

Tree–Grass Coexistence in the Everglades Freshwater System

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ABSTRACT

Mosaic freshwater landscapes exhibit tree-dominated patches—or *tree islands*—interspersed in a background of marshes and wet prairies. In the Florida Everglades, these patterned landscapes provide habitat for a variety of plant and animal species and are hotspots of biodiversity. Even though the emergence of patchy freshwater systems has been associated with climate histories, fluctuating hydrologic conditions, and internal feedbacks, a process-based quantitative understanding of the underlying dynamics is still missing. Here, we develop a mechanistic framework that relates the dynamics of vegetation, nutrients and soil accretion/loss through ecogeomorphic feedbacks and interactions with hydrologic drivers. We

show that the stable coexistence of tree islands and marshes results as an effect of their both being (meta-) stable states of the system. However, tree islands are found to have only a limited resilience, in that changes in hydrologic conditions or vegetation cover may cause an abrupt shift to a stable marsh state. The inherent non-linear and discontinuous dynamics determining the stability and resilience of tree islands should be accounted for in efforts aiming at the management, conservation and restoration of these features.

Key words: Tree islands; Peatland; Tree–grass coexistence; Alternative stable states; Resilience; Savanna; State shift.

INTRODUCTION

The Everglades freshwater wetlands exhibit a heterogeneous landscape with marshes and wet prairies punctuated by patches of woody vegetation, including trees (for example, Sklar and van der

Valk 2002). These tree patches are typically more elevated than the surrounding marshes, and are therefore known as “tree islands,” in that they often remain above the water level while the rest of the landscape is flooded. Tree islands are typically richer in nutrients, provide habitat to diverse communities of plants and animals (Sklar and van der Valk 2002), sustain high levels of productivity (Naiman and Decamps 1997; Mitsch and Gosselink 2000), and contribute to carbon storage (for example, Richardson 2000). Tree islands are a characteristic feature of the Florida Everglades (Figure 1A), though similar landforms can be found in other tropical/subtropical freshwater landscapes (for example, Okefenokee Swamp, GA;

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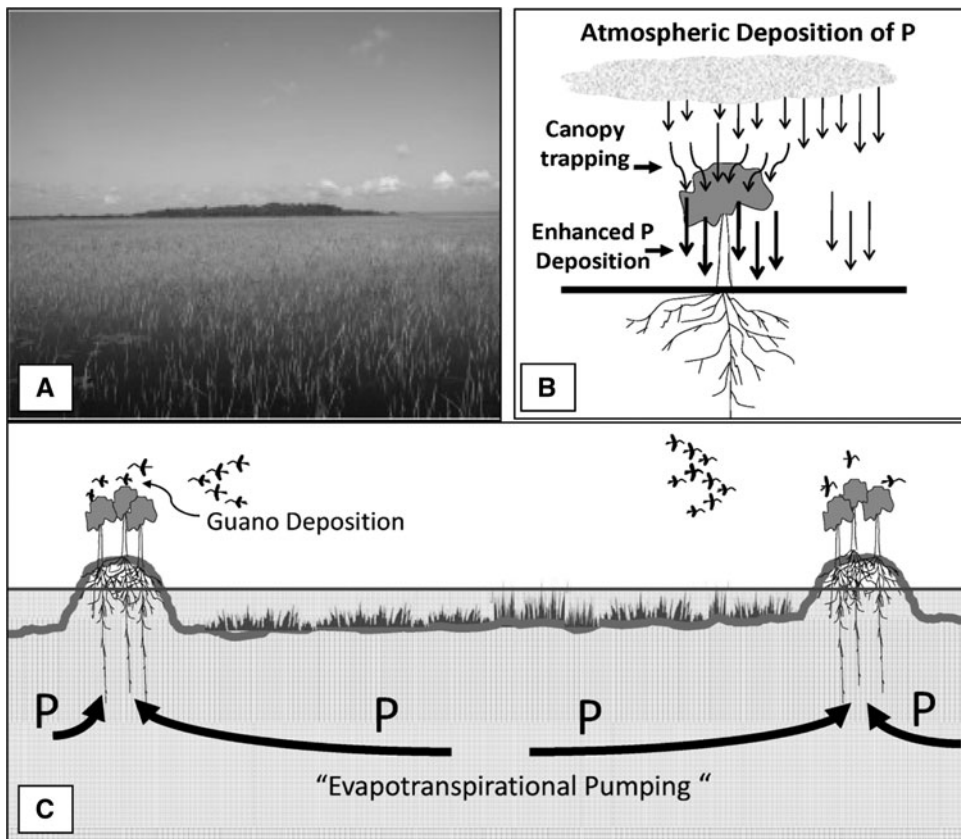


Figure 1. A A profile view of a tree island surrounded by grasses and herbaceous marsh species in Everglades, National Park. Schematic representation of the P enrichment due to the deposition feedback (B), and guano deposition or evapotranspirational pumping (C).

the Pantanal wetland in Brazil, Prance and Schaller 1982; the Okavango delta, Botswana, for example, McCarthy and Ellery 1994; the wetlands of northern Belize, Macek and others 2009); and boreal bogs (Glaser 1987, 1992; Richardson 2000).

Tree islands occurring in the ridge and slough habitat of the Everglades formed during periods of extended drought between 3500 and 500 years before present (Willard and others 2006). With the initiation of large-scale drainage projects and other hydrologic manipulations in this region, approximately one half of the tree island area in the Everglades has been lost (Davis and others 1994). Conservation of the remaining islands and the restoration of their historic aerial extent is a primary objective of Everglades restoration efforts. Ecogeomorphic models of the causal mechanisms leading to their formation and persistence are needed to guide this effort.

