

Past agricultural land use and present-day fire regimes can interact to determine the nature of seed predation

John D. Stuhler¹ · John L. Orrock¹

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Abstract Historical agriculture and present-day fire regimes can have significant effects on contemporary ecosystems. Although past agricultural land use can lead to long-term changes in plant communities, it remains unclear whether these persistent land-use legacies alter plant–consumer interactions, such as seed predation, and whether contemporary disturbance (e.g., fire) alters the effects of historical agriculture on these interactions. We conducted a study at 27 sites distributed across 80,300 ha in post-agricultural and non-agricultural longleaf pine woodlands with different degrees of fire frequency to test the hypothesis that past and present-day disturbances that alter plant communities can subsequently alter seed predation. We quantified seed removal by arthropods and rodents for *Tephrosia virginiana* and *Vernonia angustifolia*, species of conservation interest. We found that the effects of land-use history and fire frequency on seed removal were contingent on granivore guild and microhabitat characteristics. *Tephrosia virginiana* removal was greater in low fire frequency sites, due to greater seed removal by rodents. Although overall removal of *V. angustifolia* did not differ among habitats, rodents removed more seeds than arthropods at post-agricultural sites and non-agricultural sites with low fire frequencies, but not at non-agricultural sites with high fire frequencies. Land-use history and fire frequency also affected the relationship between microhabitat characteristics and removal of *V. angustifolia*. Our results suggest that

historical agriculture and present-day fire regimes may alter seed predation by shifting the impact of rodent and arthropod seed predators among habitats, with potential consequences for the establishment of rare plant species consumed by one or both predators.

Keywords Agricultural legacy · Granivory · Plant–consumer interactions · Prescribed fire · Seed removal

Introduction

Due to the widespread abandonment of land formerly used for agriculture, forest ecosystems have re-established across large portions of the USA and Europe (Flinn and Vellend 2005). Within these post-agricultural forests, agricultural land-use legacies on biodiversity can persist for centuries after the cessation of agriculture (Hermý and Verheyen 2007); sites with a history of agricultural land use generally exhibit a lasting legacy of altered understory plant community composition (Glitzenstein et al. 1990; Flinn and Marks 2007; Brudvig and Damschen 2011; Brudvig et al. 2013). Differences in understory plant communities are often characterized by the persistent rarity or absence of certain plant species on post-agricultural land compared to remnant plant communities on land not used for agriculture (Kirkman et al. 2004; Brudvig and Damschen 2011; Brudvig et al. 2013). Because the distribution and abundance of animals often depend upon the composition and structure of plant communities (Golley et al. 1965; Dueser and Shugart 1978; Van Pelt and Gentry 1985), the potential exists for past agricultural land use to generate changes in animal distribution or abundance, and thus alter plant–consumer interactions. This potential is supported by recent work showing that past agricultural land

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✉ John D. Stuhler
john.stuhler@gmail.com

¹ Department of Zoology, University of Wisconsin-Madison,
430 Lincoln Drive, Madison, WI 53706, USA

use can alter animal abundance and behavior in ways that can affect herbivory (Hahn and Orrock 2015a) and seedling establishment (Hahn 2015). However, despite evidence that present-day plant-herbivore interactions may be shaped by past land use, the degree to which other key plant–consumer interactions are affected by past agricultural land use remains unclear.

Seed predation is an important plant–consumer interaction that can inhibit the recruitment and establishment of plant species (Orrock et al. 2006; Bricker et al. 2010; Zwolak et al. 2010) and shape the composition of plant communities (Brown and Heske 1990; Hulme 1998; Howe and Brown 2000, 2001; Crawley 2013). Post-dispersal seed predation may be particularly important in the context of past agricultural land use for two reasons. First, when seed densities are low, as would be expected for plant species recolonizing post-agricultural forests, local seed predators may be particularly important for generating seed limitation and prohibiting establishment [predator limitation (Orrock et al. 2006; Crawley 2013)]. Second, changes in microclimate and vegetation generated by historical agriculture, via long-term changes in plant community composition and reduction of overall vegetation cover (Kirkman et al. 2004; Brudvig and Damschen 2011; Brudvig et al. 2013, 2014), could alter seed predation by modifying the abundance, distribution, or foraging efficacy of different guilds of seed predators (e.g., Whelan et al. 1991; Manson and Stiles 1998; Saska et al. 2010). These responses by seed predator guilds could lead to differential seed predation (e.g., Orrock and Damschen 2005) with potential consequences for the distribution and abundance of plant species (Brown and Heske 1990; Howe and Brown 2000, 2001), possibly contributing to the continued absence of entire suites of plant species several decades following agricultural land use.

