

The coconut palm, *Cocos nucifera*, impacts forest composition and soil characteristics at Palmyra Atoll, Central Pacific

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Abstract

Question: *Cocos nucifera*, the coconut palm, has a pantropical distribution and reaches near mono-dominance in many atolls, low lying islands and coastal regions. This paper examines the ecological correlation between *C. nucifera* abundance and changes in forest structure, floristic diversity and forest soil characteristics.

Location: Palmyra Atoll NWR (USA), Central Pacific Ocean.

Methods: Plant surveys were conducted on 83 transects (each 100 m²). All plants \geq 5 cm in height were identified and counted; large plants were also measured and ground cover was surveyed. Major macronutrients, pH, macro-elements/base cations, micronutrients and pedogenic elements, and thermodynamic stability levels were quantified from soil samples taken at each transect.

Results: Even in a low diversity atoll environment, we found that high abundances of *C. nucifera* corresponded with pronounced differences in forest communities including: lower diversity of established trees and regenerating understory; higher stem density and stand basal area; lower abundance of major macronutrients; and differences in macro and trace elements and energy content of soil organic matter. Historical natural experiments document that the expansion of *C. nucifera* was the likely causative agent of these changes.

Discussion: Cumulatively, these data show that *C. nucifera* has important impacts on floristic, structural and soil characteristics of forests where it becomes dominant. Given the high proportion of tropical coastal areas in which *C. nucifera* is now naturalized and abundant, this likely has important implications for coastal forest diversity and structure.

Keywords: Floristic diversity; Pacific islands; Range-expanding; Soil nutrients; Differential thermal analysis; Trace metals.

Nomenclature: Wester (1985).

Introduction

The coconut palm, *Cocos nucifera* Linnaeus 1753, is a common component of forests on many tropical and subtropical islands and coastal ecosystems around the world, occurring in 86 countries across four continents (Harries et al. 2004). It often reaches mono-dominance in many low-lying tropical atolls of the Pacific (Dombois & Fosberg 1988). It can be inferred, from fossil and molecular data, that the coconut palm likely originated in Southeast Asia and then radiated from this point of origin (Maloney 1993). While some of this movement was a result of natural (water) dispersal, much of this range expansion was likely accomplished via pre-modern anthropogenic dispersal (Ward & Brookfield 1992; Baudouin & Lebrun 2009). For thousands of years the palm has been widely used, transported and planted by humans for a variety of purposes, including as food, drink, fibre, fuel and aesthetic value (Harries et al. 2004).

Given that the species has been propagated so widely, and for such a long period of time, it would seem to have strong potential for causing large ecological changes to sites where it is not native and becomes dominant (Richardson 1998). Consistent with this potential, but undocumented risk, it is classified as a “possible” or “potential” invasive species in the Woody Invasive Species Database (Bingelli 1996). Many introduced woody plants are able to dramatically change ecosystems where they establish, causing changes in floristic composition (Brown et al. 2006), structural diversity and biomass (van Wilgen et al. 2001), water flow (Le Maitre et al. 2002) and nutrient cycling (Stock et al. 1995). While we know a great deal about the biology and horticulture of the plant, we have very little understanding of the ecological effects these palms have on systems when they reach high levels of dominance.

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In this study we examine the effects of *C. nucifera* abundance on the structure, diversity and soil properties of the forests at Palmyra Atoll, in the Central Pacific. The history of the coconut palm at Palmyra is unclear. Several early botanists presumed that it was introduced to the area by the early Polynesians (Merrill 1946; Fosberg 1960) but others have suggested it might have arrived naturally by floating, long prior to Polynesian arrival (Harries 1978). In more recent history, aerial photographs, historical reports and oral history strongly suggest the palm has expanded its range on the atoll in the past 150 years (Dawson 1959). Regardless of its history at Palmyra, the atoll now hosts a gradient of forests, ranging from mono-dominant stands of *C. nucifera* to forests composed almost exclusively of known native species. This gradient, complemented by historical manipulations of islet architecture, thus provides a convenient opportunity to examine the linkages between the expansion of *C. nucifera* and changes in forest structure, diversity and soil properties, with implications for other sites where *C. nucifera* is known to be non-native.

In this study we use the natural gradient of coconut relative abundance on Palmyra to understand the effects of *C. nucifera* dominance on forest community diversity, composition and structure, as well as more detailed understanding of the effects that the palm may be having on forest soils. Specifically we asked: (1) How do changes in relative abundance of *C. nucifera* affect the floristic diversity, composition and structure of both established and regenerating (understorey) trees? and (2) What is the effect of proliferation of *C. nucifera* on detailed soil fertility characteristics, such as the concentrations of organic material, macronutrients, macro-elements and trace elements? Addressing these questions will help us understand the mechanisms by which *C. nucifera* may be affecting the coastal and island sites where they establish and increase our understanding of the ecological importance of this species.

