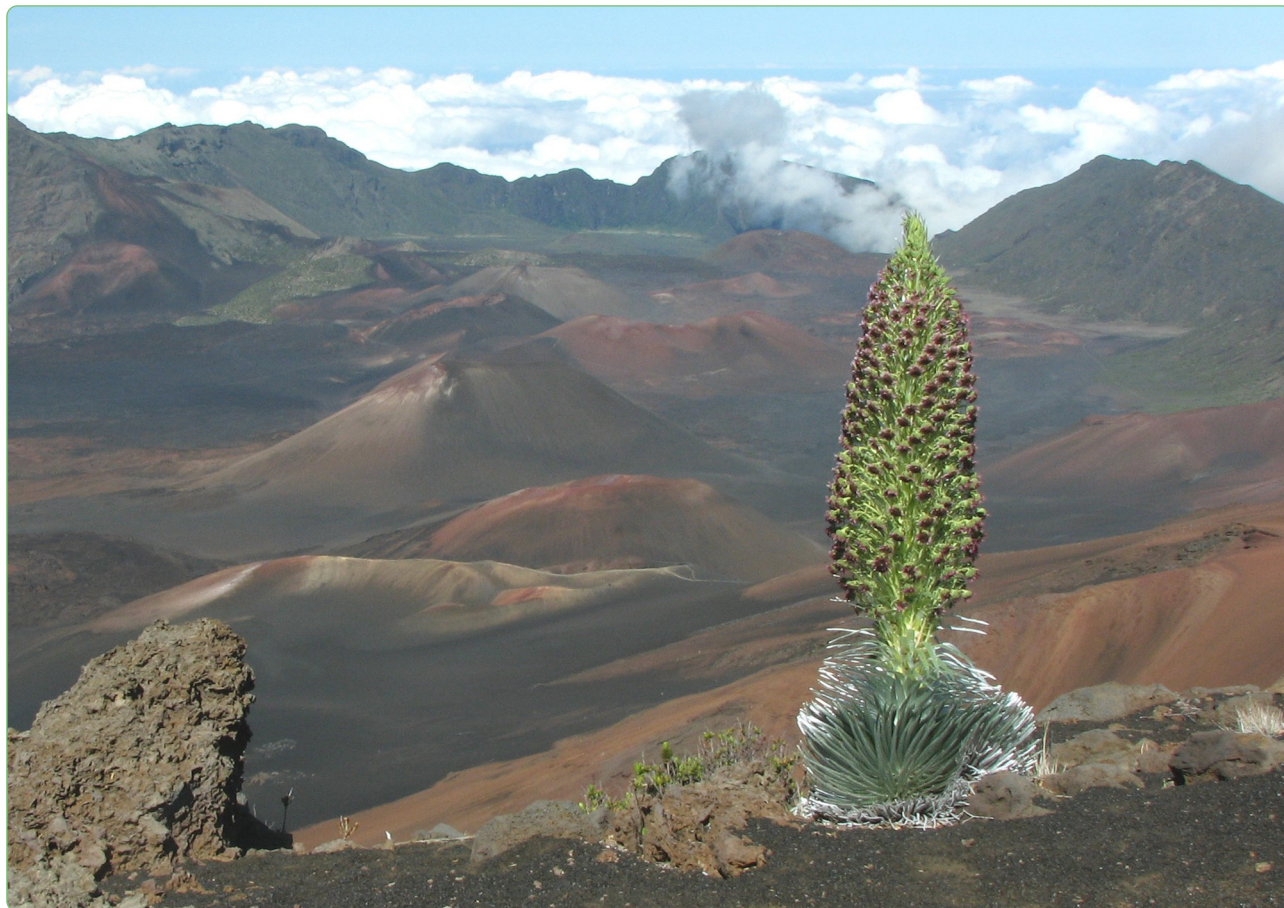# Change in trade wind inversion frequency implicated in the decline of an alpine plant

Krushelnycky *et al.*

Climate Change Responses

RESEARCH   **Open Access**

CrossMark

Change in trade wind inversion frequency implicated in the decline of an alpine plant

Paul D. Krushelnycky[1*], Forest Starr[2], Kim Starr[2], Ryan J. Longman[3], Abby G. Frazier[3], Lloyd L. Loope[4,5]
and Thomas W. Giambelluca[3]

Abstract

Background: Detailed assessments of species responses to climate change are uncommon, owing to the limited nature of most ecological and local climate data sets. Exceptions, such as the case of the Haleakalā silversword, can provide important insights into the complexity of biological responses to changing climate conditions. We present a time series of decadal population censuses, combined with a pair of early population projections, which together span the past 80 years of demographic history for this alpine plant.

Results: The time series suggests a strong population recovery from the 1930s through the 1980s, likely owing at least in part to management actions taken on its behalf. In contrast, the population is estimated to have suffered a decline of approximately 60 % since the early 1990s. Fine-scale estimates of rainfall within silversword habitat are strongly correlated with these decadal-scale population changes over the past 50 years, with rainfall estimated to be substantially lower on average during the two most recent inter-census periods (after 1991). The reversal in the silversword population trajectory, and declines in rainfall in silversword habitat, coincide with an abrupt increase in the frequency of occurrence of the trade wind inversion (TWI) in Hawai'i around 1990.

Conclusions: The shift in TWI incidence, which is linked to stronger subsidence in the Hadley circulation, has led to drier conditions in high elevation ecosystems in Hawai'i and appears to be eliciting ecological responses. Other regions influenced by the TWI could be similarly affected. The silversword case study reveals additional unexpected outcomes, such as the likely initial retraction from wetter, rather than drier, portions of the range in response to drying conditions. This pattern may stem in part from variation in drought tolerance across the range, highlighting the importance of detailed ecological and climatic information for making accurate predictions about climate change responses.

Keywords: Climate change ecology, Trade wind inversion, Silversword, Alpine plants, Population declines, *Argyroxiphium sandwicense*

Background

Empirical evidence of species response to recent climate change is usually fragmentary, owing to a shortage of long-term, comprehensive data sets. Range shifts are often estimated from limited survey data, most commonly comparing two points in time and encompassing only a portion of a species' range [1], and information on changes in population size that may or may not accompany such shifts is often lacking. At the same time, species responses to climate change are increasingly recognized and predicted to be more complex than simple poleward or upslope migration [2–5], and the incomplete nature of much ecological information likely hinders a better understanding of this complexity. This may be especially true in situations where precipitation is a key determinant of distributions and demographics, because changes to regional precipitation may be driven by complicated alterations to global circulation patterns combined with the influence of local features [6, 7], and changes in precipitation frequently act in opposition to changes in temperature [2, 3, 8].

Analyses of response patterns among large numbers of species in regional or global floras and faunas can be highly insightful and help overcome some of the

* Correspondence: pauldk@hawaii.edu
[1]Department of Plant and Environmental Protection Sciences, University of Hawai'i at Mānoa, Honolulu, HI 96822, USA
Full list of author information is available at the end of the article

Krushelnycky *et al. Climate Change Responses* (2016) 3:1

Page 2 of 12

aforementioned data limitations (e.g., [4, 5, 9, 10]). However, individual case studies that can examine more detailed ecological and climate data may be equally insightful if they reveal some of the complexity in biological responses that are obscured in large synthetic analyses. For example, McLaughlin et al. [11] found that an increase in the variability of precipitation, rather than changes in magnitude, was a key driver in extinctions of local populations of the Bay checkerspot butterfly. Similarly, the extensive ecological research on the polar bear has determined that increasing temperatures are detrimental not because they directly exceed its thermal tolerances, but instead because they affect the extent and phenology of sea ice formation and thereby impact foraging opportunity [12]. Examples such as these may be critical for defining the range of climatic drivers and ecological processes that might be considered when broader projection models are applied.

