INFLUENCE OF FIRE AND HABITAT ON THE REMOVAL OF INVASIVE PLANT SEEDS
BY GRANIVORES IN LONGLEAF PINE SAVANNAS

BY

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THESIS

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Abstract

Invasions of fire-dependent ecosystems by exotic woody plant species can disrupt fire cycles and alter successional trajectories. Prescribed fire is an important tool for managing such ecosystems, yet the role of top-down processes in mediating fire effects on invasion remain poorly understood. Fire may influence exotic woody plant species through its indirect effects on granivore activity. Given the importance of habitat structure for determining granivore activity, I focus on the role of fire-induced habitat variation at the between-habitat and landscape scales. I quantified seed removal for four species of woody exotic plants (*Elaeagnus umbellata, Albizia julibrissin*, *Triadica sebifera*, and *Melia azedarach*), in longleaf pine savanna that varied spatially in time since fire, in the Sandhills of North Carolina. I selected eight sites burnt one growing season prior, and nine sites burnt three growing seasons prior, within which I established paired plots in upland plant communities, which included *Pinus palustris, Aristida stricta,* legumes, grasses, and composites (hereafter "upland habitat"), and upland-wetland ecotone communities, which included *P. palustris, Acer rubrum*, *Liriodendron tulipifera*, shrubs, cane, and forbs (hereafter "ecotone habitat"). Over two 15-day periods, seeds were presented in depots that allowed either arthropod, or arthropod and small vertebrate access. Overall removal levels for the two presentation periods were 8.81% and 8.65%. For all exotic plant species, removal was highest in ecotone habitat, which had greater understory vegetation cover and litter depth than upland habitat. For three of four species, seed removal was highest in ecotone habitat three growing seasons post-fire. While granivores removed seeds of all four species of exotic plants, *E. umbellata* experienced significantly higher removal than other species, suggesting that granivores exhibited seed selection. Allowing vertebrate granivores access to seeds enhanced seed removal and this effect was influenced by habitat type. These findings suggest that ecotone

habitats in this system experience greater seed removal than upland habitats, particularly as time since fire increases and understory vegetation recovers. Such differences in seed removal percentages, together with seed selection, may contribute to variation in the success of exotic invaders in fire-dependent longleaf pine savannas.

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Introduction

Invasions by exotic woody plant species can be detrimental to ecosystems sensitive to changes in habitat structure, such as those which depend on frequent fire (Mandle et al. 2011). Pine savannas, for example, require fire to maintain a sparse canopy cover and continuous grass understory, conditions which in turn promote fire (Glitzenstein et al. 1995). Encroachment by woody species, including exotics, can disrupt this grass-fire cycle and alter the successional trajectory of the system (Mandle et al. 2011). In the absence of a natural fire regime, prescribed fire is increasingly used to inhibit woody 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 direct effects of fire on plant performance and competition. Such studies have yielded equivocal 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 (Kuppinger et al. 2010), and increased nutrient availability (Christensen 1977). Much less is known about the role of top-down processes in mediating fire effects on invasion, particularly through its effects on granivory.

Post-dispersal granivory is recognized as a key process influencing woody plant recruitment (Maron and Simms 2001). For instance, in fire-dependent western US savannas, removal of woody plant seeds by granivores influences the pattern and rate of encroachment by altering the distribution and viability of woody plant seeds (Weltzin et al. 1997). Small vertebrates have been found to be important granivores of woody seeds, potentially more so than arthropods (e.g. Maron and Kauffman 2006). Seed removal rates are correlated with granivore,

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especially small mammal, preference for habitat characteristics (Hulme 1994), including high levels of vegetative cover (Kotler 1984; Manson and Stiles 1998), and downed woody debris for predator refuge (McCay 2000). Reductions in vegetation cover may increase the perceived predation risk of granivores and cause them to alter their foraging patterns (Fewell 1988; Jacob and Brown 2000; Orrock et al. 2004). Litter depth has also been found to variably affect foraging activity of both arthropods (Parr et al. 2007; Ober and DeGroote 2011), and small vertebrates (Reed et al. 2006; Tester 1965). Fire may reduce litter depth (Bond and Keeley 2005), and alter vegetation cover (Krefting and Ahlgren 1974), potentially resulting in modified granivore activity. Thus, fire-induced alterations to habitat structure may result in 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. Such spatial heterogeneity may be especially apparent in fire-dependent ecosystems managed with prescribed fire (Hiers et al. 2009; Jeltsch et al. 1998). In general, prescribed fire is applied to individual land units called burn blocks, which results in landscape-scale spatial variation in length of time since fire. Additionally, because burn blocks may encompass different plant community types that differ in underlying soil moisture conditions, there may be differences in fire intensity and vegetation recovery rate that increase spatial heterogeneity at a finer scale (Dwire and Kauffman 2003; 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 plant invasions. To date, a minimal number of studies have examined the role of seed predation in exotic woody plant invasions (e.g.

Busch et al. 2012; Carrillo-Gavilan 2010; Nunez et al. 2008; Shahid et al. 2009), and none within native fire-dependent ecosystems managed with prescribed fire.

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 percentages among plant species. Seed removal percentages may be altered by morphological (Lundgren and Rosentrater 2007), chemical defense (Pearson et al. 2011), and nutritional traits (Kelrick and MacMahon 1985). 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 vertebrates (Brown and Heske 1990; Matias et al. 2009). Seed selection may also be dependent on habitat structure with time since fire, as seed preference and removal percentages may be influenced by perceived predation risk (Bowers 1990).

In this study, I investigate how fire influences exotic woody plant species through its effects on granivore activity. Given the importance of habitat structure for determining granivore activity, I focus on the role of fire-induced habitat variation at the between-habitat and landscape scales. Between-habitat heterogeneity in structure and composition of plant communities is associated with topographically mediated moisture differences that influence fire behavior and effects. Landscape-scale habitat variation is due to differences in time since fire, and is a function of the managed fire cycle, wherein the landscape is divided into units that experience similar management regimes. My specific objectives were: (1) to compare the patterns of seed removal between upland and ecotone habitats that were burned either one or three growing seasons prior, (2) to compare seed removal of four woody exotic plant species, *Elaeagnus umbellata, Albizia julibrissin*, *Triadica sebifera,* and *Melia azedarach*, which vary in life history traits and morphological characteristics such as size; and (3) assess the importance of granivore

community composition for explaining variation in removal. I expected removal to increase with vegetation structure and therefore increase with time since fire presumably due to the protection from predators afforded by vegetation structure. I further expected habitat type to modulate this effect because fire intensity and vegetation recovery vary with habitat. I expected that species would be differentially selected by arthropod and small vertebrate granivore communities potentially due to differences in exotic seed morphological 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 ^{o} 07' N, 79°10' W). The installation covers an area of 73,468 ha and ranges in elevation from 43 to 176 m (Sorrie et al. 2006). Mean temperature is 26°C during the summer and 7°C during the winter (Sorrie et al. 2006). 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 occurs near the northern extent of the former longleaf pine–wiregrass savanna ecosystem and is comprised of multiple plant community habitat 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*) and 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 seed granivores include: *Glaucomys volans*, *Microtus pinetorum*, *Mus musculus*, *Peromyscus gossypinus*, *Peromyscus leucopus*, *Reithrodontonmys humulis*, *Sciurus carolinensis*, *Scirus niger*, *Sigmodon hispidus*, and *Sylvilagus palustris* (McCallister 2011). The invertebrate granivores on site potentially include: ground beetles (Coleoptera; Carabidae), harvester ants (Hymenoptera; Formicidae) (Hooper 1996), and crickets (Orthoptera; Gryllidae) (Hanula and Wade 2003).

