Forest Ecology and Management 398 (2017) 10–24

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

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

Lauren S. Pile [a,d], G. Geoff Wang [a,*], Benjamin O. Knapp [b], Joan L. Walker [c], Michael C. Stambaugh [b]

[a] Department of Forestry and Environmental Conservation, Clemson University, Clemson, SC 29634, United States
[b] Department of Forestry, School of Natural Resources, University of Missouri, 203 Anheuser-Busch Natural Resources Building, Columbia, MO 65211, United States
[c] USDA Forest Service Southern Research Station, Clemson, SC 29634, United States
[d] USDA Forest Service, High Sierra Ranger District, Sierra National Forest, Prather, CA 93651, United States[1]

ARTICLE INFO

Article history:
Received 2 February 2017
Received in revised form 30 April 2017
Accepted 2 May 2017

Keywords:
Abandoned agriculture
Invasibility
Prescribed fire
Thinning

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

* Corresponding author.
E-mail address: gwang@clemson.edu (G.G. Wang).
[1] Current affiliation.

http://dx.doi.org/10.1016/j.foreco.2017.05.006

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 revegetation 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 forest' classification were cleared before 1939 and reforested, and stands in the 'remnant forest' classification were forested in 1939 and remained forested thereafter. A comparison of these classes was the basis for evaluating effects of land use history on species richness, composition, and forest structure to serve as a proxy for community invasibility and its possible relationship with Chinese tallow abundance.

2.2.1. Land use classification and management histories

To understand patterns of historical land use on Parris Island, aerial photograph images were collected from the University of South Carolina Map Library for 1939, 1951, and 1972, and digital orthophoto quarter quadrangles for 1994 were downloaded from the South Carolina Department of Natural Resources data clearinghouse. We used an ArcGIS 10.1 Bing basemap to derive 2011 land use data. Images were georeferenced using a 3rd order polynomial with a minimum of 20 control points and a total maximum residual of 25 m. Forest land cover was classified for each time period based on a visual estimation of land cover type. We defined remnant forest patches as those that were forested in 1939 and remained forested thereafter. Those that were not classified as remnant forests were considered disturbed forests as they were cleared at some point prior to 1939 and were re-forested. Each remnant forest layer was clipped over the next time period to determine which forest patches remained intact from 1939 through 2011 (Fig. 1). Although we were able to differentiate between post-agricultural areas and remnant maritime forests from 1939, we note that this area has had a long history of human use, from Native Americans to early European settlement. We classify sites as "remnant" but acknowledge that they were not without human influence and may have been disturbed by humans prior to 1939.

2.2.2. Vegetation plots

To describe forest composition and structure, we sampled vegetation in a random subset of the available disturbed (n = 6) and remnant (n = 4) forest stands that were at least 1.6 ha (Table 1, Fig. 2). In each stand, we established between 2 and 8 plots that were placed at least 30 meters from the forest edge and at least 50 meters apart. Each plot measured 20×40 m and was divided into eight 10×10 m subplots, with a 1 m^2 quadrat placed in the center of each subplot. For all trees $\geq$3 cm diameter at breast height (DBH) in each plot, we recorded species and DBH. In four randomly selected subplots, we recorded species and DBH of all saplings (trees >1.4 m tall and <3 cm DBH) and shrubs (> 1.4 m tall). For all herbaceous and woody species less than 1.4 m tall in each quadrat, we recorded Braun-Blanquet's cover class [1 (<0.1); 2 (0–1%); 3 (1–2%); 4 (2–5%); 5 (5–10%); 6 (10–25%); 7 (25–50%); 8 (50–75%); 9 (75–95%); 10 (>95%)], and height class [1 (<10 cm); 2 (10–50 cm); 3 (50–140 cm)] by species. We assigned each species to one of the following growth habit functional groups: forb, graminoid, shrub, subshrub, tree, or vine. Vegetation surveys were conducted in June and July 2012 for the disturbed forest and 2013 for the remnant forest. Nomenclature, plant species codes, and plant growth habit functional groups follow the USDA PLANTS Database (2014).

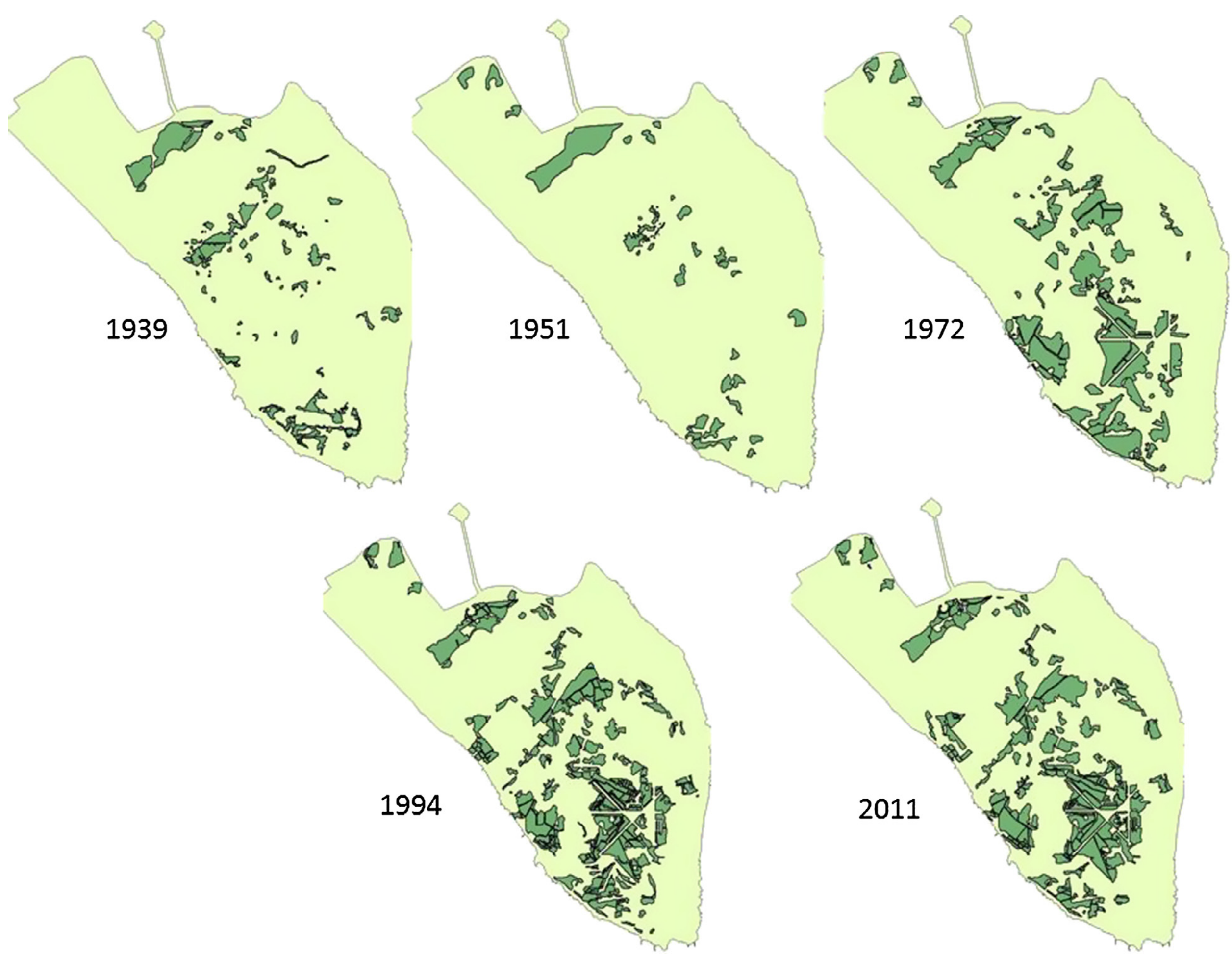

Fig. 1. Changes in forest cover through time at Parris Island, SC. Dark green polygons represent areas forested at the time of aerial image year.

Table 1
Disturbance type, size (ha), number of plots, known establishment year, number of thinning operations, thinning years, number of burns, and burn year for sampled areas at Parris Island, South Carolina.

