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Marine-derived Nutrients from Green Turtle Nests Subsidize Terrestrial Beach Ecosystems

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ABSTRACT

Spatially separated ecosystems are often linked by nutrient fluxes. Nutrient inputs may be transferred by physical vectors (*i.e.*, wind and water) or by biotic vectors. In this study, we examine the role of green turtles (*Chelonia mydas*) as biotic transporters of nutrients from marine to terrestrial ecosystems, where they deposit eggs. We compare low and high nest density sites at Tortuguero, Costa Rica, the largest green turtle rookery in the western hemisphere. Four plant species (*Costus woodsonii*, *Hibiscus pernanbucensis*, *Hymenocallis littoralis*, *Ipomoea pes-caprae*) were analyzed at both nest density sites for ^{15}N, total carbon, nitrogen, and phosphorus, and vegetation cover. Sand was analyzed for ^{15}N and total nitrogen. Vegetation at high nest density sites had higher total nitrogen, which was correlated with higher $\delta^{15}N$ values, suggesting nutrient input from a marine source. The dominant plant species changed between low and high nest density sites, indicating that turtle-derived nutrients may alter the plant community composition. The trend in $\delta^{15}N$ values of sand was similar, although less pronounced than that of the vegetation. Sand may be a poor integrator of nutrient input due to low nutrient adsorption and high rate of leaching. Sea turtles have previously been shown to deposit considerable amounts of nutrients and energy on nesting beaches. In this study, we estimate annual nitrogen and phosphorus contributions at Tortuguero are 507 and 45 kg/km, respectively, and we demonstrate that beach vegetation likely assimilates a portion of these marine-derived nutrients.

Abstract in Spanish is available in the online version of this article.

Key words: allochthonous nutrients; beach vegetation; *Chelonia mydas*; Costa Rica; nitrogen; phosphorus; sea turtles; stable isotopes.

ALLOCHTHONOUS NUTRIENTS COMMONLY FLOW between spatially separated ecosystems or habitats (Polis *et al.* 1997). While these fluxes may move by physical or biotic vectors, in many cases, animals are the transporters. Connectivity between aquatic and terrestrial habitats by animal movements often links productive marine systems to a less productive terrestrial system. Nutrient transport can occur when animals forage in one location and defecate in another (Polis & Hurd 1996, Fariña *et al.* 2003, Crait & Ben-David 2007), when terrestrial consumers utilize aquatic prey (Hilderbrand *et al.* 1999), and through secondary remains (other than excretions), such as food scraps, feathers, and egg remains at bird breeding grounds (Polis & Hurd 1995). Furthermore, these nutrient subsidies may travel through trophic levels and have consequences for population, food web, and community dynamics (Rose & Polis 1998, Anderson & Polis 1999).

Stable isotopes have increasingly been used to investigate such examples of nutrient transport, particularly when two ecosystems are isotopically distinct. Habitats often vary in their isotope distributions due to differences in biogeochemical processes that discriminate between isotopes. Therefore, stable isotopes can provide a useful tool to trace sources of energy and nutrients between habitats. Nitrogen isotope ratios (denoted as $\delta^{15}N$), in particular, can be used as indicators of marine-derived nutrients because marine ecosystems are typically ^{15}N-enriched relative to terrestrial food webs (Hobson 1999, Schindler & Lubetkin 2004). As nutrients move through food webs, baseline differences in isotopic ratios are transmitted through trophic levels (Minagawa & Wada 1984, Pajuelo *et al.* 2010). Consumers can maintain these isotopic differences as they travel between ecosystems, particularly if the turnover time of the tissue in the consumer is slow.

Sea turtles may play important roles as vectors of nutrient transport between marine and terrestrial ecosystems. For instance, loggerhead turtles (*Caretta caretta*) make substantial N, P, and organic matter contributions to nutrient-poor nesting beaches in Florida, depositing nutrients from distant foraging grounds in the form of eggs (Bouchard & Bjorndal 2000). These subsidies are derived from unhatched eggs, chorioallantoic fluid, and egg shells from hatched embryos, as well as hatchlings that do not emerge from nests. Approximately 59–66 percent of the energy, organic matter, lipids, and nutrients from nests remain in the beach ecosystem, which is then potentially available to plants, predators, detritivores, and decomposers (Bouchard & Bjorndal 2000). Despite the potential availability of these marine-derived nutrients, there are few studies using stable isotopes to trace whether such nutrients are assimilated by terrestrial organisms. One study, however, measured nutrient incorporation by dune vegetation at a beach used by nesting loggerhead and green turtles in Melbourne, Florida (Hannan *et al.* 2007). Values of $\delta^{15}N$ and total N in dune soils and in sea oats (*Uniola paniculata*), were positively correlated

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with nest density (Hannan *et al.* 2007). A second study found increased $\delta^{15}N$ values in a terrestrial insect population (*Scapteriscus didactylus*) known to damage leatherback sea turtle (*Dermochelys coriacea*) eggs in French Guiana, indicating that some of the insects fed on turtle eggs (Maros *et al.* 2006).

