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Evaluating plant community response to sea level rise and anthropogenic drying: Can life stage and competitive ability be used as indicators in guiding conservation actions?

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FLORIDA INTERNATIONAL UNIVERSITY

Miami, Florida

EVALUATING PLANT COMMUNITY RESPONSE TO SEA LEVEL RISE AND ANTHROPOGENIC DRYING: CAN LIFE STAGE AND COMPETITIVE ABILITY BE USED AS INDICATORS IN GUIDING CONSERVATION ACTIONS?

A dissertation submitted in partial fulfillment of the
requirements for the degree of
DOCTOR OF PHILOSOPHY
in
BIOLOGY
by
Kristie Susan Wendelberger

2016

To: Dean Michael R. Heithaus
College of Arts, Sciences and Education

This dissertation, written by Kristie Susan Wendelberger, and entitled Evaluating Plant Community Response to Sea Level Rise and Anthropogenic Drying: Can Life Stage and Competitive Ability be Used as Indicators in Guiding Conservation Actions?, having been approved in respect to style and intellectual content, is referred to you for judgment.

We have read this dissertation and recommend that it be approved.

Steven Oberbauer

Michael Ross

Tiffany Troxler

Eric von Wettberg

Keqi Zhang

Jennifer H. Richards, Major Professor

Date of Defense: June 17, 2016

The dissertation of Kristie Susan Wendelberger is approved.

Dean Michael R. Heithaus
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Dean Andrés G. Gil
Vice President for Research and Economic Development
and Dean of the University Graduate School

Florida International University, 2016

DEDICATION

I dedicate this dissertation to Dr. Jack Weiss (1953-2014) whose endless patience in teaching me R and ecological statistics has touched every aspect of my Masters and PhD research and will for the rest of my career. I also dedicate this dissertation to my dad, Richard Wendelberger (1941-2015), who had the plant bug and started me off on my plant saving path so long ago.

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ABSTRACT OF THE DISSERTATION

EVALUATING PLANT COMMUNITY RESPONSE TO SEA LEVEL RISE AND ANTHROPOGENIC DRYING: CAN LIFE STAGE AND COMPETITIVE ABILITY BE USED AS INDICATORS IN GUIDING CONSERVATION ACTIONS?

by

Kristie Susan Wendelberger

Florida International University, 2016

Miami, Florida

Professor Jennifer H. Richards, Major Professor

Increasing sea levels and anthropogenic disturbances have caused the world's coastal vegetation to decline 25-50% in the past 50 years. Future sea level rise (SLR) rates are expected to increase, further threatening coastal habitats. In combination with SLR, the Everglades ecosystem has undergone large-scale drainage and restoration changing Florida's coastal vegetation. Everglades National Park (ENP) has 21 coastal plant species threatened by SLR. My dissertation focuses on three aspects of coastal plant community change related to SLR and dehydration. 1) I assessed the extent and direction coastal communities—three harboring rare plant species—shifted from 1978 to 2011. I created a classified vegetation map and compared it to a 1978 map. I hypothesized coastal communities transitioned from less salt- and inundation-tolerant to more salt- and inundation-tolerant communities. I found communities shifted as hypothesized, suggesting the site became saltier and wetter. Additionally, all three communities harboring rare plants shrunk in size. 2) I evaluated invading halophyte (salt-tolerant) plant influence on soil salinity via a replacement series greenhouse experiment. I used two halophytes and two glycophytes (non-salt-tolerant) to look at soil salinity over time under 26 and 38‰ groundwater. I hypothesized that halophytes increase soil salinity as compared to glycophytes through continued transpiration during dry, highly saline periods. My results supported halophytic influence on soil salinity; however, not from higher transpiration rates. Osmotic or ionic stress likely decreased glycophytic biomass resulting in less overall plant transpiration. 3) I assessed the best plant life-stage to use for on-the-ground plot-based community change monitoring. I tested the effects of increasing salinity (0, 5, 15, 30, and 45‰) on seed germination and seedling establishment of five coastal species, and compared my results to salinity effects on one-year olds and adults of the same species. I hypothesized that seedling establishment was the most vulnerable life-stage to salt stress. The results supported my hypothesis; seedling establishment is the life-stage best monitored for community change. Additionally, I determined the federally endangered plant *Chromolaena frustrata*'s salinity tolerance. The species was sensitive to salinity >5‰ at all developmental stages suggesting *C. frustrata* is highly threatened by SLR.

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ABBREVIATIONS AND ACRONYMS

CERP	Comprehensive Everglades Restoration Plan
DEM	Digital elevation model
ENP	Everglades National Park
ENVI	Exelis Visual Information Solutions
FLAASH	Line-of-sight Atmospheric Analysis of Hypercubes
GPS	Global Positioning System
IPCC	Intergovernmental Panel on Climate Change
LiDAR	Light Detection And Ranging
NAVD	North American Vertical Datum of 1988
NCGRP	National Center for Genetic Resources Preservation
NDVI	Normalized Difference Vegetation Index
oob	Out-of-bag error estimate
SLR	Sea level rise
WV2	WorldView-2 satellite data

INTRODUCTION

Increasing sea levels and anthropogenic alterations together are resulting in a change or complete loss of coastal plant communities around the world (Nicholls and Cazenave, 2010; Terry and Chui, 2012; Kirwan and Megonigal, 2013). Shifts in plant communities from less salt- and lower inundation-tolerant to more salt- and higher inundation-tolerant community types or to open water have been documented (Ross et al., 1994; Kearney et al., 2002; Kirwan et al., 2008; Saha et al., 2011; Sharpe and Baldwin, 2012; Terry and Chui, 2012). Future SLR rate is expected to exceed both the mean global SLR rate during the 20th century (1.7mm yr^{-1}) and SLR rate since 1993 (3.6mm yr^{-1}) (IPCC, 2014). Florida has the shallowest water table in the continental US, its coastal communities are distributed across a gradient that is 0-2m above mean sea level (Hoffmeister, 1974), and it has undergone significant ecosystem drying as a result of anthropogenic changes (Davis et al., 2005). Ecosystem drying and/or hydrologic restoration and SLR effects are interacting most prominently in Florida's coastal areas, impacting its coastal plant communities.

It is expected that major changes will occur along Florida's coast over the coming decades. Previous work has found changes in Florida's coastal plant communities resulting from both SLR alone (Gaiser et al., 2006) and a combination of SLR and ecosystem drying (Alexander, 1974; Ross et al., 1994, 2000; Holmes and Marot, 1999; Holmes et al., 1999; Williams et al., 1999; Gaiser et al., 2006; Desantis et al., 2007; Krauss et al., 2011). Gaiser et al. (2006) found that while changes to plant communities along the coast of Florida have been occurring long before ecosystem drainage, the rate of change (2-4m yr^{-1} interior-ward coastal ecotone encroachment) is one or two magnitudes faster since Everglade's drainage began. Should the trends of ecosystem change along Florida's coast continue, we expect to see a decrease in area of freshwater communities and an increase in halophytic community cover. The species composition of coastal hardwood hammocks and buttonwood forests is expected to shift from glycophyte to halophyte species as the vadose zone thins and salinizes (Saha et al., 2011). This salinity change may lead to the disappearance of critically imperiled and endemic coastal species, including the federally endangered *Chromolaena frustrata* and the Florida endangered *Kosteletzkya depressa* (Saha et al., 2011).

Rare species richness tends to be negatively correlated with salinity in coastal habitats (Saha et al., 2011). Everglades National Park (ENP), which has a significant coastal extent, harbors 43 critically imperiled species as defined by Gann et al. (2002); 21 of these are threatened by SLR, including one federally endangered species, *Chromolaena frustrata* (Saha et al., 2011). To form a realistic conservation action strategy in the face of large-scale environmental change, land managers need to prioritize species under greatest extinction threat. With this information, they can decide how to allocate resources and funding for the preservation of the greatest amount of biodiversity.

In Chapter I, I used remote-sensing techniques to determine if the extent and spatial arrangement of coastal forests encompassing the mainland range of *C. frustrata* has changed over the past three decades. I assess changes and direction of change of seven major coastal plant community types (red, black, and white mangrove forests, marl prairie, tropical hardwood hammock, buttonwood forest with halophytes, and buttonwood forest with glycophytes). Chapter I was formatted to be submitted to the journal Nature Climate Change.

Many coastal vegetation processes depend on an unsaturated layer between the groundwater table and soil surface called the vadose zone. The vadose zone is a thin layer between the top of the highly brackish groundwater table and the soil surface; water is stored in the vadose zone and moved between the soil surface, root zone, and groundwater (Harter et al., 2004). During the dry season, the vadose zone can dry up, drawing more saline groundwater from below and increasing soil salinity. Conversely, during the wet season, when precipitation is high, rainwater seeps into the vadose zone, flushing salt from the soil column, recharging the freshwater lens, and freshening the groundwater table (Terry and Chui, 2012; Badaruddin et al., 2015). The seasonal desalinization process, along with slightly higher elevation, allows glycophytic (freshwater) plant communities to exist in salty coastal areas (Sternberg et al., 2007; Teh et al., 2008; Saha et al., 2015). Below ground feedback loops with both SLR (Price et al., 2006; Blanco et al., 2013) and wetland drying (Kirwan and Megonigal, 2013) occur in the soil vadose zone. Sea level rise raises the groundwater table, while wetland drying reduces the freshwater head, thinning the freshwater lens and leaving it vulnerable to permanent salinization (Sternberg and Swart, 1987; Terry and Chui, 2012).

In some cases, a plant community can out-compete an adjacent community by altering salinity regimes to favor the tolerances of the first community, thereby inhibiting the other community. The competitive effect adds a biological component to the potential causes of community change (Nosetto et al., 2007). The effect of salt on plants, communities, and halophyte:glycophyte habitat competition is well established (Jassby et al., 1995; Ungar, 1998; Spalding and Hester, 2007; Armas et al., 2010); however, there are conflicting results on the influence plants have on soil salinity. Recent, studies assessed the ability of halophytes and other plant types to desalinize soil via phytoremediation (Qadir et al., 2003, 2007; Van Oosten and Maggio, 2015). Conversely, other studies have shown that conversion of land into different habitat types can lead to higher, more saline water tables and saltier soils than what was there prior to land conversion (Nosetto et al., 2007; Jayawickreme et al., 2011). As SLR impacts coastal communities salinizing the groundwater and soil, it becomes important to understand how halophytes affect soil salinity under saline groundwater conditions (Van Oosten and Maggio, 2015).

In Chapter II, I experimentally test the ability of halophytes to alter the saline/freshwater transition zone. Because SLR modelers have assumed halophytes' ability to increase soil salinity to be a driver of change (Teh et al., 2008), validating halophytic effects on soil will help improve model accuracy and, in turn, conservation actions. Chapter II is formatted to be submitted to Proceedings of the National Academy of Sciences.

In addition to depending on the surrounding community's composition, the vulnerability of a species to environmental stressors are contingent on life stage (Parker et al., 1955; Williams et al., 1998; Chartzoulakis and Klapaki, 2000; Schiffers and Tielbörger, 2006); high salinity levels tend to impact juvenile or regenerative life stages more than adult stages (Perry and Williams, 1996). Plant community composition ultimately depends on which species are able to regenerate in an area (Keeley and Van Mantgem, 2008). In ENP coastal forests, halophyte seedling and sapling densities increased in buttonwood forests from 1998-2009, while glycophyte seedling and sapling densities decreased; buttonwood adults typically had unchanged densities. In contrast, there was no change in halophyte and glycophyte seedling densities in higher elevation hardwood hammocks (Saha et al., 2011). Because there is only a mean 6cm difference in elevation between buttonwood forests and coastal hardwood hammocks (Saha et al., 2015) and SLR is expected to increase at a rate faster than 3.6mm yr^{-1} (IPCC, 2014), coastal hardwood hammocks may exhibit changes in their community composition similar to those of buttonwood forests within the next decade.

To best monitor on-the-ground changes in coastal communities threatened by SLR and anthropogenic disturbance, one needs to know what plant life stage is most vulnerable salt stress. In Chapter III, I examined the salinity sensitivity of early life history stages of buttonwood forest and hardwood hammock understory species to better predict the species' future responses to SLR. Chapter III is formatted to be submitted to the American Journal of Botany.

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CHAPTER I

USING REMOTE SENSING TO DETECT LONG-TERM COASTAL PLANT COMMUNITY CHANGES IN THE FACE OF SEA LEVEL RISE AND EVERGLADES DRYING

Using remote sensing to detect long-term coastal plant community changes in the face of sea level rise and Everglades drying

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Author contributions: Kristie S. Wendelberger conceived the project, designed research, gathered and analyzed the data, and led the writing. Daniel Gann designed the research, conceived and contributed expertise in analysis tools, analyzed the data, and co-wrote the paper. Jennifer H. Richards analyzed the data, and co-wrote the paper.

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ABSTRACT

Increasing sea levels and anthropogenic alterations are resulting in changes in or complete loss of coastal plant communities around the world. In combination with SLR, the Everglades ecosystem has undergone large-scale drainage and restoration changing coastal vegetation throughout south Florida. Saltwater-loving communities have moved into freshwater wetlands and uplands which harbor 21 rare species threatened by SLR.

To determine the extent to which plant community shifts have occurred along the coast of Everglades National Park (ENP) between 1978 and 2011, we used remote-sensing techniques to create a map of coastal plant communities and compared it to one made with 1978 imagery. We used bi-seasonal WorldView-2 2x2m satellite imagery flown at the end of the wet (December 2011) and dry (April 2013) seasons and a supervised random forest algorithm to classify seven plant community types. Specifically, we asked whether the spatial extent and distribution of coastal plant communities has transitioned from less salt- and inundation-tolerant to more salt- and inundation-tolerant communities over the 33-year period.

We found that lowland plant communities moved up the elevation gradient, transitioning from less salt- and inundation-tolerant to more salt- and inundation-tolerant communities. White mangrove forest percent cover decreased 16% and black and red mangrove forests increased 27 and 11%, respectively, suggesting the site became saltier and wetter over the time interval. Additionally, the two highest elevation communities, tropical hardwood hammock and buttonwood forest, decreased by 4 and 6% cover, respectively. Everglades National Park is a protected national park containing unique communities and rare and some endemic species. To preserve biodiversity and ecosystem integrity, the effects of SLR and Everglades drainage on south Florida are coastal vegetation matters need to be addressed today, not in the future.

Key words: Sea level rise, climate change, anthropogenic disturbance, coastal plant community change, conservation

INTRODUCTION

Increasing sea levels and anthropogenic alterations together are resulting in changes in or complete loss of coastal plant communities around the world[1–3]. Shifts in plant communities from less salt- and lower inundation-tolerant to more salt- and higher inundation-tolerant communities or to open water have been documented[2,4–8].

In combination with SLR, the south and central Florida Everglades ecosystem has been subjected to major anthropogenic alterations. The Everglades has undergone several phases of large-scale drainage and restoration over the last 150 years[9]. Saltwater intrusion at depth in the aquifer from a reduced freshwater head and increased sea levels was documented in south Florida in the early 1950’s[10]. By the early 1980’s, it was evident that Everglades drainage was negatively affecting the environment[9]. By the late 1990’s, saltwater intrusion had extended 10-15km inland[11] and, by 2006, existed in 6 to 25 km wide zones along the coast[12]. With environmental concerns growing, in 2000, the Comprehensive Everglades Restoration Plan (CERP) was put into place[9]. The CERP is estimated to take approximately 50 years to accomplish and will cost more than $10 billion[13]. As of late 2014, overall progress of the Plan had fallen short of initial goals, but headway had been made on land acquisition, improved water deliveries to ENP, and construction of four CERP projects had begun[13]. For over 150 years, the Everglades ecosystem has undergone both hydrologic stress and the increasing press of SLR.

The combined effects of hydrologic stress and SLR have caused changes in vegetation throughout south Florida. Shifts in coastal plant composition have been documented along the Florida coast since before the early 1950's[4,7,14–21]. Saltwater-loving communities have been found moving into freshwater wetlands and uplands[17,20,21]. Since the early 1980's, restoration efforts have attempted to counteract the effects of drainage. Large-scale efforts have subsequently been directed toward restoring a more natural hydrologic regime.

In 1980, ENP biologists initiated a monitoring project to study the effects of SLR on ENP coastal plant communities[22]. As part of that project, they created a map from 1978 aerial photos of the coastal communities stretching across the Flamingo portion of ENP and sampled vegetation on a 700m transect along an elevational gradient ranging from less than 0.5m to 1.5m above mean sea level[23]. The transect included 5 of 6 coastal south Florida plant communities (black mangrove forest, coastal tropical hardwood hammock (tropical hardwood hammock), buttonwood forest, halophyte prairie, and white mangrove forest) and one transition zone (buttonwood/manchineel hammock). The transect was resampled in 1998 and 2009[7]. Saha et al.[7] found an increase in halophyte density in previously glycophytic communities, a lack of recruitment of buttonwood seedlings, and an increase in white mangrove trees and saplings in buttonwood forests along the transect. Halophytic species moved into glycophytic communities[7].

Whether these transect-level changes are representative of changes in the study area at the landscape level is unknown because of a lack of explicit spatial data for vegetation changes. To determine the extent to which plant community shifts have occurred in the study area between 1978 and 2011 and their spatial patterns, we used remote-sensing techniques to create a map of coastal plant communities in the study area and compared it to the ENP map of the same area derived from 1978 imagery. Specifically, we asked whether the spatial extent and distribution of coastal plant communities has transitioned from less salt- and inundation-tolerant to more salt- and inundation-tolerant communities over the 33-year period.

MATERIALS AND METHODS

Study area: Southern Florida is humid and subtropical with a distinct warm (mean 25^{o}C) wet season from June to October and cool (mean 16^{o}C) dry season from November to May[24]. Average annual rainfall is between 1000 to 1630mm with more than half falling between June and September and often coming from hurricanes and tropical storms; April and May usually are the driest months[24,25]. The 2011 study area is a 71km^2 strip along the coast of ENP (25°19′0″N, 80°56′0″W), Florida, U.S.A. (Fig. 1.1). To assess changes in the coastal plant community matrix over a 33-year period, we compared the 2011 map to one made in 1978. The western portion of the 1978 map overlapped with the eastern portion of the 2011 study area. The area of overlap between the 1978 map and the 2011 study area was 41km^2.

The community types mapped reside on or around the Buttonwood Embankment, which is an approximately 60x1km^2 stretch of elevated land averaging 45cm above sea level along the southern tip of Florida[15,26]. Historically, freshwater flowed from the north toward saline Florida Bay, forming fresh waterbodies to the north of the embankment[16,27]. Today, the waterbodies to the north of the embankment are brackish to marine, which has led to changes in the marsh environment[15]. Long-term transitions from freshwater to marine sediment layers in cores taken at two locations along the Embankment[15,16], coupled with the pollen cores and aerial photographs, suggest that the study area has experienced a transition in plant communities in the last half century, resulting from a combination of SLR and lack of freshwater head from the drying of the Everglades ecosystem[26].

Community types found in the 2011 research area: Seven plant communities, open water, and mud flats were the land cover types classified in the study area. We named communities using the Vegetation Classification System for South Florida Natural Areas (VCS)[28] as a guide; however, we created broader vegetative classifications than the VCS. For example, Rutchey et al.[28] classifies black mangrove into scrub and forest, divided by height class; we combined these and used black mangrove forest as a single class that encompasses both the Rutchey et al.[28] categories. Because two invasive species, *Schinus terebinthifolius* Raddi and *Colubrina asiatica* (L.) Brongn, were prominent in the area and found across several forest types, causing confusion during the classification process, we created a classification category for each of them to improve accuracy in the other community types. Mud flats were open areas of bare soil; some areas may have periphyton mats, but no vegetation.

The seven plant community types are: 1) *Black mangrove forest:* This forest is dominated by *Avicennia germinans* (L.) L. with few associated woody species[28], except for occasional *Laguncularia racemosa* (L.) C.F.Gaertn. or *Rhizophora mangle* L. found in either the canopy or understory. The forest floor is dominated by many pneumatophores. At times, areas of young black mangrove forest will have halophyte species such as *Batis maritima* L., *Sarcocornia perennis* (Mill.) A.J. Scott, and *Suaeda linearis* (Elliott) Moq. in the understory. Black mangrove forests are considered the most salt tolerant of the three mangroves found in south Florida[29].

2) *Buttonwood/glycophyte forest: Conocarpus erectus* L. is the dominant canopy species of buttonwood forests. Other woody species in the community include *Sideroxylon celastinum* (Kunth) T.D. Pennington, *Randia aculeata* L., *Cocoloba diversifolia* Jacq., *Erythrina herbacea* L., *Eugenia foetida* Pers., *Ficus aurea* Nutt., and *Piscidia piscipula* (L.) Sarg.[30]. The buttonwood understory has species such as *Alternanthera flavescens* Kunth, *Chromolaena frustrata* (B.L.Rob.) R.M.King & H.Rob., *Dicliptera sexangularis* (L.) Juss., and *Heliotropium angiospermum* Murray[30]. Temperature, salinity, tidal fluctuation, substrate, and wave energy influence the size and extent of buttonwood forests[31], which often grade into salt marsh, coastal berm, rockland hammock, coastal hardwood hammock, and coastal rock barren[31,32]. They sustain freshwater flooding during the wet season and are dry during the dry season[31]. Buttonwood forests (mean elevation 29±3cm) maintain an average groundwater table of -33±1cm and 26-29.5±0.4‰ groundwater salinity[7,30].

3) *Buttonwood/halophyte forest: Conocarpus erectus* is the only canopy tree species in buttonwood/halophyte forests. The understory is comprised of *Batis maritima, Borrichia frutescens* (L.) DC., *Distichlis spicata* (L.) Greene, *Sarcorcornia perennis, Suaeda linearis,* and other less common species[30]. Buttonwood/halophyte forest (called

Buttonwood prairies[30]) (mean elevation 18±3cm) show a mean groundwater table at -32±2cm and average groundwater table salinity of 38.8±0.6‰[30].

4) *Halophyte prairie:* These prairies are comprised of *Batis maritima*, *Borrechia frutescens*, *Distichlis spicata, Sarcorcornia perennis,* and *Suaeda linearis* and other less common species with no canopy species[30]. Halophyte prairies have marl soils and slightly higher elevation than adjacent black and white mangrove forests[33]. In halophyte prairies, standing water that is brackish to freshwater is present for months during the wet season. These communities can become hypersaline during the dry season because of evaporation and a lack of drainage [22].

5) *Coastal tropical hardwood hammocks:* Coastal hardwood hammocks are biodiverse. Typical tree and shrub species include *Capparis flexuosa* (L.) L., *Coccoloba diversifolia*, *Piscidia piscipula*, *Sideroxylon foetidissimum* Jacq., *Eugenia foetida*, *Swietenia mahagoni* (L.) Jacq., *Ficus aurea* Nutt., *Sabal palmetto* (Walt.) Lodd. ex J.A. & J.H. Schultes, *Eugenia axillaris* (Sw.) Willd., *Zanthoxylum fagara* (L.) Sarg., *Sideroxylon celastrinum* (Kunth) T.D.Penn., and *Colubrina arborescens* (Mill.) Sarg.[28,32]. Herbaceous species that occur in coastal hardwood forest include *Acanthocereus tetragonus* (L.) Hummelinck, *Alternanthera flavescens, Batis maritima* L., *Borrichia arborescens* (L.) DC., *Borrichia frutescens* (L.) DC., *Caesalpinia bonduc* (L.) Roxb., *Capsicum annuum* L. var. *glabriusculum* (Dunal) Heiser & Pickersgill, *Galactia striata* (Jacq.) Urb., *Heliotropium angiospermum* Murr., *Passiflora suberosa* L., *Rivina humilis* L., *Sarcocornia perennis* (Mill.) A.J. Scott, *Sesuvium portulacastrum* (L.) L., and *Suaeda linearis* (Elliott) Moq. Ground cover is often limited in closed canopy areas and abundant in areas where canopy disturbance has occurred or

where this community intergrades with buttonwood forest[32]. Coastal tropical hardwood hammocks are the least salt tolerant of all the coastal community types and reside at the highest elevation (mean elevation 29±3cm).

6) *Red mangrove forest:* This forest is dominated by *Rhizophora mangle* in the canopy and has little to no understory vegetation[28]. Occasional *A. germinans* are found in the canopy scattered throughout; *L. racemosa* is found even less commonly. Red mangrove forests are considered the most inundation-tolerant of the three mangrove types and less salt tolerant than black mangroves[29].

7) *White mangrove forest:* This forest is dominated by *Laguncularia racemosa* in the canopy and often halophytes such as *Batis maritima, Sarcocornia perennis,* and *Suaeda linearis* in the understory. This community is most often found in irregularly flooded areas[28] and is the least salt and inundation tolerant of the three mangrove species found in south Florida[29].

Mapping the 2011 study area:

Satellite data and image processing: Because bi-seasonal satellite imagery has been shown to be most effective in discriminating plant communities in the Everglades ecosystem[34], we used WorldView-2 (WV2) (DigitalGlobe, Westminster, Colorado) satellite imagery flown over the study area at the end of the wet (December 2011) and dry (April 2013) seasons (Fig. 1.2). The WV2 imagery has 2x2m resolution and 8-multispectral bands (coastal: 400-450nm; blue: 450-510nm; green: 510-580nm; yellow: 585-625nm; red: 630-690nm; red edge: 705-745nm; near-IR1: 770-895nm; and near-IR2: 860-1040nm). We atmospherically corrected the images using the Fast Line-of-sight Atmospheric Analysis of Hypercubes (FLAASH) module in ENVI version 5.2 (Exelis

Visual Information Solutions, Boulder, Colorado). We used the Tropical Atmosphere and Maritime Aerosol Models for both images with 80 Initial Visibility value for the April 2013 image and 40 Initial Visibility value for the December 2011 image. Images were georectified with ERDAS Imagine 2014 (Leica Geosystems, Atlanta, Georgia).

Supervised classification: To perform a supervised classification of the coastal communities in our study area, we created a training signature set by collecting GPS points using a Garmin 60Cx (Garmin International, Inc., Olathe, Kansas) with a 1-7m accuracy, in the nine known community types; we related those points to spectral signatures in the satellite images. We then used knowledge of the spectral signatures gained from the field training set to choose additional training points that we digitized using ArcMap 10.2.2[35]. A total of 17,166 training points were used in the classification. We documented community types at the GPS points with pictures in each cardinal direction, up toward the canopy, and down, creating a 2012-2015 photographic vegetation database (4,356 pictures at 730 points, Fig. 1.3), providing temporal and spatial photographic documentation of the study site.

Using the open-source program R (R Core Team 2013) and a script created by D. Gann (GIS/RS Center, FIU), we classified plant communities using a supervised random forest algorithm with built-in bootstrapping and cross validation procedures (R package randomForest[36]); this approach has been shown to effectively classify plant communities in ENP[34]. RandomForest builds unpruned trees via bootstrapped with replacement training samples generated from two-thirds of the training points[37]. We built 1,000 trees (ntree=1,000) using a different bootstrap sample from the original data for each tree[37,38]. At each tree node, a random set of *mtry* predictors ($mtry \simeq \sqrt{p}$; where p = total number of possible variables) is selected from the full set of variables choosing the best split among the random predictors. Only one of the *mtry* predictors is allowed to be used at each node[37]. The pixel level community classification is predicted by running each pixel down each of the 1,000 trees; the classification in the majority wins[36].

There were 67 possible variables to randomly select from for the *mtry* predictor (*mtry* = 8). We created 48 texture variables for (mean, range, and standard deviation) with a 3x3 pixel moving focal window deployed across each multispectral band layer of each image. We created a Normalized Difference Vegetation Index (NDVI) from the red and near infrared bands of each pixel for each satellite image. A digital elevation model (DEM) was developed with LiDAR data flown by the Florida Division of Emergency Management in 2007-2008 at 5ft resolution[39]; these data are offered to the public by the South Florida Water Management District[40] (Fig. 1.4). We stacked the texture variables, DEM, NDVI of each image, and the eight multispectral bands into a data cube with a total of 67 variable layers. For those areas in the satellite data that had clouds, we masked the clouds and used only the satellite image that did not contain clouds in that area. The areas where the clouds were masked out and only one satellite image was used were classified with 34 possible variables instead of 67; in these cases, *mtry* = 6 ($mtry \simeq \sqrt{34}$).

Model based accuracy assessment: To verify model based accuracy, cross validation was performed with out-of-bag (oob) error estimates. Each of the remaining one-third training points left out of each bootstrap iteration was run down the tree generated by that iteration of samples obtaining a test set classification for one-third of the trees. The proportion of times the oob sample was classified incorrectly is the oob error estimate[36].

Map accuracy assessment: We checked map accuracy using a 2x2m pixel stratified-random probability sampling design, stratifying by community types (53 pixels per community). The reference pixels were selected using a multinomial distribution as described by Tortora[41] and Congalton and Green[42]. Because the two invasive species, *S. terebinthifolius* and *C. asiatica*, had the smallest area and were difficult to distinguish remotely, we combined those two categories for the accuracy assessment. We used a digital stereoplotter (DAT/EM Systems International, Anchorage, Alaska) and 2009 aerial photography of the study site, ArcMap 10.3.1 (ESRI 2014) basemap (Esri, DigitalGlobe, GeoEye, i-cubed, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community), and satellite images from Google Maps (Imagery ©2015 Google, Map data ©2015 Google) to label each of the randomly sampled reference pixels without prior knowledge of the model classification. Those pixels that we could not classify remotely were verified in the field[43].

1978 Map:

The 1978 map was a hand-drawn vegetation map of the coastal area between Flamingo and Joe Bay of ENP. It was made by Olmsted et al.[22] using color aerial photography (1:7800) flown in December 1978. Olmsted et al.[22] ground-verified the map by foot, helicopter, and boat. The map was digitized and distributed to us by the National Park Service South Florida/Caribbean Inventory & Monitoring Network. The map area totaled 134km^2, of which 41km^2 coincided with the 2011 mapped area (Fig. 1.5).

Other vegetation maps of the area:

Other vegetation maps of the ENP Flamingo area were available for comparison. The University of Georgia's Center for Remote Sensing and Mapping Science created a vegetation community map (UGA map) of South Florida's National Park Service Lands in 1999. Though this map covers the entire 71km^2 area of our 2011 research site, our field-based knowledge of the site indicated that the UGA map's vegetation communities were too general for change comparisons. For example, much of the area was mapped as buttonwood forest in the UGA map; we saw numerous instances where there were dead white mangrove poles in what are now solid red mangrove forests in locations represented as purely white mangrove in the 1978 map, but as pure buttonwood forest in the UGA map (K. Wendelberger personal observations). We chose to use the 1978 map because we felt it showed the most accurate representation of the vegetation communities present at the time it was made.

Assessing plant community change between the 1978 and 2011 maps:

Data preparation: We compared spatial extents of the community types from the overlapping portions of the 2011 and 1978 maps (Fig. 1.5). Fourteen km^2 of the overlapping 1978 map was classified as mixed mangrove, a varying mixture and density of the three mangrove species and buttonwood forest. Olmsted et al.[33] suggested that the mixed mangrove stands had established since the previous hurricane; these stands were difficult to walk through in 1980 and were not thoroughly examined by Olmsted et al.[33]. A mixed mangrove community was not classified in the 2011 map because the spectral signature varies with the composition of three species. Instead, each of the 2011 communities were identified in the area of the 1978 mixed mangroves. Since the class of mixed mangrove was not available from the 2011 classification, the area covered by mixed mangroves in 1978 was excluded from the analysis of vegetation changes. The total area compared excluding the area containing the 1978 mixed mangroves was

26.8km^2. Olmsted et al.[33] further divided each community type by height class and, at times, understory type; we did not do this in the 2011 map. Therefore, we compiled and reclassified all the 1978 sub-community types into their respective larger community types for comparison with the 2011 map; all of the final community types compared were the same between the two maps: black mangrove forest, buttonwood forest, coastal tropical hardwood hammock, halophyte prairie, mud flat, open water, red mangrove forest, and white mangrove forest (Fig. 1.5).

To make the 1978 and 2011 maps comparable, we aggregated the 2011 map's minimum mapping unit from 2x2m pixel to 2m x 250 pixels by majority rule, which was approximately the smallest unit mapped in the 1978 map (Fig. 1.5). Because the *S. terebinthifolius* and *C. asiatica* categories were classified in areas smaller than the minimum mapping unit, these two categories were eliminated when we decreased the 2011 map resolution. The 1978 map did not distinguish between buttonwood forest with a glycophytic understory and buttonwood forest with a halophytic understory, so we combined those two categories in the 2011 map into buttonwood forest (Fig. 1.5).

Statistical analysis:

<u>2011 map model-based accuracy assessment:</u> Model-based accuracy is given in a confusion matrix that shows the percentage of training points for each labeled community type that was classified by the random forest algorithm as that community type versus all the other possible communities (Table 11.). Columns represent the observed training point labels; rows represent the category assigned to the training point by the random

forest algorithm. The diagonal provides the percentage of training points that were classified correctly by the model. The off-diagonal cells represent percentage of omission and commission errors.

