



Spatio-temporal pattern of plant communities along a hydrologic gradient in Everglades tree islands[☆]



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ABSTRACT

Plant communities arranged along a gradient are a product of underlying physico-chemical drivers that vary on both spatial and temporal scales. Spatial variation in the underlying drivers along the gradient usually results in the formation of boundaries between adjacent plant communities. However, the structure and composition of these communities may change over time resulting in boundary shifts. In the Everglades, tree islands are complex ecosystems, where plant communities are arranged along hydrologic and soil nutrient gradients. In these islands, temporal changes in hydrologic regime often result in a spatial shift in community composition along the gradient and determine the trajectory of community succession. We examined the interaction between hydrology and vegetation over a 12-year period in three southern Everglades tree islands. We hypothesized that drier conditions in recent decades would result in an increase in the dominance of flood-intolerant woody plants over herbaceous and flood-tolerant woody species, ultimately causing a shift in the boundaries between plant communities. The boundary between adjacent communities varied from sharp, clearly defined peaks of Bray-Curtis dissimilarity to more gradual, diffuse transition zones. In the head portion of tree island, there was little change in vegetation composition. However, in the tail portion of the islands, the relative abundance of flood-tolerant species declined, while that of moderately flood-tolerant species increased over the study period. In these islands, the effects of relatively dry conditions in recent decades resulted in small shifts in the boundaries among communities. These results suggest that tree islands are dynamic successional communities whose expansion or contraction over time depends on the strength and duration of changes in hydrologic conditions.

1. Introduction

Plant communities arranged along environmental gradients are at least in part products of ecological processes associated with spatio-temporal variation in physico-chemical drivers. Likewise, when plant communities proceed through a successional process, the conditions of drivers are modified by species-environment interactions that may contribute to changes in the environmental gradients over time. As such, these changes in environmental gradients usually result in the formation of boundaries, representing transition zones between adjacent plant communities (Allen et al., 2005). The properties and persistence of these boundaries depend on whether the variation in the drivers is abrupt or gradual (Wiens et al., 1985; Walker et al., 2003), and on the ability of adjacent plant communities also to withstand the effects of natural and/or management-induced environmental changes

(Risser, 1995; Forsy and Allen, 2002). When plant community composition responds to changes in environmental drivers beyond a certain threshold, the boundary between adjacent communities is also likely to shift (Allen et al., 2005).

In the Everglades, tree islands are an integral component of several landscapes (e.g., pine rockland, marl prairie, and ridge and slough). In the ridge and slough (R&S) landscape, tree island nucleation, formation, and development began 4000 years before present (ybp) in response to regional multi-decadal fluxes in the periodicity and duration of flooding and drought events (Willard et al., 2002). These hydrologic changes permitted the establishment and proliferation of woody vegetation in sawgrass marshes or on ridges during periods of sustained drought (Willard et al., 2002, 2006; Bernhardt, 2011). Over time, soil accretion resulting from higher productivity within the incipient tree islands led to higher surface elevations and shortened flooding periods,

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which in turn promoted the establishment of shrubs and trees. As recently as 1700 ybp, many Everglades tree islands were not fully formed and exhibited many of the characteristics of a transitional community consisting of sawgrass (*Cladium jamaicense* Crantz) and weedy annuals with a minor woody component (Willard et al., 2002). However, by around 600 ybp, following several extensive and prolonged local and regional drought episodes, the modern vegetation structure on most large tree islands in the southern Everglades had begun (Willard et al., 2002; Bernhardt, 2011).

In tree islands within the R&S landscape, plant communities vary in species composition and life-form structure along a topographic gradient. However, the degree of variation in species composition is likely correlated with habitat (resource) heterogeneity along the gradient (Davidowitz and Rosenzweig, 1998; Kumar et al., 2006). In these islands, the vegetation on the most elevated portion, called ‘Hardwood hammock’, are typically dominated by flood-intolerant trees, whereas the surrounding marsh (Mixed-marsh) has mostly flood-tolerant graminoids or broad-leaved submerged, floating, and/or emergent species. Between these two extremes, the proportion of woody plants and herbaceous species depends on the interactions between the underlying drivers and stressors (e.g., hydrology, disturbance, nutrients, etc.). As these conditions change, so does species composition and community type (Fig. 1). The most noticeable changes usually occur in the surrounding mixed-marsh and tail portion of the tree islands, where three distinct plant communities, Bayhead forest, Bayhead swamp, and Sawgrass marsh are common. These communities may be thought of as phases in a chronosequence of vegetation succession in R&S landscape. While persistent drying conditions initiate an expansion of sawgrass within the mixed-marsh or sloughs (Bernhardt and Willard, 2009), the Sawgrass marsh represents the earliest successional tree island community, analogous to the primordial marsh prior to tree island formation. Sawgrass marsh is followed by the Bayhead swamp that represents a transitional phase between the primordial Sawgrass marsh and Bayhead forest, a climax community typifying tree island maturation under wetland conditions (Fig. 1). While a Bayhead forest is less likely to transition to Hardwood hammock, an extended period of flooding beyond a critical threshold causes Hardwood hammock and other tree island woody communities to lose their characteristic woody species, and eventually may cause tree island to abruptly shift to a stable marsh (D’Odorico et al., 2011).

Hydrology is one of the major drivers of species variation within tree islands in the Everglades (Armentano et al., 2002; Ross and Jones, 2004; Espinar et al., 2011). Hence, substantial changes in hydrologic conditions, whether natural or management-induced, are likely to cause quantitative and qualitative changes in structure and composition of the tree island communities. For instance, management-related high-water levels due to compartmentalization after 1960 caused the loss of

tree islands, both in number and areal coverage, in the Water Conservation Areas (Patterson and Finck, 1999; Brandt et al., 2000; Hofmockel et al., 2008). In contrast, during periods of tree island initiation during the last four millennia, the R&S landscape experienced shorter hydroperiods than during the pre-drainage era e.g., 1800s (Willard et al., 2006). Since tree island and marsh communities are hydrologically connected (Troxler et al., 2005; Ross et al., 2006; Saha et al., 2010; Sullivan et al., 2014), prolonged and extreme dry or wet events may also affect the boundaries between these communities. The climatological records and hydrologic data from the Shark River Slough (SRS) in Everglades National Park (ENP) suggest that water level during the 1990s was well above the 30-year average (Fig. 2). In contrast, both the mean annual rainfall and water level were relatively low between 2001 and 2012. Since plant community composition on tree islands in 2001 was already impacted by high water conditions in 1990s, the dry conditions in 2000s provided an opportunity to assess response of plant communities to the shift in hydrologic regime on the islands.

Tree islands are likely to be affected by water management activities associated with the Comprehensive Everglades Restoration Plan (CERP) authorized by the Water Resources Development Act (WRDA) of 2000. The CERP is a multi-decade restoration project expected to cost approximately \$10 billion (Stern, 2014). It is the framework for the modifications and operational changes needed to restore, preserve, and protect the water resources of central and south Florida, including the greater Everglades. The overarching goal of the CERP is to repurpose freshwater outflow into the Atlantic Ocean and the Gulf of Mexico for use in environmental restoration while providing flood control and supplementing the water supply needs of south Florida’s growing population. The CERP projects are intended to restore the right quantity, quality, timing and distribution of freshwater in the Everglades through different activities, such as decompartmentalization in Water Conservation Areas and construction of Tamiami Bridges to restore the natural sheet flow and increase the water flow across the Tamiami Trail towards Everglades National Park (ENP). Within the CERP, water management decisions will result in changes in hydrologic regimes throughout R&S landscape, including the tree islands, probably affecting the balance between flood-tolerant and flood-intolerant species and resulting in shifts in species composition, community boundaries, and ultimately tree island function.

Because of the uncertainties associated with the CERP and its effect on Everglades ecosystems, specifically tree islands, it is imperative that managers understand how regional long-term changes in hydrologic regimes will affect structure and function of tree island plant communities. In this study, we describe changes in vegetation composition of three SRS tree islands between 2001 and 2012 and examine whether successional processes influenced by short-term changes in hydrologic conditions have impacted the community composition, and thus shift in

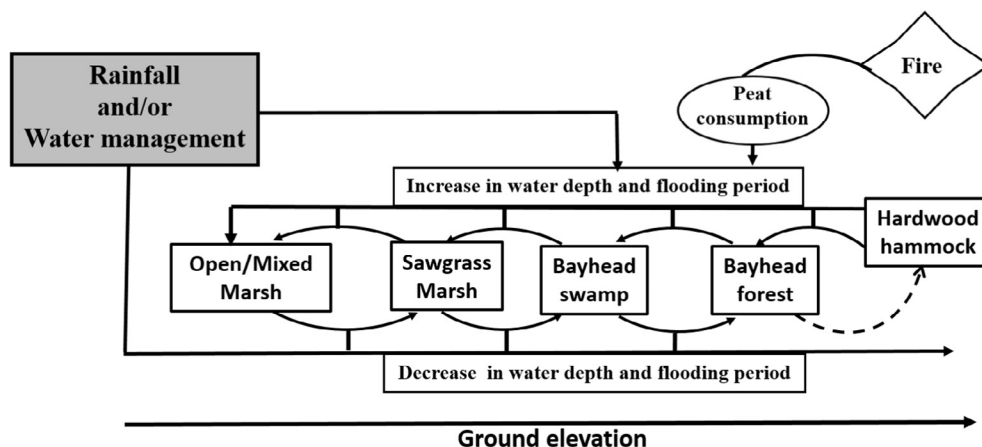


Fig. 1. Conceptual model: vegetation dynamics in Shark River Slough tree islands and surrounding marsh.

