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RESEARCH ARTICLE

Transient vegetation dynamics in a tropical coastal wetland: Sea-level rise, glycophyte retreat, and incipient loss in plant diversity

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Abstract

Aim and Questions: Sea-level rise has been responsible for extensive vegetation changes in coastal areas worldwide. The intent of our study was to analyze vegetation dynamics of a South Florida coastal watershed within an explicit spatiotemporal framework that might aid in projecting the landscape's future response to restoration efforts. We also asked whether recent transgression by mangroves and other halophytes has resulted in reduced plant diversity at local or subregional scales.

Location: Florida''s Southeast Saline Everglades, USA.

Methods: We selected 26 locations, representing a transition zone between sawgrass marsh and mangrove swamp, that was last sampled floristically in 1995. Within this transition zone, leading- and trailing-edge subzones were defined based on plant composition in 1995. Fifty-two site × time combinations were classified and then ordinated to examine vegetation–environment relationships using 2016 environmental data. We calculated alpha-diversity using Hill numbers or Shannon–Weiner index species equivalents and compared these across the two surveys. We used a multiplicative diversity partition to determine beta-diversity from landscape-scale (gamma) diversity in the entire dataset or in each subzone.

Results: Mangrove and mangrove associates became more important in both subzones: through colonization and establishment in the leading edge, and through population growth combined with the decline of freshwater species in the trailing edge. Alpha-diversity increased significantly in the leading edge and decreased nominally in the trailing edge, while beta-diversity declined slightly in both subzones as well as across the study area.

Conclusions: Recent halophyte encroachment in the Southeast Saline Everglades continues a trend evident for almost a century. While salinity is an important environmental driver, species' responses suggest that restoration efforts based on supplementing freshwater delivery will not reverse a trend that depends on multiple

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interacting factors. Sea-level-rise-driven taxonomic homogenization in coastal wetland communities develops slowly, lagging niche-based changes in community structure and composition.

KEYWORDS
coastal tropical wetland transient vegetation dynamics, Florida's Southeast Saline Everglades, USA, glycophyte retreat, halophytes encroachment, incipient loss in plant diversity, mangroves and associates' transgression, sea-level rise, wetland restoration through freshwater delivery

1 | INTRODUCTION

The natural world is replete with environmental gradients that underlie zonally arranged biotic sequences. Temperature gradients in lakes, moisture gradients in mountainous topography, light gradients beneath forest canopies come to mind. Notably, many of these gradients are or will be impacted by climate change and its byproducts. One gradient of particular interest is the transition from marine or estuarine waters to freshwater wetlands along modestly sloped coastlines. In tide-dominated coastal landscapes such as these, vegetation structure is largely determined by the interplay of sea-level across variable geomorphologic surfaces (Woodroffe, 1990). As sea-level rises in such systems, it is reasonable to hypothesize that present zonal vegetation patterns will be retained, albeit with current communities shifted in place, altered in extent, and/or changed in composition (Krauss et al., 2011; Battaglia et al., 2012). The details of these dynamics are of much interest to wetland managers and restoration practitioners who hope to maintain viable coastal wetlands into the future.

Coastal wetlands vary markedly in form and setting throughout the world. In locations experiencing rapid sea-level rise, however, environmental conditions are rearranged: the landscape is reshaped, water levels are raised, and saltwater is brought further inland. Other global environmental drivers change as well. Warming temperatures may reduce the incidence of impactful freeze events (Woodward, 1987), and changes in coastal climate often interact with human activities to alter the frequency or intensity of fire (Williams-Jara et al., 2022). These changes in the background environment, which benefit some species and are experienced as stresses by others, drive community assembly forward, but the assembled flora and fauna also have their roles to play. Positive and negative feedbacks between species and their environment create non-linear dynamics and alternative community states that are recognizable in the landscape (Beisner et al., 2003).

Coastal wetlands are distinctive in occupying environments interposed between starkly different systems, that is, marine or estuarine waters and terrestrial ecosystems. In many of these landscapes, plant species and communities are aligned in regular zonal patterns relative to the sea. These distributions have been well explored in salt marsh transitions to upland forest, where tolerance to salinity stress, resource use efficiency, and competitiveness among the resident flora seem to be determinative (Brinson et al., 1995; Penning et al., 2005; Shirley & Battaglia, 2006; Schoolmaster & Stagg, 2018). Long-term and appropriately scaled data on temporal shifts in these zonation patterns can be useful in verifying and further developing models based on these processes, but such data are currently limited. This information is especially important for accurately predicting the complex impacts of global climate change forces on landscapes that link coastal marshes or swamps with the broad set of freshwater wetlands supplied by upstream water sources (Herbert et al., 2015). In coastal wetlands moving directionally in response to sea-level rise, these would ideally focus on the boundaries between adjacent ecosystems, where one zone encroaches on the next one upslope (Smith & Goetz, 2021).

One extensive coastal wetland whose transitional character was recognized long ago is Florida's Southeast Saline Everglades (SESE; Figure 1), where the forces driving change in a mangrove-to-freshwater marsh transition were first described by Egler (1952), based on 1940 aerial photography and 1948 field observations. Noting the then-recent expansion of red mangrove (*Rhizophora mangle* L.) in the SESE marsh, Egler predicted a continuing increase in mangrove dominance throughout the coastal zone, in part due to saltwater intrusion associated with the diversion of freshwater for agricultural and residential uses. However, he did not account for the accelerating rise in sea-level that would characterize future decades, and thus did not speculate on how it would affect the dynamics of coastal zonation or the spread of *R. mangle* into the freshwater ecosystems of the southern Everglades. Egler also described a sparsely vegetated "white zone" that had separated coastal mangrove swamp from freshwater marsh. A 1995 survey of the region's coastal landscape (Ross et al., 2000) found that the white zone – whose distinctive appearance on aerial photos results from the high reflectivity of the exposed marl surface – had expanded by 1.5–3.0 km to become one of the most extensive vegetation associations in the region. The expansion of ecotonal zones under the press of global change is a form of transient vegetation dynamics that may not be unique to the SESE.

Three-quarters of a century has passed since Egler's seminal work. During this period, sea-level at nearby Key West rose by ca 19 cm (Parkinson & Wdowinski, 2022), and the South Florida canal network that effectively drains urban and agricultural lands north of the SESE was completed. The Comprehensive Everglades Restoration Program (CERP), one of the world's largest wetland restoration projects, was undertaken, with objectives that included

