

Climate-associated population declines reverse recovery and threaten future of an iconic high-elevation plant

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Abstract

Although climate change is predicted to place mountain-top and other narrowly endemic species at severe risk of extinction, the ecological processes involved in such extinctions are still poorly resolved. In addition, much of this biodiversity loss will likely go unobserved, and therefore largely unappreciated. The Haleakalā silversword is restricted to a single volcano summit in Hawai'i, but is a highly charismatic giant rosette plant that is viewed by 1–2 million visitors annually. We link detailed local climate data to a lengthy demographic record, and combine both with a population-wide assessment of recent plant mortality and recruitment, to show that after decades of strong recovery following successful management, this iconic species has entered a period of substantial climate-associated decline. Mortality has been highest at the lower end of the distributional range, where most silverswords occur, and the strong association of annual population growth rates with patterns of precipitation suggests an increasing frequency of lethal water stress. Local climate data confirm trends toward warmer and drier conditions on the mountain, and signify a bleak outlook for silverswords if these trends continue. The silversword example foreshadows trouble for diversity in other biological hotspots, and illustrates how even well-protected and relatively abundant species may succumb to climate-induced stresses.

Keywords: alpine plants, *Argyroxiphium sandwicense*, biodiversity loss, climate change ecology, hotspot, population declines, silversword

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Introduction

As temperature and precipitation regimes change, species will increasingly need to adjust their phenologies and spatial distributions to track changing environmental conditions (Parmesan, 2006). Because many species will probably be unable to adjust quickly enough, climate change has been predicted to lead to major biodiversity loss (Thomas *et al.*, 2004; Thuiller *et al.*, 2005). For mountain-dwelling species that are projected to move upslope, habitat area will decrease with increasing elevation, and species that already occupy summits may lit-

erally have nowhere to go as their habitats disappear (Diaz & Eischeid, 2007; Williams *et al.*, 2007; Raxworthy *et al.*, 2008; Dirnböck *et al.*, 2011). Despite the logic of such projections, they provide only a coarse guideline, and the scale of complexity and variation in the ecological processes that may ultimately cause such extinctions remains to be characterized (Pounds & Puschendorf, 2004). For example, even species occurring below summit areas may face extinction, if changes in precipitation regimes combine with increasing temperatures to create conditions unsuitable to population stability, as appears to have happened to Costa Rica's golden toad (*Bufo periglenes*) (Pounds *et al.*, 1999).

Moreover, much of the predicted global biodiversity extinction may go largely unnoticed by the general public and even the scientific community, either because the taxa involved are obscure and difficult for the typical

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layperson to appreciate or because they occur in remote locations and are difficult to observe. Here, we present a detailed analysis of climate-associated declining population trends and worrisome future prospects for a highly visible, eminently recognizable, and charismatic plant, the Hawaiian silversword (or ‘āhinahina). Silverswords include a handful of taxa in the larger silversword alliance, an endemic lineage that diversified dramatically from a common ancestor that colonized the archipelago about 5 million years ago (Baldwin & Sanderson, 1998). This lineage has become a textbook example of insular evolution and adaptive radiation (Futuyma, 1998). Within the alliance, alpine silverswords evolved into giant rosette plants, and the Haleakalā silversword, *Argyroxiphium sandwicense* subsp. *macrocephalum*, endemic to high elevations on Haleakalā volcano on the Island of Maui, is by far the most abundant and accessible silversword taxon. Its rosette, up to 1 m in diameter, is formed by long slender leaves densely covered with silvery pubescence. It is estimated to grow for about 20–90 years before flowering once at the end of its life (Rundel & Witter, 1994), at which time it extends a large compound inflorescence up to 2 m tall and bearing up to 600 heads. These characteristics give the silversword a striking appearance in its barren cinder habitat (Fig. S1), and have made it an iconic symbol of Hawaii’s unique ecological and evolutionary heritage and a prime attraction for the 1–2 million visitors to Haleakalā National Park each year.

The Haleakalā silversword has been considered a conservation success, with active management leading to a strong recovery from a population low in the early 20th century (Appendix S1). However, changing climatic conditions now appear to have reversed this trend in the past few decades. Consistent with trends worldwide, air temperatures in Hawai‘i have been increasing, most rapidly since 1975 and in upper mountainous areas (0.268 °C/decade, Giambelluca *et al.*, 2008). In addition, the trade wind inversion, which imposes a cap on upward movement of the prevailing moisture-laden trade winds and creates much drier atmospheric conditions above this cap, has increased in frequency in recent decades (Cao *et al.*, 2007). Together, these trends portend a shift toward warmer and drier conditions within silversword habitat, which is located above the inversion. In this study, we examine long-term climate data on Haleakalā volcano, link these to a nearly 30-year record of demographic trends of the Haleakalā silversword, and combine both with a population-wide appraisal of recent plant mortality. We use these detailed datasets to assess the likely drivers of recent unfavorable silversword population dynamics and the future prospects for this locally endemic yet widely appreciated alpine plant.

Materials and methods

Study plant and site

The Haleakalā silversword, *Argyroxiphium sandwicense* subsp. *macrocephalum* (A. Gray) Meyrat, is a federally listed threatened taxon in the family Asteraceae that occurs only on East Maui, Hawai‘i (see Appendix S1 for more information). Unspecified references to silversword plants in this study refer to the Haleakalā subspecies. Haleakalā silverswords grow on the largely barren cinder cones, cinder flats, and rocky cliffs in a single broad geographic area spanning the central to western portions of Haleakalā crater up to the summit, in the alpine zone from 2150 to 3050 m elevation. Although estimated mean annual rainfall across the silversword range varies from 1090 to 1520 mm (Giambelluca *et al.*, in press), the young, poorly developed and porous volcanic soils, combined with typically dry atmospheric conditions, create a xeric habitat with sparse vegetation that frequently experiences water stress (Leuschner & Schulte, 1991). Rainfall is concentrated in the wet season, approximately October through March: from 1950 to 2010, 70.4% of total precipitation at Haleakalā Park Headquarters (2130 m) occurred during the wet season (mean \pm SE = 926.0 \pm 56.1 mm/season), whereas 29.4% occurred during the April to September dry season (mean \pm SE = 372.6 \pm 25.8 mm/season).

