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Distribution and spread mechanisms of Chinese tallow (Triadica sebifera) at multiple spatial scales within forests in the southeastern United States

By

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Distribution and spread mechanisms of Chinese tallow (Triadica sebifera) at multiple spatial scales within forests in the southeastern United States

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The coastal plain of the southeastern United States is historically wet pine savannahs, prairie, and hardwoods. However, many exotic species have invaded this area and become a serious threat to native forest ecosystems. Among those exotic species, Chinese tallow (*Triadica sebifera*) has become one of the most pervasive tree species in the southern coastal states, including Alabama, Mississippi, Louisiana, and Texas. Therefore, to understand distribution and spread mechanisms has become important in the management and control of Chinese tallow in the southeastern United States. In this research, distribution and spread mechanisms of Chinese tallow were studied at multiple spatial scales, including regional, landscape, and stand. Effects of predisposing (community and landscape features) and inciting (natural disturbance and human activities) factors on Chinese tallow invasion had been evaluated by using a comprehensive data set (field data and Forest Inventory and Analysis data) and spatial statistical models. Results indicated that propagule pressure of Chinese tallow is the main force driving tallow dispersal at different spatial scales. Predisposing and inciting factors such as natural disturbances, anthropogenic disturbances, forest types, forestland ownerships, and landscape features are significantly related to the spread of Chinese tallow at different spatial scales. Regionally, Chinese tallow initially started to spread from southern Texas and Louisiana to the northeastern portion of the Gulf Coastal area. At landscape and stand scales, Chinese tallow has commonly invaded from edges of forests and habitats such as roads and firebreaks. Inciting factors, including hurricanes/storms and prescribed fires, could accelerate the spread of Chinese tallow at different spatial scales, especially in habitats that have previously been invaded. Compared to pine forests, it is easier for Chinese tallow to invade bottomland hardwood forests at the regional scale. The efficient dispersal distance of tallow seeds is 250-300 m, and its distribution is affected by the microtopography in forest stands. Management of Chinese tallow invasion should be focused at selected scales, such as landscape and stand levels, because of variations of site conditions.

Key words: Chinese tallow; multiple spatial scales; invasive mechanisms; spatial analysis; Forest Inventory and Analysis data; exotic species

DEDICATION

To Jesus Christ, he saved my life and led me to brightness without fear. To my wife, Nannan Cheng, you support me all the time without any complaint. To my parents, your love is the best gift I have ever received. To all other persons who love me and make me better.

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INTRODUCTION

1.1 Research background

The coastal plain of the southeastern United States is historically habitat of native species (Figure 1.1A), such as longleaf-slash pine (*Pinus palustris* and *Pinus elliottii*) savannahs and prairie. Due to varying causes, including fire suppression, climate change, biological invasion and land use change dominated by human activities, the longleaf-slash pine ecosystem has been drastically reduced to less than 5% of its original distributional area (Van Lear et al. 2005). Native ecosystems have also been threatened by the invasion of Chinese tallow (*Triadica sebifera*) which has become a very serious problem in this area (Figure 1.1B) (Lodge 1993, Simberloff 1996). The direct impacts of Chinese tallow and other exotic species on the local ecosystems have been well documented in the past several decades (Vitousek et al. 1997, Ehrenfeld and Scott 2001). However, the invasion pattern and mechanism of Chinese tallow, especially at different spatial scales, needs to undergo further investigation to fully understand factors important for tallow invasion control and local ecosystem restoration.

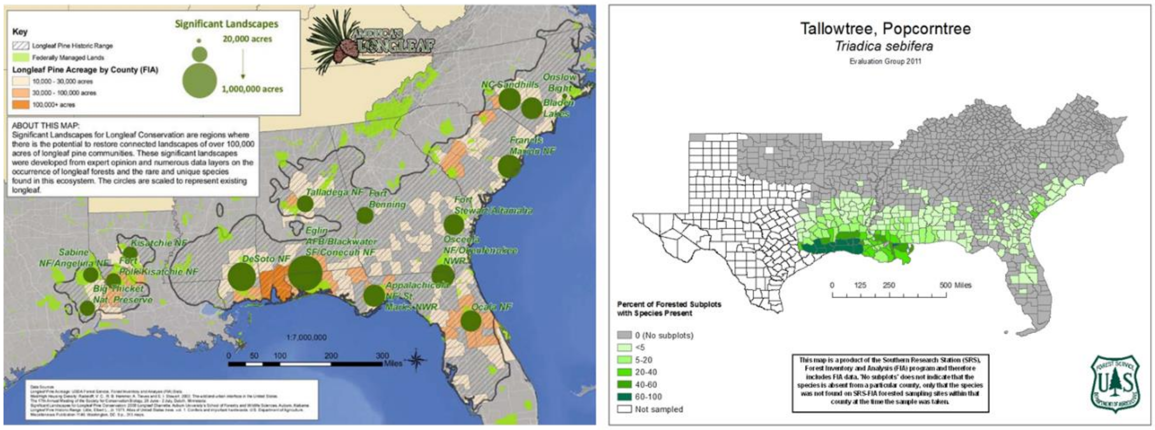

Figure 1.1 Historical distribution of longleaf pine (*Pinus palustris*) and Chinese tallow (*Triadica sebifera*) in 2011

(A) is longleaf pine distribution (Reference from *America's Longleaf*) and (B) is Chinese tallow (Reference from *Invasive. org*)

Many coastal forest ecosystems including longleaf-slash pine, loblolly-shortleaf pine, oak-pine, and oak-gum-cypress are fire dependent (Mutch 1970, Croker and Boyer 1975, Platt et al. 1988, Gilliam 1994, Grace et al. 2005). For most prairie types of coastal areas, as well as longleaf pine ecosystems, wildfire is believed to have played a critical role in the formation and maintenance of these ecosystems (Archer and Pyke 1991, Mitchell et al. 2006, Liu et al. 2013). However, due to the increase of human activities, such as farming, road building and city expansion, the frequency of wildfire is decreasing rapidly in this region, which makes prescribed fire an important tool for sustainable development of local ecosystems (Frost and Cecil 2006). Meanwhile, prescribed fire is also a key tool for controlling the expansion of invasive plants in coastal areas.

Prescribed fire has been used as a preferred tool in this area to control Chinese tallow invasion for decades, and many researchers have discovered how to control Chinese tallow invasion by using prescribed fire (Grace et al. 2005, Grace 1998). However, the use of prescribed fire has not halted the invasion of Chinese tallow in wet pine ecosystems since prescribed fire can also increase the invasive risk of tallow. Thus, how to use prescribe fire and adapt fire intervals and seasonality in southern native forests, which have been invaded by Chinese tallow, has become a critical question. The invasive patterns of Chinese tallow under different fire intervals within different spatial scales and micro-topographies may result in different outcomes with prescribed fire, however these differences are not clear as of yet. Furthermore, we cannot understand the invasive mechanism of Chinese tallow without knowing impacts of different spatial scales, such as those at the stand, landscape, and regional levels, on the Chinese tallow invasion in the southeastern United States.

With increasing human activities, wildfire is decreasing rapidly in this region, which only increases the importance of prescribed fire as a management tool for sustainable development of local ecosystems (Frost and Cecil 2006). Meanwhile, in the southern coastal area, other disturbance caused by human activities can also increase the availability of resources for invasive species (Richardson and Bond 1991, Hood and Naiman 2000, Gan et al. 2009, Fan et al. 2012, Pile et al. 2017a). For instance, road density is regarded as a salient indication of landscape disturbance (Gelbard and Belnap 2003, Watkins et al. 2003). Research to understand the invasion patterns and associated driving factors of a given site or region is necessary for management and control of invasive species (Richardson and Pyšek 2006).

Biological invasion of exotic species into a native ecosystem or region is a spatial-temporal process that can be classified into four non-discrete stages: introduction, colonization, establishment, and landscape spread (Vermeij 1996, Blackburn et al. 2011, Lockwood et al. 2013). Within each stage, characteristics of Chinese tallow invasion differ respectively. For the introduction stage, humans have been the primary dispersers of invasive species in many regions either for food, fuel, lumber, oil, and aesthetic purposes, or accidentally through a variety of other human activities such as road construction, transportation, and travel. For the colonization stage, invasive species must be able to tolerate abiotic factors and pass through survival and growth related biotic processes at the local scale. At the establishment stage, the biotic filters, such as competition from other plant species or interactions with other species, may be the major barriers for invasive species at the community scale. The spread stage occurs at the landscape and regional scale, and this stage will be influenced by landscape patterns, disturbance regimes, and climate conditions (Theoharides and Dukes 2007).

Chinese tallow has been regarded as a major exotic tree species in the southeastern coastal area for decades (Hunt 1947, Grace 1998, Renne et al. 2002, Gan et al. 2009, Fan et al. 2018). Once established, Chinese tallow may threaten the sustainability of native forest composition, structure, function, and resource productivity (Webster et al. 2006). It is difficult and expensive to control Chinese tallow, especially at regional scales. Understanding spread and distribution patterns of Chinese tallow in multiple spatial scales with different disturbances will help identify and evaluate how associated factors, such as biotic and abiotic factors, affect mechanisms of Chinese tallow invasion. This information will help land and resource managers to make scientific based optimal forest management prescriptions to control the Chinese tallow invasion in different spatial scales.

1.2 Literature review

1.2.1 Physiological characteristics of Chinese tallow

A number of characteristics of Chinese tallow contribute to its reputation as a threat to native species, both in native pine systems as well as in other community types, such as bottomland hardwood forests and prairie systems, within its range. Chinese tallow is used as a seed crop to produce oils and waxes because of its rapid growth, early reproduction, and prolific seed production (Hunt 1947, Renne et al. 2002, Miller and Fabian 2003). Chinese tallow can reach reproductive age as early as three years of age and remain reproductive for up to 100 years (Bruce et al. 1997). Cultivated mature trees in Texas can produce up to 310000 seeds per year (Gray 1950). Furthermore, Chinese tallow also has a long seed release range, which starts from September to November, and dispersal is primarily by birds and water. Local and short-distance seed dispersal occurs by flowing and impounded waters common to the wet forests of the coastal plains (Bruce et al. 1997) and by multiple species of large birds that consume the high oil content seeds (Hukui and Ueda 1999, Renne et al. 2002). Seeds of Chinese tallow can survive for several years, which can accelerate development of a seed bank and enhance its colonization capacity. Meanwhile, like most invasive species, it is easy for Chinese tallow to enter a disturbed system because of its large seeds and shade tolerant seedlings. They will grow rapidly and resist both flooding and drought once a seedling established. It has been reported that tallow is able to invade and dominate an open habitat in as few as 10 years (Bruce et al. 1995).

1.2.2 Establishment of Chinese tallow under fire

As for most prairie types of coastal areas, as well as for many other kinds of ecosystems, such as longleaf pine ecosystems, wildfire is believed to have played a critical role in the formation and maintenance of the coastal prairie (Smeins et al. 1991). Before the widespread conversion to agriculture and subdivision of the landscape by roads, wildfires spread through the prairie and longleaf ecosystems of the southern Gulf coast, on what is presumed to have been a regular disturbance. During periods of hotter and drier weather, fires would have been more frequent, while in periods of cooler or wetter weather, substantial intervals between fires would have allowed the encroachment of shrubs until the next period of hot fires (Archer et al. 1988). However, a number of human behaviors have reduced the incidences of fire in coastal areas. These include fire suppression, farmland increasing, and roadway building. However, prescribed fire is also regarded as a primary tool for controlling Chinese tallow in southern coastal areas (Grace 1998, Grace et al. 2005, Pile et al. 2017b). Meanwhile, the methods of applying herbicides and mowing are also regarded as useful tools, although they are more expensive when compared to prescribed fire. The low frequency of fire in the coastal ecosystems has led to the increased development of woody vegetation. However, native species systems such as eastern baccharis (*B. halimifolia*), which is a native coastal shrub system, are still vulnerable to fire when it finally occurs. As Chinese tallow enters those disturbed systems, this normal pattern of fire-based succession can be dramatically changed.

Chinese tallow has many adaptation traits that allow it to adapt to fire. First, as tallow grows bigger, its bark becomes thicker, which can protect tallow from fire (Eberhardt et al. 2007). Second, Chinese tallow has a strong sprouting ability, even when subjected to hot fires and it can reproduce two meters (m) of regrowth in one single growing season (Grace 1998). Therefore, this plant can recover quickly from fire disturbances. Third, when damaged by fire or mechanical cutting, tallow typically responds by root sprouting at some distance from the original stem, which can help it recover as soon as possible. Fourth, only the hottest fires are able to ignite Chinese tallow, and it does not spread as a crown fire, which is different from many trees and shrubs. The last and most important characteristic is that Chinese tallow stands are good at eliminating the fuel species which can drive fires during competition (Grace 1998, D'Antonio 2000, Mandle et al. 2011). Due to these characteristics, ecosystems are converted from being fire regulated to being tallow regulated. It is also reported that once Chinese tallow stands are well developed, soil properties may become altered (Cameron and Spencer 1989). Once Chinese tallow is established on one site, it will greatly reduce available light that can be expected to alter soil moisture profiles, microclimate, and, therefore, a wide range of habitat characteristics. Meanwhile, prescribed fire can also increase Chinese tallow regeneration because disturbed sites are easier for tallow to invade (Gan et al. 2009, Henkel et al. 2016, Pile et al. 2017a, Fan et al. 2018). The best way to use prescribed fire to control Chinese tallow establishment is before a site has become tallow regulated.

1.2.3 Chinese tallow invasion and southern native forests under fire

Fire is a type of disturbance and ecosystems are partly defined based on disturbance regimes of specific frequency (i.e., fire interval), intensity, extent, type, and seasonality (Pickett and White 1985, Moretti et al. 2006, Johnstone et al. 2016). Fire frequency can be defined as a measure of the fire cycle or the fire return interval. Fire intensity, the amount of heat released per unit of time, is related to fire severity, which is the effect of this heat release on biotic and abiotic ecosystem properties (i.e., site conditions). Fire extent includes both size and spatial homogeneity of burning. Fire type is also an important trait, which is classified as ground fire (peat-bog fires), surface fire (grass fire), and crown fire (canopy fires). Seasonality refers to the annual window of fire activity and is largely determined by the ability of fuels to ignite and carry fire.

It is known that exotic species may change the site conditions of native ecosystems, such as fuel conditions, soil properties, moisture conditions, and microclimate situations, which are related to fire regime. It is reported that fuel properties can be directly changed by the addition of invasive plants (Whisenant 1990) or indirectly changed by alteration in the amount and species composition of native plants, caused by competitive effects of invaders (D'Antonio 2000). Therefore, the fire regime cycle converts to an invasive plant-fire regime (Brooks et al. 2004). This invasive plant-fire regime model can be used to explain the relationship between fire traits and Chinese tallow invasion (Figure 1.2). Prescribed fire may increase the invasive risk of Chinese tallow for a native ecosystem, especially with stable tallow seed sources (Gan et al. 2009, Fan et al. 2012, Fan et al. 2018, Yang et al. 2019). Furthermore, high intensity (hotter and higher flames) and complete fire also can control Chinese tallow invasion (Grace 1998, Grace et al. 2005, Pile et al. 2017b). Previous research also indicates that crown fire is able to kill tallow or tops of tallow, and long-term fire during the growing season is more effective to control tallow (Grace 1998). Therefore, there is a significant correlation between fire characteristics and Chinese tallow invasion. On the other hand, Chinese tallow can also influence fire traits once it has been established in a native ecosystem. Chinese tallow can change invaded site conditions, such as moisture properties, understory fuel conditions, and microclimate. Chinese tallow has the ability to eliminate fuel species, which can make stands less likely to carry a fire. Chinese tallow will reduce the fuel of fire regime and decrease the fire intensity that is related to fuel conditions of the understory. Therefore, the effects of prescribed fire on Chinese tallow invasion is a comprehensive process and besides fire, it is also related to other predisposing (community and landscape features) and inciting factors (natural disturbance and human activities), such as natural disturbance, community features, and landscape features (Figure 1.3).

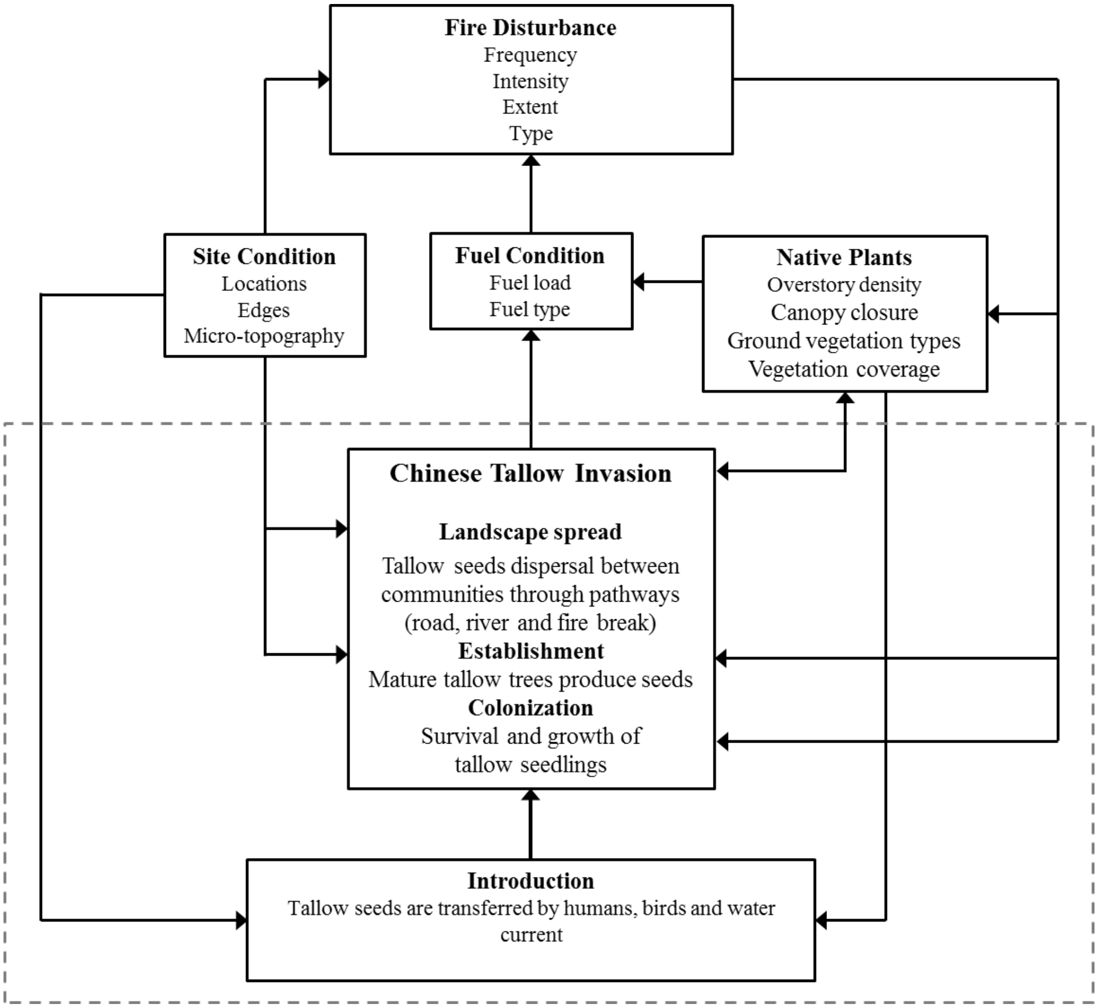

Figure 1.2 Concept model of Chinese tallow (*Triadica sebifera*) invasion under fire disturbances

Modified from Brooks et al. 2004

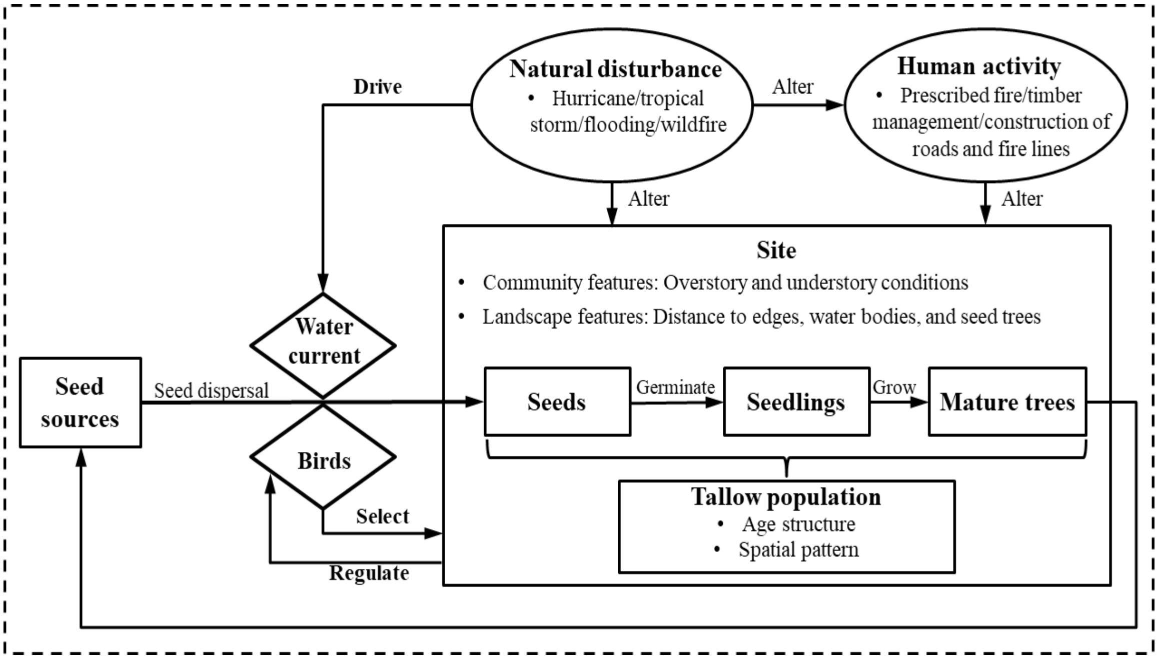

Figure 1.3 The potential mechanism (conceptual model) of Chines tallow (*Triadica sebifera*) seed dispersal and seedling recruitment along edge habitat in the southeastern United States coastal landscape

Modified from Fan et al. 2018

Fire is one of the most important factors for the ecosystems of southern coastal areas, especially for native forest ecosystems. Furthermore, ecologists have interpreted southern forest ecosystems as a “fire sub-climax” (Croker et al. 1975). Prescribed fire has been regarded as an important tool for southern forests regeneration, such as wet pine and bottomland hardwood forests, because in the southeastern coastal area forests, regeneration requires a bare soil surface and prescribed fire can burn the organic matter and vegetation above the ground providing suitable soil conditions for regeneration of native forest. For instance, longleaf pine regeneration is a kind of fire dependent behavior for almost one century. However, young seedlings that are less than two years old tend to have low survival rate under fire (Grace and Platt 1995). Therefore, how to use prescribed fire to restore the native forest ecosystem and prevent the invasion of exotic species, such as Chinese tallow, has become a serious problem because it is also related to habitat decline of certain wildlife species and ecosystem biodiversity.

1.2.4 Climate change and spread pattern of Chinese tallow

Climate conditions or climate change is another associated factor for Chinese tallow invasion. Scientists have studied the influence of climate change on forest ecosystems for decades. Climate is the key point to study the distribution or spread pattern of Chinese tallow. Previous research (Gan et al. 2009, Wang et al. 2011) reported that the mean extreme minimum temperature in winter is significant positively correlated with the Chinese tallow invasion, meanwhile it also indicates that the winter minimum extreme temperature is an important barrier to tallow invasion in the southern coastal area (Pattison and Mack 2008). Therefore, the global warming in this century will influence the spread of Chinese tallow. By using the CLIMEX model, Pattison and Mack (2008) concluded that if the minimum and maximum temperature were to rise by 2 °C, the range of tallow could extend northward 700 km beyond its current distribution. Furthermore, Gan et al. (2009) used a logistic regression model to predict the range of tallow with 2 °C warming (Figure 1.4), with observed and estimated ranges of Chinese tallow in the southern area closely matching with each other (Figure 1.4a and 1.4b). Chinese tallow has the same distribution pattern, with hot spots, in southeastern Texas and Louisiana. Chinese tallow invasion is less prevalent in Mississippi and Alabama compared to those states. If the range of Chinese tallow will continue to expand toward North and East, the infested area of Chinese tallow will increase greatly. Therefore, over 20% of invasive area may increase and as will the hot spot area transfer from the southeastern coastal area of Texas and Louisiana to the southern coastal region of Mississippi (Gan et al. 2009). Global warming could lead to tremendous challenges in combating the geographic expansion of Chinese tallow invasion. This situation may cause ecological and economic disasters for the southern United States.

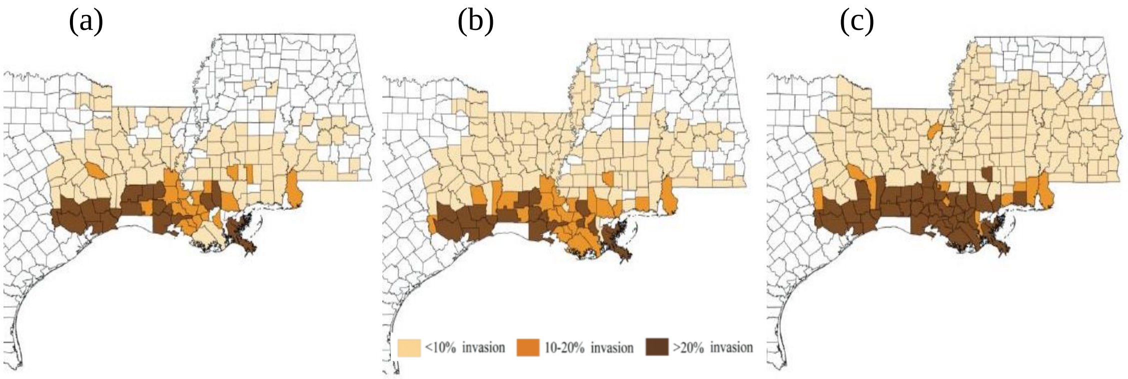

Figure 1.4 Current and predicted ranges of Chinese tallow (*Triadica sebifera*) in southern coastal area

Predictions were made only within the FIA data. (a) Observed tallow invasion, 2007; (b) predicted tallow invasion, 2007; (c) predicted tallow invasion under global climate change (2 °C warming) (Gan et al. 2009).

1.3 Objectives

The primary study objective is to construct multiscale spatial models to quantify Chinese tallow invasion patterns and evaluate the effect of associated predisposing and inciting factors on tallow invasion and spread. The next objective is to make optimal management prescriptions for tallow control and mitigation at different spatial scales.

Chapter Ⅱ will examine Chinese tallow distribution and spread patterns, and evaluate contributing factors to the observed patterns at the regional scale that includes eight southeastern coastal states (east Texas to South Carolina). Unlike previous research, two consecutive cycles of Forest Inventory and Analysis (FIA) plots are used as the analysis units for regional analysis and modeling to explore the effects of natural disturbances (i.e., hurricanes and tropical storms), landscape features (e.g., elevation), and anthropogenic disturbances on tallow invasion and spread. Chapter Ⅲ mainly focuses on distribution and spread mechanisms of Chinese tallow invasion at the landscape level and the evaluation impacts of prescribed fires and landscape structure on Chinese tallow dispersal and colonization (regeneration). Chapter Ⅳ will analyze tallow distribution patterns and invasion mechanisms at the stand scale quantifying invasion processes through spatial analysis of age structure and regeneration of Chinese tallow. Local invasibility of target communities and ecosystems and related biotic and abiotic factors will be evaluated based on community structure under a landscape context.

1.4 Research technical route

Technically, invasive patterns and mechanisms of Chinese tallow invasion will be studied in three interrelated hierarchical spatial scales: region, landscape and stand/community (Figure 1.5). The FIA database, United States Geological Survey (USGS), and National Oceanic and Atmospheric Administration (NOAA) database and the field collected data constitute the research sources related to Chinese tallow invasion. ArcGIS (Geographic Information System tool), ERDAS (Remote sensing tool), Global Positioning System tool (GPS) and R packages (statistical software) will be employed for data processing and modeling.

The regional distribution patterns and rate of spread of Chinese tallow are evaluated first by examining regional variables including elevation, spatial coordinates (latitude and longitude), road / river density, forest types, forest land ownerships, distance to the propagule pressure, and hurricane tracks and categories using classification and regression tree (CART), logistic regression (LR), and geographic weighted regression (GWR) models. At the landscape level, effects of the predisposing and inciting variables that include distance to the edges (e.g., road, firebreak and neighborhood), disturbances (e.g., prescribed fire)/regimes, density and canopy closure of overstory trees, and understory vegetation conditions on invasive patterns of Chinese tallow were modeled using the zero-inflated negative binominal (ZINB) regression model. Spatial Poisson point process models was used to evaluate the effects of distances to the stand edges, microtopography, conditions of disturbances (intensity and frequency), density and canopy closure of overstory trees, and understory vegetation conditions on stand invasibility and tallow invasive patterns.

Based on the modeling results of Chinese tallow invasion on different spatial scales, the mechanisms of Chinese tallow invasion by identified risk factors were examined in a hierarchical modeling framework, and tallow control and mitigation plans were proposed.

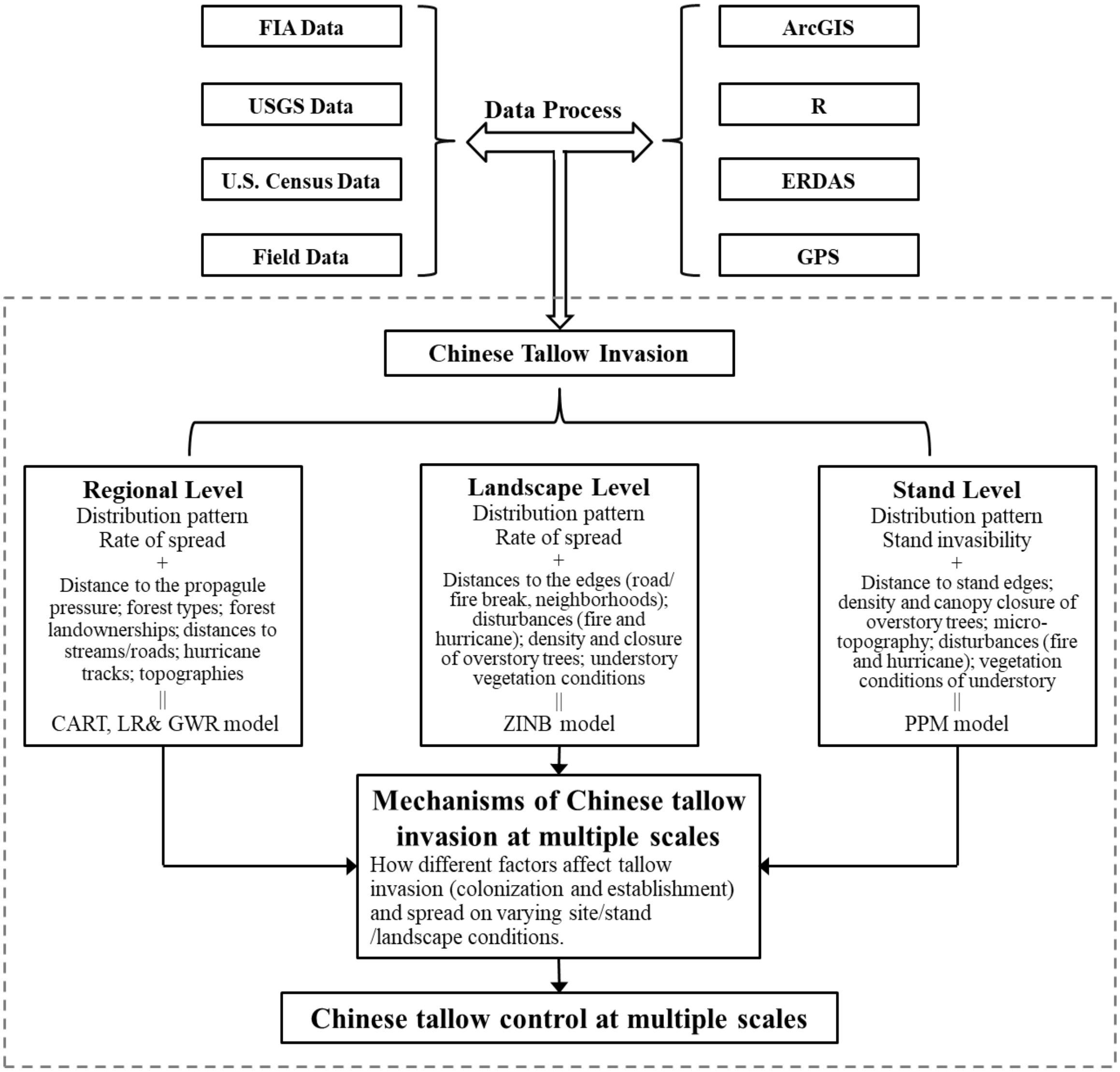

Figure 1.5 Technical route of Chinese tallow (*Triadica sebifera*) invasion and spread mechanism

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CHAPTER II

SPATIAL DISTRIBUTION AND SPREAD PATTERNS OF CHINESE TALLOW (*Triadica sebifera*) IN THE SOUTHEASTERN COASTAL AREA OF AMERICA

2.1 Introduction

The southeastern coastal area is one of the most important forest regions in the United States. Forests and forest production make great contributions to the economy and ecological services in this region (Wear and Greis 2002, Gan et al. 2009). However, the invasion of nonnative plants has become a serious problem and threatens the sustainable development of native forest ecosystems in this area (Gan et al. 2009, Wang et al. 2011, Fan et al. 2012, Pile et al. 2017a, Fan 2018, Fan et al. 2018a, Yang et al. 2019). Among those invasive species, Chinese tallow (*Triadica sebifera*) has become one of the most pervasive tree species in the southeastern coastal states, including Alabama, Mississippi, Louisiana and Texas. The U.S. government in the early 1900s promoted it as a plantation tree for the waxy oil seeds it produces that are of use in the soap industry (Hunt 1947, Gan et al. 2009, Wang et al. 2011). Currently, Chinese tallow trees have invaded and spread throughout nearly every local forest of the southeastern United States, from east Texas to South Carolina, including the coastal plain, coastal prairie plain and floodplain of the Mississippi River (Miller et al. 2008). Based on aboveground dry weight of live trees, Chinese tallow tree ranks 17th out of the 135 encountered species across the counties in the four states mentioned above (Fan et al. 2018a).

