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**Authors**

Oldfather, Meagan F
Ackerly, David D

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# Microclimate and demography interact to shape stable population dynamics across the range of an alpine plant

Meagan F. Oldfather[1,2] and David D. Ackerly[1,3]

[1] Department of Integrative Biology, University of California, Berkeley, CA 94720, USA; [2] Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO 80309, USA; [3] Jepson Herbarium, University of California, Berkeley, CA 94720, USA

## Summary

- Heterogeneous terrain in montane systems results in a decoupling of climatic gradients. Population dynamics across species' ranges in these heterogeneous landscapes are shaped by relationships between demographic rates and these interwoven climate gradients. Linking demography and climate variables across species' ranges refines our understanding of the underlying mechanisms of species' current and future ranges.
- We explored the importance of multiple microclimatic gradients in shaping individual demographic rates and population growth rates in 16 populations across the elevational distribution of an alpine plant (*Ivesia lycopodioides* var. *scandularis*). Using integral projection modeling, we ask how each rate varies across three microclimate gradients: accumulated degree-days, growing-season soil moisture, and days of snow cover.
- Range-wide variation in demographic rates was best explained by the combined influence of multiple microclimatic variables. Different pairs of demographic rates exhibited both similar and inverse responses to the same microclimatic gradient, and the microclimatic effects often varied with plant size. These responses resulted in range-wide projected population persistence, with no declining populations at either elevational range edge or at the extremes of the microclimate gradients.
- The complex relationships between topography, microclimate and demography suggest that populations across a species' range may have unique demographic pathways to stable population dynamics.

Key words: alpine plants, climate change, demography, integral projection models (IPMs), microclimate, range shifts, topography

## Introduction

Shifts in species' ranges with a changing climate are expected to have broad impacts on biodiversity, biome integrity, and ecosystem services (Bellard *et al*., 2012; Pecl *et al*., 2017). Predicting these shifts in a species' distribution requires an understanding of the fundamental mechanisms underlying biogeographic patterns. Theory suggests that, with rising temperatures species, will move poleward and to higher elevations, but cross-taxon observations show diverse responses to changing climatic conditions (e.g.

stationary range, downward shifts, topographic shifts) (Doak & Morris, 2010; Chen *et al*., 2011; Crimmins *et al*., 2011; Rapacciuolo *et al*., 2014). Local population extinction and establishment as species track suitable climatic conditions will drive range shifts, and mechanistic links between population dynamics and climate across species' ranges will refine range shift predictions (Gaston, 2009; Buckley *et al*., 2010a). Specifically, understanding the relationship between individual-based demographic rates and local climate variables, and the range-wide structure of microclimatic variation, will provide a more complete understanding of the processes that set current and future range limits (Pulliam, 2000; Ehrlen & Morris, 2015).

Dispersal, demography, local adaptation, physiological limitations, and biotic interactions, as well as spatial and temporal variability in climate, can all interact to shape a species' range (MacArthur, 1972; Kirkpatrick & Barton, 1997; Pulliam, 2000; Holt, 2003). Although the rate and magnitude of range shifts will depend on the interactions between these physical, ecological, and evolutionary processes, these all act on the species' range at the scale of the population, with climatic conditions considered a predominant force for range dynamics (Sexton *et al*., 2009; Tredennick *et al*., 2016). Range shifts will only occur with a change in climate if it influences population dynamics, be it through phenology, physiology, or behavior (Mclean *et al*., 2016). Differential population responses across the species' range will drive spatially dependent changes in the probability of establishment and extirpation as climatic suitability changes. Demography (e.g. germination, growth, fecundity, survival) places individual performance in the context of population dynamics, allowing for prediction of potential shifts in species' distributions through population expansion and contraction (Gaston, 2009; Salguero-Gómez *et al*., 2016).

Studies of range shifts are often framed as how range center or range edge populations will respond to changing climate (Hampe & Petit, 2005; Lenoir *et al*., 2008; Sexton *et al*., 2011). In addition, range shift responses are often quantified along broad geographic gradients, such as latitude or elevation, which are assumed to be correlated with climate variables: that is, populations at southern/northern latitudinal or lower/upper elevational limits of a species' range will represent climatic edges where impacts of climate change will be most evident (Lenoir & Svenning, 2014; Rapacciuolo *et al*., 2014; Halbritter *et al*., 2015). However, climate at the microclimate (< 10 m) and topoclimate (1–0.1 km) scales has been shown to be important for population-, species-, and community-level responses to changes in climate (Harrison *et al*., 2010; Scherrer & Korner, 2011; Millar *et al*., 2015; Oldfather *et al*., 2016). The use of climate data at a scale that incorporates microclimatic and topoclimatic variables relative to coarser climate data can dramatically change predictions of habitat suitability across species' ranges (Franklin *et al*., 2013; Potter *et al*., 2013). Organisms respond to climate at the scale at which they experience it, which is much finer than the scale at which many studies measure it. Others have shown that demographic rates respond to climatic gradients rather than geographic gradients, per se, as climatic drivers of demography do not always vary systematically with range position (Villellas *et al*., 2013; Pironon *et al*., 2016). If local climate conditions are variable across geographic edge sites, or vary orthogonally to the elevational or latitudinal gradient, then populations at range edges may not respond demographically to changing conditions in the same way (Aikens & Roach, 2014; Dallas *et al*., 2017).

Alpine plants, in particular, have been identified as harbingers of the biogeographic impacts of a changing climate (Gottfried *et al*., 2012; Lesica & Crone, 2016). Owing to the heterogeneous terrain in mountains, a decoupling of climatic gradients and the elevational gradient is likely across the range of alpine plants (Geiger *et al*., 2009). Steep changes in aspect, slope, and exposure can cause large variation in the climate experienced by alpine plants over short spatial scales (Isard, 1986; Körner, 2003; Ashcroft & Gollan, 2013; Lenoir *et al*., 2013). These small-scale climatic gradients have been shown to be important for alpine plant physiology and water relations (Oberbauer & Billings, 1981; Sage & Sage, 2002), phenology (Galen & Stanton, 1991; Walker *et al*., 1995), nitrogen cycling (Fisk *et al*., 1998), local distributions (Bell & Bliss, 1979; Scherrer & Korner, 2011), species richness (Stanton *et al*., 1994), and demographic rates of alpine plants (Forbis, 2003). Thus, our ability to use alpine plant range shifts as an early warning sign of biotic impacts of climate change requires an understanding of the effects of fine-scale climate on demography across a species' range. Additionally, studying the range dynamics of alpine plants in conjunction with measures of the local climate can elucidate how heterogeneous terrain may influence other species' ranges.

