Spatial pattern formation of coastal vegetation in response to external gradients and positive feedbacks affecting soil porewater salinity: a model study

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Abstract Coastal vegetation of South Florida typically comprises salinity-tolerant mangroves bordering salinity-intolerant hardwood hammocks and fresh water marshes. Two primary ecological factors appear to influence the maintenance of mangrove/hammock ecotones against changes that might occur due to disturbances. One of these is a gradient in one or more environmental factors. The other is the action of positive feedback mechanisms, in which each vegetation community influences its local environment to favor itself, reinforcing the boundary between communities. The relative contributions of these two factors, however, can be hard to discern. A spatially explicit individual-based model of vegetation, coupled with a model of soil hydrology and salinity dynamics is presented here to simulate mangrove/hammock ecotones in the coastal margin habitats of South Florida. The model simulation results indicate that an environmental gradient of salinity, caused by tidal flux, is the key factor separating vegetation communities, while positive feedback involving the different interaction of each vegetation type with the vadose zone salinity increases the sharpness of boundaries, and maintains the ecological resilience of mangrove/hammock ecotones against small disturbances. Investigation of effects of precipitation on positive feedback indicates that the dry season, with its low precipitation, is the period of strongest positive feedback.

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Introduction

Ecotones, or the abrupt transitions between vegetation types, have long been a focus of study in ecology (e.g., Clements 1907; Transeau 1935). While many transition zones, or ecotones, between floristic types are broad and diffuse, some are remarkably narrow (e.g., Oosting 1955; Walker et al. 2003). Frequently, this can

be attributed to steep environmental gradients, with further enhancement due to competition. For example, the sharp altitudinal boundary between hardwood and boreal forest at about 792 m in the Green Mountains of Vermont (and other elevations elsewhere) is attributed by Siccama (1974) in part to a climatic discontinuity near that elevation (see also Shugart et al. 1980). The boundary is reinforced by modifications of the local environment on the boreal side by the spruce and fir trees, which make conditions inhospitable for hardwoods. Similar sharp ecotones have been found in tropical montane forest (e.g., Martin et al. 2011).

The mechanism by which plants can modify their local environment to create a sharp boundary between them has been termed a 'vegetation switch' (Wilson and Agnew 1992). According to this concept, two vegetation types are each capable of occupying a particular area, and each capable of altering the local environment in its own favor. Examples of ecotones shaped by such feedbacks of vegetation on the environment include boundaries between fire-dependent (e.g., savannah) and non-fire-dependent communities, in which the former have been hypothesized to have evolved to be more flammable (e.g., Mutch 1970); treeline ecotones along smooth environmental gradients in alpine ecosystems (Wiegand et al. 2006), where modeling indicates that abrupt changes in tree density were due to positive feedback involving both facilitation and growth inhibition; the 'ridge and slough' landscape in the Everglades, in which sawgrass creates slightly higher elevations through soil accretion that separates it from more aquatic vegetation like water lily, bladderwort, and spike rush (Larsen et al. 2007); and bog habitats, in which mediation of light availability (Clymo and Hayward 1982), acidity (van Breemen 1995), temperature (Eppinga et al. 2009), and nutrient availability (Eppinga et al. 2009) have all been hypothesized to play a role in sharpening boundaries between Sphagnum and vascular plants.

Another example of the sharpening of ecotones between two vegetation types through their different effects on the environment involves mangrove vegetation and hardwood hammock vegetation (tropical hardwood trees) in southern Florida coastal areas. Typically, mangrove and hardwood hammock trees are not interspersed. Sharp 'ecotones' (transition zones) typically separate the salinity tolerant mangroves from the salinity intolerant hardwood

hammock species, which occupy the similar geographical areas of southern Florida (Snyder et al. 1990; Sternberg et al. 2007). In this case, although hammocks tend to be at slightly higher elevations, the primary environmental factor that affects their competition is soil salinity. The following mechanisms underlie the normal stability of the ecotone. Both mangroves (*Rhizophora mangle*, *Avicennia germinans*, *Laguncularia racemosa*) and hammock species (e.g., *Bursera simaruba*, *Coccoloba diversifolia*, *Eugenia axillaris*, *Sideroxylon foetissimum*, *Simarauba glauca*) obtain their water from the vadose zone (unsaturated soil zone). In coastal areas this vadose zone is underlain by highly brackish ground water, so that evapotranspiration, by depleting water in the vadose zone during the dry season, can lead to infiltration by more saline ground water. Although hardwood hammock trees tend to decrease their evapotranspiration when vadose zone salinities begin to increase, thus limiting the salinization of the vadose zone, mangroves can continue to transpire at relatively high salinities. Thus, each vegetation type tends to promote local salinity conditions that favor itself in competition, which helps explain the stability of sharp boundaries between the types, despite a very gradual elevation gradient.

