Maintaining tree islands in the Florida Everglades: nutrient redistribution is the key

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The Florida Everglades is an oligotrophic wetland system with tree islands as one of its most prominent landscape features. Total soil phosphorus concentrations on tree islands can be 6 to 100 times greater than phosphorus levels in the surrounding marshes and sloughs, making tree islands nutrient hotspots. Several mechanisms are believed to redistribute phosphorus to tree islands: subsurface water flows generated by evapotranspiration of trees, higher deposition rates of dry fallout, deposition of guano by birds and other animals, groundwater upwelling, and bedrock mineralization by tree exudates. A conceptual model is proposed, in which the focused redistribution of limiting nutrients, especially phosphorus, onto tree islands controls their maintenance and expansion. Because of increased primary production and peat accretion rates, the redistribution of phosphorus can result in an increase in both tree island elevation and size. Human changes to hydrology have greatly decreased the number and size of tree islands in parts of the Everglades. The proposed model suggests that the preservation of existing tree islands, and ultimately of the Everglades landscape, requires the maintenance of these phosphorus redistribution mechanisms.

Areas with high nutrient concentrations and rates of nutrient cycling relative to the surrounding landscape represent biogeochemical hotspots (McClain *et al.* 2003). Biogeochemical hotspots occur where the flow paths of nutrients converge, often as a result of intersecting water flows. However, wind and biological agents (plants and animals) are also known nutrient vectors. Converging flow paths, and the resulting concentration of nutrients, occur across multiple scales, from the molecular to the global (McClain *et al.* 2003). The flow of nutrients, energy, organic matter, and organisms between communities or ecosystems is often asymmetrical, resulting in spatial subsidies of these components to a particular location on the landscape, with corresponding local changes in community dynamics (Polis *et al.* 1997). The spatial coupling of component ecosystems within a larger meta-ecosystem may result in the development of nutrient sinks or sources and diversity–productivity patterns on the landscape (Loreau *et al.* 2003).

The Florida Everglades is one example of a meta-ecosystem with differentiated ecosystem components. This complex freshwater wetland ecosystem covers approximately 10 000 km^2 across the southern tip of the Floridian peninsula. Tree islands are one of four major natural landscape features that make up the Everglades (Figure 1), the others consisting of sawgrass (*Cladium jamaicense*) plains and ridges, graminoid marshes (wet prairies), and deepwater sloughs (Kushlan 1990; David 1996). We consider the Everglades a meta-ecosystem, with tree islands and non-tree islands (marshes and sloughs) as component ecosystems. In this paper we describe how the focused redistribution and differential capture of limiting nutrients between these components contributes to the spatial complexity of the Everglades landscape.

In a nutshell:

- Tree islands in the Everglades have declined substantially in number and area in the past 55 years because of human alterations to the hydrology of south Florida
- Soil phosphorus levels on tree islands are up to 100 times higher than those in the surrounding marshes and sloughs, creating biogeochemical hotspots
- Greater canopy leaf area and height may redistribute nutrients to tree islands, primarily through evapotranspirational pumping of groundwater and higher rates of dry deposition; this nutrient subsidy is believed to be essential for tree island maintenance and expansion
- The loss of tree islands has diminished landscape complexity and may have reduced an important phosphorus sink within the Everglades
- Restoring the nutrient redistribution systems associated with lost tree islands may play a key role in the restoration of the Everglades

■ Everglades tree islands as biogeochemical hotspots

The Everglades is an oligotrophic wetland system that is limited by phosphorus (Davis 1994; Noe *et al.* 2001). Total phosphorus (P) levels in natural sawgrass and slough surface waters average 10.8 ± 4.8 μg L^{-1} and < 400 mg kg^{-1} in soils (McCormick *et al.* 2002). Phosphorous is

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limited in the Everglades for two reasons. First, precipitation is the largest hydrologic input into the Everglades (86% of the total water budget), with atmospheric deposition historically contributing 90% of the total P (Davis 1994). Because the Everglades has little exposed bedrock and no natural terrigenous sediment input, geological sources of P have historically been small. Secondly, the P that does enter the system is intercepted by floating periphyton mats (Noe *et al.* 2001). High calcium (Ca) concentrations enable periphytic algae to precipitate calcium carbonate ($CaCO_3$), which leads to the precipitation of Ca–P compounds or the co-precipitation of phosphates (PO_4) with $CaCO_3$ (Otsuki and Wetzel 1972). High pH levels also enable inorganic phosphorus to be bound by magnesium, aluminum, and iron compounds in surface soils (Reddy *et al.* 1998).