Stand	Disturbance type	Size (ha)	Plots (n)	Establishment year	Thinned (n)	Thin year	Burn (n)	Burn year
1	Remnant	37.6	4		0		0	
2	Disturbed	4	4	1969	1	1992	1	2004
5	Remnant	1.6	2		0		0	
33	Disturbed	5.3	4	1965	2	1984, 1990	2	2002, 2005
38	Disturbed	3.6	4	1969	2	1990, 2004	2	2002, 2005
45	Remnant	6.1	3		0		0	
51	Disturbed	13.4	8	1957	2	1992, 2007	2	2002, 2005
123	Remnant	2	2		0		0	
131	Disturbed	7.7	4	1943	1	1998	1	1997
141	Disturbed	7.7	8	1972	3	1984, 1990, 1998	0	

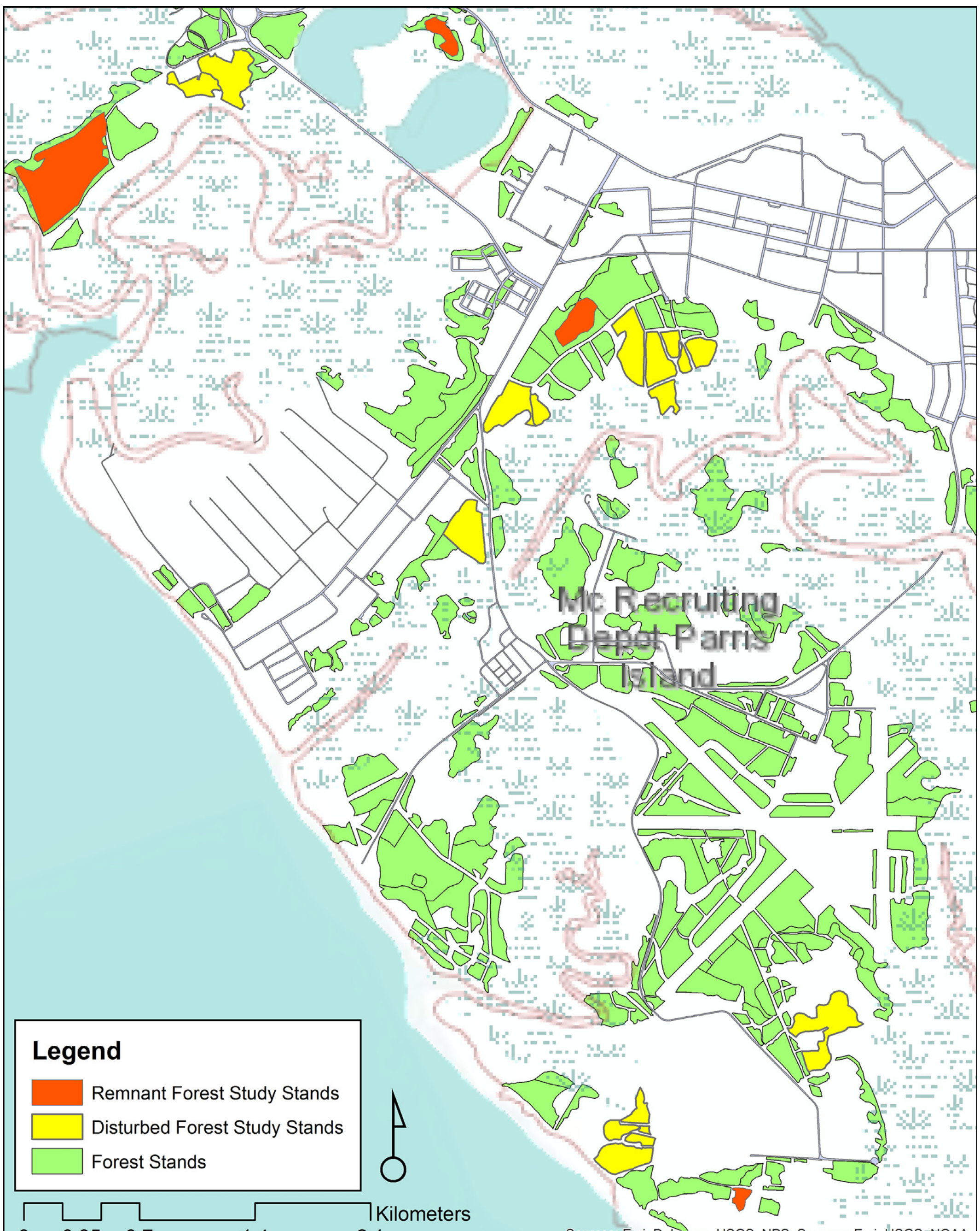

Fig. 2. Map of forest stands and selected study sites at Parris Island, SC.

We determined species richness, basal area, density (trees per hectare), and percent cover of the ground layer functional groups for each sampled vegetation plot and summarized at the stand level. Richness, basal area, density, and percent cover were compared between the two disturbance types with a two sample *t*-test using stand-level means. Percent cover was determined as the mid-point of the range for each cover class. Between-stand similarity was determined by calculating Jaccard's Coefficient of Similarity $s = \frac{p}{p+q+d}$ (Jaccard, 1912); p is the number of species that occurs in both stands, q is the number of species that occurs in stand Q but not in stand D, and d is the number of species that occur in D but not in Q. Jaccard's Coefficient of Similarity (s) has a value between 0 and 1, with 1 being equality. We then conducted a permutation-based *F*-test using a Permutational multivariate analysis of variance (PerMANOVA) to evaluate differences in woody composition and relative abundance between the two disturbance types (Anderson, 2001; McArdle and Anderson, 2001; Peck, 2016).

2.3. Effects of contemporary forest management practices on Chinese tallow abundance and establishment

To assess hypothesis 3, we used multiple regression to quantify the relationship of Chinese tallow abundance with the number of thinning entries and the number of prescribed burns within disturbed forest plots only (no thinning or burning was recorded in remnant forests). Data on the timing of contemporary prescribed burns and thinning activities by stand were collected from the Natural Resource Office at Parris Island MCRD. Data on prescribed burns were available from 1990 through present, and data from timber activities were available from 1988 through present.

We estimated the establishment year of each sampled Chinese tallow stem by developing an equation based on age at breast height (BH; 140 cm) and DBH and a second equation based on age at BH and age at the ground line. To develop the equations, we destructively sampled a total of 50 trees across 4 sites outside of the study plots at Parris Island. We measured diameter and age at BH and used regression to derive the following equation:

$$\mathrm{age}\,140 = 2.08560 + 0.91895 * \mathrm{DBH}$$
$$(\mathrm{n} = 50;\ \mathrm{MSE} = 0.18;\ F = 232.51;\ \mathrm{p} < 0.001;\ \mathrm{R}^2 = 0.83)$$

We then used age at ground line to determine the relationship between time since establishment (age0) and growth to BH (age140).

$$\mathrm{age}\,0 = 0.78421 + 1.11265 * \mathrm{age140}$$
$$(\mathrm{n} = 33;\ \mathrm{MSE} = 0.69;\ F = 674.11;\ \mathrm{p} < 0.001;\ \mathrm{R}^2 = 0.96)$$

Using this equation, we calculated the time since establishment (age0) for each measured Chinese tallow and subtracted age0 from the survey year to determine establishment year of each sampled tree.

We used a *t*-test to determine if mean establishment date was significantly different from the date of the most recent thinning or prescribed burn at the stand level. If disturbance was facilitating Chinese tallow establishment, we would expect that the *t*-test would be non-significant and establishment would occur shortly after the disturbance event.

Data were analyzed using JMP®, Version 11 (SAS Institute Inc., Cary, NC) or SAS® 9.1.3 (SAS Institute Inc., Cary, NC). PerMANOVA was conducted in PC-ORD®, Version 7 (MjM Software Design Data, Gleneden, OR). Prior to PerMANOVA analysis, abundance data were relativized by maximum across forest stands. To meet the balanced design requirements of PerMANOVA, a stratified random sample with replacement of four sample units per disturbance type were batched across 5000 runs. The PerMANOVA analysis was then bootstrapped (5000 iterations) across the batched sample units. Results of the PerMANOVA bootstrapping procedure are reported as the mean *F*-statistic and p-value across all iterations. Data are reported as means and standard errors of the mean. If necessary, data were transformed to meet the assumptions of hypothesis testing, but values are reported in original scale to aid interpretability. Each p-value less than 0.05 was considered evidence of a significant difference.

3. Results

3.1. Effects of historical land use on the abundance of Chinese tallow and the composition and structure of maritime forests

The remnant and disturbed forests differed in native species composition and abundance, including the abundance of Chinese tallow. Basal area and density of Chinese tallow were significantly different by forest type ($t = 3.6$; $p < 0.01$ and $t = 6.4$; $p < 0.01$, respectively) (Table 2). Basal area (m^2/ha) of Chinese tallow was 3.11 ± 0.67 in disturbed forests and 0.53 ± 1.90 m^2/ha in remnant forests. Density (trees/ha) was 1875 ± 392 in disturbed forest and 141 ± 135 trees/ha in remnant forest. Percent cover of Chinese tallow regeneration recorded in the ground layer of disturbed forests was 14%, and there was only one occurrence of regeneration in remnant forests.

Overall, the two disturbance types were statistically different from each other based on woody species composition (PerMANOVA: $F = 4.1$; $p = 0.03$). The Jaccard Coefficient of Similarity for woody species reflects the homogenization of these former agricultural lands as species composition was more similar among the disturbed forests (0.54 ± 0.02) than among the remnant forests (0.41 ± 0.03), and disturbed and remnant forests were dissimilar from each other (0.43 ± 0.02). Species richness was significantly different between disturbance types ($t = 2.0$; $p = 0.04$), with remnant forests having greater woody species richness (remnant = 9.6 ± 0.63; disturbed = 9.1 ± 0.37) and disturbed forests having greater richness of non-native, invasive woody plants (remnant = 0.73 ± 0.2; disturbed = 1.22 ± 0.2; $t = 2.6$; $p = 0.01$).

Disturbed forests had greater woody stem density (1530 ± 136 stems/ha) than remnant forests (237 ± 215 stems/ha) ($t = 5.1$; $p < 0.01$). However, tree basal area did not differ between disturbance types ($t = 0.65$; $p = 0.51$), indicating that the remnant forests had bigger trees than the disturbed stands. Basal area (m^2/ha) and density (trees/ha) were significantly greater for wax myrtle (*Morella cerifera* (L.) Small), slash pine, and Chinese tallow in disturbed forests than remnant forests. The densities, but not basal areas, of yaupon (*Ilex vomitoria* Aiton) and cherrybark oak (*Quercus pagoda* Raf.) were also significantly greater in disturbed forests, whereas Darlington oak (*Quercus hemisphaerica* W. Bartram ex. Willd.) and southern redcedar (*Juniperus virginiana* var. *silicicola* (Small) Silba) were denser in the remnant forests. Red mulberry (*Morus rubra* L.), Darlington oak, and live oak (*Quercus virginiana* Mill.) had greater basal areas in the remnant forests when compared to the disturbed forests.