In this study, we further investigate the potential for turtle-derived nutrients to subsidize a beach in Tortuguero, Costa Rica, which hosts the largest nesting aggregation of green turtles in the Atlantic Ocean. The beach is an ideal site to trace green turtle nutrient input, as the overall nest density at Tortuguero is much higher than at Melbourne Beach (~180,000 nests over 30 km in comparison with ~14,000 nests over 21 km; Bouchard & Bjorndal 2000, Debade *et al.* 2008). We utilize ^{15}N as well as C:N:P ratios to assess marine-derived nutrient input in vegetation and sand at the nesting beach. We predicted that sand and vegetation would exhibit elevated $\delta^{15}N$, N, and P values at higher turtle nest densities. Finally, we estimated the total mass of N and P introduced to Tortuguero beach through turtle nesting and proportion of those nutrients remaining in the beach after accounting for hatchlings that return to the ocean.

METHODS

Site description.—Tortuguero Beach is located in northeast Costa Rica on a narrow island that extends approximately 30 km north to south and is separated from the mainland by Rio Tortuguero. Low-lying rain forest covers the area immediately behind the beach. From 1955 to date, nest distributions have been recorded in units of miles, with mile 0 at the north end. As we rely on nest distribution data from Tiwari *et al.* (2005), we use miles in our study. The village of Tortuguero occurs at mile 3, and Tortuguero National Park encompasses the area from mile 3.5 to the southern end of the beach at mile 18.

Tiwari *et al.* (2005) examined the spatial distribution of green turtle nests at Tortuguero Beach between 1972 and 2000 and found no significant inter-annual variation in nesting distributions despite changes in population size and a dynamic beach environment. While the number of total nests per year varied throughout the period examined (approximately 20,000–90,000 nests; Solow *et al.* 2002), the relative distribution of nests along the beach remained constant, with a central tendency of high nest density near the middle and decreasing density to the north and south. This consistent pattern of nest distribution was used to select sample sites representing both low and high nest density within the national park at mile 4 and mile 10, with three times more nests at the high density site (Fig. 1).

The green turtle nesting season at Tortuguero typically occurs from June to November with peak nest densities in August. All sample collection of vegetation and sand occurred in December 2007 after the nesting season and when the greatest accumulation of nutrients was expected. The $\delta^{15}N$ values of green turtle nest contents at Tortuguero were not determined in this study. However, $\delta^{15}N$ values of epidermis from nesting green turtles at Tortuguero collected in 2007 ranged from 3.9 to 8.9‰ (H. Vander Zanden, unpubl. data). While there has been

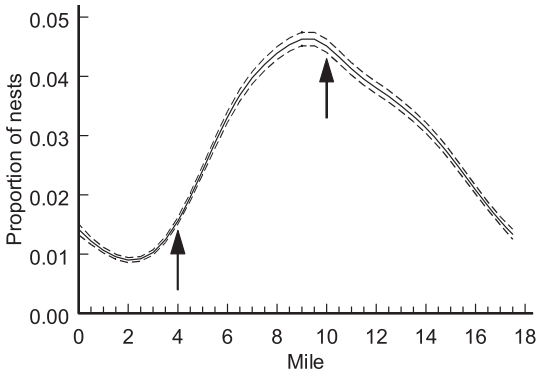

FIGURE 1. Green turtle nest distribution over 18 miles of Tortuguero beach based on 25 yr of track surveys. Solid line represents the fitted model, dashed lines represent ± 2 SE, arrows indicate sampling locations. Adapted from Tiwari *et al.* (2005).

no published discrimination factor (*i.e.*, $\delta^{15}N$ differences among tissue types) for adult epidermis and nest contents of green turtles, the $\delta^{15}N$ value of green turtle nest contents is very similar to that of adult green turtle carapace (Godley *et al.* 1998). Therefore, it was expected that the range in epidermis samples would reflect $\delta^{15}N$ values of nest contents. This potential source of N input from turtle nests has higher $\delta^{15}N$ values than that of leaf samples in terrestrial environments, which can range from −8 to 3‰ (Peterson & Fry 1987), thus allowing us to trace marine-derived inputs.

