







Sea-Level Rise and the Persistence of Tree Islands in Coastal Landscapes

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ABSTRACT

Naturally formed forest patches known as tree islands are found within lower-statured wetland matrices throughout the world, where they contrast sharply with the surrounding vegetation. In some coastal wetlands they are embedded in former freshwater marshes that are currently exposed to saltwater intrusion and mangrove encroachment associated with accelerating sea-level rise. In this study we resurveyed tree composition and determined environmental conditions in tree islands of the coastal Florida Everglades that had been examined two decades earlier. We asked whether tree islands in this coastal transition zone were differentiated geomorphologically as well as compositionally, and whether favorable geomorphology enabled coastal forest type(s) to maintain their compositional integrity against rising seas. Patterns of variation in geomorphology and soils among forest types were evident, but were dwarfed by differences between forest and adjacent wetlands.

Tree island surfaces were elevated by 12–44 cm, and ²¹⁰Pb analyses indicated that their current rates of vertical accretion were more rapid than those of surrounding ecosystems. Tree island soils were deeper and more phosphorus-rich than in the adjoining matrix. Salinity decreased interiorward in both tree island and marsh, but porewater was fresher in forest than marsh in Mixed Swamp Forest, midway along the coastal gradient where tropical hardwoods were most abundant. Little decrease in the abundance of tropical hardwood species nor increase in halophytes was observed during the study period. Our data suggest that geomorphological differences between organic tree island and marl marsh, perhaps driven by groundwater upwelling through more transmissive tree island soils, contributed to the forests' compositional stability, though this stasis may be short-lived despite management efforts.

Key words: coastal wetlands; Everglades National Park; habitat islands; Mixed Swamp Forest; mangroves; sea-level rise; soil ²¹⁰Pb analyses; Southeast Saline Everglades; tree islands; tropical hardwood forest.

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HIGHLIGHTS

- Isolated, periodically flooded forests (tree islands) in the coastal Everglades were compositionally stable in the face of sea-level rise during a recent 20-yr period.
- The species-rich Mixed Swamp Forest—which included tropical hardwood, mangroves, and trees characteristic of freshwater swamps—was common where brackish water conditions occurred seasonally but flooding was mitigated by the buildup of organic sediments above the adjacent marsh.
- The resilience of tree islands against sea-level rise appears to rest on hydrogeologic and edaphic factors associated with breaks in the marl surface continuity, in which the upwelling of fresh groundwater may play a role.

INTRODUCTION

Like oceanic islands, habitat islands surrounded by broad expanses of contrasting vegetation cover or land use may be important repositories of biodiversity and share a vulnerability to species loss (Brown 1971). Whether they originate as a result of natural processes or due to fragmentation by human activities, the isolation and limited size of habitat islands combine to make the long-term persistence of resident populations uncertain. The prognosis for these species becomes even more tenuous when there is an increase in environmental stresses like those associated with global climate change. However, in such cases, where external stressors exacerbate the demographic, genetic, and biotic challenges faced by small populations occupying isolated habitat patches, the capacity of the ecosystem to resist stress by landscape modulation (Shachak and others 2008) may forestall species decline for a time.

Habitat islands occur in many forms and sizes, and the communities they shelter respond differently to environmental change. For instance, in remnant patches left by human fragmentation of formerly extensive grassland or forest, community dynamics may be driven by extinction debt resulting from the sudden reduction in patch area (Tilman and others 1994). In habitat islands that originated outside the influence of humans, however, community responses may be less confounded by recent history, and the effects of novel environmental stresses might be more evident. The many “tree islands” found within lower-statured

wetland matrices throughout the world appear to fit this model of naturally formed but physically isolated habitats (Wetzel 2002). Though some of these forests are entirely or in part products of past human agency (Denevan 1966; Schwadron 2006), the origin of others lies in the interactions of hydrogeologic processes with biotic feedbacks provided by non-human actors, for example termites, nutrient-depositing animals, or the trees themselves (Langstroth 1996; McCarthy and others 1998; Wetzel and others 2005). As such, the self-organizing processes that led to tree island formation may play a role in maintaining ecosystem properties and resident populations against the rapid degradation that can ensue when environmental stresses increase.

Tree islands are widespread in the Florida Everglades, where they contrast dramatically with the surrounding freshwater marshes. The growing body of research on Everglades tree islands reveals them to be landscape modulators *sensu* Shachak and others (2008). That is, the habitat conditions brought on by the forest’s capacity to alter geomorphology and resource availability deviate sharply from the marshes and prairies around them (D’Odorico and others 2011). This capacity is evidenced by three notable characteristics: (1) Tree islands in the interior Everglades peatlands concentrate nutrients, especially phosphorus (P), in a wetland in which P is limiting (Wetzel and others 2005); (2) tree islands in many Everglades settings build a peat surface substantially above the level of the surrounding marshes, thereby reducing flood depth and duration and allowing less flood-tolerant species to persist (Craighead 1971); and (3) as a consequence of their relatively well-drained conditions, tree islands serve as refuges and concentrators of plant and animal diversity (Robertson and Frederick 1994), with the latter functioning as vectors of nutrient and seed input. However, unlike the random establishment of woody patches envisioned by Shachak and co-authors, tree islands in many Everglades settings nucleate on bedrock outcrops or depressions that allow for groundwater upwelling and favor the buildup of rich soils (Meeder and Harlem 2008). Due to their geologic underpinnings and self-organized nature, one might expect these landforms to be less impacted by rising water levels or saltwater intrusion than the adjacent marshes, and their tree assemblages to exhibit relative stability until an environmental threshold is reached and exceeded.

The Southeast Saline Everglades (SESE) is a coastal wetland that occupies interior positions in portions of two south Florida estuaries, Florida and

Biscayne Bays. The landscape contains many tree islands embedded in former freshwater marshes that are currently exposed to saltwater intrusion associated with accelerating sea-level rise (Wdowinski and others 2016), as well as colonization by *Rhizophora mangle* L., a native mangrove species. The encroachment of *R. mangle* into SESE marshes from its former position fringing the estuarine coastlines was noted almost 70 years ago by Egler (1952). While focusing on the effects of disturbance and environmental conditions on plant zonation patterns in this exceptionally flat wetland matrix, Egler also noted the ubiquity of the region's small, teardrop-shaped tree islands. Tree assemblages in these islands included both flood-tolerant species common in swamp forests throughout the southeastern US and tropical hardwoods that reached their northern distributional limits on well-drained sites in Florida. Though he was unaware of the pace that sea-level rise would reach decades later, Egler predicted that mangroves would become increasingly dominant in both marsh and tree island as diversion of fresh water for agricultural and residential uses increased saltwater intrusion.

Subsequent vegetation surveys by our research team in 1995–1996 confirmed the continued invasion of mangrove shrubs into freshwater marsh communities (Ross and others 2000), but found tree island composition to have been relatively stable (Ross and others 2014). Notably, distinctive tree island types were arranged in zonal patterns relative to the coast, suggesting differences in exposure or tolerance to stresses associated with brackish estuarine waters. In 2016–2018 we returned to the SESE tree islands we had visited about two decades earlier to resurvey tree composition and, for the first time, to collect environmental data pertaining to the forests' hydrologic and edaphic environments. We asked these questions: (1) Are tree islands within the coastal transition zone differentiated geomorphologically as well as compositionally? (2) Does favorable geomorphology, especially a history of building soils above those of the adjoining marsh, enable some coastal forest type(s) to maintain their compositional integrity against rising seas? (3) Has the importance of halophytes in coastal forest assemblages increased over the past two decades, and if so, did these changes lead to the extirpation of glycophytic tropical hardwood species? We conclude by considering the challenges that the changes in landscape structure and composition that would accompany continuing sea-level rise pose for coastal resource managers.