Despite the diversity and spatial organization of vegetation within the tree and grass plant communities, the landscape of the Everglades freshwater wetlands exhibits the features of a two-phase system with a distinct contrast between tree islands and marshes. Tree islands are more elevated, dominated by woody vegetation, and rich in phosphorus, whereas marshes are vegetated by herbaceous

vegetation (that is, graminoids, grasses, and forbs, hereafter generically referred to as “grasses”) and phosphorus-poor (Wetzel and others 2005, 2009). A parallel has recently been drawn between the tree–grass mosaic of tree island-marsh systems and patchy vegetation typical of dryland ecosystems, particularly of savannas (van der Valk and Warner 2009). This comparison is useful to appreciate the complexity of vegetation dynamics in heterogeneous wetland landscapes as well as to capitalize on a relatively rich literature on savanna and dryland vegetation (for example, Sarmiento 1984; Schlesinger and others 1990; Scholes and Walker 1993; Scholes and Archer 1997; Ridolfi and others 2008; D’Odorico and others 2006) to formulate research questions and hypotheses that could advance our understanding of these complex systems. Fundamental among those questions is how trees and grasses coexist in patchy freshwater landscapes and how this coexistence is affected by changes in environmental conditions. Known as “the savanna question” (Sarmiento 1984), the coexistence of trees and grasses or other herbaceous species in wetlands remains poorly investigated. In this study, we show how the stable coexistence of marshes and tree islands in the Everglades may emerge as the result of positive feedback mechanisms that

induce bi-stability in vegetation and landscape dynamics.

Tree island and marsh plant communities are found in areas with different ground surface elevations and soil nutrient contents. The persistence of bi-phase landscapes (for example, high elevation, nutrient-rich tree islands bordered by low elevation, nutrient-poor marshes) is often explained as the result of feedback mechanisms (for example, Wilson and Agnew 1992; Shachak and others 2008). In the specific case of the Everglades' freshwater landscape, complex feedbacks would contribute to soil formation and accumulation of nutrients, particularly phosphorus, the main limiting nutrient for tree island and marsh vegetation (Wetzel and others 2009). These processes are likely sustained by plant species that create their own habitat by changing the levels of available resources (for example, soil nutrients) or the disturbance regime (for example, waterlogging). Moreover, the feedbacks acting in this system involve both ecological and geomorphic processes, and are mediated by hydrological drivers, as suggested by the fact that the resulting vegetation patterns are arranged along hydrologic gradients, and landforms are oriented in the flow direction (for example, Sklar and van der Valk 2002; Sah 2004; Willard and others 2006; Watts and others 2010).

To investigate the role of ecological and geomorphic feedbacks on the existence of the alternative stable states of "marsh" and "tree island," we developed a process-based zero-dimensional model, accounting for the temporal dynamics of tree and grass biomass, soil accretion, and nutrient availability, and for feedbacks among these variables.

The major ecogeomorphic feedbacks that have been speculated to exist in the Everglades freshwater system belong to two different groups: (1) feedbacks between tree biomass and soil accretion which are either due to peat accumulation or to calcium carbonate precipitation in the root zone (see Graf and others 2008 and, for the case of the Okavango delta, McCarthy and Ellery 1994; McCarthy 2006); (2) feedbacks between vegetation and plant available phosphorus (P) which are evidenced by the higher soil P content found in the islands, suggesting that trees might contribute to P enrichment through mechanisms of autogenic fertilization (Figure 1B, C) similar to those underlying "fertility island" formation in dryland scrubs (for example, Charley and West 1975; Schlesinger and others 1990; Ridolfi and others 2008). Trees can increase P availability by enhancing phosphorous

deposition (Wetzel and others 2005; Lawrence and others 2007; Figure 1B), favoring guano deposition by birds (Frederick and Powell 1994; Givnish and others 2008; Tomassen and others 2005; Figure 1C), or through a mechanism of transpirational pumping (Figure 1C), whereby plant root uptake draws water-dissolved P into the island soils from the surrounding water body (Ross and others 2006). Regardless of the specific mechanism, P availability increases with tree biomass. Similarly, the rate of soil accumulation increases with increasing tree biomass. Thus, rather than choosing among these different mechanisms, we will refer to the two major classes of feedbacks and account for them through a generic state dependency (that is, dependency on tree biomass) in the rates of P input and soil accretion. These mechanisms are similar to those underlying P enrichment and increased soil accretion on sawgrass ridges in comparison to nearby sloughs in the Everglades (Givnish and others 2008; Hagerthey and others 2008). In fact, it has been shown that these biophysical feedbacks play a crucial role in the emergence of alternative stable states and ecogeomorphic patterns in ridge-and-slough marshes (Larsen and others 2007; Larsen and Harvey 2010). In this study, we investigate the effect of these feedbacks on the temporal dynamics of the tree island-marsh system.

METHODS

We consider as a case study the tree islands in the Everglades freshwater system. As noted, tree islands are more elevated and richer in phosphorus than the surrounding marshes and wet prairies, and the soil phosphorus content tends to increase with elevation (Figure 2; see also Wetzel and others 2009). The structure of marsh and tree island plant communities is not random in that species distribution is organized along elevation and hydroperiod (that is, inundation frequency) gradients (Sah 2004). For example, water intolerant tropical hammock species (for example, *Coccoloba diversifolia*, *Bursera simaruba*, *Simarouba glauca*, *Sideroxylon foetidissimum*, *Eugenia axillaris*) dominate the more elevated areas at the head of the tree islands, though some temperate species (for example, *Celtis laevigata*, *Quercus virginiana*) are also common. In contrast, temperate swamp species better adapted to flooding are found in lower elevation sites in the island tail (for example, *Magnolia virginiana*, *Ilex cassine*, *Salix caroliniana*, *Morella cerifera*, *Taxodium distichum*), whereas species of tropical origin such as *Annona glabra* are the exception. Similarly, marsh vegetation ranges

