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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 hydroperiod 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 (kg m^{-2}), and peat/soil accretion relative to the water table, Δh (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 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 γ_s controlling soil formation and γ_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, β , assumed homogenous across the

landscape and the accumulation due to the presence of tree biomass $\omega_p(T, r)$. Loss of phosphorous is assumed to be proportional (with proportionality constant, k_p) to the amount present at a given location of the landscape. In this manner, while not explicitly resolving P in pore water and surface flows,

$$\frac{dP}{dt} = \omega_p(T, r) + \beta - k_p P \quad (5)$$

The kernel function, $\omega_p(T, r)$, describes the spatial effects that an area with woody biomass has on phosphorous accumulation and depletion. Here, while not explicitly modeled, trees can draw down the water Table relative to the water levels in the surrounding marsh, generating an advective flux toward the tree islands (Sullivan et al., 2014). This advective flux is represented implicitly to provide both long distal inhibition of phosphorous on the landscape (the system is overall P limited) as well as contribute to phosphorous accumulation on tree islands (Ross et al., 2006; Wetzel et al., 2009). Other methods of accumulation also contribute to enhanced phosphorous on tree islands such as increased canopy trapping, and guano deposition (Givnish et al., 2008). Regardless of the specific mechanism we expect P availability to be higher in the surroundings of existing trees (short range facilitation) and lower at distance. Because P is advected by the flow, the kernel function expressing the effect of trees on P concentrations is not a symmetric function of the distance from the tree but exhibits a drift in the flow direction, x . Therefore we express the spatial interactions using a kernel function as follows,

$$\omega_p(T, r) = \int_{r'} \left[b_p (1 - \psi^2)^{3/2} \exp \left[- \left(\frac{(r - r')(1 + \psi(x - x'/r - r'))}{d_p} \right)^2 \right] - \varepsilon b_p (1 - \psi^2)^{3/2} \exp \left[- \left(\frac{(r - r')(1 + \psi(x - x'/r - r'))}{\chi d_p} \right)^2 \right] \right] T(r', t) dr' \quad (6)$$

where the b_p term specifies the magnitude of facilitation, d_p the distance at which maximum facilitation occurs; inhibition is defined to be some fraction ε of the facilitation b_p and χ is the ratio between the distance where maximum inhibition occurs in terms and d_p .

The term ψ in the exponentials describe the amount of 1-directional anisotropy in the system present due to flow conditions in the x direction. A symmetric kernel function arises when $\psi = 0$. The coefficient term $(1 - \psi^2)^{3/2}$ allows for the first moment of the kernel functions for a set parameter space $\{b_p, d_p, \varepsilon, \chi\}$ to remain constant $\omega_{p0, symmetric} = \omega_{p0, anisotropic} = \omega_{p0}$, with varying degrees of anisotropy ($0 \leq \psi < 1$). Such anisotropy is assumed to occur during increased flow periods which occur during wet season with P advection in the down flow.

2.1. Parameter constraints

Rate terms $\alpha = 0.0019$, $\omega_{p0} = 0.68$ ($\text{kg ha}^{-1} \text{y}^{-1}$), and $k_p = 0.07$ are identical to those in from D'Odorico et al. (2011). The soil accumulation rate was taken as $\omega_{\Delta h0} = 0.0037 \text{ my}^{-1}$ (Orem et al., 2003). The parameters controlling the rates of change in Eqs. (1), (3) and (5), are expected to be related as $\omega_{p0} > \alpha > \omega_{\Delta h0}$. The anisotropic term, ψ , was constrained to a value of 0.67 by setting the aspect ratio of facilitation in the kernel function to 3.1 to match the mean tree island aspect ratio which varied from 3.39 in 1940 to 2.87 in 1995 (Supplementary material). The effect of a collection of woody plants on the soil accretion rate at distance depends on many factors, rooting diameter, crown

diameter, and litterfall among others. Here we assume this spatial effect is severely limited beyond a 10 m radius of a collection of woody biomass and a value of $d_r = 10$ m was utilized. The effect of a tree island on phosphorous accumulation on a landscape was limited by both aspect ratio and average tree island areal extent (Supplementary material), which constrained d_p to around 50 m. χ was set to 1.01. The magnitude of inhibition, ε , is then limited by above parameter space, and the first moment of the kernel function, $\omega_{p0} = 0.68$ ($\text{kg ha}^{-1} \text{y}^{-1}$), but is effectively approximated as $1/\chi^2$.

