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Chinese tallow (*Triadica sebifera*) invasion in maritime forests: The role of anthropogenic disturbance and its management implication

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ABSTRACT

Land-use and forest management practices may facilitate the invasion success of non-native plants in forests. In this study, we tested if agricultural land abandonment and subsequent forest management contributed to the invasion success of Chinese tallow (*Triadica sebifera* (L.) Small) in the maritime forest of Parris Island, SC. We compared the abundance of Chinese tallow between disturbed and remnant forests, described Chinese tallow establishment patterns in relation to forest management activities, and characterized the structure and composition of disturbed and remnant forests in order to better understand relationships between stand characteristics and invasibility as indicated by Chinese tallow abundance. We found that stands in agricultural land use in 1939 but reforested with slash pine (*Pinus elliottii* Englem.) since the 1970s (i.e., disturbed forests) had significantly more Chinese tallow stems than stands that remained forested since 1939 (i.e., remnant forests). Remnant forests had significantly greater woody species richness and were more variable in species composition and structure than disturbed forests. Disturbed forests were dominated by early successional, shade intolerant species with a denser woody understory, while remnant forests included species associated with late successional habitats. The number of forest management events was positively associated with Chinese tallow abundance, explaining 34% of the total variation in stem density. Chinese tallow individuals commonly established immediately after forest thinning and their numbers increased exponentially through time. Our findings support that Chinese tallow establishment was strongly related to anthropogenic disturbance including historical agricultural land-use and forest management. This suggests that Chinese tallow invasion may be a symptom, rather than the driver, of the ecological degradation induced by persistent human perturbations.

1. Introduction

The successful invasion by a non-native, invasive species is attributed to three primary factors: the number of propagules entering the community (propagule pressure), the characteristics or traits of the invasive species (invasiveness), and the susceptibility of the community to invasion (invasibility) (Lonsdale, 1999). Although characteristics of the potential invader largely determine its invasiveness (Rejmánek and Richardson, 1996), invasibility often increases with disturbance (Hobbs and Huenneke, 1992; Burke and Grime, 1996; Lozon and MacIsaac, 1997) and thus may depend on land-use history (Vilà and Ibáñez, 2011). Disturbance and land-use legacies can affect propagule pressure by altering habitat quality and species-specific environmental filters (Mayfield et al., 2010). Therefore, understanding the role of disturbance and land use in facilitating or constraining invasions may help identify opportunities for intervention and control.

Disturbances increase invasibility by providing establishment opportunities that favor disturbance-dependent, non-native species over native species (Hobbs and Huenneke, 1992; Davis et al., 2000). Non-native, invasive species may outperform native species if the disturbance is not typical of the evolutionary history of the natives (Lockwood et al., 2013), consistent with the recognition that species exhibit suites of adaptive traits or adaptive strategies. Many of the world's most tenacious invasive species are considered '*r* strategists' (Rejmánek and Richardson, 1996), which are favored where resources are abundant and perhaps transient. This phenomenon has been described in communities ranging from

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Nomenclature

Triadica sebifera (L.) Small Chinese tallow, popcorn tree
Pinus elliottii Englem. Slash pine

coastal marshes where the timing of wrack deposition facilitates the establishment of *Phragmites australis* (Minchinton, 2002) to grasslands where overgrazing facilitates the invasion of *Centaurea* species (DiTomaso, 2000). Perhaps the most recognized disturbance in eastern North America is the conversion of forestland to agriculture. This conversion has resulted in substantial reductions in plant diversity and abundance (Vellend, 2004; Flinn and Vellend, 2005; Hermy and Verheyen, 2007), providing a 'window of opportunity' for plant invasion (Davis et al., 2000; Mosher et al., 2009) in which non-native, invasive species may establish prior to re-vegetation of native species (Pianka, 1970).

Because trees act as ecosystem engineers and regulate ecosystem function (Crooks, 2002; Belote and Jones, 2009), invasion by non-native tree species often has profound impacts on recipient forest communities (Lamarque et al., 2011). Tree invasions in forests have been associated with hierarchical effects from changes in species diversity to altered ecosystem function (Jackson et al., 2002; Yelenik et al., 2004; Pyšek et al., 2012). Because they are long-lived, studies of invasive tree species benefit from the ability to reconstruct invasion histories related to disturbance events.

