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Microhabitat heterogeneity and a non-native avian frugivore drive the population dynamics of an island endemic shrub, *Cyrtandra dentata*

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Summary

1. Understanding the role of environmental change in the decline of endangered species is critical for designing scale-appropriate restoration plans. For locally endemic rare plants on the brink of extinction, frugivory can drastically reduce local recruitment by dispersing seeds away from geographically isolated populations. Dispersal of seeds away from isolated populations can ultimately lead to population decline. For localized endemic plants, fine-scale changes in microhabitat can further limit population persistence. Evaluating the individual and combined impact of frugivores and microhabitat heterogeneity on the short-term (i.e. transient) and long-term (i.e. asymptotic) dynamics of plants will provide insight into the drivers of species rarity.

2. In this study, we used 4 years of demographic data to develop matrix projection models for a long-lived shrub, *Cyrtandra dentata* (H. St. John & Storey) (Gesneriaceae), which is endemic to the island of O'ahu in Hawai'i. Furthermore, we evaluated the individual and combined influence of a non-native frugivorous bird, *Leiothrix lutea*, and microhabitat heterogeneity on the short-term and long-term *C. dentata* population dynamics.

3. Frugivory by *L. lutea* decreased the short-term and long-term population growth rates. However, under the current level of frugivory at the field site the *C. dentata* population was projected to persist over time. Conversely, the removal of optimum microhabitat for seedling establishment (i.e. rocky gulch walls and boulders in the gulch bottom) reduced the short-term and long-term population growth rates from growing to declining.

4. Survival of mature *C. dentata* plants had the greatest influence on long-term population dynamics, followed by the growth of seedlings and immature plants. The importance of mature plant survival was even greater when we simulated the combined effect of frugivory and the loss of optimal microhabitat, relative to population dynamics based on field conditions. In the short-term (10 years), however, earlier life stages had the greatest influence on population growth rate.

5. *Synthesis and applications*. This study emphasizes how important it is to decouple rare plant management strategies in the short vs. long-term in order to prioritize restoration actions, particularly when faced with multiple stressors not all of which can be feasibly managed. From an applied conservation perspective, our findings also illustrate that the life stage that, if improved by management, would have the greatest influence on population dynamics is dependent on the timeframe of interest and initial conditions of the population.

Key-words: avian frugivory, *Cyrtandra dentata*, elasticity analysis, endangered species, microhabitat heterogeneity, plant population dynamics, restoration ecology, stage-structured demographic model, stochastic demography, transient dynamics

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Introduction

The spatial distribution and abundance of organisms are shaped by interactions with the environment. Human-induced changes in the environment, such as alterations in plant-animal interactions and degradation in abiotic conditions, influence demographic vital rates (i.e. survival, growth, and reproduction) and population dynamics, such as the population growth rate. Recent research suggests that plant endangerment is the result of the combined influence of multiple environmental stressors (Sala *et al.* 2000; Didham *et al.* 2007; Brook, Sodhi & Bradshaw 2008). To explicitly evaluate the individual or combined influence of targeted environmental change on population growth rate requires a demographic modelling approach (Morris & Doak 2002). Though many demographic studies have quantified the influence of various environmental factors on plant population dynamics, few studies have focused on the individual or combined impact of non-native frugivores and alterations in abiotic conditions (Godínez-Alvarez & Jordano 2007; Loayza & Knight 2010).

Tropical islands are biodiversity hotspots and, unfortunately, have some of the highest rates of extinction and species endangerment. For these reasons, tropical island ecosystems are often ranked as high conservation priority (Mittermeier *et al.* 1998; Myers *et al.* 2000). The high rates of extinction and species endangerment on islands are due, in part, to the sheer number of localized endemic species (Shaffer 1981; Gilpin & Soule 1986; Menges 1990; Brigham & Schwartz 2003). Due to their geographically limited ranges and adaptations to narrow ecological conditions (Brown 1984), island endemic plants are likely more sensitive to environmental change than common widespread species. As a consequence, even small-scale changes in the environment may have a disproportionally large effect on the population persistence of island plants. Thus, to effectively manage endangered species in an island context, it is critical to understand how changing environmental conditions influence population persistence (Mittermeier *et al.* 1998; Myers *et al.* 2000). Surprisingly, the demographic consequence of plant interactions with environmental stressors is rarely studied for localized island endemic species (but see, Krushelnycky *et al.* 2013; Simmons *et al.* 2012).

