Invasion of tallow tree into southern US forests: influencing factors and implications for mitigation

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Abstract: We identify species–environment relationships to predict the occurrence of Chinese tallow (*Triadica sebifera* (L.) Small) on forestlands in the southern US, where it has emerged as the most pervading, stand-replacing, alien tree species. Tallow invasions are more likely to be observed on low and flat lands, areas adjacent to water and roadways, sites recently harvested or disturbed, younger stands, and private forestlands. The winter extreme minimum temperature tends to restrain tallow northward migration. Increases in both range and severity of tallow invasions are predicted with a warming climate trend, and the situation could be worse if the warming is coupled with an increased frequency and intensity of disturbances. Monitoring and mitigation strategies are proposed to assist this region and other countries threatened by tallow invasions.

Résumé : Nous avons identifié des relations entre l'environnement et l'arbre à suif chinois (*Triadica sebifera* (L.) Small) pour prédire l'occurrence de cette espèce sur les terrains forestiers du sud des États-Unis où elle est devenue l'espèce d'arbre exotique la plus répandue capable de remplacer des peuplements. Les invasions de l'arbre à suif ont le plus de chances d'être observées sur les terres basses et plates, dans les zones adjacentes à un plan d'eau et à la chaussée, sur des sites récemment récoltés ou perturbés, dans de jeunes peuplements et dans les boisés privés. La température minimum extrême en hiver a tendance à limiter la migration de l'arbre à suif vers le nord. Une augmentation tant de l'étendue que de la sévérité des invasions de l'arbre à suif est prévue avec la tendance au réchauffement du climat et la situation pourrait être pire si le réchauffement est accompagné d'une augmentation de la fréquence et de l'intensité des perturbations. Des stratégies impliquant le suivi et des mesures d'atténuation sont proposées pour aider cette région et d'autres pays menacés par les invasions de l'arbre à suif.

[Traduit par la Rédaction]

Introduction

The southern United States' (US) forest region is one of the most productive in the country and the world. The 87 × 10^6 ha of forest resources in all 13 southern states supply 60% of the timber produced in the US and a vital array of ecological services, including biodiversity, wildlife habitats, water protection, and recreational resources (Wear and Greis 2005). Yet, the aggressive invasions of alien plants have posed a looming threat to the future prospects of the region's forest resources (Britton et al. 2004). Among these invasives, Chinese tallow (*Triadica sebifera* (L.) Small) is the most pervading, forest-stand-replacing, alien tree species in the region. It currently occupies 185 000 ha of forests, specifically their edges and openings, in the southern US, mostly in coastal plain, coastal prairie, and the Mississippi River alluvial floodplain provinces (Table 1) (Miller et al. 2008). Such a threat calls for urgent and collaborative strategic mitigation planning and an adaptive management program of response and restoration (Miller and Schelhas 2008). Effective strategies and programs must be formulated on the basis of our best understanding of spread vectors and forest characteristics that portend invasion, with updates using adaptive management cycles. Much has been studied on the expansive tallow occupation of Gulf coastal prairies (Bruce et al. 1997; Barrilleaux and Grace 2000), whereas little research has addressed the regional forest invasion. This study focuses on forestlands and aims to identify and quantify biophysical and anthropogenic factors that facilitate, control, and exasperate occupation and spread.

Tallow tree was originally introduced into coastal South Carolina and Georgia as early as the 1770s (Hunt 1947). The cultivation of tallow in China for 14 centuries for its waxy oily fruit, leaves, and wood prompted the US Department of Agriculture to establish trials and to promote Gulf coastal plain plantings in Texas during the early 1900s (Howes 1949). After abandonment of this program and a pronounced lag phase, the occupation and spread of escaped plantings escalated in wet grassland prairies and freshwater marshes in Southeast Texas and other Gulf coastal ports (Bruce et al. 1997). Tallow tree has also been planted widely as an ornamental and by beekeepers (Liuex 1975), and these plantings have been the primary vectors for long-distance spread.

Tallow tree is a deciduous tree in the Euphorbiaceae family that typically reaches a maximum height of 15 m. Reproductive age can start in as little as 3 years and remain for 100 years (Bruce et al. 1997). Cultivated mature trees in

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Table 1. Tallow tree forestland invasions by states in the southern US, 2007.

State	Completed inventory (% of subplots)	Invaded subplots No.	Invaded subplots %
Alabama	100	112	0.73
Arkansas	100	6	0.06
Florida	60	36	0.40
Georgia	100	32	0.36
Kentucky	100	0	0.00
Louisiana	100	815	8.97
Mississippi	100	206	1.45
North Carolina	100	4	0.04
South Carolina	80	40	0.44
Tennessee	100	0	0.00
Texas (east)	100	745	9.13
Virginia	60	0	0.00
Total		1996	1.68

Note: Source: USDA Forest Service 2008*b*.

