



Vegetation differentiation in the patterned landscape of the central Everglades: importance of local and landscape drivers

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ABSTRACT

Aim We present a model to account for self-assembly of the slough–ridge–tree island patterned landscape of the central Everglades in southern Florida via feedbacks among landforms, hydrology, vegetation and biogeochemistry. We test aspects of this model by analysing vegetation composition in relation to local and landscape-level drivers.

Location We quantified vegetation composition and environmental characteristics in central Water Conservation Area (WCA) 3A, southern WCA-3A and southern WCA-3B in southern Florida, based on their divergence in water management and flow regimes over the past 50 years.

Methods In 562 quadrats, we estimated species coverages and quantified maximum, minimum and average water depth, soil depth to bedrock, normalized difference vegetation index (NDVI) and proximity to the nearest tree island. We used non-metric multi-dimensional scaling (NMS) to relate compositional variation to local and landscape-level factors, and evaluated environmental differences among eight a priori vegetation types via ANOVA.

Results Water depth and hydroperiod decreased from sloughs to ridges to tree islands, but regions also differed significantly in the abundance of several community types and the hydroregimes characterizing them. NMS revealed two significant axes of compositional variation, tied to local gradients of water depth and correlated factors, and to a landscape-scale gradient of proximity to tall tree islands. Sawgrass height and soil thickness increased toward higher ridges, and NDVI was greatest on tree islands.

Main conclusions This study supports four components of our model: positive feedback of local substrate height on itself, woody plant invasion and subsequent P transport and concentration by top predators nesting on taller tree islands, compositional shifts in sites close to tree islands due to nutrient leakage, and flow-induced feedback against total raised area. Regional divergence in the relationship of community types to current hydroregimes appears to reflect a lag of a few years after shifts in water management; a longer lag would be expected for shifts in landscape patterning. Both local and landscape-level drivers appear to shape vegetation composition and soil thickness in the central Everglades.

Keywords

Cladium jamaicense, Florida, landscape ecology, peatland, *Peltandra virginica*, *Pontederia cordata*, *Sagittaria latifolia*, self-assembly, spatially coupled feedbacks, streamlined islands.

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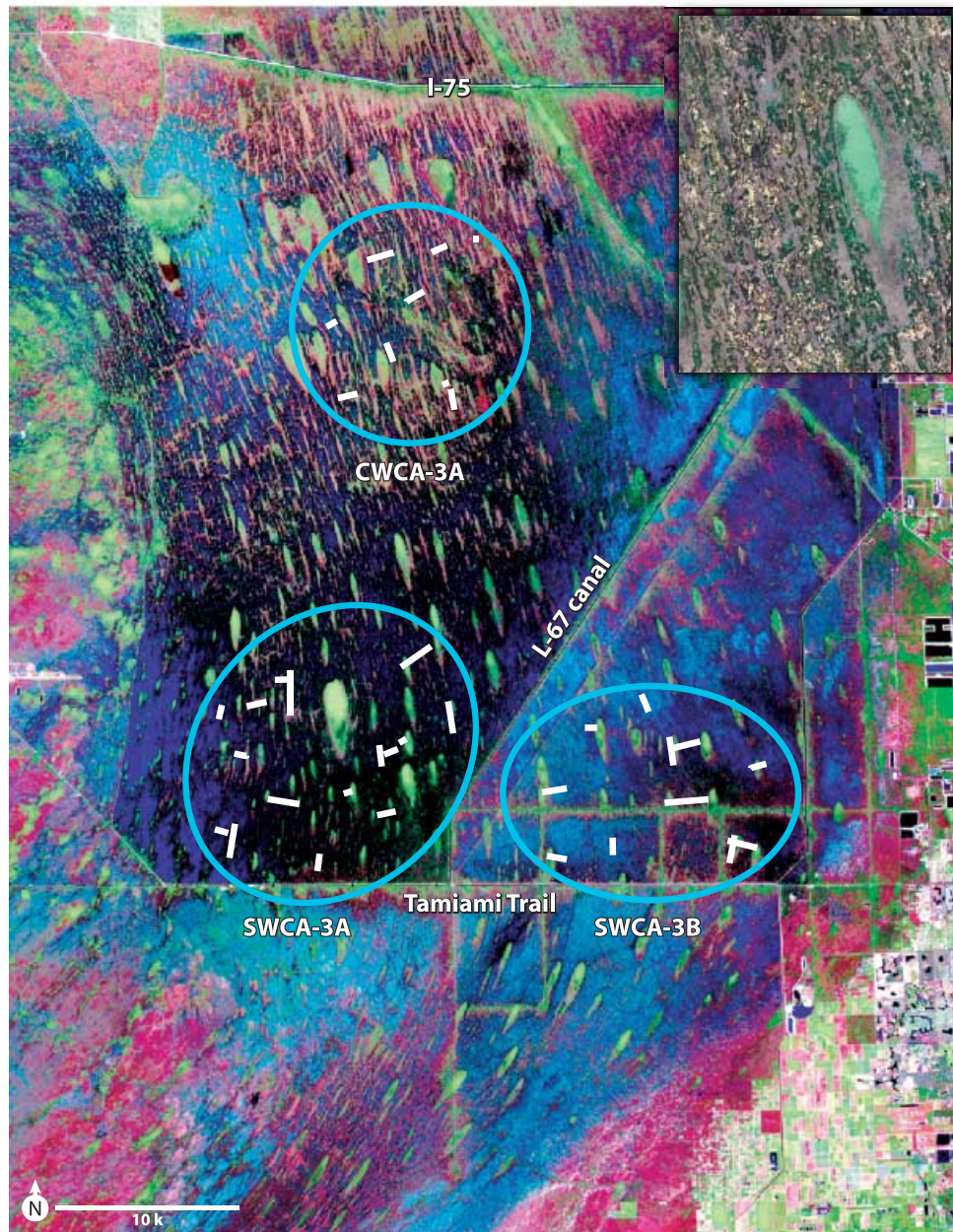


Figure 1 False-colour satellite imagery of the central Everglades, showing central and southern WCA-3A and southern WCA-3B and the location of study transects. The inset shows an aerial view of slough–ridge–tree island patterning in central WCA-3A.

INTRODUCTION

The Everglades of southern Florida are among the world's most extensive and intensively managed wetlands. Before a vast network of canals, levees and water-control structures began to crisscross the Everglades in the 1920s, surface water flowed southward from Lake Okeechobee into the Gulf of Mexico over an area of $c. 10^6$ ha (Browder & Ogden, 1999). The central Everglades are a strikingly patterned landscape, with thousands of teardrop-shaped tree islands embedded among regularly spaced, nearly linear sawgrass ridges and waterlily-dominated sloughs, all oriented in the direction of historic water flow (DeAngelis

et al., 1998; Science Coordination Team, 2003; Sklar & van der Valk, 2003; Ogden, 2005; Willard *et al.*, 2006) (Fig. 1). A substantial fraction of the biological diversity in the central Everglades reflects the differential distribution of species along a subtle microtopographic gradient of $c. 1$ m from slough bottoms to the tops of low tree islands.

Over the past several decades, historic patterns of water flow in the central Everglades have been severely disrupted, with compartmentalization and stagnation in many areas, and local reductions or increases in average water levels and hydroperiods (Davis *et al.*, 1994). At the same time, the vast populations of herons, egrets and other charismatic wading birds have

plummeted by over 80% in this region, including the Everglades National Park (Ogden, 1994). The United States of America and the State of Florida have thus committed to spending \$7.9 billion over the next 30 years to restore historic flow regimes in the central Everglades, in order to restore ecosystems and reinvigorate bird populations (USACE, 1999).

Yet relatively little is known about how these heroic efforts to replumb the Everglades – unprecedented in scope worldwide – will impact upon native ecosystems and species in the long term (NRC, 2003). Most previous analyses have taken the slough–ridge–tree island microtopographic gradient as fixed, and then asked how bands of vegetation and associated species would move up or down that gradient as water level varies (e.g. Gross *et al.*, 2003; Duke-Sylvester *et al.*, 2006). Surprisingly little attention has been paid to the fact that the Everglades are a vast peatland, with a substrate composed of partly decomposed plant remains, so that – as water levels vary and production and decomposition respond nonlinearly to changes in water-table depth – the topographic gradient may itself change. Furthermore, little attention has been paid to how flow itself – as distinct from water level or hydroperiod – might affect communities and the generation and maintenance of patterned landscapes (but see Givnish & Volin, 2003; Science Coordination Team, 2003; Wetzel *et al.*, 2005; Ross *et al.*, 2006). According to a recent review sponsored by the US National Academy of Sciences (NRC, 2003), creating and testing new models for the origin and maintenance of the slough–ridge–tree island patterned landscape is a high priority for Everglades research.

To address these questions and take up the challenge issued by the NRC (2003), we are developing and testing a conceptual model first advanced by Givnish & Volin (2003) to account for the generation and maintenance of the patterned slough–ridge–tree island landscape in the central Everglades, and to relate it to flow regime. Briefly, this model has the following components:

- (1) Sheetflow over the very gently tilted (< 0.05% slope), slightly irregular oolitic bedrock underlying the central Everglades should favour the accumulation of partly decomposed plant remains up to roughly the average water level, based on slow, mostly anaerobic decomposition below that surface.
- (2) Initial ‘bumps’ above that surface should grow, as a result of greater soil aeration increasing root function and thus plant growth and litter production, while decomposition increases only slightly. As local elevation increases, at some point increases in litter production due to this effect will slow, and decomposition (or combustion by fire during dry periods) will increase, so that the expected increase in peat surface height (dH/dt as a function of H) eventually falls to zero (Fig. 2). The curvilinear response of dH/dt to H provides a local positive feedback driving the formation of foci for ridges dominated by sawgrass (*Cladium jamaicense*).
- (3) The slowing of surface flow rates in the lee of incipient sawgrass foci would lead to the deposition there of floc and periphyton (clumps of algae, bacteria, microfauna and calcareous precipitates); this provides a spatially coupled positive feedback favouring the downstream propagation of ridges. The deposition of floc and periphyton at the edges (and interiors) of sawgrass

