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PRIMARY RESEARCH PAPER

Pattern of nutrient availability and plant community assemblage in Everglades Tree Islands, Florida, USA

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Abstract We address the relative importance of nutrient availability in relation to other physical and biological factors in determining plant community assemblages around Everglades Tree Islands (Everglades National Park, Florida, USA). We carried out a one-time survey of elevation, soil, water level and vegetation structure and composition at 138 plots located along transects in three tree islands in the Park's major drainage basin. We used an RDA variance partitioning technique to assess the relative importance of nutrient availability (soil N and P) and other factors in explaining herb and tree assemblages of tree island tail and surrounded marshes. The upland areas of the tree islands accumulate P and show low N concentration, producing a strong island-wide gradient in soil N:P ratio. While soil N:P ratio plays a significant role in determining herb layer and tree layer community assemblage in tree island tails, nevertheless part of its variance is shared with hydrology. The total species variance explained by the predictors is very low. We define a strong gradient in nutrient availability (soil N:P ratio) closely related to hydrology. Hydrology and nutrient availability are both factors influencing community assemblages around tree islands, nevertheless both seem to be acting together and in a complex mechanism. Future research should be focused on segregating these two factors in order to determine whether nutrient leaching from tree islands is a factor determining community assemblages and local landscape pattern in the Everglades, and how this process might be affected by water management.

Keywords Biogeochemical hot-spot · N:P ratio · Phosphorus · Self-assembly · Spatial patterns · Landscape ecology · Wetlands

Introduction

The maintenance of the slough-ridge-tree island landscape pattern has been targeted as a priority conservation goal in the Florida Everglades (NRC, 2003). This patterned landscape shows orientation in the direction of water flow and is composed of open water with floating-leaved plants (slough), emergent vegetation (ridge) and teardrop-shaped patches of upland and swamp forest located in elevated areas of the ridges (tree islands, hereafter TI's). The Everglades ridge and slough is considered an oligotrophic wetland in which

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P is the limiting nutrient for primary producers (Noe et al., 2001). This oligotrophy is not uniform throughout the ecosystem, however. Transects from tree islands on elevated locations through normally flooded graminoid vegetation typically show several orders of magnitude or more difference in soil P concentrations, with the highest values occurring in the most infrequently flooded forests (Wetzel et al., 2005; Ross et al., 2006). Until now, however, there is little information about nutrient distribution at a finer scale within and surrounding the TI's, and how this distribution might affect community assemblages in the oligotrophic environments nearby. Nutrient availability has been described as one of the most important forces driving succession and community structure, affecting competition among plant species, and determining species composition of plant communities (Tilman, 1985; Vitousek & Walker, 1987; DiTomaso & Aarsen, 1989; Grace & Tilman, 1990; Vitousek & Howarth, 1991). Intuitively, an area of high nutrient concentration might affect plant communities located in nutrient-poor surrounding areas, especially in wetlands, where nutrients dissolved in water move readily. Orem et al. (2002) examined the role of nutrients in the development of tree island tails, and postulated that runoff transport of P to the tails was responsible for the classic teardrop shape of the island. Ross et al. (2006) found a strong association between hydrology and leaf N:P ratio, suggesting a shift in nutrient availability along a gradient from slough to TI's.

The origin and the factors affecting the maintenance of the slough-ridge-tree island landscape pattern are poorly known. Current conceptual models related to landscape pattern in the Everglades emphasize the roles of hydrology, erosion–deposition patterns, nutrient availability, peat accretion and disturbance, all acting together through feedback mechanisms to create the patterned landscape (Ross et al., 2003, 2006; Wetzel et al., 2005; Larsen et al., 2007; Givnish et al., 2008; Hanan & Ross, 2010; Watts et al., 2010). The linear orientation of the tree island and its teardrop shape suggest that water flow must play an important role in both the mechanism and its subsequent maintenance (see Sklar & van der Valk, 2002) and strongly suggest a leaching of nutrients associated with seasonal flooding events and strongly directional flow. Both hydrology and nutrient availability might play an important role in determining plant community assemblages, but both factors seem to be correlated and their relative importance remains unknown.

In this article, we used RDA variance partitioning analysis to specifically address the effect of nutrient availability on plant community assemblages in the tree island tail and surrounding slough. Using soil N:P ratios, we explore how a shift in nutrient availability might affect community assemblage within the TI's boundaries and in surrounding areas, and the relative importance of nutrients and hydrology in determining plant species composition. We deliberately do not discuss the origin of high P of the upland areas of the tree islands, and focus instead on testing if nutrient availability might act as a driver of landscape patterning in the Everglades TI's.

