1 # Cascading community and ecosystem

2 # consequences of introduced palms in

3 # tropical islands*

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26

27 ABSTRACT

28

29 Biological invasions are a pervasive and dominant form of anthropogenic

30 disturbance. However, we seldom have the opportunity to evaluate the long-term,

31 indirect, and often slow-moving cascading effects of invasions at the community and

32 ecosystem scale. Here we synthesize the collective knowledge from 10 years of

33 study on the influence of the deep historical introduction of coconut palms (*Cocos*

34 *nucifera* L., 1753) across a series of islets at Palmyra Atoll. Through a suite of

35 pathways, we find this palm drives near-complete ecosystem state change when it

36 becomes dominant. Abiotic conditions are transformed with major soil nutrients 2.7

37 to 11.5 times lower, and water stress 15% elevated in palm-dominated forests,

38 compared with native forest. Faunal communities are likewise dramatically altered,

39 not only in composition but also in behavior, body size, and body condition. Biotic

40 interactions, including herbivory rates, palatability, and seed predation are likewise

41 changed. Cumulatively, these changes transform food webs, leading to dramatically

42 shortened and simplified food chains in invaded ecosystems. Many of these changes

43 appear to create slow-acting feedback loops that favor the palm at the expense of

44 native species. Given the widespread nature of this historical introduction, many

45 island and coastal regions of tropical oceans may be similarly transformed.

46

49

50

51   INTRODUCTION

52   Biological invasions are considered to be one of the most influential drivers of global

53   change (Tylianakis et al. 2008). Building on a deep history of invasive species

54   research (Elton 1958) we have an increasingly well-developed understanding of

55   how invasive species can shape different properties of ecosystems (Ehrenfeld 2010;

56   Vilà et al. 2011; Gaertner et al. 2014). Yet, this work, often by necessity, focuses on

57   relatively short-term effects that are relevant to most recent invasions, and thus on

58   pathways that operate over relatively short time periods.   Not only does this limit

59   the type of pathways that can be observed, but it may tend to underplay the

60   magnitude of effects. For instance, much of the debate about the extent to which

61   invasive species tend to cause extinction and declines in diversity (Gurevitch and

62   Padilla 2004; Bellard et al. 2016) are likely unresolved in part because there may

63   often be long time lags in effects following invasion, including extinction debts that

64   accrue before extinctions occur (Gilbert and Levine 2013). Indeed, the effects of

65   invasion on ecosystem processes and community structure are likely dependent on

66   both spatial (Powell et al. 2013) and temporal (Ehrenfeld 2010; Vilà et al. 2011)

67   scale of invasion, because the ecological consequences of invasion are often

68   heterogeneous, slow-occurring, and not detectable until well after impacts on

69   species and communities have occurred. Historical (multi-decadal) species

70   introductions thus provide an interesting opportunity to examine effects of

71   invasions over larger temporal as well as spatial scales.

72

73   Humans have transported non-native plants and animals with them to colonize new

74   places for thousands of years. These include both accidental introductions and the

75   intentional introduction of crop and food species (Kowarik 2003; Hulme 2009).

76   Indeed, many species that are now considered invasive were originally introduced

77   intentionally for human benefit (Vitousek et al. 1997; Mack et al. 2000; Thuiller et al.

78   2006; Tylianakis et al. 2008; Simberloff et al. 2013). In the United States alone, it is

79   estimated that 85% of the 235 invasive woody plants were intentionally introduced

80   (Reichard and White 2001). However, while the transport of new and potentially

81   invasive species to new habitats is not a new phenomenon, the rate of introduction

82   of invasive species has accelerated in modern times. For example, Polynesian arrival

83   Hawaii (between 300 and 1300 CE), appeared to drive an increase invasive species

84   colonizations increased from background rates of one species every 50,000 years to

85   3-4 species per century. In comparison, in the last few decades, it is estimated that

86   ~20 species have been introduced each year to Hawaii (Ewel et al. 1999). The

87   current high rate of global invasion poses huge biological and economic costs

88   (Pimentel et al. 2000; Hulme 2009). However, management and eradication must

89   be carefully weighed both because of the frequently large costs of implementation

90   and maintenance, and because of the potential for unintended negative

91   consequences of removal of invasive species once they have become established in

92   new systems (Zavaleta et al. 2001; Bergstrom et al. 2009).

93

94   It is thus critical to understand the extent of negative impacts of invasive species, so

95   that they can be compared with the risks and costs of management or eradication.

96   We therefore need more research exploring effects at large spatial and temporal

97   scales to not only catch abrupt and drastic state shifts (Barnosky et al. 2012; Brook

98   et al. 2013), but also the slow-acting, long-term and landscape-scale effects of

99   invasive species. Though in number they are now dwarfed by the recent global flux

100   of modern invasions, historical species introductions offer a critical opportunity to

101   fill gaps in our understanding of the impacts of invasive species.

102

103   One noteworthy historic species introduction that is now invasive in much of its

104   range is the coconut palm (*Cocos nucifera* L., 1753) (Rejmánek and Richardson

105   2013). Coconut palms are an iconic symbol of tropical coastal ecosystems

106   worldwide. Yet, this palm is thought to have originally only occurred in scattered

107   populations on islands and coastlines in the equatorial Indian and Pacific Oceans

108   (Baudouin and Lebrun 2009). Its spread was facilitated through a series of

109   introductions, likely first by Austronesian voyagers over 1500 years ago, who

110   utilized the palm for food and fiber on transoceanic journeys (Gunn et al. 2011),

111   then by early European explorers, and more recently by 19th century European

112   agricultural entrepreneurs who intensively planted coconut palms for copra

113   production. As a result, coconut palms can now be found as largely monodominant

114   forests across a wide range of tropical coastal environments (Harries 1978; Foale

115   2005). Indeed, during the boom in copra production during the 19th century,

116   coconut palm planting actively displaced hundreds of thousands of hectares of land

117   previously occupied by intact rainforests (Foale 2005). Although coconut

118   production has currently been overshadowed by other tropical crops, there are still

119   at least 12 million hectares (approximately the size of the United Kingdom) of

120   planted coconut palm distributed across nearly 90 countries in tropical regions

121   (Foale 2005). Although purposefully planted across the tropics, coconut palms are

122   considered invasive in the Pacific, Indian, and Caribbean Island regions, where

123   populations planted by Austronesian voyagers and later during the copra boom of

124   the 1800's have largely been left unmanaged in recent times (Rejmánek and

125   Richardson 2013). In some cases the positive ramifications of coconut palms for

126   humans (e.g. direct benefits from provision of non-timber forest products, indirect

127   benefits from coast line stabilization from these saline tolerant plants) may

128   outweigh the negative ecological ramifications, but to date the ecological costs have

129   not been well considered.

130

131   Like many intentional introductions that subsequently become invasive, coconut

132   palms are successful invaders in large part because of human propagation. Human

133   introduction and care reduces environmental stochasticity typically faced by

134   founder populations that might otherwise go extinct (Mack 2000), and also allows

135   new species to be introduced in large enough populations for them to become self-

136   sustaining and to grow beyond the extent of their original introduction (Kowarik

137   2003; Lockwood et al. 2005). However, as we document here, coconut palms also

138   possess traits that allow them to establish dominance in invaded systems; as, like

139   other ecosystem engineers, they create habitats suitable for their own survival

140   (Jones et al. 1994; Cuddington and Hastings 2004).

