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REVIEW

Cascading community and ecosystem consequences of introduced coconut palms (*Cocos nucifera*) in tropical islands[1]

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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.) 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 2.7–11.5 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.

Key words: invasive species, introduced species, historical introductions, ecological cascades, bottom-up processes, ecological harbingers, spatial subsidies, *Cocos nucifera*.

Résumé : Les invasions biologiques constituent une forme omniprésente et dominante de perturbation humaine. Les occasions d'en évaluer les effets de cascade indirects à long terme et souvent lents à l'échelle de la communauté et de l'écosystème sont toutefois rares. Nous présentons une synthèse des connaissances collectives découlant de 10 années d'étude sur l'influence de l'introduction historique profonde de cocotiers communs (*Cocos nucifera* L.) sur une série d'îlots dans l'atoll Palmyra. Nous constatons que, par l'entremise d'un ensemble de voies, cet arbre entraîne un changement presque complet de l'état de l'écosystème quand il devient dominant. Les conditions abiotiques sont transformées, les concentrations des principaux éléments nutritifs du sol étant de 2,7 à 11,5 fois plus faibles et le stress hydrique était 15 % plus grand dans les forêts dominées par les cocotiers que dans les forêts naturelles. Les communautés fauniques sont aussi considérablement modifiées, non seulement sur le plan de la composition, mais également du comportement, de la taille du corps et de l'embonpoint. Les interactions biotiques, y compris les taux d'herbivorie, la palatabilité et la granivorie, sont également modifiées. Combinés, ces changements transforment les réseaux trophiques, produisant des chaînes alimentaires considérablement raccourcies et simplifiées dans les écosystèmes envahis. Bon nombre de ces changements semblent créer des boucles de rétroaction lentes qui favorisent le cocotier au détriment d'espèces indigènes. Étant donné le caractère répandu de cette introduction historique, de nombreuses régions insulaires et côtières des océans tropicaux pourraient être transformées de manière semblable. [Traduit par la Rédaction]

Mots-clés : espèce envahissante, espèce introduite, introductions historiques, cascades écologiques, processus ascendants, présage écologique, apports spatiaux, *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) scales

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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 (multidecadal) species introductions thus provide an interesting opportunity to examine effects of invasions over larger temporal and 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 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, although 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 on Hawai‘i (between 300 and 1300 CE) appeared to drive an increase in invasive species colonizations from background rates of 1 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 Hawai‘i (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 to catch the slow-acting, long-term, and landscape-scale effects of invasive species. Although 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.) (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 1800s 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 nontimber 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 because, 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 10-year case study of the many cascading impacts of the historical invasion of coconut palms in the tropical Pacific, illustrating effects at both 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 (05°53′N, 162°05′W), 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 (Figs. 1A–1E). 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 5.29×10^2 to 2.60×10^6 m² and span an area of 20 km². The majority of the nutrients in this, as in other coral-derived ecosystems (Schmidt et al. 2004; Young et al. 2010*a*), come from seabird-guano fertilization. Palmyra receives, on average, 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 1940s, 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 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

