

# Using population dynamics modelling to evaluate potential success of restoration: a case study of a Hawaiian vine in a changing climate

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## SUMMARY

Demographic comparisons between wild and restored populations of at-risk plant species can reveal key management strategies for effective conservation, but few such studies exist. This paper evaluates the potential restoration success of *Alyxia stellata*, a Hawaiian vine. Stage-structured matrix projection models that compared long-term and transient dynamics of wild versus restored *A. stellata* populations, and restored populations under different levels of canopy cover, were built from demographic data collected over a four year period. Stochastic models of wild populations projected stable or slightly declining long-term growth rates depending on frequency of dry years. Projected long-term population growth rates of restored populations were significantly higher in closed than open canopy conditions, but indicated population decline under both conditions. Life table response experiments illustrated that lower survival rates, especially of small adults and juveniles, contributed to diminished population growth rates in restored populations. Transient analyses for restored populations projected short-term decline occurring even faster than predicted by asymptotic dynamics. Restored populations will not be viable over the long term under conditions commonly found in restoration projects and interventions will likely be necessary. This study illustrates how the combination of long-term population modelling and transient analyses can be effective in providing relevant information for plant demographers and restoration practitioners to promote self-sustaining native populations, including under future climates.

**Keywords:** demography, elasticity analysis, liana, life table response experiments, matrix projection models, non-timber forest products, transient analyses

## INTRODUCTION

As human impacts on ecosystems rise, the restoration of plant populations becomes increasingly important (Colas *et al.*

2008). Restoration is commonly used to re-establish extinct populations or enhance the viability of threatened populations (McKay *et al.* 2005). It can also play an integral role in the management of culturally and economically important wild plant resources such as non-timber forest products (NTFPs) (Garibaldi & Turner 2004). NTFPs represent an important source of income to millions of people worldwide and many species, while not globally threatened or endangered, have dwindling populations or have become locally extinct (Ticktin 2004). Recognizing and incorporating culturally prominent plants in restoration efforts may increase success rates through partnership with local communities (Garibaldi & Turner 2004). These activities may extend to ecosystem stewardship and conservation, and can lead to enhancement of both social and ecological integrity (Garibaldi & Turner 2004).

To be effective, restoration strategies for plants must consider not only short-term goals of establishment, growth and survival, but also reproduction and long-term persistence within natural habitats (Menges 1998; Bell *et al.* 2003). Population projection matrix (PPM) models integrate individual vital rates (growth, reproduction and survival) into measures of long-term population growth, and are powerful tools for assessing current population status and comparing the demographic effects of different current or potential management practices (Crone *et al.* 2013). Despite this, matrix modelling is not in wide use and few studies have used matrix modelling to assess the viability of, or to identify best management practices for, restored plant populations (Crone *et al.* 2011). Endels *et al.* (2005) used elasticity analysis to determine that long-term growth rates of restored populations of *Primula veris* (Primulaceae) are most sensitive to changes in the survival of reproductive adults and to seedling recruitment and based management recommendations for restoration projects on these results. Very few studies have compared the demography of wild versus restored populations even though this approach can help identify factors key to restoration success (Bell *et al.* 2003; Maschinski & Duquesnel 2007; Colas *et al.* 2008). In addition, transient (short-term) dynamics may differ significantly from the long-term asymptotic dynamics projected by matrix models, especially due to divergence of the observed population structure from the stable stage distribution (Caswell 2007; Stott *et al.* 2011). To meet restoration goals, a combination of transient analyses and PPM models can be used to project changes in both short-term and long-term dynamics.

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In the Hawaiian Islands, degradation and loss of native habitat threaten the viability of many plant populations. Over 90% of Hawai'i's native vascular flora is endemic (Goldman *et al.* 2008) and Hawai'i has more endangered species per area than any other region on the globe. More than one-third of the USA's federally listed threatened or endangered plant species are native to the Hawaiian Islands (US Fish and Wildlife Service 2013). Restoration of native vegetation communities is critical to conserve species and maintain ecosystem services, including resources important for native Hawaiian cultural practices. Previous research on restoration of Hawaiian plants has shown that closed canopy treatments support increased survival of native woody species and reduce alien grasses in Hawaiian mesic forests, at least over the short term (McDaniel & Ostertag 2010); and that both shade and invasive grass removal increase growth and survival of transplanted trees, shrubs and vine seedlings in a Hawaiian dry forest restoration (Thaxton *et al.* 2012).

*Alyxia stellata* (JR & G Forst.) Roem. & Schult. (Apocynaceae) (Middleton 2002) or maile is an indigenous woody vine and one of the most culturally important plants in Hawai'i. It is an NTFP whose stems are wild harvested for lei (garlands). *A. stellata* populations are still found in the wild but are becoming scarcer, likely as a result of habitat destruction, competition with invasive species, and disturbance by feral ungulates. Other factors such as dispersal or pollination limitation, seed predation by rats (T. Wong, unpublished data 2010; Shiels & Drake 2011) and unsustainable harvesting may also play a role. As a result, there has been growing interest and investment in *A. stellata* restoration by both conservation organizations and local communities. However, to date there have been no demographic studies on either wild or restored *A. stellata* populations and the appropriate management for, and viability of, restored populations is not known.

