicator species of longleaf pine woodlands with agricultural land-use histories, and *Cnidoscolus stimulosus* is an indicators species of longleaf pine wooldands with non-agricultural land-use histories (Brudvig and Damschen 2011). Many of our focal species play a variety of other important ecological roles. Six of our focal species are legumes (Table 1), which play a key function in replenishing nitrogen after fire in longleaf pine habitats via fixation of atmospheric N_2 (Hiers et al. 2003). Legumes are also preferred forage for many other wildlife species in longleaf pine woodlands, including gopher tortoises (*Gopherus polyphemus*), lagomorphs, and pocket gophers (*Geomys pinetis*; Miller and Miller 2005, Norden and Kirkman 2006). The seeds of these legumes are also an important component of the diets of bobwhite quail (*Colinus virginianus*), eastern wild turkey (*Meleagris gallopavo silvestris*), songbirds, and small mammals (Miller and Miller 2005, Norden and Kirkman 2006). As such, our results demonstrate an unappreciated role for post-agricultural woodlands: while these woodlands contain low-diversity plant communities, they are disproportionately rich in species that provide important forage for a wide diversity of wildlife species native to longleaf pine woodlands.

4.2. Effects of large-mammal herbivory are contingent upon disturbance regime

Our results also illustrate the important role of a contemporary disturbance, fire, in mediating the impacts of deer herbivory on deer-preferred plant species richness. While deer herbivory did not affect richness in frequently burned woodlands, herbivory significantly reduced the richness of deer-preferred plant species in sites with low fire frequencies (Fig. 2). Variation in the strength of top-down effects is sometimes attributed to variation in the ability of plants to tolerate herbivory (Hilbert et al. 1981, Maschinski and Whitham 1989, Pringle et al. 2007). Since we did not find a significant interaction between soil nutrients and herbivore access on the richness of deer-preferred species, we did not find evidence that differences in nutrient availability across habitat contexts mediated plant resistance to herbivory. Similar fire-contingent effects of large-mammal herbivory have been found in other systems (Royo et al. 2010, Burkepile et al. 2016, Crowther et al. 2016). Our results contribute to this growing knowledge by illustrating how the effects of fire on deer herbivory are not consistent across woodlands with different land-use histories (Fig. 2): deer herbivory had the largest effect on focal species richness in post-agricultural woodlands. This suggests that the effects of contemporary fire regime on herbivory may be predictably variable across landscapes containing habitats with different land-use histories.

We hypothesize that a likely mechanism by which fire mediates the effects of deer herbivory on the richness of deer-preferred species is through deer behavioral responses to fire. Past work in this system has shown that frequent fire regimes increase deer visibility to predators (i.e., coyotes; Bartel and Orrock 2021) and that deer antipredator behavior responds accordingly to this fire-mediated change in predation risk (Bartel and Orrock 2021). Research at a nearby (~400 km) site found that deer vigilance (i.e., the proportion of time spent vigilant versus foraging) was greater in recently burned longleaf-pine woodlands with no documented agricultural legacies to our knowledge (Cherry et al. 2017). Work at our study site evaluating deer behavior across longleaf-pine woodlands with varying land-use histories found that deer vigilance increased with fire frequency in post-agricultural sites and found that deer used a more proactive antipredator behavior (avoiding risky high-fire sites at risky times) in non-agricultural woodlands, suggesting that deer may be most fearful of encountering a predator in frequently burned non-agricultural woodlands (Bartel and Orrock 2021). In finding that large-mammal herbivory is less impactful when fire is frequent, particularly in post-agricultural woodlands (Fig. 2), our results indicate that deer herbivory is most pronounced in habitats where deer perceive lower predation risk. Past work suggests that deer behavioral responses to predation risk can generate cascading effects on deer-preferred plant species in recently burned longleaf-pine woodlands (Cherry et al. 2016). Our implementation of long-term herbivore exclosures across sites with varying fire regimes provide some preliminary empirical support for the potential of behaviorally-mediated trophic cascades to occur in frequently-burned woodlands because we found no effect of deer herbivory in these woodlands.

4.3. Conclusions and management implications

In this study, we found that deer-preferred species richness was greater in woodlands with agricultural legacies than in woodlands without agricultural legacies. By experimentally manipulating large-mammal herbivore access, we also found that large-mammal herbivory only impacted deer-preferred plant species richness in frequently burned woodlands, particularly those with agricultural land-use histories. These findings suggest that common management practices, such as the use of prescribed burns, may indirectly promote plant species richness by reducing deer herbivory. The effects of land-use history on deer-preferred plant species richness may be of particular importance for the management of woodland habitats in the southeastern US where deer population declines are of concern to wildlife managers (Kilgo et al. 2010). Management efforts that are directed toward creating high-quality foraging habitat for white-tailed deer should prioritize the restoration of woodland habitats in post-agricultural sites, where deer-preferred plant species may already be common. Management efforts directed toward creating foraging habitat for white-tailed deer in non-agricultural sites may require additional actions to establish populations of deer-preferred plant species, including direct seeding. Since we did not find that herbivore exclosures increased deer-preferred plant species richness in non-agricultural woodlands (Fig. 2), our results suggest that temporary herbivore exclosures may not be an effective means to restore these deer-preferred species in non-agricultural habitats. Since many of the focal deer-preferred plant species represented in our study are also preferred forage for other wildlife native to the longleaf pine ecosystem, including gopher tortoises, bobwhite quail, and eastern wild turkey, we anticipate that such management efforts to increase deer-preferred plant species richness may also benefit these wildlife species.

CRediT authorship contribution statement

Savannah L. Bartel: Conceptualization, Data curation, Formal analysis, Writing – original draft, Writing – review & editing. **John L. Orrock:** Conceptualization, Funding acquisition, Resources, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

We thank L. Brudvig, E. Damschen, C. Gratton, A. Ives, B. Peckarsky, members of the Orrock Lab, S. Leroux, and one anonymous reviewer for helpful feedback that significantly improved this paper. We thank our long-term collaborators (L. Brudvig and E. Damschen) and the USDA Forest Service-Savannah River for creating and maintaining our experimental landscapes, especially J. Blake, A. Horcher, E. Olson, K. Wright, T. Thomas, S. Breland, and other USFS-Savannah River staff. Soil and plant species data from 2010 were collected by E. Damschen and L. Brudvig. We thank L. Hakkila for assistance in the field. This work was supported by the American Society of Mammalogists through a Grants-in-Aid of Research award and Albert R. and Alma Shadle Fellowship to SLB, the USDA Forest Service - Savannah River under Interagency Agreements DE-EM0003622 and 89303720SEM000037 with the US Department of Energy, the Strategic Environmental Research and Development Program (Project RC-2705), and a UW Vilas Fellowship to JLO.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2023.121023.

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