MATERIALS AND METHODS

Study Area

As described by Egler (1952), the SESE comprises coastal wetlands adjacent to southern Biscayne Bay and northeastern Florida Bay, extending as far as Shark Slough in Everglades National Park (ENP). Although the area encompassed in this study also included coastal wetlands near the Shark Slough border, our focus was on compositional change in the eastern portions of the SESE, where islands were sampled in both 1995–1996 and 2016–2018 (Figure 1).

The climate of the SESE is warm and wet, with mean annual temperature and precipitation of 24 °C and 148 cm at nearby Homestead FL (Duever and others 1994). The strongly seasonal rainfall pattern features a May–October wet season in which 60% of annual precipitation falls and a November–April dry season during which entirely rainless months are not uncommon. The seasonality in rainfall is mirrored, with a slight lag, by water levels in the freshwater Everglades. The exceeding flatness of the coastal plain (slope ratios of about 10 cm per km, Ross and others 2002; Meeder and Parkinson 2018) means that small increases in freshwater discharge or tidal height (both typically reaching a maximum in October and November) can extend the duration of flooding across vast areas. In the easternmost portion of the study area, bordered by a sub-basin of Biscayne Bay, semidiurnal tides of 0.3 m amplitude are typical and salinity is usually in the range 15–35 psu (Wang and others 2003). In northeastern Florida Bay, tides are mostly weather-driven, and salinity averages only 18 psu in the coastal embayments below our sites (Lee and others 2008; Marshall 2017).

The marl soils (Fluvaquents of the Perrine or Pennsuco series) that predominate across SESE marshes or scrub communities (hereafter referred to generically as “matrix” vegetation) reflect their mode and conditions of formation, which revolve around the metabolic activities of a periphytic cyanobacterial community under sparse, freshwater graminoid cover (USDA 1996; Browder and others 1994). Notably, where dense scrub mangrove stands were established during the mid-twentieth century in Biscayne Bay's coastal wetlands, a distinct, root-derived organic layer formed above the carbonate sediment (Meeder and Parkinson 2018). In the small tree islands scattered throughout the SESE landscape, the soils are classified as organic-rich Medisaprists of the Terra Ceia

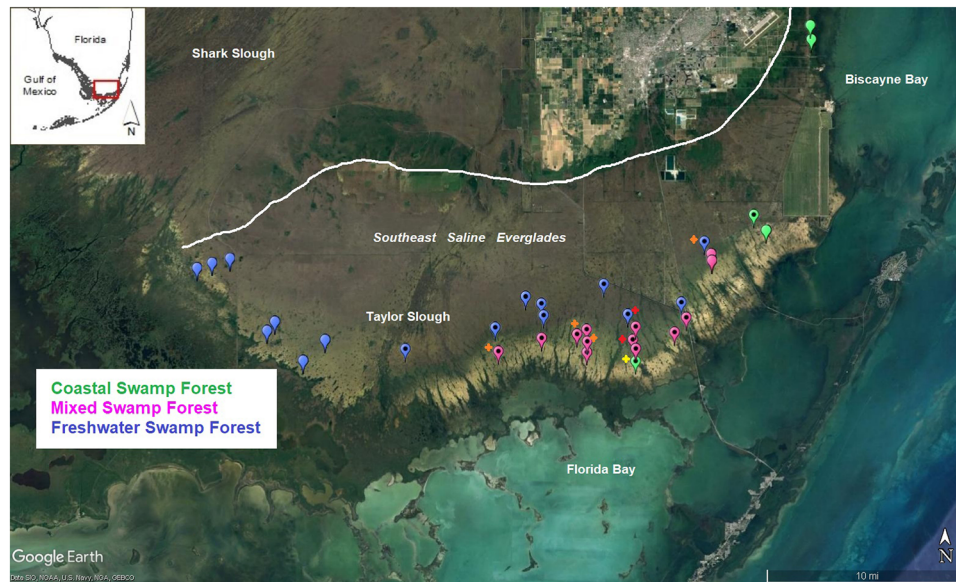


Figure 1. Tree Island site locations sampled in 1995 (symbols with black dots) and 2016 with distribution of three cluster-derived vegetation types. White line corresponds to the northern limit of the Southeast Saline Everglades region. Stars mark sites where cores used for accretion analysis (see Table 4) were collected in both tree island and adjacent marsh (in red), only in tree island (yellow) or only in marsh (orange).

or Pahokee series (USDA 1996). The lone published description of the physiography of these islands (Egler 1952) suggests substantial among-site variation. During a 1940 survey, Egler (1952) found that the organic soils in one set of SESE tree islands were underlain by a layer of marl, and the island surfaces were level with those of the adjoining marsh. Nearby, however, he also described a group of islands on which “...one can walk dry-shod...” while 2–10 cm of water was ponded on the adjacent wetland surface. This early observer recognized well the potential of tree island ecosystems to modulate the landscape through their soil-building capacities.

Vegetation and Environmental Sampling

During December–January of 2016–2017 and 2017–2018 (referred to hereafter as the 2016 survey), tree species composition and topographic conditions were assessed in 34 SESE tree islands (Figure 1). Tree composition had previously been sampled in 22 of these islands by our group in 1995–1996 (the 1995 survey), but no environmental data were collected at that time.

The abundance of tree species in the islands was estimated with identical methods in both studies: the same observer (MSR) explored the forest thoroughly for about 30 min, then ranked the canopy coverage of the resident tree species. At the same time, a team stretched a tape perpendicular to

the long axis of the tree island at its widest point, beginning in matrix vegetation 10 m outside the island and ending 10 m beyond its edge on the opposite side, comprising a transect that ranged in length from 50 to 150 m. Soil depth was determined by probing to bedrock at 5-m intervals. The location of the water table relative to the soil surface was also determined; when water was below the tree island surface, a soil auger was used to create a hole, and the depth between the surface and the water table was measured 5 min later.

At the midpoint of the transect a soil core (5.7 cm inside diameter, 30–45 cm depth) was collected and returned to the laboratory, where the profile was described and subsamples of each stratum prepared for complete soil analysis. Data presented in this paper on soil constituents are weighted means for organic matter content (OM, determined by loss on ignition at 500 °C) and total phosphorus (TP) in the top 30 cm of the core. Values for OM and TP at each location were calculated by weighting values for each stratum by its relative length and field bulk density. OM was expressed as $\text{g}\cdot\text{g}^{-1}$ and TP as $\mu\text{g}\cdot\text{cm}^{-3}$ referred to 30 cm depth. Soils in the matrix, collected on the same day and analyzed with similar methods, have been published fully elsewhere (Steinmuller and others 2021), but means for several parameters are presented for purposes of comparison in Table 2.

