



# Compositional Effects of Sea-Level Rise in a Patchy Landscape: The Dynamics of Tree Islands in the Southeastern Coastal Everglades

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**Abstract** The landscape structure of emergent wetlands in undeveloped portions of the southeastern coastal Everglades is comprised of two distinct components: scattered forest fragments, or tree islands, surrounded by a low matrix of marsh or shrub-dominated vegetation. Changes in the matrix, including the inland transgression of salt-tolerant mangroves and the recession of sawgrass marshes, have been attributed to the combination of sea level rise and reductions in fresh water supply. In this study we examined concurrent changes in the composition of the region's tree islands over a period of almost three decades. No trend in species composition toward more salt-tolerant trees was observed anywhere, but species characteristic of freshwater swamps increased in forests in which fresh water supply was augmented. Tree islands in the coastal Everglades appear to be buffered from some of the short term effects of salt water intrusion, due to their ability to build soils above the surface of the surrounding wetlands, thus maintaining mesophytic conditions. However, the apparent resistance of tree islands

to changes associated with sea level rise is likely to be a temporary stage, as continued salt water intrusion will eventually overwhelm the forests' capacity to maintain fresh water in the rooting zone.

**Keywords** Southeast Saline Everglades · Forest fragments · Coastal landscape · Salt water intrusion · C-111 basin

## Introduction

During the 1900's, worldwide sea level rose at a moderate pace of 18 cm/century (Jevrejeva et al. 2009), but by the first decade of the current century, a strong scientific consensus had formed that the rate of sea-level rise (SLR) would accelerate substantially in the near future (Meehl et al. 2007). Such acceleration would elicit changes in coastal wetland structure and composition that should be anticipated and planned for, based on a combination of direct ecological studies and modeling work. The former might include retrospective studies of past changes associated with known rates of SLR, which can provide at least some initial guidelines for model development. In reconstructing these historical scenarios, landscape context should be kept in mind, as most coastal wetlands are heterogeneous mosaics in which patch types might differ in their responses to a uniformly advancing "ramp" disturbance (Lake 2000) such as SLR. A landscape perspective is especially pertinent in places where the human footprint has been prominent, such as in the southeastern coastal Everglades.

Most if not all Everglades landscapes are comprised of a patchwork of physically, structurally, and functionally distinct ecosystems, which may respond differently to disturbance or broad-scale environmental change. For instance, in the semi-permanently flooded peatlands of the freshwater

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Everglades, self-organization processes associated with the shallow flow of water across the surface often results in a biphasic marsh in which slightly elevated, elongated, flow-parallel sawgrass (*Cladium jamaicense*) “ridges” alternate regularly with wetter, more open “sloughs” that feature floating-leaved aquatic plants (Ross et al. 2006; Larsen et al. 2007; Watts et al. 2010; Cohen et al. 2011). The “Ridge and Slough” is very sensitive to hydrologic change, as reductions in water supply can cause ridges to expand, interfering with flow and eliminating the sediment redistribution necessary to maintain landscape pattern (Larsen and Harvey 2010). In an adjacent, coastal wetland system, i.e., the Southeastern Saline Everglades (SESE) (Egler 1952), landscape heterogeneity does not develop within the wetland matrix itself, but rather in the interspersed of an expansive, low, graminoid or shrub-dominated vegetation with isolated patches of forest, or “tree islands”. Tree islands are present throughout the Everglades in many physiographic forms and compositional assemblages (Craighead 1971). In SESE, they are frequently associated with geologic discontinuities, i.e., highs or lows in the underlying limestone bedrock (Ross et al. 2003). Due to their specialized physical setting within the coastal landscape, it is reasonable to expect that tree islands there will respond differently to SLR than will the surrounding vegetation matrix.

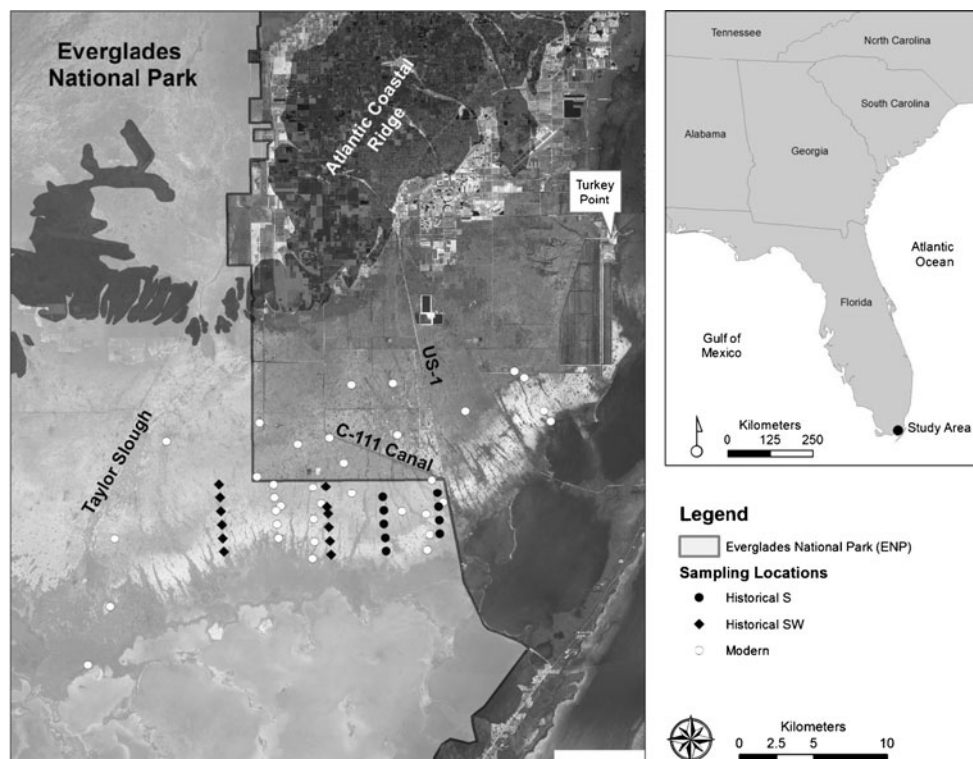
Egler (1952) described SESE—the broad band of wetlands extending from the southwest-curving Atlantic Coastal Ridge to the coast (Fig. 1)—as consisting of seven parallel zones, beginning with the interior pine rocklands, passing through a transition zone in which sawgrass-dominated freshwater

