Contingent fire effects on granivore removal of exotic woody plant seeds in longleaf pine savannas

Jacqueline S. Krall · Matthew G. Hohmann · Jennifer M. Fraterrigo

Abstract Prescribed fire is increasingly used to inhibit woody encroachment into fire-dependent ecosystems, yet its effects on other processes influencing invasion are poorly understood. We investigated how fire influences exotic woody invasion through its effects on granivore activity, and whether these effects depend on the habitat in which seed predation takes place. We quantified seed removal for four species of exotic woody plants (*Albizia julibrissin*, *Elaeagnus umbellata*, *Melia azedarach* and *Triadica sebifera*) in 17 sites in longleaf pine savanna that varied in time since fire (one or three growing seasons post-fire) in the sandhills region of North Carolina, USA. Within each site, we established paired plots in upland and upland-wetland ecotone communities and presented seeds in depots that allowed either arthropod, or arthropod and small vertebrate access. We found that differences in seed removal with time since fire were contingent on habitat and granivore community. In ecotones, three of four species had higher proportions of seeds removed from plots that were three growing seasons post-fire than plots one growing season post-fire, whereas only *T. sebifera* showed this pattern in upland habitat. Allowing vertebrate granivores access to seeds enhanced seed removal, and this effect was strongest in ecotone habitat. While granivores removed seeds of all four plant species, removal of *E. umbellata* was significantly higher than that of the other species, suggesting that granivores exhibited seed selection. These findings suggest that ecotone habitats in this system experience greater seed removal than upland habitats, particularly as time since fire increases, and differences are mainly due to the activity of vertebrate granivores. Such differences in seed removal, together with seed selection, may contribute to variation in exotic woody invasion of longleaf pine savannas.

Keywords Post-dispersal seed predation · Woody encroachment · Prescribed fire · Rodents

J. S. Krall · J. M. Fraterrigo (✉)
Department of Natural Resources and Environmental Sciences, University of Illinois at Urbana–Champaign, 1102 S. Goodwin Ave., MC-047, Urbana, IL 61801, USA
e-mail: jmf@illinois.edu

M. G. Hohmann
Construction Engineering Research Laboratory, US Army Engineer Research and Development Center, Champaign, IL 61826, USA

Introduction

Invasions by exotic woody plant species can be detrimental to native plant communities and ecosystems sensitive to changes in vegetation structure, such as those dependent on frequent fire (Mandle et al. 2011). Savannas, for example, require fire to maintain a sparse canopy cover and continuous grass understory, conditions which in turn promote fire (Bond and

Keeley 2005; Beckage et al. 2009). Encroachment by woody species, including exotics, can disrupt this grass-fire cycle and alter the successional trajectory of the system (Brooks et al. 2004; Mandle et al. 2011). In the absence of a natural fire regime, prescribed fire is increasingly used to inhibit tree and shrub encroachment into fire-dependent ecosystems (Sousa 1984), but its effects on exotic woody invasion remain poorly understood. To date, the majority of studies investigating fire effects on exotic invasion have focused on "bottom-up" control; that is, the effects of post-fire conditions on plant performance and competition. Such studies have yielded varied results. For example, research shows that fire can reduce invasive populations via seed and plant mortality (Lonsdale and Miller 1993), and reductions in fecundity (Stevens and Beckage 2010), yet may alternatively promote invasion of woody species by reducing native vegetation cover (Kuppinger et al. 2010), and increasing germination (Ne'eman et al. 2004; Todorović et al. 2010). Much less is known about how fire influences top-down processes affecting invasion, such as granivory.

Post-dispersal granivory is recognized as a key process influencing woody plant recruitment (Hulme 1998). Recent studies from diverse ecosystems show that granivores can affect the pattern and rate of woody plant recruitment by altering the distribution and viability of seeds (Schnurr et al. 2004; Côté et al. 2005; Zwolak et al. 2010; Vaz Ferreira et al. 2011). Granivory is expected to influence woody encroachment when seed limitation has a greater effect on population growth rates than establishment limitation (Clark et al. 2007). However, these constraints are not mutually exclusive and are expected to vary through space and time due to variation in fecundity, dispersal and suitability of microsites, thereby influencing invasion rates and patterns across the landscape (Nathan and Muller-Landau 2000; Satterthwaite 2007). For instance, strong seed limitation is anticipated at invasion boundaries during local range expansion because propagule pressure is often limited by dispersal capacity, low population densities, and Allee effects (Taylor and Hastings 2005; Theoharides and Dukes 2007).

Small mammals are important granivores of woody plant seeds, potentially more so than invertebrate granivores due to size related constraints on seed handling for arthropods and the positive relationship between plant height and seed size (Thompson and Rabinowitz 1989; Leishman et al. 2000). Seed removal rates are correlated with small mammals preferences for specific habitat characteristics (Hulme 1994), including high levels of vegetative cover (Kotler 1984; Manson and Stiles 1998) and downed woody debris for predator refuge (Schnurr et al. 2004). Fire may alter granivore activity by modifying habitat characteristics. For instance, fire can reduce vegetation cover, which may increase the perceived predation risk of small mammals and change their foraging patterns (Jacob and Brown 2000; Orrock et al. 2004). Fire can also reduce litter depth (Bond and Keeley 2005), increasing or decreasing small mammal and arthropod foraging activity (Tester 1965; Krefting and Ahlgren 1974; Fewell 1988; Reed et al. 2006; Gibb and Parr 2010), and leading to varied levels of seed removal.

The influence of fire on granivore activity is likely to vary across space, however, because fire both generates and responds to spatial heterogeneity in vegetation structure at multiple scales. In managed landscapes, prescribed fire is often applied to distinct land units, which results in broad scale spatial variation in length of time since fire. Additionally, because these units may encompass different plant community types that vary in underlying soil moisture conditions, there may be differences in fire intensity and vegetation recovery rate that increase spatial heterogeneity at a finer scale (Kirkman et al. 2004). Collectively, fire-induced spatial heterogeneity may lead to heterogeneous seed removal and contribute to between-habitat and landscape scale variation in exotic woody plant invasions.

Within heterogeneous landscapes created by spatial variation in plant communities and time since fire, seed selection by granivores may also contribute to differences in seed removal among plant species. Seed removal may be influenced by morphological (Lundgren and Rosentrater 2007), chemical defense (Kollmann et al. 1998), and nutritional traits (Kelrick et al. 1986). For example, small seeds are preferentially chosen by arthropods due to weight and size limitations on movement (Rey et al. 2002), whereas large seeds are more likely to be consumed by small mammals (Brown and Heske 1990; Matias et al. 2009). Seed selection may also depend on how habitat structure changes with time since fire because seed preference can be influenced by perceived predation risk (Bowers 1990).

In this study, we investigate how fire influences exotic woody plant species through its effects on granivore activity. We focus on landscape-scale variation associated with differences in time since fire and between-habitat-scale variation due to differential effects of fire within a management unit. Our specific objectives were to: (1) quantify patterns of seed removal between upland savanna and upland-wetland ecotone habitats, which represent low and high vegetation structure, respectively, (2) quantify patterns of seed removal between upland savanna and upland-wetland ecotone habitats that were burned either one or three growing seasons prior, (3) compare seed removal of four exotic woody plant species that vary in seeds traits; and (4) assess the importance of granivore community type (i.e., arthropod vs. small mammal) for explaining variation in removal. We expected seed removal to increase with vegetation structure and therefore increase with time since fire presumably due to small mammal predator avoidance behavior. We further expected habitat type to modulate this effect because fire intensity and vegetation recovery vary with habitat. We expected that species would be differentially selected by arthropod and small mammal granivores potentially due to differences in seed characteristics. By assessing the magnitude of post-dispersal exotic woody seed removal in a savanna ecosystem under threat of woody encroachment, additional insights can be gained about landscape-scale vulnerability to exotic plant invasions and focused efforts can be made to help manage emerging invasions.