There are few demographic studies of vines in general (Escalante *et al.* 2004; Nabe-Nielsen 2004; Siebert 2004; Kouassi *et al.* 2008). The studies to date indicate that vine population dynamics tend to be most sensitive to changes in the survival of juvenile and adult plants (Escalante *et al.* 2004; Nabe-Nielsen 2004; Kouassi *et al.* 2008) and that canopy cover can be a driver of population dynamics of some species (Escalante *et al.* 2004), although there have been no experimental studies on this topic. More research is needed since vine ecology remains poorly understood, despite studies that demonstrate the important role that vines can play in forest regeneration and ecosystem-level processes (Schnitzer & Bongers 2002).

We used matrix population models built from annual demographic data of restored and wild *A. stellata* populations, and transient analyses, to address the following questions: (1) What are the projected long-term population growth rates and transient dynamics of restored and wild populations? (2) How does variation in canopy cover affect long-term growth rates of restored populations? (3) What life-history transitions are most responsible for differences

in projected growth rates between wild and restored populations?

We hypothesized that (1) wild populations have higher population growth rates than restored populations since high mortality of seedlings and juveniles has been reported in restoration projects; (2) long-term population growth rates are most sensitive to changes in juvenile and adult survival; and (3) restored populations under closed canopy have higher population growth rates than those in open canopy, since wild *A. stellata* populations have been observed to proliferate in understory light conditions. Based on the above, we discuss the management practices that can maximize the potential for long-term persistence of restored populations.

## METHODS

### Study area and species

We established *A. stellata* restoration experiments at the National Tropical Botanical Garden (NTBG) Limahuli Preserve, Kaua'i Island, Hawai'i, USA. The wild populations were monitored at the NTBG Limahuli Preserve and Koke'e State Park, Kaua'i Island (Table 1; Appendix 1, Fig. S1, see supplementary material at [Journal.cambridge.org/ENC](http://Journal.cambridge.org/ENC)).

*A. stellata* plants are twining lianas, and climbing or erect shrubs with flowers that may be pollinated, or at minimum visited by moths (T. Wong, unpublished data 2010), and ovoid drupes that often form end to end (moniform) (Wagner *et al.* 1990). *A. stellata* has a widespread distribution across the Pacific Islands (Middleton 2002). In 1990 surveys of undisturbed forest vegetation in Tonga, lianas such as *A. stellata* comprised 29% of plant species in lowland rain forests and were also abundant in upland rain forests (Drake *et al.* 1996). However, surveys in Western Samoa showed that seedling germination was absent from vine patches with anthropogenic disturbance (Savage 1992).

*A. stellata* formerly grew across a range of habitats at altitudes of 50–2000 m in Hawai'i, from wet forest with closed canopy to dry open areas (Wagner *et al.* 1990). It is currently found on all the main Hawaiian islands except Kaho'olawe and Ni'ihau, and it is likely that the species grew on those islands but has become extinct due to extensive habitat disturbance (Wagner *et al.* 1990).

### Demographic monitoring of restored populations

In 2007, we transplanted 13 *A. stellata* plants into each of ten 6 × 6 m plots ( $n = 130$  transplanted individuals) at Limahuli Preserve. Transplants were approximately 12 months old and averaged  $3.00 \pm 0.60$  mm (mean  $\pm$  1SD) in basal stem diameter. All plants were greenhouse grown by NTBG Lawa'i Valley Conservation and Horticulture Center from seed collected from wild *A. stellata* populations across Kaua'i Island. Seeds were randomized before planting in the greenhouse. Since *A. stellata* restoration projects take place both in open and under forest canopy, half of the

**Table 1** Characteristics of wild and restored *A. stellata* population study sites. <sup>a</sup>> 1 SD drier than the 50-year mean.

Site	Restored site:	Wild site:	Wild site:
	Limahuli	Limahuli	Koke'e State Park
Latitude / longitude	22°12'12" N, 159°36'32" W	22°12'12" N, 159°36'32" W	22°7'49" N, 159°39'31" W
Elevation	90–140 m	180–205 m	1060–1070 m
Forest type	Remnant and restored native low elevation mesic forest, with <i>Metrosideros polymorpha</i> and <i>Acacia koa</i> . High invasive species presence	Remnant native mesic forest dominated by <i>Metrosideros polymorpha</i>	Montane mesic forest dominated by native canopy trees <i>Metrosideros polymorpha</i> and <i>Acacia koa</i>
Mean annual temperature	22.13 °C	22.13 °C	15.16 °C
Mean annual precipitation ± 1 SD (cm)   Mean wet season precipitation ± 1 SD (cm)	208.99 ± 43.76   81.79 ± 32.59	208.99 ± 43.76   81.79 ± 32.59	165.25 ± 51.92   91.67 ± 36.63
Wet season precipitation 2007–2008 (cm)	69.80	69.80	100.33
Wet season precipitation 2008–2009 (cm)	101.78	101.78	107.98
Wet season precipitation 2009–2010 (cm)	36.20 <sup>a</sup>	36.20 <sup>a</sup>	45.03 <sup>a</sup>
Wet season precipitation 2010–2011 (cm)	77.44	77.44	116.54

plots were located in open canopy conditions (100% available light) and the other half under closed canopy conditions (22–50% available light). Light levels were characterized as photosynthetically active radiation (PAR) measured as photosynthetic photon flux density (PPFD) by LI-COR LI-191 line quantum sensors (LI-COR, Lincoln, NE, USA). Light (measured as PAR) was significantly higher in open canopy than under closed canopy conditions (ANOVA,  $p < 0.05$ ). *A. stellata* transplants did not have directly adjacent trees as vertical support structures under either canopy treatment.

