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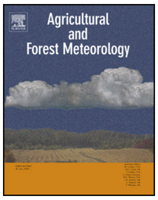

Bistability of mangrove forests and competition with freshwater plants

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ABSTRACT

Halophytic communities such as mangrove forests and buttonwood hammocks tend to border freshwater plant communities as sharp ecotones. Most studies attribute this purely to underlying physical templates, such as groundwater salinity gradients caused by tidal flux and topography. However, a few recent studies hypothesize that self-reinforcing feedback between vegetation and vadose zone salinity are also involved and create a bistable situation in which either halophytic dominated habitat or freshwater plant communities may dominate as alternative stable states. Here, we revisit the bistability hypothesis and demonstrate the mechanisms that result in bistability. We demonstrate with remote sensing imagery the sharp boundaries between freshwater hardwood hammock communities in southern Florida and halophytic communities such as buttonwood hammocks and mangroves. We further document from the literature how transpiration of mangroves and freshwater plants respond differently to vadose zone salinity, thus altering the salinity through feedback. Using mathematical models, we show how the self-reinforcing feedback, together with physical template, controls the ecotones between halophytic and freshwater communities. Regions of bistability along environmental gradients of salinity have the potential for large-scale vegetation shifts following pulse disturbances such as hurricane tidal surges in Florida, or tsunamis in other regions. The size of the region of bistability can be large for low-lying coastal habitat due to the saline water table, which extends inland due to salinity intrusion. We suggest coupling ecological and hydrologic processes as a framework for future studies.

1. Introduction

In tropical and subtropical regions, assemblages of mangrove forests parallel the coastline and riverbanks, transitioning sharply to salt-intolerant plant species, such as hardwood hammocks or freshwater marsh, farther inland. Explanations for the sharpness of the boundary between these two vegetation types have centered on abiotic environmental attributes, such as elevation, salinity, and tidal flooding, as well as biotic processes such as mangrove propagule dispersal and interspecific competition with freshwater plants (Ball, 1980; Davis et al., 2005; Lugo, 1997; Mckee, 1995; Youssef and Saenger, 1999). A widely accepted perspective is that of realized niche differentiation through a combination of abiotic limitation and competition; i.e., freshwater plants cannot survive outside of their physiological salt tolerance range, while mangrove can grow in freshwater as well as saltwater, but do not occur in strictly freshwater environments due to superior competition from freshwater plant species (Krauss et al., 2008; McKee, 2011; Medina et al., 2010; Odum and McIvor, 1990; Sternberg and Swart, 1987). This niche differentiation between halophytic and glycophytic species has been tested in transplant experiments. Transplanted salt marsh species from the intertidal zone to freshwater habitats perform well when competing plants are removed, but are suppressed by competition if freshwater plants are present (Bertness and Ellison, 1987; Cui et al., 2011; Grace and Wetzel, 1981).

An implication of the niche differentiation hypothesis is that fitness of mangrove and freshwater plants might be similar over some intermediate range of salinity levels. In this case, one would expect

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a gradual replacement of mangrove vegetation with freshwater plants as underlying environmental conditions gradually change. Yet there are sharp ecotones between halophytic forests (mangroves and buttonwood hammock) and freshwater communities, despite extremely gradual changes in topography in some regions, such as coastal areas of southern Florida (Giri et al., 2011; Ross et al., 1992; Saha et al., 2011) and East Africa (Di Nitto et al., 2014). One possible explanation for the sharp ecotones is that the environmental gradient of salinity, determined purely by abiotic factors such as tidal flux, is also sharp, separating salinity tolerant mangroves from the salinity intolerant plants. But this explanation fails to account for the boundaries located at upper intertidal zone, which are seldom inundated by tides; e.g., fringe mangrove forest (Pool et al., 1977).

Sternberg et al. (2007) hypothesized that mangrove forests compete with hardwood hammocks as alternative stable states of either pure mangrove forests or pure salt-intolerant hammock species, a case of the general phenomenon of bistability in other systems (Beisner et al., 2003; Holling, 1973; May, 1977; Scheffer et al., 2001). According to the bistability theory, a mixture of the two alternative vegetation types is rarely observed, and an initially mixed system will move toward complete dominance of one or the other type. According to the hypothesis of Sternberg et al. (2007), both mangroves and freshwater plants obtain their water from the vadose zone; that is, the unsaturated soil layer. In coastal areas, this vadose zone is underlain by highly brackish ground water, so that evapotranspiration, by depleting water in this zone during the dry season, can lead to infiltration by more saline ground water (Fass et al., 2007; Passioura et al., 1992; van Duijn et al., 1997). Although freshwater plants tend to decrease their evapotranspiration when vadose zone salinities begin to increase, thus limiting salinization of the vadose zone, mangroves can continue to transpire at relatively high salinities (Ewe and Sternberg, 2005; Sternberg et al., 2007). Each vegetation type thus tends to promote local salinity conditions that favor itself in competition. This hypothesis of boundary formation through positive feedbacks has been supported through simulation models in which the interactions of vegetation types with each other and with local salinity conditions are simulated (Jiang et al., 2012a; Teh et al., 2008).