A primary environmental driver of biodiversity loss on islands is the introduction of non-native plants and animals (Wilcove *et al.* 1998). Some of the most successful non-native animals to invade island ecosystems are non-native frugivores (Meyer & Butaud 2009; Shiels *et al.* 2014). The effectiveness of non-native frugivores to replace the role of native frugivores is dependent on the ecological similarity of the dispersal agents (Schupp, Jordano & Gómez 2010). Removal of seeds from a population to microsites that are unfavourable for germination and establishment can lead to localized recruitment depression (Godínez-Alvarez, Valiente-Banuet & Rojas-Martínez 2002; Loayza & Knight 2010). In contrast, if seeds are not destroyed following consumption and are dispersed away from the population to suitable habitat for establishment, non-native frugivores could have a positive influence on plant dynamics by decreasing conspecific competition and increasing gene flow between isolated plant populations (Slatkin 1985; Howe 1986; Bacles, Lowe & Ennos 2006; Schupp, Jordano & Gómez 2010). Island species are also threatened by habitat degradation and altered abiotic conditions (Wilcove *et al.* 1998). Altered abiotic conditions, such as a reduction of optimal microhabitats, can have a particularly pronounced impact on seedling establishment (Fetcher, Strain & Oberbauer 1983; Eriksson & Ehrlen 1992; Dostálek & Münzbergová 2013). The suitability of microhabitat for seedling establishment can be highly variable among species. Important characteristics of optimal microhabitats for seedling establishment include light availability (Denslow 1980), substrate characteristics (Dostálek & Münzbergová 2013), disturbance frequency (Crawley & Nachapong 1985), and sufficient water availability (Fetcher, Strain & Oberbauer 1983).

In this study, we investigated the combined effects of abiotic and biotic environmental factors on the dynamics of a localized endemic shrub, *Cyrtandra dentata* (H. St. John & Storey) (Gesneriaceae), confined to a narrow ecological threshold on the Island of O'ahu in Hawai'i. The biotic stressor that we examined was a non-native generalist bird, *Leiothrix lutea*, and the abiotic factor that we assessed was alterations in microhabitats that varied in suitability for seedling establishment, optimal microhabitat (rock outcrops, defined as boulders covered by moss in the gulch bottom and the rocky gulch walls) and suboptimal microhabitat (soil). To assess how these environmental factors influence local population dynamics we asked the following questions: (i) Does seed frugivory by *L. lutea* and removal of optimal microhabitat influence the short and long-term population dynamics of *C. dentata*? (ii) Under what combination of these stressors does *C. dentata* maintain positive population growth over the short and long-term? (iii) What life stages and associated vital rates have the greatest influence on population growth rate over the short and long-term? (iv) Does the intensity of these stressors influence the relative importance of life stages and associated vital rates on the short and long-term population growth rates?

Materials and methods

STUDY SPECIES

Cyrtandra dentata is an endangered long-lived shrub endemic to the island of O'ahu in Hawai'i. *Cyrtandra dentata* reaches reproductive maturity at 0·8 m (L. Bialic-Murphy, unpublished data) and produces white subumbelliform cymes, 3–9 cm long with white fleshy ovate berries, 1–2·6 cm long (Wagner, Herbst & Sohmer 1999). The mean age of first reproduction for *C. dentata* is

6 years (L. Bialic-Murphy, unpublished data). The reproductive biology of *C. dentata* is poorly understood, but the white flowers it produces suggest it is moth pollinated (OANRP 2003). The mean number of *C. dentata* seeds per mature fruit is 1873 (L. Weisenberger, unpublished data) and mean seed size is ca. 0·5 mm long (Wagner, Herbst & Sohmer 1999). The *C. dentata* fruiting season is between September and November, with peak fruiting in October (L. Bialic-Murphy, unpublished data). The long-distance dispersal agents for *Cyrtandra* species in the Pacific is unresolved but columbiform birds have been implicated (Cronk *et al.* 2005). Previous research also suggests passive transport by water is a short-distance dispersal vector for Hawaiian *Cyrtandra* species (Kiehn 2001). Adventitious roots are produced from the lower section of the main stems, anchoring plants to soil, rocky gulch walls, and boulders in the gulch bottom (L. Bialic-Murphy, pers. obs.).

Historically, *C. dentata* spanned the northern Wai'anae Mountains and the leeward side of the northern Ko'olau Mountains on the island of O'ahu, 300–610 m in elevation (Wagner, Herbst & Sohmer 1999). The typical habitat is shady gulch bottoms of mesic to wet forests. In 1996, *C. dentata* was listed as endangered and by 2010, it was restricted to five geographically isolated locations (USFWS, 2012). Of those populations, only two sites, Kahanahāiki and Pahole to West Makaleha, have >16 mature plants and are representative of plants in earlier life stages (i.e. immature plants and seedlings).