A number of individual-based models (IBMs) have been developed for mangrove forest dynamics (Doyle and Girod 1997; Chen and Twilley 1998; Berger and Hildenbrandt 2000; Doyle et al. 2003), and their applications to aspects of forecasting potential effects of global climate change have been reviewed (Berger et al. 2008). In particular, Doyle and Girod (1997) used computer simulations of their SELVA-MANGRO model of mangroves to project possible inland migration of mangroves in along the southern Florida coastline in response to projections of sea level rise. This was done using projections of the changing locations of tidal influence, given the topography of southern Florida and the assumption of a continuation of the current rate of sea level rise. However, despite this and numerous other contributions to understanding of mangrove dynamics that have come from these IBMs, we know of no applications that focus strongly on the development and maintenance of ecotones between the mangroves and other vegetation, particularly the type of hardwood hammock vegetation typical of southern Florida.

The overall aim of our study is to find out how the hypothesized 'vegetation switch' interacts with underlying environmental gradients to form sharp ecotones between mangroves and hardwood hammock vegetation. More specifically, we ask the following questions: Will the sharp boundary still exist if the self-reinforcing feedback is taken out of the model? Could the self-reinforcing feedback alone cause sharp boundaries between vegetation types under completely uniform environmental conditions? This is in the spirit of using modeling to understand the causes of patterns observed in nature (Grimm et al. 2005).

Methods

To address these issues, we built the Spatially Explicit Hammocks and Mangroves (SEHM) model, an IBM that simulates the spatial pattern of the ecotone between mangrove and hammock vegetation. SEHM omits many details that more comprehensive tree dynamics models include, such as community dynamics and competition for nutrients, in order to focus on the effects of salinity on competition between two vegetation types. We use the Overview, Design Concepts, and Details protocol (Grimm et al. 2006, 2010) to describe our model. A complete description of the model is available in Appendix A in the supplementary material. Here, we provide only an overview of SEHM.

We simulated intra- and inter- specific competition between mangroves and hammocks, including the effects of the underlying hydrodynamics of tides, soil porewater and ground water. The model links two main components, an individual-based vegetation dynamics submodel and a grid-based hydrodynamics submodel, which operate on different computational time steps, a daily time scale for physiological processes of water uptake by plants, which changes soil salinity, and a monthly time scale for vegetation dynamics. During each monthly time step, every tree can have a growth increment that is a function of neighborhood competition, and the salinity of the particular spatial cell or cells occupied by the tree's roots. Then, after a tree reaches maturity, new recruits are produced at monthly intervals by the tree. The appearance of successful new recruits depends, in part, on the salinity of the soil porewater and also on neighborhood competition. At the end of the monthly time step, death may occur due to size-dependent factors, such as low d.b.h. (diameter at breast height of tree), or from reduced growth rate caused by competition or salinity. Information on the total amount of root biomass distributed in each cell is passed to the hydrodynamics submodel, which updates water and salinity on daily time steps. Monthly average values of salinity in each cell, which affect tree growth and seedling establishment, are then returned to the vegetation dynamics submodels.

Simulation experiments

Vegetation simulations were performed in a square area that represents 1 ha, with an initially random distribution of an equal number of mangroves and hammock trees across the area. Salinity dynamics were simulated in a grid-based system with 100×100 cells. Each cell represents a 1×1 m^2 segment within a landscape typical of Florida's coastal topography, which is assumed in the model to increase locally in elevation from the coast at an average of 10 mm per meter, following (Sternberg et al. 2007; Teh et al. 2008). Although this elevation gradient is much greater than the large-scale regional gradient from the coast inland, it might not be atypical of local elevation gradients.

To investigate the relative contributions of the positive feedback mechanism and external environmental factors to the sharp ecotone between mangroves and hardwood hammocks, we used SEHM to perform two experiments.

Experiment 1

The first simulation experiment included simulations to distinguish the relative effects of the internal positive feedback mechanisms and external environmental factors. Four different trials were performed within Experiment 1. In the first trial, we used SEHM with all components of the model active, to examine whether patterns similar to field observations emerged from an initially random distribution of trees, as was done with MANHAM (Sternberg et al. 2007; Teh et al. 2008). In this full model simulation mangroves and hardwood hammock trees gradually segregated into two homogeneous stands, with a sharp boundary between them. We measured the degrees of sharpness