Chinese tallow has high seed productivity (Gray 1950), and streams (flowing water) and water bodies (impounded water) are the main pathways for Chinese tallow seed dispersal in local and short-distance along coastal areas (Bruce et al. 1997). Furthermore, some bird species that prefer the high oil content seeds could also play important roles for long-distance dispersal of Chinese tallow seeds at regional scales (Hukui and Ueda 1999, Renne et al. 2002). Human activities such as road construction, landscaping/backyard plantation, transportation, and fire suppression, could also accelerate the spread of Chinese tallow (Gan et al. 2009, Wang et al. 2011, Fan et al. 2012, Fan et al. 2018a, Yang et al. 2019). There are significant negative correlations between Chinese tallow presence and regional geographic features (slope and elevation). Meanwhile, there are no Chinese tallow trees on sites where the elevation is greater than 165 m (540 ft) or slope is steeper than 18° (Gan et al. 2009, Wang et al. 2011, Fan et al. 2012). Adjacency to water bodies correlates positively to the presence probability of Chinese tallow in the southeastern coastal area (Gan et al. 2009, Wang et al. 2011, Fan et al. 2012), because tallow seed dispersal is dependent on the water movement and birds (Barrilleaux and Grace 2000, Butterfield et al. 2004). Fires and hurricanes could also increase Chinese tallow invasion rates and presence. It is reported that Chinese tallow invasion in Louisiana increased following Hurricane Katrina (Chapman et al. 2008, Gan et al. 2009, Fan et al. 2012, Henkel et al. 2016).

Although previous research has studied the effects of associated factors on Chinese tallow distribution, mechanisms of dynamic changes of Chinese tallow invasion, especially from the aspect of invasion ecology (i.e., invasibility, degree of invasion, and invasiveness), have not been holistically and systematically studied in the southeastern coastal area of the United States. Invasion of nonnative plants into a region could be classified into four stages: introduction, colonization, establishment, and landscape spread (Vermeij 1996, Theoharides and Dukes 2007).

In each stage, invasive plants must tolerate different biotic (e.g., propagule pressure, competition or interaction with other species) and abiotic (e.g., site condition, climate) filters to successfully colonize and establish in an area (Williamson 1996, Lockwood et al. 2005, Fan et al. 2013). Contrary to previous studies, the related factors of Chinese tallow invasion in this research were divided into two functional groups, predisposing factors (community and landscape/regional features) and inciting factors (disturbances/human activities) (Fan et al. 2018a). Forest Inventory and Analysis (FIA) data between 2000 and 2016 also indicated that Chinese tallow had invaded from east Texas to South Carolina and from bottomland hardwood forests to inland pine forests, within different locations and forest ecosystems.

The major objective of this research is to understand the mechanisms of Chinese tallow distribution and spread at the regional level within different invasive stages by considering the degree of invasion (DI) of native forest ecosystems and invasiveness of Chinese tallow trees (Guo et al. 2015, Pile et al. 2017b, Fan et al. 2018b), using statistical modeling methods. Specifically, this research addressed the following objectives/questions: 1) Map the invasive stages (invasive sub-region) of Chinese tallow invasion based on the probability of presence and analyze the effects of predisposing and inciting factors on the spread of Chinese tallow within each invasive stage by using FIA data. 2) Evaluate the effects of predisposing and inciting factors on the degree of invasion of native forest ecosystems based on the cover percentage of Chinese tallow. 3) Examine the dynamic changes of Chinese tallow coverage (invasiveness) during two time periods by using the spatial statistical model and associated predisposing and inciting factors.

2.2 Methods

2.2.1 Research area

The southeastern coastal area of the United States consists of eight states: Texas, Louisiana, Arkansas, Mississippi, Alabama, Georgia, Florida, and South Carolina (Figure 2.1). Situated where several ecoregions come together (tropical and subtropical coniferous forests and tropical wet forests) (Commission for Environmental Cooperation 1997), this area is characterized by diverse native forest types such as longleaf-slash pine (*Pinus palustris* and *Pinus elliottii*) forests, loblolly-shortleaf pine (*Pinus taeda* and *Pinus echinata*) forest, oak-pine forests (*Quercus* and *Pinus spp.*), oak-hickory forests (*Quercus* and *Carya spp.*), oak-gum-cypress forests (*Quercus*, *Nyssa*, and *Taxodium spp.*), and elm-ash-cottonwood forests (*Ulmus*, *Fraxinus*, and *Populus spp.*). Across the southeastern United States, there are also many rare native habitats, such as wet pine savannas, hydric drain, bottomland hardwoods, and marshland, and these habitats are critically important to natural biodiversity (Cartwright and Wolfe 2016). However, these eight states have been invaded by Chinese tallow trees as evidenced by the presence of tallow infested FIA plots of 2016 (Figure 2.1).

The southeastern region of the United States is dominated by different varieties of the humid subtropical climate. Summers are generally very hot throughout the entire region with relatively small temperature differences for July throughout the region, as proven by Miami's July high being 32.7 °C (90.9 °F) with a coastal area as far north as Virginia Beach recording close to 31 °C (88 °F) on average for the same time period (Ingram et al. 2013). Average annual precipitation across the Southeast is 153.8 cm (60.55 inches), more than 25.4 cm (10 inches) above the 20th century average (National Climate Annual Report 2014). The main topographic types of the southeastern coastal area are very different between the southeastern and northwestern sections of this region. Landforms in the southeastern area consist of the coastal flat plain but the northwestern area includes low mountains, and gentle rolling hills which are a part of Appalachian Mountains (Napton et al. 2010).

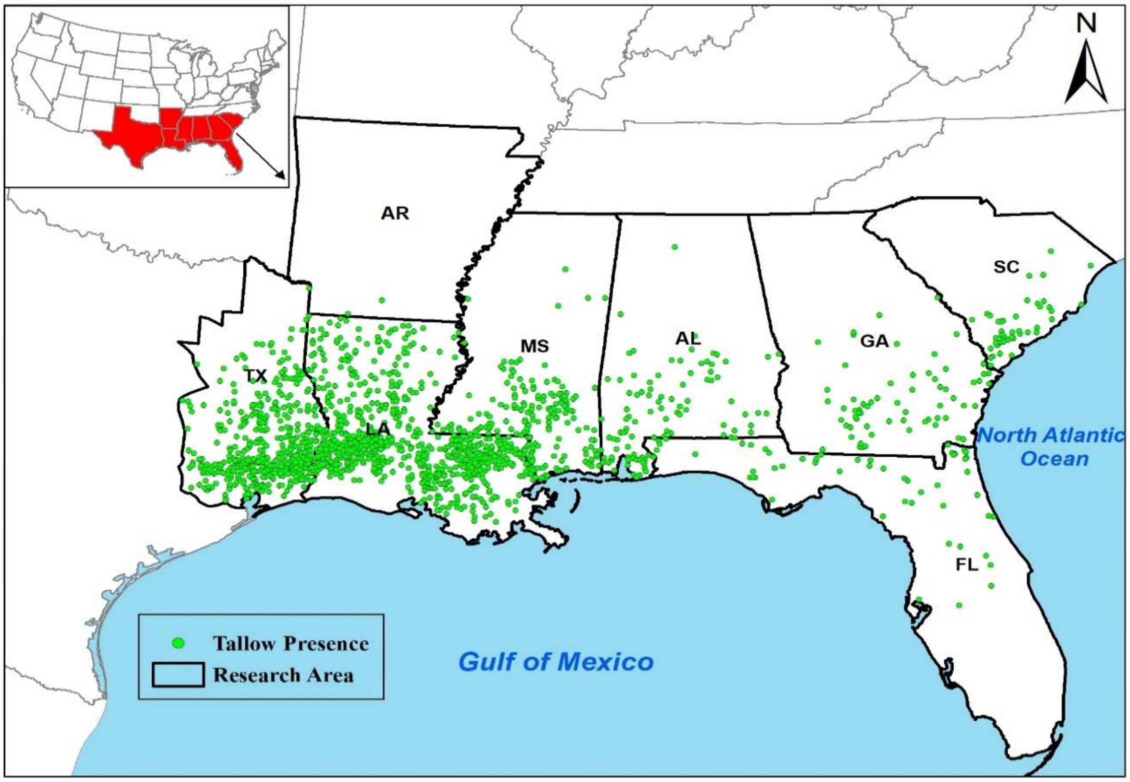

Figure 2.1 Research area and Chinese tallow (*Triadica sebifera*) infested Forest Inventory and Analysis plots (2000-2016)

2.2.2 FIA plot data and associated factors

Beginning in 2000, the FIA program changed from a periodic inventory investigation to an annual measurement scheme to monitor both annual and long-term forest change (Fan et al. 2012). However, different states have different start years for the new investigation plan. All FIA sampled plots within a state/inventory unit are measured over a 5-7 year period (one inventory cycle) with approximately 10%-20% of the plots being measured each investigation year.

According to the research objectives and requirements of data completion, the FIA plot level data from 2000 to 2016 to had been utilized to ensure each state had at least two complete cycles. Within each FIA plot, the spatial location was identified by the latitude and longitude with presence (1) or absence (0) of the tallow tree. For tallow tree invaded plots, mean cover percentage of tallow tree was calculated by four subplots and classified into five levels: none (= 0%), slight (≤ 1%), low (> 1% to ≤10%), medium (>10% to ≤ 30%), and high (> 30%). In addition, the predisposing and inciting factors associated with each FIA plot, such as forest types (6 groups, a-f), ownership (3 groups, I-III), and mature tallow density were measured and calculated based on the attribute tables of FIA plots (Table 2.1).

Regional predisposing factors, such as distance of the FIA plot to the nearest river, road, and previous infested plot (tallow seed source), were calculated by using ArcGIS 10.6 (Gan et al. 2009, Moser et al. 2009, Fan et al. 2012). The elevation of each FIA plot was extracted from the digital elevation model (DEM, 90 m resolution) of the research area. Unlike previous studies (Gan et al. 2009, Wang et al. 2011, Fan et al. 2012), effects of hurricanes/storms on the FIA plots were analyzed by using a binary variable (yes=1, no=0). In this research, effects of hurricane/storm disturbances (2000-2015, NOAA) on the FIA plots have been quantified by using their category (speed) and frequency (density) since the Chinese tallow invasion in the southeastern United States is a cumulative process affected by hurricane/storm disturbances. Based on the Saffir–Simpson scale (9 categories) (Zhang et al. 2013, Warren et al. 2016), mean speed of each category was calculated, and combined with kernel smoothing (Fan et al. 2013). The raster surface of the hurricane/storm was obtained from the interpolation of hurricane tracks. According to this surface, the quantified hurricane effects on each FIA plot were extracted (Table 2.1).

Table 2.1 Associated variables for classification trees and the logistic regression model

Data Type	Variables	Classification	Factor type	Time series	Sources
FIA plot data	Ownership	Public land (I) Corporate land (II) Nonindustrial private land (III)	Inciting	2000-2016	Forest Inventory and Analysis data mart
	Forest type	Longleaf-slash (a) Loblolly -shortleaf (b) Oak-pine (c) Oak-hickory (d) Oak-gum-cypress (e) Elm-ash-cottonwood (f)	Predisposing	2000-2016	
	Tallow presence	1: yes; 0: no	Predisposing	2000-2016	
	Tallow coverage	A. None: = 0% B. Slight: ≤ 1% C. Low: >1% & ≤ 10% D. Moderate: > 10% & ≤ 30% E. High: > 30%	Predisposing	2000-2016	
	Tallow density	Mature, DBH> 5 in (trees/ha)	Predisposing	2000-2016	

Table 2.1 (continued)

Data Type	Variables	Classification	Factor type	Time series	Sources
Landscape/ regional features	Elevation	DEM (90 m resolution), Continuous (m)	Predisposing	2016	U.S. Geological Survey
	Coordinate	Lat. & Long., continuous	Predisposing	2016	Extracting from FIA plot data
	Distance to the nearest tallow seed source	Continuous (km)	Predisposing		Extracting from FIA plot data
	Distance to the nearest river	Continuous (km)	Predisposing		Extracting from FIA plot data and rivers/streams shapefile
	Distance to the nearest road	Continuous (km)	Predisposing		Extracting from FIA plot data and roads shapefile
	Hurricane /storm	H5: 252km, continuous H4: 230 km/h, continuous H3: 193 km/h, continuous H2: 166 km/h, continuous H1: 136 km/h, continuous TS/SS: 91 km/h, continuous TD/SD: 55 km/h, continuous ET: 37 km/h, continuous DS: 28 km/h, continuous	Inciting	2000-2016	National Oceanic and Atmospheric Administration database (Hurricane tracks and categories)

2.2.3 Presence and patterns of Chinese tallow tree

From 2000 to 2016, 77396 FIA plots were measured in those eight states (Figure 2.1) including the remeasured plots because some states had multiple investigation cycles. Two complete cycles were selected from each state, and 24332 FIA plots were measured in both consecutive cycles (first cycle 2000-2009, second cycle 2006-2015). Plots were divided into four conditions according to the presence of the Chinese tallow tree (Table 2.2). To generate the current map of tallow presence probability among these eight states, all 24332 FIA plots of the second cycle were used through the kernel smoothing function. During 2000-2009, Chinese tallow trees infested 1036 out of 24332 FIA plots with an overall probability of 4.3%, but east Texas and Louisiana had higher probabilities than the other states, at 17.1% and 16.8% respectively. During the second cycle (2006-2015), tallow tree infested FIA plots increased to 1572 with an overall probability of 6.5%, and the probabilities of east Texas and Louisiana increased to 20.1% and 31.5%, respectively (Table 2.3). Compared to the first cycle, 788 FIA plots were found newly infested by the Chinese tallow tree with an overall annual increase rate of 0.54% but there were also 252 previously infested FIA plots without any tallow (Table 2.2, Table 2.3). Among these eight states, Louisiana and east Texas had the highest annual increase rates of 2.51% and 1.18%, respectively, and Arkansas had the lowest annual increase rate of 0.01% (Table 2.3).

Table 2.2 Conditions of Chinese tallow tree presence (1) and absence (0) in both cycles

	First cycle	Second cycle	Number of FIA plots and interpretation
Tallow presence	0	0	22508 non-infested plots in both cycles
	0	1	788 newly infested plots in new cycle
	1	0	252 previously infested plots but no tallow in new cycle
	1	1	784 infested plots in both cycles

Table 2.3 Probability of tallow presence in first and second cycles and the annual increase rate

State code	Total infested plots		Newly infested plots	Number of plots	Cycle period (yrs.)	Presence percentage (%)		Infestation rate (%)
	First cycle	Second cycle				First cycle	Second cycle	Annual increase
AL	61	96	62	3826	7	1.6	2.5	0.23
AR	3	2	2	3082	5	0.1	0.1	0.01
FL	38	54	36	2659	5	1.4	2	0.27
GA	36	64	42	4530	5	0.8	1.4	0.19
LA	374	702	392	2232	7	16.8	31.5	2.51
MS	122	173	97	3457	7	3.5	5	0.4
SC	29	44	28	2367	5	1.2	1.9	0.24
TX	373	437	129	2179	5	17.1	20.1	1.18
Total	1036	1572	788	24332	6	4.3	6.5	0.54

2.2.4 Regression models of data analysis

Previous research (Gan et al. 2009, Fan et al. 2012) used logistic regression to link the probability of Chinese tallow tree presence/occupation to the associated factors, including predisposing and inciting factors. Biological invasion is a non-stationary (spatially inhomogeneous) process due to the spatiotemporal autocorrelations of the propagule pressure of the invasive species (Lockwood et al. 2005, D'Antonio and Chambers 2006, Fan et al. 2018). It would be a problem to use a logistic regression model to directly estimate the spread of Chinese tallow tree at the regional level without considering the spatial autocorrelation of these associated factors because the effects could change dramatically over spatial domain. Meanwhile, the distribution of Chinese tallow tree at the regional scale is spatially autocorrelated because it varies over the spatial domain. Meanwhile, the spread of Chinese tallow is a cumulative multi-process affected by predisposing and inciting factors. Therefore, before the assessment of Chinese tallow spread, the whole region should be divided into a set of homogenous and stationary invasive sub-regions (invasive stages) to analyze effects of associated factors separately. For this objective, 24332 FIA plots (788 newly infested plots) of the second cycle and the landscape features (elevation and coordinates) were used to classify the research region through the classification and regression tree (CART) (Fan et al. 2013, Buchholz et al. 2016). Meanwhile, 22969 FIA plots (768 newly infested plots) of the second cycle within those six forest types (without other forest types and previously infested plots) were classified in each invasive sub-region. In each sub-region, a logistic regression model (Equation 2.1) (Hilbe 2009, Fan et al. 2012) was built to analyze effects of predisposing and inciting factors on the spread of Chinese tallow tree at each sub-regional scale.

$$p(Y = 1|X) = \frac{1}{1+e^{-(\alpha+X'\beta)}} \qquad (2.1)$$

where $p(Y = 1|X)$ is the expected conditional probability for a remeasured plot to be newly infested (Y =1; otherwise, Y=0 if not infested) by tallow tree within the second cycle; α is the intercept of the model; X is the vector of associated factors (Table 2.1); and β is the vector of estimated coefficients. A stepwise method with the significance level of 0.1 was chosen to select the significant factors associated with the infestation of tallow tree in a remeasured FIA plot.

To realize the second objective of this research, the DI of native forest ecosystems should be considered under each invasive sub-region (i.e., invasive stages) because of the spatial autocorrelation and non-stationary distribution of Chinese tallow tree. Based on the FIA plots in each sub-region and classifications of tallow cover percentage within each plot (Table 2.1), the relationship between DI of native forest ecosystems and associated factors (i.e., predisposing and inciting) was analyzed by using the conditional inference trees (CTree) (Hothorn et al. 2006, Hothorn et al. 2015). For each invasive sub-region, classes of tallow tree coverage were response variables, and the associated factors, such as hurricane speed, forest ownership, and forest types, were independent variables (Table 2.1). Through analyzing the results of the CTree model in each sub-region, the DI of native forest ecosystem could be evaluated in each sub-region.

Using the non-stationary spatial distribution of Chinese tallow tree at the regional scale, spatial autocorrelation had been considered when the relationship between dynamic changes of tallow cover percentage and associated predisposing and inciting factors was evaluated. To achieve the third objective, all 1492 infested FIA plots within six forest types (without other forest types) and associated factors were selected to assess the annual change of Chinese tallow cover percentage. Meanwhile, due to the spatial autocorrelation of the Chinese tallow tree, the spatial regression model, geographic weighted regression (GWR) (Equation 2.2) (Charlton et al. 2009, Wheeler 2014), was employed to analyze this relationship spatially because the non-parametric GWR was developed to analyze the relationships in a regression that varied over space or the parametric non-stationarity (Wheeler 2014). Furthermore, for the analysis of the dynamic changes of tallow cover percentage during the second cycle, one of the inciting factors, hurricane/storm disturbances, was extracted from the new raster surface that was generated based on the hurricane/storm tracks of the second cycle (2006-2015) in each state:

$$y_i = X_i\beta_i + \varepsilon_i \tag{2.2}$$

where y_i is the estimated annual changes of tallow coverage at location i; β_i is a column vector of regression coefficients; and X_i is a row vector of associated predisposing and inciting factors at location i. The vector of estimated regression coefficients at location i is

$$\beta_i = [X^T W_i X]^{-1} X^T W_i Y \tag{2.3}$$

where Y was the vector of annual change of tallow coverage; X was the design matrix of associated predisposing and inciting factors, which included a leading column of ones for the intercept; W_i was the weights matrix calculated for each calibration location i.

2.3 Results

2.3.1 Hurricane/storm disturbances and presence probability of Chinese tallow

Based on the intensity categories (wind speed) of 53 hurricane/storm tracks (18 hurricanes and 35 tropical storms) from 2000 to 2015 in the southeastern coastal area of the United States, the Gaussian kernel smoothing was used to create two raster surfaces to show the cumulative effects of hurricane/storm disturbances between 2000-2015 (entire period) and 2006-2015 (Figure 2.2). Figure 2.2A showed that the highest hurricane speed occurred in southern Florida with an average speed of 216.9 km/h and southeastern areas of east Texas, Louisiana, Mississippi, and Alabama also had higher speed than other places. However, the highest hurricane speed during the second cycle was located in southeastern Texas with an average speed of 137.9 km/h (Figure 2.2B), which was different from the speed distribution of total hurricane/storm disturbances. According to the figure 2.2A, the average speed of total hurricane/storm disturbances decreased dramatically within the region from southeast to northwest (Huang et al. 2001, Duryea et al. 2007) due to the increase of the roughness on the ground surfaces (Mehta and Pandey 1983, Wakimoto and Black 1994, Simiu et al. 2007). By using these two surfaces, the quantified effects of hurricane/storm disturbances for both inventory cycles were extracted based on the locations of all FIA plots.

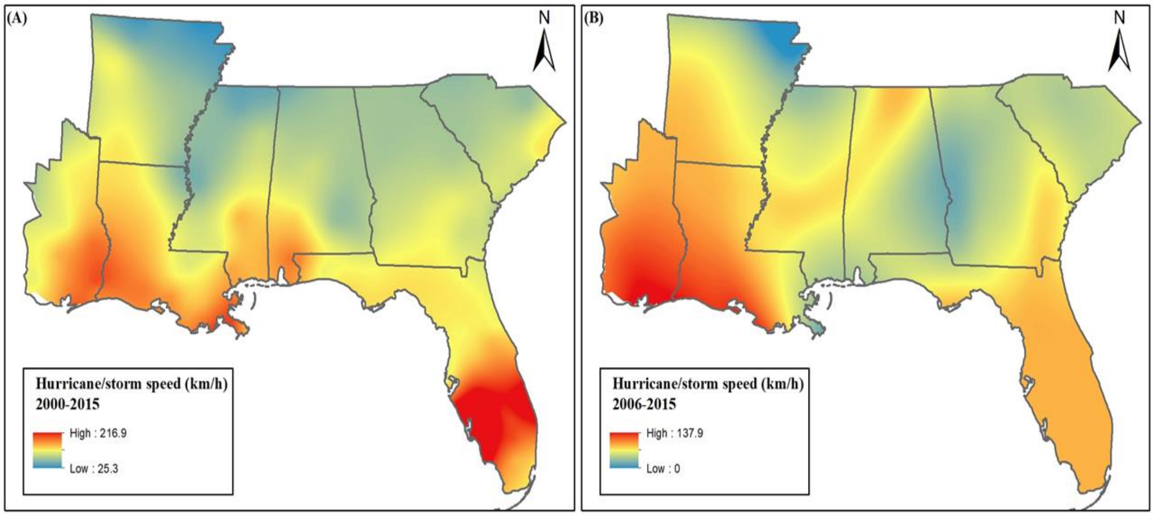

Figure 2.2 Cumulative effects of total hurricane/storm disturbances (A, 2000-2015) and cumulative effects of hurricane/storm disturbances during the second cycle (B, 2006-2015) within each state

Out of 24332 FIA plots measured during the second cycle, there were 1572 Chinese tallow infested plots and among those plots, 788 were newly infested plots. Overall presence probability in the research area was 6.5% and overall infestation probability between 2006 and 2015 was 3.2% with an average annual increase rate of 0.54% (Table 2.3, Figure 2.3). Previously infested plots were clustered in the southwestern section, mainly in southeastern Texas and Louisiana and the boundary between Louisiana and Mississippi (Gan et al. 2009, Wang et al. 2011). There were also a few clusters located in southern Alabama and South Carolina and a few infested plots scattered sporadically in the east-central portion of the research area. Newly infested plots mainly clustered with previously infested plots and some newly infested plots were found in Louisiana, Mississippi, and Alabama compared to the previously infested plots. In middle Alabama, Georgia, and South Carolina, a few newly infested plots had reached the edge of the mountain area (Figure 2.3). The smoothed presence probability map showed a similar pattern with hot spots (presence probability > 0.5) which matched the distribution of plot clusters of Chinese tallow in the research area. According to the probability map, the spread of Chinese tallow started from southern Texas and Louisiana and moved to the northeast portion of the research area. However, there was a hot spot (presence probability > 0.3) in southern South Carolina. The spread of Chinese tallow in the eastern portions (presence probability ≤ 0.1) was slower than in the southwestern portions. Compared to the southern portions, the northern portions have less or no tallow presence probability (presence probability < 0.1) (Figure 2.4). Meanwhile, compared to the cumulative effects of total hurricane/storm disturbances (Figure 2.2A), the distribution patterns of hurricane/storm speed were similar to the presence probability map of Chinese tallow (Figure 2.2, Figure 2.4) because the invasion of Chinese tallow was also a cumulative process in the research area.

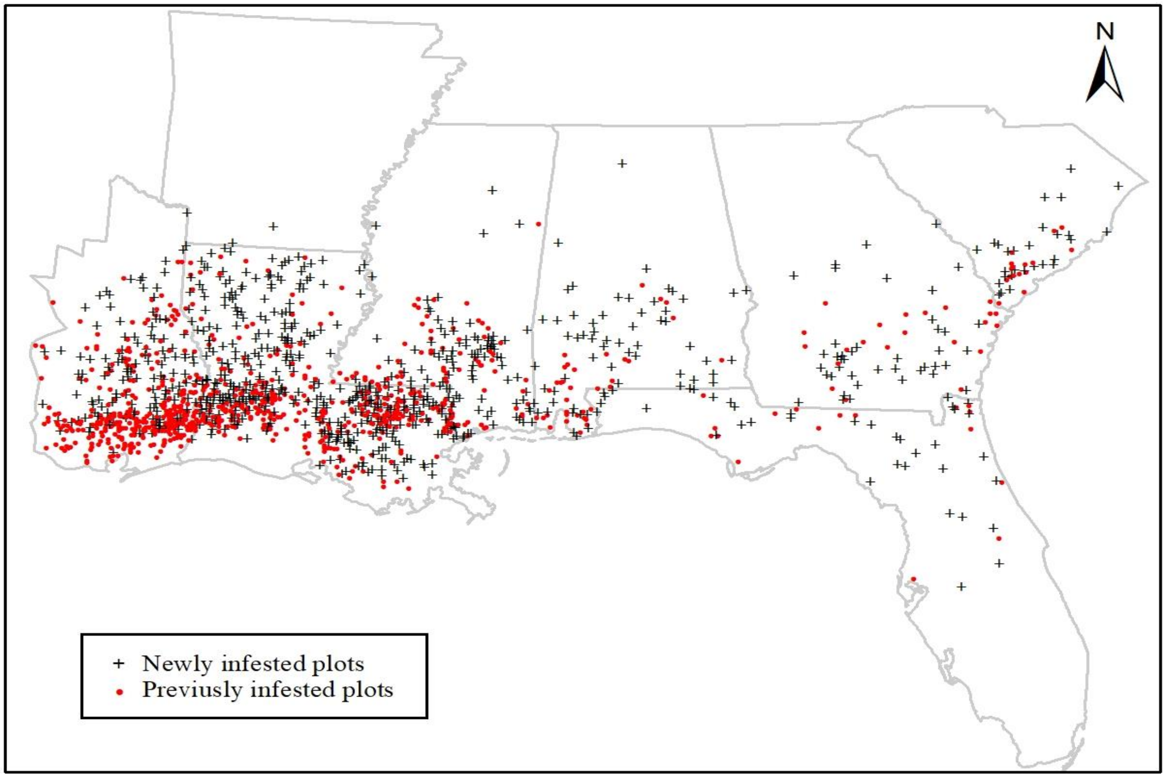

Figure 2.3 Chinese tallow (*Triadica sebifera*) newly infested plots and previous infested plots during 2000-2015

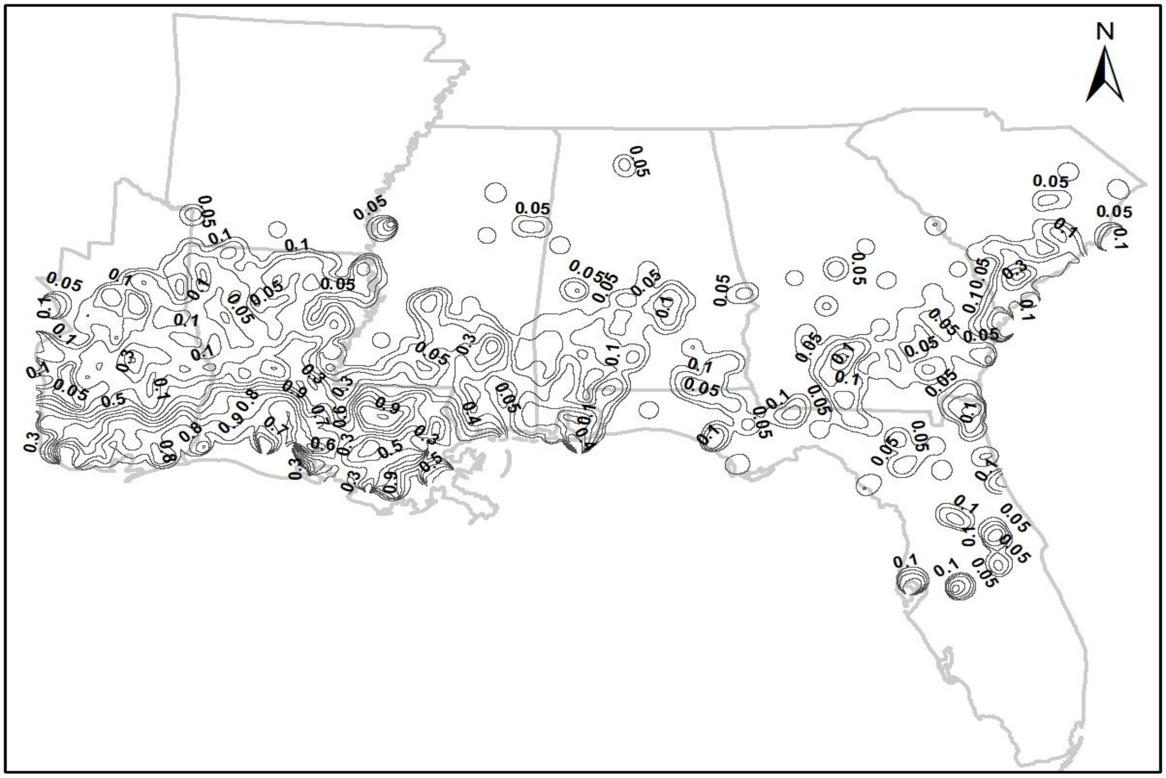

Figure 2.4 Smoothed Chinese tallow (*Triadica sebifera*) presence probability of the second cycle by 2015

2.3.2 Invasive sub-regions of CART model and logistic regression

The CART model showed (Figure 2.5) that according to the landscape features, including latitude, longitude, and elevation, all 24332 FIA plots had been classified into five nodes (S1, S3, S5, S7, and S8) each with a different presence probability for Chinese tallow. Presence probability of inland areas (S1, latitude ≥ 31.16°) was 2.7%, which was six times lower than the coastal area (S2, latitude < 31.16°). However, in the coastal area, the presence probability of the western portions of the coastal area (S4, longitude < -89.64°), involving southern Texas and Louisiana, was 12 times higher than the eastern portions (S3, longitude ≥ -89.64°), including southern Mississippi, Alabama, Georgia, and all of Florida. Based on the elevation of the western portions, the presence probability of the low elevation area (S6, elevation < 50.5 m) was as high as 61.2% compared to the presence probability of the high elevation area (S5, elevation ≥ 50.5 m). Although, node S6 had been divided into two additional nodes, this area already was the high propagule pressure region (61.2%). Therefore, in this study, the node S6 was not classified and used as the last invasive sub-region to make sure there were enough sampling plots. According to the CART model results, nodes S1, S3, S5, and S6 (a combination of S7 and S8) were converted to four invasive sub-regions/stages. All 24332 FIA plots were classified into four regions with given names: 1) inland high elevation low propagule pressure region (S1, 2.7%); 2) coastal low elevation low propagule pressure region (S3, 3.8%); 3) coastal high elevation medium propagule pressure region (S5, 23.1%); 4) coastal low elevation high propagule pressure region (S6, 61.2%) (Figure 2.6).