Methods

Study site

This work was conducted in the wet tropical forests of Palmyra atoll (5°53'N, 162°05'W) in the Northern Line Island Chain in the Central Pacific. The atoll is currently administered by the U.S. Fish and Wildlife Service as a National Wildlife Refuge. The atoll consists of a ring of coral-derived calcium

carbonate islets, encompassing a centralized salt-water lagoon system. It is approximately 12-km long and 2.5 km² in area. The climate of the atoll is hot and wet, with a mean annual temperature of 27.5°C and a mean annual rainfall around 4450 mm. The atoll has a limited history of human habitation and does not currently support, nor appears to have ever supported, indigenous human populations. It was occupied by the US military during WWII, during which time several islets were created and original islands extended, using material from lagoon dredgings. Post military abandonment, the only recent substantial inhabitation is a small research station located on one islet of the atoll (not included in these analyses).

Three forest types dominate the uninhabited islets in Palmyra: (1) forests generally consisting of tall *Pisonia grandis* (Nyctaginaceae) trees in the interior and fringing *Tournefortia argentea* (Boraginaceae) along the coast, with low abundance of *C. nucifera* (Arecaceae) in the canopy; (2) forests consisting predominantly or exclusively of *C. nucifera*; and (3) mixed forests with intermediate densities of *P. grandis*, *T. argentea*, *C. nucifera* and other species. For our analyses, we define forest type as either “high *Cocos*” (>75% basal area of *C. nucifera*), “low *Cocos*” (<25% basal area of *C. nucifera*) or “intermediate *Cocos*” ($\leq 75\%$ and $\geq 25\%$ basal area of *C. nucifera*). This classification coincides with modal classes in dominance of *Cocos* in frequency–distribution histograms of percentage of total tree basal area.

Floristic sampling

Plant surveys were conducted on paired 50×2-m transects on 14 uninhabited islets. Transects were paired such that one transect was run on the coast 5 m from the high tide line and a second interior transect was run 50 m inland from the coast. Both transects ran parallel to the coast. We placed four transect pairs evenly spaced around the perimeter of each islet, with the limitation that no transect pair be closer than 200 m to the next closest pair. Given the small size of many islets, this meant that many islets thus had less than four transect pairs. In cases where the islet was <100 m across, the interior transect was located in the centre-most area of the islet, unless the islet was <50 m in width, in which case no interior transect was surveyed. A total of 83 transects were surveyed (high *Cocos* forest $n = 33$; low *Cocos* forest $n = 26$; intermediate *Cocos* forest $n = 24$).

Vegetation surveys on these transects were conducted using Gentry's methodology (Gentry 1988), with some modifications (see López & Dirzo 2007). All plants rooted in the 50×2-m transect that had a diameter at breast height (DBH) of >1.0 cm were identified and measured. Woody plants ≤ 1.0 cm in DBH, and ≥ 5 cm in height were identified and counted and are defined as "understorey." In 1×1-m transects placed at 10 m intervals along each transect, we characterized the ground cover by describing the percentage cover of bare ground, leaf litter and herbaceous cover (herbaceous cover included both herbaceous plants and woody plants < 5 cm in height).

From the floristic data we calculated, within each forest type, the mean basal area of all trees per transect, the mean number of individuals of all woody species per transect and the mean basal area of an individual tree (not pooled by transect). We also calculated the relative density (number individuals of a species/number of individuals in a transect) and relative frequency (percentage transects in which the species occurs/sum frequency of all species occurrence) of each species. The sum of these two characteristics per species, within each forest type, was used to calculate an Importance Value (IV) for each species (Greig-Smith 1983). Relative dominance (i.e. the sum of basal areas per species) was not included as it was not relevant for understorey plants; the importance value was divided by two, to be shown on a scale of 100. We also calculated the Shannon diversity index per forest type. Since the diversity index would be strongly affected by our definition of forest type to include high abundance of *C. nucifera*, we also calculated Shannon diversity index per forest type when *C. nucifera* was excluded.

Soil sampling: chemical and thermal methods

At three positions along each of the above described vegetation transects (0, 25 and 50 m), soil samples were taken at depths of 0-5 cm and 15-20 cm. Immediately after collection, the field moist soil samples were sieved (with 2 mm sieve), roots were removed and were extracted in 2 M KCl for ammonium and nitrate assays (Keeney & Nelson 1982). The extractions, as well as the remaining soil, were frozen for subsequent analysis. Soil phosphate extractions were conducted using resin bags (Kuo 1996). All three extractions (ammonium, nitrate and phosphate) were then analysed using a discrete analyser (Westco SmartChem 200). To analyse macro-elements/base cations (S, Na, K and Mg), micronutrients (Cu, Fe, Mn, Mo, Zn and B) and

pedogenic elements (Si, Al), soil samples were first digested in a PTFE cell (Uhrberg 1982) with nitric acid using microwave-assisted digestion (Mars Xpress microwave digester) (Rodushkin et al. 1999). Digestions were diluted, filtered and analysed on a Thermo Scientific inductively coupled plasma-optical emission spectrometer (ICP-OES). Soil calcium levels were not quantified due to the high calcium coral-derived parent materials. These elements were analysed only in high *Cocos* and low *Cocos* sites (not intermediate *Cocos* sites). To estimate soil pH, we used a calibrated pH electrode to analyse a 1:1 slurry of soil and deionized water. To estimate soil organic matter, we heated all samples to 550°C in a muffle furnace for 1 h; the mass loss on ignition can be equated to the content of soil organic matter (Dean 1974).

