Hindawi Publishing Corporation
International Journal of Forestry Research
Volume 2010, Article ID 176909, 8 pages
doi:10.1155/2010/176909

Research Article

Using Florida Keys Reference Sites As a Standard for Restoration of Forest Structure in Everglades Tree Islands

Michael S. Ross,[1, 2] Danielle E. Ogurcak,[2] Jay P. Sah,[1] and Pablo L. Ruiz[1]

[1] *Southeast Environmental Research Center, Florida International University, Miami, FL 33199, USA*
[2] *Department of Earth and Environment, Florida International University, Miami, FL 33199, USA*

Correspondence should be addressed to Michael S. Ross, rossm@fiu.edu

Received 22 July 2009; Revised 29 October 2009; Accepted 9 December 2009

Academic Editor: Terry L. Sharik

In south Florida, tropical hardwood forests (hammocks) occur in Everglades tree islands and as more extensive forests in coastal settings in the nearby Florida Keys. Keys hammocks have been less disturbed by humans, and many qualify as "old-growth," while Everglades hammocks have received much heavier use. With improvement of tree island condition an important element in Everglades restoration efforts, we examined stand structure in 23 Keys hammocks and 69 Everglades tree islands. Based on Stand Density Index and tree diameter distributions, many Everglades hammocks were characterized by low stocking and under-representation in the smaller size classes. In contrast, most Keys forests had the dense canopies and open understories usually associated with old-growth hardwood hammocks. Subject to the same caveats that apply to off-site references elsewhere, structural information from mature Keys hammocks can be helpful in planning and implementing forest restoration in Everglades tree islands. In many of these islands, such restoration might involve supplementing tree stocking by planting native trees to produce more complete site utilization and a more open understory.

1. Introduction

The best developed tree islands in the Florida Everglades play many roles in the landscape: as forest refugia for wide-ranging animals and tropical hardwoods; as raised features that focus surface water flow into deeper channels; as habitat for rare ferns, epiphytes, and other shade-loving plants; as seed sources for the establishment of new islands; as carbon sinks; as attractants and sinks for nutrients, especially phosphorus, whose deficiency characterizes the surrounding marsh ecosystems [1, 2]. Having served for centuries as oases for humans as well as animals that passed through the vast and inhospitable wetland [3], their structure today carries a long legacy of human use. At the same time, natural disturbance agents play a continuing role in shaping stand structure. Their disturbance regime includes infrequent wildfires, which may kill aboveground vegetation and consume organic soils, and more frequent tropical storms and hurricanes, which topple and severely prune the exposed emergent trees in the forest canopy [4]. In many cases, the complex interaction of human and natural disturbance agents has led to open, slow-to-recover canopies that encourage the encroachment of widely dispersed vines, weedy herbs, and nonnative trees and shrubs, and may interfere with tree island function in the landscape. With tree island condition an important concern of recent efforts to restore full ecological function to the Everglades, embodied in the Comprehensive Everglades Restoration Plan [5], the ability to assess stand structure and its effects on other functions of these poorly understood forests is sorely needed.

Consideration of stand structure in ecological restoration should include both the overall utilization of the site by trees, and how site utilization is distributed among different size classes. Tree density is not a sufficient metric of site utilization, because even when a site remains fully occupied or "stocked" throughout the development of a stand, density declines as trees grow larger and compete with their neighbors [6]. Metrics by which site utilization is represented should therefore account for both tree density and size. Reineke [7] recognized that the density of trees in fully stocked, monospecific, even-aged stands of the same average stand diameter was quite constant, and largely independent of age and site productivity. Based on empirical relationships between average stand diameter and density in fully stocked stands, Reineke's Stand Density Index (SDI) projects a stand's existing size structure to the number of trees that would be present in a similarly stocked stand at an average stand diameter (ASD: diameter at breast height [DBH] of the tree of mean basal area) of 10 inches (25 cm). Long and Daniel [8] showed that Reineke's SDI could be modified to express site utilization in uneven-aged forests, and more recently Woodall et al. [9] explored the influence of species composition on the maximum attainable SDI in mixed-species stands.

Use of the stand density concept in actively managed forests involves the interdependent manipulation of tree density and average stand diameter within a zone judged to represent full stocking [10]. For instance, in his application of stand density principles to Central States hardwoods, Gingrich [11] defined a "full stocking" zone broad enough to encompass a wide range of potential forest products, including timber, wildlife, and other resources. Similarly, ecosystem restoration efforts such as those underway for Everglades tree islands require that a range of states or conditions that represent acceptable forest structure be defined. But how should such standards be determined? One approach is to settle on a limited set of reference communities, for example, old-growth forests, or "pristine" wetlands remote from human impact. In the restoration of Everglades tree islands, forests of the Florida Keys may serve well as references, for several reasons. First, a substantial proportion of Florida Keys forests have undergone little direct human disturbance since at least the 1930s, and were never subjected to the high intensity of human use that has been concentrated on many of the high Everglades tree islands. Second, successional dynamics in Keys hammocks has been thoroughly documented (e.g., [12, 13]) , while forest succession in Everglades tree islands has never been directly addressed. Finally, though growing on different substrates and in slightly different climatic regimes, Keys hammocks and Everglades tree islands are dominated by many of the same tree species, suggesting similar environmental controls.

In this paper, we examine the structure of mixed-species and uneven-aged south Florida forests, addressing not only whole-stand SDI, but also the contribution to SDI made by the full range of diameter classes present. We describe the stand structure of several regional variants of Everglades tree islands, as well as Florida Keys forests of similar composition but distinctly different disturbance history. Our primary objective in these analyses is to determine whether mature Florida Keys forests might serve as references for the establishment of structural guidelines for Everglades tree islands.

