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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

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Abstract: In the Gulf of Mexico coastal region, prescribed fire has been increasingly used as a management tool to restore declining native ecosystems, but it also increases the threat posed by biological invasion, since the treated sites are more susceptible to invasive species such as Chinese tallow (*Triadica sebifera*). We chose Mississippi Sandhill Crane National Wildlife Refuge (MSCNWR), a fire-managed landscape, to examine the potential effect of prescribed fire and landscape/community features on tallow invasion and spread. We took a complete survey of roadways and fire lines for tallow and measured a systematic sample of 144 10 × 3 m² rectangular plots along two selected roadways and a simple random sample of 56 0.04-ha circular plots across burn units. We used pair correlation function for marked point pattern data, zero-inflated negative binomial models for count data, as well as multivariate Hotelling's T² test, to analyze the effect of prescribed fire and landscape/community characteristics on tallow invasion and spread along habitat edges and into interiors. Our results show that tallow spread along habitat edges and into interiors in a spatially clustered pattern. Tallow invasion risk decreases with the distance to seed trees and shrub coverage, and with the time since last fire if seed trees are outside the effective seed dispersal range (~300 m), but increases with the time since last fire if seed trees are within the effective seed dispersal range. Tallow seedling (≤2 years old) densities increase with the time since last fire and with increasing overstory tree basal area, but decrease with the distance to seed trees. Tallow-invaded interior plots have significantly shorter mean fire return intervals (2.7 years), lower shrub coverage (8.6%), and are closer to edges (20.3 m) than non-invaded plots (4.3 years, 18.4%, 167.6 m, respectively).

Keywords: Chinese tallow; age distribution; seed trees; mean fire return interval; time since last fire; pair correlation function; zero-inflated negative binomial model

1. Introduction

In the Gulf of Mexico coastal region, prescribed fire has been recognized as a preferred approach for the restoration of native ecosystems (e.g., longleaf pine ecosystems, wet pine savannas, and coastal prairies and bogs) [1]. However, the effectiveness of prescribed fire depends on many factors such as

initial site/stand condition, fire return interval, intensity, seasonality, and length of treatment period [2]. One potential threat associated with prescribed fire is that treated areas may become more susceptible to invasion by non-native species such as the Chinese tallow tree (*Triadica sebifera*, hereafter tallow), thus preventing the restoration of native species and ecosystems [3–6]. Tallow is highly competitive and can thrive under a variety of conditions following prescribed fire, and eventually may impede the success of a prescribed fire and modify the fire regime if it successfully dominates the recipient ecosystems [5,7,8].

Native to China, tallow is an aggressive invader, able to adapt to a wide variety of ecosystems in the Gulf of Mexico coastal region [9]. Introduced to the southern coastal states in the 1900s, it has been widely planted as a crop tree throughout the southeastern United States and promoted by the Foreign Plant Introduction Division of the USDA to produce industrial materials [10,11]. In introduced regions, tallow can grow well in a suite of site/soil conditions from sandy to poorly drained to even intermittently flooded, and can tolerate and survive in a variety of light conditions for a long time due to its favorable life history traits (e.g., high specific leaf area, nutrient uptake, seed production, root/stump sprout capacity, and herbivore tolerance) [12–18]. Currently, tallow has spread from the Gulf Coast of Texas to the Atlantic Coast of North Carolina, most likely due to its advantageous life history traits and seed dispersal via various avian species such as house finches and white-winged doves [19–21]. Tallow commonly occurs in disturbed sites [22,23] such as roadsides [24,25], abandoned agricultural lands [26], urban neighborhoods [27], and hurricane-damaged forests [25,28,29]. These sites may have large seed sources and provide pathways for tallow to spread to surrounding ecosystems through habitat edges and corridors [30].

Typically, on fire-managed landscape, tallow seedlings and small trees are vulnerable to fire, but mature or large tallow trees can survive or be top-killed by fire, depending on fire intensity and timing of the burn [24]. Thick bark, a characteristic of aging, as well as vigorous basal and root sprouts following fires, allow tallow to survive and persist after low- or moderate-intensity ground fires, including those recurring at frequent intervals [7,31]. On-site experimental studies report that fire enhances tallow spread and density in some instances, but reduces tallow colonization or has little effect in other instances [32]. A variety of interacting factors including site conditions (e.g., fuel loading and continuity, soil moisture), fire characteristics (intensity, frequency, burn season, length of treatment period), and differences in the availability (abundance and spatial distribution) of seed sources cause inconsistent responses to fire [5]. The poorly understood ecological effects of prescribed fire at the landscape level, especially over longer time periods, have become a barrier to predicting forest ecosystem responses to prescribed fire treatments and biological invasion in the Gulf of Mexico coastal plain.