Texas can produce up to 310 000 seeds per year (Gray 1950). Local and short-distance seed dispersal is by flowing and impounded waters common to the wet forests of the coastal plains (Bruce et al. 1997) and by multiple species of large birds that consume the high oil content seeds (Hukui and Ueda 1999; Renne et al. 2002). Seedlings are shade tolerant, yet grow rapidly in full sun (Jones and Sharitz 1990; Barrilleaux and Grace 2000), and are extraordinarily tolerant of herbivory and plant competition (Siemann and Rogers 2003; Pattison and Mack 2008; Zou et al. 2008). Seedlings, saplings, and mature trees have been found at various elevations around bayous and lakes, with none reported in permanently wet soils (Wall and Darwin 1999; Burns and Miller 2004), whereas the full range of elevational spread potential has not been investigated.

In addition to seed dispersal by human and natural vectors, biophysical conditions play a critical role in the establishment and growth of tallow tree (Jin and Huang 1984). Bioclimatic factors are found to be correlated with the presence of tallow tree in both native and invaded ranges (Pattison and Mack 2008). Studies on plant invasibility reveal that nonclimatic factors, such as landscape features, plant biodiversity, and disturbances, are also linked to the invasions of alien species, though these have not been holistically studied for tallow tree (Huebner and Tobin 2006). These previous studies clearly indicate that natural factors can contribute to tallow spread and occupation, while anthropogenic factors have yet to be examined at larger scales.

Alien species are known to evolve or hybridize after introduction into a new region, thus altering certain characteristics and competitive capabilities (Capo-chichi et al. 2008; Zou et al. 2008). Alien species do not encounter the same complex of predators or restricting forces in invaded areas as in their native range, thus often meeting less resistance to establishment and spread (Mack et al. 2000; Peterson and Vieglais 2001). Zou et al. (2008) report that tallow tree becomes faster growing, less herbivore resistant, and more herbivore tolerant in the introduced range than in its native range because of its evolved increased competitive ability. This implies that distribution and abundance in the native range may have a limited explanatory power in predicting occupation in the introduced region (Loo et al. 2007). Hence, we attempted to determine the empirical relationships between tallow occupation on forestlands and anthropogenic and natural attributes, using logistic regression modeling.

Several modeling approaches have been examined for predicting invasive species and their spread within a new range (Heger and Trepl 2003; Cadotte et al. 2006; Herron et al. 2007). Logistic regression modeling offers several unique features suited for Forest Inventory and Analysis (FIA) and similar datasets (Sutton et al. 2007; Huebner et al. 2009). First, unlike simulations, empirical data are used to elucidate the biophysical determinants of tallow invasion. As such, results can better reflect the reality, provide details of invasions not possible with simulation modeling, and aid in testing theories of plant invasion. Second, logistic regression using observed data across the region allows the influences of both human and natural adaptations to be incorporated.

Methods and data

Study area and data sources

This study focused on four states, including Texas, Louisiana, Mississippi, and Alabama. Although tallow has invaded forests in nine southern states, the most severe occupation has taken place in these four states, with an average invasion rate of 5% on forestlands (Miller et al. 2008). It has encroached on about 9% of FIA subplots in East Texas and Louisiana, 1.5% of subplots in Mississippi, and 0.7% of subplots in Alabama (Table 1).

Data were primarily drawn from two US Forest Service Southern Region FIA datasets: the Nonnative Invasive Plants dataset and the traditional FIA dataset (Rudis et al. 2006; USDA Forest Service 2008*a*, 2008*b*). Presence or absence of tallow tree in all subplots was derived from the former dataset, whereas the latter dataset provided information on stand characteristics, site conditions, management activities, and disturbances necessary for modeling. The two datasets were merged by using FIA subplot identification numbers. In total, there were 46 865 FIA subplots used in this analysis.

The major reported climatic factors limiting tallow invasions are the winter minimum temperature affecting seed germination and the summer maximum temperature influencing growth (Pattison and Mack 2008). To delve further into climate factors, we examined for various months the mean daily minimum and maximum temperatures, mean extreme minimum and maximum temperatures, and record extreme minimum and maximum temperatures. Climate data were derived from the National Oceanic and Atmospheric Administration (NOAA 2008). The temperature data taken from NOAA were aligned with FIA data, according to the longitudes and latitudes.

Logistic regression model

We applied logistic regression modeling to link the probability of tallow occupation in a specific location (subplot) with various factors. The logistic model is a probability model that is capable of regressing a categorical or discrete variable on a set of explanatory variables via the logit link (Greene 2008). A logit is the log (base e) of the odds for an event to occur. The logistic regression model can be written as

$$[1] \qquad \text{logit}(p) = \log\left(\frac{p}{1-p}\right) = \alpha + \boldsymbol{X}'\boldsymbol{\beta}$$

where p is the probability of the occurrence of the event, $p/(1–p)$ is the odds of the occurrence, $\boldsymbol{X}$ is the vector of independent variables, α and $\boldsymbol{\beta}$ (a vector) are the regression coefficients to be estimated. Likewise, the probability is measured by

$$[2] \qquad p = \frac{\exp(\alpha + \boldsymbol{X}'\boldsymbol{\beta})}{1 + \exp(\alpha + \boldsymbol{X}'\boldsymbol{\beta})}$$