Table 2. Mean (\pm SE) Soil Characteristics of Tree Islands of Three Types in the Coastal Everglades, in Tandem with Similar Statistics for Adjacent Marsh Soils

Soil variables	Porewater salinity	Total phosphorus		Organic matter	Soil depth
Units	(psu)	($\mu\text{g cm}^{-3}$ dw)	($\mu\text{g g}^{-1}$ dw)	(g g^{-1} dw)	(cm)
Coastal Swamp Forest ($N = 5$ sites)					
Tree Island	23.42 ± 5.49	50 ± 10	513 ± 118^b	0.62 ± 0.07^b	116 ± 22^a
Marsh	29.20 ± 4.25	38 ± 2	116 ± 33^a	0.14 ± 0.02^a	94 ± 10^a
Mixed Swamp Forest ($N = 14$ sites)					
Tree Island	11.57 ± 2.09^a	62 ± 7^b	477 ± 37^b	0.56 ± 0.05^b	135 ± 9^b
Marsh	15.02 ± 2.58^b	23 ± 2^a	66 ± 5^a	0.10 ± 0.01^a	101 ± 8^a
Freshwater Swamp Forest ($N = 15$ sites)					
Tree Island	2.24 ± 0.62	36 ± 4^b	352 ± 16^b	0.79 ± 0.04^b	107 ± 7^b
Marsh	2.08 ± 0.56	25 ± 3^a	92 ± 10^a	0.19 ± 0.05^a	67 ± 7^a

Significant differences in habitat means (p value < 0.05) resulting from paired t -tests are indicated by different superscripts.

Due to the wide seasonal variation in salinity in south Florida coastal wetlands, pore water salinity was determined in the centers of all tree islands and adjacent matrix locations during a 10-day period in mid-April 2018, when dry season conditions (low water stage, high evapotranspiration and salinity) were expected to be near their annual peak. Pore water samples were collected by pushing a 10-cm-diameter PVC tube into the sediment to wall off any surface water from entering, then extracting a core from within with a 5 cm diameter \times 30-cm deep soil corer. The core hole was then pumped free of water and allowed to refill from the sides. A pore water sample of approximately 30 ml was drawn and returned to the laboratory, where salinity was determined with an YSI 30 salinity-conductivity meter.

A two-step process was used to derive site-specific patterns of inundation (hydroperiod and water depth) for each tree island. The first step was to estimate historical water levels on a daily basis in the adjacent matrix, and the second was to translate these estimates to the tree island by determining the relative elevations of the two landforms. Matrix water levels were determined by applying a hydrological model, namely MIKE Marsh Model of Everglades National Park (M3ENP), developed by Everglades National Park. M3ENP is an integrated surface and groundwater model that is scaled to a 400 \times 400 m grid throughout the terrestrial wetlands of ENP. The model is calibrated using ENP's network of long-term water level monitoring gauges and produces accurate reconstructions of historical water stages (Tachiev et al 2018). As the data produced by the model were used to calculate mean annual water depths for the 4-year period prior to both 1995 and

2016 surveys, we reconstructed water patterns beginning in January 1991 and extending through 2018. The model produced daily water stage estimates that were subsequently translated into explicit estimates of water depth using localized elevation estimates at thirty points within a 0.85 ha area adjacent to each tree island. Ground elevations from a 2018 Light Detection and Ranging (LiDAR, USGS 2018) survey of ENP were extracted for each point and then averaged to provide a local elevation offset. These were then subtracted from the M3ENP stage estimates to establish a unique sequence of daily depths for the marsh.

To apply the estimates of water regime to the tree island, we calculated a relative elevation (RE) for each island based on the measurements described earlier along our cross-island transect, using the water table as reference. RE was the mean position (in cm) of the water table relative to the soil surface at the two ends of the transect (a positive value due to flooded matrix conditions during all surveys) plus the maximum depth of the water table below the hammock surface. Elevation of the tree island surface was estimated by adding RE to the surface elevation of the surrounding marsh, allowing each island's mean annual water level and hydroperiod to be calculated by application of the M3ENP model.

We also calculated a Bedrock Convexity Index (BCI) to further explore the tree island landform. BCI was equal to the mean distance from the water surface to the underlying bedrock (in cm) at the two transect endpoints minus the mean of the same interval inside the hammock (inner 50% of points, centered on the transect midpoint); positive values indicated a convex bedrock shape, negative values a concave one. Because they are both based

on the assumption of a flat water table, both RE and BCI are rough approximations, as enhanced evapotranspiration at the center of the tree island may draw down the underlying groundwater table. However, at least one local study suggests that the water table concavity created by this process is quite small; Sullivan and others (2014) found that groundwater level beneath a peat-based bayhead (swamp forest) in the Everglades ranged from 1 to 3 cm below surface water in the surrounding marsh over an 18-month period. Given the small size and homogeneous organic soils that were found across the 34 SESE islands surveyed in 2016, we expect that our estimates yield reasonably accurate assessments of their hydrologic condition and landform character.

Finally, we used the ^{210}Pb activity in cores to document recent rates of sediment accretion in tree island and/or matrix at seven SESE locations (Figure 1). At each plot or transect center, an aluminum tube of 7.6 mm diameter and 1 m length was pushed into the soil to extract a core. Soil surfaces inside and outside the tube were compared, and cores with greater than 5% compaction were discarded and a replacement core without compaction was collected. The ^{210}Pb method, based on the disequilibrium between ^{226}Ra and its long-lived decay product ^{210}Pb ($T_{1/2} = 22.3$ y), has been widely used in coastal marine environments to obtain rates of sediment accumulation (for example, Lynch and others 1989; McTigue and others 2019). Here, cores described earlier were sectioned at 1-cm depth intervals to about 30 cm. Activities of ^{210}Pb were determined through isotope-dilution alpha spectrometry of the short-lived ($T_{1/2} = 128.4$ d) granddaughter isotope, ^{210}Po , which is in secular equilibrium with total ^{210}Pb (Flynn 1968).

The total ^{210}Pb activity measured in a sediment sample includes supported and excess ^{210}Pb ($^{210}\text{Pb}_{\text{xs}}$). Supported ^{210}Pb is produced by the decay of its parent ^{226}Ra within the sediment particles and is in equilibrium with ^{226}Ra and is calculated by determining the ^{210}Pb deep in the core where concentrations become constant with depth. Excess ^{210}Pb activity is calculated by subtracting the supported ^{210}Pb from the total ^{210}Pb activity for the intervals of interest in the surface sediment. To interpret the $^{210}\text{Pb}_{\text{xs}}$ depth distribution, we used the constant rate of supply (CRS) model (Appleby and Oldfield 1978), with dating based on the comparison of $^{210}\text{Pb}_{\text{xs}}$ inventories below a given depth with the overall $^{210}\text{Pb}_{\text{xs}}$ inventory in the surface interval.