Understanding how agricultural land-use legacies affect seed predation may require explicit consideration of both historical and contemporary disturbances because the two often coincide in space (Foster et al. 2003; Cramer et al. 2008) and because historical and contemporary disturbance processes may interact to generate unanticipated shifts in seed predation. For example, many areas affected by historical agriculture are also in fire-dependent ecosystems experiencing contemporary fire suppression (Ramankutty and Foley 1999; Briggs et al. 2005; Nowacki and Abrams 2008), and the co-occurrence of fire suppression with past agricultural land use may lead to complex shifts in the plant community (Brudvig and Damschen 2011). Fire reduces litter depth (Bond and Keeley 2005), which can affect small mammal and arthropod foraging activity (Tester 1965; Reed et al. 2004, 2006; Gibb and Parr 2010; Zwolak et al. 2010). Similarly, because shrub cover may provide a lower-risk foraging environment for rodents (e.g., Brown and Kotler 2004; Orrock et al. 2004; Mattos and Orrock 2010), the

encroachment of woody species via fire suppression (Brockway and Lewis 1997; Harrington and Edwards 1999; Briggs et al. 2005; Hiers et al. 2007) may also affect rodent foraging activity by increasing cover. For arthropods, shrub cover may affect seed predation by altering soil surface temperature (Saska et al. 2010). While the effects of fire on seed predation have been documented in some systems, an examination of how seed predation varies in the context of agricultural land-use history across different degrees of fire frequency may be critical for better understanding the dynamics of seed predators and the plant populations that they may constrain (Orrock et al. 2006; Bricker et al. 2010).

We investigated the effects of agricultural land-use legacies and fire on seed predation using a large-scale experiment in the longleaf pine (*Pinus palustris*) ecosystem in the southeastern USA. We selected two species, *Tephrosia virginiana* and *Vernonia angustifolia*, that differ in seed morphology (see Materials and methods), and thus likely in their susceptibility to different seed predator guilds (e.g., arthropod versus rodent seed predators). Both species are common in longleaf pine woodlands with no history of agricultural land use, but are conspicuously absent from forests with a history of agricultural use over 40–60 years ago (Kilgo and Blake 2005; Brudvig et al. 2013), allowing us to assess whether seed predation might contribute to the absence of these species in post-agricultural sites. Longleaf pine woodlands are diverse ecosystems that are optimal for this study: despite being characterized by high levels of diversity prior to agricultural land use (Walker 1995; Peet 2006), these plant communities exhibit persistent legacies of reduced diversity several decades after restoration (Kirkman et al. 2004; Brudvig and Damschen 2011; Brudvig et al. 2013, 2014). Coupled with evidence of high rates of post-dispersal seed predation of some species in this system (Orrock et al. 2003; Orrock and Damschen 2005; Orrock et al. 2006; Craig et al. 2011), and evidence that seed predation constrains plant abundance (Orrock et al. 2006), seed predation could be a potential mechanism prohibiting the recolonization of plants typically associated with remnant longleaf understories into post-agricultural sites. Our objectives were to (1) quantify rates of seed removal by rodents and arthropods as a function of past land use and contemporary fire frequency, and (2) evaluate the degree to which rates of seed removal by different granivore guilds are a function of the physical characteristics of the surrounding microhabitat.

Materials and methods

Study area and design

Our study was conducted at the Savannah River Site (SRS), an 80,300-ha National Environmental Research Park near

Aiken, South Carolina, USA. We used 27 sites that differed in land-use history (reforested sites used for agriculture >60 years ago vs. historically forested sites with no known history of agriculture) and fire frequency. Cultivation for agricultural use occurred in this area between 1865 and 1950, peaking in the 1920s; historical farms were small and dispersed across the landscape, leaving many pockets of untilled longleaf woodlands (Kilgo and Blake 2005). We determined historical land use across the site by examining aerial photographs taken in 1951, just before agricultural abandonment that occurred due to the creation of SRS (Brudvig et al. 2013, 2014). Mature woodlands were classified as non-agricultural woodlands and cultivated fields were classified as post-agricultural woodlands, because they were subsequently replanted with longleaf (*Pinus palustris*) or loblolly (*P. taeda*) pine trees in the 1950–1960s following abandonment (Kilgo and Blake 2005). 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; this metric was previously used to classify these sites based on characteristics of the plant community (Brudvig et al. 2014). The resulting site classification by land-use history and fire frequency created four unique habitat types interspersed across the landscape (Fig. 1). Because prescribed fire destroyed the seed-removal depots at one of our sites, our study comprised 27 total sites (six replicates within non-agricultural, high fire frequency habitats; seven replicates within each of the three other habitat types). All sites were separated by >500 m and were buffered by >50 m of similar habitat [i.e., same land-use history and fire frequency (Brudvig et al. 2014)].

We quantified post-dispersal seed predation of *Tephrosia virginiana* [Fabaceae; seed weight 9.70–11.28 mg, length 4.65–5.09 mm, and width 3.12–3.48 mm (95 % confidence intervals, $n = 15$)], and *Vernonia angustifolia* [Asteraceae; seed weight 1.14–1.52 mg, length 3.97–4.37 mm (excluding pappus), and width 0.61–0.86 mm] using paired 17 × 11 × 10-cm plastic seed-removal depots at each site; these depots have been successfully used in previous large-scale studies of seed removal in longleaf pine forests (Craig et al. 2011). Depots had two 5.5-cm-diameter openings in adjacent sides and were covered with tight-fitting lids. Lids excluded avian granivores, which have negligible impacts relative to arthropods and rodents in this study area (Orrock et al. 2003), and eliminated seed loss due to wind and rain. We confirmed that wind did not affect seed removal by conducting an ancillary experiment using *V. angustifolia* with and without a pappus, finding no difference in removal ($t = -0.71$, $df = 9$, $P = 0.49$); as such, seeds of *V. angustifolia* were presented with their pappus intact to mimic the condition of a dispersed seed. Within each pair of depots, one depot was open only to arthropods by fitting

