

**MANGROVE MORPHOLOGICAL CHANGES ALONG ENVIRONMENTAL
GRADIENTS: IMPLICATIONS FOR COMPETITIVE ABILITY IN A
CHANGING CLIMATE**

by

Hilary Standish

A Thesis Submitted to the Faculty of

Charles E. Schmidt College of Science

In Partial Fulfillment of the Requirements for the Degree of

Masters of Science

Florida Atlantic University

Boca Raton, FL

December 2016

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by

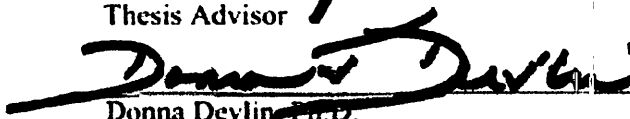
Hilary Standish

This thesis was prepared under the direction of the candidate's thesis advisor, Dr. Edward Proffitt, Department of Biology, and has been approved by the members of her supervisory committee. It was submitted to the faculty of the Charles E. Schmidt College of Science and was accepted in partial fulfillment of the requirements for the degree of Master of Science.

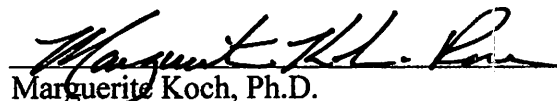
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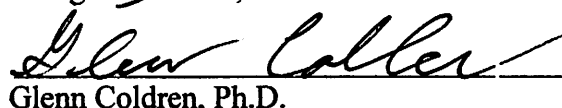
Edward Proffitt, Ph.D.
Thesis Advisor



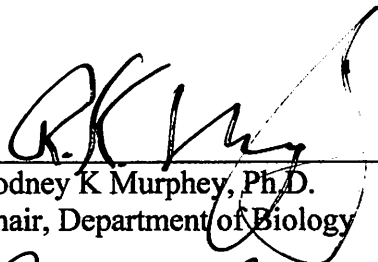
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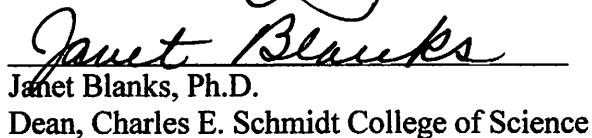
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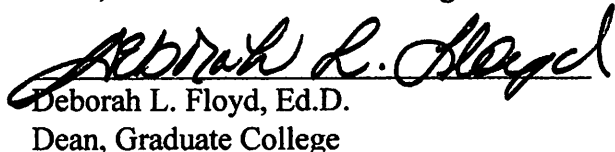
Glenn Coldren, Ph.D.



Rodney K. Murphey, Ph.D.
Chair, Department of Biology



Janet Blanks, Ph.D.
Dean, Charles E. Schmidt College of Science



Deborah L. Floyd, Ed.D.
Dean, Graduate College

December 1, 2016
Date

ACKNOWLEDGEMENTS

I would like to thank Florida Atlantic University, Harbor Branch Oceanographic Institute, and Dr. Proffitt for giving me the opportunity to conduct this research. I would also like to thank the other committee members for their help, advice, and guidance. Finally, thanks to my family for their unending support and encouragement through this process.

ABSTRACT

Author: Hilary Standish

Title: Mangrove Morphological Change Across an Environmental Gradients: Implications for Competitive Ability in a Changing Climate

Institution: Florida Atlantic University

Thesis Advisor: Dr. Edward Proffitt

Degree: Master of Science

Year: 2016

In Florida, mangroves have responded to climate change by slowly migrating northward into traditional salt marsh habitat. However, little is understood about the relationships among mangrove growth form plasticity and environmental conditions. In addition, the effects of the mangrove northward expansion on pre-existing salt marsh communities are unknown, especially any influences of differences in tree morphology. The size, canopy structure, and root structure of the three mangrove species *Rhizophora mangle*, *Avicennia germinans*, and *Laguncularia racemosa* were measured at six sites along the east coast of Florida. Structural equation modeling was used to evaluate the multivariate relationships between environmental and biotic variables. Mangrove growth form varied widely with environmental variables. The results of this study suggest that *R. mangle* expansion into salt marsh may rely on interactions with salt marsh and shading as well as on climatic variables, which has implications for future mangrove expansion northward in Florida.

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INTRODUCTION

Climate Change and Coastal Ecosystems

Human-driven increases in greenhouse gas emissions since 1850 have caused atmospheric concentrations of carbon dioxide, methane gas, and nitrous oxide to reach levels unprecedented for 800,000 years (IPCC, 2014). This in turn has caused changes in climate that pose a major threat to all of Earth's ecosystems. The Intergovernmental Panel on Climate Change has stated that the thirty years between 1983 and 2012 were likely the warmest thirty years in the last fourteen hundred years (IPCC, 2014). Land and surface mean annual temperatures have increased as much as 0.85C since 1880, and global mean sea level has risen 0.19 meters (IPCC, 2014). These changes are expected to continue through the twenty-first century, with average global surface temperatures projected to increase between 1.5 and 2 C by 2100. Sea level rise will also continue, and seventy percent of the world's coastlines are expected to be at risk from rising sea levels (IPCC, 2014).

These changes are expected to drastically impact both human and natural systems. Many natural systems are already showing evidence of climate-change-driven impacts. Species have shifted geographic ranges, migration patterns, seasonal activities, and even species interactions in response to changes in air or water temperature (Walther, et al., 2002). For example, a study on 99 species of birds, butterflies, and alpine herbs showed that species range limits have shifted 6.1 km per decade northward, or one meter per decade

upward (Parmesan & Yohe, 2003). A study of 542 plant and 19 animal species in 21 European countries demonstrated that 78% of all leafing, flowering, and fruiting events have advanced in response to changes in climate (Menzel, et al., 2006). A separate study has shown that bird populations are shifting their migration patterns to match this change in phenology, and that those populations that cannot adapt their migration patterns are declining (Moller, Rubolini, & Lehikoinen, 2008). Changing weather patterns in Costa Rican cloud forests as a result of increasing sea surface temperatures has been tied to a shift in montane bird, lizard, and anuran population demographics and geographic ranges (Pounds, Fogden, & Campbell, 1999). Extinction risk is also thought to be greatly increased with climate change, with some mid-range climate-warming scenarios for 2050 corresponding with 15-37% of species becoming committed to extinction (Thomas, et al., 2004).

Coastal ecosystems are at risk from both shifting atmospheric conditions and sea level rise, making them doubly threatened by climate change (IPCC, 2014). Rising sea levels will increase coastal flooding and change the salinity of rivers, estuaries and bays. These changes may be compounded by an increase in the frequency of severe storms (Scavia, et al., 2002). In some places, evidence of freshwater swamps converting to tidal marsh has been available as early as 1990 (Hackney & Yelverton, 1990). While sea level rise poses the largest threat, changing atmospheric conditions also threaten coastal ecosystems. As temperatures rise, more temperate coastal habitat may be replaced by tropical and subtropical habitat, and changes in precipitation regimes and increasing atmospheric carbon dioxide may also change habitat structure (Scavia, et al., 2002; Matensanz, Gianoli, & Valladares, 2010).

Mangrove forests are thought to be especially vulnerable (Duke, et al., 2007; Alongi D. M., 2008). Mangroves are salt-tolerant trees or shrubs found in intertidal conditions globally between approximately 30°N and 30°S. They are tolerant of a range of conditions, including high salinity, high temperatures, extreme flooding, high sedimentation, and anaerobic soils (Lugo & Snedaker, 1974; Tomlinson, 1984). Mangrove forests provide many valuable ecosystem services, such as assimilating excess atmospheric carbon, protecting coastlines from hurricanes, increasing vertical land development, and providing nursery habitat for fish (Alongi D. M., 2002; Nagelkerkin, et al., 2008; Lee, et al., 2014). In addition, they provide food, timber, and medicine for many cultures around the world (Alongi D. M., 2008). However, global mangrove forest cover has declined by 35% and continues to decline by 1-2% a year as a result of deforestation and conversion to aquaculture (UNEP-WCMC, 2006; Alongi D. M., 2008).

In addition to deforestation, changing climatic conditions and projected sea level rise may also threaten mangrove long-term survival (Duke, et al., 2007; Alongi D. M., 2008). Like most coastal ecosystems, the primary threat to mangroves is sea level rise (Gilman, Ellison, Duke, & Field, 2008; Krauss, et al., 2013), and the observed and predicted impacts of rising sea levels on mangroves have been well-studied. Mangroves are believed to be sediment-building organisms (Lugo & Snedaker, 1974), and therefore may act as a barrier against rising sea levels and increased storm intensity (Mazda, Magi, Ikeda, Kurokawa, & Asano, 2006; Alongi D. M., 2008).

In order for mangroves to survive in a changing climate, sediment accretion needs to keep pace with sea level rise, otherwise mangroves will retreat inland or face lethal periods of inundation (Krauss, et al., 2013). Studies indicate that mangroves can gain

elevation relatively quickly, at a rate of up to 4.1 mm year⁻¹ (McKee, Cahoon, & Feller, 2007). However, a climate-change-driven increase in hurricane intensity and frequency (Scavia, et al., 2002) may impact mangroves' ability to accumulate peat and thus increase elevation (Cahoon, et al., 2003). Some studies have indicated that mangrove mortality can lead to peat collapse and subsequent elevation loss (Sherman, Fahey, & Battles, 2000). Studies in the Caribbean have modeled a 37 mm year⁻¹ peat collapse during the first two years after a hurricane. These models also indicated that this loss may continue for at least eight more years at a reduced rate (Cahoon, et al., 2003).

Although much has been done on the impacts of sea level rise on mangrove habitats, less is understood about how increases in air and sea temperatures may affect mangrove geographic ranges, and how those changes may affect biodiversity and production. In Florida, rising atmospheric temperatures are resulting in a decline in the number of severe frost events each year (Cavanaugh, et al., 2013; Saintilan, Wilson, Rogers, Rajkaran, & Krauss, 2014). The most frost-tolerant of Florida's mangroves, the black mangrove *Avicennia germinans*, is rapidly expanding northward (Cavanaugh, et al., 2013). The number of days below -4 degrees Celsius is thought to limit *A. germinans* survival (Saintilan, Wilson, Rogers, Rajkaran, & Krauss, 2014).

This limitation may be because mangroves are particularly vulnerable to frost-induced embolisms that result in limb loss or death (Stuart, Choat, Martin, Holbrook, & Ball, 2007). These embolisms form when air bubbles in the sap freeze, then expand when the sap melts under tension and prevent water from traveling through the tree (Stuart, Choat, Martin, Holbrook, & Ball, 2007; Raven, Johnson, Losos, Mason, & Singer, 2008). However, the last bitter freeze in Florida occurred in 1989, and cold sufficient to kill

mangroves has not occurred at all in recent years (Cavanaugh, et al., 2013; Saintilan, Wilson, Rogers, Rajkaran, & Krauss, 2014). Because frost events seem to be declining, mangroves have begun to expand northward. Between 1984 and 2011, the amount of mangrove cover has doubled along the Florida coast (Cavanaugh, et al., 2013) and future range expansion is predicted to be between 2.2 to 3.2 km per year over the next fifty years (Cavanaugh, et al., 2015).

Range Expansion and Mangrove Growth Form

As mangroves expand northward, they are moving into the salt marsh habitat common along the Eastern and Gulf coasts of the United States. These salt marsh communities also have high ecological and economic importance, providing breeding habitat for many species of birds and fish (Shriver, Hodgman, Gibbs, & Vickery, 2004; MacKenzie & Dionne, 2008; Raposa, McKinney, & Beaudette, 2009). Fast growth and a high intake of nutrients also make salt marshes highly productive ecosystems (Marinucci, 1982). Salt marshes may also protect coastlines during storms (King & Lester, 1995).

The consequences of mangrove intrusion into these habitats are poorly understood. Of the three species of mangrove in Florida, *Avicennia germinans* is most resistant to frost (Saintilan, Wilson, Rogers, Rajkaran, & Krauss, 2014). Both *Rhizophora mangle* and *Laguncularia racemosa* are more prone to frost-induced embolisms, thus restricting their ability to move northward (Sobrado, 2007; Stuart, Choat, Martin, Holbrook, & Ball, 2007). The interactions between mangroves and salt marsh plants are very complex. For example, a study done along the Texas coast suggested that mangrove-salt marsh interactions are affected by latitude, elevation, and mangrove life history stage (Guo, Zhang, Lan, & Pennings, 2013). At higher latitudes, the presence of salt marsh vegetation facilitated A.

germinans seedling growth while inhibiting it at lower latitudes. However, once the seedlings grow into juvenile trees, the mangroves begin to negatively affect the salt marsh (Guo, Zhang, Lan, & Pennings, 2013).

Factors that are likely important, but poorly understood in mangrove-marsh interactions are the growth form and allometry of the mangrove trees themselves. The size and shape of the tree may impact its competitive ability (Taylor, Jinyan, & ShiQuiang, 2004; Vizoso-Arribe, Diaz-Moroto, Vila-Lameiro, & Diaz-Maroto, 2014). Presumably, a tree with a larger, more spreading canopy will produce more shade and thus preclude salt marsh growth more effectively than a tree with a narrower canopy (Vizoso-Arribe, Diaz-Moroto, Vila-Lameiro, & Diaz-Maroto, 2014). Because salt marsh species are thought to be shade-intolerant (Clarke & Hannon, 1971; Medeiros, White, & Howes, 2013), mangrove trees with large, dense canopies may greatly impact their ability to survive.

Belowground competition may be just as important, though it is difficult to directly assess. Both *R. mangle* and *A. germinans* can vary greatly in the size and extent of their root structures (Snedaker, Jimenez, & Brown, 1981; Mendez-Alonzo, Lopez-Portillo, & Riviera-Monroy, 2008). Mangrove root structures may be especially important when studying resource allocation, since mangroves need to be bottom-heavy in order to stay upright in soft, muddy soil (Mendez-Alonzo, Lopez-Portillo, & Riviera-Monroy, 2008). This may skew resource allocation in favor of root structures (Komiyama, Ong, & Pongpan, 2008). Prop roots have been shown to represent up to 37% of the aboveground biomass in *Rhizophora* in Brazil (Medeiros & Sampaio, 2008). Although no work has been done on belowground competition between mangroves and marsh plants, it is likely that a tree with expansive roots would be a better competitor with nearby salt marsh than one

with a smaller network of roots. Root structure may also be important for the vertical accretion necessary for mangroves to keep up with sea level rise (Adame, et al., 2014).

Environmental Drivers of Mangrove Growth Patterns

Trees can vary in growth form for a number of reasons, some genetic and some environmental. The ability of a plant to change its growth form or rate in response to environmental conditions is known as phenotypic plasticity (Clausen, Keck, & Hiesey, 1940; Stearns, 1989). Plasticity can play a large role a plant's ability to survive changes in their environment, and as such has received a lot of recent attention from biologists interested in climate change (West-Eberhard, 2003; Matensanz, Gianoli, & Valladares, 2010). Morphological and physiological plastic responses have been documented in plants in response to many components of environmental change, including elevated carbon dioxide, changes in water availability, and changes in temperature, among others (Gianoli & Gonzales-Teuber, 2005; Niinemets & Valladares, 2006; Bloor, Barthes, & Leadly, 2008). These plastic responses take place anywhere from the leaf level to the whole-plant level, including changes in biomass partitioning and growth pattern (Matensanz, Gianoli, & Valladares, 2010).

Phenotypic plasticity has been very poorly studied in mangrove species, but some studies have been conducted that show that mangroves do change growth form in response to environmental factors. For example, work in the Florida Keys has determined that dwarf-form *R. mangle* will accelerate growth when nutrient availability increases (Feller, 1995). When growing in soils poor in nutrients, red mangroves will allocate more resources to their roots, producing a short, stunted tree. However, when provided with excess

phosphorus or nitrogen, the aboveground biomass of *R. mangle* grew vigorously over a two-year period (Feller, 1995).

The limiting nutrient in mangrove forests appears to vary with other environmental effects. Phosphorus has been found to be more limiting further inland, while in the fringe zone along the shoreline nitrogen is the limiting nutrient (Feller, McKee, Wingham, & O'Neill, 2002). However, a subsequent study demonstrated consistent nitrogen limitation across similar zonation patterns, indicating that the nutrient dynamics of mangrove ecosystems are very complex (Feller, Wingham, McKee, & Lovelock, 2003). Further studies on mangrove growth form and nutrient availability have corroborated the idea that red mangroves adjust growth rate and resource allocation patterns according to nutrient conditions (Lovelock, Ball, Martin, & Feller, 2009).

