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

Tyler Neal McFadden, J Boone Kauffman, Rupesh Bhomia

Mangroves provide numerous ecosystem services, including biodiversity values such as nesting sites for piscivorous waterbirds. High concentrations of piscivorous birds are hypothesized to affect ecosystem dynamics, yet few studies have examined their effects in mangroves. We examined the effects of nutrient enrichment by colonial waterbirds at a mangrove rookery in the Gulf of Fonseca, Honduras. We compared macronutrient levels in the vegetation and soils between two sites — a small island that hosted large numbers of roosting waterbirds and a nearby control site with little evidence of waterbird activity. Nest density at the rookery was 1721 ± 469 nests ha^{-1} . Mangrove community structure and ecosystem carbon stocks were quantified by measuring above and belowground biomass, downed wood, and soil carbon. The nutrient input via bird guano deposition was quantified at each site. Rookery birds deposited 7.2 ± 3.4 g m^{-2} day^{-1} guano dry weight. This large nutrient influx contributed to substantially higher concentrations of biologically important nutrients in the soil and mangrove leaves. These results suggest that colonial waterbirds may significantly impact mangrove ecology and productivity at local scales. Further research is needed to understand the effects of avian delivered nutrients on mangrove growth rates, nutrient export to adjacent waters, invertebrate communities, and mangrove associated fisheries.

Key Words: mangroves, macronutrient cycling, waterbirds, guano, nutrient enrichment

Corresponding e-mail address: mcfaddty@onid.orst.edu

Introduction

Mangroves provide numerous ecosystem services, including habitat for commercially important fish and crustaceans, coastal protection from storm events, charcoal and timber, ecotourism, and carbon (C) sequestration. Mangroves are among the planet's most carbon-rich ecosystems, containing approximately 1000 tons of carbon per hectare on average (UNEP 2014). Despite their importance, mangroves are being destroyed through conversion at 3-5 times the average rate of global forest loss (FAO 2007). Greenhouse gas emissions resulting from mangrove loss now 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 (Poliodoro 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). A recent United Nations report (UNEP 2014) synthesized current knowledge of mangrove services and threats, outlining a path forward for scientists and policy makers. One suggested option was to provide financial incentives for mangrove conservation, such as Payments for Ecosystem Services (PES) or incentives for reducing emissions from deforestation and degradation (REDD+). Fair, accurate, and transparent economic valuation of ecosystem services requires sound scientific data. While our understanding of mangrove function and services has improved greatly in recent decades, knowledge gaps still exist. Further research is needed to better understand the linkages between mangroves and adjacent ecosystems, as well as the role of biodiversity in supporting mangrove health and function (McLeod et al. 2011, UNEP 2014). Both of these factors impact the capacity of mangroves to deliver ecosystem services. 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 carbon stocks.

Colonial waterbirds act as important nutrient vectors in many ecosystems (Whelan et al. 2008). These birds forage across large areas, and return to colonies (rookeries) where they deposit

nutrients in the form of guano (Ellis 2005). Previous studies in other coastal ecosystems have reported nutrient inputs comparable to fertilization rates used in intensive agriculture (Young et al. 2010). Such 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).

Mangroves provide critical foraging and nesting habitat for a variety of waterbirds, yet the role of these birds as nutrient vectors in mangrove ecosystems has received little attention in the scientific literature (Hogarth 2007, Reef et al. 2010). In this study we examined the effects of nutrient enrichment by colonial waterbirds in two mangrove sites in the Gulf of Fonseca, Honduras. The high nutrient rookery site was a small island that hosted large numbers of roosting waterbirds (Magnificent Frigatebirds, Neotropic Cormorants, Cattle Egrets, White Ibis, etc. See table 1 in results section for complete bird list). We also sampled a control site on 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, 3) Aboveground biomass would be higher at the rookery site.

Methods and Materials

Study sites

The Gulf of Fonseca is a large bay on the Pacific coast of Honduras, El Salvador, and Nicaragua (Figure 1). 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 an estimated 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).



Figure 1. Central America with arrow indicating the Gulf of Fonseca.