Until recently, few data have been available to test the bistability hypothesis. Here we link available data on two spatial scales, remote sensing and vegetation physiology, to provide further evidence that the mangrove ecotone pattern at landscape level emerges from lower-level physiological traits. We use remote sensing imagery to analyze spatial patterns of mangrove forests and hardwood hammocks in southern Florida. We also document what is known about the transpiration regime of mangrove in response to soil salinity. A mathematical model (Jiang et al., 2012b) is then applied to elucidate the bistability dynamics. In the model, environmental factors such as tidal flux, precipitation, evaporation, and soil properties etc., form a physical template that influences the competition between mangrove forests and freshwater plants, especially at the larger spatial scale. Ignoring or downgrading the contribution of physical template would overestimate the role of positive feedback. By including the positive feedback along with the physical template, we provide a framework toward more predictive large-scale vegetation changes.

2. Interspersion and juxtaposition of mangroves and hammocks

Various landscape metrics have been used to assess spatial relationships between different vegetation types in heterogeneous wetlands and other environments (Fernandes et al., 2011; Guzy et al., 2013; Shoyama and Braimoh, 2011; Stapanian et al., 2013). To evaluate horizontal interspersion and juxtaposition of hardwood hammocks and mangroves we employed Fragstats version 4.2 software, which is commonly used to analyze spatial patterns within categorical vegetation and land cover maps (Mcgarigal and Ene, 2013). Specifically, we used Fragstats to calculate the Interspersion–Juxtaposition Index (*IJI*) for an area of southern Everglades National Park where both hammocks and mangroves are found (Fig. 1). The *IJI* provides a measure of patch adjacency and is calculated as:

$$IJI = \frac{-\sum_{k=1}^{m}\left[\left(e_{ik}/\sum_{k=1}^{m}e_{ik}\right)\ln\left(e_{ik}/\sum_{k=1}^{m}e_{ik}\right)\right]}{\ln(m-1)} \times 100 \qquad (1)$$

where e_{ik} is the total length (in m) of edge in a landscape with classes i and k, and m is the number of classes present in the landscape, $m = 3$ in this study with hammocks, mangroves and others. *IJI* approaches 0 when the corresponding patch type is adjacent to same patch type and increases when a class shares a border with other classes. Further, when $IJI = 100$ the corresponding each patch type is equally adjacent to all other patch types or maximally interspersed (or intermixed) and juxtaposed to other patch types (Mcgarigal and Ene, 2013).

We obtained categorical vegetation data from the Florida Coastal Everglades Long-Term Ecological Research (LTER) website http://fcelter.fiu.edu/data/GIS/?layer=vegetation#layer, which provides highly detailed data mapped using high-resolution aerial and satellite images (Welch et al., 1999). GPS-assisted accuracy check was an average of 90% correct, with resolution of 10 m. The map delineates eight mangrove forest subtypes including stands dominated by Red mangrove (*Rhizophora mangle*), White Mangrove (*Laguncularia racemosa*), Black mangroves (*Avicennia germinans*), and Buttonwood (*Conocarpus erectus*) as well as various mixtures of these subtypes. These classes were aggregated into a single mangrove class to simplify the analysis of *IJI*. Similarly, Welch et al. (1999) also distinguished a number of hardwood vegetation types, including subtropical hardwood forest, mixed hardwood swamp forest, mixed hardwoods and bayheads, which were also aggregated into a single hardwood class (Fig. 1). All other vegetation types in the map were considered as ‘other vegetation’ or background, which was dominated mainly by graminoid vegetation types such as sawgrass marsh (*Cladium jamaicense*).

