Canadian Journal of Forest Research

Research Article

Seed removal patterns of fire-sensitive tree species on floodplain and upland sites in the absence of fire

John L. Willis[a], **Christopher M. Schalk**[b], **and Josh Pierce**[b]

[a]Southern Research Station, USDA Forest Service, Auburn, AL 36849, USA; [b]Southern Research Station, USDA Forest Service, Nacogdoches, TX 75965, USA

Corresponding author: **John L. Willis** (email: John.Willis@usda.gov)

Abstract

Surface fire is the primary ecological filter maintaining eastern North American woodlands. However, fire is not the only filter affecting species demographics, and in the absence of fire, the influence of secondary filters, such as seed predators, increases. To explore how different seed predator guilds affect individual species, we established seed offerings examining the effects of predator type (invertebrates only and invertebrates + small mammals), forest type (upland and floodplain), season (fall and summer), and offering location (beneath conspecific and heterospecific focal trees) on seed removal of four fire-sensitive tree species at two sites in the southeastern United States. Additionally, we explored the effects of forest structure on seed removal. Excluding small mammals had no impact on seed removal for any species, indicating that invertebrates were the primary seed predator. Winged elm (32%) and sweetgum (31%) seed removal in the floodplains significantly exceeded red maple (15%) and loblolly pine (6%). In the uplands, sweetgum (68%), winged elm (64%), and red maple (55%) seed removal significantly exceeded that of loblolly pine (4%). Sweetgum seeds were removed more frequently than loblolly pine regardless of focal tree identity. However, seed removal of both species beneath conspecific focal trees did not significantly exceed that recorded beneath heterospecific trees. Competing vegetation height was highest in the uplands in the summer and was positively associated with sweetgum seed removal intensity. Collectively, these results suggest that loblolly pine seeds have the highest probability of avoiding seed predator removal, potentially increasing its odds of establishing on upland sites.

Key words: mesophication, Janzen Connell, seed predation, invertebrates

Introduction

Prolonged disruptions of established disturbance regimes affect the structure and function of forest ecosystems (Johnstone et al. 2016). Structural changes often derive from the arrival of encroaching tree species previously filtered by disturbance (King and Keim 2019; Brodie et al. 2023). Once established, trees modify their surrounding environment in numerous ways based on interspecific differences in functional traits and growth strategy (Niinemets 2010; Aponte et al. 2012; Zwetsloot et al. 2018). The cumulative effects of these local environmental modifications influence ecological processes at the stand and regional scales (Chanthorn et al. 2017). Consequently, understanding the mechanisms that govern seedling establishment among encroaching species is important for projecting stand dynamics in the absence of disturbance.

Historically, frequent, low-intensity surface fire maintained distinct forest types in the southeastern United States. Low-intensity fires were common in the uplands and promoted open forests (woodlands and savannas) composed of fire-adapted species (Stambaugh et al. 2011; Flatley et al. 2023; Adams et al. 2024). In contrast, surface fire rarely penetrated the surrounding low-lying floodplains, except during interannual drought events, leading to the formation of closed canopy, multi-layered forests featuring species better adapted to survive flooding and shade than surface fire (Jin et al. 2002; Gagnon 2009; Gagnon et al. 2021). Trees growing along the forest margins annually dispersed seeds into the neighboring forest type, yet crossover recruitment was low in either direction due to vulnerability to the local disturbance regime (McKnight et al. 1981; Robertson et al. 2021). Nevertheless, decades of fire exclusion have interrupted this disturbance-maintained equilibrium, enabling fire-sensitive species to establish on upland sites creating closed-canopy forests (Hanberry et al. 2020; Hale and Peterson 2024). Moreover, due to their canopy, bark, and litter traits, many fire-sensitive species contribute to the mesophication process making upland sites less flammable and more vulnerable to future invasion from fire-sensitive species (Nowacki and Abrams 2008; Alexander et al. 2021).

Studies describing the effects of fire-sensitive species encroachment on open forests are abundant (Alexander et al. 2021). However, beyond fire exclusion, scant attention has been given to the processes that influence recruitment success among fire-sensitive species on upland sites. Overlooking these processes can lead to erroneous estimates

of species composition and subsequent function, as fire-sensitive species likely contribute unequally to the mesophication process. For example, loblolly pine (*Pinus taeda*) needles maintain a lower moisture content, dry faster, and burn at a higher intensity than red maple leaves (*Acer rubrum*) (Kreye et al. 2013; Varner et al. 2021), and likely those of sweetgum (*Liquidambar styraciflua*) and winged elm (*Ulmus alata*) (Kreye et al. 2018; McDaniel et al. 2021). Thus, understanding the filters affecting fire-sensitive species recruitment in the absence of fire is important for projecting future flammability within degraded open forests.

Seed availability is foundational for species expansion. As prolific producers of small-to-medium sized-seeds, loblolly pine, sweetgum, red maple, and winged elm aggressively expand in the absence of fire (Bey 1990; Kormanik 1990; Abrams 1998; Cain and Shelton 2001). Nevertheless, seed availability can be impacted by post-dispersal factors, such as seed predators, that can modify the relative importance of annual seed production (Janzen 1971; Orrock et al. 2006; Larios et al. 2017). Seed predators vary in their feeding strategies which can play a role in seed fate. For example, seed predators may immediately consume seeds potentially compromising their viability; alternatively, seeds can also be dispersed by scatter hoarders (e.g., squirrels) that place seeds in spaced caches and return later to consume cached seeds (Vander Wall and Beck 2012). However, not all caches are consumed, and these seeds may be deposited in microsites that facilitate germination (Vander Wall and Beck 2012). Larder hoarders (e.g., *Neotoma floridana*) cache seeds in a central location, such as their nest. However, larder hoarding is not considered to be an effective seed dispersal strategy as the seeds may be deposited in an unsuitable site (Vander Wall and Beck 2012). Food item perishability also affects feeding decisions. As such, certain seed predators are more likely to immediately consume a food item that is perishable rather than cache for later consumption (McDonald et al. 2023).

