ORIGINAL ARTICLE

WILEY **bio**TROPICA · ASSOCIATION FOR TROPICAL BIOLOGY AND CONSERVATION

Impacts of rodent eradication on seed predation and plant community biomass on a tropical atoll

Ana Miller-ter Kuile[1] 🆔 | Devyn Orr[1] | An Bui[1] | Rodolfo Dirzo[2] | Maggie Klope[1] | Douglas McCauley[1] | Carina Motta[1] | Hillary Young[1]

[1]Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, Santa Barbara, CA, USA

[2]Department of Biology, Stanford University, Stanford, CA, USA

Correspondence
Ana Miller-ter Kuile, Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, Santa Barbara, CA 93106, USA.
Email: ana.miller-ter.kuile@lifesci.ucsb.edu

Abstract

Invasive rodent eradications are frequently undertaken to curb island biodiversity loss. However, the breadth of rodents' ecological impact, even after eradication, is not always fully recognized. For example, the most widespread invasive rodent, the black rat (*Rattus rattus*), while omnivorous, eats predominantly seeds and fruit. Yet, the effects of seed predation release after eradication on plant communities and ecological functions are not well understood, posing a gap for island restoration. We examined the role of seed predation release following black rat eradication in changes to tree composition and aboveground biomass across an islet network (Palmyra Atoll) in the Central Pacific. We conducted repeated surveys of seed, juvenile, and adult tree biomass and survival in permanent vegetation plots before and after the eradication of rats. We observed a 95% reduction in seed predation for an introduced, previously cultivated tree population (*Cocos nucifera*). Juvenile tree biomass of all species increased 14-fold, with *C. nucifera* increasing the most, suggesting that eradication increased this tree's competitive advantage. Indeed, based on stage-structured demographic models, rat eradication led to a 10% increase in *C. nucifera* population growth rate. The effect of invasive rodent seed predation varies considerably among the plant species in a community and can shift competitive dynamics, sometimes in favor of invasive plants. These bottom-up effects should be considered in evaluating the costs and benefits of eradication. Documenting the variation in invasive rodent diet items, along with long-term surveys, can help prioritize island eradications where restoration is most likely to be successful.

KEYWORDS

Cocos nucifera, demography, invasive species, island conservation, Palmyra Atoll, *Rattus rattus*

1 | INTRODUCTION

We are in the midst of a global biodiversity crisis, with islands facing some of the most alarming losses of endemic species (Pimm et al., 2014). This loss is fueled by a combination of factors; one of the most detrimental being invasive mammals (Tershy, Shen, Newton, Holmes, & Croll, 2015). Invasive rodents, in particular, are found on over 80% of the world's major islands and are implicated in the extinction or suppression of 34 plant and 101 animal species (Atkinson, 1985; Towns, Atkinson, & Daugherty, 2006). Rodent eradications on over 400 islands worldwide have led to the recoveries of species across taxonomic groups, and the scale of planned and

attempted eradications continues to increase (DIISE, 2015, Jones et al. 2016).

The main goal of eradications is typically the recovery of nesting seabird populations (Jones et al., 2008, 2016). Nesting seabirds provide nutrients with their guano and perturb soil while creating burrow nests (Buxton et al., 2016; Jones, 2010). Seabird recovery, thus, can cascade to restore nutrient and soil cycling regimes which maintain island plant and consumer communities, and such recoveries have occurred across the globe (Croll, Maron, Estes, Danner, & Byrd, 2005; Fukami et al., 2006; Le Corre, 2015; Mulder et al., 2009; Figure 1).

Although the management focus of eradications is typically seabird communities, diet studies of island rodents suggest that the majority of their diet is plant-based (Shiels & Pitt, 2014). The most widespread rodent in the tropics, the black rat (*Rattus rattus*), predominantly eats seeds and fruits, including both native and introduced grasses, forbs, shrubs, and trees (Shiels, Pitt, Sugihara, & Witmer, 2014). Black rat seed predation is responsible for the suppression and extinction of plants across the tropical Pacific (Meyer & Butaud, 2009) through the effects of seed predation on plant demography, community composition, and biomass (Maron, Hajek, Hahn, & Pearson, 2018; Maron & Pearson, 2011). Black rats also disperse invasive plant species, increasing competitive pressure on native plants (Hays, Sperry, Drake, & Hruska, 2018; Shiels & Drake, 2011). Plant community responses to seed predation release following rodent control or eradication, however, are relatively under-documented (but see Grant-Hoffman, Mulder, & Bellingham, 2010a, 2010b; Pender, Shiels, Bialic-Murphy, & Mosher, 2013). This is surprising since changes to plant community composition and abundance can alter ecological functions and processes such as carbon storage, nutrient cycling, and decomposition (Chave et al., 2006; Sayer, Heard, Grant, Marthews, & Tanner, 2011), as well as shape above- and below-ground consumer communities at a comparable magnitude to seabird-driven ecosystem recovery (i.e., Drake et al., 2011; Fukami et al., 2006; Young, Mccauley, Dunbar, et al., ; Figure 1). While the release of native plants from seed predation may lead to the recovery of island ecosystems (Campbell & Atkinson, 2002; Grant-Hoffman et al., 2010a, 2010b; Pender et al., 2013; Wolf et al., 2018), release of non-native, invasive plants may lead to the establishment of additional invasive species (Bergstrom et al., 2009), or alternative ecological states (Suding, Gross, & Houseman, 2004) that endanger additional native species and create the need for supplementary management.

These ecological outcomes, including whether islands recover following eradications or not, likely vary depending on plant community composition and ecological pressure exerted by rodent seed predation (Grant-Hoffman & Barboza, 2010). On the world's tropical atolls, which are both heavily invaded by black rats and altered by human agriculture and agro-forestry, eradication responses may follow general patterns that could favor introduced plants (Harper & Bunbury, 2015; Thaman, 2016). In particular, the coconut palm (*Cocos nucifera*), which was planted across atolls in the late 1800s and early 1900s for copra production, may be a driver of post-eradication island recovery (Dawson, 1959; Thaman, 2016). Black rats are known to heavily predate the seeds of *C. nucifera* across the Pacific, targeting pre-mature seeds in the canopy (Harper & Bunbury, 2015; Wegmann, 2009). Black rat seed predation is not only likely to regulate *C. nucifera* populations, but also the populations of other seed predators that may target seeds of *C. nucifera* and other plants once they reach the ground
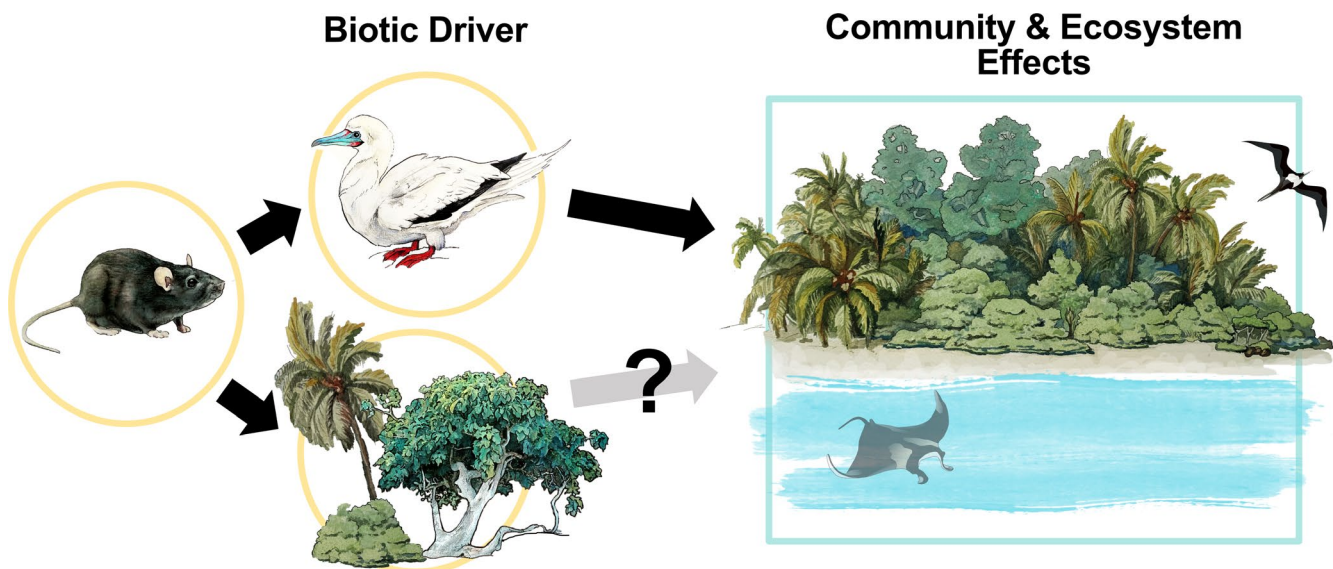
FIGURE 1 Invasive rodents are omnivores that predate important biotic drivers for island ecosystems (here, seabird and tree communities). Rodent eradications are usually undertaken to protect seabirds from rat predation, recovering the ecological processes seabirds regulate (e.g., nutrient subsidies and soil turnover; top pathway). However, less is known about how rodent eradications may directly impact (through seed predation) plant communities and the ecological processes they regulate (bottom pathway). (illustrations by Devyn Orr; vector images by Tracey Saxby and Sally Bell, Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/imagelibrary/)

