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Wading bird guano enrichment of soil nutrients in tree islands of the Florida Everglades

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HIGHLIGHTS

- Tree island soil P concentration and $\delta^{15}N$ values exceed other Everglades soils.
- Characteristics of Everglades tree island soil may indicate guano deposition.
- Deposition of stable guano P can exceed other P sources to tree island soil.

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ABSTRACT

Differential distribution of nutrients within an ecosystem can offer insight of ecological and physical processes that are otherwise unclear. This study was conducted to determine if enrichment of phosphorus (P) in tree island soils of the Florida Everglades can be explained by bird guano deposition. Concentrations of total carbon, nitrogen (N), and P, and N stable isotope ratio ($\delta^{15}N$) were determined on soil samples from 46 tree islands. Total elemental concentrations and $\delta^{15}N$ were determined on wading bird guano. Sequential chemical extraction of P pools was also performed on guano. Guano contained between 53.1 and 123.7 g-N kg^{-1} and 20.7 and 56.7 g-P kg^{-1}. Most of the P present in guano was extractable by HCl, which ranged from 82 to 97% of the total P. Total P of tree islands classified as having low or high P soils averaged 0.71 and 40.6 g kg^{-1}, respectively. Tree island soil with high total P concentration was found to have a similar $\delta^{15}N$ signature and total P concentration as bird guano. Phosphorus concentrations and $\delta^{15}N$ were positively correlated in tree island soils ($r = 0.83$, $p < 0.0001$). Potential input of guano with elevated concentrations of N and P, and ^{15}N enriched N, relative to other sources suggests that guano deposition in tree island soils is a mechanism contributing to this pattern.

1. Introduction

Determination of mechanisms controlling nutrient transport and transformations in soil is essential for wetland restoration planning and management. The Florida Everglades is a large (~10,000 km^2), primarily freshwater wetland (Wetzel et al., 2005). Drainage and flood control projects constructed within the region resulted in the conversion of wetland habitat to agriculture and urban land uses (Davis, 1994; Light and Dineen, 1994; DeBusk et al., 1994). These projects, and subsequent nutrient loading, altered historic nutrient and hydrologic regimes in the region (DeBusk et al., 1994). Restoration activities are ongoing throughout the Everglades and mostly focus on water delivery and control of phosphorus (P), a limiting nutrient in this highly oligotrophic ecosystem. An area of marsh is described as P-enriched when soil total P concentrations exceed 500 mg kg^{-1} (McCormick et al., 1999; Debusk et al., 2001).

The patches of trees and shrubs slightly elevated above the surrounding marsh are collectively described as tree islands (Sklar and van der Valk, 2002). Tree island soil P concentrations in the Everglades are reported to exceed the concentration of native marsh soil within the system, in some cases by two orders of magnitude or more (Orem et al., 2002; Wetzel et al., 2005; Ross and Sah, 2011).

Nutrient accumulation in tree island soil is primarily attributed to three mechanisms: evapotranspirational groundwater and surface water pumping by tree species, atmospheric deposition and deposition

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of animal waste (Wetzel et al., 2005; Ross et al., 2006). Accumulation of nutrients in tree island soils likely occurs at variable spatial and temporal scales among islands. If nutrient accumulation is variable among islands, differences could be attributable to the interactions between local surface and groundwater hydrologic gradients, differential vegetation patterns and wildlife distribution. Dramatic differences reported between tree island and marsh soils, and among tree island soils, may indicate that the mechanisms controlling P distribution between landforms may also influence distribution of P among islands. Soil P concentration of reconstructed tree islands, near the northern Everglades, was similar to marsh soil suggesting that tree island age may also play a role in soil nutrient accumulation (Rodriguez et al., 2014). Natural deposition or accumulation of P in high quantities may support an emerging theory for the ecology of the Everglades where high soil P and ecosystem health are no longer mutually exclusive (Wetzel et al., 2011).

Identification of P source is often challenging because of the complexity of P biogeochemistry. Wildlife species, particularly colonial nesting birds, have been described as potentially significant biovectors for nutrient transport, especially in the oligotrophic Everglades, and also in other wetland habitats (Bildstein et al., 1992; Frederick and Powell, 1994; Post et al., 1998). In the Everglades, wading birds generally forage in the emergent marshes and roost in patches of trees and shrubs dispersed throughout the ecosystem.

Spatial variation in foraging, and perching or nesting location within the ecosystem suggests a potential transport mechanism for nutrient redistribution (Frederick and Powell, 1994). Wading birds also seasonally nest in the Everglades in high density at many locations. Translocation of marine-derived nitrogen (N) and P to terrestrial island environments by seabirds, through guano deposition, is a mechanism for soil nutrient enrichment (Hutchison, 1950; Anderson and Polis, 1999; Wait et al., 2005). Similarly in the Everglades, transport of nutrients, particularly N and P, from marsh-derived prey items through bird guano deposition has been hypothesized to influence the distribution of soil P throughout the ecosystem resulting in elevated soil P concentration in tree island soils (Orem et al., 2002; Wetzel et al., 2005). For example, large nesting aggregations of birds may be capable of importing metric tonnes of P annually (Frederick and Powell, 1994). Nutrient transport alone does not comprise a mechanism for nutrient accumulation, unless the deposited nutrients have been transformed to a relatively stable form.