In July 2013 we sampled seven mangrove and shrimp pond (formerly mangrove) sites as part of the Center for International Forestry Research’s Sustainable Wetlands Adaptation and Mitigation Program. Two sites (rookery and control) were selected to examine nutrient enrichment by colonial waterbirds (Figure 2, photos 1-5 in appendix). The high nutrient site (rookery site) was a ca. 3 ha mangrove island that hosted large numbers of roosting waterbirds (Magnificent Frigatebirds, Neotropic Cormorants, Cattle Egrets, White Ibis, etc.). The island, locally known as ‘Isla de Pajaros’, is located at the mouth of a large mangrove channel, and experiences intense tidal fluctuation. Mangrove species composition 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 4-8m.

The low nutrient site (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. 500m distant) to the rookery and because it resembled 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 4-10m.



Figure 2. Location of rookery and control sites. Rookery coordinates: N 13°21.988', W 087°28.232'. Control coordinates: N 13°22.030', W 087°28.537'.

Forest structure, composition, and ecosystem carbon stocks

We determined forest structure, composition and ecosystem carbon stocks of each site following methods outlined 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 (Figure 3).

The first plot of each transect was established approximately 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.

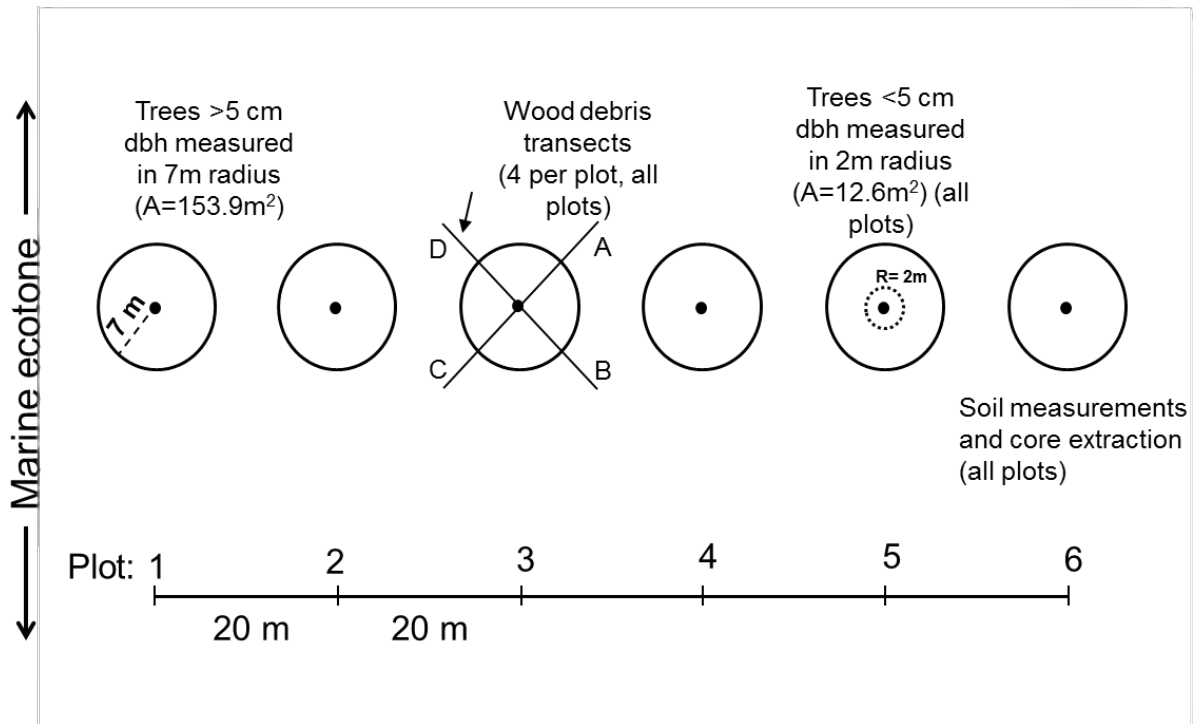


Figure 3. Sampling design used for measuring aboveground forest structure, composition, and ecosystem C stocks. Total length of transect was 100m.

