Heterogeneity of phosphorus distribution in a patterned landscape, the Florida Everglades

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Abstract The biologically mediated transfer of nutrients from one part of a landscape to another may create nutrient gradients or subsidize the productivity at specific locations. If limited, this focused redistribution of the nutrient may create non-random landscape patterns that are unrelated to underlying environmental gradients. The Florida Everglades, USA, is a large freshwater wetland that is patterned with tree islands, elevated areas that support woody vegetation. A survey of 12 tree islands found total soil phosphorus levels 3–114 times greater on the island head than the surrounding marsh, indicating that the Florida Everglades is not a homogeneous oligotrophic system. It was estimated that historically 67% of the phosphorus entering the central Everglades was sequestered on tree islands, which are ∼3.8% of the total land area. This internal redistribution of phosphorus onto tree islands due to the establishment of trees may be one reason that marshes have remained oligotrophic and may explain the spatial differentiation of the patterned Everglades landscape.

Keywords Meta-ecosystem · Nutrient redistribution · Restoration · Tree islands

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Introduction

The redistribution of nutrients and detritus has long been recognized as an important phenomenon at the landscape level. Materials, in the form of plant and animal litter, dissolved compounds, soil particles, dry fallout (dust), and feces, can be moved into and out of ecosystems by both abiotic and biotic transport mechanisms, especially wind, water, and many kinds of organisms. One of the first documented and best studied examples is the input of tree leaf litter into the

upper reaches of streams and its significance for riverine food webs (Vannote et al. 1980). Numerous other "spatially subsidized food webs" have also been recognized and studied (Polis et al. 1997, 2004; Jefferies 2000). One consequence of these inter-ecosystem transfers is an increase in the productivity of the subsidized ecosystem and a decrease in the productivity of the donor ecosystem. Another consequence, especially if the materials being transferred are limiting biological productivity, is that nutrient gradients are created that can lead to landscape heterogeneity (Rietkerk et al. 2004a). Other implications of these energy and nutrient subsidies for the subsidized and donor ecosystems continue to be a topic of great theoretical and practical interest (Jefferies 2000; Chadwick et al. 1999; Loreau et al. 2003; McClain et al. 2003; Breshears 2006).

Geomorphological changes may also result from biologically mediated inter-ecosystem transfers, a phenomena recognized by Hutchinson (1950) in his detailed survey of sea-bird guano deposits on coastal islands around the world. Guano deposited by sea bird colonies on oceanic islands often altered both their elevation and vegetation. These deposits formed because sea birds nesting on these islands exploit large "trophophoric fields" in comparison to the size of the islands. Geomorphologic changes can also result from the establishment of certain plants, causing subsequent impacts on the movement of materials within a landscape. In recent years, evidence has accumulated that suggests that geomorphological changes in landscapes due to the establishment of plants, typically tree species, are much more widespread than were previously recognized, especially in wetlands (Dangerfield et al. 1998; Wetzel 2002; Wetzel et al. 2005).

The Florida Everglades is a phosphorus limited (Noe et al. 2001), oligotrophic freshwater meta-ecosystem. It is a complex mosaic of tree islands and a variety of non-forested ecosystems. Non-forested ecosystems, which comprise most of the Everglades, include sawgrass (*Cladium jamaicense*) plains and ridges, graminoid emergent marshes (wet prairies), and deepwater sloughs (David 1996; Kushlan 1990). Hereafter, we will refer to these various non-forested wetland types as marshes. Although tree islands number in the thousands, they cover only a small percentage of the Everglades (Sklar and van der Valk 2002).

Tree islands range in size from 10 to >700,000 m^2 (70 ha). Their maximum elevations are only 0.2–2.5

m above surrounding areas. The small difference in elevation of these forested islands on the flat Everglades landscape is large enough to support a wide variety of plants and animal species that otherwise could not survive in the Everglades (Loveless 1959; Meshaka et al. 2002). Vegetation on larger tree islands is characterized by decreasing elevation and stature from the upstream head to the downstream tail and can be divided into zones described as the head, near tail, and far tail (Fig. 1; Mason and van der Valk 2002). The head, which is at the northern upstream end, has the highest elevation and the tallest vegetation. The near tail has a lower elevation and shorter vegetation than the head. The far tail has the lowest elevation and shortest vegetation which is a mix of scattered shrubs and wetland species found in the surrounding marsh. Tree islands developed over the last 1,000–3,000 years, and mature tree vegetation on two large tree islands is known to have been present for 500–1,200 years (Willard et al. 2002).

