# Dispersal, Establishment, and Influence of Black Mangrove (*Avicennia germinans)* at the Salt Marsh-Mangrove Ecotone

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# Introduction

Areas of transition can occur at multiple scales and the boundary between individuals, habitats, or ecosystems and the surround environment is called an ecotone. The focus of my dissertation is on one specific ecotone found in coastal wetlands. I sought to better understand the interactions and dynamics at the transition between temperate salt marshes and subtropical mangroves. I completed these studies at a variety of different spatial scales, from single individuals to local patches. To improve our understanding of ecotonal dynamics, I investigated: (1) dispersal at local and patch scales, (2) salt marsh and mangrove growth, survival and subsequent expansion and natural recruitment at a restoration site, and (3) tree-level interactions with surrounding salt marsh above- and belowground. Below, I provide a brief introduction that places the subsequent studies into a broader context.

Ecotones are dynamic areas of transition between two ecosystems and are influenced by a variety of abiotic and biotic factors (e.g., temperature, precipitation, fire, land use, and herbivory) (di Castri, Hansen & Naiman 1988). Consequently, ecotones are expected to be some of the first areas to shift their location with changing environmental conditions associated with global climate change, as they already represent areas encompassing boundaries between different environments (Neilson 1993). Both individual species and entire ecosystems have been shown to respond to climate change at both large and small spatial scales (Walther *et al.* 2002; Parmesan & Yohe 2003). As plant communities shift in response to changing conditions, individuals will disperse to, establish in, and survive in new areas, while interacting with incumbent communities. The three filter framework of dispersal, establishment, and survival (Lambers, Chapin & Pons 1998) states that multiple barriers for every species exist and any one of the multiple barriers may inhibit ultimate success.

Complex interactions may exist within any of these three filters and may prove to be beneficial, detrimental, or neutral during some or all stages of expansion, invasion, or restoration (Palmer, Ambrose & Poff 1997; Van der Valk 1998; Kikvidze *et al.* 2006; Guo *et al.* 2013; Wisz *et al.* 2013; Svenning *et al.* 2014; Stewart *et al.* 2015). Woody plant expansion is just one such shift in ecotones that has been observed and documented in a variety of ecosystems (e.g., deserts, savannas, tundra, grasslands) (Archer, Schimel & Holland 1995; Van Auken 2009; Saintilan & Rogers 2015). Woody plant expansion is also occurring in coastal wetlands where the salt marsh-mangrove ecotone is shifting poleward with the expansion of tropical and sub-tropical mangrove populations into temperate salt marshes.

Both observational and modeling approaches indicate that with increases in temperature in the coming century, mangroves will continue to expand poleward into previously salt marsh-dominated areas (Saintilan & Williams 1999; Saintilan, Rogers & McKee 2009; Saintilan *et al.* 2014; Osland *et al.* 2013; Cavanaugh *et al.* 2014). Studies have examined expansion worldwide, with particular emphasis on southeastern Australia and the southeastern United States focused on carbon stocks and cycling (Lovelock *et al.* 2013; Kelleway *et al.* 2016) and the United States (Perry & Mendelssohn 2009; Comeaux, Allison & Bianchi 2012; Bianchi *et al.* 2013; Henry & Twilley 2013; Doughty *et al.* 2016; Yando *et al.* 2016; Simpson *et al.* 2017), as well as inter- and intraspecific interactions (Alleman & Hester 2011a; b; Pickens & Hester 2011; Peterson & Bell 2012, 2015; Guo *et al.* 2013; Simpson, Feller & Chapman 2013). Despite this intensive and rapidly developing research area, many unanswered questions remain, which require further evaluation and present additional research opportunities (e.g., local dispersal dynamics, facilitation, local interactions, carbon storage over time, historical occupancy, and applied restoration research). The salt marsh-mangrove ecotone's overall direction may be poleward, but research focused on understanding factors influencing individuals and patches is required to truly comprehend rates of expansion and population dynamics.

In order to put range expansion of an ecosystem into perspective, it is imperative to first understand species' boundaries, ecotones' dynamics, and the processes that govern their structure. Ecotones can occur at a variety of spatial scales, from highly localized to landscape (Neilson 1993). Depending on the spatial scales of an ecotone, different factors will govern their existence, with local ecotones having many influencing factors and landscape-level ecotones having fewer (Gosz 1993). Ecotones also vary greatly in their pattern of transition, as they may be abrupt or gradual (Risser 1995). Across an ecotone, we can expect to find significant changes not only to the properties, but also to the processes and services that the habitat provides, as key drivers and constraints will differ. In some cases, intermediary states, formed from patchy mosaic environments, will provide novel attributes not found in either of the abutting ecosystems.

Expansion of species with climate change can also be compared to the spread of invasive species. The invasive species literature provides interesting parallels and contrasts to shifts in species and ecosystem ranges (Kolar & Lodge 2001; Fagan, Lewis & van den Driessche 2002; Hastings *et al.* 2005; Melbourne *et al.* 2007). Invading species are subject to the same constraints described in the three-filter framework, requiring dispersal, establishment, and survival (Lambers *et al.* 1998). Both invasion and expansion are subject to stochastic events that may inhibit both long- and short-term success and result in complex interactions and patchy distributions of invading species (Lewis & Pacala 2000).

Additionally, landscapes are not uniform and landscape heterogeneity can result in differences in the ability of individual species to establish in new environments and impact the overall rates of invasion and expansion (reviewed by Melbourne *et al.,* 2007). In examining both natural range expansion and invasion, it is necessary to understand that not all species will expand equally in time or space, particularly in highly modified landscapes (Thomas *et al.* 2001).

Both salt marshes and mangroves are ecosystems that are highly valued for many different ecosystem functions and services, but in many cases suffer from degradation (Davidson 2014). Both ecosystems also provide valuable habitat properties and processes that are beneficial to humans in the form of ecosystem services (e.g., carbon storage, improved water quality, and habitat for commercially and ecologically important species) (Barbier *et al.* 2011). Due to their importance, they are often candidates for restoration efforts. Restoration, the rehabilitation or creation of a disturbed or damaged habitat, is often an expensive venture, and in order to improve the chances of restoration success, a greater understanding of the conditions that facilitate dispersal, establishment, and survival would be helpful. The utilization of specific planting techniques in both space and time is an example of how restoration planning and design may benefit from further study (Padilla & Pugnaire 2006).

In the northern Gulf of Mexico, *Avicennia germinans,* the black mangrove, is the most frost-tolerant mangrove species in the region (Sherrod & McMillan 1985) and forms the poleward edge of mangrove expansion. *Avicennia germinans* is found in the coastal neotropics and associated subtropics, as well as portions of equatorial western Africa (Dodd *et al.* 2002). It is capable of growing up to 20 m tall in tropical locations, but is often found in stunted forms (1-3 m) at its latitudinal limits (Houck & Neill 2009). *Avicennia germinans* is typically found at higher elevations rather than low intertidal specialists (*S. alterniflora* and *Rhizophora mangle*) (Thom 1967; Patterson & Mendelssohn 1991). *Avicennia germinans* is a species that uses pneumatophores, specialized aerial roots, for gas exchange through lenticels on their surface (Andersen & Kristensen 1988). *Avicennia germinans* is cryptoviviparous with seeds germinating on the tree and then forming propagules that are retained within the pericarp (Bhosale & Mulik 1991). It does not reproduce asexually, but is capable of sprouting from its base after a disturbance (e.g., freezes, hurricanes), known as coppicing (Baldwin *et al.* 2001). Propagule set occurs during mid to late summer, and propagules disperse from the parent throughout the fall in the northern Gulf of Mexico (personal observation). Several studies have examined its tolerance to environmental conditions (Patterson, Mendelssohn & Swenson 1993; Patterson, McKee & Mendelssohn 1997; Méndez-Alonzo, López-Portillo & Rivera-Monroy 2008; Alleman & Hester 2011a; b; Pickens & Hester 2011), but much remains to be determined.

The dominant salt marsh species in the northern Gulf of Mexico include *S. alterniflora* (smooth cordgrass), *Paspalum vaginatum* (seashore Paspalum), and in some areas *Juncus romerianus* (black needlerush). In Louisiana, many areas are solely dominated by *S. alterniflora*. *Spartina alterniflora* is native to temperate regions in the western Atlantic and Gulf of Mexico coasts of North America. It reproduces through both vegetative and sexual reproduction and is able to rapidly spread in suitable conditions (Broome, Woodhouse & Seneca 1974; Metcalfe, Ellison & Bertness 1986; Trilla *et al.* 2009). Its clonal, long lived, perennial growth form allows it to rapidly spread once it disperses to a new area (Mitsch & Gosselink 2000; Pennings & Callaway 2000; Jones *et al.* 2016).

This dissertation explores the current dynamics of mangrove expansion into salt marsh at the salt marsh-mangrove ecotone in both natural and restored habitats through a compilation of case studies that examine: (1) dispersal at local and patch scales, (2) salt marsh and mangrove growth, survival, expansion, and natural recruitment at a restoration site, and (3) tree-level interactions with salt marsh above- and belowground. These studies are written and formatted for specific peer-reviewed journals. They add to a growing body of literature that explores not only the complexity of the salt marsh-mangrove ecotone, but also more general topics including dispersal, restoration, niche, and plant-soil dynamics.

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# Chapter 1: Microspatial Ecotone Dynamics at a Shifting Range Limit: Plant-Soil Variation Across Salt Marsh-Mangrove Interfaces

## 1.1 Abstract

Ecotone dynamics and shifting range limits can be used to advance our understanding of the ecological implications of future range expansions in response to climate change. In the northern Gulf of Mexico, the salt marsh-mangrove ecotone is an area where range limits and ecotone dynamics can be studied in tandem as recent decreases in winter temperature extremes have allowed for mangrove expansion at the expense of salt marsh. In this study, we assessed aboveground and belowground plant-soil dynamics across the salt marsh-mangrove ecotone quantifying micro-spatial patterns in horizontal extent. Specifically, we studied vegetation and rooting dynamics of large and small trees, the impact of salt marshes (e.g. species and structure) on mangroves, and the influence of vegetation on soil properties along transects from underneath the mangrove canopy into the surrounding salt marsh. Vegetation and rooting dynamics differed in horizontal reach, and there was a positive relationship between mangrove tree height and rooting extent. We found that the horizontal expansion of mangrove roots into salt marsh extended up to eight meters beyond the aboveground boundary. Variation in vegetation structure and local hydrology appear to control mangrove seedling dynamics. Finally, soil carbon density and organic matter did not differ within locations across the salt marsh-mangrove interface. By studying aboveground and belowground variation across the ecotone, we can better predict the ecological effects of continued range expansion in response to climate change.

## 1.2 Introduction

Range limits and ecotones are two landscape features that are likely to respond to global climate change (Noble 1993; Walther et al. 2002; Parmesan and Yohe 2003; Van der Putten et al. 2010). Both features are constrained by abiotic, biotic, and dispersal limitations that define the expansion ability of a single species and/or an entire ecosystem (Gosz 1993; Peters et al. 2006; Van der Putten et al. 2010). These dynamic areas are sensitive to change and may serve as an appropriate proxy for future shifts, but only by understanding both aboveground and belowground processes are we able to fully comprehend current changes and new interactions.

Ecosystem transitions can be examined at a variety of scales to understand the factors that maintain their existence, define their shape, and control their advance and retreat (Gosz 1993; Peters et al. 2006). Ecotones, areas of transition between two ecosystems, form as a result of changes in biotic or abiotic drivers, such as climate, fire regime, herbivory, or other edaphic conditions (Risser 1995) with areas of overlap forming a mosaic (Watt 1947). Range limits are defined as the edges of a species' "ecological niche in space" (Sexton et al. 2009), with species only persisting in habitats and locations where they can tolerate conditions, successfully establish, and ultimately survive and reproduce. Analyses of range limits and ecotones are often difficult due to challenges in assessment and comparison, as temporal and spatial variability need to be considered (Fortin and Drapeau 1995; Fortin et al. 2000). Recently, a variety of spatial detection analyses and curve fitting approaches have proven to be useful in beginning to understand, and more importantly compare, transitional patterns across range limits and ecotones (Fortin et al. 2000; Hufkens et al. 2008, 2009; Danz et al. 2013). Understanding these transitions of species and ecosystems is just as critical as understanding species range interiors and homogenous portions of each ecosystem (Lloyd et al. 2000) because landscapes and species distributions are naturally patchy and exist along a continuum (Breashers 2006). Species ranges and ecotonal transitions that respond quickly to changes in climate are valuable areas for monitoring climate change and advancing understanding of climate change impacts (Noble 1993).

The boundary between salt marsh and mangrove may be both an ecotone and the latitudinal range limit for mangroves in locations where temperature is the primary governing factor (Cavanaugh et al. 2014; Osland et al. 2017b). It may also serve as a suitable boundary for monitoring the impacts of climate change, due to the capability of coastal wetland plants to rapidly respond to changes in key drivers (Lovelock et al. 2010; Wasson et al. 2013). This ecotone can be found globally on low energy, subtropical coasts where temperate salt marshes meet tropical mangroves. The salt marsh-mangrove ecotone is determined by sea level, temperature, and precipitation at regional scales, but local factors, including dispersal, are also important (Saintilan et al. 2009, 2014; Osland et al. 2017b). In the northern Gulf of Mexico, the recent expansion of mangroves into salt marshes has been linked to a decrease in the severity, duration, and frequency of freeze events, allowing for freeze-intolerant mangroves to expand poleward (Osland et al. 2013; Cavanaugh et al. 2014). Comparisons between salt marshes and invading mangrove ecosystems have been made to predict the future implications of mangrove expansion on soil, vegetation, and both aboveground and belowground carbon dynamics (Perry and Mendelssohn 2009; Comeaux et al. 2012). Other studies have examined the structural, spatial, or temporal components of this gradient on these properties and processes (Stevens et al. 2006; Osland et al. 2012; Doughty et al. 2016; Kelleway et al. 2016; Yando et al. 2016; Gabler et al. 2017; Simpson et al. 2017), and regional analyses of literature-derived data have compared ecosystem properties in mangroves and salt marshes (Feher et al. 2017). However, studies explicitly examining ecotones at the individual tree level are scant and have not explored microspatial variation in aboveground and belowground vegetation metrics, belowground carbon dynamics, and rooting patterns.

The successful expansion from single individuals to larger patches over time will eventually result in a shifting range limit and ecotone in any ecosystem, unless a disturbance event results in mortality (Gosz 1993). The areal extent of developing mangrove patches or individuals within a salt marsh is evident aboveground, but rooting extent, belowground competition, propagule dispersal ability, and the concomitant impacts on soil properties, particularly soil carbon and organic matter, are far more cryptic. Aboveground vegetation metrics in the salt marsh-mangrove ecotone are commonly measured, and soil metrics are often used to compare edaphic conditions. Rooting metrics, however, are assessed less frequently (Comeaux et al. 2012), particularly in comparison to aboveground metrics and horizontal extent of the visible ecotone. Rooting is likely to be important due to resource competition where individual or groupings of mangroves are adjacent to other habitats (e.g. salt marsh, mudflat, salt flat, terrestrial) (Simpson et al. 2013; Howard et al. 2015), but this has not been explicitly investigated using microspatial data across the ecotone. At the salt marsh-mangrove ecotone, marsh vegetation interacts with mangroves at all life stages both aboveground and belowground. Marsh vegetation may facilitate or inhibit net expansion of mangroves by impacting resource acquisition, stress tolerance, propagule dispersal, and seedling establishment (Clarke and Hannon 1971; Kangas and Lugo 1990; McKee et al. 2007b; Pickens and Hester 2011; Peterson and Bell 2012, 2015). Finally, soil organic matter and carbon density have been shown to have no difference between salt marsh and mangrove ecosystems in the productive tidal saline wetlands of Louisiana and Florida (Perry and Mendelssohn 2009; Henry and Twilley 2013; Doughty et al. 2016) or along a structural forest gradient in either location (Yando et al. 2016), but this has not been tested at the individual tree scale. Only by understanding these responses, feedbacks, and interactions, in both the aboveground and belowground environment, will we be better able to address how this expansion occurs at both local and landscape scales (Wiens et al. 1985).

In this study, we examine plant-soil interactions within a shifting mangrove range limit and ecotonal transition from salt marsh to mangrove at the individual tree scale. This fine-scale assessment broadly addresses whether individuals of a species expanding into incumbent habitats have the same proportional relationship and extent aboveground and belowground. We hypothesized that, at the microspatial scale, 1) belowground extent would exceed aboveground extent, 2) larger trees would have greater belowground extent, 3) differences in salt marsh species and overall structural density would differentially influence aboveground and belowground mangrove dynamics, including seedling distribution, and 4) soil properties, specifically organic matter and soil carbon density, would not differ across the salt marsh-mangrove interface within our study sites.

## 1.3 Methods and Materials

### 1.3.1 Study area.

In the summer of 2013, we established field sites at two locations along the northern Gulf of Mexico where *Avicennia germinans*, the most freeze-tolerant mangrove species in the region, reaches its latitudinal limit and forms an ecotone with salt marsh species. Field site locations included Port Fourchon, Louisiana (29.11º N, 90.20º W; adjacent to Bayou

Lafourche) and Cedar Key, Florida (29.14º N, 83.03º W; between Cedar Key and Scale Key) (Fig. A1). Both locations are microtidal with mean tidal ranges of 0.37 m (Port Fourchon, Louisiana) and 0.86 m (Cedar Key, Florida) (NOAA 2014a, b). Salt marsh vegetation in the Louisiana sites is exclusively dominated by *Spartina alterniflora*, whereas the Florida sites contain a mixture of *Batis maritima*, *Paspalum vaginatum*, *Salicornia depressa,* and *S. alterniflora* (Yando et al. 2016).

### 1.3.2 Experimental design.

At each of the two locations, we identified six mangrove trees forming a discrete boundary with the surrounding salt marsh. Three replicate trees were of the large size class and three replicate trees were of the small size class, for a total of twelve trees across both locations and six trees per location. Tree sizes were relative to location. All trees were reproductive adults and represented the variation of mangroves individuals growing solitarily in salt marsh within each location. At each tree, we established a transect at the edge of the canopy (hereafter, the salt marsh-mangrove interface), positioned at 0 m and sampled 0.2-m$^2$ (0.15 m x 1.33 m) plots at set distances from each individual tree (-4 m, -2 m, -1 m, -0.5 m, 0 m, 0.5 m, 1 m, 2 m, and 4 m) (Fig. 1.1). The transect extended outwards into the salt marsh and inwards under the mangrove canopy. Plots in the salt marsh were assigned positive values that denote their distance from the salt marsh-mangrove interface, whereas mangrove plots were assigned negative values that denote their distance, in the opposite direction, from the salt marsh-mangrove interface.

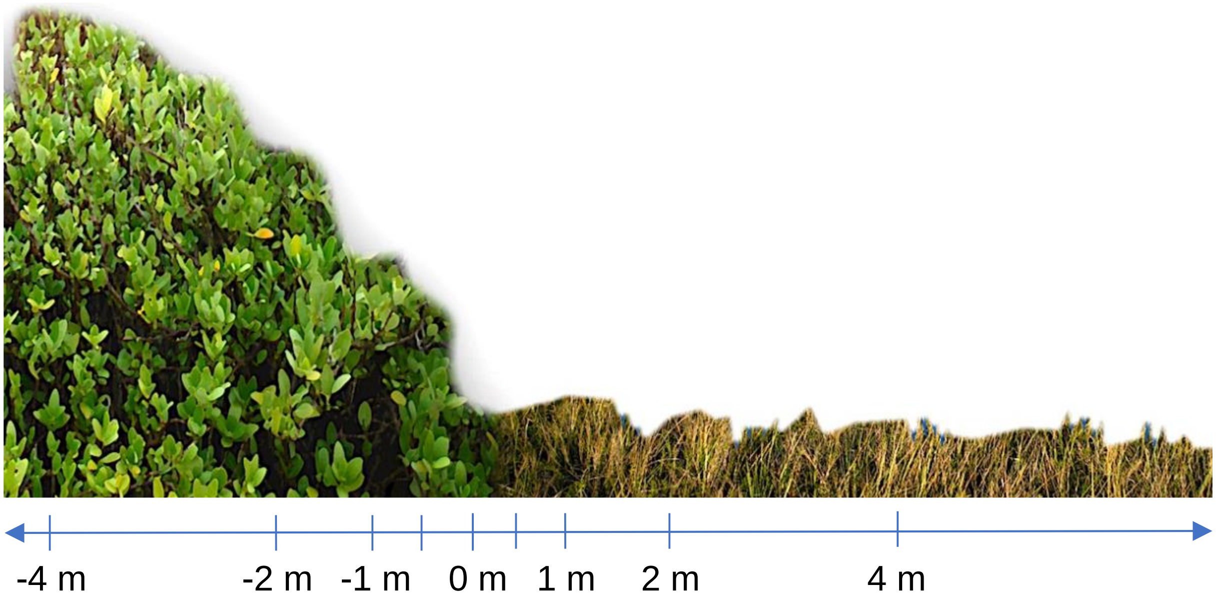

**Figure 1.1.** Idealized transect at each mangrove extending both under the mangrove canopy and out into the surrounding salt marsh.

In cases where we found mangrove pneumatophores, the aerial roots of *A. germinans*, extending to the 4 m plot in the salt marsh, additional plots were added on the transect until pneumatophores could no longer be found (e.g. at 8 m and 16 m). For small individuals, if the transect extended beyond the main trunk of the tree prior to the -4 m, -2 m, or -1 m plots, those plots were eliminated. The rectangular plots were oriented with the long axis of the plot perpendicular to the transect.

### 1.3.3 Vegetation.

Aboveground, we characterized mangrove and salt marsh plant community composition and structure within each plot. For mangroves, percent cover, number of pneumatophores, number of seedlings (i.e. trees less than 1.4 m in height), and maximum canopy height were measured at each plot along the transect. For salt marsh, we measured percent vegetation cover by species. We also collected aboveground vegetation from a 0.05-

$m^2$ subplot (0.15 m x 0.33 m). Upon returning to the lab, the collected vegetation was used to determine stem densities and individual heights for each species.