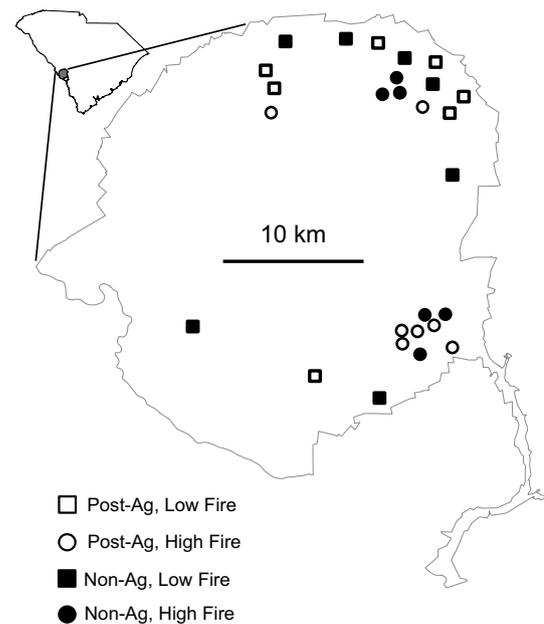


Fig. 1 Map of the study sites ($n = 27$) within upland longleaf pine woodlands at the Savannah River Site, South Carolina, USA. *Post-Ag* History of agricultural land use (>60 years since abandonment), *Non-Ag* no known history of agriculture, *Low Fire* low fire frequency (fewer than five burns since 1991), *High Fire* high fire frequency (five or more burns since 1991)

metal fencing with 1.25-cm² mesh over the openings, while the other depot allowed access by both rodents and arthropods. Pairing depots in this manner allowed us to distinguish seed removal by arthropods only and by both arthropods and rodents (e.g., Orrock and Damschen 2005; Mattos et al. 2013). Each depot contained 2 cm of sand as a substrate to mimic the natural surrounding substrate (Orrock and Damschen 2005); within each depot 20 seeds of both species were haphazardly scattered across the surface of the sand, similar to densities used in other seed-removal studies in this study system (Orrock and Damschen 2005). All seeds were collected from natural populations within the larger study region. Depots were deployed in the field for a total of 20 days between 21 July and 14 August 2012, the duration of another seed-removal study at SRS (Craig et al. 2011), and similar to other seed-removal studies in the longleaf pine ecosystem (e.g., Orrock and Damschen 2005; Krall et al. 2014). This experimental design represents a split-plot design (Littell et al. 2006), with land-use history and fire frequency as treatments applied at the level of the site and consumer access as the treatment applied to pairs of trays within a site.

We assume that seed removal is equivalent to seed predation, a common assumption in seed-removal studies (e.g., Moles et al. 2003) that was verified by observations of actual in situ seed consumption in our study (see Results)

and supported by the lack of any structures on the seeds we examined that are likely to promote arthropod dispersal (i.e., elaiosomes). Furthermore, previous work in this system shows a strong negative relationship between seed removal and recruitment of naturally occurring plants (Orrock et al. 2003, 2006), suggesting that seed removal is indicative of seed death.

Plant community data

Vegetation was sampled at each site between 7 and 12 July 2012. Within a 3.16×3.16 -m plot at each site, we visually estimated the percent cover of the foliage of all shrub species overhanging the plot, excluding trees and woody vines. Within a 1×1 -m quadrat in the corner of the plot, we visually estimated the percent cover of downed woody debris (i.e., bark, pine cones, tree branches, etc.), green vegetation, bare ground, and leaf litter. These measurements have been used previously to characterize longleaf pine understory plant communities (Brudvig and Damschen 2011; Brudvig et al. 2014). We calculated the mean proportion of visible sky in photos taken with a hemispherical lens ~1 m above the ground in the center of each plot.

Data analysis

Objective 1: quantify rates of seed removal by rodents and arthropods as a function of past land use and contemporary fire frequency

We examined the proportion of seeds removed using generalized linear mixed models with a binomial response distribution (Littell et al. 2006). To evaluate the effect of past agricultural land use and fire on seed removal by rodents and arthropods, we examined land-use history, fire frequency, and seed depot type as fixed effects with site as a random effect. Separate analyses were performed for the two species. To determine if land-use history or fire frequency affected overall seed removal of one species over the other, due to differences in seed morphology and susceptibility to different types of seed predators, we used the difference between the number of *V. angustifolia* and *T. virginiana* remaining in depots allowing access by both arthropods and rodents as the dependent variable in a mixed-model ANOVA. All mixed models used the Kenward-Roger approximation to calculate appropriate denominator *df* for testing the hypotheses of our split-plot design (Littell et al. 2006).