Tree islands are initiated by the establishment of tree species on somewhat higher ground. These points of origin can develop for many different reasons, including irregularities in the underlying bedrock, peat pop-ups, and animal and human activities (Wetzel 2002; Sklar and van der Valk 2002). Once trees become established, it is hypothesized (Wetzel et al. 2005; Ross et al. 2006) that the focused redistribution of nutrients (especially phosphorus) begins. Three major redistribution mechanisms have been identified: evapotranspirational pumping of surface and groundwater toward the island (Ross et al. 2006), higher dry fallout deposition (Wetzel et al. 2005), and the increased deposition of animal,
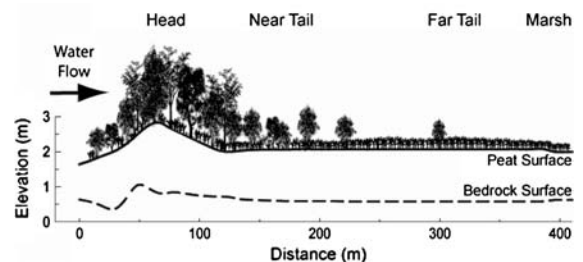

Fig. 1 Longitudinal section of a tree island from the central Everglades (peat and bedrock elevations from D. Mason, unpublished data) with the location shown of the head, near tail, far tail, and surrounding marsh. Elevation exaggerated 20×

especially bird, feces (Frederick and Powell 1994). The relative importance of these redistribution mechanisms for a given tree island is not known. Other mechanisms of phosphorus redistribution include transport of phosphorite-bearing sediments in upwelling groundwater (Wetzel et al. 2005), the mobilization of phosphorus in the limestone bedrock by tree roots and associated microorganisms (Wetzel et al. 2005), and prehistoric human activities (Carr 2002). Dry deposition and evapotranspirational pumping may be the most important nutrient redistribution mechanisms for most islands (Wetzel et al. 2005). Avian deposition of feces varies significantly from island to island, and an island with a large wading bird rookery can have annual phosphorus loadings 3,000 times annual atmospheric deposition (Frederick and Powell 1994). Most tree islands, however, do not have rookeries.

Because of the focused redistribution of phosphorus, tree islands grow in size over time, creating a positive feedback mechanism that increases the size of tree islands and the overall landscape complexity in the Everglades. The development of non-random landscape patterns that are unrelated to underlying geophysical gradients has also been described in other resource-limited landscapes such as the Okavango Delta, Botswana (Ellery et al. 1993), northern peatlands (Rietkerk et al. 2004a), and arid landscapes (Breshears 2006; Lejeune et al. 2002; Rietkerk et al. 2002). The focused redistribution of scarce resources (water, nutrients, and energy) due to the establishment of trees appears to be a unifying mechanism that can explain the spatial differentiation of many kinds of landscapes (Breshears 2006; Wetzel et al. 2005).

We predicted that if significant redistribution of phosphorus has occurred in the Everglades from marshes to tree islands, soil phosphorus levels should be higher on tree islands than in surrounding marshes. It was also hypothesized that soil phosphorus levels would be related to tree island elevation. It was expected that soil phosphorus would be greater on highly elevated islands because if phosphorus contributed to the island's expansion then phosphorus accumulation is expected to be greater on these islands. Finally, considering phosphorus redistribution across the entire Everglades landscape, we estimated the percentage of phosphorus entering the Everglades ecosystem that is expected to be redistributed onto tree islands.

