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Plants cause ecosystem nutrient depletion via the interruption of bird-derived spatial subsidies

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Plant introductions and subsequent community shifts are known to affect nutrient cycling, but most such studies have focused on nutrient enrichment effects. The nature of plant-driven nutrient depletions and the mechanisms by which these might occur are relatively poorly understood. In this study we demonstrate that the proliferation of the commonly introduced coconut palm, *Cocos nucifera*, interrupts the flow of allochthonous marine subsidies to terrestrial ecosystems via an indirect effect: impact on birds. Birds avoid nesting or roosting in *C. nucifera*, thus reducing the critical nutrient inputs they bring from the marine environment. These decreases in marine subsidies then lead to reductions in available soil nutrients, decreases in leaf nutrient quality, diminished leaf palatability, and reduced herbivory. This nutrient depletion pathway contrasts the more typical patterns of nutrient enrichment that follow plant species introductions. Research on the effects of spatial subsidy disruptions on ecosystems has not yet examined interruptions driven by changes within the recipient community, such as plant community shifts. The ubiquity of coconut palm introductions across the tropics and subtropics makes these observations particularly noteworthy. Equally important, the case of *C. nucifera* provides a strong demonstration of how plant community changes can dramatically impact the supply of allochthonous nutrients and thereby reshape energy flow in ecosystems.

Cocos nucifera | community shifts | indirect effects | seabird | tropical islands

Allochthonous nutrient subsidies shape the dynamics of a broad range of ecosystems by stimulating bottom-up productivity (1, 2). This increase in productivity can then trigger a vast array of cascading changes in recipient food webs (3–5). Several recent articles have demonstrated that introduced predators operating near the top of food webs can initiate these kinds of cascading effects on ecosystems by impacting the vectors of these subsidies, such as birds, triggering whole-scale shifts in ecosystem structure and function (6, 7). Yet top-down effects may not be the only mechanism by which spatial subsidies are disrupted. Here, we demonstrate that the proliferation of the coconut palm, *Cocos nucifera*, causes similar nutrient depletions with higher order effects by creating poor habitat for birds. Given the global proliferation of this plant in the tropics, our observations have a wide application. Even more broadly, this observation suggests that allochthonous subsidies may be blocked by the characteristics of species in the recipient system, making the recipient system a more active player in subsidy movement than has previously been acknowledged.

It is well established that the biological invasion of one species can have cascading effects across the invaded ecosystem, often through alteration of nutrient cycling (8, 9). However, in the majority of case studies where introduced plants have altered the nutrient cycle, the cascading effects have been as a result of increased inputs to the soil from the plants (either from increased litterfall or direct nitrogen fixation) (10, 11). The presumption is that introduced species generally profit from nutrient enrichment (12). However, recent work documenting that some invasive plants perform well in low-nutrient environ-

ments (13) suggests that more research on introduced plants specializing in low-nutrient systems is needed.

C. nucifera likely originated in Southeast Asia and then radiated regionally from this point of origin both via natural (water) and anthropogenic dispersal (14). Near monodominant stands of *Cocos* are now commonplace in many island and coastal forests around the tropics and subtropics of the world (see *Cocos nucifera: History and Current Status at Palmyra* in the [SI Text](#)). Working across a gradient of *C. nucifera* dominance at Palmyra atoll, this study examined the impact of *C. nucifera* proliferation on ecosystem ecology. We first examined habitat preferences of birds between *C. nucifera* and the common native tree species, *Pisonia grandis* and *Tournefortia argentea*, both on transect- and atoll-wide scales. We then examined the effects of *C. nucifera* dominance on levels of soil and foliar nutrients, and the consequent effects of changes in foliar nutrients on leaf palatability and herbivory. Finally, to document that high *C. nucifera* abundance is a cause rather than an effect of low soil nutrients (because palms are known to be able to persist in low-nutrient soils), we compared nutrient levels between islets made from dredge fill and natural islets containing different forest types. This comparison also allowed us to constrain the maximum time over which nutrient changes occur. Our results indicate that *C. nucifera* can dramatically impact allochthonous nutrients supply, with higher order effects on these ecosystems. We suggest that plant-driven alterations of spatial subsidies of the kind we observed at Palmyra are probably widespread, and can substantially shape nutrient flow across ecosystems and trigger cascading ecosystem changes.