wetlands give way to sparsely vegetated dwarf mangrove flats, and ending with a more productive mangrove fringe along the shores of Biscayne or Florida Bay. Egler predicted that vegetation zonation in SESE would shift inland in the future, in response to fire suppression and wetland drainage. In subsequent decades, concerns about salt water intrusion in south Florida continued to increase, and Everglades National Park commissioned another study of vegetation in SESE in 1967 (Tabb et al. 1968). Almost three decades later, Ross et al. (2000) demonstrated that the zonation pattern in the region had indeed shifted as predicted by Egler, attributing the change to the combination of SLR and reduction in fresh water supply to the ecosystem. While each of these studies collected information on tree island fragments as well as the surrounding wetlands, the emphasis of all three was on the dynamics of the lower vegetation which comprised the majority of landscape. In this paper, we endeavor to test whether change in the tree islands paralleled that in the surrounding wetland matrix, using compositional data collected 29 years apart (1967 and 1996) in tree islands in the coastal zone of the southeast Everglades, in conjunction with previously reported marsh dynamics from the same area (Meeder et al. 1996; Ross et al. 2000).

## Study Area

Our study of SESE landscapes was focused primarily on the C-111 basin, west of US Highway 1 and east of Taylor

**Fig. 1** Locations of tree islands sampled in 1994–96 within the Southeast Saline Everglades study area



Slough, but also included sites in Taylor Slough and several wetlands between US 1 and the Turkey Point power plant. SESE is a flat coastal plain which ascends from the surrounding bays to approximately 1 m above sea level at the base of the uplands, more than 10 km distant throughout most of the region. Below the surface decimeter or so, soils are mostly marls produced under fresh water conditions, with peat soils found locally (Leighty et al. 1965). The lower half of the SESE plain is dissected by ephemeral creeks which range in depth from several inches in the upper reaches to several feet near the coast. Much of the variation in vegetation structure, including the profusion of tree islands, appears to be associated with local undulations in bedrock topography (Craighead 1971).

The hydrology of the Southeast Saline Everglades is, as the name suggests, wet and marine-influenced. Water levels at sites in the lower SESE are primarily responsive to fluctuations in the adjacent marine waters, while levels in the interior marshes are highly correlated with stage in the C-111 Canal. Egler (1952) emphasized that periods of elevated salinity in SESE are episodic, short-lived events, while background pore water salinities in most areas are low.

In addition to drainage and compartmentalization that altered the greater Everglades ecosystem (McVoy et al. 2011), local human activities that affected SESE hydrology include: (1) the establishment of the railroad bed along the current U.S. Highway 1 in 1904; (2) dredge and fill operations involved with the construction of the adjacent road system; (3) flood protection associated with agriculture and, more recently, residential, commercial, and recreational development in the southern Biscayne Bay watershed; and (4) the establishment and management of the canals and structures associated with the Everglades National Park - South Dade Conveyance system, beginning in 1948. The system was completed in 1967 with the construction of the C-111 Canal, whose southern levee included 55 gaps along its final, southeastward leg through SESE. During periods of high canal stage, overland flow through these gaps augmented fresh water supply to wetlands to the south (Ley et al. 1995).

Mean average temperature and precipitation (1974–2011) at Homestead Air Force Base, the nearest climate station to SESE are 24.3 °C and 140.2 cm, respectively (History for Homestead AFB, FL; [www.wunderground.com/history](http://www.wunderground.com/history)). Frost events ( $\leq 0$  °C) only occurred in two of the 42 years of record analyzed by Ross et al. (2009), though chilling events capable of damaging mangroves ( $\leq 3$  °C) occur in about half of all years. Seasonal variation in temperature is small (less than 10 °C difference between the temperature of the warmest and coolest months), but rainfall varies markedly among seasons. Monthly mean precipitation in the dry season (November–April) is less than 10 cm, but during May–October ranges from 17 cm to 26 cm. A large proportion of the rainfall that occurs during the latter half of the wet

season is attributable to tropical storms and hurricanes. The climatic variables discussed above place SESE in the Dry Tropical Forest life zone (Holdridge 1947; Lugo et al. 1999), but coastward of the pine forests of the Atlantic Coastal Ridge (Fig. 1), drainage characteristics restrict the development of forests to a small portion of the area, i.e., the tree islands that were the focus of our interest.