In this study, we were interested in whether a specific site had been occupied by tallow tree, which can be measured using a binary variable. Accordingly, we employed a binary logistic regression as follows:

$$[3] \qquad p(Y = 1|\boldsymbol{X}) = \frac{\exp(\alpha + \boldsymbol{X}'\boldsymbol{\beta})}{1 + \exp(\alpha + \boldsymbol{X}'\boldsymbol{\beta})} = f(\alpha + \boldsymbol{X}'\boldsymbol{\beta})$$

where Y is a binary variable taking the value of either 1 if tallow tree is present on the site or 0 otherwise; and $p(Y = 1)$ is the probability for $Y = 1$ (i.e., the site is invaded by tallow tree).

For appropriate model specification, we next needed to identify potential explanatory variables that might have contributed to tallow invasions in the US South. We relied on existing literature to achieve this task. Previous work has identified several drivers of plant invasions, including landscape features (Higgins et al. 1999; Huebner and Tobin 2006), proximity to roads (Hansen and Clevenger 2005; Huebner and Tobin 2006), biodiversity (Wiser et al. 1998; Stohlgren et al. 1999; Kennedy et al. 2002; Collins et al. 2007), and disturbances (Lonsdale 1999; Pyšek et al. 2002). Studies on tallow invasions uncovered that climatic conditions (Pattison and Mack 2008) and hydrological zones (Wall and Darwin 1999; Burns and Miller 2004) are also attributable to its spread range. Drawing on the literature on plant invasions in general and tallow tree in particular, we selected a set of possible predictors for modeling that included landscape features, climatic factors, site and forest conditions, and disturbances. Descriptions and measurements of these variables are shown in Table 2; most of them are straightforward. One variable that probably deserves further explanation is Shannon's index of tree-species diversity (H_s). Following Liang et al. (2007) we measured it using

$$[4] \qquad H_s = -\sum_{i=1}^{n_s} \frac{B_i}{B} \log\left(\frac{B_i}{B}\right)$$

where B is the total stand basal area, B_i is the basal area of tree species i, and n_s is the number of tree species or species richness.

Five empirical models were estimated. The first model was fit using the data of all FIA subplots in the four states without data discrimination. Because tallow tree had not been recorded in many counties in these states, we also estimated models using discriminated data. The second model was fit using the data of FIA subplots (invaded and noninvaded) in only those counties where tallow presence had been observed. Additionally, we further partitioned the second dataset (containing all FIA subplots in only those invaded counties) into three subsets based on the intensity of invasions (i.e., the ratio of invaded subplots to the total subplots in each county): (1) counties with an invasion rate greater than or equal to the mean + two standard deviations, (2) counties with an invasion rate between the mean ± two standard deviations, and (3) counties with an invasion rate less than the mean – two standard deviations. The partition or discrimination of datawas based on the consideration that the invader might not have reached its maximum range in the invaded region. If this is true, the modeling results using the data from the invaded range could lead to biases (MacIsaac et al. 2000). These empirical models fit with the partitioned data are expected to help us better understand anthropogenic and natural drivers and their influences on tallow occupation at different invasion stages.

All the models were estimated using the stepwise backward procedure and the Statistical Analysis System software (SAS Institute Inc. 2004). This approach started with a temporary model that includes all potential independent variables. Next, the insignificant variable with the highest p value was removed and the model reestimated. This procedure was repeated until the Akaike Information Criterion (AIC) could not be lowered and all independent variables were statistically significant. As in ordinary regression, strong correlations among the explanatory variables could cause problems with parameter estimates and standard errors in logistic regression. Hence, we tackled this problem by deleting one of the correlated variables that had an extremely large standard error and an insignificant coefficient estimate to alleviate possible colinearity. Additionally, we used the log-likelihood ratio and Hosmer–Lemeshow test to verify the model's overall goodness of fit. According to the Hosmer–Lemeshow test, failing to reject the null hypothesis that there is no statistically significant difference between the observed and model-predicted values suggests that the model is statistically valid.

We also tested for possible zero inflation and spatial autocorrelation. We ran the zero-inflated binomial regression for each model and compared it with the corresponding logistic regression model. The coefficients of zero inflation for all five models were insignificant at the 5% level (Table 3), suggesting that there was no statistical evidence of zero inflation in our models. Meanwhile, the AIC of the zero-inflated binomial was significantly larger than that of logistic regression, implying that the logistic regression models were better than zero-inflated binomial models. To detect potential spatial autocorrelation, we calculated Moran's I index of the model residuals. The index can reveal whether a spatial pattern is clustered, dispersed, or random. The p value based on the Z-score test for all five models was greater than 5% (Table 3), indicating the null hypothesis that Moran's $I = 0$ could not be rejected at the 5% significance level. Hence, spatial autocorrelation was not an issue in our models either.

Table 2. Descriptions, measurements, and means or frequencies of possible tallow tree invasion predictors.