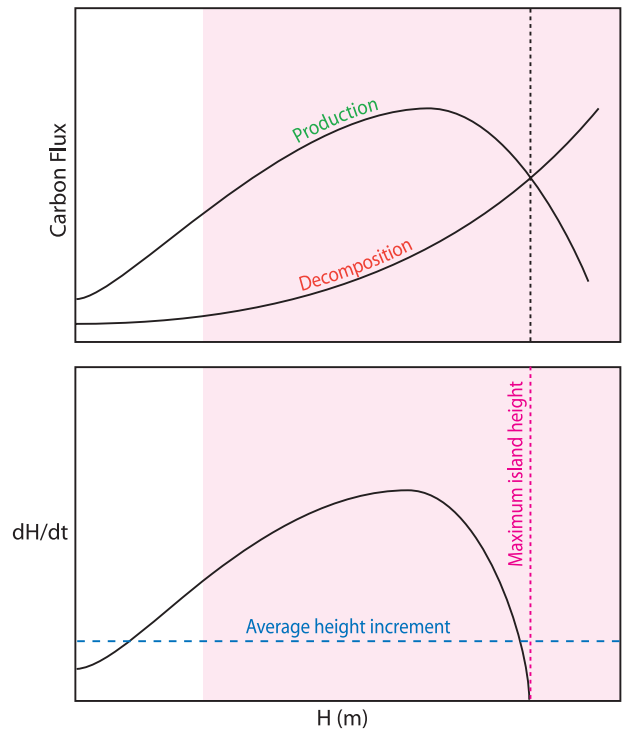


Figure 2 Schematic representation of positive and negative feedbacks in initial build-up of ridges and tree islands. As substrate height increases over an initial small rise, substrate aeration and root function increase, leading to an increase in production and litter deposition with little change in decomposition rate, resulting in an increased net rate of peat accumulation (ΔH) as a function of height relative to the water surface (H) in the landscape. When soils become sufficiently aerated to permit the invasion of woody plants (pink), ridges transition to tree islands and net rates of plant production increase further with inputs of P in animal droppings. At some point, decomposition and/or combustion increase with H faster than production, resulting in lower rates of growth; ultimately, maximum island height is set when production equals decomposition.

ridges during flood events, followed by subsequent decomposition and nutrient release, could further sharpen the ridge–slough boundary and ‘heal’ irregular fluctuations of that boundary from flowlines. Ridge peat should be rich in CaCO_3 , reflecting the importance of floc and periphyton accretion.

(4) As local peat elevation increases, at some point the substrate will become sufficiently aerated to allow invasion of woody plants. Tall shrubs and trees would provide roosting and nesting sites for herons and other wading birds; large amounts of guano deposited by such top predators, based on their foraging for prey over square kilometres of surrounding sloughs and ridges, would provide large inputs of phosphorus (the key limiting nutrient in the central Everglades; Noe *et al.*, 2001), further accelerate plant growth and provide a second positive feedback driving additional growth in peat elevation on tree islands.

(5) The slow diffusion downstream in peat pore-water of P deposited by birds on incipient tree islands should accelerate plant growth and litter production, leading to an increase in plant growth downstream of the incipient tree island. A streamlined

island tail should self-assemble, given: (a) relatively rapid movement of surface water around the island that would quickly remove any excess P entering from the groundwater at the island edge; and (b) a teardrop shape that would minimize mixing between the high-P, no surface flow, high-topography island regime and the low-P, high surface flow, low-topography ridge and slough regime. Surface peat on tree islands should be rich in P and low in CaCO₃, reflecting deposition of guano but not floc and periphyton.

(6) Island tails should be relatively short, given that they are driven by downstream diffusion of a limited amount of P from island heads; by contrast, ridges should be able to propagate downstream indefinitely, given that they are driven by the capture and accretion of biogenic floc and periphyton produced across the slough landscape, together with subsequent *Cladium* growth.

(7) As ridges and tree islands increase in abundance and extent, water must flow more deeply and longer in the intervening sloughs. This spatially coupled negative feedback would limit the extent of ridges and tree islands, and prevent loss of sloughs from the landscape.

(8) Furthermore, on a very flat peatland surface, the diversion of flow around the head of a ridge should foster, on either side of that ridge, the retention of sloughs of width comparable to the width of the ridge occluding the flow. Each ridge should grow in width until water is more likely to flow over its broad front than around it. Consequently, ridge–slough spacing should increase in areas of greater flow.

(9) Tree-island length should increase with the slope of the overall peat surface and local flow speeds, reflecting faster groundwater transport of P and greater streamlining of surface-water flow, which should result in a displacement downstream of the point at which P delivery and increased peat accretion is balanced by P removal by surface-water flow.

(10) Fire sweeping across the Everglades during drought should sharpen the edges of both ridges and tree islands, given the high flammability and fire tolerance of sawgrass and the suppression of fire-carrying grasses and sedges by shade in the understorey of tree islands.

We are now attempting to test this conceptual model by relating plant community composition and structure, production, decomposition, net peat accretion rates and landscape patterning to height above surface-water level and flow rate in three regions of the central Everglades that have diverged in flow rate, water level and hydroperiod over the past 50 years as a consequence of water management. These regions include: (1) central Water Conservation Area 3A (WCA-3A), with flow rates and water levels similar to pre-diversion conditions; (2) southern WCA-3A, with lower flows and deeper water than pre-diversion; and (3) WCA-3B, with essentially stagnant flows and rain-fed conditions (Fig. 1).

Here we present findings from the first phase of this research, relating trends in plant community composition and structure to height above surface-water level. Based on samples along 39 km of transects in all three regions, we present the first documentation of variation in central Everglades vegetation along the slough–ridge–tree island gradient in relation to surface-

water levels based on long-term hydrological data. After using non-metric multi-dimensional scaling (NMS) to extract significant axes of variation in stand composition, we relate these axes to a variety of environmental data, and test whether – as expected from our conceptual model – vegetation responds both to local conditions (e.g. height relative to surface-water level) and to landscape context (e.g. flow, proximity to P-rich islands). These findings provide one key pillar on which to base quantitative analyses of the impacts of proposed shifts in water flow and depth as part of the Comprehensive Everglades Restoration Plan (USACE, 1999). A companion paper will examine regional variation in landscape patterning associated with flow, and how patterning has shifted over a 64-year period (J.C. Volin, V.D. Owen, T.J. Givnish, V.C. Volin, K. von Ellenrieder & P.H. Glaser, unpublished data).

METHODS

Study area

The central and southern portions of WCA-3A, a managed compartment of c. 400 km², comprise the heart of the historic ridge-and-slough landscape of the central Everglades (Fig. 1). Central WCA-3A is bounded on the north by I-75; sheetflow enters it from the Big Cypress region to the west and through water-control structures that connect it with compartments to the north and east. Based on comparisons of models of water flow in the pre-drainage system with recent hydrological data, surface-water flows in central WCA-3A, although diminished, appear to be similar to historic conditions (Galloway *et al.*, 1999). As surface water moves into southern WCA-3A, bounded on the south by the Tamiami Trail, water tends to pool north of the roadway levee that restricts surface flow to the southern Everglades. WCA-3B is bounded on the west by the L-67 canal and levee, which separates it hydrologically from southern WCA-3A to its immediate west. This compartment, which is entirely surrounded by levees, receives very little surface water flow and has become primarily a rain-fed system (Science Coordination Team, 2003).

Anthropogenic inputs of N and P from upstream agriculture drop to reference conditions (and eutrophic vegetation disappears) within a few kilometres of the upper edge of WCA-2A (King *et al.*, 2004), which is upstream of – and a major source of water input to – our study areas in WCA-3A and WCA-3B. Within our study areas, the only evidence of anthropogenic eutrophication occurs within a few tens of metres of berms and canals, remote from our sampling transects. Total soil P has shown no recent (1992–2003) change over the portions of WCA-3A and WCA-3B we studied (Bruland *et al.*, 2007). Generally, peat soils a few centimetres below the water-table are anaerobic (Qualls *et al.*, 2001).

Vegetation data

In each study region, we established 9 to 16 transects (totalling 39.2 km across regions) parallel and perpendicular to the flow

Study area	No. of transects	No. of quadrats	Total length of transects (km)	Transect length (m) (mean \pm SD)
Central WCA-3A	9	121	7.08	787 \pm 408
Southern WCA-3A	16	232	17.62	1102 \pm 629
Southern WCA-3B	13	209	14.48	1104 \pm 566
Total	38	562	39.18	1031 \pm 565

Table 1 Distribution of transects and quadrats across the three study areas.

direction, spanning the slough–ridge–tree island microtopographic gradient (Fig. 1 and Table 1). Transect lines were determined at the outset of the project using infrared aerial photographs to stratify the sampling, and then located in the field using high-precision GPS (Trimble XR, Sunnyvale, CA, USA). Based on pilot surveys along a subset of these transects, we visually assigned local patches of vegetation to eight a priori categories: (1) flooded slough (open water with *Nymphaea*, *Utricularia* and periphyton dominant); (2) emergent slough (*Eleocharis* spp. often dominant); (3) slough–ridge transition; (4) short-sawgrass ridge (dominated by *Cladium jamaicense* < 125 cm tall); (5) tall-sawgrass ridge (*Cladium* > 125 cm tall); (6) ridge–tree island transition; (7) low tree island (fringes and tails of tree islands, dominated by *Annona glabra*, *Cephalanthus occidentalis* and *Salix caroliniana*); and (8) tall tree island (raised cores and bayheads dominated by a variety of subtropical trees, including *Chrysobalanus icaco*, *Ficus aurea*, *Myrica cerifera* and *Persea palustris*). Along each study transect, we sampled vegetation each time there was a shift in a priori vegetation-type; in most cases, we also sampled vegetation if no transition had been detected in the preceding 100 m of transect. At each sample point, we visually estimated the proportion of ground occupied by each non-woody species within a 1 m \times 1 m quadrat; coverage by woody species was estimated in a 2 m \times 2 m quadrat enclosing the groundlayer quadrat. On nine tree islands, herbaceous and woody plants were sampled at 5-m horizontal intervals. The maximum height of *C. jamaicense* was noted in all ridge and transitional quadrats. Vegetation sampling was conducted during winter from 18 January 2002 to 3 April 2003. No hurricanes or major fires affected the study area during this period. Species nomenclature followed Wunderlin & Hansen (2004).

Environmental data

Several measures of the physical environment were made at each quadrat. Quadrat location was determined using a high-precision Trimble XR GPS. Soil thickness (distance between soil surface and oolitic bedrock) was determined by probing with a slender steel rod. The normalized difference vegetation index (NDVI) – a widely used two-band index of total leaf coverage (Goward *et al.*, 1991; Gu *et al.*, 2007) – was assessed for each quadrat based on high-resolution, false-colour infrared photography shot for this project in February 2002 for southern WCA-3A and southern WCA-3B, and in March 2003 for central WCA-3A. Images were scanned, georectified and imported into ArcMap version 9.1 (ESRI, Redlands, CA, USA) at a resolution of 1' per pixel.

GPS coordinates were then used to locate each quadrat and calculate the NDVI. All vegetation and environmental data for each quadrat were entered in an ArcMap data base.