The Haleakalā silversword, or 'āhinahina (*Argyroxiphium sandwicense* subsp. *macrocephalum*), represents another case in which a relatively detailed data set on a charismatic species enables a more nuanced assessment of climate change response. Previous work on this alpine plant, restricted to the top (~2100–3000 m) of Haleakalā volcano on the island of Maui, Hawai'i, linked declining demographic trends over the past several decades to changing local climate conditions [13]. Although estimated mortality has been highest in the lower elevation portions of its range, consistent with an upslope tracking of temperature, the declining annual population growth rates were more tightly associated with decreasing precipitation than with increasing temperature [13]. Water limitation makes sense as a more important constraint than rising temperatures for silverswords: they grow in an alpine zone that, despite receiving considerable rainfall, is characterized by young, porous volcanic soils that support very sparse vegetation and which resembles a desert biome [14]. A change in the incidence of the trade wind inversion (TWI) was proposed as a potential mechanism underlying the pattern of declining rainfall on the mountain [13].

The TWI is a prominent feature on the high mountains of Hawai'i [15], as it is in other locales that are situated within the zone of descending air of the tropical Hadley Cell atmospheric circulation (e.g., Canary Islands [16], Hispaniola [17]). The thermally-driven Hadley circulation moves air upward within the inter-tropical convergence zone and then poleward, where it eventually subsides between 20 and 30° latitude [18]. The TWI is the result of a temperature inversion at the interface between this dry, subsiding air and the moist trade wind-driven ascending air from below. The TWI has a profound influence on montane vegetation because it limits the vertical development of clouds, thus creating a sharp

gradient in precipitation and other atmospheric conditions on mountain slopes [16, 19–21]. On average the base height of the TWI is found at about 2100–2200 m in Hawaii [22], which coincides with the lower elevation limit of the silversword range on Haleakalā. Hence, when the TWI is present, as it is on most days [22, 23], most or all of the silversword population is above the clouds and experiences clear skies and dry atmospheric conditions. Disruptions of the prevailing circulation pattern, which interrupt the TWI, are responsible for much of the moisture that reaches Hawaii's leeward mountain slopes [24], and presumably also the subalpine and alpine ecosystems above the inversion.

An increasing frequency of occurrence of the TWI in Hawai'i was detected by Cao et al. [23] over the period of 1979–2003. More recently, Longman et al. [22] examined TWI patterns from 1973–2013 and determined that the TWI incidence increased abruptly around 1990, amounting to a jump of 11–29 % in the dry season (May-October) and 16–24 % in the wet season (November-April; Fig. 1). This change was linked to stronger subsidence in the Hadley Cell in the north central Pacific [22], and while it is currently unclear whether intensified Hadley Cell subsidence is ultimately related to greenhouse gas emissions or other causes, this large-scale atmospheric circulation change could have widespread ecological repercussions. In Hawai'i, the shift in TWI incidence has been associated with average rainfall declines of 6 and 31 % in the dry and wet seasons, respectively, at meteorological stations located above 1900 m elevation on Maui and Hawai'i Island [22]. This finding provides a concrete mechanism with which to make and test predictions about ecological responses to climate in Hawai'i, particularly in ecosystems proximate to the
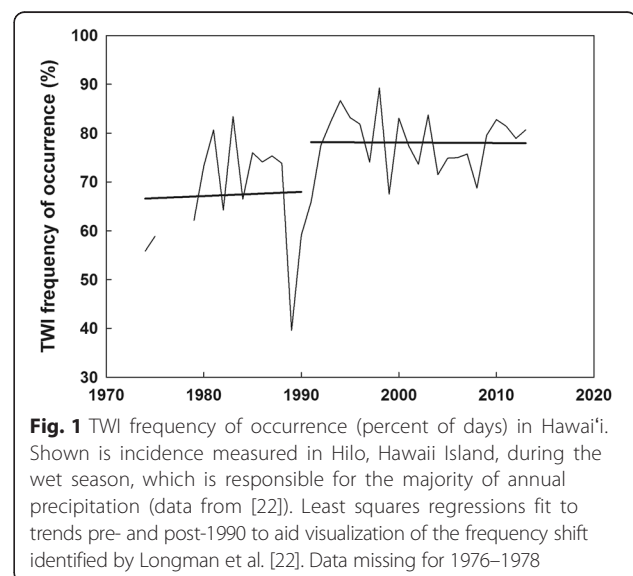
Fig. 1 TWI frequency of occurrence (percent of days) in Hawai'i. Shown is incidence measured in Hilo, Hawaii Island, during the wet season, which is responsible for the majority of annual precipitation (data from [22]). Least squares regressions fit to trends pre- and post-1990 to aid visualization of the frequency shift identified by Longman et al. [22]. Data missing for 1976–1978

Krushelnycky *et al. Climate Change Responses* (2016) 3:1

Page 3 of 12

TWI (e.g., [25, 26], and may have relevance to other locations strongly influenced by the TWI.

Previously reported population trends in the Haleakalā silversword were derived from a group of demography plots, combined with range-wide patterns in recent mortality that were inferred from a single population survey [13]. In the present study, we build on these results using a time series of population-wide censuses conducted roughly every decade since 1971, in addition to a pair of earlier projections from regional counts, which together span the past 80 years of demographic history for this species. We first use this data set to create a clearer picture of population recovery from an anthropogenically-caused low point in the early 20th century, which is thought to have represented a drastic reduction relative to the 19th century [27]. This history provides a backdrop against which we then examine the role of changing climate, including a shift in the incidence of the TWI, in influencing spatiotemporal patterns in more recent silversword population trajectories.

Results
Decadal census results
The total census counts for the five censuses, as well as total counts adjusted for differences in spatial coverage among censuses, are presented in Table 1. Of 111 count sectors demarcating the silversword population, only one appears to have lost all plants since the censuses were initiated. The aggregation of plants in this sector located on the range periphery was last verified to be extant in the 1991 census, when it numbered 106 individuals; no live plants could be found in 2001 or 2013. The coefficients of variation (CV), measured across censuses, for counts corresponding to each of 19 larger regions common to all five censuses had a wide range, from 0.16 to 1.12, indicating that the degree of temporal variation differed strongly among regions. The CV for counts on Ka Moa o Pele cinder cone from 1971–2013 was relatively low (0.34) and similar to that for the adjusted population totals for the same period (0.29). Counts for this cone and the adjusted population totals were also