Several studies have reported the spread patterns and risk factors of tallow at regional levels (in a state or across multiple states) [4,6,33] and on local scales (within a plot or stand) [25,34]. However, the patterns and mechanisms of tallow spread at a landscape or management unit level are not well understood because of the complexity of multiple factors and interactions involved and the unavailability of consistent, quality monitoring data over longer time periods. This is specifically true with tallow since the inhomogeneous spatial distribution of tallow invasion and spread varies drastically over space and time, even in similar ecosystem (patch) types [6,35]. For many invasive species, especially tallow, current condition and dynamics are primarily the effect of a sequence of disturbance events varying by landscape/ecosystem. Landscape metrics and ecosystem features mostly serve as predisposing factors indirectly affecting seed dispersal by regulating avian–vegetation relationships [36]. To date, we have not noted landscape-level studies on tallow invasion history following long-term disturbances, especially on landscapes where prescribed fire has been applied to restore the declining pine savanna and coastal prairies and bogs. Such landscapes previously dominated the coastal area and are characterized by sparse overstory and grassy understory vegetation [31]. Understanding tallow spread under varying fire return intervals, diverse stand conditions and propagule (seed trees) pressure levels will be critical for controlling tallow spread if endeavors to restore native ecosystems using fire as a tool continue.

In this study, a coastal landscape where prescribed fire has been used for restoration of native pine savanna and coastal prairies since early 1980s was selected to evaluate the spatiotemporal spread pattern of invasive tallow under repeated prescribed burns. Specifically, we intend to test the following two questions: (1) What is the spatiotemporal pattern of tallow spread and how will prescribed fire, in terms of time since last fire, in combination with other landscape metrics and site/community factors, affect the colonization of tallow seedlings along habitat edges? (2) What is the spatial pattern of tallow-invaded interior plots and how will mean fire return interval, landscape metrics and site/community factors affect the risk of tallow spread into habitat interiors? The results will help determine whether prescribed fire can be used as a tool to promote native habitat restoration and conservation as well as curb tallow occurrence.

2. Methods

2.1. Research Site

The Mississippi Sandhill Crane National Wildlife Refuge (MSCNWR) is located in southern Mississippi (30°27'3.49" N, 88°39'20.60" W) (Figure 1), contains three blocks (east, west, and south), and has a total area of 7493 ha. Situated along the gently sloping lower Gulf Coastal Plain, MSCNWR is part of the deltas of the Escatawpa and Pascagoula rivers. The climate is subtropical, which means summers are hot and humid, but winters are relatively mild [37]. Annual maximum temperatures average 24.7 °C, with July averages reaching 32.0 °C. Winters have annual minimum temperatures averaging 14.7 °C, with January averages around 5.8 °C. Light freezes are common and hard freezes occur occasionally. Average annual rainfall is approximately 1600 mm.

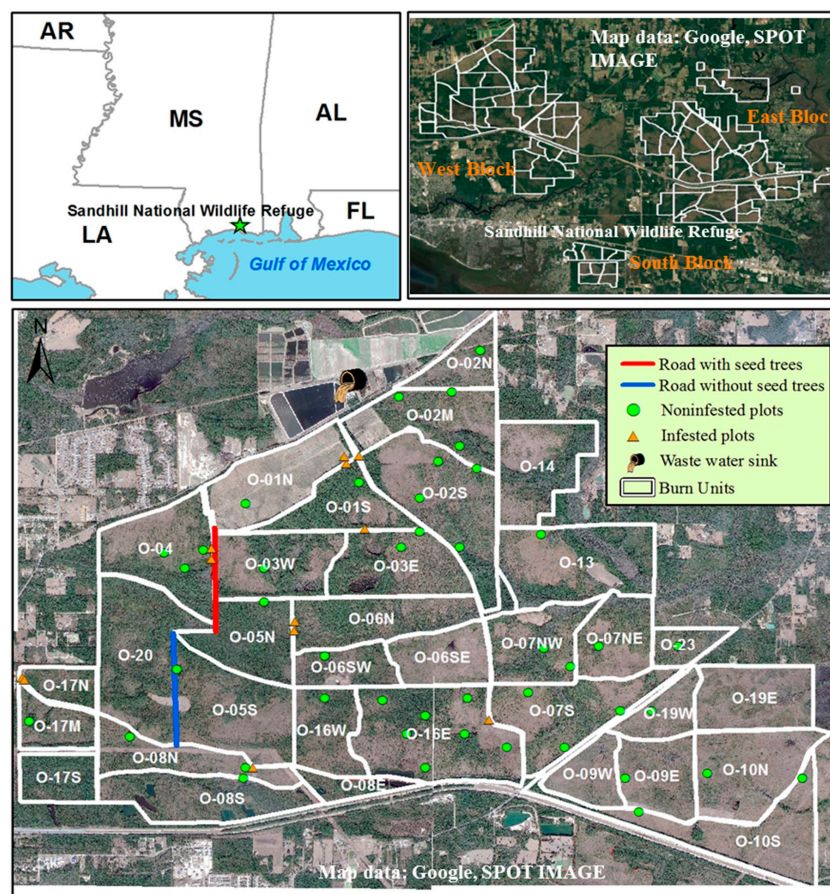


Figure 1. Map of Mississippi Sandhill Crane National Wildlife Refuge (MSCNWR) west block, showing the burn bunts, selected edges, and the locations of sample plots.