Silversword distributions within the total range on upper Haleakalā volcano are clumped, with distinct aggregations often separated by large areas devoid of individuals. These aggregations have been mapped and given “population” numbers or names by Kobayashi (1973) and subsequent researchers, although the degree to which gene flow is reduced between these entities is not known and possibly highly variable. For the sake of convenience and continuity, we follow Kobayashi in referring to these aggregations as populations, and we used his and other prior population designations for our sampling protocols whenever possible.

The total abundance of Haleakalā silverswords reached a critical low of perhaps 4,000 plants in the 1920s–1930s, owing to ungulate browsing and human vandalism (Loope & Crivellone, 1986; US Fish & Wildlife Service, 1997; Appendix S1), but subsequently rebounded with peak numbers estimated at roughly 65,000 plants in 1991. From June to September of each year, a highly variable number of mature plants flower and then die, from a low of 0 flowering plants recorded in 1970 to a high of 6,632 in 1991. Because silverswords are strongly self-incompatible (Carr *et al.*, 1986), the number of synchronously flowering plants strongly affects seed set rates (Forsyth, 2003), and therefore possibly annual seedling recruitment. The trigger for large flowering events is currently not known.

Long-term demography plots

Eleven 5 m \times 20 m plots were installed in 1982 to track silversword demography, and were sited on five different cinder cones situated on the floor of Haleakalā crater, at elevations of 2260–2387 m. A 12th plot, roughly 35 m \times 50 m, was installed in 1993 on the western rim of the crater at 2908 m

elevation (Fig. S2). All live silverswords were counted and measured in each plot during the fall, usually in October, in 1982–87, 1990, 1992, and 1996–2010 in the 11 original plots, and in 1993–2010 in the 12th plot. To assess trends in annual population growth rates, we grouped plot data in two ways: 1) six geographic localities (the five cinder cones plus the western rim), 2) two elevational zone localities (low = five cinder cone sites; high = west rim site). For each locality grouping, we calculated annual population growth rate as $\ln\lambda$, or $\ln(N_{t+1}/N_t)$, where N = total number of individuals in years t and $t + 1$ (Morris & Doak, 2002). Annual population growth rates were available for 1983–1987 and 1997–2010 for the five crater localities, and 1994–2010 for the west rim locality. We fitted a linear regression model with $\ln\lambda$ as the response variable and year, locality, and their interaction as explanatory variables for each of two time periods (1983–1987, 1994–2010).

To test associations of climate factors with the observed population growth rates, we combined growth rate data from all plots for all years in which data were available for at least five of the six localities ($n = 19$ years: 1983–1987, 1997–2010). We combined the plot data because climate data spanning the entire period of record were available for only one station (Haleakalā Ranger Station, see below), and because temporal trends in annual population growth rates were not significantly different among the six localities and exhibited parallel trends among low- and high-elevation localities (see Results). We constructed linear regression models with $\ln\lambda$ as the response variable, and the following temperature and rainfall measures as explanatory variables: mean annual temperature, total rainfall, number of days with zero rainfall, and number of days with rainfall greater than 5, 10, and 15 mm, respectively. These climate variables were chosen *a priori* as potentially important measures of temperature and the magnitude and temporal evenness of moisture availability that might influence both germination and mortality. Each climate variable was calculated for three periods for each year: wet season (Oct–Mar), dry season (Apr–Sept), and water year (Oct–Sept). We also included four silversword flowering measures as explanatory variables to test for associations with annual population growth rates: number of flowering plants in the same year, previous year, same year plus previous year, and same year plus previous 2 years. Silversword seeds remain viable in the field for up to 4 years, although most germination occurs within 1 year of flowering (Forsyth, 2002). The flowering totals were generated by summing the numbers of flowering plants (obtained from annual flowering censuses) in the regions of the park corresponding to each of the six plot localities for each year.

We generated all possible first-order models with a maximum of six terms, and evaluated the best models based on their Akaike Information Criterion (AIC_c) values, Akaike weights (w_i), and relative likelihoods computed as in Burnham & Anderson (2002). In our model selection procedures, we excluded models that yielded negative coefficients for the flowering variables, as these indicated indirect intercorrelations with other explanatory variables. Among the best first-order models, we subsequently assessed whether or not inclusion of interactions between any of the selected flowering

and climate variables improved the model fit; the large number of possible interactions made it infeasible to consider them in initial model selection. In addition, we repeated this procedure on a reduced dataset: two years had unusually high $\ln\lambda$ values owing to spikes in seedling recruitment, and these were followed 1 or 2 years later with unusually low $\ln\lambda$ values when these seedlings died. We assessed the best models with these 4 years deleted, to determine which variables best explained $\ln\lambda$ in the more ‘typical’ 15 years on record.

Large-scale census

To assess whether or not population growth rate trends in the long-term demography plots described above appeared to be representative of wider patterns across the Haleakalā silversword range, we conducted a large-scale survey of plant survival and mortality in 2010. We censused all plants within 31 populations, spanning nearly the entire silversword range (Fig. S2), from 27 May to 23 December, 2010. These were selected from a total of approximately 115 populations identified by Kobayashi (1973) and others. We excluded populations with fewer than 100 live plants, based on rough population estimates made in 2001, as well as populations located on cliffs or in other inaccessible or sensitive locations, leaving 52 populations. We divided the remaining pool into two geographic areas to maximize evenness of the elevational and spatial representation, and randomly selected 15 populations in each area. This procedure was conducted in ArcGIS 9.3 (ESRI, Redlands, CA, USA) prior to the census start to avoid selection bias in the field. We decided to split one population into two because of pronounced discontinuity of plant distributions at that site, resulting in the final 31 populations selected. In each population, we counted, geolocated (Garmin eTrex Legend H GPS units; Garmin Ltd., Olathe, KS, USA), and categorized each plant as alive or dead. Based on the long-term plots, dead silverswords can persist in the field from several to over 17 years. For a random subset of plants, rosette diameter was measured. The randomization procedure selected at least 84, and usually over 100 live plants in each population, plus a number of dead plants proportional to the overall live:dead plant ratio for the population. In four of the 31 populations, steep and loose terrain necessitated a different approach to minimize disturbance: transects were randomly placed within the populations and all plants within 1 m of the transects were counted and measured until at least 100 live plants were encountered.

