

# Effects of nesting waterbirds on nutrient levels in mangroves, Gulf of Fonseca, Honduras

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Received: 22 January 2015 / Accepted: 22 January 2016  
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**Abstract** Mangroves provide numerous ecosystem services, including biodiversity values such as nesting sites for piscivorous waterbirds. High concentrations of waterbirds at nest sites are hypothesized to affect ecosystem dynamics, yet few studies have examined their effects as a nutrient source in mangroves. We examined the effects of nutrient enrichment by colonial waterbirds at a mangrove rookery in the Gulf of Fonseca, Honduras. We compared nutrient inputs via bird guano deposition and macronutrient levels in the vegetation and soils between a small island that hosted large numbers of roosting waterbirds and an adjacent island with little evidence of waterbird activity. Nest density at the rookery was  $1721 \pm 469$  nests  $\text{ha}^{-1}$ . Rookery birds deposited  $7.2 \pm 3.4$  g  $\text{m}^{-2}$   $\text{day}^{-1}$  guano dry weight, delivering an estimated  $1.12$  Mg  $\text{ha}^{-1}$  nitrogen and  $0.16$  Mg  $\text{ha}^{-1}$  phosphorus to the island over a 120 day breeding season. This large nutrient influx contributed to substantially higher

concentrations of biologically important nutrients in the rookery soils (seven times more plant available phosphorus, eight times more nitrate, and two times more ammonium). Rookery mangrove leaves contained significantly higher concentrations of nitrogen and phosphorus compared to the control site. These results suggest that colonial waterbirds significantly influence nutrient dynamics of mangroves at local scales. Further research is needed to understand the effects of avian derived nutrients on mangrove growth rates, nutrient export to adjacent waters, invertebrate communities, and mangrove associated fisheries.

**Keywords** Mangroves · Macronutrient cycling · Waterbirds · Guano · Nutrient enrichment

## Introduction

Mangroves provide numerous ecosystem services, including habitat for wildlife, commercially important fish and crustaceans, coastal protection from storm events, charcoal and timber, ecotourism, and carbon (C) sequestration (UNEP 2014). Mangroves are among the planet's most C-rich ecosystems, containing a mean of approximately  $1000$  Mg C  $\text{ha}^{-1}$  (Alongi 2014; Donato et al. 2011). Despite their importance, mangrove deforestation rates are estimated at 3–5 times the average rate of global forest loss (FAO 2007). Greenhouse gas emissions

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**Electronic supplementary material** The online version of this article (doi:10.1007/s11273-016-9480-4) contains supplementary material, which is available to authorized users.

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resulting from mangrove loss may account for 1–9 % of global emissions from deforestation (Donato et al. 2011). Rapid declines of global mangrove extent have prompted estimates of the functional loss of mangroves in the next 100 years (Polidoro et al. 2010; Duke et al. 2007). The potential loss of mangrove ecosystem services will have severe economic and environmental consequences for coastal communities throughout the developing world.

A growing body of literature recognizing the importance of mangroves is driving international conservation measures and calls to action (e.g., Duke et al. 2007; Donato et al. 2011; IPCC 2014; UNEP 2014). One suggested option is to provide financial incentives for mangrove conservation, such as payments for ecosystem services (PES) or incentives for reducing emissions from deforestation and degradation (REDD+). Economic evaluations of ecosystem services require sound scientific data, and while our understanding of mangrove function and services has improved greatly in recent decades, knowledge gaps still exist. Research is needed to better understand the role of biodiversity in supporting mangrove health and function (Buelow and Sheaves 2015; McLeod et al. 2011; UNEP 2014). In the current study, we investigate the role of colonial waterbirds in linking mangroves with aquatic ecosystems, and how birds influence nutrient cycling, community structure and C stocks.

Colonial waterbirds act as important nutrient vectors in many coastal ecosystems (Whelan et al. 2008) and are hypothesized to facilitate biological connectivity between mangroves and adjacent aquatic ecosystems (Buelow and Sheaves 2015). Waterbirds forage across large areas, and return to colonies (rookeries) where they deposit nutrients in the form of guano (Ellis 2005). Previous studies in island ecosystems found nutrient inputs comparable to fertilization rates used in intensive agriculture (Young et al. 2010). These high nutrient inputs have been shown to increase primary production (Polis et al. 1997; Powell et al. 1989), herbivory (Onuf et al. 1977; Young et al. 2011), consumer abundance (Polis and Hurd 1996; Young et al. 2011), and even abundance of marine megafauna through nutrient export to near shore waters (McCauley et al. 2012). Such profound changes in ecosystem dynamics are likely to influence the provision of ecosystem services.

Mangroves provide critical foraging and nesting habitat for a variety of waterbirds, yet the role of birds as nutrient vectors in mangrove ecosystems has received little attention in the scientific literature (Buelow and Sheaves 2015; Reef et al. 2010). Only two studies to date have measured the effects of avian nutrient enrichment in mangroves, neither of which report nutrient inputs (Adame et al. 2015; Onuf et al. 1977). In this study we examined the effects of nutrient enrichment by colonial waterbirds in two mangrove sites in the Gulf of Fonseca, Honduras. One site was a small island that hosted large numbers of roosting waterbirds (Magnificent Frigatebirds, Neotropical Cormorants, Cattle Egrets, White Ibis, etc.) (Table 1). The other site was an adjacent island that showed little evidence of waterbird activity. Our objectives were to determine the quantity and ecological influences of avian derived nutrients on two mangrove islands; one with a large bird rookery and one without. We hypothesized that: (1) birds are a significant nutrient vector and would deposit large quantities of nutrients at the rookery site; (2) high nutrient inputs would result in higher soil and foliar nutrient levels at the rookery site; and (3) nutrient enrichment would result in increased mangrove biomass and C stocks at the rookery site.