Vegetation sampling and analysis.—Four plant species were selected for sampling due to their prevalence, taxonomic diversity, and natural zonation among beach vegetation types: *Costus woodsonii* (red/bitter cane; Costacae), *Hibiscus pernambucensis* (beach hibiscus; Malvaceae), *Hymenocallis littoralis* (spider lily; Amaryllidacae), *Ipomoea pes-caprae* (beach morning glory; Convolvulaceae). *Hymenocallis littoralis* and *I. pes-caprae* occur in the beach vegetation zone, or low-lying salt spray community (Hirth 1963). *Costus woodsonii* and *H. pernambucencis* are species found in the dense hedgerow zone of vegetation at the rear of the beach (Hirth 1963) and are considerably larger than the other two species. At each sampling site, three leaves were selected from each individual plant based on uniformity in age and minimal herbivore damage, and those leaves were pooled into a single composite sample. Leaves were collected from five individuals of each of the four species at both sites, resulting in 40 samples in total. Samples were washed with distilled water and dried at 60°C for 24 h. Dried samples were homogenized to <1 mm using a Wiley mill.

Total dry mass percent C and N plus N isotope ratios were measured for vegetation samples at the University of Florida Department of Geological Sciences Light Isotope Lab. Samples of 2.7–4.3 mg were loaded into tin capsules for combustion in a Costech ECS 4010 elemental analyzer interfaced via a ConFlo III device to a ThermoFinnigan Delta Plus XL (Bremen, Germany) isotope ratio mass spectrometer. Delta notation is used to express

stable isotope abundances, defined as parts per thousand (‰) relative to the standard:

$$\delta = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000$$

where R_{sample} and $R_{standard}$ are the corresponding ratios of heavy to light isotopes ($^{15}N/^{14}N$) in the sample and international standard (atmospheric N_2). The reference material USGS40 (L–glutamic acid) was used as a calibration standard in all runs. The standard deviation in $\delta^{15}N$ values of the reference material was 0.11‰ ($N = 10$).

Total P was determined at the University of Florida Forage Evaluation Support Laboratory. Samples of 0.25 g were digested using a variation of the aluminum block digestion procedure (Gallaher *et al.* 1975). The catalyst used was 9:1 K_2SO_4:$CuSO_4$ (1.5 g), and the digestion was conducted for at least 4 h at 375° C using 6 mL of H_2SO_4 and 2 mL H_2O_2. Phosphorus in the digestate was determined by semi-automated colorimetry using a Technicon Autoanalyzer (Hambleton 1977). All nutrient ratios reported in this study are mass-based.

At low and high nest density sites, vegetation density was assessed via point intercept along two 25 m transects along the edge of the dense hedgerow of vegetation at the rear of the beach, and total intercept length was recorded for each species. The formula (total intercept length/total transect length × 100) was used to calculate the frequency of vegetative cover for each target species.

Sand sampling and analysis.—Sand samples were collected at the time of vegetation sampling. The sand at Tortuguero has been characterized as fine to medium sand with the most abundant mineral being a highly ferruginous olivine (Hirth 1963). Three sand sampling points were randomly selected along both low and high density sites. At each site, samples were taken at the edge of the hedgerow vegetation (designated border zone) and 2 m away from the border location in the direction of the water (designated open zone). At each site, sand was sampled using an auger at two depths: 20 and 90 cm. These depths were selected to be below the surface and below the 78 cm mean depth of egg chambers (Debade *et al.* 2008). Each sand sample was a 200–300 g sub-sample from a thoroughly mixed composite of sand from three holes spaced at 0.25 m intervals parallel to the water. At both low and high density sites, 12 independent replicates were collected: three border zone points at two depths and three open zone points at two depths. Sand was prepared for isotope analysis by air-drying at the field site and oven-drying at 60°C for 24 h at the University of Florida. Large items of organic matter were removed using a 0.85 mm screen, and the sand was ground with a mortar and pestle until it passed through a 0.42 mm screen. Samples weighing 75–305 mg were loaded into tin capsules and analyzed for N isotopes at the Stable Isotope Core Laboratory at Washington State University. Samples were combusted in a Costech ECS 4010 elemental analyzer and analyzed in a ThermoFinnigan Delta Plus XP (Bremen, Germany) isotope ratio mass spectrometer. Each sample was run 2–4 times, and a mean was calculated from values of all runs for each sample. An internal reference material (Palouse topsoil) was used as a calibration standard in all runs. The standard deviation in isotope ratios of the reference material was 0.16‰ for $\delta^{15}N$ ($N = 13$). Total N was measured colorimetrically using a Technicon autoanalyzer following Kjeldahl digestion (US Environmental Protection Agency 1993, Method 352.1).