Comparison of tree island and marsh soil phosphorus levels

If phosphorus entering the Everglades is redistributed from non-forested ecosystems to tree islands, a measurable pattern should be present across the landscape and on multiple island types. We reviewed all available data, both published and unpublished (from Newman, Coronado, and Orem), on total phosphorus (TP) measurements from fixed islands (islands that form "in place" and may have small bedrock platforms or pinnacles associated with the head of the island) collected between 1998 and 2005 (Table 1, Fig. 2). The previously unpublished soil phosphorus samples were collected in the following manner. Soil cores were collected from the head, near tail, and far tail along the middle of the island parallel to the long axis of the island and in the marsh 100–350 m to the west or east of the head of the tree island. Cores were collected to a depth of 45 cm using a stationary piston coring device and then sectioned into 2–10 cm increments. Each interval of sediment was put into a plastic bag and stored on ice in a cooler until taken back to the laboratory. The samples were analyzed for TP and bulk density. These procedures were similar to the methods used to measure soil

Table 1 Total soil phosphorus concentrations at three depths on the heads, near tails, and far tails of 12 tree islands and adjacent marshes in the Everglades

Soil depth (cm)	Total phosphorus (g m^{-2a})			
	Marsh	Head	Near Tail	Far Tail
0–10				
Mean (SE)	6 (1)	421 (93)	18 (4)	21 (15)
Median	5	35	8	8
Range	2–12	6–3,576	4–233	4–80
10–20				
Mean (SE)	3 (0)	699 (131)	34 (7)	7 (1)
Median	3	67	11	7
Range	2–3	5–5,539	4–347	4–11
20–30				
Mean (SE)	2 (0)	775 (257)	36 (4)	5 (1)
Median	2	95	15	4
Range	1–3	8–6,078	3–307	3–6

[a] Square meter over a depth of 10 cm

Data sources: S. Newman and C. Coronado, South Florida Water Management District; W. Orem, U.S. Geological Survey; Jayachandran et al. 2004
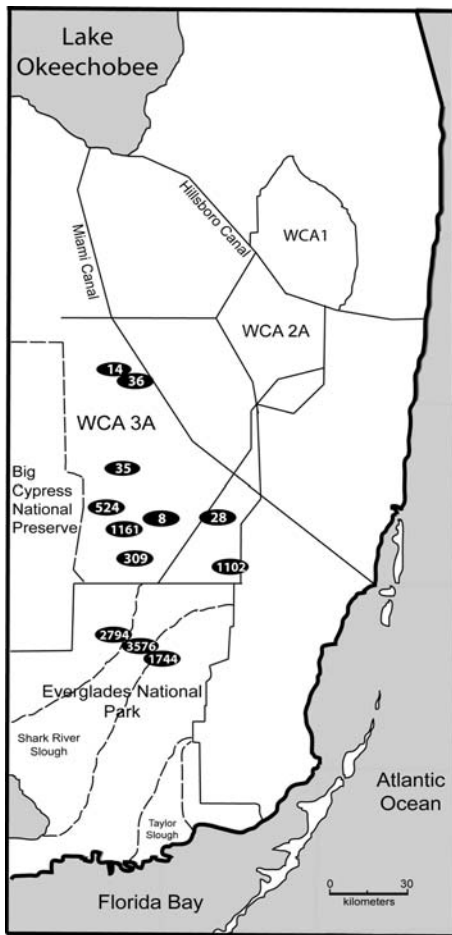
Fig. 2 Location of the tree islands analyzed in this study. Values indicate the total soil phosphorus (g TP m^{-2}) in the soil 0–10 cm depth on the heads of the tree island

phosphorus in the published data used in this article (Jayachandran et al. 2004).

On the heads of tree islands, total soil phosphorus (TP) levels in the upper 10 cm of soil averaged 421 g m^{-2} compared with 6 g m^{-2} in surrounding marshes. TP levels on the heads of islands, however, were highly variable and ranged from 6 to 3,576 g m^{-2}. Near tail TP concentrations in the upper 10 cm were about 20 times lower (18 g m^{-2}) than on heads (Table 1), and mean far tail concentrations (21 g m^{-2}) were similar to mean near tail concentrations. At lower soil depths (10–20 and 20–30 cm), where the age of the peats may be between 100 and 2,000 years (Willard et al. 2002), TP concentrations were higher on heads and near tails than in the upper 10 cm but were lower on far tails at greater depths. At 10–30

cm in the far tail, soil TP levels were comparable to those in the adjacent marshes in the upper 10 cm.

