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Past and present disturbances generate spatial variation in seed predation

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Citation: Bartel, S. L. and J. L. Orrock. 2020. Past and present disturbances generate spatial variation in seed predation. Ecosphere 11(5):e03116. 10.1002/ecs2.3116

Abstract. Seed survival is a key process for plant populations; variation in the activity and abundance of animals that consume seeds can lead to dramatic shifts in seed fate. Because granivores may respond to contemporary disturbance as well as to enduring changes in habitats caused by past disturbances, understanding seed fate requires studies capable of evaluating how past and present disturbances modify granivore communities, foraging activity, and ultimately, seed predation. Historic agricultural land use and contemporary canopy harvesting are widespread disturbances that could generate large-scale patterns of seed fate by modifying environmental characteristics that determine granivore identity and behavior. To evaluate whether land-use history and canopy harvesting affect seed–animal interactions, we conducted an experiment distributed across 80,000 ha of longleaf pine woodlands that coupled large-scale canopy harvesting at seven 4-ha sites containing both post-agricultural land use and nonagricultural land use in South Carolina, United States. We deployed a total of 28,000 nail-tagged seeds and recovered the tags to quantify seed fate. Past agricultural land use and contemporary canopy harvesting interacted to affect the rate of seed predation. Seed predation rates in harvested sites depended on land-use history: Seed predation was 30% lower in post-agricultural plots than in nonagricultural plots. This interaction was driven by the differential effect of land-use history and canopy harvesting on rodent activity. Camera traps revealed that *Sigmodon hispidus* only foraged in harvested plots and was most active in nonagricultural plots. In harvested plots, seed removal increased with *S. hispidus* activity. In unharvested plots, seed removal increased with *Sciurus niger* activity, but *S. niger* was not affected by land-use history. In finding that land-use history and canopy harvesting determine the outcomes of seed–animal interactions, we show that understanding patterns of seed predation is contingent upon the interplay of disturbances in both the distant past and recent past. These results suggest that patterns of past land use and present land use may help reconcile the considerable variation in seed fate observed in ecological communities.

Key words: canopy harvesting; disturbance; granivory; land-use history; longleaf pine; *Quercus nigra*; rodent; seed limitation; seed predation; *Sigmodon hispidus*.

Received 12 February 2020; accepted 18 February 2020. Corresponding Editor: Debra P. C. Peters.

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INTRODUCTION

Seed limitation is a key process affecting large-scale patterns of plant distributions and diversity (Louda 1982, Clark et al. 1998, Zobel et al. 2000, Orrock et al. 2006, Standish et al. 2007, Öster et al. 2009). Seed limitation occurs through two processes: Seeds may never arrive at a microsite favorable for establishment (dispersal limitation; Turnbull et al. 2000), or seeds may be destroyed by predators either before or after dispersal (predator limitation; Crawley 2000). Because seed predation may be tightly linked to the abundance and activity of animals that consume seeds (Ji-Qi and Zhi-Bin 2004), environmental characteristics that modify animal behavior,

abundance, and community composition can place important constraints on seed survival (Orrock et al. 2010, Lichti et al. 2014, 2017, Brehm et al. 2019). Despite the importance of understanding how the environment can modify seed–animal interactions, deciphering the effect of the environment can be complex because multiple environmental components can affect the activity, abundance, and community composition of foraging animals (Brown and Kotler 2004, Orrock et al. 2010, Kelt et al. 2019).

Past agricultural land use and contemporary canopy harvesting are two pervasive human disturbances that modify environmental characteristics that determine granivore identity and behavior. Agricultural land use is widespread in terrestrial systems: 42–68% of land cover has been impacted by agriculture since 1700, and land recovered from agriculture increased over this period by 10–44 $\times$ 10^6 km^2 (Hurtt et al. 2006). Agricultural legacies on plant communities can persist for centuries (Foster 1993, Flinn and Vellend 2005, Kopecký and Vojta 2009, Mattingly et al. 2015, Culbert et al. 2017). Past land use can interact with contemporary disturbances such as canopy harvesting to determine plant performance (Hahn and Orrock 2016), consumer pressure (Hahn and Orrock 2015, Stuhler and Orrock 2016), and community structure (Brudvig and Damschen 2011). Harvesting of mature trees is implemented worldwide for both commercial and restoration purposes (Toman et al. 1996, Simberloff 1999, Drever et al. 2006), and it can drive changes in seed predation by animals (Bellocq et al. 2005, Lambert et al. 2005, Chen et al. 2017). Despite evidence showing that seed limitation is fundamental in determining plant community structure after agricultural land use and canopy harvesting (Turley et al. 2017, Barker et al. 2019), it is unclear whether past agriculture and contemporary canopy harvesting generate patterns of seed predation by changing granivore identity and behavior.