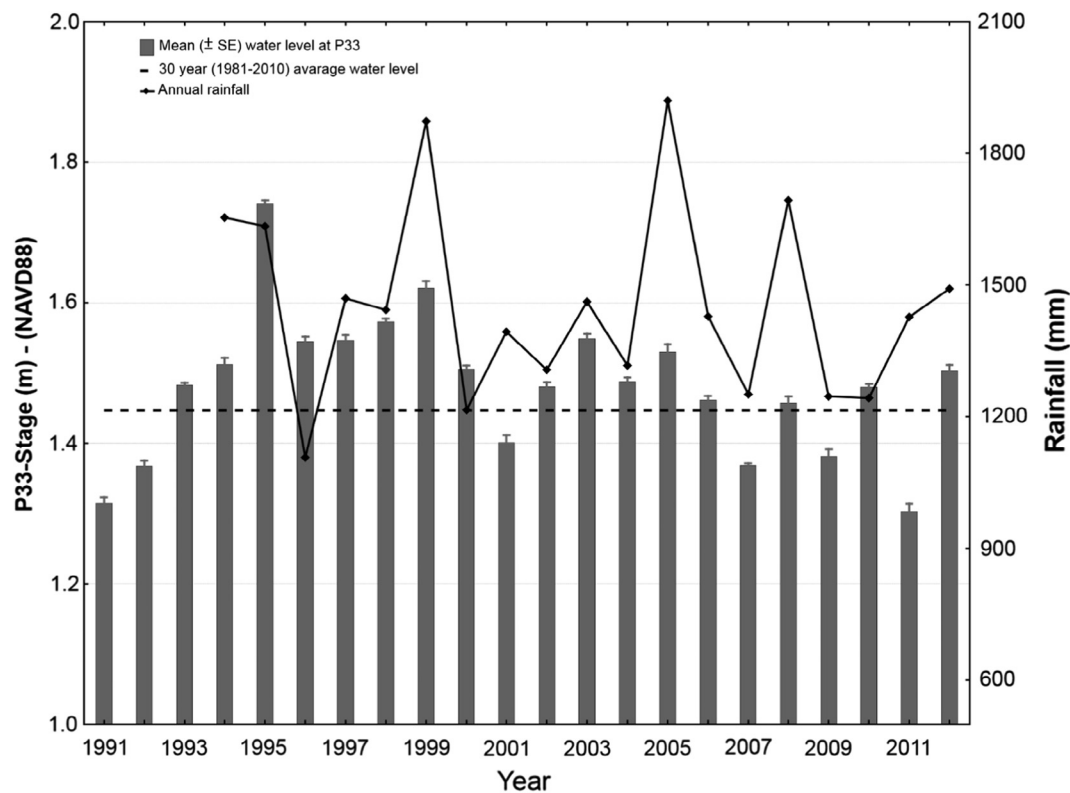


Fig. 2. Annual total rainfall and annual mean (\pm S.E.) and 30 yr (1981–2010) average (dashed line) water level at the stage recorder P33 located in Shark River Slough within Everglades National Park.

locations of boundaries between these communities within these tree islands. The objectives of this study were:

- (i) to quantify the species and life-form distribution along the environmental gradient,
- (ii) to assess the response of species composition and life-forms to the changes in hydrologic regime over time,
- (iii) to quantify changes in relative importance of woody species, and
- (iv) to evaluate the effects of change in species composition on the location and structure of boundaries between plant communities in the Everglades tree islands.

We hypothesize that hydrologic differences between the two census dates will result in, (i) an increase in dominance of woody plants over herbaceous, (ii) an increase in relative abundance of flood-intolerant over flood-tolerant tree species, and (iii) a concomitant change in the boundaries between different communities. Furthermore, an increase in dominance of woody species and flood-intolerant species suggests that tree island growth, development, and succession are dependent on hydrologic fluxes, particularly during periods of prolonged drought or below-average hydroperiod.

2. Materials and methods

2.1. Study area

The study was conducted on three SRS tree islands, Black Hammock, Gumbo Limbo and Satinleaf, within ENP (Fig. 3). These tree islands are characterized by a well-defined ‘head’ associated with a topographic high or limestone outcrop and a well-defined, extended ‘tail’ (~1–3 km long) aligned with the prevailing direction of water flow (Armentano et al., 2002). The head region of these teardrop-shaped tree islands is characterized by Hardwood hammock (Hammock), whereas Bayhead forest (Bayhead), Bayhead swamp (Swamp), and Sawgrass

marsh (Sawgrass) are present in the tail portion of these tree islands.

The hydrologic regimes of these islands are influenced primarily by annual rainfall, augmented by the water delivered from the Water Conservation Areas by pumps arrayed along the Tamiami Trail (Fig. 3). Soil characteristics also vary along the gradient from head to tail. Soils in the Hammocks are alkaline, mineral soils with extremely high P concentrations, while soils in the seasonally-flooded tail communities, Bayhead, Swamp and Sawgrass are mostly organic, with low P concentrations (Ross et al., 2006; Espinar et al., 2011). Disturbances such as hurricanes and fires have also played a large role in the ecology of SRS tree islands (Loope et al., 1994; Armentano et al., 1995, 2002; Wetzel et al., 2008; Ruiz et al., 2011).

2.2. Data collection

2.2.1. Vegetation sampling

Vegetation was sampled along four transects on each of three tree islands, Black Hammock, Gumbo Limbo and Satinleaf. One transect followed the long north–south axis of the island, hereafter termed as ‘NS transect’. The other three transects were established perpendicular to the NS transect in west–east direction (WE transects), one each through Hammock (WE1), Bayhead (WE2) and Swamp (WE3). All four transects were sampled in 2001/2002 (hereafter, 2001), but only the three WE transects were re-sampled in 2011 of the 2011/2012 (hereafter, 2012) sampling. The length of transects and the number of sites sampled in 2001 and 2012 on each transect are given in Table 1.

On each transect, vegetation was sampled every 5–10 m, and the sampling protocols included an estimate of maximum height and cover class of trees and vines by species within a 2 m radius plot, and an estimate of cover class of herbs and shrubs by species within a 1 m radius plot around each transect point. The cover classes used to estimate species cover in each stratum were: 1, 0–1%; 2, 1–4%; 3, 4–16%; 4, 16–33%; 5, 33–66%; and 6, > 66%. Soil depth was determined by probing to bedrock with a metal rod at each surveyed location.

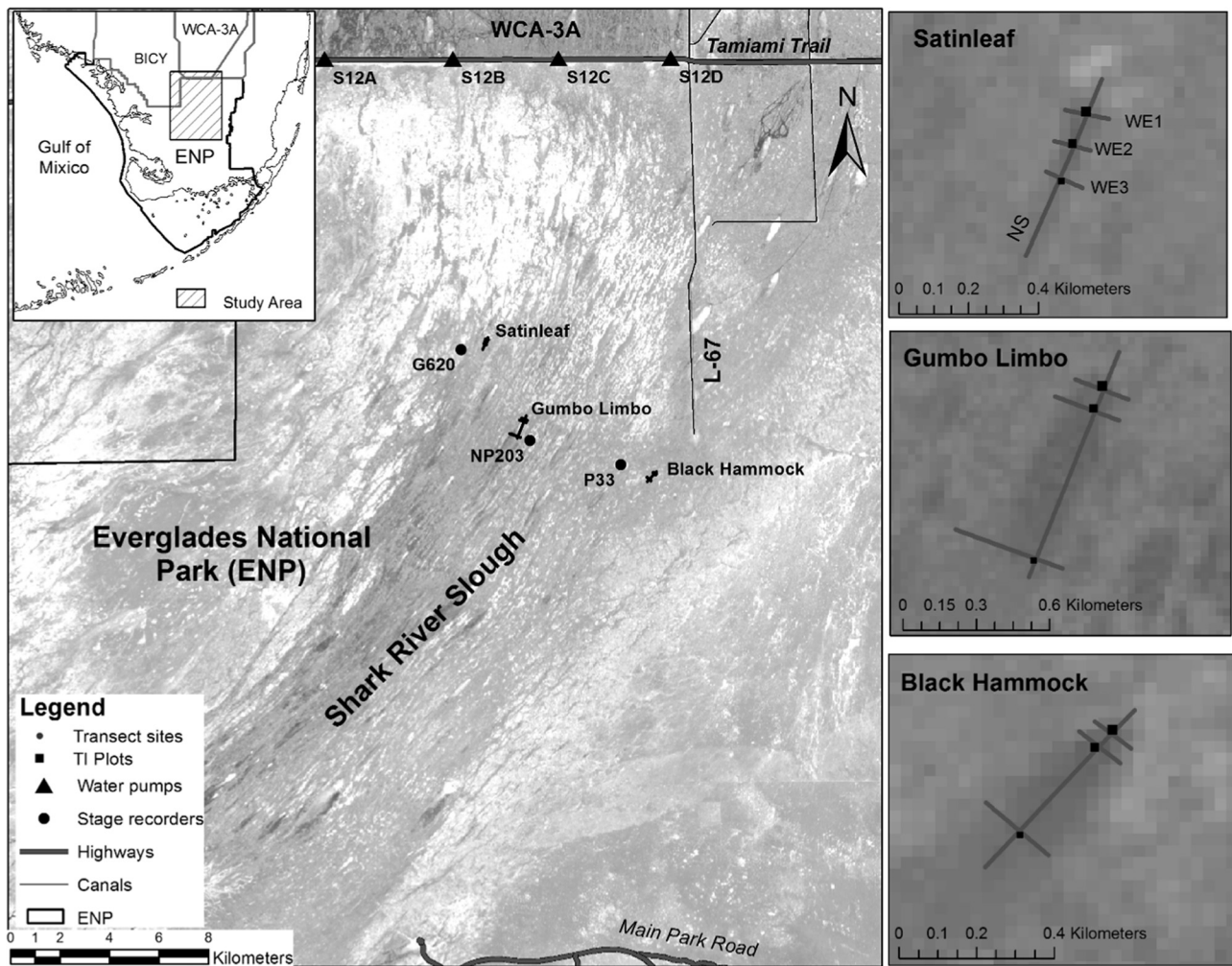


Fig. 3. Study area map showing the location of transect and plot sites on three Shark River Slough tree islands. Landsat Imagery (Feb 2003; path/row 15/42) as background.

In 2001, permanent plots of 25 × 25 m (625 m²), 20 × 20 m (400 m²) and 15 × 15 m (225 m²) were established in the Hammock, Bayhead and Swamp zones, respectively, on each of the three study tree islands, except the Black Hammock. The Hammock community in the Black Hammock was not large enough to allow the establishment of a 25 × 25 m plot. Thus, a 20 × 20 m plot was established in the Hammock of this island (Fig. 3). Each plot was gridded into 5 × 5 m cells, whose corners and midpoint were marked by 30 cm long 1/2" PVC stakes affixed to the ground. The plot and cells were set up using a

compass, measuring tape, sighting pole(s), and right-angle prism. During the 2001 census, trees (≥ 5 cm) were identified to species, tagged using numbered aluminum tags, and their diameter (cm) at breast height (DBH) was measured and recorded. The location of each tagged tree was recorded to the nearest 0.1 m using the SW corner of the plot as a reference (0, 0). Furthermore, if a tree had multiple stems ≥ 5 cm DBH, each stem was tagged with a unique ID that allowed it to be cross-referenced back to its 'parent'. The DBH (cm) of these offshoot stems was measured and recorded as well. The density of all tree

Table 1
Length of transects and number of sites sampled on each transect in three Shark River Slough tree islands.

Island	Transect	Length of the transect (m)	# of sites sampled in 2001	# of sites sampled in 2012
Black Hammock	North-South (NS)	560	72	–
	Hammock (WE1)	115	24	24
	Bayhead (WE2)	135	28	28
	Swamp (WE3)	205	41	42
Gumbo Limbo	North-South (NS)	1000	107	–
	Hammock (WE1)	230	47	47
	Bayhead (WE2)	280	57	57
	Swamp (WE3)	470	48	48
Satinleaf	North-South (NS)	500	55	–
	Hammock (WE1)	135	28	27
	Bayhead (WE2)	110	23	23
	Swamp (WE3)	115	24	24

saplings (stems ≥ 1 and < 5.0 cm in DBH) within each 5×5 m cell was recorded by species, and each individual was assigned to one of two DBH size classes: 1–2.9 cm or 3–4.9 cm. During the 2012 census, all plots were re-surveyed to assess changes in tree and sapling densities and basal area. New individuals or sprouts from existing trees were tagged and added to the database.