Maximum head elevations of the 12 islands ranged from 0.2 to 2.3 m above surrounding areas. Head TP to adjacent marsh TP ratios were positively correlated with head elevation ($r^2 = 0.81$, $P = 0.0005$; Fig. 3). The head to marsh TP ratio increased until island elevations reached 1.5 m after which the P ratio tended to level off (Fig. 3). However, there is TP data for very few high elevation islands, and this trend could be an artifact. The simplest explanation for the direct correlation of tree-island elevation and TP levels is that high elevation tree islands are older, have larger trees, and have had more time to accumulate phosphorus. Unfortunately, the ages of only a couple of these islands are known with any certainty.

It is also likely that drier conditions on the heads of tree islands which are not frequently inundated result in higher organic matter decomposition rates. This could contribute to the buildup of P in the soil over time. The upper 10 cm of soil on heads had the highest bulk density (0.26 g cm^{-3}, SE = 0.02) compared to 0.14 g cm^{-3} (SE = 0.01) on the near tail and 0.11 g cm^{-3} (SE = 0.01) in the marsh. Soils on tree island heads were peats (bulk density < 0.60 g cm^{-3}, Collins and Kuehl 2001), but the higher bulk density values indicate that they were more decomposed than peats at lower elevations in the near tail and marsh. Differences in bulk density (ca. 50%) per se between heads and tails can only account for a
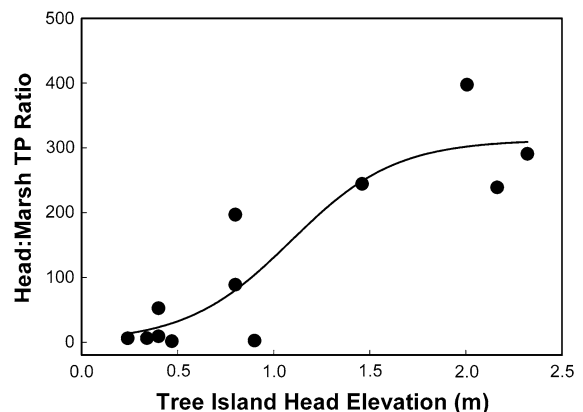

Fig. 3 Relationship between the ratios of total soil phosphorus (g m^{-2} in the upper 10 cm) on the head to the surrounding marsh and the maximum elevation of the tree island heads ($r^2 = 0.81$; $P = 0.0005$) for 12 tree islands in the Everglades

small amount of the more than 20-fold difference in their soil TP.

Little is known about the specific forms of phosphorus on tree islands. Based on samples from one tree island with an active bird rookery, inorganic phosphorus accounted for 71–92% of the TP (Orem, unpublished data). In contrast, organic phosphorus was 90% of the phosphorus stored in the surrounding marsh soils. In WCA 3, organic phosphorus makes up 80% of the total soil phosphorus (Bruland et al. 2006). Frequent oxidation of elevated heads will result in microbial mineralization of organic phosphorus to inorganic phosphorus. However, recent X-ray diffraction identified the inorganic phosphorus as an amorphous apatite, a form of phosphorus that could originate from birds (Sklar et al. 2007). Increased accumulation of phosphorus in the soil profile (0–20 cm) in association with increased uric acid (the end product of nitrogen metabolism in birds that is excreted in feces) content also supports that birds were the dominant source of phosphorus on this tree island with an active rookery (Sklar et al. 2007).

