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Sea level rise and South Florida coastal forests

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Abstract Coastal ecosystems lie at the forefront of sea level rise. We posit that before the onset of actual inundation, sea level rise will influence the species composition of coastal hardwood hammocks and buttonwood (*Conocarpus erectus* L.) forests of the Everglades National Park based on tolerance to drought and salinity. Precipitation is the major water source in coastal hammocks and is stored in the soil vadose zone, but vadose water will diminish with the rising water table as a consequence of sea level rise, thereby subjecting plants to salt water stress. A model is used to demonstrate that the constraining effect of salinity on transpiration limits the distribution of freshwater-dependent communities. Field data collected in hardwood hammocks and coastal buttonwood forests over 11 years show that halophytes have replaced glycophytes. We establish that sea level rise threatens 21 rare coastal species in Everglades National Park and estimate the relative risk to each

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species using basic life history and population traits. We review salinity conditions in the estuarine region over 1999–2009 and associate wide variability in the extent of the annual seawater intrusion to variation in freshwater inflows and precipitation. We also examine species composition in coastal and inland hammocks in connection with distance from the coast, depth to water table, and groundwater salinity. Though this study focuses on coastal forests and rare species of South Florida, it has implications for coastal forests threatened by saltwater intrusion across the globe.

1 Introduction

Sea level rise of 1 to 2 m by 2100 (Allison et al. 2009) threatens South Florida's low-lying coasts where plant communities are organized along a mild gradient in elevation, from mangroves at sea level to salinity-intolerant coastal hardwood hammocks on localized elevations generally less than 2 m above sea level (Olmsted and Loope 1980, 1984). A 30 cm increase in sea level is expected to render coastal systems erosional, preceding the complete collapse with a breach of coastal marl ridges resulting from a 60 cm rise in sea level (Wanless et al. 1994). However, even before the onset of sustained inundation there can be irreversible changes in coastal forest composition, which is the focus of this paper. While studies in southeastern United States have looked at the role of sea level rise-induced increases in flooding frequency and groundwater salinity in coastal hydric hammocks of Florida (DeSantis et al. 2007; Williams et al. 1999), pine rocklands on oceanic islands off Florida's coast (Ross et al. 1994, 2009), coastal marshes of Florida and Louisiana (Donnelly and Bertress 2001; Reed 2002), deltaic coasts of Mississippi (Blum and Roberts 2009), and tidal swamps in South Carolina (Krauss et al. 2009), coastal forests of Everglades National Park (ENP) provide a novel setting because the wide range of plant communities present differ in their salinity tolerances. Additionally, reduced freshwater inflows due to upstream water management have hastened salt-water intrusion in ENP's coastal ecosystems (Nuttle et al. 2000; Sklar and Browder 1998). Though Florida's coast lines have always been in flux, the recent acceleration in the rate of increase in sea level in conjunction with human alteration of Everglades hydrology imparts an urgency to the documentation and scientific study of the processes governing ecosystem change and the loss of rare species (Pearlstine et al. 2009).

Saltwater intrusion increases the extent of halophyte-dominated plant communities in the world's coastal tropical and subtropical ecosystems (e.g. India: Blasco 1977, Australia: Knighton et al. 1991; Lucas et al. 2002; Florida: Alexander 1974; Ross et al. 1994, 2009; Williams et al. 2007). This is also true in the southern Everglades where the coastline is dominated by mangroves (*Avicennia germinans* L., *Rhizophora mangle* L. and *Laguncularia racemosa* (L.) C.F. Gaertn.). While sea level increased by approximately 30 cm over the last century as measured in Key West, FL, seawater intrusion into the Biscayne aquifer along the Everglades coastline extended at a faster than expected rate due to the diversion of surface water flow away from the ENP with the construction of canals and levees between Lake Okeechobee and ENP (Klein and Waller 1985; Sonenshein and Koszalka 1996). By the late 1990s, saltwater intrusion extended approximately 30 km inland in the Shark River Slough region of ENP and about 10 and 15 km inland in the regions of C-111 Basin and

Taylor Slough, respectively (Fitterman et al. 1999). The boundary between fresh and saline groundwater in the region was determined to be diffuse as opposed to a sharp transition (Price et al. 2006).

In a large area of coastal Everglades, surface freshwater sheetflow is either nonexistent or seasonally limited (Langevin et al. 2005). Precipitation is the main source of fresh water, part of which is stored in the unsaturated or vadose zone of elevated coastal hammocks as soil water. Some of the soil water may percolate down to recharge the fresh groundwater lens (Fig. 1a). The lens is thin and seasonal and overlies saline ground water (Fitterman et al. 1999) that imparts a brackish signature to the lower portion of the lens (e.g. Kruse et al. 2000). Coastal forests at relatively high elevations use freshwater recharged during the wet season and lower their stomatal conductance in response to drought during the dry season, whereas plants at lower elevations shift their water source from freshwater to saline groundwater in the dry season (Ish-Shalom et al. 1992; Sternberg and Swart 1987). Dry season water stress affects both coastal and elevated inland hammocks; however, unlike the inland hammocks where some species can tap limited amounts of fresh groundwater during the dry season (up to 90% of dry season water intake; Saha et al. 2009), plants in coastal hardwood hammocks are constrained by saline groundwater (Ewe 2001). Plant communities at intermediate elevations, dominated by buttonwood (*Conocarpus erectus* L.) can shift their water source to utilize brackish groundwater (Ish-Shalom et al. 1992); however, how long buttonwoods can rely on brackish water before shutting down their stomata is currently unknown. Preliminary data show that

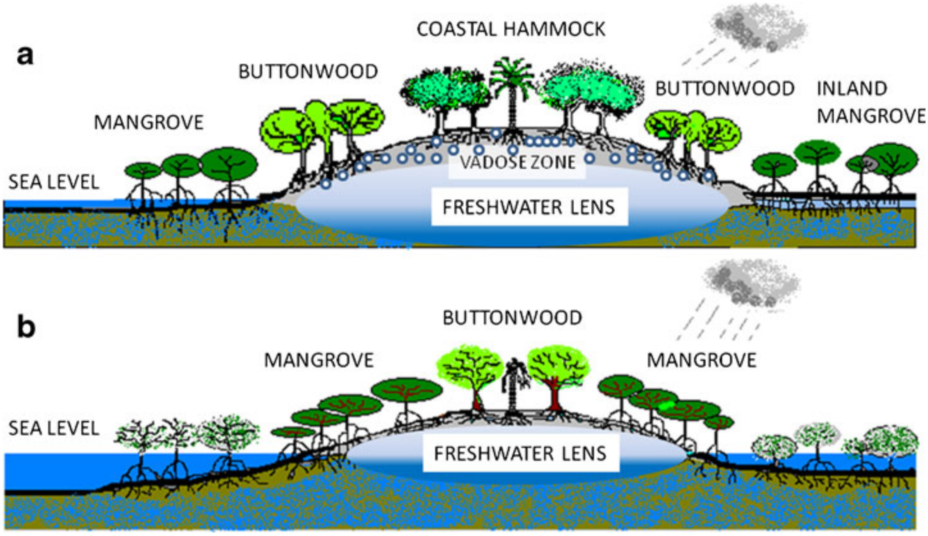


Fig. 1 **a** Sketch of a coastal hammock on an elevated rise flanked by buttonwood forests at intermediate elevations and mangrove forests at sea level. Also shown are the vadose zone (with water drops), freshwater lens (where shading indicates increasing brackishness towards the bottom of lens), and seawater. *Bottom sketch* **b** shows a rise in sea level that decreases the volume available to hold freshwater (shrinking of the freshwater lens), with consequent mortality of coastal hammocks and the migration of buttonwoods and mangroves along with the decrease in the freshwater lens. Elevation exaggerated in illustration to indicate water pools

the stomatal conductance of buttonwoods is lower in mangrove forests compared to mixed hardwood hammocks (L. Sternberg and S. Saha unpublished data) and is inversely related to salinity (S. Saha unpublished data).

Using insights from water budgets of inland hardwood hammocks where groundwater is fresh (Saha et al. 2009; Sullivan et al. 2010; Villalobos 2010) and from data on patterns of water source utilization by hardwood species in coastal hammocks, we conceptualize how sea level rise will affect freshwater availability in coastal hardwood hammocks. We suggest that the rising water table accompanying sea level rise will lead to shrinking of the vadose zone as well as increase salinity in the bottom portion of the freshwater lens (Fig. 1b), subsequently increasing brackishness of plant-available water. This will influence tree species composition of coastal hardwood hammocks and buttonwood forests based upon species-level tolerance to salinity and/or drought and may also lead to the disappearance or decline of critically imperiled coastal plant species. Such conditions already arise over the dry season, when upon shrinking of the freshwater lens, plants are exposed to the underlying saline groundwater. We thus examine the existing species composition on coastal and inland hammocks across ENP in connection with the underlying salinity gradient. With the central premise that salinity has differential impacts on transpiration of plant communities in the coastal Everglades (Sternberg et al. 2007; Teh et al. 2008) we model the change in buttonwood forests with rise in sea level. We validate the model using data on groundwater salinity (1999 to 2010) to examine the rate of seawater intrusion in coastal Everglades, and use data from coastal plant communities along the gradient in elevation to compare species abundances of glycophytes (salt-sensitive) and halophytes (salt-tolerant, sensu Glenn et al. 1999) between 1998 and 2009. Finally, using basic life history and population traits, we estimate the relative risk posed by sea level rise and habitat change to rare and endemic species.