2.2.2. Hydrology

The ground surface elevation was determined at each transect point, and at all corners of each permanent plot, by surveying via auto-level from a USGS benchmark of known elevation. We estimated hydroperiod, discontinuous number of days in a year when water level was above the surface, and mean annual relative water level (RWL), the water level in relation to ground elevation (Ross and Sah, 2011), at each transect point and plot corner. To calculate hydroperiod and RWL, we used elevation data from the topographic surveys in conjunction with long-term water level records at a stage recorder situated in the open marsh at 0.5–1.5 km distance from the head of each island. The three stage recorders used to calculate hydrologic parameters for Black Hammock, Gumbo Limbo and Satinleaf were P33, NP203, and G620, respectively (Fig. 3). Daily water level at the survey sites was estimated assuming a flat-water surface. Later, annual average hydroperiod (days) and mean annual RWL (cm) were calculated over a 7-year period for each plot. Several authors have estimated a vegetation response time of 4–6 years in marshes (Armentano et al., 2006; Zweig and Kitchen, 2008). However, in tree islands a strong correlation was found between variation in vegetation composition and 7-year annual average hydroperiod and RWL (Sah, 2004; Espinar et al., 2011). We therefore applied a mean annual hydroperiod (days) and RWL (cm) averaged over seven contiguous water years (May 1 to April 30) prior to samplings in 2001 and 2012, respectively.

2.3. Data analysis

Species cover data were summarized using the mid-point of the cover class, and both univariate and multivariate techniques were used to identify the plant communities along the environmental gradient, and change in vegetation structure and composition over time. Transect data were used for vegetation-environment relationships, and identification and shift in position of boundaries between adjacent plant communities. Plot data were used for assessing changes in basal area and importance value (IV) of the trees (≥ 5 cm dbh) and saplings (> 1 and < 5 cm dbh) between two samplings.

2.3.1. Split Moving-Window boundary analysis

We used a split moving-window (SMW) boundary analysis (Ludwig and Cornelius, 1987; Cornelius and Reynolds, 1991) to describe variation in vegetation composition and to identify boundaries between plant communities along the surveyed transects in the tree islands. In the SMW method, boundary is defined as the location of maximum variance in species-abundance based Bray-Curtis (B-C) dissimilarity between adjacent groups of sampling plots. The B-C dissimilarities were then plotted against location of the window mid-point along the transect. Results of the SMW boundary analysis are scale dependent, and are affected by the choice of window size. Use of a small window size often produces noise, resulting in many peaks that represent small-scale variation in species composition. In contrast, a wide window results in fewer peaks, overshadowing the fine scale variation. First, we explored the pattern using windows of different sizes (2, 4, 6, 8, 10 and 12) and from these we selected larger windows (6, 8, 10, and 12) because these resulted in boundaries that appeared to be ecologically meaningful. Multiple window sizes were selected to reduce the scale-dependency of SMW results (Boughton et al., 2006).

We used a Monte Carlo method to test whether a boundary identified using the SMW method has a significantly higher value than expected under a null hypothesis that no distinct boundary exists between

adjacent communities (Cornelius and Reynolds, 1991). In the Monte Carlo method, we randomized the position of each site with its species data vector intact, and repeated the calculations of SMW dissimilarities, as outlined above, for each of the selected window sizes. We repeated the randomization 1000 times, and calculated expected mean dissimilarity and standard deviation between each pair of window-halves for a given window width. We then calculated overall mean dissimilarity and standard deviation for each window width, following Cornelius and Reynolds (1991). The Monte Carlo method was performed using MATLAB v. 7.10 (Mathworks). Since our purpose was to use multiple windows in order to reduce the scale effects, we pooled the dissimilarity values of the mid-points from different window sizes. However, as dissimilarities from different window sizes are scale-dependent, we first standardized the observed dissimilarity values by calculating Z-scores for each window width. The Z-score for each mid-point for a given window-width was calculated by subtracting the observed dissimilarity value from the overall expected mean dissimilarity and dividing by the overall expected standard deviation (Cornelius and Reynolds, 1991). We averaged Z-scores for each site from four window sizes (6, 8, 10 and 12 sites), and plotted them against site positions along each transect. We considered the peaks that consisted of one or more contiguous sites with Z-scores equal or greater than 1.65 (the value in one-tailed test: 95% confidence limit) as significant and distinct boundaries between adjacent communities (Boughton et al., 2006). In a separate analysis, species were grouped according to their life-forms (i.e., trees, shrubs, graminoids, forbs, ferns, vines, seedlings). The mean cover of these groups at each sampling point was then used to calculate B-C dissimilarity.

2.3.2. Habitat heterogeneity and species turnover

The environmental underpinnings of the within- and among-island variability in composition and structure were sought through correlation between species turnover (B-C dissimilarity and beta diversity (β)) and habitat heterogeneity. To examine the relationship between the B-C dissimilarity and variation in the environmental gradient, we calculated the absolute mean differences in elevation (and its covariates hydroperiod and relative water level) and soil depth between adjacent windows. To maintain consistency between normalized B-C dissimilarity (Z-score) and environmental metrics, we calculated the absolute mean difference in the values of environmental gradient variables averaged over the sites present in each of four window sizes (6, 8, 10 and 12 sites), and then averaged the values for each mid-point for the four window sizes. We calculated beta diversity ($\beta = \gamma/\alpha$; where γ = total number of species present on a transect, and α = mean species richness per sampling plot on the transect) to represent overall species turnover along each transect. We then examined the relationship between beta diversity (β) and habitat heterogeneity, quantified by the coefficient of variation (CV) for elevation and soil depth along each WE transect and separately for 2001 and 2012 samplings.

2.3.3. NMS ordination

Non-metric multidimensional scaling (NMDS) ordination was used to examine the relationships between species composition and environmental variables representing hydrology and soil depth. The 2001 species cover data along NS transects were used for the analysis. The hydrologic variables included in the analysis were 7-year annual mean hydroperiod (days) and relative water level (cm). Relationships were examined using a vector-fitting procedure incorporated in the computer program DECODA (Minchin, 1998). Vector fitting is a form of multiple linear regression that finds the direction along which sample coordinates have maximum correlation with the fitted variable within the ordination space. The significance of the environmental vectors was assessed using a Monte-Carlo procedure permutation test with 10,000 permutations of the species data, as samples in the given ordination space are not independent (Minchin, 1998). Analysis of similarity (ANOSIM) was used to examine the differences in plant communities

between the two sampling years, 2001 and 2012.

2.3.4. Tree and sapling dynamics

For each plot, tree density and basal area were calculated for stems ≥ 5 cm DBH. For calculating sapling density and basal area, all stems (between 1 and 4.9 cm) were treated as individuals, even if they were members of a multi-stem clonal group. Finally, species' importance value (IV) of each species within each plot was calculated using the formula: $IV = (\text{Relative density} + \text{Relative basal area})/2$.

3. Results

Between 1991 and 2012, daily mean water levels at the three stage recorders (P-33, NP203, & G620) were similar within and across years. During the seven-year period that preceded the vegetation sampling, annual mean water levels (WL) prior to 2012 sampling was 13.8 cm lower at G620 (Satinleaf) and 12.5 cm lower at both P33 (Black Hammock) and NP203 (Gumbo Limbo) than during the 7-year period prior to 2001 sampling. In concurrence with the differences in annual mean WL at the stage recorders, the seven-year average hydroperiods were shorter in 2012 compared to those in 2001 by 45, 64 and 48 days for Hammock, Bayhead and Swamp, respectively (Fig. 4; Supp. Table S1). Likewise, mean hydroperiods between the two census dates had also decreased by 94 days for Bayhead and 70 days for Swamp as well, but stayed the same for the Hammock (Supp. Table S2).

3.1. Plant communities

Plant community composition in SRS tree islands followed the topographic gradient, primarily oriented along the long axis (NS transect), but also along the transects aligned perpendicular to the long axis. The SMW boundary analysis based on the 2001 species cover data along NS transects identified two significant peaks for Black Hammock and three significant peaks for each of Gumbo Limbo and Satinleaf, represented by relatively high normalized B-C dissimilarity (Z-scores > 1.65), resulting in three (Black Hammock) or four (Gumbo Limbo and Satinleaf) distinct plant communities (Fig. 5). The location of significant peaks representing high B-C dissimilarity were mostly identical in SMW analysis results based on both species and life-form abundance data. The number of significant peaks, however, differed among islands. For instance, in Gumbo Limbo, three significant peaks differentiating four communities Hammock, Bayhead, Swamp and Sawgrass marsh were clearly identifiable (Fig. 5b). In Satinleaf, only the SMW boundary analysis based on life-form abundance data revealed three significant peaks distinguishing the same four communities (Fig. 5c). In Black Hammock, however, the boundary separating Bayhead and Swamp was not distinct in either the species or life-form abundance-based analysis (Fig. 5a).

Plant communities identified along the NS transects were strongly associated with hydroperiod ($r = 0.81$, $p < 0.001$; Fig. 6). Among the three woody communities on the islands, Hammocks were dominated by flood-intolerant species such as *Bursera simaruba* (L.) Sarg., *Celtis laevigata* Willd., *Eugenia axillaris* (Sw.) Willd., *Ficus aurea* Nutt., and *Sideroxylon foetidissimum* Jacq. Bayhead forests, which were more diverse than other communities in plant species, were comprised of a mixture of moderately flood-tolerant trees (*Chrysobalanus icaco* L., *Persea borbonia* (L.) Spreng., *Morella cerifera* (L.) Small, and *Magnolia virginiana* L.), shrubs (*Cephalanthus occidentalis* L.) and ferns (*Acrostichum danaeifolium* Langsd. & Fisch., *Blechnum serrulatum* Rich. and *Thelypteris interrupta* (Willd.) K. Iwats.). Swamps were comprised of one or two flood-tolerant tree species (*Annona glabra* L., *Salix caroliniana* Michx.) and a suite of graminoids and forbs. The tree island tail, dominated by sawgrass (*C. jamaicense*), was present at the south end of the transect. Mean species cover in different plant communities along NS transects on three islands is given in Supp. Table S3. In general, tree cover decreased towards the south end of the Bayhead and was less

than 5% in the adjacent Swamp, where low shrubs and forbs were most abundant (Fig. 7). Graminoid cover increased from Hammock to the Sawgrass marsh, where sawgrass constituted $> 80\%$ of the total plant cover. Similar to tree cover, canopy height in all three islands exhibited a strong positive association ($r = 0.54$, $p < 0.001$) with surface elevation. Hammock that occupied the head of the island had the tallest canopies, followed by Bayhead, and finally Swamp (Fig. 5).