Methods

Study area and site selection

The study was carried out on Fort Bragg Army installation near Fayetteville, North Carolina (35°07′N, 79°10′W). The installation covers an area of 73,468 ha and ranges in elevation from 43 to 176 m. Mean temperature is 26 °C during the summer and 7 °C during the winter, and mean annual rainfall in the region is 120 cm with September–November and March–April being the driest months (Sorrie et al. 2006). The installation is located in the Fall-line Sandhills region near the northern extent of the former longleaf pine–wiregrass savanna ecosystem and is comprised of multiple plant community types that separate along topographic, soil, and fire gradients. Natural upland savanna sites on the installation are dominated by longleaf pine (*Pinus palustris*) and a sparse understory of wiregrass (*Aristida stricta*), legumes, scrub oaks, ericaceous shrubs, and xerophytic forbs. The ecotonal zone between upland savanna and wetland pocosins (hereafter "ecotone") are characterized by an overstory of longleaf pine, red maple (*Acer rubrum*), and tulip tree (*Liriodendron tulipifera*), as well as a dense understory that includes cane (*Arundinaria tecta*), ferns (e.g., *Osmunda cinnamomea*, *Pteridium aquilinum*), and woody shrubs (e.g., *Clethra alnifolia*, *Ilex glabra*, *Lyonia lucida*) (Sorrie et al. 2006). Small mammal survey data on Fort Bragg indicate local mammalian granivores include: *Glaucomys volans*, *Microtus pinetorum*, *Mus musculus*, *Peromyscus gossypinus*, *Peromyscus leucopus*, *Reithrodontonmys humulis*, *Sciurus carolinensis*, *Scirus niger*, *Sigmodon hispidus*, and *Sylvilagus palustris* (JM McCallister, unpubl. data). Arthropod granivores include: ground beetles (*Coleoptera; Carabidae*), harvester ants (*Hymenoptera; Formicidae*), and crickets (*Orthoptera; Gryllidae*) (M. Hohmann, personal obs.). We did not perform a separate census of the granivore community for this study because we were mainly interested in discerning general trends in removal by different granivore groups as a function of habitat type and time since fire.

Fort Bragg is under a managed fire cycle in which growing (April–July) and dormant (January–March) season fires are applied to 4.0–81.0 ha land management units locally called burn blocks approximately every 3–5 years. We selected nine burn blocks that were three growing seasons post-fire (last burned 2009), and seven burn blocks that were one growing season post-fire (last burned during the 2011 dormant season). Within each burn block we established a pair of 10 m × 40 m (0.04 ha) plots, one in upland and one in ecotone habitat. A second pair of plots was established in one of the largest recently burned blocks. All plots were separated by at least 115 m, a distance larger than the average home range of the most common small vertebrate seed predator, *P. leucopus* (32 m radius) (Lackey et al. 1985). We did not establish controls in unburned sites because such sites no longer supported plant communities characteristic of the savanna ecosystem.

Focal species

We focused on four deciduous woody exotic species: *Albizia julibrissin*, *Elaeagnus umbellata*, *Melia azedarach* and *Triadica sebifera.* All of these species are considered invasive in the southeastern USA, but are currently rare across Fort Bragg and surrounding counties. All four species have the potential to establish and bear fruit under the fire-management cycle on Fort Bragg, as well as re-sprout after fire-induced stem death (i.e., top-kill) (Munger 2003; Waggy 2009; Meyer 2010, 2011). Fruits mature locally between July and November (Weakley 2012). Seeds are primarily avian dispersed, except for *A. julibrissin*, which largely disperses via wind. Individuals of each species may produce thousands of viable seeds per growing season, and except for *E. umbellata*, have seed banks of short to moderate longevity. Disturbance promotes the establishment of all four species, which prefer full sun, but tolerate shade or partial shade.

Seeds of each species were bulk-collected from populations on or near Fort Bragg from September to November 2011 and processed to mimic the state in which they occur following primary dispersal. For *M. azedarach* and *E. umbellata*, we manually removed the fleshy coatings of fruits, rinsed off the pulp and allowed the seeds to dry for 48 h. *Albizia julibrissin* and *T. sebifera* seeds were sorted from attached pods and capsules and allowed to dry for 24 h. *Melia azedarach*, *E. umbellata* and *T. sebifera* seeds were presented still enclosed in their protective endocarp. To characterize average seed size, we measured dry seed mass, length, and width of 100 randomly chosen seeds of each species prior to storage in paper bags at room temperature (Table 1).

Field measurements

We measured substrate and vegetation characteristics within each of the 34 study plots during November and December 2011. The percent cover of ground layer understory vegetation < 2.0 m was visually estimated within fourteen 1 m^2 quadrats, one every 5 m along two parallel 40 m transects separated by 10 m. We measured litter depth at 10 points within a 1 m radius of the 5, 15, 25, and 35 m points along a 40 m transect through the plot center.

We conducted two 16-days seed removal presentations from November 5–21 and December 5–21, 2011. These time periods were chosen to coincide with the natural dispersal timing of the focal species. Multiple presentation periods allowed us to determine if removal patterns remained consistent within a single season (Boman and Casper 1995; Orrock and Damschen 2005). Presentations coincided with the timing of natural seed dispersal of the four focal species. To control for the influence of moonlight on vertebrate foraging behavior, presentations were timed to occur during similar lunar phases of waxing gibbous through waning crescent (Orrock et al. 2004). Within each plot we installed a pair of seed removal depots 1 m apart at 5, 15, 25, and 35 m along a transect that bisected the plot (n = 8 depots per plot; n = 272 depots total). Empty depots were placed in the field approximately 3 months prior to seed presentation periods. Two depot types were used: (1) accessible only to arthropods, and (2) accessible to arthropods and small mammals. All depots were inverted translucent plastic buckets 12.7 cm in height and 21.9 cm in diameter with two 15 cm $\times$ 8 cm openings on opposite sides, and the base removed. Mesh hardware cloth (1.6 cm^2 gauge) was used to bar access via the inverted base of

Table 1 Seed removal (mean $\pm$ SE) by presentation period and seed size and weight for four exotic woody species presented in seed removal depots. Species are listed in order of increasing size

Species	Seed Removal (%)		Length (mm)[b]	Width (mm)[b]	Weight (g)[a]
	November	December			
Elaeagnus umbellata	24.7 $\pm$ 2.2	19.5 $\pm$ 2.3	4.0–7.0 (5.5 $\pm$ 0.07)	1.5–2.0 (2.0 $\pm$ <0.01)	0.014 ($\pm$0.002)
Albizia julibrissin	4.4 $\pm$ 0.6	3.8 $\pm$ 0.6	4.0–9.0 (6.7 $\pm$ 0.10)	2.0–5.0 (3.1 $\pm$ 0.05)	0.037 ($\pm$0.007)
Triadica sebifera	3.8 $\pm$ 0.6	4.2 $\pm$ 0.7	5.0–10.0 (7.2 $\pm$ 0.09)	3.0–8.0 (5.3 $\pm$ 0.08))	0.116 ($\pm$0.03)
Melia azedarach	2.2 $\pm$ 0.5	1.4 $\pm$ 0.4	5.0–12.0 (9.0 $\pm$ 0.14)	5.0–11.0 (8.4 $\pm$ 0.13)	0.395 ($\pm$0.10)

[a] Values are: mean ($\pm$SD)

[b] Values are: minimum–maximum (mean $\pm$ SD)

all depots, and the side openings of the "accessible only to arthropod" depots. Similarly designed depots have been used successfully in other seed removal studies (Mattos and Orrock 2010; Craig et al. 2011). The attached bucket lid of each depot had a ¼ lip to control for incidental seed loss from natural elements such as wind or rain. Depots were secured in place with four steel landscape pins. For both seed presentations we covered the attached bucket lid of each depot with sand and deposited 10 seeds of each of the four species on the surface. After 15 d, we collected the sand and seeds from each depot, sifted the contents, and counted the remaining intact and damaged seeds.