Objective 2: evaluate the degree to which rates of seed removal by different granivore guilds are a function of the physical characteristics of the surrounding microhabitat

We performed additional analyses to examine how specific vegetation characteristics may affect seed removal

by arthropods and by rodents. Seed removal by arthropods was estimated as the proportion of seeds removed from depots allowing access by arthropods only. To quantify seed removal by rodents, we used the difference in the proportion of seeds removed between paired depots at a site. Given the potential for collinearity among habitat variables, we used principal components analysis (PCA) to reduce the habitat variables to a smaller number of principal components encapsulating environmental variation across the 27 sites. Habitat variables subjected to PCA consisted of the four cover classes (i.e., herbaceous vegetation, bare ground, litter, downed woody debris), percent visible sky in the canopy, and shrub cover. We performed a square root transformation and then centered the data prior to analysis. Following PCA, we retained principal components with eigenvalues greater than 1 (Everitt 2005). We then analyzed the principle component scores using separate linear models (ANOVA) with land-use history, fire frequency, and the interaction between land-use history and fire frequency as predictor variables to aid in interpretation of subsequent analyses.

The relationship between seed removal and habitat characteristics was evaluated with generalized linear mixed models using the proportion of seeds removed as the binomial response variable. The first principal component, land-use history, fire, and all interactions were included as fixed effects, with each observation treated as a random effect to accommodate overdispersion (Harrison 2014). We removed all non-significant higher-order interactions to simplify the model. We analyzed the two plant species separately for the two different granivore guilds (i.e., arthropods and rodents).

All analyses were performed in R (R version 3.0.2, R Core Team, Vienna, 2013) and SAS (SAS version 9.3, Cary, NC).

Results

Across both species, 660 of the 2160 (31 %) total seeds were removed from 40 of the 54 seed-removal depots placed in the field. Direct evidence of seed mortality (i.e., seed coat fragments and/or gnawed seeds) was found in 33 % of depots with rodent access and 22 % of depots with access by arthropods only.

Objective 1: quantify rates of seed removal by rodents and arthropods as a function of past land use and contemporary fire frequency

Allowing rodents access significantly increased seed removal of both species (*T. virginiana*, $F_{1,21.51} = 20.95$, $P = 0.002$; *V. angustifolia*, $F_{1,17.18} = 33.40$, $P < 0.001$; Fig. 2). The average proportion of *T. virginiana* seeds

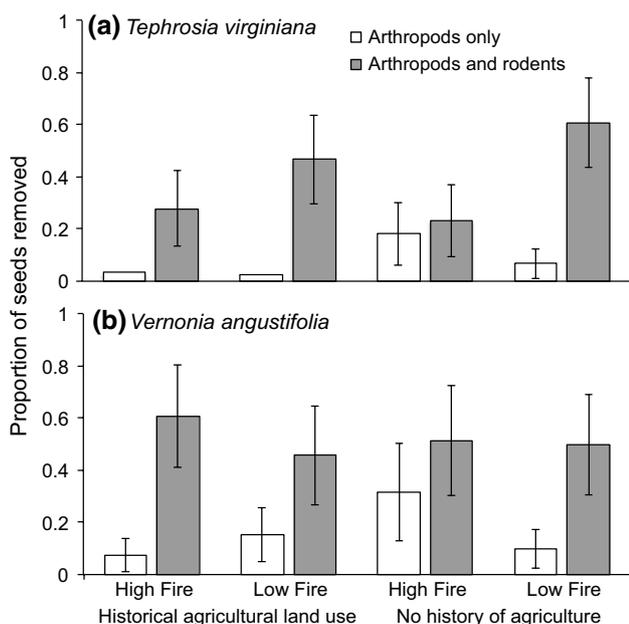


Fig. 2 The proportion of **a** *Tephrosia virginiana* and **b** *Vernonia angustifolia* seeds removed by arthropods only, or arthropods and rodents, in each of the four different habitats (i.e., land-use history and fire frequency). Bars illustrate means \pm 1 SE

removed was 0.39 ± 0.09 (SE) from seed depots open to both arthropods and rodents and 0.06 ± 0.03 from seed depots excluding rodents; the average proportion of *V. angustifolia* removed was 0.52 ± 0.10 from seed depots open to both arthropods and rodents and 0.14 ± 0.05 from seed depots excluding rodents.

For *T. virginiana*, there was no significant main effect of land-use history ($F_{1,26.18} = 1.13, P = 0.30$), fire frequency ($F_{1,26.18} = 0.14, P = 0.71$), or the interaction between land-use history and fire frequency ($F_{1,26.18} < 0.01, P = 0.99$; Fig. 2a). There was, however, a marginally significant interaction between seed depot type and fire frequency ($F_{1,21.51} = 3.66, P = 0.07$; Fig. 2a). Across both land-use histories, rodent seed removal was significantly greater than arthropod seed removal in low fire frequency sites ($F_{3,29.53} = 6.29, P = 0.002$), but not in high fire frequency sites ($F_{3,27.4} = 1.61, P = 0.21$; Fig. 2a).

