ECOSYSTEMS

Forest Resource Islands in a Sub-tropical Marsh: Soil–Site Relationships in Everglades Hardwood Hammocks

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ABSTRACT

Spatial heterogeneity in soils is often characterized by the presence of resource-enriched patches ranging in size from a single shrub to wooded thickets. If the patches persist long enough, the primary constraint on production may transition from one limiting environmental factor to another. Tree islands that are scattered throughout the Florida Everglades basin comprise nutrient-enriched patches, or resource islands, in P-limited oligotrophic marshes. We used principal component analysis and multiple regressions to characterize the belowground environment (soil, hydrology) of one type of tree island, hardwood hammocks, and examined its relationship with the three structural variables (basal area, biomass, and canopy height) indicative of site productivity. Hardwood hammocks in the southern Everglades grow on two distinct soil types. The first, consisting of shallow, organic, relatively low-P soils, is common in the seasonally flooded Marl Prairie landscape. In contrast, hammocks on islands embedded in long hydroperiod marsh have deeper, alkaline, mineral soils with extremely high P concentrations. However, this edaphic variation does not translate simply into differences in forest structure and production. Relative water depth was unrelated to all measures of forest structure and so was soil P, but the non-carbonate component of the mineral soil fraction exhibited a strong positive relationship with canopy height. The development of P-enriched forest resource islands in the Everglades marsh is accompanied by the buildup of a mineral soil; however, limitations on growth in mature islands appear to differ substantively from those that dominate incipient stages in the transformation from marsh to forest.

Key words: resource island; tree islands; limiting resource; soil phosphorus; non-carbon materials; forest production; marl prairies; sloughs; organic soil; mineral soil.

INTRODUCTION

Coincident patterns in the spatial heterogeneity of belowground resources and vegetation may be observed at a range of scales, from fine textures associated with concentrations of roots (Kleb and Wilson 1997) or individual plants (Kershaw 1962; Jackson and Caldwell 1993) to patterns expressed at larger scales associated with landscape gradients

or patches (Schimel and others 1985; Blackmore and others 1990). In wetlands, vegetation patterning may also be organized around slight discontinuities in surface topography (Huenneke and Sharitz 1986; Titus 1990), though these variations do not always translate into edaphic differences (Ehrenfeld 1995). Ecological theory suggests that environmental heterogeneity may also structure emergent properties of the plant community such as species diversity (Tilman 1988; Huston 1994; Rosenzweig 1995). However, interactions between environmental heterogeneity and vegetation structure are often reciprocal, involving positive and negative feedbacks that create a joint dynamic and common history (Pickett and others 2000).

In arid and semi-arid ecosystems, numerous investigators have found spatial heterogeneity in soils to be characterized by the presence of resource-enriched patches that range in size from the crown area of a single shrub to wooded thickets (Schlesinger and others 1990, 1996; Schlesinger and Pilmanis 1998; Titus and others 2002). The development and persistence of such patches are often dependent on feedbacks between the biota, that is, herbivores as well as primary producers, and the resource in question, usually nitrogen and/or water (Wilson and Agnew 1992; Schlesinger and Pilmanis 1998; Rietkerk and others 2002; Rango and others 2006). Through biotic responses such as canopy development, transpiration, soil accretion, or litter deposition, enhancement in a limiting resource may alter other aspects of the environmental regime, for instance microclimate, infiltration, or water retention. If the patch persists long enough, the primary constraint on production may transition from one limiting environmental factor to another. Working in the southwestern U.S., Jackson and Caldwell (1993) called such patches ''islands of fertility'', and Reynolds and others (1999) characterized them more broadly as ''resource islands''.

In wetlands as well, positive and negative feedback loops involving vegetation, nutrients and the movement of water can produce patterned landscapes in which resources are concentrated in one or more of the constituent patch types (Cohen and others 2011). In large wetland landscapes such as the Florida Everglades, geophysical variation within the basin, or management-related hydrologic alteration may result in different landscape patterning from one sub-region or management unit to another. Most of the freshwater Everglades is an oligotrophic, phosphorus-limited marsh (Noe and others 2001), but the slightly elevated forest patches, or tree islands, that are scattered throughout the basin do not exhibit similar P-deficiency. Instead, tree island soils sometimes contain extraordinary concentrations of phosphorus. Wetzel and others (2009) reported that volumetric concentrations of P in tree island heads supporting tropical hardwood species in Water Conservation Area 3, north of Everglades National Park, averaged about 1%, or 70 times higher than in adjacent marshes. Orem and others (2002) also found elevated soil P concentrations ($\sim$0.3% by weight) in two tree islands in the Central Everglades. Higher values were reported by Ross and others (2006), who found mean soil P to be nearly 5% by weight in well-drained portions of three Shark Slough (ENP) tree islands, whereas the phosphorus content of soils in swamp forests and marshes immediately downslope were one and two orders of magnitude lower, respectively. The P-enriched tree island heads serve not only as islands of fertility, but as full-fledged resource islands, providing food and cover for terrestrial wildlife, and a well-drained substrate and shaded microclimate for forest plants. Accordingly, the restoration of tree islands in areas where they have been degraded, and their maintenance in areas where they remain in good number and conditions, have provided a major rationale for embarking on the Comprehensive Everglades Restoration Project (CERP).

In this paper we present a study of one type of Everglades tree island, slightly elevated, broad-leaved forests known as hardwood hammocks, beneath which the water table fluctuates widely, affecting moisture availability in the unsaturated zone but rarely rising high enough to flood the surface. Our first objective was to describe the belowground environment (soil, hydrology) in hammocks occupying several regions of the Everglades. The survey was extensive enough to allow generalization about the nature of these rich soils, whose diagenesis is currently little understood. Our second objective was to examine associations between features of the belowground environment and several indices of forest production. We used regression analysis to indicate which soil factors might be limiting plant production in the hammocks, thereby focusing on the internal functioning of these resource islands, rather on their role in resource provision to the surrounding landscape.