Table 1 Total population estimates from each of the five decadal censuses. Actual census totals and totals adjusted for differences in spatial coverage among censuses are shown
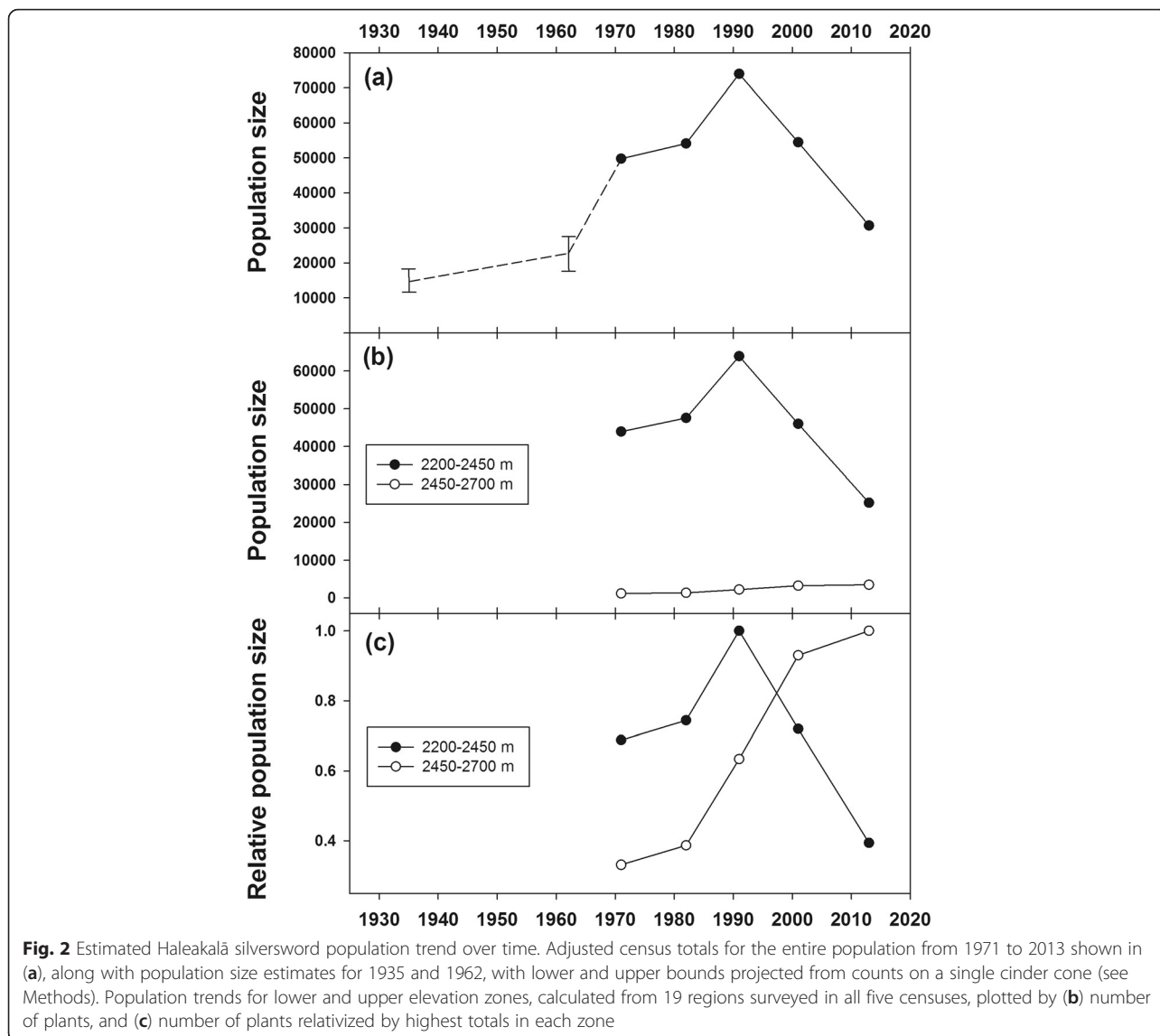
Census year	Total census count	Adjusted total census count
1971	43,325	49,750
1982	47,640	54,096
1991	64,724	73,951
2001	49,498	54,455
2013	30,709	30,709

fairly strongly correlated with one another for the five censuses (Pearson $r = 0.812$, $p = 0.095$, $n = 5$). Plants on this cone therefore appear to fluctuate in a similar fashion to that of the entire population, and two early counts on this cone may be relatively good indicators of total population size at those times. Based on the number of plants counted on Ka Moa o Pele in 1935, combined with the range in the proportion of plants on this cone relative to the total population count in the five complete censuses (1971–2013), the population size in 1935 is projected to have been between 11,587 and 18,329. The population size in 1962, using the same method, is projected to have been between 17,719 and 28,029. Our estimate for 1935 is several times higher than the prior estimate of 4000 plants calculated by projecting the number of flowering plants on Ka Moa o Pele cone as a proportion of the total number of flowering plants in 1935 [28].

The estimated population trend over time, including the two early projections, is depicted in Fig. 2. The population appeared to rebound strongly until 1991, but the two most recent censuses in 2001 and 2013 recorded strong population declines (Fig. 2a). Temporal trends over the five census periods, separated by elevation zone, are shown in Fig. 2b,c. The lower portion of the silversword range encompasses the vast majority of plants, and thus showed a trend very similar to the overall population, including strong declines since 1991 (Fig. 2b). In contrast, the upper portion, which supports relatively few plants, has continued to increase over the entire record. Trends depicted on a relativized scale suggest that rates of population growth in the two elevation zones were very similar up to 1991, but diverged sometime around this date, and that the continued growth in the higher elevation areas has slowed since 2001 (Fig. 2c).

Count error rates and estimated true population size
For 18 count sectors, the ratio of the original count to a second more accurate 'true' count ranged from 0.32 to 0.96. This indicates that all original observations undercounted the actual number of plants in the sector by varying degrees. This count error rate, which has smaller values with greater error, was negatively related to the log(observation distance) ($r^2 = 0.544$, $p < 0.001$), and positively related to the log(original count) ($r^2 = 0.417$, $p = 0.004$). The latter relationship was unexpected, but likely simply indicates that this proportional error rate is more sensitive to smaller numbers/aggregations of plants. However, these smaller aggregations contribute less to the population total, making the higher error rates less important. A multiple regression model including both log(observation distance) and log(original count) explained the most variation in the count

Krushelnycky *et al. Climate Change Responses* (2016) 3:1

Page 4 of 12

Fig. 2 Estimated Haleakalā silversword population trend over time. Adjusted census totals for the entire population from 1971 to 2013 shown in (**a**), along with population size estimates for 1935 and 1962, with lower and upper bounds projected from counts on a single cinder cone (see Methods). Population trends for lower and upper elevation zones, calculated from 19 regions surveyed in all five censuses, plotted by (**b**) number of plants, and (**c**) number of plants relativized by highest totals in each zone

error rate ($r^2 = 0.619$, $p = 0.001$, Table 2), even though log(original count) was only marginally significant when accounting for log(observation distance). We used the fitted regression with both explanatory variables to predict the count error rates, true counts, and the 95 % prediction intervals for all 111 count sectors in the 2013 census. This resulted in an estimated true total population size in 2013 of 39,355

plants (95 % prediction interval: 26,257–84,806). Because the reported prediction interval was actually a summation of the 111 individual prediction intervals, the large range includes scenarios in which most or all of the counts were subject to the widest range of errors around their individual predictions. We therefore regard the large outer bounds of the interval to be extremely conservative and highly unlikely.

Influence of climate on decadal trends

Decadal-scale population change was significantly and positively correlated with average rainfall totals for the dry (May-Oct) and wet (Nov-Apr) seasons and for the water year (Nov-Oct) during the inter-census periods (linear regression $r^2 = 0.815$, $p = 0.036$ for dry; $r^2 = 0.880$, $p = 0.018$ for wet; $r^2 = 0.919$, $p = 0.010$ for annual; $n = 5$ for each). For wet season and annual

Table 2 Multiple regression model for the count error rate in 18 count sectors censused in 2013. Total model $r^2 = 0.619$, $p = 0.001$