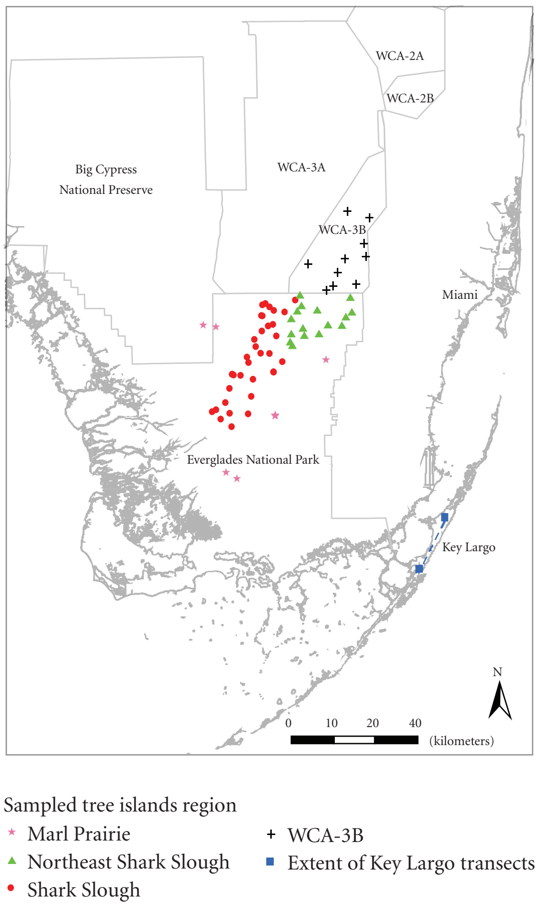

Figure 1: Map of 69 sampled tree islands included in this study, with location of reference hammocks in Key Largo.

2. Methods

2.1. Study Area. Our tree island study area included Shark Slough and adjacent prairies in Everglades National Park (ENP) and Big Cypress National Preserve, as well as state-managed wetlands in Water Conservation Area 3B (WCA-3B; Figure 1). Stretching across a latitudinal range of about 1 degree, tree islands of the area vary broadly in hydrologic conditions in the surrounding marsh, as well as in recreational use. Surrounded on all sides by levees, the peatlands in WCA-3B are dependent on local rainfall, and the area's southward-sloping topography creates deeper water in the south than in the north. While ENP marshes drain freely to the southwest, the volume and distribution of water entering the Park from the north deviates from predevelopment conditions. Overall, delivery is greatly reduced and concentrated in the western reaches of Shark Slough, while marshes in Northeast Shark Slough, south of WCA-3B, are largely rainfall dependent. Marl Prairies on the eastern and western peripheries of Shark Slough are slightly higher in elevation, and water levels are shallower than in the Slough proper.

Tree islands throughout the Everglades have a history of human use dating back at least 5000 years [14–16]. Besides providing relative comfort as sites for the hunting camps or more permanent residences of native Americans, tree islands provided seclusion for the activities of moonshiners, plume hunters, and alligator poachers. After the establishment of

ENP in 1947, access to these areas came under regulation within the Park boundaries, which have expanded from an initial 186,000 ha to 611,000 ha today. Designation of most of ENP for Wilderness Use in 1964 curtailed tree island access further. Today, public use of tree islands in ENP is limited, largely directed to a few interpretive sites near Park roads, as well as several sites in Northeast Shark Slough, the latest addition to the Park. In contrast, access to tree islands in WCA-3B is largely unrestricted, and many sites are used regularly by picnickers, campers, and hunters, and for ceremonial and other uses by members of the Miccosukee Tribe of Indians, who enjoy a right of perpetual use of state lands within the area.

Like the rest of the Everglades, tree islands are impacted by a range of natural disturbances, including lightning strikes [17], freeze events [18], fires [19], and hurricanes or tropical storms [20]. The closed canopy of tree islands moderates temperature and desiccation, and thereby provides protection from fire and freeze, especially in the interior of large islands. While the canopy architecture of tree island communities may also offer some degree of shelter from windstorms, crowns of the tallest trees on the high ground at the island center are very exposed, and are frequently pruned, damaged, or uprooted by winds.

Of the eight types of south Florida tree islands recognized by Craighead [1], hardwood hammock is the one whose surface is most elevated above the water table, and the only one to develop on well-drained soils. In contrast to the more hydric tree island types, which are often dominated by temperate species, tree assemblages in hardwood hammocks in the interior of ENP are comprised primarily of tropical species of West Indian origin [4]. With their surface a meter or more above the adjacent marsh, these hammocks are frequently ringed by swamp forests which, in portions of the peatland with strong directional flow, complete a mixed forest of tear-drop shape. Hammocks in the heads of such islands usually occupy less than 1000 m^2, while the entire tree island may encompass ten hectares or more. Small and isolated as they are, tree species richness in these hammocks does not approach that found in similar areas within the extensive forests of the nearby Florida Keys. Nevertheless, many of the common tropical species in Everglades tree islands (e.g., *Bursera simaruba, Ficus aurea, Sideroxylon salicifolia, Sideroxylon foetidissimum, Eugenia axillaris, Simarouba glauca, Coccoloba diversifolia*) are also abundant in the Keys hammocks. Soils in the large tree islands in the interior Everglades differ dramatically from those in Florida Keys hammocks. The former are deep, phosphorus-rich soils with high mineral content, while the latter are well-drained, thin, and organic-rich [21, 22]. Despite these differences, heights of dominant trees in Everglades tree islands and in hammocks of the upper Florida Keys are similar (10–12 meters at maturity).