Fire-sensitive species may avoid seed predator effects by dispersing propagules outside the floodplains, potentially escaping specialized seed predators that congregate beneath their crown or those of other conspecific trees (Janzen 1970; Howe and Smallwood 1982). However, in degraded open forests where fire-sensitive species have already established, seed predator avoidance may only occur near heterospecific trees (Janzen 1970). Variation in seed predator pressure among fire-sensitive species may also derive from differences in seed size, the frequency of disturbance that affect seed predator persistence in these habitats, and the quality of habitat for individual seed predator guilds. Small mammals generally prefer intermediate-to-large seeds and are attracted to areas with abundant vegetative cover (Brown and Kotler 2004; Orrock et al. 2004; Mendoza and Dirzo 2007; Royo and Carson 2008; Galetti et al. 2015), whereas arthropods prefer small seeds and sparse litter cover (Lundgren and Rosentrater 2007; Willis et al. 2019). Collectively, this suggests that arthropods may select small-seeded, fire-sensitive species more than small mammals, and that regular burning in the uplands could strengthen this relationship by limiting litter layer accumulation and exposing mineral soil (Willis et al. 2019; Sánchez-López et al. 2025). In contrast, annual flooding in the floodplains can increase litter layer depth by slowing decomposition and reduce seed predator pressure through limiting their local population (Wharton et al. 1981; Baker et al. 2001). Seed predator pressure can also vary seasonally with changes in food availability, temperature, moisture availability, and canopy cover (Cintra 1997; Kollmann et al. 1998; Honek et al. 2006; Doust 2011; Noroozi et al. 2016; Linabury et al. 2019; Moore et al. 2022). Among these factors, temperature and evapotranspiration increases post-dispersal seed predation by invertebrates (Peco et al. 2014) suggesting that small-seeded, fire-sensitive species may experience higher rates of seed predator pressure in the summer compared to fall due to increased invertebrate activity.

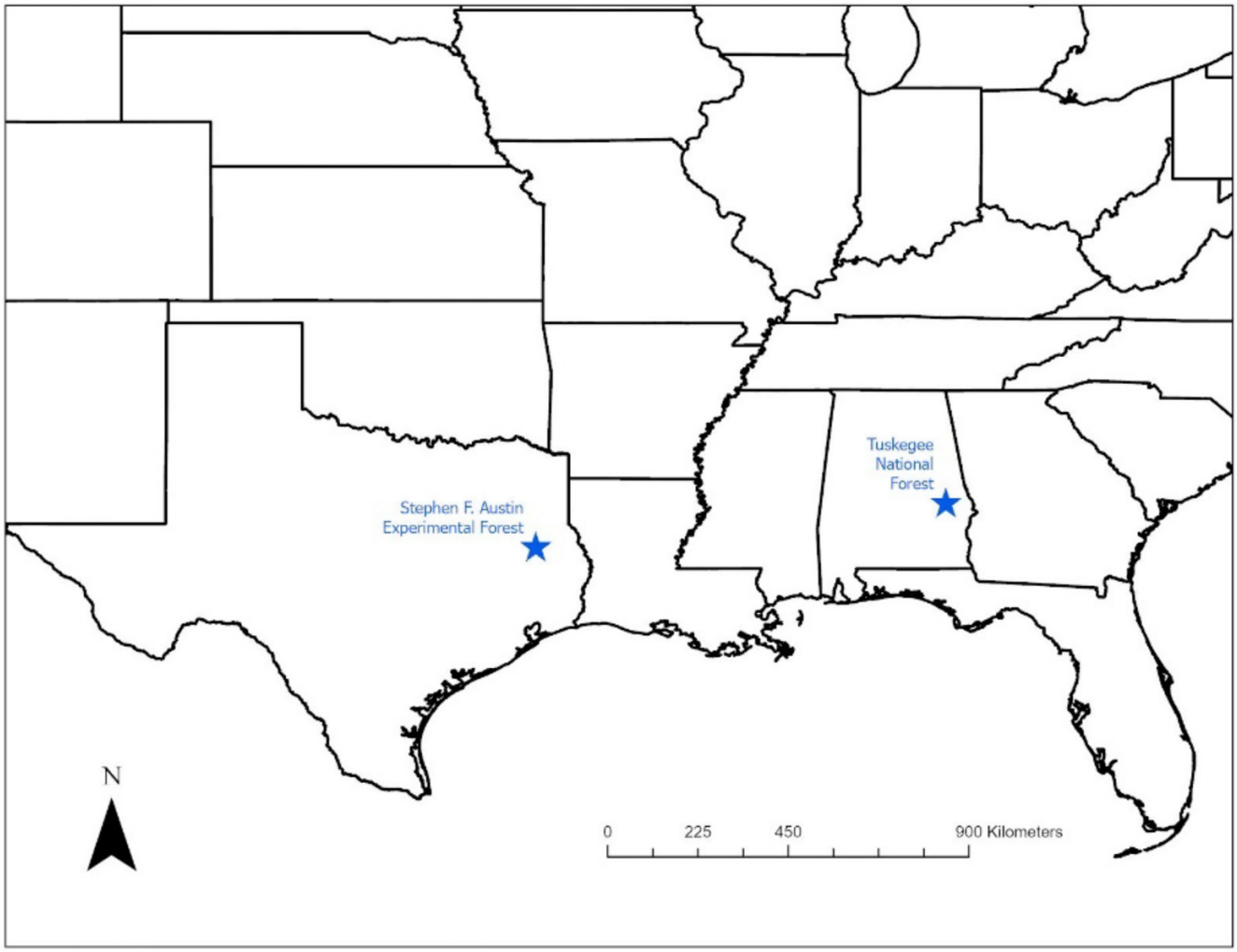
To explore how different seed predator guilds and their environment influence seed removal of fire-sensitive tree species, we conducted a series of offerings examining seed removal with different types of seed predator access (invertebrates only and invertebrates + small mammals), forest types (upland and floodplain), seasons (fall and summer), and beneath different focal species (heterospecific and conspecifics) at two sites in the southeastern United States (eastern Alabama and eastern Texas). Our objectives were to determine whether tree species seed removal varied with differences in (1) predator access type; (2) forest type in different seasons; (3) proximity to conspecific trees; and (4) forest structural conditions. Specifically, for all species, we predicted: (1) invertebrates would remove more tree seeds than small mammals; (2) seed removal in the uplands would exceed that in the floodplains in both seasons; (3) seed removal will be higher beneath conspecific trees than heterospecific trees; and (4) seed removal will decrease with increasing litter depth. The results of this study will improve our fundamental understanding of how seed predators select seeds and how forest structural characteristics modify their impact.