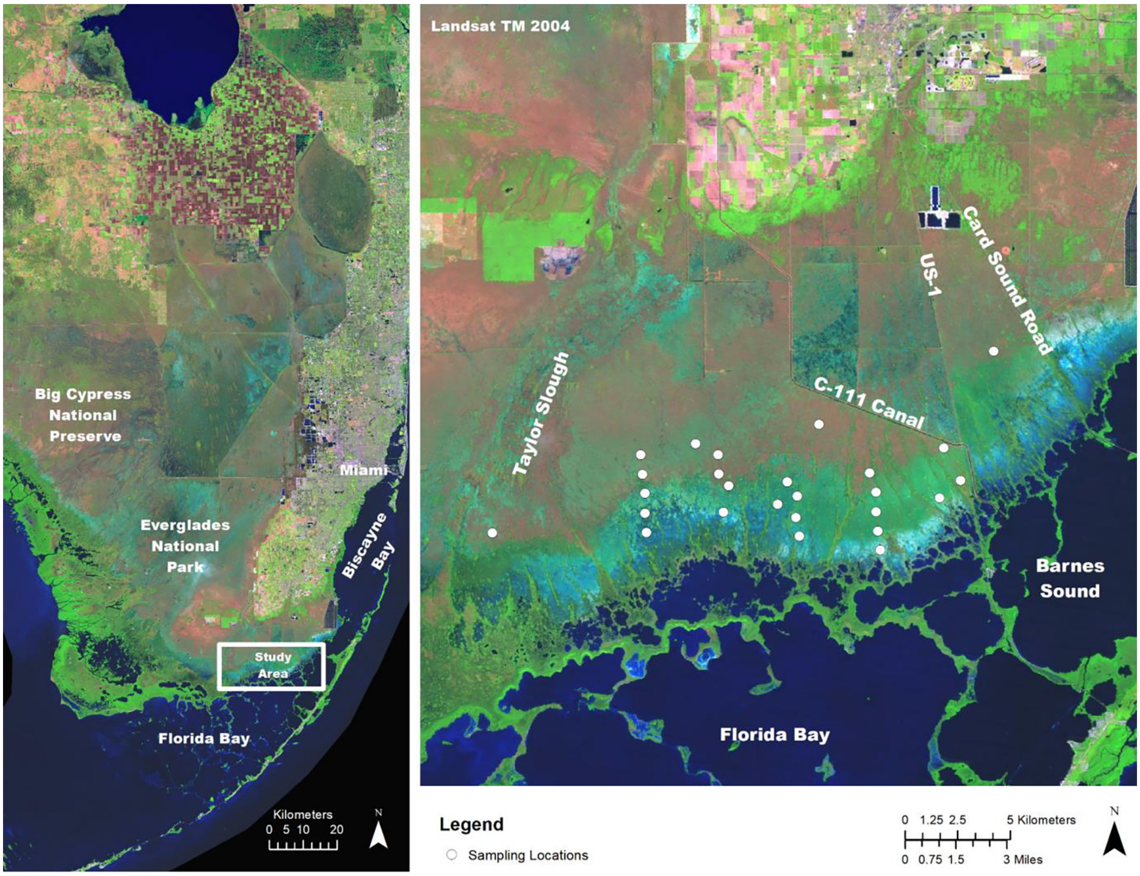


FIGURE 1 Southeast Saline Everglades USA study area and sampling points location on left and right panel respectively.

restoring freshwater flow and ecosystem function to coastal wetlands and estuaries, thereby providing a counterweight to the directional stress of sea-level rise and saltwater intrusion. To develop a prognosis for these efforts, which in the SESE have only recently begun, it is important to gain a more detailed understanding of vegetation dynamics in the coastal transition zone over an extended period (Reed et al., 2022). In this paper, we describe those dynamics based on 2016–2018 vegetation and environmental sampling within our 1995 plot network.

The rapidly rising sea-level makes management of coastal landscapes a difficult proposition, one requiring a focus on clear, long-term objectives. One of these is support of biological diversity, a prominent objective in most if not all ecological restorations (Hughes et al., 2017), including the one currently underway in the coastal Everglades (Richardson et al., 2014). While many components of biological diversity may be assessed, the focus in our study was on the diversity of vascular plants. Questions about diversity take on added dimensions when viewed at multiple scales and within a spatiotemporal context that incorporates directional movement in the landscape's initial zonal pattern. To do so, we concentrated our analyses on an elongated transition zone (Yarrow & Marin, 2007) comprising the junction of two zones that cross the SESE from east to west. The southern trailing edge of the transition zone was defined as the zone in which plant communities were dominated by *Rhizophora mangle* (red mangrove) in 1995, and hence had already exhibited substantial tidal influence by that time. In contrast, in the northern leading edge, in which *Cladium jamaicense* Crantz (sawgrass) and other Everglades freshwater marsh associates prevailed during the 1995 survey, notable coastal influence had not previously been demonstrated. Our expectations were that a re-survey of the area would reveal continued coastal transgression during 1995–2016, and that both trailing and leading-edge communities would exhibit distinct changes in both composition and patterns of plant diversity.

More specifically, we hypothesized that in the early stage of encroachment represented by the transition zone's leading edge, the expansion of white-zone assemblages into freshwater marshes would result in gains in within-plot (alpha, α)-diversity, as glycophytes, or plants whose growth is inhibited by saline soils (Oxford English Dictionary Online; but see Cheeseman, 2015), would not yet have experienced severe salt stress. Concurrently, at the trailing edge of the advancing transition zone, we expected an increase in the abundance of previously established halophytes (plants adapted to grow in saline conditions) along with extirpation or decline of the few remaining glycophytes, resulting in decreased plant diversity. Together, we anticipated that these two subregional trends and the metacommunity processes they represent would produce a broad homogenization of vegetation composition and structure, that is, reduced beta (β)-diversity across the transition zone as a whole. Though they are not directly commensurable, plant β-diversity and habitat diversity pertinent for higher trophic levels have displayed strong positive associations in some landscapes (Jankowski et al., 2013; Zellweger et al., 2017), and such parallels would amplify the impact of declining plant taxonomic diversity. In consequence, the issue of sea-level-driven biotic homogenization would extend far beyond South Florida to ecosystem function in wetlands that occupy low-gradient, undeveloped coastlines worldwide.

2 | METHODS

2.1 | Study area

The SESE today is a complex coastal landscape made up of a series of zonally arranged ecosystems bordering on estuarine waters (Figure 1). Perpendicular to the coast these zones include: (a) a narrow fringe of low mangrove or tropical hardwood forest bordering directly on Florida Bay or Barnes Sound, (b) a set of coast-parallel lakes or lagoons, bordered on the north by dense mangrove scrub, (c) a "white zone" in which scattered dwarf mangroves predominate and herbaceous associates provide sparse understorey cover above exposed marl sediments, and (d) a freshwater marsh dominated by *C. jamaicense*. Using 1940 aerial photography, Egler (1952) described a similar zonal arrangement of seven coast-parallel vegetation belts, in which the "white zone" was a region in which short-statured *R. mangle*, *C. jamaicense*, and *Eleocharis cellulosa* Torr. (spikerush) formed an open mixture that graded into sawgrass marsh to the north. While retaining its underlying zonation, recent mapping of the SESE landscape (Ruiz et al., 2017) shows substantial change since Egler's time, exemplified by an expansive interiorward shift of the white zone. Using the coastward extent of the continuous sawgrass marsh as a marker, the position of the white zone shifted northward at a rate of about 32 m year^{-1} between 1940 and 2017 (Figure 2).