Variable	Value or unit of measure	Expected sign of impact[*]	Mean or frequency[†]
Landscape features			
Elevation	m	–	93.6 (–9–451)
Slope	Degree	–	6.86 (0–77.5)
Adjacency to water bodies within 300 m	0: no	+	0: 37 248
	1: yes	+	1: 9617
Climatic conditions			
Mean extreme minimum temperature in January	1: ≤20.0°F[‡]	+	
	2: –20.1–0.0°F	+	
	3: 0.1–10.0°F	+	3: 6140
	4: 10.1–20.0°F	+	4: 35 861
	5: 20.1–32.0°F	+	5: 4864
	6: 32.1–40.0°F	+	
	7: 40.1–50.0°F	+	
	8: 50.1–60.0°F	+	
Forest and site conditions			
Stand age	Years	–	32 (0–168)
Site productivity (height–age curve categories related to volume per year)	1: 0–1.39 $\text{m}^3\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$	+/–	1: 124
	2: 1.40–3.49 $\text{m}^3\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$	+/–	2: 2430
	3: 3.50–5.94 $\text{m}^3\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$	+/–	3: 12 469
	4: 5.95–8.39 $\text{m}^3\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$	+/–	4: 17 485
	5: 8.40–11.54 $\text{m}^3\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$	+/–	5: 10 944
	6: 11.55–15.74 $\text{m}^3\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$	+/–	6: 3163
	7: >15.74 $\text{m}^3\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$	+/–	7: 250
Species diversity	Shannon's tree-species diversity	+/–	0.636 (0–2.32)
Forest management activities and disturbances			
Timber harvest	0: no	+	0: 32 771
	1: yes	+	1: 14 094
Site preparation	0: no	–	0: 43 771
	1: yes	–	1: 3094
Artificial regeneration	0: no	–	0: 33 285
	1: yes	–	1: 13 580
Natural regeneration	0: no	+/–	0: 44 894
	1: yes	+/–	1: 1971
Distance to the nearest road	1: <30 m	–	1: 2394
	2: 30–91 m	–	2: 5427
	3: 91–152 m	–	3: 5121
	4: 152–305 m	–	4: 9539
	5: 305–805 m	–	5: 14 559
	6: 805–1609 m	–	6: 7096
	7: 1609–4828 m	–	7: 2397
	8: 4828–8047 m	–	8: 199
	9: >8047 m	–	9: 133
Fire damage[§]	0: no	+	0: 45 039
	1: yes	+	1: 1826
Animal damage[§]	0: no	+	0: 46 346
	1: yes	+	1: 519
Wind damage[§] (including hurricanes and tornados)	0: no	+	0: 44 137
	1: yes	+	1: 2728
Others			
Forestland ownership	0: public	+/–	0: 4453
	1: private	+/–	1: 42 412

[*] +, postive impact; –, negative impact; ±, variable impact.

[†] Numbers inside the parentheses are the range of the variable.

[‡] Celsius temperature = [(Fahrenheit temperature – 32) × 5/9].

[§] Nominally within the past 5 years. With damage codes, at least 25% of the trees in a stand must be damaged to warrant a 1 code.

Table 3. Results of testing zero inflation and spatial autocorrelation.

	Zero inflation		Spatial autocorrelation	
Model fit with data from:	Coefficient	p value	Moran's I	p value
All counties	–8.39	0.06	0.04	0.21
Invaded counties only	–9.96	0.30	0.04	0.19
Counties with an invasion rate <mean – 2 standard deviations	–8.92	0.09	0.01	0.16
Counties with an invasion rate between the mean ± 2 standard deviations	–5.45	0.15	0.01	0.11
Counties with an invasion rate ≥mean + 2 standard deviations	–6.18	0.16	0.04	0.09

Table 4. Logistic regression results of tallow tree invasions estimated with discriminated data from invaded counties in the US South.

	Model fit with the data from counties with an invasive rate <mean – 2 standard deviations			Model fit with the data from counties with an invasion rate between the mean ± 2 standard deviations			Model fit with the data from counties with an invasion rate >mean + 2 standard deviations		
Variable	Estimated coefficient	Odds ratio	p value	Estimated coefficient	Odds ratio	p value	Estimated coefficient	Odds ratio	p value
Elevation	–0.001	0.999	0.001	–0.001	0.999	0.046	–0.001	0.999	0.024
Slope	–0.064	0.938	0.000	–0.066	0.936	0.003			
Proximity to water bodies	0.281	1.324	0.016	0.622	1.862	0.000	0.390	1.477	0.000
Mean extreme minimum temperature	1.111	3.038	0.000	0.360	1.434	0.027	0.837	2.310	0.000
Stand age	–0.005	0.995	0.060	–0.014	0.986	0.000	–0.022	0.978	0.000
Site productivity				0.164	1.179	0.009	0.109	1.115	0.000
Plant species diversity							0.246	1.278	0.002
Artificial regeneration	–0.313	0.731	0.017	–0.495	0.610	0.005	–0.739	0.478	0.000
Natural regeneration	–0.444	0.642	0.182				0.479	1.614	0.033
Distance to the nearest road	–0.061	0.941	0.055				–0.047	0.954	0.037
Fire damage				–0.639	0.528	0.176	0.328	1.388	0.047
Animal damage	1.257	3.516	0.000				0.701	2.015	0.088
Wind damage				0.523	1.686	0.033	–0.368	0.692	0.046
Land ownership	1.059	2.883	0.000	0.488	1.630	0.048	0.343	1.410	0.032
Timber harvest				0.355	1.426	0.017	0.161	1.175	0.062
Constant	–8.394	0.000	0.000	–4.318	0.013	0.000	–3.803	0.022	0.000
p value of Hosmer–Lemeshow test		0.264			0.119			0.051	
Log-likelihood ratio		1888.1			846.4			1109.5	
Akaike Information Criterion		3798.2			1716.8			2249.1	
Overall correct prediction		62.9%			63.3%			63.2%	
Number of observations		20 033			2982			3826	