## Materials and methods

### Study sites

The Gulf of Fonseca is a large bay on the Pacific coast of Honduras, El Salvador, and Nicaragua. Total mangrove area in the Gulf of Fonseca was estimated at 47,757 ha in 1999 (Rivera-Monroy et al. 2002). The Honduran part of the gulf contains ~36,700 ha of mangroves (Chen et al. 2013). The region contains a diverse array of coastal ecosystems, including mangroves, tidal creeks, mudflats, and lagoons (Rivera-Monroy et al. 2002). This diverse landscape hosts large populations of resident and migratory waterbirds and has been recognized as an Important Bird Area by Birdlife International (Devenish et al. 2009). Most of the Honduran Gulf of Fonseca (~70,000 ha) is designated as a Ramsar Wetland of International Importance (FAO 2012). The region's climate exhibits distinct wet and dry seasons with the dry season extending from November through April. The wet

**Table 1** Characteristics of sampling locations

|   | Rookery (n = 6)                                      | Control (n = 6)                                       |
|---|--|---|
| Latitude/longitude                            | 13.3668°, -87.4704°                                  | 13.3672°, -87.4756°                                   |
| Canopy height (m)                             | 4–8  | 4–10  |
| Salinity (ppt)                                | 33.0 (0.8)   | 36.5 (1.5)  |
| pH  | 6.6 (0.1)  | 6.8 (0.1)   |
| Dominant species                              | <i>R. mangle</i> (62 %)<br><i>L. racemosa</i> (28 %) | <i>R. mangle</i> (89 %)<br><i>A. germinans</i> (11 %) |
| Density (tree ha <sup>-1</sup> )              | 977 (145)  | 5300 (2390)   |
| Basal area (m <sup>2</sup> ha <sup>-1</sup> ) | 6.30 (0.83)  | 7.31 (1.42)   |
| Soil depth to marine sands (cm)               | 165 (8)  | 166 (19)  |

Values are reported as mean (SE)

season extends from May through October and is interrupted by a brief dry period in July, locally known as the canícula (Vergne et al. 1993). Average annual precipitation ranges from 1500 to 2000 mm (Hargreaves 1980). Tides are semidiurnal with a mean vertical tidal range of 2.3 m (Vergne et al. 1993).

In July, 2013 we sampled two island sites dominated by mangroves (rookery and control) to examine nutrient enrichment by colonial waterbirds (Table 1; Fig. 1). The rookery site was a ca. 3 ha mangrove island that hosted large numbers of roosting waterbirds (Fig. 2). The island, locally known as Isla de Pájaros, is located at the mouth of Estero de la Oscurana, where the Río Simisirán enters the Bahía de San Lorenzo. The rookery is unconnected to the mainland even at low tide and likely provides birds with a refuge from terrestrial mammalian nest predators (raccoon tracks were observed at the control site and other nearby mangroves but not at the rookery). Mangrove species composition at the rookery was 62 % *Rhizophora mangle* (red mangrove) and 38 % *Laguncularia racemosa* (white mangrove). The island fringe consisted almost exclusively of *R. mangle*. Canopy height ranged from approximately 4–8 m.

The most abundant bird species at the rookery at the time of sampling were Neotropic Cormorant, Cattle Egret, White Ibis, and Magnificent Frigatebird (see Supplementary Materials Table 1 for complete species list). Our sampling efforts coincided with the latter half of the breeding season for several species (Howell and Webb 1995). We observed active nests (containing eggs or chicks at various ages of maturity) of Neotropic Cormorants, Tricolored Herons, Cattle Egrets, Roseate Spoonbills, and White Ibises. No official bird censuses

have been conducted to our knowledge. According to local biologists, birds have used this rookery for at least several decades. The rookery is utilized year round, but the numbers are greatest in winter months when the region receives an influx of North American migrants (Luis Soto, personal communication, 25 July 2013). No data exists on the length of waterbird breeding seasons in the Gulf of Fonseca. Tropical birds typically breed over a longer season than temperate birds, even within the same species (Gill 2007). Using life history data of North American waterbirds, we conservatively estimated that the peak breeding season would last for 120 days at our rookery site (The Birds of North America Online 2005).

The control site was located on a larger adjacent island and showed little evidence of waterbird activity. The control site was selected for its proximity (ca. 500 m distant) to the rookery and its resemblance to the rookery site in general form and appearance. Mangrove species composition was 89 % *R. mangle* and 11 % *Avicennia germinans* (black mangrove). Canopy height was similar to that of the rookery, ranging from approximately 4–10 m.