Belowground, we characterized mangrove and salt marsh root biomass. A 30-cm deep, 4.7-cm diameter soil core was collected from the edge of each plot for root analyses so not to disturb vegetation for possible future monitoring. Rooting in this region occurs primarily in the top 30 cm, with the majority of roots occurring in the top 15 cm of soil (Darby and Turner 2008), but we acknowledge that we may be underestimating total root biomass. Cores were collected using a custom stainless-steel piano-hinge corer and stored on ice while in the field. Upon return to the laboratory, we transferred samples to a 4 ºC refrigerator until analyses were conducted. Roots were washed of soil, sorted into macro (>2 mm) and micro (<2 mm) size classes, and then sorted as either live or dead. Live roots were identified by color, turgor, and connectivity. Macro size class roots were identified as either salt marsh or mangrove. All analyses presented here focus on the macro size class.

### 1.3.4 Hydrology.

We determined the percentage of time the soil surface was flooded (hereafter, percent time flooded) by relating elevations of each plot to local hydrological data. Elevation was determined using a laser level (Spectra Precision Laser, LL300, Trimble Navigation Ltd., Sunnyvale, CA, USA) and was then related to stable benchmarks which had previously been determined using real time kinematic survey (RTK; NAVD88 Geoid 12A) (Trimble R8 Receiver & Trimble TSC3 Controller, Trimble Navigation, Ltd., Sunnydale, California). For each location, local tidal gauges were utilized to determine hourly water levels for five years prior to September 2013 (Cedar Key, FL- NOAA [National Oceanic and Atmospheric Administration], Tides and Currents-Station ID: 8727520; Port Fourchon, LA- CRMS

[Coastal Reference Monitoring System]-Station ID: CRMS0292). All water level data were collected and reported in NAVD88-Geoid 12A.

### 1.3.5 Soil and porewater properties.

For soil physicochemical analyses, we collected a 15-cm deep, 4.7-cm diameter soil core from the edge of each plot. Cores were collected and stored using the same methods as previously described for the root cores. Physicochemical analyses for the soil core included quantification of soil organic matter (SOM) and soil inorganic carbon (SIC), determined via loss on ignition in a muffle furnace at 475 ºC for 16 hours and 800 ºC for 16 hours, respectively (Wang et al. 2011). Soil bulk density was determined by simple dry weight to volume ratios (Blake and Hartge 1986), after drying soils at 65 ºC until a constant mass was achieved. Soil percent moisture was derived using the dry and wet weights. Soil total carbon (TC) was calculated from the SOM data using the following equation that was developed using data from these sites (data from Yando et al. 2016) ($TC=0.02818 + 0.4053606*SOM$) (Online Resource 2). Since bulk densities differ between these two locations, TC was converted to carbon density (i.e. mg C per $cm^3$) (C density). Soil salinity, pH, and conductivity were analyzed in the laboratory from a 1:2 soil dry weight to water ratio slurry (Jones 1999), and soil porewater temperature was measured *in situ* in the field using a handheld meter (YSI 30, YSI Inc., Yellow Springs, OH & Oakton WD 35801-00, Oakton Instruments, Vernon Hills, IL).

### 1.3.6 Data analyses.

Regression analyses (logistic, Gaussian peak, exponential, and linear) were conducted for each location and mangrove size class. Dependent variables included mangrove and salt marsh cover, mangrove and salt marsh live root biomass, density of mangrove seedlings, density of salt marsh stems, density of mangrove pneumatophores, total structural density (i.e. the sum of salt marsh stem, mangrove seedling, and mangrove pneumatophore density), and maximum pneumatophore extent from the salt marsh-mangrove interface. Independent variables included transect plot position or maximum mangrove height. Models were selected using AICc values and weights. For models where values and weights were similar, the simplest and most ecologically-relevant model was selected for direct comparison. All non-linear regressions have $R^2$ values reported despite being a pseudo-$R^2$, but we report them to make comparable analyses. For logistic regression, the inflection point (i.e. the peak of the first derivative) and the width of the area of greatest change (hereafter, width of AoC; the difference between the maximum and minimum peaks of the second derivative) were calculated to compare the position and width of transition zone between locations and mangrove size classes (for methods see Timoney et al. 1993, Hufkens et al. 2008). For Gaussian peak regression models, the peak height (P(y)), peak position (P(x)), and peak width (peak ± 2 standard deviations; Pw) were derived to compare locations and mangrove size classes. Standard errors of the mean are presented throughout the manuscript, included in figure error bars. Analysis of variance and Tukey's post hoc tests for other comparisons and analysis of regression models were conducted in RStudio (Team RStudio 2017) and JMP Pro 13 (SAS Institute Inc., Cary, North Carolina).

## 1.4 Results

### 1.4.1 Vegetation.

Mean maximum canopy heights in Florida were 5.06 ± 0.59 m and 2.16 ± 0.29 m for large and small mangroves, respectively. In Louisiana, mean maximum canopy heights were 1.55 ± 0.13 m and 1.09 ± 0.10 m for large and small mangroves, respectively. At both locations and for both size classes, mangrove vegetation cover followed a decreasing logistic pattern across transects (Fig. 1.2). The inflection point for mangrove cover was less than 0.5 m for all locations and size classes, and the width of the AoC only increased slightly with increasing tree height (Fig. 1.2; Table 1.1).

Maximum salt marsh canopy height was almost twice as tall in Louisiana than Florida ($F_{1,11}$= 113.7, p<0.0001) (Table 1.2 & A1). At both locations and for both size classes, salt marsh cover increased logistically across the transects (Fig. 1.2). Salt marsh cover in Florida large mangrove transects displayed a shifted inflection point and increased width of AoC compared to all other locations and size classes, not reaching its horizontal asymptote until 16 m from the salt marsh-mangrove interface (Fig. 1.2a; Table 1.1). All other transects had inflection points for salt marsh cover much closer to the salt marsh-mangrove interface and narrower AoC widths (Fig. 1.2b, c, d; Table 1.1). Belowground live mangrove root biomass declined with increasing distance from the mangrove-marsh interface in all transects, except for Louisiana small transects (Fig. 1.3; Table 1.1). Louisiana small transects did not change in mangrove live root biomass across the transect (Fig. 1.3d). In Florida, live mangrove roots extended out to the 8 and 4 m plots in large and small mangroves, respectively (Fig. 1.3a, b). Additionally, mangrove pneumatophores aboveground were found as far as the 8 m plot in Florida large mangrove transects and 2 m plot in Florida small mangrove transects, but were absent after the 1 m plot in Louisiana large mangrove transects and the 0.5 m plot in Louisiana small mangrove transects. There was a positive logistic relationship between maximum mangrove height and maximum mangrove pneumatophore extent (Fig. 1.4). Salt marsh live roots extended across the salt marsh-mangrove interface under the mangrove canopy in all cases (Fig. 1.3a, b, d) except for large Louisiana mangroves (Fig. 1.3c). Large

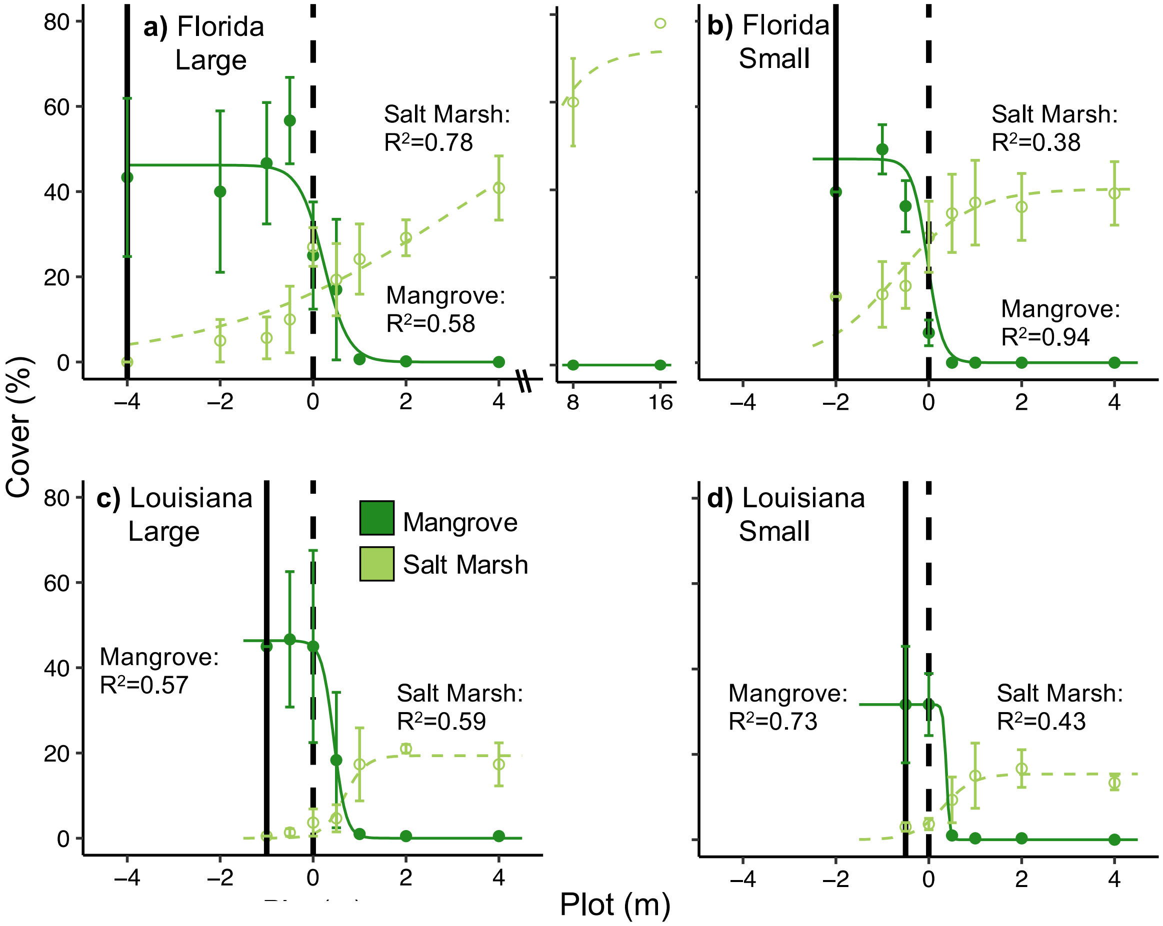

**Figure 1.2.** Comparison of vegetative cover of mangrove (solid line–dark green filled symbols) and salt marsh (dashed line–light green open symbols) plots across the salt marsh-mangrove interface in a,b) Florida and c,d) Louisiana using a logistic regression. Values are mean ± SE (N= 3). Transects were established at the edge of the canopy, positioned at 0 m (vertical dashed line) and sampled plots at set distances from either b, d) small or a,c) large trees. Note that Panel a) extends to 16 m and has a break between the 4 and 8 m plots.

**Table 1.1.** Summary of model parameters used to describe changing abundances of large and small mangroves in Florida and Louisiana. *p-values* are represented for linear and exponential regressions only (‡ $p<0.09$; * $p<0.05$; ** $p<0.01$).

| Metric type | Location | Size class | Model type | $R^2$ | *F*-statistic | Inflection point (m) | Width of AoC (m) | Peak location (m) | Peak width (m) |
|---|---|---|---|---|---|---|---|---|---|
| Mangrove cover (%) | Florida | Large | Logistic | 0.58 | | 0.23 | 0.70 | | |
| | | Small | Logistic | 0.94 | | -0.03 | 0.43 | | |
| | Louisiana | Large | Logistic | 0.57 | | 0.45 | 0.35 | | |
| | | Small | Logistic | 0.73 | | 0.38 | 0.09 | | |
| Salt marsh cover (%) | Florida | Large | Logistic | 0.78 | | 3.11 | 6.66 | | |
| | | Small | Logistic | 0.37 | | -0.69 | 2.13 | | |
| | Louisiana | Large | Logistic | 0.59 | | 0.67 | 0.62 | | |
| | | Small | Logistic | 0.4 | | 0.31 | 0.85 | | |
| Mangrove live root biomass (g) | Florida | Large | Linear | 0.14 | $5.9^{*}$ | | | | |
| | | Small | Linear | 0.12 | 3.8‡ | | | | |
| | Louisiana | Large | Linear | 0.24 | | | | | |
| | | Small | Linear | 0.16 | | | | | |
| Salt marsh live root biomass (g) | Florida | Large | Linear | 0.06 | 3.1‡ | | | | |
| | | Small | Linear | 0.33 | $11.3^{**}$ | | | | |
| | Louisiana | Large | No pattern | *NS* | | | | | |
| | | Small | No pattern | *NS* | | | | | |
| Structural density (N $m^{-2}$) | Florida | Large | No pattern | *NS* | | | | | |
| | | Small | No pattern | *NS* | | | | | |
| | Louisiana | Large | Exponential | 0.67 | $37.39^{**}$ | | | | |
| | | Small | Exponential | 0.53 | $19.99^{**}$ | | | | |
| Seedling density (N $m^{-2}$) | Florida | Large | Gaussian | 0.33 | | | | -1 | 4 |
| | | Small | Gaussian | 0.8 | | | | -1.25 | 1.75 |
| | Louisiana | Large | Linear | 0.3 | $7.3^{*}$ | | | | |
| | | Small | No pattern | *NS* | | | | | |
| Salt marsh density (N $m^{-2}$) | Florida | Large | Logistic | 0.73 | | -0.27 | 1.64 | | |
| | | Small | Logistic | 0.49 | | -0.8 | 0.6 | | |
| | Louisiana | Large | Linear | 0.2 | 4.1‡ | | | | |
| | | Small | Linear | 0.28 | $6.2^{*}$ | | | | |
| Pneumatophore density (N $m^{-2}$) | Florida | Large | Exponential | 0.8 | 121.1** | | | | |
| | | Small | Exponential | 0.83 | 101.4** | | | | |
| | Louisiana | Large | Exponential | 0.84 | 93.2** | | | | |
| | | Small | Exponential | 0.68 | 37.6** | | | | |

**Table 1.2.** Comparison of variables used to evaluate environmental differences for Large and Small trees in Florida and Louisiana. Values are means (± SE, N=3). Significant differences (*p<0.05*) are denoted by different lowercase letters within each metric across all tree sizes and locations.

| | | Florida | | Louisiana | |
|---|---|---|---|---|---|
| | | Large | Small | Large | Small |
| Vegetation | Max. salt marsh height (m) | 0.46 ± 0.03$^{b}$ | 0.48 ± 0.01$^{b}$ | 1.18 ± 0.07$^{a}$ | 1.04 ± 0.09$^{a}$ |
| Hydrology (2008-2013) | Elevation (m) | 0.42 ± 0.01$^{a}$ | 0.41 ± 0.01$^{a}$ | 0.05 ± 0.003$^{b}$ | 0.05 ± 0.004$^{b}$ |
| | Time flooded (%) | 14.8 ± 0.7$^{b}$ | 15 ± 0.5$^{b}$ | 46.5 ± 0.7$^{a}$ | 45.5 ± 0.7$^{a}$ |
| Soil properties | Bulk density (g cm$^{-3}$) | 0.3 ± 0.005$^{b}$ | 0.3 ± 0.005$^{b}$ | 0.4 ± 0.01$^{a}$ | 0.5 ± 0.01$^{a}$ |
| | Soil moisture | 77.5 ± 0.3$^{a}$ | 77 ± 0.2$^{a}$ | 66.7 ± 0.7$^{b}$ | 64.8 ± 0.9$^{b}$ |
| | SOM (%) | 29.7 ± 0.4$^{a}$ | 28.1 ± 0.4$^{a}$ | 13.1 ± 0.5$^{a}$ | 11.8 ± 0.3$^{a}$ |
| | C density (mg cm$^{-3}$) | 30 ± 0.3$^{a}$ | 30 ± 0.5$^{a}$ | 20 ± 0.7$^{b}$ | 20 ± 0.4$^{b}$ |

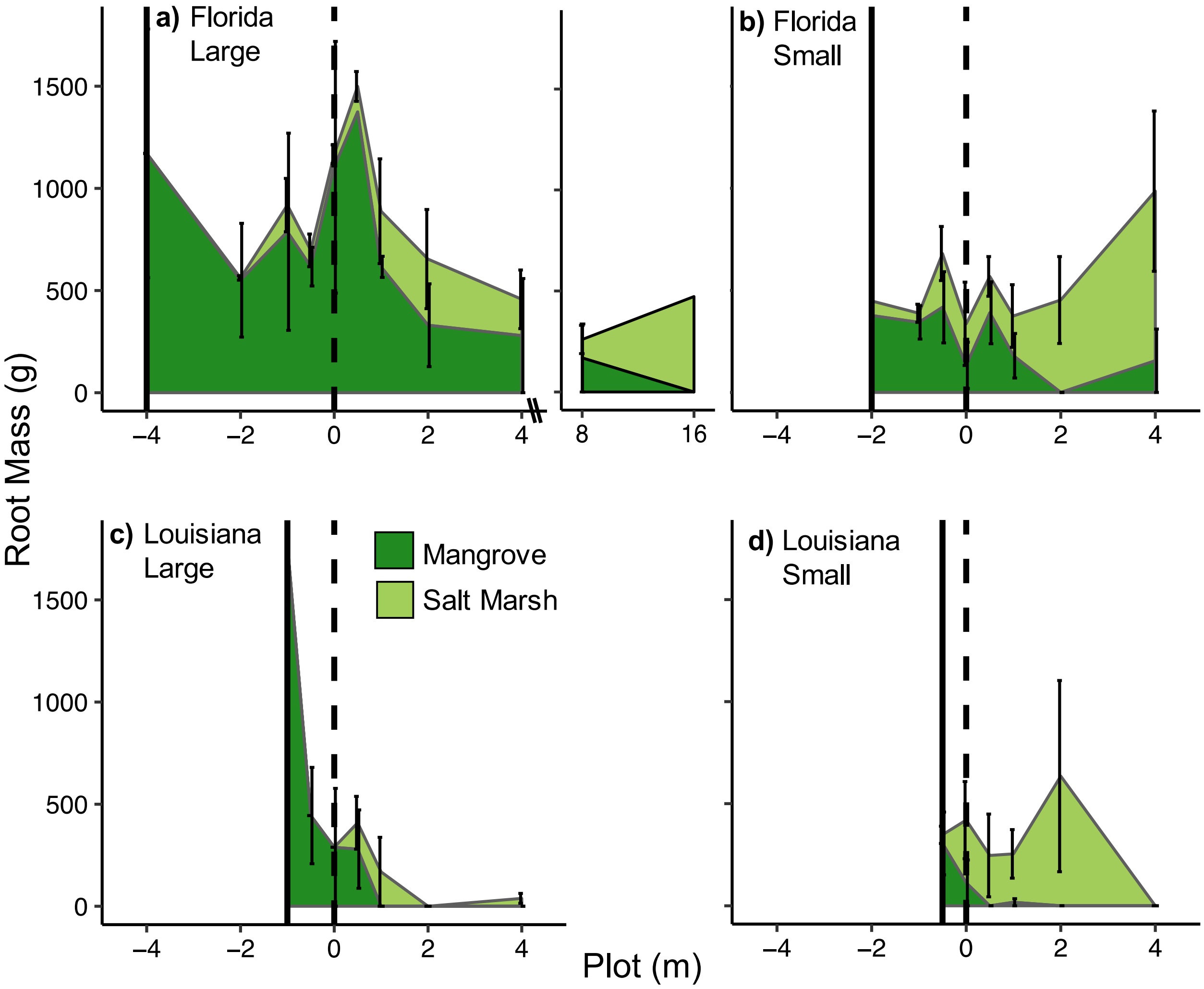

**Figure 1.3.** Comparison of live root biomass (stacked) of mangrove (dark green) and salt marsh (light green) plots across the salt marsh-mangrove interface in a,b) Florida and c,d) Louisiana. Values are mean ± SE (N= 3). Transects were established at the edge of the canopy and positioned at 0 m (vertical dashed line) and sampled plots at set distances from either b, d) small or a,c) large trees. Note that Panel a) extends to 16 m and has a break between the 4 and 8 m plots.

Fig. 4

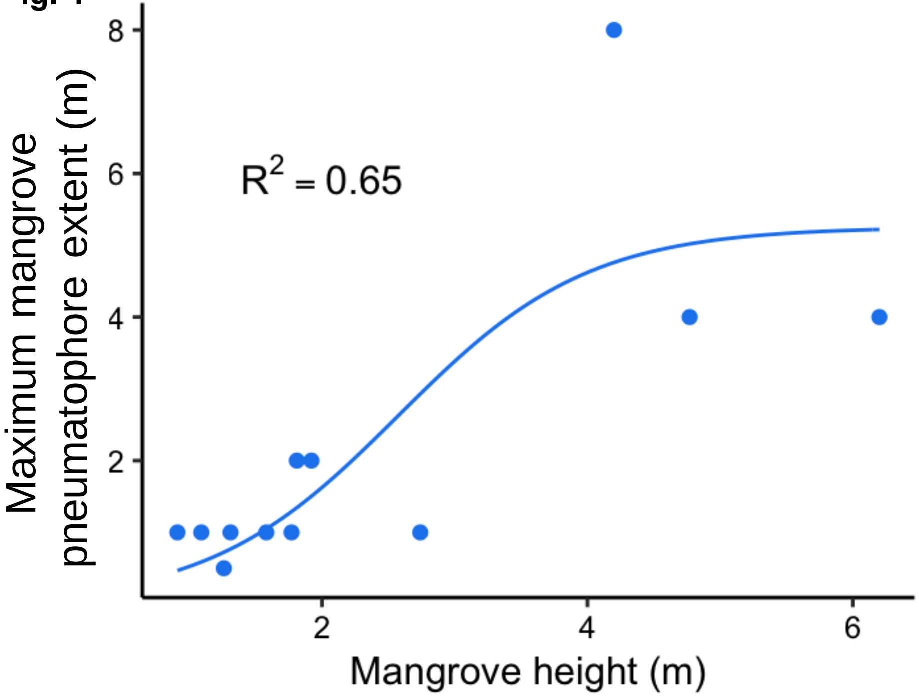

**Figure 1.4.** Maximum mangrove canopy height by maximum mangrove pneumatophore extent. All locations and size classes combined and each point represents and individual transect. Inflection point = Mangrove height of 2.6 m, Width of Area of Change = 1.8 m.