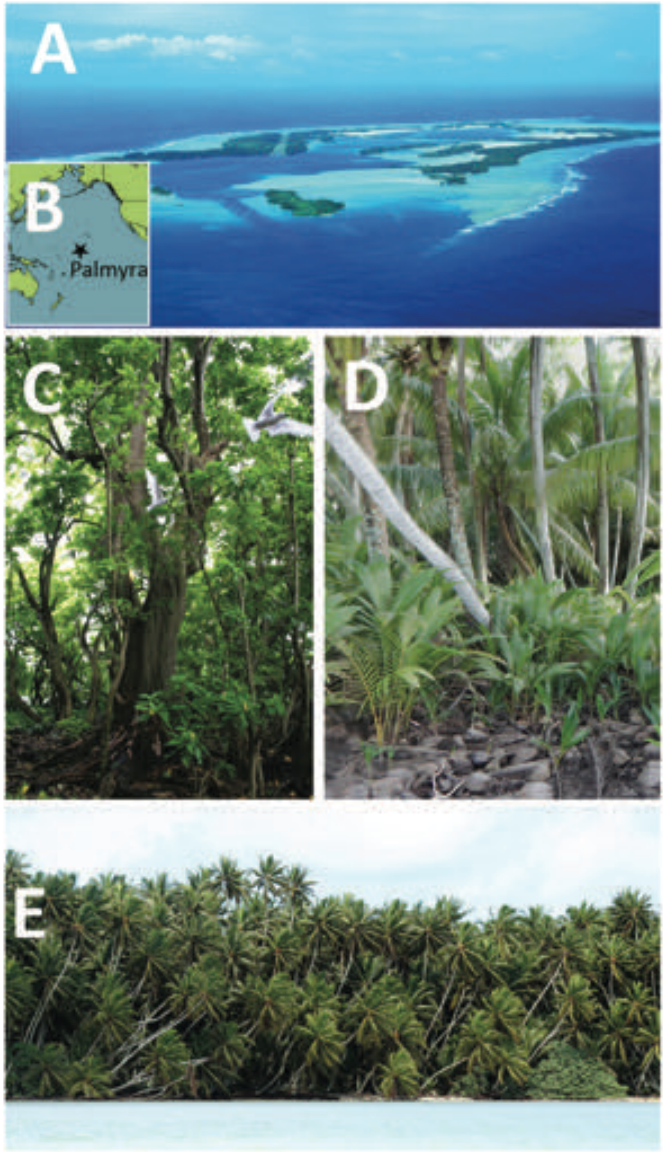


Fig. 1. All work was conducted at Palmyra Atoll (A), within the different islets, which vary strongly in dominance by coconut palms (*Cocos nucifera*), and are used as replicates. The native community of trees, dominated by grand devil's-claws (*Pisonia grandis*) and *Heliotropium foertherianum* (B), 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). Photos from K. Pollock (A) and H.S. Young (C–E). Figure appears in color on the Web.

Black Noddies (*Anous minutus* F. Boie, 1844; ~6500 individuals), as well as smaller populations of White Terns (*Gygis alba* (Sparrman, 1786)), Greater Frigatebirds (*Fregata minor* (Gmelin, 1789)), Lesser Frigatebirds (*Fregata ariel* (G.R. Gray, 1845)), Brown Noddies (*Anous stolidus* (L., 1758)), Masked Boobies (*Sula dactylatra* Lesson, 1831), Brown Boobies (*Sula leucogaster* (Boddaert, 1783)), White-tailed Tropicbirds (*Phaethon lepturus* Daudin, 1802), and Red-tailed Tropicbirds (*Phaethon 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, mainly consisting 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, beach naupaka (*Scaevola taccada* (Gaertn.) Roxb.), grand devil's-claws (*Pisonia grandis* R. Br.), thatch screwpine (*Pandanus tectorius* Parkinson ex Zucc.), and India almond (*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 (Hawai'i birdnest fern (*Asplenium nidus* L.) and monarch fern (*Phymatosorus scolopendria* (Burm. f.) Pic. Serm.)).