141

142 Here we draw on a ten-year case study of the many cascading impacts of the

143 historical invasion of coconut palms in the tropical Pacific, illustrating effects at both

144 the community and ecosystem levels. This body of work illustrates changes at

145 several spatial scales and documents how introductions can lead to long-term and

146 often slow-acting changes. This research may thus provide important insights on

147 how diverse attributes of tropical ecosystems have been fundamentally altered by

148 this species alone, while also highlighting several novel mechanisms that may

149 operate in other invasive systems. Particularly, we emphasize how the indirect

150 effects of invasion, when played out over long time periods, have influences that

151 cascade and intertwine in complex ways, often perpetuating fundamentally altered

152 ecological regimes.

153

154 **Study System: Palmyra Atoll**

155 This research was conducted in the wet tropical forest ecosystems of Palmyra Atoll

156 (162°05' W, 5°53 N), located in the Central Tropical Pacific in the Northern Line

157 Islands. This atoll is now administered as part of the Pacific Remote Islands Marine

158 National Monument and consists of a ring of approximately 23 low-lying islets

159 composed of calcium carbonate coral rubble overlaying a limestone base (Fig 1).

160 Soils range from very nutrient poor sandy coral rubble to deep phosphate rich

161 humic soils. The islets range in size over four orders of magnitude, from 5.29×10^2

162 to 2.60×10^6 square meters and span an area of 20 square kilometers. The majority

163 of the nutrients in this, as in other coral derived ecosystems (Schmidt et al. 2004;

164 Young et al. 2010*a*), come from seabird guano fertilization. Palmyra receives an

165   average of 4.5 m of rainfall a year; combined with porous sandy soils, this means

166   that extremely high rates of nutrient input are continuously required to maintain

167   soil fertility.

168

169   There is no current human inhabitation on the atoll beyond a small research center

170   established on one islet in 2005. The only history of extensive human habitation is

171   that of a brief but intense occupation during Word War II when the atoll was used as

172   a military base. During this occupation in the 1940's, major dredging and land

173   moving activity was conducted, much of the vegetation on Palmyra was modified,

174   and several new islets were constructed. After the war the atoll was largely

175   undisturbed, although some additional planting of coconut palms did occur when it

176   was briefly run as a copra plantation after the war (Dawson 1959; Collen et al.

177   2009).

178

179   Ecologically, Palmyra is best known for its relatively pristine coral reef ecosystem,

180   but it also supports large and regionally important seabird colonies. These include

181   the world's second largest population of nesting red-footed boobies (*Sula sula* L.,

182   1776) in the world (~25,000 individuals). There are also large colonies of sooty

183   terns (*Onychoprion fuscatus* L., 1766; ~875,000 individuals), and black noddies

184   (*Anous minutus* Boie, 1844; ~6,500 individuals), as well as smaller populations of

185   white terns (*Gygis alba* Sparrman, 1786), greater and lesser frigatebirds (*Fregata*

186   *minor* Gmelin, 1789; *F. ariel* Gray, 1845), brown noddies (*Anous stolidus* L., 1758),

187   masked boobies (*Sula dactylatra* Lesson, 1831), brown boobies (*Sula leucogaster*

188   Boddaert, 1783), and white tailed and red-tailed tropicbirds (*Phaethon lepturus*

189   Daudin, 1802; and *P. rubricauda* Boddaert, 1783). All of these species are truly

190   pelagic, using the atoll only for nesting or roosting habitat. Given strong global

191   declines in pelagic seabirds (Paleczny et al. 2015), Palmyra's seabird nesting

192   grounds are a critical refuge for many of these species.

193

194   Palmyra's terrestrial communities are otherwise notably species poor, and mainly

195   consist of a few plant and arthropod consumer species as might typify a remote

196   atoll. Palmyra's canopy is dominated by seven species of plants (in order of

197   abundance *C. nucifera*, *Heliotropium foertherianum* Diane & Hilger, *Scaevola taccada*

198   (Gaertn.) Roxb., *Pisonia grandis* R. Br., *Pandanus tectorius* Parkinson, and *Terminalia*

199   *catappa* L.). Of these, only *C. nucifera* and *T. catappa* are thought to be non-native; *T.*

200   *catappa* is restricted to the one inhabited islet of Palmyra. The *P. grandis* population

201   at Palmyra is one of the largest remaining intact stands in the Pacific (Handler et al.

202   2007). The understory is likewise species poor and dominated by just two ferns,

203   *Asplenium nidus* L., and *Phymatosorus scolopendria* Burm. f.

204

205   In terms of macroscopic consumers, Palmyra is thought to support approximately

206   120 species of insect and spider arthropods; >85% are presumed to be introduced

207   to the atoll (Handler et al. 2007). The only vertebrate consumers on the island are

208   three species of gecko, two native species (*Lepidodactylus lugubris* Dumeril &

209   Bibron, 1836 and Lepidodactylus sp.) that reproduce via parthenogenesis, and one

210   introduced species (*Hemidactylus frenatus,* Dumeril & Bibron 1836) that is largely

211 confined to the single inhabited islet of Palmyra. The atoll supports populations of

212 seven species of land crabs, including a healthy population of coconut crabs (*Birgus*

213 *latro* L., 1767), the world's largest terrestrial arthropod.

214

215 The history of coconut palms on Palmyra is likely typical of many other islands in

216 the Pacific. Based on best available historical evidence, it seems likely that palms

217 were brought to the region in the last 1,500 years (Matisoo-Smith and Robins 2004;

218 Gunn et al. 2011). However, coconut palm abundance on the atoll expanded

219 considerably between 1850 and 1970 due to periodic small-scale cultivation efforts.

220 Coconut palm's population in the mid-1800's was documented at approximately

221 4,000 reproductive trees, a number that has since increased to approximately

222 53,000 reproductive adults across the atoll in 2005 (Dawson 1959; Wegmann

223 2009). Currently, more than 50% of the atoll is covered in coconut palms, with

224 canopy cover of individual islets ranging from 0% to 100% palm cover. Where it

225 occurs on the atoll, it is most often a monoculture with a dense canopy (Young et al.

226 2014). As we highlight below, current data suggest this species is likely still slowly

227 encroaching on native forests on islets where both coconut palm and native

228 vegetation types occur. There is no other native palm that occurs on the atoll.

229

230 ***Cocos nucifera* dominated communities are floristically transformed**

231 By definition, palm-dominated communities (which we have categorized as forests

232 with >75% basal area of coconut palms; Young et al. 2010*a*) have very different

233 canopy compositions than do native-dominated stands. However, the floristic

234   composition and structure of palm-dominated forests also varies in many other

235   ways. Structurally, palm-dominated forests have much higher stem density both in

236   the canopy and in the understory than do native-dominated communities (40% and

237   300% higher respectively), as well as modestly higher total standing basal area (8%

238   higher) (Young et al. 2010*b*). Palm-dominated forests also have much lower plant

239   species diversity not only in the canopy (Shannon index of 0.57 in native versus 0.44

240   in palm forests) but, even more pronounced, in the understory (0.57 versus 0.27

241   respectively) (Young et al. 2010*b*). On the forest floor, palm-dominated forests tend

242   to be covered in dense, slow-decomposing litter consisting primarily of nuts and

243   fronds, with three times more total litter cover than in native forests. Growing

244   through this litter mat, herbaceous cover, primarily composed of two common ferns,

245   *A. nidus* and *P. scolopendria,* is approximately twice as high in palm as compared to

246   native forests (Young et al. 2010*b*).

