UC Berkeley
UC Berkeley Electronic Theses and Dissertations

Title

Population and Community Dynamics of Alpine Plants in a Changing Climate Across Topographically Heterogeneous Landscapes

Permalink

https://escholarship.org/uc/item/0vq6v6vs

Author

Oldfather, Meagan F

Publication Date

2018

Peer reviewed|Thesis/dissertation

Population and Community Dynamics of Alpine Plants in a Changing Climate Across Topographically Heterogeneous Landscapes

By

Meagan F. Oldfather

A dissertation submitted in partial satisfaction of the

requirements for the degree of
Doctor of Philosophy

in

Integrative Biology

in the

Graduate Division

of the

University of California, Berkeley

Committee in charge:

Professor David D. Ackerly, Chair

Professor Todd E. Dawson

Professor Steven R. Beissinger

Spring 2018

Abstract

Population and Community Dynamics of Alpine Plants in a Changing Climate Across
Topographically Heterogeneous Landscapes

by

Meagan F. Oldfather

Doctor of Philosophy, Integrative Biology

University of California, Berkeley

Professor David D. Ackerly, Chair

Understanding how species and communities shift locally and regionally poses a great challenge
as we manage for resilience in the face of a changing climate. Shifts in species distributions are
expected to be one of the largest biological effects of climate change and alpine plants are
considered early indicators of these biographic responses. However, in montane systems, highly
heterogeneous terrain results in a decoupling of climatic gradients complicating straightforward
expectations of polar or upslope distributional shifts of plants in response to warmer, drier
conditions. Species range shifts will be driven by how these interlaced climate gradients shape
current and future population performance across species ranges. This work examines how the
differential responses of life history transitions that shape population performance (demographic
rates) may mediate range shifts in a changing climate across topographically heterogeneous
landscapes.

The focal species for this work is *Ivesia lycopodioides* A. Gray var. *scandularis* (Rydb.) Ertter &
Reveal (Rosaceae), an iteroparous alpine plant with an approximate 20-year lifespan. I first
explored the importance of multiple microclimatic gradients in shaping individual demographic
rates and population growth rate in sixteen populations across the elevational distribution of this
species in the xeric White Mountains, CA USA. I found that multiple microclimate gradients
drove variation in demographic rates across this species range, and that complementary and
compensatory relationships between demographic rates lead to stable range-wide population
growth through multiple demographic pathways. This work motivated a range-wide multi-year
field experiment manipulating summertime temperature and precipitation in nine of the study
populations to investigate the degree to which climate change may perturb this population
stability.

Building integral projection modeling based on experimental demographic data, I found a
negative effect of experimentally increased summertime temperature on population growth rate
in all populations across this species range. This universal reduction is population growth in both
trailing and leading range edge populations was due to size-dependent and variable relationships
between the climate manipulation and demographic rates, and lead to predictions of population
contractions at mid elevations of the species range. These results highlight that differential and

size-dependent responses of life history transitions to changing climate influence the rate and magnitude of species range shifts and can lead to unexpected shifts.

In order to place the experimental responses of the focal species in a community context, I quantified shifts in abundances for the entire alpine plant community under manipulated climatic conditions. Under experimentally warmer conditions, I observed an increase of hot, dry adapted species relative to their surrounding community members and this effect was not ameliorated by experimental additions of summertime precipitation. Concordantly, I found that overall plant abundance increased and species richness decreased with experimental heating. Together, these results indicate that, with warmer conditions, the White Mountain alpine zone will comprise less diverse plant communities dominated by species associated with hotter, drier conditions.

ACKNOWLEDGMENTS

INTRODUCTION

Shifts in species ranges are one of the major biological effects of climate change with impacts on biodiversity, ecosystem services, and human health (Bellard *et al.* 2012; Pecl *et al.* 2017). Predicting a shift in a species range requires an understanding of the fundamental mechanisms underlying biogeographic patterns. There is strong theoretical background for the ecological and evolutionary drivers that dynamically shape species distributions, but this theory is challenging to test in natural systems (Kirkpatrick & Barton 1997; Holt 2003; Sexton *et al.* 2009). Dispersal, demography, local adaptation, physical limitations, biotic interactions, as well as spatial and temporal variability in climate all may interact to shape a species' current range (Pulliam 2000; Holt 2003; Sexton *et al.* 2009). Species range shifts in response to climate change have been highly variable (Lenoir & Svenning 2014); simple predictions of polar or upslope movement are complicated by the importance of multiple climate variables, life stage-dependent responses to climate, and species interactions (Doak & Morris 2010; Gilman *et al.* 2010; Rapacciuolo *et al.* 2014). Quantifying demographic patterns across species ranges in relation to the range-wide structure of climatic variation will improve our understanding of the species niche, the relationship between the niche and the species range, and the stability and dynamics of species ranges in response to a changing climate (MacArthur 1972; Angert 2009; Ehrlen & Morris 2015; Salguero-Gómez *et al.* 2016).

Specifically, understanding the abiotic requirements for each demographic rate (*e.g.*, reproduction, survival, growth) and how those rates coalesce to shape performance in populations across a species range will refine range shift predictions (Villellas *et al.* 2015; Pironon *et al.* 2017). For a change in climate to drive a range shift, the amount of change in climate a population experiences must have an effect on demographic rate(s) that ultimately has a large enough effect on the population growth rate to change the population trajectory toward expansion or contraction (Normand *et al.* 2014; Mclean *et al.* 2016). Many studies have experimentally modified the temperature and moisture availability and document responses in plant physiology, components of the species life-history, and community processes (Walker *et al.* 2006; Zhuoting *et al.* 2011; Franklin *et al.* 2016; Winkler, Chapin & Kueppers 2016a; Kueppers *et al.* 2017). However, few studies have examined responses to experimentally manipulated conditions across a species entire range (Buizer *et al.* 2012), and no study to our knowledge has investigated responses of all demographic rates to climate manipulations in unison across a species entire range.

Montane systems provide important early indicators of plant community responses to changing climate (Körner 2003; Grabherr, Gottfried & Pauli 2010; Rixen & Wipf 2017; Steinbauer *et al.* 2018). Climate warming is more pronounced at higher elevations (Pepin *et al.* 2015), and exposure to climate change is exacerbated in xeric mountain ranges due to shifts from snow-dominated to rain-dominated precipitation. Due to the heterogeneous terrain in mountains, a decoupling of climatic gradients and the elevational gradient is likely across the range of alpine plants (Geiger, Aron & Todhunter 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; Lenoir *et al.* 2013; Ashcroft & Gollan 2013). Studies of alpine plant responses to climate change have predominantly focused on temperature-limited systems (Körner 2003; Gottfried *et al.* 2012); however, mountain ranges in semi-arid regions, such as western North America, where temperature and moisture both play strong roles in the determination of the

distribution of alpine communities, require more research (Isard 1986; Cavieres *et al.* 2006; Lesica & Crone 2016; Winkler *et al.* 2016a).

This dissertation research was conducted in the White Mountains (California, USA), a semi-arid mountain range which has experienced marked shifts toward hotter, drier conditions with 20th century climate change (Rundel, Gibson & Sharifi 2008; Kopp & Cleland 2014; Rapacciuolo *et al.* 2014). The focal species, *Ivesia lycopodioides* A. Gray var. *scandularis* (Rydb.) Ertter & Reveal (Rosaceae) is a long-lived alpine plant (approximate 20-year lifespan) with a basal rosette of lycopod-like leaves and sensitivity to both temperature and moisture gradients (Pollak 1997). In this study, I bring together temporally and spatially replicated demography, community, and microclimatic data across the range of this alpine plant to explore how a demographic approach can refine range shift predictions in heterogeneous landscapes. By combining a field experiment manipulating summertime temperature and moisture with population modeling, I incorporated empirically verified responses of demographic rates to changing conditions into model projections of future population dynamics (Gotelli & Ellison 2006; Ehrlen & Morris 2015). Lastly, the responses of my focal species to the manipulations were placed in a community-context by examining the alpine plant community responses to the experimentally warmed conditions.

I performed demographic surveys in sixteen populations spanning the entirety of the focal species elevational range in the White Mountains in the 2014 - 2017 growing seasons. Following over 4,000 individuals across all populations, I quantified all demographic rates over three annual transitions. In each population, I also evaluated fine-scale climate conditions across all study years using temperature data loggers and biweekly soil moisture measurements. In the summers of 2015, 2016, 2017, I implemented a fully-factorial field experiment manipulating summertime temperature and precipitation in a representative subset of nine populations. The demographic, microclimatic, and community responses to these manipulations were quantified to assess how the flora of the White Mountains may respond to changing climate. I used integral projection models to examine the influence of fine-scale microclimatic gradients on range-wide population stability and the influence of climate manipulations on population performance across these microclimatic gradients. Integral projection modeling places size-dependent individual performance in the context of population dynamics, enabling prediction of shifts in species distributions through population expansion and contraction with changes in suitability across the species range (Diez *et al.* 2014; Aikens & Roach 2014; Pironon *et al.* 2017).