Little is known about the magnitude of the hypothesized mechanisms that may control nutrient accumulation and distribution in tree island soil. Deposition of high P content animal wastes such as guano, dropped food or carcasses in natural ecosystem settings can occur in discrete locations such as nesting sites of avifauna. Frederick and Powell (1994) suggested that where Everglades wading birds nest in high density, P deposition by avifauna may approach 3000 times the atmospheric P deposition rate, thereby playing an important role in nutrient redistribution. Guano deposition by avian species is one of the primary hypotheses offered to explain high concentrations of P in Everglades tree islands (Wetzel et al., 2005, 2011). Birds have been associated with nutrient focusing in wetlands and on islands located in marine environments (Post et al., 1998; Anderson and Polis, 1999; Wait et al., 2005; Macek et al., 2009). Anderson and Polis (1999) reported seabird guano deposition elevated soil P concentration up to six times higher than unaffected soil. Although an investigation conducted by Wait et al. (2005) focused on N inputs from guano deposition, their data also indicated a ~18:1 difference in soil P observed in guano affected islands versus non-guano islands.

Determination of the P concentration and forms of P in wading bird guano from the Everglades may provide insight regarding a mechanism of P transportation, and fate of P, within the ecosystem. The transport of P by birds from marsh habitat to tree islands in the Everglades, and the subsequent accumulation of P in tree island soil have been suggested as a mechanism that contributes to the oligotrophic status of the marsh (Wetzel et al., 2005). Although nutrient transport by birds to islands in marine ecosystems has been well described, similar information for the Everglades is not widely available. Contribution of P derived from bird guano to tree islands may be reflected by similarities between chemical properties of soil and guano. The purposes of this study were to: (1) chemically characterize wading bird guano collected from the Everglades, (2) investigate tree island soil characteristics and correlations among properties, and (3) estimate mass deposition of nutrients at Everglades tree islands from guano.

2. Materials and methods

2.1. Site locations, descriptions and sample collection

Soil was collected from 46 tree islands between 2005 and 2011 in the central and southern Everglades, Florida, USA (Fig. 1). All soil samples were collected from the head region of the tree island, which is the location most likely to have the highest concentration of soil P (Wetzel et al., 2009). The samples were oven-dried, and passed through a 2 mm mesh sieve prior to analysis. Soil samples were collected from depths ranging from of 0–5 cm ($n = 17$) and 0–10 cm ($n = 29$). These sampling depths were selected because this study focused on investigating shallow surface soil from numerous tree island in the Everglades and to compare P concentrations reported in subsurface soil layers at two tree islands in the Everglades by Orem et al. (2002).

Information describing survey and mapping of tree island soil in the Everglades is limited, and often soil within tree island habitat is described as peat (Wetzel et al., 2009; Ross et al., 2003; Leighty and Henderson, 1958). Coultas et al. (1998) described mineral soils within two tree islands in the southern Everglades. The few tree island locations with available soil survey data, classify the soils as Histosols (USDA, 1996).

Vegetation varies among tree islands ranging from upland species intolerant of extended periods of soil saturation, to swamp forest species capable of persisting during stages of soil saturation and standing

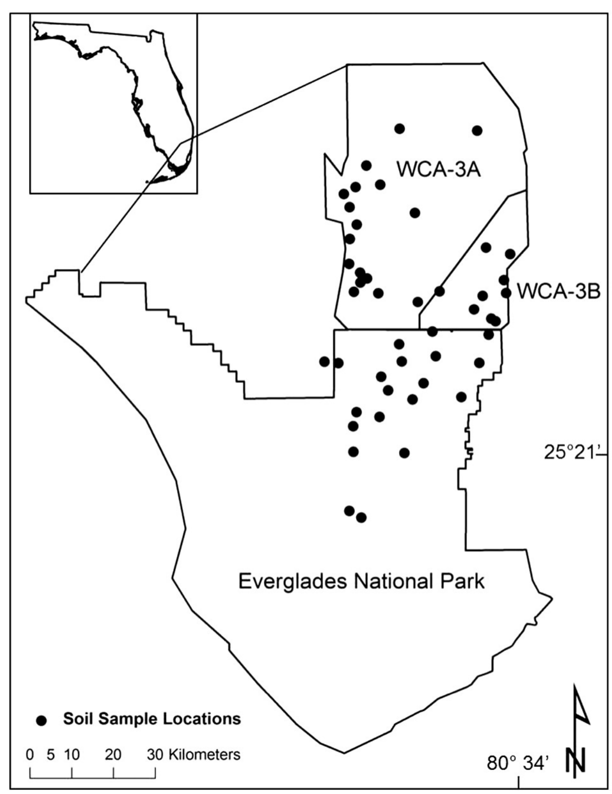

Fig. 1. Site map depicting tree island soil sample locations relative to the boundaries of Water Conservation Area 3A (WCA-3A), Water Conservation Area 3B (WCA-3B) and Everglades National Park, Florida, USA.

water. Foliar samples (n = 11) from *Magnolia virginiana*, *Salix caroliniana*, *Chrysobalanus icaco*, *Myrica cerifera*. Small *Cephalanthus occidentalis*, *Blechnum serrulatum*, and *Acrostichum danaeifolium* were collected at tree islands in the Everglades. Foliar samples were oven-dried and ground prior to analysis.