Leiothrix lutea is one of the most common non-native generalist birds in Hawai'i. The body mass of males is 21·3 ± 0·28 g and the body mass of females is 21·21 ± 0·24 g (Male, Fancy & Ralph 1998). *Leiothrix lutea* gut passage time is unknown but the average gut passage time of avian seed and pulp consumers with similar body size (i.e. 19·9–23·8 g) is 1·73 hours (Herrera 1984). The diet preference of *L. lutea* is a mix of insects and small–seeded fruits (Male, Fancy & Ralph 1998). *Leiothrix lutea* primarily forage in the understory several metres off the ground, rapidly moving from plant to plant (Male, Fancy & Ralph 1998). The home range of *L. lutea* in Hawai'i is 3·07 ± 0·32 ha for males and 2·68 ± 0·27 ha for females (Male, Fancy & Ralph 1998). *Leiothrix lutea* pair formation occurs in March and breeding season is from March to mid August. During the non-breeding season, *L. lutea* are highly nomadic, moving in large flocks (<100 individuals) (Male, Fancy & Ralph 1998).

STUDY SITE AND MANAGEMENT HISTORY

We studied the demography of *C. dentata* in the Kahanahāiki Management Unit (36 ha), located in the northern Wai'anae Mountain Range, on the island of O'ahu (21° 32′ N, −158°12′ W). Kahanahāiki is a tropical mesic forest with a mix of native and non-native flora and fauna. The mean monthly rainfall is 53–227 mm (Giambelluca *et al.* 2013), and the mean daily temperature range is 16–24 °C (Shiels & Drake 2011). The Kahanahāiki population is one of the two known *C. dentata* locations, with more than 16 mature plants and has individuals in earlier life stages (i.e. seedlings and immature plants). The population is located in the main Kahanahāiki drainage, spanning from the base of a seasonal waterfall to c. 150 m to the north. Within the Kahanahāiki drainage, the plants are scattered throughout the gulch bottom and along the steep rock walls. Though plants occur throughout the study site, they are rooted in higher density on rock outcrops than on soil.

Since 1995, the O'ahu Army Natural Resources Program (OANRP) has managed the Kahanahāiki *C. dentata* population. Restoration efforts by OANRP included the control of feral pigs (*Sus scrofa*) and semi-annual suppression of ecosystem-altering invasive vegetation (OANRP, 2009). *Sus scrofa* directly impact many plants through their physical disturbance to the forest. In general, native seedlings, saplings, and mature plants increase in density following *S. scrofa* control (Loh & Tunison 1999; Busby, Vitousek & Dirzo 2010; Cole *et al.* 2012). Non-native plants are a threat through their competitive displacement of native plants (Vitousek 1996; Ostertag *et al.* 2009; Minden *et al.* 2010). Following the suppression of these top-down stressors in the Kahanahāiki fence, *C. dentata* started establishing at higher rates leading to greater numbers of seedlings and small juvenile plants (M. Kiehn, unpublished data).

DEMOGRAPHY DATA AND PROJECTION MATRIX MODEL

The life cycle of *C. dentata* was divided into four biologically discrete life stages based on height to the apical meristem: reproductive mature (>80 cm), large immature (20 cm–80 cm), small immature (2 cm–20 cm) plants, and seedling (<2 cm). We used 80 cm as the cut off for the reproductive mature life stage because it was the minimum height that plants produced fruits at the study site. Small and large juvenile were divided into two categories based on expert opinion by conservation practitioners and observed differences in survival at the field site. In 2010, at the start of this study, the Kahanahāiki *C. dentata* population consisted of 45 mature plants, 158 immature, and 600 seedlings. For four consecutive years (2010–2014), we permanently tagged and monitored a subset of plants in the population annually. Over the study period, a total of 507 plants were tagged and monitored. For the mature and large immature life stages, all individuals were monitored. For the small immature and seedling life stages, we monitored a minimum of 60 plants annually to ensure our effects on *C. dentata* habitat were minimal. For each tagged plant, we collected data on height to apical meristem (when possible), survival, and reproduction.

We used these field data to estimate the survival, growth, and fecundity rates for each life stage and parameterize a matrix projection model (Caswell 2001):

$$n(t+1) = An(t) \qquad \text{eqn 1}$$

where the vector $n(t)$ represented the number of plants in four discrete life stages at time t and $n\ (t+1)$ was the number of plants in each life stage the following year. The transition matrix **A** was composed of eight non-zero matrix elements (a_{ij}), which represented the transition probabilities of the seedling (s), small immature (si), large immature (li), and mature (m) life stages from time t to $t+1$. Unobserved transitions over the study period were represented in matrix **A** as zeros:

$$\mathbf{A} = \begin{pmatrix} \sigma_s(1-\gamma_s) & 0 & 0 & \varphi_m \\ \sigma_s\gamma_s & \sigma_{si}(1-\gamma_{si}) & 0 & 0 \\ 0 & \sigma_{si}\gamma_{si} & \sigma_{li}(1-\gamma_{li}) & 0 \\ 0 & 0 & \sigma_{li}\gamma_{li} & \sigma_m \end{pmatrix}$$