Demographic rates may be sensitive to multiple climate variables that vary across these fine-scale gradients (Buckley *et al*., 2010b; Ettinger *et al*., 2011). In alpine systems, demography may respond to growing degree-days, season length, mean temperature, maximum temperature, nutrient availability, soil moisture decay rate, days of snow cover, and number of snow-free days over the winter (Körner, 2003; Barrett *et al*., 2015; Winkler *et al*., 2016). The variability in these climatic factors may also influence demographic responses (Boyce *et al*., 2006; Lawson *et al*., 2015), and the same climate variable may have multiple direct and indirect effects on population dynamics (Boggs & Inouye, 2012). Different demographic rates may also exhibit different levels of sensitivity to climate variables, and interactions between climate variables may influence these responses (Dalgleish *et al*., 2011; Adler *et al*., 2012; Diez *et al*., 2014). Further, demographic rates may respond in different, even inverse, ways across microclimatic gradients, leading to compensatory relationships that stabilize range-wide population growth (Doak & Morris, 2010; Dalgleish *et al*., 2011; Villellas *et al*., 2015; Compagnoni *et al*., 2016). Integration of both local population-level demography data and climate data across a species' range is necessary to determine the overall effect of these multiple relationships and predict changes in species' abundance and distributions in response to climate change (Sagarin *et al*., 2006; Gerst *et al*., 2011; Ehrlen & Morris, 2015).

We explored the role of microclimatic gradients in shaping population dynamics across the elevational range of an alpine plant species. We focused on how the demographic rates, and population growth rate, vary across the species' range as a function of field-measured temperature, soil moisture, and snowpack, and investigated the topographic determinants of these microclimate conditions. In this study, we investigated how several plant-relevant microclimate factors varied across the range of our focal species in relation to topography, how individual demographic rates were influenced by these microclimate factors, and the implications of these relationships for population growth across the ranges of species. We first hypothesize that demographic rates will be responsive to multiple microclimatic gradients shaped by topography. To understand the role of microclimate in range-wide demography more fully, we examine whether demographic rates exhibit responses to all, or a subset of, microclimatic conditions and ask whether demographic rates have similar or inverse responses to the same microclimate gradients. Finally, we examined how the responses of each demographic rate coalesced into population growth rate across microclimate gradients. Depending on whether relationships among demographic rates are largely similar or contrasting, we predict that either population growth rate will vary across multiple microclimatic gradients or, alternatively, that there will be minimal response of population growth rate due to compensatory responses to microclimatic gradients across the species' range.

## Materials and Methods

### Study system

The focal species for this work is *Ivesia lycopodioides* A. Gray var. *scandularis* (Rydb.) Ertter & Reveal (Rosaceae), an iteroparous alpine plant with a *c*. 20 yr lifespan and a basal rosette of pinnate-compound lycopod-like leaves (Pollak, 1997). This variety has a restricted range (Fig. 1) and is found predominantly in the xeric White Mountain range in eastern California. The White Mountains, located in the rain shadow of the Sierra Nevada, California, has considerably less precipitation (450 mm annually averaged over 1971–2000), even at high elevations, relative to global alpine areas (Körner, 2003; Rundel *et al*., 2005; Rundel & Millar, 2016). Populations of *I. lycopodioides* are found on granitic soils and are associated with areas of high soil moisture in the region (Ertter, 1989; Pollak, 1997). We surveyed 16 *I. lycopodioides* populations spanning the entirety of the species' elevational range in the White Mountains in the 2014–2017 growing seasons (Fig. 1). This species is an excellent candidate for studying the relationship between population dynamics and fine-scale climate across its elevation range. Individuals are delimited as genetic and physiological units without destructive sampling, it exhibits sensitivity to both temperature and moisture availability, and it is representative of obligate alpine plants with long lifespans.

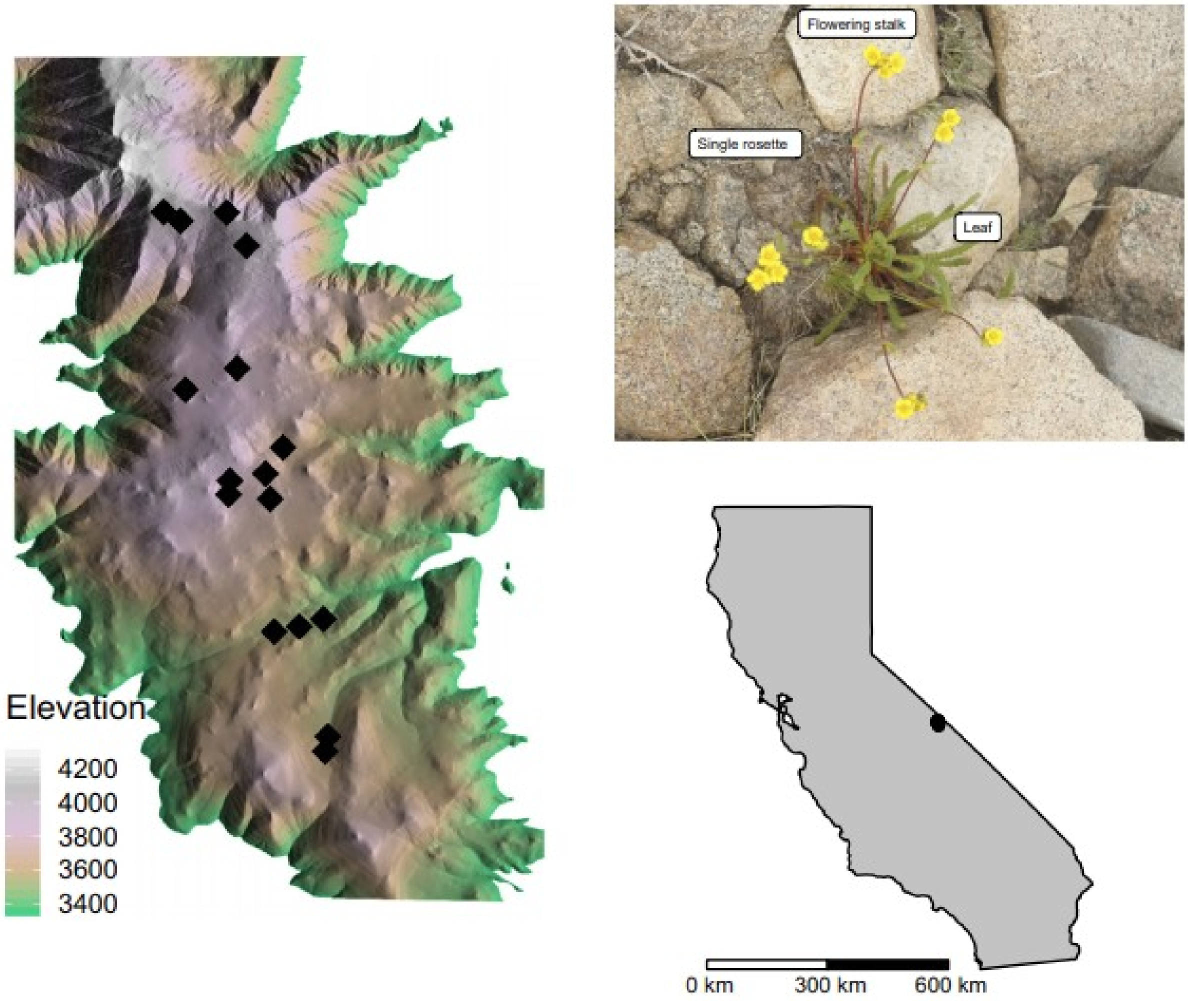

Figure 1

Map of 16 surveyed population (black diamonds) across the elevational range of *Ivesia lycopodioides* A. Gray var. *scandularis* (Rydb.) Ertter & Reveal (Rosaceae) (3460–4033 m*)* in the White Mountains, California, USA, and image of *I. lycopodioides* individual flowering with measurements of demographic survey labeled. The restricted range of this variety is shown (black points) within a map of California, USA.