Since 1985, MSCNWR has conducted prescribed fires on 400–3600 ha per year, with each stand (burn unit) on a 1–5 year fire rotation (a mean fire return interval of 2 to 3 years for the entire landscape) to restore wet pine savanna, which is the most important habitat for endangered Mississippi sandhill cranes (*Grus canadensis pulla*) [37]. Prescribed fire is used in the spring and fall to clear woody vegetation, improve areas overstocked with slash pine, and enhance the suitability of the cranes' nesting areas. Invasive species such as tallow and cogongrass have invaded this refuge in spatially clustered patterns along habitat edges or in patches frequently disturbed, and have become a serious threat to the native habitats of the cranes and declining grassland birds such as Henslow sparrows (*Ammodramus henslowii*). To date, major habitats and communities include wet pine savannas (25.3%), pinelands (flatwood and scrub) (57.5%), hydric drain (6.6%), estuarine (2.8%), agricultural land (4.2%), open water, and others (3.6%). The entire landscape has been steadily shifted to the desired habitats for the cranes and other native wildlife species postulated by the management goal [37].

2.2. Data Collection

For spatial continuity, this study will only use the data collected from the west block (2879 ha) including 34 burn units (Figure 1). Data collection was conducted in the fall of 2015. First, a complete survey of Chinese tallow clusters was conducted along all major habitat edges (roadways and fire lines) to delineate spatially separated tallow clusters. A tallow cluster is defined as a group of tallow individuals occurring closely together in similar site conditions. In each cluster, the number of tallow seed trees was counted, and the oldest (largest) tallow tree was mapped using a GPS device (Forge Echo by F4Device, <http://www.thinkf4.com/solutions/forge-echo>) and then felled to determine its age [17]. We used the geographic coordinates of the oldest tallow tree as the location of the cluster and age to infer the invasion time (year). The invasion year and location of tallow clusters were mapped to show the spatiotemporal spread pattern of tallow trees along habitat edges.

Second, two invaded roadways (one recently invaded road without seed trees and another road invaded at an earlier time with tallow seed trees) were selected, along which a number of rectangular plots with a $10 \times 3 \text{ m}^2$ area and 30 m spacing were established on each side and their spatial locations (geographic center) were mapped. Within each plot, overstory condition (overstory basal area, tree density, and canopy closure (%)), understory condition (average height and coverage (%) of shrubs and grasses/herbaceous species), time since last fire, and distance to nearest seed trees were recorded. Overstory canopy closure and understory vegetation coverage were estimated based on the presence (1) or absence (0) of target species within 20 quadrats ($1 \times 1 \text{ m}^2$) regularly set in each plot. Overstory tree density (tree/ha) and basal area (m^2/ha) were calculated based on individual tree measurement data. All tallow trees were felled at ground level to determine age and measure diameter at breast height (dbh), diameter at ground level (dgl), and total height using the method of Tian et al. [17] (Figure 2). Meanwhile, based on the age structures of tallow trees, the number of tallow seedlings (age ≤ 2 years) in each plot was determined. Time since last fire was calculated from 2000–2015 fire data provided by the Fire Management staff of the MSCNWR. Distance to the nearest tallow seed tree from a plot was calculated based on the mapped plot data and was set to zero if tallow seed trees were present.

Third, a total of 56 circular 0.04-ha plots were randomly located and mapped across burn units in the west block (Figure 1). A plot was determined as either invaded or non-invaded depending on whether tallow was present or not. Overstory and understory condition of a plot was measured and calculated using the same method as for the rectangular plot. Distance from a plot to the nearest edge was calculated using the ArcGIS Spatial Analyst tool, and mean fire return interval of the burn unit where a plot resides was calculated based on the 2000–2015 prescribed fire data from the Fire Management staff of MSCNWR.

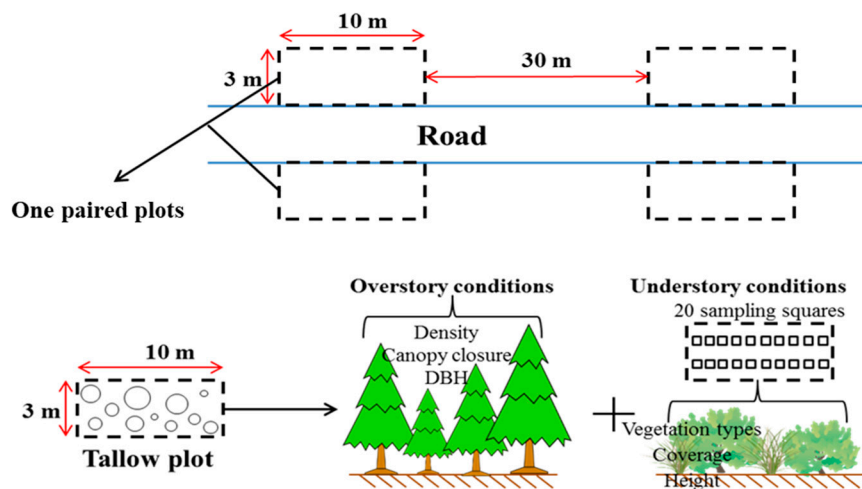


Figure 2. The design of rectangular plots and site/stand condition variables collected to study tallow colonization and spread along habitat edges (roadways and file lines).