Given the inherent complications in carbon measurements in a strong carbonate background, we also analysed organic matter for a subset ($n = 12$) of the original field collections (composited from 0- to 20-cm depth) using a Mettler-Toledo thermogravimetric-differential thermal analysis system (TGA/SDTA851e; Schwerzenbach, Switzerland) (Kasozi et al. 2009). We measured mass loss profiles from 25°C to 750°C as samples were heated in a platinum crucible in hydrocarbon-free air. The primary interference in the determination of organic C mass loss is the presence of inorganic carbonates, which are especially acute in our atoll samples. To obviate this, we compared mass loss only between 125 and 455°C (well below onset of calcium carbonate melting at 600°C). Simultaneously, we compared the differential thermal analysis (DTA) profiles of the same soils, which allowed us to understand the nature of soil organic matter (Dell'Abate et al. 2003; Plante et al. 2009), as this technique records thermodynamic changes, such as endothermal transitions associated with loss of water and exothermic reactions accompanying combustion of organic matter (Gáll et al. 1994; Kasozi et al. 2009).

To determine if changes in *C. nucifera* abundance actually cause the differences we observed in soil properties (rather than responding to different initial nutrient levels), we compared differences in macronutrients, pH, elements and organic matter (measured as loss on ignition) at artificially created islet sites where parent material was known to be identical ($n = 28$ for macronutrients, organic carbon and pH; $n = 20$ for analyses of elements). These islets were created by the US military from lagoon dredge material in the 1940s (Young et al. 2010). Both by chance and by directed human planting, approximately half of these sites became dominated

by *C. nucifera* while the other half became dominated by other plant species. Since there have been no significant inputs of anthropogenic nutrients since the islets were created, any modern differences in soil nutrients between islets hosting different plant communities should have been caused by these differences in plant community. We did not conduct this analysis on floristic variables (mean basal area, stem density, individual size), as floristic data is patchy on the landscape scale and thus sample size is not sufficiently large on this subset of data to make comparisons meaningful.

Statistical analyses

Statistics were computed in the software JMP 8 (SAS Institute, Cary, NC, USA) and in R (R Development Core Team 2008). Structural vegetation characteristics (stem density, basal area per transect and percentage ground cover) deviated significantly from the normal distribution, as assessed using a Shapiro-Wilk test. Thus structural vegetation features among forest types were compared using a Kruskal–Wallis chi-square approximation. To identify pair-wise differences in structure, we ran all possible pair-wise comparisons across the three forest types (three possible combinations) using Wilcoxon ranked sum tests with subsequent Bonferroni corrections. Soil variables were also tested for normality using a Shapiro-Wilk test and data were Box-Cox transformed, as necessary, to normalize distributions. For analysis of soil characteristics, we first used a MANOVA comparing soil characteristics by forest type. Following a significant MANOVA, we used univariate analysis of variance (ANOVA) with subsequent Tukey–

Kramer post-hoc pair-wise comparisons. All mean values are shown ± 1 SE.

To compare floristic diversity across forest types we first compared Shannon diversity index values between each of the three forest types using Hutcheson’s *t* (Zar 1999). We then also used a bootstrap analysis with 10 000 iterations based on number of species in each transect in order to create hypothetical species distributions for each of our three forest types, and compared diversity across these hypothetical species distributions (Manly 1997).

Results

Floristic diversity and structure

Palmyra atoll has a species-poor, woody plant community. A total of seven woody plants were recorded in all floristic surveys. Although the plant community is depauperate, *C. nucifera* appears to have caused significant declines in the number of species per transect, depending on the abundance of *C. nucifera*. There are more species in transects with intermediate *Cocos* transects than in high or low *Cocos* forests, both for understorey and established (> 1-cm DBH) plants (Table 1). Diversity, as measured by the Shannon diversity index, is significantly higher in low and intermediate *Cocos* forests than in high *Cocos* forests ($P < 0.001$ for both) for established trees. Richness estimates generated by bootstrapping likewise show that diversity is significantly higher in low *Cocos* and intermediate *Cocos* forests than in high *Cocos* forests ($P < 0.05$), but that there are no significant differences between low *Cocos* and intermediate *Cocos* forests. Diversity patterns in the woody understorey are similar, but in

Table 1. Diversity and structural characteristics (mean ± 1 SE) from 100 m² transects in forests dominated by *Cocos nucifera* (> 75% basal area *C. nucifera*; “high *Cocos*”), by other woody species (< 25% basal area *C. nucifera*; “low *Cocos*”) or by a mixture of *C. nucifera* and other woody species (intermediate basal area *C. nucifera*; “intermediate *Cocos*”). Letters following mean values show pair-wise significant differences, mean values with the same letters are not significantly different. All values are presented both for established plants (> 1 cm DBH), and understorey plants (plants ≤ 1 cm DBH), except basal area, as basal area was not measured for understorey plants.