For *V. angustifolia*, there was no effect of land-use history ($F_{1,14.89} = 0.11, P = 0.75$), fire frequency ($F_{1,14.89} = 0.19, P = 0.67$), or the interaction between land-use history and fire frequency ($F_{1,14.89} = 0.30, P = 0.59$; Fig. 2b) on seed removal. There was a significant three-way interaction between seed depot type, land-use history, and fire frequency ($F_{1,17.18} = 4.51, P = 0.05$; Fig. 2b). Rodents removed significantly more seeds than arthropods at sites with a history of agricultural land use (low fire frequency, $F_{1,15.57} = 7.50, P = 0.01$; high fire frequency, $F_{1,20.33} = 12.82, P = 0.002$), and at low fire frequency sites

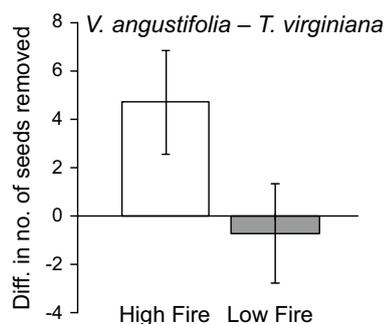


Fig. 3 The difference between the number of *V. angustifolia* and *T. virginiana* seeds removed from depots allowing access by both arthropods and rodents. Positive values indicate more *V. angustifolia* seeds were removed, whereas negative values indicate more *T. virginiana* seeds were removed. Values are averaged across both land-use histories. Bars illustrate means \pm 1 SE. For abbreviations, see Fig. 1

with no history of agricultural land use ($F_{1,15.60} = 13.62, P = 0.002$), but not at high fire frequency sites with no history of agricultural land use ($F_{1,15.34} = 2.01, P = 0.18$). This pattern was driven by increased removal of *V. angustifolia* by arthropods in high fire frequency sites with no history of agricultural land use (Fig. 2b).

Our analysis comparing the difference in removal between *V. angustifolia* and *T. virginiana* detected a marginally significant effect of fire frequency ($F_{1,23} = 3.30, P = 0.08$): there was a trend of greater removal of *V. angustifolia* seeds in high fire frequency sites. There was no significant effect of land-use history ($F_{1,23} = 0.05, P = 0.82$) or the interaction between land-use history and fire frequency ($F_{1,23} = 0.02, P = 0.89$). In high fire frequency sites across both land-use histories, more *V. angustifolia* seeds were removed compared to *T. virginiana*; i.e., the difference between *V. angustifolia* and *T. virginiana* removal was significantly different from zero (Fig. 3; $t = 2.29, df = 25, P = 0.03$). In low fire frequency sites, the difference was not significantly different from zero (Fig. 3; $t = -0.36, df = 25, P = 0.72$).

Objective 2: evaluate the degree to which rates of seed removal by different granivore guilds are a function of the physical characteristics of the surrounding microhabitat

We retained two principal components that explained 71 % of the variation in the original habitat data (Table 1). The first principal component explained 39.2 % of the variation in the original data and was a contrast between vegetation cover and downed woody debris (Table 1). This principal component did not differ by land-use history ($F_{1,23} = 2.31, P = 0.14$), fire frequency ($F_{1,23} = 1.18, P = 0.29$), or the interaction between land-use history and fire frequency

Table 1 Loadings for the first two principal components (PCs) from the analysis on seed removal related to microhabitat characteristics

Variable	PC1	PC2
Herbaceous cover (%)	−0.59	0.16
Bare ground (%)	0.05	0.66
Litter cover (%)	0.33	−0.60
Downed woody debris (%)	0.42	0.11
Visible sky (%)	0.28	0.35
Shrub cover (%)	−0.54	−0.22
Percent variance explained	39.2	31.4

($F_{1,23} = 0.07$, $P = 0.80$). The second principal component explained an additional 31.4 % of the variation in the data and was a contrast between bare ground and litter cover (Table 1). Because there were no significant main effects or interactions in analyses using the second principal component (all $P > 0.12$), results below focus on the first principal component.

The final model evaluating removal of *V. angustifolia* by arthropods with the first principal component included no significant main effect of the principal component ($F_{1,23} = 0.01$, $P = 0.81$), land-use history ($F_{1,23} = 0.94$, $P = 0.29$) or fire frequency ($F_{1,23} = 0.37$, $P = 0.53$). Furthermore, there was no significant interaction between this principal component and land-use history ($F_{1,23} = 0.70$, $P = 0.40$). However, arthropod removal of *V. angustifolia* was affected by the interaction between this principal component and fire frequency ($F_{1,23} = 4.11$, $P = 0.05$): removal of *V. angustifolia* by arthropods increased with increasing downed woody debris in low fire frequency sites, but there was no relationship between seed removal and this principal component in high fire frequency sites (Fig. 4). There were no significant main effects or interactions to describe removal of *T. virginiana* by arthropods (all $P > 0.09$).