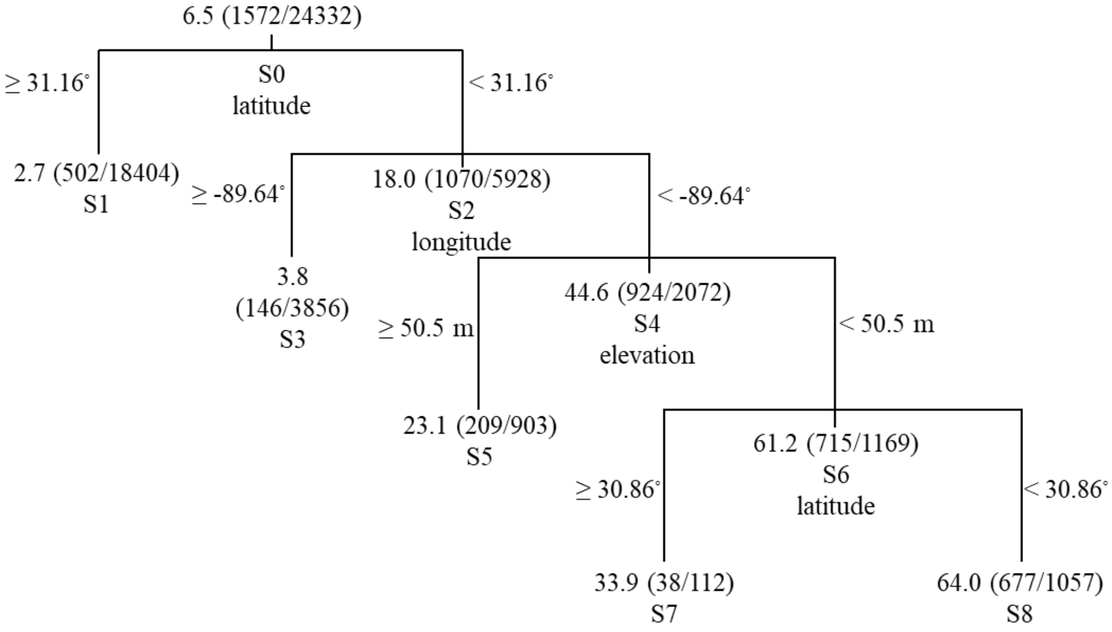

Figure 2.5 Classification tree model of Chinese tallow (*Triadica sebifera*) presence probability (%) according to elevation, latitude, and longitude of forest inventory and analysis plots

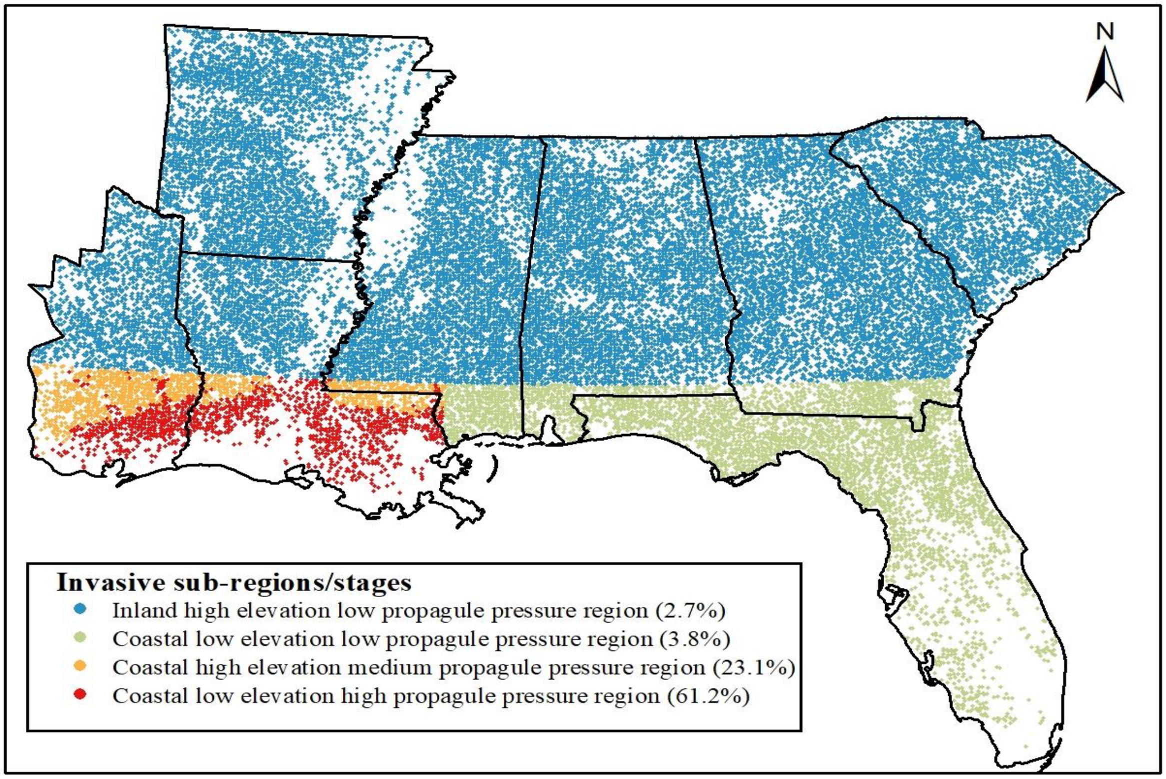

Figure 2.6 Classifications of forest inventory and analysis plots in invasive sub-regions/stages based on the CART model

Based on the predisposing and inciting factors, spread patterns of Chinese tallow in the regional level and each invasive sub-region were evaluated using the logistic regression model and 22696 FIA plots within those six forest types (Table 2.1). The overall logistic regression model for the research area (Table 2.4, S0) indicated that distance to the nearest tallow seed source (previously infested plots), distances to the nearest road and river, and elevation had a significant negative relationship ($p < 0.001$) with newly infested plots of Chinese tallow. Within those six main forest types, longleaf-slash pine had fewer infested plots compared to other forest types ($p < 0.05$) and bottomland hardwood groups (i.e., Oak-gum-cypress and elm-ash-cottonwood) had higher regression coefficients (1.176 and 1.453) than other forest types. Compared to public land, corporate and nonindustrial private lands had more newly infested FIA plots ($p < 0.001$). Another inciting factor, speed of hurricane/storm disturbances also had significant positive correlation ($p < 0.001$) with the spread of Chinese tallow at the regional level, which means hurricane/storm disturbances could accelerate the spread of Chinese tallow.

In the first invasive sub-region (Table 2.4, S1), the inland high elevation low propagule pressure region, ownership encompassing FIA plots was not a significant factor compared to the entire region. However, distances to the nearest seed sources, road and river, and elevation were still significant with Chinese tallow spread at $\alpha \leq 0.01$. For forest types, only oak-hickory, oak-gum-cypress, and elm-ash-cottonwood groups had significantly more newly infested tallow plots at the 0.05 level and the loblolly-shortleaf group was significant at the 0.1 significance level. As the last inciting factor in this sub-region, the hurricane/storm disturbances were still significant for Chinese tallow dispersal. In the coastal low elevation low propagule pressure region (Table 2.4, S3), the logistic regression model showed that compared to public and corporate lands, there were more newly tallow infested plots ($p < 0.05$) on nonindustrial private land and speed of hurricane/storm disturbances were positively correlated with the abundance of newly infested plots at the 0.05 significance level. Distances to the nearest tallow seed source and road were significant predisposing factors ($p < 0.05$), excluding the distance to the nearest rivers. Compared to the inland area (S1), elevation in this area was significant at the 0.1 significance level, which means in the coastal area, effects of elevation on the spread of Chinese tallow were not as important as in inland areas.

In the coastal high elevation medium propagule pressure region (Table 2.4, S5) and coastal low elevation high propagule pressure region (Table 2.4, S6), hurricane/storm disturbances were no longer significant in the spread of Chinese tallow. Furthermore, in the coastal high elevation medium propagule pressure region, there were three predisposing factors including distance to the nearest tallow seed sources, distance to the nearest road, and elevation which were all significant at the 0.05 significance level. Meanwhile, in the coastal low elevation high propagule pressure region, noninsutrial land, distance to the nearest tallow seed source, and distance to the nearest road were correlated with newly tallow infested plots at the 0.05 significance level. However, elevation in this area was significant at 0.1 significance level, which is similar to the coastal low elevation low propagule pressure region.

Table 2.4 Results of the logistic model for the overall area and each invasive sub-region

Node	Newly infested plots/total plots	Variables	Estimated coefficients	Standard Error	P value	Significant
S0	768/22696	Intercept	-4.229	0.311	< 0.001	***
		Public land^{+}	Reference			
		Corporate land^{+}	0.444	0.129	< 0.001	***
		Nonindustrial private land^{+}	0.485	0.129	< 0.001	***
		Hurricane/storm	0.028	0.002	< 0.001	***
		Longleaf-slash^{++}	Reference			
		Loblolly-shortleaf^{++}	0.658	0.153	< 0.001	***
		Oak-pine^{++}	0.370	0.187	0.048	*
		Oak-hickory^{++}	0.723	0.180	< 0.001	***
		Oak-gum-cypress^{++}	1.176	0.153	< 0.001	***
		Elm-ash-cottonwood^{++}	1.453	0.195	< 0.001	***
		Distance to the nearest tallow seed source	-0.063	0.004	< 0.001	***
		Distance to the nearest road	-0.100	0.016	< 0.001	***
		Distance to the nearest river	-0.070	0.017	< 0.001	***
		Elevation	-0.009	0.001	< 0.001	***
S1	330/17722	Intercept	-5.423	0.570	< 0.001	***
		Hurricane/storm	0.037	0.005	< 0.001	***
		Longleaf-slash^{++}	Reference			
		Loblolly-shortleaf^{++}	0.587	0.335	0.080	.
		Oak-hickory^{++}	1.014	0.352	0.004	**
		Oak-gum-cypress^{++}	1.300	0.339	< 0.001	***
		Elm-ash-cottonwood^{++}	1.179	0.402	0.003	**
		Distance to the nearest tallow seed source	-0.037	0.004	< 0.001	***
		Distance to the nearest road	-0.121	0.027	< 0.001	***
		Distance to the nearest river	-0.077	0.029	< 0.001	***
		Elevation	-0.006	0.002	< 0.001	***

Table 2.4 (continued)

Node	Newly infested plots/total plots	Variables	Estimated coefficients	Standard Error	P value	Significant
S3	87/3616	Intercept	-3.859	0.735	< 0.001	***
		Public land^{+}	Reference			
		Nonindustrial private land^{+}	0.857	0.329	0.009	**
		Hurricane/storm	0.012	0.006	0.048	*
		Longleaf-slash^{++}	Reference			
		Oak-gum-cypress^{++}	1.023	0.301	< 0.001	***
		Elm-ash-cottonwood^{++}	2.133	0.549	< 0.001	***
		Distance to the nearest tallow seed source	-0.044	0.008	< 0.001	***
		Distance to the nearest road	-0.165	0.055	0.003	**
		Elevation	-0.009	0.005	0.099	.
S5	104/742	Intercept	1.806	1.208	0.135	
		Distance to the nearest tallow seed source	-0.148	0.033	< 0.001	***
		Distance to the nearest road	-0.091	0.036	0.011	*
		Elevation	-0.024	0.006	< 0.001	***
S6	239/597	Intercept	0.422	0.937	0.653	
		Public land^{+}				
		Nonindustrial private land^{+}	0.697	0.277	0.012	*
		Distance to the nearest tallow seed source	-0.053	0.026	0.043	*
		Distance to the nearest road	-0.072	0.029	0.013	*
		Elevation	-0.012	0.007	0.096	.

Significant codes: '***' 0.001; '**' 0.01; '*' 0.05; '.' 0.1. Other codes: "+" ownership; "++" forest type.

2.3.3 Degree of invasion of native forest ecosystems in each invasive sub-region

Ownerships and forest types of FIA plots and hurricane/storm disturbances were selected as the independent variables in the CTree model. Classifications of tallow cover percentage in each FIA plot was the response variable. The results from the CTree model in the inland high elevation low propagule pressure region (sub-region S1) showed that all FIA plots had been divided into nine end nodes based on the predisposing and inciting factors. In each end node, the proportion of each tallow coverage class had been calculated according to the plot number in each class (Figure 2.7). Results also indicated that when the speed of a hurricane/storm was greater than 88.5 km/h, there were more tallow infested plots (node 15, 13.1%). Moreover, when forest types were oak-hickory, oak-gum-cypress, and elm-ash-cottonwood, there were more tallow infested plots and higher tallow coverage (node 17, B=5.6%, C=10.2%, D=2.0%, and E=0.2%) compared to the node of longleaf-slash pine, loblolly-shortleaf pine, and oak-pine groups (node 16, B=2.4%, C=6.0%, D=0.3%, and E=0.1%). However, when hurricane speed (< 88.5 km/h) was lower, DI of native ecosystems decreased dramatically. Nonetheless, bottomland hardwood forests (including oak-gum-cypress and elm-ash-cottonwood forests) had higher DI and tallow coverage within node 9 (B=1.0% and C=1.4%), node 13 (B=0.4%, C= 2.4%, and D=1.2%), and node 14 (B=2.7%, C=3.5%, D=0.5%, and E=0.1%).

In the coastal low elevation low propagule pressure region (sub-region S3), there were three end nodes (2, 4, and 5) and were classified based on forest types and ownership (Figure 2.8). Effects of hurricane/storm disturbances in this area were not significant compared to the inland area. Figure 2.8 showed that the area with oak-pine, oak-gum-cypress, and elm-ash-cottonwood forests had higher tallow proportion (node 3, 6.0%) compared to node of longleaf-slash pine, loblolly-shortleaf pine, and oak-hickory forests (node 2, 2.9%). Within node 3, ownership had significant ($p < 0.05$) effects on the DI and this area was classified into two end nodes (4 and 5). Compared to public and corporate lands (node 4, B=1.4%, C=2.5%), nonindustrial private land had more tallow infested plots and higher tallow coverage (node 5, B=3.4%, C=4.6%, D=0.7%, and E=0.5%).

In the coastal high elevation medium propagule pressure region (sub-region, S5), only ownership was significant and FIA plots were classified into two end nodes (Figure 2.9, nodes 2 and 3). Within public land (node 2), the proportion of tallow infested plots was 10% and the proportion of slight and low coverage classes (class B and C) was 8.4%. Compared to public land, private lands (node3, corporate and nonindustrial private lands) had higher DI with a tallow infestation rate of 24.8% and the low coverage class (class B) had the highest proportion of 15.8%. However, compared to other invasive sub-regions, the coastal low elevation high propagule pressure region (S6) was divided into four end nodes (Figure 2.10, nodes 3, 4, 6, and 7) and proportions of tallow infested plots among these four end nodes were 75.5%, 47.7%, 70.7%, and 68.7 %, respectively, which means this sub-region had the highest DI. When hurricane/storm speed was greater than 102.4 km/h and forest types were oak-pine, oak-gum-cypress, and elm-ash-cottonwood (node 7), the proportions of medium and high coverage classes (D and E) were 15.7% and 4.6% respectively which was similar to results of the coastal low elevation low propagule pressure region. Moreover, when hurricane/storm speed lower than 83.8 km/h (node 3) this resulted in the highest proportion of low coverage classes (C) at 50.6%.

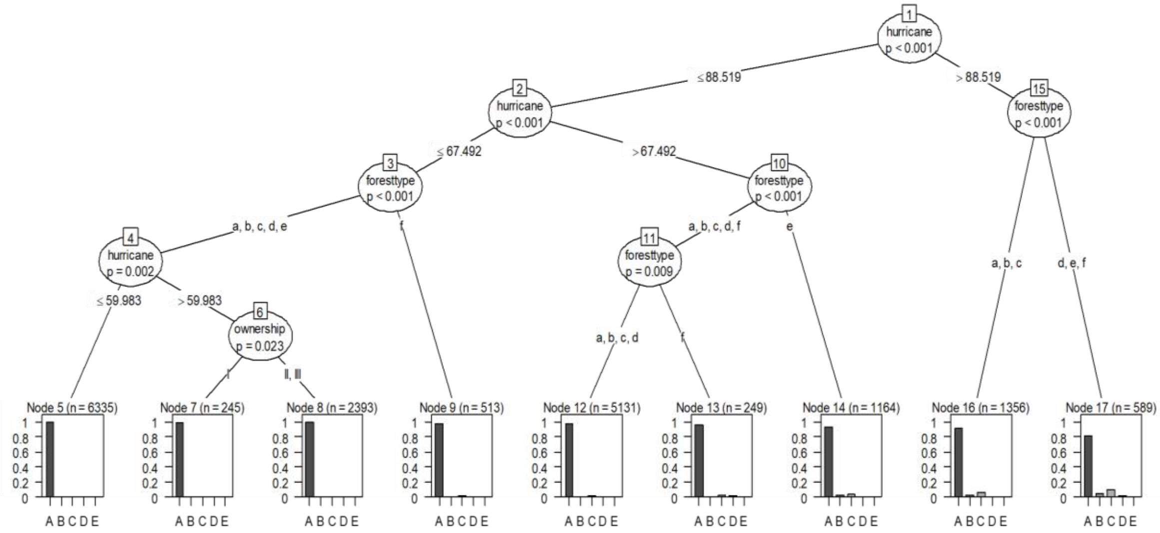

Figure 2.7 Effects of predisposing and inciting factor on the DI in inland high elevation low propagule pressure region (S1)

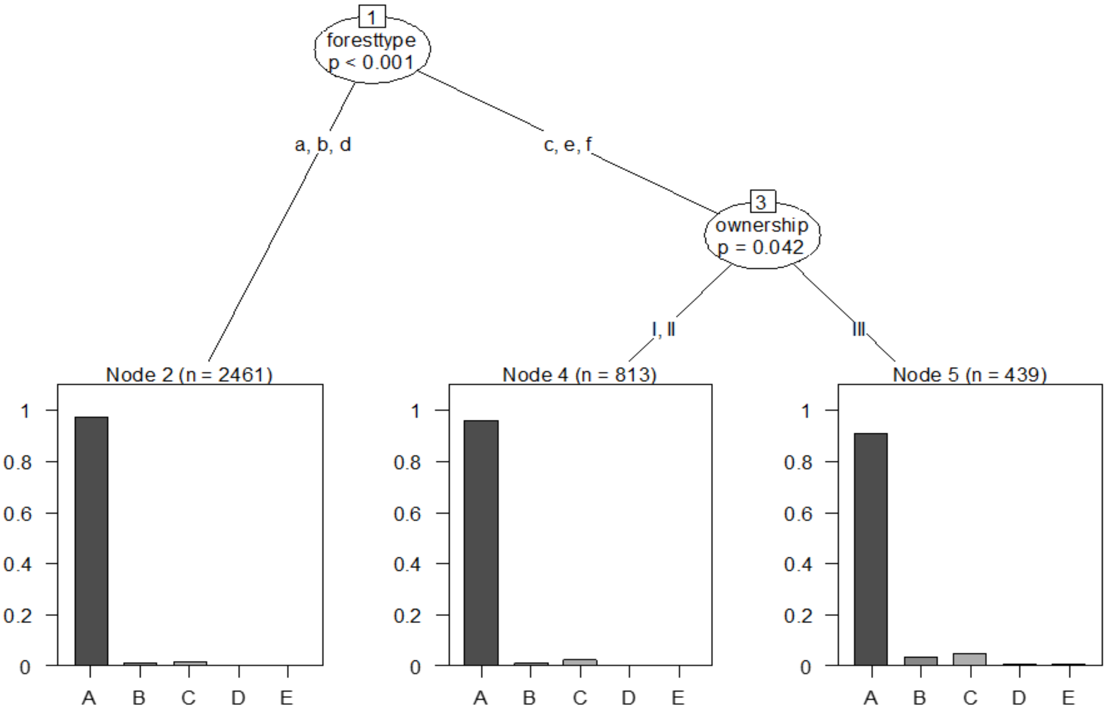

Figure 2.8 Effects of predisposing and inciting factors on the DI in coastal low elevation low propagule pressure region (S3)

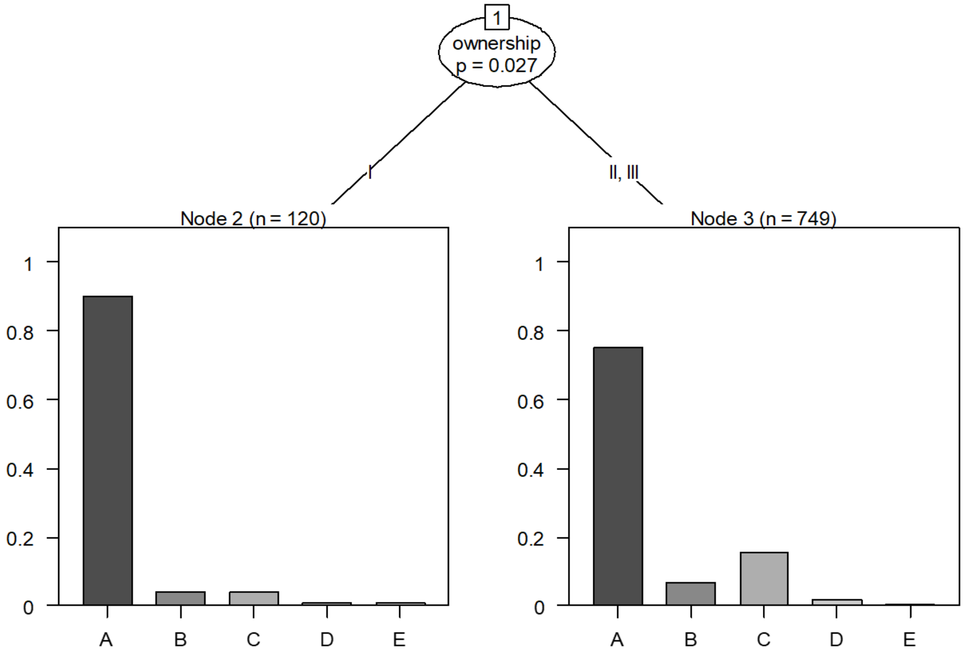

Figure 2.9 Effects of predisposing and inciting factors on the DI in coastal high elevation medium propagule pressure region (S5)

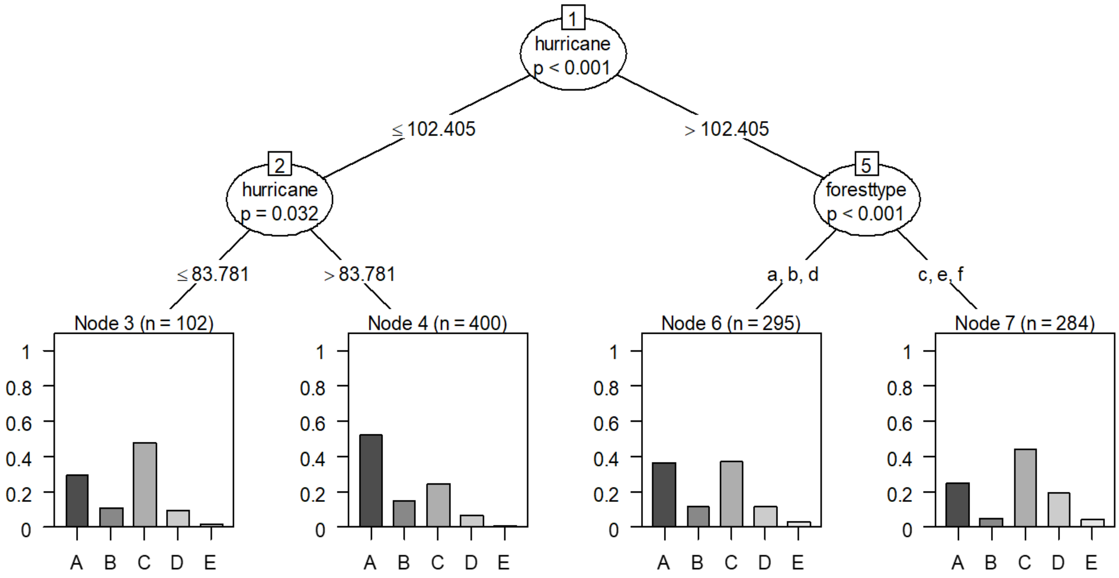

Figure 2.10 Effects of predisposing and inciting factors on the DI in coastal low elevation high propagule pressure region (S6)

2.3.4 Dynamic changes of Chinese tallow coverage

Based on the 1492 tallow infested remeasured FIA plots between first and second inventory cycles, the effects of predisposing and inciting factors on dynamic changes of Chinese tallow coverage were evaluated. GWR model results (Figure 2.11) indicated that in the coastal area of east Texas, southwestern Louisiana, and southeastern South Carolina, the annual increment of tallow coverage in some plots was negative, which means the tallow cover percentage in those plots decreased during the second inventory cycle. This phenomenon explained that previously infested plots had no tallow anymore in the second inventory cycle (Table 2.2). However, in other locations the annual increment of tallow coverage was positive, indicating a spread of Chinese tallow invasion during the second inventory cycle. The effects of predisposing and inciting factors on the dynamic changes of Chinese tallow coverage were illustrated by the regression coefficients of each variable (Table 2.5). Table 2.5 showed that variable coefficients varied at different FIA plot locations. These were called local coefficients, because dynamic changes of Chinese tallow coverage varied over spatial domain. Furthermore, there was a global coefficient for each variable to show the overall relationship between the annual cover change of Chinese tallow and the associated variable.

The global regression coefficients of the GWR model(Table 2.5) also revealed that compared to public land, the annual increment of Chinese tallow coverage was higher in private land, including corporate and nonindustrial private lands. When the speed of hurricane/storm disturbances increased, annual tallow cover percentage decreased, which was different from the results of Chinese tallow spread. Annual tallow cover percentage increased in the loblolly-shortleaf pine, oak-gun-cypress, and elm-ash-cottonwood forests compared to longleaf-slash pine, but decreased in the oak-pine and oak-hickory forests during the second inventory cycle.

Distance to the nearest tallow seed source was positively correlated with the annual increment of Chinese tallow coverage, which means tallow coverage would increase when the distance to the previously infested plot increased. Moreover, elevation and mature tallow annual increment also had positive relationships with the annual tallow cover percentage. In summary, some predisposing and inciting factors, such as hurricane/storm disturbances, distance to the nearest tallow seed source, and elevation had the opposite effects on the annual increment of Chinese tallow coverage compared to the spread of Chinese tallow (Table 2.4)

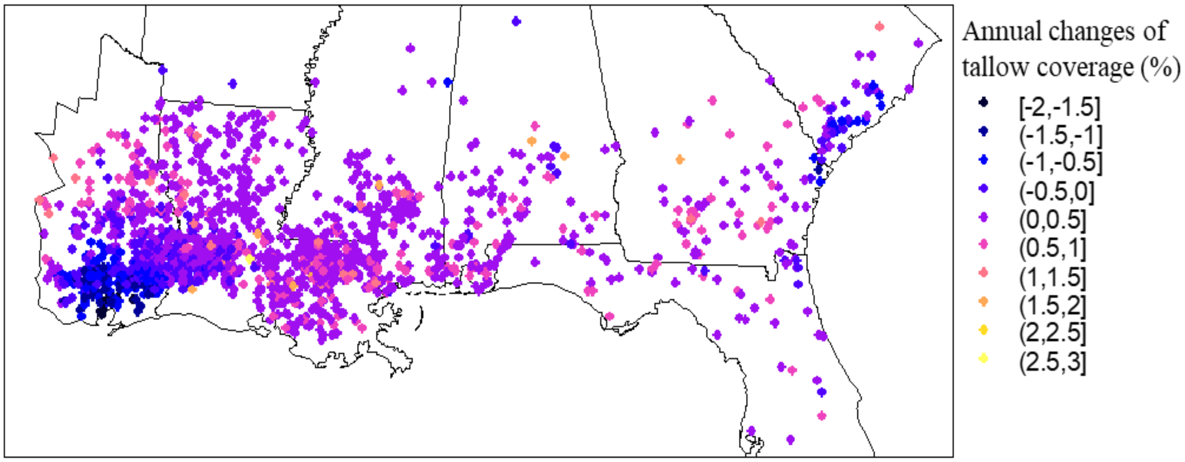

Figure 2.11 Estimated annual changes of Chinese tallow (*Triadica sebifera*) coverage at each forest inventory and analysis plot

Table 2.5 Summary of geographically weighted regression coefficient estimates of predisposing and inciting factors in each forest inventory and analysis plot

Variable	Minimum	1st quantile	Median	3rd quantile	Maximum	Global
Intercept	-1.977	0.195	0.701	3.489	8.190	0.706
Public land^{+}	Reference					
Corporate land^{+}	-0.406	-0.015	0.051	0.185	0.663	0.020
Nonindustrial private land^{+}	-0.439	0.055	0.077	0.141	0.491	0.060
Hurricane/storm	-0.077	-0.033	-0.006	0.000	0.018	-0.009
Longleaf-slash^{++}	Reference					
Loblolly-shortleaf^{++}	-0.174	0.021	0.137	0.288	0.736	0.083
Oak-pine^{++}	-0.568	-0.373	-0.104	0.120	0.621	-0.281
Oak-hickory^{++}	-0.463	-0.199	-0.045	0.109	0.486	-0.027
Oak-gum-cypress^{++}	-0.200	-0.063	0.025	0.083	0.453	0.033
Elm-ash-cottonwood^{++}	-1.225	-0.025	0.214	0.384	1.169	0.196
Distance to the nearest tallow seed source	-0.016	0.000	0.009	0.014	0.033	0.004
Elevation	-0.002	-0.001	0.001	0.002	0.010	0.003
Mature tallow annual increment	-0.008	0.002	0.007	0.009	0.026	0.006

Significant codes: '***' 0.001; '**' 0.01; '*' 0.05; '.' 0.1. Other codes: "+" ownership; "++" forest type.