We used the percentage of plants that were alive in each population as a relative inverse metric of recent mortality. It was assumed that no systematic, large-scale spatial differences occur in the duration of persistence of dead plants. A possible exception would be faster decomposition at lower and wetter sites, which would produce a bias toward lower estimated relative mortality rates at these sites.

We constructed a linear regression model to evaluate elevation, mean annual precipitation, total percent cover of all non-silversword vegetation within each population, and their interactions, as main potential explanatory factors associated with this response. Percent cover of non-silversword vegetation was used as a proxy measure for soil moisture availability,

which on a local scale is the outcome of a complex and difficult to predict range of atmospheric, topographic, and edaphic factors (Perez, 2009). Vegetative cover has been found to correlate strongly with soil moisture in tropical alpine habitats (Young, 1994), and the distribution of high-elevation Andean rosette plants was shown to be associated with areas of increased soil moisture (Perez, 1991). We measured vegetative cover using 10 randomly-placed 50 m long point-intercept transects within each population, recording live vegetation, dead vegetation, or bare ground every meter, for a total of 500 cover points per population. We obtained mean annual precipitation values from the Hawai'i Rainfall Atlas, a digital raster grid of spatial rainfall patterns averaged over the period 1978–2007 (Giambelluca *et al.*, in press). In addition, we included silversword population size (living + dead plants) in the model to control for possible density-dependent effects; number of days post census start, to control for possible mortality during the course of the census (2010 was a very dry year, receiving 40% of the 1950–2010 mean rainfall for the water year and only 26% of the 1950–2010 dry season average); and soil age to control for possible effects of differential soil development. For soil age, we used the median of the age ranges estimated for different volcanic flows on Haleakalā volcano (Sherrod *et al.*, 2008). Population size and median soil age were log transformed.

To investigate whether differential mortality among populations resulted mainly from differential rates of natural post reproductive senescence or instead from differential rates of death prior to flowering, we calculated the percentage of plants alive in each of three size classes, using the randomly measured plants in each population. We used size classes as proxies for reproductive status, because owing to decomposition it was not possible to conclusively determine whether many dead plants had flowered. The size classes were based on the size distribution of all of the plants in the entire census that had clearly flowered ($n = 1374$): plants <9 cm diameter, which includes all plants >2 standard deviations below the mean flowering size; plants >9 cm and <26 cm diameter, with 26 cm being the mean flowering size; and plants >26 cm diameter. The smallest size category therefore contained almost exclusively pre-reproductive plants, the medium size category contained a mixture of plants of reproductive and pre-reproductive age, and the large size category contained plants mainly of reproductive age. We tested whether or not the percentage of plants alive, as a function of elevation, differed among the size classes: elevation, size class, and their interaction were included in a linear regression model with percent of plants alive as the dependent variable. We used elevation as a reference because of its strong association with spatial patterns of mortality in the above analysis that included all censused plants (see Results). Simple linear regressions between percent of plants alive and elevation were subsequently modeled for individual size categories to examine significantly different trends.

To investigate patterns in recent recruitment, we calculated the proportion of living plants that were under 5 cm diameter among the randomly measured plants in each population. We chose this cutoff in part because a <5 cm class was used to

categorize plants in the long-term plots in early years, allowing us to compare size structure across time periods.

Estimating past population changes across the range

To link patterns of plant mortality in the census to past population changes, we counted the number of dead plants persisting in 2010 in the 12 long-term demography plots described above, and calculated the percentage of plants alive within each plot in 2010. We correlated these percentages with net proportional changes in silversword numbers in each plot over successively longer time periods, from one to 18 years prior to 2010, to determine how well 'percent of plants alive' performed as a metric of past population change. We then used the best-fitting relationships to estimate past population changes for the 31 populations censused in 2010. All statistical analyses were performed in JMP 9.0.2 (SAS Institute Inc., Cary, NC, USA). For all linear regression models employed, we inspected residual and leverage plots to confirm that the linear model structure was appropriate.

Climate data

We used air temperature and rainfall data for 1950–2010 from the Haleakalā Ranger Station (National Climatic Data Center), located at 2130 m elevation at National Park Headquarters and 4.1–7.7 km from the six silversword plot localities. In addition, we used HaleNet, a network of climate stations on Haleakalā volcano (HaleNet, 2011), for detailed data from 1990–2010. We used data from three stations at 2130, 2600, and 3000 m, which span the elevational range of silverswords and are located 0.6–7.7 km from the plots. We fitted linear regressions to seasonal and annual trends in rainfall, air temperature, and solar radiation anomaly (calculated as average of monthly anomalies; monthly anomalies were calculated as monthly values minus the respective long-term monthly means). We adjusted for temporal autocorrelation in the climate data using the procedure of Santer *et al.* (2000).