STUDY AREA

The freshwater wetlands of the southern Everglades fall into two broad sedimentary environments: peat-forming environments associated with marshes in the center of the historical flow-way

(including Shark Slough and Water Conservation Area 3), and marl-forming environments in the prairies on the eastern and western flanks of Shark Slough, in Everglades National Park and Big Cypress National Preserve. The peats (Lauderhill, Pennsuco series) are 80–150 cm thick over limestone, whereas the marls (Biscayne series) are thinner, usually less than 50 cm thick, interspersed with extensive areas of outcropping limestone. The critical physical driver is the hydrologic regime that characterizes each zone. The marshes of Shark Slough and WCA-3 are inundated 9–12 months per year by a water column that may approach or exceed 1 m. Peats accumulate because the flooding regime permits relatively high vascular plant production, but creates sufficiently anaerobic conditions in the sediments reducing decomposition of organic materials, especially plant roots. Immediately upslope, in what may be viewed as the floodplain of the River of Grass, the marl prairie is characterized by shallow seasonal flooding (3–8 months per year). Macrophyte production and cover are sparse in this variable environment, but conditions favor the growth of a luxuriant, benthic algal mat. The physiological activities of the algae result in precipitation of calcium carbonate from the warm, well-lit waters, contributing to the development of marl soils (Gleason 1972).

Tree islands are common inclusions in these marsh and prairie communities. As such, the islands are affected by the ecosystems that surround them, including hydrologic and sedimentologic processes in the grassy matrix. Everglades tree islands are complex forests that typically display a vegetation gradient from an open mixture of flood-tolerant trees and herbaceous plants near the marsh interface to a less hydrophytic assemblage, with a more closed canopy, at the island interior. In the most complex tree islands, the surface of the interior forest is raised well above the surrounding marsh and supports a mixture of tree species, mostly of tropical origin, that are intolerant to flooding of more than a few weeks' duration. Unlike tree islands dominated by swamp forest species, which may form above bedrock depressions or on bedrock-neutral surfaces, the hardwood hammocks occupy sites whose surface elevation is directly or indirectly attributable to the underlying bedrock; in the southern Everglades, this bedrock surface is almost always higher than the limestone that surrounds it. Some hammocks occupy outcroppings of a meter or more, but in other settings variation in the bedrock surface of 0.1 m or so is enough to initiate the development of a forest ecosystem in which the vegetation and soils differ dramatically from those of the adjacent marsh (Hanan and Ross 2010).

Tree islands with hardwood hammock vegetation are distributed widely in the Everglades, but vary regionally in number, size, orientation, and composition/structure. The density of such islands decreases from south to north, and from the peripheral marl prairies to the marshes of the central peatland. Hammocks in the center of the Everglades are usually small, but form the nuclei for large teardrop-shaped forests, comprised mostly of swamp forest species and oriented in the predominant direction of water flow. In contrast, the shape and orientation of prairie hammocks generally reflect the underlying bedrock, with less evidence of sculpting by flowing water. Hammocks in the central peatland host a limited suite of tree species, most of them among the more common in the regional flora (Armentano and others 2002). Prairie hammocks are more species-rich, including a broader selection of tropical hardwoods common in the Florida Keys (Olmsted and others 1980; Loope and Urban 1980).

Everglades tree islands are also the product of a history of human use that dates back at least 5000 years (Graf and others 2008), when the wetland was first forming. Long distance travel through the Everglades by Native Americans was most rapid by canoe. Due to the deep water which surrounded them for much of the year, the scattered, sentinel islands of the central peatland may have received more intensive use than the countless islands embedded in the marl prairie, which even in the wet season was only minimally flooded. Use of tree islands by people of European origin in the 19th and 20th centuries probably followed a similar pattern, with airboats eventually supplanting canoes as the primary means of transportation. Of course, the last century also featured the establishment and operation of roads and canals that compartmentalized the Everglades marsh, reducing flow and water levels overall, while creating hydrologic patchiness and anthropogenic gradients that induced variable responses in the tree islands. For instance, tree island density and area in Water Conservation Areas 2 and 3 declined precipitously (Hofmockel and others 2008), although similar trends have not been observed in Everglades National Park.

The tree islands we studied were distributed among four sub-regions with distinctly different physiography and/or management history (Figure 1). Three of them—Shark Slough (SS), Northeast Shark Slough (NESS), and Water Conservation Area 3B (WCA-3B)—are in the central peatland,
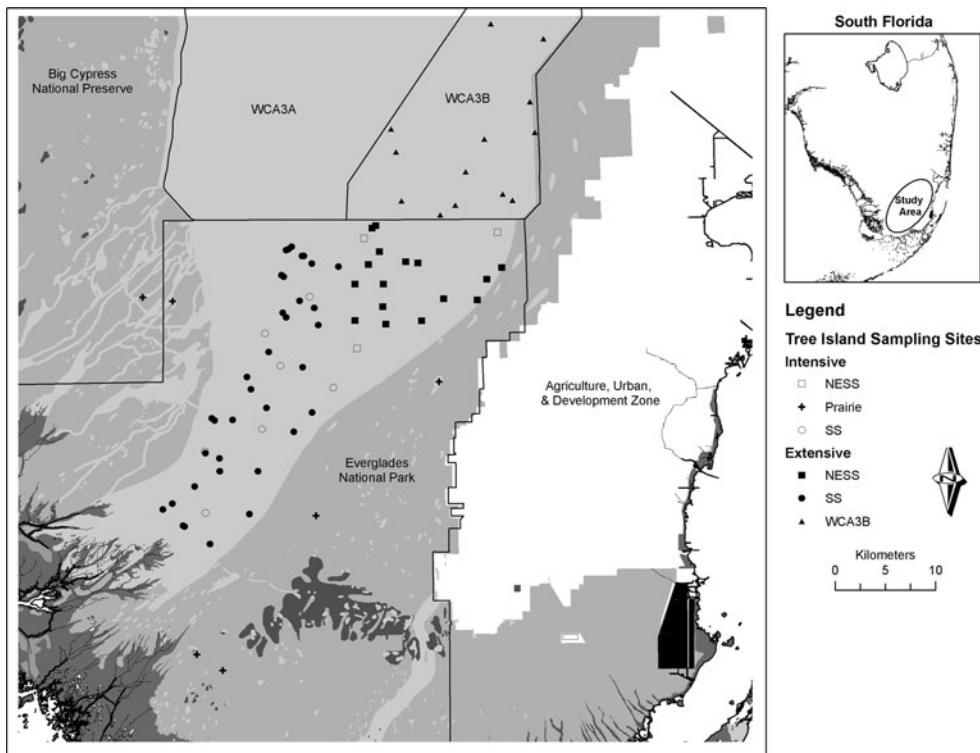
Figure 1. Study area and locations of sample tree islands.