(this includes the largest terrestrial arthropod, the coconut crab *Birgus latro*) (Nigro et al., 2017). Additionally, depending on whether black rats preferentially target *C. nucifera* seeds or the seeds of other introduced or native species, plant community composition may shift in favor of the introduced *C. nucifera* or in favor of native species. The expansion of *C. nucifera* from agricultural planting (even on isolated and uninhabited atolls) negatively influences nesting seabirds and the island food webs seabird nutrients support, and so increased expansion of this species may exacerbate these impacts (Thaman, 2016; Wegmann, 2009; Young, Miller-ter Kuile, Mccauley, & Dirzo, 2017; Young, Raab, Mccauley, & Briggs, 2010).

In this study, we examined the role of black rats (*Rattus rattus*) as seed predators on trees at Palmyra Atoll in the Central Tropical Pacific. Palmyra is a model system of the ecological shifts caused by *C. nucifera* invasion (Young et al., 2017) and provides an opportunity to assess the impacts of black rat seed predation in the absence of other canopy-feeding seed predators (Wegmann, 2009). Following black rat eradication on Palmyra Atoll in 2011, juvenile individuals of all tree species increased in abundance (Wolf et al., 2018); however, the mechanisms for this increase and its effects on species-level biomass and long-term ecosystem recovery have not been explored. We used multi-year data, which is often unavailable in eradication efforts, from both before and after black rat eradication to demonstrate that 1) the loss of black rat seed predation is a mechanism for increases of *C. nucifera* and it seems that native seed predators (*Birgus latro*) do not equal black rat in their seed predation ability, 2) increases in juvenile abundance lead to increases in juvenile biomass that vary across species with important impacts on ecosystem function, and 3) long-term effects of seed predation on tree community composition, aboveground biomass, and post-eradication ecosystem recovery, with shifts toward *C. nucifera* dominance, revealed via stage-structured demographic models.

2 | METHODS

2.1 | Study system

We conducted this study on a low-lying, currently uninhabited coral atoll (Palmyra) in the Northern Line Islands (5°53′1″N 162°4′42″W). The atoll's 230 ha of land area consists of a ring of islets surrounding three central lagoons. Palmyra Atoll has a wet tropical climate (an average 4,488 mm annual rainfall; mean annual temperature 27°C) and approximately 90% of the atoll is forested, with canopies of five species which occur in monoculture to mixed-stand gradients of *Cocos nucifera* (Arecaceae) (65% of total tree canopy area), *Pisonia grandis* (Nyctaginaceae) (12%), *Scaevola taccada* (Goodeniaceae) (12%), *Heliotropium foertherianum* (Boraginaceae) (12%), and *Pandanus tectorius* (Pandanaceae) (10%) (Lafferty et al., 2018; Young et al., 2010). Similar to many islands in the Pacific, it is believed that *Cocos nucifera* arrived from Asia with humans in the last 1,500 years (Gunn, Baudouin, & Olsen, 2011; Matisoo-Smith & Robins, 2004). On Palmyra, cultivation of *C. nucifera* for copra production between 1,850 and 1970 increased what had likely been scattered coastal

populations of this species to populations of 4,000 adult trees in the 1850s (Dawson, 1959). This population has grown to more than 53,000 reproductive adults on the atoll in 2005, and *C. nucifera* continues to expand its range into forest patches of native broadleaf tree species (Wegmann, 2009; Young et al., 2017). Black rats were likely introduced to the atoll during World War II military occupation (starting in 1941) and were successfully eradicated with aerially distributed anticoagulant rodenticide (brodifacoum) over a one-month period, June-July 2011 (Wegmann, 2009; Wolf et al., 2018; Young et al., 2017). Black rats likely died almost immediately due to the potency of brodifacoum rodenticide and the success of aerial baiting (Parkes, Fisher, & Forrester, 2011); rat absence was verified with post-eradication baiting in summer 2012, and no rats have been observed since the eradication (Wolf et al., 2018).

2.2 | Permanent plot setup

In 2007, before black rat eradication, we established seven 300-m^2 vegetation monitoring plots. These plots were established to track population dynamics among tree species over time, with a focus on understanding long-term dynamics of the dominant introduced *C. nucifera* (65% of atoll forest canopy cover; Figure 2) within the atoll ecosystem (see Young et al., 2017). Therefore, plot locations were selected either in areas already dominated by *C. nucifera* (i.e., 100% cover based on adult basal area), or areas considered potential expansion fronts, given the presence of adult *C. nucifera* in or adjacent to each plot (0%–37% basal area of *C. nucifera*, with at least one subadult *C. nucifera* present in the plot).

2.3 | Permanent plot tree measurements

At the initial survey (2007), we permanently tagged each adult tree (individuals with diameter ≥ 10 cm either at breast height (DBH; 1.3 m) or below the base of their crowns). We measured each tree DBH and determined aboveground biomass using diameter-based allometric equations (Chave et al., 2005; Appendix S1) We also counted, measured (diameter at DBH or trunk base), and tagged all subadult trees (hereafter "juveniles"; <10 cm DBH and taller than 1 m). We revisited each plot in four pre-eradication years (2007–2010) and four years post-eradication (2014–2017) during the summer season. In each of these years, we confirmed if all previously tagged adult trees were present and alive, re-counted previously marked juvenile trees, and counted and tagged all newly recruited juveniles in each plot.

