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Monitoring of Tree Island Condition in the Southern Everglades: Annual Report 2011

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Annual Report - 2011

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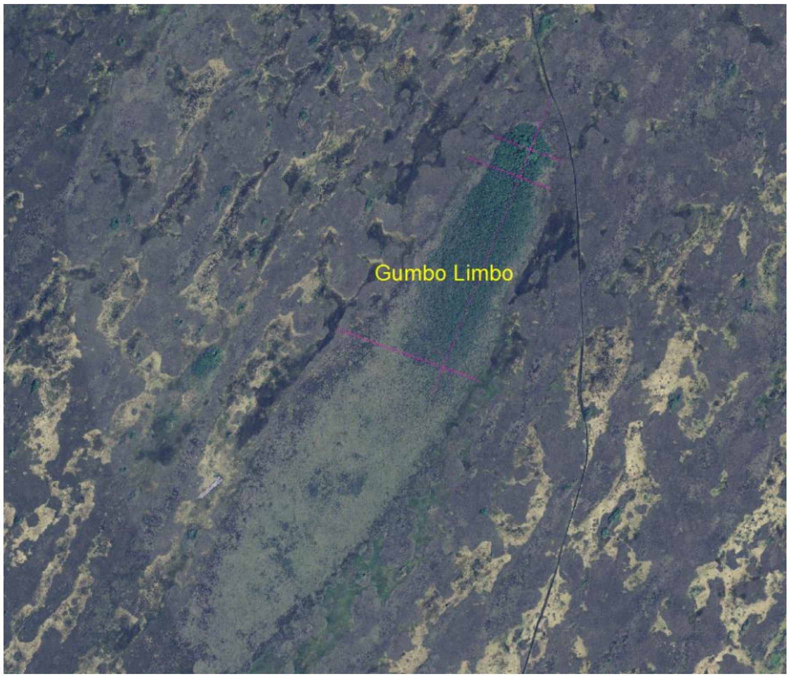

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Summary

Tree islands, a prominent feature in both the marl prairie and ridge and slough landscapes of the Everglades, are sensitive to large-scale restoration actions 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 at both local and landscape scales are likely to affect the internal water economy of islands, which in turn will influence 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 understating of reference conditions of vegetation structure and function, and their responses to major stressors is important. In this regard, a study of vegetation structure and composition in relation to associated physical and biological processes was initiated in 2005 with initial funding from Everglades National Park and South Florida Water Management District (SFWMD). The study continued through 2011 with funding from US Army Corps of Engineers (USACOE) (Cooperative Agreement # W912HZ-09-2-0019 Modification No.: P00001).

In 2011, field work was carried out on eight islands within a 16-island network established for long-term monitoring and assessment in 2005. The subset included three Shark River Slough tree islands which had been intensively studied in 2000-2002. On all eight islands, vegetation structure and compositional parameters in both canopy and ground layer were measured in permanent plots, ranging in size from 300 to 625 m^2, in the tropical hardwood hammock at the upstream end of the tree island. The vegetation survey included a tree (>5 cm dbh) census, dbh measurements of all tagged trees and in-growth, density counts of tree saplings (height >1.4 m, dbh 1-5 cm), and cover estimates of species in the shrub (height >1 m and dbh <1 cm) and herb (woody and non-woody < 1m height) strata. In addition, canopy openness was measured in the field using a spherical densiometer at the center of each cell, and a hemispherical photograph was taken with a digital camera placed at 1 m height above the ground at the same location. In two of eight islands, Satilnleaf and Grossman Hammock, seedlings were tagged in a set of randomly selected 1 m^2 subplots. Moreover, to assess vegetation change over the last ten years, transects that had been established and first sampled in 2001-2002 in Black Hammock, Gumbo Limbo and Satinleaf islands were re-sampled in the spring of 2011. At each of these sites, three cross-island transects had been established in 2000-2001, and a topographic survey was completed along each transect at 5-10 m intervals. In 2011, vegetation was resampled as before along these transects. Sampling protocols included (1) an estimate of maximum height and cover class of trees and vines by species within a 2 m radius plot; and (2) an estimate of cover class of herbs and shrubs by species within a 1 m radius plot around each transect point.

Species cover data were summarized using the mid-point of the cover class, and both univariate and multivariate techniques were used to examine the effects of environmental factors on vegetation structure and composition. The split moving-window (SMW) boundary analysis was used to analyze variation in vegetation composition and to identify boundaries between vegetation assemblages along the hydrologic gradient on the surveyed transects in the three tree

islands. Diversity indices were calculated to examine spatial and temporal species turnover along the gradient. In addition, non-metric multidimensional scaling (NMDS) ordination was used to examine relationship between environmental factors and vegetation composition along transects as well as in hardwood hammocks plots. Analysis of similarity (ANOSIM) was applied to test differences in species composition between landscape types (Ridge-Slough and Prairies), and between years. Finally, NMDS and Procrustes analyses were used to determine the relationship between overstory and understory composition along the environmental gradient.

Shark Slough tree islands revealed a more or less regular spatial pattern in plant species composition that appears to be related to topography, hydrology, and soil characteristics. On the three focal islands described in this Report, spatially differentiated vegetation occurring along the hydrologic gradient took the form of vegetation assemblages of contrasting species composition and functional representation (life forms). When plotted along the length of the transect, the boundary between adjacent vegetation assemblages varied from sharp, clearly defined peaks of B-C dissimilarity to more gradual, diffuse transition zones. However, over the last decade, the life form composition of some of these assemblages changed in response to interacting forces, including hydrology and disturbances (fire and storms). Tree cover in the hardwood hammocks, especially in Black Hammock and Gumbo Limbo, decreased whereas the cover of graminoids, including sawgrass (*Cladium mariscus* ssp. *jamaicense*) and spikerush (*Eleocharis cellulosa*) increased near the boundary between marsh and bayhead or bayhead swamp forest, and within the bayhead swamps on all islands. Further, only on a few transects, changes in the mixture of growth forms exactly paralleled changes in the boundary between adjacent assemblages. Thus, vegetation changes did not always involve a simple shift in the location of fixed species assemblages, but rather the emergence of new species and structural combinations. In general, shifts in boundaries among plant communities are presumed to initiate reductions in ecosystem resilience, resulting in regime shifts. In these three islands, however, the effects of annual variation in hydrology over the previous decade probably did not surpass the ecosystem's resilience, hence a minimal shift in boundary was observed on transects.

Within one plant community, the hardwood hammocks of rarely flooded patches in southern Everglades tree islands, response to environmental drivers and site characteristics also took place at both landscape and site levels. In these hammocks, both the overstory and understory vegetation showed similar patterns of response to site attributes (elevation above surrounding marsh and soil characteristics), resulting in differentiation in vegetation composition on islands in the marl prairie and ridge-slough landscapes. However, the responses of these two vegetation layers to hydrologic variation differed, probably due to alternative water use patterns by the plants represented in each layer. Similar differences between vegetation layers in the use of light were also present, as the overstory vegetation generally experiences the full range of light, while understory vegetation experiences a relatively narrow range and with great variation in light availability. Thus, in these islands the species composition in the overstory is not always only a good predictor of understory composition. Moreover, understory vegetation in the hammocks was mostly composed of tree seedlings. Since understory vegetation, especially dominated by tree seedlings, is tightly linked through intra- and interspecific interactions to the success of tree species in reaching to the forest canopy, understory vegetation composition and dynamics have the potential to significantly influence overstory stand structure, and to cause more long-term ecosystem responses to alterations in major natural and anthropogenic drivers.

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1. General Background

Tree islands, a prominent feature in both the marl prairie and ridge and slough landscapes of the Everglades, are sensitive to large-scale restoration actions 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 at both local and landscape scale are likely to affect the internal water economy of the islands, which in turn will influence 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 reference conditions of vegetation structure and function, and their responses to major stressors is important. In this regard, a study of vegetation structure and composition and associated biological processes was initiated in FY2005 with initial funding from Everglades National Park and South Florida Water Management District (SFWMD), and has been continued through FY2011 with funding from US Army Corps of Engineers (USACOE). The comprehensive results through FY2009 are described in Shamblin et al (2008) and Ruiz et al. (2011).

This report describes the dynamics of vegetation structure and composition on tree islands in Southern Everglades, emphasizing the work accomplished in 2011 (Cooperative Agreement # W912HZ-09-2-0019 Modification No.: P00001). In 2011, the field work was completed on eight islands that are a sub-set of a 16-island network established for long-term monitoring and assessment in 2005 (Shamblin et al. 2008). The sub-set also included three Shark Slough tree islands, Black Hammock, Gumbo Limbo, and Satinleaf which had been intensively studied in 2000-2002 (Ross and Jones 2004). Three transects on each of these three islands were re-sampled to assess the vegetation change over a ten-year period.

Tree island vegetation responds to management- and naturally-driven forces e.g., hydrology, disturbance (fire and storms). The document is organized in two sections: Section 1 describes a decadal change in vegetation composition along hydrologic gradients along transects in three islands, and Section 2 describes the understory vegetation structure and associated biological processes in hardwood hammocks on all eight islands.

2. Spatio-temporal pattern in plant communities along a gradient in the tree islands

2.1 Introduction

In a complex ecological system, plant communities arranged in a spatially hierarchical structure along a gradient can be viewed as a product of ecosystem functions or functional processes associated with underlying physico-chemical drivers that vary on both spatial and temporal scales. In general, with changes in the level of the underlying drivers in a system, specific sets of the processes result in the formation of discontinuities or boundaries, representing a transition zone between two distinct self-organizing structures (Allen et al. 2005). Structural and functional characteristics of such a boundary, often referred to as an '*ecotone*' in the plant community literature, usually depend on whether variation in the drivers is abrupt or gradual (Wiens et al. 1985; van der Maarel 1990; Gosz 1993; Walker et al. 2003). However, the persistence of the position and attributes of the boundaries in space and time depends on the ability of these self-structured identities to withstand the effects of natural and/or management-induced alterations in underlying drivers on functional processes (Risser 1995; Forys and Allen 2002). In general, self-organizing structures that maintain their functional integrity, even after some changes in their elements, are usually able to persist within their prevailing spatio-temporal domain, and the boundaries between these structural systems remain intact (Forys and Allen 2002). Hence, when there is a significant loss of the functional processes or a change in their representation within the structural system, it becomes less resilient, and its boundary is likely to get shifted (Allen et al. 2005).

In the Everglades, tree islands are integral components of the ridge-slough landscape, as well as other landscapes (e.g., pine rockland, marl prairie). They are complex ecosystems and often include different plant communities spatially arranged along topographic, hydrologic and soil nutrient gradients (Armentano et al. 2002; Ross and Jones 2004; Ross et al. 2006; Espinar et al. 2011). In these islands, physico-chemical drivers produce a range of wooded assemblages, which vary in species composition and life-form structure, represented in the proportion of plant growth forms that are present. Vegetation of the hardwood hammocks, which lie on the most elevated portion of the islands and are rarely flooded, are mostly dominated by flood-intolerant trees, whereas the surrounding marsh has mostly flood-tolerant graminoids or broad-leaved sub-merged, floating species and/or emergent species depending on the level of hydrologic conditions. In between these two extremes, the proportion of woody plants and herbaceous species varies depending on the underlying physico-chemical drivers of plant community composition (Sah 2004). For instance, on the tear-drop shaped tree islands in the ridge-slough landscape of the southern Everglades, the topographic gradient from hammock to marsh is steepest in the direction perpendicular to the water flow than along the long axis parallel to the flow (Reed and Ross 2004). Moreover, with changes in the underlying drivers, together with periodic disturbances (fire, hurricane), plant species composition may change over time, affecting the resilience of the plant communities on the islands, and ultimately the persistence of forest communities within the marsh. Paleo-ecological studies have also suggested that location of boundaries between tree island communities and surrounding low-stature marsh vegetation might have shifted in the past, depending on hydrology, climate, or fire induced changes in surface elevation (Stone and Chimura 2004), or, since the 20th century, as a result of water management (Willard et al. 2006; Bernhardt and Willard 2009).

Hydrology is one of the major drivers of species differences along topographic gradients within individual tree islands, or among various types of tree islands in the Everglades (Armentano et al. 2002; Wetzel 2002; Ross and Jones 2004; Espinar et al. 2011). Hence, substantial changes in hydrologic conditions, whether natural or management induced, are likely to impact tree island vegetation structure and composition to some extent, with extreme and prolonged changes even leading to complete degradation of forest structure and extensive change in ecosystem function. Historically, such changes in hydrologic conditions were mainly driven by annual or decadal variation in the precipitation. However, in recent years, hydrologic modifications through the operations of water structures have dramatically impacted various elements of the landscape, including the tree islands, throughout the central and southern Everglades (Sklar and van der Valk 2002). For instance, intensive hydrologic management that caused deeper and more extended flooding on the islands resulted in a reduction of more than 50% in the number and area of tree islands in the Water Conservation Areas in 60 years (Brandt et al. 2000; Patterson and Finck, 1999). Since both adjacent tree island and marsh vegetation communities are hydrologically connected (Troxler et al. 2005; Ross et al. 2006; Saha et al. 2010; Sullivan 2011), prolonged and extreme dry or wet events may also affect the boundary of tree islands. The climatological records and hydrologic data from the Shark Slough region suggest that water level during most of the last decade of the 20th century was well above the 30-year average. In contrast, both the mean annual rainfall and water level were relatively low during the most recent decade (2001-2010) (**Figure 1.1**). Such a difference in water conditions has provided an opportunity to assess the response of vegetation to the shift in hydrologic regime on three Shark Slough tree islands that were first surveyed in 2001-2002, and then in the spring of 2011.

Drying conditions usually promote the establishment and growth of woody plants in wetlands. In the Everglades, where vegetation is arranged along a hydrologic gradient from open water sloughs dominated by water lilies (*Nymphaea* sp.) and spikerush (*Eleocharis cellulosa*) to dense sawgrass (*Cladium mariscus* ssp. *jamaicense*), and finally to woody communities (Gunderson 1994; Todd et al. 2010), a decrease in water level in the landscape are expected to shift marsh species composition toward a more sawgrass-dominated community; and the expectation for tree islands include higher overall dominance of trees over herbaceous plants, and emergence of less flood tolerant trees. This study examines the spatio-temporal variation in vegetation composition in both tree and herb strata along an environmental gradient within Shark Slough tree islands by i) quantifying the species and growth form distribution along the environmental gradient, ii) identifying boundaries between vegetation assemblages, iii) assessing the response of species composition and life forms to the changes in hydrologic regime over time, and iv) evaluating the effects of change in species abundance and the representation of different life-forms on the location and structure of boundaries between vegetation assemblages.

2.2 Methods

2.2.1 Study area

The study was conducted on three Shark Slough tree islands, Black Hammock (BL), Gumbo Limbo (GL) and Satinleaf (SL), within Everglades National Park (**Figure 1.2**). The three islands, BL, GL and SL are situated in eastern, central and northwestern portions of the slough, respectively. Like most large Shark Slough tree islands, these islands are 'fixed tree islands' i.e. organized around slightly elevated (~1-2 m) limestone outcrops (Skar and van der Valk 2002), with characteristic shape and zonation. Fixed islands consist of a well-defined 'head' that supports a mixture of tree species, mostly of tropical origin, and a 'tail' dominated at its upper end by flood-tolerant trees and further downstream by tall sawgrass. These teardrop-shaped tree islands exhibit a consistent decrease in surface elevation, and canopy height from the rarely flooded heads to the seasonally flooded swamp forests and marshes in the far tail region of the islands (Armentano et al. 2002; Ross and Jones 2004). While the geomorphology of the islands has been shaped over a history that stretches back thousands of years (Stone and Chimura 2004; Willard et al. 2006), the current composition and community structure is determined to a large extent by recent hydrology. The hydrologic regimes that impact the ecology of these islands are influenced primarily by annual rainfall, augmented by the southerly flow of water delivered from the Water Conservation Areas by pumps arrayed along the east-west trending Tamiami Trail (Reed and Ross 2004). Disturbances such as hurricanes and fire have also played a large role in the ecology of Shark Slough tree islands ((Loope et al. 1994; Armentano et al. 1995, 2002; Ruiz et al. 2011).

2.2.2 Data collection

Vegetation was sampled along four transects on three tree islands, BL, GL and SL in the Shark Slough. On each tree island, one transect followed the long axis of the island, hereafter termed as 'NS transect', and the other three transects were laid in west-east direction (hereafter, WE transects), at right angles to the long transect. Out of three transects, one traversed the "head" or "hammocks", and the other two crossed the middle and lower portions of the islands; these are named as 'hammock', 'bayhead' and 'bayhead swamp' transects, respectively, based on the vegetation present at the middle of the transect. All four transects were sampled in 2001-2002, but only the three WE transects were re-sampled in the spring of 2011. The length of transects and the number of sites sampled in 2001-2002 and 2011on each transect are given in **Table 1.1**.

The ground surface elevation was determined at 5-10 m intervals along each transect by surveying via auto-level from a USGS benchmark of known elevation. Soil depth was determined by probing to bedrock with a metal rod at each surveyed location. We estimated hydroperiod (number of days per year of surface inundation) and annual mean water depth at each survey plot location along the transects, using elevation data from topographic surveys in conjunction with long term water level records at a stage recorder situated in the open marsh at 0.5 to 1.5 km distance from the head of each island. The three stage recorders used to calculate hydrologic parameters for BL, GL and SL were P33, NP203, and G620, respectively. Daily water level at the survey sites was estimated assuming a flat water surface, and an annual average hydroperiod (days) and mean annual water depth (cm) were calculated for each plot. In general, the lag time in vegetation response to hydrologic changes depends on the type of vegetation. For instance, while several authors have estimated a vegetation response time of 4-6 years in marshes (Armentano et al. 2006, Zweig and Kitchen 2009), in tree islands a strong correlation was found between variation in vegetation composition and 7-year annual average hydroperiod and water depth (Sah 2004; Espinar et al. 2011). We therefore calculated a mean annual hydroperiod (days) and water level (cm) for the sampling year 2001-2002 and 2011 for the 7-year period preceding the sampling year.

On each transect, vegetation was sampled every 5-10 m, and the sampling protocols included, (1) an estimate of maximum height and cover class of trees and vines by species within a 2 m radius plot; and (2) an estimate of cover class of herbs and shrubs by species within a 1 m radius plot around each transect point. The cover classes used to estimate species cover in each stratum were: 1, 0-1%; 2, 1-4%; 3, 4-16%; 4, 16-33%; 5, 33-66%; and 6, >66%.

Table 1.1: Length of transects and number of sites sampled on each transect in three Shark Slough tree islands.

Island	Transect	Length of the transect (m)	# of sites sampled in 2001/2002	# of sites sampled in 2011
Black Hammock (BL)	NS	560	72	-
	WE-1	115	24	24
	WE-2	135	28	28
	WE-3	205	41	42
Gumbo Limbo (GL)	NS	1000	107	-
	WE-1	230	47	47
	WE-2	280	57	57
	WE-3	470	48	48
Satinleaf (SL)	NS	500	55	-
	WE-1	135	28	27
	WE-2	110	23	23
	WE-3	115	24	24

2.2.3 Data analysis

Species cover data were summarized using the mid-point of the cover class, and both univariate and multivariate techniques were used to identify the vegetation assemblages along the environmental gradient, and change in vegetation structure and composition over time.

Split Moving-Window Boundary Analysis: We used a split moving-window (SMW) boundary analysis (Ludwig and Cornelius 1987; Cornelius and Reynolds 1991) to describe variation in vegetation composition and to identify boundaries between vegetation assemblages along the surveyed transects in the tree islands. In the SMW method, the position of boundaries, defined as the location of maximum variance in species-abundance based dissimilarities between adjacent groups of sampling plots, was identified through the following steps: i) A window of even-numbered size (the number of plots) was introduced at the beginning of the transect, (ii) The window was then divided into two half-windows, iii) The cover value of each species was averaged over the plots within each half window, iv) A species abundance-based Bray-Curtis (B-C) dissimilarity was calculated between each pair of adjacent half-windows, v) The window was then moved one plot further along the transect, repeating steps 2 and 3 until the end of the transect was reached, and vi) finally, dissimilarity profile diagrams were created by plotting dissimilarity against location of the window mid-point along the transect. In the dissimilarity profile diagram, the peaks (sharp or gradual) in dissimilarity were identified as boundaries between adjacent communities. Results of the SMW boundary analysis are scale dependent, and are affected by the choice of window size. Use of a small window size often creates noise, resulting in many peaks that represent small-scale variation in species composition. In contrast, a wide window results in fewer peaks, overshadowing the fine scale variation. First we explored the pattern using windows of different sizes (2, 4, 6, 8, 10 and 12) and from these we selected larger windows (6, 8, 10, and 12) because these resulted in boundaries which appeared to be ecologically meaningful. Multiple window sizes were selected to reduce the scale-dependency of SMW results.

We used a Monte Carlo method to test whether a boundary identified using the SMW method has a significantly higher value than expected under a null hypothesis that no distinct boundary exist between adjacent communities (Cornelius and Reynolds 1991). In the Monte Carlo method, we randomized the position of each site with its species data vector intact, and repeated the calculations of SMW dissimilarities, as outlined above, for each of the selected window sizes. We repeated the randomization 1000 times, and calculated expected mean dissimilarity and standard deviation between each pair of window-halves for a given window width. Then we calculated overall mean dissimilarity and standard deviation for each window width following Cornelius and Reynolds (1991). Since our purpose was to use multiple windows in order to reduce the scale effects, we pooled the dissimilarity value of mid-point from different window sizes. However, as dissimilarities from different window sizes are scale-dependent, we first standardized the observed dissimilarity values by calculating Z-scores for each window width. The Z-score for each mid-point for a given window-width was calculated by subtracting observed dissimilarity value from overall expected mean dissimilarity and dividing by the overall expected standard deviation (Cornelius and Reynolds, 1991). We averaged Z-scores for each site from four window sizes (6, 8, 10 and 12 sites), and plotted them against site positions along each transect. We considered the peaks that consist of one or more contiguous sites with Z-scores equal of greater than 1.65 (the value in one-tailed test: 95% confidence limit) as significant and distinct boundary between adjacent communities (Boughton et al. 2006).

In a separate analysis, species were grouped according to their life-forms (i.e., trees, shrubs, graminoids, forbs, ferns, vines, seedlings). The mean cover of these groups at each sampling point was then used to calculate B-C dissimilarity.

Habitat heterogeneity and s***pecies turnover:*** Species turnover along the transect was represented by the B-C dissimilarity between two adjacent segments of sites in SMW boundary analysis. To examine the relationship between the degree of species turnover and the environmental gradient, habitat heterogeneity was calculated as the mean absolute difference in values for elevation (and its covariates hydroperiod and water depth), and soil depth. To maintain consistency between normalized B-C dissimilarity (Z-score) and habitat heterogeneity, we first calculated absolute mean difference in the values of environmental gradient variables averaged over the sites present in each of four window sizes (6, 8, 10 and 12 sites), and then averaged the values for each mid-point for the four window sizes.

Beta diversity ($\beta = \gamma/\alpha$) was also calculated to represent overall species turnover along the gradient on each transect. To quantify overall habitat heterogeneity on the transect, we calculated coefficient of variation (CV) for elevation, hydroperiod, water depth, and soil depth. We finally used multiple-regression to quantify the relationships between species turnover and variability in elevation, hydrologic parameters, and soil depth within and across transects.

NMS Ordination: Non-metric multidimensional scaling (NMDS) ordination was used to examine the relationship between species composition and environmental variables representing hydrology and soil depth. The hydrologic variables included in the analysis were 7-year annual mean hydroperiod (days) and water depth (cm). The relationship was examined using a vector-fitting procedure incorporated in the computer program DECODA (Minchin 1998*)*. Vector fitting is a form of multiple linear regression that finds the direction along which sample coordinates have maximum correlation with the fitted variable within the ordination space. The significance of the environmental vectors was assessed using a Monte-Carlo procedure permutation test with 10,000 permutations of the species data, as samples in the given ordination space are not independent (Minchin 1998). Analysis of similarity (ANOSIM) was used to examine the differences in vegetation assemblages between two sampling years, 2001 and 2011.

2.3 Results

2.3.1 Vegetation assemblages

Vegetation composition in Shark Slough tree islands follows the topographic gradient, primarily oriented along the long axis (NS transect) parallel to the direction of the water flow, but also along the transects perpendicular to the long axis. The SMW boundary analysis of the 2001-2002 species cover data along NS transects identified 2-3 significant peaks, represented by high normalized B-C dissimilarity (z-scores > 1.65), resulting in 3-4 distinct vegetation assemblages, including the marsh vegetation at the far end of each transect (**Figure 1.3**). The peaks representing higher B-C dissimilarity between adjacent sample segments on transects were identical in both species and life-form abundance data. The number and sharpness (relatively narrow and tall) of significant peaks, however, differed among islands, suggesting that the level of distinction between vegetation assemblages and species turnover along the underlying gradient are not the same in all three islands. For instance, in GL, three significant peaks in normalized B-C dissimilarity resulted in four distinct plant communities, namely hardwood hammocks, bayhead, bayhead swamps, and sawgrass marsh (**Figure 1.3b**). In SL, only SMW boundary analysis based on life form abundance data revealed three significant peaks denoting the same four communities. In BL, however, the boundary separating two types of swamp forests was not distinct in either the compositional or life form analysis. Moreover, the sharpness of peaks separating adjacent vegetation assemblages was more distinct in GL than in BL and SL islands.

Plant communities identified along the NS transects were strongly associated with the hydrology gradient (**Figure 1.4a**). The three forest communities on the islands were: i) hardwood hammocks dominated by *Bursera simaruba, Celtis laevigata, Cocoloba diversifolia, Eugenia* *axillaris, Ficus aurea,* and *Sideroxylon foetidissimum,* ii) bayheads which were more diverse in species composition, comprised of a mixture of trees (*Chrysobalanus icaco, Persia borbonia, Morella cerifera,* and *Magnolia virginiana, Salix caroliniana),* shrubs (*Cephalanthus occidentalis)* and ferns *(Acrostichum danaeifolium, Blechunum serrulatum* and *Thelypteris interrupta*), and iii) bayhead swamp with one or two flood tolerant tree species (*Annona glabra, Salix caroliniana*) and a suite of graminoids and forbs (**Figure 1.4b**). The marsh, dominated by sawgrass (*Cladium mariscus* ssp. *jamaicense*), was present at the end of the transect. In general, tree cover decreased towards the lower end of the bayhead forests and was less than 5% in the adjacent bayhead swamp forests, where low shrubs and forbs were most abundant. Graminoid cover increased towards the tail of the island, where sawgrass constituted >80% of the total plant cover. Similar to tree cover, canopy heights in all three tree islands exhibited a strong positive association ($r = 54$, $p < 0.001$) with surface elevation. Hardwood hammocks that occupied the head of the island had the tallest canopies, followed by bayhead forest, and finally bayhead swamp forest (**Figure 1.3**).