Methods

Site characteristics

Our study was jointly conducted at the Stephen F. Austin Experimental Forest (SFAEF) in Nacogdoches County, Texas (31.501678N, −94.764018W) and the Tuskegee National Forest (TNF) in Macon County, Alabama (32.4853N, −85.5592W) (Fig. 1). At SFAEF, the coldest temperatures occur in January (2.1 °C), while the hottest temperatures occur in August (34.7 °C). Precipitation occurs almost exclusively in the form of rain averaging 1251 mm annually. Similar climatic conditions exist at TNF, the coldest temperatures occur in January (1.2 °C), the hottest temperatures in July (32.1 °C), and 1337 mm of precipitation falls annually. Both sites have gentle, rolling topography (<10% slope) featuring a combination of mature mixed pine-hardwood stands on upland sites and mature bottomland hardwood stands on low lying floodplains (Russell et al. 2002). The uplands at SFAEF are dominated by loamy, well drained soils within the Attoyac Series (fine-loamy, siliceous, semiactive, thermic Typic Paleudalfs), while the floodplains are comprised of somewhat poorly drained, loamy soils belonging to the Marietta Series (fine-

Fig. 1. Location of the Stephen F. Austin Experimental Forest, Texas, and Tuskegee National Forest, Alabama, USA. This figure was created using ArcGIS Pro Version 3.3.4 and assembled from the following data sources: United States Census Bureau. Base map from United States Census Bureau. https://www.census.gov/geographies/mapping-files/time-series/geo/cartographic-boundary.html



loamy, siliceous, active, thermic Fluvaquentic Eutrudepts). At the TNF, upland soils consist of moderately well drained loamy sands belonging to the Cowarts Series (fine-loamy, kaolinitic, thermic Typic Kanhapludult), whereas floodplains feature poorly drained, clay soils of the Bethera Series (fine, mixed, semiactive, thermic Typic Paleaquults). Shortleaf pine (*P. etchinata*), loblolly pine, sweetgum, southern red oak (*Quercus falcata*), and hickory (*Carya* spp.). are commonly found in the uplands at both sites, while longleaf pine (*P. palustris*) is also found in the uplands at TNF. Tree species commonly found in the floodplains at both sites include cherry bark oak (*Q. pagoda*), winged elm, red maple, water oak (*Q. nigra*), sweetgum, and loblolly pine. Prescribed fire is applied every 5–8 years in the uplands at SFAEF, and every 3–4 years in the uplands at TNF. The floodplains at both sites are not regularly burned. No plots used in this study had experienced timber harvesting for at least 10 years.

Experimental design

Our experiment consisted of a series of seed offerings examining the effects of seed predator type (invertebrates only and invertebrates + small mammals), forest type (upland vs. floodplain), and season (summer vs. fall) on the removal of sweetgum (average seed mass 3.6 mg), winged elm (3.7 mg), loblolly pine (24.7 mg), and red maple (9.8 mg) seeds. In October of 2023, we established plots (5 × 7 m) in the floodplains and uplands at each site. October was chosen as it corresponded with the seed dispersal window for each species except red maple, which disperses seed in the spring (Bey 1990; Kormanik 1990; Walters and Yawney 1990; Schultz 1997). Nine plots were established in each of the floodplains and uplands at SFAEF, while five plots were established in both forest types at TNF. Each plot was at least 50 m from a road edge and at least 50 m from another plot. Within each plot, we placed four "invertebrate + small mammal" seed contain-

Fig. 2. Example invertebrate + small mammal access (left) and invertebrate access only containers (right). Below depicts the grid pattern in which in the containers with established in a floodplain plot. Photographs were taken by Christopher Schalk.

ers and four "invertebrate only" containers ($N = 144$ at SFAEF, $N = 80$ at TNF).

All seed containers were constructed from plastic Tupperware (Gladware Deep Dish 64 oz) (Linabury et al. 2019). The invertebrate + small mammals (e.g., mice and voles) containers featured openings (12 × 9 cm) on the sides enabling small mammal access (Fig. 2). Large seed predators (e.g., racoons and deer) were excluded from all container types. The invertebrate only container restricted small mammal, and all other vertebrate seed predators, by covering the openings with hardware cloth (1 cm hardware mesh size) (Fig. 2). Lids were placed on top of each container to prevent seeds from washing out and to exclude birds. All containers were secured to the ground with staples.