Bird guano and mammal feces samples were also collected from tree islands in the Everglades. Guano material was collected as a single composite sample from an island on the day of each site visit. Guano samples (n = 4) were homogenized, oven dried (60 °C) and ground prior to analysis. Wading bird species present when guano samples were collected included *Eudocimus albus*, *Egretta tricolor*, *Egretta thula*, *Ardea albus*, *Egretta caerulea*, and *Mycteria americana*. Mammal feces samples (n = 10) included *Odocoileus virginianus*, *Sylvilagus floridanus*, *Sus scrofa* and *Procyon lotor*, and were identified as described by Zhu et al. (2014).

2.2. Elemental analysis

Total carbon (C) and N of soil and guano were measured by dry combustion using an elemental combustion system (Costech Analytical Technologies, Inc., Valencia, CA). Total P was determined by heating 200 mg of dried sample at 550 °C and dissolving the residual material in 6 M HCl. The P concentration in solution was then measured colorimetrically on a spectrophotometer (Beckman Instruments, Inc., Fullerton, CA) as described by Murphy and Riley (1962). The pH of guano was determined in a 5:1 solution to dry matter ratio.

The concentrations of total aluminum (Al), calcium (Ca), iron (Fe), magnesium (Mg) and potassium (K) in the same HCl solution analyzed for total P of guano were analyzed by inductively coupled plasma-optical emission spectroscopy (PerkinElmer, Inc., Waltham, MA). Although Al is not an essential plant nutrient, the concentration of Al in guano was determined because of the relationship this element has with soil phosphorus chemistry. Matrix specific standards for Al, Ca, Fe, Mg and K were utilized for instrument calibration. Replicate samples, certified reference material (SRM 1547) and matrix specific sample blanks were analyzed within each trace element analytical run.

2.3. Stable N isotope analysis

Analysis of total N stable isotopic ratios was performed by combustion using a Thermo-Finnigan MAT Delta^{Plus} XL mass spectrometer (Bremen, Germany) at the University of Florida Soil and Water Science Department Stable Isotope Mass Spectrometry Laboratory (Inglett et al., 2007). Sample isotopic ratio (R) of $^{15}N/^{14}N$ is reported as δ value (‰) relative to atmospheric N_2, where $\delta\ (‰) = [(R_{Sample} / R_{Standard}) - 1] \times 1000$. Standard material (USGS 40) was utilized for instrument calibration. Sample replicates and standard material were analyzed within each analytical run. The analytical precision for analysis of the standard material was ±0.1‰.

2.4. Phosphorus fractionation

Different forms of P were determined by a sequential chemical extraction method which was modified based on techniques developed from soil and poultry litter P characterization (Hieltjies and Liklema, 1980; Kou et al., 2009; He et al., 2010). The fractionation scheme employed sequentially separated P pools using distilled deionized water (DDI), 1.0 M KCl, 0.1 M NaOH, and 0.5 M HCl. Residue present after the 0.5 M HCl extraction was measured for total P, and is defined as residual P. Phosphorus was extracted from composite guano samples by adding 25 ml of solution and sample (sample:solution ratio of 1:50) to a 50 ml centrifuge tube. The sample and solution mixtures were shaken with a reciprocating mechanical shaker and allowed to equilibrate. Equilibration times were 1, 2, 17 and 24 h for DDI, 1.0 M KCl, 0.1 M NaOH and 0.5 M HCl respectively. After equilibration, sample solutions were centrifuged at 2100 ×*g* for 15 min, filtered (Whatman No. 42) and refrigerated at 4 °C prior to P analysis. Phosphorus measured in filtrates was assumed to be soluble inorganic P (Pi) and was determined colorimetrically as described above. Sodium hydroxide (NaOH) solutions were also measured for TP by persulfate digestion. Difference between dissolved Pi and total P in the NaOH solution is described as organic P (Po). Phosphorus recovery was within ±10% of the total P concentration for each sample. This study focused on total elemental analysis in soil and guano, and P chemical fractionation in guano. Future studies could investigate organic and inorganic pools of Ca, N and K, and electric conductivity in wading bird guano and tree island soil.

2.5. Elemental mass deposition calculation

Cation characterization of wading bird guano was utilized for calculation of nutrient deposition and loading rate. Nutrient deposition was calculated based on the mass of guano dry matter deposited per nest attempt described by Frederick and Powell (1994). Briefly, data derived from analysis of guano dry matter were used to determine the mass of each element, and P pool, deposited per nesting attempt by multiplying the dry matter nutrient concentration by the mass of dry matter deposition. Annual area-based loading rates were calculated by estimating nesting abundance at two continuously active wading bird colonies, one located in northeastern WCA-3A (~75 ha) and the other located in southwestern WCA-3A (~1.1 ha). Colony area was determined using aerial imagery. Annual nesting data for *E. albus*, *E. tricolor*, *E. thula*, *A. alba* and *E. caerulea* was compiled from South Florida Wading Bird Reports for 1998 through 2010 (Irick, 2012; Zhu et al., 2014). Areal deposition rates were determined based on the estimated annual nesting densities and mass deposition per nest.

