Impacts of fire on Chinese tallow (*Triadica sebifera*) invasion in slash-longleaf pine flatwoods and savannas in the Gulf of Mexico coastal region, United States

by

Nannan Cheng

A thesis submitted to the Graduate Faculty of
Auburn University
in partial fulfillment of the
requirements for the Degree of
Master of Forestry

Auburn, Alabama
December 12, 2020

Key words: Chinese tallow, invasion, fire, flatwoods, savannas, coastal region

Approved by

Zhaofei Fan, Chair, Associate professor, Forestry
Robert A. Gitzen, Associate professor, Wildlife Biology and Conservation
Nancy J. Loewenstein, Extension Specialist, Forestry

Abstract

The coastal area of the southeastern United States is historically wet pine savannas, prairie, and hardwoods. 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 serious invasive tree species in the southern coastal states, including Alabama, Mississippi, Louisiana, and Texas. How landscape/stand features affect Chinese tallow invasion under fire disturbances is an important consideration for the control and management of Chinese tallow invasion and restoration of native ecosystems. In this research, study plots were established in the Mississippi Sandhill Crane National Wildlife Refuge (MSCNWR) to evaluate Chinese tallow invasion at the landscape level, and plots were established in Grand Bay National Wildlife Refuge (GBNWR) to analyze Chinese tallow invasion at the stand level. At the landscape scale, under frequent and low-intensity fire pine flatwoods are more susceptible to tallow invasion than pine savannas. There was higher invasion probability and greater prevalence of seedlings and saplings encroaching in understory. Sites closer to roads and seed trees had a higher invasion probability and a greater number of Chinese tallow, suggesting that landscape fragmentation could facilitate the spread of Chinese tallow across the entire landscape. At the stand scale, invasion probability of Chinese tallow was related to distance to road and microtopography, with a higher abundance of large tallow in quadrats that were closer to a road and seed trees and at lower elevation. The abundance of tallow saplings and seedlings was highest in quadrats with greater coverage of grass. Tallow sapling and seedling abundance increased significantly after a prescribed burn. There were more tallow seedlings in pine-dominated quadrats than that in hardwood-dominated quadrats after prescribed fire, and this may

suggest that overstory pine can facilitate tallow invasion after burn while other risk factors are held unchanged or the same.

Acknowledgments

First and foremost, I would like to express my appreciation to my major professor and committee members, Dr. Zhaofei Fan, Dr. Nancy Loewenstein, and Dr. Robert Gitzen, because you helped me finish my research work. Thanks to my major professor, Dr. Fan. I really appreciate your help with my field work, data analysis, and thesis writing. Thanks to Dr. Gitzen and Dr. Loewenstein, they have helped me a lot for my thesis revision. I would like to extend my appreciation to the School of Forestry and Wildlife Sciences of Auburn University for its support of my research. I would also thank my course professors: Dr. Edward Loewenstein, Dr. Graeme Lockaby, Dr. Lori Eckhardt, Dr. John Kush, Dr. Nedret Billor, from whom I learned much professional knowledge and research methodologies. I also thank Miss Audrey Grindle, who helped me a lot during my past two years' work. I appreciate the support of the Mississippi Sandhill Crane National Wildlife Refuge and Grand Bay National Wildlife Refuge for my fieldwork. I also thank all my teachers, friends, and colleagues in my life.

Table of Contents

Abstract ii

Acknowledgments iv

List of Tables vii

List of Figures viii

Chapter I: Introduction 1

1.1 Research background 1

1.2 Literature review 3

1.2.1 Native ecosystems dominated by longleaf and slash pine in the Southeastern United States 3

1.2.2 Ecosystems invasibility 4

1.2.3 Chinese tallow invasion under fire 6

1.3 Objectives 8

1.4 References 10

Chapter II: Invasibility of coastal ecosystems to Chinese tallow tree (*Triadica sebifera*) under fire disturbances: mechanisms and key factors at the landscape level 15

2.1 Introduction 15

2.2 Methods 18

2.2.1 Research sites 18

2.2.2 Chinese tallow invasion and ecosystems invasibility: the mechanism and associated factors 20

2.2.3 Data collection 23

2.2.4 Data analysis and modeling 24
2.3 Results 26
2.3.1 Effects of prescribed fire, landscape structure and propagule on Chinese tallow invasion 26
2.3.2 The change of ecosystems invasibility with Chinese tallow invasion stages of Chinese tallow 32
2.4 Discussion 34
2.5 Conclusion 37
2.6 References 39
Chapter III: Invasion of Chinese tallow (*Triadica sebifera*) in a slash flatwood in southern Mississippi, United States: mechanisms and key factors at microscales 44
3.1 Introduction 44
3.2 Methodologies 46
3.2.1 Research sites 46
3.2.2 Data collection 47
3.2.3 Data analysis and modeling 49
3.3 Results 50
3.3.1 Effects of predisposing site and stand factors on tallow invasion 50
3.3.2 Post-fire changes of tallow saplings and seedlings by site factors 57
3.4 Discussion 62
3.5 Conclusion 64
3.6 References 66
Chapter IV: Summary 70

List of Tables

Table 2.1 Regression coefficients of binary (logistic) model of whether or not a site had been invaded by tallow (n=55 sites). 28

Table 2.2 Regression coefficients of the count (log-linear) models to predict the invasion degree of Chinese tallow by size/age class (n= 27 sites, 2018). 29

List of Figures

Figure 2.1 Distribution of study plots within the Mississippi Sandhill Crane National Wildlife Refuge 20

Figure 2.2 The mechanistic modeling framework of Chinese tallow invasion and impact on ecosystems functions and services at the ecosystem and landscape level 22

Figure 2.3 Invasion probability (A) and degree of invasion (B) of Chinese tallow by size/age classes between pine flatwoods and pine savannas by 2018. 27

Figure 2.4 Abundance of tallow seedlings by significant factors identified by the count model among the 27 tallow-invaded plots.. 30

Figure 2.5 Abundance of tallow saplings by significant factors identified by the count model among the 27 tallow-invaded plots.. 31

Figure 2.6 Abundance of large tallow trees by significant factors identified by the count model among the 27 tallow-invaded plots. 31

Figure 2.7 The scatterplot and simple linear regression trend line of the density of seedlings (A), saplings (C) and large trees (E) between tallow and pine in 2018, and the change in density of seedlings (B), saplings (D) and large trees (F) of tallow and pine between 2015 and 2018 in pine flatwood and pine savanna.. 33

Figure 3.1 Illustration of subplots of the 0.86-ha plot and 281 30-m^2 quadrats to collect field data 48

Figure 3.2 The smoothed probability density function (A) and the scatterplots (B-D) of Chinese tallow by size classes showing the typical linear trends.. 51

Figure 3.3 Changes in the invasion degree (count) of Chinese tallow by size classes with site and stand factors showing the typical linear trends. 54

Figure 3.4 The presence probability (A) and invasion degree CART models (B-D) for tallow by size class (B: large tallow; C: tallow sapling; D: tallow seedling). 56

Figure 3.5 Changes of Chinese tallow seedlings and saplings by vegetation cover types (CG=cogongrass, LC=litter covered, NG=native grass, PS=pine sapling, and SB=native shrub) before (2018) and after (2019) the prescribed burn. 58

Figure 3.6 Recovery of understory vegetation structures after burn in hardwood and pine plots (A-D hardwood plot; E-H pine flatwood plot).. 60

CHAPTER I

Introduction

1.1 Research background

The Gulf Coastal Plain of the United States was historically dominated by longleaf (*Pinus palustris Mill.*)-slash pine (*Pinus elliottii*) flatwoods and savannas characterized by high species diversity in the understory maintained by frequent, low intensity wildfires. The longleaf-slash pine flatwoods and savannas occupied more than 30 million ha before European settlement (Van Lear et al. 2005). Due to various reasons, including fire suppression, climate change, and land-use change, the longleaf-slash pine ecosystems have been reduced to less than 5% of the original occupied area (Van Lear et al. 2005). During recent centuries, biological invasion is another important factor that influences natural communities in southeastern United States (Bruce et al. 1997). Moreover, biological invasion has become an increasingly serious threat to native ecosystems because it has affected biodiversity, ecosystem structure, wildlife survival, and ecosystem dynamics and services (Duerr and Miller 2005, Gan et al. 2009). As a result, a growing number of ecologists and policymakers are concerned with how to restore native ecosystems following biological invasion (Bruce et al. 1997, Fan 2018, Gan et al. 2009, Tian et al. 2017, Pile et al. 2017, Yang et al. 2019).

Exotic invasive species may threaten the sustainability of native ecosystems by altering their compositions, structures, functions, resource productivity, and resilience, and may be difficult and expensive to manage and control invasive species (Webster et al. 2006). Quantifying biological invasion patterns and associated factors related to invasibility of given ecosystems is important for effective management and control of invasive species as well as the restoration of native plants and maintaining ecosystems productivity (Richardson and Pyšek 2006). Invasibility is the susceptibility of the recipient ecosystems to invasive species, which is an intrinsic property. It is a reflection of the interactions of multiple processes and factors, and an emergent property of a community that is the outcome of several factors, such as climate, disturbances, and competition between resident species and invasive species (Lonsdale 1999, Davis et al. 2000, Gunderson and Holling 2001). Divergent (positive or negative) relationships between biodiversity and biological invasion were observed at both small and large scales (Tilman 1997, Maron and Marler 2007). As a result, understanding how the abundance and age structures of invasive species affect invasibility, how stand factors affect invasion, and how invasion respond to disturbances at different scales will help restore native ecosystems and control invasive species (Richardson and Pyšek 2006).

Fire is a significant driver of southeastern US coastal ecosystems dynamics (Pflugmacher et al. 2012), a modifier of species composition and stand structure, and a determinant of fluxes of water, energy, and nutrients (Cohen et al. 2016). Many coastal forest ecosystems including longleaf-slash pine forests and savannas are fire-dependent (Mutch 1970, Croker 1976, Platt et al. 1999, Gilliam 1994, Grace et al. 2005). Fire was used to manage ecosystems since prehistoric times and has been influenced by humans for many years in the southeastern United States (DiTomason et al. 2006, Pyne and Vale 2003). Currently, prescribed fire is widely used in this region for forest management, including succession management, fuel management, native flora and fauna promotion, and prevention of invasive species (Grace et al. 2005). However, although prescribed fire has been used as a tool to control late-season annual broadleaf and grass species in the Southeast, it can also create ideal opportunities for invasions (Grace 1998. Mandle et al. 2011).

Chinese tallow tree (*Tricdica sebifera (L.) Small*) has become a major invasive species in the forests of the Gulf Coastal Plain, occupying 185,000 ha by early 2000s (Hunt 1947, Grace 1998, Renne et al. 2002, Gan et al. 2009, Oswalt 2010, Tan 2011, Fan et al. 2018). The advantageous life-history characteristics of Chinese tallow, such as rapid growth rate, strong resprout ability, early seed-bearing age, and resource niche after disturbances have enabled Chinese tallow to rapidly colonize, establish and spread in this region (Yang 2019, Sui 2015). It is often difficult and expensive to control Chinese tallow invasion because of its advantageous characteristics that change with the invasion/developmental stages (e.g., introduction – seeds remaining viable for at least several years, colonization – shade tolerance and rapid growth rate, establishment – strong stump and root resprout ability, and spread – multiple seed dispersal vectors including water current, birds, and humans) (Blackburn et al. 2011, Lockwood et al 2013, Pile et al. 2017, Yang 2019). Understanding how landscape/stand factors affect tallow invasion could help landowners and policy makers prescribe more effective treatments and management activities to control invasion at different stages.

1.2 Literature review

1.2.1 Native ecosystems dominated by longleaf and slash pine in the Southeastern United States

Longleaf pine ecosystems are native to nine states of the southeastern region of the United States. Across this region, longleaf pine dominated about 23 million ha and appeared in another 14 million ha in mixed stands from Virginia to Texas at the time of European settlement (Frost 1993, Brockway et al. 2005). Longleaf pine ecosystems are able to adapt to a variety of site conditions, including wet flatwoods and savannas along the Coastal Plain (Brockway et al. 2005). However, due to factors such as land-use change and long-term exclusion of fire, 97% of these ecosystems has been lost. With only 1.2 million ha remaining today (Outcalt and Sheffield 1996, U.S. Fish and Wildlife Services 2003), it has been ranked as the third most endangered ecosystems in the United States (Noss et al. 1995). Historically, frequent fire was an essential ecological process over the southeastern coastal area, shaping the vast longleaf pine-grassland ecosystems (Van Lear et al. 2005). It drove the evolution and distribution of longleaf pine dominated forest types in the Southeastern area in United States (Waldrop et al. 1992). Besides longleaf pine, slash pine and loblolly pine (*Pinus taeda L.*) are also important dormant species in the Gulf Coastal Plain. Slash pine as the primary tree of wet flatwoods should be protected from fire until the sapling stage. Loblolly pine has become the dominant pine forest in some Coastal areas due logging, land conversion, and fire exclusion (Komarek et al. 1974). Within pine flatwoods and savannas communities, prescribed fire has been regarded as a primary tool for restoring coastal longleaf-slash pine ecosystems and can contribute to the control of invasive species such as Chinese tallow tree and cogongrass (*Imperata cylindrica* (*L.*)) in the Gulf Coastal Plain (Grace et al. 2005).

1.2.2 Ecosystems invasibility

In the context of invasion ecology, invasibility, as an emergent community property, represents the susceptibility of a community or region to invasion (Guo et al. 2015) and can be measured by the potential of site being invaded by non-native species. Invasibility is affected by many factors such as species diversity, resources, disturbances, and community properties (Lonsdale 1999, Davis et al. 2000, Pearson et al. 2018). Invasibility has been a focus of ecosystems management in researches and studies of complex interactions between native and invasive species (Guo and Symstad 2008). Resident plants, including natives and established non-native species, can affect the invasibility of communities by facilitative and inhibitory interactions with invaders (Holle 2005). The invasibility of a community includes properties of the community that affect non-native species' survival (Lonsdale. 1999). However, the degree of invasion (DI) is easier to quantify than invasibility and therefore is more frequently used. Degree of invasion (DI), which is an outcome of interactions between intrinsic and extrinsic factors, measures how much the extent of a community that has already been invaded by non-native species (Catford et al. 2009, Gurevitch et al. 2011, Guo et al. 2015). Extrinsic factors include propagule pressure, disturbance, and time since invasion (Lockwood et al. 2009, Clark and Johnston 2011, Miller et al. 2014). Guo et al (2015) proposed a way to measure DI through observed exotic and total (native and non-native) richness and biomass. It is essential to understand that time and space plays different roles in the measurement of invasibility and DI. Scales, including temporal and spatial scales, could influence relationships between invasibility and landscape factors (Maron and Marler, 2007).

Communities with similar invasibility could have a different degrees of invasion (DI), although invasibility and DI often positively correlated with each other (Guo et al. 2015). Communities with lower invasibility cannot have higher DI, but communities with higher invasibility could correspond to either lower or higher DI because of impacts of external factors and different invasion stages (Guo et al. 2015, Guo and Symstad 2008). However, an increase of DI could increase competition and reduce invasibility (or susceptibility) over both the short and long term until the next disturbance. Invasibility is an intrinsic property of a community and is difficult to measure. However, the degree of invasion is an outcome of non-native species invasion and can be measured easily. This makes DI a better metric for studying existing invasive situations and ecosystems resistance (Guo and Symstad 2008, Guo et al. 2015).

The invasion of non-native species combined with increasing large-scale human activities and climate change are altering environmental conditions, ecosystems structure, and community structure (Ellis 2011, Williams and Jackson 2007, Martinuzzi et al. 2015). Invasive species that alter ecosystems functions have significant impacts on native ecosystems (Hooper et al. 2005), such as altering local abiotic conditions, species composition, and interactions between species. Non-native species invasion into a native ecosystem is a spatial-temporal process, and it can be divided into four stages: introduction, colonization, establishment, and landscape spread (Vermeij 1996, Blackburn et al. 2011, Lockwood et al. 2013). Impacts of biological invasion on ecosystems invasibility vary with spatial-temporal scales and invasion/developmental stages of invasive species (Pile et al. 2017, Yang 2019). As a result, studying how invasion affect invasibility on different levels based on invasion stages of the exotic species is necessary.

1.2.3 Chinese tallow invasion under fire

Chinese tallow tree is one of the most pervasive non-native species in Southeastern forests (Gan et al. 2009, Yang 2019). Chinese tallow tree is native to areas of Eastern Asia at similar latitudes as the southeastern United States. It has invaded diverse ecosystems including coastal prairie and forests since it was introduced in the late 1700s (Jones and Sharitz 1990, Renne et al. 2002). The population of Chinese tallow tree has increased dramatically over the past few decades. Forest Inventory Analysis data shows that it now occupies 185,000 ha of southern forests, being the most abundant at forest edges and forest openings of the southeastern Coastal Plain, and Mississippi River flood plain (Pile et al. 2017). The Chinese tallow population has increased by 500% and 174% from 1992 to 2005 in Louisiana and Texas, respectively, making it one of the most common trees in these areas (Oswalt 2010). With its advantageous biological characteristics and life-history traits, such as rapid growth rate, adaptability to various conditions, and quick nutrient uptake, Chinese tallow is expected to expand up to hundreds of miles northward and invade an array of different ecosystems and environmental conditions (Wang et al. 2011). Investigating how to control the Chinese tallow tree is important for maintaining and restoring native coastal ecosystems. Although prescribed fire is currently regarded as a primary tool for controlling the Chinese tallow tree, Chinese tallow has many traits that protect it from fire and allows it to recover quickly after a fire (Eberhardt et al. 2007, Grace 1998).

Wildfire plays an important role in the formation and maintenance of native ecosystems in southeastern coastal areas in United States (Garren 1943, Waldrop et al. 1992). However, human activities, such as fire suppression, farmland expansion, and road construction, have reduced wildfires. As a result, prescribed fire has been used to manage native ecosystems and even control invasive species, such as Chinese tallow (Grace 1998, Grace et al. 2005, Pile et al. 2017). Chinese tallow tree has physiological characteristics and life traits (e.g. strong re-sprout ability and thick bark) that allow it to adapt to fire and recover after burning, and Chinese tallow tree can convert the ecosystems from being fire regulated to being tallow regulated (Grace 1998, D'Antonio 2000, Mandle et al. 2011, Eberhardt et al. 2007). Some studies showed that prescribed fire could facilitate tallow regeneration because it is easier for tallow to invade in disturbed area (Gan et al. 2009, Henkel et al. 2016, Pile et al. 2017, Fan et al. 2018). Moreover, frequency, intensity, type, and extent of prescribed fire can affect impacts of prescribed burn on ecosystems (Lavoie et al. 2010, Ryan et al.2013). In addition, effects of prescribed burn on Chinese tallow invasion are complicated and are influenced by stand and landscape features.

As we discussed in “Ecosystem invasibility”, spatial scales could influence correlations of Chinese tallow invasion and landscape/stand factors, and invasion stages can also alter the relationships between tallow and native species. In this study, we will focus on how landscape/stand factors influence tallow invasion under fire disturbances at two scales: landscape and stand. Moreover, the analysis about tallow invasion is based on the invasion stages: seedling, sapling, and large tree. The findings will help landowners and policy makers understand how community features interact with Chinese tallow invasion, and how to use prescribed fire wisely to control tallow invasion and restore native ecosystems.

1.3 Objectives

The overarching objective of this study was to evaluate how landscape/stand factors affect Chinese tallow invasion under prescribed fire treatments at both landscape and stand levels. The results are presented in two chapters based on the spatial scale: landscape-level and stand-level.

Landscape-level

At the landscape level, the primary objective was to evaluate the effect of prescribed fire on ecosystems invasibility through a set of metrics that quantify the structure and composition of forest ecosystems in a fire-managed coastal landscape in southeastern Mississippi. Specifically, we addressed the following two questions: 1) How does prescribed fire interact with landscape/stand features and propagule pressure to affect Chinese tallow invasion at the landscape level? 2) How does ecosystems invasibility change as an invasion progress, as reflected by developmental stage (seedling, sapling, large tree) of Chinese tallow under current fire treatments?

Stand-level

At the stand level, the primary goal was to evaluate the effects of stand and site factors on Chinese tallow invasion in slash pine flatwoods. The following questions were addressed at the stand level: 1) How do the predisposing stand and site factors affect the invasion probability and degree invasion of Chinese tallow? 2) How does Chinese tallow invasion respond to fire?

