



## Original research article

## Tree island pattern formation in the Florida Everglades

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## ABSTRACT

The Florida Everglades freshwater landscape exhibits a distribution of islands covered by woody vegetation and bordered by marshes and wet prairies. Known as “tree islands”, these ecogeomorphic features can be found in few other low gradient, nutrient limited freshwater wetlands. In the last few decades, however, a large percentage of tree islands have either shrank or disappeared in apparent response to altered water depths and other stressors associated with human impacts on the Everglades. Because the processes determining the formation and spatial organization of tree islands remain poorly understood, it is still unclear what controls the sensitivity of these landscapes to altered conditions. We hypothesize that positive feedbacks between woody plants and soil accretion are crucial to emergence and decline of tree islands. Likewise, positive feedbacks between phosphorus (P) accumulation and trees explain the P enrichment commonly observed in tree island soils. Here, we develop a spatially-explicit model of tree island formation and evolution, which accounts for these positive feedbacks (facilitation) as well as for long range competition and fire dynamics. It is found that tree island patterns form within a range of parameter values consistent with field data. Simulated impacts of reduced water levels, increased intensity of drought, and increased frequency of dry season/soil consuming fires on these feedback mechanisms result in the decline and disappearance of tree islands on the landscape.

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## 1. Introduction

The Florida Everglades freshwater system is comprised of a mosaic of communities, ranging from near-continuously inundated sloughs separated by parallel, periodically-flooded sawgrass (*Cladium jamaicense*) ridges, to shorter hydroperiodic wet prairies. Isolated upland habitats interspersed among the ridge-slough and wet prairie communities are dominated by woody vegetation and referred to as “tree islands” (Sklar and Van Der Valk, 2002). These tree islands exhibit higher elevations and thereby maintain drier soils than the surrounding marshes. These islands also tend to be relatively nutrient rich compared to the surrounding habitats, particularly with regards to phosphorous (Wetzel et al., 2005, 2009), a limiting nutrient in the Everglades freshwater ecosystems. As such, these islands host a rich community of flora and fauna (Sklar and Van Der Valk, 2002) and exhibit higher levels of productivity than the surrounding marshes and wet prairies.

Earliest records of tree island deposits date to about 3500 years ago (Willard et al., 2006) and are thought to have established during periods of prolonged droughts. Tree island forms vary from round to elongated teardrop shapes (Sklar and Van Der Valk, 2002). Initial formation of round tree islands is thought to originate from buoyant floating peat masses resulting in pop up tree islands whereas teardrop shaped islands appear to originate on outcrops of limestone bedrock (Givnish et al., 2008). Flow-mediated, differential sediment transport and deposition have been cited as primary factors in the formation of the tear drop shape that tapers in the downstream direction (Ross et al., 2006). Several mechanisms leading to the high concentrations of nutrients in tree island soils have been proposed in recent studies. Transpiration-driven groundwater transport of nutrients towards the island from the surrounding areas is one such mechanism. In this process, high rates of root water uptake beneath the tree canopy generates a local hydraulic gradient which, in turn, results in flow of groundwater and solutes towards the island (Wetzel et al., 2005; Ross et al., 2006). Direct measurements of tree island-marsh hydraulic gradients, transpiration rates, stable isotope studies, and mass balance models support the hypothesis of

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transpiration-driven nutrient focusing on these islands (Saha et al., 2010; Wang et al., 2011; Sullivan et al., 2013). However, the results of Sullivan et al. (2013) also suggest the very high soil nutrient values observed in the soils at the upstream end of tree islands cannot be explained by groundwater discharge alone, indicating other mechanisms such as guano deposition and adsorption/desorption of P to carbonate minerals in response to fluctuating water levels may play a role (Sullivan et al., 2013; Troxler et al., 2014). While these recent studies have demonstrated an improved understanding of the mechanisms involved in generating the characteristic shapes and high soil nutrients of individual islands, the factors regulating the number and distribution of islands on the Everglades landscape have not been identified. In fact, while recent studies have clarified the important role of differential hydrologic exchange and particulate nutrient redistribution as dominant drivers of nutrient patchiness that drive the formation and organization of the ridge slough systems in the Everglades (Larsen and Harvey, 2010; Larsen et al., 2011, 2015; Cheng et al., 2011), tree island landscapes remain relatively poorly understood.

The partitioning of the Everglades landscape in the 1960s into water conservation areas (WCA) separated by a complex network of levees, canals and gates has modified the natural hydrologic regime under which tree islands naturally formed. During this time, tree island abundance has decreased, their size class distribution has changed and the characteristic tear drop shape of many tree islands has been degraded (Sklar and Van Der Valk, 2002). Root anoxia under persistent high water conditions in some portions of the WCA, an increase in frequency and intensity of fires during low water conditions, and invasive exotic species have all been cited as contributing factors to tree island decline in the disturbed Everglades. To date, the lack of a complete understanding of the processes that have led to the emergence of tree island landscapes and of the dynamics underlying their spatial organization is a major limitation to the evaluation of how management practices may affect the persistence and distribution of remaining tree islands.