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 called burn blocks approximately every 3-5 years. I 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 I established a pair of 10 m x 40 m (0.04 ha) plots, one in upland and one in ecotone habitat (Fig. 1). 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, *Peromyscus leucopus* (32 m radius) (Lackey et al. 1985).

Focal species

I focused on four deciduous woody species: *Elaeagnus umbellata, Albizia julibrissin, Triadica sebifera,* and *Melia azedarach.* All of these species are considered invasive in the

southeastern US. Individual species are avian dispersed except for *A. julibrissin,* which primarily disperses via wind (Table 1). Each species has the potential to establish and bear fruit within the fire-management cycle on Fort Bragg (Table 1). Individuals of each species may produce thousands of viable seeds per growing season, and except for *E. umbellata,* have short-lived seed banks (Table 1). Soil disturbance promotes the establishment of all four species (Table 1). Once established, these exotic species have the potential for fast growth (Meyer 2010, 2011; Munger 2003; Waggy 2009), potentially reaching a height and size large enough to escape mortality caused by the next "non-catastrophic" surface fire (Bond and Keeley 2005). Even if damaged during fire, all four species have the potential to re-sprout post-injury (Table 1).

Seeds of each species were bulk-collected from populations on or near Fort Bragg. To mimic avian dispersal, fleshy coatings from *M. azedarach* and *E. umbellata* fruits were manually removed; seeds rinsed clean of pulp and allowed to dry for 48 hours. *M. azedarach* and *E. umbellata* seeds were presented still enclosed in their protective endocarp. *A. julibrissin* and *T. sebifera* seeds were sorted from attached pods and capsules and allowed to dry for 24 hours. To characterize average seed size, I measured dry seed mass, length, and width of 100 randomly chosen seeds of each species prior to storage in paper bags at room temperature.

Field measurements

I 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 40 m transects. I 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.

I conducted two sixteen-day seed removal presentations from November 5th to 21st 2011 and December 5th to 21st 2011. Multiple presentation periods allowed me 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 (Table 1). 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 I 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 three months prior to seed presentation periods. Depots were inverted translucent white plastic buckets 12.7cm in height and 21.9 cm in diameter with two 15 cm x 8 cm openings on opposite sides, and the base removed. Similarly designed depots have been used successfully in other seed removal studies (e.g., Craig et al. 2011; Mattos and Orrock 2010). Two depot types were used; 1) accessible only to arthropods, and 2) accessible to arthropods and small vertebrates. Mesh hardware cloth of 1.6 cm^2 gauge was used to bar vertebrate access via openings and replace the inverted base of all depots. Depots were secured in place with four steel landscape pins. For both seed presentations I covered the attached bucket lid of each depot with 1 cup of sand and deposited 10 seeds of each of the four species on the surface. After 15 days I collected the sand and seeds from each depot, sifted the contents, and counted the remaining intact and damaged seeds.

An attempt to characterize arthropod community composition was made in four additional sites representing each time since fire x habitat combination (Fig.1). In each site I installed four depot pairs as described above and placed four pitfall traps (plastic urinalysis cups)

around each depot pair maintaining a distance of one meter between depots and traps (N=16 traps). Traps were placed flush with the soil surface and one-third of each trap was filled with propylene glycol to maintain the specimens. Traps were left in situ for 10-12 days coinciding with seed presentation periods.

Statistical analysis

Vegetation and substrate measurements were analyzed separately using a linear mixed model, with time since fire, habitat, and time since fire x habitat as fixed effects and burn block nested within time since fire as a random effect (PROC MIXED, SAS Institute 2011). I tested for simple main effects of each fixed factor in the interaction using the Slice statement.

Seed removal percentages were measured for each individual species. To analyze the main effects and interactions of habitat type, time since fire, depot type, and species on post-dispersal seed removal percentages, I constructed a generalized linear mixed model (GLMM) in SAS using the PROC GLIMMIX procedure (SAS Institute 2011). This procedure allows for the analysis of mixed models with non-normal response variables by modeling specific distribution structures (Bolker et al. 2009). I 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. I 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, I 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. Five random statements were included in the final model: burn block(time since fire), habitat x burn block(time since fire), plot x habitat x burn block(time since fire), depot pair x plot x habitat x burn block(time since fire), and depot type x depot pair x plot x habitat x burn block(time since fire). I tested for differences in seed removal percentages among different levels of fixed effects using least square means tests and a Tukey's correction for multiple comparisons. For significant interactions, I evaluated simple main effects, which are the effects of specific levels of main effects within interactions, using the Slice statement.

Results

Vegetation structure

Understory cover differed significantly with habitat type (Fig. 2). Cover was 57% higher in ecotone than upland habitat, averaging 54.7 ± 3.32 SE% and 34.84 ± 4.29%, respectively ($F_{1, 13.9}$=14.9, *P*=0.002). There was a trend for higher understory vegetation cover in ecotone habitats with time since fire, but this difference was not significant (Fig. 2).

Litter depth also varied with habitat type. On average, litter depth was 50% higher in ecotone than upland habitat (mean ± SE; 2.11 ± 0.34% and 1.41 ± 0.26%, respectively) ($F_{1, 27.5}$=5.55, *P*=0.026). 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 (2.65 ± 0.25 cm and 0.75 ± 0.13 cm, respectively) ($F_{1, 27.5}$=41.439, *P*<0.001). The effect of time since fire on litter depth did not vary with habitat type (Fig. 2).

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 8.81% in November and 8.65% in December. Several depots were damaged (six in November and one in December) making seeds irretrievable and counts impossible.

Seed removal varied considerably with habitat type (Table 2). In November, seed removal was 85% higher in ecotone than upland habitat (7.79 ± 1.19 SE % and 4.21 ± 0.72%, respectively). In December, the contrast between habitat types increased, with 218% higher seed removal in ecotone than upland habitat (8.34 ± 1.60% and 2.62 ± 0.56%, respectively) (Table 2).

Time since fire did not consistently affect seed removal during either presentation period (Table 2). Mean seed removal in plots that were three growing seasons post-fire was 5.71 ± 0.88% in November and 5.05 ± 0.96% in December. Mean seed removal in plots that were one growing season post-fire was 5.78 ± 0.98% in November and 4.40 ± 0.96% in December. There was no interaction between time since fire and habitat (Table 2).

Seed removal varied among species within habitat and by depot types; mean seed removal ranged from 0.46% to 33.9% in November and 0.25% to 42.8% in December. Overall differences in removal rates among species were During both presentation periods Overall, *E. umbellata,* the smallest seeded species, had the highest percentage removal, much greater than and followed by *A. julibrissin, T. sebifera,* and *M. azedarach* in November, and *T. sebifera, A. julibrissin,* and *M. azedarach* in December (Table 3). However, the magnitude of seed removal for each species depended on habitat type (Table 2).

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Seed removal of individual species also depended on time since fire, but only for the December presentation (Table 2). In December, *T. sebifera* removal was 114% higher in plots that were three growing seasons post-fire than in plots that were one growing season post-burn ($6.10 \pm 1.26\%$ and $2.85 \pm 0.76\%$, respectively) ($F_{1,65.16}=5.14$, $P=0.027$). There was also a significant three-way interaction between time since fire, habitat type, and species in December (Table 2). Other species also showed a trend for higher seed removal with increasing time since fire in ecotones, but these differences were not significant (Fig. 3).