Forest type (# transects)	# individuals per transect	Basal area/transect (m ²)	Shannon diversity (ln)	# species per transect
UNDERSTOREY				
High <i>Cocos</i> (33)	28.5 \pm 9.0 (a)	na	0.27 (a)	1.58 \pm 0.12 (a)
Intermediate <i>Cocos</i> (24)	34.7 \pm 10.5 (a)	na	0.39 (b)	1.96 \pm 0.14 (b)
Low <i>Cocos</i> (26)	9.8 \pm 1 (b)	na	0.57 (c)	1.50 \pm 0.15 (a)
	$P = 0.03^*$		$P < 0.001^*$	$P = 0.02^*$
ESTABLISHED PLANTS > 1-cm DBH				
High <i>Cocos</i> (33)	14.1 \pm 1.8 (a)	0.80 \pm 0.15 (a)	0.44 (a)	1.79 \pm 0.13 (a)
Intermediate <i>Cocos</i> (24)	12.9 \pm 1.2 (a)	0.76 \pm 0.09 (a)	0.56 (b)	2.38 \pm 0.15 (b)
Low <i>Cocos</i> (26)	10.5 \pm 2.4 (b)	0.73 \pm 0.22 (b)	0.56 (b)	1.54 \pm 0.14 (a)
	$P = 0.02^*$	$P = 0.03^*$	$P < 0.001^*$	$P < 0.001^*$

this case, high and intermediate *Cocos* forests both have lower diversity than low *Cocos* forests ($P < 0.001$). When Shannon diversity levels are analysed for established trees without *C. nucifera*, patterns of diversity differences across forest type remain the same, just lower (high *Cocos* = 0.34, intermediate *Cocos* = 0.45, low *Cocos* = 0.47).

The structure of the forest is very different across forest types, with significant differences in number and size of woody plants among forest types (Table 1). Low *Cocos* forests have lower stem density of individuals ≥ 1 -cm DBH than do either high *Cocos* ($Z = 2.5$, $P = 0.01$) or intermediate *Cocos* ($Z = 2.4$, $P = 0.02$) forests. Average basal area per transect is also lower in low *Cocos* than either intermediate *Cocos* ($Z = 2.3$, $P = 0.03$) or high *Cocos* ($Z = 2.2$, $P = 0.03$) forests. Densities of understorey woody plants significantly vary across forest types, with four and five times fewer individuals per transect in low *Cocos* forests than in high *Cocos* ($Z = 3.2$, $P = 0.001$) or intermediate *Cocos* ($Z = 3.4$, $P = 0.0006$) forests, respectively.

There are also significant differences between the transects in terms of ecological predominance of species, as assessed by the Importance Value (IV; Fig. 1). As would be expected, looking at plants ≥ 1 -cm DBH, *C. nucifera* is by far the most important species in both high *Cocos* forests (IV = 55%) and intermediate *Cocos* forests (IV = 42%), with two to three times the importance of the subsequent two species (*Pandanus fischerianus* (Stone 1968) and *P. grandis*). By contrast, in low *Cocos* forests, *P. grandis* is the most dominant species (IV = 39%), with *T. argentea* following closely behind (IV = 34%), and relatively little representation of *C. nucifera* (IV = 9%) or *P. fischerianus* (IV = 13%). In a regression of basal area of *C. nucifera* per transect ($n = 83$) against basal area of other species, we find a significant decline of basal area of *P. grandis* ($R^2 = 0.59$, $P < 0.0001$) and *T. argentea* ($R^2 = 0.23$, $P = 0.005$) with an increase in *C. nucifera*, but no significant effects of *C. nucifera* increase on other species. These patterns remain largely the same if relative dominance is included in calculation of importance values for established trees.

The importance value of understorey species looks quite different to that of the established plants. Both *P. fischerianus* and *C. nucifera* are well represented in all three forest types, including in low *Cocos* forests, where these two species had importance values of 22% and 31%, respectively, almost on a par with the importance value of *P. grandis* (33%), the dominant woody plant among established canopy trees in low *Cocos* forests.

Comparing all coastal forests to all interior forests, the major substantial change in species composition is the reduction in importance values of *T. argentea* and *S. sericea* in interior as compared to coastal forests. *C. nucifera* also declines in interior forests among established plants, but still remains a significant component of the community, even among only established plants (Fig. 2).

Finally, the ground cover among transects was also different. Low *Cocos* forests had nearly three times less litter on the ground than high *Cocos* forests ($Z = 4.3$, $P < 0.0001$); intermediate *Cocos* forests had intermediate levels of ground litter accumulation. Herbaceous ground cover was approximately two times higher in low *Cocos* forests as compared to high *Cocos* forests (low versus high $Z = 1.9$, $P = 0.05$); intermediate forests had intermediate cover, which was not significantly different from either forest type. Species composition of herbaceous ground cover was very simple, with more than 95% of cover composed of two ferns, *Asplenium nidens* and *Phymatosorus scolopendria*.

Soil properties

Major soil characteristics differed significantly between forest types (MANOVA, $F_{2,17} = 6.12$, $P = 0.01$; Tables 2 and 3). Soils in low *Cocos* forests were characterized by much higher levels of all macronutrients (nitrate, ammonium and phosphate) than either intermediate or high *Cocos* forests. Soil macronutrients in the top 5 cm were consistently higher than those in the lower (10–15 cm) strata. There were also small but significant differences in soil pH, with low *Cocos* forests having lower pH than either intermediate or high *Cocos* forests. Of the 12 elements analysed, five (Al, B, K, Mo, Si) differed significantly across forest types, although direction of change varied by element (Table 3).