Rodents are primary seed predators in many ecosystems (Hulme 1994, Bermejo et al. 1998, Corlett 1998, Kappler et al. 2012, Stuhler and Orrock 2016, Gómez et al. 2019); rodent seed predation can generate large-scale patterns of plant distributions (Maron and Simms 1997, Crawley 2000, Orrock et al. 2006, Bricker et al. 2010, Culot et al. 2017). Habitat structure is a particularly well-known driver of rodent foraging behavior (Dueser and Shugart 1978, Orrock et al. 2004, 2010, Zwolak 2009, Guiden and Orrock 2017); hence, disturbances that transform habitat structure could change the magnitude and spatial patterns of rodent foraging to modify seed fate (Guiden and Orrock 2017). By eliminating canopy cover and increasing understory growth, canopy harvesting can alter rodent granivore identity and foraging behavior (Sullivan and Sullivan 2001, Lambert et al. 2005, Fisher and Wilkinson 2005, Zwolak 2009, Chen et al. 2017, Jacques et al. 2017). Since agricultural legacies also modify habitat structure (e.g., increased light availability, Hahn and Orrock 2015; and decreased shrub cover, Stuhler and Orrock 2016), predicting how rodents will respond to harvesting may be contingent upon past land use. Despite the potentially important role of past agricultural legacies in determining the outcomes of contemporary disturbances, no research has investigated whether past agricultural land use interacts with a globally ubiquitous disturbance, canopy harvesting, to generate spatial variation in rodent species activity and seed predation. Considering that rodent granivores may also be essential agents of seed dispersal (Vander Wall 2001, Vander Wall et al. 2005, Jansen et al. 2012, Lichti et al. 2017), explicit tracking of seed fate after rodent handling is essential to understanding how rodent responses to disturbances are linked to spatial patterns of seed predation. Understanding the roles of past and present disturbances and rodent granivory in generating patterns of seed predation therefore requires landscape-level manipulations of past and present disturbances paired with small-scale monitoring of granivore identity, behavior, and seed fate.

In order to understand how past land use and contemporary canopy harvesting generate spatial variation in seed predation by modifying granivore identity and behavior, we monitored seed fate and rodent activity in a large-scale experiment in the longleaf pine (*Pinus palustris*) ecosystem in the southeastern United States. Agricultural history is pervasive in contemporary longleaf pine woodlands, affecting plant communities, herbivory, and habitat structure (Veldman et al. 2014, Hahn and Orrock 2015, Stuhler and Orrock 2016). In these woodlands,

seed limitation prevents the recovery of native plant species, and rodents are important seed predators (Orrock et al. 2003, 2006, Stuhler and Orrock 2016, Turley et al. 2017). Using replicated, large-scale experimental landscapes that combine a factorial manipulation of contemporary disturbance (canopy harvesting) across plots that differ in their historical land use, we used explicit tracking of seed fate and monitoring of rodent granivores to evaluate two hypotheses: (1) By modifying rodent habitat structure, past agriculture and present canopy harvesting affect rodent species activity, and (2) by modifying rodent species activity, past agriculture and present canopy harvesting affect seed predation rates.

Methods

Study area and design

We conducted our study at the Savannah River Site (SRS; Aiken, South Carolina, USA), an 80,125-ha National Environmental Research Park (NERP). SRS is within the historical range of the longleaf pine woodland, and much of this ecosystem was converted to tillage agriculture between 1856 and 1950 (Frost 2006). These agricultural lands were small and dispersed, resulting in heterogeneous landscapes with plots of tilled farmland and untilled 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). Past research at SRS shows that agricultural land-use history has a strong effect on overstory communities such that post-agricultural areas are dominated by pine and nonagricultural areas are dominated by hardwoods, an artifact of historic fire suppression (Brudvig et al. 2013). We selected seven sites, spanning an 807-km^2 area, each straddling a land-use history boundary. Each site was relatively homogenous in soil type, slope, and fire frequency (see Brudvig et al. 2013 for further details). Since fire regime is an important driver of rodent population dynamics, habitat structure, and plant communities in this system (Frost 2006, Morris et al. 2011*a*, *b*, Karmacharya et al. 2012), we selected sites that spanned a fire regime ranging from 0 to 12 yr since the last prescribed burn to capture the range of variation typical in managed longleaf pine woodlands (Frost 2006). A primary obstacle to studying land-use history is that agricultural history can be confounded with other properties of the site that were favored for agriculture (Flinn and Vellend 2005). We minimized these confounding effects by using paired plots, split by land-use history (Brudvig et al. 2013). Land-use history classification was based on aerial photography taken prior to land abandonment in 1951. Plots that were farmland in 1951 were classified as post-agricultural, and plots that were forested were classified as nonagricultural. At each site, we established four 1-ha (100 × 100 m) research plots that contained two pairs of plots on opposing sides of the land-use history boundary (Fig. 1), and we imposed a canopy harvesting treatment (8–10 mature trees remaining per ha) in 2011 to create a fully factorial manipulation of land-use history and canopy harvesting (Fig. 1).

