Cascading community and ecosystem consequences of introduced palms in tropical islands*

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ABSTRACT

Biological invasions are a pervasive and dominant form of anthropogenic disturbance. However, we seldom have the opportunity to evaluate the long-term, indirect, and often slow-moving cascading effects of invasions at the community and ecosystem scale. Here we synthesize the collective knowledge from 10 years of study on the influence of the deep historical introduction of coconut palms (*Cocos nucifera* L., 1753) across a series of islets at Palmyra Atoll. Through a suite of pathways, we find this palm drives near-complete ecosystem state change when it becomes dominant. Abiotic conditions are transformed with major soil nutrients 2.7 to 11.5 times lower, and water stress 15% elevated in palm-dominated forests, compared with native forest. Faunal communities are likewise dramatically altered, not only in composition but also in behavior, body size, and body condition. Biotic interactions, including herbivory rates, palatability, and seed predation are likewise changed. Cumulatively, these changes transform food webs, leading to dramatically shortened and simplified food chains in invaded ecosystems. Many of these changes appear to create slow-acting feedback loops that favor the palm at the expense of native species. Given the widespread nature of this historical introduction, many island and coastal regions of tropical oceans may be similarly transformed.

**Keywords:** invasive species, introduced species, historical introductions, ecological cascades, bottom-up processes, ecological harbingers, spatial subsidies, *Cocos nucifera*
INTRODUCTION

Biological invasions are considered to be one of the most influential drivers of global change (Tylianakis et al. 2008). Building on a deep history of invasive species research (Elton 1958) we have an increasingly well-developed understanding of how invasive species can shape different properties of ecosystems (Ehrenfeld 2010; Vilà et al. 2011; Gaertner et al. 2014). Yet, this work, often by necessity, focuses on relatively short-term effects that are relevant to most recent invasions, and thus on pathways that operate over relatively short time periods. Not only does this limit the type of pathways that can be observed, but it may tend to underplay the magnitude of effects. For instance, much of the debate about the extent to which invasive species tend to cause extinction and declines in diversity (Gurevitch and Padilla 2004; Bellard et al. 2016) are likely unresolved in part because there may often be long time lags in effects following invasion, including extinction debts that accrue before extinctions occur (Gilbert and Levine 2013). Indeed, the effects of invasion on ecosystem processes and community structure are likely dependent on both spatial (Powell et al. 2013) and temporal (Ehrenfeld 2010; Vilà et al. 2011) scale of invasion, because the ecological consequences of invasion are often heterogeneous, slow-occurring, and not detectable until well after impacts on species and communities have occurred. Historical (multi-decadal) species introductions thus provide an interesting opportunity to examine effects of invasions over larger temporal as well as spatial scales.
Humans have transported non-native plants and animals with them to colonize new places for thousands of years. These include both accidental introductions and the intentional introduction of crop and food species (Kowarik 2003; Hulme 2009).

Indeed, many species that are now considered invasive were originally introduced intentionally for human benefit (Vitousek et al. 1997; Mack et al. 2000; Thuiller et al. 2006; Tylianakis et al. 2008; Simberloff et al. 2013). In the United States alone, it is estimated that 85% of the 235 invasive woody plants were intentionally introduced (Reichard and White 2001). However, while the transport of new and potentially invasive species to new habitats is not a new phenomenon, the rate of introduction of invasive species has accelerated in modern times. For example, Polynesian arrival in Hawaii (between 300 and 1300 CE), appeared to drive an increase in invasive species colonizations increased from background rates of one species every 50,000 years to 3-4 species per century. In comparison, in the last few decades, it is estimated that ~20 species have been introduced each year to Hawaii (Ewel et al. 1999). The current high rate of global invasion poses huge biological and economic costs (Pimentel et al. 2000; Hulme 2009). However, management and eradication must be carefully weighed both because of the frequently large costs of implementation and maintenance, and because of the potential for unintended negative consequences of removal of invasive species once they have become established in new systems (Zavaleta et al. 2001; Bergstrom et al. 2009).

It is thus critical to understand the extent of negative impacts of invasive species, so that they can be compared with the risks and costs of management or eradication.
We therefore need more research exploring effects at large spatial and temporal scales to not only catch abrupt and drastic state shifts (Barnosky et al. 2012; Brook et al. 2013), but also the slow-acting, long-term and landscape-scale effects of invasive species. Though in number they are now dwarfed by the recent global flux of modern invasions, historical species introductions offer a critical opportunity to fill gaps in our understanding of the impacts of invasive species.