The height of each quadrat relative to a mean water-level datum is a critical environmental measure in all wetland systems, but can be extremely difficult to establish in such a way that samples across wide areas can be compared meaningfully. Our approach coupled rapid measurements of water depth in each quadrat during vegetation sampling (measured from a floating airboat) to long-term water-surface data interpolated to each transect location using the new Everglades Depth Estimation Network (EDEN) system, developed by the US Geological Survey, the South Florida Water Management District (SFWMD), Big Cypress National Preserve and the Everglades National Park (Telis *et al.*, 2006). EDEN provides water-surface data at 4- to 12-h intervals since 2000, interpolated to a 400-m grid from a network of > 230 wells and gauging stations in the Everglades. Given the extremely shallow slope of the Everglades water surface (*c.* 3 cm km⁻¹ in the absence of storm events), interpolation points within 400–800 m of a transect were assumed to track temporal shifts in water level on that transect extremely well. For each quadrat, we calculated the offset between water depth measured in the field at each quadrat and the water-surface level at the nearest EDEN grid point from the same 12-h period; and then used this offset to produce a continuous 6-year hydrograph for each of our quadrats. We note that the validity of this approach does not depend in any substantial way on the accuracy of the ground-elevation data (nominal precision < 1 cm) to which the EDEN gauge data are tied. From these data, we calculated four metrics for each quadrat: (1) maximum water depth (cm) over the 60-month period from 1 January 2000 to 31 December 2005; (2) minimum water depth over the same period; (3) average water depth; and (4) hydroperiod. Several quadrats atop tree islands were sampled when the ground there was dry; in those cases, a small well was dug, left overnight and then depth to the groundwater-table was measured the next day. Strenuous efforts were made to establish the relative elevations of the soil surface at all quadrats using high-precision GPS and a base station, and using a total station, but these generally failed due to the density of vegetation in several areas and our unwillingness to destroy vegetation in order to establish long sightlines. Inability to access and establish GPS coordinates in especially dense vegetation made it impossible to traverse and/or locate quadrats along some portions of some transects, especially in tree-island tails. Quadrats for which elevational data were unavailable were later culled from our data sets.

Table 2 Number of quadrats representing each a priori community type in the three study regions.

Study area	Community type							
	Flooded slough	Slough–ridge transition	Tall sawgrass ridge	Low tree island	Emergent slough	Short sawgrass ridge	Ridge–tree island transition	Tall tree island
Central WCA-3A	21	13	21	9	25	1	28	3
Southern WCA-3A	47	17	42	14	35	12	64	1
Southern WCA-3B	19	13	29	21	56	1	63	7
Total	87	43	92	44	116	14	155	11

For each transect, we used ArcMap to calculate the distances for each quadrat to the nearest quadrat on an immediately adjacent tree island with a minimum water depth of at least 0 cm (DistLT0) and of –10 cm (DistLT10); no attempt was made to interpolate water depths between quadrats. These two *adjacency metrics* provided landscape measures of the distance of quadrats to tree islands, which might act as sources of phosphate (see the Introduction). We calculated the mean \pm standard error for each metric of water depth, hydroperiod, adjacency, soil depth and NDVI, and used ANOVA and Tukey–Kramer tests to determine whether they showed significant differences among a priori vegetation categories. Because adjacency metrics based on increasingly tall islands can be measured on increasingly small subsets of the total number of samples, we used only the two noted, which decreased sample size to 474 and 337 quadrats, respectively. The covariance structure of the other environmental variables remained roughly unchanged in these smaller samples.

Vegetation analysis

We quantified variation in community composition and its relationship to environmental conditions using NMS as implemented in PC-ORD (McCune & Mefford, 1999; MjM Software, Corvallis OR, USA). Species occurring in fewer than 10 quadrats (0.2% of the sample universe) were excluded to improve stability of the ordination. NMS was run in autopilot mode, using ‘medium’ speed vs. thoroughness of search, Sorenson distance and 200 iterations to determine significant axes of variation in vegetation composition. Axis scores of samples were correlated with individual environmental measures to assess the ecological significance of each axis in abstract ordination space. Backwards-elimination multiple regressions involving all measures were also run for each axis using SPSS (SPSS Inc., Chicago, IL, USA), in order to obtain the best estimation of environmental variation along that axis. For each environmental measure we used PC-ORD to construct a vector whose components had the sign and magnitude of the correlation coefficient of that measure with quadrat scores of the respective axes. All vectors with magnitude (total correlation) > 0.2 were displayed in a joint-plot, to display the direction and magnitude of correlations with each ordination axis (McCune & Mefford, 1999). We overlaid the distribution of several common species on the ordination in order to obtain further insights into the nature of compositional variation along

each ordination axis and environmental gradient. ANCOVA (Sokal & Rohlf, 1995) was used to determine whether there were significant differences among regions in the slope or intercept of the relationship of water depth to axis 3 scores, the closest correlate of differences in composition associated with differences in water depth across regions. Long-term gauge data (1985 to present) on water levels in each region were examined for relatively recent shifts in hydrology that might have affected vegetation.

RESULTS

We sampled 38 transects totalling 39.2 km in length and encompassing 562 quadrats; 9 transects and 121 quadrats were located in central WCA-3A; 16 transects and 232 quadrats in southern WCA-3A; and 13 transects and 209 quadrats in southern WCA-3B (Table 1). Overall, 15% of the quadrats were classified a priori as flooded sloughs; 8% as emergent sloughs; 16% as slough–ridge transitions; 8% as short-sawgrass ridges; 21% as tall-sawgrass ridges; 2% as ridge–tree island transitions; 28% as low tree islands; and 2% as tall tree islands (Table 2). Several tall tree-island quadrats were excluded before analyses began because we were unable to establish their heights relative to long-term water-level data.

The distribution of community-types differed in a highly significant fashion among regions, whether the two rare types (ridge–tree island transition and tall tree islands) were included ($\chi^2 = 40.0, P < 0.001$ for 14 d.f.) or not ($\chi^2 = 23.5, P < 0.01$ for 10 d.f.). In the reduced data set, there was a large excess of flooded sloughs in southern WCA-3A, and a shortage in southern WCA-3B, as well as an excess of tall-sawgrass ridges in southern WCA-3B, and a shortage in southern WCA-3A (see Table 2).

As expected, water depth and hydroperiod decreased significantly in moving from sloughs to tree islands (Table 3). Across all three study regions, maximum water depth varied from 102 ± 1.9 cm in flooded sloughs to 81 ± 2.4 cm in short-sawgrass ridges, 65 ± 2.0 cm on low tree islands and 28 ± 9.8 cm on tall tree islands. Minimum water depths ranged from 27 ± 1.5 cm in flooded sloughs to -40 ± 10.4 cm on tall tree islands. In general, across study regions, flooded and emergent sloughs lay c. 15 cm lower in the landscape than short- or tall-sawgrass ridges, which in turn lay 15–20 cm lower than low tree islands and 55–60 cm lower than tall tree-island quadrats, for a total elevational/water-depth gradient of roughly 80 cm (Table 3). Hydroperiods were

Table 3 Mean \pm SE of local abiotic traits of each a priori community type across all quadrats. Values within each column (i.e. levels for a given trait in different community types) that differ at $P < 0.05$ are indicated by non-overlapping superscripts.

Community type	Abiotic trait					
	Soil thickness (cm)	Maximum water depth (cm)	Minimum water depth (cm)	Average water depth (cm)	Hydroperiod (days)	NDVI
Flooded slough	86.7 \pm 4.0 ^b	101.9 \pm 1.9 ^a	26.8 \pm 1.5 ^a	67.1 \pm 1.7 ^a	363 \pm 0.4 ^a	5.7 \pm 3.6 ^c
Emergent slough	67.6 \pm 7.7 ^a	96.9 \pm 2.6 ^a	24.0 \pm 1.9 ^a	63.6 \pm 2.4 ^b	362 \pm 0.8 ^a	-7.4 \pm 2.9 ^b
Slough-ridge transition	94.1 \pm 4.7 ^b	90.2 \pm 1.7 ^b	16.9 \pm 1.2 ^b	56.6 \pm 1.5 ^c	361 \pm 0.7 ^b	-2.0 \pm 2.0 ^b
Short sawgrass ridge	96.6 \pm 7.5 ^b	81.0 \pm 2.4 ^c	10.2 \pm 1.6 ^c	48.3 \pm 2.1 ^d	356 \pm 1.3 ^c	-13.5 \pm 3.8 ^a
Tall sawgrass ridge	114.9 \pm 3.8 ^c	80.8 \pm 1.5 ^c	10.9 \pm 1.0 ^c	48.5 \pm 1.3 ^d	357 \pm 0.8 ^c	-1.3 \pm 1.7 ^{bc}
Ridge-tree island transition	99.5 \pm 12.3 ^{bc}	92.4 \pm 6.5 ^{ab}	16.9 \pm 5.2 ^{abc}	58.2 \pm 5.9 ^{abc}	362 \pm 2.5 ^{abc}	22.4 \pm 11.7 ^{cd}
Low tree island	120.3 \pm 3.7 ^c	65.1 \pm 2.0 ^d	-6.4 \pm 1.6 ^d	32.1 \pm 1.8 ^e	317 \pm 4.8 ^d	28.0 \pm 2.5 ^d
Tall tree island	119.0 \pm 15.4 ^{bc}	36.9 \pm 8.1 ^e	-29.7 \pm 8.1 ^e	7.4 \pm 8.6 ^f	226 \pm 39.3 ^e	29.6 \pm 8.7 ^d

NDVI = (NIR - RED)/(NIR + RED), where NIR is the reflectance + emittance in the near-infrared and RED is the corresponding value for red wavelengths. NDVI ranges from -1 to +1; it achieves negative values in the sloughs due to the low value of NIR from water surfaces.

essentially year-round in the sloughs, about 10 days less on the ridges, and 50 to 170 days less on short and tall tree islands (Table 3). Flooded and emergent sloughs did not differ significantly in water depth or duration, but did in soil thickness, with the emergent sloughs occupying soils *c.* 22% (19 cm) thinner. Short- and tall-sawgrass ridges also had equivalent water depths and hydroperiods, but short-sawgrass stands occurred on soils that were *c.* 16% (18 cm) thinner than those occupied by taller sawgrass (Table 3).