Previous research (D'Odorico et al., 2011) has shown how a two state landscape such as those that occur in the Everglades (i.e., with phosphorus (P) rich tree islands and P poor marshes) may emerge as an effect of positive feedbacks between plant community composition and the limiting resources (e.g., P) or disturbance regime (e.g., waterlogging and anoxia). In this scheme, trees contribute to soil accretion through the deposition of plant organic matter that is subsequently incorporated in the soil, thereby sustaining the formation of more elevated patches (i.e., tree islands) where more trees may thrive because of the less frequent exposure to flooding. Likewise, trees can increase phosphorus availability by enhancing deposition or P concentration in the shallow groundwater (Ross et al., 2006; Wetzel et al., 2009; Sullivan et al., 2013). When applied in a spatial context, these feedbacks result in short-range facilitation (P accumulation in the surrounding of trees) and long-range competition (due to the overall P limitation in the Everglades) as has been observed in other systems and replicated in various models (Rietkerk et al., 2004; Eppinga et al., 2009; Cheng et al., 2011). This combination of near-field facilitation and far-field competition for nutrients can be used to explain the pattern of isolated, high-nutrient tree islands interspersed within a low-nutrient herbaceous landscape (Borgogno et al., 2011). Here we develop a spatially-explicit model to examine how the emergence of tree islands in a marsh landscape is related to the strength of feedback mechanisms that enhance autochthonous peat formation and phosphorus accumulation. The modeling exercise presented in this paper is focuses on identifying how abiotic factors that affect autochthonous peat formation and phosphorus accumulation influence the rate and

pattern of tree accumulation across the landscape. The use of a spatially-explicit model, allows us to define key thresholds (or feedback mechanisms) that produce characteristic patterns of tree accumulation across a chronically phosphorous limited landscape. As a result, this study focuses on the interplay of processes controlling the formation of the patterned landscape of the Everglades. Since both water management practices and the occurrence of fire on the landscape exert strong control over the rate of peat soil accumulation, our modeling process is used to investigate how water management, fire, and their interaction can affect the stability and resilience of tree island landscapes.

## 2. Methods

A spatial model was developed, which accounts for the interactions between woody biomass,  $T$  ( $\text{kg kg}^{-1} \text{m}^{-2}$ ), phosphorous,  $P$  ( $\text{kg m}^{-2}$ ), and peat/soil accretion relative to the water table,  $\Delta h$  (m). Tree establishment and growth are limited by P availability and waterlogging conditions resulting from flooding. In the absence of P limitations and frequent flooding (i.e., in P rich upland areas) trees thrive and have competitive advantage with respect to marsh vegetation. In P poor lowland areas where trees cannot establish and survive the landscape is dominated by herbaceous vegetation (sawgrass). Because the growth rate of herbaceous vegetation far exceeds the rate of tree growth, the growth of herbaceous vegetation is assumed to be instantaneous and is not explicitly modeled.

Thus, tree growth at each point on the landscape is assumed to be a function of P availability and elevation and independent of grass density. We model tree dynamics using a logistic equation (D'Odorico et al., 2011),

$$\frac{dT}{dt} = \alpha T(T_{cc}(P, \Delta h) - T) \quad (1)$$

with the carrying capacity,  $T_{cc}$ , limited by available phosphorus and dependent on elevation relative to the water table

$$T_{cc} = \begin{cases} \left(1 - \frac{1}{1 + aP^b}\right) \left(1 - \frac{1}{1 + c(\Delta h - k)^2}\right) \\ 0 \text{ if } \Delta h < k \end{cases} \quad (2)$$

Parameter values with  $a = 0.021$ ,  $b = 3$  from DeLonge et al. (2008). Following D'Odorico et al. (2011),  $c = 30 \text{ m}^{-1}$ , and the distance to the water table at which no tree growth is possible,  $k$ , is set to  $-0.4 \text{ m}$  based on data from Sah et al. (2004). Enhanced peat/soil accumulation due to the presence of woody biomass is modeled with respect to the elevation above the water table  $\Delta h(r, t)$ .

$$\frac{d(\Delta h)}{dt} = \omega_{\Delta h}(T, r) - \gamma_r(\Delta h - k) \quad (3)$$

The water table, is assumed to be spatially homogenous, with  $\gamma_s$  controlling soil formation and  $\gamma_r$  loss of soils due to respiration. The spatial term  $\omega_{\Delta h}(T, r)$ , describes the increase in soil accumulation due to the presence of a tree of biomass  $T$ , at any point  $r'(x', y')$  at distance,  $|r - r'|$  from the point  $r(x, y)$  in the landscape. The effect of such a tree decays as a function of the distance from  $r'$  according to a Gaussian function with parameter  $d_r$ . In other words  $d_r$  determines the radius of influence of a tree on soil accumulation. Thus,

$$\omega_{\Delta h}(T, r) = \int_r \left[ \gamma_s \exp \left[ -\left( \frac{r - r'}{d_r} \right)^2 \right] \right] T(r', t) dr' \quad (4)$$

The rate of phosphorus accumulation is dependent on atmospheric phosphorous deposition,  $\beta$ , assumed homogenous across the

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