The granivore community had a strong effect on seed removal. Seed removal from depots that allowed only arthropods access was appreciably lower than from depots that allowed both arthropods and small vertebrates' access. On average, seed removal from arthropod only depots was 3.63 ± 0.56 SE% in November and $1.87 \pm 0.37\%$ in December. However, the effect of depot type depended on habitat type (Table 2). Within upland habitat, removal was 83% higher in arthropod and small vertebrate than arthropod only depots in November ($F_{1,581.1}=6.21$, $P=0.013$) and 145% higher in December ($F_{1,563.5}=9.02$, $P=0.003$) (Fig. 4). Within ecotone habitat, mean removal was 227% higher in arthropod and small vertebrate than arthropod only depots in November ($F_{1,325.8}=36.1$, $P<0.001$) and 1247% in December ($F_{1,404.7}=107$, $P<0.001$) (Fig. 4). The effect of depot type also varied with species (Table 2). In November, *E. umbellata* experienced similar amounts of removal in both depot types, whereas the three other species experienced higher removal in arthropod and vertebrate depots, than arthropod only depots ($P<0.001$ for *T. sebifera* and *M. azedarach*; $P=0.057$ for *A. julibrissin* (Fig. 5). In December removal was substantially higher for all species within arthropod and small vertebrate relative to arthropod only depots (all species: $P<0.001$) (Fig. 5).

There were significant three-way interactions between habitat, depot type and species (Table 2). Within arthropod only depots, percentage removal of *E. umbellata* seeds was 117% higher in ecotone than upland habitat during the November presentation ($F_{1, 70.89}$=13.3, *P*<0.001) (Fig. 6); in December, the difference in the percentage of *E. umbellata* seeds removed from arthropod only depots between habitat types was not significant (Fig. 7). In November, within arthropod and small vertebrate depots, percentage removal was higher in ecotone than upland habitat by 370% for *M. azedarach* ($F_{1,196.7}$=21.2, *P*<0.001) and 304% for *A. julibrissin* ($F_{1,175.7}$=17.8, *P*<0.001) (Fig. 6). In December, within arthropod and small vertebrate depots, percentage removal was higher in ecotone than upland habitat by 1612% for *M. azedarach*, 832% for *T. sebifera*, 456% for *A. julibrissen*, and 148% for *E. umbellata* (all species: *P*<0.001) (Fig. 7). The greatest differences in removal by species between habitat types were in December, within arthropod and small vertebrate depots (Fig. 7).

Arthropod community

Prenolepis imparis (false honey ant) was the most abundant species collected in the pitfall traps. In upland plots, I found an average of 5.09 ± 1.07 SE individuals in November and 3.50 ± 1.55 individuals in December. In ecotone plots, I found an average of 8.0 ± 4.58 individuals in November, and no individuals in December. I also found one ant from the *Formicinae* subfamily/*Formica* genus and one ant from the *Myrmicinae* subfamily/*Monomorium* genus in ecotone habitat in November.

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 exotic woody seed removal varies spatially due to fire-induced heterogeneity in vegetation structure or have evaluated the factors that influence this relationship. Here, I found that habitat type (defined by plant community), exotic species, and granivore community strongly affected seed removal, as well as modulated 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 which allowed small vertebrates and arthropods access showed more than twofold higher removal than depots that only allowed arthropods access, indicating that small vertebrates were more effective at removing seeds of the focal species. These findings suggest that ecotone habitat supporting small vertebrate granivores experiences greater post-dispersal seed removal than upland habitat, particularly as time since fire increases and vegetation recovers. Such habitat-associated differences in removal, together with seed selection, may contribute to spatial variation in the successful establishment of exotic invaders in fire-dependent longleaf pine savannas.

Fire is an integral process that 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 indicate that pre-existing differences in vegetation associated with habitat type and length of time since fire contribute to spatial heterogeneity in vegetation cover 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 cover three growing seasons post-fire than one. Previous studies conducted in longleaf pine ecosystems

demonstrate that vegetation cover increases with time post-fire (e.g. Dwire and Kauffman 2003; Kirkman et al. 2004; Myers 1985; Myers and White 1987). In addition to greater moisture levels (Drewa et al. 2002), specialized root structures of fire-tolerant plant species (Abrahamson 1984), and larger plant size at time of burn (Rebertus et al. 1989), have been found to aid in vegetation recovery post-fire in the longleaf pine ecosystem.

Seed removal patterns strongly reflected habitat-associated differences in post-fire vegetation cover and recovery. For example, I 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 one species, it indicates that even the short three-year interval between fires in the study system can create ecologically significant differences in habitat structure that influence vertebrate granivore activity. These results are consistent with those of other studies showing higher seed removal by mammalian granivores with greater vegetation cover (e.g. Alcantara et al. 2000; Hulme 1994; Mittelbach and Gross 1984), 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). In addition to lower predation rates, habitats may be at greater risk to exotic plant invasion directly after fire as the consumption of vegetation and litter by fire increase the availability of microsites for germination (Noemi-Mazia et al. 2001). As such, the riskiest time for ecotone habitats for potential exotic woody plant invasion may be directly post-fire because, during this time, my results suggest they also experience lower seed removal. Invasion success has been found to be influenced by small differences in seed removal percentages between treatments, even as low as the low teens (Nunez et al. 2008).

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 rodents (Alcantara et al. 2000), and both arthropods and rodents (Carrillo-Gavilan et al. 2010). However, as seed size did not consistently predict removal, other seed traits may have influenced removal percentages. *M. azedarach* and *E. umbellata* were presented within their endocarp, and seed strength, impacted by seed thickness, has been shown to affect seed selection in granivores (Lundgren and Rosentrater 2007). Chemical defenses also vary among plant species to deter vertebrate granivores, which respond strongly to visual and olfactory signals (Janzen 1971). *A. julibrissin* seeds contain cyandin 3-glucoside (Ishikura et al. 1978), and *M. azedarach* seeds contain hexane and ethanol (Mikolajczak and Reed 1987). Indeed, *M. azedarach* and *A. julibrissin*, showed lower removal percentages 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 and MacMahon 1985). *T. 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 in December during the day (9.0 °C and 11.2 °C, respectively) and night (11.8 °C and 14.5 °C, respectively), the lower removal rate could potentially have been due to restrictions in arthropod movement (Pelini et al. 2011), or granivorous activity (Davis and Raghu 2010). As seed removal

from depots allowing only arthropod access did not differ by habitat type or time since fire, an effect of understory vegetation cover and litter depth associated with habitat type and time since fire was not detected to be a significant barrier to overall arthropod granivory (Denham 2008). However, owing to the broad range of potential granivore arthropods, and the limited sampling done, the pattern may have been obscured by lack of power for a detection of this effect. Within the pitfall traps, the predominant ant species found, *Prenolepis imparis,* utilizes secretions and exudates for food, while the less common *Monomorium* utilize seeds as a major food source (Fisher and Cover 2007). Individual *Monomorium* ants were only trapped in November, in ecotone sites and indeed, removal percentages were lower in arthropod only depots in December than November. Arthropods primarily removed *E. umbellata* seeds, which are smallest of the four species. Arthropods are more restricted in seed transport capabilities than small vertebrates, and at 0.014 g, *E. umbellata* is heavy for arthropod removal (Lundgren and Rosentrater 2007; MacMahon et al. 2000).

My results suggest that small vertebrates are the primary seed removers during the fall in the longleaf pine ecosystem consistent with evidence of vertebrates as the primary granivores in ecosystems experiencing frequent fire (Auld and Denham 2001; Botha and Le Maitre 1992; Broncano et al. 2008; Reed et al. 2004; Schnurr and Collins 2007), and of woody species (Diaz et al. 1999; Ostfeld et al. 1994, 1997; Plucinski and Hunter 2001; Webb and Willson 1985; Whelan et al. 1991). The depot design limits inference to small vertebrates, presumably rodents, and while birds were not explicitly excluded from either depot type, the lid likely prevented their foraging (Mattos and Orrock 2010). Not all seeds removed by vertebrates were likely consumed as all of the granivorous vertebrate species known on Fort Bragg, except *Sigmodon hispidus* (Cameron and Spencer 1981), *Sylvilagus palustris* (Chapman and Willner 1981), and

Reithrodontomys humulis (Stalling 1997), exhibit flexible feeding patterns with scatterhoarding or caching traits. Depots which allowed small vertebrate access exhibited higher seed removal in ecotone habitat than upland, consistent with studies showing comparatively greater seed removal in areas with greater vegetative cover (Caccia et al. 2006; Myster and Pickett 1993; Perez-Ramos et al. 2008; Webb and Willson 1985), presumably due to the protection from predators afforded by vegetation structure (Bowers and Dooley 1993; Diaz et al. 1999; Whelan et al. 1991). The December presentation showed the most pronounced effect of allowing vertebrate granivores access, potentially due to dwindling food resources (Haught and Myster 2008; Holmes and Froud-Williams 2005).