2.4 | Permanent plot seed counts and seed predation

For the large-seeded *C. nucifera* (2–3 kg fruit wet weight; (Dransfield & Cooke, 1999; Harries, 1978), we counted the number of predated
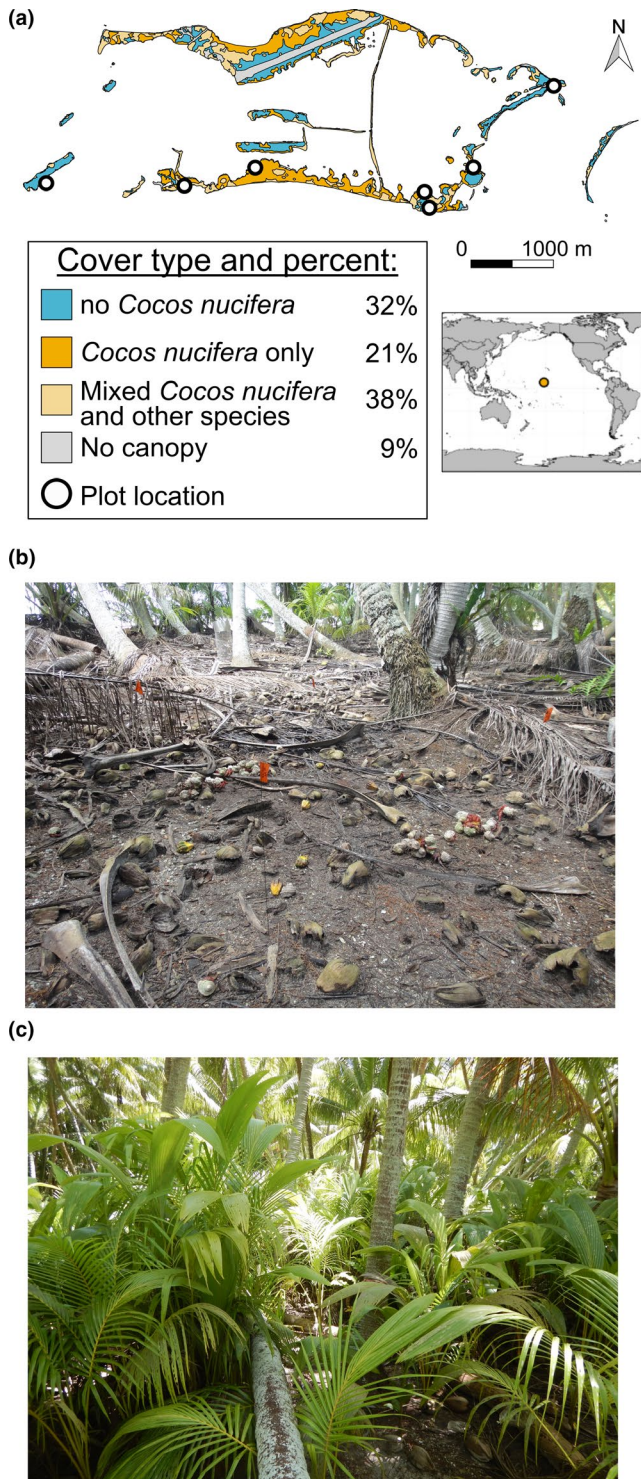
FIGURE 2 (a) Palmyra Atoll, Central Pacific, with vegetation plot distribution across the atoll. The palm tree *Cocos nucifera* occurs in mixed and monoculture stands in 65% of the forested portions of the atoll. Repeated photos taken in the same season (August-September 2010 and 2015) of one vegetation plot one year before (b) and four years after (c) rodent eradication illustrate how rodent presence limits juvenile tree recruitment. (For reference, fronds on the ground in photograph (b) are 2 meters in length; tallest understory palms in left of photograph (c) are 2.5 meters in height and the average height of seedlings in this photograph is 1.5–2 meters)

and viable drupes (hereafter referred to as "seeds") on the ground using a series of 24 1-m^2 seed count quadrats in each plot. For this tree species on Palmyra Atoll, predation always leads to seed death because seed predators burrow into the seed embryo. We included both predation of green, immature seeds (often attributed to rats gnawing into seed embryos while seeds are in the canopy) and predation of ripe, mature seeds on the ground (most likely from husking by the coconut crab *Birgus latro*) ((Harper & Bunbury, 2015). Rats are the only canopy seed predators in this system. Seed surveys were conducted in three years (2007, 2015, 2016, $n = 144$ per year). Seeds of most tree species on the atoll (not including *C. nucifera*) have previously been shown to be heavily predated by rats (Wegmann, 2009), though we did not measure predation of these seeds in our plots because these species were not present or because seeds of these species were not observed before rat eradication. We also estimated the number of immature and mature *C. nucifera* seeds in each tree in each plot in three years (2007, 2015, 2016; Appendix S4).

We established that seed predation was the mechanism of change in *C. nucifera* abundance and biomass by comparing 1) predated and 2) viable seed counts in quadrats across eradication periods using generalized linear mixed effects models. For each of the two seed types ("predated" and "viable"), we specified a full model with seed number as the response variable, eradication status as fixed effect, plot as random effect, and distributions appropriate per response variable (Zuur, Ieno, Walker, Saveliev, Anatoly, & Smith., 2009). We built all models in the *lme4* package in R (R version 3.5.0, *lme4* v 1.1–17, Bates, Maechler, Bolker, & Walker, 2015). We selected the best-fitting model by minimizing AIC values (*MuMln* package v 1.42.1, (Burnham & Anderson, 2002)) and conducted post hoc pairwise comparisons between marginal means of pre- and post-eradication periods for best-fitting models that included this fixed effect (*emmeans* package version 1.4.5). We verified that model assumptions (including heteroskedasticity and lack of overdispersion and zero inflation) were met using the *DHARMa* package (version 0.2.0; Hartig, 2018; Appendix S2).

2.5 | Short-term changes in aboveground biomass

We examined whether decreased rat seed predation led to a short-term increase in plant aboveground biomass by measuring changes in the biomass of juvenile trees of all species (non-reproductive trees < 10 cm DBH and taller than 1 m). We converted juvenile tree counts for all species to dry biomass using species-specific equations or conversions based on data collected for juveniles elsewhere on Palmyra Atoll and from literature values (Ashish, Vidyasagaran, Kumar, & Ajeesh, 2015; Chave et al., 2005; Climate Action Reserve, 2017; Young, McCauley, & Dirzo, 2011; Young, Mccauley, Guevara, et al., 2013). Because *C. nucifera* dry biomass is highly age-dependent, we determined total juvenile tree biomass in plots only for years in which all juveniles had been longitudinally tracked for at least two years and could thus be separated into age classes (pre: 2008, 2009, and 2010; post: 2016; Appendix S3).

To quantify juvenile tree biomass change, we used generalized linear mixed effects models to determine whether eradication altered juvenile biomass. We specified a full model with total juvenile biomass (in dry grams) as the response variable, eradication status as fixed effect, plot nested within year as the random effect, and a Tweedie error distribution, which is used to measure biomass values in datasets with potential zero-inflation and high skewness (Dons, Bhattarai, Meilby, Smith-Hall, & Panduro, 2016; Lecomte et al., 2013). For all models, we chose models and assessed model fits with the same model selection process used for the seed models. For these models, we used the *glmmTMB* package (version 1.0.0) to accommodate the Tweedie distribution and compared marginal means with the *emmeans* package (version 1.4.5). To verify that changes in juvenile biomass were not due to environmental conditions in the years in which biomass could be assigned, we also ran a repeated measures ANOVA for juvenile tree numbers across all sampling years (2007–2010, 2014–2017) to verify that changes were consistent and compared annual precipitation (in cm) between pre- and post-eradication years using a Mann–Whitney *U* test, (Lafferty et al., 2018, Appendix S4).

2.6 | Demographic modeling and estimates of long-term biomass change

Changes in juvenile abundance and biomass reflect immediate responses to seed predation release but are not necessarily indicative of the longer-term outcomes for the tree community. Because of the long lifespans of the trees on the atoll (70 + year lifespan with a time to maturity of 12 or more years; Malhotra & Welfare, 2017; Navarro et al., 2008) compared with the relatively short time period of this study, we used demographic models to predict how these changes may lead to long-term shifts in total plant biomass. Because we had data on all life stages for *C. nucifera* and not for other species, and because this species is the most abundant species on the atoll, we modeled this species only and assume that any changes in this species reflect a magnitude of change that is representative of biomass changes for the tree community. Because *C. nucifera* can persist in the juvenile stage using stores from their large seed for a variable amount of time (3–6 months up to one year, (U. of Hawai'i Cooperative Extension Service, 1996)) depending on growing conditions, we used stage-structured (in lieu of age-structured) demographic models, which separate populations of a species into discrete stages in which each stage shares the same probabilities of survival, growth, and reproduction (vital rates) and tracks these population stages over time given specified initial population sizes (Caswell, 2001; Rist et al., 2010).