Data Analysis

We used classification and ordination analyses to discern patterns in tree island assemblages in the SESE and to assess compositional change between the 1995 and 2016 surveys. Sites were first classified through application of an agglomerative hierarchical cluster method with flexible beta (-0.25) linkage (McCune and Mefford 2011). Analyses were applied separately to 1995 and 2016 data from islands sampled in both years, as well as islands sampled in 2016 only. Species present in less than 5% of sites were excluded from the analysis. Species cover ranks were transformed for analysis as follows: the species ranked first in each stand was assigned an abundance of 10, the species ranked second an abundance of 9, and so on; in the 31 stands with more than nine species, species ranked 10 or above were assigned an abundance of 1. These transformed ranks were applied directly in the classification analysis, but in the ordination based on the species-by-site/time matrix, the transformed ranks were relativized to the maximum abundance reached by the species in any stand (Faith and others 1987).

We then examined vegetation–environment relationships, characterizing shifts in species composition with time by locating sites and their temporal trajectories within non-metric multidimensional scaling (NMDS) ordination space in which environmental vectors (pore water salinity, mean water depth, soil organic matter content, and total P) were also expressed (Oksanen et al 2020). Relationships between species composition and potential environmental drivers, including hydro-edaphic characteristics (recorded only during the 2016 survey) and the distance between each site and the nearest coastline, were examined using a vector fitting procedure incorporated in the computer program VEGAN (Oksanen and others 2020). Vector fitting is a form of multiple linear regression that finds the direction along which sample coordinates in ordination space have maximum correlation with the fitted environmental vector. Change across islands sampled in both years was examined for each forest type, as defined on the basis of their 1995 categorization. The significance of movement was again addressed with a vector fitting procedure in VEGAN that tested for differences in ordination scores between sampling years nested within sites. Average trajectory vectors, rooted at the group centroids in 1995, were calculated for forest types that showed significant movement.

RESULTS

Tree Island Composition

The coastal Everglades' three major tree island types became clear once the classification analysis had incorporated about 70% of the information content present in the data (Figure 2). The first group to emerge was Coastal Swamp Forest (CSF), a species-poor (mean tree species number of 4 per island) assemblage of salt-tolerant species led by *R. mangle*, *Conocarpus erectus*, *Laguncularia racemosa*, and *Avicennia germinans* (Table 1). As expected, tree islands in this category were closest to the coast (Figure 1).

Among the remaining tree islands, two groups were evident: Mixed Swamp Forest (MSF) and Freshwater Swamp Forest (FSF). Islands of the former type occupied a band that paralleled the southeastern coast at 2–6 km distance, while FSF's were located further inland (Figure 1). Several flood-tolerant trees, for example *Chrysobalanus icaco*, *Morella cerifera*, *Myrsine cubana*, and *Persea palustris*, were consistently found in both types (Table 1), and two mangrove forest species (*R. mangle* and *C. erectus*) were also abundant in each. *Metopium toxiferum*, a tropical hardwood usually associated with well-drained sites, was common in FSF, but other species characteristic of the region's dry tropical forests occurred far more frequently and at higher abundance in the MSF. The affinity of tropical hardwood species for conditions in MSF contributed to its relatively high species number (mean of 12 species per island compared to 8 species per island in FSF). Variation in species number among forest types was unlikely to have resulted from differences in island size, which at the time of the 2016 survey were small and nonsignificant (mean area of 0.54 ± 0.26 , 0.38 ± 0.07 , and 0.49 ± 0.11 ha in CSF, MSF, and FSF, respectively; $p = 0.68$). The three forest types were also distinguished by their placement in the ordination diagram (Figure 3). Concentrated on the right side (positive values) of NMDS Axis 1, forests classified as Mixed Swamp Forest were associated with relatively high pore water salinity, an elevated water table (water depths that were less negative), and high soil P. In contrast, at great distance from the coast, Freshwater Swamp Forests occupied the opposite pole along Axis 1, with higher organic matter content, lower salinity and soil phosphorus, and a water table that was recessed further below the soil surface (more negative water depth). Lacking the rich tree flora of the other two forest

types, the compositionally distinct Coastal Swamp Forests were placed far to the right along Axis 1.

Soils and Geomorphology

Patterns of variation in environmental conditions between tree island and the adjacent matrix were also striking (Table 2). Organic matter content was far higher inside than outside the tree island in all three types. Soil depth (> 1 m in all three types) was significantly higher in Freshwater and Mixed Swamp Forest than in the adjacent matrix, but not in Coastal Swamp Forest. Soil P in the Mixed Swamp Forest type was about 3 times higher than in the surrounding wetland, and at 12 psu, forest soil salinity was fresher by 4 units. In contrast, at 2 psu, soil salinity in the Freshwater Swamp Forest was not different than in the adjacent marsh (Table 2).

The geomorphology of the coastal tree islands, especially their capacity to build organic soils above the level of their surroundings, is characterized in Tables 3 and 4 (see also Supplementary Figure 1). Relative elevation (RE) differed significantly among forest types ($p < 0.01$), and the Bonferroni multiple comparison test further indicated that Coastal Swamp Forests (mean = 12 cm) were less elevated above the adjacent marsh surface ($p < 0.01$) than Mixed Swamp Forests (mean = 35 cm) or Freshwater Swamp Forests (mean = 44 cm). Although the 9 cm mean RE difference between MSF and FSF was not statistically significant, this physiographic contrast was accentuated by marsh water levels that were higher in the more coastal settings where Mixed Swamp Forests were found (Ross and others unpublished manuscript). The composite effect of these factors was to produce average water tables that were 17 cm closer to the surface in MSF than FSF. Mean annual water levels during the 4-year period prior to 2016 were -0.32 , -0.15 , and -0.03 cm in FSF, MSF, and CSF, respectively, equating to hydroperiods of 11, 68, and 121 days.

The 34 tree islands exhibited considerable variation in bedrock shape around a grand mean of $BCI = +3$, suggesting a minimal trend toward convexity (Table 3). High variability in BCI was also evident within forest types, and this lack of internal consistency led to a nonsignificant difference ($p = 0.57$) among types. RE decreased nominally with increasing BCI, but the association was nonsignificant ($r = -0.25$, $p = 0.16$) (Supplementary Figure 1).

Data from the eight locations for which ^{210}Pb -based soil accretion data were available for tree is-