## Methods

### Data Collection

Data used in this study comprised both historical (1967) and recent (1994–96) sources. Historical data were the product of a study conducted for the National Park Service soon after the establishment of the C-111 Canal (Tabb et al. 1968). Tabb's research team surveyed selected plant, faunal, and environmental variables in areas south and southwest of the Canal. Their report included marsh and hammock vegetation data along a network consisting of five N-S transects 3.2 km apart, with sampling stations at 0.8 km intervals along each. In total, their network consisted of 26 sites within a strip extending about 6 km between Florida Bay and the C-111 Canal, but they sampled tree island composition at only 20 locations. Since the position of the northeast corner of the network was known, plot locations could be estimated in the absence of exact coordinates or permanently marked sampling stations.

Within a 15-month period during the winters of 1994–95 and 1995–96, we sampled vegetation and soils at 56 locations (Fig. 1). Access was by helicopter or, in a few instances, by foot from nearby roads. Site selection was non-random. Priorities in site selection were (1) sampling at locations for which historical vegetation or environmental information was available, and (2) creating a sample network that represented all portions of the Southeast Saline Everglades as described by Egler (1952). Sampling locations were predetermined in the office and located in the field with GPS. Twenty locations ("historical" sites) were those at which Tabb et al. (1968) had previously sampled tree island composition. Another thirty-six locations ("modern" sites), including the six Tabb et al. sites in which tree islands were not initially sampled, were added to more fully represent the range of conditions in the region. Twenty one of the modern sites were adjacent to hydrological stations in a network jointly maintained by Everglades National Park and the U. S. Geological Survey.

Marsh vegetation sampling, which focused on a circle of 50-m radius from the plot center, was described and interpreted in Ross et al. (2000). From the same plot center, one observer walked to the closest tree island within 500 meters and estimated the relative abundance of tree species. All

forests were small (<1 ha), and distinctly bounded by graminoid or low (<2 m) mangrove vegetation. It was therefore possible to explore the entirety of each stand within 15–20 min, and rank the tree species present in any size in terms of canopy coverage. Species ranked 1 through 4 were assigned an abundance of 10, those ranked 5 through 8 had an abundance of 5, those ranked 9 through 12 an abundance of 2, and those ranked 13 or more an abundance of 1.

Salinity data from SESE are sparse and anecdotal, both historically and in modern times. In recognition of the wide range of climatic and hydrologic conditions associated with season and irregular storm events, we decided to represent the local salinity regime with a mollusk-based Site Salinity Index (SSI) rather than with one-time, temporally variable collections of in situ porewater. From each plot center, we collected a surface (upper 2 cm) soil sample, which may be taken to represent conditions of the previous 7–20 years based on sediment accretion rates from the study area (1.0 to 3.2 mm per year; Meeder et al. 1996). Mollusks >1 mm diameter in each sample were identified and counted, and SSI was calculated as the density-weighted average of the salinity affinities of the fossil mollusk species present in the collection. Mollusk species salinity affinities were interpreted from the literature, scaling from 1 (strictly freshwater) to 5 (strictly marine) (Online Appendix 1). Using a similar approach in coastal wetlands immediately north of SESE, Gaiser et al. (2006) found that mollusk inferred salinities could be used to reliably represent observed pore water salinities.

### Analytical Methods

We used a combination of classification and ordination techniques to describe the current gradients as well as the change in tree island composition between 1967 and 1994–96 in SESE. To characterize and classify the current tree islands, we applied an agglomerative hierarchical cluster method with flexible beta (–0.25) linkage (Lance and Williams 1967) to a 56-site data collected in 1994–96. However, to assess change in composition, we applied a Non-Metric Multidimensional Scaling (NMS) (Kruskal 1964) ordination procedure to a combined data set, including our 1994–96 survey and that of Tabb et al. (1968). In the earlier study, woody species in each tree island were rated as "abundant", "consistently present", or "seedlings only". In order to treat these data as similarly as possible with those collected in 1994–96, we assigned abundances of 10, 5, and 1, respectively, to these ratings. In addition, Tabb's hammock data for one of the western transects were not available, leaving comparable hammock data from the two studies available for only 20 sites. Thus, the site x species matrix included vegetation data for 76 sites. We relativized

species abundances by the site total, calculated Bray-Curtis dissimilarities among sampling units, and then performed the NMS ordination analyses on the dissimilarity matrix. The combination of NMS ordination and the Bray-Curtis dissimilarity metric is considered to be a robust method of recovering the compositional structure associated with underlying environmental gradients (Minchin 1987). Displaying potential classification units of current forest types on the site ordination diagram helped us distinguish ecologically significant groupings. We used PCORD 6.0 (MjM Software; McCune and Mefford 2011) for classification, and DECODA (Minchin 1998) for NMS ordination.