#### Forest structure, composition, and ecosystem carbon stocks

We determined forest structure, composition and ecosystem carbon stocks of each site following methods described by Kauffman and Donato (2012). At each study site, six sampling plots were established 20 m apart along a 100 m transect, oriented along a north–south azimuth (Fig. 3). The first plot of each transect was established randomly approximately



**Fig. 1** Location of rookery and control sites. Rookery coordinates:  $13.3668^{\circ}$ ,  $-87.4704^{\circ}$ . Control coordinates:  $13.3672^{\circ}$ ,  $-87.4756^{\circ}$

15 m from the water's edge. Within each plot we collected data on standing tree biomass, measured and counted downed wood, and collected soil samples for laboratory analysis in order to calculate total ecosystem C stocks.

#### *Trees*

Composition, stem density, and basal area were quantified through measurements of species and diameter at 1.3 m height (diameter at breast height;

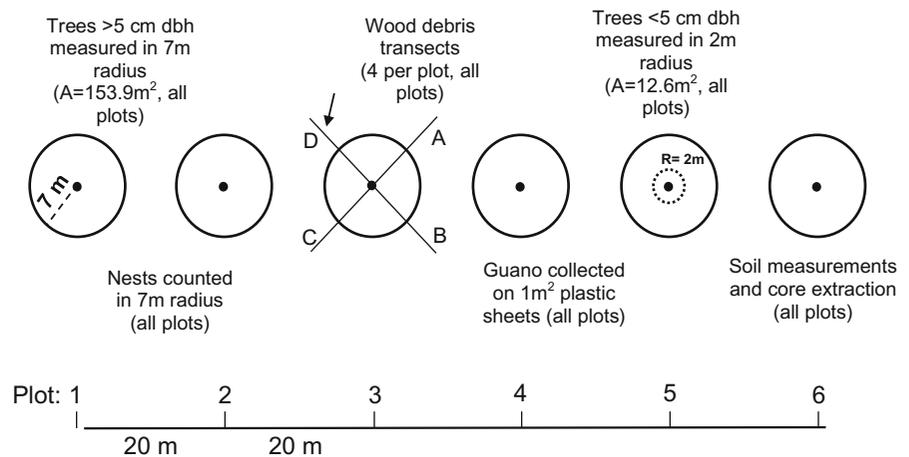


**Fig. 2** Top White ibises in *Laguncularia racemosa* (white mangrove) at the rookery site (photo credit J Boone Kauffman). Bottom Roseate spoonbill in *Rhizophora mangle* (red mangrove) at the rookery site (photo credit Rupesh Bhomia)

dbh) of all live or standing dead trees and samplings rooted within each plot. Plot size for tree measurements was  $153.9 \text{ m}^2$  (7 m radius) for trees  $>5$  cm dbh. A nested 2 m radius plot was used to measure trees  $<5$  cm dbh. The diameter of *R. mangle* trees was measured 30 cm above the highest prop root.

Allometric equations were used to calculate tree biomass for each site. We used species specific formulas provided by Fromard et al. (1998). Below-ground root biomass was calculated using the formula by Komiyama et al. (2008). Tree C was calculated by multiplying biomass by a factor of 0.47 for

**Fig. 3** Sampling design used for measuring aboveground forest structure, composition, and ecosystem C stocks. Total length of transect was 100 m



aboveground biomass and 0.39 for belowground biomass (Kauffman and Donato 2012).

Standing dead trees were also included in biomass calculations. Standing dead trees were assigned to one of three decay classes: Status 1, recently dead trees without leaves; Status 2, dead trees without secondary branches; and Status 3, dead trees without primary or secondary branches (Kauffman and Donato 2012). The biomass for each tree status was calculated using a factor for each dead tree class. After death a tree loses its leaves and branches, resulting in a lower biomass than that of live tree. Biomass of status 1 dead trees was estimated to be 97.5 % of a live tree, status 2 was estimated to be 80 % of a live tree, and status 3 trees were estimated to represent 50 % of a live tree (Miguel Cifuentes, CATIE, personal communication).

#### Dead and downed wood

Mass of dead and downed wood was calculated using the planar intersect technique parameterized for mangroves (Kauffman and Donato 2012). At the center of each plot, four 14-m transects were established. The first transect was established in a direction that was offset 45° from the azimuth of the main transect. The other three were established 90° clockwise from the first transect. At each transect, the diameter of any downed, dead woody material (fallen/detached twigs, branches, prop roots, or stems of trees and shrubs) intersecting the transect was measured. Wood that was  $\geq 2.5$  cm but  $< 7.6$  cm in diameter at the point of intersection was measured along the last 5 m of the transect. Wood  $\geq 7.6$  cm in diameter at the point of intersection was measured from the second meter to the end of the

transect (12 m in total). Wood pieces  $\geq 7.6$  cm in diameter were separated in two decay categories: sound and rotten. Wood was considered rotten if it visually appeared decomposed and broke apart when kicked.

We used data of specific gravity of downed wood as determined from the different wood classes derived from downed wood from Mexico (Adame et al. 2013). Using the specific gravity for each group of wood debris, biomass was calculated using formulas reported in Kauffman and Donato (2012). Downed wood biomass was converted to C using a factor of 50 % as reported in Kauffman and Donato (2012).

