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Monitoring of Tree Island Condition in the Southern Everglades

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General Background

Tree islands, an integral component of the Everglades in both the marl prairie and ridge and slough landscapes, are complex ecosystems. They are sensitive to activities associated with the Comprehensive Everglades Restoration Plan (CERP) authorized by the Water Resources Development Act (WRDA) 2000 to restore the south Florida ecosystem. More specifically, changes in hydrologic regimes associated with restoration projects are likely to affect the internal water economy of the islands, which in turn will influence tree island plant community structure and function. To strengthen our ability to assess the “performance” of tree island ecosystems and predict how these hydrologic alterations would translate into ecosystem response, an improved understanding of plant community structure and function, and their responses to major drivers and stressors is important. Built on a baseline study of vegetation structure and composition and associated biological processes over three years (1999-2002) on three tree islands in Shark River Slough (Ross and Jones 2004), a more extensive study was initiated in 2005 with initial funding from Everglades National Park and South Florida Water Management District (SFWMD). The study has been continued through 2017 with funding from US Army Corps of Engineers (USACOE).

The major goal of ongoing monitoring of southern tree islands is to assess structural and compositional responses of tree island vegetation to natural and management-induced hydrologic change that result in the changes in aerial extent or relative proportion of forests on tree islands and the boundary between islands and marshes. This research addresses the relevant performance measures (PM): 1) GE-15: ‘Ridge and Slough Sustainability’ 2) ‘Total System Performance Measure (RECOVER 2011). The working hypothesis of the study is expressed as *‘the loss of elongated patterns of ridges, sloughs, and tree islands in the direction of water flow in the ridge and slough landscape of the Everglades is attributed to disrupted sheet flow and related changes in water depth’* identified in the hypothesis cluster of the sub-section 3.3.7.1 of 2009 CERP Monitoring and Assessment Plan (RECOVER 2009).

The specific objectives of our ongoing research are:

- 1) To characterize relationships among the hydrologic regimes with demographic fluctuations in the hardwood forests,

- 2) To assess change in the structure and composition of both swamp forest and hardwood hammock
- 3) To develop a tree island vegetation classification scheme based on canopy and understory vegetation types.
- 4) To develop and validate methods to consistently differentiate vegetation assemblage and to delineate their boundaries from spectral signatures of bi-seasonal satellite data and aerial photography
- 5) To detect changes and trends in aerial extent of the relative proportion of different vegetation communities
- 6) To investigate the correlation of vegetation changes in response to hydrological regime changes.

This document describes the work accomplished in 2015-2017. The document is organized in two sections. Section 1 summarizes vegetation structure and composition along hydrologic gradients in tree islands, and demographic changes in tree layer composition in the hardwood hammock portions of a subset of four tree islands among a 16-island tree island network established in Everglades National Park for long-term monitoring and assessment. Section 2 explores the methodology for detecting Everglades tree island community types (hardwood hammock, bayhead forest, and bayhead swamp) in three tree islands (Chekika, SS-93 and SS-94), and differentiating them from the surrounding marsh communities using WorldView2 (WV2) multi-spectral satellite data augmented with LiDAR data available for those islands.

1 Plant communities along hydrologic gradient in tree islands

1.1 Introduction

Tree islands are a prominent feature in both the marl prairies (MP) and ridge and slough (R&S) landscapes of the Everglades, where they have undergone extensive damage from extreme flooding, drought, fire, and tropical storms (Patterson and Fink 1999; Sklar and van der Valk 2002; Wetzel et al. 2008; Ruiz et al. 2011, 2013a). These islands are also sensitive to large-scale restoration actions associated with the Comprehensive Everglades Restoration Plan (CERP) authorized by the Water Resources Development Act (WRDA) of 2000 to restore the south Florida ecosystem. More specifically, changes in hydrologic regimes associated with restoration projects, including the construction of two Tamiami Bridges and Central Everglades Project Planning (CEPP) project components (USACE 2014), are likely to alter the impact of local and landscape-level stressors such as hydrology, invasive exotics, windstorms, and fire on tree islands (Wetzel et al. 2017). While such alterations in the impact of these stressors at the broader scale influence the spatial distribution pattern of tree islands within the landscape, the hydrologic alterations also affect the internal water economy of islands, which in turn influences plant community structure and function by affecting species composition, tree regeneration and growth. In the Ecological Conceptual Model (ECM) for Greater Everglades, researchers have identified plant community composition and structure of tree islands as one of several ecological attributes that are affected by changes in hydrologic characteristics and fire regimes. It is therefore important to understand how the tree island plant community varies along the existing hydrologic gradient, and whether changes in community structure and composition influenced by natural and/or management-induced hydrologic conditions have surpassed the ability of the islands to remain functional. When plant community composition responds to changes in environmental drivers beyond a certain threshold, the tree island structure and function can be in peril, leading to the loss of the islands.

In the ridge and slough (R&S) landscape, flow-induced teardrop-shaped tree islands often include different plant communities - tropical hardwood (hammock), bayhead and bayhead swamp forests – arranged along topographic, hydrologic and soil nutrient gradients (Armentano et al. 2002; Sah 2004; Espinar et al. 2011; Sah et al. 2018). The hardwood hammock-dominated heads are of great ecological significance, as both biodiversity and phosphorus ‘hotspots’ within

the homogeneous oligotrophic landscape (Ross and Jones 2004; Wetzel et al. 2008). While hydrology plays an important role in the development and maintenance of the ridge-slough-tree island patterned landscape, the associated plant communities also influence the hydrodynamics and spatial distribution of soil resources, which in turn affect ecological processes on tree islands (Ross and Jones 2004; Wetzel et al. 2005; Ross et al. 2006, Givnish et al. 2008; Hanan and Ross 2010; Ross and Sah 2011; Sullivan et al. 2011, 2014, 2016) (**Figure 1.1**).

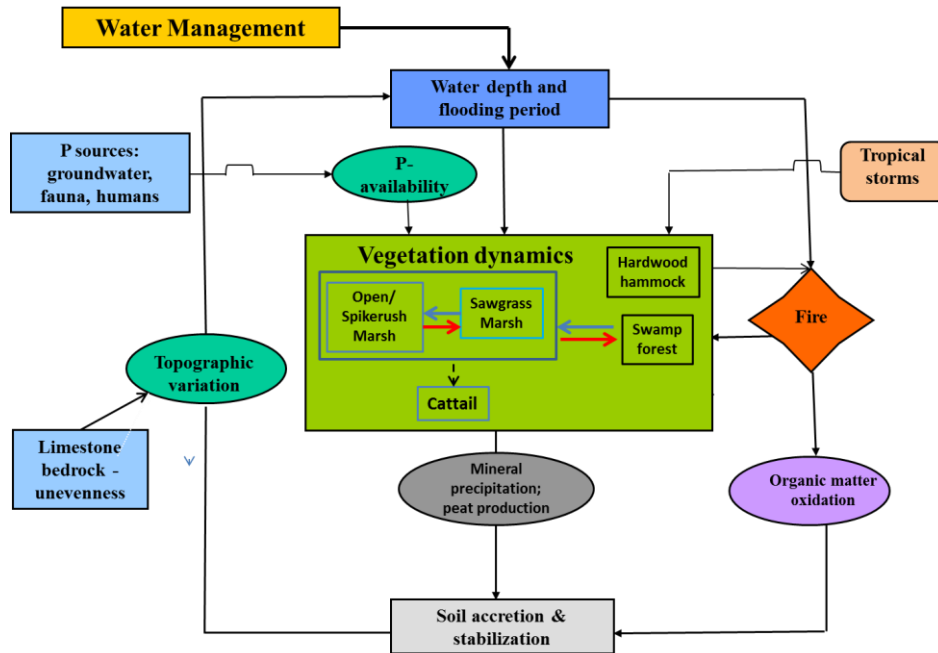


Figure 1.1: A Conceptual model: vegetation dynamics in tree islands and surrounding marsh.

Beyond the physiographic template, the species assemblages and areal extent of different plant communities on the R&S tree islands, and between tree islands and marsh fluctuate significantly over time depending on the climate and anthropogenically induced changes in hydrology and fire frequencies (Stone and Chmura 2004; Bernhardt and Willard 2009). In R&S tree islands, the swamp forests and tails are usually the areas that respond most noticeably to hydrology, whereas on an inter-annual scale the response of the tree island heads to windstorms overshadows any detectable hydrologic response (Ruiz et al. 2011; 2013b; Sah et al. 2018). Structural and compositional responses of the hardwood hammocks to hydrologic

alterations become evident primarily in extreme events. In contrast, an analysis of the multiple year historical imagery suggests that a decline in the areal extent of tree islands within Everglades National Park occurred over the last half-century (Sklar et al. 2013), and the loss was mostly concentrated in the swamp-forest dominated tail regions of the islands. Though the reason for this pattern has not yet been fully explored, one possibility is that they reflect alterations in the Everglades' hydrologic regime prior to the establishment of Everglades National Park (ENP), either directly or through their impact on other stressors such as fire and windstorms. Thus, for the RECOVER monitoring program, a strategy for tree island work that focuses on both the local and landscape-scale effects, especially those taking place along the elevation gradient of the tree islands, is important. Ecological stressors influence tree island vegetation through their effects on species composition, growth, physiological processes, soil accretion and oxidation, fire frequency and intensity. Depending on the extent of hydrologic alterations, differential recruitment and growth of flood-tolerant and flood-intolerant species of different growth forms (e.g., herbaceous or woody) are expected to exhibit spatial change, resulting in shifts in species assemblages along the hydrologic gradient.

Therefore, to understand inter-annual variability, long-term trends and the mechanisms that drive them, it is essential to delineate spatially explicit patterns of community composition and configuration at high spatial precision that allow for detection of short-term fluctuations as well as persisting long-term change. An approach that concentrates most effort on linking extensively distributed ground surveys with community patterns derived from satellite data and aerial photography interpretations (Section 2) is likely to help in reaching a more nuanced understanding of past change in tree island structure, as well as in projecting responses to future changes in water level.

This section of the report includes the results of the continued monitoring of vegetation structure and composition within permanent plots established in the hardwood hammock portion of a subset of four tree islands among a 16-island tree island network established in Everglades National Park for long-term monitoring and assessment (Shamblin et al. 2008; Ruiz et al. 2011). In addition, as a part of the continued efforts to study tree island vegetation dynamics along hydrologic gradient (Sah et al. 2015), this section also includes results from vegetation surveys conducted along transects in several tree islands to establish a more complete inventory of

spatially explicit vegetation patterns along topographic gradient across heterogeneous tree islands.

1.2 Methods

1.2.1 Study Area

The tree islands currently monitored represent a subset of those studied between 2005 and 2013. The first part of our study focused on tree recruitment and growth in the hardwood hammock portions of four tree islands in the network, including three islands (Black Hammock, Gumbo Limbo and Satinleaf) in the Shark River Slough (SRS), and one (SS-81) in the Northeast Shark Slough (NESRS) (Figure 1.2). The first three islands have been monitored since 2001 (Ross and Jones 2004). However, during initial 1999-2001 sampling, the vegetation data on these islands were collected only once. Regular monitoring began only in 2005, and since then vegetation data has been collected annually. The fourth island, SS-81, monitored since 2007, is downstream of the 1-mile bridge that has been built along the Tamiami Trail to improve water flow between Water Conservation Area (WCA)-3B and ENP.

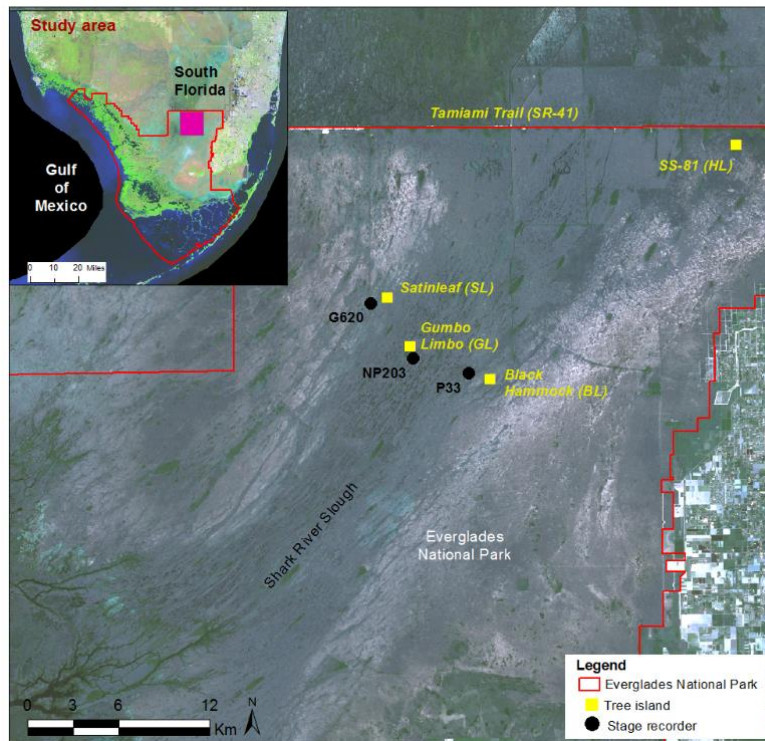


Figure 1.2: Location map of four tree islands (Black Hammock, Gumbo Limbo, Satinleaf and SS-81) on which tree dynamics in hardwood hammock is annually monitored.

The hardwood hammocks on these four islands are of different size, and they differ in elevation. Their mean (\pm SD) elevation ranges between 2.059 (\pm 0.071) m and 2.330 (\pm 0.166) m (Table 1.1). Plot elevations within individual islands are also highly variable. Among four islands, SS-81 has higher within-plot variability (Coefficient of Variation, CV= 0.140) than other islands, with low spots frequently occupied by swamp forest trees.

Table 1.1: Tree island location and topographic data (mean, minimum, and maximum) of four islands on which tree layer vegetation in the hardwood hammock was sampled.

Tree Island	Easting NAD83 (UTM_Z17N)	Northing NAD83 (UTM_Z17N)	Plot Size (m ²)	Mean (\pm 1 S.D.) Plot Elevation (m NAVD 88)	Minimum Plot Elevation (m NAVD 88)	Maximum Plot Elevation (m NAVD 88)
Black Hammock	531295	2832630	400	2.330 \pm 0.166	1.988	2.584
Gumbo Limbo Hammock	525999	2834793	625	2.059 \pm 0.071	1.916	2.24
Satinleaf	524499	2838019	625	2.221 \pm 0.076	2.082	2.368
SS-81	547639	2848113	300	2.168 \pm 0.304	1.592	2.649

The study also included vegetation sampling on transects in five islands, four (Gumbo Limbo; SS-202, SS-93 and SS-94) in the ENP, the other (WCA3B-12) in WCA 3B (Table 1.3). These islands were initially selected as potential islands for fine scale mapping. Later, instead of WCA3B-12, an island (Chekika), also in ENP, was selected for mapping. On these islands, sampling focused on the Bayhead and Bayhead Swamp parts of the tree islands (Figure 1.3), mainly to augment fine scale vegetation mapping by providing ground data in the areas of tree islands where the interpretation of spectral signature was especially difficult.

Table 1.2: Tree island location and summary of transect sites on five islands on which vegetation was surveyed along transects between WY 2015 and 2017. Plot elevation is based on field measurement of water depth and EDEN water elevation at the location on the same day.

Tree Island	Easting NAD83 (UTM_Z17N)	Northing NAD83 (UTM_Z17N)	Number of plots on transects	Mean (\pm 1 S.D.) Plot Elevation* (m NAVD 88)	Minimum Plot Elevation (m NAVD 88)	Maximum Plot Elevation (m NAVD 88)
Gumbo Limbo Hammock	525999	2834793	59	128.3 \pm 6.2	108.3	143.7
NP-202	529770	2838836	61	153.6 \pm 13.5 ^a	111.0	178.7
WCA3B-12	546325	2857390	18	148.7 \pm 1.6 ^b	146.7	151.0
SS-93	535151	2848529	14	167.8 \pm 8.1 ^c	155.3	179.3
SS-94	535517	2848771	14	169.9 \pm 10.6 ^d	154.7	185.7

* For some sites (*), elevation was missing, as there was no standing water at that site at the time of vegetation sampling. Number of missing sites: a = 1, b = 13, c = 3, and d = 4.

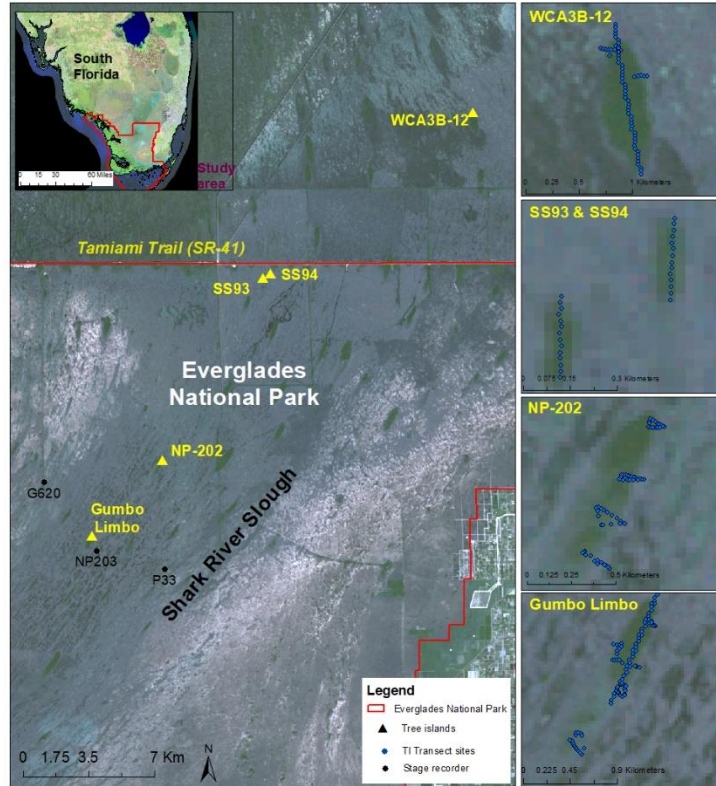


Figure 1.3: Location map of five tree islands (Gumbo Limbo, NP-202, WCA3B-12, SS-93 and SS-94) and the transect sites sampled on those islands.

1.2.2 Data Collection

1.2.2.1 Vegetation sampling

The vegetation study included two different sampling schemes; 1) tree layer sampling in permanent hardwood hammock plots, and 2) a detailed vegetation structure and compositional survey on transects along the hydrologic gradient in two islands, selected for fine scale vegetation mapping using spectral signatures from bi-seasonal satellite data.

Tree census in hardwood hammocks: Tree layer vegetation sampling was done in the hardwood hammock plots on four tree islands, Black Hammock (BL), Gumbo Limbo (GL), Satinleaf (SL) and SS-81. The monitoring plots on these islands range between 300 m² in SS-81 to 625 m² (Table 1.1). Each plot is gridded into 5×5m cells, whose corners and midpoint are marked by 30 cm long ½" PVC stakes affixed to the ground. When the plots were first established on these islands, the plot and cells were set up using compass, measuring tape, sighting pole(s), and right-angle prism. In these plots, all trees (≥5 cm) are tagged with numbered aluminum tags, and the location of each tagged tree is recorded to the nearest 0.1m using the SW

corner of the plot as a reference (0, 0). Furthermore, if a tree has multiple stems ≥ 5 cm DBH, each stem is tagged with a unique ID that allowed it to be cross-referenced back to its 'parent'. Status (live and dead) and diameter (cm) at breast height (DBH) of each individual tree was first recorded when plots were established (In BL, GL and SL in 2001, and in SS-81 in 2007). Since 2007, those measurements have been made annually.

Each year from 2014-2017, the tree census included the record of the status (live and dead) of tagged trees, and any tree that had grown into the >5 cm DBH class (hereafter called 'in-growth') since the previous year's survey. In-growths were identified to species and tagged. DBH of each tree was also measured.

Vegetation sampling on transects: In 2015 and 2016 (Year 1 and 2, respectively), in concurrence with the vegetation sampling done on nine islands during 2012-2013 study (Sah et al. 2015), we conducted vegetation surveys along transects on three islands, two (Gumbo Limbo and NP-202) in ENP, and one (WCA3B-12) in WCA3B (Figure 1.3). On these islands, however, sampling focused on the bayhead and bayhead swamp parts of the tree islands, for two reasons, 1) to provide a more complete representation of vegetation assemblages on tree islands within the R&S landscape, and 2) to augment fine scale vegetation mapping by providing the ground data in the areas of tree islands where the interpretation of spectral signature was difficult. On these transects, the sampling was done every 10 -20 m interval instead of 30 m interval done during 2012-2013.