Methods

Study area

Tree islands in the Shark Slough region of the Everglades are organized around small (~1–2 m) topographic rises in the limestone substrate, i.e., "fixed tree islands" sensu Sklar & van der Valk (2002). Above these outcroppings, the well-drained soils of the TI "head" support upland tropical dry forest species that typically reach a height of 10–15 m. In the TI "tails", flooded areas are inhabited by swamp forests, some with lush fern and herbaceous understory communities. In the swamp forest, canopy height, vegetation cover, and surface elevation decrease down the axis of the tree island. The length of this tail varies, but in the majority of cases the swamp forest constitutes most of the total surface of the TI. The vegetation in the tree island tail has previously been recognized as three discrete habitat types, based on hydrology and vegetation composition (Bayhead, Bayhead Swamp, and Marshes, see Ross et al., 2006), and these units may be recognized in the field and on aerial photos.

Sampling strategy

We selected three TI's located in Shark Slough in Everglades National Park, Florida. USA: Gumbo Limbo Hammock, (UTM 525999, 2834793), Satinleaf Hammock (UTM 524499, 2838019, and Black Hammock (UTM 531295, 2832630). These three large islands, each of which included the range of broadleaf forest types in the southern Everglades, represented hydrologic conditions in eastern, central, and western parts of the Shark Slough. Sampling included a single survey of surface elevation, soil depth, soil characteristics, and vegetation structure and composition along four transects. One transect followed the long axis of the tree island, and the other three transects were laid at right angles to the first in the TI's head, and at two locations within the tail. The elevation of the surface was determined at 10-m intervals (5-m intervals within and immediately adjacent to the hardwood hammock) along each transect by surveying via autolevel from a benchmark of known elevation. We estimated hydroperiods (HYD, number of days per year when the surface was inundated) at 138 survey plots along transects in the three islands, 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. Daily water level at the survey sites was estimated assuming a flat water surface, and an annual average hydroperiod was calculated for the 7–year period prior to vegetation sampling. Soil depth (SDPH) was determined at each point by probing to bedrock with a metal rod. Soil samples were collected with a 10 cm diameter soil auger at 5–25 m intervals along the transverse and longitudinal transects. Several samples were collected at each point to obtain a representative substrate. The samples were returned to the lab and stored in plastic bags in the refrigerator until analysis. Organic matter (OM) and carbonate (CO_3) content were determined by loss on ignition (Dean, 1974), total nitrogen (N) by Carlo Herba elemental analyzer, and phosphorus (P) by dry ashing (Solorzano & Sharp, 1980). Soil pH was determined in a 1:1 soil:demineralized water subsample homogenized in a blender for 90s (McLean, 1982).

Vegetation sampling was completed at the same locations used for elevation-soil sampling, i.e., at 5 or 10 m intervals along the transects. Sampling protocols were as follows: (1) cover class of trees and vines were estimated by species within a plot of 2 m radius around each point; (2) cover class of herbs and shrubs were estimated by species within a plot of 1 m radius centered on each point. Cover classes were: 1, 0–1%; 2, 1–4%; 3, 4–16%; 4, 16–33%; 5, 33–66%; and 6, >66%.

Data analysis

Based on plant community composition we visually assigned each plot to one of four categories: Hardwood Hammock, Bayhead, Bayhead Swamp, and Marsh. Hardwood Hammock corresponded to the TI head, and the other three units to the TI tail and ridge transition. Differences in environmental data among these four discrete microhabitats were assessed using analysis of variance (ANOVA) followed by Tukey's HSD post hoc test.

Considering the upland area of TI's as the source of nutrients, we were interested in determining how nutrient availability and other environmental factors might affect community assemblages in surrounding areas. Our analysis of vegetation–environment relationships therefore focused on only the swamp forests (Bayhead and Bayhead Swamp) of the tree islands and the marsh immediately adjacent to it.

Redundancy analysis (RDA, ter Braak, 1991), a multivariate linear technique, was used to assess the relationships between community composition (based on species cover) and the environmental variables. The environmental variables used in the analysis were hydroperiod (HYD), soil depth (SDEP), soil organic matter (OM), soil pH (pH), soil carbonate content (CAR) and soil N:P ratio (N:P). We used soil N:P ratio in our analysis instead of soil N and P concentrations separately, because the former provides a better link to plant N:P ratio, sometimes employed as a measure of the resource supply ratio of plants (Tilman, 1982, 1985, 1997; see review in Güsewell, 2004). Ross et al. (2006) detected a plant tissue N:P ratio gradient in the study area, strongly associated with hydrology.