Results and discussion

Logistic regressions yielded correct predictions ranging from 63% for the models fit with partitioned data (Table 4) to 86% for the model estimated without data partitioning (Table 5). Based on the p values of the estimated coefficients associated with individual independent variables, on Hosmer–Lemeshow test results, and on log-likelihood ratios, these models are generally well fit and robust. The observed and model-predicted ranges of tallow invasions also closely match with each other (Figs. 1*a* and 1*b*). For interpretation simplicity, all discussions that follow and are related to statistical significance, unless otherwise specified, and are based on the 5% significance level.

Landscape features

About 80% of the existing tallow invasions into southern US forests occur at elevations lower than 50 m (165 ft.) or slopes of <2°. The invasion probability diminishes quickly after these pivot points (Fig. 2). No invasion was reported in the FIA data for sites where elevation was greater than 165 m (540 ft.) or slopes were steeper than 18° (Tables 3 and 5). The odds ratios for elevation and slope in all models are approximately equal to one, suggesting that for a one-unit increase in elevation or slope, the odds ratio of tallow invasions decreases by about one. The elevation effect is consistent across all models, while the slope effect becomes insignificant only in the model estimated using data from subplots in the counties with occupation rates greater than

Table 5. Logistic regression results of tallow tree invasions into southern US forestlands.

	Model fit with the data from all counties			Model fit with the data only from invaded counties		
Variable	Estimated coefficient	Odds ratio	*p* value*	Estimated coefficient	Odds ratio	*p* value*
Elevation	–0.004	0.996	0.000	–0.003	0.997	0.000
Slope	–0.041	0.960	0.000	–0.038	0.963	0.000
Proximity to water bodies	0.283	0.328	0.000	0.319	1.376	0.000
Mean extreme minimum temperature	2.144	8.536	0.000	1.848	6.348	0.000
Stand age	–0.013	0.987	0.000	–0.014	0.986	0.000
Artificial regeneration	–0.499	0.607	0.000	–0.488	0.614	0.000
Distance to the nearest road	–0.100	0.905	0.000	–0.079	0.924	0.000
Disease damage	–1.554	0.211	0.128			
Animal damage	0.720	2.055	0.002	0.921	2.513	0.000
Wind damage	–0.170	0.844	0.122	–0.233	0.792	0.033
Land ownership	0.618	1.855	0.000	0.635	0.887	0.000
Timber harvest	0.280	1.323	0.000	0.206	1.228	0.001
Site preparation				–0.199	0.819	0.083
Constant	–11.237		0.000	–9.822		0.000
p value of Hosmer–Lemeshow test		0.101			0.821	
Log-likelihood ratio		5715.1			5429.7	
Akaike Information Criterion		11 456.1			10 885.4	
Overall correct prediction		85.6%			81.4%	
Number of observations		46 865			26 841	

Note: The models were estimated using FIA subplots in the four most severely invaded states in the US South, including Alabama, Mississippi, Louisiana, and Texas. The first model was fit using the data of FIA subplots from all counties in the four states. The second model was fit using the data of FIA subplots in only the counties with infestations. Even in those invaded countries, many subplots did not have tallow tree, allowing us to perform logistic regression.

**p* value = 0.000 indicates that it is less than 0.0005.

two standard deviations above the mean. This implies that slope emerges as a less important barrier in the latter stages of tallow invasion. Aspect was found not to be statistically significant and thus was not included in the final models.

Adjacency to rivers, streams, lakes, and ponds relates positively to the occupation of tallow tree, as shown in all models. The odds ratio for this predictor is quite large, particularly in the models estimated with discriminated data (Table 4). The main vectors of tallow seed dispersal are water movement and birds that find favorable habitat around water bodies, while high soil moisture content is favorable for germination, establishment, and growth (Barrilleaux and Grace 2000; Butterfield et al. 2004).

Site and forest conditions

Site productivity is not statistically significant with tallow occupation except in the models fit with data of medium and high invasion rates (greater than two standard deviations below the mean). This suggests that site productivity is not critical in the early stages of tallow invasion (i.e., poor or good sites have an equal chance to be invaded initially), but higher productivity furthers expansion after initial establishment.