Results

Vegetation Preference by Birds. Data collected in atoll-wide surveys indicate that birds exhibit a strong preference for the trees *P. grandis* and *T. argentea* over *C. nucifera*, even when standardized by bird biomass and estimated canopy area per tree (Fig. 1*A*) (ANOVA $F_{2,66}$ = 30.2. $P < 0.0001$; *T. argentea* vs. *C. nucifera*: $P < 0.0001$; *P. grandis* vs. *C. nucifera*: $P < 0.0001$; *P. grandis* vs. *T. argentea*: $P = 0.23$).

Bird density increases at night for all tree species; we find this means a 4-fold increase of bird biomass from day to night on *C. nucifera,* 16-fold increase on *P. grandis,* and 4-fold increase on *T. argentea* (Fig. 1*A*). Including nighttime preferences for vegetation by birds further entrenches the observed preferences by birds for native species *T. argentea* and *P. grandis* (ANOVA $F_{2,24}$= 9.8, $P < 0.001$; *T. argentea* vs. *C. nucifera*: $P < 0.01$, *P. grandis* vs. *C. nucifera*: $P < 0.01$, *P. grandis* vs. *T. argentea*: $P = 0.78$).

The same trends across forest types can be seen in analysis of vegetation transects, where vegetation is more precisely quantified and cryptic bird species are censused (but where night surveys
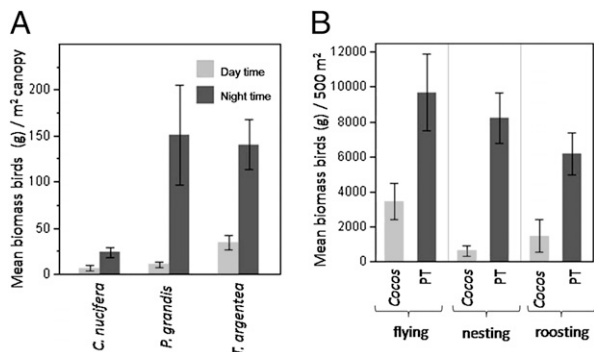
Fig. 1. Bird habitat preference by vegetation type. (*A*) Mean biomass (g) of birds per m^2 of projected canopy coverage during day and night time surveys by tree species. (*B*) Mean biomass of birds observed flying, nesting, and roosting along 500m^2 coastal transects in *Pisonia/Tournefortia* (PT) and *Cocos nucifera* (*Cocos*) forest types. Data are means (± 1 SE) pooled by islet (*n* = 10).

could not be conducted). Here again the biomass of birds flying (*t* = 2.59, *P* = 0.01) nesting (*t* = 5.16, *P* < 0.0001), and roosting (*t* = 3.07, *P* = 0.005) decline in *Cocos* forest (see *Methods*), compared to sites dominated by *P. grandis* and *T. argentea* (Fig. 1*B*) ("PT forest" hereafter; see *Methods*). Analysis at the islet level (using pooled mean basal area and bird abundances from all transect surveys on the islet) demonstrate that nesting and roosting biomass declines approximately 8-fold (*t* = 2.73, *P* = 0.04) and flying biomass declines approximately 5-fold (*t* = 3.46, *P* = 0.01) in *Cocos* forests as compared to the PT forest.

Effect of Forest Type on Soil Nutrients. Measurements of all analyzed soil nutrients were significantly lower in *Cocos* as compared to PT forests (Table 1). Soil pH was higher in *Cocos* forests and C:N ratios were lower. Measurements of nitrogen isotopes showed that δ^{15}N was significantly higher in soils from PT forests, indicating that the origin of these additional nutrients was from a high trophic-level source (Fig. 2) (*t* = 7.01, *P* < 0.0001). We found no significant difference in δ^{13}C values (*t* = 1.6, *P* = 0.12). There were no significant effects of islet size on any soil nutrients.

