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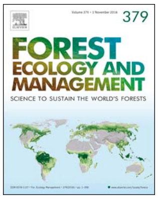

Invasibility of a fire-maintained savanna–wetland gradient by non-native, woody plant species

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ABSTRACT

Fire-promoting, open-canopy ecosystems are under threat of conversion to a fire-deterring, closed-canopy condition due to woody encroachment. This conversion of vegetation structure has been fostered by introduced woody plant species. We performed a field experiment to quantify growth, survival, and establishment success of six invasive, woody species along a managed longleaf pine savanna–wetland gradient in the Sandhills of North Carolina, USA. We investigated the effects of prescribed fire, fire history, dispersal, and abiotic conditions on the invasibility of sites along the gradient. Across 18 study sites, seeds of the six woody species were sown using three sowing methods that mimicked primary and secondary dispersal; each site contained paired plots located in savanna and savanna-wetland ecotone vegetation communities. We identified sowing treatment, abiotic conditions, seedling size, and prescribed fire as important factors for controlling woody invasion, as they prevented 5 of 6 study species from establishing in the landscape. However, the landscape was not immune to invasion. At the end of the 42-month study period, three species had established in unburned sites. In sites burned after seedling emergence, only one species, *Pyrus calleryana*, survived and established. We found *P. calleryana* survival and establishment to be a function of seedling size, soil humic matter content, and sowing treatment. Successful invasion and establishment of woody individuals in open-canopied systems increases the likelihood of fire-deterrence and further woody encroachment, threatening ecosystem integrity.

1. Introduction

Encroachment of trees and shrubs on open-canopied plant communities can alter ecosystem processes, species distributions, and biodiversity (Eldridge et al., 2011; Ratajczak et al., 2012). Possible causes of woody plant encroachment include CO_2 enrichment, nitrogen deposition, fire suppression, overgrazing, climate change, and non-native species invasions (Bond and Midgley, 2012; Kulmatiski and Beard, 2013; Van Auken, 2009). Woody plant encroachment of open-canopied communities modifies vegetation structure and, left unchecked, can result in canopy closure. Canopy closure alters understory environmental conditions and promotes woody vegetation through mechanisms that may ameliorate physical stresses, reduce competition from grasses, and reduce flammability (Smith and Johnson, 2004; Van Auken, 2009). Once the transition is made from an open- to closed-canopy structure, it is often difficult to return to an open-canopied community even after reversing the conditions that created the transition, due to hysteresis (Nowacki and Abrams, 2008; e.g., Wilson and Agnew, 1992).

Periodic disturbances that reduce the dominance of woody plants are important phenomena for maintaining open habitats. These disturbances also present opportunities (e.g., nutrients, gaps) and challenges (e.g., damage, death) for plant recruitment within landscapes (Grubb, 1988). In pyrophilic ecosystems (i.e. those that persist with reoccurring fire), for example, woody seedling establishment is both directly and indirectly influenced by fire through abiotic effects on seed banks, germination, light availability, nutrient recycling, microclimates, and safe-sites (Bond and Keeley, 2005; Hoffmann, 1996; Keeley, 1987; Lamont et al., 1993) as evidenced by the episodic recruitment of many species in fire-prone systems (Denham et al., 2010; Grubb, 1988). Whether fire can act as an effective filter (i.e. prevent establishment) against non-native woody plants is not well understood (Mandle et al., 2011).

Although fire may enhance establishment of invading species by creating favorable conditions for germination and early seedling growth (e.g., Ne'eman et al., 2004), it can kill seedlings (Gignoux et al., 2009; Green et al., 2010; Huddle and Pallardy, 1999), even those of species that become fire tolerant later in their development (e.g., Grace

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and Platt, 1995; Hoffmann et al., 2012). For such species, seedling size and growth rate should be particularly important because it will influence whether a seedling has stored adequate belowground resources to survive fire by resprouting. And for species that resist fire by avoiding topkill (i.e. loss of aerial biomass), fast-growing seedlings reach fire-resistant sizes quicker (e.g., Stevens and Beckage, 2010). Woody individuals that reach sizes that escape topkill may alter fire behavior and promote further woody encroachment (Grace et al., 2001; Stevens and Beckage, 2009).

Fire and post-fire abiotic factors (e.g., light availability, soil conditions) are undoubtedly important drivers of woody plant demography in pyrophilic systems, yet many biotic processes may also affect species recruitment (Clark et al., 1999). For example, both seed dispersal (Denham, 2008; Parr et al., 2007) and predation have been shown to be influenced by fire (Zwolak et al., 2010). Additionally, wood decay compartmentalization may influence species persistence in pyrophilic systems (Just et al., 2017; Romero et al., 2009). Unfortunately, little information on how these and other processes may influence invasive species dynamics is typically available and identifying their relative influence on seedling establishment is challenging (e.g., Clark et al., 1999).