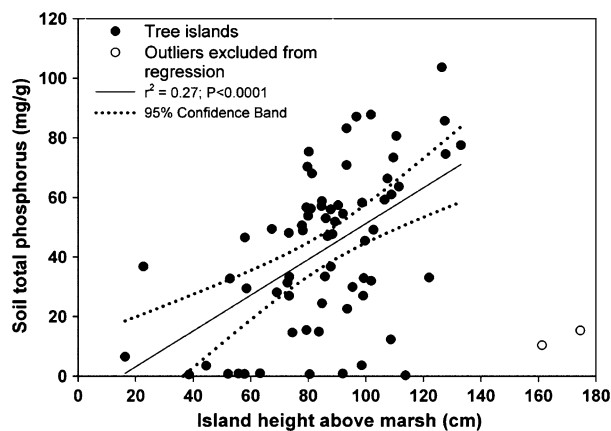


Figure 2. Soil phosphorus (P ; $\mu\text{g/g}$) content is positively correlated to tree island elevation. Soil chemistry and elevation data were collected between 2005 and 2008 on islands in Everglades National Park and in Water Conservation Area 3B north of the Park boundary. P values represent the average 0–10-cm bulk concentrations taken from three locations near the highest point of the island. Island heights were determined by topographic surveys using an auto-level to the water surface of the surrounding marsh. Marsh water surface and ground elevations were obtained from the USGS Everglades Depth Estimation Network (EDEN; <http://sofia.usgs.gov/eden/>). The two outliers (identified as SS-93 and SS-94) are located in a highly disturbed area near a major road. Regression statistical test results: Durbin–Watson = 2.35 (passed); Shapiro–Wilk normality test = 0.0745 (passed); W -statistic = 0.97 ($P = 0.05$); Constant variance test $P = 0.62$ (passed).

between sawgrass (*Cladium jamaicense*) on the crest of ridges and more elevated plains, to graminoids in wet prairies, and floating macrophytes in the sloughs (Hagerthey and others 2008; SCT 2003). However, for the purposes of this study we will group all these species into two functional types and refer to them as trees and grasses.

Ecogeomorphic Model of Tree Island Dynamics

We characterize the state of the system using four state variables, namely tree biomass (T), grass biomass (G), plant available phosphorous, (P_s), and the elevation (Δh) of the ground surface with respect to the mean water level. Both T and G are dimensionless, that is, the biomass values are normalized in a way that their maximum carrying capacity is equal to 1. The growth of tree biomass is limited by flooding conditions and P availability, consistently with the observation (Sah 2004) that trees dominate the more elevated, P -rich areas, and that they undergo severe stress in frequently flooded areas

(for example, Jones and others 2006). To reflect the fact that grasses are not abundant on tree islands, where trees thrive, the growth of grass biomass is assumed to be limited by tree biomass due to the shading effect of trees. Plant community composition and productivity in marshes are strongly dependent also on hydroperiod and P availability (for example, Hagerthey and others 2008). However, these P limitations on marsh vegetation are not accounted for in our modeling framework in that we do not explicitly represent interspecies interactions within the marsh community. Thus, on the basis of these assumptions, in the absence of P limitations and flooding, trees would outcompete grasses because they have better access to light, while grasses grow in P -poor low-elevation areas where trees cannot establish. In this case, the rate of growth of T is independent of G , and is assumed to be proportional to the existing tree biomass, T , and to the available resources, $T_c - T$, with T_c being the carrying capacity for trees, that is, the maximum amount of tree biomass allowed by the available resources and disturbance regime (that is, flooding)

$$\frac{dT}{dt} = r_1 T (T_c - T) \quad (1)$$

with r_1 (time^{-1}) expressing the rate of T growth. The carrying capacity T_c depends both on plant available phosphorous, P_s (mass per unit area), and on the flooding frequency, particularly on the exposure to extreme flood events (Wetzel 2002), which is a function of the elevation, Δh

$$T_c = T_0(\Delta h)f(P_s), \quad (2)$$

where $T_c(\Delta h)$ accounts for the effect of elevation and $f(P_s)$ accounts for the effects of phosphorous limitation on tree growth. It increases as a function of (P_s) and tends to 1 for relatively large values of (P_s), when plant available phosphorous is no longer a limiting factor (Figure 3A). We express $f(P_s)$ as

$$f(P_s) = 1 - \frac{1}{1 + aP_s^b}, \quad (3)$$

consistent with DeLonge and others (2008).

The dependence of the tree carrying capacity, T_c , on elevation is expressed as a function of the height, Δh , above (or below) the mean water level, d_0 , with $T_c \rightarrow 0$ as $\Delta h \rightarrow d_0$, consistent with the observation that tree island vegetation is typically found for values of $\Delta h > d_0 = -0.40$ m, that is, only in sites that are at most 40 cm below the mean annual water level or at higher elevations (Sah 2004)

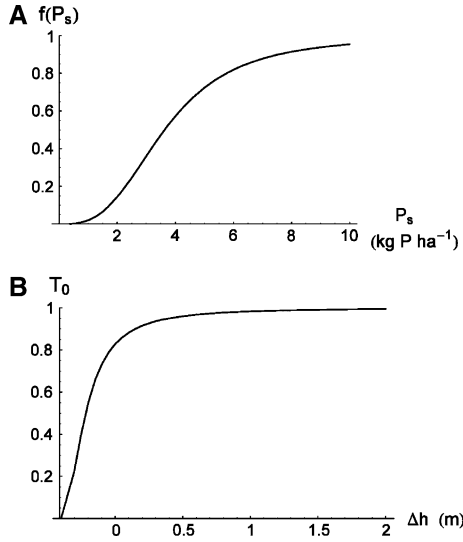


Figure 3. **A** A plot of equation (3) calculated with $a = 0.21$ and $b = 3$; **B** a plot of equation (4) calculated with $c = 30 \text{ m}^{-1}$ and $d_0 = -0.40 \text{ m}$.

$$T_c(\Delta h) = \begin{cases} 0, & \text{if } \Delta h < d_0 \\ 1 - \frac{1}{1+c(\Delta h-d_0)}, & \text{otherwise} \end{cases} \quad (4)$$

A plot of $T_c(\Delta h)$ is shown in Figure 3B. Notice that a negative value of Δh corresponds to a location that is below the mean water level and is therefore frequently flooded.

The dynamics of grass biomass, G , depend on T , with the growth rate of G being proportional to the existing grass biomass and to the resources left available by the existing trees and grasses

$$\frac{dG}{dt} = r_2 G(G_c - T - G), \quad (5)$$

where r_2 (time^{-1}) is a parameter expressing the rate of G growth, and G_c is the carrying capacity for grasses. G_c is assumed to be independent of P_s and Δh and is here taken as a constant ($G_c = 1$). Equations (1) and (5) express the fact that, while trees are in competitive advantage with respect to grasses, they are sensitive to flooding (that is, elevation) and P availability.