Species recorded only in remnant forests are more generally characterized as tolerant of shade, with habitat specificity to occur on moist, rich sites that are not subjected to fire (Burns and Honkala, 1990; Miller and Miller, 2005) (Tables 3 and 4). In contrast, species recorded only in disturbed forests are characterized as shade-intolerant pioneer species that potentially occupy a wide range of habitat types (Table 3). For species common to both disturbance types, we found a greater number of shade tolerant species in larger diameter classes (>30 cm in DBH) in the remnant forests and a greater number of shade intolerant species of smaller diameter classes in disturbed forests (Fig. 3, Table 5).

Table 2
Means and standard error of the mean for basal area (m^2/ha) and density (trees/ha) of trees and shrubs by disturbance type (disturbed vs. remnant) at Parris Island, South Carolina. Comparisons by forest stand type were determined using *t*-tests by species and disturbance.

Species	Basal area (m^2/ha)			Density (trees/ha)		
	Disturbed	Remnant	*F*(p - value)	Disturbed	Remnant	*F*(p-value)
Acer rubrum	0.71 (3.03)	0.89 (2.94)	0.12 (p = 0.75)	31 (42)	79 (35)	0.76 (p = 0.45)
Aesculus pavia		0.01 (5.10)			13 (269)	
Ailanthus altissima[a]	0.10 (4.29)			38 (2219)		
Baccharis halimifolia	0.04 (1.75)			285 (906)		
Callicarpa americana	0.06 (1.92)			1480 (992)		
Carya tomentosa		0.13 (5.10)			13 (269)	
Carya ovata	0.86 (4.29)			13 (2219)		
Celtis laevigata	0.38 (2.48)	4.28 (3.61)	1.67 (p = 0.29)	17 (12)	38 (15)	1.15 (p = 0.36)
Diospyros virginiana	0.02 (4.29)			13 (2219)		
Fraxinus pennsylvanica	2.09 (1.75)	11.43 (2.94)	3.16 (p = 0.12)	23 (7)	50 (10)	5.12 (p = 0.06)
Ilex opaca		0.03 (5.10)			13 (269)	
Ilex vomitoria	0.56 (0.76)	0.62 (1.54)	1.17 (p = 0.29)	3017 (385)	1398 (656)	**4.53 (p = 0.04)**
Juniperus virginiana var. *silicicola*	0.26 (1.36)	0.64 (5.10)	2.13 (p = 0.18)	31 (5)	88 (15)	**3.59 (p < 0.01)**
Lantana camara[a]				25 (992)		
Ligustrum sinense[a]		0.24 (2.95)			100 (156)	
Liquidambar styraciflua	1.88 (1.19)	4.23 (2.28)	1.77 (p = 0.20)	730 (354)	163 (592)	0.68 (p = 0.42)
Magnolia grandiflora		1.80 (2.08)			54 (102)	
Melia azedarach[a]	0.26 (3.03)			38 (1569)		
Morella cerifera	0.71 (0.78)	0.07 (2.55)	**19.03 (p < 0.01)**	2851 (392)	125 (135)	**19.40 (p < 0.01)**
Morus rubra	0.02 (0.75)	1.96 (0.44)	**108.4 (p < 0.01)**	13 (57)	108 (33)	2.07 (p = 0.29)
Nyssa sylvatica	0.77 (3.03)			13 (1568)		
Osmanthus americanus		0.24 (5.10)			125 (269)	
Persea borbonia		0.08 (2.08)			88 (110)	
Pinus elliottii	24.65 (1.62)	9.67 (1.70)	**16.2 (p < 0.01)**	3862 (392)	142 (90)	**8.17 (p < 0.01)**
Prunus serotina	0.41 (1.62)			70 (839)		
Quercus hemisphaerica	0.89 (1.15)	4.31 (1.92)	**8.62 (p = 0.01)**	53 (573)	138 (102)	**6.75 (p = 0.02)**
Quercus laurifolia		6.27 (2.28)			130 (120)	
Quercus nigra	0.90 (1.01)	1.19 (2.08)	0.68 (p = 0.68)	78 (496)	44 (110)	2.32 (p = 0.14)
Quercus pagoda	0.16 (1.43)	0.19 (2.94)	0.07 (p = 0.80)	81 (17)	13 (29)	**8.11 (p = 0.02)**
Quercus virginiana	2.22 (1.11)	8.06 (1.70)	**4.68 (p = 0.04)**	64 (593)	146 (90)	2.76 (p = 0.11)
Sabal palmetto	3.04 (1.92)	2.79 (2.94)	0.03 (p = 0.87)	38 (992)	33 (156)	0.05 (p = 0.83)
Tilia americana var. *caroliniana*		4.47 (3.61)			206 (190)	
Triadica sebifera[a]	3.11 (0.67)	0.53 (1.90)	**13.04 (p < 0.01)**	1875 (392)	141 (135)	**40.70 (p < 0.01)**
Vaccinium arboreum		0.09 (2.55)			31 (135)	
	32.95 (1.48)	31.03 (2.52)	0.82 (p = 0.37)	1530 (136)	237 (215)	**25.85 (p < 0.01)**

[a] Denotes non-native species.

Table 3
Ecological characteristics of woody species recorded only in disturbed forests at Parris Island, South Carolina.

Species	Ecological characteristics
Ailanthus altissima[a]	Non-native invasive. Intolerant of shade, pioneer species (Burns and Honkala, 1990)
Baccharis halimifolia	Occurs along right-of-ways and in open forests and new forest plantations as well as shore hammocks, sea beaches, salt marshes, and low grounds inland. Noxiously weedy with expansion of range along right-of-ways and disturbed areas (Miller and Miller, 2005)
Callicarpa americana	Open to shady habitats. Most frequent and abundant on moist sites under open pine canopies (Miller and Miller, 2005)
Diospyros virginiana	Grows in a wide range of conditions. Shade tolerant, slow growing (Burns and Honkala, 1990)
Lantana camara[a]	Non-native invasive
Melia azedarach[a]	Non-native invasive. Frequently associated with disturbance and is commonly associated with other early successional species such as *P. taeda* and *L. styraciflua* (Waggy, 2009)
Nyssa sylvatica	Tolerant of shade, moderate growth rate (Burns and Honkala, 1990)
Prunus serotina	Intolerant of shade. Does not live for extended periods or move up to larger size classes without moderate to heavy opening in the overstory canopy (Burns and Honkala, 1990)

[a] Denotes non-native species.

Although species richness was not significantly different between disturbance types for the ground layer vegetation (remnant = 12.5 ± 1.5 species; disturbed = 14.9 ± 0.9 species; $t = 1.4$; $p = 0.19$), abundance patterns varied. Mean total cover was greater for the disturbed forests (15.9 ± 0.6) compared to the remnant forests (8.8 ± 1.0) ($t = 6.1$; $p < 0.01$). Similarly, mean cover of several functional groups differed between disturbance types; shrubs ($t = 3.2$; $p < 0.01$), subshrubs ($t = 3.2$; $p < 0.01$), trees ($t = 6.6$; $p < 0.01$), and vines ($t = 4.8$; $p < 0.01$) had significantly greater cover in disturbed forests than in remnant forests (Fig. 4).

3.2. Chinese tallow establishment patterns in relation to contemporary anthropogenic disturbance

Chinese tallow density was significantly related to the number of entries from silvicultural practices. The number of prescribed burns (since 1990) and number of thinning entries (since 1989) explained approximately 34% of the variation in Chinese tallow density across all disturbed forest plots ($F = 10.24$; $p < 0.01$). The *t*-test showed that the establishment date of Chinese tallow was not statistically different from the timing of thinning operations ($n = 1047$; $t = 0.83$; $p = 0.41$). The mean difference between thinning and establishment date was 0.22 years, suggesting that invasion occurred coincident with thinning. In contrast, year of burn was statistically different from establishment year ($n = 740$; $t = -12.8$; $p < 0.001$). Mean difference of establishment and year of burn was −3.38 years, suggesting that establishment occurred

Table 4
Ecological characteristics of woody species recorded only in remnant forests at Parris Island, South Carolina.

Species	Ecological characteristics
Aesculus pavia	Common shrub in fertile, well-drained and moist forests, including low forests, protected sites on upland forests, and swamp margins (Miller and Miller, 2005)
Carya tomentosa	Tolerant to intolerant of shade (Burns and Honkala, 1990)
Ilex opaca	Very tolerant of shade. Mainly associated with trees of bottomlands, swamps, or other sites not subjected to fire (Burns and Honkala, 1990)
Ligustrum sinense[a]	Non-native invasive. Shade tolerant and can invade relatively undisturbed habitats following the formation of canopy gaps (Munger, 2003)
Magnolia grandiflora	Tolerant of shade. Grows on rich lowland sites, or mesic upland sites where fire is rare. Considered to be one of the major species of the potential climax forest of the southeastern coastal plain (Burns and Honkala, 1990)
Osmanthus americanus	Tolerant of shade. Understory component of mesic coastal plain forests (Fralish and Franklin, 2002)
Persea borbonia	Tolerant of shade. Occurs on the borders of swamps and swampy drains in the rich, moist, mucky soil of the lower coastal plain, or in shallow ponds, strands, and pococins of pine woods (Burns and Honkala, 1990)
Tilia americana var. *caroliniana*	Tolerant of shade. Particular in its soil and moisture requirements, cannot tolerate very wet to very dry conditions, and almost always grows on moist but well-drained soils (Burns and Honkala, 1990)
Vaccinium arboreum	Occupies a wide range of sites and conditions, and is a component of southern mixed hardwood forests which represent the dominant climax upland vegetation in the southeastern coastal plain (Tirmenstein, 1991)

[a] Denotes non-native species.

prior to burning, and thus Chinese tallow may survive fire if burned after four growing seasons of growth. The number of Chinese tallow stems that established within the disturbed plots increased exponentially through time [number = 2.3e−152 $*$ exp (0.176701 $*$ est year); R^2 = 0.89; MSE = 291.0] (Fig. 5), with a large proportion establishing within three years of disturbance.