whereas the fourth is in the Marl Prairie (MP) landscape. SS and MP have been managed essentially as wilderness areas by the National Park Service since the creation of Everglades National Park in 1947. WCA-3B, the northernmost of the sub-regions, is an impounded marsh managed by the Florida Fish and Game Commission. It is generally open to airboat use by hunters, fishers, and other recreationists. Prior to incorporation into ENP in 1989, NESS was also open to recreational users with minimal restriction.

METHODS

In this research we examined soils in 76 hardwood hammocks in central and southern Everglades tree islands (Figure 1). Based on aerial photos and helicopter overflights, we identified and sampled from all islands with significant representation of upland species in Shark Slough (41 sites), Northeast Shark Slough (19 sites), and WCA-3B (10 sites). We also collected soils from six representative islands in the marl prairie landscape on the Slough's eastern and western peripheries. The sampling method differed between two sets of islands present in these regions. The first set comprised 60 islands, on which we conducted a one-time vegetation survey in 2005–2007 (Extensive islands). The second set included 16 islands in SS, NESS, and adjacent marl prairies, where we

established permanent plots in 2005–2006 to support repeated vegetation sampling (Intensive islands). Each plot on the intensive islands was gridded into 5 × 5 m cells. In these islands, soil depth was determined at regularly spaced locations (3–5 and 9–61 points in Extensive and Intensive islands, respectively) by probing to bedrock with a metal rod. In each island, a sample was collected by auger from the surface soil (upper 10 cm) at two locations, and the samples were bulked for analysis. Measured soil parameters were total C, N, and P (TC, TN, TP); ash content, inorganic carbon (IC, based on ash %C); and pH. TC and TN were measured on a dry weight basis using a CHN analyzer (Perkin Elmer, Inc, Wellesley, Massachusetts, USA), and TP was determined colorimetrically following the method of EPA-365.1 after ashing-acid digestion (Solorzano and Sharp 1980). Total inorganic carbon (IC) was determined in ash (residual after combustion at 500°C) and scaled as % IC to total dry weight. Soil pH was determined in 1:1 (w/v) soil:water suspension using a pH meter. Organic C (OC) was determined by difference (TC − IC). The percentage of carbonate material in the soil was estimated from IC, assuming all IC to be in the form of calcium carbonate. Soil organic matter content was estimated from OC on the basis of equations developed for carbonatic and organic soils in Florida (Kasozi and others 2009). Non-carbon-based soil material (NCM) was calculated as the

percentage of soil weight not accounted for by carbonates or organic matter. Soil samples from the 16 Intensive islands were also analyzed for bulk density (Blake and Hartge 1986). These data were used to develop a linear regression ($R^2 = 0.85$; $P < 0.001$) between total organic carbon and bulk density, and the relationship was subsequently used to predict the bulk density of surface soils on the Extensive islands. Finally, using mean soil depth and the estimated bulk density values, we estimated the total phosphorus (on a volume basis) present in the soils of the hammocks.

Values of several hydrologic and landform variables were also estimated for a subset of 69 islands. Mean water level was estimated from a topographic survey from 5 to 25 regularly distributed points within the hardwood hammock portion of each island to a datum represented by the nearest free water surface, whose elevation could be estimated for the day of the survey through 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 the previous seven water years (1 May 2000 to 30 April 2007) was also derived from EDEN, and mean Relative Water Level over the period was calculated based on the difference between island and water table elevation. The topographic surveys were also used to calculate island height, that is, the difference in elevation between the surface of the tree island and the surface of the surrounding marsh, as estimated by USGS surveys (Desmond 2003; Jones and Price 2007). Beyond its influence on the relative position of the water table, tree island height may reflect the mode and timing of landform development, thereby influencing soil characteristics.

Forest structure was assessed in 15 of the 16 Intensive islands, including tree islands in MP (5 sites), SS (7 sites), and NESS (3 sites); we excluded one Intensive island because much of the surface was disturbed and lacking in tree cover. Rectangular 225–625 m^2 plots were established in 2006–2007, with each plot incorporating as much of the available extent of hardwood hammock as possible. Plots were gridded into 5 × 5 m cells, trees were mapped and tagged, and the DBH of each tree was measured in summer-fall of 2007–2009. Using individual tree diameters from 2009, we estimated basal area and biomass, on the basis of a generic equation for dry tropical forests developed by Brown and others (1989). We also measured canopy height by extending a leveled, telescoping height pole from the center of each cell, recording the height of the highest leaf that intercepted a 1-m diameter cylinder centered on the pole. The median of the 9–25 measurements taken in fall 2009 was used as a metric of canopy height.

We tested for sub-regional variation in relative water level, island height, and the seven soil variables (soil depth, TN, TP, pH, IC, OC, and NCM). Many of the variables were not normally distributed within regions, and transformations were unsuccessful in normalizing the data. Consequently, regional differences for each variable were tested with the non-parametric Kruskal–Wallis test, followed by a multiple comparison 'Z'-test when the experiment-wide result indicated a significant effect at α equal to 0.05. To reduce the dimensionality of the data for further examination of among-site patterns, we used principal component analysis (PCA) to identify a smaller number of orthogonal factors. PCA was applied to the site: environment matrix from the 69 sites for which mean relative water level, island height, and seven soil variables were available. Variable loadings of the factors with the highest explanatory value were interpreted, and the distribution of site scores for these factors was examined. Using the intensive islands, multiple stepwise regression was used to identify significant predictors of three metrics of stand stature, for example, basal area, stand biomass and canopy height. Scores for the three most important PCA factors, their squares, and first-order interaction terms were used as independent variables in the forward stepwise regression.