Nutrient input.—The potential mass of N and P introduced to the beach through green turtle nests was estimated for the year of our study. Based on track surveys, an estimated 177,260 nests were laid in the 18 miles of beach in 2007, and 110 nests were monitored throughout incubation (Debade *et al.* 2008) to determine hatching and emergence success, or the number of hatchlings that hatch out of the egg shell and the number of hatchlings that reach the beach surface, respectively (Miller 1999). Overall hatching success was 75 percent and emergence success was 67 percent with a mean clutch size of 108 eggs (Debade *et al.* 2008). It was assumed that N and P contents of green turtle eggs and hatchlings are comparable to those of fresh loggerhead eggs and hatchlings measured by Bouchard and Bjorndal (2000). Green turtle eggs and hatchlings are 16 and 25 percent larger than loggerhead eggs and hatchlings, respectively, and so we corrected for mass differences using measurements from corresponding locations for each study: loggerheads in Florida and green turtles at Tortuguero, Costa Rica (Dodd 1988, Hirth 1988).

Inputs of N and P were calculated as the number of eggs laid in the 18 miles of beach multiplied by the mean nutrient content in fresh eggs. Emergence success and nutrient content of hatchlings were used to estimate the return of N and P to the ocean in the form of hatchlings.

Statistical analysis.—There were no differences in variance estimates between low and high nest densities. Therefore, comparisons between low and high nesting densities were made using equal variance *t*-tests. The Bonferroni approach for simultaneous multiple comparisons was used to set $\alpha = 0.046$. In all cases except that of C, one-tailed *t*-tests were conducted because we expected higher nutrient content at high nest density locations. We had no prior expectations for vegetation C content with respect to nest density and therefore conducted a two-tailed *t*-test in that comparison. Each plant species was analyzed separately, and sand samples were segregated by depth and vegetation zone. Linear regression was used to examine the relationship between N and $\delta^{15}N$ in the vegetation and sand data with $\alpha = 0.05$. All statistical analyses were performed using R® (R Development Core Team 2009).

RESULTS

Vegetation.—Significant increases in $\delta^{15}N$ values of all four plant species were observed from low to high nest density