Results

Climate trends

Rainfall trends at all three elevations indicate that conditions have become drier in recent decades on upper Haleakalā volcano. Both seasonal and annual trends indicate decreasing total rainfall and increasing number of rainless days, although not all trends were statistically significant (Table S1, Fig. 1). Rainfall trends were clearest at the lowest elevation (2130 m), where the rate of declining precipitation accelerated dramatically over the past 20 years in comparison to the past 60 years. Rainfall also decreased at a rapid rate at the two higher elevations (2600 and 3000 m) over the past 20 years; however, due to greater variance many of these trends were not statistically significant. Air temperature

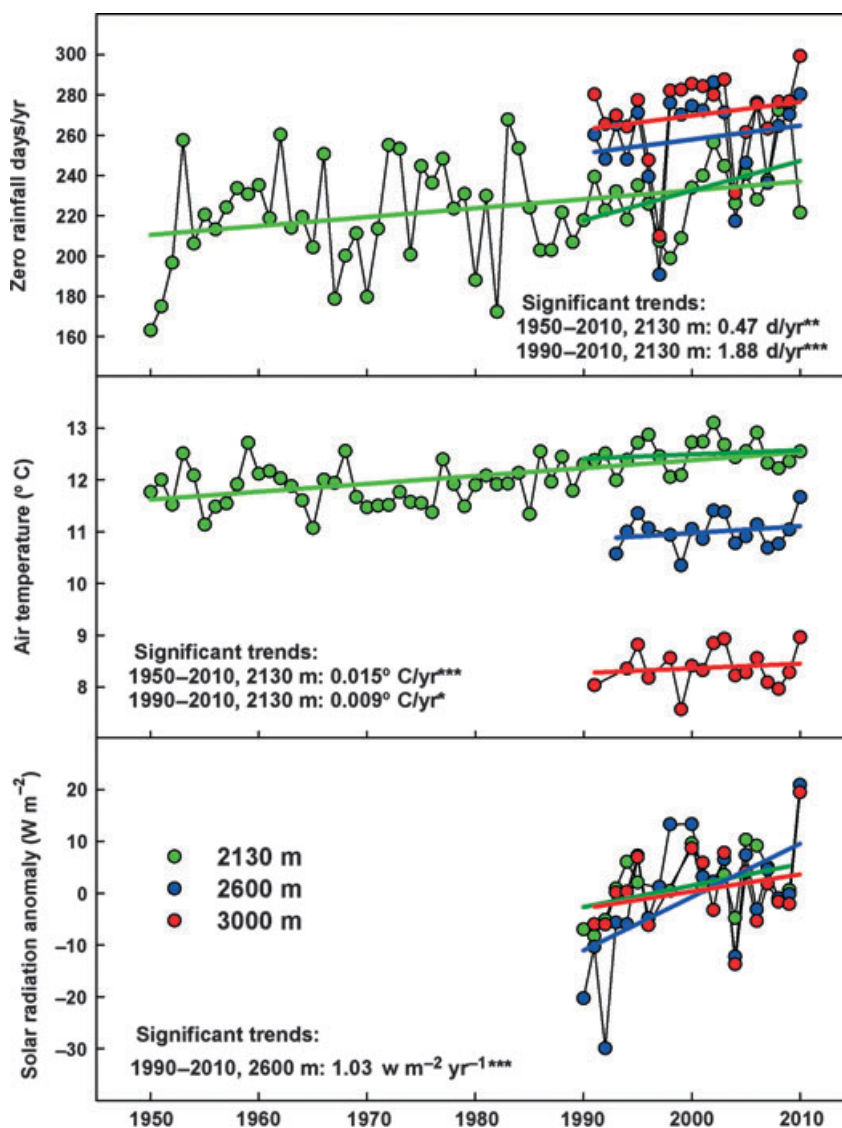


Fig. 1 Trends in number of rainless days per year (top panel), mean annual air temperature (middle), and mean annual solar radiation anomaly (bottom) at three elevations on upper Haleakalā volcano. Linear trends shown in same colors as points, but dark green lines indicate trends at 2130 m elevation for the time period 1990–2010. Significant trends listed in each panel ($P \leq 0.10^*$, $P \leq 0.05^{**}$, $P \leq 0.01^{***}$). Data prior to 1990 were not available for the two upper elevation stations (and for solar radiation at all stations). Complete seasonal and annual climate trends are presented in Table S1.

increased significantly since 1950 and marginally significantly since 1990 at the lowest elevation, but increasing temperature trends since 1990 were not significant for the two upper elevations. Mean annual solar radiation has also shown signs of increasing over the past 20 years, although this trend was significant only at 2600 m elevation.

Long-term demography plots

Numbers of live silverswords in each of the five crater floor localities fluctuated from 1982 to 1990, and then

began an almost unbroken decline after about 1990 (Fig. 2). At the high-elevation west rim locality, silversword numbers increased steadily from 1993–2000, but subsequently also began a nearly consistent decline (Fig. 2). For the period 1983–1987, no significant temporal trend in $\ln\lambda$ was found, nor were there significant differences in $\ln\lambda$ among the five plot localities (Table S2), with an overall slightly negative mean population growth rate (mean $\ln\lambda = -0.0113$). In contrast, for the period 1994–2010, a significant decreasing temporal trend in $\ln\lambda$ was found, although $\ln\lambda$ was not statistically different among the six geographic localities