For exotic invaders, escaping post-dispersal seed removal is just the first step in the establishment process, with germination success further influenced by intrinsic seed traits, and ecosystem properties (Theoharides and Dukes 2007). Seed removal does not necessarily equate to predation as seeds may be dispersed or cached (Vander Wall 1994; Vander Wall et al. 2005). However, there is overwhelming evidence that post-dispersal seed removal can negatively affect woody plant establishment and demography by decreasing the number of viable seeds that are available to establish in suitable sites (Nunez et al. 2008; Ostfeld et al. 1997; Santos and Telleria 1997; Zwolak et al 2010), when populations are limited by seeds rather than microsite availability (Turnbull et al. 2000; Orrock et al. 2006). With greater nutrient reserves for seedling development, large seeds escaping post-dispersal removal may have a competitive advantage over small seeds (Foster and Janson 1985), especially in light-limited environments such as deep litter (Turnbull et al. 1999). Seeds in sites unsuitable for germination are likely never to establish, therefore their removal is unlikely to affect plant recruitment (Maron and Simms 1997).

Germination may be suppressed through interspecific competition from dense woody and herbaceous understory layers (George and Bazzaz 1999; Royo and Carson 2008).

Although seed fate was not followed in this study, studies documenting invader establishment can provide insight into the role of seed removal for exotic invasion within the longleaf pine ecosystem. Each of the focal exotic woody 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 in the longleaf pine ecosystem (Drew et al. 1998; Herring and Judd 1995; Munger 2003; Renne et al. 2000). While time since fire likely differed between these studies, these findings suggest that seeds of all four species escaping post-dispersal predation have the potential to germinate in both upland and ecotone habitat structures.

Overall, my results indicate that in the first growing season post-fire, ecotones may be more vulnerable to exotic invasion by *E. umbellata, T. sebifera,* and *M. azedarach*, because of the presumed reduced activity of small vertebrates. Exotic woody seed removal percentages were heterogeneous due to numerous influencing factors. Assuming that these findings hold for the duration of the winter season, this suggests that there are potentially predictable sites offering escape from seed predation in this ecosystem. Generalizations about the ultimate role of any process in generating pattern, is 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 woody exotic species, and for increasing our greater understanding of invasion dynamics.

Conclusion

Conclusions

The sustained functioning of the fragmented and endangered longleaf pine ecosystem is threatened by the invasion and encroachment of exotic woody species (D'Antonio 2000; Menges et al. 1993). Woody encroachment can alter fuel loads and abiotic conditions impacting the frequent, low-intensity ground fires promoted by *P. palustris* and *A. stricta* (Provencher et al. 2000), and the high levels of plant diversity found in the understory (Hiers et al. 2007). In fire dependent ecosystems, seed removal by granivores may influence patterns of exotic woody invasion, yet few studies have examined how seed removal varies with time since fire, or have evaluated the factors that influence this relationship.

In this study, habitat and seed species played an important role in determining seed removal, as well as modulated the relationship between seed removal and time since fire in pine savannas. Although the interval between fires is only two growing seasons, seed removal within habitats, particularly ecotone appeared to be influenced by time since fire. Findings from this study suggest that ecotone habitats supporting small vertebrate granivores experience greater seed removal than upland, particularly as time since fire increases and vegetation recovers. Conversely, ecotone habitats may be more vulnerable to exotic invasion immediately following fire because of lower seed removal and potentially more amenable conditions for recruitment. Such habitat-associated differences in removal, together with seed selection, may contribute to variation in the success of exotic invaders in fire-dependent savannas. Understanding heterogeneity in seed removal resulting from multiple abiotic and biotic factors may help inform management of natural savanna ecosystems.

Future Work

As only seed removal and not seed fate was measured in this study, the relative strength to which removal influences future population establishment was not determined. Following seed fate through to germination would aid interpretation of the impact of granivores on exotic recruitment and establishment, in particular on woody invasive species (e.g. Nunez et al. 2008). A caveat to seed selection in this study is that by perching seeds on a layer of sand to mimic recent deposition, I can only infer seed fate on the soil or litter surface. A longer presentation period may have resulted in greater removal and the exaggeration or convergence of treatment effects as over time seeds may become buried, depleting visual and olfactory cues and decreasing the probability of removal (Hulme and Borelli 1999). As litter depth increases with time since fire, additional studies to determine the influence of seed burial on removal may provide even more insight to the impact of fire on exotic seed removal.
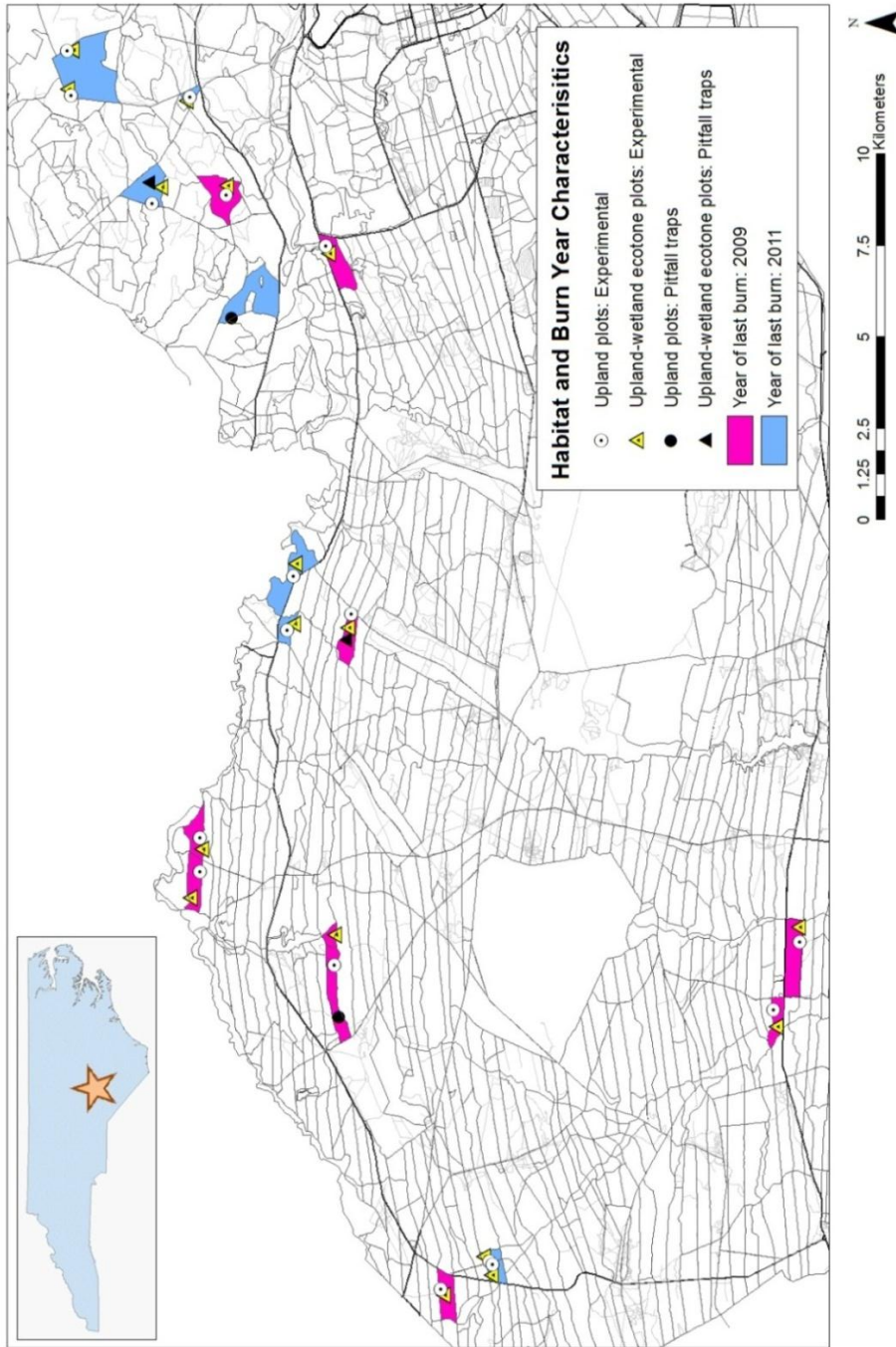
Figure 1. Locations of 34 experimental seed removal plots, and 4 pitfall trap plots established at Fort Bragg, North. Plots are in ecotone and upland habitats within 16 burn blocks last experiencing prescribed fire either one or three growing seasons prior to 15 day presentation periods in November and December 2011.