When soil nutrients and pH were examined by the source of the islet material ("fill" or "natural"), we found no significant differences in nutrients in PT sites; however, we detected significantly
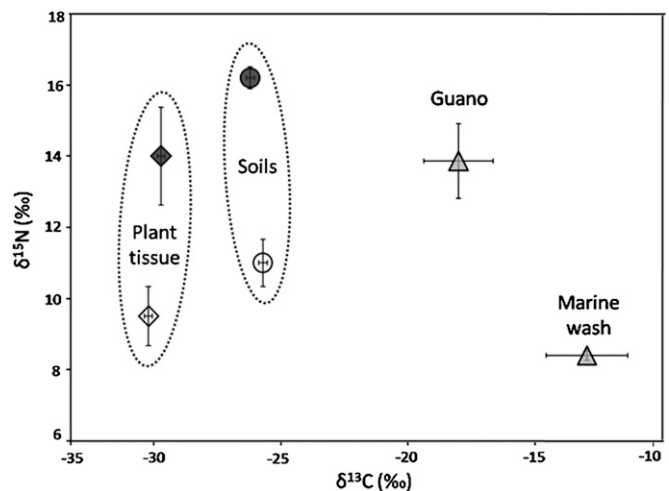

Fig. 2. Differences in soil and plant tissue stable isotope values (means ± 1 SE) measured in *Cocos*-dominated forests (*open*) and *Pisonia grandis* and *Tournefortia argentea* (PT) dominated forests (*solid black*). Enriched δ^{15}N values in PT forests are more similar to δ^{15}N of bird guano than marine wash (both *gray*), indicating that birds are major vectors of nutrient subsidies into these forests. SE bars are depicted for all sample types, but are not visible in some cases because of scaling.

lower soil nutrients in *Cocos* forests that were formed from artificial fill compared to those formed from natural material (Table 2).

Effects of Forest Type on Leaf Nutrients. Leaf nitrogen in *T. argentea*, *P. grandis*, and *C. nucifera* declined in *Cocos* forests (Table 1), although this decrease was not significant for *P. grandis*. Foliar phosphorus also declined in *Cocos* forests, but for *T. argentea* only (Table 1). The δ^{15}N and δ^{13}C values in *T. argentea* (the only tree species common enough across sites to allow for robust comparisons) were significantly lower in *Cocos* forests than in PT forests (Fig. 2) (δ^{15}N *t* = 3.0, *P* = 0.008; δ^{13}C *t* = 2.2, *P* = 0.04), also implying a lower trophic level source of foliar nitrogen in *Cocos* forests.

Stable isotopic composition of δ^{15}N for the two abundant allochthonous subsidies to this system ranges from 13.9 ‰ for bird guano (*n* = 18) to 8.4 ‰ for marine wash (predominantly algae) (*n* = 23).

Table 1. Soil and foliar nutrients by forest type

		Cocos forests Mean ± SE	*PT* forests Mean ± SE	*t* (df)	*P*
Soils					
Nitrate (µg/g)		8.04 ± 2.31	100.74 ± 26.10	6.4 (57)	<0.0001**
Ammonium (µg/g)		39.59 ± 6.21	65.09 ± 5.23	3.5 (57)	0.001**
Phosphate (µg/g)		1.63 ± 0.31	6.06 ± 0.90	5.4 (54)	<0.0001**
pH		7.57 ± 0.16	6.98 ± 0.16	2.9 (41)	0.008**
%N		0.78 ± 0.13	1.32 ± 0.14	3 (46)	0.008**
%C		14.84 ± 0.58	11.19 ± 0.30	5.5 (41)	<0.0001**
Leaves					
C. nucifera	%N	0.85 ± 0.02	1.00 ± 0.04	3.6 (29)	0.001**
	%P	0.25 ± 0.02	0.23 ± 0.01	0.8 (34)	0.45
P. grandis	%N	2.26 ± 0.13	2.49 ± 0.04	2.3 (6)	0.06*
	%P	0.34 ± 0.05	0.38 ± 0.02	0.7 (5)	0.50
T. argentea	%N	2.86 ± 0.02	3.56 ± 0.01	3.5 (22)	0.002**
	%P	0.39 ± 0.02	0.45 ± 0.02	1.8 (25)	0.07*
	C:N	16.13 ± 0.77	13.1 ± 0.51	3.3 (20)	0.004**

Soil nutrients are from transects in forests dominated (>75% basal area) by *Cocos nucifera* (Cocos forests) or by *Pisonia grandis* and *Tournefortia argentea* (PT forests). Significant results, determined using Welch's two-sample T-tests (after subsequent Bonferroni corrections) are in marked with **; near significant results are marked with *.