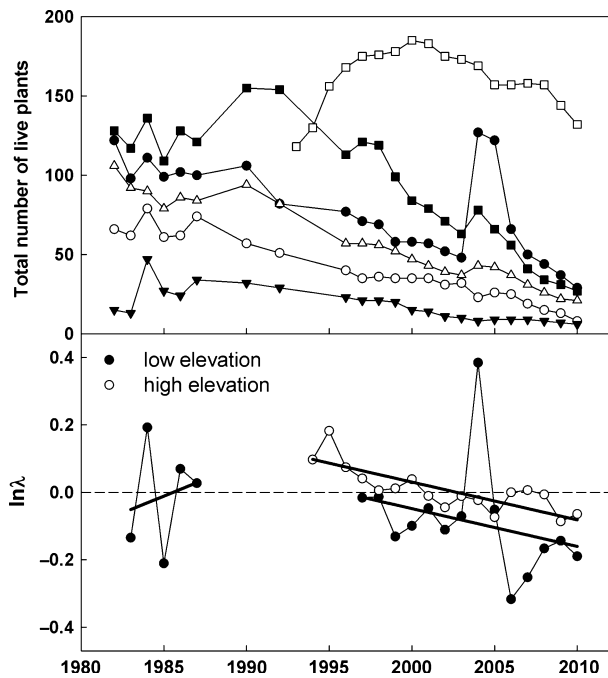


Fig. 2 Trends in 12 long-term demography plots. Top: total number of live silverswords from 1982 to 2010, plots grouped into six geographic areas: five cinder cones on the crater floor (five trends starting in 1982), plus the high elevation crater rim site (empty squares, starting in 1993). Bottom: annual population growth rates ($\ln\lambda = \ln(N_{t+1}/N_t)$) over time in low-elevation plots and high-elevation plots, for the periods 1983–1987 and 1994–2010. Reference line at $\ln\lambda = 0$ indicates a stable population. The least squares regression trend of $\ln\lambda$ over time was not significantly different from 0 for 1983–1987, whereas a decreasing trend in $\ln\lambda$ for low and high elevation plots from 1994 to 2010 was statistically significant (see Table S2).

(Table S2). However, when plots were grouped into high and low elevational zones, $\ln\lambda$ was marginally significantly different ($P = 0.057$) between the two zones. Plots in the two zones exhibited parallel declining trends in $\ln\lambda$ over time, but on average low-elevation plots had lower population growth rates and entered a period of negative population growth earlier (Fig. 2).

In our analysis of the potential effects of climate and flowering patterns on annual population growth rates, the best-fitting model for the full dataset ($n = 19$ years) included four explanatory variables that together explained 64% of the variation in $\ln\lambda$ (Table 1). We found a positive relationship of $\ln\lambda$ with the number of flowering plants in the same year and the number of days with rainfall >10 mm during the wet season, and a negative relationship with the number of zero rainfall days in the dry season and the number of days with rainfall >15 mm in the wet season. No interactions between the number of flowering plants and the three selected climate variables improved model fit. Other

Table 1 Models describing the relationships between annual population growth rates ($\ln\lambda$) in the long-term plots and various climate and flowering variables between 1983 and 2010. Top five models (lowest ΔAIC_c values) are presented for the full dataset ($n = 19$ years) and for a reduced dataset with four outlier years excluded. Best models with relative likelihoods >0.15 are in bold, with term coefficients and model fits in lower table

Model*	ΔAIC_c	Relative likelihood	w_i
All years included†			
1. A, B, C, D	0	1	0.193
2. A, C, D, E, F	2.055	0.358	0.069
3. A, B, C, D, E	2.205	0.332	0.064
4. A, B, C, D, F	2.269	0.322	0.062
5. A	2.957	0.228	0.044
Four outlier years excluded			
6. F, G	0	1	0.185
7. B, G	0.339	0.844	0.156
8. G	1.624	0.444	0.082
9. B, H	2.076	0.354	0.065
10. E, G	2.599	0.273	0.050

Term	Coef.	SE	Model R^2
Model 1	–	–	0.64
A) num flowering plants in same year	0.00010	0.00003	–
B) num zero rain days in dry season	–0.00473	0.00142	–
C) num >10 mm rain days in wet season	0.02794	0.00860	–
D) num >15 mm rain days in wet season	–0.03747	0.01048	–
Model 6	–	–	0.76
G) total rainfall in dry season	0.00015	0.00004	–
F) num zero rain days in water year	–0.00083	0.00036	–
Model 7	–	–	0.76
G) total rainfall in dry season	0.00013	0.00004	–
B) num zero rain days in dry season	–0.00146	0.00066	–

*Model terms not listed in lower table: E = number of zero rainfall days in wet season, H = number of days with >10 mm rainfall in dry season.

†No models including interactions between flowering variable (A) and any selected climate variables (B–F) yielded ΔAIC_c values <4.27 and relative likelihoods >0.118.

candidate models had a steep decline in AIC_c weights and relative likelihoods (Table 1), although most of these models included similar combinations of the same or related variables as the best fitting model.

We were unable to determine the combination of factors responsible for the two large germination events. Only one of these events coincided with a large

flowering year and moderate levels of rainfall, while the other occurred during a year of low rainfall and lagged 2 years behind a large flowering event. Multiple additional medium to large flowering events occurred during the study period. Similarly, the 2 years with unusually low population growth rates that followed the two large germination events had only moderately low levels of rainfall. These two large declines therefore appeared to reflect the influence of unusually high abundances of plants in the vulnerable seedling stage more than unusually deleterious environmental conditions. When we repeated our analysis with these 4 years removed ($n = 15$ years), two models provided similar fit to population growth rates, both explaining 76% of the variation in $\ln\lambda$ (Table 1). In both models, total dry season rainfall was strongly positively associated with $\ln\lambda$, and the number of rainless days in either the dry season or water year added explanatory power to the two models, respectively. The last two variables were negatively correlated with $\ln\lambda$. Again, other candidate models not only had substantially lower AIC_c weights and relative likelihoods (Table 1) but also suggested associations with similar climate variables.

Large-scale census

We counted 28,492 silverswords in the 31 populations in 2010. The percentage of plants that were alive varied greatly among the populations, ranging from 30.4% to 81.8%. A multiple regression model found elevation, percent vegetative cover, and their interaction, to be significantly associated with this metric (Table 2). Percent of live plants increased with both elevation and vegetative cover (Table 2). A significant interaction between these two explanatory variables signifies that the high rate of plant mortality at lower elevations was lessened in populations with higher percent cover of non-silversword vegetation, presumably indicating greater soil moisture availability in these locations. This

Table 2 Factors associated with the percentage of plants alive in 31 populations censused in 2010. Model $R^2 = 0.90$