4. Discussion

Our study provides evidence that land cleared for agriculture and then reforested to pine plantations and managed with thinning and prescribed fire resulted in persistent alterations in stand composition and structure that might have provided establishment opportunities and facilitated the growth of Chinese tallow populations. For example, disturbed stands had lower species richness, greater between-stand similarity in species composition, and reduced heterogeneity in stand structure, with smaller diameter classes dominated by a few pioneer species. The greater richness and density of all woody, non-native invasives in disturbed stands suggest that community invasibility generally increased with disturbance. Previous studies have also shown that areas cleared for agriculture often become compositionally and biogeochemically distinct from adjacent areas that have never been cleared or used for agricultural purposes (Compton and Boone, 2000; Eberhardt et al., 2003). In longleaf pine savannas, post-agricultural sites had lower species richness attributed to the depletion of soil resource availability, the increase of tree abundance, and suppression of fire (Flinn and Marks, 2007; Veldman et al., 2014). Conversion of forest to agriculture and subsequent abandonment in Quebec, Canada resulted in functionally diverse forests transitioning to functionally similar old-field communities (Mayfield et al., 2010). These human land-use alterations can make enduring changes to patterns of biodiversity that may persist for decades or longer (Vellend et al., 2007).

Maritime forests have an herbaceous layer that is typically sparse and low in species diversity, with most of the diversity being in trees and shrubs (Bellis, 1995). The dissimilarity of woody species in remnant forests in our study is consistent with Schafale and Weakley (1990), who reported that maritime forest communities vary naturally based on their physio-topographic position (e.g., distance from marsh, degree of protection from salt spray, elevation, height of water table). Our results are also consistent with those of Bratton and Miller (1994), who reported a greater abundance of vines, grasses, and forbs in former agricultural fields and grazing lands on Cumberland Island, GA than in sites without agricultural history. Changes in structure and composition of maritime forests have been attributed to historical fire suppression, land-clearing, and logging, leading to dense woody vegetation and abundant greenbriars (*Smilax* spp.) (Frost, 2005), similar to the differences seen in the remnant and disturbed forests at Parris Island (Fig. 6).

Reforestation to pine plantations following agricultural abandonment resulted in highly similar forest structure and composition dominated by four woody species (slash pine, Chinese tallow, yaupon, and wax myrtle) and a very dense shrub layer. In contrast, remnant forest communities had fewer stems per hectare but greater woody species richness and more shade tolerant species across the range of diameter classes, resulting in heterogeneous forest structure and composition. Most of the disturbed forests at Parris Island were established as part of a reforestation effort on post-agricultural lands in the 1970s, and these stands were also thinned for the management of timber resources and burned to promote military training exercises and wildlife habitat. The shift in canopy composition from hardwood to pine, and the canopy openness resulting from thinning and burning likely contributed to the observed greater abundance of ground layer vegetation in disturbed forests.

Life history traits and modes of reproduction can define a species' ability to overcome barriers to invasion and hence their ability to invade (Richardson et al., 2011). Chinese tallow is documented as being relatively shade tolerant and is more shade tolerant than native cherrybark oak (Jones and McLeod, 1989). In comparison to the other commonly occurring native woody species at Parris Island, Chinese tallow has the shortest period to maturity and the longest known period for soil seed banking (Table 5). Being relatively shade tolerant also allows Chinese tallow to establish under an intact forest canopy, while rapid growth and high tolerance to stress may allow it to outcompete less disturbance-adapted native species. These characteristics may allow Chinese tallow populations to rapidly increase and continue to grow after initial establishment.

The concept that disturbance facilitates invasions is one of the most commonly accepted ideas in invasion ecology (Lockwood et al., 2013). In our study, Chinese tallow occurred most commonly in stands with disturbance histories that included agriculture, pine plantation establishment, and ongoing forest management. These disturbances changed the structure and composition of the forest community, possibly increasing available resources and niche space for non-native plant invasion. We speculate that these disturbances facilitated Chinese tallow invasion by increasing available resources at least temporarily, as suggested by the fluctuating resource hypothesis (Davis et al., 2000; Lockwood et al., 2013). Thus, the invasibility of a community is a dynamic property that changes with time and circumstances (Lockwood et al., 2013). Our findings are similar to those of Mosher et al. (2009), who found that areas in the northeastern U.S. that had

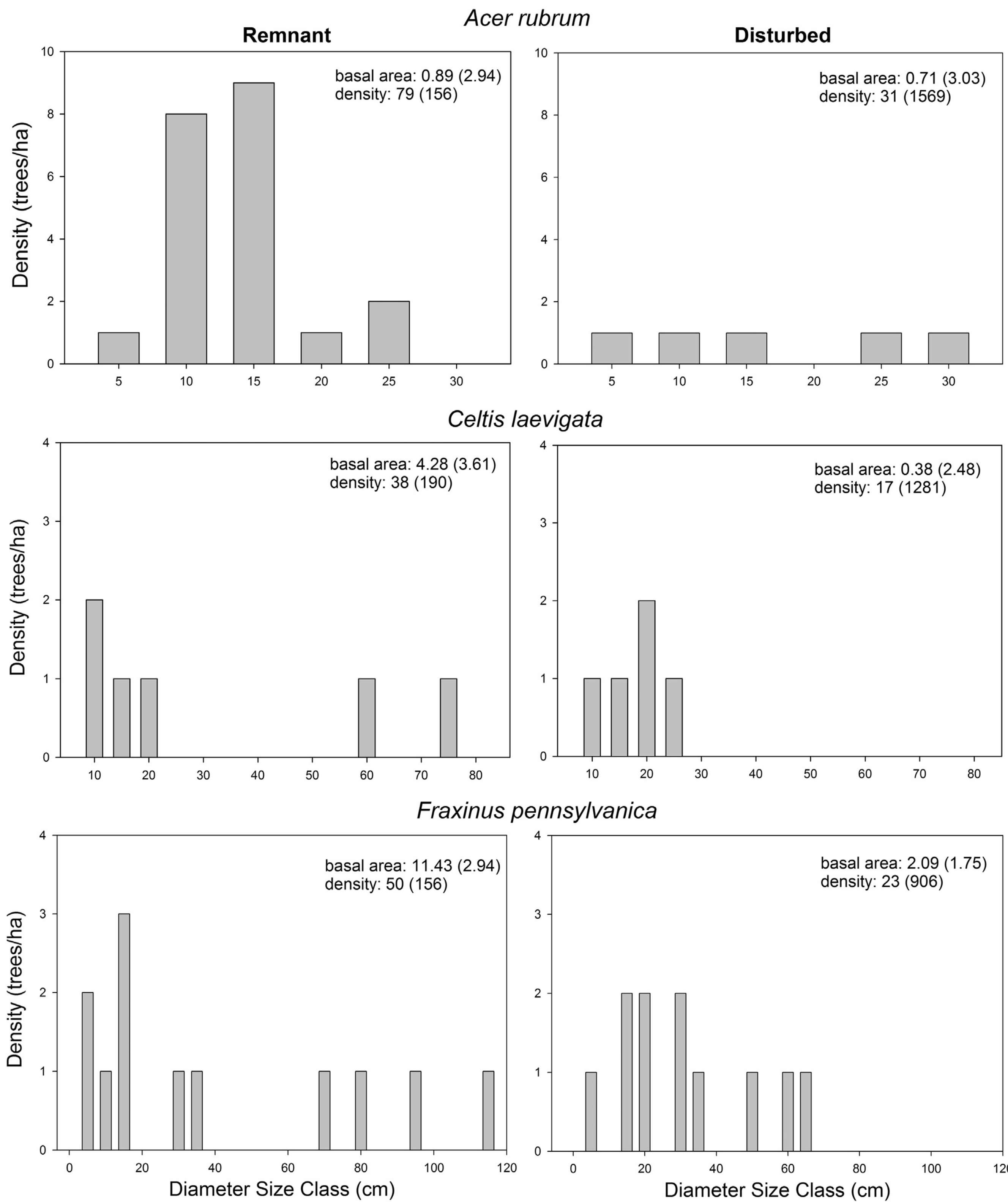

Fig. 3. Diameter distributions by density (trees/ha) of tree (>3 cm DBH) species common to both forest disturbance types (disturbed vs. remnant) at Parris Island, SC.

not undergone land use changes since 1934, remaining as either continuously forested or in constant cultivation, had the lowest incidence of woody plant invasion. In the southern Appalachian mountains, invasive plant species were found in the greatest abundance on plots that had regrown to forest from abandoned agriculture since the 1940s (Kuhman et al., 2010), suggesting that species establish in response to the changes caused by land use history. Chinese tallow was present on Parris Island prior to the

