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Spatio-temporal pattern of plant communities along a hydrologic gradient in Everglades tree islands[☆]

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ABSTRACT

Plant communities arranged along a gradient are a product of underlying physico-chemical drivers that vary on both spatial and temporal scales. Spatial variation in the underlying drivers along the gradient usually results in the formation of boundaries between adjacent plant communities. However, the structure and composition of these communities may change over time resulting in boundary shifts. In the Everglades, tree islands are complex ecosystems, where plant communities are arranged along hydrologic and soil nutrient gradients. In these islands, temporal changes in hydrologic regime often result in a spatial shift in community composition along the gradient and determine the trajectory of community succession. We examined the interaction between hydrology and vegetation over a 12-year period in three southern Everglades tree islands. We hypothesized that drier conditions in recent decades would result in an increase in the dominance of flood in-tolerant woody plants over herbaceous and flood-tolerant woody species, ultimately causing a shift in the boundaries between plant communities. The boundary between adjacent communities varied from sharp, clearly defined peaks of Bray-Curtis dissimilarity to more gradual, diffuse transition zones. In the head portion of tree island, there was little change in vegetation composition. However, in the tail portion of the islands, the relative abundance of flood-tolerant species declined, while that of moderately flood-tolerant species increased over the study period. In these islands, the effects of relatively dry conditions in recent decades resulted in small shifts in the boundaries among communities. These results suggest that tree islands are dynamic successional communities whose expansion or contraction over time depends on the strength and duration of changes in hydrologic conditions.

1. Introduction

Plant communities arranged along environmental gradients are at least in part products of ecological processes associated with spatio-temporal variation in physico-chemical drivers. Likewise, when plant communities proceed through a successional process, the conditions of drivers are modified by species-environment interactions that may contribute to changes in the environmental gradients over time. As such, these changes in environmental gradients usually result in the formation of boundaries, representing transition zones between adjacent plant communities (Allen et al., 2005). The properties and persistence of these boundaries depend on whether the variation in the drivers is abrupt or gradual (Wiens et al., 1985; Walker et al., 2003), and on the ability of adjacent plant communities also to withstand the effects of natural and/or management-induced environmental changes (Risser, 1995; Forys and Allen, 2002). When plant community composition responds to changes in environmental drivers beyond a certain threshold, the boundary between adjacent communities is also likely to shift (Allen et al., 2005).

In the Everglades, tree islands are an integral component of several landscapes (e.g., pine rockland, marl prairie, and ridge and slough). In the ridge and slough (R&S) landscape, tree island nucleation, formation, and development began 4000 years before present (ybp) in response to regional multi-decadal fluxes in the periodicity and duration of flooding and drought events (Willard et al., 2002). These hydrologic changes permitted the establishment and proliferation of woody vegetation in sawgrass marshes or on ridges during periods of sustained drought (Willard et al., 2002, 2006; Bernhardt, 2011). Over time, soil accretion resulting from higher productivity within the incipient tree islands led to higher surface elevations and shortened flooding periods,

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which in turn promoted the establishment of shrubs and trees. As recently as 1700 ybp, many Everglades tree islands were not fully formed and exhibited many of the characteristics of a transitional community consisting of sawgrass (*Cladium jamaicense* Crantz) and weedy annuals with a minor woody component (Willard et al., 2002). However, by around 600 ybp, following several extensive and prolonged local and regional drought episodes, the modern vegetation structure on most large tree islands in the southern Everglades had begun (Willard et al., 2002; Bernhardt, 2011).

In tree islands within the R&S landscape, plant communities vary in species composition and life-form structure along a topographic gradient. However, the degree of variation in species composition is likely correlated with habitat (resource) heterogeneity along the gradient (Davidowitz and Rosenzweig, 1998; Kumar et al., 2006). In these islands, the vegetation on the most elevated portion, called 'Hardwood hammock', are typically dominated by flood-intolerant trees, whereas the surrounding marsh (Mixed-marsh) has mostly flood-tolerant graminoids or broad-leaved submerged, floating, and/or emergent species. Between these two extremes, the proportion of woody plants and herbaceous species depends on the interactions between the underlying drivers and stressors (e.g., hydrology, disturbance, nutrients, etc.). As these conditions change, so does species composition and community type (Fig. 1). The most noticeable changes usually occur in the surrounding mixed-marsh and tail portion of the tree islands, where three distinct plant communities, Bayhead forest, Bayhead swamp, and Sawgrass marsh are common. These communities may be thought of as phases in a chronosequence of vegetation succession in R&S landscape. While persistent drying conditions initiate an expansion of sawgrass within the mixed-marsh or sloughs (Bernhardt and Willard, 2009), the Sawgrass marsh represents the earliest successional tree island community, analogous to the primordial marsh prior to tree island formation. Sawgrass marsh is followed by the Bayhead swamp that represents a transitional phase between the primordial Sawgrass marsh and Bayhead forest, a climax community typifying tree island maturation under wetland conditions (Fig. 1). While a Bayhead forest is less likely to transition to Hardwood hammock, an extended period of flooding beyond a critical threshold causes Hardwood hammock and other tree island woody communities to lose their characteristic woody species, and eventually may cause tree island to abruptly shift to a stable marsh (D'Odorico et al., 2011).