Louisiana mangrove transects had very limited salt marsh roots present, even in areas exclusively dominated by salt marsh (Fig. 1.3c).

Mangrove seedling density in Florida followed a Gaussian peak distribution in both large and small mangrove transects (Fig. 1.5a, b). Both Florida transects had their position of maximum density (P(x)) centered within the mangrove side of the interface, at approximately the -1m plot, with the maximum density four times greater (P(y)) and the peak width (distribution width; Pw) twice as wide in large mangrove transects than small mangrove transects (Fig. 1.5a, b; Table 1.1). Structural density in Florida did not have any trend, but remained consistently high at approximately 300 units per m$^2$ (Fig. 1.5a, b; Table 1.1) regardless of size. Louisiana large mangrove transects had a linear increase in mangrove seedling density beyond the salt marsh-mangrove interface, while Louisiana small mangrove transects displayed no pattern in seedling density distribution (Fig. 1.5c, d; Table 1.1). Structural density in both Louisiana mangrove transect types followed an exponential decrease across the salt marsh-mangrove interface (Fig. 1.5c, d; Table 1), with structural density higher beneath larger mangroves. Salt marsh reaches of the Louisiana transects had almost an order of magnitude lower structural density (i.e., ~25-50 units per $m^2$) compared to their Florida counterparts (Fig. 1.5). In both locations and size classes, pneumatophore density declined exponentially along the transect (Table 1.1 & Fig. A4-A6). In Florida, salt marsh stem density followed an increasing logistic distribution for both large and small mangrove transects with an asymptote at approximately 500 stems per $m^2$ (Table 1.1; Fig. A3-A4). In Louisiana, salt marsh stem density decreased in large mangrove transects and small mangrove transects (Table 1.1; Fig. A5-A6).

### 1.4.2 Hydrology, soil properties, and porewater

Hydrology, elevation, and soil properties did not differ along the transect from mangrove to salt marsh in any location or size class; differences were most often only between locations (Table A1). Louisiana elevations were ~35 cm lower in elevation, and percent time flooded in Louisiana was three times greater compared to Florida (Table 1.2 & A1). Florida had ~10% greater soil moisture and twice as much SOM than Louisiana (Table 1.2 & A1). Carbon density in Florida was a third greater than in Louisiana (Table 1.2 & A1). Louisiana had slightly greater overall bulk density compared to Florida (Table 1.2 & A1). Other soil and porewater variables also differed by location (Table A2), but never by transect position (Table A1 & A2).

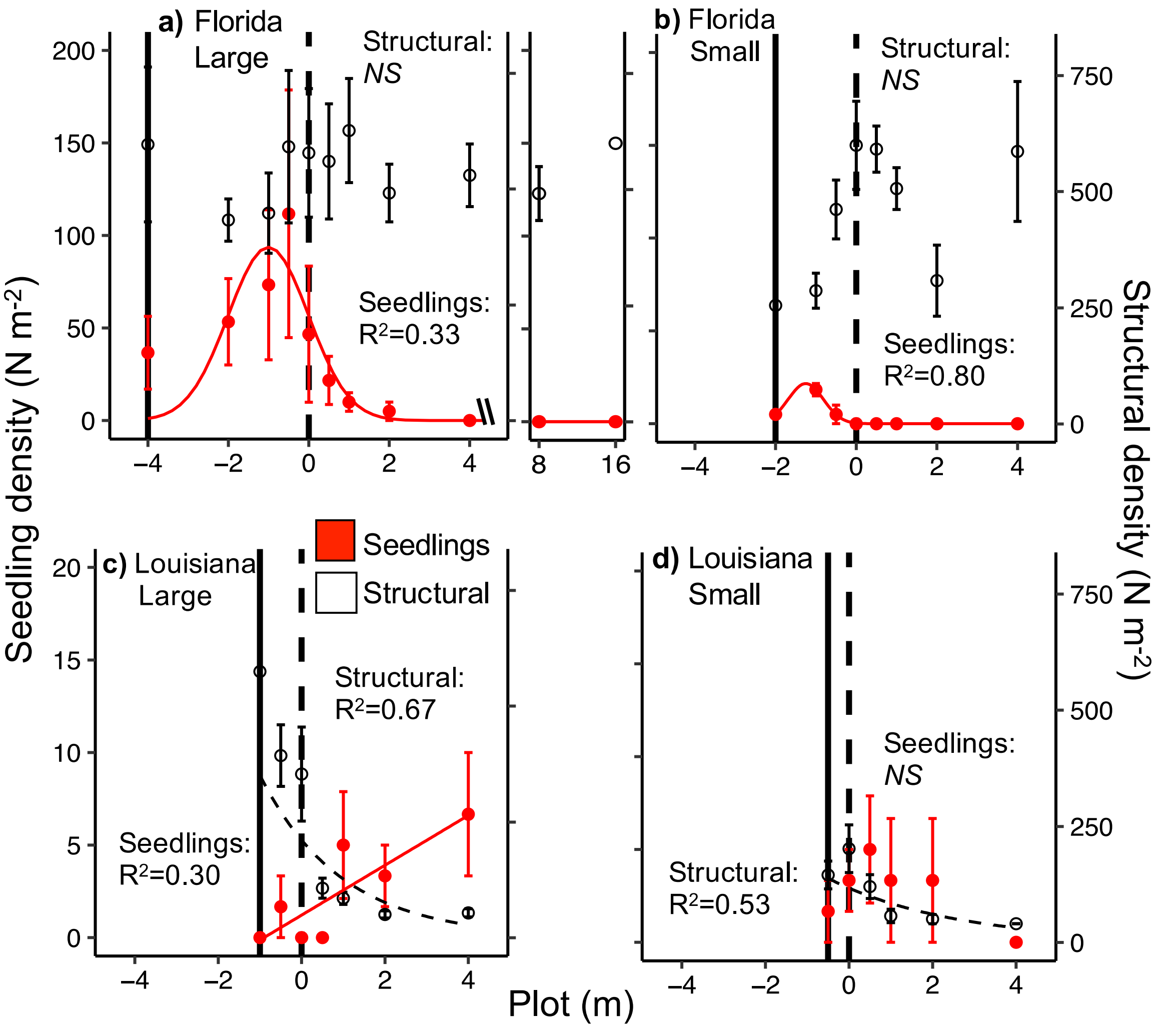

**Figure 1.5.** Comparisons of mangrove seedling (solid line-red symbols; left y axis) and total structural (dashed line-open white symbols; right y axis) density across the salt marsh-mangrove interface in a,b) Florida and c,d) Louisiana. Values are mean ± SE (N= 3). Transects were established at the edge of the canopy and positioned at 0 m (vertical dashed line) and sampled plots at set distances from either b, d) small or a,c) large trees. Note that Panel a) extends to 16 m and has a break between the 4 and 8 m plots.

## 1.5 Discussion

The results of our study highlight key differences between aboveground and belowground vegetation pattern and extent, the importance of salt marsh type and total structural density, and site-specific homogeneity in key soil metrics across the salt marsh-mangrove interface. The location-specific nature of many of our findings show the complexity of this range limit and ecotone even within the same region.

Aboveground mangrove and salt marsh vegetation cover followed logistic patterns of change along the transect, similar to the sigmoidal wave hypothesis/relationship reported in other ecotones (Cairns and Waldron 2003; Danz et al. 2013). Differences between the logistic regression in mangrove cover can be attributed to tree size, with the largest overall trees, those of the Florida large mangrove transects, also suppressing salt marsh species and resulting in a shifted pattern due presumable to competition for light (Lett and Knapp 2003) and other resources (Belsky 1994). The comparatively smaller stature of mangroves in the Florida small, Louisiana large, and Louisiana small transects resulted in smaller aboveground areal extents and did not influence salt marsh vegetation as much as their Florida large mangrove counterparts, likely due to limited light and less belowground competition (Fig. 1B,C, D) (Pickens 2012).

Neither mangrove nor salt marsh live belowground root biomass followed the logistic pattern seen in aboveground cover metrics. Mangrove live root biomass declined in all transects, but differed in horizontal extent. The disparities in mangrove and salt marsh live root biomass, and tree sizes, are likely due to a combination of duration of time since the establishment of these mangroves, local mangrove growth rates, and species-specific salt marsh interactions (Lovelock et al. 2007, 2010; Bulmer et al. 2016), similar to that of other forest systems (Hodgkins and Nichols 1977). Older mangroves and/or those with greater growth rates are likely to have had a greater opportunity for horizontal expansion and increased live root biomass within a local area, where soil and edaphic conditions are similar. Although we do not have accurate age estimates of these mangroves, due to the difficulty in aging individual mangroves of all species (Tomlinson 1994), our Florida location had much taller mangroves than our Louisiana location (Yando et al. 2016). We acknowledge that size class does not necessarily translate to age, but in this case, larger trees had a greater maximum pneumatophore extent (Fig. 4). The relationship between mangrove height and pneumatophore extent follows a logistic pattern. The pattern represented is a conservative estimate of this relationship as the asymptote may continue to rise or may shift with the inclusion of more data, particularly of larger trees (i.e. trees greater than 6 m in height). In addition to mangrove height, salt marsh species, density, and their ability to compete for space and resources belowground may also impact the ability for mangroves to expand belowground (Howard et al. 2015). During early life stages, Louisiana's *S. alterniflora*-dominated salt marshes have been shown to potentially compete with *A. germinans* belowground through their high specific root area and ability to inhibit the development of complex mangrove root architecture (McKee and Rooth 2008; Pickens 2012). The Florida salt marshes, dominated by a variety of grasses and succulents, had mangrove roots extending well into the salt marsh. The lack of salt marsh roots in large mangrove transects in both sites can likely also be attributed to age and development. Age, growth rate, and salt marsh interactions taken together start to provide an explanation for live root biomass patterns, but certainly deserve greater attention, particularly at the individual mangrove level. Research on individual shrubs in grassland systems and trees in savanna systems have highlighted the importance of belowground interactions for understanding aboveground patterns (Van der Putten 2012).

In addition to potential belowground interactions, aboveground seedling distribution of mangroves in our study appears to be controlled by surrounding vegetation structural density and percentage of time flooded. In Florida, high structural density across the entire transect and minimal inundation limit the ability for propagules to disperse away from the parent tree. The absence of seedlings in the interior mangrove areas is likely due to light limitation under the mature mangrove canopy (Smith 1987; Clarke and Allaway 1993), thus resulting in a peak density of seedlings just before the transition from mangrove to salt marsh as propagules are unable to disperse with high overall structural density. Conversely, our Louisiana site's rapidly declining structural density and greater percentage of time flooded allow for greater dispersal and establishment of mangrove propagules away from the parent mangrove. The increased density of seedlings in large Florida mangroves is likely due to the greater number of propagules produced on such large trees (Alleman and Hester 2011a) and the possibility of cold temperature protection offered by these large canopies to seedlings found underneath (Krauss et al. 2008; Ross et al. 2009; D'Odorico et al. 2013; Devaney et al. 2017). This protection of seedlings to disturbance by larger trees has previously been described as a 'shield effect' in both freeze events (Ross et al. 2009) and hurricanes (Imbert et al. 1996). The pattern of high seedling densities at the salt marsh-mangrove interface in Florida is similar to the findings by Stevens *et al.* (2006) who completed their study in nearby islands off Cedar Key, Florida. The difference in structural density can largely be attributed to salt marsh vegetation type. In the salt marsh, Florida's high structural density was composed of a mixture of *B. maritima*, *P. vaginatum*, *S. depressa,* and *S. alterniflora,* while Louisiana's low structural density was solely dominated by *S. alterniflora* (Yando *et al.* 2016). Underneath the mangrove canopy, large numbers of pneumatophores contribute to the high structural densities, except for Louisiana's small mangrove individuals, which had few pneumatophores. The combination of flooding and vegetation structure has also been suggested to be important for trapping mangrove propagules upslope as mangroves migrate inland with sea level rise (Peterson and Bell 2012, 2015), within disturbed mangrove settings (McKee et al. 2007a), and recently restored sites (Donnelly and Walters 2014). Others have also suggested that high structural density not only limits dispersal, but may also limit establishment of propagules as they are not able to root prior to desiccation (Howard et al. 2015). Comparably, within mangrove forests containing species with prop roots, density of prop roots plays an important structural role in trapping propagules and limiting dispersal (Van der Stocken et al. 2015). Vegetation density may have both positive and negative implications for mangrove dispersal, establishment, and growth depending on seasonality, location, and life history stage in mangroves (Stevens et al. 2006; Alleman and Hester 2011b; Pickens 2012) and other plant communities (Holmgren et al. 1997; Van Auken 2000). The impact of combined abiotic and biotic interactions is needed to understand dispersal once temperature limitations are released in this system and differences in the transition may be observable (similar to Walker et al. 2003), but require an objective measurement and comparison within and between locations.

Finally, soil metrics, specifically SOM and C density, did not change across the salt marsh-mangrove interface or with mangrove size class, but rather only between locations. These findings corroborate previous studies that suggest that SOM and C density do not differ in these locations between salt marsh and mangroves (Perry and Mendelssohn 2009; Henry and Twilley 2013; Doughty et al. 2016) or with mangrove structural development (Yando et al. 2016) in areas with mesic, productive salt marshes. We might expect to see changes in SOM and C density across the interface with mangroves in drier or upslope locations dominated by less productive salt marsh species (Comeaux et al. 2012; Kelleway et al. 2016; Yando et al. 2016). These findings also fit well into the broader discussion of the impacts on soil carbon of woody encroachment into grasslands with mesic locations often seeing no net change (Briggs et al. 2005) or even a decrease (Jackson and Caldwell 1993), while increases are observed in semi-arid and arid locations (Eldridge et al. 2011). Future shifts in the salt marsh-mangrove ecotone are unlikely to result in changes to these key soil properties in these mesic locations.

The findings of our study highlight the importance of examining ecotones at small microspatial scales, connecting them to broader ecosystem patterns, both in vegetation and soil properties, and realizing site specific differences. By studying "boundary dynamics", as stated by Wiens et al. (1985), we can advance understanding of local dynamics that affect landscape level processes. Within the mangrove range limit and salt marsh-mangrove ecotone, the disconnect in pattern between aboveground vegetation cover and belowground rooting metrics illustrates that aboveground vegetation is not sufficient to characterize shifts in ecosystems. Additionally, variation in the interactions with the incumbent surrounding vegetation, in this case the salt marsh ecosystem, can differentially influence expansion rates via dispersal, establishment, and competition even within the same region, thus providing a greater understanding to the drivers that influence mangrove expansion beyond just temperature and precipitation (Giri and Long 2016; Osland et al. 2017a). Surrounding vegetation and hydrology appear to be controlling the distribution of mangrove dispersal, but further research is needed to better understand short distance dispersal, individual tree expansion rates, and the impact of microclimates formed during non-lethal freeze events. The interaction between salt marshes and mangroves is far more complex than simple invasion, shading, and competition regardless of the scale being examined. Finally, the key soil metrics of SOM and C density are not likely to change with mangrove expansion into mesic, productive salt marshes. By understanding changes, or a lack thereof, at an individual level across an ecotone, we are better able to predict ecotonal dynamics and the implications of a range shift at broader scales, as well as connect aboveground and belowground patterns as invading vegetation expands into incumbent ecosystems with global change

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# Chapter 2: Patch Level Dispersal Dynamics Inform Climate-Induced Range Shifts

## 2.1 Abstract

Question: Dispersal dynamics are critical to understanding possible future shifts in species' ranges and boundaries, but are unlikely to remain constant as species expand into new areas due to global climate change. In this study, we seek to better understand patch-level dispersal dynamics at a latitudinal coastal ecotone. Specifically, we ask 1) how mangrove propagules are differentially dispersed along an elevational gradient within the salt marsh-mangrove ecotone, 2) how does vegetation influences mangrove propagule dispersal dynamics, 3) how the role of propagule predation influences propagules prior to establishment, and 4) where mangrove seedlings ultimately establish along the elevation gradient compared to where mangrove propagules strand?

Location: Coastal saline wetlands, southeastern Louisiana, USA

Methods: We collected 2,500 *Avicennia germinans* propagules during each of our two field campaigns. Batches of 500 propagules were placed at each of five different elevations, with each batch marked with a distinct color relative to its dispersal elevation. After their release, we observed dispersal dynamics over the course of the subsequent month. Additionally, we completed a simultaneous propagule predation study and a subsequent seedling establishment study.

Results: Propagule retention exponentially decreased over time, with most elevations retaining <10% of original propagules dispersed there. Propagules at the highest elevation (1% time flooded) were more likely to be retained. Retained propagules did not move up or down-slope and generally maintained their original elevations. Propagule predation accounted for ~20% of non-retained propagules, while ~80% of non-retained propagules were exported out of the study site. Vegetation density did not impact propagule retention at any of the sampling times. Finally, peak mangrove seedling density occurred at elevations flooded 20-40% of the time.

Conclusions: This study highlights the mass export of propagules in this system, a lack of vegetation influence on propagule retention within the tidal frame, the low rates of propagule predation compared to other mangal ecosystems, and the disconnect between retained propagules and established mangrove seedling distributions. By improving our understanding of dispersal and establishment dynamics at patch-level scales, we are better able to predict mangrove expansion projections and models at larger landscape scales.

## 2.2 Introduction

Dispersal plays a critical role in species survival and expansion, particularly at range limits and ecotonal boundaries (Howe & Smallwood 1982; Gaston 2009; Sexton et al. 2009). Patterns of dispersal can be examined at different spatial and temporal scales to understand species survival, expansion, and population connectivity (Nathan & Muller-Landau 2000). With changing climatic conditions, shifts in key environmental parameters will result in changes to species distributions and ecotonal boundaries (Walther et al. 2002; Parmesan & Yohe 2003; Walther 2010). Additionally, new biotic interactions may arise that will influence dispersal dynamics (Van der Putten et al. 2010). Modelling efforts often only utilize abiotic parameters at current rates to predict future species distributions in climate envelope analyses. In reality, variable rates of change in both abiotic and biotic conditions and their interactions need to be accounted for to better predict these shifting distributions, range limits, and ecotones (Sexton et al. 2009; Van der Putten et al. 2010). One portion of this complex set of interactions is a sound understanding of dispersal vectors and strategies and how incumbent ecosystems will impact dispersal patterns of expanding species.

In coastal saline wetlands, dispersal by water, or hydrochory (Dammer 1892), is a common and ecologically important dispersal vector (Nilsson et al. 2010). Mangroves, which are woody plants found on low energy tropical and subtropical coasts, utilize hydrochorous dispersal (Tomlinson 1994) despite its overall rarity in plants (Levine & Murrell 2003). Mangrove propagules are most often viviparous or cryptoviviparous in nature, as they germinate on the tree and then fall off to disperse (Bhosale & Mulik 1991; Tomlinson 1994). Tides, currents, wind, and wave action are all important factors in determining dispersal distance and direction (Howe & Smallwood 1982; Huiskes et al. 1995; Thiel & Haye 2006). Mangrove dispersal has been documented at large temporal and spatial scales (Duke 1993; Duke et al. 1998), but only a limited number of studies have examined dispersal at smaller scales (Yamashiro 1961; Clarke 1993; Sousa et al. 2007; Peterson & Bell 2015; Van der Stocken et al. 2015). The focus in the literature on long-distance dispersal does not provide adequate information to properly inform local and moderate-distance dispersal mechanisms and processes (Clarke 1993; Van der Putten et al. 2010).

Interaction dynamics of surrounding vegetation (e.g., mangrove or marsh) also play a critical role in dispersal, establishment, and survival. In stressful, early successional, or ecotonal habitats, nearby vegetation is capable of trapping propagules and ameliorating soil conditions for establishment (McKee 1995b; McKee et al. 2007), but may also inhibit dispersal (Peterson & Bell 2012; Peterson & Bell 2015) and compete for space resources (Pickens & Hester 2011; Pickens 2012; Simpson et al. 2013; Howard et al. 2015; reviewed by Saintilan et al. 2009). Guo et al. (2013) argues that mangroves at ecotonal boundaries can be governed by a biotic interaction complex that differs across environmental gradients, life history stage, and may be further driven by local edaphic conditions. The intricate nature of these interactions needs to be thoroughly examined at both local and patch-level scales to better connect plot level measurements and observations to landscape level range shifts.

Mangrove expansion at the expense of salt marshes is expected to occur on temperature-controlled mangrove range limited coastal reaches as the frequency, duration, and severity of freeze events decreases with climate change (Osland et al. 2013; Osland et al. 2017). In the southeastern United States, models predict mangrove expansion, but do not take into account the many biotic and abiotic drivers of dispersal dynamics, including potential non-stationarity in dispersal rates (Van der Putten et al. 2010; Guo et al. 2013). Dispersal at all spatial scales as well as propagule retention, establishment, survival, and predation are all key drivers of expansion and dispersal patterns (Clarke 2006). Thus, they all need to be considered and understood when predicting future mangrove expansion. Although dispersal dynamics have been previously studied within mangrove habitats (Rabinowitz 1978; Sousa et al. 2003; Sousa et al. 2007; Van der Stocken et al. 2015) and at the upslope salt marsh-mangrove ecotone (Peterson & Bell 2012; Peterson & Bell 2015), no dispersal focused studies have been conducted at the latitudinal salt marsh-mangrove ecotone in the northern Gulf of Mexico or at other temperature-controlled mangrove range limit. The northern Gulf of Mexico has been the focus of many studies examining salt marsh-mangrove interactions, mangrove seedling establishment/survival, and propagule production/predation (Patterson et al. 1993; Patterson et al. 1997; McKee & Rooth 2008; Pickens & Hester 2011; Alleman & Hester 2011b; Alleman & Hester 2011a; Osland et al. 2013; Krauss et al. 2014), but studies explicitly examining dispersal dynamics within the latitudinal salt marsh-mangrove ecotone are needed to appropriately predict future shifts in the range limits with climate.

We address this gap and inform possible salt marsh feedbacks by investigating dispersal along an elevation gradient within the salt marsh-mangrove ecotone. Specifically, we ask the following questions: 1) how are mangrove propagules differentially retained or dispersed along an elevation gradient and out of the study area, 2) how does vegetation influence mangrove propagule dispersal, 3) how does predation influence propagules prior to establishment, and 4) where do mangrove seedlings ultimately establish along the elevation gradient compared to where mangrove propagules strand? To address these questions, we dispersed marked mangrove propagules along an intertidal elevational gradient within a salt marsh-mangrove vegetation mosaic in coastal Louisiana, USA, where salt marsh and mangrove species are intermixed at their latitudinal ecotone.