The size of all individuals was recorded at the time of outplanting. We measured the diameter of each plant at the first point above the roots where the stem was standard as described by Nabe-Nielsen (2004), using digital callipers with a resolution of 0.1 mm and accuracy of  $\pm 0.3$  mm. We marked this point with paint to ensure stem measurement uniformity each time. Plants were reassessed for growth and survival every six months from 2007 to 2011. We recorded the total number of flowers, fruit and new seedlings at each census. At each census, all plots were hand weeded due to high presence of invasive species.

### Demographic monitoring of wild populations

In 2009, we tagged and measured 120 *A. stellata* plants in each wild population at Limahuli Preserve and Koke'e State Park (Table 1; Appendix 1, Fig. S1, see supplementary material at

Journal.cambridge.org/ENC) with canopy PAR conditions similar to that of the closed canopy restored populations (ANOVA,  $p > 0.05$ ). We measured the diameter of each plant as described above. We revisited all plants every six months during 2009–2011, measuring growth, survival, and emergence of new seedlings within a 3 m radius of all adults. We calculated annual fruit production by randomly selecting five fruiting branches, marked and counted all fruits present, counted total number of fruiting branches of the individual and multiplied by the average number of fruits per branch. *A. stellata* fruits develop and ripen very slowly, and persist for a long time on the plant. Therefore, monitoring and marking fruit every six months was sufficient to capture annual fruit production.

To determine if *A. stellata* maintains a seed bank, we buried 50 seeds in each of three wire baskets at each of three sites ( $n = 450$ ) in 2009 at Limahuli and at Koke'e in 2010 ( $n = 450$ ) under 10 cm of soil. One basket from each site of the three sites was recovered after one year and we counted the number of seeds that germinated *in situ* (as characterized by root breaking seed coat) and noted insect and fungal damage. We tested viability of ungerminated seeds using tetrazolium seed viability testing (TZ) according to the Apocynaceae protocol (Peters 2000).

### Population projection matrices

We divided *A. stellata* individuals into four stage classes based on size and morphology, where seedlings had a stem basal

diameter of less than 2 mm, juveniles 2.1 mm to 8 mm, small adults 8.1 mm to 20 mm, and large adults greater than 20 mm. Adult stage classes reproduce sexually (Appendix 1, Fig. S2, see supplementary material at [Journal.cambridge.org/ENC](http://Journal.cambridge.org/ENC)). For each wild population, we built  $4 \times 4$  Lefkovich stage-structured transition matrices (Caswell 2001) directly from the annual census field data for each year and site, with 30 individuals in each stage class (Appendix 1, Tables S1–6, see supplementary material at [Journal.cambridge.org/ENC](http://Journal.cambridge.org/ENC)). Since our experiments showed that *A. stellata* does not have a seedbank, the number of seedlings ( $s$ ) produced per adult was calculated as:

$$s = s_{obs} \times (f/f_{tot})$$

where  $s_{obs}$  is the number of new seedlings observed in the field,  $f$  is the number of fruit per adult, and  $f_{tot}$  is the total number of fruit of all adults.

We used the matrix model:

$$\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t)$$

where  $\mathbf{n}(t)$  is a vector of stage abundances at year  $t$ ,  $\mathbf{n}(t+1)$  is the population vector in the following year, and  $\mathbf{A}$  is the transition matrix for the population (Caswell 2001). The dominant eigenvalue  $\lambda$  represents the asymptotic finite rate of increase at the stable stage distribution.

We built one summary matrix per restored population type (closed canopy and open canopy), by pooling data over populations within each type over the four-year study period 2007–2011 (Bell *et al.* 2003; Maschinski & Duquesnel 2007; Colas *et al.* 2008). We used the mean values of adult fecundity, stasis of large adults, and growth of small to large adults obtained from the two wild populations over two years to estimate these transitions because we did not have enough adult individuals in the restored population (Appendix 1, Tables S1–6, see supplementary material at [Journal.cambridge.org/ENC](http://Journal.cambridge.org/ENC)).

For each transition matrix we calculated lambda ( $\lambda$ ), the finite rate of population growth (the rate at which a population would grow over the long term under the parameterization conditions; Caswell 2001), elasticity values of the matrix elements, and determined the 95% confidence intervals of  $\lambda$  with 2000 bootstrap runs. The last were obtained from random sampling with replacement from a stage-fate data frame of the observed transitions (Caswell 2001; Stubben & Milligan 2007). To account for temporal variation, we calculated the stochastic population growth rates ( $\lambda_s$ ) for wild populations by using the geometric mean of successive annual growth rates for both wild populations over a simulation with 50 000 iterations (Caswell 2001; Morris & Doak 2002; Stubben & Milligan 2007). Year 1 (2009–2010) had a dry wet season (Table 1). We obtained  $\lambda_s$  for scenarios where each of the two annual matrices had an equal probability of occurring and where year 1 had a 25% chance of occurring. The El Niño phase of the El Niño Southern Oscillation (ENSO) cycle occurred in 2009–2010 and commonly leads to dry wet seasons in Hawai'i (Chu 1995). ENSO indices have shown a timescale of 3–

5 years with irregularity (Wang *et al.* 2012), therefore, we chose the average estimation of this timescale (25% frequency) and higher frequency (50%) in our stochastic models to reflect potential current and future climate conditions. We used a two sample Z-test, or normal comparison, to determine the statistical support for observed differences in  $\lambda$  and  $p < 0.05$  was considered as statistically significant.