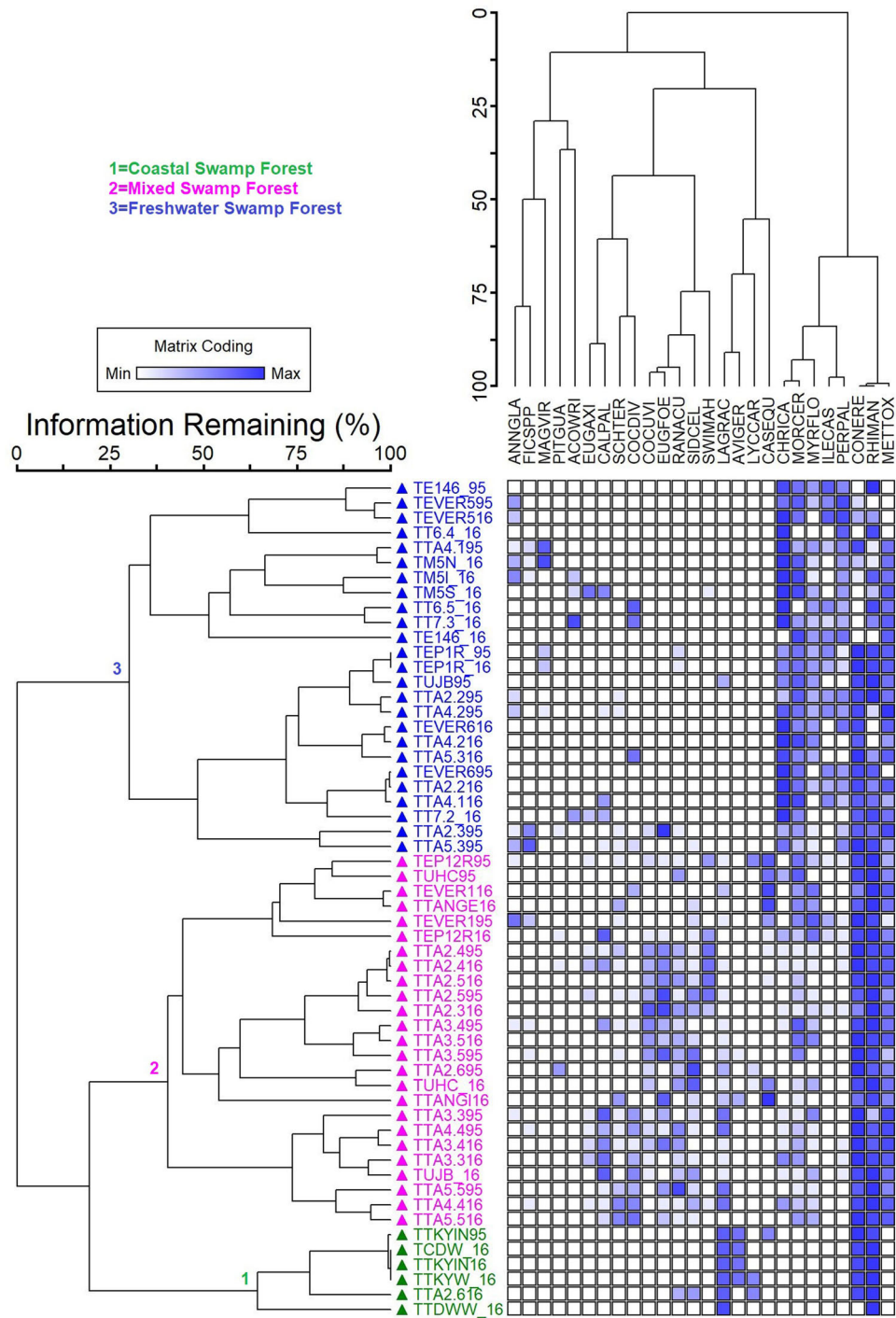


Figure 2. Two-way dendrogram showing site and species dendrograms simultaneously, adjacent to a representation of the main matrix. Shading indicates species rank abundance at each site, recoded as relative values ranging from white (minimum) to blue (maximum across all sites). Three vegetation types derived from classification of 1995 and 2016 compositional surveys are superimposed. Species codes are as in Table 1.

land or matrix indicated that the building of the tree island surface above the adjacent matrix continues today at some but not all sites (Table 4). Two tree islands accreted at rates of 4.3 and 6.4 mm y^{-1} ,

whereas a third accreted at only 0.8 mm y^{-1} . Based on this small sample, mean surface sedimentation rates were 2.38 times higher in tree island than

Table 1. Mean Rank Abundance (ten-point scale; see Methods) of 26 Species in Three Coastal Everglades Tree Island Types in 2016

Species	Coastal Swamp Forest	Mixed Swamp Forest	Freshwater Swamp Forest
<i>Rhizophora mangle</i> (RHIMAN)	10.00	9.50	5.13
<i>Laguncularia racemosa</i> (LAGRAC)	8.20	1.36	0.00
<i>Avicennia germinans</i> (AVIGER)	4.20	0.29	0.00
<i>Lycium carolinianum</i> (LYCCAR)	2.40	0.07	0.00
<i>Conocarpus erectus</i> (CONERE)	7.20	8.71	4.67
<i>Casuarina equisetifolia</i> (CASEQU)	0.00	2.57	0.00
<i>Sideroxylon celastrinum</i> (SIDCEL)	1.00	2.36	0.00
<i>Randia aculeata</i> (RANACU)	0.80	2.36	0.07
<i>Metopium toxiferum</i> (METTOX)	0.00	7.50	6.20
<i>Eugenia foetida</i> (EUGFOE)	0.00	3.14	0.00
<i>Coccoloba uvifera</i> (COCUVI)	0.00	2.14	0.00
<i>Calyptanthus pallens</i> (CALPAL)	0.00	2.64	1.00
<i>Coccoloba diversifolia</i> (COCDIV)	0.00	2.00	1.47
<i>Swietenia mahagoni</i> (SWIMAG)	0.00	1.64	0.07
<i>Schinus terebinthifolius</i> (SCHTER)	0.00	1.64	0.00
<i>Pithecellobium guadalupense</i> (PITGUA)	0.00	0.14	0.00
<i>Eugenia axillaris</i> (EUGAXI)	0.00	0.64	0.67
<i>Myrsine cubana</i> (MYRCUB)	0.00	3.07	2.87
<i>Morella cerifera</i> (MORCER)	0.00	3.36	6.47
<i>Chrysobalanus icaco</i> (CHRICI)	0.00	1.36	9.00
<i>Persea palustris</i> (PERPAL)	0.00	0.43	4.27
<i>Ilex cassine</i> (ILECAS)	0.00	0.21	2.40
<i>Ficus spp</i> (FICSPP)	0.00	0.07	0.13
<i>Annona glabra</i> (ANNGLA)	0.00	0.00	0.87
<i>Magnolia virginiana</i> (MAGVIR)	0.00	0.00	0.80
<i>Acoelorrhaphe wrightii</i> (ACOWRI)	0.00	0.00	1.27

Coastal Swamp Forest, $n = 5$; Mixed Swamp Forest, $n = 14$; Freshwater Swamp Forest, $n = 15$.

matrix ($p = 0.07$), where surface accretion averaged only 1.46 mm y^{-1} .

Forest Dynamics, 1995–2016

Although long-term data for pore water salinity or other soil variables were not available for the coastal tree islands over recent decades, water levels based on the M3ENP model were available beginning in 1991. Linear regressions on daily water stages in the coastal matrix, and by extension the adjacent tree islands, indicated an average increase of 9.4 cm over the period 1991–2016. Considered by forest type, the rates of increase were 3.5 , 3.7 , and 3.1 mm y^{-1} in the FSF, MSF, and CSF islands, respectively (Supplementary Figure 2).

Among the twenty-two 1995 sites resampled in 2016, nineteen remained in the same forest type, while three moved toward a type indicative of higher saltwater influence: two FSF to MSF, and a third from MSF to CSF (Figure 3). Across all sites, movement in ordination space was nonsignificant ($p = 0.27$), as was movement within the Mixed

Swamp Forest type ($p = 0.58$). With only one stand resampled, Coastal Swamp Forest dynamics could not be tested. However, the Freshwater Swamp Forest type exhibited a small but significant upward movement ($p = 0.047$) in Figure 3, that is, toward an area in ordination space occupied by tropical hardwood species.