Because rats are known seed predators and seedling herbivores in island ecosystems (Harper & Bunbury, 2015), eradication may have had a significant effect on both seed and seedling life stages. Rats may alter 1) fecundity (adult seed production) through pre-dispersal predation, 2) seed survival and germination through post-dispersal predation, and 3) juvenile survival and recruitment to adulthood

through herbivory of seedling apical meristems or of the large seeds attached to seedlings. Indirectly, changes in juvenile abundance may lead to altered intra- and interspecific competitive dynamics (Silva Matos, Freckleton, & Watkinson, 2013). We determined whether rats had altered each vital rate by determining each rate for each plot within a given year. We then compared vital rates among years using repeated measures ANOVAs or Wilcoxon signed-rank tests (Appendix S3). Based on the results of these tests, we created two vital rate (i.e., Leftkovich) matrices for later use in stage-structured population models, one representing vital rates with rats present in the community and one representing vital rates with rats absent. When vital rates did not vary significantly (α = 0.05) among years, we used the same vital rate across all plots and years. When vital rates varied across eradication periods (i.e., with and without rats), we averaged vital rates across plots within each eradication period, resulting in a different value for that vital rate with and without rats present.

To determine whether changed vital rates altered future aboveground biomass, we ran demographic model simulations for each vegetation plot with each of the two vital rate (Leftkovich) matrices (*n* = 14 simulations). We used a starting population vector for all simulations of population sizes for each plot in the pre-eradication time period. We ran each model over one juvenile generation (12 years). We converted the yearly population increase in each life stage from these models to biomass by multiplying the total number of new juveniles by the biomass of one age-one juvenile and the total number of new adults by the biomass of an age-twelve individual minus an age-eleven individual (thus only accounting for the biomass added as it became an adult). We summed this total biomass per plot per rodent status and tested whether the total added plant aboveground biomass was significantly different with and without seed predation using a Wilcoxon signed-rank test. In addition, we determined population growth rates (λ) for each matrix. We also determined model elasticities, which measure the relative importance of changes in each vital rate compared with all other vital rates and therefore indicate which vital rates determine population growth rate (λ).

3 | RESULTS

3.1 | Permanent plot seed counts and seed predation

Rat eradication significantly decreased the total number of predated seeds (Figure 3a) and increased the total number of viable seeds in vegetation plots (Figure 3b). We observed 44 predated seeds in 22 of 144 quadrats (15% of quadrats) pre-eradication and 15 predated seeds in 11 of 218 quadrats (5% of quadrats) post-eradication. Of these, we only observed mature predated nuts (brown with husk tearing, indicative of *B. latro* predation) following eradication and we only observed a total of 11 seeds in this category (of a total of 59 observed predated seeds). We observed 12 viable seeds in 8 of 144 quadrats (6% of quadrats) before eradication, and 87 viable seeds in 54 of 218
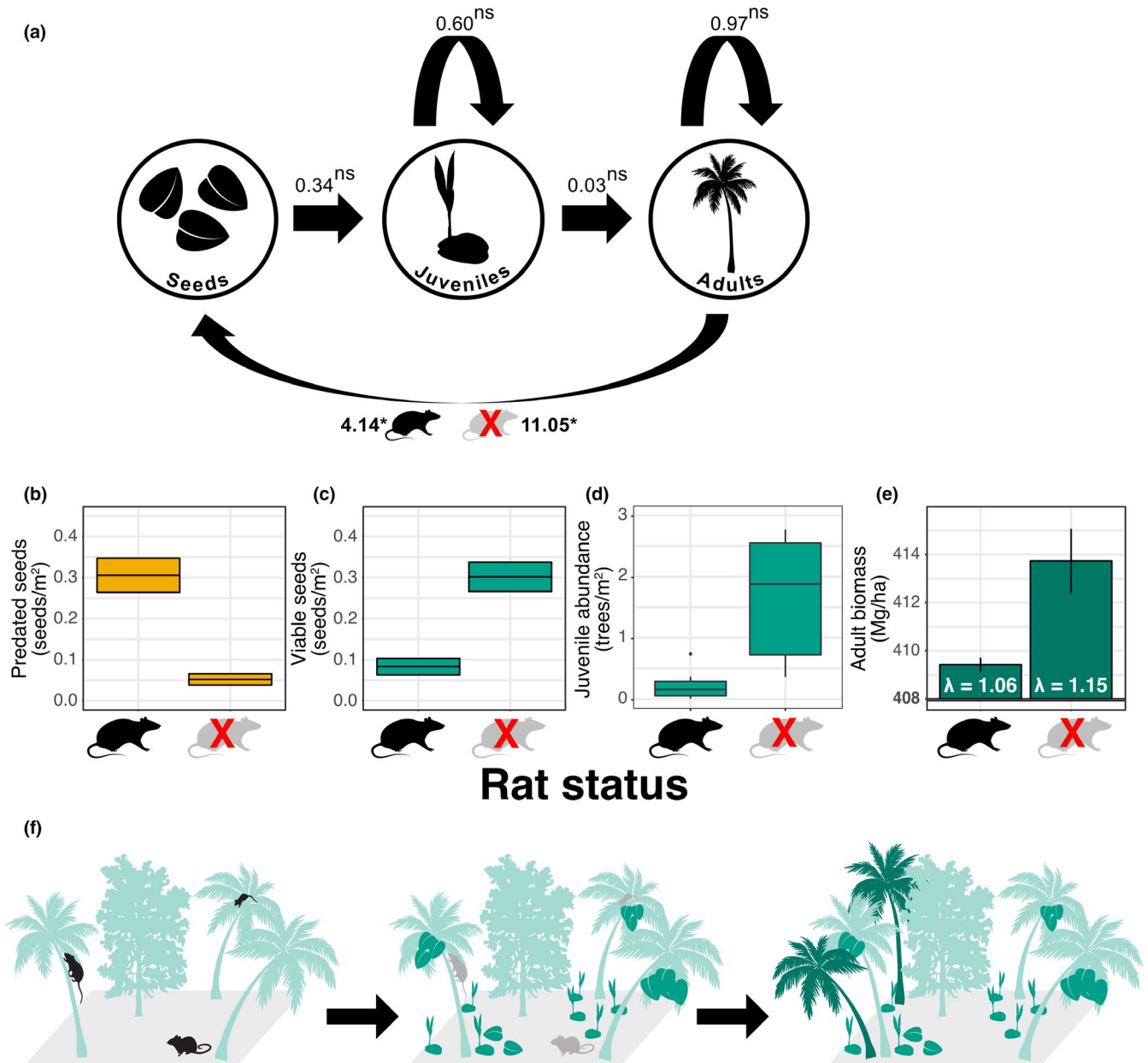
FIGURE 3 aA stage-structured demographic model for *Cocos nucifera* (a). The value on each arrow indicates a rate of survival or transition within or between stages. Only fecundity (number of mature seeds produced per adult tree per year) significantly changed following eradication. (Statistical significance across years with and without rats denoted with *, statistically indistinguishable change denoted by "ns".) Black rats predated seeds (b), controlling viable seed numbers (c) (values given in terms of the average number of seeds per square meter quadrat). Juvenile abundance (d) increased from an average 0.23 to 1.67 per square meter in each plot. In the first three generations (12 years), projected additional aboveground tree biomass in *Cocos nucifera* (e) significantly increased from an average of 1.42 to 5.73 Mg/ha as population growth rate (λ) increased. (f) Forest aboveground tree biomass along a temporal trajectory: invaded (left), immediate eradication response (center), and long-term projections of increased tree biomass in the absence of rodent seed predators (right), where changes at each temporal step are indicated by increasingly darker colors. (vector images: Ana Miller-ter Kuile and Shutterstock)

quadrats (25% of quadrats) post-eradication. The best model for the number of viable seeds had a negative binomial error structure and included eradication status as the fixed effect and plot as a random effect (*marginal* $R^2 = .13$, *conditional* $R^2 = .28$, pairwise difference between pre- and post-eradication marginal means significant with p-value < .001; Appendix S2). The best model for the number of predated seeds had a Poisson error structure and included eradication status as a fixed effect and plot as a random effect (*marginal* $R^2 = .15$,

conditional $R^2 = .58$, pairwise difference between pre- and post-eradication marginal means significant with p-value < .001; Appendix S2).