Table 2. Soil nutrients by source of island material and forest type

| | Original material | Fill material | | |
	Mean ± SE	Mean ± SE	t (df)	P
Cocos forests				
Nitrate (µg/g)	6.9 ± 1.5	3.3 ± 0.38	2.64 (30)	0.01**
Ammonium (µg/g)	53.6 ± 9.3	32.5 ± 9.2	2.25 (24)	0.03**
Phosphate (µg/g)	3.2 ± 0.57	0.6 ± 0.17	5.74 (26)	<0.0001**
pH	7.2 ± 0.23	7.9 ± 0.04	3.17 (16)	0.006**
PT forests				
Nitrate (µg/g)	138.6 ± 43.7	70.8 ± 28.7	0.79 (21)	0.44
Ammonium (µg/g)	65.4 ± 6.6	68.3 ± 3.9	0.38 (24)	0.70
Phosphate (µg/g)	7.4 ± 1.4	4.3 ± 0.9	1.67 (20)	0.11
pH	6.9 ± 0.27	7.1 ± 0.2	0.46 (18)	0.65

Soil nutrients from transects on islets naturally formed or created by fill material from dredge spoilings. Results are separated by forest type as either dominated (>75% basal area) by *Cocos nucifera* (*Cocos*) or by *Pisonia grandis* and *Tournefortia argentea* (PT forests). Significant results, determined using Welch's two-sample T-tests (after subsequent Bonferroni corrections) are marked with **.

Herbivory and Palatability of Leaves. Herbivory was higher on all species in PT forests, as compared to *Cocos* forests; this difference was significant for three of the four species analyzed (Fig. 3*A*) (Wilcoxon tests: *P. grandis* $Z_{90,78} = 2.5$, $P = 0.01$; *T. argentea* $Z_{69,72} = -2.2$, $P = 0.03$; Pearson *C. nucifera* $\chi^2_1 = 0.037$, $P = 0.04$)

Palatability trials conducted with herbivores in the lab indicate that both the katydid *Conocephalus saltator* and the crab *Coenobita perlatus* exhibited strong preferences for leaves of *P. grandis* from PT forests over those from *Cocos* forests (paired Student's *t*-tests: *C. perlatus*, $t = 3.8$, $P = 0.002$; *C. saltator*, $t = 2.6$, $P = 0.03$) consuming 12 and 23 times more leaf area, respectively, from PT forest foliage than *Cocos* forests foliage (Fig. 3*B*).

Discussion

The majority of the birds at Palmyra prefer to nest and roost in the native trees *T. argentea* and *P. grandis* over the coconut palm. This behavior creates a stark gradient of bird abundance across the islets of the atoll, with birds ≈5 to 10 times denser at sites where *T. argentea* and *P. grandis* are dominant. The reason for this preference was not examined but is likely because of (*i*) the architecture of these palms, which do not provide stable large platforms for these colonially nesting birds, and (*ii*) rats that may nest and feed in *Cocos* and also predate or harass seabirds.

Fig. 3. Measured differences in herbivory and leaf palatability between *Cocos nucifera* (*Cocos*) and *Pisonia grandis/Tournefortia argentea* (PT) dominated forests. (*A*) Mean herbivory [percent leaf area (LA) removed over 28 days, pooled by tree] for three tree species in *Cocos* (*open*) and PT (*solid black*) forests (± 1 SE). (*B*) Median, quartiles, and range of percent leaf area eaten by insect herbivore *Conocephalus saltator* and crab omnivore *Coenocephalus perlatus* in paired palatability assays of *P. grandis* leaves collected from PT (*solid black*) and *Cocos* (*open*) forests. Herbivory was generally higher in PT forests, likely because of the higher nutrient content of their leaves.

This impact of *Cocos* on bird abundance profoundly interrupts the valuable flow of allochthonous subsidies that birds provide to these impoverished terrestrial communities from the marine environment. This stark reduction in nutrient subsidies is significant. We estimate that birds vector to PT forests between 261 and 653 kg of N ha^{-1} y^{-1} and 42 to 105 kg of P ha^{-1} y^{-1} from guano, compared to between 23 and 34 kg of N ha^{-1} y^{-1} and 4 to 6 kg of P ha^{-1} y^{-1} in *Cocos* forests (see *Guano Inputs at Palmyra* in the *SI Text*). As reference, intensive agriculture fertilizer additions range between 60 and 400 kg N ha^{-1} y^{-1}, and rates of agricultural P addition above 55 kg P ha^{-1} y^{-1} are considered a taxable pollutant in some countries (15, 16).