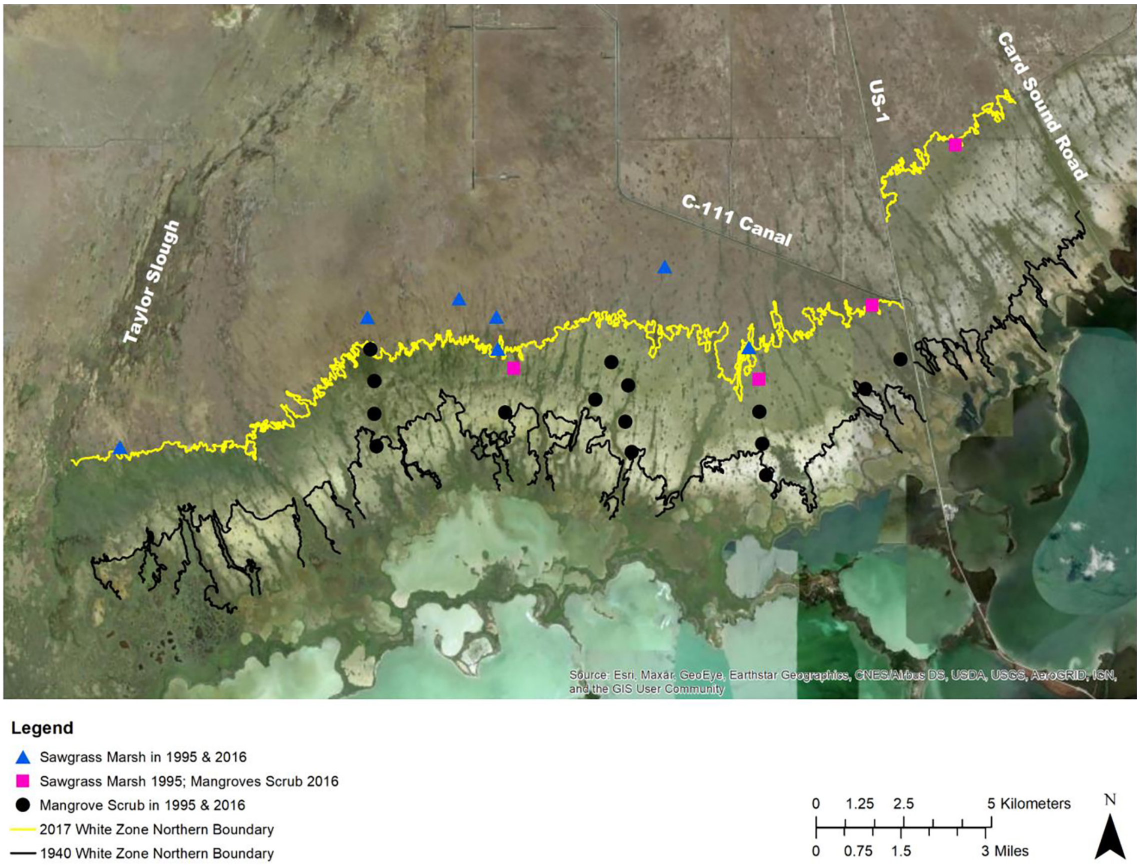
The modal soils of the wetland matrix in this region are biologically produced marls (Fluvaquents of the Perrine or Pennsuco series) formed under relatively sparse graminoid cover in freshwater marshes through the metabolic activities of a periphytic algal community (Gleason et al., 1974). Interspersed within the marsh are tree islands – slightly raised forest patches set above slight depressions or outcroppings in the limestone bedrock (Ross et al., 2021). Unlike those in the surrounding wetland matrix, tree island soils are organic-rich, primarily Medisaprists of the Terra Ceia or Pahokee series (USDA-NRCS, 1996; Steinmuller et al., 2021). The broad slope of land is negligible, with elevation typically rising by only 10 cm over distances of 1 km or more (see Ross et al., 2002; Meeder et al., 2017). Thus, small increases in freshwater discharge or water level in the adjacent estuaries can augment flooding across many hectares.

Our study focused on supratidal and non-tidal wetlands of the SESE, which extend from Taylor Slough to the east, ultimately discharging southward into Florida Bay or Barnes Sound (Figure 1). In our 1995–96 work, herein referred to as the 1995 study, we sampled matrix vegetation and adjacent tree islands at 54 locations between Taylor Slough and Biscayne Bay. In 2016–2018, referred to as the 2016 study, we used similar sampling methods to re-examine a coastal network that overlapped considerably with that of the earlier study, but focused more narrowly on transitional areas inland from the intertidal swamps, that is, the white zone and the sawgrass marsh immediately interior to it. These subregions were readily distinguished based on their vegetation composition in the 1995 study – mangrove-dominated and sawgrass-dominated, respectively – and represented the trailing and leading edges of the directional, sea-level driven SESE transition zone. We resampled 26 sites that were visited in the first study, arranged along seven coast-normal transects of 1–6 sites each (Figure 1). The easternmost "transect" is a single wetland site that drains into Barnes Sound, a subbasin of Biscayne Bay, where semidiurnal tides of 0.3 m amplitude are typical, and salinity is usually in the range 15–35 parts per thousand (ppt) (Wang et al., 2003). The next five transects comprise the headwaters of northeastern Florida Bay, where tides are irregular and frequently weather-driven; salinity averages only 18 ppt in the coastal embayments below our sites (Lee et al., 2008; Marshall, 2017). The westernmost "transect" consists of a single site in Taylor Slough, a conduit for Everglades freshwater supplying Central Florida Bay.

2.2 | Sampling methods

This paper presents analyses of the low matrix of marsh and scrub vegetation, expanding on recent research on the dynamics of adjacent tree islands within the same network (Ross et al., 2021). Surveys of vegetation and soils were done during the 2016–18 dry seasons (November through April), a six-month period during which only ca 25% of South Florida's annual precipitation normally falls (Duever et al., 1994); notably, however, the seasonal recession in Everglades water levels typically lags a month or two beyond the beginning of the climatic dry season. To characterize vegetation composition, we determined the cover of all vascular plant species in 30 1-m^2 subplots distributed evenly along a 360° arc at 50 m distance from the plot center; in all, 780 subplots were sampled across 26 sites previously sampled in 1995. Nomenclature for species follows the Atlas of Florida Plants (Wunderlin et al., 2023) (Appendix S1). Water depth was measured to the nearest 1 cm in each subplot, and soil depth was determined by probing to bedrock. A single soil core of 5.7 cm diameter and aproximately 30 cm length (average = 27 cm) was extracted and returned directly to the lab, where the profile was described, and subsamples of each stratum were prepared for complete soil analysis (Steinmuller et al., 2021). Only soil organic matter content and total phosphorus were evaluated by stratum within the profile, then summarized for the top 30 cm of soil by weighting values for each stratum by its relative length and field bulk density. Organic matter was expressed as g g^{-1} and total phosphorus (TP) as μg cm^2 surface area to 30 cm depth.

Due to the wide seasonal variation in salinity in South Florida coastal wetlands, we determined pore water salinity at all sites during an 18-day period in late April 2018, when dry-season conditions (low water stage, high evapotranspiration) were near their annual peak.



Source: Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

FIGURE 2 The interior borders of the white zone in 1940 and 2017, based on the approximate coastward extent of sawgrass marsh on images from those years. Boundaries are superimposed on 26 sampling locations with dominant vegetation in 1995 and 2016 as indicated. During 1940–2017 the white zone (sparsely vegetated area between coastal mangrove swamp and freshwater marsh whose distinctive appearance on aerial photos results from the high reflectivity of the exposed marl surface) border moved inland by an average rate of 30 m year^{-1} west of US Highway 1 (US-1) and 42 m year^{-1} east of the highway, where freshwater inflow from upstream sources is entirely interrupted by canals and levees.

Pore water samples were collected at the plot centers by pushing a 10-cm diameter PVC tube into the sediment to wall off surface water from entering, then extracting a soil core with a 5-cm diameter × 30-cm deep coring device. 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 lab, where salinity was determined with a YSI 30 salinity-conductivity meter.

2.3 | Hydrologic analyses

Site-specific patterns of inundation were estimated by applying a hydrologic model, namely M3ENP, developed by Everglades National Park (ENP), in combination with the direct measurements of water depth during vegetation sampling. M3ENP is an integrated surface and groundwater model scaled to a 400 m × 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 good reconstructions of historical water patterns (Tachiev et al., 2018). M3ENP was used to reconstruct water stages beginning in January 1991 and extending through 2015. Local ground elevation was estimated by calculating the difference between the modeled daily stage estimate on the date of field sampling and the average of the 30 water depths measured onsite on the same day. With this estimate of elevation, water depth was estimated daily throughout the periods of interest, and annual hydroperiod and mean water depth were determined for each site.

2.4 | Community compositional analyses

To facilitate comparison of matrix vegetation in the 1995 and 2016 surveys, analyses were based on species frequencies (proportion of the 30 subplots in which each species was present), as sampling in the 1995 survey included only the identity of species in each subplot, not their abundances. We classified 52 site × time combinations (26 sites sampled 1995 and resampled in 2016) based on composition by applying an agglomerative hierarchical cluster method with flexible beta (−0.25) linkage (Lance & Williams, 1967) to frequencies relativized to the maximum for each species (Faith et al., 1987) using package PC-ORD v. 6 (McCune & Medford, 2011). Species that appeared in only one site were omitted from the analysis.