In 2017 (Year 3), vegetation we conducted vegetation sampling along the N-S transect on two islands (SS-93 and SS-94). On these islands, transects run from head to tail, i.e. along the long axis (N-S) of the islands. On these transects, the sampling was done every 15m.

Vegetation sampling on the transects was done using a nested plot design. In each plot, relative abundance of species in six growth forms: tree, vine, shrub, fern, forb, and graminoid, was recorded. The overstory trees, defined here as woody individuals with a height above two meters, and woody vines were sampled within a 2.5 m radius plot, whereas shrub, fern, forb, and graminoid species were sampled within a 1 m radius plot centered within the 2.5 m plot. In different lifeform groups, cover of each species was estimated *in situ* using a modified Braun-Blanquet scale based on the following six cover categories: 1: $<1\%$; 2: $1-4\%$; 3: $4-16\%$; 4: $16-32\%$; 5: $32-66\%$; & 6: $>66\%$. In addition, the total cover of each growth form within their respective plot was also estimated.

Plant canopy height (m) within each 2.5 m plot was estimated and categorized into one of nine height categories: Cat 1: 0, 2: 0-1, 3: 1-2, 4: 2-3, 5: 3-5, 6: 5-7, 7: 7-10, 8: 10-15, and 9: >15. At each plot center, mean forest overstory density (canopy cover) was estimated by taking four densiometer readings facing in each of the four cardinal directions (i.e., North, East, South, and West) (Lemmon 1956). The densiometer has a convex mirror, engraved with 24 squares in it. It is held at breast height, and canopy closure is estimated by calculating the number of squares (or quarters of each square) covered by the image of the canopy. The total number was then multiplied by 1.04 and averaged over the four readings to calculate percent canopy cover in each plot.

1.2.1.2 Hydrology

Within each vegetation plot, three representative measurements of water depth were taken by measuring the distance between the ground surface and the water table surface above the ground. At the few plots where the water table was below the ground surface, a small 3-cm radius hole was dug and allowed to equilibrate while the vegetation sampling within the plot was completed. The water table elevation, at these plots, was then estimated by measuring down from the soil surface to the top of the water table. These measurements were recorded as negative values to indicate that the water table was below the ground surface. Measurements of water depth were not taken at the rocky “head” of the study tree islands, thus water depths at the “head” of each tree island were recorded as zero.

1.2.3 Data Analysis

1.2.3.1 Hydrologic conditions

In conjunction with EDEN (Everglades Depth Estimation Network), water surface elevation data (<http://sofia.usgs.gov/eden>), field measurements of water depth were used to estimate the hydrologic conditions at each sampling site. EDEN acquires water level data from a network of stage recorders throughout the Everglades and produces interpolated daily water surface estimates (Palaseanu and Pearlstine 2008). Ground elevation for each plot was estimated by subtracting the mean water depth from the EDEN water surface elevation for the marsh adjacent to each tree island on the day it was sampled. Mean annual water depth, and discontinuous hydroperiod (i.e., the number of days per year when the location had water depth

>0 cm for each plot) were then estimated based on ground elevation and the time series data of water surface elevation extracted from EDEN database. Previous studies have found that prairie and marsh vegetation composition are well predicted by the previous 3-5 years of hydrologic conditions (Armentano et al. 2006; Ross et al. 2006; Zweig and Kitchens 2009), whereas tree island vegetation was found strongly correlated with 7-year average hydroperiod and water depth (Sah 2004, Espinar et al. 2011; Sah et al. 2018). Thus, in this study, we averaged hydroperiod and mean annual water depth for 4-7 years water years (May 1st – April 30th) prior to each sampling event to examine the relationships between hydrologic parameters and change in vegetation characteristics.

1.2.3.2 Tree-layer vegetation dynamics

Tree census data were summarized by calculating tree mortality and in-growth, two important indicators of woody vegetation dynamics. Both tree mortality and in-growth in the islands are strongly influenced by hydrology, and other drivers and/or stressors, including tropical storms, fire, etc. In addition, tree density and basal area for each species were also calculated, and summed for each island.

Differential mortality and/or in-growth among species over time usually result in different species composition. A change in tree species composition was analyzed using non-metric multidimensional scaling (NMDS) ordination. Species abundance data used in the ordination was species' importance value (IV). Tree density and basal area for each species were summed for each plot, relativized as a proportion of the plot total, and used to calculate Importance Value (IV) of species using the following equation: $IV = 100 \cdot ((R_d + R_{ba}) / 2)$, where R_d is the species relative density and R_{ba} is the species relative basal area. Importance value (IV) data of each species were standardized to species maxima and the Bray-Curtis dissimilarity index was used as a measure of dissimilarity in the ordination.

1.2.3.3 Vegetation characterization along hydrologic gradient

Vegetation data collected on transects were used to characterize the vegetation types along the hydrologic gradient. Species cover data were summarized using the mid-point of the cover class, multivariate techniques, including cluster analysis and ordination, were used to classify the sites and characterize the plant communities along the hydrologic gradient. For both cluster analysis and ordination, Bray-Curtis dissimilarity was the distance measure. Before analyzing the data, we identified outliers, defined as a site with mean Bray-Curtis dissimilarity

and 2-standard deviation and removed them. Sites were classified using the agglomerative hierarchical cluster method with flexible beta (-0.25) linkage (McCune and Mefford 2011).

These sites were also classified, using a dichotomous key developed for site classification based on structural data (plant canopy height and cover) and relative cover of different life forms (shrub, tree, graminoid and forbs), hereafter called “structural dichotomous-key classification” (Table 1.3; Sah et al. 2015).

Table 2.3: Dichotomous key for the classification of vegetation plots within tree islands in Shark River Slough, Florida (Sah et al. 2015).

1a. Trees or shrubs on a limestone outcrop or topographic high:.....	Hardwood Hammock.
1b. Trees, shrubs, or graminoids not on a limestone outcrop or topographic high:.....	go to 2.
2a. Tree and shrub cover >10%:.....	go to 3.
2b. Tree and shrub cover < 10%:.....	go to 6.
3a. Mean vegetation height \geq 4 m.....	go to 4
3b. Mean vegetation height < 4 m.....	go to 5
4a. Mean vegetation height \geq 4 m and tree cover \geq 40%:.....	Bayhead Forest.
4b. Mean vegetation height \geq 4 m and tree cover < 40%:.....	Bayhead Swamp.
5a. Mean vegetation height < 4 m, tree cover < 40% and shrub cover between 10-100%	Bayhead Swamp.
5b. Mean vegetation height < 4, tree and shrub cover < 10%	go to 6
6a. Mean vegetation height between 1.5 and \leq 3.5 m, tree & shrub cover \leq 10%: and sawgrass cover \geq 50%)	Sawgrass Marsh.
4b. Mean vegetation height < 1.5 meters, tree and shrub cover < 1% and sawgrass cover < 50%:.....	Marsh.

Multivariate techniques, including Non-metric multidimensional scaling (NMDS) ordination (McCune and Grace 2002), was used to examine the relationships between species composition and hydrologic variables. Species cover data were relativized using species maximum observed at any site, in order to equalize the potential contributions of species to the dissimilarities (Faith et al. 1987). The hydrologic variables included in the analysis were annual mean hydroperiod (days) and relative water level (cm), averaged over one to seven years. The relationship between community composition and hydrologic variables were examined using a vector-fitting procedure incorporated in the computer program DECODA (Minchin, 1998). The

significance of the relationship was assessed using a Monte-Carlo procedure permutation test with 1,000 permutations of the species data.

Finally, we compared the vegetation types identified through cluster analysis with the classification of sites using user-defined dichotomous key that was primarily developed based on the structural variables observed in nine islands (Sah et al. 2015). We also evaluated vegetation types identified using spectral signatures of plant communities in WorldView2 (WV2) multi-spectral satellite data and LiDAR-based vegetation height data (Section 2).

1.3 Results and Discussion

1.3.1 Hardwood hammock vegetation

1.3.1.1 Hydrologic conditions

Hydrologic condition in tree island hammocks varies depending on the location of tree islands within the R&S landscape and tree island height above the surrounding marshes (Ross and Jones 2004; USACE 2009; Wetzel et al. 2017). On the four SRS tree islands (Black Hammock, Gumbo Limbo, Satinleaf and SS-81) annually monitored since 2006/07, the annual mean relative water level (RWL) ranged between -100.7 ± 14.5 cm in Black Hammock (Figure 1.4a) in 2011/12 and 49.9 ± 6.3 cm in Gumbo Limbo in 2013/14 (Figure 1.4b). The mean RWL in hammock plot was much (20 to 26 cm) lower in Black Hammock than in other three tree islands. However, the mean RWL was not uniform within the plot on each hammock. Within plot variation (Coefficient of variation, CV) in water level was significantly higher in SS-81 (CV = 33.4%) than in Black Hammock (CV = 16.4%), Gumbo Limbo (CV = 10.3%) and Satinleaf (CV = 10.9%) hammocks.

Based on their locations, SS-81 in the NESRS area that is comparatively drier than SRS, might be expected to have the lowest water level below the ground. However, it seems that hydrologic conditions on tree islands are not simply the function of regional hydrology, but also the geomorphological characteristics of tree islands, such as the tree island height, that is, the difference in elevation between the surface of the tree island and the surrounding marsh. In a study of 69 slough and prairie tree islands within the Park and WCA3B, relative water level (RWL) was negatively correlated with tree island height (Ross and Sah 2011). Among the four islands studied, Black Hammock has higher tree island height (99.1 cm) than Satinleaf (89.3 cm), Gumbo Limbo (87.8 cm) and SS-81 (79.9 cm). In addition to its influence on RWL, tree island

height may reveal the mode and timing of landform development, thus affecting soil characteristics on the islands. For instance, soil phosphorus on tree islands was positively correlated with island height (Ross and Sah 2011).

Between WY 2006/07 and WY 2011/12, the annual mean RWL, was 2 to 18 cm lower than 27- year (1991-2017) average (Figure 1.4). In contrast, the water level in the most recent 5- year period (from WY 2012/13 to 2016/17) was 2 to 12 cm above the 27-year average, except in WY 2014/15, when RWL was 5 cm below the long-term average. None of the hammock plots on these islands was inundated during these periods, except a single 5x5 sub-plot in SS-81 in NESRS slough area. A portion (one 5 x 5 cell) of the hammock plot on this island was inundated for 5 to 120 days in 7 of 11 years between WY 2006/07 and 2016/17.

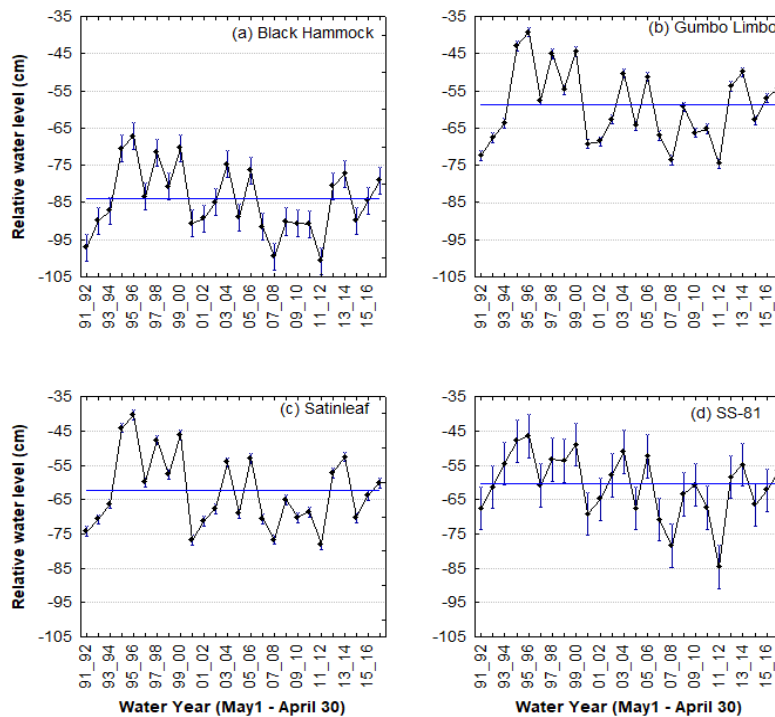


Figure 1.4: Twenty-six year (Water Year 1992-2017) average and annual mean (\pm SE) relative water level (RWL) in the hardwood hammock plots on four tree islands, (a) Black Hammock, (b) Gumbo Limbo, (c) Satinleaf, and (d) SS-81.

In general, the annual mean water level in these hammocks followed the regular dry (low) and wet season (high) pattern. However, in some years, the relative water level in the hammock plots was much higher in the dry season than the wet season due to either anomaly in weather pattern, management-induced changes in hydrologic regime or both. For instance, over the last 10 years, the most remarkable discrepancy between dry and wet season pattern was in

2010/11 and 2015/16 when the water level was higher, i.e. much closer to the ground surface in the dry season than in the wet season (Figure 1.5). This was caused by unusual high winter rain followed by the very dry wet season as well as the increased water deliveries into the Park.

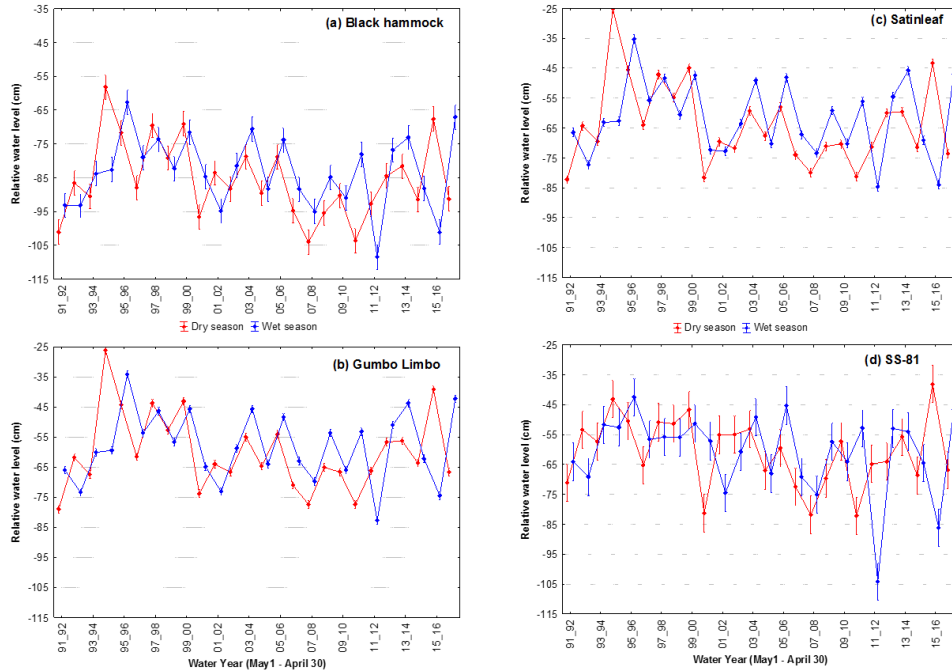


Figure 1.5: Seasonal mean (\pm SE) relative water level (RWL) in the hardwood hammock plots on four tree islands, (a) Black Hammock, (b) Gumbo Limbo, (c) Satinleaf, and (d) SS-81.

In South Florida, including the Everglades, winter rainfall is strongly linked to El Niño events. In the 2016 dry season, a strong 2015-2016 El Niño dumped more than 30 cm of rainfall resulting in high water conditions throughout South Florida. In fact, both December 2015 and January 2016 were the wettest months in several decades (Abtew and Ciuca 2017). Much higher than normal dry season rainfall in Everglades basin, especially Water Conservation Areas, resulted in extreme water level in WCA-3A, prompting emergency operations for moving water to the south, i.e. into Everglades National Park (ENP). During the 90-day emergency operation period (February 12-May 11, 2016), the Park received one-half million acre-ft of water, 60% of which flow through SRS and 40% through NESRS (Abtew and Ciuca 2017). This emergency operation period has also overlapped with the Modified Water Deliveries (MWD) Increment 1 Field Test period. Increased water delivery to the Park resulting from both MWD Increment 1 Field test and unusual emergency operation during the dry season contributed to the spatial and temporal differences in water conditions within the Everglades tree island hammocks. In fact,

mean annual relative water level in these islands in SRS and NESRS is hardly in tandem with the total annual rainfall in that region. For this analysis, the stage recorder, P33 for which a long-term rain data are available on DBHYDRO (<https://www.sfwmd.gov/science-data/dbhydro>) data resource was used. A correlation between annual total rainfall at P33 between 2007 and 2017 and mean RWL on each of these for islands was insignificant (Figure 1.6), because the hydrologic conditions in these islands partly depend on the water delivery from the adjacent WCA 3A and 3B. Thus, rain driven water delivery operational plans as envisioned in the Combined Operation Plan (COP) might help to provide natural hydrological conditions in these islands.

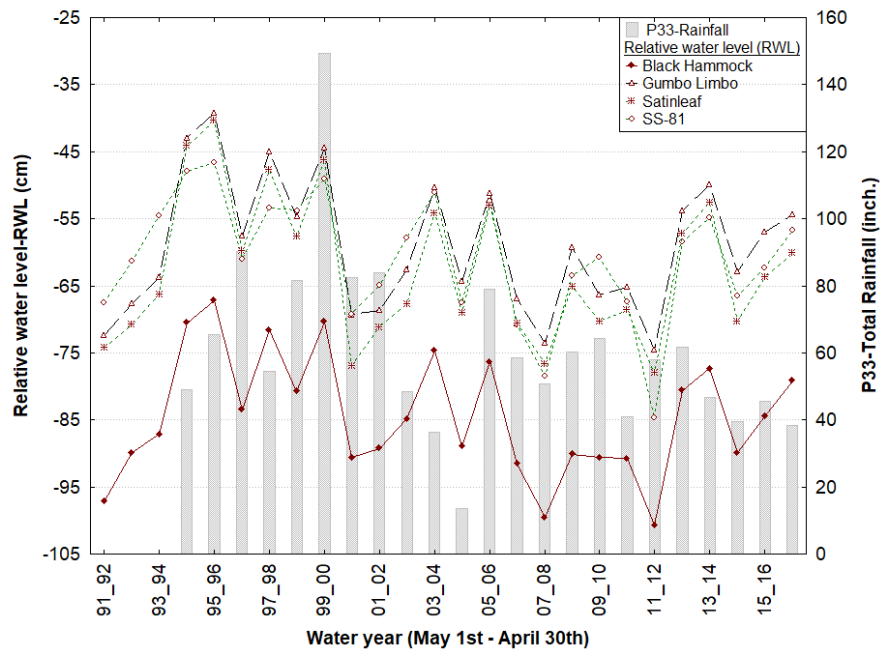


Figure 1.6: Relationship between annual total rainfall at P33 stage recorder and mean annual relative water level (RWL) four SRS tree islands (a) Black Hammock, (b) Gumbo Limbo, (c) Satinleaf, and (d) SS-81.

1.3.1.2 Tree mortality and in-growth

Tree density and basal area are the functions of tree mortality and in-growth, two important indicators of woody vegetation dynamics on tree islands. During 2007-2010 (WY 2007/08 to 2010/11), when the hardwood hammock in all 16 islands were studied, mean annual tree mortality on those islands was 3.6%, and both NESRS and R&S islands had higher mortality than MP islands (Figure 1.7). During those years, mean tree in-growth was significantly higher (paired *t*-test, $P < 0.001$) than mean tree mortality. On average, the mean tree in-growth was 104 trees ha⁻¹ year⁻¹ whereas tree mortality was 44 trees ha⁻¹ year⁻¹. In-growth on some islands was

higher also because of recovery from Hurricane Wilma in 2005. In subsequent years, i.e. between 2011 (WY 2011/12) and 2016 (WY 2016/17), when hammocks on only four islands (Black hammock, Gumbo Limbo, Satinleaf, and SS-81) were annually monitored, the both mean tree in-growth and mortality showed little variation, except in SRS islands in 2014. Mean mortality was slightly higher than in-growth. On these four islands, the mean mortality rate was almost the same as was before 2011 (3.41%) and between 2011 and 2016 (3.22%), whereas the mean in-growth rate dropped from 7.0% year⁻¹ to 2.72% year⁻¹ between these two periods. In concurrence with the trend in tree mortality and in-growths, total tree basal area on the islands slightly decreased in 5 years, between 2011 and 2016 (Figure 1.8), though the change in BA was not statistically significant. The lowest mean value of BA in WY 2015/6 was because only three tree islands were sampled in that year.