Palmyra's coral-derived soils are broadly nutrient-deficient, and the loss of bird-derived nutrient inputs in *Cocos* forests is readily evidenced in the soil nutrients of these forests, with reductions ranging from 0.5- to 12.5-fold. The smallest depletion (a 50% reduction in NH$_4^+$) is likely muted because of NH$_4^+$ nitrification (leading to particularly high changes in NO$_3^-$ pool). Because of high rainfall at Palmyra (4,500 mm per year), these direct soil measurements of nutrients almost certainly underestimate larger changes to nutrient throughflow and nutrient availability to plants. This trend for increasing soil nutrients near areas of high bird density is well established for temperate and polar zones (17, 18). However, there is considerably less understanding of the effects of these subsidies in ecosystems where rainfall is relatively high, coastal marine waters are relatively oligotrophic, and bird densities are relatively low; despite the fact that these conditions typify most of the coastal zones in the tropics (19, 20). While physical sources of subsidies (i.e., marine wash) would likely be low in these systems, inputs from highly mobile birds, which can draw nutrients from dispersed or distant but locally aggregated oceanic sources, appear to be important. The magnitude of nutrient alterations observed at Palmyra also suggest that the effects of palm proliferation might be even stronger in drier environments, where higher changes in nutrient pools have been observed (21, 22).

This trend for reductions in soil nutrients in areas where abundance of *C. nucifera* is high is mirrored, in a more subdued fashion, in foliar nutrients. We observed a 15 to 20% reduction in average foliar N, and 13% declines in foliar P for *T. argenta* only (Table 1). The magnitude of these changes in foliar nutrients is comparable with, or greater than, shifts reported in other studies conducted at sites with strong gradients in soil nutrient abundance (19, 21), although it is lower than some of the extreme changes in foliar nutrients seen in sites with higher bird densities or lower rainfall (22). Because plants use soil nutrients to advance myriad physiological processes, particularly growth, it is natural that
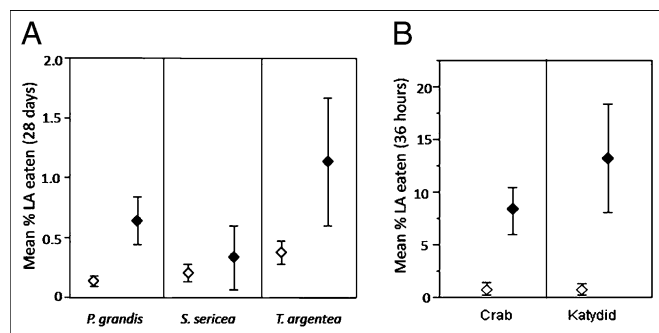
differences in foliar nutrients between forest types are not as pronounced as differences in soil nutrients.

The elevated δ^{15}N levels in both soils and plants in PT forests identify bird-derived nutrient subsidies as the most parsimonious explanation for these intersite differences in soil and plant nutrient quality. As high trophic-level marine predators, seabird δ^{15}N values are enriched, compared to most other inputs to the system, because of trophic fractionation of δ^{15}N (23). The δ^{15}N values we observe in soils and plants in PT forests closely match the elevated values we measured directly in bird guano. In contrast, the δ^{15}N values measured in *Cocos* forests are well below that of bird guano and closer to other potential N sources measured onsite (marine wash) or obtained from the literature (e.g., rain) (24, 25). δ^{15}N is known to increase in sites with more available nitrogen; still, the high δ^{15}N in PT sites is too high to be explained by this mechanism alone (26). There are no other viable, nonguano-related, alternative explanations for this δ^{15}N shift: there are no nitrogen-fixing terrestrial plants on the islets we surveyed at Palmyra (27), lightning is rare (personal observation), wind patterns in the region are not likely to deposit large quantities of transcontinental dust, and typical δ^{15}N values of surrounding seawater are low (25). There were no differences in δ^{13}C in soils. The small but significant difference in foliar δ^{13}C is most likely a result of different levels of canopy closure and light between forest types (24).

The differences we observed in the nutrient content of soils and trees in the two different forest types are reflected in processes of herbivory. Herbivores are known to preferentially select more nutrient-rich food sources (23, 28), and in our palatability trials, generalist herbivores exhibited very strong preferences for plant material derived from PT forests over material derived from the same species in *Cocos* forests. Likewise, standing herbivory was three to five times higher in PT forests than *Cocos* forests for multiple species. These observed declines in herbivory are primary indicators that the loss of bird-derived nutrients is having cascading effects on the ecology of these forests.

