

The Effect of Dune Age and Microtopography on *Triadica sebifera* (Chinese tallow tree) Recovery from Hurricane Disturbance

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Abstract

The spread and density of invasive species often reflect disturbance regimes. Coastal dunes on barrier islands, frequently impacted by hurricanes, are especially vulnerable to invasion by non-native species such as *Triadica sebifera* (Chinese tallow tree). Following Hurricane Matthew (2016), we examined the response of *T. sebifera* populations on Sapelo Island, Georgia, across a chronosequence of dunes varying in age (young, intermediate, old) and microtopography (swale, slope, ridge). Adult *T. sebifera* counts were recorded across belt transects for each dune age and microtopography. Data are included for before the hurricane, one year after (2018), and four years post-hurricane (2021). We found that *T. sebifera* had established across dunes prior to disturbance and that post-hurricane recovery was resilient across the swales and slopes. Both dune age and microtopography had significant effects on mortality and recovery, indicating strong abiotic influences on disturbance responses in *T. sebifera*. Survivorship was highest on slopes for *T. sebifera*, suggesting elevation mitigates saltwater flooding impacts. Our results demonstrate that *T. sebifera* can invade undisturbed habitats and recover aggressively following major disturbance, reinforcing its invasive threat.

Introduction

Disturbance plays a critical role in facilitating invasive plant establishment, particularly in dynamic environments such as coastal dunes (Davis et al. 2000; Sobrino et al. 2002; Burkitt and Wootton 2011; Diez et al. 2012). Hurricanes can produce highly variable spatial patterns of damage due to a combination of wind exposure and saltwater overwash. These disturbances often lead to changes in native vegetation composition and community structure, thereby increasing the vulnerability of ecosystems to colonization by non-native species (Xi et al. 2008; Bianchette et al. 2009; Henkel et al. 2016). Hurricane disturbance has been shown to promote the success of the invasive tree species, *Triadica sebifera* (Chinese tallow tree) within coastal ecosystems (Conner et al. 2005; Howard 2012; Yang et al. 2021).

Triadica sebifera is one of the most aggressive and widespread invasive species in the southeastern U.S., where it was originally introduced for oil production, ornamental use, and honey production (Howes 1949; Lieux 1975). Over the past century, it has expanded across a wide range of upland and wetland habitats, displacing native vegetation and forming dense, monospecific stands (Bruce et al. 1997; Gan et al. 2009). The invasiveness of *T. sebifera* is attributed to multipole traits, including high reproductive output, a persistent and abundant seedbank, broad tolerance of light and stress conditions, and prolific resprouting after topkill (Renne et al. 2002; Paudel and Battaglia 2015; Pile et al. 2017). The ability of *T. sebifera* to form more effective arbuscular mycorrhizal fungi (AMF) associations than *M. cerifera* is likely contributing to its competitive edge and invasional success (Paudel et al. 2014; Yang et al. 2015), especially considering the increased salt tolerance and nutrient acquisition potential with strong AMF associations (Zou et al. 2006; Evelin et al. 2009). Elsewhere, it has been shown that these fungal associations have aided in *T. sebifera*'s ability to outcompete native vegetation (Nijjer et al. 2008; Paudel et al. 2014).

Barrier island landscapes are particularly vulnerable to invasion due to their exposure to disturbance and the presence of multiple successional gradients (Bhattarai and Cronin 2014; Paudel and Battaglia 2021). On Sapelo Island, Georgia, and many other barrier islands along the southeastern coast of the United States, shoreline accretion has produced a series of parallel dune ridges of differing ages. These dunes form a chronosequence in which variation in vegetation composition, soil development, and ecological interactions are largely correlated with dune age (Foster and Tilman 2000; Tackett and Craft 2010; Walker et al. 2010). Specifically, Tackett and Craft (2010) showed that nitrogen was the major soil resource that limited primary production and was a controlling factor driving succession in this system. In addition, local microtopography associated with the dune structure (swales, slopes, and ridges) introduces variation in abiotic conditions such as light availability, soil moisture, and salinity exposure (Woods and Zinnert 2024). These gradients contribute to the development of distinct vegetation communities and may influence the capacity of invasive species to establish and persist (Foster and Tilman 2000). Young dunes at the forefront of the barrier island are typically more exposed to salt spray and sand movement, while older, inland dunes support more diverse and structurally complex vegetation communities (Tackett and Craft 2010; Sabo et al. 2024). *Morella cerifera*, a nitrogen-fixing shrub common in these dune systems, strongly influences soil development and nutrient availability across the chronosequence (Tackett and Craft 2010), potentially facilitating *T. sebifera* establishment.