These surveyed populations were selected specifically to encompass and have replication within the highest and lowest elevations of the species' range, as well as intermediate elevations within the isolated White Mountains. Before population selection, extensive field surveys were completed across this mountain range to find populations at lower and higher elevations than previously reported. We then defined three range positions of *I. lycopodioides*: lower elevation zone (< 3600 m; with five populations), range center zone (3600–3900 m; with seven populations), and upper elevation zone (> 3900 m; with four populations). The requisite study populations were selected randomly within each range position and spanned

3460–4033 m. In each population, we established 2–10, 30 × 30 $cm^2$plots ($n$ = 81 total) with plots placed randomly at least 2 m apart and with the number of plots per population not biased along the elevation gradient (Supporting Information Table S1). In every plot, all individual *I. lycopodioides* were marked with a unique combination of within-plot coordinates and colored pins for reidentification across seasons. Seedlings that emerged after the initial plot establishment were individually marked annually. Across all populations, we measured a total of 1809 (2014), 1937 (2015), 2525 (2016), and 3397 (2017) individuals.

*I. lycopodioides* individuals germinate and established individuals put out leaves in the late spring following snowmelt, mature individuals (> 5 yr) put out flowering stalks *c*. 1 month after leaf-out, and seed set and leaf senescence occur in the late summer (Pollak, 1997). For each marked individual, the number of leaves and number of flowering stalks were recorded between 10 and 26 July annually (Fig. 1). Surveys for new seedlings were also performed in this time period. For each population, we calculated emergence rate (the difference between the number of leaves at time $t + 1$ and the number of leaves at time $t$), reproduction rate (number of flowering stalks at time $t$), and survival rate (dead or alive at time $t + 1$). Plant size is correlated with demographic rates for this species (Pollak, 1997), so each demographic rate was calculated as dependent on individual size (number of leaves per individual).

## Microclimatic conditions

To quantify the climatic conditions across this species' range, we focused on three microclimate metrics shown in other studies to be ecologically important for alpine plant systems: accumulated degree-days, mean growing-season soil moisture, and days of snow cover (Körner, 2003; Winkler *et al*., 2016). Soil temperature measurements were taken every 3 or 4 h throughout the year from September 2014 to August 2017 with iButton Thermochrons in each plot (Maxim, San Jose, CA, USA). The thermochrons were put in film canisters and buried just under the surface (2 cm) to avoid radiation-induced temperature increases and to measure microclimatic conditions relevant to our focal species. Previous work has shown that alpine plant responses to soil vs air temperature measurements are similar (Barrett *et al*., 2015); however, the apical meristem of our focal species is contractile and sits at or just below the soil, making soil measurements potentially more relevant (Pollak, 1997; Körner, 2003). Soil moisture measurements were taken at a depth of 12 cm in each plot approximately every 2.5 wk during the 2014–2017 growing seasons (June–September) with a Hydrosense TDR (Campbell Scientific, Logan, UT, USA). Mean accumulated degree-days were calculated for each plot as the sum of mean daily soil temperatures for days above 0°C within the summer growing season (May–August). Temperature data were also used to estimate duration of snow cover, as the insulating effect of snowpack creates a distinctive thermal signature in winter (Harte & Shaw, 1995). Days of snow cover was calculated for each plot as the number of days between October and June with < 0.5°C diel variability (Harte & Shaw, 1995). Mean soil moisture measurements were calculated as the average across the entire growing season for each plot. Mean differences between sites and years for each microclimate variables were determined using Tukey's honest significant difference tests, and correlations between all microclimate variables (averaged by population and year) were examined with Spearman's rank tests.

We examined the relationship between these field-measured microclimatic metrics and topographic features. Elevation, slope, northness (the cosine of aspect), and topographic position index (TPI; difference in elevation between the site and a surrounding neighborhood radius of 50 m) were extracted from a 10 m digital elevation model of the White Mountains (Hijmans, 2017). North-facing aspects are predicted to be cooler than southern slopes (Geiger *et al*., 2009). At large scales, high elevation is correlated with lower temperatures, but low-elevation drainages in complex terrain can also have cooler minimum temperatures due to cold-air pooling (Fridley, 2009). TPI can provide an assessment of topography conducive to cold-air pooling across the landscape (Dobrowski, 2011). We examined this microclimate–topography relationship using a mixed effects model framework; for each microclimatic metric, a model was built with elevation, slope, northness, and TPI as fixed effects, and population and year as random intercepts. We confirmed the model assumption of no residual spatial autocorrelation using Moran's *I*.

### Demographic rate variation

To address our questions concerning the importance of multiple microclimate variables for demographic rates across a species' range, we built generalized mixed effects models in a maximum likelihood framework with the associated error structure for the following demographic rates: number of new recruits (negative binomial), individual growth (Gaussian), number of flowering stalks (Poisson), and probability of survival (binomial). Models for all demographic rates except emergence included the effect of individual size (measured as the number of leaves at time *t*) as a continuous predictor variable. For each demographic rate, we built a full model that included accumulated degree-days, mean soil moisture, and days of snow cover as both linear and quadratic predictors, as well as an interaction between individual size and each linear variable. For all demographic rate models, except emergence, random intercepts for year, population, and plot nested within population were included. The model for emergence had no random effect of plot because the number of new seedlings was quantified at the plot scale. All predictor variables were scaled and centered before being included in the models. The best model fit was determined using backward selection from a complex global model and corrected Akaike information criterion (AICc); simpler models with comparable AICc values (within 2) were selected (Tables S2–S5). AICc is a corrected estimator of model fit that has greater penalty for parameter number and may reduce overfitting (Hurvich &

Tsai, 1991). The significance of each fixed effect in the best-fit model was tested using likelihood ratio tests on nested models. The models were fit using the LME4 package (Bates *et al*., 2015). The variance explained (pseudo-$R^2$) by the fixed effects for each model was determined using the MUMINpackage (Nakagawa & Schielzeth, 2013). The mean demographic rate for each population was extracted from the best-fit model and represented the predicted value for the average-sized individual for that population averaged across all years. Correlations between mean demographic rates across populations were assessed with Spearman's rank tests. All analyses were performed in R v.3.3.3 (R Core Team, 2018).