Matrix **A** was parameterized to include the probability of survival (σ_i), growth to the next stage class (γ_i), and fecundity (φ_m). Fecundity (φ_m) was calculated by dividing the number of seedlings counted in a given year by the number of mature plants the previous year. Matrix **A** captured the population demographic transitions under management of feral pigs and invasive plant competition while including frugivory by *L. lutea*. In 2011–2012, there was unintentional impact of herbicide drift on mature plants (based on qualitative field observations). Mature plants wilted and shed their leaves 2 weeks after the control of ecosystem altering vegetation, which occurred directly around the plants. For this reason, the 2011–2012 survival of matures (σ_m = 47%) was lower than to the other transition years (σ_m = 98%–81%). Since mortality from herbicide drift was not expected to occur in the future and we wanted to make our results were generalizable to other sites, we did not use the 2011–2012 σ_m data to calculate mature plant survival for the 2011–2012 matrix **A** transition year. Instead, we used the mean survival of mature plants in 2010–2011, 2012–2013, and 2013–2014 for the 2011–2012 matrix $\mathbf{A}\cdot\sigma_m$ term.

SIMULATING THE EFFECTS OF MICROHABITAT HETEROGENEITY AND FRUGIVORY

Matrix **A** represents field microhabitat conditions while maintaining frugivory by *L. lutea*. To simulate the effects of changes in microhabitat heterogeneity and frugivory by *L. lutea* on the dynamics of the *C. dentata* population, we constructed three additional matrices **B**, **C**, and **D** by modifying matrix **A**. Based on the results of additional field experiments, we found that frugivory by *L. lutea* and the availability of optimal microhabitat impacted the fertility φ_m of matrix **A** (see Appendix S1A and S1B, Supporting Information). To construct matrix **B**, which captures the removal of frugivory while maintaining field microhabitat conditions, we increased the φ_m element of matrix **A** by the percentage of fruits consumed by *L. lutea* at our field site. To construct matrix **C**, which represents the removal of frugivory and suboptimal microhabitat, we decreased the φ_m element of matrix **B** by the difference in seedling establishment between the optimal and suboptimal microhabitat. Lastly, to construct matrix **D**, which simulates the influence of both stressors (i.e. frugivory and suboptimal microhabitat), we decreased φ_m of matrix **A** by the percent difference in seedling establishment between the optimal and suboptimal microhabitat. Given the relatively short duration of the *C. dentata* fruiting season (i.e. 3 months), we assumed *C. dentata* germination and the number of seeds per fruit was not temporally variable.

STOCHASTIC LONG-TERM POPULATION DYNAMICS

For the four scenarios **A**, **B**, **C**, and **D** we projected the stochastic long-term population growth rate λ_s. To incorporate the effect of temporal variation in demographic processes to fluctuations in environmental conditions (i.e. environmental stochasticity) on population dynamics, we used the 4 years of demographic data to develop temporally varying stochastic matrix models for each scenario **A**, **B**, **C**, and **D** previously defined:

$$n(t+1) = X(t)n(t) \qquad \text{eqn 2}$$

where $\mathbf{X}(t)$ is a random population projection selected at given time t from a pool of four yearly matrix transitions (2010–2011, 2011–2012, 2012–2013, and 2013–2014) for the corresponding scenario (**A**, **B**, **C**, and **D**). The yearly matrices had an equal probability of being selected each iteration. The stable stage distribution (SSD) was used as the initial stage structure $n(0)$. We assumed the time-varying model followed an identically independent distribution (*i.i.d.*). For each scenario, we used eqn (2) to calculate the stochastic growth rate λ_s with 95% confidence intervals by simulation using 50 000 iterations, following Tuljapurkar, Horvitz & Pascarella (2003):

$$\log \lambda_s = \lim_{t\to\infty} \left(\frac{1}{t}\right) \log[P(t)/P(0)] \qquad \text{eqn 3}$$

where $P(t)$ is the population size, i.e. the sum of the elements of $n(t)$ at a given time t. Confidence intervals were calculated using a standard bootstrap approach, as outlined in (Caswell 2001; Morris & Doak 2002). To evaluate the individual and combined influence of the microhabitat and seed consumption by *L. lutea* on population dynamics, we compared the λ_s of each scenario (**A**, **B**, **C**, and **D**). To identify the relative importance of different life stages on the stochastic population growth rate λ_s for each scenario, we calculated the elasticity $E^{\mu S}$ of λ_s to perturbation of mean matrix elements μ_{ij} following Tuljapurkar, Horvitz & Pascarella (2003).