Phosphorus sequestration on tree islands

Using an average sedimentation rate calculated from two tree islands that are well removed from any anthropogenic influences and whose development had been well studied (Orem et al. 2002), for the upper 10 cm of soil on the heads and near tails of these islands, the estimated phosphorus accumulation rate was 1.05 and 0.05 g TP m^{-2} year^{-1}, respectively, but only 0.01 g TP m^{-2} year^{-1} in the marsh. Estimates of phosphorus inputs into Water Conservation Area 3 from precipitation (rain only) are 0.033 g TP m^{-2} year^{-1} (Davis 1994) and from dust deposition (dry fallout) in southern Florida are 0.062 g TP m^{-2} year^{-1} (Redfield 2002). The much higher rate of annual phosphorus accumulation on heads provides some insight into the magnitude of total annual phosphorus redistribution to tree islands from or at the expense of surrounding marshes. Less than 10% of the annual TP input to the heads of tree islands can be ascribed to mean annual inputs associated with wet and dry fallout. In effect, 1 m^2 of tree island head seems to be sequestering annually the equivalent of the annual wet and dry fallout input on 10 m^2 of marsh.

Landscape-level phosphorus redistribution was further explored by estimating the amount of phosphorus sequestered in tree islands of WCA 3 using TP soil data from soil 0–30 cm deep. These calculations assumed that all the phosphorus in the system was eventually sequestered in the soil. All tree islands in 1940 in WCA 3, the first year aerial photographs were available, covered 3.8% (8,911 ha) of its total area. This estimate includes only tree islands whose heads and near tails were greater than 1 ha. Using the tree island area mapped in 1940, it was estimated that 67% of the TP in WCA 3 was stored on tree islands.

Nutrient data from tree islands and our estimates of phosphorus distribution on the landscape indicate that the Everglades is not a homogeneous oligotrophic system and that much of the phosphorus stored in the soil is concentrated on tree islands. These findings suggest that the internal redistribution and sequestration of phosphorus onto tree islands may be one reason that the marshes and sloughs have remained oligotrophic in the Everglades. A similar phenomenon was found in the Okavango Delta in Botswana where tree islands in that system collectively have a significant impact on the Delta's water chemistry (McCarthy and Ellery 1994). Because tree islands sequester dissolved mineral salts in the groundwater, the accumulation of mineral salts in the surface water of the wetlands is minimized, and this has prevented the Okavango from becoming a saline wetland. At the scale of the entire Okavango, tree islands collectively have a significant impact not only on the water chemistry of the Delta, but also on the geomorphology and on the distribution of its animals and plants.

Nutrient redistribution and tree island restoration

The widespread conversion of the eastern and northern Everglades over the last 65 years to agricultural, mining, and urban land uses, as well as human modifications to the hydrology of the entire system reduced the number and aerial extent of tree islands in WCA 3 and throughout the Everglades (Fig. 4). By 1995, tree islands represented 1.5% (3,434 ha) of the total area of WCA 3, a 60% reduction since 1940. If tree islands historically sequestered about 67% of the TP entering the Everglades, then this decline in the area of tree
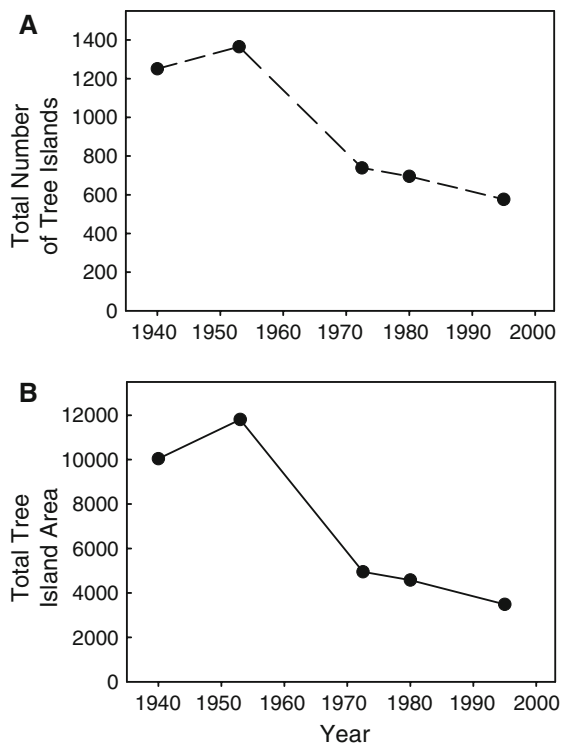
A