We carried out fixed one-way life table response experiments (LTRE; Caswell 2001) to determine which stage classes and life-history transitions were most responsible for observed differences in lambda ( $\Delta\lambda$ ) between wild populations over space and time, and between restored and wild populations. For comparisons between wild populations we used the formula:

$$\lambda^{(K)} - \lambda^{(L)} \approx \sum \left( a_{ij}^{(K)} - a_{ij}^{(L)} \right)^* \partial\lambda/\partial a_{ij}|_{A^{(m)}}$$

where  $a_{ij}$  are the transition coefficients in the matrices, and the sensitivities  $\partial\lambda/\partial a_{ij}$  are calculated from the midway matrix  $A^{(m)}$ . The midway matrices were constructed from the mean vital rates of the matrices being compared (Caswell 2001). Positive contributions represent differences in vital rates that contributed to the higher population growth rates in Koke'e wild populations.

For comparisons between years, we followed the same procedure as above, but used year 1 as the reference matrix so that positive contributions represent differences in vital rates that contributed to the higher population growth rates in year 2. Similarly, restored closed canopy was used as the reference matrix for comparisons with wild populations, and restored open canopy as reference for comparisons between restoration canopy conditions. Matrix elements with high LTRE contributions make the biggest contributions to the observed differences in  $\lambda$  between populations.

### Transient dynamics of restored populations

We examined transient dynamics of restored populations under five restoration scenarios: *A. stellata* restored under closed canopy only; *A. stellata* restored only under open canopy; and three scenarios of increased stasis of *A. stellata* outplantings under closed canopy (increased survival of juveniles by 0.20, small adults by 0.15, and combined juveniles and small adults each by 0.10). These values were chosen since it was the minimum necessary to achieve increasing populations ( $\lambda > 1$ ) and low enough to be realistic in terms of management.

To examine indices of *A. stellata* transient dynamics, we projected the restoration matrix over time. We calculated case-specific measures of transient dynamics and used the observed restoration population structure (open and closed canopy combined) as the initial population structure vector and standardized the matrices and initial structure: 0.623 seedlings, 0.377 juveniles, 0 small adults, 0 large adults (Stott *et al.* 2011). As recommended by Stott *et al.* (2011), we calculated reactivity and first-timestep attenuation (maximum



**Table 2** Finite rate of population increase ( $\lambda$ ) and 95% confidence intervals (CI) for wild and restored *A. stellata* populations.

Type	Finite rate of population increase ( $\lambda$ ) and 95% CI		
	Restored site: Limahuli	Wild site: Limahuli	Wild site: Koke'e State Park
Closed canopy	0.957 (0.938–0.977)	—	—
Open canopy	0.913 (0.904–0.923)	—	—
Year 1 observed $\lambda$	—	0.893 (0.813–0.977)	0.974 (0.920–1.000)
Year 2 observed $\lambda$	—	1.031 (0.905–1.131)	1.046 (0.966–1.132)
Stochastic $\lambda_s$ : unequal probability 25% year 1, 75% year 2	—	0.996 (0.995–0.997)	1.012 (1.011–1.013)
Stochastic $\lambda_s$ : equal probability of years	—	0.962 (0.961–0.963)	0.988 (0.987–0.989)

and minimum population growth in the first time-step relative to stable [asymptotic] growth rate), maximum amplification or attenuation (maximum short-term increase or decrease in population density relative to stable [asymptotic] growth rate), and inertia (the long-term population density relative to a population with stable growth and the same initial density). Inertia is a useful predictor of relative population densities over the short term, for example, values  $< 1$  indicate that populations are projected to decrease at a faster rate than expected of a population starting with the same initial density but with stable growth (Stott *et al.* 2011). We calculated inertia of the adults only since it is *A. stellata* adults that produce stems suitable for sustainable harvest.

All analyses were conducted in R version 2.15 statistical software (R Development Core Team 2008) with the popbio (Stubben & Milligan 2007) and popdemo (Stott *et al.* 2012) packages.

## RESULTS

### Long-term dynamics of restored and wild populations

The deterministic lambda values for the restored populations were both  $< 1$  (Table 2) indicating long-term population decline. The  $\lambda$  value of the closed canopy restored population, however, was significantly higher than that of the open canopy (two-sided *Z*-test,  $Z = 4.4$ ,  $p < 0.05$ ). There was no significant difference in  $\lambda$  for the closed canopy restored population and the mean wild Limahuli population (two-sided *Z*-test,  $Z = 0.5$ ,  $p > 0.05$ ). Projected long-term growth rates ( $\lambda$ ) of wild *A. stellata* populations ranged between 0.893 (0.813–0.977) for Limahuli in the first year to 1.046 (0.966–1.132) for Koke'e in the second year (Table 2). At both wild sites,  $\lambda$  was lower during the first year, when wet season precipitation was very low ( $> 1$  SD lower than the 50-year mean, Table 1; Appendix 2, see supplementary material at [Journal.cambridge.org/ENC](http://Journal.cambridge.org/ENC)). Stochastic lambda values ( $\lambda_s$ ) for the wild populations based on projections with equal probabilities of annual matrices occurring were both  $< 1$ , indicating projected population decline. However, for stochastic projections where low wet season precipitation (year 1) occurred only 25% of the time,  $\lambda_s$  were close to or above unity, with values of 1.012 (1.011–1.013) for Koke'e and 0.996 (0.995–0.997) for Limahuli.