247

248   **The seabird connection**

249   Many tropical seabird species, including two of the dominant and resident species in

250   this system –red-footed booby and black noddy– are tree nesting. Atoll-wide bird

251   surveys conducted in 2006 along both the coasts and interior of the islets, showed

252   that, as a group, seabirds strongly prefer to nest in native *P. grandis* and *H.*

253   *foertherianum* trees, and have a strong aversion to the use of coconut palm forests,

254   especially for nesting habitat. Only 12% of the more than 6,000 birds surveyed were

255   observed on coconut palms, and then, largely only roosting, not nesting. For the

256   large-bodied and hyper-abundant red-footed booby (more than 75% of total bird

257   biomass), only 5% of individuals were observed on palms. At the atoll scale this

258   habitat preference led to strong variation in bird abundance based on the

259   dominance of coconut palms on a given islet (Young et al. 2010*a*; Fig 2). This

260   variation in bird abundance led to strong and pronounced changes in nutrient input

261   across forest types. In the average native forests, based on estimates of bird biomass

262   and guano production rates, this equates to between 231 and 635 kg N ha^{-1} yr^{-1}, and

263   42 and 105 kg P ha^{-1} yr^{-1} in native forests (Young et al. 2010*a*). This is a rate

264   equivalent to heavily industrialized fertilization, and represents 10-20 times more

265   nitrogen and 10-18 times more phosphorous input than comparable coconut palm

266   forests.

267

268   Not surprisingly, this difference in nutrient input leads to strong depletion in plant

269   available nutrients. Soil analyses from coconut palm-dominated sites (those with

270   >75% coconut biomass) and native-dominated sites (those with <25% coconut

271   biomass) showed plant available nutrients 40-82% lower in palm forests (NO$_3^-$:

272   82%, PO$_4^-$: 73%, and NH$_4^+$: 40%) (Young et al. 2010*a*). There are also strong and

273   significant differences in trace element abundance (Al, B, K, Mo, Si); four of these

274   five elements showed significant declines, ranging from 60 to 95% reductions in

275   palm forests (one, Mo, showed significant increases in palm forests) (Fig 2) (Young

276   et al. 2010*b*). Soil pH was slightly elevated in palm forests, likely due to the lack of

277   significant inputs of acidic bird guano, and soil organic matter was greatly decreased

278   in the palm forests. The bird origin of the differences in soil nutrients can be traced

279   using natural abundance of stable isotopes, because seabirds have a distinctively

280   high δ^{15}N signature, due to their high trophic position. Accordingly, soils in palm-

281   dominated islets have substantially lower values of δ^{15}N (Fig 3).

282

283   While the observational nature of our work in this system often makes it difficult to

284   assign causality, for soil nutrients, the artificial islets created by the military during

285   World War II provide a valuable opportunity to examine causality. All artificial islets

286   were created in a short time window from nutrient-poor coral rubble dredge

287   tailings and are of similar origin and have similar elevations and essentially no

288   topography. On artificially created islets that were subsequently colonized by

289   coconut palms, plant available soil nutrients are lower than on natural coconut

290   palm-dominated islets, suggesting that the original dredge materials have received

291   very little nutrient enrichment over the past 60 years. In contrast, artificial native

292   vegetation-dominated islets now have nutrient profiles indistinguishable from

293   natural native vegetation-dominated islets, presumably due to high levels of bird

294   inputs in both systems (Young et al. 2010*a*). Combined with the isotopic data, this

295   suggests that increased palm dominance is a cause of, rather than a response to, the

296   differences in soil nutrients across sites.

297

298   The changes in soil nutrients caused impacts on plant foliar nutrients as well. Two of

299   the three dominant tree species on the atoll (*C. nucifera* and *H. foertherianum*) show

300   significant decreases in foliar N (20% and 15% respectively) when they occur in

301   high density coconut palm forests as compared to native forests (Young et al.

302   2010*a*).   This is consistent with results from a range of other seabird-dominated

303   ecosystems, which show strong effects of changes in seabird density on both soil

304   and foliar nutrient concentrations (Mulder et al. 2011).

305

306   Not surprisingly, these dramatic changes in soil nutrients in palm forests affected

307   not only plant nutrients, but also plant growth (detailed below under abiotic

308   feedbacks) and entire site productivity. Since it is challenging to directly measure

309   field productivity in tropical forests (Clark et al. 2001; Litton et al. 2007),

310   productivity was instead estimated using greenhouse experiments that measured

311   the amount of biomass, and particularly nitrogen-rich biomass produced, for one

312   plant species found across nearly all islets (the grass *Eleusine indica* (L.) Gaertn.,

313   1788) from soils taken from islets with various densities of palm invasion. These

314   experiments showed that 10% of variation in total biomass and 50% of the variation

315   in the foliar nitrogen produced (grams foliar nitrogen meters^{-2} month^{-1}) in

316   controlled conditions could be predicted based solely on the abundance of coconut

317   palms in the system where soils were sampled (Young et al. 2013*a*). These

318   controlled estimates of productivity were tightly correlated to more standard

319   measures of productivity in tropical ecosystems, such as litter throughfall inputs, for

320   the subset of sites where this information was available (Young et al. 2013*a*).

321

322   Herbivory on established plants was also impacted. Herbivores are known to prefer

323   high-nutrient plant material, and on Palmyra, this resulted in lower herbivory rates

324   in palm forest-dominated systems. Rates of herbivory (within three native species)

325   in palm-dominated forests were 3 to 4 times lower than in native-dominated

326   forests. Similarly, common Palmyra herbivores (two species, an insect and a crab)

327   subjected to cafeteria-style trials preferred *P. grandis* leaves from native forests to

328   the same species from coconut palm forests (Young et al. 2010*a*). Herbivores prefer

329   native species over palms, since coconut palms have notably unpalatable leaf tissue,

330   with low specific leaf area, low nutrient content, and very high carbon and silica

331   content in comparison to all of the dominant native plant species on Palmyra

332   (Marschner 1995; Young et al. 2011). Combined with lowered nutrient levels within

333   native species in palm-dominated forests, palm forests, thus, are likely of low value

334   to many herbivores (Young et al. 2010*a*).