Table 1. Attributes of the four exotic woody species for which seed removal was examined.

	Albizia julibrissin	Elaeagnus umbellata	Melia azedarach	Triadica sebifera
Common Name	Mimosa (silktree)	Autumn olive	Chinaberry	Chinese tallow tree
Form	Deciduous; Tree	Deciduous; Shrub	Deciduous; Tree	Deciduous; Tree
Height (feet)	10-50	10-16	30-50	24-35
Fruit Type	Legume pod	Drupe	Drupe	Capsule
Start Bearing Fruit By Year	Unknown	3-5	3-4	3-8
Seeds Mature	August/ September	September/ November	September/ October	September/ October
Average number of seeds produced	8,000	66,000	10,000	45,000
Able to produce a seed bank	Yes – for 70-150 years	Not likely	Yes - short lived	Yes – up to 7 years
Dispersal Mechanism	Wind, water, maybe animals	Avian, small mammals	Avian, gravity, potentially water	Avian, gravity, water
Suitable seed handling for germination	Scarification required	Fruit removed, enhanced by cold stratification	Fruit removed, enhanced by cold stratification for 1-3 months	Enhanced by temperature fluctuation
Habitat Preference	Full sun, tolerates shade, prefers disturbed areas	Full sun, prefers disturbed areas	Full sun, tolerates partial shade	Tolerates shade and disturbance
Establishment promoted by disturbance?	Yes	Yes	Yes	Yes
Found in upland areas?	Yes	Yes	Yes	Yes
Found in mesic areas?	Yes	Yes	Yes	Yes
Able to resprout post-fire?	Yes	Yes	Yes	Yes
Citation	Meyer 2010	Munger 2003	Waggy 2009	Meyer 2011

Table 2. Results from the significance testing of the November and December seed presentation by main effects and interactions.

	November Seed Presentation				December Seed Presentation			
	Num df	Den df	F	P	Num df	Den df	F	P
Main Effects								
Habitat	1	41.5	7.15	**0.011**	1	35.3	16.2	**<0.001**
Time since fire	1	41.5	0.0	0.96	1	35.3	0.23	0.64
Species	3	1032	229.	**<0.001**	3	1051	149.2	**<0.001**
Depot type	1	447	33.4	**<0.001**	1	481	84.8	**<0.001**
Interactions								
Species x habitat	3	1032	7.75	**<0.001**	3	1051	3.34	**0.019**
Species x time since fire	3	1032	0.62	0.60	3	1051	4.62	**0.003**
Species x habitat x time since fire	3	1032	0.02	0.99	3	1051	3.53	**0.014**
Depot type x habitat	1	447	3.90	**0.049**	1	481	22.9	**<0.001**
Depot type x species	3	1032	15.0	**<0.001**	3	1051	14.1	**<0.001**
Depot type x habitat x species	3	1032	10.1	**<0.001**	3	1051	6.78	**<0.001**
Time since fire x habitat	1	41.5	0.1	0.76	1	35.3	1.34	0.25
Time since fire x depot Type	1	447	3.86	**0.050**	1	481	0.03	0.86
Time since fire x habitat x depot type	1	447	1.49	0.22	1	481	0.37	0.55
Time since fire x depot type x species	3	1032	3.18	**0.023**	3	1051	3.52	**0.015**
Time since fire x habitat x depot type x species	3	1032	2.23	0.083	3	1051	1.54	0.20

Table 3. Mean (± SE) seed removal of the individual species presented in seed removal depots. Minimum – maximum width and length ranges, and average weight, width, and length values are reported for each species. Species are organized in order of increasing size. *Elaeagnus umbellata, Albizia julibrissin*, and *Triadica sebifera* size values are all reported for seeds. *Melia azedarach* and *E. umbellata* seeds were presented still enclosed in the protective endocarp.

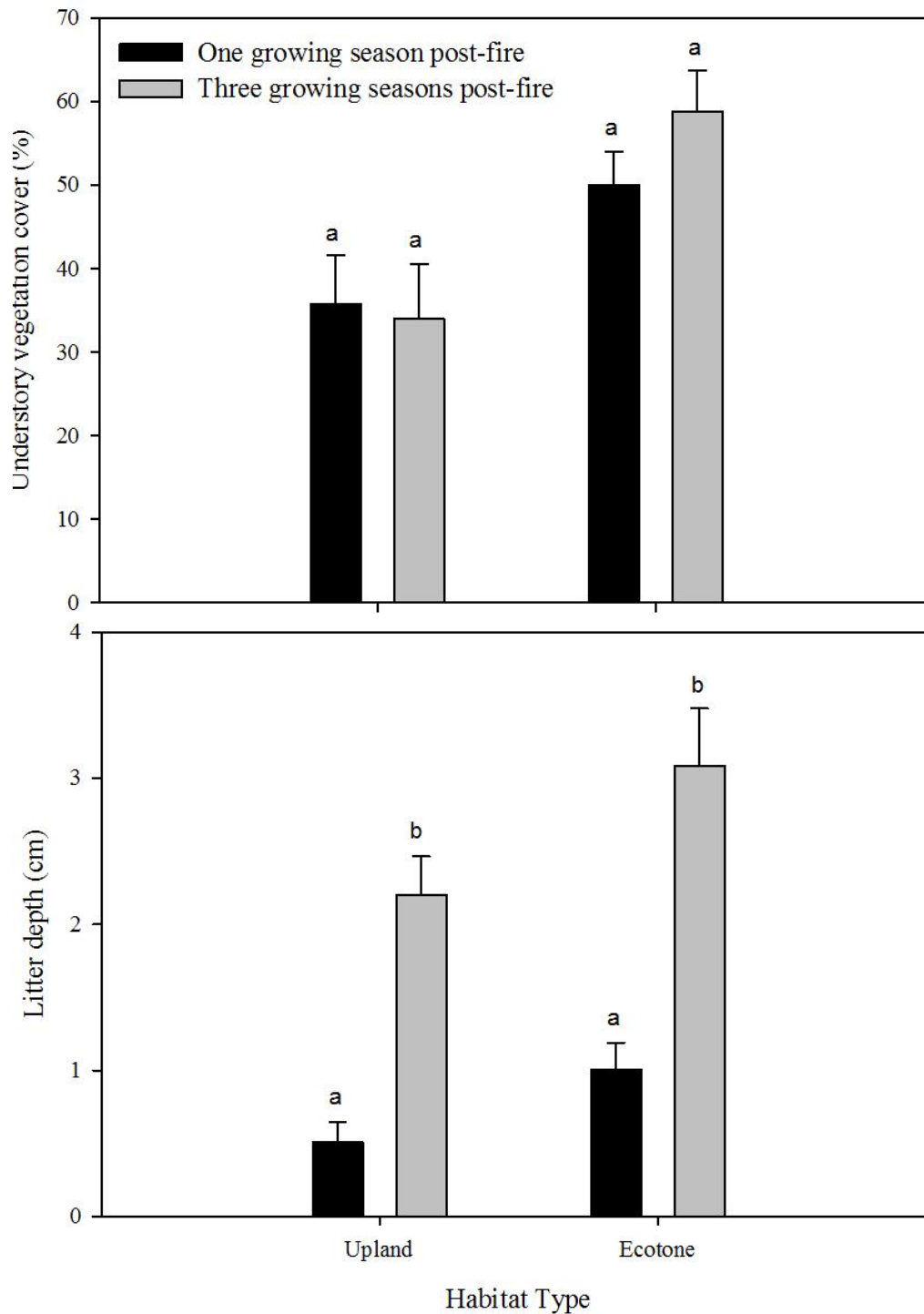|	Avg. removal (%) November	Avg. removal (%) December	Avg. seed weight (g)	Width min-max – avg. (mm)	Length min-max – avg. (mm)
Species					
Elaeagnus umbellata	24.7 ± 2.18	19.5 ± 2.25	0.014	1.5-2.0 (2.0)	4.0-7.0 (5.5)
Albizia julibrissin	4.41 ± 0.60	3.76 ± 0.61	0.037	2.0-5.0 (3.1)	4.0-9.0 (6.7)
Triadica sebifera	3.84 ± 0.55	4.18 ± 0.70	0.116	3.0-8.0 (5.3)	5.0-10.0 (7.2)
Melia azedarach	2.23 ± 0.45	1.44 ± 0.37	0.395	5.0-11.0 (8.4)	5.0-12.0 (9.0)