#### Soils

At each plot, soil samples were collected for bulk density and nutrient concentration measurements using a peat auger consisting of a semi-cylindrical chamber of 6.4 cm radius. This auger is efficient for collecting relatively undisturbed cores from wet soils under mangroves (Donato et al. 2011). The core was divided into depth intervals of 0–15 cm, 15–30 cm, 30–50 cm, 50–100 cm, and  $> 100$  cm. A relatively uniform 5 cm section of soil from these depth intervals were collected in the field. This known volume of soil was dried to a constant mass, and weighed to determine bulk density. Soil depth to parent material (marine sediments or rock) was measured at three sites near the center of each plot using a graduated aluminum pole. In each plot, pore water salinity was measured using a refractometer and soil water pH was measured using a portable pH meter.

The concentrations of C and N were determined by dry combustion or induction furnace method using

Thermo Flash EA 1112 series NC Soil Analyzer at an analytical laboratory based at Florida International University, Miami. Soil C concentration was multiplied by bulk density to determine soil C stocks. Additional analyses of surface soils (0–15 cm) were performed to determine concentrations of biologically available nutrients. These samples were analyzed by the Oregon State University Central Analytical Lab for plant available phosphorus (plant available P), nitrate ( $\text{NO}_3\text{-N}$ ) and ammonium ( $\text{NH}_4\text{-N}$ ). Plant available P was extracted using an acid–fluoride solution and measured colorimetrically based on its reaction with ammonium molybdate following Bray methods (Bray and Kurtz 1945).  $\text{NO}_3\text{-N}$  and  $\text{NH}_4\text{-N}$  were extracted in 2 M KCl for 1 h and analyzed using an Alpkem Flow Solution auto-analyzer.

### Nest counts

Bird nest density at the rookery and control sites was determined by counting the number of bird nests in each 7 m fixed-radius survey plot (six plots per site). We were unable to accurately determine the status (active or inactive) of many nests because of their location high in the canopy. Nests of different species were very similar in appearance and we could not accurately differentiate between species. The total number of nests at the rookery was estimated by multiplying the average measured nest density by the total area of mangroves on the rookery island (2.56 ha). Mangrove area was measured using Google Earth (Version 7.1.2.2041 ©2013 Google Inc.).

### Guano deposition

One square meter plastic sheets were installed underneath the tree canopy within each of the six survey plots at each site to collect bird guano. The sheets were left for 4 days and subsequently retrieved. To our knowledge no rainfall occurred at the study sites during the guano collection period. Guano was scraped off each sheet and sealed in plastic scintillation vials for later analysis. In the laboratory, the guano samples were dried for 1 day at 50 °C and homogenized using mortar and pestle. Samples were analyzed by the Oregon State University Central Analytical Lab for plant available P,  $\text{NO}_3\text{-N}$  and  $\text{NH}_4\text{-N}$ . Plant available P was extracted using an acid–fluoride solution and measured colorimetrically based

on its reaction with ammonium molybdate following Bray methods (Bray and Kurtz 1945).  $\text{NO}_3\text{-N}$  and  $\text{NH}_4\text{-N}$  were extracted in 2 M KCl for 1 h and analyzed using an Alpkem Flow Solution auto-analyzer. We used literature values of piscivorous wading bird guano nutrient content for estimates of total N and total P deposition (guano reported as 13 % N and 1.9 % P by mass, Frederick and Powell 1994). Nutrient deposition rates were calculated by multiplying the guano deposition rates by the guano nutrient concentrations. Total rookery guano deposition was calculated using a rookery mangrove area of 2.56 ha. Total breeding season nutrient inputs were calculated using a breeding season length of 120 days, which was estimated based on life history data of North American waterbirds (The Birds of North America Online 2005). The guano measurements during our sampling period represent guano deposition by resident birds during the four month peak breeding season.

### Leaf samples

We collected approximately 20 *R. mangle* leaves from each of the six survey plots at each site. We collected only mature non-senescent green leaves growing in full sun. Leaves were wiped with a damp towel to remove any guano or other contaminants that may have confounded nutrient analysis. Leaves were then stored in paper bags and dried to constant mass at 60° C. Samples were analyzed by the Oregon State University Central Analytical Lab for total phosphorus (total P) and Total Kjeldahl Nitrogen (total N). Leaf total N was determined by Kjeldahl digestion with sulfuric acid ( $\text{H}_2\text{SO}_4$ ) and analyzed using an Alpkem Flow Solution auto-analyzer. To measure total P, samples were dry-ashed, extracted with 5 %  $\text{HNO}_3$  and analyzed for total P using Inductively Coupled Plasma Spectrometry.

### Statistical analysis

Differences among soil and leaf nutrient concentrations were tested using Welch's two sample *t* test. Welch's *t* test is an adaptation of the Student's *t* test used when comparing two populations with possibly unequal variances (Ramsey and Schafer 2002). Soil and leaf nutrient concentrations at the rookery and control sites were predicted to have unequal standard deviations as a result of spatial variability in guano

deposition. Differences among salinity, pH, forest structure, and carbon stocks were tested using two sample *t* tests. Normality was assessed using probability plots and Shapiro–Wilk tests. Soil NO<sub>3</sub>-N, soil NH<sub>4</sub>-N and stem density data were log transformed to comply with normality assumptions. Leaf P could not be normalized by log transformation, so differences between sites were tested using Wilcoxon Rank Sum test. All values are expressed as mean ± SE. Statistical analyses were performed in RStudio (Version 0.97.18, ©2009–2012 RStudio, Inc.).

