Forest Science, 2021, **67**, 491–500
DOI: 10.1093/forsci/fxab019
Advance access publication 22 July 2021
Research Article

Biometrics

Spatiotemporal Invasion Severity of Chinese Tallow (*Triadica sebifera*) and Invasibility of Forest Types in Southern US Forestlands

Sunil Nepal, W. Keith Moser, and Zhaofei Fan

Sunil Nepal (szn0044@auburn.edu), Zhaofei Fan (zzf0008@auburn.edu) School of Forestry and Wildlife Sciences, Auburn University, 602 Duncan Drive, Auburn, AL 36849, USA. W. Keith Moser (warren.k.moser@usda.gov) US Department of Agriculture, Forest Service, Rocky Mountain Research Station, 2500 S. Pine Knoll Dr., Flagstaff, AZ 86001, USA.

Abstract

Quantifying invasion severity of nonnative invasive plant species is vital for the development of appropriate mitigation and control measures. We examined more than 23,250 Forest Inventory and Analysis (FIA) plots from the southern coastal states of the United States to develop an alternative method to classify and map the invasion severity of Chinese tallow (*Triadica sebifera*). Remeasured FIA plot-level data were used to examine the spatiotemporal changes in the presence probability and cover percentage of tallow. Four invasion severity classes were identified by using the product of presence probability and cover percentage. Chinese tallow invasion severity increased over time with 90 and 123 counties being classified into the highest severity class for the first and second measurement, respectively. Further, the invasibility of major forest-type groups by severity class was examined using the product of the county-level mean presence probability and mean cover percentage of Chinese tallow as a proxy of invasibility. Longleaf/slash pine (*Pinus palustris/P. elliottii*) forests were highly resilient to the Chinese tallow invasion. In contrast, elm/ash/cottonwood (*Ulmus spp./Fraxinus spp./Populus deltoides*) and oak/gum/cypress (*Quercus spp./Nyssa spp./Taxodium spp.*) forest-type groups were vulnerable to invasion.

Study Implications: In the southern United States forestland, differences in invasion severity and vulnerability of forest types to Chinese tallow invasion have been observed across time and space. Our findings provide insight into spatial variations in the severity of Chinese tallow invasion and the relative susceptibility of different forest-type groups in the region to inform monitoring and management of this invasive species. High invasion severity occurs in the lower Gulf of Mexico coastal region of Texas, Louisiana, and Mississippi and the Atlantic coastal region of South Carolina and Georgia, with the longleaf/slash pine and oak/gum/cypress forest-type groups being most susceptible to Chinese tallow invasion. Based on these results, we recommend that management efforts be tailored to the different invasion severity classes. Forests in the high-severity class need a management program coordinated across different agencies and landowners to curb the increase of tallow populations to prevent stand replacing risks. The monitoring of Chinese tallow spread should focus on longleaf/slash pine, loblolly/shortleaf pine, and oak/gum/cypress groups, because the spread rate was higher in these forest-type groups. A better use of scarce resources could be to treat lands in the moderate- and low-severity classes to reduce the propagule pressure levels and post-invasion spread. For those counties with a minimal-severity condition, early detection and eradiction measures should be taken in a timely maner to prevent tallow from invading noninvaded neighboring counties. Managers may be able to treat a larger area of these lands for a given investment compared with lands already severely invaded.

Keywords: Chinese tallow, invasion severity, invasibility, forest inventory and analysis (FIA), classification and regression tree

The southern region of the US is often known as the "wood basket" of the nation (Oswalt et al. 2019). Both forest biodiversity and productivity are high in the southern states, although not always in the same location. Southern forests are an important economic driver in the region because they are a substantial contributor to the economy and to five million private forest landowners of the region. The future benefits of these forests can only be assured if those forests are sustainably managed. However, the future of the forests in this region is severely threatened by the invasion of nonnative invasive plants (NNIP). NNIPs can cause significant ecological and economic damage to a forest. For example, they can compete and displace native and desirable species, degrade timber production and recreational values, lower carbon sequestration and biodiversity, change stand structure, and alter fire and natural disturbance regimes (Macdonald 1992, Pimentel et al. 2005, Moser et al. 2009a, Eviner et al. 2012). The degradation of ecosystem functions and services is related to the abundance and invasion severity of NNIPs as well as the invasibility (susceptibility) of an ecosystem to an invasive species. More than 300 potentially invasive plants have been identified in the southern states, and some are deemed serious threats to the local ecosystem. Miller et al. (2013) noted that more than 9% of the forested land in the South was infested with one or more NNIP species. Further, NNIPs are expanding in extent and affecting forest productivity and ecosystem function (Moser et al. 2009b, Miller et al. 2013).

Chinese tallow (*Triadica sebifera,* hereafter, tallow) tree, an NNIP of considerable concern, is increasingly characterized as a threat to southern forestlands (Wear and Greis 2013). Tallow has been spreading at an unprecedented rate in the

Received: December 22, 2020. **Accepted:** May 26, 2021
Published by Oxford University Press on behalf of the Society of American Foresters 2021.

region since it was initially introduced into coastal areas of South Carolina and Georgia in the late 1700s and was planted widely by the US Department of Agriculture in southeast Texas in the 1900s for the soap industry (Howes 1949, Miller et al. 2013, Pile et al. 2017b). Tallow cover has been expanding at an increasing rate (Fan et al. 2012, Suriyamongkol et al. 2016) and has the capability to replace native forest species in the native forest stand (Gan et al. 2009). In eastern Texas alone, the estimated tallow cover exceeded 160,000 acres between 2001 and 2003 (Rudis et al. 2006). Scientists expect the rate of spread to continue in many heavily infested areas and beyond (Gan et al. 2009, Miller et al. 2013).

