Invasive Plant Science and Management

cambridge.org/inp

Research Article

Cite this article: Fan Z, Yang S, Liu X (2018) Spatiotemporal Patterns and Mechanisms of Chinese Tallowtree (*Triadica sebifera*) Spread along Edge Habitat in a Coastal Landscape, Mississippi, USA. Invasive Plant Sci Manag 11:117–126. doi: 10.1017/inp.2018.21

Received: 9 April 2018
Revised: 20 July 2018
Accepted: 23 August 2018

Associate Editor:
Songlin Fei, Purdue University

Key words:
Age structure; distance to seed trees; invasion history; soil seedbank; seedling recruitment

Author for correspondence:
Zhaofei Fan, School of Forestry and Wildlife Sciences, Auburn University, 602 Duncan Drive, Auburn, AL 36849.
(Email: zzf0008@auburn.edu)

© Weed Science Society of America, 2018.

Spatiotemporal Patterns and Mechanisms of Chinese Tallowtree (*Triadica sebifera*) Spread along Edge Habitat in a Coastal Landscape, Mississippi, USA

Zhaofei Fan[1], Shaoyang Yang[1,2] and Xia Liu[3]

[1]Associate Professor (ORCID: 0000-0003-0653-0646), School of Forestry and Wildlife Sciences, Auburn University, Auburn, AL, USA, [2]Graduate Research Assistant, Department of Forestry, Mississippi State University, Mississippi State, MS, USA and [3]Professor, College of Forestry, Nanjing Forestry University, Nanjing, Jiangsu 210037, China

Abstract

Chinese tallowtree [*Triadica sebifera* (L.) Small] has reached unprecedented prevalence in coastal landscapes in the Gulf of Mexico, especially along edge habitat with low competition and abundant resource (e.g., light) availability. This study investigated the spatiotemporal patterns and mechanisms of *T. sebifera* spread along roadways and fire lines. *Triadica sebifera* individuals and landscape and community features were surveyed in equally spaced, spatially mapped plots. All *T. sebifera* individuals were felled to determine tree age and status (seed trees or non-seed bearing trees), and *T. sebifera* seed and seedling (≤2 yr old) densities and community and landscape features (over- and understory conditions, distance to seed trees) were measured. A zero-inflated negative binomial model was used to evaluate factors affecting *T. sebifera* seed dispersal and seedling recruitment contributing to the observed spatiotemporal patterns. Introduced into the Grand Bay National Wildlife Refuge around 30 yr ago, *T. sebifera* trees distribute in clustered patterns along roadways and fire lines and exhibit an exponential growth in density. High *T. sebifera* seed and seedling densities mainly occurred in sites that are ≤250 m from seed trees or have sparse overstory and high understory grass/herb coverage. With respect to the avian seed dispersal mechanism, the spatiotemporal patterns of *T. sebifera* spread along roadways and fire lines could be simply characterized by using landscape and community features that influence avian behaviors, including distance to seed trees, overstory tree density, and ground grass/herb coverage.

Introduction

Habitat fragmentation creates edges with elevated resource (e.g., light) availability that often allow for the easy establishment and spread of invasive plants and as a result facilitate biological invasions in a landscape (Fahrig 2003; Vitousek et al. 1997). Plant invasion patterns often follow routes and edges that act as vectors for the introduction and spread of plant propagules (Fahrig 2003; Fletcher 2005; Ries et al. 2004). One particular invasive, Chinese tallowtree [*Triadica sebifera* (L.) Small], formerly *Sapium sebiferum*), is of high importance along the Gulf Coast of the United States. As for many other invasives, *T. sebifera* spread along edge habitat is often facilitated by disturbances. To date, it has invaded nine southeastern states, with the most severe occupations in the northern Gulf of Mexico coastal counties. Oswalt (2010) reported an up to 5-fold increase in the number of *T. sebifera* trees in Mississippi, Louisiana, and eastern Texas from the mid-1990s to late 2000s. Based on the most recent inventory data, *T. sebifera* has exceeded most native species, ranking 17 out of the 135 most encountered species in aboveground dry weight across the 67 coastal counties in northern Florida, Alabama, Mississippi, Louisiana, and eastern Texas (J Chappell, Forest Inventory and Analysis Coordinator, Alabama Forestry Commission, personal communication).

Favorable life history traits of *Triadica sebifera* (e.g., high specific leaf area, nutrient uptake, seed production, root/stump sprout capacity, and herbivore tolerance) in introduced regions enable it to grow well in a suite of soils such as sandy, clay, poorly drained, and even intermittently flooded areas, and its seedlings can tolerate a variety of light conditions (Barrilleaux and Grace 2000; DeWalt et al. 2011; Paudel and Battaglia 2015; Renne et al. 2001; Rogers and Siemann 2002; Tian et al. 2017; Zou et al. 2008). The significant threat of *T. sebifera* to native coastal ecosystems lies not only in its negative impact on native ecosystems through competition with native species, but also in its alteration and transformation of soil properties, composition, and structure of native ecosystems such as wetlands and

https://doi.org/10.1017/inp.2018.21 Published online by Cambridge University Press

Management Implications

Great effort has gone into the restoration of degraded, native ecosystems (e.g., longleaf pine [*Pinus palustris*]) and creating habitat for wildlife biodiversity in the Gulf of Mexico coastal region. It is imperative to evaluate the potential biological invasion risk associated with management activities such as timber extraction, understory release, prescribed fire, and snag retention to design efficient and effective methods to reduce ecological and economic losses. Part of the challenge has been to understand factors driving the invasion processes, including individual colonization and establishment, population expansion in native ecosystems, and postinvasion spread in a landscape from an integrated, multiscale perspective. Through spatial and quantitative analyses of factors associated with Chinese tallowtree [*Triadica sebifera* (L.) Small] invasion and spread along edge habitat, this study provided information on how to reduce *T. sebifera* invasion in restoring and managing native coastal ecosystems. Land and resource managers could base the observed spatiotemporal patterns of *T. sebifera* and risk factors (landscape and community features) to identify hot spots for landscape-level planning to prioritize control measures. With the coincidence between large-scale *T. sebifera* invasion and disturbance, a postdisturbance survey should be taken before the full establishment of *T. sebifera* in highly susceptible areas (e.g., habitat edges) and control measures such as prescribed burn, mechanical removal, or herbicide treatment should be conducted in a timely manner. With most *T. sebifera* seeds and individuals found within a distance of 250 m from seed trees, removal of seed trees may significantly impede seed dispersal and encroachment of *T. sebifera* in surrounding areas.

coastal prairies (Pile et al. 2017). If no active measures are taken, it may completely change native ecosystems, natural disturbance regimes, and ecosystem services (Donahue et al. 2006; Pile et al. 2017). The challenge in controlling *T. sebifera* in the coastal landscape, however, is primarily due to its strong, nonstationary, stochastic seed (propagule) dispersal and unprecedented spread rate, which are enabled by multiscale factors such as avian species, landscape and community features, and disturbances (e.g., flooding, hurricanes, storm water, fire, land-use change) (Conner et al. 2014; Fan et al. 2012; Gan et al. 2009; Henkel et al. 2016; Renne et al. 2000, 2002).