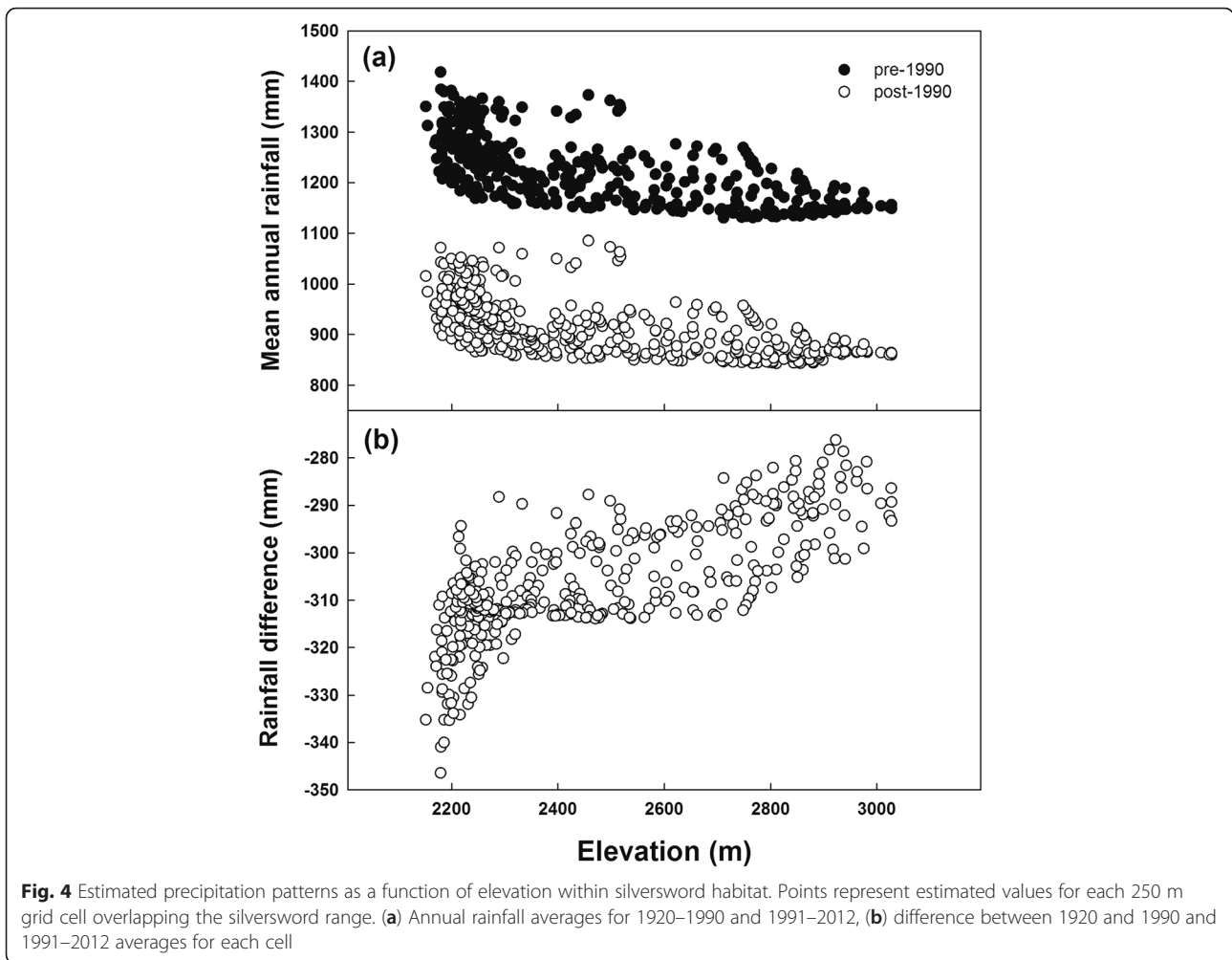| Term	Coefficient	SE	t	p
intercept	0.622	0.358	1.74	0.103
log(observation distance)	−0.219	0.078	−2.82	0.013
log(original count)	0.217	0.126	1.72	0.106

Krushelnycky *et al. Climate Change Responses* (2016) 3:1

Page 5 of 12

rainfall averages, these relationships were best fit with quadratic equations, and the strongest relationship existed between percent population change per decade and the average annual rainfall over the water year during the inter-census period (Fig. 3a; $r^2 = 0.991$, $p = 0.009$). Relationships between decadal-scale population change and average air temperatures during the inter-census periods were negative but not statistically significant (linear regression $r^2 = 0.546$, $p = 0.154$ for dry season; $r^2 = 0.475$, $p = 0.198$ for wet season; $r^2 = 0.548$, $p = 0.153$ for annual; $n = 5$ for each). Quadratic equations did not improve the fit for temperature. The negative relationship between decadal-scale population change and average TWI frequency during the inter-census periods was statistically significant for the dry season (linear regression $r^2 = 0.918$, $p = 0.042$; $n = 4$; Fig. 3b) but not for the wet season ($r^2 = 0.663$, $p = 0.186$; $n = 4$).

On an annual scale, estimated rainfall in silversword habitat was significantly and negatively related to TWI frequency of occurrence from 1973 to 2013 in both the dry ($r^2 = 0.289$, $p = 0.001$; $n = 38$) and wet ($r^2 = 0.371$, $p < 0.001$; $n = 37$) seasons, although there was considerable variance around these relationships. For decadal averages, wet season rainfall was significantly and negatively associated with wet season incidence of the TWI ($r^2 = 0.946$, $p = 0.027$; $n = 4$), but dry season rainfall was not significantly related to dry season TWI incidence ($r^2 = 0.359$, $p = 0.401$; $n = 4$). Plots of average annual rainfall in silversword habitat across elevation show that precipitation was considerably lower after 1990 than before 1990, and that precipitation generally decreased with increasing elevation during both periods (Fig. 4a). However, differences between the periods displayed a distinct nonlinear, threshold-type relationship with elevation, wherein the
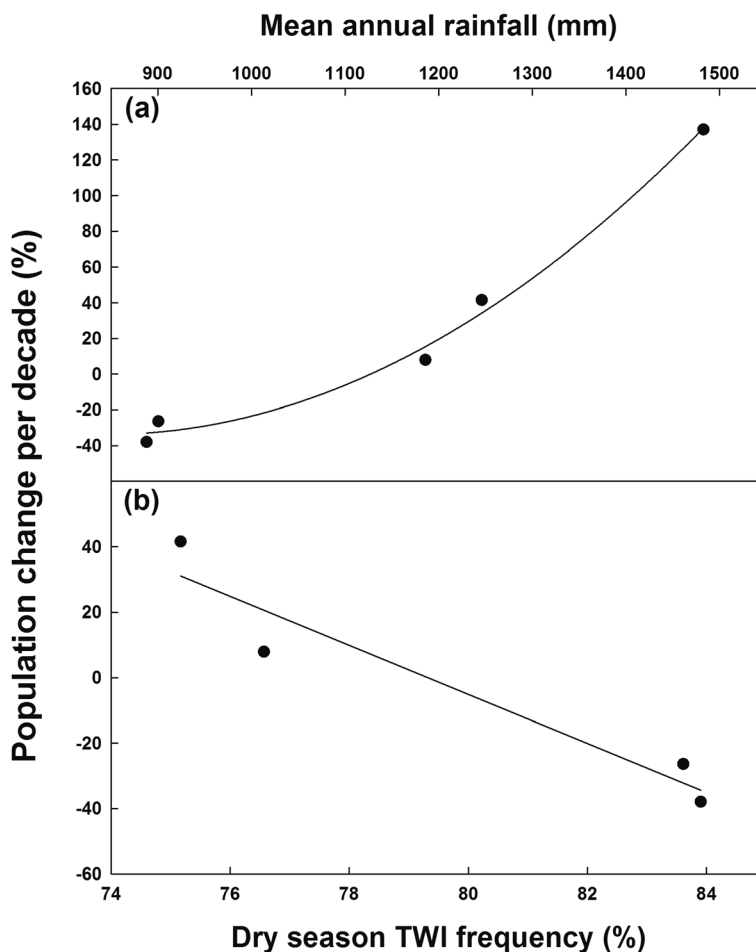
Fig. 3 Relationships between decadal-scale population change and climate. Silversword population change was significantly associated with several climate measures, including (**a**) average annual rainfall during the inter-census periods ($r^2 = 0.991$, $p = 0.009$), and (**b**) average dry season TWI frequency of occurrence during the inter-census periods ($r^2 = 0.918$, $p = 0.042$)

Krushelnycky *et al. Climate Change Responses* (2016) 3:1

Page 6 of 12

Fig. 4 Estimated precipitation patterns as a function of elevation within silversword habitat. Points represent estimated values for each 250 m grid cell overlapping the silversword range. (**a**) Annual rainfall averages for 1920–1990 and 1991–2012, (**b**) difference between 1920 and 1990 and 1991–2012 averages for each cell

post-1990 rainfall difference grew substantially more negative below approximately 2350 m elevation (Fig. 4b). This pattern was also apparent for wet and dry season rainfall (not shown).