As the severity and extent of NNIPs has increased across the region, species-specific decision support tools such as spread models and maps have assumed increasing importance (Fan et al. 2018). The increasing economic damage and resulting cost of control suggest that efforts to control tallow should target the establishment phase (Webster et al. 2006, Moser et al. 2009a). The invasion severity of NNIPs describes the likelihood of invasion and the potential harm to native forest ecosystems (Venette et al. 2010). Several approaches have been tested to quantify invasion severity. For example, Bazzichetto et al. (2018) used nonnative invasive species distribution models to predict invasion severity. Invasion severity typically reports risk as the relative likelihood of invasive species presence (Yemshanov et al. 2009, Bazzichetto et al. 2018); however, this term fails to express the impact on the ecosystem. Venette et al. (2010) suggested including impact of invasion on the forested area. Invasion severity may be described as the potential area of infestation and the seriousness of invasion. Rudis et al. (2006) used invasive species cover percentage data to classify FIA plots into different severity classes. A higher percentage cover of an invasive species suggests greater levels of severity. Using this protocol, Rudis et al. (2006) used total cover to describe the severity of tallow invasion in eastern Texas.

Invasion severity based on the presence probability and coverage of NNIPs is one of the recommended measures to quantify invasion severity and potential threats to native ecosystems (Catford et al. 2012). An index of invasion severity should not only aid in the assessment of the extent of NNIPs, reveal spatial and temporal trends, and act as an early warning sign of ecological degradation, but also help to guide management efforts. Bradley et al. (2018) also suggested that a robust assessment of the invasion risk or invasibility of an ecosystem can be achieved using both presence and coverage information of an invasive species. Many distribution maps have been created based on the presence or absence of NNIPs or some specific invasion indicators such as alien species richness, abundance, and relative abundance at the regional level (Gan et al. 2009, Fan et al. 2012, Iannone et al. 2015). In this study, we had access to a comprehensive data source—the US Forest Service's Forest Inventory and Analysis program (FIA) database—which provides extensive spatial and temporal data for NNIPs with presence and cover percentage at the plot level. These variables can be used to classify invasion severity (Catford et al. 2012, Bradley et al. 2018, Fan et al. 2018).

In this study, we intend to evaluate county-level invasion risk and severity of tallow across southeastern US forestlands using repeatedly measured FIA plots during the most recent two inventory cycles. Our specific objectives in this study are to quantify and classify invasion severity and examine the trends over time for tallow and to compare the invasibility of selected forest-type groups to tallow invasion by identified severity classes.

Materials and Methods

Study Area

For this study we chose seven heavily forested coastal states of the southern US: eastern Texas, Louisiana, Mississippi, Alabama, Florida, Georgia, and South Carolina. The forests of the southern coastal states are highly diverse, ranging from upland oak/hickory forest to lowland gum/cypress swamp (Wear and Greis 2012). Six major forest-type groups that were identified in the regions are elm/ash/cottonwood, loblolly/shortleaf pine, longleaf/slash pine, oak/gum/cypress, oak/hickory, and oak/pine. Upland oak forests are dominant in the northern part of the region, especially in the Appalachian Mountains and the associated foothills. Pine forests tend to be dominant throughout the coastal plain (Fig. 1).

FIA Data

The US Forest Service continually monitors US forests via the FIA program. FIA data are recognized as the most comprehensive forest dataset in the USA (Tinkham et al. 2018). FIA collects data at an intensity of one plot for every 2,428 hectares (6,000 acres) (McRoberts et al. 2005). Each FIA plot is divided into four subplots: one in the center and three each located 36.6 meters (120 feet) away at azimuths of 360, 120, and 240 degrees, respectively (O'Connell et al. 2015a). FIA monitors selected NNIPs at the subplot level. Tallow presence/absence and cover percentage data were collected from each subplot. Forest-type groups and location (coordinates) of each plot were derived from the FIA data by using subplot/plot condition and other required data base variables downloaded from the FIA DataMart (FIA DataMart 2019).

Previously, state forest inventories were measured on a periodic basis with complete state inventories conducted at intervals of approximately 7–15 years. Based on the legislation contained in the Farm Bill of 1998, the inventories began the transition from a periodic inventory to an annual system (USDA Forest Service 2016). Depending on the state, each FIA annual inventory cycle is designed to be completed in approximately 5–7 years (O'Connell et al. 2015b). A new cycle starts only after all FIA plots in a state in the current cycle have been sampled. About 10–20% of FIA plots were measured annually in the southern states. Because of the staggered start to the annual inventory system across states, the cycle length, number of completely measured cycles, and starting year of annual FIA plots differed among states. For instance, the annual inventory program began in Georgia in 1998, South Carolina in 1999, Texas, Alabama, and Louisiana in 2001, Florida in 2002, and Mississippi in 2005. By 2019, South Carolina had uploaded four completely measured annual FIA inventory cycles of data in the FIA DataMart; Texas and Alabama had uploaded three cycles, and Florida, Mississippi, and Louisiana had uploaded two completely measured inventory cycles into the FIA DataMart.

As a result, there is asynchrony in cycle length and cycle starting point among states, which makes it challenging to compare tallow invasion trends at the regional level. Although many states in the region had completed more than two annual inventory cycles, only two completely measured annual plots can be found at the regional level. Hence, we considered only the two most recent and completely measured FIA cycles from each state in this analysis. The most recently completed cycle (2009–2019) is designated T2 throughout the article and the second most recently completed cycle (2002–2012) in