A landscape-level survey conducted in 2012 and 2013 in the Grand Bay National Wildlife Refuge (GBNWR) in southeast Mississippi found *T. sebifera* to be extraordinarily abundant in clustered patterns along roadways, fire lines, ditches, and trails (Stoklosa and Fan 2013). Using these edges as footholds, *T. sebifera* aggressively spread to surrounding areas and forest interiors, and the observed spread patterns suggest that the role of risk factors may change (facilitate or hinder) with scales, spatially and temporally, and by ecosystem (Fan 2018; Fan et al. 2012). In this study, we intend to understand the mechanisms underlying *T. sebifera* spread and quantify the effect of landscape metrics and community features on the spatiotemporal patterns along roadways and fire lines. As primary, permanent structures maintained or disturbed consistently by humans, roadways and fire lines contribute greatly to the rapid spread of *T. sebifera* in the coastal landscape via linking or separating different patches of ecosystems. Specifically, we aim to answer the following questions: (1) What are the factors associated with the spatiotemporal patterns of *T. sebifera* along roadways and fire lines in the GBNWR? (2) How do these factors affect *T. sebifera* seed dispersal and seedling recruitment that contribute to the observed patterns? Answers to these questions will improve understanding of the invasion history and key factors that contribute to the spread of *T. sebifera* as well as the development of effective management strategies to control *T. sebifera* in the coastal landscape.

Materials and Methods

Study Area

Grand Bay National Wildlife Refuge (GBNWR), located on the Mississippi/Alabama state line in Jackson County, MS (30.42°N, 88.42 °W), was established in 1992 to help protect one of the largest remaining expanses of endangered Gulf Coast wet pine savanna/flatwood habitat (Figure 1). Of the 7,305 ha within its boundary, there are 1,386 ha of private inholdings and 5,919 ha of public lands and waters. In addition to the wet pine savanna/flatwood, other habitats include maritime forest, tidal and nontidal wetlands, salt marshes, salt pannes, bays, and bayous (GBNWR 2009; https://www.fws.gov/refuge/grand_bay).

GBNWR lies within the gently sloping, lower Gulf Coastal Plain and is part of a retrograding delta of the Escatawpa River. It has a subtropical climate with hot, humid summers characterized by afternoon thunderstorms. Average annual maximum temperatures are 24.7 C, with July averages reaching 32.0 C. Winters are mild, with annual minimum temperatures averaging 14.7 C and January averages at 5.8 C. Light freezes are common, and hard freezes occasionally occur. Average annual rainfall is approximately 1.6 m, and extreme precipitation events may result in 0.25 to 0.76 m of rainfall over a short period of time (e.g., during a landfalling tropical cyclone) (Peterson et al. 2007). Such events have caused serious flooding along the nearby Escatawpa River (Wieland 2007).

The invasion of *T. sebifera* into the GBNWR originated from the private inholdings with large (old) *T. sebifera* trees distributed around property boundary lines and roadsides (Stokalosa and Fan 2013). Established in multiple sites along roadsides, *T. sebifera* is encroaching into fire lines, trails, and ditches, where disturbances occur most frequently, and into forest interiors due to avian seed dispersal following natural and anthropogenic disturbances (Fan 2018; Stokalosa and Fan 2013).

The Mechanisms of Triadica sebifera Spread along Roadways and Fire Lines

Roadways and fire lines are highly susceptible landscape features and serve as dispersal corridors for *T. sebifera* to spread into patch interiors and the entire landscape. Multiple factors across varying spatial and temporal scales interact and drive the spread of *T. sebifera* (Fan et al. 2012; Gan et al. 2009; Theoharides and Dukes 2007). Unlike previous studies, selected factors were organized into three functional groups (driving factors, predisposing factors, and inciting factors) based on the roles they play in three key processes—seed dispersal, seed germination, and seedling recruitment (growth)—to understand the mechanisms behind *T. sebifera* spread (Figure 2). Driving factors include birds and water currents that disperse *T. sebifera* seeds to a new site. The abundance of *T. sebifera* seeds and individuals (propagule pressure) on a site is proportionally related to the frequency and intensity of driving factors such as *T. sebifera* seed-dispersing bird

https://doi.org/10.1017/inp.2018.21 Published online by Cambridge University Press

activities (e.g., perching, foraging, roosting, nesting) and the flow or circulation of water current. Predisposing factors include community and landscape features such as canopy closure, tree density, the cover of ground vegetation, edge types (roadway and fire line), ecosystem type (e.g., maritime forest, pine flatwood, pine savanna, salt marsh), and distance to seed sources. These factors are the primary determinants of the spatial patterns of *T. sebifera* populations, regulating driving factors for seed dispersal and providing critical resources (e.g., light, moisture, substrate) for seed germination and seedling recruitment. Inciting factors include natural and anthropogenic disturbances such as hurricanes, tropical storms, timber extraction, prescribed fires, and construction of roads and fire lines. These factors usually initiate or facilitate *T. sebifera* invasion and alter the age structure (dynamics) by regulating and altering driving factors and predisposing factors. As a result, *T. sebifera*'s spatiotemporal distribution and age structure reflect the interactions of these factors across spatial and temporal scales (Figure 2).

Data Collection and Statistical Analysis

As a retrospective study, we surveyed *T. sebifera* trees along two major roadways (Missala Road and Bayou Heron Road) and two fire lines (numbered 1 and 2) to investigate *T. sebifera* invasion history, spread patterns, and associated factors (Figure 1). First, the presence (1) or absence (0) of *T. sebifera* was recorded within each of a sequence of 30 by 3 m^2 transects along both sides of the selected roadways and fire lines. A rectangular 10 by 3 m^2 plot was then taken in the center of each 30 by 3 m^2 transect, and the geographic coordinates of the center of each plot were recorded using a GPS device (Forge Echo, F4Device, http://www.thinkf4.com/solutions/forge-echo). Plots were equally spaced, and each was mapped for spatial data analysis.

Within each plot, overstory tree dbh (diameter at breast height of ~1.3 m) >10 cm, density (trees ha^{-1}), and basal area (m^2 ha^{-1}) by species and as a whole were calculated using individual tree dbh data. Canopy closure (%) was estimated using a densitometer, based on the readings of 1 (covered) or 0 (open) from a regular grid of 20 sampling points spaced at 1 by 1 m. In the understory, ground vegetation was classified as the grass/herbaceous layer and the woody shrub layer. The mean height (m) and coverage (%) of both layers were measured using the same regular grid of 20 sampling points spaced at 1 by 1 m. Finally, all *T. sebifera* individuals in each plot were felled to determine their age and distinguish them as either seed trees or non-seed trees (Tian 2017). Based on the age data, *T. sebifera* trees were grouped into three age cohorts: old (>21 yr), middle (11 to 20 yr), and young (1 to 10 yr); and *T. sebifera* density (trees ha^{-1}) by age