In this study, we examined the effects of hurricane disturbance on the persistence and recovery of invasive *T. sebifera* populations across a dune chronosequence on Sapelo Island. We hypothesized that survivorship and recovery of *T. sebifera* would be influenced by both dune age and microtopographic position. Specifically, we predicted that mortality rates would be highest in low-lying swales due to flooding and saltwater exposure, while survivorship would be greater on elevated slopes and ridges. Furthermore, we expected that older dunes, with their more developed soils and vegetation, would support higher pre-disturbance densities of *T. sebifera* and demonstrate greater resilience following disturbance.

Methods

Study Site Description

Research was conducted on Sapelo Island, Georgia, part of the Georgia Coastal Ecosystems Long-Term Ecological Research network. The study area comprised three dune ridges of different ages representing a chronosequence formed through shoreline accretion: a 37 year old dune (young), 49 year old dune (intermediate), and 72 year old dune (old) (Fig. 3). Each dune ridge was subdivided into three distinct microtopographic zones: swale (low point between dunes), slope (dune face), and ridge (dune crest).

Prior to the hurricane, the youngest dune was in the early stages of succession, where shrub colonization in the swale was starting to facilitate the establishment of new species, but slopes and ridges were predominantly vegetated by grasses and herbs. Due to its proximity to the oceanfront, it remained exposed to strong winds and frequent sand movement. Grasses on this dune played a key role

in trapping windblown sand, contributing to the formation of tall dune ridges. The slopes of this dune were the steepest among the three dune ages, and the ridge lay one or two meters above the adjacent swale.

In contrast, the intermediate and old dunes were buffered from wind and salt spray by the elevated ridge of the young dune. Without continual sand deposition, these older dunes had gradually eroded, developing broader swales and more gently sloping ridges. On the intermediate dune, swales supported patchy populations of *T. sebifera* and *Spartina patens*, although much of the area lacked dense cover. The slopes were more vegetated, containing *T. sebifera*, *M. cerifera*, and *P. taeda*. The old dune exhibited the most developed soils and vegetation of the three. In its eastern portion, the swale was particularly wide—approximately 100 meters—and was intersected by a back-channel creek, making it the only dune with standing water. The ridge of the old dune was low, heavily eroded, and supported some woody vegetation, including mature native trees such as: *Juniperus virginiana*, *Sideroxylon tenax*, and *Pinus taeda*.

In October 2016, Hurricane Matthew passed just offshore of Sapelo Island, producing storm surge and wind damage that differentially impacted vegetation across the dunes. Matthew (H3) was the strongest hurricane to pass within 150 kilometers of Sapelo since Hurricane Gracie (H4) in 1959 (NOAA Historical Hurricane Tracker 2025). Each dune experienced different types and severities of hurricane disturbances. The youngest dune was overwashed by saltwater from sea swells and the intermediate and old dune experienced back-channel flooding which originated from the saltmarsh. The oldest dune appears to have experienced more severe backchannel flooding than the intermediate dune.

T. sebifera was first discovered on Sapelo Island in the early 1990's along roadsides (Fred Hay pers. comm 2019). At the time of its discovery no individual was over five years old, which places the beginning of the *T. sebifera* invasion between the late 1980's and the early 1990's. According to Landsat and aerial imagery (EROS 2020), *M. cerifera* shrub colonization was already present on the intermediate and old dunes prior to 1985. This strongly suggests that *Morella cerifera* shrub populations were already in place at the time of initial *T. sebifera* invasion.

Population Surveys

At each of the three dunes (old, intermediate, and young), we selected three random locations where we established three parallel 2m × 100m belt transects, positioned along the swale, slope, and ridge microtopographies—totaling 27 transects. Each transect was monumented with permanent markers, and GPS coordinates were recorded for both endpoints.

Adults, Saplings and Seedlings

In spring 2018, one growing season after Hurricane Matthew, we counted the living and dead adults (> 2m in height) of *Triadica sebifera* and *Morella cerifera* (greater than 5cm in diameter at 1m in height). From these data we estimated pre-hurricane population densities of adult *T. sebifera* and *M. cerifera*

within the transects. In 2018, we also censused the number of saplings (0.5m – 2m in height). Seedlings of *T. sebifera* (< 0.5m in height) in each transect were recorded by counting individuals within 0.5m on either side of the transect line and then scaled to the area of the belt transect (2m × 100m). In 2021, we recensused adults, saplings and seedlings of *T. sebifera* in all transects in the same fashion.