Trees

Composition, tree density, and basal area were quantified through measurements of species and diameter at 1.3m height (diameter at breast height; dbh) of all trees rooted within each plot. Plot size for tree measurements was 153.9 m² (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 from French New Guinea provided by Fromard et al. (1998). Belowground 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 aboveground 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 class 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.

Dead and Downed wood

Mass of dead and downed wood was calculated using the planar intersect technique adapted 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 ≥ 2.5 cm but < 7.5 cm in diameter at the point of intersection was measured along the last 5 m of the transect. Wood ≥ 7.5 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 ≥ 7.5 cm in diameter was 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 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 near the center of each plot using a graduated aluminum pole.

The concentrations of C and N were determined by combustion method using Thermo Flash EA 1112 series NC Soil Analyzer at an analytical lab based in 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 Bray phosphorus (Bray-P), nitrate (NO₃) and ammonium (NH₄). Phosphorus was extracted using an acid-fluoride solution and measured colorimetrically based on its reaction with ammonium molybdate. NO₃ and NH₄ were extracted in 2M KCl for 1 hour and analyzed using an Alpkem Flow Solution auto-analyzer.

Nest counts

Bird nest density 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 survey plot to collect bird guano (photos 6 and 7 in appendix). The sheets were left for four days and subsequently retrieved. Guano was scraped off each sheet and stored in plastic scintillation vials at room temperature for later analysis. Upon return to the United States, the guano samples were dried for one day in a 50°C oven and homogenized using mortar and pestle. Samples were

analyzed by the Oregon State University Central Analytical Lab for Bray phosphorus (Bray-P), nitrate (NO_3) and ammonium (NH_4). Phosphorus was extracted using an acid-fluoride solution and measured colorimetrically based on its reaction with ammonium molybdate. NO_3 and NH_4 were extracted in 2M KCl for 1 hour 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 sampling area of 2.56 ha. Total breeding season nutrient inputs were estimated using a breeding season length of 120 days.

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 contaminant that may have confounded nutrient analysis. Leaves were then stored in paper bags and dried in a 60° C oven for several days. Samples were analyzed by the Oregon State University Central Analytical Lab for total phosphorus (P) and Total Kjeldahl Nitrogen (TKN). Leaf TKN was determined by kjeldahl digestion with sulfuric acid (H_2SO_4) and analyzed using an Alpkem Flow Solution auto-analyzer. To measure total P, samples were dry-ashed, extracted with 5% 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-tests were used because standard deviations were expected to vary wildly between the rookery and control sites. Differences among forest structure and carbon stocks were tested using two sample t-tests. Normality was assessed using probability plots and Shapiro-Wilk tests. Soil NO_3 , soil NH_4 , 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 \pm SE. Statistical analyses were performed in RStudio (Version 0.97.18, ©2009-2012 RStudio, Inc.).

Results

Avian community

The rookery hosted a large and diverse avian community (Table 1). The most abundant species at the time of sampling were Neotropic Cormorant, Cattle Egret, White Ibis, and Magnificent Frigatebird. Our sampling efforts likely coincided with the tail end of the breeding season for several species (Howell and Webb, 1995). We observed active nests (containing eggs or chicks) of Neotropic Cormorants, Tricolored Herons, Cattle Egrets, Roseate Spoonbills, and White Ibises. 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 (Personal communication, Luis Soto, 25 July 2013). No official bird censuses have been conducted to our knowledge. We measured nest density at 1721 ± 469 nests ha^{-1} . We observed but did not quantify variation in nest density between the island fringe and interior. The island fringe contained fewer nests than the interior, but was used by many roosting birds, particularly magnificent frigatebirds. We estimate the rookery to contain 4407 ± 2941 nests at the time of sampling.

Table 1. List of bird species observed at Isla de Pajaros, Honduras (rookery site) in approximate order of abundance. Sources for diet information: The Birds of North America Online (2005) and Ramos et al. (2010).