When samples were segregated by study region, many of the environmental differences among community types just described persisted. For example, on average, sloughs lay *c.* 15 cm lower than ridges, 30 cm lower than low tree islands and 30–80 cm lower than tall tree islands (Table 4). However, there was almost as great a difference in each measure of water depth among study regions for a given community type as there was among community types within a study region: quadrats with a particular form of vegetation in southern WCA-3A tended to be 15 cm deeper than those in central WCA-3A, and 30 cm deeper than those in southern WCA-3B, and these differences were frequently statistically significant (Table 4). This pattern corresponds to known shifts in hydroregime in each WCA since the late 1940s, caused by the emplacement and operation of various water-control structures, levees and canals, and evident even on satellite imagery (Fig. 1), with surface flow from central WCA-3A pooling at the southern end of WCA-3A, and with lack of flow (and possible groundwater infiltration into the oolite aquifer) in southern WCA-3B associated with rapid growth of vegetation and loss of landscape patterning there (V.C. Volin, T.J. Givnish, and V.D. Owen, unpublished data). Paralleling this pattern, for many community types soils were significantly thicker in southern WCA-3B than in southern WCA-3A, which in turn were significantly thicker than those in central WCA-3A. Hydroperiods showed a similar trend, though differences among study areas for a given community type were usually not significant (Table 4). Soils were significantly thinner under emergent-leaved

vs. floating-leaved sloughs only in southern WCA-3A. Soils were also significantly thinner under short- vs. tall-sawgrass ridges only in southern WCA-3A, but the same pattern held qualitatively in the two other study areas (Table 4). In all three regions, soil thickness was 15–34 cm greater under low tree islands than under floating sloughs, pointing to similar amounts of soil (peat) buildup in all three regions, and to the ability of such differences in soil thickness (as opposed to added variation in bedrock elevation) to account for much of the 30–40 cm topographic relief between sloughs and low tree islands. Across the entire gradient, depth to bedrock (estimated as soil thickness plus water depth) showed no obvious linear trend across the composition gradient regardless of whether depth to bedrock was estimated as soil thickness plus maximum water depth, or as soil thickness plus minimum water depth (Fig. 3). There was also no significant correlation of depth of bedrock to position on the compositional gradient as represented by NMS axis-3 score, tied to relative topographic position (Fig. 3; see below). In central and southern WCA-3A, bedrock depth was significantly shallower under tall tree islands than elsewhere; however, in southern WCA-3B, bedrock was not significantly shallower than elsewhere, and in fact averaged deeper than under emergent sloughs and short-sawgrass ridges.

NMS ordination of all 562 quadrats produced three significant axes, of which only the second and third showed strong relationships to measured environmental variables (Table 5). Within this interpretable, two-dimensional ordination space, NMS placed quadrats from the eight a priori community types in coherent fashion in a triangular cloud (Fig. 4). Emergent and floating sloughs lay near one pole, low on axis 3; short- and tall-sawgrass ridges lay near a second pole, higher on both axes 2 and 3, and separated from the first pole by communities transitional between slough and ridges; and tall tree islands lay near a third pole, high on axis 3, with low tree islands extending toward both sloughs and ridges to complete the remaining two legs of the triangle (Fig. 4). Axis 3 showed a strong negative correlation with

Table 4 Comparison of abiotic factors for each community-type in the three study regions; each value represents mean \pm SE. Values within each column (i.e. levels for a given trait in different community-types) that differ at $P < 0.05$ are indicated by non-overlapping superscripts. Values for ridge-tree island transition and tall-tree island with no reported SE have no tests for differences due to small sample sizes.

	Abiotic trait					
	Soil thickness (cm)	Maximum water depth (cm)	Minimum water depth (cm)	Average water depth (cm)	Hydroperiod (days)	NDVI
Flooded slough						
Central WCA-3A	58.5 \pm 3.3 ^a	92.6 \pm 1.4 ^b	16.1 \pm 1.3 ^a	55.6 \pm 1.2 ^b	364 \pm 0.2 ^a	-6.6 \pm 1.7 ^a
Southern WCA-3A	86.9 \pm 5.5 ^b	114.3 \pm 2.0 ^c	36.0 \pm 1.6 ^b	78.4 \pm 1.9 ^c	365 \pm 0.1 ^a	18.8 \pm 5.8 ^b
Southern WCA-3B	117.4 \pm 7.5 ^c	81.3 \pm 1.6 ^a	15.8 \pm 1.3 ^a	51.6 \pm 1.3 ^a	359 \pm 1.3 ^b	-13.3 \pm 4.8 ^a
Emergent slough						
Central WCA-3A	51.6 \pm 6.3 ^b	90.9 \pm 2.2 ^b	14.9 \pm 1.9 ^a	54.2 \pm 1.8 ^a	363 \pm 0.5 ^a	-5.2 \pm 2.0 ^a
Southern WCA-3A	35.0 \pm 7.7 ^a	114.7 \pm 1.9 ^c	36.9 \pm 1.3 ^b	80.9 \pm 1.8 ^b	365 \pm 0.1 ^a	-5.2 \pm 6.1 ^a
Southern WCA-3B	126.2 \pm 10.9 ^c	79.8 \pm 2.0 ^a	16.2 \pm 1.9 ^a	50.3 \pm 1.7 ^a	357 \pm 2.1 ^b	-12.5 \pm 4.8 ^a
Slough-ridge transition						
Central WCA-3A	65.6 \pm 3.7 ^a	84.1 \pm 1.5 ^b	7.2 \pm 1.4 ^a	47.2 \pm 1.4 ^a	361 \pm 0.8 ^b	-4.0 \pm 2.1 ^{ab}
Southern WCA-3A	82.2 \pm 6.8 ^b	102.7 \pm 2.2 ^c	24.3 \pm 1.8 ^c	67.3 \pm 2.1 ^b	363 \pm 0.9 ^c	1.8 \pm 3.7 ^b
Southern WCA-3B	132.1 \pm 6.4 ^c	76.7 \pm 1.4 ^a	13.3 \pm 1.0 ^b	47.9 \pm 1.1 ^a	357 \pm 1.3 ^a	-6.1 \pm 3.0 ^a
Short sawgrass ridge						
Central WCA-3A	65.3 \pm 3.6 ^a	81.0 \pm 3.6 ^b	5.4 \pm 3.3 ^a	44.0 \pm 3.1 ^a	359 \pm 1.7 ^b	-0.7 \pm 2.9 ^b
Southern WCA-3A	64.9 \pm 11.1 ^a	97.6 \pm 3.5 ^c	20.6 \pm 3.2 ^b	63.3 \pm 3.6 ^b	365 \pm 0.2 ^c	-9.9 \pm 5.3 ^{ab}
Southern WCA-3B	131.1 \pm 9.2 ^b	69.9 \pm 1.7 ^a	5.4 \pm 3.3 ^a	40.2 \pm 1.0 ^a	349 \pm 1.4 ^a	-21.4 \pm 6.6 ^a
Tall sawgrass ridge						
Central WCA-3A	79.2 \pm 3.9 ^a	80.5 \pm 1.9 ^b	3.9 \pm 1.8 ^a	43.6 \pm 1.7 ^a	358 \pm 1.7 ^b	2.1 \pm 1.9 ^a
Southern WCA-3A	99.5 \pm 6.5 ^b	99.1 \pm 2.2 ^c	21.9 \pm 1.8 ^b	63.6 \pm 2.1 ^b	363 \pm 1.0 ^c	-5.6 \pm 2.5 ^b
Southern WCA-3B	140.5 \pm 4.3 ^c	69.5 \pm 1.2 ^a	7.2 \pm 0.8 ^a	41.3 \pm 1.0 ^a	353 \pm 1.1 ^a	-0.1 \pm 2.9 ^{ab}
Ridge-tree island transition						
Central WCA-3A	38.0	85.0	14.0	50.0	364	-2.0
Southern WCA-3A	99.0 \pm 12.1	96.9 \pm 6.2	19.4 \pm 5.6	62.2 \pm 5.9	364 \pm 0.3	33.7 \pm 9.0
Southern WCA-3B	167.0	45.0	-11.0	19.0	330	-88.0
Low tree island						
Central WCA-3A	73.9 \pm 5.2 ^a	66.0 \pm 3.2 ^b	-9.0 \pm 3.0 ^a	29.3 \pm 3.0 ^b	318 \pm 12.1 ^a	19.2 \pm 4.4 ^a
Southern WCA-3A	120.2 \pm 5.0 ^b	80.0 \pm 3.3 ^c	1.0 \pm 3.1 ^b	44.3 \pm 3.2 ^c	330 \pm 8.8 ^a	20.7 \pm 3.0 ^a
Southern WCA-3B	141.0 \pm 4.5 ^c	49.4 \pm 1.7 ^a	-12.8 \pm 1.5 ^a	21.0 \pm 1.6 ^a	303 \pm 5.3 ^a	39.3 \pm 4.5 ^b
Tall tree island						
Central WCA-3A	61.3 \pm 9.2 ^a	9.3 \pm 4.7 ^a	-62.7 \pm 4.7 ^a	-26.7 \pm 4.7 ^a	57 \pm 18 ^a	42.0 \pm 6.9 ^a
Southern WCA-3A	90.0	80.0	1.0	47.0	356	-45.0
Southern WCA-3B	134.1 \pm 20.4 ^b	36.5 \pm 12.8 ^b	-30.9 \pm 13.3 ^a	5.6 \pm 13.0 ^b	247 \pm 44 ^b	36.6 \pm 2.3 ^a

all measures of water depth and hydroperiod ($-0.503 < r < -0.541$), and slightly weaker positive correlations with NDVI ($r = 0.359$) and soil thickness ($r = 0.311$). Axis 3 also showed (as would be expected) moderately negative correlations with both adjacency metrics ($-0.270 < r < -0.373$) (Table 5), with points lower on axis 3 representing sites more distant from tall tree islands (mainly at the high end of axis 3). Axis 3 thus appears to represent the classic microtopographic gradient from sloughs to ridges to tree islands, with quadrats along that gradient (and axis 3) differing primarily in local elevation and correlated factors.

Axis 2, in contrast, showed much weaker relationships to various measures of water depth ($r^2 < 0.033$, vs. $r^2 > 0.282$ for axis 3), soil thickness ($r^2 < 0.0004$, vs. $r^2 > 0.096$) and hydroperiod ($r^2 < 0.088$, vs. $r^2 > 0.253$), and showed positive correlations with

both adjacency metrics ($r = 0.350$ for DistLT10, 0.234 for DistLT0) (Table 5). Axis 2 thus appears to represent a landscape-proximity gradient, with rather comparable sites – at least in terms of a priori vegetation type and elevation relative to the water surface – varying from those close to tall tree-island areas on the left of Fig. 4, to those more distant from tall tree islands on the right. The landscape-proximity gradient actually runs skew to both axes 2 and 3, given the comparable magnitude (but opposite sign) of correlations of adjacency metrics to those axes (Fig. 4). Backwards-elimination multiple regressions retained DistLT0 and DistLT10 as predictors of axis-2 scores when one or the other were initially entered with soil thickness, hydroperiod and all measures of water depth; similar regressions retained only DistLT0 as a predictor of axis-3 scores. Axis 1 (not shown) showed weak relationships ($r^2 < 0.025$) to all environmental variables.