Term	Coef.	SE	t	P
elevation	0.0419	0.0105	4.00	<0.001
precipitation	-0.0655	0.0413	-1.58	0.128
vegetative cover	1.7218	0.3008	5.72	<0.001
elevation \times precipitation	-0.0003	0.0002	-1.28	0.213
elevation \times veg cover	-0.0052	0.0011	-4.62	<0.001
precipitation \times veg cover	0.0031	0.0040	0.76	0.456
log(population size)	-1.0954	3.1741	-0.35	0.733
log(median soil age)	-0.8450	2.3680	-0.36	0.725
days post census start	-0.0838	0.0253	-3.31	0.003

ameliorating effect of increased water availability was much weaker in higher-elevation populations, where percentage of plants alive was consistently high. If a methodological bias toward higher percentages of live plants at lower elevations was created by faster decomposition and disappearance of dead plants in these areas (see Materials and Methods), then the observed elevational trend in mortality was more conservative than the actual trend. Number of days post census start was also significantly (negatively) associated with percentage of plants alive, indicating mortality during the 6-month census, although this effect was relatively weak compared to the other significant effects. Together, these variables accounted for 88% of the variation in percentage of plants alive across the populations (whereas total model $R^2 = 0.90$). Patterns of mortality among populations were unrelated to median soil age, population size, or long-term spatial patterns in mean annual precipitation. Intercorrelations between elevation and soil age ($r = 0.70$) and between elevation and mean annual precipitation ($r = -0.39$), however, make it difficult to rule out completely the roles of these two factors.

The relationship between percentage of plants alive and elevation was significantly different among plant size classes (Table S3). Small (pre-reproductive) plants, as well as medium plants (including pre-reproductive and potentially reproductive individuals), both showed a significant trend of increasing mortality with decreasing elevation (Fig. 3). However, the average rate of survivorship at a given elevation was significantly higher for medium plants as compared to small plants (Fig. 3). Plants in the largest class, containing mainly individuals of reproductive size, showed no relationship between mortality and elevation (Fig. 3). The latter suggests that mortality in this size class may have been largely represented by natural postreproductive death that occurred at similar rates across the entire range.

The proportion of living plants that were under 5 cm diameter was consistently low (mean = 0.049 ± 0.010 SE), with only two of the 31 populations exhibiting proportions over 0.082. This indicates very low levels of seedling recruitment in recent years in nearly all parts of the silversword range; in comparison, this proportion averaged 0.316 ± 0.023 SE in the long-term demography plots from 1982 to 1987, years when population growth rates were on average nearly stable.

Estimating past population changes across the range

The percentages of plants alive in 2010 in the 12 long-term demography plots were strongly correlated to net proportional changes in silversword numbers in the plots over past time intervals. This relationship reached

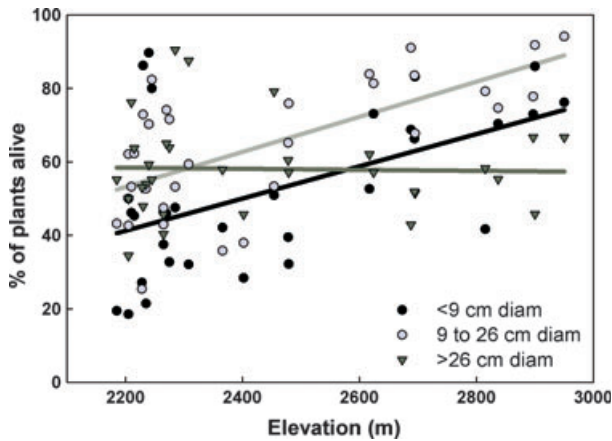


Fig. 3 Relationship between percentage of plants alive in 31 populations censused in 2010 and elevation for three size classes of silverswords. While additional variation would be explained by other factors (as in Table 2), this figure indicates that elevation was significantly associated with rates of mortality for small and medium-sized plants, but not for larger plants. (Small plants, black line: $R^2 = 0.26$, $P = 0.003$; medium plants, light gray line: $R^2 = 0.44$, $P < 0.001$; large plants, dark gray line: $R^2 = 0.001$, $P = 0.883$).

its strongest correlation for the 7-year period prior to 2010 ($r = 0.82$, $P = 0.001$), but was strong ($r > 0.76$) for all time intervals ranging from 7 to 14 years prior to 2010 (Fig. S3). We therefore estimated net proportional change for each of the 31 populations censused in 2010, using both the 7 and 14 year relationships (Fig. 4), because these two relationships largely bracketed the range of estimates produced with all of the relationships between 7 and 14 years prior to 2010.

Discussion

Haleakalā silverswords currently number in the tens of thousands, and aided by federal protection the persistence of this taxon has appeared relatively secure for the foreseeable future. However, long-term demography plots installed to study silversword recovery now indicate that this view is no longer justified. Silversword numbers in these plots fluctuated with no clear trend from 1982 until the early to mid 1990s, but subsequently began declining sharply to 2010 (Fig. 2). Annual population growth rates were negative by the late 1990s in lower-elevation plots and continued to decline over time, whereas population growth rates transitioned from positive to negative in the early 2000s in the high-elevation plot (Fig. 2).

We found that these declining population growth rates were associated with changing climatic conditions on upper Haleakalā volcano. Since 1950, and especially after 1990, air temperature and solar radiation have