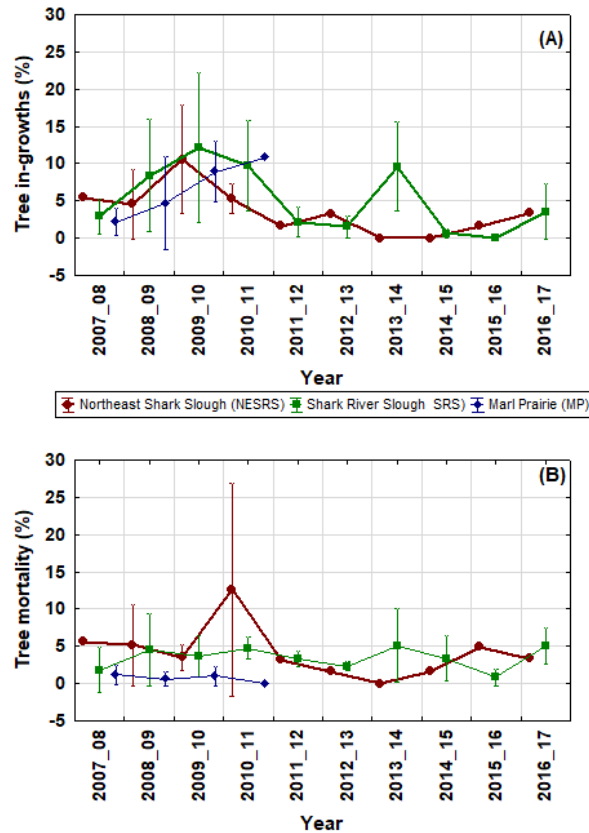


Figure 1.7: Annual mean (\pm) tree in-growth (A) and mortality (B) on the tree islands monitored in Shark River Slough (SRS) and Northeast Shark River Slough (NESRS) within the Everglades National Park between 2007 and 2017. The number of tree islands studied varied among years. Since 2011, hardwood hammocks on four islands (Black Hammock, Gumbo Limbo, Satinleaf and SS-81) were studied.

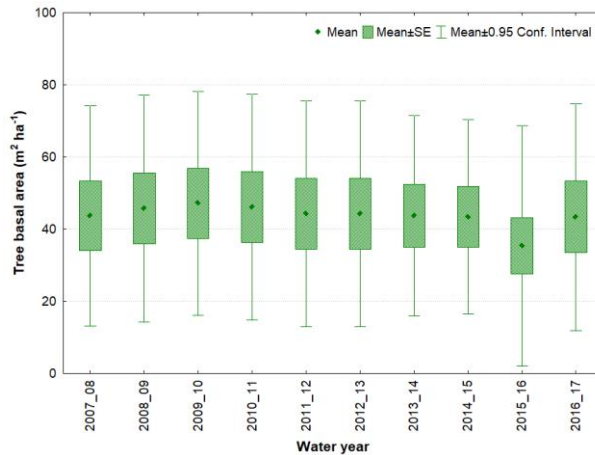


Figure 1.8: Box-plot showing the trend in tree basal on four tree islands monitored within the Everglades National Park between 2007 (WY 2007/08) and 2016 (WY 2016/17). In WY 2015/16, only three tree islands were sampled.

As reflected by variation in annual mean tree mortality and in-growth, the short-term trend of tree dynamics observed in the hardwood hammocks is in accord with variation in hydrologic condition, though, the relationship between mean annual RWL and tree mortality on these islands was weak ($r = 0.05$; Figure 1.9). Hardwood hammocks have primarily flood-intolerant species. Water level above or near the ground surface for longer periods, especially in the dry season, adversely impacts the survival and growth of those tree species (Stoffella et al. 2011). During the 2016 (WY 2015/16) dry season, water level in the SRS tree islands was very close (<40 cm) to the ground surface for a longer period (Figure 1.5), which may have affected tree growth and mortality in subsequent years.

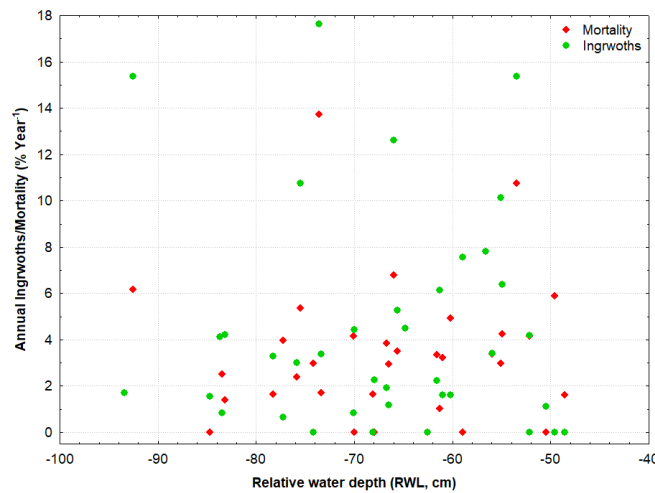


Figure 1.9: Scatter-plot showing the relationship between relative water level and tree in-growth and mortality on four tree islands monitored within the Everglades National Park between 2007 and 2017.

1.3.1.3 Tree layer vegetation dynamics

In the hammocks on four islands (Black hammock, Gumbo Limbo, Satinleaf, and SS-81), tree species composition, as represented by species' important value index (IVI), has somewhat changed over time. The changes were obvious on three tree islands that have been monitored since 2002. A nonparametric multi-dimensional scaling (NMDS) ordination, based on species' IVI and B-C similarity, revealed that in these three tree islands, the species composition in 2002/2003 was slightly different from the composition in recent years (Figure 1.10). For instance, over the sampling period, in Black Hammock, the IVI of Sugarberry (*Celtis laevigata*) decreased, whereas the IVI of White stopper (*Eugenia axillaris*) significantly increased. Likewise, the IVI values of Wild mastic (*Sideroxylon foetidissimum*) and Satinleaf (*Chrysophyllum oliviforme*) in Gumbo Limbo and Satinleaf hammock, respectively, doubled in 15 years (Figure 1.11). In these islands, however, there has not been much shift in species composition in recent years (Water Years: 2010-2017). A minimal shift in species composition in the tree layer was also observed in the hammock of SS-81, which has been annually monitored since WY 2008.

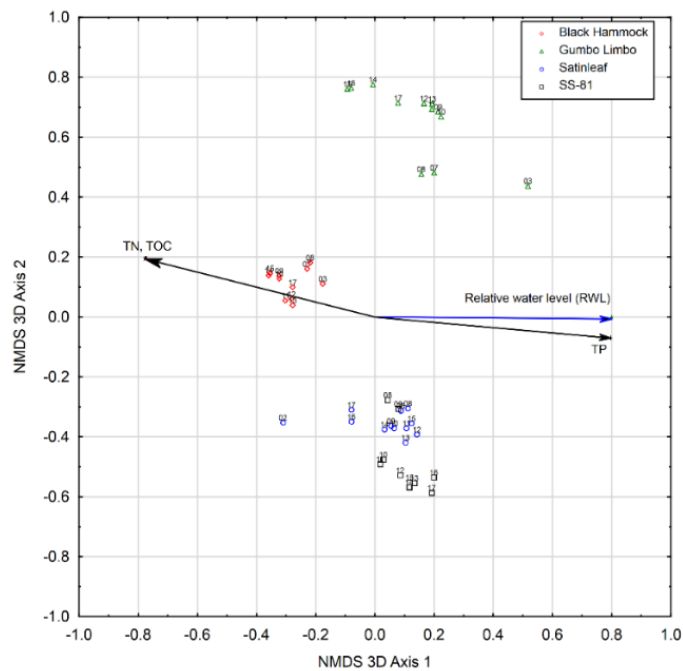


Figure 1.10: Scatter-plot of 3-D NMDS ordination based on tree species IVI in four tree island hammocks sampled between Water Year (WY) 2002 and 2017. Fitted vectors are relative water level (RWL), soil phosphorus (TP) and total organic carbon (TOC).

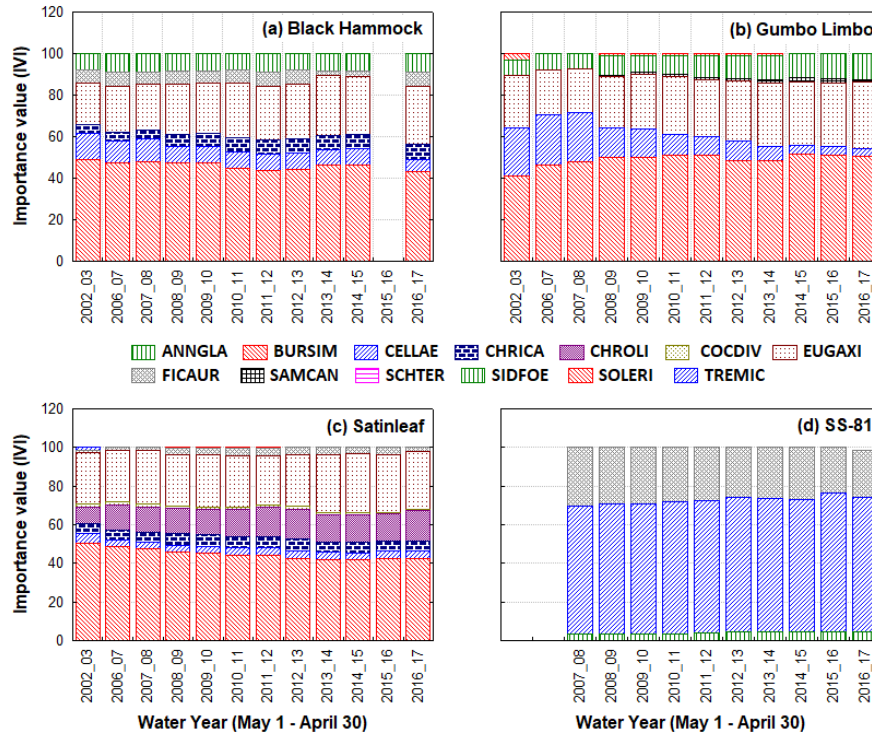


Figure 1.11: Importance value index (IVI) of tree species in hardwood hammocks of four tree islands. ANNGLA = *Annona glabra*; BURSIM = *Bursera simaruba*; CELLAE = *Celtis laevigata*; CHRICA = *Chrysobalanus icaco*; CHROLI = *Chrysophyllum oliviforme*; COCDIV = *Coccoloba diversifolia*; EUGAXI = *Eugenia axillaris*; FICAUR = *Ficus aurea*; SAMCAN = *Sambucus canadensis*; SCHTER = *Schinus terebinthifolius*; SIDFOE = *Sideroxylon foetidissimum*; SOLERI = *Solanum erianthum*; TREMIC = *Trema micranthum*.

In general, hydrology is the major driver of differences in species composition among various plant communities arranged along topographic gradient within a tree island (Armentano et al., 2002; Wetzel 2002; Ross and Jones, 2004; Espinar et al., 2011; Sah et al. 2018). However, in the hardwood hammocks which rarely get flooded, and mean annual water table is often below 40 cm (Figure 1.5), tree species composition is probably more the legacy of long-term interaction between hydrology and other physical processes, including recurrent disturbances. In some of these islands, high tree mortality was observed until 3-4 years after hurricane Wilma in 2005. In those hammocks, higher mortality in the 3rd and 4th than in the 1st and 2nd post-hurricane years was attributed to the interaction of multiple disturbances, e.g., hurricane and drought (Ruiz et al. 2011). In September 2017, Hurricane Irma, a category 4 storm hurricane hit the southwest coast of Florida. However, its impact was felt in most of south Florida. A preliminary analysis of 2017 (WY 2017/18) tree data has revealed severe damage to the tree layer vegetation in eight tree

islands for which we had pre-Irma data (Figure 1.12). A detailed account of the effects of Hurricane Irma on vegetation on those islands will be described in the next (Year-4) report.

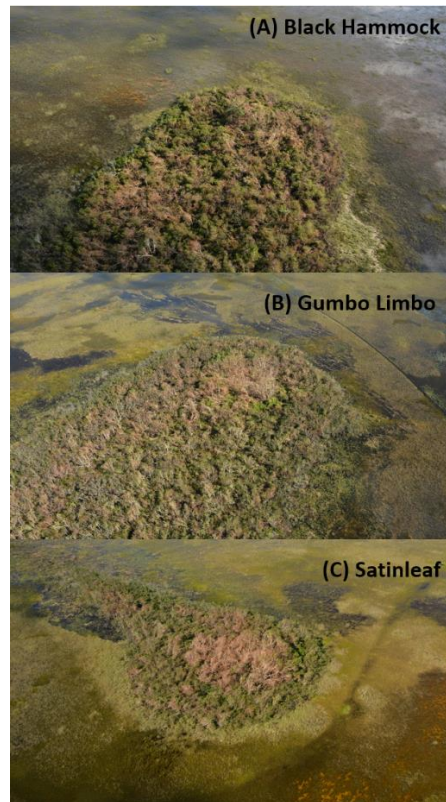


Figure 1.12: Photo of three tree islands (Black Hammock, Gumbo Limbo and Satinleaf) showing the damage from Hurricane Irma. (Photo credit – Jed Redwine, NPS)

1.3.2 Vegetation along the hydrologic gradient

A cluster analysis of vegetation data, collected at 164 sites on transects in five tree islands, revealed a suite of plant community types. The classification based on relative cover of species identified major plant community types, described for SRS tree islands (Armentano et al. 2002; Sah et al. 2018). While the distinctive composition of Bayhead Forest, *Cladium* marsh, and sparse graminoid marsh was evident (Figure 1.13), Hardwood hammock was not so distinct. Based on vegetation structure and compositional percentage of different lifeforms, the characterization of sampled sites also revealed very few Hardwood hammocks, primarily because sampling on these transects focused on the Bayhead forest and Bayhead swamp parts of the islands. In contrast, Bayhead swamp, a transitional vegetation between Sawgrass marsh and Bayhead forest (Ruiz et al. 2011), was widely present on these islands. The Bayhead swamp is a heterogenous community type, consisting of herbaceous vegetation mixed with various

proportions of flood-tolerant woody plants (*Annona*, *Salix*, *Morella*, *Ilex*, etc.), usually <4m high. The other heterogenous community is the broad-leaved or graminoid herbaceous marsh mixed with short shrubs.

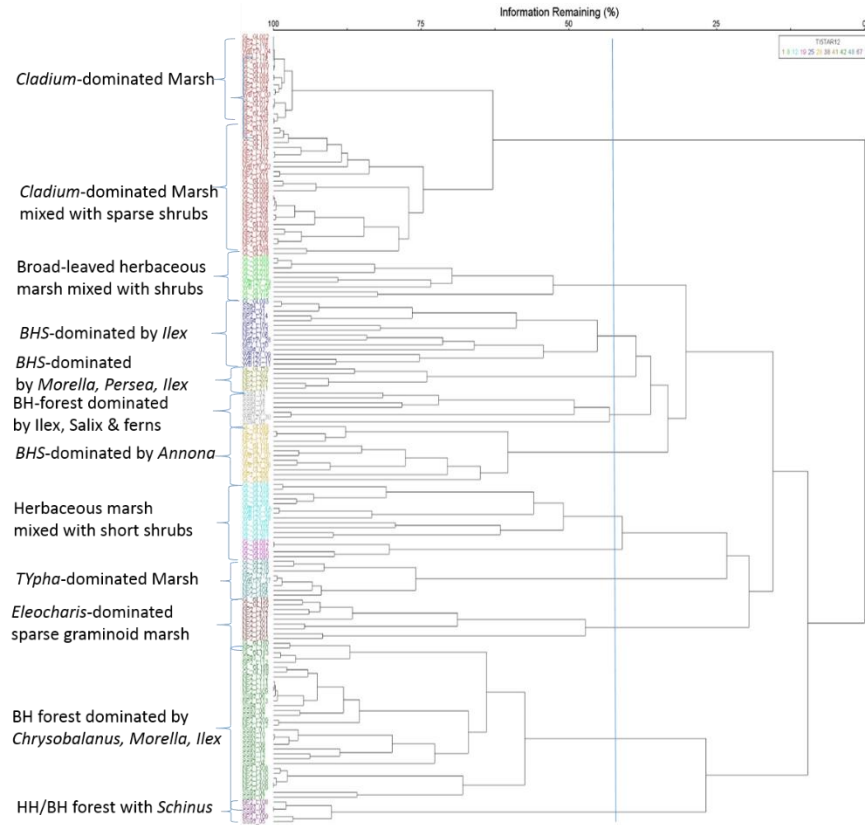


Figure 1.13: Vegetation types identified through cluster analysis of species cover values at 164 sites (nested plots) sampled on transect in five tree islands. Information remaining (%) is based on Wishart’s objective function, following McCune and Grace (2002).

A non-metric multidimensional scaling (NMDS) ordination shows that the sites are more or less arranged along the hydrology gradient (Figure 1.14). However, most of sites had the vegetation types that were the characteristic of relatively wet conditions, because sampling on these transects was targeted to supplement fine-scale vegetation mapping. In Gumbo Limbo and NP 202, the sites for ground sampling were selected in the areas of tree islands where the interpretation of spectral signature was relatively difficult. In two islands, SS-93 and SS-94, sampling was done on transects parallel to the main axis of islands, but these islands are small and have very limited area of hardwood hammock. Since the classification was also used to

characterize the sites in vegetation mapping (see Section 2), there is a fair agreement between the vegetation classification and the mapped vegetation classes. A slight difference is probably due to the discrepancies in vegetation classes among individual islands.

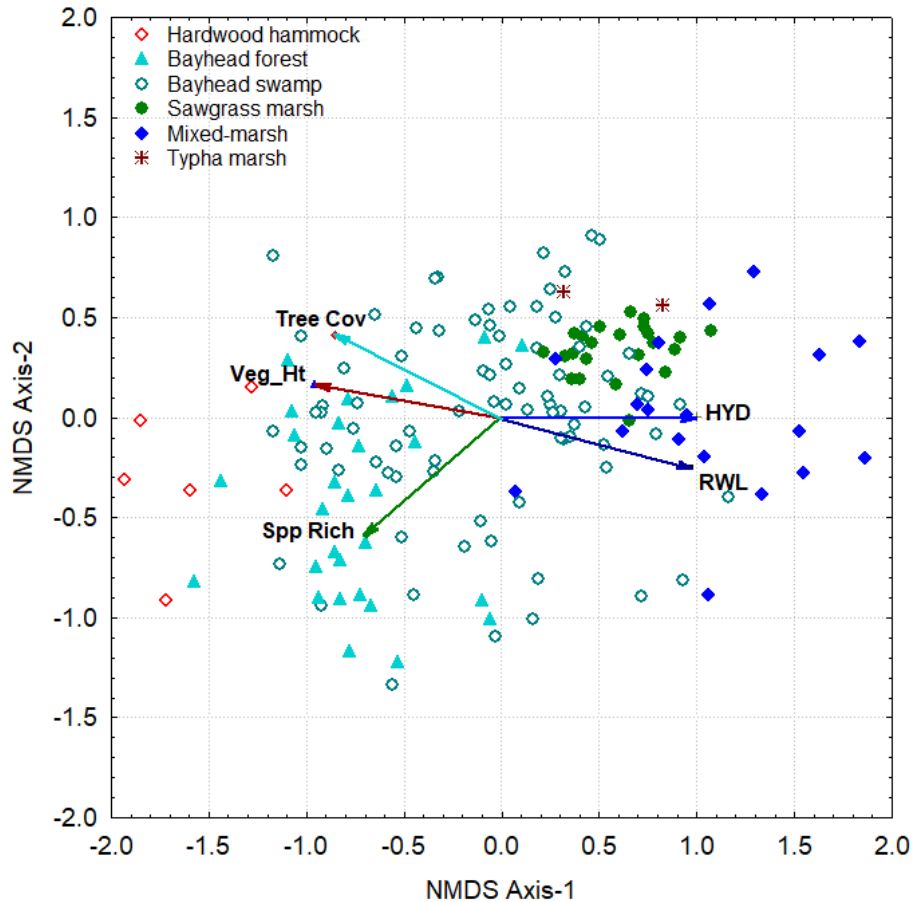


Figure 1.14: Scatter-plot of 3d NMDS ordination, based on both tree and understory species cover recorded in 166 plots on transects in five tree islands (see Table 1.2). Community types identified in cluster analysis are grouped in broader classes to match with the vegetation structure and lifeform-based classification. Fitted vectors are hydroperiod (Hyd), relative water level (RWL), percent tree cover (Tree_Cov), mean vegetation height (Veg_Ht), and species richness (Spp_rich).