2.3. Spatial Data Analysis and Modeling

To evaluate the spatiotemporal pattern and associated risk factors of tallow spread along habitat edges (question 1), the cumulative number of tallow clusters by year was plotted to demonstrate the annual rate of spread of tallow clusters along habitat edges (Figure 3A). Differentiated by the pivotal year of 2011, the average spread rate of tallow (the number of tallow clusters formed annually) was estimated via the slope coefficient of the derived simple linear regression models for the two time periods: before and after 2011. The spatiotemporal spread process (Figure 3B) of tallow along habitat edges was then modeled using a marked point pattern in the R spatstat package using the (x, y) coordinates as the location and derived invasion time (before and after 2011) as the mark [38,39]. The pair correlation function (PCF) (Figure 3C) was used to estimate spatial correlation between tallow clusters formed in the two different time periods [40]. The PCF measures the spatial scale (linear length, expressed by the x-axis) on which individual clusters are positively (the PCF curve is above the shaded envelope), negatively (the PCF curve is below the shaded envelope), or randomly (the PCF curve is within the shaded envelope) distributed. Therefore, it can be used to infer the critical spatial scale at which favorable resource alternates or is available for tallow to colonize and spread within a specific time period.

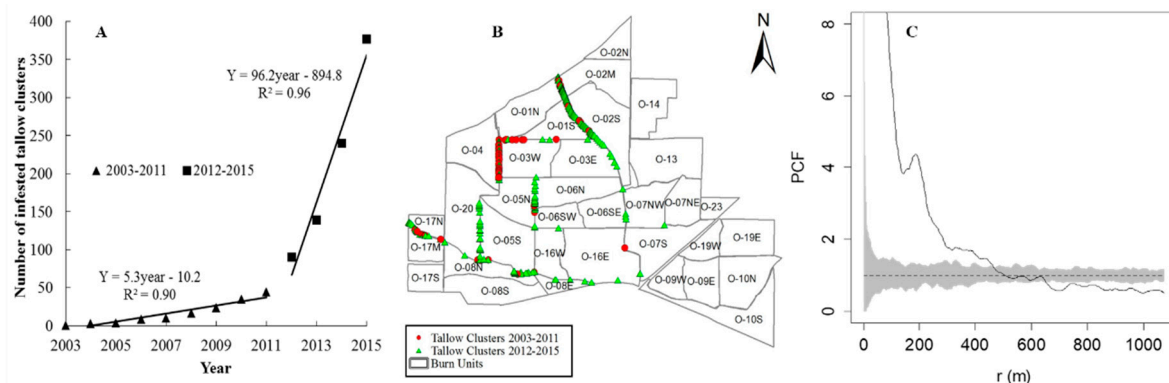


Figure 3. (A) Cumulative increases of tallow clusters between 2003–2011 and 2012–2015, (B) spatiotemporal spread patterns of tallow clusters along habitat edges (roadways and fire lines) and (C) the spatial relationship of tallow clusters between 2003–2011 and 2012–2015.

Using age data collected from rectangular plots (80 plots along the earlier invaded road and 64 plots along the recently invaded road), age distribution and cumulative density (number/ha) of tallow trees were plotted to visualize tallow colonization at microscales (plot) (Figure 4). Taking the count number of tallow seedlings ≤ 2 years old in each plot as the response variable, and the measured overstory and understory condition, distance to the nearest seed trees, and time since last fire as the predictor variables, the mixture zero-inflated negative binomial models (ZINB) were used to evaluate potential factors contributing to tallow colonization [36]. The ZINB count and binary (logit) regression models aim to predict the mean number of tallow seedlings ≤ 2 years and the probability of having no tallow seedlings ≤ 2 years within a rectangular plot of $10 \times 3 \text{ m}^2$, respectively, with respect to a subset of selected predictor variables using the maximum likelihood method (Table 1). Change in density of tallow seedlings with respect to significant predictor variables identified by the ZINB models was plotted to visualize their relationships (Figure 4).

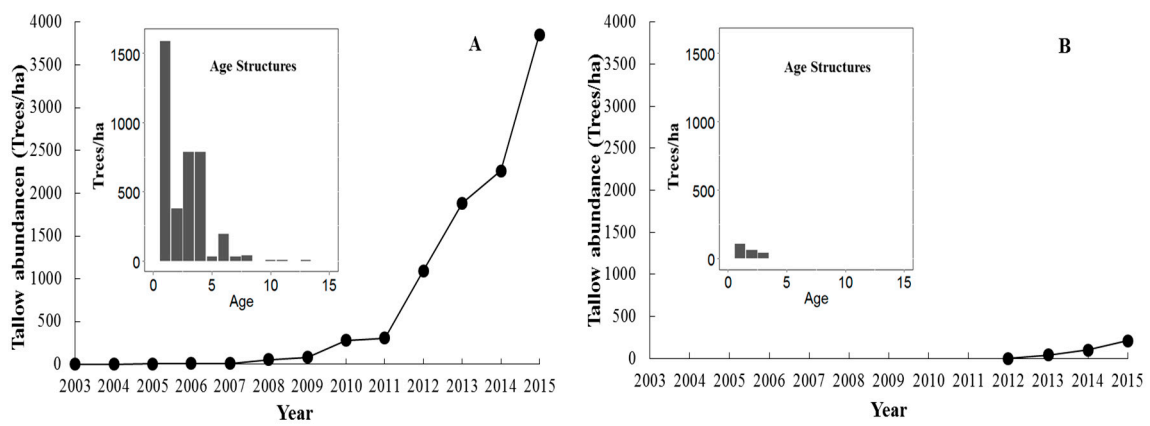


Figure 4. The cumulative increase in density and age structure (inserted) of tallow trees along selected roadways: (A) With seed trees; (B) without seed trees.