(*SI*) by means of technique borrowed from the entropy of mixing. Mangroves and hardwood hammocks were considered as analogous to two substances mixing on a surface. Maximum entropy (E_{max}) represents perfectly random mixing of two vegetation types (Macchiato et al. 1992). The *SI* was calculated by,

$$SI = \omega \left(1 - \frac{E}{E_{max}} \right)$$

where E the is entropy of the system, which is calculated by $E = -\sum p_i \log p_i$, and p_i is the fraction of one species (e.g., mangroves) in a spatial cell i with respect to the total number of mangrove trees. (For the purpose of calculating the p_is, we summed trees across the rows of cell, so that the 100×100 grid of cells reduced to a single column of 100 cells along the elevation gradient.) The value of E would become E_{max} if every cell along the column had the same fraction p_i. The minimum E would occur when the fractions were all equal to 1 below some cell number and all equal to 0 in and above that cell number. The parameter ω is a normalization coefficient based on an optimally sharp ecotone, which corresponds to mangroves being evenly distributed below mean tidal height and hardwood hammocks evenly distributed above mean tidal height.

In the second trial, we removed the feedback between vegetation and soil porewater salinity. Vegetation growth rate and regeneration rate were still able to be affected by soil porewater salinity. But soil porewater salinity was not able to be affected by changes in vegetation; in particular, a constant water uptake (or evapotranspiration) of 2.1 mm/day was assumed uniformly across the model landscape. We explain the choice of 2.1 mm/day in more detail in the Results and Discussion. Other values of water uptake ranging from 1.0 to 3.0 mm/day were also simulated. A sign test was used to quantify the difference in the degree of sharpness of the ecotone for the first two trials.

In the third trial, we kept only the self-reinforcing feedback, and made the underlying environmental conditions completely uniform across space, such that there was the same elevation for all the cells and there was no tidal effect. If self-reinforcing feedback alone can maintain a sharp boundary, we would expect aggregation patterns of the two vegetation types to emerge; that is, a pattern of homogeneous clumps of vegetation of each type. We measured the degree of clumpedness of overall landscape patterns by focusing on the aggregation of the rarer vegetation (whether mangrove or hammock) on the model landscape in any given simulation. In this technique, the dominant vegetation type was considered as background habitat, and the trees of the rare vegetation type were the test objects. Simulations leading to fewer than 5 individuals of the rare type on the landscape were considered as monospecific and not used to calculate aggregation indices. For simulations leading to coexistence of the two types on the model landscape, each individual tree of the rare type was identified as either the same as or different from each of its neighbors within 3 meters. The aggregation index was computed by dividing the links between trees of the same vegetation type by the total number of links. Since the third trial required the assumption of a constant water table salinity and distance to water table, we also chose other higher and lower constant water table salinities and distance to water table, separately. Nine sets of constant values were simulated. A Kruskal–Wallis test, followed by an all-pairwise comparison of the Dwass–Steel–Critchlow–Fligner test, was used to test the effects of the two factors.

In the fourth trial, similar to the use of a control group in field experiments, we removed positive feedback and simulated the model under uniform environmental conditions. In this completely uniform spatial arena, without feedbacks, we expected a relatively intermixed distribution between the two vegetation types for this trial. All the trials are repeated 20 times, estimated by power analysis.

Experiment 2

In the field, soil porewater salinity differs between the wet and dry seasons, although the spatial pattern of mangrove/hardwood hammock does not respond to salinity changes on a short time scale (Semeniuk 1983). We predicted that it is primarily high salinity during the dry season that defines the long-term ecotones between the hardwood hammock community and the mangroves, because salinity stress should be the highest then and because there is insufficient time for vegetation to shift back towards the hardwood hammock community during the following wet season.

To investigate seasonality of precipitation on the distribution of mangroves and hardwood hammock we first tested the effect of precipitation on spatial pattern. All components of the SEHM model were working the same as in the third trial in experiment 1, which removed environmental gradients, except for experimental control of the precipitation amount. We also tested the effect of precipitation using the full version of SEHM, to completely understand the interaction between positive feedback and precipitation effect on spatial pattern. Finally, we investigated the monthly variation of soil porewater salinity after the vegetation distribution reached equilibrium.

Results

Comparison of mechanisms (Experiment 1)

The combined mechanisms of positive feedback and an environmental gradient (first trial) resulted in a clear boundary between hammocks and mangroves (Fig. 1a), and showed a strong resemblance to typical patterns of coastal vegetation distribution. The model contains both tidal effects, which directly influence soil porewater, and the positive feedback mechanism discussed earlier, in which each vegetation type has a self-reinforcing effect on itself by influencing soil porewater salinity in its favor. Starting from an initially random distribution of the two tree types across the landscape, a vegetation pattern emerged with full mangrove coverage within 30 m of the seaward end of the landscape to full hammock coverage at higher elevations. This is shown by the circles and the solid line fit in Fig. 2, where the relative percentage of hammock basal area is plotted versus distance from the seaward edge of the transition.