2011 map accuracy assessment: To quantify accuracy of the map and estimate area of each community type across the 71km^2 area, we created an error matrix of the map label versus reference pixel labels[43] (Table 1.2). The error matrix represents the proportion of area for each community type that would be found if a complete census of the community type was performed. The main diagonal shows the proportion of correctly classified pixels while the off-diagonal cells represent the proportion of producer's accuracy and user's accuracies (Table 1.2). Using the probabilities generated from the error matrix, we calculated the adjusted area and overall map, user's, and producer's accuracies with standard errors and 95% confidence intervals[43,44] (Table 1.3).

1978 map: The area and percent cover were calculated for all the reclassified community types in the 41km^2 area of the reclassified 1978 map. We included the mixed mangrove forest category in this analysis so comparisons could be made between the 1978 mixed mangrove forest and what that area was classified as in 2011 (Table 1.4).

Comparing the 1978 and 2011 maps: We compared overall area (ha) and percent cover, as well as area (ha) and percent area change of each of the community types between the maps within the 26.8km^2 area that excluded the 1978 mixed mangrove forest (Table 1.5). We then cross-tabulated how much area of each community changed into another community from 1978 to 2011 (Tables 1.6 and 1.7). Using the diffeR package in R[45] we created a site change map delineating paired community changes (original community - changed community) throughout the area.

RESULTS

2011 vegetation map:

<u>2011 map model-based accuracy assessment:</u> Overall model-based map accuracy was 87.9%, and each community type showed its own model-based accuracy, depending on model confusion between the communities (Table 1.1). Black and red mangrove forests and tropical hardwood hammock training points had accuracies > 87% and were confused the most with each other (Table 1.1). Buttonwood/glycophyte forest and buttonwood halophyte forest had lower accuracies (app. 69%). Buttonwood/glycophyte forest was confused the most with black mangrove forest and tropical hardwood hammock (Table 1.1). Buttonwood/halophyte forest showed the most model confusion with halophyte prairie (Table 1.1), as did mud flats (Table 1.1). White mangrove forest, with 75.81% accuracy, was confused with black mangrove forest and halophyte prairie (Table 1.1). Water and halophyte prairie training points were accurately classified 99.2 and 95.3% of the time, respectively, with little confusion with the other community types (Table 1.1). The two invasive species, *S. terebinthifolius* and *C. asiatica*, had the lowest accuracies (67%) and were confused primarily with tropical hardwood hammock (Table 1.1).

<u>2011 map accuracy assessment:</u> The accuracy assessment showed an 85.66% overall map accuracy prior to adjusting for the proportional errors. Water was the most proportionally accurate community type (1.00; Table 1.2). Of the natural plant communities mapped, buttonwood/halophyte and white mangrove forests were the most proportionally accurate communities (0.91; Table 1.2), and tropical hardwood hammocks

were the least accurate (0.74; Table 1.2). The combined invasive species category showed the least accuracy of all the classified types (0.62; Table 1.2).

2011 adjusted map areas and cover: The adjusted map accuracy after taking into account proportional errors across the communities was 86.02%. The plant communities covered from 183 (CI 154.2; 211.6) to 2,015 (CI 1890.4; 2138.6) ha in the 71km^2 study area (Table 1.3). Black mangrove forest maintained the most area and percent cover of all the community types (28.5% cover; Table 1.3; Fig. 1.6). Red mangrove was second most dominant (20.8% cover; Table 1.3; Fig. 1.6), followed by halophyte prairie (10.0% cover; Table 1.3; Fig. 1.6). All the other community types showed less than 10% cover each (Table 1.3; Fig. 1.6). Of all the natural plant communities mapped, tropical hardwood hammock was the least common (2.6% cover; Table 1.3; Fig. 1.6) followed by mud flats (3.4% cover; Table 1.3; Fig. 1.6). When combining the two invasive species, *S. terebinthifolius* and *C. asiatica,* they showed 3.2% cover together (Table 1.3; Fig. 1.6). *Schinus terebinthifolius* tended to be found in tropical hardwood hammock and red mangrove forest (K. Wendelberger personal observations).

The communities were distributed across the elevation patterns at the site. The DEM shows patterns of higher elevation interwoven with lower elevation throughout the 2011, 71km^2 study site (Fig. 1.4). Tropical hardwood hammock, buttonwood/glycophyte and buttonwood/halophyte forests tended to follow a sequential pattern (Fig. 1.6). Tropical hardwood hammocks were found at the highest elevation, buttonwood/glycophyte forest found on slightly lower elevation at either side of tropical hardwood hammocks, and buttonwood/halophyte forest on the lower sides of buttonwood/glycophyte forests (Figs. 1.4 and 1.6). Halophyte prairie was frequently located in low spots adjacent to buttonwood/halophyte forests. Black and red mangroves were located in the lowest elevations in the area (Figs. 1.4 and 1.6).

Reclassified 1978 map:

The plant communities in the 1978 map differed in area and percent cover across the 41km^2 research site. Mixed mangrove forest had the greatest area (1,386ha) and percent cover (34.1%) of all the community types (Table 1.4; Fig. 1.5). Of the remaining communities, buttonwood forest was most abundant (20.7% cover; Table 1.4). White mangrove forest was second most abundant (16.9% cover; Table 1.4; Fig. 1.5), followed by halophyte prairie (14.8% cover; Table 1.4; Fig. 1.5). Pure red mangrove forest—not including that found in the mixed mangrove stands—was the least abundant community type (0.6% cover; Table 1.4; Fig. 1.5). Tropical hardwood hammock showed more coverage than either red or black mangrove forests outside of the mixed mangrove areas (tropical hardwood hammock: 5.4% cover, black mangrove forest: 2.5% cover; Table 1.4; Fig. 1.5).

Vegetation changes 1978 to 2011:

Large changes in plant communities from less salt- and inundation-tolerant to more salt- and inundation-tolerant community types have occurred over the 33-year period from 1978 to 2011 (Table 1.4 and 1.5; Fig. 1.7). After excluding the areas containing the 1978 mixed mangrove category from the analysis and using the unadjusted 2011 areas, we found red and black mangrove forests have increased the most in the study area (289ha and 730ha increase and 1,145% and 720% change, respectively; Table 1.4 and 1.5; Fig. 1.7). White mangrove forest, halophyte prairie, and tropical hardwood hammock showed the greatest decrease in area (-436, -310, and -95ha and -64, -51, and -43% area change, respectively; Table 1.4 and 1.5; Fig. 1.7).

Community relative abundances in 2011 in the 41km^2 area that overlapped with the 1978 map differed from the entire 71km^2 map. Black mangrove forest was still the most abundant (31% cover; Table 1.4; Fig. 1.5); however, buttonwood forest, which included both buttonwood/glycophyte and buttonwood/halophyte forest, was the second most abundant community (25% cover; Table 1.4; Fig. 1.5). Red mangrove forest showed the third highest cover (12% cover; Table 1.4; Fig. 1.5), closely followed by halophyte prairie (11% cover; Table 1.4; Fig. 1.5) and white mangrove forest (9.3% cover; Table 1.4; Fig. 1.5). Mud flat showed the least cover (1.5 % cover; Table 1.4; Fig. 1.5) and tropical hardwood hammock the second least (4.7% cover; Table 1.4; Fig. 1.5).

There was not a direct landward transition in coastal plant communities. Instead, the areas of change tended to move from lower to higher elevation within the elevation matrix of the study area. Communities found at the top of a ridge (e.g., tropical hardwood hammock) were replaced by lower elevation communities (e.g., buttonwood forest) from the lower and outer edge of the upland community; communities found in a trough of elevation changed from the center of the trough and moved up the edge toward higher elevation (Fig. 1.5); for example, the large area of white mangrove (which was buttonwood forest in 1978; Fig. 1.5) to the center and bottom of Fig. 1.6 shows an edge of buttonwood/halophyte prairie, suggesting the changes in this area came from within the previous community as opposed to the edge. The highest elevation tropical hardwood hammock was the exception, with the community shrinking from the edge (Figs. 1.6 and 1.7). The majority of halophyte prairie changed into black mangrove and buttonwood forest (184 and 110ha, respectively; Table 1.5; Fig. 1.7). White mangrove transitioned into black and red mangrove forests (416 and 210ha, respectively; Table 1.5; Fig. 1.7). Tropical hardwood hammocks changed into buttonwood forest (109ha; Table 1.5), and buttonwood forests converted mostly to white mangrove forest (164ha; Table 1.5; Fig. 1.7). Halophyte prairies showed the largest transition into black mangrove forest (183ha; Table 1.5; Fig. 1.7) and second largest into buttonwood forest (110ha; Table 1.5; Fig. 1.7).

The 1978 mixed mangrove forest (14km^2) was mapped as distinct vegetation communities in 2011. Red and black mangrove forests covered the majority of the area in 2011 (Table 1.6), followed by white mangroves and buttonwood forest (Table 1.6); tropical hardwood hammock and halophyte prairie covered the least of the 1978 mixed mangrove area in 2011 (Table 1.6).

Those areas that did not change between 1978 and 2011 tended to be the lowest elevation communities. Of the area covered by black and red mangrove forests in 1978, 82% and 44%, respectively, were still those community types (Fig. 1.7 and Table 1.5). White mangrove forest changed the most; only 5.8% of the area covered by white mangrove in 1978 was still white mangrove in 2011. The area covered by the highest elevation buttonwood forests and tropical hardwood hammock in 1978 were 52% and 37% unchanged, respectively, in 2011 (Fig. 1.7 and Table 1.5). The above results were generated by direct comparison between the 1978 and 2011 maps; a plant community change accuracy assessment including confidence intervals of the change categories is needed. We will be performing the accuracy assessment prior to peer-reviewed publication.

DISCUSSION

Lowland plant communities along the coast of south Florida have moved up the elevation gradient, transitioning from less salt- and inundation-tolerant to more salt- and inundation- tolerant communities. Of the three mangrove species found in our study area, white mangroves reside highest in elevation and are the least salt tolerant[29,46]. Black mangroves are known to be the most salt tolerant of the three species[29] and red mangroves the most flood tolerant[46], outcompeting white mangroves in increasingly salty and flooded environments[46]. White mangrove forest cover decreased 16% since 1978; 61% of the area covered by white mangrove forest in 1978 was black mangrove forest by 2011 and 31% was red mangrove forest. Further, halophyte prairie showed a 12% decrease in cover over the 33 year period with the majority (184ha) transitioning into more inundation-tolerant black mangrove forest. Overall, black and red mangrove forests increased 27 and 11% in cover, respectively, over the 33 year period in the area we analyzed, suggesting the site became saltier and wetter since 1978. Additionally, the two highest elevation communities—tropical hardwood hammock and buttonwood forest[30] (mean elevation 0.29 ± 0.007m and 29 ±3cm, respectively)—decreased by 6% (172ha) and 4% (95ha) cover, respectively, during the study period. White mangrove forest replaced 20% of buttonwood forest and buttonwood forest replaced 49% of tropical hardwood hammocks since 1978.

Plant communities change from environmental stress when there is a shift in their regeneration niches that prevent the current community from reproducing. Seedlings are more susceptible to changing microsite ecology, usually losing their ability to establish sooner than adults die[47,48] (Chapter 3 this dissertation). When a community cannot reproduce, it results in a population of relic adults from the former community with an understory of either establishing seedlings from a new community more suited to the changed environment or no regenerating individuals[7,47]. Pulse disturbances, e.g., hurricanes and storm surges, tend to be the final event eliminating relic adults[49,50], leaving saplings from the new community to grow into the canopy or, in cases where no regeneration is present, open water[3,47]. Changes finalized by pulse events appear from above to be rapid transitions of large land areas, but, in fact, they occurred slowly over time[47]. Large-scale plant community transitions along the coast of ENP detectable via remote sensing technologies indicate that changes in belowground conditions and regeneration niches have been happening in the area for quite some time. Though attempts to further dry the Everglades ceased decades ago, the system continues to move in the direction of salty and inundation-tolerant coastal communities.

Florida's coastal communities have been changing from SLR since the end of the last glacial maximum; however, reduction of freshwater flow and increasing rates in SLR have substantially increased the modern rate of change found in the past century[4,7,15–21,51]. Williams et al.[47] showed increases in salinity along the Gulf Coast of Florida decreased upland *Sabal palmetto* (Walter) Lodd. ex Schult. & Schult.f. (cabbage palm) seedling establishment and increased adult *S. palmetto* die off, resulting in a replacement of *S. palmetto* forest by salt marsh. Ross and O'Brien[4] determined that mortality of *Pinus elliotti* Engelm. var *densa* Little & Dorman (South Florida slash pine) and replacement by lower elevation halophytic communities on Sugarloaf Key in the Florida Keys coincided with increasing sea levels. Ross et al.[17] found that freshwater graminoid marshes in the eastern portion of the southern Everglades transitioned into mangrove scrub between 1952 and 2000. In addition to drying, there has been more than a 23cm increase in sea level along the south Florida coast in the last century[52]. A large increase in red mangrove forest—the most flood tolerant of the three mangroves—and a decrease in tropical hardwood hammock—the highest elevation community along the coast and the least salinity-tolerant community—suggests that an increase in groundwater elevation and flooding from rising sea levels contributed to the changes we found in our study.

A diverse coastal plant community matrix is critical to the health of the greater community, both human and natural alike[29,53–57] and a hotspot for sequestering CO_2 at high rates[56,57]. Our map, which provides a fine-scale baseline for monitoring future change, shows that in 2011, the ENP coastal communities were still quite diverse, maintaining a matrix of complex community composition of black and red mangrove forests, halophyte prairie, two buttonwood communities (glycophyte and halophyte), white mangrove forest, and tropical hardwood hammock. Of the natural communities, tropical hardwood hammock showed the least amount of cover at 3%. However, if the decreases in upland communities seen in the subset data between 1978 and 2011 continue, there will be a homogenization of communities along the coast of ENP. Our study site encompasses a portion of the buttonwood embankment, a ridge along the southern coast of Florida formed from historic coasts and storm surges[16]. There is over 8km of dwarf red mangrove forest between the most northern hardwood hammocks and buttonwood forests in our study site and lands with high enough elevation to support the two communities. Therefore, an inland migration of hardwood hammock and buttonwood forests is not likely. Upland coastal plant communities in ENP maintain 21 rare plant species that are threatened by SLR, including the federally endangered plant *Chromolaena frustrata*[7]. Further shrinking in cover of the habitats that support the rare species increases threats to them; some may become extirpated or extinct[7]. Although red and black mangrove forests have increased in our study area, a continuation in rising seas may lead to a collapse of these forests[3,53], losing natural area, CO_2 sequestering forest, and coastal buffer to south Florida's human populations[55].

Creating a healthy Everglades ecosystem through increased freshwater flow would eliminate one of two major stressors driving the vegetative changes that have been seen throughout the Florida coast. Sea level rise alone plays a small role in predicted global wetland loss when human alterations are not included in the forecast[3,57]. The coupled stress of anthropogenic landscape modifications and SLR tend to be the driving factors in coastal wetland loss[3]. Therefore, restoring the hydrologic regime of the Everglades ecosystem is critical if we want a coastal community matrix that is as resilient to SLR as possible. The objective of the Comprehensive Everglades Restoration Project is to increase freshwater flow into ENP. A stronger freshwater head would push back coastal saltwater intrusion, allowing a freshwater lens to form in areas where it no longer exists or is thinning[53]. Potentially, the highest elevation communities that harbor the most rare plant species would be able to either expand or at least maintain their current area, giving species and people time to adapt to the press of SLR. The landscape-scale changes found in our and others' research show that if we want to preserve biodiversity and ecosystem integrity, the effects of SLR and Everglades drying on coastal south Florida are matters to be addressed today, not in the future.

TABLES

	Black Mangrove Forest	*Schinus terebinthifolius*	Buttonwood/ glycophyte Forest	Buttonwood/ halophyte Forest	*Colubrina asiatica*	Water	Halophyte Prairie	Tropical Hardwood Hammock	Mud Flat	Red Mangrove Forest	White Mangrove Forest
Black Mangrove Forest	**91.73**	6.02	12.25	1.97	3.41	0.00	0.45	1.62	1.62	7.63	10.44
Schinus terebinthifolius	0.03	**66.61**	0.18	0.00	1.14	0.00	0.02	0.34	0.00	0.00	0.00
Buttonwood/glycophyte Forest	0.11	1.64	**68.65**	5.82	0.00	0.00	0.00	1.29	0.00	0.04	0.14
Buttonwood/halophyte Forest	0.08	0.36	3.96	**69.06**	0.00	0.00	1.02	0.00	0.22	0.00	2.45
Colubrina asiatica	0.00	0.00	0.36	0.00	**67.05**	0.00	0.00	0.17	0.00	0.00	0.00
Water	0.00	0.00	0.00	0.00	0.00	**99.24**	0.00	0.00	0.00	0.00	0.00
Halophyte Prairie	1.00	0.00	0.00	20.04	1.14	0.00	**95.28**	0.00	8.10	0.50	9.72
Tropical Hardwood Hammock	1.85	20.07	9.01	0.21	27.27	0.00	0.02	**93.91**	0.00	4.34	0.07
Mud Flat	0.08	0.00	0.18	0.00	0.00	0.76	1.52	0.00	**89.31**	0.00	0.22
Red Mangrove Forest	4.63	4.20	3.42	0.00	0.00	0.00	0.00	2.68	0.00	**87.33**	1.15
White Mangrove Forest	0.50	1.09	1.98	2.91	0.00	0.00	1.68	0.00	0.76	0.17	**75.81**
Total number of training points	3783	548	555	963	88	131	4408	1789	926	2399	1389
% error	8.27	33.39	31.35	30.94	32.95	0.76	4.72	6.09	10.69	12.67	24.19
Random forest classifier	numTree	oob	accuracy								
	1000	12.1	87.9%								

Table 1.1. Model based accuracy confusion matrix for the 2011, 71km^2 map, Flamingo, Everglades National Park, Florida. Columns are the training point labels; rows represent the label the algorithm assigned to the training points. The cell data are the % of training points in each column that were classified as each row community by the model. The diagonal (in bold) provides the % of training points that were classified correctly by the model. The off-diagonal cells are % omission and commission errors. The % error gives class-specific model error for each community type. The overall map model accuracy is 87.9%.

	Black Mangrove Forest	Buttonwood/ glycophyte Forest	Buttonwood/ halophyte Forest	Water	Halophyte Prairie	Tropical Hardwood Hammock	Invasive Species (*S. terebinthifolius/ C. asiatica*)	Mud Flat	Red Mangrove Forest	White Mangrove Forest
Black Mangrove Forest	**0.85**	0.08	0.02	0.00	0.00	0.00	0.00	0.00	0.04	0.02
Buttonwood/glycophyte Forest	0.06	**0.89**	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Buttonwood/halophyte Forest	0.00	0.06	**0.91**	0.00	0.04	0.00	0.00	0.00	0.00	0.00
Water	0.00	0.00	0.00	**1.00**	0.00	0.00	0.00	0.00	0.00	0.00
Halophyte Prairie	0.02	0.04	0.02	0.00	**0.89**	0.00	0.00	0.04	0.00	0.00
Tropical Hardwood Hammock	0.06	0.00	0.11	0.00	0.02	**0.74**	0.04	0.00	0.04	0.00
Invasive Species (*S. terebinthifolius/ C. asiatica*)	0.02	0.00	0.15	0.00	0.02	0.06	**0.62**	0.00	0.13	0.00
Mud Flat	0.02	0.00	0.00	0.06	0.04	0.00	0.00	**0.89**	0.00	0.00
Red Mangrove Forest	0.08	0.00	0.00	0.00	0.00	0.02	0.00	0.00	**0.89**	0.02
White Mangrove Forest	0.00	0.02	0.08	0.00	0.00	0.00	0.00	0.00	0.00	**0.91**
Accuracy : 85.66%	95% CI : (0.8238, 0.8853)									

Table 1.2. Stratified-random probability accuracy assessment error matrix, stratifying by community types (53 pixels per community) for the 2011, 71km^2 study area, Flamingo, Everglades National Park, Florida. Rows are classification derived map labels; columns are the reference labels. The main diagonal (in bold) shows the proportion of correctly classified pixels; the off-diagonal cells represent the proportion of producer's and user's accuracies. Because it was difficult to distinguish pixels of the two invasive species, *Schinus terebinthifolius* and *Colubrina asiatica*, and their area was small, we combined those two categories for the accuracy assessment. The map accuracy prior to adjusting for proportion correct is 85.66%; (95% CI: 0.8238, 0.8853).

Community	Area (ha)	proportional area (ha)	Adj. area (ha)	% Cover of adj. area	Adj. area std. error	Adj. area lower 95% CI	Adj. area upper 95% CI	Proportional area Bias	Proportion adj. user's accuracy	Adj. user's accuracy std. error	Adj. user's accuracy lower 95% CI	Adj. user's accuracy upper 95% CI	Proportion adj. producer's accuracy	Adj. producer's accuracy std. error	Adj. producer's accuracy lower 95% CI	Adj. producer's accuracy upper 95% CI
Black Mangrove	2158.5	0.31	2014.5	28.5	124.1	1890.4	2138.6	0.85	0.85	0.10	0.75	0.95	0.91	0.06	0.85	0.97
Invasive Species	16.4	0.00	227.4	3.2	81.6	145.8	309.0	0.89	0.91	0.08	0.84	0.99	0.07	0.08	-0.02	0.15
Buttonwood/ glycophyte	429.8	0.06	615.2	8.7	63.9	551.4	679.1	0.91	0.91	0.08	0.83	0.99	0.63	0.13	0.51	0.76
Buttonwood/ halophyte	653.2	0.09	667.5	9.5	8.1	659.4	675.6	1.00	1.00	0.00	1.00	1.00	0.98	0.02	0.96	1.00
Water	408.6	0.06	409.7	5.8	28.4	381.3	438.1	0.89	0.89	0.09	0.80	0.97	0.89	0.09	0.79	0.98
Halophyte Prairie	899.5	0.13	703.5	9.9	62.3	641.2	765.8	0.74	0.74	0.12	0.62	0.86	0.94	0.078	0.86	1.02
Hardwood Hammock	239.2	0.03	182.9	2.6	28.7	154.2	211.6	0.62	0.62	0.13	0.49	0.76	0.82	0.21	0.61	1.02
Mud Flat	253.7	0.04	240.9	3.4	15.5	225.4	256.4	0.89	0.89	0.09	0.80	0.97	0.94	0.08	0.85	1.02
Red Mangrove	1493.0	0.21	1470.6	20.8	90.8	1379.8	1561.4	0.89	0.89	0.09	0.80	0.97	0.90	0.08	0.82	0.98
White Mangrove	511.6	0.07	532.6	7.5	53.7	478.9	586.3	0.91	0.91	0.08	0.83	0.99	0.87	0.16	0.71	1.03
Total	7063.5	1.00	7064.8	100	Adjusted accuracy			86.02%								

Table 1.3. Original and adjusted post accuracy assessment of classified community types in the 2011, 71km^2 study area, Flamingo, Everglades National Park, Florida. Columns are mapped area (ha), proportion of area covered (ha), adjusted area (ha) account for proportional errors, adjusted area %cover, unadjusted community area bias proportion, proportion adjusted user’s and producer’s accuracies, standard errors, and upper and lower 95% confidence intervals. Because it was difficult to distinguish pixels of the two invasive species, *Schinus terebinthifolius* and *Colubrina asiatica*, and their area was small, we combined those two categories (called Invasive Species in the table) for the accuracy assessment. Map accuracy after adjusting for map error was 86%.

	1978 Area (ha)	2011 Area (ha)	Area (ha) Change	% Area Change	1978 % Cover	2011 % Cover	% Cover Change
Black Mangrove Forest	101.39	831.08	729.69	719.69	3.78	30.98	27.20
Buttonwood Forest	841.46	669.94	-171.52	-20.38	31.37	24.97	-6.39
Water	177.68	160.03	-17.65	-9.94	6.62	5.97	-0.66
Halophyte Prairie	601.87	292.05	-309.82	-51.48	22.44	10.89	-11.55
Tropical Hardwood Hammock	220.21	124.93	-95.28	-43.27	8.21	4.66	-3.55
Mud Flat	29.10	40.38	11.28	38.75	1.08	1.51	0.42
Red Mangrove Forest	25.27	314.70	289.43	1145.33	0.94	11.73	10.79
White Mangrove Forest	685.57	249.46	-436.11	-63.61	25.56	9.30	-16.26
Total	2682.55	2682.55	0.00	1715.10	100.00	100.00	0.00

Table 1.4. Total area (ha), percent cover, area (ha) change, and percent cover change of each plant community type compared between the 1978 map and the 2011 map, Flamingo, Everglades National Park, Florida. Because we excluded the amount of area covered by the 1978 mixed mangrove category, the study area for this analysis was 26.8km^2. The 1978 map did not distinguish between buttonwood forest understory types; therefore, we combined the two 2011 buttonwood forest types for this analysis. The 2011 areas used were from the mapped values not the proportionally adjusted area values.

		2011								
	Units = hectare	Black Mangrove Forest	Buttonwood Forest	Water	Halophyte Prairie	Tropical Hardwood Hammock	Mud Flat	Red Mangrove Forest	White Mangrove Forest	Total area (ha) 1978
1978	Black Mangrove Forest	**82.83**	4.28	0.85	7.39	0.15	1.14	4.75	0.00	101.39
	Buttonwood Forest	116.53	**436.57**	0.12	48.80	36.29	0.23	39.00	163.91	841.46
	Water	3.38	0.07	**155.18**	0.12	0.04	2.02	16.71	0.16	177.68
	Halophyte Prairie	183.87	110.47	0.41	**216.79**	4.90	16.00	25.62	43.81	601.87
	Tropical Hardwood Hammock	11.31	108.51	0.21	9.27	**81.64**	0.53	7.06	1.68	220.21
	Mud Flat	4.16	0.00	2.32	2.39	0.00	**20.12**	0.11	0.00	29.10
	Red Mangrove Forest	13.51	0.00	0.45	0.00	0.00	0.00	**11.03**	0.28	25.27
	White Mangrove Forest	415.49	10.04	0.49	7.28	1.91	0.33	210.41	**39.62**	685.57
	Total area (ha) 2011	831.08	669.94	160.03	292.05	124.93	40.38	314.70	249.46	2682.55

Table 1.5. Cross-tabulation table showing how the total area (ha) of each community type mapped in the 41km^2 study area, Flamingo, Everglades National Park changed from 1978 (rows) to 2011 (columns). The diagonal (in bold) represents the unchanged area (ha). Off-diagonal cells represent the area each community type was in 1978 (lower cells) versus 2011 (upper cells). A mixed mangrove community class was not defined in the 2011 map; therefore, the area contained by the 1978 mixed mangrove forest community class was not analyzed in this analysis. The 1978 map did not distinguish between buttonwood forest understory type; therefore, we combined the two 2011 buttonwood forest types for this analyses.

Units = hectare	2011								
	Black Mangrove Forest	Buttonwood Forest	Water	Halophyte Prairie	Tropical Hardwood Hammock	Mud Flat	Red Mangrove Forest	White Mangrove Forest	Total area (ha) 1978
1978 Mixed Mangrove Forest	485.23	63.73	2.22	9.52	10.26	1.01	715.71	98.38	1386.06

Table 1.6. A cross-tabulation table showing the amount of area (ha) of the 1978 mixed mangrove forest that had changed into each of the 2011 community types in the 41km^2 study area, Flamingo, Everglades National Park. We did not specifically analyze the differences between years for this community. The 1978 map did not distinguish between buttonwood forest understory type; therefore, we combined the two 2011 buttonwood forest types for this analyses.

FIGURES

Figure 1.1. Digitalglobe WorldView-2 satellite image (red, green, blue bands displayed) of 71km ^{2} study site along the coast with Florida Bay to the south, Flamingo, Everglades National Park (ENP). The inset shows Florida with ENP outlined and the location of the study area indicated. The ENP road to Flamingo is seen in the image. The orange outline is the 41km^2 area where the 1978 ENP map overlapped and where we performed plant community change analysis.

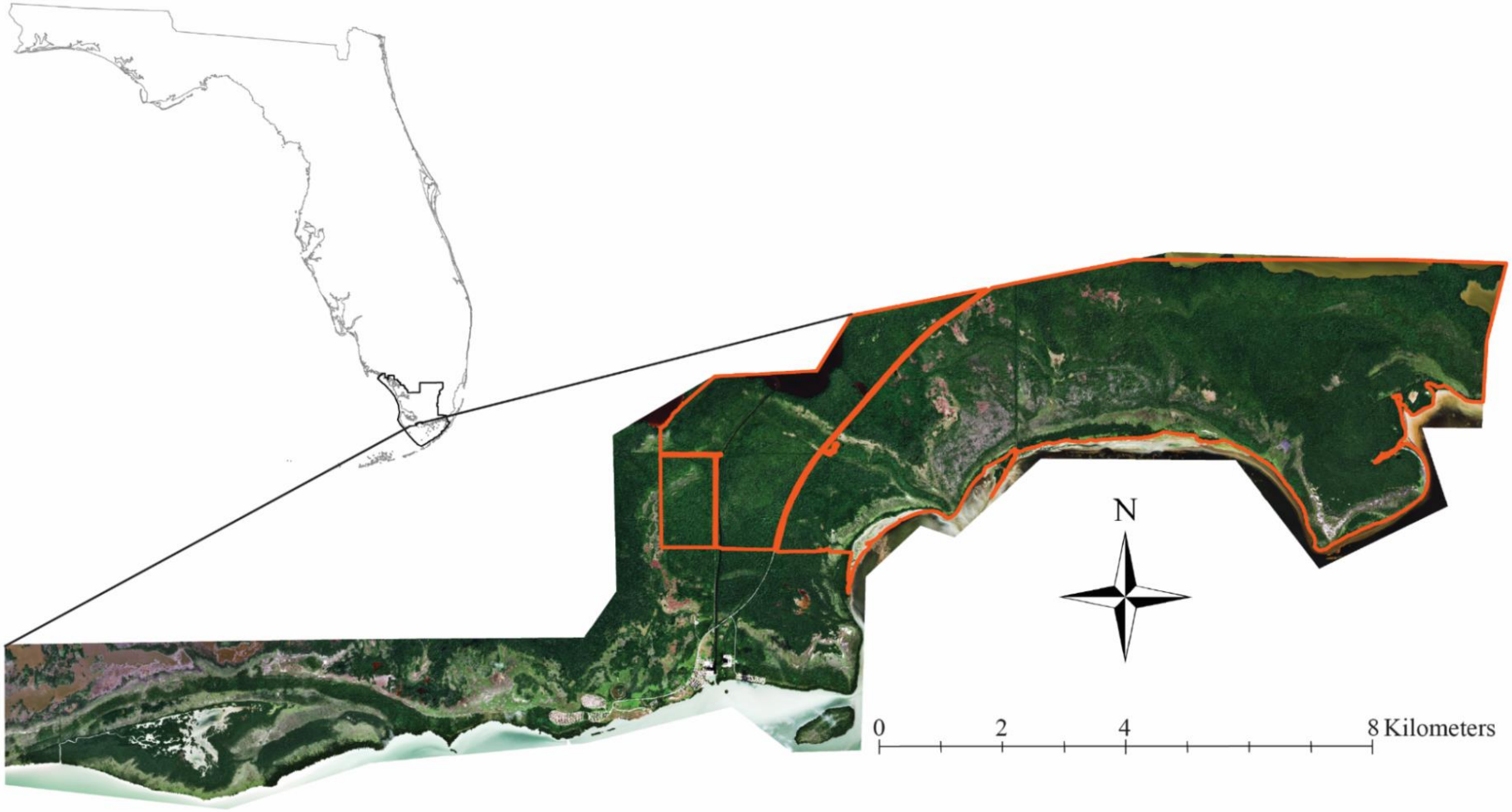


Figure 1.2. WorldView-2 satellite 2x2m imagery used to create the 2011, 71km^2 plant community map, Flamingo, Everglades National Park (red, green, blue bands displayed with a 0.5 min/max percent clip Gamma Stretch 0.75, 0.75, 0.75). The images were taken at the end of the wet season, December 2011 (A) and the end of the dry season, April 2013 (B).