Within the plots, all containers were randomly placed in a 1 × 1 m grid pattern (Fig. 2). Each tree species was assigned to one container from both predator access types (invertebrate only and invertebrate + small mammals) through a stratified random process. All containers were placed in the plots for at least 1 week prior to trial initiation to allow for acclimation. After the acclimation period, seed offerings began by adding a Petri dish partially filled with sand and ten naked (detached from cones or samaras) tree seeds to each container. Adhesive tack was used to secure the Petri dish to the container. Seeds were allowed to sit in situ for 2 weeks before the Petri dishes were collected and counted in the lab. Any seed that was missing or present but damaged was considered removed. The same procedure was followed in August of 2024 to detect the influence of seasonality. All offerings occurred in the same plots at each site.

Based on our initial results and lack of red maple and winged elm representation in the overstory in the uplands, we conducted an additional experiment examining whether loblolly pine and sweetgum seed removal is higher beneath conspecific or heterospecific trees (i.e., negative density dependence). In spring 2025, we randomly selected 10 mature sweetgum and 10 mature loblolly pine trees as plots for our density-dependence trials at both sites ($N = 40$). All focal trees were established on upland sites and were at least 50 m from the road edge, at least 100 m apart, and separated from the opposite focal species by at least 30 m (e.g., no mature sweetgum was within 30 m of a focal loblolly pine tree). At SFAEF, 12 containers were established alternating container type and seed species ~1 m apart in a circle around each focal tree at approximately mid-crown position ($N = 240$) (e.g., three invertebrate + small mammal and three invertebrate access only container per species). At TNF, 8 containers were established around each focal tree following a similar protocol ($N = 160$) (e.g., three invertebrate + small mammal access and one invertebrate only container per species). Containers were once again allowed to acclimate for at least 1 week before the offering began. Offerings were conducted over 2 weeks at both sites and followed the above-described counting procedures.

Forest structure measurements

Within each plot, we quantified a variety of forest structural metrics to explore the effects of the local environment on seed removal. Percent canopy closure was estimated using a spherical densiometer over each container within plots. Woody vegetation (shrubs and seedlings), herbaceous vegetation (grass, forbs, and ferns), mineral soil, leaf litter, and coarse woody debris were visually estimated to the nearest 5% across the entire plot. Measurements falling below 5% were measured to the nearest percent. Litter depth (mm) was measured at three random locations within each plot. Similarly, we measured vegetation height (cm) at three random locations within each plot. Tree seedlings (≤1.37 m) were counted by species within a 10 m^2 circular plot. All measurements were conducted in the summer and fall to capture seasonal changes in forest structure.

Statistical methods

Effects of species, predator type, forest type, and seasonality

All analyses were conducted in R Studio (version 4.5) (Posit team 2025). Graphics were produced within the ggplot2 package (Wickham 2016). We first explored the effects of species, seed predator type, forest type, and season on seed removal with a generalized linear mixed model assuming a binomial distribution within the glmmTMB package (Brooks et al. 2017). The model included the proportion of seeds removed as a response variable, species, predator type, forest type, and season as categorical main effects, two-way interac-

Table 1. Differences in mean ± one standard deviations canopy cover, wood cover, herbaceous cover, litter cover, mineral soil cover, litter layer depth, coarse woody debris cover, and mid-story vegetation height between forest cover types and seasons in east Texas and east Alabama, USA.

Plot metric	Floodplains fall	Uplands fall	Floodplains summer	Uplands summer
Canopy cover (%)	76 (6)ab	57 (6)b	85 (6)a	66 (6)ab
Woody cover (%)	3 (3)c	18 (3)b	3 (3)c	27 (3)a
Herbaceous cover (%)	16 (4)	13 (4)	11 (4)	19 (4)
Litter cover (%)	63 (7)a	52 (7)ab	42 (7)b	38 (7)b
Mineral soil (%)	10 (5)b	11 (5)b	34 (5)a	10 (5)b
Litter layer depth (mm)	28 (4)a	22 (4)ab	16 (4)ab	12 (4)b
Coarse woody debris (%)	6 (1)	6 (1)	8 (1)	6 (1)
Vegetation height (cm)	17 (5)b	35 (5)ab	15 (5)b	40 (5)a

Note: Categories with different letters were statistically different ($P < 0.05$).

tions between species and predator type, forest type, and season, a two-way interaction between forest type and season, a three-way interaction between species, forest type, and season, and plot nested within site as a categorical random effect (Table A1). Model diagnostics were evaluated in the Dharma package (Hartig 2024). All statistically significant interactions and main effects ($P < 0.05$) not contained within interactions were further tested with Tukey's post hoc tests using the emmeans package (Lenth 2016).

Forest structural differences and effects

To investigate seasonal effects on structural characteristics between forest types, we tested for differences in canopy closure, woody vegetation cover, herbaceous vegetation cover, litter cover, mineral soil cover, litter depth, coarse woody debris cover, and vegetation height in separate one-way linear mixed models using the lmer function. Prior to analysis, all plot-level measurements of canopy closure, litter depth, and vegetation height were pooled to represent average plot conditions. Each model contained one of the above-described structural metrics as a response variable, forest type and season as a single fixed main effect (e.g., uplands summer, floodplain summer, uplands fall, floodplain fall), and plot nested within site as a random factor. If the combined main effect was statistically significant, we compared all combinations of forest type and season using previously described post-hoc procedures.