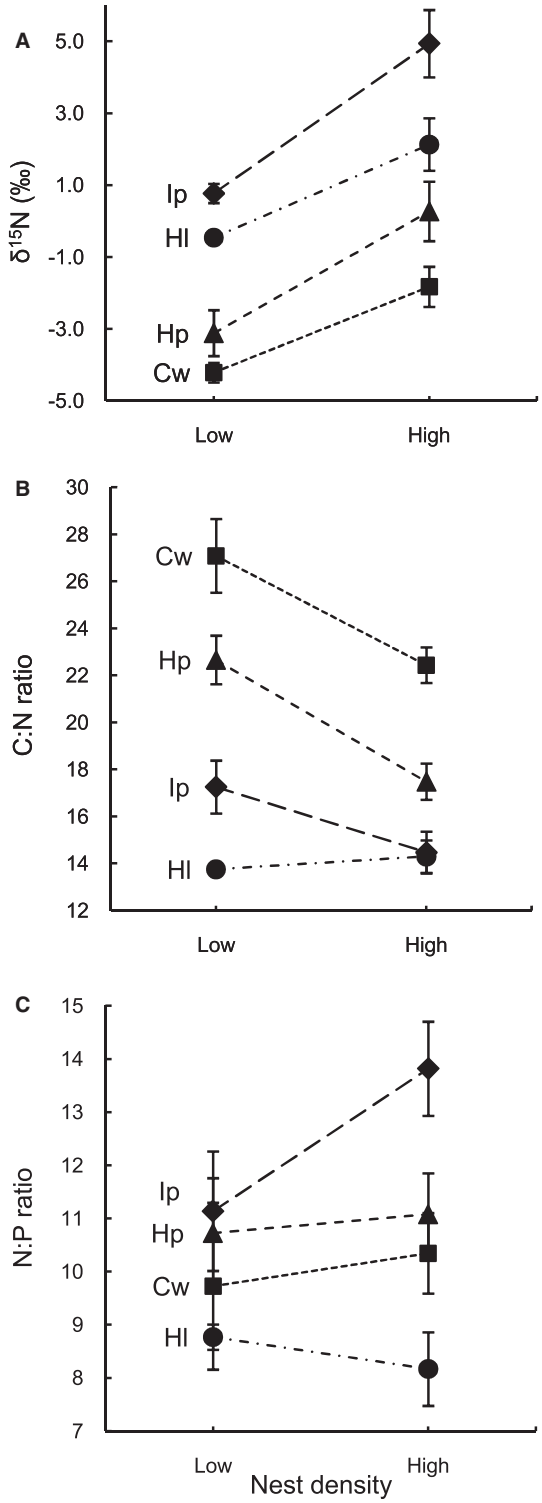

FIGURE 2. Mean (±SE) isotope and nutrient content of each plant species at low and high green turtle nest density (N = 5). (A) All four species had significantly higher $\delta^{15}N$ values at the high nest density site. (B) All species except *H. littoralis* had significantly lower C:N ratios at the high nest density site. (C) Only *I. pes-caprae* had a significant increase in the N:P ratio at high nest density. Cw, *Costus woodsoonii*; Hp, *Hibiscus pernanbucensis;* Hl, *Hymenocallis littoralis*; Ip, *Ipomoea pes-caprae*.

(Fig. 2A; Table 1). The mean $\delta^{15}N$ difference between low and high density averaged over all species was 3.1‰. A significant increase in N from low to high nest density was observed in three of the four plant species (mean increase of 0.5%) (Table 1), and the C:N ratio significantly decreased for the same three species (Fig. 2B) due to increased N (Table 1). Increases in N of the plant tissue corresponded to a significant increase in $\delta^{15}N$ (Fig. 3), indicating that additional nitrogen uptake by the plant occurred from a more enriched source. Patterns in P were less clear, with significant increases from low to high nest density in only two of the four species (Table 1). As *C. woodsonii* and *H. pernambucensis* had higher N at high nest density, the N:P ratio remained unchanged. A small but significant increase in the N:P ratio occurred in *I. pes-caprae*, for which N increased but P did not (Fig. 2C; Table 1).

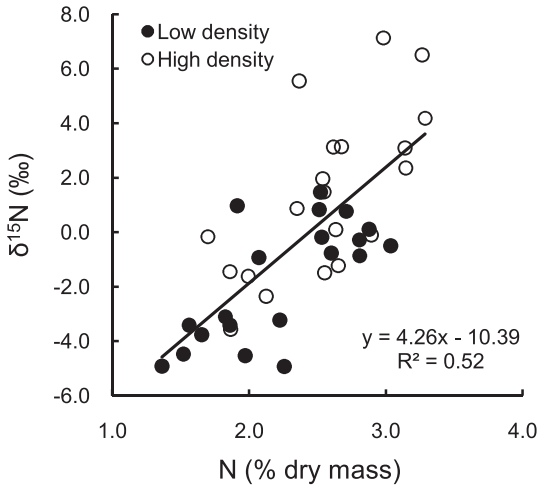

FIGURE 3. Foliage $\delta^{15}N$ values increase significantly with increasing N when all plant samples from both low and high nest density are plotted together. (F = 40.43, df = 38, P < 0.001).

TABLE 1. *P-values from one-tailed* t*-tests for all comparisons except C in which a two-tailed test was performed. For each species, comparisons were made between low and high nest density sites for $\delta^{15}N$, C, N, P, C:N ratios, and N:P ratios. Significant values are highlighted in bold; + or − indicates high nest density site is higher/lower than low nest density site.*

Species	n	$\delta^{15}N$	C	N	P	C:N	N:P
Costus woodsonii	10	**0.003+**	0.052	**0.02+**	**0.016+**	**0.014-**	0.26
Hibiscus pernambucensis	10	**0.006+**	0.64	**0.002+**	**0.004+**	**0.002-**	0.36
Hymenocallis littoralis	10	**0.004+**	0.27	0.62	0.41	0.76	0.68
Ipomoea pes-caprae	10	**0.001+**	0.55	**0.03+**	0.69	**0.044-**	**0.005+**

TABLE 2. *Dominance (% cover) of each plant species in the border zone, based on point intercept along two 25 m transects at each site.*

Species	Low density	High density
Costus woodsonii	35	2
Hibiscus pernambucensis	7	48
Hymenocallis littoralis	2	7
Ipmoea pes-caprae	0	1

The dominant species in the vegetation coverage changed between sites, with greater coverage of *C. woodsonni* at low nest density and *H. pernambucensis* at high nest density (Table 2). As all transects were positioned in the border zone and not in the open zone where *H. littoralis* and *I. pes-caprae* are typically found, these two species were observed infrequently in this assessment.