3.2 | Short-term changes in aboveground biomass

There was a significant increase in juvenile tree biomass following eradication (Figure 3c), increasing from an average of 0.69 (*SD* 0.50)
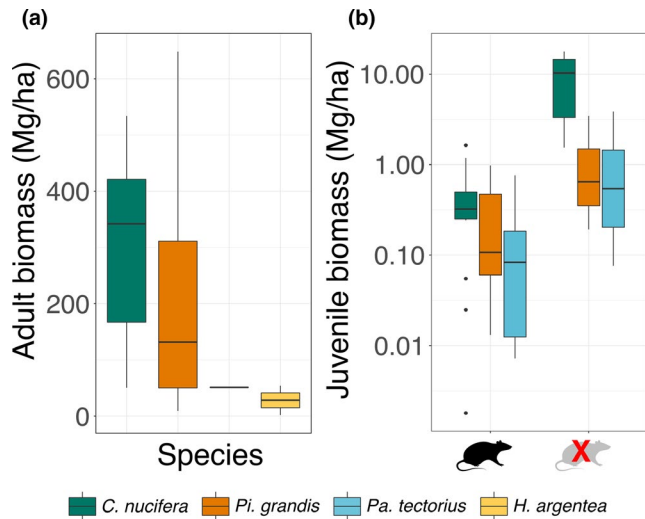
FIGURE 4 aIn our plots, *C. nucifera* is the species with highest adult tree biomass (a) and juveniles of this species had the most marked biomass response to black rat eradication (b). (vector image: Shutterstock)

to 9.48 (*SD* 5.97) Mg/ha (*n* = 27). This increase was primarily driven by increases in juvenile *C. nucifera*, which accounted for 73% of the total increased juvenile biomass, though two other species (*Pa. tectorius* and *Pi. grandis*) also increased in biomass (Figure 4). Juvenile biomass was best predicted by a model with eradication status as fixed effect and plot as random effect (pairwise difference between marginal means: *p*-value < .001; Appendix S2). This is consistent with results from yearly juvenile abundance repeated measures ANOVA. Precipitation was not significantly different across pre- and post-eradication years (Appendix S4).

3.3 | Demographic modeling and estimates of long-term biomass change

Modeled future aboveground biomass significantly increased following eradication (Figure 3d). Fecundity significantly increased following eradication, increasing from 4.14 (*SD* 8.99) to 11.05 (*SD* 12.23) viable seeds per tree per year. No other vital rates significantly changed between pre- and post-eradication (Table 1, Appendix S3). In the first juvenile generation (12 years), there was an increase in the added aboveground biomass in the plots (Wilcoxon signed-rank test, *p*-value = .02), with aboveground biomass added via recruitment increasing from an average of 1.42 (*SD* 0.82) to 5.73 (*SD* 3.62) Mg/ha per plot. Examination of elasticities for both models shows adult survival has the greatest effect on population growth rate (Table 1).

4 | DISCUSSION

Black rats, through seed predation, reduced juvenile recruitment and aboveground biomass of the introduced palm tree species *C. nucifera*

TABLE 1 Rates of survival, growth, and reproduction (vital rates), elasticities (relative importance of each rate for population growth), and population growth rates (λ) for stage-structured demographic models of *Cocos nucifera* with and without rat seed predation (vital rate determinations in Appendix S3)

Model (growth rate, λ)	Vital rate (per year)	Value	Elasticity
With rats (λ = 1.06)	Seed to juvenile transition	0.34	0.06
	Juvenile survival	0.60	0.09
	Juvenile to adult transition	0.03	0.06
	Adult survival	0.97	0.72
	Fecundity	4.04[a]	0.06
Without rats (λ = 1.15)	Seed to juvenile transition	0.34	0.11
	Juvenile survival	0.60	0.11
	Juvenile to adult transition	0.03	0.11
	Adult survival	0.97	0.57
	Fecundity	11.05[a]	0.11

[a]Significantly different based on quadrat seed counts.

(a 24-fold increase). Through seed predation or seedling herbivory, black rats also limited juvenile recruitment and biomass of at least two native tree species (*Pa. tectorius* and *Pi. grandis*), but to a lesser degree (11-fold). These data support a previous finding of the recent increases in seedling abundance on Palmyra Atoll (Wolf et al., 2018) and further elaborate on the mechanisms driving these increases. Specifically, the present study illustrates that rat seed predation operated as a key control on introduced *C. nucifera* populations. Here, we show, based on demographic models informed by repeatedly surveyed permanent plot data, how increases in fecundity (undamaged seed production) and juvenile recruitment in *C. nucifera* will lead to an increase in adult recruitment in this species, increasing total aboveground biomass and changing the species composition of biomass pools on the island. In this system, in particular, the negative effects of the non-native *C. nucifera* on island food webs, even in the presence of black rats, are well-established (*C. nucifera* deters nesting seabirds, thus removing guano subsidies; reviewed in Young et al., 2017). This study demonstrates that this negative effect could be compounded by the eradication of an introduced seed predator (black rats), thus highlighting the need for further management intervention. More broadly, while island rodents are known to consume seeds and fruit (Drake et al., 2011), this study provides an important demonstration of how seed predation can influence entire island ecosystems from short-term changes for plant community composition, to long-term shifts in ecological functions related to plant biomass, such as carbon storage and decomposition (i.e., ecosystem-level eradication: Zavaleta, Hobbs, & Mooney, 2001).

The ecological and conservation outcomes on Palmyra Atoll highlight the importance of considering seed predation as a

critical management element associated with the removal of invasive rodents. On Palmyra, juvenile recruitment and biomass of an introduced tree (*C. nucifera*) responded at greater magnitudes (2–5 times) than other tree species to seed predation release, even though all these tree species were heavily targeted by rodent seed predators and have seen some population recovery following eradication (Wegmann, 2009; Wolf et al., 2018). The differential responses of plant species to rat eradication may be due to rat food preference, inability to effectively kill seeds of a species (thus providing a benefit as a seed disperser), the reproductive ability of the tree, the tree's ability to escape predation by other seed predators when rats are not in the system, or a combination of these or other factors (Clark, 1981; Hayes & Barry, 2008; Nigro et al., 2017; Young, Mccauley, Guevara, et al., 2013). In this system, it is likely that the differential advantage of *C. nucifera* comes from the natural history of the tree, since evidence from rat husking stations on Palmyra Atoll suggest that rats predate seeds of most of the canopy trees in this system and cause seed mortality in the majority of predation events for all seed species, thus providing little or no benefit as a seed disperser for this or other tree species (Wegmann, 2009). Although we saw some evidence that the coconut crab (*Birgus latro*), the only native seed predator effective at predating *C. nucifera* seeds once they reach the ground, is predating some seeds in the absence of rats, the relative rarity of this predation compared to rat predation suggests that coconut crabs will not compensate for rats in the short term. However, the increased frequency with which coconut crabs are now observed in *C. nucifera* forests following black rat eradication suggests this is a process that warrants longer-term monitoring (Nigro et al., 2017). *B. latro* and other terrestrial crabs in this system (hermit crabs: *Coenobita brevimanus* and *Coenobita perlatus* and land crabs: *Cardisoma carnifex* and *Cardisoma rotundum*) preferentially predate seeds of rare tree species, so the disproportionate immediate benefit to *C. nucifera* may only be exacerbated by seed selection of native seed predators for seeds of rarer canopy trees (Nigro et al., 2017; Young, Mccauley, Dunbar, et al.,). The conservation implications of the increased competitive advantage of an introduced tree (*C. nucifera* in this case) means that the detrimental effects of yet another invasive species become magnified by rat eradication (i.e., Bergstrom et al., 2009). On Palmyra, the negative effects of this tree species are already known: *C. nucifera* deters seabird nesting on Palmyra, thus stopping the provision of seabird guano to native plant communities dependent on these subsidies. In this system, in particular, the effects of rat eradication on *C. nucifera* make imperative an extensive secondary intervention to remove and control this invasive species.