335

336   **Community Effects: Consumer Communities**

337   Given the strong direct and indirect effects that coconut palms have on forest

338   structure, plant growth rates, nutrient availability, and herbivory, it is thus

339   unsurprising that these changes cascade to impact a wide range of consumers, from

340   direct plant consumers (e.g. herbivorous insects) to species with only indirect links

341   to forest dynamics (e.g. rat stomach parasites, and pelagic manta rays). The effects

342   include not only changes in abundance, but also changes in ecology, behavior and

343   body condition. These responses appear to be partly driven by direct effects of

344   changes in forest structure, food type, and habitat availability on composition of

345   consumer communities in regions altered by the invasive palm. However, these

346   direct effects are compounded by, and often superseded by the indirect effects of

347   palm abundance on site productivity, driven by changes in seabird-derived

348   nutrients. Essentially the decreased availability of energy at the bottom of the food

349   web in palm forests has bottom-up effects that percolate through multiple trophic

350   levels, and ultimately transforms and simplifies the entire structure of food webs in

351   coconut palm-dominated forests.

352

353   Invertebrates are the most abundant and diverse group on the atoll; the group also

354   includes many herbivorous and detritivorous species. As such they are a natural

355   first group to examine for consumer responses to changes in palm dominance.

356   Trapping of ground-dwelling invertebrates showed a strong change in composition

357   across forest types. Specifically, Isopoda and Formicidae decrease dramatically in

358   palm forests while Amphipoda show strong increases in palm forests (Briggs et al.

359   2012). Trapping of flying invertebrates –e.g. Diptera, Lepidoptera, Hymenoptera–

360   also revealed decreases in diversity and species richness in low productivity, largely

361   palm-dominated islets. There was also a tendency for the number of individuals to

362   decline with increasing coconut palm density, but this pattern was only marginally

363   significant (P = 0.07, R^2 =0.18). However, other insect taxa (*Dysmicoccus* sp., Order:

364   Hemiptera*; Phisis holdhausi* Karny 1926*,* Order: Orthoptera*)*, which were surveyed

365   using targeted visual surveys, showed marked decreases in abundance in low

366   productivity, palm-dominated islets (Young et al. 2013*a*).

367

368   These changes in abundance and composition of prey also trickle up to impact

369   predator communities. Among the most abundant predators groups (and some of

370   the few terrestrial vertebrates at Palmyra) are two species of geckos from the

371   *Lepidodactylus* genus. These geckos are top predators on the atoll and are both

372   abundant and pervasive in the system. The abundance of geckos did not change

373   across forest types, but the diets of the two species were very different in palm

374   forests than in native forests. These diet differences closely paralleled changes seen

375   in the invertebrate community at large; gecko diets in palm-dominated forests

376   tended to be lower in diversity, with a higher abundance of amphipods (family

377   Talitridae), and reduced abundance of isopods (family Philosciidae) and ants (family

378   Formicidae) (Briggs et al. 2012).

379

380   Beyond these dietary changes, both gecko species showed significant reductions

381   (17-19%) in body condition (mass per snout-ventral length (mg/mm)) in palm-

382   dominated forests as compared to native-dominated forests. In this case, analysis

383   suggested that these body condition effects were best explained by structural

384   variation across forest types; mean stem size, not nutrient availability, was the best

385   explanatory variable for changes in body condition (Briggs et al. 2012). One species

386   of gecko (*L. lugubris*) and one other common predator, an abundant spider

387   (*Heteropoda venatoria* Latreille 1804) also had statistically larger body sizes on

388   more productive islets (Briggs et al. 2012; Young et al. 2013a). Larger animals are

389   likely able to forage more effectively in structurally open habitats and may also be

390   able to more effectively competitively exclude smaller conspecifics in areas with less

391   structure.

392

393   Even parasites of these free-living consumers appear to be impacted. From its

394   introduction in the middle of the 20th century during US military occupation until

395 2011 when an atoll-wide eradication effort was completed, the roof rat (*Rattus*

396 *rattus* Linnaeus 1758*)* was the only other large terrestrial vertebrate predator on

397 the atoll. In 2009, rats were surveyed across 13 islets, and a subset (n = 169) was

398 dissected for parasites. While rat abundance is difficult to survey in these complex

399 habitats, catch per unit effort showed no effect of the dominance of coconut palms

400 on the abundance, size, or body condition of rats (Lafferty et al. 2010). However, the

401 intensity of infestation with the stomach nematode, *Mastophorus muris* Gmelin 1790

402 strongly and significantly increased in palm-dominated habitats (15 worms per rat

403 versus 2 in native-dominated forests). The reason for this was not established, but

404 as *M. muris* requires an insect intermediate host, changes in insect community in

405 palm dominated forests may change the availability of this host. Changes in

406 microclimate or microhabitat might also change survivorship for free-living stages

407 in this nematode.

408

409 Perhaps most surprisingly, the effects of increased coconut palm dominance even

410 percolate into surrounding marine ecosystems. A study looking at how increases in

411 palm-dominance might impact lagoon dynamics found that nitrogen in runoff was

412 26.5 times higher off coastlines of native- as compared to palm-dominated forests.

413 Phytoplankton growth rates in surrounding waters, measured using moored, in-situ,

414 phytoplankton growth chambers along the coast of palm- and native forest-

415 dominated islets, showed significant declines in productivity near palm forests. This

416 then led to decreases in biomass and body size of an important group of

417 zooplankton, Copepoda, around palm-dominated sites. This, in turn, affected the

418   foraging ecology of at least one large obligate plankton consumer, the giant manta

419   ray (*Manta birostris* Wallbaum 1792*)*, which was recorded to forage more regularly

420   along the coastlines of native-dominated forests as compared to the surrounding

421   coconut palm-dominated islets. Isotopic tracing of nutrients at each of the steps

422   along this pathway demonstrates that this effect is largely driven by bird-derived

423   nutrients (McCauley et al. 2012). This observation remains a rare example of how an

424   invasive plant species can influence the behavior of large marine fish and

425   demonstrates the extreme ecological distances that changes engineered by invasive

426   species can propagate to, affecting both land and sea.

427

428   While each of these effects on consumers is itself noteworthy, the most compelling

429   demonstration of the strong and pervasive effects of increased palm dominance on

430   consumer communities comes from isotopic analysis of food chain length across

431   islets. In this work, isotopes are used to estimate trophic position of a range of

432   consumers, from herbivores to top predators, after correcting for site-level

433   differences in isotopic baseline. It was found that higher-level consumers occupy

434   relatively higher trophic positions when found on native forest-dominated islets

435   than on palm-dominated islets (Fig 3). The magnitude of this effect is larger for

436   carnivores than for herbivores, suggesting that small changes in trophic dynamics

437   accumulate up the food chain, driven by the aggregated effects of higher levels of

438   reduced productivity at the bottom of the food chain (Young et al. 2013*a*). In

439   aggregate, these small changes in trophic positions, likely the result of subtle

440   changes in foraging ecology and behavior, lead to strong changes in overall food web

441   structure. Indeed, there is a strong negative relationship between coconut palm

442   dominance and food chain length (Fig 4), with food webs in palm-dominated islands

443   (>75% coconut palm basal area) lacking more than two trophic levels represented

444   on native-dominated islets.