The communities identified along the NS transects were also distinguishable within each of the Hammock, Bayhead and Swamp transects (WE transects). However, the SMW analysis revealed that the boundaries between identifiable plant communities were not always distinct. Boundaries were more distinct on Hammock (WE1) and Bayhead (WE2) transects than on Swamp (WE3) transects (i.e., Sawgrass marsh and Swamp are more similar than other adjacent pairs), and more distinct in Black Hammock and Gumbo Limbo than Satinleaf (Fig. 8). For instance, on the Hammock transects (WE1), the peaks separating Hammock and Bayhead communities were generally significant. However, unlike on the NS transect, where three woody vegetation were identifiable, the Bayhead on both Hammock (WE1) and Bayhead (WE2) transects transitioned directly into Sawgrass or mixed-marsh, as elevation decreased. On these transects, the Swamp community was either absent, or if present, occupied a very narrow zone that was indistinguishable in the selected window sizes in the SMW boundary analysis.

3.2. Environmental heterogeneity and species turnover

Bray-Curtis dissimilarity between adjacent communities was positively correlated with absolute differences in hydroperiod and mean annual RWL, along the transects (Table 2). On the NS transects, many of the significant peaks (Z-score > 1.65) that represented relatively high B-C dissimilarity, i.e. species turnover co-occurred with absolute differences in elevation of 48 cm or more (Fig. 5), corresponding to a difference in mean annual hydroperiod of ≥ 185 days. Along the WE transects, however, such values were much higher in the Hammock (WE1) transect, where the sharpest gradient in elevation occurred (Fig. 8). In contrast, in the Bayhead (WE2) and Swamp (WE3) transects, high B-C dissimilarity was associated with just 15–20 cm difference in elevation i.e. a difference in hydroperiod of < 100 days.

Beta-diversity differed significantly (One-way ANOVA: 2001: $F_{2,6} = 4.95$, $p = 0.05$; 2012: $F_{2,6} = 5.8$, $p = 0.04$) among the three woody communities, and was higher on the Hammock (WE1) than on Swamp (WE3) transects (Fig. 9). The mean β -diversity on Bayhead (WE2) transects was not significantly different from that on either Hammock (WE1) or Swamp (WE3) transects. Averaged over all transects, the mean β -diversity was significantly (paired t -test: $t = 7.0$, $p < 0.001$) higher in 2012 than in 2001, suggesting greater micro-habitat heterogeneity. The mean (\pm SE) β -diversity were 6.18 (± 0.49) and 7.56 (± 0.56) in 2001 and 2012, respectively. The β -diversity in both years 2001 and 2012, was positively correlated ($r = 0.83$ and $r = 0.84$, respectively) with habitat heterogeneity, represented by CV of elevation on each transect. However, the relationship between β -diversity and soil depth was not significant.

3.3. Vegetation change (2001–2012)

3.3.1. Vegetation dynamics along transects

From 2001 to 2012, the degree of change in plant community composition varied within and among SRS tree islands. Analysis of similarity (ANOSIM) reveals that, in general, the plant communities in the Hammocks in each island did not change between 2001 and 2012 (Table 3). The changes in overall plant community composition were higher in the Swamp than in Bayhead for each island, and these differences were greater in Gumbo Limbo and Satinleaf than in Black Hammock.

Along the nine WE transects in the islands, the change in tree cover

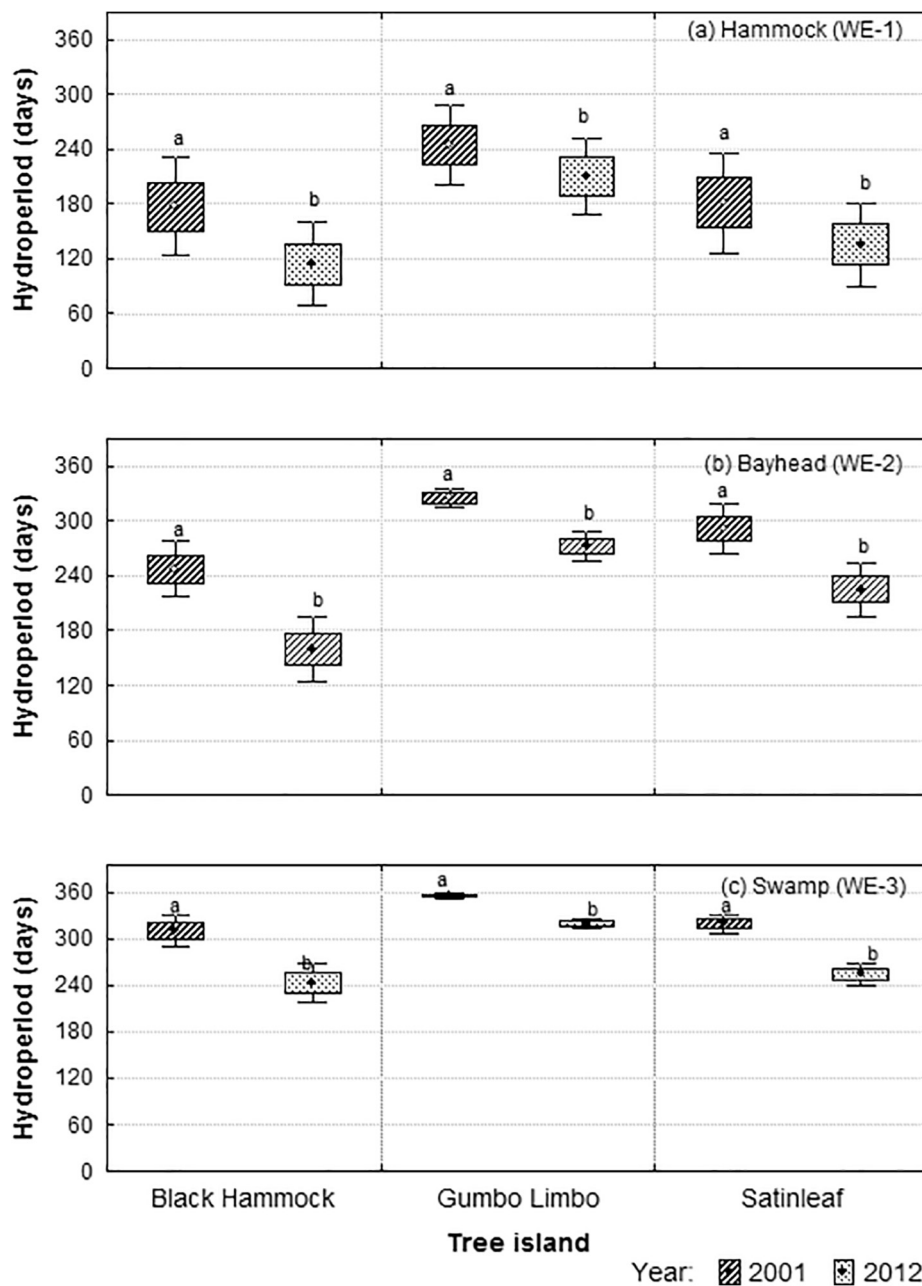


Fig. 4. Boxplots (Mean, 1.SE, and 95% CI) showing mean annual hydroperiod averaged over 7 years prior to sampling along three west-east (WE) transects - Hammock (WE1), Bayhead (WE2) and Swamp (WE3) - in three Shark River Slough tree islands, Black Hammock, Gumbo Limbo and Satinleaf. Different letters show significant (Paired *t*-test; $p < 0.05$) difference in mean hydroperiod between 2001 and 2012.

showed mixed results (Table 4). Tree cover significantly decreased in the Bayhead (WE2) transect of Black Hammock (paired *t*-test: $t = 2.23$, $df = 27$; $p = 0.03$), and in both the Hammock (WE1; paired *t*-test: $t = 4.85$, $df = 46$; $p < 0.001$) and Swamp (WE3; paired *t*-test: $t = 2.51$, $df = 56$; $p = 0.015$) transects of Gumbo Limbo. In contrast to Black Hammock and Gumbo Limbo, tree cover in Satinleaf was not significantly different between two censuses. Tree layer vegetation on the tree islands included both flood-intolerant and flood-tolerant species. Between 2001 and 2012, when averaged over all WE transects, the mean (\pm S.E.) cover of *Annona glabra*, a flood-tolerant species, decreased significantly from 11.1 (± 1.23) to 6.53 (± 0.78) percent (paired *t*-test: $t = 4.3$, $df = 318$, $p < 0.001$), while the mean cover of *Chrysobalanus icaco*, a moderately flood-tolerant species, increased from 9.1% to 12.3%. Among other woody species, shrub cover increased in most transects, though the increase was statistically significant (paired

t-test, $p < 0.05$) only in the Swamp (WE3) transect of Black Hammock (Table 4). By far the most striking change in vegetation composition in all study islands was an increase in the cover of graminoids, particularly *Cladium jamaicense*. The increase in graminoids was statistically significant (paired *t*-test; p -value < 0.005) in all transects except the Hammock (WE1) transect in Satinleaf (Table 4). However, on the Hammock (WE1) and Bayhead (WE2) transects, the increase in *C. jamaicense* cover was limited to the Sawgrass marsh portion of the transects.

3.3.2. Tree and sapling dynamics in plots

In the Hammock plots, in which only the tree layer was resampled in 2012, mean tree density and basal area, averaged over all three islands, increased by 7.3% and 5.1%, respectively. However, the pattern of temporal change in both tree density and basal area differed among