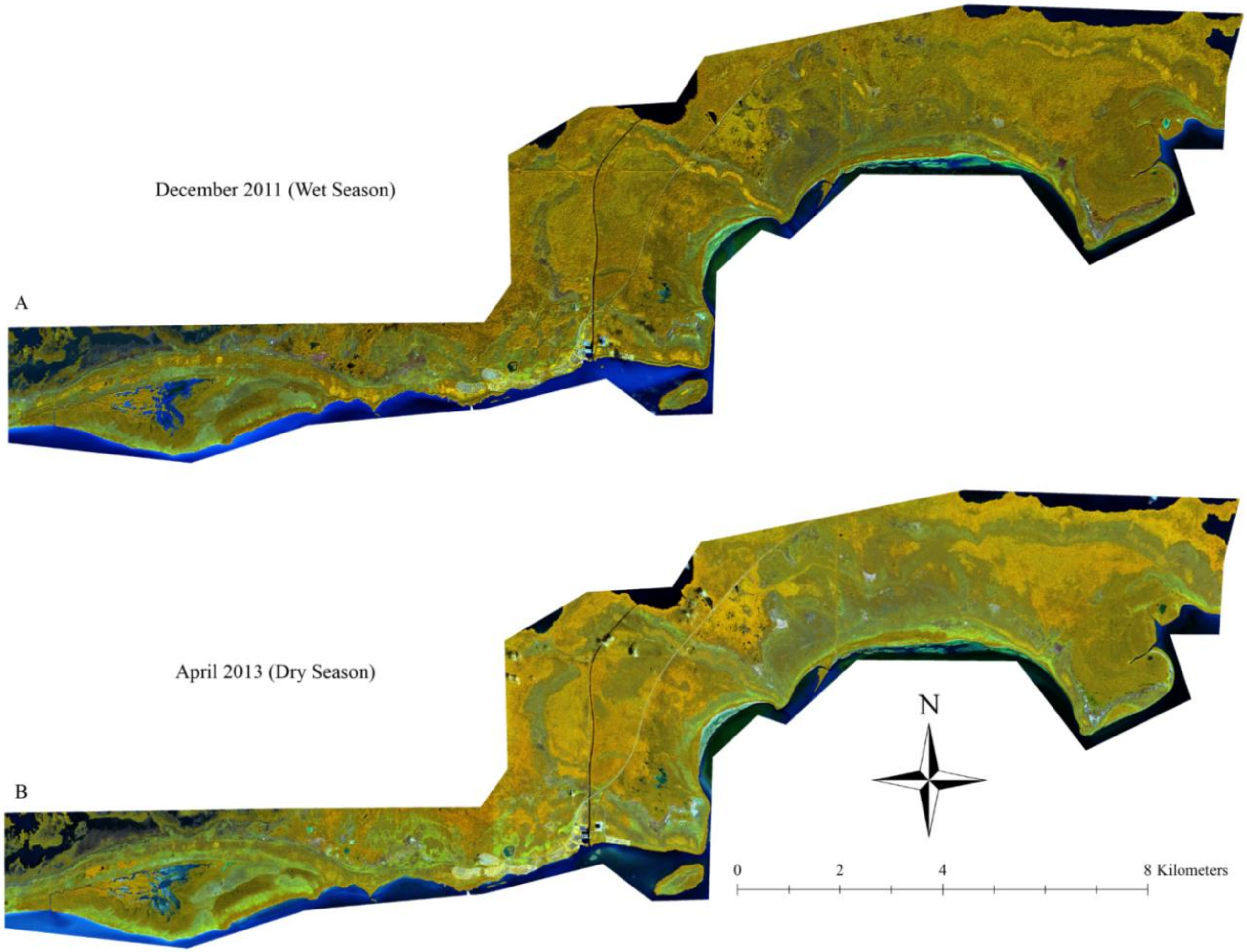


Figure 1.3. Mapped GPS points that are associated with the 2012-2015 photographic database of the 71km^2 study area, Flamingo, Everglades National Park.

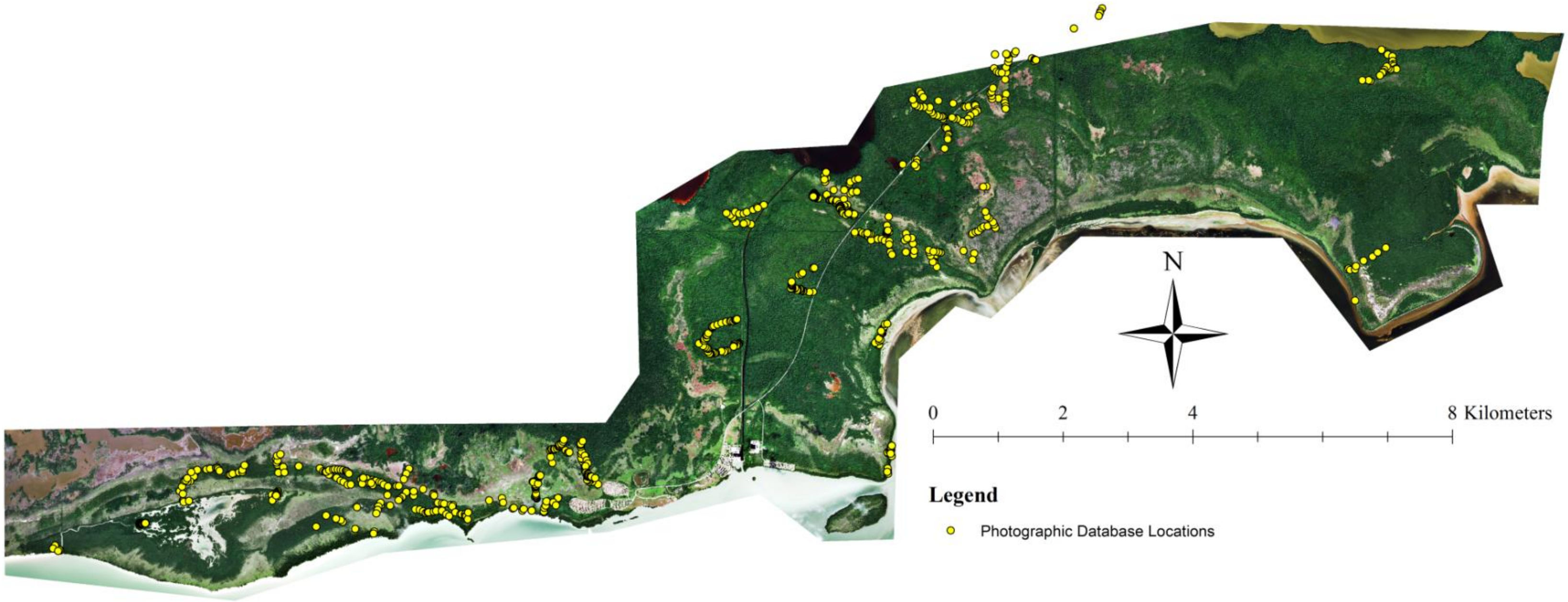


Figure 1.4. Digital Elevation Model (DEM) of the 2011 71km^2 study site, Flamingo, Everglades National Park. Areas with highest elevations are the brightest; areas with lowest elevation are the darkest. The higher elevation buttonwood embankment is seen as the highest elevation natural areas throughout the study site. The circles of high elevation along the Buttonwood Canal (center of image) are likely spoil piles from when the canal was built. The roads and campgrounds also show as high elevation. The DEM was created with LiDAR data flown by the Florida Division of Emergency Management in 2007-2008 at 5ft resolution (FDEM 2015), tiled and offered to the public by the South Florida Water Management District (SFWMD 2015).

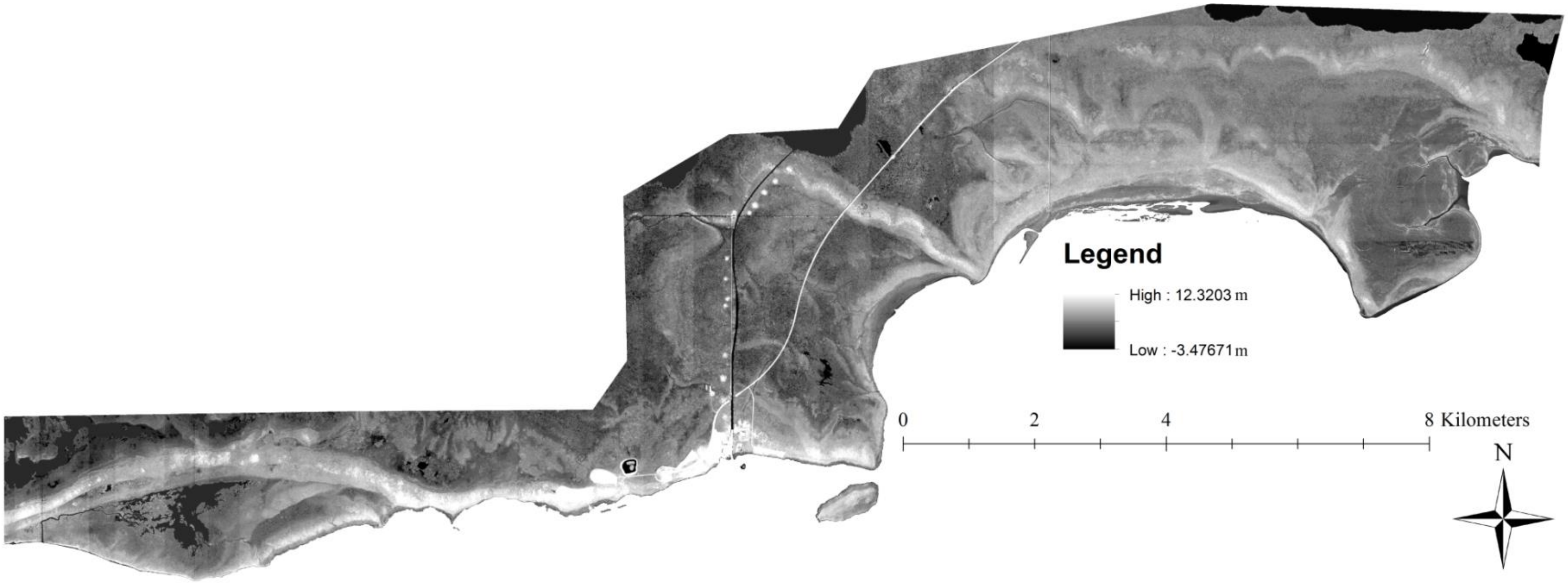


Figure 1.5. The 41km^2 study area, Flamingo, Everglades National Park, comparing changes in the plant community matrix between 1978 and 2011. (A) 2011 vegetation map where the minimum mapping unit was aggregated from 2x2m to 250x250m, approximately matching the smallest unit mapped in 1978. (B) 1978 vegetation map. Both maps were reclassified to match plant community names, except the 1978 mixed mangrove forest (gray) which did not have a matching class in the 2011 map.

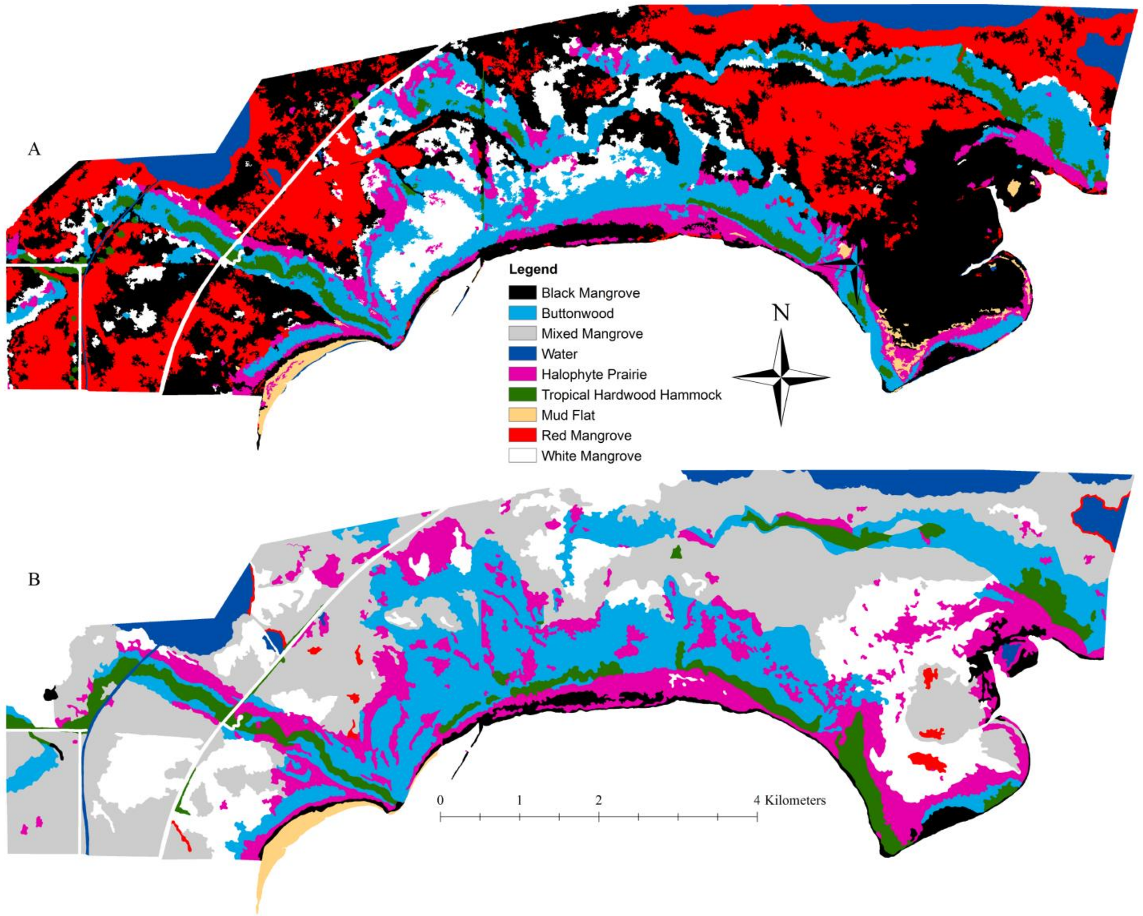


Figure 1.6. The 2011 2x2m resolution vegetation map of the 71km^2 study area, Flamingo, Everglades National Park. The overview is the entire 71km^2 area. (A) The eastern portion of the map; (B) the western portion.

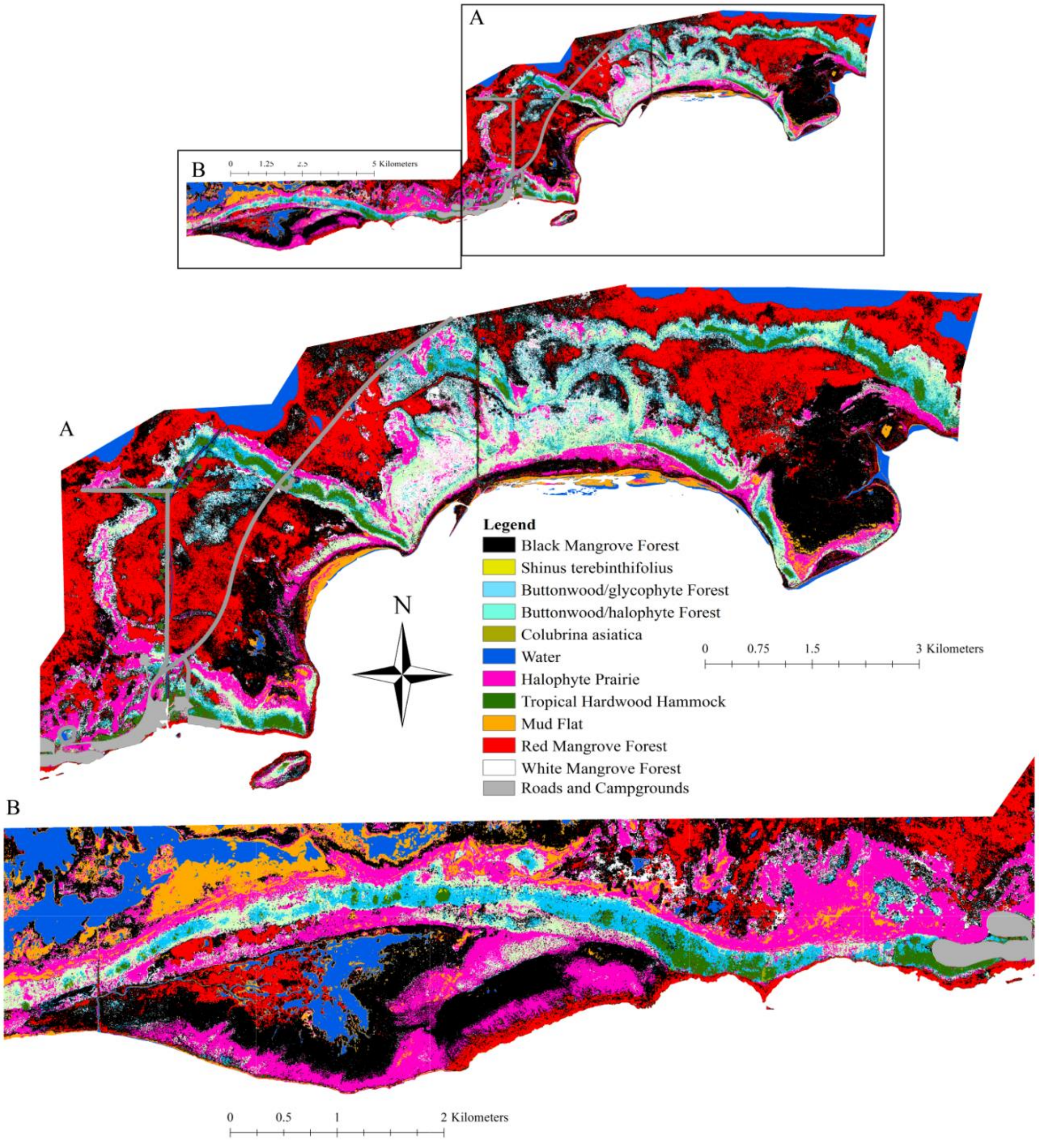
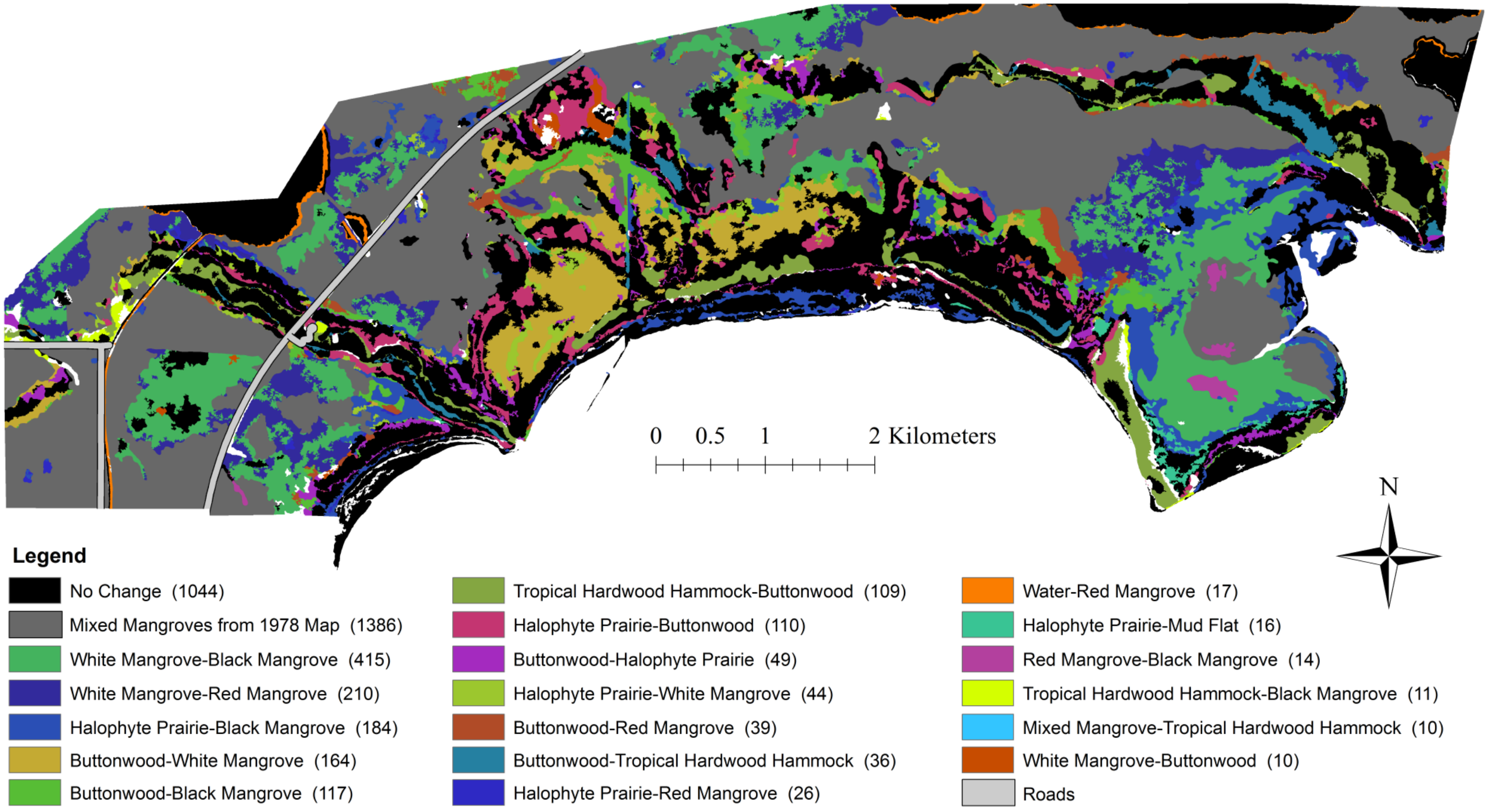


Figure 1.7. Community change map between 1978 and 2011of the 41km^2 study area, Flamingo, Everglades National Park. The numbers in parentheses are hectares each community change represents on the map. In the Legend labels, the first community named was present in the 1978 map, while the second community named was present at that location in the 2011 map.



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CHAPTER II

CAN HALOPHYTES SALINIZE SOIL WHEN COMPETING WITH GLYCOPHYTES, INTENSIFYING EFFECTS OF SEA LEVEL RISE IN COASTAL COMMUNITIES?

Halophytes can salinize soil when competing with glycophytes, intensifying effects of sea level rise in coastal communities

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ABSTRACT

Anthropogenic disturbances and sea level rise (SLR) have caused the world's coastal plant communities to decline 25-50% over the last 50 years. Along the coast of Florida, SLR and large-scale ecosystem drying have worked together to increase groundwater salinity driving shifts in plant community composition. Halophytic (salt-tolerant) understory species have been documented moving into glycophytic (salt-intolerant) communities. There is debate as to whether halophytes entering a system result in higher or lower soil salinity. Halophytes are thought to transpire under higher salinity levels than glycophytes. Continued transpiration under dry, saline conditions may draw up saline groundwater leading to increased soil salinity levels; however, halophytes may also transport soil salts into their leaves freshening soils. We hypothesized that halophytes increase soil salinity as compared to glycophytes through continued transpiration during dry, highly saline periods, drawing saline groundwater up through the soil column via capillary rise.

Our results show that, indeed, halophytes increased soil salinity with increasing halophyte density; however, not directly from higher transpiration rates. Instead, either osmotic or ionic stress caused a decrease in biomass resulting in overall less plant transpiration even though per unit area stomatal conductance was the same for both halophytes and glycophytes after salinity treatments began. Once halophytic individuals establish they increase soil salinity throughout the soil column making conditions more conducive to further halophyte establishment adding a biological component to observed plant community turnover. Our study suggests that coastal plant community turnover may occur faster than would be predicted from SLR and anthropogenic disturbance alone.

Keywords: Halophyte, Glycophyte, Competition, Soil salinity, Sea level rise, Climate Change, Coastal vegetation shifts

SIGNIFICANCE STATEMENT

We demonstrate that changes in coastal plant community composition attributed to anthropogenic disturbances and sea level rise (SLR) are also, in part, as a result of halophytic (salt-tolerant) individuals increasing soil salinity as they invade upland glycophytic (non-salt-tolerant) communities. Once halophytes establish they increase soil salinity throughout the soil column making conditions more conducive to further halophyte establishment. We did not find a difference in per unit area stomatal conductance under increased groundwater salinity between our study halophytic and glycophytic species. Therefore, halophyte influence on soil salinity is likely from higher salt tolerance rather than shutting stomata to prevent water loss. Our results suggest that coastal plant community turnover may occur faster than would be predicted from SLR and anthropogenic disturbance alone.

INTRODUCTION

Increasing sea levels and anthropogenic disturbances are causing changes in coastal plant communities around the world (1–3). Shifts from less salt- and lower inundation- tolerant to more salt- and higher inundation-tolerant community types or to open water have been documented (1, 3–7). Over the past 50 years, the world’s coastal vegetation declined in area 25-50% (8) because of a combination of sea level rise (SLR) and anthropogenic alterations (9). Future SLR rate is expected to exceed both the mean global SLR rate during the 20th century (1.7mm yr^{-1}) and SLR rate since 1993 (3.6mm yr^{-1}) (10), further threatening coastal habitats. A diverse coastal plant community matrix is critical for healthy coastal ecosystems, both human and natural alike (8, 11–15), and is a hotspot for CO_2 sequestration (8, 14, 15). Increases in groundwater salinity and inundation periods and depth drive shifts in plant community composition (4, 9); however, organisms themselves can act as ecosystem engineers, modifying habitats to increase their survival (16). The effect of salt on plants, communities, and plant competition is well established (17–20), but there are conflicting results on whether and how plants influence soil salinity (21–25). As SLR salinizes coastal groundwater and soil, it becomes important to understand how halophytes (salt-tolerant plants) invading glycophytic (non-salt-tolerant) communities affect soil salinity (24), to determine whether a biological component should be added to the causes of community change predicted with SLR.

Plants can influence soil salinity via below-ground feedback loops in the soil vadose zone. The vadose zone is a thin layer between the top of the brackish groundwater table and the soil surface where water is stored and moved between the land surface, root zone, and groundwater (26). Low precipitation or over-extraction of water for human use, coupled with evapotranspiration, dries the vadose zone, drawing up saline groundwater via capillary rise and salinizing the freshwater lens and rhizosphere (1, 23). Seasonal precipitation infiltrates the vadose zone, freshening the soil and forming a freshwater lens above the seawater/groundwater table (1, 23). The seasonal desalinization process, along with slightly higher elevation, allows glycophytic plant communities to exist in coastal areas that might not support them otherwise (27–29). Sea level rise and anthropogenic disturbances such as wetland drying can result in the groundwater table becoming saltier and higher, thinning the freshwater lens and leaving it vulnerable to permanent salinization (1, 3, 30). Increasing groundwater and vadose zone salinity impacts the overlying plants.

Changes in plant communities aboveground can alter vadose zone and groundwater salinity levels (21, 31, 32). Halophytes and glycophytes have differing physiological responses to salt stress. In freshwater-limited systems glycophytes shut stomata above threshold salinity levels (33, 34), enabling the vadose zone to recharge with freshwater. Halophytes, however, continue to transpire and, in some cases, transpire more under higher salinity levels (33, 34). A reasonable hypothesis is that as groundwater salinity increases from SLR, halophytes will increase vadose zone and rhizosphere salinity via higher transpiration rates, creating a positive feed-back loop that allows them to out-compete glycophytes, resulting in plant community turnover. This study addresses the issue of halophytes' effects on vadose zone salinity in southern Florida coastal communities.

Beginning in 1909, Florida Everglades' drainage resulted in a broad front of saltwater intrusion along the shore and up drainage canals (35). By the late 1990's, saltwater intrusion had extended 10-15km inland (36) and in 2006 existed in 6 to 25km wide coastal zones (37). Saltwater intrusion has been attributed to SLR and large-scale anthropogenic drying of the Everglades watershed (35, 37, 38). The Comprehensive

Everglades Restoration Plan is working to restore freshwater flows into the Everglades watershed, decrease saltwater intrusion, and mitigate nutrient input (39). Sea level rise, however, counteracts this restoration effort. The Intergovernmental Panel on Climate Change predicts a sea level increase from 0.45 to 0.82m in the next 50-100 years (10). Restoration and SLR effects will interact most directly in the coastal areas of Everglades National Park (ENP).

Increases in sea level and saltwater intrusion are threatening rare plant species in the coastal buttonwood hammocks of ENP (6). We examined possible causes of change in ENP coastal understory species composition by experimentally testing the ability of halophytes to alter soil salinity levels during the dry season under varying glycophyte/halophyte ratios. We hypothesized that in freshwater-limited systems halophytes alter soils as compared to glycophytes by increasing salinity levels through continued transpiration during dry periods, drawing saline water up through the soil column.

MATERIALS AND METHODS

Area of interest: The ENP coastal buttonwood hammock and buttonwood prairies reside on the Buttonwood Embankment, which is a coastal ridge separating the tip of the Florida peninsula from Florida Bay, U.S.A (40–42). Southern Florida is humid and subtropical with a distinct warm (mean 25^{o}C) wet season from June to October and cool (mean 22^{o}C) dry season from November to May. Average annual rainfall is between 100 and 163cm with more than half falling between June and September, assisted by hurricanes and tropical storms; April and May usually are the driest months (43, 44).

Two coastal communities, buttonwood hammock and buttonwood prairies, were the focus of this research.

Buttonwood hammocks (mean elevation 29+3cm) sustain freshwater flooding during the wet season and are dry during the dry season (45). Buttonwood hammocks have an average groundwater table of -33+1cm and 26-29.5 groundwater salinity (6, 29). *Conocarpus erectus*, buttonwood, is the dominant canopy species, but a number of other woody species are also present (29). The buttonwood understory has species such as *Alternanthera flavescens* Kunth, *Chromolaena frustrata*, *Dicliptera sexangularis* (L.) Juss., and *Heliotropium angiospermum* Murray (29).

Buttonwood prairies are halophytic prairies that have marl soils and slightly lower elevation than adjacent buttonwood hammocks (46). During the wet season, buttonwood prairies have months of standing water that is brackish to freshwater and can become hypersaline during the dry season because of evaporation and a lack of drainage (47). Buttonwood prairies (mean elevation 18+3cm) show a mean groundwater table at -32+2cm and average groundwater table salinity of 38.8+0.6‰ (29). Scattered *Conocarpus erectus* is the only canopy tree species in buttonwood prairies. The understory is comprised of *Batis maritima* L., *Borrichia frutescens* (L.) DC., *Distichlis spicata* (L.) Greene, *Sarcocornia perennis* (Mill.) A.J. Scott, and *Suaeda linearis* (29).

Study species: Because halophyte encroachment has been found to be an early indicator of change in buttonwood hammock understories (6), in our experiments we used two halophyte species commonly found invading coastal buttonwood hammocks in ENP (*Batis maritima* and *Sarcocornia perennis*) and two glycophyte species commonly found in buttonwood hammock understory (*Heliotropium angiospermum* and *Alternanthera flavescens*) (29).

Propagation protocol: Cuttings of each species were made from *in-situ* plants found along the Coastal Prairie Trail, ENP, between February and April 2011 (ENP Scientific Research and Collecting Permit# EVER-2011-SCI-0019). Freshly cut ends were dipped in rooting hormone (Shultz Take Root Rooting Hormone, Shultz Company, Bridgeton, MO), wrapped in damp paper towels, and placed in plastic bags for transport. The cuttings were immediately processed at the Florida International University (FIU) greenhouse, where they were planted in trays of perlite and placed on a misting bench with a 15s mist every five minutes for 16 hours/day. Once roots formed, the cuttings were planted into 10cm^3 pots with standard seedling potting soil mix (Fafard® 4 Mix, Sun Gro Horticulture Canada LTD, Agawam, MA, USA) and fertilized with a slow release granular fertilizer (Nutricote® Total 18-6-8, Chisso-Asahi Fertilizer Co., LTD, Tokyo, Japan). They were maintained as such until planting for the experiment.

Because coastal ENP buttonwood prairies reside on marl soils (48), we planted the final experiment in locally collected marl. We dug up the marl from a private wetland and transported it to the FIU greenhouse, where we manually removed large rocks and root debris, mixed the soil, and used immediately.

Study design: The ability of halophytes to alter soil salinity was tested via a replacement series experiment. Five replicates of paired halophyte/glycophyte combinations (*B. maritima* versus *H. angiospermum*; *B. maritima* versus *A. flavescens*; *S. perennis* versus *H. angiospermum*; and *S. perennis* versus *A. flavescens*) were planted with the following halophyte/glycophyte ratios: 0:4, 1:3, 2:2, 3:1, 4:0. We planted into

9.5L pots (44cm deep) filled with marl soil. We used pots 44cm deep to simulate the vadose zone—the lowest average depth to water table in the buttonwood communities was -33cm in buttonwood hammocks (29). We planted 4cm below the top of the pot and set each replicate combination in trays of treatment water that was 3cm deep, leaving a 37cm soil column/root zone/vadose zone. To mimic dry season effects where plants only have groundwater as their water supply, plants were watered from the bottom only; no watering was administered to the top of the pots once the experiment began. Upon experiment initiation, the replicates were given 26‰ saline water (average buttonwood hammock soil salinity) (6) for the first month and 38‰ water—average dry season soil salinity in buttonwood prairies (29)—for the following three months. The south Florida dry season lasts for six months; therefore the high salinity three month treatment was half the time of the dry season under buttonwood prairie groundwater conditions. Saline solutions were created by dissolving measured amounts of Instant Ocean Aquarium Sea Salt Mix (Spectrum Brands, Blacksburg, VA) with tap water and pouring the solution into the trays containing the experimental pots. Salinity levels were monitored three days a week using a portable hand-held salinity refractometer (RHS-10ATC, Agriculture Solutions, Strong, ME) and adjusted as needed to maintain appropriate salinity levels. To provide access to soil for sampling, 2cm diameter holes were cut in each pot at 9, 18, and 30cm from the water surface. The openings were sealed between sampling using the hole cut outs and duct tape. The highest soil column measurement, 30cm, was 7cm below the soil surface.