Statistical analysis

Vegetation and substrate measurements were analyzed separately using a linear mixed model, with time since fire, habitat, and time since fire × habitat as fixed effects and burn block nested within time since fire as a random effect (PROC MIXED, SAS v.9.3, Cary, NC, USA). We examined simple main effects to evaluate the influence of specific levels of each factor within interactions using the Slice statement.

To analyze the main effects and interactions of habitat type, time since fire, depot type, and species on post-dispersal seed removal, we fit a generalized linear mixed model to percentage seed removal using the PROC GLIMMIX procedure (SAS v.9.3, Cary, NC, USA). This procedure allows for the analysis of mixed models with non-normal response variables by modeling specific distribution structures (Bolker et al. 2009). We initially compared the same model structure with two distributions for the response variable, the binomial and Poisson, to determine which distribution best fit the data (Johnson and Omland 2004). A binomial distribution and logit link function, which utilizes an "event per trial" response variable, yielded the lowest AICc value and was selected. We analyzed presentation periods separately using individual linear mixed models with habitat type, time since fire, depot type, species, and all interactions as fixed effects. Random variables included terms for plots and depot pairs to represent the sampling structure with nesting of random variables (Onofri et al. 2010). Following model selection, we compared multiple combinations of random statements using the covariance parameter estimates to

determine the random variable structure that minimized redundancy and accounted for the most variation in the data. We tested for differences in seed removal among different levels of fixed effects using least square means tests and a Tukey's correction for multiple comparisons. Simple main effects were examined with the Slice statement in the PROC GLIMMIX procedure.

Results

Vegetation structure

Understory cover differed significantly with habitat type (Fig. 1). Cover was 57 % higher in ecotone than upland habitat, averaging 55 ± 3 SE % and 35 ± 4 %, resp. ($F_{1,13.9} = 14.9$, $P = 0.002$). There was a trend for higher understory vegetation cover in ecotone habitats
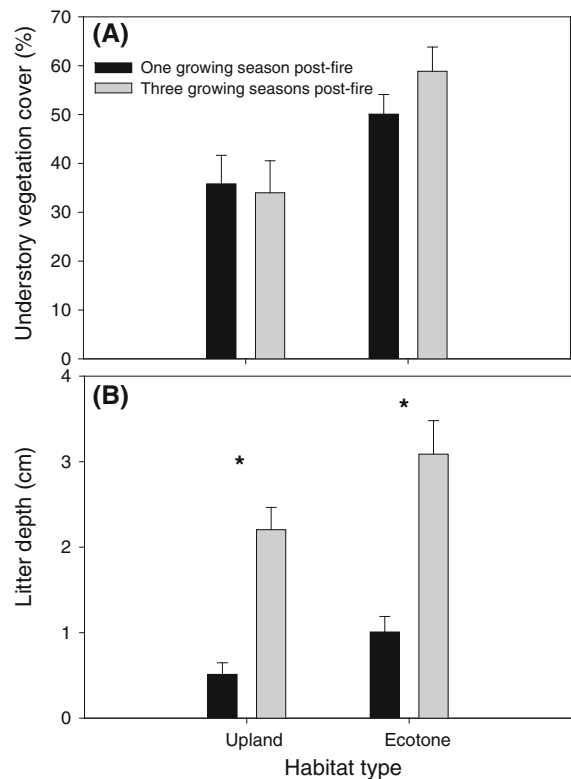
Fig. 1 Mean (+SE) understory vegetation cover (**a**) and litter depth (**b**) in upland and ecotone habitats one or three growing seasons post-fire. The means and standard errors displayed here are not corrected for the nested design of the study. *Asterisks* represent statistically significant differences within habitat types between time post-fire groups (*$P \leq 0.05$)

with time since fire, but this difference was not significant (Fig. 1a).

Litter depth also varied with habitat type. On average, litter depth was 50 % higher in ecotone than upland habitat (mean ± SE; 2.1 ± 0.3 and 1.4 ± 0.3 %, respectively) ($F_{1,27.5} = 5.6$, $P = 0.03$). Time since fire had a significant effect on litter depth, which was on average 253 % higher in plots three growing seasons post-fire than in plots one growing season post-fire (2.7 ± 0.3 cm and 0.8 ± 0.1 cm, resp.) ($F_{1,27.5} = 41.4$, $P < 0.001$). The effect of time since fire on litter depth did not vary with habitat type (Fig. 1b).

Seed removal

Overall, the number of depots experiencing seed removal was similar between presentation periods, with at least one seed removed from 246 depots in November and 222 depots in December. Average seed removal was 8.8 % in November and 8.7 % in December. Several depots were damaged (six in November and one in December) making seeds irretrievable and counts impossible.

Habitat type, species and depot type had strong main effects on seed removal during both presentation periods (Table 2). Seed removal was 77 % higher in ecotone than upland habitat [15.2 ± 1.1 % (SE) and 8.6 ± 0.7 %, resp.] in November, and 201 % higher in ecotone than upland habitat (20.3 ± 1.3 and 6.8 ± 0.6 %, resp.) in December. Among species, mean seed removal ranged from 6.4 to 27.6 % in November and 8.5 to 24.3 % in December. In both periods, removal of *E. umbellata*, the smallest seeded species, was more than twofold higher than that of other species (Table 1; Fig. 2). Seed removal was also consistently higher from depots that allowed both arthropods and small mammals access than from those that allowed only arthropods [November: 14.9 ± 1.1 % (SE) and 9.0 ± 0.8 %, resp.; December: 21.2 ± 1.3 and 5.8 ± 0.6 %, resp.].

There were also significant three-way interactions among these factors in both periods (Table 2). In November, seed removal from arthropod only depots was higher in ecotone than upland habitat for *E. umbellata* ($F_{1,70.98} = 13.8$, $P < 0.001$), and similar for all other species (*M. azedarach* and *A. julibrissin*: $P > 0.14$; *T. sebifera*: $F_{1,418.2} = 3.07$, $P = 0.08$)

Table 2 ANOVA results testing for significance of seed removal by main effects and interactions during November and December seed presentations

	November seed presentation				December seed presentation			
	Num *df*	Den *df*	F	*P*	Num *df*	Den *df*	F	*P*
Main effects								
Time since fire	1	41.5	0.0	0.96	1	35.3	0.23	0.64
Habitat	1	41.5	7.15	**0.011**	1	35.3	16.2	**<0.001**
Species	3	1,032	229.	**<0.001**	3	1,051	149.2	**<0.001**
Depot type	1	447	33.4	**<0.001**	1	481	84.8	**<0.001**
Interactions								
Time since fire × habitat	1	41.5	0.1	0.76	1	35.3	1.34	0.25
Time since fire × species	3	1,032	0.62	0.60	3	1,051	4.62	0.003
Time since fire × depot type	1	447	3.86	**0.050**	1	481	0.03	0.86
Habitat × species	3	1,032	7.75	**<0.001**	3	1,051	3.34	**0.019**
Habitat × depot type	1	447	3.90	**0.049**	1	481	22.9	**<0.001**
Species × depot type	3	1,032	15.0	**<0.001**	3	1,051	14.1	**<0.001**
Time since fire × habitat × species	3	1,032	0.02	0.99	3	1,051	3.53	**0.014**
Time since fire × habitat × depot type	1	447	1.49	0.22	1	481	0.37	0.55
Time since fire × species × depot type	3	1,032	3.18	**0.023**	3	1,051	3.52	**0.015**
Habitat × species × depot type	3	1,032	10.1	**<0.001**	3	1,051	6.78	**<0.001**
Time since fire × habitat × species × depot type	3	1,032	2.23	0.083	3	1,051	1.54	0.20