Hydrology is one of the major drivers of species variation within tree islands in the Everglades (Armentano et al., 2002; Ross and Jones, 2004; Espinar et al., 2011). Hence, substantial changes in hydrologic conditions, whether natural or management-induced, are likely to cause quantitative and qualitative changes in structure and composition of the tree island communities. For instance, management-related high-water levels due to compartmentalization after 1960 caused the loss of tree islands, both in number and areal coverage, in the Water Conservation Areas (Patterson and Finck, 1999; Brandt et al., 2000; Hofmockel et al., 2008). In contrast, during periods of tree island initiation during the last four millennia, the R&S landscape experienced shorter hydroperiods than during the pre-drainage era e.g., 1800s (Willard et al., 2006). Since tree island and marsh communities are hydrologically connected (Troxler et al., 2005; Ross et al., 2006; Saha et al., 2010; Sullivan et al., 2014), prolonged and extreme dry or wet events may also affect the boundaries between these communities. The climatological records and hydrologic data from the Shark River Slough (SRS) in Everglades National Park (ENP) suggest that water level during the 1990s was well above the 30-year average (Fig. 2). In contrast, both the mean annual rainfall and water level were relatively low between 2001 and 2012. Since plant community composition on tree islands in 2001 was already impacted by high water conditions in 1990s, the dry conditions in 2000s provided an opportunity to assess response of plant communities to the shift in hydrologic regime on the islands.

Tree islands are likely to be affected by water management activities associated with the Comprehensive Everglades Restoration Plan (CERP) authorized by the Water Resources Development Act (WRDA) of 2000. The CERP is a multi-decade restoration project expected to cost approximately $10 billion (Stern, 2014). It is the framework for the modifications and operational changes needed to restore, preserve, and protect the water resources of central and south Florida, including the greater Everglades. The overarching goal of the CERP is to repurpose freshwater outflow into the Atlantic Ocean and the Gulf of Mexico for use in environmental restoration while providing flood control and supplementing the water supply needs of south Florida's growing population. The CERP projects are intended to restore the right quantity, quality, timing and distribution of freshwater in the Everglades through different activities, such as decompartmentalization in Water Conservation Areas and construction of Tamiami Bridges to restore the natural sheet flow and increase the water flow across the Tamiami Trail towards Everglades National Park (ENP). Within the CERP, water management decisions will result in changes in hydrologic regimes throughout R&S landscape, including the tree islands, probably affecting the balance between flood-tolerant and flood-intolerant species and resulting in shifts in species composition, community boundaries, and ultimately tree island function.

Because of the uncertainties associated with the CERP and its effect on Everglades ecosystems, specifically tree islands, it is imperative that managers understand how regional long-term changes in hydrologic regimes will affect structure and function of tree island plant communities. In this study, we describe changes in vegetation composition of three SRS tree islands between 2001 and 2012 and examine whether successional processes influenced by short-term changes in hydrologic conditions have impacted the community composition, and thus shift in

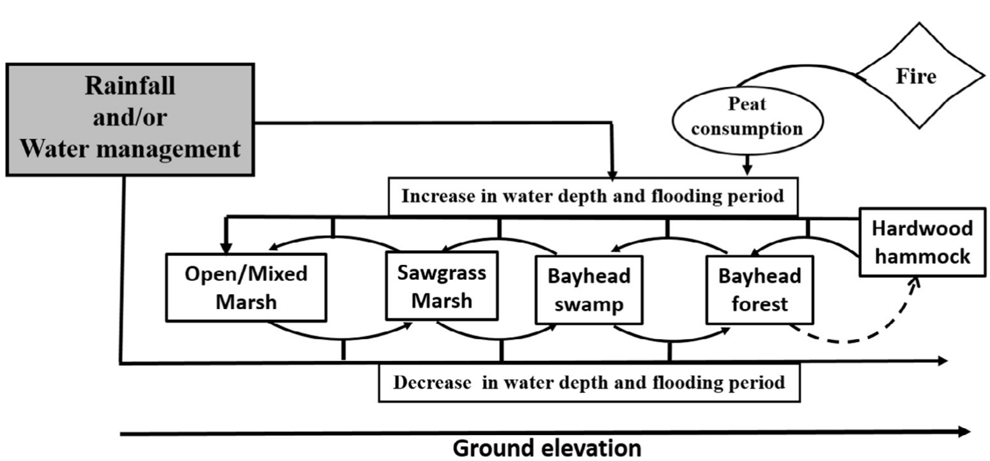

Fig. 1. Conceptual model: vegetation dynamics in Shark River Slough tree islands and surrounding marsh.