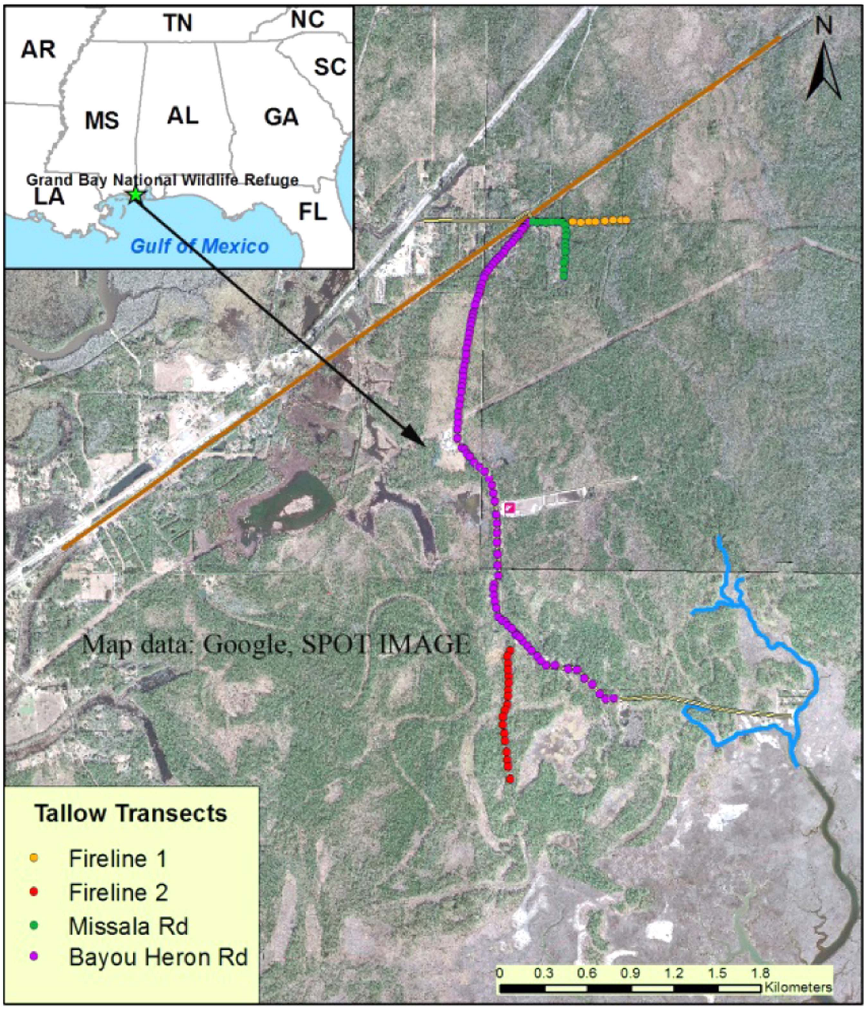

Figure 1. Google map showing the vegetation conditions and sampled plots along roadways and fire lines infested by *Triadica sebifera* in the Grand Bay National Wildlife Refuge and vicinity (circled in red), Mississippi.

https://doi.org/10.1017/inp.2018.21 Published online by Cambridge University Press

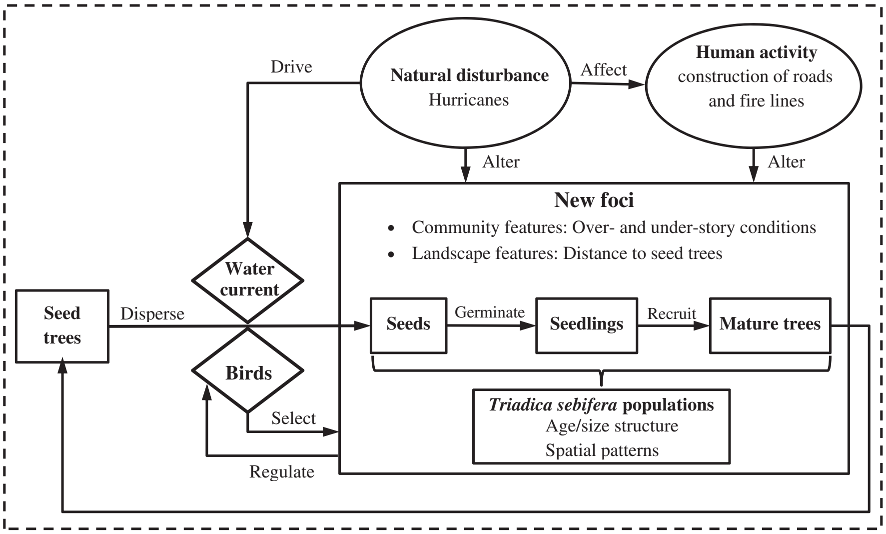

Figure 2. The potential mechanism (conceptual model) of *Triadica sebifera* seed dispersal and seedling recruitment along edge habitat in the coastal landscape. *Triadica sebifera* spread to new foci is driven by three processes—seed dispersal, seed germination, and seedling recruitment—which are affected by birds and water current (driving factors), community and landscape features (predisposing factors), and natural disturbance and human activities (inciting factors), respectively.

cohort and as a whole was calculated. *Triadica sebifera* seed density (no. m^{-2}) in the litter/humus and the top soil layer (0 to 2.5 cm) was counted in three regularly spaced 30 by 23 cm rectangular sampling areas for each plot. The nearest distance from each plot to *T. sebifera* seed trees was calculated using the mapped plot and seed tree data.

For Question 1, the runs test was first conducted to test the statistical significance of the observed spatially clustered patterns by using data on the presence or absence of *T. sebifera* within each transect of 30 by 3 m^2 along the selected roadways and fire lines. The age structure of *T. sebifera* trees by edge was plotted, and rank correlations in the number of *T. sebifera* individuals between different age classes were computed to characterize the temporal patterns (invasion history) of *T. sebifera*. The density of *T. sebifera* individuals by age cohort and soil *T. sebifera* seeds was mapped to show the spatiotemporal patterns of *T. sebifera* spread and spatial variations of propagule levels.

For Question 2, the total count of *T. sebifera* seeds and seedlings ≤2 yr for each plot or sample area was used to estimate the potential impact of measured variables/factors on seed dispersal and seedling recruitment. Because the count of *T. sebifera* seeds and seedlings in each plot followed a right-skewed, zero-inflated, and overdispersed (variance > > mean) discrete distribution, the mixture zero-inflated negative binomial model (ZINB, Equations 1 and 2) was used (Zeileis et al. 2008).

$$P(Y=y\mid \mu,\theta)=\begin{cases} P+(1-P)\left(1+\frac{\mu}{\theta}\right)^{-\theta}, y=0 \\ (1-P)\frac{\Gamma(\theta+y)}{y!\,\Gamma(\theta)}\left(1+\frac{\mu}{\theta}\right)^{-\theta}\left(1+\frac{\theta}{\mu}\right)^{-y}, y=1,2,\ \ldots \end{cases} \qquad [1]$$

where $\mu = E(Y)$ is the mean of the response variable Y (here, count of *T. sebifera* seeds and seedlings in the sample plot, respectively) and θ is a scale parameter quantifying the amount of overdispersion. The ZINB regression model regresses μ (the mean of the response variable Y) and P (the probability for the response variable Y to be zero) on a set of covariates X and Z via

$$\log(\mu) = X\beta \text{ and } \operatorname{logit}(P) = Z\Upsilon \qquad [2]$$

where β and Υ are the regression coefficients used to estimate μ and P via the maximum-likelihood method, and X and Z are the predisposing factors (community and landscape features), respectively. With the final ZINB models (with minimum Akaike information criterion [AIC] and randomly dispersed residuals), *T. sebifera* seed and seedling density changes against significant predisposing factors were plotted to examine the strength of resultant correlations or associations. All statistical analyses were conducted using the ‘pscl’ (Zeileis et al. 2008) and other base packages within the R statistical environment (R Development Core Team 2014).