Surprisingly, the presence of cattail (*Typha domingensis*) and Brazilian pepper (*Schinus terebinthifolius*) on these islands was also evident. On some of the SRS islands, such as Gumbo Limbo, that were first studied in 2001/2002, cattail cover had increased in 10 years (Sah et al. 2015). Similarly, out of 474 sites sampled on transects in 12 islands (9 in ENP, 2 in WCA3A, and 1 in WCA3B) between 2012 and 2017, Brazilian pepper was present at 28 sites on seven islands, while *Lygodium* and *Melaleuca* were present on five islands, at one site in each island. The total frequency of all these three exotic plants was higher on the islands (42.9%, 37.9%,

21.4% and 15.0% in SS-93, SS-81, SS-94 and Chekika, respectively) close to the Tamiami Trail than the interior islands (<5%) (Figure 1.15), suggesting some role of disturbances in spreading the invasive exotic species on these islands.

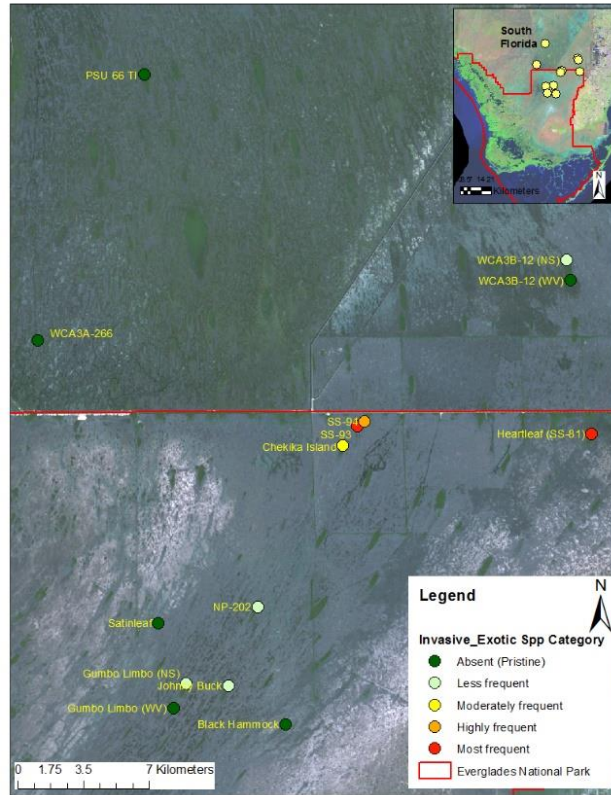


Figure 1.14: Frequency of invasive exotic species on tree islands sampled between 2012 and 2017.

1.4 Summary

In the hardwood hammocks on SRS tree islands between 2007 and 2016 (WY2008 and 2017), the annual mean RWL remained well below the soil surface. Thus, slight increases in marsh hydroperiod or water depth in Everglades National Park are unlikely to have any significant impact on tropical hardwood hammock communities. However, an incremental upward shift in the RWL could cause a shift in species composition and productivity of these islands. In contrast, over the period of this study, such a shift in vegetation in response to hydrologic change commonly occurred in the wetter communities (Bayhead and Bayhead swamp) (Sah et al. 2018). In the four islands currently monitored, Bayhead and Bayhead swamp

plots are scheduled to be sampled in 2018, and that will help to assess a more comprehensive response of tree island vegetation to hydrologic changes in these years. Moreover, most of south Florida, including these tree islands felt the impact of Hurricane Irma, a category 4 storm hurricane hit the southwest coast of Florida. A preliminary analysis of 2017 (WY 2017/18) tree data has revealed severe damage to the tree layer vegetation in eight tree islands for which we had pre-Irma data. The detailed account of the effects of Hurricane Irma on vegetation on those islands will be described in the next (Year-4) report.

Plant communities on sampled transects were arranged along hydrologic gradients, though the community types identified were more of wetter types primarily because sampling on these transects was targeted in those areas to supplement fine-scale vegetation mapping. Vegetation data collected in this study at 166 sites on transects in five islands are merged with the larger dataset compiled over several years, between 2001 and 2017. Altogether, the dataset has now vegetation structure and composition data, collected using a similar methodology, for 1025 sites (nested circular plots) on transects along hydrologic gradient in 12 tree islands (9 in ENP, 2 in WCA3A, and 1 in WCA3B). Of the 1025 sites, 321 sites were sampled twice, first time during 2000-2002 study, and then in 2011-2012. Characterization of vegetation from both studies and the results of vegetation change over a decade on these sites have already been described (Sah 2004; Sah et al. 2018). Vegetation data collected at 309 sites during 2009-2012 study are summarized in Sah et al. 2015. The data collected at these 309 sites were also used to develop a relationship between plant community types and hydrologic characteristics at those sites. After determining the hydrologic characteristics of plant communities, the Everglades Vegetation Succession Model (ELVeS), a simulation tool developed by South Florida Natural Resources Center, ENP (Pearlstine et al. 2011) was used to model the response of those tree island communities to hydrologic conditions under four restoration scenarios. (Wetzel et al. 2017). In the next step in our modeling effort, we plan to use all 1025 sites and additional sites from any other study that has used similar methodology in vegetation data collection for determining the hydrologic characteristics of plant communities followed by vegetation dynamics modeling using ELVeS tool.

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2. Plant Community Detection on Chekika, SS-93 and SS-94 from Bi-Seasonal WorldView2 and LiDAR Data – Signature Extension Evaluation

- Daniel Gann, Allison Jirout, Paulo Olivas and Ximena Mesa

2.1 Introduction

The Everglades is a mosaic of complex ecosystems where the landscape dynamics are primarily driven by hydrology. In a landscape dominated by ridge and slough, tree islands are important components of the landscape that affect the occurrence and distribution of species that are less tolerant to waterlogged conditions. In turn, these landscape features are sensitive to hydrological alteration and, therefore, to activities associated with the Comprehensive Everglades Restoration Plan (CERP) authorized by the Water Resources Development Act (WRDA) 2000 to restore the south Florida ecosystem. The information described in this document contributes with the improvement of our understanding of the response of the tree islands and surrounding marsh ecosystems to hydrological changes.

The previous methodology evaluated the use of spectral signature extension, which consists in using locally extracted spectral signatures of representative regional plant communities to map larger landscapes. The idea of this methodology is that if similar environmental conditions (including hydrology) lead to quasi identical or very similar plant communities across the larger landscape, it can be expected that similar spectral reflectance patterns of electromagnetic radiation can be associated with each community. As a result, locally extracted spectral signatures of those communities can be used to successfully map greater extents.

This report focuses in the description of the improvement of the spectral signature extension methodology for detecting Everglades tree island community types (hardwood hammock, bayhead forest, and bayhead swamp) and differentiating them from the surrounding marsh communities. The previous methodology used WorldView2 (WV2) multi-spectral satellite data to detect changes in the communities, which resulted in some community class confusion when the spectral signatures were similar. Therefore, to reduce community class confusion a LiDAR data layer was added to the classification. The inclusion of LiDAR data in the form of vegetation height, can improve the differentiation between not only marsh and tree island

communities but also of the structure within the tree islands making possible to distinguish between trees and shrubs.

2.2 Methods

2.2.1 Study Area

This study considered three tree islands located within 1 km of each other within Everglades National Park: Chekika, tree island head located at N 25.745° W 80.657° (WGS 84), SS93 located at N 25.757° W 80.646°, and SS94 located at N 25.754° W 80.649° (Figure 2.1). The main criteria for island selection were that all islands should be located within the footprint of a satellite image acquired on the same day, and that LiDAR data came from the same data set (same year). Using images acquired on the same day assures that spectral differences across islands are a result of differences in plant communities and spectral variability of communities and not seasonal effects such as phenological cycles of the vegetation types or variability in atmospheric conditions. Ideally, the LiDAR data should also be collected at the same time to ensure that the vegetation height extracted from the data reflects the vegetation type present. However, given the high cost of the acquiring LIDAR data and the relative large differences in vegetation height between marsh communities and tree island communities and between trees and shrubs, LiDAR data acquired sometime before or after the satellite images should still be representative of the different plant communities.

2.2.2 Classification Scheme

After initial field visits, a classification system with 11 classes was developed to represent tree island and marsh community types located within a 200 m buffer around the approximate boundaries of each island. Tree island vegetation classes included hardwood hammock (tH) with trees or woody species with heights greater than 5m that are not typically found in standing water, bayhead forest (tB) with trees or woody species, Brazilian pepper trees (tB_Shin), *Schinus terebinthifolius*, bayhead swamp (sB) representing shrubs, or woody species having heights less than 5m (Table 2.1). Marsh classes were divided into those dominated by dense *Cladium jamaicense*, sawgrass (gM_Clad), those dominated by sparse *Cladium jamaicense*, sawgrass (gM_Clad_sp), those dominated by graminoids typically found in deeper sloughs (gM_sp), a mixed graminoid class of denser graminoids (gM), and those dominated by

Typha domingensis, cattails, (gM_Typha). Two additional categories for classes found typically within tree island tails and edges were a class of herbaceous marsh (hM) and herbaceous marsh mixed with shrubs, typically *Cephalanthus occidentalis* (s_hM) (Table 2.1).

2.2.3 Image Data Processing

For its high spatial and spectral resolution properties, we chose the WorldView 2 (WV2) sensor to detect vegetation communities. Since previous studies within the larger Everglades showed that bi-seasonal data increased mapping accuracies significantly (Gann, Richards, & Biswas, 2012; Gann, Richards, Lee, & Gaiser, 2015; Gann & Richards, 2009), two images with minimal cloud cover containing both islands were obtained for the dry season (04/06/2013) and wet season (10/20/12). Images were first geometrically corrected in ERDAS Imagine (Intergraph, 2013), then radiometrically calibrated and atmospherically corrected in ENVI (Exelis Visual Information Solutions, 2013). Atmospheric correction for each image was completed using the FLAASH module in ENVI (ENVI, 2009). Selection of an atmospheric model in FLAASH was based on local air temperature at the time of image acquisition while the aerosol model chosen was based on wind direction and time of year. Local texture layers were generated for each pixel during the stacking procedures in R (R Development Core Team & R Core Team, 2013) using the focal function in the raster package (Hijmans & van Etten, 2010). We calculated local mean and range including the surrounding 8 pixels for each pixel of each of the 8 WV2 bands. Finally, NDVI was calculated for both the wet and dry season images for each pixel and stacked with all other data layers, which resulted in a bi-seasonal data cube of 51 layers or variables.

We used LiDAR data collected in May, 2015 using the G-LiHT sensor (Goddard's LiDAR, Hyperspectral & Thermal Imager) operated by NASA (National Aeronautics and Space Administration). LIDAR data were acquired at a 1m resolution and subsequently aggregated at a 2m to match the resolution of WV2 images. Digital surface (DSM) and terrain (DTM) models were created using first and last returns from the point cloud, respectively. A canopy height model (CHM) was derived by subtracting the DTM from the DSM. The CHM is a representation of the height of the vegetation.

2.2.4 Island and Training Point Digitization

The approximate boundaries of each tree island were digitized from 2009 color infrared aerial imagery (CIR) imagery at a resolution of 1:1,000. A buffer of 200 m was added to each island to include a hydrological gradient from tree island to surrounding marsh communities. Outlines of clouds, cloud shadows, and man-made structures overlapping the tree island and buffer areas were digitized in a separate mask layer. The three islands included a small boardwalk and a building, included in the digitized mask layer. The areas covered with the masks were classified as missing data.

Training points for each vegetation class were added iteratively using a combination of field surveys, both aerial surveys by helicopter and ground surveys, and high resolution aerial photography in stereo view. For aerial surveys, coordinates of points of interest were determined using satellite images and aerial photographs, subsequently these points were found in the field using a Trimble GPS unit with 1 m accuracy. On the ground, a Trimble GPS with real-time correction allowed for sub-meter accuracy. The 2009 CIR imagery was also used to identify and digitize training samples for all vegetation classes for training purposes. Training points were not located in areas of digitized clouds, cloud shadows, or man-made structure shadows. A total of 1,753 training points were digitized on Chekika, and 5,372 on SS93 and SS94 combined.

2.2.5 Spectral Signature Evaluation

For all training samples, signatures were extracted from the 51-layer data cube. A random forest classifier was established for all community types with consideration of all training samples across all three tree islands. All data analysis was performed with Revolution R 7.4. For classification we used the unifying modeling framework of the ‘caret’ package (Kuhn et al., 2015), using its ‘rf’ function for random forest. We determined from test runs that 1000 decision trees was a safe threshold beyond which no significant increase in model-based classification accuracy was observed ($\alpha = 0.05$) (Kuhn et al., 2015). The parameter for the optimal number of random variables selected at each split (“mtry”) was established for each random forest model through build-in tuning routines considering all possible options from 2 to 51, the maximum number of all variables in the variable set.

2.2.6 Model selection

Although, we expected that based on previous research models using bi-seasonal data would produce models with higher accuracies (Gann, Richards, & Biswas, 2012; Gann, Richards, Lee, & Gaiser, 2015; Gann & Richards, 2009), we evaluated four models constructed using: 1) wet season image only, 2) dry season image only, 3) bi-seasonal (wet-dry), and 4) bi-seasonal plus LiDAR.

2.2.7 LiDAR evaluation

Previous work (Guo et al., 2017; Rapinel et al., 2015) suggested that the use of LiDAR data should increase the accuracy of the classification of trees and shrubs. Therefore, we further evaluated the effect of the LiDAR data in the accuracy on these classes using a design-based accuracy assessment. We evaluated the change in the commission and omission errors in the tree and shrub classes.

2.2.8 User-Based Accuracy Assessment

Stratified random samples were selected for each island to perform a model with the highest design-based accuracy. The number of samples selected for accuracy assessment was determined assuming multinomial distribution of errors with an expected map confidence of 95% and a 95% precision of the estimate (Congalton & Green, 1999). An equal number of samples were selected for each of the eleven classes for a total of 770 samples. Pixel centroids selected for accuracy assessment were greater than 1 m away from training pixels (no overlap). Each of the samples was evaluated from aerial photography in stereo view at a fixed zoom of 1:500 and a class label was assigned. Confusion matrices were constructed from predicted and reference class labels for all islands, and overall and class-specific user's and producer's accuracies were calculated adjusted for inclusion probabilities associated with the stratified random sample design (Equations based on Olofsson et al., 2014; Olofsson, Foody, Stehman, & Woodcock, 2013; Stehman, 2013). Finally, bias adjusted areas were calculated for each class (Olofsson et al., 2013). All sampling, accuracy assessment and bias adjusted area calculation was coded in R (R Development Core Team & R Core Team, 2013).

2.2.9 Final vegetation map

Classifiers were applied to all pixels of all the islands. Pixel clumps were generated from the classified maps using the clumping and sieving functions in the R package ‘raster’ (Hijmans & van Etten, 2010). The clumps were generated taking into account 8 adjacent cells. The minimum mapping unit was established as 20 m², resulting clumps of a minimum of 5 adjacent pixels. Clumps smaller than 5 pixels were reclassified using the most common class within a 3x3 kernel.

2.3 Results and Discussion

2.3.1 Model selection

Similar to the findings of previous research, single season models (wet image: 85% and dry image: 85%) presented lower accuracy than models that used bi-seasonal data (bi-seasonal: 91% and bi-seasonal plus LiDAR: 92%) (Table 2.2).

2.3.2 LiDAR evaluation

We found that the use of LiDAR data improves the classification of shrubs and trees, with a decrease of 3% in the omission error for shrub classes and 6% for tree Classes. We found a commission error of 5% in the shrub class and 4% in the tree class (Table 2.3).

Given that trees and shrubs are likely to have very similar spectral signatures, the inclusion of LiDAR data for the classification improves the ability to differentiate between these two classes. This result has important implications for change detection, such as the expansion or contraction of hardwood hammocks, bayhead forest, and shrubland.

2.3.3 Mapping Accuracy

Maps of vegetation communities on Chekika, SS93, and SS94 show the configuration of vegetation communities on each island as classified using training points located on all three islands. Mapping resulted in an overall map accuracy of $93.3 \pm 2.2\%$ (estimated standard error)

The highest accuracy was achieved for graminoid marsh dominated by *Typha domingensis* (gM_Typha) reaching 100%. (Table 2.2). Except for the sparse sawgrass class (gM_Clad_sp), all other classes reached accuracies of 92.6% or greater.

2.3.4 Areal Coverage and Relative Abundance

For the islands and their surrounding marshes, sawgrass (gM_Clad) was the most abundant class, covering approximately 40% of the entire study area surface (Table 2.4). Considering only the tree and shrub classes, the most abundant class was the herbaceous marsh and shrub mixed class (s_hM) representing 48.8% of the study area, followed by bayhead shrub (sB) with 29.3 % cover. Bayhead forest (tB) and hardwood hammock (tH) were represented with 19.7 % and less than 1% cover, respectively. The invasive Brazillian pepper tree class (tB_Shin) represents 1.2% of the tree and shrub classes. It is likely that Brazillian pepper is present within the bayhead shrub class, but it was not possible to determine what percentage is present.

2.4 Conclusion

While very high overall accuracies for the islands suggests that signature extension for plant communities of tree islands and their adjacent marshes is valid, significant differences exist between communities. Woody tree and shrub classes were rarely confused with graminoid and broadleaved vegetation in the tails and surrounding marshes. These results indicate that the differentiation between tree islands and their tails and marsh communities is very reliable and that, given the spatial resolution of 2 m for WV2 data, expansion or contraction of tree islands can be detected as they occur. Considering the spatial accuracy of 1-2 m expansion or contraction of tree island communities could be detected reliably when community boundaries shift by about 3-4 m on the ground.

Confusion between the various graminoid and sawgrass classes was expected given their similar species composition. The addition of LiDAR data may not be helpful in this circumstance due to the fact that these species heights typically do not vary based on how sparse or dense they grow. Majority of the marsh was represented with a height of less than 1m.

We mapped points on all three islands, integrated the use of LiDAR height data, and completed multiple site visits to reach a high accuracy of our finalized map. This method results in training sample inclusion across a spatially balanced sample of islands of different sizes with integration of height data used to differentiate classes with similar spectral signatures.

Tables and Figures

Table 2.1: Vegetation class codes and corresponding class descriptions.