We ran separate analyses for the herb and tree layer composition. Species occurring less than three times in all the plots sampled were excluded. In the analysis of herb species composition, we also included tree cover (TCOV, calculated as the sum of all tree and vine species (*Cissus sicyoides* and *Mikania scandens*) cover in each plot cover of the vines, as a predictor variable, because tree canopy might influence the structure and composition of ground vegetation by modifying light availability and soil moisture. In all statistical analyses, soil N:P ratio was log transformed to meet conditions of normality and homogeneity of variance. The significance level was fixed at $P \leq 0.05$ for all analyses.

We used an RDA variance partitioning technique (Borcard et al., 1992) because it allowed us to address several analytical issues directly. The first issue was isolation of the role of landscape-scale spatial variation and tree island identity in explaining community assemblage. We assumed that differences in the locations of our three TI's within the landscape may have some effects on the relationships between environmental variables and community composition, and therefore incorporated this spatial component, expressed as tree island identity, as a predictor in the RDA analysis. Our approach therefore resembled that of Totland & Nylehn (1998) in its intent to distinguish species variance explained by spatial components from species variance due to environmental variables. We created a spatial component by coding individual TI's as dummy variables, i.e., spatial variables TI-1, TI-2, and TI-3. We constructed four RDA analyses, using (1) environmental predictor only, (2) the spatial variable only, (3) environmental variables as predictor and spatial variable as the covariable, and (4) the spatial variable as the predictor and environmental variables as covariables. Based on these analyses, the variance partitioning technique allows determination of the percentage of variance accounted by environmental and spatial components (TI identity).

Secondly, we were interested in partitioning the pure and shared effects of nutrient availability in relation to other environmental variables in determining community assemblages. We ran five RDA analyses, using (1) soil N:P ratio only, (2) all other environmental variables, excluding soil N:P ratio, (3) other environmental variables as the predictors and soil N:P ratio as the covariable, (4) Soil N:P ratio as a predictor and all other environmental variable as covariables, and (5) all variables. To test the significance of the first and second RDA axes and the overall model we used a Monte Carlo test with 499 restricted permutations, including in the design "transect" as covariable (ter Braak, 1991).

Result

Environmental variables

Environmental variables measured in our study varied strongly among the four Everglades communities: hardwood hammock, bayhead, bayhead swamp, and marsh (Table 1). In general, a gradient from the hammocks to the marshes was evident. Differences in topography created a flooding gradient from the upland areas (Hammock), with an average of less than 5 days of flooding per year, to the outer edge of the tree islands (Marshes), with an average of 342 days of flooding per year. Hydroperiods of all vegetation types except Bayhead Swamp and Marsh differed significantly. Soil P concentration was extremely high in the hammock and decreased toward the marsh; soil N showed the reverse, i.e.,

Table 1 Environmental variables and tree cover measure at the sample locations along transect in three Shark Slough TI's in Everglades National Park

Variable	Upland forest (TI's head)	Swamp forest and marshes (TI's tail and ridge boundaries)		
	Hammock	Bayhead	Bayhead swamp	Marshes
Soil depth	0.33 ± 0.01^{a}	0.79 ± 0.05^{b}	0.92 ± 0.085^{bc}	0.63 ± 0.077^{b}
pH	7.63 ± 0.06^{a}	6.38 ± 0.1^{b}	6.04 ± 0.09^{b}	6.63 ± 0.1^{bc}
Organic matter	25.66 ± 0.66^{a}	71.07 ± 2.99^{b}	76.64 ± 3.09^{b}	70.39 ± 3.75^{b}
Carbonates	10.81 ± 0.81^{a}	6.72 ± 0.83^{b}	8.43 ± 1.14^{ab}	9.12 ± 1.34^{ab}
Phosphorus	5.57 ± 0.32^{a}	0.81 ± 0.24^{b}	0.55 ± 0.33^{b}	0.08 ± 0.02^{b}
Nitrogen	1.1 ± 0.04^{a}	2.7 ± 0.11^{b}	3.34 ± 0.07^{c}	3.24 ± 0.14^{c}
N:P ratio	0.27 ± 0.053^{a}	26.53 ± 2.94^{b}	48.78 ± 4.85^{c}	70.76 ± 12.18^{d}
Hydroperiod	4.79 ± 2.29^{a}	238.37 ± 12.88^{b}	322.41 ± 8.28^{c}	342.24 ± 6.03^{c}
Tree cover	125 ± 5.76	65 ± 6.04	12 ± 3.6	0