Wildfire suppression was widely practiced in the United States during the 20th century, and anthropogenically fragmented landscapes have further reduced the extent of burned areas (Duncan and Schmalzer, 2004). Reduced burning of fire-adapted, open-canopied communities has resulted in increased woody encroachment and canopy closure (Nowacki and Abrams, 2008). Importantly, these changes have been accompanied by the arrival of invasive, woody species which can further alter vegetation structure and fire regimes (e.g., Arianoutsou and Vilà, 2012; Mandle et al., 2011). In some landscapes where natural fire regimes have been altered or lost, prescribed fire has been used to prevent native woody encroachment, thereby conserving and restoring pyrophilic communities (Peterson and Reich, 2001; Twidwell et al., 2013). However, the extent to which prescribed fire can inhibit non-native woody encroachment is not well documented (Mandle et al., 2011). Integrated studies of the role of fire relative to other biotic and abiotic factors on invasive species recruitment are needed if it is to be used as an effective management tool.

Here we test invasibility along a gradient from longleaf pine (*Pinus palustris*) savanna to wetland in the southeastern USA by a suite of non-native, woody plants. Longleaf pine ecosystems are dependent on periodic fire disturbance (Chapman, 1932), and are among the most species-rich systems in North America (Noss et al., 2015), but currently occupy 3% of their maximum historical range (Frost, 1993; Simberloff, 1998), with approximately 19% of existing area under active fire management (Stambaugh et al., 2011). Fire is considered important in preventing woody plant encroachment in these systems (Glitzenstein et al., 2012). We performed a field experiment to test the effects of prescribed fire, fire history, seed dispersal, vegetation community, seedling size, and abiotic (soil and light) conditions on non-native species recruitment. We examined growth, survival, and establishment of six woody, non-native, avian-dispersed species that are extant, but currently not abundant in a longleaf pine savanna landscape that is actively maintained with prescribed fire.

2. Materials and methods

2.1. Study site

This study was conducted at Fort Bragg Army installation (73,468 ha), located within the Sandhills physiographic region of North Carolina, USA (35 °07′N, 79 °10′W). The dominant vegetation community at Fort Bragg is longleaf pine savanna (known locally as xeric Sandhill scrub; Schafale 2012) which tends to occur on upland ridges of sandy soils (Sorrie et al., 2006). These sand ridges are remnants of ancient marine coastal features and aeolian processes (Swezey et al., 2016). Some areas of the Sandhills are perched atop a less permeable clay substrate, resulting in the lateral movement of ground water (Oliver, 1978), which exits at lower slopes forming wetlands (known locally as streamhead pocosins and sandhill seeps; Weakley and Schafale, 1991) that are embedded within the savanna landscape matrix (Schafer and Just, 2014).

Mean annual precipitation in the study area is 1275 mm and mean temperature ranges from 6.9 °C in the coldest months to 26 °C in the warmest months (Sorrie et al., 2006). The conditions during the first 12 months following our experimental sowing approximated mean conditions; the precipitation total was 1270 mm, and the mean temperatures for the coldest and warmest months were 7.7 and 25.6 °C, respectively (Ft. Bragg, NC RAWS data station; https://raws.dri.edu). Elevation ranges from 43 to 176 m. The landscape at Fort Bragg has been divided into discrete burn compartments of which one-third burn annually (Schafer et al., 2013), approximating the estimated, historic mean fire frequency (2.2 years) of longleaf pine savannas (Stambaugh et al., 2011). Prescribed fires are started in the upland savanna and allowed to burn downslope towards wetland (Lashley et al., 2014).

2.2. Study species

We studied six avian-dispersed, non-native woody species that are generally considered invasive in the southeastern USA: *Elaeagnus umbellata* Thunb., *Ligustrum sinense* Lour., *Melia azedarach* L., *Nandina domestica* Thunb., *Pyrus calleryana* Dcn., and *Triadica sebifera* (L.) Small (Table 1; nomenclature follows USDA NRCS (2016)). These species have been documented to occur in longleaf pine landscapes in both xeric and mesic communities (Drew et al., 1998; Herring and Judd, 1995; Hohmann et al., 2013; Jenkins and McMillan, 2009; Noss, 2012; Renne et al., 2002). Moreover, each of these non-native species have been found at Fort Bragg, with the greatest abundances in residential and urban areas, where fire is suppressed and some species have been planted ornamentally. Each of the six species resprouts after a topkilling event as adults or established plants (Culley and Hardiman, 2007; Faulkner, 1989; Grace, 1998; Herrero et al., 2015; Miller, 2003). Seeds of each species were bulk-collected from on or near Fort Bragg during November 2011 and then processed according to pre-germination treatments outlined in Bonner and Karrfalt (2008) before sowing (March 2012). Sowing density (Table 1) was based on seed availability and densities of invasive tree seedlings reported in a recent meta-analysis (Delmas et al., 2011).

2.3. Experimental design

This research was performed along gradients between longleaf pine savanna and wetland. Sites were identified from vegetation community and fire history (i.e. number of years since last prescribed fire) GIS data. We first selected burn compartments that contained both longleaf pine savanna and wetland communities. We then selected sites that were scheduled to burn 1, 2, or 3 years after sowing. From this subset, we

Table 1
Woody species used in this experiment.