Elasticity values varied among populations and years (Fig. 1a–f). Elasticity values for wild and restored populations at Limahuli indicated that stasis of the large adults contributed most to the population growth rate but, depending on the year, stasis of juveniles and small adults also had moderate values. Elasticity of stasis of juveniles and small and large adults was high for both wild populations (Fig. 1a–d), with large adults' stasis highest for Limahuli (Fig. 1a,b). For Koke'e, elasticity was dominated by stasis of small adults in both years, though this was even more prominent in year one (Fig. 1c, d). Restoration populations under closed canopy had high elasticity for stasis and growth (includes survival and growth to the next stage class) of juveniles, and small and large adults (Fig. 1e, f). Open canopy restoration populations had predominantly high elasticity values for stasis of large adults and marginal values for small adults (Fig. 1e, f).

### Life table response experiments

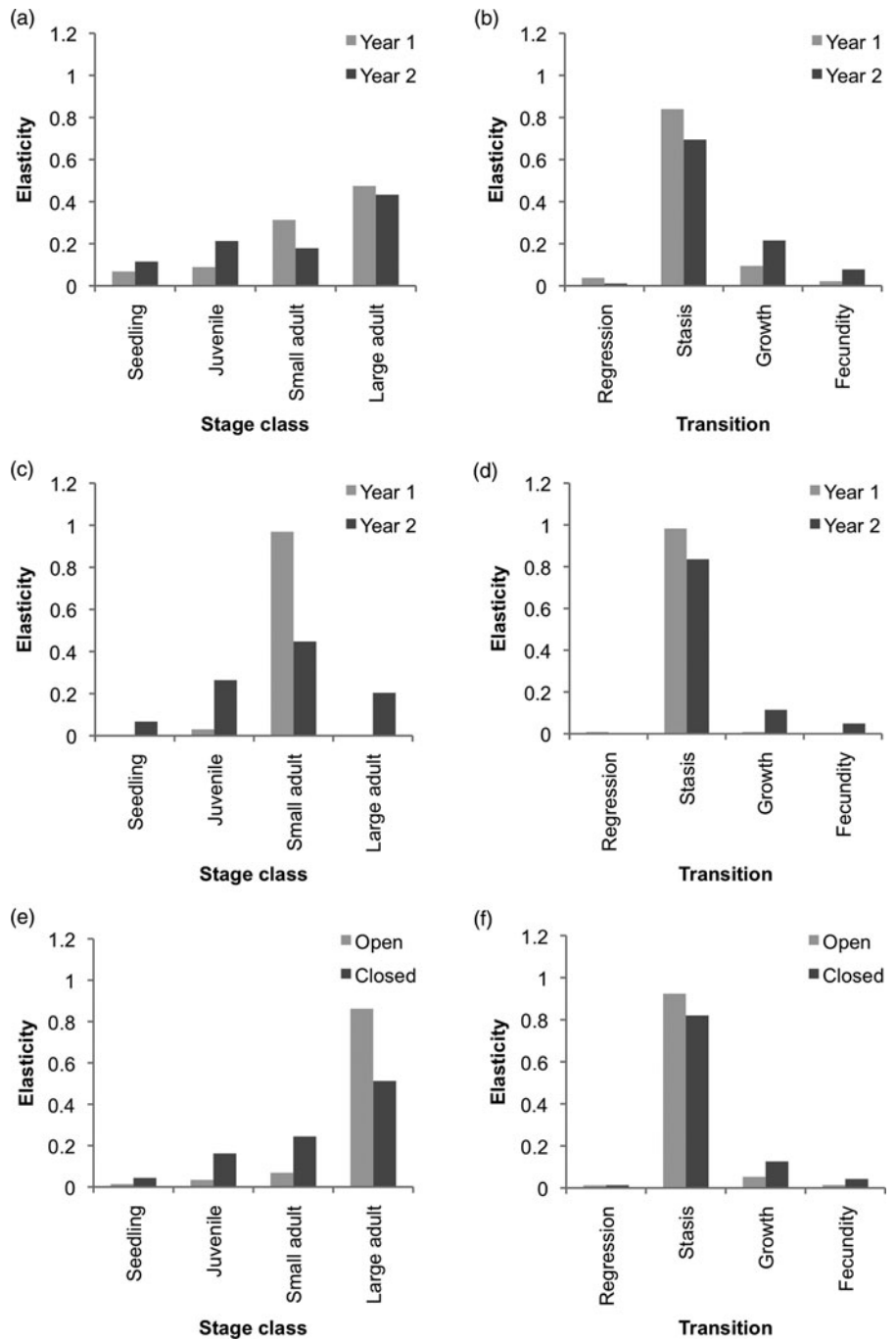
For wild *A. stellata* populations, higher growth of seedlings, juveniles and large adults, and higher fecundity, made the biggest contributions to the higher lambda values observed during the second year (with average precipitation) versus the first year (with low precipitation) (Fig. 2a, b). Greater stasis of small adults was the largest contributor to the higher growth rate observed in wild Koke'e versus wild Limahuli populations in both years (Fig. 2c, d).