We planted the replicates 5th – 8th November 2012, and watered with fresh water from above for one month to allow acclimation prior to salinity treatments. To assess the effects of treatment on relative soil salinity, pre-treatment soil samples were taken shortly after planting, 10th – 18th November, 2012. On 17th December, 2012, the plants were exposed to the first 26‰ salinity treatment. Soil samples were then collected one month after treatment (21st – 25th January, 2013). On the 28th January, 2013, the saline solution was increased to 38‰. Final soil samples were collected on 12th – 13th June 2013. For each soil collection date, one 2g soil sample was collected from the 30, 18, and 9cm extraction ports of each pot, totaling 360 samples collected. Soil samples were dried at 70°C in a drying oven (OV35545, Thermolyne, United States) for three weeks. The dry soil was crushed through a 2mm sieve to ensure even particle size. One gram of sieved soil was weighed and placed in a 20ml glass scintillation vial, 5ml of DI water was added to each vial, and the vials were gently shaken on a mechanical shaker for one hour. After one hour, the solution was filtered using a 90mm diameter qualitative filter paper (Cat No 1001 090, Whatman, United States), and electrical conductivity (EC) (*u*S/cm) measurements were taken using a dual channel pH/Ion/Conductivity meter (AR 50, Fisher Scientific Accumet Research, United States). EC measurements were converted to parts per thousand for analysis: ppt = (*u*S/cm*0.64)/1000. Because salinity was determined via a 1:5 soil/water extraction, the extracts give a relative soil salinity level (49).

Stomatal conductance was measured on all four species using a steady-state porometer (LI-1600m, LI-COR, Inc, Lincoln, NE). Stomatal conductance (mmol m^{-2} s^{-1}) was measured one month after planting but before treatments began (freshwater; 11 December, 2012), after one month of exposure to 26‰ groundwater (25th January, 2013), one month after 38‰ (27th February, 2013), and after 3 months at 38‰ (14th June, 2013).

One to three of the most recently matured leaves of each species from pots with all four individuals of the same species were measured. When the leaves were too small to completely fill the porometer chamber, leaf area inside the chamber was measured (mm^2). Because the LI-1600m does not adjust for boundary layer resistance, the boundary layer resistance and an adjustment for leaf area were made to find the true conductance value (50).

Shoot and root biomass were measured for each plant after the final soil samples were taken. Roots were cleaned by washing and cut from the shoot. Roots and shoots were placed in separate brown paper bags for drying. The samples were dried at 70°C in a drying oven (OV35545, Thermolyne, United States) for 7-10 days; dry samples were weighed to 0.01g on a balance (PG2002-S, Metler Toledo, Columbus, OH).

Statistical Analysis: To test the effects of halophyte/glycophyte ratio on soil column salinity under freshwater, 26‰, and 38‰ groundwater salinity, we used linear mixed effects models fit by maximum likelihood with soil salinity as the dependent variable, halophyte/glycophyte ratio and soil column depth as interacting fixed effects, and treatment tray as the random effect. We then assessed pairwise comparisons of halophyte/glycophyte ratio and soil column depth with Tukey post hoc tests. We utilized Analyses of Variance and Tukey post hoc tests to evaluate the effects of freshwater, 26‰, and 38‰ groundwater salinity on stomatal conductance of each of the four test species, where stomatal conductance was the response variable and species was the fixed effect. To address the effects of halophyte/glycophyte ratio on average individual biomass per species, we employed a linear mixed effects model fit by maximum likelihood with shoot or root biomass as the dependent variable, halophyte/glycophyte ratio as the fixed effect, and treatment tray as the random effect. We used Tukey post hoc tests to determine statistical differences in root or shoot biomass across the various ratios of the respective species.

All analyses were executed in the R statistical environment (v3.0.2; R Core Team 2013). The linear mixed effects models were performed using the nlme package (51), and Tukey post hoc tests for the linear mixed effects models were completed with the lsmeans package (52). Readers can access the data in this paper through the Florida Coastal Everglades LTER data repository (53).

RESULTS

Halophyte ratio affected relative soil salinity, and the effects increased when groundwater salinity increased. There were no significant differences in relative salinity after one month of fresh groundwater across halophyte/glycophyte densities or species combinations, except for *Sarcocornia perennis/Heliotropium angiospermum* (*S1* and *S2*). For this species combination at 18cm above treatment water, pots with all halophytes (*S. perennis*) showed significantly higher soil salinity than pots with one halophyte and three glycophytes (*H. angiospermum*) ($p < 0.001$; *S1* and *S2*) and two halophytes and two glycophytes ($p = 0.001$; *S2*), and at 9cm, pots with four and three *S. perennis* showed significantly higher salinity than those with three and four *H. angiospermum* (all: $p < 0.001$; *S1* and *S2*). Though soils were mixed prior to planting, it is possible that a pocket of higher salinity soil was detected in the above analysis.

Small changes in soil salinity were seen when groundwater was increased to 26‰ salinity for one month. Soil salinity at 30cm above the water level did not significantly differ between any of the species combinations or halophyte/glycophyte densities (Fig. 2.1; *S1* and *S2*). At 18cm above the groundwater level, pots with four *Alternanthera flavescens* showed significantly higher salinity than those with four *Batis maritima* and those with four *S. perennis* (Fig. 2.1; *S1* and *S2*); otherwise, no differences were seen at this level and groundwater salinity. At 9cm above the groundwater, differences were seen among halophyte/glycophyte densities between both glycophytes and *S. perennis* but with *B. maritima.* Comparing *S. perennis* versus *A. flavescens*, pots with only *S. perennis* showed significantly lower soil salinity than any of the other *A. flavescens/S. perennis* ratios and were not different from the control soils (Fig. 2.1; *S1* and *S2*). Pots with all *H. angiospermum* and pots with three *S. perennis* were both significantly different from the control, but none of the other species ratio combinations differed significantly (Fig. 2.1; *S1* and *S2*). All combinations of *B. maritima* and either glycophyte showed significantly higher soil salinity than control pots but not between the glycophyte/halophyte combinations (Fig. 2.1; *S1* and *S2*).

Strong patterns in halophyte ratio effects emerged after three months at 38‰ groundwater salinity. Pots with all halophytes show significantly more relative soil salinity than those with just glycophytes in all four species combinations and at all three soil strata except *S. perennis* versus *A. flavescens* at 18cm, where there was no significant difference (Fig. 2.1; *S1* and *S2*). All pots showed a steady increase in soil salinity at all three soil strata as halophyte ratio increased, regardless of which glycophyte species was paired with the halophyte (Fig. 2.1; *S1* and *S2*). The highest soil salinity (22‰) occurred in pots with only *B. maritima* at 38‰ and at 9cm above groundwater.

Stomatal conductance changed with increasing salinity in all four species. When taking measurements from plants in pots with only that species (4:0 and 0:4), in freshwater, *B. maritima* showed significantly less stomatal conductance than *H. angiospermum* (Fig. 2.2; *S3*). *Sarcocornia perennis* showed similar stomatal conductance to *B. maritima* and *A. flavescens,* while *A. flavescens* and *H. angiospermum* maintained similar stomatal conductance (Fig. 2.2; *S3*). All species significantly decreased stomatal conductance when treatment water was increased to 26‰ salinity for one month, except *B. maritima,* which significantly increased (Fig. 2.2; *S4*). After one month at 26‰ salinity and for both 38‰ samplings, all four species exhibited similar stomatal conductance among each other and within the species, except *A. flavescens,* which displayed significantly less stomatal conductance than *S. perennis* at one month of 38‰ (Fig. 2.2; *S3* and *S4*).

As the ratio of one plant type (halophyte or glycophyte) increased, so did average biomass per plant of that type. Halophyte biomass tended to be more sensitive to halophyte/glycophyte ratio, showing larger increases in biomass with increasing halophyte ratio (Fig. 2.3; *S5*). *Batis maritima* had the most consistent increase in biomass with increasing ratio regardless of which glycophyte it was paired with (Fig. 2.3; *S5*); *B. maritima* individuals in pots with only *B. maritima* displayed significantly greater shoot and root biomass as compared to individuals growing in all other ratio and species combinations (Fig. 2.3). *Sarcocornia perennis* also exhibited significant increases in root and shoot biomass with increasing *S. perennis* ratio; however, when paired with *A. flavescens,* only those with all *S. perennis* showed significantly more root and shoot biomass (Fig. 2.3; *S5*). When paired with *H. angiospermum,* those individuals with three or four *S. perennis* were similar and either trending towards being larger plants or were significantly larger than those in other ratio combinations, respectively (Fig. 2.3; *S5*). Both glycophyte species showed largest biomass when only glycophytes were in the pot and gradual decreases in biomass with decreases in glycophyte ratio (Fig. 2.3; *S5*).

DISCUSSION

The results of this study show that halophytes can eco-engineer their environment to increase vadose zone salinity, resulting in increased competitive ability for halophytes as compared to glycophytes as soils become more saline. When all four species in our study were subjected to regular freshwater watering, glycophytes transpired more than halophytes, supporting findings of greater glycophyte competitiveness against halophytes under abundant freshwater (54, 55). A reduction in stomatal conductance was seen in three of the four species between the freshwater and one month of 26‰ measurements, rendering similar stomatal conductance between all four species for the remainder of the study. As the halophyte/glycophyte ratio increased, so did relative soil salinity rejecting our hypothesis that decreased glycophytic transpiration rates drove differences in soil salinity between the plant types.

Soil salinity after one month at 26‰ showed no significant differences across the species or ratio combinations, as would be expected with similar transpiration rates. Soil salinity was higher at 9cm above treatment water levels than soils at 18 and 30cm. All four species were transpiring at the same rate and leaves of glycophytes and halophytes had not changed dramatically in size by this monitoring date (K. Wendelberger personal observations). Perhaps increased salinity at the lower stratum was the early sign of transpiration drying soils, resulting in capillary action bringing salty groundwater into the pots and raising soil salinity at 9cm.

A distinct pattern of halophytic influence on soil salinity as the halophytic/glycophytic ratio increased was seen after three months at 38‰ groundwater. Soil salinity across all three soil strata was significantly higher in pots with all halophytes as compared to pots with only glycophytes regardless of the species combination. Additionally, there was a general trend of increasing soil salinity as halophyte ratio increased across the replicates. Per unit area stomatal conductance was similar across the four species at both one and three months of 38‰ groundwater; however, when looking at root and shoot biomass, plant size differed.

As halophytes increased in ratio in our experiment, mean individual halophyte shoot and root biomass increased significantly. Conversely, glycophyte root and shoot biomass showed a trend of decreasing size as glycophyte/halophyte ratio and decreased significantly at different ratios, depending on the species combination. Further, glycophyte leaves of both species decreased in size, while leaves of both halophyte species increased over the course of the experiment (K. Wendelberger personal observations). Though shoot and leaf growth was not measured, the steady-state porometer chamber area was consistent for all measurements. Both glycophyte species' leaves were larger than the chamber area during the freshwater and one month after 26‰ treatment measurements. Both halophytes' leaves were small, and it was difficult to fill the chamber with leaf material for the freshwater and 26‰ treatments. After three months at 38‰, both halophyte species' leaves had grown to sizes that easily filled the chamber, while 26% of *A. flavescens* and 95% of *H. angiospermum* leaves were smaller than the chamber area. Changes in chamber area covered by both halophytic and glycophytic species suggests that halophyte leaf area increased under 38‰ salinity, while glycophyte leaf area diminished. Additionally, mature leaves had dried and fallen from both glycophytes by the end of the study while both halophytes showed no sign of leaf senescence (K. Wendelberger personal observation). Osmotic stress causes a reduction in rate of young leaf expansion and reduced mature leaf stomatal conductance, while ionic stress shows as an increase in older leaf senescence rate (34). Reduction in leaf area decreases total plant transpiration and photosynthesis (34). Perhaps the combination of higher soil salinities and salinity exposure time acted together to stress the glycophytes to a point where biomass production was no longer feasible and halophytes were more competitive. Larger halophyte plants under higher halophyte densities results in more plant material transpiring per pot, increasing soil saltwater intrusion via capillary action. Further studies need to be conducted to pinpoint whether it is halophytic resistance to osmotic or ionic toxicity that drives their ability to eco-engineer soils as they invade into glycophytic communities.

Coastal plant communities around the world are threatened by halophytic movement into upland glycophytic communities (1–3, 56). Sea level rise coupled with anthropogenic disturbance has been found to be the major contributors to the loss of coastal communities (3). Simulation models are predicting large scale changes in coastal plant community composition from SLR (28, 57–59), and rates of SLR are expected to increase in the coming years (10), further threatening already changing systems.

The current study suggests that changes may occur faster than would be predicted from SLR and anthropogenic disturbance. Once halophytic individuals establish and increase soil salinity throughout the soil column, conditions become more conducive to further halophyte establishment. Eventually, soil salinity levels may be too high to support glycophyte survival and establishment, resulting in a turnover in plant communities from less salt tolerant to more salt tolerant community types (e.g. (4, 6, 56). The process of increasing soil salinity via increasing halophyte density in glycophytic communities brings a biological component to SLR- related coastal plant community shifts.

In south Florida, the Buttonwood Ridge is a ridge line following the coast that has a slightly higher elevation than lands to the north or south (40, 60). Upland plant communities in coastal ENP harbor 21 rare plant species that are threatened by SLR (6). Understanding the feedback loops enhancing the rate of change expected from SLR is important when evaluating conservation actions such as when to collect seeds or germplasm, perform assisted migration, and/or form *ex-situ* conservation collections. Because lower elevation species have already been documented invading higher elevation communities in the area (6, 56), one can expect underground salinity and inundation changes are occurring that will only further promote losses of upland habitats. The time for conservation action on our most threatened coastal species is now, before further habitat loss occurs.

FIGURE LEGENDS

Fig. 2.1. Linear mixed effects models and Tukey post hoc tests looking at the effects of 26‰ and 38‰ groundwater relative soil salinity and varying halophyte/glycophyte ratios across soil column depths of four species combinations (Batis maritima (H) vs Alternanthera flavescens (G), B. maritima (H) vs Heliotropium angiospermum (G), Sarcocornia perennis (H) vs A. flavescens (G), S. perennis (H) vs H. angiospermum (G)). The red, blue, and green hued whisker plots are data from soil samples taken at 30, 18,

and 9 cm above the treatment water, respectively. Lettering indicates statistical significances in soil salinity levels at that soil depth for the halophyte:glycophyte combinations; different letters signify significantly different results. The legend gives the number of halophytes to glycophytes (H:G). The black bar in the middle of the boxes represents the median, vertical lines represent the upper and lower extremes of the data set.

Fig. 2.2. Analysis of Variance and Tukey post hoc tests looking at the difference in mean stomatal conductance (mmol $m^{-2}s^{-1}$) between two halophytes (Batis maritima and Sarcocornia perennis) and two glycophytes (Alternanthera flavescens and Heliotropium angiospermum) across varying salinity treatments and time. Plunge bars represent the standard deviation. Small lettering indicates statistical significances across species for each salinity treatment; capital lettering indicates statistical significances within each species across treatments and time. Different letters signify significantly different results.

Fig. 2.3. Average shoot and root biomass (g) per plant of four species planted in varying densities and species combinations (Batis maritima (H) vs Alternanthera flavescens (G), B. maritima (H) vs Heliotropium angiospermum (G), Sarcocornia perennis (H) vs A. flavescens (G), S. perennis (H) vs H. angiospermum (G)). Measurements were taken at the end of the experiment. Black and grey plots represent glycophyte shoot and root biomass, respectively. Dark and light blue boxes represent halophyte shoot and root biomass, respectively. Plunge bars are standard deviations. Lettering indicates statistical differences between shoots or roots of the respective species across different halophyte/glycophyte ratios; different letters signify significantly different results.

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FIGURES

Figure 2.1.

Linear mixed effects models and Tukey post hoc tests looking at the effects of 26‰ and 38‰ groundwater relative soil salinity and varying halophyte/glycophyte ratios across soil column depths of four species combinations.

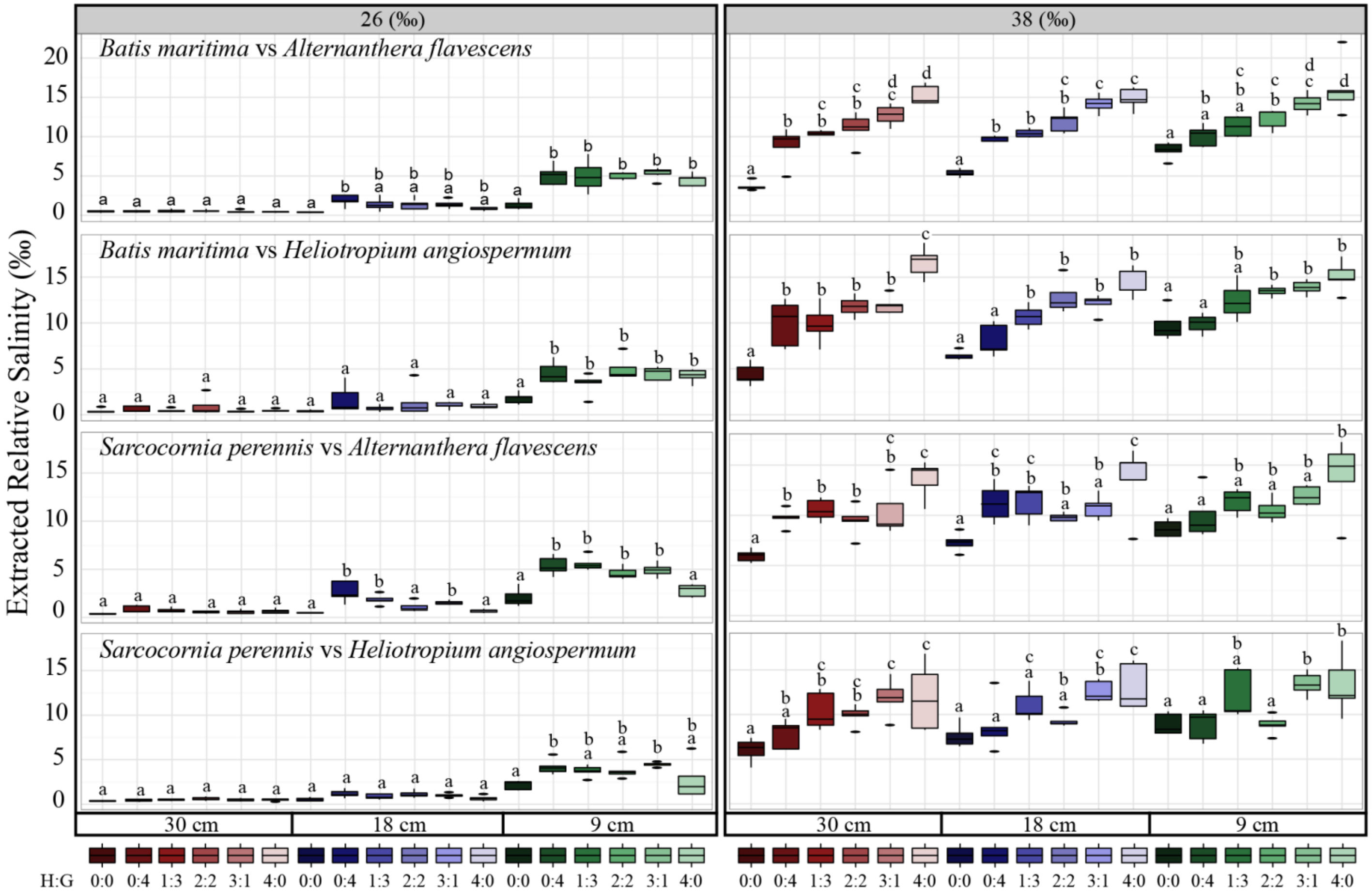


Figure 2.2. Analysis of Variance and Tukey post hoc tests looking at the difference in mean stomatal conductance (mmol $m^{-2}s^{-1}$) between two halophytes (Batis maritima and Sarcocornia perennis) and two glycophytes (Alternanthera flavescens and Heliotropium angiospermum) across varying salinity treatments and time.

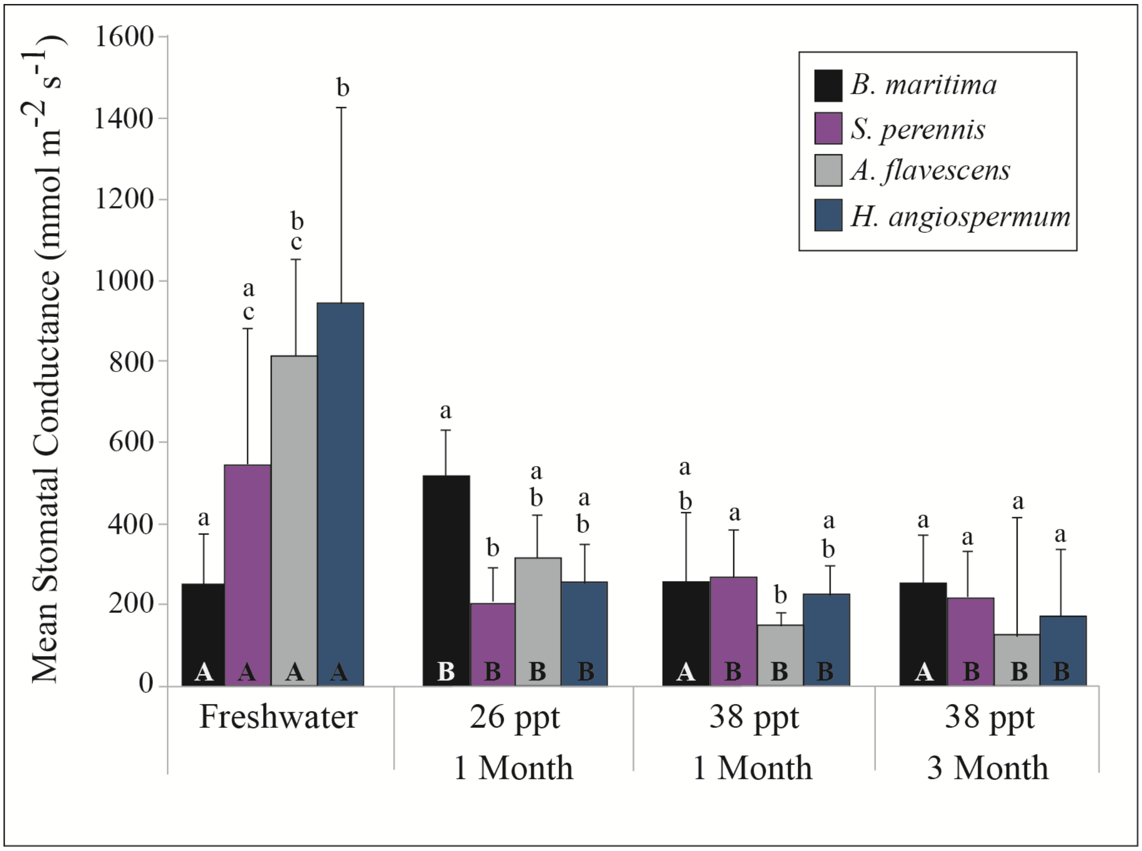
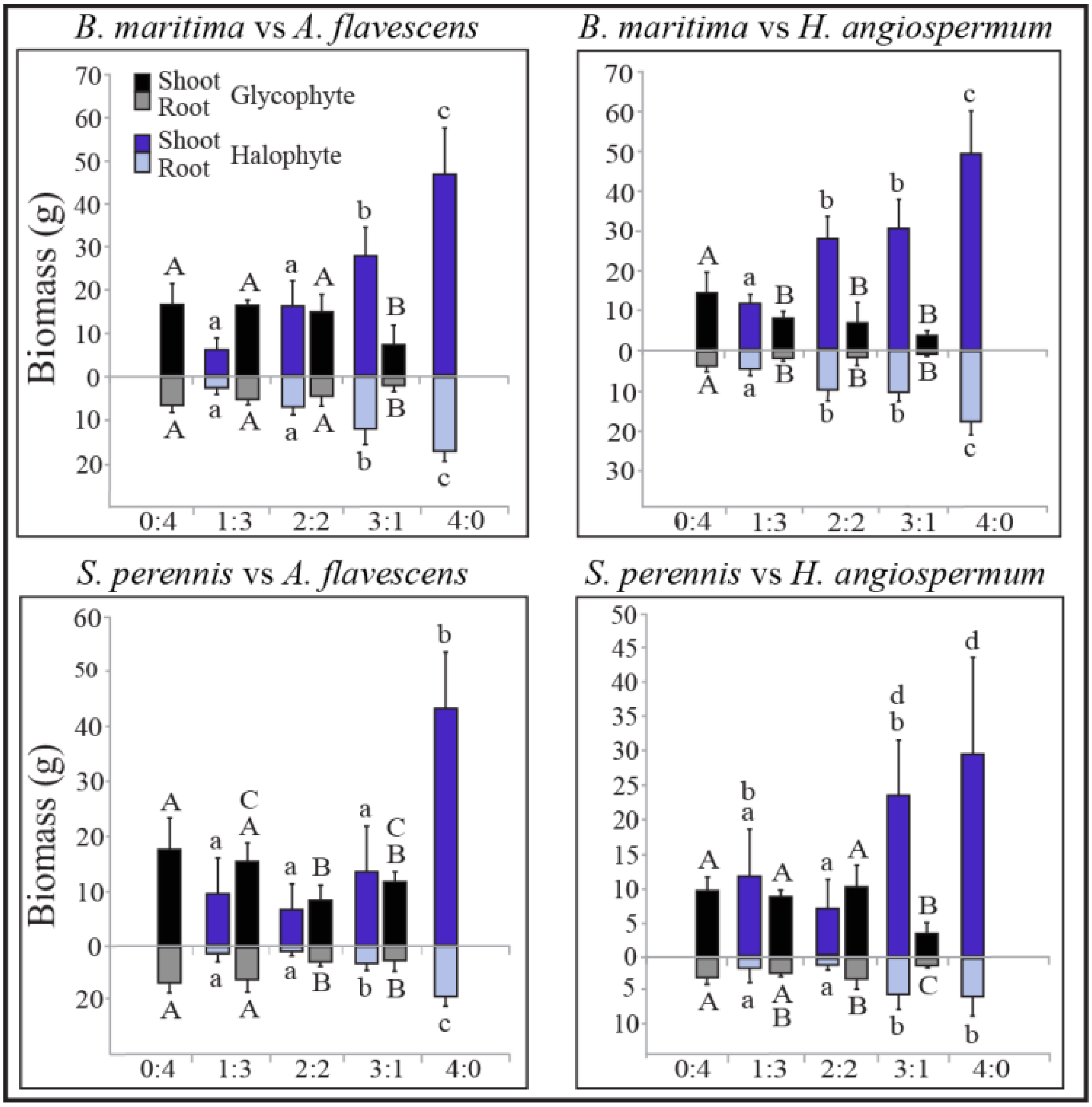


Figure 2.3. Average shoot and root biomass (g) per plant of four species planted in varying densities and species combinations (Batis maritima (H) vs Alternanthera flavescens (G), B. maritima (H) vs Heliotropium angiospermum (G), Sarcocornia perennis (H) vs A. flavescens (G), S. perennis (H) vs H. angiospermum (G)).



SUPPLEMENTAL INFORMATION

S1. Mean salinity levels (‰) of each of the species combinations (*Batis maritima* (H) vs *Alternanthera flavescens* (G), *B. maritima* (H) vs *Heliotropium angiospermum* (G), *Sarcocornia perennis* (H) vs *A. flavescens* (G), *S. perennis* (H) vs *H. angiospermum* (G)), soil column levels, and halophyte/glycophyte ratio combination.

Batis maritima vs *Alternanthera flavescens*

Freshwater	**9cm**	**18cm**	**30cm**
0:0	0.42	0.40	0.43
0:4	0.44	0.48	0.47
1:3	0.52	0.49	0.44
2:2	0.54	0.52	0.53
3:1	0.53	0.50	0.50
4:0	0.54	0.53	0.49
26‰			
0:0	1.78	0.44	0.42
0:4	5.07	2.20	0.64
1:3	5.00	1.40	0.44
2:2	5.05	1.60	0.54
3:1	5.36	1.42	0.54
4:0	4.38	0.90	0.46
38‰			
0:0	8.90	6.69	5.01
0:4	10.02	10.49	9.30
1:3	11.27	10.44	10.44
2:2	12.26	11.94	11.05
3:1	14.23	14.17	12.76
4:0	15.62	14.79	15.93

Batis maritima vs *Heliotropium angiospermum*

Freshwater	**9cm**	**18cm**	**30cm**
0:0	0.42	0.40	0.43
0:4	0.47	0.56	0.48
1:3	0.60	0.53	0.58
2:2	0.51	0.50	0.51
3:1	0.57	0.57	0.44
4:0	0.54	0.53	0.49
26‰			
0:0	1.78	0.44	0.42
0:4	4.38	1.45	1.27
1:3	3.39	0.72	0.46
2:2	5.03	1.62	0.96
3:1	4.51	1.03	0.41
4:0	4.38	0.64	0.46
38‰			
0:0	8.90	6.69	5.01
0:4	9.39	8.43	8.89
1:3	12.39	10.69	9.88
2:2	13.47	12.85	11.79
3:1	13.87	12.08	11.94
4:0	15.62	14.79	15.93

Sarcocornia perennis vs *Alternanthera flavescens*

Freshwater	**9cm**	**18cm**	**30cm**
0:0	0.42	0.40	0.43
0:4	0.44	0.48	0.47
1:3	0.48	0.48	0.49
2:2	0.51	0.50	0.47
3:1	0.50	0.49	0.48
4:0	0.51	0.52	0.45
26‰			
0:0	1.78	0.44	0.42
0:4	5.07	2.20	0.64
1:3	5.24	1.71	0.67
2:2	4.32	1.06	0.50
3:1	4.61	1.41	0.52
4:0	2.67	0.64	0.53
38‰			
0:0	8.90	6.69	5.01
0:4	10.02	10.49	9.30
1:3	11.38	11.35	10.53
2:2	10.50	9.80	9.47
3:1	11.94	10.80	10.45
4:0	13.61	13.35	12.76

Sarcocornia perennis vs *Heliotropium angiospermum*

Freshwater	**9cm**	**18cm**	**30cm**
0:0	0.42	0.40	0.43
0:4	0.47	0.56	0.48
1:3	0.37	0.41	0.38
2:2	0.41	0.41	0.45
3:1	0.54	0.46	0.47
4:0	0.51	0.52	0.45
26‰			
0:0	1.78	0.44	0.42
0:4	4.38	1.45	1.27
1:3	3.72	0.86	0.49
2:2	3.88	1.14	0.64
3:1	4.47	0.96	0.50
4:0	2.67	0.64	0.53
38‰			
0:0	8.90	6.69	5.01
0:4	9.39	8.43	8.89
1:3	12.21	11.07	10.37
2:2	8.88	9.36	9.90
3:1	13.42	12.58	11.90
4:0	13.61	13.35	12.76

S2. Results of linear mixed effects models and Tukey post hoc tests looking at the effects of Freshwater, 26‰ and 38‰ groundwater salinity and varying halophyte/glycophyte ratios across soil column depths of four species combinations (*Batis maritima* (H) vs *Alternanthera flavescens* (G), *B. maritima* (H) vs *Heliotropium angiospermum* (G), *Sarcocornia perennis* (H) vs *A. flavescens* (G), *S. perennis* (H) vs *H. angiospermum* (G)). Significant *p*-values are in bold.