The final model evaluating removal of *V. angustifolia* by rodents with the first principal component included no significant main effect of the principal component ($F_{1,23} = 0.04$, $P = 0.73$), land-use history ($F_{1,23} = 0.14$, $P = 0.64$), or fire frequency ($F_{1,23} = 0.68$, $P = 0.48$). However, rodent removal of *V. angustifolia* was affected by the interaction between this principal component and fire frequency ($F_{1,23} = 7.61$, $P < 0.01$): in high fire frequency sites, there was a positive relationship between removal of *V. angustifolia* by rodents and increasing downed woody debris, whereas there was a trend of decreasing removal of *V. angustifolia* by rodents with increasing downed woody debris in low fire frequency sites (Fig. 5a). Similarly, rodent removal of *V. angustifolia* was affected by a marginally significant interaction between this principal component

Removal of *V. angustifolia* by arthropods

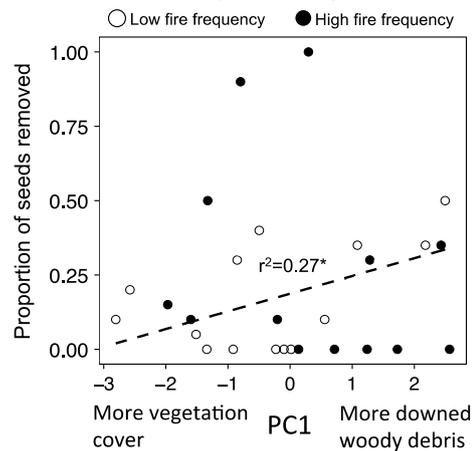


Fig. 4 The relationship between removal of *V. angustifolia* seeds by arthropods and the first principal component (PC1), pooled by fire frequency. The dashed line indicates a significant relationship between seed removal and the PC in low fire frequency sites (open circles; $*P < 0.05$). There was no relationship between seed removal and the PC in high fire frequency sites

and land-use history ($F_{1,23} = 5.42$, $P = 0.07$). There was no relationship between rodent seed removal and this principal component in non-agricultural sites, but there was a significant positive relationship between removal of *V. angustifolia* and increasing downed woody debris in post-agricultural sites (Fig. 5b). There were no significant main effects or interactions to explain removal of *T. virginiana* by rodents (all $P > 0.12$).

Discussion

The results of our large-scale study indicate that past and present-day human activities may act, alone or in concert, to determine the nature of seed predation in contemporary landscapes. Because the ultimate effect of past land use and contemporary fire frequency depended largely on the traits of specific seed species, our results also highlight how the effect of past and present disturbance on seed predation may depend critically upon seed characteristics that determine susceptibility to particular consumers (e.g., small seeds that are consumed by both rodents and arthropods). Moreover, our results not only illustrate the potential for historical agriculture and contemporary fire to alter seed removal, but we also found that it modifies the relationship between microhabitat characteristics and seed removal. As such, predicting how seed predation will vary based upon habitat characteristics may require knowledge of past and present disturbance. Below, we expand on each of these implications.

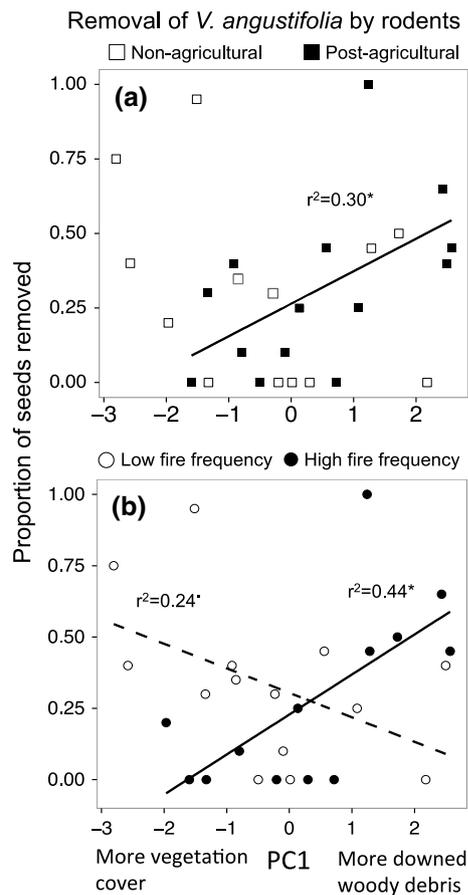


Fig. 5 The relationship between removal of *V. angustifolia* seeds by rodents and PC1 pooled by **a** land-use history and **b** fire frequency to show significant two-way interactions involving the PC. Regression lines (*dashed* or *solid*) indicate significant relationships. $\cdot P < 0.1$, $*P < 0.05$

Past and present disturbance can modify the nature of contemporary seed predation

Although seed removal can be affected by contemporary management activities such as fire (e.g., Reed et al. 2004; Zwolak et al. 2010; Krall et al. 2014), our work illustrates that past agricultural land use may also lead to changes in seed removal. Importantly, our results highlight how the ultimate effect of land-use history and fire on seed predation depends upon the granivore guild with access to seeds (e.g., arthropods or rodents) and the seed species (i.e., *T. virginiana* or *V. angustifolia*). In particular, the effect of past agricultural land use was most evident for *V. angustifolia*: allowing rodents access to seeds resulted in significant increases in seed removal in post-agricultural sites and non-agricultural sites with low fire frequencies. However, arthropods alone were just as effective as both arthropods and rodents in non-agricultural sites with high fire frequencies (Fig. 2b). This habitat-specific shift in the importance

of arthropod versus rodent seed predation may be magnified in situations where seeds may be buried due to wind or rain. Rodents can exhume buried seeds, whereas arthropods generally only consume seeds on the soil surface (Reichman 1979; Hulme 1994). As such, burial would be expected to lead to greater survival of *V. angustifolia* seeds in frequently burned non-agricultural habitats, because *V. angustifolia* is more likely to be buried because of its smaller size (Bekker et al. 1998), providing refuge from arthropods. In post-agricultural habitats and non-agricultural habitats with low fire frequencies, *V. angustifolia* would be less likely to escape consumption via burial, because rodents are significant seed predators in these habitats (Fig. 2b).