2.6. Data analysis

All statistical analyses were conducted using SAS version 9.2 (SAS Institute, Inc.). Samples were characterized using descriptive statistics. Soil samples were also categorized based on total P concentration using 1 g kg^{-1} as the threshold between low- and high-P soils. This threshold was established because it is twice the concentration (0.5 g kg^{-1}) typically considered as an indicator of P enrichment in Everglades soils (McCormick et al., 1999). Prior to classifying the soils based on P concentration, correlation coefficients for soil total P with total C and N, and $\delta^{15}N$ were determined in order to justify combining soil samples collected from different depths. Correlation of soil total P concentration with total C and N, and $\delta^{15}N$ signature was described using Pearson Product–moment Coefficient. The differences in soil properties between soil P categories, and differences of total P concentration and $\delta^{15}N$ signature of bird guano and mammal feces evaluated using a Student's T-test. Total P concentration of tree island plant leaves were also compared for differences with bird guano using a Student's T-test. Data were log transformed prior to analysis.

3. Results

3.1. Guano characterization and deposition

Guano pH was near neutral, and based on dry weight was 23% C (Table 1). Total Ca, N and P cumulatively comprised approximately 30% of the guano mass (Table 1). In addition to Ca, N and P comprising a relatively large proportion of the guano, it was enriched in ^{15}N relative to atmospheric N and the $\delta^{15}N$ signature varied among samples ranging from 7.8 to 10.6‰ (Table 1; Irick, 2012; Zhu et al., 2014). The combined concentrations of total Al, Fe, K and Mg in the guano samples on average accounted for less than 1% of the guano mass (Table 1). The estimated range of nutrient deposition (g $nest^{-1}$ yr^{-1}) per nest attempt, and potential nutrient loading rates (g m^{-2}), followed the same pattern as the guano characterization data (Table 2).

The primary form of P in wading bird guano was HCl extractable P, which averaged 88.2% and ranged from 82.2 to 96.8% of the total P

Table 1
Characterization of wading bird guano (n = 4) from the Everglades, Florida, USA.

Parameter (unit)	Mean (±1 SE)	Max.	Min.
pH	6.90 ± 0.04	6.99	6.81
Total C (g kg^{-1})	230.3 ± 19.1	285.2	197.9
Total nitrogen (g kg^{-1})	92.0 ± 14.6	123.7	53.1
Total phosphorus (g kg^{-1})	41.6 ± 8.9	56.7	20.7
δ^{15}nitrogen (‰)[a]	8.8 ± 0.7	10.6	7.8
Total aluminum (mg kg^{-1})	233 ± 120	569	49.3
Total calcium (g kg^{-1})	154 ± 28.5	229	101
Total iron (mg kg^{-1})	994 ± 199	1324	479
Total potassium (mg kg^{-1})	5700 ± 1767	9567	1606
Total magnesium (mg kg^{-1})	2536 ± 710	4195	917

[a] Data from Zhu et al. (2014) and Irick (2012).

(Fig. 2). Water soluble and KCl extractable P, i.e., labile or readily available P, cumulatively accounted for 9.6 ± 5.8% of the total P in bird guano and water soluble P comprised a higher proportion relative to KCl-P (Fig. 2.). Very little guano P was alkaline extractable (Fig. 2). Residual and alkaline extractable organic P on average was less than 3% of the total P. The estimated mass deposition (g nest^{-1} yr^{-1}) per nest attempt, and potential loading rates (g m^{-2}), of available and stable P were similar to the relative proportions of each P pool measured in guano (Table 2).

3.2. Characteristics of soil and potential nutrient sources

Soil total C, N and δ^{15}N signature showed a similar relationship with total P concentration regardless of sample depth. When data for soil samples collected from 0–5 cm and 0–10 cm depths were combined for analysis, soil total P and δ^{15}N measured at tree islands in this study showed significant positive correlation ($n = 46$, $r = 0.83$, $p < 0.0001$). Total P and C were negatively correlated ($n = 46$, $r = -0.93$, $p < 0.0001$). Soil total N and P were also negatively correlated ($n = 46$, $r = -0.815$, $p < 0.0001$).

The δ^{15}N signature of high-P tree island soil, defined as ≥1000 mg-P kg^{-1}, was significantly ($t = 8.0$, $p < 0.0001$) greater than the δ^{15}N signature of low-P tree island soil (Table 3). On average the δ^{15}N signature of high-P island soil was 6.4‰ greater than low-P island soil. The total C and N concentrations of high-P island soil were significantly ($t = 6.1$, $p < 0.0001$; and $t = 4.0$, $p < 0.001$; respectively) less than low-P island soil.

The total P concentration of mammal feces and plant leaves collected from Everglades tree islands were significantly ($t = 7.0$, $p < 0.0001$; and $t = 10.4$, $p < 0.0001$; respectively) less than the total P concentration of bird guano (Fig. 3). On average the total P concentration of guano was 8 times greater than mammal feces and 40 times greater than plant leaves. Similarly, the mean total P concentration of tree island soils was 6 to 30 times greater than mammal feces and plant leaves, respectively (Table 3). The δ^{15}N signature of bird guano was also significantly

Table 2
Annual estimated mass deposition and loading rate of total elements and phosphorus pools from colonial wading birds that may nest or roost in tree islands in the Florida Everglades, USA.