2 Methods

2.1 Species composition and seawater intrusion

2.1.1 Study location and species composition

We sample forests/hammocks/tree islands in the ENP, which vary in their distances from the coast and the freshwater/saltwater interface (FWSWI). Our objective is to investigate if there are distinctions in species composition based on distance from the coast and FWSWI. The closer a site is to the coast, the greater would be the salinity of groundwater. Species composition of hardwood hammocks dominated by tropical species (forests and hammocks are used interchangeably) and buttonwood forests located in ENP are determined and then examined in relation to the underlying salinity gradient.

Sampled hammocks occurred at different distances from the coast; hammocks in Long Pine Key (an elevated ridge of limestone that separates the Taylor Slough and Shark River Slough, the two main drainages of ENP) averaged 22 km from the coast; plots located in mahogany (*Swietenia mahagoni* (L.) Jacq.)- dominated hammocks southwest of LPK averaged 17 km; and tree islands in Shark River Slough basin averaged 29 km (Fig. 2a). Hammocks, buttonwood forests and tree islands were

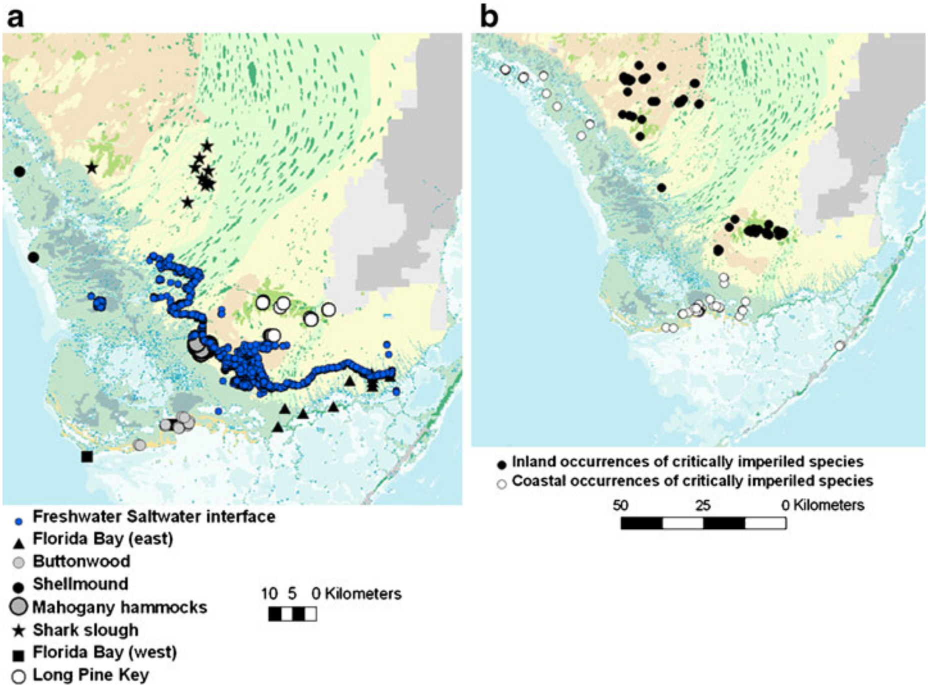


Fig. 2 **a** Study site locations in relation to Freshwater–Saltwater interface. **b** Distribution of critically imperiled species in the ENP in coastal and inland habitats

sampled immediately north of Florida Bay's shoreline. Hardwood and buttonwood hammocks north of western Florida Bay averaged 1.4 and 1.76 km from the coast, respectively, while tree islands north of eastern Florida Bay averaged 2.94 km from the coast. In addition, seven plots from discrete shell mounds along the coast of Gulf of Mexico (at the mean distance of 0.5 km from the coast) were included in the analysis.

Hardwood hammocks of ENP are dominated by tropical woody plants and rarely flood, as they are on higher ground (ridges) marshes, mangroves, and buttonwood forests (Armentano et al. 2002; Olmsted and Loope 1980). Shell mounds are hardwood hammocks created by Amerindians along the coasts of Florida, and have long been of interest to botanists due to their unusual floristic composition (Craighead 1971; Small 1927; Stalter and Kincaid 2004). Buttonwood forests occupy intermediate elevations and may have standing water in the rainy season (S Saha personal observations). Everglades National Park alone harbors 1000 ha of buttonwood forests on two nearly continuous ridges composed of calcitic marl overlain by a thin layer of organic detritus (Craighead 1971; Olmsted et al. 1981) and/or sediment deposited from Florida Bay during periodic hurricanes and tropical storms (Holmes et al. 2000); despite their abundance the biology of buttonwoods is poorly understood (Tomlinson 1980).

Coastal hammocks and buttonwood forests of Florida Bay experience tidal amplitude of ∼15 cm, while those off the Gulf of Mexico experience much greater amplitude, in the range of 100–200 cm (Doyle et al. 2010; Wanless et al. 1994). The lack of large tides along Florida Bay might be an important factor permitting the existence of these salinity-intolerant communities on low marl berms in eastern ENP.

We obtained published data on presence–absence of woody plants in tree islands within coastal wetlands adjoining eastern Florida Bay (100 m^2) from Meeder et al. (1996). For all other sites we used unpublished data collected by S. Saha and J. Sadle (Fig. 2a).

2.1.2 Seawater intrusion

We examined the groundwater salinity gradient created by saltwater intrusion from three independent sources—(1) Fitterman et al. (1999) resistivity studies, (2) salinity data from groundwater wells, and (3) reconstruction of groundwater salinity and depth to water table for all sampled plots based on the species-environment relationships derived from the Florida Keys (Ross et al. 1992).

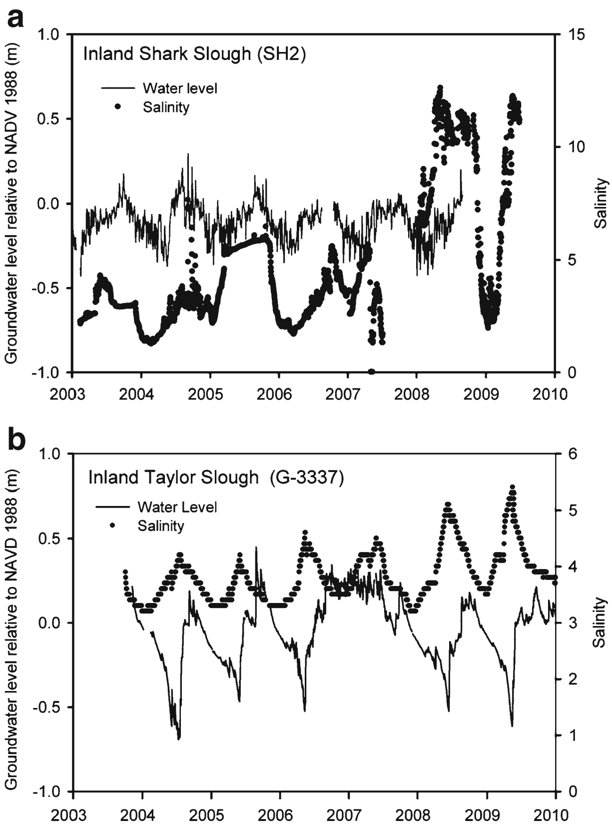
The freshwater–saltwater interface (FWSWI) was defined by Fitterman et al. (1999) as values of formation resistivity of less than 10 ohm-m as obtained from a resistivity survey of the Biscayne Aquifer across ENP. They found that the depth of the FWSWI varied from near the ground surface along the coastline to a depth of greater than 20 m at its most inland extent. The position of the FWSWI as determined by Fitterman et al. (1999) was plotted on a map. We obtained the map coordinates for locations that had resistivity around 10 ohm-m at a depth of 5–10 m (U.S. Department of Interior 2007) corresponding to maximum plant water uptake depth and plotted them to indicate the freshwater–saltwater transition zone as of 1999. Sampled hammock locations were then plotted in relation to the FWSWI contour (Fig. 2a).

Shallow groundwater (<4 m) salinity has been continuously monitored along the coastline at several United States Geological Survey (USGS) and ENP wells located in Shark and Taylor Sloughs from October 2003 until present. Groundwater salinity and water level data from those wells was obtained from (http://waterdata.usgs.gov) as well as directly from the USGS (Fig. 3a and b). These data were used to investigate temporal trends in saltwater intrusion as well as to contour the spatial extent of saltwater intrusion in 2009 (Fig. 4). In addition, we had a limited dataset on groundwater salinity and depth to water table from Long Pine Key (Villalobos 2010), one-time data from soil pits in coastal hardwood hammocks by Olmsted and Loope (1980), and in buttonwood hammocks by S. Saha (unpublished results).