The results from Fragstats reveal values of *IJI* of 13.49 and 37.55 for mangroves and hardwoods, respectively. These values suggest that mangroves are not highly intermixed and that hardwoods are moderately interspersed and juxtaposed to mangroves. This finding is likely explained in part by the dominance of mangroves relative to hardwoods in the area analyzed (Fig. 1). In comparison to ecological studies in other regions that have employed the *IJI* metric, the two main vegetation types in this portion of the southern Everglades appear to have relatively high adjacency. For example, Coops et al. (2010) showed that in a disturbed boreal forest landscape, *IJI* ranged from approximately 35–60 over a period of 14 years during which forest fragmentation increased. Further, Guzy et al. (2013) showed that mean *IJI* ranged from 7.2 to 65.3 for a range of aquatic vegetation types found across different rural to urban environments. In general, the literature suggests that *IJI* values are somewhat lower in wetlands than for terrestrial ecosystems (consistent with sharp zonation patterns that characterize coastal wetlands), although a systematic comparative study of *IJI* values across a range of ecosystems appears to be lacking (Cifaldi et al., 2004; Li et al., 2010; Torbick et al., 2006). Nonetheless, the *IJI* metric as well as Fig. 1 suggest mangroves tend to be relative clumped rather than intermixed with hardwood hammocks. Although there are uncertainties of what cause the bistability, sharp boundaries between mangroves and hardwood hammocks are consistent with the hypothesis advanced by Sternberg et al. (2007).

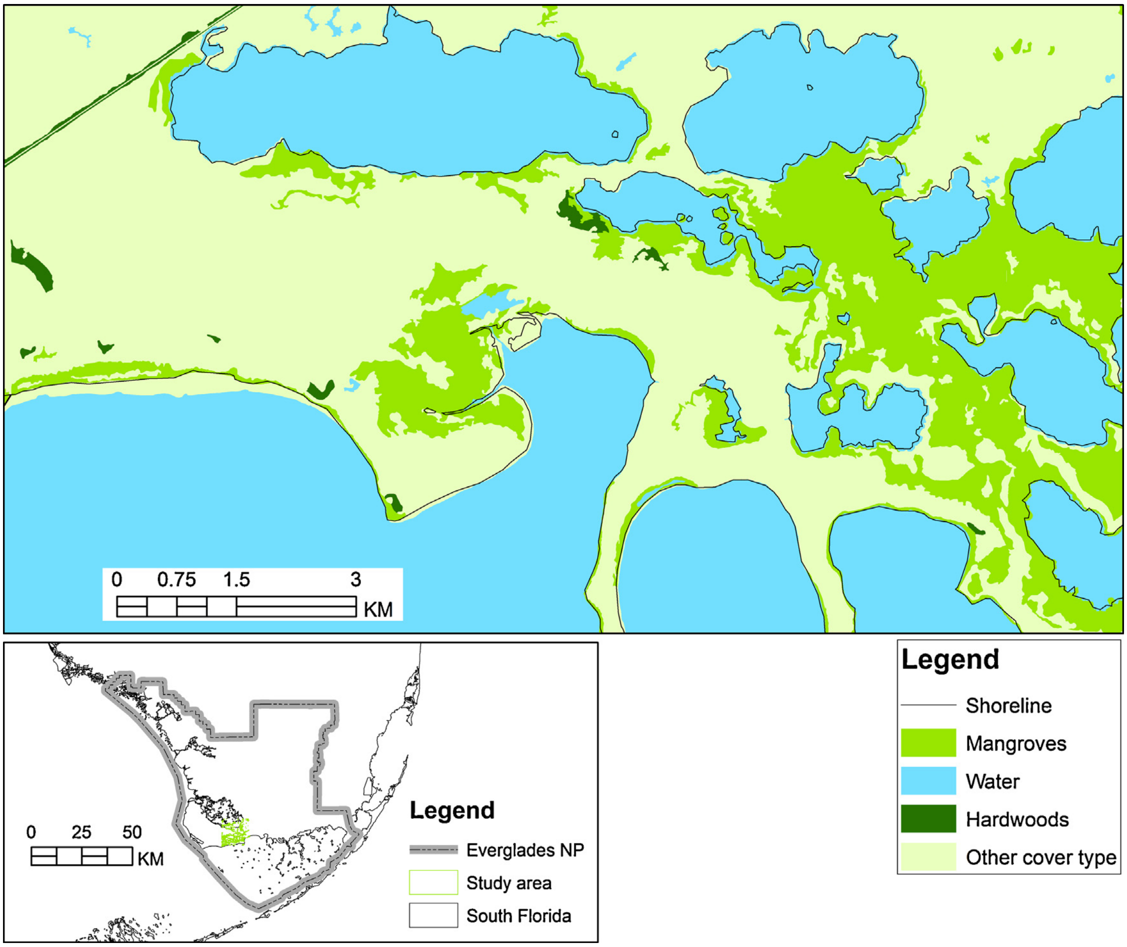

Fig. 1. A map of southern Everglades National Park classifying vegetation types into mangrove, hardwood hammocks and others.