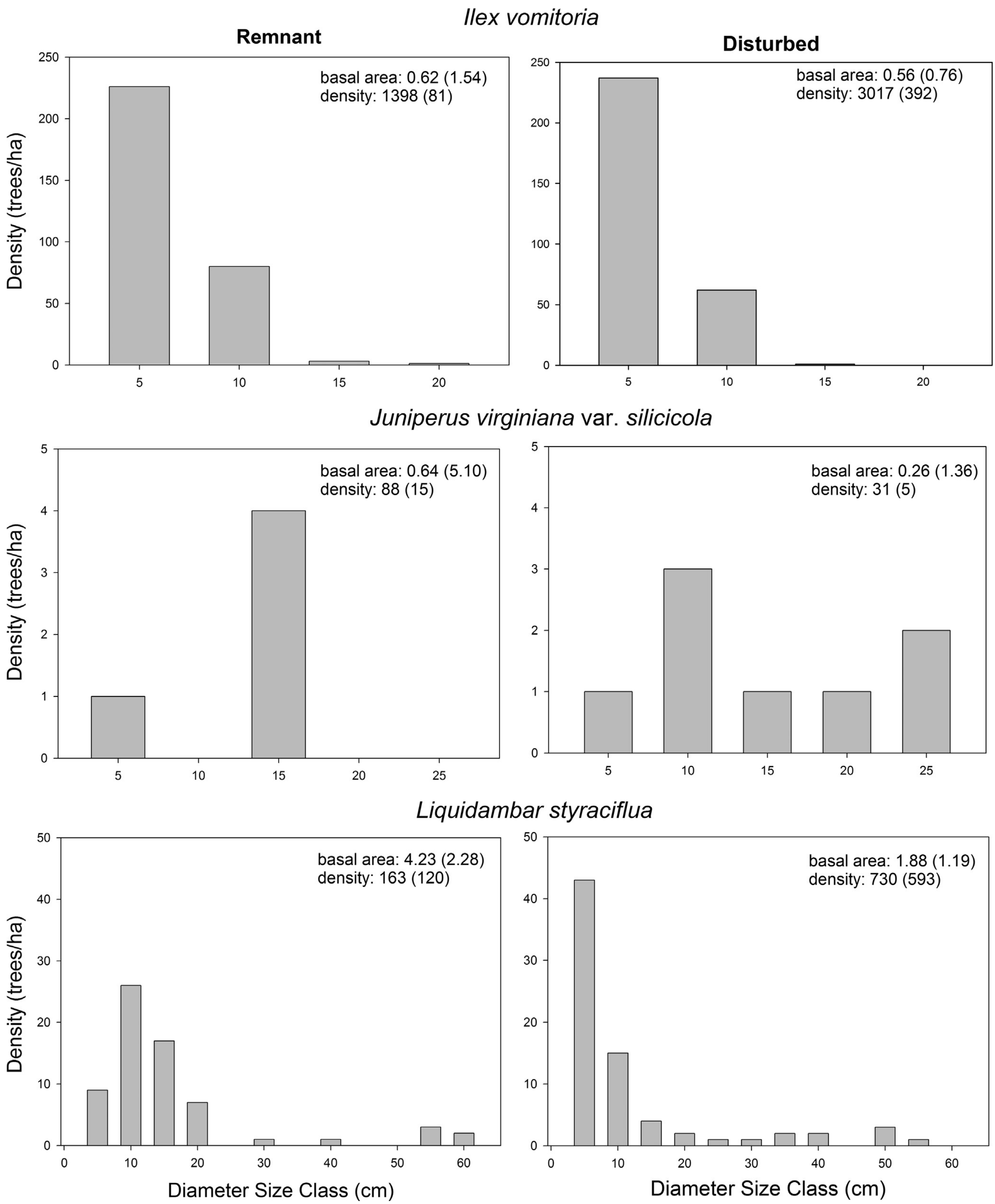

Fig. 3 (*continued*)

establishment of plantation forests. While maintained as agricultural fields, these sites may have resisted invasion by Chinese tallow due to repeated mowing. However, after conversion to pine plantations, reduced mechanical disturbance may have allowed Chinese tallow to invade, grow, and reproduce at these sites.

Forest operations, such as thinning, can provide favorable conditions for plant establishment, including increased sunlight to the forest floor, exposed mineral soil, and reduced competition. Thinning and burning have been documented to have positive effects on some non-native plant species (Nelson et al., 2008).

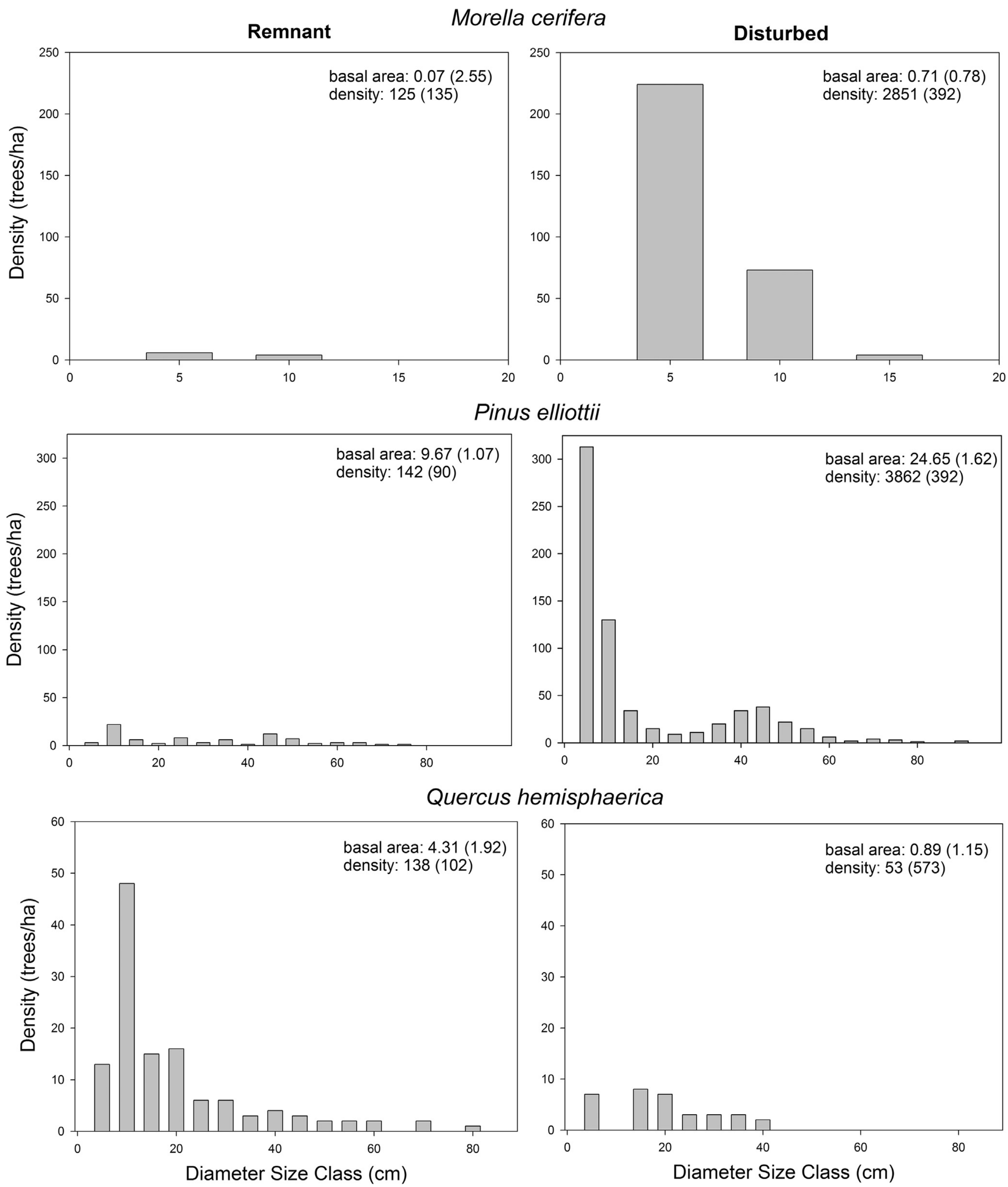

Fig. 3 (*continued*)

We found that thinning facilitated the establishment in Chinese tallow in the disturbed forests, and remnant forests, which had not been actively managed, had few established Chinese tallow individuals. Although we are unable to separate effects of land-use history from contemporary forest thinning effects on Chinese tallow establishment, the coincidence of Chinese tallow establishment year and year of thinning event suggests that this practice provided an additional opportunity for establishment. Additionally, our results indicate that Chinese tallow has the ability to survive low intensity surface fires and may have a greater likelihood of survival if burning occurs at least 4-years after establishment.