Seed-tracking experiment

To test how land-use history and canopy harvesting alter rodent activity and seed fate, we employed an acorn-tracking method that has been successfully used in past studies examining seed predation and seed dispersal (Sork 1984, Moore et al. 2007, Lichti et al. 2014, Guiden and Orrock 2017). We obtained *Quercus nigra* seeds from a commercial supplier (Louisiana Forest Seed Company, Lecompte, Louisiana, USA), which we tagged with 12-mm brad nails (Sork 1984, Moore et al. 2007, Lichti et al. 2014, Guiden and Orrock 2017). *Quercus nigra* is a common oak species found in both post-agricultural and nonagricultural areas at our sites. We deployed 1000 nail-tagged *Q. nigra* seeds in the center of every 1-ha plot at all seven sites for a period of four weeks in July 2017 (Fig. 1). Within a site, we painted the nails for each plot a unique fluorescent color to make it possible to determine between-plot movement events. To focus on seed foraging by rodents, we secured a 0.5 × 0.5 m hardware-cloth box around tagged acorns to create a seed depot. The seed depot contained a 7 × 7 cm hole that allowed rodent access and prohibited seed foraging by larger, non-focal taxa (e.g., turkeys and deer). At the end of the deployment period, we used a metal detector (Bounty Hunter Platinum, First Texas Products, El Paso, Texas, USA) to survey the area within a 30-m radius of each depot for the nails. Preliminary

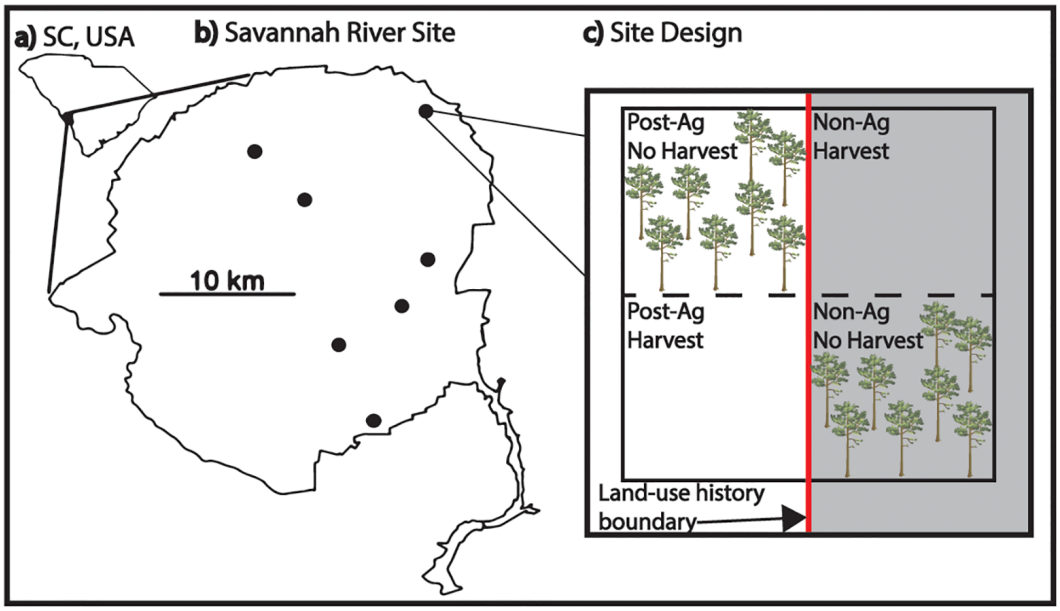

Fig. 1. We conducted this experiment in South Carolina (a) at the Savannah River Site (b). The location of the seven sites utilized in this study at SRS is depicted as black dots on the SRS map (b). Each of our seven sites straddled a land-use history boundary, on top of which we imposed a fully factorial manipulation of canopy harvesting (c). Each site contained four 1-ha plots.

tests verified that our metal detector was able to detect a nail 15 cm below the surface, which greatly exceeds the published range of cache depths: 0.26–9 cm (Vander Wall 2003, Vander Wall et al. 2009, Lichti et al. 2014, Dittel et al. 2017). Once a tagged acorn or nail was recovered, we recorded the distance and compass bearing from the depot and whether or not the seed was consumed. By counting the number of seeds remaining in the depot, we were able to estimate the number of seeds removed and determine recovery rates. Because *Glaucomys volans* nest boxes and *Peromyscus polionotus* burrows in the southeastern United States have been shown to contain the remains of consumed acorns and never intact acorns (Moore 1947, Gentry and Smith 1968, Goertz et al. 1975, Heidt 1977), we assume, consistent with other studies that follow acorn fate (Steele et al. 2001, Guiden and Orrock 2017), that unrecovered acorns are likely to be nonviable because they have been moved to arboreal or deep subterranean caches where they are likely to be consumed or are incapable of successful germination and emergence. Habitat structure was measured at each depot by using four 1-m^2 quadrats where percent cover for bare soil, leaf litter, woody debris, and vegetative cover (herbaceous and woody plants) was visually estimated. All data were collected by the same observer.