Figure 2. Mean (± SE) litter depth and understory vegetation cover in upland and ecotone habitats one or three growing seasons after prescribed fire. Lower-case letters represent statistically significant differences (*P*≤0.05) within habitat types between time since fire.
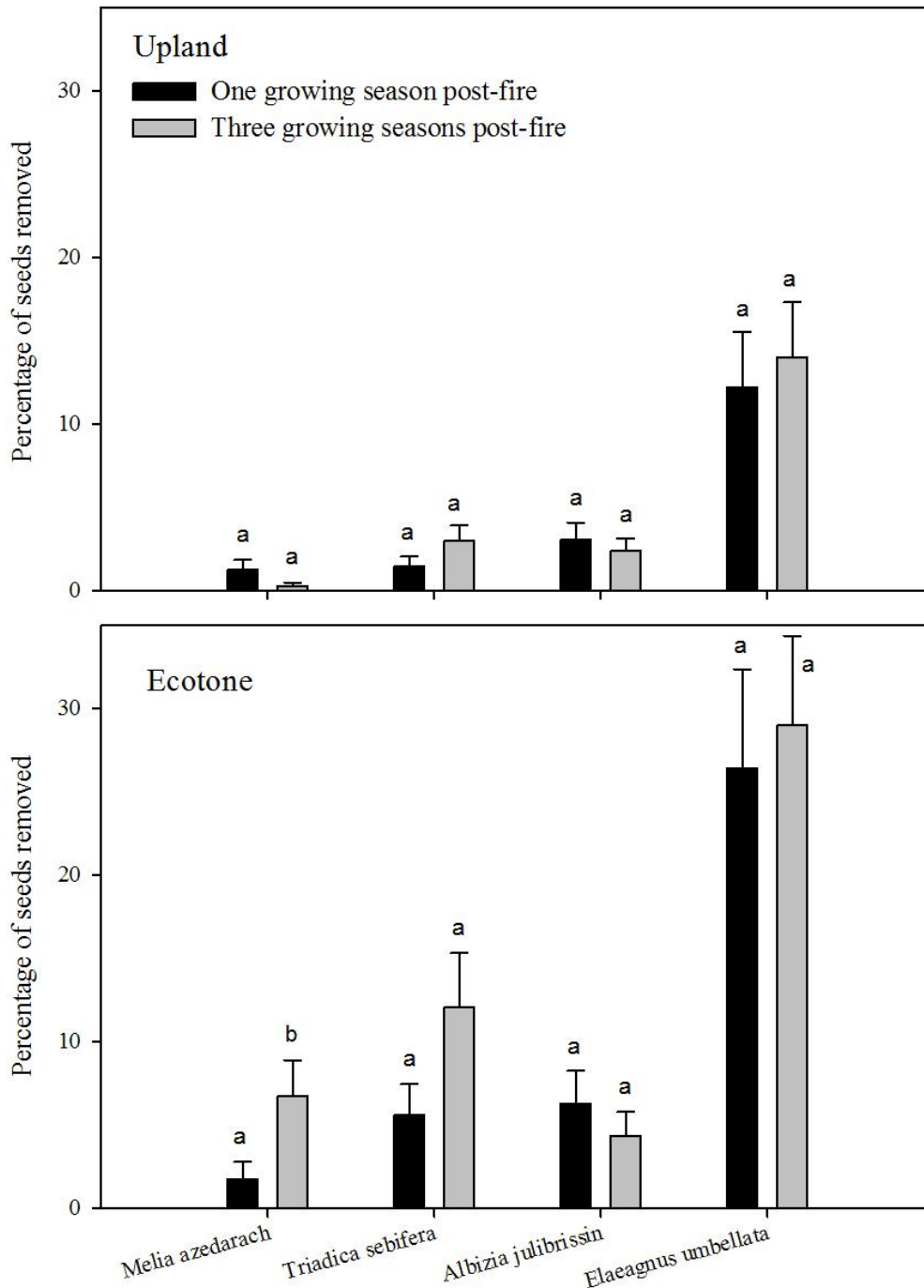
Figure 3. Mean (± SE) seed removal in December by species, from seed depots placed in sites one or three growing seasons post fire in upland and ecotone habitats. Individual species are ordered by decreasing seed size. Lower-case letters represent statistically significant differences ($P{\leq}0.05$) within species between sites one or three growing seasons since fire, by habitat type.
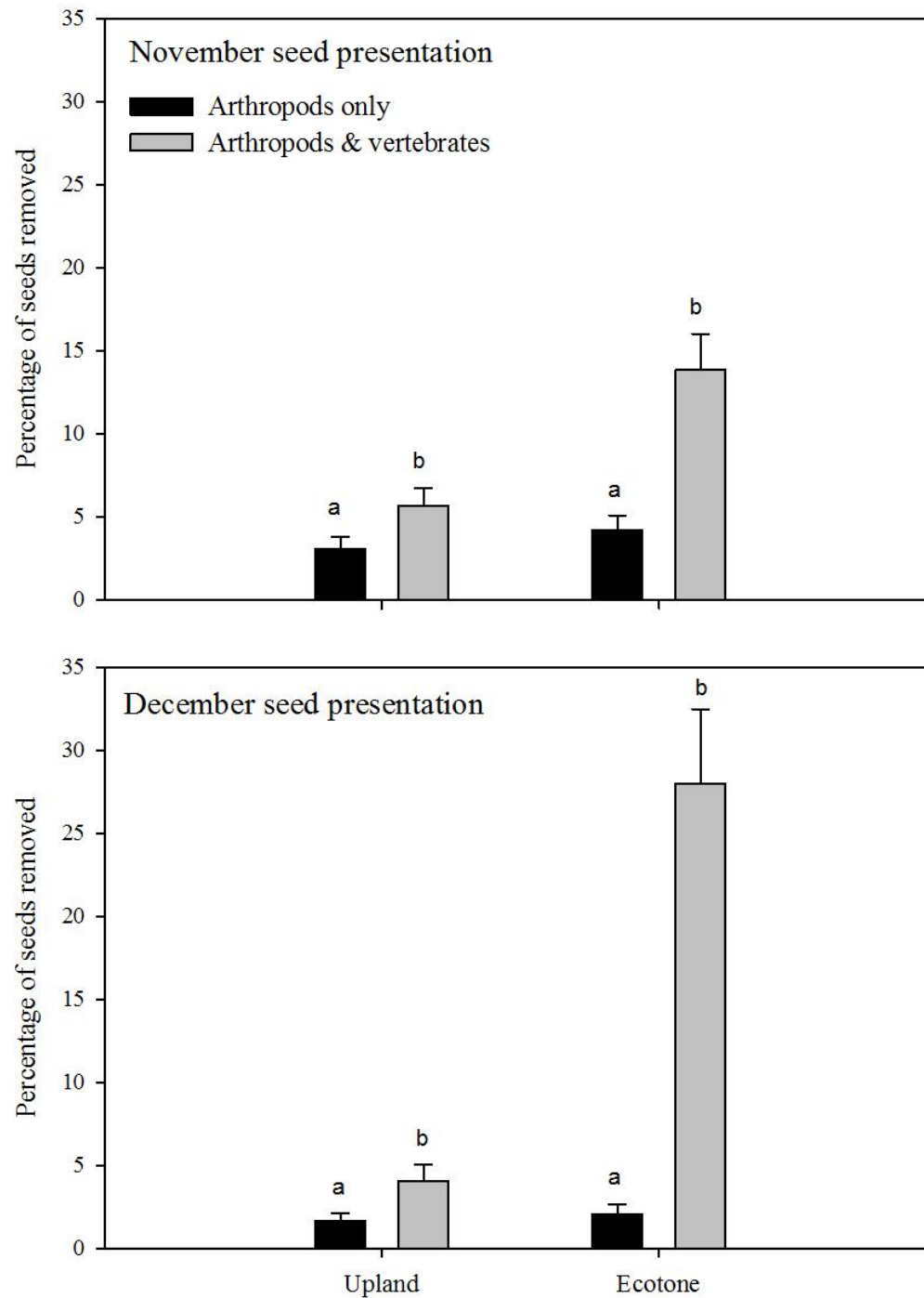