Common name	Latin name	Diet	Observed breeding
Neotropic Cormorant	<i>Phalacrocorax brasilianus</i>	Fish, shrimp	X
Cattle Egret	<i>Bubulcus ibis</i>	Fish, arthropods, amphibians	X
White Ibis	<i>Eudocimus albus</i>	Aquatic crustaceans	X
Magnificent Frigatebird	<i>Fregata magnificens</i>	Fish, squid	
Great Egret	<i>Ardea alba</i>	Fish, crustaceans	
Tricolored Heron	<i>Egretta tricolor</i>	Small fish	X
Black-crowned Night-Heron	<i>Nycticorax nycticorax</i>	Insects, crustaceans, mollusks, fish, mammals, birds/eggs	
Snowy Egret	<i>Egretta thula</i>	Worms, insects, crustaceans, fish	
Brown Pelican	<i>Pelecanus</i>	Fish	

	<i>occidentalis</i>		
Roseate Spoonbill	<i>Platalea ajaja</i>	Fish, crustaceans, aquatic insects	X
Boat-billed Heron	<i>Cochlearius cochlearius</i>	Fish, crustaceans	
Anhinga	<i>Anhinga anhinga</i>	Fish	

Avian derived nutrients

Birds delivered large quantities of nutrient rich guano to the rookery. Mean guano deposition to the rookery was measured at $7.15 \pm 3.43 \text{ g m}^{-2}$ per day. In four days of sampling we recorded no guano deposition at the control site. Guano samples contained very high concentrations of biologically available nutrients. Guano contained $3658 \pm 368 \text{ mg kg}^{-1}$ bray-P, $29.3 \pm 6.2 \text{ mg kg}^{-1}$ NO_3 , and $2192.7 \pm 196.3 \text{ mg kg}^{-1}$ NH_4 . Mean daily nutrient inputs from guano was $281 \pm 146 \text{ g ha}^{-1}$ bray-P, $3.0 \pm 1.8 \text{ g ha}^{-1}$ NO_3 , and $185 \pm 95 \text{ g ha}^{-1}$ NH_4 .

Deposition rates of total P and total N were calculated using literature values reported by Frederick and Powell (1994). Frederick and Powell reported that piscivorous wading bird guano composition was 1.9% P and 13% N by dry weight. By combining these published nutrient concentrations 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.

Soil and foliar nutrients

Soil nutrient levels were significantly higher at the rookery compared to the control site (Figure 4). Mean soil bray-P was seven times greater at the rookery than at the control site ($80.5 \pm 21.1 \text{ mg kg}^{-1}$ compared to $11.2 \pm 0.7 \text{ mg kg}^{-1}$, $p = 0.022$). Mean soil NO_3 was nearly eight times greater at the rookery than at the control site ($10.5 \pm 2.9 \text{ mg kg}^{-1}$ compared to $1.4 \pm 0.7 \text{ mg kg}^{-1}$, $p = 0.0009$). Mean soil NH_4 at the rookery was nearly twice that of the control site ($15.6 \pm 2.1 \text{ mg kg}^{-1}$ compared to $8.9 \pm 0.9 \text{ mg kg}^{-1}$, $p = 0.009$).