The vegetation assemblages identified along the NS transects were also distinguishable on the WE transects, established in three forest zones on each island. However, the SMW analysis revealed that the boundaries between identifiable vegetation assemblages were not always distinct. The peaks representing the transition zone between adjacent communities were more distinct on hammock and bayhead transects than on bayhead swamp transects (i.e., marsh and bayhead swamp are more similar than other adjacent pairs), and more distinct in BL and GL than SL (**Figure 1.5**). For instance, on the hammock transects, the peaks separating hardwood hammock and bayhead forests were generally significant. However, unlike on the NS transect, where three forests zones were identifiable, the bayhead forests on both hammock and bayhead transects transitioned directly into the marsh. On these transects, bayhead swamp forests were either absent or, if present, occupied a very narrow zone that was indistinguishable in the selected window sizes in the SMW boundary analysis. A relatively narrow or absent bayhead swamp forest along the gradient suggests a sharp drop in tree island elevation in the direction perpendicular to the axis of the tree island.

2.3.2 Environmental heterogeneity and species turnover

The environmental underpinnings of the within- and among-island variability in composition and structure illustrated in **Figures 1.3 and 1.5** were sought through regression analysis with metrics of habitat heterogeneity. Calculated as the mean absolute differences in elevation, or its covariates hydroperiod and water depth, habitat heterogeneity was positively correlated with B-C dissimilarity along both NS and WE transects (**Figure 1.6; Table 1.2**). On the NS transects, many of the significant peaks (z-score > 1.65) that represented relatively high species turnover co-occurred with absolute differences in elevation of 48 cm or more, corresponding to a difference in mean annual hydroperiod of ≥ 185 days. Along the WE transects, however, such values were much higher in the transect through the tree island head, where the sharp decreases in elevation occur. In contrast, in the bayhead and bayhead swamp zones, high species turnover could occur in association with just 15-20 cm difference in elevation, i.e. a difference in hydroperiod of <100 days (**Appendix A.1**).

Considering the transects as a whole, β-diversity differed significantly (One-way ANOVA: $F_{2,6}$ = 5.7, p = 0.03) among the three habitat zones (hardwood hammock, bayhead and bayhead swamp), and was higher on the hardwood hammock transects than on bayhead swamp transects (**Figure 1.7**). β-diversity on bayhead transects was not significantly different from that on either hardwood hammock or bayhead swamp transects. Species turnover (β) in both years 2001 and 2011, was positively correlated (r = 0.83 and r = 0.84, respectively) with habitat heterogeneity, represented by CV of elevation (**Figure1.8**). However, the relationship between species turnover and soil depth was not significant and thus, not presented here. Across all transects, β diversity was significantly (paired t-test: t = 7.0, $p < 0.001$) higher in 2011 than in 2001, suggesting greater microhabitat heterogeneity. The mean (± SE) β values were 6.18 (± 0.49) and 7.56 (± 0.56) in 2001 and 2011, respectively.

Table 1.2: Pearson Correlation coefficient (r) and p-values for the relationship between mean normalized Bray-Curtis dissimilarity (Z-Score) and difference in (a) hydroperiod, and (b) water depth on nine transects, three each in Black Hammock, Gumbo Limbo and Satinleaf tree islands. HH = Hardwood Hammock, BH = Bayhead, BHS = Bayhead swamp.

			2001				2011			
Tree Island	Transect	n	Hydroperiod		Water depth		Hydroperiod		Water depth	
			r	p-value	r	p-value	r	p-value	r	p-value
Black Hammock	HH (WE-1)	19	0.68	0.001	0.47	0.040	0.60	0.007	0.16	ns
	BH (WE-2)	23	0.79	<0.001	0.81	<0.001	0.82	<0.001	0.80	<0.001
	BHS (WE-3)	37	0.79	<0.001	0.76	<0.001	0.57	<0.001	0.50	0.002
Gumbo Limbo	HH (WE-1)	42	0.47	0.002	0.37	0.014	0.51	<0.001	0.53	<0.001
	BH (WE-2)	52	0.27	0.050	0.43	0.001	0.23	ns	0.10	ns
	BHS (WE-3)	43	0.13	ns	0.18	ns	0.55	<0.001	0.60	<0.001
Satinleaf	HH (WE-1)	22	0.61	0.002	0.47	0.023	0.67	<0.001	0.55	0.009
	BH (WE-2)	18	0.76	<0.001	0.73	<0.001	0.81	<0.001	0.74	<0.001
	BHS (WE-3)	19	0.10	ns	0.13	ns	0.36	ns	0.35	ns

2.3.3 Vegetation change (2001-2011)

Over the period of a decade (2001-2011), the degree of change in plant community composition varied within and among Shark Slough tree islands. Much of the change was either near the boundary between forest and marsh communities along the hardwood hammock transect, or within the bayhead and bayhead swamp forests on other transects. Analysis of similarity (ANOSIM) reveals that, in general, vegetation on hardwood hammock transect on all three islands was not significantly different between 2001 and 2011 (**Table 1.3**). Moreover, the change in overall vegetation composition was higher in bayhead swamp forest than in bayheads, and in GL and SL than in BL. The effect of hydrology on vegetation composition also varied among community types as well as among islands (**Figure 1.9**). While bayhead vegetation showed a drying trend in all three islands, changes in vegetation composition in bayhead swamps did not show any relationship to hydrology, suggesting that factors other than inter-annual hydrologic variation were also responsible for change in swamp forest composition. An obvious change was in the bayhead swamp of GL where two types of bayhead swamp forest became more distinct in 2011 than they had been in 2001. The mean dissimilarity between these two assemblages was 70.6%, and the characteristic species in the eastern portion of bayhead swamp forest were sawgrass (*Cladium marsicus* ssp. *jamaicense*), willows (*Salix caroliniana*) and cattail (*Typha domingensis*), whereas the assemblage covering the western one-third of bayhead swamp forest was primarily dominated by *Cephalanthus occidentalis* (mean cover 46%).

Table 1.3: Global R and *p*-values from analysis of similarity (ANOSIM) testing for differences in vegetation composition between two sampling years, 2001-2002 and 2011.

Tree island	Transects					
	Hardwood Hammock		Bayhead		Bayhead swamp	
	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**

In general, even after ten years, boundaries between two forest types or between a forest and marsh in the head region of the islands remained distinct, suggesting that the underlying factors that define the forest zones on elevated ground elevation in these islands were resistant to small-scale annual variation in hydrology. However, the sharpness of peaks separating forest and marsh communities was more distinct in 2011 than in 2001, especially in the transition between marsh and bayhead or bayhead swamp forests (**Figure 1.5**). Despite a general trend in resistance by these communities from expansion and contraction in spatial extent, there was some noticeable change in community composition at the boundaries. A few sites located at the boundaries between marsh and bayhead were marsh/bayhead swamp type in 2001, but had changed to bayhead swamp/bayhead type by 2011 (**Appendix A.2**). Those changes occurred mostly in eastern portions of the GL and SL hardwood hammock transects, suggesting a drying trend in the area. In contrast, sites at the boundary in the western portion of the bayhead and bayhead swamp transects in BL and GL were more characteristic of marsh in 2011 than in 2001, mainly resulting from an increase in sawgrass cover that corresponded with a decrease in woody cover.

The temporal variation in vegetation composition is also summarized by the pattern of change (increase or decrease) in total cover of different life-forms on nine WE transects surveyed in ten years apart (**Figure 1.10**). In contrast to our expectation that tree, shrub and/or woody vine cover would be higher in 2011 than it was ten years earlier, the change in the cover of these life forms were inconsistent. In general, tree cover decreased on all BL and GL transects except the bayhead swamp transect in GL (**Figure 1.10**). However, the decrease in tree cover was statistically significant only in the bayhead transect of BL (paired t-test: t = 2.23, df = 27; p =0.03) (**Figure 1.11**), and in both the hammock (paired t-test: t = 4.85, df = 46; p < 0.001) and bayhead (paired t-test: t = 2.51, df = 56; p =0.015) transects of GL (**Figure 1.12**). On the GL hammock transect, mean tree cover in 2011 (46.2±40.7%) declined by almost half from 2001 (79.2±68.7%), with the decline in cover distributed throughout the transect, encompassing both the hardwood hammock and bayhead forests. In contrast to the trend in BL and GL, tree cover in SL showed an increasing trend, though not statistically significant (**Figure 1.13**). In this island, the increase in tree cover was mostly concentrated in the western half of the transects (**Figure 1.14**), indicating a difference in underlying causes between two sides of the island.

Tree layer vegetation on the Shark Slough islands included both flood intolerant and tolerant species. Hence, change in total tree cover was confounded by the differential response of tree species, which depended on their tolerances to flooding. Between 2001 and 2011, while the mean (± S.E.) cover of pond apple (*Annona glabra*), a flood tolerant species, decreased significantly from 11.1 (±1.23) to 6.53 (±0.78) percent (paired t-test: t = 4.3, df = 318, p<0.001), mean cover of cocoplum (*Chrysobalanus icaco*), a moderately flood tolerant species increased from 9.1% to 12.3%. Among other woody species, shrub cover increased significantly (paired t-test, p < 0.05) in the bayhead swamp transect of BL (**Figure 1.11**). Mean shrub cover also increased in GL bayhead and GL and BL bayhead swamp transects (**Figure 1.12**), though these increases were not statistically significant. Shrub cover significantly decreased in the GL hammock and SL bayhead swamp transect (**Figure 1.13**). Most of the increase in shrub cover in bayhead swamps of BL and GL was due to an increase in the cover of *Cephalanthus occidentalis,* whose mean (± S.E.) cover increased from 0.8 (± 0.3) in 2001 to 14.7% in 2011. Moreover, cover of woody vines significantly increased on hammock transects in BL and GL, and bayhead transect in GL.

By far the most striking change in vegetation composition in all study islands was an increase in the cover of graminoids (**Figure 1.10**), particularly sawgrass (*Cladium mariscus* ssp. *jamaicense*) and spikerush (*Eleocharis cellulosa*) (**Appendix A.3**). The increase in graminoids was statistically significant (paired-t test; p-value < 0.005) in all transects except the SL hardwood hammock (**Figures 1.11-1.13**). Mean graminoid cover was 1.5 to 8.0 times higher in 2011 than in 2001. Sawgrass cover increased throughout the three bayhead swamp transects. However, in the forested portion of hardwood hammock and bayhead transects, the increase in sawgrass cover was limited to the with bayhead swamp and marsh zones (**Figure 1.15**), suggesting that sawgrass was responding to a change in marsh water level in recent years in comparison to the late1990s.

Besides the graminoids, several other herbaceous species with overall mean cover ≥1% either increased or decreased over the course of the study (**Appendix A.3**). Among them, the change in cover of cattail (*Typha domigensis*) was of special interest. In ten years, cattail increased in cover on the three transects where it was present in 2001, i.e., bayhead in BL and bayhead swamps in BL and SL. Furthermore, it was recorded for the first time on three other transects (bayhead swamp in BL and GL, and hammock transect in SL) in 2011 (**Figure 1.16**). The increase in cattail was most evident in the bayhead swamp and marsh of GL, where its cover reached 50% at some sites.

2.4 Discussion

Shark Slough tree islands exhibit a spatial pattern in plant species composition that is related to variation in topography, hydrology, and soil characteristics. Vegetation assemblages that are distinct in both species composition and functional representation (life forms) are found along the hydrologic gradient in these islands. These assemblages are dynamic, having changed over time in response to interacting forces, including hydrologic conditions and disturbances (hurricanes and fire). Despite these internal changes, we found minimal alteration in the position of the boundary between adjacent assemblages over the period between 2001 and 2011.

Vegetation characteristics of the three Shark Slough tree islands are in accord with patterns described for ‘fixed tree islands’ present within ridge-slough landscape throughout central and southern Everglades (Loveless, 1959; and others). Four distinct vegetation assemblages - hardwood hammock, bayhead, and bayhead swamp forests, and tall sawgrass marsh were expressed most clearly along the primary axis parallel to the direction of water flow, but also were evident along secondary axes in the direction perpendicular to flow. On these secondary axes, their relative areal extent varied in a consistent way depending on the location of transect along the length of the island (**Figure 1.5**). Ultimately, vegetation zonation within tree islands is a result of water flow patterns and associated ecological processes, including biotic feedbacks that alter the local topography. In the Everglades, proposed models for the development of ridge-slough-tree island landscape have emphasized the role of water flow and the distribution of nutrients (Wetzel et al 2005; Ross et al. 2006; Bazante et al. 2006; Givnish et al. 2008, Cheng et al. 2011; Lago et al. 2011). According to these models, evapotranspiration-induced convergent flow of water is one mechanism that causes the accumulation of nutrients (mainly phosphorus) and the formation of a tree island head on topographically high ground. However, it is the strong regional water flow gradient that causes the nutrient to spread downstream in the direction of flow and to form longitudinally arranged vegetation zones (Ross et al. 2006; Givnish et al. 2008; Cheng et al. 2011). A similar process operating in directions perpendicular to flow appears to create nutrient gradients between P-rich forests on relatively high ground to P-limited marshes along the flanks of the tree islands. These gradients are concentrated within a relatively short distance, resulting in the narrow vegetation zones. In the tree islands we studied, relatively narrow vegetation zones were present near the ends of the transects, especially in the head and bayhead regions.

Within a tree island, boundaries between adjoining plant communities were not always distinct. While the transition between hammock and bayhead was well-defined in the study tree islands, the transition from bayhead to bayhead swamp to tall sawgrass marsh was subtle, and boundaries were sometimes difficult to distinguish. While several flood tolerant tree species that occur in bayheads are also present in bayhead swamps, e.g., *Morella cerifera, Magnolia virginiana*, and *Salix caroliniana*, their growth is stunted in the later. Similarly, sawgrass, whose hydrologic range is very wide, grows together with flood-tolerant tree species in bayhead swamps. Thus, a boundary between bayhead swamp with high cover of sawgrass in the understory and adjacent sawgrass marsh may not always be distinct, and changes over time depend upon the change in cover of sawgrass and other associated species. Rapid changes in sawgrass cover were largely responsible for a change in boundary characteristics along the bayhead swamp transect in GL and SL. On this transect in GL, none of the peaks were significant in 2001, whereas in 2011 three significant peaks were identified (**Figure 1.5**).

The physical factors that influence the position of boundaries among adjacent communities are likely to be the same that affect the distributions of individual species. A related concept, the spatial heterogeneity hypothesis, suggests that greater habitat (resource) heterogeneity allows the coexistence of more species (MacArthur and MacArthur 1961; Davidowitz and Rosenzweig 1998; Kumar et al. 2006). Thus, along an environment gradient, a positive relationship between habitat heterogeneity and degree of species turnover is expected. In the Shark Slough tree islands, we observed a positive relationship between normalized B-C dissimilarity and habitat heterogeneity in all transects, suggesting that processes that enhance habitat heterogeneity along the gradient will result in sharp inter-community boundaries, which represent zones of high species turnover. Moreover, β-diversity was higher in 2011 than in 2001, suggesting that habitat resource heterogeneity in the tree islands was higher in recent years than a decade earlier. Generally, in periodically flooded ecosystems, such as floodplains, continuous flooding and high water level are known to form homogeneous habitat, whereas during the low water level habitat heterogeneity increases (Thomaz et al. 2007). In contrast, a fluctuating water level with periodic dry-down is likely to increase habitat heterogeneity, especially in topographically heterogeneous areas. In the Shark Slough also, annual mean precipitation and water level varied greatly in last ten years than a decade earlier. Thus the increased β-diversity in recent years could be due to both relatively dry conditions and inter-annual variability in water depth.

Tree island vegetation responds to management- and naturally-driven forces e.g., hydrology, disturbance (fire and storms), or internal ecological feedbacks. The absence of a significant increase in woody vegetation cover following a drier-than-normal decade was unexpected. In fact, in the hardwood hammocks of BL and GL islands and in the bayhead forest of GL, tree cover significantly decreased. This finding may result from several interacting phenomena, including the disturbances. In 2005, the study islands were hit by two major hurricanes, Hurricane Katrina and Hurricane Wilma. The latter brought relatively high wind speeds (Knabb et al. 2006; Pasch et al. 2006) that caused significant tree damage on the study islands (Ruiz et al. 2011). For three years after the hurricane, cumulative tree mortality values were 17.5% and 6.2% in the hardwood hammock forests of GL and BL, respectively. The high tree mortality on these islands in post-hurricane years could also be the result of interaction of multiple disturbances, which are capable of impacting the resilience of forests, resulting in surprise outcomes (Buna and Wessman 2011). The drought that prevailed for 1-3 years (2006-2008) after Hurricane Wilma might have accentuated tree mortality on these islands. In drought years, particularly during the dry season when hammock plants use regional ground water (Saha et al. 2010), water level fell more than 70 cm below ground, which might have reduced access to ground water, causing high mortality in hurricane-stressed trees.

In a Shark Slough tree island, herbaceous cover, including graminoids, generally increases along the hydrologic gradient from upland hammocks to marsh. With this reference, an increase in sawgrass cover over a decade would be indicative of an increase in water depth. In this study, however, the increase in sawgrass cover in the bayhead swamps and at the fringes of hammocks and bayheads, evident in the 2011 survey, occurred despite 7-year mean annual water level being 13 cm lower than the equivalent period preceding the 2001 survey, and a shorter hydroperiod by 56 days. High water level in the mid- to late-1990s might have caused increased velocity around the tree island, and thus a reduction in sawgrass cover. In the early 2000s, however, low water level must have favored an increase in sawgrass. In general, the emergent vegetation, including spikerush and sawgrass, has high filtration efficiencies, i. e. they are capable of capturing more floc than sparsely vegetated aquatic communities (Huang et al. 2008). With the recession of the prolonged flooding of the 1990s, followed by reduced flow that accompanied low water stages of the early 2000s, once sawgrass and spikerush started increasing in cover in the area, they may have further slowed down the flow velocities resulting in more floc deposition. Flow velocity is generally negatively correlated with vegetation bio-volume, which is relatively high on the sawgrass-dominated ridges (Harvey et al. 2009). Moreover, once the flocs are transported onto densely vegetated ridges, they are likely to be settled on it (Larsen et al. 2009), resulting in further reduction in water depth and an increase in sawgrass cover. Hence, once the process started, seasonally high water levels might not have been high enough to break the positive feedback, but might be high enough to prevent woody species from establishing in the marshes. This sequence could explain the minimal shift in boundaries observed over the period of ten years.

Olmsted and Armentano (1997) postulated that a prolonged high water level during the mid-1990s followed by brief dry period was responsible for “sawgrass die-off”, a pronounced, spatially extensive, and episodic decadence observed in mono-dominant stands of sawgrass in some areas of Shark Slough. In our 2001 sample, opening in the herb layer due to sawgrass die-off was most evident in bayhead swamp transect of GL (**Figure 17**), where the mean cover of sawgrass was only 5.5%, one-fourth of the value observed in the equivalent transect in BL. In the Everglades, researchers have often reported sawgrass decadence, for which various reasons including, the reduced fire frequency, nutritional imbalance, fungal infection, a boring larva (*Scirpophaga perstrialis*), and hurricane caused periphyton deposition, have been suggested (Hofstetter and Parson 1975; Wade et al. 1980; Alexander and Cook 1984; Olmsted and Armentano 1997; Clark et al. 2009). In the present study, we have not thoroughly investigated the cause of sawgrass die-off. However, it could have occurred due to a mix of reasons, including extreme flooding in the mid-1990s.

In the area of sawgrass die-off, the succession of plants within an affected area may start within months (Alexander 1967), but years may pass before full vegetation recovery is achieved. In parts of Shark Slough where open water sites due to sawgrass die-off prevailed in 2000-2001, sawgrass was still very sparse in 2007 (Ross et al. 2001; Cline et al. 2007). Wade et al. (1980) had reported that extensive area of sawgrass decadence observed in early 1970s were not different from a healthy sawgrass stand in 1980. These studies suggest that vegetation recovery in the area of sawgrass die-off could occur within 7-10 years. In the present study also, areas within the transects that were affected by sawgrass die-off were fully vegetated with dense tall sawgrass ten years later. While these areas of sawgrass die-off seem to have recovered to something approaching their previous conditions, periodic sawgrass die-off events within the ridge-slough landscape have important implications. In general, sawgrass die-off on ridges negatively impact long-term viability of the ridge-slough mosaic through shrinkage of the elevation difference between these two important features (Clark et al. 2009). Likewise, sawgrass die-off near tree islands may have effects on island development through various mechanisms. For instance, in sawgrass die-off areas, water flow velocity is usually higher than in adjacent sawgrass-vegetated area (Bazante et al. 2006). Slowdown of soil accretion process associated with greater floc transport mediated through increased flow and reduced biomass production might also exacerbate the elevation difference between the island and adjacent marsh. Such an increase in the elevation difference then could accentuate positive feedback for differential transpiration and P-accumulation, a mechanism suggested by researchers for the development and persistence of tree islands (D'Odorico et al. 2011). The resulting elevation difference between island and adjacent marsh then would sharpen the boundary between these components of the landscape. This may be the reason the boundaries between forest and marsh in GL were sharper in 2011 than in 2001. Nonetheless, in coming years the recent increases in sawgrass may disrupt such feedback, resulting in more diffuse boundaries.

Fire is also known to sharpen the edges of both ridges and tree islands (Givnish et al. 2008; Wetzel et al. 2008). In the last ten years, two fires, the Airboat fire of 2006 and the Mustang Corner fire of 2008 burned the marshes close to Black hammock. These fire must have not only killed woody plants, if any were growing in marshes in reduced flow conditions, but also must have consumed the peat layer, thus causing a greater difference in elevation and sharpening the boundary between forest and marsh.

In the Everglades, expansion of cattail in existing sawgrass marsh is widespread, especially in the northern and central Everglades. Cattail usually spreads into areas of prolonged hydroperiod, if nutrient conditions, especially phosphorus levels, are relatively high (Newman et al. 1998; Hagerthey et al. 2008). They largely spread into adjacent sawgrass areas by underground rhizomes, but usually do not penetrate dense vegetation until something like a peat fire or a senescent patch of sawgrass creates an opening. In this study, increase in cattail in GL was possibly associated with sawgrass die-off, which was evident as early as in late 1990s in the area adjacent to the bayhead swamp zone of the island (**Figure 1.17**).

A shift in boundary among plant communities occurs when a change in system's ecological processes cause reduction of its resilience, resulting in regime shifts (Folke et al. 2004; Hagerthey et al. 2008). In the study islands, change in hydrology over a decade probably has not affected each community enough to exceed its "tipping point", hence a minimal shift in boundary was observed. In a recent study, macrofossil analysis of a tree island in WCA-3A has shown that the island habitat expanded in response to the dry conditions in late 1980s, followed by a reduction during wet conditions in the 1990s (Brock et al. 2012). This implies that extreme hydrologic events are more important than average annual hydrologic conditions in shaping tree island vegetation. Moreover, in plant communities arranged along an ecological gradient, high species turnover usually occurs at the edge of discontinuities. Since there is high variability in composition within the transition zone, the turnover appears to be adaptive. Hence, communities that have low turnover at the boundary, particularly when the boundary is diffused, may have little adaptive capacity and relatively low resilience (Allen et al. 2005). In the study islands also, there was lower degree of species turnover at the boundaries between bayhead swamp, and thus the boundary between them are prone to shift, especially when they are impacted by the extreme events of flooding or droughts.

In summary, in the Shark Slough tree islands, spatially differentiated vegetation occurring along the hydrologic gradient consists of vegetation assemblages of contrasting species composition and functional representation (life forms). Over the last decade, while the life form composition of some of these assemblages changed in response to interacting forces, including hydrology and disturbances (fire and storms), only on a few transects, such changes in the mixture of growth forms exactly paralleled the changes in the boundary between adjacent assemblages. Thus, vegetation changes does not always involve a simple shift in the location of fixed species assemblages, but rather the emergence of new species and structural combinations. In general, shifts in boundaries among plant communities are presumed to initiate reductions in ecosystem resilience, resulting in regime shifts. In these three islands, however, the effects of annual variation in hydrology over the previous decade probably did not surpass the ecosystem's resilience, hence a minimal shift in boundary between vegetation assemblages was observed on most transects.

3. Understory vegetation composition and dynamics in tropical hardwood hammock tree islands in the southern Everglades

3.1 Introduction

Tree islands, a characteristic feature of the Everglades, often include one or more types of plant communities, namely tropical hardwood hammock, bayhead and bayhead swamp forests, arranged along a gradient of increasing wetness (Olmsted and Loope 1984; Gunderson 1994; Armentano et al. 2002; Sah 2004). Hardwood hammocks, the most elevated portions of tree islands, are rarely flooded, broad-leaved forests comprised of flood-intolerant tropical and temperate tree species. Vegetation capable of occupying these sites pass through an environmental filter posed by several interacting factors, including the underlying bedrock topography, hydrologic conditions, soil nutrients, and various disturbances, such as fire and windstorms (Gunderson 1994; Armentano et al. 2002; Wetzel et al. 2002, 2008; Ross and Sah 2011; Ruiz et al. 2011). Hydrologic conditions of the region, however, have been greatly modified by implementation of a complex water management system (Light and Dineen 1994), resulting in altered water flows, and changes in frequency and duration of flooding and drying events. These management-induced changes in hydrologic regimes, along with disturbances like fire and windstorms, act as major stressors that impact hardwood hammock structure and composition. However, the nature of effects of hydrologic modifications on the hammock vegetation depends on both the severity and duration of extreme environmental events. For instance, longer hydroperiod due to prolonged flooding first causes physiological changes in flood-intolerant trees before they exhibit any visible changes or altering tree layer composition (Kozlowski 2002). In contrast, a disturbance that physically impacts tree canopy structure, caused by either breakage of branches or tree mortality, results in a modified understory light environment, and in turn affects the ground layer vegetation and tree seedling density.

In forested communities, where vegetation is arranged in different height strata, understory vegetation accounts for a substantial part of plant diversity (Gilliam 2007), depending on the availability of resources such as soil water, nutrients, and light (Small and McCarthy 2005). Spatial and temporal alterations in these resources, caused by natural events or anthropogenic disturbances, affect the diversity and cover of understory plant species, which may impact tree regeneration and forest dynamics (Royo and Carson 2006).

In tree island hammocks, understory vegetation has particular importance due to its influence on continuing overstory composition and growth. This is especially so for hammocks potentially affected by the hydrologic changes associated with restoration efforts under the Comprehensive Everglades Restoration Plan (CERP), authorized by the Water Resources Development Act (WRDA) 2000. Within CERP, changes in water management associated with hydrologic restoration are likely to impact local and landscape-level tree island stressors such as hydrology, invasive exotics, windstorms, and fire. While broad-scale alterations in the impact of these stressors will influence the spatial distribution pattern of tree islands within the landscape, the local and landscape scale hydrologic alterations are likely to affect the internal water economy of islands, which in turn will influence tree island plant communities, including understory vegetation composition.