For the second trial, positive feedback was removed from the model by not allowing the vegetation to have any effect on the soil porewater salinity, so porewater salinity was determined by abiotic effects alone; i.e., tides, precipitation, and salinity diffusion between cells. Nevertheless, salinity was still able to affect vegetation growth. Specifically, plant effects on salinity in the previous trial were removed by assuming a constant water uptake rate (evapotranspiration) by plants across the landscape, regardless of vegetation type and soil salinity. With the feedback removed,

the simulation output still produced a boundary (Fig. 1b), corroborating the idea that the tidal effect alone can maintain the boundary. Notice that with the assumption of constant water uptake of 2.1 mm/day, there is some shifting upward of the elevation boundary, with mangroves moving a few meters inland to higher elevations that were initially fully covered by hammock vegetation (Fig. 2). We compared trial 1 and trial 2 near the seaward end and near the inland edge separately (Fig. 1a, b). At the seaward end, which is affected by tidal flux, salinity was too high for hammocks to persist, so we found no difference there between trial 1 and trial 2; in both trials vegetation was dominated by mangroves near the seaward end. Near the inland end, with positive feedback in trial 1, hammock trees reduced their evapotranspiration and kept the soil porewater in that area at a low salinity level.

To determine if the difference in sharpness of the ecotone observed between the first and second trials represents a general rule, 20 simulations were performed for each case, and a sign test of SI showed a significant difference ($P < 0.01$), with a mean difference of degree of sharpness of 0.57 versus 0.37 for the first and second trials, respectively. When water uptake of only 1.8 mm/day was assumed, however, the sharpness index of Trial 2 was not significantly different from that of Trial 1 ($P = 0.12$). To examine the effects of other values of water uptake, a range from 1.0 to 3.0 mm/day was used and degree of sharpness was plotted against water uptake (Fig. 3). With an extremely low constant rate of water uptake, which reduced the capillary rise of saline water, the external tidal effect played an important role, and a sharp ecotone continued to be maintained. But the relative effect of tidal flux diminished as water uptake increased (Fig. 3), showing the importance of the magnitude of evapotranspiration on the salinity and vegetation dynamics.

With positive feedback alone, with no gradient (trial 3), an aggregation pattern resulted (Fig. 1c), with a mean value of aggregation index of 0.65. This is significantly higher than that of the null model (trial 4; Fig. 1d), in which both positive feedback and environmental gradient were removed, which showed a weak aggregation pattern, with a mean value of 0.46. In trial 3, the distance from the soil surface to the water table and the water table salinity were assumed to be the same for all cells across the area and there was no
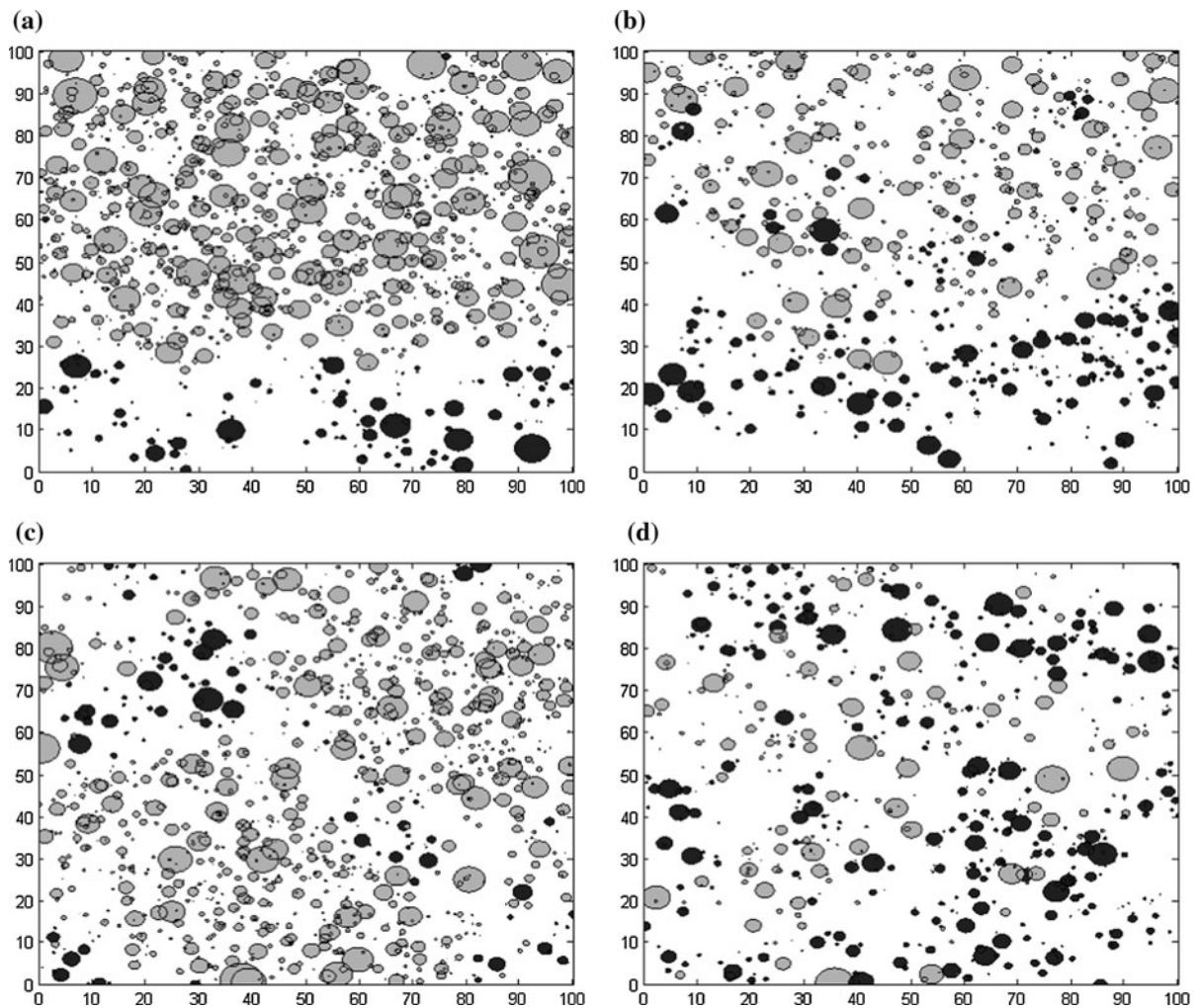
(a)