2.2. Steady state solutions

Homogenous steady state solutions are obtained from Eqs. (1), (3), and (5) in the case of spatially and temporally constant state variables, T , and Δh ; after simple manipulations the equilibrium solutions P_{eq} , Δh_{eq} and T_{eq} can be expressed as

$$P_{eq} = \frac{\omega_{p0} T_{eq} + \beta}{k_p} \quad (7)$$

$$\Delta h_{eq} = \frac{\omega_{\Delta h0} T_{eq} + k}{\gamma_r} \quad (8)$$

$$0 = \alpha T_{eq} \left[\left(1 - \frac{1}{1 + c(\Delta h_{eq} - k)^2} \right) \left(1 - \frac{1}{1 + a(P_{eq})^b} \right) - T_{eq} \right] \quad (9)$$

where ω_{p0} and $\omega_{\Delta h0}$ are the first moment of the kernel functions, $\omega_{p0} = \pi(b_p d_p^2 - \varepsilon b_p d_p^2 \chi^2)$ and $\omega_{\Delta h0} = \pi \gamma_s d_r^2$ respectively.

Eqs. (7) and (8) can be substituted into Eq. (9) to arrive at an equation defining the equilibria states of tree biomass

$$0 = T_{eq} \left[\left(1 - \frac{1}{1 + c((\omega_{\Delta h0}/\gamma_r) T_{eq})^2} \right) \left(1 - \frac{1}{1 + a(\omega_{p0} T_{eq} + \beta/k_p)^b} \right) - T_{eq} \right] \quad (10)$$

These equilibria depend on the first moment of the kernel functions $\omega_{\Delta h0}$, ω_{p0} , soil respiration (i.e., γ_r), atmospheric phosphorous deposition β and the loss rate of phosphorous k_p . Real solutions of Eq. (10) include the trivial solution $T_{eq} = 0$; other unstable or stable equilibria exist under different model parameterizations (i.e., $0.35 < \omega_{\Delta h0}/\gamma_r < 1.4$, and $0 < \beta/k_p < 5 \text{ kg ha}^{-1} \text{y}^{-1}$). As such, we can examine the solutions of Eq. (10) as a function of $\omega_{\Delta h0}/\gamma_r$ (which expresses the relative importance of soil accretion and loss), and $\omega_{p0} T_{eq} + \beta/k_p$ (i.e., the rate of phosphorous accumulation, relative to the rate of phosphorous loss) in order to find unstable or stable equilibria.

2.3. Numerical simulations

Non-spatially explicit trajectories of the coupled Eqs. (1), (3), (5) can be examined to determine what initial elevations and woody biomass might be necessary for the slow establishment of trees. Eqs. (1), (3), and (5) are solved using a 7–8th order Runge–Kutta approach within the parameter range: $0.35 < \omega_{\Delta h0}/\gamma_r < 1.4$, and $0 < \beta/k_p < 5 \text{ kg ha}^{-1} \text{y}^{-1}$.

Full spatial numerical simulations were performed on a half year time step for a 3500 year period on a 256 by 256 grid with a 5 m grid size. Simulations were seeded with a heterogenous landscape randomly generated around initial values, Δh , P , and T .

2.4. Fires

The impact of fire on the landscape is modeled as a process which removes some proportion of the woody biomass, and soil elevation. Fires frequency is bounded at 3 years which is roughly the time needed for adequate fuel to develop with a severe burn occurring approximately 6–15 years (Gunderson and Snyder, 1994; Beckage and Platt, 2003; Beckage et al., 2003). While fire return interval indicates high likelihood for burns to occur, fire rotation for a point on the landscape is roughly 33.6 years (Taylor, 1981). As such, fire arrival times are modeled as a Poisson process and their recurrence interval is exponentially distributed with mean of 33.6 years. Tree island edges are assumed to be more susceptible to fires (Matlaga et al., 2010), as some evidence (Silveira, 1996) suggests that the core portion of larger tree islands are also less impacted by fires and specified an approximate 30 m distance from a tree island edge as the distance at which fires have little impact in their modeling efforts. Contrastingly, peat smoldering interior to tree islands can be more severe than near the edges (Matlaga et al., 2010). With larger islands characterized by higher elevations, fire severity on peat elevations is modeled simply as a function of relative distance to the water table. Thus after a fire occurrence the ground surface elevation (with respect to the water surface) decreases from an “old” to a “new” value as