Comparisons of nutrient levels from artificially created islets only show the same patterns as observed above. All three macronutrients and pH levels were significantly lower in artificial islets with high *Cocos* forests as compared to those with low *Cocos* forests. Of the five elements that showed significant differences across all sites, four also showed significant differences across forest types when the analysis was constrained only to artificially created islets. Differences in Mo were only nearly significant (See Young et al. 2010 and SI Table S1). All differences in elements between artificial sites occurred in the same direction as they did in analyses of the full data set.

Organic carbon (from muffle combustion) was much higher in low *Cocos* sites; this pattern remained

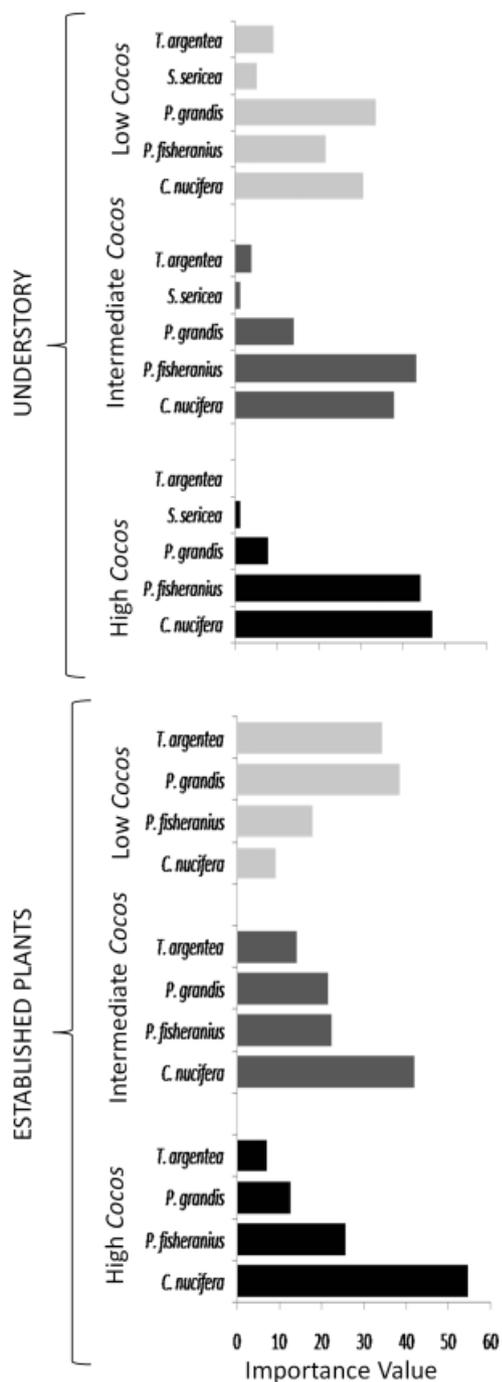


Fig. 1. Importance values (percentage) of five most common tree species (*Cocos nucifera*, *Pandanus fischerianus*, *Pisonia grandis*, *Tournefortia argentea*, *Scaevola sericea*) by forest type for both understory (regeneration) plants (≤ 1 cm DBH) and established plants (> 1 -cm DBH). Forest type definitions are “high *Cocos*” ($> 75\%$ basal area of *C. nucifera*), “low *Cocos*” ($< 25\%$ basal area of *C. nucifera*) or “intermediate *Cocos*” ($\leq 75\%$ and $\geq 25\%$ basal area of *C. nucifera*).

significant when only those sites composed of fill material were considered. This was consistent with results from the differential thermal analysis system (DTA) (Fig. 3a). Low *Cocos* soils demonstrated accelerated mass loss between 230°C and 370°C , while high *Cocos* soils significantly delayed the loss of mass upon heating to $> 520^{\circ}\text{C}$, and never achieved mass loss on heating as large as in soils under low *Cocos* forests, regardless of the temperature range over which the groups are compared. The DTA profiles (Fig. 3b) also demonstrated alterations in the energy content of organic materials (causing the distinct mass loss profiles in Fig. 3a). We can deduce this from: (1) the altered number and temperature onsets for exothermic and endothermic transitions, and (2) the “apparent enthalpies” of soil organic matter fractions disappearing at various temperature intervals. By comparison with an authentic lab-grade calcium carbonate (Fig. 3c), it is straightforward to recognize the two characteristic endotherms at 59°C and 590°C ; these same features can be seen underlying the thermograms of the high *Cocos* soils. There is an additional endotherm from water loss from soil organic matter that overlaps the first limestone endotherm common to all the Palmyra soils; no such ambiguity arises for the second endotherm. The organic matter estimated using the thermogravimetric data was 51.6% (± 14.4) for low *Cocos* forests and 7.20% (± 2.05) for high *Cocos* forests.

Discussion

Several important and unintuitive features emerge in examining the importance values of species by forest type. Most striking is the relatively high importance value of *C. nucifera* in the understory of all forest types, including low *Cocos* forests where *C. nucifera* is not an important part of the canopy (Fig. 1). Indeed, *C. nucifera* is as important as any other species in the understory in these low *Cocos* forests, and is equally important in low *Cocos* forest understory as it is in high and intermediate *Cocos* forest understory. While the relatively high importance of *C. nucifera* in the understory may be caused by the large seed size of *C. nucifera*, which allows it to persist in the seedling bank, it does also suggest that increased *C. nucifera* establishment in low *Cocos* forests is not limited by propagule availability. There may be other factors at these low *Cocos* forests, such as differences in light and soil fertility, that place *C. nucifera* at a competitive disadvantage, creating persistent barriers to the establishment of this species.