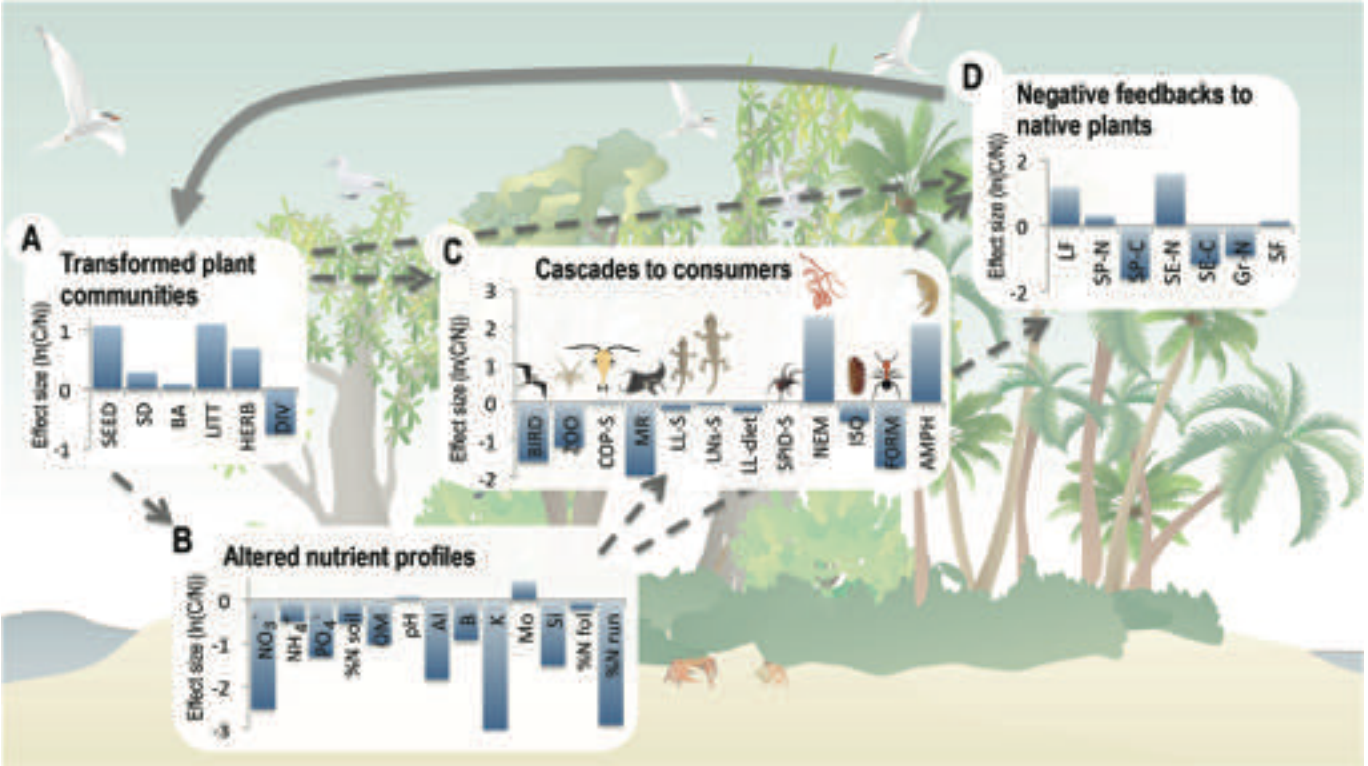
In terms of macroscopic consumers, Palmyra is thought to support approximately 120 species of insect and spider arthropods; >85% are presumed to be introduced to the atoll (Handler et al. 2007). The only vertebrate consumers on the island are three species of gecko: two native species (Mourning Gecko (*Lepidodactylus lugubris* (Duméril and Bibron, 1836)) and Indo-Pacific Gecko (species of the genus *Lepidodactylus* Fitzinger, 1843)) that reproduce via parthenogenesis and one introduced species (Common House Gecko (*Hemidactylus frenatus* Schlegel, 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 1500 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. The population of coconut palms in the mid-1800s was documented at approximately 4000 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. 2010*a*) 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. 2010*b*). Palm-dominated forests also have much lower plant species diversity not only in the canopy (Shannon index of 0.57 in native forests versus 0.44 in palm forests) but, even more pronounced, in the understory (0.57 versus 0.27, respectively) (Young et al. 2010*b*). 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

Fig. 2. A change from low (<25%) to high (>75%) dominance of coconut palms (*Cocos nucifera*) (as a 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 (LITT), density of herbaceous cover (HERB), and strong declines in plant diversity (DIV). 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 (NO_3^-), ammonium (NH_4^+), phosphate (PO_4^-), bulk nitrogen, soil organic matter (OM), aluminum (Al), boron (B), potassium (K), and silica (Si), while modestly increasing soil pH (pH) and molibdinum (Mo). These changes in soil nutrients, particularly nitrogen, affect plant nutrients, including percent foliar nitrogen (%N fol) and 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 the text in more detail. Specific references for each response are provided in the Supplementary material.[2]



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 forests compared with native forests (Young et al. 2010*b*).