## Results

### Avian derived nutrients

Birds delivered large quantities of nutrient-rich guano to the rookery. Mean guano deposition at the rookery was  $7.15 \pm 3.43 \text{ g m}^{-2}$  per day. In 4 days of sampling we recorded no guano deposition at the control site. Guano samples contained very high concentrations of biologically available nutrients. Guano contained  $3658 \pm 368 \text{ mg kg}^{-1}$  plant available P,  $29 \pm 6 \text{ mg kg}^{-1}$  NO<sub>3</sub>-N, and  $2193 \pm 196 \text{ mg kg}^{-1}$  NH<sub>4</sub>-N. Mean daily nutrient inputs from guano were  $281 \pm 146 \text{ g ha}^{-1}$  plant available P,  $3 \pm 2 \text{ g ha}^{-1}$  NO<sub>3</sub>-N, and  $185 \pm 95 \text{ g ha}^{-1}$  NH<sub>4</sub>-N.

By combining published nutrient concentrations (Frederick and Powell 1994) with our measurements of guano deposition, we estimate daily deposition of total P and total N at  $1360 \pm 650 \text{ g ha}^{-1}$  P and  $9300 \pm 4450 \text{ g ha}^{-1}$  N. We estimate that birds delivered  $420 \pm 200 \text{ kg P}$  and  $2860 \pm 1370 \text{ kg N}$  to the rookery in the course of a 120 day breeding season.

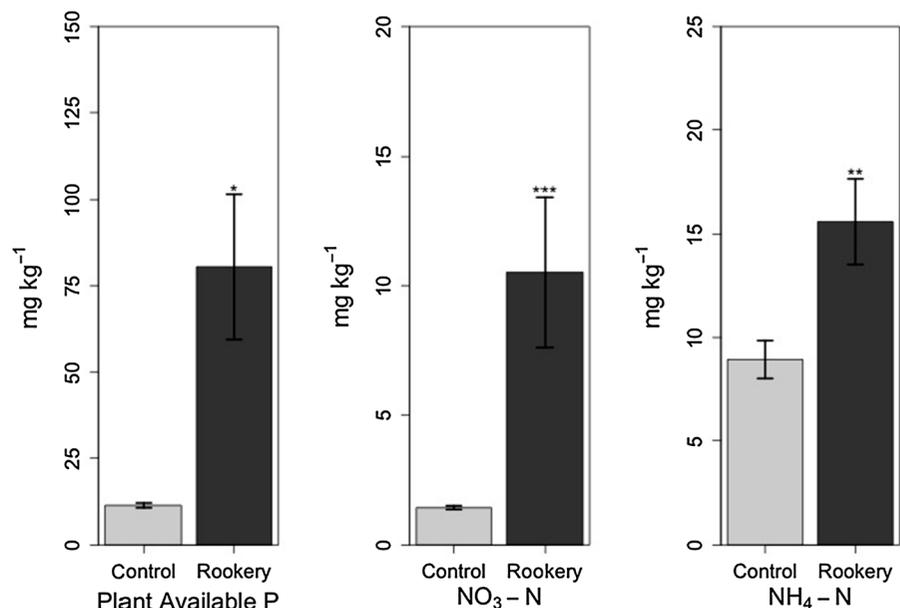
Nest density at the rookery was measured at  $1721 \pm 469 \text{ nests ha}^{-1}$ . Nest density at the control site was measured to be zero. We estimate that the 2.56 ha rookery contained  $4407 \pm 2941$  nests at the time of sampling.

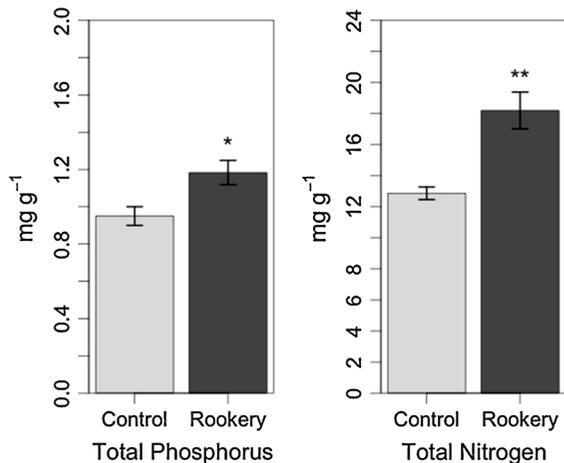
### Soil and foliar nutrients

Soil nutrient levels were significantly higher at the rookery compared to the control site (Fig. 4). Mean soil available P was seven times greater at the rookery than at the control site ( $80.5 \pm 21.1 \text{ mg kg}^{-1}$  compared to  $11.2 \pm 0.7 \text{ mg kg}^{-1}$ ,  $t_{(5,0)} = 3.29$ ,  $p = 0.022$ ). Mean soil NO<sub>3</sub>-N was nearly eight times greater at the rookery than at the control site ( $10.5 \pm 2.9 \text{ mg kg}^{-1}$  compared to  $1.4 \pm 0.7 \text{ mg kg}^{-1}$ ,  $t_{(5,4)} = 6.69$ ,  $p = 0.001$ ). Mean soil NH<sub>4</sub>-N at the rookery was nearly twice that of the control site ( $15.6 \pm 2.1 \text{ mg kg}^{-1}$  compared to  $8.9 \pm 0.9 \text{ mg kg}^{-1}$ ,  $t_{(9,9)} = 3.28$ ,  $p = 0.009$ ).