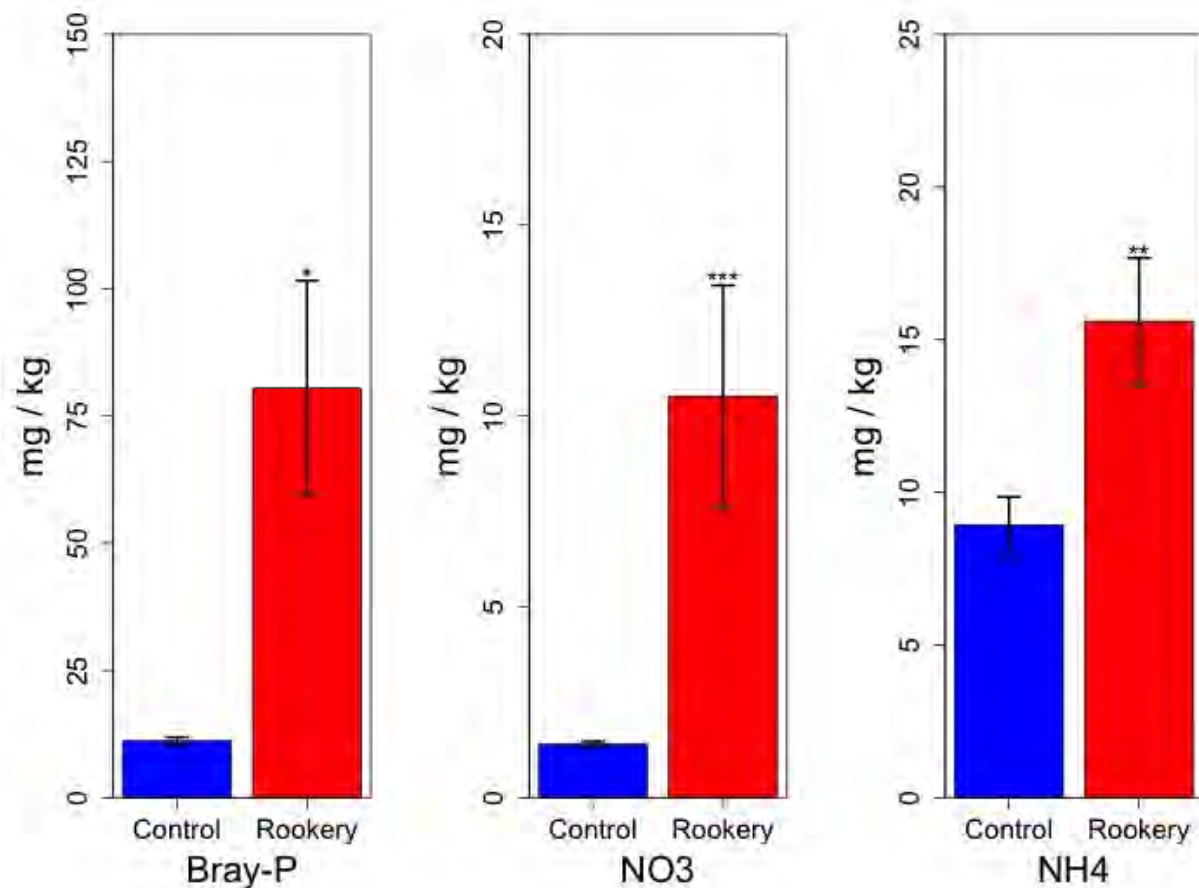


Figure 4. Soil concentrations of plant available phosphorus (Bray-P), nitrate (NO₃), and ammonium (NH₄). Error bars represent mean±SE. *: p < 0.05, **: p < 0.01, ***: p < 0.001.

Foliar nutrient concentrations were significantly higher at the rookery compared to the control site (Figure 5). Total P concentrations were 0.12 ± 0.007 % at the rookery compared to 0.10 ± 0.005 % at the control site ($p = 0.031$). TKN concentrations were 1.82 ± 0.12 % at the rookery compared to 1.29 ± 0.04 % at the control site ($p = 0.005$). Nitrogen to phosphorus ratios (N:P) in the leaves was greater at the rookery than at the control site, but the difference was not significant ($p = 0.089$). Mean N:P values were 15.4 ± 0.7 and 13.7 ± 0.6 at the rookery and control sites, respectively.