The cause of varying densities of *C. nucifera* at Palmyra is unknown, but likely the result of some combination of historical chance (where palms arrived or were planted) and incomplete gradual spread from these sites via competitive exclusion. This is an aspect that warrants further research. Further evidence that *C. nucifera* dominance drives the observed nutrient differences via changes in bird abundance, rather than responding to low nutrients or to unmeasured intrinsic site differences, was found in comparing nutrient levels on Palmyra's naturally produced islets to its recent man-made islets. This provides a large-scale natural experiment on the effect of forest change. All nutrients on *C. nucifera*-dominated islets created in the 1940s are lower than those in *C. nucifera*-dominated islets of natural origin, suggesting that (*i*) dredge materials are of low nutrient quality, (*ii*) little nutrient enrichment has occurred at these sites in the past 70 years, and (*iii*) nutrient levels on natural islets dominated by *C. nucifera* may yet fall further, especially those in which *C. nucifera* establishment was recent. The case of PT forest islets provides a sharp contrast. Man-made PT forest islets are nutrient rich and are indistinguishable from PT-dominated islets of natural origin. This finding suggests that 70 years is ample time for nutrient-poor man-made islets to be converted to nutrient-rich ecosystems when they host PT forests, which facilitate the import of bird-derived subsidies. Given the rates of bird inputs into PT forests, it is likely that this occurs much more quickly.

Coconut palms have rapidly expanded their range in the last several millennia to achieve their current pantropical distribution; for the most part, perceptions of this expansion are neutral or positive (see *SI Text*). The scale of nutrient depletions and higher order ecosystem changes that we have observed to be underway at Palmyra as a result of the expansion of this species suggest that the implications of the global expansion of the coconut should be more closely monitored and considered.

Broad-scale changes to the resource budgets of ecosystems, such as we observed, are well documented for introduced or range-expanding plants that increase soil nutrients (29, 30). However, this study provides an interesting example of how an expanding plant population may create and thrive in nutrient-poor conditions. We suggest that examples of introduced plants reducing available nutrients in this fashion may be more abundant than have been previously documented (30).

These results also expand our understanding of the range of mechanisms that can interrupt allochthonous subsidy transfers. Numerous cases are available, demonstrating how predators may reduce densities of birds or other animal vectors of nutrients and cause large-scale ecosystem alterations as a result of nutrient loss from these animal vectors (6, 7). We provide here an example of how a plant can play the same role, with equally important consequences for ecosystem function. In bird systems alone, there are multiple examples of plants that deter birds, suggesting that our observations at Palmyra have wide-reaching importance (31, 32). However the implications of these results extend far beyond bird-dominated systems. Given the ubiquitous importance of spatial subsidies across a wide breadth of scales and system types (33, 34), we contend that more attention should be paid to the role plants play in governing transfers of spatial subsidies between ecosystems.

Methods

Study Site. We studied the effects of *Cocos* expansion on the ecology of wet tropical forests at Palmyra Atoll (162°05′ W, 5°53′ N; 4,500 mm annual rainfall) in the Northern Line Island Chain in the Central Pacific. Currently administered by the United States Fish and Wildlife Service as a National Wildlife Refuge, Palmyra has no indigenous human population and a limited history of human habitation (World War II military occupation). The atoll is composed of a ring of coral-derived islets, which encircle a centralized saltwater lagoon system. Some islets at Palmyra are not natural, having been created in the 1940s from dredged coral sand and rock. Two forest types dominate islets in Palmyra: forests generally consisting of tall *P. grandis* trees in the interior and fringing *T. argentea* along the coast, and forests of *C. nucifera*. Both forest types can include low densities of six other tree species. For most analyses, we define forest type as either a "PT forest" (>75% basal of *P. grandis* and *T. argentea* combined) or a "*Cocos* forest" (>75% basal area of *C. nucifera*). Mixed species sites (with <75% basal area of either *Cocos* or *P. grandis* and *T. argentea*) are not included in these analyses. The avifauna on Palmyra is comprised entirely of seabirds and shorebirds. Boobies (*Sula* spp.) make up the largest proportion of the bird biomass on the atoll, but smaller terns (*Sterna fuscata* and *Gygis alba*) and noddies (*Anous* spp.) are also abundant, as well as multiple less common species. Open areas on Palmyra also provide excellent habitat for seabirds; however, they must be actively maintained or they revert to forest.