(b)

(c)

(d)

Fig. 1 Simulation output showing distribution of mangrove (*dark*) and hardwood hammocks (*gray*) in 100 × 100 m² landscape, from **a** trial 1, complete SEHM model; **b** trial 2, removing only positive feedback between vegetation and soil porewater salinity; **c** trial 3, removing only environmental gradient of salinity; and **d** trial 4, removing both mechanisms. Diameter of each circle is four times d.b.h.

tidal effect, so there was no preferential ecotone along the transect from seaward to inland. The different vegetation types adjusted evapotranspiration response to soil porewater salinity, and evapotranspiration in turn changed the soil porewater salinity through capillary rising of the saline water. Two factors, distance to water table and water table salinity, combined with evapotranspiration, can affect soil porewater salinity. In the real world, greater distance from the soil surface to the water table is related to higher elevation at the inland end of the elevation gradient, so we used a series of different values of distance of soil surface to water table. Significant

differences were found for the aggregation index depending on the values of distance to water table and water table salinity (Fig. 4). The aggregation index was high when water table salinity was high, such that the positive feedback between vegetation and soil porewater salinity was strong. We found a significantly lower aggregation index at high elevations for which distance to the water table also was large. At high elevations, soil porewater salinity dynamics slowed because of the thickness of the soil layer above the water table. Thus, soil porewater salinity increased less at high elevations than at low elevations, when mangroves were present within hammock
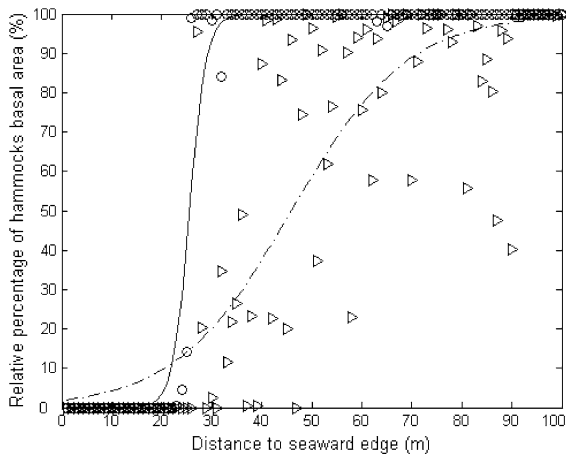
Fig. 2 Relative percentage of hammock basal area is plotted versus distance from the seaward end of the transect. The *circles* and *solid line* represent trial 1 output and a logistic regression fit, respectively. The *triangles* and *dashed line* represent trial 2 output with constant water uptake 2.1 mm/day and a logistic regression fit, respectively
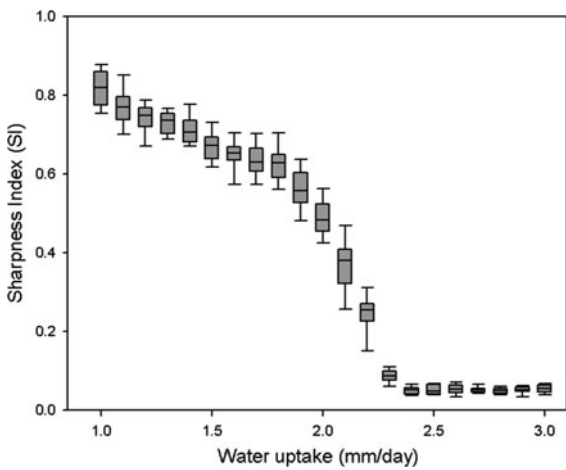