All five models demonstrate that invasions are less likely in mature forest stands than in young ones. Also, in general, tree-species diversity is not a significant barrier to invasion, as similarly reported by Lonsdale (1999), Stohlgren et al. (1999), and Collins et al. (2007). Diversity is statistically significant only in the model of highly invaded counties (with an invasion rate greater than two standard deviations above the mean). This may be because immigration processes rather than species competition dominate tallow invasions (Pattison and Mack 2008). It may also suggest that the plant communities invaded by tallow tree have not been saturated, since tallow tree is shade tolerant and able to persist with other species (Jones and McLeod 1990; Jones and Sharitz 1990). Additionally, as mentioned earlier, tallow tree is more likely to occupy low and productive lands that also tend to be more species diverse (Wall and Darwin 1999; Burns and Miller 2004) and where competition has not been shown to be so influential compared with other test cohorts (Pattison and Mack 2008). Furthermore, tallow tree is capable of evolution of increased competitive ability in introduced ranges (Zou et al. 2008).

Climatic conditions

Among the climate variables considered, only mean extreme minimum temperature in January is significant. As shown in Table 5, the odds ratio for the mean extreme minimum temperature in January is the largest in the models, 2–3 times larger than the next largest odds ratio. Additionally, the FIA data reveal that no invasion was detected in survey sites where the mean extreme minimum temperature in January was below –12 °C (10°F). This implies that the winter minimum extreme temperature indeed serves as an important barrier to tallow invasions, as also reported by Pattison and Mack (2008).

Global temperature is highly likely to rise in the decades to come owing to greenhouse gas emissions and other factors, as predicted by the Intergovernmental Panel on Climate

Fig. 1. Current and predicted ranges of tallow tree in the forests of Alabama, Mississippi, Louisiana, and Texas. (Note: Predictions were made only within the FIA data range). (*a*) Observed tallow tree invasions, 2007; (*b*) predicted tallow tree invasions, 2007; and (*c*) predicted tallow tree invasions under global climate change (2 °C warming).