No comprehensive, spatially explicit, appropriately scaled environmental data (e.g., water depth, nutrient availability, disturbance history) were available for tree islands of the study area. Therefore, two variables were considered in our examination of vegetation-environment interactions: SSI and Distance to the Coast (DTC), i.e., the shortest distance between the site and the coastline of Florida Bay or Biscayne Bay. In all likelihood, DTC represented a composite of many unmeasured environmental factors. For both variables, we used least-square regression to explore the relationships between their values at each site and the coincident NMS Axis I scores. We used linear, quadratic, power and log functional forms, and compared the percent of variance accounted for by each model.

Using historical data (Tabb et al. 1968) in conjunction with the data collected in 1994–96, we asked two questions about the tree islands coastward from the C-111 Canal: (1) Was there an overall change in the composition of tree islands of the area between 1967 and 1994–96? and (2) If such change did occur, was it manifested differently in areas south v southwest of the C-111 Canal? Areas directly south of the Canal received overflow through gaps in its southern levee during periods of high water, while areas to the southwest did not. We reasoned that if the amount of water exiting the C111 canal for the southern marshes was ecologically significant, we should see a trend toward freshwater species in that area in comparison to marshes to the southwest. We note that precipitation in south Florida throughout most of the period of interest was lower than normal, in conjunction with a cool phase in the Atlantic Multidecadal Oscillation (Enfield et al. 2001), but the period ended with several extremely wet years (1994 and 1995).

We assessed vegetation change by applying analysis of covariance to the NMS Axis 1 scores for the 20 historical sites sampled in both periods. Eight of these sites were directly south of the C111 canal, and twelve were located to its southwest (Historical-S and Historical-SW sites in Fig. 1). We analyzed the data using analysis of covariance, with Distance to Coast as the covariate, Position (south or southwest of the canal) and Time (1967 or 1994–96) as the main effects. In addition to the ANOVA assumptions, tests

for linearity and homogeneity of regression slopes showed that the assumptions for covariance were also satisfied. The sites included in the covariance analysis were within 6 km from the coast, and the NMS Axis-1 score showed a linear relationship with DTC within that range. Likewise, the interactions between the covariate (DTC), and both independent variables were not significant, showing that the regression slopes were homogeneous. Since the assumptions were met, no transformation of data was required. The STATISTICA program (Statsoft Inc.) was used for the statistical analyses.

## Results

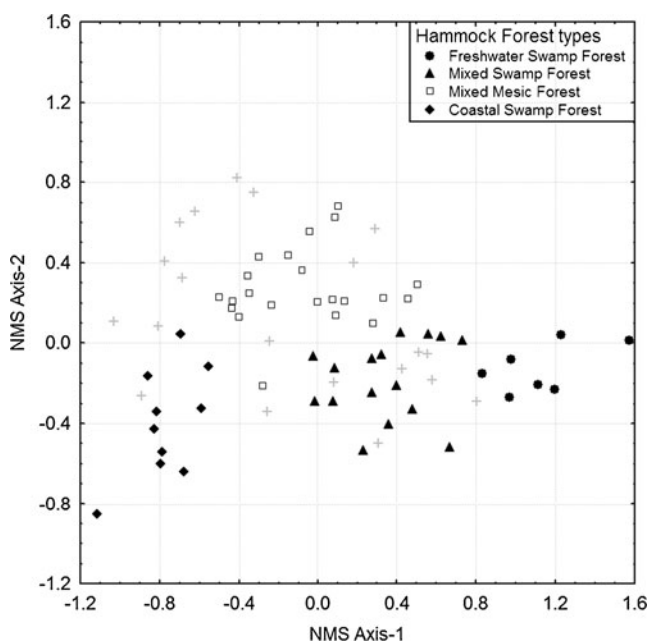
The results of NMS ordination of sites based on species abundances in SESE tree islands, with groupings suggested by the cluster analysis, are presented in Fig. 2. In the analysis we recognized four ecologically meaningful groups, which accounted for 68 % of the species information (McCune and Grace 2002). Variation in species composition across the data set was effectively summarized in a 2-D NMS ordination (stress=0.14). Three of the four groups were distinguished along Axis 1 of the NMS ordination, which appeared to represent a gradient between relatively salt-tolerant and salt-intolerant swamp forests. The fourth group, the Mixed Mesic Forest, occupied a broad, intermediate position along Axis 1, but was separated from the other

groups along NMS Axis 2, which may be interpreted as a gradient in surface elevation.

Freshwater and Mixed Swamp Forest units (Groups 1 and 2) shared several of the same fresh water swamp species of more temperate distribution, e.g., red bay (*Persea borbonia* (L.) Spreng.) and wax myrtle (*Morella cerifera* (L.) Small) (Table 1). A tropical species, cocoplum (*Chrysobalanus icaco* L.) was also equally important in both groups. The Freshwater Swamp Forest was distinguished by a relative abundance of