2.2. Sampling Design and Analytical Methods. Analysis of stand structure was based on three data sets, each derived from different sampling techniques. The most extensive of these was a one-time vegetation survey of 52 tree islands in Shark Slough, Northeast Shark Slough, and WCA-3B, conducted in 2005–2007 (“Extensive” survey). A second set of 16 permanent tree island plots in Shark Slough and adjacent marl prairies was established in 2005-2006, and sampled most recently in 2008-2009 (“Permanent Plot” survey). Finally, structural data representing Florida Keys hammocks (“Keys” survey) were derived from 23 sites examined in Key Largo in 1994 (Figure 1).

Prior to initiating both the Extensive and Permanent Plot surveys in 2005, we used 1999 aerial photographs to examine Shark Slough and WCA-3B tree islands for evidence of the relatively high (compared to adjacent swamp forests) canopies associated with hardwood hammock forests. We then completed a reconnaissance flight by helicopter over both study areas, confirming or rejecting that each of the islands identified on the aerial photos contained a patch of hardwood hammock at least 10 × 10 m in size. Ten of the hardwood hammocks in Shark Slough were selected for the establishment of permanent plots based on distribution and logistical factors, while the rest of the islands were sampled using Extensive survey methods. The set of permanent plots was supplemented by six additional hammocks, selected from the many tree islands scattered throughout the marl prairies adjoining Shark Slough on the east and west.

Sampling in the Extensive survey plots employed multiple nested circular subplots for estimation of canopy cover in understory and overstory layers, as well as the community structure of tree species. In most cases, five subplots were sampled at the center of the hammock and midway between the center and the edges of the stand along its major and minor axes, respectively. In each subplot, four concentric circles rooted at the subplot center were delineated for sampling of different forest elements. Tree seedlings <1 m in height were counted by species in the inner, 0.57-m radius circle. Herb cover, and density of shrubs (>1 m height) and saplings (1–5 cm DBH) were determined by species in a 1-m radius circle. The species and diameter (5-cm classes) of trees 5–25 cm in DBH were enumerated in a 2-m radius circle, and trees >25 cm were sampled similarly in a 3-m radius circle. Individual stems of multitrunked trees were measured, and a DBH equivalent was computed based on their composite cross-sectional area. Using a spherical densiometer [23, 24], we estimated overstory canopy cover on the basis of a pair of north- and south-facing readings from the subplot center.

Permanent plot size was fit to the dimensions of each hammock; all were square or rectangular and 225–625 m^2 in area. Each plot was gridded into 5 × 5 m cells, and herbs, seedlings, and shrub stems were sampled as in the extensive plots, that is, in 0.57-m and 1-m radius circular plots surrounding a stake at the center of each cell. Saplings were counted by size class throughout the plot, while the diameter of each tree (>5 cm DBH) throughout the plot was measured. Multistemmed trees were treated as in the Extensive survey plots.

Florida Keys sampling represented a chronosequence of known time since abandonment from agriculture or other human activities in Key Largo. Examination of sequential aerial photos indicated that the youngest stands sampled had been cleared 14 years prior to our 1994 survey, while five stands showed no evidence of human disturbance since at

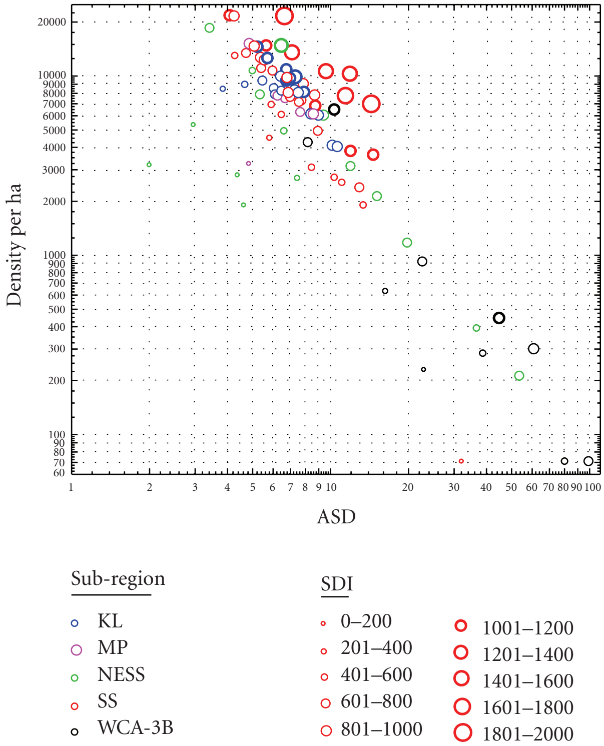

Figure 2: Tree density, Average Stand Diameter (ASD), and SDI in 92 south Florida tropical hardwood hammocks. Subregions include: Key Largo (KL), Marl Prairie (MP), Shark Slough (SS), Northeast Shark Slough (NESS), and WCA-3B.

least 1926. Since the northern portions of Key Largo had been dealt a glancing blow from Hurricane Andrew (August 1992) only two years prior to our survey, we recorded species and DBH of both live and hurricane-killed trees along belt transects 60–100 m long. We measured all stems 1–10 cm DBH within 1 meter of the transect, all trees 10.1–25.0 cm in diameter within 2 meters of the line, and all trees >25 cm DBH within 5 meters of the transect. Successional relationships suggested by the composition of these stands have previously been described [12].