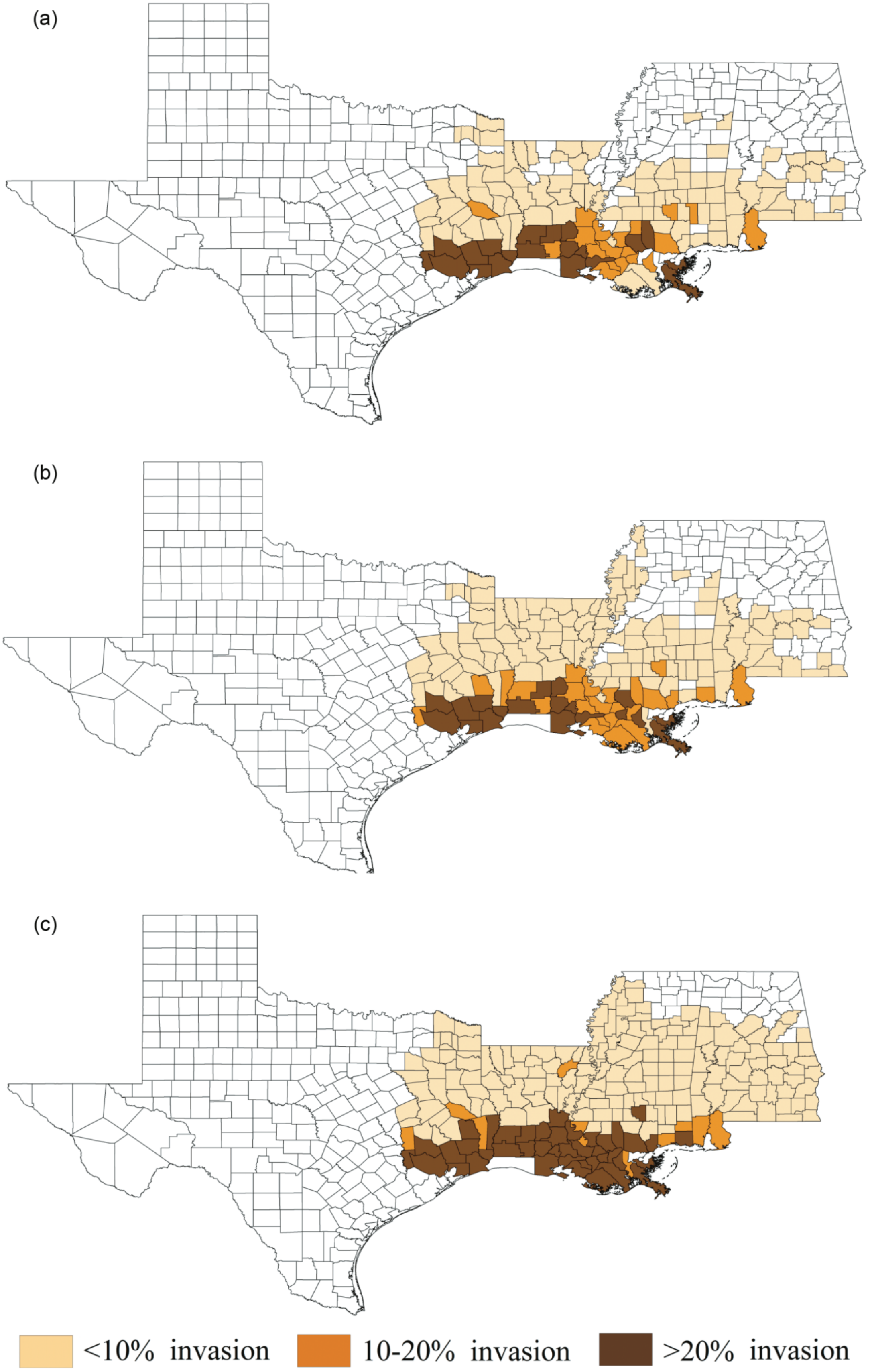
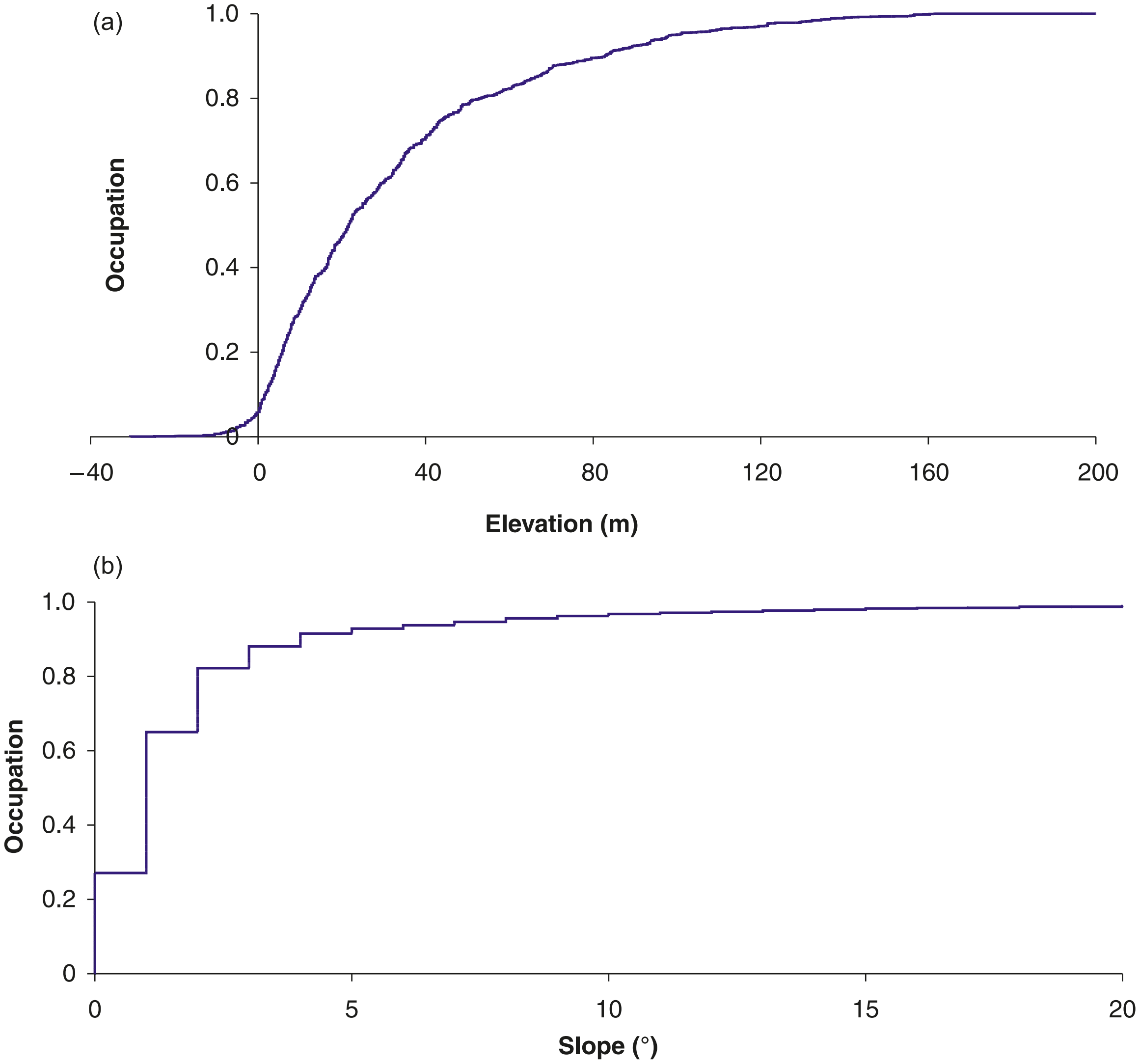


Fig. 2. Cumulative probability of tallow tree occupation across elevation gradients (*a*) and slope gradients (*b*).



