

RESEARCH ARTICLE

# Tree islands: the bellwether of Everglades ecosystem function and restoration success

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Everglades tree islands are patches of woody vegetation ranging in size from 0.1 to 70 ha embedded in a marsh matrix. Tree islands are an essential component of the tree island–ridge–slough topographic continuum and the trees provide a mechanism for the accumulation of phosphorus in the landscape, enhancing landscape biocomplexity. This article reviews the literature of tree island ecology and describes the predicted effects of five ecosystem restoration scenarios on tree islands. Elevations of the highest points on 404 islands across the Everglades were used to assess the effects of the scenarios at a landscape level, while the plant communities of nine islands were modeled to assess local effects. Evaluation of the restoration scenarios were based on three critical components needed to maintain and restore tree islands: hydrology that allows the survival of woody species, seasonally appropriate water flow to move nutrients off the heads of islands, and oligotrophy. All restoration options generally improved water conditions for tree growth, although flooding of islands in some areas was predicted to increase. Scenarios with the greatest amount of decompartmentalization and largest capacity to remove phosphorus from water entering the Everglades provided the best chance of delivering vigorous pulses of sheet flow in directions parallel to historic flows and maintaining oligotrophy. Tree islands are “bellwethers” of restoration actions because their maintenance on the landscape requires multiple ecosystem functions.

**Key words:** decompartmentalization, ecosystem processes, hydrology, restoration scenarios, wetlands

## Implications for Practice

- Like keystone species, the presence of certain landscape features reflect the integration of multiple ecosystem processes. When these features are readily visible they can be used to gauge progress of ecosystem deterioration or restoration.
- Use of restoration scenarios developed to address policy-maker questions is a useful method to predict ecosystem outcomes that are relevant for policymakers.
- Tree islands provide a useful landscape feature by which to evaluate restoration scenarios in patterned peatlands.

## Introduction

Tree islands are patches of woody vegetation embedded in a sawgrass ridge and marsh-patterned landscape (Fig. 1) (Sklar et al. 2003; Wetzel et al. 2011). The slough–ridge–tree island landscape forms a topographic continuum where tree islands are the driest end of the continuum; the heads of the tree islands rise from 18 to 120 cm above the slough bottoms (Wetzel et al. 2008), while ridges rise from 8 to 32 cm above the sloughs in well conserved areas of the Everglades (Watts et al. 2010). Everglades tree islands come in a variety of shapes that are organized into nonrandom spatial patterns: round clumps of trees surrounded by water lily sloughs, teardrop-shaped islands oriented in the direction of surface water flow (Fig. 1) and surrounded by sloughs, long strands integrated with and parallel

to sawgrass or marsh ridges interspersed with sloughs, and a labyrinth of trees with gaps occupied by herbaceous communities. Tree islands number in the thousands and range in size from 0.01 to 70 ha. The area covered by tree islands varies by region, averaging approximately 14% in the northern Everglades (Loxahatchee National Wildlife Refuge; Brandt et al. 2000) and 3.8% of the area in the central Everglades (Patterson & Finck 1999).

While tree islands were not identified as a feature of the Everglades that “people care about” in the Synthesis of Everglades Research and Ecosystem Services (SERES) analyses (Everglades Foundation 2011), Everglades’ ecologists recognize their pivotal role in the Everglades ecosystem. Most importantly, tree islands provide a mechanism for the accumulation of phosphorus in the landscape, making every tree island a biogeochemical hot spot in the ecosystem (Wetzel et al. 2005; Ross et al. 2006; Wetzel et al. 2011). Tree islands also promote inorganic nitrogen (N) retention on the landscape by providing a reactive substrate and a supply of dissolved organic carbon (Troxler & Childers 2010). Tree islands were found to be a N

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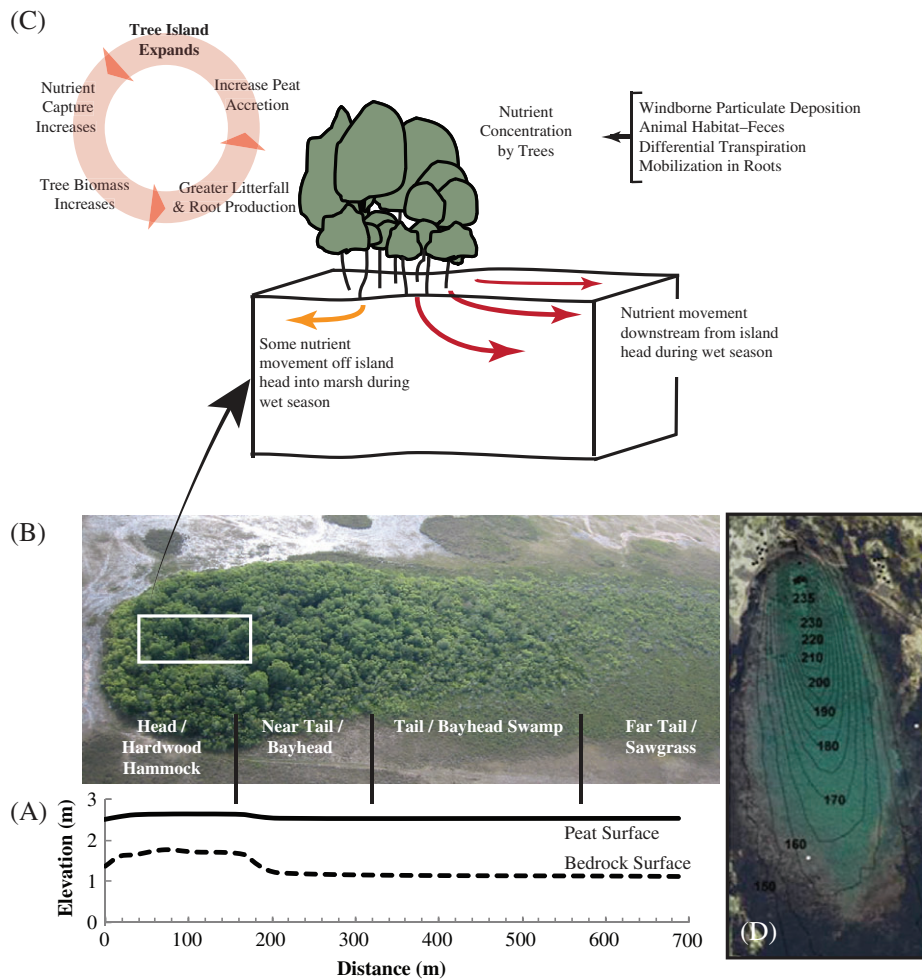


Figure 1. Description of a teardrop-shaped tree island and model of how trees concentrate nutrients on the landscape and the resulting development of tree islands. (A) Longitudinal cross section of a tree island (identified in other studies as 3AS3) with average peat and bedrock elevations (D. Mason, unpublished data). Elevation exaggerated 50× compared with distance. (B) Aerial photo of a tree island located in WCA 3A (photo by D. Kilbane). Tree island vegetation communities defined by vegetation and hydrology are labeled. (C) Conceptual model of nutrient concentration on the landscape by trees and resulting development of tree islands. The presence of trees on the flat landscape concentrates nutrients, eventually increasing tree biomass and peat accretion. During the wet season water flow moves nutrients downstream and, to a much lesser extent, laterally off the island head. Plant biomass increases and tree islands develop in line with water flow. (D) Example of tree island topography. Contour lines in 5 cm increments. (Data from Owen et al. 2009).

sink and Troxler and Childers (2010) estimated that tree islands in their study could retain 55% of the dissolved inorganic N entering the wetland landscape. The ability of tree islands to concentrate phosphorus (P) and nitrogen allows them to maintain their elevation and potentially grow, both in elevation and areal extent. The resulting drier hydrology of the highest elevations on tree islands also provides keystone habitats, as upland and/or dry refugia from wet marsh conditions, for plants, invertebrates, amphibians, reptiles, mammals, and birds—both resident and migratory (Craighead 1971; Brandt et al. 2002; Gawlik 2002; Meshaka et al. 2002). In addition, larger tree islands that have ground elevations above normal seasonal flooding were, and still are, culturally important to Native Americans (Carr 2002; Graf et al. 2008). Thus, the pivotal role of tree islands in the biogeochemistry of the Everglades landscape, as keystone habitats that increase overall biodiversity, and as important

anthropological sites, made them an important resource to be evaluated for the restoration alternatives.