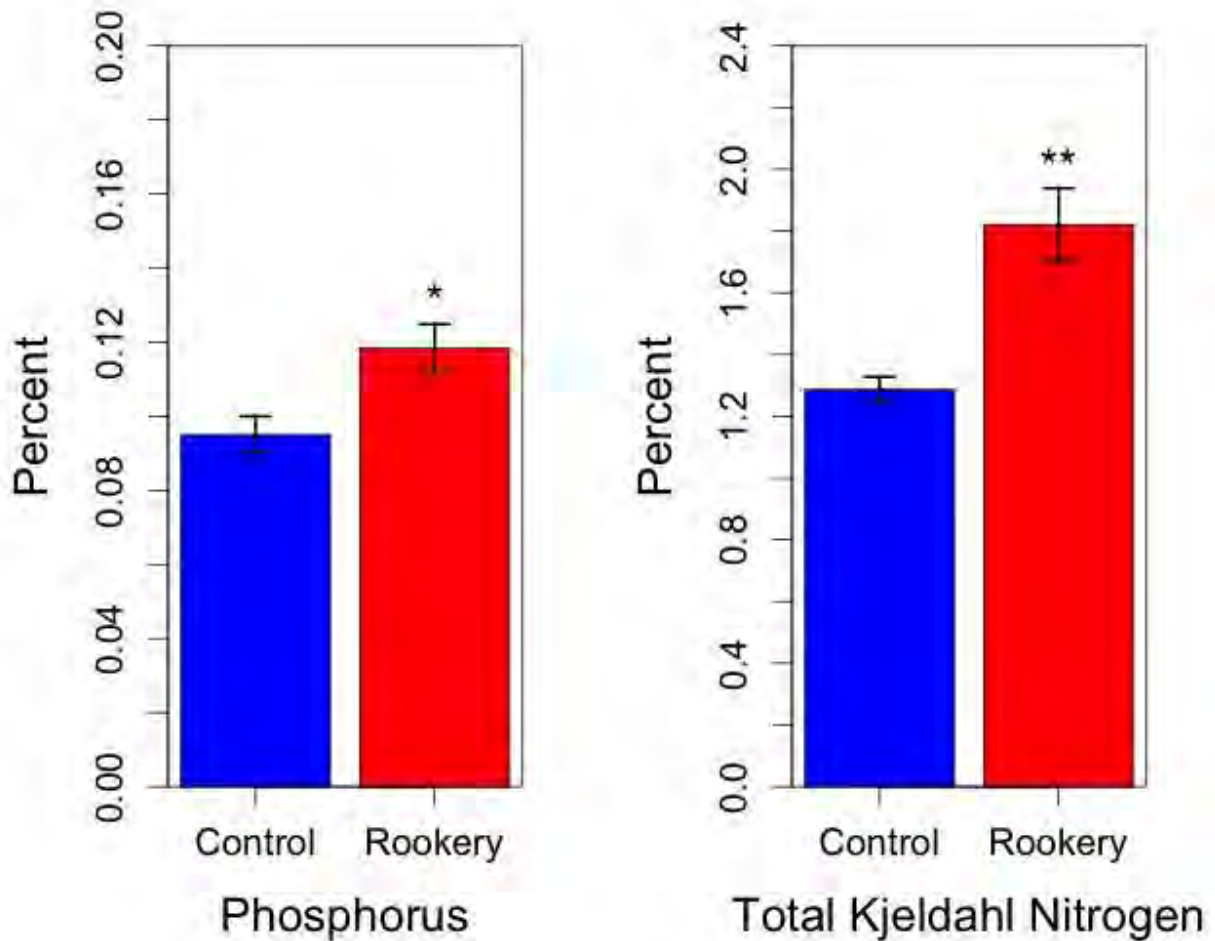


Figure 5. Foliar concentrations of phosphorus and TKN. Error bars represent mean \pm SE. *: $p < 0.05$, **: $p < 0.01$.

Aboveground forest structure and ecosystem C stocks

The presence of birds appeared to result in few differences in mangrove ecosystem structure. Basal area was slightly higher at the control site, but the difference was not significant ($7.31 \pm 1.42 \text{ m}^2 \text{ ha}^{-1}$ at the control vs. $6.30 \pm 0.83 \text{ m}^2 \text{ ha}^{-1}$, $p = 0.553$). 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, $p = 0.185$). 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, $p = 0.470$). Ecosystem carbon stocks (Figure 6) were almost identical between the two sites ($411 \pm 11 \text{ Mg ha}^{-1}$ at the control vs. $400 \pm 61 \text{ Mg ha}^{-1}$ at the rookery, $p = 0.857$).