A general assumption in forest ecosystem management practices is that dominant species have the largest impact on ecosystem function, and therefore the study of tree layer associations will lead to an understanding of ecosystem structure and function. However, several researchers (McCune and Antos 1981; Rogers 1981; Sagers and Lyon 1997) have questioned whether all vegetation layers respond similarly to the same environmental gradients. In this section, our objectives were to describe the understory vegetation composition, and to examine whether plant community composition in both the overstory and understory layers in southern Everglades tree islands respond similarly to the major environmental gradients.

3.2 Methods

3.2.1 Study area

The study area included a long-term monitoring network of 16 hardwood hammocks established in Everglades National Park (**Figure 2.1; Appendix A.4**). Within the Park, the hammocks vary regionally in shape and size, soil characteristics, and vegetation structure and composition (Armentano et al. 2002; Ruiz et al. 2011). Hammocks in the Park's ridge-slough landscape in Shark Slough (SS) region are small, usually located on the most elevated and upstream locations within large tear-shaped tree islands that are oriented in the direction of water flow (north-northeast to south-southwest). In contrast, hammocks in the marl prairie (short hydroperiod wet prairie, WP) landscape flanking the ridge-slough vary in shape and size depending on the underlying bedrock sculpture. The hammocks in these two landscapes also have distinct soul characteristics (Ross and Sah 2011). The mineral soils in the ridge-slough hammocks are not deep (usually < 1 m), but so rich in phosphorous that they are considered hotspots embedded in the phosphorus poor oligotrophic landscape. The prairie hammocks, however, are characterized by shallower organic, relatively low-P soils. The forest flora in both hammock types are comprised mostly of tree species of tropical, West Indian origin, though the prairie hammocks are more species-rich and include several trees whose U.S. distributions are otherwise restricted to the Florida Keys (Ross et al. 2010).

3.2.2 Field sampling

Vegetation structure and compositional parameters in both canopy and ground layers were measured in permanent plots, ranging in size from 225 to 625 m^2. Three plots were established in 2000-2001, and the others were established and first sampled in 2005-2006. Each plot was gridded into 5 x 5 m cells. Vegetation parameters included size structure of individual trees (>5 cm dbh), density of tree saplings (height >1.4 m, dbh 1-5 cm), cover of species in shrub (height >1 m and dbh <1 cm) and herb strata (woody and non-woody ≤ 1m height), and tree seedling density. DBH (diameter at the breast height) and height of all tagged trees were measured. Saplings present in each 5x5 sub-plot were distinguished in two size classes (1-3 and 3-5 cm). In the herb layer, plants present within a 1-m radius plot centered at the middle of each cell, were identified to species, and cover of each species was estimated using a modified *Braun-Blanquet* scale (1 = 0-1%, 2 = 1 - 4%; 3 = 4-16%; 4 = 16-33%; 5 = 33 - 66%; and 6 = > 66%).

We characterized the soils in the islands by determining soil depth and soil nutrient parameters. Soil depth was determined at 9-61 regularly spaced points within the plot by probing to bedrock with metal rod. In each island, surface soil samples (top 10 cm) were also collected and analyzed in the laboratory. Measured soil parameters were pH, nitrogen (TN), phosphorus (TP), and organic carbon (TOC). Soil analysis methods are described in detail in Ross and Sah (2011).

We used mean annual distance to water table (Dist_WT) to characterize the hydrologic regime of the plots. The distance to water table for each hammock plot was calculated using ground elevation of the plots and surface water level adjacent to each island over the period from Jan 1, 2000 to Dec, 31 2010. Ground elevation was determined by either topographic survey from the nearest bench mark or to a datum represented by the nearest water surface, whose elevation could be estimated for the day of the survey through water surface elevation from the Everglades Depth Estimation Network (EDEN; *http://sofia.usgs.gov/eden/*) model (Palaseanu and Pearlstine 2008). The position of the water surface at each location over ten water years (1 May 2000 to 30 April 2010) was also derived from EDEN, and mean distance to water table (Dist_WT) over the period was calculated based on the difference between mean hammock plot and the EDEN-estimated water table elevation for each island. The topographic surveys were also used to calculate island height (TI_Ht), that is, the difference in elevation between the surface of the tree island and the surrounding marsh, as estimated by USGS surveys (Jones and Price 2007).

Canopy openness, the percentage of the canopy gaps for a specified sky region, and leaf area index (LAI), the ratio of the total one-sided leaf area to the projected ground area (Parker 1995), were used as a surrogate measures of understory light availability. Canopy openness was measured in the field using a spherical densiometer (Lemmon 1956) at the center of each cell. A hemispherical photograph was also taken with a digital camera (Nikon Coolpix 995; Nikon, Japan) and a hemispherical lens (Nikon Fisheye Converter FC-E8 0.21x) placed at 1 m height above the ground at the center of the plot. The photos were taken when the sun was not directly above the canopy to minimize sun flecks, and the north was always aligned with the bottom of the photo. The photo number identifying the plot was recorded for future reference. Canopy openness and the 4-ring leaf area index (LAI) were determined from hemispherical photographs using the software Gap Light Analyzer (GLA), version 2.0 (Frazer et al. 1999).

3.2.3 Data Analysis

Herb and shrub layer species cover data were summarized using the mid-point of the cover class. We calculated frequency and mean percent cover of each species for each island. Then, importance values (IV) for each species were calculated from the relative frequency and cover values by using the equation: IV = (Relative frequency + Relative cover)/2. To characterize the abundance of plant species in tree and sapling layers, we calculated density and basal area, which then were used to calculated importance values (IV).

Multivariate techniques, including non-metric multidimensional scaling (NMDS) ordination and analysis of similarity (ANOSIM), were used to examine the effects of environmental factors on understory vegetation, and the differences in composition between landscape types (Ridge-Slough and Prairies). The relationships between herb layer species composition and environmental variables, including hydrology, soil characteristics, and canopy structure were examined using a vector-fitting procedure incorporated in the computer program DECODA (Minchin 1998). Vector fitting is a form of multiple linear regression that finds the direction along which sample coordinates have maximum correlation with the values of fitted variable within the ordination space. The significance of the environmental vectors was assessed using a Monte-Carlo procedure permutation test with 10,000 permutations of the species data, as samples in the given ordination space are not independent (Minchin 1998). Additionally, we used Similarity Percentage (SIMPER) analysis in the Primer Software (Clarke and Warwick 2001) to ascertain the species that contributed most to within group similarity among the sites in the prairie and ridge-slough landscape. The differentiation of understory species along the environmental vectors was assessed by calculating species centroids as weighted averages of sample scores, and plotted them in the NMDS ordination space with sample points and fitted environmental vectors.

Relationship between overstory composition and understory composition was also examined using Procrustes analysis (least squares orthogonal mapping) conducted in DECODA (Minchin 1998). The analysis was used to quantify how well the NMDS ordination solutions based on species data from different tree/sapling and herb/shrub strata fit with each other. In this analysis, a test statistic, usually scaled root mean square (RMS) residual, is estimated to examine the similarity in site scores from two ordination configurations with same number of dimensions when a test ordination is rotated to fit within a target ordination space (Minchin 1987; Peres-Neto and Jackson 2001). In this study, the test and target ordinations were based on understory and overstory species data, respectively. The RMS residual is the square root of the mean squared distances between corresponding points in the two ordinations being compared. In the analysis, the RMS residual was calculated by selecting the option 'normalization' which adjusts the scaling such that the average distance between points and the centroid of the target ordination is 1.0.

Procrustes analysis was also used to examine temporal changes in understory composition. However, this analysis was limited to understory species data from a subset of eight islands that were sampled till 2010. The subset included five islands (Black Hammock, Chekika Island, Grossman Hammock, Gumbo Limbo, and Satinleaf) that had pre-Hurricane Wilma as well as 2-5 years of post-hurricane species abundance data.

3.3 Results

In the understory layer of the tree island hammocks in the Everglades National Park, a total of 144 plant species were recorded, including 7 epiphytes, 13 ferns, 11 graminoid, 29 forb, 15 shrub, 28 vines, 30 tree species. Based on species' importance value (IV), the most abundant, species was *Eugenia axillaris*. However, many species had restricted distribution, as 59 species were present in only one hammock.

Variation in understory species composition in the hammocks was well summarized by a species' importance value-based 3-d NMDS ordination (stress = 0.16) which revealed that WP and SS hammocks were different in understory composition (**Figure 2.2a, b**). However, within each group, there was a wide variation in species composition, as revealed by the wide spread of sites of both categories along the 2nd and 3rd axes in the ordination. There was a significant difference (ANOSIM; R = 0.692, p = 0.001) in understory composition between two groups of hammocks, and the mean Bray-Curtis dissimilarity between the groups was 81.4%. In general, WP tree islands were richer in understory species than SS islands. Mean (± SD) number of species was 6.7 (±2.9) and 4.5 (±1.9) species per 1 m^2 plot in WP and SS islands, respectively. Results of the SIMPER analysis revealed that white stopper (*Eugenia axillaris*) was commonly dominant in both types of islands (**Table 2.1**). However, its annual mean abundance (IV) was more than two times higher in SS (IV = 25.74 ± 14.0) than WP (11.96 ± 9.1) islands. Specifically, the understory vegetation in SS hammocks were characterized by the dominance of tree seedlings (*Eugenia axillaris*, *Celtis lavevigata, Sideroxylon foetidissimum Myrsine floridana, Bursera simaruba, Chrysobalanus icaco*), shrub (*Rivina humilis*), vines (*Parthenocissus quinquefolia*), and ferns (*Thelypteris kunthii*, *Nephrolepis exaltata*). In the WP hammocks, the characteristic species in the understory vegetation were *Eugenia axillaris, Psychotria nervosa, Ardisia escallonoides, Chrysobalanus icaco, Coccoloba diversifolia, Toxicodendron radicans, Nectandra coriacea, Metopium toxiferum, Sideroxylon salicifolium, Morella cerifera,* among others (**Table 2.1**).

The environmental vectors representing island elevation above marsh (TI_Ht), distance to water table (Dist_WT), soil total nitrogen (TN), total organic carbon (TOC), and total phosphorus (TP) were significantly correlated with ordination configuration (**Table 2.2**), suggesting that understory vegetation on the study islands is arranged along the gradients defined by these environmental variables. However, soil depth was marginally non-significant. The vector fitting results revealed that the difference in understory vegetation composition between SS and WP islands was mainly associated with the gradient represented by the island elevation above marsh, soil depth and soil nitrogen, organic carbon and phosphorus content (**Figure 2.2a**). The SS islands had deeper soil and higher phosphorus content than the WP islands. Likewise, soil nitrogen and organic carbon content were relatively high in WP islands. Within each group, however, variation in understory vegetation composition was primarily influenced by tree cover, which influences understory light condition. All three variables, total tree and sapling basal area (S&T_BA), canopy openness (CanOpen), and leaf area index (LAI), that characterized the tree canopy and understory light, were strongly correlated with ordination configuration (**Table 2.2**). The sites in both SS and WP regions were widely spread along the gradient associated with canopy characteristics (**Figure 2.2b**).

Understory species were well differentiated along the environmental gradients in the ordination space (**Figure 2.3**). Several species (e.g. *Psychotria nervosa (*PSYNER*), Ardisia escallonoides* (ARDSEC), *Coccoloba diversifolia* (COCDIV), *Toxicodendron radicans* (TOXRAD), *Nectandra coriacea* (NECCOR), *Metopium toxiferum* (METTOX), *Sideroxylon salicifolium* (SIDSAL), and *Morella cerifera* (MORCER)) that were identified by SIMPER analysis as characteristic of WP islands occupy the left part of the ordination and are found in the area with low soil phosphorus and high nitrogen. Similarly, the characteristic species of SS islands are in the right part of the ordination. Consistent with its much higher abundance (IV) in SS than in WP islands, *Eugenia axillaris,* is also present among the clouds of species that are characteristic of SS islands. Species are also arranged along the light gradient, represented by canopy openness and LAI vectors in the ordination. The species that were abundant in open canopy areas included mostly herbaceous species, e.g. *Andropogon virginicus, Mikania scandens, Aster carolinianus, Sida rhombifolia,* among others. In the herb and shrub vegetation layers, tree and woody vines were present mostly in low to medium light conditions, as represented by increasing LAI vector in the ordination (**Figure 2.3**).

Table 2.1: Results of SIMPER analysis showing the importance species in contributing to the mean similarity between sites within each group of Wet Prairie and Shark Slough tree islands.

Species	Spp. Code	Average Abundance (%)	Contribution to within group similarity (%)
	Wet Prairie tree islands		
Eugenia axillaris	EUGAXI	10.96	17.77
Psychotria nervosa	PSYNER	8.40	11.67
Ardisia escallonoides	ARDESC	5.94	9.38
Chrysobalanus icaco	CHRICA	8.73	7.79
Myrsine floridana	MYRFLO	4.51	7.26
Coccoloba diversifolia	COCDIV	4.16	6.28
Toxicodendron radicans	TOXRAD	3.33	5.78
Nectandra coriacea	NECCOR	6.63	5.25
Smilax bona-nox	SMIBON	2.70	3.37
Nephrolepis exaltata	NEPEXA	2.53	3.36
Thelypteris kunthii	THEKUN	3.05	2.72
Parthenocissus quinquefolia	PARQUI	1.78	2.19
Vitis rotundifolia	VITROT	1.56	1.71
Sideroxylon salicifolium	SIDSAL	1.57	1.70
Blechnum serrulatum	BLESER	2.18	1.67
Metopium toxiferum	METTOX	1.24	1.52
Campyloneurum phyllitidis	CAMPHY	1.30	1.09
	Shark Slough tree islands		
Eugenia axillaris	EUGAXI	25.74	47.13
Celtis laevigata	CELLAE	8.19	12.57
Rivina humilis	RIVHUM	8.83	8.20
Parthenocissus quinquefolia	PARQUI	4.14	5.66
Chrysobalanus icaco	CHRICA	4.27	5.04
Sideroxylon foetidissimum	SIDFOE	4.29	3.43
Nephrolepis exaltata	NEPEXA	3.90	3.24
Myrsine floridana	MYRFLO	3.73	2.17
Bursera simaruba	BURSIM	2.44	1.92
Thelypteris kunthii	THEKUN	3.44	1.83

Table 2.2: Correlation (r) and statistical significance of fitted community (species richness) and environmental vectors with species importance value (IV)-based 3-dimensional ordination configuration.

Variable	r	p
Canopy openness (CanOpen)	0.486	<0.001
Leaf Area Index (LAI)	0.486	<0.002
Tree Basal Area (S&T_BA)	0.582	<0.001
Tree island height (TI_Ht)	0.830	<0.002
Distance to water table (Dist_WT)	0.558	0.044
Soil depth (SoilDep)	0.657	0.051
Soil total nitrogen (TN)	0.694	0.013
Soiol total phosphorus (TP)	0.673	0.045
Soil total organic matter (TOC)	0.766	0.006
Species Richness	0.776	< 0.001

The procrustes analysis, used to examine the relationship between overstory and understory species composition, revealed that the ordinations based on vegetation data from these two strata matched well in identifying and interpreting differences in species composition between SS and WP islands. For instance, though the standardized root-mean squared (RMS) residual value (0.753) was relatively high, only 18.6% of that was attributable to the gradient on which the two types of islands were well separated (Axis 1), primarily represented by TI_Ht and soil characteristics (**Figure 2.3: Table 2.3**). The alignment of sites in two groups along the same gradient in two independent ordinations suggested that vegetation composition in both strata on these islands were strongly influenced by the same environmental factors that differed between the two types of islands. However, most differences in site scores between the two ordinations were attributable to the hydrology and canopy characteristic (understory environmental) gradients. Of the total standardized RMS residual, 49.1% and 32.3% were related to Axis 2 and Axis 3, respectively (**Table 2.3**). These two axes were closely aligned with hydrology (Dist_WT) and canopy characteristic (CanOpen and LAI) vectors (**Figure 2.4**). Moreover, differences in the responses of overstory and understory vegetation to the environmental gradients were not the same in both types of islands. The mean (±SD) standardized RMS residual was significantly (One-way ANOVA; $F_{1,66} = 9.9$, p = 0.002) higher in WP (0.86 ± 3.1) than in SS (0.57 ± 0.37) islands.

Table 2.3: Results of procrustes analysis showing the total scaled root mean square (RMS) and the percentage attributable to the axes derived from 3-d non-metric multidimensional scaling (NMDS) ordination.

Total RMS	Percent of RMS attributable to NMDS axes		
	Axis-1	Axis-2	Axis-3
0.753	18.6	49.1	37.3

During the sampling period (2001-2010), a change in understory vegetation composition was observed on the islands, especially those which were impacted by the hurricanes in 2005. Results of Procrustes analysis, used to examine before and after hurricane species composition on the five islands (Black Hammock, Gumbo Limbo, Satinleaf, Chekika Island, and Grossman

Hammock) which had pre-hurricane data, revealed that the difference in understory vegetation composition between pre-hurricane and the 2nd post-hurricane year was relatively high (**Table 2.4**). In subsequent years, however, the change in composition did not show a definite pattern. While the understory composition in the 3rd year after the hurricane was more similar to that in pre-hurricane, understory vegetation took a different trajectory in the following two years (4th and 5th year after hurricane), as revealed by relatively high mean standardized RMS residuals between pre-hurricane and those two years (**Table 2.4**).

Table 2.4: Results of procrustes analysis showing the total scaled root mean square (RMS) residuals between pair of NMDS ordination configurations, each representing the understory vegetation composition in pre- and post-hurricane years.

Year	Sampling years				
	Pre-Hurricane	2006	2007	2008	2009
2006	0.488				
2007	0.588	0.610			
2008	0.364	0.529	0.505		
2009	0.593	0.661	0.659	0.463	
2010	0.610	0.645	0.732	0.528	0.453

3.4 Discussion

The understory vegetation in hardwood hammocks of the southern Everglades respond to environmental drivers and site characteristics that apparently vary at both landscape and site level. At the landscape level, hammock understory vegetation composition differs between two distinct wetland regions, ridge slough (RS) and wet prairies (WP), the latter with greater species richness and abundance. The difference in understory vegetation between the regions is attributable to the site factors (elevation above surrounding marsh, soil characteristics) that also influence the overstory vegetation. In general, vegetation in Everglades tree islands, encompassing a wide range of hydrologic conditions, is strongly influenced by hydrologic parameters (hydroperiod and mean water depth), with trees dominating on the rarely flooded heads of the islands and the proportion of herbaceous species gradually increasing with increased wetness towards the tail (Armentano et al. 2002; Sah 2004; Espinar et al. 2011; *see also Section. 2*). However, in ecosystems where soil water is relatively uniform, other environmental factors such as soil characteristics and light also play important role in determining the plant community composition in the lower strata. Although the hammocks in the WP and SS islands significantly differed in elevation above the adjacent marsh, the mean annual depth to water table was not different between these two island types (Ruiz et al. 2011). Nonetheless, the islands in two regions were different in soil characteristics (Ross and Sah 2011). SS islands had deeper soil and higher phosphorus content than the WP islands. Likewise, soil nitrogen and organic carbon content was relatively high in WP islands (Ross and Sah 2011). Moreover, topographic variation is higher in WP islands than SS islands (Ruiz et al. 2011), which may result in more heterogeneous soil and water resources, and thus the relatively high species richness in WP islands. In par with the ‘resource heterogeneity hypothesis’, several studies (Beatty 1984; Small and McCarthy 2005) have shown that resource heterogeneity mediated through spatial topographic variability or variation in the local hydrologic regime favors growth of a range of species capable of thriving in disparate levels of above and below ground resources, resulting in an increase in species diversity.

Vegetation layers within forests may respond to similar or different environmental gradients. However, the response of vegetation layers to similar gradients may also differ spatially, affecting the correspondence between them (Rogers 1981; Sagers and Lyon 1997). In this study, both overstory and understory vegetation showed similar pattern in response to the soil nutrient gradient, resulting in differentiation in vegetation composition between SS and WP islands. However, only understory vegetation composition was significantly correlated with water table depth, our metric of hydrology, and with canopy characteristics. Discrepancy in the relationships of vegetation layers with water depth may be due to differences in water use pattern by the plants in these layers. Trees usually use rain water during the wet season and the ground water in the dry season (Saha et al. 2010). Whether shrubs and herbaceous plant in south Florida hammocks exhibit similar pattern in water use, has not yet been fully explored. However, in other ecosystems, researchers have shown that understory herbs and shrubs are more dependent on rainwater regardless of their topographic position (Sagers and Lyon 1997). Similar differences between vegetation layers exist in using light resources. Overstory vegetation uses broader range of light, but herb and shrub layer vegetation in the understory experiences relatively narrow range of light (Sagers and Lyon 1997). Incongruence between these two layers in the use pattern of light resources could be also due to differences in the variability of available light resources. It is likely to be more variable in understory than in overstory, as the light available in understory has to pass through all layers of overstory, thus is affected by overall overstory structures. On the study islands, we did not measure the light availability in different layers of tree canopy. In the understory, however, the mean canopy openness and LAI, surrogate measures of light availability, ranged from 3.7 to 46.5%, and 0.75 to 3.76, respectively (*also see* Ruiz et al. 2011). Species in the understory layer probably differentiate along the light gradient irrespective of the overstory species composition, but it only depends on overstory canopy structure that affects the light availability in the understory. In this study, islands such as E-4200 SS-37, SS-81, Chekika and Panther Mound, that had relatively low LAI, were very different in overstory composition (**Figure 2.4**), but some of them had several understory species in common. For instance, *Andropogon virginicus*, which is known to be a shade-intolerant species, occupying mostly dry and open areas in the late stages of forest development, was present only on two islands, one each in WP (E4200) and SS (SS-81) regions.

The relationship between overstory and understory vegetation is also shaped by their differential responses to disturbances (Gilliam et al. 1995; Sagers and Lyon 1997; Tobisch and Standovar 2005). In the Everglades, researchers have documented the effects of disturbances on tree layer structure and composition in the tree island hammocks (Loope et al. 1994; Armentano et al. 1995, 2002; Ruiz et al. 2011). However, disturbances such as tropical storms, which are common in South Florida, might affect the tree layer and understory vegetation differently. In general, the dynamics of many understory plants in forests is driven by changes in canopy cover above them. Hence, some of the storms that may have little impact on tree species composition can create openings by causing physical damage to upper forest canopy, in turn affecting environmental conditions and species composition in the understory. In 2005, several islands were impacted Hurricane Wilma and Hurricane Katrina which made landfall in South Florida with maximum sustained winds of 70 and 105 knots, respectively (Knabb et al. 2006; Pasch et al. 2006). While the storms had minimal effects on the tree layer composition (Ruiz et al. 2011), they caused extensive canopy damage, resulting in alterations in the light availability, and thus affected understory vegetation composition.

In summary, understory vegetation composition in the southern Everglades hammocks varies at both regional landscape and local levels. Since overstory and understory vegetation associations may differ in their response to similar environmental factors, species composition in the overstory is not always a good predictor of understory associations. Moreover, understory vegetation in the hammocks is mostly composed of tree seedlings. Since understory vegetation, especially dominated by tree seedlings, are tightly linked, through competitive interactions, to the success of tree species in reaching to the forest canopy, understory vegetation composition and dynamics has the potential to significantly influence overstory stand structure, and broader ecosystem responses to alterations in major natural and anthropogenic ecological drivers.

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References

Alexander, T.R., 1967, Effects of Hurricane Betsy on the southeastern Everglades: *The Quarterly Journal of the Florida Academy of Sciences* 39: 10-24.

Alexander, T. R. and A. G. Crook. 1984. Recent vegetational changes in South Florida. p. 199-210. *In* P.J. Gleason (ed.) Environments of South Florida: Present and Past II, second edition. Miami Geological Society, Coral Gables, FL, USA.

Allen, C. R., L. Gunderson and A. R. Johnson. 2005. The use of discontinuities and functional groups to assess relative resilience in complex systems. *Ecosystems* 8: 958-966.

Armentano, T. V., R. F. Doren, W. J. Platt and T. Mullins. 1995. Effects of Hurricane Andrew on coastal and interior forests of southern Florida: overview and synthesis. *Journal of Coastal Research* 21: 111-1444.

Armentano T. V., D. T. Jones, M. S. Ross and B. W. Gamble. 2002. Vegetation pattern and process in tree islands of the southern Everglades and adjacent areas. In: F.H. Sklar and A. van der Valk (Eds). Tree islands of the everglades. pp 225–81. Dordrecht: Kluwer.

Armentano, T. V., J. P. Sah, M. S. Ross, D. T. Jones, H. C. Cooley, and C, S. Smith. 2006. Rapid responses of vegetation to hydrological changes in Taylor Slough, Everglades National Park, Florida, USA. *Hydrobiologia* 569: 293-309.

Bazante, J., G. Jacobi, H. M. Solo-Gabriele, D. Reed, S. Mitchell-Bruker, D. L. Childers, L. Leonard and M. S. Ross. 2006. Hydrologic measurement and implications for tree island formation within Everglades National Park. *Journal of Hydrology* 329: 606-619.

Beatty, S. W. 1984. Influence of microtopography and canopy species on spatial patterns of forest understory plant. *Ecology* 65:1406-1419.

Bernhardt, C. E. and D. A. Willard. 2009. Response of the Everglades ridge and slough landscape to climate variability and 20th century water management. *Ecological Applications* 19: 1723-1738.

Boughton, E. A., P. F. Quintana-Ascencio, E. S. Menges, and R. K. Boughton. 2006. Association of ecotones with relative elevation and fire in an upland Florida landscape. *Journal of Vegetation Science* 17: 361-368.

Brandt, L. A., K. M. Portier, and W. M. Kitchens. 2000. Patterns of change in tree islands in Arthur R. Marshall Loxahatchee National Wildlife Refuge from 1950 to 1991. *Wetlands* 20: 1-14.

Brock, J., C. McVoy, M. Oates, F. Santamaria, C. J. Saunders, T. Schall and E. Wunderlich. 2011. Landscape. In: F. Sklar, T. Dreschel and R. Stanek (eds). 2012 South Florida Environment Report – Chapter 6: Everglades Research and Evaluation.

Buma, B. and C. A. Wessman. 2011. Disturbance interactions can impact resilience mechanism of forests. *Ecosphere* 2:art64. doi:10.1890/ES11-00038.1

Cheng, Y., M. Stieglitz, G. Turk and V. Engel. 2011. Effects of anisotropy on pattern formation in wetland ecosystems. *Geophysical Research Letters* 38: L04402, doi: 10.1029/2010GL046091

Clark, M. W., M. J. Cohen, T. Z. Osborne, D. Watts, and T. Oh. 2009. Evaluating decomposition dynamics, community composition, and ridge-top senescence in the ridge-slough mosaic in response to climate change and water management. Annual Report 2009.