To augment the salinity gradient insights gained from the limited number of groundwater wells, in the absence of an extensive well network, we employ the distance of hammocks from the coast as a proxy for the salinity gradient. The limited set of field data were then used to check the proxy. The distance of a hammock from the coast (hammock sampling mentioned above) is a qualitative indicator of underlying salinity because in general the salinity of groundwater decreases as distance from the coast increases (Fig. 4).

We also looked at the relationship between distance from the coast and underlying salinity from the perspective of plant species and communities occurring across the salinity gradient. As mentioned earlier, both groundwater salinity and depth to the water table can influence plant species composition via species-specific salinity and drought tolerances. These species-specific values were obtained during 1989–92 from Florida Keys forests whose composition overlapped with hardwood hammocks in ENP (Ross et al. unpublished data). In 1989–90, tree species density and basal area

Fig. 3 **a** Groundwater salinity (*black dots*) along with groundwater level (*black line*) at USGS site SH2 in Shark River Slough. **b** Groundwater salinity in parts per thousand (*black dots*) along with groundwater level (*black line*) at USGS site G-3337 in Taylor Slough



were determined in twenty-two 10 × 60 m plots, representing the broad spectrum of Keys forest vegetation. Ground water depth and salinity were sampled from the top of the water table monthly for three years using a refractometer (Ross et al. 1992). Abundance-weighted means for each species were calculated for both these parameters, using the relative basal area of each species in each plot as the weighting factor. We used these abundance-weighted salinity and depth to water table values for the constituent species from Ross et al. (1992) to obtain a site or a plot value for salinity and depth to water table for ENP plots by averaging across the constituent species per ENP site used in this study.

2.1.3 Data analysis

We performed detrended correspondence analysis (DCA) ordination to describe species composition based on presence–absence on data collected in 100 m^2 plots located all across ENP. Twelve plots each of Long Point Key, Mahogany and Buttonwood hammocks; sixteen plots at Florida Bay (east); four plots at Florida Bay (west); and seven plots each in tree islands of Shark River Slough basin and coastal shell mounds were sampled. Axis I of the DCA ordination was regressed against distance from the coast. Distance from the coast was also regressed against

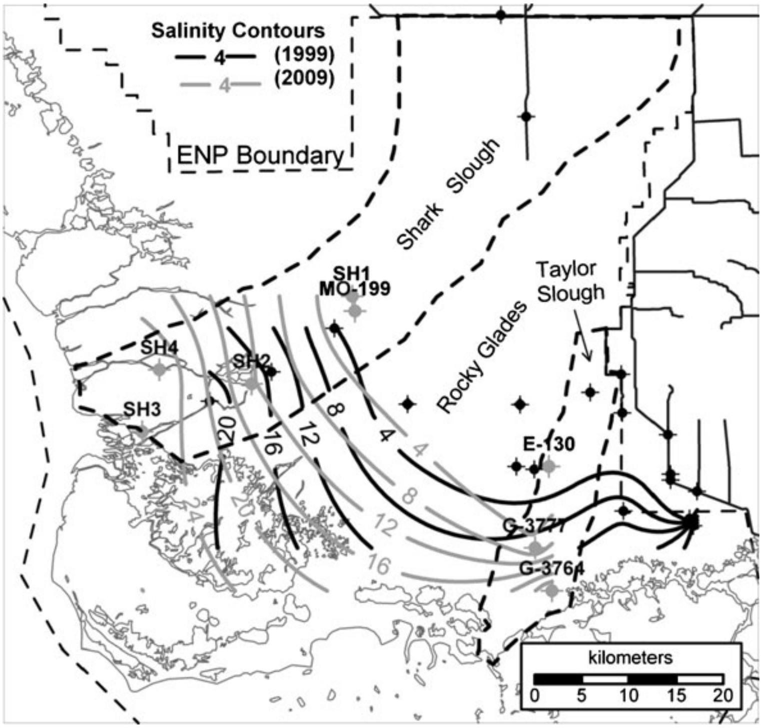


Fig. 4 Extent of saltwater intrusion in the Biscayne Aquifer on June 11–24, 1999 (*black contours*) and June 1, 2009 (*grey contours*). The contours are in increments of 4‰ and represent groundwater salinity at depth of less than 4 m (figure adapted from Price et al. 2003 and augmented with 2009 data from the USGS). *Black dots* represent wells sampled in 1999, while *grey dots* represent wells sampled in 2009

the respective reconstructed depth to water table and groundwater salinity with the expectation that the salinity would decrease as the distance from the coast increases, and the depth to water table would increase positively with distance from the coast. Two-way Indicator Species Analysis (TWINSPAN) was performed to characterize species distribution among study sites.

2.2 Modeling the effects of saltwater intrusion on coastal forests along the elevation gradient

To understand how Florida's coastal forests respond to sea level rise, we extended a previously published spatially explicit simulation model of hardwood hammocks and mangroves to include buttonwoods (see Sternberg et al. 2007 for description of parameters and model equations). The basic assumptions and model structure are similar to previous simulations of this model. The mangrove–hammock model (MANHAM) assumes that mangroves are better adapted to high salinity areas compared to glycophytic hammock species. At lower salinities, however, mangroves are out-competed by hammock species. Both vegetation types interact with the unsaturated soil (vadose zone) salinity by regulating their transpiration. Their respective transpiration and associated water uptake regimes have a feedback effect upon the vadose zone salinity, by driving different degrees of recharge of the vadose zone from the underlying saline water table to replenish the water absorbed by the plant. Thus, each vegetation type tends to promote local salinity conditions that favor their own establishment and maintenance. We extend this model to include a third community, buttonwood forests, with salinity tolerance intermediate to mangroves and hammocks.

Uptake of water as a function of salinity by hammocks and mangroves were described in detail in Sternberg et al. (2007). Here we add buttonwood to the model and propose the following empirical relation between buttonwood transpiration (R) and vadose zone salinity (Sv):

$$R = \frac{5.78}{2 + e^{0.15(\mathrm{Sv}-10)}}$$

The relationship between transpiration and salinity of buttonwoods is less sensitive to salinity compared to hammocks, but more sensitive compared to mangroves. Buttonwood is dominant in brackish water areas, whereas few coexist with mangrove at higher salinity levels (Urrego et al. 2009). To check this relationship, buttonwood leaf transpiration data measured with a porometer (Li-Cor 1600, Lincoln NE, USA) from two days in an on-going experiment growing buttonwood plants at four different salinity levels (0‰, 5‰, 15‰ and 30‰, S. Saha unpublished) were utilized.

In the model used by Sternberg et al. (2007), the rate of transpiration for both mangroves and hammocks at the salinity of 0 parts per thousand (‰) was 2.6 mm day^{-1}. For convenience, we use the same value of maximum transpiration for buttonwoods. Buttonwoods are known to tolerate some salinity, and show a decline in growth rate when transpiration is lower than 0.78~0.97 mm/day (Diaz et al. 2006), which corresponds to salinity around 20‰ in our empirical relation between buttonwood transpiration and vadose zone salinity (Fig. 4). In the field, buttonwood density is very low if the salinity is higher than 20‰, at sites where mangroves are dominant (Urrego et al. 2009). We assume that mangroves will replace buttonwoods when the 2-year running average of transpiration is less than 0.89 mm/day at salinity of 20‰. On the other hand, if salinity is <20‰, buttonwoods are maintained and will replace mangroves.

The revised MANHAM model was simulated in a grid-based system with 100 × 100 cells. Each cell (or pixel) represents a 1 m^2 segment within a landscape typical of Florida's coastal topography that increases in elevation at an average of 10 mm per meter (Sternberg et al. 2007; Teh et al. 2008). Each cell can be populated either by hammock species, buttonwood, or mangrove species. Initial conditions are set such that the cells are randomly populated with one of the above species. We expect that these communities will self organize into a typical spatial pattern observed in coastal Florida; i.e., hammocks species at the highest elevation, mangroves at the lowest elevation, and buttonwood forests 'sandwiched' between hammocks and mangroves. To investigate the effects of SLR, mean tidal heights and water table heights were assumed to increase 3 mm/year until they reached 100 mm above initial conditions. SLR simulations were run only after the vegetation structure reached equilibrium under initially constant sea level conditions.

2.3 Changes in species composition along an elevation gradient in coastal forests

Changes in abundance of common woody plant species in coastal forests along an elevational gradient were monitored in ENP's Coot Bay Hammock (25°12′24.13″N, 80°55′47.48″W), which borders Coot Bay and whose salinity is influenced by Whitewater Bay, to which it is directly connected. The salinity data suggest an increasing trend over time (data from hydrological station maintained by ENP). Coot Bay Hammock is an ideal study site because hardwood hammocks occur at the highest, and mangroves and coastal prairies occur at the lowest end of the gradient in elevation, while buttonwood dominated forests and mixed hammocks with buttonwood, manchineel (*Hippomane mancinella* L.), and Spanish stopper (*Eugenia foetida* Pers.) occupy intermediate elevation. The baseline data in the Coot Bay community complex were established in 1980, when depth to groundwater, elevation, and groundwater salinity were determined. Additional censuses were conducted in 1998 by Armentano et al. (2002) and in 2009 by K. Wendelberger and S. Saha.