Fig. 3 Box-and-Whisker plot of sharpness index versus water uptake (evapotranspiration) of plants in trial 2, which removed the positive feedback between plants and salinity dynamics. The boundary of the box indicates the 25th and 75th percentile. The line within the box marks the median. *Whiskers* (*error bars*) above and below the box indicate the 90th and 10th percentiles

Fig. 4 The aggregation index in trial 3, in which the environmental gradient was removed, at different levels of water table salinity and distance to water table. *Error bars* show the standard error of the mean (SEM). *Bars marked with same letters* do not differ statistically by all-pairwise comparisons Dwass–Steel–Critchlow–Fligner test following the Kruskal–Wallis test

Effect of precipitation on ecotones (Experiment 2)

At permanent very high or very low precipitation levels, hammock trees or mangroves, respectively, outcompeted the other vegetation type. Aggregation indices on a uniform landscape, with no environmental gradient effects, were high over a range of low precipitation values, and declined as precipitation increased (Fig. 5). At very high precipitation, hammocks dominated the whole habitat, and mangroves were scattered in gaps among the hammock trees instead of occurring a distinct mangrove habitats.

We also used a full version of SEHM, which included both positive feedback and environmental gradient, to simulate the effect of precipitation on ecotone pattern. A clear ecotone line did not emerge along the elevation gradient when the precipitation was permanently low, which created conditions in which the positive feedback was strong. In that case, positive feedback maintained clumping of mangroves within inland hammock habitats, and tidal flux created mangrove-dominate habitats at the seaward edge. However, an ecotone line was clear at a constant high precipitation, because high precipitation favored hammocks at all points without tidal effects, while the intertidal zone was dominated by mangroves because of periodic saline ocean water inundation.

dominated habitats. This also means that only weak positive feedback occurred at high elevations. Inter-action effects also were significant; for example, extremely high water table salinity could overcome stagnancy of soil porewater salinity dynamics at high elevation (Fig. 4).
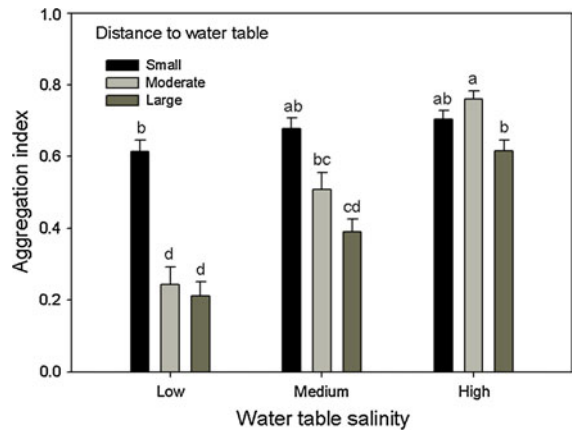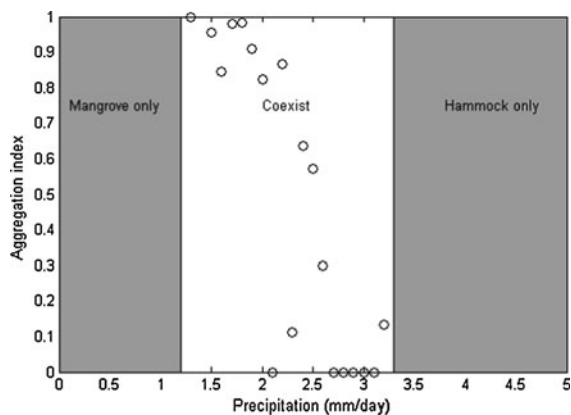
Fig. 5 Aggregation index versus precipitation when environmental gradients were removed. *Gray* areas show where one vegetation type completely dominates the other type, so that an aggregation index cannot be calculated

The salinity pattern varied seasonally, as shown in monthly snapshots (Appendix B in the supplementary material), even though the vegetation aggregation pattern persisted during a specific year (Fig. 1c). The spatial pattern of salinity was relatively homogeneous at the end of December (Fig. 6b), but highly heterogeneous at the end of June (Fig. 6a), although the vegetation pattern was the same. Mangrove habitats maintained high salinities, while hammock habitats still maintained low salinities. Temporal variation of spatial salinity pattern of soil porewater followed the shape of the precipitation pattern, but with a delay of about 2 months. The dry season in the model ended at the end of April, while salinity of mangrove habitats reached their highest levels at the end of June. This is similar to field observations at the Harney River estuary, Everglades National Park (Anderson et al. 2003). The lag probably results from delayed capillary rise of salinity depending upon soil layer depth.