The sampled points are organized following four discrete microhabitat previously described (see "Methods" section). Hydroperiod (days flooding year $^{-1}$), soil depth (m), and organic matter, carbonates, total carbon, nitrogen, and phosphorus (in % soil dry weight)

Significance of between-microhabitat post hoc comparisons is indicated with letters increasing from Hammock to Marsh. These opposite trends create a strong gradient in soil N:P ratio, with values in the range of 0.27–70.76, and with significant differences across all vegetation types. Mean pH in Swamp forest (<6.5) was significantly lower than in the Hammocks (7.63). Significant differences in soil organic matter between upland forest and swamp forest were observed, but differences among swamp vegetation types were not significant. In contrast, soil depth was lower in both the Hammocks and Marshes than in Bayhead and Bayhead Swamp, where the means were close to 1 m.

Correlation coefficients showed that variance inflation factors (VIF) were always less than 2, indicating absence of collinearity (ter Braak & Šmilauer, 2002) (Table 2).

Environment and spatial components

The result of variance partitioning of environmental and spatial variables (Table 3) showed that in the case of herb layers "pure" environmental factors explained 18.8% ($P = 0.002$) of the compositional variance. After partitioning out the effect of environmental factors, the "pure" spatial component is not significant, while the "shared" spatial effect accounted for 2% of variance explained. In the case of the tree layer, "pure" environmental factors explained 23.8% ($P = 0.002$)

Table 2 Correlation matrix between the environmental factors used in the RDA analysis and *P* values

	pH	OM	CO_3	N:P	HYD	TCOV
SDEP	−0.56**	0.25*	0.04	0.38**	0.39**	−0.17
pH		−0.46**	0.20	−0.48***	−0.43***	0.12
OM			−0.50**	0.54***	0.25*	−0.12
CO_3				0.043	0.04	−0.18
N:P					0.61***	−0.46**
HYD						−0.62***

Only significance level in correlation coefficients are indicated as follows: * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$

Table 3 Result of RDA variance partitioning of environmental and "spatial" (TI's identity) component in (a) herb and (b) tree layer of tree islands swamp forest in the Everglades Shark Slough

External constraints RDA	Sum of all canonical eigen values	Variance explained (%)	*P*
(a) Herb			
1. Environmental variables only	0.188	18.8	0.002
2. "Spatial" variable only	0.046	4.6	0.1
3. Environmental variable, "spatial" as covariable	0.168	16.8	0.02
4. Spatial variable, environmental as covariable	0.014	1.4	0.24
Pure Spatial (4)		1.4	
Share Spatial (1–3)		2	
Pure environment (3)		16.8	
Residual (100% − (1 + 4))		79.8	
(b) Trees			
1. Environmental variables only	0.239	23.8	0.002
2. "Spatial" variable only	0.022	2.2	0.1
3. Environmental variable, "spatial as covariable	0.243	24.3	0.002
4. Spatial variable, environmental as covariable	0.035	3.5	0.52
Pure Spatial (4)		3.5	
Share Spatial (1–3)		0.5	
Pure environment (3)		24.3	
Residual (100% − (1 + 4))		72.7	

of the compositional variance, the percentage explained by the "pure" spatial component is not significant (Table 3). These results indicate that measured environmental variables were responsible for most of the accounted variance in species, and the responses of species to environmental variables were consistent across TI's. We, therefore, concentrated on the RDA using only the environmental variables. Note that in the case of the herb layer 79.8% of the variance remained unexplained by both environmental factors and spatial structure. For the tree layer, this unexplained variance was 72.7%.

Variance partitioning of N:P soil ratio

Table 4 shows the results of the RDA variance partitioning among environmental variables, focusing on the "pure" and "shared" effects of soil N:P ratio. For the herb layer, where total variance explained was 18.8% ($P = 0.002$); soil N:P ratio shared 1.9% of variance, while its "pure" effects accounted for 2.5% variance ($P = 0.05$). All other variables together accounted for 15.1% ($P = 0.002$), i.e., 78% of the explained variance. A similar result was obtained for the tree layer. However, "pure" N:P ratio accounted for only 8% of total variance explained, while the shared effect of N:P ratio was much higher than that of "pure" effects, accounting for 25% of total variance explained.