2.4 Discussion

2.4.1 Distribution and spread of Chinese tallow at regional level

By 2015, based on the presence probability of Chinese tallow in the research area, there were two hot spots of Chinese tallow invasion: one was southern Texas and Louisiana with an average presence probability of 0.5; another area was southeastern South Carolina with an average presence probability of 0.3 (Figure 2.4). Results indicated that Chinese tallow trees initially started to spread from these two spots because of early introduction of Chinese tallow occurred in those regions (Hunt 1947, Bruce et al. 1997, Renne et al. 2000). Movement was then to the northeastern and southeastern portions of the research area due to the increasing propagule pressure and driving factors of seed dispersal. Previous research (Renne et al. 2002, Gan et al. 2009, Wang et al. 2011, Pile et al. 2017b) evaluated factors associated with the dispersal and occurrence of Chinese tallow by using simulation models directly without considering repeated inventory cycles, effects of spatial domain, or invasive stages. In this study, FIA plots measured in two consecutive inventory cycles were used to evaluate associated factors and Chinese tallow spread combined with invasive stages. Based on the latitude, longitude, and elevation of each FIA plot, and presence and absence of Chinese tallow, FIA plots were classified into four invasive sub-regions with different presence probabilities of Chinese tallow. Landscape features were selected as the classification variables because the distribution of Chinese tallow infested plots was non-stationary and clustered. Spatial coordinates, such as latitude and longitude, could be used to distinguish Chinese tallow infested plots from non-infested plots directly. Elevation was correlated to topography, temperature, soil moisture, and forest types and all these variables were related to the distribution of Chinese tallow trees (Gan et al. 2009, Wang et al. 2011, Fan et al. 2012, Wang et al. 2014). Therefore, invasive sub-regions of S1 and S3 were identified by using latitude and longitude and S5 and S6 were elected based on elevation (Figure 2.5, Figure 2.6). The high propagule pressure area was mainly located in sub-region S6 where the elevation was lower than 50.5 m, which was as same as Gan et al. (2009). These four invasive sub-regions also represented invasive stages of Chinese tallow based on the presence probability of Chinese tallow. The inland high elevation low propagule region (S1, 2.7%) and the coastal low elevation low propagule pressure region (S3, 3.8%) were in early invasive stages (introduction and colonization) because of the low presence probability of Chinese tallow trees. The coastal high elevation medium propagule pressure region (S5, 23.1%) and coastal low elevation high propagule pressure region (S6, 61.2%) were in the late invasive stages (establishment and landscape spread) due to the high presence probability of Chinese tallow trees (Figure 2.5, Figure 2.6).

In this study, invasion patterns of Chinese tallow and associated predisposing and inciting factors varied across the different invasive sub-regions (Figure 2.5, Table 2.4). Results of the CART model and logistic regression models of sub-regions provide a complete and accurate way to evaluate effects of associated factors on the spread of Chinese tallow in the entire southeastern United States. Usually, one model could not adequately fit the data and would result in inaccurate estimates of associated factors and subsequently inefficient management to control biological invasion. For instance, the speed of hurricane/storm disturbances was a significant factor in the regions of early invasive stage (S1 and S3) but was not in the regions of late invasive stage (S5 and S6) (Table 2.4). That is because the succession of biological invasion is originally related to the propagule pressures and dispersal pathways (driving factors) (Lockwood et al. 2005, Warren et al. 2012, Fan et al. 2018a) and hurricanes could more likely disperse tallow seeds from the southwestern high propagule pressure area to the northeastern low propagule pressure area (Figure 2.2A, Figure 2.3). Floods and extreme windstorms caused by hurricanes (Chen et al. 2013, Henkel et al. 2016) and the damaged native forests were able to facilitate the invasion by Chinese tallow, especially in the coastal area of the United States (Pattison and Mack 2008, Fan et al. 2012, Wang et al. 2012, Fan et al. 2018a). As the inciting factor, hurricane/storm disturbances were more important for the spread of Chinese tallow in the early invasive stages compared to the late invasive stages. Due to the decrease of spatial domain and increase of propagule pressure, predisposing factors, such as the distance to the nearest tallow seed source (i.e., propagule pressure), distance to the nearest road, and elevation were more significant to the spread of Chinese tallow in the coastal area frequently disturbed by hurricanes (Table 2.4). In the coastal low elevation regions (S3 and S6), nonindustrial private land had more newly infested FIA plots compared to public land, but it was not significant in high elevation regions (S1 and S5). Meanwhile, the elevation was significant at 0.001 level in the high elevation regions but in the coastal low elevation regions, it was significant at 0.1 level (Table 2.4). These results suggested that in high elevation regions, spread of Chinese tallow was limited by elevation compared to the low elevation regions. Furthermore, there were more anthropogenic activities on nonindustrial private land in low elevation regions compared to high elevation regions and the frequent anthropogenic activities (e.g., forest harvesting, farming, prescribed fire, and road construction) could increase the risk of Chinese tallow dispersal (Grace 1998, Mooney and Cleland 2000, Paudel and Battaglia 2013, Pile et al. 2017c, Fan 2018, Schwartz 2018). In all invasive sub-regions, distance to the nearest road was significant to the spread of Chinese tallow because as edges of habitats and landscapes, roadside forests could be used as perches for birds and drive seed dispersal of tallow trees along these edges (Renne et al. 2002, Fan et al. 2018a). In late invasive stages, due to the high propagule pressure of Chinese tallow (presence probability > 0.5) (Figure 2.4), all the forest types had been invaded by Chinese tallow and forest types were not significant with Chinese tallow spread in these regions. However, in the early invasive stages, bottomland hardwood forests, such as oak-hickory, oak-gum-cypress, and elm-ash-cottonwood, had more newly infested plots as compared to pine forest types (Table 2.4) because of frequent disturbances of hurricane/storm, prescribed fires, low elevation, and water current (Bennett et al. 2015, Henkel et al. 2016).

2.4.2 Degree of invasion of native forest ecosystems and Chinese tallow management

Degree of invasion (DI) is used to quantify how much the community has been invaded by exotic species and is an outcome of previous interactions between invasibility and extrinsic factors (i.e., predisposing and inciting factors) (Guo et al. 2015). In this study, the effects of predisposing and inciting factors on the DI of native forest ecosystems varied in each invasive sub-region/stage (Figures 2.1, 2.7-2.10). Therefore, DI of native forest ecosystems was evaluated in each invasive stage. For instance, in the inland high elevation low propagule region, the high intensity hurricane/storm (> 88.5 km/h) disturbed forest had higher DI compared to low intensity hurricane/storm (≤ 88.5 km/h) disturbed forests. High or low intensity hurricane/storm disturbed forests and bottomland hardwood forests (i.e., oak-hickory, oak-gum-cypress, and elm-ash-cottonwood forests) were easier to be invaded by Chinese tallow and had higher tallow coverage compared to pine forests. That is because high soil moisture, low altitude, and fire-suppressed habitats of bottomland hardwood forest could enhance the probability of survival and establishment of tallow regenerations (Figure 2.7) (Brown et al. 2011, Chen et al. 2013, Henkel et al. 2016). Chinese tallow seedlings are tolerant of shade and can survive beneath the fully covered canopy of bottomland hardwood forests (Jones and McLeod 1990, Lin et al. 2004, Paudel and Battaglia, 2015). In bottomland hardwood forests, tallow trees could dominate the overstory once a forest gap is created by hurricanes because the rapid height growth of tallow trees and the richness habitats in bottomland hardwood forests with high soil moisture (Renne et al. 2002, Zheng et al. 2005) but in the pine forests, due to low soil moisture and high intensity burns, the growth of tallow trees would be limited and could only be the midstory in pine forests. However, in the coastal low elevation low propagule region, hurricane/storm disturbances were not significant. Instead, nonindustrial private forests of oak-pine, oak-gum-cypress, and elm-ash-cottonwood were more sensitive to the Chinese tallow invasion because the inciting factor of anthropogenic activities were more important for Chinese tallow invasion compared to other factors (Figure 2.8). For the coastal high elevation medium propagule pressure region, corporate and nonindustrial private forests had higher DI compared to the public forests due to the high propagule pressure (Figure 2.9). The coastal low elevation high propagule pressure region had the highest DI, either in the high intensity hurricane/storm disturbed forests or in the different forest types because the invasion of Chinese tallow in this region had reached the stage of landscape spread (late invasive stage) (Figure 2.10).

Based on the DI of each invasive sub-region/stage, results suggested that in the regions of early invasive stage (S1 and S3), Chinese tallow management should be focused on the hurricane disturbed bottomland hardwood forests (oak-hickory, oak-gum-cypress, and elm-ash-cottonwood) that are owned by nonindustrial private forest landowners. In those forests, the propagule pressure should be removed first, which means the tallow seed trees should be removed from infested forests first. It is better to use herbicides or mechanical methods to control Chinese tallow trees in the bottomland hardwood forests compared to prescribed fire because the latter is not an effective method in wetland areas and it may also increase the probability of Chinese tallow spread (Mandle et al. 2011, Fan 2018, Yang et al. 2019). In low soil moisture and high elevation forests, prescribed fire could be used to control regeneration (i.e., seedling and sapling) of Chinese tallow (Grace 1998, Burns and Miller 2004, Pile et al. 2017a). Meanwhile, private forests owners should be trained to understand the harm of Chinese tallow and learn how to eliminate them, especially mature trees, from their property (Gan et al. 2009). For regions at an early invasive stage, management prescriptions for Chinese tallow control should be specific and located to the particular forest stand. For regions at a late invasive stage (S5 and S6), with the great presence probability of infested plots (Figure 2.3) and high intensity and frequency of natural disturbances, eradication or control of tallow trees will be extremely difficult and costly. In these regions, spread of Chinese tallow could still be controlled and limited through stand management practices that could enhance forest health and reduce seed tree density. Previous research (Müller-Schärer et al. 2004, Wheeler and Ding 2014, Wheeler et al. 2017, Pile et al. 2017b) has reported that biological control (e.g., fungal pathogens and insect pests) could be used to manage Chinese tallow because it is an efficient and low cost method. However, any biological method has its own limitations and it could result in non-impact. Biological methods are a double-edged sword and the introduction of any new fungal pathogen and arthropod from China to the United State is not advisable without complete and scientific tests (Wheeler and Ding 2014).

2.4.3 Comparisons between spread and cover changes of Chinese tallow

According to the results (Table 2.4 and Table 2.5), the same predisposing and inciting factors had opposite effects between the spread of Chinese tallow and dynamic changes of Chinese tallow coverage. The speed of hurricane/storm disturbances had a positive correlation with the spread of Chinese tallow but it had a negative correlation with the annual increment of Chinese tallow coverage. This is because all tallow infested FIA plots during the second inventory cycle were used to analyze the dynamic changes of Chinese tallow coverage but only newly infested FIA plots were used to evaluate the spread of Chinese tallow. Meanwhile, high intensity hurricane/storm disturbances could also decrease the coverage of Chinese tallow when the speed was greater than 100 km/h (Figure 2.12), especially in southeastern Texas and Louisiana where such disturbances occurred during the second inventory cycle (Figure 2.2B, Figure 2.11). Therefore, the hurricane/storm disturbances could decrease the annual cover percentage of Chinese tallow in the coastal area, but in the inland area hurricanes could increase annual cover percentage of Chinese tallow since it could recover quickly when compared to native hardwood species and had an explosion in the habitats of hurricane damaged bottomland hardwood forests (Gagnon and Platt 2008, Henkel et al. 2016, Babin 2017, Fan et al. 2018a). As the distance from the regions of high propagule pressure (S5 and S6) increased, the speed of hurricane/storm disturbances decreased and annual cover percentage of Chinese tallow increased (Figure 2.2B, Figure 2.11). This explained why the annual increment of Chinese tallow coverage had positive relationships with elevation and distance to the nearest tallow seed source when the locations moved to the northeastern portion of the research area (Table 2.5).

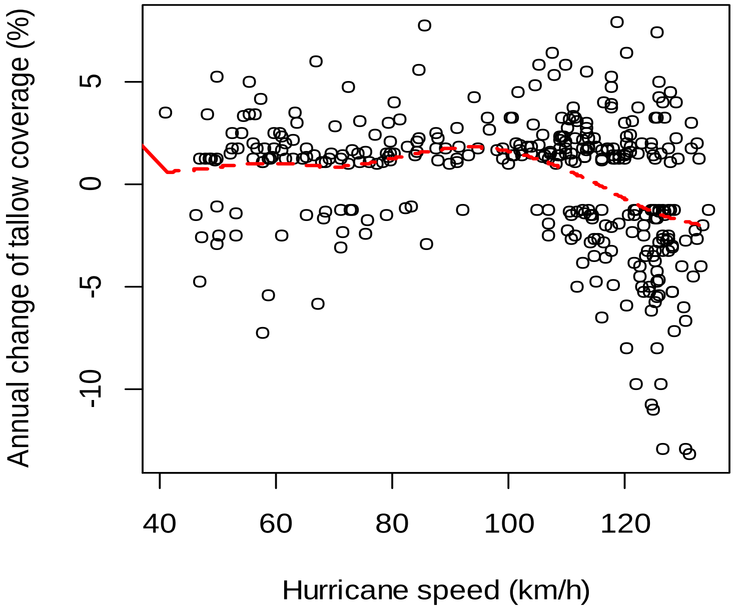

Figure 2.12 Relationships between hurricane speed and annual increase of Chinese tallow (*Triadica sebifera*) coverage

2.5 Conclusions

In this study, the distribution patterns and presence probabilities of Chinese tallow had been identified in the southeastern United States during 2000-2015 according to remeasured FIA plots. Hot spots of Chinese tallow invasion were located in southeastern Texas, Louisiana, and South Carolina and tallow trees initially started to spread from those regions. Meanwhile, hurricane/storm disturbances had cumulative effects on the distribution of Chinese tallow and they had spatial correlations with each other. Four invasive sub-regions or stages were classified in the research area based on the presence or absence of tallow-infested plots. The most significant predisposing and inciting factors in regard to the spread of Chinese tallow had been identified in each invasive sub-region. Close proximity to previously infested plots and roads, coastal bottomland and lowland areas, hurricane/storm disturbances, and anthropogenic disturbance were related to the spread of Chinese tallow throughout the research area. High DI and spread rate occurred in the bottomland/lowland hardwood forests, such as oak-hickory, oak-gum-cypress, and elm-ash-cottonwood, characterized by high soil moisture, low altitude, fire suppression and high intensity natural/human disturbances in native forest habitats. Compared to the bottomland hardwood forests, Chinese tallow trees were not likely to invade southern pine forests because of the low soil moisture, high altitude, and frequent fire disturbance in pine forests. In the inland and coastal low propagule regions (i.e., early invasive stages), hurricane/storm disturbances could accelerate the spread of Chinese tallow but in the coastal high propagule regions (i.e., late invasive stages) this factor was not significant. Hurricanes could enhance the spread of Chinese tallow but in the coastal area, high intensity hurricane/storm disturbances were able to decrease the cover percentage of tallow trees; however, the quick recovery of tallow trees could also cause an explosion of these trees in the disturbed forests. Among those predisposing factors, elevation was the limiting factor for Chinese tallow spread in the high elevation regions but it was not a limitation in low elevation coastal area.

According to the DI of each invasive sub-region, it was suggested that the management of Chinese tallow invasion should be focused on the disturbed bottomland hardwood forests and removal of the tallow seed trees should occur first. Reduction of propagule pressure of tallow trees could limit the seed sources for tallow dispersal. Restoration and reforestation should be applied on harvested and disturbed native forests immediately after the disturbances. Management prescriptions for Chinese tallow invasion should be specific and located in particular forest stands to ensure optimal efficiency. Mechanisms and control of Chinese tallow invasion at landscape and stand levels should be fully studied to help the forest managers and nonindustrial private forest landowners make specific prescriptions. Compared to traditional treatments, biological control (e.g., fungal pathogens and insect pests) is regarded as the new method to manage Chinese tallow invasion at the regional level. However, biological methods could not be used without complete scientific tests. Moreover, more efforts should be made to educate and train nonindustrial private forest landowners. Let them learn the dangers of Chinese tallow, and understand how to control tallow trees and restore the infested forests within their own forest land.

This study already talked about the distribution and spread of Chinese tallow at the regional level. As it had been discussed above, the implementable management for Chinese tallow invasion should be located at landscape and stand level forest land within different forest ecosystems. Future studies should be focused on the spread and distribution mechanisms of Chinese tallow invasion at these levels in the coastal area of the southeastern United States.

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CHAPTER III

SPATIO-TEMPORAL INVASION PATTERNS OF CHINESE TALLOW (*Triadica sebifera*) IN A FIRE-REGULATED LANDSCAPE IN THE COASTAL REGION OF MISSISSIPPI

3.1 Introduction

In southeastern coastal region of the United States, prescribed fire has been utilized as a preferred approach to restore native ecosystems (e.g., longleaf-slash pine ecosystems, wet pine savannas, and coastal prairies) (Lavoie et al. 2010). However, the effectiveness of prescribed fire is related to many contributing factors such as initial site/stand condition, fire return interval, intensity, seasonality, and length of treatment period (Ford et al. 2010). One possible threat of prescribed fire is that the disturbed area may become more susceptible to invasion by exotic species such as the Chinese tallow (*Triadica sebiferum*), changing the restoration direction from developing native ecosystems to promoting invasion of non-native species (Gan et al. 2009, Meyer 2011, Fan et al. 2012, Fan et al. 2018). Chinese tallow is a highly competitive species and can survive under a variety of site/stand conditions after prescribed fire, and eventually it may cause suppression of a prescribed fire and modify fire behavior once it successfully dominates native forest ecosystems (Grace 1998, D’Antonio 2000, Brooks et al. 2004, Meyer 2011, Pile et al. 2017a).

As an Asian native species, Chinese tallow has become an aggressive invader and is able to adapt to a wide variety of ecosystems in southeastern coastal region of the United States

(Jubinsky and Anderson 1996, Grace et al. 2005, Pile et al. 2017b, Fan 2018). Since introduced to the southeastern coastal states in the 1900s, it has been widely planted as a crop tree throughout all the southern states and promoted by the Foreign Plant Introduction Division of the United States Department of Agriculture (USDA) to produce industrial materials (wax and oil) (Hunt 1947, Randall and Marinelli 1996, Renne et a. 2002, Miller 2003). Currently, tallow has spread regionally from southeastern Texas to the southern coastal area of North Carolina because of its advantageous life history traits and seed dispersal via various avian species and hurricanes/storm disturbances (Flack and Furlow 1996, Burns et al., 2004, Pattison and Mack 2008, Howard 2012, Henkel et al. 2016). Chinese tallow is commonly found in disturbed sites (Nolfo-Clements 2006, Battaglia et al. 2007, Pile et al. 2017b) such as roadsides (Zomlefer et al. 2013, Fan 2018), abandoned agricultural lands (Ramsey 2005, Pile et al. 2017b), urban neighborhoods (Loewenstein and Loewenstein 2005, Fan et al. 2018), and hurricane-damaged forests (Conner et al. 2005, Keeland and Gorham 2009, Henkel et al. 2016, Fan 2018). These areas usually have high propagule pressure from Chinese tallow (large seed trees) and provide pathways for it to spread to surrounding landscapes through habitat edges and streams (Vance et al. 2003, Gan et al. 2009, Fan et al. 2012, Fan et al. 2018).

On fire regulated landscapes, tallow seedlings and small trees are vulnerable to fire, but mature trees or large tallow saplings are able to survive or just be top-killed by fire, depending on characteristics of the fire and burning seasons (Grace and Allain 2000, Grace et al. 2005). Thick bark, a characteristic of aging, as well as vigorous basal and root sprouts following fires allow tallow to survive and persist after low- or moderate- intensity ground fires, even those ground fires at frequent intervals (Grace 1998, Grace et al. 2005, Pile et al. 2017c). Experimental studies report fire could enhance Chinese tallow invasion and density at burned sites in some particular instances, but reduce tallow colonization or have no significant effect in other instances (Samuels 2004, Huang et al. 2011, Pile et al. 2017a). A series of associated factors including site conditions (e.g., fuel loading and continuity) and fire characteristics (e.g., intensity, frequency, burn season, length of treatment period), and differences in the availability (i.e., abundance and spatial distribution) of seed sources cause inconsistent responses to fire (Meyer 2011). The incomplete understandings of ecological effects of prescribed fire at the ecosystem/landscape level, especially over long periods, have become a barrier to predicting forest ecosystem responses to prescribed fire treatments and developing effective fire treatments in southeastern coastal area of the United States.

Previous research reported spread patterns and impact factors of tallow at the regional level (Gan et al. 2009, Wang et al. 2011, Fan et al. 2012, Wang et al. 2014) and at local scales (e.g., Henkel et al. 2016, Fan 2018). However, distribution patterns and mechanisms of Chinese tallow spread at the landscape level are not well documented because of the nonstationary stochasticity at this level. Chinese tallow invasion and spread vary drastically over space and time, even in similar ecosystem types (Theoharides and Dukes 2007, Fan et al. 2012, Fan et al. 2018). For many invasive species, especially Chinese tallow, current conditions and dynamics are primarily the effect of a sequence of disturbance events in diverse ecosystems, and landscape metrics and ecosystem features mostly serve as predisposing factors indirectly affecting seed dispersal by regulating avian-vegetation relationships (Fan 2018, Fan et al. 2018). Currently, landscape-level studies on tallow invasion history following long-term disturbances was not noted yet, especially on landscapes where prescribed fire has been applied to restore the declining wet pine savannahs and coastal prairies. Those landscapes are characterized by sparse overstory and grass-covered ground vegetation, and they are the native habitats that previously dominated the coastal area (Grace et al. 2005, Osland et al. 2013). Understanding the long-term, cumulative effect of prescribed fire on tallow spread under varying fire return intervals, diverse stand conditions and propagule (seed trees) pressure levels will be critical for controlling tallow spread while endeavors using fire as a tool to restore native ecosystems proceed.

In this study, a fire-regulated landscape where prescribed fire was used for restoration of native pine savanna was selected to evaluate distribution and spread mechanisms of Chinese tallow invasion and examine how prescribed fire will affect the spread of tallow trees at landscape level. Specifically, this study intends to answer the following three questions: 1) What is the spatiotemporal pattern of tallow spread and how will prescribed fire affect the spread of tallow trees along habitat edges at the landscape level? 2) How will the time since last fire and other landscape metrics and site/community factors affect colonization of tallow seedlings along habitat edges? 3) What is the spatial pattern of tallow-invaded interior plots and how will mean fire return interval, landscape metrics and site/community factors affect the risk of tallow spread into habitat interiors? Answers to these questions will help evaluate whether prescribed fire can be used as a tool to promote native habitat restoration and conservation as well as curb tallow trees. Subsequently, we will also be able to evaluate effectiveness of prescribed fire in controlling tallow at the landscape level.

3.2 Methods

3.2.1 Research area

Mississippi Sandhill Crane National Wildlife Refuge (MSCNWR) is located in southern Mississippi (30°27'3.49"N, 88°39'20.60"W) and contains three blocks (east, west, and south) with total area of 7492.73 ha (18514.93 ac) (Figure 3.1). Situated along the gently sloping, lower Gulf coastal plain, MSCNWR is part of the deltas of the Escatawpa and Pascagoula Rivers. The climate is subtropical, which means summers are hot and humid, but winters are relatively mild. Annual maximum temperatures average 24.7° C (76.5° F), with July averages reaching 32.0° C (89.7° F). Winters have annual minimum temperatures averaging 14.7°C (58.5° F), with January averages around 5.8° C (42. 4° F). Light freezes are common and hard freezes occasionally occur. Average annual rainfall is approximately 1600 mm (63 inches). Major habitats and communities include wet pine savannas (25.3%), pinelands (flatwood and scrub) (57.5%), hydric drain (6.6%), estuarine (2.8%), agricultural land (4.2%), and open water and others (3.6%). The MSCNWR has been intensively burned using fire to restore wet pine savanna, the most important habitat for endangered Mississippi sandhill cranes (*Grus canadensis pulla*). Prescribed fire occurs in the spring and fall to clear woody vegetation, improve areas overstocked with slash pine (*Pinus elliottii*), and enhance the suitability of nesting areas of the cranes. Since 1985, MSCNWR has conducted prescribed fires on 400-3,600 ha (1,000-9,000 acres) per year, with each stand on a two to five-year fire rotation. Invasive species such as Chinese tallow (*Triadica sebifera*) and cogongrass (*Imperata cylindrica*) have invaded this refuge in spatially clustered patterns and have become a serious threat to the native habitats of the cranes and declining grassland birds such as Henslow sparrows (*Ammodramus henslowii*) (US Fish and Wildlife Service 2007).

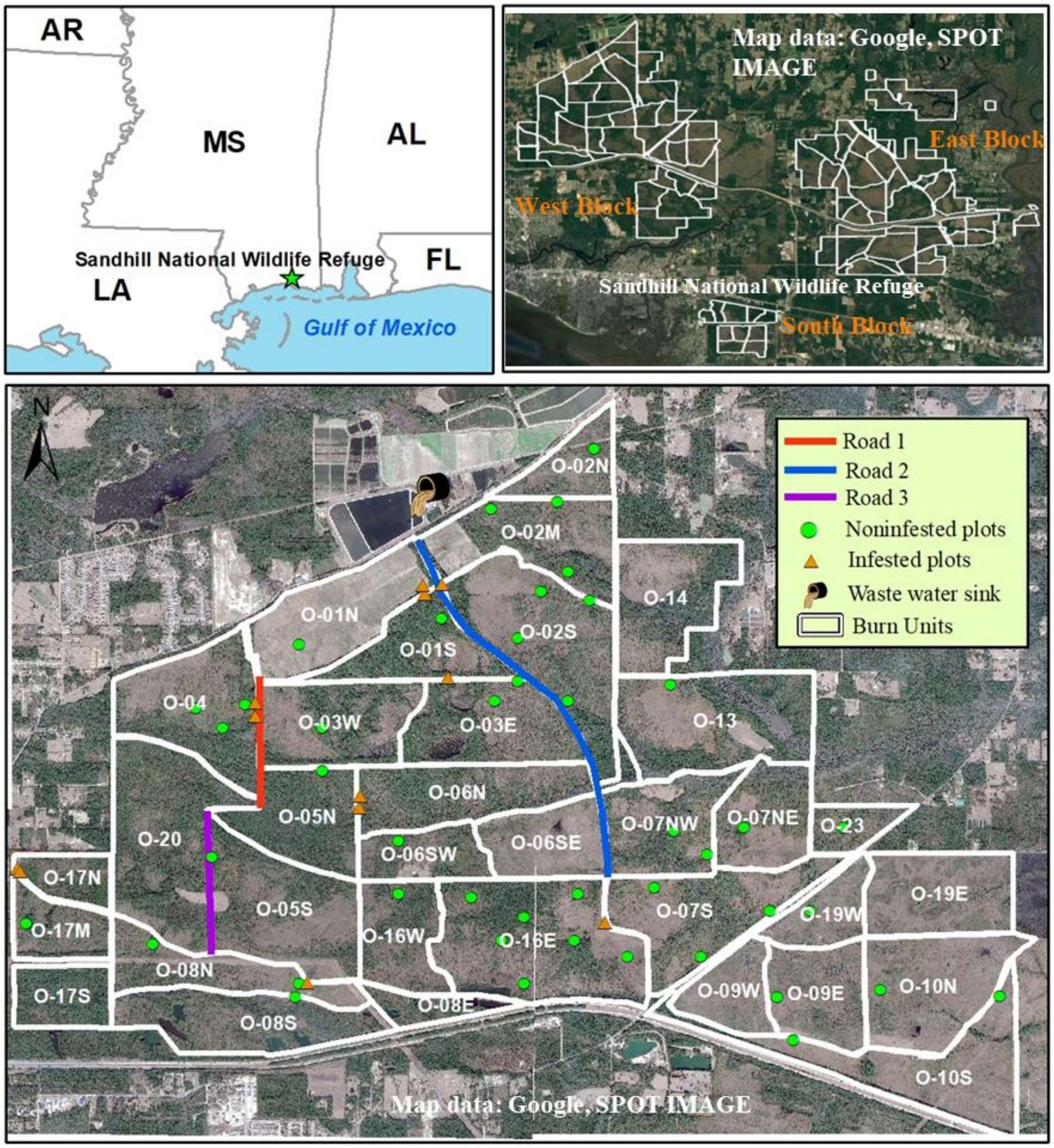

Figure 3.1 Mississippi Sandhill Crane National Wildlife Refuge (MSCNWR)

3.2.2 Data collection

For spatial continuity, this study will only use data collected from the west block (2,879 ha) of the MSCNWR (Figure 3.1). Data collection was conducted in the fall of 2015. First, a complete survey was conducted along all major habitat edges (i.e., roads and firebreaks) to delineate spatially separated tallow clusters. A tallow cluster is defined as a group (≥ 1) of tallow individuals occurring closely together in similar site conditions. In each cluster, the number of tallow seed trees was counted, and the oldest (largest) tallow tree was mapped using a GPS device (Forge Echo by F4Device) and then felled to determine its age (Tian et al. 2017). The geographic coordinates of the oldest tallow tree was used as the location of the cluster and the age to infer the invasion time (year). Mapped clusters data was used to analyze the spatiotemporal spread pattern of tallow trees along habitat edges and contributing factors (Question 1).

Second, three invaded roadways (1, 2, and 3) were selected (Figure 3.1), along which a sequence of rectangular plots with an area of $10\times3\ m^2$ ($33\times10\ ft^2$) and 30 m spacing on each side were set up and their spatial locations (geographic center) mapped. Within each plot, overstory condition [i.e., overstory basal area, tree density, and canopy closure (%)], understory condition [average height and coverage (%) of shrubs and grasses/herbaceous species], the time since last fire, and distance to nearest seed trees were measured. Overstory canopy closure and understory vegetation coverage were estimated based on the presence (1) or absence (0) of targets within 20 quadrats ($1\times1\ m^2$) regularly set in each plot. Overstory tree density (tree/ha) and basal area (m^2/ha) were calculated based on individual tree measurement data. All tallow trees were felled at the ground base to determine the age and measure dbh (diameter at breast height), dgl (diameter at ground level), and total height (Figure 3.2). The time since the last fire was calculated from the fire data provided by the Fire Management staff of the MSCNWR. Distance to the nearest tallow seed trees from a plot was calculated based on the mapped plot data and was set to zero if tallow seed trees were present. These data were used to quantify the effect of risk factors on tallow colonization at micro-scales (plot) (Question 2).

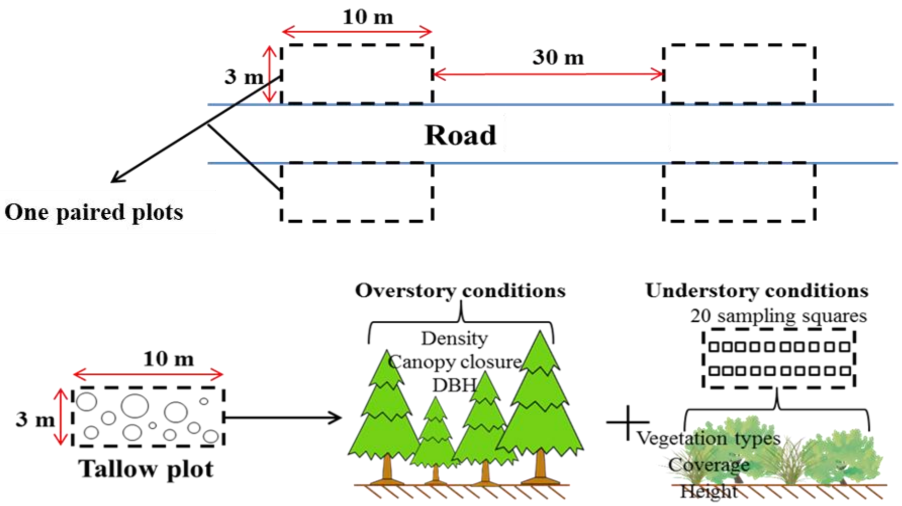

Figure 3.2 Design of rectangular plots and site/stand condition variables collected along habitat edges (i.e., roadways and fire lines)

Third, 56 circular plots of 0.04-ha (1/10th acre) were randomly located and mapped across burn units in the west block. Each plot was determined as invaded plot or non-invaded plot depending on whether tallow was present or not. The overstory and understory condition of a plot was measured and calculated using the same method as for the rectangular plot. Distance from a plot to the nearest edge was calculated using the ArcGIS Spatial Analyst tool, and the mean fire return interval was calculated based on the 2000-2015 prescribed fire data from the Fire Management staff of the MSCNWR. These data were used to analyze tallow spread into habitat interiors and related risk factors (Question 3).