Results and Discussion

The age data (Figure 3) showed that *T. sebifera* was introduced into the GBNWR along Missala Road and Bayou Heron Road around 30 (1987) and 24 (1994) yr ago, respectively. By the survey year (2017), *T. sebifera* had spread into 76.1% and 38.6% of the transects along both roadways, respectively. In contrast, fire lines 1 and 2 were invaded in later years (1998 and 2006), with 54.2% and 69.8% of the transects being colonized by *T. sebifera*. Temporally, *T. sebifera* invaded in an intermittent manner before the mid-2000s, followed by a consecutive recruitment that resulted in an exponential increase in the number of individuals colonized (Figure 3). Significant positive correlations of the number of *T. sebifera* between consecutive, young age classes (<10 yr) was observed ($P < 0.05$), but there were no correlations between consecutive age classes in the intermittent middle and old age cohorts (Table 1).

Triadica sebifera was distributed in significantly clustered patterns along Bayou Heron Road ($P < 0.0001$) and fire line 2 ($P = 0.0226$) compared with *T. sebifera* along Missala Road ($P = 0.2576$) and fire line 1 ($P = 0.6487$). The spatial distribution maps of *T. sebifera* by age cohort (Figure 4) showed that *T. sebifera* invasion mainly occurred in the northern areas along Missala Road and Bayou Heron Road before 1997 (Figure 4A). Then *T. sebifera* gradually spread into fire line 1, the southern areas around Bayou Heron Road and fire line 2 from 1997 to 2007 (Figure 4B). Since 2007, *T. sebifera* populations have increased persistently along all roadways and fire lines, and by 2017, the density of *T. sebifera* individuals in the young age cohort had

https://doi.org/10.1017/inp.2018.21 Published online by Cambridge University Press

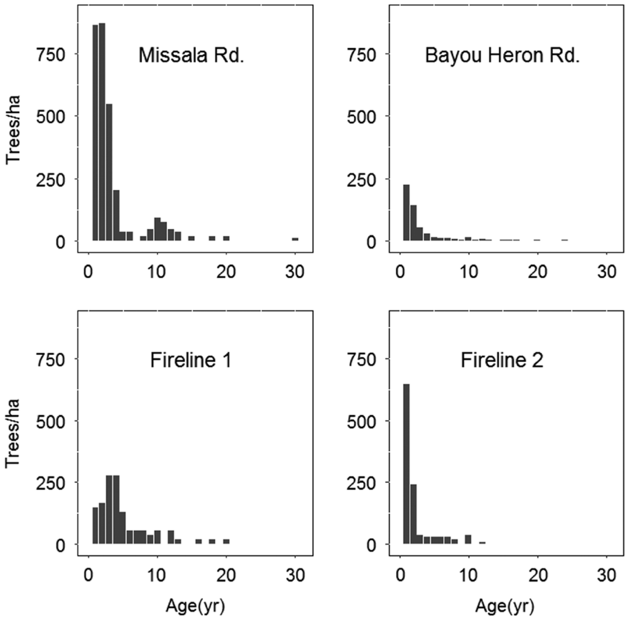

Figure 3. Age structure of *Triadica sebifera* populations along roadways and fire lines, showing the three age cohorts: old (>20 yr), middle (11–20 yr), and young (1–10 yr) which correspond to the three invasion stages (see Figure 4A–C): sporadic invasion stage, intermittent invasion stage, and consecutive annual invasion stage of *Triadica sebifera* invasion in the Grand Bay National Wildlife Refuge.

reached >15,000 trees ha^{-1} in certain northern clusters (Figure 4C). Great spatial variations in soil *T. sebifera* seedbank were also observed, and the density of *T. sebifera* seeds at northern clusters approached upward of 1,000 seeds m^{-2} (Figure 4D).

Distance to seed trees played a pivotal role in *T. sebifera* seed dispersal and seedling recruitment as shown by its significance level (Table 2) and the distribution of *T. sebifera* seeds and seedlings in relation to seed trees (most seeds and seedlings were distributed within a range of 0 to 250 m from seed trees) (Figure 5). At the landscape level, *T. sebifera* seed density decreased significantly with distance to seed trees, especially for sites with high overstory density, as shown by the significant interaction between distance to seed trees and overstory density. However, seedling distribution by predisposing factors other than distance to seed trees changed focally with edge and ecosystem type. *Triadica sebifera* seedling density increased with understory grass cover (%) along fire lines, and decreased with overstory pine density along Bayou Heron Road in the pine flatwood, but no predisposing factors were found to be statistically significant along the Missala Road and Bayou Heron Road in the mixed forest (Table 2; Figure 5). The binary models did not find any factors significantly related to the absence of *T. sebifera* recruitment along the fire lines and along Missala Road and Bayou Heron Road in the mixed forest. However, overstory pine density was negatively correlated to the probability of the absence of *T. sebifera* seedlings along Bayou Heron Road in the pine flatwood (Table 2).

Triadica sebifera was introduced into the GBNWR around 30 yr ago, and since then it has spread along roadways and fire lines (Figures 3 and 4). The reversed, J-shaped age structures characterized by consecutive, young age classes and intermittent, middle, and old age classes showed a rapidly expanding population after a slow, intermittent, focal recruitment of ~3 to 17 yr (Theoharider and Dukes 2007). Disturbance has proved to be an important driver or facilitator of biological invasion and is significantly associated with the occurrence of *T. sebifera* (Conner et al. 2014; Fan et al. 2012; Gan et al. 2009; Lockwood et al. 2013; Paudel 2013; Pile et al. 2017). In light of the conceptual model (Figure 2), the impact of natural and human-mediated disturbance (inciting factors) on *T. sebifera* invasion lies in disturbance, which can alter community/landscape features (predisposing factors) (e.g., releasing resources) and drive or regulate water current, and *T. sebifera* seed-eating bird activities (driving factors). A close cross-examination of GBNWR's natural disturbance and management data against *T. sebifera* age structures showed that the early invasion of *T. sebifera* into roadways was attributed to anthropogenic factors (local inhabitants), because the oldest *T. sebifera* trees were distributed in rows along the front line of the abandoned private inholdings. However, the early infestation of *T. sebifera* in fire lines was most likely by birds, with the oldest *T. sebifera* trees distributed sporadically underneath large slash pine (*Pinus elliottii* Engelm.) trees that are attractive to birds. Along all roadways and fire lines, the consecutive, annual colonization and rapid expansion of *T. sebifera* all co-originated around 12 to 13 yr ago, concurrent in time with the devastating hurricane Katrina. According to Evans et al. (2012), hurricane Katrina seriously affected the GBNWR and its vicinity, resulting in a large decrease (32%) in evergreen forest and the conversion of evergreen forest into grassland. We speculate that Katrina initiated and facilitated the rapid, consecutive, annual recruitment by creating favorable site/community conditions for *T. sebifera* seed-dispersing birds to distribute seeds to the disturbed sites (Conner et al. 2014; Pile et al. 2017). Significant, positive correlations in the count of *T. sebifera* trees between consecutive age classes <10 yr (Table 1) might suggest that propagule pressure (seed density) following Katrina was no longer a limiting factor for *T. sebifera* spread, as it was in the early years, when occurrence of *T. sebifera* was confined spatially within separated clusters (Figure 4A and B). Therefore, unlike fire line 1 and roadways, the latterly constructed fire line 2 did not experience the intermittent, focal colonization. Current propagule pressure (seed trees and seedbank) has rendered GBNWR highly susceptible to the postinvasion spread of *T. sebifera* following a disturbance.