To assess structural variation in Everglades tree islands and Keys hammocks, we calculated tree density, basal area, Average Stand Diameter (ASD), and Stand Density Index (SDI) based on all trees >1 cm DBH. We chose a low diameter limit because of the ubiquity and importance of small trees in the species-rich south Florida hammocks, where a number of common taxa rarely exceed 10 cm. SDI was calculated as

$$\mathrm{SDI} = \sum \mathrm{tph}_i \left(\frac{\mathrm{DBH}_i}{25}\right)^{1.6}, \tag{1}$$

where tph_i is tree density in the ith diameter class, and DBH_i is the DBH of the class midpoint [25]. We also calculated the proportion of SDI attributable to each 5-cm diameter class through 50 cm diameter, and to trees that exceeded 50 cm.

Principal Component Analysis (PCA) was applied to the combined data set consisting of 92 sites from the three study areas. Six variables were used: SDI and the proportional contribution to SDI from five tree-size categories at each site. Of the 23 Keys stands, 21 were defined as reference sites within the PCA site ordination; two 14 year-old forests were deemed inappropriate to serve as structural references due to their immature developmental condition. Using the standard distance tool in ArcMap 9.3, a 2-s.d. circle was created around the geometric mean center of the PCA distribution of the 21 reference hammocks [26]. Islands were divided into groups based on this analysis; Everglades tree islands falling within this circle were identified as "Keys-like," while those islands falling outside this circle were considered "Not Keys-like." Mean overstory canopy cover, understory cover, and seedling density of the two groups were compared through T-tests, once assumptions of homogeneity of variance were met.

3. Results

Based on the 92 hardwood hammocks sampled across the region, south Florida sites supported forests of mean tree (≥ 1 cm DBH) density of ~7300 stems $\cdot$ ha^{-1}, comprising a basal area of ~34 m^2 $\cdot$ ha^{-1}, with means for ASD of 12.2 cm and SDI of 803. Around these means, considerable intraregional variation in SDI and associated stand-level metrics was also observed (Table 1). Mean SDI was the highest in Key Largo and Shark Slough forests, but the former were relatively homogeneous in this and other parameters, while the latter were far more variable. This is illustrated in Figure 2, where Key Largo stands are restricted to a small range in tree density, ASD, and SDI, Shark Slough hammocks are more broadly distributed. For instance, the six densest stands sampled, with SDI's exceeding 1400, were all located in Shark Slough, but many stands with SDI < 600 were also present within the subregion. SDI never exceeded 1200 in WCA-3B; mean ASD in this subregion was much greater than elsewhere, but tree densities were consistently low (Table 1; Figure 2). Mean SDI was significantly lower in Northeast Shark Slough than in either Key Largo or Shark Slough (Table 1), but Northeast Shark Slough tree islands displayed the broadest range in tree density and ASD of the five subregions (Figure 2). The few Marl Prairie islands sampled were characterized by low ASD and basal area, but SDI and tree density were intermediate.

As suggested above, hammocks in the five subregions differed not only in stand-level structural characteristics, but also in how these attributes were distributed among the tree-size classes that comprised each stand. In Figure 3, mean proportional contributions of individual 5-cm DBH classes to SDI are expressed as cumulative curves for each subregion. Three patterns emerge from these curves. Small size classes were very important in Key Largo and Marl Prairie forests, with ≥80% of SDI due to trees 20 cm DBH and less, and little or no contribution from trees more than 30 cm DBH. Trees less than 20 cm DBH also played a substantial role in site occupancy in Shark Slough and Northeast Shark Slough stands, but larger trees were also structurally important. In WCA-3B, small size classes were generally absent, and most of SDI was due to large (>40 cm DBH) trees.

Table 1: Means (±S.E.) for four structural parameters in hardwood hammocks in five south Florida subregions. Site means within a column followed by same superscript do not differ at $\alpha = 0.05$.

Subregion	n	Tree density (ha^{-1})	Basal area ($\mathrm{m}^2 \cdot \mathrm{ha}^{-1}$)	Average stand diameter (cm)	Stand density index
Key Largo	23	8584 (489)^{a}	31.6 (1.7)^{a}	7.0 (0.3)^{b}	925 (41)^{a}
Marl prairies	6	7677 (1654)^{ab}	24.8 (4.1)^{a}	6.5 (0.6)^{b}	679 (102)^{ab}
NESS	17	5516 (1238)^{ab}	25.0 (4.1)^{a}	12.0 (3.3)^{b}	568 (81)^{b}
SS	36	8968 (917)^{a}	38.9 (4.1)^{a}	8.8 (0.8)^{b}	897 (69)^{a}
WCA-3B	10	1368 (691)^{b}	41.8 (7.8)^{a}	40.4 (9.8)^{a}	654 (97)^{ab}

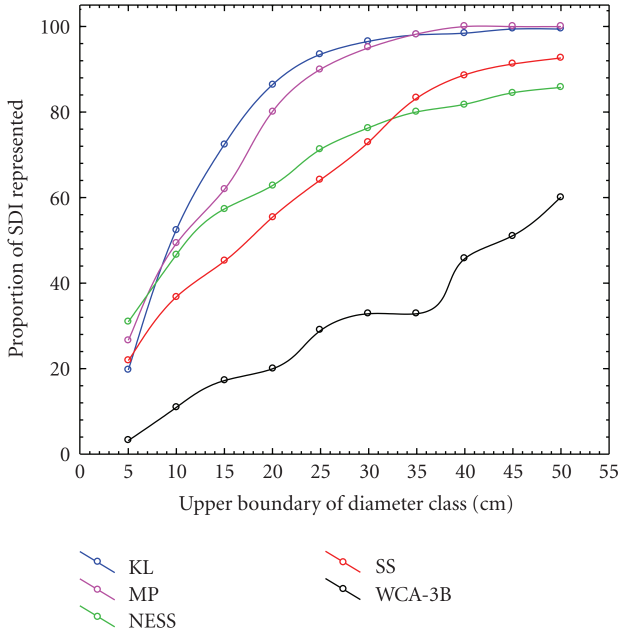

Figure 3: Cumulative SDI curves for Key Largo (KL old and mature sites), Marl Prairie (MP), Shark Slough (SS), Northeast Shark Slough (NESS), and WCA-3B hardwood forests.