RESULTS

Soils, Landforms, and Hydrology

On average, the surfaces of hardwood hammocks in the Everglades marsh were 87 cm above the surrounding marsh, and 65 cm above the mean water table. As a group, hammock surface soils in Everglades tree islands were less than 0.5 m deep, and characterized by a basic reaction (mean pH = 8.12) and very high (mean = ~42,165 µg/g) phosphorus concentrations (Table 1). The latter are especially notable, in that mean P not only exceeded mean N by more than 2× in the same set of islands, it also exceeded background P concentrations in Everglades marsh soils by more than two orders of magnitude (Ross and others 2006). Based on volumetric weight, the upper 10 cm of soil of the hammocks held a mean total phosphorus of 1,489 (±1,030) g/m^2, with a range from 2.1 to 3,809 g/m^2. Although the organic fraction (mean organic C = 15.82%) was abundant in tree island surface soils, carbonate compounds, represented in

Table 1. Environmental Characteristics[1] of Hardwood Hammocks in the Everglades Landscape

Environmental characteristics (unit)	Mean	Median	Min	Max
Island height (cm)	87.5	87.2	16.3	174.5
Relative water level (cm)	−64.6	−65.1	−136.0	10.0
Soil depth (cm)	46.5	34.5	8.4	150.0
pH	8.12	8.18	6.36	8.76
TP (µg/gdw)	42,165	47,311	239	103,660
TN (%)	1.21	1.00	0.40	2.49
IC (%)	3.13	2.89	0.60	9.12
OC (%)	15.82	12.62	5.96	40.60
NCM (%)	49.70	51.41	13.36	81.46
Soil bulk density (g/cc)	0.262	0.287	0.060	0.451

[1]Estimates based on samples from 76 islands, except for soil bulk density (n = 15).

Table 1 by a mean inorganic carbon concentration of 3.1%, were important in many soils. Still, organic and carbonate fractions together accounted for only about half of soil weight, with the remainder (49.7%) being NCM.

Figure 2 illustrates the strong sub-regional patterns that underlie the regional means described above. The most consistent distinction was between MP hammocks and tree islands in the three sub-regions of the central peatland. Among the soil variables, MP forests were lowest in soil P, pH, inorganic carbon, and non-carbon materials, and highest in organic C and nitrogen content. With their high soil organic content, low bulk density and shallow soil depth, MP forest soils held a mean of only 41 g/m^2 phosphorus in the surface 10 cm, compared to 1,598 g/m^2 in slough hammock soils.
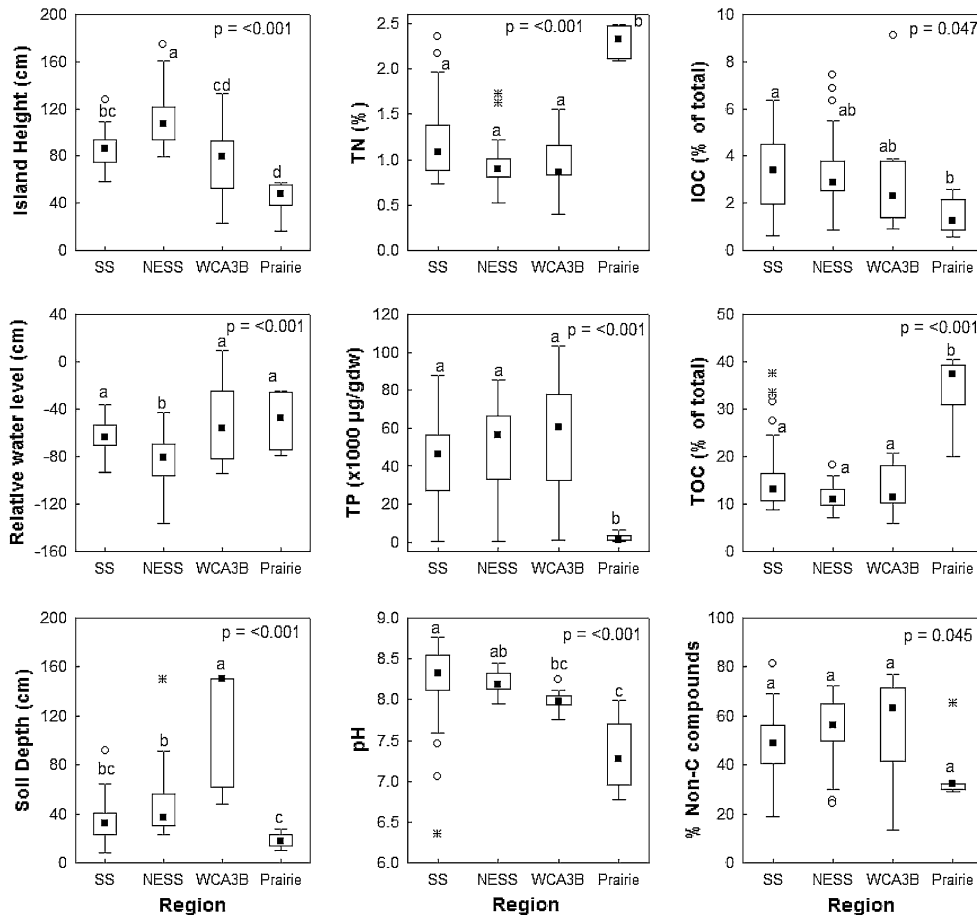

Figure 2. The distribution of nine physiographic and edaphic variables within the four sub-regions. *Box plots* represent boxes with 1st quartile, median, and 3rd quartile, whiskers with non-outlier range of data (the maximum or minimum value within 1.5 times the quartile), outliers (*circle*), and extreme (*) values. *P* values represent the Kruskal–Wallis test of the effect of sub-region on median values of each variable. Sub-regions followed by the same letter did not differ at $\alpha = 0.05$.