1.4 References

Blackburn, T. M., P. Pyšek, S. Bacher, J. T. Carlton, R. P. Duncan, V. Jarošík, J. R. U. Wilson, and D. M. Richardson. 2011. A proposed unified framework for biological invasions. Trends Ecol. Evol. 26(7):333–339.

Brockway, D. G., K. W. Outcalt, D. J. Tomczak, and E. E. Johnson. 2005. Restoring longleaf pine forest ecosystems in the southern United States. P. 501-519 in Restoration of Boreal and Temperate Forests, Stanturf, John A., and Madsen Palle (eds.). CRC Press, Boca Raton.

Bruce, K. A., G. N. Cameron, P. A. Harcombe, and G. Jubinsky. 1997. Introduction, impact on native habitats, and management of a woody invader, the Chinese tallow tree, Sapium sebiferum (L.) Roxb. Natural Areas Journal. 17(3):255–260.

Catford, J. A., R. Jansson, and C. Nilsson. 2009. Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. Divers. Distrib. 15(1):22–40.

Clark, G. F., and E. L. Johnston. 2011. Temporal change in the diversity-invasibility relationship in the presence of a disturbance regime. Ecol. Lett. 14(1):52–57.

Cohen, W. B., Z. Yang, S. V. Stehman, T. A. Schroeder, D. M. Bell, J. G. Masek, C. Huang, and G. W. Meigs. 2016. Forest disturbance across the conterminous United States from 1985-2012: The emerging dominance of forest decline. For. Ecol. Manage. 360:242–252

Croker, T.C., 1976. Regenerating longleaf pine naturally. US Department of Agriculture, Forest Service, Southern Forest Experiment Station, New Orleans, La. 26 p.

D'Antonio, C.M., 2000. Fire, plant invasions, and global changes. P. 65-93 in Invasive species in a changing world. Island Press, Washington, DC.

Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: A general theory of invasibility. J. Ecol. 88(3):528–534.

DiTomaso, J. M., M. L. Brooks, E. B. Allen, R. Minnich, M. Rice, G. B. Kyser. 2006. Control of Invasive Weeds with Prescribed Burning. Weed Technol. 20(2):535–548.

Duerr, D.A. and Miller, J.H. 2005. Understanding and controlling nonnative forest pests in the South. P. 133-154 in Southern Forest Science: Past, Present, and Future Forest Health, Asheville, NC.

Eberhardt, T. L., X. Li, T. F. Shupe, and C. Y. Hse. 2007. Chinese tallow tree (Sapium sebiferum) utilization: Characterization of extractives and cell-wall chemistry. Wood Fiber Sci. 39(2):319–324.

Ellis, E. C. 2011. Anthropogenic transformation of the terrestrial biosphere. Philos. Trans. R. Soc. A Math. Phys. Eng. Sci. 369(1938):1010–1035.

Fan, Z. 2018. Spatial analyses of invasion patterns of Chinese tallow (Triadica sebifera) in a wet slash pine (Pinus elliottii) flatwood in the coastal plain of Mississippi, USA. For. Sci. 64(5):555–563.

Fan, Z., S. Yang, and X. Liu. 2018. Spatiotemporal patterns and mechanisms of Chinese tallowtree (Triadica sebifera) spread along edge habitat in a coastal landscape, Mississippi, USA. Invasive Plant Sci. Manag. 11(3):117–126.

Frost, C. C. 1993. Four centuries of changing landscape patterns in the longleaf pine ecosystem. Proc. Tall Timbers Fire Ecol. Conf. 18(18):17–43.

Gan, J., J. H. Miller, H. Wang, and J. W. Taylor. 2009. Invasion of tallow tree into southern US forests: Influencing factors and implications for mitigation. Can. J. For. Res. 39(7):1346–1356.

Garren, K. H. 1943. Effects of fire on vegetation of the southeastern United States. Bot. Rev. 9(9):617–654.

Gilliam, J. W. 1994. Riparian wetlands and water quality. J. Environ. Qual. 23(5):896–900.

Grace, J. B. 1998. Can prescribed fire save the endangered coastal prairie ecosystem from Chinese tallow invasion? Endanger. Species Updat. 15(5):70–76.

Grace, J. B., L. K. Allain, H. Q. Baldwin, a G. Billock, W. R. Eddleman, a M. Given, C. W. Jeske, and R. Moss. 2005. Effects of prescribed fire in the coastal prairies of Texas. 46 p.

Guo, Q., S. Fei, J. S. Dukes, C. M. Oswalt, B. V. I. III, and K. M. Potter. 2015. A unified approach for quantifying invasibility and degree of invasion. Ecology. 96(10):2613–2621.

Guo, Q., and A. Symstad. 2008. A two-part measure of degree of invasion for cross-community comparisons. Conserv. Biol. 22(3):666–672.

Gurevitch, J., G. A. Fox, G. M. Wardle, Inderjit, and D. Taub. 2011. Emergent insights from the synthesis of conceptual frameworks for biological invasions. Ecol. Lett. 14(4):407–418.

Gunderson, L.H., 2001. Panarchy: understanding transformations in human and natural systems. Island press. London, United Kingdom. 65p.

Henkel, C., P. D. Muley, K. K. Abdollahi, C. Marculescu, and D. Boldor. 2016. Pyrolysis of energy cane bagasse and invasive Chinese tallow tree (Triadica sebifera L.) biomass in an inductively heated reactor. Energy Convers. Manag. 109(225):175–183.

Holle, B. V. O. N. 2005. Biotic resistance to invader establishment of a southern Appalachian plant community is determined by environmental conditions. Journal of Ecology. 93(1):16–26.

Hooper, D. U., I. F. S. Chapin, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, et al. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological monographs, 75(1):3–35.

Hunt, K. W. 1947. The Charleston woody flora. Am. Midl. Nat. 37(3):670–756.

Jones, R.H. and Sharitz, R.R., 1990. Effects of root competition and flooding on growth of Chinese tallow tree seedlings. Canadian Journal of Forest Research, 20(5):573-578.

Komarek, E.V., 1974. Effects of fire on temperate forests and related ecosystems: southeastern United States. Fire and ecosystems, 24:255- 277.

Lavoie, M., G. Starr, M. C. MacK, T. A. Martin, and H. L. Gholz. 2010. Effects of a prescribed fire on understory vegetation, carbon pools, and soil nutrients in a longleaf pine-slash pine forest in Florida. Nat. Areas J. 30(1):82–94.

Lockwood, J. L., P. Cassey, and T. M. Blackburn. 2009. The more you introduce the more you get: the role of colonization pressure and propagule pressure in invasion ecology. Divers. Distrib. 15(5):904–910.

Lockwood, J.L., Hoopes, M.F. and Marchetti, M.P., 2013. Invasion ecology. John Wiley & Sons, West Sussex, United Kingdom. 456p.

Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. Ecology. 80(5):1522–1536.

Mandle, L., J. L. Bufford, I. B. Schmidt, and C. C. Daehler. 2011. Woody exotic plant invasions and fire: reciprocal impacts and consequences for native ecosystems. Biol. Invasions. 13(8):1815–1827.

Maron, J., and M. Marler. 2007. Native plant diversity resists invasion at both low and high resource levels. Ecology. 88(10):2651–2661.

Martinuzzi, S., G. I. Gavier-Pizarro, A. E. Lugo, and V. C. Radeloff. 2015. Future land-use changes and the potential for novelty in ecosystems of the United States. Ecosystems. 18(8):1332–1342.

Miller, A. L., J. M. Diez, J. J. Sullivan, S. R. Wangen, S. K. Wiser, R. Meffin, and R. P. Duncan. 2014. Quantifying invasion resistance: the use of recruitment functions to control for propagule pressure. Ecology. 95(4):920–929.

Mutch, R. W. 1970. Wildland fires and ecosystems—a hypothesis. Ecology. 51(6):1046–1051.

Noss, R.F., LaRoe, E.T. and Scott, J.M., 1995. Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. Washington, DC, USA: US Department of the Interior, National Biological Service. 58p.

Oswalt, S. N. 2010. Chinese Tallow (Triadica sebifera (L.) Small) population expansion in Louisiana, East Texas, and Mississippi. USDA publication. 20:1–4.

Outcalt, K.W. and Sheffield, R.M., 1996. The longleaf pine forest: trends and current conditions. Resour. Asheville, NC: US Department of Agriculture, Forest Service, Southern Research Station. 23p.

Pearson, D. E., Y. K. Ortega, D. Villarreal, Y. Lekberg, M. C. Cock, Ö. Eren, and J. L. Hierro. 2018. The fluctuating resource hypothesis explains invasibility, but not exotic advantage following disturbance. Ecology. 99(6):1296–1305.

Pflugmacher, D., W. B. Cohen, and R. E. Kennedy. 2012. Using Landsat-derived disturbance history (1972-2010) to predict current forest structure. Remote Sens. Environ. 122:146–165.

Pile, L. S., G. G. Wang, B. O. Knapp, J. L. Walker, and M. C. Stambaugh. 2017. Chinese tallow (Triadica sebifera) invasion in maritime forests: the role of anthropogenic disturbance and its management implication. For. Ecol. Manage. 398:10–24

Platt, W.J., 1999. Southeastern pine savannas. Savannas, barrens, and rock outcrop plant communities of North America, Cambridge University Press, Cambridge, United Kingdom. 484p.

Pyne, S. and Vale, T.R., 2003. Fire, native peoples, and the natural landscape. Restoration Ecology: BOOK REVIEW, 11(2):257-259.

Renne, I. J., W. C. Barrow, L. A. Johnson Randall, and W. C. Bridges. 2002. Generalized avian dispersal syndrome contributes to Chinese tallow tree (Sapium sebiferum, Euphorbiaceae) invasiveness. Divers. Distrib. 8(5):285–295.

Richardson, D. M., and P. Pyšek. 2006. Plant invasions: merging the concepts of species invasiveness and community invasibility. Prog. Phys. Geogr. 30(3):409–431.

Ryan, K. C., E. E. Knapp, and J. M. Varner. 2013. Prescribed fire in North American forests and woodlands: history, current practice, and challenges. Front. Ecol. Environ. 11(SUPPL. 1).

Sui, Z., 2015. Modeling tree species distribution and dynamics under a changing climate, natural disturbances, and harvest alternatives in the southern United States. D.Sc. dissertation Mississippi State University, Starkville, MS, United States. 194p.

Tan, Y., 2011. Predicting the potential distributions of major invasive species using geospatial models in southern forest lands. M.Sc. thesis, Mississippi State University, Starkville, MS, United States. 76p.

Tian, N., Z. Fan, T. G. Matney, and E. B. Schultz. 2017. Growth and stem profiles of invasive Triadica sebifera in the Mississippi coast of the United States. For. Sci. 63(6):569–576.

Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. Ecology. 78(1):81–92.

U.S. Fish and Wildlife Service, 2003. Longleaf pine ecosystem fact sheet.http://www.southeast.fws.gov/pfwpine.html (accessed 4 November 2003).

Van Lear, D. H., W. D. Carroll, P. R. Kapeluck, and R. Johnson. 2005. History and restoration of the longleaf pine-grassland ecosystem: implications for species at risk. For. Ecol. Manage. 211(1–2):150–165.

Vermeij, G. J. 1996. An agenda for invasion biology. Biol. Conserv. 78(1–2):3–9.

Waldrop, T. A., D. L. White, and S. M. Jones. 1992. Fire regimes for pine-grassland communities in the southeastern United States. For. Ecol. Manage. 47(1–4):195–210.

Wang, H. H., W. E. Grant, T. M. Swannack, J. Gan, W. E. Rogers, T. E. Koralewski, J. H. Miller, and J. W. Taylor. 2011. Predicted range expansion of Chinese tallow tree (Triadica sebifera) in forestlands of the southern United States. Divers. Distrib. 17(3):552–565.

Webster, C. R., M. A. Jenkins, and S. Jose. 2006. Woody invaders and the challenges they pose to forest ecosystems in the eastern United States. J. For. 104(7):366–374.

Williams, J. W., and S. T. Jackson. 2007. Novel climates, no-analog communities, and ecological surprises. Front. Ecol. Environ. 5(9):475–482.

Yang, S., Z. Fan, X. Liu, A. W. Ezell, M. A. Spetich, S. K. Saucier, S. Gray, and S. G. Hereford. 2019. Effects of prescribed fire, site factors, and seed sources on the spread of invasive Triadica sebifera in a fire-managed coastal landscape in southeastern Mississippi, USA. Forests. 10(2):175.

Yang, S., 2019. Distribution and spread mechanisms of Chinese tallow (Triadica sebifera) at multiple spatial scales within forests in the southeastern United States. D.Sc. dissertation, Mississippi State University, Starkville, MS, United States. 150p.

CHAPTER II

Invasibility of coastal ecosystems to Chinese tallow tree (*Triadica sebifera*) under fire disturbances: mechanisms and key factors at the landscape level

2.1 Introduction

In invasion ecology, the term "invasibility" has been coined to describe the susceptibility of recipient ecosystems to invasive species, which is an intrinsic property and a manifestation of the interactions of multiple processes and factors (Lonsdale 1999, Davis et al. 2000). There was an initial belief that higher biodiversity reduces the susceptibility of recipient ecosystems to nonnative invasive species (Elton 1958). Essentially, the negative biodiversity-invasibility relationship is based on the biotic resistance assumption and has mostly been observed in small-scale experimental studies in certain ecosystem types (e.g. grassland) while other factors are held constant (Tilman 1997, Maron and Marler 2007). However, observational studies have shown divergent (either positive or negative) relationships between native species diversity and biological invasion at both small and large scales. Numerous hypotheses and theories such as scaling effects, productivity, heterogeneity and fluctuating resource availability of recipient ecosystems, propagule pressure, disturbance, life-history traits of invasive species, and positive interactions between native species and nonnative invasive species have been proposed to explain observed invasion patterns (Lonsdale 1999, Alpert et al. 2000, Davis et al. 2000, D'Antonio et al. 2001, Sax 2002, Cleland et al. 2004, Fridley et al. 2007, Bulleri et al.

2008). However, none of these explanations can be mechanistically applied to all species and ecosystems across varying spatial and temporal scales (Davies et al. 2007, Sandel and Corbin 2010).

Biological invasions are context-dependent and that invasibility, as an emergent ecosystems property, is affected by multiple processes and factors that interact and covary across multiple spatial and temporal scales (Richardson and Pysek 2006, Hui et al. 2016, Pearson et al. 2018). For a specific invasive species and ecosystem type, invasibility is largely determined by the competitive interactions (ecosystems resistance) between the non-native and resident species, which are often regulated by community structure, propagule pressure, disturbance/stress regime, and invasion stages of exotic species (Alpert et al. 2000, Davis et al. 2000, D'Antonio et al. 2001, Fan et al. 2018). In order to understand the mechanisms of biological invasion and to evaluate ecosystems invasibility, appropriate spatial and temporal scales should be selected to sufficiently characterize these processes and factors, particularly in frequently disturbed ecosystems (D'Antonio et al. 2001, Kamenova et al. 2017).

Historically, frequent, low-intensity wildfires ignited by lightning and humans (e.g., native Americans) have been a key ecological process in sustaining the once expansive pine flatwood and savanna ecosystems primarily dominated by longleaf pine (*Pinus palustris Mill.*) and slash pine (*Pinus elliottii*) in the southern Coastal Plain. However, a century-long period of logging, land conversion (e.g., urbanization, tree plantations, agriculture), and fire suppression following European settlement significantly reshaped the historical vegetation and fire regimes (Van Lear et al. 2005). The longleaf pine ecosystems have experienced a drastic reduction in area, from over 38 million acres to today's 2 million acres, as tree plantations and dense mixed forests have become increasingly dominant since the arrival of the first European settlers (Noss et al. 1995, Frost 2007). The use of prescribed fire in combination with appropriate vegetation management practices (e.g., removal of overstory species) has been recognized as a preferred approach of restoring longleaf pine ecosystems and sustaining biodiversity and resilience (Lavoie et al. 2010).

However, the effectiveness of prescribed fire for managing these ecosystems has been compromised by the unprecedented biological invasion by non-native invasive species (NNIS), as the burned areas are more susceptible to invasion by NNISs. Out of those NNISs, Chinese tallow (*Tricdica sebifera (L.) Small*) has been recognized by landowners and government agencies as one of the most threatening NNISs due to its rapid spread rate (King and Grace 2000, Brooks et al. 2004, Oswalt 2010, J Chappell, Forest Inventory and Analysis Coordinator, Alabama Forestry Commission, personal communication). Chinese tallow trees are highly competitive and can spread under a variety of conditions, preventing the establishment and growth of longleaf pine and slash pine seedlings, among other native species (Yang 2019, Sui, 2015). Moreover, Chinese tallow trees can modify fire regimes, resulting in an irreversible shift from desired states, as the degree of invasion reaches a certain threshold (e.g., Meyer 2011).

Reports on Chinese tallow invasion and its effects on coastal ecosystems are often inconsistent and even contradictory, largely a result of most studies being confined to small-scale field and greenhouse experiments. Furthermore, few address critical factors such as the context, invasion degree, and long-term consequences of disturbances (e.g., fire). The results are also difficult to generalize and thus, have little management value (Pile et al. 2017). The poor understanding of ecological consequences of prescribed fire at the ecosystem/landscape level, especially over long periods, has become a barrier to predicting forest ecosystems response to prescribed fire treatments and biological invasion in the Gulf Coastal Plain. Understanding the relationships between prescribed fire and the competition between dominant longleaf/slash pine and invasive species such as Chinese tallow at local and landscape levels, could lead to better methods for the restoration of degraded native ecosystems (Yang 2019).

The primary objective of this study was to evaluate the effect of prescribed fire on ecosystems invasibility by Chinese tallow in relation to the structure and composition of forest ecosystems in a fire-managed coastal landscape in southeastern Mississippi. Specifically, our goals were to answer the following two questions: 1) How does prescribed fire interact with landscape/stand features and propagule pressure level to affect tallow invasion at the landscape level? 2) How does ecosystems invasibility (quantified by invasion probability and invasion degree) change with the developmental stage (seedling, sapling, large tree) of Chinese tallow under current fire treatments?

2.2 Methods

2.2.1 Research sites

Located in the Gulf Coastal Plain within 8-km of the Gulf of Mexico (30°27’3”N, 88°39’20”W), the Mississippi Sandhill Crane National Wildlife Refuge (MSCNWR) has a flat topography and low elevation of 1.5 to 6 m above mean sea level (Teaford et al. 1995). MSCNWR has a subtropical climate with hot, humid summers and relatively mild winters (U.S. Almanac 2004). The average day and night temperatures in January, the coldest month, are about 16.2 °C and 5.8 °C, respectively (Southeast Regional Climate Center 2005). The average maximum temperature in July and August, the hottest months, is 32.0 °C. MSCNWR receives substantial rainfall, averaging 1,600 mm a year, mainly in the summer months, from June to August.

Pine flatwoods and savannas are the two largest ecosystems in the MSCNWR, occupying 57.5% and 25.3% of the landscape, respectively. Since 1985, MSCNWR has conducted prescribed fires on between 1,000 and 9,000 acres (400~3,600 ha) per year. Each stand (burn unit) is on a 1 to 5-year fire rotation resulting in a mean fire return interval of 2 to 3 years for the entire landscape. The objective of this fire regime is to restore and conserve the pine flatwood and savanna ecosystems, which provides critical habitat for endangered Mississippi ylindri cranes (*Grus ylindrica pulla*) and declining grassland birds such as the Henslow sparrow (*Ammodramus henslowii*) (US Fishes and Wildlife Service 2007). Prescribed fire is applied in the spring and fall to clear woody vegetation, improve areas overstocked with longleaf/slash pine, and enhance the suitability of the cranes' nesting areas. To implement prescribed burns, MSCNWR has three management units (west block, east block, and south block) which are classified into 45 burning units (100+ sub-units), each with varying stocking levels of longleaf/slash pine (Figure 2.1).

Surrounded by non-industrial private land and residential areas that have abundant Chinese tallow seed sources, MSCNWR was invaded by Chinese tallow tree in the late 1990s. Populations of invading Chinese tallow tree were distributed in spatially clustered patterns along forest edges and in frequently disturbed areas. The increasing numbers of Chinese tallow in combination with other invaders such as cogongrass (*Imperata ylindrical (L.) Beauv*) have become a serious threat to the pine flatwoods and savannas, and the wildlife species they support (*Ammodramus henslowii*) (Yang et al. 2019, MSCNWR Comprehensive Conservation Plan 2007).