$$\Delta h_{\text{new}} = \Delta h_{\text{old}} - \left[\frac{\Delta h - h_{\text{min}}}{h_{\text{max}} - h_{\text{min}}} \right] r_{\Delta h} \quad (11)$$

where $r_{\Delta h}$ is the maximum potential burn depth set here to 5 cm. The parameters h_{max} , and h_{min} , determine the relative elevation where fires have the maximum (0.5 m), and the minimum impact (−0.4 m), respectively.

The effects of fire on woody biomass are modeled to be dependent on distance to an edge. In areas affected by a fire occurrence tree biomass is reduced by an amount ΔT proportional to the pre-burn value of T ,

$$\Delta T = \bar{T}_r T \quad (12)$$

The proportionality coefficient, \bar{T}_r , is calculated as the spatial average within radius of 30 m from each point on the landscape of a fire reduction term T_r . T_r varies from point to point and accounts for the fact that fires are expected to be more intense at the edges of a tree patch where flammable grass biomass is more abundant (during the dry season) than in the middle of a closed canopy area where grass fuel is either scarce or lacking. Thus T_r depends on the local value of T , and such dependency is here expressed by a step function with respect to a critical value of biomass T_{cr} (set here to 0.1).

$$T_r = \begin{cases} 0 & \text{if } T \geq T_{\text{cr}} \\ 0.5 & \text{if } T \leq T_{\text{cr}} \end{cases} \quad (13)$$

In this manner, as the tree biomass within a 30 m radius of a point begins to exceed the critical value, that point is “internal” to an island, or in this sense, is at least a distance of 30 m from an edge or low biomass region and $\bar{T}_r \rightarrow 0$ resulting in no burn for that point. As more points with low or no tree biomass enter within the 30 m radius, $\bar{T}_r \rightarrow 0.5$. With this approach, biomass near the “edges” of tree islands are most impacted by fires, with fires having little to no impact on “internal” regions. The total simulation area is considered affected when a fire occurs.

3. Results

Self organization and pattern formation typically require both a local or short range facilitation (or “activation”, i.e., the positive feedbacks discussed before) and long range inhibition (e.g., Borgogno et al., 2009). These activation-inhibition dynamics (i.e., local facilitation and long range competition) have the effect of destabilizing the homogeneous state of the system. Known as “symmetry-breaking instability” this process is often a mechanism of self-organized pattern formation in nature (e.g., Murray, 2002). The inhibition resulting from P limitations is a decreasing function of atmospheric phosphorus deposition. It is therefore important to determine the range of parameter values within which self-organized patterns may emerge. In order to determine where in