Species	Common name	Family	No. seeds per subplot
Elaeagnus umbellata Thunb.	autumn olive	Elaeagnaceae	40
Ligustrum sinense Lour.	Chinese privet	Oleaceae	40
Melia azedarach L.	Chinaberry	Meliaceae	40
Nandina domestica Thunb.	nandina	Berberidaceae	25
Pyrus calleryana Dcn.	Callery pear	Rosaceae	30
Triadica sebifera (L.) Small	Chinese tallow tree	Euphorbiaceae	20

selected 18 sites distributed over 134 km^2 of Fort Bragg, with a mean minimum distance of 692 m between sites. All sites were greater than 2 km from any known populations of the six study species, and unlikely to receive any naturally dispersed seeds (Bullock et al., 2017; Vittoz and Engler, 2007).

At each site, we established one rectangular plot (2.5 × 5 m) within savanna and one downslope within the savanna-wetland ecotone. Each plot was divided into 18 circular subplots (diameter: 30 cm) for 648 subplots (six species × three seed sowing treatments) in this experiment. We had three sowing treatments mimicking the range of conditions seeds may be exposed to during emergence: (1) undisturbed, (2) litter removal and undisturbed soil, and (3) litter removal and covered with loose soil. The undisturbed treatment consisted of placing seeds atop existing litter (e.g., pine needles, broadleaves), emulating primary dispersal by birds. The litter removal and undisturbed soil treatment consisted of removing litter and duff to bare soil, emulating litter removal by fire prior to seed arrival. In the final treatment, we removed litter and then covered seeds with 1 cm of loose soil, simulating seed caching (secondary dispersal) (Vander Wall, 1992) by scatter hoarding mammalian granivores in this system (e.g., *Peromyscus gossypinus*, *P. leucopus*, *Sciurus carolinensis*, *S. niger*; JM McCallister, unpublished data). Krall et al. (2014) reported evidence of post-dispersal seed removal and granivory for three of our study species at Fort Bragg. To reduce seed removal and herbivory by vertebrates, we erected steel mesh (1.27 cm^2 mesh size) exclosures for each of our subplots. Assignment of species and sowing treatment to subplots was random.

Five of the study sites were burned in 2013 (1 year after sowing), four were burned in 2014 (2 years after sowing), and eight were burned in 2015 (3 years after sowing). In total, 13 sites were burned and four of these sites burned twice, once in 2013 and again in 2015.

2.4. Field measurements

At the end of the first summer (September 2012), we recorded the number of emerged seedlings per subplot and surveyed the space between subplots for emerged seedlings. At one-year intervals after sowing (May 2013–2015), and again at the end of the study period (September 2015), we counted the number of surviving individuals and measured height and basal diameter of each with digital calipers. For analyses considering seedling size, we calculated the conical stem volume (cm^3) for each individual using stem height and diameter measurements.

In summer 2013 we sampled the surface soil (0–10 cm) of each community plot ($n = 36$). Soil samples were analyzed by the North Carolina Department of Agriculture's Agronomic Division. Soil pH was determined on a 1:1 soil to water volume ratio. Exchangeable acidity (Ac; meq 100 cm^{-3}) was assessed using the Mehlich et al. (1976) method. Percent humic matter was determined with a NaOH digestion and colorimetry (Mehlich, 1984a). Soil amounts of Ca, Cu, K, Mg, Mn, Na, P, and Zn (mg dm^{-3}) were determined with the Mehlich 3 soil text extractant method (Mehlich, 1984b). Cation exchange capacity (CEC; meq 100 cm^{-3}) was calculated as the summation of extractable Ca, K, Mg, and Ac. Base saturation (BS; %) and soil bulk density (g cm^{-3}) were also reported. These soil variables were examined due to their importance for plants in longleaf pine ecosystems (e.g., Christensen, 1977) and to compare the soil properties of savanna and ecotone communities.

Volumetric soil moisture content (0–20 cm) was measured at five locations per community plot four times per year (2012–15) with a HydroSense II soil-moisture sensor (Campbell Scientific, Logan, UT, USA) and recorded as the mean. Canopy cover (%) was estimated with a concave spherical densiometer (Lemmon, 1956) at five locations per community plot four times per year (2012–15) and recorded as the mean.

At the end of the study all established individuals were hand pulled from subplots and subplots were monitored through May 2016 to ensure no additional seeds emerged and established.