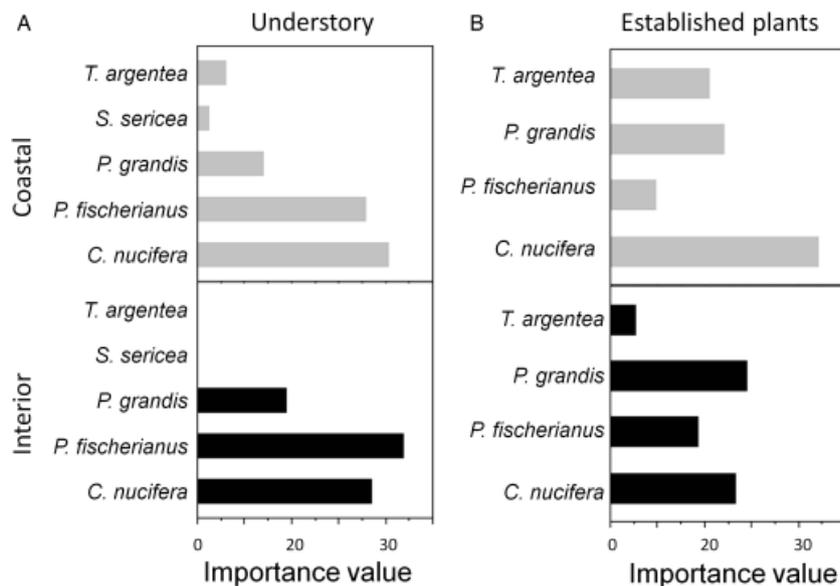


Fig. 2. Importance values of five most common tree species (*Cocos nucifera*, *Pandanus fischerianus*, *Pisonia grandis*, *Tournefortia argentea*, *Scaevola sericea*) pooled across forest type by proximity to the coast for both understory plants (≤ 1 cm DBH) and established plants (> 1 cm DBH).

Table 2. Soil nutrients (mean \pm 1 SE) by forest type and soil depth (0–5 cm and 10–15 cm). Forest type definitions are the same as in Fig. 1. Significant differences are denoted with an asterisk (*).

	Depth (cm)	<i>P</i>	<i>n</i>	High <i>Cocos</i>	Intermediate <i>Cocos</i>	Low <i>Cocos</i>
Nitrate ($\mu\text{g g}^{-1}$)	0–5	< 0.0001*	75	7.2 \pm 2.0	30.5 \pm 14.2	130.8 \pm 35.8
	10–15	< 0.0001*	73	9.1 \pm 4.4	12.8 \pm 5.8	90.8 \pm 24.0
Ammonium ($\mu\text{g g}^{-1}$)	0–5	< 0.0001*	75	54.2 \pm 8.4	45.6 \pm 6.6	78.6 \pm 5.8
	10–15	< 0.01*	73	26.8 \pm 4.9	21.4 \pm 4.0	49.7 \pm 4.7
Phosphate ($\mu\text{g g}^{-1}$)	0–5	< 0.0001*	71	2.2 \pm 0.4	2.7 \pm 0.5	6.7 \pm 0.9
	10–15	< 0.0001*	67	1.4 \pm 0.3	3.1 \pm 0.8	5.7 \pm 1.2
pH	0–5	< 0.01*	59	7.5 \pm 0.2	7.6 \pm 0.1	7.0 \pm 0.1
	10–15	< 0.01*	58	7.5 \pm 0.1	7.6 \pm 0.1	7.1 \pm 0.2
Soil Organic Matter (%)	0–5	< 0.01*	43	15.5 \pm 3.0	20.7 \pm 4.9	42.6 \pm 6.8
	10–15	< 0.01*	41	10.0 \pm 2.2	11.5 \pm 6.2	25.3 \pm 4.6

Alternatively, it may be that *C. nucifera* is increasing in abundance at the atoll, and the high importance of *C. nucifera* in the understory presages increased importance of *C. nucifera* throughout the atoll. Related to this, while there is somewhat lower importance of *C. nucifera* in established plants in the interior as opposed to the coast, such differences dissipate in the understory plants. This suggests lack of propagule limitation of *C. nucifera* to interior sites, and may also be indicative of future changes to come, which began on the coast and are moving from the edge towards more interior sites. An on-going, long-term demographic study will shed light on these findings.

Increases in abundance of *C. nucifera* seem to be primarily correlated with reductions in importance *P. grandis* and *T. argentea*. Both of these species

have lower importance in the understory of all forest types than in established plants, which is suggestive of potential for future decline (but see Condit et al. (1998)). Given that *P. grandis* is declining locally and throughout much of its range (Handler et al. 2007; Batianoff et al. 2010), and that both these species commonly provide important habitat to seabirds, this could have important conservation implications. However, increases in *C. nucifera* do not equally impact all other plant species. *P. fischerianus*, for example, actually increases in importance in high and intermediate *Cocos* forests as compared to low *Cocos* forests.