The clustered patterns of *T. sebifera* occurrences (Figure 4) suggest that *T. sebifera* spread in a landscape is subject to some limiting factors. Generally, landscape fragmentation, heterogeneity in vegetation composition and structure, and selective behaviors of *T. sebifera* seed-dispersing birds (perching, foraging, roosting, and nesting) should be the primary reasons or factors (Renne et al. 2000, 2002). In another study in GBNWR, for instance, we found that the density of *T. sebifera* decreased significantly with distance to road (the edge effect) and more *T. sebifera* trees were clumped underneath the range of an overstory slash pine tree's crown and around snags of high-decay classes in forest interiors (the snag effect) (Fan 2018). Other studies also report bird-mediated dispersal limitation and patchy distribution of invasive species at the landscape level (Bartuszevige et al. 2006; Schetter et al. 2013). Mechanistically, three key processes—seed dispersal, seed germination, and seedling recruitment (growth)—are involved in *T. sebifera* spread in the landscape (Figure 2). The rate of spread and spatiotemporal patterns of an invasive species following disturbance are basically determined by the interaction between propagule pressure (e.g., seed density) and habitat suitability (or invasibility), such as the amount of resources released or empty niches (Warren et al. 2012). According to the ZINB

https://doi.org/10.1017/inp.2018.21 Published online by Cambridge University Press

Table 1. Spearman's rank correlation coefficients (* statistical significance at α=0.05) between age classes of *Triadica sebifera*.

Age	[1]	[2]	[3]	[4]	[5]	[6]	[7]	[8]	[9]	[10]	[11]	[12]	[13]	[15]	[16]	[17]	[18]	[20]	[24]	[30]
[1]	1.0																			
[2]	0.3*	1.0																		
[3]	0.2*	0.3*	1.0																	
[4]	0.0	0.2*	0.4*	1.0																
[5]	0.1	0.1	0.3*	0.5*	1.0															
[6]	0.1	0.1	0.0	0.2* −0.1	1.0															
[7]	0.1	−0.1	−0.0	0.1	−0.0	0.4*	1.0													
[8]	−0.1	−0.0	0.0	0.1	0.1	0.1	0.2*	1.0												
[9]	−0.0	0.1*	0.1	0.2*	−0.0	0.2*	0.3*	0.3*	1.0											
[10]	0.1	−0.0	0.1	−0.0	0.0	−0.1	0.1*	0.2*	0.1	1.0										
[11]	−0.1	0.1	0.1	−0.0	−0.0	0.2*	0.2*	−0.0	−0.0	−0.0	1.0									
[12]	0.1	0.1	0.1	0.1	0.1	0.2*	−0.0	−0.0	−0.0	0.1	0.2*	1.0								
[13]	0.1	0.1	0.0	0.0	0.1	−0.0	−0.0	−0.0	−0.0	0.1	−0.0	−0.0	1.0							
[15]	0.1	0.1	0.2*	−0.0	−0.0	−0.0	−0.0	−0.0	0.3*	−0.0	−0.0	−0.0	−0.0	1.0						
[16]	0.0	−0.1	−0.1	−0.0	−0.0	−0.0	−0.0	−0.0	−0.0	−0.0	−0.0	−0.0	−0.0	−0.0	1.0					
[17]	−0.0	−0.0	−0.0	−0.0	−0.0	−0.0	−0.0	0.3*	−0.0	−0.0	−0.0	−0.0	−0.0	−0.0	−0.0	1.0				
[18]	0.0	0.0	0.2*	0.1	−0.0	−0.0	−0.0	−0.0	−0.0	−0.0	−0.0	−0.0	−0.0	−0.0	−0.0	−0.0	1.0			
[20]	0.1	0.1	0.1*	0.1	−0.0	−0.0	−0.0	−0.0	0.2*	−0.0	−0.0	−0.0	0.2*	−0.0	−0.0	−0.0	−0.0	1.0		
[24]	−0.0	−0.0	−0.0	−0.0	−0.0	−0.0	−0.0	−0.0	−0.0	−0.0	−0.0	−0.0	−0.0	−0.0	−0.0	0.0	−0.0	−0.0	1.0	
[30]	−0.0	0.1*	−0.0	−0.0	−0.0	−0.0	−0.0	−0.0	−0.0	−0.0	−0.0	−0.0	−0.0	−0.0	−0.0	0.0	−0.0	−0.0	0.0	1.0

model (Table 2), distance to seed trees and overstory density were shown to be the most significant limiting factors of *T. sebifera* seed dispersal by birds and seedbank size for all roadways and fire lines. There was a larger seedbank in the northern portion (mixed forests) than in the southern portion (pine forests, marsh) (Figure 5). *Triadica sebifera* seed density along roadways and fire lines decreased significantly with distance to seed trees, and few or no seeds existed under either high overstory density or open canopy (Figure 5), most likely due to limited activities of *T. sebifera* seed-dispersing birds. Soil seed densities were properly fit using one parsimonious ZINB model, suggesting that the effect of the distance to seed trees and overstory density on seed dispersal at the landscape level did not change with edge (roadway vs. fire line) and patch (mixed forest vs. pine forest) types.

In contrast to seed dispersal regulated primarily by overstory condition, the recruitment of *T. sebifera* seedlings depends on two processes: seed germination and seedling growth restricted by both over- and understory conditions (biotic factors) and abiotic factors (e.g., light, temperature, moisture, salinity, and burial) (Barrilleaux and Grace 2000; Battaglia et al. 2009; Howard 2012; Paudel 2013; Paudel and Battaglia 2015). Compared with the single, parsimonious seed density model, the effect of community characteristics on seedling recruitment varied by edge type (roadways vs. fire lines) and patch type (mixed forests vs. pine flatwood), reflecting the interaction between propagule pressure and community and landscape characteristics. Distance to seed trees remained important as a prerequisite in the recruitment of *T. sebifera* seedlings, because it is the only statistically significant factor in all models for both roadways and fire lines. Spatially, seedling density was positively correlated with seed density, though the trend was weak and not statistically significant due to great variations at the sampling scale (10 by 3 m^2) used by this study. This may suggest that community characteristics affect seedling recruitment differently, resulting in the disparity in invasibility among communities or habitats observed at local and regional scales (Fan 2018; Fan et al. 2012; Moser et al. 2016; Nijjer et al. 2007). In this study, no over- and understory conditions were shown to be statistically significant along Missala Road and Bayou Heron Road in the mixed forest patch (in the northern portion of GBNWR), but overstory density had a significant, negative impact on seedling recruitment along Bayou Heron Road in the pine flatwood patch (in the southern portion of GBNWR). Based on our field observations, one possible explanation is that the former had more homogeneous over- and understory characteristics, but the latter passed through very different patches from cleared powerline strips to sparse pine flatwoods, dense pine forests, prairies, and marshlands. *Triadica sebifera* mainly occurred along the roadside of sparse pine flatwoods and pine forests, and few or no *T. sebifera* trees occurred along Bayou Heron Road, which passes through the cleared powerline strips, prairies, and marshlands. In both fire lines, the overstory was more uniform in species composition and structure

https://doi.org/10.1017/inp.2018.21 Published online by Cambridge University Press