One noteworthy historic species introduction that is now invasive in much of its range is the coconut palm (*Cocos nucifera* L., 1753) (Rejmánek and Richardson 2013). Coconut palms are an iconic symbol of tropical coastal ecosystems worldwide. Yet, this palm is thought to have originally only occurred in scattered populations on islands and coastlines in the equatorial Indian and Pacific Oceans (Baudouin and Lebrun 2009). Its spread was facilitated through a series of introductions, likely first by Austronesian voyagers over 1500 years ago, who utilized the palm for food and fiber on transoceanic journeys (Gunn et al. 2011), then by early European explorers, and more recently by 19th century European agricultural entrepreneurs who intensively planted coconut palms for copra production. As a result, coconut palms can now be found as largely monodominant forests across a wide range of tropical coastal environments (Harries 1978; Foale 2005). Indeed, during the boom in copra production during the 19th century, coconut palm planting actively displaced hundreds of thousands of hectares of land previously occupied by intact rainforests (Foale 2005). Although coconut production has currently been overshadowed by other tropical crops, there are still
at least 12 million hectares (approximately the size of the United Kingdom) of planted coconut palm distributed across nearly 90 countries in tropical regions (Foale 2005). Although purposefully planted across the tropics, coconut palms are considered invasive in the Pacific, Indian, and Caribbean Island regions, where populations planted by Austronesian voyagers and later during the copra boom of the 1800’s have largely been left unmanaged in recent times (Rejmánek and Richardson 2013). In some cases the positive ramifications of coconut palms for humans (e.g. direct benefits from provision of non-timber forest products, indirect benefits from coast line stabilization from these saline tolerant plants) may outweigh the negative ecological ramifications, but to date the ecological costs have not been well considered.

Like many intentional introductions that subsequently become invasive, coconut palms are successful invaders in large part because of human propagation. Human introduction and care reduces environmental stochasticity typically faced by founder populations that might otherwise go extinct (Mack 2000), and also allows new species to be introduced in large enough populations for them to become self-sustaining and to grow beyond the extent of their original introduction (Kowarik 2003; Lockwood et al. 2005). However, as we document here, coconut palms also possess traits that allow them to establish dominance in invaded systems; as, like other ecosystem engineers, they create habitats suitable for their own survival (Jones et al. 1994; Cuddington and Hastings 2004).
Here we draw on a ten-year case study of the many cascading impacts of the historical invasion of coconut palms in the tropical Pacific, illustrating effects at both the community and ecosystem levels. This body of work illustrates changes at several spatial scales and documents how introductions can lead to long-term and often slow-acting changes. This research may thus provide important insights on how diverse attributes of tropical ecosystems have been fundamentally altered by this species alone, while also highlighting several novel mechanisms that may operate in other invasive systems. Particularly, we emphasize how the indirect effects of invasion, when played out over long time periods, have influences that cascade and intertwine in complex ways, often perpetuating fundamentally altered ecological regimes.

**Study System: Palmyra Atoll**

This research was conducted in the wet tropical forest ecosystems of Palmyra Atoll (162°05’ W, 5°53 N), located in the Central Tropical Pacific in the Northern Line Islands. This atoll is now administered as part of the Pacific Remote Islands Marine National Monument and consists of a ring of approximately 23 low-lying islets composed of calcium carbonate coral rubble overlaying a limestone base (Fig 1). Soils range from very nutrient poor sandy coral rubble to deep phosphate rich humic soils. The islets range in size over four orders of magnitude, from $5.29 \times 10^2$ to $2.60 \times 10^6$ square meters and span an area of 20 square kilometers. The majority of the nutrients in this, as in other coral derived ecosystems (Schmidt et al. 2004; Young et al. 2010a), come from seabird guano fertilization. Palmyra receives an...
average of 4.5 m of rainfall a year; combined with porous sandy soils, this means that extremely high rates of nutrient input are continuously required to maintain soil fertility.

There is no current human inhabitation on the atoll beyond a small research center established on one islet in 2005. The only history of extensive human habitation is that of a brief but intense occupation during World War II when the atoll was used as a military base. During this occupation in the 1940’s, major dredging and land moving activity was conducted, much of the vegetation on Palmyra was modified, and several new islets were constructed. After the war the atoll was largely undisturbed, although some additional planting of coconut palms did occur when it was briefly run as a copra plantation after the war (Dawson 1959; Collen et al. 2009).

Ecologically, Palmyra is best known for its relatively pristine coral reef ecosystem, but it also supports large and regionally important seabird colonies. These include the world’s second largest population of nesting red-footed boobies (Sula sula L., 1776) in the world (~25,000 individuals). There are also large colonies of sooty terns (Onychoprion fuscatus L., 1766; ~875,000 individuals), and black noddies (Anous minutus Boie, 1844; ~6,500 individuals), as well as smaller populations of white terns (Gygis alba Sparrman, 1786), greater and lesser frigatebirds (Fregata minor Gmelin, 1789; F. ariel Gray, 1845), brown noddies (Anous stolidus L., 1758), masked boobies (Sula dactylatra Lesson, 1831), brown boobies (Sula leucogaster
Boddaert, 1783), and white tailed and red-tailed tropicbirds (*Phaethon lepturus* Daudin, 1802; and *P. rubricauda* Boddaert, 1783). All of these species are truly pelagic, using the atoll only for nesting or roosting habitat. Given strong global declines in pelagic seabirds (Paleczny et al. 2015), Palmyra’s seabird nesting grounds are a critical refuge for many of these species.