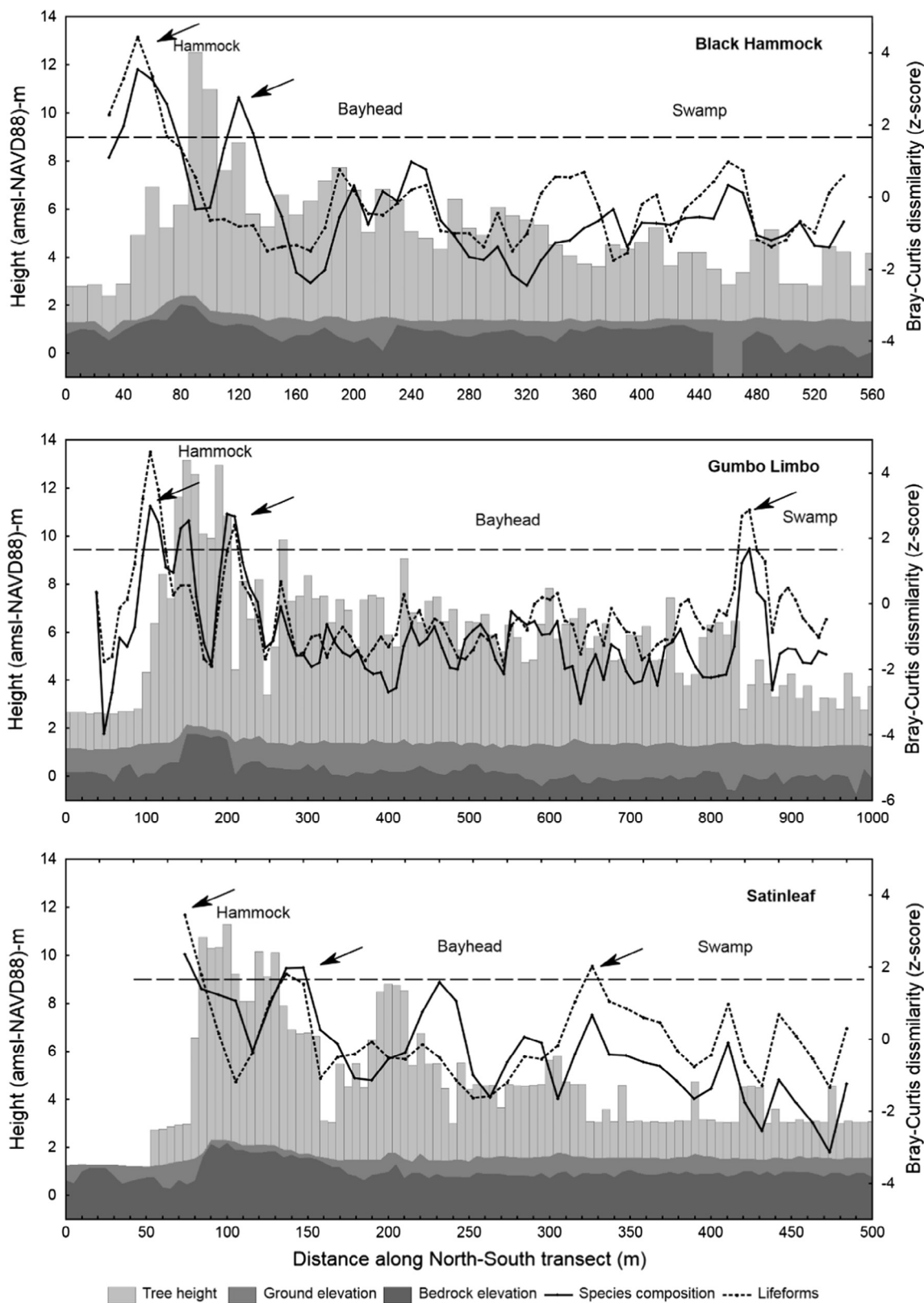


Fig. 5. Canopy height, bedrock elevation, soil depth, and normalized Bray-Curtis (B and C) dissimilarity (Z-Score) based on species composition during 2001 sampling along NS transects on three Shark River Slough tree islands. In split-moving window analysis, the Z-scores were averaged over four window sizes (window with of 6, 8, 10, and 12). Arrows indicate the peaks (boundaries) that consisted of one or more contiguous sites with Z-scores equal or greater than 1.65 (dashed line - the value in one-tailed test: 95% confidence limit).

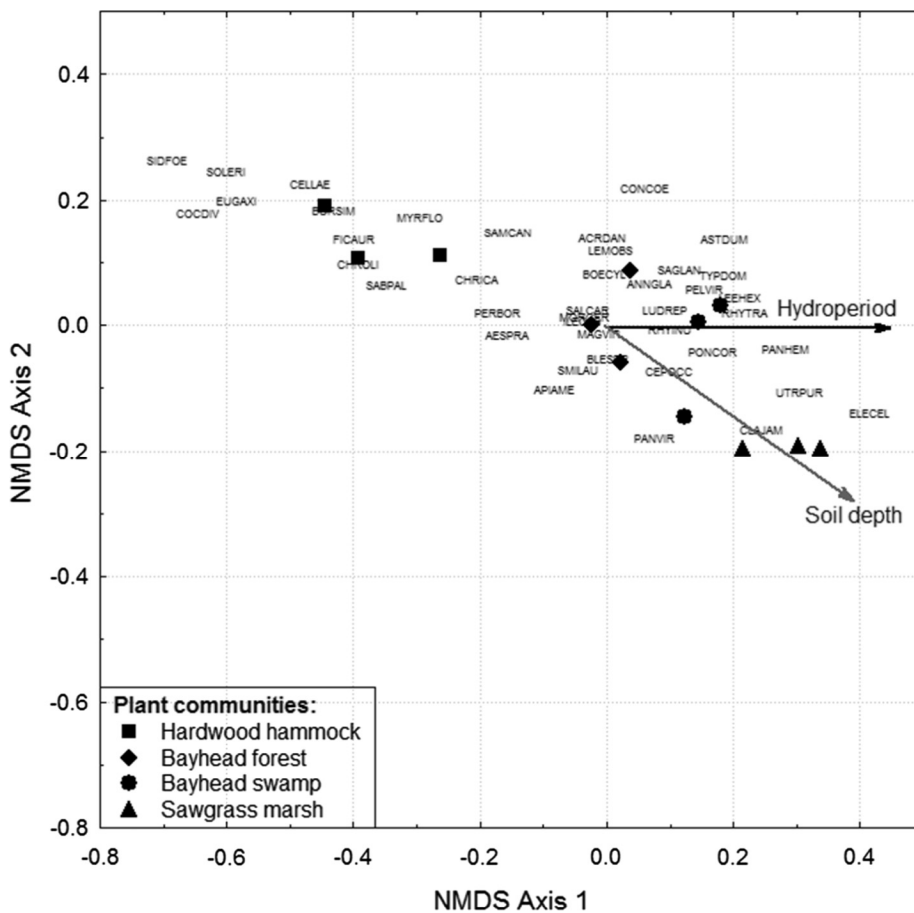


Fig. 6. Bi-plots of site species scores from two-dimensional nonmetric multidimensional scaling (NMDS) ordination of species cover data collected during 2001 sampling at the sites along NS transects on three Shark River Slough tree islands. Environmental vectors fitted in the ordination spaces represent the direction of their maximum correlation with ordination configuration. Full name of species are in Supplementary Table S3.

islands (Fig. 10). While both the density and basal area in the Hammock plot of Gumbo Limbo decreased during the ten-year period, tree density increased by 7.3% and 23.5% in Black Hammock and Satinleaf, respectively. Moreover, the basal area decreased in Black Hammock by 6.5%, but increased in Satinleaf by 37.4%, from 36.5 m² ha⁻¹ to 50.1 m² ha⁻¹.

Across all Bayhead plots, the average importance value (IV) of most tree species declined between 2001 and 2012 (Table 5). However, the IV of three tree species *Ilex cassine*, *Salix caroliniana*, and *Chrysobalanus icaco* increased during this period. The most notable increase was in the IV value of *C. icaco*. Its IV increased across all Bayhead plots and in one of the Swamp plots (Fig. 11a). In the sapling layer, the IV of *C. icaco* remained almost unchanged in Black Hammock and Gumbo Limbo, but increased in Satinleaf (Fig. 11b). In contrast to the increase in IV of *C. icaco*, the flood-tolerant species *Annona glabra* and *Morcer cerifera* decreased in most Bayhead plots, but remained relatively unchanged in the Swamp plots.

The IV of sapling species showed much greater variability between plots and census dates than did those of the tree species. For example, in the Bayhead plots, IV of flood-tolerant species like *Annona glabra* decreased at second sampling (Table 6). In contrast, less dominant sapling species like *Persea borbonia*, *Sambucus nigra* ssp. *canadensis* (L.) R. Bolli, and *Ficus aurea* increased in IV between 2001 and 2012. This pattern, however, was not observed in the Swamp plots, in which the average IV of the three dominant sapling species, *A. glabra*, *Magnolia virginiana*, and *Salix caroliniana*, remained unchanged between census dates, as did most of the other sapling species (Table 6).

3.3.3. Vegetation change and boundaries

In general, even after ten years, the position of boundaries between two forest types or between forest and marsh along the Hammock

(WE1) transects remained intact. However, the sharpness of peaks separating forest and marsh communities was more distinct in 2012 than in 2001, especially in the transition between Sawgrass marsh and Bayhead or Swamp (Fig. 8). A few plots, located at the boundaries between Sawgrass marsh and Bayhead that were Sawgrass or Swamp in 2001 changed to Swamp or Bayhead, respectively, by 2012, indicating an increase in woody components at the boundaries.

4. Discussion

In the fixed, teardrop-shaped, tree islands within the ridge and slough landscape of the Everglades, plant communities that differ in both species composition and functional representation (life-forms) are arranged along a topographic and hydrologic gradient. These communities are dynamic, and responds to changes in hydrologic conditions. Our results show that periodic fluxes in the hydrologic regime, resulting in below average water levels and shorter hydroperiods over a period as short as one decade, promote the growth of sawgrass in the marsh, and the establishment and growth of woody plants within the tree islands. However, despite these internal changes, we found minimal alteration in the position of the boundary between adjacent plant communities, with the exception of the far tail regions of the islands.

Vegetation characteristics of the three study tree islands are in accord with patterns described for ‘fixed tree islands’ present within the R & S landscape of the central and southern Everglades (Sklar and van der Valk, 2002). Four distinct plant communities - Hardwood hammock, Bayhead forest, Bayhead swamp, and Sawgrass marsh - were expressed most clearly along the primary axis of the islands parallel to the direction of water flow, but also were evident along secondary axes in the direction perpendicular to flow. On these secondary axes, their relative areal extent varied consistently depending on the location of the