Seeds

In 2018, three 10 cm³ holes were dug at each transect at the 25, 50, and 75 meter marks on the centerline. The soil from the three holes was combined into a composite sample. Soil was sieved and tallow seeds were extracted and counted. Seed data were scaled to density within the 2m × 100m belt transect.

Soil Nutrient Characterization

In order to describe soil differences with the study site, soil samples from each of the nine locations along the belt transects were collected and analyzed using the soil sampled for seed density (see above). Soil was oven dried and analyzed for nutrient concentration by Waypoint Analytical laboratories (Memphis, TN) for extractable nutrient concentrations including phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg), as well as Total Nitrogen (N).

Our analysis of five macronutrients in the soil samples showed that as dune age progressed from young to old, Mg, N, and K increased while Ca and P decreased (Fig. 2). Similarly, as microtopography increased from swale to ridge, magnesium, nitrogen, and potassium decreased while calcium and phosphorus increased (Fig. 2). These data characterizes the microtopographies by variation in soil nutrient availability along the chronosequence within the study site.

Statistical Analyses

Spearman's rank correlation was used to test whether *T. sebifera* adult density was correlated with *M. cerifera* density with pre-hurricane data. Generalized linear mixed models (GLMMs) with a negative binomial error distribution were used to test whether adult stem counts of *T. sebifera* varied with year, dune age, or microtopography, and their interactions. Dune age and microtopography were each treated as fixed factors with three levels (young, intermediate, old; swale, slope, ridge). Plot (a unique combination of dune age, microtopography, and transect) was included as a random intercept to account for repeated measures within plots. All GLMM tests were conducted as Type III Wald χ^2 tests using the car package in R. All analyses were performed in R (R Core Team 2025).

Results

Pre-Hurricane Invasion History

Triadica sebifera first became established at the study site in the early 1990s, during a period with no major hurricane activity. Just prior to the impact of Hurricane Matthew on Sapelo Island in 2016, *T. sebifera* was abundant on both the intermediate and old dunes (Fig. 3). Densities were higher in swales compared to slopes (Fig. 3). Across all periods—pre-hurricane, 2018, and 2021—*T. sebifera* remained largely absent from the young dune and from the ridge microtopographies of the intermediate and old dunes (Fig. 3). There was a strong correlation between *M. cerifera* density and *T. sebifera* adult density pre-hurricane throughout the study site ($\rho = 0.496$, $p < 0.001$).

Triadica sebifera Population Response

There were significant interactions of year by microtopography ($\chi^2 = 31.998$, $p = < 0.001$; Table S1), signifying that both mortality (Pre-2018) and recovery (2018–2021) of *T. sebifera* were significantly influenced by their microtopographic location. In 2018, following the 2016 hurricane disturbance, density declined significantly in the swales (Fig. 3; Table S2). Mortality was significantly higher in the swales ($z = 5.839$, $p = < 0.001$) than on the slopes ($z = 1.090$, $p = 0.827$). Among the few adult trees that survived the hurricane, nearly all were located on slopes, with very few persisting in the swales (Fig. 3). The swales also showed significant recovery ($z = -6.319$, $p = < 0.001$), where the slopes did not ($z = 0.192$, $p = 1.000$; Table S2), demonstrating further evidence that slopes experienced a relatively more stable adult density than the swales which were most influenced by the effects of the hurricane. Throughout all dune ages and time intervals, *T. sebifera* maintained low adult densities on the ridge (Fig. 3). Additionally, *T. sebifera* seeds were most concentrated on the slopes of the intermediate and old dunes one growing season after Hurricane Matthew, while seedlings were more abundant in the swales during this period (Fig. 4). Seedlings in 2021 were most concentrated in the swale of the intermediate dune, and more evenly distributed across all microtopographies in the old dune (Fig. 4). Sapling densities were severely low throughout all microtopographies and dune ages in 2018 following the hurricane, but rebounded in the intermediate and old dunes particularly in the swales in 2021 (Fig. 4).

Mortality and recovery were significantly influenced by dune age ($\chi^2 = 12.502$, $p = 0.014$; Table S3). The young dune showed significant mortality between the pre-hurricane period and 2021 ($z = 2.422$, $p = 0.046$; Table S4), suggesting reduced suitability for *T. sebifera* establishment regardless of disturbance. The intermediate dune experienced significant mortality ($z = 2.424$, $p = 0.046$) with near-significant recovery ($z = -2.343$, $p = 0.057$), whereas the old dune exhibited marginal mortality ($z = 2.330$, $p = 0.059$) but significant recovery ($z = -2.440$, $p = 0.044$; Table S4). Together, these results indicate that dune age modulates population fluctuations of *T. sebifera* following hurricane disturbance.