The dynamics of plant available phosphorus, P_s , are complex and involve a number of processes that would be hard to account for in the minimalistic modeling framework developed in this article. These dynamics are here expressed in a simplistic manner considering the balance between major inputs (P_{in}) and outputs (P_{out}) of P

$$\frac{dP_s}{dt} = P_{in} - P_{out}. \quad (6)$$

The input of P from external sources is associated with mechanisms that are independent of vegetation cover (for example, background levels of atmospheric deposition) and with plant-related inputs in the form of guano, transpirational pumping, or canopy trapping of atmospheric P (for example, dust, aerosols, water vapor condensation). Thus, to account for this feedback between trees and P inputs we express P_{in} as (DeLonge and others 2008)

$$P_{in} = \alpha T + \beta. \quad (7)$$

with β being the rate of canopy-independent P deposition, and αT accounting for autogenic mechanisms of P fertilization. Thus, β depends for example on the specific geographic location, while α expresses the strength of the fertilization feedback and depends on the specific autogenic mechanism. The output of plant available phosphorus due to soil leaching, erosion, or loss of litter and debris during flood events is here expressed as proportional to the existing amount of phosphorus, $P_{out} = kP_s$. In some systems it has been found that trees contribute to reduce these losses presumably through effective root uptake mechanisms thereby further enhancing P availability in treed areas (for example, Lawrence and others 2007). However, this effect is difficult to assess and quantify and is therefore not invoked by this study as one of the possible mechanisms explaining P enrichment in tree islands.

The dynamics of soil accretion occur on relatively long time scales. For example, in the Everglades the rates of tree island accretion have been estimated in the range $0.11\text{--}0.17 \text{ mm y}^{-1}$, with maximum values around 0.37 mm y^{-1} (Orem and others 2002). As noted, the build-up of tree island soils can be due either to the precipitation of carbonates in the soil solution within the root zone or to the accumulation of organic matter (litterfall, dead roots, and other plant residues) that does not decompose, due to anaerobic conditions associated with the frequent occurrence of water logging. Thus, the first mechanism contributes to the formation of mineral soils (McCarthy and Ellery 1994; Graf and others 2008), whereas the second contributes to the accumulation of organic soil in the form of peat (for example, Richardson 2000). In both the cases, the rate of soil formation depends on T , whereas the loss of organic soil depends on microbial respiration and fire (for example, Armentano 1980; Luken and Billings 1985; Raich and Schlesinger 1992). Because both of these processes are favored by soil aeration, the rate of soil loss should be an

increasing function of Δh (for example, Moore and Knowles 1989). Thus the overall dynamics of Δh can be expressed as

$$\frac{d(\Delta h)}{dt} = \gamma_S T - \gamma_R (\Delta h - d_0) \quad (\text{if } \Delta h > d_0) \quad (8)$$

where γ_S and γ_R are two parameters measuring the rates of soil accretion (for example, by peat formation) and soil loss (for example, by respiration or fire), respectively, while the term proportional to d_0 accounts for the fact that soil respiration tends to zero as $\Delta h \rightarrow d_0$. Because for $\Delta h < d_0$ both soil respiration and the carrying capacity of trees (T_c) are zero (that is, $T \rightarrow 0$), in flooded areas Δh remains constant, though we acknowledge that in the Everglades, herbaceous vegetation may maintain low rates of soil accretion in the flooded marsh areas (Larsen and others 2007).

Equilibrium States

The equilibrium states of the system are determined setting to zero the first-order derivatives in equations (1), (5), (6), and (8). Thus, using equation (7) we express the plant available phosphorus, P_s , at equilibrium, as

$$P_s = \alpha' T + \beta' \quad \text{with} \quad \alpha' = \frac{\alpha}{k} \quad \text{and} \quad \beta' = \frac{\beta}{k} \quad (9)$$

Similarly, we find that at equilibrium soil elevation is related to tree biomass as

$$\Delta h_{eq} = \gamma T + d_0 \quad (\text{if } \Delta h > d_0). \quad (10)$$

with $\gamma = \frac{\gamma_S}{\gamma_R}$ expressing the relative importance between the rates of soil formation and soil loss.

Inserting equation (9) in (2), and (2) in equation (1) we determine the equilibrium, T_{eq} , states of T as a function of the parameters a , b , α' , β' , d_c , and of the elevation Δh

$$T_{eq} [T_0(\Delta h)f(T_{eq}) - T_{eq} = 0]. \quad (11)$$

This equation allows us to investigate the steady states of the system as a function of surface elevation, Δh . Over relatively long timescales, however, Δh tends to equilibrium, Δh_{eq} . Thus, using (10), equation (11) becomes

$$T_{eq} [T_0(\Delta h_{eq})f(T_{eq}) - T_{eq}] = 0. \quad (12)$$

The solutions of (12) provide the steady states of the dynamics of tree biomass as a function of the parameters a , b , α' , β' , d_0 , and γ . The steady states of plant available phosphorus and ground elevation can be then calculated as a function of T_{eq} using equations (9) and (10), respectively, whereas the

stable state, G_{eq} , of grass biomass is obtained from equation (5), as $G_{eq} = G_c - T_{eq}$. Notice that the equilibrium solution $G_{eq} = 0$ is unstable, unless $T_c = T_{eq} = 1$. Similarly, the equilibrium solution $T_{eq} = 0$ is unstable unless $T_c = 0$. The equilibrium solution $G_{eq} = T_{eq} = 0$ is always unstable. Any non-local transport mechanism of seeds (for example wind, water flow, bird droppings) would allow for progression away from the unstable equilibria.

Parameter Estimation

The modeling framework presented in this study is suitable to qualitatively investigate the dynamics of tree island freshwater landscapes in general. In this study, we show an application to the case of the Everglades. To this end, the parameters were determined using data from the Everglades or from other neotropical forests, when data from the Everglades were not available.