The seabird connection

Many tropical seabird species, including two of the dominant and resident species in this system (i.e., Red-footed Booby and Black Noddy) are tree nesting. Atoll-wide bird surveys conducted in 2006 along both 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 6000 birds surveyed were observed on coconut palms, and then, largely only roosting, not nesting. For the large-bodied and hyperabundant Red-footed Booby (>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. 2010*a*; Figs. 2A–2D). This variation in bird abundance led to strong and pronounced changes in nutrient input across forest types. In the typical native forests, based on estimates of bird biomass and guano production rates, this equates to between 231 and 635 kg $N \cdot ha^{-1} \cdot year^{-1}$ and between 42 and 105 kg $P \cdot ha^{-1} \cdot year^{-1}$ (Young et al. 2010*a*). 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 palm-dominated sites (those with >75% coconut biomass) and native-dominated sites (those with <25% coconut biomass) showed plant-available nutrients were 40%–82% lower in palm forests (NO_3^-: 82%; PO_4^-: 73%; NH_4^+: 40%) (Young et al. 2010*a*). 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 (Mo showed significant increases in palm forests) (Figs. 2A–2D)

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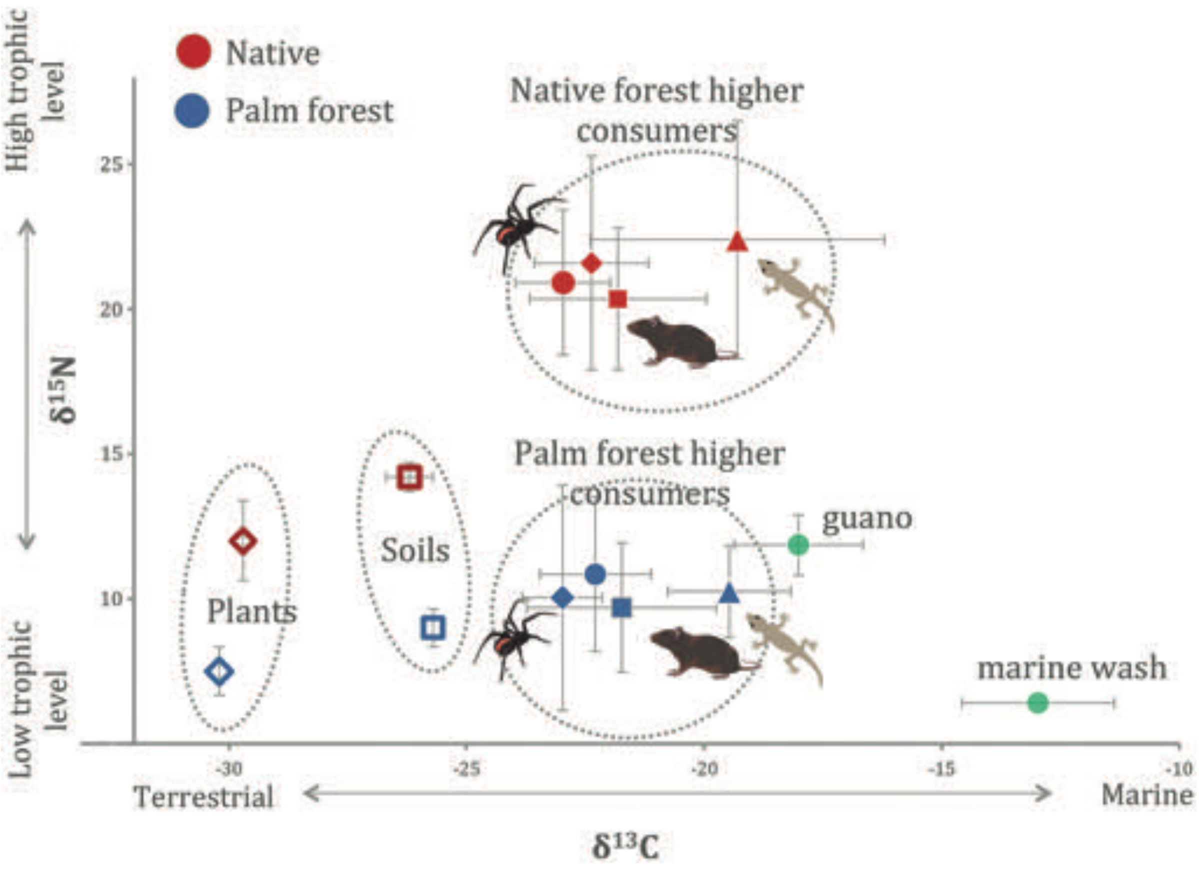
[2] Supplementary material is available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2016-0107.