While nutrient availability is important to mangrove growth rate and form, it is not the only environmental factor that can affect mangroves. Light availability is another factor that may contribute to differences in mangrove growth forms. A tree growing in a narrow forest gap may grow tall and thin as it struggles to reach the sunlight, while one in a more open environment may be shorter overall but put out more branches (Harja, Vincent, Mulia, & van Noordwijk, 2012). This trend has been demonstrated in other tree species (Delagrange, Messier, Lechowicz, & Dizengremel, 2004; Harja, Vincent, Mulia, & van Noordwijk, 2012). Because mangroves are very light-dependent (Dov Por & Dor, 1984) they may respond very strongly to the availability of light.

As halophytes, mangroves are affected by the salinity of the water and soil (Tomlinson, 1984). At high salinities, it is harder for mangroves to control their salt balance, and the salt must be excluded, secreted, or diluted (Raven, Johnson, Losos, Mason,

& Singer, 2008). In addition, increases in salinity makes water transport through the plant less efficient (Ball, Cochrane, & Rawson, 1997; Sobrado, 2007). Some species can tolerate higher salinity better than others (Adame, et al., 2014; Naskar & Palit, 2015). In Florida, the most salt-tolerant species is thought to be the black mangrove *A. germinans*, which has been recorded growing at salinities greater than 90 ppt (Macnae, 1968; Odum, McIvor, & Smith, 1982). The white mangrove *L. racemosa* is the next most tolerant, while the red mangrove *R. mangle* may be limited at salinities above 60-65 ppt (Odum, McIvor, & Smith, 1982). Salt tolerance has been observed to be linked to relative growth rate, with more salt-tolerant species having a lower relative growth rate (Ball, Cochrane, & Rawson, 1997). Individual mangrove trees may also have a lower growth rate when in hypersaline conditions (Ball, 1988).

Research of the effects of salinity on *Spartina alterniflora* indicates that shoot number, total biomass, and leaf area all decrease at higher salinities (Ma, Chai, & Shi, 2011; Medeiros, White, & Howes, 2013). The white mangrove *L. racemosa* produces smaller but thicker leaves with increasing salinity (Sobrado, 2007). Salinity has also been found to affect the growth and size of *A. germinans*. Increasing salinities correspond with an increase in leaf mortality and a decrease in the net accumulation of leaves (Suarez & Medina, 2005; Neveu, 2013). In addition, both high and low salinity was found to negatively affect branch length in mangroves (Neveu, 2013). Salinity may also influence the belowground growth of roots, but studies conflict on whether root growth is positively or negatively correlated with salinity (Adame, et al., 2014). High salinity can also inhibit the survival and growth of *A. germinans* seedlings (Dangremond, Feller, & Sousa, 2015).

One of the most important—and most variable—environmental factors within mangrove forests are tidal fluctuations. Surface elevation within mangroves determines the frequency and duration of tidal events (Medeiros, White, & Howes, 2013). Elevation also influences drainage patterns and therefore directly contributes to other environmental parameters, such as soil salinity and oxygen availability (Jimenez & Sauter, 1991). These play an important part in mangrove establishment, survival, and growth, since waterlogged soils are lower in oxygen than dry soils, and can often become completely anoxic (Hogarth, 1999).

Mangroves have adapted to these conditions in many ways, the most obvious of which is the development of aerial root systems. While *Rhizophora* species tend to have large, arching aerial roots that can extend meters above the ground, species of *Avicennia* have systems of shallow, underground roots that radiate outward for many meters and support pneumatophores that emerge from the surface (Hogarth, 1999; Naskar & Palit, 2015). While the architecture of these root structures varies by species, it has also been shown to vary according to environmental conditions. In the northern Red Sea, individuals of *Avicennia marina* that are regularly inundated by the tide have abundant pneumatophores, while those higher up the coast in dryer sand have relatively few (Hogarth, 1999). In addition, *L. racemosa* can produce small pneumatophores or prop roots, and even though the exact reason for this is unclear, it most likely has to do with soil salinity or flooding (Odum, McIvor, & Smith, 1982).

Tidal characteristics are also important for mangrove overall growth and survival. They play a role in determining the survival of established mangroves, and to some degree determining physical characteristics. A study on Caribbean mangroves demonstrated that

in a flooded stand, *Rhizophora racemosa* are taller and slenderer, while *Avicennia bicolor* in the same stand are thicker and shorter. However, in a drier conditions, *A. bicolor* had better growth and survival at larger sizes (Jimenez & Sauter, 1991). This study indicates that both of these species are affected by the tidal regime, though the magnitude and direction of the effect are species-specific. Duration of immersion has been shown to affect physical characteristics of other salt marsh plants. *Spartina anglica* grown under different flooding regimes changed biomass allocation patterns depending on the length of immersion (Li, et al., 2011) and *Tecticornia pergranulata* ceases all shoot growth when submerged in order to conserve carbohydrates (Colmer, Vos, & Pederson, 2009).

Latitude may also play an important role, as latitude has a direct influence on both temperature and the length of the growing season. Many plant species are affected by latitude, becoming shorter, slenderer, or both at higher latitudes (Li, et al., 2011; Lines, Zavala, Purves, & Coomes, 2012; Osland, Day, Larriviere, & From, 2014). An increase in temperature can greatly affect a plant's aboveground vegetative growth (Kirwan, Guntenspergen, & Morris, 2009; DeFrenne, et al., 2011), while colder temperatures can kill branches or whole trees with frost (Stuart, Choat, Martin, Holbrook, & Ball, 2007).

A study on the black mangrove *A. germinans* on the Gulf Coast of Mexico demonstrated that those mangroves became shorter and skinnier with latitude, with the tallest trees found further south. Additionally, as height and diameter decreased, leaf mass per area increased, demonstrating that, at higher latitudes, black mangroves may allocate more resources to leaf production and shoot growth (Mendez-Alonzo, Lopez-Portillo, & Riviera-Monroy, 2008). *Avicennia marina* demonstrates a similar negative correlation with latitude in the Red Sea (Price, et al., 1987). In addition, more poleward mangroves

are susceptible to frost events that may kill back branches, which can lead to higher lateral branch production (Osland, Day, Larriviere, & From, 2014). This may result in trees that are shorter and shrubbier in more northern latitudes.

Aims of the Current Study

Very little is understood about the interaction between salt marsh and mangrove species, especially in the mangrove expansion zone (Guo, Zhang, Lan, & Pennings, 2013; Osland, Day, Larriviere, & From, 2014). Furthermore, little has been done on how the growth form of mangroves affects the ecology of the local patch, including competitive interactions with salt marsh and other mangroves. The purpose of this study is to establish patterns in how environmental conditions affect mangrove growth form and subsequent marsh interactions. Elevation and latitude are of special interest, as these are factors that will be greatly affected by climate change and have already produced changes in mangrove distribution along the Florida coast (Cavanaugh, et al., 2013; Osland, Day, Larriviere, & From, 2014). The relationship between mangrove growth form and marsh plant interactions will also be investigated, as well as the intraspecific competitive effect of mangrove growth form on mangrove seedlings. As such, there are three main questions this study will attempt to address:

- 1) How does mangrove growth form change with environmental conditions that vary over latitude?
- 2) How does this response vary between mangrove species?
- 3) How does competition between salt marsh and mangroves affect the growth and survival of both?

The nature of environment-plant interactions and plant-plant interactions are very complex, with multiple factors contributing to multiple potential responses. I present several multivariate alternative hypotheses, to be tested using partial least squares path modeling.

MATERIALS AND METHODS

Study Sites

Surveys were conducted at six field sites along the eastern coast of Florida, United States. Site locations ranged from Coral Gables, FL in the south (25.68N, 80.26W) to St. Augustine, FL in the north (29.90N, 81.31W), a distance of approximately 510 kilometers (see Figure 1). Four of these sites are within the Indian River Lagoon, which represents a transitional zone between the southern mangroves and northern salt marsh. The northernmost site is near the current latitudinal limit of mangrove species on the East Coast of Florida.

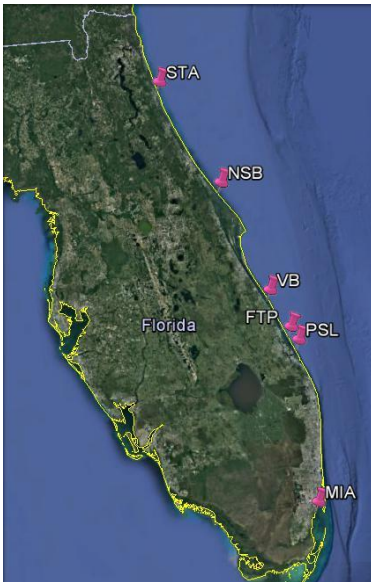


Figure 1: Locations of the six sites along the east coast of Florida, USA. Each site is abbreviated with a 3-letter code: Miami=MIA; St. Lucie=PSL; Fort Pierce=FTP; Vero Beach=VB; New Smyrna Beach=NSB; St. Augustine=STA.

Florida mangrove communities are comprised of *Rhizophora mangle*, *Laguncularia racemosa*, and *Avicennia germinans*, while Florida salt marsh contains a number of species, including *Spartina alterniflora*, *Spartina patens*, *Batis maritima*, *Sarcocornia ambigua* (formerly *Salicornia virginica*), *Sesuvium portulacastrum* and *Distichlis spicata*, among others.

Mangrove and Salt Marsh Surveys

Surveys were conducted at each site to measure mangrove morphological characteristics, such as height, diameter at 137cm (diameter at breast height, or DBH), and canopy diameter and volume. For *R. mangle*, morphology of the above-ground prop roots was also characterized. Nine trees were selected for measurement at each site and their coordinates recorded with a handheld GPS. Trees were selected in a stratified random process. First, areas of mangrove forest were identified that corresponded to one of three zones based on light availability. “Open Canopy” zones were defined as areas of high sun penetration without a closed mangrove canopy that contained both salt marsh and mangroves. “Closed Canopy” zones were defined as areas of mangrove within a fully closed canopy. “Partial Canopy” zones were in between the two, generally along the edges of an open area. Mangroves in this zone generally had part of their canopy extending into the gap and part within the forest canopy. Once a zone was identified, individual trees were selected at random. An attempt was made to select one tree of each species in each habitat type, though at some sites this was made impossible due to the complete absence of one or more mangrove species or the scarcity of certain habitat types.

The height of each tree was measured visually using the trigonometric equation

$$h = \tan A \times d + e$$

A_1 represents the measurement angle between the eye and the top of the tree, while A_2 represents the measurement angle between the eye and the base of the tree. All angles were measured using the mobile app iHandy Carpenter for an iPhone 6 (iHandySoft, Inc, 2013).

DBH was measured via calipers. Measurements were taken twice on each stem at perpendicular angles, then averaged for the DBH measurement. For trees with multiple stems, DBH measurements were taken for each stem, and both the average and the maximum DBH of the tree were determined from those measurements. Crown area and volume were calculated from two perpendicular canopy diameter measurements. Crown area was determined using the formula for the area of an ellipse

$$A = \pi \left(\frac{a}{2} * \frac{b}{2} \right)$$

where a and b represent the canopy diameter measurements. In order to gain a better understanding of mangrove morphology, the height of the tree was accounted for by calculating the “relative” maximum crown diameter, defined as the maximum diameter divided by the height. This metric allows an understanding of the ratio between height and crown diameter, which may display different patterns than maximum diameter alone.

Crown length was measured by subtracting the height of the lowest foliage from the total height of the tree, and overall crown volume calculated by multiplying crown length by crown area (Osland, Day, Larriviere, & From, 2014). Lowest foliage was selected over lowest branching because mangrove branches can grow very long before producing any leaves. Therefore, using the lowest branch might give an inaccurate representation of foliage height. Similar to relative crown diameter, relative crown length was calculated by dividing crown length by tree height to obtain the proportion of the total height occupied by the crown.

The area and volume of *R. mangle* prop roots were also calculated from diameter and height measurements. The area of prop root spread around the trunk was measured with two perpendicular measurements of the diameter of roots along the ground. The height of the highest prop roots was also measured. Prop root area was determined using the same formula as that for crown area. Prop root volume was determined by the formula for an elliptical cone

$$V = \frac{1}{3}\pi abh$$

where a and b represent the two diameter measurements and h the height of the roots on the trunk.

All measured mangroves were divided into four morphological categories encompassing height, DBH, crown diameter, and crown length. Mangroves were categorized as “Tall” if their heights were above the median measured height (447 cm) and “Short” if below that threshold. Similarly, “Girthy” mangroves were those with a measured maximum DBH above the median of 40 mm, while “Slender” mangroves fell below the median. Mangroves had a “Long” crown if the relative crown length exceeded the median of 0.75, and a “Wide” crown if the relative crown diameter exceeded the median of 0.65. Finally, mangroves were further categorized as either multi-or single-stemmed.

In addition to morphological measurements, community structure around the tree was also determined using 1 m² plots. Eight plots were placed at each tree, four under the canopy and four just outside the canopy. The under-canopy (“inner”) plots were placed with one corner at the base of the tree, at each of the four cardinal directions. The outside-canopy (“outer”) plots were placed just outside of the reach of the canopy, which was determined visually. Within each plot, the number of mangrove seedlings was determined.

Seedlings were divided into two categories based on the numbers of leaves and leaf scars: young of the year (YOY), and those older than one year, hereafter referred to as seedlings. Mangrove saplings and adults were also counted and recorded.

Salt marsh presence was measured by an estimated percent occurrence. Each 1m²-plot was divided into ten equal sections of 10 cm² each. The number of sections containing salt marsh were counted and taken as an estimate of percent salt marsh coverage within the plot. Salt marsh species richness was determined for each plot. Finally, canopy photos were taken with a fisheye lens from the center of each plot. Photos were taken with the Fisheye Pro app (Watson, 2015) for iPhone 6. The phone was held on a telescoping photography pole (“selfie stick”) at a height of 10cm off the ground. These photos were then analyzed in ImageJ (Shindelin, Rueden, & Hiner, 2015) to determine the amount of light penetrating the canopy. The iPhone was chosen over a traditional camera because of the ability to label photos in the field with plot, tree, and field site identifiers and backup photos to the cloud.

Environmental Variables

Latitude and elevation were determined by handheld GPS and were measured once per tree. Pore-water salinity was determined once per plot type (inner vs outer) by digging down to the pore water and using a handheld refractometer to calculate salinity. Due to the margin of error present in elevation data, the depth of the water table was used to corroborate it. Since water table depth is likely constant throughout a given site, changes in its depth are likely due to changes in surface elevation. Therefore, the difference between the site mean water table depth and the individual measurements of water depth was calculated as an approximation of change in elevation for each plot. These data were

regressed against measured elevation, and the regression equation was used to calculate a new estimate of elevation.

Tidal information, such as the height and time of the high tide, mean monthly tidal range, and monthly maximum high tide was collected from the online National Oceanic and Atmospheric Association (NOAA) Tides and Currents Database (NOAA, 2016). The yearly minimum, maximum, and average temperatures for 2015 as well as annual mean precipitation were obtained from NOAA's National Centers for Environmental Information Climate Data Online (NOAA, 2016) and U.S. Climate Data (U.S. Climate Data, 2016).

Multivariate Hypothesis Testing

Partial least-squares path modeling (PLS-PM) was chosen over traditional structural equation modeling techniques due to the relatively small number of samples in comparison to the number of variables, as well as issues of non-normality and a high degree of correlation among the predictor variables. As a technique with less rigid assumptions, PLS-PM is better able to handle non-normal and highly correlated data (Monecke & Leisch, 2012; Sanchez, 2013). In addition, PLS-PM has been found to work well for complex phenomena that are defined by a combination of several different variables (Carrascal, Galvan, & Gordo, 2009).

The PLS-PM analysis was done using the package `pls-pm` in R (Sanchez, Trinchera, & Russolillo, 2015). The path weighting scheme was used for the inner estimates, and the bootstrapping sample was set to 500. Latent variables were identified based on preliminary data analyses. Several models were tested first, each with its own set of *a priori* multivariate hypotheses.

Figure 2 shows the final hypothesized model between the latent and measured variables. The model is comprised of both reflective and formative latent constructs, another advantage of PLS-PM over traditional covariance methods (Sanchez, 2013).