Rodent species activity

To examine how land-use history and canopy harvesting affected rodent activity and community composition, we positioned a motion-activated digital trail camera one meter from each depot for one week while nail-tagged seeds were deployed (Fig. 1). We recorded the date and time of each photograph and the species captured in it. Since the identification of the two common *Peromyscus* species in our study area, *Peromyscus gossypinus* and *Peromyscus polionotus*, requires morphological measurements, we did not identify this genus to the species level. To create an estimate of rodent species activity from the camera-trap data that were relevant for seed predation and dispersal, we quantified the total number of foraging bouts per rodent species at each depot. Because our camera traps were positioned to capture rodents entering, exiting, and

foraging inside of the depot, a bout was defined as a single visit to the depot.

Data analysis

We calculated the proportion of seeds removed from the depot and the average distance seeds were moved at each plot. All analyses were conducted in R ver. 3.5.1, and linear mixed models were constructed using the lme4 package (Bates et al. 2015; see Appendix S1: Table S1 for list of hypotheses and models). To test the hypothesized effects of land-use history and canopy harvesting on habitat structure, we used multivariate analysis of variance (MANOVA) with percent ground cover variables (bare, litter, vegetation, and woody debris) as response variables and canopy harvesting and land-use history as fixed effects. If a significant result from MANOVA analysis was detected, we used univariate analysis of variance (ANOVA) to test the effects of land-use history and harvesting on specific ground cover variables (Scheiner 2001). To test the hypothesized effects of land-use history and canopy harvesting on the proportion of seeds removed, we used a binomial generalized linear mixed model (GLM) with a random intercept for site and varying slopes for land-use history. To test how land-use history and canopy harvesting affected the spatial extent of rodent foraging, we used linear mixed-effects models with a random intercept for site and varying slopes for land-use history. To test how activity of individual rodent species was related to the proportion of seeds removed, we used separate binomial GLMs (Table 1) with a random intercept for site and different slopes for land-use history. For species that were only found in one harvesting treatment group, we had to subset the data by harvesting treatment for analyses. For rodent species whose activity had a significant effect on seed removal, we used linear mixed-effects models to test how land-use history and canopy harvesting affected the activity with a random intercept for site.

Results

The average seed-removal rate at each plot was 31.5 ± 5.6% (SE) seeds, and the average nail recovery rate was 66 ± 5% (SE). Our average recovery rate was higher than that of other acorn metal-tagging studies (17–37%; Sork 1984, Steele et al. 2001, Lichti et al. 2014, Guiden and Orrock 2017). The longest distance a nail was recovered was 10.3 m, and the average distance at which moved nails were recovered was 0.9 ± 0.2 (SE) m. A total of 49 (< 0.01%) seeds were removed from the depot and found intact. We did not find any intact seeds that had been cached (i.e., buried under litter or soil). The farthest distance an intact seed was moved was 7.5 m, and the average distance was 1.1 m. Camera traps captured 11,124 photographs of animal activity, including 1,103 photographs of *Peromyscus* spp., 2476 photographs of *Sigmodon hispidus*, 5,145 photographs of *Sciurus niger*, and 1936 photographs of *G. volans* foraging in the seed depots.

Canopy harvesting had a significant effect on ground cover ($F_{4,21} = 21.23$, $P < 0.001$), and the interaction of harvesting and land-use history also significantly affected ground cover ($F_{4,21} = 4.66$, $P = 0.008$). Litter cover was significantly lower in harvested plots ($P < 0.001$; Fig. 2). Vegetation cover was significantly higher in harvested plots ($P < 0.001$; Fig. 2). Land-use history and harvesting interacted to affect vegetation cover ($P < 0.034$; Fig. 2) such that land-use history only affected vegetation cover in harvested plots where nonagricultural plots had greater cover.

Land-use history and canopy harvesting interacted to affect seed-removal rates ($\chi^2 = 10.71$, $P = 0.001$). The lowest seed-removal rates were in harvested, post-agricultural plots, and the highest rates were in harvested, nonagricultural plots (Fig. 3a). Canopy harvesting altered rodent species activity such that *Sciurus niger* and *G. volans* were only observed in unharvested plots, and *Sigmodon hispidus* was largely observed in harvested plots (Fig. 2). Bouts by *S. niger* were positively correlated with seed removal in unharvested plots (Table 1), and there was no effect of land-use history on *S. niger* bouts in unharvested plots ($F_{1,6} = 2.25$, $P = 0.184$). Land-use history and canopy harvesting marginally interacted to affect *S. hispidus* bouts ($F_{1,27} = 3.53$, $P = 0.077$), and harvested post-agricultural plots had fewer bouts (Fig. 3b). Bouts by *S. hispidus* were positively correlated with seed removal in harvested plots (Table 1; Fig. 3c). Seed movement distances were not affected by land-use history ($F_{1,13} = 2.26$,

Table 1. Coefficients, test statistics, and *P*-values for our eight single-species models evaluating the effects of each rodent species' foraging activity on the proportion of seeds removed (binomial GLMs) and the average distance seeds were moved (linear mixed-effects models).