Clarke, K. R. and R. M. Warwick. 2001. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation, 2nd edition. PRIMER-E, Plymouth, United Kingdom.

Cornelius, J. M. and J. F. Reynolds. 1991. On determining the statistical significance of discontinuities within ordered ecological data. *Ecology* 72: 2057-2070.

Davidowitz, G. and M. L. Rosenzweig. 1998. The latitudinal gradient of species diversity among North American grashoppers within a single habitat: a test of the spatial heterogeneity hypothesis. *Journal of Biogeography* 25: 553-560.

D'Odorico, P., V. Engel, J. Carr, S. F. Oberbauer, M. S. Ross and J. P. Sah. 2011. Tree-grass coexistence in the Everglades freshwater system. *Ecosystems* 14: 298-310.

Espinar, J., M. S. Ross and J. P. Sah. 2011. Pattern of nutrient availability and plant community assemblage in Everglades tree islands, Florida USA. *Hydrobiologia* 667: 89-99.

Folke, C., S. R. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. H. Gunderson and C. S. Holling. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology and Systematics* 35:557–581.

Forys E. A. and C. R. Allen. 2002. Functional group change within and across scales following invasions and extinctions in the Everglades ecosystem. *Ecosystems* 5: 339-347.

Frazer, G. W., C. D. Canham, and K. P. Lertzman, 1999. Gap light analyzer (GLA). *Version 2.0. Imaging software to extract canopy structure and gap light transmission indices from true-color fisheye photographs: users' manual and program documentation.* Simon Fraser University, Burnaby, BC, Canada. 36 p.

Gilliam, F. S. 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. *BioScience* 57: 845-858.

Gilliam, F. S., N. L. Turtill and M. B. Adams. 1995. Herbaceous layer and overstory species in clear-cut and mature central Appalachian hardwood forests. *Ecological Applications* 5: 947-955.

Givnish, T. J., J. C. Volin, V. D. Owen, V. C. Volin, J. D. Muss and P. H. Glaser, 2008. Vegetation differentiation in the patterned landscape of the central Everglades: importance of local and landscape drivers. *Global Ecology and Biogeography*17: 384–402.

Gosz, J. R. 1993. Ecotone hierarchies. *Ecological Applications* 3: 369-376.

Gunderson, L. 1994. Vegetation of the Everglades: Determinants of Community composition. In: S. M. Davis and J. C. Ogden. Everglades: The Ecosystem and Its Restoration. Delray Beach, Florida.: St. Lucie Press: 323-340.

Hagerthey, S. E., S. Newman, K. Rutchey, E. P. Smith and J. Godin. 2008. Multiple regime shifts in a subtropical peatlnad: community-specific thresholds to eutrophication. *Ecological Monographs* 78: 547-565.

Harvey, J. W., R. W. Schaffranek, G. B. Noe, L. G. Larsen, D. Nowacki and B. L. O'Connor. 2009. Hydroecological factors governing surface water flow on a low-gradient floodplain. *Water Resources Research* 45, W03421. doi:10.1029/2008WR007129.

Hofstetter, R. H. and F. Parsons. 1975. Effects of Fire in the Ecosystem: An Ecological Study of the Effects of Fire on the Wet Prairie, Sawgrass Glades and Pineland Communities of South Florida. Final Report Part 2. USDA National Park Service. EVER-N-48 NTIS No. BP 264463.

Huang, Y. H., J. E. Saiers, J. W. Harvey, G. B. Noe and S. Mylon. 2008b. Advection, dispersion, and filtration of fine particles within emergent vegetation of the Florida Everglades. *Water Resources Research* 44, W04408. doi:10.1029/2007WR006290.

Jones J. W. and S. D. Price. 2007. Initial Everglades depth estimation network (EDEN) digital elevation model research and development. U. S. Geological Survey, Open File Report 2007–1304, Reston, Virginia. 29 p.

Kline, M. M. S. Ross, P. L. Ruiz, B. Shamblin, J. P. Sah, E. Hanan and S. Stoffella. 2007. Marl Prairie/Slough Gradients; patterns and trends in Shark Slough and adjacent marl prairies. CERP monitoring activity 3.1.3.5. Third Annual Report. Dec 31, 2007. 26 pp.

Knabb, R. D., J. R. Rhome and D. P. Brown. 2006. Tropical cyclone report Hurricane Katrina 23-30 August 2005. 43pp.

Kozlowski, T. T. 2002. Physiological-ecological impacts of flooding on riparian forest ecosystems. *Wetlands* 22: 550-561.

Kumar S, T. J. Stohlgern and G. W. Chong. 2006. Spatial heterogeneity influences native and nonnative species richness. *Ecology* 87:3186–3199

Lago, M. E., F. Miralles-Wilhelm, M. Mahmoudi and V. Engel. 2010. Numerical modeling of the effects of water flow, sediment transport and vegetation growth of the spatiotemporal patterning of the ridge and slough landscape of the Everglades wetland. *Advances in Water Resources* 33: 1268-1278.

Larsen, L., J. W. Harvey, G. B. Noe, and J. P. Crimaldi. 2009. Predicting organic floc transport dynamics in shallow aquatic ecosystems: insights from the field, the laboratory, and numerical modeling. *Water Resources Research* 45, W01411, doi:10.1029/2008WR007221.

Lemmon, P.E. 1956. A spherical densitometer for estimating forest overstory density. *Forest Science* 2: 314-320.

Light, S. S. and J. W. Dineen. 1994. Water control in the Everglades: a historical perspective. p. 47–84. In S. M. Davis and J. C. Ogden (eds.) Everglades. The Ecosystem and Its Restoration. St. Lucie Press, Delray Beach, FL, USA.

Loope, L., M. Duever, A. Herndon, J. Snyder and D. Jansen. 1994. Hurricane impact on uplands and freshwater swap forest. *BioScience* 44: 238-246.

Loveless, C. M. 1959. A study of the vegetation in the Florida Everglades. *Ecology* 40:1-9.

Ludwig, J. A. and J. M. Cornelius. 1987. Locating discontinuities along ecological gradients. *Ecology* 68: 448-450.

MacArthur, R. H. and J. W. MacArthur. 1961. On bird species diversity. *Ecology* 42:594–598.

McCune, B. and J. A. Antos. 1981. Correlations between forest layers in the Swan Valley, Montana. *Ecology* 62: 1196-1204.

Minchin, P. 1987. An evaluation of the relative robustness of techniques for ecological ordination. *Plant Ecology* 69: 89-107.

Minchin P. 1998. DECODA: Database for Ecological Community Data. Anutech Pty. Ltd., Canberra, Australia.

Newman, S., J. Schuette, J. B. Gracce, K. Rutchey, T. Fontaine, K. R. Reddy and M. Peitrucha. 1998. Factors influencing cattail abundance in the northern Everglades. *Aquatic Botany* 60: 265 – 280.

Olmsted, I. C., and L. L. Loope. 1984. Plant communities of Everglades National Park. In: P.J. Gleason, (Ed). Environments of South Florida: Present and Past II. pp. 167-184. Miami Geological Society, Coral Gables.

Olmsted, I. and T.V. Armentano 1997. Vegetation of Shark Slough, Everglades National Park. South Florida Natural Resources Center, Technical Report 97-001. National Park Service, Everglades National Park, Homestead, FL, USA.

Palaseanu M. and L. Pearlstine. 2008. Estimation of water surface elevations for the Everglades, Florida. *Computers and Geosciences* 34:815–26.

Parker, G.G. 1995. Structure and microclimate of forest canopies. *In*: M. Lowman and N. Nadkarni, (eds.), Forest canopies: a review of research on a biological frontier. Academic Press, San Diego, CA.

Pasch, R. J., E.S. Blake, H.D. Cobb III and D.P. Roberts. 2006. Tropical cyclone report Hurricane Wilma 15-25 October 2005. 27 pp.

Patterson, K. and R. Finck. 1999. Tree Islands of the WCA-3 Aerial Photointerpretation and 1775 Trend Analysis Project Summary Report. Report by Geonex Corporation, St. Petersburg, FL, 1776 submitted to South Florida Water Management District, West Palm Beach, FL.

Peres-Neto, P. R. and D. A. Jackson. 2001. How well do multivariate data sets match? The advantages of a Procrustean superimposition approach over the Mantel test. *Oecologia* 129:169-178.

Reed, D. and M. S. 2004. Hydrologic variation among and within tree islands of Shark Slough. pp. 5-16. *In* M. S. Ross & D. T. Jones (eds), Tree islands in the Shark Slough landscape: interactions of vegetation, soils, and hydrology. Final report to Everglades National Park, Homestead, FL, USA. September 2004.

Risser, P.G. 1995. The status of the science examining ecotones. *BioScience* 45: 318–325.

Rogers, R. S. 1981. Mature mesophytic hardwood forest: community transitions, by layer, from east-central Minnesota to southeastern Michigan. *Ecology* 62: 1634-1647.

Ross, M. S., P. L. Ruiz, D. L. Reed,, K. Jayachandran, C. L. Coultas, J. P. Sah and M. T. Lewin, 2001. Assessment of Marsh Vegetation Responses to Hydrological Restoration in Shark Slough, Everglades National Park. Final Report, (Cooperative Agreement 5280-9021). June 27, 2001. 102 pp.

Ross, M. S. and D. T. Jones (Eds.). 2004. Tree islands in the Shark Slough landscape: interactions of vegetation, soils, and hydrology. Final report to Everglades National Park, Homestead, FL, USA. September 2004.

Ross, M. S. and J. P. Sah. 2011. Forest resource islands in a sub-tropical marsh: soil-site relationships in Everglades hardwood hammocks. *Ecosystems* 14: 632-645.

Ross, M. S., D. E. Ogurcak, J. P. Sah and P. L. Ruiz. 2010. Using Florida Keys reference sites as a standard for restoration of forest structure in Everglades tree islands. *International Journal of Forestry Research*. Volume 2010, Article ID 176909; 8 pp. doi:10.1155/2010/176909.

Ross, M. S., S. Mitchell-Brucker, J. P. Sah, S. Stothoff, P. L. Ruiz, D. L. Reed, K. Jayachandran and C. L. Coultas, 2006. Interaction of hydrology and nutrient limitation in the Ridge and Slough landscape of the southern Everglades. *Hydrobiologia* 569: 37–59.

Royo, A. A. and W. P. Carson, 2006. On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. *Canadian Journal of Forest Research* 36:1345–1362.

Ruiz, P. L., J. P. Sah, M. S. Ross, D. Rodriguez and A. Lambert. 2011. Monitoring of Tree Island Conditions in the Southern Everglades: The Effects of Hurricanes and Hydrology on the Status and Population Dynamics of Sixteen Tropical Hardwood Hammock Tree Islands. USACOE – US Army Engineer Research and Development Center. Cooperative Agreement: W912HZ-09-2-0019. 136 pp.

Sagers, C. L. and J. Lyon. 1997. Gradient analysis in a riparian landscape: contrasts among forest layers. *Forest Ecology and Management* 96: 13-26.

Sah, J. P. 2004. Vegetation structure and composition in relation to the hydrological and soil environments in tree islands of Shark Slough. p. 85-111. *In* M. S. Ross and D. T. Jones (eds), Tree islands in the Shark Slough landscape: interactions of vegetation, soils, and hydrology. Final report to Everglades National Park, Homestead, FL, USA. Sept. 2004.

Saha, A. K., L. S. Sternberg, M. S. Ross and F. Miralles-Wilhelm. 2010. Water source utilization and foliar nutrient status differs between upland and flooded plant communities in wetland tree islands. *Wetlands Ecology and Management* 18: 343-355.

Shamblin, B., M. S. Ross, S. F. Oberbauer, D. Gomez, L. Sternberg, A. Saha, and X. Wang, 2008. CERP monitoring and assessment program: tree island conditions in the southern Everglades. Annual Report for 2007 submitted to the South Florida Natural Resources Center, Everglades National Park, Homestead, FL.

Sklar, F. H. and A. G. van der Valk, 2002. Tree islands of the Everglades: an overview. In Sklar, F. H. & A. G. van der Valk (eds), Tree Islands of the Everglades. Kluwer Academic Publishers, Netherlands.

Small, C. J. and B. C. McCarthy. 2005. Relationship of understory diversity to soil nitrogen topographic variation, and stand age in an eastern oak forest, USA. *Forest Ecology and Management* 217: 229-243.

Stone, P. A. and G. L. Chimura. 2004. Sediments, stratigraphy, and aspects of succession, chronology, and major prehistoric disturbance in the principal type of large tree island in

Shark Slough. In Ross, M. S. and D. T. Jones (eds.), Tree Islands in the Shark Slough Landscape: Interactions of Vegetation, Hydrology and Soils. Final Report. Everglades National Park, Homestead: 17–29.

Sullivan, P. 2011. Ground Water-Surface Water Interactions on Tree Islands in the Everglades, South Florida. A Ph.D. Dissertation. Florida International University, Miami, FL.

Thomaz, S. M., L. M. Bini and R.L. Bozelli. 2007. Floods increase similarity among aquatic habitats in river-floodplain systems. *Hydrobiologia* 579: 1-13.

Tobisch, T. and T. Standovar. 2005. A comparison of vegetation patterns in the tree and herb layers of a hardwood forest. *Community Ecology* 6: 29-37.

Todd, M. J., R. Muneepeerakul, D. Pumo, S. Azaele, F. Miralles-Wilhelm, A. Rinaldo and I. Rodriguez-Iturbe. 2010. Hydrological drivers of wetland vegetation community distribution within Everglades National Park, Florida. *Advances in Water Resources* 33: 1279-1289.

Troxler Gann, T., D. L. Childers and D. N. Rondeau. 2005. Ecosystem structure, nutrient dynamics, and hydrologic relationships in tree islands of the southern Everglades, Florida, USA. *Forest Ecology and Management* 214:11–27.

van der Maarel, E. 1990. Ecotones and ecoclines are different. *Journal of Vegetation Science* 1: 135-138.

Wade, D., J. Ewel and R. Hofstetter. 1980 . Fire in South Florida ecosystems. U.S. Department of Agriculture and Forest Service., General Technical Report SE-17. 125 p. Southeast Forest Experimental Station. Asheville, N.C.

Walker, S., J. B. Wilson, J. B. Steel, G. L. Rapson, B. Smith, W. M. King and Y. H. Cottam, 2003. Properties of ecotones: evidence from five ecotones objectively determined from a coastal vegetation gradient. *Journal of Vegetation Science* 14: 579-590.

Wetzel, P. R. 2002. Analysis of tree island vegetation communities: hydrologic and fire impacts over a decade. p. 357-389. *In* F.H. Sklar and A. van der Valk (eds.) Tree Islands of the Everglades. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Wetzel, P. R., A. G. van der Valk, S. Newman, D. E. Gawlik, T. Troxler Gann, C. A. Coronado-Molina, D. L. Childers and F. H. Sklar, 2005. Maintaining tree islands in the Florida Everglades: nutrient redistribution is the key. *Frontiers in Ecology and the Environment* 3: 370–376.

Wetzel, P. R., T. Pinion, D. Towles and L. Heisler. 2008. Landscape analysis of tree island head vegetation in Water Conservation Area 3, Florida Everglades. *Wetlands* 28: 276-289.

Wiens, J. A., C. S. Crawford and J. R. Gosz, 1985. Boundary dynamics: a conceptual framework for studying landscape ecosystems. *Oikos* 45: 421-427

Willard, D. A., C. E. Bernhardt, C. W. Holmes, B. Landacre, and M. Marot. 2006. Response of Everglades tree islands to environmental change. *Ecological Monographs* 76:565–583.

Zweig, C. L., W. M. Kitchens. 2008. Effects of landscape gradients on wetland vegetation communities: Information for large-scale restoration. *Wetlands* 28: 1086-1096.

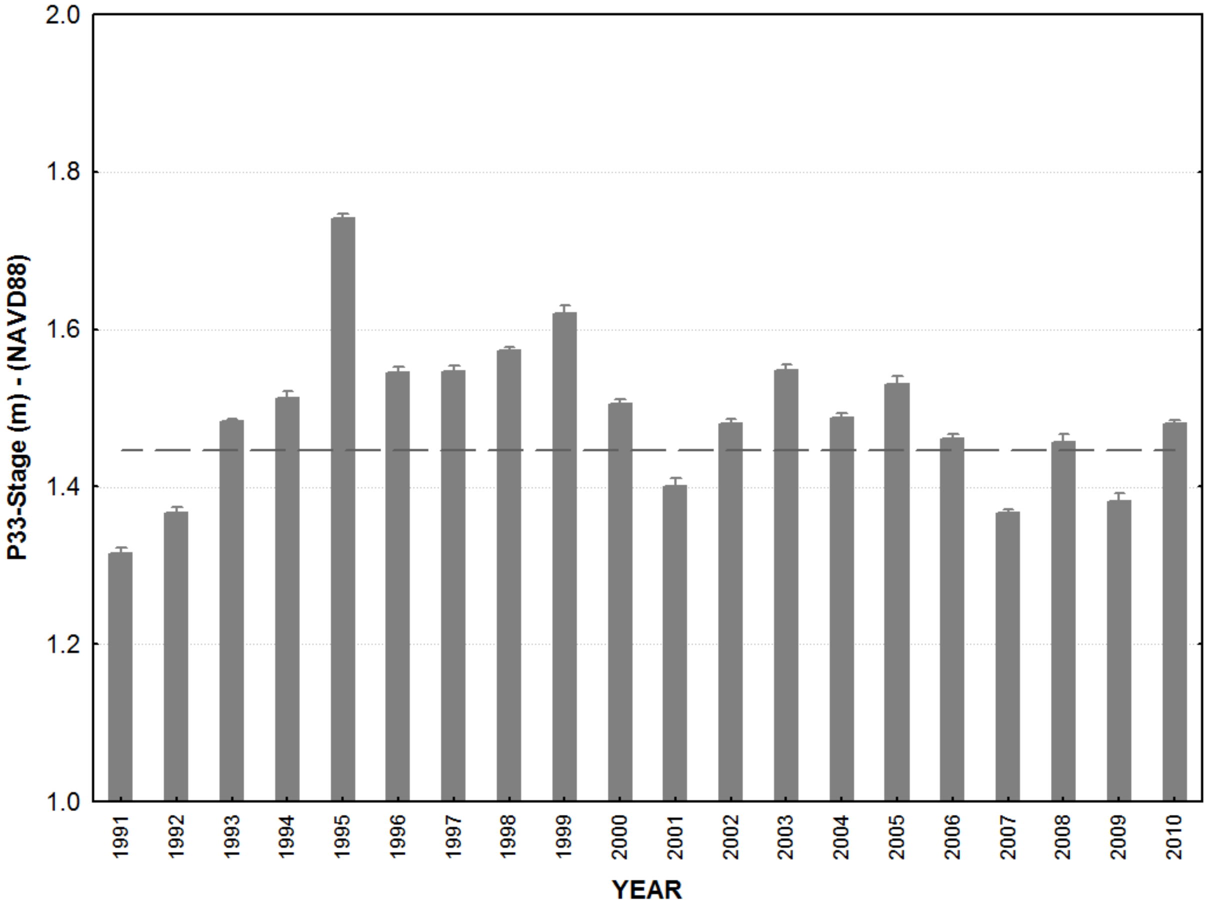


Figure 1.1: Mean (± S.E.) annual and 30-Yr (1981-2010) average water level at the stage recorder P-33 located in Shark River Slough within Everglades National Park.

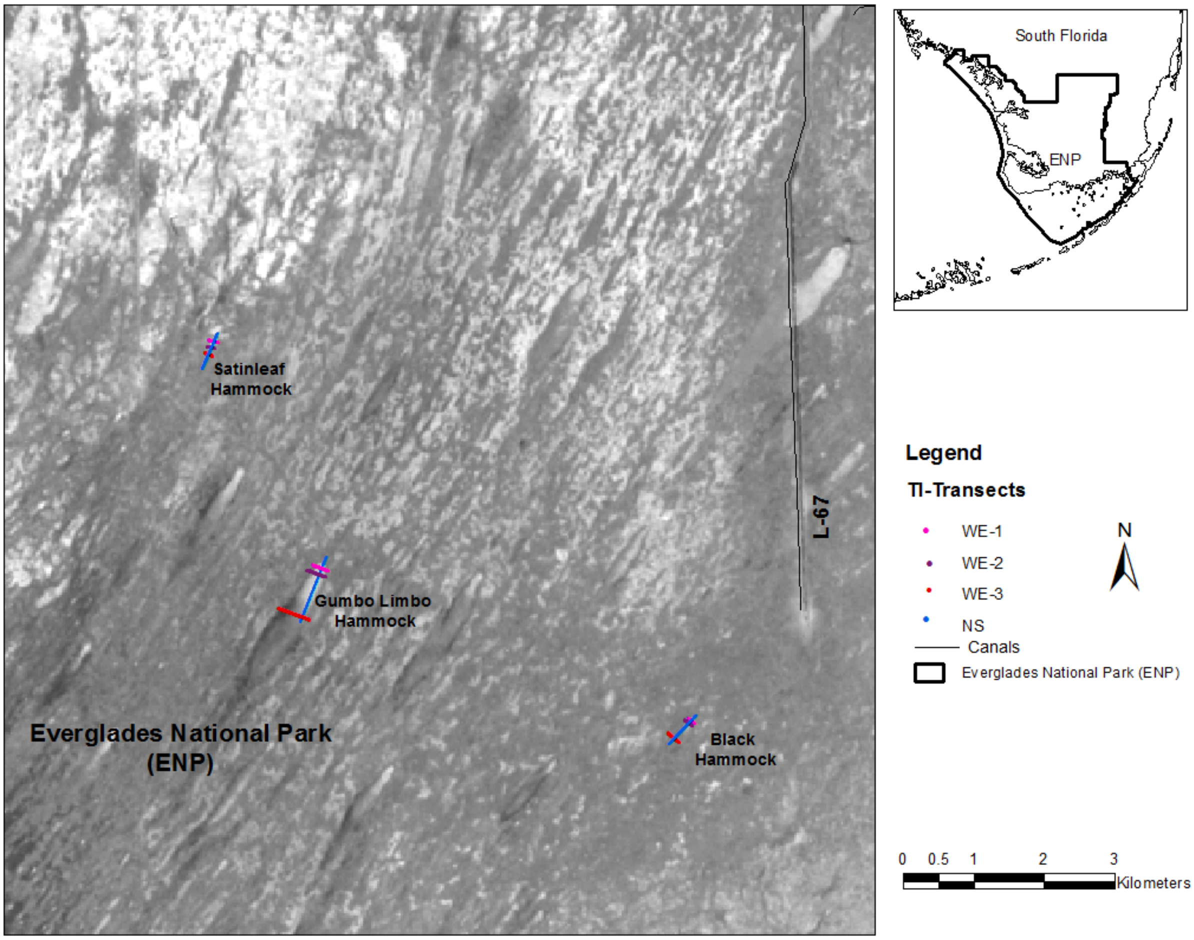


Figure 1.2: Study area map showing the location of transects on three Shark Slough tree islands

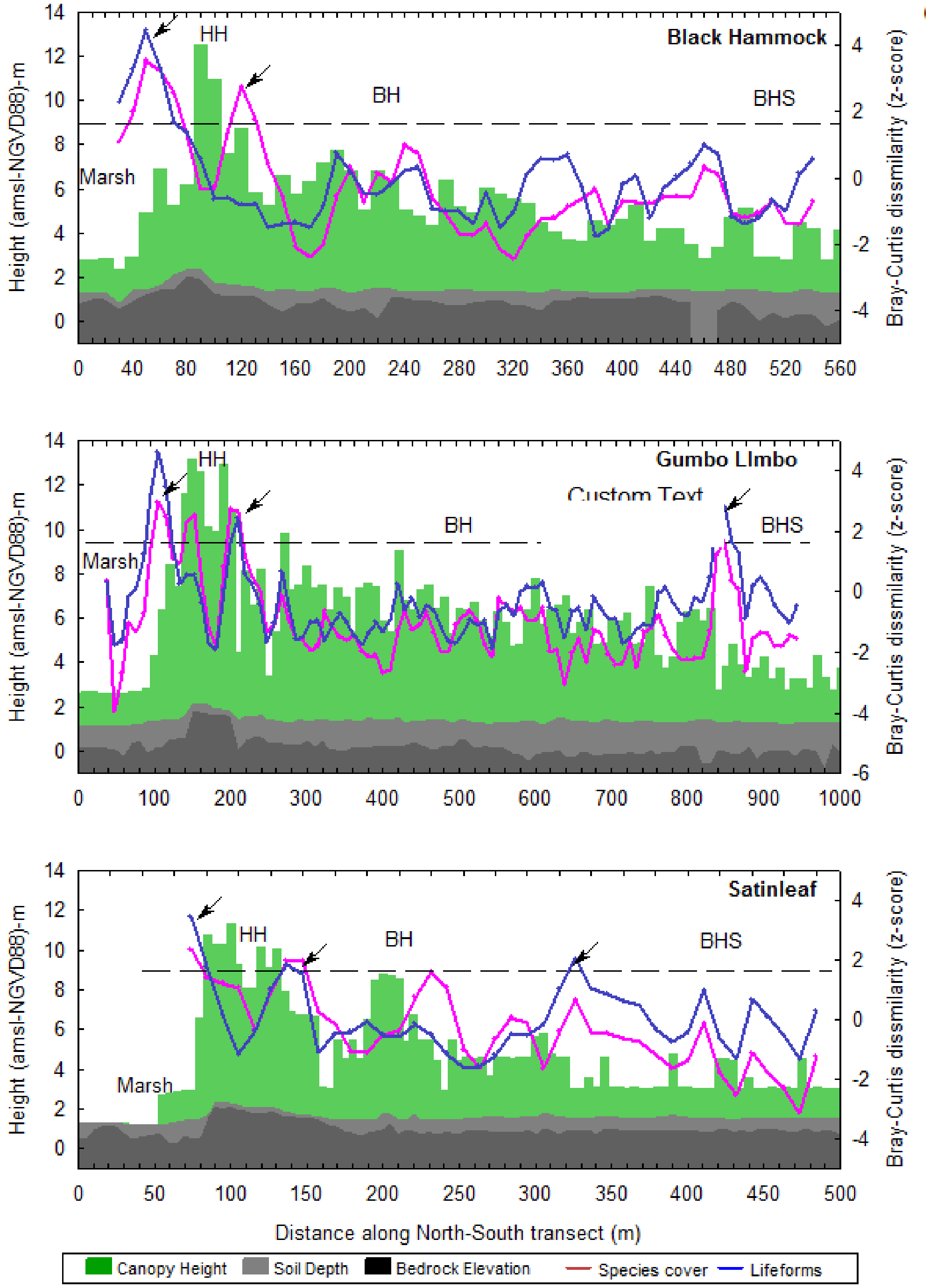


Figure 1.3: Canopy height, bedrock elevation, soil depth, and normalized Bray-Curtis dissimilarity (Z-Score) based on species cover and life form cover along N-S transects on three Shark Slough islands. In split-moving window analysis, the Z-scores were averaged over 4 window sizes (window with of 6, 8, 10, and 12). HH = Hardwood hammock, BH = Bayhead, BHS = Bayhead swamp.