### Range-wide population growth

For each of the 16 populations, a separate integral projection model (IPM) was built to determine population growth rates across this species' range. An IPM is a generalization of the matrix projection model allowing for a continuous stage-structure and the inclusion of other parameters of interest, such as climate (Easterling *et al*., 2000; Ramula *et al*., 2009; Merow *et al*., 2017). The probabilities of survival, reproduction, and growth were determined for each population separately using generalized mixed effects models parameterized from data across all populations and years. Each of the models used to estimate the probabilities of survival (binomial), reproduction (Poisson), and growth (Gaussian) included size as a fixed effect and random intercepts of population, plot, and year. The growth and reproduction models also included random intercepts of individual and random slopes of size within population. The random effect structure was determined with AICc. The relationships between the demographic rates and size across all populations were explored visually to determine the predictability of our state variable (Fig. S1). The effect of size, population, and size by population interactions were extracted from each of these regressions to estimate probabilities used in the IPM kernel estimates of growth, reproduction, and survival. The IPM sub-kernel for growth and survival $P\ (z', z)$ was calculated based on the size-dependent survival and growth. The reproduction sub-kernel $F\ (z', z)$ was calculated based on the size-dependent reproduction (number of flowering stalks per individual), the viable seed production per flowering stalk, the probability of seedling establishment, and the size distribution of the seedlings. Establishment probability was determined as the number of new recruits at time $t + 1$ divided by the seed availability in a population at time $t$. The size estimates for seedling recruits (mean = 1.67 leaves, SD = 0.8 leaves; Fig. S1) and viable seed production per flowering stalk (15 seeds/stalk; as determined from inflorescence collections in 2014 across all populations) were assumed to be constant across populations and years. Although alpine plants can have seed banks in xeric mountain ranges (Wenk & Dawson, 2007), we have no evidence of seed bank dynamics for this species, and this species does not appear to be seed limited across the study populations (see the Results section).

The model was integrated over 0.9 times the minimum plant size to 1.1 times the maximum plant size of each population to allow for realistic plant sizes that were not observed, and 100 mesh points were used (Easterling *et al*., 2000; Ellner *et al*., 2016). All population modeling was performed in R v.3.3.3 (R Core Team, 2018) and was based on previously published code for the modeling of perennial plant populations (Merow *et al*., 2014). We calculated 95% confidence intervals for population growth for each population by bootstrapping the data 2000 times, keeping the total number of observations within each population constant for each sample. The sample data were then used to rebuild the regressions on which the IPM is based, and a new lambda value was calculated. To estimate the proportional effect of the demographic rates on population growth rate, we performed an elasticity analysis for each of the 16 populations; higher elasticity values indicate a larger influence of transition(s) on the population growth rate (Benton & Grant, 1999; Caswell, 2001). This prospective perturbation analysis was done at the level of the IPM additive sub-kernels of survival–growth $P(z', z)$ encompassing persistence, progression, and retrogression) and reproduction (encompassing number of flowering stalks and emergence) $F(z', z)$ in order to separate the elasticity values for the major groups of demographic rates (Griffith, 2017). Each element in the sub-kernels was perturbed by 0.001 and the sub-kernel elasticities were then summed to compare the proportional influence of survival–growth and reproduction in all populations.

## Data accessibility

All demographic and microclimatic data are available at 10.6084/m9.figshare.7239233.

## Results

### Microclimatic conditions

Between 2014 and 2017 we observed large variation in all three microclimatic conditions, decoupling the variables both spatially and temporally (Fig. 2). Snowpack was much more persistent in spring 2017 relative to the drought years of 2014 ($F = 16.57$, $P = 0.04$) and 2015 ($P < 0.001$). However, for both soil moisture and accumulated degree-days there was no clear effect of year on microclimate conditions due to the idiosyncratic responses of each site to annual environmental stochasticity. There were also no significant correlations between any of the three microclimatic variables (soil moisture–degree-days: $r = -0.15$, $P = 0.58$; soil moisture–snow days: $r = 0.344$, $P = 0.19$; snow days–degree-days: $r = -0.447$, $P = 0.08$). Further, the minima and maxima of the microclimatic conditions for each variable occurred in different populations across the elevation gradient each year, and occurred in locations that spanned the entire elevational gradient (Fig. 2). Topography shaped the microclimatic conditions in the populations. Accumulated degree-days increased with slope, with warmer sites on steeper slopes (Table 1). Soil moisture increased with northness and decreased with elevation, indicating that populations at lower elevation north-facing slopes were wetter throughout the growing season (Table 1). Days of snow cover had no relationships with any of the topographic metrics (Table 1).

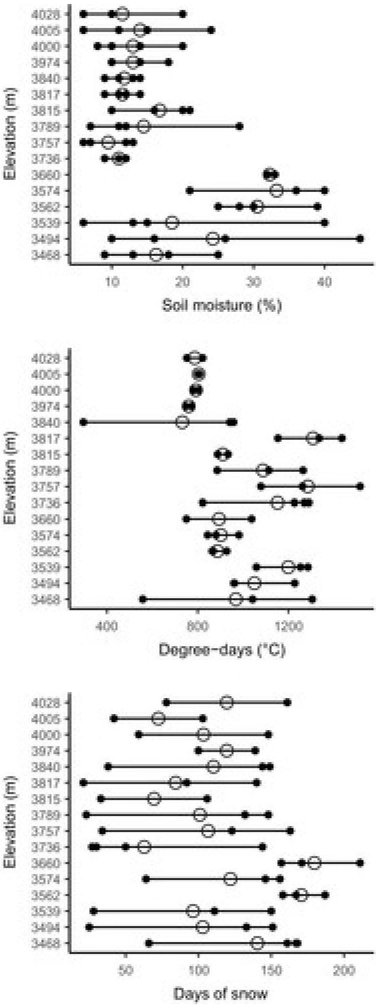

Figure 2

Variation in soil moisture and accumulation of degree-days for the 2014–2017 summer growing seasons (top and center, respectively) across the elevation gradient. Variation in the days of snow cover for 2015, 2016, and 2017 winters across the elevation gradient (bottom). Both site means for each year (closed circles) and site mean across all years (open circles) are shown. Certain climate measurements are missing in different years at some sites, leading to less data for some year, site, climate variable combinations.