Palmyra’s terrestrial communities are otherwise notably species poor, and mainly consist of a few plant and arthropod consumer species as might typify a remote atoll. Palmyra’s canopy is dominated by seven species of plants (in order of abundance *C. nucifera*, *Heliotropium foertherianum* Diane & Hilger, *Scaevola taccada* (Gaertn.) Roxb., *Pisonia grandis* R. Br., *Pandanus tectorius* Parkinson, and *Terminalia catappa* L.). Of these, only *C. nucifera* and *T. catappa* are thought to be non-native; *T. catappa* is restricted to the one inhabited islet of Palmyra. The *P. grandis* population at Palmyra is one of the largest remaining intact stands in the Pacific (Handler et al. 2007). The understory is likewise species poor and dominated by just two ferns, *Asplenium nidus* L., and *Phymatosorus scolopendria* Burm. f.

In terms of macroscopic consumers, Palmyra is thought to support approximately 120 species of insect and spider arthropods; >85% are presumed to be introduced to the atoll (Handler et al. 2007). The only vertebrate consumers on the island are three species of gecko, two native species (*Lepidodactylus lugubris* Dumeril & Bibron, 1836 and *Lepidodactylus* sp.) that reproduce via parthenogenesis, and one introduced species (*Hemidactylus frenatus*, Dumeril & Bibron 1836) that is largely
confined to the single inhabited islet of Palmyra. The atoll supports populations of
seven species of land crabs, including a healthy population of coconut crabs (*Birgus
latro* L., 1767), the world’s largest terrestrial arthropod.

The history of coconut palms on Palmyra is likely typical of many other islands in
the Pacific. Based on best available historical evidence, it seems likely that palms
were brought to the region in the last 1,500 years (Matisoo-Smith and Robins 2004;
Gunn et al. 2011). However, coconut palm abundance on the atoll expanded
considerably between 1850 and 1970 due to periodic small-scale cultivation efforts.
Coconut palm’s population in the mid-1800’s was documented at approximately
4,000 reproductive trees, a number that has since increased to approximately
53,000 reproductive adults across the atoll in 2005 (Dawson 1959; Wegmann
2009). Currently, more than 50% of the atoll is covered in coconut palms, with
canopy cover of individual islets ranging from 0% to 100% palm cover. Where it
occurs on the atoll, it is most often a monoculture with a dense canopy (Young et al.
2014). As we highlight below, current data suggest this species is likely still slowly
encroaching on native forests on islets where both coconut palm and native
vegetation types occur. There is no other native palm that occurs on the atoll.

*Cocos nucifera* dominated communities are floristically transformed

By definition, palm-dominated communities (which we have categorized as forests
with >75% basal area of coconut palms; Young et al. 2010a) have very different
canopy compositions than do native-dominated stands. However, the floristic
composition and structure of palm-dominated forests also varies in many other ways. Structurally, palm-dominated forests have much higher stem density both in the canopy and in the understory than do native-dominated communities (40% and 300% higher respectively), as well as modestly higher total standing basal area (8% higher) (Young et al. 2010b). Palm-dominated forests also have much lower plant species diversity not only in the canopy (Shannon index of 0.57 in native versus 0.44 in palm forests) but, even more pronounced, in the understory (0.57 versus 0.27 respectively) (Young et al. 2010b). On the forest floor, palm-dominated forests tend to be covered in dense, slow-decomposing litter consisting primarily of nuts and fronds, with three times more total litter cover than in native forests. Growing through this litter mat, herbaceous cover, primarily composed of two common ferns, *A. nidus* and *P. scolopendria*, is approximately twice as high in palm as compared to native forests (Young et al. 2010b).

**The seabird connection**

Many tropical seabird species, including two of the dominant and resident species in this system –red-footed booby and black noddy– are tree nesting. Atoll-wide bird surveys conducted in 2006 along both the coasts and interior of the islets, showed that, as a group, seabirds strongly prefer to nest in native *P. grandis* and *H. foertherianum* trees, and have a strong aversion to the use of coconut palm forests, especially for nesting habitat. Only 12% of the more than 6,000 birds surveyed were observed on coconut palms, and then, largely only roosting, not nesting. For the large-bodied and hyper-abundant red-footed booby (more than 75% of total bird
biomass), only 5% of individuals were observed on palms. At the atoll scale, this habitat preference led to strong variation in bird abundance based on the dominance of coconut palms on a given islet (Young et al. 2010a; Fig 2). This variation in bird abundance led to strong and pronounced changes in nutrient input across forest types. In the average native forests, based on estimates of bird biomass and guano production rates, this equates to between 231 and 635 kg N ha\(^{-1}\) yr\(^{-1}\), and 42 and 105 kg P ha\(^{-1}\) yr\(^{-1}\) in native forests (Young et al. 2010a). This is a rate equivalent to heavily industrialized fertilization, and represents 10-20 times more nitrogen and 10-18 times more phosphorous input than comparable coconut palm forests.