## 2.3 Methods and methods

### 2.3.1 Study area and experimental design.

During the winters of 2015 and 2016, we conducted dispersal studies in a restored coastal saline wetland adjacent to Bayou Lafourche in Port Fourchon, Louisiana (29.127° N, 90.222° W) (Fig 2.1a). The area received dredged sediment slurry from a nearby canal when the slurry spilled over a retention levee, forming an elevation gradient within the study site. We established five elevation contours along the elevation gradient using a laser level (Spectra Precision Laser, LL300, Trimble Navigation Ltd., Sunnyvale, CA, USA) and related contours to a previously measured nearby stable benchmark. Contours were reestablished and reference to the benchmark each year using real time kinematic survey (RTK); NAVD88 Geoid 12A (Trimble R8 Receiver & Trimble TSC3 Controller, Trimble Navigation, Ltd., Sunnydale, California) and the real-time Continuous Monitoring Reference Station (CORS) network (Louisiana State University, GULFNet). The elevation contours corresponded to ~75 %, 50 %, 25 %, 10 %, and 1 % of time the marsh surface was flooded (hereafter referred to as percent time flooded) (5-year average; NOAA 2015) (Fig. 2.1b). Five sectors of ~ 4 m were established along each elevation contour to further divide the site for spatial analyses. The greater Fourchon area is microtidal with a mean tide range of 0.37 m (NOAA 2014), and is heavily influenced by meteorological forces (Hester & Mendelssohn 1989). The overall relationship of flooding was the same for the two sampling campaigns (Fig. B1 & Table B2). The site included a mosaic of mangrove, salt marsh, and succulent vegetation at varying densities (Fig. 2.2).

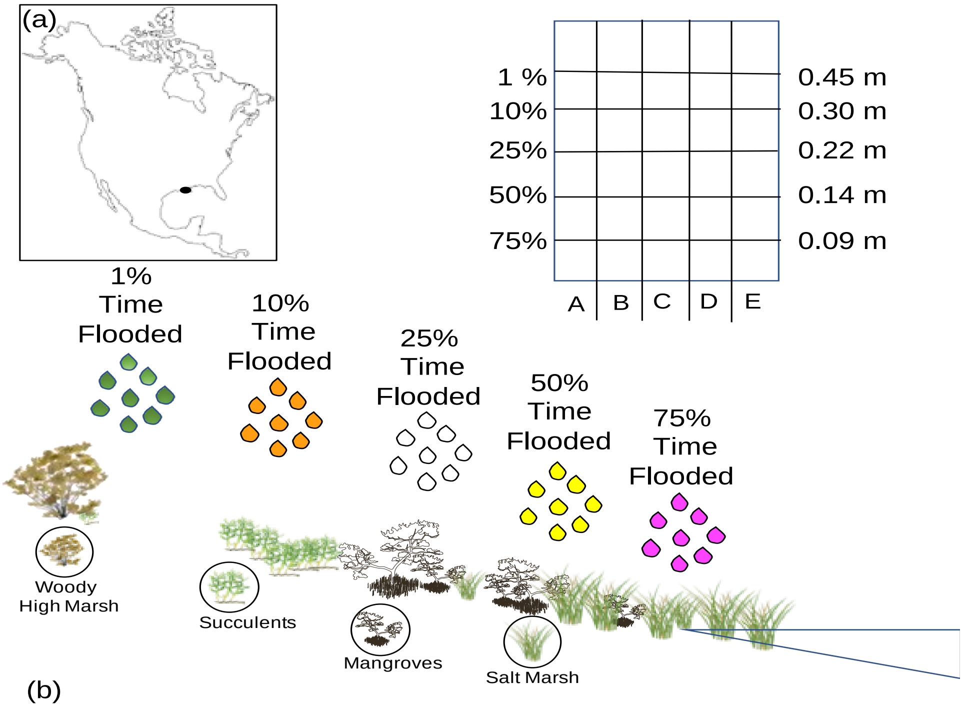

**Figure 2.1.** (a) Map of study site location in Louisiana (USA) and (b) diagram of painted propagules located along an elevational gradient with corresponding percent time flooded and elevations (NAVD88-Geoid12A) in a salt marsh-mangrove vegetation mosaic. Images of vegetation courtesy of Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/imagelibrary/).

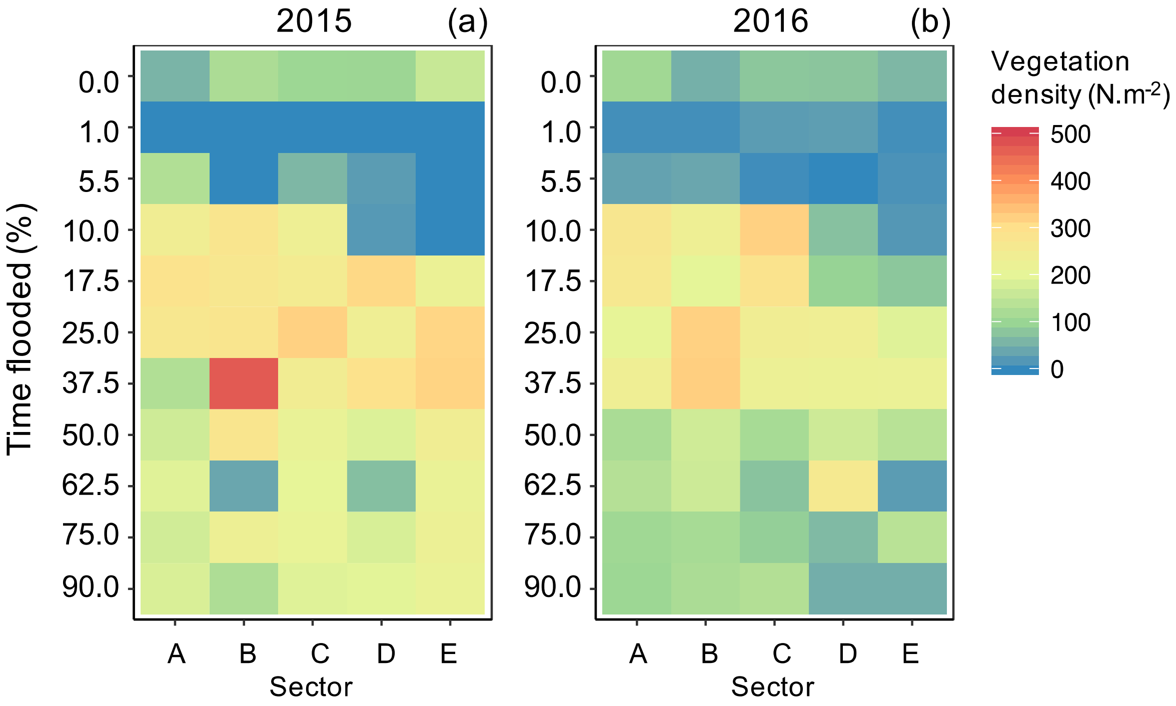

**Figure 2.2.** Map of vegetation density with respect to the amount of time flooded in 2015 (a) and 2016 (b) by sampling sector.

### 2.3.2 Propagule dispersal.

During each field campaign (2015 & 2016), 2,500 mangrove propagules were collected. Pericarps were removed after a brief soaking period, propagules were allowed to dry, and were

then painted in batches of 500 with five different colors of spray paint (similar to Sousa et al., 2007- Appendix A) (methods and color specifics in Appendix C and Table B2). These propagules were only studied for each month-long dispersal campaign, not the subsequent establishment experiment. Each batch of 500 propagules were placed linearly along their respective elevation contours (Fig. 2.2) (100 per sector) that represent a gradient of percentage of time the marsh surface was flooded [hereafter time flooded (%)]. Sampling of contours was completed at 1, 5, and 36 days (2015) and 1, 3, 18, and 31 days (2016) after initial placement throughout the study site and divided by sector. We also sampled a 50-m buffer surrounding the area. All sampling utilized a methodical multi-person visual line search. Elevation, minimum distance traveled, and vegetation density and type were measured for each propagule located during sampling. We determined propagule elevation using a laser level (Spectra Precision Laser, LL300, Trimble Navigation Ltd., Sunnyvale, CA, USA) and related elevations to previously mentioned nearby benchmarks. Minimum distance traveled was measured using a range finder to determine distance from the propagule to the closest possible release point (TruPulse 200, Laser Technology Inc., Centennial, Colorado, USA). Vegetation type and density in 0.11-$m^2$ quadrats (0.33 x 0.33 m) centered on each propagule. Propagules that dispersed out of system were defined as exported and propagules preserved within our study system were defined as retained.

#### 2.3.3 Propagule predation and buoyancy.

To calculate propagule predation and herbivory (hereafter predation), ten propagules were tethered along each elevation contour using dental floss attached to steel landscaping stakes during each sampling effort. Five paired propagules (one painted to match the elevation contour, one unpainted) were placed along each elevation contour for a total of 50 propagules. Propagule presence/absence and predation damage were quantified at 35 days (2015) and 29 days (2016) (Table B3). Buoyancy of both each paint color on propagules was also tested and compared to unpainted propagules in a laboratory experiment (Table B2).

#### 2.3.4 Propagule establishment.

We calculated local seedling establishment rates by sampling 15 0.11-$m^2$ (0.33 x 0.33 m) quadrats per elevation contour 3 and 6 months after the 2016 sampling campaign.

Seedlings, individuals 30 cm or less in height, were counted, as these plants are two years old or less. Presence or absence of cotyledons was also noted.

#### 2.3.5 Data analyses.

Data analyses included regression in a mixed model framework (linear, exponential, quadratic, square root power function) using package ‘nlme’ (Pinheiro et al. 2017) in R-Studio (Team RStudio 2017) to appropriately analyze our repeated measures design (Zuur et al. 2009) (Table 1). Dependent variables included propagules retained, estimated propagules lost to predation, propagules exported, propagule density, and seedling density. The fixed portion of all models included sampling day, sampling campaign, and % time flooded, month and % time flooded for the seedling density model, or vegetation density and sampling day for the propagule density model. The random portion of all models included sampling day nested within sampling campaign or plot identification nested within sampling month for the seedling density and propagule density models. To address heterogeneity in propagule density models we modeled error variance for each sampling day and removed values of zero vegetation structure for analyses. All random portions were utilized to appropriately account for independence due to the repeated nature of these analyses (Zuur et al. 2009). Model selection was based on AICc values and eliminating non-significant model terms to form the simplest model.

For elevation, buoyancy, and predation experiments, analysis of variance and Tukey’s post-hoc tests were utilized. Independent variables included: % time flooded and sampling campaign for elevation analyses, sampling campaign and paint color for the buoyancy analyses, and sampling campaign, % time flooded, and paint color for predation analyses. Dependent variables included: elevation and observed % time flooded for the elevation experiment, number of days propagules remained buoyant for the buoyancy experiment, and confirmed propagule predation, propagule removal, and conservative total propagule predation for the predation experiment.

## 2.4 Results

### 2.4.1 Propagule dispersal.

The number of propagules retained within the site declined exponentially regardless of field campaigns (Fig. 2.3a; Table 2.1). Propagules that started at elevation contours of 10 - 75 % of the time flooded had < 5% propagule retention the study system at the end of the field campaigns. Those at the highest elevation (1% time flooded elevation contour) also saw an exponential decrease, but differed in their rate of decline from other elevations with approximately 20% propagules retention after 36 days (Fig. 2.3a; Table 2.1). For those propagules not found in the system during each sampling time a 20% predation rate was calculated (data in present study) and the remainder were estimated to have been exported (Fig. 2.3b,c; Table 2.1). Both propagules lost to predation and exported propagules followed a square root function regression.

Retained propagules generally stayed at their original elevation contour over time (Fig. 2.4) regardless of sampling campaign. Propagule density was not influenced by vegetation density (Fig. 2.2 & 2.5; Table 2.1), but was highly variable in both sampling campaigns (Fig. B2). Propagule density did decrease in time after release regardless of vegetation (Fig. B2) as shown by other analyses.

### 2.4.2 Propagule predation and buoyancy.

Confirmed predation ranged from 0 - 40 % depending on elevation contour and paint color (Table B3). Additionally, some tethered propagules were removed due to unknown

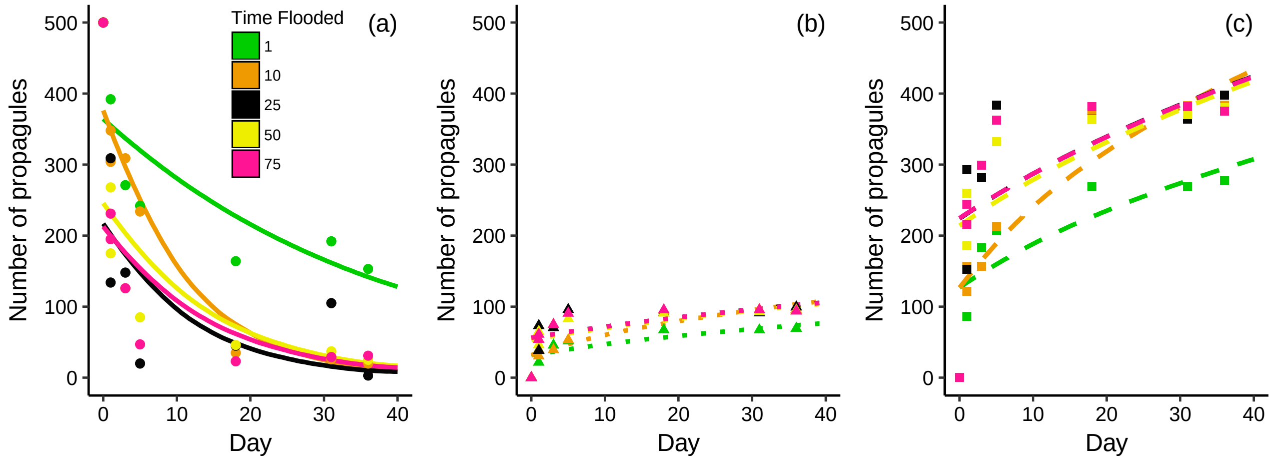

**Figure 2.3.** Number of propagules retained within site (a; circles, solid lines) on each observed sampling day for both sampling campaigns with exponential regression fit shown. Estimated predation (b; triangles, dotted lines) and export (c; squares, dashed lines) utilizing square root power function regression fit for sampling days for both sampling campaigns. See Table 1 for statistical information.

**Table 2.1.** Mixed model regression types, model factors, F-statistics and p-values for all regression analyses. (* $p<0.05$; ** $p<0.01$; *** $p<0.001$)

| Metric | Regression Type | Dispersal Days | Elevation Contour | Dispersal Days x Elevation Contour |
|---|---|---|---|---|
| Found | Exponential | $F_{1,6}$=26.3** | $F_{4,28}$=5.6** | $F_{4,28}$=3.3* |
| Herbivory | Square Root | $F_{1,6}$=18.9** | $F_{4,28}$=9.7*** | $F_{4,28}$=2.9* |
| Export | Square Root | $F_{1,6}$=18.9** | $F_{4,28}$=9.7*** | $F_{4,28}$=2.9* |
| | | Month | Elevation Contour^2 | Month x Elevation Countour^2 |
| Establishment | Quadratic | $F_{1,16}$= 25.3 *** | $F_{2,16}$=7.0** | $F_{2,16}$=5.23* |
| | | Vegetation Density | Sampling Day | Vegetation Density * Sampling Day |
| Propagule Density 2015, 2016 | Linear | *NS*, *NS* | $F_{3,138}$= 13.5***, $F_{2,92}$= 19.0*** | *NS*, *NS* |

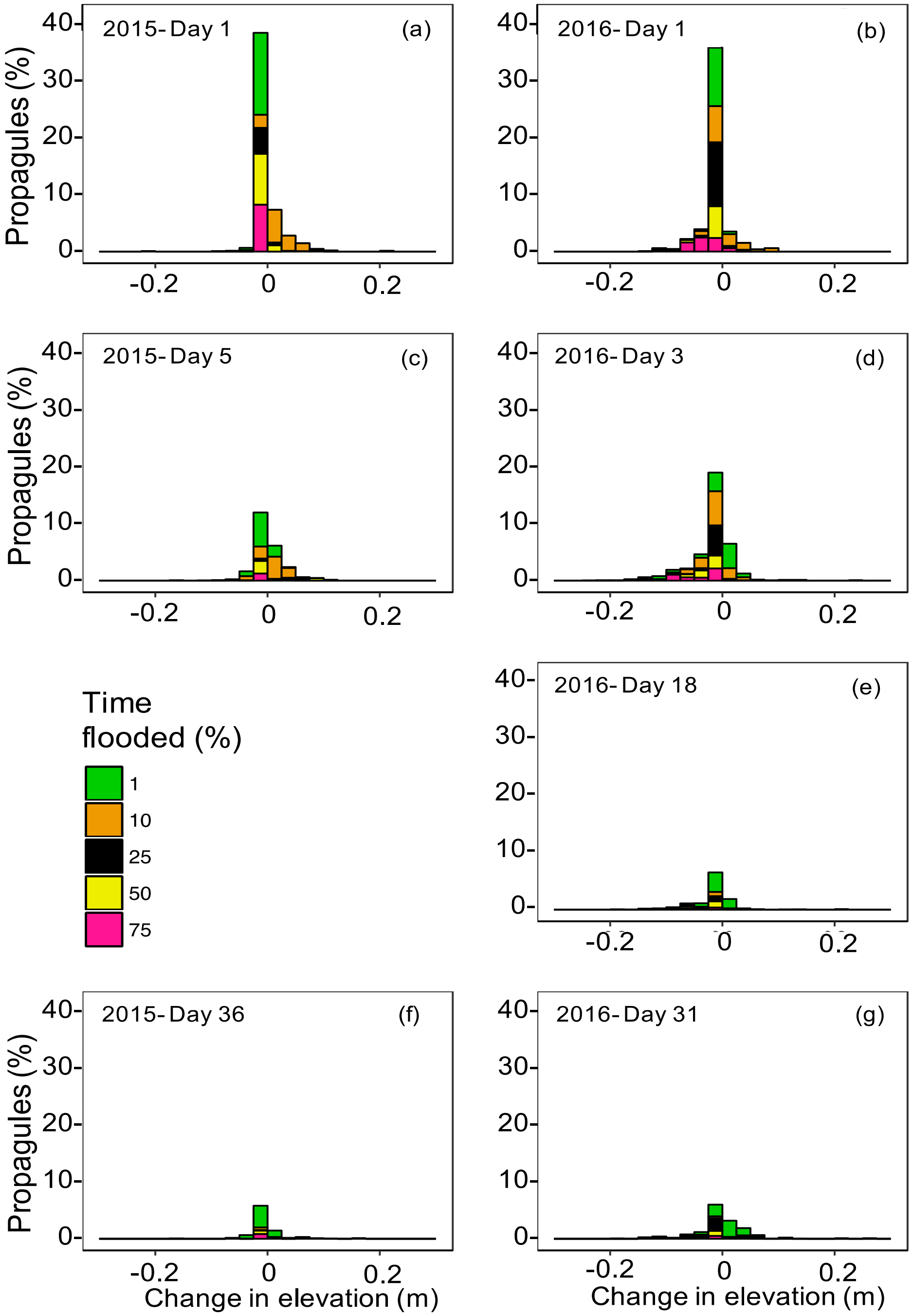

**Figure 2.4**. Stacked histogram of propagule change in elevation by percentage of total propagules found by percent time flooded elevation contour during both sampling campaigns. 2015 Day 1 (a), Day 5 (c), Day 36 (f) and 2016 Day 1 (b), Day 3 (d), Day 18 (e), Day 31 (g). Binned by 0.02 m intervals.

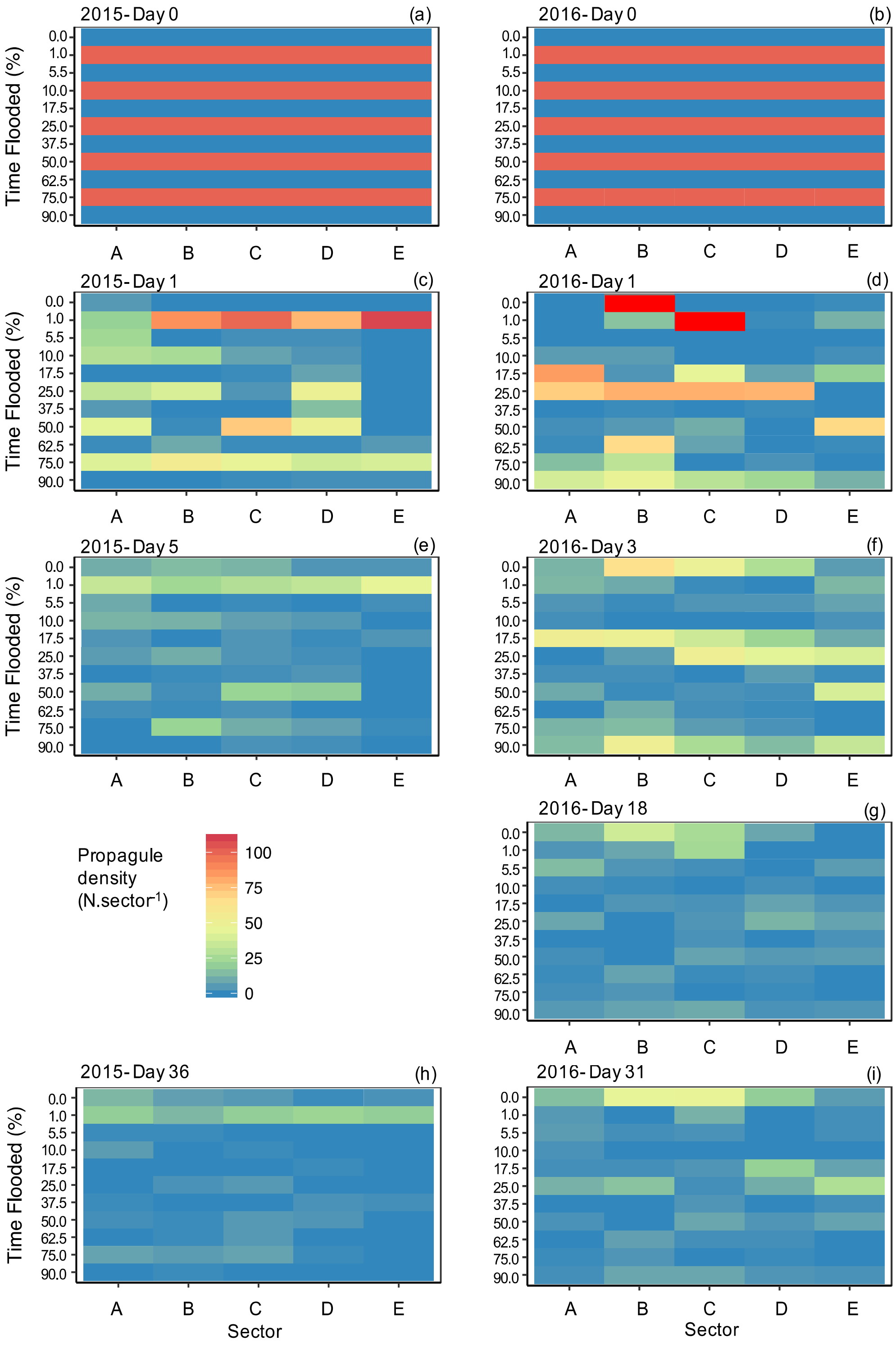

**Figure 2.5.** Density map of propagules (N. sector$^{-1}$) along time flooded elevation contours by partitioned sector sampled for both field sampling campaigns. 2015- Day 0 (a), Day 1 (c), Day 5 (e), Day 36 (h) and 2016- Day 0 (b), Day 1 (d), Day 3 (f), Day 18 (g), Day 31 (i).

causes (e.g., predation, tidal action, rotting). To account for this unknown loss, we conservatively added 20% of unknown removed propagules to the known propagule predation rates. This conservative total predation estimate did not differ by sampling campaign, paint treatment (painted or unpainted, color), or time flooded elevation contour and yielded a 22 ± 2.3%) predation rate for the whole system (Table B3).