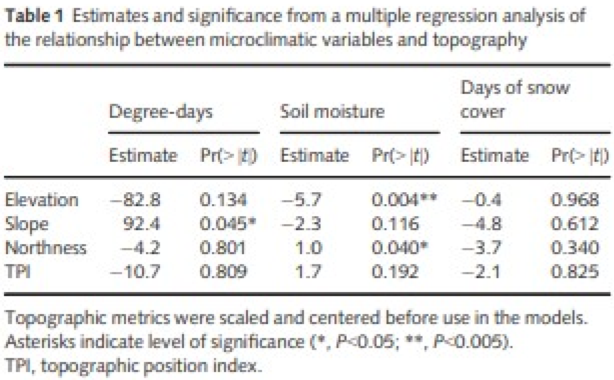

**Table 1** Estimates and significance from a multiple regression analysis of the relationship between microclimatic variables and topography

| | Degree-days | | Soil moisture | | Days of snow cover | |
|---|---|---|---|---|---|---|
| | Estimate | Pr(> \|$t$\|) | Estimate | Pr(> \|$t$\|) | Estimate | Pr(> \|$t$\|) |
| Elevation | −82.8 | 0.134 | −5.7 | 0.004** | −0.4 | 0.968 |
| Slope | 92.4 | 0.045* | −2.3 | 0.116 | −4.8 | 0.612 |
| Northness | −4.2 | 0.801 | 1.0 | 0.040* | −3.7 | 0.340 |
| TPI | −10.7 | 0.809 | 1.7 | 0.192 | −2.1 | 0.825 |

Topographic metrics were scaled and centered before use in the models.
Asterisks indicate level of significance (*, $P$<0.05; **, $P$<0.005).
TPI, topographic position index.

## Demographic rate variation

Average density of individuals per population across years ranged from *c.* 160 to 944 $m^{-2}$(Table S1). Density decreased across the elevation gradient (estimate = −0.76, $P$ = 0.005, $R^2$ = 0.40), with denser populations at the species' lower elevation edge. Density increased with both mean soil moisture (estimate = 15.68, $P$ = 0.002, $R^2$ = 0.49) and days of snow cover (estimate = 3.1, $P$ = 0.011, $R^2$ = 0.38). Mean size of individuals responded to the gradients in the opposite way, increasing with elevation (estimate = 0.02, $P$ = 0.008, $R^2$ = 0.36) and decreasing across soil moisture (estimate = −0.46, $P$ = 0.013, $R^2$ = 0.32) and snow-covered gradients (estimate = −0.1, $P$ = 0.014, $R^2$ = 0.31). Denser populations consistently had smaller individuals (estimate = −0.02, $P < 0.001$, $R^2$ = 0.58).

For emergence (number of seedlings that germinated each season), a model including all microclimate variables, either as linear or quadratic effects, was the best fit (marginal $R^2$ = 0.36; Table S2). Mean soil moisture had a positive linear effect on the number of new seedlings (estimate = 1.12, $P < 0.001$), with much higher emergence in wetter sites (Fig. 3a). The quadratic of accumulated degree-days (estimate = −0.41, $P$ = 0.012) was also a significant predictor of emergence rates. More seedlings emerged at intermediate levels of degree-days (Fig. 3a). Days of snow cover was also included in the best-fit model, but it only had a nonsignificant linear negative effect on the number of germinating seedlings each season.

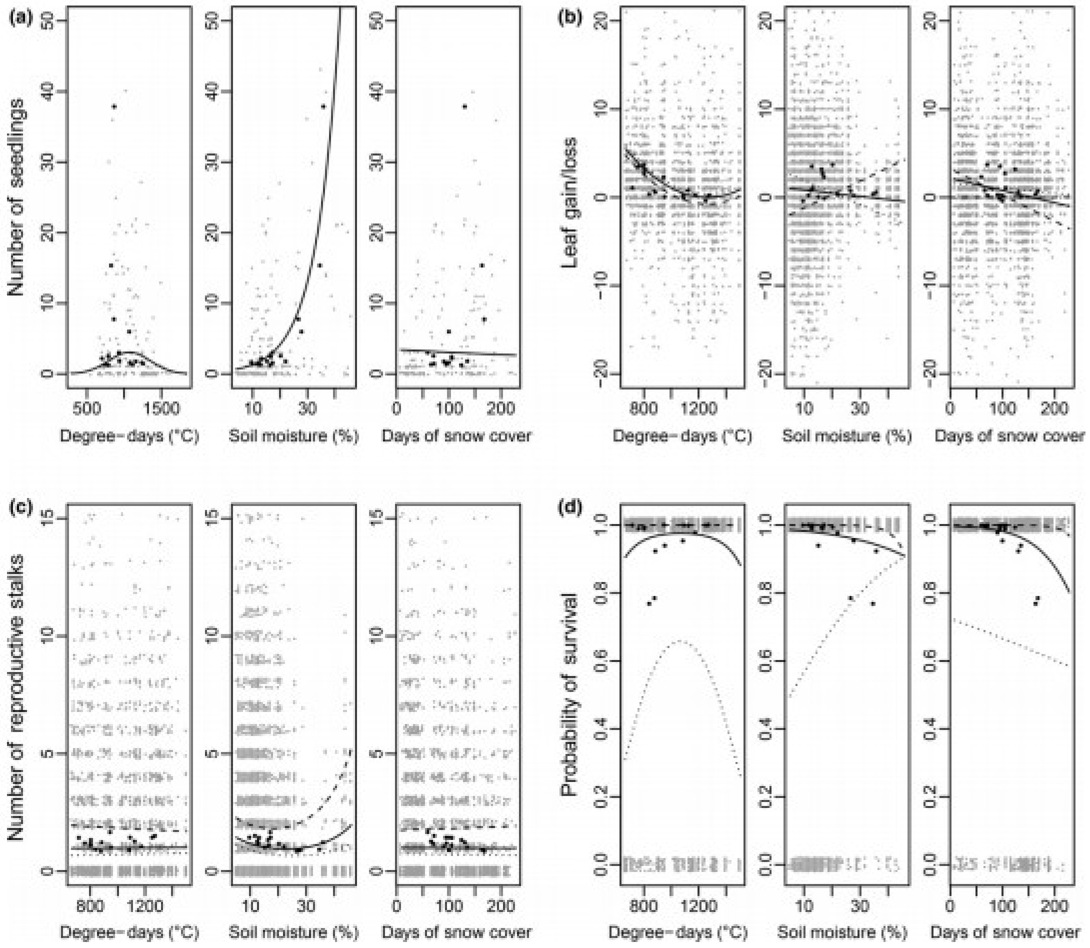

Figure 3

(a) Numbers of seedlings, (b) individual gain or loss of leaves between seasons, (c) number of flowering stalks, (d) probability of survival (alive = 1, dead = 0) across all populations of *Ivesia lycopodioides* and years shown as gray points for the three microclimate variables of interest. Black points show the average demographic rate for each population for an average-sized individual in that population. Lines represent marginal effect of accumulated degree-days (left), mean growing season soil moisture (center), and days of snow cover (right) from best-fit model for each demographic rate. The line types, when applicable, represent different quantiles of size (leaf number) with dotted = 10th percentile size class, solid = 50th percentile size class, and dashed = the 90th percentile size class.