Not surprisingly, this difference in nutrient input leads to strong depletion in plant available nutrients. Soil analyses from coconut palm-dominated sites (those with >75% coconut biomass) and native-dominated sites (those with <25% coconut biomass) showed plant available nutrients 40-82% lower in palm forests (NO\(_3\)\(-\): 82%, PO\(_4\)\(-\): 73%, and NH\(_4\)\(+\): 40%) (Young et al. 2010a). There are also strong and significant differences in trace element abundance (Al, B, K, Mo, Si); four of these five elements showed significant declines, ranging from 60 to 95% reductions in palm forests (one, Mo, showed significant increases in palm forests) (Fig 2) (Young et al. 2010b). Soil pH was slightly elevated in palm forests, likely due to the lack of significant inputs of acidic bird guano, and soil organic matter was greatly decreased in the palm forests. The bird origin of the differences in soil nutrients can be traced using natural abundance of stable isotopes, because seabirds have a distinctively
high $\delta^{15}N$ signature, due to their high trophic position. Accordingly, soils in palm-dominated islets have substantially lower values of $\delta^{15}N$ (Fig 3).

While the observational nature of our work in this system often makes it difficult to assign causality, for soil nutrients, the artificial islets created by the military during World War II provide a valuable opportunity to examine causality. All artificial islets were created in a short time window from nutrient-poor coral rubble dredge tailings and are of similar origin and have similar elevations and essentially no topography. On artificially created islets that were subsequently colonized by coconut palms, plant available soil nutrients are lower than on natural coconut palm-dominated islets, suggesting that the original dredge materials have received very little nutrient enrichment over the past 60 years. In contrast, artificial native vegetation-dominated islets now have nutrient profiles indistinguishable from natural native vegetation-dominated islets, presumably due to high levels of bird inputs in both systems (Young et al. 2010a). Combined with the isotopic data, this suggests that increased palm dominance is a cause of, rather than a response to, the differences in soil nutrients across sites.

The changes in soil nutrients caused impacts on plant foliar nutrients as well. Two of the three dominant tree species on the atoll ($C. nucifera$ and $H. foertherianum$) show significant decreases in foliar N (20% and 15% respectively) when they occur in high density coconut palm forests as compared to native forests (Young et al. 2010a). This is consistent with results from a range of other seabird-dominated
ecosystems, which show strong effects of changes in seabird density on both soil
and foliar nutrient concentrations (Mulder et al. 2011).

Not surprisingly, these dramatic changes in soil nutrients in palm forests affected
not only plant nutrients, but also plant growth (detailed below under abiotic
feedbacks) and entire site productivity. Since it is challenging to directly measure
field productivity in tropical forests (Clark et al. 2001; Litton et al. 2007),
productivity was instead estimated using greenhouse experiments that measured
the amount of biomass, and particularly nitrogen-rich biomass produced, for one
plant species found across nearly all islets (the grass Eleusine indica (L.) Gaertn.,
1788) from soils taken from islets with various densities of palm invasion. These
experiments showed that 10% of variation in total biomass and 50% of the variation
in the foliar nitrogen produced (grams foliar nitrogen meters\(^{-2}\) month\(^{-1}\)) in
controlled conditions could be predicted based solely on the abundance of coconut
palms in the system where soils were sampled (Young et al. 2013a). These
controlled estimates of productivity were tightly correlated to more standard
measures of productivity in tropical ecosystems, such as litter throughfall inputs, for
the subset of sites where this information was available (Young et al. 2013a).

Herbivory on established plants was also impacted. Herbivores are known to prefer
high-nutrient plant material, and on Palmyra, this resulted in lower herbivory rates
in palm forest-dominated systems. Rates of herbivory (within three native species)
in palm-dominated forests were 3 to 4 times lower than in native-dominated
forests. Similarly, common Palmyra herbivores (two species, an insect and a crab) subjected to cafeteria-style trials preferred *P. grandis* leaves from native forests to the same species from coconut palm forests (Young et al. 2010a). Herbivores prefer native species over palms, since coconut palms have notably unpalatable leaf tissue, with low specific leaf area, low nutrient content, and very high carbon and silica content in comparison to all of the dominant native plant species on Palmyra (Marschner 1995; Young et al. 2011). Combined with lowered nutrient levels within native species in palm-dominated forests, palm forests, thus, are likely of low value to many herbivores (Young et al. 2010a).

**Community Effects: Consumer Communities**

Given the strong direct and indirect effects that coconut palms have on forest structure, plant growth rates, nutrient availability, and herbivory, it is thus unsurprising that these changes cascade to impact a wide range of consumers, from direct plant consumers (e.g. herbivorous insects) to species with only indirect links to forest dynamics (e.g. rat stomach parasites, and pelagic manta rays). The effects include not only changes in abundance, but also changes in ecology, behavior and body condition. These responses appear to be partly driven by direct effects of changes in forest structure, food type, and habitat availability on composition of consumer communities in regions altered by the invasive palm. However, these direct effects are compounded by, and often superseded by the indirect effects of palm abundance on site productivity, driven by changes in seabird-derived nutrients. Essentially the decreased availability of energy at the bottom of the food
web in palm forests has bottom-up effects that percolate through multiple trophic
levels, and ultimately transforms and simplifies the entire structure of food webs in
cococonut palm-dominated forests.

Invertebrates are the most abundant and diverse group on the atoll; the group also
includes many herbivorous and detritivorous species. As such they are a natural
first group to examine for consumer responses to changes in palm dominance.