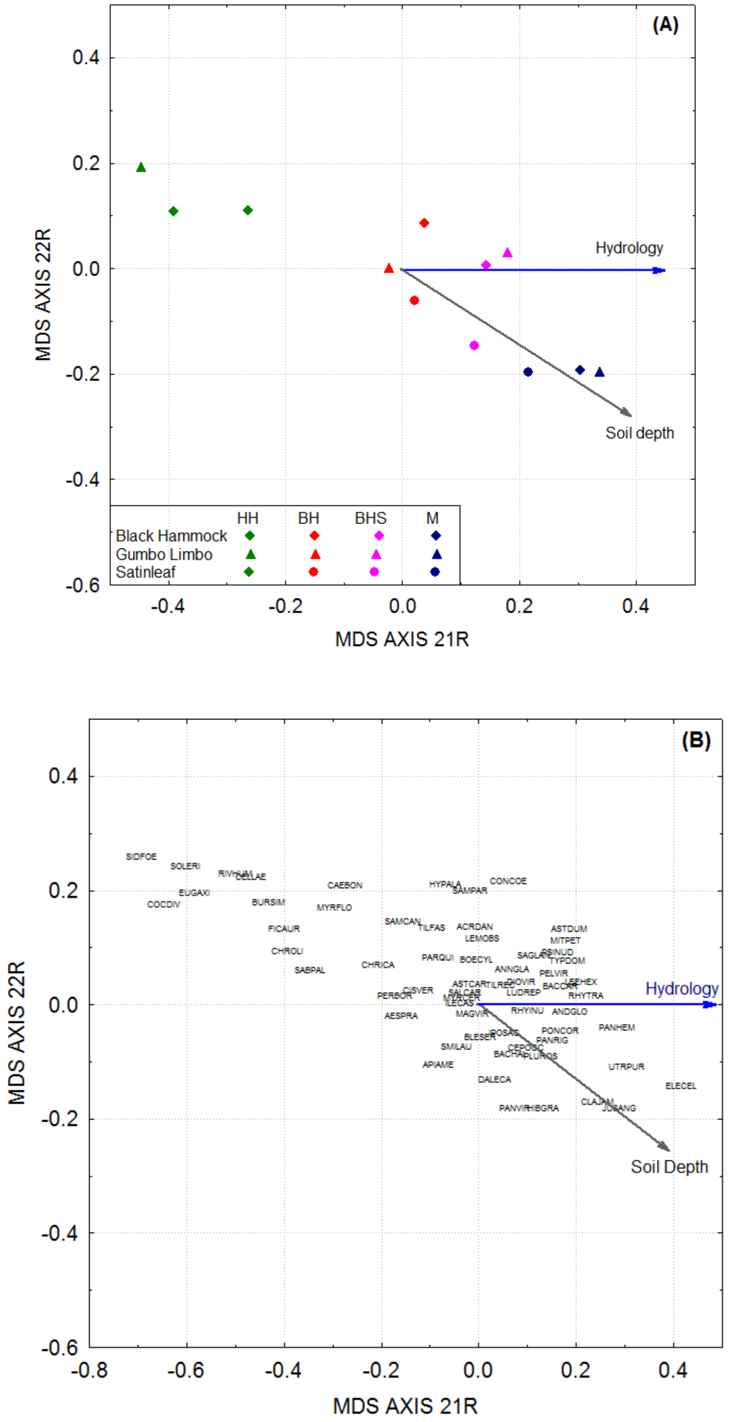


Figure 1.4: Bi-plots of (a) site, and (b) species scores from two-dimensional non-metric multidimensional scaling (NMDS) ordination of species cover data collected at the sites along N-S transects on Shark Slough islands. Environmental vectors fitted in the ordination spaces represent the direction of their maximum correlation with ordination configuration.

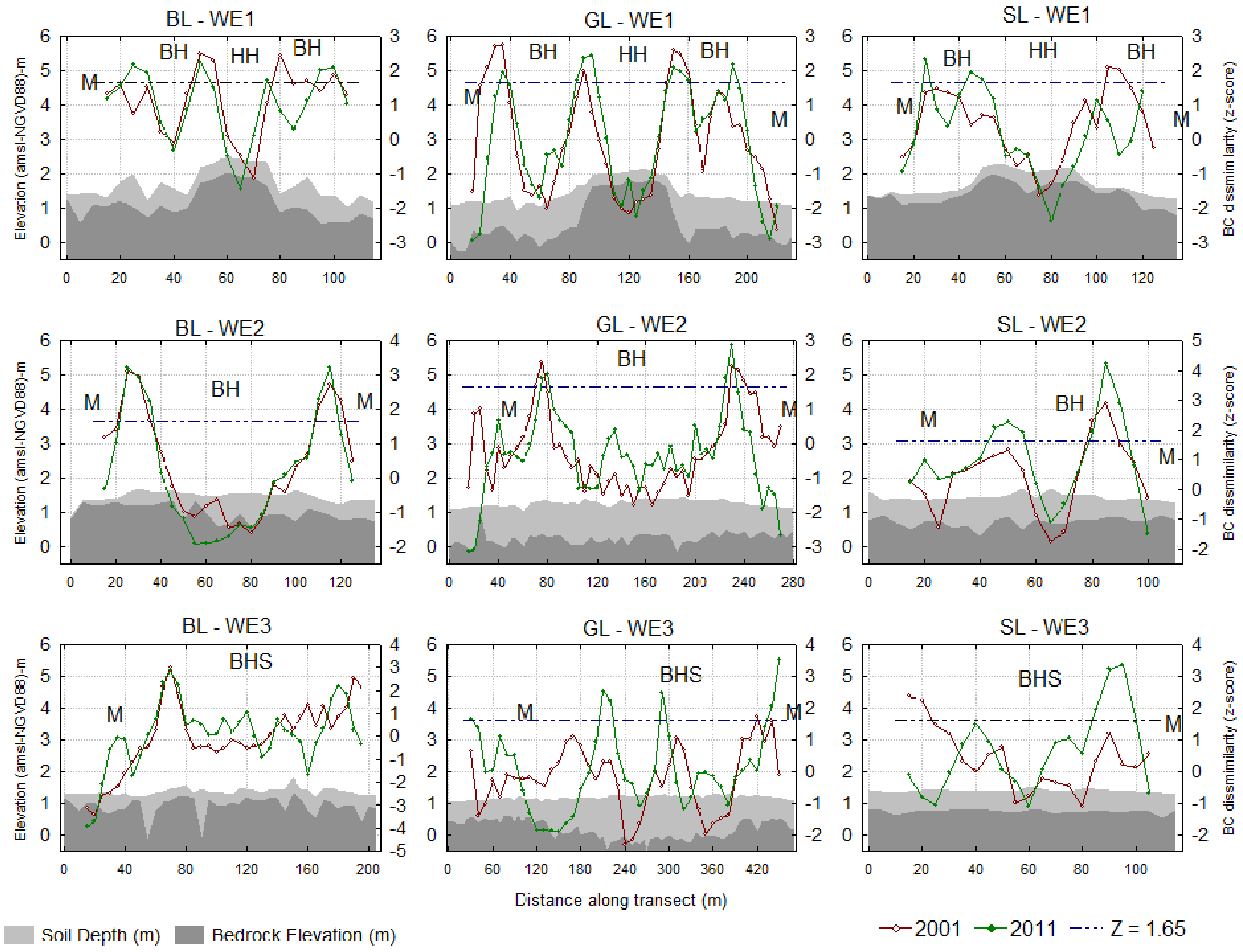


Figure 1.5: Bedrock elevation, soil depth, and normalized Bray-Curtis dissimilarity (Z-Score) based on species cover along W-E transects on three Shark Slough islands. In split moving-window analysis, the Z-scores were averaged over 4 window sizes (window with of 6, 8, 10, and 12 sites) separately for 2001 and 2011 samples. HH = Hardwood hammock, BH = Bayhead, BHS = Bayhead swamp.

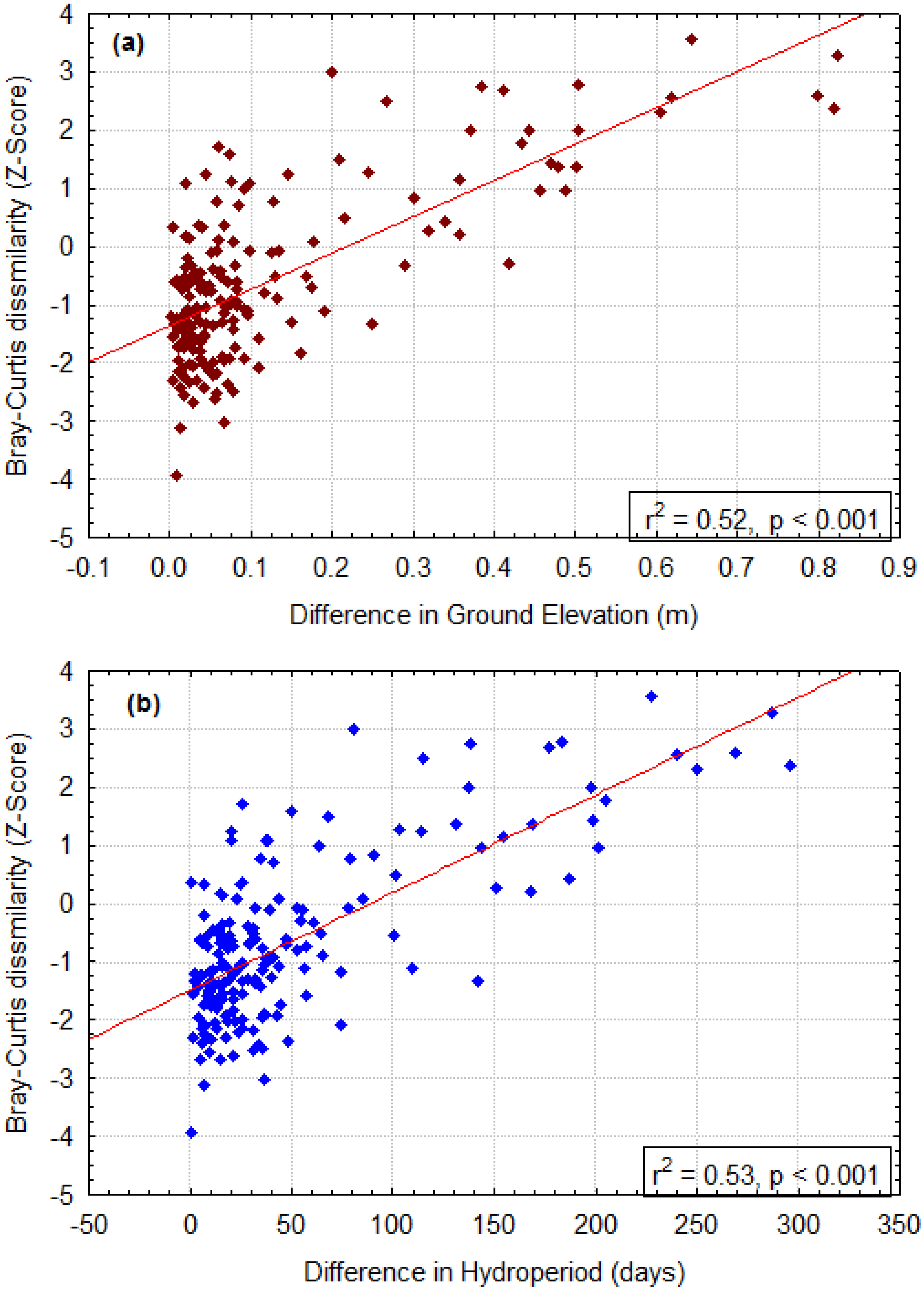


Figure 1.6: Relationship between mean normalized Bray-Curtis dissimilarity (Z-Score) and absolute difference in (a) elevation, and (b) hydroperiod on three N-S transects, one each in Black Hammock, Gumbo Limbo and Satinleaf tree islands.

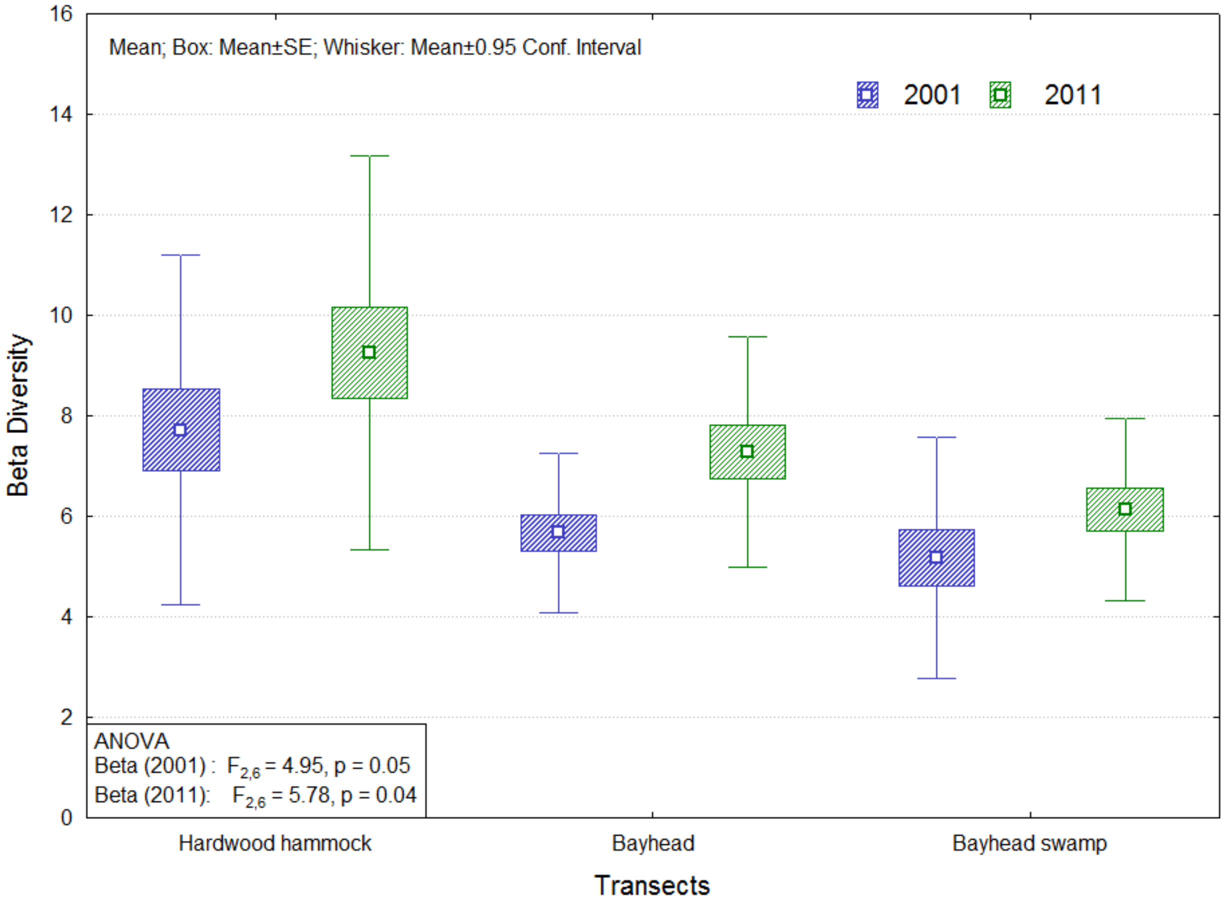


Figure 1.7: Box plots showing the mean (±SE) of Beta diversity (β) in 2001 and 2011 on the transects that crossed the head (hardwood hammock), middle (bayhead) and lower (bayhead swamp) portions of Shark Slough tree islands.

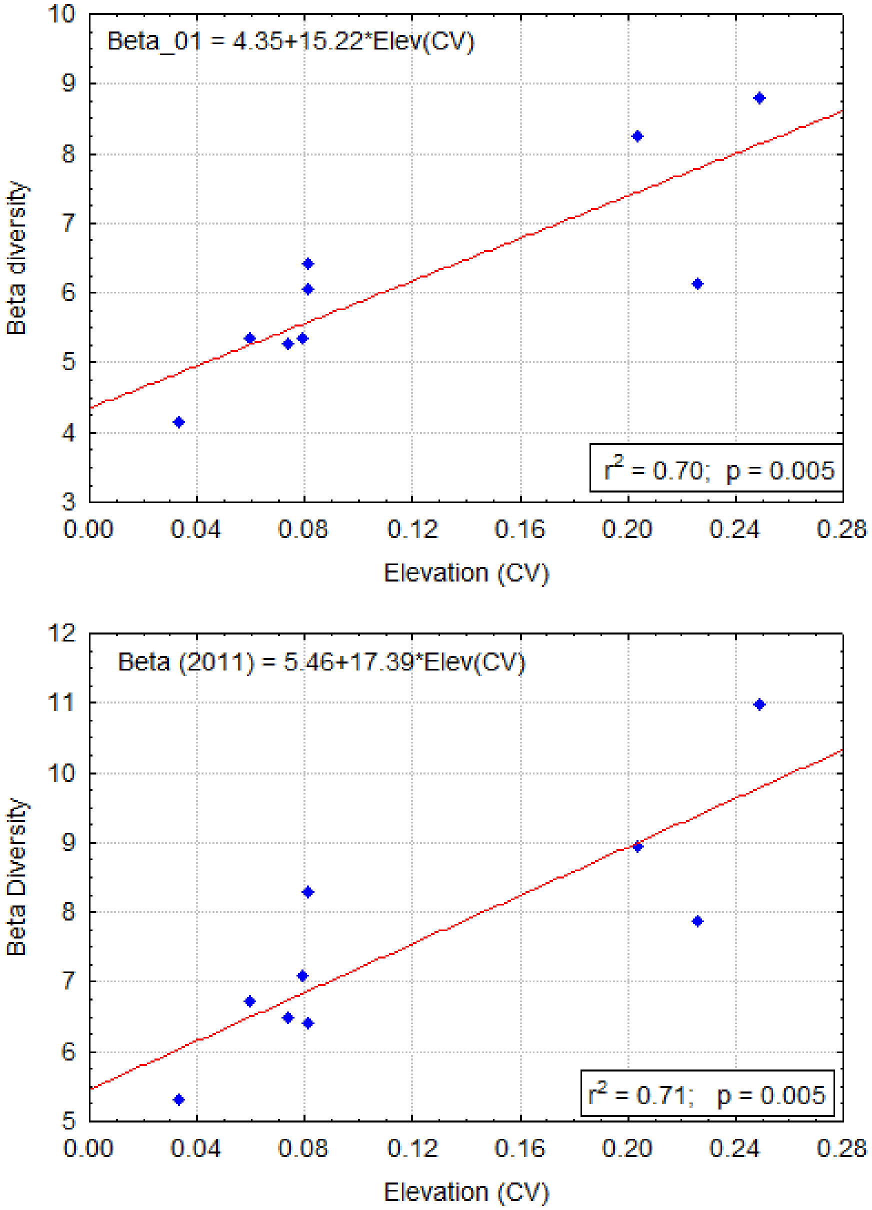


Figure 1.8: Relationship between mean Beta diversity (β) and habitat heterogeneity (Coefficient of variation of Elevation) on nine transects in Shark Slough tree islands

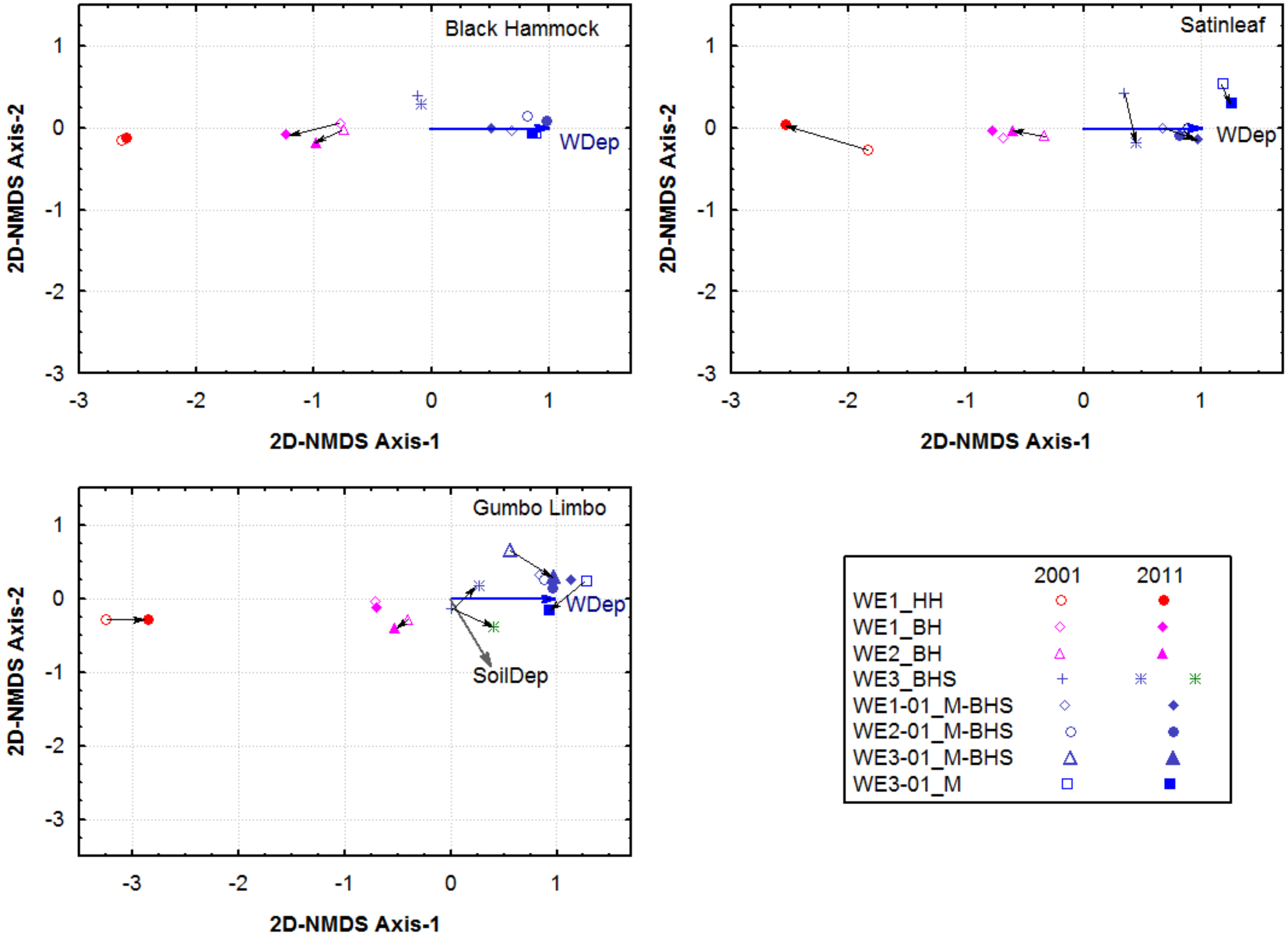
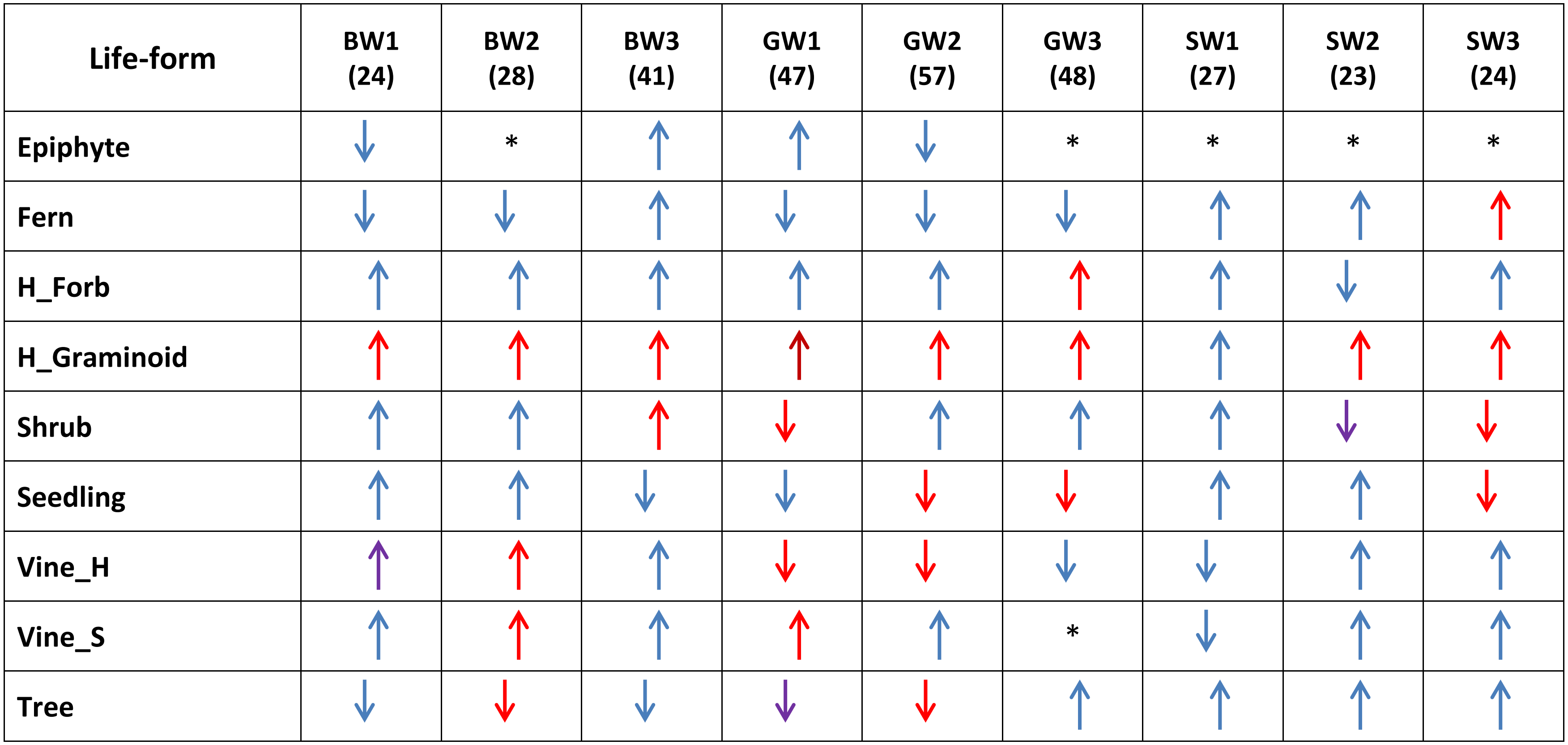


Figure 1.9: Bi-plots of site scores of centroids of sites, grouped by vegetation types, from two-dimensional non-metric multidimensional scaling ordination of species cover data collected at the sites along W-E transects on Shark Slough islands. Environmental vectors fitted in the ordination spaces represent the direction of their maximum correlation with ordination configuration. WDep = Water depth (cm); HH = Hardwood hammock, BH = Bayhead, BHS = Bayhead swamp, M = Marsh.