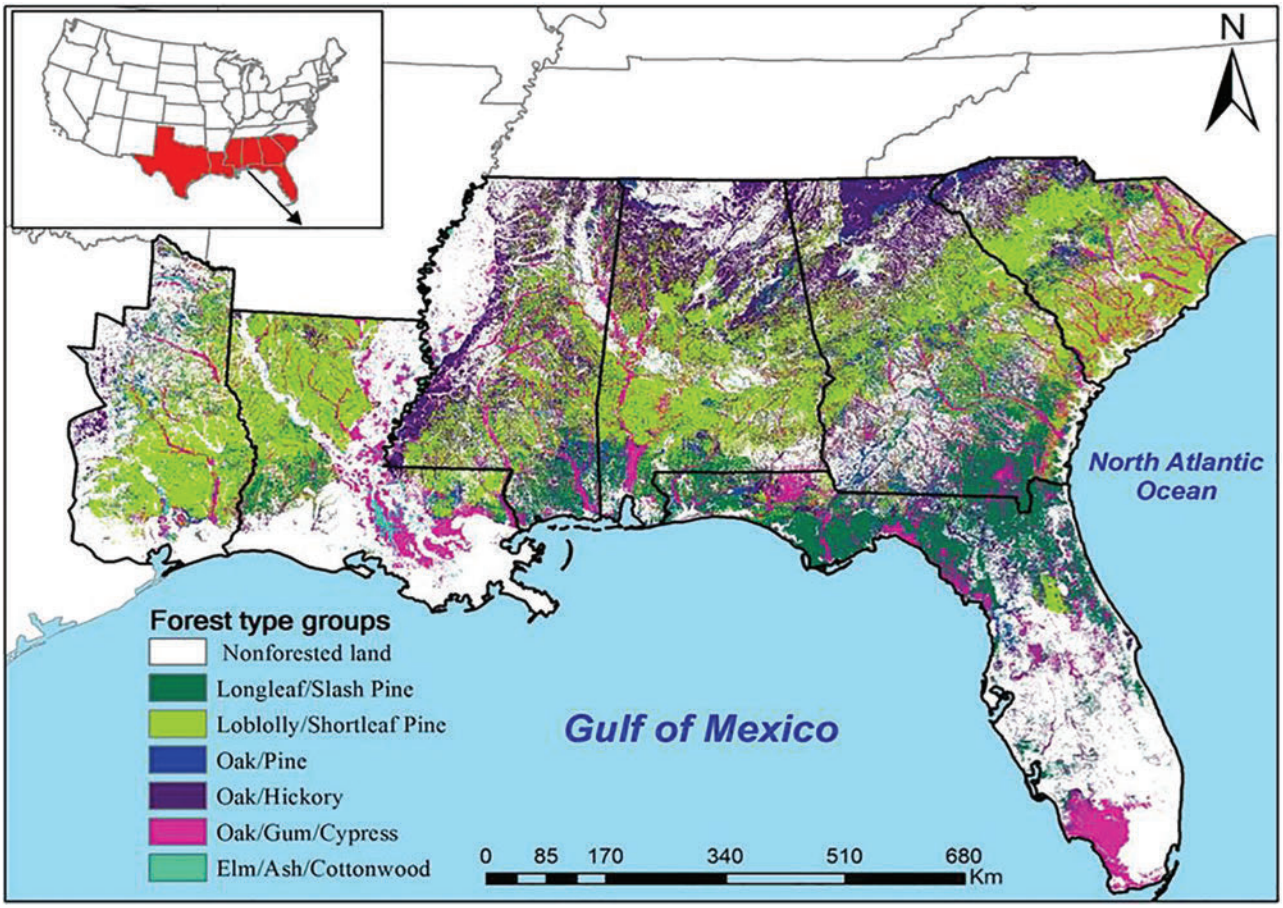

Figure 1. Map of major forest-type groups invaded by tallow in the seven southeastern coastal states, United States (Ruefenacht et al. 2008).

each state is T1. We assume population expansion or change can be detected using repeatedly measured cycles (i.e., T1 and T2) across states.

Aggregating FIA Data at the County Level

We examined 528 counties from seven southern coastal states. We found that 211 counties in T1 and 250 counties in T2 had at least one subplot infested with tallow. We found 128 out of 211 counties with five or fewer tallow-infested plots in T1 and 118 out of 250 in T2. In contrast, we found 83 counties in T1 and 132 in T2 with more than five infested plots.

In our analysis, we used both presence probability and cover percentage to describe the invasion risk and severity. Presence probability accounts for the number of infested plots and total number of plots in a county. Cover percentage was calculated as the mean tallow cover percentage of all FIA plots at a county level.

Not all counties had the same number of FIA plots; some had sufficient numbers whereas others had limited data. To overcome this problem, we used a neighborhood smoothing function to calculate the smoothed presence probability and cover percentage of each county. This approach is similar to that used by Fan et al. (2018).

$$P_i = \frac{\sum_{i}^{nb_i} S_i}{\sum_{i}^{nb_i} N_i} \tag{1}$$

Here, P_i is the presence probability of tallow for a county i using a neighbor smoothing function. S_i is the number of tallow presence plots in a county i, N_i is the total number of plots in a county i, and nb_i is the set of neighboring counties that share a boundary with a county i.

A similar approach was used to calculate tallow cover percentage at the county level.

$$C_i = \frac{\sum_{i}^{nb_i} T_i}{\sum_{i}^{nb_i} N_i} \tag{2}$$

Here, C_i is the cover percentage of tallow for a county i using a neighbor smoothing function, T_i is the sum of tallow cover in a county i, N_i is the total number of plots in a county i, and nb_i is the set of neighboring counties that share a boundary with a county i.

Mapping Invasion Severity

In this study, the product of the estimated presence probability and mean cover rate (percent) that measure both the abundance and dominance of an invasive species was used as a proxy to quantify the invasion severity of tallow in a county. The empirical cumulative distribution function (ECDF, a sigmoid or exponential or spherical curve) of the product was calculated to quantify the distribution of the county-level invasion severity. A classification and regression tree (CART) model was used to partition the

ECDF into different segments or categories by using the product as the only predictor, so that all counties were classified into different severity classes (Fan et al. 2018, Figure 2). Those counties with varying invasion severities were then mapped spatially to reflect the geospatial invasion patterns of tallow across the southeastern coastal states. The initial CART model was then pruned using an optimal complexity parameter value derived through the cross-validation approach. The terminal nodes of the pruned CART model explicitly specify the severity classes of infested counties. The T1 data were used to construct the CART model to delineate the severity classes of infested counties. This model (same variables and cutoff values) was then applied to T2 data to delineate potential changes in severity during the most recent inventory cycle (2009–2019).