Palynologic evidence indicates that some tree islands are longtime landscape features, initially developing between 1,200 and 500 years ago (Willard et al. 2006; Bernhardt & Willard 2009). The original vegetation on islands sampled in the central Everglades consisted of sloughs or sawgrass plant communities. If such communities become dry enough to support woody plants, nascent tree islands may begin to form (Wetzel et al. 2005; Givnish et al. 2007; Bernhardt & Willard 2009). The presence of trees allows the focused concentration of nutrients from guano or dust deposition onto the nascent island, causing litter and peat to accumulate at a higher rate than on the surrounding ridges or sloughs (Fig. 1). Changes in the hydrology of the Everglades from human activities over the last 75 years have greatly reduced both the number and aerial extent of tree islands. This

is particularly true in Water Conservation Area (WCA) 2 and WCA 3 where the number of islands in WCA 3A decreased by 54% while tree island area declined by 67% (Patterson & Finck 1999).

This article provides a brief literature review of tree island ecology and describes the predicted effects of five ecosystem restoration scenarios on tree islands. The restoration scenarios used in the analyses were Existing Conditions Baseline (ECB), Comprehensive Everglades Restoration Plan (CERP), Partial CERP (PC), Expanded Storage and Decompartmentalization (ESD), and Maximum Storage and Decompartmentalization (MSD) (Table 1; see Wetzel et al. this volume for detailed descriptions of the restoration scenarios). To predict the effects of the restoration scenarios, elevations of the highest points on 404 islands across the Everglades were used to assess the effects of the scenarios at a landscape level, and the plant communities of nine islands were modeled based on the predicted hydrology. The goal of the scenario analysis was not to find the best restoration plan, but rather to understand the relative importance of different restoration elements.

### The Role of Tree Islands in the Everglades

#### Trees Concentrate Nutrients on the Landscape

Tree islands are now recognized as a mechanism for the accumulation of phosphorus in the landscape, with the result that every tree island is a biogeochemical hot spot in the ecosystem (Wetzel et al. 2005; Ross et al. 2006; Wetzel et al. 2011). Total phosphorus (TP) measured in soils 0–10 cm deep on tree island heads was 3–170 times greater than in the surrounding marsh (Wetzel et al. 2009; Wetzel et al. 2011). A similar local gradient exists for TP in soil pore water and vegetation foliage (Ross et al. 2006). Within an island, soil TP decreases downstream from the head to its lowest level in the tail (Wetzel et al. 2005; Wetzel et al. 2009; Espinar et al. 2011; Troxler et al. 2014). Total nitrogen (TN) levels in the soil, pore water, and foliage did not follow the same pattern and were slightly lower or similar on the tree island head compared with the marsh (Ross et al. 2006; Wetzel et al. 2011). Accordingly, Ross et al. (2006a) and Espinar et al. (2011) found that vegetation communities on the head were nitrogen limited, while marsh communities were phosphorus limited as described by many other researchers.

The soil TP level on tree island heads creates a landscape pattern of increasing concentration from north to south (Table 2). TP levels on tree island heads in the Everglades National Park (ENP) are four times greater than islands in WCA 3B and on average 28 times greater than soil TP levels on island heads in WCA 1 (Wetzel et al. 2011; Table 2). The reason for this pattern is not clear, although Sullivan et al. (2012) suggest that it may be due to spatial variations of rainfall (which decrease from north to south), hydrologic properties, and tree stand structure based on their findings of ET rates from constructed wetlands. Geology may also play a role, as sand generally underlies the WCAs while limestone containing phosphorus is found beneath the surface of ENP (Price et al. 2003; Harvey et al. 2006).

**Table 1.** Water storage, flow, and ecological features of the SERES Everglades restoration scenarios: ECB, CERP, PC, ESD, and MSD. ASR, Aquifer Storage and Recovery.

Scenario Options	Water Storage			Water Flow			Ecology				
	Lake Okeechobee ASR (acre-feet/year)	Everglades Agricultural Area/Lake Belt Reservoir (acre-feet/year)	Predicted Level of Historic Water Flows Reaching the Gulf of Mexico (%)	Reduction of Internal Barriers to Flow (%)	Additional Storm Water Treatment Areas Needed (acres)	Wading Bird Flock Abundance Annual Increase (%)	Fish Density Annual Increase (%)	Overall Fire Risk (%)	Florida Bay Salinity Reduction (% closer to target)	Nearly every other year	Too salty
ECB	0	0	>50	12.5 miles of levees	Current area	90% lost	0 (multi-decadal decline)	78	50		
CERP	2,456,000	504,000	87	54	60,000	10	12	78	50		
PC	822,700	360,000	79	54	33,000	9	12	-67	25		
ESD	0	1,300,000	91	69	28,500	8	13	-36	50		
MSD	0	2,700,000	90	75	47,000	9	15	-89	50		

**Table 2.** Landscape mean values of TP in soil from tree island heads (0–30 cm) compared with marsh soils (0–10 cm). Sources: <sup>a</sup>Ewe (2008), <sup>b</sup>Corstanje et al. (2006), <sup>c</sup>Bruland et al. (2006), and <sup>d</sup>Osborne et al. (2011).

Location	Tree Island TP $\pm$ S.E. (mg/kg dry wt.) <sup>a</sup>	Marsh TP $\pm$ S.E. (mg/kg <sup>-1</sup> dry wt.)
Water Conservation Area 1	1,478 $\pm$ 31 (n = 4)	405 $\pm$ 14 (n = 131) <sup>b</sup>
Water Conservation Area 3A	2,777 $\pm$ 1,122 (n = 40)	402 $\pm$ 12 (n = 189) <sup>c</sup>
Water Conservation Area 3B	10,329 $\pm$ 3,315 (n = 35)	371 $\pm$ 22 (n = 54) <sup>c</sup>
Everglades National Park	41,073 $\pm$ 3,097 (n = 70)	312 $\pm$ 10 (n = 310) <sup>d</sup>

Similar to the positive feedback mechanisms believed to create ridges, the focused redistribution of phosphorus on tree islands causes the islands to accumulate biomass at a greater rate than the surrounding sloughs, through the production of tree roots and organic matter accumulation on the island surface (Givnish et al. 2007). The presence of trees concentrates nutrients on the island, some of which may move downstream off the island head by leaching into shallow groundwater (Espinar et al. 2011; Wetzel et al. 2011; Troxler et al. 2014; Fig. 1). As the tree island grows more nutrients are captured by the island, creating a positive feedback mechanism that increases the size of tree islands (D'Odorico et al. 2011). This positive feedback allows the islands to continue to grow in size until some disturbance (fire or flooding) reduces tree abundance and therefore the mechanisms of focused nutrient redistribution. The mechanisms that focus nutrients onto tree islands and their relationship to restoration activities are discussed below.