Discussion

Our results broadly support the hypothesis that microtopography and dune age influence survivorship and recovery of *Triadica sebifera* in coastal dune communities. Specifically, mortality was concentrated in the swales, while slopes and ridges experienced lower mortality. Contrary to our prediction, old dunes

did not host the highest pre-hurricane densities, nor did they show greatest resilience. Instead, intermediate dunes consistently supported the highest adult densities across all time intervals.

Despite major population reductions following Hurricane Matthew, *Triadica sebifera* re-established abundant populations within four growing seasons, suggesting that its spatial distribution across the dune system was not permanently altered by disturbance. Recovery patterns mirrored pre-hurricane distribution, indicating that the same environmental constraints (dune age and microtopographic position) controlled both decline and recolonization. These factors are likely proxies for soil moisture and nutrient availability, with swales of intermediate and old dunes showing elevated Mg, N, K concentrations, and supporting the highest *T. sebifera* densities.

Fine-scale elevation gradients strongly influenced survivorship, as small vertical differences (tens of centimeters) altered saltwater exposure duration.. The highest survivorship occurred in a narrow “Goldilocks zone” at the swale–slope boundary (identified in Fig. 5), where flooding was minimal, but access to moisture and nutrients likely remained high. Woods and Zinnert (2024) describe this zone as the ideal habitat for *M. cerifera* as well. Most *T. sebifera* individuals tagged in 2018 and still alive in 2021 were located in this transitional zone, emphasizing the ecological importance of fine-scale topography to disturbance response within coastal dune systems.

Post-hurricane patterns revealed new, spatially stratified age structure within the *T. sebifera* population on Sapelo. Older individuals were now primarily found on slopes, while younger recruits were concentrated in the swales, indicating a shift from a previously mixed age distribution across the site. This spatial stratification may be one of the most enduring effects of the disturbance and future interpretation of this structure would be difficult without pre-disturbance data.

Recovery mechanisms in *T. sebifera* appeared to be mostly seed-driven, involving persistent seedbanks. While the species is capable of root sprouting (Enloe et al. 2015), excavations revealed only seedlings contributed to the post-hurricane population response. The swales and slopes of the intermediate and old dunes contained large *T. sebifera* seedbanks (Fig. 4). Additionally, recovery was not driven by post-storm seed dispersal. High levels of seedling recruitment in isolated swales, where perching trees had been eliminated, suggested that post-storm seed rain was improbable and that the seed source here was likely persistent seedbanks. This is consistent with the species’ known seed longevity and rapid germination capacity which can confer a competitive advantage in early successional environments (Cameron et al. 2000; Zhang et al. 2020). Seedlings also manifest a high level of salt tolerance (Conner et al. 1997; Chen et al. 2013; Yang et al. 2015) and this may further explain their ability to recover in flooded areas.

By 2021, *T. sebifera* had largely returned to pre-hurricane levels in swales and slopes, while ridges remained marginal habitats. Historically, the young and intermediate dunes on Sapelo would have supported a *Morella*-dominated shrubland with occasional *Pinus taeda* (Stallins 2003). Following invasion, and with little competition from native canopy-forming species, these areas have become occupied with dense *T. sebifera* stands. Since *Morella cerifera* populations were already established

prior to *T. sebifera* invasion, and the densities of both species are highly correlated, it is possible that the presence of *M. cerifera* helped facilitate the establishment of *T. sebifera* through its contribution of nitrogen to dune soil development on Sapelo (Tackett and Craft 2010).

As *Triadica sebifera* stands mature, they create dense, closed-canopy forests that threaten native biodiversity and alter dune ecosystem processes (Henkel et al. 2016; Chapman et al. 2008; Gan et al. 2009; Battaglia et al. 2009; Bruce 1993; Bruce et al. 1995). The displacement of *M. cerifera* reduces available fruit for migratory birds that rely on barrier islands as stopover habitat (Borgmann et al. 2004). *T. sebifera* leaf litter adds nutrients to the soil which could shift ecosystem productivity (Cameron and Spencer 1989), as well as reducing dissolved oxygen and lowering soil pH, which has been shown to impair the survival of amphibians like the southern leopard frog (*Lithobates sphenoccephalus*) and other native anurans (Adams and Saenz 2012; Laerm et al. 1999). Additionally, *T. sebifera* has become a host for multiple invasive scale insects, raising the possibility of invasional meltdown (Lucas et al. 2024).