Discussion

Some studies investigating ecotones have focused on the mechanism of positive feedback alone (Zeng and Malanson 2006; Cutini et al. 2010), but gradients of external environmental conditions are also important. Our results suggest that mechanisms of spatial pattern formation of coastal vegetation are more complex than previously suggested, and patterns may not be simply the outcome of either effects of positive feedback or environmental gradients alone.

Relative contribution of positive feedback to sharp ecotones

A combination of positive feedback and environmental gradients is likely responsible for the sharp boundary between mangrove and hammock vegetation types in coastal habitats. Our first simulations supported this (Fig. 1a). The pattern is similar to earlier simulations using MANHAM (see Sternberg et al. 2007; Teh et al. 2008), and is consistent with environmental gradients being important in establishing vegetation ecotones. However, it was difficult to determine the contribution of positive feedback on this boundary from simulation of MANHAM alone. Our Trial 3 (Fig. 1c) simulation showed that positive feedback between plants and soil porewater salinity contributed to the sharp ecotone between hammock and mangroves. The strength of the positive feedback is represented by how fast the salinity of soil porewater changes due to the alternating processes of capillary rising from the saline water table versus infiltration of precipitation. As shown in Fig. 4, a combination of a high water table and high salinity of the water table created a strong positive feedback and resulted in a relatively high aggregation index. In nature, high water table salinity is usually associated with low elevation at the intertidal zone. This implies strong positive feedback around the intertidal zone, while weak positive feedback occurs at high elevations associated with low water table salinity where hammocks dominate.

Our results indicate that positive feedback may not necessarily be essential to boundary formation, at least for the elevation gradient that we used. The effects of positive feedback relative to environmental gradient were evidenced by trial 2 in which positive feedback was removed. In trial 2, when we fixed water uptake at a constant value of 2.1 mm/day across the whole landscape (the average water uptake in trial 1), salinity increased and benefitted mangroves. There exists a certain level of soil porewater salinity at which there is a balance in the competitive relationship between hammock trees and mangroves. This is because hammock vegetation is competitively dominant over mangroves under low salinity conditions, while mangrove vegetation is dominant under high salinities. Therefore, one may expect a salinity level at which the two vegetation types are approximately equal competitively, which prevails at the boundaries of these
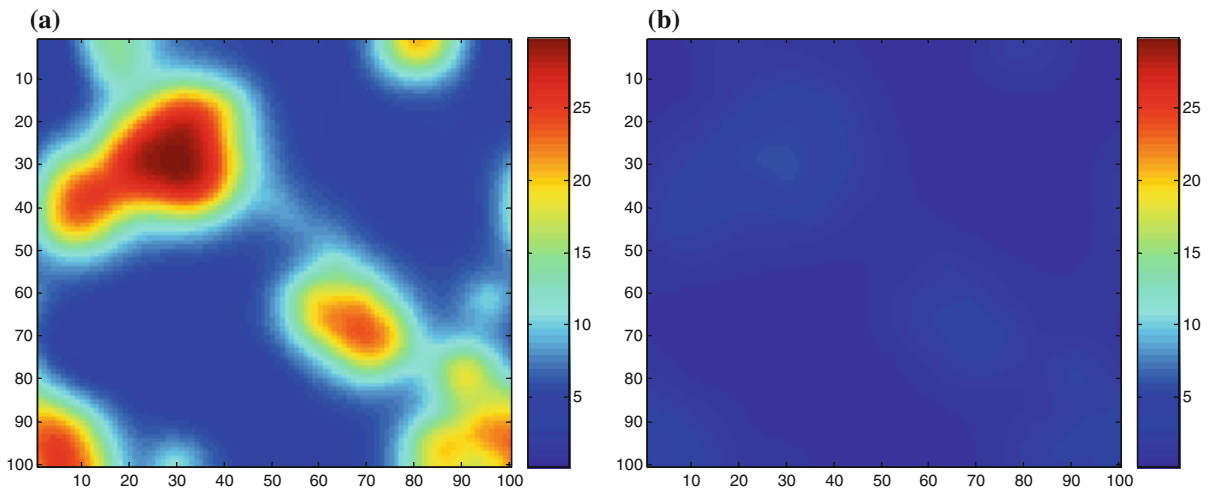
(a)   **(b)**