Tree growth was monitored on 10 tree islands located in Everglades National Park. On each of those islands, band dendrometers (Felker and Diaz-De Leon 2005) were installed on 6–15 trees and were measured bi-annually or more frequently from mid 2007 until late 2008. The trees were located in 3–5 randomly located $5 \times 5 \text{ m}^2$ cells on the most elevated portions of the islands, typically classified as a tropical hardwood hammock (Craighhead 1971; Armentano and others 2002). All trees larger than 5-cm diameter at breast height in the sample cells were equipped with dendrometers. The most common trees measured include *Bursera*, *Eugenia*, *Celtis*, and *Sideroxylon* spp. (Table 1). Tree basal area was converted to aboveground biomass (kg) using the allometric equations provided by Brown and others (1989). The total standing biomass, T_s , on an island is estimated as the sum of the individual tree biomass values divided by the total area of sample cells (15–25 m^2), and expressed as kg ha^{-1} . Notice that, unlike T (in equation (1)), T_s is a dimensional variable. The change in total standing tree biomass from mid 2007 to late 2008 was used to estimate annual growth rates (dT_s/dt , $\text{kg m}^{-2} \text{ y}^{-1}$) on each island. The maximum total standing biomass on Everglades tree islands (T_{cs}) is unknown due to natural (for example, hurricane) and anthropogenic disturbances, and this term is expected to vary with soil nutrients and water levels in the surrounding marshes. However, the tree islands included in this analysis are all found near the center of the Shark River Slough in Everglades National Park, in areas with similar water depths, and are relatively undisturbed by human activity. Consequently, a single T_{cs} is

Table 1. Tree Island Names, Locations, Species Lists, and Heights Above Average Water Level (Δh) in Shark River Slough, Everglades National Park for which Bimonthly Dendrometer Measurements from Mid 2007 to Late 2008 were used in Figure 4

Island name	UTM Easting (NAD83)	UTM Northing (NAD83)	Species (# individuals) with dendrometers	Δh^* (m)
Manatee	518560	2820117	EUGAXI (5), BURSIM (2) CELLAE (2), SIDFOE (1)	0.64
Gumbo	525999	2834793	EUGAXI (6), BURSIM (5)	0.62
Black	531295	2832630	BURSIM (7), CHRICA (2) EUGAXI (1), SIDFOE (1)	0.78
Chekika	534372	2847485	SIDFOE (7), EUGAXI (5) CELLAE (2), MYRFLO (1)	0.79
SS-37	518488	2826245	CELLAE (3), COCDIV (3)	0.58
Panther	524189	2828472	BURSIM (4), CELLAE (3) EUGAXI (1), FICAUR (1) SOLERI (1)	0.63
Irongrape	533651	2836523	CELLAE (4), SIDFOE (4) EUGAXI (2)	0.74
Satinleaf	524499	2838019	EUGAXI (8), CHROLI (2) CHRICA (1), CELLAE (1) BURSIM (1)	0.63
Vulture	528918	2841667	CELTIS (6), EUGAXI (3) SIDFOE (1), BURSIM (1)	0.93
SS-81	547639	2848113	CELLAE (10)	0.25

*Island heights surveyed to surrounding water table. Average marsh water depths and surface elevations (2000–2009) surrounding islands are derived from USGS Everglades Depth Estimation Network (EDEN: <http://sofia.usgs.gov/eden/>). Species include *Bursera simaruba* (BURSIM), *Eugenia axillaris* (EUGAXI), *Sideroxylon foetida* (SIDFOE), *Celtis laevigata* (CELLAE), *Coccoloba diversifolia* (COCDIV), *Chrysobalanus icaco* (CHRICA), *Myrsine floridana* (MYRFLO), *Ficus aurea* (FICAUR), *Chrysophyllum oliviforme* (CHROLI), *Solanum erianthum* (SOLERI).

considered sufficient to describe these stands, and we conservatively estimate the theoretical maximum tree island aboveground biomass as approximately 1.5 times the maximum biomass measured in these stands. The slope of a least-squares linear regression between the terms dT_s/dt and $T_s(T_{cs} - T_s)$ was then used to estimate r_1 ($r_1 = 0.0019$; $P = 0.0003$) as shown in Figure 4. Assuming T_{cs} equals 1, 2, or 3 times the maximum observed tree biomass produces r_1 values equal to 0.0023, 0.0011, and 0.0006, respectively, a variation of +21 to -68% of the initial estimate. More data are needed to better constrain r_1 . However, the steady states of the system as predicted by the tree island-grassland model are independent of the r_1 and r_2 parameters (see equations (9)–(12)). Thus, the slope of the regression in Figure 4 is not used directly in model calibration or simulations. Rather, these results are presented here to validate the functional relation used in equation (1) to express the temporal dynamics of tree biomass and provide a basis for comparisons between Everglades tree islands and other forests.

No data from the Everglades were available to determine the parameters a and b in equation (3). Therefore, in Figure 3A (and in the rest of the

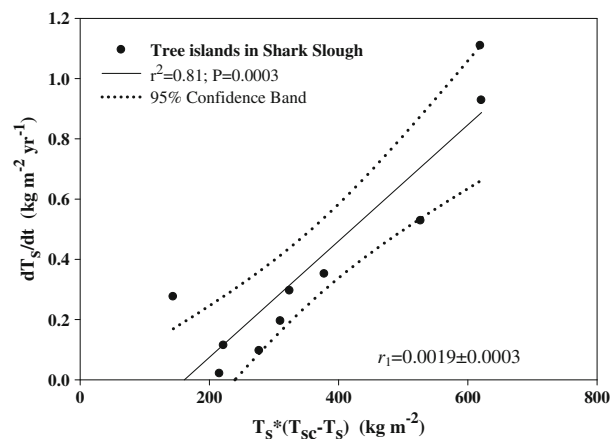


Figure 4. The rate of tree growth (dT_s/dt) measured with dendrometers on 10 islands in Shark Slough (Everglades National Park) is dependent on the existing standing tree biomass (T_s) and the difference between T_s and the carrying capacity of islands (T_{cs}). For this analysis, T_{cs} is estimated at 50 kg ha^{-1} , approximately 1.5 times the maximum biomass found on these islands. The slope of the expression is equivalent to r_1 in equation (1). See Table 1 for island locations and dendrometer species lists. Regression statistical tests: Durbin–Watson Statistic = 2.058 (passed), Shapiro–Wilk normality test $P = 0.123$ (passed); W -statistic = 0.88 ($P = 0.05$); Constant variance test $P = 0.123$ (passed).