Discussion

Total population censuses conducted roughly every decade since 1971, combined with population estimates for two earlier points in time, create an informative picture of population trends of the Haleakalā silversword over much of the last century (Fig. 2a). The estimated trend documents the strong population resurgence that followed, and presumably resulted at least in part from, both the regulatory protection of silverswords from human collecting that began in the 1930s, and the resource management efforts to exclude invasive browsing ungulates that culminated in the complete fencing of the park in the 1980s. The estimated trend also confirms a strong population decline since the early 1990s that was recently inferred from demography plot data and which

was tied to drying conditions on upper Haleakalā volcano [13].

The population trends depicted in Fig. 2 show census totals that do not adjust for observer error, mainly in the form of undercounting small or obscured plants, because all censuses prior to the most recent one did not attempt to quantify error rates. Earlier reports acknowledged the considerable uncertainty inherent in the census methodology [27], and our most recent effort confirmed that a substantial portion of the population is unavoidably missed. However, trends from 1971 onward should be reasonably accurate on a relative scale, since census methods were consistent over time. Examining trends across the entire population, or large portions of it, should also improve accuracy by averaging out smaller-scale errors. To the extent that systematic bias exists, it is likely to have resulted in higher undercounting rates in earlier censuses, because most of the population decline in recent decades can be attributed to mortality among smaller plants [13]. This makes it likely that a lower proportion of smaller and more difficult to

Krushelnycky et al. Climate Change Responses (2016) 3:1

Page 7 of 12

observe plants existed at the times of the most recent censuses. In this respect, the 58.5 % estimated decline in population size from 1991 to 2013 may be viewed as conservative. Using an independent method and data source, Krushelnycky et al. [13] arrived at a similar estimate of the magnitude of population declines over the past two decades in the lower portion of the silversword range, which encompasses the vast majority of the population.

Average annual rainfall was very strongly correlated with decadal-scale changes for the population as a whole (Fig. 3a). This also supports the findings of Krushelnycky et al. [13], which documented a negative relationship between annual population growth rates in demography plots and annual and seasonal measures of rainfall. The congruence between these results measured at two different spatial and temporal scales strengthens the interpretation that declines in the Haleakalā silversword population since the early 1990s have been caused by changes in climate patterns. There are no obvious alternate explanations for the increase in plant mortality and decline in seedling recruitment during this period [13], such as plant diseases, invasive pests, or loss of pollinators [29]. Unlike rainfall, air temperature was not found to be significantly correlated with population changes either on the decadal scale evaluated here, or on the annual scale assessed by Krushelnycky et al. [13]. However, statistical power to detect such relationships was low in the present study, and temperature is often linked to other climate variables on a regional scale, including rainfall. This can make it difficult to separate their effects, especially when sample sizes are small. In reality, it is likely that a suite of climate variables were affected by the increased frequency of the TWI around 1990 [22, 30].

The synchrony between the upward shift in TWI incidence and the abrupt reversal in the silversword population trajectory is striking, and makes this climatic shift a compelling mechanism that may be responsible, at least in part, for strengthening water deficits in the alpine habitat and for causing deteriorating silversword demographic trends. TWI incidence was negatively correlated with rainfall totals in silversword habitat on both annual and decadal time scales, most consistently during the wet season. Coefficients of determination were relatively low (but highly statistically significant) on the annual scale, suggesting that additional factors are important in determining the magnitude of rainfall from year to year. For instance, TWI incidence may be strongly tied to the frequency of precipitation events above its base height, but may be more loosely linked to precipitation totals. Beyond precipitation, TWI presence affects other climate variables that also influence plant water status. For example, on upper Haleakalā, trends since 1990

indicate conditions that have undoubtedly promoted greater water stress for silverswords and other plants, including decreases in rainfall, relative humidity and cloud attenuation of sunlight, and associated increases in solar radiation, vapor pressure deficit and potential evapotranspiration [30, 31]. Ultimately, TWI incidence during the dry season was a significant predictor of decadal-scale silversword population changes (Fig. 3b), while wet season TWI incidence was not. However, as previously noted, a longer time series could result in stronger statistical relationships between wet season and/or annual TWI incidence and silversword population growth rates.

Differences in population trends across elevation also point to a heterogeneous spatial response to the changing conditions described above. Although we detected considerable variation among census regions in the degree to which they fluctuated over time, a coherent divergence in trajectories was apparent when grouping the lower and upper portions of the population (Fig. 2b,c). The decadal censuses, therefore, confirmed a gradient in mortality across elevation that was previously and independently inferred from spatial patterns of live and dead plants [13]. The divergence among lower and upper portions of the population occurred around 1990, when lower elevation areas began their decline while upper elevation areas continued to grow rapidly until around 2000, at which point this rate of growth slowed. Relevant to this pattern, spatial rainfall estimates indicate that while there was greater rainfall at low elevations than at high elevations both before and after 1990 (Fig. 4a), the magnitude of change in rainfall across this temporal inflection point was distinctly non-linear with respect to elevation. Specifically, areas below approximately 2350 m experienced notably larger precipitation declines than areas above this elevational threshold (Fig. 4b). The zone below the threshold corresponds to the area that is typically directly above the TWI base height, suggesting that an increase in TWI incidence impacts precipitation directly above it most strongly, by more frequently restricting upward flow of moist air that would otherwise ascend higher on the mountain. It is unknown whether this magnitude of intensified precipitation decline is ecologically meaningful for silverswords, but it may underestimate the actual degree of moisture reduction for plants in this zone. A lower frequency of clouds rising above the average TWI base height would also reduce the opportunity for fog interception, which is thought to be an important source of water for silverswords [32].

Differences in silversword mortality across elevation may therefore be tied to spatial differences in precipitation change, rather than to spatial differences in absolute precipitation. Such a pattern could arise in several ways.

Krushelnycky *et al. Climate Change Responses* (2016) 3:1

Page 8 of 12

One possibility is that variation in drought tolerance exists across the population. Specifically, plants located at higher elevations, which are almost always situated above the TWI, may have acquired a greater tolerance to water stress by virtue of local adaptation or a phenotypic response to development in more arid conditions. In comparison, plants in lower elevation/higher precipitation zones have experienced greater mortality from rainfall reductions despite receiving more rainfall, contemporaneously, than higher elevation plants. Inherent differences in drought tolerance across elevation and rainfall gradients have been suggested in other plants, including tropical alpine rosette species [33–36]. Alternatively, the magnitude of deviation from the norm may be more important than, or act synergistically with, any possible differences in drought tolerance. For example, greater dieback in low elevation populations that experience more intense water stress during episodes of severe drought has been documented for other plants [37–39]. Identifying the relative importance of these mechanisms as causes of differential silversword mortality is the subject of current research.

The long-term census record shows that, given protection from collection and grazing and with sufficient rainfall, silverswords are capable of relatively rapid population growth, as occurred in the 1960s and again in the 1980s. If the rate of undercounting we measured in the most recent census is typical or even conservative, it is likely that the population reached or exceeded 95,000 plants by the late 1980s. Even the current estimate of approximately 40,000 plants represents a considerable improvement over the estimated number of plants around the 1930s, which proved to be an adequate remnant for successful recovery later in the century. However, the strong links between population growth rates and climate conditions mean that future persistence or recovery will be dependent on a wetter climate regime, particularly as temperatures rise and potentially lead to higher rates of evapotranspiration. Unfortunately, recent downscaled climate projections for Hawai'i predict a higher frequency and lower base height for the TWI [40], as well as decreased precipitation in both the wet and dry seasons for upper Haleakalā under future warming scenarios [7].

Conclusions

This case study provides several illustrations of how the incorporation of greater climatic and organismal detail can better characterize the range of possible ecological responses to climate change [41]. First, while the general pattern of intensified mortality at the lower end of the silversword range matches simple predictions of upslope tracking of rising temperatures, closer examination indicates that silverswords are likely responding to a combination of changes in precipitation, insolation, and evaporative demand (which is influenced by temperature). These changes appear to be mediated locally by a shift in the TWI prevalence, and perhaps more broadly by alterations to larger atmospheric circulation patterns, rather than by steadily rising air temperatures.