3. Mechanisms of bistability

Fundamental to the bistability hypothesis (Jiang et al., 2012a; 2012b; Sternberg et al., 2007; Teh et al., 2008) is the assumption that during the dry season mangroves will continue to transpire despite the high salinity of the vadose zone, causing capillary rise of saline water from water table and a consequent increase in the salinity of the vadose zone. Freshwater plants during the dry season, on the other hand, will decrease or cease transpiration, thus maintaining a low salinity of the vadose zone. Precipitation plays a role also, reducing vadose zone salinity in both habitat types during the wet season, but dry season salinity is the major determinant of vegetation type and is much higher under mangrove vegetation (Fass et al., 2007; Saha et al., 2012). Here we compare transpiration regimes of the two plant types responding to vadose zone salinity and demonstrate how the differential transpiration regimes influence vadose zone salinity. A simple mathematical model that can capture the mechanism is presented to describe population dynamics at the landscape scale, showing how bistability can emerge from functional traits of transpiration response to salinity and the ability of mangrove to alter soil salinity patterns.

3.1. Physiological level transpiration regime

Effects of water stress caused by salinity on transpiration reduction are well documented in salt-sensitive plants (Achenbach et al., 2013; Meiri and Poljakoff-Mayber, 1970; Volkmar et al., 1998). When dissolved salt concentrations in soil increase, water potential gradients from soil to plant root decrease, lowering the water movement from the soil through root membranes and into the plant. In addition to this osmotic effect, ion flux to shoots causes stomatal closure (Hasegawa et al., 2000). Coastal freshwater plants may tolerate short periods of high salinity, by ceasing or diminishing transpiration during the dry season and resuming transpiration when precipitation increases and washes salinity from the soil. In a South Carolina watershed, for example, baldcypress (*Taxodium distichum*) reduces water uptake by more than 75% as a response to short-term salinity stress (Krauss and Duberstein, 2010). In the saline southeastern Everglades ecotone, sawgrass (*C. jamaicense*) may survive for short episodes of exposure to high salinities during the dry season (Ewe et al., 2007), despite sawgrass annual net primary productivity declining when salinity increases (Childers et al., 2006).

The status of sapflow or transpiration of mangroves in response to salinity is still a controversial topic, although there is agreement that mangroves can tolerate high salinities in the rhizosphere through salt exclusion, salt secretion and salt accumulation (Tomlinson, 1994). Mangroves may reduce transpiration in response to salinity increases, indicating conservative rates of water use (Becker et al., 1997; Krauss et al., 2012). By extensive literature review (see Appendix A for the method), however, we show that in mangroves, species with higher salt tolerance display less reduction in transpiration (Fig. 2). Tolerant and very tolerant species reduce transpiration 28% and 13%, respectively, in response to per 10 ppt salinity increase. We did not analyze the responses of all freshwater plant species to salinity, but in general we can say that most salt-sensitive species cannot survive above 10 ppt. By comparing native southern Florida glycophytic species to

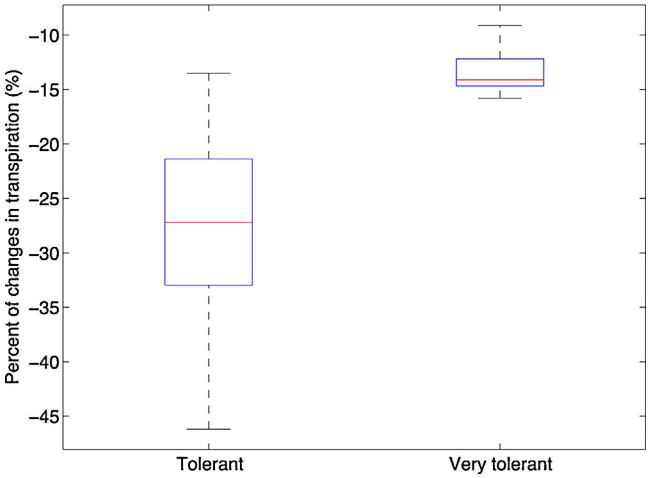

Fig. 2. Percentage of transpiration reduction in response to a 10 ppt increase of salinities for tolerant and very tolerant mangroves. On each box, the central mark is the median, the edges of the box are the 25th and 75th percentiles. Data are extracted from (Ball, 1988; Ball et al., 1997; Ball and Munns, 1992; Clough and Sim, 1989; Ewe and Sternberg, 2005; Kao et al., 2001; Lin and Sternberg, 1992; Lopez-Hoffman et al., 2007; Lopez-Hoffman et al., 2006; Lovelock et al., 2006; Muller et al., 2009; Naidoo and Vonwillert, 1995; Reef et al., 2012; Santiago et al., 2000; Sobrado, 1999; Sobrado, 2000, 2001a, 2001b, 2005, 2006, 2007; Takemura et al., 2000; Wei et al., 2008a, 2008b; Ye et al., 2005; Youssef, 2007).