Lambda values for wild and closed canopy restored Limahuli populations were similar, but in the wild population higher fecundity and juvenile regression made positive contributions, while stasis of small adults contributed positively in the restored populations (Fig. 2e). Higher stasis of small adults was the biggest contributor to the higher lambda observed in the wild Koke'e population versus the closed canopy restored population (Fig. 2f). The largest contributors to the higher lambda values in the closed versus open canopy restored populations were higher values of stasis and growth for seedlings, juveniles and small adults (Fig. 2g, h).

### Transient dynamics of restored populations

The transient dynamics of restored *A. stellata* populations varied widely depending on the canopy conditions and on

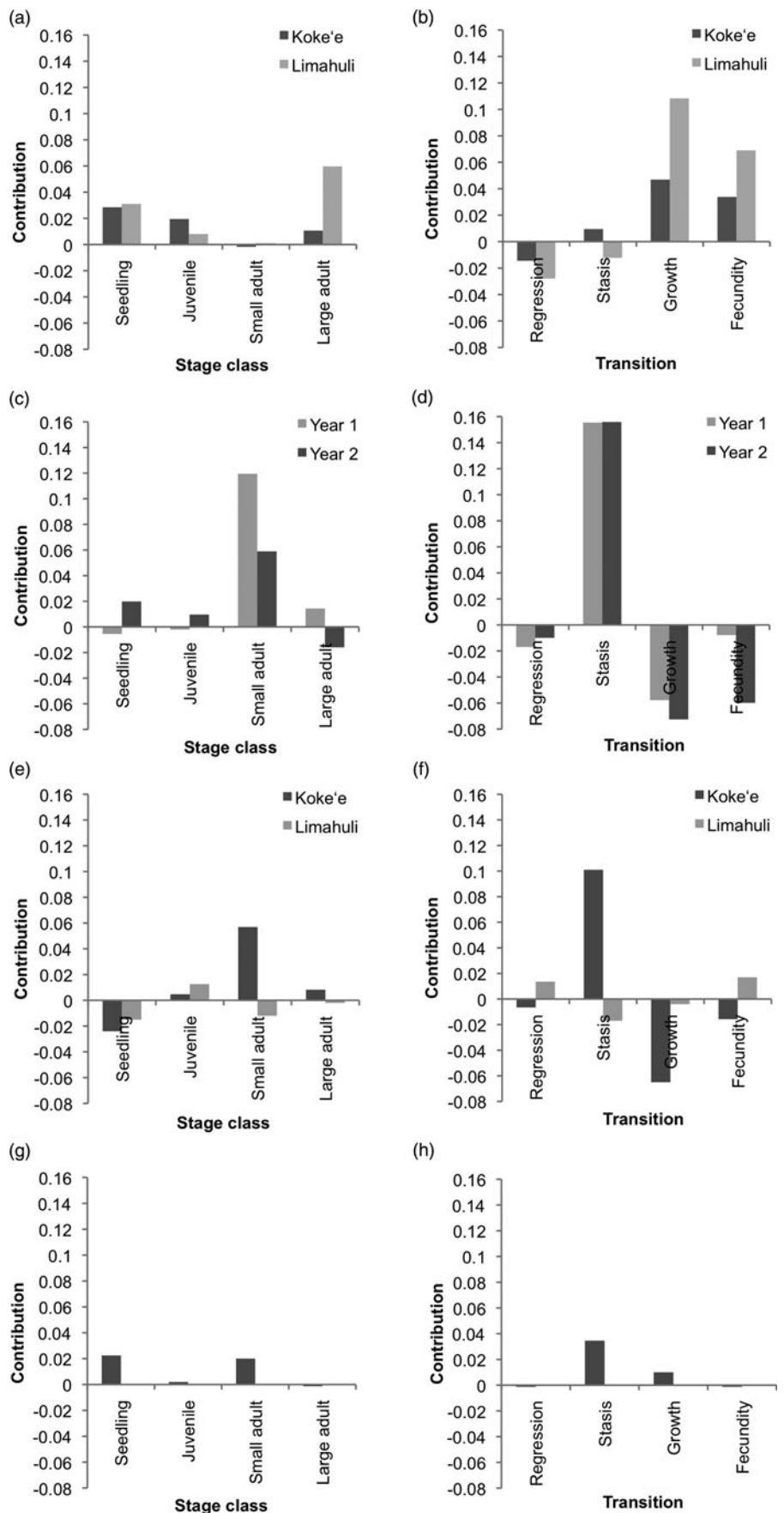
**Figure 1** Elasticity values summed per stage class and vital rate for wild *A. stellata* populations at: (a, b) Limahuli (c, d) Koke'e, and (e, f) under closed and open canopy for restored Limahuli populations.