2.5. Analyses

Statistical analyses were performed in R 3.2.2 (R Core Team, 2016). Emergence (i.e. the ratio of seedlings to seeds sown), survival (i.e. proportion of emerged seedlings that survived until May 2014), and establishment (i.e. proportion of seeds that emerged and survived until the end of the 42-month study period) were recorded per species per subplot. Given that seedling emergence, survival, and establishment follow a binomial distribution (0–100% success), we analyzed our data with generalized linear mixed-effect models (GLMM) with a binomial error structure and a logit link function (Giménez-Benavides and Milla, 2013) using R package *lme4* (Bates et al., 2015). We tested for effects of vegetation community, sowing treatment, abiotic variables, or fire history on our seedling responses. We built separate models for burned and unburned subplots. Our models used the Laplace approximation of maximum likelihood, and we considered site as a random effect. Models were evaluated for overdispersion, and when the ratio of residual deviance to degrees of freedom was greater than 1.5 we added an observation-level random effect to account for the overdispersion (Harrison, 2015). For cases with too few observations across sites, relationships were analyzed with generalized linear models (GLM). We examined the significance of each model variable with Wald test statistics (Zurr et al., 2009). Models were assessed with Nakagawa and Schielzeth's goodness-of-fit statistic 'marginal R^2' (R^2_m), which measures the variance explained by fixed effects (Johnson, 2014; Nakagawa and Schielzeth, 2013).

To build our 1-yr seedling survival model, we identified important variables by evaluating the full model versus reduced models using P values for type II Wald χ^2 tests derived from the R package *car* (Fox and Weisberg, 2011). The full model was constructed with all variables previously identified as statistically significant (when considered individually) as predictors. We tested the full model versus a reduced model (i.e. one variable removed at a time); variables were removed if there was no difference in explanatory power between the full and reduced model.

Linear mixed-effect models (LMM) were used for to test for the influence of abiotic and biotic variables on seedling size (individual plants as sampling unit), and we used Satterthwaite's approximation of denominator degrees of freedom to calculate P values in R package *lmerTest* (Kuznetsova et al., 2012).

Selected soil properties were summarized with a principal-component analysis (PCA) with R package *caret* (Kuhn, 2008). Each selected soil property was Box-Cox transformed, centered, and standardized before the PCA was performed.

3. Results

3.1. Effect of vegetation community, sowing, fire, and fire history on seedling emergence, survival, and establishment

Seedlings of all six species emerged within subplots by the end of the first growing season (Table 2), while none were observed within other portions of plots or near plots. Emergence varied across species from 1.1 to 9.6% (df = 5, $\chi^2 = 52.82$, $P < 0.001$), with a mean of 6.1%. Across all species, vegetation community had no effect on seedling emergence (df = 1, $\chi^2 = 0.50$, $P = 0.23$), but when tested within species, *L. sinense* had higher emergence in savanna (1.5%) than in the ecotone (0.6%; df = 1, $\chi^2 = 8.31$, $P = 0.003$). Across all species, mean emergence differed among seed sowing treatments (df = 2, $\chi^2 = 101.78$, $P < 0.001$), with greatest emergence occurring where litter was removed and seeds were covered with soil (Fig. 1). The effect of seed sowing treatment was significant for each species when tested individually (Table 3). We did not observe an effect of pre-sowing fire history on emergence (not shown).

Table 2
Mean emergence, survival, and establishment for our six study species. Emergence is defined as the proportion of seedlings to seeds sown at the end of the first growing season. Two-year survival is defined as the proportion of emergent seedlings that survived until May 2014. Establishment is defined as the proportion of seedlings at the end of the study period to seeds sown.

Species	Emergence	Two-year survival Unburned, burned	Establishment Unburned, burned
E. umbellata	3.56 (0.84)	3.04 (2.26), 0 (0)	0 (0), 0 (0)
L. sinense	1.06 (0.32)	0 (0), 0 (0)	0 (0), 0 (0)
M. azedarach	5.65 (0.84)	11.44 (4.99), 0 (0)	0 (0), 0 (0)
N. domestica	9.56 (1.93)	49.21 (10.76), 0 (0)	3.87 (2.58), 0 (0)
P. calleryana	8.24 (1.47)	61.85 (9.71), 21.82 (12.20)	9.78 (3.62), 1.07 (0.45)
T. sebifera	8.61 (1.45)	43.21 (8.52), 0 (0)	7.83 (3.51), 0 (0)

Standard errors of the mean are in parentheses.