Growth rate (change in leaf number across growing seasons) was influenced by microclimate directly and by an interaction between microclimate and individual size (marginal $R^2 = 0.11$; Table S3). Size at time $t$ had a negative effect, with smaller individuals growing more and/or losing fewer leaves across seasons (estimate = −0.59, $P < 0.001$). Degree-days had an overall negative effect on growth rate (linear estimate = −1.32, $P < 0.001$; quadratic estimate = 0.74, $P < 0.001$) across all sizes (Fig. 3b). The number of days with persistent snow also decreased individual growth (estimate = −0.91, $P = 0.002$), and this effect was greatest for the largest individuals (estimate = −0.66, $P < 0.001$) (Fig. 3b). A positive interaction between size and the mean soil moisture was also significant (estimate = 1.40, $P < 0.001$), indicating more growth for large individuals in wetter sites (Fig. 3b).

For reproductive output (number of flowering stalks per individual), a model with soil moisture as a linear and quadratic predictor, as well as with size by microclimate interactions for all three microclimate variables, was supported (marginal $R^2 = 0.19$; Table S4). Mean soil moisture had a negative linear effect (estimate = −0.12, $P = 0.032$), with individuals having fewer flowering stalks in wetter sites. However, in the very wettest sites, the magnitude of reproduction again increased due to a positive quadratic effect of soil moisture (estimate = 0.12, $P = 0.008$) (Fig. 3c). Larger individuals across all environmental conditions had more inflorescences per individual (estimate = 0.299, $P = < 0.001$). However, the effect of individual size varied across microclimatic gradients, with larger individuals flowering more in wetter sites (estimate = 0.09, $P < 0.001$) and in sites with more snow cover (estimate = 0.02, $P = 0.007$), but flowering less in warmer sites (estimate = 0.04, $P < 0.001$) (Fig. 3c).

Probability of survival was also influenced by all three microclimate variables; however, very little variation in survival was explained (marginal $R^2 = 0.02$; Table S5). Smaller individuals had higher mortality rates, with a significant positive effect of size at time $t$ on survival (estimate = 4.58, $P < 0.001$). The quadratic of degree-days had a negative effect on survival probability, with lower survival rates in both the coolest and warmest populations (estimate = −0.43, $P = 0.019$) (Fig. 3d). By contrast, both mean soil moisture and number of snow-covered days decreased survival rates, with higher mortality in the wettest and snowiest sites for the average-sized individual (Fig. 3d). There was also significant negative interaction between size and mean soil moisture (estimate = −1.46, $P < 0.001$), as well as size and number of snow-covered days (estimate = −1.41, $P = 0.003$) (Fig. 3d). The survival rates of larger individuals were less influenced by the microclimatic conditions, and in the wettest sites there is some evidence that what may be a favorable site for survival of small individuals is unfavorable for large individual survival.

Mean demographic rates across the populations were predominantly not correlated with one another; however, survival probability was correlated with both reproductive output and emergence rates (Fig. 4). The mean number of reproductive stalks for an average-sized individual increased with the probability of survival. By contrast, the number of new seedlings decreased with the probability of survival for an average-sized individual. There was also a nonsignificant negative relationship between the mean number of reproductive stalks and the number of new seedlings. There were no significant correlations between growth and any of the other demographic rates (Fig. 4).

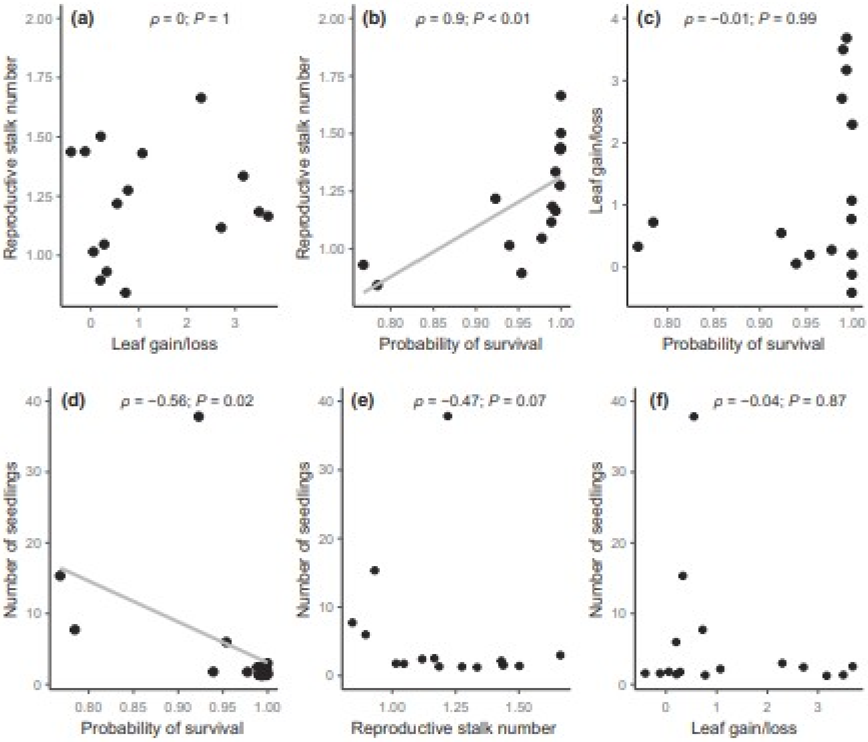

Figure 4

Correlations between population mean demographic metrics of *Ivesia lycopodioides* averaged across year and individual size predicted by best-fit demographic rate–microclimates regressions. (a) Leaf gain/loss vs reproduction, (b) survival probability vs reproduction, (c) survival probability vs leaf gain/loss, (d) survival probability vs seedling emergence, (e) reproduction vs seedling emergence, and (f) leaf gain/loss vs seedling emergence. Spearman's rank test used for all correlation coefficient and significance tests. Significant relationships between demographic rates shown with gray lines.

## Range-wide population growth

Across the 16 populations, population growth rate $\lambda$ ranged from 0.99 to 1.72, indicating stable or increasing populations across this species’ entire range. The 95% confidence intervals of six of the populations across this species’ range included population growth rate of one. Population growth rate did not change predictably across the elevational gradient of the species’ range (Fig. 5). Further, no significant relationships between population growth and any microclimate conditions were found (Fig. 5). The elasticity of growth–survival was larger than the elasticity for reproduction for most populations across this species’ range (Fig. 6), with 14 of the 16 populations having a summed elasticity value for growth–survival over 0.70. However, for one population at mid-elevations, reproduction had a higher elasticity value (0.60), highlighting the variability of elasticity for populations occupying different microclimates across a species’ range.