First, I found highly variable responses of the demographic rates to the multiple microclimatic gradients across the focal species range. Bringing together all of these responses of the individual demographic rates, I found that population growth rate was consistently stable or slightly increasing across this species entire range. 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 that 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 spatio-temporal variation in multivariate microclimate suggests that populations behave idiosyncratically across a species range and that there may be multiple demographic pathways to population stability (Csergő *et al.* 2017). The climate manipulations allowed me to investigate how changing climate may impact this range-wide population stability. I found a negative effect of experimentally increased summertime temperature on population growth rate in all populations across this species range, and no amelioration of this negative effect with experimentally increased summertime precipitation. The

multiple demographic pathways that led to stability also had unique vulnerabilities to changing climate driving this universal reduction. These unique vulnerabilities were shaped by 1) size-mediated and variable relationships between the climate manipulations and demographic components, 2) changes in the effects of the climate manipulations across climate gradients for each demographic component, and 3) spatial variation in proportional influence of each demographic rate across the species range. The alpine plant community also shows sensitivity to changing climate conditions; under experimentally warmer conditions, I observed increased abundance of the hottest, driest adapted species, an increase in overall abundance, and a decrease in species richness

Understanding spatial variation in demographic rates and its role in governing species range limits is a fundamental question in population ecology (MacArthur 1972; Sutherland *et al.* 2013). 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). My results indicate that care needs to be taken when predicting and quantifying range shifts when there is a decoupling of geography and climate gradients at the scale important for populations dynamics. 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; Pironon *et al.* 2017). These differences in responses of germination, growth, survival to a changing climate also influence community dynamics with growth of warm-adapted species occurring prior to mortality of cool-adapted species (Alexander *et al.* 2017). This work suggests that for long-lived species with ranges in heterogeneous landscapes, we should not assume that presence or abundance is a useful proxy for population performance and vulnerability to a changing climate across species ranges.

CHAPTER 1: MICROCLIMATE AND DEMOGRAPHY INTERACT TO SHAPE STABLE POPULATION DYNAMICS ACROSS THE RANGE OF AN ALPINE PLANT

ABSTRACT
Highly heterogeneous terrain in montane systems results in a decoupling of climatic gradients across the range of alpine plants and these complex relationships between multiple climate variables and demographic rates shape population dynamics across species ranges. Linking demography and climate across species ranges will refine the underlying mechanisms of species current ranges and enhance predictions of range shifts with climate change through population extinction and establishment. I explored the importance of multiple microclimatic gradients in shaping individual demographic rates, as well as population growth rate, across the elevational distribution of an alpine plant (*Ivesia lycopodioides* var. *scandularis*) in the White Mountains, CA USA. I ask how each rate varies across three microclimate gradients: accumulated degree-days, growing season soil moisture, and days of snow-cover using both mixed effects models and integral projection modeling. Variation in all demographic rates was best explained by a combination of multiple microclimatic variables shaped by fine-scale topography. Demographic rates exhibited both complimentary and contrasting responses to the same microclimatic gradient and the relative importance of each microclimate gradient varied, most often through interactions with plant size. These variable relationships resulting in invariant population persistence across this species range, with no relationship between population growth and any of the microclimate variables. The manifold relationships between topography, microclimate and demography suggest that populations across a species range have unique demographic pathways to stable population dynamics.

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 pole-ward 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). Range shifts will occur with local population extinction and establishment as species track suitable climatic conditions and mechanistically linking population dynamics and climate across species ranges will refine range shift predictions (Gaston 2009; Buckley *et al.* 2010b). 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, climate acts on the species range at the scale of the population (Sexton *et al.* 2009; Tredennick, Hooten & Adler 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, Strauss & Rice 2011). In addition, range shift responses are often quantified along geographic gradients such as latitude or elevation which are assumed to be correlated with climate variables: i.e. 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, topo- and micro-climate have been shown to be important for population, species, and community level response to changes in climate (Harrison, Damschen & Grace 2010; Scherrer & Korner 2011; Millar *et al.* 2015; Oldfather *et al.* 2016). The use of climate data at a scale that incorporates topo- and micro-climatic variables relative to coarser climate data can dramatically change predictions of habitat suitability across species ranges (Franklin *et al.* 2013; Potter, Arthur Woods & Pincebourde 2013). Others have shown that demographic rates respond to climatic gradients rather than geographic gradients, *per se* (Villellas, Morris & Garcia 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, Decker & Hastings 2017).

Alpine plants have been identified as harbingers of the biogeographic impacts of a changing climate (Gottfried *et al.* 2012; Lesica & Crone 2016). Due 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; Lenoir *et al.* 2013; Ashcroft & Gollan 2013). These small-scale topographic 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, Ingersoll & Webber 1995), nitrogen cycling (Fisk, Schmidt & Seastedt 1998), local distributions (Bell & Bliss 1979; Scherrer & Korner 2011), species richness (Stanton, Rejmánek & Galen 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 across the species range.

Demographic rates may be sensitive to multiple climate variables that vary across these topographic gradients (Buckley *et al.* 2010a; Ettinger, Ford & Hille Ris Lambers 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.* 2016a). 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, Dalgleish & Ellner 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, Gaines & Gaylord 2006; Gerst, Angert & Venable 2011; Ehrlen & Morris 2015).

In this study, I explored the role of microclimatic gradients in shaping population dynamics across the entire range of an alpine plant species. I 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 snow-pack, and investigated the topographic determinants of these microclimate conditions. With this range-wide demographic analysis, I 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, I 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 gradient. Finally, I 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 complimentary or compensatory, I predict that either population growth will vary across multiple microclimatic gradients, or alternatively, that there will be minimal response of population growth to microclimatic gradients across this alpine plant species range.

MATERIALS & 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 an approximate 20-year lifespan and a basal rosette of pinnate-compound lycopod-like leaves (Pollak 1997). This variety is found in the xeric White Mountains in eastern California. The White Mountain range, located in the rain-shadow of the Sierra Nevada, California has considerably less precipitation, even at high elevations, relative to global alpine areas (Körner 2003; Rundel, Gibson & Sharifi 2005). 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). I surveyed sixteen *I. lycopodioides* populations spanning the entirety of the species elevational range in the White Mountains in the 2014 - 2017 growing seasons (Figure 1). These surveyed populations encompass the highest and lowest elevations of the species range, as well as intermediate elevations, and spanned 3460 m to 4033 m. I defined three *I. lycopodioides'* range positions: lower elevation zone (<3600 m; with five populations), range center zone (3600 – 3900m; with seven populations), and upper elevation zone (>3900m; with four populations). In each population, I established three to ten, 30 x 30 cm plots (N = 81 total) with plots placed at least 2 m apart (Table 1). In every plot, all individual *I. lycopodioides* were marked with a unique combination of within plot coordinates and colored pins for re-identification across seasons. Seedlings that emerged after the initial plot establishment were individually marked annually. Across all populations, I measured a total of 1,809 (2014), 1,937 (2015), 2,525 (2016) and 3,397 (2017) individuals.

For each marked individual, the following measurements were taken between July 10th and July 26th annually: number of rosettes, number of leaves, number of flowering stalks and the length of the longest leaf (Figure 1). For each population, I calculated emergence rate (number of new seedlings at time *t* per plot), individual growth rate (number of leaves at time *t+1* – 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, I 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.* 2016a). Soil temperature measurements were taken every three or four hours throughout the year from September 2014 to August 2017 with iButton Thermochrons in each plot (Maxim, San Jose USA). The ibuttons were put in film canisters and buried just under the surface (2cm) 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 versus 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 12cm in each plot approximately every 2.5 weeks during the 2014-2017 growing seasons (June – September) with a Hydrosense TDR (Campbell Scientific, Logan 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 less than 0.5°C diel variability (Harte and 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.

I 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 10m digital elevation model of the White Mountains (Hijmans, Etten & Mattiuzzi 2015). 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). I 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 (n = 16). I 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, I built generalized mixed effects models 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, I 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 prior to being included in the models. The best model fit was determined using AICc; simpler models with comparable AICc values were selected (Table 2 – Table 5). 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 model was tested using likelihood ratio tests on nested models. All analyses were performed in R 3.3.3 (R Core Team 2017). The models were fit using the lme4 package (Bates *et al.* 2013). The variance explained (pseudo-R^2) by the fixed effects for each model was determined using the MuMin package (Nakagawa & Schielzeth 2013).

Range-wide Population Growth

For each of the sixteen 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 (Easterling, Ellner & Dixon 2000; Ramula, Rees & Buckley 2009; Ellner, Childs & Rees 2016). The probability of survival, reproduction, and growth were determined using generalized mixed effects models parametrized 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 effect of size, site, 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. Establishment probability was determined as seed availability in a population at time t divided by the number of new recruits at time $t+1$. The size estimates for seedling recruits (mean =1.67 leaves, sd = 0.8 leaves) and viable seed production per flowering stalk (15 seeds/stalk) were assumed to be constant across populations and years. The model was integrated over 0.9 times the minimum plant size and 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 3.3.3 (R Core Team 2017) and was based on previously published code for the modeling of perennial plant populations (Merow *et al.* 2014). I calculated 95% confidence intervals for population growth for each population by bootstrapping the data 2,000 times keeping the total number of observation within each population constant.

RESULTS

Microclimatic Conditions

Between 2014 and 2017 I observed large variation in all three microclimatic conditions, decoupling the variables both spatially and temporally (Figure 2). Snowpack was much more persistent in spring 2017 relative to the drought years of 2014 ($F = 16.57$, $p = 0.04/0.02$) 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. The minima and maxima of the microclimatic conditions for each variable occurred in a different population across the elevation gradient each year, and occurred in locations that spanned the entire elevational gradient (Figure 2). Topography shaped the microclimatic conditions in the populations. Accumulated degree-days increased with slope, with warmer sites on steeper slopes (Table 6). Soil moisture increased with northness and decreased with elevation indicating that population at higher elevation, north-facing slopes were wetter throughout the growing season (Table 6). Days of snow cover had no relationships with any of the topographic metrics (Table 6).