We compare community composition across 1998–2009 for buttonwood forests, mixed-hammock, and hardwood hammock communities. Woody vegetation in buttonwood (0.6–0.7 m above msl), mixed hardwood hammocks (elevations 0.7–0.9 m), and hardwood hammocks (elevation 0.9–1.5 m) was inventoried in rectangular plots of 5 × 20 m. All plants <0.6 m tall were classified as seedlings, individuals >0.6 m and <2 cm diameter at breast height (DBH) were classified as saplings, and all individuals >2 cm DBH as adult trees. Three plots were established per community type. We compared the densities of dominant species in buttonwood, mixed hammocks, and hardwood hammocks between 1998 and 2009 to test if halophytes increased and glycophytes showed a decline, a pattern that would parallel the trend exhibited by increasing salinity of Whitewater Bay.

2.4 Rare species in coastal ecosystems of South Florida

We compiled data on all plant species ranked as critically imperiled in South Florida and known to be extant within different habitats of ENP (Table 1). Critically imperiled species were chosen as the suite of rare species for analysis because that ranking is based on quantitative information that considers both number of occurrences and number of total individuals in the South Florida floristic region defined by Gann et al. (2002). Occurrence data was obtained from Gann et al. (2010), herbarium specimens, and field observations (Sadle, unpublished data). Occurrences within ENP were defined as discreet groupings of rare plants separated by unsuitable habitat or by at least 1 km of suitable habitat. For example, observations of a critically imperiled plant species in two coastal hardwood hammocks separated by tidal swamp were considered two occurrences. Population estimates were compiled by combining estimates or counts recorded at each occurrence during field surveys between November 2005 and September 2010. Historical and extirpated species were excluded from the analysis. Life history traits of each species were included in the analysis when relevant to impacts of sea level rise.

Coastal habitats were divided or grouped into units based on similarities in relative elevation, soil type, and species composition. These habitats include beach dune, buttonwood hammock, coastal hardwood hammock, midden or shell mound, coastal

Table 1 Critically imperiled (sensu Gann et al. 2002) plant species that naturally occur in Everglades National Park

Species	Midden or shell mound	Buttonwood hammock	Coastal hardwood	Tidal swamp	Salt marsh	Coastal rockland hammock	Non coastal
Acacia tortuosa (L.) Willd.	X						
Adiantum melanoleucum Willd.							X
Anemia wrightii Baker							X
Basiphyllaea corallicola (Small) Ames							X
Bourreria cassinifolia (A. Rich.) Griseb.							X
Celtis iguanaea (Jacq.) Sarg.	X						
Cenchrus myosuroides Kunth					X		
Ceratopteris pteridoides (Hook.) Hieron.							X
Cheilanthes microphylla (Sw.) Sw.	X						
Chromolaena frustrata (B.L. Rob.) R.M. King & H. Rob	X	X	X				
Croton lobatus L.							X
Cyperus floridanus Britton ex Small	X						
Cyrtopodium punctatum (L.) Lindl.		X			X		X
Desmodium lineatum DC.							X
Digitaria pauciflora Hitchc.							X
Eltroplectris calcarata (Sw.) Garay & H.R. Sweet	X						X
Exostema caribaeum (Jacq.) Schult.						X	
Galeandra bicarinata G.A. Romero & P.M. Br.							X
Helenium flexuosum Raf.							X
Hypelate trifoliata Sw.						X	X
Ionopsis utricularioides (Sw.) Lindl.				X			

Table 1 (continued)

Species	Midden or shell mound	Buttonwood hammock	Coastal hardwood	Tidal swamp	Salt marsh	Coastal rockland hammock	Non coastal
Kosteletzkya depressa (L.) O.J. Blanch. et al.		X	X				
Lomariopsis kunzeana (Underw.) Holttum							X
Malachra urens Poit.	X	X	X				
Najas wrightiana A. Braun							X
Oncidium ensatum Lindl.							X
Passiflora sexflora Juss.							X
Pavonia paludicola Nicolson ex Fryxell	X			X			
Pecluma plumula (Humb. & Bonpl. ex Willd.) M.G. Price							X
Peperomia humilis A. Dietr.		X					
Ponthieva brittoniae Ames							X
Scirpus robustus Pursh					X		
Spiranthes costaricensis Rchb. f.							X
Sporobolus compositus (Poir.) Merr.							X
Tephrosia angustissima var. *corallicola* (Small ex Rydb.) Isely	X						
Thelypteris reticulata (L.) Proctor							X
Thelypteris serrata (Cav.) Alston							X
Trichocentrum undulatum (Sw.) Ackerman & M.W. Chase		X		X			
Trichostigma octandrum (L.) H. Walter	X						
Vallesia antillana Woodson	X						
Vanilla phaeantha Rchb. f.				X			
Wolffiella oblonga (Phil.) Hegelm.							X
Xylosma buxifolia A. Gray							X
Total in each habitat	11	6	3	4	3	2	24

rockland hammock, salt marsh, and tidal swamp (mixed mangrove). Buttonwood and coastal hardwood hammock habitats occur on slightly elevated marl soils as a relatively linear band along the northern coast of Florida bay. Middens and shell mound habitats comprise of elevated anthropogenic landscape features found sporadically along the entire Everglades coast and support mixed upland tropical hardwood species. Coastal rockland hammock habitat is restricted in ENP to Key Largo, occur on elevated limestone, and are comprised of mixed tropical hardwood species. Salt marsh includes low elevation, open, saline habitats dominated by grass species or shrubs such as Batis (*Batis maritima* P. Browne). Tidal swamp habitat includes single species or mixed mangrove forests on peat soils that are found throughout the coastal Everglades. All non-coastal habitats were classified as other.

Extrinsic threats such as climate change and intrinsic life-history traits can be integrated to derive species extirpation risk (Freville et al. 2007). Here we use quantitative data on occurrences and population size and categorical data on distribution (habitat and extent), and observations on life history traits to predict the relative risk of extirpation for each species from sea level rise. Critically imperiled species that did not occur in any of the coastal habitats were excluded from the risk assessment. Species with a single occurrence were considered more vulnerable than species with more than one occurrence regardless of the total number of plants at any one occurrence. Population size was divided into three relative risk categories based on similarities in population size between groups of species. Species with less than 500 individuals were considered high risk, species with 500–1,000 individuals were considered moderate risk, and species with greater than 1000 individuals were considered low risk. Species with an entirely coastal distribution in ENP were considered more vulnerable than those that occurred in both coastal and inland habitats.

Habitat vulnerability was predicted by combining relative elevation with the ability of that habitat to migrate. Tidal swamp and salt marsh are both low elevation, but the ability of these communities to migrate suggests they are at low risk of loss. The remaining habitats are considered stationary in the landscape due to their occurrence on isolated, elevated geologic features. These habitats were ranked as higher risk than tidal swamp and salt marsh. Within fixed habitats, those at lower elevations were considered to be a greater risk than higher elevation sites. Coastal rockland hammock (3 m) and midden or shell mound habitats (1–5 m reported in Schwadron 2010) were considered to be less vulnerable than buttonwood hammock (0.75–0.85 m reported in Olmsted and Loope 1980) and coastal hardwood hammock (0.85–1 m reported in Olmsted and Loope 1980).

Epiphytic species were considered less vulnerable than terrestrial plants because they are not directly impacted by salinization of the vadose zone. Salt tolerant species were considered to be less vulnerable than plants that are salt intolerant or with unknown salt tolerance.

A whole number value (0, 1, or 2) was assigned to each risk category. Higher values were given to factors with greater relative risk to sea level rise. Relative risk values for habitat were averaged when a species occurred in more than one habitat. Each critically imperiled species was scored for each factor. Numerical scores were created for each species by summing all its risk scores for each category (Table 2).