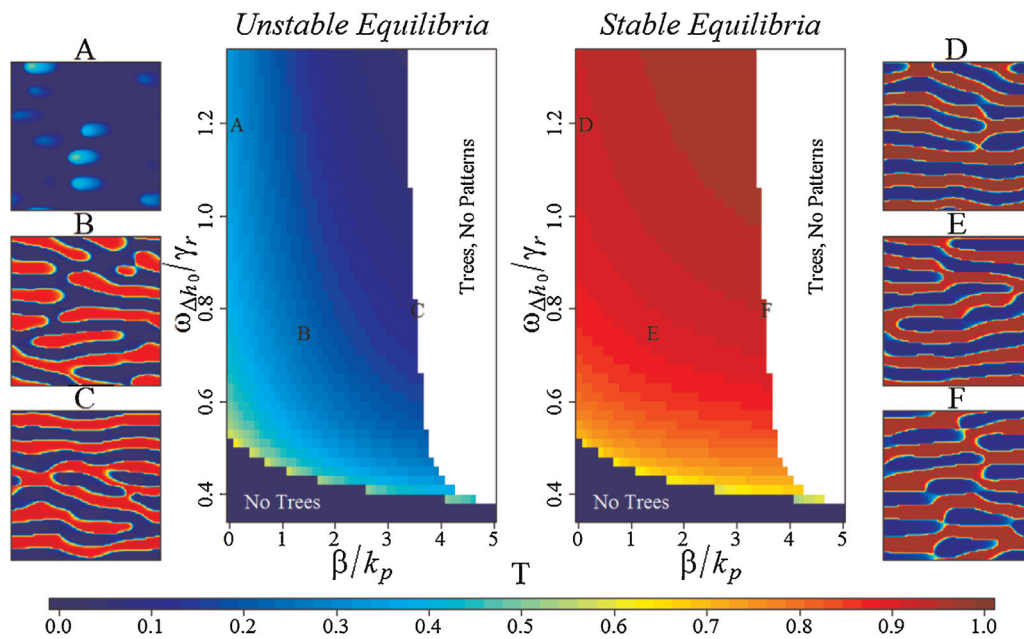


Fig. 1. Emergence of different patterns through self organization from unstable (A–C) and stable (D–F) equilibria of tree biomass (T) under the primary model parameters soil formation to loss ratio, $0.35 < \omega_{\Delta h_0}/\gamma_r < 1.4$, and atmospheric phosphorous deposition to loss ratio $0 < \beta/k_p < 5 \text{ kg ha}^{-1} \text{ y}^{-1}$. The white regions define the parameter space where patterns fail to form under small perturbations. Insets (A–F) display that pattern emerging from unstable (A–C) and stable equilibria (D–F) at corresponding locations in the atmospheric phosphorous deposition to loss ratio and soil formation to loss ratio phase space.

the parameter space self-organized landscapes have the potential to occur we perform a linear stability analysis and examine the propagation of small perturbations to the steady state homogeneous solution of Eqs. (1), (3), and (5) (i.e., Eqs. (7)–(9)). To simplify the mathematical development of this stability analysis we consider a case with no anisotropy in the kernel function and no fires, and search for conditions of marginal stability (Supplementary material), while we rely on numerical simulations for the anisotropic case with fires. Within an interval of the parameter space ($\omega_{\Delta h_0}/\gamma_r, \beta$) small perturbations propagate and patterns develop, whereas with higher atmospheric phosphorus deposition rates (i.e., higher β) and soil formation relative to soil respiration rates ($\omega_{\Delta h_0}/\gamma_r$), the effect of the inhibition becomes negligible and self-organized patterns are unable to form (Fig. 1). As noted, linear stability analysis (Fig. 1, central panels) was here performed on the isotropic case. Numerical simulations of the anisotropic dynamics show the emergences of patterns with elongated structures (maze like or island) in the direction of the flow.

The linear stability analysis (e.g., Borgogno et al., 2009; Supplementary materials) provides some indications on whether the stable homogeneous state obtained as the solution of Eqs. (7)–(10) is actually unstable with regards to small perturbations and patterns may emerge for a given set of parameters. However, it does not predict the pattern geometry. Numerical simulations show substantial differences in the shape of the emerging patterns depending on the initial conditions (e.g., D’Odorico et al., 2006). Interestingly, maze-like, quasi-parallel patterns form (Fig. 1D–F) when the stable homogeneous states (e.g., stable equilibria solutions of equation 10, or high biomass forested landscapes) are used as the initial condition. Whereas, starting from the unstable homogeneous equilibrium state (e.g., unstable equilibria solutions of equation 10, low biomass forested landscape), isolated patches of forests to maze-like patterns appear (Fig. 1A–C). However, depending on the parameters, model runs with no spatial interactions reveal that with minimal tree biomass, an increase in the relative elevation of the ground surface (with respect to the water table), induced by drought alone may not be enough to promote the initiation of tree island formation (Fig. 2).