3.2.3 Spatial data analysis and modeling

For Question 1, the spread process (Figure 3.3) of tallow clusters along habitat edges was modeled using a marked point pattern in the R *spatstat* package using the x,y coordinates as the location and derived invasion time as the mark (Cressie 1992, Baddeley and Turner 2004, Fan 2018). The pair correlation function (PCF) was used to estimate the spatial relationships (the spatial scale on which individual clusters are positively, negatively or randomly distributed) between newly formed tallow clusters in a specific year and previous tallow clusters (Figure 3.4, Lutz et al. 2014). The cumulative number of tallow clusters by year was plotted to show the annual rate of spread of tallow clusters. Simple linear regression was run to quantify the relationship between number of tallow seed trees and number of tallow clusters by habitat edge. To estimate the effect of prescribed fire on tallow spread, number of tallow clusters formed in a year following a fire was regressed against the number of tallow clusters formed in a year before a fire. The estimated value of the regression slope was used to quantify fire effect.

In regard to Question 2, using age data collected from the rectangular plots (80 plots along road1, 180 plots along road 2, and 64 plots road 3), the age distribution and cumulative density (number/ha) of tallow trees were plotted to visualize tallow colonization at micro-scales (plot). Taking the count of tallow seedlings ≤ 2 years in each plot as the response variable and measured overstory and understory condition, the distance to the nearest seed trees and time since last fire as the predictor variables, the mixture zero-inflated negative binominal models (ZINB) [equations (3.1) and (3.2)] were used to evaluate potential factors contributing to tallow colonization (Fan 2018).

$$P(Y = y|\mu, \theta) = \begin{cases} p + (1-p)\left(1 + \frac{\mu}{\theta}\right)^{-\theta}, \ y = 0 \\ (1-p)\frac{\Gamma(\theta+y)}{y!\Gamma(\theta)}\left(1 + \frac{\mu}{\theta}\right)^{-\theta}\left(1 + \frac{\theta}{\mu}\right)^{-y}, y = 1, 2, \dots \end{cases} \qquad (3.1)$$

With $E(Y) = (1-p) \cdot \mu$ and $Var(Y) = (1 + p)\mu\left(1 + p\mu + \frac{\mu}{\theta}\right)$, respectively. The ZINB regression models μ (the mean of the response variable Y) and p (the probability for the response variable Y to be zero) with respect to covariates X and Z via

$$\log(\mu) = X\beta \;\text{ and }\; logit\,(p) = Z\gamma, \tag{3.2}$$

where β and γ are the regression coefficients to estimate μ and p, respectively, using the maximum likelihood method. The change in the density of tallow seedlings with respect to significant covariates identified by the ZINB models was plotted to visualize their relationships.

For Question 3, the 56 spatially mapped interior plots were examined as marked point pattern data with the presence (1) or absence (0) as the mark in the *spatstat* package of R. Again, the PCF was used to detect the spatial relationship between tallow invaded and non-invaded plots. Then, the 2-sample (tallow invaded and non-invaded plots) multivariate Hotelling's T^2 test was run to test the differences in distance to edge, mean fire return interval, overstory basal area, tree density, canopy closure, and coverage (%) of shrubs and grass/herbaceous species between invaded and non-invaded plots.

All statistical analysis was conducted using the R-3.4.2 statistical environment for the Windows (R Development Core Team 2014). R base packages and contributed packages including *spatstat* version 1.53-2 (Baddeley and Turner 2004) for spatial analysis and *pscl* version 1.5.2 for ZINB regression analysis (Zeileis et al. 2008) were used.

3.3 Results

3.3.1 Spread of tallow cluster along habitat edges

Chinese tallow spread along habitat edges in this fire-regulated landscape originating in the northwest part in 2003, which is neighbored with residence communities and a wastewater sink (Figures 3.1, 3.3). By 2015 (the sampling year), 377 clusters of varying sizes had been identified and mapped. Temporally, the spread process consisted of two distinct phases based on the rate of spread (number of new tallow clusters formed in a year): a slow spread phase (2003-2011 with an average of five clusters established annually) followed by a rapid spread phase

(2012-2015 with an average of 96 clusters established annually) (Figures 3.3, 3.5A). During the earlier period (2003-2011), tallow was mainly confined to habitat edges encompassing the northwest and west burn units; however, after 2011, it quickly spread to most habitat edges encompassing the central burn units. Few instances of tallow were found along habitat edges in the east and southeast part (Figure 3.3). Except for the first five years (2003-2007), the PCF showed that tallow clusters newly formed in a subsequent year were consistently positively correlated with previously established clusters at spatial scales of 200-600 m (Figure 3.4). The number of tallow clusters was positively correlated with number of tallow seed trees ($R^2 = 0.960$) (Figure 3.5B). Prescribed fire affected tallow spread differently: fire had little effect (regression slope = 1) on tallow spread from 2003 to 2011, but facilitated (regression slope = 1.34) tallow spread after 2011 since the number of tallow clusters formed after a fire was statistically 1.34 (regression slope) times more than that before a fire (Figure3.5C).

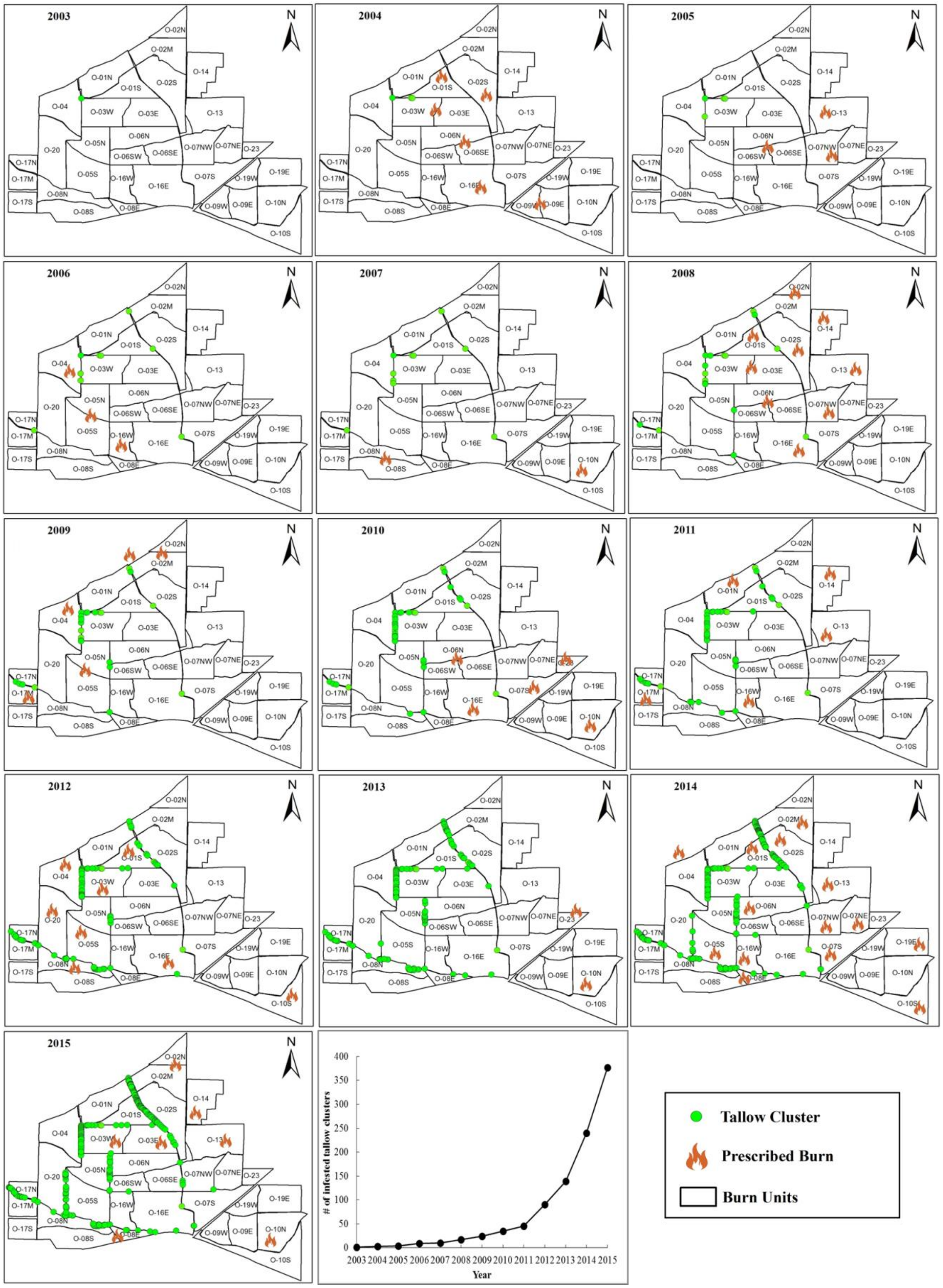

Figure 3.3 Spread patterns of Chinese tallow (*Triadica sebifera*) clusters along habitat edges (i.e., roadways and fire lines) by year

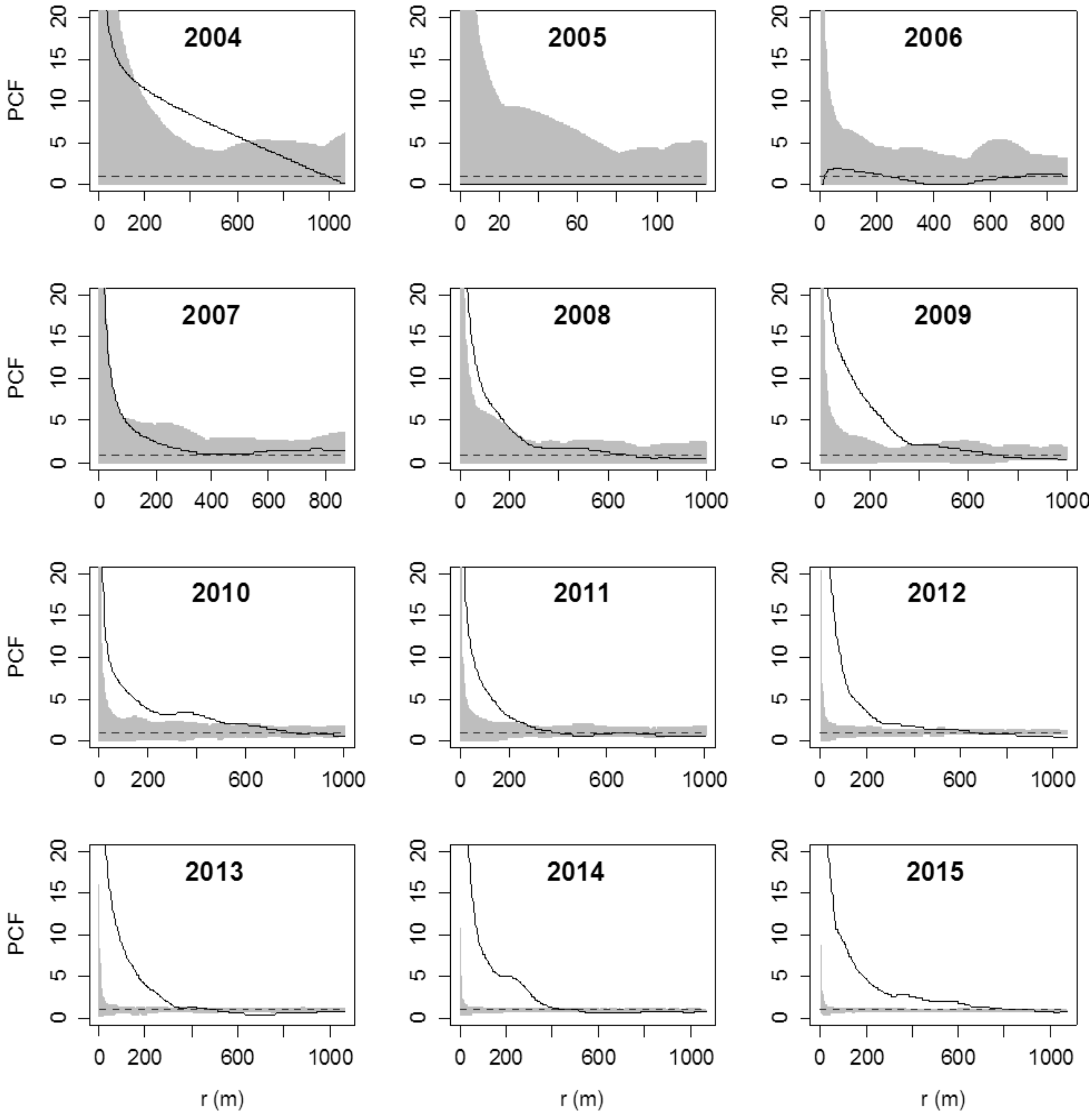

Figure 3.4 Pair Correlation Function (PCF) curve and envelop between newly formed Chinese tallow tree (*Triadica sebifera*) clusters and previously formed clusters by year

A curve above, within and below the envelop represents a positive (attractive), random (independent) and negative (repulsive) relationship in space, respectively.

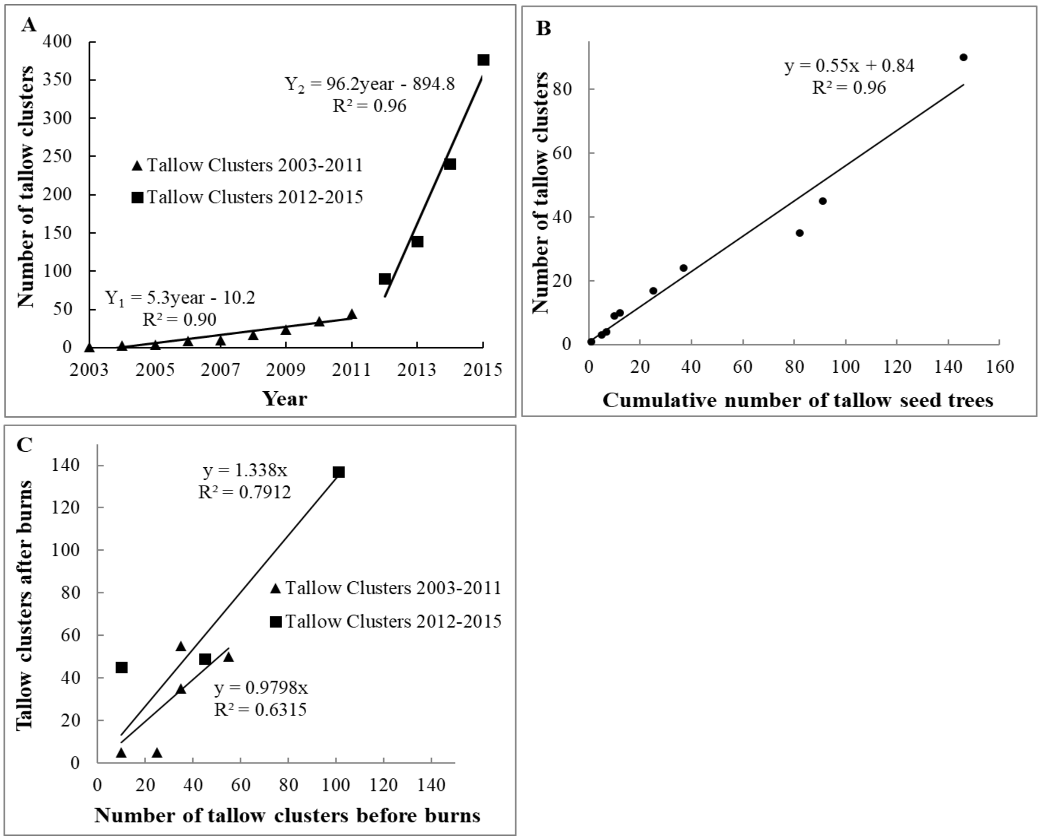

Figure 3.5 Cumulative increase of Chinese tallow (*Triadica sebifera*) clusters and effects of propagule pressure and fire disturbances on cluster increase

Cumulative increases of tallow clusters between 2003-2011 and 2012-2015 (A); effects of tallow seed trees on the increment of tallow clusters (B); and effects of prescribed fires on the increment of tallow clusters (C).

3.3.2 Colonization of tallow seedlings along roadways

Chinese tallow had a reversed J-shape age structure along all three sampling roads, and age structures showed three propagule pressure statues and invasive stages along these roads. These pressures were described as high propagule along road 1 (landscape spread), medium propagule along road 2 (establishment), and low propagule along road 3 (introduction and colonization) (Figure 3.6). Along the early invaded road (road1), tallow tree densities in the rectangular plots from 2003 to 2015, derived from the age data, followed a trend similar to the landscape-level spread of tallow clusters: a slow increase from 2003 to 2011, followed by a rapid increase from 2012 to 2015 and started to spread at landscape level (Figure 3.6A). Along the road 2, tallow density did not have a rapid increase until 2013 but before 2013, the increase rate was slow (Figure 3.6B). Compared to road 1 and road 2, the newly invaded road (road 3, without seed trees), tallow tree densities were still in a slow increase mode (Figure 3.6C).

Of all factors contributing to tallow colonization in the count models (Table 3.1), the time since last fire appeared to be most significant for road 1 and road 3 but it was not significant along road 2. Specifically, tallow seedling densities tended to increase with the time since last fire (Figure 3.7B). Furthermore, tallow seedling densities were found to decrease significantly with the distance to seed trees along the roads that with seed trees ($p < 0.05$, Figure 3.7A) and increase with overstory basal area along the road without seed trees ($p<0.05$, Figure 3.7C). For road 2, Chinese tallow invaded north of the road and moved slightly south from the northern residence area creating a hot spot of tallow regeneration ($p<0.001$) (Table 3.1). The binary models showed that time since last fire remained most significant out of all risk factors contributing to tallow invasion, but influenced the invasion risk along roads (road 1 and road 3) with and without seed trees in the opposite manner (Table 3.1). Longer periods since last fire would increase a site's invasion risk along the road with seed trees, but decrease invasion risk along the road without seed trees. Similar to overstory basal area, canopy closure could also increase invasive risk of Chinese tallow along the road with medium propagule pressure ($p<0.05$). A site's invasion risk would decrease with shrub coverage for all roads (Figure 3.7D), but along the roads (road 1 and road 2) with seed trees, the invasion risk was shown to decrease with distance to seed trees as well as the distance to residences (Table 3.1).

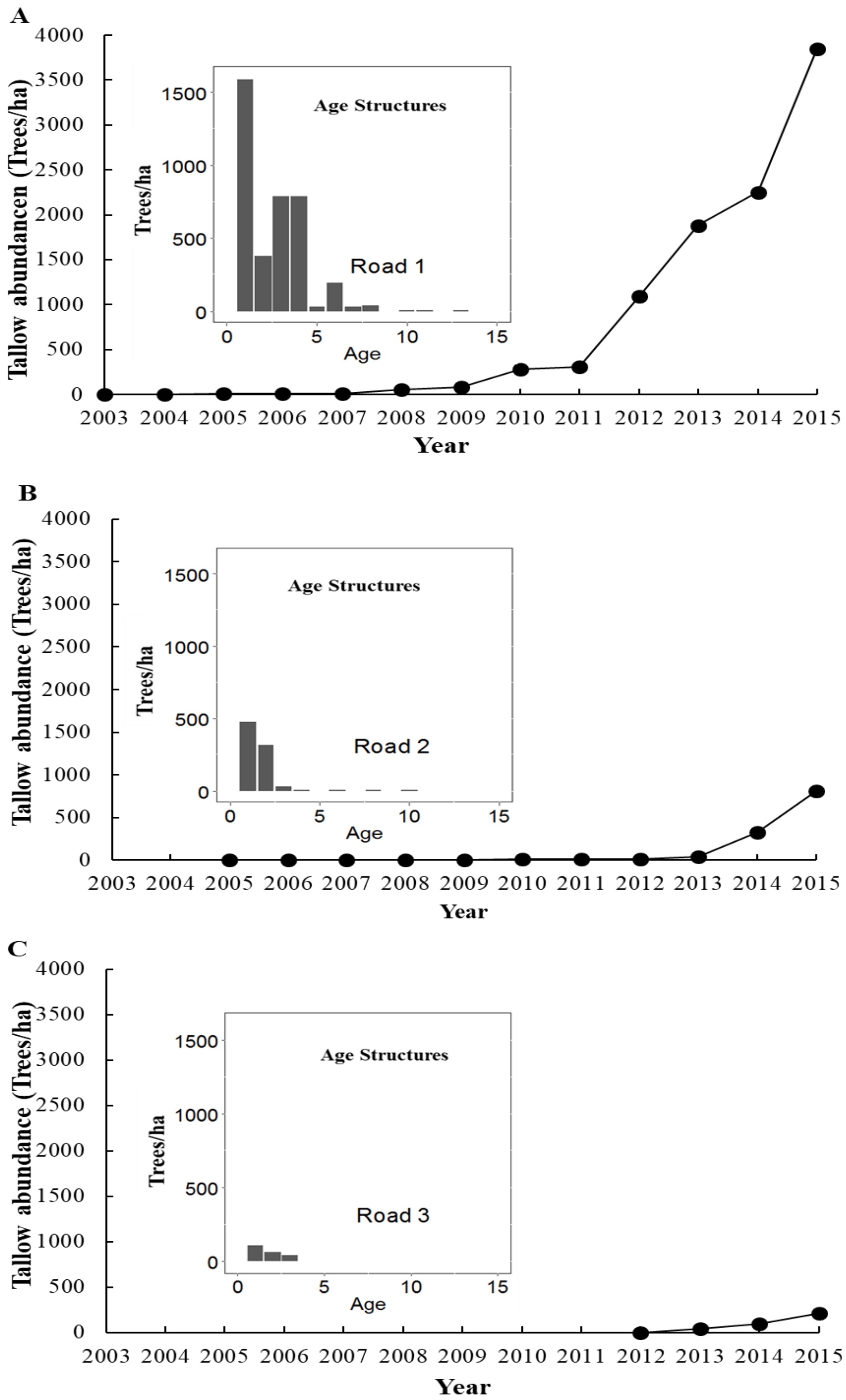

Figure 3.6 Age structures and the net increase of Chinese tallow (*Triadica sebifera*) along selected roads in the west block of the MSCNWR by October 2015

A: road1, high propagule pressure with seed trees; B: road 2, medium propagule pressure with seed trees; C: road 3, low propagule pressure without seed trees.

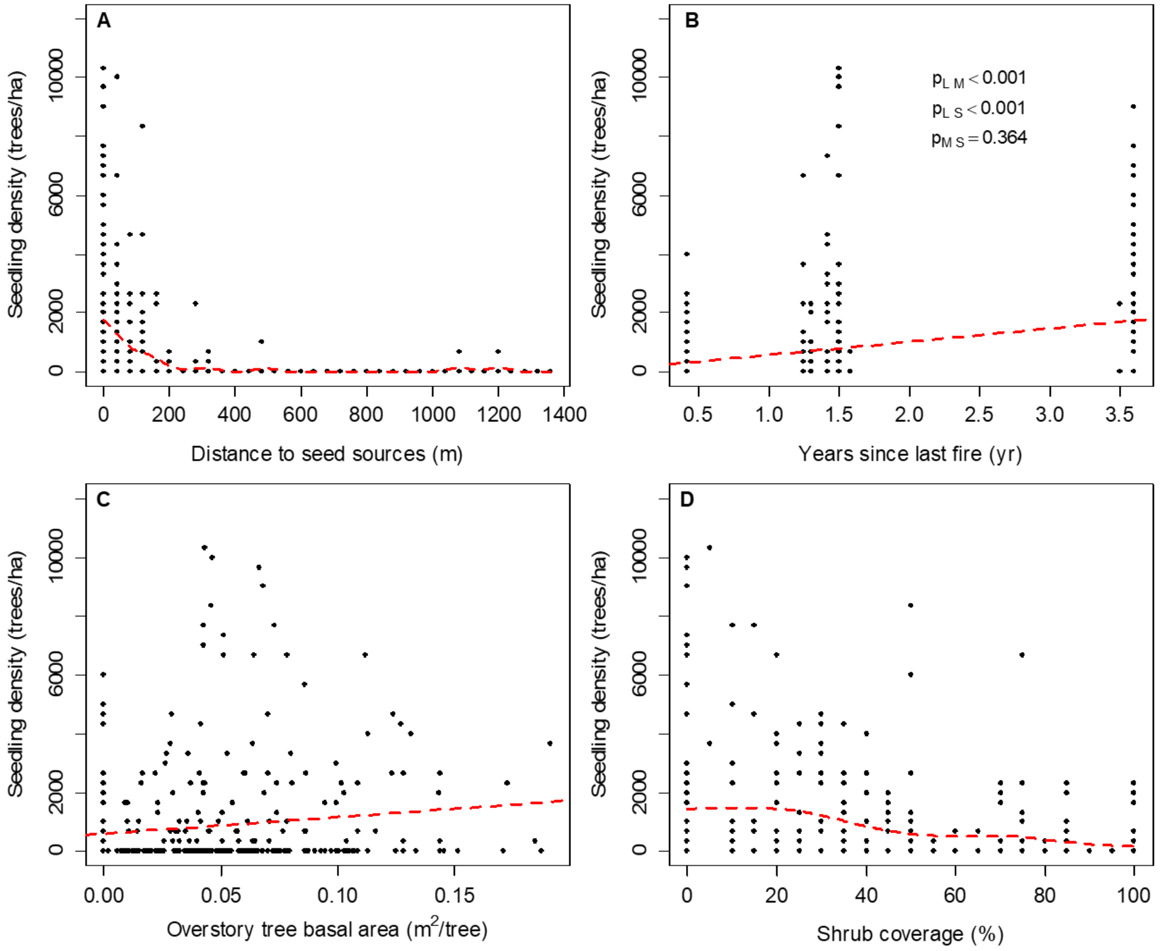

Figure 3.7 Change of Chinese tallow (*Triadica sebifera*) seedling (≤ 2 yrs) densities by associated factors

A: distance to seed sources; B: year since last fire; C: overstory basal area; D understory woody shrub coverage.

Table 3.1 Estimated coefficients of the zero-inflated negative binomial model for roads of habitat edges

	Estimate	Std. error	z value	Pr(>|z|)
Road 1 high propagule pressure with seed trees				
Count model:				
Intercept	7.587	0.809	9.385	0.000
Distance to seed trees	-0.009	0.004	-2.025	0.043
Year since last fire	0.320	0.061	5.286	0.000
Log(theta)	0.849	0.167	5.076	0.000
Binary model:				
Intercept	7.580	3.431	2.209	0.027
Shrub coverage	0.021	0.013	1.647	0.100
Distance to seed trees	0.034	0.015	2.242	0.025
Year since last fire	-0.662	0.259	-2.553	0.011
Distance to neighborhood	4.676	1.869	-2.502	0.012
Road 2 medium propagule pressure with seed trees				
Count model:				
Intercept	10.963	1.504	7.287	0.000
Shrub coverage	-0.012	0.006	-2.054	0.040
Distance to seed trees	-0.003	0.001	-3.000	0.003
Distance to neighborhood	1.175	0.368	-3.193	0.001
Log(theta)	0.805	0.186	4.339	0.000
Binary model:				
Intercept	8.490	2.122	4.002	0.000
Canopy closure	-0.023	0.010	-2.270	0.023
Shrub coverage	0.021	0.008	2.538	0.011
Distance to neighborhood	2.068	0.538	-3.843	0.000
Road 3 low propagule pressure without seed trees				
Count model:				
Intercept	5.196	0.923	5.632	0.000
Overstory basal area	0.724	0.366	1.977	0.048
Year since last fire	0.924	0.398	2.324	0.020
Log(theta)	1.452	0.414	3.507	0.000
Binary model:				
Intercept	-1.231	1.172	-1.050	0.294
Shrub coverage	0.024	0.013	1.792	0.073
Year since last fire	1.135	0.505	2.247	0.025

3.3.3 Spread of tallow into habitat interiors

By 2015, approximately 21.4% (12 of 56 plots) of interior plots had been invaded by tallow with an annual spread rate of 1.8%. Spatially, invaded plots were independent from non-invaded plots at all spatial scales since the PCF curve was within the simulated envelope (the shaded area) (Figure 3.8A). Based on Hotelling's T^2 tests, invaded interior plots were significantly different from non-invaded interior plots on distance to nearest edge, understory shrub coverage, and mean fire return interval. Chinese tallow invaded plots were located significantly closer to roads and fire lines with a mean distance of 20.3 m in contrast to 167.6 m for the non-invaded plots ($p < 0.001$, Figure 3.8B). Invaded plots had lower shrub coverage (8.57 ± 3.23 % vs. 18.42± 2.60 %, $p = 0.025$) and shorter mean fire return interval (2.7 ± 0.17 years vs. 4.3 ± 0.31 years, $p < 0.001$) than the non-invaded plots (Figure 3.8C and 8D). Additionally, invaded plots tended to have higher overstory basal area (16.08 ± 4.33 m^2/ha vs. 8.62 ± 1.50 m^2/ha, $p=0.126$) and canopy closure (44.17 ± 10.42 % vs. 25.86 ± 3.89 %, $p = 0.122$) (Figures 3.8E, 3.8F) even though the differences were not significant at a significance level of 0.05 (Figure 3.9).

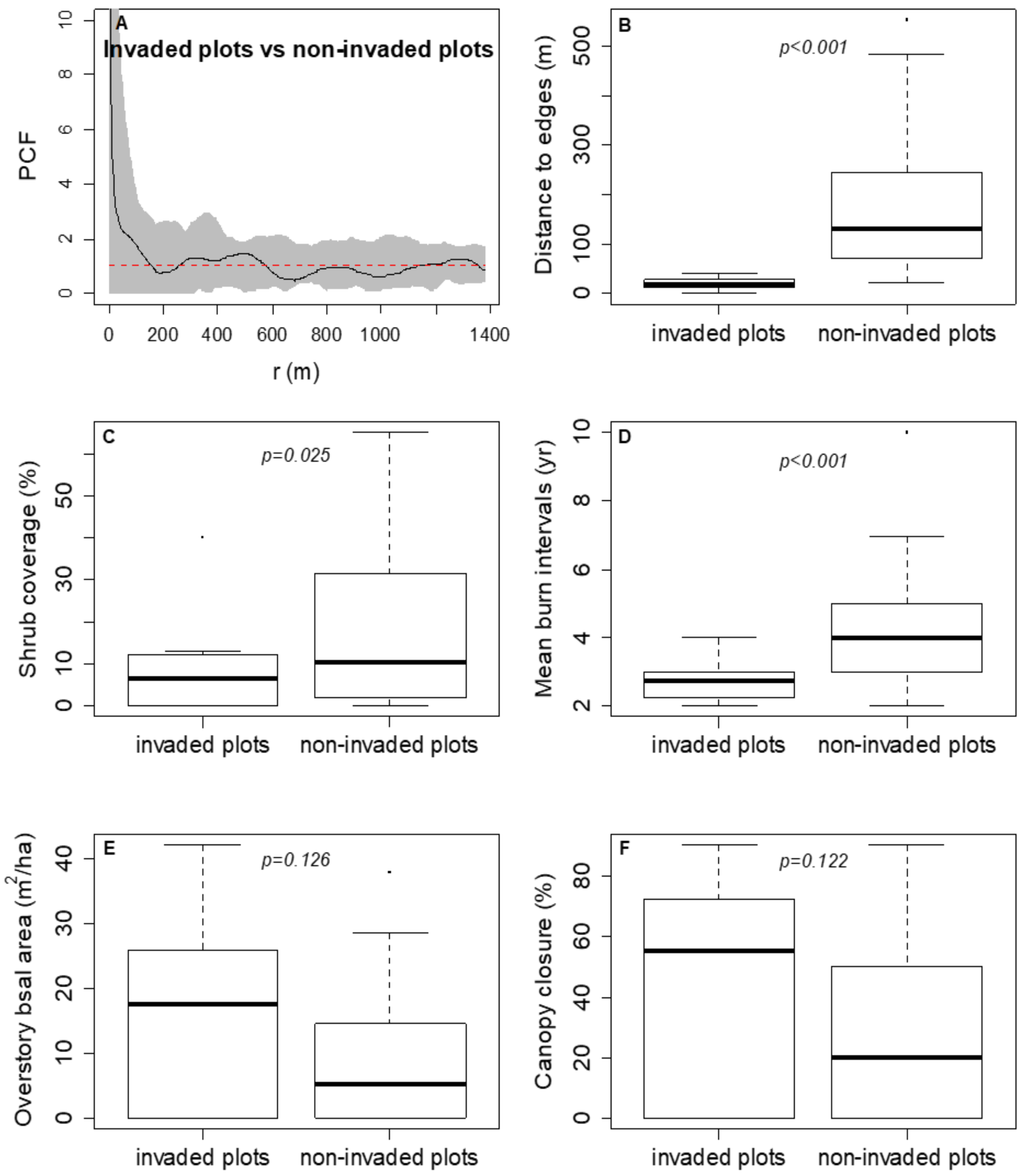

Figure 3.8 Spatial relationships and site conditions between Chinese tallow (*Triadica sebifera*) invaded plots and non-invaded plots

A: PCF curve shows the invaded plots and non-invaded plots are spatially independent. B: tallow invaded plots are significantly closer to roads than non-invaded plots. C: tallow invaded plots have significantly lower shrub coverage than non-invaded plots. D: tallow invaded plots have significantly shorter mean fire return intervals than non-invaded plots. E: tallow invaded plots have higher overstory basal area than non-invaded plots. F: tallow invaded have higher canopy closure than non-invaded plots.