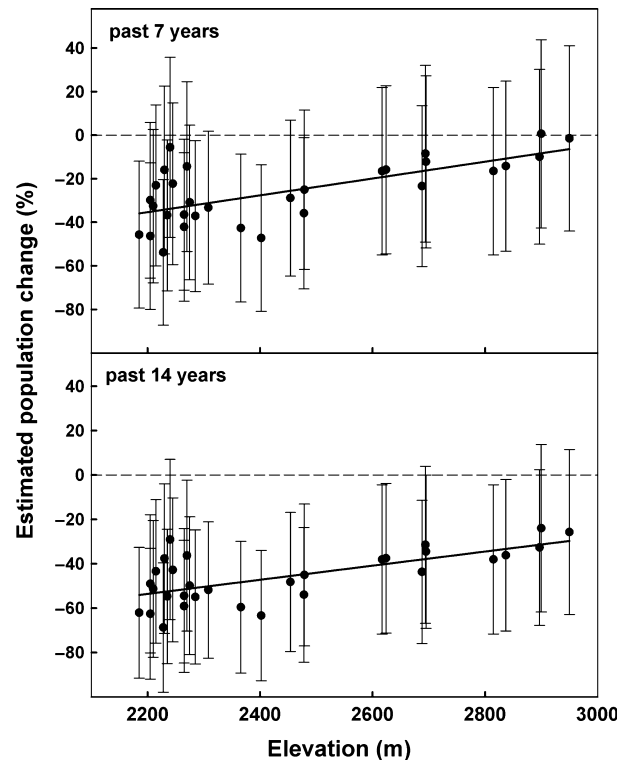


Fig. 4 Estimated past population changes ($\pm 95\%$ prediction intervals) for 31 silversword populations censused in 2010. Estimates were made using relationships between percentage of plants alive and known population changes in the long-term demography plots (Fig. S3), and were calculated separately for relationships over the past 7 (top) and 14 years (bottom). Trends fitted by least squares regression.

been increasing, and total rainfall has been decreasing while frequency of rainless days has risen (Table S1, Fig. 1). Multiple regression models indicated that annual population growth rates were strongly tied to rainfall patterns, as well as to the number of plants that flowered the same year (Table 1). Fewer rainless days during the dry season were associated with higher population growth rates, whereas frequency of higher rainfall days in the wet season had variable relationships with growth rates. The latter result could indicate that moderate rainfall days (>10 mm/day) enhance recruitment and survival, whereas numerous high rainfall events (>15 mm/day) may be deleterious by causing erosion of the loose cinder substrate (Loope & Crivellone, 1986) or perhaps owing to intercorrelations with other climate factors.

Two years had exceptionally high population growth rates resulting from large germination events. The specific combination of factors responsible for these events is not clear, and it is likely that a much longer time series would be required to resolve this. Nevertheless, infrequent successful recruitment events can be a

key feature of population persistence among long-lived plants living in resource-limited environments (García & Zamora, 2003). For such species, long-term survival of adults confers substantial resilience to instability in other demographic rates that may be tied to varying climatic or other conditions (Morris *et al.*, 2008; Chacastaldo & Inouye, 2011). In fact, a stage-based demographic matrix model for Haleakalā silverswords predicted that survival of adult plants, as well as germination and survival of seedlings, were the main contributors to positive population growth (Forsyth, 2002), suggesting that the Haleakalā population may have a strong capacity to rebound despite recent high rates of mortality among smaller plants. However, this is contingent on the periodic occurrence of favorable conditions lasting long enough for seedlings to recruit and pass through the most vulnerable stage, which likely lasts for several or more years. For example, the vast majority of the large cohort that germinated in the plots during the relatively wet year of 2004 perished from 2005 to 2008. Therefore, if climate trends continue their tendency toward less favorable conditions on Haleakalā, it seems likely that the frequency and success rate of such rare recruitment events will decline.

Moreover, we found that population growth rates in the more typical intervening years (excluding the two large germination events and the two subsequent large mortality events) were tied even more strongly to the quantity and timing of precipitation, especially dry season rainfall (Table 1). Overall, our models accounted for most of the variation in annual demographic rates ($R^2 = 0.64$ and 0.76 for full and reduced datasets, respectively), providing an unusually strong link between changing climatic conditions and deteriorating biological outcomes (see also van Mantgem & Stephenson, 2007; Beever *et al.*, 2010, 2011; Regehr *et al.*, 2010; Giménez-Benavides *et al.*, 2011). At the lower elevational end of the silversword range, the fitted climate trends correspond to a decrease of $531 (\pm 93 \text{ SE})$ mm/yr in rainfall and $38 (\pm 8 \text{ SE})$ additional rainless days per year in 2010 vs. 1990. The high rates of silversword mortality in the demography plots over the past 10–20 years appear to be directly tied to these and related climate changes. It is important to note that temperature and rainfall experience significant multi-decadal-scale variability associated with the Pacific Decadal Oscillation (PDO, Mantua *et al.*, 1997). Positive phases of the PDO coincide with warm (Giambelluca *et al.*, 2008) and dry (Frazier *et al.*, 2011) climate anomalies in Hawai'i. Hence, the relatively rapid warming and drying of recent decades may be partly explained by natural variability. However, in the context of long-term secular trends in temperature (Cao *et al.*, 2007), rainfall (Chu & Chen, 2005), and solar radiation (Longman,

2011), future cool-wet climate phases in Hawai'i are likely to be less pronounced, limiting silversword recruitment and population rebound, whereas subsequent warm-dry phases are likely to be more severe.

Our large-scale census of 31 populations spanning the entire geographic range of the Haleakalā silversword supported the patterns documented in the long-term demography plots. It confirmed that recent silversword recruitment has been very low across the range and that mortality has been widespread, and it revealed a strong elevational pattern in this mortality: populations at 2950 m averaged 75% of plants alive, whereas those at 2185 m averaged only 47% alive. On the basis of the tight relationships between percentage of live plants and changes in abundance in the demography plots over the preceding 7–14 years (Fig. S3), we estimate that most of the lower elevation populations, and perhaps even many of the higher elevation populations, have likely undergone substantial declines over this period (Fig. 4). Importantly, most populations currently occur near the lower elevational end of the silversword range (Fig. S2). Mortality was concentrated among small to medium-sized plants (Fig. 3, Table S3), indicating that the elevational pattern was not caused by differential rates of flowering and natural post reproductive death. Some low elevation populations exhibited higher than typical survival rates (Fig. 4), apparently owing to increased soil moisture availability at these sites (Table 2). Such refuges are created by unusual microhabitat conditions, for example, seeps at the bases of some cinder cones, and outcrops with rock faces that intercept and channel water from wind-driven rain and fog to their bases. While important for revealing the factors influencing silversword survival, these refuges are small, relatively uncommon, and unlikely to significantly counteract the prevailing pattern of extensive mortality.