Under climate change, increasing hurricane frequency and intensity (Knutson and Tuleya 2004; Webster et al. 2005; Hellmann et al. 2008; Wuebbles et al. 2014) may continue to enhance *T. sebifera*'s opportunities for expansion. Impacts of climate change, such as increased wave activity and warming temperatures, are expected to facilitate its spread, both regionally and latitudinally (Pattison and Mack 2008; Gabler and Siemann 2013). Our data suggest that *T. sebifera* is highly resilient to natural disturbances and without active management, it will likely remain a persistent invader. Current control efforts using fire and herbicide treatments show mixed success (Jubinsky and Anderson 1996; Grace 1998; Enloe et al. 2015; Schwartz 2018), and further research should include spatial mapping approaches (Young et al. 2011) to guide targeted interventions.

Conclusions

Storm disturbance, interacting with fine-scale environmental heterogeneity, shapes *T. sebifera* invasion patterns in coastal dune ecosystems. *T. sebifera* experienced substantial mortality in swales following Hurricane Matthew, but recovered rapidly via seedbank recruitment, returning to pre-disturbance densities within a few years. Projected increases in storm frequency and intensity may disproportionately benefit invasive species like *T. sebifera*. These results show that the rapid invasion of a tree species can precipitate fundamental changes in the composition and structure of coastal dune communities over time. Our findings highlight the need for coastal management strategies that incorporate both abiotic factors (e.g., dune age, elevation) and biotic responses to disturbance in order to better predict and mitigate future invasion trajectories in these systems.

Declarations

Author Contribution

J.E. was responsible for study conception and design. Material preparation and data collection were performed by J.E. and G.B. Data analysis was conducted by J.M. and J.E. Figure preparation was conducted by J.M. and G.B. The first draft of the manuscript was written by J.E. and G.B. and all authors edited and approved the final version of the manuscript.

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Figures

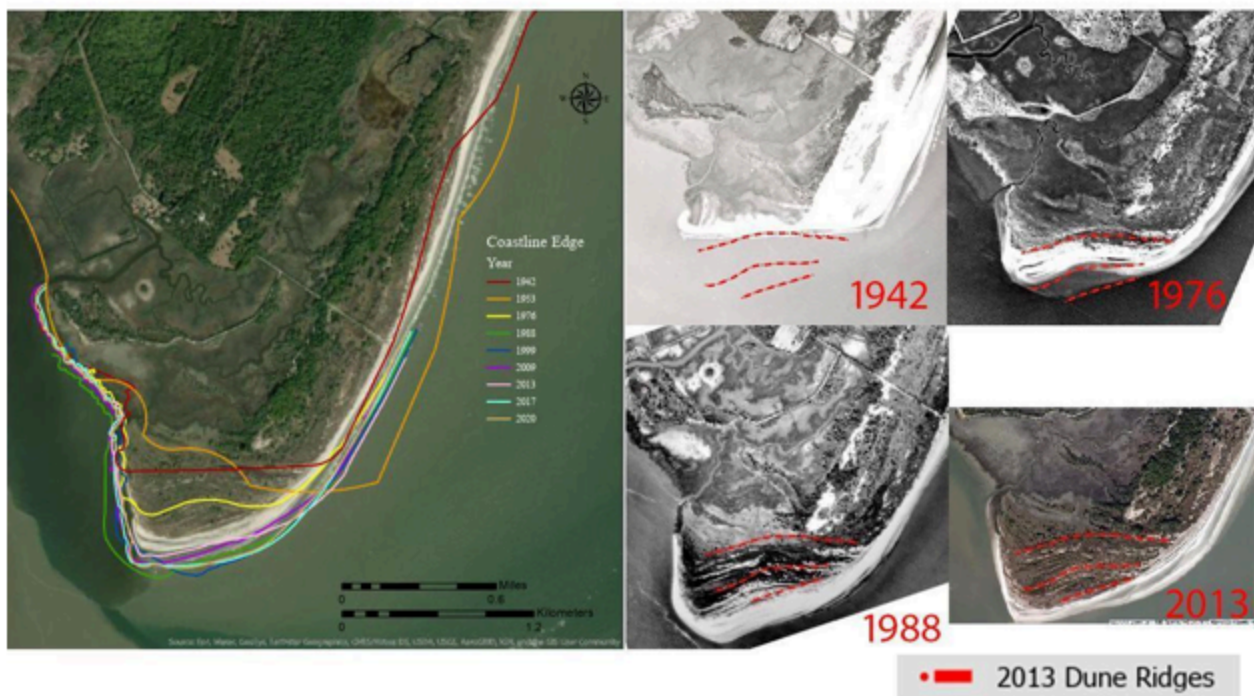


Figure 1

The history of the development of the dune system on the south end of Sapelo Island. Each red dashed line represents the georeferenced location of young, intermediate, and old dunes in our study. Source of aerial imagery: Georgia Coastal Systems, Long-term Ecological Research