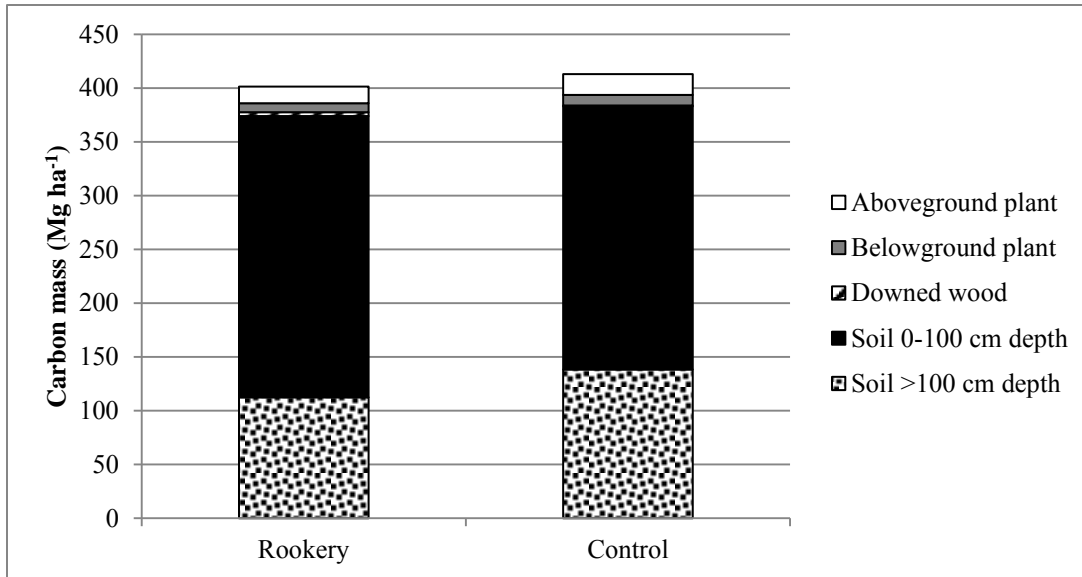


Figure 6. Ecosystem carbon stocks of the two study sites, reported by carbon pool.

Discussion

Waterbirds as nutrient vectors

We found that nesting waterbirds can be significant nutrient vectors, transporting large quantities of nutrients from the aquatic environment to their mangrove nest sites. We estimated that at the Isla de Pajaros (the rookery site) birds delivered between 4.9 and $13.8 \text{ kg N ha}^{-1}$ per day and between 0.7 and 2.0 kg P ha^{-1} per day to the rookery. These rates far exceed typical fertilizer application rates used for corn in the United States of America. For comparison, average annual rates of fertilization for corn are approximately 156 kg N ha^{-1} and 30 kg P ha^{-1} (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. In total we estimate that birds delivered 22 metric tons of guano (dry weight) to the rookery mangroves in the course of the four month breeding season. Total breeding season N and P inputs are estimated at 2.86 metric tons and 0.42 metric tons.

Five of the twelve waterbird species observed at the rookery were observed tending active nests (containing eggs, chicks, or fledglings). Three of the four most abundant bird species were breeding in large numbers (Neotropic Cormorant, White Ibis, and Cattle Egret). To our

knowledge, 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). Tropical birds will frequently make multiple nesting attempts within one year, and typically produce smaller clutch sizes than their temperate conspecifics (Gill 2007). Using life history data of North American waterbirds, we conservatively estimated that the peak breeding season would last for four months at our rookery site (The Birds of North America Online, 2005). According to local biologists, bird numbers increase at the rookery in winter with the arrival of North American migrants. Even though bird numbers increase in winter, guano deposition to the rookery may not increase. Migrant birds may spend less time at the rookery because they do not have nests to tend. Migrant individuals typically begin to arrive in August and leave the following April (Howell and Webb, 1995). We consider our guano measurements to be representative of the guano deposition by resident birds during the four month breeding season.

Deposition rates of plant-available nutrients (Bray-P, NO_3 , and NH_4) were smaller but still substantial. These rates however underestimate the total nutrient contribution that birds make to the rookery for several reasons. First, Bray-P is a measure of plant-available phosphorus, and does not account for phosphorus that may become available after deposition (Bray and Kurtz 1945). Second, much of the nitrogen initially present in the guano was likely lost to volatilization in the field. Smith and Johnson (1995) experimentally demonstrated that in a humid environment, nearly 60% of total nitrogen in fresh guano was lost to ammonia volatilization within four days. Our guano samples were exposed for up to four days in very hot and humid weather during the sampling period and therefore our estimates are likely quite low. Guano that is intercepted by the canopy likely experiences a similar loss of nitrogen to volatilization. However, guano that passes the canopy (such as what we measured), would typically fall in water during high tides or would be covered in water within 12 hours. For these reasons, we estimated total N and total P inputs using literature values for piscivorous wading bird guano deposition (guano reported as 13% N and 1.9% P by mass; Frederick and Powell 1994). These concentrations fall at the lower end of the spectrum 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 phosphorus (bray-P) were seven-fold greater and NO_3 concentrations were eight-fold greater at the rookery than at the control site. Rookery NH_4 concentrations were nearly twice those of the control site. NH_4 is typically the most abundant form of nitrogen in mangrove soils and is highly available for plant uptake (Reef et al. 2010). Foliar concentrations of total P and TKN were both significantly greater at the rookery site, indicating that mangroves utilized avian delivered nutrients.