Increased mortality at the lower elevational ends of species distributions during periods of drought has been documented in an increasing number of tree and herbaceous plant species (Allen & Breshears, 1998; Foden *et al.*, 2007; van Mantgem & Stephenson, 2007; Worrall *et al.*, 2008; McDowell *et al.*, 2010; Giménez-Benavides *et al.*, 2011). The physiological mechanisms underlying these patterns have varied among sites and species, and in many cases remain unresolved. Silverswords, like other tropical alpine rosette plants (Smith & Young, 1987), possess a specialized suite of traits that allows them to withstand the harsh conditions typical of their habitats (Robichaux *et al.*, 1990), such as high solar radiation, extreme daily temperature fluctuations, low soil water availability, and periodic drought. Nevertheless, tropical alpine rosette species must also actively manage their water budgets to endure periods

of water shortage. When dry conditions create low leaf water potentials and high potential transpiration, stomata close to reduce water loss (Baruch, 1979; Smith & Young, 1987; Robichaux *et al.*, 1990). This reduction in gas exchange greatly slows photosynthesis and carbon assimilation (Baruch, 1979). At the same time, higher temperatures increase rates of respiration and carbon loss (Baruch, 1979; Goldstein *et al.*, 1996). Unusually warm and dry conditions may create persistent negative carbon balances and lead to mortality through carbon starvation, either due to eventual depletion of carbon stores (McDowell *et al.*, 2008) or to water stress-induced interruption of stored carbon transport (Sala *et al.*, 2010). Alternatively, severe water stress may kill plants through hydraulic failure (Anderegg *et al.*, 2012).

At Haleakalā, a commonly observed phenomenon among water-stressed silverswords is a gradual shrinkage in live tissue volume as peripheral leaves die. This pattern appears more consistent with carbon starvation rather than hydraulic failure. However, these mechanisms are not mutually exclusive, and plant shrinkage may also result in part from an active reallocation of water and nutrients from peripheral leaves to the younger central leaves of the rosette when conditions become extreme (e.g. Tuffers *et al.*, 1995; Neuner *et al.*, 1999). Sacrifice of older leaves may preserve a limited capacity for thermal regulation and photosynthesis by allowing some gas exchange in the reduced central portion of the plant. Warmer temperatures at the lower end of the silversword range apparently cause greater evaporative water loss from soils (Perez, 2009), which may mean that during prolonged drought, plants at lower elevations can resort to this mechanism for a shorter period before succumbing than can those at higher elevations. Higher rates of respiration due to warmer temperatures may also lead to greater carbon deficits at lower elevations, depending on the degree to which this dynamic is counteracted by homeostatic acclimation (Larigauderie & Körner, 1995; Goldstein *et al.*, 1996). Together, these interactions between temperature and water stress may partly explain the elevational pattern in silversword mortality. It is also possible that silverswords possess greater inherent drought tolerance at higher elevations, as in some Andean alpine rosette plants (Baruch, 1979; Meinzer *et al.*, 1985), perhaps mediated by differences in leaf capacitance (Robichaux & Morse, 1990), root-shoot ratio, cellular resistance to negative water potentials, or other means.

Although the precise combination of mechanisms responsible for climate-related silversword mortality remains to be determined, increasingly warm and dry conditions on upper Haleakalā can be expected to push suitable silversword habitat upslope and into shrinking

lower elevation refuges. As the lowest elevation at which silverswords can maintain stable populations shifts upward, habitat area will shrink rapidly (Fig. S4). Estimates of range shifts required to track increasing temperatures may often be overestimated, because nearby suitable microhabitat sites may typically occur in alpine environments owing to fine-scale variation in environmental conditions (Scherrer & Körner, 2010). However, our documentation of high rates of silversword mortality and low levels of recent recruitment across most of the plant's current range suggests that short distance movement to suitable microhabitats is unlikely to be possible on a routine basis. Moreover, upslope migration has already been recorded in an increasing number of montane plant species around the world (e.g. Grabherr *et al.*, 1994; Peñuelas & Boada, 2003; Walther *et al.*, 2005; Lenior *et al.*, 2008; Feeley *et al.*, 2011; Jump *et al.*, 2011).

Whereas large-scale, climate-related die-offs of trees around the world have the potential to result in profound ecological and biogeochemical shifts (Allen *et al.*, 2010), the decline of the Haleakalā silversword highlights different aspects of global climate change. Because of its iconic status, and because it is viewed and appreciated by millions of park visitors, it is positioned to become one of the most visible examples of climate change-induced biodiversity loss if climate trends on the mountain do not reverse course. Furthermore, although the impacts of climate change can often be expected to interact in complicated ways with other threats (Parmesan *et al.*, 2011), in this case climate can be isolated as the main current driver of silversword population declines on Haleakalā volcano. The chief historical impacts, from human collection and feral ungulate browsing (Loope & Crivellone, 1986; Appendix S1), have been removed via legal protection and a fence encircling the park. The demise of the Haleakalā silversword may therefore proceed in spite of intensive, costly, and previously highly successful management actions implemented by the National Park. As a consequence, it may become emblematic of the extreme challenges that global climate change will impose on the preservation of biodiversity in island ecosystems, as well as in other hotspots that are characterized by small species ranges and high levels of endemism (Malcolm *et al.*, 2006; Williams *et al.*, 2007).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Additional details on the study plant, site and history.

Figure S1. Haleakalā silversword in bloom, with Haleakalā crater in background.

Figure S2. Map of study site.

Figure S3. Relationships between percentage of plants alive in 2010 and net population change in the 12 long-term demography plots.

Figure S4. Total surface area within Haleakalā National Park as a function of elevation, from the lowest silversword population to the summit of Haleakalā volcano.

Table S1. Trends in total rainfall, zero rainfall days, air temperature and solar radiation on upper Haleakalā volcano over two time periods.

Table S2. Linear regression models examining the effects of time and locality on annual population growth rates in the long-term demography plots.

Table S3. Linear regression models examining the effects of elevation, plant size class and their interaction on the percentage of live plants in 31 populations censused in 2010.