Foliar nutrient concentrations were significantly higher ( $p < 0.05$ ) at the rookery compared to the control site

**Fig. 4** Soil concentrations of plant available phosphorus (plant available P), nitrate (NO<sub>3</sub>-N), and ammonium (NH<sub>4</sub>-N). Error bars represent mean ± SE. \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$



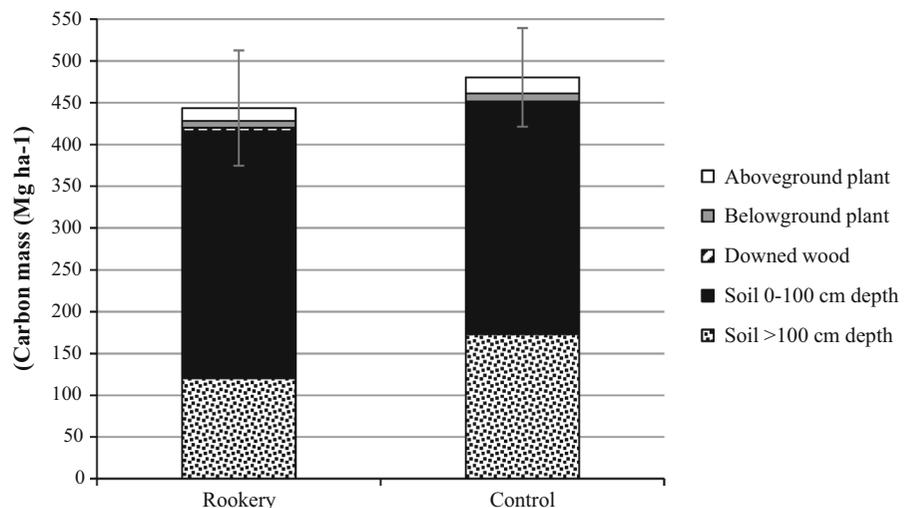


**Fig. 5** Foliar concentrations of total phosphorus and total nitrogen. Error bars represent mean  $\pm$  SE. \* $p < 0.05$ , \*\* $p < 0.01$

(Fig. 5). Total P concentrations were  $1.2 \pm 0.07 \text{ mg g}^{-1}$  at the rookery compared to  $1.0 \pm 0.05 \text{ mg g}^{-1}$  at the control site ( $W = 31, p = 0.031$ ). Total N concentrations were  $18.2 \pm 1.2 \text{ mg g}^{-1}$  at the rookery compared to  $12.9 \pm 0.4 \text{ mg g}^{-1}$  at the control site ( $t_{(6,2)} = 4.25, p = 0.005$ ). Nitrogen to phosphorus ratios (N:P) in the leaves were greater at the rookery than at the control site, but the significance was marginal ( $t_{(10)} = 1.89, p = 0.089$ ). Mean N:P ratios were  $15.4 \pm 0.7$  and  $13.7 \pm 0.6$  at the rookery and control sites, respectively.

Mean salinity was slightly higher at the control site, but the significance was marginal ( $36.5 \pm 1.5 \text{ ppt}$

**Fig. 6** Ecosystem carbon stocks of the rookery and control sites, reported by carbon pool. Error bars represent mean  $\pm$  SE



compared to  $33.0 \pm 0.8 \text{ ppt}$ ,  $t_{(10)} = -2.10, p = 0.062$ ). Mean pH did not differ between the two sites ( $6.8 \pm 0.1$  at the control vs.  $6.6 \pm 0.1$  at the rookery,  $t_{(10)} = -1.48, p = 0.171$ ).

#### Aboveground forest structure and ecosystem C stocks

There were few differences in mangrove ecosystem structure between the rookery and adjacent control site. Basal area was slightly higher at the control site, but the difference was not significant ( $7.3 \pm 1.4 \text{ m}^2 \text{ ha}^{-1}$  at the control vs.  $6.3 \pm 0.8 \text{ m}^2 \text{ ha}^{-1}$ ,  $t_{(10)} = -0.61, p = 0.553$ ). Mean stem density was higher at the control site but the difference was not significant ( $5300 \pm 2390 \text{ stems ha}^{-1}$  at the control vs.  $977 \pm 145 \text{ stems ha}^{-1}$  at the rookery,  $t_{(10)} = -1.51, p = 0.162$ ). Aboveground biomass did not differ significantly between the two sites ( $39.0 \pm 8.4 \text{ Mg ha}^{-1}$  at the control vs.  $31.0 \pm 6.5 \text{ Mg ha}^{-1}$  at the rookery,  $t_{(10)} = -0.75, p = 0.470$ ). Ecosystem carbon stocks (Fig. 6) were also similar between the two sites ( $478 \pm 59 \text{ Mg ha}^{-1}$  at the control vs.  $442 \pm 69 \text{ Mg ha}^{-1}$  at the rookery,  $t_{(10)} = -0.40, p = 0.697$ ).