Class Code	Vegetation Class Description
gM	Graminoid marsh, includes short graminoids
gM_Clad_sp	Sparse <i>Cladium</i> dominated marsh
gM_Clad	<i>Cladium</i> dominated marsh
gM_sp	Sparse graminoid marsh
gM_Typha	<i>Typha</i> dominated marsh
hM	Herbaceous marsh
s_hM	Herbaceous marsh mixed with shrubs with heights less than 4m
sB	Bayhead swamp, dominated by woody species with heights less than 4m
tB	Bayhead forest, dominated by woody species with heights greater than 4m
tB_Shin	Bayhead forest, dominated by <i>Schinus</i> with heights greater than 4m
tH	Hardwood hammock, dominated by species that do not tolerate inundation

Table 2.2: Comparison of all model-based accuracy assessments

Vegetation Class	Dry		Wet		Biseasonal		bi+LiDAR	
	User's	Producer's	User's	Producer's	User's	Producer's	User's	Producer's
gM	86.4	85.6	84.5	86.3	92.3	91.5	92.5	92.0
gM_Clad	80.6	92.8	80.8	91.8	86.3	96.1	86.3	95.8
gM_Clad_sp	90.9	91.3	91.3	92.7	95.2	94.3	95.1	95.0
gM_sp	94.6	91.7	93.8	94.6	97.9	97.4	98.1	97.7
gM_Typha	93.0	78.1	92.0	77.1	96.3	82.1	95.3	81.9
hM	83.4	79.8	85.9	75.4	90.3	84.7	90.7	85.5
s_hM	85.3	79.9	79.6	75.8	87.7	87.0	88.5	86.1
sB	77.6	68.5	79.3	74.4	86.2	77.9	96.1	93.8
tB	73.8	79.0	73.7	77.2	81.8	84.9	91.4	94.7
tB_Shin	80.9	79.1	90.2	88.8	92.3	90.4	92.8	89.8
tH	89.3	91.9	91.0	86.6	90.6	94.3	97.9	95.5
Overall	85		85		91		92	

Table 2.3: Effect of LiDAR data in the accuracy of tree and shrub classes

User's Accuracy					
Class Code	Biseasonal		LiDAR		Difference %
	Accuracy	SE	Accuracy	SE	
Shrub Classes	96.8%		99.8%		3%
Tree Classes	93.8%		99.7%		6%

Producer's Accuracy					
Class Code	Biseasonal		LiDAR		Difference %
	Accuracy	SE	Accuracy	SE	
Shrub Classes	94.9%		99.8%		5%
Tree Classes	96.1%		99.7%		4%

Table 2.4: percent cover of classes of entire study area and for tree and shrub classes only

Class Code	% Cover of all classes	% Cover of tree and shrub classes only
gM	7%	--
gM_Clad_sp	21%	--
gM_Clad	40%	--
gM_sp	9%	--
gM_Typha	1%	--
hM	1%	--
s_hM	10%	49%
sB	6%	29%
tB	4%	20%
tB_Shin	<1%	1%
tH	<1%	<1%

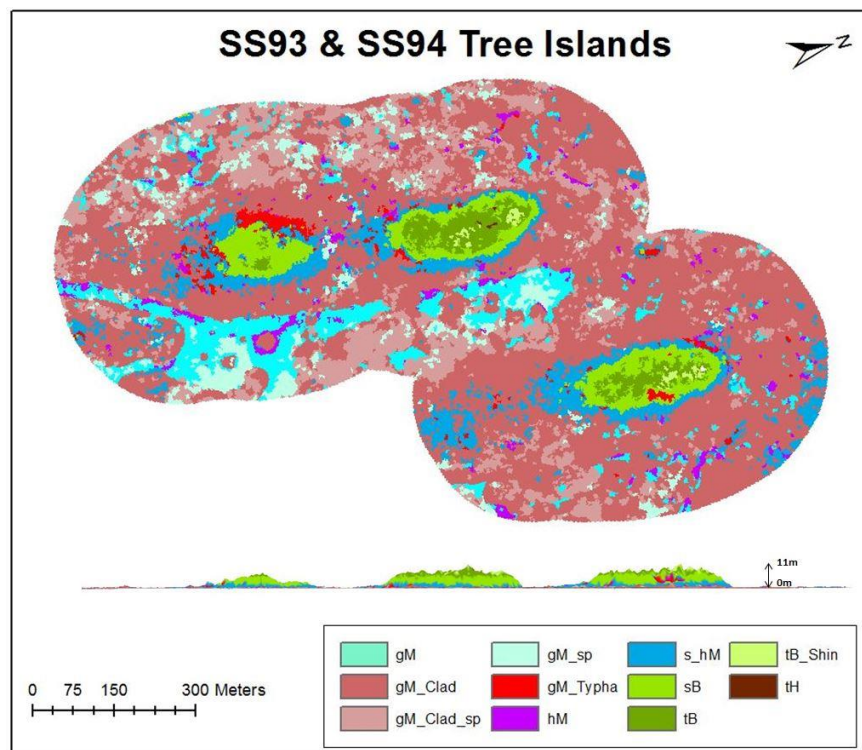
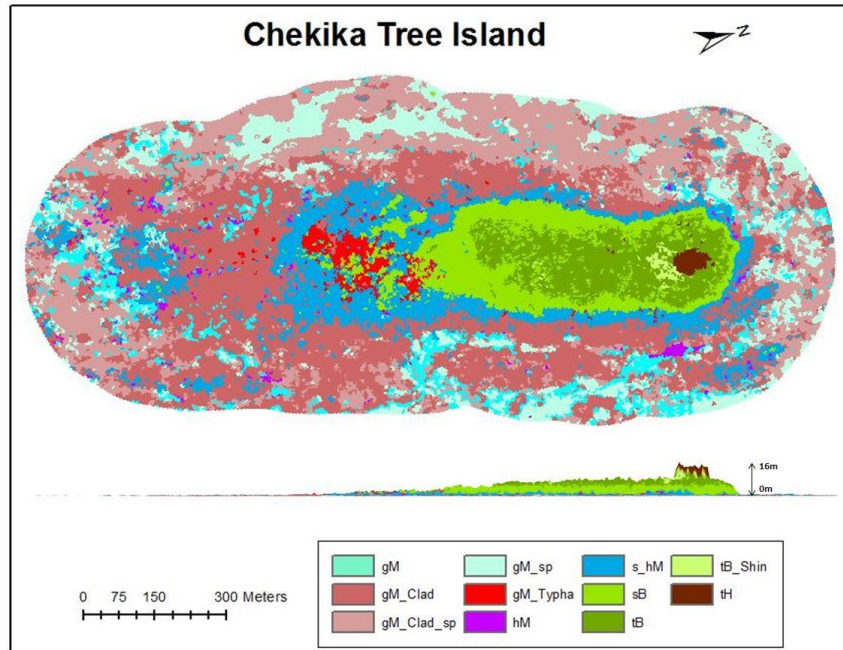


Figure 2.1: Chekika, SS93 and SS94 tree islands map classification. Class Codes: gM = graminoid marsh, gM_Clad = *Cladium* marsh, gM_Clad_sp = sparse *Cladium* dominated marsh, gM_sp = sparse graminoid marsh, gM_Typha = *Typha* dominated marsh, hM = herbaceous marsh, sHm = herbaceous marsh mixed with shrubs (<4m), sB = bayhead shrub (swamp), tB = bayhead tree (forest), tB_Shin = bayhead forest, dominated by *Schinus* with heights (> 4m), tH = hardwood hammock tree.

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1 **Spatio-temporal pattern of plant communities along a hydrologic gradient in Everglades**
2 **tree islands**

3

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16

17 **Abstract**

18

19 Plant communities arranged along a gradient are a product of underlying physico-
20 chemical drivers that vary on both spatial and temporal scales. Spatial variation in the
21 underlying drivers along the gradient usually results in the formation of boundaries between
22 adjacent plant communities. However, the structure and composition of these communities may
23 change over time resulting in boundary shifts. In the Everglades, tree islands are complex
24 ecosystems, where plant communities are arranged along hydrologic and soil nutrient gradients.
25 In these islands, temporal changes in hydrologic regime often result in a spatial shift in
26 community composition along the gradient and determine the trajectory of community
27 succession. We examined the interaction between hydrology and vegetation over a 12-year
28 period in three southern Everglades tree islands. We hypothesized that drier conditions in recent
29 decades would result in an increase in the dominance of flood in-tolerant woody plants over
30 herbaceous and flood-tolerant woody species, ultimately causing a shift in the boundaries
31 between plant communities. The boundary between adjacent communities varied from sharp,

32 clearly defined peaks of Bray-Curtis dissimilarity to more gradual, diffuse transition zones. In
33 the head portion of tree island, there was little change in vegetation composition. However, in the
34 tail portion of the islands, the relative abundance of flood-tolerant species declined, while that of
35 moderately flood-tolerant species increased over the study period. In these islands, the effects of
36 relatively dry conditions in recent decades resulted in small shifts in the boundaries among
37 communities. These results suggest that tree islands are dynamic successional communities
38 whose expansion or contraction over time depends on the strength and duration of changes in
39 hydrologic conditions.

40

41 **Key words:** Everglades, Tree islands, Hydrology, Split Moving Window, Vegetation change.

42

43

44 **Introduction**

45 Plant communities arranged along environmental gradients are at least in part products of
46 ecological processes associated with spatio-temporal variation in physico-chemical drivers.
47 Likewise, when plant communities proceed through a successional process, the conditions of
48 drivers are modified by species-environment interactions that may contribute to changes in the
49 environmental gradients over time. As such, these changes in environmental gradients usually
50 result in the formation of boundaries, representing transition zones between adjacent plant
51 communities (Allen et al. 2005). The properties and persistence of these boundaries depend on
52 whether the variation in the drivers is abrupt or gradual (Wiens et al. 1985; Walker et al. 2003),
53 and on the ability of adjacent plant communities also to withstand the effects of natural and/or
54 management-induced environmental changes (Risser 1995; Forsy and Allen 2002). When plant
55 community composition responds to changes in environmental drivers beyond a certain
56 threshold, the boundary between adjacent communities is also likely to shift (Allen et al. 2005).

57 In the Everglades, tree islands are an integral component of several landscapes (e.g., pine
58 rockland, marl prairie, and ridge and slough). In the ridge and slough (R&S) landscape, tree
59 island nucleation, formation, and development began 4,000 years before present (ybp) in
60 response to regional multi-decadal fluxes in the periodicity and duration of flooding and drought
61 events (Willard et al. 2002). These hydrologic changes permitted the establishment and
62 proliferation of woody vegetation in sawgrass marshes or on ridges during periods of sustained
63 drought (Willard et al. 2002; Willard et al. 2006; Bernhardt 2011). Over time, soil accretion
64 resulting from higher productivity within the incipient tree islands led to higher surface
65 elevations and shortened flooding periods, which in turn promoted the establishment of shrubs
66 and trees. As recently as 1700 ybp, many Everglades tree islands were not fully formed and
67 exhibited many of the characteristics of a transitional community consisting of sawgrass
68 (*Cladium jamaicense* Crantz) and weedy annuals with a minor woody component (Willard et al.
69 2002). However, by around 600 ybp, following several extensive and prolonged local and
70 regional drought episodes, the modern vegetation structure on most large tree islands in the
71 southern Everglades had begun (Willard et al. 2002; Bernhardt 2011).

72 In tree islands within the ridge and slough (R&S) landscape, plant communities vary in
73 species composition and life-form structure along a topographic gradient. However, the degree of
74 variation in species composition is likely correlated with habitat (resource) heterogeneity along

75 the gradient (Davidowitz and Rosenzweig 1998; Kumar et al. 2006). In these islands, the
76 vegetation on the most elevated portion, called ‘Hardwood hammock’, are typically dominated
77 by flood-intolerant trees, whereas the surrounding marsh (Mixed-marsh) has mostly flood-
78 tolerant graminoids or broad-leaved submerged, floating, and/or emergent species. Between
79 these two extremes, the proportion of woody plants and herbaceous species depends on the
80 interactions between the underlying drivers and stressors (e.g., hydrology, disturbance, nutrients,
81 etc.). As these conditions change, so does species composition and community type (Figure 1).
82 The most noticeable changes usually occur in the surrounding mixed-marsh and tail portion of
83 the tree islands, where three distinct plant communities, Bayhead forest, Bayhead swamp, and
84 Sawgrass marsh are common. These communities may be thought of as phases in a
85 chronosequence of vegetation succession in R&S landscape. While persistent drying conditions
86 initiate an expansion of sawgrass within the mixed-marsh or sloughs (Bernhardt and Willard
87 2009), the Sawgrass marsh represents the earliest successional tree island community, analogous
88 to the primordial marsh prior to tree island formation. Sawgrass marsh is followed by the
89 Bayhead swamp that represents a transitional phase between the primordial Sawgrass marsh and
90 Bayhead forest, a climax community typifying tree island maturation under wetland conditions
91 (Figure 1). While a Bayhead is less likely to transition to Hammock, an extended period of
92 flooding beyond a critical threshold causes Hammock and other tree island woody communities
93 to lose their characteristic woody species, and eventually may cause tree island to abruptly shift
94 to a stable marsh (D’Odorico et al. 2011).

95 Hydrology is one of the major drivers of species variation within tree islands in the
96 Everglades (Armentano et al. 2002; Ross and Jones 2004; Espinar et al. 2011). Hence,
97 substantial changes in hydrologic conditions, whether natural or management-induced, are likely
98 to cause quantitative and qualitative changes in structure and composition of the tree island
99 communities. For instance, management-related high-water levels due to compartmentalization
100 after 1960 caused the loss of tree islands, both in number and areal coverage in the Water
101 Conservation Areas (Patterson and Finck 1999; Brandt et al. 2000; Hofmockel et al. 2008). In
102 contrast, during periods of tree island initiation during the last four millennia, the R&S landscape
103 experienced shorter hydroperiods than during the pre-drainage era e.g., 1800’s (Willard et al.
104 2006). Since tree island and marsh communities are hydrologically connected (Troxler et al.
105 2005; Ross et al. 2006; Saha et al. 2010; Sullivan et al. 2014), prolonged and extreme dry or wet

106 events may also affect the boundaries between these communities. The climatological records
107 and hydrologic data from the Shark River Slough (SRS) in Everglades National Park (ENP)
108 suggest that water level during the 1990s was well above the 30-year average (Figure 2). In
109 contrast, both the mean annual rainfall and water level were relatively low between 2001 and
110 2012. Since plant community composition on tree islands in 2001 was already impacted by high
111 water conditions in 1990s, the dry conditions in 2000s provided an opportunity to assess
112 response of plant communities to the shift in hydrologic regime on the islands.

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

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

136 composition, and thus shift in locations of boundaries between these communities within these
137 tree islands. The objectives of this study were:

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

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

151

152 **Materials and Methods**

153 **Study Area**

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

161 The hydrologic regimes of these islands are influenced primarily by annual rainfall,
162 augmented by the water delivered from the Water Conservation Areas by pumps arrayed along
163 the Tamiami Trail (Figure 3). Soil characteristics also vary along the gradient from head to tail.
164 Soils in the Hammocks are alkaline, mineral soils with extremely high P concentrations, while
165 soils in the seasonally-flooded tail communities, Bayhead, Swamp and Sawgrass are mostly
166 organic, with low P concentrations (Ross et al. 2006; Espinar et al. 2011). Disturbances such as

167 hurricanes and fires have also played a large role in the ecology of SRS tree islands (Loope et al.
168 1994; Armentano et al. 1995, 2002; Wetzel et al. 2008; Ruiz et al. 2011).

169

170 **Data Collection**

171 *Vegetation sampling:*

172 Vegetation was sampled along four transects on each of three tree islands, Black
173 Hammock, Gumbo Limbo and Satinleaf. One transect followed the long north-south axis of the
174 island, hereafter termed as ‘NS transect’. The other three transects were established
175 perpendicular to the NS transect in west-east direction (WE transects), one each through
176 Hammock (WE1), Bayhead (WE2) and Swamp (WE3). All four transects were sampled in
177 2001/2002 (hereafter, 2001), but only the three WE transects were re-sampled in 2011 of the
178 2011/2012 (hereafter, 2012) sampling. The length of transects and the number of sites sampled
179 in 2001 and 2012 on each transect are given in Table 1.

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

186 In 2001, permanent plots of 25 x 25 m (625 m²), 20 x 20 m (400 m²) and 15 x 15 m (225
187 m²) were established in the Hammock, Bayhead and Swamp zones, respectively, on each of the
188 three study tree islands, except the Black Hammock. The Hammock community in the Black
189 Hammock was not large enough to allow the establishment of a 25 x 25 m plot. Thus, a 20 x 20
190 m was established in the Hammock of this island (Figure 3). Each plot was gridded into 5 x 5 m
191 cells, whose corners and midpoint were marked by 30 cm long ½” PVC stakes affixed to the
192 ground. The plot and cells were set up using a compass, measuring tape, sighting pole(s), and
193 right-angle prism. During the 2001 census, trees (≥ 5 cm) were identified to species, tagged using
194 numbered aluminum tags, and their diameter (cm) at breast height (DBH) was measured and
195 recorded. The location of each tagged tree was recorded to the nearest 0.1 meter using the SW
196 corner of the plot as a reference (0, 0). Furthermore, if a tree had multiple stems ≥ 5 cm DBH,
197 each stem was tagged with a unique ID that allowed it to be cross-referenced back to its 'parent'.

198 The DBH (cm) of these offshoot stems was measured and recorded as well. The density of all
199 tree saplings (stems ≥ 1 and < 5.0 cm in DBH) within each 5 x 5 m cell was recorded by species,
200 and each individual was assigned to one of two DBH size classes: 1 to 2.9 cm or 3 to 4.9 cm.
201 During the 2012 census, all plots were re-surveyed to assess changes in tree and sapling densities
202 and basal area. New individuals or sprouts from existing trees were tagged and added to the
203 database.

204 ***Hydrology:***

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

222

223 **Data Analysis**

224 Species cover data were summarized using the mid-point of the cover class, and both
225 univariate and multivariate techniques were used to identify the plant communities along the
226 environmental gradient, and change in vegetation structure and composition over time. Transect
227 data were used for vegetation-environment relationships, and identification and shift in position
228 of boundaries between adjacent plant communities. Plot data were used for assessing changes in

229 basal area and importance value (IV) of the trees (≥ 5 cm dbh) and saplings (>1 and <5 cm dbh)
230 between two samplings.

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

245 We used a Monte Carlo method to test whether a boundary identified using the SMW
246 method has a significantly higher value than expected under a null hypothesis that no distinct
247 boundary exists between adjacent communities (Cornelius and Reynolds 1991). In the Monte
248 Carlo method, we randomized the position of each site with its species data vector intact, and
249 repeated the calculations of SMW dissimilarities, as outlined above, for each of the selected
250 window sizes. We repeated the randomization 1000 times, and calculated expected mean
251 dissimilarity and standard deviation between each pair of window-halves for a given window
252 width. We then calculated overall mean dissimilarity and standard deviation for each window
253 width, following Cornelius and Reynolds (1991). The Monte Carlo method was performed using
254 MATLAB v. 7.10 (Mathworks). Since our purpose was to use multiple windows in order to
255 reduce the scale effects, we pooled the dissimilarity values of the mid-points from different
256 window sizes. However, as dissimilarities from different window sizes are scale-dependent, we
257 first standardized the observed dissimilarity values by calculating Z-scores for each window
258 width. The Z-score for each mid-point for a given window-width was calculated by subtracting
259 the observed dissimilarity value from the overall expected mean dissimilarity and dividing by the

260 overall expected standard deviation (Cornelius and Reynolds, 1991). We averaged Z-scores for
261 each site from four window sizes (6, 8, 10 and 12 sites), and plotted them against site positions
262 along each transect. We considered the peaks that consisted of one or more contiguous sites with
263 Z-scores equal or greater than 1.65 (the value in one-tailed test: 95% confidence limit) as
264 significant and distinct boundaries between adjacent communities (Boughton et al. 2006). In a
265 separate analysis, species were grouped according to their life-forms (i.e., trees, shrubs,
266 graminoids, forbs, ferns, vines, seedlings). The mean cover of these groups at each sampling
267 point was then used to calculate B-C dissimilarity.

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

283 ***NMS Ordination:*** Non-metric multidimensional scaling (NMDS) ordination was used to
284 examine the relationships between species composition and environmental variables representing
285 hydrology and soil depth. The 2001 species cover data along NS transects were used for the
286 analysis. The hydrologic variables included in the analysis were 7-year annual mean hydroperiod
287 (days) and relative water level (cm). Relationships were examined using a vector-fitting
288 procedure incorporated in the computer program DECODA (Minchin 1998). Vector fitting is a
289 form of multiple linear regression that finds the direction along which sample coordinates have
290 maximum correlation with the fitted variable within the ordination space. The significance of

291 the environmental vectors was assessed using a Monte-Carlo procedure permutation test with
292 10,000 permutations of the species data, as samples in the given ordination space are not
293 independent (Minchin 1998). Analysis of similarity (ANOSIM) was used to examine the
294 differences in plant communities between the two sampling years, 2001 and 2012.

295 ***Tree and Sapling Dynamics:*** For each plot, tree density and basal area were calculated
296 for stems ≥ 5 cm DBH. For calculating sapling density and basal area, all stems (between 1 and
297 4.9 cm) were treated as individuals, even if they were members of a multi-stem clonal group.
298 Finally, species' importance value (IV) of each species within each plot was calculated using the
299 formula: $IV = (\text{Relative density} + \text{Relative basal area})/2$.

300

301 **Results**

302 Between 1991 and 2012, daily mean water levels at the three stage recorders (P-33,
303 NP203, & G620) were similar within and across years. During the seven-year period that
304 preceded the vegetation sampling, annual mean water levels (WL) prior to 2012 sampling was
305 13.8 cm lower at G620 (Satinleaf) and 12.5 cm lower at both P33 (Black Hammock) and NP203
306 (Gumbo Limbo) than during the 7-year period prior to 2001 sampling. In concurrence with the
307 differences in annual mean WL at the stage recorders, the seven-year average hydroperiods were
308 shorter in 2012 compared to those in 2001 by 45, 64 and 48 days for Hammock, Bayhead and
309 Swamp, respectively (Figure 4; Supp. Table S.1). Likewise, mean hydroperiods between the two
310 census dates had also decreased by 94 days for Bayhead and 70 days for Swamp as well, but
311 stayed the same for the Hammock (Supp table S.2).