Fig. 6 Snapshot of soil porewater salinity along the 100 × 100 landscape at **a** June, the most heterogeneous salinity pattern; **b** December, a relatively homogeneous salinity pattern. Color change from *blue* to *red*, represent salinity value from 0 to 30 ppt

two vegetation types. In our simulation experiments, if a high level of water uptake was assumed (e.g., >2.3 mm/day in Fig. 3), the balance was destroyed and mangroves dominated the whole area. If an extremely low level of water uptake was assumed, the balance was destroyed in the opposite direction and much of the area should be dominated by hammock. But even in that case, because the seaward end of the area was frequently inundated by saline tides, a sharp boundary between hammocks and mangroves near the mean tide level occurred in the simulation, even sharper than outputs of trial 1. This implies that positive feedback would not be a necessary mechanism for sharpness of the boundary, under conditions in which water uptake was permanently low. However, water uptake typically varies between 2.0 and 2.5 mm/day (relatively high) when salinity is low, and at this level, the boundary became vague in trial 2, with the positive feedback removed. This indicates that under certain conditions positive feedback is an essential mechanism for maintaining a sharp ecotone, and that an environmental gradient alone only determines that a diffuse boundary exists.

Dry seasons are the major determinant of the vegetation distribution pattern

We studied the aggregation pattern when the environmental gradient was removed and different levels of precipitation were assumed, and found that aggregations of two coexisting vegetation types occurred over

a certain range of low precipitation, but not at extremely low precipitation, at which level positive feedback predominated and mangroves dominated the whole region. At somewhat higher levels of precipitation, positive feedback still favors mangroves in the dry season, during which salt, rising through capillary action, accumulates in the soil porewater and stresses hammock trees. But it is possible that local aggregations of hardwood hammock trees could occur and prevent invasion of mangroves.

Temporal variation in soil porewater salinity resulting from fluctuations in precipitation, coupled with positive feedback between vegetation and salinity, resulted in spatio-temporal variation of the salinity pattern through the seasons (Fig. 6). Nevertheless, vegetation distributions were relatively stable and coincided with the salinity pattern at the end of June, a 1–2 month time lag following the end of the dry season. This implies that strong positive feedback during the periodic dry season resulted in a highly heterogeneous aggregation of salinity and vegetation pattern. The following wet season prevented mangroves from continuously invading hardwood hammock habitats, but was not enough for dominance to shift back to hammock.

These theoretical results need empirical support. Cases of sharp ecotones between mangroves and hardwood hammocks are well documented in southern Florida; for example, in the Florida Keys (Sternberg et al. 1991; Ross et al. 1992), Waccasassa Bay on the west coast of Florida (Williams et al. 2003), and

Turkey Point on the southeast coast of Florida (Pool et al. 1977). But our simulation results suggest that there could be patchiness of mangroves in more inland habitats, where there are no tidal effects, but occasional storm surge inundations occur. Inland isolated mangroves have been reported on the island of Inagua in the Bahamas (Lugo 1981), island of Barbuda, West Indies (Stoddart et al. 1973), and southwest of Moreton Island at Australia (Manson et al. 2003). But there are no reports so far of this pattern of inland mangrove amidst southern Florida hardwood hammocks stands. This could be due to high precipitation of southern Florida during the wet season, and less extreme droughts during the dry season.

Implications for coastal ecosystem pattern with sea level rise and changes in water management

The objective of SEHM is to help make better projections of possible changes in coastal vegetation patterns in southern Florida that may result from both the rise of mean sea level and from saline overwash resulting from storm surges. Simulations of a simpler forerunner of SEHM, MANHAM, indicated that broad areas of freshwater vegetation (hardwood hammocks) could theoretically undergo regime shift to halophytic (mangrove) vegetation under a sufficiently large storm surge. Using SEHM, we have studied the environmental and autogenic factors maintaining the ecotone between freshwater and halophytic vegetation more carefully. SEHM still makes a number of simplifications of the actual coastal hydrology. For example, the subsurface advection of freshwater (e.g., see Wilson 2005), and other aspects of groundwater dynamics are ignored. We will take these into account in future versions of SEHM. It is also relevant to note that the expected increase in freshwater sheet flow from the implementation of the Comprehensive Everglades Restoration Plan (CERP), which will affect both surface and groundwater flow. This may have similar effect to increased precipitation (Perry 2004), although we have not explicitly simulated this effect here. The potential effects of CERP on future water flows are currently being simulated (Swain et al. 2003) and will be taken into account in SEHM.

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