Table 4 Result of RDA variance partitioning of environmental factor in (a) herb layer and (b) tree layer of three tree islands swamp forest in the Everglades Shark Slough

	External constraints RDA	Explained variance %	*P*
(a) Herb			
1	N:P and others	18.8	0.002
2	N:P	4.7	0.002
3	Others	17.0	0.002
4	N:P with others as covariable	2.5	0.054
5	Others with N:P as covariable	15.1	0.002
A	Pure others	15.1 (78% total explained)	
B	Pure N:P	2.5 (12% total explained)	
C	Share (3–5)	1.9 (10% total explained)	
D	Residual	81.2	
(a) Trees			
1	N:P and others	23.8	0.002
2	N:P	9	0.002
3	Others	22.3	0.002
4	N:P with others as covariable	2	0.27
5	Others with N:P as covariable	16.2	0.002
A	Pure others	16.2 (68% total explained)	
B	Pure N:P	2 (8% total explained)	
C	Share (3–5)	6.1 (25% total explained)	
D	Residual	76.2	

Environment and community composition

For the herb layer, a Monte Carlo test showed that the first RDA axis ($P = 0.004$, $F = 10.86$) and the overall model ($P = 0.002$, $F = 2.81$) were significant. The first axis accounted for most (11.7%) of the explained variance, and appeared to represent the combined effects of soil N:P-Hydroperiod (correlations −0.26 and −0.31, respectively) as well as tree cover (TCOV) (0.39). The second axis mainly represented a gradient in soil depth (−0.50), as well as soil N:P ratio again (−0.38) (Table 5). Twenty eight species were included in the herb layer analysis, including submerged macrophytes, emergent macrophytes, shrubs and vines. *Rhynchospora inundata*, *Eleocharis cellulosa*, *Pontederia cordata*, and *Sacciolepsis striata*, occupying the bottom-left part of the ordination cloud (Fig. 1), were associated with long hydroperiod, low tree cover and low nutrient concentration, mainly low P (high soil N:P ratio). In contrast, *Sagittaria lancifolia*, *Leersia hexandra* and *Peltanda virginica*, occupying the upper part of the ordination cloud, were associated with shorter hydroperiod, higher P concentration (low soil N:P ratio), and shallow soils with high pH, and high tree cover. *Cladium mariscus* ssp. *jamaicense* and *Panicum hemitomon*, which are associated with medium P soil concentration and more balanced N:P values, occupied the left part of the ordination cloud. Finally, the bottom-right part of the ordination was occupied by *Typha dominguensis* and all the fern species present in the analysis (see Fig. 1 for details). These taxa were associated with deeper soil with low or medium tree cover, low pH and high organic matter content.

Fifteen tree species and two vines were included in the tree layer analysis. Monte Carlo testing indicated that the first RDA axis ($P = 0.002$, $F = 14.0$) and the overall model ($P = 0.002$, $F = 3.5$) were significant,

Table 5 Result of RDA analysis of herb and tree layers in 91 plots located along transect in three TI'S in the Everglades

	RDA axis 1	RDA axis 2	RDA axis 3
Herbs			
Eigen values	0.114	0.039	0.018
% cumulative variance	11.7	15.7	17.6
Correlation with variables			
Soil depth	0.152	−0.500	−0.034
pH	−0.045	0.268	0.054
Organic matter	−0.035	−0.255	−0.125
Soil carbonates	0.038	0.036	0.247
Soil N:P	−0.26	−0.388	0.039
TCOV	0.39	0.123	0.140
Hydroperiod	−0.311	−0.283	0.077
Trees			
Eigen values	0.168	0.038	0.014
% cumulative variance	17.2	21.6	23.0
Correlation with variables			
Soil depth	−0.2965	0.113	−0.089
pH	0.222	0.126	0.0291
Organic matter	−0.181	−0.204	−0.182
Soil carbonates	−0.237	0.364	0.007
Soil N:P	−0.479	−0.061	0.043
Hydroperiod	−0.585	−0.192	0.035

Monte Carlo Test of herb layer ($F = 2.57$, $P = 0.002$) and tree layer ($F = 3.50$, $P = 0.002$). The table shows only three first significant axes of a total of four, total variance explained was 23.8% for trees and 17.1% for herb

explaining 23.8% variance. The first axis was mainly related to the soil N:P ratio-hydroperiod gradient (correlations −0.48 and −0.58, respectively), and explained most of the variance (17.2%). The second axis was related primarily to soil carbonate content (0.36) and organic matter (−0.20).