Fig. 3. Isotopes of nitrogen in soils (open squares) and plants (open diamonds) indicate that the sources of nitrogen in native-dominated islets (red) are different than those in coconut 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 (Mourning Gecko, *Lepidodactylus lugubris* (triangles); Indo-Pacific Gecko, *Lepidodactylus* ns (circles)), the Huntsman spider (*Heteropoda venatoria*) (diamonds), and the roof rat (*Rattus rattus*) (squares; now eradicated from the atoll).



(Young et al. 2010*b*). 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 owing to their high trophic position. Accordingly, soils in palm-dominated islets have substantially lower values of $\delta^{15}N$ (Fig. 3).

Although 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 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. 2010*a*). 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 nitrogen (20% and 15%, respectively) when they occur in high-density coconut palm forests compared with native forests (Young et al. 2010*a*). 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. As 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 crowsfoot grass (*Eleusine indica* (L.) Gaertn.)) 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 (g foliar $N \cdot m^{-2} \cdot month^{-1}$) in controlled conditions could be predicted based solely on the abundance of coconut palms in the system where soils were sampled (Young et al. 2013*a*). 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. 2013*a*).

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 systems dominated by palm forests. Rates of herbivory (within three native species) in palm-dominated forests were 3–4 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. 2010*a*). Herbivores prefer native species over palms, because coconut palms have notably unpalatable leaf tissue, with low specific leaf area, low nutrient content, and very high carbon and silica content compared with all of the dominant native plant species on Palmyra (Marschner 1995; Young et al. 2011). Combined with reduced nutrient levels within native species in palm-dominated forests, palm forests are thus likely to be of low value to many herbivores (Young et al. 2010*a*).

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 not surprising 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., parasites in rat stomachs 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 that are 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 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, whereas 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 ($R^2 = 0.18$, $P = 0.07$). However, other insect taxa (species of the genus *Dysmicoccus* Ferris, 1950 (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. 2013*a*).

These changes in abundance and composition of prey also trickle up to impact predator communities. Among the most abundant predator groups (and some of the few terrestrial vertebrates at Palmyra) are two species of geckos from the genus *Lepidodactylus* Fitzinger, 1843. 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).