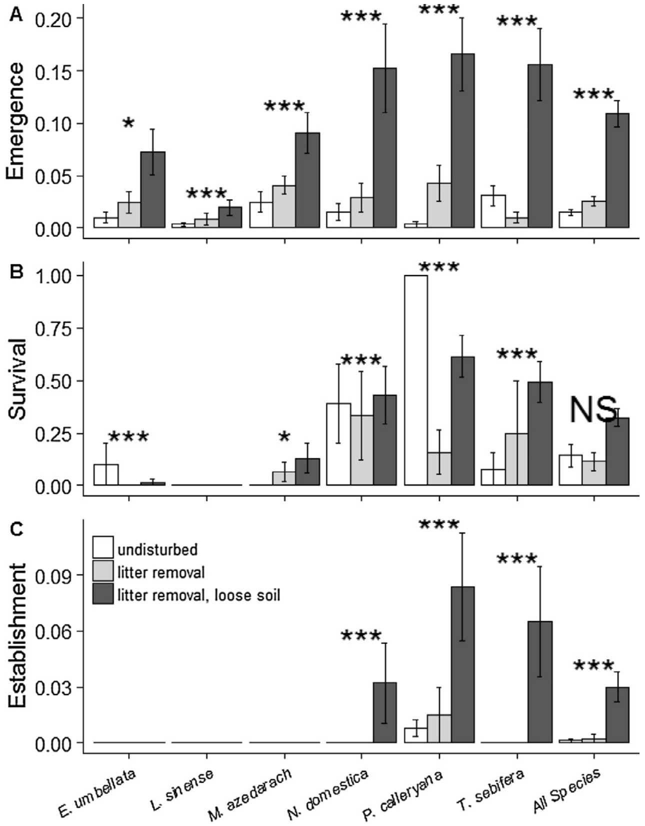

Fig. 1. Effect of sowing treatment (undisturbed [white], litter removal and undisturbed soil [light gray], litter removal and covered with loose soil [dark gray]) on seedling emergence, survival, and establishment. (a) Emergence is the proportion of seedlings to seeds sown at the end of the first growing season (September 2012). (b) Two-year survival is the proportion of emergent seedlings that survived until May 2014. (c) Establishment is the proportion of seedlings at the end of the study period (September 2015) to seeds sown. Error bars represent the standard error of the mean. Significance levels for type II Wald χ^2 test statistic: $^{***}P < 0.001$, $^{**}P < 0.01$, $^{*}P < 0.05$, NS = not significant.

However, burning after seedling emergence substantially reduced survival, so post-emergence survival was analyzed separately for plots that were not burned in 2013, when seedlings were approximately 1 year old. For these unburned sites, mean 2-yr survival of all species was 29.1%, no *L. sinense* seedlings survived, and community type did not affect survival (Table 3). However, testing each species individually revealed an effect of vegetation community on 2-yr survival for *N. domestica* and *P. calleryana* (Table 3) with each experiencing greater survival in savanna than at the wetland ecotone. We did not observe an effect of sowing treatment on 2-yr seedling survival in unburned subplots. Analyzing each species separately, we observed an effect of sowing treatment on 2-yr survival, except for *E. umbellata* (Table 3, Fig. 1). The 2-yr survival rate differed among species (df = 4, $\chi^2 = 166.36$, $P < 0.001$; Table 3). At burned sites, only *P. calleryana* survived, and there was an effect of community type on survival (df = 1, $\chi^2 = 5.26$, $P = 0.02$), with 60.0 ± 24.5% mean survival in savanna and no survival in ecotone. We also observed an effect of sowing treatment on survival of *P. calleryana* seedlings burned after emergence (Table 3); the greatest survival rate was observed for the litter removal with covered soil treatment. For comparison, *P. calleryana* had a mean survival rate of 21.8 ± 12.2% in burned sites, and 61.9 ± 9.7% in unburned sites. We did not observe an effect of pre-sowing fire history on 2-yr seedling survival.

Invasion success depends on both emergence and subsequent survival, each of which were presented above. To examine the net outcome of both, we defined establishment as the proportion of seeds that emerged and survived until the end of the 42-month study period. Across all study species, the mean establishment success was 7.2 ± 1.8% in unburned subplots and 0.4 ± 0.2% in subplots burned after seedling emergence. Only three species (*N. domestica*, *P. calleryana*, *T. sebifera*) had individuals remaining at the end of the study, and *P. calleryana* was the only species with individuals remaining in sites that burned (Table 3, Fig. 1). Across these three species, establishment within unburned subplots was 8.7 ± 3.0% in savanna and 5.6 ± 2.3% in the savanna-wetland ecotone (df = 1, $\chi^2 = 10.50$, $P = 0.001$), but establishment success did not differ between vegetation communities when considering species separately ($P > 0.05$). Across the established species, there was an effect of sowing treatment on establishment (df = 2, $\chi^2 = 151.12$, $P < 0.001$) in unburned subplots; establishment was 19.0 ± 5.0% where litter was removed and seeds were buried and 0.7 ± 0.4% and 1.8 ± 1.8% for the undisturbed and litter removal treatments, respectively. Species differed in their establishment rates in unburned subplots (df = 2, $\chi^2 = 22.81$, $P < 0.001$; *N. domestica*, 3.9 ± 2.6%; *P. calleryana*, 9.8 ± 3.6%; and *T. sebifera*, 7.8 ± 3.5%). In burned subplots, establishment success of *P. calleryana* was 1.1 ± 0.5%, and 88% of established individuals received the litter removal and soil covering sowing treatment (Table 4). We did not observe an effect of pre-sowing fire history on establishment success.

3.2. Effect of abiotic conditions and seedling size on 1-yr survival

We observed no difference in percent canopy cover between savanna and ecotone plots, however ecotone plots had greater humic matter and soil moisture, and savanna plots had greater soil bulk density (Table 5). A PCA of soil Ac, BS, Ca, CEC, Cu, K, Mg, Mn, Na, P, pH, and Zn showed that 33.7% of the variance of these selected soil properties was accounted for by the first principal component (Table A1). This soil fertility composite variable (i.e. PC1) was used in subsequent seedling survival and size analyses.