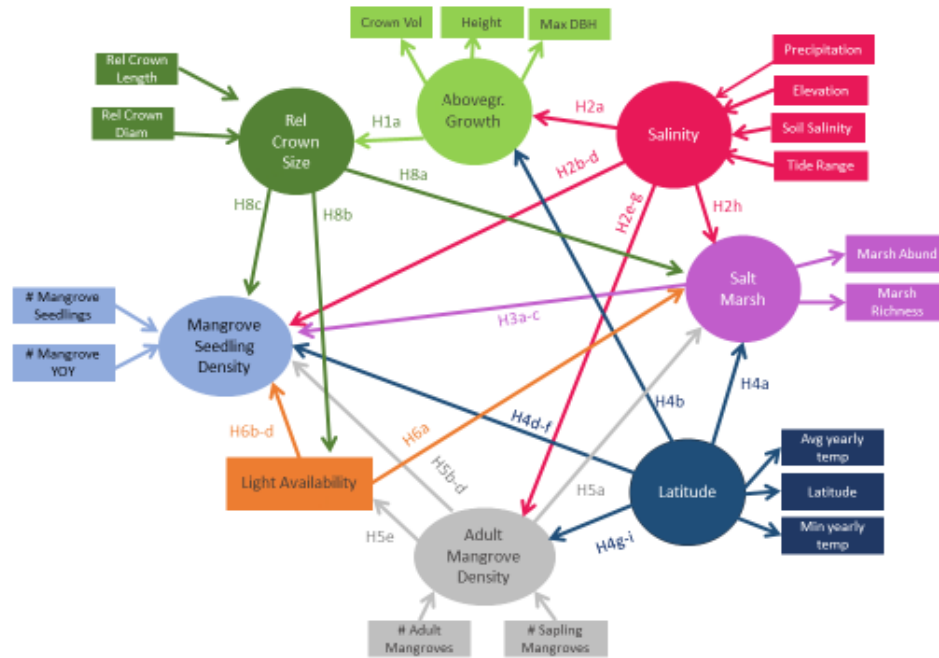


Figure 2: Predicted PLS path diagram between environmental and biotic variables in mangrove-salt marsh habitats. Ovals represent latent variables, rectangles measured variables. Numbers beside each arrow indicate a hypothesized effect. For the sake of simplicity, the adult and seedling densities of all three species are shown lumped into one variable, but effects were tested on each species. Direct and indirect effects of adult densities of all three mangroves on seedling densities of all three mangroves are discussed in the text.

Reflective variables, of the type common in traditional covariance-based SEM, are constructs that represent an underlying cause of a group of measured variables. Formative variables are constructs that are assumed to be affected by their measured variables. Seven latent variables, three reflective and four formative, are included in the model, along with one measured variable.

The reflective variable *Aboveground Growth* is hypothesized to affect measured crown volume, tree height, and maximum DBH. *Salt Marsh* is also a reflective variable, affecting salt marsh species richness and abundance. An underlying factor that drives

patterns in abundance and richness is assumed to be influencing this variable. *Latitude* is a reflective variable that affects the minimum annual temperature, the average annual temperature, and the measured variable latitude. As temperature changes along a latitudinal gradient, these variables are clearly affected by latitude.

The formative variable *Salinity* is hypothesized to be comprised of elevation, soil salinity, precipitation, and tidal exchange. *Salinity* was predicted to be formative, rather than reflective due to the fact that the actual salinity mangroves experience is going to be the result of several different contributing factors. It would be hard to argue, however, that some environmental construct affects both tidal regimes and elevation.

Laguncularia Adult Density, *Avicennia Adult Density*, and *Rhizophora Adult Density* were all formative variables as well. Adult densities were hypothesized to be combination of both measured adult density and measured sapling densities. It is possible to argue that, similar to salt marsh, an underlying factor is driving these patterns, instead of being driven by them. However, one of the primary questions of this study addresses how environmental variables affect mangrove competitive ability. *Density* as a formative variable allows a direct examination of the effects of, for example *Latitude* on density of adult mangroves. *Avicennia*, *Laguncularia*, and *Rhizophora* seedlings are formative variables for the exact same reason. These variables are comprised of both seedling and young-of-the-year (YOY) abundance, and thus the latent variable itself can respond to environmental conditions.

The final variable, *Relative Crown Size*, is a formative variable comprised of relative crown length and relative crown diameter. These measured variables were obtained by dividing the measured diameter and length of the crown by the total height of

the tree. *Relative Crown Size* gives an idea of how large the canopy is relative to the height of the tree, and thus is a simple measurement of “morphological structure.”

Direct relationships between latent variables are hypothesized as follows:

Aboveground Growth

H1a: Aboveground growth will likely positively affect relative crown size.

Salinity

H2a: High salinity is expected to decrease mangrove aboveground growth. It has been shown that mangroves will direct more resources to belowground growth when subjected to high salinity stress (Ball, 2002). As a result, aboveground growth may be reduced.

H2b-d: Higher salinity is expected to negatively affect the density of seedlings of all three mangrove species. The stress of higher pore water salinity and higher elevation may limit seedling growth and establishment (Ball, 2002; Bompy, Lequeue, Imbert, & Dulormne, 2014).

H2e-g: Adult and sub-adult mangrove densities of all three species are expected to decrease with higher salinity due to salinity stress (Sobrado, 2007).

H2h: Salinity is expected to decrease salt marsh abundance and diversity. Salinity stress and infrequent flooding will likely negatively affect salt marsh survival (Colmer, Vos, & Pederson, 2009; Ma, Chai, & Shi, 2011; Medeiros, White, & Howes, 2013). This effect upon salt marsh may lead to an indirect effect of salinity on mangrove seedling densities.

Salt Marsh

H3a-c: Increased salt marsh abundance is expected to negatively affect seedling densities of all three species. Although marsh may aid in the initial trapping and establishment of mangrove seedlings (McKee, Rooth, & Feller, 2007; Peterson & Bell, 2012; Guo, Zhang, Lan, & Pennings, 2013), competition for resources and increased shading will likely have an overall negative effect on seedling survival.

Latitude:

H4a: Salt marsh abundance and diversity is expected to increase with latitude, as salt marsh begins to outcompete mangrove in colder climates (Kirwan, Guntenspergen, & Morris, 2009). The effect of latitude on salt marsh may result in indirect effects between latitude and mangrove seedlings.

H4b: Mangrove aboveground growth is expected to decrease with latitude. Cold temperatures are known to limit mangrove height and stunt growth (Sobrado, 2007; Stuart, Choat, Martin, Holbrook, & Ball, 2007).

H4c-e: Mangrove seedling densities are expected to be affected by latitude. *R. mangle* and *L. racemosa* are less frost tolerant than *A. germinans*, (Pickens & Hester, 2011; Osland, Day, Larriviere, & From, 2014) and thus are likely to be less common further north. *A. germinans* seedling density is expected to increase with latitude, following the pattern of increasing *A. germinans* dominance with latitude (Cavanaugh, et al., 2013).

H4f-h: The density of adult and sapling mangroves is likewise anticipated to be affected by latitude. *A. germinans* is expected to increase with latitude, as this species will likely become more abundant at ranges where it is the only mangrove

able to survive (Cavanaugh, et al., 2013). The densities of adult and sapling *L. racemosa* and *R. mangle* are expected to decrease with latitude, as these species are less frost-tolerant (Sobrado, 2007; Cavanaugh, et al., 2015).

Adult Density

H5a: Adult mangrove density will likely negatively affect salt marsh abundance and density.

H5b-d: Adult mangrove density will likely negatively affect seedling growth and survival through shading, as well as through competition for nutrients, space, and other resources. However, species-specific effects will likely apply, and facilitation between conspecifics may occur (Vogt, et al., 2014).

A. germinans and *R. mangle* adult densities will likely negatively affect *L. racemosa* density, as prior studies have shown that in established mangrove stands, *A. germinans* and *R. mangle* are more efficient long-term competitors (Proffitt & Devlin, 2005).

H5e: Adult mangrove density will likely negatively affect light availability by shading. This effect on shading will likely lead to indirect effects of adult mangrove density of salt marsh and mangrove seedlings through light availability.

Light Availability

H6a: Salt marsh is expected to be positively affected by increased light availability. Light availability may have indirect affects through salt marsh on mangrove seedling abundance.

H6b-d: Increased availability of light is expected to positively affect abundance of mangrove seedlings. Species-specific responses are anticipated, with seedlings of

L. racemosa likely being the most abundant in high-light areas, as this species is known to be a rapid early colonizer (Proffitt & Devlin, 2005).

Relative Crown Size

H7a: As relative crown size increases, salt marsh is expected to decrease. Larger aboveground structures will likely outcompete saltmarsh for resources both above and below ground (Guo, Zhang, Lan, & Pennings, 2013; Saintilan, Wilson, Rogers, Rajkaran, & Krauss, 2014).

H7b: Relative crown size is expected to be negatively correlated with light availability. Shorter, squatter mangroves with broader and lower crowns will likely produce more shade.

H7c-e: The density of mangrove seedlings is expected to be negatively affected by the morphology of the central mangrove. Increased tree height and canopy size will likely increase competitive ability and thus may preclude other mangroves from growing to adulthood.

Univariate Data Analysis

In addition to the multivariate techniques, several univariate hypotheses were formed to test the relationship between mangrove morphology and environmental variables. One-way ANOVA was used to determine between-species variation in mangrove aboveground morphological characteristics and the effects of target mangrove species on salt marsh and seedling densities. In order to determine the interactive effects of light availability at latitude, a two-way ANOVA was performed using site and light availability zone (closed-canopy, open-canopy, and partial-canopy) as predictor variables and mangrove morphological characteristics as responses. Multiple regression was used

to determine the most important determining factors behind *R. mangle* prop root density, as sample sizes of *R.mangle* were too low for those data to be included in the PLS model. Differences in density of salt marsh and mangrove adults and seedlings between the inner and outer plots was determined via Kruskal-Wallis nonparametric test.

Variables were transformed as needed to meet assumptions of normality and heterogeneity of variance. All univariate analyses were done using R version 3.3.1 (R Core Team, 2016). The package ggplot2 was used for graphics (Wickham, 2009).

RESULTS

Partial Least Squares Path Modeling

Due to limited sample size, constructing a single model containing the adult and seedling densities of all three species of mangrove was not possible. Therefore, separate models were constructed with different combinations of adult and mangrove seedling densities, and the model with the best predictive power was chosen as the final model. This model is shown in Figure 3.

Because no criterion yet exists that can adequately estimate overall goodness-of-fit in PLS path modeling (Henseler & Sarstedt, 2013), PLS path models must be analyzed based on the validity and predictability of each part of the model (Guo, Yuan, Archer, & Connelly, 2011). Measures of convergent validity and composite reliability are used to validate each part of the model and assess whether each construct adequately reflects its measurement variables (Monecke & Leisch, 2012). In addition, the overall predictive power of the model is assessed based on R^2 and factor loading values.

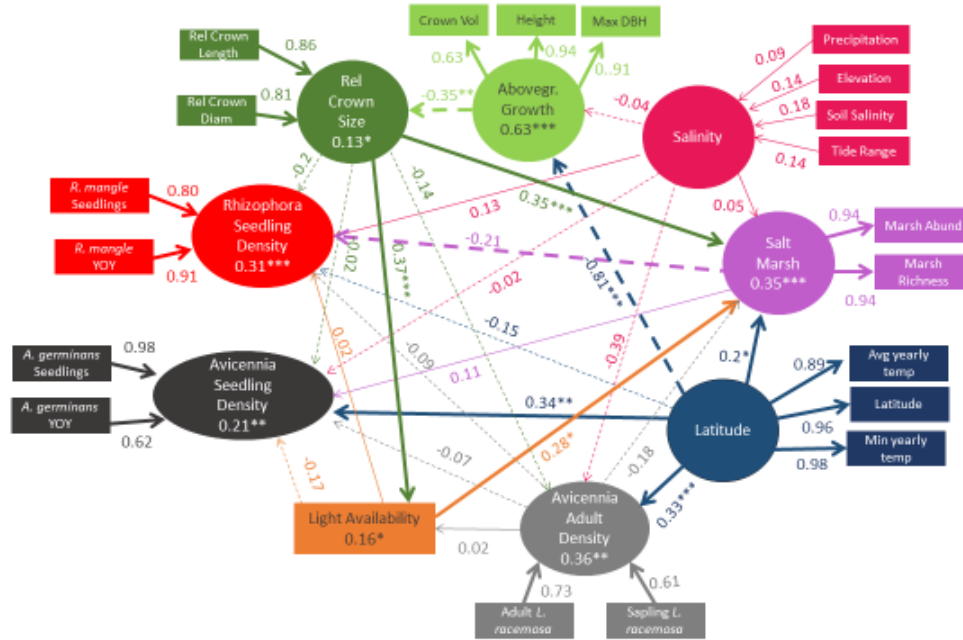


Figure 3: PLS analysis results. Large arrows represent a significant ($p < 0.05$) relationship as indicated by a 500 subsample bootstrap. Negative effects are indicated with dashed arrows; positive with solid. R^2 values are listed for each dependent variable. Significance is indicated as: * ($p < 0.05$); ** ($p < 0.01$), or *** ($p < 0.001$). Note that while all adult and seedling mangroves were tested, the final model was formed based on those species that responded most to environmental parameters.

Convergent validity of the measurement model is generally achieved if the following three criteria are met: (1) all item factor loadings are significant and greater than 0.7; (2) the average variance extracted (AVE) is greater than 0.5; and (3) the composite reliability indices for each construct should be greater than 0.8 (Guo, Yuan, Archer, & Connelly, 2011). Table 1 lists the outer loadings and cross-loadings of each measurement variable. All but three of the twenty variables had loadings of greater than 0.7. The loading of YOY of *A. germinans* on *Avicennia Seedlings* was 0.620. The loading of all variables on *Salinity* were low, but they were retained in the model for two reasons. Retaining variables with low loadings is permitted if the loadings of the other variables on that construct are high (Chin, 2010), or if the variables in question have a very logical or biological reason for loading on that construct (Sanchez, 2013). Furthermore, all variables

loaded more strongly on their respective constructs than on any other constructs, verifying these results.

Table 1: Factor loadings (bolded) and cross-loadings. Factor 1=Aboveground Growth; 2=A. germinans Seedlings; 3=L. racemosa Density; 4=Latitude; 5=R. mangle Seedlings; 6=Salinity; 7=Salt Marsh

	SAL	LAT	ABG	RCS	AAD	SM	RSD	ASD
Elevation	0.262	-0.157	0.189	-0.890	0.024	-0.096	0.171	0.094
Soil Salinity	0.511	-0.404	0.290	-0.261	-0.171	-0.056	0.221	0.080
Tide Range	0.802	-0.168	0.068	-0.312	-0.496	-0.048	0.209	-0.212
Latitude	-0.542	0.956	-0.789	0.357	0.563	0.162	-0.365	0.357
An. Min Temp	-0.301	0.987	-0.825	0.258	0.418	0.138	-0.307	0.347
An. Avg Temp	-0.097	0.892	-0.585	0.157	0.275	0.135	-0.194	0.266
Max DBH	0.156	-0.713	0.913	-0.178	-0.327	-0.082	0.272	-0.196
Height	0.286	-0.742	0.941	-0.471	-0.359	-0.236	0.488	-0.253
Crown Vol	-0.123	-0.530	0.633	0.196	-0.188	0.090	0.032	-0.153
Rel Crown Lng	-0.258	0.214	-0.196	0.863	0.64	0.466	-0.359	0.096
Rel Crown Wd	-0.451	0.268	-0.389	0.814	0.043	0.330	-0.305	0.030
# Avi Saplings	-0.498	0.444	-0.363	0.146	0.990	-0.043	-0.305	0.069
# Avi Adults	-0.487	0.429	-0.311	0.026	0.822	-0.113	-0.206	0.069
Marsh Rchnes	-0.138	0.073	-0.073	0.495	-0.057	0.939	-0.334	-0.050
Marsh Abund	-0.026	0.217	-0.244	0.405	-0.054	0.939	-0.300	-0.114
# Rhiz YOY	0.207	-0.313	0.397	-0.441	-0.210	-0.297	0.909	-0.158
# Rhiz Sdlgs	0.377	-0.220	0.294	-0.208	-0.217	-0.287	0.807	-0.151
# Avi YOY	-0.050	0.180	-0.083	0.020	0.123	0.094	-0.156	0.620
# Avi Sdlgs	-0.124	0.329	-0.222	0.068	0.092	0.096	-0.187	0.976

Table 2 presents the composite reliability scores, AVE, and the Fornell-Larcker (1981) criterion for discriminate validity for the three reflective variables present in the study. All three variables had composite reliability of greater than 0.8, and AVE of greater than 0.5. Cronbach's Alpha and rho A were above the suggested 0.6 (Sanchez, 2013) indicating that these reflective variables are sufficiently correlated with their measurement

variables. Discriminate validity, calculated as the square root of the AVE, was also high for each reflective variable.