Demographic Rate Variation

Average density per population across years ranged from approximately 160 individuals per m^2 to 944 individuals per m^2 (Table 1). Density decreased across the altitudinal gradient (estimate = -0.76, $p = 0.005$, R$^2 = 0.40$,) with denser population at the species lower 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, $p = 0.011$, 1R$^2 = 0.38$). Wetter sites with more persistent

snowpack had denser populations. 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 2). 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 (Figure 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 (Figure 3A). Days of snow-cover was also included in the best fit model, but only had a non-significant linear negative effect on the number of germinating seedlings each season.

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 3). 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 (Figure 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) (Figure 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 (Figure 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 4). 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) (Figure 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) (Figure 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 5). Smaller individuals had much 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) (Figure 3D). In 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 (Figure 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) (Figure 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.

Range-wide Population Growth

Across the sixteen populations, population growth rate (λ) ranged from 0.99 - 1.72, indicating stable or increasing populations across this species entire range. The 95% confidence intervals of six of the population 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 (Figure 4). Further, no significant relationships between population growth and any microclimate conditions were found (Figure 4).

DISCUSSION

Microclimate was an important driver of all demographic rates across the entire elevational range of the long-lived alpine plant *I. lycopodioides*. These relationships led to large variations in observed demographic rates within the same range position (i.e., elevation band). Although all demographic rates were sensitive to microclimatic gradients, the relative importance of the microclimate variables differed among demographic rates. Some demographic rates were influenced by microclimate directly while other rates were only sensitive to microclimatic conditions through interactions with individual size. Each demographic rate also showed dissimilar responses, in both direction and magnitude, to the same microclimatic gradient. Bringing together all of these responses of the individual demographic rates with population modeling, I found that population growth rate was consistently stable or slightly increasing across this species entire range. There was no pattern of population growth across any of the microclimate variables, despite the influence of microclimate on the demographic rates. This latter result suggests compensatory relationships between demographic rates are stabilizing population growth across these gradients. These complex relationships between topography, microclimate and individual demographic rates across a species range have important implications for the quantification and prediction of range shifts across geographic and climatic space with a changing climate.

The distinction between geographic and climatic space across a species range becomes necessary in heterogeneous landscapes where climatic dissimilarity is not parallel to physical distance between populations (Pironon *et al.* 2016). While there were general trends towards cooler, drier conditions at higher elevations, annual measured microclimate variables were not all strongly correlated with the elevational gradient of the species range. Instead, slope and aspect shaped the microclimatic conditions experience by each population. 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, Samis & Eckert 2014; Pironon *et al.* 2015; Chardon *et al.* 2015). Environmental variables may be correlated across elevational gradients for some species ranges, but in the alpine fellfields fine-scale topography creates substantial amount of environmental variation across small spatial extents (Scherrer & Korner 2011). Furthermore, the relationship between topography and microclimate conditions also varied across years, and I 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, populations in the center of this species range were the last to melt out. This results 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 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). I found that all demographic rates responded to multiple microclimatic variables, but with different patterns and magnitudes. Emergence of new seedlings was strongly influenced by soil moisture, but responded weakly to accumulated degree-days and days of snow cover. In contrast, individual growth showed a similar response to all three microclimatic variables. Significant size-by-microclimate interactions were 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), where measuring all demographic rates across a range of individual sizes is necessary for range shift predictions.

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, I did not find similar responses of the demographic rates to the microclimatic gradients. For a single microclimate gradient, the demographic rates had very different responses. Soil moisture had a positive effect on emergence of new recruits, but a negative effect on the number of flowering stalks for larger individuals. New recruitment was highest at intermediate levels of snow cover and degree-day accumulation, however individual growth was lowest at sites with the most accumulated degree-days. Survival across this species range presents an interesting case where wetter sites have less mortality for smaller individuals, but higher mortality for larger individuals. 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 that 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). A mosaic of demographic responses to spatio-temporal variation in multivariate microclimate suggests that populations behave idiosyncratically across a species range (Csergő *et al.* 2017).

The different responses of each demographic rate to the microclimatic gradients resulted in inverse relationships among demographic rates that loosely follow life-history trade-offs between different life stages (Salguero-Gómez *et al.* 2016). For example, both new seedling emergence and survival was highest at intermediate accumulated degree-days, but emergence and large individual survival had inverse relationships across the soil moisture gradient. The individual demographic rates coalesce to form the overall population growth, which will not only be shaped by the microclimate gradients, but also by the proportional influence of each demographic rate on the population growth rate (Mclean *et al.* 2016). The inverse responses of some demographic rates 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, I found there was very little variation in population growth rates across the microclimatic gradients. Neither climatic nor geographic edge populations had 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 corroborates 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 climate and population dynamics spanning the entire elevational range and climatic gradients of a species distribution using field-measured microclimatic data.

Conclusions

Understanding spatial variation in demographic rates and its role in governing species range limits is a fundamental question in population ecology (MacArthur 1972; Sutherland *et al.* 2013). 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). These results indicate that care needs to be taken when predicting and quantifying range shifts when there is a decoupling of geography and climate gradients at the scale important for populations dynamics. Due to variation in response of demographic rates to different microclimatic conditions capturing the relationships between climate and multiple life-history stages is critical 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 continued compensatory relationships to buffer population growth. Buffered population response may lead to reduce range shifts as long as combined climatic conditions stay within the range currently experienced across this species distribution. Although collecting demographic data requires considerable effort, a focus on this individual-level response across environmental gradients is critical to our understanding of the biogeographic responses to climate change (Schurr *et al.* 2012; Coutts *et al.* 2016).

TABLES AND FIGURES

Table 1. Site characteristics for each of the sixteen populations. Elevation, number of individuals (indvs) tracked and population density averaged across plots and across years (2014 - 2017). The populations are ordered by elevation (ascending).

Range Position	Elevation (m)	Number of Plots	Number of Indvs Tracked	Density (per m^2)
Lower Edge	3468	3	144	500
Lower Edge	3494	4	306	539
Lower Edge	3539	10	858	508
Lower Edge	3562	2	278	944
Lower Edge	3573	2	156	681
Center	3660	3	99	331
Center	3735	4	107	238
Center	3757	10	186	186
Center	3789	4	122	236
Center	3815	4	94	189
Center	3816	10	304	220
Center	3840	3	80	295
Upper Edge	3974	10	72	160
Upper Edge	4000	4	378	368
Upper Edge	4005	4	84	206
Upper Edge	4028	4	129	301

Table 2. Model structures for all models fits for the emergence rate with corresponding AICc value. All models include random intercept of year and site (not shown). ΔAICc represent difference between model and most supported model (bolded).

Model Structure	AIC_c	ΔAIC_c
Y ~ vwc + degree days + snow days + vwc^2 + degree days^2 + snow days^2	814	3
Y ~ vwc + degree days + snow days + vwc^2 + degree days^2	814	3
Y ~ vwc + degree days + snow days + vwc^2	818	7
Y ~ vwc + degree days + snow days + degree days^2	813	2
Y ~ vwc + degree days + degree days^2	816	5
Y ~ vwc + snow days + degree days^2	811	0
Y ~ vwc + degree days^2	814	3
Y ~ snow days + degree days^2	843	32
Y ~ vwc + snow days	888	77
Y ~ vwc + snow days + vwc^2 + degree days^2	812	1
Y ~ vwc + snow days + vwc^2 + degree days^2 + snow days^2	812	1

Table 3. Model structures for all models fits for the growth/regression rate with corresponding AICc value. All models include random intercept of year, site, and plot (not shown). ΔAICc represent difference between model and most supported model (bolded).

Model Structure	AICc	ΔAICc
Y ~ size + vwc + degree days + snow days + vwc^2 + degree days^2 + snow days^2 + size:vwc + size:degree days + size:snow days	12287	3
Y ~ size + vwc + degree days + snow days + vwc^2 + degree days^2 + snow days^2 + size:vwc + size:degree days	12300	16
Y ~ size + vwc + degree days + snow days + vwc^2 + degree days^2 + snow days^2 + size:vwc + size:snow days	12285	1
Y ~ size + vwc + degree days + snow days + vwc^2 + degree days^2 + snow days^2 + size:snow days	12327	43
Y ~ size + vwc + degree days + snow days + vwc^2 + degree days^2 + size:vwc + size:snow days	12284	0
Y ~ size + vwc + degree days + snow days + vwc^2 + size:vwc + size:snow days	12290	6
Y ~ size + vwc + degree days + snow days + degree days^2 + size:vwc + size:snow days	12286	2
Y ~ size + vwc + degree days + vwc^2 + degree days^2 + size:vwc + size:snow days	12289	5
Y ~ size + vwc + snow days + vwc^2 + degree days^2 + size:vwc + size:snow days	12290	6
Y ~ size + degree days + snow days + vwc^2 + degree days^2 + size:vwc + size:snow days	12284	0
Y ~ degree days + snow days + vwc^2 + degree days^2 + size:vwc + size:snow days	12297	13
Y ~ size + snow days + vwc^2 + degree days^2 + size:vwc + size:snow days	12294	10
Y ~ size + degree days + vwc^2 + degree days^2 + size:vwc + size:snow days	12288	4
Y ~ size + degree days + snow days + degree days^2 + size:vwc + size:snow days	12284	0
Y ~ size + degree days + snow days + size:vwc + size:snow days	12292	8
Y ~ size + degree days + snow days + degree days^2 + size:snow days	12329	45
Y ~ size + degree days + snow days + degree days^2 + size:vwc	12295	14

Table 4. Model structures for all models fits for the reproduction rate with corresponding AICc value. All models include random intercept of year, site, and plot (not shown). ΔAICc represent difference between model and most supported model (bolded).