Figure 4. Mean (± SE) seed removal from seed depots allowing only arthropods or arthropods and vertebrates placed in ecotone and upland habitats during the November and December presentation periods. Lower-case letters represent statistically significant differences (*P*≤0.05) within habitat types between depot types.
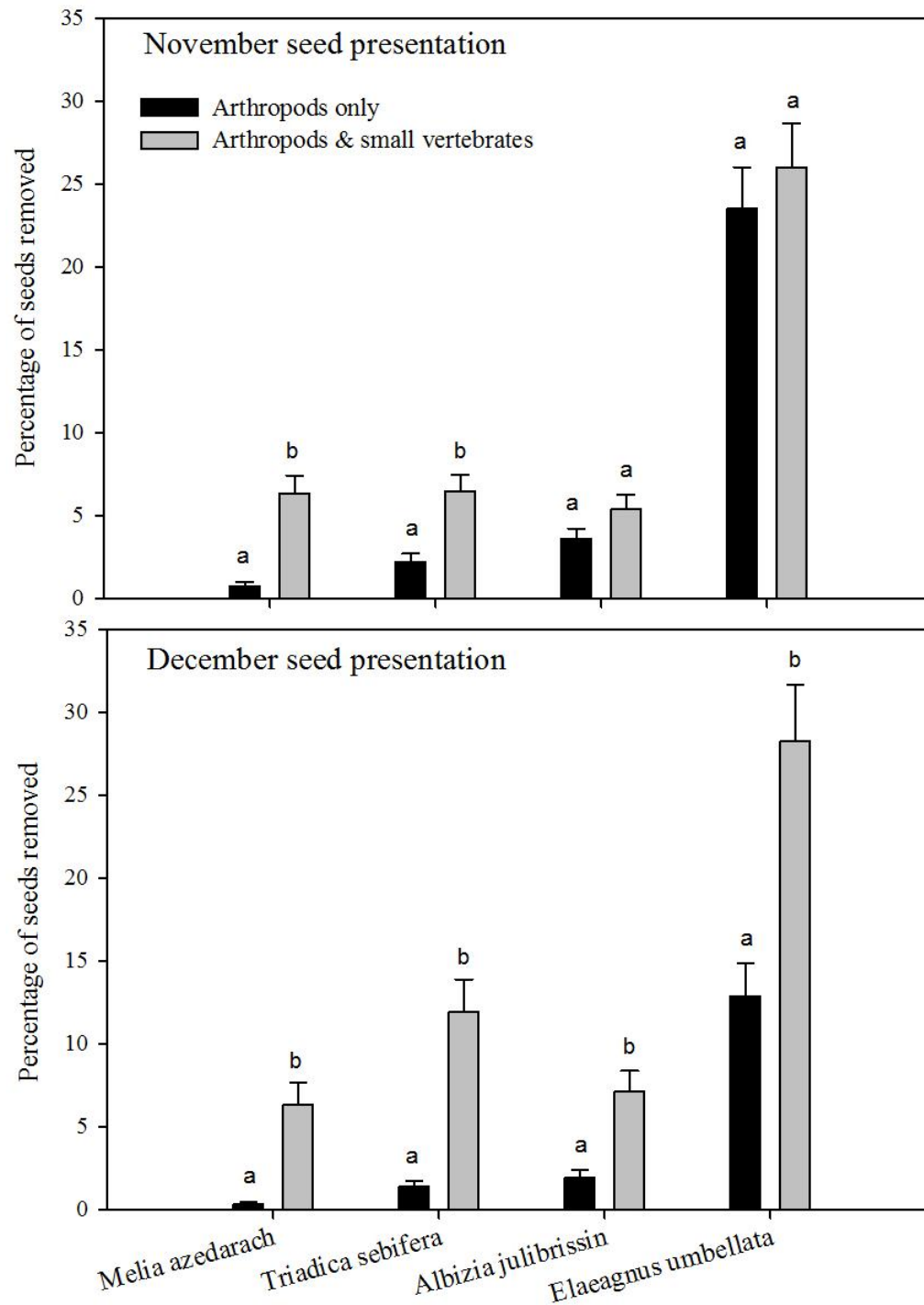
Figure 5. Mean (± SE) seed removal by species from seed depots allowing only arthropods or arthropods and vertebrates placed during the November and December presentation periods. Lower-case letters represent statistically significant differences ($P \leq 0.05$) within species between depot types.
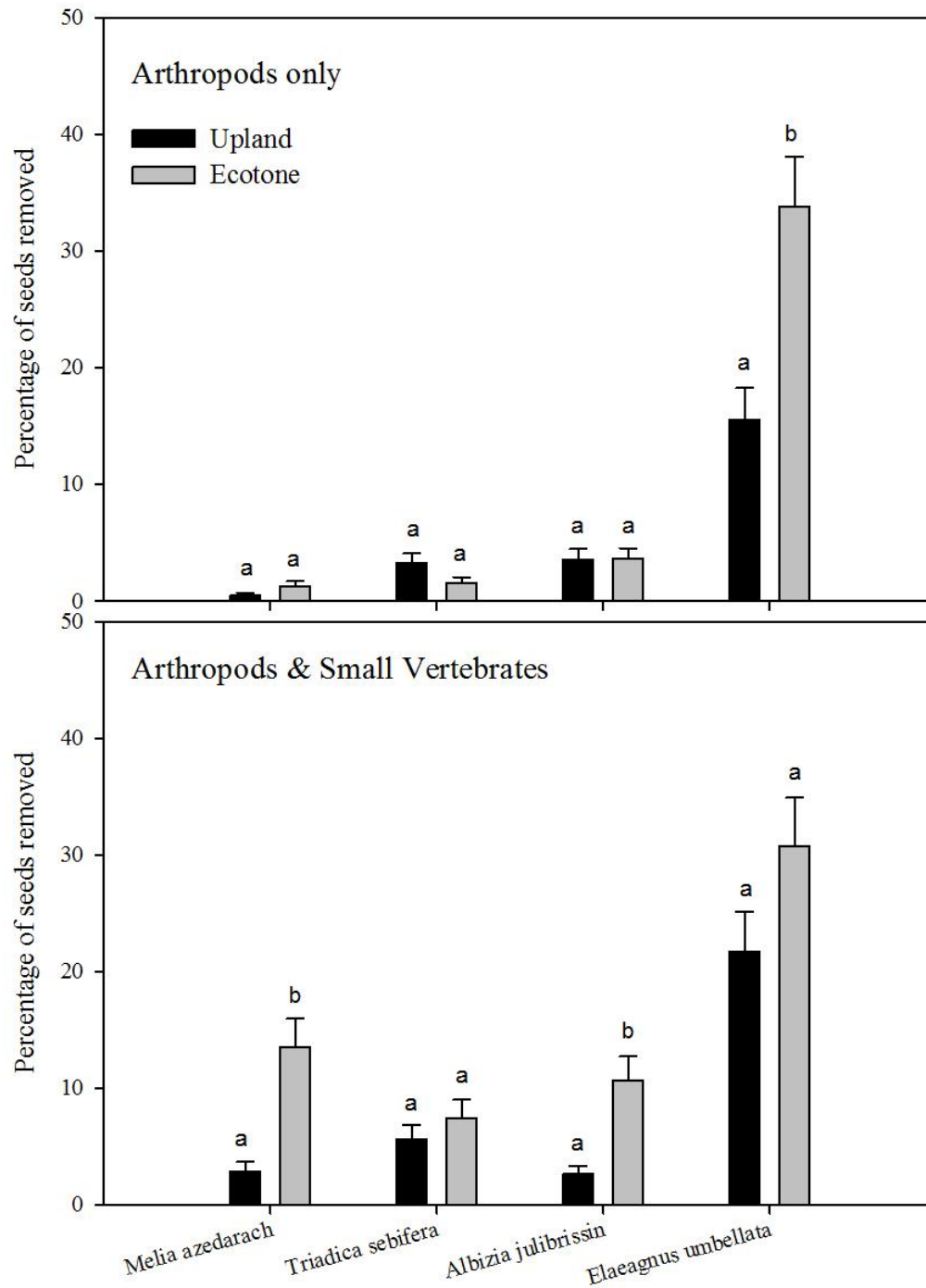
