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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

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