Quantifying Invasibility of Forest-type groups to Tallow Invasion

Invasibility of the recipient forest-type groups was examined by using the mean presence probability and cover percentage for all severity classes. Using mean presence probability as the x-axis and mean cover percentage as the y-axis, a triangle (half of the rectangle) was plotted for each forest-type group in each severity class for both inventory cycles T1 and T2. The area of the triangle and its change between inventory cycles were used as a proxy for measuring invasibility, with a larger area representing greater invasibility and vice versa, with a smaller area representing that a forest-type group is more resistant to tallow invasion.

The presence probability and cover percentage were bootstrapped 1,000 times and the area of the corresponding triangle was computed for each forest-type group by severity

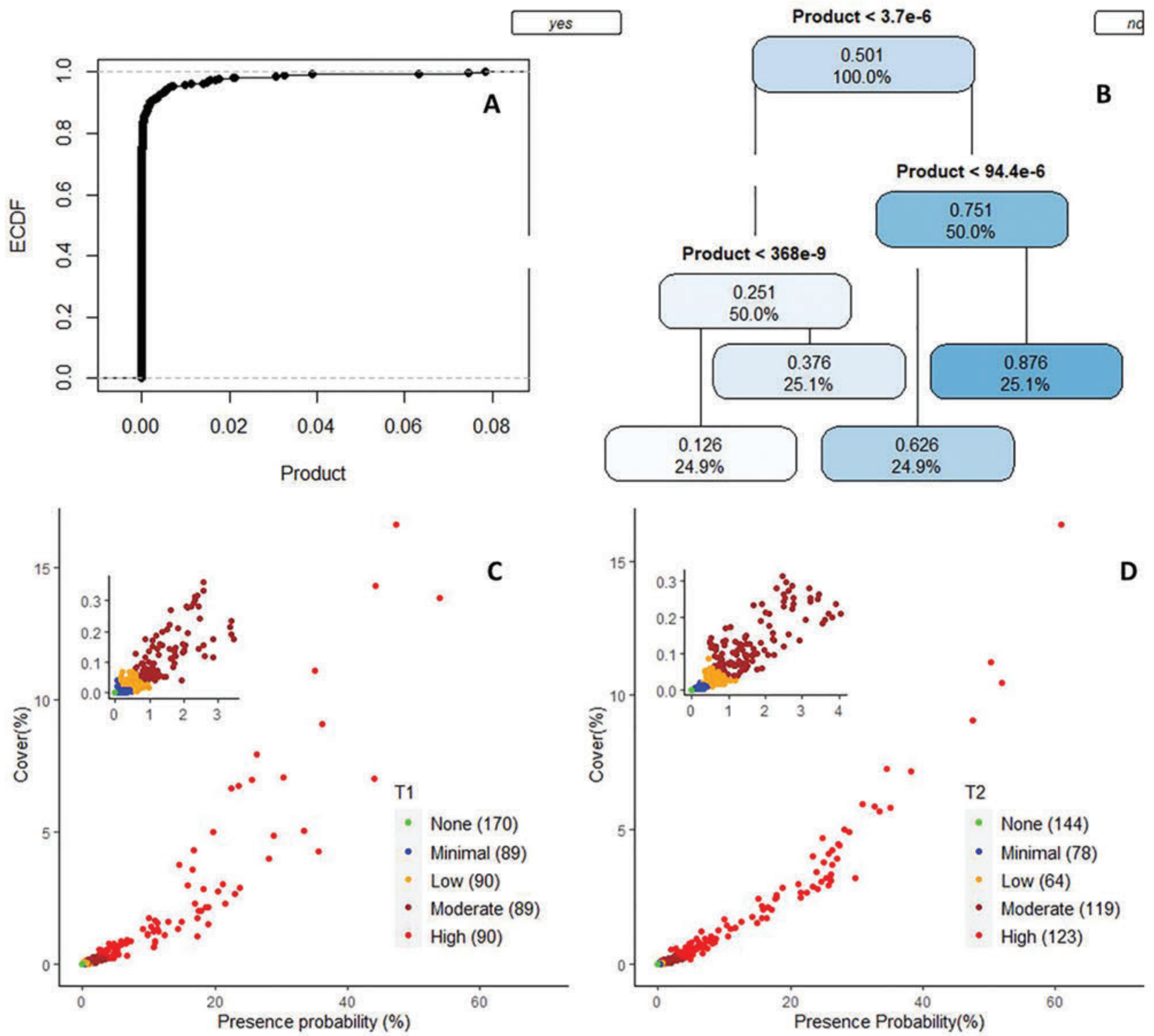

Figure 2. The empirical cumulative density function (ECDF) curve of the product of presence probability and cover percent of tallow, a proxy of invasion severity (A), four invasion severity classes identified by the classification and regression tree (CART) model (B), and the relationship between presence probability and cover percent by severity class in cycle T1 (C) and T2 (D). Number of counties in each severity class is shown in the legend.

class. The Student's *t*-test was conducted to compare the statistical significance in the change of the area inside a triangle for each forest type over time. All analyses were done using the R language (R Development Core Team, 2014) and an a priori significance level of $\alpha = 0.05$ was set for statistical tests. The CART model of invasion severity was constructed using the *rpart* package, and other analyses, including Student's *t*-test, were conducted using the R *base* package.

Results

Mapping Invasion Severity

More than 72% of the counties in the region contained at least one FIA plot infested with tallow in two periods. The CART model of invasion severity (the product of presence probability and cover percentage at the county level) classified the infested counties into four (high, moderate, low, and minimal) severity classes using three cutoff values of the product (Fig. 2 A and B). In T1, 90, 89, 90, and 89 counties and in T2, 123, 119, 64, and 78 counties were classified as high, moderate, low, and minimal severity, respectively (Fig. 2 C and D). The number of counties with high and moderate invasion severity have increased over time (Fig. 3). We found nearly 31% of all counties moved into a higher severity class between T1 and T2, suggesting further focal expansion of tallow populations. We also observed that nearly 39% of the counties remained in the same severity class over time and 5% of the counties showed a decrease in severity class. Negative changes were found mostly on the edges of the invasion range, where a lower level of risk already existed. In contrast, no change or increase was observed in areas with higher levels of invasion (Fig.3).