Table 2 Relative vulnerability of rare species to impacts of sea level rise

Species	Epiphyte	Salt tolerance	Habitat vulnerability	Number of occurrences	Number of individuals	Coastal only	Sum
Celtis iguanaea (Jacq.) Sarg.	1	1	1	1	2	1	7
Exostema caribaeum (Jacq.) Schult.	1	1	1	1	2	1	7
Peperomia humilis A. Dietr.	0	1	2	1	2	1	7
Vallesia antillana Woodson	1	1	1	1	2	1	7
Acacia tortuosa (L.) Willd.	1	1	1	0	2	1	6
Cheilanthes microphylla (Sw.) Sw.	1	1	1	0	2	1	6
Eltroplectris calcarata (Sw.) Garay & H.R. Sweet	1	1	1	1	2	0	6
Hypelate trifoliata Sw.	1	1	1	1	2	0	6
Tephrosia angustissima var. *corallicola* (Small ex Rydb.) Isely	1	1	1	1	1	1	6
Trichostigma octandrum (L.) H. Walter	1	1	1	0	2	1	6
Cyperus floridanus Britton ex Small	1	1	1	0	1	1	5
Ionopsis utricularioides (Sw.) Lindl.	0	1	0	1	2	1	5
Vanilla phaeantha Rchb. f.	0	1	0	1	2	1	5
Chromolaena frustrata (B.L. Rob.) R.M. King & H. Rob	1	1	1.67	0	0	1	4.67
Cenchrus myosuroides Kunth	1	0	0	0	2	1	4
Cyrtopodium punctatum (L.) Lindl.	0	1	1	0	2	0	4
Kosteletzkya depressa (L.) O.J. Blanch. et al.	1	0	2	0	0	1	4
Trichocentrum undulatum (Sw.) Ackerman & M.W. Chase	0	1	1	0	1	1	4
Malachra urens Poit.	1	0	1.67	0	0	1	3.67
Pavonia paludicola Nicolson ex Fryxell	1	0	0.5	0	1	1	3.5
Scirpus robustus Pursh	1	0	0	0	0	1	2

Higher scores indicate greater risk. Scores were assigned as follows: epiphytic plant = 0, terrestrial = 1; salt tolerant = 0, salinity tolerance low or unknown = 1; Salt marsh and tidal swamp = 0, hardwood hammock and shell mound/midden = 1, buttonwood hammock = 2; more than 1 occurrence = 0, single occurrence = 1; and population size greater than 1000 = 0, between 500 and 1000 = 1 and less than 500 = 2

3 Results

3.1 Species composition

Distance from the coast explained the distribution of woody species based on presence–absence data and also indicated whether the groundwater was fresh or brackish. DCA Axes I and II explained 52% and 13% of variation in hammock species composition (Fig. 5a). DCA Axis I was significantly correlated with distance from the coast ($r^2 = 0.46$, $P < 0.05$).

The significant variation in salinity across sites in the ENP was related to distance from the coast by a polynomial relationship (Fig. 5b) whereby salinity decreased linearly with distance from the coast up to a point ($\mathit{Salinity} = 15.05 - 0.15 \times x + 0.0011 \times x^2 + 0.00005 \times x^3$, $r^2 = 0.49$, $P < 0.001$). Depth to groundwater (Fig. 5b) increased linearly with distance from the coast ($\text{Depth to water table} = 79.43 + 1.89 * x$, $r^2 = 0.47$, $P < 0.001$). Depth to water table per plot, derived by averaging species optima from the Florida Keys, closely resembled the actual depth to water table measured by piezometer and by using soil pits. For example, we derived a mean depth to water table of 81–147 cm for LPK hammocks, which resembled the piezometer water depth measurement of 101–187 cm (Villalobos 2010). Similarly, the species weighted depth to water table ranging from 45–79 cm for buttonwood forests

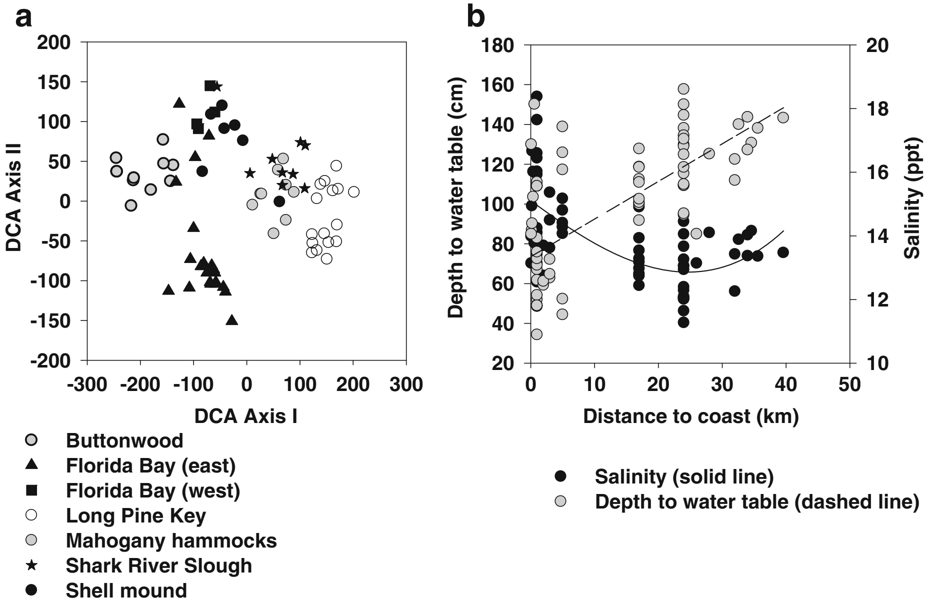


Fig. 5 **a** DCA ordination showing plots in species space. Buttonwood forests are the furthest from Long Pine Key hammocks. Lower panel plots (distance from the coast against salinity and depth to water table. **b** As the distance from the coast increases, so does the depth to water table while the salinity decreases. The relation is polynomial for salinity and distance from the coast ($\text{Salinity} = 15.05 - 0.15 \times x + 0.0011 \times x^2 + 0.00005 \times x^3$, $r^2 = 0.49$, $P < 0.001$), and linear for depth to water table and distance from the coast ($\text{Depth to water table} = 79.43 + 1.89 \times x$, $r^2 = 0.47$, $P < 0.001$)

resembled the water table depth of 23–70 cm obtained with soil pits at buttonwood forests in early dry season.

The DCA ordination clearly separates two categories of plant communities. To the extreme right are the plots from LPK, Shark River Slough and mahogany hammocks, which are furthest from the coast, while plots in buttonwood forests, which lie south of the FWSWI and are closest to the coast, constitute the other extreme of the continuum (Fig. 5a). Mahogany hammocks occur at the cusp of FWSWI, and are closest in species composition to the hammocks in LPK. Tree islands of Shark River Slough basin were intermediate in species composition between mahogany hammocks and coastal hardwood hammocks of the shell mounds and of sites north of Florida Bay (east and west). Coastal forests occupying intermediate locations along the continuum in distance from the coast also showed two distinct groups. Hardwood hammocks located in shell mounds and north of eastern and western Florida Bay were distinct from the tree islands located in eastern Florida Bay region (Fig. 5a).

Level 1 division of TWINSPAN separated hammocks into two categories: hammocks occurring south of FWSWI fell into one category, while the hammocks at the cusp of FWSWI and north of the FWSWI, along with the shell mounds at the periphery of the Shark River Slough basin, were classified into a freshwater category (eigenvalue = 0.53). The Level 1 division also discerned three groups of species based on their distribution. Of 70 species, 14 occurred in sites exclusively south of FWSWI, 16 were exclusively found in hammocks north of FWSWI, and 7 species occurred in the majority of sites both north and south of FWSWI. Species occurring in the hardwood hammocks north of FWSWI with fresh groundwater were: *Calyptranthes zuzygium* Griseb., *Lysiloma latisiliquum* (L.) Benth., *Ocotea coriacea* (Sw.) Britton, *Prunus myrtifolia* (L.) Urb., *Quercus virginiana* Mill., *Sideroxylon* salicifolium (L.) Lam., and *Simarouba glauca* DC. Species occurring only at locations south of FWSWI with brackish to saline groundwater were: *E. foetida, Capparis flexuosa* (L.) L., *H. mancinella* (Manchineel), *Piscidia piscipula* (L.) Sarge., *Pithecellobium keyense* Britton ex Britton & Rose, *R. mangle*, and *Sideroxylon celastrinum* (Kunth.) T.D. Penn. Examples of cosmopolitan species that occur at all sites including the north, south, and cusp of FWSWI, and in the buttonwood forests as well are: *Coccoloba diversifolia* Jacq., *C. erectus*, *Erythrina herbacea* L., *Metopium toxiferum* (L.) Krug & Urb., *Randia aculeata* L., *Rapanea punctata* (Lam.) Lundell, and *Sabal palmetto* (Walter) Lodd ex Schult. & Schult. f. The FWSWI boundary does not extend northwards along the west coast of ENP where shell mounds are located; however, we assume that the water table in the shell mounds is saline due to their intimate proximity with the coast and tidal inlets.

3.2 Extent of seawater intrusion

The maximum extent of seawater intrusion (shallow groundwater well (<4 m) data for June 1, 2009) did not differ substantially from June 1999 as depicted by the 4‰ salinity contour lines in the Shark River Slough region (Fig. 4). However, inspection of daily salinity data from the Shark River Slough site SH2, located in the sawgrass marsh– mangrove transition zone, indicated that the trend in maximum groundwater salinity in that region has been variable over the last 7 years. Low values of salinity (between 2‰ and 5‰) were recorded at SH2 in 2003–2004, but then increased through the years to a high value near 12‰ in 2009 (Fig. 3a). Likewise, in Taylor

Slough, there appears to be no significant shift in the landward extent of seawater intrusion between 1999 and 2009, as indicated by the 4‰ salinity contour lines (Fig. 4). However, a general increase in salinity from 3.9‰ to above 5‰ was observed in the Taylor Slough groundwater well G-3777 between 2003 and 2009 (Fig. 3b).