#### Mechanisms of Nutrient Concentration by Trees

It is the trees themselves, growing in an oligotrophic landscape, that create the conditions that concentrate TP onto the islands. Several mechanisms of nutrient capture by the trees have been suggested (Wetzel et al. 2005) and continue to be investigated. Trees are attractive to wading birds as roosting and nesting sites and to other animals (including humans) which increases the deposition of feces and animal bones on islands (Lund 1957; Burton et al. 1979; Frederick & Powell 1994; Coultas et al. 2008; Irick et al. 2013). Frederick and Powell (1994) estimated that wading birds deposited an average of approximately 13 metric tons of nitrogen and 5.1 metric tons of phosphorus onto tree island colony sites annually. A medium-sized nesting colony (approximately 5,450 nests over 352 ha) was estimated to deposit 20.3 g m<sup>-2</sup> yr<sup>-1</sup> nitrogen and 0.90 g m<sup>-2</sup> yr<sup>-1</sup> phosphorus, an input that is 20 times the historical atmospheric input of phosphorus (Davis 1994) and for denser colonies up to 3,000 times more phosphorus than was deposited by precipitation (Frederick & Powell 1994). Clearly, wading birds concentrate nutrients on tree islands, but not all tree islands are used as bird colony sites. So, other nutrient concentration mechanisms must come into play on the landscape.

Trees may also act as traps for dry fallout as they sway in the wind, 3–10 m above the surrounding vegetation (Weathers et al. 2001; Krahl et al. 2004). Summer air flow patterns generally originate from the North African coast and contain a higher dust content than air masses reaching the Everglades in the winter (Prospero et al. 2001; Holmes & Miller 2004). Aeolian deposition in south Florida on mechanical traps averaged 41  $\pm$  33 mg P m<sup>-2</sup> yr<sup>-1</sup> (Ahn & James 2001), ranging from 16 to 118 mg P m<sup>-2</sup> yr<sup>-1</sup> (Redfield 2002). These preliminary findings suggest that dust will be a significant nutrient input to tree islands, but the phenomenon needs further study.

Transpiration of the tree patches is also a possible mechanism of nutrient concentration on tree islands (Wetzel et al. 2005). Trees on tree islands transpire tremendous amounts of groundwater especially during the late dry season when daily evapotranspiration ranges from 3.4 to 9.9 mm/day (Wetzel et al. 2011; daily mean = 5.3  $\pm$  0.5 mm from Troxler et al. 2014). This is enough water to lower the water level in the root zone between 1.0 and 3.0 cm each day during the dry season (Ross et al. 2006; Wetzel et al. 2011), resulting in a depressed groundwater table under the tree patch (Sullivan et al. 2012). Surprisingly, this diurnal flux in water level could also be seen (at a lower magnitude between 0.4 and 0.8 cm/day) in wells 8 m deep located on the tree island head (Wetzel et al. 2011). The diurnal fluxes in water level at all well depths were highly synchronized with the photosynthetic activity of trees on the island as measured by the peak sap flow fluxes. However, during the wet season the diurnal water level signature was muted or not apparent, even though photosynthetic activity was the same as during the dry season (Wetzel et al. 2011).

Tree transpiration and the resulting ion exclusion through root water uptake during the dry season concentrates carbonate minerals under the tree island head (Sullivan et al. 2011; Wetzel et al. 2011; Sullivan et al. 2014; Troxler et al. 2014) and, as Sullivan et al. (2014) recently reported on a tree island in the ENP, in areas immediately downstream of the head of the island. The strong dry–wet seasonality in the Everglades, where evapotranspiration exceeds precipitation during the dry season, results in the formation of calcrete layers, which may contribute to local topographic differences between tree islands and the surrounding marsh (Graf et al. 2008; Ross & Sah 2011; Sullivan et al. 2014, 2016; Troxler et al. 2014).

The important question concerning tree patch transpiration is whether nutrients are pulled toward the island and concentrated. Supersaturation of carbonate minerals observed under the tree island head certainly suggests that such a mechanism exists. Additional insight from stable isotope analyses determined that during the wet season, trees and ferns on the tree island head and near tail use P-enriched shallow soil water. As these surface waters become scarcer in the dry season, trees and ferns draw water from the deeper, regional water pool adjacent to the island (Saha et al. 2010; Sullivan et al. 2014). Saha et al. (2010) suggest that nutrient buildup on tree islands would occur over long time periods even though regional water has low P concentrations. However, intensive study of a tree island in the ENP led Sullivan et al. (2014) to conclude the P in the water of the shallow, unsaturated soil of the tree island head originates



locally from the dissolution of apatite. Apatite is a class of crystalline, inorganic minerals containing phosphorus and calcium with high concentrations of  $\text{OH}^-$ ,  $\text{F}^-$ , and  $\text{Cl}^-$  ions.

### Water Flow Moves Nutrients on the Island

The dry–wet seasonality of the Everglades plays an important role in moving P concentrated on the tree island head laterally to other parts of the island. Troxler et al. (2014) found that the rewetting of tree island head soils during precipitation events mobilized the largest fluxes of P, and that 67% of the annual vertical P flux occurred during the wet season between April and August. The mobilized and reprecipitated P is moved laterally by the gradient between the island head and lower, downstream elevations and surface water flow during the wet season. The tree island head is the initiation point of island P dynamics because the area is elevated above the regional groundwater level. Soil and root exposure above the regional groundwater table is necessary for both mineral concentration at the tree roots during tree transpiration and to allow the wet season rewetting of dry soil that enables P mobilization and lateral transfer (Troxler et al. 2014). The lower topographic positions of the wet head, near tail, and far tail areas of the tree island (Fig. 1) are often inundated with regional groundwater and do not always allow mineral concentration during transpiration (Sullivan et al. 2014) or remineralization of P during soil rewetting.

Groundwater does move away from the island footprint during the wet season and appears to bring nutrients with it. Sullivan et al. (2014) found that groundwater did flow from a tree island head to the marsh during the wet season, but did not measure nutrients in that flow. Givnish et al. (2007) detected a vegetation gradient of dense *Sagittaria latifolia* and *Peltandra virginica* communities in close proximity to tall tree islands across the Everglades landscape; *S. latifolia* and *P. virginica* growth was more limited by nutrient availability than *Cladium jamaicense* (Daoust & Childers 1999) and their association with tree islands suggests that a portion of the P on the island head leaches off the island and may permit the existence of this vegetation community.

The loss of the nutrient-concentrating function of trees on the Everglades landscape would mean that the marshes will naturally receive a higher nutrient load, which may affect the oligotrophy of the entire system (Wetzel et al. 2005; Wetzel et al. 2009). Wetzel et al. (2009) estimated that in WCA 3A, 1 m<sup>2</sup> of tree island head annually sequestered the equivalent of the annual wet and dry fallout input on 10 m<sup>2</sup> of marsh. They further estimated that historically 67% of the TP in WCA 3A was stored on tree islands, highlighting the importance of tree islands on the Everglades nutrient cycling and in Everglades restoration.