Ordination was applied to the same data described above. Vegetation–environment relationships were examined and shifts in species composition with time were characterized by locating sites and their temporal trajectories within non-metric multidimensional scaling (NMDS) ordination space in which environmental vectors were also fitted (Oksanen et al., 2022). Environmental vectors were based on values associated with the 2016 survey, including soil OM, total P, pore water salinity, and water depth (mean of the four-year period prior to 01/01/2016), as well as distance to coast, which reflected each site's position within the estuarine wetland. The ordinations were applied to site × time combinations for the 26 sites. Inclusion of species and relativization of their frequencies in the ordination were treated as described above for the classification analysis. Relationships between species composition and environmental vectors were examined using a vector-fitting procedure (Faith & Norris, 1989; Kantvilas & Minchin, 1989) incorporated in the R package *vegan* (Oksanen et al., 2022). Ordination axes were rotated so that Axis 1 was aligned with the distance to the coast vector. Change across the 26 plots was examined for each 1995 vegetation type by a vector-fitting procedure between the ordination scores (adjusted to their centroids) and the sampling year nested within site. We delineated vegetation type trajectories on the ordination diagram as vectors that began at each group's 1995 centroid and extended with length and direction defined based on the mean change in site scores on Axes 1 and 2.

We used a paired *t*-test to identify the species that have changed in a significant way between 1995 and 2016 throughout the sites in each vegetation type using the function "tpaired.krandtest.R" available in package *adespatial* (Dray et al., 2023).

2.5 | Diversity analyses

We used classical metrics, calculated directly from measures of gamma (γ, regional) and (α, local) diversity, and a multiplicative approach for calculation of β-diversity (Whittaker, 1960, 1972; Tuomisto, 2010). Diversity is reported using Hill numbers or species equivalents of the Shannon–Weiner index (exp (H')), to allow for independence in measures of α- and β-diversity (Jost, 2007). Gamma-diversity was calculated by pooling abundances for each species across all relevant local units and dividing by the mean α. Diversities were obtained for the whole study area and for the leading and trailing edges in both sampling years. Leading and trailing edges are denoted hereon as subzones within the transition zone, as defined by 1995 vegetation composition (see below). Diversity indices were calculated using the function "multipart" in the R package *vegan*.

It has been proposed that variation in composition among communities can also be defined as β-diversity (Legendre & De Caceres, 2013). Dissimilarity in species composition is described by two different patterns: *species replacement* and *species abundance difference*. Both patterns may be attributed to different mechanisms. Species replacement (also called turnover) is observed along ecological gradients in which some species disappear and are replaced by others, often related to environmental filtering but also to competition and patterns of dispersal, while species abundance difference (species' gain and loss without replacement, or its special case, nestedness) may be caused by changes in local abiotic conditions leading to larger or smaller ecological niches. Several methods to partition a dissimilarity matrix into different components have been reviewed by Legendre (2014). We followed Baselga's method (2013) to separate components of abundance-based dissimilarity calculated using the Bray–Curtis index. Function "beta.multi.abund" available in the R package *betapart* (Baselga & Orme, 2012) was used to partition β-diversity into components of species replacement and abundance difference.

3 | RESULTS

3.1 | Plant assemblages

Cluster analysis of the 52 assemblages (26 sites sampled during two periods) yielded two major vegetation types: Sawgrass Marsh, representing the freshwater Everglades, and Mangrove Scrub, representing coastal brackish-water wetlands (Figure 3). During the 1995 survey, Sawgrass Marsh and Mangrove Scrub were both well represented in the sampling network, with 11 and 15 sites respectively, occupying opposite sides of a line that roughly coincided with the interior limit of the white zone at that time. *Cladium jamaicense* was omnipresent in Sawgrass Marsh, in mixture with *E. cellulosa*, aquatic herbs and scattered *R. mangle* (Figure 3). In direct contrast, *R. mangle* was dominant in Mangrove Scrub; several epiphytic bromeliad species were attached to its branches, and *E. cellulosa* and the floating-leaved bladderwort *Utricularia purpurea* Walter were common below. Based on these analyses, we recognized two subzones within the transition zone: a leading edge consisting of sites that were Sawgrass Marsh in 1995, and a trailing edge that included sites that were Mangrove Scrub in the same year (Figure 2).

3.2 | Compositional dynamics during 1995–2016

Environmental variables measured during the 2016 survey were consistent with expectations for the coastal gradient. Pore water salinity determined during our April 2018 sampling event decreased with increasing distance from the saltwater source in Florida Bay ($r = -0.50$, $p < 0.05$) – a pattern in close accord to one generated through a more intensive, seasonally balanced SESE sampling program during 2011–2018 (Troxler et al., 2021). In contrast, soil organic matter increased marginally with distance to coast, in association with peat building in surface soils of the sawgrass marsh ($r = 0.38$, $p < 0.10$), but soil P and water depth did not differ significantly along the gradient. Results of the M3ENP modeling did indicate a regional increase in water level of 8.5 cm (SE = 0.6 cm) between 1991–1994 and 2012–2015.

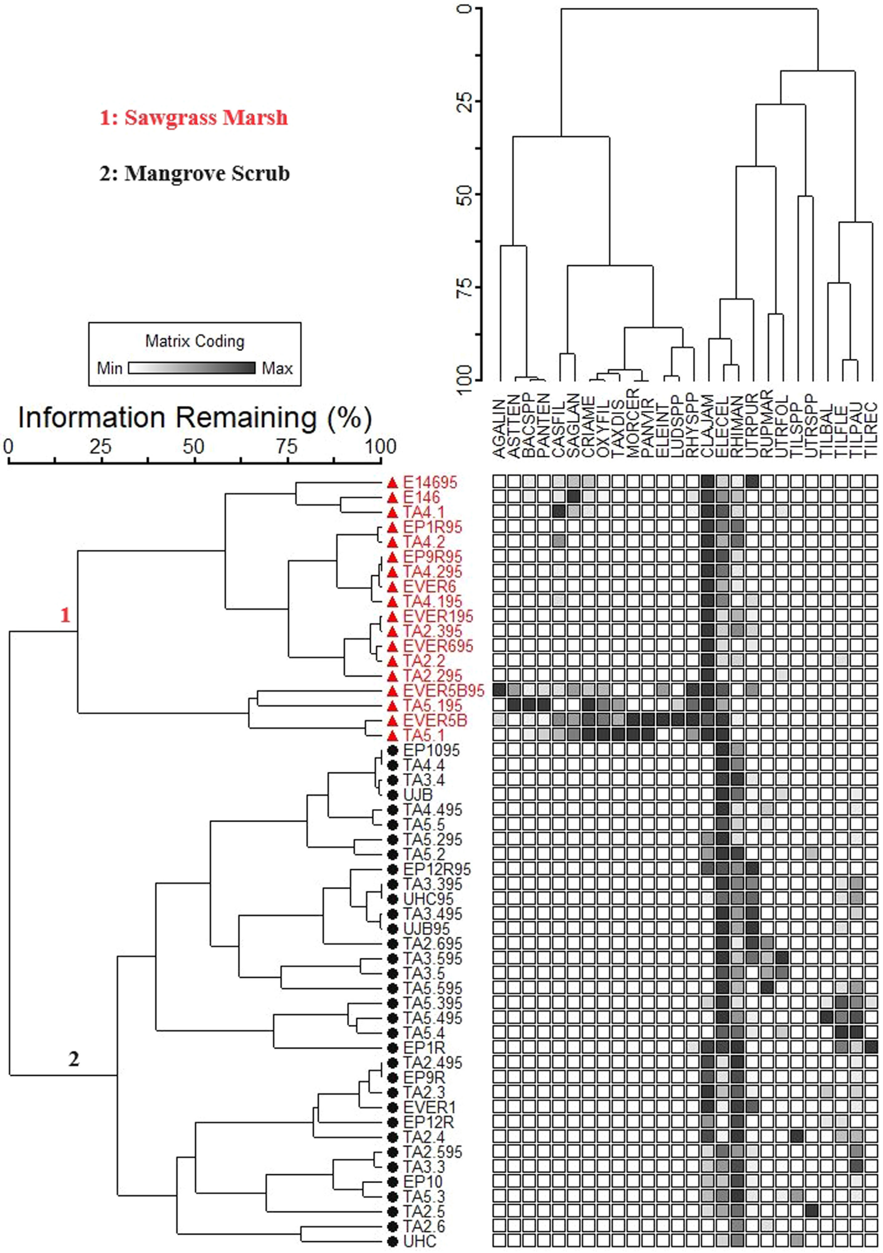


FIGURE 3 Two-way dendrogram showing site and species dendrograms simultaneously. Data include 52 site × time combinations collected in 1995 and 2016; #95 is appended to labels of samples obtained in 1995. Shading indicates species frequency in each sample, re-coded as relative values ranging from white (minimum) to black (species maximum across all sites). The cluster analysis distinguished samples in two vegetation types – sawgrass marsh and mangrove scrub – indicated in red and black, respectively. Full species names and six-letter codes are listed in Appendix S1.