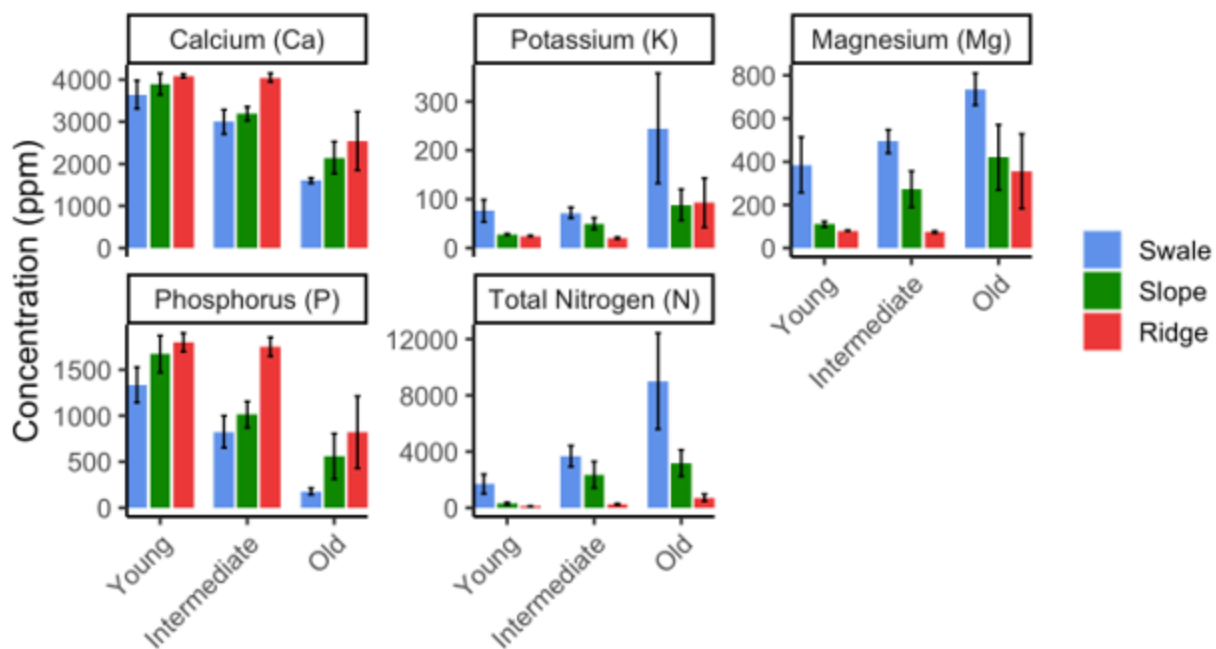


Figure 2

Macronutrient concentrations (ppm) as a function of dune age and microtopography

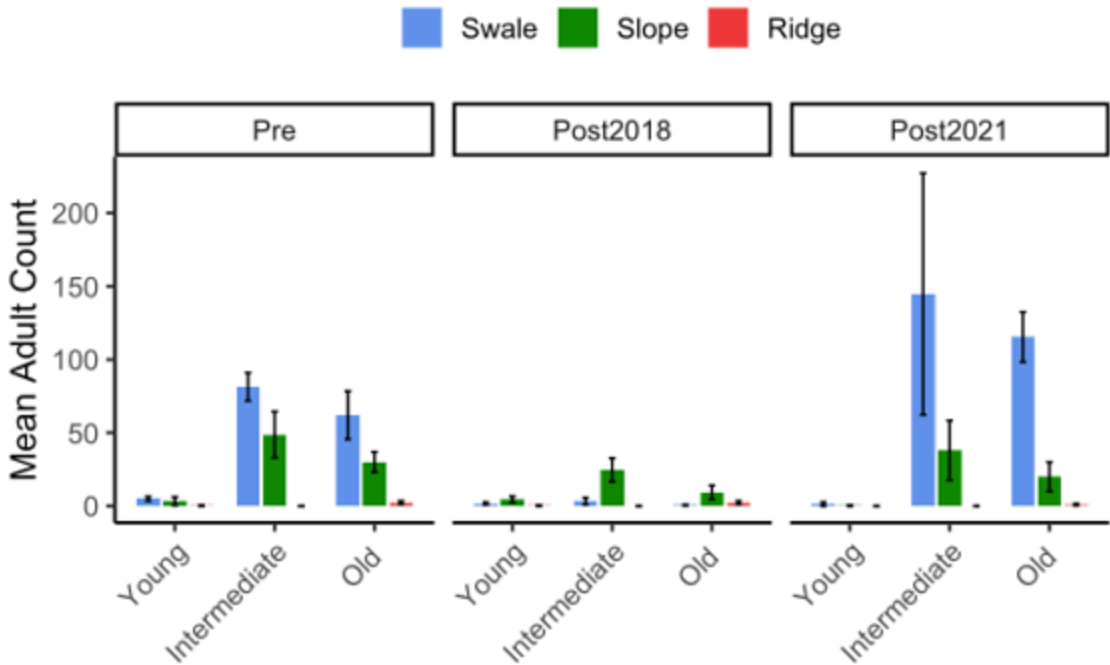


Figure 3

Triadica sebifera density (mean adult