312 ***Plant communities***

313 Plant community composition in SRS tree islands followed the topographic gradient,
314 primarily oriented along the long axis (NS transect), but also along the transects aligned
315 perpendicular to the long axis. The SMW boundary analysis of the 2001 species cover data
316 along NS transects identified two significant peaks for Black Hammock and three significant
317 peaks for each of Gumbo Limbo and Satineaf, represented by relatively high normalized B-C
318 dissimilarity (Z-scores > 1.65), resulting in three (Black Hammock) or four (Gumbo Limbo and
319 Satinleaf) distinct plant communities (Figure 5). The location of significant peaks representing
320 high B-C dissimilarity were mostly identical in SMW analysis results based on both species and
321 life-form abundance data. The number of significant peaks, however, differed among islands.

322 For instance, in Gumbo Limbo, three significant peaks differentiating four communities
323 Hammock, Bayhead, Swamp and Sawgrass marsh were clearly identifiable (Figure 5b). In
324 Satinleaf, only the SMW boundary analysis based on life-form abundance data revealed three
325 significant peaks distinguishing the same four communities (Figure 5c). In Black Hammock,
326 however, the boundary separating Bayhead and Swamp was not distinct in either the species or
327 life-form abundance-based analysis (Figure 5a).

328 Plant communities identified along the NS transects were strongly associated with
329 hydroperiod ($r = 0.81$, $p < 0.001$; Figure 6). Among the three woody communities on the
330 islands, Hammocks were dominated by flood-intolerant species such as *Bursera simaruba* (L.)
331 Sarg., *Celtis laevigata* Willd., *Eugenia axillaris* (Sw.) Willd., *Ficus aurea* Nutt., and *Sideroxylon*
332 *foetidissimum* Jacq. Bayhead forests, which were more diverse than other communities in plant
333 species, were comprised of a mixture of moderately flood-tolerant trees (*Chrysobalanus icaco*
334 L., *Persea borbonia* (L.) Spreng., *Morella cerifera* (L.) Small, and *Magnolia virginiana* L.),
335 shrubs (*Cephalanthus occidentalis* L.) and ferns (*Acrostichum danaeifolium*, *Blechnum*
336 *serrulatum* and *Thelypteris interrupta*). Swamps were comprised of one or two flood-tolerant
337 tree species (*Annona glabra* L., *Salix caroliniana* Michx.) and a suite of graminoids and forbs.
338 The tree island tail, dominated by sawgrass (*C. jamaicense*), was present at the south end of the
339 transect. Mean species cover in different plant communities along NS transects on three islands
340 is given in Supp. Table S.3. In general, tree cover decreased towards the south end of the
341 Bayhead and was less than 5% in the adjacent Swamp, where low shrubs and forbs were most
342 abundant (Figure 7). Graminoid cover increased from Hammock to the Sawgrass marsh, where
343 sawgrass constituted >80% of the total plant cover. Similar to tree cover, canopy height in all
344 three islands exhibited a strong positive association ($r = 0.54$, $p < 0.001$) with surface elevation.
345 Hammock that occupied the head of the island had the tallest canopies, followed by Bayhead,
346 and finally Swamp (Figure 5).

347 The communities identified along the NS transects were also distinguishable within each
348 of the Hammock, Bayhead and Swamp transects (WE transects). However, the SMW analysis
349 revealed that the boundaries between identifiable plant communities were not always distinct.
350 Boundaries were more distinct on Hammock (WE1) and Bayhead (WE2) transects than on
351 Swamp (WE3) transects (i.e., Sawgrass marsh and Swamp are more similar than other adjacent
352 pairs), and more distinct in Black Hammock and Gumbo Limbo than Satinleaf (Figure 8). For

353 instance, on the Hammock transects (WE1), the peaks separating Hammock and Bayhead
354 communities were generally significant. However, unlike on the NS transect, where three woody
355 vegetation were identifiable, the Bayhead on both Hammock (WE1) and Bayhead (WE2)
356 transects transitioned directly into Sawgrass or mixed-marsh, as elevation decreased. On these
357 transects, the Swamp community was either absent, or if present, occupied a very narrow zone
358 that was indistinguishable in the selected window sizes in the SMW boundary analysis.

359 ***Environmental heterogeneity and species turnover***

360 Bray-Curtis dissimilarity between adjacent communities was positively correlated with
361 absolute differences in hydroperiod and mean annual RWL, along the transects (Table 2). On
362 the NS transects, many of the significant peaks (Z -score > 1.65) that represented relatively high
363 B-C dissimilarity, i.e. species turnover co-occurred with absolute differences in elevation of 48
364 cm or more (Figure 5), corresponding to a difference in mean annual hydroperiod of ≥ 185 days.
365 Along the WE transects, however, such values were much higher in the Hammock (WE1)
366 transect, where the sharpest gradient in elevation occurred (Figure 8). In contrast, in the
367 Bayhead (WE2) and Swamp (WE3) transects, high B-C dissimilarity was associated with just
368 15-20 cm difference in elevation i.e. a difference in hydroperiod of < 100 days.

369 B-diversity differed significantly (One-way ANOVA: 2001: $F_{2,6} = 4.95$, $p = 0.05$; 2012:
370 $F_{2,6} = 5.8$, $p = 0.04$) among the three woody communities, and was higher on the Hammock
371 (WE1) than on Swamp (WE3) transects (Figure 9). B-diversity on Bayhead (WE2) transects was
372 not significantly different from that on either Hammock (WE1) or Swamp (WE3) transects.
373 Averaged over all transects, the mean β -diversity was significantly (paired t-test: $t = 7.0$, $p <$
374 0.001) higher in 2012 than in 2001, suggesting greater microhabitat heterogeneity. The mean (\pm
375 SE) β -diversity were $6.18 (\pm 0.49)$ and $7.56 (\pm 0.56)$ in 2001 and 2012, respectively. The β -
376 diversity in both years 2001 and 2012, was positively correlated ($r = 0.83$ and $r = 0.84$,
377 respectively) with habitat heterogeneity, represented by CV of elevation on each transect.
378 However, the relationship between β -diversity and soil depth was not significant.

379

380 *Vegetation change (2001-2012)*

381

382 ***Vegetation dynamics along transects:*** From 2001 to 2012, the degree of change in plant
383 community composition varied within and among SRS tree islands. Analysis of similarity
384 (ANOSIM) reveals that, in general, the plant communities in the Hammocks in each island did

385 not change between 2001 and 2012 (Table 3). The changes in overall plant community
386 composition were higher in the Swamp than in Bayhead for each island, and these differences
387 were greater in Gumbo Limbo and Satinleaf than in Black Hammock.

388 Along the nine WE transects in the islands, the change in tree cover showed mixed results
389 (Table 4). Tree cover significantly decreased in the Bayhead (WE2) transect of Black Hammock
390 (paired t-test: $t = 2.23$, $df = 27$; $p = 0.03$), and in both the Hammock (WE1; paired t-test: $t = 4.85$,
391 $df = 46$; $p < 0.001$) and Swamp (WE3; paired t-test: $t = 2.51$, $df = 56$; $p = 0.015$) transects of
392 Gumbo Limbo. In contrast to Black Hammock and Gumbo Limbo, tree cover in Satinleaf was
393 not significantly different between two censuses. Tree layer vegetation on the tree islands
394 included both flood-intolerant and flood-tolerant species. Between 2001 and 2012, when
395 averaged over all WE transects, the mean (\pm S.E.) cover of *Annona glabra*, a flood-tolerant
396 species, decreased significantly from 11.1 (± 1.23) to 6.53 (± 0.78) percent (paired t-test: $t = 4.3$,
397 $df = 318$, $p < 0.001$), while the mean cover of *Chrysobalanus icaco*, a moderately flood-tolerant
398 species, increased from 9.1% to 12.3%. Among other woody species, shrub cover increased in
399 most transects, though the increase was statistically significant (paired t-test, $p < 0.05$) only in
400 the Swamp (WE3) transect of Black Hammock (Table 4). By far the most striking change in
401 vegetation composition in all study islands was an increase in the cover of graminoids,
402 particularly *Cladium jamaicense*. The increase in graminoids was statistically significant (paired
403 t-test; p -value < 0.005) in all transects except the Hammock (WE1) transect in Satinleaf (Table
404 4). However, on the Hammock (WE1) and Bayhead (WE2) transects, the increase in *Cladium*
405 *jamaicense* cover was limited to the Sawgrass marsh portion of the transects.

406 ***Tree and Sapling Dynamics in plots:*** In the Hammock plots, in which only the tree layer
407 was resampled in 2012, mean tree density and basal area, averaged over all three islands,
408 increased by 7.3% and 5.1%, respectively. However, the pattern of temporal change in both tree
409 density and basal area differed among islands (Figure 10). While both the density and basal area
410 in the Hammock plot of Gumbo Limbo decreased during the ten-year period, tree density
411 increased by 7.3% and 23.5% in Black Hammock and Satinleaf, respectively. Moreover, the
412 basal area decreased in Black Hammock by 6.5%, but increased in Satinleaf by 37.4%, from 36.5
413 $m^2 ha^{-1}$ to 50.1 $m^2 ha^{-1}$.

414 Across all Bayhead plots, the average importance value (IV) of most tree species declined
415 between 2001 and 2012 (Table 5). However, the IV of three tree species *Ilex cassine*, *Salix*

416 *caroliniana*, and *Chrysobalanus icaco* increased during this period. The most notable increase
417 was in the IV value of the moderately *C. icaco*. Its IV increased across all Bayhead plots and in
418 one of the Swamp plots (Figure 11a). In the sapling layer, the IV of *C. icaco* remained almost
419 unchanged in Black Hammock and Gumbo Limbo, but increased in Satinleaf (Figure 11b). In
420 contrast to the increase in IV of *C. icaco*, the flood-tolerant species *Annona glabra* and *Morcer*
421 *cerifera* decreased in most Bayhead plots, but remained relatively unchanged in the Swamp
422 plots.

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

431
432 ***Vegetation change and boundaries:*** In general, even after ten years, the position of
433 boundaries between two forest types or between forest and marsh along the Hammock (WE1)
434 transects remained intact. However, the sharpness of peaks separating forest and marsh
435 communities was more distinct in 2012 than in 2001, especially in the transition between
436 Sawgrass marsh and Bayhead or Swamp (Figure 8). A few plots, located at the boundaries
437 between Sawgrass marsh and Bayhead that were Sawgrass or Swamp in 2001 changed to Swamp
438 or Bayhead, respectively, by 2012, indicating an increase in woody components at the
439 boundaries.

440

441 **Discussion**

442 In the fixed, teardrop-shaped, tree islands within the ridge and slough landscape of the
443 Everglades, plant communities that differ in both species composition and functional
444 representation (life-forms) are arranged along a topographic and hydrologic gradient. These
445 communities are dynamic, and responds to changes in hydrologic conditions. Our results show
446 that periodic fluxes in the hydrologic regime, resulting in below average water levels and shorter

447 hydroperiods over a period as short as one decade, promote the growth of sawgrass in the marsh,
448 and the establishment and growth of woody plants within the tree islands. However, despite these
449 internal changes, we found minimal alteration in the position of the boundary between adjacent
450 plant communities, with the exception of the far tail regions of the islands.

451 Vegetation characteristics of the three study tree islands are in accord with patterns
452 described for ‘fixed tree islands’ present within the R&S landscape of the central and southern
453 Everglades (Sklar and van der Valk 2002). Four distinct plant communities - Hardwood
454 hammock, Bayhead forest, Bayhead swamp, and Sawgrass marsh - were expressed most clearly
455 along the primary axis of the islands parallel to the direction of water flow, but also were evident
456 along secondary axes in the direction perpendicular to flow. On these secondary axes, their
457 relative areal extent varied consistently depending on the location of the transect along the length
458 of the island (Figure 8). Ultimately, vegetation zonation within tree islands is a result of
459 hydrologic patterns and associated ecological processes, including biotic feedbacks that alter the
460 local topography. In the Everglades, proposed models for the development of ridge-slough-tree
461 island landscape have emphasized the role of water flow and the distribution of nutrients (Wetzel
462 et al 2005; Ross et al. 2006; Bazante et al. 2006; Givnish et al. 2008, Cheng et al. 2011; Larsen et
463 al. 2011). According to these models, the strong regional water flow causes nutrients to spread
464 downstream in the direction of flow and to form longitudinally arranged vegetation zones. A
465 similar process operating in directions perpendicular to flow appears to create nutrient gradients
466 between P-rich forests on relatively high ground to P-limited marshes. However, in those
467 directions, the gradients are concentrated within a shorter distance, resulting in narrow vegetation
468 zones.

469 Within a tree island, boundaries between plant communities are not always distinct.
470 While the transition between Hammock and Bayhead was well defined in the tree islands we
471 studied, the transition from Bayhead to Swamp to Sawgrass marsh was subtle, and boundaries
472 were sometimes difficult to distinguish. Several flood-tolerant tree species e.g., *Morella*
473 *cerifera*, *Magnolia virginiana*, and *Salix caroliniana* that occur in Bayhead were also present in
474 Swamp. However, their growth was stunted in the latter. Similarly, sawgrass, whose hydrologic
475 range is wide, grows together with flood-tolerant tree species within the Bayhead swamp zone.
476 Thus, a boundary between Swamp with high cover of sawgrass in the understory and adjacent
477 Sawgrass marsh may not always be distinct, and changes over time depend upon the change in

478 cover of sawgrass and other associated species. Rapid changes in sawgrass cover were largely
479 responsible for a change in boundary characteristics along the Swamp transect in Gumbo Limbo
480 and Satinleaf. On this transect in Gumbo Limbo, none of the peaks were significant in 2001,
481 whereas in 2012 three significant peaks, representing high normalized B-C dissimilarities and
482 sharp boundaries between adjacent communities were identified (Figure 8).

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

502 In contrast to our expectation of ubiquitous increase in woody plant cover because of
503 relatively dry conditions during 2001-2012, the change in woody cover along the transects
504 showed mixed results. In fact, in the Hammock transect of Black Hammock and Gumbo Limbo
505 islands and in the Bayhead of Gumbo Limbo, tree cover even decreased. This finding may be the
506 result of several interacting phenomena, including disturbances. In 2005, the study islands were
507 hit by two hurricanes, Hurricanes Katrina and Wilma. The latter brought relatively high wind
508 speeds (Knabb et al. 2006; Pasch et al. 2006) and caused significant tree damage on the study

509 islands. For three years after the hurricane, cumulative tree mortality values were 17.5% and
510 6.2% in the Hammock plots of Gumbo Limbo and Black Hammock, respectively (Ruiz et al.
511 2011). The high tree mortality on these islands in post-hurricane years could also be the result of
512 interactions of multiple disturbances, which can intensify the effects of disturbances and affect
513 the resilience of forests (Buma and Wessman 2011). The drought that prevailed from 2006 to
514 2008 after Hurricane Wilma might have accentuated tree mortality on these islands. In drought
515 years, particularly during the dry season when hammock plants use regional ground water (Saha
516 et al. 2010), water level fell more than 70 cm below the ground surface potentially limiting
517 access to ground water and leading to high mortality in hurricane-stressed trees.

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

531 Distribution of tree species in tree islands, and the loss of tree islands have normally been
532 viewed in relation to prolonged high-water conditions. However, tree island plant communities
533 and the boundaries between them or between an island and adjacent mixed-marsh are also
534 susceptible to the direct and indirect effects of disturbance, such as fire, particularly during
535 drought conditions like those observed in 2007-2008. Fires not only kill trees, but also consume
536 the rich organic soils, in the process altering water regime by lowering the surface elevation.
537 Under these circumstances, immediate post-fire flooding can be detrimental to tree island
538 recovery, and may lead to their recession or elimination (Ruiz et al. 2013b). Furthermore, fire is
539 also known to sharpen the edges of both ridges and tree islands (Givnish et al. 2008; Wetzel et al.

540 2008). Between 2001 and 2012 samplings, two fires burned the marshes close to Black
541 Hammock. These fires might have killed any woody plants growing in the marshes, and
542 consumed marsh peat, accentuating the difference in elevation and sharpening the boundary
543 between tree island and adjacent marsh.

544 A shift in the boundary between plant communities occurs when a change in community
545 characteristics cause reduction of its resilience beyond some threshold (Allen et al. 2005). In the
546 study islands, change in hydrology over a decade caused changes in the relative abundance of
547 herbaceous and woody species. However, these changes did not exceed the “tipping point” for
548 any tree island community. Hence, a minimal shift in boundary was observed. In a recent study,
549 macrofossil analysis of a tree island in an area adjacent to Everglades National Park, Water
550 Conservation Area-3A (WCA3A; Figure 3) showed that the island expanded in response to the
551 dry conditions of the late 1980s, and contracted during wet conditions in the 1990s (Brock et al.
552 2012). This implies that extreme hydrologic events are more important than average annual
553 hydrologic conditions in shaping tree island vegetation. Moreover, in plant communities
554 arranged along an ecological gradient, high species turnover usually occurs at the interface
555 between adjacent communities. Since there is high variability in composition within the
556 transition zone, the turnover appears to be adaptive. Hence, communities that have low turnover
557 at the boundary, particularly when the boundary is diffuse, may have relatively low resilience
558 (Allen et al. 2005). In the study islands, species turnover was relatively high along the
559 Hammock and Bayhead transects (Figure 9), where boundaries did not shift in position,
560 suggesting that those communities have higher resilience. However, species turnover was lower
561 on the Swamp transects, and thus the boundaries between Swamp community and the adjacent
562 Sawgrass marsh were prone to shifting, especially when impacted by extreme instances of
563 flooding or drought.

564 The strong correlation between tree island vegetation structure and hydrology suggests
565 that hydrologic modifications caused by Comprehensive Everglades Restoration Plan (CERP), a
566 multi-decade restoration project that is underway to restore, preserve and protect the Everglades
567 ecosystems, will affect tree island dynamics throughout the Everglades. Depending on the
568 magnitude of hydrologic alterations achieved by the CERP, the balance between flood-tolerant
569 and flood-intolerant woody and herbaceous vegetation within tree islands is likely to change.
570 The magnitude and direction of such changes will vary spatially in response to regional

571 differences in tree island condition and the extent of hydrologic modification achieved by the
572 CERP. It is likely that tree islands currently under hydrologic stress or in a highly degradative
573 state, e.g., ghost islands (Ewe et al. 2009), could see a recovery if hydrologic conditions
574 conducive to woody plant establishment and growth are achieved and sustained. In an
575 evaluation of several restoration scenarios for the Everglades that were based on questions of
576 policy makers and managers, Wetzel et al. (2017) showed improved water conditions for tree
577 growth in WCA3A, where tree islands have long been exposed to a stressful flooding regime.
578 Their results support our findings of an increase in abundance of flood-intolerant and moderately
579 flood-tolerant species in study SRS tree islands in response to relatively dry conditions during
580 2001-2012 period. While such a dry conditions during that period in SRS was a function of both
581 low rainfall and restricted water delivery, under the CERP projects, there are plans to increase
582 the water delivery to ENP in coming years. Under those conditions, the trend in tree island
583 community change observed in this study is likely to be reversed, favoring herbaceous over
584 woody life forms. However, Wetzel et al. (2017) showed that while some tree islands in ENP
585 and WCA3B will experience the wetter conditions in all restoration scenarios than existing
586 condition, the plant communities in the modeled islands in these regions would experience
587 minimal change in the proportions of tree island woody communities. Our study suggests that the
588 CERP should strive to achieve hydrologic conditions that result in a spatially balanced mosaic of
589 plant communities in different successional states on tree islands. System wide homogeneity in
590 tree island structure, composition, and type should be discouraged, since it might cause local
591 extirpation of rare flora and fauna, which would reduce the overall species diversity of tree
592 islands. System wide homogeneity in tree islands significantly increases the chances of a system
593 wide or regional perturbation event having catastrophic consequences.