Considering the species with surviving individuals, mean seedling stem volume (mean of all individuals per subplot) at the beginning of the second growing season (May 2013) did not differ between savanna and ecotone community plots ($P > 0.10$) for any species (*E. umbellata* was not tested due to sample size [$n = 6$]). Mean stem volume did not differ among seed sowing treatments ($F_{2,96} = 0.13$, $P = 0.88$) when considering all species, or when considering each species separately ($P > 0.20$), except for *M. azedarach* ($F_{2,7} = 25.78$, $P < 0.001$).

Mean seedling stem volume (May 2013) was not correlated with abiotic variables, except for a weak positive relationship with soil bulk density (df = 103.3, $t = 2.35$, $P = 0.020$, $R^2_m = 0.02$), when all species were considered. Only *M. azedarach* and *P. calleryana* had significant correlations between mean stem volume and abiotic variables (Table A2), and only *P. calleryana* had a $R^2_m \geq 0.10$ (humic matter; df = 57.7, $t = 4.78$, $P < 0.001$, $R^2_m = 0.19$). Fire history prior to sowing had no effect on seedling stem volume for any species (Table A2).

The 1-yr seedling survival rate, the proportion of seedlings that

Table 3
Type II Wald χ^2 test statistic values from generalized linear mixed-effect models (GLMM) evaluating the effect of vegetation community (df = 1), sowing treatment (df = 2), or species identity on emergence, survival, and establishment for our six study species and all species combined. Emergence is the proportion of seedlings to seeds sown at the end of the first growing season (September 2012). Survival is the proportion of emergent seedlings that survived until May 2014. Establishment is the proportion of seedlings at the end of the study period (September 2015) to seeds sown.

	Elaeagnus umbellata	*Ligustrum sinense*	*Melia azedarach*	*Nandina. domestica*	*Pyrus calleryana*	*Triadica sebifera*	All species
Emergence							
Community	0.001	8.31**	1.62	1.00	1.55	0.28	0.05
Treatment	6.08*	17.10***	18.67***	25.25***	50.76***	30.33***	101.78***
Species (df = 5)	–	–	–	–	–	–	52.82***
Survival							
Unburned							
Community	3.66	–	0.50	6.94**	4.68*	0.51	0.31
Treatment	1.60	–	32.02***	26.41***	16.38***	15.12***	0.56
Species (df = 4)	–	–	–	–	–	–	166.36***
Survival							
Burned							
Community	–	–	–	–	5.26*	–	–
Treatment	–	–	–	–	16.77***	–	–
Establishment							
Unburned							
Community	–	–	–	6.21*	2.98	0.64	0.07
Treatment	–	–	–	15.00**	10.61**	38.38***	22.97***
Species (df = 2)	–	–	–	–	–	–	0.67
Establishment							
Burned							
Community	–	–	–	–	0.37	–	–
Treatment	–	–	–	–	11.18**	–	–

Significance levels for type II Wald χ^2 test statistic.
*** $P < 0.001$.
** $P < 0.01$.
* $P < 0.05$.

survived from May 2013–2014 (this period was evaluated because it had the greatest number of individuals and a fire event), in unburned sites was not correlated with abiotic variables nor fire history when species were examined collectively (Table A3). The correlations between 1-yr survival and abiotic variables for individual species were idiosyncratic and we did not observe general patterns among the four species (*E. umbellata* was censored due to sample size; Table A3). For burned *P. calleryana* subplots, there was an effect of each environmental variable on 1-yr seedling survival except soil moisture (Table A4).

Over all species, larger seedlings in May 2013 had higher seedling survival rates in unburned plots ($z = 5.33$, $P < 0.001$, $R^2_m = 0.47$). When examining species individually, stem volume was positively correlated with survival for *N. domestica*, *P. calleryana*, and *T. sebifera*, but not *M. azedarach* (Table A5). For the only species surviving fire, *P. calleryana*, 1-yr post-fire survival was also positively correlated with pre-burn stem volume ($z = 2.38$, $P = 0.02$, $R^2_m = 0.64$). Individuals that had acquired a stem volume of 0.45 cm^3 had greater than a 50% chance of surviving fire (Fig. 2). Only 8.4% of surviving individuals had reached this size by May 2013, 9.6% by May 2014, and 16.8% by May 2015. As only *P. calleryana* seedlings were observed to resprout following fire, we examined the determinants of fire survival more closely. The final, reduced model ($R^2_m = 0.60$) included two predictors, humic matter (df = 1, $\chi^2 = 30.1$, $P < 0.001$) and sowing treatment (df = 2, $\chi^2 = 8.9$, $P = 0.01$).

Table 5
Mean soil properties and environmental variables within study plots (Welch's unequal variance *t*-test).