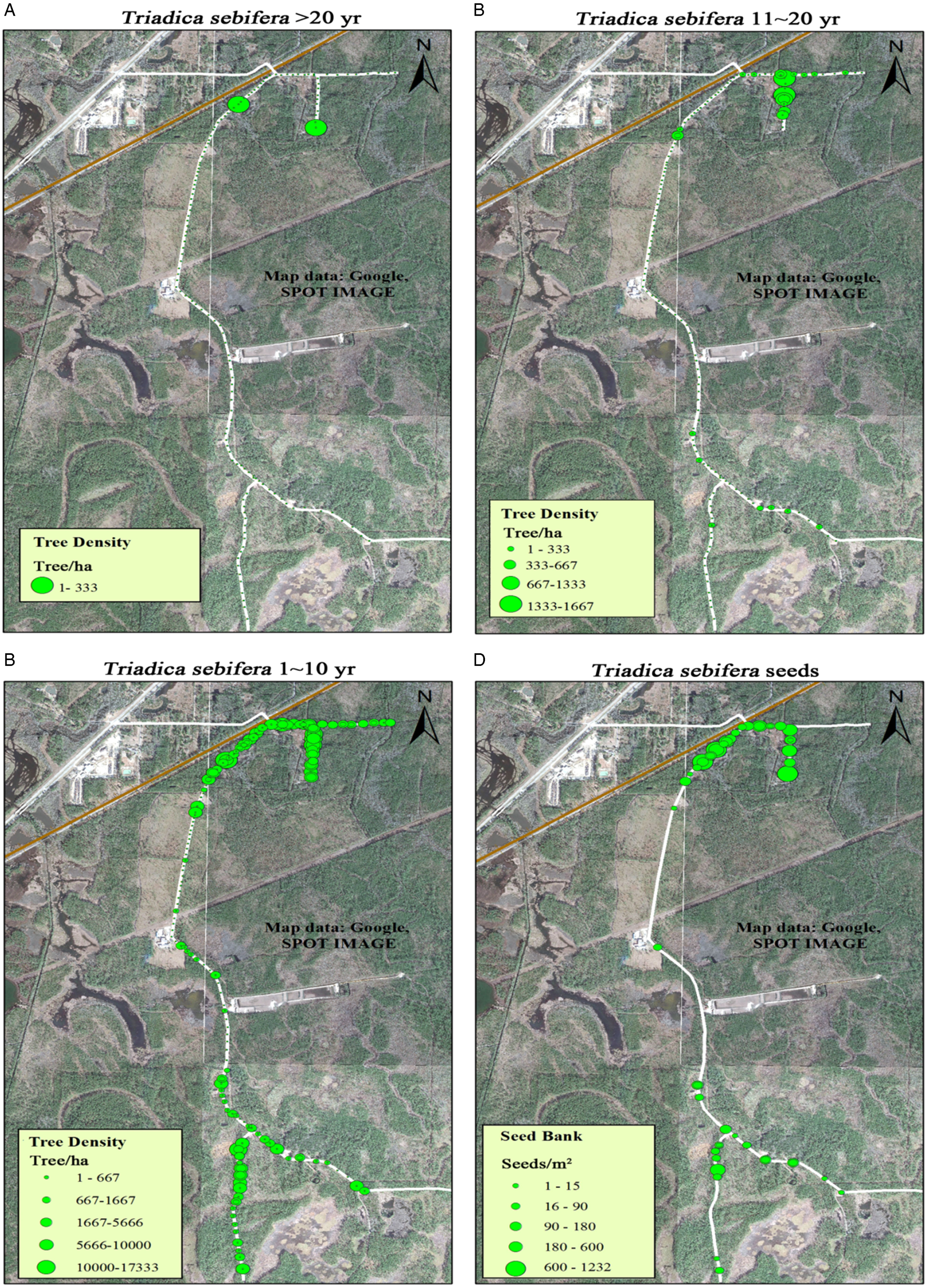

Figure 4. Spatiotemporal distribution of *Triadica sebifera* by age cohort and soil seedbank, showing the sporadic invasion (A), intermittent invasion (B), consecutive annual invasion (C), and soil seed bank (D) of *Triadica sebifera* in the Grand Bay National Wildlife Refuge.

(canopy openness), but understory grass and shrub cover varied with microtopography. *Triadica sebifera* seedlings occurred mostly in areas with high grass cover (low shrub cover) as found in forest interiors (Fan 2018). Generally, few or no seeds or seedlings occurred in areas with either open canopy, high canopy closure, or dense shrub layers. This differs from observations in other studies in which more *T. sebifera* trees grew in canopy gaps or abandoned fields (Pile et al. 2017). One possible explanation is that birds were the primary seed-dispersal agent in GBNWR, while in other studies *T. sebifera* seeds might have

https://doi.org/10.1017/inp.2018.21 Published online by Cambridge University Press

Table 2. Results of the ZINB (zero-inflated negative binomial) regression models showing factors associated with seed dispersal and seedling recruitment of *Triadica sebifera.*

Seed dispersal along habitat edges (roadways and fire lines) sampled				
Count model coefficients (negative binomial with log link):				
	Estimate	SE	*z*-value	Pr(> |z|)
(Intercept)	2.259	0.301	7.551	<0.000***
Overstory density x	− 0.002	0.001	− 2.079	0.038*
Distance to seed trees				
Distance to seed trees	− 0.002	0.001	− 2.790	0.005**
Log(theta)	− 0.873	0.492	− 1.774	0.076
Zero-inflation model coefficients (binomial with logit link):				
	Estimate	SE	*z*-value	Pr(> |z|)
(Intercept)	−1.301	1.058	− 1.229	0.219
Seedling establishment along fire lines 1 and 2				
Count model coefficients (negative binomial with log link):				
	Estimate	SE	*z*-value	Pr(> |z|)
(Intercept)	0.576	0.368	1.567	0.117
Grass cover (%)	0.015	0.005	2.841	0.004**
Distance to seed trees	−0.007	0.003	− 2.294	0.022*
Log(theta)	0.571	0.594	0.962	0.336
Zero-inflation model coefficients (binomial with logit link):				
	Estimate	SE	*z*-value	Pr(> |z|)
(Intercept)	−1.007	0.549	− 1.834	0.067
Seedling establishment along Bayou Heron Road in the pine flatwood patch				
Count model coefficients (negative binomial with log link):				
	Estimate	SE	*z*-value	Pr(> |z|)
(Intercept)	1.609	0.464	3.465	0.001***
Overstory density	−0.251	0.109	− 2.308	0.021*
Distance to seed trees	− 0.001	0.000	− 2.156	0.031*
Log(theta)	− 0.269	0.489	− 0.550	0.583
Zero-inflation model coefficients (binomial with logit link):				
	Estimate	SE	*z*-value	Pr(> |z|)
(Intercept)	2.071	0.655	3.161	0.002 **
Overstory density	−2.086	0.808	− 2.583	0.010 **
Seedling establishment along Missala Road and Bayou Heron Road in the mixed forest patch				
Count model coefficients (negative binomial with log link):				
	Estimate	SE	*z* value	Pr(> |z|)
(Intercept)	1.761	0.335	5.254	0.000***

https://doi.org/10.1017/inp.2018.21 Published online by Cambridge University Press

