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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).