445

446   **Abiotic feedbacks**

447   There are several examples of invasive species that alter abiotic or biotic conditions

448   in ways that then facilitate their own further encroachment, or the further

449   establishment of other invasive species. For example, the invasion of ice plant

450   (*Mesembryanthemum crystallinum* Linnaeus 1753) on Santa Barbara Island

451   accumulates salt, which makes an osmotic environment intolerable to native plants

452   but highly suited to the ice plant as well as to other weedy invasives (Vivrette and

453   Muller 1977). In a similar fashion, *Morella faya* Wilbur 1994, an introduced

454   nitrogen-fixing leguminous shrub, alters soils in a manner that fosters further

455   invasion by *M. faya,* as well as by the introduced strawberry guava (Vitousek 1986;

456   Hughes et al. 1991), introduced earthworms (Aplet 1990), and Japanese white-eye

457   birds (Vitousek and Walker 1989). These positive feedback loops not only

458   facilitate the advance of invasion (the controversial "invasion meltdown"

459   hypothesis; O'Dowd et al. 2003), but also make it much more likely to see entire

460   ecosystem state changes following invasion (O'Dowd et al. 2003; Simberloff 2006)

461

462   We found evidence for several such feedback loops in the Palmyra system. First,

463   and perhaps most critically, the effects of the loss of bird-derived nutrients in palm-

464   dominated sites appeared to disproportionately impact recruitment and growth of

465   native plants, creating a feedback loop that entrenches persistence of the invasive.

466   This feedback likely partially explains the tendency for local monodominance by

467   coconut palms and also facilitates their further spread. The disproportionate impact

468   of reduced guano input on native species was initially demonstrated through

469   nursery greenhouse fertilization experiments, which grew seedlings of coconut

470   palms and the three most common native species (*P. grandis, S. taccada,* and *H.*

471   *foertherianum)* in controlled environments, that varied only in the amount of

472   nutrient inputs they received; these nutrient levels simulated low, moderate, and

473   high densities of birds at Palmyra. The addition of nutrients had much stronger

474   effects on growth, nutrient concentration, and chlorophyll levels for common native

475   trees than for coconut palms. All three native trees showed substantial differences

476   in above ground biomass (at least double over the first three months of growth) as

477   well as strong increases in chlorophyll concentration when exposed to fertilization

478   rates simulating high or moderate as compared to low densities of birds (Young et

479   al. 2011). In contrast, coconut palms showed no differences across treatments in

480   either above ground biomass or chlorophyll concentration, even after 180 days of

481   treatment (Young et al. 2011) .

482

483   The greenhouse results were paralleled by results in the field, where outplanted

484   seedlings of native species grew approximately three times larger over the course of

485   one year in native-dominated forests than in palm-dominated forests. In contrast,

486   coconut palm seedlings experienced only a very small increase in growth rates

487   (<10%) when grown in more nutrient rich native-dominated forests as compared

488   with growth in palm-dominated forests (Young et al. 2013*b*). Cumulatively, these

489   results suggest a feedback loop where the nutrient depletions that occur as a result

490   of coconut palm establishment have a disproportionately negative effect on native

491   plants, giving a competitive advantage to coconut palm seedlings that are

492   comparatively tolerant to low nutrient conditions.

493

494   In addition to the effects the invasive coconut palms have on nutrients, they also

495   seem to affect water availability. Coconut palms use a considerable amount of water

496   and appear to be strong competitors for water (Jayasekara and Jayasekara 1993;

497   Roupsard et al. 2006; Gomes and Prado 2007; Krauss et al. 2015). Accordingly,

498   native plants experience significantly reduced water use when in proximity to

499   coconut palms, likely due to aggressive use of water by coconut palms. *Pisonia*

500   *grandis* appeared to exhibit some stress from this water competition, as

501   demonstrated by 46-63% reductions in sap flow when growing near coconut palms,

502   as compared to growing in native-dominated stands (Krauss et al. 2015) . This may

503   be particularly important to native tree survivorship in dry years, when drought

504   may significantly stress native trees (Krauss et al. 2015). As with negative effects of

505   coconut palms on nutrients, this thus appears likely to create a regime whereby

506   palm encroachment changes abiotic conditions that disproportionately and

507   negatively impact native plants.

508

509   **Biotic Feedbacks**

510   In addition to the abiotic feedback loops, there appear to be at least two biotic

511   feedback loops that occur: 1) via increases in patterns of seed and seedling

512   predation on native species in palm-dominated forests and 2) via increases in

513   litterfall damage rates to seedlings in palm-dominated forests. Based on camera trap

514   surveys of seed predation events, most seed and seedling mortality on Palmyra is

515   driven by highly abundant land crab species. This is common in many tropical and

516   coastal ecosystems, where consumption from land crabs can be critical in

517   structuring forest communities (Green et al. 1997; Lindquist and Carroll 2004;

518   Lindquist et al. 2009). These crabs are highly effective seed and seedling predators.

519   In seed predation experiments, more than 95% of seeds from the common small-

520   seeded native trees (*H. foertherianum, P. grandis,* and *S. sericea*) were predated

521   within one month of placement (Young et al. 2013*b*). However, these already high

522   rates of seed predation increased dramatically –to upwards of 99%- in palm-

523   dominated forests. Consequently, the native seeds placed in unprotected locations

524   in invasive coconut palm forests never successfully germinated, while germination

525   was repeatedly observed (albeit at low rates) in native forests. Similarly, for

526   unprotected transplanted seedlings of these common native tree species, less than

527   5% survived in coconut palm-dominated forests within one year while 36%

528   survived through this first year in native forests. In contrast, coconut seeds and

529   seedlings suffered very low total rates of seed (0-5% within one month) and

530   seedling (4 to 13% within 1 year) predation in either forest type; and the rates were

531   actually significantly reduced in coconut palm-dominated as compared to native-

532   dominated forests (Young et al. 2013*b*). The net effect is that native plants

533   experience dramatically reduced rates of growth (leaf area per plant; Fig 5) and

534   establishment in native forests, while coconut palms experience little negative

535   consequences (Fig 5) and, indeed, likely perform even better when in palm-

536   dominated forests when both seed and seed predation effects are included.

537   Mathematical simulations suggest this feedback mechanism alone is sufficient to

538   drive near total replacement of most native species, and can create the

539   monodominant structure of coconut palms that is empirically observed at Palmyra

540   and elsewhere (Young et al. 2013*b*). Given the slow rates of natural encroachment

541   of coconut palms, this in turn, leads to a patchy landscapes with higher than

542   anticipated levels of beta diversity, and low levels of alpha diversity (Young et al.

543   2013*b*).

544

545   The high dominance of coconut palm also provides a second source of elevated

546   seedling mortality via high rates of seedling damage caused by heavy falling palm

547   fronds and palm nuts (e.g. mean nut size >1.5 kg). Litterfall inputs were measured

548   to be 5 times higher in coconut forests (mean 2.3 kg per month) than in native

549   forests (mean 0.4 kg per month) (Young et al. 2014). Using artificial seedlings made

550   of wire and straws to record damage rates, we found that severe damage rates to

551   seedlings were more than three times higher in palm forests (16.1%) than in native

552   forests (4.9%) (Young et al. 2014). Tree species are known to vary in their ability to

553   resist and recover from litterfall damage (Gilman et al. 2003; Peters et al. 2004).