Values in bold are significant at alpha ≤ 0.05
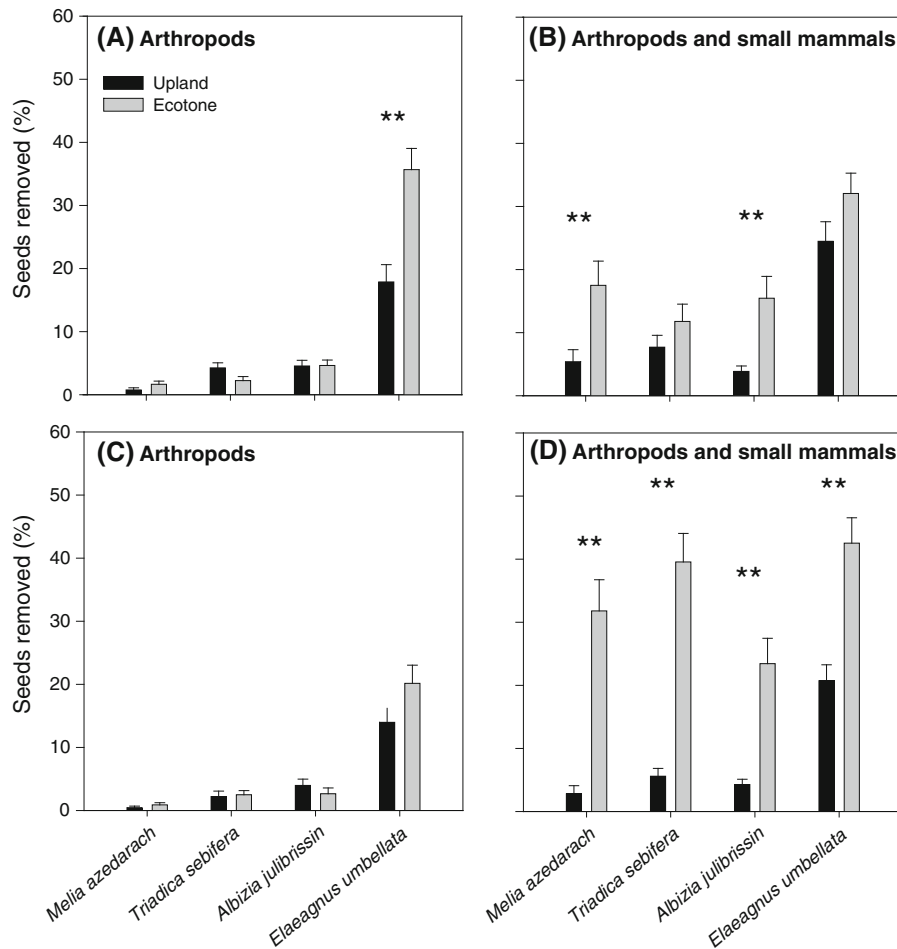
Fig. 2 Mean (+SE) seed removal by species, from arthropod only (**a**, **c**) and arthropod and small mammal (**b**, **d**) depots placed in ecotone and upland habitats for November (*top panels*) and December (*bottom panels*) presentations. The means and standard errors displayed here are not corrected for the nested design of the study. Individual species are ordered by decreasing size. *Asterisks* represent statistically significant differences within species between habitat types, by depot type ($*P \leq 0.05$, $**P \leq 0.01$)

(Fig. 2). In contrast, all species showed a trend for higher seed removal in ecotone than upland habitat when seeds were placed in depots that allowed access to both arthropods and small mammals. Differences were significant for *M. azedarach* and *A. julibrissin* (for both, $P < 0.001$), but not for *E. umbellata* ($F_{1,70.25} = 2.83$, $P = 0.09$) and *T. sebifera* ($F_{1,130.6} = 0.85$, $P = 0.36$) (Fig. 2) Species-level patterns in seed removal in December were comparable to those of November. Removal from arthropod only depots was higher in ecotone than upland habitat for *E. umbellata* ($F_{1,61.52} = 2.62$, $P = 0.11$) and similar between habitat types for all other species ($P > 0.31$). Seed removal from depots that allowed

small mammals access was higher in ecotone than upland habitat for all species ($P < 0.001$) (Fig. 2).

Seed removal did not vary consistently with time since fire during either presentation period (Table 2). Mean seed removal in areas one and three growing seasons post-fire was 12.2 ± 1.0 % (SE) and 11.6 ± 0.9 % in November and 11.8 ± 1.0 and 15.1 ± 1.1 % in December. There were, however, significant two- and three-way interactions with time since fire (Table 2), indicating that fire effects on seed removal were contingent on other factors.

Habitat influenced the effects of time since fire primarily in December (Table 2). In this period, seed removal in upland habitat was 402 % higher in plots one

growing season post-fire than three growing seasons post-fire for *M. azedarach* [2.8 ± 1.4 % (SE) and 0.6 ± 0.3 %, resp.; $F_{1,440.1} = 3.59$, $P = 0.05$], but similar for all other species ($P > 0.16$) (Fig. 3). We observed the opposite pattern in ecotone habitat, such that seed removal was 41 % lower in areas one growing season post-fire than those three growing seasons post-fire for *M. azedarach* (11.9 ± 3.6 and 20.0 ± 4.2 %, resp.; $F_{1,240.8} = 4.18$, $P = 0.04$) and 47 % lower for *T. sebifera* (14.1 ± 3.7 % and 26.8 ± 4.0 %, resp.; $F_{1,52.14} = 3.23$, $P = 0.07$) (Fig. 3). Seed removal for the other species was similar with time since fire in ecotone habitat ($P > 0.43$) (Fig. 3).

Depot type also influenced the effect of time since fire on seed removal for *M. azedarach* and *T. sebifera*. Removal of *M. azedarach* seeds from depots allowing access to both arthropods and small mammals was significantly higher in November in plots one growing season post-fire than in plots three growing seasons post-fire [15.2 ± 3.5 % (SE) and 8.3 ± 2.7 %, resp.; $F_{1,196.9} = 10.7$, $P = 0.001$; data not shown]. In contrast, removal of *T. sebifera* was significantly lower in December in plots one growing season post-fire than in plots three growing seasons post-fire (14.6 ± 3.7 and 29.3 ± 3.9 %, resp.; $F_{1,84.87} = 11.1$, $P = 0.001$; data not shown). Removal of all other species was similar between fire treatments within depot types ($P > 0.13$).