STOCHASTIC SHORT-TERM POPULATION DYNAMICS

We calculated the stochastic short-term population growth rate for each management scenario (**A**, **B**, **C**, and **D**), using the following formula:

$$r(t_1, t_{10}) = \frac{1}{t_{10} - t_1} \log \frac{N(t_{10})}{N(t_1)} \qquad \text{eqn 4}$$

The transient population growth rate was calculated as the average of a 1000 independent sample paths of length t = 10 years. The stage structure at $n\ (t + 1)$ was calculated using eqn (2). For a given year t (t < 10), and for each management scenario, we randomly selected one of the four yearly transition matrices (2010–2011, 2011–2012, 2012–2013, and 2013–2014) with equal probability to account for the effect of environmental variability. The timeframe of t = 10 years was used because it is the recommended timeframe to evaluate population dynamics of critically endangered plants by the IUCN red listing guideline (IUCN, 2001) and a reasonable length of time of a restoration management plan. Lower survival of mature plants in 2011–2012, due to herbicide drift, likely resulted in a lower proportion of individuals with high reproductive value in 2014 than would otherwise be expected. If the stage structure of the population had not been affected by herbicide drift, the short-term growth rate would likely have been slightly higher (i.e. population amplification) prior to SSD being achieved. However, in order to simulate short-term projections that could be used by conservation practitioners to manage the Kahanahāiki *C. dentata* population, we chose to use the observed population size in 2014 as the initial stage structure $n(0)$.

To identify the relative importance of life stages on the short-term population growth rate, we conducted stochastic transient elasticity analyses with respect to small changes in matrix elements to unperturbed stage structure, $e_{1,i,j}$ (Haridas & Tuljapurkar 2007; Haridas & Gerber 2010). The $e_{1,i,j}$ distribution for each scenario (**A**, **B**, **C**, and **D**) was iteratively calculated by simulation, using 1000 iterations. The four yearly transition matrices $\mathbf{X}(t)$ were selected with equal probability each iteration.

Results

STOCHASTIC LONG-TERM POPULATION GROWTH RATES

The stochastic growth rate of the *C. dentata* population for scenario **A** (i.e. frugivory and field microhabitat conditions) was positive (λ_s = 1·032, 95% CI [1·028–1·037]), indicating a moderately growing population in the long-term (Fig. 1a). Removal of frugivory by *L. lutea* while maintaining field microhabitat conditions (scenario **B**) increased the stochastic population growth rate by 1·7% (λ_s = 1·049, 95% CI [1·044–1·054]), relative to scenario **A** (Fig. 1a).

Maintaining frugivory while removing optimal microhabitat (scenario **C**) shifted the population growth rate from positive to negative (λ_s = 0·968, 95% CI [0·964–0·971]). The combined influence of both stressors (scenario **D**) decreased the stochastic population growth rate (λ_s = 0·955, 95% CI [0·952–0·959]) and led to a declining population trajectory (Fig. 1a).

STOCHASTIC SHORT-TERM POPULATION GROWTH RATES

Over the short-term, the *C. dentata* population was projected to grow moderately under current field conditions (i.e. frugivory and field microhabitat conditions) (r_s = 1·087, 95% CI [1·083–1·091]; Fig. 1b). Similar to long-term projections, removal of frugivory increased the short-term population growth rate (r_s = 1·119, 95% CI [1·115–1·124]). Removal of optimal microhabitat reduced the short-term population growth rate (r_s = 0·973, 95% CI [0·969–0·976]). The combined impact of frugivory and the removal of optimal microhabitat had the greatest negative impact on the population growth rate (r_s = 0·941, 95% CI [0·938–0·944]).

STOCHASTIC SHORT AND LONG-TERM ELASTICITY

In the long-term, the survival of mature plants had the greatest proportional impact on the population growth rate, followed by the growth of seedlings, small immature, and large immature plants and fertility (Fig. 2a). Removal of optimal microhabitat for seedling establishment and frugivory increased the relative importance of the survival of mature plants on the long-term population growth rate. It also decreased the relative importance of the survival and growth of seedling, small immature, and large immature plants on the population growth rate (Fig. 2a).

In the short-term, fecundity had the greatest relative importance on the population growth rate followed by the growth of seedlings to the small immature life stage (2b). The individual and combined impacts of seed consumption by *L. lutea* and removal of optimal microhabitat (scenario **A**, **C**, and **D**) reduced the relative importance of the fecundity and growth of seedlings to the small immature life stage (Fig. 2b).

Discussion

The influence of abiotic factors (e.g. light, soil type, elevation) on plant population dynamics has been well examined (Alvarez-Buylla *et al.* 1996; Brys *et al.* 2005; Colling & Matthies 2006; Dahlgren & Ehrlén 2009; Souther & McGraw 2014). However, the influence of frugivorous animals or the combined effects of frugivory and microhabitat heterogeneity on plant population dynamics are rarely measured, and studies on this topic have produced mixed results (Godínez-Alvarez & Jordano 2007; Loayza