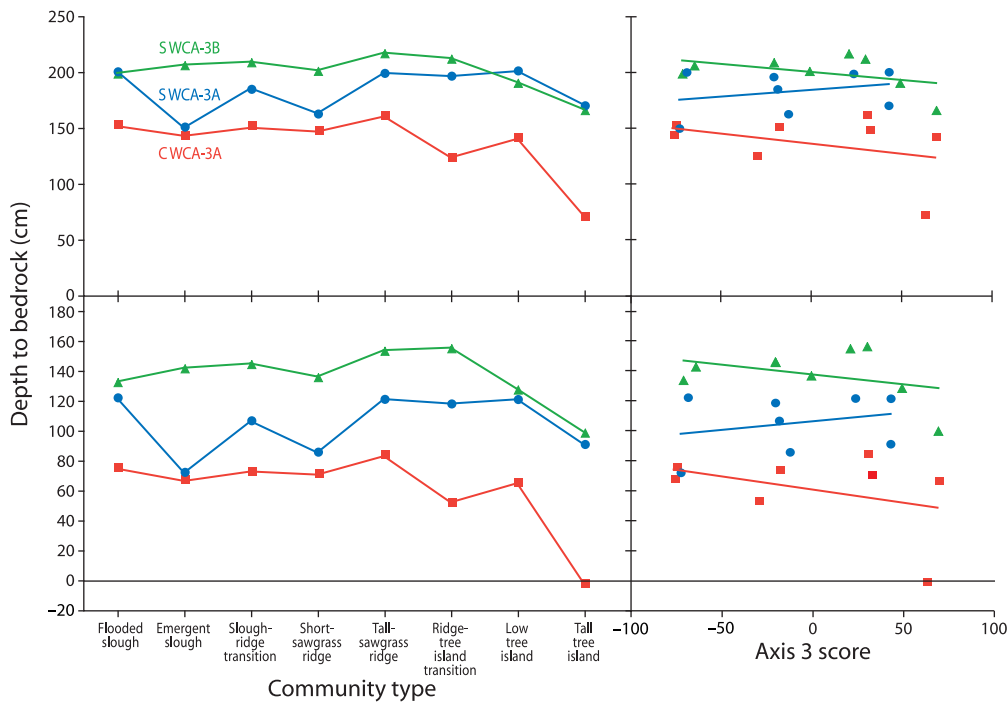


Figure 3 Relationship of depth to bedrock to compositional gradient: the top figures show bedrock depth based on maximum water depth, while the bottom figures show bedrock depth based on minimum water depth. Left: depth to bedrock vs. a priori vegetation type in central WCA-3A, southern WCA-3A and southern WCA-3B; points represent mean \pm SE. Right: depth to bedrock as a function of NMS axis-3 score, a measure of community composition related to relative topographic position (see text); none of the linear regressions indicated are statistically significant.

Table 5 Correlations (r) of environmental factors to axis scores of the NMS ordination. Correlations accounting for more than 5% of the variance in individual factors are highlighted in bold. For the first six factors, sample size was 562. For the adjacency metrics DistLT0 and DistLT10, the sample sizes were 474 and 337 quadrats, respectively.

Environmental factor	Axis 1	Axis 2	Axis 3
Soil thickness	0.035	-0.019	0.311***
Minimum water depth	-0.126**	0.183***	-0.540***
Maximum water depth	-0.144***	0.130**	-0.531***
Average water depth	-0.134**	0.153***	-0.541***
Hydroperiod	-0.134**	0.295***	-0.503***
NDVI	0.025	-0.378***	0.359***
DistLT0	-0.043	0.234***	-0.270***
DistLT10	-0.072	0.350***	-0.373***

** $P < 0.01$; *** $P < 0.001$.

A total of 33 species (including ‘periphyton’) were included in the NMS ordination. Most taxa were restricted to a small portion of ordination space; not surprisingly, several were strongly associated with the a priori community types they helped to define. For example, periphyton and *Utricularia* occurred primarily in flooded and emergent sloughs (Fig. 5a,b); *Nymphaea odorata* and *Hymenocallis latifolia* in flooded sloughs and slough–ridge transitions (Fig. 5c,d); *Eleocharis cellulosa* in emergent sloughs (Fig. 5e) and *Nymphoides aquatica* and *Crinum americanum* in

slough–ridge transitions (Fig. 5f,g). *Cladium jamaicense* dominated short- and tall-sawgrass ridges (Fig. 5h) and was significantly shorter ($P < 0.0001$) in the former (81.0 ± 5.7 cm) than the latter (213.0 ± 2.9 cm); these differences were maintained robustly in all three study regions. Several woody species (e.g. *Annona glabra*, *Cephalanthus occidentalis*, *Salix caroliniana*) were restricted mainly to the lower-lying edges and tails of tree islands (Fig. 5i,j), while many others (e.g. *Chrysobalanus icaco*, *Ficus aurea*, *Myrica cerifera*, *Persea palustris*) were found primarily in the higher cores and bayheads of tree islands (Fig. 5k,l). Several ferns (*Acrostichum danaeifolium*, *Blechnum serrulatum*, *Thelypteris kunthii*) were also strongly associated with tree islands (Fig. 5m,n), while *Osmunda regalis* (Fig. 5o) was more common on island edges and tails.

Of special interest were the species populating the ‘western’ and ‘north-eastern’ margins of the triangular ordination cloud. These taxa, in some way, differentiate the tree island–slough gradient from the tree island–ridge gradient; the remaining ‘south-eastern’ margin of the ordination cloud is clearly inhabited by slough–ridge transition species (Figs 4 & 5c–g). *Sagittaria latifolia* and *Peltandra virginica* were common in the western margin (Fig. 6a,b), while *Pontederia cordata* and *C. jamaicense* were common in the north-eastern margin (Figs 6c & 5h). Elsewhere in the eastern USA, *S. latifolia* and *P. virginica* often grow most densely on nutrient-rich mucks – as in lower reaches of freshwater tidal marshes in the mid-Atlantic region (Simpson et al., 1983) and along slow-moving streams carrying rich silt loads in the Upper Midwest (e.g. Trempealeau River in Wisconsin).

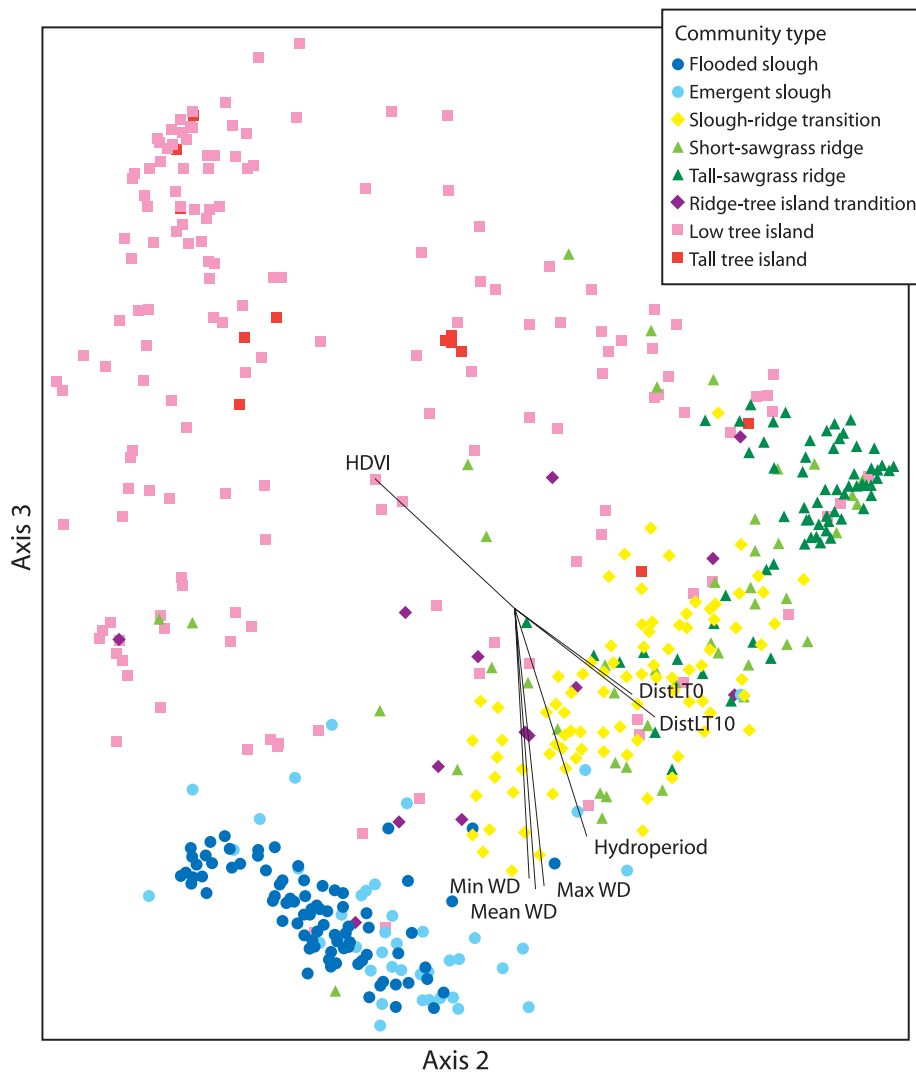


Figure 4 Non-metric multi-dimensional scaling (NMS) ordination of quadrats, showing the distribution of a priori vegetation types, and the strength and direction of correlations between environmental factors and score on the leading two axes. The x - and y -components of each vector correspond to the Spearman correlation coefficient (r) between the environmental factor and score on axes 2 and 3, respectively. Note the strong relationship of maximum water depth and other factors related to local elevation with axis 3, and the relationship of proximity measures to both axes. NDVI, normalized difference vegetation index; WD, water depth; DistLT0 and DistLT10, distances to the nearest quadrat on an immediately adjacent tree island with a minimum water depth of at least 0 cm and -10 cm, respectively.