	Mass deposition[a]	Loading rate[b]
Parameter	Range (g nest^{-1} yr^{-1})	Range (g m^{-2})
Total nitrogen	163–2186	3.3–37.2
Total phosphorus	74–987	1.7–19.6
Total calcium	272–3649	8.9–100.1
Total potassium	10–135	0.2–2.3
Total magnesium	4.5–60	0.1–1.0
Available phosphorus	6.2–83	0.08–0.83
Stable phosphorus	69–926	1.6–18.4

[a] Data calculated using dry matter deposition from Frederick and Powell (1994).
[b] The range for estimated loading rate is based on the mass deposition calculation and bird colony areal extent. Some data have been rounded to the next decimal, and the rounding reflects differences from the approximate range factor.

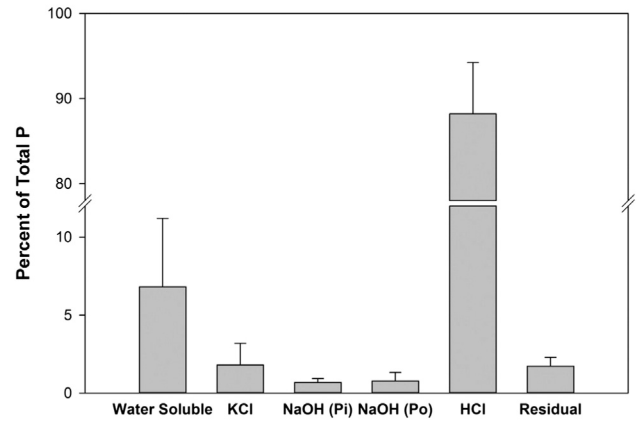

Fig. 2. Distribution of phosphorus pools in wading bird guano (n = 4) collected from tree islands in the Florida Everglades, USA. Bar values indicate mean and error bars (±1 SE).

($t = 9.2$, $p < 0.0001$) greater than the signature of mammal feces ($\delta^{15}N = 2.0 \pm 0.3$ SE). Tree island soil categorized as high-P soil had a similar mean value of δ^{15}N signature and total P concentration as bird guano (Table 1; Table 3).

4. Discussion

Guano deposition is one of the three main hypotheses explaining elevated P in tree island soil (Wetzel et al., 2005). Guano pH was similar to the range reported for seabird guano, and samples of poultry manure and litter (Gillham, 1956; Codling, 2006; Dail et al., 2007). The range of organic matter content observed in the guano may indicate different proportions of urine and fecal matter present in different samples of guano because avian excrement consists of two parts: fecal matter and urine. Bird guano C:N ratios have been reported to range from 1.2 to 3.7, and relate well with C:N ratio of guano characterized in this study (Mitzutani and Wada, 1988; Bird et al., 2008).

Frederick and Powell (1994) estimated Everglades wading bird guano contained 1.9% P, which is half of the mean value of P reported in this study but close to the measured minimum P concentration (Table 1). Scherer et al. (1995) estimated a bird guano P concentration of 1.87% based on literature of migratory waterfowl for determining P loading at an urban lake. A range of P concentrations, 1.9 to 8.3%, have been reported for colonial wading bird species (Stinner, 1983; Bildstein et al., 1992). Veerbek and Boason (1984) reported alpine passerine species droppings were 3.7% P. Data for P reported in our study and by others are similar to classical datasets compiled and reported

Table 3
Total phosphorus (P), carbon (C), and nitrogen (N), and stable nitrogen isotope ratio (δ^{15}N) of soil P classes from tree islands in the Everglades, Florida, USA. Different letters within each row indicate significant differences ($p < 0.05$) of soil properties between soil P classes.

Parameter (unit)		Soil P class	
		<1 g-P kg^{-1} (n = 13)	>1 g-P kg^{-1} (n = 33)
Total P (g kg^{-1})[a]	Mean (±1 SE)	0.71 ± 0.05	40.6 ± 5.6
	Max.	0.92	88.1
	Min.	0.52	1.1
Total C (g kg^{-1})	Mean (±1 SE)	437.1 ± 9.3a	220.9 ± 19.3b
	Max.	475	461.6
	Min.	375.4	95.5
Total N (g kg^{-1})	Mean (±1 SE)	21.8 ± 0.85a	14.3 ± 1.2b
	Max.	25.9	30.2
	Min.	15.9	6.7
δ^{15}N (‰)	Mean (±1 SE)	2.3 ± 0.5a	8.6 ± 0.5b
	Max.	5.5	13.9
	Min.	−0.7	2.7

[a] Mean values were not analyzed for statistical differences between soil P classes.

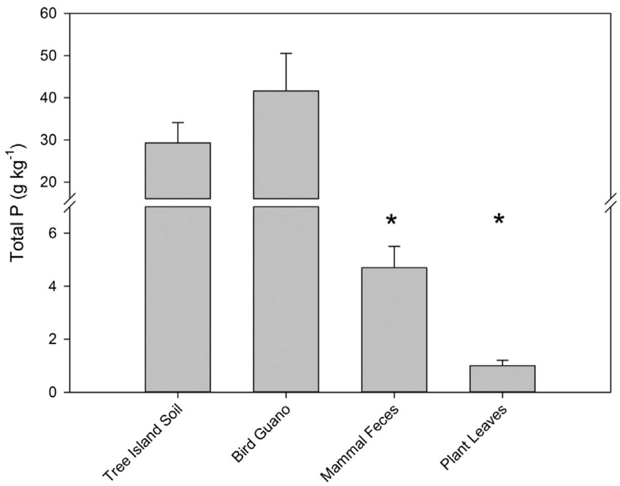

Fig. 3. Total phosphorus (P) concentration of soil (n = 46), wading bird guano (n = 4), plant leaves (n = 11), and mammal feces (n = 10) collected from tree islands in the Florida Everglades, USA. Bar values indicate mean with errors bars (±1 SE). Asterisks indicate a significant ($p < 0.05$) difference between total P concentration of guano and plant leaves or mammal feces.