B

Fig. 4 Tree island change in Water Conservation Area 3 of the Florida Everglades between 1940 and 1995. (**a**) Change in the number of tree islands ≥1 ha in area. (**b**) Change in tree island area (only tree islands ≥1 ha in area were included)

islands (up to 90% locally) suggests that phosphorus is now more uniformly sequestered in the Everglades. In addition, over the last 100 years the number of wading birds in the Everglades has declined up to 90% (Ogden 1994). Thus, some historic and extant tree islands may not have accumulated phosphorus at pre-drainage rates, further reducing the redistribution of phosphorus on the landscape. Both factors are predicted to result in the gradual eutrophication of the marshes in the Everglades. An increase in slough and marsh productivity in certain areas, coupled with a decline in tree islands and historical water velocity rates through the system, could result in the further reduction of the microtopography that characterizes the ridge-slough-tree island landscape of the Everglades (Sklar et al. 2003).

Recently developed models of arid-patterned ecosystems identified shrubs as a spatially explicit resource concentration mechanism to explain landscape vegetation patterns (Lejeune et al 2004; Rietkerk et al. 2004b). These spatial models indicate

that the presence of a resource concentration mechanism creates an ecosystem with patterned and homogenous alternative stable states. It appears that changing levels of the limiting resource will affect the level of self organization or amount of patterning on the landscape. If the limiting resource is scarce, then a patterned stable state exists. But if the limiting resource increases then the ecosystem shifts to a homogeneous stable state (Lejeune et al 2004; Rietkerk et al. 2004b). Thus, a catastrophic shift from one alternative state to the other can result from the loss of the resource concentration mechanism or a change in the level of the limiting resource.

In the Everglades, human induced hydrologic changes have both eliminated the resource concentration mechanism (reduced tree island area) and potentially increased the overall level of soil phosphorus in the marshes. In areas of the Everglades where agricultural runoff increased soil phosphorus levels threefold since the 1970s (McCormick et al. 2002), the landscape patterns have disappeared. The alternative stability domains of the marshes in these disturbed areas, which are defined by the soil nutrient content (Gunderson and Walters 2002), are characterized by a shift in the dominant vegetation from tree islands surrounded by sawgrass and wet prairies to no or few tree islands and cattail. In areas without direct agricultural runoff but with a highly modified hydrological regime that reduced or eliminated tree islands (the nutrient concentration mechanism), a less patterned homogenous stability domain also prevails. If the spatially explicit models of Lejeune et al (2004) and Rietkerk et al. (2004b) accurately describe the Everglades ecosystem, then in areas without direct agricultural runoff the resource concentration mechanism must be restored to enable the ecosystem to shift to a patterned stable state. Restoring the resource concentration mechanism onto the Everglades landscape will thus require the restoration of tree islands, which will likely require the re-establishment of hydroperiods similar to historic conditions and the planting of trees on the heads of former tree islands.

Summary

In summary, the Everglades is not a homogeneous oligotrophic system. The focused redistribution of

phosphorus from marshes to tree islands has significant implications for understanding why its marshes have remained oligotrophic. The available data suggest that the redistribution of phosphorus onto tree islands is the major reason why marshes have remained oligotrophic in spite of thousands of years of non-anthropogenic phosphorus inputs from outside. A similar phenomenon was found in the Okavango Delta in Botswana where tree islands in that system collectively have prevented the salinization of the surrounding wetland (McCarthy and Ellery 1994).

The ongoing multi-billion dollar restoration of the Everglades has tree islands as a performance measure but has not yet designated tree island restoration as one of its goals due to many uncertainties (Sklar et al. 2005; Wetzel et al. 2005). Available data on the role of tree islands in the overall phosphorus biogeochemistry of the Everglades suggest that the focused redistribution of phosphorus within this meta-ecosystem is essential for its long-term survival. Without tree island restoration as part of the Comprehensive Everglades Restoration Plan, it may not be possible to completely restore the functionality of the Everglades meta-ecosystem.

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