Removal of *T. virginiana* seeds was minimal across all sites from depots that allowed access by arthropods only (Fig. 2a), suggesting that *T. virginiana* is too large for many arthropods; this was corroborated by field observations, where the most abundant ant species at our study sites (*Solenopsis invicta*) could only physically remove seeds in 20 % of trials with *T. virginiana*, but 90 % of trials with *V. angustifolia* [$n = 10$ trials per species (Stuhler and Orrock, unpublished data)]. As such, the reduced impact of rodent seed predators in high fire frequency sites led to lower rates of overall predation of *T. virginiana* seeds in those habitats (Fig. 2a). Similarly, Hiers et al. (2000) documented lower rates of pre-dispersal seed predation of *T. virginiana* following fire. The effects of pre- and post-dispersal seed predation are likely additive; because *T. virginiana* is capable of persisting in the seed bank for at least 8 years (Kaeser and Kirkman 2012), our results suggest that heightened rates of seed predation by rodents in low fire frequency sites may exacerbate the threat of fire suppression to legume conservation (Leach and Givnish 1996).

The importance of rodents as primary seed predators in our system is illustrated by significantly higher seed removal from rodent-accessible trays (Fig. 2) and reinforced by our observations of depredated seeds inside the depots. While this finding is consistent with studies implicating rodents as significant seed predators (e.g., Reichman 1979; Brown and Heske 1990; Orrock et al. 2003), our research highlights the contribution of rodents to seed predation of rare species in post-agricultural forests, which are increasingly widespread (Flinn and Vellend 2005), in addition to areas with no history of agriculture. Because granivores foraging from our seed-removal depots also forage outside of them, and common granivorous rodent species in this system (i.e., *Peromyscus gossypinus* and *P. polionotus*) may consume a variety of foods (Gentry and Smith 1968; Wolfe and Linzey 1977), one possible explanation for the different consumption of *T. virginiana* seeds in non-agricultural sites with different fire frequencies may be that there are more alternative food sources in habitats with high fire frequencies. Because we were primarily

Table 2 Attributes for each of the four habitat types (i.e., land-use history and fire frequency)

Variable	Post-agricultural		Non-agricultural	
	High fire	Low fire	High fire	Low fire
Number of sites	7	7	6 ^b	7
Herbaceous cover (%)	19.7 ± 6.9	19.7 ± 7.5	23.2 ± 12.4	28.0 ± 10.5
Bare ground (%) ^a	23.6a ± 11.1	4.7b ± 3.4	13.0a,b ± 8.8	0c ± 0
Litter cover (%)	45.0 ± 12.0	66.3 ± 7.7	56.7 ± 14.6	64.9 ± 9.7
Downed woody debris (%)	11.7 ± 3.2	9.3 ± 2.9	7.2 ± 1.5	7.0 ± 2.0
Visible sky (%) ^a	61.2a ± 4.0	41.5b ± 3.3	43.6b ± 4.5	42.7b ± 5.6
Shrub cover (%) ^a	5.4a ± 2.2	7.4a ± 2.3	6.5a ± 1.5	24.4b ± 5.5

Values are mean ± SE. *Different lowercase letters* indicate significant differences among habitats (Tukey's honest significant difference, $P < 0.05$) for variables that were affected by land-use history and fire frequency

Post-agricultural History of agricultural land use (>60 years since abandonment), *Non-agricultural* no known history of agriculture, *Low Fire* low fire frequency (fewer than five burns since 1991); *High Fire* high fire frequency (five or more burns since 1991)

^a Variables for which differences exist among habitats

^b One site was removed from analyses due to a prescribed burn during the experiment

interested in rates of seed removal across different habitats, we did not conduct a comprehensive survey of the food sources available to granivores at our sites, but research suggests that prescribed fire can lead to significant changes in foods for rodent granivores by altering flower production (Hiers et al. 2000), seed production (Buckner and Landers 1979), and arthropod abundance (Hanula and Wade 2003). A more complete examination of possible food sources for omnivorous consumers could be a profitable next step to understand habitat-related patterns.

Past and present disturbance mediates the relationship between microhabitat and seed removal

Microhabitat characteristics are often significantly associated with seed predation (e.g., Kotler 1984; Whelan et al. 1991; Manson and Stiles 1998). Our results show, for the first time, that past and present human activities may alter the relationship between microhabitat characteristics and patterns of seed removal. Greater vegetation cover likely lowers the perceived predation risk experienced by rodents (e.g., Morris and Davidson 2000; Manson et al. 2001; Wolf and Batzli 2004), which may lead to heightened rates of seed predation (Manson and Stiles 1998). In our study, non-agricultural sites with low fire frequencies had greater shrub cover than all other habitats (Table 2); within this habitat type, greater seed removal occurred in sites with greater shrub cover. In sites with less vegetation cover, rodent removal of *V. angustifolia* increased with downed woody debris (Fig. 5). Cotton mice (*P. gossypinus*), likely the primary rodent seed predators at our sites (Golley et al. 1965; Cothran et al. 1991; Loeb 1999; Hinkelman et al. 2011), use downed woody debris as daytime refuges, travel

routes, and foraging sites (McCay 2000; Hinkelman et al. 2011). Because the amount of downed woody debris was not different among habitats (Table 2), the importance of downed woody debris as a microhabitat feature affecting rodent seed predation is likely greatest where there is less vegetation cover. This shift in the use of different structures among habitats may also illustrate why *P. gossypinus* abundance and survival are not different in burned versus unburned longleaf pine forests (Morris et al. 2011).