Increased abundance of *C. nucifera* is strongly correlated with changes in forest structure and diversity. High abundance of *Cocos* is associated with reduced forest diversity (as measured by the

Table 3. Soil elemental composition (mg element/kg dry weight soil) by forest type from 0–5-cm depth. Soil nutrients are from transects in forests dominated by *Cocos nucifera* (>75% basal area *C. nucifera*; “high *Cocos*”), and from transects with low dominance of *C. nucifera* (<25% basal area *C. nucifera*, “low *Cocos*”). Significant differences after Bonferonni correction are denoted with an asterisk (*).

	<i>P</i>	<i>N</i>	High <i>Cocos</i>	Low <i>Cocos</i>
Al	<0.0001*	37	121.7 ± 172.1	762.1 ± 533.1
B	<0.0001*	37	335.01 ± 33.38	847.5 ± 92.6
Cu	0.54	37	8.14 ± 2.07	9.47 ± 2.2
Fe	0.68	37	238.2 ± 87.5	180.6 ± 36.6
K	<0.0001*	37	283.8 ± 26.5	5991.9 ± 55.2
Mg	0.39	37	6736.8 ± 628.5	7420.4 ± 632.5
Mo	0.002*	37	1.88 ± 0.13	1.19 ± 0.16
Mn	0.32	37	6.5 ± 0.9	8.0 ± 2.3
Na	0.40	37	3268.3 ± 198.6	3492 ± 145.0
Si	<0.0001*	37	2276.3 ± 786.9	10432.5 ± 1380.6
S	0.06	37	5008.8 ± 319.2	4399.4 ± 209.6
Zn	0.36	37	81.8 ± 26.2	135.7 ± 39.2

Shannon diversity index) in these already low diversity systems. Structurally, high and intermediate *Cocos* forests tend to have more individuals per unit area than low *Cocos* forests; this increased stem density leads to higher total basal area in high and intermediate *Cocos* forests as compared to low *Cocos* forests. As expected, intermediate *Cocos* forests have structural characteristics intermediate between the high *Cocos* and low *Cocos* forest types, although structural values tend to be statistically indistinguishable from high *Cocos* forests. Diversity in intermediate forests, for established trees, is similar to that in the low *Cocos* species forest type. This is also not surprising, since they have species typical of both low *Cocos* and high *Cocos* forests.

The abundance of *C. nucifera* is strongly correlated to changes in soil features, as has been observed in several woody species (Versfeld & VanWilgen 1986; Musil 1993), although patterns observed here are different from those in other studies. Soil differences between forest types were pronounced for the major macronutrients (nitrate, ammonium and phosphate) measured in both soil horizons. Both mass loss on combustion and thermal analyses suggest that higher amounts of soil organic matter accumulate in soils below low *Cocos* forests. The energy content of this soil organic matter is higher on a mass basis than soil organic matter accumulating under high *Cocos* forests. Comparisons of differences between recently created artificial islets derived from the same parent material but having differing patterns of *Cocos* dominance strongly suggest that *C. nucifera* actually causes all

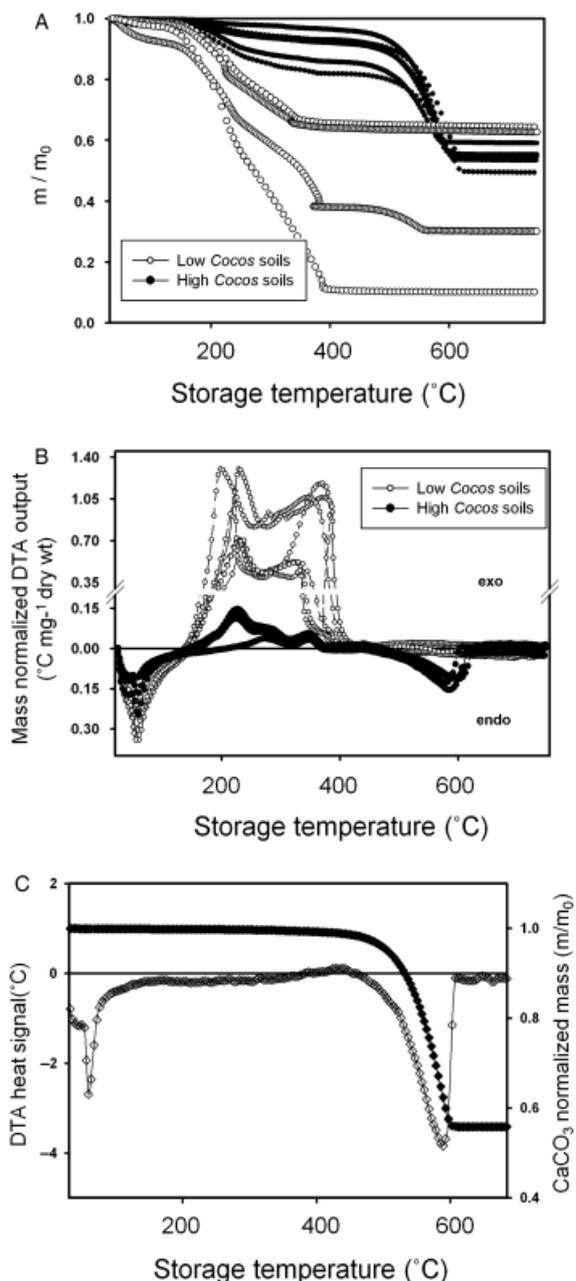


Fig. 3. Thermal analysis of composited soils from either low *Cocos* ($n = 6$) or high *Cocos* ($n = 6$) soils. (a) Temperature profile of mass loss (TG), normalized to initial mass. (b) Differential thermal analysis (DTA) heating curves of the same soil samples as in (a), mass-normalized. Points above the zero line arise from exothermic transitions, points below from endothermic events. (c) Pure lab standard of solid calcium carbonate, with both TG (filled symbol) and DTA (open symbol) profiles shown.