Additionally, habitat and depot type jointly influenced the effect of time since fire on removal of *M. azedarach* and *T. sebifera* seeds (Fig. 4). In ecotone habitat in December, seed removal from depots allowing both arthropod and small mammal access was 38 and 49 % lower in plots one growing season post-fire than in plots three growing seasons post-fire for M. *azedarach* ($F_{1,58.3} = 4.99$, $P = 0.03$) and *T. sebifera* ($F_{1,56.4} = 10.2$, $P = 0.002$), respectively. In upland habitat, however, removal of M. *azedarach* seeds from arthropod and small mammal depots was 398 and 500 % higher in plots one growing season post-fire in November ($F_{1,344} = 9.63$, $P = 0.002$) and December ($F_{1,395} = 5.14$, $P = 0.02$), respectively (Fig. 4). There was also a trend in December for lower seed removal for *T. sebifera* in upland plots one growing season post-fire than in plots three growing seasons post-fire (Fig. 4), but the difference was not significant ($F_{1,56.4} = 2.80$, $P = 0.09$). For *A. julibrissin* and *E. umbellata*, seed removal was similar one and three growing seasons post-fire within each combination of habitat and depot type.
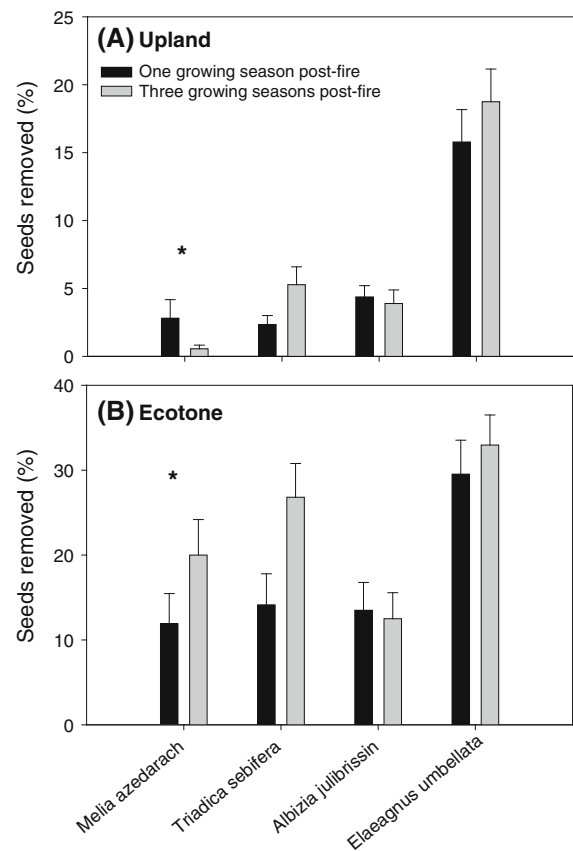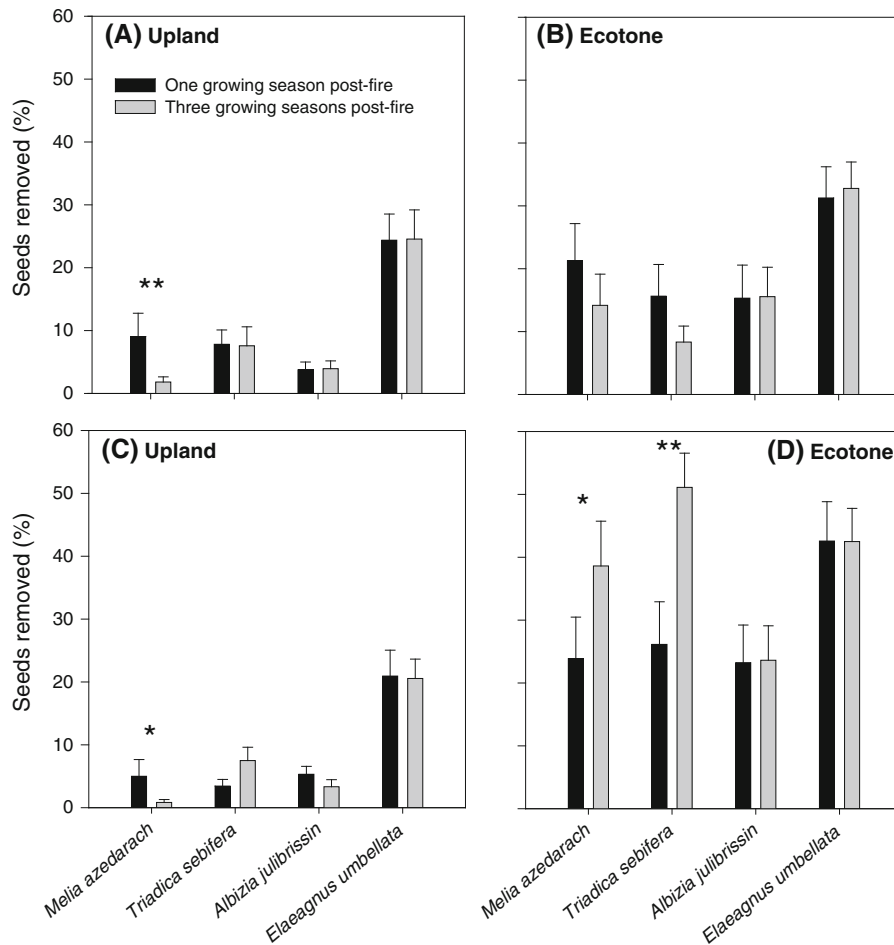

Fig. 3 Mean (+SE) seed removal in December by species, from seed depots located in plots one or three growing seasons post-fire in upland (**a**) and ecotone (**b**) habitats. The means and standard errors displayed here are not corrected for the nested design of the study. Individual species are ordered by decreasing seed size. *Asterisks* represent statistically significant differences within species, between plots one or three growing seasons post-fire, by habitat type (*$P \leq 0.05$)

Discussion

In fire-dependent ecosystems, recent fire history may influence patterns of exotic woody invasion by altering granivore activity. Few studies, however, have examined how fire effects vary spatially due to heterogeneity in time since fire or vegetation structure, or have evaluated the factors that modulate these relationships. We found that habitat type (defined by plant community), exotic species, and granivore community strongly affected seed removal, as well as influenced the relationship between time since fire and seed removal in longleaf pine savannas. For three of four species, seed removal was highest in ecotones three growing seasons post-fire. Seed depots that

Fig. 4 Mean (+SE) seed removal by species from seed depots that allowed access to both arthropod and small mammals and were placed in plots one or three growing seasons post-fire in upland (**a**, **c**) and ecotone (**b**, **d**) habitats for November (*top panels*) and December (*bottom panels*) presentations. The means and standard errors displayed here are not corrected for the nested design of the study. Individual species are ordered by decreasing seed size. *Asterisks* represent statistically significant differences within species between plots one or three growing seasons post-fire, by habitat type (*$P \leq 0.05$, **$P \leq 0.01$)

allowed small mammals and arthropods access showed more than twofold higher removal than depots that only allowed arthropods access, indicating that small mammals were more effective at removing seeds of the focal species. These findings suggest that ecotone habitat supporting small mammal granivores experiences greater post-dispersal seed removal than upland habitats; and, for at least two species, post-dispersal seed removal increases in ecotone habitat as time since fire increases and vegetation recovers.

Fire both drives and responds to spatial and temporal variation in vegetation structure within the longleaf pine ecosystem (Kirkman et al. 2004). Results from this study support this idea, and suggest that differences in vegetation structure associated with habitat type and length of time since fire contribute to spatial heterogeneity at between-habitat and landscape scales. Vegetative cover was higher in ecotone than upland habitat; and for ecotone habitat, time played a role in recovery, with greater percentage cover three growing seasons post-fire than one. Previous studies show that vegetation recovery following fire in the longleaf ecosystem is affected by fire behavior (Thaxton and Platt 2006; Ellair and Platt 2012), microsite conditions (Olson and Platt 1995; Drewa et al. 2002), component species' morphological and physiological traits (Hiers and Mitchell 2007; Romero et al. 2009), and plant size at time of burn (Rebertus et al. 1989; Grady and Hoffmann 2012).