Ficus aurea, *Bursera simaruba*, *Sarcostemma clausum*, *Parthenocissus quinquefolia*, *Morella cerifera*, *Vitis aestivali*s, *Salix caroliniana*, *Persea borbonia*, *Chrysobalanus icaco*, and *Cissus sicyoides* were organized in the upper-right part of the ordination cloud, and were associated with high pH and relatively low soil N:P ratio, short flooding duration, and low organic matter content (Fig. 2). The species that occupied the upper-left part of the ordination, i.e., *Aster carolinianus*, *Ampelopsis arborea*, and *Ilex cassine* were associated in our data with high CO_3 content and deep soils. *M. scandens*, *Ipomoea sagittata*, *Magnolia virginiana*, and *Annona glabra* occupied the bottom-left part, which was characterized by high organic matter, long hydroperiod, and high N:P ratio.

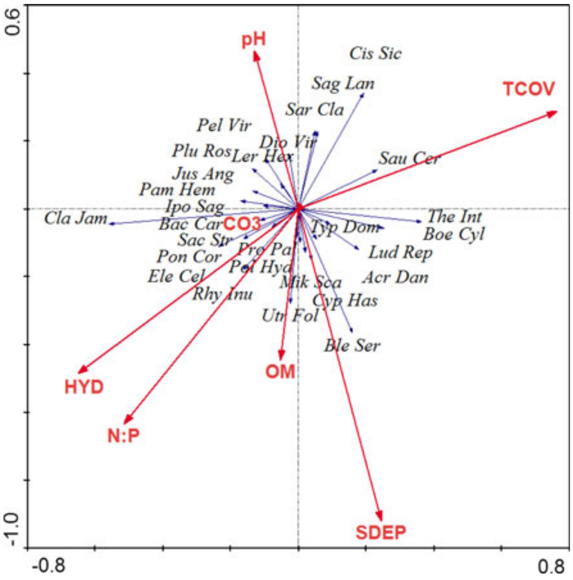

Fig. 1 Result of RDA ordination of 91 floristic sample locations along transects in three Shark Slough tree islands. Environmental variable includes soil depth (SDEP), soil N:P ratio (N:P), hydroperiod (HYD), soil organic matter (OM), soil carbonates (CO3), soil pH (pH) and tree cover (TCOV). The species names and codes are indicated as follows: *Acrostichum danaeifolium* (Ard Dan), *Bacopa caroliniana* (Bac Car), *Blechnum serrulatum* (Ble Ser), *Boehmeria cylindrical* (Boe Cyl), *Cissus sicyoides* (Cis Sic), *Cyperus haspan* (Cyp Has), *Diodia virginiana* (Dio Vir), *Eleocharis cellulosa* (Ele Cel), *Ipomoea sagittata* (Ipo Sag), *Justicia angusta* (Jus Ang), *Mikania scandens* (Mik Sca), *Peltandra virginica* (Pel Vir), *Panicum hemitomon* (Pam Hem), *Proserpinaca palustris* (Pro Pal), *Polygonum hydropiperoides* (Pol Hyd), *Pontederia cordata* (Pon Cor), *Pluchea rosea* (Plu Ros), *Rhynchospora inundata* (Rhy Inu), *Saururus cernuus* (Sau Cer), *Sacciolepis striata* (Sac Str), *Sagittaria lancifolia* (Sag Lan), *Sarcostemma clausum* (Sar Cla), *Thelypteris interrupta* (The Int), *Leersia hexandra* (Ler Hex), *Ludwigia repens* (Lud Rep), *Typha domingensis* (Thy Dom), *Utricularia foliosa* (Utr Fol), *Cladium mariscus ssp. jamaicense* (Cla Jam)

Discussion

Nutrient status

The amount of phosphorus observed in the upland portions of the tree islands constitutes an unusual