Figure 3.9 Chinese tallow (*Triadica sebifera*) stands formed in late 1990s in burn units O4 and O1

These stands are believed to be formed primarily due to the accidental discharge of wastewater (Figure 3.3.1) and serves as seed sources for tallow to spread across the entire west block of the MSCNWR.

3.4 Discussion

3.4.1 Spatiotemporal pattern and spread of Chinese tallow along habitat edges

In the southeastern Gulf of Mexico coastal landscape, the unprecedented spread of tallow trees has been ascribed to natural and anthropogenic disturbances (Chapman et al. 2008, Gan et al. 2009, Fan et al. 2012, Henkel et al. 2016, Pile et al. 2017b). Tallow is a disturbance-dependent species, and any disturbance causing alteration of resources will inevitably facilitate its invasion (Theoharides and Dukes 2007, Harcombe et al. 2009, Conner et al. 2014, Pearson et al. 2018). Earliest Chinese tallow invasions in the west block of the MSCNWR was caused by accidental discharge of wastewater into this refuge in the mid-1990s (personal communication with the Fire Management staff of the MSCNWR). Tallow seeds were likely transferred into the refuge by wastewater current from the adjoining urban area since old (large) tallow trees were mostly distributed along ditches and in flooded areas by waste water in bordering burn units (O1 and O4) (Figure 3.1). Tallow was introduced into these burn units around 1998, six years earlier than the initial invasion of surrounding roads and fire breaks in 2003.

By 2015 and since 2003, tallow clusters had been distributed widely along most roads and fire breaks in the western part of the landscape (Figure 3.3). Among the factors contributing to the spatiotemporal patterns of tallow clusters, the abundance and spatial location of roadside tallow seed trees should be the primary determinant as shown by strong associations between the numbers of tallow clusters and seed trees (Figures 3.4, 3.5B) and the spatial relationship indicating most tallow seedlings were clumped within a distance of approximately 300 m from seed trees (Figure 3.7A). Fan et al. (2018) reported a similar value (250 m) for the effective seed dispersal distance and the spatial relationship between tallow seed trees and seedlings in the Grand Bay National Wildlife Refuge. Accordingly, a conservative estimate for the effective seed dispersal distance along habitat edges might be approximately 250-300 m in coastal landscape of the southeastern United States where was dominated by longleaf pine ecosystems and pine savannas with birds as the primary disperser of tallow seeds (Grace 1998, Renne et al. 2000, 2002). The positive correlation between newly formed and previously established tallow clusters at a spatial scale of 200 to 600 m (300 m from seed trees on each side) after 2007 could be directly related to the interactions between tallow seed dispersal birds and roadside tallow seed trees, while the negative correlation at large spatial scales > 600 m might reflect the heterogeneity of resource availability between early invaded and latterly invaded habitat edges (Wiser et al. 1988, Theoharides and Dukes 2007) (Figure 3.4).

The lag phase and subsequent slow spread process (2003-2011) were most likely caused by low propagule pressure (i.e., lack of seed trees) (Theoharides and Dukes 2007, Aikio et al.

2010) (Figure 3.5A). This was consistent with survey results that a great number of tallow trees began bearing seeds at 4-year or younger (Scheld and Cowles 1981). Therefore, it was speculated that early tallow seeds were dispersed by birds from these interior seed trees to roadsides and fire breaks (Warren et al. 2012). This might explain why tallow clusters were spatially independent and spread slowly in the early years (2003-2007) (Figures 3.4, 3.6). The phenomenal increase in spread after 2011 (Figure 3.5A) was believed to result from the refuge wide road construction and reconstruction in 2011 funded by the Federal Road Initiative Program (personal communication with the Fire Management staff of the MSCNWR). Anthropogenic disturbances often act as vectors for the introduction and spread of plant propagules and have more profound and lasting effects on the habitat and subsequent biological invasion (Lockwood et al. 2013, Taylor and Cruzan 2015). Mechanistically, clustered pattern of tallow spread along habitat edges suggests that tallow spread is mostly based on short-distance dispersal, for few or no tallow clusters were found along the roads and fire breaks in the east and southeast part and tallow colonization along habitat edges without seed trees was notably slow (Figures 3.5A, 3.6).

For anthropogenic disturbances, prescribed fire may affect tallow spread by altering habitat characteristics that may change the behavior of tallow seed dispersing birds as well as influencing seed germination and seedling establishment (Renne et al. 2002, Fan et al. 2018). The research data showed that the effect size of fire at the landscape level might vary with abundance of tallow seed trees (i.e., propagule pressure). Fire effect was trivial (the regression slope approached 1) before 2011 due to the limited number of seed trees, but after 2011, fire had greatly promoted tallow spread as shown by the value (1.34) of the regression slope (Figure 3.5B). Abundant tallow seed trees and expanding areas burned in recent years (2012-2015) accelerate the spread of tallow trees along roadways and fire breaks in the western part of the landscape (Figure 3.3).

3.4.2 Colonization of tallow seedlings along habitat edges

As shown in Figure 3.6A, the formation of a tallow cluster was characterized by a slow, intermittent colonization phase (2003-2011) followed by a fast colonization phase (2012-2015) that was similar to the landscape-level spread of tallow clusters. This similarity or coincidence in time again emphasizes the importance of tallow seed trees for tallow colonization at micro-scales. Taking the distance to seed trees as a simple measure of propagule pressure (Fan et al. 2018), the relationship between propagule pressure and invasion risk measured by the density of tallow seedlings less than 2 years old was nonlinear and influenced by multiple factors such as fire as well as overstory and understory condition (Figure 3.7, Table 3.1). In an experimental study to test the propagule pressure-invasion risk relationship, Houseman et al. (2014) reported that community invasion risk could be predicted by incorporating propagule pressure, disturbances and soil fertility into an asymptotic model. However, results showed tallow seedling density varied drastically with the distance to seed trees and other risk factors (Figure 3.7A). This was intrinsically caused by the stochasticity and complexity of avian and water current-driven seed dispersal as well as interactions of multiple factors across diverse scales both spatially and temporally (Fei et al. 2016, Fan et al. 2018). The change in the density of tallow seedlings with the distance to seed trees (Figure 3.7A) may suggest sites within the effective seed dispersal range (≤ 300 m from seed trees) are highly susceptible to tallow invasion.

The time (year) since last fire has a significant, as positive effects were shown on the local colonization of tallow seedlings for roads both with and without seed trees (Table 3.1). The density of tallow seedlings for long return times (around 3.5 years) is significantly higher than that for moderate return times (around 1.5 years) and short return times (around 0.5 years), but the difference between moderate return times and short return times is not significant (Figure 3.7B). Fire effect on tallow colonization is two-fold as fire can 1) top or completely kill tallow seedlings/saplings and 2) promote seedling growth by clearing understory vegetation for seed germination thereby reducing vegetative competition. The ZINB count models suggested that frequent burns (return intervals < 3 years) would kill most if not all tallow seedlings and subsequently subdue tallow colonization. However, with long intervals most tallow seedlings will likely survive from repeated low-intensity fires due to its thick bark or be top-killed due to its strong resprouting ability like other hardwood species (Hammond et al. 2015). In the field, it was observed that fire could kill most 1-year old and some 2-year old seedlings, but tallow of more than two years could only be top-killed in most situations and resprout vigorously after prescribed fires in this landscape mostly burned with low-intensity ground fires. As a strong sprouter, Chinese tallow has thick bark and is fire resistant (Grace 1998, Burns and Miller 2004, Grace et al. 2005). Unless the site is burned repeatedly in short intervals, tallow will likely grow to a size that is resistant to fire due to its fast growth and strong sprouting ability.

As to how prescribed fire affects the invasion risk, the ZINB binary model (Table 3.1) shows that the invasion probability tends to increase with the time since last fire at sites with tallow seed trees, but decrease at sites without tallow seed trees. This disparity is most likely due to the spatially nonstationary nature of soil seed bank (Fan 2018) and viability of tallow seeds in the soil seed bank (Cameron et al. 2000). At sites with tallow seed trees, fire will help clear understory vegetation for seed germination and seedling colonization, and long return intervals will allow tallow to grow into sizes that are resistant to fire. In contrast, at sites without tallow seed trees, fire will be unlikely to cause new seedling recruitment due to few or no seeds in the soil. Short interval burns will help kill new seedlings originating from seeds dispersed from other areas. The effect of prescribed fire on a site's invasion risk to Chinese tallow depends on not only fire return intervals, but also the soil seed bank and site conditions (Pile et al. 2017a, Fan et al. 2018).

Note that in addition to the time since last fire, basal area and canopy closure of overstory appears to be a significant factor influencing tallow seedling density along the roads with low and medium propagule pressures (i.e., lack of tallow seed trees) (Table 3.1). These tallow seeds most likely came from nearby seed sources and were dispersed by birds. Since tallow seed-eating birds prefer large pine trees for foraging and roosting (White and Stiles 1992, Renne et al. 2000, Renne et al. 2002, Bartuszevige and Gorchor 2006), more tallow seedlings were found around large pine trees (Fan 2018, Fan et al. 2018), which resulted in a positive association between overstory basal area/canopy closure and tallow seedling density. The ZINB binary models also showed that the invasion risk decreases when the coverage (%) of shrubs increases, which means current efforts to restore understory vegetation dominated by grass and herbaceous species by using frequent prescribed fires could increase the risk of tallow colonization, particularly in areas containing tallow seed trees (Fan 2018 Fan et al. 2018) (Table 3.1, Figure 3.7D). For roads with tallow seed trees, the invasion risk decreased with the distance to the residence - a "neighborhood" effect. Tallow age data indirectly supported the neighborhood effect since tallow became younger going from the north to south (Figure 3.3).

3.4.3 Spread of tallow into habitat interiors

Tallow spread into habitat interiors has a salient edge effect with invaded plots having a mean distance to edge of 20.3 m that is less than mean distance of non-invaded plots to forest edges (Figure 3.8B). Interestingly, the mean distance to edge for invaded plots was nearly the same as the total range of most tallow trees in another study site where prescribed fire was not an active management action (Fan 2018). In greatly fragmented landscapes such as the MSCNWR, the edge effect is most likely related to the fact that bird richness and abundance along edges and surrounding areas are much higher than forest interiors (Terraube et al. 2016). This may explain why forest edges and surrounding areas are highly susceptible to tallow invasion. Understory vegetation (e.g., shrub coverage) contributes more for tallow, taking habitat edges as footholds, to invade interiors than overstory conditions (i.e., basal area, density, canopy closure) as shown by significant differences between the invaded and non-invaded interior plots ($p = 0.025$). It means that frequent (short interval) burn efforts to restore grass and herbaceous species coverage and remove woody shrub layers will potentially increase the risk for tallow to invade from habitat edges to interiors at the landscape level (Figure 3.8 C and D) (Lavoie et al. 2010). Even though, differences of basal area and canopy closure of overstory between invaded and non-invaded plots are not significant (Figure 3.8 E and F), it still shows that compared to open grassland and savanna, Chinese tallow prefers the sparse forested sites with large overstory trees because those sites are the best habitats for birds to disperse tallow seeds (Renne et al. 2000, Renne et al. 2002). This makes it a challenge for land and resource managers to conserve native bird species and diversity, but prevent tallow invasion. One possible solution is to adjust the time and fire intervals based on the condition of seed sources to create a habitat that is unfavorable for seed dispersal, germination and establishment (e.g., high shrub cover or dense overstory). For instance, creating a 20 m wide shrub covered buffer along habitat edges in areas with abundant tallow seed sources may greatly reduce tallow spread into habitat interiors (Fan 2018, Fan et al. 2018).

3.5 Conclusions

3.5.1 Mechanisms of Chinese tallow invasion at a landscape level

This study examined the spatiotemporal spread pattern of Chinese tallow trees in the MSCNWR, a landscape managed intensively using prescribed fire to restore declining native habitats-pine savannah for the endangered Mississippi Sandhill Crane. Originating from the adjacent neighborhood, invasive tallow was introduced into the landscape by the accidental discharge of wastewater and tallow seed-eating birds. Subject to short dispersal distance (≤ 300 m), tallow distributed in clustered patterns along habitat edges and tallow clusters were positively correlated at a distance of 200-600 m. Temporally, the spread of tallow consists of a slow spread phase (2003-2011) with limited propagule pressure (tallow seed trees) followed by a rapid spread phase beginning in 2012 which was caused by large-scale road construction and reconstruction.

Spatial distribution and abundance of seed trees (propagule pressure) are the predominating determinant of tallow spread rate. Furthermore, prescribed fire (disturbances), landscape structure, and site/stand characteristics have also proved to be significant factors.

At the landscape level, frequent fires (mean interval around three years) generally tend to significantly increase risk of tallow spread into habitat interiors, especially those areas within a mean distance of 20 m (0-50 m) from habitat edges compared to infrequent fires (mean interval greater than four years). At microscales, tallow invasion was influenced not only by fire but also by site/stand characteristics and propagule levels measured by distance to seed trees. The invasion risk will decrease with the increase in the distance to seed trees and shrub coverage. Fire, however, has a very contrasting effect on invasion risk depending on availability of seed trees: the risk will increase with the time since last fire if seed trees are present in surrounding areas, but decrease if there are no seed trees or if seed trees are out of the range of the effective seed dispersal distance (> 300 m). As soon as tallow colonization occurs at a site, tallow seedling density will increase with the time since last fire and overstory basal area/canopy closure. Therefore, using prescribed fire to control and manage invasive tallow should carefully consider all aforementioned factors.

3.5.2 Management of Chinese tallow invasion at a landscape level

Chinese tallow invasion at landscape-level is a cumulative and complicated process associated with many factors and management of tallow invasion is a costly and time consuming process but not a simple linear process. In the MSCNWR, driven by the spatial distribution and abundance of tallow seed trees, fire regime and landscape/community features, tallow spread in the fire-managed landscape takes a clustered spatiotemporal pattern along habitat edges and surrounding areas (< 50 m from edges). Effective fire treatments at the landscape level should explicitly consider the “seed tree effect”, “edge effect”, and “neighborhood effect” with burn schedules (e.g., determination of fire intervals and seasonality) that not only shorten the window of invasion but also prevent tallow seedlings from growing into mature trees. Therefore, the management of Chinese tallow invasion is a comprehensive process not only in the MSCNWR, but also in other similar landscapes and habitats in the southeastern coastal area of the United States. A specific management prescription is required based on particular conditions of the Chinese tallow invasion in a landscape.

In the MSCNWR, to reduce tallow spread from edge to interior in this fire-maintained landscape intertwined with pine savannas and pine flatwoods, it is recommended that along the edges such as roads and fire breaks, all tallow seed trees should be felled within a 250-300 m radius range from seed trees by using mechanical and chemical treatments (Pile et al. 2017a) to reduce the propagule pressure. Subsequently, a 25-50 m wide native shrub covered buffer should be built from edges to interior forests or savanna to increase resistance of native ecosystems and maintain a healthy understory vegetation structure. Within this shrub buffer along habitat edges, interspecific competition between tallow seedlings and shrubs could limit the growth of Chinese tallow. Furthermore, once the shrub buffer is established, it should not be burned when prescribed fires are deployed. After the removal of tallow seed trees, prescribed fire could be used to control the growth of tallow seedlings and saplings in a landscape area. Previous research reported that frequent fires with a short interval (≤ 2 years) could have an efficient effect on Chinese tallow regeneration (Grace 1998, Grace et al. 2005, Pile et al. 2017a) because short fire intervals may limit regeneration window of Chinese tallow but the regeneration window of Chinese tallow is not clear yet. Therefore, for highly susceptible habitat (< 50 m from invaded roads and fire breaks), fire treatments and timber management should be carefully designed to create more resistant vegetation structure (e.g., high woody shrub layers, dense overstory) to curb tallow invasion into the interior habitats (pine savanna) in coastal areas of the southeastern United States. In the future, the optimal fire intervals of prescribed fire, effects of fire on tallow seeds visibility, and regeneration window of Chinese tallow after burning, should be studied systematically because these questions are directly related to the management of tallow invasion.

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CHAPTER IV

DEVELOPMENT OF CHINESE TALLOW (*Triadica sebifera*) INVASION PROCESSES IN FIRE REGULATED FOREST STANDS

4.1 Introduction

Chinese tallow (*Triadica sebifera*) is known as one of the most aggressive exotic species and invader in the southern coastal area of the United States since it was introduced in the 1770s (Hunt 1947, Oswalt 2010, Meyer 2011). It was widely planted as a commercial crop in the early 1900s across the Gulf Coast by the federal government because of its high productivity of oily and waxy seeds that were important industrial resources at that time (Scheld and Cowles 1981, Jones and McLeod 1989, Bruce et al. 1997). Chinese tallow has invaded several native plant communities including the coastal prairies and many other types of forests (e.g., wet pine forests and oak forests) in the southeastern United States (Lodge 1993, Simberloff 1996, Gan et al. 2009, Wang et al. 2011a). By 2008, it has occupied 185,000 ha of southern forests from east Texas to south Florida (Oswalt 2010). It has been reported that Chinese tallow commonly occurs on disturbed sites (Battaglia et al. 2007, Nolfo-Clements 2006, Howard 2012, Conner et al. 2014, Pile et al. 2017a) such as fire disturbed or hurricane damaged wet pine forest stands or hardwood and wet pine mixed forest stands in the southern coastal area. Moreover, these two forest types are appropriate habitats for Chinese tallow to colonize and establish at the stand level (Fan et al. 2012, Fan 2015, Fan 2018).

In native forest ecosystems, prescribed fire has been regarded as a feasible method to control Chinese tallow in Texas coastal prairies (Grace et al. 2005). Other research indicated that frequent burning could kill tallow seedlings and damage old tallow trees, especially during the growing season (Grace 1988). However, other researchers reported that fire disturbance, especially infrequent burns, could increase the risk of Chinese tallow invasion due to its ability to establish under other types of disturbance (Neyland. and Meyer 1997, Conner et al. 2002, Pile et al. 2017a). Chinese tallow has many biological traits (e.g., rapid growth rates, shade tolerance, nutrient uptake, seed production, and root sprout) which enable it to adapt to a variety of site conditions (shade to full sun) and soil types (acidic to alkaline, wet to dry), and it is able to modify the stand conditions and reduce understory fuels which may have negative effects on burns (Bogler and Batcher 2000, DeWalt et al. 2011, Paudel and Battaglia 2015, Tian et al. 2017). Colonization and establishment of tallow in a site following its introduction is greatly restricted by the local environmental conditions (Chesson 2000, Sakai et al. 2001, Pattison and Mack 2008), including impacts of overstory trees (abundance and location), understory vegetation types, and micro-topographic conditions of forest sites/stands (Levine et al. 2004).

The southern wet pine forest is one of the most important coastal ecosystems and is also the native ecosystem that is easy for Chinese tallow to invade because of its open stand structure and frequent disturbances (e.g., fire, flooding, and hurricane). Mechanisms of Chinese tallow invasion (i.e., colonization and establishment) on different site/stand conditions have not been well-studied, especially when considering the relationship between Chinese tallow distribution and site conditions, recruitment of Chinese tallow, and effects of disturbances (fire and hurricanes) on Chinese tallow age structures (Rogers and Siemann 2002, Tian et al. 2017, Pile et al. 2017b, Fan 2018). Therefore, understanding mechanisms (i.e., establishment, regeneration, and spread) of Chinese tallow invasion within wet pine forest stands, especially for stands with disturbances, has become important for Chinese tallow control.

In this study, underlying mechanisms driving tallow colonization and establishment/growth on different site and stand conditions, especially the microtopography, were analyzed through spatial analysis of age and size structure of tallow populations and mapped stem data. Meanwhile, by using statistical modeling methods, mechanisms of Chinese tallow spread in the stands of southern coastal forests were evaluated in different forest stands. Specifically, this research addressed the following objectives/questions: 1) How will the microtopography inside the forest stands affect the distribution and spread pattern of Chinese tallow with consideration of other site conditions, overstory structures, understory vegetation cover and edges? 2) How will prescribed fire affect age structures and spread rate of Chinese tallow with cumulative propagule pressure under different microtopography conditions within pine flatwoods? 3) How will overstory conditions (Trees per acre, basal area, and canopy closure), understory vegetation (vegetation types and coverage), and propagule pressure (tallow seed trees) affect the regeneration of tallow seedlings (seed germination)?

4.2 Methods

4.2.1 Research area

Mississippi Sandhill Crane National Wildlife Refuge (MSCNWR) is located in southern Mississippi (30°27'3.49"N, 88°39'20.60"W) and contains three blocks (east, west, and south) with total area of 7492.73 ha (18514.93 ac) (Figure 4.1). This refuge was established in 1975 under the authority of the Endangered Species Act to protect the critically endangered Mississippi Sandhill cranes (*Grus canadensis pulla*) and their unique, and itself endangered, wet pine savanna habitat. The refuge also protects and restores the last large expanses of wet pine savanna, primarily through the utility of prescribed fire, thus this refuge has been divided into 99 sub-burn units for fire management. The wet pine savanna is one of the most diverse ecosystems in the U.S. with more than 30 species of plants found in a square meter of land (MSCNWR website, https://www.fws.gov/refuge/Mississippi_Sandhill_Crane/about.html). In addition to the wet pine savanna (25.3%), the major habitat in this area is pinelands (pine flatwoods) which occupy 57.5% of the MSCNWR (MSCNWR Comprehensive Conservation Plan 2007).

The Sandhill Crane National Wildlife Refuge has hot, humid summers and relatively mild winters. Average maximum temperatures are 16° C (61° F) in January, the coldest month of the year, and average minimum temperatures are 6° C (42° F) for the same month (National Climate Report 2005). The refuge has its highest temperatures in July and August, with an average maximum temperature of 32° C (90° F). Like most of Mississippi and the Southeast, this area receives substantial rainfall, averaging more than 162.6 cm a year. Located in the Gulf Coastal Plain within 8 km of the ocean, the refuge is characterized by flat topography and a low elevation just a few feet above mean sea level (US Fish and Wildlife Service 2007).

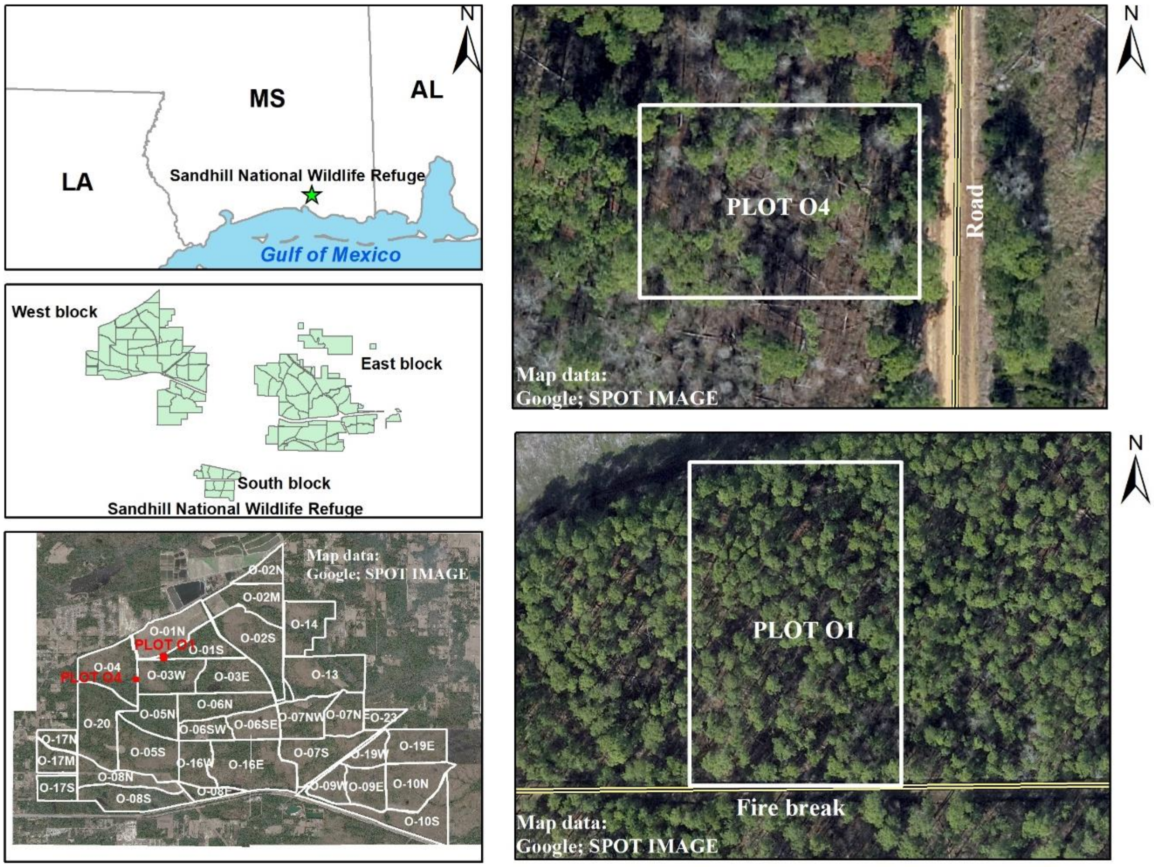

Figure 4.1 MSCNWR west block and research sites

4.2.2 Data collection

In this research, study sites were located in the west block of the MSCNWR that has been invaded by Chinese tallow. Two fire burn units (Unit O4 and Unit O1S) were selected in the west block of the MSCNWR to establish investigation plots (Figure 4.1). In the spring of 2016, two plots were sampled along the edge of these two burn units. One plot is located in unit O4 and called plot o4 (March 2016) and another plot is located in unit O1S and called plot o1 (March 2016). Plot o4 and plot o1 are rectangular plots with area of 1750 m^2 (50 m ×35 m) and 6834 m^2 (67 m × 102 m). Both plots were established in slash pine (*Pinus elliottii*) flatwoods (Figure 4.1).

In each plot, all trees (i.e., overstory trees and tallow trees) were mapped using a high resolution GPS (Global Positioning System) unit. Diameter at breast height (DBH) of overstory pine trees was recorded. Total height and DBH/GLD (ground level diameter) of Chinese tallow trees were recorded. All tallow trees in plot o4 and plot o1 were then felled at ground level and a disk was removed for age determination in the field. In plot o4 and plot o1, 699 (377 in plot 04 and 322 in plot o1) tallow saplings and mature trees (height > 1 m) were cut and measured separately. According to the average difference of relative altitude [Digital Elevation Model (DEM 3 m resolution)] obtained from United States Geological Survey (USGS)) data, and field condition, each plot was divided into two parts (upland area and lowland area). In each plot, tallow trees were mapped by age groups (Figure 4.2), that were determined by prescribed fire history from 1998 to 2016 (Fire Department of the MSCNWR).

Both plots were divided into investigation quadrats with equal areas based on the spatial domain of each plot. Plot o4 and plot o1 had 35 and 66 quadrats, respectively. In each quadrat, the number of 1-year tallow seedlings (height ≤ 1 m), vegetation type and coverage of understory, and canopy closure of overstory (using a densiometer) were measured and recorded. To study impacts of prescribed fire on age differences between above and below ground growth of Chinese tallow trees, roots of 44 resprout Chinese tallow trees were excavated and age data of each root was measured in burn unit O1S.

4.2.3 Spatial data analysis and modeling

For Question 1, spread process (Figure 4.2) of different tallow age groups within plots o4 and o1 under different prescribed fire disturbances and micro-topographies was mapped using a marked point pattern in the R *spatstat* package using the (x, y) coordinates as the location and derived invasion time (tree age) as the mark (Baddeley and Turner 2004, Fan 2018). The pair correlation function (PCF) was used to estimate spatial relationships (spatial scale on which tallow groups are distributed positively, negatively or randomly) between newly formed tallow age groups after specific fire disturbances and previous tallow age groups (Figure 4.3), and also the spatial relationship between tallow trees and overstory trees (Lutz et al. 2014, Fan 2018). To analyze effects of overstory tree density, distance from the edge (road/fire break), and the microtopography (DEM) on the distribution of tallow trees, nonparametric (smoothed) spatial association (rho function) analysis had been used (Baddeley and Turner 2004, Baddeley et al. 2012, Fan 2018). To quantify spatial distribution of Chinese tallow trees (spatial intensity), and examine significances of site conditions such as overstory tree density, canopy closure, and microtopography, on distribution of Chinese tallow in the pine flatwoods, the Spatial Poisson Regression (SPR) model was applied. The equation is as follows:

$$log\left(\hat{\lambda}(s)\right) = \alpha \cdot f(s) + \beta \cdot g(U, s) \qquad (4.1)$$

where $\hat{\lambda}(s)$ is the predicted tallow tree intensity at a spatial location *s*; *f(s)* is a function of locations (x, y coordinates), reflecting the trend, and *g(U, s)* is a function of spatial covariates (DEM, canopy closure, distance to the edge and shrub coverage), reflecting the interaction and dependence.

To answer Question 2, age structure differences of tallow trees with respect to different micro-topographies were tested by using Student's t-test (Ruxton 2006, Pile et al. 2017a).

Average annual increment rate (spread rate) of each tallow age group with different prescribed fire disturbances in two different topographic landforms was used to show development of tallow colonization under prescribed fire disturbances. Polynomial regression and Cox-test (Davidson and MacKinnon 1981, Greene 1994, Greene 2003) were used to examine the effects of fire disturbance and cumulative propagule pressure (tallow seed trees, age ≥ 4 yr) on the annual increment rate of tallow colonization separately.

In regard to Question 3, the count of tallow seedlings (1 year old) in each of the 44 quadrats in plot o4 and 66 quadrats in plot o1 were response variables. Measured overstory canopy closure (X_1) and basal area (X_2), tallow tree basal area (X_3, seed sources), and understory vegetation type (X_4, 1=shrub, 0=grass) were the predictor variables. The Poisson regression model was used to evaluate potential factors contributing to tallow recruitment by using the following equation:

$$l\,n(\hat{\lambda}) = b_0 + b_1X_1 + b_2X_2 + b_3X_3 + b_4X_4 \qquad (4.2)$$

where $\hat{\lambda}$ is the predicted count number of tallow seedlings, X_1 and X_2 are the canopy closure and basal area of overstory trees, X_3 is the basal area of mature tallow trees, and X_4 is the vegetation type of understory by using dummy code.