Seed removal patterns strongly reflected habitat-associated differences in post-fire vegetation cover and recovery. For example, we found that overall seed removal was higher in ecotone than upland habitat regardless of time since fire. Additionally, for three of the four species studied, seed removal was highest in ecotone habitat three growing seasons post-fire. While this difference was only significant for two species, it indicates that even the short 3-year interval between fires in the study system can create ecologically significant differences in habitat structure that influence small mammal granivore activity. These results are consistent with those of other studies showing higher seed removal by mammalian granivores with greater vegetation cover (e.g., Mittelbach and Gross 1984; Hulme 1994; Alcantara et al. 2000), and are presumably due to the decreasing perceived predation risk of granivores with increasing vegetation cover (Bowers 1993; Garcia-Castano et al. 2006; Pons and Pausas 2007). However, they are in contrast to other studies that have shown seed removal increases after fire in both grasslands (Reed et al. 2004) and forests (Côté et al. 2005; Zwolak et al. 2010), due to increased granivore foraging efficiency (Reed et al. 2005; Zwolak et al. 2012). Furthermore, the opposing effects of time since fire on removal of *M. azedarach* and *T. sebifera* seeds between habitats and presentation periods emphasize the importance of examining potential spatial, temporal and species-specific variation in seed removal. Ecotone habitats may be at greater risk to exotic woody plant invasion directly after fire not only due to reduced seed removal, but also because the consumption of vegetation and litter by fire can increase the availability of microsites for germination (e.g., Kuppinger et al. 2010; Mazia et al. 2010).

Although granivores removed seeds of all four woody exotic species, the smallest seeded species, *E. umbellata*, was both strongly selected and the only species for which direct evidence of in situ seed predation was found, in the form of empty endocarps. Using seeds of a similar weight and size as this experiment, others have found similar selective removal of smaller seeds by small mammals (Alcantara et al. 2000), and both arthropods and small mammals (Carrillo-Gavilan et al. 2010). However, as seed size did not consistently predict removal rates, other seed traits may have influenced removal. For example, seed strength, impacted by seed thickness,

has been shown to affect seed selection in granivores (Lundgren and Rosentrater 2007). Seed chemical defenses also vary among plant species to deter vertebrate granivores, which respond strongly to visual, gustatory olfactory signals (Janzen 1971). Seeds of several *Albizia* species and many other legumes contain chemicals toxic to rodent granivores (Duncan et al. 1953; Grant et al. 1995), and *M. azedarach* fruits contain toxic tetranortriterpenes (Oelrichs et al. 1983). Indeed, *M. azedarach* and *A. julibrissin* were removed less often from depots that allowed small vertebrates access than the other species, which have no known chemical defenses. Nutritional differences among seeds may also be important in influencing granivore foraging behavior (Kelrick et al. 1986). *Triadica sebifera* seeds have high levels of short- and long-chain fatty acids (Terigar et al. 2010), and were primarily removed when small vertebrates were allowed access, rather than arthropods only.

Arthropod granivores removed relatively few seeds of the focal species during the November and December seed presentation periods. With colder average temperatures during the night (9.0 and 11.2 °C, resp.) and day (11.8 and 14.5 °C, resp.), the low removal rates could have been due to restrictions in arthropod activity (Golley and Gentry 1964; Niehaus et al. 2012). Seed removal from depots allowing only arthropod access did not differ by habitat type or time since fire, which suggests understory vegetation cover and litter depth had no effect on arthropod foraging. This is inconsistent with other studies which show arthropod seed predation is higher on bare ground than litter covered substrates (Crist and Wiens 1994) and that fire increases arthropod foraging distances (McCoy and Kaiser 1990) and seed predation (Côté et al. 2005). However, we may not have been able to detect any effects of habitat or time since fire due to low removal rates. When seed removal could be unequivocally attributed to arthropod granivores, *E. umbellata* seeds were selected. Arthropods are more restricted in seed transport capabilities than small vertebrates, and at 0.014 g, *E. umbellata* seeds are likely heavy for arthropod removal (MacMahon et al. 2000; Lundgren and Rosentrater 2007).

Our results suggest that small vertebrates are the primary post-dispersal granivores of the focal species during the fall across the longleaf pine ecosystem

studied. This is consistent with evidence suggesting that vertebrates are the primary granivores in ecosystems regularly experiencing fire (Auld and Denham 2001; Reed et al. 2004), and of woody species having comparably sized seeds (Ostfeld et al. 1997; Whelan et al. 1991). The depot design limits inference to small mammals, presumably rodents, and while birds were not explicitly excluded it is unlikely they removed seeds (Mattos and Orrock 2010). The December presentation showed the most pronounced effect of allowing small mammal granivores access, potentially due to dwindling food resources (Haught and Myster 2008). However, not all seeds removed by small mammals were likely consumed, as all of the granivorous rodents known on Fort Bragg, except *S. hispidus* (Cameron and Spencer 1981), *S. palustris* (Chapman and Willner 1981), and *Reithrodontomys humulis* (Stalling 1997), exhibit flexible feeding patterns with scatterhoarding or caching traits.

The observed differences in removal suggest that habitat type and fire may jointly influence the spatial distribution of the seeds of woody exotic species within fire-dependent longleaf pine savannas. Yet the implications of these findings for the establishment and spread of woody exotic species remain unclear because we did not follow the seeds post-removal. Granivores could have consumed, dispersed or cached seeds following removal (Vander Wall et al. 2005). Moreover, seeds in sites unsuitable for germination are likely never to establish, and therefore their removal is unlikely to affect plant recruitment (Maron and Simms 1997). When populations are limited by seeds rather than microsite availability, however, there is consistent evidence suggesting that post-dispersal seed removal negatively affect woody plant establishment and demography by decreasing the number of viable seeds that are available to establish in suitable sites (Ostfeld et al. 1997; Santos and Telleria 1997; Orrock et al. 2006; Nunez et al. 2008; Zwolak et al. 2010). In the longleaf pine ecosystem, each of the focal species is known to invade xeric upland (Kush and Meldahl 2000; Provencher et al. 2000; Renne et al. 2000; Stocker and Hupp 2008) and mesic ecotone plant communities (Herring and Judd 1995; Drew et al. 1998; Renne et al. 2000), which suggests that seeds of all four species have the potential to germinate in both upland and ecotone habitats if they escape post-dispersal predation. Despite this, invasion of our study system by the focal species remains rare. This is

evidence that the focal species are seed limited, despite the large number of seeds a single tree can produce. Given these findings and the observed differences in seed removal patterns, we conclude that granivores are limiting exotic woody invasions in ecotone habitat, but hypothesize that the influence of granivores in ecotone habitat is diminished during the first growing season post-fire. By corollary, and assuming that these findings hold for the duration of the winter season, there may be predictable sites offering escape from seed predation in this ecosystem. Studies evaluating establishment limitation should be conducted to assess invasion vulnerability in such areas.

Generalizations about the ultimate role of any process in generating pattern are limited by our knowledge about how the process varies in space and time. Biological invasions are inherently a spatially and temporally dynamic phenomenon. With regard to invasive plants, post-dispersal establishment is affected by multiple biotic and abiotic factors. An understanding of the patterns of post-dispersal seed removal may be useful for managing natural savanna ecosystems that are under the threat of encroachment from exotic woody species, and for increasing our understanding of invasion dynamics.