Freshwater		*B. maritima* vs *A. flavescens*	*B. maritima* vs *H. angiospermum*	*S. perennis* vs *A. flavescens*	*S. perennis* vs *H. angiospermum*
All Combined		$F_{1,65} = 293.94$ $\boldsymbol{p < 0.001}$	$F_{1,68} = 708.26$ $\boldsymbol{p < 0.001}$	$F_{1,65} = 244.6$ $\boldsymbol{p < 0.001}$	$F_{1,68} = 539.40$ $\boldsymbol{p < 0.001}$
Pairwise		*p*-value	*p*-value	*p*-value	*p*-value
30 cm	0:0 vs 0:4	1.00	1.00	0.85	1.00
	0:0 vs 1:3	1.00	0.75	0.08	0.78
	0:0 vs 2:2	0.94	1.00	0.37	1.00
	0:0 vs 3:1	1.00	1.00	0.18	1.00
	0:0 vs 4:0	1.00	1.00	0.92	1.00
	0:4 vs 1:3	1.00	1.00	1.00	0.94
	0:4 vs 2:2	1.00	1.00	1.00	1.00
	0:4 vs 3:1	1.00	1.00	1.00	1.00
	0:4 vs 4:0	1.00	1.00	1.00	1.00
	1:3 vs 2:2	0.91	1.00	1.00	0.95
	1:3 vs 3:1	1.00	0.61	1.00	0.67
	1:3 vs 4:0	1.00	1.00	0.99	0.60
	2:2 vs 3:1	1.00	1.00	1.00	1.00
	2:2 vs 4:0	0.99	1.00	1.00	1.00
	3:1 vs 4:0	1.00	1.00	1.00	1.00
18 cm	0:0 vs 0:4	0.32	0.08	1.00	0.99
	0:0 vs 1:3	0.97	0.78	0.27	1.00
	0:0 vs 2:2	0.56	0.97	0.07	1.00
	0:0 vs 3:1	0.87	0.25	0.20	1.00
	0:0 vs 4:0	0.13	0.96	0.61	0.19
	0:4 vs 1:3	1.00	1.00	0.97	0.47
	0:4 vs 2:2	1.00	0.99	0.79	0.48
	0:4 vs 3:1	1.00	1.00	0.95	1.00
	0:4 vs 4:0	1.00	0.98	1.00	0.99
	1:3 vs 2:2	1.00	1.00	1.00	1.00
	1:3 vs 3:1	1.00	1.00	1.00	1.00
	1:3 vs 4:0	1.00	1.00	1.00	**0.00**
	2:2 vs 3:1	1.00	1.00	1.00	1.00
	2:2 vs 4:0	1.00	1.00	1.00	**0.01**
	3:1 vs 4:0	1.00	1.00	1.00	0.22
9 cm	0:0 vs 0:4	1.00	0.43	1.00	0.99
	0:0 vs 1:3	0.97	0.07	0.93	0.98
	0:0 vs 2:2	0.87	0.95	0.64	1.00
	0:0 vs 3:1	0.95	0.35	0.77	0.40
	0:0 vs 4:0	0.12	0.99	1.00	0.19
	0:4 vs 1:3	0.90	1.00	1.00	1.00
	0:4 vs 2:2	0.66	1.00	1.00	1.00

	0:4 vs 3:1	0.82	1.00	1.00	**0.00**
	0:4 vs 4:0	0.04	1.00	1.00	**0.00**
	1:3 vs 2:2	1.00	1.00	1.00	1.00
	1:3 vs 3:1	1.00	1.00	1.00	**0.00**
	1:3 vs 4:0	0.99	0.93	1.00	**0.00**
	2:2 vs 3:1	1.00	1.00	1.00	0.11
	2:2 vs 4:0	1.00	1.00	1.00	**0.04**
	3:1 vs 4:0	0.98	1.00	1.00	1.00
26‰		*B. maritima* vs *A. flavescens*	*B. maritima* vs *H. angiospermum*	*S. perennis* vs *A. flavescens*	*S. perennis* vs *H. angiospermum*
All Combined		$F_{1,68}$ = 464.92 **p < 0.001**	$F_{1,68}$ = 384.61 **p < 0.001**	$F_{1,68}$ = 2339.45 **p < 0.001**	$F_{1,68}$ = 255.14 **p < 0.001**
Pairwise		p-value	p-value	p-value	p-value
30 cm	0:0 vs 0:4	1.00	1.00	1.00	0.39
	0:0 vs 1:3	1.00	1.00	1.00	1.00
	0:0 vs 2:2	1.00	1.00	1.00	1.00
	0:0 vs 3:1	1.00	1.00	1.00	1.00
	0:0 vs 4:0	1.00	1.00	1.00	1.00
	0:4 vs 1:3	1.00	1.00	1.00	0.55
	0:4 vs 2:2	1.00	1.00	1.00	0.73
	0:4 vs 3:1	1.00	1.00	1.00	0.56
	0:4 vs 4:0	1.00	1.00	1.00	0.55
	1:3 vs 2:2	1.00	1.00	1.00	1.00
	1:3 vs 3:1	1.00	1.00	1.00	1.00
	1:3 vs 4:0	1.00	1.00	1.00	1.00
	2:2 vs 3:1	1.00	1.00	1.00	1.00
	2:2 vs 4:0	1.00	1.00	1.00	1.00
	3:1 vs 4:0	1.00	1.00	1.00	1.00
18 cm	0:0 vs 0:4	**0.01**	0.29	**< 0.001**	1.00
	0:0 vs 1:3	0.57	1.00	**0.00**	1.00
	0:0 vs 2:2	0.15	0.55	0.69	1.00
	0:0 vs 3:1	0.34	1.00	**0.05**	1.00
	0:0 vs 4:0	1.00	1.00	1.00	1.00
	0:4 vs 1:3	1.00	0.70	0.33	1.00
	0:4 vs 2:2	1.00	1.00	**0.00**	1.00
	0:4 vs 3:1	1.00	0.99	**0.02**	1.00
	0:4 vs 4:0	0.34	0.98	**< 0.001**	1.00
	1:3 vs 2:2	1.00	0.90	0.70	1.00
	1:3 vs 3:1	1.00	1.00	1.00	1.00
	1:3 vs 4:0	1.00	1.00	**0.01**	1.00
	2:2 vs 3:1	1.00	1.00	1.00	1.00
	2:2 vs 4:0	0.87	1.00	0.98	1.00
	3:1 vs 4:0	0.98	1.00	0.28	1.00
9 cm	0:0 vs 0:4	**< 0.001**	**< 0.001**	**< 0.001**	**0.04**
	0:0 vs 1:3	**< 0.001**	**0.03**	**< 0.001**	0.36
	0:0 vs 2:2	**< 0.001**	**< 0.001**	**< 0.001**	0.19
	0:0 vs 3:1	**< 0.001**	**< 0.001**	**< 0.001**	**0.01**
	0:0 vs 4:0	**< 0.001**	**< 0.001**	0.53	1.00
	0:4 vs 1:3	1.00	0.39	1.00	1.00

	0:4 vs 2:2	1.00	1.00	0.49	1.00
	0:4 vs 3:1	1.00	1.00	0.99	1.00
	0:4 vs 4:0	0.99	1.00	**< 0.001**	0.52
	1:3 vs 2:2	1.00	**0.05**	0.10	1.00
	1:3 vs 3:1	1.00	0.49	0.74	1.00
	1:3 vs 4:0	1.00	0.89	**< 0.001**	0.96
	2:2 vs 3:1	1.00	1.00	1.00	1.00
	2:2 vs 4:0	1.00	0.98	**< 0.001**	0.87
	3:1 vs 4:0	0.72	1.00	**< 0.001**	0.19
38‰		*B. maritima* vs *A. flavescens*	*B. maritima* vs *H. angiospermum*	*S. perennis* vs *A. flavescens*	*S. perennis* vs *H. angiospermum*
All Combined		$F_{1,68}$ = 5306.96 **$p < 0.001$**	$F_{1,68}$ = 5098.27 **$p < 0.001$**	$F_{1,68}$ =2339.45 **$p < 0.001$**	$F_{1,68}$ = 512.18 **$p < 0.001$**
Pairwise		*p*-value	*p*-value	*p*-value	*p*-value
30 cm	0:0 vs 0:4	**< 0.001**	**< 0.001**	**0.02**	0.96
	0:0 vs 1:3	**< 0.001**	**< 0.001**	**0.00**	**0.00**
	0:0 vs 2:2	**< 0.001**	**< 0.001**	**0.05**	**0.02**
	0:0 vs 3:1	**< 0.001**	**< 0.001**	**0.00**	**< 0.001**
	0:0 vs 4:0	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**
	0:4 vs 1:3	0.94	1.00	1.00	0.55
	0:4 vs 2:2	0.41	0.86	1.00	0.86
	0:4 vs 3:1	**0.00**	0.67	1.00	**0.01**
	0:4 vs 4:0	**< 0.001**	**< 0.001**	**0.02**	**0.01**
	1:3 vs 2:2	1.00	0.75	1.00	1.00
	1:3 vs 3:1	0.35	0.50	1.00	0.99
	1:3 vs 4:0	**< 0.001**	**< 0.001**	0.18	0.99
	2:2 vs 3:1	0.78	1.00	1.00	0.90
	2:2 vs 4:0	**0.00**	**< 0.001**	**0.01**	0.89
	3:1 vs 4:0	0.13	**< 0.001**	0.15	1.00
18 cm	0:0 vs 0:4	**< 0.001**	0.91	**0.01**	1.00
	0:0 vs 1:3	**< 0.001**	**< 0.001**	**0.01**	**0.08**
	0:0 vs 2:2	**< 0.001**	**< 0.001**	0.56	0.97
	0:0 vs 3:1	**< 0.001**	**< 0.001**	0.06	**0.00**
	0:0 vs 4:0	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**
	0:4 vs 1:3	1.00	0.12	1.00	0.73
	0:4 vs 2:2	0.42	**< 0.001**	1.00	1.00
	0:4 vs 3:1	**< 0.001**	**0.00**	1.00	**0.02**
	0:4 vs 4:0	**< 0.001**	**< 0.001**	0.64	**0.00**
	1:3 vs 2:2	0.97	0.53	0.99	0.97
	1:3 vs 3:1	**0.00**	0.96	1.00	0.99
	1:3 vs 4:0	**0.00**	**0.00**	0.73	0.90
	2:2 vs 3:1	0.31	1.00	1.00	0.15
	2:2 vs 4:0	**0.05**	0.82	**0.02**	**0.04**
	3:1 vs 4:0	1.00	0.14	0.32	1.00
9 cm	0:0 vs 0:4	0.74	1.00	1.00	1.00
	0:0 vs 1:3	**0.06**	0.11	0.40	0.12
	0:0 vs 2:2	**0.00**	**0.01**	0.94	1.00
	0:0 vs 3:1	**< 0.001**	**0.00**	0.11	**0.00**
	0:0 vs 4:0	**< 0.001**	**< 0.001**	**< 0.001**	**0.00**

	0:4 vs 1:3	1.00	0.18	1.00	0.10
	0:4 vs 2:2	0.45	**0.01**	1.00	1.00
	0:4 vs 3:1	**< 0.001**	**0.00**	0.88	**0.00**
	0:4 vs 4:0	**< 0.001**	**< 0.001**	**0.01**	**0.00**
	1:3 vs 2:2	1.00	1.00	1.00	0.11
	1:3 vs 3:1	**0.05**	0.94	1.00	1.00
	1:3 vs 4:0	**< 0.001**	0.10	0.57	1.00
	2:2 vs 3:1	0.55	1.00	1.00	**0.00**
	2:2 vs 4:0	**0.00**	0.96	0.09	**0.00**
	3:1 vs 4:0	0.56	1.00	0.91	1.00

S3. Analysis of Variance and Tukey post hoc tests looking at the difference in mean stomatal conductance (mmol $m^{-2}s^{-1}$) between two halophytes (*Batis maritima* and *Sarcocornia perennis*) and two glycophytes (*Alternanthera flavescens* and *Heliotropium angiospermum*) within each salinity treatment (Freshwater-one month; 26‰-one month; 38‰-one month; 38‰-three months).

	Freshwater – 1 Month	26‰ - 1 Month	38‰ - 1 Month	38‰ - 3 Months
All combined	$F_{3,36} = 9.59$ $p < 0.001$	$F_{3,12} = 3.25$ $p = 0.06$	$F_{3,36} = 3.04$ $p = 0.04$	$F_{3,79} = 1.95$ $p = 0.13$
Pairwise	*p*-value	*p*-value	*p*-value	*p*-value
B. maritima - A. flavescens	< 0.001	0.22	0.06	0.11
B. maritima - H. angiospermum	< 0.001	0.16	0.93	0.47
S. perennis - A. flavescens	0.23	0.68	0.04	0.39
S. perennis - H. angiospermum	0.03	0.96	0.88	0.86
B. maritima - S. perennis	0.18	0.04	1.00	0.90
A. flavescens - H. angiospermum	0.80	0.96	0.20	0.88

S4. Analysis of Variance and Tukey post hoc tests looking at the difference in mean stomatal conductance (mmol $m^{-2}s^{-1}$) of two halophytes (*Batis maritima* and *Sarcocornia perennis*) and two glycophytes (*Alternanthera flavescens* and *Heliotropium angiospermum*) across salinity treatments (Freshwater-one month; 26‰-one month; 38‰-one month; 38‰-three months).

		Initial - 26‰ (1 Month)	Initial - 38‰ (1 Month)	Initial - 38‰ (3 Months)	26‰ (1 Month) - 38‰ (1 Month)	26‰ (1 Month) – 38‰ (3 Months)	38‰ (1 Month) -38‰ (3 Months)
Species	All combined	*p*-value	*p*-value	*p*-value	*p*-value	*p*-value	*p*-value
Batis maritima	$F_{3,39} = 3.63$ $p = 0.03$	**0.030**	1.000	1.000	**0.040**	**0.020**	1.000
Sarcocornia perennis	$F_{3,42} = 7.78$ $p < 0.001$	**0.010**	**0.008**	< **0.001**	0.953	1.000	0.911
Alternanthera flavescens	$F_{3,44} = 23.46$ $p < 0.001$	**0.001**	< **0.001**	< **0.001**	0.518	0.379	0.999
Heliotropium angiospermum	$F_{3,38} = 21.83$ $p < 0.001$	**0.001**	< **0.001**	< **0.001**	0.997	0.943	0.946

S5. Results of linear mixed effects models and Tukey post hoc tests for shoot and root biomass (g) of four species found in varying densities and species combinations (*Batis maritima* (H) vs *Alternanthera flavescens* (G), *B. maritima* (H) vs *Heliotropium angiospermum* (G), *Sarcocornia perennis* (H) vs *A. flavescens* (G), *S. perennis* (H) vs *H. angiospermum* (G)). The second and fifth columns indicate halophyte or glycophyte ratio; 1-2 means pots with one halophyte (or glycophyte) compared to pots with two halophytes (or glycophytes). Significant *p*-values are in bold.

		Halophyte Root	Halophyte Shoot		Glycophyte Root	Glycophyte Shoot
B. maritima - A. flavescens	All combined	$F_{1,12}$ = 370.15 ***p* < 0.001**	$F_{1,12}$ = 167.82 ***p* < 0.001**	All combined	$F_{1,12}$ = 133.94 ***p* < 0.001**	$F_{1,12}$ = 112.24 ***p* < 0.001**
	Pairwise	*p*-value	*p*-value	Pairwise	*p*-value	*p*-value
	1-2	**0.01**	0.06	4-3	0.26	0.99
	1-3	**< 0.001**	**< 0.001**	4-2	**0.01**	0.72
	1-4	**< 0.001**	**< 0.001**	4-1	**< 0.001**	**< 0.001**
	2-3	**< 0.001**	**0.003**	3-2	0.75	0.59
	2-4	**< 0.001**	**< 0.001**	3-1	**< 0.001**	**< 0.001**
	3-4	**< 0.001**	**< 0.001**	2-1	**< 0.001**	**< 0.001**
B. maritima – H. angiospermum	All combined	$F_{1,12}$ = 225.12 ***p* < 0.001**	$F_{1,12}$ = 372.87 ***p* < 0.001**	All combined	$F_{1,12}$ = 107.65 ***p* < 0.001**	$F_{1,12}$ = 112.27 ***p* < 0.001**
	Pairwise	*p*-value	*p*-value	Pairwise	*p*-value	*p*-value
	1-2	**< 0.001**	**< 0.001**	4-3	**0.005**	**0.006**
	1-3	**< 0.001**	**< 0.001**	4-2	**0.03**	**0.007**
	1-4	**< 0.001**	**< 0.001**	4-1	**< 0.001**	**< 0.001**
	2-3	0.60	0.60	3-2	1.00	0.99
	2-4	**< 0.001**	**< 0.001**	3-1	0.21	0.16
	3-4	**< 0.001**	**< 0.001**	2-1	0.20	0.36
S. perennis - A. flavescens	All combined	$F_{1,12}$ = 94.14 ***p* < 0.001**	$F_{1,12}$ = 85.78 ***p* < 0.001**	All combined	$F_{1,12}$ = 186.95 ***p* < 0.001**	$F_{1,12}$ = 193.45 ***p* < 0.001**
	Pairwise	*p*-value	*p*-value	Pairwise	*p*-value	*p*-value
	1-2	0.76	0.91	4-3	0.86	0.66
	1-3	**0.005**	0.76	4-2	**< 0.001**	**< 0.001**
	1-4	**< 0.001**	**< 0.001**	4-1	**< 0.001**	**0.01**
	2-3	**< 0.001**	0.35	3-2	**0.003**	**0.001**
	2-4	**< 0.001**	**< 0.001**	3-1	**0.001**	0.16
	3-4	**< 0.001**	**< 0.001**	2-1	1.00	0.29
S. perennis – H. angiospermum	All combined	$F_{1,12}$ = 63.03 ***p* < 0.001**	$F_{1,12}$ = 75.98 ***p* < 0.001**	All combined	$F_{1,12}$ = 116.65 ***p* < 0.001**	$F_{1,12}$ = 256.20 ***p* < 0.001**
	Pairwise	*p*-value	*p*-value	Pairwise	*p*-value	*p*-value
	1-2	1.0	0.79	4-3	0.40	0.76
	1-3	**0.004**	0.10	4-2	0.78	0.99
	1-4	**0.003**	**0.002**	4-1	**< 0.001**	**< 0.001**
	2-3	**0.001**	**0.006**	3-2	0.06	0.56
	2-4	**0.001**	**< 0.001**	3-1	**0.001**	**< 0.001**
	3-4	1.0	0.62	2-1	**< 0.001**	**< 0.001**

CHAPTER III

EFFECTS OF VARYING SALINITY ON EARLY LIFE HISTORY STAGES OF SUBTROPICAL COASTAL SPECIES

Effects of varying salinity on early life history stages of subtropical coastal species

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The authors declare no conflict of interest.

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ABSTRACT

Premise of the study: In south Florida, anthropogenic drying and sea level rise (SLR) have resulted in upland coastal plant communities shrinking while lowland mangrove communities expand, threatening 21 rare plant species in Everglades National Park (ENP). To understand on-the-ground coastal community change and assess where conservation actions are best implemented, one needs to know what plant life-stage is most vulnerable to environmental stress. We hypothesized that seedling establishment was the most vulnerable life-stage to salt stress and, therefore, the largest driver of community change. An additional goal was to determine the salinity tolerances of *Chromolaena frustrata*, a federally endangered plant species.

Methods: We examined the effects of increasing salinity (0, 5, 15, 30, and 45‰) on seed germination and seedling establishment of 5 coastal species and compared our results to a prior study that examined salinity effects on one-year old and adult individuals of the same species.

Key results: We found seedling establishment showed the most disparate responses across salinity treatments and between species and the life-stage best monitored for community change.

Conclusions: Changing microsite conditions regulating seedling establishment is likely the driver of upland plant community shifts in our study area. *Chromolaena frustrata* was sensitive to salinity levels greater than 5‰ at all developmental stages suggesting this species is highly threatened by SLR. Our results show that when species of concern are found in the understory, on-the-ground monitoring of seedling establishment may be the

best approach for determining when conservation action is needed before understories change and species are lost.

Key Words: See germination; seedling establishment; life stage; community change; salinity; sea level rise

INTRODUCTION

Because Florida has the shallowest water table in the continental U.S. and its coastal communities are distributed across a gradient that is 0-2m above mean sea level (Hoffmeister, 1974), its coastal communities are imminently threatened by sea level rise (SLR) (Zhang, 2011). Everglades National Park (ENP), which has a significant coastal extent, harbors 43 critically imperiled species as defined by Gann et al. (2002). Because rare species richness tends to be negatively correlated with salinity in coastal habitats (Saha et al., 2011), 21 of ENP's rare species are threatened by SLR (Saha et al., 2011). With increased ocean warming and glacial and ice sheet melt, the future SLR rate is expected to exceed both the mean global SLR rate during the 20th century (1.7mm yr^{-1}) and SLR since 1993 (3.6mm yr^{-1}) (IPCC, 2014), further threatening coastal species and increasing the need to take proactive conservation measures.

Groundwater and salinity are important drivers of ecological processes in wetland communities (Williams et al., 1998; Graham et al., 1999; Ross et al., 2000; Price et al., 2006; Hancock et al., 2009; Harvey and McCormick, 2009; Saha et al., 2011) and dictate plant community composition (Jassby et al., 1995; Ross et al., 2000; Saha et al., 2011). In the Everglades coastal uplands areas, groundwater table mean depth and salinity vary with elevation and season from buttonwood prairies (38.8‰ average salinity) at lowest elevations to buttonwood forests (29.5‰) to the highest elevation hardwood hammocks (22.8‰) (Saha et al., 2015). Between the groundwater table and soil surface lays an aerated zone of soil called the vadose zone. In coastal south Florida, this zone's soil pore water is less salty than that of the groundwater table beneath, forming a freshwater layer during the wet season that is utilized by upland glycophyte (salt intolerant) species (Sternberg et al., 2007). As sea level rises, the vadose zone will shrink above the rising water table, and more saline groundwater will infiltrate the rhizosphere.

The species composition of coastal forest communities has responded to these changes in salinity and the vadose zone by shifting up the elevation gradient, causing upland communities to shrink as more salt-tolerant communities replace them (Saha et al., 2011; Chapter 1 this dissertation). Thus, salinity change may lead to the extirpation of critically imperiled and endemic coastal species, including the federally endangered *Chromolaena frustrata* (B.L.Rob.)R.M.King & H.Rob. and the Florida endangered *Kosteletzkya depressa* (L.)O.J.Blanchard et al. (Saha et al., 2011).

A species' vulnerabilities to environmental stressors are contingent on life stage (Nicholls et al., n.d.; Parker et al., 1955; Williams et al., 1998; Chartzoulakis and Klapaki, 2000; Schiffers and Tielbörger, 2006); high salinity levels tend to impact juvenile or regenerative life stages more than adult stages (Perry and Williams, 1996). Glycophytes typically respond to the presence of saline soils by reducing leaf size, total plant leaf area, and/or stomatal conductance, which inhibits gas exchange and thus photosynthesis (Pezeshki et al., 1990; Munns, 2002; Saha et al., 2011). If gas exchange and photosynthesis is reduced enough, a net negative carbon balance occurs killing the plant (Pezeshki et al., 1990; Munns, 2002). Plant community composition ultimately depends on which species are able to regenerate in an area (Keeley and Van Mantgem, 2008). In ENP coastal forests, halophyte seedling and sapling densities increased in buttonwood forests from 1998-2009, while glycophyte seedling and sapling densities decreased; buttonwood adults typically had unchanged densities. In contrast, halophyte and glycophyte seedling densities were unchanged in higher elevation hardwood hammocks (Saha et al., 2011). Additionally, Wendelberger et al. (Chapter 1 this dissertation) found hardwood hammocks have shrunk and have been replaced by buttonwood forest in the study area between 1978 and 2011. Because there is only a mean 6cm difference in elevation between buttonwood forests and coastal hardwood hammocks (Saha et al., 2015), and SLR is expected to increase at a rate faster than 3.6mm yr^{-1} (IPCC, 2014), coastal hardwood hammocks in our study area are under threat of disappearing.

In order to better monitor coastal forest community change, we need to examine the effects of increasing salinity on all life stages of key species found in these communities. The purpose of this study was to determine seed germination and seedling establishment responses to increasing soil salinity levels in five coastal species found in varying dominance in southern Florida buttonwood forest and hardwood hammocks. We hypothesized that seedling establishment was a larger driver of change than seed germination under increasing salinity levels. An additional goal was to determine the salinity tolerances of *C. frustrata*, a federally endangered coastal buttonwood forest species.

MATERIALS AND METHODS

Study site— Seeds used in this study were collected from species found in buttonwood forests and hardwood hammocks along the coast of ENP (25°19′0″N, 80°56′0″W), Florida, U.S.A. (Figure 3.1). Southern Florida is humid and subtropical with a distinct warm (mean 25°C) wet season from June to October and cool (mean 15°C) dry season from November to May (SOFIA, 2015). Average annual rainfall is between 100 to 163cm with more than half falling between June and September often coming from hurricanes and tropical storms; April and May usually are the driest months (FCC, 2015; SOFIA, 2015).

The communities and species of interest in this study reside on the Buttonwood Embankment, which is a coastal ridge separating the tip of the Florida peninsula from Florida Bay. The Buttonwood Embankment is an approximately 60x1km^2 stretch of elevated land averaging 45cm in height (Holmes and Marot, 1999; Holmes, Willard, Brewster-Wingard, et al., 1999). Historically, freshwater flowed from the north toward saline Florida Bay forming fresh water bodies to the north of the embankment (Craighead Jr., 1964; Holmes, Willard, Brewster-Wingard, et al., 1999). Today, the waterbodies to the north of the embankment are brackish to marine, which has led to changes in the marsh environment (Holmes, Willard, Brewster-Wingard, et al., 1999). Long-term transitions from freshwater to marine sediment layers, coupled with the pollen cores and aerial photographs, suggest that the study area has experienced a transition in plant communities in the last half century, resulting from a combination of SLR and lack of freshwater head from the drying of the Everglades ecosystem (Holmes and Marot, 1999).

Plant communities of interest— Our study focuses on species found in coastal buttonwood forests and tropical hardwood hammocks along the buttonwood ridge, Flamingo, ENP, Florida. Buttonwood forest is dominated by *Conocarpus erectus* L. (buttonwood) in the canopy. Other woody species in the community include *Sideroxylon celastinum* (Kunth) T.D. Pennington, *Randia aculeata* L., *Cocoloba diversifolia* Jacq., *Erythrina herbacea* L., *Eugenia foetida* Pers., *Ficus aurea* Nutt., and *Piscidia piscipula* (L.) Sarg. (Saha et al., 2015). The buttonwood understory has species such as *Alternanthera flavescens* Kunth, *Chromolaena frustrata* (B.L.Rob.) R.M.King & H.Rob., *Dicliptera sexangularis* (L.) Juss., and *Heliotropium angiospermum* Murray (Saha et al., 2015). Temperature, salinity, tidal fluctuation, substrate, and wave energy influence the size and extent of buttonwood forests (FNAI, 2010), which often grade into salt marsh, coastal berm, rockland hammock, coastal hardwood hammock, and coastal rock barren (FNAI, 2010; USFWS, 2012). They sustain freshwater flooding during the wet season and are dry during the dry season (FNAI, 2010). Buttonwood forests (mean elevation 29±3cm) maintain an average groundwater table of -33±1cm and 26-29.5±0.4‰ groundwater salinity (Saha et al., 2011, 2015).

Coastal tropical hardwood hammocks are biodiverse. Typical tree and shrub species include *Capparis flexuosa* (L.) L., *Coccoloba diversifolia*, *Piscidia piscipula*, *Sideroxylon foetidissimum* Jacq., *Eugenia foetida*, *Swietenia mahagoni* (L.)Jacq., *Ficus aurea* Nutt., *Sabal palmetto* (Walt.) Lodd. ex J.A. & J.H. Schultes, *Eugenia axillaris* (Sw.) Willd., *Zanthoxylum fagara* (L.) Sarg., *Sideroxylon celastrinum* (Kunth)T.D.Penn., and *Colubrina arborescens* (Mill.) Sarg. (Rutchey et al., 2006; USFWS, 2012). Herbaceous species that occur in coastal hardwood hammock include *Acanthocereus tetragonus* (L.) Hummelinck, *Alternanthera flavescens, Batis maritima* L., *Borrichia arborescens* (L.) DC., *Borrichia frutescens* (L.) DC., *Caesalpinia bonduc* (L.) Roxb., *Capsicum annuum* L. var. *glabriusculum* (Dunal) Heiser & Pickersgill, *Galactia striata* (Jacq.) Urb., *Heliotropium angiospermum* Murr., *Passiflora suberosa* L., *Rivina humilis* L., *Sarcocornia perennis* (Mill.) A.J. Scott, *Sesuvium portulacastrum* (L.) L., and *Suaeda linearis* (Elliott) Moq. Ground cover is often limited in closed canopy areas and abundant in areas where canopy disturbance has occurred or where this community intergrades with buttonwood forest (USFWS, 2012). Coastal tropical hardwood hammocks are the least salt tolerant of all the coastal community types and reside at the highest elevation (mean elevation 29±3cm).

Study species— Species studied included the shrubby federally-endangered *Chromolaena frustrata*, and four coastal forest species, as described below.

Chromolaena frustrata (Cape Sable thoroughwort; Asteraceae) is a federally endangered (USFWS, 2012) shrub endemic to coastal buttonwood forest, hardwood hammock, coastal berm, coastal rock barren, and rockland hammock in Miami-Dade and Monroe Counties, Florida (Gann et al., 2002). This species grows to 1.5m, has lavender to blue flowers arranged in heads, and produces wind-dispersed achenes (Nesom, 2006). Little is known about *C. frustrata's* reproductive biology (Bradley and Gann, 2004), but the invasive congener, *C. odorata,* is known to show some tolerance to salinity on seed germination and requires light to germinate (Chauhan and Johnson, 2008).

Conocarpus erectus L. (Buttonwood; Combretaceae) is a tree distributed across coastal tropical America, West Africa (Tomlinson, 1986; Boitani et al., 2008), the Caribbean south to Brazil, and Mexico through Central America to Ecuador (Howard, 1989). The species is the dominant woody species found in buttonwood forests (44%) and the only canopy species in buttonwood prairies (Saha et al., 2015). *Conocarpus erectus* flowers and fruits year-round with very high seed production (Tomlinson, 1986); however, this species is known to have low seed viability (< 12%), < 5% seed germination during the dry season, and 1.6% seedling survival to reproduction (Hernandez and Espino, 1999).

Eugenia foetida Pers. (Spanish stopper; Myrtaceae) is a tree found in Florida, throughout the Caribbean, the Yucatan in Mexico, Belize, and Guatemala (Little Jr. et al., 1974; Howard, 1989). In Florida, the species is typically a small tree in buttonwood forests but is larger and has been found up to 43% of the canopy in hardwood hammocks in the coastal Everglades (Saha et al., 2015). *Eugenia foetida* fruits are fleshy blue/black berries that are bird and lizard (Godinez-Alvarez, 2004) dispersed and have low germination rates— Bohl Stricker and Stiling (2013) obtained 25% germination in freshwater conditions. Some *Eugenia* species are known to have recalcitrant seeds (Andrade et al., 2003; Masetto et al., 2008); it is not known if *E. foetida* is recalcitrant, however, the species is known to take months to germinate.

Piscidia piscipula (L.) Sarg. (Jamaica-dogwood; Fabaceae) is a tree common in southern Florida, the Bahamas, Cuba, Haiti, Jamaica, Mexico, Honduras, Belize, and Guatemala (Rudd, 1969; NaturServe, 2016). In Florida the species averages 12% of the canopy cover in hardwood hammocks and is a less common woody species in buttonwood forests of the coastal Everglades (Saha et al., 2015). *Picidia piscipula* pods are 4-winged with 3-8 seeds per pod (Rudd, 1969). Seeds show high germination rates (80%) when nicked and planted above soil (K. S. Wendelberger unpublished data).

Swietenia mahagoni (L.) Jacq. (West Indian mahogany; Meliaceae) is a widely cultivated tree native to south Florida, the Bahamas, and the Greater Antilles, except Puerto Rico (Howard, 1989; IUCN, 1998). The species is Florida State threatened (FDACS, 1998) and considered endangered (A1cd) by the IUCN (1998). In Florida, *S. mahagoni* is a common canopy species found in coastal hardwood and rockland hammocks (Gann et al., 2002; Saha et al., 2015). *Swietenia mahagoni* seeds easily germinate in freshwater conditions—Howard et al. (1988) found 90% germination after 20 days and 100% germination after 2 months.

Seed collection— All seeds were collected from the Flamingo area of ENP and from more than 10 individuals of each species (ENP permit # EVER-2011-SCI-0019, EVER-2012-SCI-0013, EVER-2013-SCI-0033). Seeds were pooled by species for each experiment. Seeds were cleaned by hand and stored at room temperature until experiments began. Seeds of *C. frustrata* were collected in April 2011, *C. erectus* in January 2012, *E. foetida* in January 2013, *P. piscipula* in October 2012, and *S. mahagoni* in March 2011. All seeds were collected during the dry season except for *P. piscipula,* whose seeds were collected at the end of the wet season.

Seed germination experiments— To test the effects of increasing salinity levels on the five species, twenty seeds per petri dish were sown into 5 replicate petri dishes (150 x 15mm for *C. erectus* and *S. mahagoni* seeds and 90 x 10mm for all other species) per salinity treatment (0, 5, 15, 30, and 45‰), for 100 seeds per treatment and 500 seeds in total. All seeds were soaked in 5% bleach for five minutes then rinsed prior to sowing to help prevent molding. Because of low *C. erectus* germination rates, 100 seeds per petri dish for a total of 2,500 seeds were used. Each petri dish was filled 1/4 with large-grain silica sand and treated with its respective saline solutions. Saline solutions were created by dissolving measured amounts of Instant Ocean Aquarium Sea Salt (Spectrum Brands, Blacksburg, Virginia) with distilled water, then diluting to treatment concentrations. Parafilm was placed around each dish to prevent drying and consequent changes to the salinity solution. The dishes were placed in a growth chamber (GC8-2H, Environmental Growth Chambers, Chagrin Falls, Ohio) on a 12 hour light/12 hour dark cycle at 80% humidity and a constant 26°C. Seeds were monitored for germination, defined by emergence of the radicle from the seed coat, one to three times a week for six weeks or until germination no longer occurred. Germinated seedlings were removed as counted. Study initiation and termination dates are found in Appendix I.