by Hutchinson (1950) for a variety of bird guano. Mean Ca concentration, and the range of N concentration observed in the samples agree well with estimates of Ca and N used by Frederick and Powell (1994).

Little information is available about the concentration of other elements (Al, Fe, K and Mg) in bird guano, which may influence soil P dynamics and nutrient availability (Table 1). Cation concentrations in Everglades wading bird guano described here are much lower than recent data reported for poultry manure (Dail et al., 2007; He et al., 2010). Dietary differences among wild and domesticated species may explain discrepancies among elemental content.

4.1. Guano P form and accumulation

There is no literature available for P forms in wild bird guano from colonial wading bird species. Recent characterization studies related to poultry litter and manure, and dairy manure have investigated the distribution of P in those respective materials (Codling, 2006; Dail et al., 2007; He et al., 2010). In order to maintain some degree of comparability with our data, we used recent literature from poultry litter and manure research to explain and provide context to the observations made with regard to P forms in wild bird guano.

Inorganic P accounted for more than 90% of the total P in bird guano (Fig. 2). The primary form of P in wading bird guano was HCl extractable P, which averaged 88.2% and ranged from 82.2 to 96.8% of the total P (Fig. 2). Dail et al. (2007) also found HCl extractable P as the primary P form in oven-dried poultry manure, however the proportion was much lower and accounted for approximately 35–55% of the total P. He et al. (2010) reported HCl extractable P accounted for 40–45% of the total P in poultry litter. Generally, HCl-P is described as P bound with Ca or Mg.

Stoichiometry provides an indication of which elemental associations are more likely dominant in the guano. Mean molar ratios for Ca:P and Mg:P were >2 and <1, respectively. This rapid assessment based on elemental composition suggests that Ca–P is the primary form, although some Mg–P may be present. He et al. (2010) showed no significant relationship between extractable P and Mg in poultry litter across different extracting solutions which suggests that Mg phosphate interactions may not be as significant in avian excrement as compared to Ca phosphate.

Crystalline phosphate minerals were not identified in the bird guano using X-ray diffraction (data not shown); however, Bates et al. (2010) reported amorphous apatite present in tree island soil in northern WCA-3A and attributed the Ca–P mineral to guano derived P. Irick et al. (2013) observed apatite in multiple hardwood hammock surface soils in tree islands in the southern Everglades and suggested the apatite is derived from bone fragments also observed in the soil. Toor et al. (2005) reported that Ca:P ratios near 1 indicated dicalcium phosphate ($CaHPO_4 \cdot 2H_2O$) as the dominant Ca–P mineral in broiler and turkey litters while hydroxylapatite ($Ca_5(PO_4)_3OH$) was dominant at Ca:P ratios >2. In another study of poultry litter, non-crystalline hydroxylapatite was reported to comprise 50% of the total P present (Shober et al., 2006).

Water soluble and KCl extractable P, i.e., labile or readily available P, cumulatively accounted for 9.6 ± 5.8% of the total P in bird guano and water soluble P comprised a higher proportion relative to KCl-P (Fig. 2.) Approximately 4000 mg of P per kg of guano dry matter is readily available for biological activity or mobilization in rain or surface water, based on mean guano total P concentration (Table 1) and proportion of water soluble and KCl extractable P. If this proportion of P in wading bird guano is mobilization, leaching of dissolved P could contribute to increased P concentrations reported in sub-surface soil layers in tree islands (Orem et al., 2002). These data provide new insight toward tree island formation in the Everglades hypotheses indicating that birds not only focus nutrients but also bring an immediate supply of plant available P to nesting or perching habitat. A future study could focus on sample collection from deeper soil horizons and quantification of P leaching to describe the fate of P in tree island soil in the Everglades.

The reported effect of guano deposition on the spatial extent, productivity, and composition of plant communities is variable (Verbeek and Boasson, 1984; Ryan and Watkins, 1989; Tomassen et al., 2005; Wait et al., 2005; Mulder et al., 2011). Ryan and Watkins (1989), suggested that plant cover was negatively affected by guano deposition. Verbeek and Boasson (1984) suggested that P deposition by passerine species altered vegetation dynamics in an alpine ecosystem by creating and maintaining what they describe as “bird hummocks” which consisted of deeper soil and different vegetative characteristics relative to the low emergent surrounding vegetation. Tree species growth in northern ombrotrophic bogs responded positively at sites with bird guano nutrient inputs which reduced P and K limitation (Tomassen et al., 2005).