TABLE 1 Mean difference in percent frequency (proportional occurrence in 30 1-m^2 plots) between paired sites in 1995 and 2016 of four dominant plant species in two subzones.

	Leading edge	Trailing edge
Cladium jamaicense	−3.9 ($t = 1.96$, $p = 0.08$)	+1.4 ($t = -0.40$, $p = 0.33$)
Eleocharis cellulosa	+8.2 ($t = -0.79$, $p = 0.18$)	−31.0 ($t = 3.78$, $p < 0.01$)
Rhizophora mangle	+29.1 ($t = -4.26$, $p < 0.01$)	+33.0 ($t = -4.96$, $p < 0.01$)
Utricularia purpurea	+12.1 ($t = 0.99$, $p = 0.14$)	−37.1 ($t = 3.23$, $p < 0.01$)

Note: Mean difference significantly different from zero ($p < 0.05$). Degrees of freedom are 11 and 14 for the leading and trailing edge, respectively.

By 2016, four local assemblages classified as Sawgrass Marsh in 1995 had transitioned to Mangrove Scrub, while none shifted in the opposite direction. These changes were primarily the result of dynamics among the four most abundant species, especially the expansion of *R. mangle* in sites initially classified as Sawgrass Marsh (Table 1). Other significant changes evident in Table 1 – the large increase in *R. mangle* and decreases in *E. cellulosa* and *U. purpurea* in Mangrove Scrub – did not cause sites to be reclassified. Salinities and mean water depths in the SESE ranged from less than 1–24 ppt and 5–35 cm, respectively (Figure 4). Salinities in sites classified as Sawgrass Marsh in both years were less than 8 ppt, but notably, mangrove dominance also extended into freshwater sites; measured salinities in two of the four communities that transitioned from Sawgrass Marsh to Mangrove Scrub in 2016 were less than 2 ppt.

Compositional dynamics explored through a two-dimensional NMDS ordination of data from both surveys converged at a stress level of 0.11 (Figure 5). While soil organic matter, phosphorus, and water depth vectors were uncorrelated with the ordination, vectors for pore water salinity and distance to coast both showed highly significant ($p < 0.001$) relationships. With strong salinity and distance to coast vectors pointing in opposite directions, Axis 1 represents the coastal physical gradient and its strong influence on the study area's vegetation. The placement of sites characterized as Sawgrass Marsh in 1995 on the right (freshwater) side of the gradient and those classified as Mangrove Scrub on the left (more saline) side of Figure 5 is a further reflection of the strength of this gradient.

The vectors joining the positions of individual sites in ordination space in 1995 and 2016 show that substantial directional change in composition took place between the two sampling periods (Figure 5). This visual impression was supported by tests of the effect of year nested within site, which were significant for both Sawgrass Marsh ($p < 0.01$) and Mangrove Scrub ($p < 0.001$) groups. The translated group vector for Sawgrass Marsh was the shorter of the two, but vectors for both types pointed to the left, indicating movement to a more coastal composition and environment.

Table 1 provides some clarification of the trajectories displayed in Figure 5 by showing how group mean frequencies of four dominant coastal Everglades plant species changed between 1995 and 2016. The shift to a more coastal composition of sites classified as Sawgrass Marsh in 1995 was brought about in part by a small decrease in *C. jamaicense* and an increase of more than 30% in *R. mangle* frequency. Table 1 also suggests that the leftward trajectory of Mangrove Scrub in the ordination was likewise a product of the expansion of *R. mangle*, in this case at the expense of *E. cellulosa* and its associate *U. purpurea* (Figure 6). Unlike *C. jamaicense*, which is restricted to low salinity conditions, both *E. cellulosa* and *R. mangle* appear capable of occupying most of the environmental (salinity × water depth) space available in the SESE (Figure 7), so the observed trajectory from *E. cellulosa* to *R. mangle* dominance in the Mangrove Swamp is not easily attributed to known environmental changes.

3.3 | Alpha- and beta-diversity

Between 1995 and 2016, no change was observed in mean α-diversity across the study area (Table 2). However, *α-diversity* increased significantly in the leading edge of the transition zone (paired *t*-test, $t = -2.7$, $p < 0.05$), while remaining stable across the trailing-edge sites (paired *t*-test, $t = 1.32$, $p = 0.21$). Beta-diversity, defined as the effective number of discrete local communities in a region (Jost, 2010), showed a slightly declining trend between 1995 and 2016 for the whole transition zone as well as for the two strata (Table 2).

In the β-diversity decomposition analyses, species replacement was responsible for most compositional dissimilarity among sites across the study area as well as within the two subzones in both years (Figure 7). The proportions of β-diversity attributable to replacement and abundance difference changed slightly between 1995 and 2016, with an increase in the replacement component in the leading edge of the transition zone and decreases in replacement in the trailing edge and the study area as a whole.

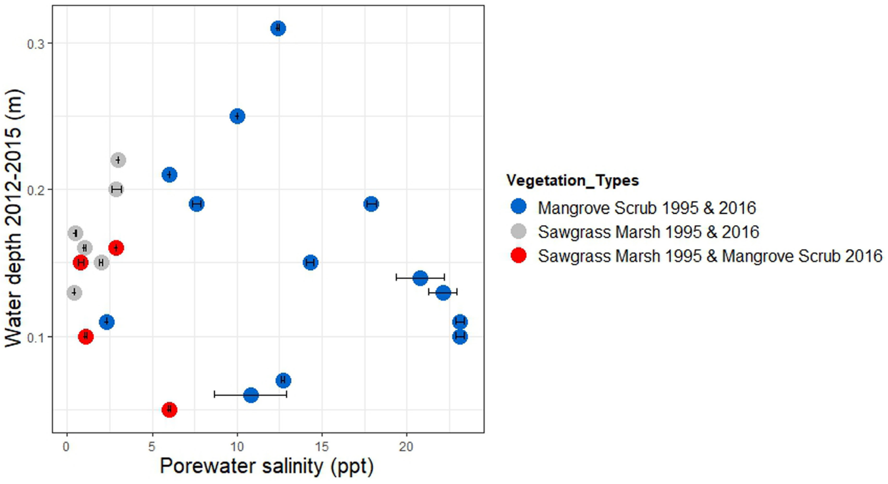


FIGURE 4 Relationship between porewater salinity measured in April 2018 and water depth in the period 2012–2015 for all sites sampled in 2016 and as classified in the same year. Horizontal bars correspond to porewater salinity mean standard error for each site.