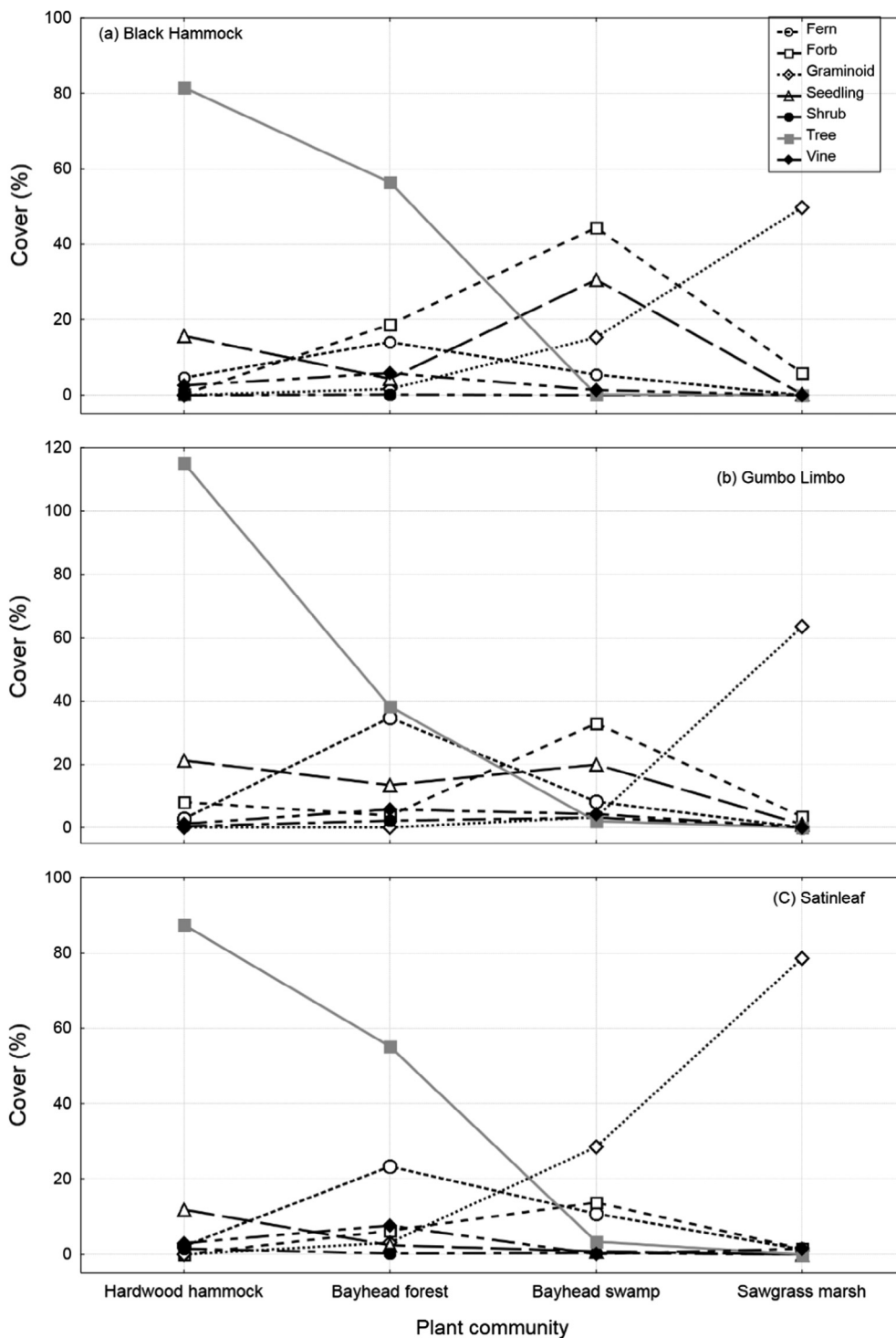


Fig. 7. Mean cover of life-forms based on 2001 sampling in four plant communities along NS transect on three Shark River Slough tree islands.

transect along the length of the island (Fig. 8). Ultimately, vegetation zonation within tree islands is a result of hydrologic patterns and associated ecological processes, including biotic feedbacks that alter the local topography. In the Everglades, proposed models for the development of ridge-slough-tree island landscape have emphasized the role of water flow and the distribution of nutrients (Wetzel et al., 2005; Ross et al., 2006; Bazante et al., 2006; Givnish et al., 2008, Cheng et al., 2011; Larsen et al., 2011). According to these models, the strong regional water flow causes nutrients to spread downstream in the direction of flow and to form longitudinally arranged vegetation zones. A

similar process operating in directions perpendicular to flow appears to create nutrient gradients between P-rich forests on relatively high ground to P-limited marshes. However, in those directions, the gradients are concentrated within a shorter distance, resulting in narrow vegetation zones.

Within a tree island, boundaries between plant communities are not always distinct. While the transition between Hammock and Bayhead was well defined in the tree islands we studied, the transition from Bayhead to Swamp to Sawgrass marsh was subtle, and boundaries were sometimes difficult to distinguish. Several flood-tolerant tree species

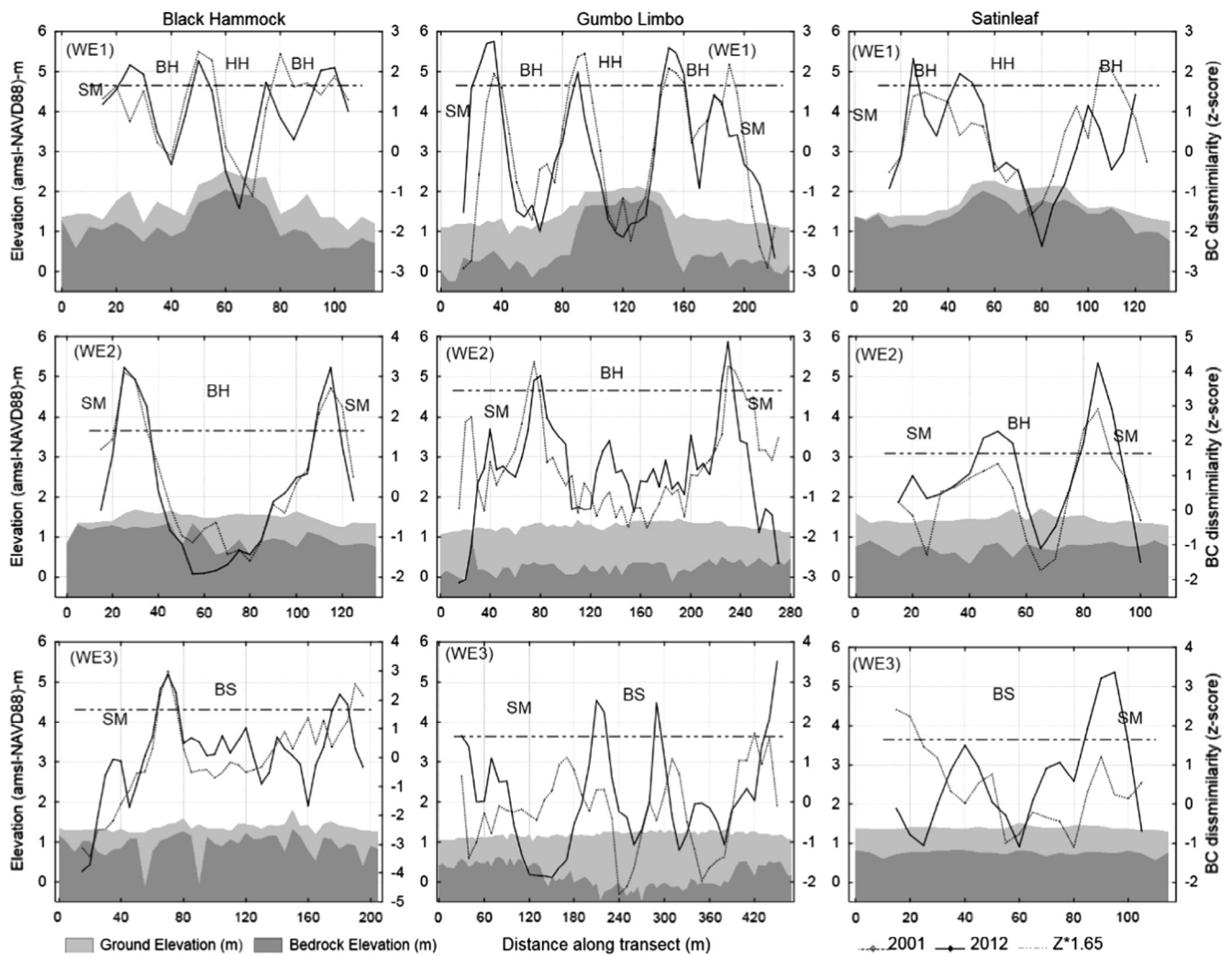


Fig. 8. Bedrock elevation, soil depth, and normalized Bray-Curtis dissimilarity (Z-score) based on species composition along WE transects on three Shark River Slough tree islands. In split moving-window analysis, the Z-scores were averaged over four window sizes (window with of 6, 8, 10, and 12 sites) separately for 2001 and 2012 samples. HH = Hardwood hammock, BH = Bayhead, BS = Bayhead swamp; SM = Sawgrass marsh. The peaks (boundaries) that consisted of one or more contiguous sites with Z-scores equal or greater than 1.65 (dashed line - the value in one-tailed test: 95% confidence limit) were significant.

e.g., *Morella cerifera*, *Magnolia virginiana*, and *Salix caroliniana* that occur in Bayhead were also present in Swamp. However, their growth was stunted in the latter. Similarly, sawgrass, whose hydrologic range is wide, grows together with flood-tolerant tree species within the Bayhead swamp zone. Thus, a boundary between Swamp with high

cover of sawgrass in the understory and adjacent Sawgrass marsh may not always be distinct, and changes over time depend upon the change in cover of sawgrass and other associated species. Rapid changes in sawgrass cover were largely responsible for a change in boundary characteristics along the Swamp transect in Gumbo Limbo and

Table 2

Pearson Correlation coefficient (r) and p-values for the relationship between mean normalized Bray-Curtis dissimilarity (Z-Score) and difference in (a) hydroperiod, and (b) relative water level (RWL) on nine transects, three each in Black Hammock, Gumbo Limbo and Satinleaf tree islands.

Tree island	Transect	n	2001				2012			
			Hydroperiod		Relative water level (RWL)		Hydroperiod		Relative water level (RWL)	
			r	p-value	r	p-value	r	p-value	r	p-value
Black Hammock	Hammock (WE1)	19	0.68	0.001	0.47	0.040	0.60	0.007	0.16	ns
	Bayhead (WE2)	23	0.79	< 0.001	0.81	< 0.001	0.82	< 0.001	0.80	< 0.001
	Swamp (WE3)	37	0.79	< 0.001	0.76	< 0.001	0.57	< 0.001	0.50	0.002
Gumbo Limbo	Hammock (WE1)	42	0.47	0.002	0.37	0.014	0.51	< 0.001	0.53	< 0.001
	Bayhead (WE2)	52	0.27	0.050	0.43	0.001	0.23	ns	0.10	ns
	Swamp (WE3)	43	0.13	ns	0.18	ns	0.55	< 0.001	0.60	< 0.001
Satinleaf	Hammock (WE1)	22	0.61	0.002	0.47	0.023	0.67	< 0.001	0.55	0.009
	Bayhead (WE2)	18	0.76	< 0.001	0.73	< 0.001	0.81	< 0.001	0.74	< 0.001
	Swamp (WE3)	19	0.10	ns	0.13	ns	0.36	ns	0.35	ns

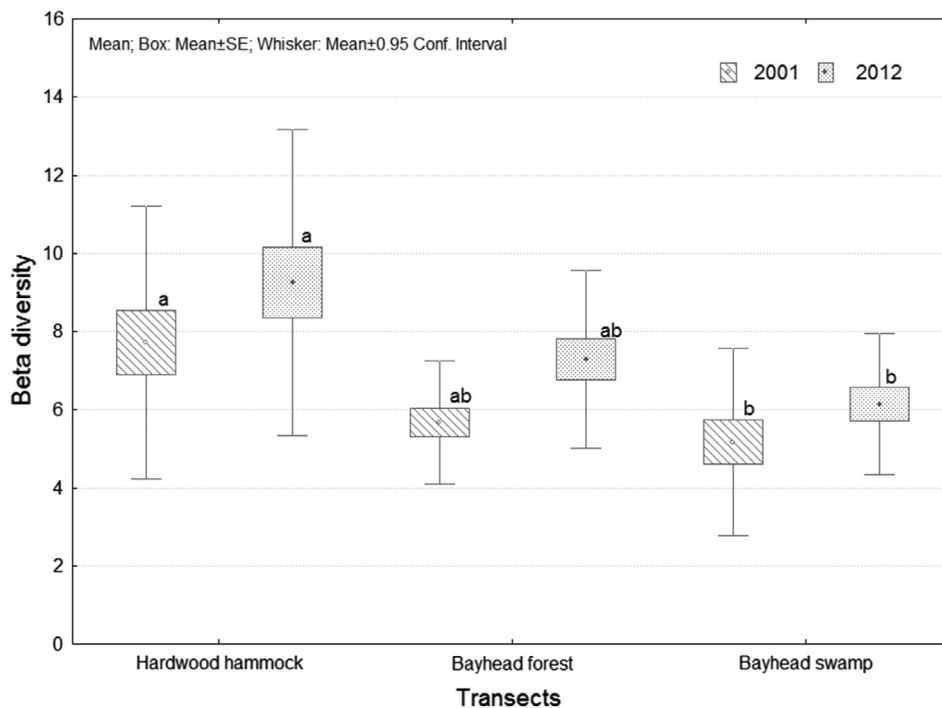


Fig. 9. Box plots showing the mean (\pm SE) of beta diversity (β) in 2001 and 2012 on three WE transects – Hammock (WE1), Bayhead (WE2) and Swamp (WE3) – on three Shark River Slough tree islands. Different letters show significance (One-way ANOVA: Bonferroni test, $p < 0.05$) difference between transects within sampling year.