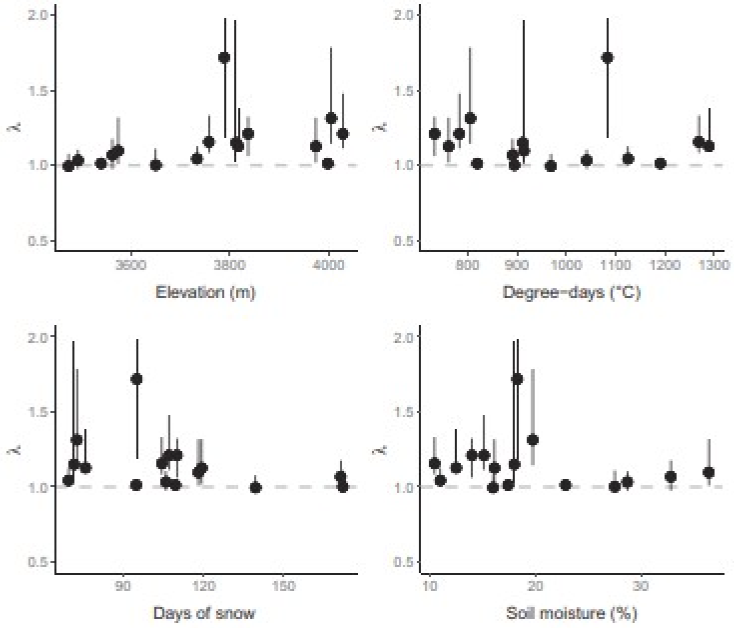

Figure 5

Population growth rate of all 16 *Ivesia lycopodioides* populations regressed against elevation and all measured microclimate variables show no significant relationships. Dashed line indicates where population growth rate is stable ($\lambda = 1$). The 95% confidence intervals are shown for each population.

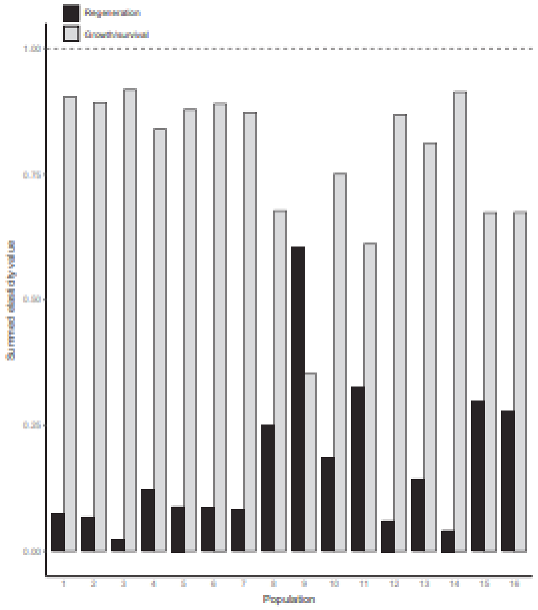

Figure 6

Elasticity values for reproduction/recruitment and growth/survival based for each *Ivesia lycopodioides* population ordered by increasing elevation. Owing to the summed elasticity being proportional (sums to one) the values can be compared across populations.

## Discussion

Understanding spatial variation in demographic rates and its role in governing a species' range limits is a fundamental question in population ecology (MacArthur, 1972; Sutherland *et al*., 2013). Further, range shifts will occur through population establishment and population extinction, and therefore quantifying population dynamics in relation to climate across a species' range will aid in refining range shift predictions with a changing climate (Halbritter *et al*., 2015; Mclean *et al*., 2016; Merow *et al*., 2017). In this study, we explored the importance of multiple microclimatic gradients in shaping individual demographic rates and population growth rate across the elevational range of an alpine plant in the xeric White Mountains, California, USA. We performed demographic surveys and quantified microclimatic gradients in 16 populations spanning the entirety of the species' elevational range in the White Mountains for the 2014–2017 growing seasons. We found highly variable and size-dependent responses of the demographic rates to the multiple topographically shaped microclimatic gradients across the focal species' range (Fig. 3). Bringing all of these responses together with integral projection modeling, we found that population growth rate was stable or slightly increasing across the species' entire range (Fig. 5). Despite the responses of the individual demographic rates to the microclimatic gradients, population growth rate did not vary predictably across the microclimatic or elevational gradients. In this discussion, we explore the possible mechanisms that could be driving this discrepancy, including the impact of spatially and temporally variable combinations of microclimatic conditions on demographic rates, spatial variation in proportional influence of the demographic rates on population growth rates, and inverse relationships between demographic rates across climatic gradients. We frame these different mechanisms by how they may shape the influence of topography, microclimate, and demography on range shifts across geographic and climatic space with a changing climate.

The distinction between geographic and climatic space across a species' range becomes important in heterogeneous landscapes, where climatic dissimilarity is not parallel to physical distance between populations (Pironon *et al*., 2016). Although there were general trends across our study populations towards cooler, drier conditions at higher elevations, measured microclimate variables were not all strongly correlated with the elevational gradient of the species' range (Fig. 2). Instead, slope and aspect shaped the microclimatic conditions experience by each population (Table 1). Environmental variables may be correlated across elevational gradients for some species' ranges, but fine-scale topography creates substantial amount of environmental variation across small spatial extents in the alpine fellfields (Scherrer & Korner, 2011). Therefore, the geographic edge (in terms of elevation or latitude) may not be the edge of climatic conditions considered suitable for the species (Sagarin *et al*., 2006; Hargreaves *et al*., 2014; Chardon *et al*., 2015; Pironon *et al*., 2015). Furthermore, the relationship between topography and microclimate conditions also varied across years, and we observed the maxima and minima of the microclimate variables in different parts of the species' range depending on the variable and year. For example, in years with less snow, higher elevations melted the latest, but after the 2017 above-average snow year the populations in the center of this species' range were the last to melt out. This result indicates that making predictions for edge vs center populations or across elevation gradients misses important nuances and may lead to erroneous assumptions about a species' biogeographic sensitivity to climate change (Pironon *et al*., 2015). If a species does not respond at the range edge, this may not indicate lack of sensitivity, but instead may be due to these edge populations not being at the climatic edges of the species' distribution.

The concept of the climatic edge of a species' range is complicated by the inclusion and importance of multiple climate variables that may not respond to topography in the same way. There has also been increasing recognition that these multiple climatic variables have simultaneous and interactive effects on plant phenology, distributions, and community dynamics (Rapacciuolo *et al*., 2014; Harsch & Hille Ris Lambers, 2016). We found that all demographic rates responded to multiple microclimatic variables, but with different patterns and magnitudes (Fig. 3). Significant size-by-microclimate interactions were also common, indicating that the effect of microclimate varies for even a single demographic rate depending on individual size. For example, more persistent snowpack had a considerable negative effect on survival for the average-sized individual, but a negligible effect on the largest individuals. These unique combinations of responses to climate for each demographic rate pose a potential difficulty in predicting species' responses to climate change (Ettinger & Hille Ris Lambers, 2013). Such predictions may require measurement of all demographic rates across a range of individual sizes.