SAND.—While there were trends for increased $\delta^{15}N$ values of sand between low and high nest density for a given depth or beach zone, none of these comparisons was significant (Fig. 4). When sand samples from both low and high nest densities were combined, however, samples at 90 cm depth (below the mean depth of green turtle nests) had significantly higher $\delta^{15}N$ than those at 20 cm (Fig. 5). A significant negative relationship was observed between $\delta^{15}N$ and N values after a point identified with the Bonferroni test for outliers (Bonferonni $P = 0.017$) was removed (Fig. 5). This relationship in sand samples was the opposite of trend observed in vegetation samples.

NUTRIENT INPUT.—Green turtle nesting was estimated to have introduced approximately 507 kg/km of N and 45 kg/km of P in 2007. Hatchlings that returned to the ocean accounted for approximately 259 kg/km of N and 31 kg/km of P, leaving 248 kg/km (49%) of N and 14 kg/km (31%) of P in the beach ecosystem.

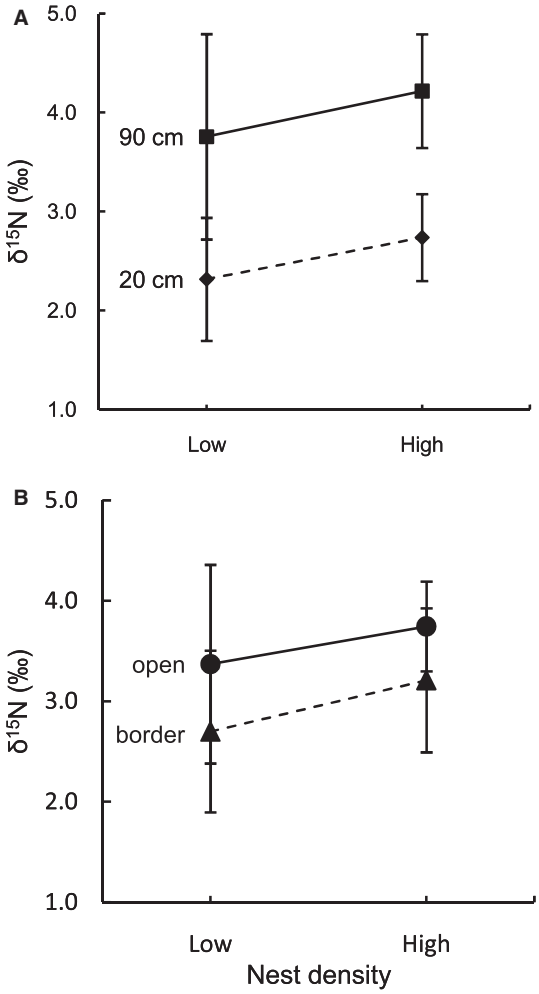

FIGURE 4. Mean (±SE) $\delta^{15}N$ values of sand at low and high green turtle nest density at (A) depths of 20 and 90 cm or (B) open and border zones ($N = 6$). While there are trends for increase in $\delta^{15}N$ at high nest density, none of the relationships is significant.

DISCUSSION

VEGETATION.—Foliar tissue at high nest density sites had both higher $\delta^{15}N$ and N values. Across all samples, N content was positively related to $\delta^{15}N$ values, indicating assimilation of a ^{15}N-enriched source of N in these plants, presumably derived from green turtle nests. This pattern is similar to that observed in sea oats on a Florida loggerhead-nesting beach (Hannan *et al.* 2007). It appears that the plants, regardless of beach zone, accessed and assimilated marine-derived N. While there are differences in baseline $\delta^{15}N$ values of each plant species, the magnitude of ^{15}N-enrichment observed from low to high nest density was approximately the same. The relative differences in species' overall $\delta^{15}N$ values could be due to various reasons, including variation in discrimination against $\delta^{15}N$ during uptake, assimilation, or internal distribution of N; as well as the form of N used (Högberg 1997, Evans 2001).