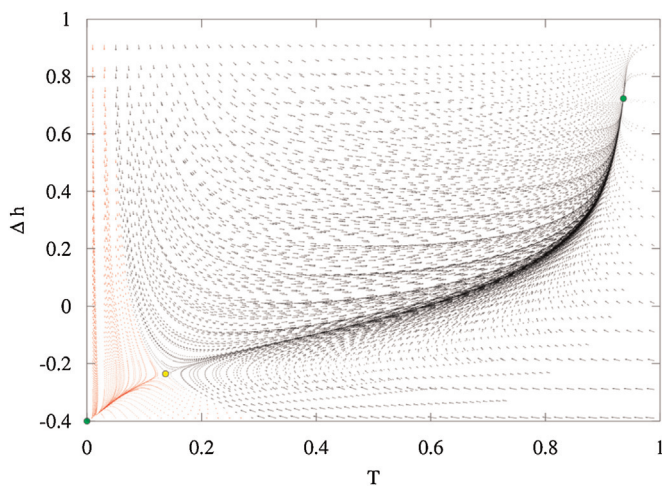


Fig. 2. Trajectories in the phase space of scaled tree biomass (T) and height relative to the water table (Δh in meters) with $\omega_{\Delta h_0}/\gamma_r = 1.2$ and $\beta/k_p = 1.4$. Unstable equilibria (yellow circle), and stable equilibria (green circles) are clearly evident. Red trajectories proceed towards submerged conditions with no tree biomass while black trajectories proceed towards a stable elevated region with tree biomass. Note that for low enough initial tree biomass ($T < 0.06$), even high elevations are unable to support long term establishment of trees. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

In fact, at low atmospheric phosphorus deposition, even treeless islands with relatively high elevations with respect to the water Table (e.g., severe drought conditions for prolonged periods) remain stable as grass-dominated communities. Examples of treeless areas of relatively high elevation compared to the surrounding marsh are found in the Everglades and known as “ghost islands”. Once functioning tree islands, ghost islands formed after prolonged high water conditions, which caused the decline and loss of flood-intolerant woody species. Lowering water levels in some of these areas has not resulted in the reestablishment of trees. Islands lost to burning in the recent past also have not been observed to return to a forested state.

Increasing atmospheric phosphorus deposition causes self-organized patterns to switch from islands to a maze type pattern into raised ridges (Fig. 3) and then finally into fully covered forested landscape (not shown). Maze like tree patterns and fully covered forested landscapes are not observed in the Everglades, presumably because of the effect of phosphorus limitations and fires. In fact, these patterns are significantly modified by the fires: at low atmospheric phosphorus deposition rates fires can fully inhibit the formation of tree islands (Fig. 3). Moreover, patterns emerging when the effect of fires is accounted for differ in that fire tends to (1) reduce island size both laterally and vertically, (2) maintain distinct island edges, effectively inhibiting downstream elongation with the development of raised ridge patterns and (3) remove smaller islands from the landscape.

4. Discussion

The complexity of the Florida Everglades landscape is governed by interacting feedbacks and processes involving soil accretion, phosphorus accumulation, and vegetation dynamics, which act under the effect of dynamic drivers such as fire, climate and hydrologic fluctuations. As an example, the central portion of Water Conservation Area 3A is roughly a 500 square mile area in which tree islands have been stable during the last century, while drained areas of northern WCA 3 and northeastern Shark Slough in Everglades National Park have experienced near total loss of tree islands in the last 100 years. The soil accumulation and P accumulation patterns in these different areas are hypothesized to be drivers of either tree island stability or rapid loss among these different areas. Tree establishment and growth in the Everglades requires phosphorus concentrations above those occurring in the expansive marshes of this ecosystem. It has been argued that trees might act as “ecosystem engineers” (Jones et al., 1994) and contribute to the formation and maintenance of their own habitat by increasing P availability through positive feedbacks with atmospheric deposition (D’Odorico et al., 2011). Likewise, trees tend to be flood intolerant and to thrive only in more elevated areas that are therefore exposed to less frequent flooding than the surrounding marshes. Because of their high productivity woody plants are able to contribute to soil accretion through organic matter accumulation. Thus, another positive feedback should exist between tree establishment/growth and island accretion (D’Odorico et al., 2011; see Sullivan et al., 2013 for observations supporting this conclusion). Both feedbacks can explain the co-emergence of marsh communities in low elevation areas with low P and tree islands (treed areas with higher elevation and higher P) as alternative stable states of the landscape (D’Odorico et al., 2011). Our results show that this bistability manifests in organized patches of tree islands and marshes on the landscape depending on how the spatial interaction among soil accretion, tree growth and P deposition are represented.