Trapping of ground-dwelling invertebrates showed a strong change in composition
across forest types. Specifically, Isopoda and Formicidae decrease dramatically in
palm forests while Amphipoda show strong increases in palm forests (Briggs et al.
2012). Trapping of flying invertebrates –e.g. Diptera, Lepidoptera, Hymenoptera–
also revealed decreases in diversity and species richness in low productivity, largely
palm-dominated islets. There was also a tendency for the number of individuals to
decline with increasing coconut palm density, but this pattern was only marginally
significant ($P = 0.07$, $R^2 =0.18$). However, other insect taxa (Dysmicoccus sp., Order:
Hemiptera; Phisis holdhausi Karny 1926, Order: Orthoptera), which were surveyed
using targeted visual surveys, showed marked decreases in abundance in low
productivity, palm-dominated islets (Young et al. 2013a).

These changes in abundance and composition of prey also trickle up to impact
predator communities. Among the most abundant predators groups (and some of
the few terrestrial vertebrates at Palmyra) are two species of geckos from the
Lepidodactylus genus. These geckos are top predators on the atoll and are both
abundant and pervasive in the system. The abundance of geckos did not change across forest types, but the diets of the two species were very different in palm forests than in native forests. These diet differences closely paralleled changes seen in the invertebrate community at large; gecko diets in palm-dominated forests tended to be lower in diversity, with a higher abundance of amphipods (family Talitridae), and reduced abundance of isopods (family Philosciidae) and ants (family Formicidae) (Briggs et al. 2012).

Beyond these dietary changes, both gecko species showed significant reductions (17-19%) in body condition (mass per snout-ventral length (mg/mm)) in palm-dominated forests as compared to native-dominated forests. In this case, analysis suggested that these body condition effects were best explained by structural variation across forest types; mean stem size, not nutrient availability, was the best explanatory variable for changes in body condition (Briggs et al. 2012). One species of gecko (L. lugubris) and one other common predator, an abundant spider (Heteropoda venatoria Latreille 1804) also had statistically larger body sizes on more productive islets (Briggs et al. 2012; Young et al. 2013a). Larger animals are likely able to forage more effectively in structurally open habitats and may also be able to more effectively competitively exclude smaller conspecifics in areas with less structure.

Even parasites of these free-living consumers appear to be impacted. From its introduction in the middle of the 20th century during US military occupation until
2011 when an atoll-wide eradication effort was completed, the roof rat (*Rattus rattus* Linnaeus 1758) was the only other large terrestrial vertebrate predator on the atoll. In 2009, rats were surveyed across 13 islets, and a subset (n = 169) was dissected for parasites. While rat abundance is difficult to survey in these complex habitats, catch per unit effort showed no effect of the dominance of coconut palms on the abundance, size, or body condition of rats (Lafferty et al. 2010). However, the intensity of infestation with the stomach nematode, *Mastophorus muris* Gmelin 1790 strongly and significantly increased in palm-dominated habitats (15 worms per rat versus 2 in native-dominated forests). The reason for this was not established, but as *M. muris* requires an insect intermediate host, changes in insect community in palm dominated forests may change the availability of this host. Changes in microclimate or microhabitat might also change survivorship for free-living stages in this nematode.

Perhaps most surprisingly, the effects of increased coconut palm dominance even percolate into surrounding marine ecosystems. A study looking at how increases in palm-dominance might impact lagoon dynamics found that nitrogen in runoff was 26.5 times higher off coastlines of native- as compared to palm-dominated forests. Phytoplankton growth rates in surrounding waters, measured using moored, in-situ, phytoplankton growth chambers along the coast of palm- and native forest-dominated islets, showed significant declines in productivity near palm forests. This then led to decreases in biomass and body size of an important group of zooplankton, Copepoda, around palm-dominated sites. This, in turn, affected the
foraging ecology of at least one large obligate plankton consumer, the giant manta ray (Manta birostris Wallbaum 1792), which was recorded to forage more regularly along the coastlines of native-dominated forests as compared to the surrounding coconut palm-dominated islets. Isotopic tracing of nutrients at each of the steps along this pathway demonstrates that this effect is largely driven by bird-derived nutrients (McCauley et al. 2012). This observation remains a rare example of how an invasive plant species can influence the behavior of large marine fish and demonstrates the extreme ecological distances that changes engineered by invasive species can propagate to, affecting both land and sea.

While each of these effects on consumers is itself noteworthy, the most compelling demonstration of the strong and pervasive effects of increased palm dominance on consumer communities comes from isotopic analysis of food chain length across islets. In this work, isotopes are used to estimate trophic position of a range of consumers, from herbivores to top predators, after correcting for site-level differences in isotopic baseline. It was found that higher-level consumers occupy relatively higher trophic positions when found on native forest-dominated islets than on palm-dominated islets (Fig 3). The magnitude of this effect is larger for carnivores than for herbivores, suggesting that small changes in trophic dynamics accumulate up the food chain, driven by the aggregated effects of higher levels of reduced productivity at the bottom of the food chain (Young et al. 2013a). In aggregate, these small changes in trophic positions, likely the result of subtle changes in foraging ecology and behavior, lead to strong changes in overall food web
Indeed, there is a strong negative relationship between coconut palm dominance and food chain length (Fig 4), with food webs in palm-dominated islands (>75% coconut palm basal area) lacking more than two trophic levels represented on native-dominated islets.