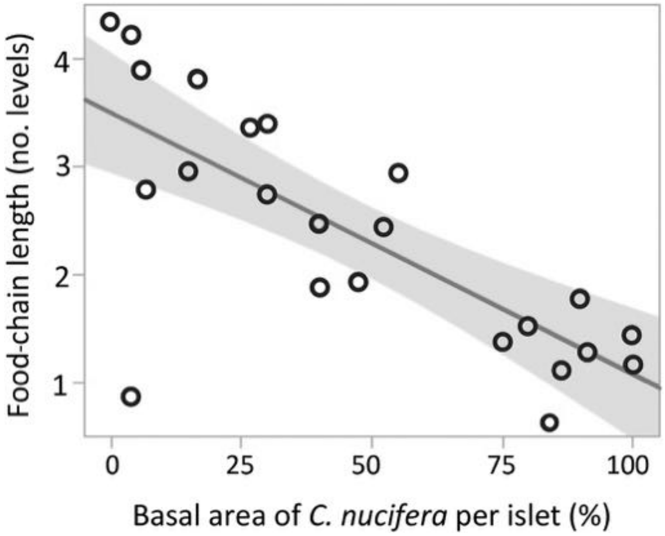
Beyond these dietary changes, both gecko species showed significant reductions (17%–19%) in body condition (mass per snout–vent length; $\mathrm{mg \cdot mm^{-1}}$) in palm-dominated forests compared with native-dominated forests. In this case, analysis suggested that these body-condition effects were 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 (the Huntsman spider, *Heteropoda venatoria* (L., 1767)), also had statistically larger body sizes on more productive islets (Briggs et al. 2012; Young et al. 2013*a*). 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 U.S. military occupation until 2011 when an atoll-wide eradication effort was completed, the roof rat (*Rattus rattus* (L., 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. Although 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 worms per rat 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 of the free-living stages of 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-dominated forests compared with palm-dominated forests. Growth rates of phytoplankton in surrounding waters, measured using moored, in-situ, phytoplankton growth chambers along the coast of islets dominated by coconut palms and native forests, 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. In turn, this affected the foraging ecology of at least one large obligate plankton consumer, the giant manta ray (*Manta birostris* (Walbaum, 1792)), that was recorded to forage more regularly along the coastlines of native-dominated forests compared with the surrounding 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.

Although 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 cor-

Fig. 4. Increases in coconut palms (*Cocos 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.



recting for site-level differences in isotopic baseline. It was found that higher level consumers occupy relatively higher trophic positions when found on islets dominated by native forests than on islets dominated by coconut palms (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. 2013*a*). 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 structure. 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 the ice plant (*Mesembryanthemum crystallinum* L.) 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 invasive plants (Vivrette and Muller 1977). In a similar fashion, the firetree (*Morella faya* (Aiton) Wilbur), 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 (*Psidium cattleyanum* Sabine) (Vitousek 1986; Hughes et al. 1991), introduced earthworms (Aplet 1990), and Japanese White-eyes (*Zosterops japonicus* Temminck and Schlegel, 1845) (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 species. 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 aboveground biomass (at least double over the first 3 months of growth) and strong increases in chlorophyll concentration when exposed to fertilization rates simulating high or moderate density of birds compared with low density of birds (Young et al. 2011). In contrast, coconut palms showed no differences across treatments in either aboveground biomass or chlorophyll concentration, even after 180 days of treatment (Young et al. 2011).