of these observed patterns. Isotopic analysis of soils also strongly suggests that the mechanism of change of nitrogen levels is disruption to seabird-derived

subsidies, since seabirds do not nest and roost in *C. nucifera* in substantial numbers (Young et al. 2010).

Of the 12 macronutrients and trace elements analysed, five (Si, B, Mo, K and Al) showed significant differences between high *Cocos* and low *Cocos* forest types, although the patterns varied by element. The elements that changed were not strongly bird-associated, and thus it seems likely that other properties of the palm dominance drive these patterns. While we have not specifically examined mechanisms, we suggest several probable pathways, given changes observed in other soil and litter properties and known chemical properties of palms. Si and B were depleted in soils in high *Cocos* forests and we hypothesize that this is due to higher above-ground accumulation of these nutrients in *C. nucifera* than in other dicotyledenous species. Palms are well known Si accumulators, with both leaf and stem concentrations in the several per cent dry weight range (Marschner 1995). Palms may also be B-accumulating species and may be more tolerant of high B (Nable et al. 1997). Mo, in contrast, was elevated in high *Cocos* sites. Mo is naturally scarce in soils, and only found in sizable amounts in association with standing litter (Wichard et al. 2009), especially on coarse-textured soils, as found in our transects. This pattern may thus be due to observed increases in standing litter in high *Cocos* forests. In the case of K and Al, we saw enrichment of both elements in low *Cocos* forests. Soil organic matter was likewise higher under this forest type as compared to intermediate *Cocos* and high *Cocos* forests, and soil pH was slightly depressed. These soil conditions directly impact the availability of Al in the soil solution, as pH and dissolved organic carbon are principal controllers of $[Al^{+3}]$ solubility (Sposito 1989). There is some evidence for the systematic substitution of Al for Si in woody dicot stems (Carnelli et al. 2002). Thus, we may be seeing support for cycling of silica below high *Cocos* forests substituted by accelerated K/Al cycling below low *Cocos* forests. Though we believe bird subsidies may drive the K changes, the mechanism must be different in the case of Al.

While it is quite possible that WWII activities could have impacted total levels of metals and other trace elements at Palmyra, there is no evidence that military activities differed systematically across different forest types. Furthermore, the metals that would most likely be affected by such anthropogenic disturbance, Zn, Cu and Mn, did not vary significantly by forest type.

It seems likely that differences in nutrient and trace element properties are driven both by effects of

changes in bird-derived subsidy arrival (Young et al. 2010) and by specific differences in growth habits, ground cover and foliar nutrient properties of *C. nucifera*, as compared to other dominant species. Other researchers studying soil-forming processes in the Central and South Pacific have expressed surprise at the variety of soil types that seemed to develop under the often depauperate vegetation and have noted different soil features with different vegetation patterns, including elevated bird-associated elements under *T. argentea* (Morrison 1990; Morrison & Woodroffe 2009). This study suggests that *C. nucifera* may play an important role in creating these different soil properties via multiple pathways.

Given the current pantropical distribution of this palm, and its tendency to reach near monodominance, particularly in remote tropical islands, the results of this study suggest that the palm may have important, widespread impacts on soil properties and on floristic diversity. Detailed long term studies of longitudinal change over time in areas of recent *C. nucifera* establishment would improve our understanding of the nature, mechanisms and time periods of these potential effects.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Photo S1. The coconut palm, *Cocos nucifera*, often reaches monodominance at Palmyra atoll and

throughout the world, changing forest structure, soil composition and plant diversity in the process (photo credit TC Robbins).

Photo S2. When coconut palms, *Cocos nucifera*, become dominant at Palmyra Atoll, there are strong changes in forest structure, diversity and soil nutrients. This may be partially mediated by associated changes in the seabird community (photo credit RB Dunbar).

Photo S3. Coconut palms may affect large changes in floristic and soil properties in sites when they replace other species (photo credit V Chen).

Photo S4. When coconut palms, *Cocos nucifera*, become dominant at Palmyra Atoll, there are strong changes in forest structure, diversity and soil nutrients. This may be partially mediated by associated changes in the seabird community.

Table S1. Soil elemental composition (mg element/kg dry weight soil) by forest type from 0–5 cm depth from only those transects placed on sites artificially created by military activity. Soil nutrients are from transects in forests dominated by *Cocos nucifera* (>75% basal area *C. nucifera*, “high *Cocos*”), and from transects with low dominance of *C. nucifera* (<25% basal area *C. nucifera*, “low *Cocos*”). Differences that are significant after Bonferonni correction are denoted with an asterisk (*).

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