Seedling establishment experiments— To determine the effect of salinity on seedling growth from 0 to 3 months, seedling establishment experiments for each species were conducted in a greenhouse on the Florida International University campus. All seedlings were planted just after cotyledon emergence into standard seedling potting soil mix (Fafard® 4 Mix, Sun Gro Horticulture Canada LTD, Agawam, Massachusetts, USA, a soil-less medium made from Canadian Sphagnum peat moss (45%), processed pine bark, vermiculite, starter nutrients, wetting agent and dolomitic limestone; pH range was 5.5-6.5 after wetting). Seedlings were allowed to acclimate in freshwater for one week prior to treatment. Seedlings were obtained by mixing seedlings from the germination experiments and, in some cases, seedlings germinated separately to compensate for low germination rates. Seeds of *C. frustrata, C. erectus,* and *E. foetida* were planted one per 6cm^2 x 5cm deep subunits in plastic potting 6-packs; because of their larger seedling size, *P. piscipula* and *S. mahagoni* seedlings were planted into individual 6.5cm^2 x 9cm deep plastic pots. Seedlings were grown in 0, 5, 15, 30, and 45‰ salinity for 3 months. For each species and treatment, we planted 4 replicates of 16 individuals per replicate, totaling 64 plants per treatment (320 seedlings total). Because of poor germination, *P. piscipula* had fewer seedlings available for the seedling establishment experiments; seven pots per replicate with three replicates per salinity treatment were used for a total of 21 individuals per treatment (84 seedlings total); no 45‰ treatment was performed. Because *E. foetida* grew slowly in all treatments, this species' seedling establishment experiments continued for 200 days. Each replicate set was placed in one seedling flat that lacked drainage holes, and the flats were filled with 2.5 liters of their respective saline solutions so that the potted seedlings sat in but were not submerged in the solution. Saline solutions were created by dissolving measured amounts of Instant Ocean Aquarium Sea Salt (Spectrum Brands, Blacksburg, Virginia) with tap water. Salinity levels were monitored three days a week using a portable hand-held salinity refractometer (RHS-10ATC, Agriculture Solutions, Strong, Maine) and adjusted with the Instant Ocean solution as needed to maintain appropriate salinity levels. Study initiation and termination dates, average temperature, and average day length are found in Appendix II.

To document seedling morphology at the beginning of the experiment, seedling height (mm) from the soil surface was measured and the number of fully opened photosynthetic leaves excluding cotyledons, if present, was counted. As individuals died or at the end of the experiment, additional measurements were taken: height from the soil to the shoot tip (cm); number of leaves present on the stem; length and width (mm) of the newest matured leaf; and the length of the internode below the newest matured leaf (mm). Total leaf number per plant was determined by counting leaf scars and adding that to the number of leaves present. Plants were removed from pots and soil washed away, then length of the longest root measured. Root and shoot dry biomass were determined by cutting the seedlings at the soil surface and placing the roots and shoots in separate envelopes; these were dried in a 70°C drying oven (OV35545, Thermolyne, United States) for 3-5 days; dry mass was then weighed on a balance (AE240 for small samples and PG2002-S for large samples, Metler Toledo, Columbus, Ohio).

To examine the effect that increasing salinity levels had on seedling stomatal conductance, five seedlings per treatment were placed in one tray per treatment and watered from the bottom with their respective salinity treatments. Stomatal conductance was taken on one leaf per plant using a steady-state porometer (LI-1600M, LI-COR, Inc, Lincoln, Nebraska). Some seedling leaves were too small to completely fill the porometer's chamber; in this case, leaf area inside the chamber was measured (mm^2). Because the LI-1600m does not adjust for boundary layer resistance, the boundary layer resistance and an adjustment for leaf area were made to find the true conductance value (LI-COR, 1989).

Study initiation and termination dates, when stomatal conductance was taken, and seedling age at time of measurements are found in Appendix III.

Statistical analysis— Seed germination— Generalized linear models and Tukey post hoc tests were used to assess the effects of increasing salinity level on mean seed germination fractions (number of germinated seeds/total number of seeds) assuming a binomial response variable and using a logit link function (McCullagh and Nelder, 1989). To test the effects of varying salinity level on time-to-germination, cox proportional hazards survival analyses were performed (Onofri et al., 2010). In cases where there was no germination at 30 and/or 45‰, these treatments were removed from analysis—only treatments with germinated seeds were compared.

Seedling establishment— Cox proportional hazards survival models were used to assess the effects of increasing salinity level on seedling survival. Because *C. erectus* showed 100% seedling survival in all treatments except 45‰ (1 seedling survived) and *P. piscipula* showed 100% seedling survival in all treatments except 30‰ (19% survival), survival analyses were not performed on these two species.

To test the effects of varying salinity on morphological trait development while accounting for within tray correlation we used linear mixed effects models and Tukey post hoc tests. Seedling height, root length, shoot biomass, root biomass, shoot:root biomass, most recently matured leaf position, internode length just below the newest matured leaf, area of most recently matured leaf, number of leaves at the time of harvest, and total number of leaves produced were the dependent variables, salinity was the fixed-effect, and tray was the random effect in the model. To test the effects of increasing salinity on seedling stomatal conductance, one-way ANOVAs and Tukey post hoc tests were performed where salinity was the fixed main effect.

All analyses were executed in R (R Core Team, 2013). The linear mixed effects models were performed using the nlme package (Pinheiro et al., 2013), and Tukey post hoc tests for the linear mixed effects models were completed with the lsmeans package (Lenth, 2014). Cox proportional hazard models and Kaplan-Meier survival plots were executed with the survival package (Therneau and Grambsch, 2000; Therneau, 2014). Tukey post hoc tests for the generalized linear model were completed using the multcomp package (Hothorn et al., 2008)—all other analyses utilized the base package provided in R. Readers can access the data in this paper through the Florida Coastal Everglades LTER data repository (FCE LTER, n.d.).

RESULTS

Seed germination— Seed germination decreases with increasing salinity levels in all five species. Mean seed germination was similar in 0 and 5‰ in all species (Table 3.1 and 3.2; Figure 3.2a-e). Seeds sown in 15‰ sand germinated significantly less than those in 0 and 5‰ and significantly more than those in 30‰ treatments in all species (Table 3.1; Figure 3.2). No seeds germinated in 45‰ sand, while *C. erectus* and *E. foetida* were the only species to show germination at 30‰ (mean 0.2 and 2.6 seeds germinated, respectively; Table 3.1; Figure 3.2).

Time to germination was significantly different across salinity treatments for all five species. Seeds germinated similarly in 0‰ treatments versus 5‰ treatments in all species (Table 3.3; Fig. 3.3a-e) except *S. mahagoni,* where seeds in 0‰ germinated sooner than those in 5‰ treatments (Table 3.3, Fig. 3.3a-e). Seeds sown in 15‰ germinated significantly more slowly than those in 0 and 5‰ treatments and significantly faster than 30‰ treatments in all species (Table 3.3; Fig. 3.3a-e).

Seedling establishment— Seedling survival, morphological development, and stomatal conductance decreased significantly across salinity levels in all five species. Species showed differing sensitivity to increasing salinity levels, depending on the species (Tables 3.4-3.5; Figs. 3.4-3.10). All species showed a significant decrease in stomatal conductance after one week of being subjected to salinity treatments while *C.*

erectus and *E. foetida* appeared to adjust to the increased salinity with time—with some salinity treatments conducting similarly to the control after one month (Table 3.5; Fig. 3.10).

Chromolaena frustrata— Chromolaena frustrata seedling survival dropped significantly with increasing salinity, as compared to the control (0‰), even at low salinity levels (X^2 = 384.9, P less than 0.001; Table 3.4). While *C. frustrata* seedlings growing in 5‰ soil showed better survival than those in 0‰ early on (Fig. 3.4a), there was a significant decline in survival in 5‰ soils (8% survival) up to 45 days compared to 0‰ (88% survival); seedlings in 15, 30, and 45‰ all showed 0% survival to 45 days (Table 3.4; Fig. 3.4a).

Seedling development differed across salinity treatments with a reduction in shoot and root length, leaf area, number of leaves, and root and shoot biomass as salinity increased; in most cases the largest reductions occurred between 0 and 5‰ treatments (App. IV; Figs. 3.5a-j). *Chromolaena frustrata* seedlings showed significantly less overall plant growth and leaf production between 0‰ and 5‰ and no difference in these parameters as salinity increased (App. IV; Figs. 3.5a-d;i-j). *Chromolaena frustrata* allotted significantly more energy to shoot production as opposed to root production in 5‰ treatments as compared to all other treatments; the difference in shoot and root production was insignificant between 15, 30 and 45‰ treatments (App. IV; Fig. 3.5e). Though control seedlings (0‰) showed similar shoot:root biomass to those growing in 45‰ soils, both shoot and root biomass were significantly less in 45‰ as compared to 0‰ when looked at separately (App. IV; Fig. 3.5c-e). Leaf area was significantly smaller between 0, 5, 15, and 30‰ treatments; there was no difference in leaf area between seedlings growing in 30 and 45‰ soils (App. IV; Fig. 3.5h).

Increases in salinity had little effect on *C. frustrata* seedling stomatal conductance. After one week, *C. frustrata* seedlings showed significantly less stomatal conductance between 0 and 45‰ and 15 and 45‰ treatments—all other treatment combinations were not significantly different ($F_{4,20} = 5.36$, $P = 0.004$). After one month there were no significant difference between treatments; however, all the seedlings in 30 and 45‰ treatments had died by one month and could not be evaluated (Table 3.5; Fig. 3.10).

Conocarpus erectus— When looking at survival, *C. erectus* seedlings showed the least sensitivity to increasing salinity of all the species in this study. All *C. erectus* seedlings survived to 105 days at all salinity levels except 45‰, where only one seedling survived (Fig. 3.4b); therefore, survival analyses were not performed.

In most cases, *C. erectus* seedlings did not show a significant decrease in morphological development or plant size until the 15‰ salinity treatments; only root biomass and the total number of leaves produced were significantly less in 5‰ compared to 0‰ (App. IV; Fig. 3.6a-j). *Conocarpus erectus* seedlings showed similar shoot and root production in 0, 5, and 15‰ treatments; at 30‰ seedlings began to produce significantly more shoots than roots, but shoot production declined in 45‰ treatments (App. IV; Fig. 3.6e).

Conocarpus erectus seedling stomatal conductance was negatively impacted at higher salinity levels after one week ($F_{4,20} = 13.99$, *P* less than 0.001; Table 3.5, Fig. 3.10). After one week, *C. erectus* showed significantly higher stomatal conductance in control treatments as compared to 15 (57% less than control), 30 (82% less), and 45‰ (95% less) treatments and significantly higher stomatal conductance in 5‰ treatments compared to 30 and 45‰ treatments; after one month, seedlings in 5, 15, and 35‰ treatments showed similar stomatal conductance to control seedlings; only 45‰ seedlings had significantly less stomatal conductance (88% less) than control; seedlings in 15‰ showed higher stomatal conductance than 45‰ seedlings (Table 3.5, Fig. 3.10).

Eugenia foetida— *Eugenia foetida* seedlings showed significant differences in survival between all treatments (X^2 = 220.2; P less than 0.001; Table 3.4, Fig. 3.4c). Seedlings growing in 0‰ soils had the highest survival up to 200 days (91%), and survival decreased with increasing salinity; no seedlings survived past 104 days at 45‰ (Table 3.4, Fig. 3.4c).

Overall, seedlings showed marked decreases in growth and morphology between 0 and 5‰ treatments and little difference between all remaining treatment combinations (App. IV, Fig. 3.7a-j). *Eugenia foetida* seedlings showed no difference in root length between all five salinity treatments (App. IV, Fig. 3.7b). The shoot:root biomass indicated a slight decrease in shoot production between 5 and 30‰ that was maintained through 45‰ treatments, but no difference between 0, 5, and 15‰ treatments (App. IV; Fig. 3.7e). The internode length was similar for all treatments except those seedlings growing in 30‰ soils which had shorter internodes than those growing in 0‰ soils (App. IV; Fig. 3.7g). The mean number of leaves produced decreased significantly (over 50% decrease) between control and 5‰ then showed no significant difference in leaf production across all other treatments (App. IV; Fig. 3.7j).

Eugenia foetida seedling stomatal conductance decreased significantly with increasing salinity (one week: $F_{4,20} = 33.96$, *P* less than 0.001; one month: $F_{4,20} = 20.05$, *P* less than 0.001). After one week, seedlings in 0‰ showed significantly more stomatal conductance than all other treatments (5‰ showed 42% less conductance, 15‰ 61% less, 30‰ 71% less, and 45‰ 84% less conductance than control). After one month, 5‰ seedling stomatal conductance was no longer significantly different to that of those in 0‰ soils (18% less conductance) while showing significantly more stomatal conductance than 15‰ (52% higher conductance); all other combinations were the similar (Table 3.5; Fig. 3.10).

Piscidia piscipula— *P. piscipula* survival showed the second lowest sensitivity to increasing salinity levels. Seedlings growing in 0, 5, and 15‰ soils showed 100% survival to 100 days. Those seedlings growing in 30‰ soils showed an 80% chance of survival to 100 days (Table 3.4; Fig. 3.4d); therefore, no analysis was performed for survival on this species.

Overall *P. piscipula* seedling morphology and growth followed a pattern of significant decreases in size and number between 0, 5, and 15‰ treatments (App. IV; Fig. 3.8a-j). Seedlings showed significantly shorter roots between 0 and 5‰, then no differences thereafter (App. IV; Fig. 3.8b). Seedlings growing in 5, 15, and 30‰ treatments allotted the same amount of energy to shoots as roots; those growing in 5‰ showed slightly more shoot biomass than root biomass than seedling in 0 or 15‰ treatments (App. IV; Fig. 3.8e). Leaf development followed the same pattern as shoot:root biomass, decreasing significantly between 5 and 15‰ treatments then again between 15 and 30‰ (App. IV; Fig. 3.8f and i-j).

Piscidia piscipula seedlings showed a marked decline in stomatal conductance with increasing salinity and time ($F_{4,20}$ = 20.05, *P* less than 0.001 after one week; $F_{4,16}$ = 10.35, *P* = 0.001 after one month; Table 3.5; Fig. 3.10). After one week of the study, *P. piscipula* seedlings in 0‰ had higher stomatal conductance than all other treatments (5‰ showed 48% less conductance than control, 15‰ 54% less, 30‰ 72% less, and 45‰ 86% less); 5 and 15‰ treatments showed significantly greater stomatal conductance than those in 45‰ treatments, while all other combinations were not different (Table 3.5; Fig. 3.10). After one month, seedlings in control treatments continued to show significantly more conductance than all treatments (5‰ 57%, 15‰ 75%, 30‰ 84%, and 45‰ 91% less conductance than control); no other treatment combination was significantly different (Table 3.5; Fig. 3.10).

*Swietenia mahagoni— Swietenia mahagoni s*eedling survival showed a tolerance for increasing salinity up to 15‰, after which a marked decline was noted (X^2 = 497.8.5, *P* less than 0.001; Table 3.4; Fig. 3.4e). Seedlings growing in 0 and 5‰ soils had 98% survival, those in 15‰ had 73% survival to 94 days, all seedlings in 30‰ died by 70 days, and those in 45‰ died by 35 days (Table 3.4; Fig. 3.4e).

Most changes in morphology and growth for this species occurred starting at the 15‰ treatment level, then again at 30‰, where significant decreases in size and number where seen (App. IV; Fig. 3.9a-j). There was a small but significant increase in energy for shoot biomass production compared to root biomass between 0 and 30‰ treatments (App. IV; Fig. 3.9e). Internode length and leaf area all decreased in size and number between 0‰ and 5‰ treatments, then again between 15 and 30‰, while the other treatments remained the same (App. IV; Fig. 3.9f and h). Mean number of leaves at time of harvest and total leaves produced had little change between 0, 5, and 15‰, then large decreases 15 and 30‰ (Table 3.5; Fig. 3.9i and j). Stomatal conductance was not measured on this species.

DISCUSSION

We found seed germination responded similarly to increased salinity in all five coastal, upland species—decreasing with increased salinity—while seedling establishment showed disparate responses across salinity treatments and between species. Changing microsite salinity conditions regulating seedling establishment is a more likely driver of upland plant community shifts in our study area. In addition to our work, Saha et al. (2012), Wendelberger (Florida International University, unpublished data), and Saha et al. (2015) examined the same species, respectively, looking at salinity effects (0, 5, 15, and 30‰ soil salinity) on one-year-old plants, one-year-old *Chromolaena frustrata*, and isotopic signatures (δ^{18}O and δ^{2}H) of in situ adults assessing where in the soil column and salinity of the water they uptake at the study site (*S. mahagoni* adults were not examined). Three of the five study species (*C. frustrata*, *E. foetida*, and *S. mahagoni*) showed lower percent seedling survival at the higher salinity levels than one-year-old plants of the same species grown in equivalent soil salinities (Table 3.7; Saha et al., 2012, Wendelberger unpublished data). *Eugenia foetida* is more dominant and found as larger trees in upland hardwood hammocks than buttonwood forests, where the species tends to be a smaller mid-story tree or shrub (Saha et al., 2012); this reduction in plant size was seen starting at the seedling life history stage. We found decreases in stomatal conductance associated with reduced growth and morphological responses in *E. foetida* seedlings in 5‰ soils; seedlings showed similar responses in nearly all measured parameters with increasing saline treatments. These results may explain the decrease in *E. foetida* dominance and plant size in the lower elevation, more saline buttonwood forest as compared to upland hardwood hammocks. *Swietenia mahagoni,* showed a distinct stepwise reduction with dramatic decreases in growth and development between 5 and 15‰ then again between 15 and 30‰ soils, indicating a higher sensitivity to increased salinity levels than *E. foetida* and a possible reason as to why this species is rarely found in buttonwood forests while being common in hardwood hammocks (Saha et al., 2012).

Piscidia piscipula was the only species to show better seedling survival at high salinity levels as compared to saplings (Saha et al., 2012); however, a cold snap during the sapling experiments resulted in *P. piscipula* dropping its leaves. Those saplings growing in higher salinity soils did not recover from the cold as well as those growing in lower salinity soils (Saha et al., 2012, Wendelberger personal observations); likely, high salinity levels and the cold temperatures that resulted in a reduction in leaf tissue and, therefore, a net negative carbon balance, acted as covariates resulting in sapling survival that may have been lower than what would have been had the cold snap not occurred (Saha et al., 2012). Interestingly, though *P. piscipula* seedlings showed dramatic reductions in most developmental parameters between controls and 5‰, then again between 5 and 15‰ treatments, and similar reductions in stomatal conductance across salinity treatments starting at 5‰, this species showed the second highest survival rates in all salinity treatments compared to the other five species. *Piscidia piscipula* has been seen as a first colonizer in collapsed hardwood hammocks following hurricane disturbance (Wendelberger personal observations); the mechanism for how this species is capable of waiting out periods of increased salinity levels (e.g. storm surges) better than other hardwood hammock species is not known and in need of further examination. *Conocarpus erectus* showed 100% survival in all treatments for both seedlings and saplings (Saha et al., 2012). That *C. erectus* did so well at both life stages in high salinity treatments is not surprising—the species is the dominant tree found in buttonwood forest canopies (Saha et al., 2012), where the average soil salinity is 35.5‰ (Saha et al., 2015), and seedling stomatal conductance adjusted to higher salinity levels over time, further suggesting a strong tolerance for varying salinity regimes. Adults of all species except *C. frustrata* accessed salty belowground and deep soil water throughout the year during the wet and/or dry season, showing greater tolerance for salinity at this life stage than at the seedling establishment stage (Saha et al., 2015). As groundwater rises with sea level, the vadose zone supplying freshwater for buttonwood and hardwood hammock species is shrinking; upland communities are transitioning into lower elevation, more salt tolerant communities. Our results and those of others (Williams, Williams, et al., 1999; Ross et al., 2000; Saha et al., 2011) show that the transition will first be seen in the understory as a change in the species that establish seedlings in the area.

Additionally, our results corroborate those of Saha et al. (2011, 2015) regarding the conservation of the federally endangered *C. frustrata*. This species is endemic to the Florida Keys and the coastal portion of ENP on the mainland (Gann et al., 2002; Bradley and Gann, 2004; USFWS, 2012). *Chromolaena frustrata* has been extirpated from half the Florida Keys islands where it once occurred (Bradley and Gann, 2004; USFWS, 2012). The majority of this species' population is found in the understory of the lower elevation, highly saline, buttonwood forests of the Buttonwood Embankment (Gann et al., 2002; Service, 2012; Saha et al., 2015). *Chromolaena frustrata* seedlings showed poorer seedling establishment than both *C. erectus* and *E. foetida.* Because *E. foetida* is more dominant in hardwood hammocks where freshwater is more abundant (Saha et al., 2015), it would be expected to be less tolerant to salinity than lower elevation *C. frustrata*. There was a marked decline in *C. frustrata* stomatal conductance across all treatments, including the control, between the pre-treatment and one week measurements. Interestingly, control seedlings did not show a reduction in development reflective of what would be expected with decreases in conductance, while all other treatments including 5‰ showed marked declines in growth and development. Flooding is known to result in a decline in photosynthetic rates in flood sensitive species (Pezeshki et al., 1990); perhaps constant inundation during the seedling establishment experiments acted as a covariate with salinity reducing growth and survival while freshwater control seedlings were able to survive and grow without the combined stress of salt. As the groundwater levels rise with rising sea levels, inundation depth, duration, and salinity level will also increase, suggesting that even in times when salinity levels are low enough for germination, *C. frustrata* seedlings may not be able to establish with the added stress of increased inundation.

Intolerance to increases in salinity was seen in *C. frustrata* adults, as well. Saha et al. (2015) found wild *C. frustrata* abundance is greater in locations with the widest freshwater recharge zone and highest freshwater supply. During the dry season, *C. frustrata* adults were the only species tested by Saha et al. (2015) that tended to access shallow soil water that resembled the isotopic signatures of rainwater. The species accesses ground water and deep soil water during the wet season when salinity levels are lowest in these layers (Saha et al., 2015), suggesting an aversion to high salinity at all life stages and further emphasizing the importance of ephemeral freshwater microsites for *C. frustrata* establishment and survival. As the sea rises and salinity levels increase along the southern coast of Florida, it will become more difficult for *C. frustrata* to establish new and maintain old populations where it currently exists. Land to the north of the Buttonwood Embankment is lower in elevation, leaving no close place for this species to migrate as these northern lands become inundated before habitats on the Buttonwood Embankment. Conservation actions need to be evaluated and implemented for *C. frustrata*. Fairchild Tropical Botanic Garden has stored 4,505 seeds from 42 maternal lines of this species in the National Center for Genetic Resources Preservation (NCGRP) in Ft. Collins, CO (Goodman et al., 2007). Studies performed at the NCGRP suggest that *C. frustrata* seeds are intermediate between orthodox and recalcitrant (J. Maschinski, Fairchild Tropical Botanic Garden, personal communication, Kennedy et al., 2012). Studies need to determine if seeds of this species can survive in long-term cryogenic storage and whether seed storage is enough, or are other conservation actions, such as ex-situ storage or assisted migration, required for the protection of this species.

Upland forest communities changing from press events such as SLR tend to change from the inside out—microsites supporting seedling establishment shift, leaving a non-regenerating relic community in the overstory with an understory of seedlings and saplings from the new community (Williams, Williams, et al., 1999; Saha et al., 2011). Pulse disturbances, e.g. hurricanes and storm surges, tend to be the final event eliminating the relic adult community (Baldwin and Mendelssohn, 1998; Ross et al., 2009), allowing saplings from the new community to grow into the overstory. This creates what appears from above to be a rapid transition of a large land area that, in fact, occurred more slowly over time (Williams, Williams, et al., 1999). When monitoring changes over large landscapes, biologists tend to look for shifts in the edges of plant communities to move in one direction or another along the environmental gradient (Ross et al., 2000; Pauli et al., 2012; Smith et al., 2013). Monitoring edge shifts in plant communities has its value. Being able to discern changes in the landscape community matrix helps us understand how large scale environmental stressors are affecting the overall health of the landscape. Ross et al. (2000) found shifts northward in the white zone (a zone of vegetation appearing white in aerial photographs due to dead plant material, salt accumulation, and soil surface wetness) of southeastern ENP associated with areas most effected by local drainage and cut off from its former freshwater supply. Documenting this information is important and helps inform us on a landscape level of changes often associated with anthropogenic disturbance; however, our results and others (Williams, Williams, et al., 1999; Ross et al., 2000; Armentano et al., 2006; Spalding and Hester, 2007; Saha et al., 2011) show that when monitoring for conservation purposes and specific species of concern, assessing movement of forest edge may not be an effective strategy. If one waits to see large scale changes in the forest overstory, it may be too late for conservation action in the understory—the community and plants of concern may have disappeared or significantly diminished in population size long before what appears to be one forest type transitions into another. Instead, when the species of concern are found in the understory, on-the-ground monitoring of seedling establishment may be the best approach for determining when conservation action is needed before the understory community changes and species are lost.

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TABLES

	Chromolaena frustrata		*Conocarpus erectus*		*Eugenia foetida*		*Piscidia piscipula*		*Swietenia mahagoni*	
Salinity (‰)	Mean	Std. Error	Mean	Std. Error	Mean	Std. Error	Mean	Std. Error	Mean	Std. Error
0	15.2	0.81	24.2	0.98	13	0.77	17.8	0.92	17.6	0.62
5	13.6	1.15	19.8	1.38	13.6	1.08	17	1.31	17.2	0.87
15	8.4	1.15	3.2	1.38	8.6	1.08	9.8	1.31	2.8	0.87
30	0	-	0.2	1.38	2.6	1.08	0	-	0	-
45	0	-	-	-	0	-	0	-	0	-

Table 3.1. Mean seed germination across salinity treatments (0, 5, 15, 30, and 45‰) of five plant species (*Chromolaena frustrata, Conocarpus erectus*, *Eugenia foetida*, *Piscidia piscipula*, and *Swietenia mahagoni*) found along the coast of Everglades National Park, Florida, USA. Note: No seeds germinated in 45‰ treatments.

	Chromolaena frustrata	*Conocarpus erectus*	*Eugenia foetida*	*Piscidia piscipula*	*Swietenia mahagoni*
All combined	$Z = 4.923$; $df = 14$; $P < 0.001$	$Z = -10.934$; $df = 19$; $P < 0.001$	$Z = 2.953$; $df = 19$; $P = 0.003$	$Z = 6.542$; $df = 14$; $P < 0.001$	$Z = 6.475$; $df = 14$; $P < 0.001$
Salinity (‰)	*P*-value	*P*-value	*P*-value	*P*-value	*P*-value
0 vs 5	0.42	0.16	0.97	0.68	0.98
0 vs 15	< 0.001	< 0.001	0.01	< 0.001	< 0.001
0 vs 30	--	< 0.001	< 0.001	--	--
5 vs 15	< 0.001	< 0.001	0.002	< 0.001	< 0.001
5 vs 30	--	< 0.001	< 0.001	--	--
15 vs 30	--	0.03	< 0.001	--	--

Table 3.2. Generalized linear models and Tukey post hoc tests assessing seed germination across salinity treatments (0, 5, 15, 30, and 45‰) of five plant species (*Chromolaena frustrata, Conocarpus erectus, Eugenia foetida, Piscidia piscipula*, and *Swietenia mahagoni*) found along the coast of Everglades National Park, Florida, USA. Note: No seeds germination at 30‰ in *C. frustrata, P. piscipula,* or *S. mahagoni.*

	Chromolaena frustrata		*Conocarpus erectus*		*Eugenia foetida*		*Piscidia piscipula*		*Swietenia mahagoni*	
Salinity (‰)	X^2	*P*-value	X^2	*P*-value	X^2	*P*-value	X^2	*P*-value	X^2	*P*-value
All combined	57.33	< 0.001	210.4	< 0.001	93.45	< 0.001	33.67	< 0.001	169.4	< 0.001
0 vs 5	3.85	0.05	3.98	0.05	0.01	0.94	1.39	0.24	3.62	< 0.001
0 vs 15	58.92	< 0.001	96.67	< 0.001	19.62	< 0.001	33.28	< 0.001	47.2	< 0.001
0 vs 30	--	--	135.2	< 0.001	69.01	< 0.001	--	--	--	--
5 vs 15	34.45	< 0.001	69.31	< 0.001	22.51	< 0.001	18.48	< 0.001	18.48	< 0.001
5 vs 30	--	--	107.1	< 0.001	75.61	< 0.001	--	--	--	--
15 vs 30	--	--	13.48	< 0.001	23.05	< 0.001	--	--	--	--

Table 3.3. Log-rank Test and pairwise comparisons looking at time-to-germination across salinity treatments (0, 5, 15, 30, and 45‰) of five plant species (*Chromolaena frustrata, Conocarpus erectus, Eugenia foetida, Piscidia piscipula,* and *Swietenia mahagoni*) found along the coast of Everglades National Park, Florida, USA.

	Chromolaena frustrata		*Eugenia foetida*		*Swietenia mahagoni*	
Salinity (‰)	X^2	*P*- value	X^2	*P*- value	X^2	*P*- value
All combined	384.9	< 0.001	220.2	< 0.001	497.8	< 0.001
0 vs 5	79.57	< 0.001	34.36	< 0.001	0	0.99
0 vs 15	103.4	< 0.001	62.46	< 0.001	19.3	< 0.001
0 vs 30	105.8	< 0.001	84.38	< 0.001	162.1	< 0.001
0 vs 45	111.4	< 0.001	97.85	< 0.001	172.1	< 0.001
5 vs 15	33.16	< 0.001	11.25	< 0.001	19.35	< 0.001
5 vs 30	87.44	< 0.001	38.15	< 0.001	163	< 0.001
5 vs 45	137.5	< 0.001	83.18	< 0.001	172.1	< 0.001
15 vs 30	30.27	< 0.001	17	< 0.001	116.2	< 0.001
15 vs 45	92.31	< 0.001	65.65	< 0.001	153.1	< 0.001

Table 3.4. Log-rank Test and pairwise comparisons assessing seedling survival across salinity treatments (0, 5, 15, 30, and 45‰) of five plant species (*Chromolaena frustrata, Conocarpus erectus, Eugenia foetida, Piscidia piscipula,* and *Swietenia mahagoni*) found along the coast of Everglades National Park, Florida, USA. Note: Because there was 100% survival in all but one treatment on *C. erectus* and *P. piscipula,* no analysis was performed.

	Salinity (ppt)	*Chromolaena frustrata*	*Conocarpus erectus*	*Eugenia foetida*	*Piscidia piscipula*
Pre-treatment	All combined	$F_{4,19} = 2.28$; $p = 0.10$	$F_{4,20} = 1.49$; $p = 0.24$	$F_{4,20} = 0.26$; $p = 0.90$	$F_{4,20} = 1.86$; $p = 0.16$
1 week after treatment	All combined	$F_{4,20} = 5.26$; $p = 0.004$	$F_{4,20} = 13.99$; $p < 0.001$	$F_{4,20} = 33.96$; $p < 0.001$	$F_{4,20} = 20.05$; $p < 0.001$
	Pairwise	*p*- value	*p*- value	*p*- value	*p*- value
	0 vs 5	0.28	0.06	< 0.001	0.001
	0 vs 15	1.00	0.003	< 0.001	< 0.001
	0 vs 30	0.12	< 0.001	< 0.001	< 0.001
	0 vs 45	0.01	< 0.001	< 0.001	< 0.001
	5 vs 15	0.25	0.66	0.16	0.97
	5 vs 30	0.99	0.05	0.02	0.19
	5 vs 45	0.54	0.01	< 0.001	0.02
	15 vs 30	0.10	0.49	0.79	0.46
	15 vs 45	0.01	0.16	0.08	0.05
	30 vs 45	0.82	0.94	0.49	0.72
1 month after treatment	All combined	$F_{2,11} = 3.16$; $p = 0.08$	$F_{4,20} = 7.58$; $p = 0.001$	$F_{4,20} = 13.53$; $p < 0.001$	$F_{4,16} = 10.35$; $p = 0.001$
	Pairwise	*p*- value	*p*- value	*p*- value	*p*- value
	0 vs 5	--	0.54	0.64	0.01
	0 vs 15	--	0.43	0.002	< 0.001
	0 vs 30	--	0.24	< 0.001	< 0.001
	0 vs 45	--	0.03	< 0.001	0.002
	5 vs 15	--	0.03	0.03	0.77
	5 vs 30	--	0.98	0.003	0.52
	5 vs 45	--	0.46	0.004	0.50
	15 vs 30	--	0.01	0.77	0.99
	15 vs 45	--	< 0.001	0.85	0.94
	30 vs 45	--	0.80	1.00	1.00

Table 3.5. One-way analysis of variances and Tukey post hoc tests comparing seedling stomatal conductance across salinity treatments (0, 5, 15, 30, and 45‰) of four plant species (*Chromolaena frustrata, Conocarpus erectus, Eugenia foetida,* and *Piscidia piscipula*) found along the coast of Everglades National Park, Florida, USA. Note: Because there was no significant difference in stomatal conductance across treatments of *C. frustrata* seedlings after one month, no pairwise comparisons were performed.