Buoyancy of propagules was only impacted in one case and was changed for the second field campaign, but did not impact results from the field experiments (Table B3).

### 2.4.3 Propagule establishment

Seedling density was greatest at ~37 % time flooded at 3 months and ~25 % time flooded at 6 months (Fig. 2.6; Table 2.1). The number of seedlings significantly decreased between the two sampling campaigns (Fig. 2.6).

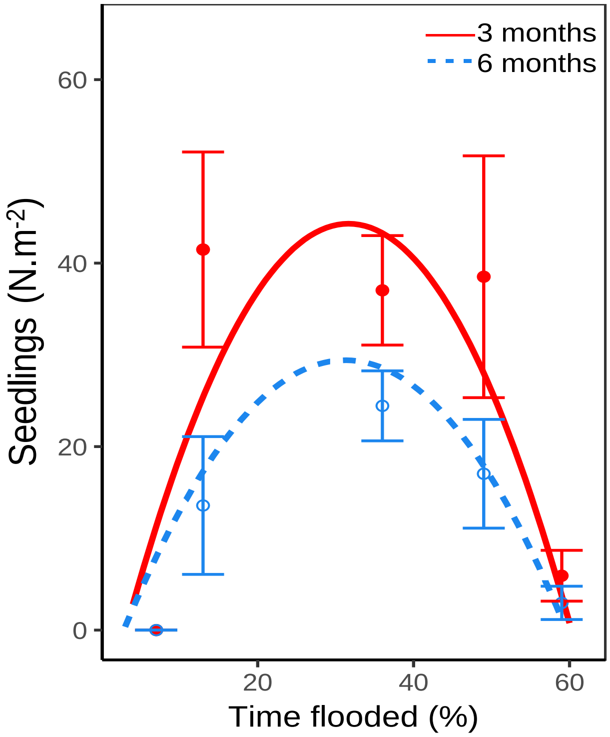

**Figure 2.6.** Number of established seedlings per square meter (mean±SE) with respect to time flooded (%) at three (red, solid line; quadratic model) and six (blue, dashed line; quadratic model) months after the second field campaign.

## 2.5 Discussion

Dispersal is an important aspect of survival and expansion of any species. In this study, we highlight the importance of understanding local patch-scale hydrochorous dispersal dynamics along an elevation gradient. Our experimental results emphasize the export of dispersing propagules out of the local study system and highlights the lack of influence of the surrounding vegetation on retaining propagules. This study has implications for understanding the importance of scale in a shifting ecotone and provides information on how to use or not use propagules for restoration practices.

Retention dynamics of dispersing propagules within the salt marsh-mangrove ecotone have only been examined tangentially through seedling and adult mangrove distributions within the latitudinal salt marsh-mangrove ecotone in the southeastern United States. Our findings show that 10 % or less of marked propagules were retained within the system after one month, with the exception of propagules placed at the highest elevation, which were retained at a rate of ~20-25 %. The number of propagules retained within the site is much lower than other mangrove dispersal studies: 60 % in Belize after 4 weeks for *A. germinans* (Sousa et al. 2007), 48 % and 85 % for *Ceriops tagal* and *Rhizophora macronata*, repectively, after 3 days in Kenya (Van der Stocken et al. 2015), and in Florida, 60-70 % after 6 weeks for *A. germinans* (Peterson & Bell 2015). In other coastal halophytic plants, a broad range of propagule retention has been recorded, but mass export is commonly seen (Huiskes et al. 1995).

Predation of propagules is a potential mechanism of propagule loss in our study. We estimated 22 % of propagules were lost due to predation, regardless of paint color and elevation. These rates are similar to other *A. germinans* predation studies which reported 11 % propagule predation in coastal Louisiana (Patterson et al. 1997), ~20 % in Belize (Sousa et al. 2007), 25 % in Panama (Sousa & Mitchell 1999), and 10 - 40 % for *A. marina* in southeastern Australia (Clarke 1993). Higher predation rates (60 - 100 %) of both *A. germinans* and other *Avicennia* species in both tropical and sub-tropical locations have also been reported in the literature (Smith et al. 1989; McKee 1995a; McGuinness 1997; Van Nedervelde et al. 2015; Langston et al. 2017). Possible predators of *A. germinans* propagules in Louisiana were previously reported as the square back marsh crab [*Armases cinerum* (previously *Sesarma cinerum*)] and the marsh periwinkle (*Littorina irrorata*) (Patterson et al. 1997). *Avicennia germinans* mangrove propagules have large, nutritious cotelydons and low levels of defense compounds compared to other mangrove species.

Although propagule predation accounted for some of the propagules removed from our system, the majority of the propagule loss (~70 %) was from dispersing propagules exporting out of the system. Export is driven primarily by tidal currents (Huiskes et al. 1995) with wind also playing an important role (Feller & Sitnik 1996; Van Der Stocken et al. 2015). Coastal Louisiana’s microtidal environment (~30 cm - 40 cm tidal range), coupled with significant winter storms, may enhance propagule export as cold-front passages can drastically lower water levels (Hester & Mendelssohn 1989) pulling propagules away from the parent plant. Despite our two sampling campaigns having different average water levels and frequency and amplitude of higher water events, rates of propagule retention and loss did not differ. This is likely a function of time as dispersing propagules within the system are found early in the sampling efforts. Export out of the system potentially provides a mechanism for moderate and even long distance dispersal to other suitable areas (Huiskes et al. 1995). This, however, is stochastic in nature and success is likely limited, despite being highly important at larger temporal and spatial scales (Duke et al. 1998; De Ryck et al. 2012). In the greater area, large numbers of propagules have often been seen stranded in a variety of areas and are often found in the water column (Yando, per. obs.). The precocious reproduction rates at the latitudinal range limit of other mangrove species in the region have also been examined (Dangremond & Feller 2016) and our work further supports the massive reproductive effort and subsequent export of mangrove propagules.. Furthermore, it may play a key role in the expansion strategy of species at range limits and ecotones with species realizing their new climatic envelope (sensu Box 1981; Pearson & Dawson 2003) with global climate change.

Of those propagules that were retained within the system, most did not move significantly up or down slope. This lack of transport has been reported in other halophytic coastal plants (Huiskes et al. 1995; Rand 2000; Sousa et al. 2007). Yamashiro (1961) reported only 2 % retention under maternal trees, similar to our own study with very low overall retention. Furthermore, dispersal in our study does not appear to be influenced by vegetation structural density (Fig. 2 & 5). Other studies have shown the importance of propagule trapping and facilitation by surrounding vegetation in both mangrove and nearby marsh species (McKee et al. 2007; Peterson & Bell 2012; Guo et al. 2013; Peterson & Bell 2015). These differences may be due to time scale or differences in vegetation density, but perhaps most importantly the dominant role of hydrology in propagule dispersal and export. This has significant implications for restoration of coastal wetlands, particularly in areas where both mangroves and salt marsh coexist. The major role of hydrology indicates that propagule dispersal may not be able to be controlled even if propagules are dispersed to the correct elevation, and rather suitable habitat should be constructed to allow mangroves to disperse on their own if source populations are available nearby (Lewis 2005).

The few propagules that were retained within the system, primarily those found at the highest elevations, followed a similar pattern of stranding on ebb tides as seen by Clark (1993). This highest elevation was too high in the tidal frame for successful establishment, and propagules were often observed to be desiccated after the first few sampling days (Yando, pers. obs.). Balke et al.'s (2011) "window of opportunity" hypothesis fits well with this observation, as propagules require suitable environmental conditions, proper stranding and establishment windows within the tidal cycle, and a suitable substrate. The seedling establishment experiment confirms our observation that the highest elevations are too high for survival (Fig. 6), with no seedlings present at these elevations likely due to a lack of tidal inundation, hypersalinity, water stress, and possibly seedling predation (Clarke & Allaway 1993; Clarke & Myerscough 1993; Patterson et al. 1997; Clarke & Kerrigan 2002). Furthermore, observed peak seedling densities regardless of sampling date were midway through the intertidal zone, areas likely receiving daily inundation on most tidal cycles, and are very close to values reported for both seedlings and adults by Alleman and Hester (2011a) and Guo et al. (2013).

This study addresses the importance of understanding and accounting dispersal dynamics at the patch scale. In this system and at this scale, propagule export is high, with those propagules that are retained generally persisting at their natal elevations. Furthermore, vegetation interactions do not appear to play a role in this system at a month-long time scale, evincing the dominant role of hydrology in structuring dispersal dynamics. This difference, compared to other studies, highlights the importance of scale on factors influencing propagule dispersal and how the relative importance of interactions may differ across environmental gradients. With shorter time scales and smaller areas different drivers are likely to control dispersal [microtopography, vegetation structure/height, storm events, wave height, time flooded (%), predation rates] compared to moderate times and patch-level scales [time flooded (%), predation rates] (similar to Gosz, 1993). Furthermore, many of factors influencing dispersal dynamics are likely to be scale dependent (Morton et al. 2018). As retained propagules were primarily found at elevations not suitable for establishment, mangroves in this system must produce a vast number of propagules in order to expand into surrounding marsh habitat, as similarly suggested by Alleman & Hester (2011b). Thus, the mechanisms and potential rates of mangrove expansion into incumbent marsh habitat are potentially different depending on the spatial and temporal scale being examined. Relying solely on temperature changes ignores both patch and local level dynamics as well as longer term stochastic events, such as hurricanes and freezes, that are important for range expansion (Rodriguez et al. 2016). By achieving greater insights into dispersal and establishment factors at patch-level scales, a more mechanistic understanding of mangrove expansion dynamics is possible at the latitudinal salt marsh-mangrove ecotone throughout the tidal setting.

## 2.6 Acknowledgements

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# Chapter 3: Jump-Starting Ecological Restoration:

# A Comparison of Marsh and Mangrove Foundation Species

## 3.1 Abstract

1. During coastal wetland restoration, foundation plant species play a critical role as they create habitat, modulate ecosystem functions, and support entire ecological communities. Following restoration of desired hydrologic regimes, foundation plant species can help stabilize sediments and jump-start ecosystem development. However, foundation species may have different early life history traits and environmental tolerances. Thus, there is a pressing need for studies that compare these traits and tolerances from a restoration perspective.
2. Where tropical and temperate climates meet, coastal wetland restoration practitioners can choose between salt marsh and mangrove foundation species. Here, we compared the early life stage traits of two foundation species: (1) a salt marsh grass (*Spartina alterniflora*); and (2) a mangrove tree (*Avicennia germinans*). We utilized a recently-restored coastal wetland in southeastern Louisiana, USA to better understand differences between the early life history traits and environmental tolerances of these foundation species. Over an 18-month study, we examined growth and survival strategies along an elevational gradient, and compared expansion and natural recruitment rates in an adjacent experiment.
3. We found that the rapid growth, expansion, and recruitment of the salt marsh grass foundation species (*S. alterniflora*) make it an ideal species to quickly establish ecological structure, at suitable elevations.

4. The slower growth, limited expansion, and general lack of early natural recruitment of the mangrove tree foundation species (*A. germinans*) highlight its limited capability in immediate structural restoration, especially in habitats where it co-occurs with fast-growing, perennial salt marsh foundation species like *S. alterniflora*.
5. *Synthesis and applications:* Our findings suggest that the structural attributes that are desperately needed in recently-restored areas can be achieved rapidly using fast-growing salt marsh grass foundation species. Following grass establishment, mangrove tree foundation species can be used to further assist ecosystem development. This work highlights how the appropriate foundation plant species can help jump-start ecosystem development to meet short-term (e.g., erosion control, vegetation structure) and long-term restoration objectives (e.g., plant community development and restoration of ecosystem processes and functions).

### 3.2 Introduction

Foundation species have a disproportionate influence on the structure, function, and maintenance of ecosystems (Dayton, 1972). Loss of these species can have a significant impact on ecosystem stability, function, and the supply of ecosystem services (Ellison et al., 2005). Structural characteristics are one of the most well-studied attributes that foundation species provide with numerous examples from terrestrial forests, salt marshes, kelp forests, seagrass beds, and mangrove forests (e.g., Angelini, Altieri, Silliman, & Bertness, 2011; Ellison et al., 2005; Gedan & Bertness, 2010; Gedan, Kellogg, & Breitburg, 2014; Osland, Enwright, Day, & Doyle, 2013). The ecological structure provided by foundation species, often by autotrophic primary producers, is valued by humans for the many ecosystem services that are supported (e.g., carbon storage and cycling, water filtration, nursery habitat, wave attenuation, erosion control, and water management) (Barbier et al., 2011). During restoration, foundation species often play a pivotal role in rapidly creating structure and habitat and enabling ecosystem development.

The comparison of multiple foundation species was a key component of Dayton's (1972) seminal study, which has introduced and provided the definition for foundation species. Interactions between foundation species have been studied in marine, terrestrial, and aquatic ecosystems. (Altieri, Silliman, & Bertness, 2007; Angelini et al., 2011; Gedan et al., 2014; Osland et al., 2013; Osland, Enwright, & Stagg, 2014). In species-poor ecosystems, where few species are capable of surviving stressful conditions, there is typically only a single dominant foundation species that is able to occupy a given portion of a particular environmental gradient (Angelini et al., 2011). Other foundation species are likely to be found in alternate adjacent patches due to differ abiotic conditions, different stress tolerances, and/or competition (Altieri, Bertness, Coverdale, Herrmann, & Angelini, 2012; Angelini et al., 2011; Levine, Brewer, & Bertness, 1998). This is most common where environmental gradients are steep (e.g., intertidal and alpine ecosystems). In some ecosystems, different foundation species can play similar functional roles in the same or overlapping patches (Gedan et al., 2014; Osland et al., 2013), however, this overlap in functionality is likely only to occur at species range limits, near local thresholds along environmental gradients, or in areas that are currently recovering from disturbance.

In coastal wetlands, an area of foundation species overlap occurs at the poleward salt marsh-mangrove ecotone, where both salt marsh grass and mangrove tree plant communities exist (Alongi, 2009; Bertness & Ellison, 1987; Osland et al., 2013). Salt marshes are dominated by herbaceous vegetation and exist in temperate and sub-polar regions (Mitsch &

Gosselink, 2000), whereas mangroves are dominated by freeze-intolerant, woody trees and shrubs on tropical and sub-tropical coasts (Duke, 1993). Interactions between these grass and tree foundation species have been studied at a variety of life history stages (Clarke & Myerscough, 1993; Patterson, Mendelssohn, & Swenson, 1993; Pickens & Hester, 2011; Stevens, Fox, & Montague, 2006; Yando, Osland, & Hester, 2018) and through the lens of global climate change. Little work, however, has been done to understand their interactions and tradeoffs in growth strategies along environmental gradients from a restoration perspective.

Ecosystem restoration is becoming an increasingly valuable tool in systems that are destroyed, degraded, or perturbed by both natural and human disturbances. Salt marsh and mangrove ecosystem have experienced some of the highest relative levels of disturbance worldwide (Airoldi & Beck, 2007; Kennish, 2001; Leadley et al., 2013; Richards & Friess, 2016). Despite their high levels of loss and degradation in many areas, both salt marshes and mangroves are highly valued for their ecosystem services (e.g., wave attenuation, carbon storage, erosion control, nursery habitat) (Barbier et al., 2011). In the northern Gulf of Mexico, and particularly in coastal Louisiana, where a dynamic salt marsh-mangrove ecotone exists, the rate of coastal saline wetland loss, due to relative sea level rise, is among the highest in the world (Penland et al., 1990; Turner, 1997). To compensate for this loss, large-scale coastal restoration efforts have been implemented and coastal wetland restoration is a key component (e.g., The Louisiana Master Plan) (Porthouse & Rouge, 2005). During ecological restoration, practitioners must balance critical short-term constraints, including site creation or manipulation (e.g., erosion control, soil compaction, sediment type), with long-term objectives (e.g., provision of habitat, targeted species assemblages and communities, and key ecosystem services and functions) (Hilderbrand, Watts, & Randle, 2005). The planting of key salt marsh and mangrove foundation species in restoration projects is common, but direct comparisons of survival, expansion and natural recruitment along elevational gradients are lacking, particularly the during the critical early stages after physical restoration (Crewz & Lewis, 1991; Lewis & Dunstan, 1975).

In this study, we utilized a recently restored coastal saline wetland to understand: 1) how the growth strategy and survival of two foundation species differs along an elevation gradient, 2) how rates of expansion and recruitment differ between two foundation species, and 3) which foundation species is better suited for the rapid formation of necessary structural attributes? We compared a common salt marsh grass foundation species (*Spartina alterniflora*) to a mangrove tree foundation species (*Avicennia germinans*). Our overarching aim was to advance understanding of the importance of the early life history strategies and interspecies interactions between these foundation species, thereby providing valuable information to coastal scientists and restoration practitioners.

## 3.3 Methods and Materials

### 3.3.1 Study site.

We completed this study in a previously operational canal in Port Fourchon, Louisiana, USA (Fig. 3.1a) (29.132°N, 90.224°W). This canal has been the site of an ongoing wetland restoration with adjacent sections completed in 2012, 2013, and 2014 utilizing dredge spoil sediments from the nearby Bayou Lafourche. This experiment was started in March of 2015 in the most recently filled sections (2013 & 2014) and planted with both *A. germinans* (hereafter *Avicennia*) and *S. alterniflora* (hereafter *Spartina*). Planting was completed in coordination with the Coalition to Restore Coastal Louisiana (CRCL), with over fifty volunteers directed and overseen by ESY to plant individuals according to the study design described herein. The site was monitored at 3 months, 7 months, 12 months, and 18 months after initial planting (March 2015 to September 2016). Two experimental areas were established (Fig. 3.1b & 3.1c).

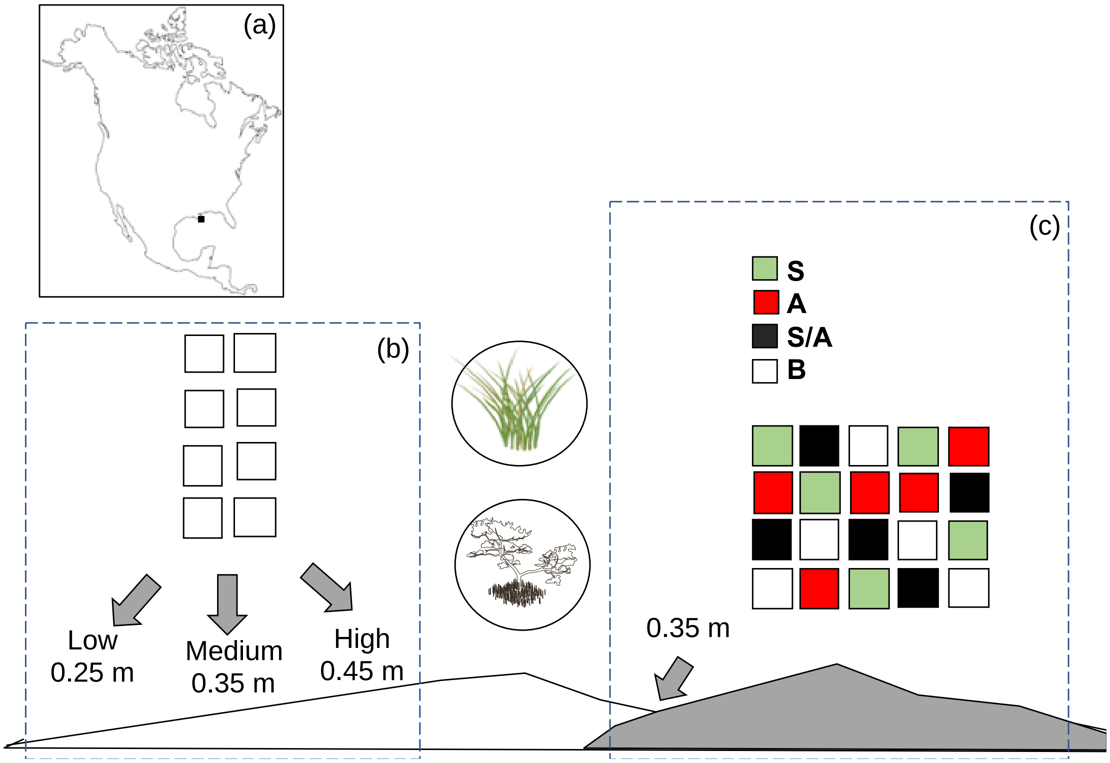

**Figure 3.1.** (a) Map of location of study site in Port Fourchon, Louisiana (USA). (b) Layout of Experimental Area I at low, medium, and high elevations in the 2013 fill site (white polygon). (c) Layout of Experimental Area II in the overlap between the 2013 and 2014 fill sites (gray polygon) (S = *Spartina*; A= *Avicennia*; S/A = *Spartina/Avicennia*; B = Bare). Circles indicate marsh (top [*Spartina alterniflora*]) and mangrove (bottom [*Avicennia germinans*]) foundation species that were planted in both experimental areas.