Very little guano P was alkaline extractable (Fig. 2). Residual and alkaline extractable organic P on average was less than 3% of the total P. The majority, 89.0 ± 6.3%, of P deposited by wading birds is in the Everglades is relatively stable and suggests that guano derived P would likely accumulate in tree island soils. The weathering of guano likely results in removal of soluble and available forms of P, while stable P remains relatively unchanged and therefore may accumulate in tree island soil. Deposition of seabird guano has been reported to increase total P, and the Ca or Mg bound P in organic soil in the arctic (Ziótek and Melke, 2014). The presence of relatively stable P, in soil affected by seabird guano deposition, was suggested to control P limitation and supplement plant available P (Hawke and Condron, 2014).

4.2. Nutrient deposition

To illustrate that bird guano deposition could greatly exceed other N and P sources to tree islands, and that deposited guano P was deposited in a stable form that could result in accumulation, guano nutrient deposition was calculated using guano chemistry data and available nesting data at active colonies within the Everglades. This information was then used to provide a comparison with available nutrient loading data and atmospheric deposition rates in the region. Available estimates of N and P loading at Everglades wading bird colonies range from 20 to 331 g-N m^{-2} and 0.9 to 120 g-P m^{-2} (Frederick and Powell, 1994). The recommended application rates for seasonal vegetable crops grown in Florida range from 0 to 9.8 g-P m^{-2}, depending on the crop and site specific soil P availability (Liu et al., 2015). We estimated N and P loading rates ranging from 3.3 to 37.2 g-N m^{-2} and 1.7 to 19.6 g-P m^{-2} from the documentation of *A. alba*, *E. albus*, *E. tricolor*, *E. thula* and *E. caerulea* presence at tree islands in the Central Everglades.

A limitation to these estimates is that they are based on known nesting density and wading bird species composition at active colonies. The estimates do not take into account raptor species which also likely utilize Everglades tree islands. Also, many tree islands are either not continuously utilized for nesting or not utilized at all by wading birds for nesting habitat. However, tree islands provide locations for birds to perch or roost within the marsh. Annual monitoring of wading birds and hydrologic characteristics may be useful indicators of nutrient removal from marshes and redistribution if models can be developed to couple ecosystem-scale hydrologic patterns with wildlife presence. Until quantitative estimates of other wildlife use of Everglades tree islands emerge, nutrient loading rates based on wading bird nesting density provide at minimum a range of potential nutrient inputs that are important for comparison with other components of tree island nutrient budgets.

Troxler and Childers (2010) described the wet-season N budget for a tree island in the southeastern Everglades with import rates for hydrologic, atmospheric and N_2 fixation of 26.8, 0.65 and 0.44 g-N m^{-2}, respectively. At the same location seasonal contribution of plant litter accounted for the deposition of 4.93 g-N m^{-2} (Troxler and Childers, 2010). The N loading reported by Troxler and Childers (2010) may not be indicative of the N budget for all Everglades tree islands, but it provides a baseline for comparison of N sources which may influence the isotopic signature of soil N. We assert that, based on the differences in potential N deposition from birds at tree islands versus other possible N sources, soil $\delta^{15}N$ signature in tree islands might reflect a contribution of guano-derived N.

We utilized Davis's (1994) system-wide atmospheric P deposition rate of 0.036 g m^{-2} to compare potential loading rate from guano P. Our results indicated guano P loading at tree islands may have occurred at rates of 47 to 544 times greater than at tree islands only receiving atmospheric P. The large proportion of inorganic P forms in guano indicates most guano P deposited at tree islands is in an inorganic form (Fig. 2). The highest deposition rate calculated for stable (i.e. HCl extractable and residual) P was approximately 500 times greater than atmospheric deposition. If atmospheric P is considered soluble and available for biological activity, a more appropriate comparison would be with the pool of guano P that is likely bioavailable. Guano derived available P loading rates ranged from 2 to more than 20 times the atmospheric load. The distribution of P pools in guano and potential loading rates elucidates that guano could serve as both an available P supplement that enhances soil fertility and also as a source of stable P that could lead to P accumulation.

Average annual atmospheric deposition rates measured in south Florida (Station FL11) from 1998–2010 for Ca, K, and Mg were 0.18, 0.09 and 0.10 g m^{-2}, respectively (NRSP-3, 2007). Except for the minimum estimated deposition rate for Mg, which was similar to the atmospheric deposition rate, guano deposition of Ca, K, and Mg was 2 to 500 times the rate of atmospheric deposition (Table 3; NRSP-3, 2007). This suggests that the deposition of guano derived nutrients may play an important role in tree island soil characteristics and P chemistry.

4.3. Soil properties

The observation of a high proportion of relatively stable inorganic P present in guano, which may be deposited at a greater rate relative to other sources, supports the hypotheses that guano deposition could contribute to P accumulation in tree island soil. Soil P accumulation in organic soil in the Everglades marsh has been reported to account for removal and storage of external sources of P (Craft and Richardson, 1993). Accumulation of guano derived P was reported to account for <1.0% of historic inputs to organic soil at a seabird breeding colony (Hawke and Newman, 2004).

Tree islands in the Everglades may function similarly to islands in marine ecosystems where birds play an important role in nutrient transport from aquatic to terrestrial habitats. Only a small percentage of tree islands are likely to consistently receive guano deposition, and the utilization and occupation of islands by wading birds likely changes overtime depending on the quality of nesting habitat. Accumulation of P in tree island soil may be an indication of previous bird utilization (Fukami et al., 2006). Wildlife use may also result in the accumulation of nutrients to tree island soil from bones, feathers, or other animal waste.