Through mechanisms that are still not completely clear, tree islands are biogeochemical hot spots for phosphorus as a result of material fluxes of a limiting resource operating at multiple spatial and temporal scales. The concentration of TP by trees from a large spatial area to specific points on the landscape establishes a small-scale (within the island) positive feedback loop that increases the size of the tree island and allows an even

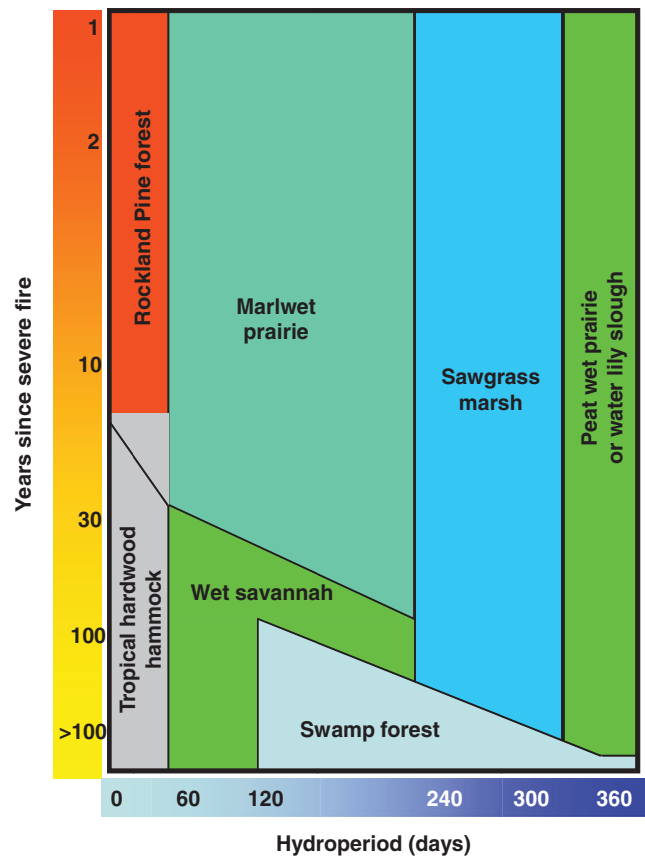


Figure 2. Distribution of seven broad Everglades vegetation categories along axes of time since fire and hydroperiod. Modified from Lockwood et al. (2003).

greater capture of the limiting resource. The result is an increase in landscape biocomplexity (Shachak et al. 2008) with strong local hydrologic and nutrient gradients.

### Drivers of Tree Island Plant Community Composition and Structure

The composition and structure of tree island plant communities are controlled by three primary environmental drivers: water level, nutrient availability, and disturbance, including fire, tropical storms and droughts. These environmental drivers act at both landscape and local scales, as well as at various temporal scales (Gunderson 1994; Fig. 2). The interplay of these scales complicates the relationship between vegetation and Everglades hydropatterns as larger spatial scales tend to change at a slower rate than finer ones (Gunderson 1994; Gunderson & Walters 2002; Sah et al 2014; Troxler et al 2014). The following sections summarize the effects of hydrology and fire on tree island plant communities at the intermediate to fine spatial and temporal scales.

### Hydrology

Hydrology is a complex environmental driver that consists of water level, length of time on the landscape, and seasonal

variation. Most simply, plant communities may be classified by their response to hydroperiod (the average number of days per year that the water level is at or above the soil surface). Hydrology greatly influences the structure and composition of tree island vegetation communities (Loveless 1959; McPherson 1973; Zaffke 1983; Armentano et al. 2002; Heisler et al. 2002; Mason & van der Valk 2002; Sah 2004; Troxler Gann & Childers 2006; Givnish et al. 2007; Ruiz et al. 2013b) and the elevation of the island relative to the surrounding marsh will determine its hydroperiod.

There is considerable variation in the height of the heads of Everglades tree islands above the marsh surface, and this variability, in combination with marsh water levels that vary regionally in the Everglades, creates the moisture regimes to which trees on the islands are exposed. Figure 3 illustrates the hydroperiods experienced on tree islands in WCA 3 and the interior of the ENP during 2000–2007. At the landscape scale, inundation periods on the islands generally increase with ponding depths from north to south in WCA 3A. In comparison, the islands in WCA 3B show significantly shorter hydroperiods, resembling the values observed on the islands in the ENP. Beyond these broad patterns, one may easily find low, wet islands intermixed in the landscape with high-elevation dry islands.

The heads of the most highly elevated tree islands (e.g. tropical hardwood hammocks) are inundated only 3–7% of the year, or may never be inundated (Armentano et al. 2002; Sah 2004; Ross et al. 2006)—a hydroperiod of 0–45 days/year (Fig. 4). Lower elevation tree islands or areas downstream of the tree island heads known as bayhead or bayhead-swamp may be flooded 25% of the year or more, and even all year during particularly wet years (Armentano et al. 2002; Wetzel 2002; Wetzel et al. 2008). The near tail, tail, and far tail sections of the tree island are lower in elevation and flood more frequently than the head. For comparison, marl wet prairies are the driest Everglades freshwater marshes, with a hydroperiod of 60–200 days/year, while sawgrass, spikerush, and cattail marshes have moderate to long hydroperiods between 180 and 330 days/year. Hydroperiods of individual woody species of these plant communities were described by Armentano et al. (2002) (Fig. 4).

However, other components of hydrology are important to plant community development and structure. For example, many wetland woody and herbaceous seeds will not germinate under water but require an extended dry period (van der Valk & Davis 1978; Dalrymple et al. 2003). Longer hydroperiods (>180 days) also affect tree sapling establishment in wetter areas of tree islands or on tree islands that have extended hydroperiods. Ruiz et al. (2013b) found that sapling density and basal area declined as much as 75% in long hydroperiod (>330 days) environments. Finally, a number of studies found that hydrologic extremes, that is, extreme drought or flooding events, exert a greater effect on woody plant communities than seasonal means (Heisler et al. 2002; Wetzel 2002; Givnish et al. 2007; Wetzel et al. 2008). In a related finding, Ruiz et al. (2013b) reported that both tree density and basal area declined as hydroperiod became longer.

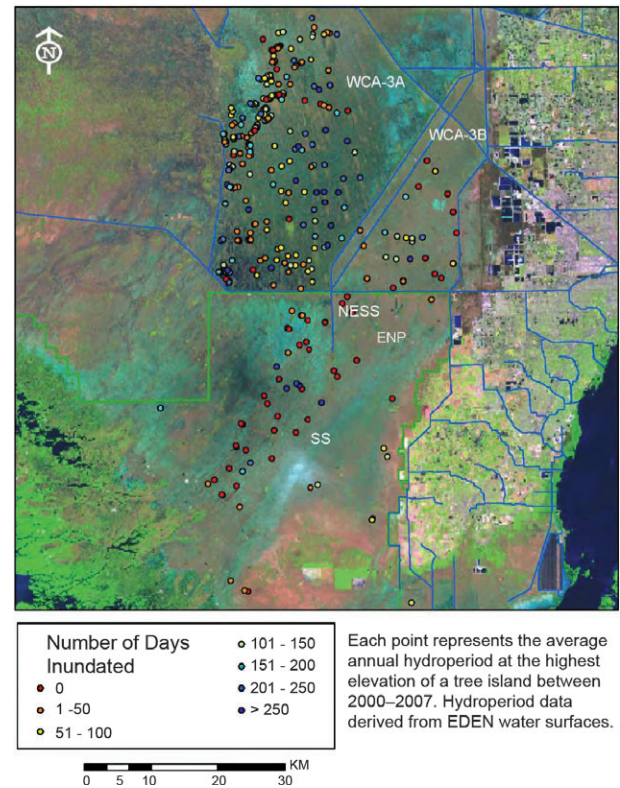


Figure 3. Average annual hydroperiods at the highest elevation of tree islands within WCA 3 and Everglades National Park between 2000 and 2007. Source: Modified from Comprehensive Everglades Restoration Plan, 2009 System Status Report; Restoration Coordination and Verification (RECOVER). Greater Everglades Ridge and Slough Pattern and Tree Islands, September 2010.

Tree island plant communities are dynamic, expanding and contracting with changing hydrologic fluxes (Wetzel et al. 2005; Ruiz et al. 2013b). Extended dry periods promote the growth and expansion of woody species in the tail areas of the tree island. During these dry events areas downstream of the tree island bayhead experienced increases in species richness, basal area, and canopy development (Ruiz et al. 2013b). In addition, the sequence of flood and drought disturbance events and the presence or absence of an intervening period of average hydrologic conditions have also been found to affect growth and mortality of different woody species (Miao et al. 2009). In some sequences growth and mortality was stimulated or depressed, depending on the species. The effects and time frame of the hydrologic disturbance sequence is not well understood and has not been investigated on the plant community level. Although hydrology is an important environmental driver for plant community composition and succession, its interaction with fire and nutrient levels must also be considered, especially in the parts of the Everglades highly modified by humans.