Life-form	BW1 (24)	BW2 (28)	BW3 (41)	GW1 (47)	GW2 (57)	GW3 (48)	SW1 (27)	SW2 (23)	SW3 (24)
Epiphyte	↓	*	↑	↑	↓	*	*	*	*
Fern	↓	↓	↑	↓	↓	↓	↑	↑	↑
H_Forb	↑	↑	↑	↑	↑	↑	↑	↓	↑
H_Graminoid	↑	↑	↑	↑	↑	↑	↑	↑	↑
Shrub	↑	↑	↑	↓	↑	↑	↑	↓	↓
Seedling	↑	↑	↓	↓	↓	↓	↑	↑	↓
Vine_H	↑	↑	↑	↓	↓	↓	↓	↑	↑
Vine_S	↑	↑	↑	↑	↑	*	↓	↑	↑
Tree	↓	↓	↓	↓	↓	↑	↑	↑	↑

↑ Increase in cover; ↓ Decrease in cover. * = not present in any of two samplings. Red color = Significant (Paired T-test; alpha = 0.05); Blue color = not significant at alpha = 0.05. Number in the parenthesis represents the number of sites on each transect.

Figure 1.10: Change pattern (increase or decrease) in mean cumulative cover (%) of different life forms in ten years (2001-2010) at the sites on the WE transects in three Shark Slough islands.

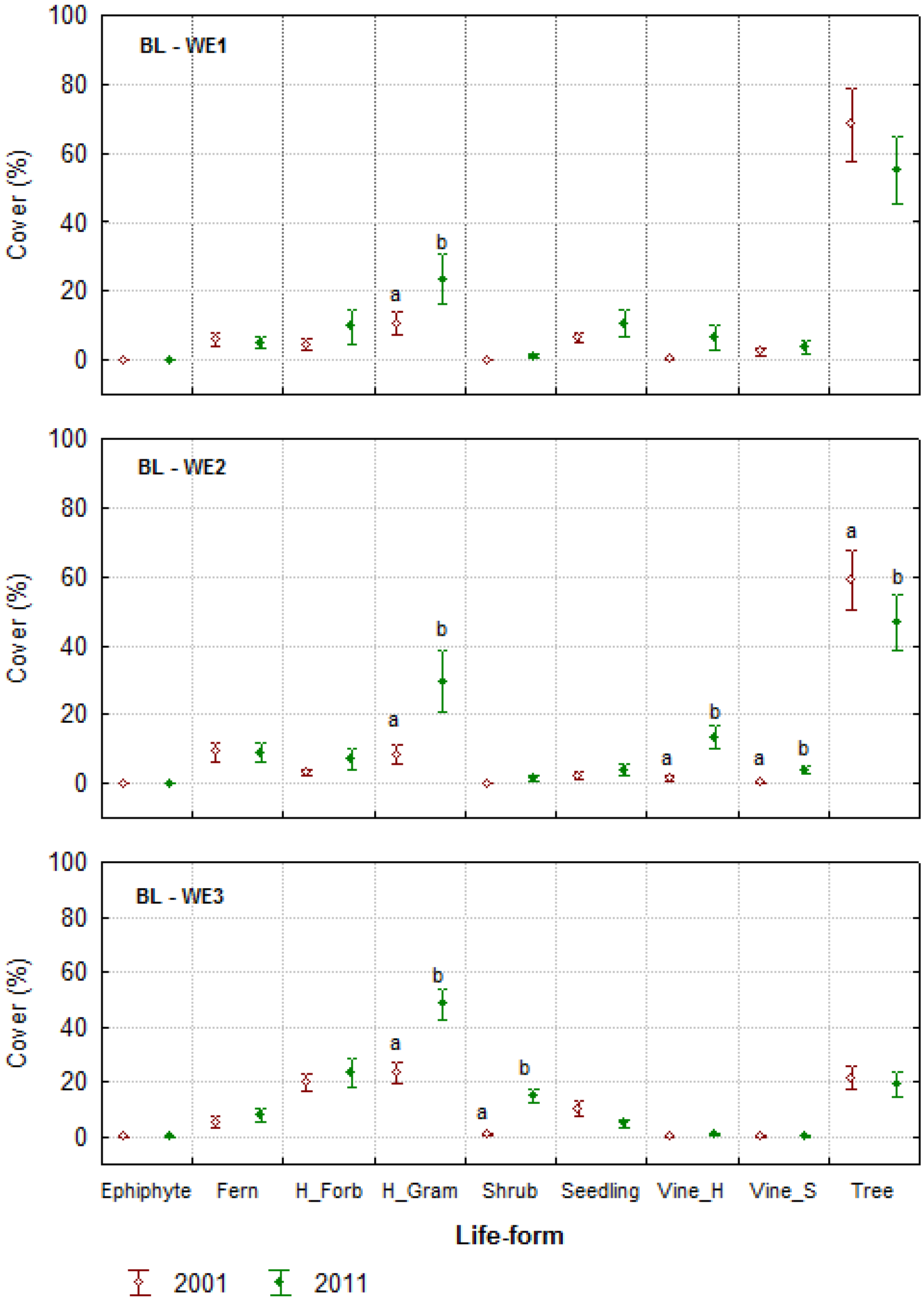


Figure 1.11: Mean (± S. E.) cover (%) of different life forms in 2001 and 2011 on three transects in Black Hammock.

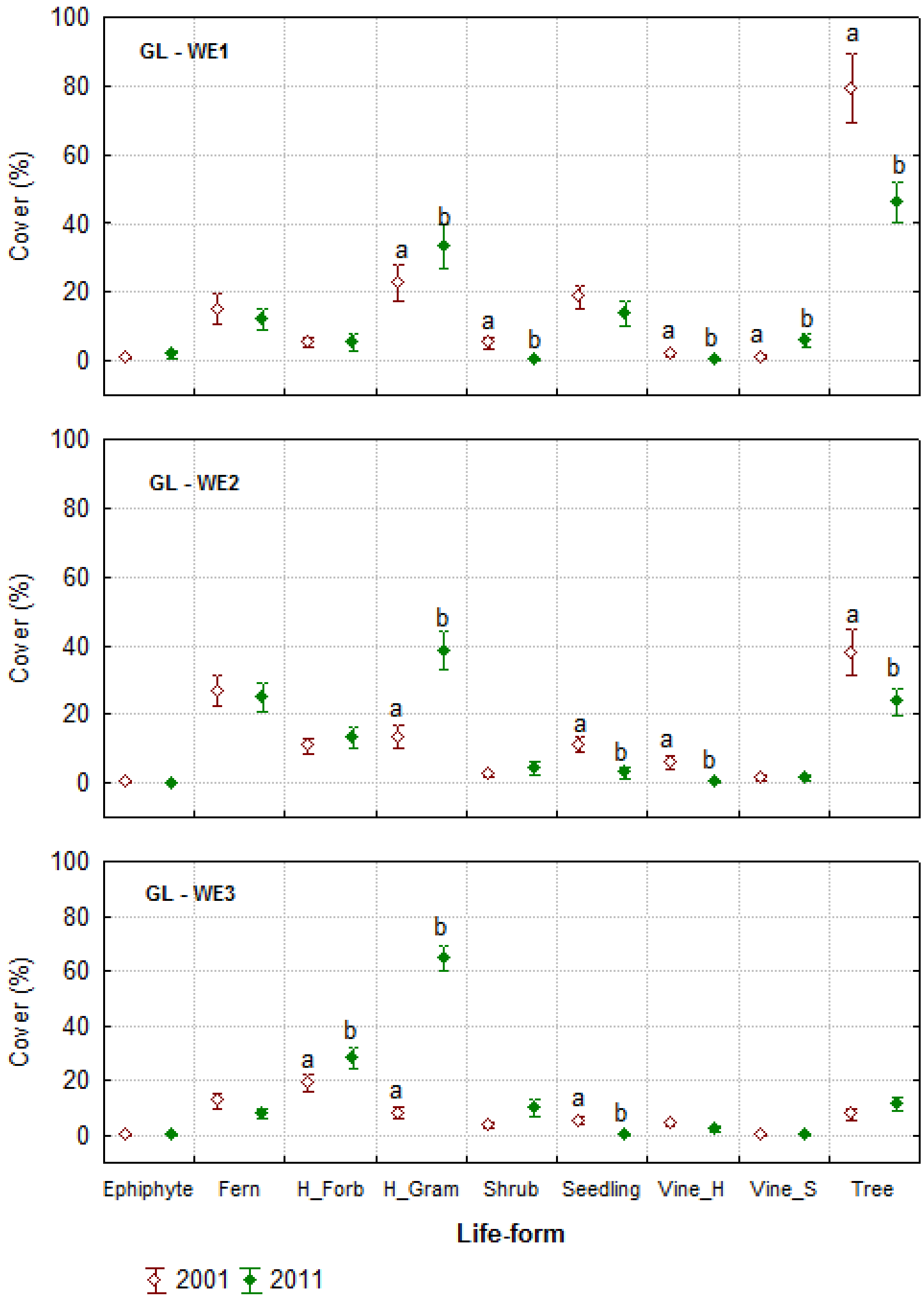


Figure 1.12: Mean (± S. E.) cover (%) of different life forms in 2001 and 2011 on three transects in Gumbo Limbo.

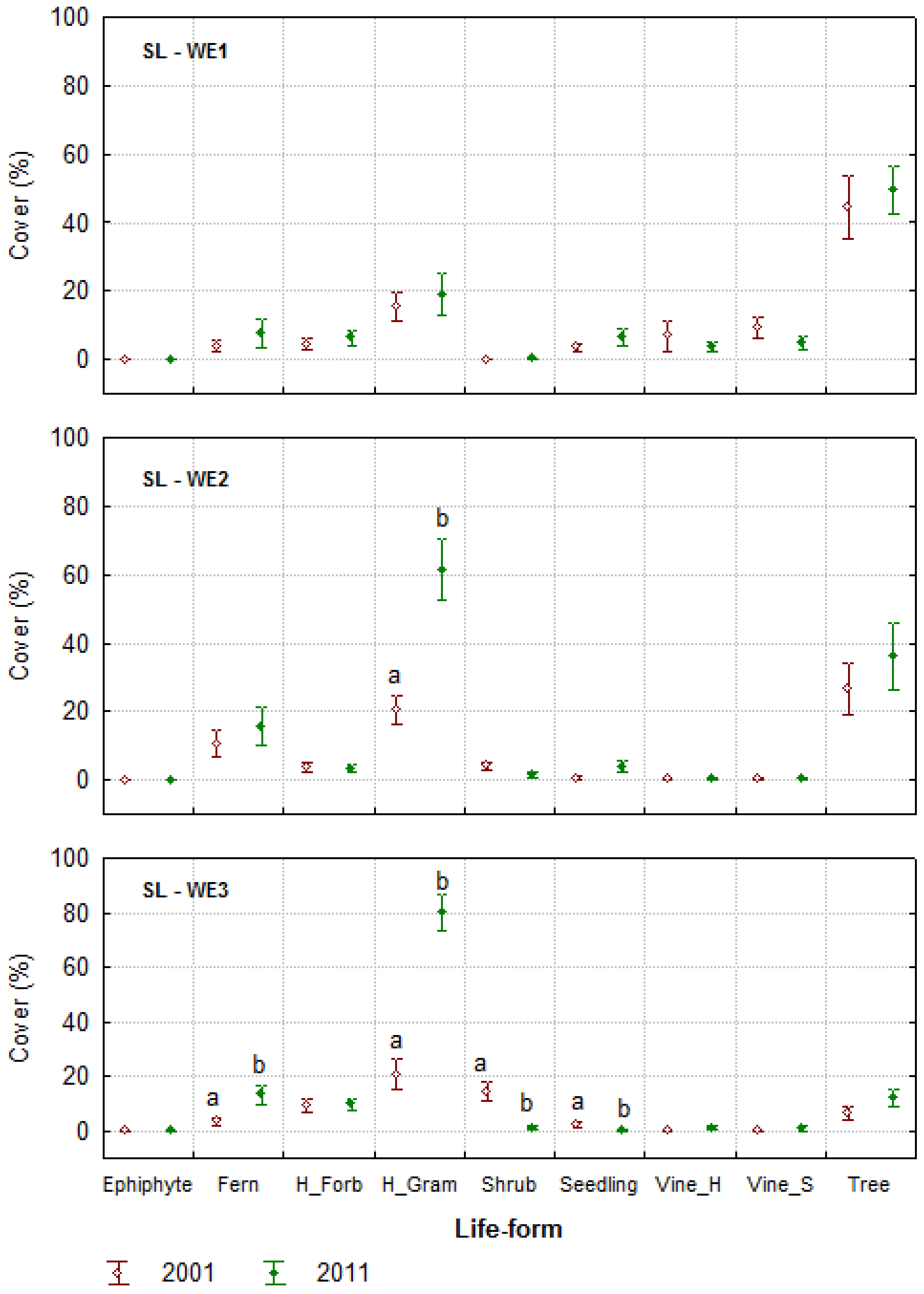


Figure 1.13: Mean (± S. E.) cover (%) of different life forms in 2001 and 2011 on three transects in Satinleaf.

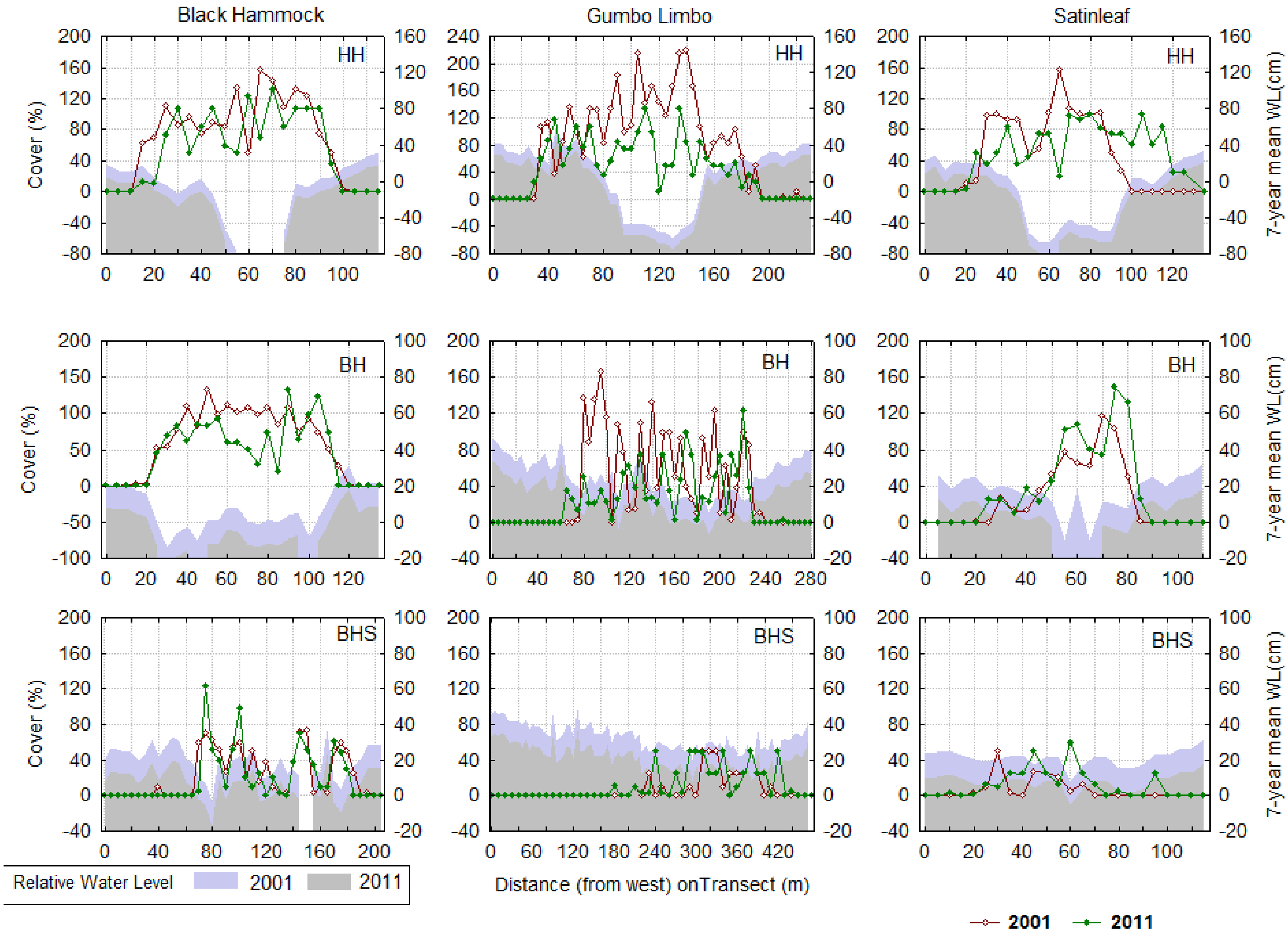


Figure 1.14: Graminoid cover in 2001 and 2011 and annual mean water level for seven years before sampling on the transects in three Shark Slough tree islands. Three transects are HH = hardwood hammock, BH = Bayhead, and BHS = Bayhead Swamp.

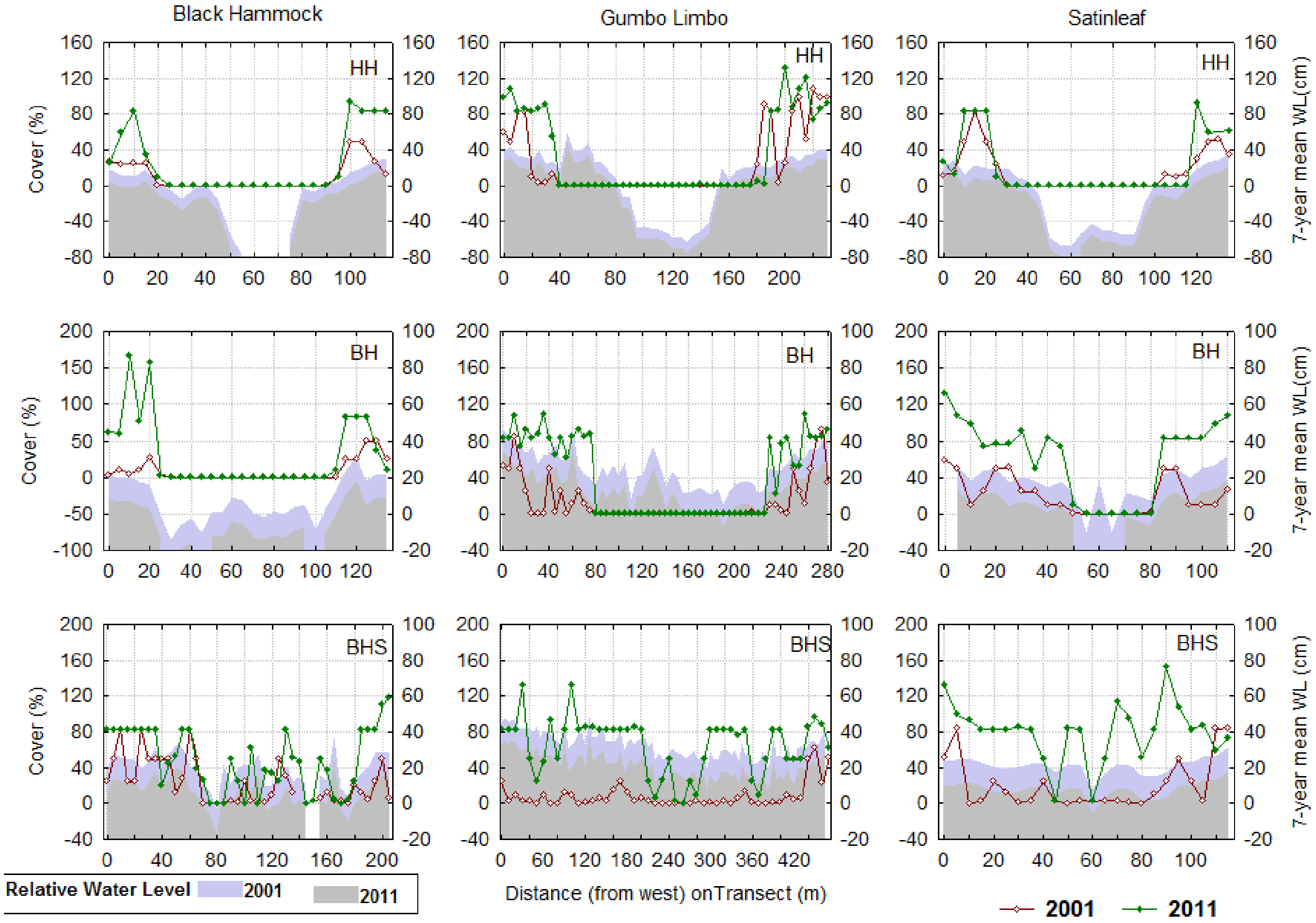


Figure 1.15: Sawgrass (*Cladium mariscus* ssp. *jamaicense*) cover in 2001 and 2011 and annual mean water level for seven years before sampling on the transects in three Shark Slough tree islands. Three transects are HH = hardwood hammock, BH = Bayhead, and BHS = Bayhead Swamp.

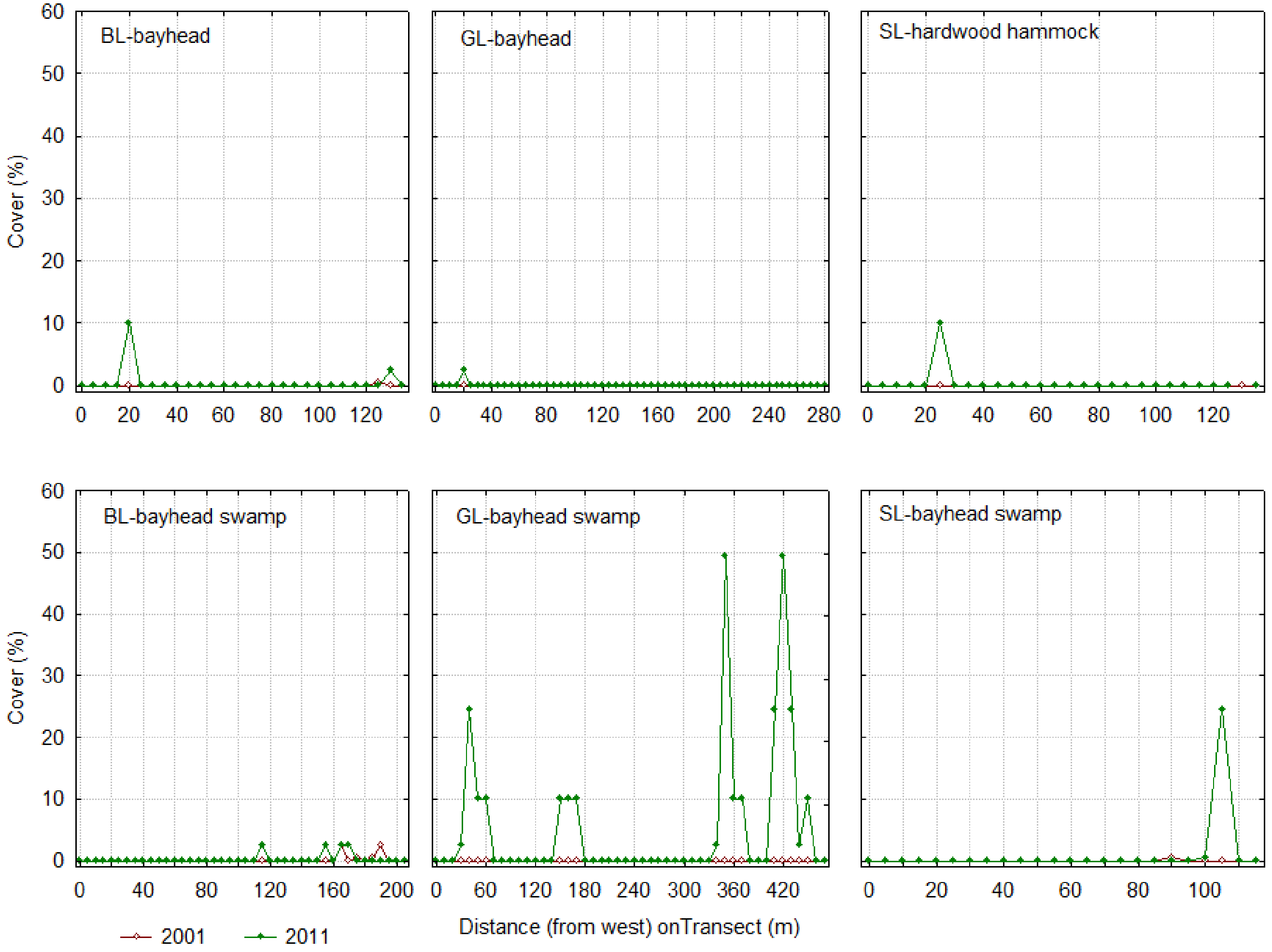


Figure 1.16: Cattail (*Typha domingensis*) cover in 2001 and 2011 on six transects in three Shark Slough tree islands.