MP hammocks also had the lowest island heights, but median water table depth overlapped broadly with that found in hammocks in other sub-regions. Variation in hammock soil or physiography among peatland sub-regions was less pervasive. Significant differences were observed for four variables: island height (NESS > SS, NESS > WCA-3B), relative water level (NESS < SS, NESS < WCA-3B), soil depth (WCA-3B > SS, WCA-3B > NESS), and pH (SS > WCA-3B).

The Spearman rank correlation analyses showed that several physiographic and edaphic variables were significantly inter-correlated. Several of the P associations are of special interest. For instance, island height above the marsh surface was positively correlated with soil P (Spearman $R = 0.407$) (Table 2). Soil P was also positively correlated with pH and NCM (Spearman $R = 0.351$ and 0.766, respectively), negatively correlated with OC (Spearman $R = -0.588$), and uncorrelated with IC. The first three axes of the PCA explained more than 85% of the variation in the eight soil, landform, and hydrology variables (Table 3). Factor 1 (eigenvalue = 3.78) distinguished alkaline, high P soils on the one hand from organic- and N-rich soils on the other. Factor 2 (eigenvalue = 2.39) represented a gradient from high-NCM soils to carbonate-rich sediments, and Factor 3 (eigenvalue = 1.49) represented an axis from high, well-drained sites to lower, less distinctive landforms with shallow water tables. Figure 3 portrays the distribution of sites in PCA factor space. MP sites are restricted to the negative (organic-rich) side of Factor 1, whereas sites from the three peatland sub-regions are grouped together toward the positive, P-rich side. Analysis of variance confirmed a significant effect of sub-region on Factor 1 scores ($F_{(3,65)} = 27.05$, $P < 0.001$), with HSD post-hoc comparison indicating that Factor 1 scores for MP were less than

each of the other sub-regions (which did not differ among themselves). Unlike Factor 1, sites from the four sub-regions appear to be inter-mixed on Factors 2 and 3 (Figure 3), and ANOVA identified no sub-regional effects.

Forest Structure and Growth Relationships

Median basal area, biomass, and canopy height in the 15 tropical hardwood forests sampled were modest, at 25.96 m^2 ha^{-1}, 130.13 Mg ha^{-1}, and 8.4 m, respectively (Table 4). Medians for all three variables were lowest in MP, but no effect of sub-region was indicated by Kruskal–Wallis tests, due to substantial within-region variation and minimal replication (Table 4).

Regressions predicting forest structure from PCA factor scores gave different results depending on the metric used. Stepwise regression analysis identified Factor 2 as an independent predictor of canopy height, suggesting that soil composition weighted toward non-carbon materials was beneficial to growth (Figure 4). However, neither basal area nor biomass exhibited a significant relationship to any single factor or combination.

DISCUSSION

Hardwood hammocks in the southern Everglades grow on two very distinct soil types. The first, consisting of shallow organic soils developed directly on limestone bedrock outcroppings, is common in tree islands in the seasonally flooded Marl Prairie landscape. In contrast, hammock soils on islands embedded in long hydroperiod marshes in the central Everglades peatland are deeper, with much higher mineral content, alkaline pH, and extremely high P concentrations. However, our

Table 2. Spearman Rank Correlation Matrix of Environmental Characteristics of Hardwood Hammocks in the Everglades

Environmental characteristics (unit)	Island height (cm)	Relative water level (cm)	Soil depth (cm)	pH	TP (µg/gdw)	TN (%)	IC (%)	OC (%)
Relative water level (cm)	**−0.829**							
Soil depth (cm)	0.134	−0.096						
pH	0.034	0.043	**0.260**					
TP (µg/gdw)	**0.407**	**−0.346**	0.224	**0.351**				
TN (%)	**−0.315**	0.196	**−0.391**	**−0.476**	**−0.543**			
IC (%)	−0.073	0.109	**0.421**	**0.497**	−0.173	**−0.414**		
OC (%)	**−0.310**	0.216	**−0.353**	**−0.484**	**−0.588**	**0.920**	**−0.356**	
NCM (%)	**0.372**	**−0.296**	−0.007	0.087	**0.766**	−0.215	**−0.627**	**−0.307**

Correlations significant at $P < 0.05$ are in bold. $n = 69$.

Table 3. Factor Loadings of First Three Factors of Principal Component Analysis, Applied to Two Physiographic and Seven Edaphic Variables Measured at 69 Everglades Hardwood Hammocks

	Factor 1 Alkaline, high P	Factor 2 Non-carbon materials	Factor 3 Well-drained
Eigenvalue	3.78	2.39	1.49
% of total variation	42.0	26.6	16.6
Variable			
Island height	0.61	0.27	**0.70**
Relative water level	−0.46	−0.38	**−0.76**
Soil depth	0.18	−0.63	−0.14
pH	**0.79**	−0.22	−0.23
Total P	**0.73**	0.48	−0.32
Total N	**−0.91**	0.27	0.08
IC	0.33	**−0.89**	0.23
OC	**−0.94**	0.20	0.17
NCM	0.42	**0.78**	−0.40

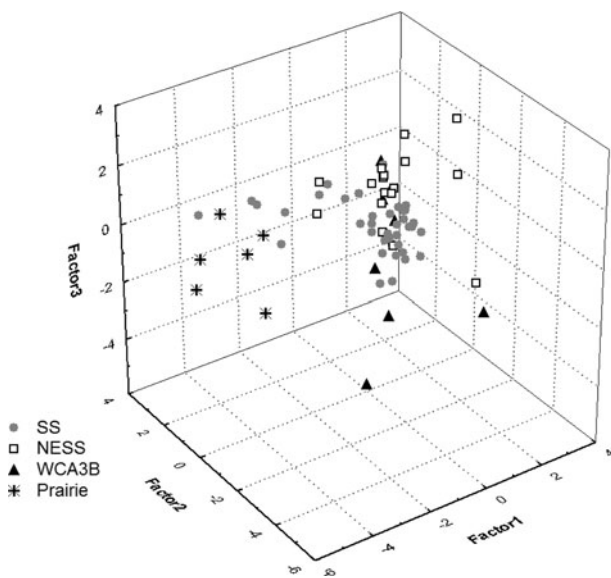*Most important variables on each factor are printed in bold face.*

Figure 3. Projection of tree islands, grouped by subregion, in the factor space formed by PCA Axes 1, 2, and 3.

data suggest that this edaphic variation does not result in clear differences in forest structure and production between Marl Prairie and Slough hammocks.