It should be noted that Everglades P dynamics are highly complex, involving many biotic and abiotic processes that produce anisotropic distributions across the landscape. Landscape-scale

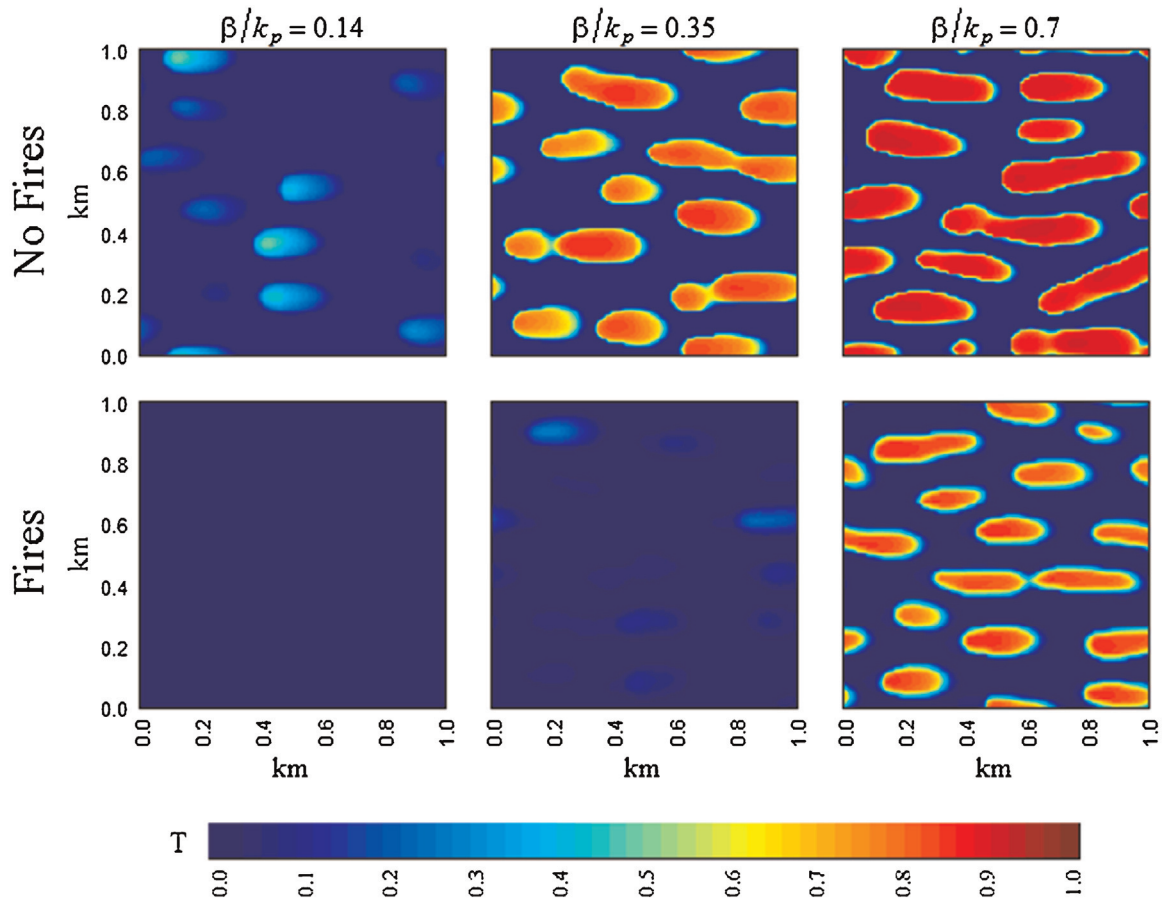


Fig. 3. The effect of fires and increasing β/k_p on pattern formation.

data needed to parameterize a mechanistic, spatial model is not currently available, yet models of tree island patterning are needed to improve understanding of their changing distributions and the potential consequences of hydrologic management strategies.

As landscape scale data is not available, we instead apply a kernel function as a means to simulate local concentration of nutrients and biomass (positive feedbacks) and distal inhibition (negative feedbacks), as has been done for other patterned systems (Lefever and Lejeune, 1997; Lejeune et al., 2002; D'Odorico et al., 2006) and which reflects the conditions observed within the Everglades (i.e. isolated tree patches with very high P).