While shifts in plant communities led to immediate changes for the island ecosystem (i.e., Nigro et al., 2017; Wolf et al., 2018), our demographic models highlight that the effects of seed predation release on island ecosystems can potentially reverberate through decades (or even longer periods) of succession dynamics. Similar to other systems modeling palm demography, population growth rate (and thus total biomass) is disproportionately determined by changes in the number of seedlings that germinate, survive, and reach adulthood (Pinard & Putz, 1992). Increased total tree biomass in *C. nucifera* on Palmyra will likely alter a diverse range of ecological functions on the atoll, including carbon storage, nutrient cycling, and primary productivity (Bello et al., 2015; Chave et al., 2006; Sayer, 2006; Sayer et al., 2011, 2012; Sayer, Powers, & Tanner, 2007). Currently, the increase in the proportion of biomass in juvenile life stages (an increase from 0.08% to 1.43%) has likely altered rates of decomposition and soil respiration through an increase in the number of juveniles germinating and then dying in the understory (Chomel et al., 2016; Quested, Eriksson, Fortunel, & Garnier, 2007). In the long term, a shift in the species composition, and therefore of productivity and biomass (increasingly more *C. nucifera* -dominated), has the potential to substantially alter rates of decomposition and nutrient cycling (Quested et al., 2007). The demographic models ignore potential responses in other seed predators (here, land crabs) or stochastic events that may alter successional dynamics (i.e., storms, climatic conditions) but highlight that island responses to seed predation release may occur on long time scales and in other island systems successional trajectories may be reasonably predicted using modeling approaches.

These ecosystem-level effects of invasive rodents and their eradication have important implications for the management and restoration of islands and island biodiversity. While the ecological regime-shifting potential of invasive rodents on seabird islands has been observed across many islands in New Zealand (Fukami et al., 2006), this work from Palmyra Atoll contributes to a smaller body of literature examining ecological regime shifts through the mechanisms of seed predation and the ecosystem effects of rodent seed predator eradication (Grant-Hoffman et al., 2010a, 2010b). In the case of Palmyra, unlike on the islands of New Zealand, the effects of seed predation are decoupled from those of burrowing seabirds since Palmyra does not have nesting populations of these seabirds and demonstrates that seed predation alone can be an important ecological driver. In all these cases, invasive plants often become common on islands following eradications, making subsequent management necessary or advised to curb island ecosystem degradation (Grant-Hoffman et al., 2010b). On Palmyra as with other tropical atolls where abandoned agro-forestry has shifted plant communities in favor of cultivated crops, the effects of rat eradication may increase the rate of spread of naturalized crop plants, putting much of the remaining habitats for important island species (i.e., island endemics and nesting seabirds) in greater jeopardy (Thaman, 2016; Young et al., 2017). These studies emphasize the need to view eradications as part of holistic management plans to avoid ecological regime shifts (i.e., Zavaleta et al., 2001).

The observed plant responses on Palmyra suggest important insights for future island rodent eradications. Foremost, it is imperative to revisit the trophic ecology of invasive rodents and refine eradication efforts considering all organisms likely to respond to eradications. Specifically, as seeds and fruit constitute the majority of the diet of black rats (Shiels & Pitt, 2014), eradication efforts of this species need to document plant responses. This may

change the prioritization of islands for rodent eradication based on the restoration of important elements of the flora that support island fauna (Capizzi, Baccetti, & Sposimo, 2010; Harris, Gregory, Bull, & Courchamp, 2012; Holmes, 2019). Incorporating plant responses into eradication monitoring may require a combination of field and modeling approaches since many plants, including those in this study, respond on longer time scales than the time span of most eradication monitoring programs. Appropriate temporal scales need to be built into eradication programs because long-lived trees are foundational species that shape ecosystem structure and function (Ellison et al., 2005). With Palmyra Atoll as a case study, the immediate recoveries of island communities following release from the effects of rats may be outweighed by the long-term expansion of invasive tree species, favoring ecosystem processes that are actively detrimental to native biodiversity (Young et al., 2017). Many islands host multiple invasive species and often these species interact, so eradications should be done with care to ensure recovery of stable and regenerating ecosystems rather than deteriorated alternative ecological states (Suding et al., 2004; Tershy et al., 2015). Indeed, understanding the interactions between invasive species on islands and how these influence ecosystems therein is an important area of current and future study that starts with understanding the breadth of ecological effects of invasive species.

ACKNOWLEDGEMENTS

AUTHOR CONTRIBUTIONS

AM-tK, DO, HY, and RD conceived the ideas and designed methodology; HY, RD, and DM received funding for this project; AM-tK, DO, AB, RD, MK, DM, CM, and HY collected data; AM-tK, DO, and MK analyzed the data; AM-tK led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.xsj3tx9cp (Miller-ter Kuile et al., 2020).

ORCID

Ana Miller-ter Kuile https://orcid.org/0000-0003-2599-5158

REFERENCES

Ashish, S. S., Vidyasagaran, K., Kumar, V., & Ajeesh, R. (2015). Evaluation of leaf biomass production and fibre properties of *Pandanus tectorius* in the coastal plains of Thrissur District, Kerala. India. *Indian Journal of Tropical Biodiversity*, 23, 69–73.

Atkinson, I. (1985). The spread of commensal species of *Rattus* to oceanic islands and their effects on island avifaunas. In P. Moors (Ed.), *Conservation of Island Birds* (pp. 35–81). Cambridge: ICBP Technical Publication.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48.

Bello, C., Galetti, M., Pizo, M. A., Magnago, L. F. S., Rocha, M. F., Lima, R. A. F., … Jordano, P. (2015). Defaunation affects carbon storage in tropical forests. *Science Advances*, 18, 1–10.

Bergstrom, D. M., Lucieer, A., Kiefer, K., Wasley, J., Belbin, L., Pedersen, T. K. and Chown, S. L. (2009). Indirect effects of invasive species removal devastate World Heritage Island. *Journal of Applied Ecology*, 46, 73–81.

Burnham, K. P., & Anderson, D. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*, 2nd ed. New York, NY: Springer-Verlag.

Buxton, R., Taylor, G., Jones, C., Lyver, P. O. B., Cree, A., Towns, D., … Towns, D. (2016). Spatio-temporal changes in density and distribution of burrow-nesting seabird colonies after rat eradication. *New Zealand Journal of Ecology*, 40, 88–99.

Campbell, D. J., & Atkinson, I. A. E. (2002). Depression of tree recruitment by the Pacific rat (*Rattus exulans* Peale) on New Zealand's northern offshore islands. *Biological Conservation*, 107, 19–35.

Capizzi, D., Baccetti, N., & Sposimo, P. (2010). Prioritizing rat eradication on islands by cost and effectiveness to protect nesting seabirds. *Biological Conservation*, 143, 1716–1727.

Caswell, H. (2001). *Matrix population models*. Sunderland, MA: Sinauer Associates Inc.

Chave, J., Andalo, C., Brown, S., Cairns, M. A., Chambers, J. Q., Eamus, D., … Yamakura, T. (2005). Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia*, 145, 87–99.

Chave, J., Muller-Landau, H. C., Baker, T. R., Easdale, T. A., Hans Steege, T. E. R., & Webb, C. O. (2006). Regional and phylogenetic variation of wood density across 2456 neotropical tree species. *Ecological Applications*, 16, 2356–2367.

Chomel, M., Guittonny-Larchev, M., Fernandez, C., Gallet, C., Desrochers, A., Pare, D., … Baldy, V. (2016). Plant secondary metabolites: A key driver of litter decomposition and soil nutrient cycling. *Journal of Ecology*, 104, 1527–1541.

Clark, D. (1981). Foraging patterns of black rats across a desert-montane forest gradient in the Galapagos Islands. *Biotropica*, 13, 182–194.