	Binomial GLMs				Linear mixed-effects models			
	Seeds foraged				Average distance			
Effect	β	χ^2	AIC	*P*	B	*F*	AIC	*P*
Glaucomys volans bouts†	0.04	0.91	173.8	0.340	0.00	0.11	38.9	0.749
Peromyscus spp. bouts	0.01	0.03	365.2	0.869	0.03	1.27	101.0	0.271
Sciurus niger bouts†	0.14	5.28	170.1	0.022*	−0.01	0.38	37.5	0.548
Sigmodon hispidus bouts†	0.05	9.08	187.8	0.003**	−0.01	0.59	64.9	0.458

Note: Levels of significance are expressed as $*P < 0.05$ and $**P < 0.01$.

† Models in which a subset of the data was analyzed due to the absence of bout data across a canopy harvesting treatment for the rodent species. Only data from the canopy harvesting treatment that contained bout data for the species were analyzed in these models.

$P = 0.184$), canopy harvesting ($F_{1,13} = 3.73$, $P = 0.077$), the interaction of land use and harvesting ($F_{1,27} = 0.51$, $P = 0.487$), or rodent species bouts (Table 1).

Discussion

Seed limitation structures plant populations in a wide array of terrestrial ecosystems (Clark et al. 1998, Turnbull et al. 2000, Zobel et al. 2000, Standish et al. 2007, Öster et al. 2009, Turley et al. 2017). Our study demonstrates that past agricultural land use, which is known to have lasting legacies on plant communities (Foster 1993, Flinn and Vellend 2005, Kopecký and Vojta 2009, Brudvig et al. 2014), may also interact with contemporary canopy harvesting to yield significant changes in an essential component of seed limitation, seed predation. Moreover, we find that the effect of past land use on seed predation is contingent upon contemporary disturbance, in the form of canopy harvesting (Fig. 3a). These significant changes in seed predation arise because of the varying effects of land-use history and canopy harvesting on different rodent species (Fig. 3b, c). Our findings have several implications. First, our results suggest that understanding seed predation may require knowledge of both past and present disturbances. Second, in finding a strong link between habitat characteristics that modify the activity of different rodent species and the magnitude of seed predation, our work suggests that studies relating rapid environmental changes to shifts in animal behavior may provide unappreciated insight into spatial patterns of seed fate.

Past and present disturbances modify the magnitude of seed predation

Agricultural land-use history decreased seed predation rates when canopy harvesting was imposed, but there was no effect of land-use history in unharvested plots. Harvesting amplified agricultural legacies on seed predation by shifting rodent species activity, such that species only found in harvested plots exhibited reduced activity with historic agriculture. A notable limitation to generalizing these results is that we tracked the fate of one, large-seeded species, *Q. nigra*. Since seed traits can modify rodent foraging decisions (Lichti et al. 2017), the fate of *Q. nigra* seeds may not represent the fate of all seeds handled by rodents. However, our results do illuminate a possible mechanism behind well-documented patterns of *Q. nigra* regeneration in restored post-agricultural areas (Shear et al. 1996, Allen 1997, Allen et al. 1998). *Quercus nigra* and related southeastern oaks are known to have low rates of natural establishment in post-agricultural areas with suitable abiotic conditions (Shear et al. 1996, Allen 1997, Allen et al. 1998), and our results from explicit tracking of *Q. nigra* seed fates support the common assumption that these species are limited by infrequent dispersal events and high rates of seed predation. In fact, guidelines for hardwood reforestation in the southeast often emphasize the necessity of actively planting *Q. nigra* (e.g., direct seeding or planting saplings) in order to enable its establishment (Allen 1997, Allen et al., 2001). In a Louisiana study investigating the cause of failed reforestation efforts involving oak direct seeding in the late 1980s, it was found that seed predation by