### 3.3.2 Elevational gradient - experimental area I.

Utilizing the elevational gradient formed from the placement of dredge spoil material, three distinct planting elevations were identified at 0.25 m, 0.35 m, and 0.45 m (± 0.025 m) NAVD88 (Geoid12A). Elevation for all plots was determined by first establishing stable benchmarks, which had previously been measured using a high-precision Global Navigation Satellite System (GNSS) (Trimble R8 and TSC3), in combination with a real-time Continuously Operating Reference Station (CORS) network (Louisiana State University's GULFNet network) and then using a laser level (Spectra Precision Laser, LL300, Trimble Navigation Ltd., Sunnyvale, CA, USA) to identify suitable areas of each elevation. Elevations were related to local tidal gauges (CRMS-CPRA, 2017) to determine the percentage of time the marsh surface was flooded (hereafter referred to as percent time flooded). At each elevation, eight 16-$m^2$ plots (4 m x 4 m) were established (Fig. 1b). All plots were planted with *Avicennia* at 1.52-m spacing [this spacing (5 ft.) is common in Louisiana restoration plantings] with an additional four individuals in the center 1-$m^2$ subplot for a total of 13 mangrove transplants per plot with initial heights that ranged from 30-45 cm. Plots were also planted with *Spartina* at high (0.3-m spacing) or low (1.52-m spacing) densities, but this treatment was not statistically significant at any time point nor for any measurement, so these treatments were combined. After 18 months, elevations were remeasured, and although significant elevation increases were detected (4-6 cm) these differences are within the margin of error of the RTK and fluctuations in soil surface elevation due to subsurface hydrological variation (Nuttle, Hemond, & Stolzenbach, 1990). Nonetheless, relative differences were maintained and over the course of the 18-month study, the low, medium, and high elevations were flooded 27, 11, and 3 % of the time, respectively.

*Avicennia* tree height, total biomass, and percent survival were measured at each sampling period. Percent live and dead cover were visually estimated at the plot level. Tree height was measured and total biomass was calculated using an allometric equation during each sampling point (Osland, Day, Larriviere, & From, 2014). Specific leaf area (SLA) was measured at the 18-month sampling period from five representative *Avicennia* leaves from five different trees in each plot. If less than five trees were present, then the five leaves were equally taken from the available individuals. SLA was determined by dividing leaf area by dry leaf mass. The area of each leaf was calculated using ImageJ software (Rasband, 2017) and dry mass of leaves was measured after drying at 65 °C for two weeks.

*Spartina* percent live and dead cover were measured at the plot level and mean *Spartina* canopy heights determined at each sampling period. Additionally, during the 18-month sampling period, a 0.11-$m^2$ (0.33 m x 0.33 m) plot was randomly selected and all salt marsh aboveground biomass was clipped at the soil surface and stored at 4 °C until processed. Collected stems were counted and all stems were dried at 65 °C for two weeks for total dry biomass (g). Adjusted biomass for each plot was calculated at the meter-squared level using the plot cover estimates.

### 3.3.3 Expansion and recruitment - experimental area II.

To examine expansion and recruitment, a second experimental area was established in an adjacent portion of the same restoration site. We established twenty 16-$m^2$ plots (4 m x 4 m) and planted them with one of four treatments: 1) *Avicennia*, 2) *Spartina*, 3) *Avicennia*/*Spartina*, or 4) bare (not planted) in a randomized design (Fig. 1c). All plantings were at 1.52-m spacing for a total of nine plants per species per plot. We measured *Avicennia* and *Spartina* live and dead percent cover and calculated percent survival of *Avicennia* within each plot. At the 12-month sampling period, the number of *Spartina* progenitor clumps (original transplants or natural recruits), and rates of lateral expansion were measured from the previous year’s dead stems to the external expanding edge. Elevations were measured prior to the experiment and after 18 months. Elevations were related to local tidal gauges

(CRMS-CPRA, 2017) to determine percent time flooded. A 0.32 m (± 0.01) (NAVD88-Geoid12A) elevation was maintained for the duration of the experiment and percent time flooded was 15 %.

#### 3.3.4 Soil.

For all plots we collected a 15-cm deep, 5.08-cm diameter soil core prior to the start of the experiment (0 months) and at each sampling period. Cores were collected and stored at 4 ºC until analyses were completed. All soils were dried at 65 ºC until constant mass was achieved, and bulk density was determined by simple dry weight to volume ratio (Blake & Hartge, 1986). Quantification of soil organic matter (SOM) was determined via loss on ignition in a muffle furnace at 500 ºC for 5 hours (similar to Wang et al. 2011).

#### 3.3.5 Data analyses.

Data analyses included linear and quadratic regression in a mixed model framework using package ‘nlme’ (Pinheiro et al., 2017) in R-Studio (Team RStudio, 2017) to analyze our repeated measures design. Dependent variables included *Avicennia* survival, tree height, biomass, and cover along with *Spartina* cover and canopy height. Independent variables included fixed effects (month, sampling elevation, planting treatment) and random effects (plot identification [used to account for the non-independence in repeated measure]). Model selection was completed by using AICc values and eliminating non-significant model terms.

For comparisons at 12- and 18-month measurements, analysis of variance and Tukey’s post-hoc tests were utilized. Dependent variables for these measurements included elevation, *Avicennia* SLA, *Spartina* biomass, *Spartina* stem density, and *Spartina* expansion rate, whereas independent variables included sampling elevation or treatment type. All means are presented with standard error.

## 3.4 Results

### 3.4.1 Elevational gradient - experimental area I.

*Avicennia* percent survival declined over time, with greater survival at low elevations compared to high elevations ($p<0.01$; Fig. 3.2a; Table 3.1; Table D1). Tree height and total mangrove biomass increased over time, but did not differ by elevation (Fig. 3.2c,e; Table 3.1 & D1). At the 18-month sampling period, SLA was significantly greater at low elevations (78.1 ± 3.0 $cm^2$ $g^{-1}$) compared to both medium (47.5 ± 8.0 $cm^2$ $g^{-1}$; $p<0.01$) and high elevations (42.4 ± 6.6 $cm^2$ $g^{-1}$; $p<0.01$) (Table 3.1). *Avicennia* cover in this experimental area ranged from 0 - 15 % over the monitoring period, but was highly variable and patchy.

*Spartina* live cover increased over time at all elevations, with the lowest elevation displaying a faster rate of increase compared to both medium and high elevations ($p<0.001$; Fig. 3.2b; Table 3.1 & D1). *Spartina* canopy heights also increased over time but had significantly greater canopy heights at the lowest elevations ($p<0.05$; Fig. 3.2d; Table 3.1& D1). *Spartina* stem density at 18 months did not differ statistically by elevation, but had high variability at all elevations (Low: 139 ± 21.9 stems $m^{-1}$; Medium: 114 ± 25.16 stems $m^{-1}$; High: 56 ± 23.2 stems $m^{-1}$). Adjusted biomass did differ at 18 months in *Spartina*, with significantly greater biomass in low elevation plots compared to medium ($p<0.005$) and high elevation plots ($p<0.001$) (Fig. 3.2f; Table 3.1 & D1).

Soil metrics in this experimental area had increasing bulk densities over time for all elevations, but were lower in low elevation plots at all time points compared to high elevations ($p<0.001$) (Table 3.1 & D1). SOM did not differ over time, but was lower in high (3.4 ± 0.3 %) and medium elevation plots (2.9 ± 0.3 %) compared to low elevation plots (4.7 ± 0.3 %; $p<0.001$) (Table 3.1 & D1).

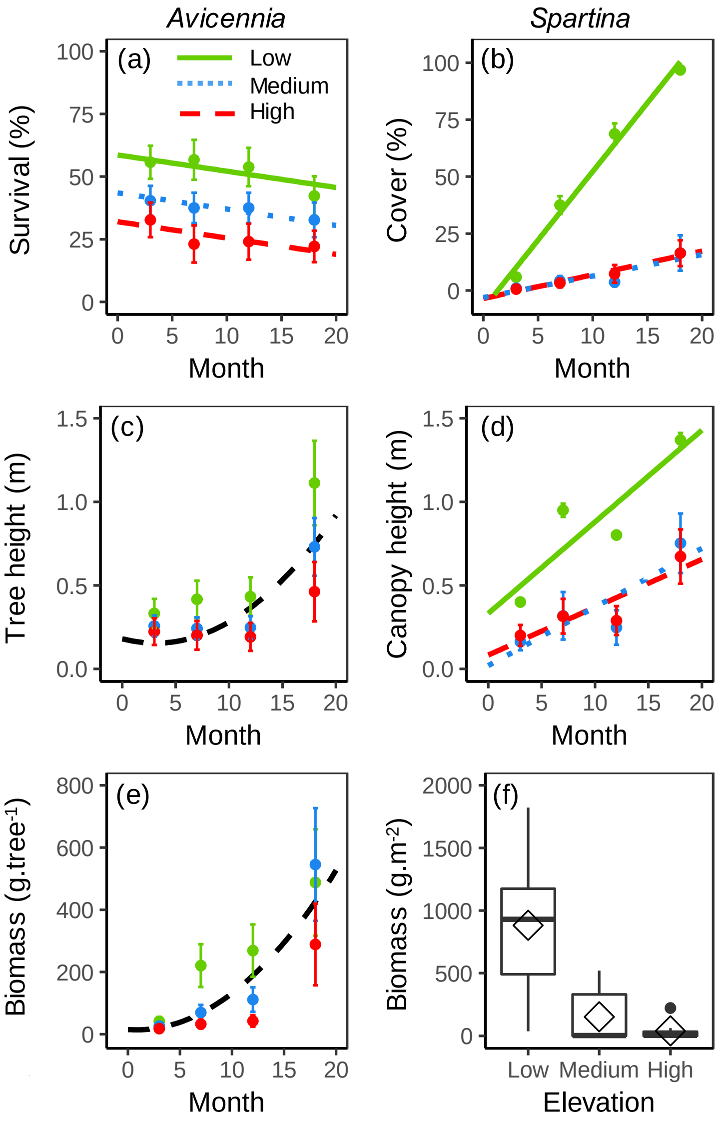

**Figure 3.2.** Relationship between time and (a) *Avicennia* survival, (b) *Spartina* cover (c) *Avicennia* tree height, (d) *Spartina* canopy height, and (e) *Avicennia* tree biomass and (f) boxplot of *Spartina* biomass between elevations at 18-month sampling. All linear regressions (a, b, d) have low (green-solid), medium (blue-dotted), and high (red dashed) elevations with means (± SE). All quadratic regressions (c, e) have mean (±SE) values for low (green), medium (blue), and high (red). Interior diamonds in boxplot (f) represent mean values.

**Table 3.1.** Model type, degrees of freedom, F-statistic, and p-value for time, elevation, time x elevation, treatment, and time x treatment for all metrics in both experimental areas.

| Experimental Area I | | Model Type | Time | Elevation | Time x Elevation | Treatment | Time x Treatment |
|---|---|---|---|---|---|---|---|
| *Avicennia* | Survival | Linear | $F_{1,71}=10.8$** | $F_{2,21}=4.9$* | NS | | |
| | Tree height | Quadratic | $F_{1,70}=28.6$*** | NS | NS | | |
| | Biomass | Quadratic | $F_{2,69}=37.0$*** | NS | NS | | |
| | Specific leaf area | ANOVA | | $F_{2,21}= 9.62$*** | | | |
| *Spartina* | Cover | Linear | $F_{1, 69}=283.1$*** | $F_{2,21}=104.0$*** | $F_{2,69}=111.5$*** | | |
| | Canopy height | Linear | $F_{1,69}=108.0$*** | $F_{2,21}=11.6$*** | $F_{2,69}=4.3$* | | |
| | Stem density | ANOVA | | NS | | | |
| | Adjusted biomass | ANOVA | | $F_{2,21}= 13.21$*** | | | |
| Soil & Hydrology | Bulk density | Linear | $F_{1,94}=10.7$ * | $F_{2,21}=5.7$** | NS | | |
| | SOM | Linear | NS | $F_{2,21}=9.3$** | NS | | |
| | Elevation | Linear | $F_{1,23} = 72.6$*** | $F_{2,21}= 211.1$*** | NS | | |
| Experimental Area II | | | | | | | |
| *Avicennia* | Cover | Linear | $F_{1,56}=13.9$*** | | | $F_{3,16}=9.1$*** | $F_{3,56}=7.2$*** |
| *Spartina* | Cover | Linear | $F_{1,56}=231.5$** | | | NS | $F_{3,56}=3.3$* |
| | Number of progenitor clumps | ANOVA | | | | $F_{3,16} = 7.96$*** | |
| Soil & Hydrology | Bulk density | Quadratic | $F_{2,76}=10.9$** | | | NS | NS |
| | SOM | Linear | NS | | | NS | NS |
| | Elevation | Linear | NS | | | NS | NS |

* = p<0.05; ** = p<0.01; *** = p<0.001

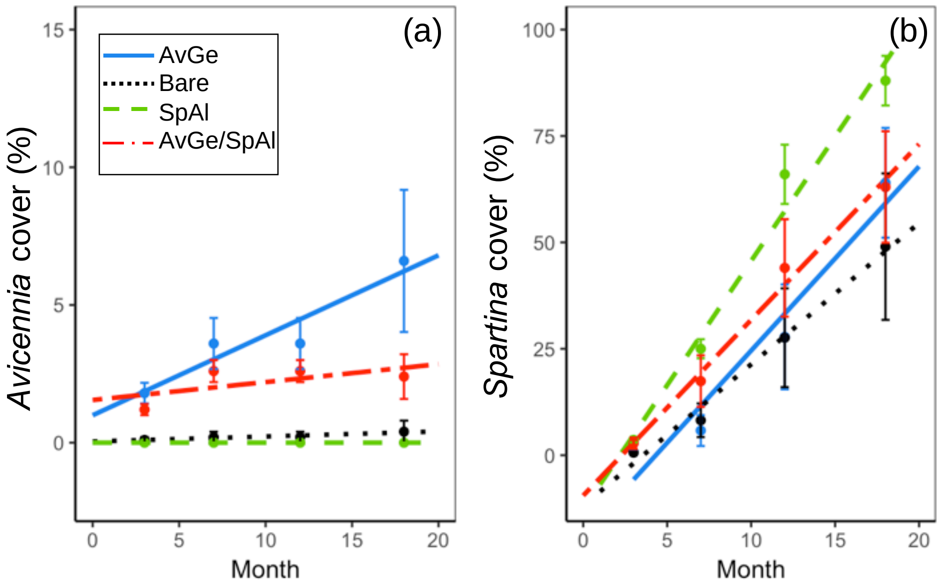

**Figure 3.3.** Avicennia (a) & Spartina (b) cover over time by planting treatment with means (± SE) and linear regressions. Treatments: AvGe (Avicennia; blue-solid), Bare (black-dotted), SpAl (Spartina; green-dashed), and SpAl/AvGe (Spartina/Avicennia; red-dashed-dot). Note differences in y-axes.

### 3.4.2 Expansion and recruitment- experimental area II.

*Avicennia* live cover increased significantly faster in the *Avicennia* monoculture treatment ($p<0.005$), while the *Spartina/ Avicennia*, *Spartina*, and bare treatments did not increase in *Avicennia* live cover nor did they differ in cover amounts (Fig. 3.3a; Table 3.1 & D2. Natural recruitment of *Avicennia* was only observed once in one bare treatment plot. *Spartina* live cover increased in all treatments, and increased faster in plots planted with only *Spartina* compared to bare treatments ($p<0.005$; Fig. 3.3b, Table 3.1 & D2.). After one year, the mean rate of *Spartina* lateral expansion was 0.94 ± 0.05 m regardless of treatment. The number of progenitor clumps, however, did differ after one year ($p< 0.002$; Table 3.1) with a greater number of progenitor clumps present in the *Spartina* treatment (5.2 ± 0.5 N plot$^{-1}$), compared to the bare (1.8 ± 0.4 N plot$^{-1}$; $p<0.005$) and *Avicennia* treatments (2.0 ± 0.6 N plot$^{-1}$; $p<0.005$). The *Spartina*/*Avicennia* treatment had an intermediate number of progenitor clumps (3.4 ± 0.8 N plot$^{-1}$) that did not differ from any of the other treatments.

Soil bulk density in this experimental area displayed a quadratic relationship over time with a peak bulk density at ~ 5 months after planting (Table 3.1 & D2.), but did not differ between treatment (Table 3.1 & D2.). SOM did not differ by time or treatment and ranged between 4 and 7 % SOM (Table 3.1 & D2.).

## 3.5 Discussion

The direct comparison of foundation species survival, growth, expansion, and recruitment along elevational gradients is needed to advance our understanding of ecosystem development during the critical early stages after physical restoration. Our study highlights key differences between these salt marsh and mangrove foundation species and can thus inform scientists and restoration practitioners of how selection of appropriate foundation species can lead to rapid structural and functional attributes needed to jumpstart long-term ecosystem restoration goals and natural ecosystem function.

Our study's comparison of these two foundation species along an elevation gradient highlights where they overlap and do not overlap in the landscape, while providing metrics of growth and survival success in the critical period after physical restoration. *Spartina* was more strongly influenced by the elevational gradient compared to *Avicennia* as observed in several metrics. *Spartina* displayed rapid increases in cover and biomass at the lowest elevations, and a progressively muted response with increasing elevation. Eighteen months after planting, we observed similar aboveground biomass at the lowest elevation as reported in other natural *Spartina* dominated marshes, but the values in this study were on the lower end of values previously observed in Louisiana (reviewed by Stagg et al. 2016). Medium and high elevations, however, had lower biomass compared to reference locations. *Spartina* growth at medium and high elevation sites was lower, but continued to increase over time, likely due to asexual reproduction (clonal growth) and subsequent resource sharing that can occur between ramets in stressful conditions (Pennings & Callaway, 2000). *Avicennia*'s lack of response to the elevational gradient is likely due to its slower growth rates (Alleman & Hester, 2011b), lack of asexual expansion (Baldwin et al. 2001), possible growth inhibition by surrounding *Spartina*, and stressful abiotic conditions (McKee & Rooth, 2008; Patterson et al., 1993; Pickens, 2012). *Avicennia* was able to grow at all elevations with varying survival, but differences between individuals only manifested themselves in SLA. At the lowest elevation, SLA was significantly greater indicating a lack of water stress (Knight & Ackerly, 2003), but also may be indicative of possible shading from the surrounding *Spartina* community (Liu et al., 2016). Tree height and biomass increased over time and did not differ by elevation but did show some differences in growth morphology by 18 months. Low elevation individuals maintained tall, narrow growth forms, while medium and high elevation trees were shorter and stouter. This is likely a function of light availability and competition, with trees forced to grow vertically when surrounded by *Spartina* at low elevations (Iwasa, Cohen, & Leon, 1985), a trend that we expect to become more pronounced over time. Despite an area of overlap at low and medium elevations and likely changes to interactions over time, our study clearly shows that as a foundation species, *Spartina* provides significantly faster structural development compared to *Avicennia* after 18 months.

Expansion and recruitment are critical to the structural provisioning that foundation species provide in all restoration sites and are key to integration within the greater landscape complex. Species interactions are also important to consider as species disperse, expand, and establish, and as suitable spaces in the environment are filled. Our findings show that in 18 months, *Avicennia* expanded relatively little and had very few new recruits, while *Spartina* had rapid expansion as well as some recruitment. *Avicennia*'s slow expansion and lack of natural recruitment rate may be attributed to a variety of factors including slower growth capacity (Alleman & Hester, 2011b), difficulty competing with surrounding marsh at early life stages (Howard et al., 2015; McKee & Rooth, 2008; Patterson et al., 1993; Pickens, 2012), a lack of asexual reproduction (Baldwin, Egnotovich, Ford, & Platt, 2001), and only one reproductive period prior to the end of the experiment. *Spartina*, on the other hand, displayed expansion rates of ~1 m per year for progenitor clumps, similar to other documented expansion rates in the literature (Hartman, 1988; Proffitt, Travis, & Edwards, 2003). The rapid expansion can be largely attributed to asexual reproduction, as *Spartina* does not have a persistent inter-annual seedbank (Xiao, Zhang, & Zhu, 2009). Seedlings from the previous year made up only a small number of overall stems (Yando, pers. obs.), and most areas had clearly expanded asexually from existing progenitor clumps. *Spartina* regularly tillers via ramets from its rhizomatous base, quickly filling in gaps once established in an area (Jones, Stagg, Krauss, & Hester, 2016). Other studies have highlighted the importance of clonal growth in expanding into highly stressful conditions, particularly in saline and hypersaline environments (Pennings & Callaway, 2000). Moreover, in terms of natural recruitment, we observed large numbers of broken fragments of *Spartina* stems and rhizomes strewn throughout the site at the 12-month and 18-month sampling periods. We attribute this high number of vegetative fragments to feral hogs (*Sus scrofa*), which were regularly present at the site and were observed via camera traps rooting into soil at the base of *Spartina* patches and pulling up plants with their rhizomes intact (Yando, pers. obs.). This behavior resulted in vegetative fragments gaining the opportunity to disperse to favorable areas for establishment and forming new progenitor clumps (Yando, pers. obs.). Additionally, we believe this behavior may also lead to increased asexual expansion rates through the breaking up of dense soils (Sloey & Hester, 2015), but may have negative effects on soil development (Persico, Sharp, & Angelini, 2017) as well as long term marsh sustainability.