Satinleaf. On this transect in Gumbo Limbo, none of the peaks were significant in 2001, whereas in 2012 three significant peaks, representing high normalized B-C dissimilarities and sharp boundaries between adjacent communities were identified (Fig. 8).

The physical factors that influence the position of boundaries among adjacent communities are likely to be the same that affect the distributions of individual species. A related concept, the spatial heterogeneity hypothesis, suggests that greater habitat (resource) heterogeneity allows the coexistence of more species (MacArthur and MacArthur, 1961; Davidowitz and Rosenzweig, 1998; Kumar et al., 2006). Thus, along an environmental gradient, a positive relationship between habitat heterogeneity and degree of species turnover is expected. In the SRS tree islands, we observed a positive relationship between normalized BC dissimilarity and habitat heterogeneity in all transects, suggesting that the processes that enhance habitat heterogeneity along the gradient will result in sharp intercommunity boundaries, which represent zones of high species turnover. Moreover, β -diversity was higher in 2012 than in 2001, suggesting that habitat resource heterogeneity also increased in the tree islands between the two periods. Generally, in periodically flooded ecosystems, such as floodplains, flooding in large area and high-water levels are known to form homogeneous habitat, whereas during the low water level habitat heterogeneity increases (Thomaz et al., 2007). In contrast, a fluctuating water level with periodic dry-down is likely to increase habitat heterogeneity, especially in topographically heterogeneous areas. In SRS, mean annual water levels were lower and varied more between 2001 and 2012 than the period between 1993 and 2000. Thus, we conclude

that relatively dry conditions and inter-annual variability in the water level in the recent decade resulted in increased β -diversity in SRS tree islands.

In contrast to our expectation of ubiquitous increase in woody plant cover because of relatively dry conditions during 2001–2012, the change in woody cover along the transects showed mixed results. In fact, in the Hammock transect of Black Hammock and Gumbo Limbo islands and in the Bayhead of Gumbo Limbo, tree cover even decreased. This finding may be the result of several interacting phenomena, including disturbances. In 2005, the study islands were hit by two hurricanes, Hurricanes Katrina and Wilma. The latter brought relatively high wind speeds (Knabb et al., 2006; Pasch et al., 2006) and caused significant tree damage on the study islands. For three years after the hurricane, cumulative tree mortality values were 17.5% and 6.2% in the Hammock plots of Gumbo Limbo and Black Hammock, respectively (Ruiz et al., 2011). The high tree mortality on these islands in post-hurricane years could also be the result of interactions of multiple disturbances, which can intensify the effects of disturbances and affect the resilience of forests (Buma and Wessman, 2011). The drought that prevailed from 2006 to 2008 after Hurricane Wilma might have accentuated tree mortality on these islands. In drought years, particularly during the dry season when hammock plants use regional ground water (Saha et al., 2010), water level fell greater than 70 cm below the ground surface potentially limiting access to ground water and leading to high mortality in hurricane-stressed trees.

Our results reinforce the concept that tree islands are dynamic communities that expand and contract over time in response to

Table 3

Global R and p-values from analysis of similarity (ANOSIM) testing for differences in vegetation composition between two sampling events, 2001 and 2012.

Tree island	Transects							
	Hammock (WE1)		Bayhead (WE2)		Swamp (WE3)			
	R-statistic	p-value	R-statistic	p-value	R-statistic	p-value		
Black Hammock	0.011	0.272	0.071	0.024	0.131	0.001		
Gumbo Limbo	0.009	0.218	0.055	0.007	0.384	0.001		
Satinleaf	0.009	0.292	0.114	0.006	0.348	0.001		

Table 4
Mean cover of different life-forms in plots along transects sampled in 2001 and 2012 in three Shark River Slough tree islands. The value in bold are significantly different (Wilcoxon Matched Paired test, $p < 0.05$) between 2001 and 2012 samplings.

Transect/Life-forms	Black Hammock		Gumbo Limbo		Satinleaf	
	2001	2012	2001	2012	2001	2012
<i>Hammock (WE1)</i>						
Epiphyte	0.04		0.74	1.96		
Fern	5.88	5.08	15.13	12.26	3.84	7.52
Herb/Forb	4.54	9.71	5.45	5.55	4.34	6.35
Herb/Graminoid	10.50	23.54	22.82	33.34	15.54	18.98
Shrub	0.00	1.04	5.28	0.54	0.04	0.19
Seedling (woody)	6.63	10.65	18.70	13.81	3.57	6.56
Vine (woody)	2.50	3.94	1.18	6.20	9.45	4.72
Tree	68.40	54.92	79.23	46.24	44.59	49.54
<i>Bayhead (WE2)</i>						
Epiphyte			0.27	0.04		
Fern	9.21	9.05	26.85	24.89	10.74	15.72
Herb/Forb	3.16	7.07	10.82	13.37	3.78	3.35
Herb/Graminoid	8.30	29.63	13.42	38.55	20.59	61.41
Shrub	0.11	1.41	2.40	4.29	1.52	
Seedling (woody)	2.34	3.89	11.25	2.96	0.70	3.91
Vine (woody)	0.23	4.00	1.34	1.49	0.43	0.46
Tree	58.89	46.59	38.03	23.62	26.67	36.13
<i>Swamp (WE3)</i>						
Epiphyte	0.02	0.06				
Fern	5.48	8.19	12.63	7.98	3.65	13.29
Herb/Forb	19.54	23.32	19.40	28.28	9.38	9.79
Herb/Graminoid	23.09	48.32	8.20	64.90	20.79	80.06
Shrub	0.82	14.99	3.65	9.96	14.50	1.25
Seedling (woody)	10.35	4.95	5.28	0.27	2.25	0.15
Vine (woody)	0.16	0.37				1.02
Tree	21.35	19.25	7.74	11.24	6.46	12.00

hydrologic fluxes (Stone and Chmura, 2004). Between 2001 and 2012, Bayhead and Swamp plots saw increases in tree density and basal area. In general, sapling densities decreased in the Swamp plots, possibly in response to intra and interspecific competition for nutrients and light resulting from canopy closure and forest maturation. However, in those plots an increase in the number of trees and a new cohort of saplings indicate a slow but steady progression in the succession of the Swamp into a Bayhead community. Temporal changes in species importance values (IV), further reinforce the concept of a successional model of tree island development over time, though a precise interpretation of changes in IV between 2001 and 2012 is difficult because of species differences in hydrologic tolerance. In general, however, flood-tolerant species like *Annona glabra* and *Salix caroliniana* saw their IV decline while moderately flood-tolerant species like *Chrysobalanus icaco* and *Ilex cassine*, and flood-intolerant species like *Ficus aurea* increased.

Distribution of tree species in tree islands, and the loss of tree islands have normally been viewed in relation to prolonged high-water conditions. However, tree island plant communities and the boundaries between them or between an island and adjacent mixed-marsh are also susceptible to the direct and indirect effects of disturbance, such as fire, particularly during drought conditions like those observed in 2007–2008. Fires not only kill trees, but also consume the rich organic soils, in the process altering water regime by lowering the surface elevation. Under these circumstances, immediate post-fire flooding can be detrimental to tree island recovery, and may lead to their recession or elimination (Ruiz et al., 2013). Furthermore, fire is also known to sharpen the edges of both ridges and tree islands (Givnish et al., 2008; Wetzel et al., 2008). Between 2001 and 2012 samplings, two fires burned the marshes close to Black Hammock. These fires might have killed any woody plants growing in the marshes, and consumed marsh peat, accentuating the difference in elevation and sharpening the boundary between tree island and adjacent marsh.

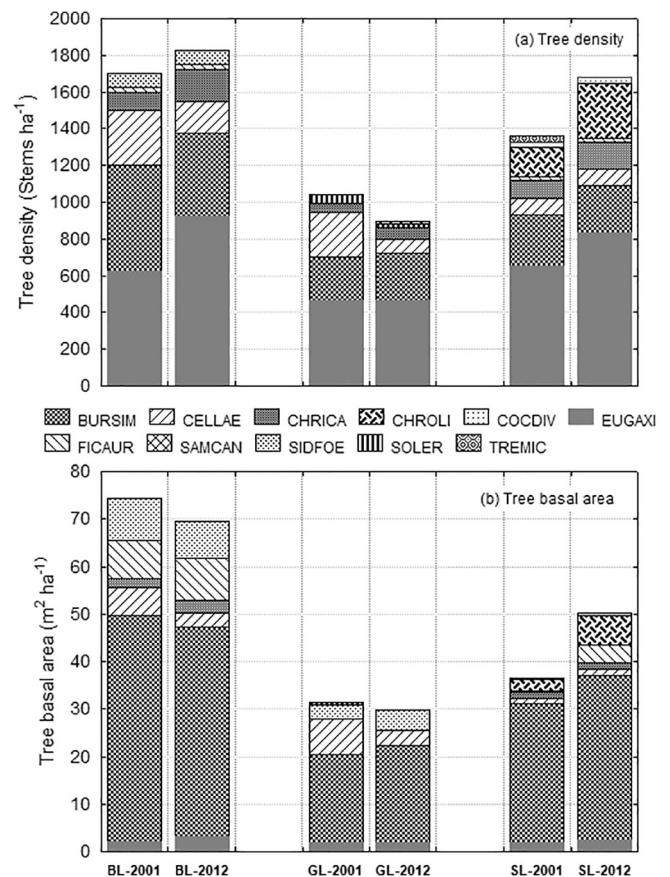


Fig. 10. Tree density (stems ha⁻¹) and basal area (m² ha⁻¹) in Hardwood hammock plots on Shark River Slough tree islands sampled in 2001 and 2012. BL = Black Hammock, GL = Gumbo Limbo, SL = Satinleaf. Full name of species are in Supplementary Table S3.

Table 5
Mean (± 1 S.E.) tree importance value (IV) in Bayhead forest and Bayhead swamp plots sampled in 2001 and 2012. The IV values were averaged over all three Shark River Slough tree islands.