Tree islands cover only a small percentage of the Everglades (Sklar and van der Valk 2002), but they number in the thousands, with more than 2000 in Water Conservation Area 1 (WCA–1) alone (Brandt *et al.* 2002). (The historic Everglades north of the Everglades National Park is divided into five large water conservation areas, or WCAs, completely or partially surrounded by levees that allow the manipulation of water levels.). Tree islands range in area from 10 m^2 to >700 000 m^2 (70 ha) and typically have elevations only 0.2–1.0 m above surrounding areas. Nevertheless, in this flat landscape, this is enough elevation to provide environmental conditions that can support a wide variety of trees, shrubs, and other plants and animals that otherwise could not exist in the Everglades (Loveless 1959; McPherson 1973; Meshaka *et al.* 2002). Tree islands have a variety of shapes, including tear-drop, elongated oval, and round. Vegetation on larger islands can be divided

Figure 1. *Tree islands in the Everglades landscape on the edge of the Big Cypress National Preserve, in WCA–3. Tree islands are embedded in a matrix of sawgrass plains and ridges, emergent marshes, and deepwater sloughs.*

into zones, characterized by decreasing elevation and stature of vegetation from the upstream head to the downstream tail (Figure 2; Mason and van der Valk 2002).

It has only recently been discovered that tree islands are biogeochemical hotspots. Soil P levels on the heads and near tails of tree islands (Figure 2) are 6 to 100 times higher than in the surrounding marsh (Orem *et al.* 2002; Jayachandran *et al.* 2004). On tree islands, higher P levels also occur in soil pore water, as compared to the surrounding marsh (Table 1). Furthermore, a sharp nutrient gradient exists within each tree island, such that the highest P levels are found on the head and the lowest generally at the far tail (Figure 2).

■ Changes in hydrology and declining tree islands

The Everglades has a neotropical climate, characterized by a wet season (May–October) with high water levels (50–150 cm) and a dry season (November–April) with low water levels (10–50 cm; Thomas 1974). Surface water generally flows south from Lake Okeechobee through an intricate system of sloughs (and now canals), collects in the low areas of the Loxahatchee Channel, Tamiami Basin, and Shark River Slough, and finally flows into the Gulf of Mexico and Florida Bay (Fennema *et al.* 1994; Gleason and Stone 1994). It is clearly apparent, based on the orientation and comet shape of many tree islands, that surface waters historically flowed from north to south through the Everglades.

Groundwater flow patterns are less well understood, but generally flow from the center of the Everglades towards the coasts

Table 1. Mean values of total P, NO_3, Ca, Cl, and pH in soil pore water from two tree islands

Island	Parameter	Head		Near tail		Tail		Slough	
3AS3	Total P	0.23	(0.01)	0.07	(0.04)	0.06	(0.01)	0.00	
	NO_3	0.01	(0.00)	0.02	(0.01)	0.01	(0.00)	0.01	(0.00)
	Ca	130.79	(13.61)	85.77	(4.96)	46.25	(3.74)	63.10	(2.81)
	Cl	123.00	(54.77)	23.78	(1.45)	17.47	(0.64)	15.75	(0.74)
	pH	7.2	(0.1)	6.3	(0.1)	6.4	(0.1)	6.2	(0.1)
3BS1	Total P	0.44	(0.06)	0.13	(0.04)	0.01	(0.00)	0.01	(0.01)
	NO_3	0.24	(0.10)	0.01	(0.00)	0.01	(0.00)	0.04	(0.03)
	Ca	61.66	(2.68)	53.08	(2.51)	49.13	(3.40)	71.44	(7.87)
	Cl	34.60	(5.66)	28.46	(3.35)	26.23	(3.75)	31.29	(2.56)
	pH	6.8	(0.1)	6.6	(0.1)	6.7	(0.1)	6.7	(0.1)