Table 2. (*Continued*)

Seed dispersal along habitat edges (roadways and fire lines) sampled				
Distance to seed trees	−0.012	0.006	− 1.891	0.058
Log(theta)	− 0.651	0.575	− 1.132	0.257
Zero-inflation model coefficients (binomial with logit link):				
	Estimate	SE	*z* value	Pr(> |z|)
(Intercept)	−1.818	1.837	− 0.990	0.322

*P = 0.05.
**P = 0.01.
***P = 0.001.
"." P = 0.1

been dispersed by multiple agents (e.g., birds, flooding, storm surge, and the like).

Owing to the nonstationary, stochastic nature of biological invasion, specifically *T. sebifera* invasion and spread (Theoharides and Dukes 2007), this study aims to quantify the effect of easily measured landscape and community characteristics on *T. sebifera* spread through evaluating the logical, mechanistic relations between the observed spatiotemporal patterns and associated biotic factors based on their functional roles (Figure 2). The information presented (e.g., Table 2; Figures 3, 4, and 5) is useful for comparing and evaluating the invasibility of different ecosystems and for developing integrated, landscape-level control measures. The demographic (age-structure) data (Figure 3) indicated an edge habitat's invasion history characterized by three distinct phases: the sporadic invasion phase (the old age cohort, before 1997), the intermittent invasion phase (the middle age cohort, from 1997 to 2007), and the consecutive invasion phase (the young age cohort, after 2007). Land and resource managers could use this information in combination with the spatial maps of *T. sebifera* by invasion phase (age cohort) (Figure 4) and seed and seedling distribution by important biotic factor (Figure 5) to prioritize control treatments. For instance, chemical (herbicide) treatments were planned or conducted in areas that are highly susceptible to *T. sebifera* invasion (e.g., pine flatwood, mixed forest) and clumped with *T. sebifera* seed trees. Soil seed density predominantly attributed to the activities of seed-dispersing birds is subject to distance to seed trees and overstory density. Seedling recruitment, however, is subject to both the distance to seed trees and overstory density as well as ground cover (%) of grasses/herbs. Either high overstory density or open canopy might impede *T. sebifera* seed dispersal and seedling recruitment, as indicated by low seed density. Compared with woody shrubs, the high grass/herb cover tended to be more favorable to *T. sebifera* seedling recruitment, perhaps due to low competition and high light availability. Integrating these findings with Google imagery of vegetation condition, an endeavor to map habitat invasion risk for landscape-level planning and monitoring is ongoing in the GBNWR.

In conclusion, classifying factors contributing to the observed spatiotemporal patterns into driving factors, predisposing factors, and inciting factors and quantifying their effects on key underlying invasion processes based on their functional roles should be helpful to the design of effective and efficient control methods (Blackburn et al. 2011; Pysek et al. 2012). Using the easily measured landscape metrics and community features (predisposing factors) to model invasion risk at diverse scales will be critical for future planning and management of invasive species (Fan et al. 2012; Pile et al. 2017).

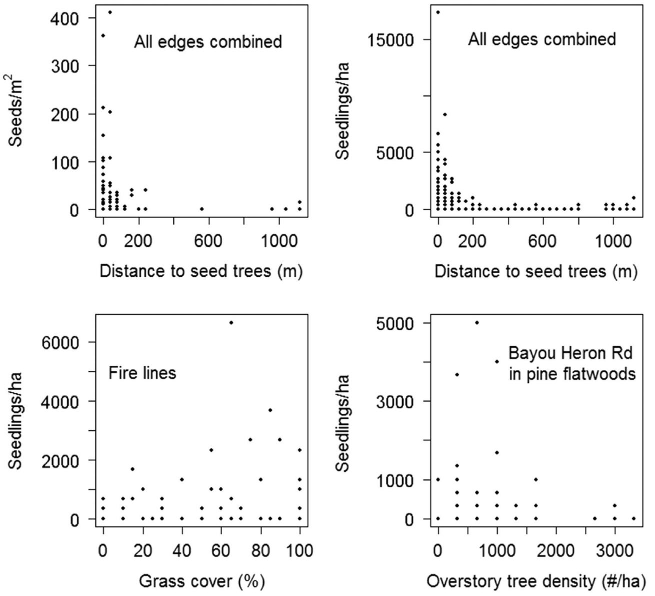

Figure 5. Distribution of seed trees and seedlings (≤2 yr) by significant factors identified by the ZINB (zero-inflated negative binomial) models.

Acknowledgments. Sunil Nepal, Nannan Cheng, Alison Stoklosa, Zhen Sui, and Nana Tian participated in field data collection. We are grateful to the research staff from Grand Bay National Wildlife Refuge, Mississippi Sandhill Crane Wildlife Refuge, for logistic support. Jonathan Pitchford from the Grand Bay National Wildlife Refuge and Lin Fan from Stanford University helped review this article. We are also grateful to two anonymous reviewers for their constructive comments, which improved this article. This work was funded partially by the McIntire Stennis Program funds NI17MSCFRXXXG064 through the School of Forestry and Wildlife Sciences, Auburn University. No conflicts of interest have been declared.

References

Barrilleaux TC, Grace JB (2000) Growth and invasive potential of *Sapium sebiferum* (Euphorbiaceae) within the coastal prairie region: the effects of soil and moisture regime. Am J Bot 87:1099–1106

Bartuszevige AM, Gorchov DL, Raab L (2006) The relative importance of landscape and community features in the invasion of an exotic shrub in a fragmented landscape. Ecography 29:213–222

Battaglia LL, Denslow JS, Inczauskis JR, Baer SG (2009) Effects of native vegetation on invasion success of Chinese tallow in a floating marsh ecosystem. J Ecol 97:239–246

https://doi.org/10.1017/inp.2018.21 Published online by Cambridge University Press

Blackburn TM, Pysek P, Bacher S, Carkton JT, Duncan RP, Jarosik V, Wilson JRU, Richardson DM (2011) A proposed unified framework for biological invasions. Trends Ecol Evol 26:333–339

Conner WH, Duberstein JA, Day JW, Hutchinson S (2014) Impacts of changing hydrology and hurricanes on forest structure and growth along a flooding/elevation gradient in a south Louisiana forested wetland from 1986 to 2009. Wetlands 34:803–814

DeWalt SJ, Siemann E, Rogers WE (2011) Geographic distribution of genetic variation among native and introduced populations of Chinese tallow tree, *Triadica sebifera* (Euphorbiaceae). Am J Bot 98:1128–1138