Mangroves are very productive ecosystems but are often limited by nutrient availability (Reef et al. 2010). Nutrient limitation in mangroves is most frequently attributed to either N or P limitation. Which nutrient is limiting 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 at the control site in our study was 13.8 ± 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. Rookery N:P ratios were higher than at the control site, but not significantly so (mean = 15.4 ± 0.7 , $p=0.089$). Elevated N:P ratios at the rookery would further suggest N limitation, because the mangroves took up relatively more N than P, even though both nutrients were present in high concentrations.

Mangroves are highly sensitive to variation in nutrient availability (Boto and Wellington 1983, Feller 1995, Feller et al. 2003). Numerous studies have documented the ecological impacts of avian guano inputs in other ecosystems. Authors have reported a wide range of effects, from increased primary production to increased abundance of terrestrial and aquatic consumers (Polis et al. 1997, Young et al. 2011, Polis and Hurd 1996, McCauley et al. 2012). 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. Onuf et al. (1977) measured increased growth rates and insect herbivory of *R. mangle* in response to N enrichment by a seasonal bird colony in Florida. To our knowledge, this is the only previously published study to address avian nutrient enrichment in mangroves.

We would expect primary productivity at the rookery to increase as a result of nutrient enrichment. However we found no significant differences in aboveground forest structure, aboveground carbon stocks, or ecosystem carbon stocks between the two sites. Although no differences in forest structure were quantified, the sites were not identical. The control site mangroves had denser and taller prop roots than the rookery, even though stem density did not differ between the two sites. One possible explanation for this difference 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). Other possible explanations for this difference are structural damage from perching birds, or damage from the rookery's greater exposure to tidal energy. We would also expect to see increased insect herbivory of mangrove tissues due to elevated N concentrations (i.e. increased nutritive value). Increased herbivory damage may counteract any potential increases in primary production.

Much of the nutrients that birds deliver are likely deposited directly in the water, or are quickly washed away by the tides. Given the value of mangroves to commercial and artisanal fisheries, the aquatic fate of avian derived nutrients 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. 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.

Conclusion

Mangroves are complex ecosystems, characterized by strong linkages with adjacent ecosystems, and high biodiversity. Conservation mechanisms such as Payments for Ecosystem Services 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 overlooked role of colonial waterbirds in mangrove nutrient cycles. Our findings demonstrate that waterbirds can transfer large quantities of nutrients from the sea to the mangroves. This large nutrient influx contributed to substantially higher concentrations of biologically important nutrients in mangrove soils and vegetation at our study site. Waterbird rookeries provide a unique opportunity to study mangrove nutrient limitation and the effects of nutrient enrichment on mangrove ecology and function. Mangrove conservation measures would benefit from further research examining the effects of avian derived nutrients on mangrove growth rates, nutrient export to adjacent waters, invertebrate communities, and mangrove associated fisheries.

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Appendix



Photo 1. Isla de Pajaros (rookery), Gulf of Fonseca, Honduras. Photo taken from the control site.



Photo 2. Rookery site. Photo courtesy of Rupesh Bhomia.



Photo 3. Control site.



Photo 4. White ibises perched in *L. racemosa* at the rookery. Photo courtesy of J Boone Kauffman.



Photo 5. Roseate spoonbill perched in *R. mangle* at the rookery. Photo courtesy of Rupesh Bhomia.



Photo 6. Guano collection sheet installed beneath the canopy at the rookery.



Photo 7. Guano collection sheet after four days installed below the canopy at the rookery.