Parameters measured on the head, near tail, and tail on each island and from the surrounding slough. All parameters are mg L^{-1} except pH. Standard errors in parentheses. Courtesy of S Newman, South Florida Water Management District.
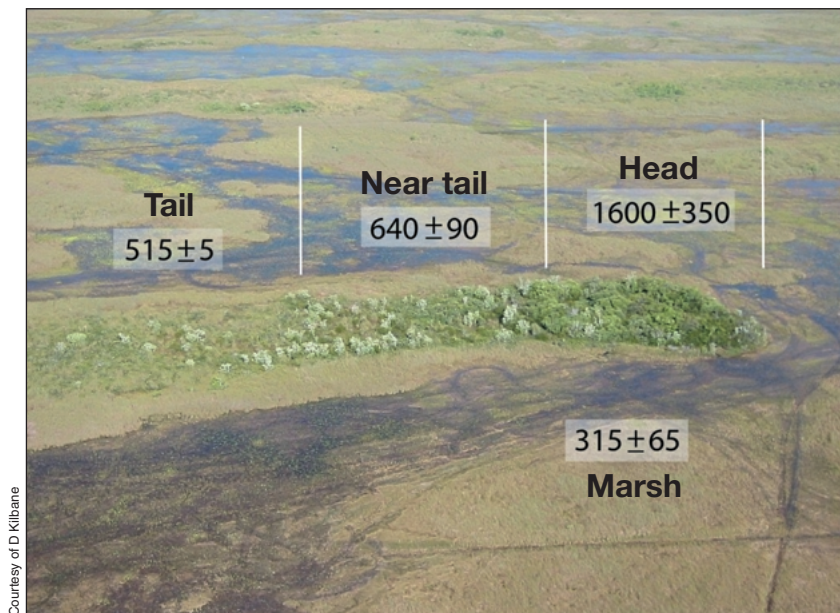
Figure 2. Most tree islands have distinctive vegetation zones that correlate with specific island locations. The most upstream position on the island is termed the head; this area has the highest elevation, largest trees, and greatest number of upland species. Total soil P concentrations on the head of tree islands could be 6 to 100 times higher than the surrounding marsh (values shown in this figure are means from Orem et al. [2002] and S Newman unpublished). Surrounding the head, at a slightly lower elevation, is the near tail, which contains smaller, woody trees. Downstream of the near tail is the tail, an area of sparse shrubs and trees, ferns, marsh plants, and sparse sawgrass. Dense sawgrass dominates the far tail of the island (not shown), the area of lowest elevation and furthest downstream of the head. Total soil P levels generally decrease from head to tail.

(Fennema *et al.* 1994). The groundwater system flows through a karstic limestone and dolomite bedrock that is honeycombed with fissures, vertical fractures, and solution holes that create a highly permeable aquifer system with extensive interaction between the upper Floridian aquifer system and surficial aquifers (Johnston and Bush 1988). Phosphorite-bearing sediments (Hawthorn Group) underlie much of the southern Florida peninsula (Compton 1997; Brand 2002) and groundwater has the potential to bring this P to the surface.

Today, canals and levees have greatly modified the hydrology of the entire Everglades (Sklar *et al.* 2002). A change in hydrologic regime that results in shorter or longer hydroperiods can kill the woody vegetation on a tree island as a result of increased fire frequency and intensity, or by drowning the trees (Figure 3a). Over the past 55 years, both the number of tree islands and the area they cover have declined substantially in the Everglades, especially in WCA–2 and WCA–3. A comparison of all tree islands greater than 1 ha in the central Everglades (WCA–3; Figure 3b) was made using aerial photographs taken between 1940 and 1995; the results showed that tree island area declined by 67%, while the number of islands declined by 54% (Patterson and Finck 1999).

Other parts of the Everglades have undergone even greater changes in tree island area and number. In WCA–2A the total number of tree islands declined by 87% between 1953 and 1995 (Hofmockel 1999). This loss of islands was not uniform across all island size classes. The number of small islands (< 3.2 ha) decreased by 98%, while the number of large islands (> 43.3 ha) remained the same. The loss of most of the small islands led to a decrease in island density, from 16 to three islands per 100 ha, and the nearest distance from one island to another increased from 253 m in 1953 to 874 m in 1995. This loss of tree islands has resulted in a reduction in overall landscape complexity (Sklar *et al.* 2004).