3.3 Transpiration, salinity and model simulations

Preliminary data from the ongoing experiment indicates that buttonwood plants grown under higher salinity conditions had lower transpiration than plants grown under lower salinity conditions (Fig. 6a). The model equation predicting transpiration from salinity fits well with these measured transpiration values (Fig. 6b).

In the simulations, under stable environmental conditions, hardwood hammocks occupied the higher elevation cells, mangroves occupied the lower elevation cells, and buttonwood woodland occupied the landscape between hammocks and mangroves (Fig. 7a). There exists a clear, sharp boundary between buttonwoods and mangroves, except for some mangroves scattered in the buttonwood woodland, which is similar to the hammock/mangrove ecotone described in Sternberg et al. (2007). The presence of mangroves in a more glycophytic community can be explained by observations that mangroves have a greater tolerance to salinity and are able to utilize low salinity water as well as the high salinity water lethal to both buttonwoods and hammock species (Sternberg and Swart 1987). Buttonwood

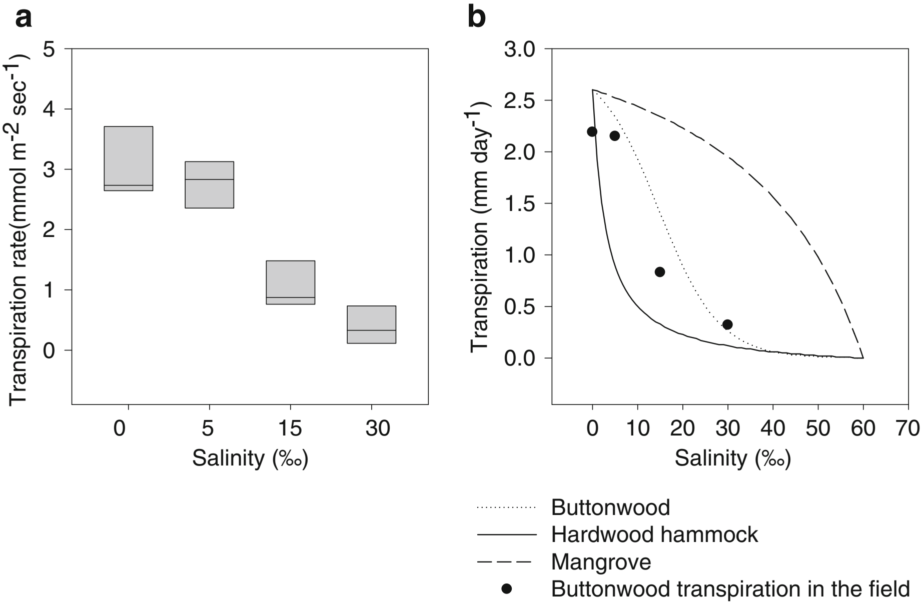


Fig. 6 **a** Transpiration rate of buttonwoods grown at 4 different salinity treatments (A: 0‰, B: 5‰, C: 15‰ and D: 30‰). **b** Model output of transpiration (mm/day) of mangrove, buttonwood, and hardwood hammock as a function of vadose pore water salinity while the circles denote model predictions using actual transpiration data

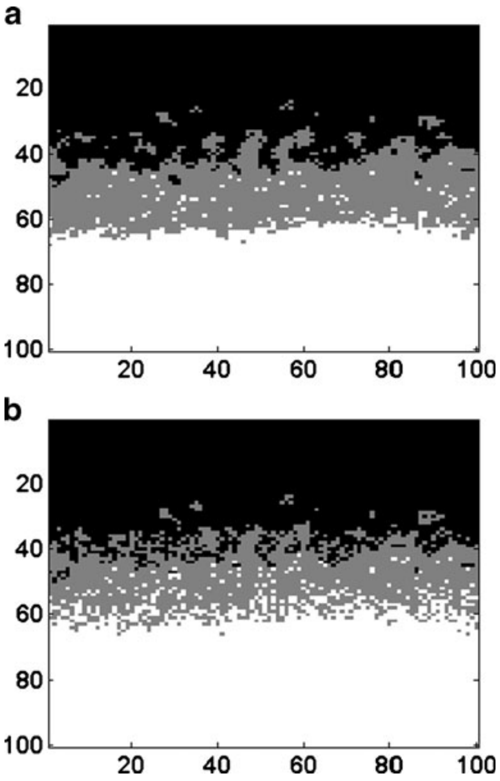


Fig. 7 **a** Horizontal view 100×100 m^2 grid cells showing distribution of mangrove (*white*), buttonwood (*grey*) and hammock (*black*) 33.3 years after stable pattern formed without sea level rise, and **b** subject to sea level rise 3 mm/year. In these two graphs, upper *x* axis depicts inland side while lower *x* axis the seaward side

and hammock species can coexist in certain areas, with hammock aggregates in buttonwood woodland or vice versa (Fig. 7a).

As sea level rises at a rate of 3 mm/year for about 33.3 years, the original buttonwood dominated areas are replaced by mangroves (Fig. 7b). This invasion does not occur as a solid front, but rather by fragmentation of the original buttonwood stand. Similarly, buttonwood invades the hammock area as individuals and small aggregates, not as a solid front. Overall, during sea level rise the buttonwood forest is squeezed out of the intermediate salinity niche between mangroves and hammocks. Buttonwood frequency decreases from 26.3% before sea-level rise to 19.9% after an increase in sea level of 100 mm.

3.4 Changes in species composition over a decade

3.4.1 Buttonwood forests

Results from a Mann–Whitney test indicate that the buttonwood trees did not exhibit differences in density (number of individuals per 100 m^2) between 1998 and 2009 (9 and 10.00, $P = 0.448$, Fig. 8a). White mangrove tree (1 and 4.00, $P = 0.04$, Fig. 8a) and sapling density increased significantly from 1998 to 2009 (1 and 11, $P = 0.032$, Fig. 8a). Buttonwood saplings did not show any change between years (3 and 2, $P = 0.245$, Fig. 8a). Buttonwood and white mangrove seedling (were absent from

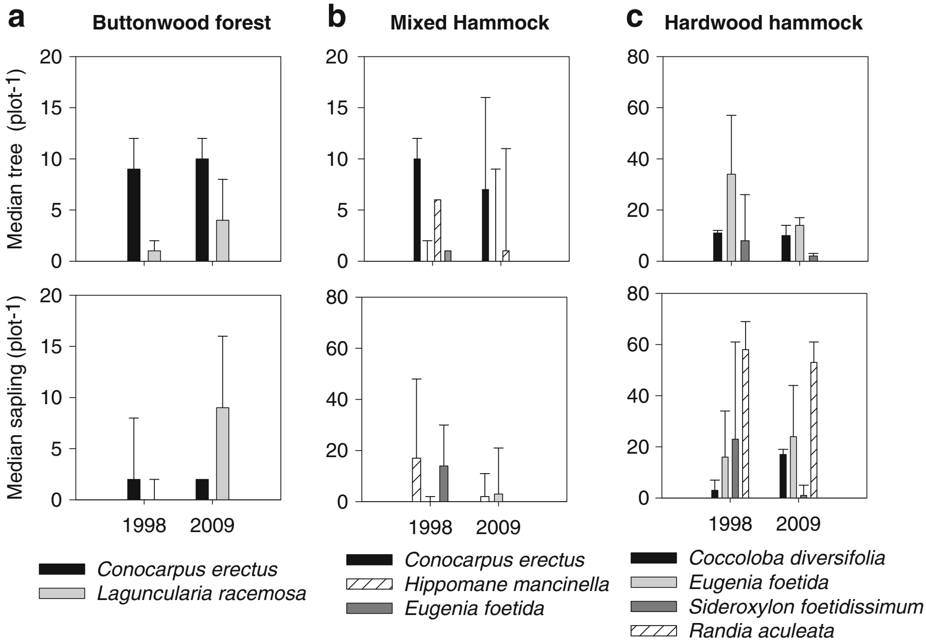


Fig. 8 Changes in densities of adult trees and saplings from 1998 to 2009 in a coastal complex of **a** buttonwood forests, **b** buttonwood–hardwood (mixed) hammocks, and **c** hardwood hammocks in Everglades National Park

the buttonwood forest understory during both censuses. Density of *B. maritima*, a halophyte, significantly increased from 1998 to 2009 (18 and 39, $P = 0.042$), while *Sarcocornia perennis* (Mill.) A.J. Scott densities decreased from 1998 to 2009 (27 and 11, $P = 0.05$), and *C. flexuosa* showed no change (0 and 0, $P = 0.30$).

3.4.2 Mixed buttonwood and hardwood hammock

Significant changes were observed in hardwood *E. foetida* tree density, which was lost from the canopy in 2009 (1 to 0, $P = 0.048$; Fig. 8b) while white mangrove showed an increase from 1998 to 2009 (1 and 3.00, $P = 0.04$; Fig. 8b). *H. mancinella* (5 and 3.00, $P = 0.07$) and buttonwood (9 and 8, $P = 0.42$) densities were comparable across years.