References

Alcantara JM, Rey PJ, Sanchez-Lafuente AM, Valera F (2000) Early effects of rodent post-dispersal seed predation on the outcome of the plant-seed disperser interaction. Oikos 88:362–370

Auld TD, Denham AJ (2001) The impact of seed predation by mammals on post-fire seed accumulation in the endangered shrub *Grevillea caleyi* (Proteaceae). Biol Conserv 97:377–385

Beckage B, Platt WJ, Gross LJ (2009) Vegetation, fire and feedbacks: a disturbance-mediated model of savannas. Am Nat 174:805–818

Bolker MB, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol Evol 24:127–135

Boman JS, Casper BB (1995) Differential postdispersal seed predation in disturbed and intact temperate forest. Am Midl Nat 134:107–116

Bond WJ, Keeley JE (2005) Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. Trends Ecol Evol 20:387–394

Bowers MA (1990) Exploitation of seed aggregates by Merriam's kangaroo rat: harvesting rates and predatory risk. Ecology 71:2334–2344

Bowers MA (1993) Influence of herbivorous mammals on an old-field plant community: years 1–4 after disturbance. Oikos 67:129–141

Brooks ML, D'Antonio CM, Richardson DM, Grace JB, Keeley JE, DiTomaso JM, Hobbs RJ, Pellant M, Pyke D (2004) Effects of invasive alien plants on fire regimes. Bioscience 54:677–688

Brown JH, Heske EJ (1990) Control of a desert-grassland transition by a keystone rodent guild. Science 250:1705–1707

Cameron GN, Spencer SR (1981) *Sigmodon hispidus*. Mammalian Species 158:1–9

Carrillo-Gavilan MA, Lalague H, Vila M (2010) Comparing seed removal of 16 pine species differing in invasiveness. Biol Invasions 12:2233–2242

Chapman JA, Willner GR (1981) *Sylvilagus palustris*. Mammalian Species 153:1–3

Clark CJ, Poulsen JR, Levey DJ, Osenberg CW (2007) Are plant populations seed limited? A critique and meta-analysis of seed addition experiments. Am Nat 170:128–142

Côté M, Ferron J, Gagnon R (2005) Invertebrate predation of postdispersal seeds and juvenile seedlings of black spruce (*Picea mariana*) in the boreal forest of eastern Canada. Can J For Res 35:674–681

Craig MT, Orrock JL, Brudvig LA (2011) Edge-mediated patterns of seed removal in experimentally connected and fragmented landscapes. Landscape Ecol 26:1373–1381

Crist TO, Wiens JA (1994) Scale effects of vegetation on forager movement and seed harvesting by ants. Oikos 69:37–46

Drew MB, Kirkman LK, Gholson AK (1998) The vascular flora of Ichauway, Baker County, Georgia: a remnant longleaf pine/wiregrass ecosystem. Castanea 63:1–24

Drewa PB, Platt WJ, Moser EB (2002) Fire effects on resprouting of shrubs in headwaters of southeastern longleaf pine savannas. Ecology 83:755–767

Duncan WH, Piercy PL, Starling RJ (1953) Toxicological studies of southeastern plants. I. Leguminosae. Econ Bot 9:243–255

Ellair DP, Platt WJ (2012) Fuel composition influences fire characteristics and understory hardwoods in pine savanna. J Ecol 101:192–201

Fewell JH (1988) Energetic and time costs of foraging in harvester ants, *Pogonomyrmex occidentalis*. Behav Ecol Sociobiol 22:401–408

Garcia-Castano JL, Kollmann J, Jordano P (2006) Spatial variation of post-dispersal seed removal by rodents in highland microhabitats of Spain and Switzerland. Seed Sci Res 16:213–222

Gibb H, Parr CL (2010) How does habitat complexity affect ant foraging success? A test using functional measures on three continents. Oecologia 164:1061–1073

Golley FB, Gentry JB (1964) Bioenergetics of the southern harvester ant, *Pogonomyrmex badius*. Ecology 45:217–225

Grady JM, Hoffmann WA (2012) Caught in a fire trap: recurring fire creates stable size equilibria in woody resprouters. Ecology 93:2052–2060

Grant G, More LJ, McKenzie NH, Dorward PM, Buchan WC, Telek L, Pusztai A (1995) Nutritional and haemagglutination properties of several tropical seeds. J Agric Sci 124:437–445

Haught JE, Myster RW (2008) Effects of species, density, season and prairie-type on post-dispersal seed removal in Oklahoma. Am Midl Nat 159:482–488

Herring BJ, Judd WS (1995) A floristic study of Ichetucknee Springs State Park, Suwannee and Columbia counties, Florida. Castanea 60:318–369

Hiers JK, Mitchell RJ (2007) The influence of burning and light availability on N_2-fixation of native legumes in longleaf pine woodlands. J Torrey Bot Soc 134:398–409

Hulme PE (1994) Post-dispersal seed predation in grassland: its magnitude and sources of variation. J Ecol 82:645–652

Hulme PE (1998) Post-dispersal seed predation: consequences for plant demography and evolution. Perspect Plant Ecol Evol Syst 1:32–46

Jacob J, Brown JS (2000) Microhabitat use, giving-up densities and temporal activity as short- and long-term anti-predator behaviors in common voles. Oikos 91:131–138

Janzen DH (1971) Seed predation by animals. Annu Rev Ecol Syst 2:465–492

Johnson JB, Omland KS (2004) Model selection in ecology and evolution. Trends Ecol Evol 19:101–108

Kelrick MI, MacMahon JA, Parmenter RR, Sisson DV (1986) Native seed preferences of shrub-steppe rodents, birds and ants: the relationship of seed attributes and seed use. Oecologica 68:327–337

Kirkman LK, Goebel PC, Palik BJ, West LT (2004) Predicting plant species diversity in a longleaf pine landscape. Ecoscience 11:80–93

Kollmann J, Coomes DA, White SM (1998) Consistencies in post-dispersal seed predation of temperate fleshy-fruited species among seasons, years and sites. Funct Ecol 12:683–690

Kotler BP (1984) Risk of predation and the structure of desert rodent communities. Ecology 65:689–701

Krefting LW, Ahlgren CE (1974) Small vertebrates and vegetation changes after fire in a mixed conifer-hardwood forest. Ecology 55:1391–1398

Kuppinger DM, Jenkins MA, White PS (2010) Predicting the post-fire establishment and persistence of an invasive species across a complex landscape. Biol Invasions 12:3473–3484

Kush JS, Meldahl RS (2000) Composition of a virgin stand of longleaf pine in south Alabama. Castanea 65:56–63

Lackey JA, Huckaby DG, Ormiston BG (1985) *Peromyscus leucopus*. Mammalian Species 247:1–10

Leishman MR, Wright IJ, Moles AT, Westoby M (2000) The evolutionary ecology of seed size. In: Fenner M (ed) Seeds: the ecology of regeneration in plant communities. CAB International, Wallingford, pp 31–57

Lonsdale WM, Miller IL (1993) Fire as a management tool for the tropical woody weed: *Mimosa pigra* in northern Australia. J Environ Manage 39:77–87

Lundgren JG, Rosentrater KA (2007) The strength of seeds and their destruction by granivorous insects. Arthropod Plant Interact 1:93–99

MacMahon JA, Mull JF, Crist TO (2000) Harvester ants (*Pogonomyrmex* spp.): their community and ecosystem influences. Annu Rev Ecol Syst 31:265–291

Mandle L, Bufford JL, Schmidt IB, Daehler CC (2011) Woody exotic plant invasions and fire: reciprocal impacts and consequences for native ecosystems. Biol Invasions 13:1815–1827

Manson RH, Stiles EW (1998) Links between microhabitat preferences and seed predation by small vertebrates in old fields. Oikos 82:37–50

Maron JL, Simms EL (1997) Effect of seed predation on seed bank size and seedling recruitment of bush lupine (*Lupinus arboreus*). Oecologia 111:76–83

Matias L, Mendoza I, Zamora R (2009) Consistent pattern of habitat and species selection by post-dispersal seed predators in a Mediterranean mosaic landscape. Plant Ecol 203:137–147

Mattos KJ, Orrock JL (2010) Behavioral consequences of plant invasion: an invasive plant alters rodent antipredator behavior. Behav Ecol 21:556–561

Mazia CN, Chaneton EJ, Machera M, Uchitel A, Feler MV, Ghersa CM (2010) Antagonistic effects of large- and small-scale disturbances on exotic tree invasion in a native tussock grassland relict. Biol Invasions 12:3109–3122