Species	Tree - importance value (%)			
	Bayhead forest		Bayhead swamp	
	2001	2012	2001	2012
<i>Annona glabra</i>	44.0 \pm 13.4	34.3 \pm 4.0	13.8 \pm 13.8	50.1 \pm 28.7
<i>Chrysobalanus icaco</i>	4.4 \pm 4.4	18.9 \pm 9.8		2.0 \pm 2.0
<i>Ficus aurea</i>	11.7 \pm 11.7	9.5 \pm 9.0		
<i>Ilex cassine</i>	2.8 \pm 1.8	3.5 \pm 2.2		4.2 \pm 4.2
<i>Magnolia virginiana</i>	14.9 \pm 9.5	10.6 \pm 5.7		6.7 \pm 6.7
<i>Morella cerifera</i>	3.1 \pm 1.8	2.5 \pm 0.7	4.1 \pm 4.1	4.3 \pm 4.3
<i>Persea borbonia</i>	0.7 \pm 0.7			
<i>Salix caroliniana</i>	17.0 \pm 3.6	20.2 \pm 0.2	15.5 \pm 15.5	
<i>Sambucus nigra</i> ssp. <i>canadensis</i>	1.5 \pm 0.8	0.4 \pm 0.4	0.0 \pm 0.0	

A shift in the boundary between plant communities occurs when a change in community characteristics cause reduction of its resilience beyond some threshold (Allen et al., 2005). In the study islands, change in hydrology over a decade caused changes in the relative abundance of herbaceous and woody species. However, these changes did not exceed the “tipping point” for any tree island community. Hence, a minimal shift in boundary was observed. In a recent study, macrofossil analysis of a tree island in an area adjacent to Everglades National Park, Water Conservation Area-3A (WCA3A; Fig. 3) showed that the island expanded in response to the dry conditions of the late 1980s, and

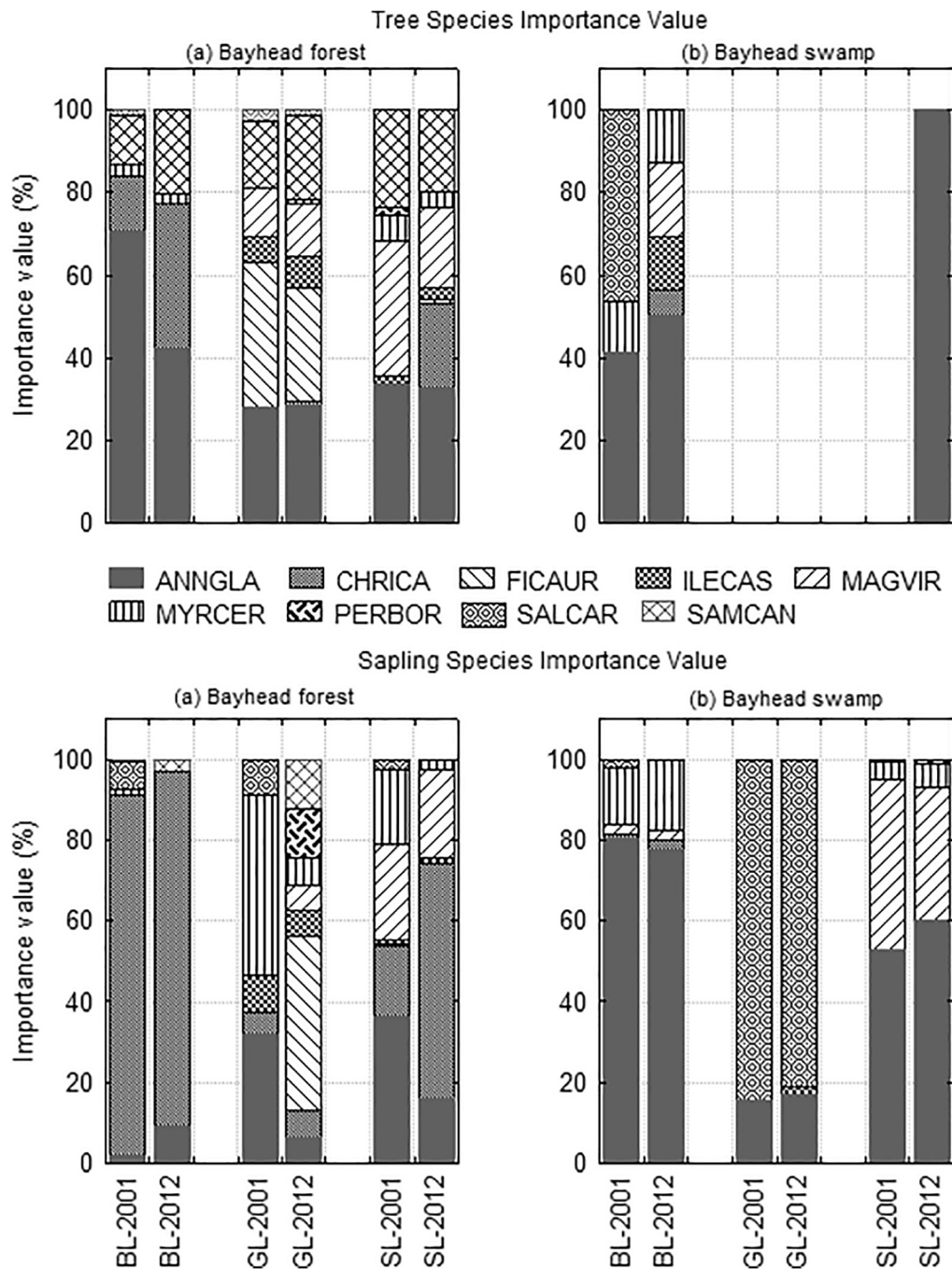


Fig. 11. Tree and sapling importance value (IV) in (a) Bayhead forest and (b) Bayhead swamp plots in three Shark River Slough tree islands sampled in 2001 and 2012. BL = Black Hammock, GL = Gumbo Limbo, SL = Satinleaf. . Full name of species are in [Supplementary Table S3](#).

contracted during wet conditions in the 1990s (Brock et al., 2012). This implies that extreme hydrologic events are more important than average annual hydrologic conditions in shaping tree island vegetation. Moreover, in plant communities arranged along an ecological gradient, high species turnover usually occurs at the interface between adjacent communities. Since there is high variability in composition within the transition zone, the turnover appears to be adaptive. Hence, communities that have low turnover at the boundary, particularly when the boundary is diffuse, may have relatively low resilience (Allen et al., 2005). In the study islands, species turnover was relatively high along the Hammock and Bayhead transects (Fig. 9), where boundaries did not shift in position, suggesting that those communities have higher resilience. However, species turnover was lower on the Swamp transects, and thus the boundaries between Swamp community and the adjacent

Sawgrass marsh were prone to shifting, especially when impacted by extreme instances of flooding or drought.

The strong correlation between tree island vegetation structure and hydrology suggests that hydrologic modifications caused by Comprehensive Everglades Restoration Plan (CERP), a multi-decade restoration project that is underway to restore, preserve and protect the Everglades ecosystems, will affect tree island dynamics throughout the Everglades. Depending on the magnitude of hydrologic alterations achieved by the CERP, the balance between flood-tolerant and flood-intolerant woody and herbaceous vegetation within tree islands is likely to change. The magnitude and direction of such changes will vary spatially in response to regional differences in tree island condition and the extent of hydrologic modification achieved by the CERP. It is likely that tree islands currently under hydrologic stress or in a highly

Table 6

Mean (± 1 S.E.) sapling importance value (IV) in Bayhead forest and Bayhead swamp plots sampled in 2001 and 2012. The IV values were averaged over all three Shark River Slough tree islands.

Species	Sapling – importance value (%)			
	Bayhead forest		Bayhead swamp	
	2001	2012	2001	2012
<i>Annona glabra</i>	23.6 \pm 10.8	10.7 \pm 2.9	49.6 \pm 18.8	51.7 \pm 18.0
<i>Chrysobalanus icaco</i>	37.2 \pm 26.2	50.7 \pm 23.7	0.2 \pm 0.2	0.8 \pm 0.8
<i>Ficus aurea</i>	0.2 \pm 0.2	14.4 \pm 14.4	0.1 \pm 0.1	0.1 \pm 0.1
<i>Ilex cassine</i>	3.3 \pm 2.8	2.6 \pm 2.0		0.5 \pm 0.5
<i>Magnolia virginiana</i>	8.0 \pm 8.0	9.4 \pm 6.4	14.9 \pm 13.8	11.7 \pm 10.5
<i>Morella cerifera</i>	21.3 \pm 12.6	3.1 \pm 1.9	6.1 \pm 4.2	7.8 \pm 5.0
<i>Persea borbonia</i>		4.1 \pm 4.1	0.2 \pm 0.2	0.4 \pm 0.3
<i>Salix caroliniana</i>	6.2 \pm 1.8		28.8 \pm 27.8	27.1 \pm 27.1
<i>Sambucus nigra</i> ssp. <i>canadensis</i>	0.2 \pm 0.2	5.1 \pm 3.7		

degradative state, e.g., ghost islands (Ewe et al., 2009), could see a recovery if hydrologic conditions conducive to woody plant establishment and growth are achieved and sustained. In an evaluation of several restoration scenarios for the Everglades that were based on questions of policy makers and managers, Wetzel et al. (2017) showed improved water conditions for tree growth in WCA3A, where tree islands have long been exposed to a stressful flooding regime. Their results support our findings of an increase in abundance of flood-intolerant and moderately flood-tolerant species in study SRS tree islands in response to relatively dry conditions during 2001–2012 period. While such a dry conditions during that period in SRS was a function of both low rainfall and restricted water delivery, under the CERP projects, there are plans to increase the water delivery to ENP in coming years. Under those conditions, the trend in tree island community change observed in this study is likely to be reversed, favoring herbaceous over woody life forms. However, Wetzel et al. (2017) showed that while some tree islands in ENP and WCA3B will experience the wetter conditions in all restoration scenarios than existing condition, the plant communities in the modeled islands in these regions would experience minimal change in the proportions of tree island woody communities. Our study suggests that the CERP should strive to achieve hydrologic conditions that result in a spatially balanced mosaic of plant communities in different successional states on tree islands. System wide homogeneity in tree island structure, composition, and type should be discouraged, since it might cause local extirpation of rare flora and fauna, which would reduce the overall species diversity of tree islands. System wide homogeneity in tree islands significantly increases the chances of a system wide or regional perturbation event having catastrophic consequences.

In summary, SRS tree islands consist of plant communities of contrasting species composition and functional representation (life-forms). Between 2001 and 2012, cover of flood-tolerant tree species decreased, while cover of moderately flood-tolerant and flood-intolerant species increased along transects, as well as in plots within Hammock, Bayhead and Swamp communities. While the life-form composition of plant communities changed on only a few transects, such changes in the mixture of life-forms exactly paralleled the changes in the boundary between adjacent communities. Thus, vegetation changes do not always involve a simple shift in the location of fixed species assemblages, but rather the emergence of new species' and structural combinations. In these three islands, however, the effects of annual variation in hydrology over the previous decade probably did not surpass the communities' resilience, possibly because the period of the study may just not have been long enough. Hence, a minimal shift in boundary between tree island plant communities was observed on most transects.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2018.03.022>.

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