Sapling density of *H. mancinella* (17 and 2, $P = 0.029$), *E. foetida* (14 and 0, $P = 0.043$), and *C. flexuosa* (18 and 0, $P = 0.027$) decreased significantly from 1998 to 2009 (Fig. 8b) and that of white mangrove increased (0 and 3, $P = 0.046$; Fig. 8b). Seedlings of *B. maritima* in mixed hammocks increased significantly (3 and 54, 0.049), *S. perennis* showed a marginally non-significant increase (0 and 6, $P = 0.059$), and *H. mancinella* seedling densities were comparable between years (1 and 0, $P = 0.15$).

3.4.3 Hardwood hammock

No halophytic plants were observed in either of the two censuses. Some changes or reshuffling of rank-order occurred among years. *E. foetida* was more common in 1998 than 2009 (34 and 14, $P = 0.048$, Fig. 8c), density of *C. diversifolia* did not change significantly between 1998 and 2009 (11.00 and 10.00, $P = 0.083$, Fig. 8c). *Sideroxylon foetidissimum* Jacq., the third most common tree in 1998, declined significantly in 2009 (8 and 2, $P = 0.038$, Fig. 8c).

Common species in the sapling cohort showed reshuffling of ranks similar to adult trees. Saplings of *R. aculeata* (58 and 53) and *E. foetida* (16 and 24) were comparable across years, while *S. foetidissimum* densities were significantly lower in 2009 (23 and 1, $P = 0.011$). Saplings of *C. diversifolia* showed a significant increase in density from 1998 and 2009 (3 and 24, $P = 0.02$, Fig. 8c). Seedlings of *E. foetida* (59 and 42, $P = 0.037$) and *R. aculeata* (5 and 1, $P = 0.047$) decreased from 1998 to 2009, and those of *Ardisia escallonioides* Schiede & Deppe ex Schltdl. & Cham. remained the same.

3.5 Rare species

Forty-three critically imperiled species are currently extant in ENP, 21 (49%) of which occur in the coastal habitats defined in this paper (Table 1). Three of the 21 coastal species are also found in inland habitats, whereas the remaining 18 are found exclusively in coastal habitats. We report 54 occurrences of critically imperiled species in the coastal habitats of ENP (Fig. 2b). These are largely restricted to buttonwood and coastal hardwood hammocks of central ENP, middens and shell mounds throughout the park, and coastal rockland hammocks on Key Largo (Fig. 2b).

Number of species per habitat ranged from 0 (beach dune) to 11 (midden and shell mound). Seven species are found only on shell mound or midden habitat and four species are found only in buttonwood and coastal hardwood hammock habitats. Five species occur as epiphytes in coastal systems, 12 are herbs or shrubs, and 4 are trees. Number of occurrences ranged from 1 to 9 and population size ranged from 1–10,000.

Relative risk scores ranged from 2–7 with 4 of the 21 species ranked at the highest score (Table 2). All four of the species with the highest score had population sizes of less than 500 and were restricted to a single occurrence. Habitat for the species with the highest calculated risk included shell mound or midden, buttonwood hammock, and coastal rockland hammock. Both epiphytic and terrestrial species were included in this group. All of the highest ranked species were restricted to coastal habitats within ENP and were not also found in inland communities. Number of occurrences was the single factor common to the lowest ranked species. All species with a score of 4 or less (lowest 7 species) had more than one occurrence. Habitat for this group of species includes buttonwood hammock, coastal hardwood hammock, shell mound or midden, salt marsh, and tidal swamp.

4 Discussion

4.1 Species composition and freshwater availability: coastal hardwood hammocks on the brink

This study examines patterns of species composition in hardwood hammocks throughout the coastal and inland ENP with respect to the underlying salinity gradient caused by saltwater intrusion. Studies describing patterns of species distribution in tree islands and hardwood hammocks of ENP have invoked elevation-driven flooding and disturbance, especially fire (Armentano et al. 2002; Gunderson 1994; Olmsted and Loope 1984) as a primary mechanism. Ours is a novel approach, which highlights the role of drought resulting from salinity stress in explaining distribution of woody plants in ENP.

Our ordination analysis indicated a distinction between two main habitats: one with saline groundwater occurring to the south or seaward of the FWSWI (defined as the limit of the saltwater intrusion at <5 m depth), and the other with fresh groundwater lying to the north of the FWSWI. Although both habitats share several tree and shrub species, 20% are exclusive to inland hammocks and 22% are exclusive to coastal hammocks and buttonwood forests. Plots in Shark River Slough basin are an exception, harboring a few coastal species that are absent from locations north of FWSWI. The presence of coastal species in Shark Slough is hypothesized to be anthropogenic. Virtually all Shark River Slough tree islands contain aboriginal middens, and movement of plants may explain disjunct coastal species in this area (Schwadron 2010). Tidal seawater inflow along the rivers draining Shark River Slough increase salinity values inland, suggesting that the effective distance from the coast is actually less than the values used here. These two aspects of Shark River Slough tree islands may have resulted in the polynomial relationship between distance from the coast and salinity.

Similar patterns of species distribution in relation to groundwater and salinity occur in coastal forests of the Florida Keys, albeit within a smaller area and more fragmented in relation to ENP. Distribution of tree species in the Florida Keys is not homogeneous across all islands, and can be distinguished based upon the presence or absence of freshwater lenses. For example, species like *C. zuzygium*, *S. glauca*, and *O. coriacea*, which are limited to freshwater hammocks in the Everglades, are absent or rare in small low-lying islands of the Florida Keys (Gann et al. 2008) where freshwater lenses are poorly developed, such as Little Torch Key and Sugarloaf Key (Meadows et al. 2004). On the other hand, large islands like Key Largo, Big Pine Key, and Key West have deeper freshwater lenses, which may turn brackish but sustain tropical hammock vegetation (Kruse et al. 2000; Langevin et al. 1998), including species restricted to sites where fresh groundwater occurs. Thus it was not surprising to find that the same species occurring in ENP hammocks sort themselves in relation to distance from the coast, which is correlated to depth to water table and salinity of water table.

Distance from the coast explained the distinction between buttonwood forests harboring salt-tolerant species from the inland hammocks and tree islands but did not explain the entire pattern. Coastal plant communities such as coastal hardwood hammocks, though closer to saline water of the Florida Bay and Gulf of Mexico, were comparable to buttonwood at intermediate locations along DCA Axis I. Here we postulate that tolerance to drought generates the observed pattern of species distribution in relation to distance from the coast, with species occurring on the coast at higher elevation compared to buttonwood forests and mangroves, are better competitors in an environment where seasonal droughts, caused by shortage of freshwater, or physiological drought, caused by brackish-saline water, are common. Cosmopolitan species, occurring in both coastal and inland sites, are able to tolerate seasonal and physiological drought, or alternatively, exhibit plasticity in rooting depths (Armas et al. 2010). Deep rooting among glycophytes is not an option in coastal sites, due to their intolerance of brackish-saline groundwater (Ewe 2001).

The degree of drought tolerance demonstrated by the trees of inland hardwood hammocks reflects their location along a water availability gradient, from year-round (Shark River Slough) to seasonal (Long Pine Key). Accordingly, hardwood hammocks in Shark River Slough have more evergreen species, while the hammocks in Long Pine Key experience significantly greater water stress and are more drought-deciduous, with greater regulation of stomatal conductance (Saha 2009). It is yet to be documented how the hardwood species of coastal hammocks, especially those restricted to coastal sites, respond to drought. Trees in coastal uplands (such as hammocks) have the ability to access pockets of fresh water, and can tolerate only mild salinities up to 5‰ (Sternberg and Swart 1987). *S. palmetto*, a common palm of coastal hammocks, tolerates salinity up to 8‰ without showing decline in photosynthetic rates (Perry and Williams 1996). Initial responses to increase in salinity might trigger responses similar to drought, while prolonged exposure may lead to irreversible toxicity caused by accumulation of salts (Munns 2002). For example, declines in the density of the hardwood obligate cactus *Pilosocereus polygonus* (Lam.) Byles & G.D. Rowley in the Florida Keys were linked to soil salinity in the Florida Key's hammocks (Maschinski et al. 2009). A comparison of ecological factors that may have contributed to mortality of plants in a Lower Keys population between 1994 and 2007 revealed that salinity was 1.5 times greater near dying and dead plants than near live plants. One population that experienced 95% plant mortality had significantly lower elevation (0.3 m) and 27% less canopy cover than an adjacent population, which experienced only moderate mortality (20% plants; Maschinski et al. 2009).

We predict that with rise in sea level the coastal hardwood communities, especially those on the coast of Florida Bay, will be pushed to the edge of their drought tolerance and eventually collapse (Fig. 2b). The pathway of hammock collapse will be via the decrease in freshwater recharge volume or shrinking of the vadose zone due to rising water table; this is different from the increases in tidal flooding documented by Williams et al. (1999) in the hydric hammocks of Florida's Gulf Coast. The results of this study are relevant for the hardwood hammocks of the Florida Keys as well, where decline in pines and pine ecosystems are already underway (Ross et al. 1994, 2009).