**Table 1** Mean relative abundance of tree species in four forest community types in the Southeast Saline Everglades

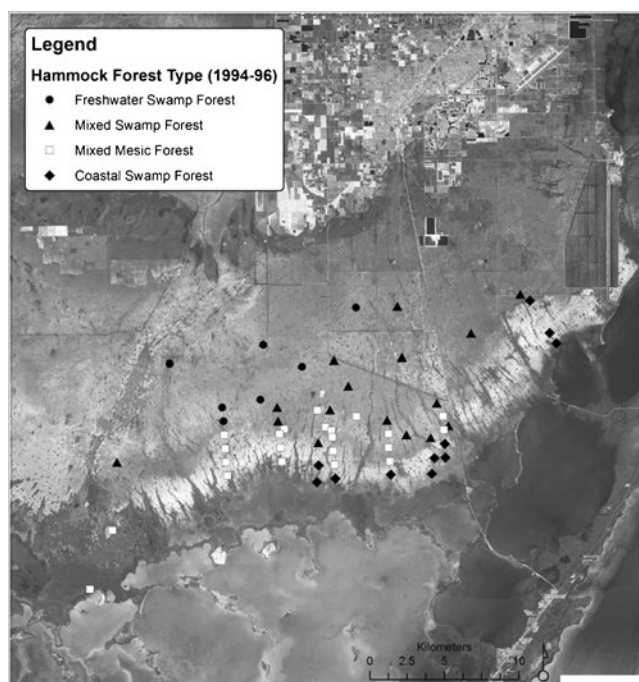
Name of Species	Hammock Forest Type			
	Freshwater Swamp	Mixed Swamp	Mixed Mesic	Coastal Swamp
<i>Taxodium distichum</i>	15.29			
<i>Morella cerifera</i>	15.16	14.60	6.95	1.65
<i>Chrysobalanus icaco</i>	12.36	11.66	3.98	
<i>Persea borbonia</i>	11.81	6.66	1.75	
<i>Ilex cassine</i>	8.90	6.83	0.18	
<i>Salix caroliniana</i>	8.51	1.48	0.14	
<i>Annona glabra</i>	7.00	1.83	1.57	
<i>Myrsine floridana</i>	6.29	6.40	4.74	
<i>Magnolia virginiana</i>	4.91	2.11		
<i>Metopium toxiferum</i>	3.12	9.32	10.86	0.71
<i>Ficus sp.</i>	2.74	0.64	2.66	
<i>Conocarpus erectus</i>	2.02	14.76	14.25	16.19
<i>Rhizophora mangle</i>	1.48	12.76	11.83	20.74
<i>Schinus terebinthifolius</i>	0.41	2.15	4.68	
<i>Casuarina equisetifolia</i>		2.92	0.72	1.01
<i>Sabal palmetto</i>		1.53	0.13	
<i>Laguncularia racemosa</i>		1.03	4.80	15.19
<i>Randia aculeata</i>		1.03	3.86	4.03
<i>Swietenia mahagoni</i>		0.88	1.50	
<i>Lycium carolinianum</i>		0.42		12.61
<i>Calyptanthus pallens</i>		0.38	5.37	
<i>Sideroxylon celastrinum</i>		0.18	3.12	9.42
<i>Coccoloba uvifera</i>		0.17	2.78	1.11
<i>Eugenia foetida</i>		0.08	5.30	
<i>Eugenia axillaris</i>		0.08	3.19	
<i>Quercus virginiana</i>		0.08		
<i>Coccoloba diversifolia</i>			3.79	
<i>Forestiera segregata</i>			0.71	
<i>Piscidia piscipula</i>			0.34	
<i>Pithecellobium keyense</i>			0.27	0.71
<i>Zanthoxylum fagara</i>			0.21	
<i>Avicennia germinans</i>			0.19	9.97
<i>Sideroxylon salicifolium</i>			0.07	
<i>Ardisia escallonioides</i>			0.06	
<i>Jacquinia keyensis</i>				6.66



**Fig. 2** Two-axis non-metric multidimensional scaling ordinations, including 20 samples from 1967 (Tabb et al. 1968) and 56 samples from 1994 to 1996. 1967 samples are designated as +, and 1994–96 samples are identified by forest type as determined by cluster analysis

baldcypress (*Taxodium distichum* (L.) Rich.), willow (*Salix caroliniana* Michx.), pondapple (*Annona glabra* L.), and sweet bay (*Magnolia virginiana* L.). The Mixed Swamp Forest also included some species associated with more mesic conditions, e.g., poisonwood (*Metopium toxiferum* (L.) Krug & Urb.), and often harbored halophytes such as red mangrove (*Rhizophora mangle* L.) and/or buttonwood (*Conocarpus erectus* L.) along island flanks. While the Mixed Mesic Forest (Group 3) is a heterogeneous group in which nearly any SESE tree species may be found, it is characterized by mesic species whose centers of distribution lie to the south, e.g., poisonwood, spice-wood (*Calyptanthes pallens* Griseb.), pigeon plum (*Coccoloba diversifolia* Jacq.), white stopper (*Eugenia axillaris* (Sw.) Willd.), and spanish stopper (*Eugenia foetida* Pers.) (Table 1). Finally, tree islands categorized as Coastal Swamp Forest (Group 4) included a much more diverse mixture of woody halophytes than are found in the zonal mangrove swamps of the SESE or other portions of South Florida. Besides buttonwood and the three mangrove species (red mangrove, black mangrove (*Avicennia germinans* (L.) L.) and white mangrove (*Laguncularia racemosa* (L.) C.F. Gaertn.), common associates were Christmas berry (*Lycium carolinianum* Walter), saffron plum (*Sideroxylon celastrina* (Kunth) T.D. Penn), joewood (*Jacquinia keyensis* Mez), and indigo berry (*Randia aculeata* L.) (Table 1).