Ultimately, a critical question at the latitudinal salt marsh-mangrove ecotone is which foundation species is better to plant in recently restored coastal wetland locations to maximize rapid structural provisioning after physical restoration? Our findings clearly demonstrate that the salt marsh grass foundation species, *Spartina,* is far more suited for rapid structural provisioning after physical restoration due to its growth, survival, expansion, recruitment strategy, and performance compared to the mangrove tree foundation species, *Avicennia*. If planting mangrove tree foundation seedlings at a restoration site is desired, our findings demonstrate that *Avicennia* would need to be planted at prohibitively high densities in order to compete with the structural density attained by *Spartina* at low and intermediate elevations. These findings agree well with studies from Florida that highlight the role of *Spartina* in mangrove restoration projects to rapidly expand, prevent erosion, and capture sediment in recently restored sites (Lewis, 1982; Lewis & Dunstan, 1975). At high elevations, *Avicennia* may be suitable to plant as *Spartina* does not survive well, if at all. This partial niche overlap in the tidal frame has been previously documented between these two species (Alleman & Hester, 2011a; Patterson & Mendelssohn, 1991), but is often ignored by restoration practitioners (although see Lewis & Dunstan, 1975). The highest elevations in the present study are only suitable for *Avicennia,* but are also at the upper elevational range for naturally established, mature *Avicennia* adults in Louisiana as reported by Alleman & Hester (2011b). *Spartina* clonal growth may eventually expand into these high elevation areas (Crewz & Lewis, 1991; Pennings & Callaway, 2000) or succulent dominated communities may naturally establish via seed. Alternatively, project engineers could design sites with lower maximum soil elevations (< 0.35 m NAVD-Geoid12A), as has successfully been completed in newer adjacent portions of this same restoration site (e.g., Experimental Area II). Eventually most of this site is likely to be covered by *Avicennia* regardless of the initial planting scheme (Lewis & Dunstan, 1975; Osland et al., 2012), as nearby mangrove source populations are readily found, and copious numbers of mangrove propagules have been observed at the site after the 18-month sampling period (Yando, pers. obs.). While it has been argued that habitat complexity/mosaics may be more desirable for overall resiliency and diverse function of landscapes (Bell, Fonseca, & Moten, 1997; Corbin & Holl, 2012), this area is within the salt marsh-mangrove ecotone and large patches of both salt marsh and mangrove can be found nearby. *Avicennia'*s susceptibility to freeze impacts may also make areas planted with mangrove vulnerable to diebacks if and when future freeze events of sufficient intensity occur, as has been previously observed in southeastern Louisiana (Osland et al., 2017; Stevens et al., 2006). By planting *Spartina*, rapid vegetative restoration can be attained, limiting risk of die-off from freeze events and providing the needed structure for long-term restoration of multiple ecosystem processes and functions.

These findings have critical implications for understanding foundation species interactions within the context of restoration. By utilizing foundation species that are capable of quickly providing structure in a recently restored location it may be possible to jump-start long-term restoration and ecosystem development. This study helps improve our understanding of interactions and attributes of foundation species and provides solutions to meet both short-term and long-term restoration objectives.

### 3.6 Acknowledgements

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# Appendix A

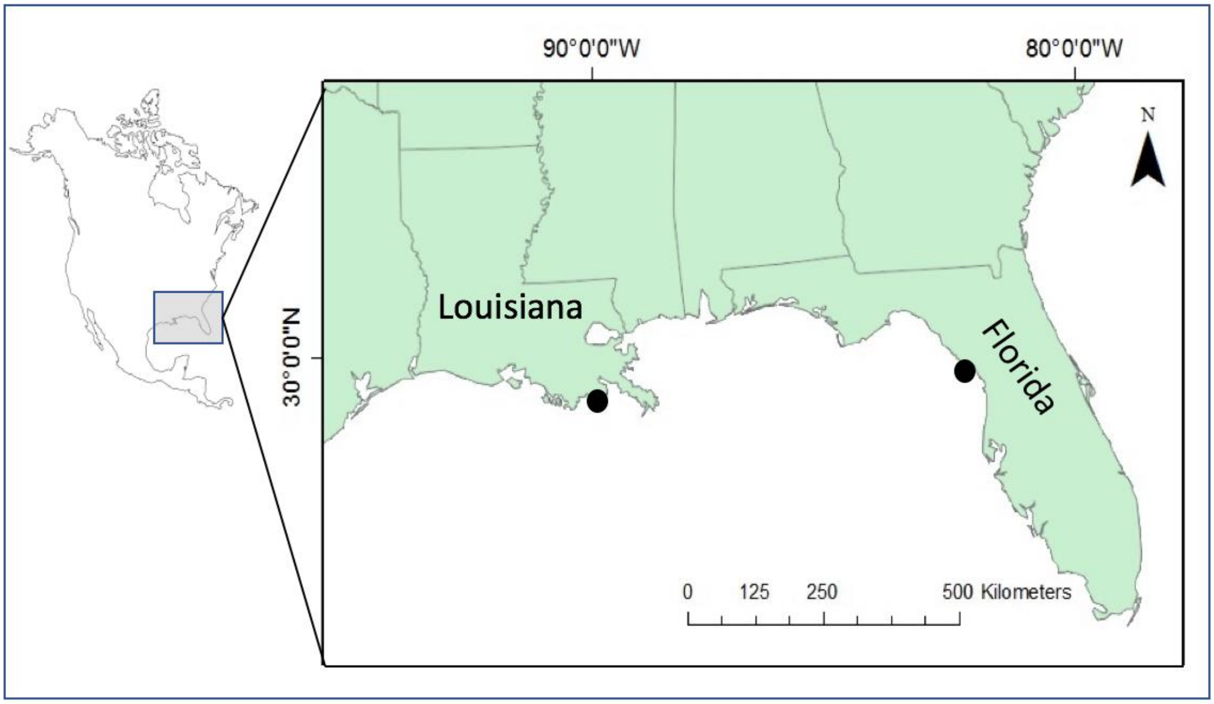

**Figure A1.** Map of sampling locations for this study: Port Fourchon (Louisiana) and Cedar Key Florida (Florida).

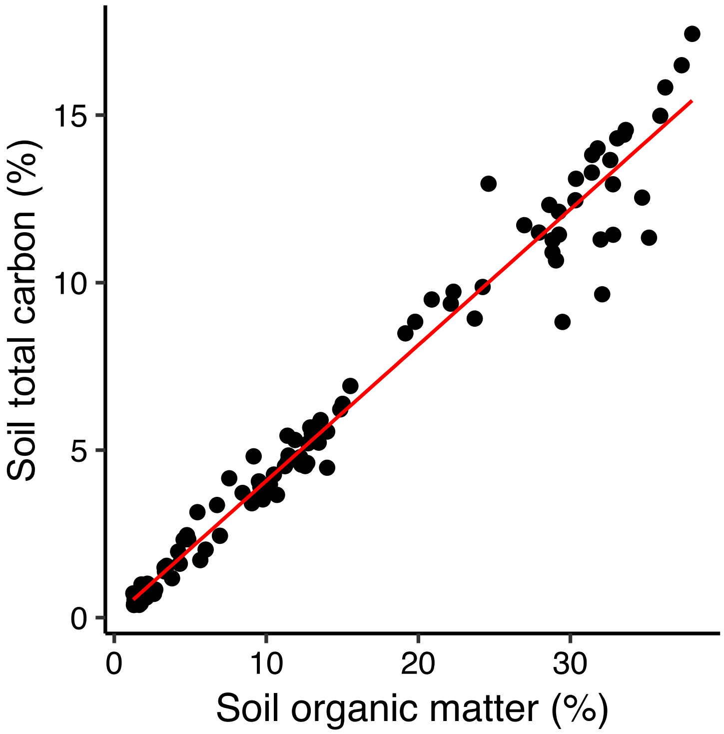

**Figure A2.** Soil organic matter (SOM) (%) by soil total carbon (TC) (%) with linear regression (TC= 0.02818 + 0.405361*OM; $r^2$ = 0.97; $F_{1,104}$=3088; $p<0.0001$). Data from northern Gulf of Mexico dataset contained within Yando et al. (2016).

**Table A1.** Summary of model parameters for vegetation, hydrology, soil, and porewater properties. Columns show *F* statistic with symbols indicating p-value significance: * <0.05, ** <0.01, ***<0.001; N/A= not applicable to metric; † indicates non-biologically significant result

| | Metric | Plot | Site | Size | Plot x Site | Plot x Size | Site x Size |
|---|---|---|---|---|---|---|---|
| Vegetation | Maximum salt marsh height | N/A | 124*** | 1 | N/A | N/A | 2 |
| Hydrology (2008-2013) | Elevation (m) | 0.1 | 1792*** | 0.0 | 0.0 | 0.7 | 0.4 |
| | Time flooded (%) | 0.1 | 1927*** | 0.2 | 0 | 0.2 | 0.8 |
| Soil properties | Bulk density (g $cm^{-3}$) | 3 | 699*** | 7*† | 0.1 | 1 | 2 |
| | Soil moisture (%) | 3 | 505*** | 4 | 0.5 | 0.09 | 2 |
| | SOM (%) | 3 | 1435*** | 10**† | 0 | 1 | 0 |
| | C density (mg $cm^{-3}$) | 1 | 228*** | 0.3 | 0.5 | 0.7 | 0.5 |
| | SIC (%) | 2 | 71*** | 0.2 | 0.5 | 0.01 | 0.1 |
| Porewater | pH | 0.1 | 124*** | 4 | 4.6*† | 0.03 | 1.4 |
| | Salinity (ppt) | 0.2 | 138*** | 0.08 | 0.6 | 0.05 | 1 |
| | Conductivity (mS) | 0.08 | 143*** | 0.001 | 1.4 | 0.3 | 0.5 |
| | Temperature (°C) | 0.4 | 152*** | 16*** | 0.08 | 0.25 | 11** |

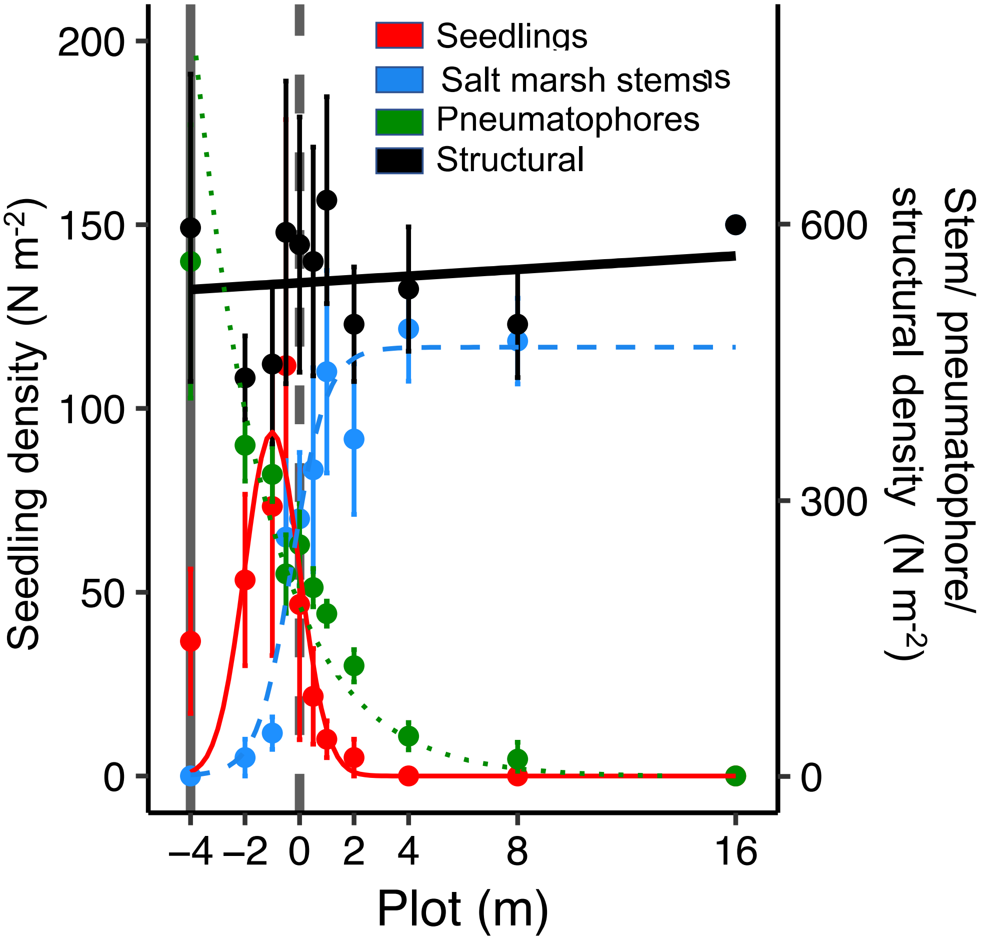

**Figure A3.** Comparisons of mangrove seedling (solid-red; left y axis; Gaussian peak), salt marsh stem (dashed-blue; right y axis; logistic), mangrove pneumatophore (dotted-green; right y axis; exponential), and total structural (thick solid-black; right y axis; non-significant) density across the salt marsh-mangrove interface in Florida-Large Transects. Values are mean ± SE (N= 3). Transects were established at the edge of the canopy and positioned at 0 m (vertical dashed line) and sampled plots at set distances. See Table 1.1 for all statistics.

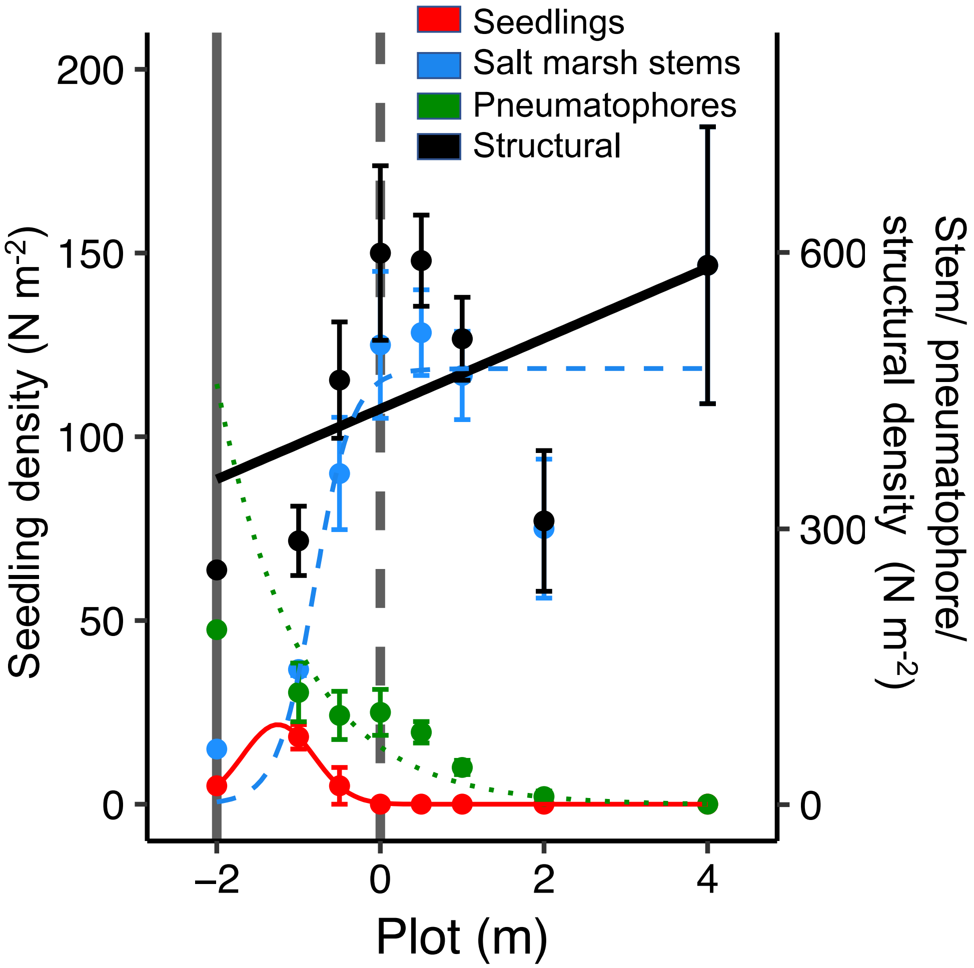

**Figure A4.** Comparisons of mangrove seedling (solid-red; left y axis; Gaussian peak), salt marsh stem (dashed-blue; right y axis; logistic), mangrove pneumatophore (dotted-green; right y axis; exponential), and total structural (thick solid-black; right y axis; non-significant) density across the salt marsh-mangrove interface in Florida-Small Transects. Values are mean ± SE (N= 3). Transects were established at the edge of the canopy and positioned at 0 m (vertical dashed line) and sampled plots at set distances. See Table 1.1 for all statistics.

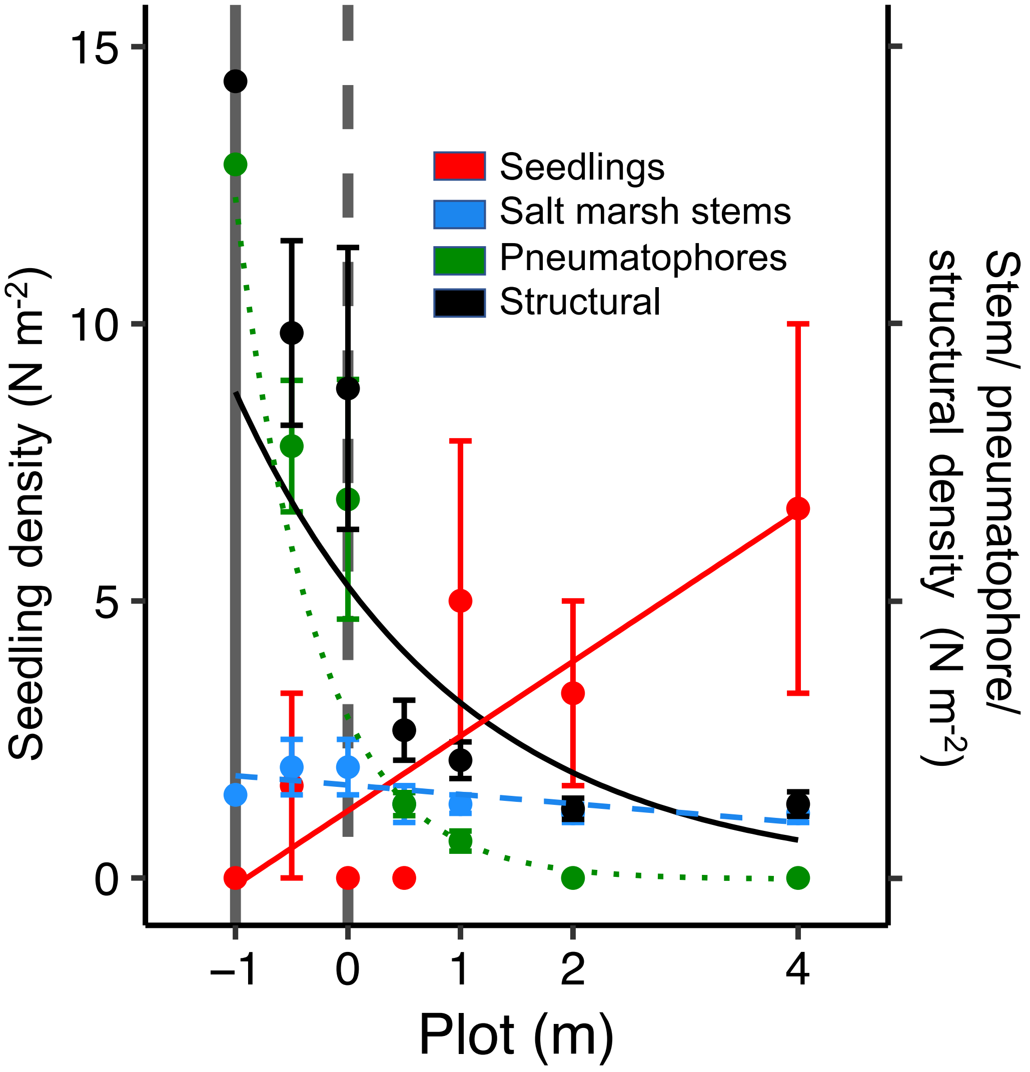

**Figure A5.** Comparisons of mangrove seedling (solid-red; left y axis; Gaussian peak), salt marsh stem (dashed-blue; right y axis; logistic), mangrove pneumatophore (dotted-green; right y axis; exponential), and total structural (thick solid-black; right y axis; non-significant) density across the salt marsh-mangrove interface in Louisiana-Large Transects. Values are mean ± SE (N= 3). Transects were established at the edge of the canopy and positioned at 0 m (vertical dashed line) and sampled plots at set distances. See Table 1.1 for all statistics.