## Discussion

### Waterbirds as nutrient vectors

We found that nesting waterbirds were significant nutrient vectors, transporting large quantities of

nutrients from the aquatic environment to their mangrove nest sites. We estimated that birds delivered between 4.9 and 13.8 kg N ha<sup>-1</sup> per day and between 0.7 and 2.0 kg P ha<sup>-1</sup> per day to Isla de Pájaros (the rookery site). These rates far exceed typical fertilizer application rates used for industrial corn production in the United States of America. For comparison, average annual rates of fertilization for corn are approximately 156 kg N ha<sup>-1</sup> and 30 kg P ha<sup>-1</sup> (Lander and Moffitt 1996). Birds at the rookery site would deliver this quantity of N in just 16 days and this quantity of P in just 22 days. We estimated that birds delivered 22,000 kg guano (dry weight) to the rookery mangroves in the course of a four month breeding season. Total breeding season nutrient inputs are estimated at 2860 kg N ha<sup>-1</sup> and 420 kg P ha<sup>-1</sup>.

Deposition rates of bioavailable nutrients (plant available P, NO<sub>3</sub>-N, and NH<sub>4</sub>-N) were substantial but underestimate the total nutrient contribution that birds make to the rookery for two reasons. First, plant available P as measured by the Bray methods does not account for P that may become available after deposition (Bray and Kurtz 1945). Second, much of the N initially present in the guano was likely lost to volatilization before collection. Smith and Johnson (1995) experimentally demonstrated that in a humid environment, nearly 60 % of total N in fresh guano was lost to ammonia volatilization within 4 days. Our guano samples were exposed for up to 4 days in very hot and humid conditions during the sampling period and therefore our estimates are likely low. Guano that is intercepted by the canopy likely experiences a similar loss of N to volatilization. However, guano that passes through the canopy (such as what we measured) would typically fall in water during high tides or would be covered in water within 12 h. For these reasons, we estimated total N and total P inputs using literature values for piscivorous wading bird guano deposition (Frederick and Powell 1994). Our estimates are reasonably conservative as these concentrations fall at the lower end of the range of published waterbird guano nutrient concentrations (Allaway and Ashford 1984, Powell et al. 1989, Young et al. 2010).

#### Soil and foliar nutrients and ecological implications

Rookery soils contained highly elevated levels of biologically available nutrients. Concentrations of

plant available P were seven-fold greater and NO<sub>3</sub>-N concentrations were eight-fold greater at the rookery than at the control site. Rookery NH<sub>4</sub>-N concentrations were nearly twice those of the control site. NH<sub>4</sub>-N is typically the most abundant form of N in mangrove soils and is highly available for plant uptake (Reef et al. 2010). Foliar concentrations of total N and total P were both significantly greater at the rookery site, suggesting that mangroves received and took up the avian delivered nutrients. The observed 41 % increase in foliar N at the rookery site is consistent with increases in *R. mangle* foliar N measured at mangrove bird rookeries relative to control sites in the Yucatan Peninsula, Mexico (25 %, Adame et al. 2015) and Florida, USA (33 %, Onuf et al. 1977).

Mangroves are highly sensitive to variation in nutrient availability (Boto and Wellington 1983; Feller 1995; Feller et al. 2003). Nutrient limitation in mangroves is most frequently attributed to either N or P limitation, but varies regionally and site to site. In general, N is the limiting nutrient in fringe and oceanic mangroves, whereas P is generally limiting in interior mangroves that receive less tidal flushing (Boto and Wellington 1983; Feller et al. 2003; Reef et al. 2010). Foliar N:P ratios are frequently used to assess nutrient limitation. In mangroves, N:P ratios >32 generally indicate P limitation (Reef et al. 2010). Mean N:P ratio in *R. mangle* leaves at the control site in our study was 13.7 ± 0.6, indicating N limitation. This conclusion is corroborated by the site's location—as a fringe mangrove, we would expect the site to be nitrogen limited.

The effects of avian derived nutrients are well documented in a variety of coastal ecosystems. Authors have reported a wide range of effects, from increased primary production to increased abundance of terrestrial and aquatic consumers (McCauley et al. 2012; Polis and Hurd 1996; Polis et al. 1997; Young et al. 2011). In one of the few studies of avian derived nutrients in mangroves, Onuf et al. (1977) measured increased growth rates and leaf biomass in response to N enrichment by a seasonal bird colony in Florida. Given the high rates of nutrient deposition at the rookery, as well as elevated soil and foliar nutrients, we would expect to see similar higher order effects as in previous studies. However, we found no significant differences in aboveground forest structure, aboveground biomass, or ecosystem carbon stocks between the two sites. Indirect effects of nutrient enrichment on

the rookery mangroves may have precluded any increases in primary production. When a limiting nutrient is added to a community, increased growth may lead to increased demands on other resources, which may themselves become limiting (Tilman 1984). For example, experimental evidence from a P limited mangrove in Belize suggests that potassium limitation may develop when N or P limitation is relieved (Feller 1995). High nutrient inputs at water-bird rookeries can lead to ammonium toxicity in some plant communities (Ellis 2005), however this is unlikely to occur in mangroves because they are adapted to high levels of ammonium and likely use it as their primary N source (Reef et al. 2010). We would also expect increased insect herbivory of mangrove tissues at the rookery due to elevated N concentrations (i.e., increased nutritive value). Onuf et al. (1977) measured four times greater losses to herbivores at a mangrove bird rookery than at a control site without birds. Foliar N concentrations in the current study were even greater than in Onuf et al. ( $18.2 \pm 1.2 \text{ mg g}^{-1}$  vs.  $16.0 \pm 1.0 \text{ mg g}^{-1}$ ), suggesting that mangroves at our rookery site may experience similar or potentially greater rates of herbivory. Such substantial losses to herbivory may counteract any potential increases in growth rates associated with nutrient enrichment.