#### Fire

The distinct annual winter dry period and summer wet period weather cycles of the Everglades create conditions that

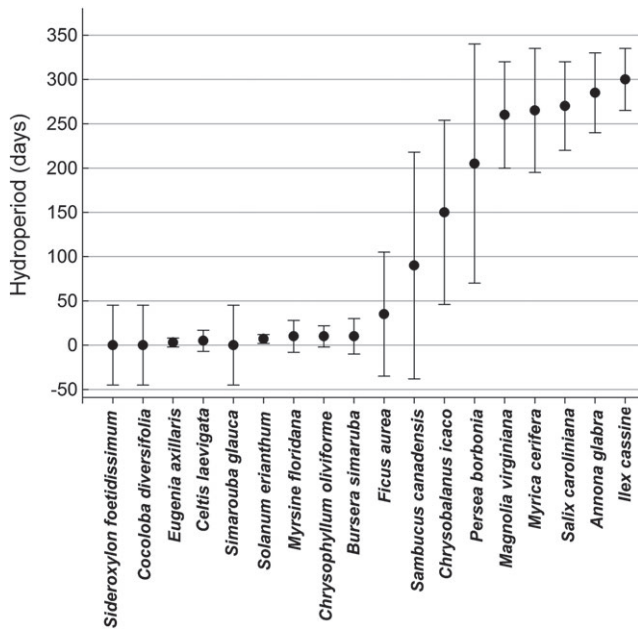


Figure 4. Mean annual (optima) and range of hydroperiods (tolerance) of 18 common tree species found on tree islands in the central and southern Everglades. From Sah (2004).

**Table 3.** Size of areas burned and their frequency of occurrence in a given year for each fire size level in the Everglades National Park (Beckage et al. 2003). The estimated area of muck and hammock soil fires from 1948 to 1979, as a percentage of the total area burned in a given year (data from Taylor 1981). SEM, standard error of the mean.

Annual Area Burned (ha)	Periodicity (years)	Percent of Burned Area That Muck or Hammock Soil Was Burned (SEM)
20,000–80,000	12.3	42 (11) $n = 6$
2,000–20,000	3.4–5.0	33 (8) $n = 10$
0–2,000	1.0	47 (11) $n = 6$

support wildfires. These wildfires, in addition to prescribed fires and incendiary fires (started as acts of vandalism), create an ecologically important disturbance in the Everglades. The dry season typically begins in early October and extends through April and early May (Duever et al. 1994). Nearly 80% of the total annual burned area is burned in April and May during the transition from the dry to the wet season, when water levels are lowest (Taylor 1981; Gunderson & Snyder 1994; Beckage et al. 2003). Generally, fires in the Everglades occur at three different combinations of spatial and temporal scales: large fires on 12.3-year cycles, intermediate size fires on 3.4–5-year cycles, and small fires on a 1-year cycle (Table 3). The effect of the annual dry–wet cycle is reflected in the 1-year fire regime (Beckage et al. 2003) in which 0–2,000 ha may burn annually (Table 3).

Usually one or two fires burn most of the annual burned area (Beckage et al. 2003). Years when large areas burned,

20,000–80,000 ha, occurred approximately every 12 years and were correlated with the La Niña phase of the El Niño Southern Oscillation and an associated decrease in dry season rainfall and lower surface water levels (Table 3). In modern times natural fire frequencies are often modified by human-initiated prescribed burns that are set to reduce fuel loads, control invasive exotics, or improve wildlife habitat (Lockwood et al. 2003).

Everglades fires are of two intensities: either severe peat-burning fires (muck fires) or less severe surface fires. The average area in which muck or hammock soils were burned during severe peat burning fires generally ranges from 33 to 47% of the total annual burned area (Taylor 1981), and the extent of muck fires are greater during large 12-year fire events. Severe peat-burning fires can reduce the soil surface of tree islands by 10–20 cm and destroy hammocks and tree islands (Loveless 1959; Loope & Urban 1980; Zaffke 1983; Newman et al. 1998). Smoldering ground fires can also create large holes in the peat, often burning deeper into soils at the base of trees (Watts & Kobziar 2013). The lowering of the peat surface after a muck fire will alter plant communities and initiate a new succession pathway. For example, wet prairies were observed to succeed to plant communities with longer hydroperiods (Loveless 1959; Davis et al. 1994; Newman et al. 1998) and muck fires reduced small tree island patches to herbaceous plant communities (Zaffke 1983, personal observation). Ruiz et al. (2013a) describe tree islands in the Marl Prairie region subjected to intense fire as skeleton islands. After burning, these islands have little or no soil, less than 10% vegetation cover and little probability of recovery. Fires that burn the surface vegetation and not the peat soil generally do not cause one plant community to succeed to another.

How vulnerable are tree islands to fire? The susceptibility of tree islands to fire varies and the conditions that allow tree islands to burn are not entirely understood. Tree island size may be a factor, as the cores of large tree islands have been observed to be less susceptible to fire although the margins of these islands burn (Wade et al. 1980; Silveira 1996). Once formed, tree islands may become fire-proof under climatic conditions of a moderate year, by developing a cool, moist understory microclimate and organic soils with a capacity to store moisture. Less fuel in the understory, in the form of herbaceous plants, to carry a fire may also be a factor. Hanan et al. (2010) also reported anecdotal information that large groups of tree islands deflect fire and interfered with its movement across the landscape. Such occurrences could perpetuate island clusters, especially during periods of low fire intensity events, and influence island patterning on the landscape.

In a study of tree islands in short hydroperiod marl prairies where tree islands range in size from several square meters to a few hectares, Ruiz et al. (2013a) found that marsh water level was the most important factor in determining whether an island burned or not during a large (16,250 ha) fire. The probability of a tree island burning increased as the water level decreased. The water level averaged about 30 cm higher near nonburned islands compared with burned islands. Tree island size was also negatively correlated with the probability of burning, but this was not as strong a predictor as marsh water level. However,



after 3 years larger tree islands were found to recover from the fire much better than smaller islands and tree island size was a strong predictor of tree island recovery from fire (Ruiz et al. 2013a). In their study about 4% of the tree islands that burned showed no signs of recovery. In a study of cypress domes in Big Cypress National Preserve, an ecosystem with tree patches like the Everglades, Watts et al. (2012) found that tree mortality was the same in large and small domes (tree patches); however, fire severity was greater on the dome edges than in the dome centers.

When fire history is known and included in factors that shape vegetation community analyses, fire is always identified as a major driver of tree island vegetation characteristics. Overall plant species richness increases on burned tree islands and is the result of a proliferation of herbaceous species (Wetzel 2002; Wetzel et al. 2008). However, canopy species richness was reduced on islands that experienced severe fire (Wetzel et al. 2008). Certain woody species tolerate fire better than other species and these fire-tolerant species are more common on frequently burned islands (Wetzel 2002). Multi-stemmed woody species that were burned generally resprout unless fire burns into the peat and kills the tree roots. Rapid flooding after a fire can eliminate or slow the recovery of woody species compared with the recovery of tree islands where water levels increased gradually (Sah et al. 2012; Ruiz et al. 2013a). Tropical hardwoods growing in hammocks were capable of resprouting after a fire of low or moderate intensity, surviving fires at approximately 5-year intervals (Loope & Urban 1980).