McCoy ED, Kaiser BW (1990) Changes in foraging activity of the southern harvester ant *Pogonomyrmex badius* (Latreille) in response to fire. Am Midl Nat 123:112–123

Meyer R (2010) *Albizia julibrissin*. In: Fire effects information system, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: http://www.fs.fed.us/database/feis/. 20 Jan 2013

Meyer R (2011) *Triadica sebifera*. In: Fire effects information system, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: http://www.fs.fed.us/database/feis/. 20 Jan 2013

Mittelbach GG, Gross KL (1984) Experimental studies of seed predation in old-fields. Oecologia 65:7–13

Munger GT (2003) *Elaeagnus umbellata*. In: Fire effects information system, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: http://www.fs.fed.us/database/feis/. 20 Jan 2013

Nathan R, Muller-Landau HC (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends Ecol Evol 15:278–285

Ne'eman G, Goubitz S, Nathan R (2004) Reproductive traits of *Pinus halepensis* in the light of fire—a critical review. Plant Ecol 171:69–79

Niehaus AC, Wilson RS, Storm JJ, Angilletta MJ (2012) Fall field crickets did not acclimate to simulated seasonal changes in temperature. J Comp Physiol B 182:199–207

Nunez MA, Simberloff D, Relva MA (2008) Seed predation as a barrier to alien conifer invasions. Biol Invasions 10:1389–1398

Oelrichs PB, Hill MW, Vallely PJ, MacLaod JK, Molinski TF (1983) Toxic tetranortriterpenes of the fruit of *Melia azedarach*. Phytochemistry 22:531–534

Olson MS, Platt WJ (1995) Effects of habitat and growing season on fires on resprouting of shrubs in longleaf pine savannas. Vegetatio 119:101–118

Onofri A, Carbonell EA, Piepho HP, Mortimer AM, Cousens RD (2010) Current statistical issues in *Weed Research*. Weed Res 50:5–24

Orrock JL, Damschen EI (2005) Corridors cause differential seed predation. Ecol Appl 15:793–798

Orrock JL, Danielson BJ, Brinkerhoff RJ (2004) Rodent foraging is affected by indirect, but not by direct, cues of predation risk. Behav Ecol 15:433–437

Orrock JL, Levey DJ, Danielson BJ, Damschen EI (2006) Seed predation, not seed dispersal, explains the landscape-level abundance of an early-successional plant. Ecology 94:838–845

Ostfeld RS, Manson RH, Canham CD (1997) Effects of rodents on survival of tree seeds and seedlings invading old fields. Ecology 78:1531–1542

Pons J, Pausas JG (2007) Rodent acorn selection in a Mediterranean oak landscape. Ecol Res 22:535–541

Provencher L, Herring BJ, Gordon DR, Rodgers HL, Tanner GW, Brennan LA, Hardesty JL (2000) Restoration of northwest Florida sandhills through harvest of *Pinus clausa*. Restor Ecol 8:175–185

Rebertus AJ, Williamson GB, Moser EB (1989) Longleaf pine pyrogenicity and turkey oak mortality in Florida xeric sandhills. Ecology 70:60–70

Reed AW, Kaufman GA, Kaufman DW (2004) Influence of fire, topography, and consumer abundance on seed predation in tallgrass prairie. Can J Zool 82:1459–1467

Reed AW, Kaufman GA, Kaufman DW (2005) Rodent seed predation and GUDs: effect of burning and topography. Can J Zool 83:1279–1285

Reed AW, Kaufman GA, Kaufman DW (2006) Effect of plant litter on seed predation in three prairie types. Am Midl Nat 155:278–285

Renne IJ, Gauthreaux SA, Gresham CA (2000) Seed dispersal of the Chinese tallow tree (*Sapium sebiferum* (L.) Roxb.) by birds in coastal South Carolina. Am Midl Nat 144:202–215

Rey PJ, Garrido JL, Alcantara JM, Ramirez JM, Aguilera A, Garcia L, Manzaneda AJ, Fernandez R (2002) Spatial variation in ant and rodent post-dispersal predation of vertebrate-dispersed seeds. Funct Ecol 16:773–781

Romero C, Bolker BM, Edwards CE (2009) Stem responses to damage: the evolutionary ecology of *Quercus* species in contrasting fire regimes. New Phytol 182:261–271

Santos T, Telleria JL (1997) Vertebrate predation on Holm oak, *Quercus ilex*, acorns in a fragmented habitat: effects on seedling recruitment. For Ecol Manage 98:181–187

Satterthwaite WH (2007) The importance of dispersal in determining seed versus safe site limitation of plant populations. Plant Ecol 193:113–130

Schnurr JL, Canham CD, Ostfeld RS, Inouye RS (2004) Neighborhood analysis of small-mammal dynamics: impacts of seed predation and seedling establishment. Ecology 85:741–755

Sorrie BA, Gray JB, Crutchfield PJ (2006) The vascular flora of the longleaf pine ecosystem of Fort Bragg and Weymouth Woods, North Carolina. Castanea 71:129–161

Sousa WP (1984) The role of disturbance in natural communities. Annu Rev Ecol Syst 15:353–391

Stalling DT (1997) *Reithrodontomys humulis*. Mammalian Species 565:1–6

Stevens JT, Beckage B (2010) Fire effects on demography of the invasive shrub Brazilian pepper (*Schinus terebinthifolius*) in Florida pine savannas. Nat Areas J 30:53–63

Stocker R, Hupp KVS (2008) Chapter 6: fire and nonnative invasive plants in the southeast bioregion. USDA For Serv Gen Tech Rep 6:91–112

Taylor CM, Hastings A (2005) Allee effects in biological invasions. Ecol Lett 8:895–908

Terigar BG, Balasubramanian S, Boldor D (2010) Effect of storage conditions on the oil quality of Chinese tallow tree seeds. J Am Oil Chem Soc 87:573–582

Tester JP (1965) Effects of a controlled burn on small vertebrates in a Minnesota oak savanna. Am Midl Nat 74:240–243

Thaxton JM, Platt WJ (2006) Small-scale fuel variation alters fire intensity and shrub abundance in a pine savanna. Ecology 87:1331–1337

Theoharides KA, Dukes JS (2007) Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. New Phytol 176:256–273

Thompson K, Rabinowitz D (1989) Do big plants have big seeds? Am Nat 133:722–728

Todorović S, Božić D, Simonović A, Filipović B, Dragićević M, Giba Z, Grubišić D (2010) Interaction of fire-related cues in seed germination of the potentially invasive species *Paulownia tomentosa* Steud. Plant Species Biol 25:193–202

Vander Wall SB, Kuhn KM, Beck MJ (2005) Seed removal, seed predation, and secondary dispersal. Ecology 86:801–806

Vaz Ferreira A, Bruna EM, Vasconcelos HL (2011) Seed predators limit plant recruitment in Neotropical savannas. Oikos 120:1013–1022

Waggy MA (2009) *Melia azedarach*. In: Fire effects information system, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: http://www.fs.fed.us/database/feis/. 20 Jan 2013

Weakley AS (2012) Flora of the southern and mid-Atlantic states. University of North Carolina at Chapel Hill, North Carolina Botanical Garden, University of North Carolina Herbarium (Producer). Available: http://www.herbarium.unc.edu/flora.htm. 20 Jan 2013

Whelan CJ, Willson MF, Tuma CA, Souza-Pinto I (1991) Spatial and temporal patterns of postdispersal seed predation. Can J Bot 69:428–436

Zwolak R, Pearson DE, Ortega YK, Crone EE (2010) Fire and mice: seed predation moderates fire's influence on conifer recruitment. Ecology 91:1124–1131

Zwolak R, Pearson DE, Ortega YK, Crone EE (2012) Mechanisms driving postfire abundance of a generalist mammal. Can J Zool 90:51–60