Second, predictions of climate change impacts on montane biota have commonly focused on changes in the base height of the TWI [21, 26, 42–45], as well as on changes in the lifting condensation level, which corresponds to the cloud base height [46, 47], because of the obvious repercussions on montane cloud forests. Changes in the base height of the TWI in Hawai'i are not yet apparent [22], but our results strongly suggest that changes in TWI incidence alone can have severe ecological impacts.

Finally, although very little climate-related range reduction has occurred for silverswords thus far, the pattern of mortality indicates that the wetter, rather than drier, portions of the current range will likely be the first to see retractions in response to drying conditions. This counterintuitive outcome may be a consequence of an interaction between regional differences in drought tolerance, the distribution of such differences relative to precipitation and temperature gradients on the mountain, and the way in which atmospheric circulation changes have altered these gradients. Unexpected spatial responses such as this have been predicted in situations where species have locally-adapted populations, because the narrower climate envelopes of constituent populations render projections based on species-wide tolerances inaccurate [48, 49]. Continued monitoring and physiological research on the Haleakalā silversword may provide documentation of this type of complex distributional effect of climate change.

Methods
Study site and species
The Haleakalā silversword, *Argyroxyphium sandwicense* subsp. *macrocephalum* (A. Gray) Meyrat, is a federally-listed threatened taxon in the family Asteraceae that occurs only on East Maui, Hawai'i. The Mauna Kea silversword (*Argyroxyphium sandwicense* subsp. *sandwicense* (A. Gray) Meyrat), is sister to the Haleakalā silversword, and is a federally-listed endangered subspecies growing at high elevations on Mauna Kea volcano, Hawai'i Island. Two additional silversword taxa grow on West Maui and Mauna Loa, Hawai'i Island. Unspecified references to silversword plants in this study refer to the Haleakalā subspecies.

The Haleakalā silversword is a long-lived (estimated 20–90 year, [50]), monocarpic, acaulescent rosette plant that today grows on the largely barren cinder cones, cinder flats, and rocky cliffs in a broad geographic

Krushelnycky *et al. Climate Change Responses* (2016) 3:1

Page 9 of 12

area spanning the central to western portions of Haleakalā crater up to the summit, in the alpine zone from 2150 to 3050 m elevation (roughly 2300 ha). Long-term averages of annual rainfall across the silversword range are estimated to vary from 1018 to 1352 mm [51], with approximately 70 % of this falling in the wet season (November-April, [13]. 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 were first comprehensively mapped and censused by H. Kobayashi in 1971 [32]. Following Kobayashi's recommendations, a total population census was subsequently repeated approximately every decade (see below).

Early accounts suggest that the silversword population underwent a dramatic decline around the turn of the 19th century, owing to ungulate browsing and human vandalism [27]. Anecdotal descriptions by several visitors to Haleakalā crater in the 1800s imply a large abundance of plants, including the description of "thousands of silverswords … making the hillside look like winter or moonlight" in 1873 [52]. By the 1920s, however, serious concern arose among National Park staff and local residents, as it was apparent that the population had been decimated by feral goats and cattle and by zealous over-collection by people [27]. As before, no numbers were attached to these observations, with the exception of an estimate of "barely 100 plants" for the entire population made by a botanist in 1927 [53]. This was almost certainly a drastic underestimate, as a careful count of plants on one cinder cone, Ka Moa o Pele, in 1935 recorded 1470 plants [27]. This 1935 count, and a repeated count of the same cone in 1962, are the only reliable figures for silversword abundances prior to 1971. The 1935 count was previously used to estimate a total population of approximately 4000 in that year [28], by projecting the proportion of flowering plants on Ka Moa o Pele (88 of 1470) onto the entire population (in which 217 flowering plants were counted). In response to the aforementioned concern regarding silversword persistence, rigorous protections against plant collection were instituted by the National Park Service in the 1930s, and feral ungulates were controlled through hunting and were eventually completely excluded in the 1980s with a fence encircling the park [27].

Census procedures
Total population censuses were conducted in 1971, 1982, 1991, 2001 and 2013. In all censuses prior to 2013, one to three observers attempted to count all plants during a two to four week period. For this purpose, the silversword range was divided into 82 sectors that corresponded to a combination of known silversword aggregations and topographical features such as cinder cones

or portions of cinder cones, and observers visited as many of these sectors as possible during each census. Total number of plants in each sector was estimated by counting all visible live plants with either the naked eye or with binoculars, depending on the observer's distance. Observation distances are known to have varied tremendously, from several meters or tens of meters in flat regions that can be traversed on foot, to several hundreds of meters in regions situated on steep cinder cone faces or on distant cliffs. However, these observation distances and/or vantage points were not recorded. Methods of earlier censuses are also reported in Kobayashi [32] and Loope & Crivellone [27].

In the 2013 census, the procedure was modified to allow comparison with prior censuses while improving methods for future censuses. Four observers completed the census between October 2013 and March 2014, using the same methods described above. However, the count sectors were modified to more accurately represent current boundaries of silversword aggregations, rather than relying more heavily on topographic features, and the resulting 111 sectors were mapped in GIS (Geographic Information Systems) to allow more accurate relocation and delineation in future censuses (Additional file 1: Figure S1). In addition, observation distances were estimated for each region, either by estimating average distances to plants in regions that were walked through, or by using ArcGIS™ 10.2.2 (ESRI, Redlands, CA, USA) to measure the distances from observer vantage points to the midpoints of sectors in cases where binoculars were used. Finally, more effort was expended in the 2013 census, compared to prior censuses, to visit all previously reported locations supporting silverswords, making it the most thorough census to date.

Census comparisons over time
Because each census counted plants in a slightly different subset of sectors, and because these sectors were modified somewhat in 2013, we delineated 19 regions that were fully counted in all five censuses, grouping multiple sectors within each region, to enable comparison between censuses (Additional file 1: Figure S1). Sectors were generally grouped by cinder cone or contiguous lava flows. These 19 regions comprised from 86.7 to 99.6 % of the actual total counts in each census, with the lowest percentage (86.7 %) corresponding to 2013, the most spatially complete census. Therefore, the summed totals of the 19 regions in common for each census were subsequently divided by 0.867 to calculate an adjusted total count for each census, which accounted for areas missed and made the censuses directly comparable. This procedure assumes that the small minority of areas not counted in

Krushelnycky *et al. Climate Change Responses* (2016) 3:1

Page 10 of 12

the 1971 to 2001 censuses fluctuated in the same manner as the remainder of the population.

Counts of plants on Ka Moa o Pele cinder cone were 1470 in 1935 and 2248 in 1962 [32]. This cone accounted for between 8.0 and 12.7 % of the five adjusted census totals (1971–2013). We therefore used this range to calculate a rough estimate of the lower and upper bounds for the total population in 1935 and 1962, by dividing the Ka Moa o Pele counts in those years by 0.127 and 0.080. We feel that this is likely to be a more accurate method for estimating the total population size than the one used previously, in which the proportion of plants flowering on the cone was projected to the entire population [28]. This is because proportions of plants flowering are known to vary considerably from region to region in a given year, much more so than the magnitude of variation observed in the proportion of plants on Ka Moa o Pele cone relative to the estimated population total over the five censuses.

Related work has suggested that silversword population declines over the past two decades have been most severe in lower elevation portions of the range [13]. To assess whether the decadal censuses have recorded a similar pattern, the 19 common geographic regions described above, which spanned an elevation of approximately 2200 m to 2700 m, were split into two even elevation zones (2200–2450 m, 2450–2700 m), and temporal trends between 1971 and 2013 were compared in each zone. We took this approach of lumping plant numbers across large geographic areas, rather than relating percent population change within each region to its elevation, because strong temporal variation and/or counting error in smaller geographic units led to very high and probably unrealistic variation in the resultant percent population changes, making spatial patterns difficult to detect.