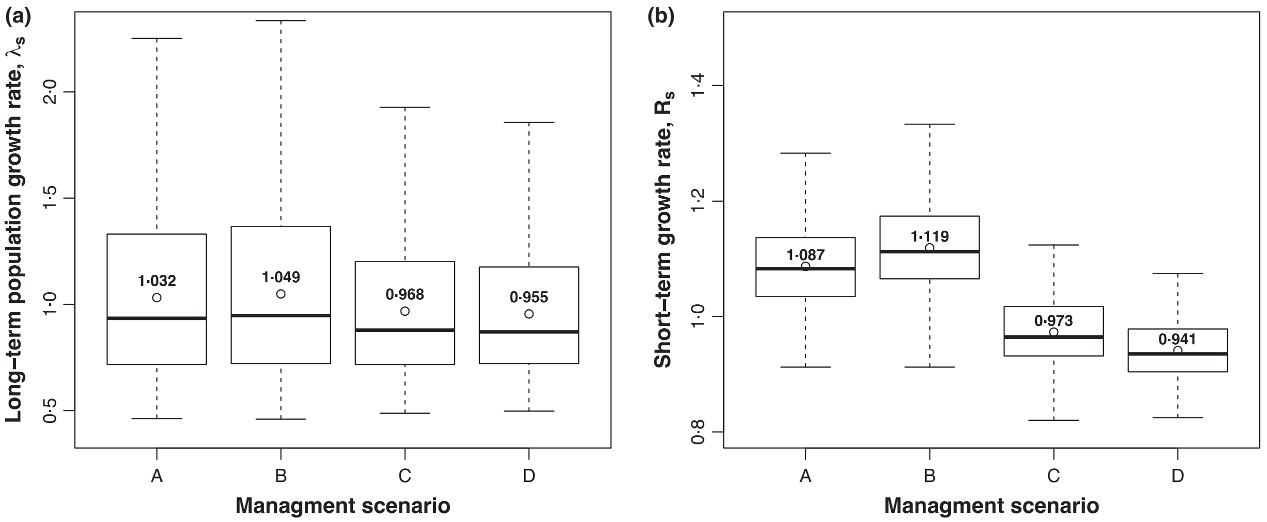

Fig. 1. Stochastic short (R_s) and long-term (λ_s) population growth rates of *Cyrtandra dentata*. The black bar is the median and the boxes represent the inter-quartile range. The limits of the whiskers are 1·5× the inter-quartile range. The open circle is the mean of each management scenario. Scenario **A** = Field conditions (i.e. field microhabitat conditions and frugivory), **B** = No frugivory while maintaining field microhabitat conditions, **C** = No frugivory and suboptimal microhabitat, **D** = Frugivory and suboptimal microhabitat.

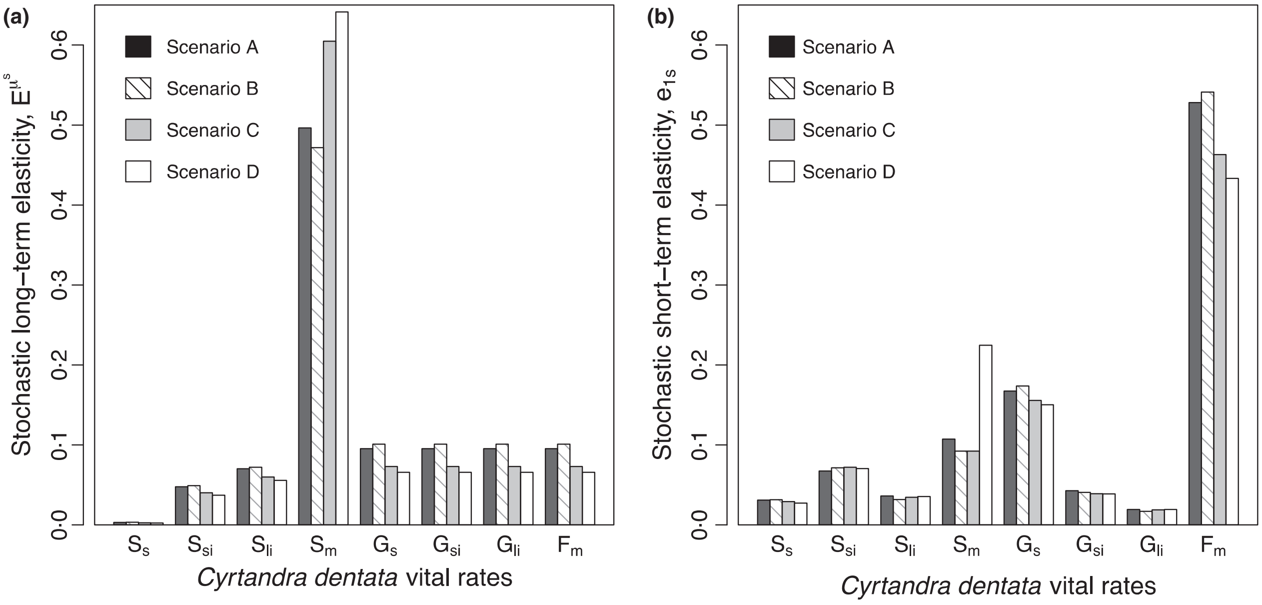

Fig. 2. Stochastic elasticities of *Cyrtandra dentata* (a) long- and (b) short-term growth rates to perturbation of mean vital rates. The vital rates are survival (S), growth (G), and fertility (F) and the life stages are seedling (*s*), small immature (*si*), large immature (*li*), and mature (*m*). Scenario **A** = Field conditions (i.e. field microhabitat conditions and frugivory), **B** = No frugivory while maintaining field microhabitat conditions, **C** = No frugivory and suboptimal microhabitat, **D** = Frugivory and suboptimal microhabitat.