count) by dune age and microtopography for all periods

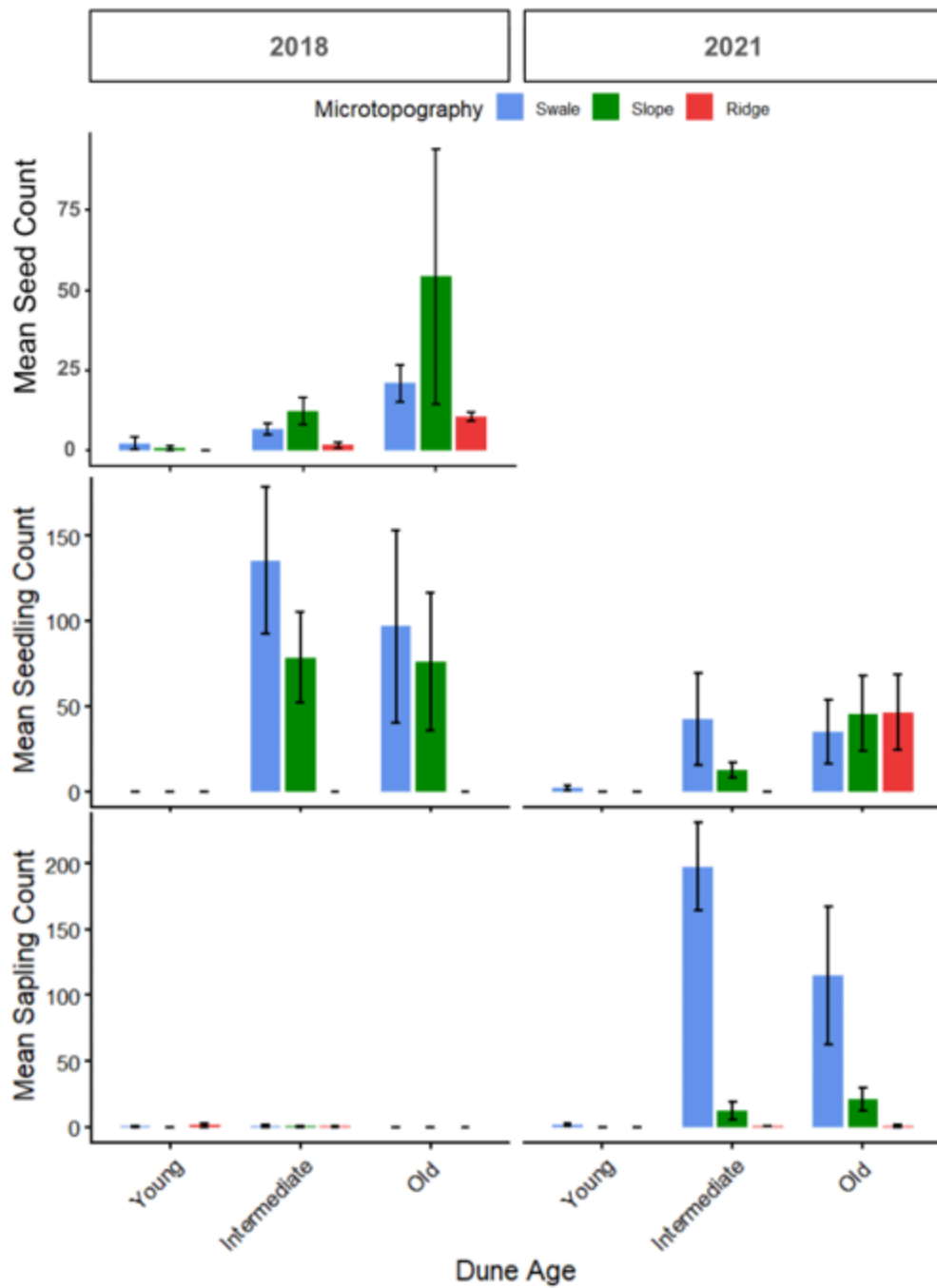


Figure 4

Triadica sebifera density (mean counts) for seeds, seedlings, and saplings by dune age and microtopography for 2018 and 2021.