article) we used parameters consistent with those obtained for plant available phosphorus along a biomass gradient in a Brazilian savanna (DeLonge and others 2008). The parameters of equation (4) were determined based on the observation that in the Everglades freshwater system woody vegetation is generally found only at elevations above -0.40 m with respect to the mean water level (Sah 2004). Therefore, d_0 is equal to -0.40 m. No direct estimate of the parameters α' and β' is available for tree island vegetation in the Everglades. As noted, the value of α' depends also on the specific mechanism invoked to explain the autogenic fertilization of tree island soils. Values of α and k used for dry seasonal forests ($\alpha = 0.68$ kg P ha $^{-1}$ y $^{-1}$, $k = 0.07$ y $^{-1}$) are reported by DeLonge and others (2008) in the case of autogenic P enrichment due to occult precipitation (that is, fog deposition and canopy condensation) or dust trapping by the canopy. In the case of the tree islands in the Everglades evapotranspirational pumping and other mechanisms (Figure 1) are likely to play a major role in the feedback between tree cover and P availability (Ross and others 2006). Thus, we will also assess the sensitivity of the dynamics to larger values of α . The values of the parameters β' and γ depend on the geographic location and on the relative importance of the processes of soil formation and soil loss. The analyses presented in the following sections will explore the dependence of the dynamics on these two parameters.

RESULTS

The dynamics expressed by equations (1), (5), (6), and (8) occur at different time scales; changes in plant community composition (equations (1) and (5)) are expected to occur at multidecadal time scales as observed in vegetation response to drought cycles and water management over the past 50 or more years (Sklar and van der Valk 2002; Kwon and others 2006; Willard and others 2006). For example, in those areas where water management has maintained unusually high water levels, tree vegetation has been lost from lower elevation tree islands. In many cases, tree species have disappeared entirely from historic island locations observed in aerial photography. The shape and outline of these treeless islands can still be observed in the landscape, leading to their characterization as “ghost islands” (for example, Sklar 2001). The persistence of these features in aerial photos over the past several decades suggests that the geomorphic processes associated with changes in soil elevation in tree islands (equation (8)) occur at much

longer time scales than the changes in plant community. Thus, although peat elevation in ridge and slough landscapes may respond to water level changes more quickly than vegetation composition (Watts and others 2010), the dynamics of tree island vegetation appear to be faster than those of peat accretion. Therefore, we first investigate the properties of the system at decade-to-century time scales assuming that the elevation, Δh , remains constant. To this end, we use equation (11) to determine the stable states of the system and analyze their dependence on elevation. The results are shown in Figure 5 for different values, β' , of canopy-independent phosphorus input (for example, background levels of deposition in the region). It is found that for all elevations and low values of β' (thick lines), P inputs are inadequate to sustain the establishment and growth of woody vegetation. Thus, in this case trees rely on their ability to enhance phosphorus available through the feedback mechanisms discussed in the previous sections. For regions with tree biomass less than some critical value (Figure 5, thick dashed line), this enhancement is not strong enough for self maintenance and a tree island becomes a ghost island. These feedbacks play a crucial role in the dynamics of tree island vegetation, as they are found to induce bistability in the system.

Over longer time scales, however, Δh is not a constant but a dynamic variable that varies in time at a rate that depends on T as in equation (8). In this case, the equilibrium states, T_{eq} , of the system

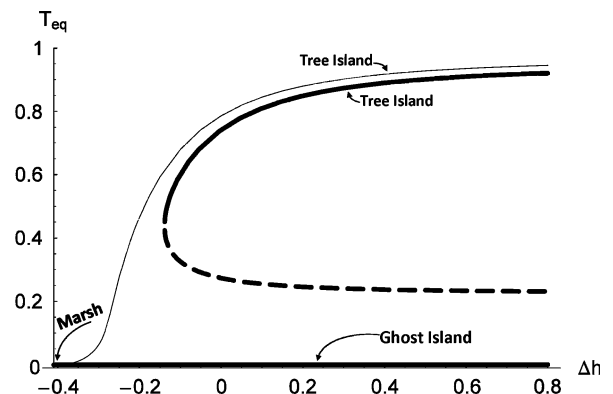


Figure 5. Stable (*solid*) and unstable (*dashed*) equilibrium states of tree biomass as a function of the elevation, Δh . In this analysis Δh is an assigned parameter, rather than being modeled as a function of T (equation (8)). The thick and the thin lines correspond to the case with $\beta' = 0.2$ kg P ha $^{-1}$ and $\beta' = 2.0$ kg P ha $^{-1}$, respectively. The other parameters are $\alpha' = 9.75$ kg P ha $^{-1}$ (that is, $\alpha = 0.68$ kg P ha $^{-1}$ y $^{-1}$, $k = 0.07$ y $^{-1}$) whereas a , b , c , and d_0 are as in Figure 3.

are obtained as solutions of (12) for different values of the parameters. Here, we keep constant the values of a , b , d_0 , and α' (see “Parameter estimation”) and investigate the dependence of T_{eq} on the rate of canopy-independent phosphorus input, β' , and on the parameter γ , expressing the relative importance of soil formation and soil loss processes. We find that for suitable values of β' and γ the system is bi-stable, that is, it exhibits two possible stable equilibria, $T_{eq} = 0$ and $T_{eq} \approx 1$ (Figure 6). The dependence of the states of the system on the phosphorus and soil accretion dynamics is shown in Figure 7 as a function of the parameters β' and γ . Low elevation marshes and wet prairies are stable for low values of β' and γ . As these two parameters increase, the dynamics become bi-stable, with tree islands and low elevation marshes/prairies becoming both stable states of the system.