Life Stage	Species	0‰	5‰	15‰	30‰	45‰
Seed germination	*C. frustrata*	76	68	38	0	0
Seedling establishment	*C. frustrata*	88	8	0	0	0
1 year old plants	*C. frustrata*	98	100	92	80	62
Seed germination	*C. erectus*	24	20	3	.2	0
Seedling establishment	*C. erectus*	100	100	100	100	1.5
1 year old saplings	*C. erectus*	100	100	100	100	--
Seed germination	*E. foetida*	65	68	43	13	0
Seedling establishment	*E. foetida*	78	32	11	0	0
1 year old saplings	*E. foetida*	100	100	97	92	--
Seed germination	*P. piscipula*	89	85	49	0	0
Seedling establishment	*P. piscipula*	100	100	100	19	--
1 year old saplings	*P. piscipula*	100	93	79	70	--
Seed germination	*S. mahagoni*	88	86	17	0	0
Seedling establishment	*S. mahagoni*	98	98	73	0	0
1 year old saplings	*S. mahagoni*	100	96	93	80	--

Table 3.6. Comparing probability of seeds germinating and percent survival of seedlings and one-year-old plants across treatments (0, 5, 15, 30, and 45‰) of five plant species (*Chromolaena frustrata, Conocarpus erectus, Eugenia foetida, Piscidia piscipula,* and *Swietenia mahagoni*) found along the coast of Everglades National Park, Florida, USA. Notes: Data from one-year-old plant survival comes from Saha et al. 2012 except *C. frustrata* (Wendelberger, Florida International Univerisity, unpublished data). Dashed lines indicate no studies were performed at that salinity level.

FIGURE LEGENDS

Fig. 3.1. Map of Florida, USA with the Everglades National Park boundary denoted in black and the study area, Flamingo, ENP, shown by satellite imagery.

Fig. 3.2. Mean seed germination across salinity treatments (0, 5, 15, 30, and 45‰) of five plant species (Chromolaena frustrata, Conocarpus erectus, Eugenia foetida, Piscidia piscipula, and Swietenia mahagoni) found along the coast of Everglades National Park, Florida, USA. Notes: Lettering represents significant (different letter) and non-significant (same letter) differences between salinity levels based on results from generalized linear models. Error bars represent the standard error. No seeds germinated in 45‰ treatments; only C. erectus and E. foetida showed germination in 30‰ treatments.

Fig. 3.3. Kaplan-meier survival plots assessing the probability of a population of seeds germinating over time across salinity treatments (0, 5, 15, 30, and 45‰) of five plant species ((A) Chromolaena frustrata, (B) Conocarpus erectus, (C) Eugenia foetida, (D) Piscidia piscipula, and (E) Swietenia mahagoni) found along the coast of Everglades National Park, Florida, USA.

Fig. 3.4. Kaplan-meier survival plots assessing the probability a population of seedlings surviving over time across salinity treatments (0, 5, 15, 30, and 45‰) of five plant species ((A) Chromolaena frustrata, (B) Conocarpus erectus, (C) Eugenia foetida, (D) Piscidia piscipula, and (E) Swietenia mahagoni) found along the coast of Everglades National Park, Florida, USA.

Fig. 3.5. Mean growth and morphological responses across salinity treatments (0, 5, 15, 30, and 45‰) of Chromolaena frustrata seedlings. Notes: Lettering symbolizes significant (different letter) and non-significant (same letter) differences between salinity levels based on results from linear mixed-effects models. Error bars represent the standard error.

Fig. 3.6. Mean growth and morphological responses across salinity treatments (0, 5, 15, 30, and 45‰) of Conocarpus erectus seedlings. Notes: Lettering symbolizes significant (different letter) and non-significant (same letter) differences between salinity levels based on results from linear mixed-effects models. Error bars represent the standard error.

Fig. 3.7. Mean growth and morphological responses across salinity treatments (0, 5, 15, 30, and 45‰) of Eugenia foetida seedlings. Notes: Lettering symbolizes significant (different letter) and non-significant (same letter) differences between salinity levels based on results from linear mixed-effects models. Error bars represent the standard error.

Fig. 3.8. Mean growth and morphological responses across salinity treatments (0, 5, 15, 30, and 45‰) of Piscidia piscipula seedlings. Notes: Lettering symbolizes significant (different letter) and non-significant (same letter) differences between salinity levels based on results from linear mixed-effects models. Error bars represent the standard error.

Fig. 3.9. Mean growth and morphological responses across salinity treatments (0, 5, 15, 30, and 45‰) of Swietenia mahagoni seedlings. Notes: Lettering symbolizes significant (different letter) and non-significant (same letter) differences between salinity levels based on results from linear mixed-effects models. Error bars represent the standard error.

Fig. 3.10. Mean stomatal conductance responses across salinity treatments (0, 5, 15, 30, and 45‰) of five plant species (Chromolaena frustrata, Conocarpus erectus, Eugenia foetida, Piscidia piscipula, and Swietenia mahagoni) found along the coast of Everglades National Park, Florida, USA. Notes: Lettering symbolizes significant (different letter) and non-significant (same letter) differences between salinity levels at each monitoring event (initial, 1 week, 1 month) based on results from linear mixed-effects models. Error bars represent the standard error. No C. frustrata seedlings planted in 30 or 45‰ soils survived to one month.

FIGURES

Figure 3.1. Map of Florida, USA with the Everglades National Park boundary denoted in black and the study area, Flamingo, ENP, shown by satellite imagery.

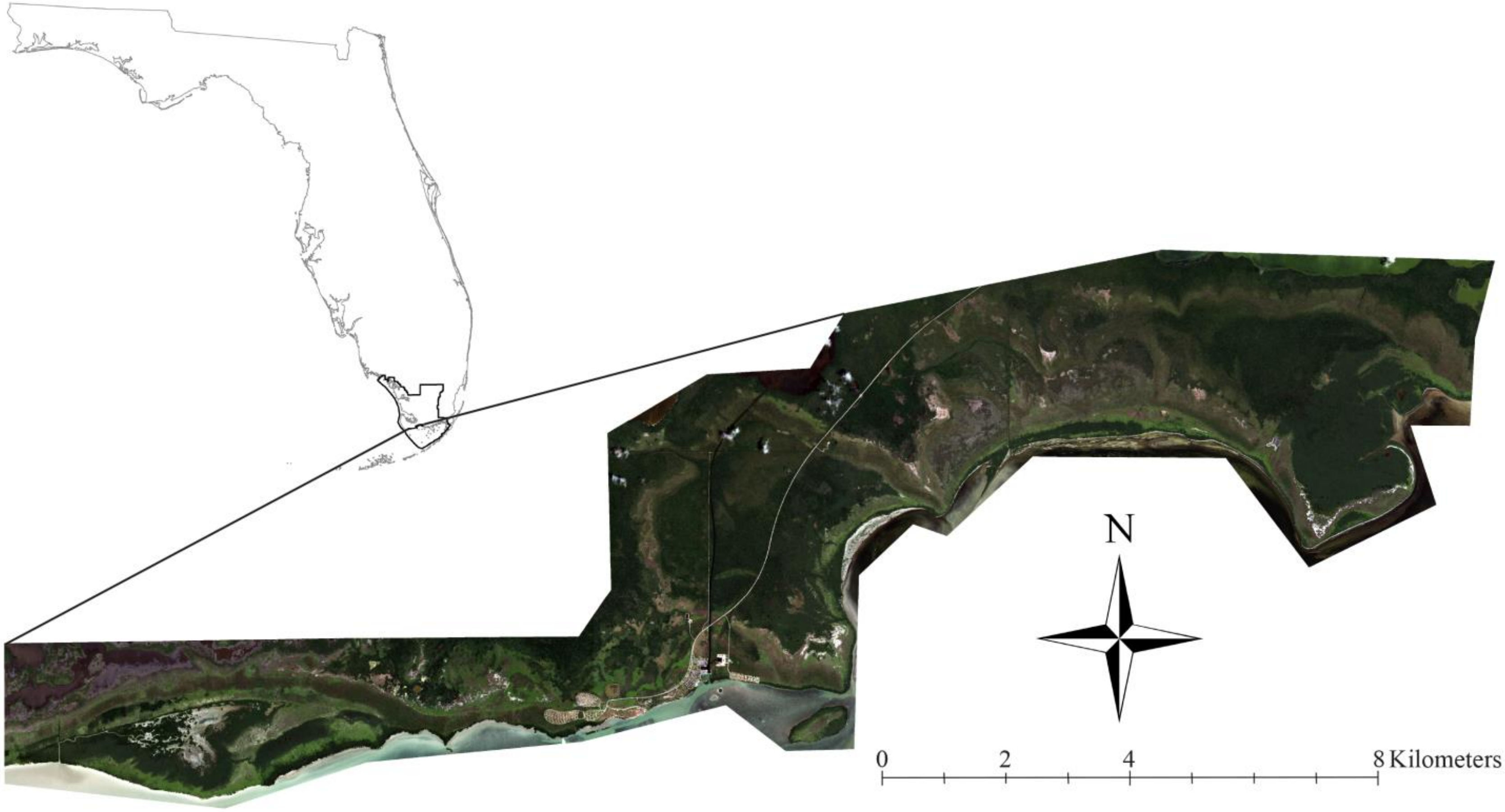


Figure 3.2. Mean seed germination across salinity treatments (0, 5, 15, 30, and 45‰) of five plant species (Chromolaena frustrata, Conocarpus erectus, Eugenia foetida, Piscidia piscipula, and Swietenia mahagoni) found along the coast of Everglades National Park, Florida, USA.

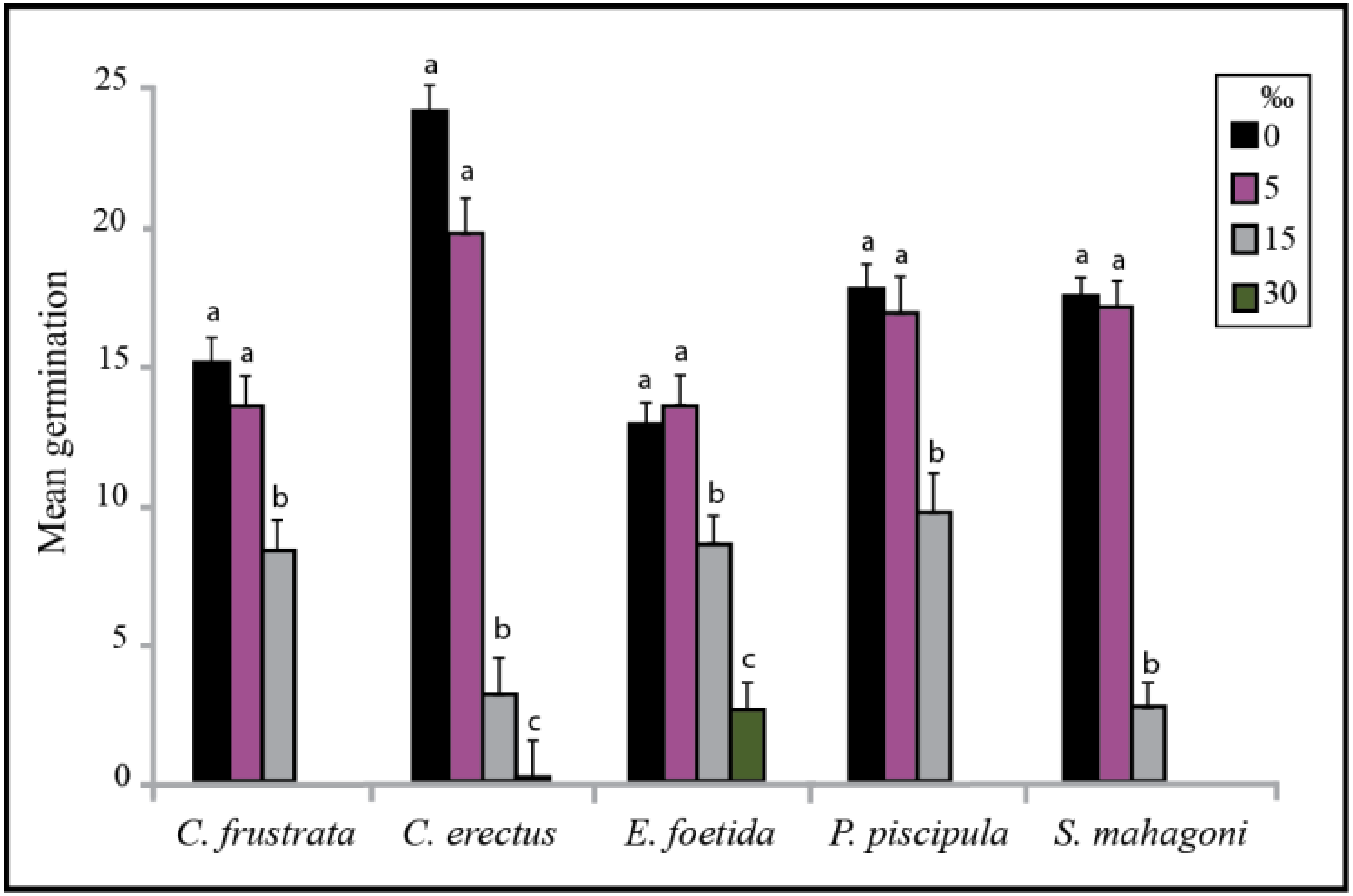


Figure 3.3. Kaplan-meier survival plots assessing the probability of a population of seeds germinating over time across salinity treatments (0, 5, 15, 30, and 45‰) of five plant species ((A) Chromolaena frustrata, (B) Conocarpus erectus, (C) Eugenia foetida, (D) Piscidia piscipula, and (E) Swietenia mahagoni) found along the coast of Everglades National Park, Florida, USA.

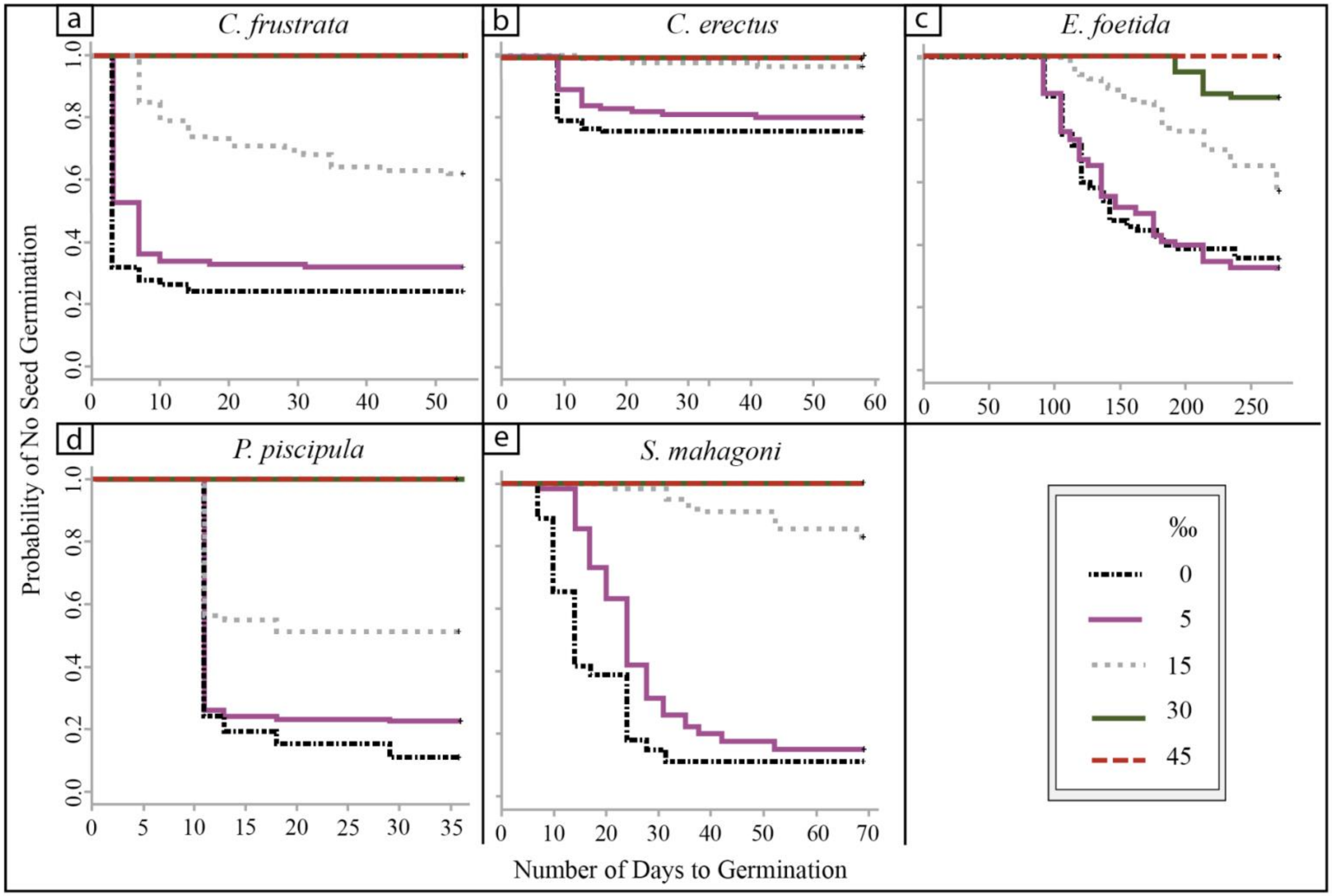


Figure 3.4. Kaplan-meier survival plots assessing the probability a population of seedlings surviving over time across salinity treatments (0, 5, 15, 30, and 45‰) of five plant species ((A) Chromolaena frustrata, (B) Conocarpus erectus, (C) Eugenia foetida, (D) Piscidia piscipula, and (E) Swietenia mahagoni) found along the coast of Everglades National Park, Florida, USA.

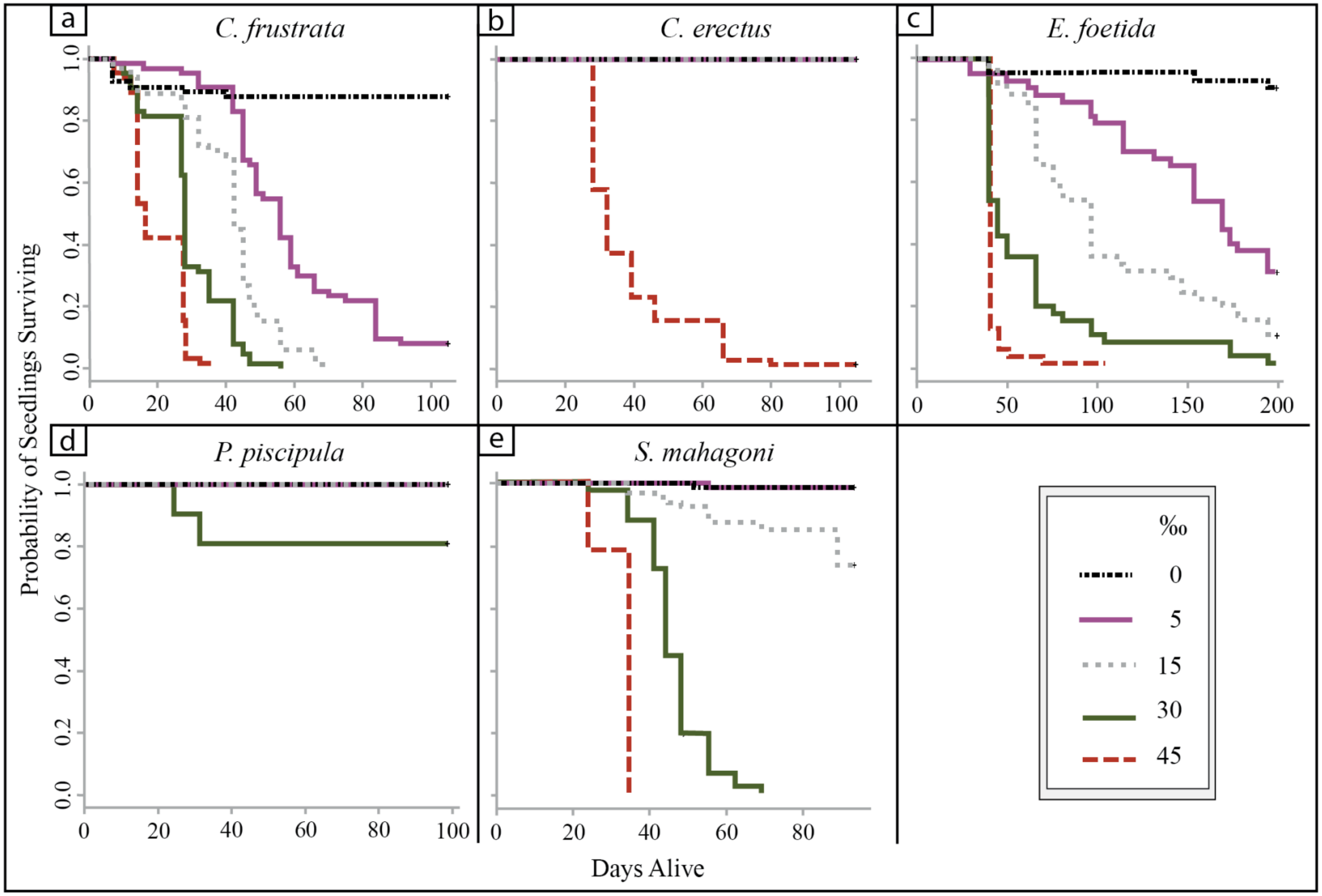


Figure 3.5. Mean growth and morphological responses across salinity treatments (0, 5, 15, 30, and 45‰) of Chromolaena frustrata seedlings. Notes: Lettering symbolizes significant (different letter) and non-significant (same letter) differences between salinity levels based on results from linear mixed-effects models. Error bars represent the standard error.

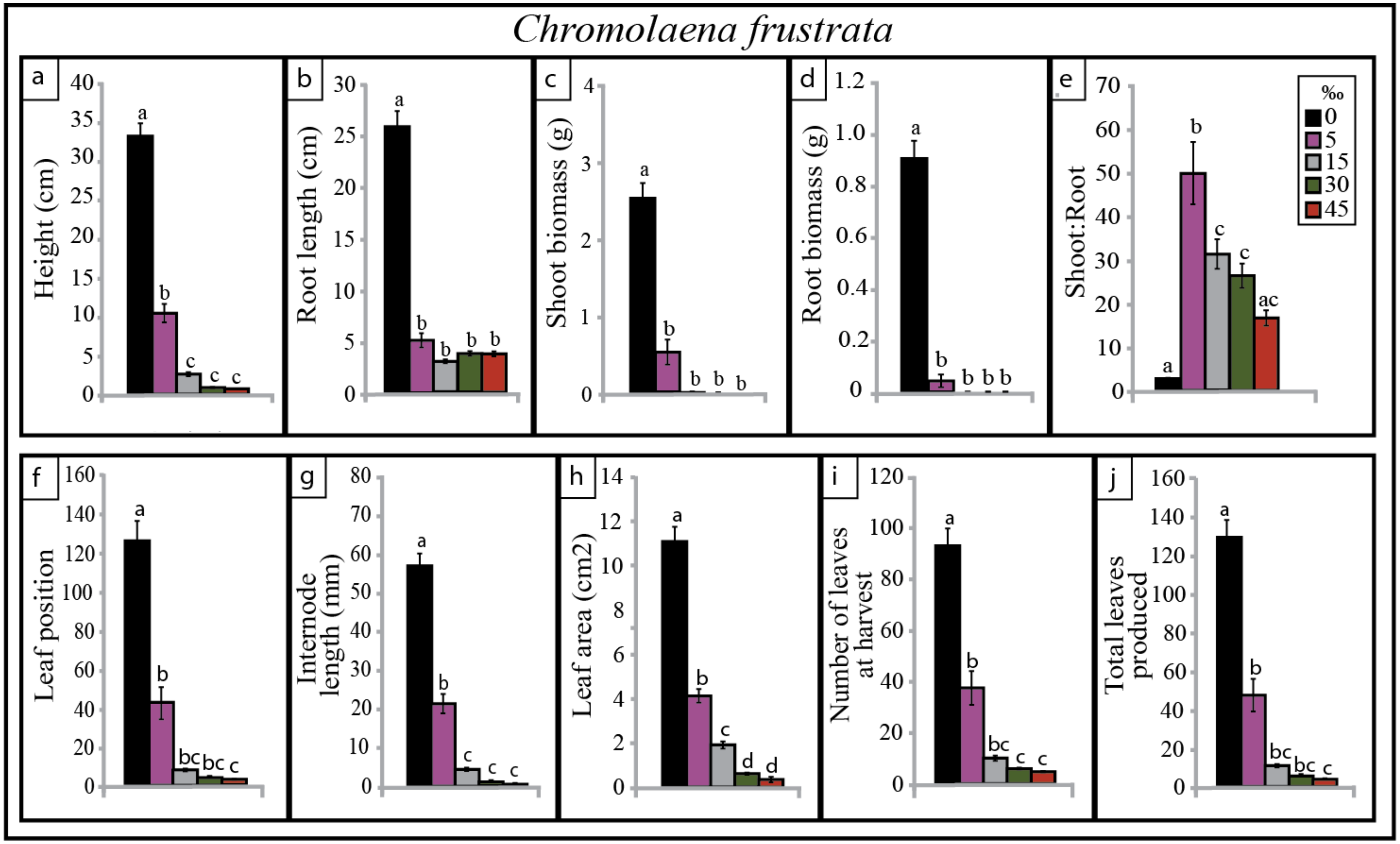


Figure 3.6. Mean growth and morphological responses across salinity treatments (0, 5, 15, 30, and 45‰) of Conocarpus erectus seedlings. Notes: Lettering symbolizes significant (different letter) and non-significant (same letter) differences between salinity levels based on results from linear mixed-effects models. Error bars represent the standard error.

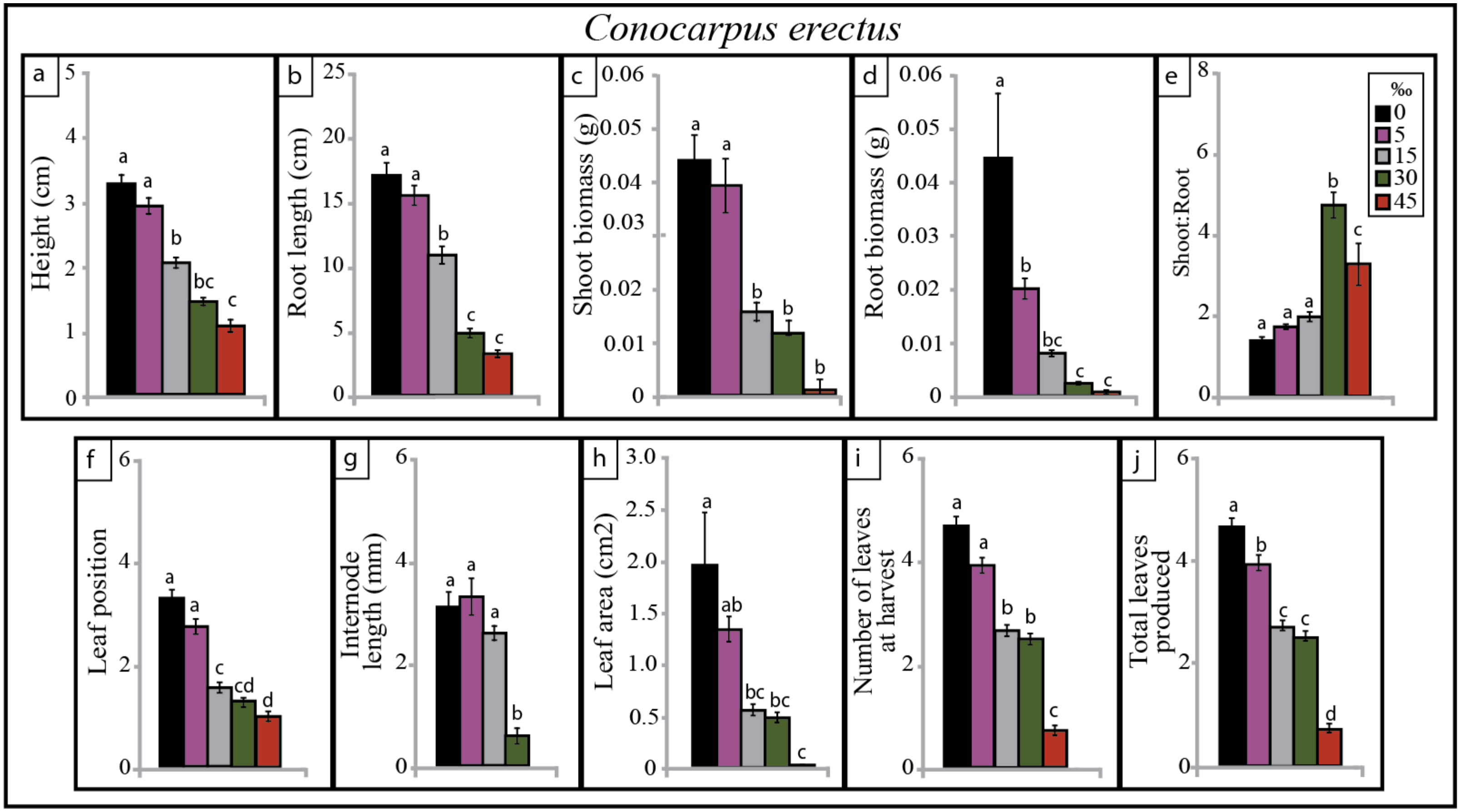


Figure 3.7. Mean growth and morphological responses across salinity treatments (0, 5, 15, 30, and 45‰) of Eugenia foetida seedlings. Notes: Lettering symbolizes significant (different letter) and non-significant (same letter) differences between salinity levels based on results from linear mixed-effects models. Error bars represent the standard error.

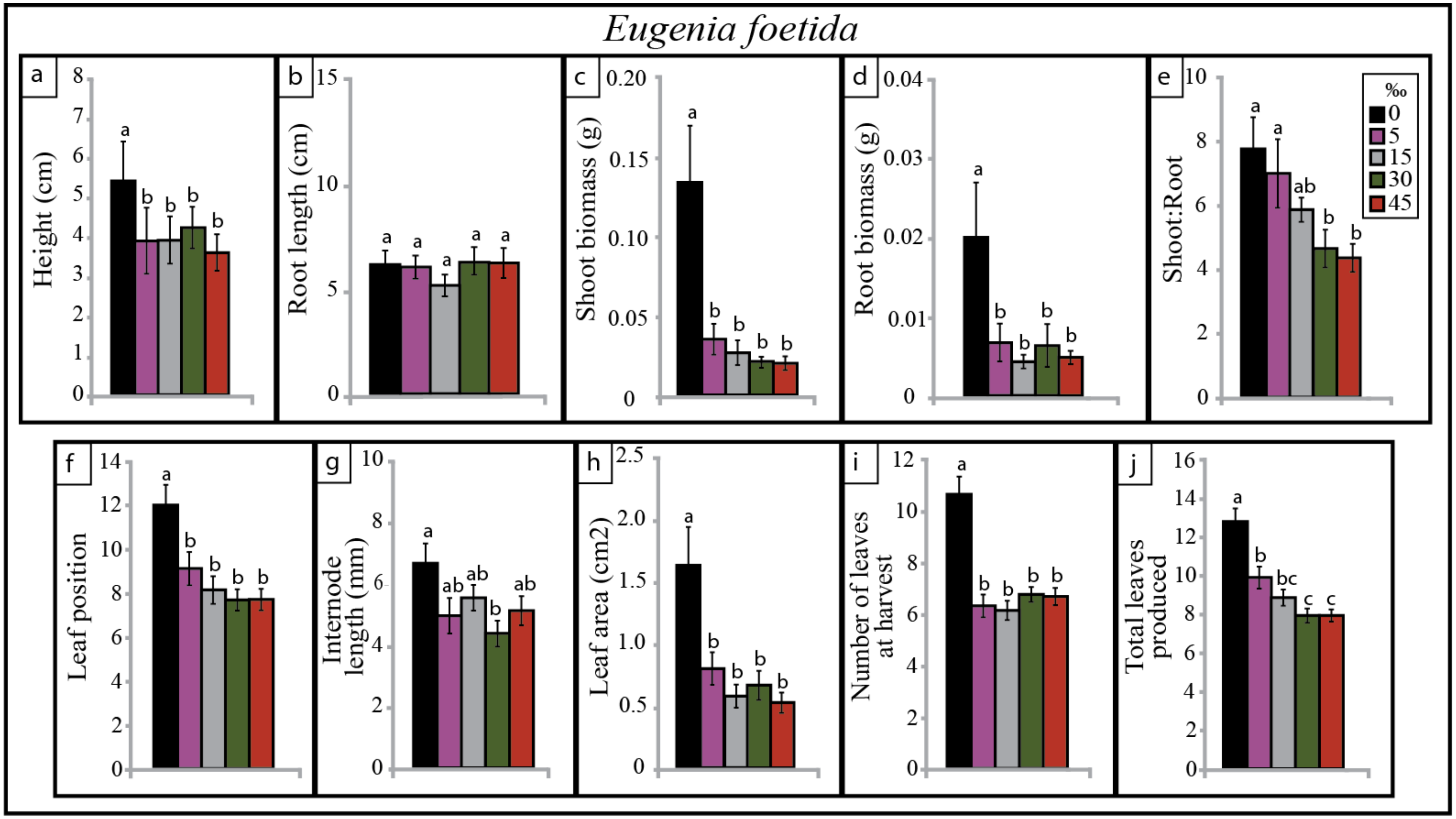


Figure 3.8. Mean growth and morphological responses across salinity treatments (0, 5, 15, 30, and 45‰) of Piscidia piscipula seedlings. Notes: Lettering symbolizes significant (different letter) and non-significant (same letter) differences between salinity levels based on results from linear mixed-effects models. Error bars represent the standard error.