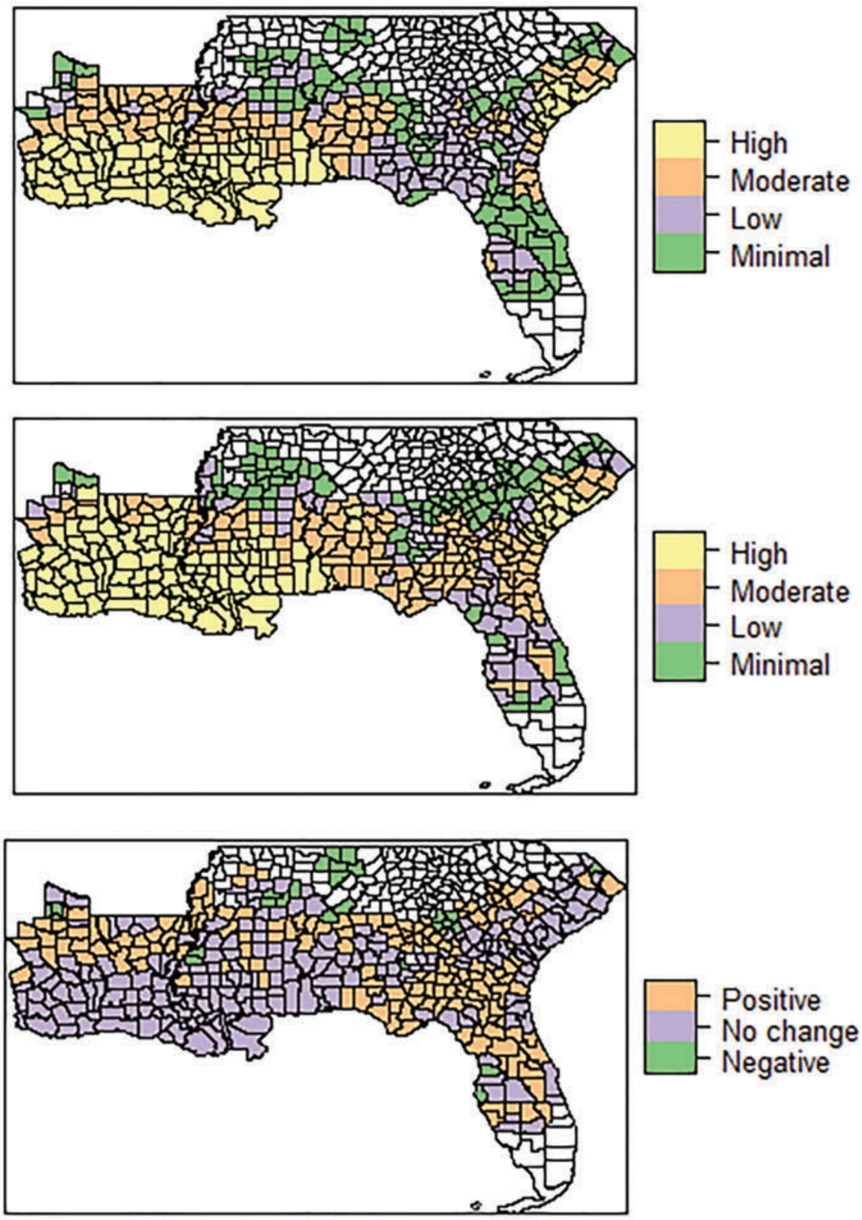

Figure 3: Spatial representation of invasion severity of Chinese tallow showing the distribution of different severity classes in cycle T1 (A), in cycle T2 (B), and changes between T1 and T2 (C). Of the 528 counties, 166 counties showed a positive change, 205 showed no change, 26 showed a negative change, and 131 remained noninfested.

Invasibility of Forest-type groups

The highest invasibility (the largest area of the triangle) was observed in the elm/ash/cottonwood forest-type group (Fig. 4 and Tables 1 and 2). In contrast, the longleaf/slash pine forest-type group had the lowest invasibility. This trend existed in both cycles across all severity classes (Fig. 4). High invasibility was also observed in the oak/gum/cypress forest-type group in both cycles in all severity classes. We observed increases in the presence probability over time for almost all forest-type groups, although the cover percentage did not follow the same pattern. For instance, cover percentage in the high-severity class increased in the longleaf/slash pine, loblolly/shortleaf pine, and oak/gum/cypress forest-type groups and decreased in the oak/hickory, oak/pine, and elm/ash/cottonwood forest-type groups (Table 1). The Student's *t*-test showed that in the high-severity class, the area of the triangle significantly increased between T1 and T2 for all forest-type groups except the oak/hickory forest-type group (Table 2). Detailed comparisons for other forest-type groups by severity class are shown in Table 2 and Figure 4.