DISCUSSION

This study provides insight into the possible mechanisms underlying the coexistence of trees and herbaceous freshwater marshes in mixed landscapes such as those of the Everglades. It has

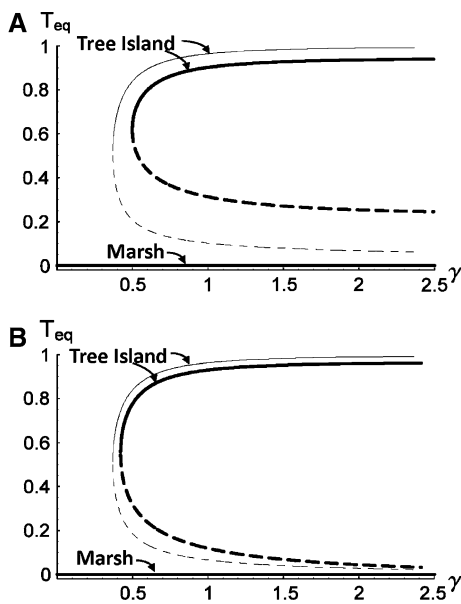


Figure 6. Stable (solid) and unstable (dashed) equilibrium states of tree biomass as a function of the parameter, γ expressing the relative importance of soil formation and soil erosion. In this analysis Δh is modeled as a function of T (equation (8)). Thus, at equilibrium low values of T correspond to low elevation (that is, more flooded) sites. **A** $\beta' = 0.2$ kg P ha⁻¹ and **B** $\beta' = 2.0$ kg P ha⁻¹. The other parameters are $\alpha' = 9.75$ kg P ha⁻¹ (thick lines) and $\alpha' = 30$ kg P ha⁻¹ (thin lines) whereas a , b , c , and d_0 are as in Figure 3.

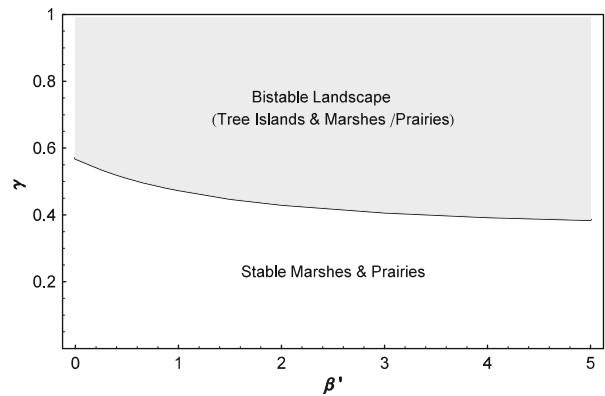


Figure 7. Domains of the parameter space corresponding to stable marsh and bistable island/marsh conditions.

been noted (van del Valk and others 2009) that these landscapes share many of the attributes of arid and semiarid ecosystems, including (a) the heterogeneity and patchiness of vegetation, which is mirrored by a heterogeneous distribution of soil resources as in the case of fertility (or resource) “islands” found in dryland environments (Charley and West 1975; Schlesinger and others 1990; Vet-aaas 1992; Wang and others 2007); (b) the presence of geomorphic features (that is, the islands) in association with tree cover, which is reminiscent of similar landforms typical of arid landscapes such as coppice (or “nabkha”) dunes found in many deserts around the world (Khalaf and others 1995; Dougill and Thomas 2002; Nickling and Wolfe 1994; Ravi and others 2007) where woody vegetation also plays a crucial role in the processes controlling soil accretion; (c) the susceptibility to fire occurrences during the dry season and the crucial role of fires in determining vegetation composition and structure (for example, Brandt and others 2002; Richardson 2009); (d) the apparently stable coexistence of trees and grasses in different patches within the same landscapes, similar to the case of savanna ecosystems, where clusters of trees are found dispersed within a grass matrix (for example, Scholes and Walker 1993; Scholes and Archer 1997). Questions on the mechanisms underlying tree–grass coexistence and its stability and resilience have been addressed in the last four decades with reference to arid and semiarid savannas (Walter 1971; Noy-Meir 1975; Walker and others 1981; Walker and Noy-Meir 1982). The same questions are also relevant to the case of heterogeneous wetland environments, where the processes controlling the formation, persistence, and sensitivity to disturbance of tree islands and marshes remain poorly understood.

Drawing from a rich body of literature on dryland, peatland, marsh, and riparian vegetation (Noy-Meir 1975; Walker and others 1981; Walker and Noy-Meir 1982; Dublin and others 1990; Anderies and others 2002; Rietkerk and others 2004; Ridolfi and others 2006; Marani and others 2007) we developed a minimalist model of tree island dynamics. The zero-dimensional model presented in this article shows how alternative stable states may arise in the ecogeomorphic dynamics of tree islands as an effect of positive feedback mechanisms that have been documented for these systems. These mechanisms include the mutual dependence among vegetation dynamics, soil accretion, and processes of tree island fertilization associated with atmospheric deposition (Wetzel and others 2005), bird nesting (Frederick and Powell 1994), or transpiration-induced groundwater flow (Ross and others 2006). This model is used here to show how the resilience of tree islands may change in response to changes in environmental conditions. The model is mainly conceptual and its major objective is to provide a process-based understanding of the dynamics underlying tree island systems and of their susceptibility to possible shifts to the alternative state of freshwater marsh. This study does not investigate the mechanisms underlying the high degree of spatial organization of tree island patterns (for example, Borgogno and others 2009), the oblong shape, the orientation with the flow, the typical size, and the regular spacing of tree islands. The analysis of these patterns requires a spatially explicit framework (for example, Rietkerk and others 2004; Lago and others 2010), which is beyond the scope of this study because of the lack of data (for example, measurements of rates of seedling dispersal, phosphorus fluxes, and tree island lateral growth) for the parameterization of a spatial tree island model for the Everglades. Thus, this study focuses on the temporal dynamics and on possible equilibrium states of the ecosystem.