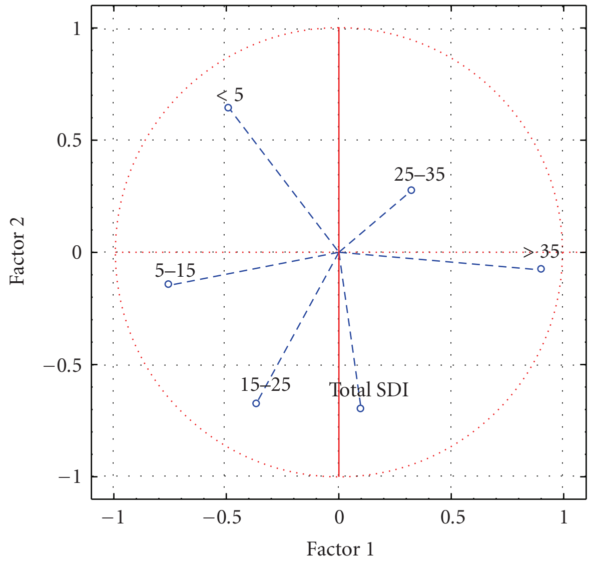

Figure 4: Projection of six structural variables on the factor plane formed by PCA Axes 1 and 2. 92 sites from hardwood hammocks in the Keys and Everglades were analyzed, and the first two PCA axes accounted for 55% of the total variation.

Factors 1 and 2 of the PCA explained 31% and 24%, respectively, of the total variation in the structural data from all sites (Figure 4). Factor 1 generally distinguished stands in which large trees were major contributors to SDI (high scores) from stands in which small trees were especially important (low scores). SDI was the strongest correlate with Factor 2; high SDI was associated with a large proportional contribution from mid-size (DBH 15–25 cm) trees, and a lower than normal sapling (<5 cm) contribution (Figure 4). The distribution of sites in the PCA ordination space is presented in Figure 5. Mature and old-growth Key Largo forests grouped together in the lower left corner of the graph (high SDI, many small and medium-sized trees, few saplings). Marl Prairie tree islands were mostly clustered nearby, but Shark Slough and Northeast Shark Slough islands were spread throughout the ordination space. WCA-3B islands were mostly confined to the far right of the figure (high Factor 1). Still, at least two representatives of each tree island type were located within 2 s.d. of the centroid of the reference Keys stands, that is, a total of 18 "Keys-like" islands. These islands had significantly higher canopy cover and lower ground cover than the 51 "Not Keys-like" islands that were distant from the reference group in PCA space (Figures 6(a)-6(b)). While seedling density did not differ significantly between the two groups, there was a tendency for higher densities beneath the more disturbed, open canopies in the "Not Keys-like" stands (Figure 6(c)).

4. Discussion

In this study, we quantified and assessed several aspects of the structure of one type of tree island community, the tropical hardwood hammock, across a swathe of the southern and central Everglades, using for reference similar forests from nearby Key Largo, which in the recent years have received much less human disturbance. Compared to the Key Largo reference group, Everglades tree islands exhibited high variability within and among subregions in stand-level structural characteristics, that is, SDI, basal area, ASD, and tree density. In Northeast Shark Slough and especially WCA-3B, where recent human impact was most extensive, high average tree size, low tree density, and low SDI were the rule. Repeated episodes of clearing and reversion to forest concentrated growth on a few very large trees, and site

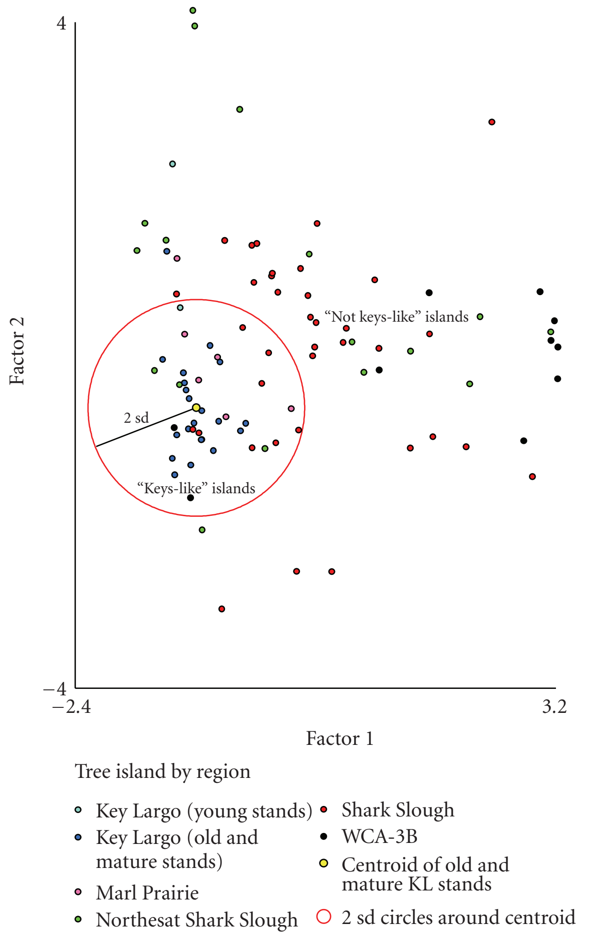

Figure 5: Factor coordinates of cases from PCA ordination of 6 structural variables. Factors 1 and 2 are represented on the X and Y axes, respectively. A 2 s.d. circle from the centroid of the Key Largo mature and older stands separates "Keys-like" islands from "Not Keys-like" islands.