Change (2007). As minimum temperatures rise, the probability of tallow colonization farther northward will increase considerably. Using our empirical model fit with nondiscriminated data, we predicted the range and intensity of tallow tree in the study region with a 2 °C warming and everything else unchanged (Fig. 1*c*). Please note that invasion predictions were made only for those counties where general FIA data were collected. In other words, no prediction was made for geographic areas beyond the FIA data range. Our results clearly indicate that both range and intensity of tallow invasions would be augmented if the presumed warming occurs. Tallow tree could then occur in all of East Texas and Louisiana and most of Alabama and Mississippi, except the far north of these two latter states. Using the CLIMEX model, Pattison and Mack (2008) predicted an even more northern spread to southern Illinois and Pennsylvania with a 2 °C rise. Thus, global warming could result in tremendous challenges for combating the geographic expansion of this invasive stand-replacement species, and the invasions, if not contained, could lead to considerable ecological and economic consequences in the US South and beyond.

Forest management activities and disturbances

All five models reveal that artificially regenerated forest stands have lowered the risk of tallow invasion. These stands are usually more intensively managed, and silvicultural measures are applied to enhance vigor of the planted species and control competition from unwanted species. Burns and Miller (2004) observed that prescribed burning decreased tallow seed germination, which is a common site preparation treatment. These activities combine to lessen the chance of alien plant establishment.

Tallow invasions are positively correlated with natural regeneration only in highly invaded stands (with an invasion rate greater than two standard deviations above the mean). Timber harvesting would generally enhance the probability of tallow invasions (Table 5), although its statistical significance is less obvious in the models fit with the data containing only high or low invasion rates (Table 4). Harvesting bares soil and creates openings that reduce competition from dominant species, thus creating conditions for tallow establishment. Less well documented was the finding that tallow tree is more frequent along roads and decreases with departure from vicinity of roadside. Although common roadside observations would suggest a connection between adjacency to roads and invasive potential of specific species, little research has yet documented similar findings (Parendes and Jones 2000; Fei et al. 2008).

Animal damage, wind storms, and fire occurrence show significant effects on tallow occupation. Animal-damaged stands were found highly susceptible to tallow invasion, as evidenced by the fact that the odds ratio associated with this predictor is consistently among the top two largest values in all models. However, high invasion rates are also more likely in wind- or fire-damaged stands, which often cause broader, more severe, and longer lasting disturbances than animals, and are common to Gulf coastal plain forests owing to hurricanes and the use of prescribed burning. The increased presence of tallow tree has recently been reported in Louisiana forests following hurricane damage (Chapman et al. 2008). Damage by disease and insect pests were also considered but found insignificant and were excluded in the final models.

Forest ownership

Private forestlands are far more apt to have tallow tree than public forestlands (Tables 3 and 5), and the odds ratio for private ownership is higher than that for many other predictors included in the models (Table 4). There are at least two reasons for the higher probability of finding tallow occupation on private forestlands than on public forestlands. (1) Private lands in general are less closely monitored and managed, more frequently harvested, and covered with younger trees than public lands (Smith et al. 2004), all contributing to tallow invasion. (2) The lack of policy incentives for private landowners to implement invasion prevention and mitigation (Colton and Alpert 1998) is another reason for the more extensive presence of tallow tree on private lands.

Conclusions

We identified key species–environment relationships of tallow invasions and estimated likelihoods of local and regional expansions in the southern US. Tallow tree is more likely to be observed on low and flat lands, areas adjacent to water and roadways, and younger stands. Disturbances including timber harvesting and damage caused by animals, wind, and fire stimulate tallow invasions. However, when harvesting occurs, site preparation and artificial regeneration tend to reduce tallow colonization. Additionally, more severe invasions are found on private forestlands than on public ones, which are often characterized with more mature trees, less frequent harvests, and better monitoring and control of invasives. The mean extreme minimum temperature in January inhibits tallow tree movement northward.

Our results have several implications for monitoring and mitigating tallow invasions in the US and other countries facing the similar challenge. Monitoring and mitigating efforts should target lands with low elevations and gentle slopes, close to water and roads, recently harvested or disturbed, and covered by young stands established with minimum site preparation. Harvested or disturbed sites should be promptly reforested or restored employing adequate site preparation. The complementarity between mitigating disturbances and preventing tallow invasions suggests that holistic and coordinated efforts to enhance forest health would be more cost-effective. More efforts should be directed to educate private forestland owners and engage them in tallow prevention and restoration of infested stands. As the winter minimum temperature restrains tallow invasions, this invasive plant could pose a much greater threat than just US southern ecosystems with the predicted global warming. This would be even more alarming when climate change is coupled with the increased frequency and intensity of disturbances.

This study focused on forestlands only. Future studies can integrate tallow occupation in various ecosystems, including forestlands, grasslands, and others in different countries. Analyses across different ecosystems and regions will lead to a more profound and comprehensive understanding of tallow invasions, which will be of greater value for guiding the monitoring and mitigation of this widely spread invasive species.

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