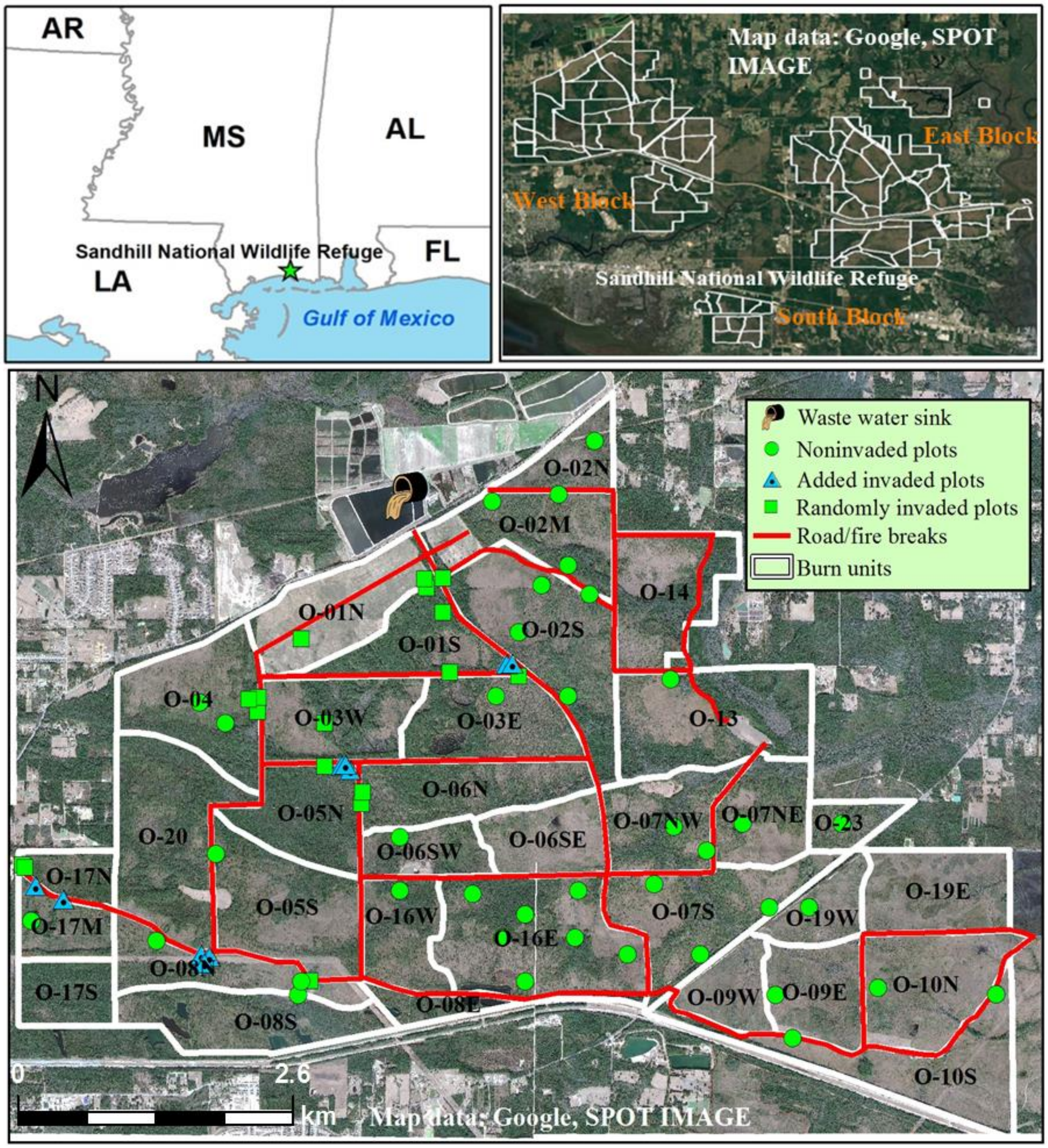


Figure 2.1 Distribution of study plots within the Mississippi Sandhill Crane National Wildlife Refuge.

2.2.2 Chinese tallow invasion and ecosystems invasibility: the mechanism and associated factors

The invasibility of an ecosystem or landscape by biological invaders is determined by ecosystem structure, local disturbance regimes, propagule pressure, and the biological traits of the invasive species (Davis et al. 2000). In the Gulf Coastal Plain, the invasion of native ecosystems by Chinese tallow is primarily attributed to 1) its advantageous life-history traits such as high specific leaf area, quick nutrient uptake, high seed production, strong root/stump sprout capacity, and herbivore tolerance (Barrilleaux and Grace, 2000, Rogers and Siemann 2003, Zou et al. 2008) and 2) frequent, intense disturbances such as fire, hurricanes, tropical storms, and human activities (Gan et al. 2009, Fan et al. 2012). The fluctuating resources theory (FRT) (e.g., Davis et al. 2000), provides a mechanistic modeling framework (Figure 2.2) through which Chinese tallow invasion at the ecosystem and landscape levels is divided into four interrelated stages/processes: seed dispersal (spread), seedling recruitment (colonization), sapling accumulation (establishment) and large tree development (growth). The framework also shows the interactions and feedbacks between these stages/processes, ecosystem and landscape features, and natural and human disturbances. All of the factors contributing to Chinese tallow invasion are mechanistically classified as either driving factors, predisposing factors or inciting factors based on the roles they play in the identified invasion stages/processes. Driving factors include birds, water currents (watershed hydrology) and human activities that disperse tallow seeds are the direct driver of seed dispersal. The number of Chinese tallow trees and seeds in an ecosystem is proportionally related to the frequency and intensity of the driving factors. Predisposing factors include ecosystem and landscape features, such as overstory and understory species composition and structure, hydrological condition, density of edges/corridors, and spatial distribution of Chinese tallow trees and seeds (propagule pressure level). The predisposing factors are the primary determinants of the spatial patterns of Chinese tallow establishment, as they influence seed dispersal and affect the condition of critical resources necessary for tallow recruitment (seed germination, survival and growth). Given explicit spatial and temporal scales, ecosystems invasibility is basically a function or manifestation of predisposing factors and can be measured by the degree or rate of invasion. Inciting factors include natural and anthropogenic disturbances such as prescribed fires, hurricanes, tropical storms, and timber extraction. The inciting factors affect and modify predisposing factors and driving factors and subsequently influence the state and dynamics of ecosystems, biological invasion, and ecosystems functions, dynamics and services. Although numerous factors contribute to tallow invasion, this study will focus on evaluating how landscape- and community- features and fire disturbance will affect tallow invasion and ecosystem invasibility.

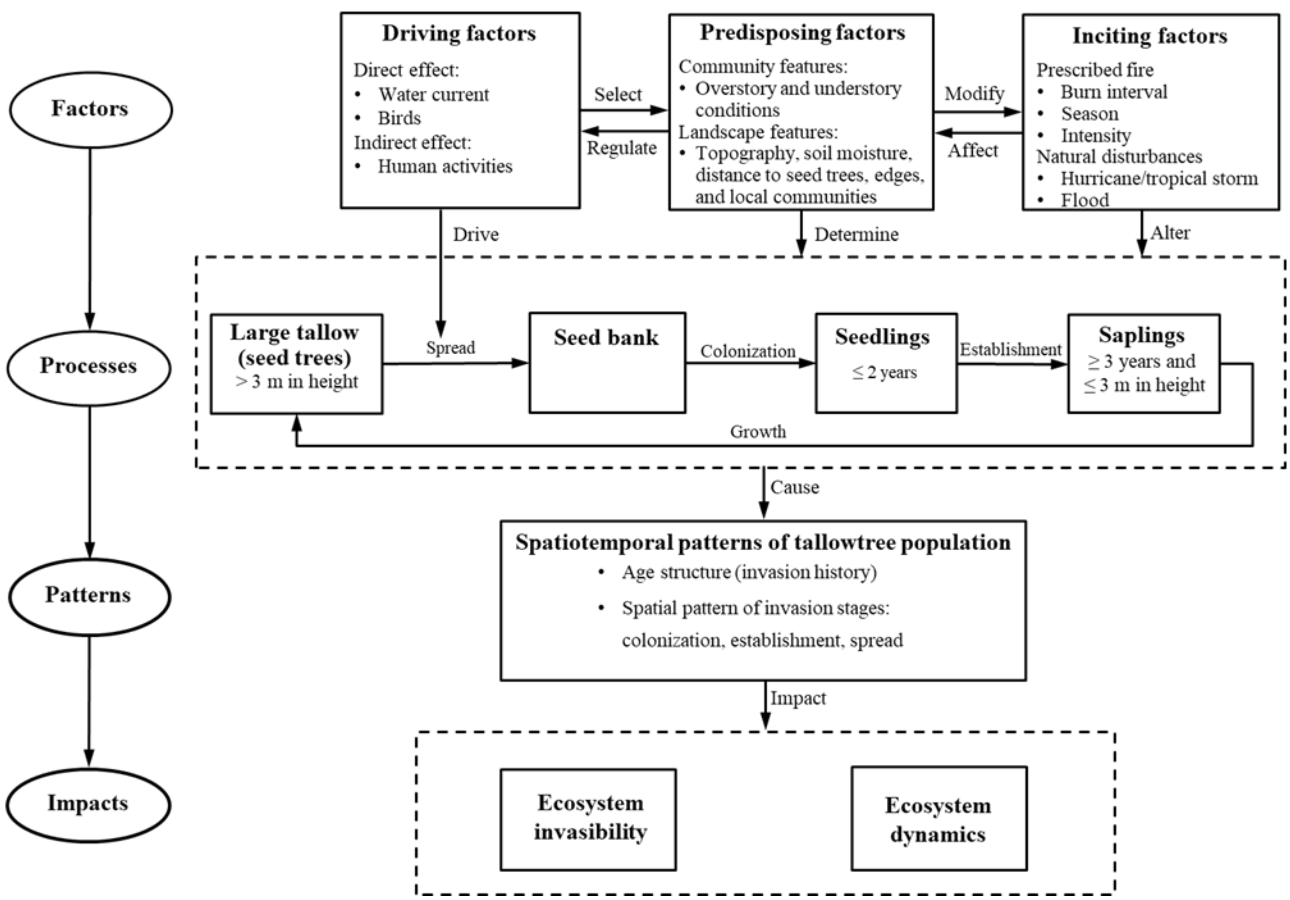


Figure 2.2 The mechanistic modeling framework of Chinese tallow invasion and impact on ecosystems functions and services at the ecosystem and landscape level, showing the interactions and feedbacks between tallow invasion and associated driving, predisposing, and inciting factors.

2.2.3 Data collection

MSCNWR encompasses three separate management units (Ocean Springs, Gautier, and Fontainbleau) of approximately 7,800 ha in total. For spatial continuity, only the West block unit was used for this study (Figure 2.1). A random sample of 55 0.1-ac (0.04-ha) permanent circular plots was set up across the study landscape in May and June of 2015. To allow for future remeasurement and monitoring, plot centers were mapped using a GPS device (Forge Echo by F4Device, http://www.thinkf4.com/solutions/forge-echo). Within each plot, the overstory condition, including canopy closure (%), the species and diameter at breast height (dbh) of all overstory trees were measured, and the total basal area (m^2/ha) and tree density (#/ha) were calculated. To measure the understory condition, three 2×2 m^2 quadrats were set up to measure the dbh, total height, and numbers of pine saplings. Within three nested 1×1 m^2 sub-quadrats, the number of pine seedlings and the mean height (m) and coverage (%) of the grass/herbaceous and woody shrub layers were measured. The number, total height and dbh (if present) of Chinese tallow were counted and measured across the whole plot.

Additional measurements included: the ecosystem types (e.g., pine flatwood, pine savanna) of each plot and the presence/absence (a binary variable) of tallow seed trees. The nearest distance from a plot center to both the forest edge/road and the local community (potential tallow seed sources) were generated using ArcGIS. To quantify fire disturbance and potential effects, the mean fire return interval and the length of time (year) since the last fire at each plot was determined from the 2000-2019 prescribed fire data provided by site managers from the Fire Department of MSCNWR. Time since last fire of pine flatwoods (1.69 years) was shorter than that of pine savannas (6.85 years), burn interval in pine flatwoods (5.4 years) was longer than that in pine savannas (3.3 years), and the difference of the distance to road between these two ecosystem types was not significant. All plots were initially measured in May and June of 2015 and remeasured in late October 2018 and mid-March of 2019.

2.2.4 Data analysis and modeling

To assess the impacts of prescribed fire, propagule pressure, and ecosystem/ landscape-factors on the invasion probability and abundance (degree of invasion) of Chinese tallow (goal 1), plants were grouped into three size/age classes: seedlings (< 1 m height), saplings (1-3 m,) and large trees (> 3 m). These classes represent the colonization, establishment and post-invasion spread (bearing seeds) stages/processes, respectively, as specified in the mechanistic modeling framework (Figure 2.2). Seedlings are mostly one or two years old and located in the grass/herbaceous layer, saplings are mostly more than three years old and surpass the grass/herbaceous layer into the shrub layer, and large tallow surpass the shrub layer into the mid- and over-story layer. This classification is based on extensive field observations and the age-height relationship developed through aging felled Chinese tallow (Yang 2019). All plots (n=55) were first classified into either tallow-invaded (1, n=17) or non-invaded (0, n=38) plots. A two-sample test for equality of proportions without continuity correction was conducted to compare the difference in invasion probability between the pine flatwoods and pine savannas based on the 2×2 contingency table (Newcombe 1998). The invasion probability was calculated as the proportion ($\hat{p}$) of invaded plots among all plots and its standard error was calculated as $\sqrt{\hat{p}(1-\hat{p})/n}$. Logistic regression was then conducted to evaluate the effect of prescribed fire, propagule pressure, and ecosystem/landscape-factors on the invasion probability (Fan et al. 2012).

$$\mathrm{P}(y=1|\mathrm{X}) = \frac{1}{1+e^{-(\alpha+X'\beta)}})$$

where $p(y = 1|X)$ is the expected conditional probability for a plot to be invaded (y=1) by Chinese tallow; α is the intercept of the model; X is the vector of associated factors; β is the vector of estimated coefficients. The associated factors include distance to road and local community, canopy closure, overstory basal area, seed tree presence (1 if present or 0 if absent), shrub cover, grass cover, mean burn interval, and time since last fire.

The abundance of Chinese tallow seedlings, saplings, and large trees were used to estimate the potential impact of measured factors on degree of invasion by size classes. The count (Poisson regression) model was applied (Consul and Famoye 1992):

$$\log(\mathrm{u}) = \beta_0 + \sum_{i=1}^{n} \beta_i x_i + \varepsilon_i$$

Where u is the abundance of Chinese tallow seedlings, saplings, and large trees; β_i and x_i are the estimated coefficients and associated factors; ε_i is the random errors, respectively. We first conducted over dispersion test on Poisson regression models and quasipoisson regression was applied with the over-dispersion count data to obtain estimates of significant factors by using the dispersion-test function in the R package *AER*. We applied the stepwise method with significance level of 0.05 to select the significant factors associated with Chinese tallow invasion for the Logistic regression and Poisson regression models by using the *stepAIC* function in the R package MASS.

To address the second goal—how ecosystems invasibility changed with the invasion stages of Chinese tallow—ten tallow plots from another Chinese tallow invasion study measured at the same period of time were combined with the seventeen tallow-invaded plots for this study. The combined 27 tallow invaded plots (n=27) were used for statistical tests to compare the difference in the abundance of tallow seedlings, saplings and large trees between pine flatwoods and pine savannas. Student's t-test was applied to compare the difference in the abundance of tallow seedlings, saplings, and large trees between pine flatwoods and pine savannas. A Poisson regression was applied to quantify the impact of the identified risk factors on the abundance of Chinese tallow by size/age classes. The change in the density of seedlings, saplings and large tree of native species (longleaf and slash pine) and Chinese tallow between 2015 and 2019 were compared using a paired t-test as well as graphically. Ecosystems invasibility was evaluated based on the abundance of Chinese tallow in different size/age classes and their changes between 2015 and 2019 in relative to native species (longleaf and slash pine). An ecosystem is deemed more susceptible to an invasion stage if it has more abundant tallow trees and larger increase in density in the corresponding tallow size class (Guo eta l. 2015). All statistical analyses were conducted using the base packages within the R statistical environment (R Development Core Team 2014).

2.3 Results

2.3.1 Effects of prescribed fire, landscape structure and propagule on Chinese tallow invasion

By late 2018, 17 out of 55 monitoring plots were invaded by Chinese tallow resulting in an invasion probability of 0.31 for the entire landscape. Pine flatwoods (12 out of 23 flatwoods were invaded, invasion probability = 0.52) were more susceptible to tallow invasion than pine savannas (5 out of 32 savannas were invaded, invasion probability = 0.16) ($p = 0.002$) (Figure 2.3 A). Pine flatwoods had more Chinese tallow seedlings and saplings than pine savannas ($p < 0.001$). However, there was a greater number of large tallow in pine savannas than that in pine flatwoods, although the difference was marginally significant ($p = 0.07$) (Figure 2.3 B).

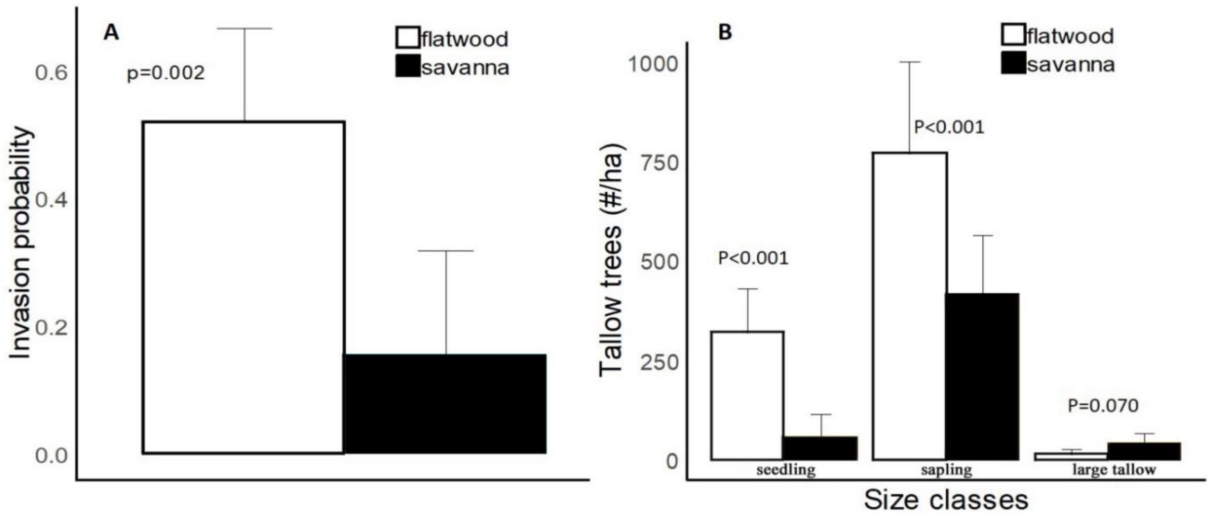


Figure 2.3 Invasion probability (A) and degree of invasion (B) of Chinese tallow by size/age classes between pine flatwoods and pine savannas by 2018.

The logistic regression model (Table 2.1) showed that the invasion probability was positively related to the overstory basal area, but negatively related to the burn interval and understory shrub cover, suggesting that overstory trees tended to increase the invasion probability by Chinese tallow while high shrub cover and long burn interval tended to decrease the invasion probability by Chinese tallow. The count models (Table 2.2) further quantified factors affecting the abundance (degree of invasion) of Chinese tallow by size class. The abundance of seedlings was positively related to the presence of tallow seed trees and canopy closure and was negatively related to the distance to the road and time (in years) since last fire (Figure 2.4). The abundance of saplings was positively related to the presence of seed trees but negatively related to mean burn interval (Figure 2.5). The abundance of large trees was positively correlated to the presence of tallow seed trees, canopy closure, and mean burn interval (Figure 2.6).

Table 2.1 Regression coefficients of binary (logistic) model of whether or not a site had been invaded by tallow (n=55 sites).