Much of the nutrients that birds deliver are deposited directly in the water during high tides, quickly washed away by the subsequent tide, or transported in groundwater as dissolved organic or particulate matter (Alongi 2014). Given the value of mangroves to commercial and artisanal fisheries, the aquatic fate of avian derived nutrients and their influence on fishery productivity is an important area of future research. Young et al. (2011) reviewed the effects of seabird derived nutrients on aquatic ecosystems. Effects were highly variable, but generally had positive or neutral impacts on water column nutrient levels, as well as producer and consumer abundances. Only one of the studies reviewed by Young et al. (2011) focused on mangroves. While nutrient enrichment may benefit some ecosystems, eutrophication is a major threat to many coastal ecosystems, including some mangroves (Reef et al. 2010). The potential for negative effects of nutrient enrichment is particularly high in small bays or reef lagoons (Young et al. 2011). Future research should attempt to identify under which conditions avian derived nutrients may contribute to

eutrophication, and how these nutrient contributions compare to and interact with anthropogenic nutrient sources.

One limitation of natural experiments, such as the current study, is that the sampling locations may differ in ways other than those being studied. While the rookery and control sites are similar in many aspects, several differences can be observed which may influence our results. Little is known about the underlying geology and hydrology of the two sites. From satellite imagery (Fig. 1), it appears that the rookery is a fluvial island. It is possible that nutrient deposition and sedimentation from upstream explains some of the variation in nutrient levels between the rookery and control sites. However, the sandy substrate at the rookery site (compared to the finer organic substrate at the control site) suggests that the elevated soil nutrients at the rookery are not due to terrigenous sedimentation. Fine sediments generally contain more plant available P (phosphates) than coarse substrates because phosphate retention is more efficient in fine sediments (Saenger 2002). Despite this bias against high P levels at the rookery, rookery soils contained seven times more plant available P than the control site. In the field, certain structural differences between the sites were observed. Mangroves at the control site had denser and taller prop roots than at the rookery, even though stem density was not significantly different between the two sites. The rookery trees also had wider crowns and a more open canopy. These structural differences may be due to a variety of factors. One possible explanation is that mangroves growing in high nutrient soils invest a larger proportion of their energy in new shoot growth, as opposed to root growth (Reef et al. 2010). Birds may also physically damage the canopy or roots when perching, taking flight, or landing. Elevated foliar nutrients at the rookery may lead to increased herbivory and mortality of seedlings, reducing recruitment and maintaining a more open forest. Finally, the rookery mangroves may have wider crowns if they were recently recruited into an open habitat following a disturbance. Hurricane Mitch caused extensive damage to Gulf of Fonseca mangroves in 1998, primarily due to debris flow, flooding, changes in soil elevation, and canopy damage (Castañeda-Moya et al. 2006). Such a disturbance could have created an open habitat in which re-establishing mangroves developed wider crowns and a more open canopy than is seen in undisturbed sites.

## Conclusions

Mangroves are complex ecosystems, characterized by strong linkages with adjacent ecosystems, and high biodiversity. Conservation mechanisms such as PESs and REDD+ require an understanding of the linkages between ecosystems and the role of biodiversity in maintaining ecosystem function (McLeod et al. 2011; UNEP 2014). Our study provides insight into the role of colonial waterbirds in mangrove nutrient dynamics and adds to a growing body of literature recognizing the importance of vertebrates in mangrove nutrient cycling (Adame et al. 2015; Buelow and Sheaves 2015; Reef et al. 2014). Waterbirds transferred large quantities of nutrients from the sea to their mangrove rookery. This large nutrient influx contributed to substantially higher concentrations of biologically important nutrients in mangrove soils and vegetation at our study site. While our study did not document significant changes in aboveground biomass or C stocks, avian nutrient enrichment has the potential to influence mangrove growth rates, C sequestration, and the provision of other ecosystem services such as artisanal fisheries. Additionally, waterbird rookeries provide a unique opportunity to study mangrove nutrient limitation and the effects of nutrient enrichment on mangrove ecology and function. Future research should examine the effects of avian derived nutrients on mangrove growth rates, organic matter decomposition, nutrient export to adjacent waters, invertebrate communities, and mangrove associated fisheries.

**Acknowledgments** This work was part of the Sustainable Wetlands Adaptation and Mitigation Program (SWAMP), a collaborative effort by the Center for International Forestry Research, Oregon State University, and the United States Forest Service, with support from the United States Agency for International Development (USAID). Additional funding came from the Oregon State University Honors College and the Oregon State University College of Agricultural Sciences in support of the undergraduate thesis by the senior author. We wish to thank Ian Drysdale, Luis Turcios, Wendy Naira and Claudia Vallejo for logistical support in Honduras, as well as Johnathon Lainez and the Honduran Secretariat of Natural Resources and the Environment (SERNA) for their collaboration. We also wish to acknowledge Dr. Fourqueren of Florida International University for the carbon analysis of soils. We are grateful to all of the participants of the Gulf of Fonseca SWAMP workshop for their local knowledge and contributions to data collection in the field.

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