Soil Development

The arrangement of tree island surface soils along a gradient from circumneutral organic soils on the one hand, to highly alkaline, mineral soils on the other is a common theme in south Florida wetlands, but has not been previously described for these forested inclusions in the Everglades marsh. In the palustrine portions of the Everglades, flooding depth and duration are critical drivers of soil formation, through their effects on the primary producers and the rate of organic matter decomposition (Mitsch and Gosselink 2007). In semi-permanently flooded (8–12 months y^{-1}) marshes, emergent graminoid or floating-leaved aquatic macrophytes are the dominant primary producers, and their detrital remains decompose slowly. In seasonally flooded (3–8 months y^{-1}) prairies,

Table 4. Median Values for Three Structural Variables in Tropical Hardwood Forests in Tree Islands in Three Southern Everglades Sub-regions

Region	*n*	Basal area (m^2 ha^{-1})	Biomass (Mg ha^{-1})	Canopy height (m)
SS	7	29.37(16.26, 72.64)	149.70(80.92, 365.14)	8.98(4.76, 11.41)
NESS	3	23.45(17.96, 33.19)	130.13(88.82, 153.98)	8.75(5.47, 9.75)
Prairie	5	23.17(20.98, 33.49)	91.94(75.52, 158.74)	7.75(6.50, 8.18)
All	15	25.96(16.26, 72.64)	130.13(75.52, 365.14)	8.40(4.76, 11.41)

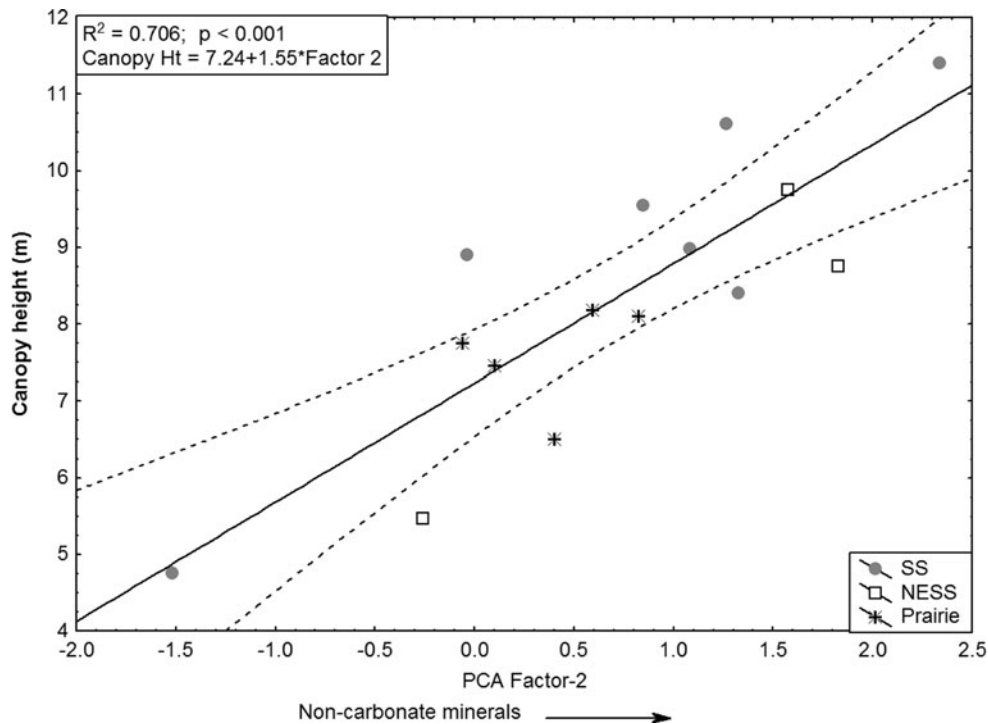*Minimum and maximum values for each category are in parentheses.*

Figure 4. Regression model for prediction of canopy height of Everglades tropical hardwood forest structure from PCA factor 2.

macrophyte productivity is lower, and periphytic and benthic algal communities predominate (Davis and others 2005; Ewe and others 2006). The photosynthetic consumption of CO_2 within the water column by these algae leads to the precipitation of calcium carbonate and the formation of mineral soils (marls) (Gleason and Spackman 1974). However, although the peatland and marl prairie environments may influence soil development in the hammocks, there is little evidence that hammock soils developed under flooded conditions, or that palustrine developmental models apply.

Surface soils in MP hammocks are characterized by relatively high OC and total N, low IC and total P, and neutral to slightly basic pH (Figure 2). On the Miami-Dade County soil survey (USDA 1996), these soils are mapped as Dania or Matecumbe mucks, and Craighead (1971) described them as Gandy Peats. In both physical and chemical characteristics, they resemble the Folists (Lithic Troposaprists) that support hardwood hammock vegetation in the upper Florida Keys (Ross and others 2003). Fibric organic soils that develop in upland settings, Folists are especially common on limestone or young volcanic surfaces (Collins and Kuehl 2001). Maintenance and development of an organic soil in a well-drained, subtropical environment requires high aboveground production, because decomposition is likely to be rapid. In the most productive Key Largo hammocks, decomposition rates are initially rapid, approaching 60% in

the first 24 months after leaf drop, but leaving recalcitrant materials behind that form the bulk of the soils (Ross and others 2003). The same is likely in Marl Prairie tree islands, where litter turnover rates (net annual litterfall/average detrital biomass) above 1 have been observed (Ross, unpublished data). As in the Keys, soil development in the Marl Prairie tree islands in the present study consists primarily of a reprocessing of dead roots and remains of aboveground organic materials.