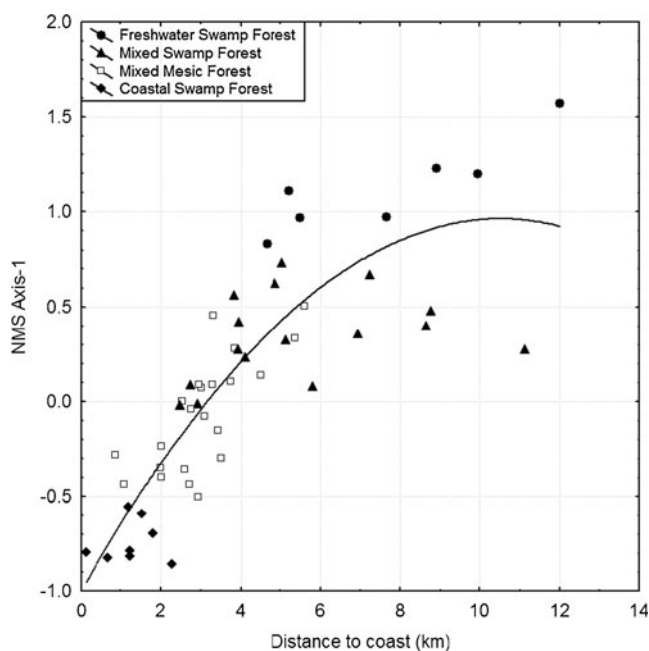
The distribution of tree islands in the study area resembled that of SESE marsh vegetation (Ross et al. 2000), i.e., hammocks of similar composition were arranged in roughly concentric bands parallel to the coast (Fig. 3). The compositional



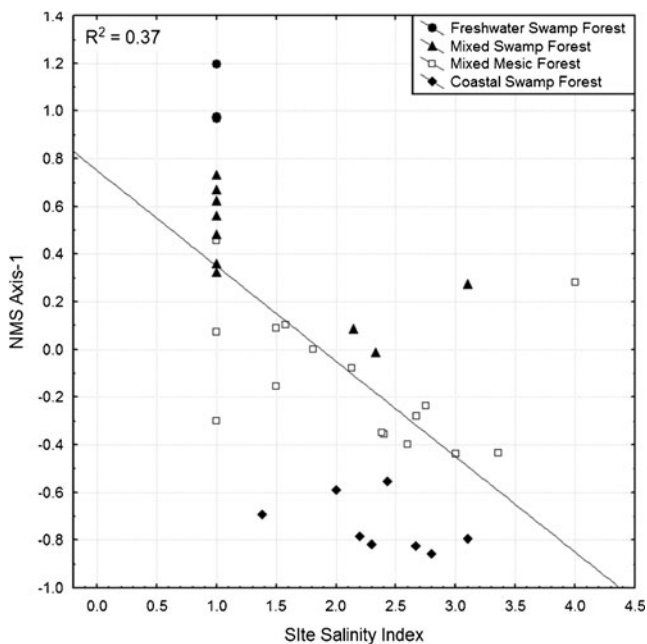
**Fig. 3** The distribution of four forest types within the Southeast Saline Everglades, 1994–96

change in SESE hammocks with increasing distance to the coast is displayed more quantitatively in Fig. 4. Beginning at the coastline, species composition along NMS Axis I changed in a more or less linear fashion for about 6 km inland; beyond that distance, variation was non-linear. A quadratic regression model offered the best fit ( $R^2=0.72$ ), suggesting that an extensive zone of relatively constant tree species composition occurred near the interior of the study area. The negative relationship ( $R^2=0.37$ ) between NMS Axis 1 scores and SSI (Fig. 5) suggests that forest types were roughly arranged along a salinity gradient.

The results of the analysis of covariance for changes in hammock species composition below the C-111 Canal between 1967 and 1996 are summarized in Table 2. The results revealed that after the controlling for the effects of DTC, tree island composition showed a significant effect ( $F_{1,35}=37.0$ ,  $p<0.001$ ) of Position and a non-significant Time effect (Table 2). After DTC, Position accounted for 51.4 % of the remaining variance in tree island composition. The effect of the Position  $\times$  Time interaction on composition was marginally non-significant ( $p=0.08$ ), indicating some level of change in the effects of position on composition over time. While mean NMS Axis 1 scores for the SW-sites did not show any change, the mean score for S-sites was significantly higher (paired ‘*t*’ test;  $n=8$ ;  $p=0.037$ ) in 1996 than in 1967 (Fig. 6), suggesting an impact of freshwater input on the composition of tree islands located south of the C111 Canal.