554   Given the much larger and stronger stem size of *C. nucifera* as compared to that of

555   other native species, we expect that, as in other palm forests (Gillman et al. 2003;

556   Peters et al. 2004) this dramatic increase in litterfall damage will disproportionately

557   impact the survivorship and recruitment of smaller-stemmed and thus more

558   vulnerable native species. Invasive palm litterfall damage is yet another important

559   factor that contributes to the near total lack of native species recruitment

560   underneath coconut palm canopies.

561

562   **Conclusion**

563   The Palmyra system, with its relatively long-term historical time period and

564   replicated islets, offers important insight into the diverse pathways and complex

565   dynamics by which invasive species affect ecosystem structure and function across

566   entire landscapes. While knowledge of the impacts on invasive species on

567   ecosystems has grown rapidly in the past several decades (Ehrenfeld 2010; Vila et

568   al. 2011; Pysek et al. 2012; Gaertner et al. 2014), there are still gaps in the

569   understanding of such impacts and their underlying driving factors. The Palmyra

570   palm example addresses a few, including: 1) how invasive species lead to regime

571   shifts, 2) the long time frame needed to fully understand invasive species impacts,

572   and 3) novel and interacting higher-order mechanisms and effects of invasion.

573

574   Coconut palms have transformed the forest community, altered nutrient profiles,

575   changed the abundance and ecology of consumers across trophic levels, and altered

576   the magnitude and direction of species interactions. Coconut palms act as many

577   ecosystem engineers (sensu Jones et al. 1994) do; by creating a habitat more

578   suitable to their survival than the survival of other species (Cuddington and

579   Hastings 2004). Through these effects, they perpetuate and extend their dominance

580   throughout Palmyra, a trend that is likely to have occurred or be occurring in many

581   island systems where coconut palms are invasive across the tropics. As these palms

582   may have created alternative stable states in invaded systems it is not clear if

583   eradication would lead to restoration of original forests; more research is thus

584   needed to inform management of these sites. However, any new plantings of

585   coconut palms in other sites, particularly where seabird colonies occur, should be

586   carefully considered in light of the risk of strong ecological ramifications, and

587   managers in lightly invaded sites should strongly consider removal of these palms

588   before invasion proceeds further. Notably, the case of the coconut palm expansion is

589   now being mirrored (and overshadowed) by the recent global proliferation of the

590   African oil palm (*Elaeis guinneensis),* now being cultivated on between 13 and 16

591   million ha worldwide (Fitzherbert et al. 2008). Impacts of coconut palm expansion

592   may serve as an "ecological harbinger" of some effects now occurring with the rapid

593   expansion of oil palm.

594

595   As an historical invasion, coconut palms have been present and invasive on the

596   Palmyra landscape long enough (likely present for at least 1,500 years, and actively

597   expanding for at least the last 50-150 years) to result in process shifts that play out

598   over both short and long ecological time spans. For instance, while the interruption

599   of seabird nutrient inputs at small scales was likely relatively abrupt, the associated

600   trickle down effects to other consumers and to island-scale nutrient budgets very

601   likely has taken many years to develop. This case study thus suggests that modern

602   invasions may lead to large-scale changes that will last and extend across

603   landscapes and seascapes.

604

605   The Palmyra system also highlights the rich and diverse mechanisms by which

606   impacts occur, including several relatively novel mechanisms. While some

607   ecosystem impacts of invasive species have been fairly robustly documented

608   (including a tendency to cause nutrient enrichment and change nutrient cycling

609   (Ehrenfeld 2010)), the Palmyra example illustrates that structural changes (forest

610   canopy, litter, and understory in this case) are important impacts that can lead to

611   large-scale change. And while coconut palm invasion does ultimately lead to

612   substantial changes in nutrient regimes and cycling, it is through different feedbacks

613   than are commonly cited (usually nitrogen fixation, litter, and soil biota (Gaertner et

614   al. 2014)). Additionally, while some studies highlight the indirect effects of invasive

615   species, these have generally occurred via top-down forces and trophic cascades

616   (Estes and Palmisano 1974; Croll et al. 2005). The coconut palm example illustrates

617   that these indirect effects can have complex pathways dictated by bottom-up as well

618   as top-down processes. Future studies should, then, focus on broadening the

619   definition of ecosystem-level impacts, and be more ambitious in the search for

620   tracing the diverse pathways through which this change can be engineered.

621   Undertaking this effort will help bring to light the true ecological extent by which

622   invasive species influence ecosystems, the deep temporal reach by which this

623   change becomes manifest, and the complex biotic and abiotic interrelationships that

624   give rise to these effects.

625

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636   **FIGURE CAPTIONS:**

637

638   Fig 1: All work was conducted at Palmyra atoll (A), within the different islets, which

639   vary strongly in dominance by coconut palms, and are used as replicates. The native

640   community of trees, dominated by *P. grandis* and *H. foertherianum* (B), have been

641   replaced in many areas with nearly monodominant stands of coconut palms (C).

642   These palm forests are structurally transformed, with higher stem density and total

643   basal area, more standing litter, and dense seedling canopies composed almost

644   entirely of coconut palms. Many islets are now nearly completed dominated by

645   coconut palms (D). Photo credits: Kydd Pollock (A) and Hillary Young (C-E)

646

647   Fig 2: A change from low (<25%) to high (>75%) dominance of coconut palms (as

648   proportion of basal area) transforms plant communities (Panel A), causing increases

649   in number seedlings (SEED), stem density (SD), total standing basal area (BA),

650   standing litter (LITT), density of herbaceous cover (HERB), and strong declines in

651   plant diversity. Through strong negative impacts on birds (BIRD, panel C), this

652   causes radical changes in ecosystem nutrient dynamics (Panel B) including strong

653   declines in soil nitrate (NO_3^-), ammonium (NH_4^+), phosphate (PO_4^-), bulk nitrogen,

654   soil organic matter (OM), aluminum (Al), boron (B), potassium (K), and silica (Si),

655   while modestly increasing soil pH (pH) and molibdinum (Mo). These changes in soil

656   nutrients, particularly nitrogen, affect plant nutrients, including percent foliar

657   nitrogen (%N fol) as well as nitrogen in runoff (%N run). The combination of

658   physically changed plant communities and chemically changed soil parameters

659   alters abundance of a wide range of consumers (Panel C) including zooplankton

660   (ZOO), manta rays (MR), parasitic nematodes (NEM), isopods (ISO), ants (FORM),

661   and amphipods (AMPH). It also impacts a range of other consumer parameters such

662   as body size of two species of geckos (LL-S and LNs-S) and one abundant spider

663   species (SPID-S) and the diet diversity of one gecko species (LL-diet). These changes

664   cumulatively cause a suite of negative feedbacks to native plants (Panel D),

665   including via physical processes such as increased litterfall (LF), anf biological

666   processes such as increased seed predation (SP-N) and seedling (SE-N) predation on

667   natives (SP-N), but decreased seed and seedling predation on coconut palms (SP-C

668   and SE-C), decreased growth rates (GR) of native species, and increased water stress

669   as indicated by sap flow (SF). All differences shown here are significant and are

670   discussed in text in more detail. Specific references for each response are provided

671   in SI 1.