Discussion

Invasion Severity of Chinese Tallow Over Time

In the southern US, tallow invasion has increased over time. Infestation intensity was higher in two sub-regions (Miller et al. 2013): the Gulf of Mexico coastal plain, stretching from Texas to Florida (western epicenter) and the Atlantic coastal plain of South Carolina and Georgia (eastern epicenter). The increase in infested area and infestation intensity extended

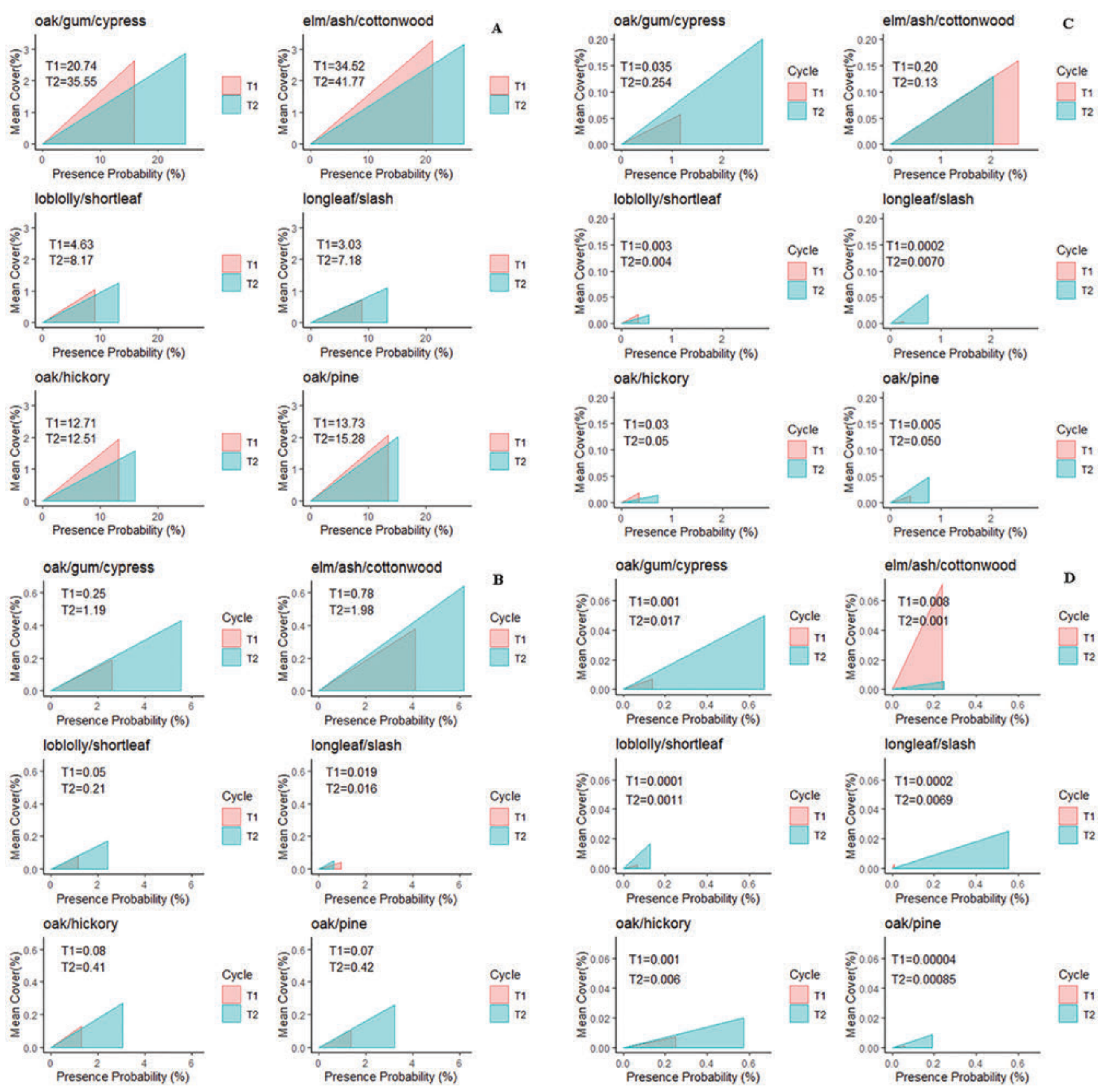

Figure 4: Area inside triangles for different forest-type groups over two cycles in the high (A), moderate (B), low (C), and minimal (D) severity classes. The numbers reported for T1 and T2 are the area of each triangle.

northeast from the western epicenter and northwest from the eastern epicenter. Infestation intensity was higher in the western epicenter than in the eastern epicenter. Other research identified those areas as locations where tallow was historically introduced for commercial planting (Howes 1949, Pile et al. 2017b, Miller et al. 2013). Our findings from the remeasured FIA data found that these epicenters of tallow infestation became more pronounced over time both in extent and intensity.

Tallow invasion severity classes in this study were quantitatively derived from the FIA plot data in the southern coastal states. A similar approach was applied in Fan et al. (2018) using one-time measured FIA data to classify invasion severities of nonnative invasive plant species in the midwestern US. Remeasured data provided an opportunity to compare invasion severity over time at the regional level. Counties in the high invasion severity class were concentrated around the two epicenters in both cycles. Examination of temporal changes in invasion severity showed that most of the counties with the highest level of invasion severity stayed at that level. Some counties with a lower number of infested plots, especially at the outer edge of the epicenter, decreased in invasion severity. Increases in severity occurred outside of but adjacent to the two epicenters.

Using remeasured FIA plot-level data, Yang (2019) used a CART model to classify four subregions based on tallow presence in the southern US. Yang (2019) classified the low elevation coastal plain near the western epicenter (i.e., near Texas) as the area with the most severe tallow invasion. Our classification approach differed in that we considered both presence probability and cover percentage of FIA plots and aggregated them to the county level before classification. As such, we identified high-severity zones in both the eastern and western epicenters.