Donahue C, Rogers WE, Siemann E (2006) Restoring an invaded prairie by mulching live *Sapium sebiferum* (Chinese tallow trees): effects of mulch on *Sapium* seed germination. Nat Area J 26:244–253

Evans ED, Anjaneyulu Y, Tchnouwou PB (2012) Effects of Hurricane Katrina on land cover within the Grand Bay National Estuarine Research Reserve in Mississippi, USA. Pages 173–Pages 188 *in* Vitale K, ed. Environmental and Food Safety and Security for South-East Europe and Ukraine. Dordrecht, Netherlands: Springer

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annu Rev Ecol Syst 34:487–515

Fan Z (2018) Spatial analyses of invasion patterns of Chinese tallow (*Triadica sebifera*) in a wet slash pine (*Pinus elliottii*) flatwood in the coastal plain of Mississippi, USA. Forest Sci, 10.1093/forsci/fxy014

Fan Z, Tan Y, Crosby MK (2012) Factors associated with the spread of Chinese tallow in East Texas forestlands. Open Journal of Ecology 2:121–130

Fletcher RJ Jr (2005) Multiple edge effects and their implications in fragmented landscapes. J Anim Ecol 74:342–352

Gan J, Miller JH, Wang H, Taylor JW (2009) Invasion of tallow tree into southern US forests: influencing factors and implications for mitigation. Can J For Res 39:1346–1356

[GBNWR]Grand Bay National Wildlife Refuge (2009) Comprehensive Conservation Plan of Grand Bay National Wildlife Refuge, Jackson County, Mississippi and Mobile County, Alabama. Atlanta, GA: U.S. Department of the Interior Fish and Wildlife Service, Southeast Region. 156 p

Henkel TK, Chambers JQ, Baker DA (2016) Delayed tree mortality and Chinese tallow (*Triadica sebifera*) population explosion in a Louisiana bottomland hardwood forest following Hurricane Katrina. For Ecol Manag 378:222–232

Howard JJ (2012) Hurricane Katrina inpact on a leveed bottomland hardwood forest in Louisiana. Am Midl Nat 168:56–69

Lockwood JL, Hoopes MF, Marchetti MP (2013) Invasion Ecology. 2nd ed. West Sussex, UK: Wiley. 444 p

Moser CS, Wier TP, Grant JF, First MR, Tamburri MN, Ruiz GM, Drake LA (2016) Quantifying the total wetted surface area of the world fleet: a first step in determining the potential extent of ships' biofouling. Biol Invasions 18:265–277

Nijjer S, Rogers WE, Siemann E (2007) Negative plant–soil feedbacks may limit persistence of an invasive tree due to rapid accumulation of soil pathogens. Proc R Soc Lond B Biol Sci 274:2621–2627

Oswalt SN (2010) Chinese tallow (*Triadica sebifera* (*L.*) Small) population expansion in Louisiana, east Texas, and Mississippi. Knoxville, TN: USDA Forest Service, Southern Research Station Publication 20. Pp 1–4

Paudel S (2013) Climate Change, Shifts in Tropical Storm Regimes and *Triadica sebifera* Invasion in Coastal Mississippi, United States. Ph.D dissertation. Carbondale, IL: Southern Illinois University Carbondale. Paper 694. http://opensiuc.lib.siu.edu/dissertations. Accessed: October 22, 2017

Paudel S, Battaglia LL (2015) The role of light, soil and human factors on the probability of occurrence of an invasive and three native plant species in coastal transitions of coastal Mississippi, USA. J Plant Ecol 8:491–500

Peterson MS, Waggy GL, Woodrey MS (2007) Grand Bay National Estuarine Research Reserve: An Ecological Characterization. Moss Point, MS: Grand Bay National Estuarine Research Reserve. 268 p

Pile LS, Wang GG, Knapp BO, Walker JL, Stambaugh MC (2017) Chinese tallow (*Triadica sebifera*) invasion in maritime forests: the role of anthropogenic disturbance and its management implication. For Ecol Manag 398:10–24

Pysek P, Jarosok V, Hulme PE, Pergl J, Hejda M, Schaffner U, Vila M (2012) A global assessment of invasive plants impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. Global Change Biol 18:1725–1737

R Development Core Team (2014) R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. http://www.R-project.org. Accessed: June 26, 2017

Renne IJ, Barrow WC Jr, Johnson Randall LA, Bridges WC Jr (2002) Generalized avian dispersal syndrome contributes to Chinese tallow tree (*Sapium sebiferum*, Euphorbiaceae) invasiveness. Divers Distrib 8:285–295

Renne IJ, Gauthreaux SA Jr, Gresham CA (2000) Seed dispersal of the Chinese tallow tree (*Sapium sebiferum* (L.) Roxb.) by birds in coastal South Carolina. Am Midl Nat 144:202–215

Renne IJ, Spira TP, Bridges WC Jr (2001) Effects of habitat, burial, age and passage through birds on germination and establishment of Chinese tallow tree in coastal South Carolina. Journal of the Torrey Botanical Society 109–119

Ries L, Fletcher RJ Jr, Battin J, Sisk TD (2004) Ecological responses to habitat edges: mechanisms, models, and variability explained. Annu Rev Ecol Evol Syst 35:491–522

Rogers WE, Siemann E (2002) Effects of simulated herbivory and resource availability on native and invasive exotic tree seedlings. Basic Appl Ecol 3:297–307

Schetter TA, Walters TL, Root KV (2013) A multi-scale spatial analysis of native and exotic plant species richness within a mixed-disturbance oak savanna landscape. Environ Manag 52:581–594

Stoklosa AM, Fan Z (2013) Invasion patterns and population structure of Chinese tallow (*Triadica sebifera* (L.) Small) in the Grand Bay National Estuarine Research Reserve. Pages 56–63 *in* Merry K, Bettinger P, Brown T, Cieszewski C, Hung I-K, Meng Q, eds. Proceedings of the 9th Southern Forestry and Natural Resource Management GIS Conference. Athens, GA: University of Georgia

Theoharides KA, Dukes JS (2007) Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. New Phytol 176:256–273

Tian N, Fan Z, Matney TG, Schultz EB (2017) Growth and stem profiles of invasive *Triadica* in the Mississippi coast of United States. For Sci 63:569–576

Vitousek PM, D'Antonio CM, Loope LL, Reimanke M, Westbrooks R (1997) Introduced species: a significant component of human-caused global change. NZ J Ecol 21:1–16

Warren RJ II, Bahn V, Bradford MA (2012) The interaction between propagule pressure, habitat suitability and density-dependent reproduction in species invasion. Oikos 121:874–881

Wieland RG (2007) Habitat types and associated ecological communities of the Grand Bay National Estuarine Research Reserve. Pages 104–147 *in* Peterson MS, Waggy GL, Woodrey MS, eds. Grand Bay National Estuarine Research Reserve: An Ecological Characterization Moss Point, MS: Grand Bay National Estuarine Research Reserve

Zeileis A, Kleiber C, Jackman S (2008) Regression models for count data in R. J Statist Softw 27:1–25

Zou J, Rogers WE, Siemann E (2008) Increased competitive ability and herbivory tolerance in the invasive plant *Sapium sebiferum*. Biol Invasions, 10:291–302

https://doi.org/10.1017/inp.2018.21 Published online by Cambridge University Press