672

673   Fig 3: Isotopes of nitrogen in soils (unfilled squares) and plants (unfilled diamonds)

674   indicate that the sources of nitrogen in native-dominated islets (red) are different

675   than those in palm- (*Cocos nucifera*) dominated forests (blue), likely driven by the

676   higher relative importance of high-trophic level guano-derived nutrients in native

677   forests. The difference between consumer nitrogen isotopes across forest types is

678   much stronger than that seen in plants and soils, indicating not only a different

679   source of nitrogen, but differences in feeding ecology of consumers, or differences in

680   overall food web structure on native-dominated islets. The four consumers shown

681   are some of the most abundant top predators and include two species of geckos –

682   *Lepidactlyus lugubris* (triangles) and *Lepidactlus ns* (circles), a spider Heteropoda

683   venatoria (diamonds), and the roof rat, *Rattus rattus* (squares, now eradicated from

684   the atoll).

685

686   Fig 4: Increases in coconut palms (*C. nucifera*) affect abundance, diversity and body

687   size of many consumer groups, largely through their effects on site productivity.

688   These effects trickle up to drive changes in entire food web structure, reflected in a

689   significant decline in total food chain length with coconut palm abundance.

690

691   Fig 5: Increased rates of herbivory, litterfall damage, and seedling predation,

692   combined with lower rates of soil nutrients in palm-dominated forests combine to

693   cause greatly reduced survivorship and growth (leaf area per plant) for

694   transplanted seedlings, after two years, for native *Pisonia grandis* (A)*.* In contrast,

695   there is no significant effect of forest type on growth or survivorship of transplanted

696   coconut palms across forest types (B) (from Young et al. 2013). Combined with

697   differential seed predation for native versus coconut palm plants in palm-dominated

698   forests, this creates a negative feedback loop making it difficult for native plants to

699   persist in palm-dominated forests

700

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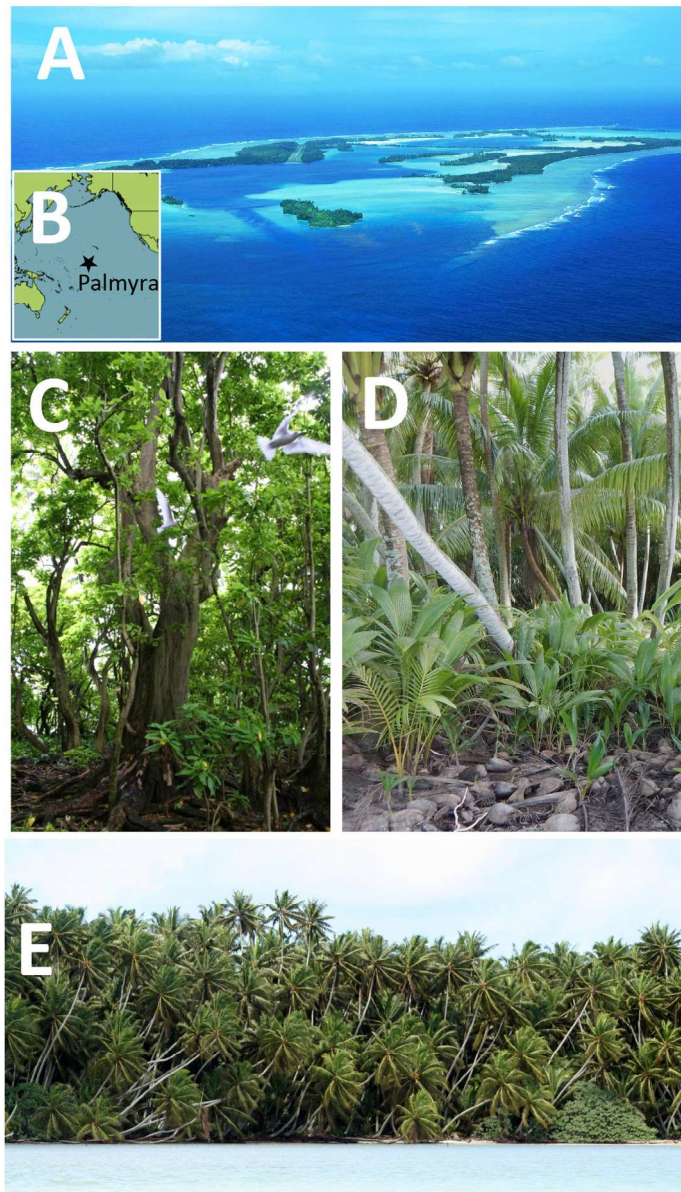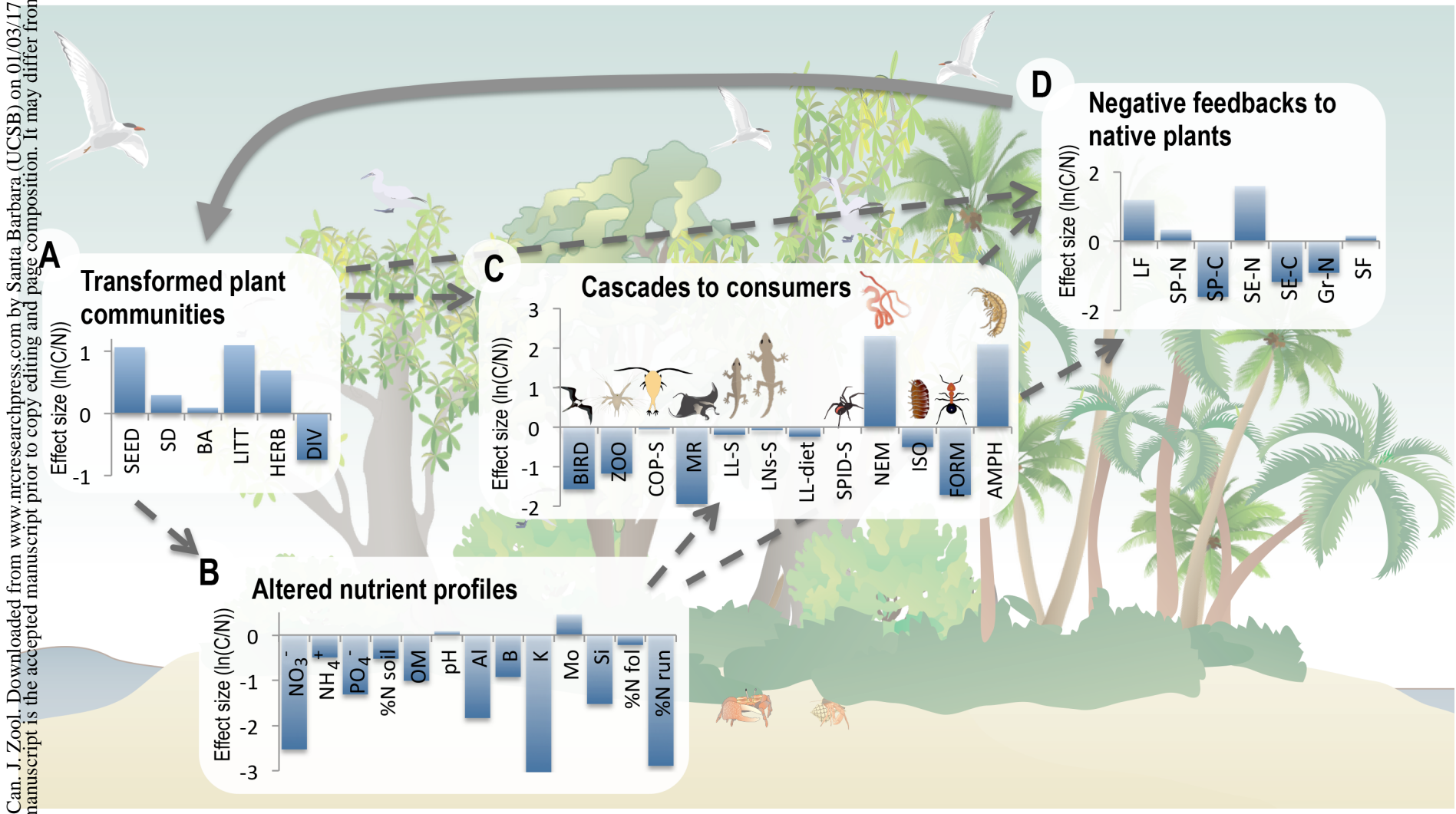
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Fig 1: All work was conducted at Palmyra atoll (A), in the central Pacific Ocean (B), within the different islets, which vary strongly in dominance by coconut palms, and are used as replicates. The native community of trees, dominated by P. grandis 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 completed dominated by coconut palms (E). Photo credits: Kydd Pollock (A) and Hillary Young (C-E)