Table 2: Assessment of the convergent validity of the measurement model. For a model to demonstrate convergent validity, composite reliability should be greater than 0.7; AVE should be >0.5. Cronbach's alpha and rho A should both >0.6.

	Discriminate Validity	Average Variance Extracted	Cronbach's Alpha	Rho A
Aboveground Growth	0.841	0.707	0.828	0.898
Latitude	0.947	0.896	0.942	0.963
Salt Marsh	0.939	0.882	0.866	0.937

The hypotheses were assessed by examining the structural model parameters. The R^2 of the dependent variables indicate the predictive ability of the theoretical model, while the path coefficients between constructs indicates the strength of the relationships. Significance of these paths was estimated via a complete bootstrapping with 500 subsamples. These results are shown in Figure 3. All of the dependent variables have a significant R^2 of greater than the suggested minimum of 0.10, meaning that the theoretical model likely demonstrates substantial predictive power (Guo, Yuan, Archer, & Connelly, 2011). The model explains 63% of the variance in *Aboveground Growth*, 35% of the variance in *Salt Marsh*, 36% of the variance in *A. germinans Density*, 16% of the variance in *Light Availability*, 21% of the variance in *A. germinans Seedlings*, and 31% of the variance of *R. mangle Seedlings*.

Several variables also displayed significant indirect relationships, some of which were significant even when the direct effect was not. The total effects of each variable on each other are displayed in Appendix A. Both indirect and direct effects were considered when interpreting the results.

Aboveground Growth had a significant negative effect on *Relative Crown Diameter* ($\beta = -0.35$, $p = 0.001$). This led to significant indirect effects of *Aboveground Growth* on *Light Availability* ($\beta = -0.13$, $p = 0.011$) and *Salt Marsh* ($\beta = -0.17$, $p = 0.006$), as well as a marginally significant positive effect on *Rhizophora Seedling Density* ($\beta = 0.10$, $p = 0.052$).

Salinity did not significantly affect any of the response variables, nor did it have any significant indirect effects. There was a marginally insignificant negative trend between *Salinity* and *Avicennia Adult Density* ($\beta = -0.39$, $p = 0.085$). *Salt Marsh* had a significant negative effect on *Rhizophora Seedling Density* ($\beta = -0.21$, $p = 0.006$), but did not significantly affect mangrove seedlings of the other two species.

Latitude had a significant negative effect on *Aboveground Growth* ($\beta = -0.81$, $p < 0.001$). As a result, *Relative Crown Size* displayed a significant positive indirect response to *Latitude* ($\beta = 0.28$, $p = 0.009$). Through this relationship, *Latitude* was also found to have a significant positive effect on *Light Availability* ($\beta = 0.10$, $p = 0.015$). *Latitude* had significant positive effects on *Salt Marsh* ($\beta = 0.20$, $p = 0.040$), *Avicennia Seedling Density* ($\beta = 0.34$, $p = 0.002$), and *Avicennia Adult Density* ($\beta = 0.34$, $p < 0.001$). *Latitude* did not directly affect either adult or seedling density of *Laguncularia* or *Rhizophora*. However, when indirect pathways through *Salt Marsh*, *Aboveground Growth*, and *Relative Crown Size* are considered, the total effect of *Latitude* on *Rhizophora Seedling Density* was significantly negative ($\beta = -0.29$, $p = 0.001$).

Avicennia Adult Density did not significantly affect seedling densities of any of the three mangroves. The effect of *Avicennia Adult Density* on *Salt Marsh* was marginally insignificant, suggesting a negative trend between the two variables ($\beta = -0.18$, $p = 0.079$). There were no significant relationships between adult densities of *Avicennia*, *Rhizophora*,

and *Laguncularia*. Densities of adult *Rhizophora* and *Laguncularia* did not significantly affect seedling densities of any species. Adult mangrove density did not significantly affect *Light Availability*.

Light Availability had significant positive effects on *Salt Marsh* ($\beta=0.28$, $p=0.011$). *Light Availability* did not significantly affect mangrove seedling density of any species, even when indirect pathways were accounted for. *Rhizophora Seedling Density* had a significant negative effect on *Laguncularia Seedling Density* ($\beta= -0.16$, $p<0.001$). There were no significant effects between seedling densities of *Avicennia* and *Rhizophora* or *Avicennia* and *Laguncularia*.

Relative Crown Size had significant positive effects on *Salt Marsh* ($\beta=0.35$, $p<0.001$) and *Light Availability* ($\beta= 0.37$, $p<0.001$). The indirect pathway through *Light Availability* increased the magnitude of the effect of *Relative Crown Size* on *Salt marsh* to $\beta= 0.49$. *Relative Crown Size* did not significantly affect mangrove seedling densities of any species; however, when indirect effects through *Light Availability* and *Salt Marsh* are accounted for, *Rhizophora Seedling Density* displays a significant negative response ($\beta= -0.29$, $p=0.009$). *Relative Crown Size* did not significantly affect densities of adult mangroves of any species.

Site and Sunlight Effects on Mangrove Morphology

Table 3 lists the results of the two-way ANOVAs testing the effects of latitude and light availability on mangrove morphological characteristics. The interaction between the two factors was significant in every case, indicating that the response of mangroves to one factor changes with changes in level of the other.

Table 3: Two-Way ANOVA results on the variation of mangrove morphology with site, light availability, and the interaction term.

	Site		Light Availability		Interaction	
	F _(5,84)	p	F _(2,84)	p	F _(10,84)	p
Height	82.29	<0.001	19.84	<0.001	2.05	0.034
Max DBH	71.31	<0.001	1.37	0.259	2.86	0.004
Crown Volume	22.95	<0.001	16.79	<0.001	7.46	<0.001

Figure 4 shows the change in mean mangrove height across all six sites. Mangroves within all three light categories decreased significantly in height with latitude. Both site and light zone were significant ($F_{(5,84)}=82.89$ $p<0.001$, and $F_{(2,84)}=19.84$ $p<0.001$, respectively), as was the interaction between the two ($F_{(10,84)}=2.05$, $p=0.034$).

Mean closed-canopy mangrove height decreased 90.28% from $1548.46\text{cm} \pm 233.99$ cm in Miami to $150.50\text{cm} \pm 4.27\text{cm}$ in St. Augustine. In mangroves growing in partial sun, mean height decreased 90.98% from $1330.26\text{cm} \pm 140.77\text{cm}$ in Miami to 120cm in St. Augustine. Because only one tree was able to be measured in this zone, there is no variance or margin of error. Mean height of open-canopy zone mangroves decreased 78.69% from $659.03\text{cm} \pm 65.15\text{cm}$ in Miami to $178.50\text{cm} \pm 13.50\text{cm}$ in St. Augustine.

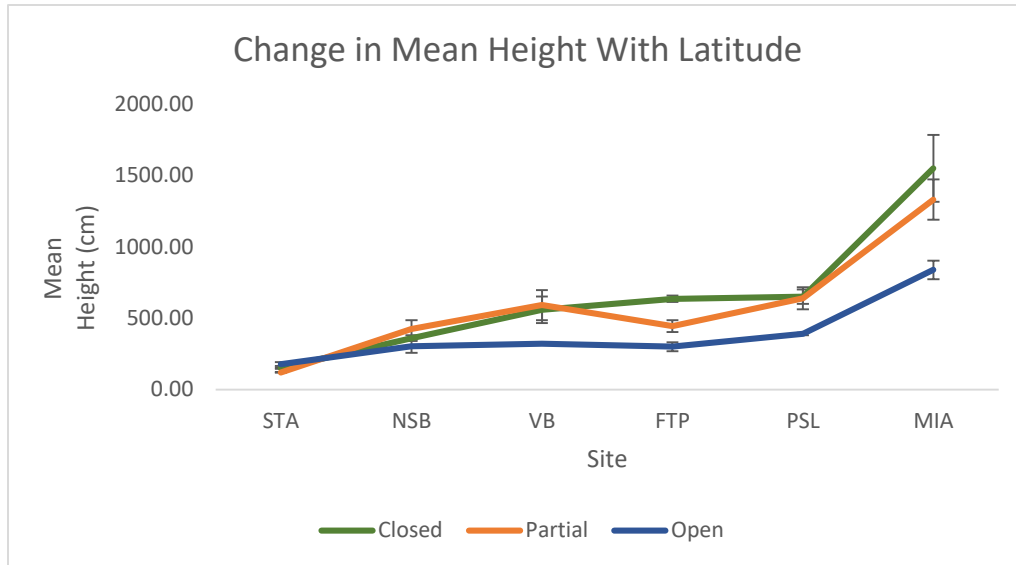


Figure 4: Change in mean mangrove height with latitude in all three types of canopy. Error bars represent standard error. Data shown are untransformed for clarity.

Post-Hoc Tukey comparisons reveal that across all sites, closed- and partial-canopy mangroves did not differ significantly in height ($p=0.448$), but closed- and open-canopy mangroves and open- and partial-canopy mangroves did significantly differ in height ($p<0.001$ for both). Comparison of between-light zone means at different sites reveals that mangroves in open-canopy zones were shorter than those in closed or partial canopy zones in Miami, Jensen Beach, Fort Pierce, Vero Beach, and New Smyrna Beach. In St. Augustine, open-canopy trees averaged taller than either closed or partial canopy trees.

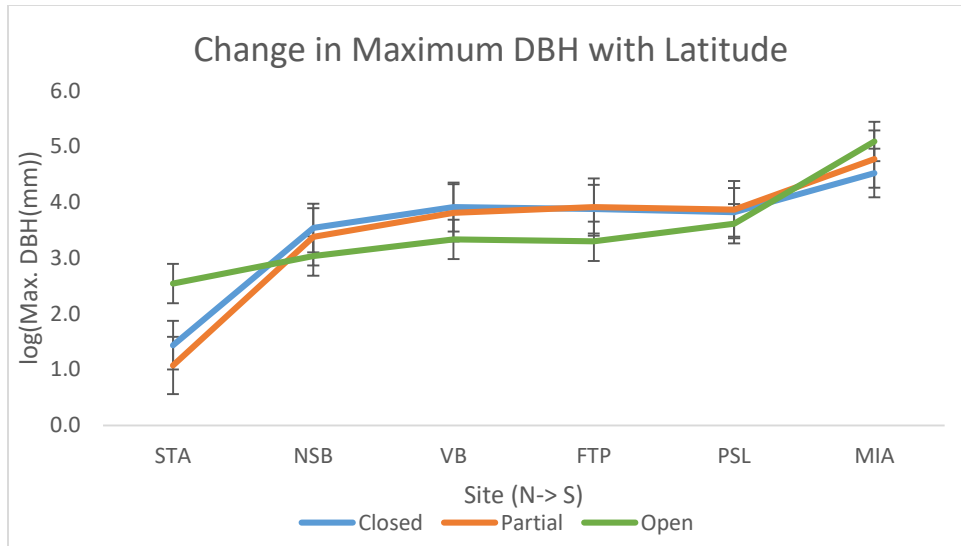


Figure 5: Change in maximum DBH across six sites for trees within all three light availability zones. Data values on the y-axis have been log-transformed. Sites go from north to south.

Maximum DBH was log-transformed in order to meet ANOVA assumptions of normality and homogeneity of variance. Figure 5 shows the change in mean maximum DBH across all six sites. DBH was significantly affected by latitude ($F_{(5,84)} = 71.81$, $p < 0.001$) but not light ($F_{(2,84)} = 1.37$, $p = 0.259$), though the interaction between the two was significant ($F_{(10,84)} = 2.86$, $p = 0.004$).

Mangroves decreased in DBH with latitude in all three light zones. Closed-canopy zone mean log maximum DBH decreased 68.21% from 4.53 ± 0.227 in Miami to 1.44 ± 0.103 in St. Augustine. In partial-canopy zones, mean log maximum DBH decreased 77.62% from 4.78 ± 0.051 in Miami to 1.07 in St. Augustine. In open-canopy zones, mean log maximum DBH decreased 50.10% from 5.09 ± 0.244 in Miami to 2.54 in St. Augustine.

The main effect of light zone was not significant, suggesting that DBH does not vary based on light availability. However, between-group means were still compared due to the significance of the interaction term. Comparisons of between-light zone means at each site reveals that site differences are only driven by Miami and St. Augustine, which

differ significantly from all other sites. None of the other sites were significantly different from each other in terms of maximum DBH. Therefore, presence of true latitudinal trend cannot be identified from these data.

Figure 6 shows the change in mangrove crown volume with latitude for all three light zones. Crown volume varied significantly by site ($F_{(5,84)} = 22.95$, $p < 0.001$) and sunlight ($F_{(2,84)} = 16.79$, $p < 0.001$). The interaction between them was also significant ($F_{(10,84)} = 7.46$, $p < 0.001$), indicating that crown volume response to one factor differs with levels of the other.

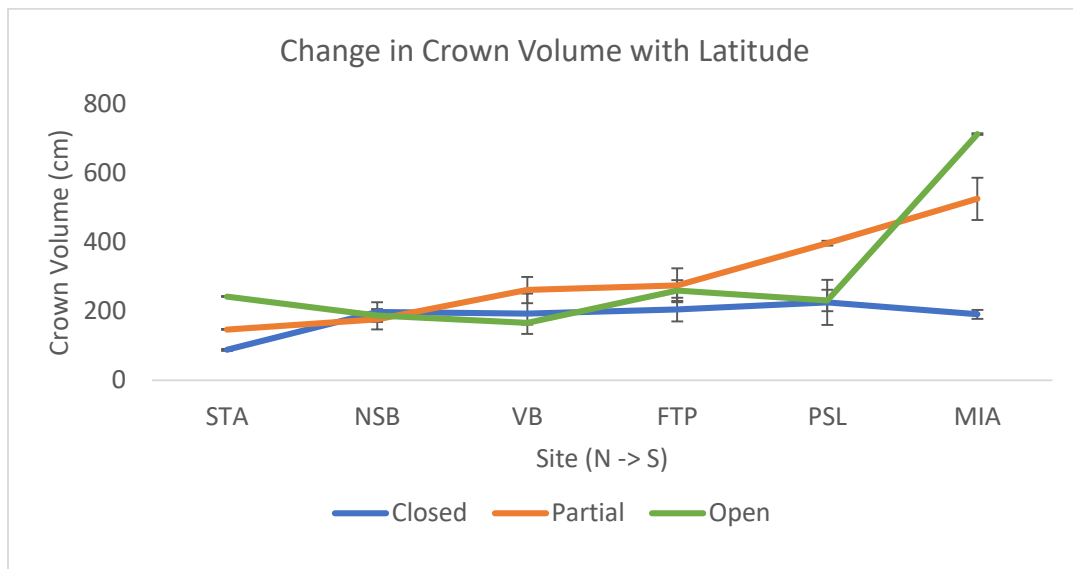


Figure 6: Change in crown volume over latitude in all three light zones. Error bars represent standard error. Y-axis values have been cubed to meet assumptions of ANOVA.

Overall, mean crown volume of closed-canopy zone mangroves decreased 53.77% from $190.87\text{cm} \pm 12.89\text{cm}$ in Miami to $88.24\text{cm} \pm 2.76\text{cm}$ in St. Augustine. Crown volume actually increased slightly in closed-canopy zones between Miami and Port. St. Lucie, remained relatively constant between Port. St. Lucie and New Smyrna Beach, and then only dropped off again between New Smyrna Beach and St. Augustine. Partial-canopy zone mangroves decreased in crown volume in a much more constant fashion, from

525.87cm ± 61.25 in Miami to 146.98cm ± 0.89cm in St. Augustine, a decrease of 72.05%. Open-canopy zone mangroves decreased 66.00% between Miami and St. Augustine, but the bulk of that decrease occurred between Miami and Port St. Lucie. Open-canopy Miami mangroves averaged 712.97cm ± 2.27cm, decreasing to 231.19cm ± 31.37cm in Port St. Lucie. Canopy volume fluctuated across sites in open-canopy mangroves, but ultimately did not decrease further between Port St. Lucie and St. Augustine.

Interspecies Variation in Mangrove Morphological Characteristics

Of the eight morphological variables compared across the three species of mangrove, three displayed a significant difference (see Table 4). The number of main stems varied between species ($F_{(2,99)}=10.7$, $p<0.001$). Multiple stems are significantly less prevalent in *R. mangle* than in *A. germinans* or *L. racemosa*, though the latter two do not differ significantly from each other (see Figure 7).