Variables	Estimate	Std. Error	Z value	Pr(>|z|)
Intercept	10.732	4.400	2.439	0.015
Shrub cover (%)	-0.051	0.026	-1.949	0.051
Burn interval (year)	-3.955	1.711	-2.311	0.021
Overstory basal area (m^2/ha)	0.251	0.111	2.268	0.023

Table 2.2 Regression coefficients of the count (log-linear) models to predict the invasion degree of Chinese tallow by size/age class (n= 27 sites, 2018).

	Estimate	**Std. Error**	**Z value**	**Pr(>|z|)**
Seedlings ≤ 2 years (height ≤ 1 m)				
Intercept	1.214	0.341	3.556	0.000
Distance to road (m)	-0.011	0.004	-2.902	0.004
Seed tree (yes, no)	2.051	0.139	14.771	0.000
Canopy closure (%)	0.016	0.003	4.751	0.003
Time since last fire (year)	-0.136	0.046	-2.943	0.001
Saplings (height ≤ 3 m)				
Intercept	4.254	0.491	8.688	0.000
Seed tree (yes, no)	1.154	0.344	3.356	0.004
Mean fire interval (year)	-0.285	0.125	-2.275	0.036
Large (height > 3 m)				
Intercept	-10.368	2.996	-3.460	0.001
Seed tree (yes, no)	4.247	0.985	4.312	0.000
Canopy closure (%)	0.040	0.014	2.873	0.004
Mean fire interval (year)	1.294	0.342	3.784	0.000

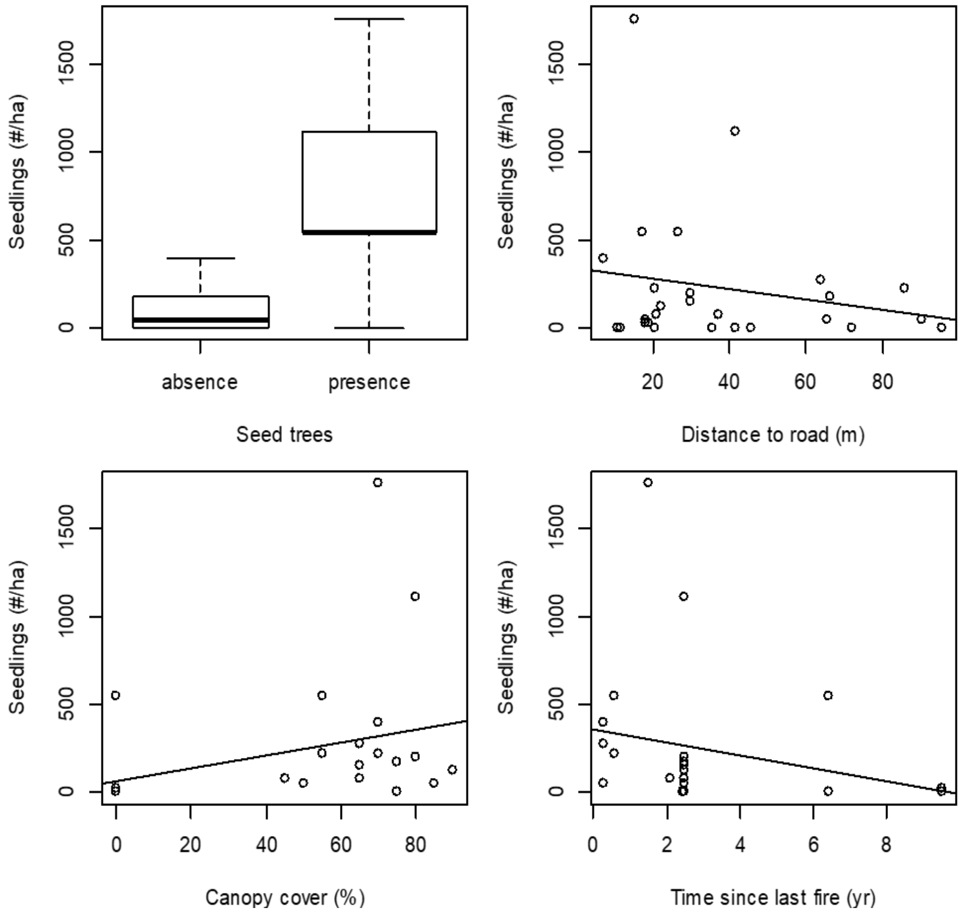


Figure 2.4 Abundance of tallow seedlings by significant factors identified by the count model among the 27 tallow-invaded plots. The straight line shows the simple linear regression trend line and the bold line and box plot represent the median (50^{th} percentile) and the first-quartile (25^{th} percentile) and third-quartile (75^{th} percentile) of tallow seedlings, respectively.

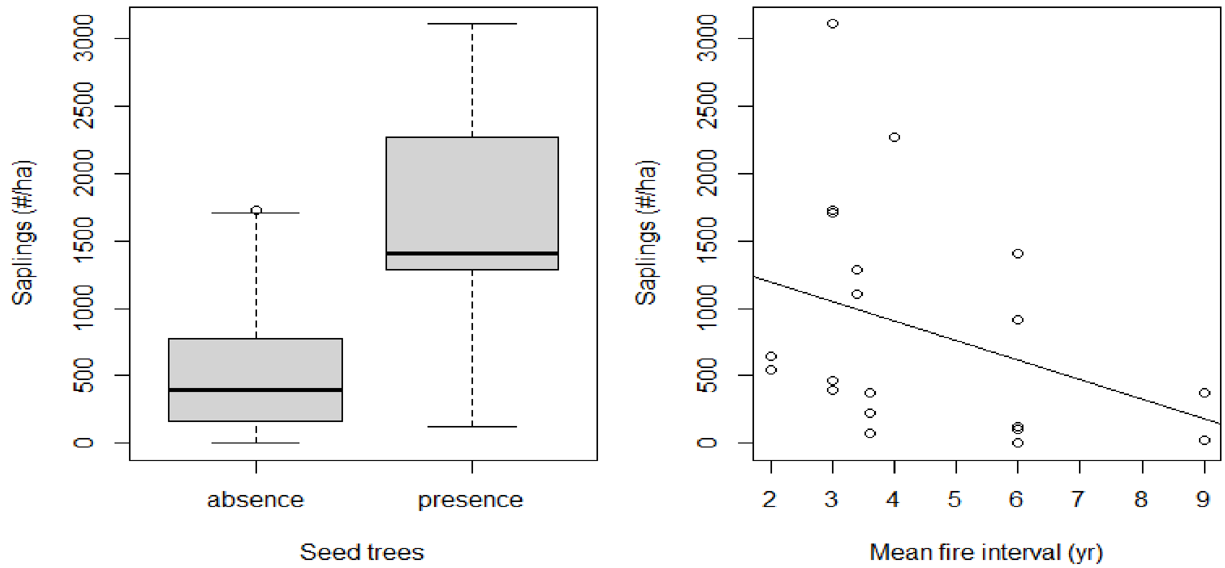


Figure 2.5 Abundance of tallow saplings by significant factors identified by the count model among the 27 tallow-invaded plots. The straight line shows the simple linear regression trend line and the bold line and box plot represent the median (50th percentile) and the first-quartile (25th percentile) and third-quartile (75th percentile) of tallow saplings, respectively.

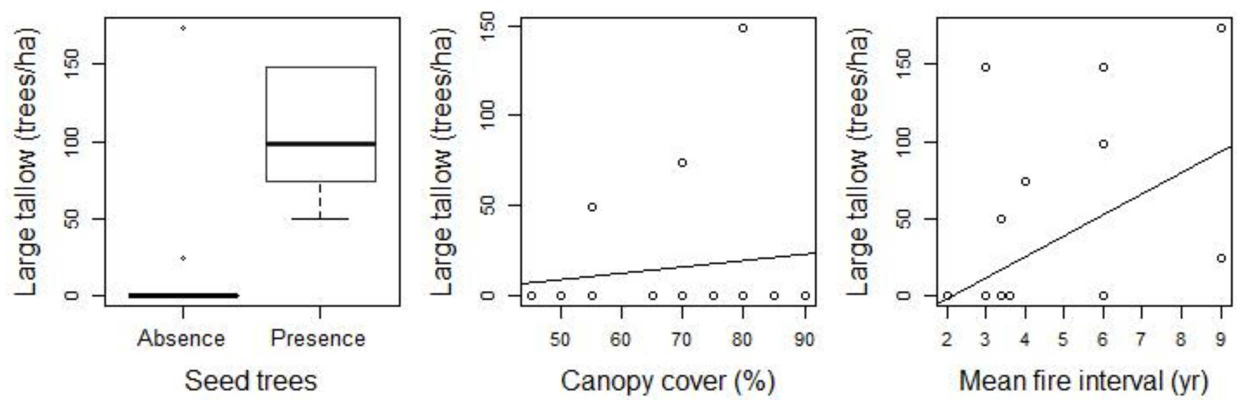


Figure 2.6 Abundance of large tallow trees by significant factors identified by the count model among the 27 tallow-invaded plots. The straight line shows the simple linear regression trend line and the bold line and box plot represent the median (50th percentile) and the first-quartile (25th percentile) and third-quartile (75th percentile) of large tallow trees, respectively.

2.3.2 The change of ecosystems invasibility with Chinese tallow invasion stages of Chinese tallow

Overall, the seedling densities of tallow and pines were positively correlated ($p < 0.001$), whereas the sapling densities were negatively correlated ($p = 0.040$) among all 27 tallow invaded plots. The densities of Chinese tallow and pine large trees showed a slight negative correlation, but the relationship was not statistically significant ($p = 0.238$) (Figure 2.7 A, C, E). The results suggest that pine saplings and large trees have negative correlations with tallow saplings and large tallow trees due to the interspecific competition for light and other resources.

A closer examination of the change in the density of Chinese tallow and pine by ecosystem types between 2015 to 2018 revealed disparities between the pine flatwoods and pine savannas. In pine savannas, there was a concurrent decrease in the density of both the Chinese tallow and pine seedlings from 2015 to 2018, although the decrease was not statistically significant ($p = 0.25$ and $p = 0.18$). In pine flatwoods, however, the density of pine seedlings increased significantly ($p = 0.01$) while tallow seedlings tended to decrease ($p = 0.31$) (Figure 2.7 B). Numbers of pine and tallow saplings increased from 2015 to 2018 in both flatwoods and savannas, but in flatwoods the increase in number of tallow saplings was greater than that of pine saplings. In pine savannas, there was a greater increase in pine saplings (Figure 2.7 D). In both pine savannas and flatwoods, number of large tallow trees increased as large pines decreased or remained unchanged. Savannas had a greater number of large tallow trees than pine flatwoods ($p = 0.07$) (Figures 2.7 F, 2.3 B). The changes in tallow and native pine density indicate that pine flatwoods were more susceptible to the colonization and establishment of tallow seedlings and saplings, but pine savannas were more favorable for development of large tallow trees.

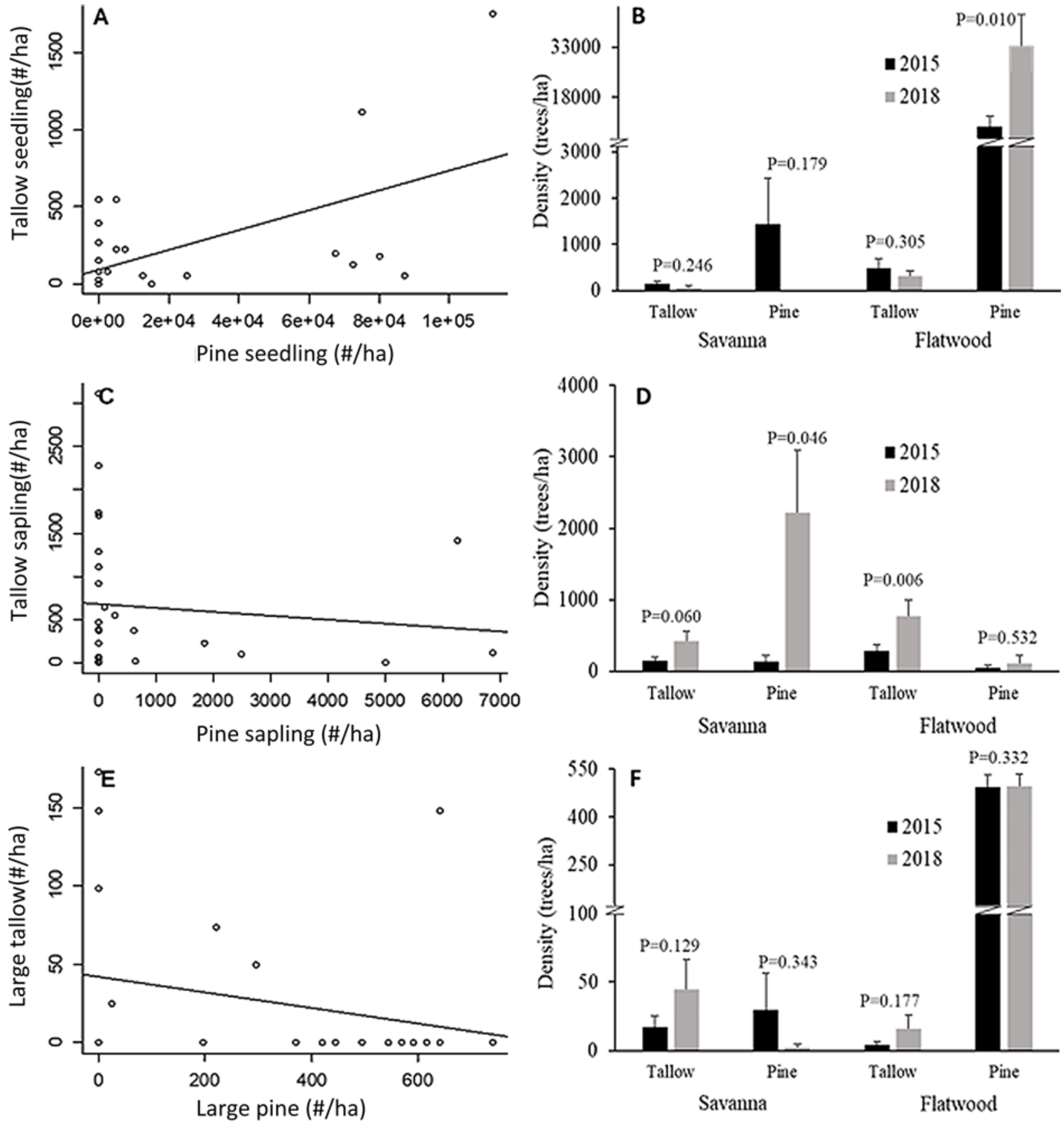


Figure 2.7 The scatterplot and simple linear regression trend line of the density of seedlings (A), saplings (C) and large trees € between tallow and pine in 2018, and the change in density of seedlings (B), saplings (D) and large trees (F) of tallow and pine between 2015 and 2018 in pine flatwood and pine savanna. Vertical bars and lines represent means and standard errors of tree density, and the p-value of paired t-test to test whether there is a significant change in the density between 2015 and 2018 are labeled.

2.4 Discussion

The FRT-based model framework illustrates the interactions and feedbacks between Chinese tallow invasion stages and key factors from a landscape perspective. In the framework, invasibility, as an intrinsic property of an ecosystem, is primarily determined by predisposing factors – metrics measuring landscape/ecosystem structure and condition including overstory condition (basal area and canopy closure), understory condition (% of grass cover and shrub cover), distance to roadway, and the presence of seed trees (Davis et al. 2000, Richardson and Pysek 2006, Fan et al. 2018). In this study, the invasion probability and abundance (number per ha) of Chinese tallow by size/age classes were used to quantify the invasibility of longleaf/slash pine flatwood and savanna ecosystems. With a significantly higher invasion probability and a greater number of tallow seedlings and saplings, pine flatwoods appeared to be more susceptible in terms of seed dispersal, seedling colonization and sapling recruitment compared to pine savannas under frequent, low-intensity fires (Figure 2.3). The high invasibility of pine flatwoods is correlated with its larger overstory tree density and basal area but relatively lower understory shrub cover compared to pine savannas. Overstory trees, particularly large trees (alive or dead), provide perches for tallow seed-eating birds and can greatly facilitate avian seed dispersal (Renne et al. 2000, Renne et al. 2002), causing tallow seedlings and saplings to be distributed mostly under crowns of overstory pine trees and/or in sites with high grass cover but low shrub cover (low vegetative competition from native species) (Fan 2018, Fan et al. 2018, Yang et al. 2019). Forest edges (e.g., roads, fire lines) and propagule pressure could affect invasion probability and degree significantly (Fan, et al. 2018, Yang et al. 2019). Evidence that fire serves as an inciting factor on Chinese tallow invasion and ecosystems invasibility stems from two characteristics of fire: 1) fire helps clear understory vegetation to promote seed germination and seedling recruitment, and 2) fire can kill or top-kill small Chinese tallow (Meyer 2011). The cumulative effect of prescribed fire on Chinese tallow varied with the invasion stages (Grace 1998). Short fire intervals tended to increase the invasion probability and the accumulation of seedlings and saplings, but decreased large tallow (Tables 2.1, 2.2). The increase of invasion probability with short fire intervals is explained by the fact that fire helps to clear the site and release resources for seed germination. However, short fire intervals are more likely to kill or top-kill seedlings and saplings before they grow into larger sizes that can survive low-intensity fires, which result the decrease of large tallow tree abundance (Smith et al. 1997).

The invasion risk and abundance of Chinese tallow may vary with the ecosystems condition, fire regimes (e.g., fire frequency, intensity and seasonality), and their interactions (Fan et al. 2018, Yang et al. 2019). According to Yang et al. (2019), Chinese tallow invaded into this landscape began in the late1990s. This was ten years after the reintroduction of prescribed fire on the landscape. The delay in Chinese tallow invasion may reflect a lack of seed sources in the landscape and vicinity (Williamson and Fitter 1996, Lonsdale 1999). The low propagule pressure limited the spread of Chinese tallow across the landscape in earlier years until after 2011, when a phenomenal increase was seen following the refuge-wide road construction and reconstruction (Yang et al. 2019). Because of variations and nonsignificant statistically relationships between tallow and native pine, it is difficult for us to quantify tallow spread rate in a short period time (2015-2018). Because of the dynamic nature of tallow invasion propagule pressure, the qualification of ecosystems invasibility should be ideally conducted in a spatiotemporally explicit manner and over a relatively long period to design practical fire management scenarios for the future restoration of native ecosystems and controlling of Chinese tallow invasion. The effective management for Chinese tallow invasion control should consider all factors including ecosystems context, propagule pressure, and fire regimes.

To date, published studies are mostly based on data collected within a relatively short period of time before/after fire treatments, and the findings are more descriptive and confined to a particular ecosystem; therefore, they are more difficult to generalize for prescribing fire treatments (e.g., Grace 1998, Bates et al. 2006, Richardson 2011, Pile et al. 2017). Taking a 2,900-ha fire-managed landscape as a sampling frame, this study quantified the invasion probability and abundance of Chinese tallow in two interlaced ecosystems—longleaf/slash pine flatwoods and savannas. Moreover, the landscape has been actively managed by using frequent (a mean return interval of two to three years) low-intensity fires since the mid-1980s.

The mean fire return interval in the study landscape for pine flatwoods and pine savannas is 3.3 years and 5.4 years, respectively (Yang 2019). Compared with the pine savannas, pine flatwoods are more susceptible to Chinese tallow invasion due to their large overstory tree density/basal area, but relatively low grass and shrub cover under current fire intervals. In pine savannas of lower canopy closure (less competition from pine trees above), there are greater numbers of large tallow trees. As a result, pine savannas could be the seed source of post-invasion spread once invaded by Chinese tallow. Under current Chinese tallow invasion patterns, maintaining a shorter burn interval of 2-3 years to reduce accumulation of large tallow trees (potential seed source) should be recommended in pine savannas. For pine flatwoods, a longer fire interval of 5-6 years should be recommended to reduce invasion probability and abundance of tallow seedlings and saplings in the understory. Because Chinese tallow seedlings and saplings may outcompete native species and dominate the site when the overstory is removed (Henkel et al. 2016). Moreover, other methods such as mechanical treatments should also be considered to reduce Chinese tallow stocking in the invaded pine flatwoods with large number of seedlings and saplings encroaching in the understory.