107x186mm (300 x 300 DPI)

A Transformed plant communities

Effect size (ln(C/N))

SEED, SD, BA, LITT, HERB, DIV

B Altered nutrient profiles

Effect size (ln(C/N))

NO_3^-, NH_4^+, PO_4^-, %N soil, OM, pH, Al, B, K, Mo, Si, %N fol, %N run

C Cascades to consumers

Effect size (ln(C/N))

BIRD, ZOO, COP-S, MR, LL-S, LNs-S, LL-diet, SPID-S, NEM, ISO, FORM, AMPH

D Negative feedbacks to native plants

Effect size (ln(C/N))
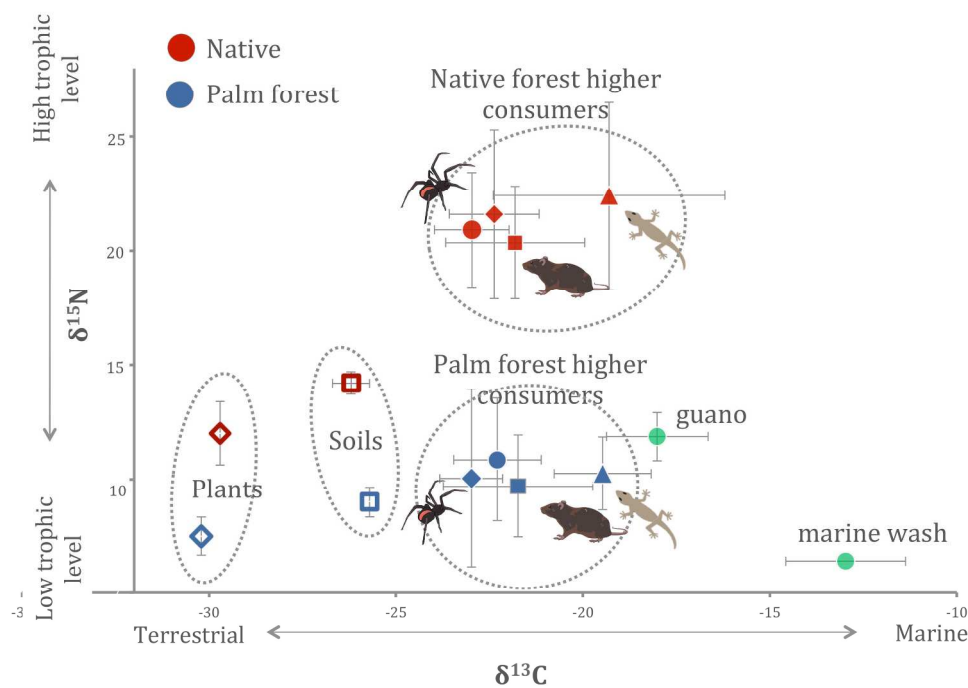
LF, SP-N, SP-C, SE-N, SE-C, Gr-N, SF

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 – Lepidactlyus lugubris (triangles) and Lepidactlus ns (circles), a spider Heteropoda venatoria (diamonds), and the roof rat, Rattus rattus (squares, now eradicated from the atoll).

233x162mm (300 x 300 DPI)
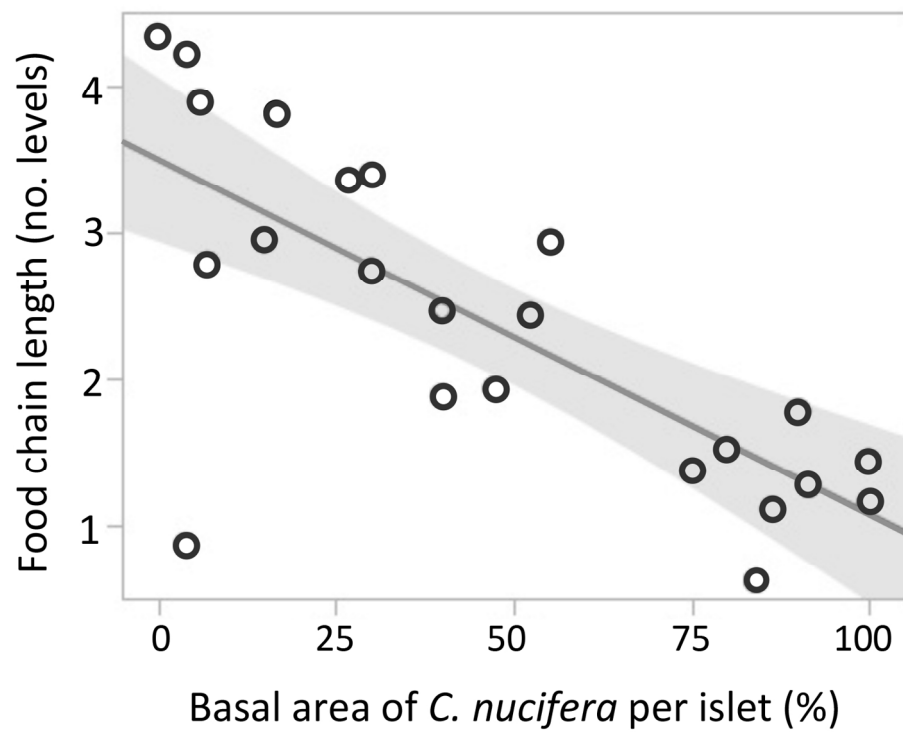
Increases in coconut palms (C. nucifera) affect abundance, diversity and body size of many consumer groups, largely through their effects on site productivity. These effects trickle up to drive changes in entire food web structure, reflected in a significant decline in total food chain length with coconut palm abundance.

144x109mm (300 x 300 DPI)