Table 4: Results of the one-way ANOVA comparing mangrove morphological traits between species

	$F_{(2,99)}$	P
Height	0.977	0.360
Max. DBH	0.130	0.878
# Stems	10.7	<0.001
Max Crown Diameter	0.991	0.009
Relative Crown Diameter	5.13	0.008
Crown Length	1.353	0.263
Relative Crown Length	2.253	0.110
Crown Volume	0.12	0.887

Difference in Number of Main Stems in Three Mangrove Species

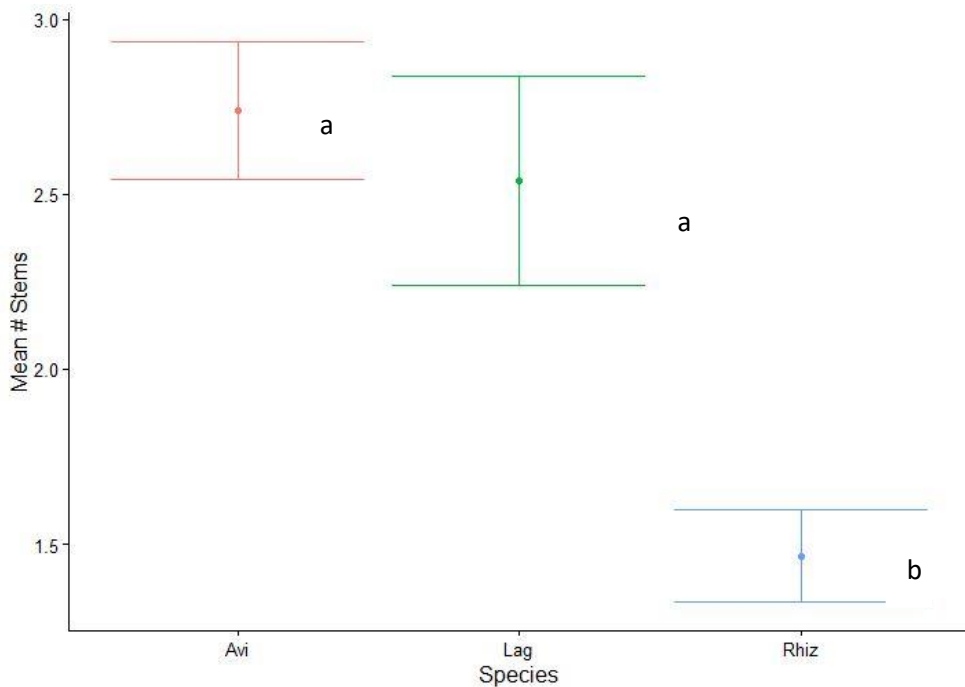


Figure 7: Mean number of main stems of each of the three mangrove species. Letters indicate significant differences in one-way ANOVA. Bars represent standard error, points, the mean

Both absolute and relative maximum crown diameter also differed significantly between species ($F_{(2,99)}=0.991$, $p=0.009$ and $F_{(2,99)}=5.13$, $p=0.008$, respectively). However, upon analysis of post-hoc pairwise tests, the differences in mean absolute crown diameter between species was nonsignificant, while significant differences between pairs did occur in terms of relative crown diameter (see Figure 8). *A. germinans* displayed larger crown diameters in relation to overall tree height than did *R. mangle*. *L. racemosa* did not differ significantly from either of the other two species.

Inter-Specific Comparison of Crown Diameter and Crown:Height Ratio in Mangroves

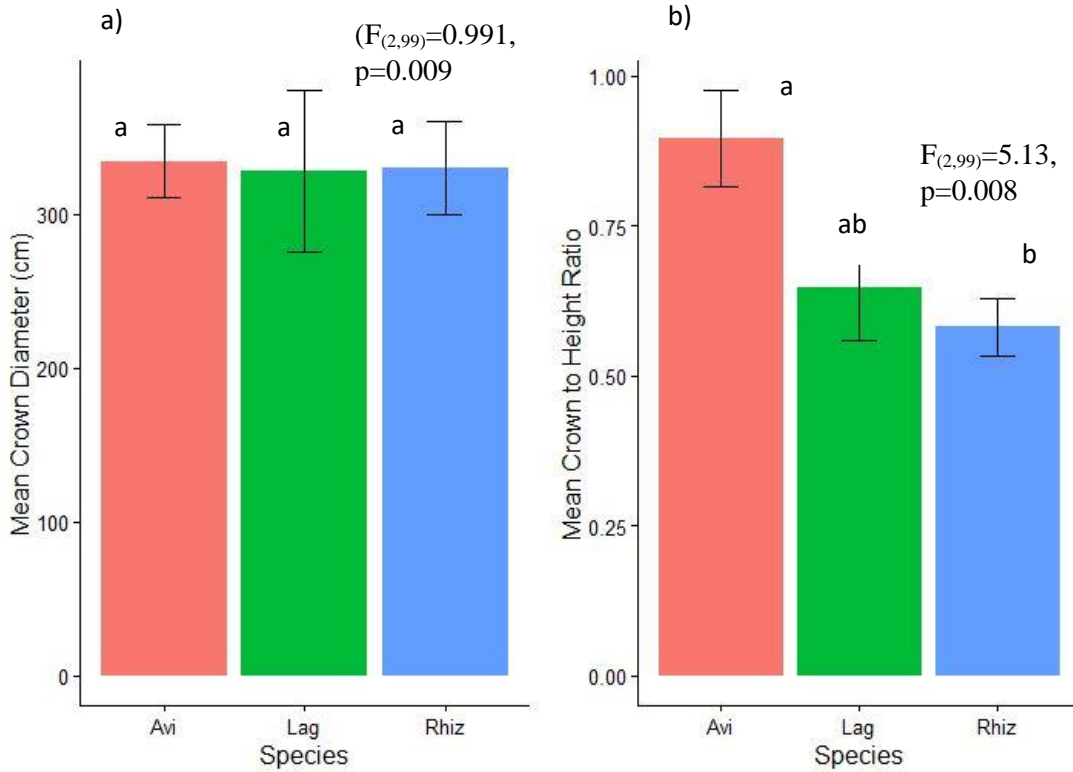


Figure 8: Differences in a) measured crown diameter; and b) crown to height ratio between three species of mangrove. F and p values result from a one-way ANOVA, and a's and b's post-hoc Tukey analysis. Error bars represent standard error.

Species-Specific Responses of Mangrove Morphology to Latitude

A two-way ANVOA was used to compare the response of mangrove morphological variables of the three different species to site. Table 5 lists those results. As other results demonstrate, site was a significant factor in determining mangrove height and crown volume. Mangroves demonstrated a species-specific response only in terms of height, and the interaction term between site and species was also significant in terms of height, suggesting that mangrove height changes with latitude depending on species.

Table 5: Two-Way ANOVA results comparing mangrove morphology to site and species.

	Site		Species		Interaction	
	F _(5,86)	p	F _(2,86)	p	F _(8,86)	p
Height	55.92	<0.001	4.63	0.012	3.59	0.001
Crown Volume	13.61	<0.001	0.605	0.524	0.79	0.614

Figure 9 shows the pattern of height change in all three mangrove species with latitude. Mangroves of all three species were tallest in Miami and much shorter throughout the other five sites. *A. germinans* averaged 1622.7 cm \pm 230.54cm in Miami, and decreased to an average of 583.61 cm \pm 86.82cm in Port St. Lucie. Between Port St. Lucie and Vero Beach, *A. germinans* mean height further decreased only 37.41cm, but began decreasing much faster north of Vero Beach to a mean height in St. Augustine of 152.3cm \pm 6.9cm.

R. mangle did not differ significantly from *A. germinans*. *R. mangle* height averaged 1403.96cm \pm 129.8cm in Miami and dropped to an average of 573.96 \pm 68.68cm in Port St. Lucie. *R. mangle* height did not change significantly between Port St. Lucie and Vero Beach, but then decreased to a mean of 334.06cm \pm 72.79cm in New Smyrna Beach. *L. racemosa* height in Miami was lower than the other two species, averaging 853.53cm \pm 40.77cm in Miami. This decreased to 521.18cm \pm 67.52cm in Port St. Lucie. Unlike the other two species, *L. racemosa* height continued to decrease between Port St. Lucie and Fort Pierce, to a mean of 412.27cm \pm 52.97cm. Mean *L. racemosa* height did not decrease north of Vero Beach, though only one individual of this species was found in New Smyrna Beach that could be measured

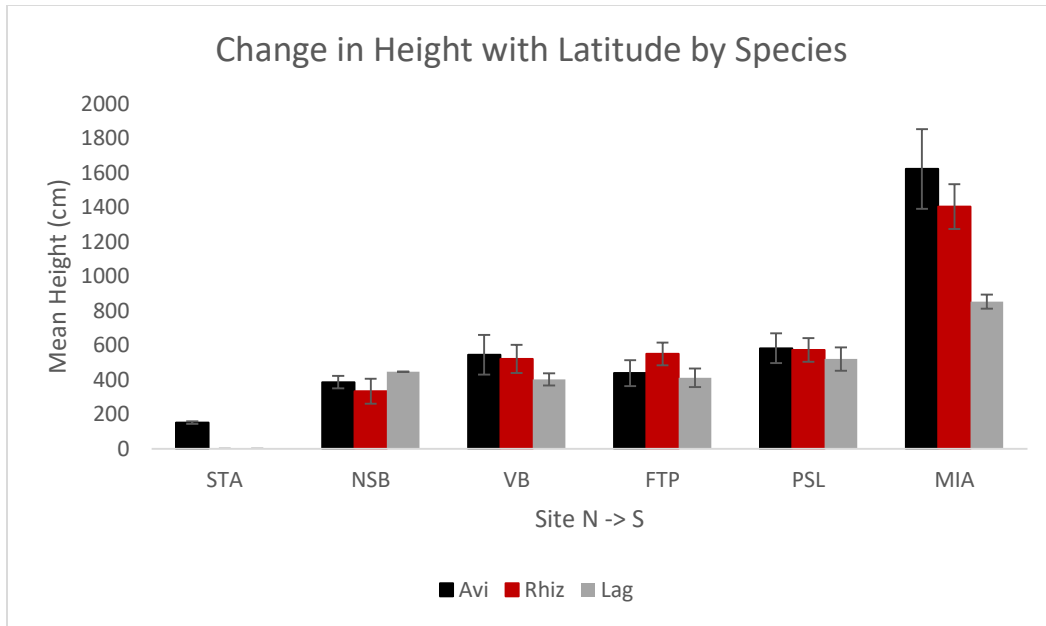


Figure 9: Species-specific changes in height with latitude between three mangrove species. Error bars represent standard error.

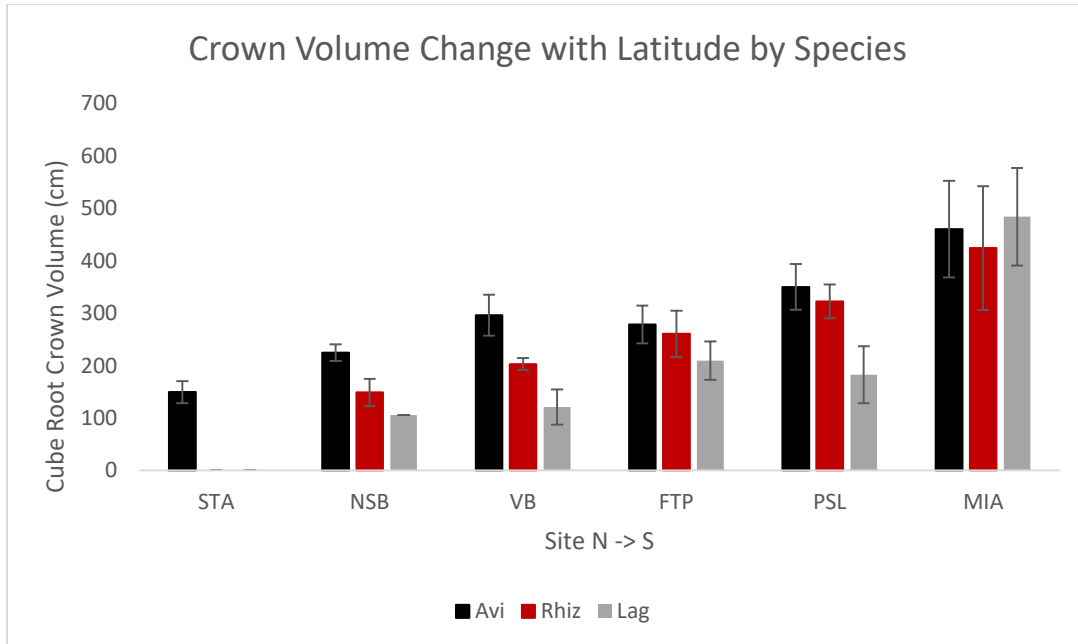


Figure 10: Species-specific changes in crown volume with latitude between three mangrove species. Error bars represent standard error.

Crown volume was also largest in Miami, as figure 10 demonstrates, but crown volume changed less with latitude than height. These data were transformed to meet ANVOA assumptions by taking the cube root of the data. *A. germinans* averaged a 459.93 ± 91.88 cm crown in Miami, which decreased to $349.93\text{cm} \pm 43.65\text{cm}$ in Port St. Lucie. Crown volume in this species remained relatively constant until north of Vero Beach, before decreasing to a mean of $149.41\text{cm} \pm 20.83\text{cm}$ in St. Augustine.

R. mangle displayed a much more linear decrease in crown volume with latitude, starting from a mean of $423.93\text{cm} \pm 118.04\text{cm}$ in Miami and decreasing consistently to a mean of $148.86\text{cm} \pm 25.80\text{cm}$ in New Smyrna Beach. *L. racemosa* dropped in mean crown volume size from $483.49\text{cm} \pm 92.75\text{cm}$ in Miami to $182.52\text{cm} \pm 54.28\text{cm}$ in Port St. Lucie, after which further decreases in crown volume were not significant.

Environmental Variation in Salt Marsh and Mangrove Seedlings

Salt Marsh: Salt marsh abundance varied greatly between sites, but overall there was no trend with latitude (GLM, $\chi^2=0.51$, $p=0.477$). Figure 11 shows the differences in abundance between sites. Latitudinal effects on the two most abundant salt marsh species, *Batis maritima* and *Spartina alterniflora* were tested separately. *B. maritima* did not significantly vary in abundance across a latitudinal gradient (GLM, $\chi^2=0.76$, $p=0.384$), but *S. alterniflora* was significantly more abundant in the north than in the south (GLM $\chi^2=14.69$, $p<0.001$). However, this is not a true latitudinal trend as *S. alterniflora* abundance was at or near zero at every other site except the northernmost (see Figure 11).

Density of Salt Marsh Along a Latitudinal Gradient

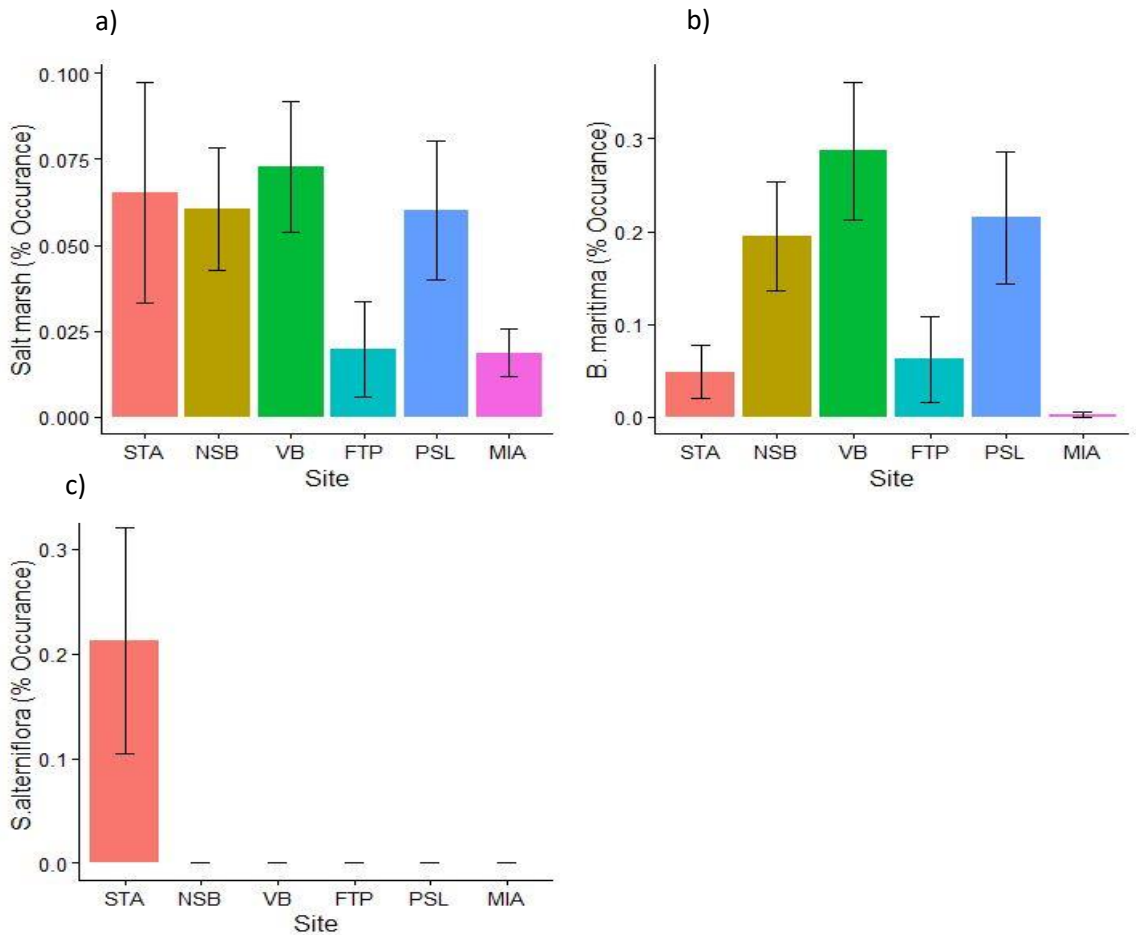


Figure 11: Mean abundance of a) all salt marsh; b) *Batis maritima* and c) *Spartina alterniflora* at each site. Abundance was measured as percent occurrence. Error bars represent standard error.