■ Phosphorus redistribution mechanisms

The mechanisms by which nutrients are redistributed from marshes and sloughs to tree islands are not well studied. However, field observations and studies from the Everglades and from other patterned wetlands suggest that there are three major redistribution mechanisms: (1) subsurface water flows to islands, generated by evapotranspiration of trees; (2) higher deposition rates of dry fallout; and (3) deposition of guano on islands by birds and other animals (Figure 4). Over time, other sources of nutrients may also increase the total mass of P on tree islands. These include groundwater upwelling beneath or adjacent to islands, and bedrock mineralization. We will first review what is known about major nutrient redistribution mechanisms and then briefly consider other possible sources of nutrients.

Major redistribution mechanisms

We suggest that evapotranspiration rates are higher on tree islands than in the surrounding marshes and sloughs, causing the groundwater and dissolved nutrients to flow towards tree islands. Groundwater levels in wells on and around several tree islands in the Everglades have been observed to drop from the period between approximately 0900–1800 hrs each day during the dry season, indicating higher transpiration rates on tree islands than in the surrounding marsh and slough communities (Reed and Ross 2004; S Krupa unpublished). A similar pattern of diurnal water level changes under tree islands has also been observed in the Okavango Delta (Botswana). Here, when the precipitation of dissolved compounds from groundwater is taken up by trees, it is believed to be responsible for the vertical and horizontal growth of tree islands (McCarthy *et al.* 1993). Nutrient mass flow driven by differential transpiration has also been proposed as an expla-
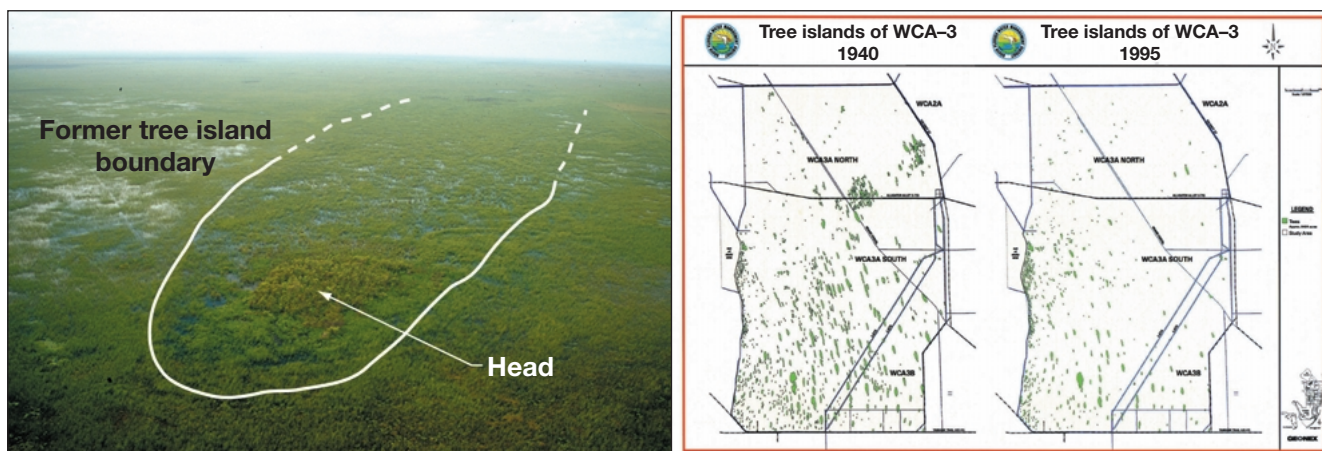
Figure 3. *(a) A degraded tree island in WCA–2A. (b) A comparison of tree islands in the central Everglades (WCA–3) between 1940 and 1995.*

nation for vegetation patterning in northern bog ecosystems (Rietkerk *et al.* 2004).