In the short term, soil elevation can be considered constant. Trees establish only in relatively elevated and P-rich areas that are not prone to frequent flooding. Marsh species establish in areas that are not suitable for tree growth, that is, low elevation flooded sites, or on relatively P-poor soils. P availability depends both on canopy-independent supply, and on autogenic mechanisms of canopy-enhanced phosphorus input. Figure 5 shows how on relatively elevated sites this positive feedback between P and tree dynamics may induce bistability in systems receiving only relatively small amounts of P in the form of canopy-independent input (that is, small values of β'). This result is

consistent with those by DeLonge and others (2008) for the case of dry seasonal neotropical forests. In these bistable systems the dynamics are stable both in the presence and in the absence of a tree canopy. In the first case, the presence of the canopy enhances phosphorous inputs, thereby allowing for the persistence of woody vegetation. Conversely, in the absence of trees the background levels of P input (that is, β') are insufficient to sustain woody vegetation. Thus, at low β' , the system is also stable when relatively elevated areas exhibit no tree cover. With higher values of β' , canopy-independent P inputs are sufficient to maintain adequate levels of plant available phosphorus even in the absence of a tree canopy. In this case, tree establishment and growth are limited only by flooding (that is, elevation) but is independent of any pre-existing tree cover. Thus, the treeless configuration would not be stable in relatively elevated sites. Therefore, for sufficiently high values of β' these dynamics exhibit only one stable state (Figure 5, thin line).

When the underlying dynamics are bistable, tree island vegetation has only a limited resilience. In fact, if woody vegetation is disturbed beyond a critical level the system shifts to the alternative state of an island with no trees (“ghost island”). Due to the stability of this state, the system may not revert back to the tree island state even if the disturbance is eliminated. Moreover, Figure 5 (thick lines) shows a discontinuous response of tree islands to changes in water level. As the elevation above the mean water level decreases—for example, as a result of water management—tree biomass does not change substantially until Δh reaches a critical value marking the transition from bistable to stable behavior. In this case, the lower elevation islands (with respect to mean water level) would be expected to shift to a “ghost island” state. Figure 5 shows that this shift is abrupt and potentially irreversible. Thus, in areas of the Everglades where islands have been lost due to flooding, simply lowering water levels may not lead to the formation of island communities that were characteristic of the pre-disturbance state. However, this does not exclude the possibility that “ghost” tree islands might be recolonized by more flood tolerant species at first, and then, after some time of building soil, the flood-intolerant (that is, drought tolerant) hardwood hammock species would again begin to dominate. In most instances, this regime shift is hard to predict (Scheffer and others 2001) and the model here suggests that relatively minor changes in mean water levels may lead to unexpected changes in the state of the system. Our model does

not take into account any shifts from flood tolerant to flood-intolerant tree species that might accompany changes in water management. These species shifts are not expected to change the conclusions regarding the steady-state bi-stability and resilience of the tree island-marsh system as suggested by the model. However, competition among tree species with variable flood tolerances may induce time-lags in the shifts between alternative stable states in the Everglades, particularly in areas where the changes in water management are moderate or where they are implemented slowly with respect to the time-scales of community dynamics. Figure 5 shows that in a phosphorus-poor environment the dependence of steady-state tree biomass on elevation is qualitatively different from the case of phosphorus rich landscapes. Thus, ongoing anthropogenic increases in P availability may strongly modify tree island dynamics. Some of these changes involve an increase in the rates of soil organic matter decomposition (Troxler and Childers 2009) and shifts in grass community composition (for example, Hagerthey and others 2008), which are not captured by the model presented in this article. These shifts may have an important impact on the dynamics of ghost islands. For example, increased P favors the replacement of sawgrass (*Cladium jamaicense*) by the invasive *Typha* (cattail). The enhanced carbon sequestration in ghost island soils resulting from the higher productivity of cattail (Hagerthey and others 2008) could favor the persistence of ghost islands, whereas their re-colonization by trees would depend on the competitive relations between cattail and woody vegetations. Thus, the success of tree island restoration efforts could depend on the management of P concentration levels and the associated invasions of cattail.

Over longer timescales soil elevation does not remain constant but changes with the tree biomass, T (equation (8)). In this case, the system may still exhibit bistable behavior, depending on the rates of P deposition and soil accretion (Figure 6). These results differ from those in Figure 5 (that is, with constant Δh); in this case, bistability occurs even for high values of β' (compare Figure 6A, B), that is, when no important P limitations may determine a dependence of T on autogenic fertilization. Thus, the emergence of multiple stable states in Figure 6 is not induced by interactions between vegetation and phosphorus dynamics, but by feedbacks with soil accretion processes (equation (12)). However, stronger feedbacks between P input and tree island vegetation (that is, higher values of α' ; see Figure 6, thin lines) increase the range in parameter values for which the dynamics are bistable. Moreover,

using equations (8) and (10) we find that the state $T_{\text{eq}} = 0$ corresponds to low elevation points of the landscape, $\Delta h_{\text{eq}} < d_0$. This suggests that the “ghost island” state in Figure 5 (that is, $T_{\text{eq}} = 0$ and elevated Δh values) is a transient feature that tends to disappear over longer time scales, with long-term equilibrium values of Δh_{eq} less than the current mean water depth. The dependence of the states of the system on the rates of P input (β') and on the relative importance between soil accretion versus erosion (γ) shows (Figure 7) how tree islands are prone to catastrophic shifts to the marsh/wet prairie state characterized by lower elevations and lower soil P contents. In fact, although marshes can exist as stable states of the system, tree islands can only occur as metastable states, that is, as one stable state in the bistable ecogeomorphic dynamics. The existence of the alternative stable state of marsh (Figure 7) limits the resilience of tree islands in that disturbances and environmental change may cause an abrupt regime shift in the system.

These analyses explain the stable persistence of tree islands but do not shed light on the possible causes of their formation. It is relevant to wonder how tree islands became established starting from freshwater marsh conditions. What caused the shift from the stable marsh to the stable tree island state? Why did this happen only in some points and not in the whole landscape? It has been argued that tree island formation dates back to periods of extended droughts, when the lack of flooding pressure favored the establishment of trees on topographic highpoints associated with limestone outcrops (Willard and others 2006). However, peat-based islands, which are also elevated above the surrounding marshes, are found in many parts of the Everglades, and peat-based tree communities are frequently found downstream of islands formed on the limestone outcrops. In this case, the autogenic process is affecting the shape of the island, but not its formation.

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