Fire treatments can be spatially applied for specific stands or ecosystems based on distance to forest edges and seed source, because Chinese tallow invasion appeared in spatially clustered patterns along forest edges (road, fire line) (Fan et al. 2018, Yang et al. 2019). Knowing the propagule pressure (seed bank) and removing tallow seed trees are important to control post invasion spread after disturbances (Miller et al.2014). Evaluating the propagule pressure levels, invasion probability, and invasion degree of an exotic species is important to design effective prescribed burn.

2.5 Conclusion

Longleaf/slash pine flatwood and savanna ecosystems play an important role in the ecological functions and services of the Gulf Coastal Plain. Prescribed fire has been used to restore these ecosystems that have experienced a substantial shift away from desired conditions due to the drastic change in land use following European settlement and fire suppression throughout the 20th century (Platt 1999). The reintroduction of prescribed fire accompanied by increasing natural and anthropogenic disturbances make coastal landscapes and ecosystems more susceptible to biological invasion from nonnative invasive plants such as tallow (Sui 2015). This study on a fire-managed coastal landscape (Mississippi Sandhill Crane National Wildlife Refuge) integrated prescribed fire data spanning 20 years with Chinese tallow data collected from 2015 to 2018 and examined the factors affecting tallow invasion and ecosystems invasibility from a landscape perspective. The findings will aid in the restoration of endangered native ecosystems such as longleaf/slash pine flatwoods and savannas, and will specifically benefit the design of prescribed fire treatments for use in mitigating and controlling Chinese tallow invasion.

Under frequent (a mean return interval of two to three years), low-intensity fires, pine flatwoods in this study were more susceptible to tallow invasion than pine savannas as indicated by the high invasion probability and the greater prevalence of seedlings and saplings encroaching in the understory. This was largely due to their large overstory tree density/basal area and low shrub and grass cover. Compared to pine flatwoods, however, more large tree of Chinese tallow were found in pine savannas. This could be a function of lower canopy closure and less competition from overstory pine trees in the savannas. Invaded pine savannas may serve as potential seed sources for tallow’s rapid spread to surrounding ecosystems and forests. Both distance from roads and abundance of seed trees, which reflected propagule pressure, had a significant impact on the degree of invasion and ecosystems invasibility, as sites closer to roads and seed trees had a higher invasion probability and a larger number of Chinese tallow. This suggests that landscape fragmentation will facilitate the spread of Chinese tallow across the entire landscape.

2.6 References

Alpert, P., E. Bone, and C. Holzapfel. 2000. Perspectives in plant ecology, evolution and systematics invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. Perspect. Plant Ecol. Evol. Syst. 3(1):52–66.

Barrilleaux, T. C., and J. B. Grace. 2000. Growth and invasive potential of Sapium sebiferum (Euphorbiaceae) within the coastal prairie region: the effects of soil and moisture regime. Am. J. Bot. 87(8):1099–1106.

Bates, J. D., R. F. Miller, and K. W. Davies. 2006. Restoration of quaking aspen woodlands invaded by western juniper. Rangel. Ecol. Manag. 59(1):88–97 Available online at: http://dx.doi.org/10.2111/04-162R2.1.

Brooks, M.L., D'antonio, C.M., Richardson, D.M., Grace, J.B., Keeley, J.E., DiTomaso, J.M., Hobbs, R.J., Pellant, M. and Pyke, D., 2004. Effects of invasive alien plants on fire regimes. BioScience, 54(7):677-688.

Bulleri, F., J. F. Bruno, and L. Benedetti-Cecchi. 2008. Beyond competition: incorporating positive interactions between species to predict ecosystem invasibility. PLoS Biol. 6(6):1136–1140.

Cleland, E. E., M. D. Smith, S. J. Andelman, C. Bowles, K. M. Carney, M. C. Horner-Devine, J. M. Drake, S. M. Emery, J. M. Gramling, and D. B. Vandermast. 2004. Invasion in space and time: non-native species richness and relative abundance respond to interannual variation in productivity and diversity. Ecol. Lett. 7(10):947–957.

Consul, P. and Famoye, F., 1992. Generalized Poisson regression model. Communications in Statistics-Theory and Methods, 21(1):89-109.

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

Davies, K. F., S. Harrison, H. D. Safford, and J. H. Viers. 2007. Productivity alters the scale dependence of the diversity-invasibility relationship. Ecology. 88(8):1940–1947.

Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. J. Ecol. 88(3):528–534.

Elton, C.S., 1958. The ecology of invasions by animals and plants. Methuen & Co. Ltd., London, 261p.

Fan, Z. 2018. Spatial analyses of invasion patterns of Chinese tallow (Triadica sebifera) in a wet slash pine (Pinus elliottii) flatwood in the coastal plain of Mississippi, USA. For. Sci. 64(5):555–563.

Fan, Z., Y. Tan, and M. K. Crosby. 2012. Factors associated with the spread of Chinese tallow in East Texas forestlands. Open J. Ecol. 02(03):121–130.

Fan, Z., S. Yang, and X. Liu. 2018. Spatiotemporal patterns and mechanisms of Chinese tallowtree (Triadica sebifera) spread along edge habitat in a coastal landscape, Mississippi, USA. Invasive Plant Sci. Manag. 11(3):117–126.

Fridley, J.D., Stachowicz, J.J., Naeem, S., Sax, D.F., Seabloom, E.W., Smith, M.D., Stohlgren, T.J., Tilman, D. and Holle, B.V., 2007. The invasion paradox: reconciling pattern and process in species invasions. Ecology, 88(1):3-17.

Frost, C., 2007. History and future of the longleaf pine ecosystem. P. 9-48 in The longleaf pine ecosystem. Springer, New York, NY.

Gan, J., J. H. Miller, H. Wang, and J. W. Taylor. 2009. Invasion of tallow tree into southern US forests: influencing factors and implications for mitigation. Can. J. For. Res. 39(7):1346–1356.

Grace, J. B. 1998. Can prescribed fire save the endangered coastal prairie ecosystem from Chinese tallow invasion? Endanger. Species Updat. 15(5):70–76.

Guo, Q., S. Fei, J. S. Dukes, C. M. Oswalt, B. V. I. III, and K. M. Potter. 2015. A unified approach for quantifying invasibility and degree of invasion. Ecology. 96(10):2613–2621.

Henkel, T.K., Chambers, J.Q. and Baker, D.A., 2016. Delayed tree mortality and Chinese tallow (Triadica sebifera) population explosion in a Louisiana bottomland hardwood forest following Hurricane Katrina. Forest Ecology and Management, 378:222-232.

Hui, C., D. M. Richardson, P. Landi, H. O. Minoarivelo, J. Garnas, and H. E. Roy. 2016. Defining invasiveness and invasibility in ecological networks. Biol. Invasions. 18(4):971–983.

Kamenova, S., T. J. Bartley, D. A. Bohan, J. R. Boutain, R. I. Colautti, I. Domaizon, C. Fontaine, et al. 2017. Invasions toolkit: current methods for tracking the spread and impact of invasive species. In Advances in Ecological Research. 56:85-182.

King, S.E. and Grace, J.B., 2000. The effects of gap size and disturbance type on invasion of wet pine savanna by cogongrass, Imperata cylindrica (Poaceae). American Journal of Botany, 87(9):1279-1286.

Lavoie, M., G. Starr, M. C. MacK, T. A. Martin, and H. L. Gholz. 2010. Effects of a prescribed fire on understory vegetation, carbon pools, and soil nutrients in a longleaf pine-slash pine forest in Florida. Nat. Areas J. 30(1):82–94.

Lonsadle, W. M. 1999. Global Patterns of Plant Invasions and the concept of invasibility. Ecology. 80(5):1522–1536.

Maron, J., and M. Marler. 2007. Native plant diversity resists invasion at both low and high resource levels. Ecology. 88(10):2651–2661.

Meyer, R., 2011. Fire effects information system: Triadica sebifera. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. Retrieved January. 10:2014.

Miller, A. L., J. M. Diez, J. J. Sullivan, S. R. Wangen, S. K. Wiser, R. Meffin, and R. P. Duncan. 2014. Quantifying invasion resistance: the use of recruitment functions to control for propagule pressure. Ecology. 95(4):920–929.

Newcombe, R.G., 1998. Interval estimation for the difference between independent proportions: comparison of eleven methods. Statistics in medicine, 17(8):873-890.

Noss, R.F., LaRoe, E.T. and Scott, J.M., 1995. Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. Washington, DC, USA: US Department of the Interior, National Biological Service. 58p

Oswalt, S. N. 2010. Chinese tallow (Triadica sebifera (L.) Small) population expansion in Louisiana, east Texas, and Mississippi. USDA publication. 20:1-4.

Pearson, D. E., Y. K. Ortega, D. Villarreal, Y. Lekberg, M. C. Cock, Ö. Eren, and J. L. Hierro. 2018. The fluctuating resource hypothesis explains invasibility, but not exotic advantage following disturbance. Ecology. 99(6):1296–1305.

Pile, L. S., G. G. Wang, B. O. Knapp, J. L. Walker, and M. C. Stambaugh. 2017. Chinese tallow (Triadica sebifera) invasion in maritime forests: the role of anthropogenic disturbance and its management implication. For. Ecol. Manage. 398:10–24.

Platt, W.J., 1999. Southeastern pine savannas. P. 23-51 in Savannas, barrens, and rock outcrop plant communities of North America, Anderson, R.C. Fralish, J.S. and Baskin, J.M. (eds). Cambridge Press, United Kingdom.

R Development Core Team. 2014. R: A language and environment for statistical computing. P. 409 in R Found Statistical Computing. Vienna, Austria.

Renne, I. J., S. A, G. Jr., and C. A. Gresham. 2000. Seed dispersal of the Chinese tallow tree (Sapium Sebiferum (L .) Roxb.) by birds in coastal South Carolina. Am. Midl. Nat. 144(1):202–215.

Renne, I. J., W. C. Barrow, L. A. Johnson Randall, and W. C. Bridges. 2002. Generalized avian dispersal syndrome contributes to Chinese tallow tree (Sapium sebiferum, Euphorbiaceae) invasiveness. Divers. Distrib. 8(5):285–295.

Richardson, D. M., and P. Pyšek. 2006. Plant invasions: merging the concepts of species invasiveness and community invasibility. Prog. Phys. Geogr. 30(3):409–431.

Richardson, D.M., 2011. Invasion science: the roads travelled and the roads ahead. P. 397-407 in Fifty years of invasion ecology: the legacy of Charles Elton. Blackwell Published Ltd, West Sussex, UK.

Rogers, W.E. and Siemann, E., 2003. Effects of simulated herbivory and resources on Chinese tallow tree (Sapium sebiferum, Euphorbiaceae) invasion of native coastal prairie. American Journal of Botany, 90(2):243-249.

Sandel, B., and J. D. Corbin. 2010. Scale, disturbance and productivity control the native-exotic richness relationship. Oikos. 119(8):1281–1290.

Sax, D. F. 2002. Native and naturalized plant diversity are positively correlated in scrub communities of California and Chile. Divers. Distrib. 8(4):193–210.

Smith, G.F., Nicholas, N.S., Zedaker, S.M., 1997. Auccession dynamics in a maritime forest following Hurricane Hogo and fuel reduction burns. Forest Ecology and Management, 95(3):275-283.

Sui, Z., 2015. Modeling tree species distribution and dynamics under a changing climate, natural disturbances, and harvest alternatives in the southern United States. D.Sc. dissertation Mississippi State University, Starkville, MS, United States. 194p.

Teaford, J.W., P.L.Lewis and Johnson. 1995. Mississippi pine savannas, pine flatwoods, and forested bay heads: wetland delineation, evaluation, and mitigation considerations. J.W. Teaford and Company, Vicksburg, Mississippi. 53p.

Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. Ecology. 78(1):81–92.

US Fish and Wildlife Service. 2007. Mississippi Sandhill Crane National Wildlife Refuge Comprehensive Conservation Plan; US Department of the Interior Fish and Wildlife Service Southeast Region: Atlanta, GA, USA. 151p.

Van Lear, D. H., W. D. Carroll, P. R. Kapeluck, and R. Johnson. 2005. History and restoration of the longleaf pine-grassland ecosystem: implications for species at risk. For. Ecol. Manage. 211(1–2):150–165.

Williamson, M. H., and A. Fitter. 1996. The characters of successful invaders. Biol. Conserv. 78(1–2):163–170.

Yang, S., Z. Fan, X. Liu, A. W. Ezell, M. A. Spetich, S. K. Saucier, S. Gray, and S. G. Hereford. 2019. Effects of prescribed fire, site factors, and seed sources on the spread of invasive Triadica sebifera in a fire-managed coastal landscape in southeastern Mississippi, USA. Forests. 10(2):175.

Yang, S., 2019. Distribution and spread mechanisms of Chinese tallow (Triadica sebifera) at multiple spatial scales within forests in the southeastern United States. D.Sc. dissertation, Mississippi State University, Starkville, MS, United States. 150p.

Zou, J., W. E. Rogers, and E. Siemann. 2008. Increased competitive ability and herbivory tolerance in the invasive plant Sapium sebiferum. Biol. Invasions. 10(3):291–302

.

CHAPTER III

Invasion of Chinese tallow (*Triadica sebifera*) in a slash flatwood in southern Mississippi, United States: mechanisms and key factors at microscales

3.1 Introduction

Chinese tallow (*Triadica sebifera, (L.) Small),* which is native to Japan and central China, was introduced into the southern region of the United States in the late 1700s as an ornamental and potential oil species (Bruce 1993, Myers et al. 2000). In the 1900s, the U.S. Department of Agriculture introduced Chinese tallow to the Gulf of Mexico coastal region to build its own soap industries (Bruce et al. 1997, Jones and McLeod 1989). By the early 2000s, Chinese tallow occupied 185,000 ha of southern forests from Texas to south Florida (Oswalt 2010, Tan 2011). Based on the U.S. Department of Agriculture Forest Service's Forest Inventory and Analysis (FIA) data, Wang et al. (2011a) estimated that Chinese tallow could occupy more than 1.5 million ha of forests by 2023. An analysis of most recent FIA from across the 67 coastal counties of northern Florida, Alabama, Mississppi, Louisiana and eastern Texas data shows that Chinese tallow has outcompeted many native species, ranking 17th out of the 135 encountered species in aboveground dry weight (Personal communication with James Chappell, Forest Inventory and Analysis Coordinator, Alabama Forestry Commission). Chinese tallow has become one of the most prevalent invasive species, causing serious threats to native ecosystems in the Gulf of Mexico coastal region (Miller et al. 2008, Meyer 2011, Pile et al. 2017).

Adaptability to various environments, as seen in Chinese tallow, is an important factor for successful invasion (Reichard and Hamilton 1997, Williamson and Fitter 1996), such as seedling shade tolerance, flood tolerance, and long seed dormant season. The physiological characteristics and life history traits of Chinese tallow such as large leaf area, quick nutrients uptake, strong sprout capacity, rapid growth rate, and herbivore resistance make it able to invade quickly and successfully (Zou et al. 2008, Rogers and Siemann 2003, Fan et al. 2018b). Furthermore, the forest types in the Gulf coastal region are favorable for Chinese tallow invasion because similar latitude to its native region according to USDA Forest Service FIA data (Tian et al. 2017). Chinese tallow tree invasion along edges could be facilitated by disturbances. Other environmental conditions such as light, soil moisture, and temperature, can also significantly influence its colonization, establishment, and spread (Sakai et al. 2001, Pattison and Mack 2008). The primary factors that affect Chinese tallow invasion include site biodiversity, distance to road, site quality, slope, and overstory density (Fan et al. 2018a). Resources availability influences Chinese tallow establishment at the stand level, and its growth rate varies with different light levels (Urbatsch 2000, Rogers and Simann 2003). Moreover, Chinese tallow has higher growth rates than native trees at the same light level, and its seedlings could outcompete with herbivory when light is limited (Rogers et al. 2000).

Prescribed fire combined with other vegetation management has been regarded as a preferred tool to restore native ecosystems and control Chinese tallow invasion of coastal areas (Grace et al. 2005, Lavoie et al. 2010). Some researches indicated that frequent burning could kill Chinese tallow seedlings and damage saplings during growing season, and other researches showed that fire disturbances may increase Chinese tallow invasion risk due to the availability of resources (Grace 1998, Pile et al. 2017, Conner et al. 2022). The southern wet pine forest is an important coastal ecosystem type, and it is easy to be invaded by Chinese tallow due to its open stand structure and frequent disturbances (e.g., fire, flood, and hurricane). Invasion of Chinese tallow can not only threaten native species directly and can also transform soil properties, and community structure, and composition, making Chinese tallow one of the most influential invasive species (Van and Richardson 2014). Native species can also affect Chinese tallow invasion directly or indirectly by facilitating or impeding conditions for Chinese tallow establishment or spread (Lankau et al. 2004). Historically, wet pine flatwood ecosystems occupied broad areas of the Gulf coastal plain (Yang 2019). Wet pine flatwoods are important native ecosystems because of their critical ecological functions and services, but their stand structures and properties appear to facilitate Chinese tallow invasion (Fan et al. 2018a, Fan et al. 2018b, Yang et al. 2019). Therefore, in this study, a flatwoods wet pine-hardwood plot with changing understory conditions (before and after prescribed burn) was selected to evaluate the effects of microscale stand and site factors on Chinese tallow invasion at microscales. Specifically, this research addressed the following two questions: 1) How do predisposing stand and site factors affect the invasion probability and degree of Chinese tallow invasion? 2) How does Chinese tallow invasion respond to fire?

3.2 Methodologies

3.2.1 Research sites

Grand Bay National Wildlife Refuge (GBNWR) was established in 1992 with a primary objective of restoring wet savanna/flatwood ecosystems. Located on the Mississippi/Alabama state line in Jackson County, MS (30°25'12"N, 88°25'12" W) (Figure 3.1) (Fan 2018), GBNWR occurs within the deltas of the Escatawpa and Pascagoula rivers, and it is located in the lower Gulf Coastal Plain. The total area of the refuge is 7,285 ha, and 81% of the area is public lands and waters. The major cover types in this area are wet pine savanna and pine flatwood, along with salt marshes, maritime forest, wetlands, and bays. The climate of GBNWR is a subtropical climate with hot and humid summers. The average annual maximum and minimum temperatures are 24.7 ℃ (76 ℉) and 14.7 ℃ (58 ℉), respectively. The annual rainfall is around 1.6m, and extreme rainfall events can lead to serious riparian flooding (Wieland 2007). The invasion of Chinese tallow to GBNWR is thought to have originated from plants occurring on private inholdings and around roads and boundaries since 1990s (Stokalosa and Fan 2013).

3.2.2 Data collection

In March 2018, a study plot of 0.86 ha in a wet pine-hardwood flatwood was established. A hiking trail with clumps of Chinese tallow distributed along other side passes through the plot (Figure 3.1). All overstory trees (native and Chinese tallow trees) were mapped using a high-resolution GPS (Global Positioning System) unit. The species of over-story and diameter at breast height (dbh) were recorded and measured. The plot was then divided into 281 evenly-spaced 30-m^2 quadrats to measure Chinese tallow invasion and overstory and understory conditions.

As a first step, all measured tallow trees were divided into three size classes: large tallow trees (> 3 m in height), saplings (1 m < height ≤ 3 m) and seedlings (height ≤ 1 m and 1-year-old), and the number of Chinese tallow by size classes and total overstory trees (including pine and hardwoods) were counted for each quadrat. Within each quadrat, thirty evenly-placed 1 m^2 sub-quadrats were further set up to record the vegetation types: cogongrass, native grass, shrub, litter, pine sapling. Based on the records of the 30 sub-quadrats of each quadrat, we calculated the coverage (%) of cogongrass, shrub, and native grass. For the litter depth, we set up 5 points in the 30 m^2 quadrat to measure the depth and calculated the mean value. For height of pine saplings, we measured the height of all saplings and calculated the mean value. We sued Crown Densiometer to measure the canopy closure (%) of each quadrat. The distance from each quadrat to a tallow-invaded road and hiking trail (seed sources) was also measured using ArcGIS. The digital elevation model (DEM, 3m resolution) was obtained from the United States Geological

Survey (USGS) to show the topographic conditions of the study plot. The mean elevation (m) of each quadrat was extracted from the DEM to show the change of micro-topography.