Assessment of count error rate and true total population estimate

For 18 of the 111 count sectors in the 2013 census, we performed a second 'true' count, in which every live plant was individually approached and coordinates were recorded using a Garmin eTrex Legend H GPS unit (Garmin Ltd., Olathe, KS, USA). The ratios of the initial counts to the second true counts were used as estimates of count error rates for these sectors. Error rates were then regressed against the log-transformed observation distance and the log-transformed initial count (number of plants). These relationships were subsequently used to estimate count error rates (and 95 % prediction intervals) and to predict the true plant numbers for all 111 sectors in the 2013 census, based on the observation distances and number of plants estimated for each of these sectors. To avoid negative as well as unreasonably high

predictions, we bounded the lower ends of the 95 % prediction intervals for the count error rates to 0.1, which seems reasonable given that the lowest measured count error rate was 0.32 (see Results). The resultant predicted true counts and 95 % intervals were summed to estimate the true total population size in 2013.

Influence of climate on decadal trends

We examined the explanatory power of patterns in rainfall, air temperature and the frequency of occurrence of the TWI on the magnitude and direction of decadal-scale population changes. For rainfall, we used a database of spatially-explicit (250 m grid cell resolution) hind-casted monthly rainfall estimates for the island of Maui from 1920 through 2012 [54]. We extracted all grid cells coinciding with the silversword distribution, and used these to calculate the average dry season (May-October), wet season (November-April) and annual (by water year, November-October) rainfall across the silversword range during each inter-census period. Rainfall data for 2012–2013 were taken from the average of six weather stations installed across the silversword range in 2010. Monthly mean air temperature data through 2010 were taken from the Haleakalā Ranger Station located at the park headquarters, 2125 m elevation (National Climatic Data Center). Air temperature data from 2010 to 2013 were taken from HaleNet station 151, also located at the Haleakalā NP headquarters [55]. We used the combined data to calculate average dry season, wet season, and annual air temperatures for each inter-census period. Frequency of occurrence of the TWI was calculated from atmospheric sounding data collected daily at 2 pm HST in Hilo, Hawaiʻi Island, from 1973 to 2013; these data are maintained by the University of Wyoming and can be accessed at http://weather.uwyo.edu/upperair/sounding/html. TWI presence was determined according to the methods in Longman et al. [22], and frequency of daily occurrence (%) was calculated for all dry seasons, wet seasons and water years possessing at least 75 % of daily readings. This resulted in TWI data gaps during the 1971–1982 inter-census period: for the dry season and wet season, respectively, 64 and 54 % of seasons had available data, while only 45 % of water years had available data during this period. We therefore chose to not use the water year data, and only calculated average dry season and wet season TWI frequency of occurrence for each inter-census period. There were no gaps in the TWI data after the 1970s.

We used the above inter-census climate averages as explanatory variables in simple linear regressions with percent decadal change in population size as the response variable. For the latter, we used the adjusted census totals, and standardized the percent population

Krushelnycky *et al. Climate Change Responses* (2016) 3:1

Page 11 of 12

change between each census to ten year periods. Because there are only four inter-census periods, we added a fifth period, 1962–1971, to increase sample size, by using the average of the lower and upper bounds of the 1962 total population estimate (however, only rainfall and temperature data were available for this earlier period). Because non-linearity was suggested in some of the fitted relationships, we also attempted quadratic regressions against the rainfall and temperature data, but not against the TWI data which only had four data points. Due to the small sample sizes and intercorrelations, we did not fit multiple regressions using combinations of explanatory climate variables.

To test the influence of the TWI on rainfall patterns in Haleakalā silversword habitat, we regressed seasonal rainfall totals against TWI frequency of occurrence for all years with available data between 1973 and 2013 ($n = 38$ and 37 for dry and wet seasons, respectively); we also regressed the decadal averages of dry and wet season rainfall on decadal averages of TWI incidence ($n = 4$ for each). We further examined graphically how the reported shift in TWI frequency around 1990 may have differentially affected rainfall across elevation within silversword habitat. To do this, we plotted the mean estimated annual rainfall for the periods 1920–1990 and 1991–2012, for each 250 m grid cell within silversword habitat ($n = 377$), as a function of elevation. We also plotted the difference between these two time periods (pre- and post-1990) relative to elevation.

Additional file

Additional file 1: Figure S1. Map of the top of Haleakala volcano, showing census counting areas. Red polygons indicate 111 count sectors, black polygons indicate the 19 larger regions that were surveyed in all five censuses. (PDF 371 kb)

Author details
[1]Department of Plant and Environmental Protection Sciences, University of Hawaiʻi at Mānoa, Honolulu, HI 96822, USA. [2]Pacific Cooperative Studies Unit, University of Hawaiʻi at Mānoa, Honolulu, HI 96822, USA. [3]Department of Geography, University of Hawaiʻi at Mānoa, Honolulu, HI 96822, USA. [4]Pacific Island Ecosystems Research Center, US Geological Survey, Honolulu, HI 96813, USA. [5]Present address: 751 Pelenaka Pl., Makawao, HI 96768, USA.

References
1. Parmesan C. Ecological and evolutionary responses to recent climate change. Annu Rev Ecol Syst. 2006;37:637–69.
2. Crimmins SM, Dobrowski SZ, Greenberg JA, Abatzoglou JT, Mynsberge AR. Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. Science. 2011;331:324–7.
3. Tingley MW, Koo MS, Moritz C, Rush AC, Beissenger SR. The push and pull of climate change causes heterogeneous shifts in avian elevational ranges. Glob Change Biol. 2012;18:3279–90.
4. VanDerWal J, Murphy HT, Kutt AS, Perkins GC, Bateman BL, Perry JJ, et al. Focus on poleward shifts in species' distribution underestimates the fingerprint of climate change. Nat Clim Chang. 2012;3:239–43.
5. Gillings S, Balmer DE, Fuller RJ. Directionality of recent bird distribution shifts and climate change in Great Britain. Glob Chang Biol. 2015;21:2155–68.
6. IPCC. Summary for policymakers. In: Stocker TF et al., editors. Climate change 2013: The physical science basis. Contribution of working group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge: Cambridge University Press; 2013.
7. Elison Timm O, Giambelluca TW, Diaz HF. Statistical downscaling of rainfall changes in Hawaiʻi based on the CMIP5 global model projections. J Geophys Res-Atmos. 2015;120:92–112.
8. Dobrowski SZ, Abatzoglou J, Swanson AK, Greenberg JA, Mynsberge AR, Holden ZA, et al. The climate velocity of the contiguous United States during the 20th century. Glob Chang Biol. 2013;19:241–51.
9. Parmesan C, Yohe G. A globally coherent fingerprint of climate change impacts across natural systems. Nature. 2003;421:37–42.
10. Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA. Fingerprints of global warming on wild animals and plants. Nature. 2003;421:57–60.
11. McLaughlin JF, Hellmann JJ, Boggs CL, Ehrlich PR. Climate change hastens population extinctions. Proc Natl Acad Sci U S A. 2002;99:6070–4.
12. Stirling I, Derocher AE. Effects of climate warming on polar bears: a review of the evidence. Glob Change Biol. 2012;18:2694–706.
13. Krushelnycky PD, Loope LL, Giambelluca TW, Starr F, Starr K, Drake DR, et al. Climate-associated population declines reverse recovery and threaten future of an iconic high-elevation plant. Glob Change Biol. 2013;19:911–22.
14. Leuschner C, Schulte M. Microclimatological investigations in the tropical alpine scrub of Maui, Hawaiʻi: evidence for a drought-induced alpine timberline. Pac Sci. 1991;45:152–68.
15. Giambelluca TW, Nullet D. Influence of the trade-wind inversion on the climate of a leeward mountain slope in Hawaiʻi. Clim Res. 1991;1:207–16.
16. Fernández-Palacios JM, de Nicolás JP. Altitudinal pattern of vegetation variation on Tenerife. J Veg Sci. 1995;6:183–90.
17. Martin PH, Fahey TJ. Mesoclimatic patterns shape the striking vegetation mosaic in the Cordillera Central, Dominican Republic. Arct Antarct Alp Res. 2014;46:755–65.
18. Diaz HF, Bradley RS. The Hadley circulation: present, past and future. Dordrecht: Kluwer; 2004.
19. Kitayama K, Mueller-Dombois D. Vegetation of the wet windward slope of Haleakala, Maui, Hawaii. Pac Sci. 1992;46:197–220.
20. Crausbay SD, Hotchkiss SC. Strong relationships between vegetation and two perpendicular climate gradients high on a tropical mountain in Hawaiʻi. J Biogeogr. 2010;37:1160–74.
21. Martin PH, Fahey TJ, Sherman RE. Vegetation zonation in a neotropical montane forest: environment, disturbance and ecotones. Biotropica. 2010;43:533–43.
22. Longman RJ, Diaz HF, Giambelluca TW. Sustained increases in lower tropospheric subsidence over the central tropical North Pacific drives a decline in high elevation rainfall in Hawaiʻi. J Clim. 2015;28:8743–59.
23. Cao G, Giambelluca TW, Stevens DE, Schroeder TA. Inversion variability in the Hawaiian trade wind regime. J Clim. 2007;20:1145–60.