In terms of the number of tree islands, island size, and woody vegetation survival fire is a force that structures the Everglades landscape. Silveira (1996) created a simple model to predict changes in the Loxahatchee tree island communities with different fire severities through time. Fire controlled the number and sizes of tree islands through time. Short fire frequencies were predicted to reduce the number of small tree islands (75% of the islands in Loxahatchee are <1,500 m<sup>2</sup>; Brandt et al. 2002), but larger islands were left intact. As fire intervals increased 20–60 years, far beyond the 12-year severe fire frequency calculated by Beckage et al. (2003), the area of woody vegetation increased until tree islands lost the integrity of their shape (Silveira 1996; Brandt et al. 2002). While Silveira's (1996) model may not be entirely realistic, tree islands affect fire movement across the landscape and fire clearly shapes tree island vegetation communities and the presence and absence of tree islands on the landscape.

### Restoration Scenario Analyses

Our understanding of the ecology of tree islands and their role in the Everglades landscape identified three critical components necessary for their existence and continued function: the presence of trees, seasonally appropriate water flow, and oligotrophy. Trees capture nutrients in a large spatial area on the landscape from dust, roosting birds and through transpiration and concentrate them onto a small area. The concentration of nutrients increases plant growth, producing more organic matter and, over the years, increases the tree island elevation and footprint. Water flow moves captured nutrients downstream on

the island, eventually increasing its size, as well as shaping the island's outline and orientation. Oligotrophy in the surrounding marsh is necessary so that a nutrient gradient develops between the island and the surrounding landscape. If the surrounding marsh becomes as nutrient rich as the islands, the islands are overgrown and the landscape patterning created by tree islands disappears.

While several tree islands have been intensively studied, basic physical and biological information on a large number of tree islands across the landscape is limited. Evaluation of the effects of the SERES scenarios on tree islands required the use of existing information and needed to be tied to changing water levels as modeled by the SWMM model (South Florida Water Management District, West Palm Beach, FL, v. 5.0). The highest elevation points of 404 tree islands scattered throughout the WCA and the ENP were known and these elevations were compared with predicted water levels modeled for each scenario. Knowing the hydroperiods of common tree island woody species allowed the prediction of how well trees would thrive, thus tying the scenario evaluation to the presence of trees, one of the critical components of tree island existence. Tree island plant communities on nine islands were also modeled relative to water level for a more detailed analysis of potential scenario effects.

Data related to the other critical components of tree island existence and function, water flow and oligotrophy, did not exist for tree islands. However, the restoration scenarios investigated focused on different combinations of decompartmentalization and water storage, which produced varying levels of water flow, as well as P reduction which varied through the creation of storm water treatment areas (STAs). Five options were analyzed: ECB, CERP, PC, ESD, and MSD (Table 1). The reduction of barriers to surface water flows in the scenarios investigated ranged from 54% for the CERP and PC options to 90% reduction for the ESD and MSD scenarios with corresponding increases in water flows that were predicted to travel through the Everglades historically (Table 3). Choi and Harvey (this issue) predicted that the ESD and MSD options generally doubled the water flow speed (cm/second) in most regions compared with the existing conditions. They also predicted that the angle of water flow alignment to be similar to historic orientations for all options in all regions except northern WCA 3A and WCA 3B. There was little difference between scenarios ESD and MSD in either of these criteria.

To improve the reduction of P in overland flow with STAs their total acreage increased from 29,000 to 33,000 acres in the CERP and PC options from 39,000 to 47,000 acres in the ESD and MSD scenarios (Table 1). So, while water flow and oligotrophy information were not available to specifically apply to tree islands there is enough information on tree island ecology to assume that scenarios that increased water flow and reduced P will improve conditions over scenarios that do not have these benefits. Full descriptions of the scenarios are given in Wetzel et al., this issue.

### Landscape Level Tree Island Analysis

The average tree island head elevation for 404 tree islands spread throughout the Everglades were measured. Of the total



number of islands measured, 311 islands were located in WCA 3A, 29 islands in WCA 3B, and 64 islands in ENP. The islands in the ENP were located in Northeast Shark Slough (NESS) and further south in Shark Slough (SS). Daily water levels near each of the islands were modeled under the conditions of five scenarios with the SWMM model using weather data from 1965 to 2000. For each scenario, the percentage of time that the water level was above the surface of the tree island head was calculated for each island during the period of record (POR). The percentages were grouped together in the following categories:  $\leq 10\%$ , 11–25%, 26–50%, 51–75%, 76–99%, and 100%. The  $\leq 10\%$  and 11–25% groupings were calculated to capture tree islands that would support tree species with hydroperiods less than 36 days or between 37 and 91 days (Fig. 4). A category of 100% was calculated to determine the number of islands that would be permanently flooded in each scenario. The other categories covered the remaining range of hydroperiods.

A number of simplifying assumptions were made for this analysis. First, tree island elevations were measured on the island's area of highest elevation—the tree island head. This point represents a small area of the entire tree island, typically less than 0.1 ha or about 3–6% of the total area of the tree island (Heisler et al. 2002; Mason & van der Valk 2002). Because only the island head was compared with modeled water levels, plant communities at lower elevations on islands that are flooded for long periods will be altered or drowned. This analysis also made no attempt to determine water depth or the length of flooding on an island, two hydroperiod parameters that are critical for predicting plant community types at lower elevations. Therefore, if an island is predicted to be flooded for an extended period of time each year (on average 58 or 74% for example) it is not unreasonable to assume that the aerial extent of the island will shrink and that the plant communities on the island will be altered to plant communities that tolerate hydroperiods.

Second, not all flooding categories are expected to be present on all islands. This is especially true for the Hardwood Hammock community which is found in the southern Everglades. The hydroperiods of the major tree island plant communities—hammock (flooded 0–8% annually), bayhead (flooded 20–82% annually), bayhead-swamp (flooded 59–93% annually), and sawgrass (59–96% of the year) (Armentano et al. 2002; Ross et al. 2003; Ross et al. 2006; Sah et al. 2015)—could be used as a guide to predict how changing water levels in each scenario will affect the plant community on the tree island head. Predicting plant community changes from these scenarios is not precise as the hydroperiods of the plant communities overlap each other and the topography of the tree islands was not available.

Finally, model water depths were computed relative to the mean ground surface elevation over a approximately 10-km<sup>2</sup> model grid cell while island heights were measured relative to local benchmarks. Given the uncertainty of the hydrologic model, the imprecision of comparing model and field elevations, and the limited range of elevation points on an island, this analysis does not attempt to predict actual flooding durations or plant changes of specific islands. The predicted outcomes of

the analyses are relative to each other and the strength of this analysis is through comparison of the different scenarios.

### Plant Community Level Analysis

Changes of specific tree island plant communities on tree islands from the predicted hydrologic changes of the four restoration scenarios were modeled to consider community level changes. Vegetation structure and composition were recorded at 309 sites along hydrologic gradients on the nine tree islands, distributed in four water management regions. Four islands were in Central SS, two in NESS, two in WCA 3A, and one in WCA 3B. Plots were spaced at 30–42.2 m intervals coinciding with the centroidal coordinate of Landsat TM 30×30 m pixels. Vegetation was sampled using a nested plot design, and in each plot three representative water depth measurements were taken. Using field measurement of water depth and the Everglades Depth Estimation Network (EDEN) water surface elevation data of the same date, the ground elevation of each plot was estimated. For the plots on the head of seven tree islands within ENP and WCA 3B, where water level was below ground at the time of sampling, the ground elevation was based on the elevation survey from the water edge in the marsh to five locations in the hammocks (Ross & Sah 2011). Likewise, the ground elevation data for tree island hammock plots in WCA 3A were obtained from Furdi and Volin (2007). The ground elevation data were then used to calculate hydrologic characteristics of the sites using both the EDEN time series water surface elevation data, as well as hydrologic model output for the five restoration scenarios. Using a user-defined dichotomous key based on vegetation structure, the vegetation on the sites were classified into five groups—hardwood hammock, bayhead, bayhead-swamp, sawgrass, and marsh. The vegetation communities differed in hydroperiod and mean annual water depth, with some overlap among communities along the hydrologic gradient.