Variable	Savanna plots	Ecotone plots	*t*-value
Soil bulk density (g cm^{-3}; df = 31)	1.16 (0.01)	1.01 (0.01)	−3.66**
Humic matter (%; df = 34)	0.96 (0.03)	1.47 (0.03)	2.71*
Soil moisture (%; df = 24)	7.36 (0.12)	10.58 (0.24)	2.73*
Canopy closure (%; df = 34)	69.21 (0.83)	71.25 (0.89)	0.38

Standard errors of the mean are in parentheses. Significance levels for *t*-test between savanna and ecotone plots.
** $P < 0.01$.
* $P < 0.05$.

4. Discussion

We investigated the role of fire, dispersal, vegetation community, seedling size, and abiotic conditions on recruitment success of six woody, invasive plant species along a savanna-wetland gradient. Seedling establishment is an important early step in woody encroachment of open-canopied ecosystems. Our results demonstrated that sowing treatment (dispersal surrogate), species identity, seedling size,

Table 4
Number and proportion (seedlings per seeds sown) of established seedlings by sowing treatment (undisturbed [UD], litter removal and undisturbed soil [LRU], litter removal and covered with loose soil [LRS]) in unburned and burned sites.

Species	UD		LRU		LRS	
	Unburned	Burned	Unburned	Burned	Unburned	Burned
N. domestica	0, 0%	0, 0%	0, 0%	0, 0%	29, 11.60%	0, 0%
P. calleryana	6, 2.00%	3, 0.37%	16, 5.33%	0, 0%	66, 22.00%	22, 2.93%
T. sebifera	0, 0%	0, 0%	0, 0%	0, 0%	47, 23.50%,	0, 0%

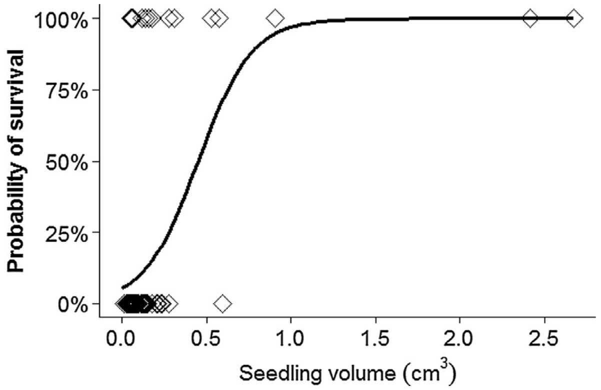

Fig. 2. Line is the predicted probability of a *P. calleryana* seedling surviving a topkilling fire based on seedling stem volume ($\chi^2 = 20.3$, $P < 0.001$, $R^2_m = 0.20$). Diamonds represent observed data points ($n = 24$).

abiotic constraints, and fire were all important factors for determining seedling survival and establishment success within this longleaf pine landscape. At the end of the study period (42 months), there were 189 seedlings remaining from 21,060 sown seeds and three of the six study species had surviving individuals (Fig. 1). Of these 189 seedlings, 164 established in the treatment where litter was removed and the seeds were buried. Only *P. calleryana* survived fire, with a total of 25 seedlings established (from 3240 seeds sown) in sites burned 9–36 months after emergence; 23 of these seedlings were in the sowing treatment where litter was removed and the seeds were buried (Table 4).

Dispersal is a primary driver of species invasion dynamics, and for each of the six species, in both burned and unburned sites, we found that sowing treatment was an important determinant of seedling emergence rates and that it exerted persistent effects on species' subsequent survival and establishment. For example, the greatest rates of survival and establishment occurred in the litter removal and soil covering treatment, which emulated secondary dispersal by scatter hoarding rodents (Table 4). This speaks to the potentially important role that secondary dispersal may play in establishment of the study species in this system (e.g., Vander Wall, 2003). Post-dispersal seed removal by vertebrate granivores has been documented in savanna and ecotone vegetation communities for three of the study species (*E. umbellata*, *M. azedarach* and *T. sebifera*; Krall et al., 2014), but without additional information about rates of seed consumption versus caching (Lichti et al., 2017), we are limited in our ability to explicitly quantify the beneficial versus the detrimental consequences for species' establishment. Still, Zwolak and Crone (2011) have suggested that the ratio of seedling emergence on the ground surface to emergence from artificial caches can be used to elucidate the relative benefit likely provided to species from granivore interactions. When the ratio is very small, one can be confident that granivory is beneficial; conversely, granivores are unlikely to enhance recruitment if the ratio is large. Interestingly, only *P. calleryana* exhibited a value for this ratio (0.05) that suggested benefits; the other species had ratios that suggested either ambiguous or negative consequences for recruitment (Zwolak and Crone, 2011). Additional information about granivore utilization of *P. calleryana* seeds would be helpful for interpreting the threat posed by this recent invader within this system (Culley and Hardiman, 2007).

Longleaf pine ecosystems in the Sandhills are nutrient and water limited (Hatchell and Marx, 1987; Wells and Shunk, 1931), resulting in slow vegetation growth rates. Slow growth combined with periodic fires, create obstacles to seedling survival, and individuals in this environment may need prolonged periods to reach fire-tolerant sizes, as compared to less stressful environments. Seedling size had a positive effect on survival of each of the three species that established by the end of the study period (Table A5).