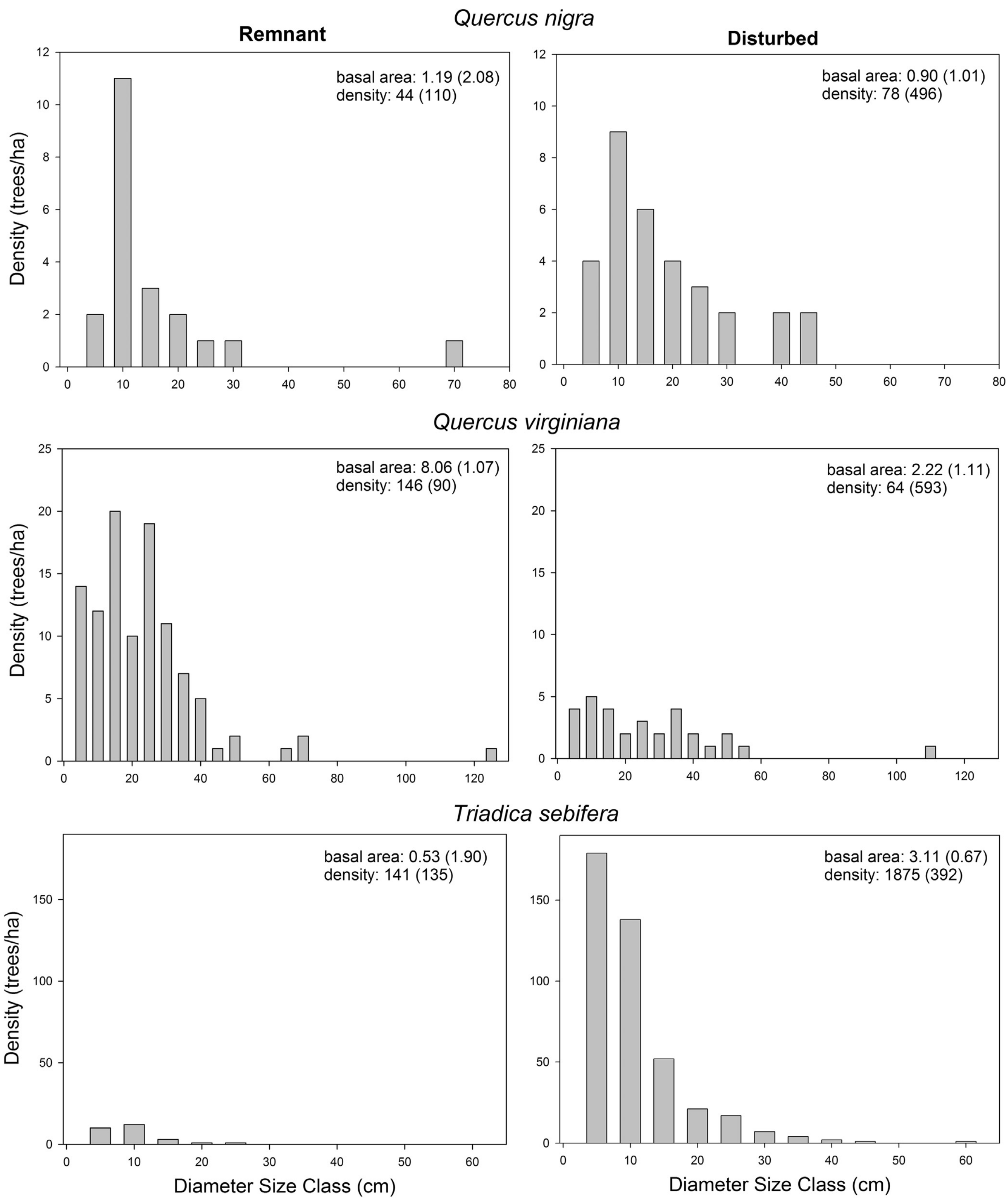

Fig. 3 (*continued*)

The lag phase of Chinese tallow establishment in the disturbed stands is evident from the 1970s, when reforestation began, to the late 1990s when the exponential increase began (Fig. 5). The high rate of seed production of Chinese tallow has been cited as important to its invasiveness (Conway et al., 2000). Chinese tallow has been cultivated in China for 14 centuries as a seed producing crop species (Bruce et al., 1997), and the invasive success of Chinese tallow could be a result of the artificial selection for high seed

Table 5
Physiological and seed characteristics of the most common tree species found in both disturbance types at Parris Island. Information gathered from Burns and Honkala (1990).

Species	Shade tolerance	Age to reproductive maturity (years)	Growth rate	Seed bank (years)
Acer rubrum	Tolerant	4	Rapid when young	1
Celtis laevigata	Tolerant	15	Moderate to fast	
Fraxinus pennsylvanica	Intermediate to intolerant	8–10 cm DBH (or 40+ years)	Moderate	4
Juniperus virginiana var. *silicicola*	Intolerant to very intolerant	10	Moderate to slow	
Liquidambar styraciflua	Intolerant	20 to 30	Fast	
Morus rubra	Tolerant	10		
Pinus elliottii	Intolerant	10 to 15	Rapid	
Quercus hemisphaerica	Tolerant	15 to 20	Fast	
Quercus nigra	Intolerant	20	Slow early growth; rapid on favorable sites	
Quercus pagoda	Intermediate to intolerant	25	Fast	
Quercus virginiana	Intermediate	50	Rapid when young	
Triadica sebifera[a]	Intermediate to intolerant	3	Rapid	5

[a] Denotes non-native species.

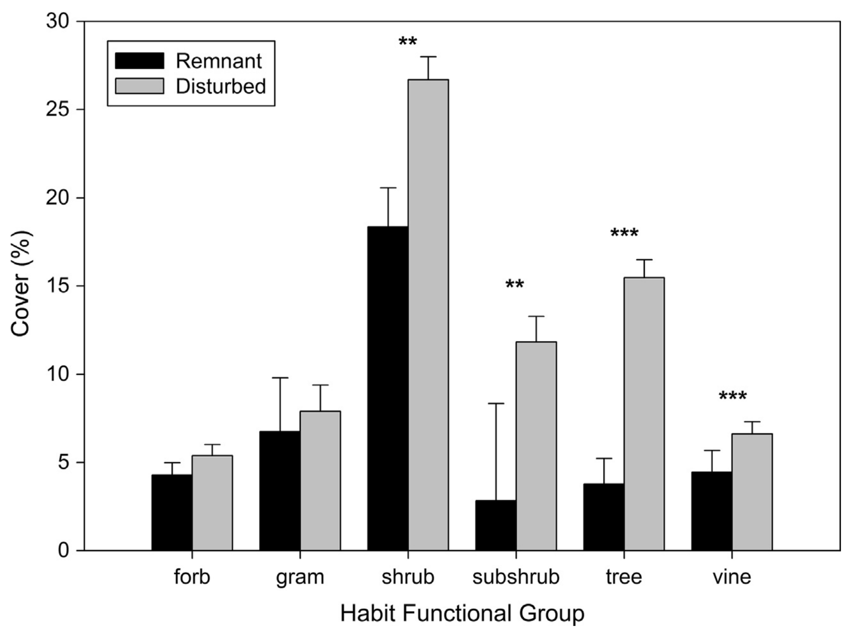

Fig. 4. Cover of plant habit functional groups (mean and standard error) recorded in 1 × 1 m ground layer quadrats at Parris Island by disturbance type (asterisks depict level of significance: ** significance of $p < 0.01$; *** significance of $p < 0.001$).

production prior to its introduction to North America (Butterfield et al., 2004). In addition, Chinese tallow seeds are consumed in large numbers by diverse bird assemblages (Renne et al., 2000, 2001). In the absence of disturbance, the lag phase for invasion in the remnant stands may be longer as the propagules continue to accumulate through active seed dispersal from adjacent disturbed forest into the remnant forest, especially as Chinese tallow seeds are known to remain viable for at least 5-years in the soil seed bank (Cameron et al., 2000).

Human-mediated disturbance events have been previously cited as facilitating Chinese tallow invasions. In South Carolina, the greatest density and largest reproductive Chinese tallow trees were found predominately on highly impacted spoil dredge areas and other very disturbed sites (Renne et al., 2001). Forest disturbances from timber management practices, including forest restoration, have also been shown to facilitate Chinese tallow establishment (Johns et al., 1999). Chinese tallow was reported as a minor component of three pine plantations prior to harvest in an effort to restore bottomland forests in Texas, after which Chinese tallow invaded and was the dominant species in all three areas (Johns et al., 1999). In eastern Texas, more than 50% of the forests invaded by Chinese tallow were documented as managed forest stands less than 30 years old (Wang et al., 2014).

Although disturbance events may drive the initial establishment of Chinese tallow, increased propagule supply can lead to continued establishment without additional disturbance. Community resistance to invasion can be overwhelmed as the propagule supply increases, and, as a result, even small-scale disturbances (e.g., single tree mortality, soil disturbance from faunal inhabitants, weather events) could lead to increased establishment in the nearby remnant forests. High propagule supply will increase the likelihood of seeds and seedlings finding refuge (i.e., "safe sites" for establishment) from competition (D'Antonio et al., 2001). The exponential increase in Chinese tallow establishment through time in our study is characteristic of biological invasions, suggesting that as an increasing number of individuals become established the propagule pressure also increases.