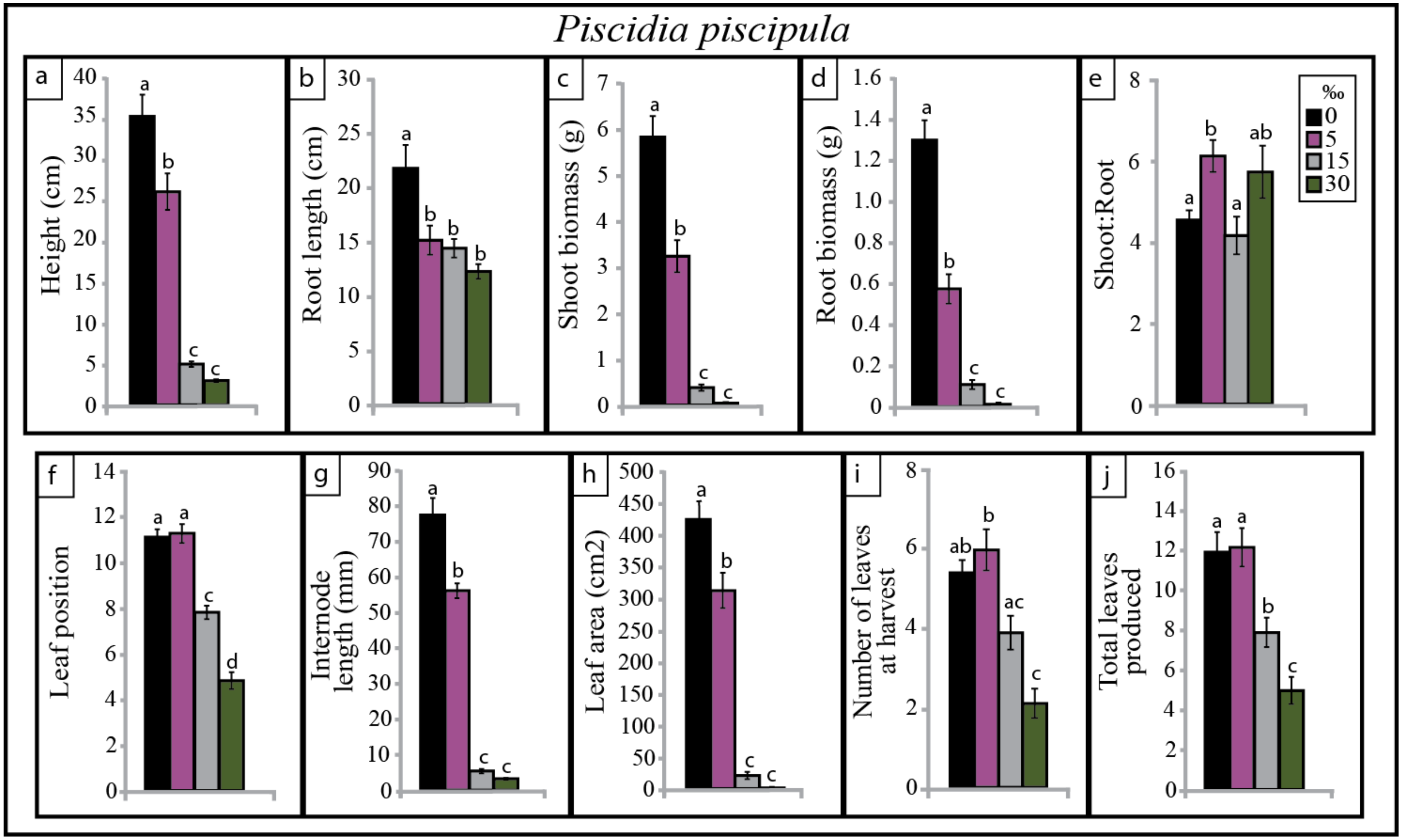


Figure 3.9. Mean growth and morphological responses across salinity treatments (0, 5, 15, 30, and 45‰) of Swietenia mahagoni seedlings. Notes: Lettering symbolizes significant (different letter) and non-significant (same letter) differences between salinity levels based on results from linear mixed-effects models. Error bars represent the standard error.

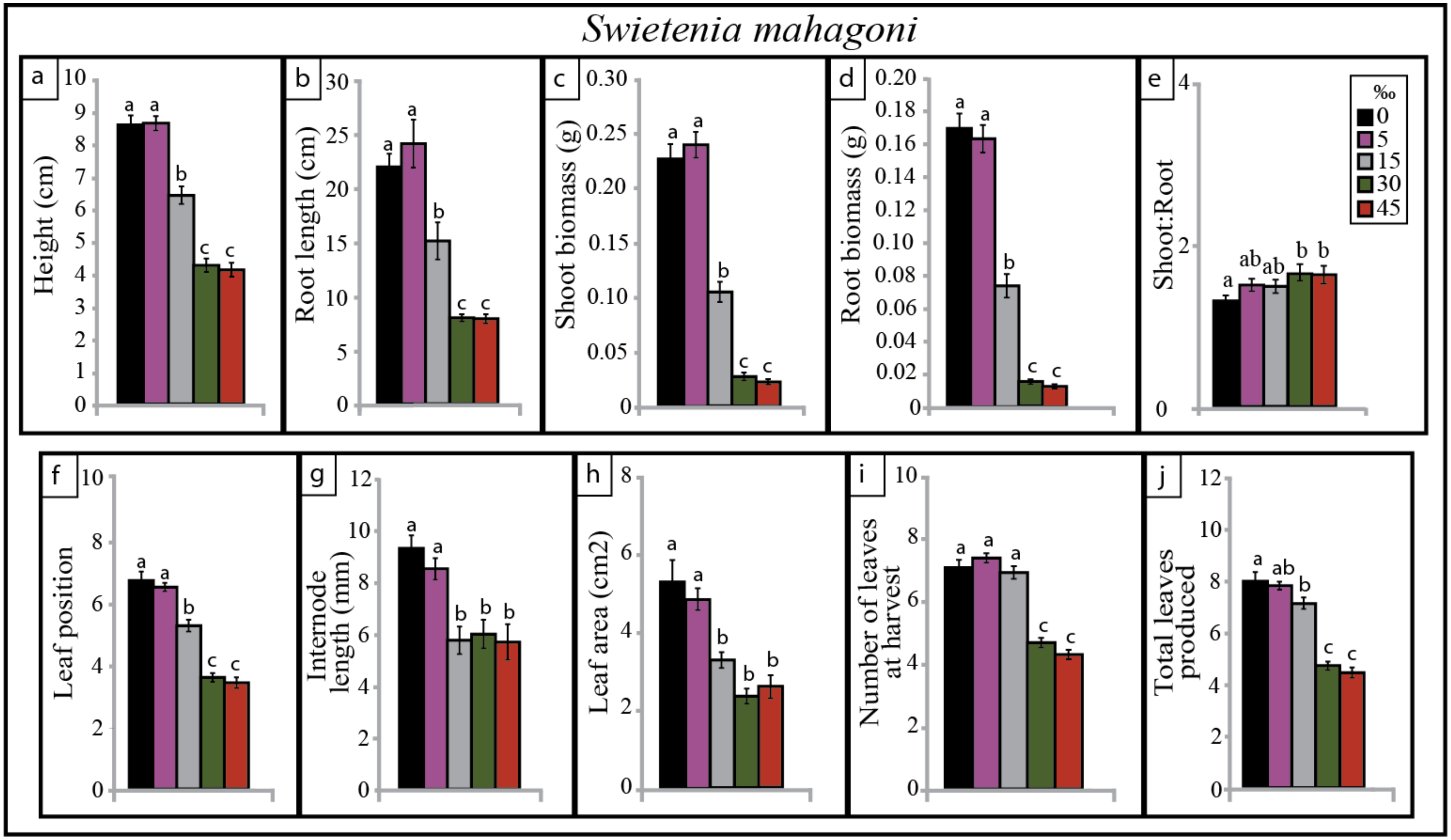
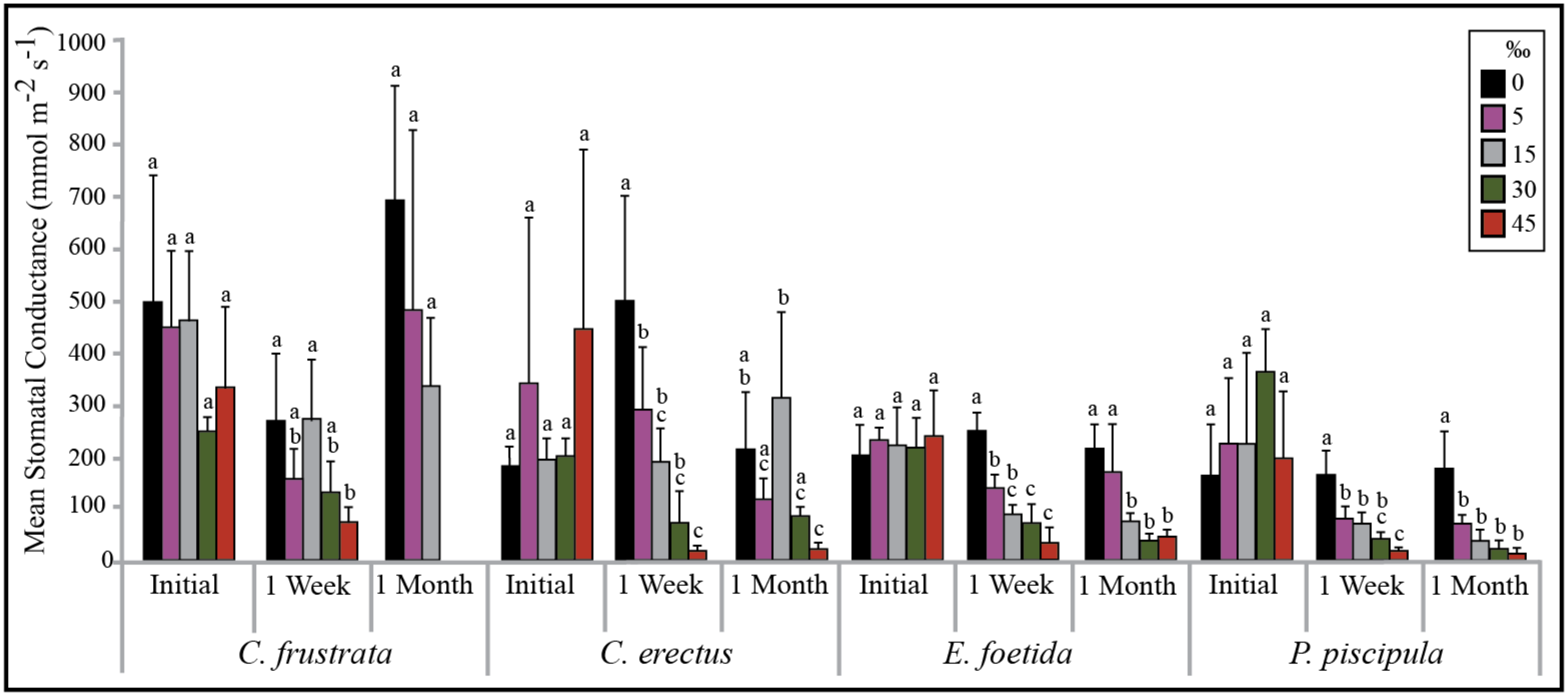


Figure 3.10. Mean stomatal conductance responses across salinity treatments (0, 5, 15, 30, and 45‰) of five plant species (Chromolaena frustrata, Conocarpus erectus, Eugenia foetida, Piscidia piscipula, and Swietenia mahagoni) found along the coast of Everglades National Park, Florida, USA. Notes: Lettering symbolizes significant (different letter) and non-significant (same letter) differences between salinity levels at each monitoring event (initial, 1 week, 1 month) based on results from linear mixed-effects models. Error bars represent the standard error. No C. frustrata seedlings planted in 30 or 45‰ soils survived to one month.



APPENDICES

Appendix I. Seed collection and germination study data for seed germination experiments of five plant species (*Chromolaena frustrata*, *Conocarpus erectus*, *Eugenia foetida*, *Piscidia piscipula*, and *Swietenia mahagoni*) found along the coast of Everglades National Park, Florida, USA.

Species	Date Collected	Season	Study Initiation Date	Study Termination Date
Chromolaena frustrata	April-11	Dry	December 2, 2011	January 23, 2012
Conocarpus erectus	January-12	Dry	April 16, 2012	January 11, 2013
Eugenia foetida	January-13	Dry	February 15, 2013	April 12, 2013
Piscidia piscipula	October-12	Wet	January 17, 2013	February 22, 2013
Swietenia mahagoni	March-11	Dry	December 2, 2011	February 8, 2012

Appendix II. Seedling establishment study dates, average greenhouse temperatures, and daylight hours for five plant species (*Chromolaena frustrata*, *Conocarpus erectus*, *Eugenia foetida*, *Piscidia piscipula*, and *Swietenia mahagoni*) found along the coast of Everglades National Park, Florida, USA.

Species	Study Initiation Date	Study Termination Date	Temperature °C	Average Day Length
Chromolaena frustrata	April 13, 2012	July 7, 2012	Average: high 42 Average : low 23 Max high: 46 Max low: 16	13 hours 11 min
Conocarpus erectus	August 22, 2011	December 5, 2011	Average: high 42 Average : low 23 Max high: 46 Max low: 13	11 hours 44 min
Eugenia foetida	October 2, 2012	April 19, 2013	Average: high 39 Average : low 19 Max high: 45 Max low: 7	12 hours 22 min
Piscidia piscipula	March 22, 2013	June 28, 2013	Average: high 42 Average : low 22 Max high: 46 Max low: 8	12 hours 57 min
Swietenia mahagoni	July 29, 2011	December 31, 2011	Average: high 42.2 Average : low 23 Max high: 47 Max low: 13	11 hours 58 min

Appendix III. Stomatal conductance experiment data of five plant species (*Chromolaena frustrata, Conocarpus erectus, Eugenia foetida, Piscidia piscipula,* and *Swietenia mahagoni*) found along the coast of Everglades National Park, Florida, USA.

Species	Study Initiation Date	1 week	1 month	Time	Seedling Age
Chromolaena frustrata	May 8, 2013	May 17, 2013	June 17, 2013	10:30-1:00 pm	3 month
Conocarpus erectus	June 15, 2012	June 21, 2012	July 21, 2012		2 month
Eugenia foetida	May 10, 2013	May 23, 2013	17-Jun-13	11:00-1:00 pm	7 month
Piscidia piscipula	March 3, 2013	March 27, 2013	May 6, 2013	11:00 - 1:00 pm	2 month

Appendix IV. Linear mixed effects models and Tukey pairwise comparisons looking at growth under five salinity treatments (0, 5, 15, 30, and 45‰) of five plant species (*Chromolaena frustrata, Conocarpus erectus, Eugenia foetida, Piscidia piscipula,* and *Swietenia mahagoni*) found along the coast of Everglades National Park, Florida, USA. Notes: *C. erectus* only developed one leaf above the cotyledons at 45‰, therefore, no measurement was taken for internode length for this species. *Eugenia foetida* showed no difference in root length across treatments, therefore, no pairwise comparisons were performed. No *P. piscipula* seedlings were grown in 45‰ soils.

	Salinity (‰)	Height (cm)	Root length (cm)	Shoot biomass (g)	Root biomass (g)	Shoot: Root	Most recently mature leaf position	Internode length below most mature leaf (mm)	Area of most mature leaf (cm^2)	Number of leaves at time of harvest	Total number of leave produced
Chromolaena frustrata	All combined	$F_{4,15} = 68.86$ $p < 0.001$	$F_{4,15} = 22.77$ $p < 0.001$	$F_{4,15} = 41.56$ $p < 0.001$	$F_{4,15} = 111.68$ $p < 0.001$	$F_{4,15} = 14.08$ $p < 0.001$	$F_{4,15} = 28.01$ $p < 0.001$	$F_{4,15} = 56.15$ $p < 0.001$	$F_{4,15} = 193.82$ $p < 0.001$	$F_{4,15} = 25.51$ $p < 0.001$	$F_{4,15} = 22.77$ $p < 0.001$
	Pairwise	p- value	p- value	p- value	p- value	p- value	p- value	p- value	p- value	p- value	p- value
	0 vs 5	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
	0 vs 15	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
	0 vs 30	< 0.001	< 0.001	< 0.001	< 0.001	0.003	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
	0 vs 45	< 0.001	< 0.001	< 0.001	< 0.001	0.21	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
	5 vs 15	0.01	0.71	0.18	0.87	0.04	0.12	0.002	< 0.001	0.07	0.15
	5 vs 30	0.001	0.92	0.14	0.86	0.003	0.06	< 0.001	< 0.001	0.02	0.06
	5 vs 45	< 0.001	0.93	0.13	0.86	< 0.001	0.05	< 0.001	< 0.001	0.02	0.05
	15 vs 30	0.95	0.99	1.0	1.0	0.94	1.0	0.95	0.03	0.99	1.0
	15 vs 45	0.93	0.99	1.0	1.0	0.16	1.0	0.91	0.004	0.99	1.0
	30 vs 45	1.0	1.0	1.0	1.0	0.58	1.0	1.0	1.0	1.0	1.0
Conocarpus erectus	All combined	$F_{4,15} = 33.69$ $p < 0.001$	$F_{4,15} = 22.77$ $p < 0.001$	$F_{4,15} = 15.91$ $p < 0.001$	$F_{4,15} = 15.78$ $p < 0.001$	$F_{4,15} = 26.50$ $p < 0.001$	$F_{4,15} = 28.01$ $p < 0.001$	$F_{3,12} = 11.43$ $p < 0.001$	$F_{4,15} = 7.38$ $p = 0.002$	$F_{4,15} = 59.77$ $p < 0.001$	$F_{4,15} = 59.77$ $p < 0.001$
	Pairwise	p- value	p- value	p- value	p- value	p- value	p- value	p- value	p- value	p- value	p- value
	0 vs 5	0.59	0.44	0.96	< 0.001	0.9	0.04	0.97	0.49	0.05	0.05
	0 vs 15	< 0.001	< 0.001	< 0.001	< 0.001	0.55	< 0.001	0.76	003	< 0.001	< 0.001
	0 vs 30	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.001	< 0.001	< 0.001

	0 vs 45	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	--	< 0.001	< 0.001	< 0.001
	5 vs 15	< 0.001	< 0.001	0.002	0.31	0.97	< 0.001	0.49	0.25	< 0.001	< 0.001
	5 vs 30	< 0.001	< 0.001	< 0.001	0.04	< 0.001	< 0.001	< 0.001	0.17	< 0.001	< 0.001
	5 vs 45	< 0.001	< 0.001	< 0.001	0.02	< 0.001	< 0.001	--	0.01	< 0.001	< 0.001
	15 vs 30	0.06	< 0.001	0.97	0.91	< 0.001	0.69	< 0.001	1.0	0.95	0.95
	15 vs 45	< 0.001	< 0.001	0.18	0.8	0.001	0.04	--	0.68	< 0.001	< 0.001
	30 vs 45	0.48	0.43	0.5	1.0	0.006	0.53	--	0.79	< 0.001	< 0.001
Eugenia foetida	All combined	$F_{4,15} = 8.39$ $p < 0.001$	$F_{4,15} = 1.30$ $p = 0.32$	$F_{4,15} = 15.84$ $p < 0.001$	$F_{4,15} = 7.87$ $p = 0.001$	$F_{4,15} = 8.12$ $p = 0.001$	$F_{4,15} = 15.79$ $p < 0.001$	$F_{4,15} = 3.07$ $p = 0.05$	$F_{4,15} = 16.01$ $p < 0.001$	$F_{4,15} = 17.79$ $p < 0.001$	$F_{4,15} = 17.51$ $p < 0.001$
	Pairwise	*p*- value	*p*- value	*p*- value	*p*- value	*p*- value	*p*- value	*p*- value	*p*- value	*p*- value	*p*- value
	0 vs 5	< 0.001	--	< 0.001	< 0.001	0.83	< 0.001	0.09	< 0.001	< 0.001	< 0.001
	0 vs 15	< 0.001	--	< 0.001	< 0.001	0.06	< 0.001	0.46	< 0.001	< 0.001	< 0.001
	0 vs 30	0.005	--	< 0.001	< 0.001	< 0.001	< 0.001	0.007	< 0.001	< 0.001	< 0.001
	0 vs 45	< 0.001	--	< 0.001	< 0.001	< 0.001	< 0.001	0.15	< 0.001	< 0.001	< 0.001
	5 vs 15	1.0	--	0.99	0.95	0.5	0.54	0.92	0.68	1.0	0.52
	5 vs 30	0.87	--	0.92	1.0	0.009	0.16	0.91	0.94	0.96	0.03
	5 vs 45	0.91	--	0.91	0.98	0.002	0.17	1.0	0.45	0.98	0.03
	15 vs 30	0.9	--	1.0	0.97	0.44	0.95	0.43	0.98	0.86	0.67
	15 vs 45	0.88	--	1.0	1.0	0.23	0.96	0.97	1.0	0.92	0.67
	30 vs 45	0.35	--	1.0	0.99	1.0	1.0	0.81	0.89	1.0	1.0
Piscidia piscipula	All combined	$F_{3,8}= 83.73$ $p < 0.001$	$F_{3,8}= 9.76$ $p = 0.005$	$F_{3,8}= 78.55$ $p < 0.001$	$F_{3,8}= 95.68$ $p < 0.001$	$F_{3,8}= 5.50$ $p = 0.024$	$F_{3,8}= 87.03$ $p < 0.001$	$F_{3,8}= 108.74$ $p < 0.001$	$F_{3,8}= 115.31$ $p < 0.001$	$F_{3,8} = 10.38$ $p = 0.004$	$F_{3,8}= 85.73$ $p < 0.001$
	Pairwise	*p*- value	*p*- value	*p*- value	*p*- value	*p*- value	*p*- value	*p*- value	*p*- value	*p*- value	*p*- value
	0 vs 5	< 0.001	0.002	< 0.001	< 0.001	0.02	0.99	< 0.001	< 0.001	0.86	0.97
	0 vs 15	< 0.001	< 0.001	< 0.001	< 0.001	0.90	< 0.001	< 0.001	< 0.001	0.18	< 0.001
	0 vs 30	< 0.001	< 0.001	< 0.001	< 0.001	0.16	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
	5 vs 15	< 0.001	0.98	< 0.001	< 0.001	0.002	< 0.001	0.002	< 0.001	0.03	< 0.001
	5 vs 30	< 0.001	0.39	< 0.001	< 0.001	0.90	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
	15 vs 30	0.82	0.65	0.86	0.65	0.03	< 0.001	0.97	0.90	0.07	< 0.001

	All combined	$F_{4,15}$ = 85.29 $p < 0.001$	$F_{4,15}$ = 31.99 $p < 0.001$	$F_{4,15}$ = 147.11 $p < 0.001$	$F_{4,15}$ = 162.66 $p < 0.001$	$F_{4,15}$ = 3.89 $p = 0.02$	$F_{4,15}$ = 55.83 $p < 0.001$	$F_{4,15}$ = 11.93 $p < 0.001$	$F_{4,15}$ = 14.93 $p < 0.001$	$F_{4,15}$ = 70.59 $p < 0.001$	$F_{4,15}$ = 81.26 $p < 0.001$
Swietenia mahagoni	Pairwise	*p*- value	*p*- value	*p*- value	*p*- value	*p*- value	*p*- value	*p*- value	*p*- value	*p*- value	*p*- value
	0 vs 5	1.0	0.8	0.8	0.95	0.29	0.94	0.76	0.89	0.69	0.97
	0 vs 15	< 0.001	0.002	< 0.001	< 0.001	0.34	< 0.001	< 0.001	< 0.001	0.97	0.009
	0 vs 30	< 0.001	< 0.001	< 0.001	< 0.001	0.004	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
	0 vs 45	< 0.001	< 0.001	< 0.001	< 0.001	0.009	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
	5 vs 15	< 0.001	< 0.001	< 0.001	< 0.001	1.0	< 0.001	< 0.001	0.01	0.29	0.06
	5 vs 30	< 0.001	< 0.001	< 0.001	< 0.001	0.54	< 0.001	0.003	< 0.001	< 0.001	< 0.001
	5 vs 45	< 0.001	< 0.001	< 0.001	< 0.001	0.65	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
	15 vs 30	< 0.001	0.002	< 0.001	< 0.001	0.47	< 0.001	1.0	0.32	< 0.001	< 0.001
	15 vs 45	< 0.001	0.001	< 0.001	< 0.001	0.59	< 0.001	1.0	0.61	< 0.001	< 0.001
	30 vs 45	0.99	1.0	1.0	1.0	1.0	0.98	0.99	0.99	0.52	0.83

CONCLUSIONS AND FUTURE DIRECTIONS

Increasing sea levels and anthropogenic alterations together are resulting in a change or complete loss of coastal plant communities around the world (Nicholls and Cazenave, 2010; Terry and Chui, 2012; Kirwan and Megonigal, 2013). Shifts in plant communities from less salt- and lower inundation-tolerant to more salt- and higher inundation-tolerant community types or to open water have been documented (Ross et al., 1994; Kearney et al., 2002; Kirwan et al., 2008; Saha et al., 2011; Sharpe and Baldwin, 2012; Terry and Chui, 2012). Florida has the shallowest water table in the continental US, its coastal communities are distributed across a gradient that is 0-2m above mean sea level (Hoffmeister, 1974), and it has undergone significant ecosystem drying as a result of anthropogenic changes (Davis et al., 2005). Ecosystem drying and/or hydrologic restoration and SLR effects are interacting most prominently in Florida’s coastal areas, impacting its coastal plant communities.

Rare species richness tends to be negatively correlated with salinity in coastal habitats (Saha et al., 2011). Everglades National Park, which has a significant coastal extent, harbors 43 critically imperiled species as defined by Gann et al. (2002); 21 of these are threatened by SLR, including one federally endangered species, *Chromolaena frustrata* (Saha et al., 2011). To form a realistic conservation action strategy in the face of large-scale environmental change, land managers need to prioritize species under greatest extinction threat. Understanding how and in what direction the system is changing will help land managers decide how to allocate resources and funding for the preservation of the greatest amount of biodiversity. I addressed this need in Chapters I-III.

Chapter I provided evidence that lowland plant communities along the coast of south Florida have moved up the elevation gradient, transitioning from less salt- and inundation-tolerant to more salt- and inundation- tolerant communities between 1978 and 2011. More than half of the area covered by white mangrove forest in 1978 transitioned into black and red mangrove forest by 2011. Halophyte prairie decreased transitioning into more inundation-loving black mangrove forest. Black and red mangrove forests increased. Additionally, the two highest elevation communities—tropical hardwood hammock and buttonwood forest—and those harboring the most rare species decreased; white mangrove forest replaced buttonwood forest and buttonwood forest replaced tropical hardwood hammocks. The direction of change we found suggests the site became saltier and wetter during the 33 year study period.

In Chapter II, I looked at how competitive ability of halophytes may be playing a role in the transitions found in Chapter I between halophytic and glycophytic communities. I showed that halophytes create a positive feedback, increasing soil salinity throughout the soil column, thus making it more conducive to halophyte establishment in increasingly saline soils. Pots with all halophytes showed significantly higher soil salinity than pots with only glycophytes regardless of species or location within the soil strata. Interestingly, increases in soil salinity were not directly from higher transpiration rates of halophytes. Instead, either osmotic or ionic stress caused a decrease in glycophyte biomass and leaf area resulting in overall less plant transpiration. As halophytes invade a glycophytic community, soil salinity levels may become too high to support glycophyte survival and establishment, resulting in a turnover in plant communities from less salt tolerant to more salt tolerant community types (e.g. Ross et al., 1994; Saha et al., 2011; Chapter I this dissertation). The process of increasing soil salinity via increasing halophyte density in glycophytic communities brings a biological component to SLR-related coastal plant community shifts. This study suggests that changes may occur faster than would be predicted from SLR alone negatively impacting rare plants in the area sooner than later.

A species' vulnerabilities to environmental stressors are contingent on life stage (Parker et al., 1955; Williams et al., 1998; Chartzoulakis and Klapaki, 2000; Schiffers and Tielbörger, 2006). High salinity levels tend to impact juvenile or regenerative life stages more than adult stages (Perry and Williams, 1996). To preserve the most biodiversity possible before large-scale plant community turnover occurs, on-the-ground plot-based monitoring for change is essential. Understanding which life stage is most vulnerable to salinity stress can help land managers monitor for on-the-ground changes in a way that is detectable before large-scale community turnover occurs. Chapter III addresses these monitoring needs with species found in the rare plant-harboring buttonwood and tropical hardwood hammock communities.

In Chapter III, I showed that seedling establishment is the life stage most sensitive to increasing salinity levels in the five species we studied and can be used as an indicator to change in on-the-ground surveys. Seed germination responded similarly to increased salinity in all five coastal, upland species—decreasing with increased salinity—while seedling establishment showed disparate responses across salinity treatments and between species. In addition to our work, Saha et al. (2011, 2015); Wendelberger unpublished data examined the same species, respectively, looking at salinity effects (0, 5, 15, and 30‰ soil salinity) on one-year-old plants, one-year-old *Chromolaena frustrata*, and isotopic signatures (δ^{18}O and δ^{2}H) of *in-situ* adults assessing where in the soil column and salinity of the water they uptake at the study site (*S. mahagoni* adults were not examined). Three of the five study species (*C. frustrata*, *E. foetida*, and *S. mahagoni*) showed lower percent seedling survival at the higher salinity levels than one-year-old plants of the same species grown in equivalent soil salinities (Saha et al., 2015; Wendelberger unpublished data). Our results and that of others (Williams, Williams, et al., 1999; Ross et al., 2000; Saha et al., 2011) show that plant community change will first be seen in the understory as a change in species composition of seedlings in the area.

Additionally, our results corroborate those of Saha et al. (2011, 2015) regarding the conservation of the federally endangered *C. frustrata.* The majority of this species' population is found in the buttonwood forest understory (Gann et al., 2002; USFWS, 2012; Saha et al., 2015). Buttonwood forests have decreased in cover in our study area since 1978. There was a marked decline in *C. frustrata* stomatal conductance across all treatments, including the control, between the pre-treatment and one week measurements. Flooding is known to result in a decline in photosynthetic rates in flood sensitive species (Pezeshki et al., 1990); perhaps constant inundation during the seedling establishment experiments acted as a covariate with salinity reducing growth and survival while freshwater control seedlings were able to survive and grow without the combined stress of salt. As the groundwater levels rise with rising sea levels, inundation depth, duration, and salinity level will also increase, suggesting that even in times when salinity levels are low enough for germination, *C. frustrata* seedlings may not be able to establish with the added stress of increased inundation.

Conservation actions need to be evaluated and implemented for *C. frustrata*. Studies performed at the National Center for Genetic Resources Preservation suggest that *C. frustrata* seeds are intermediate between orthodox and recalcitrant (J. Maschinski, Fairchild Tropical Botanic Garden, personal communication, Kennedy et al., 2012). Studies need to determine if seeds of this species can survive in long-term cryogenic storage and whether seed storage is enough, or are other conservation actions, such as *ex situ* storage or assisted migration, required for the protection of this species.

A diverse coastal plant community matrix is critical to the health of the greater community, both human and natural alike (Odum, 1988; Davis et al., 2005; Alongi, 2008; Langley et al., 2009; McLeod et al., 2011) and a hotspot for sequestering CO_2 at high rates, helping to decrease climate change (Barr et al., 2010; McLeod et al., 2011). If the decreases in upland communities seen between 1978 and 2011 continue, there will be a homogenization of communities along the coast of ENP. Tropical hardwood hammocks and buttonwood forests will disappear along with the rare species they harbor.
Creating a healthy Everglades ecosystem through increased freshwater flow would eliminate one of two major stressors driving the vegetative changes that have been seen throughout the Florida coast. Therefore, restoring the hydrologic regime of the Everglades ecosystem is critical, if we want to preserve biodiversity and ecosystem integrity.

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