Table 1. Estimated coefficients of the ZINB model for the early invaded roadway (with seed trees) and the roadway invaded latterly (without seed trees).

	Estimate	Std. Error	z Value	Pr (> z)
For the early invaded roadway (with seed trees)				
Count model:				
Intercept	7.587	0.809	9.385	0.000
Distance to seed trees	−0.009	0.004	−2.025	0.043
Year since last fire	0.320	0.061	5.286	0.000
Log(theta)	0.849	0.167	5.076	0.000
Binary model:				
Intercept	7.580	3.431	2.209	0.027
Shrub coverage	0.021	0.013	1.647	0.100
Distance to seed trees	0.034	0.015	2.242	0.025
Year since last fire	−0.662	0.259	−2.553	0.011
Distance to neighborhood	0.468	1.869	−2.502	0.012
For the latterly invaded roadway (without seed trees)				
Count model:				
Intercept	5.196	0.923	5.632	0.000
Overstory basal area	0.724	0.366	1.977	0.048
Year since last fire	0.924	0.398	2.324	0.020
Log(theta)	1.452	0.414	3.507	0.000
Binary model:				
Intercept	−1.231	1.172	−1.05	0.294
Shrub coverage	0.024	0.013	1.792	0.073
Year since last fire	1.135	0.505	2.247	0.025

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

All statistical analysis was conducted using the R-3.4.2 statistical environment for Windows (R Development Core Team 2014). R base packages and contributed packages including *spatstat* version 1.53-2 [39] for spatial analysis and *pscl* version 1.5.2 for ZINB regression analysis [41] were used.

3. Results

3.1. The Spatiotemporal Pattern and Associated Risk Factors of Tallow Spread along Habitat Edges

Tallow spread along habitat edges in this fire-managed landscape around 2003 (Figure 3A). By 2015 (the sampling year), a total of 377 clusters of varying sizes had been identified. Temporally, the spread process consisted of two distinct phases based on the spread rate: a slow spread phase (2003–2011, with an average of 5.3 clusters established annually) and a rapid spread phase (2012–2015, with an average of 96.2 clusters established annually), distinguished by year 2011 (Figure 3A). During the earlier period (2003–2011), tallow was mainly confined to habitat edges encompassing the northwest and west burn units and after 2011 it quickly spread to most habitat edges, encompassing the central burn units (Figure 3B). Less tallow was found along habitat edges in the east and southeast part. Tallow clusters were positively spatially correlated at small spatial scales (<500 m) but negatively correlated at large spatial scales (>650 m) between the clusters established in the two spread phases (Figure 3C).

Tallow trees had a reverse J-shaped age structure for roadways both with and without seed trees (Figure 4). Along the early invaded roadway (with seed trees), tallow tree densities in rectangular plots from 2003 to 2015, derived from the age data, followed a trend similar to the landscape-level spread of tallow clusters: a slow increase from 2003 to 2011, followed by a rapid increase from 2012 to 2015 (Figures 3A and 4A). For the newly invaded roadway (without seed trees), tallow tree densities were still in a slow increase mode (Figure 4B). Of all factors contributing to tallow colonization in count models (Table 1), time since last fire appeared to be most significant (minimum p values) for both roadways, and specifically, tallow seedling densities tended to increase with time since last fire (Figure 5B). Furthermore, tallow seedling densities were found to decrease significantly with distance to seed trees along the roadway with seed trees ($p = 0.043$, Figure 5A) and to increase with increasing overstory tree basal area along the roadway without seed trees ($p = 0.048$, Figure 5C). Binary models showed that time since last fire remained most significant out of all risk factors, but influenced the colonization risk along the roadway with and without seed trees in an opposite manner (Table 1). Longer time periods since last fire would increase a site's colonization risk along the roadway with seed trees, but decrease colonization risk along the roadway without seed trees. Colonization risk decreased with shrub coverage for both roadways (Figure 5D), but along the roadway with seed trees, colonization risk was shown to decrease with increasing distance to seed trees as well as increasing distance to residences (Table 1).