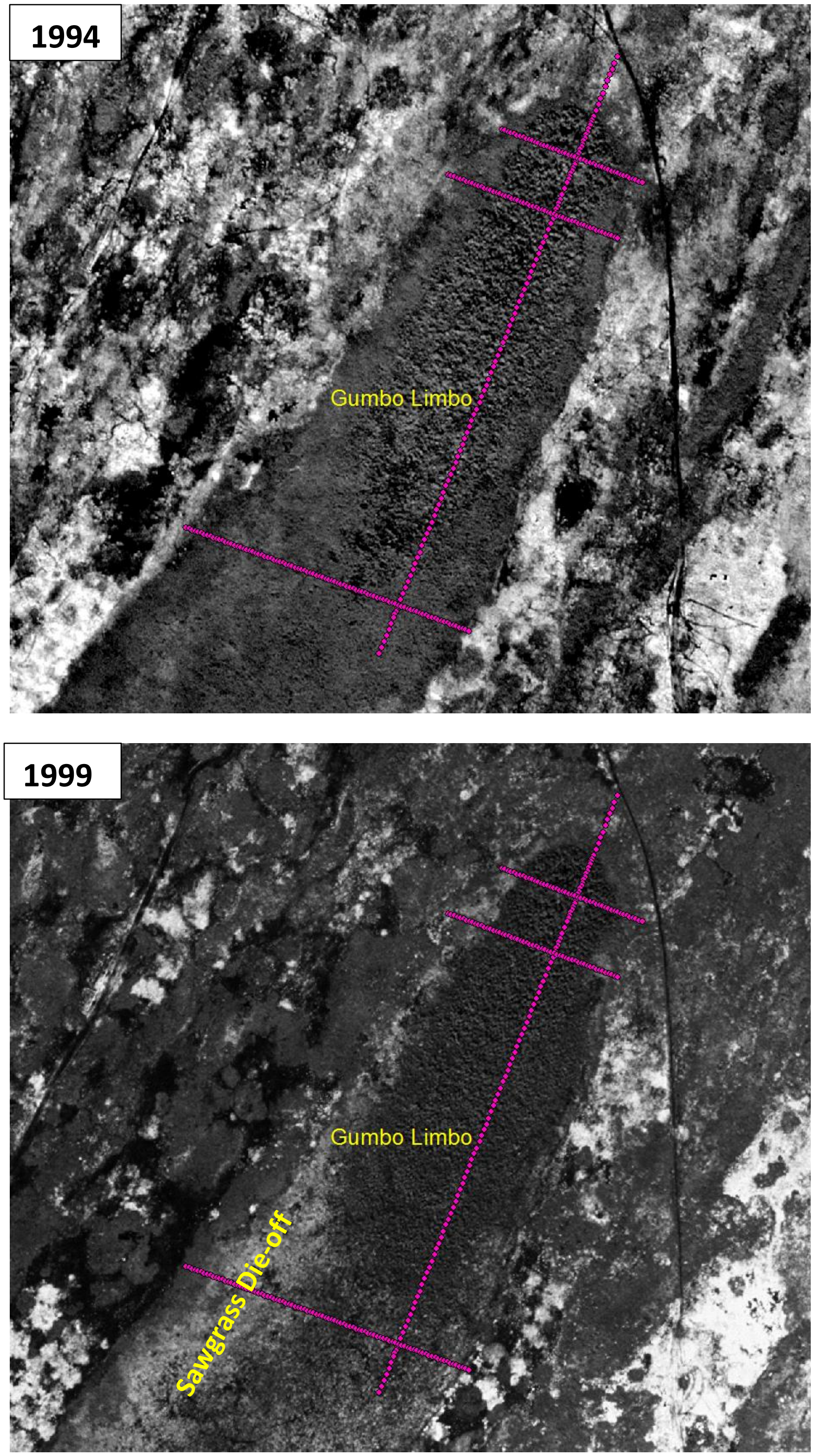


Figure 1.17: Images of Gumbo Limbo in 1994 and 1999, showing the area of sawgrass die-off present in 1999.

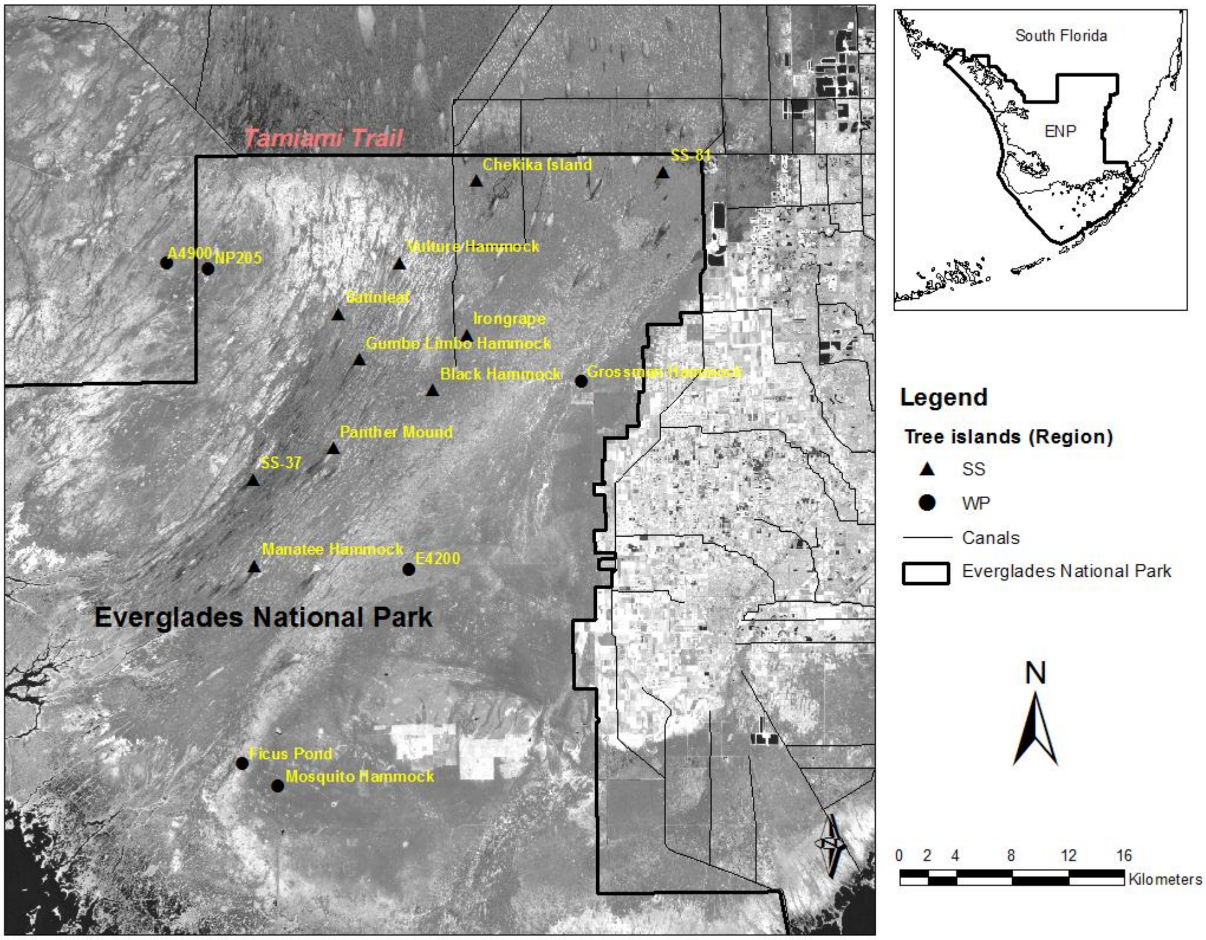


Figure 2.1: Location of study islands in Shark Slough and Wet Prairie landscape within Everglades National Park.

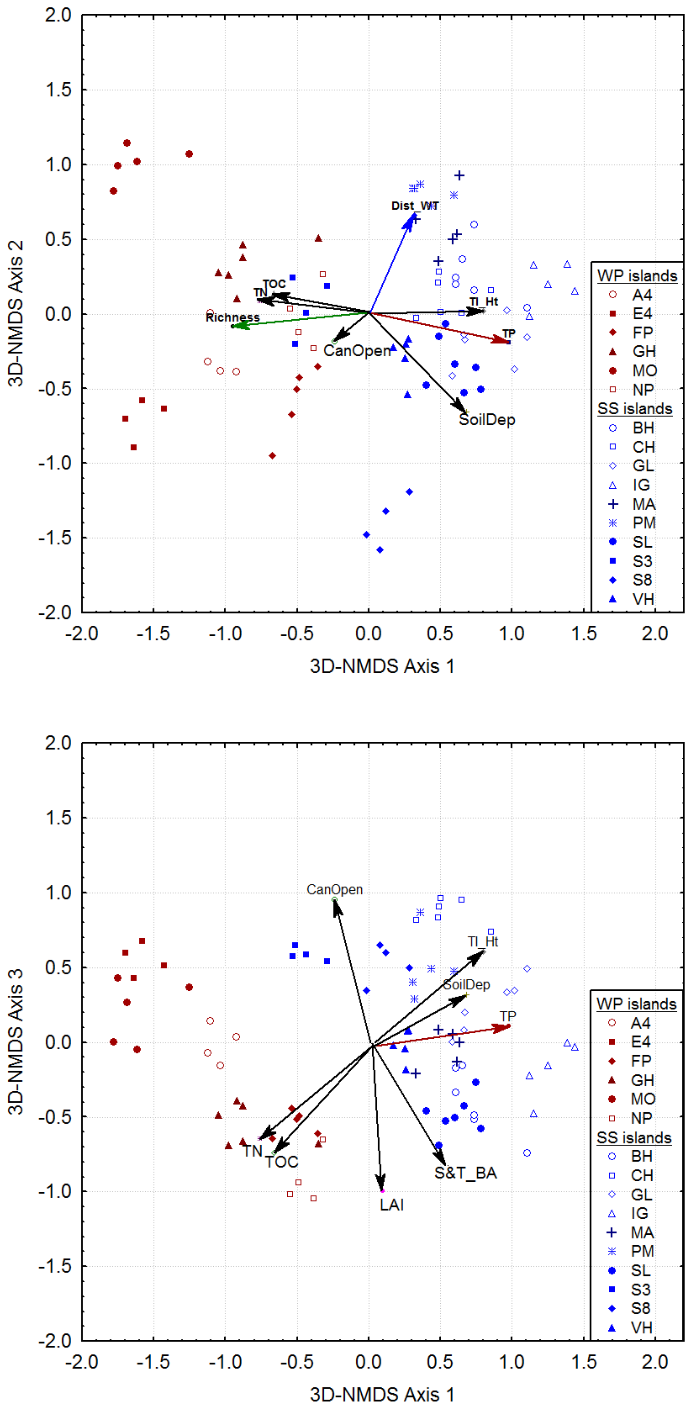


Figure 2.2: Bi-plots of axis scores derived from understory species' importance value (IV) – based three-dimensional non-metric multidimensional ordination (NMDS) of 16 hardwood plots sampled in multiple years between 2001 and 2010. Fitted environmental and species richness vector represent the direction of maximum correlation between the variable and ordination configuration. The name of islands and their codes are given in Appendix A.4.

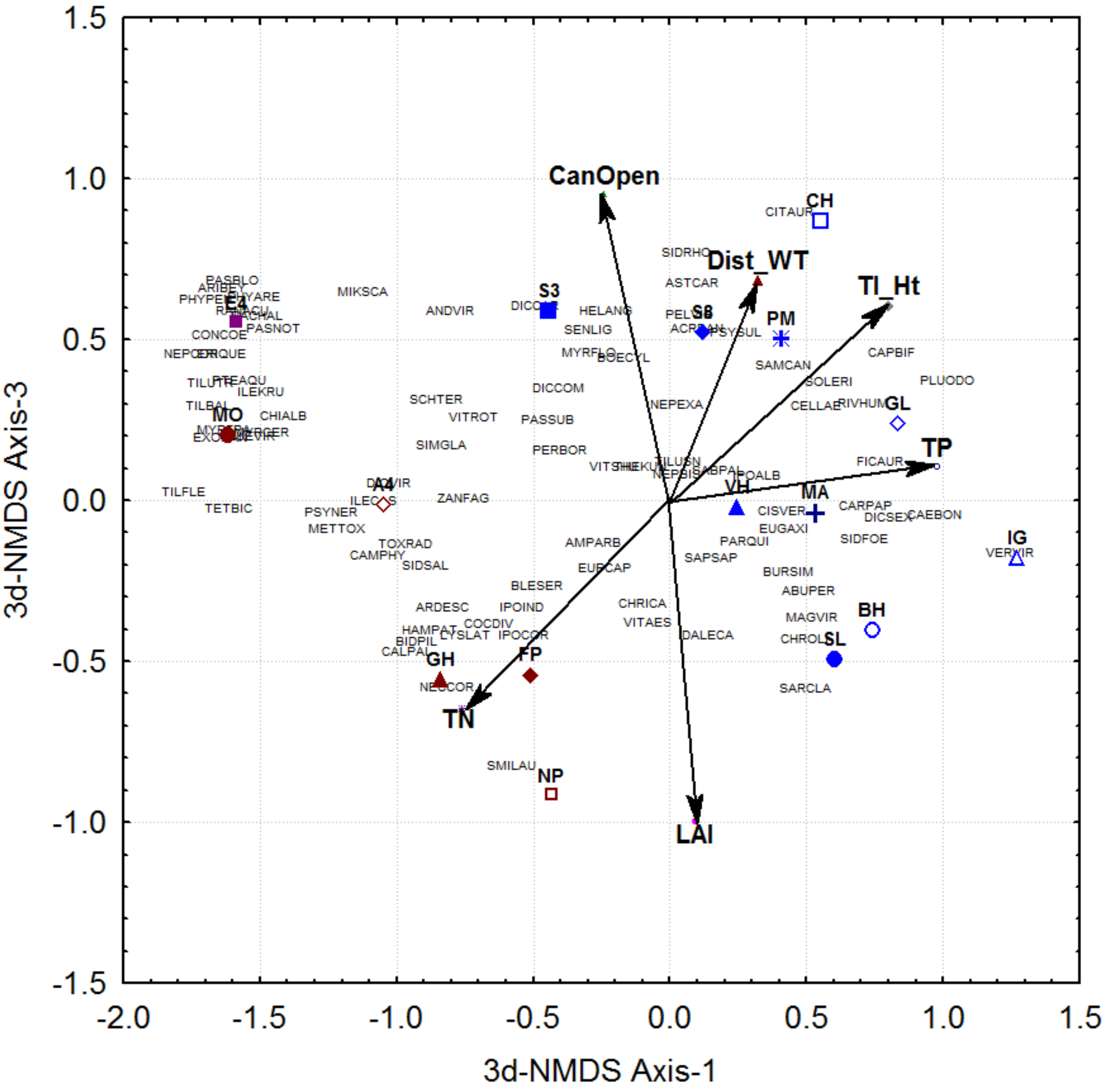


Figure 2.3: Bi-plots of species scores derived from weighted averaging of the site-scored derived from derived from understory species' importance value (IV) –based three-dimensional non-metric multidimensional ordination (NMDS) of 16 hardwood plots sampled in multiple years between 2001 and 2010. Fitted environmental and species richness vector represent the direction of maximum correlation between the variable and ordination configuration. The name of species and their codes are given in Appendix A.5.

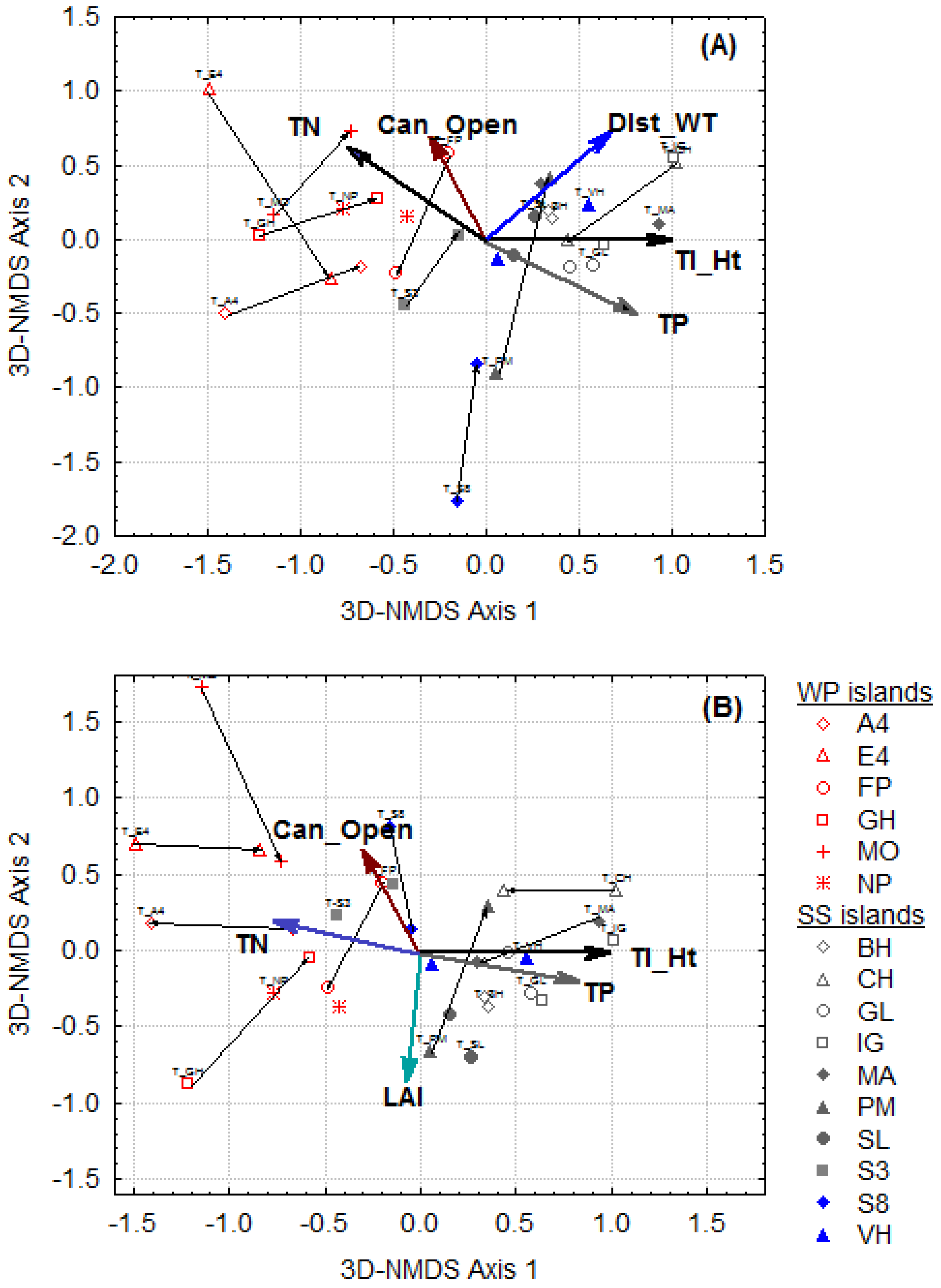


Figure 2.4: Overlay of the three-dimensional NMDS ordinations based on species' abundance (Importance Value) in overstory (sapling and tree) and understory (herb and shrub) vegetation layers. The understory-based ordination configuration was fitted on the overstory vegetation-based ordination using procrustes analysis. The fitted vectors represent the direction of maximum correlation between the variable and ordination configuration. Prior to procurstes analysis ordination configurations were rotated so that the vector for TI_HT was aligned with Axis-1. The name of islands and their codes are given in Appendix A.4.

Appendix A.1: Linear regression co-efficient, coefficient of variation (r^2), and p-value for the relationship between hydrological parameters (7-year average hydroperiod and mean water depth) and normalized Bray-Curtis dissimilarity (Z-Score). N-S = North South, HH = Hardwood hammock, BH = Bayhead, BHS = Bayhead swamp; ns = not significant. N-S transects were not sampled in 2011.

Hydroperiod									
Tree island	Transect	2001				2011			
		a	b	r^2	p	a	b	r^2	p
Black Hammock	N-S	-1.201	0.016	0.637	<0.001				
	HH	-0.502	0.014	0.460	0.001	-0.063	0.012	0.361	0.007
	BH	-0.964	0.023	0.621	<0.001	-1.483	0.023	0.68	<0.001
	BHS	-1.191	0.043	0.626	<0.001	-1.160	0.022	0.325	<0.001
Gumbo Limbo	N-S	-1.747	0.019	0.471	<0.001				
	HH	-0.714	0.009	0.222	0.002	-0.925	0.012	0.26	<0.001
	BH	-0.618	0.019	0.073	0.052	ns			
	BHS					-0.748	0.056	0.304	<0.001
Satinleaf	N-S	-1.195	0.014	0.514	<0.001				
	HH	-0.561	0.009	0.376	0.002	-1.013	0.014	0.454	<0.001
	BH	-1.212	0.033	0.576	<0.001	-1.002	0.036	0.659	<0.001
	BHS	ns				ns			
Water depth									
Black Hammock	N-S	-1.041	0.054	0.652	<0.001				
	HH	0.346	0.021	0.225	0.040	ns			
	BH	-1.052	0.156	0.663	<0.001	-1.468	0.175	0.635	<0.001
	BHS	-1.889	0.244	0.580	<0.001	-1.095	0.154	0.25	0.002
Gumbo Limbo	N-S	-1.757	0.081	0.518	<0.001				
	HH	-0.705	0.033	0.141	0.014	-1.002	0.048	0.284	<0.001
	BH	-0.998	0.139	0.188	0.001	ns			
	BHS					-1.061	0.365	0.364	<0.001
Satinleaf	N-S	-1.012	0.050	0.451	<0.001				
	HH	-0.296	0.026	0.223	0.023	-0.773	0.034	0.301	0.008
	BH	-1.154	0.189	0.526	<0.001	-0.858	0.219	0.551	<0.001
	BHS	ns				ns			

Appendix A.2: A change in vegetation type at sites within the transition zone between vegetation assemblages on the transects in three Shark Slough islands. HH = hardwood hammock, BH = Bayhead, BHS = Bayhead swamp, M = Marsh. Species codes are according to Appendix A.3.

Island	Tran sect	Meter	Vegetation type		Major change in species' cover
			2001	2011	
Black Hammock	BW1	45	HH	BH	BURSIM & CELLAE decreased, SALCAR appeared
Black Hammock	BW1	75	HH	BH	BURSIM & EUGAXI not present in 2011
Black Hammock	BW2	10	BHS	M	ANNGLA decreased, CLAJAM, ELECEL 83%
Black Hammock	BW2	15	BHS	M	ANNGLA decreased, CLAJAM, ELECELincreased
Black Hammock	BW2	115	BH	BHS	ANNGLA, SALCAR decreased, CLAJAM increased
Black Hammock	BW2	120	BHS	M	ANNGLA decreased, ClADIUM increased
Black Hammock	BW3	185	BHS	M	ANNGLA decreased, CLAJAM 83%
Gumbo Limbo	GW1	30	M	BHS	ANNGLA & CEPOCC increased, ELECEL also increased
Gumbo Limbo	GW1	150	HH	BH	BURSIM, FICUS absent
Gumbo Limbo	GW1	185	BHS	BH	Fern increased, MAGVIR increased
Gumbo Limbo	GW1	190	BHS	BH	MAGVIR present
Gumbo Limbo	GW1	195	BHS	M	MAGVIR decreased, CLAJAM & ELECEL increased
Gumbo Limbo	GW1	200	BHS	M	CEPOCC decreased, CLAJAM & ELECEL increased
Gumbo Limbo	GW1	210	BHS	M	ANNGLA decreased
Gumbo Limbo	GW1	220	BHS	M	ANNGLA decreased
Gumbo Limbo	GW2	40	M/BHS	M	CLAJAM increased
Gumbo Limbo	GW2	45	M/BHS	M	CLAJAM increased
Gumbo Limbo	GW3	170	BHS/M	M	CLAJAM increased
Gumbo Limbo	GW3	180	BHS	BHS/M	CLAJAM increased
Gumbo Limbo	GW3	190	BHS	BHS/M	CLAJAM increased
Gumbo Limbo	GW3	200	BHS	BHS/M	CLAJAM increased , CEPOCC decreased
Gumbo Limbo	GW3	420	M	BHS	SALCAR & CEPOCC increased
Satinleaf	SW1	100	BHS	BH	ANNGLA & CHRICA increased
Satinleaf	SW1	105	BHS	BH	ANNGLA & CHRICA increased
Satinleaf	SW1	110	BHS	BH	ANNGLA & CHRICA increased
Satinleaf	SW1	115	BHS	BH	CHRICA increased
Satinleaf	SW1	120	M	BHS	ANNGLA, SALCAR increased
Satinleaf	SW1	125	M	BHS	DALECA, MAGVIR increased
Satinleaf	SW2	25	M	BHS	ANNGLA increased
Satinleaf	SW3	20	BHS	BHS/M	High CLAJAM Cover - uniform
Satinleaf	SW3	25	BHS	BHS/M	High CLAJAM Cover - uniform
Satinleaf	SW3	30	BHS	BHS/M	High CLAJAM Cover - uniform
Satinleaf	SW3	90	M	BHS	CEPOCC decreased, CLAJAM & ELECEL increased
Satinleaf	SW3	95	M	BHS	MAGVIR increased

Appendix A.3: Mean species cover on the transects in three Shark Slough tree islands sampled in 2001/2002 and 2011. Three transects are: HH = Hammock, BH = Bayhead, and BHS = Bayhead Swamp. Tree species in the seedling (height <1 m) layer are listed separately.