The frequency and duration of bird use of tree islands in the Everglades likely plays an important role in soil characteristics and P chemistry. Fukami et al. (2006) reported soil total P concentrations were lower by roughly 50% at islands in a marine environment where the presence of predators reduced bird use. Wait et al. (2005) reported similar findings, and observed available P concentrations were approximately 20 times greater in soils from seabird islands when compared with soil from non-seabird islands. A general trend of increased soil P concentration with seabird use was also observed by Mulder et al. (2011) in their recent review of the characteristics of seabird islands. Island habitat affected by seabird guano derived nutrient inputs also showed lower soil C:N ratio than islands where soil was unaffected by guano (Wait et al., 2005). A similar pattern was observed between low- and high-P Everglades tree island soil, based on the mean values of total C and N (Table 3). Stable isotopes have been used to indicate deposition of marine derived nutrients within terrestrial environments and nutrient transport within terrestrial environments (Mitzutani et al., 1985; Mitzutani and Wada, 1988; Anderson and Polis, 1999; Macek et al., 2009; Mulder et al., 2011). Soil $\delta^{15}N$ has been used as an indicator to demonstrate the influence of guano deposition by avian species on seabird island ecosystems (Wait et al., 2005; Mulder et al., 2011). Zhu et al. (2014) showed a positive correlation between $\delta^{15}N$ signature and total mercury (Hg) concentration in Everglades tree island soil and suggested that bird guano contributed to the pattern. The positive correlation ($n = 46$, $r = 0.83$, $p < 0.0001$) between soil $\delta^{15}N$ and P may also be an indicator of bird guano-derived P in tree island soils.

Cohen et al. (2011) also suggested animal waste, likely bird guano, as an explanation for enrichment (≤2‰) of $\delta^{15}N$ in tree island soil compared to marsh soil and a positive relationship between soil $\delta^{15}N$ and TP. A wider difference (~6‰) of surface soil $\delta^{15}N$ signature between tree island soil and marsh soil was found at an island in the central Everglades (Gu et al., 2013). Ammonia volatilization could also influence differences observed among these soil $\delta^{15}N$ values, and volatilization of ammonia derived from animal wastes would likely increase tree island soil $\delta^{15}N$ values within the Everglades (Mitzutani et al., 1985; Frank et al., 2004).

Wang et al. (2011) found a similar pattern in mean foliar $\delta^{15}N$ signature of Everglades tree island plants at high soil P islands (foliar $\delta^{15}N = 6.1$‰) and low soil P islands (foliar $\delta^{15}N = -1.6$‰). The difference of foliar $\delta^{15}N$ signature between high and low soil P islands was suggested to indicate lack of isotopic discrimination against ^{15}N during plant uptake due to N limitation (Wang et al., 2011). Enrichment of wetland plant foliar and soil $\delta^{15}N$ signatures have also been described in marsh habitat of the northern Everglades along a P concentration gradient (Inglett and Reddy, 2006; Inglett et al., 2007). Maeck et al. (2009) showed foliar $\delta^{15}N$ signature of wetland plants growing in areas of frequent wading bird use was 5.7‰ higher than plants growing in areas without bird use, and soil P was also higher in areas of bird use.

Tree island soil with high total P concentration was found to have a similar $\delta^{15}N$ signature and total P concentration as bird guano (Table 1; Table 2). This similarity may reflect the influence of guano on the characteristics of tree island soil. The TP concentration of bird guano on average was approximately 40 times greater than plant leaves, and 8 times greater than mammal feces, collected from tree islands (Fig. 3). Mean foliar $\delta^{15}N$ signature for tree island plants and mammal feces have also been reported at lower values than bird guano (Zhu et al., 2014).

Total C and P concentrations were negatively correlated ($n = 46$, $r = -0.92$, $p < 0.0001$) in tree island soil suggesting that the accumulation of P is not associated with C, and likely accumulates as an inorganic form of P. Deposition of bird guano and accumulation of stable inorganic P forms could contribute to the correlation observed between total C and P concentrations in tree island soil. Further investigation and quantification of wildlife use of tree island habitat will improve estimations of nutrient budgets and transfers throughout the ecosystem. Future estimations of nutrient balances in tree islands should likely consider wildlife inputs if animals utilizing the islands forage in the surrounding marsh and nest or take refuge in tree island habitat.

5. Conclusion

This work provides new insight toward the guano contribution hypothesis by characterizing a P source to tree island soil and elucidating an isotopic indication of P source. Bird guano had high concentrations of P and N, and the guano N is enriched in ^{15}N. Approximately 90% of P deposited as guano was a relatively stable (HCl extractable or residual) form derived from consumed biomass, which could accumulate in tree island soil. Deposition of stable guano P and ^{15}N enriched N can occur at rates greatly exceeding other sources of P and N to tree island soil and P concentrations and $\delta^{15}N$ were positively correlated in tree island soil. Potential input of guano with elevated concentrations of N and P, and ^{15}N enriched N, relative to other sources suggest that guano deposition in tree island soils is a mechanism contributing to this pattern. Nutrient transport and transformation from marsh areas to tree islands by wildlife is a mechanism that should be considered in wetland restoration planning and management.

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