Climate Action Reserve (2017) Hawaii wood density values. Biomass equations - For. Carbon Protoc. Retrieved from http://www.climateactionreserve.org/how/protocols/forest/biomass-equations/ [Accessed December 17, 2018]

Croll, D. A., Maron, J. L., Estes, J. A., Danner, E. M., & Byrd, G. V. (2005). Introduced predators transform subarctic Islands from Grassland to Tundra. *Science*, 307, 1959–1961.

Dawson, E. Y. (1959). Changes in palmyra atoll and its vegetation through the activities of man, 1913–1958. *Pacific Nature*, I, 1–51.

Diise (2015). The Database of Island Invasive Species Eradications. Isl. Conserv. Coast. Conserv. Action Lab. UCSC, IUCN SSC Invasive Species Spec. Group, Univ. Auckl. Landcare Res. New Zeal.

Dons, K., Bhattarai, S., Meilby, H., Smith-Hall, C., & Panduro, T. E. (2016). Indirect approach for estimation of forest degradation in non-intact dry forest: Modelling biomass loss with Tweedie distributions. *Carbon Balance and Managment*, 11(14), 1–10.

Drake, D. R., Bodey, T., Russell, J. C., Towns, D. R., Nogales, M., & Ruffino, L. (2011). Direct impacts of seabird predators on island biota other than seabirds. In C. P. H. Mulder, W. B. Anderson, D. R. Towns & P. J. Bellingham (Eds.), *Seabird Islands: Ecology, invasion, and restoration*, (91–132). Oxford, UK: Oxford University Press.

Dransfield John, Cooke David (1999). Plate 355. Cocos nucifera Arecaceae. *Curtis's Botanical Magazine*, 16, (1), 2–9. http://dx.doi.org/10.1111/1467-8748.00188

Ellison, A. M., Bank, M. S., Clinton, B. D., Colburn, E. A., Elliott, K., Ford, C. R., ... Webster, J. R. (2005). Loss of foundation species: Consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment*, 3, 479–486. https://doi.org/10.1890/1540-9295(2005)003[0479:LOFSCF]2.0.CO;2

Fukami, T., Wardle, D. A., Bellingham, P. J., Mulder, C. P. H., Towns, D. R., Yeates, G. W., ... Williamson, W. M. (2006). Above- and below-ground impacts of introduced predators in seabird-dominated island ecosystems. *Ecology Letters*, 9, 1299–1307. https://doi.org/10.1111/j.1461-0248.2006.00983.x

Grant-Hoffman, M. N., & Barboza, P. S. (2010). Herbivory in invasive rats: Criteria for food selection. *Biological Invasions*, 12, 805–825. https://doi.org/10.1007/s10530-009-9503-7

Grant-Hoffman, M. N., Mulder, C. P. H., & Bellingham, P. J. (2010a). Effects of invasive rats and burrowing seabirds on seeds and seedlings on New Zealand islands. *Oecologia*, 162, 1005–1016. https://doi.org/10.1007/s00442-009-1500-0

Grant-Hoffman, M. N., Mulder, C. P. H., & Bellingham, P. J. (2010b). Invasive rats alter woody seedling composition on seabird-dominated islands in New Zealand. *Oecologia*, 163, 449–460. https://doi.org/10.1007/s00442-009-1523-6

Gunn, B. F., Baudouin, L., & Olsen, K. M. (2011). Independent origins of cultivated coconut (*Cocos nucifera* L.) in the old world tropics. *PLoS One*, 6, e21143. https://doi.org/10.1371/journal.pone.0021143

Harper, G. A., & Bunbury, N. (2015). Invasive rats on tropical islands: Their population biology and impacts on native species. *Global Ecology and Conservation*, 3, 607–627. https://doi.org/10.1016/j.gecco.2015.02.010

Harries, H. C. (1978). The evolution, dissemination and classification of *Cocos nucifera* L. *Botanical Review*, 44, 265–319.

Harris, D. B., Gregory, S. D., Bull, L. S., & Courchamp, F. (2012). Island prioritization for invasive rodent eradications with an emphasis on reinvasion risk. *Biological Invasions*, 14, 1251–1263.

Hartig, F. (2020). DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.3.2.0.. https://CRAN.R-project.org/package=DHARMa

Hayes, K. R., & Barry, S. C. (2008). Are there any consistent predictors of invasion success? *Biological Invasions*, 10, 483–506.

Hays, B. B. R., Sperry, J., Drake, D. R., & Hruska, A. M. (2018). Husking stations provide insight into the diet of non-native rodents on O'ahu, Hawai'i. *Pacific Science*, 72, 335–344.

Holmes N. D., Spatz D. R., Oppel S., Tershy B., Croll D. A., Keitt B., ... Butchart S. H. M. (2019). Globally important islands where eradicating invasive mammals will benefit highly threatened vertebrates. *PLOS ONE*, 14(3), e0212128. https://doi.org/10.1371/journal.pone.0212128

Jones, H. (2010). Seabird islands take mere decades to recover following rat eradication. *Ecological Applications*, 20, 2075–2080.

Jones, H. P., Holmes, N. D., Butchart, S. H. M., Tershy, B. R., Kappes, P. J., Corkery, I. ... Croll, D. A. (2016). Invasive mammal eradication on islands results in substantial conservation gains. *Proceedings of the National Academy of Sciences USA*, 113, 4033–4038.

Jones, H. P., Tershy, B. R., Zavaleta, E. S., Croll, D. A., Keitt, B. S., Finkelstein, M. E., & Howald, G. R. (2008). Severity of the effects of invasive rats on seabirds: A global review. *Conservation Biology*, 22, 16–26.

Lafferty, K. D., Mclaughlin, J. P., Gruner, D. S., Bogar, T. A., Bui, A., Childress, J. N., ... Young, H. S. (2018). Local extinction of the Asian tiger mosquito (*Aedes albopictus*) following rat eradication on Palmyra Atoll. *Biology Letters*, 14, 1–5.

Le Corre, M.,Danckwerts, D. K., Ringler, D., Bastien, M., Orlowski, S., Morey Rubio, C., Pinaud, D. and Micol, T. (2015). Seabird recovery and vegetation dynamics after Norway rat eradication at Tromelin Island, western Indian Ocean. *Biological Conservation*, 185, 85–94.

Lecomte, J. B., Benoît, H. P., Ancelet, S., Etienne, M. P., Bel, L., & Parent, E. (2013). Compound Poisson-gamma vs. delta-gamma to handle zero-inflated continuous data under a variable sampling volume. *Methods in Ecology and Evolution*, 4, 1159–1166.

Malhotra, S. K., & Welfare, F. (2017). Diagnosis and management of soil fertility constraints in coconut (*Cocos nucifera*): A review. *Indian Journal of Agricultural Sciences*, 87, 711–726.

Maron, J. L., Hajek, K. L., Hahn, P. G., & Pearson, D. E. (2018). Rodent seed predators and a dominant grass competitor affect coexistence of co-occurring forb species that vary in seed size. *Journal of Ecology*, 106, 1795–1805.

Maron, J. L., & Pearson, D. E. (2011). Vertebrate predators have minimal cascading effects on plant production or seed predation in an intact grassland ecosystem. *Ecology Letters*, 14, 661–669.

Matisoo-Smith, E., & Robins, J. H. (2004). Origins and dispersals of Pacific peoples: Evidence from mtDNA phylogenies of the Pacific rat. *Proceedings of the National Academy of Sciences of the United States of America*, 101, 9167–9172.

Meyer, J. Y., & Butaud, J. F. (2009). The impacts of rats on the endangered native flora of french Polynesia (Pacific Islands): Drivers of plant extinction or coup de grâce species? *Biological Invasions*, 11, 1569–1585.

Miller-ter Kuile, A., Orr, D., Bui, A., Dirzo, R., Klope, M., Mccauley, D., ...Young, H. (2020). Data from: Impacts of rodent eradication on seed predation and plant community biomass on a tropical atoll. Dryad Digital Repository, https://doi.org/10.5061/dryad.xsj3tx9cp

Mulder, C. P. H., Grant-Hoffman, M. N., Towns, D. R., Bellingham, P. J., Wardle, D. A., Durrett, M. S., ... Bonner, K. I. (2009). Direct and indirect effects of rats: Does rat eradication restore ecosystem functioning of New Zealand seabird islands? *Biological Invasions*, 11, 1671–1688.