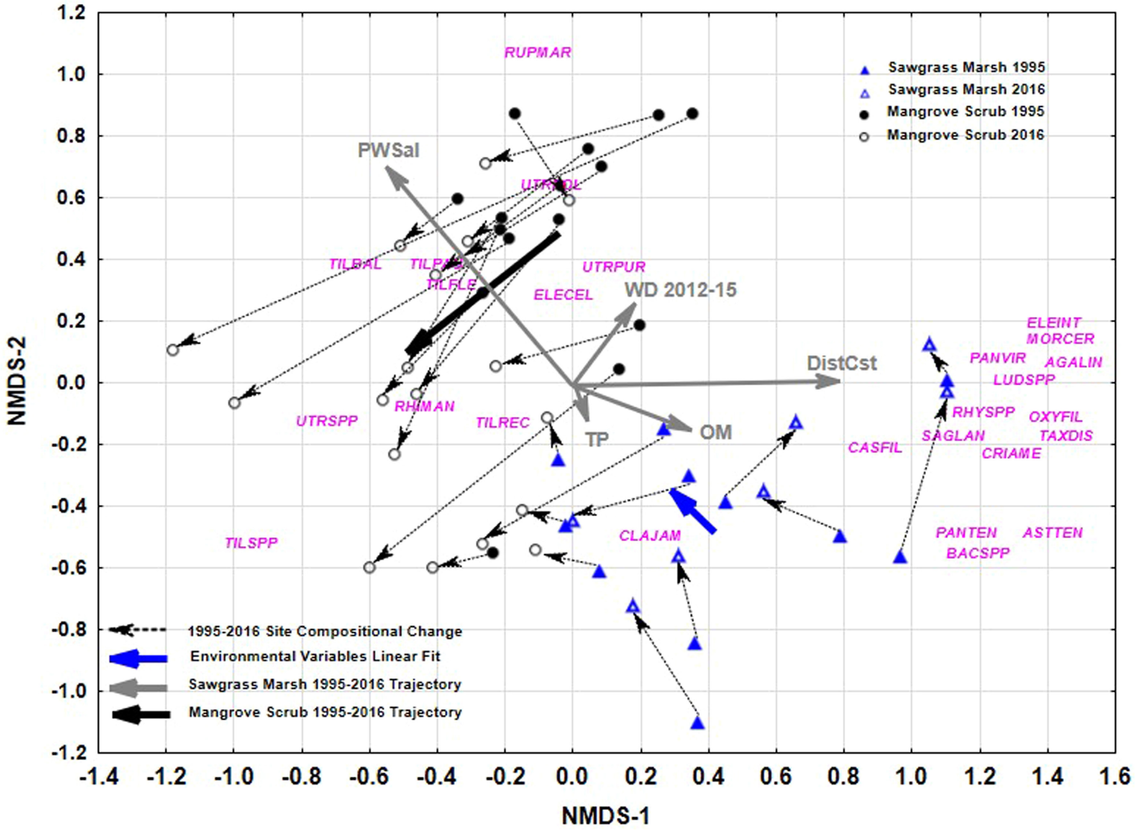


FIGURE 5 Ordination of marsh communities in two-dimensional non-metric multidimensional scaling (NMDS) space, based on site × species abundances determined in 1995 and 2016. Environmental variables strength and direction of best linear fit to ordination (PWSal: porewater salinity, WD_2012–15: four-year period water depth, DistCst: distance to coast, TP: total phosphorus, OM: organic matter); only PWSal and DistCst were significantly related to the ordination ($p < 0.001$). Average 1995–2016 trajectory of sites classified as Sawgrass Marsh and Mangrove Scrub, respectively, in 1995; effect of year nested within site was significant ($p < 0.01$, 0.001, respectively) for both groups. Full species names and six-letter codes are listed in Appendix S1.

4 | DISCUSSION

4.1 | Recent changes in SESE wetlands

The Southeast Saline Everglades is a landscape displaying gradual, progressive spatial change between continuous mangrove forests near the coast and sawgrass marshes downslope from the Miami Rock Ridge. As such, it can be characterized as an ecocline in which coastal influence is the primary environmental driver, but divergent factors allow the recognition of discrete communities along the gradient (van der Maarel, 1990; Attrill & Rundle, 2002). Within the SESE, the transition zone we studied stretches northward from the sparsely vegetated, mesohaline white zone, distinguished by its white-gray marl surface, into short, oligohaline sawgrass marshes growing on more organic-rich surface soils. Egler (1952) noted that the border between these two communities was indistinct compared to more sharply bounded zones within the SESE. The low productivity of the white zone has been attributed to low phosphorus availability in the carbonate sediments, perhaps exacerbated by inhibition of root function by the anaerobic soils (Koch & Snedaker, 1997). *Cladium jamaicense*, the foundational macrophyte in the sawgrass marsh, is a strong competitor in long hydroperiod, P-limited peat-forming freshwater wetlands, and is well adapted to disturbances caused by fire, freeze, or hurricane that have long been potent ecological forces in the Everglades (Lodge & Davis, 2023).

The trajectory toward halophyte dominance undergone by transition zone vegetation during the two decades between surveys (Figure 5) suggests that saltwater intrusion was an important driver, though not necessarily the only one. Long-term data on porewater salinity in the wetlands of the study area are not available. However, data from 2000 to 2020 in two embayments that are immediate sources of saline waters to the study area indicate that surface water salinities increased significantly over the period, rising from 12 to 16 ppt in Joe Bay, and from 20 to 27 ppt in Long Sound (Menne et al., 2012). Even if salinity in these water bodies had remained stable, the documented rise in sea-level in Florida Bay would have brought these brackish waters further into the wetland, where evaporation processes might well have caused porewater salinities to increase. Further evidence for increasing saltwater influence in the SESE is provided by the transgressive advance of preserved marine mollusks