(Nichols, 1999). Both *Sagittaria* and *Pontederia* have wide ecological ranges, and inhabit the shores of both oligotrophic and mesotrophic ponds in Wisconsin (Nichols, 1999). However, dense monocultures of *Pontederia* in the Upper Midwest are typically common around nutrient-poor ponds and lakes (T.J. Givnish, pers. obs.); in freshwater tidal marshes, *Pontederia* occurs primarily in frequently disturbed, low-coverage microsites along stream banks and in interior ponds (with relatively little current silt deposition), in contrast to both *Sagittaria* and *Peltandra* (Simpson *et al.*, 1983). *Cladium* competes successfully only in highly oligotrophic wetlands throughout the Caribbean, and is favoured by frequent fire (Steward & Ornes, 1983; Imbert & Delbé, 2006).

Based on ANCOVA, the relationship between axis-3 scores (an index of community composition related to depth) and maximum water depth shows significant differences in intercept ($P < 0.01$) but no significant differences in slope among regions. Paralleling our findings for a priori vegetation types, comparable axis-3 scores occur at maximum water depths *c.* 12 cm deeper in central WCA-3A than in southern WCA-3B, and *c.* 17 cm deeper in southern WCA-3A than in central WCA-3B (Fig. 7). Water-level data since 1985 for three gauges used as a basis for the EDEN network show that: (1) water levels in southern WCA-3B have been roughly consistent since 1994; (2) water levels in central and southern WCA-3A increased by 15 to 25 cm from 2000 through the period of vegetation sampling; and (3) the seasonal

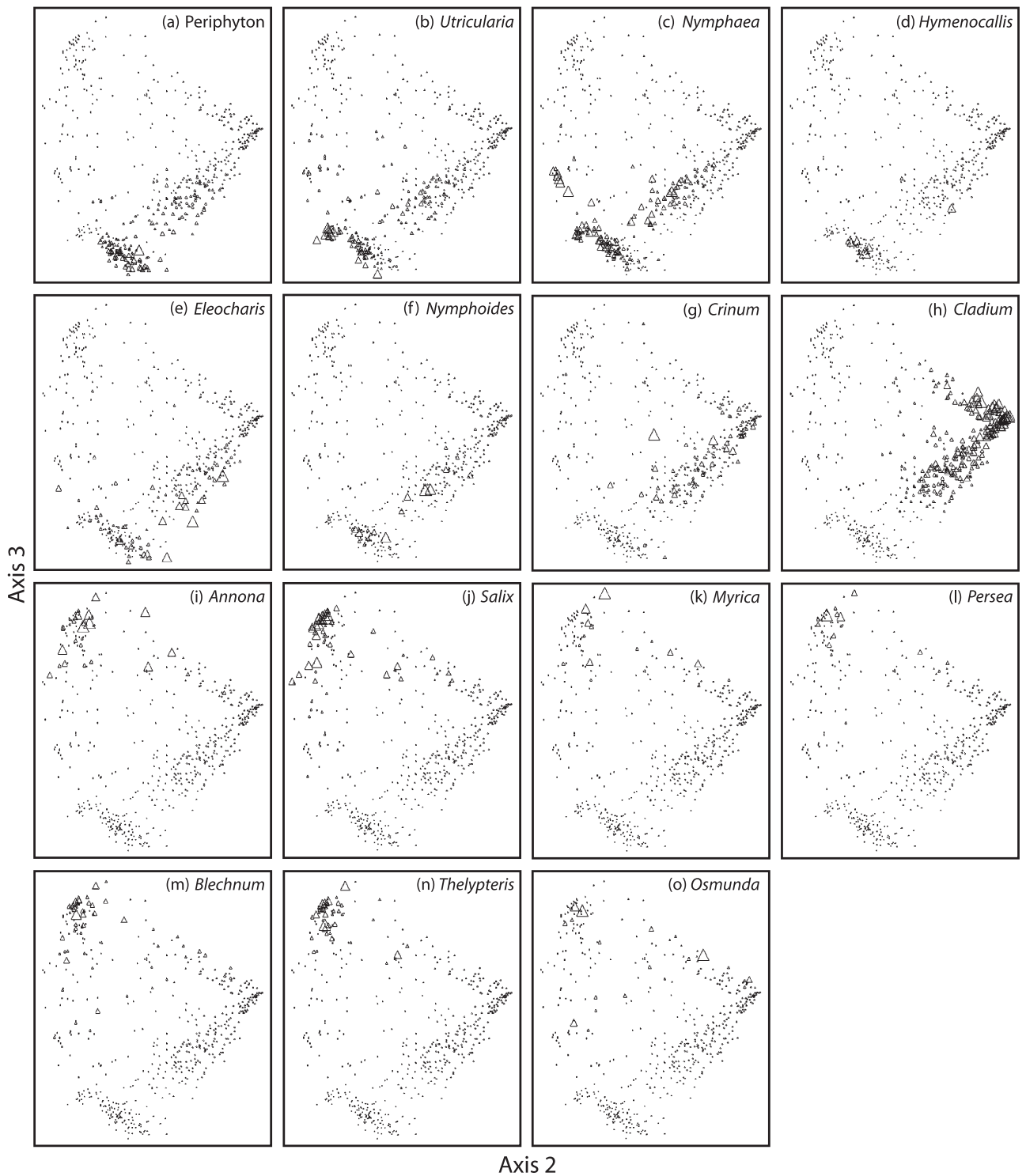


Figure 5 Distribution of species in ordination space; the width of each triangle increases with coverage by the focal species in each quadrat, with zero coverage being specified by the smallest symbols (thus, all quadrats are plotted on all graphs): (a) periphyton; (b) *Utricularia* spp.; (c) *Nymphaea odorata*; (d) *Hymenocallis latifolia*; (e) *Eleocharis cellulosa*; (f) *Nymphoides aquatica*; (g) *Crinum americanum*; (h) *Cladium jamaicense*; (i) *Annona glabra*; (j) *Salix caroliniana*; (k) *Myrica cerifera*; (l) *Persea palustris*; (m) *Blechnum serrulatum*; (n) *Thelypteris kunthii*; (o) *Osmunda regalis*.

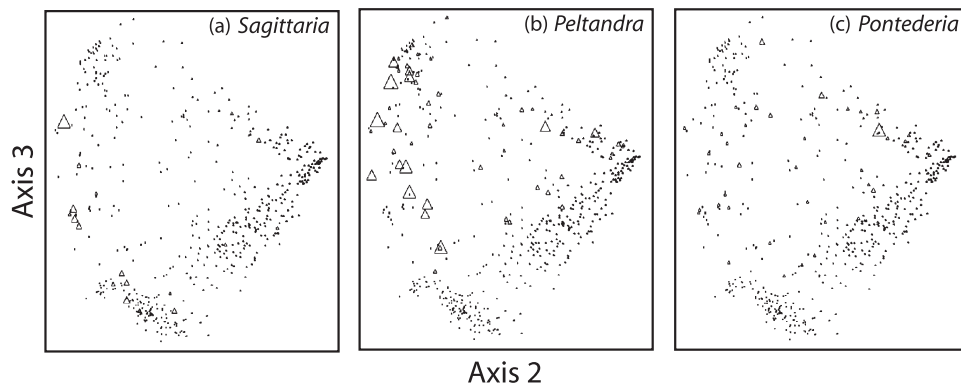


Figure 6 Species whose distribution in low tree islands, ridges and slough–ridge transitions appear sensitive to proximity to tall tree islands under similar hydrological regimes: (a) *Sagittaria latifolia* and (b) *Peltandra virginica* are distributed closer to tree islands, while (c) *Pontederia cordata* and *Cladium jamaicense* (see Fig. 5 h) are distributed further from tree islands.

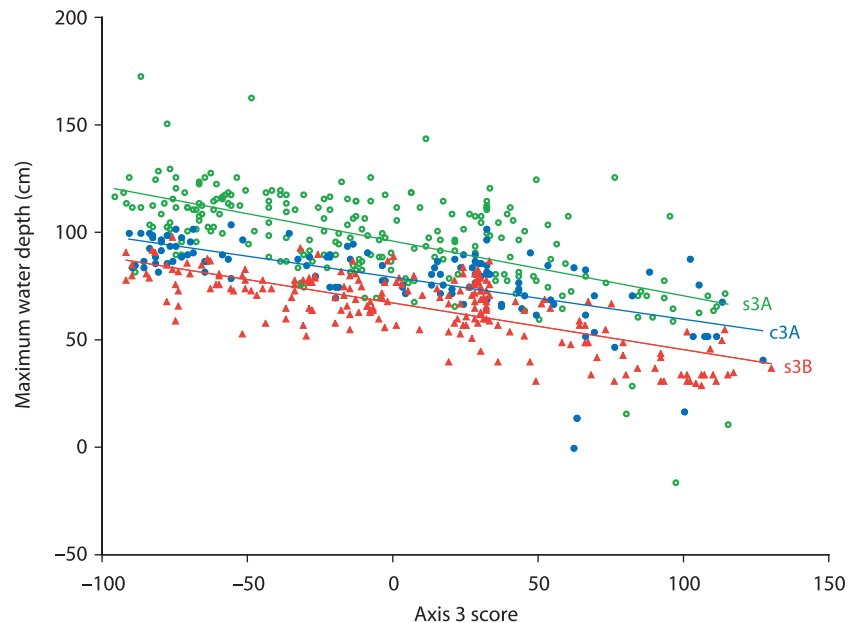


Figure 7 Relationship of axis-3 scores (a proxy for depth-related variation in vegetation composition) and maximum water depth, showing significant differences in elevation but not in slope for all three regions. Regressions are as follows: southern WCA-3A, $y = -0.254x + 96.1$ ($r^2 = 0.37$); central WCA-3A, $y = -0.195x + 79.4$ ($r^2 = 0.42$); southern WCA-3B, $y = -0.217x + 67.4$ ($r^2 = 0.54$). All regressions are significant at $P < 0.001$.

amplitudes of fluctuation in water levels in both central and southern WCA-3A have been roughly twice that in southern WCA-3B (Fig. 8). The latter difference presumably reflects a divergence between flow-fed and rain-fed regions. Absolute water levels at gauges reflect idiosyncratic differences among sites in placement of the reference level, and not general differences between regions in water depth.

DISCUSSION

Local and landscape-level drivers of vegetation differentiation

Using offsets from water levels interpolated for the EDEN well network to produce virtual recording gauges for each quadrat

was extremely important, because it allowed us to relate vegetation to various aspects of the hydroregime over extended areas and periods of time. Although water depth and hydroperiod are manifestly important in determining vegetation composition in the Everglades (Loveless, 1959; DeAngelis *et al.*, 1998; Kushland, 1990; Mason & van der Valk, 2003), our study is the first to relate these parameters to vegetation composition and structure over geographically extensive areas, permitting an evaluation of these relationships in regions that have experienced radically different hydroregimes over the past 50 years, and allowing a search for factors that affect vegetation other than those tied immediately to relative elevation.