occupancy was slow to recover between disturbances. Even in Shark Slough, where the tree islands have been protected within ENP for decades, variation in disturbance history has left many stands with SDI far below the maximum for the type. With their high canopies extending far above the surrounding landscape, residual emergent trees in Shark Slough tree islands are very exposed to the hurricanes that periodically cross the area, and many canopy species are vulnerable to breakage or uprooting even in less severe windstorms. Most of these species resprout reliably, but the success of seedling regeneration in gap-filling is limited by the encroachment of native and nonnative vines, and by the rooting activities of feral hogs that frequent the tree islands. Despite these impediments, tropical hardwood forests with stocking levels above the mean for the reference stands in Key Largo can be found here and there throughout ENP.

Mature and old Key Largo hammocks are products of an extended successional sequence that features a sharp turnover in species composition within the first century following catastrophic disturbance [12, 13]. Given their

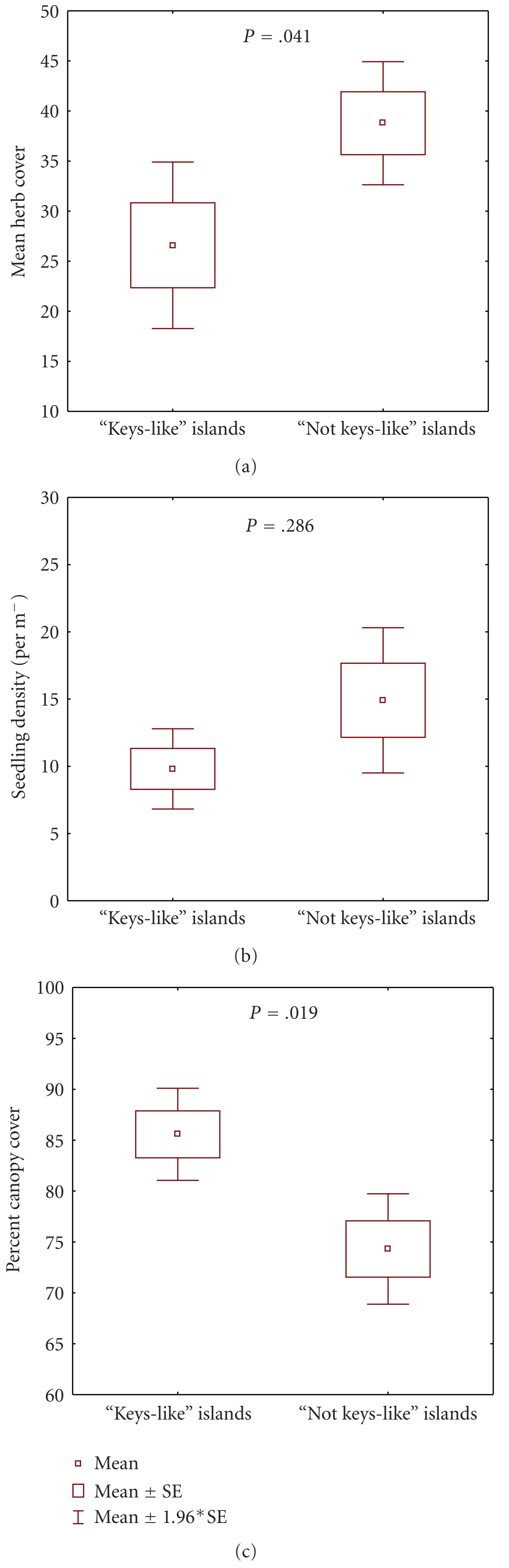

Figure 6: Box plots comparing three forest characteristics in "Keys-like" islands and "Not Keys-like" islands. (a) Percent herb cover, (b) seedling density, and (c) percent canopy cover.

close compositional affinities with Everglades tree islands, it is likely that, in the absence of human disturbance, the latter would follow a similar trajectory, also taking on an uneven-aged stand structure. While SDI effectively expresses site occupancy in such stands [8], it communicates nothing about their internal, within-stand structure, which is a fundamental concern in the management of uneven-aged forests [6]. In summarizing stand structure for our combined data set, we therefore supplemented SDI with information about tree diameter distribution, expressed as the proportional contribution of each size class to SDI. These analyses highlighted important subregional variation in tree island structure, with small trees the majority contributors to SDI in Key Largo and Marl Prairie tree islands, very large trees the overwhelming contributors in WCA-3B, and relatively even contributions from small and large trees in Shark Slough and Northeast Shark Slough. Disturbances of human or natural origin that affect SDI are also likely to affect the size structure of forests, and certainly have a role in the subregional patterns. Another possible factor is site quality, as self-thinning may be less intense or slower to develop on low-productivity sites, enabling small trees to survive longer in competition with their larger neighbors [27]. The grouping of Key Largo and Marl Prairie stands is notable in this context, as the thin, low P soils on which both of these hammock variants are found may provide less rooting volume and nutrient availability than the richer and deeper sediments of the Shark Slough, Northeast Shark Slough, and WCA-3B islands [21, 22], possibly leading to lower inherent site productivity. Two studies that used similar methods to monitor litterfall in Key Largo and Shark Slough found about 35% higher production in the latter [12, 28].