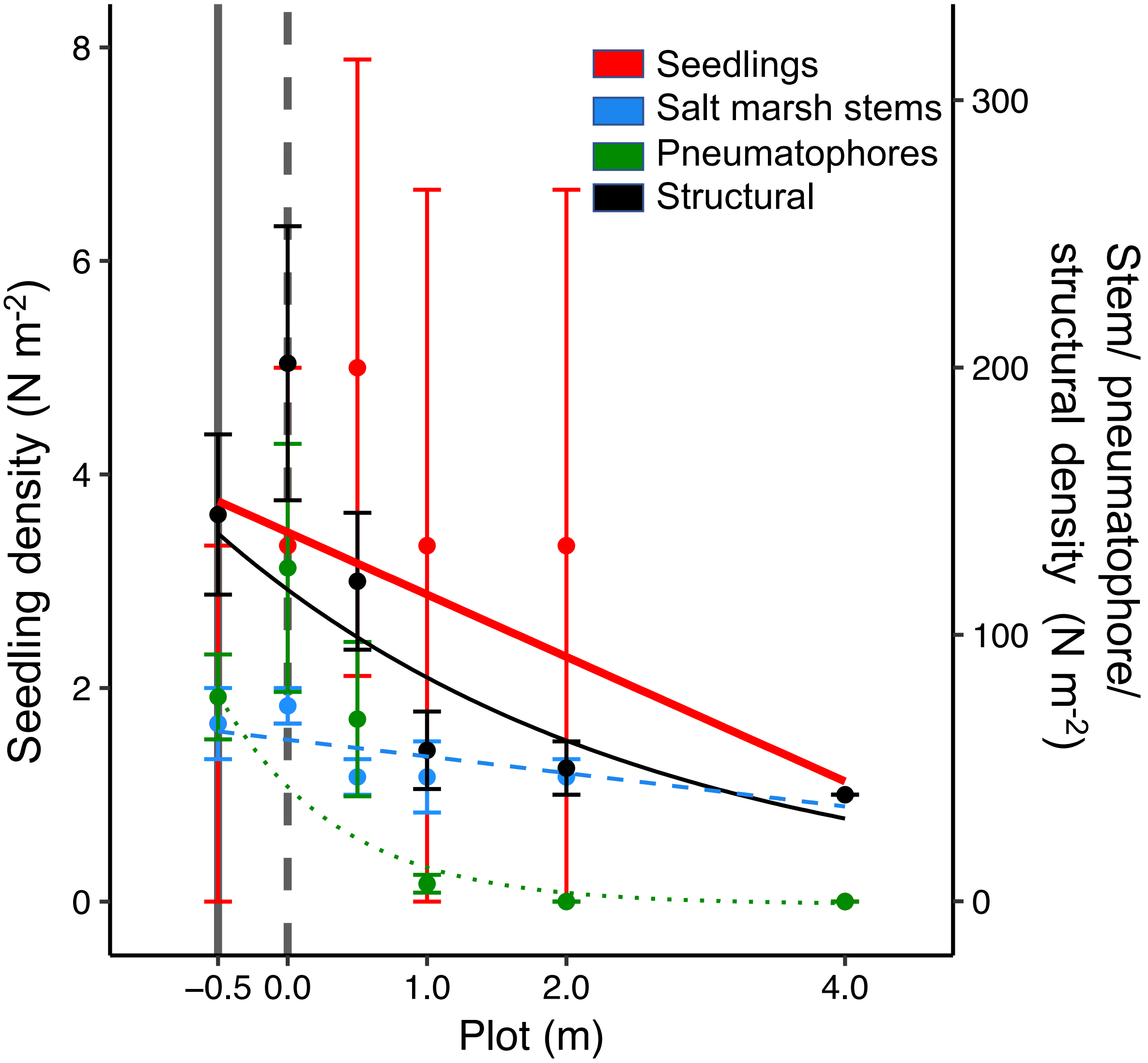

**Figure A6.** Comparisons of mangrove seedling (solid-red; left y axis; Gaussian peak), salt marsh stem (dashed-blue; right y axis; logistic), mangrove pneumatophore (dotted-green; right y axis; exponential), and total structural (thick solid-black; right y axis; non-significant) density across the salt marsh-mangrove interface in Louisiana-Small Transects. Values are mean ± SE (N= 3). Transects were established at the edge of the canopy and positioned at 0 m (vertical dashed line) and sampled plots at set distances. See Table 1.1 for all statistics.

**Table A2.** Comparison of soil and porewater properties used to evaluate environmental differences for Large and Small trees in Florida and Louisiana. Values are means (± SE, N=3). Significant differences ($p<0.05$) are denoted by different lower-case letters within each metric across all tree sizes and locations.

| | | Florida | | | | Louisiana | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Large | | Small | | Large | | Small | |
| Soil properties | SIC (%) | 4.0 | ± 0.1$^{a}$ | 3.9 | ± 0.1$^{a}$ | 3.1 | ± 0.1$^{b}$ | 3.1 | ± 0.1$^{b}$ |
| Porewater | Salinity (ppt) | 35.2 | ± 1.3$^{a}$ | 35.8 | ± 0.8$^{a}$ | 23.9 | ± 0.5$^{b}$ | 22.4 | ± 0.8$^{b}$ |
| | Conductivity (mS) | 46.3 | ± 1.5$^{a}$ | 47.1 | ± 0.9$^{a}$ | 32.2 | ± 0.7$^{b}$ | 31.1 | ± 1.0$^{b}$ |
| | pH | 6.3 | ± 0.03$^{a}$ | 6.4 | ± 0.04$^{a}$ | 5.5 | ± 0.10$^{b}$ | 5.7 | ± 0.10$^{b}$ |
| | Temperature (°C) | 26.3 | ± 0.15$^{b}$ | 25.5 | ± 0.07$^{c}$ | 27.5 | ± 0.10$^{a}$ | 27.5 | ± 0.07$^{a}$ |

# Appendix B

**Table B1.** Elevation and observed time flooded for 2015 and 2016 sampling campaigns by idealized time flooded contour. Values show means and standard errors. Letters denote statistically different values as derived from Tukey post-hoc analysis.

| | Idealized time flooded contour (%) | 2015 | | 2016 | |
|---|---|---|---|---|---|
| Elevation (NAVD88-Geoid12A) | 1 | 0.458 | ±0.004$^{A}$ | 0.4218 | ±0.009$^{B}$ |
| | 10 | 0.315 | ±0.011$^{C}$ | 0.2912 | ±0.007$^{C}$ |
| | 25 | 0.221 | ±0.002$^{D}$ | 0.1936 | ±0.005$^{D}$ |
| | 50 | 0.152 | ±0.008$^{E}$ | 0.1386 | ±0.003$^{E}$ |
| | 75 | 0.087 | ±0.019$^{F}$ | 0.0962 | ±0.003$^{F}$ |
| Observed time flooded (%) | 1 | 7 | | 8 | |
| | 10 | 13 | | 26 | |
| | 25 | 36 | | 44 | |
| | 50 | 49 | | 58 | |
| | 75 | 59 | | 71 | |

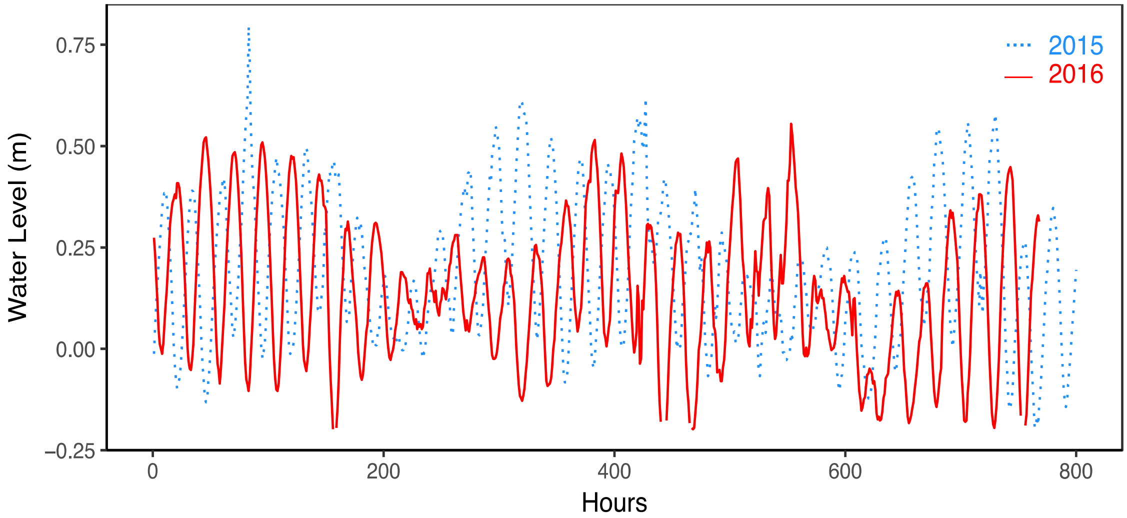

**Figure B1.** Water level fluctuations over the duration of the study (NAVD88-Geoid12A) for 2015 (blue, dashed line) and 2016 (solid, red line) sampling campaigns. Data derived from CRMS Database (CRMS-CPRA 2017).

**Table B2.** Number of days (mean ± SE) propagules remained buoyant by color painted or unpainted for 2015. Letters denoted significant differences within each year.

| Paint Color | 2015 | | 2016 | |
|---|---|---|---|---|
| Green | 30.6 | ±8.0$^{A}$ | N | / A |
| Orange | 30.6 | ±8.0$^{A}$ | N | / A |
| Pink | 43.0 | ±0.0$^{A}$ | N | / A |
| White* | 6.7 | ±2.4$^{B}$ | 22.6 | ±4.3$^{A}$ |
| Yellow | 43.0 | ±0.0$^{A}$ | N | /A |
| Unpainted | 43.0 | ±0.0$^{A}$ | 29.0 | ±0.4$^{A}$ |

*Secondary white color tested in 2016 against unpainted propagules

**Table B3.** Confirmed predation, removal, and estimated conservative total predation percentages for painted and unpainted propagules by elevation within sampling campaign.

| Year | Elevation contour | Propagule type | Confirmed predation (%) | Removal (%) | Conservative total predation (%) |
|---|---|---|---|---|---|
| 2015 | 1% | Natural | 20 | 0 | 20 |
| | | Painted | 40 | 0 | 40 |
| | 10% | Natural | 20 | 0 | 20 |
| | | Painted | 20 | 0 | 20 |
| | 25% | Natural | 0 | 20 | 4 |
| | | Painted | 0 | 40 | 8 |
| | 50% | Natural | 20 | 40 | 28 |
| | | Painted | 20 | 20 | 24 |
| | 75% | Natural | 0 | 80 | 16 |
| | | Painted | 0 | 80 | 16 |
| 2016 | 1% | Natural | 20 | 20 | 24 |
| | | Painted | 20 | 20 | 24 |
| | 10% | Natural | 20 | 20 | 24 |
| | | Painted | 20 | 20 | 24 |
| | 25% | Natural | 40 | 20 | 44 |
| | | Painted | 20 | 20 | 24 |
| | 50% | Natural | 20 | 80 | 36 |
| | | Painted | 0 | 80 | 16 |
| | 75% | Natural | 0 | 60 | 12 |
| | | Painted | 0 | 80 | 16 |

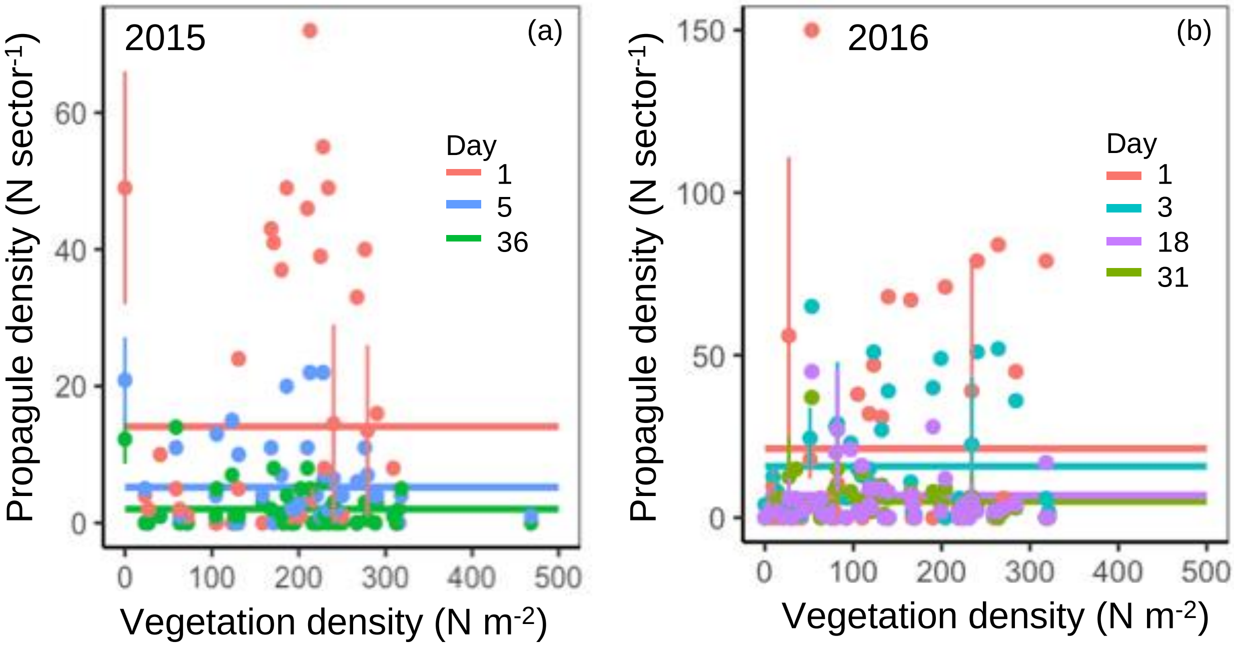

**Figure B2.** Propagule density in relation to vegetation density by sampling day in (a) 2015 and (b) 2016 field campaigns.

# Appendix C

Methods for Propagule Painting and Testing Buoyancy:

A laboratory buoyancy experiment using the 5 colors of paint (500 with five different colors of spray paint (Orange: FL- 9 “Caution Orange”, PlastiKote Premium Florescent, Valspar Corporation Minneapolis, Minnesota, USA; Yellow: “Fluorescent Yellow” #1942830, Green “Fluorescent Green” #1932830, Pink: “Fluorescent Pink” #1959830, Rust-Oleum Specialty Fluorescent; White (2015) “Flat White” #20009, ColorPlace Interior/Exterior Fast Dry Spraypaint, Walmart Stores Inc., Bentonville, Arkansas, USA; White (2016): “Gloss White” # 7592838, High Performance Enamel Spray, Rust-Oleum Corporation, Vernon Hills, Illinois, USA) and unpainted propagules was conducted to determine if the spray paint affected propagule buoyancy.(n=6). Propagules were independently assigned to a randomized block design. Propagules were placed in 150 mL of 24 ppt salt water (Instant Ocean Aquarium Sea Salt Mixture, Instant Ocean, Blacksburg, Virginia, USA). Water was changed every other week and observations were made every 2-3 days for 36 days. The white paint from the second sampling campaign was tested separately using the same methods.

# Appendix D

**Table D1.** Means (± SE) for soil, *Avicennia*, and *Spartina* metrics for Experimental Area I at low, medium, and high elevations at all sampling points.

| | | Soil | | | | Avicennia | | | | | | Spartina | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Month | Elevation | Bulk Density (g. cm$^{-3}$) | | SOM (%) | | Survival (%) | | Tree height (m) | | Biomass (g tree-$^{1}$) | | Cover (%) | | Canopy height (m) | | Biomass (g m-2) | |
| 0 | Low | 0.75 | ±0.08 | 6.2 | ±0.6 | | | | | | | | | | | | |
| | Medium | 0.82 | ±0.09 | 4.5 | ±0.6 | | | | | | | | | | | | |
| | High | 1.00 | ±0.07 | 2.2 | ±0.2 | | | | | | | | | | | | |
| 3 | Low | 0.81 | ±0.05 | 3.5 | ±0.4 | 56 | ±7 | 0.33 | ±0.09 | 42.0 | ±13.9 | 6 | ±1.4 | 0.40 | ±0.02 | | |
| | Medium | 0.78 | ±0.02 | 1.8 | ±0.2 | 40 | ±6 | 0.26 | ±0.06 | 26.5 | ±10.2 | 1 | ±0.5 | 0.16 | ±0.05 | | |
| | High | 0.76 | ±0.02 | 6.0 | ±0.6 | 33 | ±7 | 0.22 | ±0.08 | 18.1 | ±6.3 | 1 | ±0.2 | 0.20 | ±0.06 | | |
| 7 | Low | 0.80 | ±0.05 | 4.9 | ±0.5 | 57 | ±8 | 0.42 | ±0.11 | 220.7 | ±68.9 | 38 | ±3.9 | 0.95 | ±0.04 | | |
| | Medium | 0.87 | ±0.03 | 3.4 | ±0.4 | 38 | ±6 | 0.24 | ±0.07 | 69.6 | ±24.8 | 4 | ±2.1 | 0.32 | ±0.14 | | |
| | High | 0.87 | ±0.03 | 1.7 | ±0.2 | 23 | ±7 | 0.20 | ±0.09 | 32.8 | ±14.3 | 3 | ±1.9 | 0.32 | ±0.1 | | |
| 12 | Low | 0.66 | ±0.05 | 5.4 | ±0.5 | 54 | ±8 | 0.43 | ±0.11 | 269.0 | ±84.0 | 69 | ±4.6 | 0.80 | ±0.02 | | |
| | Medium | 0.90 | ±0.05 | 3.7 | ±0.5 | 38 | ±6 | 0.25 | ±0.07 | 111.4 | ±39 | 4 | ±2 | 0.25 | ±0.1 | | |
| | High | 1.04 | ±0.02 | 1.5 | ±0.2 | 24 | ±7 | 0.19 | ±0.08 | 42.5 | ±18.6 | 7 | ±3.9 | 0.29 | ±0.09 | | |
| 18 | Low | 0.87 | ±0.06 | 3.4 | ±0.5 | 42 | ±8 | 1.11 | ±0.25 | 487.9 | ±170.9 | 97 | ±1.3 | 1.37 | ±0.04 | 916 | ±212 |
| | Medium | 0.89 | ±0.08 | 3.7 | ±0.9 | 33 | ±7 | 0.73 | ±0.17 | 545.5 | ±181.1 | 16 | ±7.8 | 0.75 | ±0.18 | 550 | ±208 |
| | High | 1.10 | ±0.09 | 3.7 | ±0.5 | 22 | ±6 | 0.46 | ±0.18 | 288.7 | ±131.2 | 16 | ±5.7 | 0.67 | ±0.16 | 111 | ±67 |

**Table D2.** Means (± SE) for soil, *Avicennia*, and *Spartina* metrics for Experimental Area II in all treatments at all sampling points.

| | | Soil | | *Avicennia* | *Spartina* |
|---|---|---|---|---|---|
| Month | Treatment | Bulk density (g cm-3) | SOM (%) | Cover % | Cover % |
| 0 | *Avicennia* | 0.65 ±0.09 | 5.1 ±0.8 | | |
| | Bare | 0.42 ±0.1 | 6.9 ±1.0 | | |
| | *Spartina* | 0.6 ±0.04 | 5 ±0.5 | | |
| | *Spartina/Avicennia* | 0.49 ±0.04 | 5 ±0.6 | | |
| 3 | *Avicennia* | 0.87 ±0.08 | 4.2 ±0.7 | 1.8 ±0.4 | 0.7 ±0.1 |
| | Bare | 0.89 ±0.08 | 4.6 ±0.8 | 0.1 ±0.1 | 0.6 ±0.2 |
| | *Spartina* | 0.7 ±0.06 | 6 ±1.2 | 0.0 ±0 | 3.6 ±0.6 |
| | *Spartina/Avicennia* | 0.81 ±0.05 | 4.7 ±0.4 | 1.2 ±0.2 | 2.8 ±1.3 |
| 7 | *Avicennia* | 0.82 ±0.11 | 5.1 ±1.0 | 3.6 ±0.9 | 5.8 ±3.6 |
| | Bare | 0.74 ±0.08 | 5.7 ±0.7 | 0.2 ±0.2 | 8.2 ±4 |
| | *Spartina* | 0.85 ±0.10 | 4.4 ±1.0 | 0.0 ±0 | 25.0 ±2.2 |
| | *Spartina/Avicennia* | 0.7 ±0.06 | 6 ±0.6 | 2.6 ±0.4 | 17.4 ±6 |
| 12 | *Avicennia* | 0.72 ±0.06 | 5.7 ±0.8 | 3.6 ±0.9 | 27.8 ±12.3 |
| | Bare | 0.77 ±0.09 | 5 ±0.9 | 0.2 ±0.2 | 27.6 ±11.6 |
| | *Spartina* | 0.72 ±0.06 | 6.3 ±1.0 | 0.0 ±0 | 66.0 ±7 |
| | *Spartina/Avicennia* | 0.85 ±0.05 | 4.6 ±0.8 | 2.6 ±0.4 | 44.0 ±11.4 |
| 18 | *Avicennia* | 0.78 ±0.03 | 4.8 ±0.4 | 6.6 ±2.6 | 64.0 ±12.9 |
| | Bare | 0.79 ±0.07 | 4 ±0.6 | 0.4 ±0.4 | 49.0 ±17.2 |
| | *Spartina* | 0.66 ±0.04 | 4.9 ±0.6 | 0.0 ±0 | 88.0 ±5.8 |
| | *Spartina/Avicennia* | 0.63 ±0.06 | 5.6 ±0.8 | 2.4 ±0.8 | 63.0 ±13.1 |

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Major: Environmental and Evolutionary Biology
Title of Dissertation: Dispersal, Establishment, and Influence of Black Mangrove (*Avicennia germinans)* at the Salt Marsh-Mangrove Ecotone
Dissertation Director: Dr. Mark Hester
Pages in Dissertation: 122; Words in Abstract: 185

## Abstract

Interactions between species are dynamic and are likely to shift with changes in species ranges due to climate change. With the expansion of new species into incumbent ecosystems a variety of abiotic and biotic factors shape the rate, pattern, and method of invasion. This dissertation utilizes one such boundary of transition, the salt marsh-mangrove ecotone, located in the northern Gulf of Mexico. This dynamic coastal wetland has recently seen the expansion of sub-tropical mangrove species into a previously salt marsh dominated system. This collection of works provides pointed case studies seeking to understand local and patch scale dispersal dynamics, expansion, recruitment, growth, and survival rates along an elevational gradient, and understanding interactions both above- and belowground between mature mangroves and the surround salt marsh. We find that dispersal is overwhelmingly dominated by propagule export, that black mangrove and smooth cordgrass differ in their ability to provide structural provisioning in the short term after restoration, and that mature mangroves have much greater belowground extent than aboveground. By better understanding species-specific interactions at the salt marsh-mangrove ecotone, a greater understanding of future expansion rates can be gained.

# Biographical Sketch

Reared in the forests, swamps, and coastlines of New England and the Baltic coast of Finland, the son of Maarit and John Yando, Erik's affinity for exploration of the natural world has led him to many places, but he feels most at home knee deep in mud on a brilliant sunny day. Erik's childhood and curiosity were shaped by his siblings' (Karl and Hanna) inquisitive nature into a wide variety of topics. He attended Connecticut College, majoring in biological sciences and botany, and attained a M.S. degree in biology at the University of Louisiana at Lafayette. When not found working in the lab, writing, or preparing for his next field excursion, Erik enjoys spending time with his dog, Chappie, and wife, Taylor, walking through Acadiana's swamps, fields, and forests. He is a lover of water-based activities, cool temperatures, and a perfectly balanced pale ale.