Model Structure	AICc	ΔAICc
Y ~ size + vwc + degree days + snow days + vwc^2 + degree days^2 + snow days^2 + size:vwc + size:degree days + size:snow days	10507	6
Y ~ size + vwc + degree days + snow days + vwc^2 + degree days^2 + snow days^2 + size:vwc + size:degree days	10511	10
Y ~ size + vwc + degree days + snow days + vwc^2 + degree days^2 + snow days^2 + size:vwc + size:snow days	10517	16
Y ~ size + vwc + degree days + snow days + vwc^2 + degree days^2 + snow days^2 + size:degree days + size:snow days	10522	21
Y ~ size + vwc + degree days + snow days + vwc^2 + degree days^2 + size:vwc + size:degree days + size:snow days	10506	5
Y ~ size + vwc + degree days + snow days + vwc^2 + size:vwc + size:degree days + size:snow days	10505	4
Y ~ size + vwc + degree days + snow days + size:vwc + size:degree days + size:snow days	10509	8
Y ~ size + vwc + degree days + vwc^2 + size:vwc + size:degree days + size:snow days	10503	2
Y ~ size + vwc + vwc^2 + size:vwc + size:degree days + size:snow days	10501	0
Y ~ vwc + vwc^2 + size:vwc + size:degree days + size:snow days	11854	1344
Y ~ size + vwc^2 + size:vwc + size:degree days + size:snow days	10503	2
Y ~ size + vwc + size:vwc + size:degree days + size:snow days	10506	5
Y ~ size + vwc + vwc^2 + size:degree days + size:snow days	10516	15
Y ~ size + vwc + vwc^2 + size:vwc + size:snow days	12050	1549
Y ~ size + vwc + vwc^2 + size:vwc + size:degree days	10789	288

Table 5. Model structures for all models fits for the survival rate with corresponding AICc value. All models include random intercept of year, site, and plot (not shown). ΔAICc represent difference between model and most supported model (bolded).

Model Structure	AICc	ΔAICc
Y ~ size + vwc + degree days + snow days + vwc^2 + degree days^2 + snow days^2 + size:vwc + size:degree days + size:snow days	1030	2
Y ~ size + vwc + degree days + snow days + vwc^2 + degree days^2 + snow days^2 + size:vwc + size:degree days	1037	9
Y ~ size + vwc + degree days + snow days + vwc^2 + degree days^2 + snow days^2 + size:vwc + size:snow days	1030	2
Y ~ size + vwc + degree days + snow days + vwc^2 + degree days^2 + snow days^2 + size:snow days	1059	31
Y ~ size + vwc + degree days + snow days + vwc^2 + degree days^2 + size:vwc + size:snow days	1032	4
Y ~ size + vwc + degree days + snow days + vwc^2 + size:vwc + size:snow days	1034	6
Y ~ size + vwc + degree days + snow days + degree days^2 + size:vwc + size:snow days	1030	2
Y ~ size + vwc + degree days + degree days^2 + size:vwc + size:snow days	1039	11
Y ~ size + vwc + snow days + degree days^2 + size:vwc + size:snow days	1028	0
Y ~ size + snow days + degree days^2 + size:vwc + size:snow days	1032	4
Y ~ vwc + snow days + degree days^2 + size:vwc + size:snow days	1327	1
Y ~ size + vwc + snow days + degree days^2 + size:vwc	1035	8
Y ~ size + vwc + snow days + degree days^2 + size:snow days	1059	31
Y ~ size + vwc + snow days + size:vwc + size:snow days	1736	708

Table 6. Estimates and significance from a multiple regression analysis of the relationship between microclimatic variables and topography. Topographic metrics were scaled and centered before use in the models. Stars indicate level of significance.