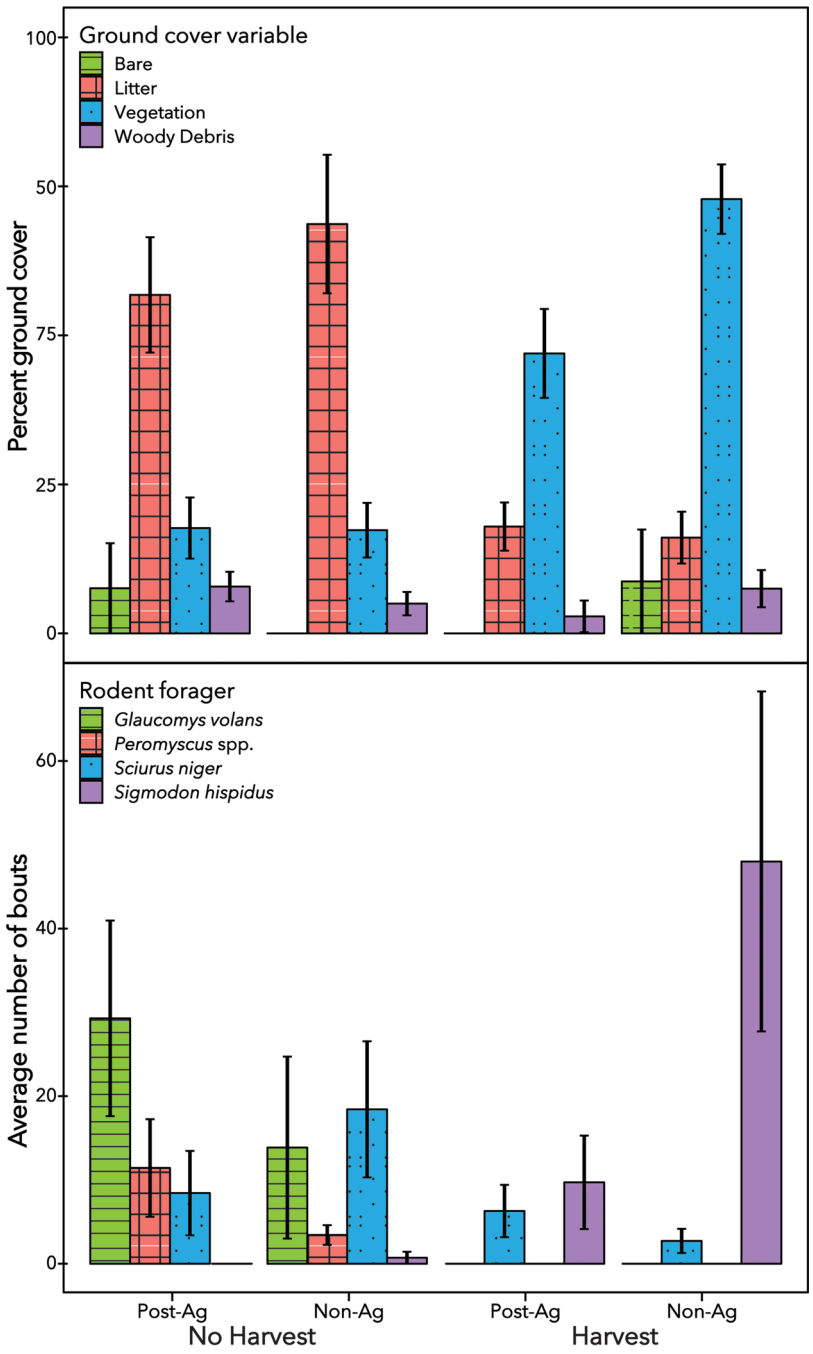

Fig. 2. Canopy harvesting and past land use caused shifts in percent ground cover and rodent species activity. Litter cover was significantly lower in harvested plots ($P < 0.001$). Vegetation cover was significantly higher in harvested plots ($P < 0.001$). Land-use history and harvesting interacted to affect vegetation cover ($P = 0.034$) such that land-use history only affected vegetation cover in harvested plots where nonagricultural plots had greater cover. *Sciurus niger* and *Glaucomys volans* were only active in unharvested plots and were not affected by land-use history. *Sigmodon hispidus* was almost exclusively active in harvested plots. *Peromyscus* spp. activity did not change with harvesting or land-use history. Error bars represent one standard error.