The differentiation of a priori vegetation-types by maximum water depth and related measures of local elevation (Tables 3 & 4) and by NMS axis 3 (Fig. 4) is consistent with the traditional

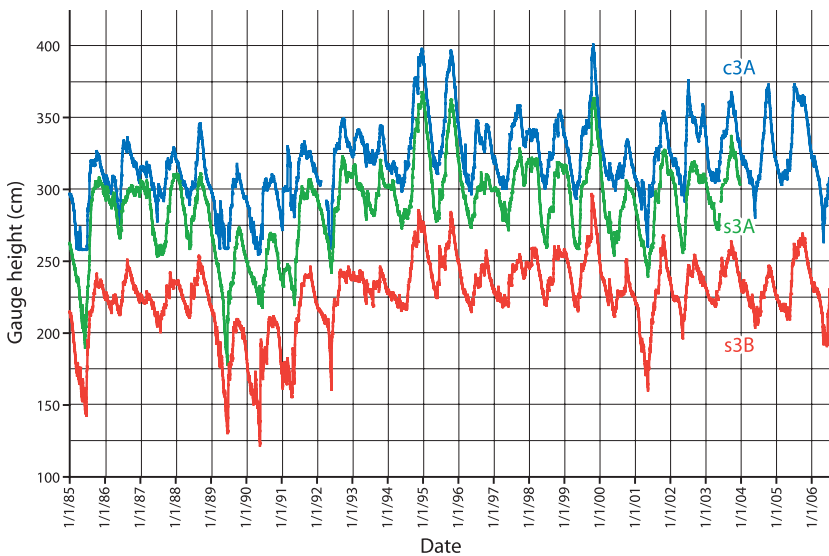


Figure 8 Shifts in water levels from 1985 to 2006 at selected gauges in central WCA-3A, southern WCA-3A and southern WCA-3B. Data are relative to (arbitrary) reference levels at each gauge; note the shift to deeper water levels in both parts of WCA-3A just prior to the study period, the relatively constant levels in southern WCA-3B over the previous decade and the greater amplitude of annual fluctuations in water level in flow-fed WCA-3A than in precipitation-fed WCA-3B.

view of the major environmental gradient running from tall tree islands to deep, flooded sloughs. The substantial excess of flooded sloughs in southern WCA-3A, the corresponding shortages of tall-sawgrass ridges in southern WCA-3A and of flooded sloughs in WCA-3B, and excess of tall-sawgrass ridges in southern WCA-3B (see Results) corresponds to expectations based on our model on the flooding of southern WCA-3A caused by the Tamiami Trail and on the elimination of flow in southern WCA-3B. Flooding in WCA-3A has apparently tended to convert tall-sawgrass ridges to short-sawgrass ridges and flooded sloughs, as would be expected simply from a rise in general water levels. Elimination of flow in southern WCA-3B appears to have eliminated some flooded sloughs and increased the incidence of tall-sawgrass ridges, as would be expected by the relaxation of the spatially coupled negative feedback of raised areas caused by an absence of flow (point 7 of our model; see the Introduction). It is important, however, to keep in mind that our study involved a stratified, not random, sample of the landscape, so that the abundance of each community type in the three regions is not strictly proportional to the abundance on our transects; our vegetation mapping of each region from aerial photography (V.C. Volin, T.J. Givnish and V.D. Owen, unpublished data) shows, for example, that sloughs have largely disappeared in WCA-3B and been replaced by sawgrass ridges.

Our detection of a second major environmental gradient in vegetation of the slough–ridge–tree island province – tied not to differences in local elevation, water depth, hydroperiod or soil thickness, but instead to proximity to tall tree islands (Figs 4 & 6) – is a key new finding. This proximity gradient was predicted by one aspect of our model for the self-assembly of patterned landscapes in the Everglades – namely, the leaching of phosphate from tree islands into the surrounding groundwater and surface-water flows, with effects on the composition and productivity of local vegetation. Such a gradient had not been recognized or predicted by previous studies (e.g. Loveless, 1959; McPherson,

1973; Kushlan, 1990; Davis *et al.*, 1994; DeAngelis *et al.*, 1998; Heisler *et al.*, 2003; Mason & van der Valk, 2003; Sklar & van der Valk, 2003; Willard *et al.*, 2003, 2006; Lodge, 2005; Wetzel *et al.*, 2005), and its existence clearly points to the operation of landscape-level driver(s) affecting vegetation, in addition to the obvious drivers of water depth, hydroperiod and soil thickness operating at a local scale.

Additional studies, including experiments, are required to determine whether the observed landscape-level gradient is indeed driven by phosphate-rich groundwater and runoff leaking from tree islands. The data currently in hand, however, are supportive of this leakage mechanism. Very high levels of phosphorus input to tree islands have been documented (Orem *et al.*, 2003; Willard *et al.*, 2003; Jayachandran *et al.*, 2004; Wetzel *et al.*, 2005; Orem, 2006) and tied to guano deposition by egrets, herons, ibis and other wading birds that fish in the adjacent marshes, nest on the tree islands and thereby concentrate P on those islands in an otherwise P-poor system (see Lund, 1957; Burton *et al.*, 1979; Frederick & Powell, 1994; Noe *et al.*, 2001; McCormick *et al.*, 2002). Furthermore, once birds have delivered large amounts of P, the effects on luxuriant plant growth can persist for many decades (Frederick & Powell, 1994), and can thus be integrated over long periods with and without rookeries present. Experiments by Chiang *et al.* (2000) showed that P fertilization of sawgrass and sawgrass/cattail communities in the Everglades led both to greatly increased production and to increases in readily exchanged P, not closely bound to organic matter or CaCO₃ and therefore mobile. Finally, supporting another central assumption of our model (point 4), Craft and Richardson (1993) used field experiments in WCA-2A (upstream of our study area) to demonstrate that increased P loading increased the rate of net peat accretion up to two-fold over control conditions.

Alternative hypotheses that P is concentrated on tree islands (and sawgrass ridges) by groundwater focusing driven by higher

evaporation or higher rates of dry deposition on those topographic rises (e.g. Wetzel *et al.*, 2005; Ross *et al.*, 2006) seem implausible. Simulations by Ross *et al.* (2006) incorporate a level of peat hydraulic conductivity (1000 m day^{-1}) that is at least two orders of magnitude too high; measurements in WCA-2A by Harvey *et al.* (2000) yielded a mean K_{peat} of 0.01 m day^{-1} , with values ranging up to 10 m day^{-1} . By incorporating such enormous levels of conductivity in their simulation, Ross *et al.* (2006) introduce a huge bias in favour of their proposed mechanism. In addition, these simulations ignore important constraints on local geochemistry: P in groundwater in the central Everglades is likely to be intercepted and immobilized by marl scattered throughout the peat substrate, as well as by periphyton scattered atop that substrate. Observed patterns of evapoconcentration by tree islands in the Okavango Delta of Botswana (McCarthy & Ellery, 1994) are not really comparable. As Bauer-Gottwein *et al.* (2007) state, of an average of $300 \text{ m}^3 \text{ s}^{-1}$ of water entering the Okavango Delta, only about $10 \text{ m}^3 \text{ s}^{-1}$ leave. This makes the Okavango Delta an evaporite environment – involving the death by evaporation of a river in a semi-desert, and it should come as no surprise that tree islands there are ringed by salt deposits. The Florida Everglades are wholly different – their high rainfall and high humidity mean that the ratio of precipitation to evapotranspiration (P/E) exceeds 1 in most years (German, 2000). As a consequence, there is far stronger flushing of nutrients from the upper soil (especially on tree islands above surface water) by rainfall in the Everglades, which would work strongly against the proposed evapoconcentration mechanism.

The appearance of ridge-like elongations of higher ground in simulations by Ross *et al.* (2006) is an artefact of their having placed initial points of higher ground in columns on a grid, and thus is spurious. Wetzel *et al.* (2005) themselves admit that guano deposition is likely to provide an input of P at least 20 times that via other mechanisms. Trophic concentration of P on the tree islands by birds (or other large vertebrates, such as alligators) that forage in the sloughs and nest on islands provides a highly plausible mechanism for elevating P on islands. It also does not require an exquisite balance of groundwater flow to islands, with the general flow being high – but not so high that it prevents nutrients from moving away and downslope from islands, creating tails. Perhaps most importantly, none of the mechanisms advanced by Sklar and van der Valk (2003), Ogden (2005), Wetzel *et al.* (2005) and Ross *et al.* (2006) can account for the initial development of sawgrass ridges from the marshes (sloughs) that originally occupied much of the Everglades, as Willard *et al.* (2006) have documented based on stratigraphic data. While these papers may consider the processes driving the origin and maintenance of tree islands as different from those initiating the ridges themselves, the key question regarding ridge origin remains. It must be recognized that, before today's tree islands were formed, water depths may have been as much as 0.5 to 1.0 m deeper than they have been recently (Willard *et al.*, 2006). Such a difference in water level may have occasioned higher rates of surface flow, which in turn may have affected the possibility of ridges being sculpted by erosional or depositional processes.

Under present-day circumstances, however, known flow rates are too low to resuspend and move much material, except for floc and periphyton during storm events (V.C. Volin, T.J. Givnish and V.D. Owen, unpublished data).

Much of the attention previously given to feedbacks focused on the potential role of erosive processes. McVoy (in South Florida Water Management District, 2000) and the Science Coordination Team (2003) proposed that erosion is a primary force creating and maintaining ridges in the central Everglades, arguing that it should proceed more rapidly and longer in sloughs, scouring flocculent organic carbon and transporting it downstream. According to these authors, such erosion might be highly episodic, difficult to observe and associated with severe storms. This hypothesis remains untested and problematic, given the extremely shallow topographic gradients driving flow in the Everglades; the likelihood for scouring to be greater on ridges (not sloughs) at high water levels; and the general tendency for erosion to create dendritic drainages rather than innumerable, parallel channels. Such erosion-based models also overlooked several important feedbacks. We believe that spatially coupled, positive and negative feedbacks – involving soil oxygenation, root nutrient uptake, downstream transport and deposition of floc, ecological concentration of P on tree islands, groundwater vs. surface-water transport of P leaking from such islands and its impact on plant growth, flow-induced inhibition of island initiation and spread, and spread of fire-favouring vs. fire-dampening domains – underlie the development of the slough-ridge-tree island topography typical of the central Everglades, and may ultimately prove to be the most important set of long-term controls on vegetation, hydrology and substrate in the region.