& Knight 2010). Due to their adaptation to narrow ecological conditions and limited geographical distribution, localized endemics are likely to suffer stronger effects of such stressors. Thus, to fully understand the drivers of species decline, it is critically important to evaluate the individual and combined impact of environmental change, such as alterations in abiotic conditions and non-native frugivores, on the short-term (i.e. transient) and long-term (i.e. asymptotic) dynamics of rare species.

In this study, we found that rock outcrops (i.e. rocky gulch walls and small boulders in the gulch bottom) were an optimal microhabitat for *C. dentata* seedling establishment. Though the mechanism underpinning higher seedling establishment on rock outcrops is unknown, previous research suggests that rocks covered by moss can maintain a moist microsite favourable for seedling establishment (Ren *et al.* 2010). We also found that *C. dentata* seeds that were not contributing to local dynamics were consumed by *L. lutea* and dispersed away from the population. Under current field conditions (i.e. intensity of frugivory by *L. lutea* and microhabitat conditions at the field site), *C. dentata* was projected to persist in the long-term. Removal of frugivory moderately increased the long-term population growth rate, as compared to field conditions. Under suboptimal microhabitat conditions the long-term population growth rate was negative, regardless of frugivory pressure. These results suggest that for *C. dentata*, the removal of optimal microhabitat availability for seedling establishment would have a greater influence on population dynamics than frugivory by *L. lutea*. Furthermore, we found that the short-term transient growth rate (i.e. over 10 years) was slightly higher than the long-term growth rate. However, for each scenario, the projected direction of the short and long-term growth rates was not different. Additionally, there was more variation in the long-term projections than in the short-term projections (Fig. 1). In the transient phase, the population dynamics are strongly influenced by the initial condition of the population (Ellis & Crone 2013). Conversely, the stochastic long-term dynamics are strongly influenced by variation in vital rates (Ellis & Crone 2013). Thus, greater variation in long-term dynamic than in the short-term dynamics of *C. dentata* can be explained, in part, by the effects of the year to year differences in targeted vital rates, after the strong effects of initial population structures has damped out. Though herbicide drift altered the stage structure of the population by decreasing the proportion of plants with high reproductive value, the population was still projected to persist in the short-term. If herbicide drift had not occurred, however, the population would likely have grown faster in the short-term (i.e. transient amplification), which is important to consider when evaluating the population dynamics of other *C. dentata* population not experiencing this demographic disturbance.

Dispersal agents can provide enemy escape from predators in close proximity to parent plants, reduce conspecific seedling competition, and increase seed germination for species reliant on gut passage to maintain high seed viability (Howe & Smallwood 1982; Willson & Traveset 2000). For species that produce more seeds than are needed to maintain a persistent population, dispersal away from geographically isolated populations can have a positive effect on metapopulation dynamics. However, for species on the brink of extinction the removal of seeds away from a population can shift the population trajectory from persistent to declining. In this study, we found that a majority of the seedlings at the field site either established slightly down gulch or underneath the crown of reproductively mature plants. This observation supports previous studies that suggest passive transport by water is a short-distance dispersal strategy for *Cyrtandra* species in Hawaii (Kiehn 2001). We also found that seed germination from whole *C. dentata* fruits was relatively high, which suggest this taxon is not dependent on gut passage by frugivores to maintain high seed viability (see Appendix S1, Fig. 2). These results suggest *C. dentata* is not reliant on avian dispersal to maintain locally persistent populations.

Following massive extinction of native Hawaiian birds it is likely that many native species are dispersal limited, which may eventually reduce plant fitness by decreasing gene flow between populations. However, decreased gene flow between populations may be mitigated by cross-pollination between populations. For *C. dentata*, there are only five known extant populations, only two of which, Kahanahāiki and Pahole to West Makaleha, have >16 mature plants and individuals in earlier life stages (i.e. immature plants and seedlings). Of those populations, Pahole to West Makaleha was the only population closer to Kahanahāiki (<3 ha) than the home range of *L. lutea*. If rare long-distance dispersal between the Kahanahāiki and Pahole to West Makaleha populations is occurring by *L. lutea*, it may have an effect on plant fitness over time by increasing gene flow between populations. However, to fully understand the effect of rare long-distance dispersal would require a metapopulation approach, incorporating extinction and re-colonization events, and this is beyond the scope of this study.