mangroves, Ewe and Sternberg (2005) found reductions of 54% and 15% in stomatal conductance for glycophytic species *Randia aculeata* and the mangrove *R. mangle*, respectively. Evapotranspiration (ET) in a mangrove dominated area is also much higher than in an equivalent sawgrass area, and is the largest water loss in an estuary wetland, as estimated by a water budget model (Saha et al., 2012).

Based on the differential transpiration regimes described above, mangrove and freshwater plants have different abilities to change salinities of soil porewater through transpiration. Less reduction in water uptake of mangroves at high salinity conditions can lead to vadose zone salinity increases (Passioura et al., 1992; van Duijn et al., 1997). Fass et al. (2007) demonstrated that mangrove forests could lead to high chloride concentrations in ground water; for example, in an Australian river delta chloride concentration was almost three times that of ocean water.

3.2. *Scale to landscape level vegetation competition*

When one considers the ability of mangroves to change vadose zone salinity, competition between mangroves and freshwater plants becomes a complex issue. Hardwood hammock species are competitively superior in low salinity areas, suggesting that halophytic species will usually be excluded from areas farther from tidal influence by competitive exclusion (Kenkel et al., 1991; La Peyre et al., 2001; Silander and Antonovics, 1982). In areas of intermediate salinity, however, mangrove vegetation, once established, can influence vadose zone salinity in its favor. Alternatively, hardwood hammocks, when in high abundance, can compete effectively with mangroves and maintain low salinity. Thus the distribution of the two plant types is controlled by a combination of the externally imposed physical template and emergent self-organization (Sheffer et al., 2013). Over a certain range of this physical template, feedbacks between mangroves and freshwater plants can affect soil salinity and result in bistability (Fig. 3).

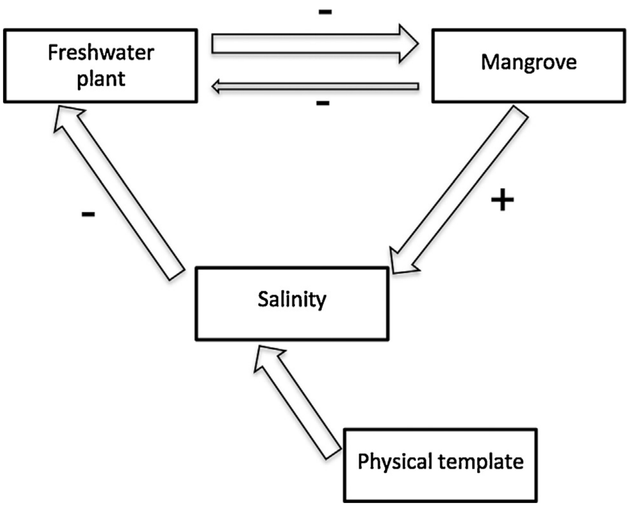

Fig. 3. Schematic diagram showing that the physical template controls soil salinity, while, simultaneously, the mangrove has a positive effect on soil salinity, which has a negative effect on freshwater plant growth. The freshwater plant is assumed to be a superior competitor against mangrove under low salinity conditions.

Jiang et al. (2012b) developed a simple mathematical model integrating the feedbacks between halophytic and glycophytic vegetation to a physical template of baseline salinity gradient. These equations describe the change in biomass of mangroves ($\mathrm{d}M/\mathrm{d}t$), freshwater plants ($\mathrm{d}F/\mathrm{d}t$), and the pore water salinity ($\mathrm{d}S/\mathrm{d}t$) on a unit time step (e.g., per year). Change of mangrove biomass is a function of standing mangrove biomass (M) and its maximum relative growth rate (ρ), modulated by salinity stress ($m_{(S)}$) and intraspecific ($\alpha_{MM}M$) or interspecific ($\alpha_{MF}F$) competition. Likewise, change of freshwater plant biomass is modulated by salinity stress ($f_{(S)}$), intraspecific ($\alpha_{FF}F$) and interspecific ($\alpha_{FM}M$) competition.

$$\frac{\mathrm{d}M}{\mathrm{d}t} = M\left(\rho m_{(S)} - \alpha_{MM}M - \alpha_{MF}F\right) \tag{2}$$

$$\frac{\mathrm{d}F}{\mathrm{d}t} = F\left(\rho f_{(S)} - \alpha_{FF}F - \alpha_{FM}M\right) \tag{3}$$

where Eqs. (2) and (3) constitute a classic Lotka–Volterra two-species competition model.