Examination of temporal change at the species level amplified the patterns suggested in the ordination. Only 2 of 26 species changed in abundance between 1995 and 2016 (Figure 4); *Annona glabra* and *Ficus aurea*, which were minor components of the Freshwater Swamp Forest, decreased in abundance over the period. Among the 24 species whose abundance did not change between surveys were the mangroves and mangrove associates. Most notable of these was *R. mangle*, which was already well established in tree islands in 1995, but expanded its coverage in the adjacent matrix over the 1995–2016 interval (Ross and others unpublished manuscript). Tropical hardwood species associated

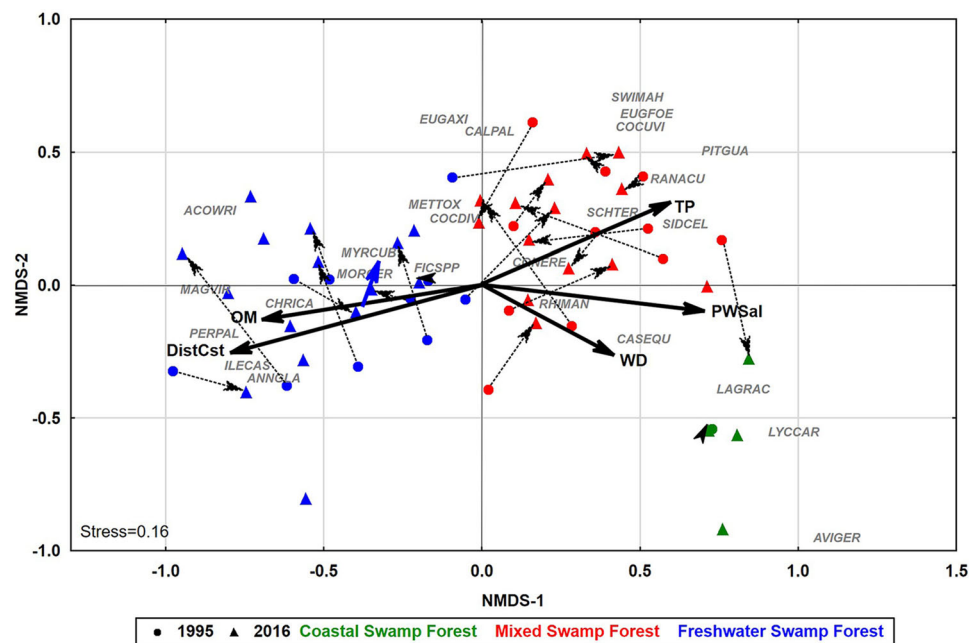


Figure 3. Ordination of tree island communities in two-dimensional NMDS space, based on Site \times Species abundances determined in 1995 and 2016. Dashed arrows indicate 1995–2016 compositional change at individual sites sampled in both years. Solid black arrows indicate strength and direction of best linear fit to ordination for environmental variables determined in 2016 (PWSal = Pore Water Salinity; TP = Total Phosphorus; WD = Water Depth; OM = Organic Matter; DistCst = Distance to Coast). Solid blue arrow indicates average trajectory of sites classified as Bayhead Forest in 1995, the only type to exhibit a significant shift in position between years. Species codes are as in Table 1.

Table 3. Mean (\pm SE) Relative Elevation and Bedrock Convexity Index in Three Coastal Everglades Tree Island Types

Vegetation types	Relative elevation (cm)	Bedrock Convexity Index
Coastal Swamp Forest	12.20 \pm 4.69 ^a	13.77 \pm 5.06 ^a
Mixed Swamp Forest	35.16 \pm 3.12 ^b	0.28 \pm 8.17 ^a
Freshwater Swamp Forest	44.05 \pm 4.11 ^b	1.49 \pm 5.76 ^a

Means superscripted by the same letter do not differ (Bonferroni multiple comparisons test, p value < 0.05).

Table 4. Surface Accretion Rates Determined at nine Tree Island or Marsh Sites in the Coastal Everglades

Site	Landcover	Forest type	Accretion (mm y^{-1})	Depth interval (cm)
2.2	Forest	Freshwater Swamp	4.3	0–14.5
2.4	Forest	Mixed Swamp	6.4	0–7.5
2.6	Forest	Mixed Swamp	0.8	0–3.5
2.2	Marsh	–	2.2	0–7.5
2.4	Marsh	–	1.45	0–6.5
3.4	Marsh	–	1.45	0–4.5
5.5	Marsh	–	1.4	0–6.5
EP10R	Marsh	–	1.7	0–7
EVER1	Marsh	–	0.53	0–8.5

with the Mixed Swamp Forest likewise exhibited no change in rank abundance over the period.

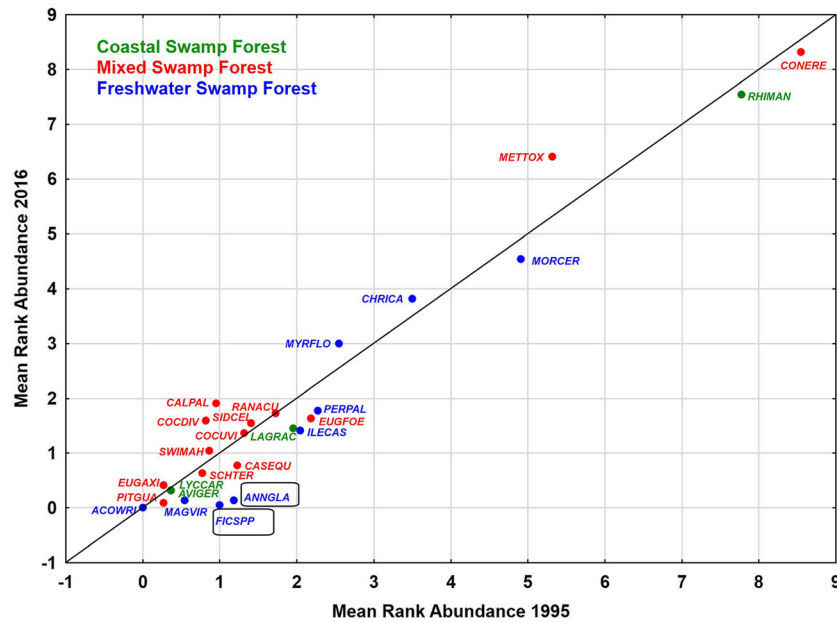


Figure 4. Mean rank abundances of species in 22 tree islands sampled in both 1995 and 2016. Species categorizations are based on the forest type in which they achieved their highest rank abundance in 2016 (see Table 1). Species codes are as in Table 1. Species with significantly different mean rank abundances between years (p value < 0.05) are enclosed in rectangles.

DISCUSSION

In wetlands of the southeastern coastal Everglades, tree islands arranged in a zonal pattern relative to the Florida Bay coast exhibited little change in composition during 1995–2016, a period during which sea level at nearby Key West increased by 8.5 cm (<http://www.psmsl.org>, accessed November 9, 2020). Mesophytic tropical hardwood species remained an important component of the tree assemblages, despite the continued dominance of halophytes such as red mangrove (*R. mangle*) and buttonwood (*C. erectus*). The stasis we observed in the tree islands contrasted sharply with rapid vegetation change that prevailed over the same period in the adjacent marshes, where halophytic and salt-tolerant species replaced freshwater-dependent species across the upper reaches of the watershed (Ross and others unpublished manuscript). An important contributing factor in the stability of the tree islands was their inherent capacity to build organic soils above the level of the surrounding wetland surface. While the vegetation dynamics in marsh and forest continue to unfold, the environmental data assembled in this study provide further clues regarding the future response of the tree islands.