	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
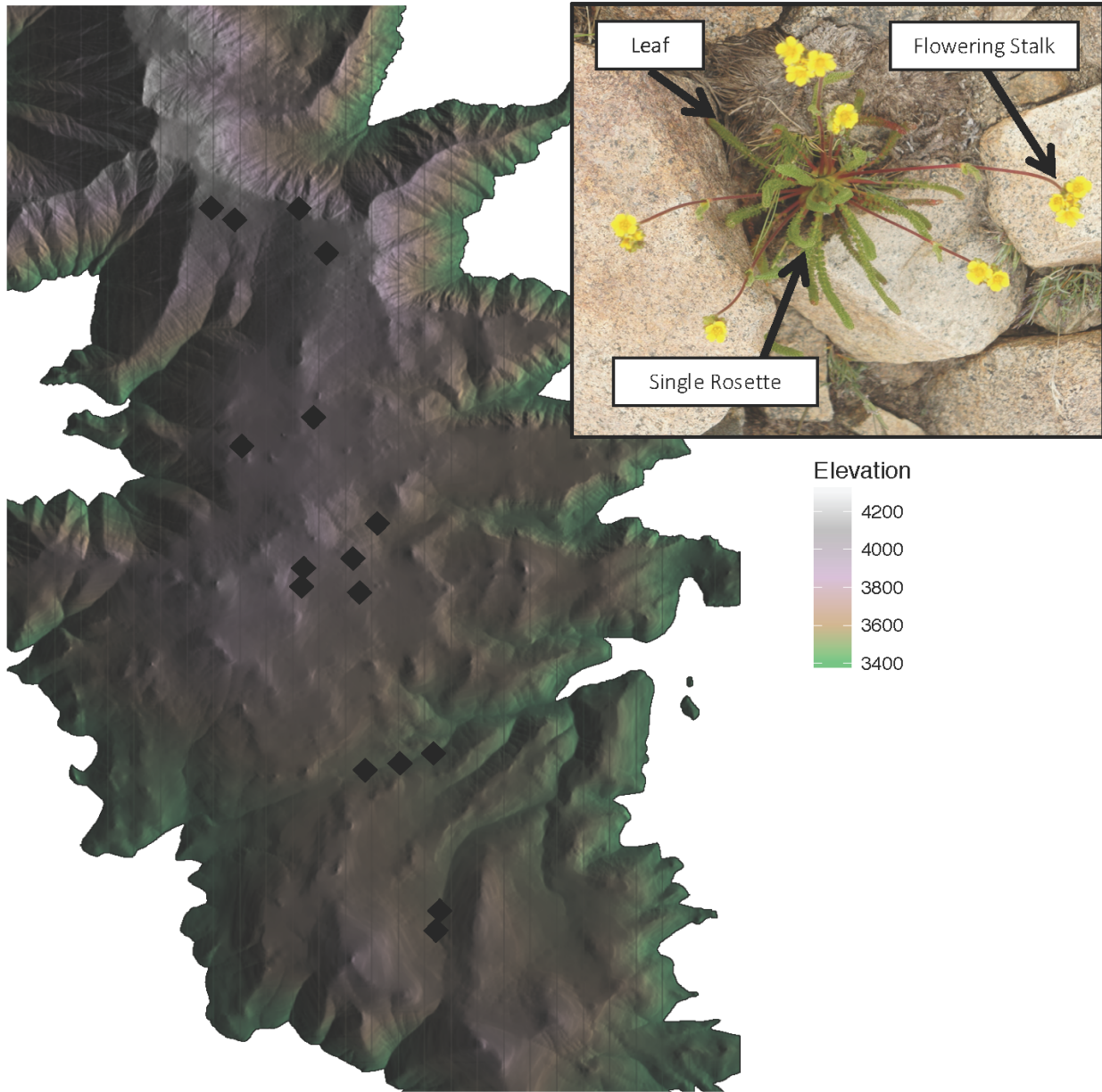
Figure 1. Map of 16 surveyed population (black diamonds) across the elevational range of *I.lycopodioides* (3460 m to 4033m*)* in the White Mountains, CA USA and image of *I.lyocopdioides* individual flowering with measurements of demographic survey labeled.
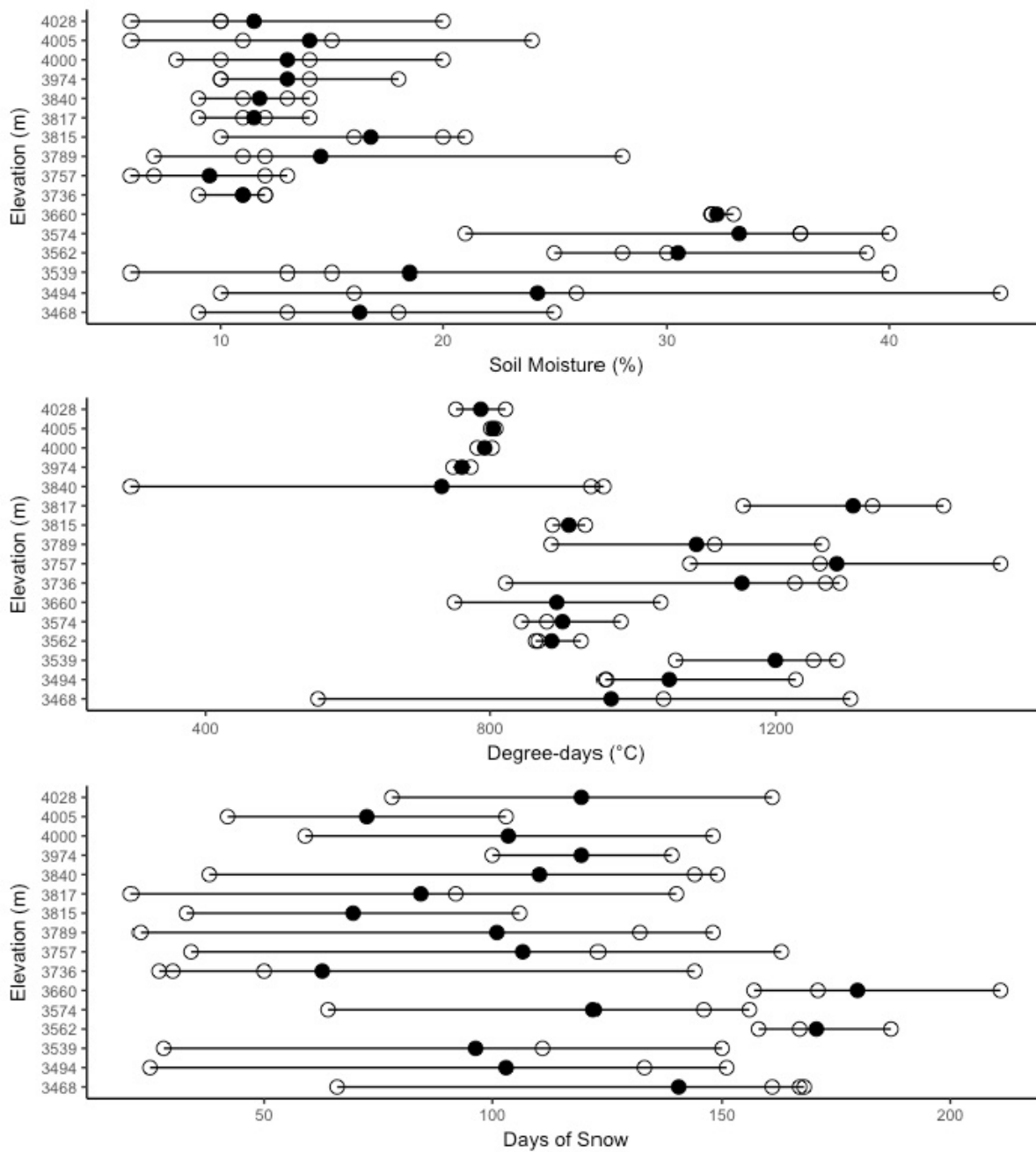
Figure 2. Variation in soil moisture and accumulation of degree-days for the 2014 – 2017 summer growing seasons (top, center) across the elevation gradient. Variation in the days of snow cover for 2015, 2016, and 2017 winters across the elevation gradient (bottom). Both site means for each year (open circles) and site mean across all years (filled circles) shown.
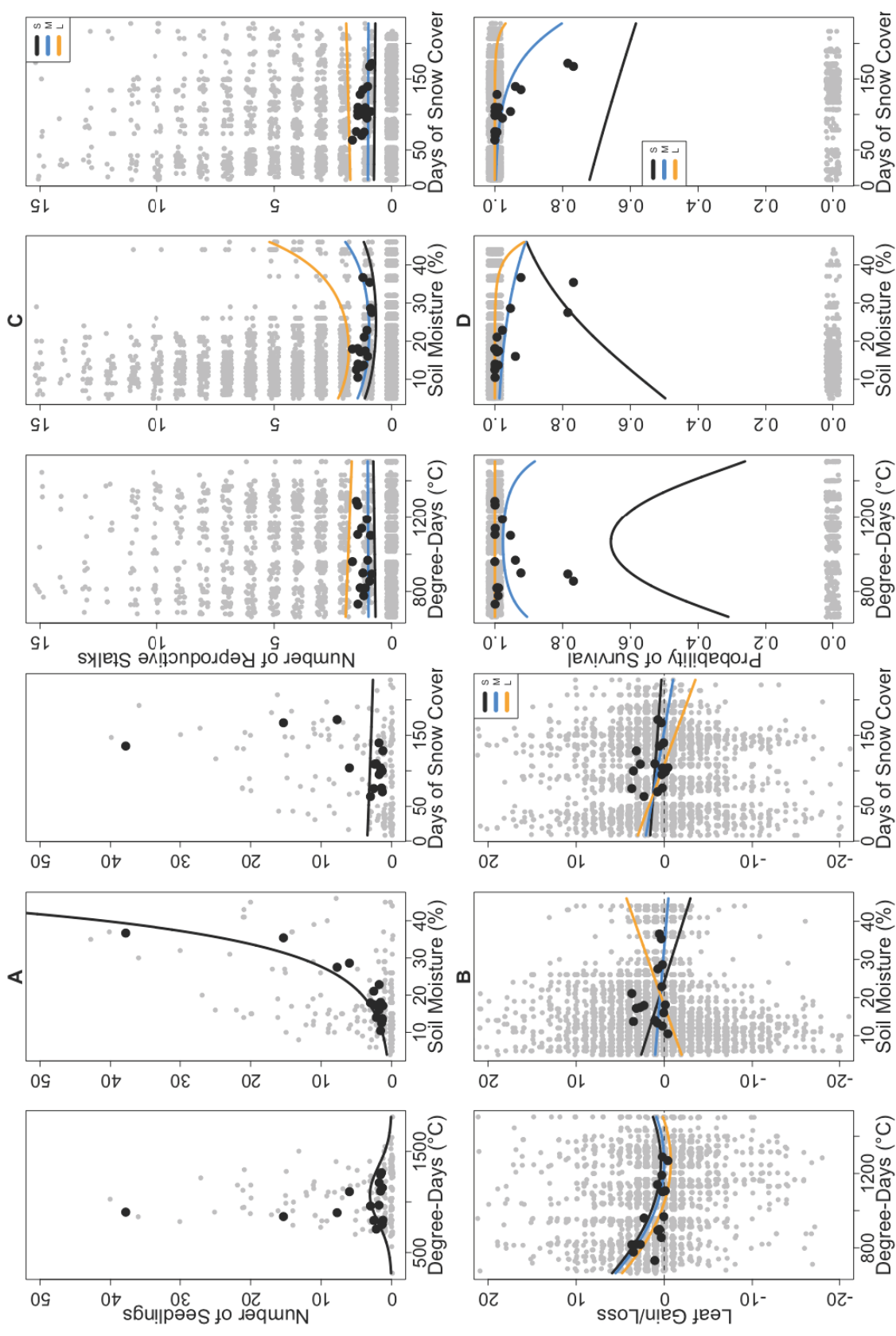
Figure 3. A) Numbers of seedlings B) Individual gain or loss of leaves between seasons C) Number of flowering stalks D) Probability of survival (Alive=1, Dead=0) across all populations and years shown as gray points for the three microclimate variables of interest. Solid Lines represent marginal effect 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 colors, when applicable, represent different quantiles of size (leaf number) with $S = 10^{th}$ percentile size class, $M = 50^{th}$ percentile size class, and $L =$ the 90th percentile size class. Black points show the average demographic rate for each population for an average-sized individual in that population.
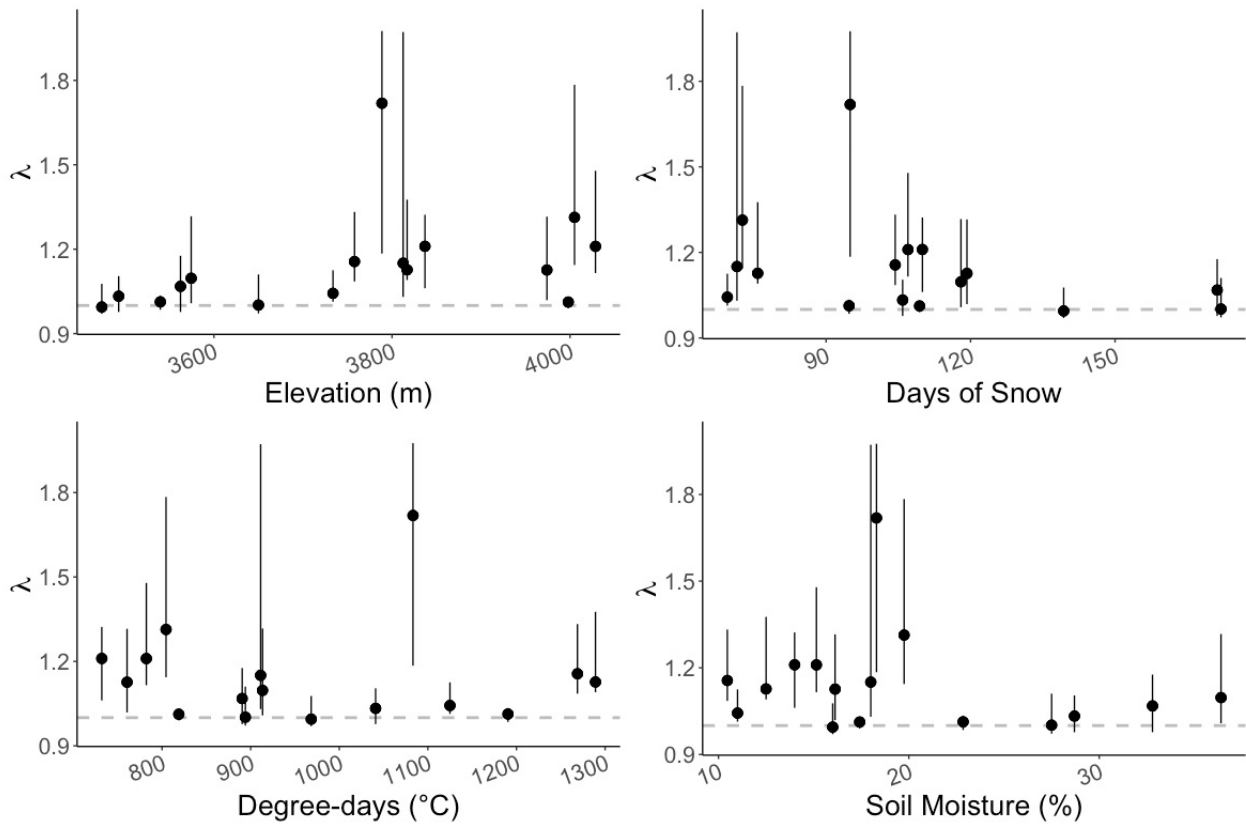
Figure 4. Population growth rate (shown with 95% confidence intervals) of all 16 populations regressed against elevation and all measured microclimate variables show no significant relationships. Dashed line indicates where population growth rate is stable ($\lambda = 1$).