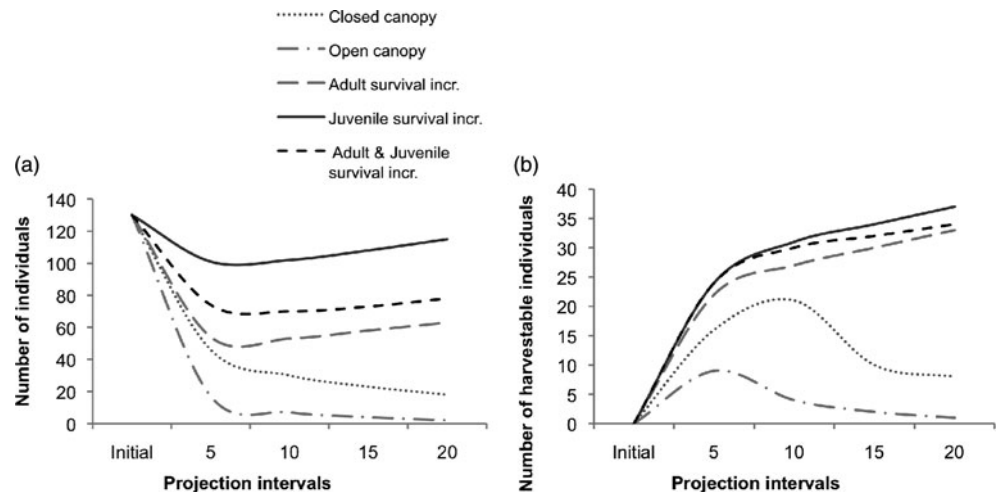
whether management to increase survival (stasis) was directed at juveniles, small adults, or both (Fig. 3a, b). Under the observed closed and open canopy conditions, populations plummeted in the first five years. If, under closed canopy, survival of small adults was increased by 0.15, or both juveniles and small adults by 0.10, total density began to stabilize after five years at approximately half the initial planting density. If survival of juveniles was increased by 0.20, density stabilized with less dramatic losses and began to reach initial density after 20 years.

The range of inertia values was 0.112–0.652 (Table 3), which indicated population decline at a faster rate than that expected of a population starting with the same initial density but with stable growth. Maximum attenuation of restored populations under the different scenarios was generally the same as the inertia values, indicating that populations were projected to consistently decrease before stabilizing (Table 3). In terms of harvestable *A. stellata* individuals for open and closed canopy, densities peaked at five and 10 years respectively, then declined. Increases in small adult and

**Figure 2** Life table response experiments for *A. stellata* populations summed per stage class and vital rate. (a, b) Positive values represent contributions to higher long-term population growth rates ( $\lambda$ ) observed in the average precipitation year 2 (2010–2011) versus dry year 1 (2009–2010) for wild populations; (c, d) positive values represent contributions to higher  $\lambda$  observed in wild Koke'e populations versus Limahuli by year; (e, f) positive values represent contributions to higher  $\lambda$  in wild populations than in closed canopy restored populations; (g, h) positive values represent contributions to higher  $\lambda$  in closed canopy than in the open canopy restored populations.



**Figure 3** Transient dynamics of restored *A. stellata* populations under open and closed canopy, and under three different management scenarios under closed canopy: increased survival (stasis) of small adult survival by 0.15; increased juvenile survival by 0.20; and increased small adult and juvenile survival, each by 0.10. Lines represented the projected number of (a) total *A. stellata* plants and (b) harvestable plants over time.



**Table 3** Indices of *A. stellata* transient dynamics in restored populations under open and closed canopy, and under three different management scenarios under closed canopy.

Population type	First-timestep attenuation	Maximum attenuation	Inertia
Closed canopy	0.762	0.325	0.325
Open canopy	0.461	0.112	0.112
Increased small adult stasis by 0.15	0.717	0.340	0.346
Increased juvenile stasis by 0.20	0.793	0.652	0.652
Increased small adult and juvenile stasis each by 0.10	0.758	0.468	0.468

combined juvenile and small adult survival (by 0.15 and 0.10, respectively) allowed for harvesting of *A. stellata* after five years (Fig. 3a, b). Increases in juvenile survival by 0.20 allowed for consistent harvest after five years (Fig. 3a, b). Since harvesting involves only cutting shoots of the plant, we considered harvest viable if the density of harvestable sized individuals were projected to stay stable or increase over time.

## DISCUSSION

### Projected fate of restored populations

Multiple *A. stellata* restoration programmes have been initiated in Hawai'i to address concerns of decreasing populations and some programmes occur in open canopy. These programmes vary, with direct planting of seedlings as a common method. Some programmes have involved removing non-native grass and watering nursery raised outplants via drip irrigation during establishment. Our results suggest that many of these restored populations, whether under open or closed canopy, may not be viable over the long term. While closed canopy populations fared much better than open canopy populations in our study, both had  $\lambda$  that were significantly  $< 1$ , projecting long-term population decline. Due to slow transitions between stages and our therefore being unable to document the vital rates of large adults in the restored populations, continued long-term monitoring is

necessary to further assess population viability of this long-lived species.

Our LTREs revealed that, in comparison to closed canopy restored populations, higher fecundity and juvenile regression in Limahuli and higher stasis of small adults in Koke'e made positive contributions to long-term growth rates in wild populations. Similar to our findings in Limahuli, a comparison of wild versus restored populations of the perennial herb *Centaurea corymbosa* in southern France showed differences in population dynamics, yet no significant difference in lambda values. In that case, higher survival in restored populations compensated for their lower fecundity (Colas *et al.* 2008), yet both wild and restored populations had  $\lambda < 1$ . As in our case and that of other species (Bell *et al.* 2003), restored populations were not projected to be viable. Transient analyses indicated that short-term decline was projected to occur even faster than predicted by asymptotic dynamics. This emphasizes the importance of analysing both long-term and transient dynamics of restored populations to ensure that current management can lead to self-sustaining populations. Increasing initial population size is recommended since small restoration populations are highly vulnerable to environmental, demographic and genetic stochasticity (Lande 1988; Menges 1991; Bell *et al.* 2003), and Bell *et al.* (2003) found that initial stage class greatly affected restoration population growth rates.