Invasibility of Forest-type groups

Invasibility of forest-type groups was examined using presence probability, cover percentage, and the product of both in different severity classes. In prior work, Fan et al. (2012) explored tallow invasion solely in eastern Texas, where they found the highest presence probability in the oak/gum/cypress forest-type group, followed by longleaf/slash pine, elm/ash/cottonwood, loblolly/shortleaf, and oak/hickory groups. Most of the counties in eastern Texas and Louisiana were classified as high severity in our analysis. Furthermore, this study was regional and covered a wider range, with overall presence probabilities that were relatively lower than Fan et al. (2012). However, our results for the high-severity class were similar to those of Fan et al. (2012). The most severely infested forest-type groups in both cycles were elm/ash/cottonwood and oak/gum/cypress. In general, tallow can invade both wet and dry sites (Miller 2003), but the severe infestation sites were wet forest sites and coastal prairies (Miller 1998). Our findings also support this conclusion, as we found that elm/

Table 1. The presence probability and cover percentage of Chinese tallow by identified severity classes in the southern US

Severity Class	Forest-Type Groups	T1		T2		Change	
		Presence percent	Cover percent	Presence percent	Cover percent	Presence percent	Cover percent
High	EAC	21.15	3.29	26.50	3.15	5.35	-0.14
	LSL	8.98	1.03	13.06	1.25	4.08	0.22
	LLS	8.79	0.70	13.28	1.07	4.49	0.37
	OGC	15.78	2.62	24.64	2.87	8.86	0.25
	OH	13.11	1.94	15.95	1.57	2.84	-0.37
	OP	13.34	2.05	15.05	2.04	1.71	-0.01
Moderate	EAC	4.08	0.37	6.16	0.64	2.08	0.27
	LSL	1.16	0.08	2.42	0.17	1.26	0.09
	LLS	0.94	0.04	0.63	0.05	-0.31	0.01
	OGC	2.61	0.19	5.52	0.43	2.91	0.24
	OH	1.30	0.14	3.05	0.27	1.75	0.13
	OP	1.35	0.11	3.25	0.26	1.90	0.15
Low	EAC	2.55	0.17	2.03	0.13	-0.52	-0.04
	LSL	0.33	0.02	0.53	0.02	0.20	0.00
	LLS	0.27	0.00	0.75	0.06	0.48	0.06
	OGC	1.18	0.06	2.79	0.20	1.61	0.14
	OH	0.35	0.02	0.72	0.03	0.37	0.01
	OP	0.40	0.01	0.76	0.05	0.36	0.04
Minimal	EAC	0.24	0.07	0.25	0.00	0.01	-0.07
	LSL	0.07	0.00	0.13	0.02	0.06	0.02
	LLS	0.10	0.00	0.54	0.02	0.44	0.02
	OGC	0.14	0.01	0.67	0.05	0.53	0.04
	OH	0.26	0.01	0.57	0.02	0.31	0.01
	OP	0.06	0.00	0.18	0.01	0.12	0.01

EAC, elm/ash/cottonwood; LSL, loblolly/shortleaf pine; LLS, longleaf/slash pine; OGC, oak/gum/cypress; OH, oak/hickory; OP oak/pine

Table 2. Results of Student's *t*-test performed to compare area inside triangles between two cycles (T1 and T2) in each severity class for all forest-type groups using bootstrapping (n = 1,000)

Severity Class	Forest-Type Groups	Mean (SD); n = 1,000		P^a	Relative Change
		T1	T2		
High	EAC	34.68(6.64)	41.9(5.95)	<0.001	0.21
	LSL	4.65(0.5)	8.21(0.64)	<0.001	0.77
	LLS	3.07(0.69)	7.19(1.03)	<0.001	1.34
	OGC	20.76(2.26)	35.59(2.78)	<0.001	0.71
	OH	12.77(1.89)	12.52(1.57)	<0.001	-0.02
	OP	13.78(2.29)	15.34(2.1)	<0.001	0.11
Moder-ate	EAC	0.8(0.42)	2.01(0.67)	<0.001	1.52
	LSL	0.05(0.01)	0.2(0.03)	<0.001	3.33
	LLS	0.02(0.01)	0.02(0.01)	<0.001	-0.22
	OGC	0.25(0.07)	1.19(0.23)	<0.001	3.75
	OH	0.09(0.03)	0.41(0.09)	<0.001	3.66
	OP	0.07(0.04)	0.42(0.12)	<0.001	4.64
Low	EAC	0.23(0.16)	0.15(0.13)	<0.001	-0.32
	LSL	<0.01(<0.01)	<0.01(<0.01)	<0.001	NA
	LLS	<0.01(<0.01)	0.02(0.01)	<0.001	NA
	OGC	0.04(0.02)	0.28(0.08)	<0.001	7.01
	OH	<0.01(<0.01)	0.01(0.01)	<0.001	NA
	OP	<0.01(<0.01)	0.02(0.01)	<0.001	NA
Minimal	EAC	0.02(0.03)	<0.01(<0.01)	<0.001	NA
	LSL	<0.01(<0.01)	<0.01(<0.01)	<0.001	NA
	LLS	<0.01(<0.01)	0.01(0.01)	<0.001	NA
	OGC	<0.01(<0.01)	0.02(0.01)	<0.001	NA
	OH	<0.01(<0.01)	0.01(0)	<0.001	NA
	OP	<0.01(<0.01)	<0.01(<0.01)	<0.001	NA

[a]significance values based on bootstrapping
EAC, elm/ash/cottonwood; LSL, loblolly/shortleaf pine; LLS, longleaf/slash pine; OGC, oak/gum/cypress; OH, oak/hickory; OP oak/pine

ash/cottonwood and oak/gum/cypress were severely infested by tallow invasion in both measurement cycles.

At the other end of the invasion spectrum, we found longleaf/slash pine and loblolly/shortleaf pine forest-type groups were the least infested in both cycles at the regional level. The greatest changes in presence probability over time were observed in oak/gum/cypress, elm/ash/cottonwood, longleaf/slash pine, and loblolly/shortleaf pine. Presence probabilities in these forest-type groups increased by 8.86, 5.35, 4.49, and 4.08%, respectively. Fan et al. (2012) also found the highest spread rate in oak/gum/cypress forests. In our analysis, we found invasibility was already higher in oak/gum/cypress in T1, and the rate of change in presence probability was higher than for other forest-type groups. Thus, the oak/gum/cypress forest-type group is highly susceptible to tallow invasion compared with other forest-type groups across severity classes.