As noted earlier, atmospheric deposition (wetfall plus dryfall) was the primary source of P for the historic Everglades ecosystem (Davis 1994; Noe *et al.* 2001). Estimates of mean P deposition rates in the Everglades and southern Florida are between 40.7 and 62 mg P m^{-2} year^{-1} and range from 11.3 to 118 mg P m^{-2} year^{-1}, with the interior of the peninsula experiencing the lowest deposition rates (Redfield 2002). Dry atmospheric deposition has not been measured on tree islands in the Everglades; however, we hypothesize that it should be considerably higher on islands because forest edges are very effective at trapping dry fallout (Weathers *et al.* 2001; Redfield 2002) and tree islands are, in effect, mostly forest edges. Dry deposition has been found to make substantial contributions to the nutrient cycles of many other wetland ecosystems (Blank *et al.* 1999; Krah *et al.* 2004). In the Okavango, which is in a sandy, arid region of Africa, so much dust is trapped by tree islands that it can directly increase their elevations over time (Krah *et al.* 2004).

Wading birds also move nutrients from the sloughs, where they feed on fish, frogs, and invertebrates, to their rookeries on tree islands (Kahl 1964; Burton *et al.* 1979). Such nesting sites can significantly elevate soil P levels on tree islands (Lund 1957). For example, a nesting colony of 5450 nests in 1987 was calculated to deliver 900 mg P m^{-2} yr^{-1} to a tree island, a P input of about 20 times the annual input from other sources (Frederick and Powell 1994). P loading from larger colonies could have been 3000 times the annual atmospheric deposition rate (Frederick and Powell 1994). In the Everglades, the bird guano deposition under rookeries results in luxuriant vegetation, which has been observed to persist for up to 50 years following aban-

donment (Frederick and Powell 1994). Major nesting colonies probably changed location over time, though little is known about how long rookeries were used and where they were located in the past (Ogden 1994). There are, however, many more tree islands than there are wading bird rookeries. The establishment of a rookery would result in a major nutrient input, and this could have a considerable impact on rate of growth of islands and their eventual size. Many other animals (eg migrating passerines, alligators, deer, etc) also use tree islands (Meshaka *et al.* 2002), and they could also redistribute nutrients there.

Other sources of nutrients

Phosphorous in phosphorite-bearing sediments (formed in the Miocene Period by diagenesis and later reworked into Pleistocene deposits; Compton 1997) may be transported to
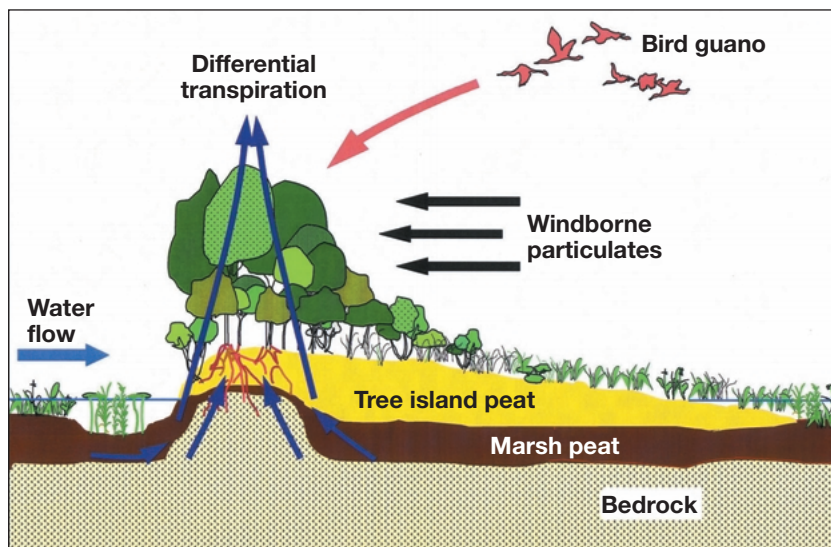