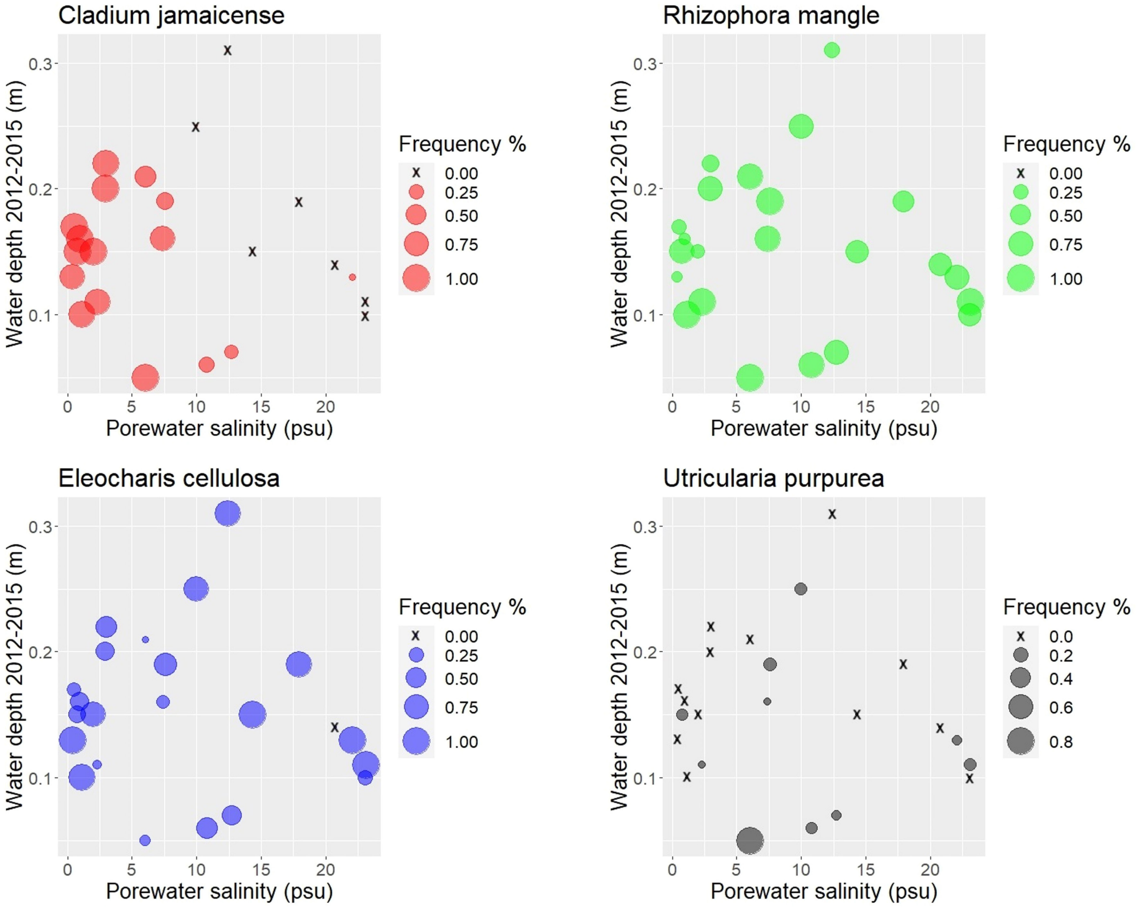


FIGURE 6 Relationship between porewater salinity measured in April 2018 and water depth in the period 2012–2015 for the four most frequent species in all sites sampled in 2016. Bubble size represents species frequency in percentage as the proportion of the 30 subplots in which the species was present in each site.

found in stratigraphic analyses of soil cores along five transects perpendicular to the coast, including three within the study area (Meeder et al., 2017).

Compositional change was dominated by variations in two of the study area's most abundant species: a precipitous 1995–2016 decline in *E. cellulosa*, a characteristic sedge of the freshwater Everglades, in the scrub mangrove communities, and sharp increases in *R. mangle* throughout the study area (Table 1). By the time of the 2016 survey, *R. mangle* had become overwhelmingly dominant in scrub mangrove stands in which the two species were growing in relatively even mixture in 1995. The brackish dry-season porewater salinities we observed in these sites (2–23 ppt) likely strain the tolerance of *E. cellulosa*, but the increasing abundance of *R. mangle* may cause additional stresses. During water uptake, red mangrove excludes salt at the soil–root interface (Werner & Stelzer, 1990), causing competitors in close proximity of its rhizosphere to experience elevated salinity (Passioura et al., 1992; Jiang et al., 2012). Moreover, even in the dwarf form *R. mangle* takes on in scrub mangrove ecosystems, it is a superior competitor for light compared to the barely emergent *E. cellulosa*. Likewise, interspecific competition is also a potential driver of the initial invasion of *C. jamaicense* marsh by *R. mangle*. An agent-based model that incorporated both the relative salt tolerances of the major species and modeled porewater salinities was applied to a nearby wetland that was entirely sawgrass-dominated in 1973; the model was reasonably successful in reproducing observed *R. mangle* encroachment by 2015 (Park et al., 2019). While greenhouse studies have found *R. mangle* seedling growth benefits from small additions of NaCl (Lin & Sternberg, 1992), there is little evidence that the species' distribution is restricted by freshwater conditions. Instead, the inland advance of *R. mangle* may be accelerated by flooding events that redistribute propagules, followed by water levels appropriate for seedling establishment – conditions which are extended further into the Everglades interior with rising sea-level (Dessu et al., 2018).

Our study documented the transgression of mangroves away from local coastlines, over distances of hundreds to thousands of meters. Changes of similar scale and type were also demonstrated in the Ten Thousand Islands National Wildlife Refuge (TTINWR) in southwest Florida, where mangrove coverage increased by 35% over a 78-year period, primarily through the replacement of interior brackish and saltmarsh (Krauss et al., 2011). Elsewhere, most attention to the expansion of mangrove communities has been on processes operating at larger scales, that is, allowing mangroves to extend their poleward limits. In these studies, mangrove expansion has been attributed to the reduced incidence of killing

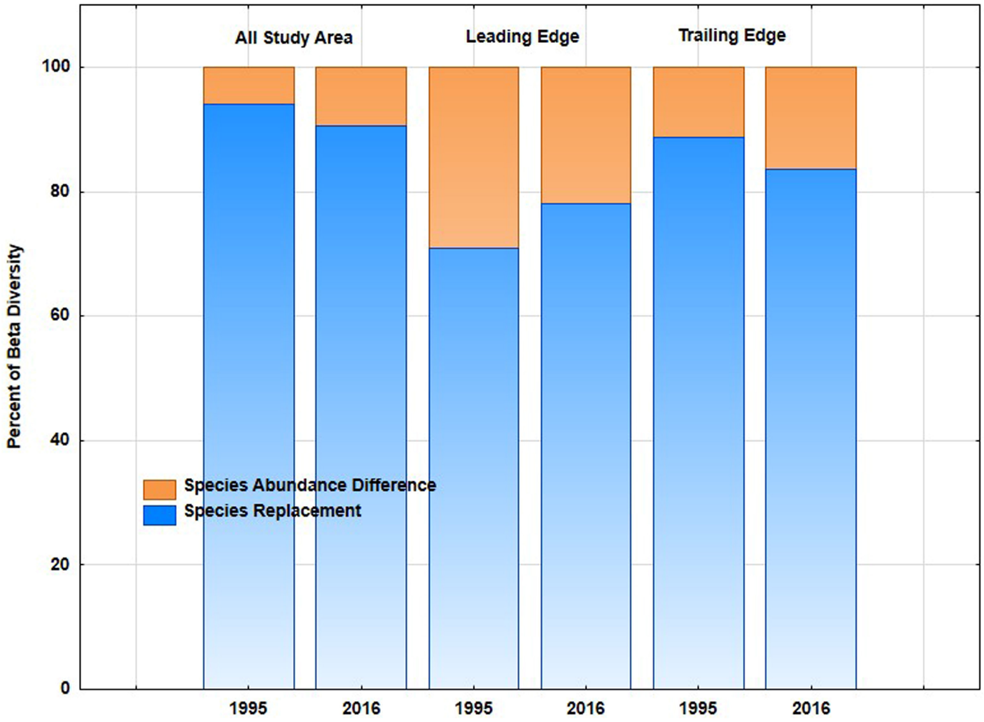


FIGURE 7 Species replacement and abundance difference expressed as percent of total β-diversity calculated using abundance-based Bray–Curtis dissimilarities for the whole study area, leading and trailing edge in 1995 and 2016.

TABLE 2 Beta-diversity by multiplicative partition (γ/α) using Shannon index species equivalents.

Diversities	1995	2016	Leading edge 1995	Leading edge 2016	Trailing edge 1995	Trailing edge 2016
α	3.76^a	3.89^a	4.09^a	4.87^b	3.52^a	3.18^a
β	2.01	1.89	1.76	1.66	1.53	1.46
γ	7.57	7.37	7.18	8.10	5.40	4.63

Note: If followed by different subscripts, mean alpha values for the entire study area, or individual subzones differed significantly ($p < 0.05$) between 1995 and 2016; hence, alpha diversity differed between years only in the Leading edge.

freezes (e.g., Saintilan et al., 2014). However, cold temperatures may also play a role in the distribution of mangroves within their existing latitudinal range. For instance, extensive dieback of South Florida mangroves has been observed at temperatures as high as 2°C (Ross et al., 2009), but such cold-temperature events have become less frequent in recent years. Temperature records from Flamingo along the Florida Bay coast ca 30 km west of the study area reveal that winter minimum temperatures increased by 2.4°C between 1961 and 2020. During the first half of the period daily minimum temperatures of 2°C or below were reached on 39 occasions, compared to only 24 occasions during a similar 30-year period beginning in 1991.