3.2. The Spread of Tallow into Habitat Interiors

By 2015, approximately 21.4% of interior plots (12 out of 56 plots) had been invaded by tallow, with an annual spread rate of 1.8%. Spatially, invaded plots were independent from non-invaded plots at all spatial scales since the PCF curve was within the simulated envelope (the shaded area) (Figure 6A). Based on Hotelling's T^2 tests, invaded interior plots were significantly different from non-invaded interior plots in terms of distance to nearest edge, understory shrub coverage and mean

fire return interval ($p < 0.0001$). Invaded plots were located significantly closer to roadways and fire lines with a mean distance of 20.3 m in contrast to 167.6 m for the non-invaded plots ($p < 0.001$, Figure 6B), and had lower shrub coverage ($8.57 \pm 3.23\%$ vs. $18.42 \pm 2.60\%$) ($p = 0.025$, Figure 6C) and shorter mean fire return interval (2.7 ± 0.17 years vs. 4.3 ± 0.31 years) than non-invaded plots ($p < 0.001$, Figure 6D).

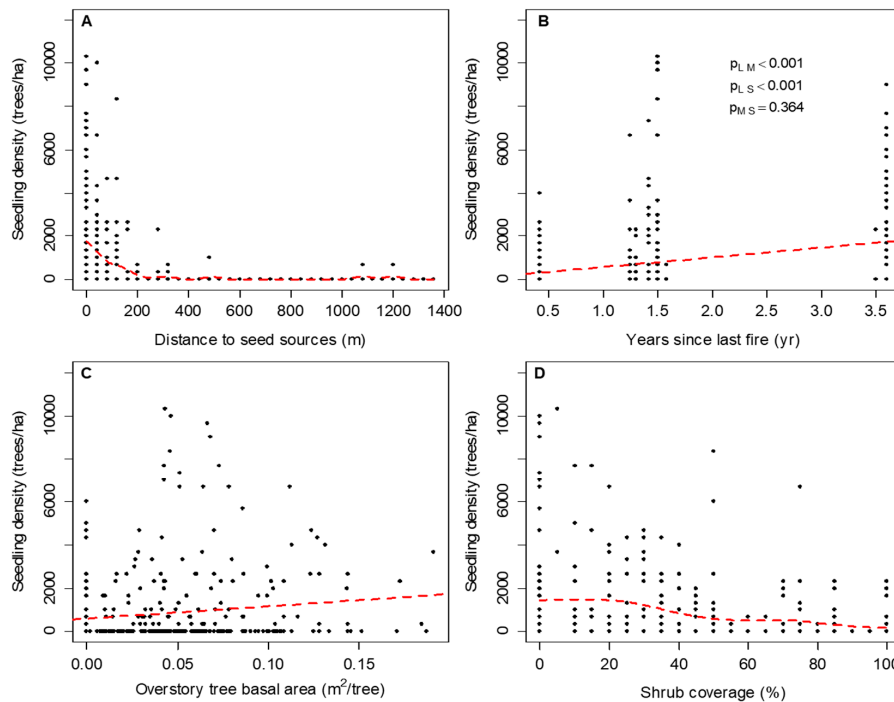


Figure 5. Change of tallow seedling (≤ 2 years) densities by risk factors: (A) Distance to seed sources; (B) year since last fire; (C) overstory tree basal area; and (D) understory shrub coverage.

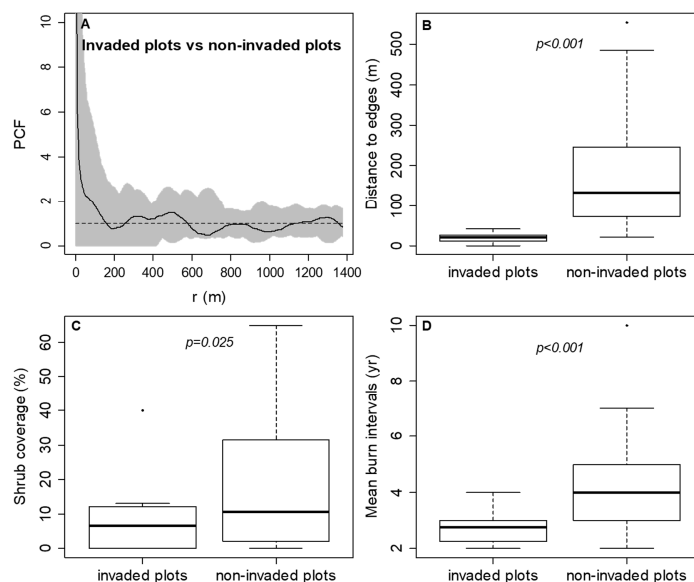


Figure 6. The spatial relationship and site conditions between tallow-invaded plots and non-invaded plots: (A) The PCF curve shows the invaded plots and non-invaded plots are spatially independent; (B) tallow-invaded plots are significantly closer to roads than non-invaded plots; (C) tallow-invaded plots have significantly lower shrub coverage than non-invaded plots; (D) tallow-invaded plots have significantly shorter mean fire return intervals than non-invaded plots.