The increase in soil salinity (S) can be described in terms of salinity infiltration upwards into the vadose zone from the saline water table (g) through capillary action, replacing soil water that is lost through evaporation at a rate $\beta_0 g$, which is equal to ground water salinity times the coefficient β_0. We assume that water table salinity, g, has a spatial gradient along the physical template, increasing from inland toward the coast, and is not affected by plants. Additional salinity increases in the vadose zone by mangrove plants follow a Monod equation with a maximum rate of β_1 and half-saturation coefficient k. The salinity increase is countered by salinity washout (ε) due to precipitation or other freshwater inputs at a rate of ε. The equation describing vadose zone salinity can thus be written as

$$\frac{\mathrm{d}S}{\mathrm{d}t} = \beta_0 g + \frac{\beta_1 M}{k+M} g - \varepsilon S. \tag{4}$$

All parameter values are positive and the same as in Jiang et al. (2012b). The model can be shown to imply, along a certain range of values of g, the possibility of alternative stable states of either a high salinity state dominated by mangroves or a low salinity state dominated by freshwater plants in a three-dimensional ‘stability landscape’ (Fig. 4). In the sense of the familiar stability landscape in the form of ‘valley’ and ‘hilltop’ (Walker et al., 2004), the 3D stability landscape, or state space, has two regions separated by a boundary, or separatrix. The ball can settle to a stable equilibrium in each region, having some degree of resilience to perturbations. These regions are called ‘basins of attraction’ in mathematics. The larger the size of the basin of attraction, and the steeper its slope, the more resilience the system has to a perturbation away from the

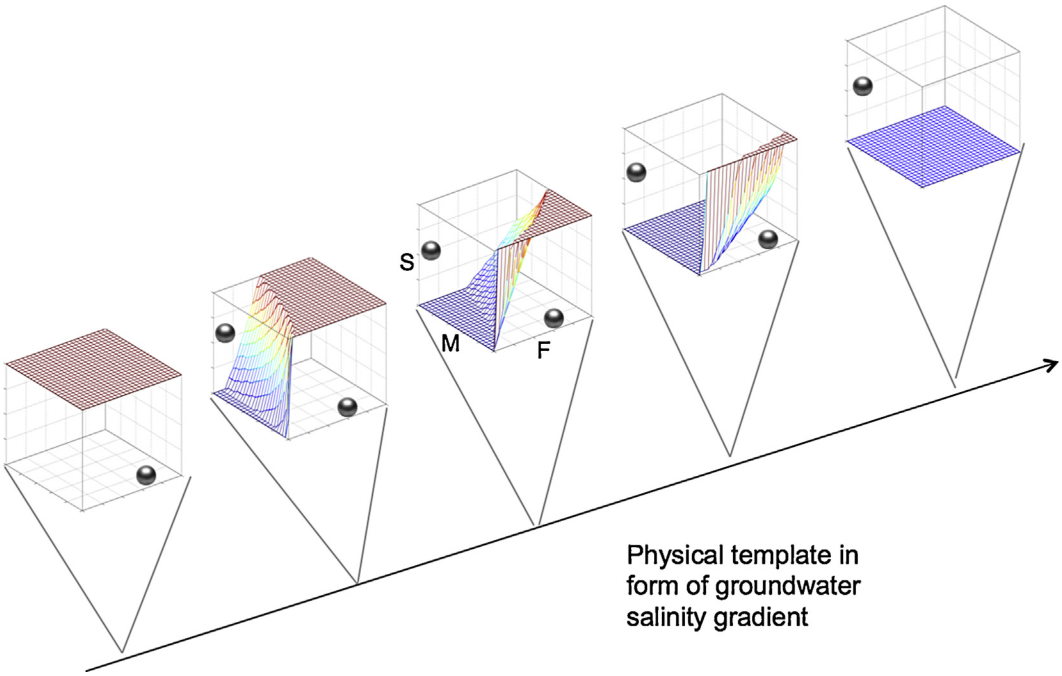

Fig. 4. Stability landscape of mangrove system shows boundaries between mangrove states and freshwater plant states. The balls above and below the curved boundary surface (separatrix) represent mangrove states and freshwater plant states, respectively. Size of each basin indicates relative resilience of each state. M, F and S represent mangroves, freshwater plant and salinity, respectively.

stable state within that basin. However, a disturbance that is large enough can cause the ball to cross over the separatrix from one basin of attraction to the other one, which will result in a regime shift.