Having determined the hydrologic characteristics of the five major tree island plant communities, the Everglades Vegetation Succession Model (ELVeS), a simulation tool developed by South Florida Natural Resources Center, ENP (Pearlstone et al. 2011) was used to model the response of those tree island communities to hydrologic conditions under the different restoration scenarios. Twelve-year (2001–2012) average values of two hydrologic variables, discontinuous hydroperiod and mean annual water depth, were used in this analysis. A frequency histogram was created by calculating binned counts of the two hydrologic metric values within each tree island vegetation class. Skewed normal distributions were fit to these histograms using the Java Program, ELVeSkew (Ecological Modeling Team, South Florida Natural Resource Center, ENP), and the curves for each plant community were normalized to fit between 0 and 1. A temporal lag routine incorporated in ELVeS was used to ensure that in a changed environmental condition, an existing vegetation community was replaced by another community only after a defined inertial period. Different temporal lag probabilities were set for each vegetation community. Following Pearlstone et al. (2011), starting values were set for each community at 0.001, and end values were set as 4.5, 7.0,

10.0, 12.0, and 15.0 for marsh, sawgrass, bayhead-swamp, bayhead, and hammock, respectively. The model was run separately for each island and each restoration scenario.

### Landscape Level Results

For tree islands to function, environmental conditions must allow tree survival. Existing conditions of the Everglades ecosystem have created groups of tree islands that are either flooded too long each year causing woody vegetation to be drowned or that are so dry that flowing water is not available to rewet soils and move nutrients downstream off the tree island head, preventing islands from expanding. Islands in dry areas may also be more susceptible to peat fires that destroy the roots of woody vegetation (Zaffke 1983; Worth 1988). Results of the landscape level analysis were divided into three geographic regions—WCA 3A, WCA 3B, and the ENP—and restoration goals for tree islands depend on where the tree islands are located. For example, restoration goals for southern WCA 3A are to reduce water ponding caused by roadway levees. In the Shark River Slough the restoration goal is to increase water flow. Islands in those areas contain flood-intolerant species that are rarely flooded (Fig. 3), although some additional inundation would be tolerated, as long as it is less than 60 days annually (Sah 2004).

Under the existing hydrologic conditions most of the islands in WCA 3A are flooded between 11 and 75% annually (Table 4). This hydroperiod range indicates that these 232 islands are generally wetter islands with bayhead vegetation on their heads and bayhead-swamp vegetation in their near-tail and tail vegetation zones. They also probably have large sawgrass zones. Existing conditions in WCA 3B are drier, with nearly half of the islands sampled flooded  $\leq 10\%$  annually (Table 5), indicating a hardwood hammock type vegetation at least on the tree island heads. Most of the other islands in WCA 3B are flooded between 50 and 100% annually (Table 5) suggesting islands with predominately bayhead-swamp and sawgrass vegetation communities. Existing conditions in the islands sampled in the ENP are also drier with 73% of the islands sampled having island heads flooded  $\leq 10\%$  annually (Table 6). Most other islands sampled in the ENP were flooded long enough to support bayhead vegetation on their heads.

In terms of tree survival in WCA 3A, the compartmentalization modeled in all restoration scenarios increased the number of islands predicted to flood  $\leq 10\%$  annually from 108 to 173%, with the greatest increase predicted in the ESD scenario (Table 4). Many of the islands predicted to be drier were annually flooded between 51 and 75% under existing conditions. Except for two islands that would be permanently flooded in all but the CERP restoration scenarios, all of the restoration scenarios reduced flooded conditions in southern WCA 3A and improved the hydrology for the tree islands there. The MSD scenario produced the wettest conditions and had the lowest percent change of islands in all hydroperiods compared with existing conditions, a result of moving the greatest amount of water through the Everglades of any restoration option.

Hydrologic conditions in area WCA 3B were predicted to be generally wetter in the restoration scenarios compared with existing conditions and all scenarios produced roughly the same conditions for trees (Table 5). The number of dry islands (flooded  $\leq 10\%$  annually) decreased by 42% compared with existing conditions in all scenarios. Many of these islands were predicted to experience much wetter conditions. Between four and seven additional islands were predicted to be flooded between 76 and 99% annually for all scenarios (Table 5).

The restoration scenarios also created slightly wetter conditions for tree islands sampled in the ENP, with all scenarios predicted to create conditions that will make about 9% of the islands shift from the drier hydrologic regimes to the moderate (51–75%) and greater flooding regimes (76–99%) (Table 6). Nearly all of the islands currently experiencing annual flooding of  $\leq 10\%$  at their highest points will retain a hydrology that supports hardwood hammock tree communities, although their bayhead and bayhead-swamp communities may experience flooding. About 12% more of the islands were predicted to be flooded over 50% of the time each year compared with existing conditions, potentially encouraging those island plant communities to shift from bayhead to bayhead-swamp and sawgrass. The predicted results of flooding on tree islands in the ENP were similar across all restoration scenarios.

### Plant Community Level Results

Hydrologic modeling of all restoration scenarios predicted that NESS, SS, and WCA 3B will experience wetter conditions and extended periods of annual flooding compared with existing conditions. Wetter conditions reflect the goal of these scenarios to move more water southward through the Everglades ecosystem. However, the mean annual water depth in the tree island communities will not increase uniformly across all three regions. Our modeling predicted that water depth will increase by 5–10 cm in central SS, and by 15–20 cm in both NESS and WCA 3B. In contrast, on the two tree islands WCA 3A the plant communities will experience greatly reduced water levels and hydroperiods. Bayhead and Bayhead-Swamp communities, which are flooded for 60–70% of a year in the existing condition, will remain flooded for only 20–40% of a year, a notable drying trend within islands of that area.

Despite the model predictions of wetter conditions in NESS, SS, and WCA 3B, the plant communities on the seven islands modeled in those regions showed little or no change for any of the restoration scenarios compared with the existing conditions (results not shown). In contrast, the drier conditions predicted by the restoration scenarios in WCA 3A are expected to increase the relative abundance of woody species on the two tree islands modeled. The number of sites with bayhead communities will increase about 80% for all scenarios, accompanied by a decrease in the number of shrub (–75%) and marsh (–53%) communities (Fig. 5).

The ELVeS model produced a result that appears to happen in a time frame faster than expected. This was the occurrence of sawgrass/marsh in the model results at sites where other woody communities are found because conditions during the second

**Table 4.** Tree islands in WCA 3A (311 islands total) with mapped average high points and the percent time they are expected to flood annually under different restoration scenarios. The percent change in the number of islands compared with the existing conditions is also given for the four different restoration scenarios.

Island Hydroperiod (% time flooded annually)	Number of Islands					Percent Change in Number of Islands Compared With Existing Conditions			
	Existing Conditions (ECB)	CERP	PC	ESD	MSD	CERP	PC	ESD	MSD
≤10	71	184	175	194	148	159	146	173	108
11–25	71	48	51	47	57	–32	–28	–34	–20
26–50	70	43	50	45	64	–39	–29	–36	–9
51–75	91	26	27	15	36	–71	–70	–84	–60
76–99	8	10	6	8	4	25	–25	0	–50
100	0	0	2	2	2	0	200	200	200

**Table 5.** Tree islands in WCA 3B (29 islands total) with mapped average high points and the percent time they are expected to flood annually under different restoration scenarios. The percent change in the number of islands compared with the existing conditions is also given for the four different restoration scenarios.