Vegetation and Soil Surveys. To compare forest and soil characteristics to bird density, we conducted detailed sampling of vegetation and soils on 14 islets free from any contemporary human activity. We only sampled islets that were separated by distances ≥ 250 m or by deep seawater channels, considering such islets independent from one another.

Forest type was characterized using 50 × 2 m belt transects (*n* = 77). In each transect we measured and identified all plants >1 cm diameter at breast height and calculated basal area from the diameter-at-breast height measurements (35). Transects were spaced evenly around the coast of each islet (maximum of 10, minimum of 2 transects per islet; scaled to islet size). When possible, transects were arranged in pairs: one coastal transect 5 m in from the high-tide line parallel to the coast, and one interior transect laid 50 m inland and parallel to the coastal transect. If the islet was ≤ 100 m in width, no interior transect was conducted. Each pair of transects was at least 250 m from the next nearest pair.

On each transect we took six soil samples: one sample at 0 to 5 cm depth and a second one at 10 to 15 cm depth at three evenly spaced positions along the transects. Soils from the same transect at the same depth were homogenized before analysis. We collected samples of mature, nonsenescent leaves in full sun, from three individual trees of *T. argentea*, *P. grandis*, and *Cocos* when they were available on each transect. The leaf samples from the three individuals of each species were homogenized before analysis. We classed each sampled islet as a natural or artificial fill (created from military

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dredge spoilings) site. These designations were made by overlaying a map of Palmyra generated in 1874 (36) with a current map of the atoll; sites that completely overlaid land masses in the 1874 map were deemed to be "natural" ($n = 35$; 18 *Cocos*-dominated, 17 PT-dominated), while sites that fell completely or partially in water in the 1874 map were deemed to be of "artificial fill" origin ($n = 28$; 16 *Cocos*-dominated, 12 PT-dominated).

Bird Surveys and Nutrient Inputs. Bird communities were surveyed at two spatial scales: at the atoll level and at the transect level. For the atoll-level surveys we counted all nesting and roosting birds visible from the coast, within 10 m of the high-tide line, around the perimeter of all islets in the atoll. To examine bird preferences for vegetation, we identified the tree species upon which each bird was observed nesting/roosting, counted all adult plants (>2 m height) that did not have birds, and determined the species and breeding status (i.e., nesting or only roosting) of every bird censused. We complemented atoll-wide coastal surveys with 32 randomly located belt transects (10 m in width) that ran across the interior of each islet, beginning 10 m from the high-tide line. Densities of birds calculated on these interior transects were used to extrapolate overall interior densities of birds across each islet. For bird surveys conducted at the vegetation/soil transect level, we counted all birds nesting or roosting within a 50 × 10 m band directly overlaying each vegetation/soil transect, as well as the number of birds observed flying directly over the transect area in a 3 min period. All bird surveys were conducted over a 2-week period (Aug 2007) during daytime hours (1000–1700). In sum, 8,641 trees were surveyed, including 6,224 *C. nucifera*, 1,671 *T. argentea*, 356 *P. grandis*, and 390 of all other species combined.

Bird abundances increase at night when birds return from foraging. To determine if nighttime preferences differed from diurnal habitat preferences, we conducted 10 additional surveys in which we counted the number and location of birds present in a given area every 4 h for a 24 h period using spotlights. We analyzed relative nighttime bird abundance per tree species for the three tree species that composed more than 5% of basal area across all vegetation surveys (*C. nucifera*, *P. grandis*, and *T. argentea*).

Bird numbers were converted to biomass using established conversion factors from species in this region (37). To account for interspecific variability in tree-canopy size, the number of trees were converted to average canopy coverage by measuring the horizontal length of the crown of 30 individuals of each species and assuming each tree covered a roughly circular area of ground. Thus, the final metric used for analysis of bird density was bird biomass per square meter of projected canopy coverage.

To quantify isotopic values of nonbird-derived marine inputs to terrestrial soil and vegetation, we collected and homogenized organic marine wash (primarily algae), a known contributor to other island nutrient cycles, from randomly located 10 m beach transects (38).