The overall population response across a species' range is moderated by the individualistic response of each demographic rate to each microclimatic variable (Jongejans & De Kroon, 2005). Overall, we did not find uniform responses of the demographic rates to the microclimatic gradients. For a single microclimate gradient, some combinations of demographic rates had inverse responses. For example, soil moisture had a positive effect on emergence of new recruits, but a negative effect on the number of flowering stalks for larger individuals (Fig. 3). Survival across this species' range presents an interesting case where wetter sites have lower mortality for smaller individuals but higher mortality for larger individuals (Fig. 3). Although current range shift predictions often assume a single response of a species' fitness to variation in climate, these results join a growing literature that suggests the direction and magnitude of responses to climatic gradients is not consistent across demographic rates (Doak & Morris, 2010; Dalgleish *et al*., 2011; Compagnoni *et al*., 2016). This mosaic of demographic responses to spatiotemporal variation in multivariate microclimate supports other work that indicates populations behave idiosyncratically across a species’ range and have unique pathways to stability (Csergő *et al*., 2017).

The individual demographic rates coalesce and contribute to overall population growth shaped by the proportional influence of each demographic rate on the population growth rate (Morris & Doak, 2002). Responses of individual demographic rates, without a corresponding response of population growth rates to a geographic/climatic gradient, could in part be driven by a decoupling between the more variable demographic rates and those that have the largest proportional influence on the population growth rate (Mclean *et al*., 2016). We found that, generally across all populations, survival and growth had the largest proportional influence on population growth rates, as expected for a long-lived alpine plant (Fig. 6). These demographic rates with high elasticity were less influenced by the microclimates than reproduction and germination were. Although we saw some responses of survival and growth to microclimate, their overall influence was complicated by interactions with size. For survival, only small individuals were highly responsive to microclimate, but average and larger individuals were not. For growth, the limited responses to microclimate were in different directions for individuals of different sizes, potentially negating an overall impact. Overall, the longevity of the focal species, and therefore its reliance on large individual survival rates, may explain the limited population growth rate response to highly temporally variable microclimatic conditions (Morris *et al*., 2008). We also observed elasticity varying across the species range, with regeneration (reproduction and germination) having more of a proportional influence at mid-elevations (Fig. 6). This spatial variation in elasticity may shape the pattern of range-wide stable or growing population growth rates, with reduced demographic rates having less influence in the populations where conditions are less suitable for that life-history transition.

An additional, but not mutually exclusive, hypothesis to explain the lack of population growth response across the complex microclimate gradients is that demographic rates show compensatory relationships between demographic rates (Villellas *et al*., 2015). We also see evidence of this; in one case, the different responses of each demographic rate to the microclimatic gradients resulted in an inverse relationship loosely following life-history trade-offs between different life stages (Salguero-Gómez *et al*., 2016). There was a negative relationship between germination rates and the survival rate of adult individuals across the populations, indicating that some microclimatic conditions beneficial for survival are not beneficial for germination (Fig. 4d). The inverse relationships between demographic rates, potentially driven by inverse responses to the same microclimate gradient, indicate that the population growth rates across a species’ range may be shaped by compensatory relationships between demographic rates (i.e. demographic compensation), reducing the overall variation in population growth (Doak & Morris, 2010; Jongejans *et al*., 2010; Villellas *et al*., 2015).

Indeed, we found there was very little predictable variation in population growth rates across the microclimatic gradients. The geographic edge populations did not exhibit reduced population growth rate, suggesting that range edges may not be ubiquitously marginal from a demographic perspective (Sexton *et al*., 2009; Abeli *et al*., 2014; Chardon *et al*., 2015). The observed stable or increasing population growth rates corroborate other work showing that the demographic strategies that maintain populations vary widely across a species' range (Villellas *et al*., 2015; Csergő *et al*., 2017; Pironon *et al*., 2017). This study is one of few showing these proposed complex relationships between field-measured climate and population dynamics driving stable population dynamics spanning the entire elevational range and climatic gradients of a species' distribution.

More spatially replicated studies of population across species distributions are needed to determine whether these conclusions can be generalized. Owing to the limitations of an observational study, we cannot discount the effect of unmeasured climatic conditions, such as frost events, nitrogen availability, or drought stress. Nor can we discount the effect of climate responses of unmeasured demographic transitions, such as seed viability or seed bank dynamics, as driving the range limits of the focal species. Extreme climatic events not captured during the study period, which was limited relative to the average lifespan of the focal species (4 yr compared with 20 yr), may also constrain range-wide population growth and shape species' distributions (Smale & Wernberg, 2013). We observed a large variation in density across our study populations, suggesting that density may mediate the influence of these microclimatic variables on demography as well. Although we focus here on climate impacts, many other ecological and evolutionary processes can impact the population stability, and therefore range stability of species (Sexton *et al*., 2009). Disturbance, in this system represented predominantly by frost heaving, may be an explanation for lower survival rates of smaller individuals (Pollak, 1997). Community interactions through pollination, herbivory, or direct competition can also limit population growth at range edges (Louthan *et al*., 2015), and the effect of these interactions on demography can also be mediated by the microclimatic conditions (Blonder *et al*., 2018).

Overall, our results indicate that caution is warranted when predicting and quantifying range shifts if geography and climate gradients are decoupled at the scale important for population dynamics. Owing to variation in the response of demographic rates to different microclimatic conditions, it is critical to capture the relationships between climate and multiple life-history stages to make robust range shift predictions. Further, in response to a changing climate, the combined effect of multiple changing climate variables in heterogeneous terrain may allow compensatory relationships to buffer population growth. Buffered population response may lead to reduce range shifts as long as climatic conditions stay within the range currently experienced across this species' distribution. Currently, the large magnitude of spatiotemporal microclimatic gradients is larger than the predicted changes from climate change in this region (He *et al*., 2018), suggesting that this species' range may not contract with climate change, but instead the populations may shift their demographic strategies for persistence (Pironon *et al*., 2017). Further, range shifts studies need to consider the potential for life-history components to interact with changing climatic conditions in different ways (Doak & Morris, 2010; Csergő *et al*., 2017). This work suggests that, for long-lived species occupying heterogeneous landscapes, we should not assume that presence, abundance, or a single demographic rate is a useful proxy for population performance and vulnerability to a changing climate. Across a species' range, populations may have different demographic pathways to stability; interestingly, this could also imply that each population may have different vulnerabilities to a changing climate that may disrupt this stability.

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