Tree Island Geomorphology

Tree islands in the SESE developed in a different geological setting than in other areas of South Florida. In these coastal wetlands, an impervious basal marl sediment blankets the Pleistocene limestone bedrock and serves to decouple the fluctuations of surface water from the groundwater (Gleason and Stone 1994). Tree islands with organic soils form where there are breaks in the basal marl due to karst processes such as surface depressions, intense epikarst development or erosional remnant bedrock (Meeder and Harlem 2019). These isolated organic landforms serve as outlets for fresh groundwater when hydraulic pressure from upstream in the Everglades is high (Tropical BioIndustries 1990). An additional freshwater source, recharge by precipitation, is enabled by the slight elevation of the island surfaces above the adjacent marsh, which is greater in the interior forest types than in Coastal Swamp Forest. Access to these two freshwater sources helps to buffer the forests against saltwater intrusion—an effect that was most evident in Mixed Swamp Forest, where the surrounding marshes sometimes develop high soil salinities. In addition, a geochemical trait that tree islands of the coastal plain share with those in other settings is their function as sinks for phosphorus, the limiting nutrient in most Everglades wetlands. Though P concentrations in coastal tree

islands were 1–2 orders of magnitude less than those observed in “fixed” islands formed on bedrock outcrops in the interior Everglades (Wetzel and others 2011; Ross and others 2006), P storage in coastal tree island sediments far exceeded those in the adjacent matrix (Table 3). Relative to these adjoining ecosystems, the favorable soil, water, and nutrient conditions in coastal Everglades tree islands serve to explain their apparent productivity and prominence in the landscape.

Forest Composition

In the eastern portion of the study area, we found strong zonal patterning among the compositional assemblages identified by cluster analysis: Mixed Swamp Forest was sandwiched in a narrow band between Coastal Swamp Forest near the shoreline and Freshwater Swamp Forest extending into the interior (Figure 1). This well-defined pattern draws attention not only to the strength of coastal influence in this area but also to the responses of dominant or locally diagnostic species to the environmental factors associated with it, especially to interiorward decreases in water level, salinity, and soil phosphorus, and increases in organic matter content (Figure 3). However, due to its large complement of tropical hardwood species, the Mixed Swamp Forest’s intermediate positioning with respect to water depth along the environmental gradient was unexpected. Elsewhere in the region, these species are associated with rarely flooded limestone substrates, and we had anticipated that relative elevation in these forests would rise to a high enough level that similar mesic conditions would prevail in the SESE islands. Though MSF islands are elevated by an average of 35 cm above the adjacent wetland, high surrounding water level produces tree island flooding for several months per year and likely causes the organic soils to be saturated for much of the annual cycle.

The Mixed Swamp Forest is a melting pot for tree species of disparate ecological settings. Ross and others (2014) divided this community into two units (Mixed Swamp Forest and Mixed Mesic Forest), but our current analysis did not justify that subdivision. Notably, the Mixed Swamp Forest includes both species usually associated with South Florida’s halophytic forests (*R. mangle* and *C. erectus*) and freshwater swamp forests (*M. cerifera* and *C. icaco*), in significant and sometimes exceptionally high abundances. Mixed with these are distinctive tropical hardwood species common to the extensive tropical forests of the Florida Keys, either in interior (*M. toxiferum*, *E. foetida*, *C. pallens*, and *S.*

mahagoni) or edge positions (*S. celastrinum*, *R. aculeata*, *C. uvifera*, and the invasive exotic *S. terebinthifolius*). Saha and others (2011) described forests of comparable mixed composition on sands and rocklands exposed to brackish water conditions near the Florida Bay coast, and a recent vegetation map of south Florida recognized a similar species mixture as Transitional Bayhead Forest, which extended in a coast-parallel zone along much of the southern Everglades (Ruiz and others 2017). Tree islands in which tropical hardwoods characteristic of upland settings occur in mixture with mangroves and freshwater swamp forest trees have also been reported from the coastal peten region of northern Yucatan, where fresh groundwater from the interior periodically mixes with saline coastal waters (Wilson and Williams 1987; Olmsted 1993). Unlike the SESE tree islands, these petenes—circular forested islands set over limestone depressions serviced by freshwater springs—feature mineral soils recessed from or level with the surrounding wetland surface. Despite their ready access to fresh groundwater, the petenes seem to lack the soil-building capacity of the SESE islands and therefore share a vulnerability to rapid sea-level rise.

Compositional Dynamics

Three resampled stands changed to a type indicative of higher salt-tolerance during the two decades after our initial study, but community- and species-level analyses both suggested that changes in tree composition in SESE tree islands were minor and difficult to attribute to a single environmental factor (Figures 3 and 4). Small but significant shifts in community composition and species abundance were observed in the Freshwater Swamp Forest and several taxa associated with it. However, in light of the proximity of Mixed Swamp Forests to a coast experiencing rising seas, the absence of change in this forest type, which harbors a broad mixture of glycophytic, mesophytic, and halophytic trees, was perplexing. The existing literature indicates that the high salinities observed in MSF stretch the limits expected for trees of the freshwater swamp (Krauss and others 2007). Elevated soil salinity may not be as problematic for the tropical hardwoods, which are all common in upper Florida Keys rockland forests where groundwater salinity may exceed 20 psu (Ross and others 1992) and which have a range of responses to drought stress that may allow them to tolerate or avoid episodically high salinity. However, the water table in Keys hardwood forests is usually 50 cm or more below the thin soil surface, so these

brackish water conditions are rarely combined with the periodic inundation and extended soil saturation that characterize the tree islands of the mainland coast. Moreover, tropical hardwoods in the Keys do not grow in intimate mixture with mangroves, which are thought to increase salinities in the vadose zone through their capacity to transpire at high soil salinities (Sternberg and others 2007; Subedi and others 2020). Thus, only the mangrove species, whose presence in the MSF forest might increase the stress experienced by their tropical hardwood neighbors, seem to have both the salt- and flood-tolerance necessary to thrive in all tree island types sampled here. Given the sea-level rise-driven saltwater intrusion taking place in the region (Park and others 2019), one might hypothesize that the MSF assemblage in particular is unstable and transient. What then explains its recent stability?

The first possibility, of course, is that the premise for our hypothesis is incorrect and that the fundamental environmental niches of the tropical hardwood and bayhead species in the mixture—especially the capacities of their root systems to function in saturated soils with elevated porewater salinities—are broader than previously believed. With the possible exception of the halophyte *R. mangle*, the environmental tolerances of none of the tree species we encountered are known in detail for the combination of soil and water conditions experienced by the MSF assemblages. Thus, the hypothesis that this rare Everglades community is stable under current conditions cannot be discounted.