Figure 4. *Major mechanisms that redistribute nutrients from marshes and sloughs to tree islands in the Everglades. Tree islands capture more windborne particulates than surrounding marshes because of their taller plant canopies. Subsurface water flows towards them because of higher evapotranspiration rates, and they attract birds and other animals to nest or rest, resulting in guano deposits on the island.*
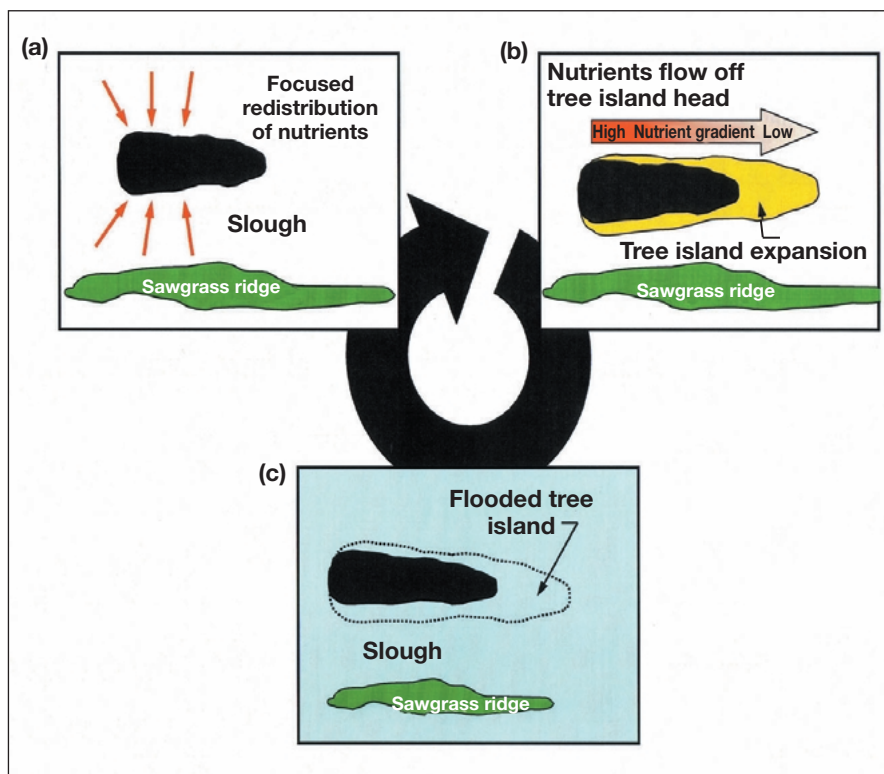
Figure 5. *Cycle of tree island expansion and contraction. (a) Nutrients are redistributed from the surrounding landscape onto the tree island. (b) Nutrients leach from the head as a result of surface and groundwater flows, creating a nutrient gradient that is highest on the tree island head and lowest on the tail. This increases primary productivity behind the head and results in increased rates of peat deposition, which in turn increases the elevation and size of the island. (c) Islands can continue to expand until a disturbance (eg prolonged flooding, fire) reduces tree abundance. As long as some trees remain on the head after the disturbance, focused redistribution will replenish lost nutrients and another period of expansion will begin (ie back to [a]).*

tree islands. This is suggested by the fact that there are tree islands (eg those that form floating mats of vegetation or peat) that do not have access to P in underlying bedrock.

■ A model of tree island expansion

The mechanisms that allow for the differential distribution of nutrients require that tree islands already exist. The initiation of tree islands on the landscape may involve a completely different suite of mechanisms, which are not addressed in this paper. Instead, we propose a conceptual model to explain how the focused redistribution of nutrients is necessary for the expansion of tree islands (Figure 5). In our model, P is transported to tree islands, at the expense of nearby marshes and sloughs, by tree evapotranspirational pumping of groundwater, differential dry fallout, and animals (Figures 4, 5a). This focused redistribution of nutrients increases local primary production, which in turn increases the rate of peat deposition and thus the magnitude (eg height or area) of a tree island. The pattern of P distribution within an island (Figure 2) suggests that P deposited on the head of the island moves downstream, where its increases plant growth and/or results in higher rates of peat accumulation, ie tail formation (Figure 5b). Nutrients from decomposing plant material on the head may then be moved off the island head in several possible ways: (1) by erosion during extreme flow events; (2) by leaching into surface water passing over the head during the wet season; or (3) by leaching into shallow groundwater (Sklar and van der Valk 2002). As islands grow, more trees and shrubs become established. The resulting positive feedback loop means that islands can continue to grow in size until some disturbance (fire or flooding) reduces tree abundance (Figure 5c). Our model suggests that tree island size and age are correlated and that larger tree islands have higher total amounts of P per unit area, but this has not yet been tested.