To further explore the impacts of structural characteristics on seed removal, we examined the effects of each measured structural metric in species-specific hurdle models. Coarse woody debris was omitted from this analysis due to its low coverage across plots. Only trials conducted with invertebrate + small mammal access were included in this analysis, as we were broadly interested in the combined effects of both guilds. Hurdle models were selected because they provide insights into two relevant ecological processes: whether seeds were discovered and removed by predators (binary event) and, if so, how many seeds were removed (removal count) potentially representing seed preference. To produce the most parsimonious species-specific models, we first ran a full model, including each structural metric (continuous main effects) and plot nested within site (categorical random effect) for each part of the hurdle model separately. The zero-inflation model was fit with a binomial distribution, while the conditional model was fit with a Poisson distribution. We then checked for multicollinearity among coefficients within each model by examining variance inflation factors (VIF) using the performance package (Lüdecke et al. 2021). If high collinearity (VIFs > 5) was detected within the models, coefficients with the largest VIFs were removed iteratively until all residual coefficients had VIFs < 5. We then searched for the most parsimonious model (AICc) using the dredge function within the MUMIn package (Bartoń 2025). The best zero-inflation and conditional models detected by the dredge function were then combined into a hurdle model and run in the glmmTMB package.

Density-dependent seed offerings

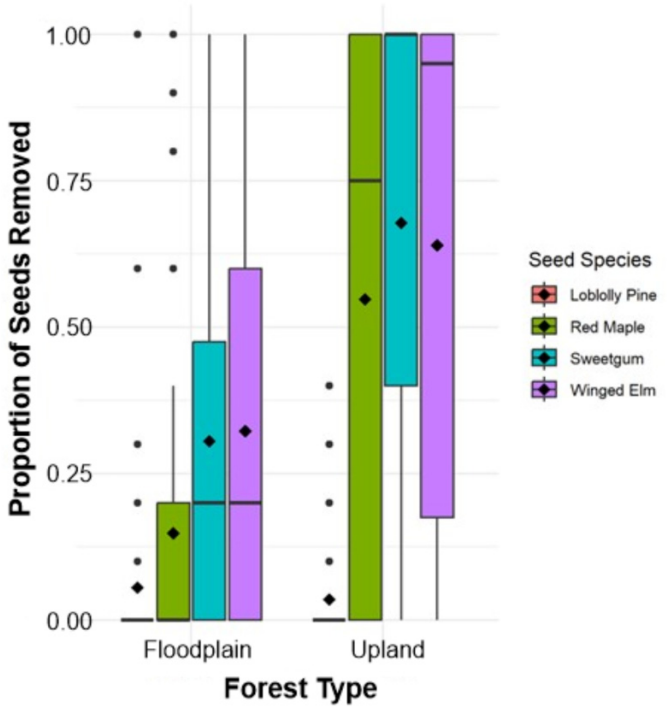
All replicate containers surrounding focal trees were pooled prior to analysis. Modeling of density-dependent effects followed the same procedures used in our previous generalized linear mixed model analysis. The density-dependent model contained the proportion of seeds removed as the response variable, species, focal tree type, predator type as categorical fixed main effects, interactions between species* predator type, species*focal tree type, predator type*focal tree type, species* focal tree type* predator type, and focal tree nested within site as a categorical random effect.

Results

Effects of species, predator type, forest type, and seasonality on seed depredation

Numerous seasonal differences in forest structure were detected between forest types. Canopy cover was nearly 30% higher in the floodplains in the summer than upland forests in the fall ($\chi 2 = 12.09$, $P = 0.0071$) (Table 1). Relatedly, litter cover was highest in the floodplains during the fall significantly exceeding litter cover of either forest type in

Fig. 3. Boxplots depicting the effect of forest type on loblolly pine, red maple, sweetgum, and winged elm seeds removed by seed predators pooled from sites in east Alabama and east Texas, USA. Whiskers extend to the highest/lowest value within 1.5 times the inter-quartile range (IQR). Points represent values beyond 1.5 * IQR. Circles represent outliers. Diamonds represent the mean seed removal value.



the summer ($\chi2 = 15.32$, $P = 0.0016$) (Table 1). Litter layer depth was also highest in the floodplains during the fall, which significantly exceeded litter depth in the uplands during the summer ($\chi2 = 11.35$, $P = 0.0099$) (Table 1). Moreover, mineral soil was 3 × higher in floodplain forests in the summer than any other forest type season combination ($\chi2 = 16.54$, $P = 0.0009$) (Table 1). In contrast to forest canopy and substrate dynamics, woody vegetation cover in the understory was a more prominent component in upland forests. Woody vegetation cover in upland forests was 9× higher in the summer, and 6× higher in the fall, compared to woody cover in floodplain forests ($\chi2 = 60.65$, $P < 0.0001$) (Table 1). Additionally, midstory vegetation height in the uplands was double the height of woody vegetation in the floodplains in any season ($\chi2 = 15.26$, $P = 0.0016$) (Table 1). No statistical differences in herbaceous vegetation cover ($\chi2 = 4.52$, $P = 0.2106$) or coarse woody debris ($\chi2 = 2.39$, $P = 0.4937$) were detected between forest types in any season (Table 1).

Seed removal varied significantly among species between forest types ($\chi2 = 34.64$, $P < 0.0001$) (Fig. 3) (Table A1). In the floodplains, winged elm (32% ± 6) and sweetgum (31% ± 5) seed removal was nearly 6× greater than loblolly pine and 2× greater than red maple (Fig. 3). Significant differences in seed removal between winged elm and sweetgum, and red maple (15% ± 3) and loblolly pine (6% ± 2), were not detected (Fig. 3). In the uplands, sweetgum (68% ± 6), winged elm (64% ± 5), and red maple (55% ± 6) seeds, were statistically removed more frequently than loblolly pine (4% ± 1) (Fig. 3). Additionally, sweetgum seeds were removed significantly more often than those of red maple (Fig. 3). Seed removal among species in different forest types did not statistically differ between seasons ($\chi2 = 3.89$, $P = 0.2737$) (Table A1).