594 In summary, SRS tree islands consist of plant communities of contrasting species
595 composition and functional representation (life-forms). Between 2001 and 2012, cover of flood-
596 tolerant tree species decreased, while cover of moderately flood-tolerant and flood-intolerant
597 species increased along transects, as well as in plots within Hammock, Bayhead and Swamp
598 communities. While the life-form composition of plant communities changed on only a few
599 transects, such changes in the mixture of life-forms exactly paralleled the changes in the
600 boundary between adjacent communities. Thus, vegetation changes do not always involve a
601 simple shift in the location of fixed species assemblages, but rather the emergence of new

602 species' and structural combinations. In these three islands, however, the effects of annual
603 variation in hydrology over the previous decade probably did not surpass the communities'
604 resilience, possibly because the period of the study may just not have been long enough. Hence,
605 a minimal shift in boundary between tree island plant communities was observed on most
606 transects.

607

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609

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624

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Tables

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

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778 **Table 2:** Pearson Correlation coefficient (r) and p-values for the relationship between mean
 779 normalized Bray-Curtis dissimilarity (Z-Score) and difference in (a) hydroperiod, and (b) relative
 780 water level (RWL) on nine transects, three each in Black Hammock, Gumbo Limbo and
 781 Satinleaf tree islands.
 782

Tree Island	Transect	n	2001		2012		2012		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

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784

785 **Table 3:** Global R and p-values from analysis of similarity (ANOSIM) testing for differences in
 786 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

787

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

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Transect/Life-forms	Black Hammock		Gumbo Limbo		Satinleaf	
	2001	2012	2001	2012	2001	2012
Hammock (WE1)						
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
Bayhead (WE2)						
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	4.09	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
Swamp (WE3)						
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

792

793

794 **Table 5:** Mean (± 1 S.E.) tree importance value (IV) in Bayhead forest and Bayhead swamp plots
 795 sampled in 2001 and 2012. The IV values were averaged over all three Shark River Slough tree
 796 islands.
 797

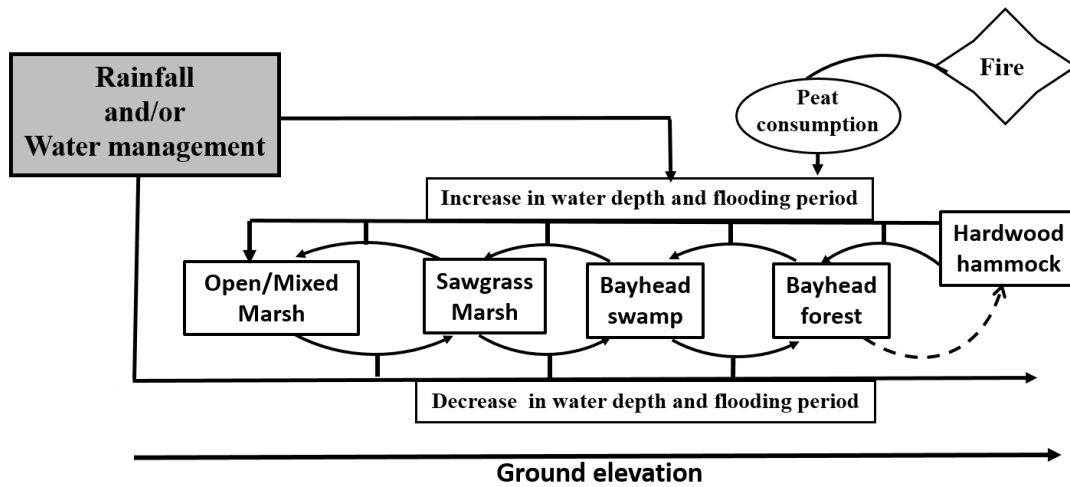
Species	Tree - importance value (%)			
	Bayhead forest		Bayhead swamp	
	2001	2012	2001	2012
<i>Annona glabra</i>	44.0 \pm 13.4	34.3 \pm 4.0	13.8 \pm 13.8	50.1 \pm 28.7
<i>Chrysobalanus icaco</i>	4.4 \pm 4.4	18.9 \pm 9.8		2.0 \pm 2.0
<i>Ficus aurea</i>	11.7 \pm 11.7	9.5 \pm 9.0		
<i>Ilex cassine</i>	2.8 \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	

798
 799
 800 **Table 6:** Mean (± 1 S.E.) sapling importance value (IV) in Bayhead forest and Bayhead swamp
 801 plots sampled in 2001 and 2012. The IV values were averaged over all three Shark River Slough
 802 tree islands.
 803

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		

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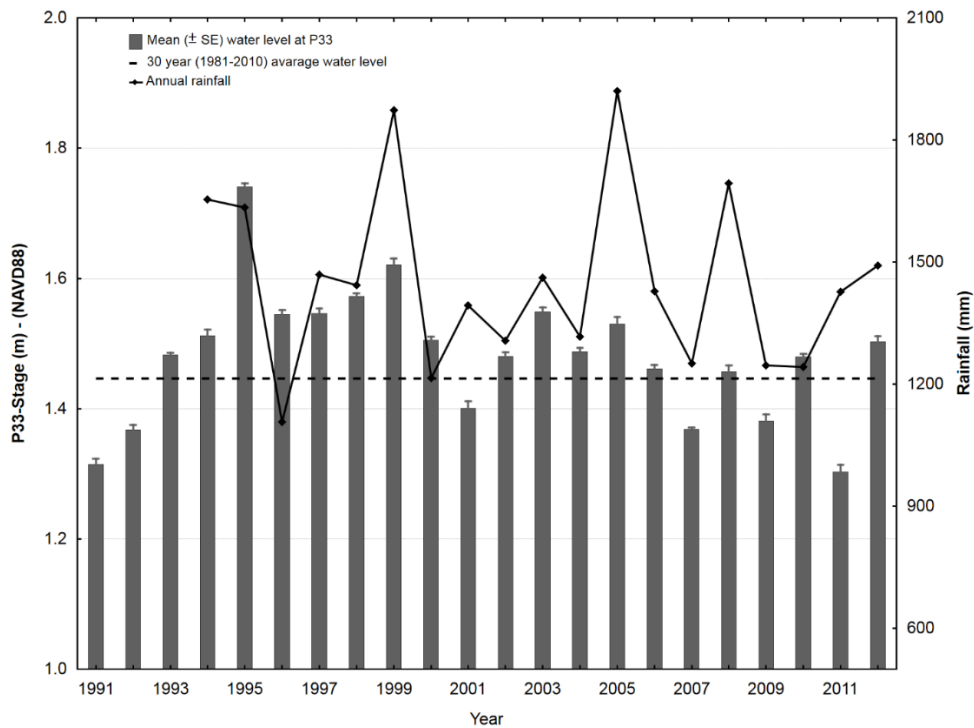
Figures



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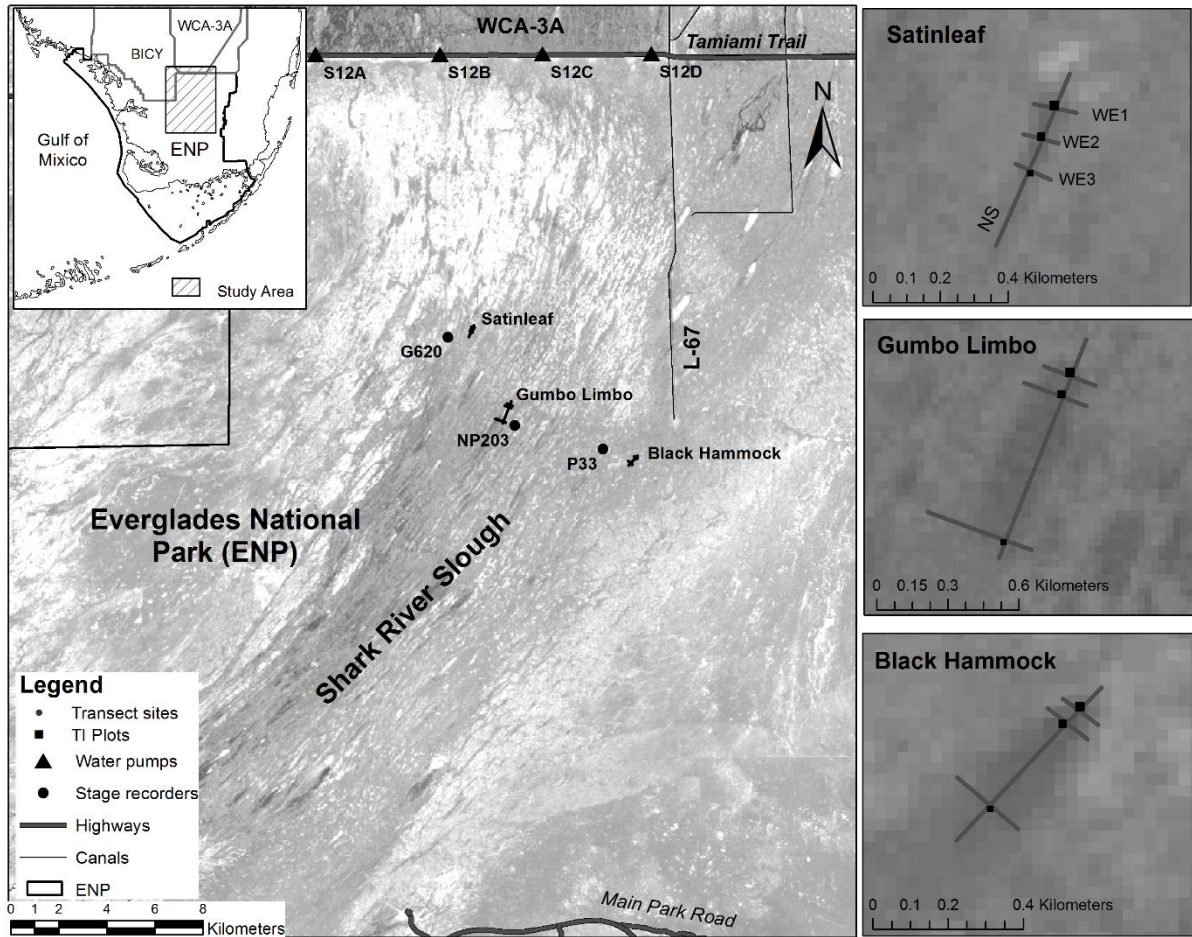
810 **Figure 1:** Conceptual model: vegetation dynamics in Shark River Slough tree islands and
 811 surrounding marsh.

812



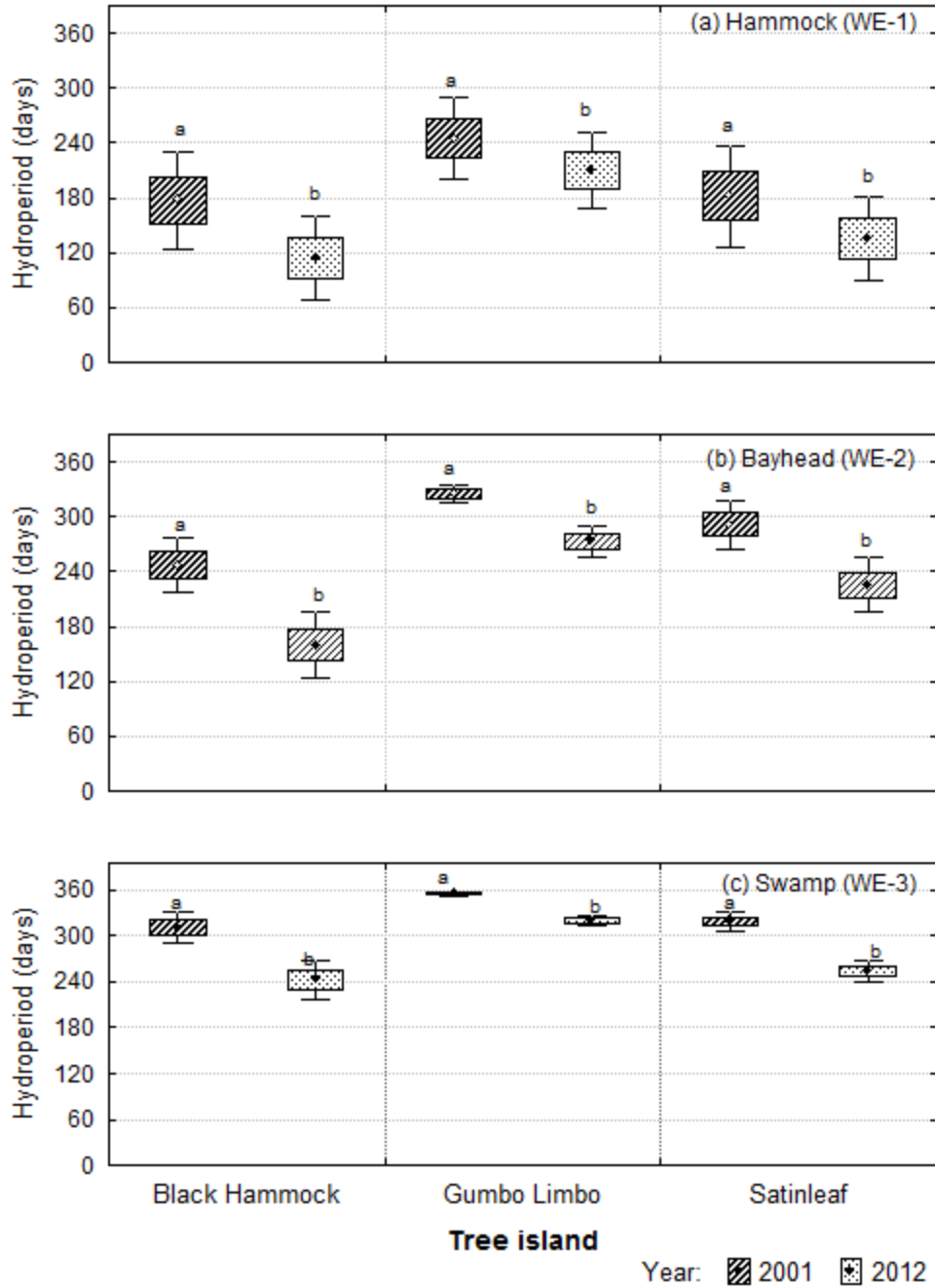
813

814 **Figure 2:** Annual total rainfall and annual mean (± S.E.) and 30Yr (1981-2010) average
 815 (dashed line) water level at the stage recorder P33 located in Shark River Slough within
 816 Everglades National Park.



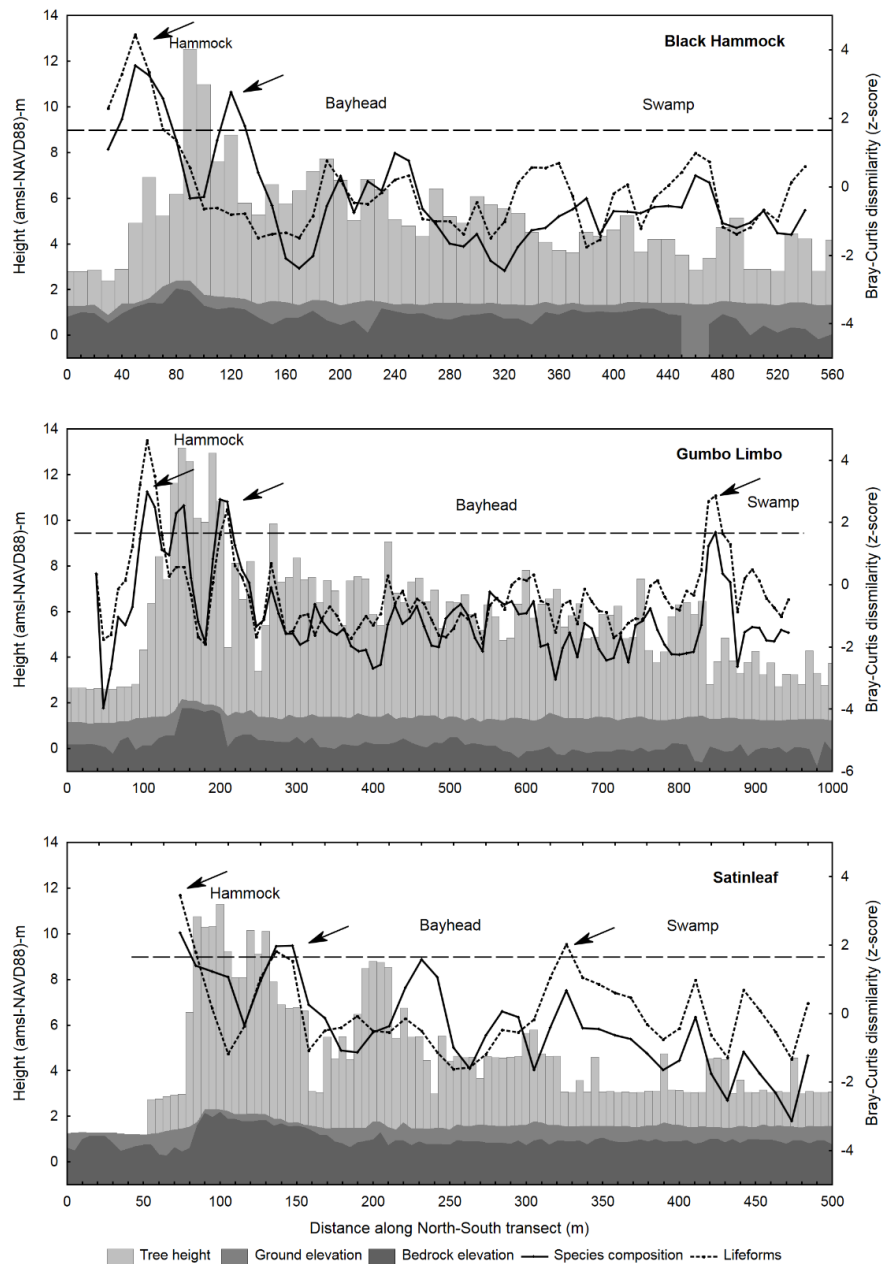
817

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

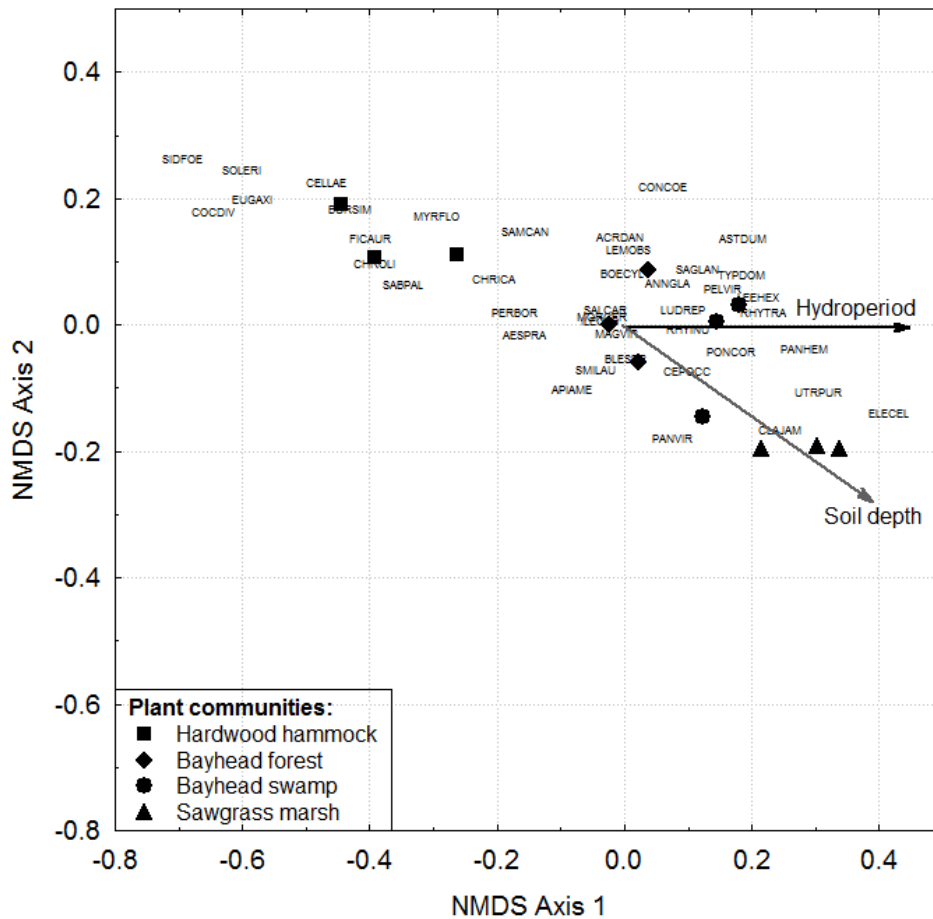


820

821 **Figure 4:** Boxplots (Mean, 1.SE, and 95% CI) showing mean annual hydroperiod averaged over
 822 7 years prior to sampling along three west-east (WE) transects - Hammock (WE1), Bayhead (WE2)
 823 and Swamp (WE3) - in three Shark River Slough tree islands, Black Hammock, Gumbo Limbo
 824 and Satinleaf. Different letters show significant (Paired t-test; $p < 0.5$) difference in mean
 825 hydroperiod between 2001 and 2012.