In June and August 2019, the plot was remeasured again after a prescribed burn in May 2019. In each 30-m^2 quadrat, the number of Chinese tallow seedlings and saplings (including re-sprouted and grew from seedling) regenerated were measured and recorded. We also remeasured the coverage and height of shrubs and grasses/herbaceous species and coverage and depth of litter in each quadrat. Based on these measurements, each quadrat was classified into five substrate conditions: native grass (NG), pine seedlings and saplings (PS), shrubs (SB), cogongrass (CG), and litter cover (LC).

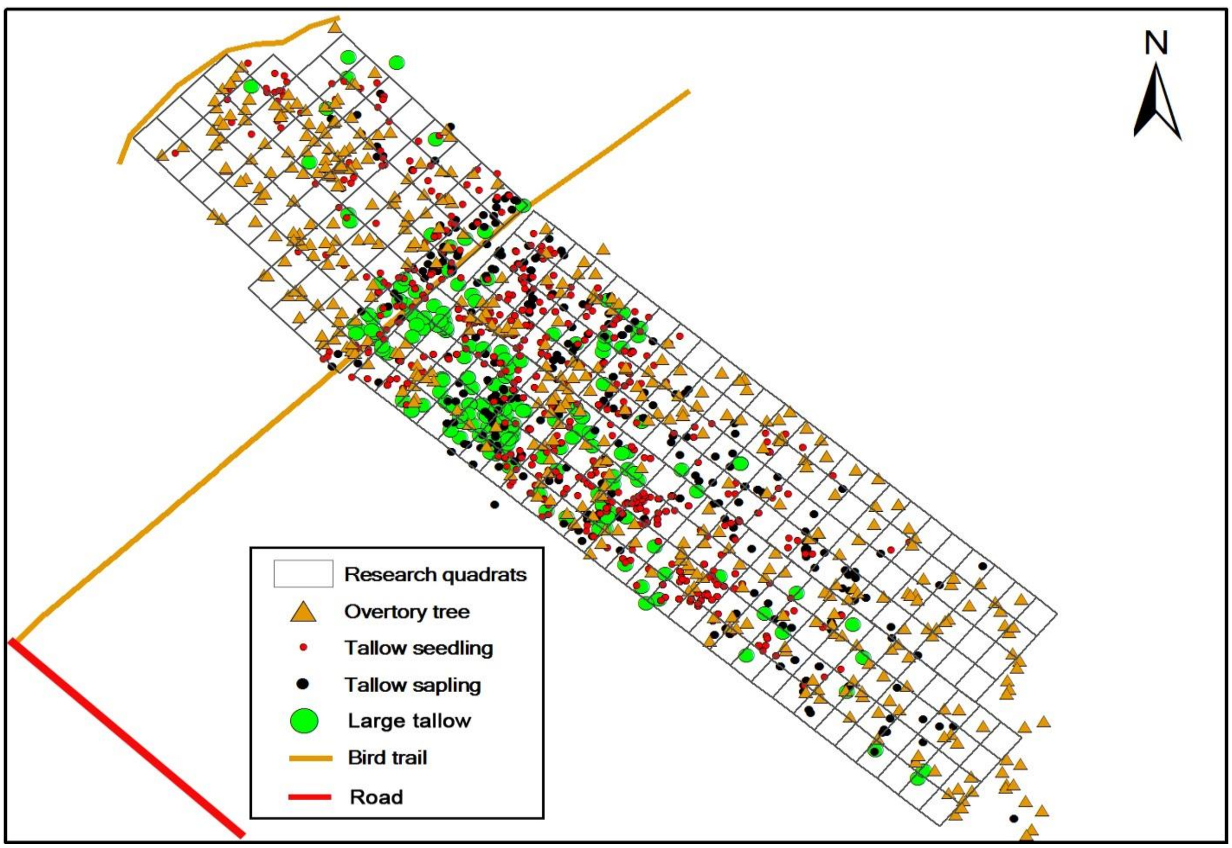


Figure 3.1 Illustration of subplots of the 0.86-ha plot and 281 30-m^2 quadrats to collect field data.

3.2.3 Data analysis and modeling

To quantify the invasion degree of Chinese tallow in the slash pine flatwood and evaluate the effects of site and stand factors (objective 1), we first plotted the smoothed probability density function of Chinese tallow by size classes and the bivariate scatterplots between size classes (large tallows, saplings, seedlings) based on the data collected from quadrats (n = 281). The smoothed probability density was calculated by Kernel Density Smoothing by using Chinese tallow data by size classes of the 281 quadrats (Fan and Crosby 2012). Next, we plotted the number of Chinese tallow by size classes against measured site and stand factors to show how Chinese tallow invasion degree varied with site conditions. Based on the aforementioned exploratory analyses, we applied the nonparametric classification and regression tree model (CART) of quadrat data to quantify the effects of site and stand factors on tallow invasion probability and degree of invasion (number/quadrat). CART is a predictive model that explains how an outcome variable's values can be predicted based on other values. Its output is a decision tree where each fork is a split in a predictor variable and each end note contains a predictor for the outcome variable. A quadrat was classified into absence (0) and presence (1) based on whether or not tallow was found. Using the binary variable (invaded-1 or noninvaded-0) and the count of large tallows, saplings and seedlings in each quadrat as the response variable and site and stand factors as the predictors. CART estimated the invasion probability and degree of tallow by selected significant factors and displayed the interactions between factors. To prevent the over-fit, CART was pruned based on the complexity measure to achieve the minimum relative error. Evaluation of selected factors was based on the pruned CART (the best model). R packages *rpart* and *rpart.plot* were used for developing and plotting the CART models. To address how does Chinese tallow invasion respond to fire, the analysis of covariance

(ANCOVA) and post-hoc multiple comparisons were conducted to evaluate post-fire change in the number of Chinese tallow seedlings and saplings by substrate condition (factor) and covariates including the coverage of shrubs, grass/herbaceous species and litter.

3.3 Results

3.3.1 Effects of predisposing site and stand factors on tallow invasion

Within the study plot, 66 (23.5%) out of 281 quadrats were invaded by tallow. The number of Chinese tallow (large trees, saplings and seedlings) in the 30-m^2 quadrats followed a skewed-to-right distribution with a mean of 0.6 large tallows, 1.4 saplings and 4.1 seedlings per quadrat, respectively (Figure 3.2A). Although there was a positive relationship (trend) between Chinese tallow size classes (large tree vs. saplings, large tree vs. seedlings, saplings vs. seedlings), great variations among quadrats were large. This suggested Chinese tallow invasion was controlled by multiple factors and changed across both space and measurement time (Figure 3. 2 B, C and D). The invasion degree (abundance) of Chinese tallow generally decreased with the distance to the road and trail, overstory tree density, shrub coverage, litter coverage and depth, and elevation, but increased with canopy closure and grass coverage (Figure 3.3).

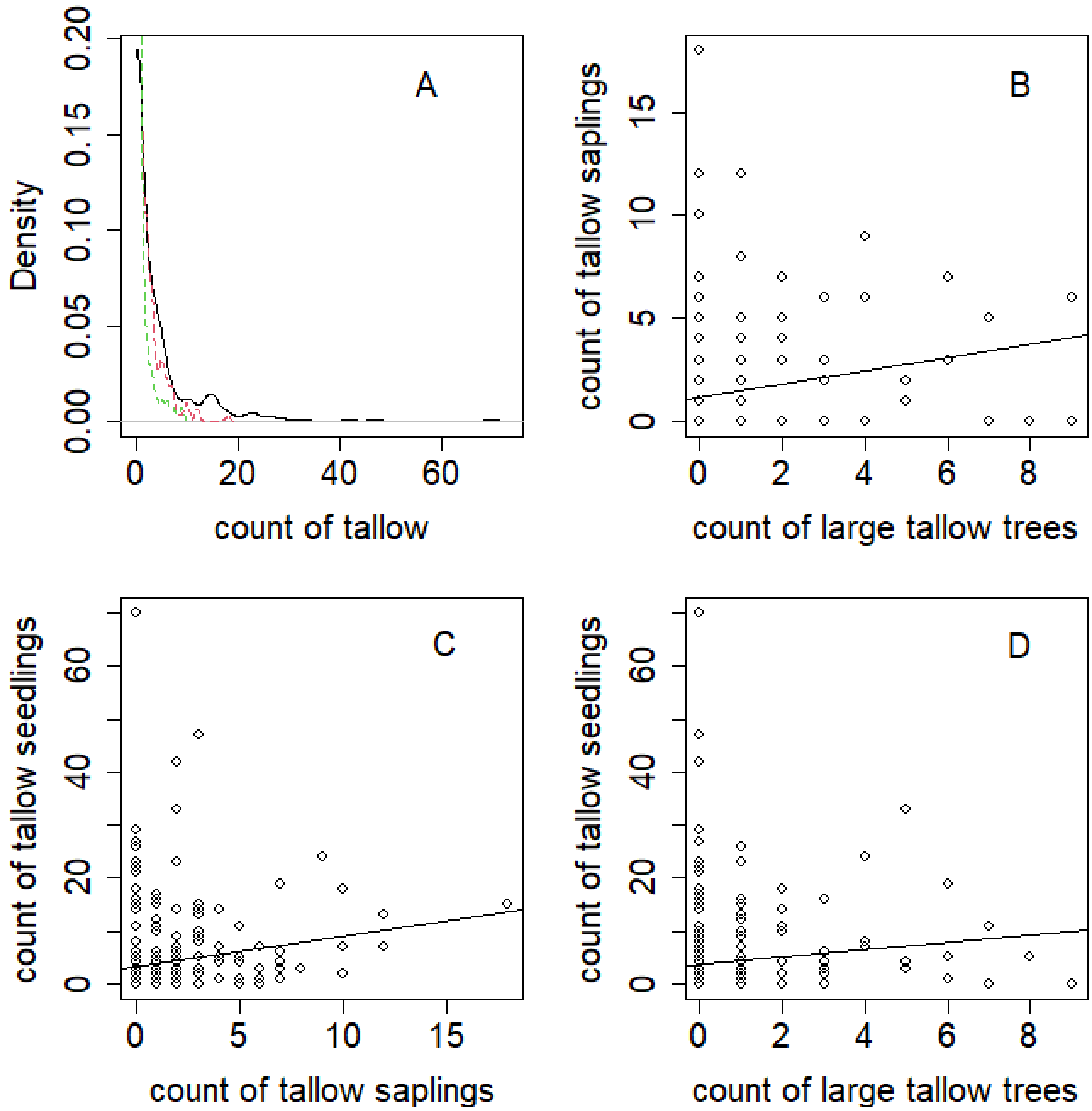
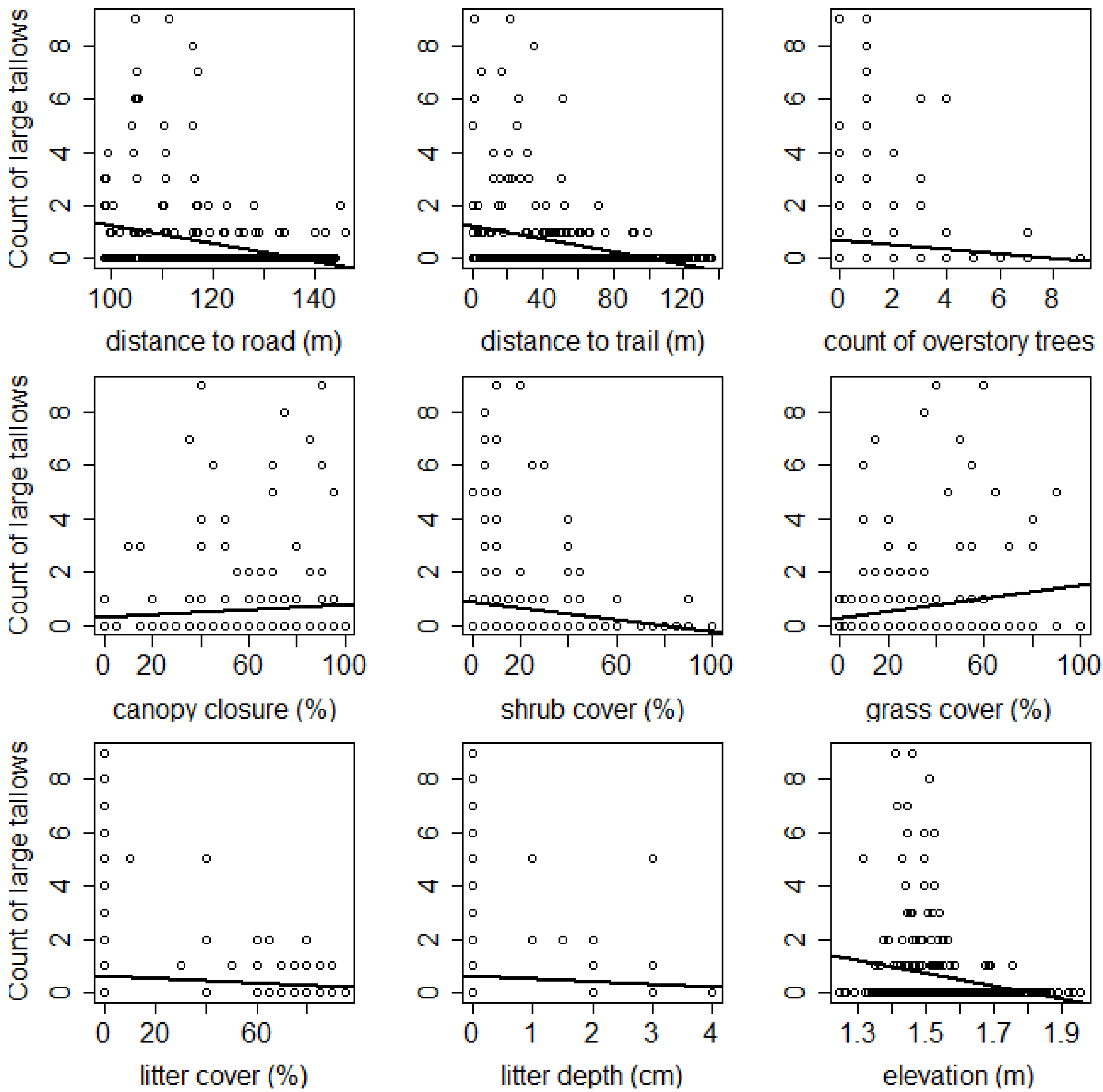
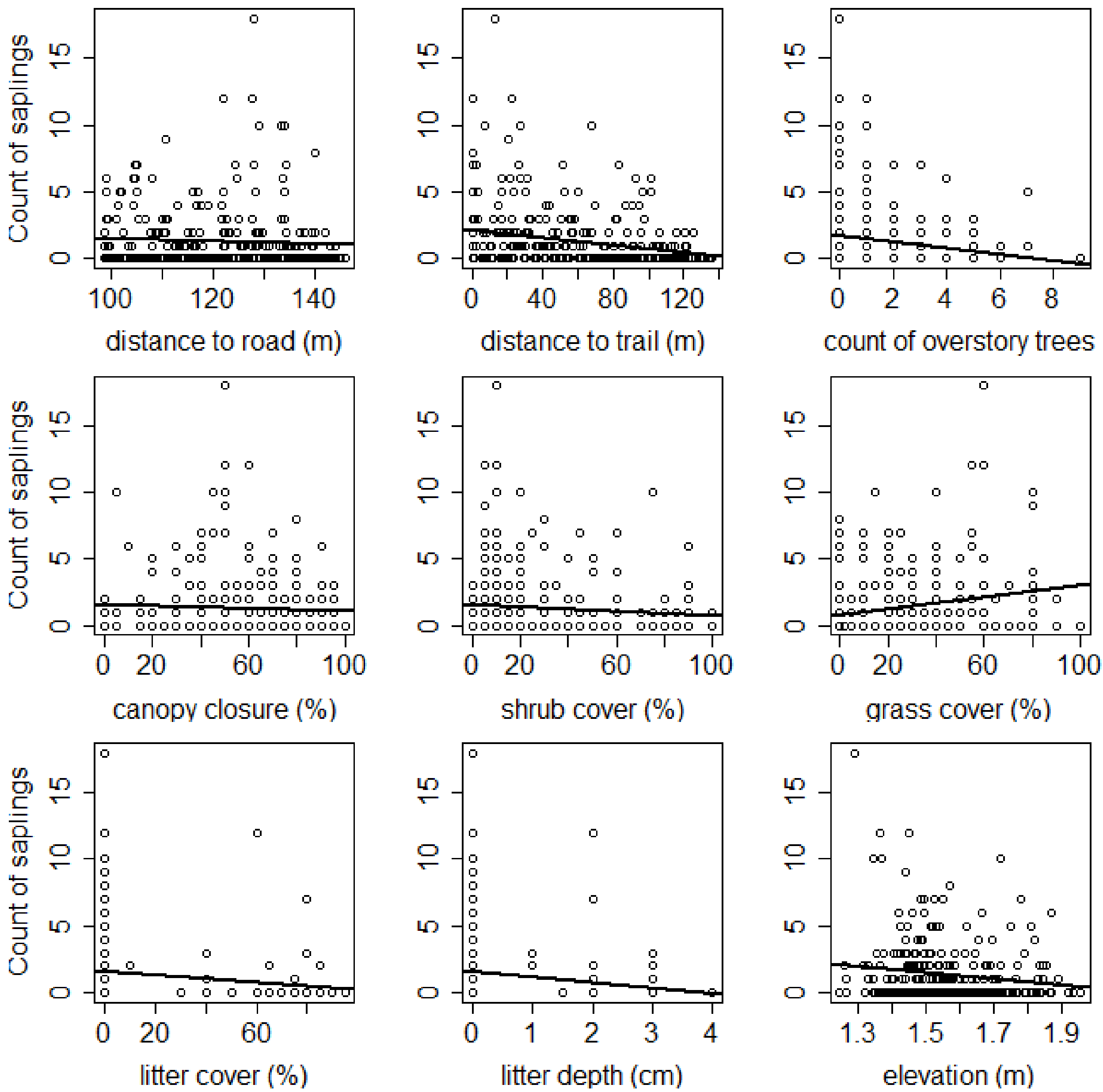


Figure 3.2 The smoothed probability density function (A) and the scatterplots (B-D) of Chinese tallow by size classes showing the typical linear trends. The straight line represents the linear trend line.