This model is formulated to place the D'Odorico et al., 2011 model in a spatial context, thereby allowing for examination of the types of landscape patterns generated by altering the relative strengths of feedbacks between tree growth, soil formation and P-concentrating mechanisms occurring at the scale of individual tree islands. The model structure also allows us to simulate disturbances to tree biomass, similar to what happens during fire events and examine the emergence, or lack thereof, of patterns.

Self-organized pattern formation resulting from instability of a uniform configuration typically requires that the local facilitation of tree vegetation (either by increasing P availability or soil elevation) translates into a negative feedback (or "inhibition") at greater distances. In the absence of this inhibition no process would preclude the entire landscape in the model from turning into woodlands. However, this would be unrealistic result given the P limitations in the Everglades. We account for such limitations as well as for the positive feedback between trees and P deposition through the use of the kernel function (6) introduced into Eq. (5) to

represent the spatial interactions. For low levels of background P deposition (β), these spatial interactions lead to the emergence of Tree Island and maze-like patterns. The drift effect of deposition in the presence of the one-directional flow was accounted for through anisotropy in the kernel. In the presence of such anisotropy tree islands grow with elongated shapes aligned to the flow (Fig. S1).

Tree island patterns on the landscape depend on the fire regime. Fires tend to reduce the extent and modify the geometry of treed areas (Hanan et al., 2010; Ruiz et al., 2013) as shown in Fig. 3. Smaller islands do not form and maze-like patterns are converted into isolated tree islands in simulations including fire. The impacts of large size fires on soil loss (Taylor, 1981), timing of larger fires corresponding to lower water levels associated with the La Nina phase of the southern oscillation (Beckage et al., 2003) and the significant loss of peat soils, and destruction of a large number of tree islands during the Mustang Corner fire in May 2008 (Ruiz et al., 2010) all indicate the important role of fires in shaping the landscape. Furthermore, analysis of dry season fire frequency and tree island loss in the Shark River Slough (Supplementary material) indicate both declines in total tree island area (Supplementary material, Fig. S2) as well as fewer tree islands in areas where dry season fires are more frequent over a six decade period. The combination of fire dynamics and P limitation may explain why maze like patterns are not found in the Everglades ridge and slough system. Since the model framework does not clarify the magnitude of evapotranspirational pumping or other P concentrating processes needed to create long-range inhibition, or the relative importance of locally deposited P versus accumulated P from

surrounding areas, the conclusions regarding the role of additional factors (fire, reduced water levels) on tree island persistence in the landscape must be drawn carefully.

Rather than destabilization of a relatively homogenous landscape into patterns through self organization mechanisms, patterns may also result from a random initial condition with trees scattered across the landscape as a Poisson type process (D'Odorico et al., 2006). This can be likened to the random occurrence of a floating peat mat becoming the nursery for development of a pop-up tree island and/or the initial distribution of small raised bedrock limestone areas. In this case, island evolution on the landscape is still a function of landscape productivity, bio-geomorphological feedbacks and fire, however, the number, shape and extent of islands on the landscape is also determined by a more stochastic process of tree island initiation that has not been included in this study.

5. Conclusion

Different pattern geometries are obtained by perturbing the stable or the unstable homogeneous state, indicating that the history of the trajectory of the landscape in the phase space determines the ultimate form of the spatial patterns rather than a single stable patterned landscape to which all trajectories converge, at least within the time frame of tree island formation in the Everglades fresh water system. As such, these modeling results suggest that the extant patterns have formed by emerging up, via some successional sequence (Larsen et al., 2011), through an unstable equilibrium point rather than being formed from destabilization of a more contiguous forested landscape. The gradual development from tree islands across the Everglades landscape is consistent with both the geological history of vegetation development in the region (Willard et al., 2001) as well as the comparatively higher amount of forest coverage in nearby Big Cypress National Preserve—a similarly low nutrient marsh (Sobczak et al., 2011) that has been developing over a much longer geologic timeframe (Thornberry-Ehrlich, 2008). This finding coincides with the theories of tree establishment during prolonged droughts on raised elevation areas (Sklar and Van Der Valk, 2002).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecocom.2016.03.007>.

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