For arthropods, the importance of downed woody debris in affecting seed removal may reflect differences in the arthropod communities of different habitats. Niwa and Peck (2002) found that carabid beetles were generally more abundant in unburned forested sites compared to recently burned forested sites. Additionally, downed woody debris is an important habitat feature for many beetle species (Ulyshen et al. 2004), suggesting that the positive relationship between seed removal and downed woody debris may be driven by more abundant granivorous beetles in low fire frequency sites. In contrast, ants may be more significant seed predators in high fire frequency sites, as suggested by a weak, positive trend between ant mound abundance and removal of *V. angustifolia* seeds in these habitats (Stuhler and Orrock, unpublished data). Understanding how these potential differences in arthropod communities translate to seed survival could be an important avenue for future research.

Implications for conservation and restoration of post-agricultural sites

By evaluating rates of seed removal in non-agricultural versus post-agricultural forests, our work may have

implications for the management of plant communities. First, although overall seed removal in post-agricultural sites did not differ from seed removal in non-agricultural sites (Fig. 2), the impact of seed predation may still be greater in post-agricultural sites where there are fewer adult plants (Kirkman et al. 2004; Brudvig and Damschen 2011; Brudvig et al. 2013) because seeds at low densities are more susceptible to being limited by consumers (Crawley 2013). The overall rates of seed removal that we observed were consistent with other work in the longleaf pine ecosystem examining seed removal of species of conservation interest [*Anthaenantia villosa*, *Carphephorus bellidifolius* (Craig et al. 2011)], indicating that rates of seed predation may be high for rare, native species in this system. Although seed addition may aid restoration by compensating for consumer effects (Myers and Harms 2009; Orrock et al. 2009), seeds that survive predation in post-agricultural habitats may still experience reduced recruitment due to the more compacted soils compared to habitats not used for agriculture (Mattingly and Orrock 2013).

Finally, our work shows that prescribed fire may influence seed consumption within these habitats, and this effect is not always dependent upon land-use history. For example, our work predicts that large-seeded species (e.g., legumes), which are more likely to be suppressed primarily by rodent seed predators (e.g., Brown and Heske 1990), will perform better in sites managed with prescribed burns where predation of these plant species by rodents is likely to be reduced. For small- and intermediate-seeded species, which are more likely to be susceptible to both rodent and arthropod seed predators, our work predicts that, all else being equal, small-seeded plant species will be more vulnerable in frequently burned sites (Fig. 3). We also show that understanding the impacts of prescribed burns on seed predation is likely to require an understanding of the characteristics of the surrounding environment (e.g., shrub cover versus downed woody debris), and how the role of these habitat characteristics in affecting consumer pressure may be modified by disturbance. Future work that addresses whether these differences in seed survival are sufficient to produce changes in the relative abundance of established plants will be essential for further understanding the consequences of past and present disturbance on important plant–consumer interactions.

Although seed predation may be an important factor shaping plant populations and communities (Howe and Brown 2000, 2001; Bricker et al. 2010; Crawley 2013), other factors like microsite availability, dispersal limitation, and competition may be important and can act in concert to synergistically limit plant establishment and community composition (Crawley 2013). In longleaf systems, fire (Hiers et al. 2000; Brudvig et al. 2014; Veldman et al. 2014), agricultural land use (Brudvig et al. 2013, 2014;

Veldman et al. 2014), canopy density (Veldman et al. 2013), and connectivity (Brudvig and Damschen 2011) are all known to affect plant populations and communities. For example, fire increases the number of available microsites (i.e., open patches of soil close to the soil surface), although seed predation may prevent those microsites from being filled (Orrock et al. 2006). Biotic processes other than seed predation, such as herbivory, may also be important in affecting plant growth (Hahn and Orrock 2015b) and seedling establishment (Hahn 2015). In our work, we find that the potential scope for seed mortality via seed predation can be very high (e.g., over 50 %), in general agreement with other studies of seed predation in this system (Orrock and Damschen 2005; Craig et al. 2011; Krall et al. 2014). This magnitude of seed predation is likely to be significant given the importance of early seed survival stemming from relatively low seedbank longevity in longleaf systems (Kaeser and Kirkman 2012). Moreover, studies that have manipulated dispersal limitation and granivores have found that seed predation can be a more important determinant of plant establishment than seed dispersal. However, this work was done in an experiment where microsites were not limiting and other factors (e.g., prescribed fire) were carefully controlled. Consequently, factorial experiments that manipulate multiple factors (e.g., fire regime, seed predation, seed dispersal, canopy density) will be necessary to construct a robust framework for understanding the unique, and potentially interactive, role of seed predation in affecting plant populations and communities.

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