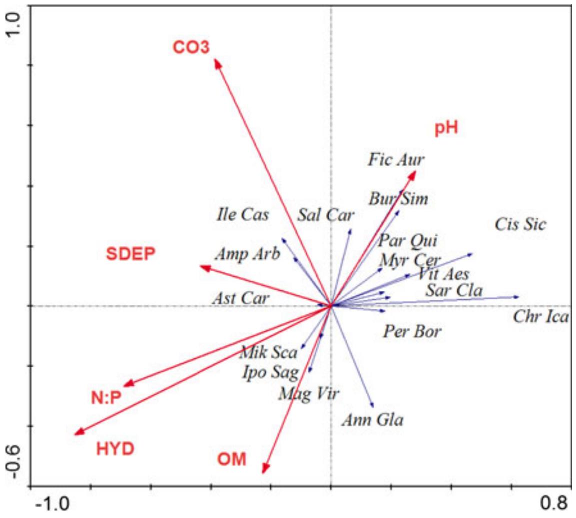

Fig. 2 Result of RDA ordination of 91 floristic sample locations around transect in three Shark Slough tree islands. Environmental variable includes soil depth (SDEP), soil N:P ratio (N:P), hydroperiod (HYD), soil organic matter (OM), soil carbonates (CO3), and soil pH (pH). The species names and codes are indicated as follows: *Ampelopsis arborea*, (Amp Arb), *Annona glabra* (Ano Gla), *Aster carolinianus* (Ast Car) *Bursera simaruba* (Bur Sim), *Cissus sicyoides* (Cis Sic), *Chrysobalanus icaco* (Chr Ica), *Ficus aurea* (Fic Aur), *Ipomoea sagittata* (*Ipo Sag*), *Ilex cassine* (Ile Cas), *Magnolia virginiana* (Mag Vir), *Mikania scandens* (*Mik Sca*), *Morella cerifera* (Myr Cer), *Parthenocissus quinquefolia* (Par Qui), *Persea borbonia* (Per Bor), *Salix caroliniana* (Sal Car), *Sarcostemma clausum* (Sar Cla), *Vitis aestivalis* (Vit Aes)

pattern in an oligotrophic system. The presence of high P concentrations in hardwood hammocks has been highlighted recently by several authors (Orem et al., 2002; Jayachandran et al., 2004; Wetzel et al., 2005, 2009; Ross et al., 2006; Ross & Sah, 2011). This study confirms this pattern, and places it within the context of surrounding vegetation. The head of the tree islands we examined accumulated P (average 70 times greater than surrounding marshes) and showed low nitrogen concentration (three times lower than surrounding marshes). N depletion on the tree island head might be promoted by the high mineralization of organic matter in this non-flooded area, and by the high N demand of the relatively productive forest. Ross et al. (2006) suggested that the heads of Shark Slough TI's were N-limited, based on the N:P ratio of leaf tissue from resident species.

The opposing trends observed in the spatial distributions of N and P within the tree islands resulted in a strong gradient in soil N:P ratios from head to tail of the TI's. Given the high rainfall in the Everglades area (German, 2000), the elevated topography of the TI's, the low P concentration in the slough, and an Everglades-wide geochemistry that favours P remobilization from P enriched to P unenriched areas (Bostic & White, 2007; Bostic et al., 2010) a strong mechanism of phosphorus retention must be in place for such a strong concentration gradient to be maintained between hammock, surrounding swamp forest, and adjacent marsh. The ability of wetland soil to retain P depends on the physico-chemical characteristics of the sediment and overlying water. Accumulation of inorganic P onto sediments is usually due either to adsorption of phosphate onto Fe(OOH) or, especially in hard water systems, by the precipitation of P with Ca ions (i.e., apatite formation). The relative importance of the two processes are controlled by the concentration of Fe(OOH) in sediments, and by pH and Ca ions concentration in overlying water (see Golterman, 1995a, b, 2004). However in calcareous systems with high Fe, Mg, and Al, and high H_2S content, the combined effects of redox potential and pH might play an important role in controlling P flux between sediments and overlying-water (Olila & Reddy, 1997). Jayachandran et al. (2004) indicated that most P in Shark Slough hammocks was adsorbed to calcium rather than iron or aluminum. That is more likely to be case, especially at high P- concentrations (Zhou & Li, 2001). Variation in sediment pH, P availability, soil carbonate content, and the lack of frequent flooding may combine to maintain a strong P retention mechanism on the TI's head.

Community assemblage and environmental variables

Nutrient enrichment is well recognized as an important factor affecting species composition and productivity in wetlands, and may result in a change in species composition and invasion by exotic species (Bedford et al., 1999). Using N:P plant tissue ratio as an indicator of N or P limitation, some authors suggested that shifts in limitation can lead changes in community composition (Koerselman & Meuleman, 1996; Verhoeven et al., 1996; Roem & Berendse, 2000). Our results show that soil N:P ratio plays an important role in determining Everglades herb and tree layer community assemblages, and perhaps in the formation and downstream expansion of TI's. Soil N:P ratios exhibit pure and shared effects on both herb and tree layer assemblages. Nevertheless, the percentage of total species variance explained by all variables is very low, and part of the variance accounted for by soil N:P ratio is shared with hydrology. It is notable that the total effect of soil N:P ratio (shared + pure) accounts for a higher percentage of the total explained variance for the tree layer (33%) than for the herb layer (22%), due to a larger shared N:P effect (25 and 10%, respectively). The response of trees must reflect environmental conditions across a long time frame, thus reflecting the long term tendency in nutrient status and hydrology to act in tandem and through a complex mechanism.