The high mineral content observed in almost all sites in our extensive survey of central peatland hammock surface soils is consistent with two full soil profiles recently described by Coultas and others (2008) at Crandon and Heartleaf Hammocks in NESS. Profiles in both hammocks exceeded 1.5 m in depth, and included abundant bones, shells and artifacts throughout. Organic matter was 10–15% at the surface, but decreased downward in the profile, such that the soils were classified morphologically as Mollisols (Fluventic Calciudoll and Cumulic Hapludoll, respectively). Most notably, a petrocalcic layer of approximately 20 cm thickness was present mid-profile, beginning about 60 cm below the surface. The mechanism of development of the petrocalcic layer was uncertain, but was hypothesized by the authors to involve the precipitation of calcite from calcium-rich capillary waters originating in the shallow water table. McCarthy and others (1993) documented a similar subsurface precipitation of calcium, magnesium,

silica and sodium minerals in tree islands developing in anastamosing channel systems in the Okavango Delta of Botswana. Water movement into the islands was driven by the transpiration of large trees, and mineral precipitation was responsible for soil accretion and landform aggradation. Both physicochemical and biological mechanisms (that is, exclusion of cations at the root surface) were responsible for the precipitation of minerals from solution. Because the process depended on the proximity of tree roots to the groundwater table, soil accretion would proceed only when the islands were surrounded by permanent surface water, and ceased when the channel system shifted away from the islands.

In the Everglades context, McCarthy and others' model may apply well to incipient tree islands embedded in the continuously flooded conditions of the central peatland. Wetzel and others (2011) reported high Na and Cl ionic concentrations in groundwater beneath an elevated tree island in Water Conservation Area 3, particularly during the dry season. These observations suggest the focused transport and deposition documented in the Botswanan islands, with salts being drawn toward the island in the transpiration stream, but then excluded at the root interface. Besides a groundwater source, the high mineral content of hammock sediments in interior Everglades tree islands could be derived from other allochthonous sources (dust, bones and human artifacts) or from residuum remaining after partial dissolution of the underlying limestone bedrock. Although the origin of these soils remains an open question, future development of models to explain the dynamics of patterned Everglades peatlands (Cohen and others 2011; Larsen and Harvey 2010) should endeavor to incorporate the minerogenic nature of these embedded elements.

Phosphorus and Other Soil Properties

The mechanism(s) by which extremely high concentrations of soil P have developed in some Everglades tree islands is controversial. Most thinking has revolved around the means by which P arrives at the island (Wetzel and others 2005; Ross and others 2006). Alternatives include (1) faunal deposition by animals feeding elsewhere, (2) entrapment of aerosol-P by tree crowns, (3) disposal of P-rich bones in kitchen middens by native Americans, who used the islands as temporary or more permanent campsites, or (4) the drawing-in of dilute-P marsh water to the tree island in response to the rapid transpiration stream of trees

in mesic sediments and favorable growing conditions. Less attention has been paid to the means and efficiency with which P is sequestered in tree island soils once it arrives, though Jayachandran and others (2004) and Ross and others (2006) hypothesized that P may be especially prone to fixation in insoluble forms in Ca-rich tree island soils. In fact, despite the recent interest in the origin of these P hot spots, our study is the first to describe the associations between P concentrations and other soil and hydrologic parameters in hardwood hammocks across a broad spatial landscape.

One important finding of our analysis was the strong positive association of soil P content and soil alkalinity (Table 2), with enormous concentrations found in soils of pH above 8. This suggests that much of the phosphorus sequestered in Everglades tree islands may be in forms unavailable to plants, as P availability generally declines sharply at pH values outside the range 5.5–7.5 (Black 1968; Wright and others 2009). Although the predominant forms of phosphorus in hammock soils are not well known at present, our findings do provide some direction in this regard. Soil P was negatively associated with the organic fraction (Table 2), in direct contrast to the pattern exhibited over a wide range of Everglades marl and peat marshes (Scheidt and Kalla 2007), including P-enriched marshes (Noe and others 2001; Craft and Richardson 2008). Given the relationship with pH discussed above, the absence of correlation between soil P and IC was surprising. Instead, P exhibited a strong positive association with non-carbon materials, which represented, on average, about half of soil weight in the sampled islands. Working with soils from the agricultural areas immediately east of the Everglades, Zhou and Li (2001) also found phosphorus-sorption to be strongly correlated with non-carbonate clays at low P-concentrations, though carbonates became important in binding P at high concentrations. Several studies have shown that amorphous and crystalline calcium phosphate compounds can form secondarily in association with calcite surfaces (Freeman and Rowell 1981; von Wandruszka 2006). However, if P-sorption in the hammocks was primarily through reaction with calcite, a positive association between P and IC likely would have resulted. Another possibility is that much of the P was deposited in bound form, as hydroxylapatite ($Ca_{10}(PO_4)_6(OH)_2$) in the bones that suffused the profiles described by Coultas and others (2008). In any case, the large volumes of bones present in these soil profiles are indicative of amplified human activity, which is likely to have been more concentrated on the taller islands than

others, resulting in high soil phosphorus in those islands. The nature of P-sorption in hammock soils remains very much an open question.

Resource Islands and Forest Production

The data presented above clearly mark Everglades tree islands as islands of fertility in a nutrient-limited wetland landscape. However, they are also distinguished from the rest of the landscape by attributes of the belowground environment other than their nutrient contents. Soils have built up to present a surface raised well above the water table, and their mineral component prominently includes a non-carbonate fraction whose presence has not been reported elsewhere in the southern Everglades. Most importantly, these soils are occupied and influenced by trees, which are known to alter soils by their impacts on microclimate, and on the cycling and redistribution of water, nutrients, and materials (Binkley and Giardina 1998). Like the ecosystems that form around desert shrubs, tree island ecosystems play an essential role in the life cycles of many organisms and in the biogeochemistry of the landscape (Givnish and others 2008; Wetzel and others 2009), and are resource islands in the broadest sense. Our study focused on mature tree islands well beyond the individual tree stage, in which processes of resource island formation may be inferred. We therefore examined our data for associations that might suggest which belowground resources or stresses might limit the productivity of tree islands, once formed.