All statistical analyses and modeling were conducted using the R statistical environment of the Windows base version (R Development Core Team 2014). R base packages and contributed packages including *spatstat* version 1.53-2 (Baddeley and Turner 2004) for spatial analysis and the SPR modeling and *stats* for the Poisson regression analysis were used.

4.3 Results

4.3.1 Spread processes of Chinese tallow tree age groups within pine flatwoods

Dynamic distribution maps of tallow age groups in plot o4 showed that the earliest tallow trees invaded this plot from the north highland in 1998 (Figure 4.2A). By 2016 (the sampling year), there were 377 tallow stems (height > 1 m and age > 1 year) in this plot and these were divided into five age cohorts using prescribed fire history (1998, 2002, 2006, 2009, and 2012). Temporally, there were three distinct phases of spread based on the rate of spread (number of new tallow trees formed in a year): 1) a slow spread phase (1998-2005, five trees/yr average annual increment) with most tallow trees located in the north highland of the plot with the spread rate in the north upland higher than in the south lowland; 2) a rapid spread phase (2006-2011, 20 trees/yr average annual increment) in which tallow trees started to move to the southeastern lowland of the plot and the spread rate of tallow trees in the lowland was higher than the upland compared to the former phase; and 3) a dramatic spread phase (2012-2015, 56 trees/yr average annual increment) in which tallow trees started to move to the eastern edge (road) and there was a clustered distribution pattern in the southeastern lowland area. According to the distribution map of overstory trees in plot o4, there was a large canopy gap in the southeastern lowland of the plot where the tallow tree cluster occurred.

Compared to plot o4, plot o1 was invaded by tallow trees in 1999 which was similar to plot o4, but there were different invasive patterns in plot o1 (Figure 4.2B). In plot o1, tallow trees invaded from the southern edge (fire break), and by 2016 (the sampling year) there were 322 tallow trees in this plot which were divided into six age cohorts based on prescribed fire history (1999, 2001, 2004, 2008, 2012 and 2014). Based on the spread rate of tallow trees, spread processes of plot o1 also had three phases: 1) a slow spread phase (1999-2003, four trees/yr average annual increment) in which tallow trees were mainly located in the southeast lowland area and began to move north; 2) a rapid spread phase (2004-2011, 12 trees/yr average annual increment) in which most newly germinated tallow trees dispersed inside the lowland area and there was a tallow cluster in the southeast lowland; and 3) a dramatic spread phase (2012-2015, 49 trees/yr average annual increment) which was different from the other two phases, new tallow trees increased dramatically in the upland area and the spread rate was greater than the lowland which had almost no new tallow trees. Compared to plot o4, there was no large canopy gap within plot o1 and tallow trees dispersed from the south lowland to the north highland.

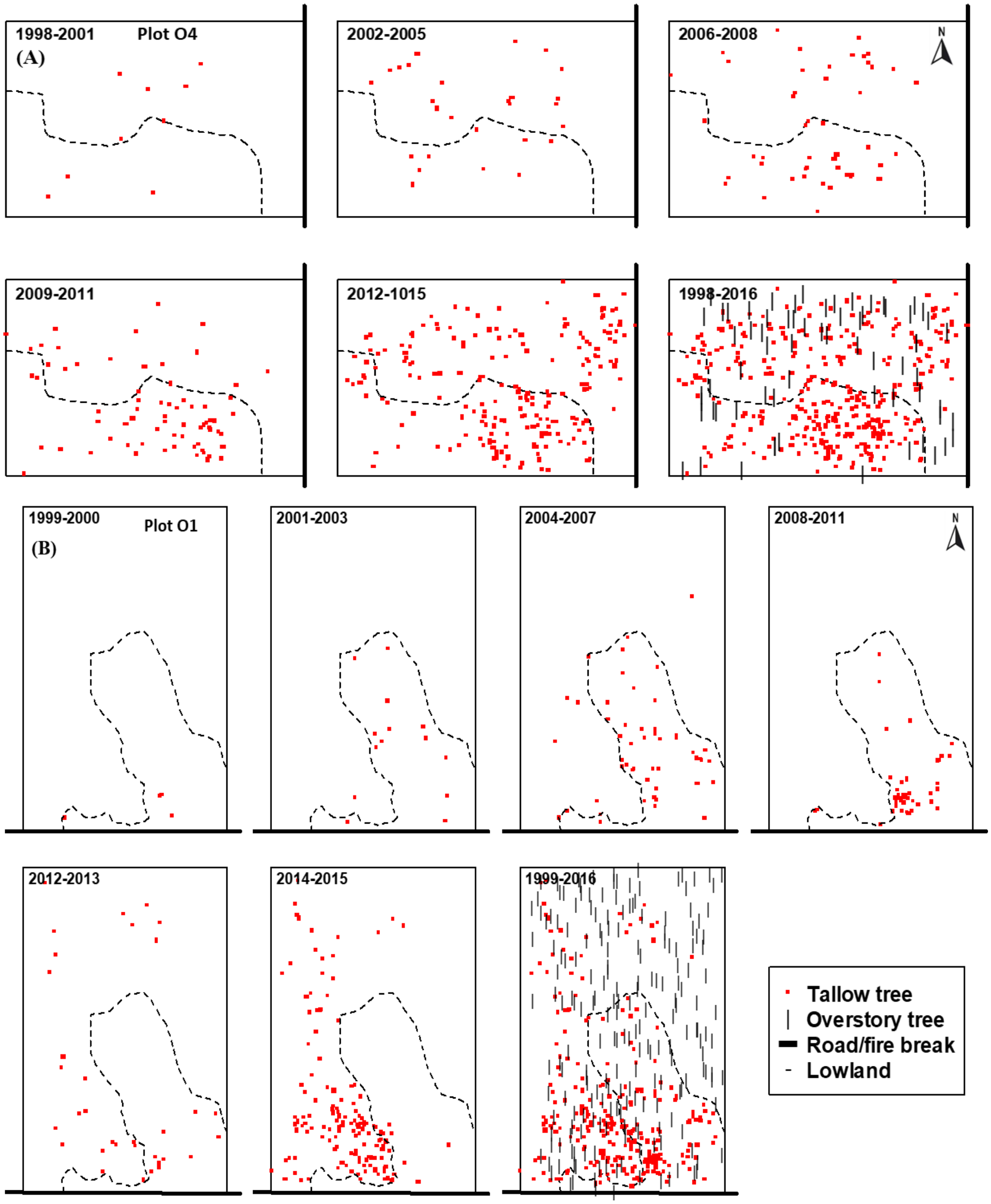

Figure 4.2 Distribution and spread pattern of Chinese tallow (*Triadica sebifera*) in plots o4 and o1

With prescribed fire determined age groups and microtopography boundary (inside the dash line is the lowland area).

4.3.2 Distribution patterns of Chinese tallow trees with site conditions

Results of PCF (Figure 4.3A) indicated that in the upland portion of plot o4, the newly formed tallow age cohort was not spatially correlated with previously established tallow (random relationship). However, after 2005, the newly formed tallow age cohorts were positively correlated with previous age cohorts within a spatial scale of 6 m in the lowland area (Figure 4.3B). For plot o1, only the tallow age cohorts formed after 2012 had a positive spatial correlation with newly formed age cohorts (2014-2015) at a spatial scale of 4-10 m (Figure 4.3C). After 2004, in the lowland area there were positive spatial correlations between former age cohorts and later age cohorts within a spatial scale of 4-10 m (Figure 4.3D).

Figure 4.4 A and B indicated that upland tallow trees had a random spatial relationship with overstory pine trees in plot o4 but lowland tallow trees had a significant negative spatial correlation with overstory trees. Most tallow trees clustered along the stand edge within 15-20 m of the road, and as the distance to the edge increased, tallow intensity deceased ($p< 0.001$). Rho function results suggested that tallow trees had a significant negative relationship with elevation (microtopography, $p< 0.\ 01$) (Table 4.1). In lowland areas, tallow trees clustered at moderate canopy openness (100-300 trees/ha overstory density) which was similar to earlier results (Fan 2018), but in upland areas, there was a random distribution pattern between tallow and overstory pine trees (Figure 4.4 A and B). However, there was still a negative spatial correlation between tallow trees and overstory density (canopy closure, $p< 0.001$) (Table 4.1). Upland tallow trees in plot o1 had a positive spatial correlation with overstory pine trees at a spatial scale of 4 m that was different from the plot o4 highland area but in lowland area, tallow trees had no spatial correlation with overstory pine trees (Figure 4.4 C and D). Upland tallow trees were clumping along forest stand edges (< 20 m from the firebreak) with an overstory density of 200-500 trees/ha where the elevation was 13.3-13.4 m. Lowland tallow trees originated 10 m from forest stand edges with two kinds of overstory densities (100-200 trees/ha and 400-500 trees/ha), and were mainly distributed at the elevation of 13.2-13.4 m (Figure 4.4D). The SPR results implied that spatial covariates such as canopy closure, distance to the edge, and DEM were negatively correlated with spatial intensity of tallow trees (Table 4.1).

Table 4.1 Spatial Poisson regression results of Chinese tallow trees in plots o4 and o1

Plot o4	Estimate	Std. Error	Z value	Z test
Intercept	17.834	5.768	3.092	**
Canopy closure	-0.015	0.003	-4.979	***
Shrub coverage	-0.020	0.005	-3.914	***
Distance to the edge	-0.039	0.006	-6.065	***
DEM	-1.427	0.465	-3.066	**
Plot o1				
Intercept	25.164	7.561	3.328	***
Canopy closure	-0.015	0.004	-4.256	***
Shrub coverage	-0.012	0.003	-3.459	***
Distance to the edge	-0.032	0.005	-6.51	***
DEM	-1.976	0.57	-3.465	***

Significant codes: '***' 0.001; '**' 0.01; '*' 0.05; '.' 0.1

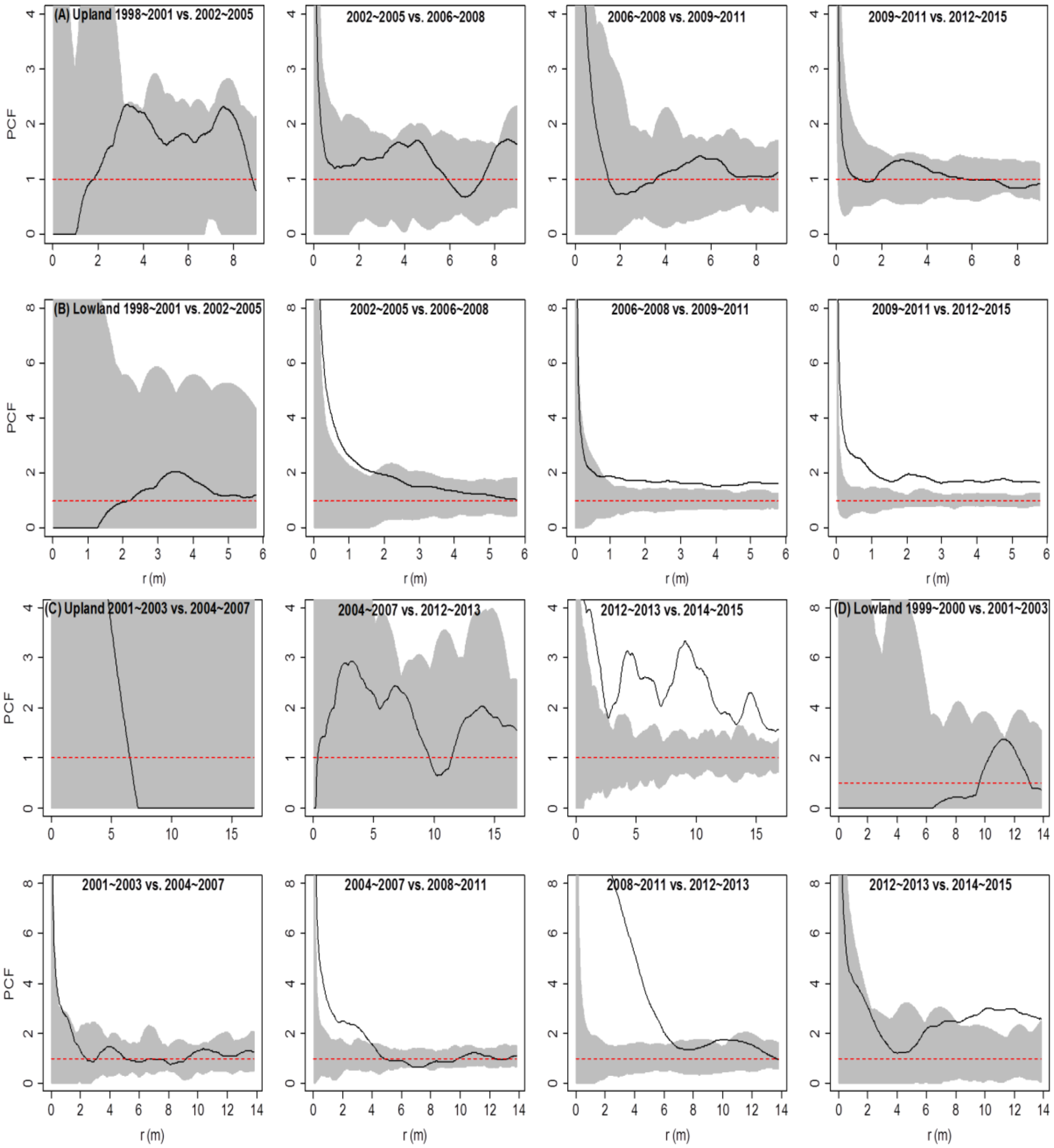

Figure 4.3 Spatial relationships between different Chinese tallow (*Triadica sebifera*) age groups in plots o4 and o1

A and B refer to plot o4 and C and D refer to plot o1 with consideration of the microtopography

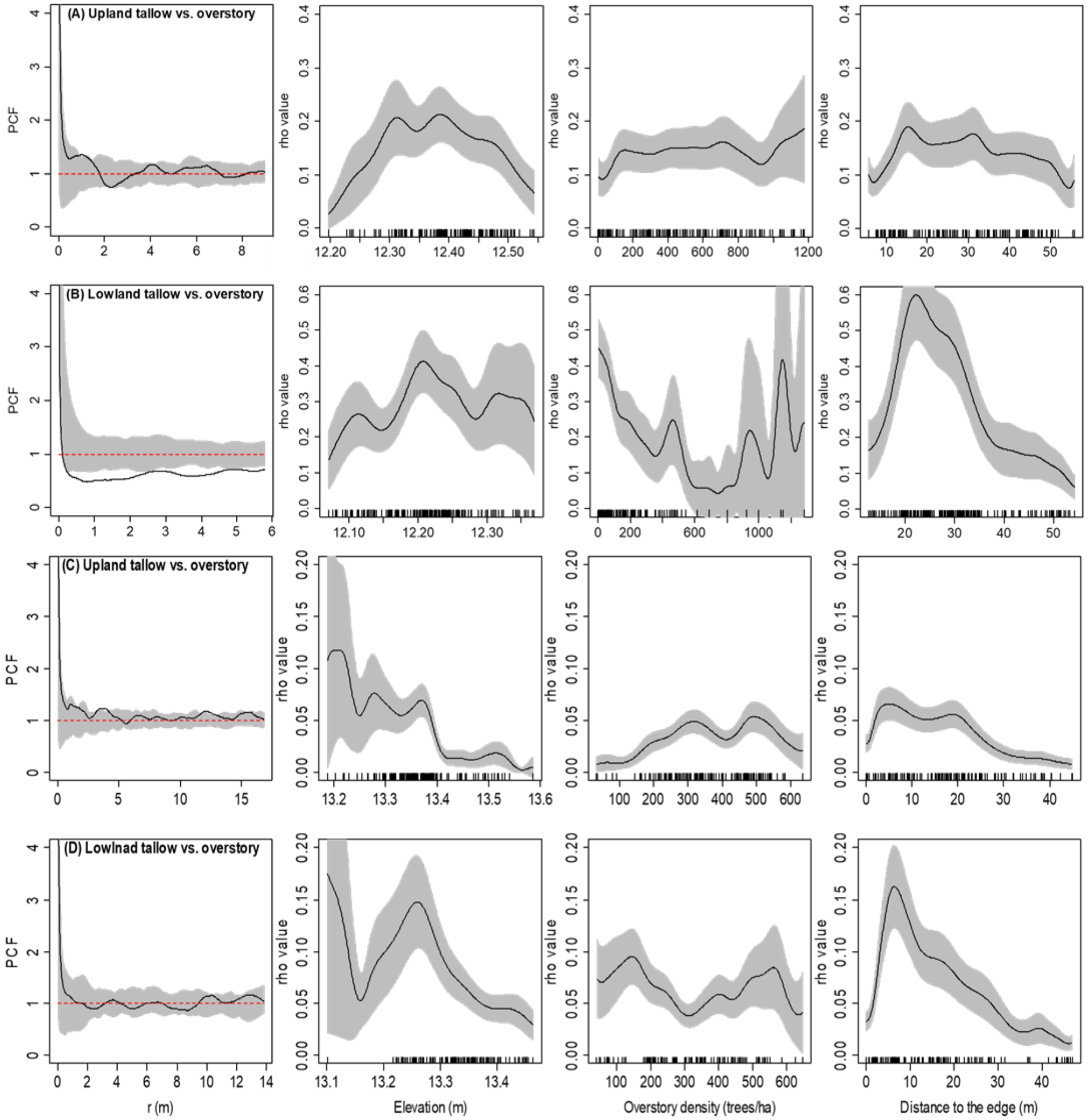

Figure 4.4 Spatial relationships and distribution patterns between Chinese tallow (*Triadica sebifera*) trees and site conditions in plots o4 and o1

With consideration of the microtopography, A and B refer to plot o4; C and D refer to plot o1.

4.3.3 Effects of prescribed fires and propagule on colonization and spread of Chinese tallow trees

The t-test of tallow tree age between upland and lowland areas in plot o4 (Figure 4.5A) indicated that the age of tallow trees in the lowland was higher than the upland although the difference was not significant ($p = 0.85$). Lowland tallow age was significantly greater than in the upland in plot o1 ($p < 0.001$) (Figure 4.5B). Average annual increment data coupled with prescribed fire history (Figure 4.6) showed that lowland tallow trees in plot o4 had a “J” shaped increasing curvature (Figure 4.6A) and the annual increment rate was greater than in upland area since the prescribed fire of 2002. However, the annual increment rate of tallow trees in the lowland area of plot o1 displayed a “bell” shaped curve compared to the upland area which had a “J” shaped curve, and after 2012, the increment rate of upland areas had a substantial increase and was greater than in the lowland (Figure 4.6B).

Quadratic polynomial regression indicated that the annual increment rate of tallow trees in lowland areas of plot o4 increased as the propagule pressure increased at first, but when the propagule pressure reached 700 trees/ha, increment rates for the years without prescribed fires started to decrease ($p < 0.01$) (Figure 4.7A). Even though increment rates for the years with fires continued rising, the decreasing trend appeared when propagule pressure reached 900 trees/ha ($p < 0.01$). Under the same propagule pressure, annual increment rates with fires were higher than those without fires ($p < 0.001$) in the lowland area of plot o4. In the upland area of plot o4, annual increment rate was positively correlated with propagule pressure ($p < 0.05$), and increment rates had no significant difference between the years with and without prescribed fires ($p=0.468$) (Figure 4.7B). Compared to lowland areas, tallow annual increment rate was lower in upland areas under the same propagule pressure, and propagule pressure in lowland areas was also higher than in upland areas. In plot o1 lowland areas, the annual increment of tallow trees was similar to plot o4 lowland (Figure 4.7C). Increment rates of tallow trees with fires increased as propagule pressure increased but when it reached 250 trees/ha, increment rates began to decline (from 90 trees/ha to 30 trees/ha) ($p = 0.18$). Increment rates without fires showed a weak increase and decrease curve ($p = 0.45$) with a lower increment rate ($p < 0.001$) compared to the curve with fires before propagule pressure reached 400 trees/ha. For the upland area of plot o1, increment rates of tallow trees suddenly increased which was different from the plot o4 upland area, and there was no significant difference between the years with and without prescribed fires (Figure 4.7D). In both plots, propagule pressure at lowland areas was greater than in upland areas which means tallow seed trees had a higher survival rate in lowland areas which might be related to fire intensity in these areas (Figure 4.8).

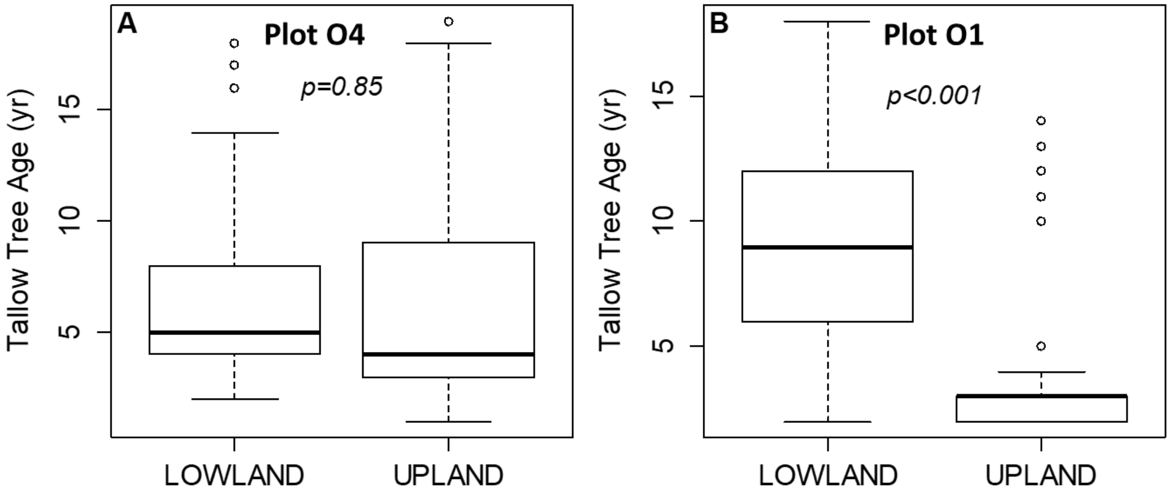

Figure 4.5 Age differences of Chinese tallow (*Triadica sebifera*) trees between lowland and upland areas in plots o4 and o1

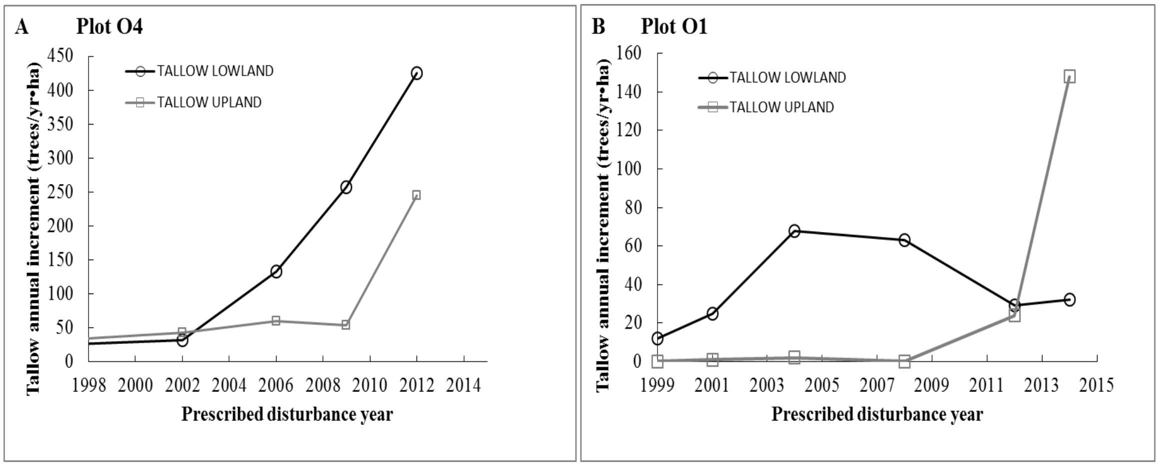

Figure 4.6 Average annual increment of Chinese tallow (*Triadica sebifera*) trees between upland and lowland areas in plots o4 and o1 with prescribed fires

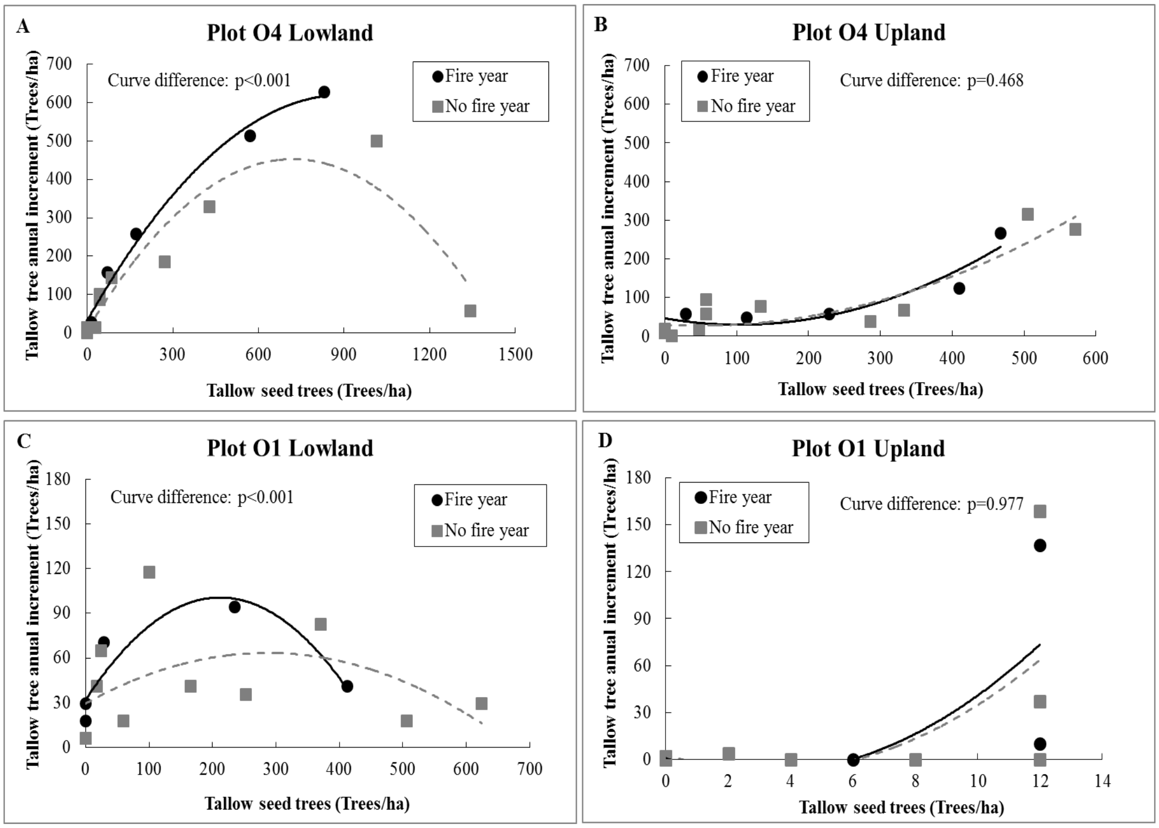

Figure 4.7 Effects of fire and increasing propagule pressure on the annual increase of Chinese tallow (*Triadica sebifera*) trees

Within the pine flatwoods considering the microtopography; A and B belong to plot o1; C and D belong to plot o4; p -value shows the significance between two regression curves.

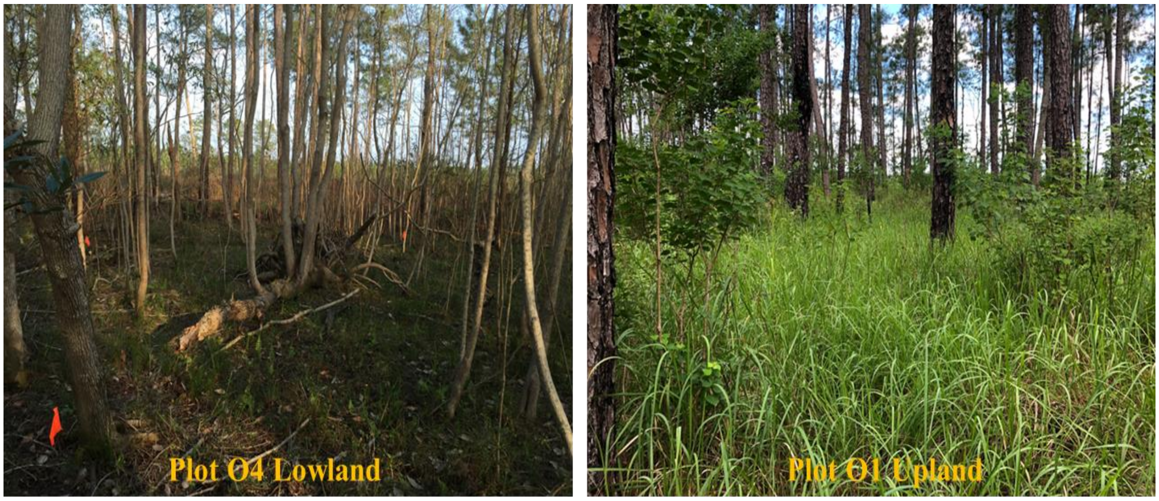

Figure 4.8 Differences of understory vegetation cover between lowland and upland areas in pine flatwoods invaded by Chinese tallow (*Triadica sebifera*) trees

4.3.4 Effects of site conditions on regeneration of seed germinated tallow seedlings

Results from scatter plots of tallow seedlings (1 year seed germinated) coupled with four site condition covariates (i.e., canopy closure, understory vegetation type, and basal area of tallow trees and overstory trees) in plots o4 and o1 suggested that tallow seedlings had the same trends and correlation patterns with these contributing variables (Figure 4.9). Seedling data from these plots was combined for modeling which indicated that tallow regeneration had a negative correlation with canopy closure ($p < 0.05$) indicating light was an important factor for tallow seedlings (Table 4.2). More tallow seedlings could be found in bare soil or grass covered areas compared to shrub covered areas ($p < 0.001$). Quadrats with high tallow basal area (i.e., large seed trees) had more tallow seedlings ($p < 0.001$), and tallow seedlings had a positive correlation with the basal area of overstory pine trees (large pine trees, $p < 0.001$).

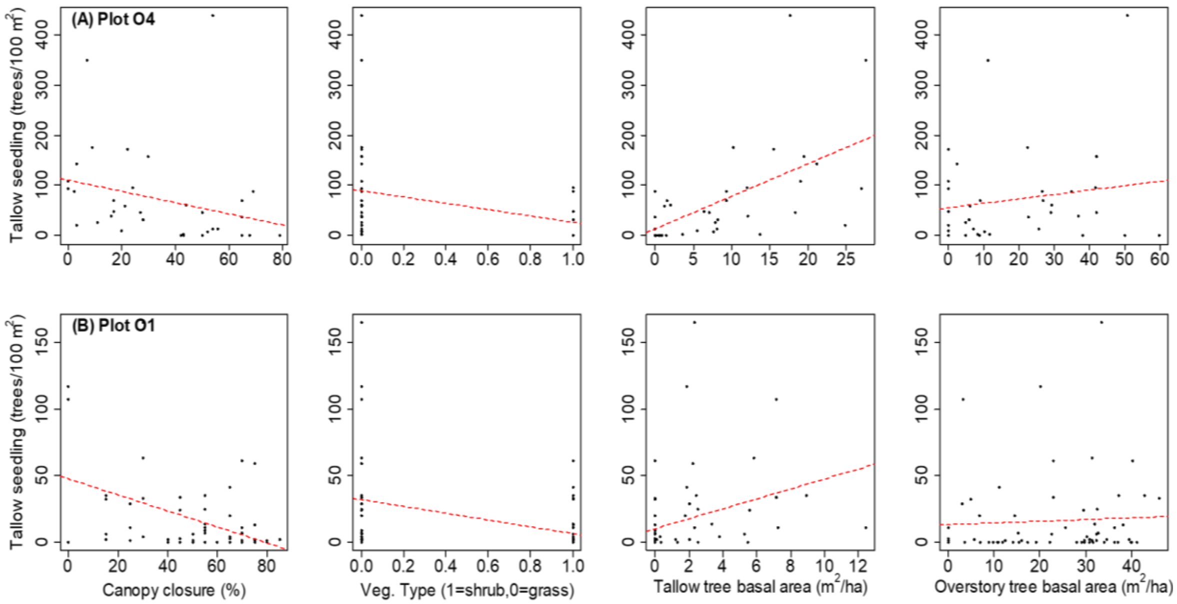

Figure 4.9 Effects of different stand conditions on the spread of Chinese tallow (*Triadica sebifera*) seedlings

A: relationships between stand conditions and tallow seedlings in plot o4; B: relationships between stand conditions and tallow seedlings in plot o1.