Figure 6. Mean (± SE) seed removal in November by species, from arthropod only and arthropod and small vertebrate depots placed in ecotone and upland habitats in forests. Individual species are ordered by decreasing size. Lower-case letters represent statistically significant differences ($P \leq 0.05$) within species between habitat types, by depot type.
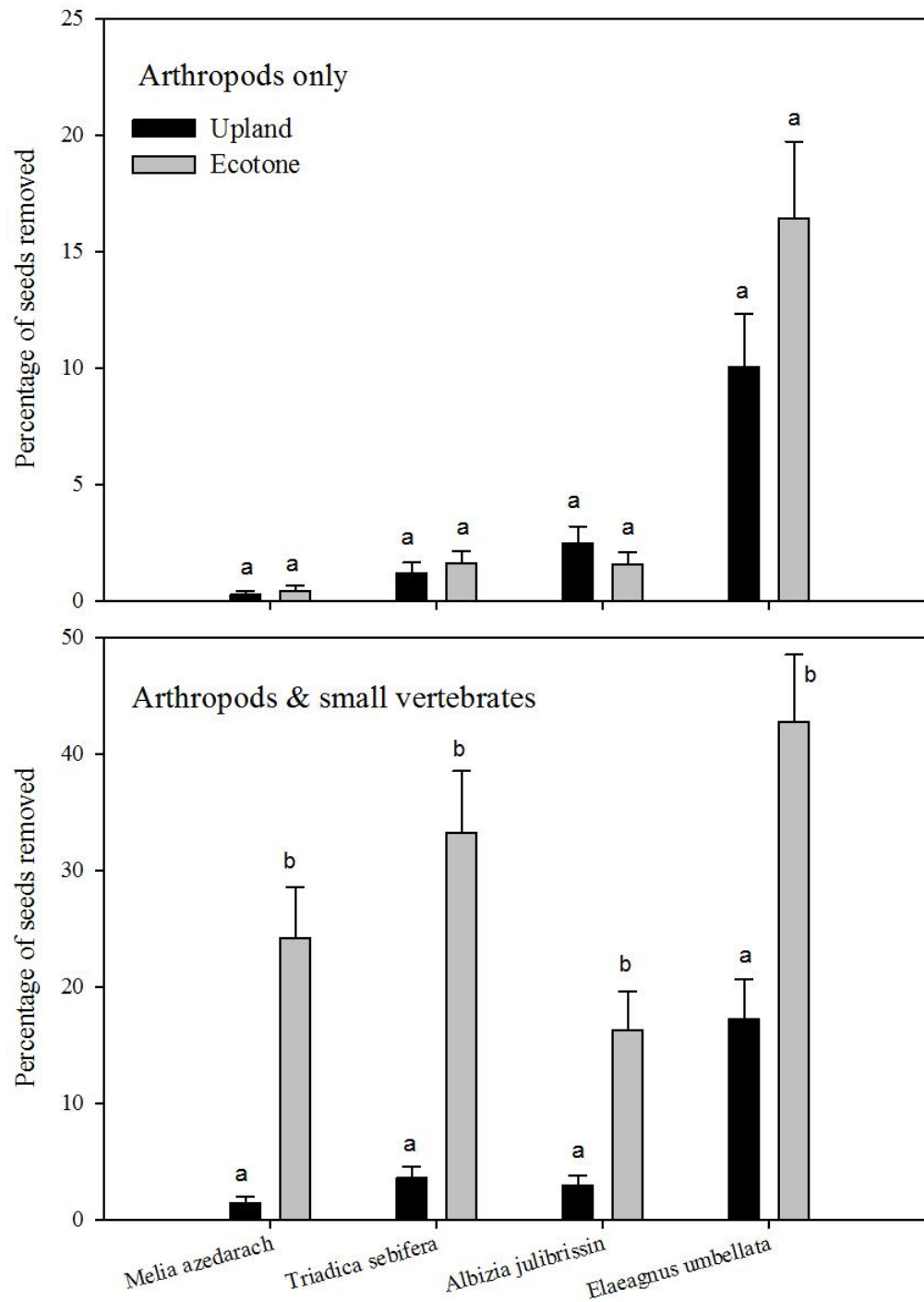
Figure 7. Mean (± SE) seed removal in December by species, from arthropod only and arthropod and small vertebrate depots placed in ecotone and upland habitats. Individual species are ordered by decreasing size. Lower-case letters represent statistically significant differences (*P*≤0.05) within species between habitat types, by depot type.

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