Both salt marsh abundance and richness were negatively affected by shading (GLM, $\chi^2=1.39$, $p<0.001$; GLM, $\chi^2=12.07$, $p<0.001$, respectively). *B. maritima* was also negatively affected by shading (GLM, $\chi^2=1.98$, $p=0.030$). *S. alterniflora* was tested against shade only in St. Augustine, since abundance of this species was at or near zero in all other sites. Where *S. alterniflora* is present, shading has a negative effect on the abundance of this species (GLM, $\chi^2=2.79$, $p=0.009$).

Comparisons were also made between inner (those directly under the canopy) and outer (those just outside the canopy edge) plots. The percentage of available light differed

significantly between inner and outer plots (one-way ANOVA, $F_{(1,100)}=13.52$, $p<0.001$). Plots just outside the edge of the canopy had significantly more light than did those directly underneath (see Figure 12). Despite this, salt marsh abundance and richness did not vary between inner and outer plots (Kruskal-Wallis test, $\chi^2=1.47$, $p=0.226$; $\chi^2=1.992$, $p=0.158$). Neither *B. maritima* or *S. alterniflora* varied significantly between inner and outer plots (Kruskal-Wallis test, $\chi^2=0.271$, $p=0.603$, $\chi^2=0.358$, $p=0.550$, respectively).

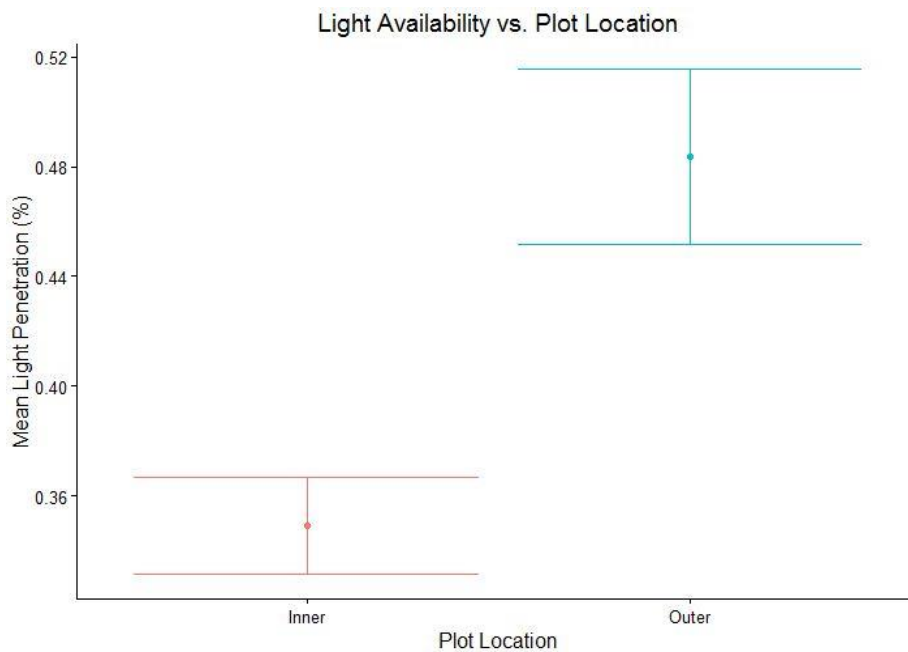


Figure 12: Percentage of available light between plots directly underneath and plots just outside a mangrove canopy. F and p values generated from a one-way ANOVA. Error bars represent standard error.

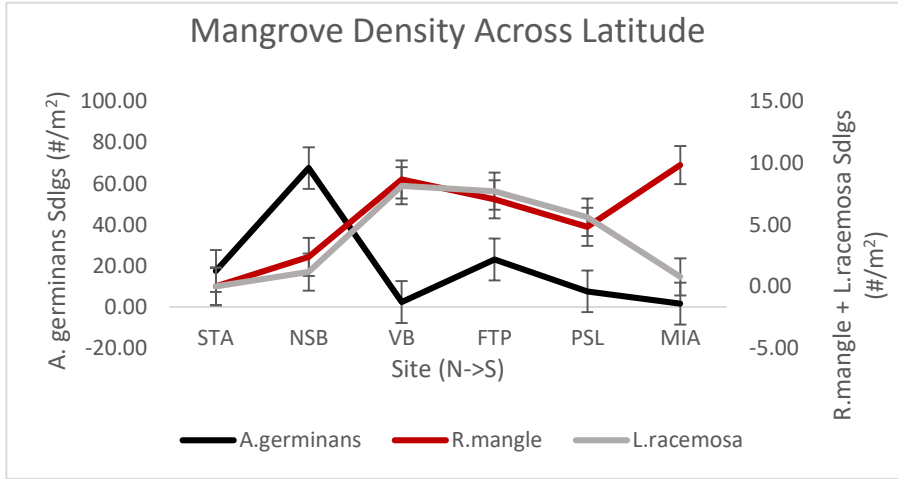
Mangrove Density: Figure 13 displays the latitudinal trends in mangrove adult and seedling abundance for all three species. *R. mangle* seedlings were much more abundant in the south, and decreased significantly with latitude (GLM, $\chi^2=13.53$, $p<0.001$). *A. germinans* seedlings were significantly higher in the northern latitudes than further south (GLM $\chi^2=23.65$, $p<0.001$). *L. racemosa* seedlings did not vary significantly by latitude (GLM, $\chi^2=1.794$, $p=0.181$); however, further analysis by ranked one-way ANOVA revealed

that *L. racemosa* seedlings were significantly more abundant within the three Indian River Lagoon sites ($F_{(5,96)}=5.17$, $p<0.001$).

While densities of adult *R. mangle* and *L. germinans* did not vary with latitude (GLM, $\chi^2=5.25$, $p=0.488$, and $\chi^2=2.51$, $p=0.113$), Kruskal-Wallis test revealed that the between-site differences visible in Figure 13 are significant for both *R. mangle* ($\chi^2=35.99$, $p<0.001$) and *L. racemosa* ($\chi^2=32.77$, $p<0.001$). The increase with latitude in adult density of *A. germinans* was significant (GLM $\chi^2=62.69$, $p<0.001$).

Light availability did not affect abundances of seedlings of *R. mangle* (GLM, $\chi^2=1.57$, $p=0.210$), *A. germinans* (GLM, $\chi^2=3.17$, $p=0.075$), or *L. racemosa* (GLM, $\chi^2=0.001$, $p=0.972$). Plot location (inner or outer) also did not affect abundance of seedlings of *R.mangle* (Kruskal-Wallis test, $\chi^2=0.06$, $p=0.808$), *A. germinans* (Kruskal-Wallis test, $\chi^2=0.14$, $p=0.713$) or *L. racemosa* (Kruskal-Wallis test, $\chi^2=0.06$, $p=0.814$).

a)



b)

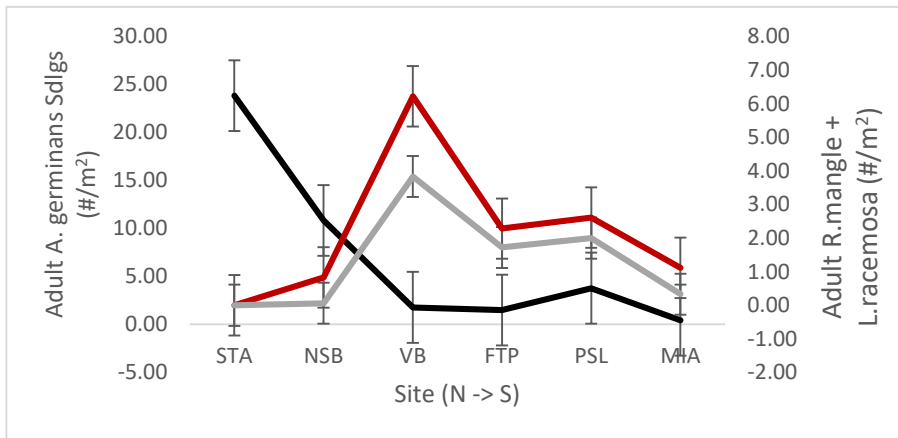


Figure 13: Mean mangrove a) seedling density; and b) adult density across all six sites. *A. germinans* is graphed on a separate axis due to extremely high abundance in northern sites. Error bars represent standard error.

Effect of Environment on Prop Root Volume

Due to the relatively small sample size of *R. mangle*, prop root volume could not be analyzed within the multivariate path model. Therefore, a multiple linear regression was calculated in order to predict how the prop root volume of *R. mangle* varies with environmental conditions. A significant regression equation was found ($F_{(4,23)}=11.95$, $p<0.001$), with an adjusted R^2 of 0.62. Cube root transformed prop root volume is equal to $-0.001 + 3.390(\text{soil salinity}) + 0.350(\text{latitude}) + 0.122(\text{tree height}) + 4.233(\text{\# of prop roots})$. Cubed root volume increased 3.39 cm with each ppm of salinity, 0.35 cm for every degree of latitude, 0.122 for every cm of tree height, and 4.233 cm for every additional prop root.

DISCUSSION

Main Findings and Conclusions

The effects of latitude and cold on mangrove morphology have been well documented. However, few, if any, studies have addressed how interactions between climate and other abiotic factors affect mangrove morphology. Furthermore, few studies to date have examined the multivariate effects of morphology, environmental variables, salt marsh competition, and latitude on mangrove seedling recruitment in regions of mangrove expansion into salt marsh. The results of this study offer evidence that patterns of mangrove distribution on the east coast of Florida are not due solely to latitudinal variables. Complex relationships between salt marsh abundance, light availability, and the crown morphology of adult mangroves play a role in determining *R. mangle* seedling establishment latitudinal patterns. Whether or not *R. mangle* seedlings are able to recruit into new areas therefore probably depends on a balance between environmental stressors and biotic interactions.

This study aimed to address three main questions. Through the use of partial least squares path modeling, as well as traditional analysis techniques, all three questions were able to be answered.

Question 1: How does mangrove growth form change with environmental conditions that vary over latitude? PLS path model results demonstrate that mangrove growth form varies strongly with latitude, while analysis of trees growing in differing light levels

demonstrates that variables such as height and crown volume are further affected by the availability of sunlight. This study has demonstrated how interactions between different environmental variables produce changes in mangrove morphology.

Question 2: How does this response vary between mangrove species? Overall, variation in morphology did not differ between the three species. This suggests that the change in morphology between Miami and St. Augustine is not due to the change in species composition, but is a true reflection of changing environmental conditions.

Question 3: How does competition between salt marsh and mangroves affect the growth and survival of both? The PLS model demonstrated the critical role of mangrove morphology in affecting the local patch. Growth form directly impacted the amount of available light, which carried implications for salt marsh and mangrove seedling survival. *R. mangle* seedlings, in particular, were highly affected by light availability and salt marsh presence, suggesting that the predicted migration northward of this species may depend equally on biotic and abiotic factors.

Morphological Changes with Latitude

The overall pattern of growth form change with latitude demonstrated in this study is consistent with other studies that have found decreasing height and increasing aboveground biomass allocation with latitude, in both mangroves (Medeiros & Sampaio, 2008; Mendez-Alonzo, Lopez-Portillo, & Riviera-Monroy, 2008; Cavanaugh, et al., 2013; Osland, Day, Larriviere, & From, 2014; Saintilan, Wilson, Rogers, Rajkaran, & Krauss, 2014) and in other species of plants (Li, Suzuki, & Hara, 1998; DeFrenne, et al., 2011; Lines, Zavala, Purves, & Coomes, 2012). The PLS path model indicates that, while tree height and DBH decrease with latitude, there is a corresponding increase in the crown size:

height ratio. The positive indirect pathway between *Latitude* and *Relative Crown Size* suggests that mangroves further north are allocating more resources to crown and leaf production than their counterparts of similar height further south.

Using crown size:height ratios in the PLS model instead of absolute measurements of crown diameter, volume, and area was designed to investigate specifically how morphology changes with latitude. Crown size is, by necessity, limited by the height of the tree. Therefore, as mangroves decrease in height with latitude, crown measurements will also decrease simply because the tree is shorter, and not because of any underlying change in resource allocation patterns. By using the ratio between crown size and height, the actual morphology of the tree can be quantified and its effects included in the model.

Furthermore, estimating patterns of resource allocation are difficult, if not impossible, without destructive sampling methods. It can be argued that the ratio between the crown and the height of the tree is a better indicator of how that tree is distributing resources than is the absolute size of the crown itself. For example, a crown 300 cm in diameter would be relatively small on a ten-meter-tall tree, and that tree would likely be putting more energy into vertical growth than into branch production. However, a 300cm-wide crown on a two-meter-tall tree would be suggestive of a very different pattern of resource allocation, even though the measured crown diameter is the same.

Given this, the fact that the variable *Relative Crown Size* increases with latitude is interesting, because it suggests that crown size and tree height respond differently to latitude. In other words, if *Relative Crown Size* showed no change with latitude, the crown would likely be changing at a similar rate as overall height. Crown size is clearly limited by the height of the tree, as indicated by the negative relationship between *Aboveground*

Growth and Relative Crown Size. However, results from other analyses indicate that crown volume and diameter may be less affected by latitude than is height (see figures 6 and 10).

The few other studies done on mangrove morphological changes with latitude have found similar results suggesting an increase in the allocation of resources to branches and leaves with latitude. A 2008 study in Mexico found that, while mangrove height decreases with latitude, leaf size and the leaf area index (LAI) increases, suggesting that more leaves are being produced at higher latitudes (Mendez-Alonzo, Lopez-Portillo, & Riviera-Monroy, 2008). The reasons behind this has to do with the way frost affects plants. Growing tips and young shoots are thought to be more vulnerable to frost embolisms than older, more established shoots (Sobrado, 2007). If these growing tips are “pruned” during cold snaps, trees produce a bushier, fuller crown in response (Osland, Day, Larriviere, & From, 2014).

A decrease in mangrove crown with latitude may be expected to a certain extent due to changes in height. However, at latitudes where cold events become more common, it appears that mangrove crown size ceases to decrease at the same pace that mangrove height does, likely due to the effects of colder air temperatures forcing an allocation of growth to branches and leaves. These mechanisms explain why *Relative Crown Size* increases with latitude even as *Aboveground Growth* decreases.

Effects of Salinity on Mangrove Morphology

Salinity was also expected to affect mangrove growth form. Previous studies on the effects of salinity on mangroves have shown that individuals growing in high salinity may have a decreased growth rate (Ball, 1988; Bompy, Lequeue, Imbert, & Dulormne, 2014), possibly due to a lowered efficiency of water transport within the plant (Sobrado,

2007). In addition, studies have shown salinity to affect the branch length of *A. germinans*, with too-high or too-low salinity resulting in a decrease in branch length (Neveu, 2013). Aboveground growth was therefore expected to decrease with increasing salinity.

Contrary to these expectations, the PLS path model found no pattern between *Salinity* and *Aboveground Growth*. In fact, none of the variables included in the model were significantly affected by *Salinity*. However, it is unlikely that salinity plays no effect in determining mangrove forest characteristics. Rather, the lack of significance in this relationship likely has to do with both the structure of the latent variable and the range of pore water salinity present in this study.