The possibility of alternative stable states occurs only over a certain range of the physical template, or values of water table salinity, *g* (Fig. 4), which can be imagined as a transect from the ocean side, with high water table salinity, to an inland point with much lower groundwater salinity. At both ends of the physical template, that proximate to the ocean side and the inland end of the transition, only one stable state exists. This can be explained by the niche differentiation hypothesis, that freshwater plant cannot tolerate high salinity; and that mangroves are excluded by competition at low salinity end. Over a certain range of water table salinities, however, a bistable region that can be, alternatively, either mangroves or freshwater plants, exists; but the relative resilience of each state is controlled by details of the physical template. Analysis of Eqs. (2), (3) and (4) provides a theoretical range of the physical template over which bistability exists, but the actual size of the range depends on a whole complex of factors that are not explicit in the model; abiotic factors such as precipitation, landscape morphology, and depth and salinity of the water table; and biotic factors such as the physiological and competitive properties of local vegetation and age or size class of plants. Jiang et al. (2012a) developed a more complex spatially explicit, individual-based simulation model to disentangle the relative contributions of the physical template and bistability mechanism in the formation of sharp ecotone. This model was based on a simpler spatially explicit model, MANHAM (Sternberg et al., 2007; Teh et al., 2008), in which vegetation was not modeled as individual-based, but as state variables representing fractional occupation of spatial cells. The model of Jiang et al. (2012a) uses parameters estimated from general mangrove types, and the same simplified hydrology process as the original MANHAM used. The emergence of bistability suggests that including positive feedback mechanism in more realistic hydrology models is necessary to provide more realistic predictions of vegetation changes.

4. Implication for large-scale vegetation changes

Much of what has been documented concerning the spatial and temporal shifts of mangroves along coastal habitats can be explained by gradual environmental changes (Berger et al., 2008; Chen and Twilley, 1998; Doyle et al., 2003). Sea level rise and anthropogenic decreases in freshwater flow cause salinity intrusion and a landward shift of the mangrove bands. For example, Doyle et al. (2003) used computer simulations to project possible inland migration of mangroves along the southern Florida coastline in response to sea level rise. This was done using projections of the inland movement of tidal influence, given the topography of southern Florida. However, even if spatial location of mean tidal influence does not change in the future, the bistability hypothesis implies that sufficiently large storm surge disturbances, if they maintain salt intrusion for some time period, could still result in an inland shift in mangroves beyond what would be predicted from sea level rise alone. This could happen if the resultant salinity input to freshwater habitat is large enough to tip an existing stable freshwater vegetation state to the alternative mangrove stable state. The model MANHAM (Teh et al., 2008) simulated competition between mangroves and hardwood hammock vegetation on two-dimensional grid of square spatial cells, where the sides of each cell were assumed to be in the range of a few to several meters. Vadose zone salinity in each cell was modeled as a function of tidal flux, precipitation, groundwater salinity, and evapotranspiration. The two vegetation types were represented as state variable for fractions occupying each cell. From simulations of MANHAM it was found that in the event of a light storm surge, accompanied by mangrove propagules, hardwood hammocks were able to restore the salinity to low levels in a short time period. After 50 years, hardwood hammocks still dominated the cells at higher elevation but the patches of mangrove-dominated cells were larger compared to the case without a storm surge event. A medium surge event that saturated the vadose zone at 15 ppt caused the mangroves to invade the cells at higher elevation that were initially dominated by hardwood hammocks. A heavy surge caused the mangroves to take over the entire domain inundated by the surge after 50 years. Therefore, consistent with the bistability hypothesis, simulations with MANHAM indicated that broad areas of hardwood hammocks could theoretically undergo regime shift to mangrove vegetation under a single sufficiently large storm surge (Sternberg et al., 2007; Teh et al., 2008; Williams et al., 2003).

Mechanisms of ecological bistability influenced by environmental gradients, especially salinity gradients caused by tidal flux, should be considered in the study of large-scale vegetation changes. Within the region of bistability, exact location of the ecotone between the two vegetation states depends on initial conditions; i.e., which vegetation type got there first. Although the ecotone within the region of bistability can change as a result of large perturbations, it may be fairly resilient to small disturbances caused by sea level rise or minor storm surges. Jiang et al. (2014) applied the model to a section of the mangrove-freshwater marsh ecotone on the southwestern coast of the Everglades. Based on recorded data from Hurricane Wilma at a USGS monitoring site, the model indicated that salinity at that site would probably persist in the soil for only a short period of time after the hurricane, and the model projected that the ecotone would be resilient to that minor disturbance. But scenarios of longer period of salinity intrusion and passive transports of mangrove propagules via storm surge could cause a shift of freshwater marsh to mangrove forest.