**Fig. 4** Relationship between non-metric multidimensional scaling Axis 1 scores and Distance to Coast for 56 tree islands sampled in 1994–96. Line representing the best-fit regression model (quadratic form) is included



**Fig. 5** Relationship between non-metric multidimensional scaling Axis 1 scores and Site Salinity Index for 56 tree islands sampled in 1994–96. Line representing the best-fit regression model (linear form) is included

## Discussion

Tree islands and the matrix of lower-statured wetlands that surround them are both subject to the same environmental forcings, including sea-level rise, but due to their distinctive physiographic settings, they experience these forces differently. Matrix wetlands in the southeastern Everglades are usually rooted in 40–120 cm of heavy calcareous sediments that over centuries have precipitated above a rough limestone surface (Meeder et al. 1996). Soils drain slowly, and salts can accumulate when storm tides pond and slowly evaporate. In contrast, tree islands in the area occupy two geologic settings: modest outcroppings in the limestone, or peat mounds formed over bedrock depressions. While tree islands of both types have likely been common in SESE for centuries, soil formation in some depressional islands

**Table 2** Analysis of covariance (ANCOVA) for NMS Axis 1 score of tree islands sampled in 1967 and in 1994–96 ( $n=40$ ). Distance to coast (DTC) is a covariate in the analysis, and Position and Time are main effects

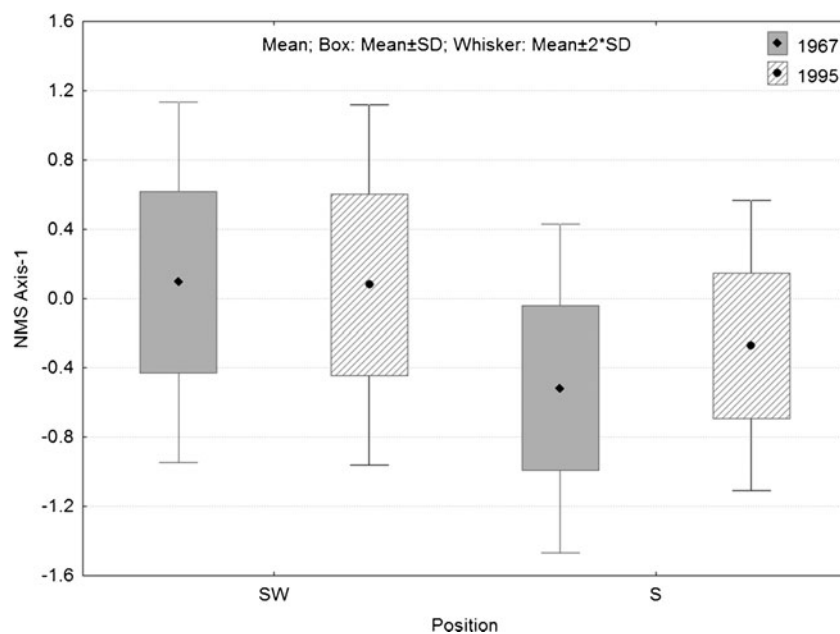
	df	MS	F	<i>p</i>	Partial eta-squared
Distance to Coast	1	6.93	132.9	0.000	0.792
Position	1	1.93	37.0	0.000	0.514
Time	1	0.13	2.5	0.125	0.066
Position*Time	1	0.16	3.2	0.084	0.083

appear to date back to a time when sea level was at least 3 m lower than today (Ross et al. 2003). Development of both types of landform results in a positive surface feature that is less frequently inundated by storm tides or seasonal high water stages than adjacent wetlands. In some cases, the elevation of these tree islands is sufficient to allow a local lens of fresh groundwater to form in response to recharge by rainfall (Saha et al. 2011). In comparison to the sparse production that prevails in the surrounding wetland communities, trees on the islands make reasonable growth, due to adequate drainage, reduced porewater salinity, and superior groundwater exchange (Meeder and Harlem 2008). In contemplating the coastal landscape, it is interesting to consider whether the hydrologically buffered, relatively productive tree islands display the same zonation patterns that have previously been described for the unproductive wetland matrix in which they are embedded, or have changed at the same rate and in the same direction in response to SLR and variable fresh water delivery.

**Spatial Pattern** As it proved to be for the marsh vegetation (Ross et al. 2000), coastal influence was evident in SESE tree islands, especially in the strong relationship between species composition (as exemplified by NMS Axis 1) and distance to coast (Fig. 4). Our mollusk-based Site Salinity Index indicated that salinity likely plays an important role in the environmental gradient represented by distance to coast (Fig. 5), but other factors expected to vary with location within the coastal zone, especially disturbances, may also affect patterns in forest composition. Fires can leave a profound and long-lasting mark on tree islands (Robertson 1955), but matrix fuels in SESE are typically sparse and moist, and fires are infrequent in the area. During the period 1948–2007, Everglades National Park records show only 30 fires (average size=266 ha) within SESE, indicating a fire return interval of about 310 years; nearly all large fires burned within the northern one-third of the study area. Cold temperature events periodically damage or kill exposed, frost-sensitive species throughout south Florida, but temperatures are moderated substantially within forest canopies, so that tree islands are affected superficially if at all (Olmsted et al. 1993; Ross et al. 2009). The disturbances most likely to contribute to the distribution patterns we observed (Fig. 3) are those hurricanes accompanied by large storm surges, which bring saltwater deep into the Everglades and may bury forest soils with transported sediment (Craighead 1964). These are likely to be most influential within a few km of the coast, as the depth of mud deposits become thinner toward interior areas, thereby reducing their ecological impact (Ross et al. 2002; Castaneda-Moya et al. 2010).