The distribution of herb layer species in the RDA analysis merits special attention (Fig. 1). Some species representative of Slough and Ridge boundaries (i.e. *E. cellulosa*, *R. inundata*, *P. cordata*, *S. lancifolia*, *L. hexandra*, *Panicum hemitomon*, *P. virginica*, and *Cladium mariscus* ssp. *jamaicense*) seem to be organized along the aforementioned gradient in nutrient availability and hydrology. The distribution of *E. cellulosa*, *R. inundata*, *P. cordata*, species which grouped together in the lower portion of Fig. 1, have been shown to have high competitive ability in low nutrient, flooded areas. *E. cellulosa* is well adapted to flooding (Edwards et al., 2003), its biomass increasing under flooding conditions (Busch et al., 2004). In both *E. cellulosa* and *Rhynchospora* spp, P availability has been found positively related to aboveground biomass (Busch et al., 2004). *R. inundata*, which inhabits nutrient-poor peat marshes, has higher aboveground biomass in continuously flooded and alternately dry–wet conditions than in dry conditions, where its growth is limited by N availability (Gerritsen & Greening, 1989). *P. cordata* shows good growth under both N and P limitation (Daoust & Childers, 1999), thus explaining its intermediate position in the N:P gradient. *C. mariscus* ssp. *jamaicense* is far apart from the gradient in a position of medium flooding and nutrient requirement too, and low tree cover. *Cladium mariscus* ssp. *jamaicense* appears to have a low P requirement (Daoust & Childers, 1999). Species that were far from the low P species in Fig. 1, i.e., *S. lancifolia*, *L. heaxandra*, *P. virginica*, and *P. hemitomon*, are known to exhibit high competitive ability under high nutrient (especially P) and short hydroperiod conditions. *S. lancifolia* exhibited considerable biomass increase in a P addition experiment, concurrent with a reduction in leaf N:P ratio from around 45 to 15 (Richards & Ivey, 2004). Yanbuaban et al. (2007) indicated that *L. hexandra* can accumulate a high amount of P and demonstrated a great capacity to induce N fixation in flooded soils. In this species and in *P. hemitomon*, N and P tissue contents decrease along the gradient from dry to flooding conditions (Miller & Sharitz, 2000). Delaune et al. (1986) found that in freshwater Louisiana marshes N addition increased the nitrogen content in tissue and above ground biomass of *P. hemitomon*. *P. virginica* seems to be a high N-demanding species (Daoust & Childers, 1999). Summarizing, all these species seem to be organized along a nutrient-flooding gradient, reflecting their competitive ability in the swamp forest surrounding the head of the TI's.

The linear orientation of the tree island and its teardrop shape suggest that water flow must play an important role in both the mechanism and its subsequent maintenance (see Sklar & van der Valk, 2002) and strongly suggest a leaching downstream of nutrients associated with seasonal flooding events. Both hydrology and spatially differentiated availability of nutrients might play an important role in determining plant community assemblages but both factors seem to be correlated and their relative importance remains unknown. Our analysis does support a strong role for nutrient leaching from TI's in local patterning in nearby vegetation, based on measured soil N:P ratios. Nevertheless, because hydrology and N:P ratio share a large part of the explained variance, and the overall percentage of species variance explained is low, other factors may also be playing a major role in determining plant community assemblages in the TI's we studied.

Conclusion and remarks

In this article, we established a baseline of physico-chemical soil properties of TI's, with the main focus on N and P concentrations and their spatial variation along the hydrologic gradient. The data presented indicate that (1) N depletion is present on the head of the tree island, (2) the opposing N and P gradients together create a strong N:P soil ratio gradient from the head to the tail and nearby ridge and slough landscape, and (3) N:P soil ratio explains part of herb and tree layer species variation in the tree island tails. However, part of its effect is shared with hydroperiod, especially in the tree layer.

Independent of the mechanism of P enrichment on tree islands, the presence of high P concentrations on the upland portions of the islands, and its decreasing concentration toward the swamp forest areas, suggest a process of P leaching from upland to the nearby marshes. Nutrient availability (measured as soil N:P ratio) affects plant community assemblages in TI's tail and surrounding marshes.

Our analysis shows that nutrient availability and hydroperiod are factors closely linked in explaining plant community assemblages in the tree islands-ridge-slough landscape. Experimental studies segregating the effects of both factors are required in order to determine whether nutrient leaching from TI's is a factor determining community assemblages and a local landscape driver in Everglades landscape patterning.

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