Humic matter was the only abiotic factor with a significant effect on seedling size, and only for *P. calleryana* (Table A2), and was one of the two predictors included in our model predicting *P. calleryana* survival after fire. Humic matter has both direct and indirect positive correlations with plant growth (Nardi and Pizzeghello, 2002; Trevisan et al., 2010). Regardless of whether the effect of humic matter is direct or indirect, it is an indicator of favorable conditions that support faster growth rates and, thus, reduce the effectiveness of fire as a filter, because individuals reach fire resistant sizes more quickly.

Fire return intervals, one aspect of fire regimes, affect encroachment and invasibility of pyrophilic ecosystems (Higgins et al., 2007; Keeley, 2006; Sankaran et al., 2005). Frequent fires may exhaust energy reserves of topkilled seedlings, or kill seedlings that are not yet physiologically capable of resprouting (Ryan and Williams, 2011). On the other hand, very infrequent fires may result in a landscape with unfavorable recruitment conditions (Denham et al., 2010). The current fire management of our study landscape utilizes a three-year fire return interval based on an estimated historical average. This fire interval has been documented to reduce or topkill hardwoods and other closed-canopy species in longleaf pine ecosystems (Glitzenstein et al., 2012; Kirkman et al., 2004) and appears to be largely effective at preventing the establishment of seedlings from these non-native species; it filtered from the landscape two of three study species that successfully established in the absence of fire. Similarly, Pile et al. (2017) found low survival rates of *T. sebifera* in maritime forest when burning occurred within four years of establishment.

Yet, this does not indicate that the landscape is altogether immune to increased invasion rates by woody plants as longleaf pine ecosystems can support many woody seedlings and resprouts in the absence of fire (Menges, 2007; Varner et al., 2005). Importantly, in unburned sites, individuals of three species successfully established during the study period (Fig. 1). In spite of the regular use of prescribed fire as a management tool, fires are heterogeneous, leaving unburned patches that may provide seedlings a window to establish and potentially encroach upon savanna. Moreover, the effect of fire on both native and non-native woody seedlings is generally unknown. Managers are now considering conservation and restoration techniques for pyrophilic communities that are more temporally and spatially heterogeneous with respect to prescribed fire (Ryan et al., 2013), but it is important to note that the effect of fire on both native and non-native woody seedlings in longleaf pine systems is generally unknown.

While we did not observe great differences in emergence, survival, or establishment between the savanna and ecotone communities, differences in vegetation structure along the savanna-wetland gradient are nevertheless important for invasibility because of its influence on flammability. Despite a mean fire interval of 3 years in the upland savanna, mean intervals increase to 7.5 years in adjacent wetland at the site (Just et al., 2016). This longer fire return interval would greatly increase the opportunity for successful establishment, particularly for shade-tolerant species capable of establishing in the shrub-dominated pocosin wetlands. Four of the six study species, *E. umbellata* (Brym et al., 2011), *L. sinense* (Webster et al., 2006), *N. domestica* (Knox and Wilson, 2006), and *T. sebifera* (Jones and Mcleod, 1989) are shade tolerant, and so the longer fire-free periods at the wetter end of the gradient may provide adequate time for individuals to establish and become fire tolerant.

Seedling establishment is a critical demographic bottleneck in woody plant invasions. Understanding the numerous mechanisms that may influence the establishment success of a native or non-native seed after its arrival within this savanna-wetland gradient is a complex task. Fire (even prescribed fire) occurrence and intensity varies spatially and temporally (Knapp and Keeley, 2006; Ryan et al., 2013), as do the many other biotic and abiotic processes that determine seed fates (García and Houle, 2005; Kauffman and Maron, 2006) and seedling establishment (Rey and Alcántara, 2000). Although little is known about these processes for the majority of our study species, we documented several strong ecological filters that differentially influenced establishment of the six species in our study landscape. Our observed establishment rates indicate that the combined effects of biotic interactions (dispersal), species identity, abiotic conditions, seedling size, and fire management practices appear to be largely effective at filtering five of these six species from the landscape. However, at least three of the species still pose an invasion threat; *N. domestica*, *P. calleryana*, and *T. sebifera* can be expected to establish where seeds arrive in unburned portions of the landscape. Additional monitoring of woody invaders, beyond the seedling stage, is necessary to determine their potential to contribute to long-term encroachment of savanna and canopy in-filling. Furthermore, we anticipate that *P. calleryana* poses a particular threat because a number of 1-year old seedlings also survived topkilling fire. Still, more information is needed to understand the response of *P. calleryana* seedlings to successive fires. Finally, we acknowledge the great ecological complexity surrounding invasion, which suggests that while the studied longleaf pine – wetland gradient seems fairly resistant to invasion, it is not exempt from increased invasion rates from these or other species.

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Competing interest statement

The authors have no competing interests to declare.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2017.09.052.

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