The coastal gradient in tree island composition is complicated by an effect of surface elevation, which appears to

**Fig. 6** Box plots representing non-metric multidimensional scaling Axis 1 scores for tree islands sampled in 1967 and 1994–96 in areas south and southwest of the C-111 Canal



be expressed on Axis 2 of the NMS ordination (Fig. 2). We infer that Axis 2 represents a topographic gradient, based on the separation of Mixed Mesic Forest from the three Swamp Forest types along this axis. Mixed Mesic Forest is characterized by a substantial component of species of tropical origin that are restricted to well-drained, infrequently flooded sites, e.g., *C. pallens*, *E. foetida*, *E. axillaris*, *C. diversifolia* (Craighead 1971; Ross et al. 1992). Within the study area, this forest type is aligned along a variably wide band paralleling the coast at several km distance (Fig. 3). No similarly located zone has been described in any study of the vegetation of the surrounding wetland matrix. We suspect that the localized distribution of Mixed Mesic Forest in SESE is the result of patterns in the underlying geology, in conjunction with groundwater dynamics, but we were not able to further examine the physical environment of these landforms in this study. We conclude that the distribution of coastal forest fragments follows much the same pattern as the marsh/swamp matrix in SESE, with an additional layer of variation associated with their peculiar physiography.

**Temporal Dynamics** Consideration of tree island compositional change (1967–1996) is best framed by the dynamics of *C. jamaicense* (sawgrass), the quintessential plant of the Everglades fresh water marsh, during 1940–1996 (Ross et al. 2000) and 1967–1996 periods (Meeder et al. 1996). Along a transect southwest of the C-111 Canal, the border between sawgrass marsh and more coastal vegetation receded toward the interior by 3.3 km between 1940 and 1996, concurrent with a substantial inland encroachment of mangroves (Ross et al. 2000). During the 1967–1996 period alone, the frequency of sawgrass in 1 m<sup>2</sup> plots in the same region decreased by 30–50 %, but increased by about 10 % in the area directly south of

the C-111 Canal (Meeder et al. 1996). The authors attributed the increase in sawgrass abundance south of the canal to augmented southeasterly flow of water through openings in the southern canal wall beginning in 1967.

Despite slightly different sampling methods in the 1967 and 1994–96 surveys, the current study documented a parallel but more muted response among SESE tree islands. As expressed by scores along the dominant NMS ordination axis, the marginally significant changes in forest composition south of the C-111 Canal were consistent with increased fresh water flow during the period, but the absence of change southwest of the Canal contrasted sharply with results cited above from the marsh (Table 2, Fig. 6). To what can the relatively high resilience of tree islands to changes pressed by SLR be attributed? One possibility is that this apparent stability is a condition of our sampling methods, which were cover-based, and therefore influenced predominantly by large trees, and less affected by seedlings. Elsewhere in Florida, at Wacassassa Bay, where forest retreat is currently occurring due to SLR, Williams et al. (1999) demonstrated that regeneration of the major fresh water tree species failed well before mature trees succumbed, leaving behind relict stands of mature individuals with scant future prospects. While we did not sample seedlings directly, we observed no dearth of reproduction of the dominant trees. Instead, our observations may in fact reflect the capacity of SESE tree island surfaces to build up rapidly enough to maintain a hydrologic buffer against the effects of salt water intrusion, at least at current rates. Though their origin and trajectories are often geologically-determined, Everglades tree islands are biologically constructed, self-organized ecosystems that concentrate nutrients, draw in water via their transpiration streams, and build soils at rates that set them apart from the surrounding wetlands (Ross and Sah 2011; Sullivan et al.



2011). While likely higher than the 1–3 mm per year accretion rates estimated for SESE marshes (Meeder et al. 1996), estimates of sediment accretion in coastal tree islands are unknown. However, in order for these communities to maintain their current composition and structure, accretion will need to match the local rate of SLR, which is projected to rise from the current 2.3 mm per year to 5.0–14.5 mm per year through 2100 (USACE 2009). Moreover, even if the tree islands could attain such high accretion rates, growth might be counterbalanced by accelerated erosion if the adjacent wetland matrix was not able to keep pace. Thus, the productivity-based resilience recently exhibited by tree islands to SLR, a ramp disturbance whose intensity is predicted to increase, is one whose effectiveness will probably erode in the future.

The results described in this paper and our earlier work (Meeder et al. 1996; Ross et al. 2000) provide parallel analyses of compositional changes in the two major components of a biphasic, coastal landscape subject to SLR. Our data showed rapid change toward more salt-tolerant species in the low marsh matrix, but relative stasis in the scattered tree islands that comprise much the smaller component of the landscape over a 29-year period. The two-component landscape present in 1996 controlled or created emergent properties, e.g., the propagation of disturbances, the movement and persistence of organisms, the redistribution of matter and nutrients, and the fixing of carbon, in ways likely to reverberate throughout the Everglades ecosystem (Turner 1989). However, given projected increases in the rate of SLR, the structure of the landscape in 1996 will almost certainly prove to be a temporary condition, with the fresh water-dependent species in the tree islands replaced by the same mangrove species that dominate the lower vegetation around them. Even in this more monotonous landscape, the juxtaposition of extensive shrub communities with scattered patches of forest is likely to remain for some time, creating a new set of emergent properties.

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