Focused nutrient redistribution leading to the development of tree islands has been documented in other large peatlands, including northern Minnesota (Glaser *et al.* 1981; Siegel 1981), Mexico's Yucatán Peninsula (Rico-Gray 1982), and in non–peatlands such as the Okavango Delta (Ellery *et al.* 1998). There is, however, remarkably little detailed information on the annual input of nutrients into the Everglades' tree islands by any redistribution mechanism. Consequently, we know very little about the relative importance of the various redistribution mechanisms.

tree islands by ground-water upwelling. In the Everglades, there is an extraordinary degree of hydrologic connection between surface waters, surficial aquifers, and tree islands, as demonstrated by the high hydraulic conductivities (the rate at which water moves through the ground) around tree islands (Harvey *et al.* 2000; Bevier and Krupa 2001). Elevated chloride concentrations, an indicator of groundwater, have been reported in the pore water on some tree islands (Table 1; S Newman unpublished). It is not known how often tree islands are located in areas of groundwater discharge.

When the limestone bedrock is close to the surface, as occurs in some tree islands, the potential exists for nutrients in the limestone to become available to the trees. Plants commonly release organic acids from their roots and this acidification of the rhizosphere allows immobilized inorganic P to be released or desorbed from the limestone into the soil solution (Gillespie and Pope 1990; Mengel and Kirkby 2001). Microorganisms (bacteria and fungi) can also solubilize inorganic P by producing organic acids, making the P available to plant roots (Kucey *et al.* 1989; Vazquez *et al.* 2000). However, the mining of P from limestone by trees is probably a minor component of the overall P budget of

Conclusions

Our observations indicate that tree islands in the Everglades store large amounts of P, which is transported to tree islands by numerous focused redistribution mechanisms acting concurrently. We predict that for most tree islands the continuous nutrient inputs from subsurface water flow due to tree evapotranspiration and dry deposition are more important than episodic inputs from wading birds and other animals, as nutrient inflow resulting from these two mechanisms remains relatively constant year round. We also hypothesize that episodic, large nutrient inputs are needed in order for islands to grow beyond a certain size. The establishment of a wading bird rookery on a tree island may be such an event.

Changes in the hydrology of the Everglades have resulted in the loss of a substantial number of tree islands. Field observations and a few studies (Wetzel 2002) indicate that both indirect effects (eg increased period of flooding) and direct effects (eg increased fires) were responsible. With the loss of large numbers of tree islands the local redistribution of nutrients in the Everglades meta-ecosystem also ceased in many places, reducing the effectiveness of an important internal P sink in this region, which may result in increasing nutrient levels in the rest of the Everglades. As the number and area of tree islands decline, marsh and slough ecosystems should receive more nutrients, become more productive, and begin to accumulate more organic matter. This in turn could reduce the ridge and slough topography that historically was found throughout the Everglades, and may account for the measured reduction of landscape complexity in some areas (Sklar *et al.* 2004).

The current restoration plan for the Everglades emphasizes the restoration of historic hydrologic flow and periodicity and a reduction of anthropogenic sources of P. Restoring traditional hydrologic flows should reduce the extended flooding or drying of tree islands. Keeping P levels at historic concentrations will maintain localized nutrient gradients between tree islands and the surrounding marsh. Low P levels in the ecosystem will also reduce the ability of invasive exotics to become established and spread. Both of these efforts are essential for the preservation of the remaining tree islands.

However, restoration of lost tree islands is currently not a goal of the Everglades restoration plan (Restoration Coordination and Verification 2005). In addition to preserving the remaining tree islands, complete restoration of the Everglades may require restoring lost tree islands to increase the landscape complexity needed to re-establish important nutrient redistribution mechanisms and P sinks. Such an effort will require future studies that focus on hydrologic management favorable to functional tree islands, methods to replant trees on damaged islands, and techniques to initiate new tree islands from levees that will be degraded as part of the hydrologic restoration.

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