Initial analyses revealed a significant relationship between species and seed predator type ($\chi2 = 20.61$, $P = 0.0001$) (Table A1); however, within post hoc comparisons were not statistically significant. Season had no statistical impact on seed removal among species ($\chi2 = 2.51$, $P = 0.4739$) or between forest types ($\chi2 = 3.05$, $P = 0.0809$) (Table A1).

Effects of forest structure on seed removal

The odds of red maple seed removal occurring (binary model) was best predicted by woody vegetation cover, canopy cover, and mineral soil cover ($R^2 = 0.70$). Increasing canopy (−0.05 ± 0.02 SE) and woody vegetation cover (−0.16 ± 0.08) significantly reduced the odds of a red maple seed being removed (Table 2). Mineral soil cover had the opposite effect on red maple seed removal but was not statistically significant (Table 2). No structural factor investigated significantly predicted the intensity of red maple seed removal (Table 2). The odds of loblolly pine seed removal occurring was best predicted by litter layer depth ($R^2 = 0.16$). Increasing litter depth (0.05 ± 0.03) significantly increased the odds of a loblolly pine being removed (Table 2). However, no investigated structural factor statistically predicted the intensity of loblolly pine removal (Table 2). The odds of sweetgum seed removal occurring was not statistically predicted by any structural factor quantified (Table 2), but sweetgum seed removal intensity was significantly predicted by mineral soil cover and vegetation height ($R^2 = 0.43$). Increasing mineral soil cover (−0.02 ± 0.01) reduced the number of sweetgum seeds removed, while vegetation height statistically had the opposite effect (0.02 ± 0.01) (Table 2). Winged elm seed removal occurrence ($R^2 = 0.03$) and the intensity of seed removal ($R^2 = 0.07$) were not statistically predicted by any measured factor (Table 2).

Negative density-dependence

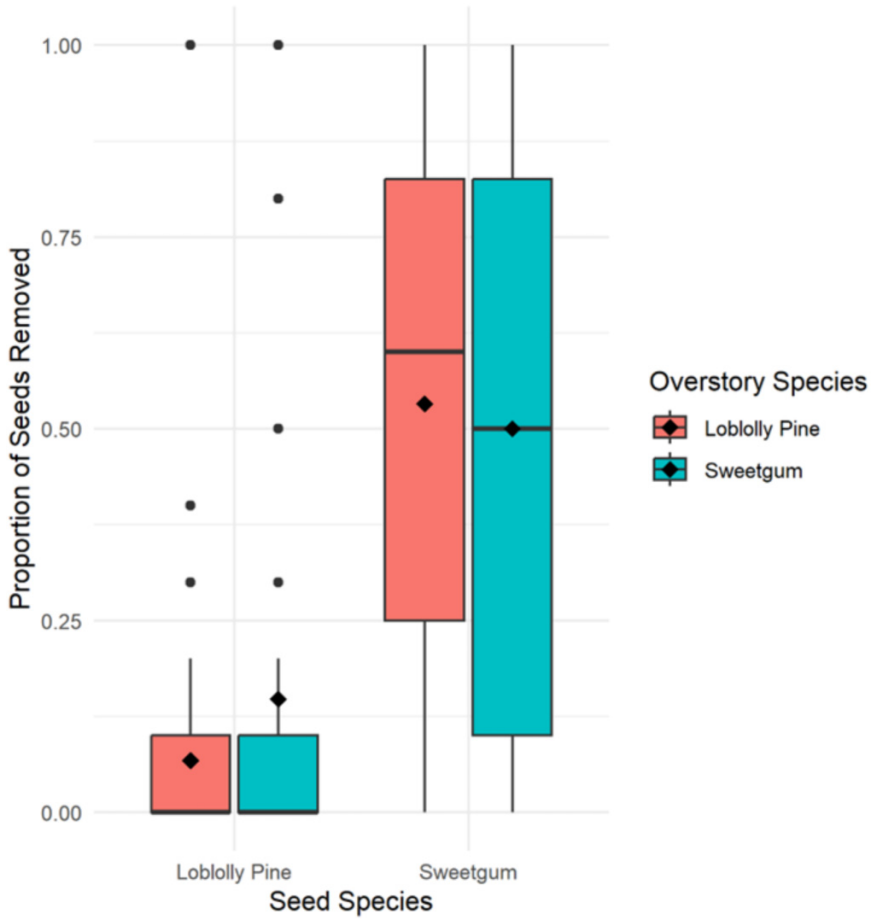
Sweetgum seed removal was 7.5× higher than loblolly pine seeds beneath loblolly pine focal trees, and 3× higher beneath sweetgum focal trees ($\chi2 = 7.30$, $P = 0.0069$) (Fig. 4) (Table A2). However, neither sweetgum nor loblolly pine seed removal beneath conspecific focal trees significantly exceeded that beneath heterospecific trees (Figure 4). Between predator types, loblolly pine seed removal was 2× higher when invertebrates and vertebrate predators were allowed access compared to when vertebrates were excluded ($\chi2 = 12.28$, $P = 0.0005$) (Table A2). Sweetgum seed removal did not significantly differ between seed predator types. No statistical relationship was found between seed species beneath either focal tree species with differing types of seed predator access ($\chi2 = 1.05$, $P = 0.3061$).

Table 2. Statistical results from hurdle models examining the effects of forest structural attributes on the probability of seed removal occurring and the intensity of seed removal for red maple, loblolly pine, sweetgum, and winged elm.