5. Management implications

Disturbed forests should be a high management priority for the treatment and monitoring of Chinese tallow due to its ability to

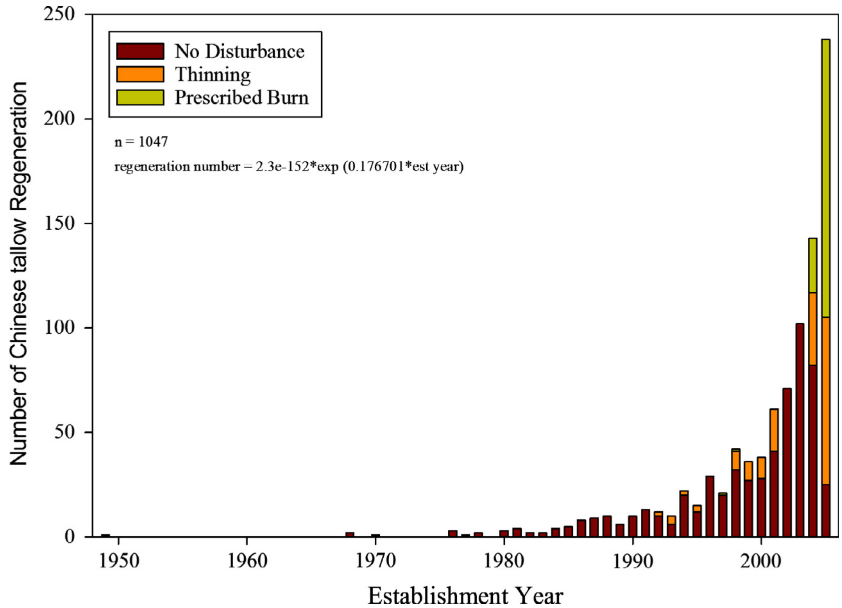

Fig. 5. The total number of Chinese tallow regeneration by year, with the colors depicting the number of regeneration that occurred within a three year time period following a disturbance event (thinning or prescribed burn) or establishment with no associated disturbance.

Fig. 6. Photographs providing examples of disturbed forest stands (left) and remnant forest stands (right) at Parris Island, SC. Disturbed forests are characterized by high stem density of smaller diameter trees and a ground layer vegetation dominated by woody species. Remnant forests have multiple strata in the forest canopy and a sparse herbaceous layer.

rapidly establish and obtain dominance following disturbance events. Invasive species management in disturbed forests should take a proactive approach to restore desired native communities or a novel assemblage of desired species to create an ecological community that may have greater resistance to invasion by Chinese tallow.

Our study found that contemporary silvicultural practices such as thinning and prescribed burning facilitated the establishment of Chinese tallow. Therefore, in forests that are currently managed for timber resources and wildlife habitat and readily exposed to propagules of Chinese tallow, innovative management practices that can reduce the invasion of non-native invasive species and promote native species diversity must be developed and adopted. Combined management approaches that build community resistance to invasion and/or the use of biological control agents may provide effective options for the Chinese tallow control (Wheeler and Ding, 2014; Wheeler et al., 2017; Pile et al., in press). More research is required to better understand the effects of management activities such as thinning and prescribed burning on Chinese tallow recruitment, establishment, and persistence.

Existing remnant forests are important for many reasons, including the provision of propagules to foster a resilient landscape, serving as the reference for the restoration of maritime forests, and providing important ecosystem services. Therefore, these remnant forests should be given a high conservation priority, avoiding anthropogenic activities that may promote the invasion of Chinese tallow or other exotic plants.

Acknowledgements

This research was supported by the Department of Defense and the Cooperative Ecosystem Studies Unit, Fort Worth District. We would like to thank the natural resource staff at Parris Island MCRD: John Holloway Jr., Van Horton, and Charles Pinckney for their help and support on the project. We would also like to especially thank our research technicians, Hunter M. Hadwin and Steven C. Broom who helped collect data during the hot and humid coastal summers at Parris Island MCRD. In addition, we would like to thank Dr. Robert Baldwin who inspired the idea and two anonymous reviewers who provided insightful comments and suggestions on the manuscript. We would also like to thank Drs. Tom Waldrop and Patricia Layton for their comments on previous versions of the manuscript.

References

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecol. 26, 32–46. http://dx.doi.org/10.1111/j.1442-9993.2001.01070.pp.x.

Bellis, V.J., 1995. Ecology of maritime forests of the southern Atlantic coast: a community profile. In: Opler, P.A. (Ed.), Biological Report. DTIC Document.

Belote, R.T., Jones, R.H., 2009. Tree leaf litter composition and nonnative earthworms influence plant invasion in experimental forest floor mesocosms. Biol. Invasions 11, 1045–1052.

Bratton, S.P., Miller, S.G., 1994. Historic field systems and the structure of maritime oak forests, Cumberland Island National Seashore, Georgia. Bull. Torrey Bot. Club, 1–12.

Bruce, K.A., Cameron, G.N., Harcombe, P.A., 1995. Initiation of a new woodland type on the Texas coastal prairie by the Chinese tallowtree (*Sapium sebiferum* (L.) Roxb.). Bull. Torrey Bot. Club 122, 215–225.

Bruce, K.A., Cameron, G.N., Harcombe, P.A., Jubinsky, G., 1997. Introduction, impact on native habitats, and management of a woody invader, the Chinese tallow tree, *Sapium sebiferum* (L.) Roxb. Nat. Areas J. 17, 255–260 <http://www.jstor.org/stable/43911684>.

Burke, M.J., Grime, J., 1996. An experimental study of plant community invasibility. Ecology 77, 776–790.

Burns, R.M., Honkala, B.H., 1990. Silvics of North America: 1. Conifers; 2. Hardwoods, Agriculture Handbook 654. U.S. Department of Agriculture, Forest Service, Washington, DC.

Butterfield, B.J., Rogers, W.E., Siemann, E., 2004. Growth of Chinese tallow tree (*Sapium sebiferum*) and four native trees under varying water regimes. Tex. J. Sci. 56, 335–346.

Camarillo, S.A., Stovall, J.P., Sunda, C.J., 2015. The impact of Chinese tallow (*Triadica sebifera*) on stand dynamics in bottomland hardwood forests. For. Ecol. Manage. 344, 10–19. http://dx.doi.org/10.1016/j.foreco.2015.02.013.

Cameron, G.N., Glumac, E.G., Eshelman, B.D., 2000. Germination and dormancy in seeds of *Sapium sebiferum* (Chinese tallow tree). J. Coastal Res. 16, 391–395. <http://www.jstor.org/stable/4300048>.

Cameron, G.N., Spencer, S.R., 2010. Entomofauna of the introduced Chinese tallow tree. Southwest. Naturalist 55, 179–192. http://dx.doi.org/10.1894/JC-28.1.

Compton, J.E., Boone, R.D., 2000. Long-term impacts of agriculture on soil carbon and nitrogen in New England forests. Ecology 81, 2314–2330. http://dx.doi.org/10.2307/177117.

Conner, W.H., 1994. The effect of salinity and waterlogging on growth and survival of baldcypress and Chinese tallow seedlings. J. Coastal Res. 10, 1045–1049 <http://www.jstor.org/stable/4298295>.

Conner, W.H., Askew, G.R., 1993. Impact of saltwater flooding on red maple, redbay, and Chinese tallow seedlings. Castanea 58, 214–219.

Conway, W.C., Smith, L.M., Bergan, J.F., 2000. Evaluating germination protocols for Chinese tallow (*Sapium sebiferum*) seeds. Tex. J. Sci. 52, 267–270.

Crooks, J.A., 2002. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. Oikos 97, 153–166. http://dx.doi.org/10.1034/j.1600-0706.2002.970201.x.

D'Antonio, C., Levine, J., Thomsen, M., 2001. Ecosystem resistance to invasion and the role of propagule supply: a California perspective. J. Mediterranean Ecol. 2, 233–246.

Davis, M.A., Grime, J.P., Thompson, K., 2000. Fluctuating resources in plant communities: a general theory of invasibility. J. Ecol. 88, 528–534. http://dx.doi.org/10.1046/j.1365-2745.2000.00473.x.

DiTomaso, J.M., 2000. Invasive weeds in rangelands: species, impacts, and management. Weed Sci. 48, 255–265. http://dx.doi.org/10.1614/0043-1745(2000) 048[0255:IWIRSI]2.0.CO;2.

Dukes, J.S., 2001. Biodiversity and invasibility in grassland microcosms. Oecologia 126, 563–568. http://dx.doi.org/10.1007/s004420000549.

Eberhardt, R.W., Foster, D.R., Motzkin, G., Hall, B., 2003. Conservation of changing landscapes: vegetation and land-use history of Cape Cod National Seashore. Ecol. Appl. 13, 68–84. http://dx.doi.org/10.2307/3099951.

EPA, 2003. Level III and IV Ecoregions of the Continental United States. In: National Health and Environmental Effects Research Laboratory (Ed.). United States Environmental Protection Agency.

Flinn, K.M., Marks, P., 2007. Agricultural legacies in forest environments: tree communities, soil properties, and light availability. Ecol. Appl. 17, 452–463.

Flinn, K.M., Vellend, M., 2005. Recovery of forest plant communities in post-agricultural landscapes. Front. Ecol. Environ. 3, 243–250.

Fralish, J.S., Franklin, S.B., 2002. Taxonomy and Ecology of Woody Plants in North American Forests (Excluding Mexico and Subtropical Florida). John Wiley & Sons, Hoboken, NJ.

Frost, C., 2005. Rapid assessment reference condition model - R9MARF Maritime Forest. In: USDA Forest Service (Ed.). LANDFIRE, USDA Forest Service.

Gan, J., Miller, J.H., Wang, H., Taylor, J.W., 2009. Invasion of tallow tree into southern US forests: influencing factors and implications for mitigation. Can. J. For. Res. 39, 1346–1356. http://dx.doi.org/10.1139/X09-058.

Hermy, M., Verheyen, K., 2007. Legacies of the past in the present-day forest biodiversity: a review of past land-use effects on forest plant species composition and diversity. In: Sustainability and Diversity of Forest Ecosystems. Springer, pp. 361–371.

Hobbs, R.J., Huenneke, L.F., 1992. Disturbance, diversity, and invasion: implications for conservation. Conserv. Biol. 6, 324–337.