Initiation of ridges via greater oxygenation and leaf allocation in *Cladium*

Our model (Givnish & Volin, 2003, and above) provides a simple but overlooked mechanism by which sawgrass ridges could arise from more deeply submerged sloughs: increased plant growth on slightly raised substrates that are somewhat better oxygenated (thus enhancing root function at a given energetic investment), coupled with little or no increase in decomposition rate. Shallower water may also increase plant production by reducing allocation to relatively unproductive stem tissue and/or permitting leaves to be borne in a taller, thicker canopy. Childers *et al.* (2006) have shown that annual net primary productivity (ANPP) of *C. jamaicense* in the southern Shark River Slough increased dramatically toward shallower water: $\text{ANPP} (\text{g m}^{-2} \text{ year}^{-1}) = 1126 - 231 \ln \text{depth (cm)}$. *Cladium* height decreased sharply with water depth in WCA-2A (Weisner & Miao, 2004). Increased production toward shallower water or higher redox potentials has also been observed in *Eleocharis cellulosa* growing in emergent sloughs (Edwards *et al.*, 2003) and mesocosms (Chen *et al.*, 2005). Lissner *et al.* (2003) used experimental hydroponic mesocosms to show that reduced redox potential (similar to conditions in flooded soils) substantially decreases P uptake and whole-plant growth by *Cladium*, especially at low P levels.

Our own data show: (1) that *Cladium* is more than twice as tall (213 cm vs. 81 cm) on tall- vs. short-sawgrass ridges; (2) that tall-sawgrass ridges occur on surfaces that are c. 8 cm shallower than short-sawgrass ridges (Table 3); and (3) that total soil thickness (i.e. the depth of accreted peat) is some 20 cm thicker under taller sawgrass (Table 3). These findings are each consistent with an increase in plant productivity and net rate of peat deposition on slightly higher surfaces that are less deeply and less frequently inundated. Such positive feedback should help initiate the formation of ridges – and ultimately tree islands – from initial random decreases in microsite depth caused by variations in bedrock height, local production, or peat ‘pop-ups’. The stratigraphic data of Willard *et al.* (2006) can be interpreted as being consistent with such positive feedback in several cases. For example, at Manatee Hammock in southern Shark River Slough, rates of peat accumulation over the past 600–2700 years have been almost four times higher in the near tail (0.43 mm year⁻¹) than in the deeper adjoining marsh (0.11 mm year⁻¹). At T3 Island in WCA-2A, recent rates of peat accumulation have been about two times higher in the near tail (0.53 mm year⁻¹) than in the adjoining marsh (0.30 mm year⁻¹). While deviations from this pattern exist (e.g. Treece’s Island in WCA-2A), such exceptions could be an artefact of greater peat combustion on tree islands vs. sloughs during exceptional droughts or fire.

The claim by Willard *et al.* (2006) that tree islands generally develop over topographic highs in the underlying oolitic bedrock mirrors earlier proposals by Loveless (1959), Heisler *et al.* (2003), Sklar and van der Valk (2003) and many other authors. However, this view is contradicted by the fact that tree islands can occur over rises, flats or depressions in the underlying bedrock (Sklar & van der Valk, 2003), and our finding that – at least in southern WCA-3B – there was no significant difference in depth to bedrock between tall tree islands and other a priori community types (Fig. 4). We found a few tree islands in the other two study regions whose depth to bedrock was also greater than sites on the same transect. These findings argue against at least the universal validity of the claim that tree islands develop over highs in the oolitic bedrock. However, we cannot yet state decisively that bedrock depth is not a universal (or frequent) determinant of the location of tree-island bayheads, given that we were unable to determine water depth – and hence, depth to bedrock relative to various metrics of local water level – on several tall tree islands.

Landscape-level variation in limiting nutrients

The association of *P. virginica* and *S. latifolia* with proximity to tree islands (Fig. 5), and presumably with higher nutrient levels (especially phosphorus), corresponds to their association with richer soils elsewhere (see Results). In addition, leaf-tissue N:P ratios suggest that *Peltandra* is especially demanding of nutrients, particularly N (Daoust & Childers, 1999). Due to the high P requirements of N-fixers (e.g., cyanobacteria), increased P supply can also enhance N supply in both terrestrial and aquatic ecosystems (Vitousek & Field, 1999). Conversely, *Pontederia* – associated with distance from tree islands and with

poorer substrates elsewhere, and more similar in its distribution to *Cladium* than to *Peltandra* and *S. latifolia* (Figs 4 & 5) – was identified by leaf chemistry as insensitive to the availability of N and P (Daoust & Childers, 1999). *Cladium* has an especially high foliar N:P ratio and thus appears to have unusually low P requirements (Daoust & Childers, 1999). Foliar N:P ratios identified *Hymenocallis* – associated in our study with sloughs – as being entirely N-limited; this seems readily explicable, given that N-fixation is likely to be strongly inhibited by constant flooding. Foliar N:P ratios also indicate that tree-island forests are often N-limited (Ross *et al.*, 2006), as would be expected from high inputs of P from birds.

Modest additions of P increase growth of both *C. jamaicense* and *E. cellulosa* in the field and in mesocosms (Weisner & Miao, 2004; Chen *et al.*, 2005). Weisner and Miao (2004) found significant effects of site (a proxy for P supply along WCA-2A enrichment gradient), year (a proxy for rainfall, and thus for water depth) and year × P interactions on plant growth and biomass allocation in *Cladium* growing in WCA-2A, with growth increasing in shallower water and at higher P concentrations. Craft and Richardson (1998) dated soil cores using ¹⁴C, ²¹⁰Pb, and ¹³⁷Cs to show that net rates of peat accumulation in northern WCA-2A had increased to 5.8–6.7 mm year⁻¹ since the early 1960s, a three- to five-fold increase over the rates in parts of the Everglades that had not received P enrichment from agricultural runoff. Collectively, these data strongly suggest support for yet another component of our model, entailing increased plant growth and peat deposition around and especially in the lee of tree islands.

Overall, our data and the literature cited above provide partial support for points 2, 4, 5 and 7 of our model: positive feedback of peat accretion via increased aeration and shallower water on higher microsites; trophic P concentration on tree islands; fertilization of areas around and in the lee of tree islands, with subsequent shifts in composition and net peat accretion; and negative feedback of total raised area on itself driven by flow. The most important contribution of this paper is its indication that both local and landscape-level drivers shape vegetation composition and soil thickness in the central Everglades. The relatively small fluctuation in depth to peat surfaces vs. depth to bedrock across the Everglades (C. McVoy, pers. comm. cited by Science Coordination Team, 2003) supports point 1 of our model; massive amounts of marl in peat under sawgrass ridges in the central Everglades (Glaser *et al.*, 2006) provides partial support for point 3. As research continues, we expect to find support for the remaining assumptions and predictions of our model, as well as some ancillary features not included in the model presented here – including the effect of waterlilies corroding and lowering the level of peat in deep sloughs, as a consequence of internal ‘winds’ (Dacey, 1981) carrying oxygen to their roots and leaking into the substrate (Givnish & Volin, 2003) and of waterlilies and associated aquatic plants having tissues with much lower C:N and C:P ratios, which thus decompose at higher rates than the dead tissues of nutrient-poor *Cladium*. Both of these processes could add positive feedbacks leading to the differentiation of sloughs and ridges, and help account for the highly decomposed

nature of peat in sloughs vs. ridges, which has long been recognized (Harshberger, 1914).

Vegetation and hydrology at non-equilibrium

While the occurrence of sloughs, ridges and low tree- and tall tree-island communities at distinct levels of water depth, hydroperiod, soil thickness and proximity to tall tree-island areas *within regions* argues that these variables have a strong effect on vegetation composition (and, presumably, on production, decomposition and net peat accretion), the fact that similar communities today occupy very different levels of water depth and hydroperiod *among regions* (Table 3 and Fig. 7) argues forcefully that vegetation is not in equilibrium across the areas studied. This lag might arise because vegetation: (1) has not yet responded fully to regional shifts in Everglades hydrology wrought by humans over the past 60 years; (2) has not equilibrated in response to much more recent shifts in hydrology; or (3) actually has equilibrated with hydrology but is responding to a multi-dimensional combination of conditions, including not only water depth (or hydroperiod) but yearly amplitude of fluctuation in depth.

Explanation (1) seems highly unlikely: aquatic plants generally respond to local hydrological conditions over periods of months to a few years, not decades (see Welling *et al.*, 1988; Squires & van der Valk, 1992; van der Valk, 1994; van der Valk *et al.*, 1994). Explanation (2) is far more likely, given the increase in water levels by *c.* 15–25 cm in central and southern WCA-3A over the 2–3 years before our vegetation sampling commenced (Fig. 8). We cannot exclude explanation (3), but the fact that water depth alone was a strong correlate of vegetation composition in each region, with nearly identical slope (Fig. 7), while yearly amplitude of water depth had almost no correlation with vegetation composition within regions (data not shown), argues against vegetation in different regions of the central Everglades being strongly affected by an interaction between water depth and water-depth amplitude.

More generally, however, local and coupled differences in vegetation, topography, hydrology and biogeochemistry in the central Everglades are unlikely to have yet come into equilibrium with the changes in regional hydrology caused by humans over the past several decades. The fact that soil and pore-water levels of phosphorus remain high on tree islands (Wetzel *et al.*, 2005), decades after a collapse of 90% or more in the abundance of wading birds (Ogden, 1994), argues that the processes leading to the patterned Everglades landscape have not come into equilibrium with the changed biological scene over the same time-frame. Gunderson and Walters (2002) raise the possibility that anthropogenic changes in ecological conditions could change not the equilibrium point but instead the *resilience* of Everglades ecosystems – that is, their ability to remain within the same stability domain – specifically envisioning how the cumulative effects of P loading by agricultural run-off might ultimately push ridge ecosystems away from sawgrass to cattails. We believe it is unlikely that such an override of ecosystem resilience, or fundamental change in ecological trajectory, has yet occurred in

WCA-3A or WCA-3B. Slow approaches to equilibrium in the central Everglades are to be expected, given the slow movement of groundwater in a landscape with extremely gentle slopes; slow rates of peat accretion, measured in millimetres or tenths of millimetres per year; and slow movement of P within and through the Everglades ecosystems, in periphyton, floc, guano and surface and groundwater flows. Such slow-moving processes are, we believe, the reason why a patterned landscape still exists in the Everglades despite massive hydrological and geochemical changes over the last several decades. By the same token, the existence of these processes almost ensures that spending billions of dollars to replumb the Everglades – while essential for ecosystem restoration and the continued viability of Everglades National Park – will also not have immediate beneficial effects on patterning, even if there are prompt effects of shifts in hydroregime on other features of Everglades ecology, including the population densities of wading birds.

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