As N and P are typically limiting nutrients for plant growth, we expected that Tortuguero turtle nests might also provide a source of P to beach vegetation. An increase in P at high nest density sites, however, was only observed in two of the four species. It is likely that the plant community is N-limited based on N:P ratios in these samples (Fig. 2C, mean for all samples = 10.5), as N:P ratios below 14 (by mass) are indicative of N-limitation (Koerselman & Meuleman 1996, Högberg 1997). In addition, the introduced fraction of P remaining in the beach ecosystem is smaller than the remaining fraction of N (31% and 49%, respectively). Therefore, we believe that these N-limited plants benefit more from the N subsidy than P subsidy from turtle nests.

Plant access to nutrients from green turtle nests may occur when nests are placed within the rooting depth of the plant or when roots grow directly into nests. Bouchard and Bjorndal (2000) found that 23 percent of sea turtle nests in Melbourne Beach, Florida had been invaded by plant roots, and roots have been documented to directly penetrate developing and

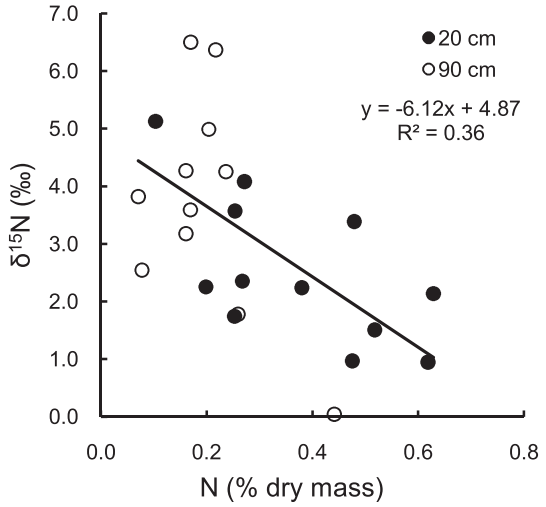

FIGURE 5. The $\delta^{15}N$ values in the sand decrease significantly as N increases when all sand samples at depths of 20 and 90 cm are plotted together ($F = 11.58$, df = 21, $P = 0.003$). Sand samples at 90 cm have significantly higher $\delta^{15}N$ values than those at 20 cm ($t = -2.15$, df = 22, $P = 0.021$). Deeper samples also appear to have lower N, but the difference is not significant ($t = 1.45$, df = 22, $P = 0.08$).

decomposing sea turtle eggs (Witherington 1986). Root penetration into nests can destroy nests and eggs (Witherington 1986).

The observed difference in nitrogen assimilation at low and high nest density sites may also affect plant community composition (Tilman 1984). We found a spatial shift in the dominant species of the four species in this study. Therefore, the turtle nesting may be driving patterns of species abundance in the plant community. Similarly, salmon-derived nutrient enrichment has been found to change riparian vegetation cover (Bartz & Naiman 2005), understory plant density, and species diversity (Bilby *et al.* 2003). Plant cover is important to turtle nesting, as it promotes beach stability and prevents erosion, thus securing sea turtle nests during incubation and for future generations. Moreover, sea turtles exhibit temperature-dependent sex-determination, and plant cover at Tortuguero, Costa Rica, has been found to significantly influence sea turtle hatchling sex ratios (Spotila *et al.* 1987).

While measures of productivity were beyond the scope of this study, it is also possible that the additional nutrient input at high nest density sites may lead to increased plant productivity. Increases in plant biomass have been correlated with nutrient input from seabird guano during wet years on desert islands in the Gulf of California (Anderson & Polis 2004). Therefore, in addition to altering the plant community composition, turtle nesting may also influence the total biomass and growth of the beach vegetation, thereby further stabilizing the nesting beach.

SAND.—While not significant, the trend of ^{15}N enrichment in sand at high nest density was in the expected direction, and is consistent with the pattern in the vegetation. Turtle-derived nutrients are likely responsible for this pattern, yet total sand N was extremely low (<1%). Nutrients from turtle nests are probably not retained for extended periods of time, given the low organic matter content of sand, the high leaching potential of labile N, the high water table at Tortuguero, and heavy rainfall that exceeds 5 m annually at Tortuguero (Myers 1981, Horikoshi 1992).