**Abiotic feedbacks**

There are several examples of invasive species that alter abiotic or biotic conditions in ways that then facilitate their own further encroachment, or the further establishment of other invasive species. For example, the invasion of ice plant (*Mesembryanthemum crystallinum* Linnaeus 1753) on Santa Barbara Island accumulates salt, which makes an osmotic environment intolerable to native plants but highly suited to the ice plant as well as to other weedy invasives (Vivrette and Muller 1977). In a similar fashion, *Morella faya* Wilbur 1994, an introduced nitrogen-fixing leguminous shrub, alters soils in a manner that fosters further invasion by *M. faya*, as well as by the introduced strawberry guava (*Vitousek* 1986; Hughes et al. 1991), introduced earthworms (Aplet 1990), and Japanese white-eye birds (*Vitousek* and *Walker* 1989). These positive feedback loops not only facilitate the advance of invasion (the controversial “invasion meltdown” hypothesis; O’Dowd et al. 2003), but also make it much more likely to see entire ecosystem state changes following invasion (*O’Dowd* et al. 2003; Simberloff 2006)

We found evidence for several such feedback loops in the Palmyra system. First, and perhaps most critically, the effects of the loss of bird-derived nutrients in palm-
dominated sites appeared to disproportionately impact recruitment and growth of native plants, creating a feedback loop that entrenches persistence of the invasive. This feedback likely partially explains the tendency for local monodominance by coconut palms and also facilitates their further spread. The disproportionate impact of reduced guano input on native species was initially demonstrated through nursery greenhouse fertilization experiments, which grew seedlings of coconut palms and the three most common native species (*P. grandis, S. taccada*, and *H. foertherianum*) in controlled environments, that varied only in the amount of nutrient inputs they received; these nutrient levels simulated low, moderate, and high densities of birds at Palmyra. The addition of nutrients had much stronger effects on growth, nutrient concentration, and chlorophyll levels for common native trees than for coconut palms. All three native trees showed substantial differences in above ground biomass (at least double over the first three months of growth) as well as strong increases in chlorophyll concentration when exposed to fertilization rates simulating high or moderate as compared to low densities of birds (Young et al. 2011). In contrast, coconut palms showed no differences across treatments in either above ground biomass or chlorophyll concentration, even after 180 days of treatment (Young et al. 2011).

The greenhouse results were paralleled by results in the field, where outplanted seedlings of native species grew approximately three times larger over the course of one year in native-dominated forests than in palm-dominated forests. In contrast, coconut palm seedlings experienced only a very small increase in growth rates
When grown in more nutrient rich native-dominated forests as compared with growth in palm-dominated forests (Young et al. 2013b). Cumulatively, these results suggest a feedback loop where the nutrient depletions that occur as a result of coconut palm establishment have a disproportionately negative effect on native plants, giving a competitive advantage to coconut palm seedlings that are comparatively tolerant to low nutrient conditions. In addition to the effects the invasive coconut palms have on nutrients, they also seem to affect water availability. Coconut palms use a considerable amount of water and appear to be strong competitors for water (Jayasekara and Jayasekara 1993; Roupsard et al. 2006; Gomes and Prado 2007; Krauss et al. 2015). Accordingly, native plants experience significantly reduced water use when in proximity to coconut palms, likely due to aggressive use of water by coconut palms. Pisonia grandis appeared to exhibit some stress from this water competition, as demonstrated by 46-63% reductions in sap flow when growing near coconut palms, likely due to aggressive use of water by coconut palms. This may be particularly important to native tree survivorship in dry years, when drought conditions are prevalent.
In addition to the abiotic feedback loops, there appear to be at least two biotic feedback loops that occur: 1) via increases in patterns of seed and seedling predation on native species in palm-dominated forests and 2) via increases in litterfall damage rates to seedlings in palm-dominated forests. Based on camera trap surveys of seed predation events, most seed and seedling mortality on Palmyra is driven by highly abundant land crab species. This is common in many tropical and coastal ecosystems, where consumption from land crabs can be critical in structuring forest communities (Green et al. 1997; Lindquist and Carroll 2004; Lindquist et al. 2009). These crabs are highly effective seed and seedling predators.

In seed predation experiments, more than 95% of seeds from the common small-seeded native trees (*H. foertherianum*, *P. grandis*, and *S. sericea*) were predated within one month of placement (Young et al. 2013b). However, these already high rates of seed predation increased dramatically—to upwards of 99%—in palm-dominated forests. Consequently, the native seeds placed in unprotected locations in invasive coconut palm forests never successfully germinated, while germination was repeatedly observed (albeit at low rates) in native forests. Similarly, for unprotected transplanted seedlings of these common native tree species, less than 5% survived in coconut palm-dominated forests within one year while 36% survived through this first year in native forests. In contrast, coconut seeds and seedlings suffered very low total rates of seed (0-5% within one month) and seedling (4 to 13% within 1 year) predation in either forest type; and the rates were actually significantly reduced in coconut palm-dominated as compared to native-dominated forests (Young et al. 2013b). The net effect is that native plants
experience dramatically reduced rates of growth (leaf area per plant; Fig 5) and establishment in native forests, while coconut palms experience little negative consequences (Fig 5) and, indeed, likely perform even better when in palm-dominated forests when both seed and seed predation effects are included. Mathematical simulations suggest this feedback mechanism alone is sufficient to drive near total replacement of most native species, and can create the monodominant structure of coconut palms that is empirically observed at Palmyra and elsewhere (Young et al. 2013b). Given the slow rates of natural encroachment of coconut palms, this in turn, leads to a patchy landscapes with higher than anticipated levels of beta diversity, and low levels of alpha diversity (Young et al. 2013b).