CHAPTER 2: EXPERIMENTAL HEATING DECREASES POPULATION GROWTH ACROSS AN ALPINE PLANT'S GEOGRAPHIC RANGE

ABSTRACT

Expectations of expansions at leading range edges and contractions at trailing range edges with climate change have been complicated in part by the importance of multiple climate variables and the potential for diverse responses of different life stages to changing climatic conditions. I test the robustness of the leading-trailing hypotheses for range shift predictions by experimentally manipulating climate and measuring population growth responses in multiple populations across an alpine plants species range. Our approach brings together 1) range-wide spatial replication of demography and microclimate measurements, 2) experimental climate manipulations of summertime temperature and precipitation, and 3) quantification of population growth responses to climate manipulations using integral projection modeling. This approach allows attribution of range shift predictions through population contraction and expansion to changes in climatic conditions. The effect of experimental manipulation on individual demographic components was partially consistent with our predictions that heating would have a negative effect and watering would have a positive effect on populations in hotter, drier, and more exposed sites. However, these responses did not result in changes in population growth rates that would predict range expansion at the cool, wet leading range edge and a contraction at the hot, dry trailing range edge. I instead observed a de-coupling of the temperature and soil moisture gradients and a negative effect of heating on population growth rate for all populations across this species range. These impacts lead to predictions of population contractions at mid elevations of the species range and I proposed that this unexpected result is due to size-mediated and variable relationships between the manipulations and demographic rates, different effects of climate manipulation effects across climatic gradients, and spatial variation in the proportional influence of each demographic rate across the species range.

INTRODUCTION

Shifts in species distributions are expected to be the largest biological effect of climate change (Pecl *et al.* 2017). Predicting these shifts requires a comprehensive understanding of the mechanisms that influence species current ranges, an elusive goal in and of itself for most, if not all, species (Gaston 2009; Sexton *et al.* 2009; Schurr *et al.* 2012). If a species range represents its climatic niche, we would predict expansions at the cool range edge (leading edge) and contractions at the hot range edge (trailing edge) with climate change (Hargreaves *et al.* 2014; Lee-Yaw *et al.* 2016). However, cross-taxon observed range shifts in response to climate change have been highly variable and even counterintuitive (Tingley *et al.* 2009; Chen *et al.* 2011; Crimmins *et al.* 2011; Lenoir & Svenning 2014). Straightforward expectations of polar or upslope distributional shifts of plants in response to warmer, drier conditions have been complicated in part by the importance of multiple climate variables (*e.g.* temperature, precipitation, snowpack), the interactive effects of these variables on species physiology and demography, and the potential for diverse responses of different life stages to changing climatic conditions (Doak & Morris 2010; Rapacciuolo *et al.* 2014; Alexander *et al.* 2017; Sheth & Angert 2018). Therefore, understanding the abiotic requirements for each demographic rate, and how these rates coalesce to shape population persistence across species entire ranges may be crucial for predicting the biogeographic effects of climate change (Normand *et al.* 2014; Coutts *et al.* 2016). I test the robustness of the leading-trailing hypotheses for range shift predictions by experimentally manipulating climate and measuring the response in population growth across a species range.

A demographic approach may clarify when predictions of upslope, polar shifts with climate change are likely, and allow exploration of the mechanisms driving unexpected shifts (Schurr *et al.* 2012; Normand *et al.* 2014). Process-based as opposed to correlative-based species distribution models mechanistically link population dynamics with climate, refining predictions of range shifts through population expansion and contraction dynamics (Buckley *et al.* 2010b; Evans *et al.* 2016; Fordham *et al.* 2018). Population response to a change in climate will be shaped by the following parameters: 1) exposure, the extent of change in climate in the local area, 2) environmental sensitivity, the magnitude of fluctuations in demographic rates driven by climate, and 3) elasticity, each demographic rates' proportional influence on the overall population growth. For a change in climate to drive a range shift, the amount of change in climate a population experiences (exposure) must have an effect on a demographic rate(s) (environmental sensitivity) that ultimately has a large enough effect on the population growth rate (demographic elasticity) to change the population trajectory (Normand *et al.* 2014; Mclean *et al.* 2016). Hierarchical demographic transition models can incorporate these components as comparative metrics for populations across a species range (Figure 1).

It is well established that demographic rates (*e.g.* germination, growth, reproduction, survival) are influenced by spatial and temporal climate variation in different ways (Dalgleish *et al.* 2011; Diez *et al.* 2014; Dahlgren, Bengtsson & Ehrlen 2016) and that the limiting climate driver(s) of each demographic rate may shift across the species range (Morris & Doak 2002; Villellas *et al.* 2015; Compagnoni *et al.* 2016; McCullough *et al.* 2016). In addition, these relationships between climate and demographic rates can be mediated by size (Ettinger & Hille Ris Lambers 2013; Máliš *et al.* 2016). For many long-lived species, different life-stages may be differentially responsive to climate variables, as well as to the variation in those climate variables across their geographic distributions (Ettinger & Hille Ris Lambers 2013; Máliš *et al.* 2016). It is

often considered that younger or smaller individuals will be more sensitive to climate variation; the "regeneration niche" of a species is more limited than the adult species niche (Grubb 1977). Further, the spatial variation in the influence of each size-dependent demographic rate on population growth across a species range has the potential to drive a large variety of range shift patterns (Svenning & Sandel 2013; Lenoir & Svenning 2014; Sheth & Angert 2018). These life-stage or size-dependent responses have been shown to be an important factor for population stability, and therefore species range stability, in response to past and current climate change (Jackson *et al.* 2009; Serra-Diaz *et al.* 2016).

Integral projection modeling specifically places size-dependent individual performance in the context of population dynamics, enabling prediction of shifts in species distributions with changes in suitability across the species range (Diez *et al.* 2014; Aikens & Roach 2014; Pironon *et al.* 2017). However, these population models still assume stationary mean demographic rates, limiting these powerful tools if mean environmental conditions change through time (Ezard *et al.* 2010; Crone *et al.* 2013). This fundamental limitation points to a need for integrating experimental manipulations and population modeling for populations across a species range to mechanistically project future range-wide population dynamics (Gotelli & Ellison 2006; Buckley *et al.* 2010b). Experiments allow the elucidation of mechanisms, and have been crucial in detecting and attributing plant responses to climate change (Franklin *et al.* 2016). Many studies have experimentally modified the temperature and moisture availability and seen responses in plant physiology, components of the species life-history, and community processes (Zhuoting *et al.* 2011; Winkler *et al.* 2016a; Kueppers *et al.* 2017). However, few studies have examined responses to experimentally manipulated conditions across a species entire range (Buizer *et al.* 2012), and no study to our knowledge has looked at responses of all demographic rates to climate manipulations in unison across a species entire range. Combining both an experimental and population modeling approach draws from the strengths of both approaches. Quantifying the effect of climate manipulations of all demographic rates in multiple populations allows for incorporation of empirically verified responses of demographic rates into model projections of future population dynamics (Gotelli & Ellison 2006; Ehrlen & Morris 2015).

For the focal species, I found that heterogeneous microclimate gradients drove variation in demographic rates across this species range, but that complementary and compensatory relationships between demographic rates across these complex climate gradients lead to stable range-wide populations growth (Chapter 1). This work motivated a range-wide experiment investigating the degree to which climate manipulations may perturb this system. By experimentally manipulating climate and measuring the demographic response, we gain a more mechanistic understanding of how the interaction between demographic elasticity, environmental sensitivity, and local exposure shape a population's overall growth rate in both ambient and modified conditions (Gotelli & Ellison 2006; Ehrlen *et al.* 2016).

With this analysis, I examine the effects of warmer or wetter conditions on all demographic components and population growth rate within each population asking:

1. How do the responses of each demographic component to the experimental manipulations coalesce to shape the overall population growth rate response across a species range?