Fire is another disturbance that can control the advance of mangroves, but its occurrence and effect are not independent of the extant vegetation. Egler (1952) posited that dry-season fires ignited by indigenous people had a critical role in limiting the encroachment of mangroves into the Everglades interior. For pioneering *R. mangle* to be culled by such fires, however, the mangroves must have been scattered within a dense herbaceous assemblage that provided a continuous layer of fine fuels. Once the mangroves become dominant, fire ceases to be an important process in shaping the landscape. Everglades National Park fire records indicate that only two fires have occurred in the SESE since 1948, initiated recently under Park prescription.

The factors that appear to have played a part in the still-unfolding vegetation changes in the coastal Everglades therefore include background changes in the physical environment (salinity and water level increases associated with sea-level rise), long-term changes in disturbance regime (reduction in freeze and fire frequency), and internal feedbacks resulting from the vegetation responses themselves. In locations in which one foundational species is replaced by another, as in the four SESE sites that transformed from sawgrass to mangrove dominance (Figure 3), these vegetation responses serve to stabilize an ecosystem condition that will be difficult to reverse. The role of sea-level rise in the transition from one alternative *stable* state to another has recently been described for coupled transitions between tidal mudflat and salt marsh in the intertidal zone (McGlathery et al., 2013). In other situations, however, the stability of alternative states is more apparent than real, and the term alternative *transient* state is more appropriate (Fukami & Nakajima, 2011; Francis et al., 2021). Neilson (1993) pointed out that directional climate change effects in regions such as the SESE transition zone are likely to be blurry and transient. Thus, at the temporal scale addressed in our study, sampling sites and subzones will shift among alternative transient states, that is, novel assemblages at the front of a well-established, advancing wave of ecosystem change.

4.2 | Species diversity and the geography of SESE vegetation change

4.2.1 | Local (alpha) diversity

Having confirmed that the interiorward advance of salt-tolerant species recognized by Everglades ecologists as early as the mid-20th century had continued through 2016 (Figure 5), we examined the parallel dynamics of plant diversity. The layered, hierarchical design that divides the moving wave of halophyte transgression into leading and trailing edges (sawgrass- or mangrove-dominated as of 1995) can also be interpreted temporally as two stages of the same process: colonization and consolidation, respectively. In the colonization stage (or leading edge) we expected local diversity to increase, due to enhanced dispersal and establishment of salt-tolerant, coastal species in freshwater marshes in the absence of substantial increases in salt stress on species already present. In the consolidation stage (or trailing edge) we expected diversity to decline due to selective loss of glycophytic plants ill-adapted to increasing salinity in the mesohaline white zone. Our expectations were largely realized, with α-diversity during 1995–2016 increasing significantly in the leading edge and decreasing nominally in the trailing edge (Table 2). This pattern implies that at the front of the SESE transgression wave halophyte invasion did precede the decline of freshwater plants, while at the rear of the wave, consolidation and population expansion of salt-tolerant species coincided with glycophyte species loss.

We are unaware of other studies that directly address the temporal dynamics of plant diversity in coastal wetlands, and whether the pattern described above applies more generally or is particular to a landscape in which *R. mangle*, the foremost colonizing species, is quite capable of persisting in freshwater marshes. In this context, the low plant diversity of the SESE coastal wetlands (3–5 species equivalents per plot) is notable. Alpha-diversity is particularly low in trailing-edge plots, which occupy brackish-water conditions in the white zone. Research in other estuaries proposes that diversity of plants and many faunal groups reaches a minimum in mesohaline (5–18 ppt) environments, where neither freshwater nor marine species are well adapted (Attrill & Rundle, 2002; Whitfield et al., 2012).

4.2.2 | Among-plot (beta) diversity

The 1995–2016 changes in β-diversity throughout the study area as well as in each subzone were small but notable in the consistency of their decline (Table 2). Furthermore, the decomposition of β-diversity into its component parts, that is, replacement vs abundance difference, illustrated in Figure 7 makes clear that among-plot diversity in the SESE transition zone is principally a product of different community-level responses to the driving coastal environmental gradient (Baselga, 2012). Decreases in the replacement component of diversity across the transition zone and in its trailing edge during 1995–2016 (Figure 7) are small but may be signs of a weakening of gradient effects as coastal transgression proceeds and glycophytic assemblages are eliminated. Continuation of this process of transition from colonization to consolidation stage over a long and still indeterminate time period would result in loss of half or more of the species pool – a form of biotic homogenization.

4.2.3 | Implications for Everglades restoration

The fundamental ecological goals of CERP are the restoration or re-creation of the Everglades' historical landscape pattern and processes (National Research Council [NRC], 2003; Sklar et al., 2005). During the early years of the project (which began in 2001), sea-level rise was not an important consideration in accomplishing those objectives, despite that its rapid current acceleration was already well underway (Parkinson & Wdowinski, 2023). Once the complications brought on by rising seas began to be recognized, coastal wetland restoration plannersç focus settled on enhancing flow, with the intent of pushing back the white zone and the mangrove front to the narrow coastal band they once occupied. Increasing freshwater delivery to coastal wetlands has several benefits, including potentially improving the quality and distribution of water that reaches the nearshore environment of the surrounding estuaries. However, it is not an action that will stem the tide of invasion by *R. mangle* and its halophytic associates, nor will it recreate the historical coastal landscape in the SESE.

Several of the weaknesses of the "just-add-water" approach envisioned in CERP have been illustrated in our findings. One is that it fails to reestablish the disturbance regime – frequent fires and freezes – that formerly prevented mangroves from successfully invading the sawgrass marsh. It may still be possible to use prescribed fire for this purpose in places where productive grasslands remain, but the recent rise in winter temperatures suggests that freeze or near-freeze events are receding as an ecological force in the region. A second limitation of the current approach is that supplementing freshwater delivery does more than dilute the salts already present in the wetland; combined with sea-level rise, it pushes water levels closer to a tipping point where the capacity of even the mangroves to persist is exceeded, resulting in open-water conditions. Evidence of the transition of mangrove swamp to open water, especially in conjunction with storm surge from tropical storms, is already mounting in other South Florida coastal environments (Meeder & Parkinson, 2018; Osland et al., 2020; Lagomasino et al., 2021).

Sea-level's absence of stationarity, or the likelihood that it will continue to reside within its range of past variability (Milly et al., 2008), makes setting goals for coastal wetland restoration challenging. Recent projections (Sweet et al., 2022) have sea-level in South Florida rising 40 cm above a 2000 baseline by 2050, or ca 30 cm provided by the Interagency Sea Level Scenario Tool (2022). Two tenets may be applicable for landscapes like the one described in these pages: (1) recognize the reality of the changing present; and (2) plan for an achievable future in which biological production and diversity are maximized. Tenet 1 means accepting that the movement of alternative transient states that coastal researchers have been tracking in the SESE for nearly a century is inexorably approaching a stable state, with *R. mangle* serving as its foundational species. Tenet 2 means that restoration practitioners should focus their efforts on reestablishing, to the extent possible, the timing and volume of water flow from upstream water sources believed to have prevailed in the predevelopment Everglades, and removal or modification of structures that hinder the ongoing transitional process. We anticipate that these limited actions will lead to a productive coastal landscape of high biological diversity, extending beyond the structurally important macrophytes reported here to the entire complement of life forms that will occupy the future wetland. In the vast Everglades ecosystem, it should be possible to maintain the full marine–freshwater coastal gradient elsewhere, though not in its current position.

AUTHORS CONTRIBUTIONS

Michael S. Ross, John F. Meeder, Jay P. Sah and Leonard J. Scinto conceived of the research idea; Michael S. Ross, Susana L. Stoffella and Rosario Vidales collected data; Michael S. Ross, Suresh C. Subedi and Susana L. Stoffella performed statistical analyses with contributions from Peter R. Minchin. Pablo L. Ruiz provided GIS expertise. Michael S. Ross and Susana L. Stoffella wrote the initial draft of the paper; all authors participated in editing subsequent drafts.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Six-letters codes for all species present in 1995 and 2016.

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