		Conditional model	
Species	Metric	Estimate (SE)	*P*-value
Red maple	Mineral soil cover	−0.02 (0.01)	0.0868
Loblolly pine	Mineral soil cover	−0.04 (0.02)	0.06709
Sweetgum	Mineral soil cover	−0.02 (0.01)	0.0061
	Vegetation height	0.02 (0.01)	0.0007
Winged elm	Vegetation height	0.01 (0.01)	0.0937
		Zero-inflation model	
Red maple	Woody vegetation cover	−0.16 (0.08)	0.0456
	Canopy cover	−0.05 (0.03)	0.0349
	Mineral soil cover	0.03 (0.02)	0.0858
Loblolly pine	Litter depth	0.05 (0.03)	0.0459
Sweetgum	Woody vegetation cover	−0.05 (0.04)	0.2210
Winged elm	Canopy cover	−0.03 (0.02)	0.2770

Note: Displayed models represent the most parsimonious model selected with AICc.

Fig. 4. Boxplots depicting the effects of focal tree species identity on seed predator removal of loblolly pine and sweetgum seeds pooled from sites in east Texas and east Alabama, USA. Whiskers extend to the highest/lowest value within 1.5 times the inter-quartile range (IQR). Points represent values beyond 1.5 * IQR. Circles represent outliers. Diamonds represent the mean seed removal value.



Discussion

Red maple, sweetgum, and winged elm seeds were overwhelmingly removed by seed predators compared to loblolly pine in upland forests. This result indicates that loblolly pine may gain an indirect advantage over other fire-sensitive species due to its avoidance of seed predators, which can contribute to loblolly pine establishment in the absence of fire (Spring et al. 1974; Mohler et al. 2021). Thus, while seed predators have been widely recognized as problematic for pine natural regeneration (Boyer 1964; Castro et al. 1999; Lucas-Borja et al. 2016), the effects of seed predators on tree species that compete with pine for growing space has been scarcely addressed, potentially leading to a mischaracterization of the role of seed predators in stand dynamics.

Observed patterns in seed removal may be attributed to the seed mass of our investigated species (winged elm: 3.6 mg, sweetgum: 3.7 mg, red maple: 9.8 mg, loblolly pine: 24.7 mg) and the lack of small mammal activity at our sites. The lack of small mammal effects may have been particularly impactful, as they generally remove intermediate sized seeds and are the primary post-dispersal predator of conifers (Plucinski and Hunter 2001; Wang and Chen 2009; Lobo 2014; Dylewski et al. 2020). While not necessarily a large-seeded species, loblolly pine seeds are twice as heavy as red maple and approximately 8× heavier than sweetgum and winged elm. Indeed, the only example of seed predator type significantly influencing seed removal came in the density-dependent offerings with loblolly pine. However, even in these offerings, loblolly pine seed removal was limited to 15% of offered seeds.

We did not measure the relative abundance or occurrence of specific seed predators during this study, limiting our ability to explain the lack of small mammal effects. However, the simplest explanation for this pattern is that our study corresponded with periods of reduced small mammal density, as population fluctuations are common (Batzli 1992). Our experimental design, featuring geographically distinct sites (Texas and Alabama) and sampling over 3 years (Fall 2023 to Spring 2025), partially buffers against climate, local resources, and seed predator enemies that influence small mammal populations (Steen et al. 1996), but we cannot rule out that any of these factors may have contributed to our results. The seasonal timing of our seed offerings may have also unintentionally emphasized the importance of invertebrates over vertebrates, as invertebrate surface activity is highest in summer (Vogt et al. 2003), while seed removal by rodents increases in winter months when resources are comparatively scarce (Plucinski and Hunter 2001). Finally, the summer deployment of seeds is outside the natural dispersal window of the species examined in this study, which may have led to small mammals choosing alternative food sources that are abundant in the growing season (Adams et al. 2024). While population dynamics of seed predators remain outside the scope of this study, our finding of sweetgum seed removal preference is consistent with other studies where small mammals were excluded (Willis et al. 2021).

Another emergent pattern from our offerings was the consistently greater removal of hardwood seeds in the uplands compared to the floodplains. One plausible explanation for this trend may be tied to the differing disturbance regime of the forest types. Floodplains are subjected to seasonal flooding events with high water cycles that are attributed to winter rainfall in the southeastern United States. After floodwater recession in the spring, species vulnerable to inundation recolonize floodplains, but at different rates. Ants, likely the dominant invertebrate seed predator at our sites, are vulnerable to rising floodwaters and slow to colonize floodplains after the inundation period (Uetz et al. 1979; Wharton et al. 1981). Indeed, arthropod species richness, including ants, is lower in floodplains compared to uplands (Uetz et al. 1979). Similarly, rodent diversity and relative abundance decline in response to high water periods and recolonization can be slow as water levels recede due to reduced food availability and cover (Chamberlain and Leopold 2003). As such, the reduction in hardwood seed removal in the floodplains compared to the uplands may be related to temporary reductions in seed predator abundance associated with disturbance frequency.

Increased seed predator pressure in the uplands may also be linked to a slight discordance with the historical burn regime at SFAEF. Historically, mixed pine hardwood upland sites in east Texas burned every 1–5 years (Guyette et al. 2012; Stambaugh et al. 2014). In contrast, the prescribed fire return interval at SFAEF is approximately 5–7 years (Adams et al. 2022, 2024). Consequently, the extended time between prescribed fires may have enabled both invertebrate and vertebrate seed predators to maintain or increase their population across space and time at SFAEF. Seed predators may also have been attracted to the habitat in the uplands due to high woody cover and vegetation height (Kollmann and Buschor 2003; Meiss et al. 2010; Penn and Crist 2018). These structural factors could account for the high rates of sweetgum seed removal in the uplands, as vegetation height was positively associated with seed removal intensity.