The $\delta^{15}N$ values were significantly higher below the depth of turtle nests, yet there was less total N at this depth. While we expected higher $\delta^{15}N$ values below turtle nests due to enriched inputs, we would also expect higher N. The relationship between $\delta^{15}N$ values and N in the sand was opposite to the pattern observed in the vegetation. A possible explanation for this difference is that leaf litter provides most N near the sand surface, whereas the more ^{15}N-enriched, turtle-derived N is available at the lower depth, and the turtle N is leached more quickly from sand than from leaf litter due to the high water table and lower organic matter content. The increasing $\delta^{15}N$ values and decreasing N content observed with soil depth is not necessarily unusual (Nadelhoffer & Fry 1988, Evans 2007, Hobbie & Ouimette 2009), yet this trend is usually most pronounced between 0 and 20 cm (above the 90 cm depth of this study) and has typically been reported for forest and grassland soils. Furthermore, the corresponding ^{15}N-enrichment of plant species at high nest density supports a marine-derived N source interpretation.

In addition, $\delta^{15}N$ patterns in sand may differ from those in vegetation because bulk soil $\delta^{15}N$ values may not represent plant-available forms, and biologically active forms can change considerably over short time periods (Högberg 1997, Houlton *et al.* 2007). We conclude that the vegetation in this study may represent a better integration of turtle-derived nutrients, and that the sand, subject to high leaching and variable nutrient adsorption, may not be as reliable in reflecting nutrient input from green turtle nesting.

IMPLICATIONS.—The number of green turtle nests fluctuates from year to year, with an overall increasing trend from 1971 to 2003 (Troëng & Rankin 2005). The spatial distribution of nesting at Tortuguero, however, has been highly stable over a similar time period (Tiwari *et al.* 2005), and we conclude that the high nest density site has been receiving a substantially larger annual nutrient subsidy from sea turtle nests than the low nest density site through time. We do not expect any other potential source of nutrient input at Tortuguero, such as sea spray or algal wrack, to contribute a comparable magnitude of nutrients to that of sea turtle nesting. In addition, on islands with marine bird nutrient input, such 'background' sources of nutrients have been found to be minimal (Anderson & Polis 2004). We do not calculate the total N and P budget in this study, and we are unaware of any nutrient budgets that have been determined for sea turtle nesting beaches. Such budgets would be helpful for interpreting the importance of this green turtle subsidy in comparison with other 'background' sources of nutrient input.

Our calculations of green turtle nutrient input are only approximations. While 51 percent of the N and 69 percent of the P are contained in the hatchlings that successfully emerge from nests, an unknown proportion of these hatchlings is depredated as they cross the beach, potentially augmenting the amount of

nutrients remaining in the beach ecosystem. We also did not account for the small proportion of N (~5%) that is lost to metabolic heat and gases during the incubation period (Bouchard & Bjorndal 2000).

While ecological roles of sea turtles have been considered mostly in the marine ecosystem as prey, consumer, competitor, host, and engineer of the physical environment, there are fewer examples of sea turtles fulfilling ecological roles in the terrestrial environment (Bjorndal & Jackson 2003). Green turtles at Tortuguero appear to provide a substantial nutrient subsidy to terrestrial beach vegetation through nesting. These nutrients are likely assimilated by the vegetation and potentially influence productivity and community structure of the coastal vegetation. As plant quality has ramifications for consumer growth and reproduction, effects of the nutrient flux may be transferred up the food web. Egg-derived nutrients may be available directly to predators, scavengers, and detritivores, thus influencing community dynamics with the annual pulse of nesting (Madden *et al.* 2008). In addition, at Tortuguero, nesting green turtles act as a direct source of nutrients to jaguars. Annual reports from the Sea Turtle Conservancy provide a minimum number of green turtles depredated by jaguars each year. Between 1998 and 2009, the minimum has ranged from 9 to 97 (Sea Turtle Conservancy Website 2011).

Finally, this nutrient input can be considered in the context of historic green turtle population sizes. As green turtle populations in the Caribbean are severely reduced from their pre-Columbian sizes—current populations are only 3–7 percent of pre-exploitation levels—this nutrient subsidy would have been much larger historically (Jackson *et al.* 2001, Bjorndal & Jackson 2003). At the carrying capacity of Tortuguero Beach, approximately 2 million nests would be deposited each year (Tiwari *et al.* 2006), resulting in 5720 kg/km of N and 510 kg/km of P input to the beach, which is an order of magnitude greater than the current nutrient input. Reduced population sizes have resulted in declines in sea turtles fulfilling their roles in marine ecosystems and in terrestrial beach ecosystems. Understanding the role of sea turtles in maintaining the structure and function of marine and adjacent terrestrial ecosystems can help to provide more meaningful goals for their conservation.

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