Krushelnycky *et al. Climate Change Responses* (2016) 3:1

Page 12 of 12

24. Giambelluca TW, Schroeder TA. The physical environment: climate. In: Juvik SP, Juvik JO, editors. Atlas of Hawai'i. 3rd ed. Honolulu: University of Hawai'i Press; 1998. p. 49–59.
25. Banko PC, Camp RJ, Farmer C, Brinck KW, Leonard DL, Stephens RM. Response of palila and other subalpine Hawaiian forest bird species to prolonged drought and habitat degradation by feral ungulates. Biol Conserv. 2013;157:70–7.
26. Crausbay SD, Frazier AG, Giambelluca TW, Longman RJ, Hotchkiss SC. Moisture status during a strong El Nino explains a tropical montane cloud forest's upper limit. Oecologia. 2014;175:273–84.
27. Loope LL, Crivellone CF. Status of the Haleakalā silversword: past and present. Technical report CNPRSU-58. Honolulu: University of Hawai'i; 1986.
28. USFWS. Recovery plan for the Maui plant cluster. Portland: US Fish and Wildlife Service; 1997.
29. Krushelnycky PD. Evaluating the interacting influences of pollination, seed predation, invasive species and isolation on reproductive success in a threatened alpine plant. PLoS ONE. 2014;9(2):e88948. doi:10.1371/journal.pone.0088948.
30. Longman RJ, Giambelluca TW, Nullet MA, Loope LL. Climatology of Haleakalā. Technical report CNPRSU-193. Honolulu: University of Hawai'i; 2015.
31. Longman RJ, Giambelluca TW, Alliss RJ, Barnes ML. Temporal solar radiation change at high elevations in Hawai'i. J Geophys Res-Atmos. 2014;119. doi:10.1002/2013JD021322.
32. Kobayashi HK. Ecology of the silversword, *Argyroxiphium sandwicense* DC. (Compositae), Haleakalā Crater, Hawai'i. PhD Thesis. Honolulu: University of Hawai'i; 1973.
33. Baruch Z. Elevational differentiation in *Espeletia schultzii* (Compositae), a giant rosette plant of the Venezuelan Paramos. Ecology. 1979;60:85–98.
34. Meinzer FC, Goldstein GH, Rundel PW. Morphological changes along an altitude gradient and their consequences for an Andean giant rosette plant. Oecologia. 1985;65:278–83.
35. Zhang H, DeWald LE, Kolb TE, Koepke DF. Genetic variation in ecophysiological and survival responses to drought in two native grasses: *Koeleria macrantha* and *Elymus elymoides*. West N Am Naturalist. 2011;71:25–32.
36. Vasques A, Chrino E, Vilagrosa A, Vallejo VR, Keizer JJ. The role of seed provenance in the early development of *Arbutus unedo* seedlings under contrasting watering conditions. Environ Exp Bot. 2013;96:11–9.
37. Allen CD, Breshears DD. Drought-induced shift of a forest-woodland ecotone: rapid landscape response to climate variation. Proc Natl Acad Sci U S A. 1998;95:14839–42.
38. McDowell NG, Allen CD, Marshall L. Growth, carbon-isotope discrimination, and drought-associated mortality across a *Pinus ponderosa* elevational transect. Glob Chang Biol. 2010;16:399–415.
39. Worrall JJ, Egeland L, Eager T, Mask RA, Johnson EW, Kemp PA, et al. Rapid mortality of *Populus tremuloides* in southwestern Colorado. USA Forest Ecol Manag. 2008;255:686–96.
40. Lauer A, Zhang C, Elison-Timm O, Wang Y, Hamilton K. Downscaling of climate change in the Hawai'i Region using CMIP5 results: on the choice of the forcing fields. J Clim. 2013;26:10006–30.
41. Helmuth B, Russell BD, Connell SD, Dong Y, Harley CDG, Lima FP, et al. Beyond long-term averages: making biological sense of a rapidly changing world. Clim Chang Responses. 2014;1:6.
42. Loope LL, Giambelluca TW. Vulnerability of island tropical montane cloud forests to climate change, with special reference to East Maui, Hawai'i. Clim Chang. 1998;39:503–17.
43. Sperling FN, Washington R, Whittaker RJ. Future climate change of the subtropical North Atlantic: implications for the cloud forests of Tenerife. Clim Chang. 2004;65:103–23.
44. Lloret F, González-Mancebo JM. Altitudinal distribution patterns of bryophytes in the Canary Islands and vulnerability to climate change. Flora. 2011;206:769–81.
45. Harter DEV, Irl SDH, Seo B, Steinbauer MJ, Gillespie R, Triantis KA, et al. Impacts of global climate change on the floras of oceanic islands – Projections, implications and current knowledge. Perspect Plant Ecol. 2015;17:160–83.
46. Pounds JA, Fogden MPL, Campbell JH. Biological response to climate change on a tropical mountain. Nature. 1999;398:611–5.
47. Foster P. The potential negative impacts of global climate change on tropical montane cloud forests. Earth-Sci Rev. 2001;55:73–106.
48. O'Neill GA, Hamann A, Wang T. Accounting for population variation improves estimates of the impact of climate change on species' growth and distribution. J Appl Ecol. 2008;45:1040–9.
49. Kuo ESL, Sanford E. Geographic variation in the upper thermal limits of an intertidal snail: implications for climate envelope models. Mar Ecol-Prog Ser. 2009;388:137–46.
50. Rundel PW, Witter MS. Population dynamics and flowering in a Hawaiian alpine rosette plant, *Argyroxiphium sandwicense*. In: Rundel PW, Smith AP, Meinzer FC, editors. Tropical alpine environments: plant form and function. New York: Cambridge Univ. Press; 1994. p. 295–306.
51. Giambelluca TW, Chen Q, Frazier AG, Price JP, Chen Y-L, Chu P-S, et al. Online Rainfall Atlas of Hawai'i. B Am Meteorol Soc. 2013;94:313–6. doi:10.1175/BAMS-D-11-00228.1.
52. Bird IL. Six months in the Sandwich Islands. London: John Murray; 1890.
53. Degener O. Plants of Hawai'i National Parks. Ann Arbor: Braum-Blumfield; 1930.
54. Frazier AG, Giambelluca TW, Diaz HF, Needham HL. Comparison of geostatistical methods to spatially interpolate month-year rainfall for the Hawaiian Islands. Int J Climatol. 2015. doi:10.1002/joc.4437.
55. HaleNet. HaleNet Haleakalā climate network. 2015. http://climate.socialsciences.hawaii.edu/HaleNet/HaleNet.htm. Accessed 15 March 2015.