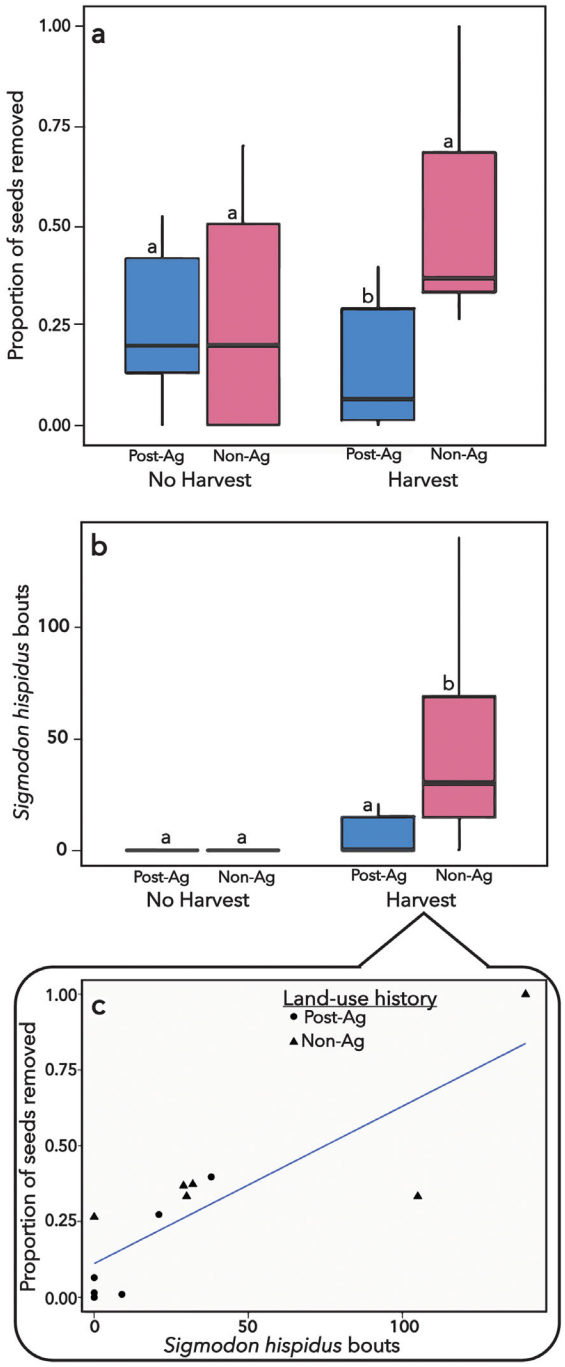

Fig. 3. (a) The interaction of land-use history and canopy harvesting had a significant effect on seed-removal rates ($P = 0.001$). Land-use history did not affect seed removal in unharvested plots. With canopy harvesting, post-agricultural plots had significantly lower seed-removal rates than nonagricultural plots. (b) The interaction of land-use history and canopy harvesting had a marginally significant effect on *Sigmodon hispidus* activity ($P = 0.069$), and *S. hispidus* was significantly more active in harvested post-agricultural sites than harvested nonagricultural sites ($P = 0.015$). (c) The proportion of seeds removed from depots in harvested sites increased with *S. hispidus* activity ($P = 0.003$). We therefore expect that the negative effect of agricultural history on seed removal in harvested sites is driven by a reduction in *S. hispidus* activity.

rodents, particularly *S. hispidus*, was a primary limitation to oak establishment (Buchholz 1996). Our results provide further evidence of *S. hispidus*' role as an important seed predator of southeastern oaks and illuminate the effects of past land use on *S. hispidus* seed predation.

Environmental change that creates spatial variation in animal behavior may generate spatial patterns in seed predation

Our study suggests that contemporary disturbances that generate rapid environmental change can modify animal behavior and transform the strength of land-use legacies. Canopy harvesting increased the strength of post-agricultural effects on seed predation by driving a shift in rodent species activity (Figs. 2, 3). There was no effect of land-use history in unharvested plots on seed predation or the activity of *S. niger*, the primary seed predator in unharvested plots (Table 1); however, canopy harvesting drove a shift in rodent species activity such that *S. hispidus* was the primary seed predator and was most active in nonagricultural plots, which had higher vegetation cover than post-agricultural plots (Table 1; Fig. 2). These results show that changes in habitat structure caused by canopy harvesting may modify the relationship between rodent seed removal and past land use. The effects of land-use history on *S. hispidus* foraging activity in harvested plots are likely driven by differences in vegetation cover in post-agricultural vs. nonagricultural habitats after harvesting because it is known to prefer dense understories to reduce predation risk (Fleharty and Mares 1973, Conner et al. 2013). Since herbaceous ground cover was lower in harvested post-agricultural plots, agricultural land-use history may enhance predation

risk in harvested plots. In a separate experiment comparing seed removal by rodents in unharvested longleaf-pine woodlands of different land-use histories and fire regimes, Stuhler and Orrock (2016) found that seed predation by *P. gossypinus* increased with vegetation cover in nonagricultural sites with low fire frequencies, which were habitats with generally higher vegetation cover than high-fire nonagricultural sites and all post-agricultural sites. In the other habitat types with generally lower vegetation cover, *P. gossypinus* seed predation increased with woody debris cover. This contingency of habitat structure on the relationship between microhabitat characteristics and rodent seed removal reflects our study's findings that rodent seed predation was greater in habitats with higher vegetation cover (i.e., nonagricultural plots) in harvested plots, which had generally higher vegetation cover than unharvested plots. Alternatively, since harvesting increases seed production (Turley et al. 2017), it is possible that *S. hispidus* is responding to changes in food availability. Food supplementation in nonagricultural longleaf-pine woodlands can amplify *S. hispidus* populations (Morris et al. 2011*a*); however, *S. hispidus* space use is more strongly affected by perceived predation risk than food availability (Conner et al. 2013). Viewed in light of this past work, our results suggest that *S. hispidus* may generally prefer harvested sites for food availability, but they concentrate their foraging activity in nonagricultural harvested areas where there is greater herbaceous cover to reduce predation risk. Future studies quantifying *S. hispidus* antipredator behavior in these habitats, for example, via giving-up densities (Brown 1988), could help evaluate this hypothesis.

Rodent populations can vary both spatially and temporally, which is important for the generality of our results across space and time. Spatial variation in rodent populations in our study system is well-documented (Hinkelman and Loeb 2007, Morris et al. 2011*a*); given our experimental design's large-scale replication, we are confident in the spatially consistent patterns of rodent behavior and seed fate shown in our results. Furthermore, experiments conducted at our study site in habitats similar to our harvested and unharvested plots in previous years have shown similarly high levels of rodent seed predation and similar effects of past land use on seed predation for multiple years (Orrock et al. 2003, 2006, Orrock and Damschen 2005, Stuhler and Orrock 2016). Past work in our system has also found no variation in rodent seed predation across seasons (Orrock and Damschen 2005). These consistencies across multiple years and seasons indicate that the effects of past and present disturbance on seed predation in our results are unlikely to have significant temporal variation.