2. What predictions can be made about potential future range shifts with a changing climate?

With the assumption that altitudinal range limits correspond to climatic niche limits (Lee-Yaw *et al.* 2016), I hypothesize that experimental heating will have a negative effect on both demographic components and overall population growth rate at the hotter, drier populations (low elevation edge), and a positive effect at the cooler, wetter sites (upper elevation edge). I also hypothesize that experimental increases in precipitation will ameliorate the negative impacts of heating in driest populations, and exaggerate the positive effects of heating in the wettest populations. These overall responses would result in a range expansion at the cool, wet edge of the species range and a contraction at the hot, dry edge.

METHODS

Study System

Our focal species, *Ivesia lycopodioides* A. Gray var. *scandularis* (Rydb.) Ertter & Reveal (hereafter *I. lycopodioides*; Rosaceae) is a long-lived alpine plant (approximate 20-year lifespan) with a basal rosette of lycopod-like leaves found in the xeric White Mountains of eastern California. The White Mountain range, located in the rain-shadow of the Sierra Nevada, is drier relative to global alpine areas with significantly less winter precipitation than the nearby Sierras Nevada (Körner 2003). Populations of *I. lycopodioides* are found at elevations from 3444 – 4115m on granitic soils and are associated with areas of higher soil moisture in the White Mountains (Ertter 1989; Pollak 1997). This species is an excellent candidate for studying the effect of population dynamics on overall range stability with a changing climate. Individuals are easily delimited as genetic and physiological units without destructive sampling, dense populations allow replication of experimental treatments within a small area, and the species exhibits sensitivity to both temperature and moisture availability (Pollak 1997). In the last two decades temperature has increased and precipitation has decreased in the White Mountains (Kopp & Cleland 2014), and a previous study suggests that this species could lose 98% of its range with a 3°C increase in temperature (Van de Ven, Weiss & Ernst 2007).

From 2014 - 2017 I performed demographic surveys in nine populations of *I. lycopodioides* that span the entirety of its altitudinal range in the White Mountains, CA (Figure 2). In each of these populations, 8-10 30x30cm plots were established in 2014 with all present individuals marked with unique pins and coordinate combinations. Within each plot the following metrics were recorded for each individual annually: number of rosettes, leaves, stalks, inflorescences, and length of the longest leaf. Newly recruited individuals that were recorded in 2015, 2016, or 2017 were also individually marked. Following over 4,000 individuals across all populations, I have quantified germination (number of new seedlings at time t per plot), survival (dead or alive at time $t +1$), growth (number of leaves at time $t+1$ – number of leaves at time t), and flowering probability (flowering at time t) and number of flowering stalks (at time t) over three annual transitions.

In each plot, fine-scale climate conditions were also evaluated across all transition years. Soil moisture was recorded biweekly during the growing season (June – September) with a Hydrosense TDR (Campbell Scientific, Logan USA). Mean soil moisture was calculated as the average across the entire growing season for each plot. Temperature measurements were recorded every 3-4 hours throughout the year with iButton Thermochrons (Maxim, San Jose USA) buried 2cm below the soil surface. 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 also indicates the duration of snow cover, as the insulating effect of snow creates a distinctive thermal signature in winter. Days of snow

cover was calculated for each plot as the number of days between October and June with less than 0.5°C diel variability (Harte and Shaw 1995).

Experimental Manipulations

In the summers of 2015, 2016 and 2017, 8 plots in each of the populations were randomly assigned to one of four treatments in a replicated, full-factorial design: 1) increased summertime temperature 2) increased summer precipitation, 3) both increased summer precipitation and temperature, or 4) ambient conditions (Figure 2). Summertime temperature was increased with passive warming chambers placed on the plots each summer immediately after snow melt-out (Figure 2). The chambers were hexagonal and constructed of double-walled poly-carbonate with a height of 30.5 cm and a width of 60 cm at the widest point. The passive warming chambers were designed to increase the mean daily temperature by 1.5°C and this effect was driven primarily by slower cooling in nighttime temperatures (*personal observation*). Summer precipitation was manipulated with the addition of 1 liter of water per plot in each of 5 "storm" events spaced evenly through summer growing season (approximately every 2 weeks), resulting in approximate 55% increase in summer precipitation (Kopp & Cleland 2014). The water was added with a back-pack sprayer and the watering order was randomized by population for each event. Both climate variables were manipulated simultaneously as interactions between temperature and soil moisture may be more important for montane systems in western North America due to the cold, dry conditions at high elevations (Rundel *et al.* 2005; Winkler *et al.* 2016a). Within each population, I quantified the shifts in climate conditions and demographic components in manipulated plots relative to ambient plot for all annual transitions.

Demographic Responses to Manipulations

The effect of the manipulations on all demographic components was assessed for all populations across the species ranges and for interactions between the manipulations and geographic gradient (elevation) or climatic gradients (accumulated degree-days, soil moisture, number of snow-covered days). I built generalized mixed effects models for the following demographic components: germination (Poisson error structure), individual growth (Gaussian error structure), probability of flowering (Binomial error structure), number of flowering stalks (Poisson error structure), and probability of survival (Binomial error structure). To look for range-wide effects of climate manipulations, models for all demographic components except germination included the fixed effects of year (*t*), individual size (number of leaves at time *t*), experimental heating, experimental watering, and the interactions between size, heating and watering. These models also included random intercepts of site, plot, and individual id. The model for germination had a similar structure except it did not include a size parameter or random intercepts of *plot* and *id* as it is count data taken at the level of *plot*. In order to explore differences in the effect of the manipulations across the species range, I built separate models for each demographic component with the same structure as above, and also included elevation, accumulated degree-days, mean soil moisture, or days of snow cover, as well as an interaction between size, the experimental manipulations, and each geographic and climatic gradient. These gradient parameters were population averages taken across all years for only ambient plots. Significance of each parameter from all models was estimated with Type II Wald χ^2 tests. All mixed-effects modeling was performed in R 3.4.3 with lme4 (Bates *et al.* 2013; R Core Team 2017).

Population Growth Response to Manipulations

I built Integral Projection Models (IPM) to examine the overall population response from the individualistic responses of each demographic component to the climatic manipulation in each population. An IPM is a generalization of the matrix projection model allowing for a continuous stage-structure, and facilitating the incorporation of other parameters, such as experimental status, into models of population dynamics (Easterling *et al.* 2000; Ramula *et al.* 2009; Merow *et al.* 2016). For each of the nine populations, an IPM was parameterized with hierarchical regressions to determine population growth rates under four treatments (ambient, heated, watered, heated and watered); a total of 36 IPMs were produced.

These IPMs were parametrized with regressions based on data from all years, populations and treatments. Generalized mixed-effects models were built for probability of survival (Binomial error structure), growth (Gaussian error structure), probability of flowering (Binomial error structure), and number of flowering stalks (Poisson error structure). These models all included 1) fixed effects of year, size, heating, watering and the interaction between the latter three parameters, 2) random intercepts of population, plot, and individual id, and 3) a random slope of heating by watering for each population. Treatment status was determined as a Bernoulli vector of heating and a Bernoulli vector of watering. The effects of population, size, treatment, and size by treatment interactions were extracted from each of these regressions to estimate probabilities used in the IPM kernel estimates of growth and survival for all populations in all experimental states (Table 1). Establishment probability was determined as seed availability in a plot within a population at time *t* divided by the number of new recruits in a plot at time *t+1*, and then averaged to get a single establishment probability for each treatment in each population (Table 2). The size estimates for seedling recruits (mean = 1.7, sd = 0.8) and viable seed production per flowering stalk (5 seeds/stalk) were assumed to be constant across populations and years.

The models were integrated over 0.9 times the minimum plant size and 1.1 times the maximum plant size of each population in order to take into account realistic plant sizes not observed, and 100 mesh points were used (Easterling *et al.* 2000; Ellner *et al.* 2016). All population modeling was performed in R 3.4.3 (R Core Team 2018) and was based on previously published code for the modeling of perennial plant populations (Merow *et al.* 2014). Population growth was calculated as the dominant eigenvalue of the kernel (matrix representing all possible size transitions including births and deaths) (Caswell 2001). I calculated bias-corrected 95% confidence intervals for population growth for each treatment status in each population by bootstrapping the data 1,000 times keeping the total number of observation within each population, treatment combination constant and excluding the random effects of individual and plot in the IPM's regressions (Caswell 2001). Mixed effects models were used to assess the effect of the manipulations on overall population growth rates both across all sites and in interaction with the geographic or climatic gradients (based on ambient conditions). Population growth was regressed against the fixed effects of the gradient, heating, watering, and their three-way interaction, as well as a random intercept of population. Significance of each parameter was estimated with Type II Wald χ^2 tests and differences between treatment groups was determined by contrast tests with Tukey adjustments to account for multiple comparisons.

Elasticity Analysis Across Sites and Treatments

I performed an elasticity analysis in order to estimate the proportional effect of the demographic rates on population growth rate across this species range (Benton & Grant 1999;

Caswell 2001). The elasticity of a demographic rate gives a sense of the importance of that transition for overall population dynamics with higher values indicating larger influence on the population growth rate. This prospective perturbation analysis was done at the level of the IPM additive sub-kernels of survival-growth ($P(z',z)$) and reproduction (encompassing flowering probability, number of flowering stalks, and germination) ($F(z',z)$) in order to separate the elasticity values for the major groups of demographic rates (Griffith 2017). Each matrix element in the sub-kernels were perturbed by 0.001. The sub-kernel elasticities were then summed to compare the proportional influence of survival-growth and reproduction in all populations. Elasticity values were calculated for each population in non-manipulated conditions

RESULTS

Range-wide Climate Conditions

      Across the elevational gradient of *I. lycopodioides* range, accumulated degree-days were the highest and most variable in the mid elevation populations and the lowest and least variable at populations at the upper elevational edge (Figure 3). Soil moisture and the number of snow-covered days both decreased with elevation, but were also highly variables across years (Figure 3).