However, a more likely explanation for the lack of compositional change lies in recognizing that transitions from one stable state to another involve nonlinear relationships among multiple species, structural guilds, and processes (for example, Burkett and others 2005). One result of this complexity is that the time and place at which ecological thresholds will be exceeded cannot be directly inferred from a few environmental factors, even very influential ones. Moreover, biological inertia (Von Holle and others 2003) may cause an environmental threshold, once passed, to be masked for some time (Milchunas and Lauenroth 1995). In such cases, the true state of affairs may not appear contemporaneously across all elements of the community and may not become widely evident until the system is pushed beyond its tolerance thresholds by a major disturbance.

An example of time lag in the ecosystem transition process comes from freshwater forest islands on Florida's Gulf of Mexico coast. Here, failures of

recruitment among the dominant tree species *Sabal palmetto* and *Juniperus virginiana* provided the first evidence that stresses associated with increased tidal flooding and salinization of the rooting environment were leading to major community changes (Williams and others 1999). However, it was only in the aftermath of a multi-year drought that mortality among adult trees accelerated, eventually cascading into large-scale changes in the wetland habitat mosaic (Williams and others 2003; DeSantis and others 2007; Langston and others 2017). Unlike the Williams and others (1999) research, sampling in the SESE tree islands did not address regeneration failure, but the recent history of natural disturbances in the area is well known. Extensive fires have not been noted in the region since 1948 (Redwine and others 2019), and in the eastern section of the study area the last instance in which temperatures dropped low enough to impact sensitive mangrove vegetation was in 1996 (Zhang and others 2016). During the interval between our two sampling periods, several hurricanes delivered maximal tidal surges on the Gulf Coast region of ENP (<https://www.nhc.noaa.gov/data/#tracks>), but Hurricanes Katrina and Wilma (2005) did not affect the SESE tree islands (Ruiz and others 2017), nor did Hurricane Irma (2017). Given the marked changes that have already taken place in the composition of adjacent marsh communities (Ross and others unpublished manuscript), one might imagine that the next major disturbance event to directly strike the SESE biotic landscape could initiate the inevitable loss of the freshwater swamp and tropical hardwood components from the diverse Mixed Swamp Forests.

Management Considerations

As a distinctive component of the coastal habitat mosaic, tree islands have long provided a characteristic group of plant and animal species with resources unavailable elsewhere nearby. Despite the relative stability of their composition over the last two decades, the Mixed Swamp Forests and Freshwater Swamp Forests we studied are clearly at different places along a path to becoming mangrove hammocks (Lugo and Snedaker 1974), a forest type associated with interior basins in coastal carbonate settings worldwide (Woodroffe 1992). The biphasic nature of the freshwater landscape presents ENP managers—whose mandate emphasizes maintenance of whole landscapes above protection of individual components within them—with the challenge of providing conditions beneficial for both matrix and forest. Logically, the water regime

that produced one phase also produced the other, so the goal should be to recreate that water regime. However, rising seas and salinities in the coastal zone complicate the task, particularly due to the more rapid response of the marsh matrix to such changes (Ross and others 2014; Ross and others unpublished manuscript). The management conundrum is therefore to come up with solutions that raise the collective habitat value of the landscape value as much as possible. Directing more fresh water toward coastal wetlands appears to be the primary way to contribute to this goal.

Water management of most SESE tree islands is controlled by the South Florida Water Management District in cooperation with the US Army Corps of Engineers. Given the NPS mission to: "...preserve intact our natural resources for the enjoyment of future generations" (Organic Act of 1916; National Parks and Recreation Act of 1978), the goal of management is to stabilize this landscape as much as possible through the delivery of freshwater. As prescribed in Florida Statute Section 373.042, state law requires consistent flows (no less than 105,000 acre* ft 365 day moving sum) through the five coastal creeks between Taylor River and the C-111 canal. This legal framework helps reduce the risk of high salinity for long durations. Based on vegetation–environment relationships such as those presented here, resource managers believe that enhanced freshwater deliveries beyond those mandated by law are needed to alleviate the primary stress associated with saltwater intrusion, and plans to enhance water delivery are ongoing as part of the Comprehensive Everglades Restoration Program (CERP). The essence of this strategy is restoring freshwater flows to include both high volumes during wet conditions and consistent flows as long as possible during dry times, thereby flushing residual salts from soil porewater. However, the ecological effects of freshwater flooding itself are likely to vary along a subsidy-stress gradient (Odum 1979), introducing considerable uncertainty into stewardship of the landscape and the tree islands within it. By 2060 it is expected that annual rates of SLR might increase three–fivefold (Park and others 2017) and extreme events will continue to occur unpredictably, so we recommend an adaptive management framework that is firmly based on documented ecosystem responses and a willingness to change course if necessary.

The current composition of SESE tree islands may change abruptly as a consequence of an extreme event, or an interaction of events occurring sometime in the next four decades, but their con-

tinued presence as forested patches within a low scrub mangrove matrix promises to provide important habitat services for many years to come. Cross-referencing recent accretion rates (Table 4) and observed soil depths (Table 2) suggests that they have persisted for hundreds of years or more as productive organic islands in a carbonate coastal plain. Moreover, the structural stability they have exhibited during the recent era of more rapid change in sea level is remarkable compared to the decline of tree islands in the Everglades peatland, where dewatering and fires have led to systematic loss of woody cover since the 1950's (Redwine and others 2019).

Based on intermediate sea-level rise projections (Sweet and others 2017; Park and others 2017), a continuation of the two highest ^{210}Pb -derived sediment accretion rates listed in Table 4—which to our knowledge are the first reported for coastal tree islands—would allow them to remain as emergent landforms for many more years, as they have for centuries. In contrast, recent soil accretion in the third island we sampled (0.8 mm y^{-1}) lagged far below the current rate of sea-level rise, illustrating the spatial and perhaps temporal variability in productive capacity (and long-term prognosis) that is likely to define the fate of these landforms as sea-level rises.

So rising seas will alter but not eliminate the hydrogeologic conditions responsible for the stable persistence of tree islands in the coastal landscape. Mangrove tree islands are common along many south Florida coastlines (including the southern reaches of our study area), where they provide reliable habitat for migrating and resident passerines (J. Lorenz personal communication), and roosting and nesting sites for large flocks of wading birds (SFWMD 2019). While accelerating sea-level rise may have already surpassed the rate of soil accretion in these landforms, their value as forested centers of biological activity should persist until water levels become too deep for mangroves to reestablish after periodic disturbances.

As the landscape changes over the next four decades, only the most productive tree islands will remain present as increasingly isolated, freshwater-supplemented, nutrient-rich islands in a saltwater-intruded wetland. The sharp ecological distinction between tree island and surrounding wetland vegetation may be obscured for a time. However, the high inherent productivity of many of the tree islands, built on hydrologically and sedimentologically stable characteristics of the landscape, will allow these features to persist for many years, supporting their capacity to build organic soils and

maintain their surfaces above the level of the encroaching sea.

Well past 2060, as the wetlands around them are eventually submerged and merge into an expanded Florida Bay, it seems likely that the few tree islands that do manage to persist through these profound changes will become increasingly isolated, but their functions as biological refuges and geomorphologic landmarks in this watery landscape may only be enhanced. The fate of any individual tree island in the next millenia cannot be known. However, the geophysical and ecological information collected over several decades and presented here highlights the resilience of these slightly elevated forested landforms in the coastal Everglades and focuses attention on the use of freshwater flow to maintain their existing species composition for the next four decades.

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