The graphical tool (Figure 4) provides a useful approach to compare the invasibility of different communities by simultaneously considering the presence probability (abundance) and cover percentage (dominance) of nonnative plants involved (Catford et al. 2012, Fan 2015, Fan et al. 2018). The largest areas inside a triangle were observed in the elm/ash/cottonwood forest-type group in both cycles whereas the smallest was in the longleaf/slash pine forest-type group. Invaded area increased over time in all but the oak/hickory forest-type group at the regional level. Although the longleaf/slash pine forest-type group had the lowest severity of invasion, it has the highest relative increment between T2 and T1 (> 134%). We also found higher rates of increment in the area under the triangle in the loblolly/shortleaf pine (>77%), oak/gum/cypress (>72%), and elm/ash/cottonwood (>21%) forest-type groups between T2 and T1. In the moderate-severity class, areas inside a triangle were significantly higher in T2 than in T1 for all forest-type groups except longleaf/slash pine. The highest relative increment in area inside a triangle between the two cycles was seen in the oak/pine forest-type group (>464%), followed by the oak/gum/cypress forest-type group (>375%).

In the high-severity class, tallow presence (abundance) increased across all forest-type groups but cover percentage (dominance) increased, primarily in pines (lowland flatwoods) and oak/gum/cypress (bottomland). In elm/ash/cottonwood, oak/pine, and oak/hickory forest-type groups, the mean dominance declined, although tallow presence increased. These results suggest that monitoring of tallow spread should focus on longleaf/slash pine, loblolly/shortleaf pine, and oak/gum/cypress forest-type groups. Further, the longleaf/slash pine forest-type group demonstrated a higher level of invasibility at the regional level, whereas elm/ash/cottonwood forest-type groups displayed a lower level of invasibility by tallow. Further, Fan (2012) compared the invasibility of loblolly/shortleaf pine and oak/gum/cypress forest-type groups in eastern Texas and suggested that oak/gum/cypress was more susceptible to tallow invasion than was loblolly/shortleaf pine. Our results are consistent with those findings. In both cycles, we found a significantly higher level of tallow invasion in the oak/gum/cypress forest-type group as compared with the loblolly/shortleaf pine forest-type group.

There are multiple potential confounding factors influencing community invasibility, including disturbance, climate, and geographic features. That comparisons of the invasibility of different forest-type groups were made by invasion severity class helped to a certain degree to filter out the potential impact of these confounding factors, because each subregion identified in this study is more homogeneous in invasion severity (propagule pressure), geographical features, climate, and disturbance regimes (Fan et al. 2012). Specifically, geographical features (e.g., slope and elevation), propagule pressure levels, and disturbances (e.g., hurricanes, flooding, wildfires, and management activities) tend to increase the presence probability of tallow between inventory cycles, but climate and community conditions will have greater effects on the change in dominance of the invasive tallow (Yang et al. 2021). The western epicenter seemed to expand more rapidly than the eastern epicenter between the two inventory cycles, as more counties around the western epicenter had been converted to the high-severity class in the most recent inventory cycle. This might be related to more favorable climate (e.g., high temperatures and rainfall), flat terrain, and more frequent and intensive disturbances such as hurricanes and tropical storms along the western Gulf coastal plain. Moser et al. (2016) stated that the oak/hickory and elm/ash/cottonwood forest-type groups were highly susceptible to invasive shrubs in the midwestern US. These Midwestern-forest types were heavily exposed to disturbance because of their proximity to human development and the history of forest management and exploitation of those types; such disturbances were likely facilitators of the invasive species spread (Moser et al. 2009a). Pile et al. (2017a) compared the invasibility of natural and disturbed forests to tallow infestation and found that natural forests were more resistant to the invasion because of greater woody species richness and biomass. Other factors, including physiographic zone, hurricanes, storms, distance to nearest road and water, stand age, treatments, and land ownership play important roles in the extent and severity of tallow infestation (Yang 2019, Gan et al. 2009). Gan et al. (2009) also showed that slope was the key factor for tallow invasibility in flat areas, as flooding and higher soil moisture levels facilitate its invasion. We examined only forest-type groups in relation to tallow invasion severity classes. In the future, these other variables should be included in analyses of temporal changes in invasion severity.

Conclusions

Based on the US Forest Service's FIA data, tallow has become one of the most aggressive invaders in diverse southern forestlands. Using the product of presence probability and cover percentage as a proxy, we classified tallow invasion severity into four classes in the south coastal US states from eastern Texas to South Carolina. The highest severity class occurred in counties in coastal South Carolina and Georgia and at the oppposite end of the region in western Louisiana and eastern Texas. Among all severity classes, elm/ash/cottonwood and oak/gum/cypress forest-type groups were most susceptible to tallow invasion, followed in a descending order by oak/pine, oak/hickory, loblolly/shortleaf pine, and longleaf/slash pine forest-type groups, based on the invasibility measure: the area of the triangle that reflects both the abundance (presence probability) and dominance (cover percentage) of invading tallow populations. The invasion severity and invasibility measures provide useful tools to assess the relative threats of different forest communities across the southern forestland, allowing forest managers to prioritize risk areas and forest types to control and mitigate the invasion and postinvasion spread of tallow. Management of tallow invasion should be focused on the highly susceptible oak/gum/cypress and elm/ash/cottonwood forests. In addition, considering the high value and rapid increase of tallow's cover percent in longleaf/slash pine forests in the high-, low-, and minimal-severity regions, mechanical and chemical treatments to remove tallow should be used to protect and conserve this endangered ecosystem. Because tallow is largely disturbance-dependent and may completely replace the invaded forest and form a monoculture stand, intensive monitoring is critical in frequently disturbed coastal areas (e.g., high- and moderate-severity counties) so that proactive measures can be implemented in a timely manner. For instance, prescribed fire in combination with stand management has been recommended to mitigate tallow's growth to prevent stand-replacement incidence.

Acknowledgment

This research was supported by the Alabama Agricultural Experiment Station and the Hatch program and the McIntire-Stennis program of the National Institute of Food and Agriculture, US Department of Agriculture.

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