Table 4.2 Poisson regression results for Chinese tallow seedlings in plots o4 and o1

Plot o4	Estimate	Std. Error	Z value	P value	Z test
Intercept	2.965	0.077	38.570	< 0.001	***
Veg. types	-0.592	0.073	-8.130	< 0.001	***
Canopy closure	-0.004	0.002	-2.500	< 0.05	*
Overstory basal area	0.002	0.000	18.150	< 0.001	***
Tallow basal area	0.007	0.000	24.000	< 0.001	***
Plot o1					
Intercept	3.755	0.076	49.575	< 0.001	***
Veg. types	-1.002	0.076	-13.198	< 0.001	***
Canopy closure	-0.027	0.002	-16.378	< 0.001	***
Overstory basal area	0.002	0.000	7.819	< 0.001	***
Tallow basal area	0.008	0.001	7.870	< 0.001	***

Significant codes: '***' 0.001; '**' 0.01; '*' 0.05; '.' 0.1

4.4 Discussion

4.4.1 Mechanisms of tallow spread under the effects of site conditions in pine flatwoods

Tallow trees in plot o4 moved from the north end of the plot to the southeast where the lowland area occurred with a large overstory gap. By 2016, there was an obvious tallow cluster created inside the overstory gap of the lowland area and, after 2005, the annual increment rate of tallow trees in lowland areas exceeded the rate in upland areas (Figure 4.6A). This suggested that more tallow trees colonized lowland areas with increasing propagule pressure. By 2009, propagule pressure (i.e., seed trees/seed sources) in upland areas was still higher than in lowland areas, but the annual increment of tallow trees in lowland areas had exceeded the rate in upland areas since 2006. This indicated that propagule pressure of tallow trees had been transferred to lowland areas by that time. Results supported the probability that this transformation of propagule pressure was caused by tallow seed dispersal by water since it is one natural way to enhance dispersal (Bruce et al. 1997, Renne et al. 2000, Pile et al. 2017b). Only water dispersal could lead to a sudden increase of propagule pressure and deposition of tallow seeds within lowland areas. In plot o1, the tallow tree invaded from the south lowland (low elevation) area in 1999 and started to spread to the north high elevation area in 2001(Figure 4.2B). After 2008, a tallow tree cluster was created in the southeast lowland area by increasing propagule pressure because microtopography was characterized by a limited low elevation area. There were still some tallow trees dispersed in high elevation areas and this was attributed to another driving factor of tallow seed dispersal, birds (Bruce et al. 1997, Renne et al. 2002, Pile et al. 2017b). Only birds can resist gravity and disperse seeds to high elevation areas.

In the pine flatwoods, microtopography could affect tallow tree dispersal indirectly through controlling water movements to modify the transformation of propagule pressures of tallow trees within low elevation areas. During water dispersal, this process could also build a soil seed bank of tallow trees (Bennett et al. 2015, Henkel et al. 2016). Birds, especially species of tallow seed predators such as the red-bellied woodpecker (*Melanerpes carolinus*), northern cardinal (*Cardinalis cardinalis*), northern flicker (*Colaptes auratus*), and American robin (*Turdus migratorius*) among others, are another major factor for tallow seed dispersal within pine flatwoods because they prefer forest edges and moderately open pine flatwoods as their habitats in southeastern coastal areas (Renne et al. 2000, Renne et al. 2002, Fan 2018, Fan et al. 2018). In addition to microtopography, other contributing factors in plots o4 and o1, such as canopy gap, forest edges, and understory vegetation cover, could also affect the tallow tree distributions as results indicated (Figure 4.4, Table 1). In both plots, microtopography was the prerequisite of tallow cluster creation, providing enough tallow seeds within a limited time, and canopy gap of overstory trees was the decisive factor for creation of the tallow tree clusters because cluster size was determined by size of the canopy gap (Figures 4.2, 4.3). Tallow clusters in both plots were located in lowland areas, initiating positive spatial clustered distributions of different tallow age cohorts in lowland areas (Figure 4.3 B and D). In upland areas, because of the interaction of seed dispersal caused by water and birds, most tallow age cohorts had random spatial distribution patterns with each other with the exception of the relationship between age cohorts 2012-2013 and 2014-2015 in plot o1which were dominated by bird dispersal and small overstory gaps (Figure 4.3 A and C). The distance to forest edge had a significant negative spatial correlation with the intensity of tallow trees (Table 1), and most tallow trees clumped along the edges within a 20 m spatial scale (Figure 4.4). Forest edges and large crown overstory pines could provide appropriate snags for tallow seed-eating birds to brood and nest (Renne et al. 2000, Pile et al. 2017a, Fan 2018, Fan et al. 2018). This explains the phenomenon that tallow trees were positively associated with overstory pines in the spatial domain of plot o1 (Figure 4.4 C). The unimodal distribution of tallow tree density with overstory pine density and distance to the road seems to suggest that birds particularly favor moderate canopy openness (100-300 trees/ha) and sites near the road (e.g., < 20 m), causing these sites to be most susceptible to tallow tree invasion (Figure 4.4).

4.4.2 Colonization and establishment of tallow trees within fire regulated pine flatwoods

According to the Figure 4.5, average age of tallow trees in lowland areas was greater than that in upland areas for both plots. However, in plot o1, the result was significant supporting the idea that microtopography may also affect the age structures of tallow trees. In plot o4 the average annual increment of each age cohort (divided by fire disturbance) had a stable increasing rate and reached 450 trees/ha during 2012-2015 in lowland areas compared to 250 trees/ha in upland areas where the increasing rate did not improve until 2009 (Figure 4.6A). In plot o1, average annual increment of tallow age cohorts was also higher than in upland areas until 2012 (Figure 4.6B). Indicating, the establishment of tallow trees was affected by microtopography, propagule pressure, and prescribed fires in pine flatwoods. In plots o4 and o1, propagule pressure in lowland areas (1400 trees/ha and 700 trees/ha by 2015) was higher than in upland areas (600 trees /ha and 12 trees/ha by 2015) (Figure 4.7) with the same fire disturbances. This suggested that the survival rate of tallow trees in lowland areas was higher compared to upland areas because lowland areas were usually flooded seasonally with high soil moisture and lower understory vegetation cover (Table1, Figure 4.8) causing suppression of prescribed fire intensity within burned forest stands (Grace 1998, Hibdon 2005). This provided another explanation for differences in propagule pressure between lowland and upland areas beside the modification of seed dispersal, and also indicated tallow trees have a higher probability to colonize and establish in lowland areas of fire-regulated forest stands.

Results of fire analysis also showed that in lowland areas of plots o1 and o4, prescribed fire was able to improve the spread rate of tallow trees compared to years without a prescribed fire within a limited propagule pressure (Figure 4.7). It was possible that fire disturbances could release site resources, such as light, nutrients, and space (Lockwood et al. 2013, Pile et al. 2017a), through decreasing understory vegetative coverage and modifying overstory structures (e.g., open canopies), thereby triggering the regeneration of tallow trees within pine flatwoods. For a fire-regulated pine flatwood with a 3-4 years fire interval, it was easier for tallow trees to colonize and establish themselves (Samuels 2004, Gan et al. 2009).This is especially true when there were stable seed sources (i.e., tallow seed trees), due to a fire-caused regeneration window, however, the length of the regeneration window after burn was not documented yet. In upland areas of plots o1and o4, prescribed fires had no significant effect on the tallow increment which was different from the lowland areas. This difference was caused by the variation of fire intensity. In lowland areas, the understory fuel load (i.e., vegetation coverage) was lower than in upland areas (Figure 4.8), and hotter fires in upland areas top-killed some tallow trees, especially in plot o1 upland areas. This may explain the sudden increase of tallow trees after 2014 (Figures 4.2B, 4.6B) in the upland area of plot o1 (Figure 4.7D) because these tallow trees were resprouts of previously top-killed tallow trees and most of them may have already colonized upland areas before 2014 (Figure 4.10). Even in the same forest stand, variation of fire behavior caused by different site conditions could lead to different effects on colonization and establishment of tallow trees.

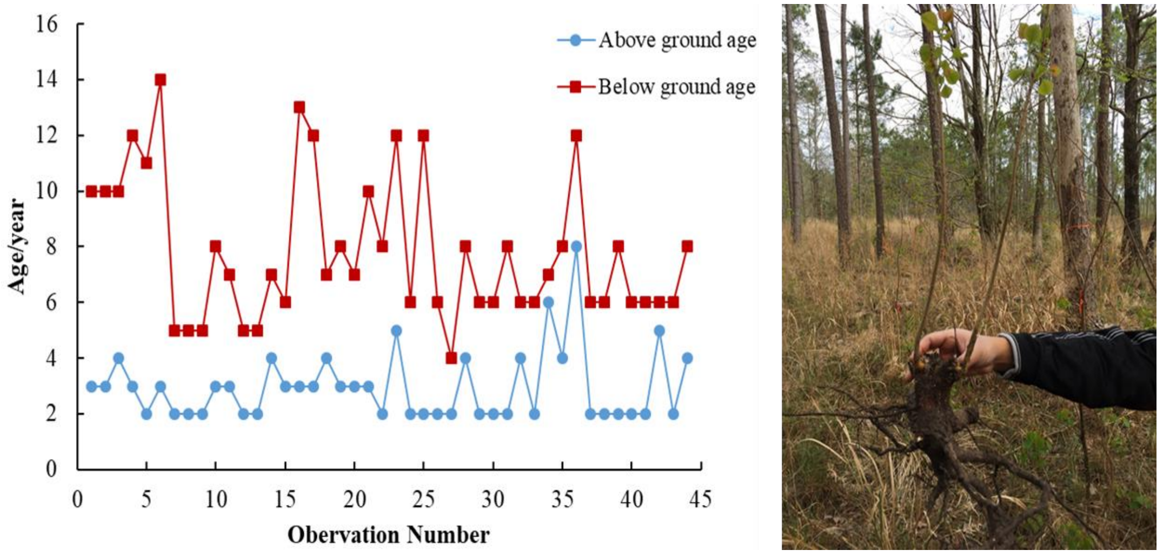

Figure 4.10 Age differences of Chinese tallow (*Triadica sebifera*) tree sprouts between above ground and below ground after prescribed fire disturbances

As shown in Figure 4.7 A and C, annual increment of tallow trees in lowland areas of plots o1 and o4 plotted as “bell” shaped curves with propagule pressure with or without fire. Although fire disturbance and propagule pressure could enhance the spread rate of tallow trees in low elevation areas, this process could not continually increase and other contributing factors could affect tallow tree colonization within pine flatwoods. This factor could be gap size in overstory trees because light and space are indispensable factors for the growth of Chinese tallow even though tallow seedlings are capable of growth in the shade (Renne 2000, Siemann and Rogers 2003, Wang et al. 2011b, Pile et al. 2017b). Compared to the overstory gap (515 m^2) in plot o4 lowland area, the overstory gap in plot o1 (135 m^2) was smaller. The limitation of environmental resources increased intraspecific competition of tallow trees with population increase causing the decline of tallow tree annual increment. In lowland areas of fire disturbed pine flatwoods, tallow trees have a higher probability to colonize and establish, and forest structures (resources limitation) could also affect the invasive process by affecting the ecosystem resistance (invasibility) (Lockwood et al. 2013, Pile et al. 2017b). In upland areas of plots o1 and o4, annual increment rates of tallow trees increased with the development of tallow propagule pressures (Figure 4.7 B and C) and there were no significant differences between burn years and non-burn years. Upland areas of pine flatwoods previously had more understory vegetation cover compared to lowland areas (Figure 4.8), and fire intensity in upland areas was higher than the lowland areas. Due to high understory vegetation coverage and fire intensity, colonization of tallow trees in upland areas of pine flatwoods faced a stronger community resistance causing a slow increment rate or top-kill after fire disturbance. The population of tallow trees in upland areas of plots o1 and o4 did not reach the carrying capacity of the environment compared to the lowland areas leading to the continuous increase. This suggests that prescribed fires could control and postpone the process of Chinese tallow tree invasion and spread under some specific circumstances in upland or even elevation areas with fine fuel loads (Smith et al. 1997, Grace et al. 2005, Pile et al. 2017c).

4.4.3 Colonization of tallow seedlings within fire-regulated pine flatwoods

Tallow seedlings (1-year seed germinated) had negative correlations with canopy closure and vegetation types in both plots o4 and o1 (Figure 4.9, Table 2). This may be due to temperature, soil moisture, and light being initial environmental factors for tallow seed germination, as tallow seedlings grow most rapidly in full sun (Jones and McLeod 1989, 1990). Understory vegetation, such as shrubs, could compete with tallow seedlings, and thick shrub coverage could also prevent tallow seeds from germinating, especially on the sites without prescribed fires (Fan 2018, Fan et al. 2018). In addition to canopy closure and understory vegetation types, there were positive correlations between tallow seedlings, basal area of mature tallow trees, and overstory pine trees (propagule pressure). High basal area of tallow trees was related to more, large seed trees. High overstory tree basal area was caused by large pine trees, providing appropriate snags for tallow seed eating birds (Renne et al. 2002, Fan 2018, Fan et al. 2018) to create tallow seed banks around large overstory pine trees. Therefore, in pine flatwoods, understory vegetation coverage could prevent the regeneration of tallow seedlings, especially shrub coverage. Canopy gaps of overstory trees are able to improve the colonization of tallow seedlings. This suggested that fire disturbances could cause new regeneration of tallow trees by destroying understory vegetation cover. Abundance of tallow seedlings is also affected by the basal area of mature tallow trees and pine trees due to the increase of propagule pressures.

4.5 Conclusions

4.5.1 Distribution patterns and colonization of Chinese tallow trees

This research examined the spatiotemporal spread pattern and colonization of Chinese tallow trees in fire-regulated pine flatwoods of the MSCNWR. These forest stands are managed intensively using prescribed fire to restore declining native habitats-pine savannah and coastal prairies for the endangered Mississippi Sandhill Crane. Originating from adjacent areas, invasive tallow trees were introduced into pine flatwoods of the MSCNWR around 1998 by accidental discharge of wastewater (Jackson County, Mississippi wastewater pond) and/or tallow seed-eating birds, and colonized and spread within the pine forests. The invasive process and spread of Chinese tallow within a pine flatwood were mainly driven by propagule pressures (Lockwood et al. 2005, Lockwood et al. 2013, Fan 2018) and native community traits (i.e., site/habitat properties) (Pyšek and Richardson 2010, Pile et al. 2017b, Fan 2018), including biotic and abiotic factors (e.g., vegetation cover, overstory structures, microtopography, soil moisture, and disturbance). Tallow trees usually distribute themselves in clustered patterns in low elevation areas (lowland) of pine flatwoods compared to high elevation areas (upland) because of the microtopography modifications on seed dispersal and fire behavior. Microtopography can change seed dispersal through controlling water current. Low elevation areas in forest stands are usually seasonally flooded areas, especially in the southeastern coastal area, and have high soil moisture which could also reduce fire intensity and increase the survival rate of tallow trees. In addition to microtopography, tallow clustered distribution is also related to gap size in overstory trees with a large overstory gap being able to create a bigger tallow cluster within pine flatwoods. Forest edges, such as roads and fire breaks, and overstory pine density are correlated with tallow distribution at the stand level, with most tallow trees clumping along edges (< 20 m from the edge) and having positive spatial correlation with moderate overstory pine density (100 trees/ha- 300 trees/ha) due to the seed dispersal of seed-eating birds (Renne 2000, 2002, Fan 2018).

Based on field investigation, tallow trees were more likely to invade pine flatwoods compared to open grassland and savannah in the MSCNWR (Renne et al. 2000, Fan et al. 2018). Once Chinese tallow established in a pine flatwood, understory coverage, especially shrub coverage, will be reduced (Grace 1998, Grace et al. 2005). In addition, the resistance of the native forest community will also be destroyed (Lockwood et al. 2013) increasing invasibility of pine flatwoods in southeastern coastal regions (Fan 2018, Fan et al. 2018). The reduction of understory vegetation cover could also result in fire suppression in these invaded pine flatwoods where prescribed fire has been used as a favorite tool for restoration of native habitats (Reilly et al. 2016, Huffman et al. 2017, Waldrop et al. 2018).

Colonization and establishment of tallow trees in pine flatwoods is primarily determined by the propagule pressure, and the increase of propagule pressure could increase the probability of establishment success (Drake and Lodge 2006, Lockwood et al. 2013, Pile et al. 2017a, Fan 2018). In pine flatwoods of the MSCNWR, microtopography could increase propagule pressure indirectly by changing the direction of water dispersal of tallow seeds and suppressing fire intensity because of the reduction of understory vegetation coverage and high soil moisture in low elevation area. Results support the contention that in a fire regulated pine flatwood with a 3-4 year fire interval, Chinese tallow is more likely to colonize and establish in the low elevation areas or seasonally flooded areas, especially when there are stable seed sources (i.e., seed bank/seed trees) as compared to relatively high elevation or dry areas. Spread rates of tallow trees in lowland areas show a logistic trend (Drake and Kramer 2011) and have a rapid spread rate at an early stage of colonization due to overstory gap (environmental resources) and fire disturbance (regeneration promotion). However, in high elevation areas, spread rate of tallow trees implies a weak Allee effect (Courchamp et al. 2008, Drake and Kramer 2011, Garnier et al. 2012, Lockwood et al. 2013) with a slow spread rate at the early stage of colonization. The population of tallow trees in upland areas does not reach a sufficient population size (Keitt et al. 2001, Lockwood et al. 2013). This indicated that prescribed fires in high elevation areas of pine flatwoods are able to restrain the spread of tallow trees, especially at an early stage of colonization. A low population with a strong Allee effect could lead to extinction of the population (Drake and Kramer 2011). Even though the appropriate fire interval for tallow tree control is not clear yet, Results suggest that in high elevation areas of pine flatwoods, a regulated fire interval less than 3 years (< 3 years) could control tallow tree invasion efficiently (Harcomb 1989, Grace 1998, Pile et al. 2017c). Use of fire can result in resprouts of tallow trees after burns (Grace 1998, Miller 2003, Pile et al. 2017b). This was observed in upland areas of plot o1 and resulted in a sudden increase of tallow trees. However, sprouting capacity after repeated top kill has not been studied in Chinese tallow (Pile et al. 2017c). In this study, a 3-year (year 2014) tallow resprout had a 14-year old root (year 2003), which means this tallow tree had experienced four prescribed fires before being felled. This indicates that the mechanisms of tallow sprouting capacity and physiological characteristics under frequent fires need to be studied in the future.

In the pine flatwoods of the MSCNWR, once tallow trees are established, regeneration of tallow trees is positively related to basal area of tallow trees, which means the abundance of tallow seedlings is related to large tallow seed trees but not related to tallow density since high tallow density could have negative effects on tallow seedlings (Nijjer et al. 2007). Basal area of overstory pine trees also has a positive correlation with tallow seedlings due to the tallow seed bank created by seed-eating birds around the crown of large pine trees (Fan 2018). However, shrub coverage of the understory and canopy closure of the overstory could suppress germination of tallow seeds (Siemann and Rogers 2003, Fan 2018, Fan et al. 2018). Maintaining a high understory shrub coverage and healthy overstory structure (i.e., high canopy closure) could control tallow seedlings effectively in pine flatwoods.

4.5.2 Management and control of Chinese tallow trees in pine flatwoods

In conclusion, invasion of Chinese tallow in pine flatwoods of the southeastern coastal area of the United States is a comprehensive process due to the complexity of invasion ecology which includes biology, ecology, physiology, climatology, geography and so on (Lockwood et al. 2013). According to previous research (Jubinsky and Anderson1996, Grace 1998, DiTomaso et al. 2006, Pile et al. 2017b), there is no universal prescription for Chinese tallow control in the southeastern United States because each forest stand or community has its unique characteristics, and it is difficult to manage a comprehensive invasion process using a single option (Pile et al. 2017c). Results suggest that we could control and manage Chinese tallow invasion by using a "precision strike strategy" (PSS) combined with a specific treatment (e.g., mechanical treatment, herbicides, and prescribed fire) based on site conditions and community traits of the pine flatwoods. Pile's (2017c) research shows that comprehensive treatments, including mastication, herbicides, and prescribed fire are more effective in reducing tallow density within a forest stand but the expense of applying the comprehensive treatments to different large forest stands is a concern. Most research (71%) of invasive plant control do not evaluate the cost and limitations of spatiotemporal scope (Kettenring and Adams 2011). Therefore, PSS should be considered for management and control of Chinese tallow invasion in pine flatwoods to minimize costs (ecological and economic). This could also maximize benefits through utilizing the resistance of native forest ecosystems (e.g., competition of native species), and subsequently applying control treatments, because the long-term control treatments could also have deleterious effects on native ecosystems (Myers 2000, Kettenring and Adams 2011).

By using PSS, we first need to classify pine flatwoods as tallow invaded or non-invaded. For non-invaded, especially those with high potential for invasion with an overstory density 100-300 trees/ha and low understory shrub coverage (< 50%), prevention is the major concern. Within a 250 m radius along forest edges, all tallow seed trees should be removed according to the Fan et al (2018). This would eliminate propagule pressure of tallow trees. Moreover, a 20 m wide shrub covered buffer should be maintained from the edge to the interior stand to prevent Chinese tallow invasion from the edges (Fan 2018). It is necessary to decease the frequency and intensity of disturbances within non-invaded pine flatwoods to maintain the original understory vegetation coverage, especially for shrub coverage (Fan 2018, Fan et al. 2018), and reduce the risk of Chinese tallow invasion (Ewel and Putz 2004, Lockwood et al. 2013, Paudel and Battaglia 2015, Pile et al. 2017a).

For tallow invaded pine stands, we could also divide them into two types, those with tallow seed trees and those without tallow seed trees. For stands without tallow seed trees (early stage of colonization) and with even elevation, frequent fires (≤ 2 yrs) during growing season (Grace 1998, Grace et al. 2005, Pile et al. 2017c) could suppress the spread of tallow trees, especially for young or small diameter tallow saplings (Pile et al. 2017c) by enhancing the Allee effect (Drake and Kramer 2011). If there is a low elevation area, or seasonally flooded area inside of the pine stand causing fire suppression, herbicides and mechanical treatments should be applied after prescribed fires. Maintaining understory native shrub coverage in low elevation or seasonally flooded areas after treatments is also important to control Chinese tallow invasion

(Fan 2018, Fan et al. 2018). When tallow invaded stands have tallow seed trees (i.e., stable seed sources), especially stands with overstory gaps and seasonally flooded areas, prescribed fires could increase the probability of colonization success. For areas with established tallow trees, seed trees within the stand and a 250 m radius range from the stand should be removed by using mechanical or herbicide treatments to reduce propagule pressure (Lockwood et al. 2013, Pile et al. 2017a, Fan 2018). After removing tallow seed trees, regulated prescribed fires with two-year fire intervals could control tallow saplings and seedlings (seed bank germinated) effectively at relatively high elevation areas. For seasonally flooded areas and overstory gaps, restoration of understory shrub coverage is important to control recruitment of Chinese tallow trees. Therefore, the PSS should be an effective idea to control Chinese tallow invasions under specific conditions in pine flatwoods, while also providing a feasible and economic method for managing Chinese tallow invasion of pine flatwoods in the southeastern coastal area of the United States. In the future, further studies should focus on Chinese tallow invasion in bottomland hardwoods to determine if Chinese tallow trees have the same invasive mechanisms in bottomland hardwoods as in the pine flatwoods. Meanwhile, effects of prescribed fires on resprout ability and below ground growth of tallow trees should be studied systematically to fully understand the mechanism of Chinese tallow invasion under fire disturbances.

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CHAPTER V

CONCLUSION SUMMARY

5.1 Chinese tallow invasion in coastal area of the southeastern United States

In southeastern coastal area of the United States, Chinese tallow initially started to spread from southern Texas and southeastern South Carolina where it was originally introduced. However, the average presence probability of Chinese tallow is 50% in southern Texas but in southeastern South Carolina, it is 30%. According to the presence probability of Chinese tallow, the coastal area of the southeastern United States was classified into four sub-regions: Inland high elevation low propagule pressure, coastal low elevation low propagule pressure, coastal high elevation medium propagule pressure, and coastal low elevation high propagule pressure. Meanwhile, these invasive sub-regions also stand for different invasive stages of Chinese tallow.

In southeastern coastal area, distribution and spread of Chinese tallow is affected by predisposing and inciting factors, such as landscape features (i.e., elevation, latitude, longitude, and road and river distribution), propagule pressure, forest landownership, and natural disturbances (e.g., hurricane and storms). In inland and coastal areas with low propagule pressure, hurricane/storm disturbances could accelerate the spread of Chinese tallow at a large spatial scale but for costal high propagule pressure areas, hurricane effects are now not significant. Propagule pressure of Chinese tallow is the most important factor that drives the spread of Chinese tallow in the regional area. Distribution of Chinese tallow is also significantly affected by elevation and presence probability decreases dramatically when elevation increases in this area. High propagule pressure areas of Chinese tallow are located in the region where elevation is lower than 50 m. In low elevation areas, nonindustrial private forests have higher spread rates than corporate owned and public forests compared to high elevation areas. Compared to other forest types, hurricane/storm frequently disturbed bottomland hardwood forests (i.e., oak-hickory, oak-gum-cypress, and elm ash cottonwood) owned by nonindustrial private forest landowners have higher degree of invasion. Even though, hurricanes or storms could enhance the spread of Chinese tallow, they could also reduce the coverage of Chinese tallow and other native species when the speed of a hurricane/storm is over 100 km/h. High intensity and frequent disturbances of a hurricane/storm in coastal areas may change recovery direction of invaded native forests to Chinese tallow dominant direction.

In coastal areas of the southeastern United States, management and mitigation of Chinese tallow invasion should focus on areas with high degree of invasion and make specific prescriptions based on particular conditions of Chinese tallow invasion. For areas with low propagule pressures, conservation and restoration of native forests after disturbances to increase resistances of native ecosystems should be a priority. For areas that have been in late invasive stages, mechanical and chemical treatments should be used to remove tallow seed trees and reduce the propagule pressure first, and subsequently combined with prescribed fire to prevent the colonization of tallow seedlings/saplings. Edges of forest habitats, such as roads and water bodies, also need to be managed because they could provide pathways for Chinese tallow dispersal. Chinese tallow invasion is a cumulative and comprehensive process that could not be simulated by a simple linear process. Therefore, management and control of Chinese tallow should be operated under specific invasive stages and circumstances, especially under limited spatial scales such as landscape and stand levels, because a smaller spatial scale could provide a more particular management prescription for Chinese tallow invasion.

5.2 Chinese tallow invasion in a fire regulated landscape area

In a fire regulated landscape area of the pine flatwood, Chinese tallow is originally introduced into the landscape by birds or water current from surrounding tallow seed sources. Subsequently, tallow trees will disperse along edges (e.g., roads and firebreaks) of a landscape with a clustered pattern from areas where there is high propagule pressures. Spatial distribution and abundance of seed trees (propagule pressure) are the predominating determinant of Chinese tallow spread rate. Results indicate that the efficient dispersal distance of tallow seeds in the landscape area is 250-300 m and tallow clusters are positively correlated within a 200-600 m spatial scale. In the landscape area, prescribed fires with a mean interval around three years could increase risk of Chinese tallow spread into habitat interiors, especially for areas with a mean distance of 20 m from habitat edges, compared to infrequent fires that mean fire intervals are greater than four years. Meanwhile, the invasion risk of tallow will decrease when the distance to the seed trees and shrub coverage increases. The invasion risk of tallow will increase along habitat edges when the time since last fire increases, as long as seed trees are present in surrounding areas. However, there would be decreases if there are no seed trees within a 300m spatial scale. Furthermore, for low propagule pressure areas, colonization of tallow seedlings will increase when there are high basal area overstory trees that could provide canopy for birds' perching and nesting.

The management of Chinese tallow invasion in a southern coastal forest landscape is a comprehensive process that many associated predisposing and inciting factors should be considered. For instance, treatments of prescribed fires should be used carefully, especially when determining fire intervals. At the landscape level, to reduce tallow spread from edge to interior, it is recommended that along the edges of roads and firebreaks, all tallow seed trees should be removed within a 250-300 m radius range and subsequently a 20-50 m wide native shrub covered buffer should be established from the forest/savanna edge to its interior to increase the resistance of native forest ecosystems. Furthermore, for highly susceptible habitat (< 50 m from invaded roads and fire breaks), fire treatment and timber management should be carefully designed to create more resistant vegetation structure (i.e., high woody shrub layers and dense overstory) to curb tallow invasion into the interior habitat (pine savanna) in coastal areas of the southeastern United States. In the future, the optimal fire intervals of prescribed fire, effects of fire on tallow seeds visibility, and regeneration window of Chinese tallow after burning, should be studied systematically because these questions are related to the management of tallow invasion directly.

5.3 Chinese tallow invasion in fire regulated forest stands

In fire regulated pine flatwood stands, Chinese tallow was introduced into stands by accidental discharges of wastewater and tallow seed-eating birds, which is similar to Chinese tallow invasion at the landscape level. In native forest stands, distribution of tallow trees are mainly affected by propagule pressure and other associated predisposing and inciting factors, such as microtopography, understory vegetation types and coverage, overstory tree density and gap, and fire disturbances. At the stand level, tallow trees usually distribute in clustered patterns within the areas having low elevation and overstory gaps. Microtopography could affect the distribution of tallow trees through changing the movement of tallow seeds and fire suppression. Results indicate that prescribed fire could increase risk of tallow invasion, especially in the low elevation areas, compared to high elevation areas in forest stands. In high elevation areas, prescribed fires are able to mitigate colonization and establishment of tallow trees due to the Allee effect. However, effects of prescribed fire on resprout abilities of Chinese tallow are not clear yet because many tallow trees could sprout after a top kill that causes age differences between above and below ground growth of tallow trees. In addition to fire, edges of forest stands such as roads and firebreaks could also affect the distribution of tallow trees, with most tallow trees clumping in the area that is 20 m from forest edges. Tallow trees have positive spatial correlation with moderate overstory density (100 trees/ha -300 trees/ha) and negative spatial correlation with shrub coverage, especially for tallow seedlings. Regeneration of Chinese tallow is related to basal area of tallow and overstory trees, understory shrub coverage, and canopy closure of overstory.

The invasion of Chinese tallow is a complicated process and there is no universal prescription to control it. As a forest stand is the basic level for forest management, it is suggested using a “precision strike strategy” (PSS) that is combined with a specific treatment (i.e., mechanical treatment, herbicides, and prescribed fire) based on site conditions and community traits of pine flatwoods, to minimize costs (ecological and economic) and maximize benefits through utilizing the resistance of native forest ecosystems. For instance, in tallow invaded forest stands, tallow seed trees could be removed from forest stands and surrounding areas within a 300 m radius range. Subsequently, for high elevation areas, the short-interval (≤ 2 years) prescribed fire could be applied to control colonization of tallow seedlings and saplings through enhancing Allee effect. Meanwhile, understory shrub coverage should be restored to increase resistance of forest stands. In low elevation areas, mechanical and chemical methods should be used to remove all tallow trees because of fire suppression. Restoration of understory and overstory vegetation is applied immediately after mechanical and chemical treatments. In the future, further studies need to focus on Chinese tallow invasion in the bottomland hardwoods. For fire-regulated forest stands, it is necessary to figure out the effects of prescribed fires on resprout ability and below growth of Chinese tallow trying to fully understand the mechanism of Chinese tallow invasion.