Laboratory Analyses. Field moist-soil samples were sieved (<2 mm) and extracted in KCl for ammonium and nitrate immediately after collection (39). Phosphates were extracted from soils using resin bags (40). Ammonium, nitrate, and phosphate extractions were analyzed using a discrete analyzer (Westco SmartChem 200). The pH of soils was measured from a 1:1 mixture of soil and water with a pH electrode. The %N, %-organic C content, δ^{15}N, and δ^{13}C of soils were measured using oven-dried, ball-milled samples in an elemental analyzer coupled with a mass spectrometer at the Stanford Stable Isotope Biogeochemistry Laboratory (Thermo Finnegan Delta-Plus IRMS). These samples were each run twice: once unadulterated for δ^{15}N and %N, and once after repeated acidifications to remove $CaCO_3$ for analyses of δ^{13}C and % organic C. Leaf samples (washed, oven dried, and milled) were Kjeldahl-digested and then analyzed for %N and %P on a continuous flow autoanalyzer (Alpkem Flow Solution IV). Leaf powder from *T. argentea* (the most widely distributed tree species), the homogenized bird guano, and marine wash powders, were also analyzed for %C, δ^{15}N, and δ^{13}C at the Stanford Stable Isotope Biogeochemistry Laboratory.

Higher-Order Effects: Herbivory Measurements and Foliage Palatability. We performed field herbivory measurements and laboratory palatability trials to assay the biological significance of any observed differences in nutrient quality of leaves in different forest types. To measure herbivory in the field, we marked 10 undamaged leaves (from same phylotaxis position) or leaflets (for *Cocos*) on 10 *P. grandis*, *T. argentea*, *C. nucifera*, and *Scaevola sericea* growing in PT forests and 10 individuals of the same species growing in *Cocos* forests (total 800 leaves). We collected the individual leaves after 1 month and assessed cumulative percent-area eaten from scanned images of leaves using the program Sigma Scan (41). Herbivory on *C. nucifera* was very low and dominated by damage from leaf-mining insects. This damage was not readily quantifiable using scanning software, so all *C. nucifera* leaflets were instead visually scored in blind trials for the presence or absence of herbivory. For analysis, leaves were pooled by tree, with statistics conducted on mean herbivory per tree.

For laboratory palatability trials, we collected *P. grandis* leaves from trees growing in *Cocos* and PT forests (each leaf from a different tree). We then presented these leaves as pairs (one from each forest type) in cafeteria-type assays (42) to the generalist herbivore *Conocephalus saltator* (Orthoptera) ($n = 10$ replicates), and the omnivorous hermit crab, *Coenobita perlatus* ($n = 14$ replicates). Before the experiments, the animals were fed ad libitum with lettuce for 3 h, and then starved for 10 h. We then offered one *P. grandis* leaf square from each forest type (1 × 1 cm for *C. saltator*, 8 × 8 cm for *C. perlatus*) to individual animals. Leaf squares were left with herbivores for 12 (*C. perlatus*) or 36 h (*C. saltator*), after which we measured the leaf area consumed from each pair.

Statistical Analyses. All statistics were computed in JMP 7 (SAS Institute). Datasets were tested for normality using a Shapiro-Wilk test. When necessary, data were Box-Cox transformed to normalize distributions. Comparisons were made using Welch's *t*-test or analysis of variance (ANOVA) with subsequent Tukey-Kramer posthoc pairwise comparisons. Data from herbivory trials could not be normalized and were analyzed using a Wilcoxon ranked-sum test. For linear regression analyses, residuals were checked for conformation to normality. When multiple dependent variables (i.e., various metrics of bird abundance, soil quality, or leaf quality) were analyzed against the same independent variable (e.g., forest type), sequential Bonferroni corrections were conducted. All graphs and tables depict untransformed data and all mean values are shown with ± 1 SE.

Most analyses presented compare *Cocos* vs. PT forests. Such a classification is simplistic, as actual forests span a gradient of *C. nucifera* abundance and include some intermediate sites that fit neither of these designations (14 of 77 sampled transects were omitted in this type of analysis). Still, this analysis was deemed preferable to regression by basal area of *C. nucifera*, because intermediate sites often contained a high abundances of species uncommon elsewhere on the atoll, and basal area of *C. nucifera* may overestimate canopy importance of *C. nucifera*, because these palms have particularly high basal area-to-canopy cover relationships. However, to document that *C. nucifera* has a roughly linear effect on bird abundance and nutrient levels, we also analyzed the relationship between dependent variables of interest and differing densities of *C. nucifera* basal area using linear regressions; such analyses encompassed data from all sampled transects, including intermediate sites. For all variables, the direction and the significance (using α of 0.05) of the effects (not presented) were consistent with other (Welch's *t*-test or ANOVA) analyses.

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