Information from reference sites can be used to define restoration goals, develop site-specific restoration plans, and assess restoration success [29]. In forest ecosystems, where canopy structure exerts a profound influence on ecosystem processes in subordinate layers, restoration assessments should include effective metrics of stand structure. In this study, we used SDI, which was initially developed as a metric of site utilization in managed, even-aged forests of the western U.S. [7], but has only recently been extended to uneven-aged forests more characteristic of the Eastern U.S., especially the tropical and subtropical hardwood forests of south Florida and the Caribbean basin [8, 9]. Our statistical approach, which incorporated both SDI and the contributions to SDI attributable to different tree size classes, was aimed at summarizing the variability inherent in unmanaged stands. In the ordination of sites based on these structural variables, Key Largo forests grouped together, but were joined by a substantial cohort of similarly-structured Everglades tree islands. Among the few associated variables we measured, "Keys-like" stands had more closed canopies and lower understory cover, both characteristics of old-growth south Florida tropical forests [30], than neighboring, structurally different tree islands. Because stand structure drives many biological functions taking place within the forest [27], the "Keys-like" structure of these islands may translate as well to other desirable forest characteristics, for example, high species diversity and trophic complexity, moderated microclimate, and closed nutrient cycles [31–33].

The use of reference sites as targets of restoration effort is a staple of the science. However, caution must be applied in each case, because the developmental history and environmental conditions that produced the reference stands are never an exact match for those of the restoration sites. In the south Florida situation we described, variation in site potential and natural disturbance regime experienced at reference and restoration sites are undoubtedly ecologically significant at some level of detail, and their impacts should be studied further. Still, the Key Largo hardwood hammocks are recognized to be among the best examples of old-growth tropical hardwood hammock remaining in the region [30], and can provide guideposts for restoration of tropical forests on the south Florida mainland. In particular, they may serve at least initially as references for activities (e.g., underplanting, exotic species control) needed to augment site occupancy by native trees, and develop a more balanced uneven-aged stand structure on under-stocked Everglades tree islands. In the Everglades, such restoration activities would take place within a large-ecosystem restoration project that is based on the axiom "Get the water right" [5]. Suitable hydrologic conditions are necessary but not sufficient for restoration of ecological function in Everglades tree islands. Achievement of the habitat-specific targets indicated in this study would also require active management to increase site utilization by trees in many poorly stocked stands.

Acknowledgments

The authos thank the following people for long, hard days collecting the data reported on here: Brooke Shamblin, Nate Colbert, Lawrence Lopez, Cara Dodge, Erin Hanan, Susana Stoffella, Jessica Heinrich, Rafael Travieso, David Jones, Joe O'Brien, and Laura Flynn. The Everglades tree island work has been funded by Everglades Park and the South Florida Water Management District, and ably managed by Vic Engel, Tom Armentano, and Jana Newman. The Keys work was funded by the U.S. Fish and Wildlife Service, under Jon Andrews' supervision. The tree island research was enhanced by collaboration with the Florida Coastal Everglades Long-Term Ecological Research program (funded by the National Science Foundation, no. DBI-0620409 and no. DEB-9910514). This is SERC Contribution no. 454.

References

[1] F. C. Craighead, *The Trees of South Florida. Volume 1: The Natural Environments and Their Succession*, University of Miami Press, Coral Gables, Fla, USA, 1971.

[2] P. R. Wetzel, A. G. van der Valk, S. Newman, et al., "Heterogeneity of phosphorus distribution in a patterned landscape, the Florida Everglades," *Plant Ecology*, vol. 200, no. 1, pp. 83–90, 2009.

[3] R. S. Carr, "The archaeology of Everglades tree islands," in *Tree Islands of the Everglades*, F. H. Sklar and A. van der Valk, Eds., pp. 187–206, Kluwer Academic Publishers, Dordrecht, The Netherlands, 2002.

[4] T. V. Armentano, D. T. Jones, M. S. Ross, and B. W. Gamble, "Vegetation pattern and process in tree islands of the southern Everglades and adjacent areas," in *Tree Islands of the Everglades*, F. H. Sklar, A. van der Valk, et al., Eds., pp. 225–281, Kluwer Academic Publishers, Dordrecht, The Netherlands, 2002.

[5] F. H. Sklar, M. J. Chimney, S. Newman, et al., "The ecological—societal underpinnings of Everglades restoration," *Frontiers in Ecology and the Environment*, vol. 3, no. 3, pp. 161–169, 2005.

[6] B. J. Enquist and K. J. Niklas, "Invariant scaling relations across tree-dominated communities," *Nature*, vol. 410, no. 6829, pp. 655–660, 2001.

[7] L. H. Reineke, "Perfecting a stand-density index for even-aged forests," *Journal of Agricultural Research*, vol. 46, pp. 627–638, 1933.

[8] J. N. Long and T. W. Daniel, "Assessment of growing stock in uneven-aged stands," *Western Journal of Applied Forestry*, vol. 5, pp. 93–96, 1990.

[9] C. W. Woodall, P. D. Miles, and J. S. Vissage, "Determining maximum stand density index in mixed species stands for strategic-scale stocking assessments," *Forest Ecology and Management*, vol. 216, no. 1–3, pp. 367–377, 2005.