As with our study, high elasticity values for juvenile and adult stages is typical for slow-growing woody species and has been found for other vines (Escalante *et al.* 2004; Nabe-Nielsen 2004; Kouassi *et al.* 2008). Increasing population growth rates by supplementing with juveniles and adults instead of with seedlings may reduce the demographic cost of reintroduction, especially for species with slow maturation (Bell *et al.* 2003; Guerrant & Fiedler 2003). Since outplanting adults may be cost prohibitive and could result in decreased fecundity due to lower fitness of greenhouse plants (Bell *et al.* 2003), increasing survival of juveniles through annual supplementation may be more practical for some species (Escalante *et al.* 2004; Maschinski & Duquesnel 2007). Increasing juvenile and adult survival could potentially be achieved using various management approaches such as irrigation during drought and supplemental outplanting after major disturbance or tree fall events.

### Dynamics of wild populations

Although vines play important roles in forest regeneration and ecosystem processes (Schnitzer & Bongers 2002), their demography and its drivers are still poorly understood. *A. stellata* has been hypothesized to play a key role in native Hawaiian forests as a species whose population dynamics has a strong effect on the other species in the community (Mueller-Dombois 2005). It is a culturally iconic species and *A. stellata* lei are used by many sectors of society for cultural events such as hula, weddings, graduations and inaugurations (Abbott 1992). The demand for *A. stellata* has continued to rise and the supply to decrease, and most *A. stellata* lei are currently imported from elsewhere in the Pacific.

A study assessing the long-term population growth rate of another liana showed that the shade-tolerant neotropical species, *Machaerium cuspidatum*, had a slightly increasing population ( $\lambda = 1.033$ , 95% CI = 1.000–1.056) in shaded understorey (Nabe-Nielsen 2004). Our results illustrate that projected long-term growth rates (deterministic  $\lambda$  values) for wild *A. stellata* populations were close to unity during the average precipitation year (2010–2011), but lower during the dry year (2009–2010). Stochastic population growth rates for these populations were close to unity when dry years occurred 25% of the time, but significantly below one when dry years occurred 50% of the time, indicating long-term population decline. Our LTREs showed that lower growth of seedlings, juveniles and large adults, and lower fecundity were the main contributors to lower lambda values during the dry year. Lower stasis and growth of seedlings, juveniles and small adults were main contributors to lower lambda in open versus closed canopy restoration populations, and this appeared to be due to desiccation (T. Wong, personal observation 2007–2011).

Our elasticity analyses showed that elasticity of stasis for small adults (Koke'e) and small and large adults (Limahuli) was highest during the dry year (year 1). In the Koke'e wild population, mortality of small adults was high and observed to

be due to tree falls. Increased mortality of these stage classes due to storms and tree falls, habitat destruction, competition with invasive species and ungulate disturbance may have large negative effects on population growth rates.

While it is difficult to directly attribute precipitation as a causal factor due to only two years of observation, these results suggest that wild *A. stellata* populations may be sensitive to drought. The El Niño phase of the ENSO cycle occurred in the first year of our wild populations study (2009–2010) often resulting in dry periods in Hawai'i's wet seasons (Chu 1995), as seen in our study (Table 1). The pattern of increased plant mortality following droughts linked with ENSO has been documented in many studies of other tropical rainforests (Leighton & Wirawan 1984; Condit *et al.* 1995; Carlos Lola da Costa *et al.* 2010). Moreover, lianas have been shown to be generally more susceptible to mortality due to drought than either trees or palms (Nepstad *et al.* 2007). Central-Pacific El Niño events have occurred more frequently in recent decades (Wang *et al.* 2012). Our stochastic population growth rates show that *A. stellata* populations may be at risk of long-term population decline if there are increasing drought years in the future as predicted for Kaua'i and O'ahu islands (Timm & Diaz 2009; Chu *et al.* 2010). Adverse effects of low precipitation may be compounded where changes in climate lead to habitat shifts such as reduced canopy cover. Our analyses are limited by the short duration of our study, the limited number of populations we studied, and the fact that our data from wild populations was collected for two of the four years of our restoration project. Longer-term monitoring over more populations would provide greater insight.

### CONCLUSIONS

The application of a combination of analyses, including projected long-term population growth rates, LTRE contributions, elasticity values and transient indices, can greatly improve efforts to ensure the viability of restored populations and more effective use of resources. For *A. stellata*, our results suggest that viability of restored populations may be tightly connected to canopy conditions and survival of particular stage classes. Further research is needed to assess the effects of harvest on maile population dynamics to identify optimal management strategies.

Transient dynamics projected our study populations to stabilize at half the initial size, therefore, increasing initial population size is recommended. To buffer against stochastic losses, restoration approaches that involve multiple years paired with multiple sites may also be necessary (Maschinski & Duquesnel 2007). This may become even more important if increasing drought predictions in certain regions are realized (Timm & Diaz 2009; Chu *et al.* 2010). Finally, conservation and restoration of culturally important species like maile can greatly benefit from collaboration with cultural practitioners and local communities, and future partnerships should be a priority.

## Supplementary material

To view supplementary material for this article, please visit [Journal.cambridge.org/ENC](http://Journal.cambridge.org/ENC).

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