The latent variable *Salinity* as present in the PLS model was, overall, not a good representation of its measured variables, which likely contributes greatly to its lack of overall effect within the model. None of the measured variables had a loading of greater than the suggested 0.7. This is not, however, to suggest that salinity is not affected by precipitation, tidal exchange, elevation, or pore water salinity, but rather that it is extremely likely that the response of mangroves to any of those variables depends on levels of the other. For example, tidal exchange is likely not important at higher elevations, and rainfall likely is much more important at higher elevations than low. Measurements of soil salinity itself are likely to result from combinations of all the aforementioned variables. This further illustrates how closely intertwined environmental variables can be, and the difficulty of combining them into single latent constructs.

The values for pore water salinity in this study ranged from 1 PPT to 27 PPT. Abundant rainfall during the time of sampling (May-July 2016) likely contributes to these

low salinity values, illustrating the difficulty in assessing salinity via one-time pore water sampling. Neveu (2013) found that mangroves produce longer branches and more leaves when salinity is at an optimum, and growth decreases when salinity is too far above or below. Decreases in plant growth have been demonstrated when salinity is close to or greater than that of seawater (Bompy, Lequeue, Imbert, & Dulormne, 2014). Those values are above those found in this study, possibly explaining why mangrove growth appears to have no relation to salinity. In addition, salinity within mangrove soils fluctuates greatly due to tidal incursions, precipitation, and biotic factors. It is likely that this fluctuation is equally as important in driving mangrove growth responses as is the yearly average salinity (Bompy, Lequeue, Imbert, & Dulormne, 2014).

Despite its lack of effect on aboveground growth, soil salinity was found to affect the production of prop roots by *R. mangle*. Measurements of aboveground prop roots reflect only a fraction of mangrove belowground processes, but are still valuable as a proxy for these processes. Prop root volume varied in response to both environmental and biotic variables. Not surprisingly, larger trees produce a larger volume of prop roots, and a higher number of prop roots results in a larger volume. However, the relationship between salinity and prop root production is not as straightforward. It has been suggested that mangroves may allocate more resources to belowground growth when salinity stress is high (Ball, 1988; Ball, Cochrane, & Rawson, 1997). Other studies have found the opposite—that mangrove belowground production decreases with increasing salinity (Ball, 2002; Krauss, et al., 2013).

It is unclear whether or not increased root production at higher salinity is beneficial to mangroves. While an increase in root production would aid in water uptake at higher

salinity, this response does not appear to be constant among mangrove species (Krauss, et al., 2013). Furthermore, physiological studies on *L. racemosa* have shown that the structure of the xylem changes at higher salinities to better aid in water transport (Sobrado, 2007) suggesting that mangroves deal with increasing salinity in a number of complex ways.

Prop root production was documented in both *L. racemosa* and *A. germinans* at three out of the six sites (see figure 14). This anomaly has been noted in Florida before (Snedaker, Jimenez, & Brown, 1981; Osland, Day, Larriviere, & From, 2014), but the causes and mechanisms remain unknown. Unfortunately, only two examples of *L. racemosa* and one of *A. germinans* with prop roots were found, so no statistical analyses were able to be performed. Prop roots on *L. racemosa* occurred in Fort Pierce and Vero Beach, in areas of high elevation and firm, sandy soil. The stand of *A. germinans* was found in New Smyrna Beach, in an interior stand with no flooding and dense clay mud. Although no analyses of this phenomenon were possible, these findings confirm that the findings by Osland, et al. (2014) did not occur in isolation. In addition, while prop roots have previously been reported on *A. germinans*, they have not been reported to develop in *L. racemosa* until now. Studies focusing on this phenomenon are clearly required.

a)



b)



Figure 14: Prop root growth on a) *A. germinans* in New Smyrna Beach; and b) *L. racemosa* in Vero Beach.

Interactions between Latitude and Light Availability

Both latitude and light availability were predicted to be important predictors of mangrove morphology. As latitude and potential stress from cold events increases, the effect of light availability was expected to increase, especially in closed-canopy zones where competition for sunlight is more pronounced. Adult mangroves growing under the combined pressure of both colder temperatures and lack of sunlight were expected to

display the most dramatic changes in terms of height and crown parameters. Low light, closed-canopy zone trees were expected to be tallest and have the shortest, narrowest crowns regardless of latitude. Mangroves growing in full sunlight, however, are not constrained by a need to grow out from under the canopy and also have the physical space to extend their crown laterally. Therefore, these trees were predicted to be the shortest, with the longest and widest crowns. Mangroves found along the edge of the forest partially under canopy cover and partially in sunlight were expected to fall somewhere in the middle.

Consistent with this prediction, closed-canopy or partial-canopy zone mangroves displayed larger decreases in height and DBH than did open-canopy zone mangroves. Crown size was expected to be the least affected by latitude in closed-canopy zones, as lack of both physical space and sunlight would presumably constrain lateral crown expansion regardless of latitude. As predicted, closed-canopy zone mangrove crown volume displayed no change with latitude across the majority of the site, suggesting no relation to latitudinal variables.

There is a distinct difference in how mangrove crown volume changes with latitude between the three light zones. If crown volume was responding solely to colder temperatures, it would be expected that volume would decrease with latitude, as longer branches are more susceptible to frost embolisms (Sobrado, 2007; Stuart, Choat, Martin, Holbrook, & Ball, 2007). Partial-canopy zone mangroves are the only mangroves to display this kind of consistent decrease in volume with latitude. Closed-canopy zone mangroves decrease slightly between New Smyrna Beach, while open-canopy zone mangroves only decrease between Miami and Port St Lucie, and actually increase in crown volume north of Vero Beach (see Figure 6).

These patterns indicate a strong interaction between latitude and sunlight in terms of mangrove morphological trends. While mangroves in all light zones were shorter and shrubbier in the north, differences exist in exactly how growth form changes. Low-light mangroves, switch from tall and slender to short and shrubby primarily because of a reduction in height, with little corresponding change in crown volume. However, mangroves growing in abundant sunlight do not change much in height, and may begin to increase in crown volume north of Vero Beach.

The interaction between sunlight and latitude is a strong indicator of phenotypic plasticity in mangroves. Under ideal circumstances, trees growing in shaded conditions generally allocate more energy towards height growth at the expense of branch production, while those growing in full sun generally allocate energy towards branching and leaf production in order to maximize photosynthesis. The fact, therefore, that closed-canopy mangroves decrease greatly in height while open-canopy mangroves don't is suggestive that latitudinal changes are made where the tree is allocating most of its energy. Furthermore, the fact that canopy volume in open canopy is so variable suggests that, when sunlight is abundant, other stressors or resources, such as salinity or nutrient availability may become more important.

An interesting pattern in crown volume changes becomes apparent north of Vero Beach. North of this site, which is located at approximately 27.75°N , the effects of frost seem to take effect. Figure 6 shows that, north of the Vero Beach site, crown volume in open-canopy mangroves may be increasing, rather than decreasing. It is possible that this increase could be due to the increasing chance of temperatures low enough to damage growing tips. The crown volume of partial-canopy mangroves appears to level off north of

New Smyrna beach, which may suggest a similar trend for these trees. Interestingly, closed-canopy mangrove crown volume decreases the most north of that same site. Although no direct measures of temperature were taken in this study, it is possible that slightly cooler conditions exist in the shadier zones. In the two northernmost sites, this slight decrease in temperature could be enough to increase the risk of frost embolisms affecting entire branches, rather than just growing tips and new shoots. Conversely, in high-sunlight zones the warmth of the sun might offset cooler air temperatures.

These interactions make it abundantly clear that mangrove survival and growth is limited by both sunlight and latitude. Further research, however, is needed into the factors that affect mangrove crown size. Crown volume varied very little in low-sunlight zones, but was extremely variable when sunlight was abundant. Research is needed in order to determine what other factors, such as salinity, elevation, flooding, or nutrient availability, affects crown volume when sunlight is no longer limiting.

Response of Belowground Growth to Environmental Variables

The results of this study focused on the response of aboveground growth to environmental change, but belowground structures have been found to make up the majority of mangrove biomass (Hogarth, 1999). Understanding how these processes relate to environmental variables is, therefore, crucial to a complete understanding of how mangrove growth form changes with environment. As the results of this study have shown, many different variables affect aboveground growth, and those variables, as well as others, likely also affect belowground processes.

Some studies have been done on mangrove belowground growth. Lovelock et al., (2009) found that nutrient enrichment over the long term increased mangrove mortality

from storm events. As has been documented in prior studies, nutrient enrichment increases the allocation of resources to aboveground growth, which the study found corresponded to a decrease in belowground growth. This pattern led to a taller, heavier tree with less belowground support, making these mangroves more vulnerable to storm or flooding damage (Lovelock, Ball, Martin, & Feller, 2009). Other studies have found differing responses of belowground growth in mangroves to nutrient enrichment. Adame et al. (2014) found that root biomass and production actually increases with phosphorus availability in regions where soil salinity is high. This study highlights the variation in the response of mangrove growth to belowground conditions.

The belowground processes of mangroves are important not just as a reflection of mangrove morphological change. Belowground growth in mangroves has received increasing attention due to the capacity for belowground carbon storage, soil stabilization, and resistance to sea level rise. Murdiyarso et al (2009) found that mangroves in Indonesia have an exceptionally large capacity for carbon storage in comparison to most forest types, and that the majority of that carbon storage occurs belowground. Further studies have found that 0.5% of global coastlines occupied by mangroves contributes to 10-15% of coastal sediment carbon accumulation (Alongi D. M., 2014). These studies illustrate not only the importance of better understanding mangrove belowground processes and patterns of resource allocation, but also the importance of mangrove ecosystems in mitigating climate change.

However, due to the difficulty of assessing mangrove belowground growth in non-destructive ways, few studies have been able to assess how belowground and aboveground resource allocation work in relation to each other in mangroves, and how those processes

might be affected by combinations of environmental drivers. The belowground component is likely important in terms of the long-term survival of mangroves in a changing climate. Increased root production leads itself to better soil stabilization and tolerance to changes in flooding regimes (Hogarth, 1999; Alongi D. M., 2008). Furthermore, some studies have linked the structure of mangrove prop roots with fish community structure. A 2010 study found that fish abundance changed depending on the orientation of artificial mangrove prop roots, with some species preferring upright roots and others preferring hanging roots (Nagelkerken, et al., 2010). Therefore, belowground architecture and growth form may very well affect more than overall mangrove survival in a changing climate, and further research is needed to determine how these processes are affected by all environmental conditions, but especially those likely to be affected by climate change.

Adaptability in response to environmental changes is likely going to be beneficial in the coming decades. As rising seas force mangroves to migrate landward (Scavia, et al., 2002; Krauss, et al., 2013) and rising air temperatures allow them to expand northward (Cavanaugh, et al., 2013; Saintilan, Wilson, Rogers, Rajkaran, & Krauss, 2014), mangroves will encounter a high degree of variability in terms of environmental parameters. Plasticity has been shown to give plants an advantage when it comes to climate change (West-Eberhard, 2003; Matensanz, Gianoli, & Valladares, 2010), and this study provides new evidence suggesting the existence of adaptability, if not plasticity, in mangroves. Further lab and field studies are required in order to determine the exact nature of mangrove morphological change, but current evidence suggests that mangrove growth form is highly responsive to changes in environmental conditions.

Species-Specific Responses to Environmental Conditions

The response of mangroves to environmental conditions was expected to vary by species, as the three species present in Florida have different optimum ranges and tolerances for different conditions (Odum, McIvor, & Smith, 1982). However, the patterns of morphological change in *A. germinans*, *R. mangle*, and *L. racemosa* were very similar, with a few exceptions.

A. germinans and *L. racemosa* were more likely than *R. mangle* to have more than one main stem. This is partially consistent with the predictions that *L. racemosa* would produce the highest number of main stems. This prediction was based largely on qualitative observations of mangroves in the field, as few studies have been conducted on *L. racemosa* physiology or growth. However, the number of main stems of an individual mangrove was not found to correlate well with any other morphological characteristic.

Canopy volume, tree height, and other morphological characteristics did not vary significantly between species. This indicates that the change in morphology as seen along the latitudinal gradient is not due to a change in species composition. Because *A. germinans* does not differ in height or crown volume from the other two species, the transition to a shorter, bushier growth form cannot be attributed solely to the change to *A. germinans* dominance in northern sites.

When changes across latitude were compared across species in a two-way ANOVA, several interesting patterns emerged. Crown volume was shown to decrease with latitude in *R. mangle* and *L. racemosa*, but remained relatively constant in *A. germinans*, except at the very northern edge of the range. Furthermore, *A. germinans* crown volume was significantly larger than that of the other two species in Vero Beach and New Smyrna

Beach, suggesting that mangroves may experience some effect of colder temperatures as far south as Vero Beach. These larger crowns found in *A. germinans* are likely due to the increased frost tolerance of this species. Cavanaugh et al. (2015) found that mortality occurs in *L. racemosa* at -2.77°C , in *R. mangle* at -3.99°C , and in *A. germinans* at -4.62°C . However, sublethal effects of effects of freezing such can occur at warmer temperatures (Stuart, Choat, Martin, Holbrook, & Ball, 2007; Osland, Day, Larriviere, & From, 2014).

Due to their lower tolerance to frost, *L. racemosa* and *R. mangle* likely experience damage to outer branches and growing tips in latitudes where *A. germinans* does not. Thus, their crown volume would shrink faster and further south than that of *A. germinans*, which is exactly the pattern seen in the crown volume changes seen in figure 10. The fact that *R. mangle* and *L. racemosa* crown size shrinks while *A. germinans* remains relatively constant also explains why the relative crown diameter of *A. germinans* is overall larger than those of the other two species (see figure 8).

Environmental conditions were also expected to have species-specific effects on the density of mangrove adults and seedlings. Density of adult *A. germinans* increased with latitude, but *R. mangle* and *L. racemosa* did not significantly vary in density with latitude. However, the PLS path model assumes a linear relationship between variables, and univariate analysis of these data reveal that the relationship between mangrove abundance and latitude, while present, proves to be nonlinear.

Adults and seedlings of both *R. mangle* and *L. racemosa* increased in density between Miami and Vero Beach, and then declined sharply further north (see Figure 13). As expected, therefore, all three species do show a relationship with latitude, with *A. germinans* increasing with increasing latitude and the other two species decreasing sharply

once conditions are no longer favorable. These patterns are true for both adults and seedlings, as would be expected. Latitude, does, therefore, affect mangrove density, but not in a linear way. There was no evidence of intraspecific interactions between adults the three species. Despite predictions to the contrary, none of the species responded to the any of the others in terms of abundance.

However, these results should be taken with a grain of salt. Data from this study was collected at only one site at each latitude, meaning that site-specific conditions likely affect mangrove density independent of latitude. Disturbance history in particular is likely important in terms of patterns of species dominance.

While the exact disturbance history of many of these sites is unknown, the Fort Pierce and Port St. Lucie sites are known to have been affected by Hurricane Wilma in 2005, which made landfall almost directly atop the Fort Pierce site and is known to have decimated the majority of the mangrove cover in the area. These two sites, therefore, must be considered to be relatively young, as most of the growth present in the current study has only occurred in the last ten years. Dominance patterns in Florida mangroves are thought to be affected by the age of the stand. Generally, *L. racemosa* is an abundant early colonizer, but later is outcompeted by *A. germinans* and *R. mangle* depending on salinity and flooding regime (Proffitt & Devlin, 2005) . Thus, hurricane disturbance and age of the stand may be having an effect on observed patterns of species dominance.

The development of mosquito impoundments in the Indian River Lagoon creates a unique disturbance history to these sites. Mosquito impoundments alter vegetation cover, salinity, and tidal and flooding regimes and thus may dramatically affect mangrove cover (Sweat, 2009). Studies of the effects of these impoundments on mangrove density have

indicated that *R. mangle* and *A. germinans* density changes based on impoundment type and history. Rotational impoundment management sites tend to be dominated by *R. mangle*, while *A. germinans* was more dominant in natural areas (Middleton, Devlin, Proffitt, McKee, & Cretini, 2008). This may explain why *A. germinans* density was so low in the Vero Beach, Fort Pierce, and Port St. Lucie sites.

These questions of disturbance history site age, and local peculiarities arise whenever sites are used to extrapolate to a larger geographical area. More data is needed before any solid conclusions can be drawn about mangrove dominance patterns across latitude. Future studies investigating mangrove dominance patterns across latitude should include disturbance and age as factors.