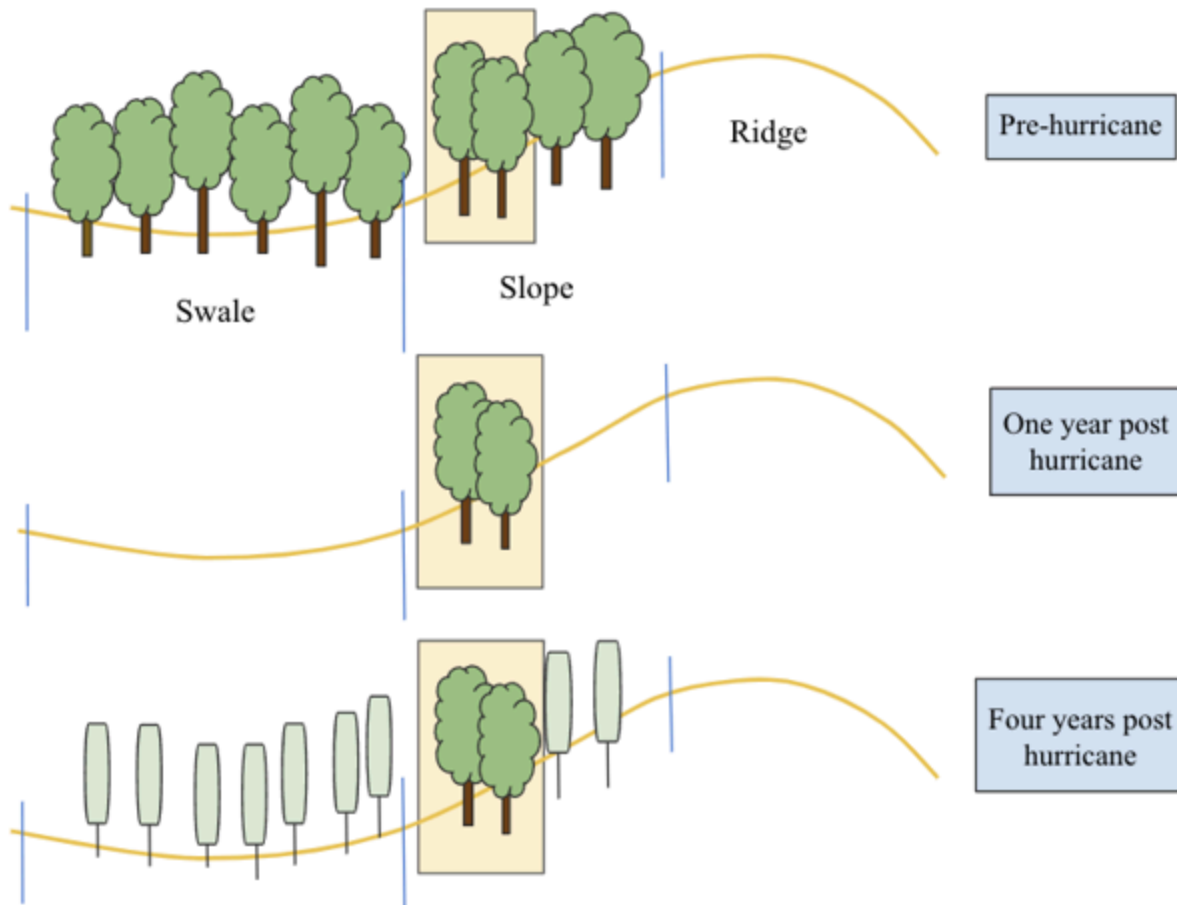


Figure 5

A schematic diagram of *Triadica sebifera* invasion across a topographic gradient on an intermediate age dune before and after hurricane disturbance. Dark green trees represent original and surviving adults and light green trees represent saplings and newly recruited adults. The yellow box highlights a region on the lower portion of the slope in which *T. sebifera* survivorship since Hurricane Matthew (2016) was the highest

Supplementary Files

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