Maritime forests are globally imperiled ecosystems with high risks of extinction (NatureServe, 2012), partly due to invasive species. In the southeastern U.S., maritime forests are considered one of the rarest and least studied biological communities (Bellis, 1995). Chinese tallow (*Triadica sebifera* (L.) Small) is a highly invasive, non-native tree species that poses a significant threat to these ecosystems. It is fast-growing (Scheld and Cowles, 1981), shade tolerant (Jones and McLeod, 1989), and able to thrive under various conditions, including bottomlands with anoxic soil conditions, dry upland forests, and soils with moderate levels of salinity (Conner and Askew, 1993; Conner, 1994; Butterfield et al., 2004). Furthermore, Chinese tallow can reach sexual maturity in 3 years (Bruce et al., 1997) and is highly fecund (Scheld et al., 1984), with seeds that are bird dispersed (Renne et al., 2000) and persist in the soil seed bank for up to 5 years (Cameron et al., 2000). Chinese tallow has the potential to create monocultures and invade intact forests (Bruce et al., 1995; Gan et al., 2009), leading to losses of biodiversity (Cameron and Spencer, 2010; Camarillo et al., 2015). Given that southeastern maritime forests are exposed to high levels of both natural and anthropogenic disturbance, understanding the role of disturbance in facilitating Chinese tallow invasion is especially important.

The goal of this study was to better understand the relationships between anthropogenic disturbance and Chinese tallow invasion in maritime forests. We compared the abundance of Chinese tallow among forest stands representing two classes of disturbance history: remnant sites with no significant disturbance other than low severity agricultural uses in the 1700s (i.e., the remnant forest) and a more intensive disturbance history of agriculture use through the 1950s followed by the establishment and subsequent management of slash pine plantations (i.e., the disturbed forest). We reasoned that if disturbance events facilitate Chinese tallow establishment, there would be a relationship between the timing of disturbance and the age of Chinese tallow cohorts. Additionally, informal observation suggested that Chinese tallow was not as successful in remnant compared to disturbed forests, even though, based on their proximity to each other, they were exposed to similar propagule pressure through time. We reasoned that, in addition to the absence of acute disturbance events, the remnant forest may exhibit compositional and structural characteristics reportedly associated with reduced invasibility, such as high species richness or structural complexity (Tilman, 1997; Naeem et al., 2000; Dukes, 2001; Munro et al., 2009). We hypothesized that: (1) Chinese tallow is more abundant in disturbed forests than remnant forests; (2) remnant forests are more species-rich and structurally diverse than disturbed forests, consistent with decreased community invasibility; and (3) Chinese tallow abundance is positively related to the number of forest thinning and prescribed fire events and the timing of Chinese tallow establishment is positively related to the occurrence of forest management practices.

2. Methods

2.1. Site description and history

Parris Island Marine Corps Recruit Depot (referred to as 'Parris Island', hereafter) is located in Beaufort County, SC (Lat. 32.3289N, Long. −80.6947W). It comprises 3257 hectares, of which 608 ha are managed forests, 1538 hectares are salt water marsh and tidal streams, and 1111 hectares are developed (housing, military training facilities) or cultivated (parks, golf course). Parris Island is located in the Southern Coastal Plain eco-region (EPA, 2003) and has flat topography, with elevations that range from 0 to 7 m above mean sea level. Mild winters and hot summers characterize the study area. Soils in the study area are generally described as fine sands to fine loamy sands. Soil series include Wando fine sands (sandy marine sediments, very deep and well-drained), Wahee fine sandy loam (clayey and loamy marine sediments, very deep and somewhat poorly drained), Murad fine sand (loamy marine deposit, moderately well to somewhat poorly drained), Williman loamy fine sand (loamy marine deposit, poorly drained), and Seewee fine sand (sandy marine deposits, somewhat poorly drained) (Soil Survey Staff, 2013). All soil types in our study area are known to be cultivated for row crops and pasture (Soil Survey Staff, 2013).

Most of Parris Island remained forested during early European settlement due its saline soils. Beginning in the 1740s some forests were cleared for the establishment of indigo (*Indigofera* spp. L.), and during the 1790s, Sea Island cotton (*Gossypium barbadense* L.) replaced indigo as the primary agricultural crop. By 1825, the plantations were divided and most of the arable land was used for cotton farming, leaving few remaining wooded patches. Civilian residents remained on Parris Island until 1938, when the Marine Corps expanded the Recruit Depot operations to encompass the entire island. Most of the previous agricultural lands were maintained as open fields until slash pine (*Pinus elliottii* Engelm.) was planted in the 1970s.

2.2. Historical land-use effects on Chinese tallow abundance

To assess hypotheses 1 and 2, we classified forest stands into two types based on historical land-use: stands in the 'disturbed