Whether such storm-surge induced pulses could lead to long-term effects on vegetation depend on many factors: the physiological and competitive properties of local vegetation, precipitation, overland freshwater flow, elevation gradient, and depth and salinity of groundwater. Thus, predicting the likelihood of such shifts requires detailed modeling of coupled ecological-hydrologic processes. Coupling vegetation dynamics with underling environmental models is a state-of-the-art of modeling approach and depends on spatial scale (Runyan et al., 2012). At the scale of individual trees, salinity can affect plant transpiration, but individual plants hardly change soil salinity, as the effect of a single plant is overwhelmed by regional hydrological dynamics. At a larger scale, an assembly of mangrove forests may exert strong engineering force on vadose zone salinity. Our modeling framework suggests hydrology models that take into account the balance of physical template and positive feedback between plants and soil conditions could determine how large a spatial scale the bistability pattern would emerge.

5. Concluding remarks and future direction

We demonstrated here how interactions between mangroves, freshwater plants and local soil conditions could result in bistability along an environmental gradient of water table salinity. Sharp ecotones are usually indicators of positive feedbacks that cause bistability between differing vegetation types, such as forest-grassland, forest-mire, Alpine treelines, etc. (Agnew et al., 1993; Wiegand et al., 2006). The mangrove forest—salt marsh transitions are also suggested to result from positive feedback between vegetation and local temperature (D'Odorico et al., 2013). But abrupt spatial changes between two vegetation types are not always evidence for bistability (Wilson and Agnew, 1992). Peterson (1984) pointed out "Only by experiment could one convincingly demonstrate multiple stable states by showing that the very same site could come to be occupied by different, self-replicating communities". But the "very same site" condition is difficult to prove in this case since feedback loops driven by mangrove alter the salinity conditions. Wet season salinity, which is least influenced by vegetation, might be a good candidate for a criterion for comparing similar sites. Sites with the same wet season salinity, assuming other factors are the same as well, will insure that the observed difference in salinity of the vadose zone at the end of the dry season is caused by the presence of the particular plant functional type that occurs there and not by other factors.

The bistability hypothesis is proposed based on the fundamental assumption that differential transpiration regimes of the particular plant functional type in response to salinity, and the ability for this to influence salinity of the vadose zone. Although empirical studies support this assumption, no direct experimental data are available to derive the response function. Furthermore, daily ET values at landscape level are highly dependent on the level of solar radiation. Future theoretical and empirical studies should consider seasonality of radiation on the response function of transpiration to salinity.

Identification of the region of bistability is necessary for projecting large-scale vegetation changes as well as for developing potential management plans. The lower intertidal zone is limited to halophytic vegetation, while on higher elevation that lacks frequent salinity overwash or a saline water table, freshwater plants are always competitively dominant. However, the coastal Everglades and the Florida Keys contain large areas of saline water table, which provide potential areas for region of bistability. Accurate predictions of bistability will require sophisticated hydrology models coupled with landscape vegetation dynamics.

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Appendix A. Meta-analysis based on literature review on transpiration of mangroves in response to salinity increase

Using a meta-analysis approach, we assessed if mangroves reduce transpiration in response to salinity increases. We conducted a literature search on Web of Knowledge and Google Scholar, using combinations of the search terms mangrove, salinity and any of terms with sap flow, transpiration, stomatal conductance, shoot evaporation or water use. After screening the initial list of over 800 articles generated by our data base searches, we retained only studies that measured water-related characteristics at multiple salinity levels. Most of studies measured stomatal conductance; there were relatively few with direct data on transpiration, shoot evaporation or sap flow. We extracted raw data from tables or scatter plots using GETDATA GRAPH DIGITIZER 2.24 (Fedorov, 2013). Since reduction of stomatal conductance follows the same pattern as transpiration in response to salinity increase (Youssef, 2007), we calculated the dimensionless percent of reduction in response to 10 ppt increases of salinity. From all the studies, we extracted 27 articles with 32 tests of hydrologic characteristics in response to salinity changes, which were reported for 16 species. Relative tolerances of the species were classified as very tolerant and tolerant modified from Clough (1992).

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