The high dominance of coconut palm also provides a second source of elevated seedling mortality via high rates of seedling damage caused by heavy falling palm fronds and palm nuts (e.g. mean nut size >1.5 kg). Litterfall inputs were measured to be 5 times higher in coconut forests (mean 2.3 kg per month) than in native forests (mean 0.4 kg per month) (Young et al. 2014). Using artificial seedlings made of wire and straws to record damage rates, we found that severe damage rates to seedlings were more than three times higher in palm forests (16.1%) than in native forests (4.9%) (Young et al. 2014). Tree species are known to vary in their ability to resist and recover from litterfall damage (Gilman et al. 2003; Peters et al. 2004). Given the much larger and stronger stem size of C. nucifera as compared to that of other native species, we expect that, as in other palm forests (Gillman et al. 2003;
Peters et al. 2004) this dramatic increase in litterfall damage will disproportionately impact the survivorship and recruitment of smaller-stemmed and thus more vulnerable native species. Invasive palm litterfall damage is yet another important factor that contributes to the near total lack of native species recruitment underneath coconut palm canopies.

Conclusion

The Palmyra system, with its relatively long-term historical time period and replicated islets, offers important insight into the diverse pathways and complex dynamics by which invasive species affect ecosystem structure and function across entire landscapes. While knowledge of the impacts on invasive species on ecosystems has grown rapidly in the past several decades (Ehrenfeld 2010; Vila et al. 2011; Pysek et al. 2012; Gaertner et al. 2014), there are still gaps in the understanding of such impacts and their underlying driving factors. The Palmyra palm example addresses a few, including: 1) how invasive species lead to regime shifts, 2) the long time frame needed to fully understand invasive species impacts, and 3) novel and interacting higher-order mechanisms and effects of invasion.

Coconut palms have transformed the forest community, altered nutrient profiles, changed the abundance and ecology of consumers across trophic levels, and altered the magnitude and direction of species interactions. Coconut palms act as many ecosystem engineers (sensu Jones et al. 1994) do; by creating a habitat more suitable to their survival than the survival of other species (Cuddington and
Hastings 2004). Through these effects, they perpetuate and extend their dominance throughout Palmyra, a trend that is likely to have occurred or be occurring in many island systems where coconut palms are invasive across the tropics. As these palms may have created alternative stable states in invaded systems it is not clear if eradication would lead to restoration of original forests; more research is thus needed to inform management of these sites. However, any new plantings of coconut palms in other sites, particularly where seabird colonies occur, should be carefully considered in light of the risk of strong ecological ramifications, and managers in lightly invaded sites should strongly consider removal of these palms before invasion proceeds further. Notably, the case of the coconut palm expansion is now being mirrored (and overshadowed) by the recent global proliferation of the African oil palm (*Elaeis guineensis*), now being cultivated on between 13 and 16 million ha worldwide (Fitzherbert et al. 2008). Impacts of coconut palm expansion may serve as an “ecological harbinger” of some effects now occurring with the rapid expansion of oil palm.

As an historical invasion, coconut palms have been present and invasive on the Palmyra landscape long enough (likely present for at least 1,500 years, and actively expanding for at least the last 50-150 years) to result in process shifts that play out over both short and long ecological time spans. For instance, while the interruption of seabird nutrient inputs at small scales was likely relatively abrupt, the associated trickle down effects to other consumers and to island-scale nutrient budgets very likely has taken many years to develop. This case study thus suggests that modern
invasions may lead to large-scale changes that will last and extend across landscapes and seascapes.

The Palmyra system also highlights the rich and diverse mechanisms by which impacts occur, including several relatively novel mechanisms. While some ecosystem impacts of invasive species have been fairly robustly documented (including a tendency to cause nutrient enrichment and change nutrient cycling [Ehrenfeld 2010]), the Palmyra example illustrates that structural changes (forest canopy, litter, and understory in this case) are important impacts that can lead to large-scale change. And while coconut palm invasion does ultimately lead to substantial changes in nutrient regimes and cycling, it is through different feedbacks than are commonly cited (usually nitrogen fixation, litter, and soil biota [Gaertner et al. 2014]). Additionally, while some studies highlight the indirect effects of invasive species, these have generally occurred via top-down forces and trophic cascades [Estes and Palmisano 1974; Croll et al. 2005]. The coconut palm example illustrates that these indirect effects can have complex pathways dictated by bottom-up as well as top-down processes. Future studies should, then, focus on broadening the definition of ecosystem-level impacts, and be more ambitious in the search for tracing the diverse pathways through which this change can be engineered. Undertaking this effort will help bring to light the true ecological extent by which invasive species influence ecosystems, the deep temporal reach by which this change becomes manifest, and the complex biotic and abiotic interrelationships that give rise to these effects.
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Figure Captions:

Fig 1: All work was conducted at Palmyra atoll (A), within the different islets, which vary strongly in dominance by coconut palms, and are used as replicates. The native community of trees, dominated by *P. grandis* and *H. foertherianum* (B), have been replaced in many areas with nearly monodominant stands of coconut palms (C). These palm forests are structurally transformed, with higher stem density and total basal area, more standing litter, and dense seedling canopies composed almost entirely of coconut palms. Many islets are now nearly completely dominated by coconut palms (D). Photo credits: Kydd Pollock (A) and Hillary Young (C-E)

Fig 2: A change from low (<25%) to high (>75%) dominance of coconut palms (as proportion of basal area) transforms plant communities (Panel A), causing increases in number seedlings (SEED), stem density (SD), total standing basal area (BA), standing litter (LIT), density of herbaceous cover (HERB), and strong declines in plant diversity. Through strong negative impacts on birds (BIRD, panel C), this causes radical changes in ecosystem nutrient dynamics (Panel B) including strong declines in soil nitrate (NO3-), ammonium (NH4+), phosphate (PO4-), bulk nitrogen, soil organic matter (OM), aluminum (Al), boron (B), potassium (K), and silica (Si), while modestly increasing soil pH (pH) and molybdenum (Mo). These changes in soil nutrients, particularly nitrogen, affect plant nutrients, including percent foliar nitrogen (%N fol) as well as nitrogen in runoff (%N run). The combination of physically changed plant communities and chemically changed soil parameters
alters abundance of a wide range of consumers (Panel C) including zooplankton (ZOO), manta rays (MR), parasitic nematodes (NEM), isopods (ISO), ants (FORM), and amphipods (AMPH). It also impacts a range of other consumer parameters such as body size of two species of geckos (LL-S and LNs-S) and one abundant spider species (SPID-S) and the diet diversity of one gecko species (LL-diet). These changes cumulatively cause a suite of negative feedbacks to native plants (Panel D), including via physical processes such as increased litterfall (LF), and biological processes such as increased seed predation (SP-N) and seedling (SE-N) predation on natives (SP-N), but decreased seed and seedling predation on coconut palms (SP-C and SE-C), decreased growth rates (GR) of native species, and increased water stress as indicated by sap flow (SF). All differences shown here are significant and are discussed in text in more detail. Specific references for each response are provided in SI 1.

Fig 3: Isotopes of nitrogen in soils (unfilled squares) and plants (unfilled diamonds) indicate that the sources of nitrogen in native-dominated islets (red) are different than those in palm- (Cocos nucifera) dominated forests (blue), likely driven by the higher relative importance of high-trophic level guano-derived nutrients in native forests. The difference between consumer nitrogen isotopes across forest types is much stronger than that seen in plants and soils, indicating not only a different source of nitrogen, but differences in feeding ecology of consumers, or differences in overall food web structure on native-dominated islets. The four consumers shown are some of the most abundant top predators and include two species of geckos –
Fig 4: Increases in coconut palms (*C. nucifera*) affect abundance, diversity and body size of many consumer groups, largely through their effects on site productivity. These effects trickle up to drive changes in entire food web structure, reflected in a significant decline in total food chain length with coconut palm abundance.

Fig 5: Increased rates of herbivory, litterfall damage, and seedling predation, combined with lower rates of soil nutrients in palm-dominated forests combine to cause greatly reduced survivorship and growth (leaf area per plant) for transplanted seedlings, after two years, for native *Pisonia grandis* (A). In contrast, there is no significant effect of forest type on growth or survivorship of transplanted coconut palms across forest types (B) (from Young et al. 2013). Combined with differential seed predation for native versus coconut palm plants in palm-dominated forests, this creates a negative feedback loop making it difficult for native plants to persist in palm-dominated forests.
REFERENCES CITED


are associated with coconut (*Cocos nucifera*) habitat at Palmyra Atoll.


Fig 1: All work was conducted at Palmyra atoll (A), in the central Pacific Ocean (B), within the different islets, which vary strongly in dominance by coconut palms, and are used as replicates. The native community of trees, dominated by P. grandis and H. argentea (C), have been replaced in many areas with nearly monodominant stands of coconut palms (D). These palm forests are structurally transformed, with higher stem density and total basal area, more standing litter, and dense seedling canopies composed almost entirely of coconut palms. Many islets are now nearly completely dominated by coconut palms (E).

Photo credits: Kydd Pollock (A) and Hillary Young (C-E)
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Increases in coconut palms (C. nucifera) affect abundance, diversity and body size of many consumer groups, largely through their effects on site productivity. These effects trickle up to drive changes in entire food web structure, reflected in a significant decline in total food chain length with coconut palm abundance.
### Pisonia grandis

- **Native**
- **Palm forest**

### Cocos nucifera

- **Native**
- **Palm forest**

**Leaf Area (cm²)**

**Days after planting**