Species	SPCODE	Black Hammock						Gumbo Limbo						Satinleaf					
		WE1 (HH)		WE2 (BH)		WE3 (BHS)		WE1 (HH)		WE2 (BH)		WE3 (BHS)		WE1 (HH)		WE2 (BH)		WE3 (BHS)	
		2001	2011	2001	2011	2001	2011	2001	2011	2001	2011	2001	2011	2001	2011	2001	2011	2001	2011
Acrostichum danaeifolium	ACRDAN	2.06	1.04	5.59	1.89	0.01	1.19	7.28	3.00	12.78	6.80	2.48	0.31			2.26	1.07		
Aeschynomene pratensis	AESPRA		0.10				0.30					0.02	0.22		0.19	0.02		0.02	0.10
Ampelopsis arborea	AMPARB	0.02	0.52					0.35	0.53	1.30	0.02				0.39				
Andropogan glomeratus	ANDGLO													0.54					
Annona glabra	ANNGLA	11.63	3.58	20.30	4.95	12.67	9.82	18.19	11.48	17.32	6.73	0.01	0.08	1.59	4.94	8.43	12.65	4.35	4.27
Annona glabra_seedling	ANNGLA-S	0.67	1.15	0.54	1.00	4.95	3.74	1.90	0.05	2.25	0.21	0.44		0.39	0.02	0.15	0.24	1.73	0.13
Apios americana	APIAME		6.33		13.23					0.04									
Aster carolinianus	ASTCAR				0.09		1.13	0.02			0.09	0.52	0.48				0.02		
Aster dumosus	ASTDUM			0.46															
Bacopa caroliniana	BACCAR	1.69	1.96	0.45	2.82	2.82	2.26	0.85	0.53	1.55	1.57		0.52	1.07		1.26	1.41	0.77	1.77
Baccharis halimifolia	BACHAL												0.05						
Bacopa monnieri	BACMON														0.46				0.94
Blechnum serrulatum	BLESER	3.27	1.65	2.38	3.95	5.45	7.00	5.11	5.51	9.26	9.72	9.88	7.61	3.20	4.94	8.20	11.11	3.65	13.29
Boehmeria cylindrica	BOECYL	0.17	2.58	0.48	0.71	0.04	0.55	0.16	0.07	1.17	0.02	0.22	0.10	0.21	0.19	0.07		0.02	
Bursera simaruba	BURSIM	12.17	3.50					12.38	7.37					4.41	3.48				
Bursera simaruba_seedlimng	BURSIM-S							0.05	0.01										
Caesalpinia bonduc	CAEBON								4.45										
Celtis laevigata	CELLAE	3.00	1.02					14.18	0.73					0.73	0.37				
Celtis laevigata_seedling	CELLAE-S	0.02	0.52					0.10	0.12										
Cephalanthus occidentalis	CEPOCC		0.94	0.11	1.41	0.82	14.69	1.50	0.48	2.40	4.29	3.63	9.69			4.07	1.52	14.48	1.15
Chrysobalanus icaco	CHRICA	20.83	27.71	23.02	27.41	0.30	4.00	13.15	11.61	2.08	2.56			15.23	15.17	5.76	14.65		
Chrysobalanus icaco_seedling	CHRICA-S	4.79	2.48	1.77	2.00	4.80		7.99	2.16	3.89	2.48		0.05	1.45	2.09	0.48	3.20		
Chrysophyllum oliviforme	CHROLI													11.80	9.83				
Chrysophyllum oliviforme_seedling	CHROLI-S													0.09	0.19				
Cissus verticillata	CISVER	0.94	0.94	0.13	0.54			0.47	0.89	0.04	1.47			5.86	2.28				
Cladium mariscus ssp. jamaicense	CLAJAM	8.65	19.40	7.88	16.71	20.80	35.89	12.65	12.10	10.54	20.87	5.51	53.73	11.20	14.41	17.09	43.98	10.10	53.08
Coccoloba diversifolia	COCDIV														3.11				
Coccoloba diversifolia_seedling	COCDIV-S													0.36	0.11				
Cyperus haspan	CYPHAS					0.24	0.71	0.06	0.05	0.06		0.21	0.06						0.52

Species	SPCODE	Black Hammock						Gumbo Limbo						Satinleaf					
		WE1 (HH)		**WE2 (BH)**		**WE3 (BHS)**		**WE1 (HH)**		**WE2 (BH)**		**WE3 (BHS)**		**WE1 (HH)**		**WE2 (BH)**		**WE3 (BHS)**	
		2001	2011	2001	2011	2001	2011	2001	2011	2001	2011	2001	2011	2001	2011	2001	2011	2001	2011
Cyperus ligularis	CYPLIG															0.04		0.04	
Cyperus odoratus	CYPODO	0.02				0.02													
Dalbergia ecastaphyllum	DALECA													2.84	0.37	0.43	0.46		
Dichanthelium commutatum	DICCOM								0.05										
Dichanthelium dichotomum	DICDIC																	0.02	
Diodia virginiana	DIOVIR			0.04				0.01	0.21	0.13		0.17		0.98		0.07		0.06	
Echinochloa crusgalli	ECHCRU					0.09						0.04							
Eleocharis caribaea	ELECAR																	0.02	
Eleocharis cellulosa	ELECEL	0.35	1.54	0.11	9.29	0.06	3.15	9.01	19.05	2.15	13.91	1.25	7.79	3.54	2.74	3.39	13.65	9.40	22.92
Eleocharis elongata	ELEELO												0.51						
Eleocharis interstincta	ELEINT										1.46		0.51						
Eugenia axillaris	EUGAXI	8.65	6.96					13.54	8.47					3.71	6.59				
Eugenia axillaris_seedling	EUGAXI-S	0.94	4.08					6.64	10.64					1.18	3.13				
Eupatorium leptophyllum	EUPLEP																		0.02
Ficus aurea	FICAUR				0.36			0.21	0.13		0.04			0.36					
Ficus aurea_seedling	FICAUR-S							0.21		0.01				0.02					
Fuirena breviseta	FUIBRE						2.25	0.09	0.32	0.12	0.76	0.11	1.68	0.02	0.37	0.02		0.19	0.44
Habenaria sp.	HABXXX						0.13												
Hibiscus grandiflorus	HIBGRA													0.04					
Hydrolea corymbosa	HYDCOR							0.52			0.05						0.11		0.42
Hymenocallis palmeri	HYMPAL											0.01	0.01						
Hyptis alata	HYPALA														0.09				0.10
Ilex cassine	ILECAS			0.45					0.21	2.93	1.26								
Ilex cassine_seedling	ILECAS-S			0.02		0.06	0.24		0.01	1.39	0.05								
Ipomoea alba	IPOALB									0.05									
Ipomoea sagittata	IPOSAG	0.02	0.31		0.09		0.55	0.07		0.12	0.03	0.02	0.50	0.02	0.74	0.04	0.22	0.04	0.63
Ipomoea sp.	IPOXXX				0.09				0.04		0.02				1.93				
Justicia angusta	JUSANG			0.02	0.04			0.04	0.03	0.03	0.01	0.24	0.84	0.02	1.93	0.04	0.43	1.67	0.54
Kosteletzkya virginica	KOSVIR											0.05	0.05						
Leersia hexandra	LEEHEX	0.02		0.18		0.65	0.19	0.36	0.06	0.01	0.38	0.01	0.01		0.91	0.02	2.24		1.65
Ludwigia alata	LUDALA			0.02		0.01	2.05					0.04	0.01		0.46	0.04	0.11		0.73
Ludwigia curtissii	LUDCUR													0.04					

Species	**SPCODE**	**Black Hammock**						**Gumbo Limbo**						**Satinleaf**					
		WE1 (HH)		**WE2 (BH)**		**WE3 (BHS)**		**WE1 (HH)**		**WE2 (BH)**		**WE3 (BHS)**		**WE1 (HH)**		**WE2 (BH)**		**WE3 (BHS)**	
		2001	2011	2001	2011	2001	2011	2001	2011	2001	2011	2001	2011	2001	2011	2001	2011	2001	2011
Ludwigia repens	LUDREP		0.52	0.14	0.02	2.33	0.65	1.05	2.82	1.39	0.01		0.01	0.46				0.13	
Magnolia virginiana	MAGVIR			0.02	0.71	1.04	0.65	2.06	1.10	3.22	2.73			0.09	0.91	4.43	7.41	2.06	7.10
Magnolia virginiana_seedling	MAGVIR-S				0.09	0.13	0.01	1.59		1.18	0.11					0.02	0.22	0.52	0.02
Melothria pendula	MELPEN							0.02		0.08									
Mikania scandens	MIKSCA	0.06		0.05		0.33	0.13	0.01		0.18	0.18	0.23	1.57	0.13		0.11	0.11	0.19	0.42
Mitreola petiolata	MITPET											0.01		0.11					
Morella cerifera	MORCER	2.60	1.46	2.73	3.00	5.60	4.13		0.95	1.26	3.12		0.51	1.77	0.37	1.72	0.98	0.04	
Myrica cerifera_seedling	MORCER-S	0.06	0.02	0.02	0.16	0.32	0.35	0.05		0.46	0.05				0.56	0.04	0.22		
Myrsine floridana	MYRFLO							0.28	0.52					1.86					
Myrsine floridana_seedling	MYRFLO-S							0.06	0.68					0.02					
Nectandra coriacea_seedling	NECCOR-S								0.05										
Nephrolepis exaltata	NEPEXA		0.42		0.09														
Nymphoides aquatica	NYMAQU												0.05						
Nymphaea odorata	NYMODO											0.05	0.68						
Oeceoclades maculata	OECMAC		0.10						0.13		0.01								
Osmunda regalis	OSMREG										0.04								
Oxypolis filiformis	OXYFIL													0.02					
Panicum hemitomon	PANHEM		1.67	0.13	0.46	0.16	4.23	0.27	0.12		0.02	0.21	0.28	0.04	0.46			1.02	0.10
Panicum rigidulum	PANRIG					0.09		0.05								0.02			
Panicum virgatum	PANVIR						0.06												0.83
Parietaria floridana	PARFLO								0.06										
Parthenocissus quinquefolia	PARQUI	0.10	2.38	0.11	2.23	0.10	0.24	0.03	0.33					0.75	1.69				
Paspalidium geminatum	PASGEM		0.42		0.09	0.01						0.22	0.06	0.11					
Passiflora pallens	PASPAL														1.00				
Passiflora suberosa	PASSUB				0.02														
Passiflora sp.	PASXXX						0.06												
Peltandra virginica	PELVIR	1.17		0.73	0.36	11.39	1.79	0.12		0.05	0.09	1.52	0.36			0.04	0.22	0.08	
Persea borbonia	PERBOR	0.02				0.90	0.64	0.70		0.24									
Persea borbonia_seedling	PERBOR-S	0.02	0.21		0.09	0.06	0.62	0.01	0.02	0.61	0.05		0.01	0.07			0.02		
Pluchea rosea	PLUROS	0.02	1.04	0.02		0.09	2.42		0.06	0.01	0.05	0.01		0.02	0.09	0.26	0.04	0.17	0.21
Polygonum hydropiperoides	POLHYD	0.04	0.21	0.39	0.09	0.02	0.30	0.01	0.02	0.08	0.04	1.45	1.38			0.28			
Pontederia cordata	PONCOR	0.15	0.10	0.14	0.09	1.77	1.54	1.10	0.13	1.05	0.62	2.27	1.43	1.00		1.57	0.13	6.19	0.85

Species	SPCODE	Black Hammock						Gumbo Limbo						Satinleaf					
		WE1 **(HH)**		**WE2** **(BH)**		**WE3** **(BHS)**		**WE1** **(HH)**		**WE2** **(BH)**		**WE3** **(BHS)**		**WE1** **(HH)**		**WE2** **(BH)**		**WE3** **(BHS)**	
		2001	2011	2001	2011	2001	2011	2001	2011	2001	2011	2001	2011	2001	2011	2001	2011	2001	2011
Proserpinaca palustris	PROPAL		1.44			0.13	6.51	0.01	0.01	0.13	0.45	0.53	0.28		0.02		0.11	0.06	0.23
Psilotum nudum	PSINUD		0.10			0.01							0.05						
Pteridium aquilinum var. *caudatum*	PTECAU													0.38					
Rhynchospora colorata	RHYCOL								0.21										
Rhynchospora divergens	RHYDIV				0.88														
Rhynchospora inundata	RHYINU		0.42		1.23		1.83	0.29	1.27	0.49	1.11	0.33	0.05		0.09		1.41		0.52
Rhynchospora microcarpa	RHYMIC				0.88					0.01							0.11		
Rhynchospora miliacea	RHYMIL																0.02		
Rhynchospora tracyi	RHYTRA		0.10		0.09	0.07		0.02	0.11	0.01	0.04		0.21	0.11					
Rivina humilis	RIVHUM							3.78	0.06										
Sabal palmetto_seedling	SABPAL-S	0.04	0.02						0.01										
Sacciolepis striata	SACSTR	1.46		0.02		0.89		0.02		0.03		0.29							
Sagittaria lancifolia	SAGLAN	0.04	0.63		0.18	0.02	0.24				0.74		6.58	0.02			0.33		2.21
Salix caroliniana	SALCAR	5.40	4.50	12.38	10.16	0.84		3.47	1.57	10.97	7.18	7.73	10.65	3.02	4.67	6.33	0.43		0.63
Salix caroliniana_seedling	SALCAR-S	0.04	2.06		0.55	0.02		0.10		1.49		4.84	0.21				0.02		
Sarcostemma clausum	SARCLA	0.04		1.36	0.09	0.02	0.01	2.11	0.35	5.55	0.35	4.03	0.30	6.84		0.13	0.22		
Saururus cemuus	SAUCER	0.04	1.13	0.23	0.45	0.46	1.50	0.83	0.27	1.46	0.54			0.39	1.00	0.15		0.21	
Setaria magna	SETMAG											0.01							
Sideroxylon foetidissimum	SIDFOE	4.10	6.19					1.05	1.32										
Sideroxylon foetidissimum_seedling	SIDFOE-S	0.04	0.10						0.05										
Simarouba glauca	SIMGLA													0.02	0.09				
Simarouba glauca_seedling	SIMGLA-S														0.46				
Smilax bona-nox	SMIBON						0.12												
Smilax laurifolia	SMILAU					0.06													1.02
Solanum erianthum	SOLERI							0.01	0.79										
Thelypteris interrupta	THEINT	0.54	1.88	1.25	3.13			1.69	3.53	4.81	8.32			0.27	2.57	0.28	3.54		
Thelypteris kunthii	THEKUN							1.05	0.21		0.01								
Thelypteris palustris var. pubescens	THEPAL											0.27							
Tillandsia balbisiana	TILBAL										0.01								
Tilandsia fasiculata	TILFAS					0.01		0.10	1.85										
Tillandsia flexuosa	TILFLE							0.05		0.18	0.03								
Tillandsia paucifolia	TILPAU							0.06	0.05										

Species	**SPCODE**	**Black Hammock**						**Gumbo Limbo**						**Satinleaf**					
		WE1 (HH)		**WE2 (BH)**		**WE3 (BHS)**		**WE1 (HH)**		**WE2 (BH)**		**WE3 (BHS)**		**WE1 (HH)**		**WE2 (BH)**		**WE3 (BHS)**	
		2001	2011	2001	2011	2001	2011	2001	2011	2001	2011	2001	2011	2001	2011	2001	2011	2001	2011
Tillandsia recurvata	TILREC					0.01	0.06	0.51	0.05	0.04									
Tillandsia usneoides	TILUSN	0.04						0.01		0.04									
Tillandsia utriculata	TILUTR							0.01											
Typha domingensis	TYPDOM			0.02	0.45	0.15	0.24				0.04		5.42		0.37			0.02	1.04
Utricularia foliosa	UTRFOL	1.13		0.02	1.77	0.30	2.00	0.70	0.11	2.40	2.22	12.30	5.77		1.74				0.21
Utricularia purpurea	UTRPUR	0.10						0.02	1.04	1.31	6.81		4.30				0.43		0.52
Vallisneria americana	VALAME									0.05									
Vitis sp.	VITXXX	1.44	0.10		1.23		0.01	0.33											
Unkown sp1	XXX001				0.02		0.01												
Xyris sp.	XYR001						0.01		0.05		0.01								

Appendix A.4: Tree island plot attributes and their location (Ruiz et al. 2011).

Region	Island Code	Tree Island	Year established	Plot Size (m^2)	No. of 5 x5 m cells	Easting NAD83 (UTM_Z17N)	Northing NAD83 (UTM_Z17N)
NESS	CH	Chekika Island	2005	400	16	534372	2847485
NESS	IG	Irongrape	2006	400	16	533651	2836523
NESS	S8	SS-81	2007	300	12	547639	2848113
SS	BH	Black Hammock	2001/2002	400	16	531295	2832630
SS	GL	Gumbo Limbo Hammock	2001/2002	625	25	525999	2834793
SS	MA	Manatee Hammock	2006	400	16	518560	2820117
SS	PM	Panther Mound	2006	400	16	524189	2828472
SS	SL	Satinleaf	2001/2002	625	25	524499	2838019
SS	S3	SS-37	2007	300	12	518488	2826245
SS	VH	Vulture Hammock	2006	400	16	528918	2841667
WP	A4	A4900	2007	400	16	512305	2841611
WP	E4	E4200	2007	400	16	529566	2819857
WP	FP	Ficus Pond	2005	225	9	517701	2806030
WP	GH	Grossman Hammock	2005	400	16	541819	2833205
WP	MO	Mosquito Hammock	2005	450	18	520271	2804429
WP	NP	NP205	2007	400	16	515279	2841219

Appendix A.5: Mean abundance (Importance Value) of plant species present in herb and shrub layer in 16 hardwood hammocks in Shark Slough (SS) and short hydroperiod wet prairies (WP) landscapes in Everglades National Park. Values were averaged over multiple samplings between 2001/2002 and 2010. The name of islands is given in Appendix A.4.

Species	Spp. Code	Tree islands															
		Wet Prairie						Shark Slough									
		A4	E4	FP	GH	MO	NP	BH	CH	GL	IG	MA	PM	SL	S3	S8	VH
Abutilon permolle	ABUPER											2.33		0.46			
Acrostichum danaeifolium	ACRDAN									0.00						2.58	
Ampelopsis arborea	AMPARB		0.46	0.08	0.00			0.03		0.00				0.06	0.02		0.03
Andropogon virginicus	ANDVIR		5.21													2.68	
Anemia adiantifolia	ANEADI				0.00	0.25											
Annona glabra	ANNGLA					0.00				0.01			0.03			0.16	
Ardisia escallonoides	ARDESC	7.95	0.05	0.67	1.10	0.92	1.73					0.08					0.01
Aristida beyrichiana	ARIBEY		0.07														
Aster carolinianus	ASTCAR															0.03	
Baccharis halimifolia	BACHAL		1.65			0.01										0.03	
Bidens pilosa	BIDPIL				0.19												
Blechnum serrulatum	BLESER	2.14		0.32	0.00		2.53								1.32	1.69	
Boehmeria cylindrica	BOECYL	0.25								0.01		0.06			0.25	0.80	
Bursera simaruba	BURSIM	0.13	0.00		0.03	0.01	0.07	0.28		0.22		1.68	0.27	0.61	0.43		0.03
Caesalpinia bonduc	CAEBON							0.11	0.27	0.61	3.42						0.04
Calyptranthes pallens	CALPAL				0.37												
Campyloneurum phyllitidis	CAMPHY				0.62	0.49									0.52		
Capraria biflora	CAPBIF								0.02	0.14							
Carica papaya	CARPAP							0.46	0.12		0.02	1.36		0.13			0.11
Celtis laevigata	CELLAE				0.01			0.07	2.40	1.52	0.99	3.94	0.94	0.87	0.83	6.09	1.20
Chamaecrista fasciculata	CHAFAS		0.59														
Chiococca alba	CHIALB		0.50		0.03												
Chrysobalanus icaco	CHRICA	1.53		9.60	0.01	0.43	2.71	1.10	0.01	0.12	0.04	1.20	0.08	0.82	3.19		2.28
Chrysophyllum oliviforme	CHROLI				0.03									0.85			0.16
Cissus verticillata	CISVER				0.02		0.06	0.04	0.00	0.54		0.09	0.19	0.07	0.14	0.01	0.21
Citrus aurantium	CITAUR								0.06								
Coccoloba diversifolia	COCDIV	1.86	0.88	0.92	1.12		1.58	0.07			0.00		0.09	0.08	1.07		0.01
Conoclinium coelestinum	CONCOE		2.30														
Crotalaria pumila	CROPUM		0.52														
Cyperus retrorsus	CYPRET		3.32														
Dalbergia ecastaphyllum	DALECA	0.02												0.01			
Dichondra carolinensis	DICCAR														0.03		
Dichanthelium commutatum	DICCOM	0.39	0.61			0.30				0.74		1.15			6.15		0.43

Species	Spp. Code	Tree islands															
		Wet Prairie						Shark Slough									
		A4	E4	FP	GH	MO	NP	BH	CH	GL	IG	MA	PM	SL	S3	S8	VH
Dicliptera sexangularis	DICSEX		0.12								0.95						
Diodia virginiana	DIOVIR	0.03	0.00														
Emilia sonchifolia	EMISON															0.04	
Encyclia tampensis	ENCTAM					0.06											
Erechtites hieracifolia	EREHIE															1.23	
Erigeron quercifolius	ERIQUE		0.01														
Eugenia axillaris	EUGAXI	3.34	0.36	4.03	1.35	0.04	3.84	12.23	6.69	17.31	31.49	5.40	5.14	6.77	5.72		7.78
Eupatorium capillifolium	EUPCAP						0.10								0.08	0.19	
Exothea paniculata	EXOPAN					1.61											
Ficus aurea	FICAUR										0.04		0.03	0.01		0.01	
Galactia volubilis	GALVOL											0.00			0.02		
Hamelia patens	HAMPAT				0.00												
Heliotropium angiospermum	HELANG									0.02					0.36		
Ilex cassine	ILECAS	0.20															
Ilex krugiana	ILEKRU					0.19											
Ipomoea alba	IPOALB			0.09	0.01	0.00	0.01	0.01		0.01	0.10	1.25	0.19		0.13		0.00
Ipomoea cordatotriloba	IPOCOR			0.04													
Ipomoea indica	IPOIND	0.01				0.02	0.01										0.02
Ipomoea sp.	IPOXXX			0.06		0.02	0.02	0.07		0.30	0.03		0.05	0.13			0.07
Iresine diffusa	IREDIF		0.33														
Jasminum fluminense	JASFLU				0.00												
Lasiacis divaricata	LASDIV					0.07				0.00							
Lysiloma latisiliquum	LYSLAT	0.10					0.04										
Magnolia virginiana	MAGVIR	0.00												0.01			
Mecardonia acuminata var. *peninsularis*	MECACU		0.43														
Melothria pendula	MELPEN	0.00							0.08	0.52	0.04	0.09	0.00	0.05		0.06	0.05
Metopium toxiferum	METTOX	0.07	0.27	0.03		0.51	0.28										
Mikania cordifolia	MIKCOR				0.02										3.24	0.01	
Mikania scandens	MIKSCA		0.03						0.00								
Muhlenbergia capillaris ssp. *filipes*	MUHCAP		0.06														
Myrica cerifera	MYRCER	0.60	0.02			0.65											
Myrsine floridana	MYRFLO	3.82	4.98	0.29	0.35	1.75	0.04	0.01	3.62	0.14		0.81		0.00	3.30		0.69
Myrcianthes fragrans	MYRFRA					1.88											
Nectandra coriacea	NECCOR			0.03	7.92	0.34	2.61	0.03						0.01			0.05
Nephrolepis biserrata	NEPBIS	1.25			0.28						0.07	2.48	3.13				
Nephrolepis cordifolia	NEPCOR					0.08											
Nephrolepis exaltata	NEPEXA	1.94		1.85	0.49	0.47		0.84	3.40	3.86	0.60		5.96		8.32		
Nephrolepis sp.	NEPXXX					0.28											

Species	Spp. Code	Tree islands															
		Wet Prairie						Shark Slough									
		A4	E4	FP	GH	MO	NP	BH	CH	GL	IG	MA	PM	SL	S3	S8	VH
Oeceoclades maculata	OECMAC				0.04		0.79	0.10	0.00	0.94		0.35	0.16	0.13	0.09	0.01	0.19
Oplismenus hirtellus	OPLHIR											3.28			0.03		
Palm	PALM			0.02													
Parietaria floridana	PARFLO							3.71		3.01		0.45	1.47			6.48	
Parthenocissus quinquefolia	PARQUI	0.13	0.10	0.08	0.49	0.08	0.00	0.41	0.02	0.67	0.19	1.25	0.20	0.54	0.23	1.42	1.17
Paspalum blodgettii	PASBLO		0.25														
Paspalum notatum	PASNOT		1.95														
Passiflora suberosa	PASSUB	0.20	0.36					0.01			0.03			0.03	0.34		0.02
Passiflora sp.	PASXXX					0.08											
Peltandra virginica	PELVIR															0.37	
Persea borbonia	PERBOR	0.69	0.01	0.01		0.08	0.00	0.00	0.00	0.02		0.01		0.02	0.13	0.08	
Phlebodium aureum	PHLAUR					0.11											
Physalis angustifolia	PHYANG		1.17														
Physalis arenicola	PHYARE		0.11														
Phyllanthus pentaphyllus var. *floridanus*	PHYPEN		0.02														
Pleopeltis polypodioides ssp. *michauxiana*	PLEPOL				0.01	1.79											
Pluchea odorata	PLUODO									0.01							
Psilotum nudum	PSINUD			0.05	0.00	0.04					0.00						
Psychotria nervosa	PSYNER	2.45	3.34		3.53	6.94	0.02	0.01							1.05		
Psychotria tenuifolia	PSYSUL	0.32											25.14		4.78		0.05
Pteridium aquilinum var. *caudatum*	PTEAQU		0.67			0.91											
Quercus virginiana	QUEVIR		0.25		0.01	2.50						0.01					
Randia aculeata	RANACU	0.00	4.35														
Rhus copallinum	RHUCOP		0.36														
Rhynchospora colorata	RHYCOL		0.12														
Rhynchospora inundata	RHYINU		2.65														
Rivina humilis	RIVHUM	0.05			0.22			1.43	0.47	18.94	5.61	5.46	11.80	0.00	0.35	9.67	
Sabal palmetto	SABPAL		0.08			0.22	0.19	0.11	0.00			0.35	0.30	0.00	0.01		0.00
Sambucus nigra ssp. *canadensis*	SAMCAN									0.09						0.07	
Sapindus saponaria	SAPSAP				0.00												0.03
Sarcostemma clausum	SARCLA						0.01	0.02				0.06		0.00			
Schoepfia schreberi	SCHCHR					0.16											
Schinus terebinthifolius	SCHTER		2.31		0.18				0.00							0.34	0.02
Senna ligustrina	SENLIG		1.98		0.01				0.44					0.00			0.36
Serenoa repens	SERREP	1.66															
Sideroxylon foetidissimum	SIDFOE				0.00		0.19	2.28	0.08	0.31	10.03	0.63		0.02			2.81

Species	Spp. Code	Tree islands															
		Wet Prairie						Shark Slough									
		A4	**E4**	**FP**	**GH**	**MO**	**NP**	**BH**	**CH**	**GL**	**IG**	**MA**	**PM**	**SL**	**S3**	**S8**	**VH**
Sida rhombifolia	SIDRHO		0.42						0.33			0.05	0.06				
Sideroxylon salicifolium	SIDSAL	0.00	0.57	0.71	0.01	0.16	0.02										
Simarouba glauca	SIMGLA	0.95			0.06										0.64		
Smilax auriculata	SMIAUR			0.06	0.00	0.00											
Smilax bona-nox	SMIBON	0.17	3.84	0.40	0.12	0.00	0.97										
Smilax laurifolia	SMILAU				0.02		0.09										
Smilax sp.	SMIXXX				0.00	0.01											
Solanum erianthum	SOLERI								0.62	0.24		0.10	0.19	0.24			0.00
Solidago stricta	SOLSTR		0.48														
Tetrazygia bicolor	TETBIC					0.33											
Thelypteris kunthii	THEKUN	4.16	0.21	2.79						0.83		0.59	0.07	0.12	1.08	11.83	7.07
Tillandsia balbisiana	TILBAL					0.01											
Tilandsia fasiculata	TILFAS					0.29											
Tillandsia flexuosa	TILFLE			0.01													
Tillandsia setacea	TILSET					0.04											
Tillandsia usneoides	TILUSN		0.18														0.09
Tillandsia utriculata	TILUTR					0.26											
Tillandsia sp.	TILXXX					0.06											
Toxicodendron radicans	TOXRAD	1.03	4.28	0.56	0.16	0.04	0.12	0.00						0.00	0.01	0.01	
Verbesina virginica	VERVIR										13.13						
Vitis cinerea var. floridana	VITAES				0.34			0.02				0.01	0.10	0.03	0.03		0.18
Vitis rotundifolia	VITROT	0.27	3.26		0.08	0.60	0.00			0.01	0.03		0.46	0.01	0.05		0.73
Vitis shuttleworthii	VITSHU	0.06	0.14	0.08	0.04				0.04		0.03		0.04	0.01	0.13	0.25	0.10
Vitis sp.	VITXXX				0.01				0.11	0.01							
Zamia pumila	ZAMPUM		1.19			2.11											
Zanthoxylum fagara	ZANFAG	0.01			0.03										0.18		