Island Hydroperiod (% time flooded annually)	Number of Islands					Percent Change in Number of Islands Compared With Existing Conditions			
	Existing Conditions (ECB)	CERP	PC	ESD	MSD	CERP	PC	ESD	MSD
≤10	12	7	7	7	7	–42	–42	–42	–42
11–25	1	3	3	1	2	200	200	0	100
26–50	3	3	3	4	4	0	0	33	33
51–75	8	4	5	6	7	–50	–38	–25	–13
76–99	5	12	11	11	9	140	120	120	80
100	0	0	0	0	0	0	0	0	0

half of the 1990s, which is also the final years of the model period, were very wet, and the probability of occurrence of the relative wet sawgrass/marsh community was much higher in those conditions. As the model period ended in similarly wet conditions, much different from the drier conditions in the first decade of the 21st century, those communities did not get reversed to woody communities. A more robust temporal lag routine may improve the sensitivity of the model parameters and robustness of the model output and make the output closer to observations of tree island community dynamics. However, if we assume that any error due to uncertainty in the model runs were the same in the four regions across all scenarios, the model results highlight important findings relative to each other.

## Conclusions

Tree islands have limited resilience as field observations, our literature review, and mechanistic modeling have shown (D’Odorico et al. 2011). Extended disturbances of hydrology on the woody vegetation beyond a critical threshold shift tree islands to ghost islands and eventually marshes. Even if the disturbance that caused tree islands to shift from woody patches to marsh were removed, the marshes are themselves stable and tree islands will not be restored. Limited tree island resilience and the potential lack of recovery after tree islands become ghost or skeleton islands presents a challenge for restoration.

The existence and maintenance of tree islands requires three critical aspects of ecosystem function in the Everglades: water

levels that allow the regeneration and survival of trees, seasonally appropriate pulsed water flow, and oligotrophy. Examination of the restoration scenarios analyzed by the SERES team found that when compared with the existing conditions, all of the restoration scenarios investigated appeared to improve or be neutral to the survival of trees on tree islands located in WCA 3A and the ENP. All of the proposed restoration options greatly increased the number of island heads predicted to be flooded ≤10% annually in WCA 3A. A reduction in shrub and marsh sites was also predicted on the two islands with the detailed vegetation analyses. A small area of Hardwood Hammock communities was also predicted to occur on the two islands under all scenarios, where none had existed in the baseline conditions.

In the ENP, the hydrology of most islands did not change although 12% of the islands analyzed were predicted to have wetter conditions. Wetter conditions were predicted for tree islands in WCA 3B, where half of the islands analyzed moved from the driest to the wettest categories. While the landscape analyses predicted differences between regions, there was little difference between the predicted outcomes of tree survival for the different scenarios.

While a specific restoration scenario did not stand out as best for tree survival (except ESD for WCA 3A, which had the highest number of islands with hydrology less than 10% annually), scenarios ESD and MSD are expected to produce high flow events, conditions needed to produce vigorous pulses of sheetflow for weeks per year in a direction parallel to the



**Table 6.** Tree islands in Everglades National Park (64 islands total) with mapped average high points and the percent time they are expected to flood annually under different restoration scenarios. The percent change in the number of islands compared with the existing conditions is also given for the four different restoration scenarios.

Island Hydroperiod (% time flooded annually)	Number of Islands					Percent Change in Number of Islands Compared With Existing Conditions			
	Existing Conditions (ECB)	CERP	PC	ESD	MSD	CERP	PC	ESD	MSD
≤10	47	45	46	45	45	-4	-2	-4	-4
11–25	2	2	2	2	2	0	0	0	0
26–50	8	2	3	2	2	-75	-63	-75	-75
51–75	4	9	7	9	9	125	75	125	125
76–99	3	6	6	6	6	100	100	100	100
100	0	0	0	0	0	0	0	0	0

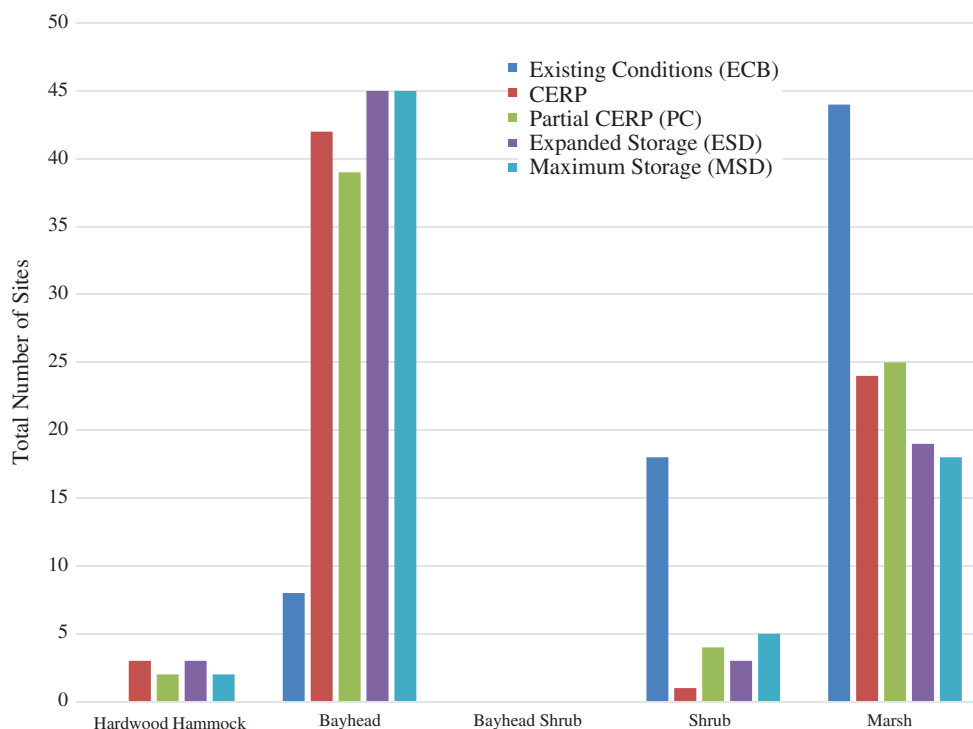


Figure 5. Numbers of different vegetation communities predicted by the ELVeS model after 36 years (1965–2000) on two tree islands in Water Conservation Area 3A under five hydrologic options.

grain of the remnant landscape patterning. Managing for such landscape-scale flow patterns is very likely to be effective in halting further degradation of the ridge–slough–tree island mosaic in areas where remnant ridge–slough topography still exists. These two options also had the greatest area of additional STAs, which are expected to maintain oligotrophic conditions in the Everglades. Given these two major advantages, our analyses identified either ESD or MSD as the preferred restoration scenario.

None of the scenarios appear to be catastrophic in their predicted effects. However, the landscape analysis and, to a lesser extent, the community-level analysis suggests that all scenarios will change, and on many islands, greatly alter the vegetation communities. This is not surprising as the Everglades

was grossly under-hydrated for approximately 100 years. Our knowledge of Everglades’ soil dynamics suggests that similar low water levels in the past probably caused tree islands to lose elevation (Givnish et al. 2007; Larsen et al. 2011)—possibly up to 4 mm/year as measured on a strand island in WCA 2A over a recent 36-year period (Aich et al. 2014). Such a reduction in elevation results from physical soil compaction and aerobic decomposition. These elevation-reducing actions would be offset by vegetation accumulation each growing season. It is hard to know whether elevation reduction or elevation accumulation processes have dominated during the drainage of the Everglades. However, it is safe to expect that most tree islands lost elevation as the Everglades was drained. It should be remembered that tree islands are dynamic and it is expected that tree islands will be

able to adjust to some extent to the new hydroperiods created by restoration.

Our tree island analyses did not consider all factors that are known to be important to tree island maintenance and preservation and it only considered a fraction of the tree islands. Each of the restoration scenarios considered will jeopardize the survival of certain individual tree islands; however, the overall results are predicted to be a great improvement over existing conditions. Monitoring and measuring landscape and local tree island restoration indicators will be essential for a truly successful restoration of the slough–ridge–tree island landscape.

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