Factors Affecting Seedling and Salt Marsh Abundance

Mangrove seedlings: Mangrove seedling abundance was expected to show species-specific responses. *R. mangle* and *L. racemosa* seedling densities were expected to closely follow patterns of adult densities, and therefore be quite abundant throughout most of the study area, but decrease sharply in abundance in the northern sites due to climate. These patterns were supported by this study, (see Figure 13) and likely arise from a suite of interacting effects.

First, it is important to note that the survey was conducted occurred in May and June of 2016. Seedlings present and counted in this study, therefore, represent those that have survived since the previous year's seedfall and not necessarily total seedling recruitment. It is likely that seedling mortality due to unfavorable conditions occurred well before data collection was begun. This may explain why adult and seedling densities of the same species are uncorrelated. An area with a high density of adult *R. mangle*, for

example, would be predicted to also have a high density of *R. mangle* seedlings, but it is likely that the majority of those seedlings would not survive the first year.

Regardless, several patterns in seedling density and distribution are present. *A. germinans* seedling density was directly affected by the latitudinal gradient, in keeping with studies that found that mangrove range expansion is primarily driven by raising annual minimum temperatures and the recent lack of severe frosts (Mendez-Alonzo, Lopez-Portillo, & Riviera-Monroy, 2008; Cavanaugh, et al., 2013; Saintilan, Wilson, Rogers, Rajkaran, & Krauss, 2014). However, *R. mangle* recruitment was not significantly affected by the latitudinal change directly; rather, decreasing seedling recruitment with latitude in this species appears mainly due to competition with increasing salt marsh.

R. mangle recruitment was also significantly affected by *Relative Crown Size* through two indirect pathways. First, the increase in *Light Availability* with *Relative Crown Size* led to a positive effect of relative crown size on seedling recruitment. Second, *Light Availability* has a significant direct effect on *Salt Marsh*, which in turn negatively affects *R. mangle*. As a result, *Relative Crown Size* has a large positive total effect on *Rhizophora Seedling Density*.

The positive effect of *Relative Crown Size* on *Light Availability* is surprising. The PLS model results suggest that, as mangroves become shorter and shrubbier, the amount of available light under the crown increases. This is in direct contrast to the expectation of increased shade with increased crown size. It is important to note, however, that the relationship between *Aboveground Growth* and *Relative Crown Size* is negative—that is, as aboveground growth increases, relative crown size decreases. Consequently,

Aboveground Growth has an indirect negative effect on *Light Availability*, which does fit with predictions.

Competition is clearly an important key to the expansion of mangroves into salt marsh. Both adult mangrove morphology and salt marsh presence affect the establishment and survival of *R. mangle* seedlings. Studies conflict, however, on exactly how salt marsh affects mangrove seedling recruitment and survival. In China, a study on the effects of the invasive *S. alterniflora* on native mangrove recruitment have indicated that the salt marsh either represses or facilitates mangrove seedling establishment depending on other environmental factors such as salinity and canopy closure (Zhang, Huang, Wang, Chen, & Lin, 2012). Howard *et al.* (2015) demonstrated that salt marsh can suppress *A. germinans* and *L. racemosa* seedling establishment and slow mangrove encroachment into salt marsh. Similar to the studies in China, the magnitude of the suppression of mangrove seedling growth by salt marsh was mediated by environmental variables.

L. racemosa seedling abundance was not affected by any measured environmental variables. Rather, the abundance of *L. racemosa* seedlings was primarily affected by the abundance of *R. mangle* seedlings. This relationship may partially explain the results shown in Figure 13. At lower latitudes, competition with abundant *R. mangle* seedlings may prohibit *L. mangle* establishment, while at higher latitudes, cooler temperatures and latitudinal effects restrict seedling survival. This relationship between *R. mangle* and *L. racemosa* leads to an indirect positive effect of *Salt Marsh* on *L. racemosa* seedling density. A facilitative effect of salt marsh has been found in *L. racemosa* seedlings before, and this competitive pathway may contribute to that process.

As air temperatures increase globally, the zone in which mangroves are able to survive is expected to grow (Cavanaugh, et al., 2015). This study indicates that *A. germinans* expansion will likely occur independently of salt marsh, as its abundance at both seedling and adult stages was most strongly affected by latitude. The extremely low direct effect of salt marsh on *A. germinans* seedlings is likely due to the fact that *A. germinans* has been documented to undergo both competition and facilitation with salt marsh (Guo, Zhang, Lan, & Pennings, 2013; Zhang, Huang, Wang, Chen, & Lin, 2012), leading to a net zero effect.

R. mangle and *L. racemosa* respond very differently to environmental variables. Once no longer limited by frost events, the results of this study suggest that interactions between established mangroves and salt marsh will determine the ability of *R. mangle* and *L. racemosa* to expand further north. Currently, decreasing aboveground growth further north allows more light to penetrate the canopy. This increase of light with latitude has both direct and indirect effects on *R. mangle*. While increasing light availability positively affects seedling survival, the concurrent positive effect on salt marsh survival leads to a negative effect of light on *R. mangle* seedling survival.

If temperatures increase enough to allow larger growth forms in northern latitudes, canopy closure may occur, and large mangroves may outcompete salt marsh. However, *R. mangle* seedling survival is positively affected by relative crown size—and thus negatively associated with absolute measures of aboveground growth. It is interesting to note that these patterns of *R. mangle* abundance appear to apply only to the seedling stage. Abundances of adult *R. mangle* did not vary with any of the environmental variables in this

study, suggesting that once stands are well-established, survival is no longer as strongly affected by environmental conditions.

Salt marsh: The direct increase of salt marsh abundance and species richness with latitude was anticipated due to the ecotone along which this study occurred. However, it is interesting to note that indirect pathways increase the total effect of *Latitude* on *Salt Marsh* by changing the availability of light. Both *Latitude* and *Relative Crown Size* indirectly influence the amount of light, and thus have indirect positive effects on *Salt Marsh*. Latitudinal patterns of salt marsh abundance, therefore, are likely a result of both climate and light availability. As mangroves continue to move northward, it is likely that the light availability will decrease. The climatic drivers behind shrubbier growth in *A. germinans* may weaken as air temperatures continue to increase (Stuart, Choat, Martin, Holbrook, & Ball, 2007; Cavanaugh, et al., 2015).

Salt marsh was also affected positively by *Relative Crown Size*, which is surprising given that one would expect the opposite. It is possible that, as mangroves allocate more resources to the aboveground structures such as branches and leaves that make up a larger crown, allocation to belowground resources suffers as a consequence. This reduction in belowground growth might then lead to a reduction in belowground competition between mangroves and salt marsh for water and nutrients, allowing salt marsh to become more abundant under these trees. This study was unable to measure belowground production, and studies of belowground competition are difficult to conduct, but this is likely why trees with larger crowns can support higher abundances of salt marsh.

The Use of Partial Least Squares Path Modeling in Ecology

This study is, to the author's knowledge, the first to utilize PLS path modeling in ecology. This technique is relatively new, but has gained traction in business and social sciences as an alternative to conventional covariance-based structural equation modeling. At first glance, PLS path modeling may seem uniquely suited for ecological studies. Ecological data—especially count and abundance data—are often highly non-normal and suffer from issues of zero covariance and autocorrelation. In addition, sample sizes in ecological field studies are often small, and the predicted relationships between variables are usually many and complex (Carrascal, Galvan, & Gordo, 2009). These kinds of data are difficult, if not impossible, to analyze with covariance-based SEM, but can be handled by PLS models (Guo, Yuan, Archer, & Connelly, 2011; Sanchez, 2013).

However, the lack of any global criterion of goodness-of-fit means is a major drawback and means that PLS techniques are not universally appropriate (Henseler & Sarstedt, 2013). PLS path modeling is generally considered less suitable than conventional SEM for studies dealing with theory testing or confirmation, or the comparison of alternate theories or models (Joreskog & Wold, 1982). PLS techniques are most appropriate for studies aimed at identifying key drivers or relationships, when the structural model is likely highly complex, and when sample sizes are small (Hair, Hult, Ringle, & Sarstedt, 2014). Traditional covariance-based SEM is more appropriate for studies where the goal is theory testing or comparing between models, and when a global goodness-of-fit criterion is needed (Hair, Ringle, & Starstedt, 2011).

This study aimed to identify important patterns in the relationship between mangroves, salt marsh, and environment, and PLS path modeling was an appropriate way

to analyze these data. Because this is the first study to analyze relationships between mangrove morphology, salt marsh, and mangrove seedling recruitment in a multivariate fashion, the primary goal of this study was to identify potential patterns and the key biotic and abiotic drivers behind variation in the morphology and distribution. To that end, the PLS technique was successful, as complex patterns were identified. Despite the drawback of an accurate way to measure global goodness-of-fit, PLS techniques are still useful for identifying the drivers behind ecological variability.

CONCLUSIONS AND FUTURE RESEARCH DIRECTIONS

This study has provided further data on morphological variability within mangroves, including how these species react to several different environmental factors at once. Specifically, light availability, latitude, and salinity, and the interactions between these variables, all significantly affected mangrove morphological characteristics in neotropical mangroves. This suggests the presence of plasticity in these species, a trait that may help mangroves adapt to changing climatic conditions. However, more work is needed in order to corroborate these results. Suggested research directions include experimental studies on the effects of latitude and light availability on mangrove morphology as well as identifying the genetic components of mangrove growth form.

This study also investigated whether or not mangrove growth form affects salt marsh survival and seedling recruitment. Changes in growth form from tall and slender to short and shrubby corresponded with an increase in light penetration, which affected both salt marsh and mangrove seedlings, though the response of seedlings is species-dependent. These findings suggest that species interactions and biotic effects are as important as climate in determining the future of mangroves and salt marsh in eastern Florida. Further work is also needed here, as this is the first study to utilize multivariate techniques in the study of mangrove intrusion into salt marsh.

Finally, this study demonstrates the use of partial least squares path modeling in ecology. This technique has emerged in business and the social sciences, but its application

in ecology has thus far been limited, if not non-existent. However, ecological data are generally well-suited for PLS path modeling, as they are often non-normal and autocorrelated, and sample sizes tend to be small. PLS techniques allow these kinds data to be investigated in a multivariate way, though the current lack of an adequate measure of model fit limits its application. That being said, PLS path modeling works well for exploratory analyses and identifying multivariate relationships in ecological data.

APPENDICES

Appendix A: Total Effects

Total effects of the structural PLS model are listed in the table below. Effects significant at the 0.05 level are in bold. Abbreviations for latent variables are as follows: SAL=Salinity; LAT=Latitude; ABG=Aboveground Growth; RCS=Relative Crown Size; AAD= Avicennia Adult Density; RAD=Rhizophora Adult Density; LAD=Laguncularia Adult Density; LA=Light Availability; SM=Salt Marsh; ASD=Avicennia Seedling Density; RSD=Rhizophora Seedling Density; LSD=Laguncularia Seedling Density

Pathway	Direct Effect	P	Total Effect	P
SAL-ABG	-0.044	0.629	-0.044	0.629
SAL-RCS	-	-	0.011	0.727
SAL-AAD	-0.385	0.085	-0.387	0.087
SAL-RAD	0.227	0.623	0.196	0.635
SAL-LAD	0.185	0.572	0.177	0.614
SAL-LA	-	-	0.001	0.984
SAL-SM	0.047	0.708	0.121	0.354
SAL-RSD	0.127	0.360	0.137	0.230
SAL-ASD	-0.017	0.942	0.019	0.915
SAL-LSD	0.106	0.726	0.044	0.715
LAT-ABG	-0.808	0.000	-0.808	0.000
LAT-RCS	-	-	0.278	0.009
LAT-AAD	0.327	0.000	0.287	0.000
LAT-RAD	0.092	0.478	0.109	0.382
LAT-LAD	0.094	0.568	0.11	0.365
LAT-LA	-	-	0.104	0.015
LAT-SM	0.195	0.040	0.272	0.005
LAT-ASD	0.344	0.002	0.331	0.001
LAT-RSD	-0.146	0.145	-0.286	-0.001
LAT-LSD	-0.072	0.589	0.044	0.715
ABG-RCS	-0.345	0.001	-0.345	0.001
ABG-AAD	-	-	0.049	0.397
ABG-LSD	-	-	0.002	0.982
ABG-LA	-	-	-0.129	0.011

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	-	-		
ABG-SM			-0.169	0.006
ABG-RSD	-	-	0.099	0.052
ABG-ASD	-	-	0.003	0.932
ABG-LSD	-	-	-0.034	0.458
RCS-AAD	-0.137	0.370	-0.137	0.374
RCS-RAD	0.038	0.797	-0.052	0.652
RCS-LAD	-0.056	0.831	-0.005	0.984
RCS-LA	0.367	0.000	0.373	0.000
RCS-SM	0.352	0.000	0.487	0.000
RCS-RSD	-0.196	0.147	-0.284	0.009
RCS-ASD	-0.024	0.867	-0.006	0.953
RCS-LSD	-0.003	0.987	0.102	0.398
AAD-LA	0.018	0.879	0.018	0.879
AAD-SM	-0.177	0.079	-0.170	0.119
AAD-RAD	0.078	0.508	0.078	0.508
AAD-LAD	0.013	0.937	0.02	0.896
AAD-RSD	-0.094	0.311	-0.057	0.503
AAD-ASD	-0.065	0.736	-0.085	0.646
AAD-LSD	-0.077	0.399	-0.108	0.222
ASD-RSD	-0.082	0.129	-0.082	0.129
ASD-LSD	0.144	0.560	0.144	0.560
LA-SM	0.284	0.011	0.284	0.011
LA-RSD	-0.012	0.899	-0.074	0.391
LA-ASD	-0.126	0.237	-0.096	0.420
LA-LSD	-0.045	0.813	-0.014	0.939
SM-RSD	-0.211	0.006	-0.211	0.006
SM-ASD	0.105	0.388	0.105	0.388
SM-LSD	0.168	0.458	0.213	0.291
RAD-SM	-0.152	0.414	-0.152	0.429
RAD-LA	-0.078	0.623	-0.053	0.742
RAD-LAD	0.094	0.719	0.094	0.719
RAD-RSD	0.133	0.382	0.159	0.319
RAD-LSD	-0.058	0.837	-0.104	0.726
RAD-ASD	-0.131	0.418	-0.135	0.369
RSD-LSD	-0.156	0.000	-0.156	0.000
LAD-LA	-0.122	0.470	0.112	0.467
LAD-SM	0.075	0.576	0.109	0.500
LAD-RSD	-0.166	0.375	-0.135	0.311
LAD-ASD	-0.108	0.475	-0.092	0.492
LAD-LSD	0.162	0.660	0.188	0.599

Appendix B: Tables of Means

Means of morphological characteristics at each of the six sites. Standard deviation is included after the mean.

Site	Lat/Long	Hieght (cm)	DBH (mm)	Crown Diam. (cm)
STA		152.33±23.91	5.52±3.56	213.17±128.15
NSB		376.08±131.02	33.94±17.02	209.17±71.48
VB		490.09±204.49	45.72±27.39	260.06±164.30
FTP		459.94±159.85	44.93±21.42	352.89±110.76
PSL		559.59±174.55	46.71±18.03	366.22±144.80
MIA		1293.40±487.17	126.99±52.21	546.44±248.00

Mean density (individuals/m²) of mangrove seedlings and adults. Mean percent occurrence of salt marsh at each of the six sites. Standard deviation is included after each mean.

Site	Lat/Long	R. mangle		A. germinans		L. racemosa	
		Adults	Seedl.	Adults	Seedl	Adults	Seedl
STA		0±0	0±0	23.83±20.88	17.50±23.26	0±0	0±0
NSB		0.83±1.54	2.39±4.27	10.83±9.18	67.61±69.26	0.056±0.23	1.17±2.64
VB		6.22±5.14	8.67±8.67	1.78±2.56	2.39±3.65	3.83±3.96	8.17±15.83
FTP		2.28±9.17	7.06±11.97	1.50±3.55	23.11±53.16	1.72±2.30	7.72±10.36
PSL		2.61±3.50	4.83±4.84	3.78±4.19	7.56±7.06	2.00±2.35	5.61±6.83
MIA		1.11±1.18	9.83±9.57	0.44±0.78	1.61±2.90	0.33±0.59	0.78±1.17

Site	Spartina alterniflora	Batis maritima
STA	0.211±0.37	0.049±0.10
NSB	0±0	0.195±0.25
VB	0±0	0.287±0.31
FTP	0±0	0.063±0.19
PSL	0±0	0.215±0.03
MIA	0±0	0.003±0.01

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