4. Discussion

4.1. The Spatiotemporal Pattern and Associated Risk Factors of Tallow Spread along Habitat Edges

In the Gulf of Mexico coastal landscape, the unprecedented spread of tallow trees has been ascribed to natural and anthropogenic disturbances [4,6,34,42]. Tallow is a disturbance-dependent species, and any disturbance causing alteration of resources will inevitably facilitate its invasion [35,43–45]. The earliest tallow invasion into the west block of MSCNWR is believed to have been caused by accidental discharge of waste water into the refuge in the mid-1990s (personal communication with the Fire Management staff of the MSCNWR). Tallow seeds were likely transferred into the refuge by waste water current from the adjoining urban area since old (large) tallow trees are mostly distributed along ditches and in flooded areas by waste water in bordering burn units (O-1 and O-4) (Figure 1). Tallow was dated to have invaded the two burn units around 1997, 6 years earlier than the initial invasion of surrounding roadways and fire breaks in 2003. The lag phase and subsequent slow spread process (2003–2011) were most likely caused by low propagule pressure (lack of seed trees) [35,46]. This is consistent with our survey results which showed that a great number of tallow trees began bearing seeds at 4 years or even younger [47]. Therefore, we speculate that early tallow seeds were dispersed by birds from these interior seed trees to roadsides and fire breaks [48].

The phenomenal increase in spread after 2011 is believed to result from the refuge-wide road construction and reconstruction in 2011 funded by the Federal Road Initiative Program (personal communication with the Fire Management staff of the MSCNWR). Anthropogenic disturbances often act as vectors for the introduction and spread of plant propagules and have profound and lasting effects on the habitat and subsequent biological invasion [49,50]. Mechanistically, the contribution of disturbances to tallow invasion mostly lies in the alteration of resource availability and habitat characteristics that may change the behavior of tallow seed-dispersing birds [51] as well as influence seed germination and seedling establishment [25]. The positive correlation between tallow clusters established at small spatial scales <500 m could be directly related to interactions between tallow seed dispersal birds and roadside tallow seed trees (i.e., effective seed dispersal distance) [48], while the negative correlation at large spatial scales >650 m might reflect the heterogeneity of resource availability between early invaded and latterly invaded habitat edges [35,52]. The strong clustered pattern of tallow spread along habitat edges suggests that tallow spread is mostly based on short-distance dispersal, for few or no tallow clusters were found along the roadways and fire breaks in the east and southeast parts and tallow colonization along habitat edges without seed trees is notably slow (Figure 3; Figure 4). Similar spatiotemporal spread patterns along habitat edges were observed in the Grand Bay National Wildlife Refuge, where prescribed fire was not used as an active management tool [36]. As for tallow spread along habitat edges, a conservative estimate for effective seed dispersal distance by birds might be approximately 250–300 m in the Gulf of Mexico coastal landscape, dominated by longleaf pine ecosystems and pine savannas (Figure 3C) [7,51,53].

Formation of a tallow cluster is characterized by a slow, intermittent colonization phase (2003–2011) followed by a fast colonization phase (2012–2015) which is similar to the landscape-level spread of tallow clusters (Figures 3A and 4A). The colonization risk, measured by the density of tallow seedlings less than 2 years old, decreases drastically with the distance to tallow seed trees and understory shrub cover, but increases with the time since last fire and overstory tree size (Figure 5 and Table 1), emphasizing the importance of propagule pressure level (tallow seed trees) and community structure [54–57]. In an experimental study to test propagule pressure–invasion risk relationships, Houseman et al. [58] reported that community invasion risk can be predicted by incorporating propagule pressure, disturbances, and soil fertility into an asymptotic model. But for tallow invasion in pine savanna and pine flatwood managed by prescribed fire, community structure (e.g., overstory tree size and shrub coverage) is much more important than soil physical characteristics considering tallow seed-dispersing birds' selective behavior regarding habitat features [25,51].

Time since last fire has a significant, positive effect on the local colonization of tallow seedlings for roadways both with and without seed trees (Table 1). Density of tallow seedlings for long return intervals (around 3.5 years) is significantly higher than that for short (~0.5 years) or moderate (~1.5 years) return intervals, but the difference between moderate return intervals and short return intervals is not statistically significant (Figure 5B). Fire effect on tallow colonization is two-fold: Fire can 1) top or completely kill tallow seedlings and 2) promote seedling growth by clearing understory vegetation for seed germination, thereby reducing vegetative competition. The ZINB count model suggests that frequent burns (return intervals <3 years) will kill most, if not all, tallow seedlings and subsequently subdue tallow colonization. With long intervals, however, most tallow seedlings will likely survive repeated low-intensity fires due to their thick bark, or be only top-killed due to their strong resprouting ability (as with other hardwood species) [59]. In the field, we observed that fire could kill most 1-year-old and some 2-year-old seedlings, but tallow of >2 years can only be top-killed in most situations and can sprout vigorously after low-intensity ground fires. As a strong sprouter, tallow has thick bark and is fire resistant [7,20,31]. Unless the site is burned repeatedly at short intervals, tallow will likely grow to a size that is resistant to fire due to its fast growth and strong sprouting ability.

As to how prescribed fire affects invasion risk, the ZINB binary model (Table 1) shows that the invasion probability tends to increase with the time since last fire at sites with tallow seed trees, but decrease at sites without tallow seed trees. This disparity is most likely due to the spatially nonstationary nature of the soil seed bank [25] and the viability of tallow seeds in the soil seed bank [60]. At sites with tallow seed trees, fire will help clear understory vegetation for seed germination and seedling colonization, and long return intervals will allow tallow to grow to sizes that are resistant to fire. In contrast, at sites without tallow seed trees, short interval burns will help kill new seedlings originating from seeds dispersed from other areas.