The timing of our experiment may also be important for rodent caching behavior. Secondary seed dispersal by rodents can help seeds of various sizes reach favorable microsites and most often occurs in the fall (Herrera 2002, Vander Wall et al. 2005, 2017). In North America, plants dispersed by scatter-hoarding rodents are most prevalent in the southeastern and southern part of the continent (Vander Wall et al. 2017); however, no research to our knowledge has investigated scatter-hoarding behavior in the southeastern United States. The closest approximation to our knowledge was a seed-tracking study conducted in Kentucky in which fox squirrels were largely seed predators, dispersing only 0.02% of the acorns presented (Cilles et al. 2016). Less than 0.01% of the acorns we deployed were effectively dispersed in that they were both moved and not consumed. These generally high rates of seed predation and low rates of seed dispersal reflect patterns of acorn fate found in other seed-tracking experiments that more closely approximate the seasonal timing of acorn production (Sork 1984, Lichti et al. 2014, Guiden and Orrock 2017). Our dispersal rate, however, is lower than other experiments that have investigated dispersal by rodents using our nail-tagging methods with a search radius of 30 m (1–10%; Sork 1984, Lichti et al. 2014, Guiden and Orrock 2017). Additionally, our study was unique in that we did not detect a single cache. While our recovery rate (66%) was nearly double that of other nail-tagging experiments that did detect caches in other ecosystems (17–37%; Sork 1984, Steele et al. 2001, Lichti et al. 2014, Guiden and Orrock 2017), it is possible that some of the unrecovered seeds were cached. In our system, unrecovered seeds are likely to have been consumed in arboreal nests by *G. volans* or subterranean nests by *P. polionotus*. Consumed remains of

acorns have been found in both settings, while intact acorns were not found (Moore 1947, Gentry and Smith 1968, Goertz et al. 1975, Heidt 1977). It is possible that the uniquely low dispersal rates found in our experiment are due to its timing 2–4 weeks prior to natural *Q. nigra* maturation. Future studies on seed fate that capture a larger temporal range are needed to determine the frequency of seed dispersal by rodents in the southeastern United States. It is worth noting, however, that despite the natural maturation of *Q. nigra* seeds occurring in September, direct seeding of oak species in the southeast occurs year-round and often during the summer (Buchholz 1996, Allen et al. 2001). Our findings that seed predation by *S. hispidus* is modified by past agricultural land use illustrate the potentially significant role of disturbance histories in determining the outcomes of these restoration efforts. Finally, while oak species in some ecosystems are able to overcome seed limitation by satiating predators through masting (Kelly 1994, Vander Wall 2001), vertebrate seed predation has been shown to limit oak recruitment in a variety of ecosystems (Santos and Telleria 1997, Gómez 2004, Sun et al. 2004, Pé Rez-Ramos and Marañon 2008, Cilles et al. 2016, Bogdziewicz et al. I*n press*). Our results indicate that past and present disturbances that affect granivore behavior could subsequently determine when oaks may overcome seed limitation through masting. Future research that explicitly links seed fate with oak recruitment in the southeastern United States is exceedingly needed to understand these potential dynamics.

Conclusions

Land-use legacies and contemporary disturbances can interact to modify animal behavior and generate spatial patterns in seed predation. As agricultural land abandonment increases and management practices are implemented to restore these secondary lands (Hurtt et al. 2006, Turley et al. 2017), studying the ways in which these past and present disturbances transform species interactions is increasingly relevant. In this study, we found that the effects of past agricultural land use on rodent seed predation were contingent upon a contemporary canopy harvesting whereby past land use only had an effect on the magnitude of seed predation in harvested plots. Our work highlights several areas of research that require further investigation. First, further investigation is needed to understand whether past land use and contemporary disturbance change the activity of predators, the effects of predators on rodent foraging under different habitat contexts, and the potential for predators to elicit cascading effects on seed predation and ecosystem recovery. Additionally, further research is needed to understand the breadth of species interactions (e.g., predator–prey interactions of large mammals) that show spatial variation in response to past and present disturbances.

Acknowledgments

We thank the U.S. Forest Service-Savannah River for creating and maintaining the large-scale experimental landscapes. The support from John Blake, Andy Horcher, Ed Olson, Kim Wright, and other USFS-Savannah River staff was essential to the completion of this work. We thank Lars Brudvig for leadership in creating the large-scale experiment and L. Brudvig and Sabrie Breland for logistical support. We also thank L. Brudvig, Pete Guiden, Jen Cruz, and Angela Larsen for helpful feedback. The support was provided by the Department of Energy—Savannah River Operations Office through the U.S. Forest Service—Savannah River under Interagency Agreement DE-EM0003622 and by the Strategic Environmental Research and Development Program (Project RC-2705).

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3116/full