4.2 Salinity gradient and changes in species composition

Groundwater salinity shows an increasing trend over time in both Shark and Taylor Sloughs (Fig. 3a, b) between salinity in the tidally-influenced Shark River Slough do not correspond to the lowest water levels; this may signify that both groundwater salinity and water levels are more affected by seawater intrusion. This difference in salinity regimes between Shark and Taylor sloughs, the major drainages of the Everglades, likely contributes to the differences in plant community types present.

The extent of seawater intrusion also varied interannually as suggested by long-term groundwater salinity records in the region. Between 1999 and 2003, the seawater front receded coastward, while from 2003 to 2009 the seawater front has migrated inland to a position similar to that observed in 1999. There may have been a slight seawater shift in the extent of seawater intrusion in Taylor Slough between 1999 and

2009, as indicated by the 4‰ salinity contour lines (Fig. 4). However, the difference between the well depths used in 1999 (<25 m) and 2009 (<4 m) may explain the apparent shift as seawater intrudes into a coastal aquifer at an angle, with the extent of seawater intrusion occurring further inland, deeper in the aquifer.

Interannual variation in precipitation and water management is transmitted into annually varying freshwater flows, which together with interannual variability in sea level rise then lead to annually varying salinity. Thus, a plant community may face different salinity regimes (both salinity levels and duration) in different years. The back-and-forth variation, however, will not necessarily induce an equivalent back-and-forth oscillation in distribution of plant communities based on salinity-intolerance, because a salinity-intolerant plant when faced with saline conditions for as little as a few weeks can become water stressed. Saline conditions persisting over an entire season can fatally stress the plants, permitting colonization by more salinity-tolerant species, thereby leading to an irreversible composition change even if the salinity is lower over the subsequent 2–3 years before increasing again.

Several Everglades wetlands have turned saline over time, including Whitewater Bay, as indicated by temporal increases in salinity. Results from observational studies conducted in Coot Bay hammock show increases in halophyte densities at the expense of glycophytes, and model simulations resonate with reports of saltwater intrusion and erosion leading to changes in species composition among coastal uplands elsewhere. Mixed hammocks at higher elevation witnessed a significant increase in halophytes such as white mangrove and *B. maritima* and a steep decline in *H. mancinella* (a glycophyte). In hardwood hammocks, *S. foetidissimum* declined, while the density of cosmopolitan *C. diversifolia* increased. Using historical aerial photographs, Barry (2009) documented vegetation change between 1940 and 2007 in Ten Thousand Islands National Wildlife Refuge (TTINWR). They reported a decline in shell mound habitat from 45 ha in 1940 to 39 ha in 2007 as a result of peripheral buttonwood die-off and replacement by mangroves.

4.3 Buttonwood forest is a vulnerable ecosystem

Our findings suggest that buttonwood forests are vulnerable to sea level rise. Comparison of forest plots over a period of 11 years shows an increase in numbers and proportion of halophytes, while glycophyte adults have not increased, and in some cases decreased with no recruitment. The density of white mangrove increased in buttonwood forests, while buttonwood tree density remained the same. Vast stands of buttonwood-dominated coastal forests occurred historically in South Florida (Craighead 1964; Olmsted et al. 1981). Saltwater intrusion has implications for continued existence of buttonwood-dominated plant communities and the rare species associated with these communities.

DeSantis et al. (2007) and Williams et al. (1999) documented rapid changes in understory in response to sea level rise, as the tree seedlings and saplings in hydric hammocks showed greater susceptibility to salinity than adults. Our data indicate that such a change in the coastal forest complex of ENP may have already begun, and this situation warrants careful monitoring of species-specific responses to salinity and changes in flooding regime.

Using the framework outlined in a model (Sternberg et al. 2007; Teh et al. 2008), we show that buttonwood forests at intermediate salinity and elevation could exhibit fragmentation and decline in cover because of saltwater intrusion. Simulations generate a sharp boundary between buttonwoods and mangroves, except for some mangroves scattered in buttonwood forests, which is similar to the hammock/ mangrove ecotone described in Sternberg et al. (2007). Mangroves have a large range of salinity tolerance and are able to utilize and thrive in high salinity, which is lethal to both buttonwoods and hammocks (Sternberg and Swart 1987). Buttonwoods and hammocks can coexist in certain areas, with hammock species aggregating in buttonwood forests (Fig. 7a). Positive correlations between plants and environments are believed to be one of the mechanisms for aggregation (Pielou 1960). The buttonwood/hammock boundary occurs at a higher elevation, where tidal flux cannot reach even after an increase in sea level of 100 mm. The vadose zone pore water salinities in these areas are only affected by infiltration of saline ground water. We have previously observed that the sustenance of hammocks may be due to their remarkable ability to harvest rainfall water retained in the highly organic soil layer (Saha et al. 2009) and as modeled here, cease transpiration when this water is no longer available. This occurs even when the underlying water table is saline (Ish-Shalom et al. 1992). Therefore, we propose here that the squeezing of buttonwood woodland by sea level rise is caused by ability of hardwood hammocks to utilize entrapped rainwater, lower their transpiration during the dry season, and thereby resist the invasion of buttonwoods.

4.4 Implications for rare species

Coastal wetlands and uplands provide essential habitat for nearly half of the critically imperiled plant species in Everglades National Park. Loss or degradation of these habitats directly resulting from sea level rise or in combination with diversion of freshwater flow, hurricanes, and exotic plant species infestations will result in the reduction or loss of rare plant populations. Sea level rise impacts are expected to occur before actual flooding from ocean water occurs, leaving a relatively short window of opportunity for study of these species and implementing potential mitigation actions.

All of the coastal uplands that support rare plant species in ENP are restricted to relatively immobile geologic features separated by large expanses of flooded, inhospitable wetland, leading us to conclude that these habitats will not be able to migrate as sea level rises. Tidal swamp and salt marsh, on the other hand, are wetland communities that occur in large expanses, and are capable of migrating toward the interior in low-lying south Florida, unless they are prevented from doing so by roads, levees, or other human infrastructure. Rare plant species in these habitats may be able to migrate with their respective communities. Groundwater impacts predicted for buttonwood hammocks and coastal hardwood hammocks also apply to other coastal upland communities in ENP and their constituent imperiled species. Salinization of groundwater in these communities will take longer due to their higher elevation but will nonetheless occur in time.

Based on the risk assessment carried out for this study, the impacts of sea level rise on rare plant species in ENP will have the largest effect on imperiled taxa with few occurrences and small population sizes that do not also occur inland. Upland species were identified as more vulnerable than wetland species. The most vulnerable species were not all from a single plant community due to the extreme rarity of some species on shell mound or midden habitat (*Celtis iguanaea* and *Vallesia antillana*), buttonwood hammocks (*Pepromia humilis*), and coastal rockland hammocks (*Exostema caribaeum*). Therefore, focusing studies or conservation measures on upland species in general may provide greater overall benefit to the suite of coastal rare species in ENP compared to those that study all imperiled taxa in a particular habitat.

Unfortunately, little is currently known about rare plant populations in coastal ENP outside of the distributional information presented in this paper. Even the existing distributional data lacks information for significant areas that have yet to be surveyed. Surveys conducted between 2005 and the present have led to the discovery of numerous previously unrecorded occurrences of critically imperiled species as well as three species previously unreported from ENP. These data provide a starting point to assess the relative risk to these species from sea level rise. Improved understanding of demographics, basic life history traits, and habitat requirements of coastal rare species would lead to a more refined risk assessment and may provide a better means of directing limited resources toward managing the loss of these species. In addition, studying these species prior to their loss will provide a historical ecological account that currently does not exist. This information will also be applicable to management decisions further inland as sea level rise submerges more and more of the Florida peninsula. In the interim, direct conservation measures including seed banking and establishment of ex situ conservation collections of all rare coastal species should be carried out to prevent the loss of genetic resources and to enable reintroduction elsewhere. The results of this risk assessment may serve as a guideline for determining which species may need the most immediate attention.

5 Summary

Coastal hammocks and buttonwood forests are compositionally different from inland hammocks in the ENP, with unique combinations of common and rare species. Importantly, whereas all hammocks in the estuarine/coastal zone rely upon localized freshwater for much of the year, periods of drought force the plants to either use saline water or tolerate some measure of drought. We predict a decline in the extent of coastal hardwood hammocks and buttonwood forests with the initial rise in sea level before the onset of sustained erosional inundation. The change in the extent of hardwood and buttonwood forests will be brought about by decline in freshwater recharge volume in conjunction with an increase in porewater salinity, which will push the hardwood species to the edge of their drought (freshwater shortage and physiological) tolerance. Along with the coastal hammocks and buttonwood forests, scores of critically imperiled and or endemic species will be jeopardized, and possibly be extirpated from the United States. Reductions in freshwater inflows into the estuarine portion of the Everglades will accelerate the loss of salinity-intolerant coastal plant communities. Restoring freshwater inflow might be the only mechanism to mitigate, in the short term, the effects of rising sea levels in the Everglades.

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