For long-lived species, it is expected that later life stages will have a larger impact than earlier life stages on the long-term population growth rate (Silvertown *et al.* 1993; Haridas & Gerber 2010). The importance of later life stages on population dynamics of long-lived species is commonly explained by life history strategy. High survival of mature plants can insulate long-lived species from environmental variability and thus is the most important vital rate for maintaining population persistence in the long-term. However, recent research suggests that long-term elasticity does not always adequately describe the importance of life stages and associated vital rate in the short-term (Haridas & Tuljapurkar 2007; Haridas & Gerber 2010). In some scenarios, earlier life stages disproportionally contributed to the population growth rate of long-lived species over the short-term (e.g. 10 years), relative to later life stages (Haridas & Tuljapurkar 2007; McMahon & Metcalf 2008; Ezard *et al.* 2010; Haridas & Gerber 2010; Gaoue 2016). Consistent with these studies, we also found a shift in the short and long-term elasticity patterns of the *C. dentata* population growth rate to perturbation of vital rates. *Cyrtandra dentata* long-term stochastic elasticity was dominated by the survival of mature plants. However, in the short-term, the establishment of *C. dentata* seedlings had the greatest influence on the population growth rate. These results have several management implications for *C. dentata*. First, with high mature plant survival (81% – 97%), there is likely little that can be done to improve that vital rate. However, the importance of mature plants on the long-term population growth rate emphasizes the gravity of maintaining high survival of matures over time. Secondly, management actions that increase seedling establishment would have the greatest positive impact on the population growth rate in the short-term.

Studying the demography of rare and endangered species is challenging due to limited replication (Morris & Doak 2002). Despite the constraint of limited replication valuable insight can be gained from population dynamic studies of endangered species, such as quantifying the likely outcome of management actions and assessing the potential impact of environment parameters on population dynamics (Morris *et al.* 2002; García 2003; Ellis, Weekley & Menges 2007; Marrero-Gómez *et al.* 2007; Crone *et al.* 2011; Dostálek & Münzbergová 2013). It can also provide a proactive method of predicting the likely outcome of management actions, which would otherwise take several generations to detect (Menges 2000). For this study, we were limited to one study site because it was the only *C. dentata* population that was composed of more than several individuals that we had permission to access. Thus, results from this study may not be extrapolated across varying habitat and ecological conditions. Future integrative studies on the combined impact of plant interactions with multiple environmental parameters would benefit from having replication across multiple study sites. Plant population response to environmental stressors should be studied for more species varying in life history in order to investigate if generalized patterns emerge, which could be used to effectively manage rare plants and the habitat that they depend on.

Regardless of the difficulties of studying endangered species, the results of this study emphasize the importance of protecting optimal microhabitat for seedling establishment to maintain a positive population trajectory for endangered species that are sensitive to fine-scale environmental change. For *C. dentata*, a management strategy that would prevent degradation of optimal abiotic conditions for seedling establishment is the suppression of competitive vegetation. One of the most invasive ecosystem altering species at Kahanahāiki is *Blechnum appendiculatum*, which is a non-native fern that forms large clonal colonies and prevents germination of many native species in Hawaii (Wilson 1996). *Blechnum appendiculatum* has started to encroach on rock outcrops at the Kahanahāiki *C. dentata* field site. If left uncontrolled, *B. appendiculatum* will ultimately degrade optimal microhabitat for seedling establishment and negatively impact local population dynamics. The influence of fine-scale abiotic conditions on population dynamics also emphasizes the importance of selecting reintroduction sites with appropriate microhabitat for *C. dentata*, which will be necessary to delist this taxon following the United States Fish and Wildlife criteria (USFWS, 1998). The results of this study also illustrate that for localized endemic species on the brink of extinction, such as *C. dentata*, non-native frugivores can reduce local seedling recruitment of geographically isolated populations. In combination with other environmental stressors, such as degradation of abiotic conditions, frugivory by non-native birds can shift the population growth rate of endangered plants from growing to declining over time.

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Data accessibility

Matrices used to simulate short and long-term population dynamics of each scenario are deposited in Dryad Digital Repository https://doi.org/10.5061/dryad.35b38 (Bialic-Murphy, Gaoue & Kawelo 2017).

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Supporting Information

Details of electronic Supporting Information are provided below.

Appendix S1. (A) Results of frugivory by *Leiothrix lutea* and (B) Results of microhabitat heterogeneity.

Fig. S1. (1) Typical laceration markings on the remaining pericarp of mature *Cyrtandra dentata* fruits. Incisor marks (white arrows) are indicative of fruit consumption by birds. (2) Seedling germination from a mature *C. dentata* fruit when places on a mist bench in the greenhouse.