Jaccard, P., 1912. The distribution of the flora in the alpine zone. New Phytol. 11, 37–50.

Jackson, R.B., Banner, J.L., Jobbágy, E.G., Pockman, W.T., Wall, D.H., 2002. Ecosystem carbon loss with woody plant invasion of grasslands. Nature 418, 623–626. http://dx.doi.org/10.1038/nature00910.

Johns, D.T., Williams, B., Williams, H.M., Stroupe, M., 1999. Seedling survival and natural regeneration for a bottomland hardwood planting on sites differing in site preparation. In: Haywood, J. (Ed.), 10th Biennial Southern Silvicultural Research Conference, USDA For. Serv., Gen. Tech. Rep. SRS-30, Southern Research Station, Asheville, NC, pp. 145–150.

Jones, R.H., McLeod, K.W., 1989. Shade tolerance in seedlings of Chinese tallow tree, American sycamore, and cherrybark oak. Bull. Torrey Bot. Club 116, 371–377. http://dx.doi.org/10.2307/2996627.

Kuhman, T.R., Pearson, S.M., Turner, M.G., 2010. Effects of land-use history and the contemporary landscape on non-native plant invasion at local and regional scales in the forest-dominated southern Appalachians. Landscape Ecol. 25, 1433–1445.

Lamarque, L.J., Delzon, S., Lortie, C.J., 2011. Tree invasions: a comparative test of the dominant hypotheses and functional traits. Biol. Invasions 13, 1969–1989. http://dx.doi.org/10.1007/s10530-011-0015-x.

Lockwood, J.L., Hoopes, M.F., Marchetti, M.P., 2013. Invasion Ecology. John Wiley & Sons, West Sussex, UK.

Lonsdale, W.M., 1999. Global patterns of plant invasions and the concept of invasibility. Ecology 80, 1522–1536. http://dx.doi.org/10.2307/176544.

Lozon, J.D., MacIsaac, H.J., 1997. Biological invasions: are they dependent on disturbance? Environ. Rev. 5, 131–144.

Mayfield, M.M., Bonser, S.P., Morgan, J.W., Aubin, I., McNamara, S., Vesk, P.A., 2010. What does species richness tell us about functional trait diversity? Predictions and evidence for responses of species and functional trait diversity to land-use change. Glob. Ecol. Biogeogr. 19, 423–431.

McArdle, B.H., Anderson, M.J., 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology 82, 290–297. http://dx.doi.org/10.1890/0012-9658(2001) 082[0290:FMMTCD]2.0.CO;2.

Miller, J.H., Miller, K.V., 2005. Forest Plants of the Southeast and Their Wildlife Uses. University of Georgia Press, Athens, Georgia.

Minchinton, T.E., 2002. Disturbance by wrack facilitates spread of *Phragmites australis* in a coastal marsh. J. Exp. Mar. Biol. Ecol. 281, 89–107.

Mosher, E.S., Silander Jr, J.A., Latimer, A.M., 2009. The role of land-use history in major invasions by woody plant species in the northeastern North American landscape. Biol. Invasions 11, 2317–2328.

Munger, G.T., 2003. *Ligustrum* spp. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: <http://www.fs.fed.us/database/feis/> (2014, December 2).

Munro, N.T., Fischer, J., Wood, J., Lindenmayer, D.B., 2009. Revegetation in agricultural areas: the development of structural complexity and floristic diversity. Ecol. Appl. 19, 1197–1210. http://dx.doi.org/10.1890/08-0939.1.

Naeem, S., Knops, J.M.H., Tilman, D., Howe, K.M., Kennedy, T., Gale, S., 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. Oikos 91, 97–108. http://dx.doi.org/10.1034/j.1600-0706.2000.910108.x.

NatureServe, 2012. NatureServe Conservation Status. In: NatureServe <http://www.natureserve.org/explorer/ranking.htm>.

Nelson, C.R., Halpern, C.B., Agee, J.K., 2008. Thinning and burning result in low-level invasion by nonnative plants but neutral effects on natives. Ecol. Appl. 18, 762–770. http://dx.doi.org/10.1890/07-0474.1.

Peck, J.E., 2016. Multivariate Analysis for Ecologists: Step by Step. MjM Software Design, Gleneden Beach, OR.

Pianka, E.R., 1970. On r- and K-selection. Am. Nat. 104, 592–597. http://dx.doi.org/10.2307/2459020.

Pile, L.S., Wang, G.G., Waldrop, T.A., Walker, J.L., Bridges, W.C., Layton, P.A., in press. Managing an established tree invader: developing control methods for Chinese tallow (*Triadica sebifera*) in maritime forests. J. For. http://dx.doi.org/10.5849/jof.2016-022 (in press).

Pyšek, P., Jarošík, V., Hulme, P.E., Pergl, J., Hejda, M., Schaffner, U., Vilà, M., 2012. A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. Glob. Change Biol. 18, 1725–1737. http://dx.doi.org/10.1111/j.1365-2486.2011.02636.x.

Rejmánek, M., Richardson, D.M., 1996. What attributes make some plant species more invasive? Ecology 77, 1655–1661. http://dx.doi.org/10.2307/2265768.

Renne, I.J., Gauthreaux Jr, S.A., Gresham, C.A., 2000. Seed dispersal of the Chinese tallow tree (*Sapium sebiferum* (L.) Roxb.) by birds in coastal South Carolina. Am. Midland Naturalist 144, 202–215.

Renne, I.J., Spira, T.P., Bridges, W.C.J., 2001. Effects of habitat, burial, and passage through birds on germination and establishment of Chinese tallow tree in Coastal South Carolina. J. Torrey Botanical Soc. 128, 109–119.

Richardson, D.M., Pysek, P., Carlton, J.T., 2011. A compendium of essential concepts and terminology in invasion ecology. In: Richardson, D.M. (Ed.), Fifty Years of Invasion Ecology: The Legacy of Charles Elton. Blackwell Publishing Ltd, Oxford, UK, pp. 409–420.

Schafale, M.P., Weakley, A.S., 1990. Classification of the natural communities of North Carolina. Third approximation. North Carolina Department of Environment, Health, and Natural Resources, Division of Parks and Recreation, Natural Heritage Program. Raleigh, NC.

Scheld, H.W., Cowles, J.R., 1981. Woody biomass potential of the Chinese tallow tree. Econ. Bot. 35, 391–397.

Scheld, H.W., Cowles, J.R., Engler, C.R., Kleiman, R., E.B., S.J., 1984. Seeds of the Chinese tallow tree as a source of chemicals and fuels. In: Schultz Jr., E.B., Morgan, R.P. (Eds.), Fuels and chemicals from oil seeds: tecnology and policy options. Westview Press, American Association for the Advancement of Science, Boulder, CO, pp. 81–101.

Soil Survey Staff, 2013. Gridded Soil Survey Geographic (gSSURGO) Database for Beaufort, South Carolina. In: United States Department of Agriculture, N.R.C.S. (Ed.). United States Department of Agriculture, Natural Resources Conservation Service.

Tilman, D., 1997. Community invasibility, recruitment limitation, and grassland biodiversity. Ecology 78, 81–92. http://dx.doi.org/10.1890/0012-9658(1997)078[0081:CIRLAG]2.0.CO;2.

Tirmenstein, D.A., 1991. *Vaccinium arboreum*. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: <http://www.fs.fed.us/database/feis/> (2015, October 7).

Veldman, J.W., Brudvig, L.A., Damschen, E.I., Orrock, J.L., Mattingly, W.B., Walker, J.L., 2014. Fire frequency, agricultural history and the multivariate control of pine savanna understorey plant diversity. J. Veg. Sci. 25, 1438–1449. http://dx.doi.org/10.1111/jvs.12195.

Vellend, M., 2004. Parallel effects of land-use history on species diversity and genetic diversity of forest herbs. Ecology 85, 3043–3055. http://dx.doi.org/10.2307/3450544.

Vellend, M., Verheyen, K., Flinn, K.M., Jacquemyn, H., Kolb, A., Van Calster, H., Peterken, G., Graae, B.J., Bellemare, J., Honnay, O., 2007. Homogenization of forest plant communities and weakening of species–environment relationships via agricultural land use. J. Ecol. 95, 565–573.

Vilà, M., Ibáñez, I., 2011. Plant invasions in the landscape. Landscape Ecol. 26, 461–472.

Waggy, M.A., 2009. *Melia azedarach*. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: <http://www.fs.fed.us/database/feis/> (2014, December 2).

Wang, H.-H., Buchhorn, J.L., Grant, W.E., 2014. Effects of management on range expansion by Chinese Tallow in the forestlands of eastern Texas. J. Forest. 112, 346–353.

Wheeler, G.S., Ding, J., 2014. Is Chinese tallowtree, *Triadica sebifera*, an appropriate target for biological control in the United States? Invasive Plant Sci. Manage. 7, 345–359. http://dx.doi.org/10.1614/IPSM-D-13-00061.1.

Wheeler, G.S., Steininger, M.S., Wright, S., 2017. Quarantine host range of *Bikasha collaris*, a potential biological control agent of Chinese tallowtree (*Triadica sebifera*) in North America. Entomol. Exp. Appl. 163, 184–196. http://dx.doi.org/10.1111/eea.12573.

Yelenik, S., Stock, W., Richardson, D., 2004. Ecosystem level impacts of invasive *Acacia saligna* in the South African fynbos. Restor. Ecol. 12, 44–51.