One factor that did not influence sweetgum and loblolly pine seed removal was their proximity to conspecific trees. This finding supports cumulative evidence suggesting density-dependent mortality effects are stronger in the seedling than seed stage (Comita et al. 2014; Song et al. 2021). Seed predator preference for sweetgum under both focal species also suggests that small seeds are not necessarily better protected against seed predators than large seeds (Moles et al. 2003; Fricke and Wright 2016). Collectively, the lack of density-dependent effects for either species is not particularly surprising considering that both often dominate the seedling layer despite not possessing a high degree of shade tolerance (Chapman 1945; Adams et al. 2015). This indicates that constraints on the seed to seedling transition are not inhibiting either species recruitment. Nevertheless, it should be acknowledged that our study did not consider other mechanisms of density-dependent mortality, such as fungus or bacteria, which can also inhibit germination under tree canopies (O'Hanlon-Manners and Kotanen 2006).

There are several important caveats of our experiment that should be considered when evaluating the influence of seed predators on stand dynamics. For example, our seed containers excluded the influence of birds and large mammals. Their potential effects may override the influence of invertebrates

and small mammals. It is also worth noting that many of the structural conditions associated with seed removal patterns (e.g., high canopy cover and litter depth) may only be present in degraded open forests. Readers should also recognize that our results were interpreted under the conditions of equal seed inputs and do not consider the influence of annual variation in seed production. We encourage future studies to examine seed predation patterns with varying levels of seed inputs. Our investigation of seasonality was limited to a single season replicate, therefore may not fully capture important annual variability deriving from differences in climate and seed predator density. Finally, we do not know the specific invertebrate or vertebrate species responsible for seed removal. Vertebrate seed predators that cache (e.g., *Peromyscus* spp., *Reithrodontomys humulis*), larder hoarders soft and hard mast (e.g., *Neotoma floridana*), and scatter hoarders mostly hard mast (i.e., *Scuridae*) likely occur at both sites (M.V. Cove, pers. comm.; Ostfeld et al. 1997; McDonald et al. 2023). Invertebrates can also function as either seed consumers or dispersers (Penn and Crist 2018). As such, we do not know the fate of the seeds that were removed (i.e., consumed or dispersed), only the number of seeds removed for each species. It could be that these seed predators may be contributing to the establishment and spread of these fire-sensitive species in upland forests through their role as dispersers which can alter mesophytic establishment dynamics.

Conclusion and management implications

Mesophytic encroachment on upland sites represents an existential threat to open forest ecosystems. Prescribed fire is regularly applied to quell the momentum of mesophication. However, the scale of degradation across the landscape, and contemporary challenges to implement prescribed fire, often cause lengthened or missed burn rotations creating opportunities for further encroachment. Our results demonstrate that seed predators remove mesophytic hardwood species more frequently than loblolly pine on upland sites in the absence of fire.

Preferential removal of mesophytic hardwood seeds over loblolly pine suggests that seed predators may be indirectly helping to retain understory flammability by constraining the recruitment of fire dampening species (Varner et al. 2021). While loblolly pine is not the preferred pine species in open forest restoration in the Southeast, its flammable litter and thick bark make it a viable surrogate for longleaf and shortleaf pine (Kirkman et al. 2007; Willis et al. 2024). Moreover, even if loblolly pine seeds survive to become seedlings, they can be killed by prescribed fire more effectively than mesophytic hardwood species due to minimal post-fire sprouting (Wade 1993; Willis et al. 2025).

Acknowledgements

The authors thank Edward Andrews, Tina Ciaramataro, James Childress, Rick Schaefer, and Katelyn Anderson for help with field and lab work. We also thank Mike Cove and Gabriel Andrade Ponce for informative discussions on small mammal foraging strategies. Finally, we thank the two anonymous reviewers for their helpful comments. The findings and conclusions in this publication are those of the authors and should not be construed to represent an official USDA, Forest Service, or United States Government determination or policy.

Article information

History dates

Received: 13 January 2026
Accepted: 16 April 2026
Accepted manuscript online: 21 April 2026
Version of record online: 15 May 2026

Copyright

Data availability

Data generated or analyzed during this study are available from the corresponding author upon reasonable request.

Author information

Author ORCIDs

John L. Willis https://orcid.org/0000-0003-0238-0003

Author contributions

Conceptualization: JLW, CMS, JP
Data curation: JLW, CMS, JP
Formal analysis: JLW
Investigation: CMS, JP
Methodology: JLW, CMS, JP
Project administration: JLW
Resources: JLW, CMS, JP
Software: JLW
Supervision: JLW
Validation: CMS
Writing – original draft: JLW
Writing – review & editing: JLW, CMS, JP

Competing interests

The authors have nothing to declare.

Funding information

Funding for this study was provided by the USDA Forest Service Southern Research Station.

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Appendix A

Table A1. The statistical results of zero inflated generalized linear mixed models examining the effects of tree species, predator type, forest type, season, and their interactions on the proportion of red maple, loblolly pine, sweetgum, and winged elm seeds removed in seed offerings.

Factor	$\chi 2$	Degrees of freedom	*P*-value
Species	15.17	3	0.0017
Predator type	16.89	1	<0.0001
Forest type	5.23	1	0.0221
Season	3.12	1	0.0915
Species*forest type	34.64	3	<0.0001
Species*predator type	20.61	3	0.0001
Species*season	2.51	3	0.4739
Forest type*season	3.05	1	0.0809
Species*forest type*season	3.89	3	0.2737

Table A2. The results of zero inflated generalized linear mixed models examining the effects of tree species, predator type, focal tree type, and their interactions on the proportion of loblolly pine and sweetgum seeds removed in seed offerings.

Factor	$\chi 2$	Degrees of freedom	*P*-value
Species	63.47	1	<0.0001
Predator type	7.67	1	0.0056
Focal tree type	2.49	1	0.1149
Species*predator type	12.28	1	0.0005
Species*focal tree	7.30	1	0.0069
Predator type*focal tree	0.05	1	0.8237
Species*predator type*focal tree	1.05	1	0.3061