Count of large tallows
distance to road (m)
distance to trail (m)
count of overstory trees
canopy closure (%)
shrub cover (%)
grass cover (%)
litter cover (%)
litter depth (cm)
elevation (m)



Count of saplings
distance to road (m)
distance to trail (m)
count of overstory trees
canopy closure (%)
shrub cover (%)
grass cover (%)
litter cover (%)
litter depth (cm)
elevation (m)

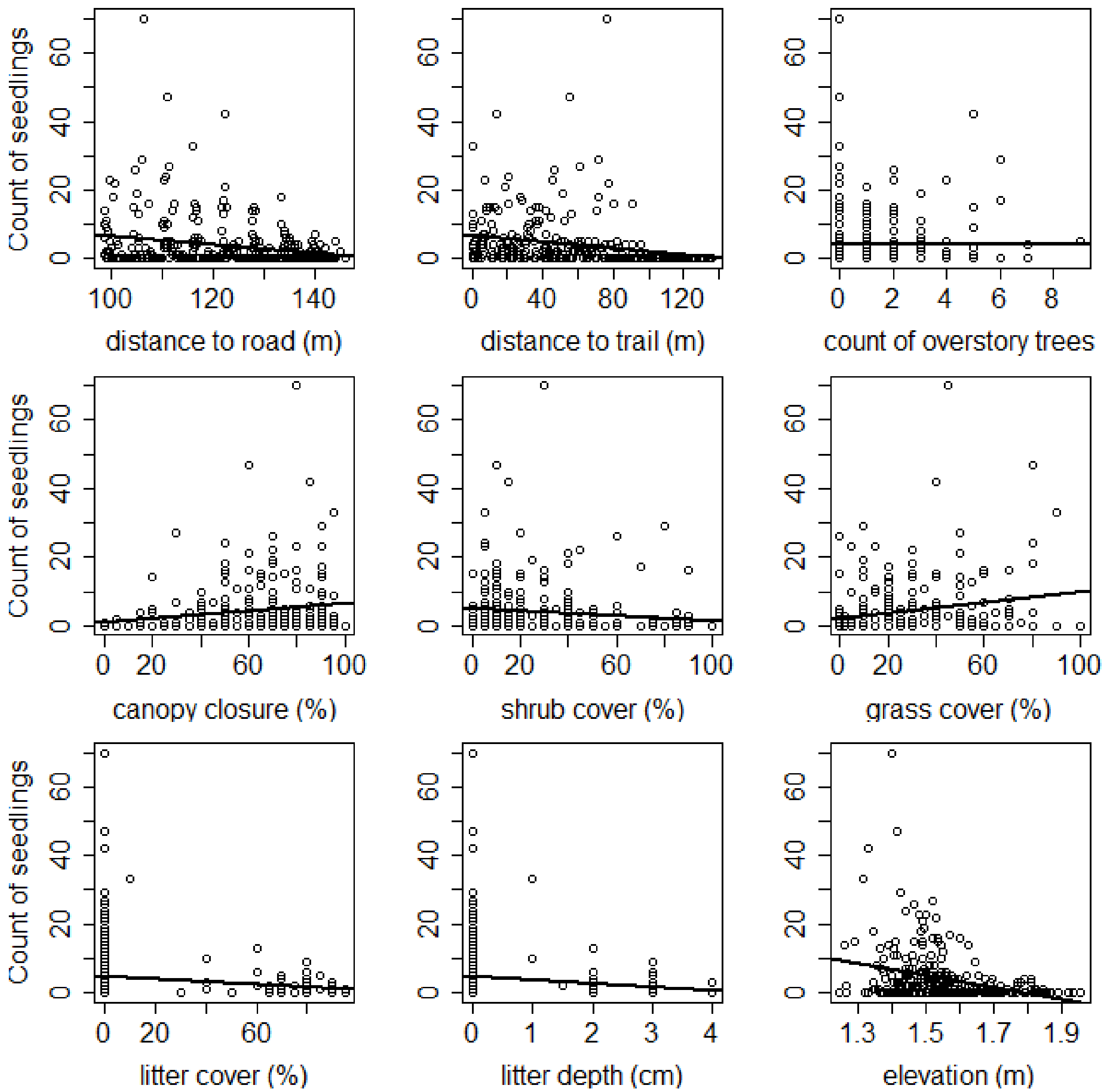


Figure 3.3 Changes in the invasion degree (count) of Chinese tallow by size classes with site and stand factors showing the typical linear trends. The straight line represents the linear trend line.

Results indicated that the presence of Chinese tallow was a function of two factors: distance to the road (a proxy of propagule pressure) and elevation (Figure 3.4A). Quadrats < 117 m from the road had an invasion probability of 0.41, which was 3.7 times higher than quadrats ≥ 117 m (invasion probability = 0.11). Within the quadrats < 117 m from the road, quadrats < 1.6 m in elevation had an invasion probablity of 0.69, which was 11.5 times higher than quadrats > 1.6 m in elevation. The CART (regression tree) model of the invasion degree of large tallow trees was equivalent to the presense proabability model in significant variables and their cutoff values (Figure 3.4B). The total number of large tallow tree was 162 among the 281 quadrats, approximately 87 % (141/162) of large tallow trees were found in 120 quadrats < 117 m from the road (the right terminal node) with the remaining 13% (21/162) occurring in 161 quadrats ≥ 117 m (the left terminal node). Among those quadrats < 117 m from the road, nearly all large tallow trees (97.9%, 138/141) were found in quadrats with low elevation < 1.6 m (Figure 3.4B). Results suggested that recent tallow invasion (saplings and seedlings) continue to be confined to previous invasion areas (areasn with large tallow trees) which were correlated with distance to the road and elevation. Recent colonization and establishment of Chinese tallow saplings and seedlings were mainly controlled by the distance to the trail (Figures 3.4 C and D). Other variables including distance to the road, elevation, canopy closure and grass coverage approved to be important as well. Quadrats with shorter distance to road, lower elevation, smaller canopy clsure, and larger grass cover may have more Chinese tallow saplings and seedlings (Figure 3.4 C D). Generally, more Chinese tallow saplings and seedlings were found in quadrats with shorter distances to the road and the trail, lower elevation and canopy closure, but higher grass coverage. The presence probability model (Figure 3.4A) and the invasion degree models (Figure 3.4 B-D) indicated that propagule pressure and overstory and understory conditions play significant roles in tallow invasion.

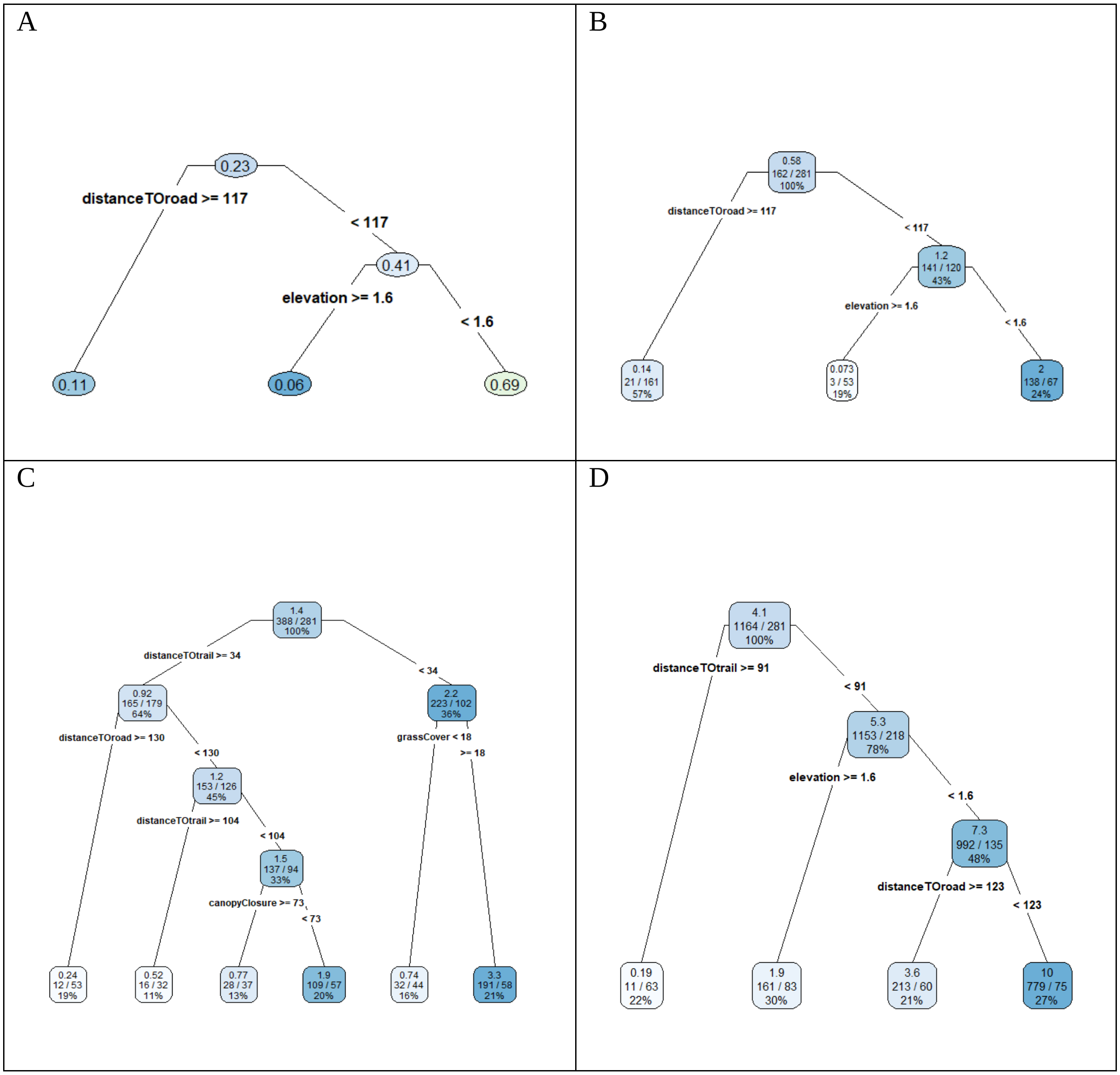


Figure 3.4 The presence probability (A) and invasion degree CART models (B-D) for tallow by size class (B: large tallow; C: tallow sapling; D: tallow seedling). The number in each node in figure A represents invasion probability among the quadrats that meet the splitting criteria. The top, middle and bottom numbers in each node in Figure B-D represent the average number of tallow trees in a quadrat, total number of tallow trees/total number of quadrats, and the proportion of quadrats falling within a node.

3.3.2 Post-fire changes of tallow saplings and seedlings by site factors

The area dominated by native grasses had the most Chinese tallow seedlings ($p<0.05$) before (2018) and after the burn (2019), but the number of tallow seedlings increased dramatically after burn (Figures 3.5 A and B). The number of Chinese tallow seedlings in the litter-, cogongrass- and shrub-covered areas also increased after burn ($p< 0.05$) (Figures 3.5 B). The number of Chinese tallow saplings in native grass covered areas was larger than that of other vegetation covered quadrats (shrub-, litter-, and pine sapling-covered) except cogongrass covered areas ($p< 0.05$) in 2018 (Figures 3.5 C) and 2019 (Figure 3.5 D). Figure 3.5 E showed that more large tallow trees were located in the native grass covered area compared to other vegetation types. This could explain why there were more tallow saplings and seedlings in native grass covered areas after burn, as the native grass covered areas had more large tallow seed-trees.

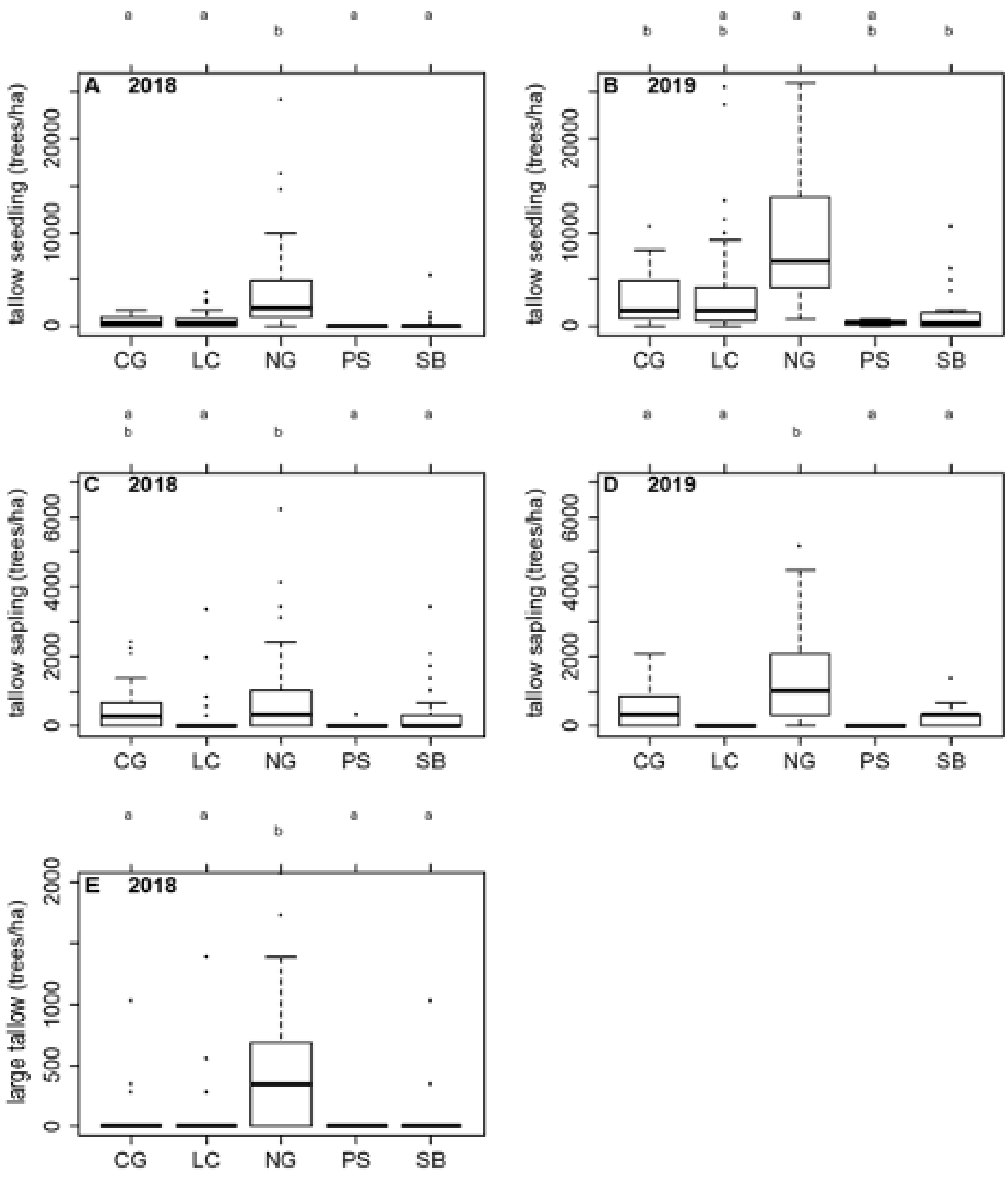


Figure 3.5 Changes of Chinese tallow seedlings and saplings by vegetation cover types (CG=cogongrass, LC=litter covered, NG=native grass, PS=pine sapling, and SB=native shrub) before (2018) and after (2019) the prescribed burn.

To better understand the relationship between understory condition and tallow invasion, the changes in predisposing site factors after the burn were compared in the hardwood-dominated and the pine-dominated quadrats separately. Within the hardwood-dominated quadrats (Figure 3.6A), the understory litter cover decreased dramatically ($p< 0.01$) after prescribed burn and the medium value of litter coverage had dropped to 35% in 2019. Litter depth also decreased significantly ($p< 0.01$) after the prescribed burn in 2019 (Figure 3.6 B). The number of Chinese tallow saplings was not significantly altered, but the number of Chinese tallow seedlings increased dramatically (medium value increased from 200 trees/ha to 2000 trees/ha, $p< 0.01$) (Figures 3.6 C and D). In contrast to what was observed in the hardwood-dominated quadrats, the grass cover increased significantly ($p< 0.01$) in the pine-dominated quadrats after the prescribed burn (Figure 3.6 E). Meanwhile, the shrub coverage decreased significantly ($p<0.01$, Figure 3.6 F). There was no litter cover and depth in the pine plots before the burn and no significant changes following the burn. The numbers of Chinese tallow seedlings and saplings also increased significantly in pine plots following burning ($p< 0.01$, Figures 3.6 G and H).

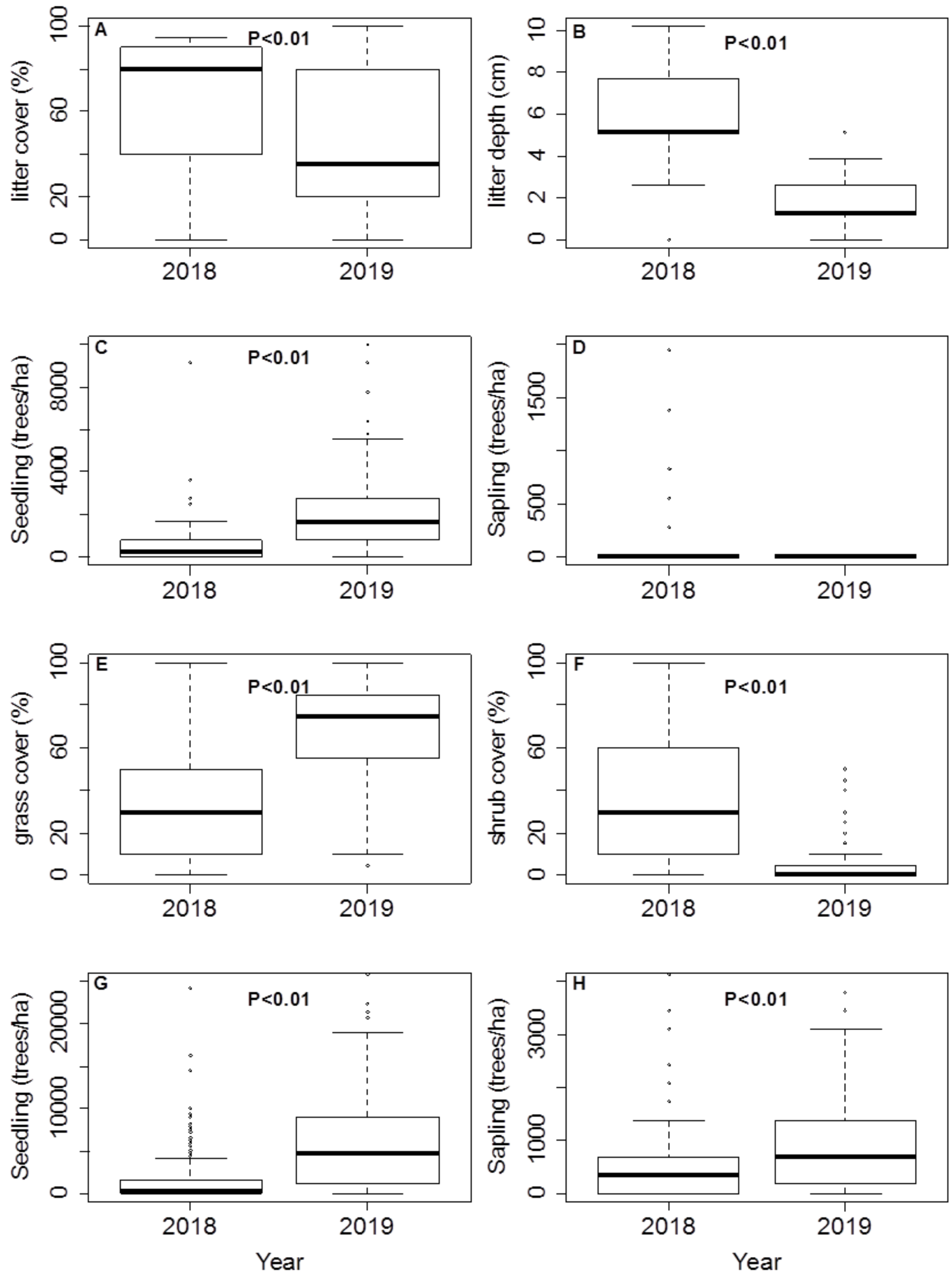


Figure 3.6 Recovery of understory vegetation structures after burn in hardwood and pine plots (A-D hardwood plot; E-H pine flatwood plot). The changes of Chinese tallow seedlings and saplings abundance in 2018 and 2019 (C D E F). The changes of litter cover (%) and litter depth (cm) in 2018 and 2019 (A B). The changes of grass cover (%) and shrub cover (%) (G H).

Following the prescribed fire, ANCOVA results indicated that compared to the cogongrass covered area, the native grass covered areas had more Chinese tallow saplings ($p < 0.001$) and fewer Chinese tallow saplings in shrub covered areas ($p < 0.001$). There was not a significant difference in the number of Chinese tallow saplings ($p = 0.98$) between the hardwood-dominated quadrats and pine-dominated quadrats after the burn. However, the number of Chinese tallow saplings increased significantly as the shrub coverage decreased ($p < 0.001$) after the prescribed burn in hardwood-dominated plots. There were more Chinese tallow seedlings in native grass covered areas ($p < 0.001$) compared to cogongrass and litter covered areas before burn. However, in areas with pine saplings and native shrubs, there were fewer Chinese tallow seedlings ($p < 0.001$). There were more Chinese tallow seedlings in the pine-dominated quadrats than that in the hardwood-dominated quadrats after the prescribed burn ($p < 0.001$). Chines tallow seedlings had significant negative correlations with the shrub and cogongrass cover compared to Chinese tallow saplings ($p < 0.001$). There was a significant negative correlation between litter depth and the number of Chinese tallow seedlings ($p < 0.001$) after the prescribed burn in 2019.