Note that in addition to the time since last fire, overstory basal area appears to be a significant factor influencing tallow seedling density along the roadway without tallow seed trees (Table 1). These tallow seeds most likely came from nearby seed sources and were dispersed by birds. Since tallow seed-dispersing birds prefer large pine trees for foraging and roosting [51,53,61,62], more tallow seedlings were found around large pine trees [25], which resulted in a positive association between overstory basal area and tallow seedling density. Binary models also shows that invasion risk decreases with shrub coverage (%), which means current efforts to restore understory vegetation dominated by grass and herbaceous species by using frequent prescribed burns could increase the risk of tallow colonization, particularly in areas containing tallow seed trees [25]. For the roadway with tallow seed trees, we also found invasion risk decreases with distance to the residence—a “neighborhood” effect—as tallow trees became younger from north (close to residential area) to south.

4.2. The Spread of Tallow into Habitat Interiors

Tallow spread into habitat interiors has a salient edge effect with invaded plots having a mean distance to edge of 20.3 m, much less than that of non-invaded plots (Figure 6). In greatly fragmented landscapes such as the MSCNWR, the edge effect is most likely related to the fact that bird richness and abundance along edges and surrounding areas are much higher than forest interiors [63]. This may explain why forest edges and surrounding areas are highly susceptible to tallow invasion. Understory vegetation (shrub coverage) contributes more to tallow’s ability to invade interiors, by taking habitat edges as footholds, than do overstory conditions (basal area, density, canopy closure) as shown by statistically significant differences between the invaded and non-invaded interior plots ($p = 0.025$). This means that frequent (short interval) burn efforts to restore grass and herbaceous species coverage and remove woody shrub layers will potentially increase the risk of tallow invading from habitat edges to interiors at the landscape level (Figure 6C,D) [1,37].

5. Conclusions

Our study examined spatiotemporal spread patterns of Chinese tallow trees in the MSCNWR, a landscape managed intensively using prescribed fire to restore declining native habitats (pine savanna and coastal prairies) for the endangered Mississippi sandhill crane. Originating from the adjacent neighborhood, invasive tallow was introduced into the landscape by the accidental discharge of waste water and/or tallow seed-eating birds. Subject to relatively short effective seed dispersal distances (≤ 300 m), tallow are distributed in clustered patterns along habitat edges and tallow clusters are positively correlated at a distance of < 500 m. Temporally, the spread of tallow consisted of a slow spread phase (2003–2011) with limited seed trees followed by a rapid spread phase beginning in 2012 which was caused by large-scale road construction and reconstruction. Spatial distribution and abundance of seed trees (propagule pressure) are the predominating determinants of tallow spread rate. Furthermore, prescribed fire (disturbances), landscape structure, and site/stand characteristics have also proved to be significant factors.

At the landscape level, frequent fires (short return intervals of ≤ 3 years) generally tend to significantly increase risk of tallow spread into habitat interiors, especially those areas within a mean distance of 20 m (0–50 m) from habitat edges, compared to infrequent fires (long return intervals of > 3 years). At microscales, tallow invasion is influenced not only by fire but also by site/stand characteristics and propagule levels measured by distance to seed trees. The invasion risk will decrease with the increase in the distance to seed trees and shrub coverage. Fire, however, has a totally contrasting effect on invasion risk depending on availability of seed trees: The risk will increase with the time since last fire if seed trees are present in surrounding areas, but decrease if there are no seed trees or if seed trees are out of the range of the effective seed dispersal distance (> 300 m). As soon as tallow colonization occurs at a site, tallow seedling density will increase with the time since last fire and with overstory basal area. Therefore, using prescribed fire to control and manage invasive tallow should carefully consider all aforementioned factors.

Driven by the spatial distribution and abundance of tallow seed trees, fire regime, and landscape/community features, tallow spread in the fire-managed landscape takes a strong clustered spatiotemporal pattern along habitat edges and surrounding areas (< 50 m from edges). Effective fire treatments at the landscape level should explicitly consider the “seed tree effect”, “edge effect”, and “neighborhood effect” with burn schedules (e.g., determination of fire intervals and seasonality) that not only shorten the window of invasion but also prevent tallow seedlings from growing into mature trees. To reduce tallow spread from edge to interior in this fire-maintained landscape intertwined with pine savannas and pine flatwoods, we recommend that mechanical and/or chemical treatments be conducted in a timely manner along invaded roadways and fire lines to remove tallow seed trees and seedlings and saplings to reduce the propagule pressure. For highly susceptible habitats (< 50 m from invaded roadways and fire lines), fire treatment and timber management should be carefully designed to create more resistant vegetation structure (e.g., high woody shrub layers, dense overstory) to curb tallow invasion into pine savanna, the interior habitat for endangered Mississippi sandhill cranes.

Author Contributions: Z.F. and S.Y. developed the study design. S.Y. collected the field data. S.Y. and Z.F. analyzed the data and wrote the manuscript. X.L., A.W.E., M.A.S. and S.G.H. revised the manuscript. S.K.S. and S.G. provided the fire history data and logistic support to field data collection.

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