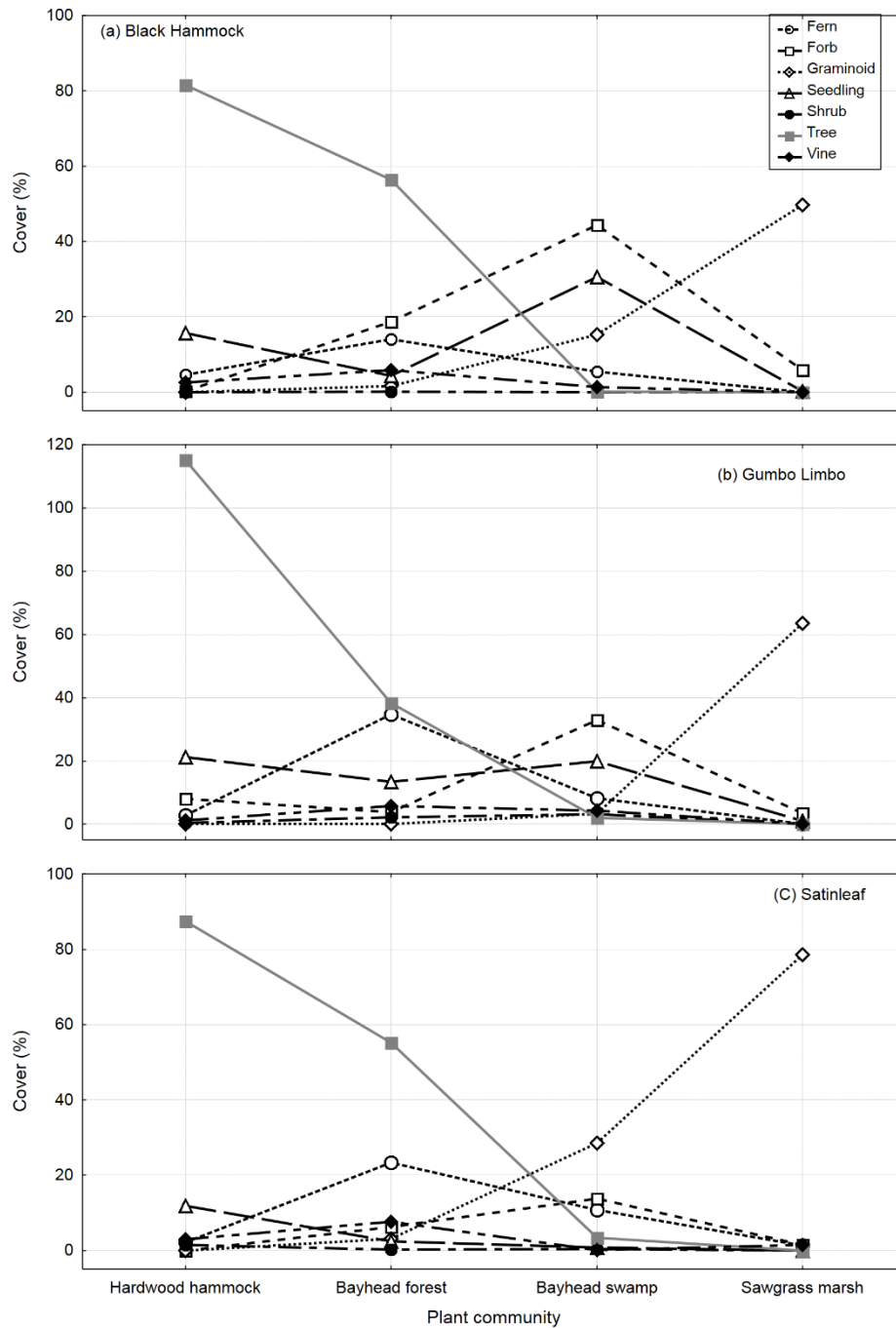


827 **Figure 5:** Canopy height, bedrock elevation, soil depth, and normalized Bray-Curtis (B-C)
 828 dissimilarity (Z-Score) based on species composition during 2001 sampling along NS transects
 829 on three Shark River Slough tree islands. In split-moving window analysis, the Z-scores were
 830 averaged over four window sizes (window with of 6, 8, 10, and 12). Arrows indicate the peaks
 831 (boundaries) that consisted of one or more contiguous sites with Z-scores equal or greater than
 832 1.65 (dashed line - the value in one-tailed test: 95% confidence limit).



833

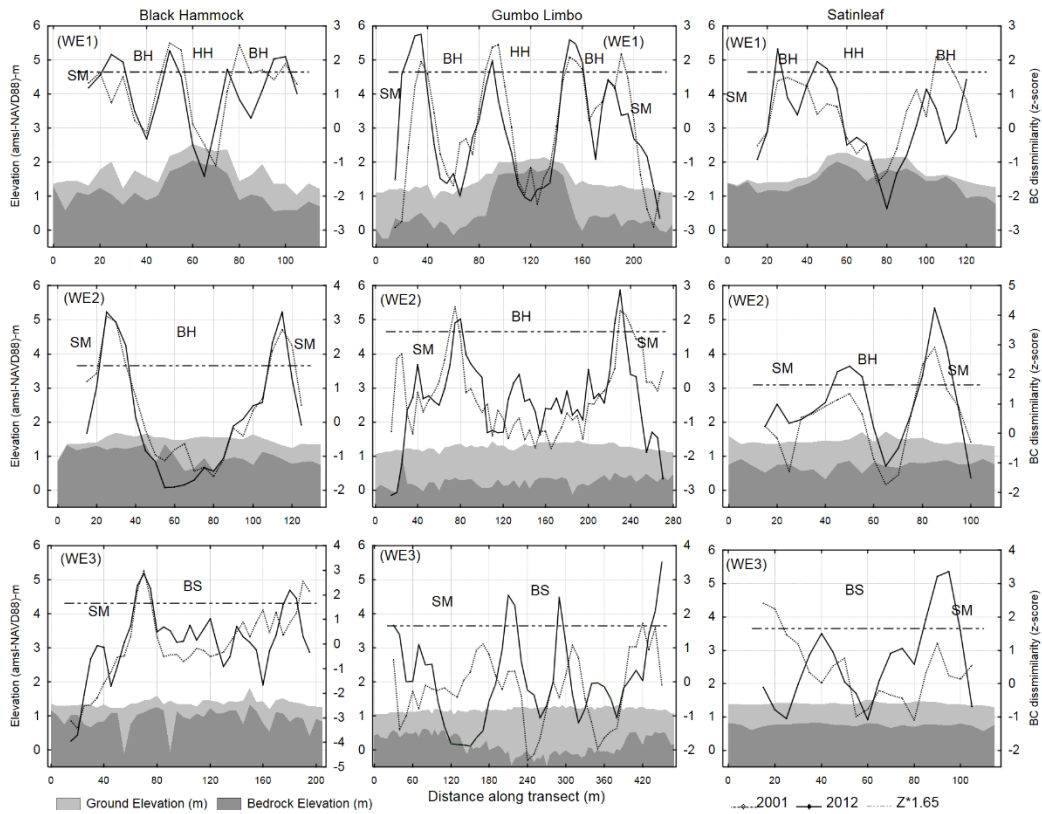
834 **Figure 6:** Bi-plots of site species scores from two-dimensional nonmetric multidimensional
 835 scaling (NMDS) ordination of species cover data collected during 2001 sampling at the sites along
 836 NS transects on three Shark River Slough tree islands. Environmental vectors fitted in the
 837 ordination spaces represent the direction of their maximum correlation with ordination
 838 configuration. Full name of species are in Supplementary Table S.3.



839

840 **Figure 7:** Mean cover of life-forms based on 2001 sampling in four plant communities along NS

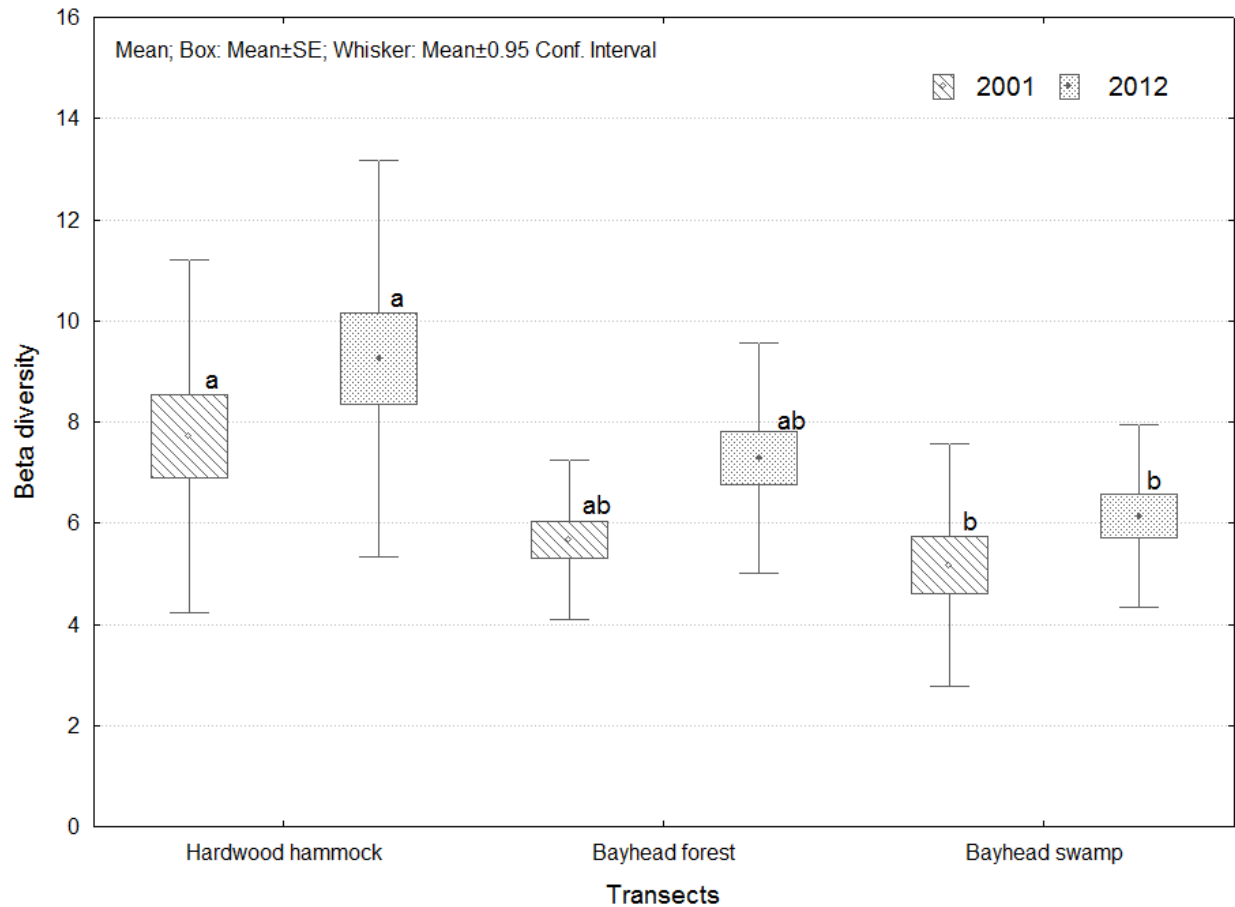
841 transect on three Shark River Slough tree islands.



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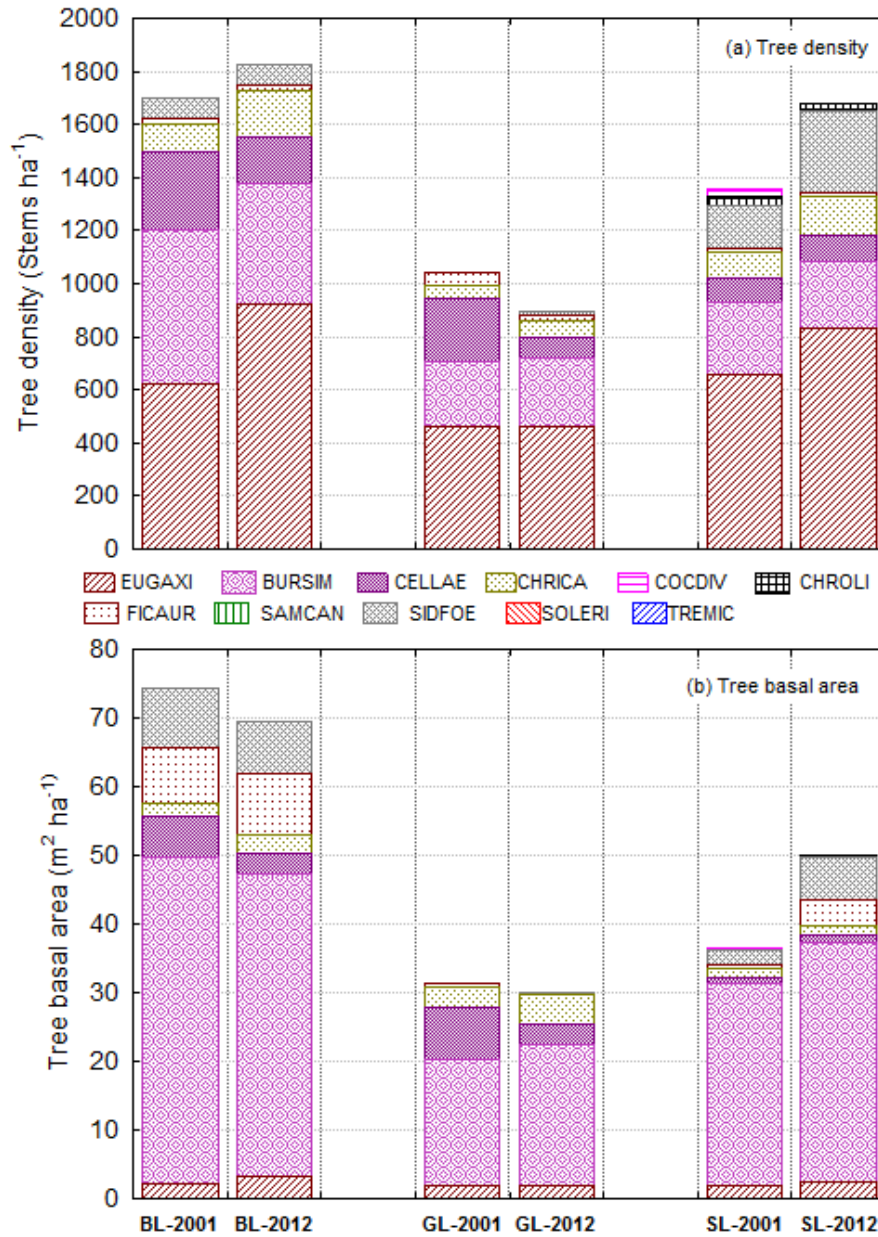
843

844 **Figure 8:** Bedrock elevation, soil depth, and normalized Bray-Curtis dissimilarity (Z-Score) based
 845 on species composition along WE transects on three Shark River Slough tree islands. In split
 846 moving-window analysis, the Z-scores were averaged over four window sizes (window with of 6,
 847 8, 10, and 12 sites) separately for 2001 and 2012 samples. HH = Hardwood hammock, BH =
 848 Bayhead, BS = Bayhead swamp; SM = Sawgrass marsh. The peaks (boundaries) that consisted of
 849 one or more contiguous sites with Z-scores equal or greater than 1.65 (dashed line - the value in
 850 one-tailed test: 95% confidence limit) were significant.



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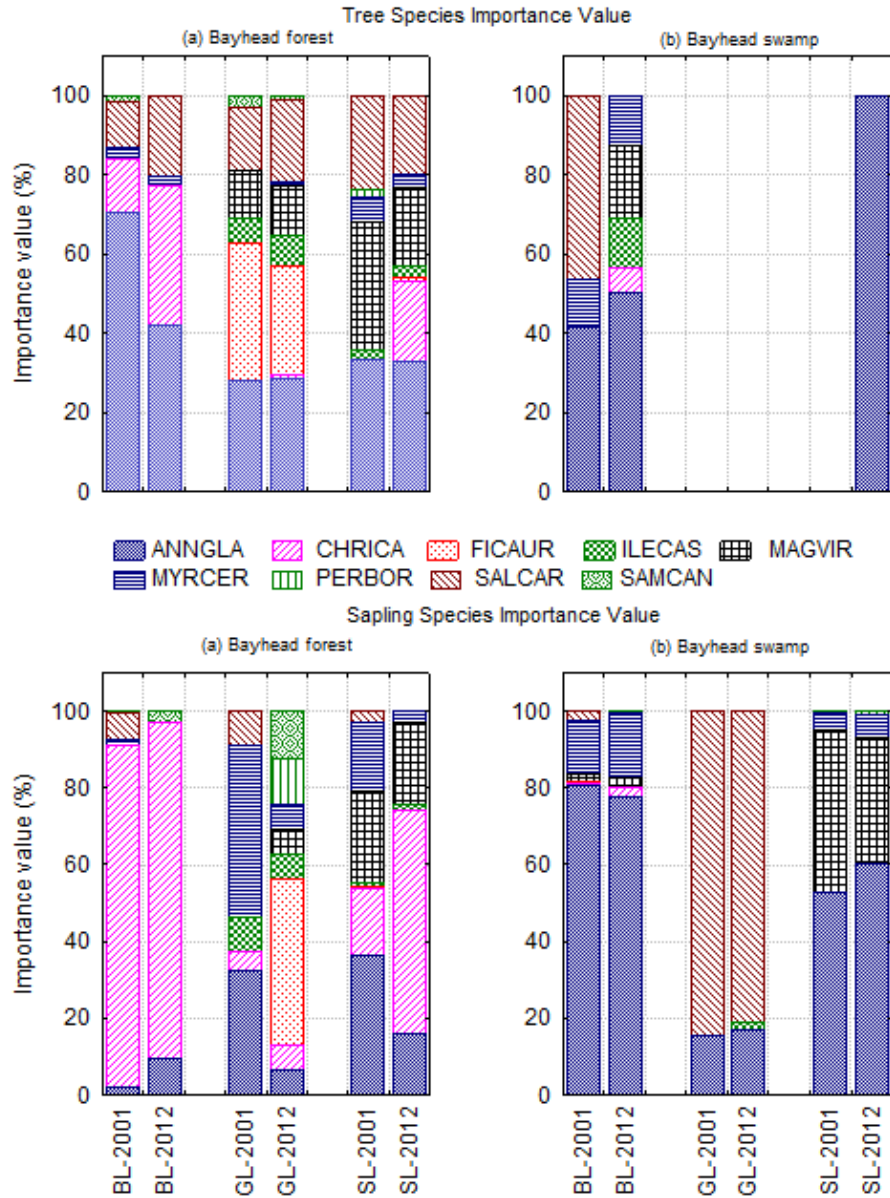
852 **Figure 9:** Box plots showing the mean (\pm SE) of beta diversity (β) in 2001 and 2012 on three WE
 853 transects – Hammock (WE1), Bayhead (WE2) and Swamp (WE3) – on three Shark River Slough
 854 tree islands. Different letters show significance (One-way ANOVA: Bonferroni test, $p < 0.05$)
 855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



856

857 **Figure 10:** Tree density (stems ha⁻¹) and basal area (m² ha⁻¹) in Hardwood hammock plots on
 858 Shark River Slough tree islands sampled in 2001 and 2012. BL = Black Hammock, GL = Gumbo
 859 Limbo, SL = Satinleaf. Full name of species are in Supplementary Table S.3.

860



861

862 **Figure 11:** Tree and sapling importance value (IV) in (a) Bayhead forest and (b) Bayhead
 863 swamp plots in three Shark River Slough tree islands sampled in 2001 and 2012. BL = Black
 864 Hammock, GL = Gumbo Limbo, SL = Satinleaf. . Full name of species are in Supplementary
 865 Table S.3.

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