We tested for relationships of site variables representing soil constituency, soil depth, and water table position with three structural indicators of relative site productivity. The relationships that emerged should be interpreted with caution, because the structural response variables we employed are likely to be imperfect indicators of production in subtropical hardwood forests of the Everglades. Stand structure in these forests is mixed-species and uneven-aged, reflecting not only site potential but also the forests' long history of human use. Furthermore, fragment size is irregular, variable and small (<0.1 ha to several ha), creating edge effects such as increased exposure to natural disturbances, especially tropical storms and hurricanes, with influences on forest structure that may be independent of site. Among the structural variables examined, basal area and biomass are not only sensitive to these disturbances, but are also slow to recover in their aftermath, as replacement of killed gap-forming trees by ingrowth of seedlings and advance regeneration

requires many years, even in the absence of further disturbance (Weaver 1986). Gap-filling by new individuals may be an especially prolonged process in forests used intensively prior to the creation of Everglades National Park, and many such stands show evidence of severe understocking (Ross and others 2010). Although canopy height also can be substantially reduced by windstorms, it may serve as a better indicator of site potential than basal area or biomass, because canopy recovery after disturbances that leave significant live structural legacy requires only the relatively rapid reiteration and expansion of the crowns of residual trees, a relatively speedy process. In our earlier work in the Florida Keys, we found that canopy height correlated well with direct measures of forest production (tree biomass increment and litter production), and adequately reflected a climatically controlled productivity gradient from islands near the south Florida mainland to more distal locations (Ross and others 1992, 2003). Presuming, then, that canopy height represents a good structural indicator of stand productivity, how then are we to interpret the relationships that were revealed by the regression analyses—both soil nutrients and the relative position of the water table without apparent effects, but a positive association between productivity and the proportion of non-carbon materials in the mineral soil component?

The finding that production does not vary along the gradient in soil N:P ratio (Factor 1) seems at first rather remarkable, given more than a 100-fold difference in total P in the sample data, and the extensive P-limitation of growth reported for Everglades marshes. However, several authors have suggested that tree islands with very high soil P in the Everglades interior may become nitrogen-limited, based on leaf N:P ratio (Ross and others 2006) or leaf $\delta^{15}N$, which becomes enriched when high P availability increases plant demand for nitrogen (Inglett and others 2007; Wang and others 2010). With phosphorus potentially limiting growth at one end of the Factor 1 gradient, and nitrogen limiting growth at the other, it is not surprising to find no relationship across the data set.

The absence of an association between productivity and water table depth (Factor 3) is likewise unexpected, until one considers the relatively narrow range of hydrologic conditions represented among the sample locations from which canopy height data were available. Tear-drop shaped tree islands in the interior Everglades exhibit a consistent decrease in canopy height and litter production from elevated, rarely flooded heads to the

seasonally flooded swamp forests in the islands' tails (Armentano and others 2002; Sah 2004). However, the 15 hardwood hammocks in our data set included only well-drained sites, with mean water table position recessed 25–92 cm from the surface. Our analysis suggests that within this narrow range, seasonal fluctuations in the water table do not in themselves create soil drought or saturation severe enough to limit forest growth.

Complete interpretation of the strong increase in canopy height from high-carbonate soils to soils high in non-carbon materials (Figure 4) await further study, including a full elaboration of the composition of the mineral fraction in the sample tree islands. Nevertheless, some informed speculation is possible based on the published literature. Sodek and others (1990) described minerals in the clay size class from several south Florida soils, including the marl prairies that surround some of the islands, as well as sites that support slightly elevated pine rockland forests. Calcite predominated in the prairie soils, but silicate materials, particularly hydroxy-interlayered vermiculite, were proportionally abundant within the relatively small clay fraction in the rockland soils. If vermiculite clays are similarly well-represented in the much larger mineral component of tree island soils, then positive effects on growth may ensue. Vermiculite clays have high cation exchange capacity, enhance water retention, and thus may improve moisture and nutrient availability to plants. The capacity of south Florida tropical hardwood forests to grow rapidly on shallow, organic-rich soils frequently beset by mid-summer rainless periods has previously been noted (Ross and others 2003), and the role of clay minerals in the process deserves more study.

CONCLUSION

In this study, we examined soils of well-drained tree islands embedded in Everglades marshes, finding them to be distinct in character from those in the surrounding landscape, and also exhibiting considerable regional variation. Tree island soils in the short-hydroperiod prairies most closely resembled the shallow organic soils reported from hammocks in the Florida Keys (Ross and others 2003). In contrast, the P-rich mineral soils we found in central peatland tree islands had no local analogue, differing from the sandy profiles described for hammocks in the Big Cypress National Preserve, for instance (Craighead 1971; Duever and others 1986).Viewed from either below- or above-ground perspectives, both of these distinctive Everglades ecosystems serve as excellent examples of resource islands. From below, the well-aerated soils include sharply elevated concentrations of phosphorus, not present in abundance in adjacent, anaerobic marsh sediments. From above, the forests provide shade, cover, and feeding opportunities for a broad faunal assemblage of permanent residents or seasonal opportunists drawn there from elsewhere in the ecosystem. Moreover, data presented here and by others suggest that the resources provided by soil and forest are interdependent, developing in tandem over many years. At early stages in their development, the establishment of communities dominated by woody plants may have depended on the availability of phosphorus, but in the mature forest ecosystems we examined there was no evidence of P-limitation to growth. Just as multiple resources may alternate in limiting individual or community production over periods of days to years (Chapin and others 1987), the resource fundamentally limiting tree island function may have changed drastically over the millennia of their development.

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