3.4 Discussion

The extremely right skewed pdfs (probability density functions) and positive trends between the number of large tallow trees, saplings and seedlings among the 281 contiguous quadrats within thirty 1m^2 sub-quadrats provided strong evidence of clustered invasion patterns or coexistence of Chinese tallow of different size classes by potential limiting factors to the invasion processes (Lockwood et al. 2005, Fan and Crosby 2012). Basically, the invasion probability and degree of Chinese tallow are related to a set of variables reflecting the change in both propagule pressure (e.g., distance to the road and to the hiking trail) and overstory- and understory- conditions. This showed that invasion probability and degree decreased with the increase of distance to the road and trail, overstory tree density, shrub coverage, litter coverage and depth, and elevation, but the increased with the increase of canopy closure and grass coverage (Figure 3.3). At microscales (e.g., 30 m^2), the great variations of Chinese tallow invasion degree (count) by these factors provided further evidence that Chinese tallow invasion was a stochastic process controlled by multiple limiting factors. The CART models (Figure 3.4) explicitly showed the critical role of propagule pressure and its interactions with overstory- and understory-conditions in Chinese tallow invasion processes (Wang et al. 2011a, Yang et al. 2019, Zomlefer et al, 2008, Sui 2015). Propagule pressure and microtopography were the major determinant of large tallow trees and seedlings. However, Chinese tallow saplings were determined by propagule pressure, elevation, canopy closure, and grass coverage. Areas close to forest edge (e.g., road, fire line) and/or with low elevation are more likely to be invaded by Chinese tallow because of high propagule pressure - a large soil seed bank stored up by birds and/or water current (Bruce et al. 1997, Renne et al. 2000, Pile et al. 2017). As seen in this study, invasion probability was about 3.7 times higher in quadrats < 117 m to roads than those that were >= 117 to roads. The invasion probability of quadrats < 1.6 m in elevation was 11.5 times higher than quadrats > 1.6 m in elevation (Figure 3.4 A). Moreover, about 87% of large tallow trees were found in 120 quadrats < 117 m to the road, and nearly all these large tallow trees (97.9%) were found in quadrats with elevation < 1.6 m (Figure 3.4 B).

As a pioneer or disturbance-dependent species, Chinese tallow establishment and growth depends on sufficient light; however, Chinese tallow seedlings can tolerate a wide range of light conditions (Jones and McLeod 1989, Nijjer et al. 2007, Siemann and Rogers 2001, Wang et al. 2011b, Pile et al. 2017). This explains why large numbers of Chinese tallow saplings can only be found under low or moderate canopy closure (< 0.7), whereas numerous seedlings can colonize under high canopy closure (≥ 0.7) (Yang 2019). The role of understory vegetation cover in tallow establishment (from seedlings to saplings) are owing to the negative competition from native species for light, nutrient, water, and growing space, and large numbers of tallow saplings mostly occur in areas with high grass/herbaceous species coverage (low shrub coverage) (Fan 2018, Fan et al. 2018b, Yang et al. 2019). Therefore, the efforts to create sparse canopy structure and to restore grass dominated understory vegetation will inevitably increase the risk for Chinese tallow invasion and establishment in areas with high propagule pressure. To mitigate or control the risk, proactive treatments to reduce the propagule pressure by removing seed trees is critical prior to overstory and understory treatments such as thinning and prescribed burn.

Prescribed fire plays an important role in nutrient recycling, regulating plant succession and maintaining wildlife surroundings, and it is an essential tool to protect and restore native ecosystems in southern U.S. (Rideout and Oswald, 2002, Mutch 1994). Prescribed fire is also applied as a tool to control insect and invasive species (DiTomaso et al. 2006, Richburg and Patterson 2003). However, the effectiveness of fire in terms of maximizing the diversity of native species and minimizing the invasion risk of invasive species may change with understory conditions or different ecosystems. In this study, different understory vegetations were observed in species or life-form (e.g., shrub, grass, herbaceous species) compositions. In litter covered and grass/herbaceous species dominated areas, prescribed fire facilitated Chinese tallow invasion. Prescribed fire consumed large amount of litter and understory vegetation that can impede the invasion of Chinese tallow. As a result, frequent prescribed fires tend to promote grass/herbaceous species dominance (suppressing shrubs) and thus could increase the risk of Chinese tallow invasion (Lavoie et al. 2010, US fish and wildlife service 2007).

The number of Chinese tallow seedlings increased dramatically after the prescribed burn in 2019 both in hardwood-dominated quadrats and pine-dominated quadrats, but the number of Chinese tallow saplings followed fire increased significantly only in pine-dominated quadrats (Figure 3.6). Overall, the number of Chinese tallow saplings and seedlings in pine-dominated quadrats was higher than that in hardwood-dominated quadrats (Figure 3.6), which suggest that pine-dominated quadrats has lower resistance and were more susceptible to tallow invasion followed prescribed burn. In the pine-dominated quadrats, less litter accumulated in the understory compared with the deeper litter layers observed in hardwoods-dominated quadrats, but fire can consume litter and create suitable environmental conditions for Chinese tallow seed germination and seedling colonization. Overstory may interact with understory to affect fire behavior and tallow invasion.

3.5 Conclusion

Chinese tallow invasion is a serious threat to native ecosystems, such as longleaf pine and slash pine forest, coastal prairies, and hardwood forests in the southeastern Coastal Plain (Gan et al. 2009, Wang et al. 2011b). Prescribed fire is an important tool for restoring native ecosystems, but its effects on Chinese tallow invasion varies with invasion stages (Sui 2015, DiTomaso et al. 2006, Richburg and Patterson 2003). This study used the invasion probability and degree of invasion of Chinese tallow to evaluate effects of microscales (30 m^2) stand and site factors on tallow invasion and how Chinese tallow invasion responds to prescribed burns.

The invasion probability of Chinese tallow was influenced by distance to road and elevation. Invasion degree of large tallow was higher in quadrats with shorter distance to road/trail and lower elevation. Larger numbers of Chinese tallow saplings and seedlings were found in quadrats with shorter distances to the road and the trail, lower elevation and canopy closure, but higher grass coverage. The invasion probability and invasion degree of Chinese tallow showed that propagule pressure and overstory and understory conditions significantly affect Chinese tallow invasion process. The invasion degree of Chinese tallow sapling and seedling in quadrats with grass covered was higher than that in other understory vegetation types and increased significantly followed a burn (2019). The reason might be that there was more large tallow in native grass covered quadrats which could provide seed banks. There were more tallow seedlings in pine-dominated plot than that in hardwood-dominated plot after prescribed fire, and this may suggest that pine-dominated quadrats are more susceptible to tallow invasion and establishment following prescribed fire treatments.

3.6 References

Bruce, K.A., 1993. Factors affecting the biological invasion of the exotic Chinese tallow tree, Sapium sebiferum, in the Gulf Coast Prarie of Texas. D.Sc. dissertation, University of Houston, Houston, TX, United States. 155p.

Bruce, K.A., Cameron, G.N., Harcombe, P.A. and Jubinsky, G., 1997. Introduction, impact on native habitats, and management of a woody invader, the Chinese tallow tree, Sapium sebiferum (L.) Roxb. Natural Areas Journal, 17(3):255-260.

Conner, W. H., I. Mihalia, and J. Wolfe. 2002. Tree community structure and changes from 1987 to 1999 in three Louisiana and three South Carolina forested wetlands. Wetlands 22(1):58-70.

DiTomaso, J.M., Brooks, M.L., Allen, E.B., Minnich, R., Rice, P.M. and Kyser, G.B., 2006. Control of invasive weeds with prescribed burning. Weed technology, 20(2):535-548.

Fan, Z., Tan, Y. and Crosby, M.K., 2012. Factors associated with the spread of Chinese Tallow in east Texas forestlands. Open Journal of Ecology, 2(3):121-130.

Fan, Z., 2018. Spatial analyses of invasion patterns of Chinese tallow (Triadica sebifera) in a wet slash pine (Pinus elliottii) flatwood in the coastal plain of Mississippi, USA. Forest Science, 64(5):555-563.

Fan, Z., Moser, W.K., Crosby, M.K., Yu, W., Zhang, Y., Hansen, M.H. and Fan, S.X., 2018a. Mapping the invasion stage and invasiveness of major nonnative invasive plants in the upper midwest forestlands, USA. Mathematical and Computational Forestry & Natural Resource Sciences, 10(2):68.

Fan, Z., Yang, S. and Liu, X., 2018b. Spatiotemporal patterns and mechanisms of Chinese tallowtree (Triadica sebifera) spread along edge habitat in a coastal landscape, Mississippi, USA. Invasive Plant Science and Management, 11(3):117-127.

Gan, J., Miller, J.H., Wang, H. and Taylor, J.W., 2009. Invasion of tallow tree into southern US forests: influencing factors and implications for mitigation. Canadian journal of forest research, 39(7):1346-1356.

Grace, J. B. 1998. Can prescribed fire save the endangered coastal prairie ecosystem from Chinese tallow invasion? Endanger. Species Updat. 15(5):70–76.

Grace, J. B., L. K. Allain, H. Q. Baldwin, a G. Billock, W. R. Eddleman, a M. Given, C. W. Jeske, and R. Moss. 2005. Effects of prescribed fire in the coastal prairies of Texas. 46 p.

Jones, R.H. and McLeod, K.W., 1989. Shade tolerance in seedlings of Chinese tallow tree, American sycamore, and cherrybark oak. Bulletin of the Torrey Botanical Club, 116(4):371-377.

Jones, R.H. and McLeod, K.W., 1990. Growth and photosynthetic responses to a range of light environments in Chinese tallowtree and Carolina ash seedlings. Forest science, 36(4):851-862.

Lankau, R.A., Rogers, W.E. and Siemann, E., 2004. Constraints on the utilisation of the invasive Chinese tallow tree Sapium sebiferum by generalist native herbivores in coastal prairies. Ecological Entomology, 29(1):66-75.

Lavoie, M., Starr, G., Mack, M.C., Martin, T.A. and Gholz, H.L., 2010. Effects of a prescribed fire on understory vegetation, carbon pools, and soil nutrients in a longleaf pine-slash pine forest in Florida. Natural Areas Journal, 30(1):82-94.

Lockwood, J.L., Cassey, P. and Blackburn, T., 2005. The role of propagule pressure in explaining species invasions. Trends in ecology & evolution, 20(5):223-228.

Meyer, R., 2011. Fire effects information system: Triadica sebifera. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. Retrieved January. 10: 2014.

Miller, J.H. and Schelhas, J., 2008. 15 adaptive col laborative restoration: a key concept in invasive plant management. P. 9-251 in Invasive plants and forest ecosystems, Kohli R.K., Joes, S., Singh, H.P. and Batish, D.R. (eds). CRC Press, Boca Raton, FL.

Mutch, R.W., 1994. Fighting fire with prescribed fire: a return to ecosystem health. Journal of forestry, 92(11):31-33.

Myers, J.H., Simberloff, D., Kuris, A.M. and Carey, J.R., 2000. Eradication revisited: dealing with exotic species. Trends in ecology & evolution, 15(8):316-320.

Nijjer, S., Rogers, W.E. and Siemann, E., 2007. Negative plant–soil feedbacks may limit persistence of an invasive tree due to rapid accumulation of soil pathogens. Proceedings of the Royal Society B: Biological Sciences, 274(1625):2621-2627.

Oswalt, S.N., 2010. Chinese tallow (Triadica sebifera (L.) Small) population expansion in Louisiana, east Texas, and Mississippi. USDA Publication, 20:1-4.

Pattison, R.R. and Mack, R.N., 2008. Potential distribution of the invasive tree Triadica sebifera (Euphorbiaceae) in the United States: evaluating CLIMEX predictions with field trials. Global Change Biology, 14(4):813-826.

Pile, L.S., Wang, G.G., Knapp, B.O., Walker, J.L. and Stambaugh, M.C., 2017. Chinese tallow (Triadica sebifera) invasion in maritime forests: the role of anthropogenic disturbance and its management implication. Forest ecology and management, 398:10-24.

Reichard, S.H. and Hamilton, C.W., 1997. Predicting invasions of woody plants introduced into North America: predicción de invasiones de plantas leñosas introducidas a Norteamérica. Conservation Biology, 11(1):193-203.

Renne, I.J., Gauthreaux, S.A. and Gresham, C.A., 2000. Seed dispersal of the Chinese tallow tree (Sapium sebiferum (L.) Roxb.) by birds in coastal South Carolina. The American Midland Naturalist, 144(1):202-216.

Richburg, J.A. and Patterson III, W.A., 2003. Can northeastern woody invasive plants be controlled with cutting and burning treatments. Proceedings, Using Fire to Control Invasive Plants: What's New, What Works in the Northeast, 1-3p.

Rideout, S. and Oswald, B.P., 2002. Effects of prescribed burning on vegetation and fuel loading in three east Texas state parks. The Texas Journal of Science, 54(3):211-226

Rogers, W.E., Nijjer, S., Smith, C.L. and Siemann, E., 2000. Effects of resources and herbivory on leaf morphology and physiology of Chinese tallow (Sapium sebiferum) tree seedlings. Texas Journal of Science, 52(4, Supplement):43-56.

Rogers, W.E. and Siemann, E., 2003. Effects of simulated herbivory and resources on Chinese tallow tree (Sapium sebiferum, Euphorbiaceae) invasion of native coastal prairie. American Journal of Botany, 90(2):243-249.

Sakai, A.K., Allendorf, F.W., Holt, J.S., Lodge, D.M., Molofsky, J., With, K.A., Baughman, S., Cabin, R.J., Cohen, J.E., Ellstrand, N.C. and McCauley, D.E., 2001. The population biology of invasive species. Annual review of ecology and systematics, 32(1):305-332.

Siemann, E. and Rogers, W.E., 2001. Genetic differences in growth of an invasive tree species. Ecology Letters, 4(6):514-518.

Sui, Z., 2015. Modeling tree species distribution and dynamics under a changing climate, natural disturbances, and harvest alternatives in the southern United States. D.Sc. dissertation Mississippi State University, Starkville, MS, United States. 194p.

Tan, Y., 2011. Predicting the potential distributions of major invasive species using geospatial models in southern forest lands. M.Sc. dissertation, Mississippi State University, Starkville, MS, United States.76p.

Tian, N., Fan, Z., Matney, T.G. and Schultz, E.B., 2017. Growth and stem profiles of invasive Triadica sebifera in the Mississippi coast of the United States. Forest Science, 63(6):569-576.

Urbatsch, L., 2000. Chinese tallow tree (Triadica sebifera (L.) Small. plant guide. Natural Resources Conservation Service (NRCS).

US Fish and Wildlife Service, 2007. Mississippi Sandhill Crane National Wildlife Refuge comprehensive conservation plan. US Department of the Interior Fish and Wildlife Service Southeast Region, Atlanta, GA.

Van Wilgen, B.W. and Richardson, D.M., 2014. Challenges and trade-offs in the management of invasive alien trees. Biological invasions, 16(3):721-734.

Wang, H.H., Grant, W.E., Swannack, T.M., Gan, J., Rogers, W.E., Koralewski, T.E., Miller, J.H. and Taylor, J.W., 2011a. Predicted range expansion of Chinese tallow tree (Triadica sebifera) in forestlands of the southern United States. Diversity and Distributions, 17(3):552-565.

Wang, R., Hanna, M.A., Zhou, W.W., Bhadury, P.S., Chen, Q., Song, B.A. and Yang, S., 2011b. Production and selected fuel properties of biodiesel from promising non-edible oils: Euphorbia lathyris L., Sapium sebiferum L. and Jatropha curcas L. Bioresource technology, 102(2):1194-1199.

Wieland, R.G., 2007. Habitat types and associated ecological communities of the Grand Bay National Estuarine Research Reserve. Grand Bay National Estuarine Research Reserve: An Ecological Characterization (Peterson, MS, GL Waggy and MS Woodrey, editors). Grand Bay National Estuarine Research Reserve, Moss Point, Mississippi, 104-147p.

Williamson, M.H. and Fitter, A., 1996. The characters of successful invaders. Biological conservation, 78(1-2):163-170.

Yang, S., 2019. Distribution and spread mechanisms of Chinese tallow (Triadica sebifera) at multiple spatial scales within forests in the southeastern United States. D.Sc. dissertation, Mississippi State University, Starkville, MS, United States. 150p.

Yang, S., Fan, Z., Liu, X., Ezell, A.W., Spetich, M.A., Saucier, S.K., Gray, S. and Hereford, S.G., 2019. Effects of prescribed fire, site factors, and seed sources on the spread of invasive triadica sebifera in a fire-managed coastal landscape in southeastern Mississippi, USA. Forests, 10(2):175.

Zomlefer, W.B., Giannasi, D.E., Bettinger, K.A., Echols, S.L. and Kruse, L.M., 2008. Vascular plant survey of Cumberland Island National Seashore, Camden County, Georgia. Castanea, 73(4):251-282.

Zou, J., Rogers, W.E. and Siemann, E., 2008. Increased competitive ability and herbivory tolerance in the invasive plant Sapium sebiferum. Biological Invasions, 10(3):291-302.

CHAPTER IV

Summary

Based on the most recent US Forest Service's Forest Inventory and Analysis (FIA) data, Chinese tallow has become well established across the 67 coastal counties in the Gulf of Mexico, ranking 17th out of the 135 encountered species. Studies showed that fire-managed landscapes were highly susceptible to Chinese tallow invasion and fire may facilitate Chinese tallow spread. This study proposed a multiscale (stand, landscape) approach to study the mechanisms of Chinese tallow invasion and factors influencing Chinese tallow establishment and spread under fire disturbance. It will provide an integrated approach to control and mitigate Chinese tallow spread as fire is widely used as a tool to restore the native coastal ecosystems.

Will fire increase the risk of tallow invasion across the Gulf coastal region? Chapter 2 showed that fire return interval interacts with propagule pressure level and landscape/stand factors to affect Chinese tallow invasion probability and abundance in a fire-managed landscape. Under frequent, low-intensity fires, pine flatwoods were more susceptible to Chinese tallow invasion than pine savannas largely due to its larger overstory basal area and relatively lower understory shrub coverage. Large overstory basal area is needed for Chinese tallow seed disperdal birds, while low shrub coverage benefits the colonization and establishment of Chinese tallow seedlings and saplings. Therefore, more Chinese tallow seedlings and saplings are found in the understory of pine flatwoods, which may rapidly take over the site as soon the overstory is removed, either by hurricances or mechnically through clearcutting. To manage pine flatwoods, a longer fire interval such as five to six years is recommend to reduce Chinese tallow invasion and the accumulation of large numbers of tallow seedlings and saplings accumulated in the understory so that the density of tallow populations can be controlled to a managable level (a threshod) if it is difficult or impossible to be completely eradicated. To manage pine savannas, however, a shorter fire return interval such as two to three years should be adopted to kill or top-kill tallow seedlings and saplings to prevent the development of large tallow (seed) trees.

Restricted by the small sample size (n = 55 plots) and the sparseness of Chinese tallow-invaded plots (n = 17 plots), the landscape level study did not consider spatial autocorrelation among the plot-level data in statistical modeling and parameter estimation. More plots should be measured in the future and spatial regression models (e.g., spatial logisical regression, simutaneous or conditional autoregressive regression models) be used to refine model parameters. The spatial regreesion models will provide more insightful information of the nonstationary nature of tallow invasion and spread by selected predisposing factors and be capble to estimate the impact of inciting factors such as fire and hurricane on tallow invasion more accurately by reducing or removing potential correlations in data.

How will fire interact with site and stand factors to affect seed germination and the establishment of Chinese tallow seedlings and saplings in invaded stands? Chapter 3 examined impacts of selected site and stand factors on Chinese tallow invasion at microscales (30 m^2). At the mircroscale, propagule pressure represented by the distance to road/trail remain to be a primary limiting factor as shown by the CART models, and propagule pressure and microtopograpy (elevation) as major determinants of Chinese tallow seed bank, to a large degree, determining the abundance of Chinese tallow seedlings followed fire. We also noted the difference in the abundance of tallow seedlings and saplings by overstory species compositions: there were more tallow seedlings and saplings in pine-dominated areas than that in hardwoods-dominated areas, primarily due to the difference in soil seed bank as more tallow seed dispresal birds often use the pine trees. In addition, hardwoods-dominated areas have thick litter layers which impede tallow seed germination. But low-intensity ground fire may consume litter layers and stimulate seed germination and the recruitment of tallow seedlings as shown by thinner litter layers but increasing numbers of tallow seedlings after the prescsribed burn in May of 2019.

The findings of Chinese tallow invasion at microscales indicate that the role of fire may change with site and stand conditions. A future study will be evaluating the effect of fire on the mortality and rate of germination of tallow seeds in the soil or litter seed bank.