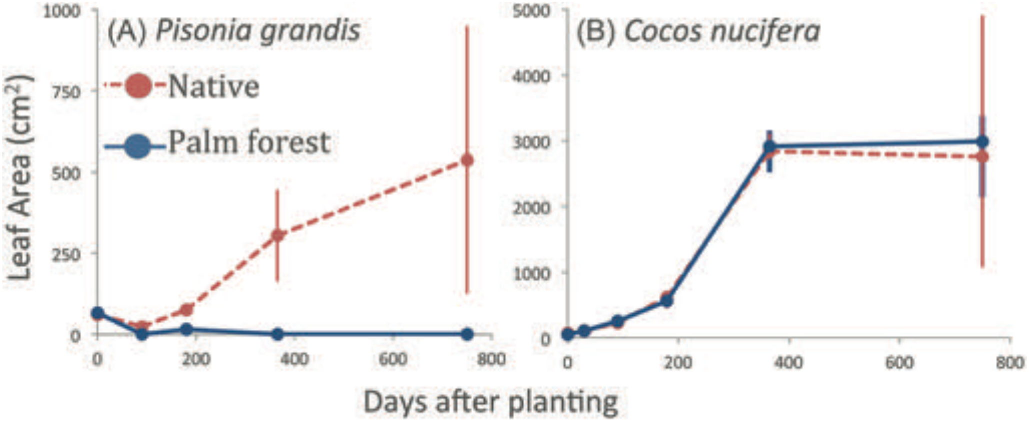
The greenhouse results were paralleled by results in the field, where outplanted seedlings of native species grew approximately three times larger over the course of 1 year in native-dominated forests than in palm-dominated forests. In contrast, coconut palm seedlings experienced only a very small increase in growth rates (<10%) when grown in more nutrient-rich native-dominated forests compared with growth in palm-dominated forests (Young et al. 2013*b*). 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 of 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, compared with growing in native-dominated stands (Krauss et al. 2015). This may be particularly important to the survivorship of native trees in dry years, when drought may significantly stress native trees (Krauss et al. 2015). As with negative effects of coconut palms on nutrients, this thus appears likely to create a regime whereby palm encroachment changes abiotic conditions that disproportionately and negatively impact native plants.

Biotic feedbacks

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, >95% of seeds from the common small-seeded native trees (*H. foertherianum*, *P. grandis*, and *S. sericea*) were predated within 1 month of placement

Fig. 5. Increased rates of herbivory, litterfall damage, and seedling predation, combined with lower rates of soil nutrients in coconut palm (*Cocos nucifera*) dominated forests, cause greatly reduced survivorship and growth (leaf area per plant) for transplanted seedlings, after 2 years, of native grand devil's-claws (*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 that makes it difficult for native plants to persist in palm-dominated forests. Figure appears in color on the Web.



(Young et al. 2013*b*). 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, whereas germination was repeatedly observed (albeit at low rates) in native forests. Similarly, for unprotected transplanted seedlings of these common native tree species, <5% survived in palm-dominated forests within 1 year, whereas 36% survived through this 1st year in native forests. In contrast, coconut seeds and seedlings suffered very low total rates of seed (0%–5% within 1 month) and seedling (4%–13% within 1 year) predations in either forest type; the rates were actually significantly reduced in palm-dominated forests compared with native-dominated forests (Young et al. 2013*b*). The net effect is that native plants experience dramatically reduced rates of growth (leaf area per plant; Fig. 5A) and establishment in native forests, whereas coconut palms experience little negative consequences (Fig. 5B) and, indeed, likely perform even better 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. 2013*b*). Given the slow rates of natural encroachment of coconut palms, this in turn leads to patchy landscapes with higher than anticipated levels of beta diversity and low levels of alpha diversity (Young et al. 2013*b*).

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 five times higher in coconut forests (mean 2.3 kg·month^{-1}) than in native forests (mean 0.4 kg·month^{-1}) (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 >3 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 (Gillman et al. 2003; Peters et al. 2004). Given the much larger and stronger stem size of *C. nucifera* compared with 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. Although knowledge of the impacts on invasive species on ecosystems has grown rapidly in the past several decades (Ehrenfeld 2010; Vila et al. 2011; Pyšek 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 (*i*) how invasive species lead to regime shifts, (*ii*) the long time frame needed to fully understand the impacts of invasive species, and (*iii*) 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 do (sensu Jones et al. 1994), 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 species across the tropics. Because these palms may have created alternative stable states in invaded systems, it is not clear if eradication would lead to restoration of original forests; thus, more research is 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* Jacq.), now being cultivated on 13–16 million hectares 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 1500 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, although 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. Thus, this case study 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. Although 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 which can lead to large-scale change. And although 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, although 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 and 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 inter-relationships that give rise to these effects.

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