Navarro, M. N. V., Jourdan, C., Sileye, T., Braconnier, S., Mialet-Serra, I., Saint-Andre, L., ... Roupsard, O. (2008). Fruit development, not GPP, drives seasonal variation in NPP in a tropical palm plantation. *Tree Physiology*, 28, 1661–1674.

Nigro, K. M., Hathaway, S. A., Wegmann, A. S., Miller-ter Kuile, A., Fisher, R. N., & Young, H. S. (2017). Stable isotope analysis as an early monitoring tool for community-scale effects of rat eradication. *Restoration Ecology*, 25, 1015–1025.

Parkes, J., Fisher, P., & Forrester, G. (2011). Diagnosing the cause of failure to eradicate introduced rodents on islands: Brodifacoum versus diphacinone and method of bait delivery. *Conservation Evidence*, 8, 100–106.

Pender, R. J., Shiels, A. B., Bialic-Murphy, L., & Mosher, S. M. (2013). Large-scale rodent control reduces pre- and post-dispersal seed predation of the endangered Hawaiian lobeliad, *Cyanea superba* subsp. *superba* (Campanulaceae). *Biological Invasions*, 15, 213–223.

Pimm, S. L., Jenkins, C. N., Abell, R., Brooks, T. M., Gittleman, J. L., Joppa, L. N., ... Sexton, J. O. (2014). The biodiversity of species and their rates of extinction, distribution, and protection. *Science*, 344, 987. https://doi.org/10.1126/science.1246752

Pinard, M. A., & Putz, F. E. (1992). Population matrix models and palm resource management. *Bulletin De L'institut Français D'études Andines*, 21, 637–649.

Quested, H., Eriksson, O., Fortunel, C., & Garnier, E. (2007). Plant traits relate to whole-community litter quality and decomposition following land use change. *Functional Ecology*, 21, 1016–1026. https://doi.org/10.1111/j.1365-2435.2007.01324.x

Rist, L., Kaiser-Bunbury, C. N., Fleischer-Dogley, F., Edwards, P., Bunbury, N., & Ghazoul, J. (2010). Sustainable harvesting of coco de mer, Lodoicea maldivica, in the Vallée de Mai, Seychelles. *Forest Ecology and Management*, 260, 2224–2231. https://doi.org/10.1016/j.foreco.2010.09.032

Sayer, E. J. (2006). Using experimental manipulation to assess the roles of leaf litter in the Functioning of forest ecosystems. *Biological Reviews*, *81*, 1–31. https://doi.org/10.1017/S1464793105006846

Sayer, E. J., Heard, M. S., Grant, H. K., Marthews, T. R., & Tanner, E. V. J. (2011). Soil carbon release enhanced by increased tropical forest litterfall. *Nature Climate Change*, *1*, 304–307. https://doi.org/10.1038/nclimate1190

Sayer, E. J., Joseph Wright, S., Tanner, E. V. J., Yavitt, J. B., Harms, K. E., Powers, J. S., ... Turner, B. L. (2012). Variable responses of lowland tropical forest nutrient status to fertilization and litter manipulation. *Ecosystems*, *15*, 387–400. https://doi.org/10.1007/s10021-011-9516-9

Sayer, E. J., Powers, J. S., & Tanner, E. V. J. (2007). Increased litterfall in tropical forests boosts the transfer of soil CO_2 to the atmosphere. *PLoS One*, *2*, 1–6. https://doi.org/10.1371/journal.pone.0001299

Service, U. OF H. C. E (1996). Coconut Palms from Seed. Univ. Hawaii, Manoa Coll. Trop. Agric. Hum. Resour. Fact Sheet Ornamentals Flowers.

Shiels, A. B., & Drake, D. R. (2011). Are introduced rats (Rattus rattus) both seed predators and dispersers in Hawaii? *Biological Invasions*, *13*, 883–894. https://doi.org/10.1007/s10530-010-9876-7

Shiels, A. B., & Pitt, W. C. (2014). a review of invasive rodent (Rattus spp. and Mus musculus) diets on Pacific Islands. *Proceedings of the Vertebrate Pest Conference*, *26*, 161–165. https://doi.org/10.5070/V426110336

Shiels, A. B., Pitt, W. C., Sugihara, R. T., & Witmer, G. W. (2014). Biology and Impacts of Pacific Island Invasive Species. 11. *Rattus rattus*, the Black Rat (Rodentia: Muridae). *Pacific Science*, *68*, 145–184.

Silva Matos, D. M., Freckleton, R. P., & Watkinson, A. R. (2013). The role of density dependence in the population dynamics of a tropical palm. *Ecology*, *80*, 2635–2650. https://doi.org/10.1890/0012-9658(1999)080[2635:TRODDI]2.0.CO;2

Suding, K. N., Gross, K. L., & Houseman, G. R. (2004). Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology & Evolution*, *19*, 46–53. https://doi.org/10.1016/j.tree.2003.10.005

Tershy, B. R., Shen, K. W., Newton, K. M., Holmes, N. D., & Croll, D. A. (2015). The importance of islands for the protection of biological and linguistic diversity. *BioScience*, *65*, 592–597. https://doi.org/10.1093/biosci/biv031

Thaman, R. R. (2016). Atolls of the tropical pacific Ocean: Wetlands under threat. In C. Finlayson, G. Milton, R. Prentic, & N. Davidson (Eds.), *The Wetland Book*, (1–25). Dordrecht, The Netherlands: Springer. https://doi.org/10.1007/978-94-007-6173-5_270-1

Towns, D. R., Atkinson, I. A. E., & Daugherty, C. H. (2006). Have the harmful effects of introduced rats on islands been exaggerated? *Biological Invasions*, *8*, 863–891. https://doi.org/10.1007/s10530-005-0421-z

Wegmann, A. (2009). *Limitations to tree seedling recruitment at Palmyra Atoll*. Honolulu: University of Hawaii at Manoa.

Wolf, C. A., Young, H. S., Zilliacus, K. M., Wegmann, A. S., Mckown, M., Holmes, N. D., ... Croll, D. A. (2018). Invasive rat eradication strongly impacts plant recruitment on a tropical atoll. *PLoS One*, *13*(7), 1–17.

Young, H. S., McCauley, D. J., & Dirzo, R. (2011). Differential responses to guano fertilization among tropical tree species with varying functional traits. *American Journal of Botany*, *98*, 207–214. https://doi.org/10.3732/ajb.1000159

Young, H. S., Mccauley, D. J., Guevara, R., & Dirzo, R. (2013). Consumer preference for seeds and seedlings of rare species impacts tree diversity at multiple scales. *Oecologia*, *172*, 857–867. https://doi.org/10.1007/s00442-012-2542-2

Young, H. S., Miller-ter Kuile, A., Mccauley, D. J., & Dirzo, R. (2017). Cascading community and ecosystem consequences of introduced coconut palms (*Cocos nucifera*) in tropical islands. *Canadian Journal of Zoology*, *95*, 139–148.

Young, H. S., Raab, T. K., Mccauley, D. J., Briggs, A. A., and Dirzo, R. (2010). The coconut palm, *Cocos nucifera*, impacts forest composition and soil characteristics at Palmyra Atoll, Central Pacific. *Journal of Vegetation Science*, *21*, 1058–1068.

Zavaleta, E. S., Hobbs, R. J., & Mooney, H. A. (2001). Viewing invasive species removal in a whole-ecosystem context. *Trends in Ecology & Evolution*, *16*, 454–459. https://doi.org/10.1016/S0169-5347(01)02194-2

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*, New York: Springer.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Miller-ter Kuile A, Orr D, Bui A, et al. Impacts of rodent eradication on seed predation and plant community biomass on a tropical atoll. *Biotropica*. 2021;53:232–242. https://doi.org/10.1111/btp.12864