[10] T. W. Daniel, J. A. Helms, and F. S. Baker, *Prinicples of Silviculture*, McGraw-Hill, New York, NY, USA, 1979.

[11] S. F. Gingrich, "Measuring and evaluating stocking and stand density in upland hardwood forests in the central states," *Forest Science*, vol. 13, no. 1, pp. 38–53, 1967.

[12] M. S. Ross, M. Carrington, L. J. Flynn, and P. L. Ruiz, "Forest succession in tropical hardwood hammocks of the Florida keys: effects of direct mortality from Hurricane Andrew," *Biotropica*, vol. 33, no. 1, pp. 23–33, 2001.

[13] J. R. Redwine, *Leaf morphology scales multi-annual trends in nutrient cycling and leaf, flower, and fruiting phenology among species in the sub-tropical hardwood forests of the northern Florida Keys*, Ph.D. dissertation, Florida International University, Miami, Fla, USA, 2007, http://digitalcommons.fiu.edu/dissertations/AAI3279233.

[14] J. W. Griffin, *Archaeology of the Everglades*, edited by J. T. Milanich and J. J. Miller, University Press of Florida, Gainesville, Fla, USA, 2002.

[15] M. Schwadron, "Everglades tree islands prehistory: archaeological evidence for regional Holocene variability and early human settlement," *Antiquity*, vol. 80, no. 310, 2006.

[16] M.-T. Graf, M. Schwadron, P. A. Stone, M. Ross, and G. L. Chmura, "An enigmatic carbonate layer in Everglades tree island peats," *Eos*, vol. 89, no. 12, pp. 117–118, 2008.

[17] T. J. Smith III, M. B. Robblee, H. R. Wanless, and T. W. Doyle, "Mangroves, hurricanes, and lightning strikes. Assessment of Hurricane Andrew suggests an interaction across two differing scales of disturbance," *BioScience*, vol. 44, no. 4, pp. 256–262, 1994.

[18] I. Olmsted, H. Dunevitz, and W. J. Platt, "Effects of freezes in Everglades National Park Florida, USA," *Tropical Ecology*, vol. 34, pp. 17–34, 1993.

[19] D. Wade, J. Ewel, and R. Hofstetter, "Fire in South Florida ecosystems," Forest Service General Technical Report SE-17, p. 125, USDA, Washington, DC, USA, 1980.

[20] T. V. Arrmentano, R. F. Doren, W. J. Platt, and T. Mullins, "Effects of Hurricane Andrew on coastal and interior forests of Southern Florida: overview and synthesis," *Journal of Coastal Research*, vol. 21, pp. 111–144, 1995.

[21] M. S. Ross, C. L. Coultas, and Y. P. Hsieh, "Soil-productivity relationships and organic matter turnover in dry tropical forests of the Florida Keys," *Plant and Soil*, vol. 253, no. 2, pp. 479–492, 2003.

[22] C. L. Coultas, M. Schwadron, and J. M. Galbraith, "Petrocalcic horizon formation and prehistoric people's effect on Everglades tree island soils, Florida," *Soil Survey Horizons*, vol. 49, pp. 16–21, 2008.

[23] P. E. Lemmon, "A spherical densitometer for estimating forest overstory density," *Forest Science*, vol. 2, pp. 314–320, 1956.

[24] S. R. Englund, J. J. O'Brien, and D. B. Clark, "Evaluation of digital and film hemispherical photography and spherical densiometry for measuring forest light environments," *Canadian Journal of Forest Research*, vol. 30, no. 12, pp. 1999–2005, 2000.

[25] C. W. Woodall, C. E. Fiedler, and K. S. Milner, "Stand density index in uneven-aged ponderosa pine stands," *Canadian Journal of Forest Research*, vol. 33, no. 1, pp. 96–100, 2003.

[26] ESRI, *Using ArcMap: ArcGIS 9*, ESRI Press, Redlands, Calif, USA, 2004.

[27] A. J. Larson, J. A. Lutz, R. F. Gersonde, J. F. Franklin, and F. F. Hietpas, "Potential site productivity influences the rate of forest structural development," *Ecological Applications*, vol. 18, no. 4, pp. 899–910, 2008.

[28] J. P. Sah, "Vegetation structure and composition in relation to the hydrological and soil environments in tree islands of Shark Slough," in *Tree Islands in the Shark Slough Landscape: Interactions of Vegetation, Hydrology, and Soils*, M. S. Ross and D. T. Jones, Eds., Final Report to Everglades National Park on Study EVER 00075, p. 183, 2004, http://digitalcommons.fiu.edu/sercrp/42004.

[29] P. S. White and J. L. Walker, "Approximating nature's variation: selecting and using reference information in restoration ecology," *Restoration Ecology*, vol. 5, no. 4, pp. 338–349, 1997.

[30] K. W. Outcalt, "An old-growth definition for tropical and subtropical forests in Florida," General Technical Report SRS-13, p. 8, U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC, USA, 1997.

[31] K. S. McCann, "The diversity-stability," *Nature*, vol. 405, no. 6783, pp. 228–233, 2000.

[32] G. Aussenac, "Interactions between forest stands and microclimate: ecophysiological aspects and consequences for silviculture," *Annals of Forest Science*, vol. 57, no. 3, pp. 287–301, 2000.

[33] P. M. Vitousek and R. L. Sanford Jr., "Nutrient cycling in moist tropical forest," *Annual Review of Ecology and Systematics*, vol. 17, pp. 137–167, 1986.