Experimental Manipulations

      The passive heating chambers had positive effect of 0.8°C on daily minimum temperature ($\chi^2 = 54.78$, df = 1, p < 0.001) approximately mimicking the change observed in temperature over the last half century in the White Mountains (Kopp & Cleland 2014). This effect led to an increase in the accumulated degree-days during the summer growing season by 53°C/days (5% increase of the mean accumulated degree-days under ambient conditions) on average across all populations and years ($\chi^2 = 11.006$, df = 1, p = 0.009). The heating treatment was also consistent across all populations and years, with no population by treatment interaction indicating evidence of a larger or smaller treatment effect in different populations along the geographic and climatic gradients ($\chi^2 = 141$, df = 1, p = 0.905). Heating did not have a measurable drying effect on soil moisture ($\chi^2 = 328$, df = 1, p 0.214) and there was also no measurable effect of the watering treatment on the soil moisture in any of the populations across any of the years ($\chi^2 = 141$, df = 1, p = 0.792). Although I did not see an effect on the climatic conditions, I do see responses in the demographic components to the watering treatment (see *Demographic Responses to Manipulations*). This lack of an abiotic effect was not surprising because soil moisture measurements were usually taken 1-2 days after the experimental watering and granitic soils have low water-holding capacity (Wenk & Dawson 2007); the climatic effect of the watering treatment was only evident in 1-2 hours after the treatment was applied (*personal observation*). Neither of the manipulations affected the number of snow-days observed for each population across years as the treatments were performed after snow melt each year.

Demographic Responses to Manipulations

      All demographic components varied in response to the experimental manipulations in at least some of the populations across the geographic or climatic gradients of the species range. However, the effect of the manipulations on the demographic components were predominantly through interactions with individual size. Individual size had a significant positive effect on survival ($\beta_{size} = 2.901$, p < 0.001), probability of flowering ($\beta_{size} = 2.319$, p < 0.001), the number

of flowering stalks (β_{size} = 0.304, p < 0.001) and negative effect on growth (β_{size} = -0.421, p<0.001). This size-dependency of the demographic components supports building a size-structured population model, and requires considering how the climate manipulations influence demography both in interaction with the population conditions (geographic and climatic) and the size structure of the population.

There was no consistent effect of the experimental heating and watering on survival across all populations in this species range (χ^2_{heat} = 2.907, df = 1, p = 0.088; χ^2_{water} = 0.007, df = 1, p = 0.931; $\chi^2_{heat*water}$ = 0.0528, df = 1, p = 0.818). Survival also did not vary predictably across the gradients of elevation ($\chi^2_{elevation}$ = 2.745, df = 1, p = 0.097), accumulated degree-days ($\chi^2_{degree.days}$ = 0.058, df = 1, p = 0.809) mean number of snow-covered days (χ^2_{snow} = 1.868, df = 1, p = 0.171). However, for each these gradients there were significant three-way interaction between individual size, the gradient and the watering treatment. Watering had a larger negative effect on smaller individuals at higher elevation, cooler populations ($\beta_{size*elevation*water}$ = 1.014, p = 0.040; $\beta_{size*degree.days*water}$ = -1.032, p = 0.003) and watering had a larger positive effect on large individuals in snowier sites (β_{snow} = 0.905, p = 0.022). Survival increased with soil moisture ($\beta_{soil.moisture}$ = 0.660, p < 0.001) and the effect of heating varied across this gradient. Heating had a less negative effect on survival in wetter sites ($\beta_{soil.moisture * heat}$ = 0.833, p = 0.001), and this effect was exaggerated for larger individuals ($\beta_{soil.moisture * heat *size}$ = 0.905, p = 0.022), leading to the highest mortality for small individuals under experimental heating in dry sites (Figure 4).

There was also no consistent effect of the experimental heating and watering on individual growth across all populations (χ^2_{heat} = 0.002, df = 1, p = 0.962; χ^2_{water} = 0.027, df = 1, p = 0.867; $\chi^2_{heat*water}$ = 0.208, df = 1, p = 0.648). Growth did not vary predictably across the elevation gradient ($\chi^2_{elevation}$ = 0.972, df = 1, p = 0.324), nor were then any significant interactions between the elevation gradient and the manipulations. Growth increased with the population's accumulated degree-days ($\beta_{degree.days}$ = 0.487, p < 0.001) and watering had a positive effect on growth in hotter sites ($\beta_{degree.days *water}$ = 0.561, p = 0.001). Heating and watering had a positive effect of growth of larger individuals in cooler sites ($\beta_{degree.days *water*heat*size}$ = 1.021, p = 0.001) (Figure 4). Growth did not vary predictably across the soil moisture or snow persistence gradients ($\chi^2_{soil.moisture}$ = 1.1, df = 1, p = 0.294; χ^2_{snow} = 1.69, df = 1, p = 0.194). However, across these gradients, heating had a negative effect in drier populations ($\beta_{soil.moisture*heat}$ = 0.792, p = 0.004) and watering had a negative effect in populations with more persistent snowpack ($\beta_{snow*water}$ = 0.65, p = 0.012).

Germination across all populations increased with heating (β_{heat} = 0.214, p = 0.026) or watering (β_{water} = 0.0159, p < 0.001), but was greatly reduced by the combination of heating and watering ($\beta_{heat.water}$ = -1.034, p < 0.001). Across the elevation gradient, germination was lower at higher elevations ($\beta_{elevation}$ = -0.866, p < 0.001) and heating had a more negative effect on germination at lower elevations ($\beta_{elevation*heat}$ = 0.427, p < 0.001). Germination was also reduced in sites with higher accumulated degree-days ($\beta_{degree.days}$ = -0.1, p < 0.001), and in the coldest sites watering had a larger positive effect ($\beta_{degree.days*water}$ = -0.1, p = 0.038), and heating and watering had a larger negative effect ($\beta_{degree.days*heat*water}$ = -0.1, p < 0.001). Germination increased with soil moisture ($\beta_{soil.moisture}$ = 1.226, p < 0.001), and in these wettest sites, heating had a more negative effect on germination ($\beta_{soil.moisture*heat}$ = -0.239, p < 0.001). Germination also increased with the number of snow-covered days (β_{snow} = 0.430, p < 0.001), and in the snowiest sites, heating had a positive effect ($\beta_{snow*heat}$ = 0.064, p = 0.004), but the combination of heating and

watering had a large negative effect on germination ($\beta_{snow*heat*water}$ = -0.790, p < 0.001) (Figure 4).

Flowering probability did not respond consistently to experimental heating and watering across all populations (χ^2_{heat} = 0, df = 1, p = 0.998; χ^2_{water} = 0.283, df = 1, p = 0.594; $\chi^2_{heat*water}$ = 0.269, df = 1, p=0.604). Across the elevation gradient, mean flowering probability increased ($\beta_{elevation}$ = 2.105, p < 0.001). In higher elevation populations, heating had a negative effect on flowering probability ($\beta_{elevation*heat}$ = -0.298, p = 0.023), and the combination of heating and watering had a positive effect ($\beta_{elevation*heat*water}$ = 1.33, p = 0.003) (Figure 4). Flowering probability did not vary predictably across the accumulated degree-days gradient ($\chi^2_{degree.days}$ = 3.045, df = 1, p = 0.081), but heating had a negative effect in hotter sites for smaller individuals ($\beta_{size*degree.days*heat}$ = -0.456, p = 0.044). In wetter sites, mean flowering probability increased ($\beta_{soil.moisture}$ = 0.424, p < 0.001) and heating further increased this probability for large individuals ($\beta_{size*soil.moisture*heat}$ = 0.913, p = 0.001). Flowering probability did not vary predictably across the snow persistence gradient ($\chi^2_{snow.days}$ = 0.436, df = 1, p = 0.509), but in snowier sites heating again increased flowering probability for large individuals ($\beta_{size*snow*heat}$ = 0.695, p = 0.042). Across all populations, the number of flowering stalks per individual increased with a combination of heating and watering for large individuals ($\beta_{size*heat*water}$ = 0.186, p = 0.001). The number of flowering stalks had a positive relationship with elevation ($\beta_{elevation}$ = 0.341, p < 0.001), but no relationship with any of the climatic gradients ($\chi^2_{degree.days}$ = 1.355, df = 1, p = 0.244; $\chi^2_{soil.moisture}$ = 3.052, df = 1, p = 0.981; χ^2_{snow} = 0.037, df = 1, p = 0.346). For all of the gradients, there were no significant interactions between the experimental manipulations and temperature gradient.

Population Growth Response to Manipulations

Population growth across all the populations and treatments ranged from 0.944 to 1.205. Population were in a state of contraction (λ <1), expansion (λ >1), and stability (λ ~ 1) under ambient conditions (2 contracting, 4 expanding, 2 stable) as well as under experimental conditions: heating (0 contracting, 4 expanding, 5 stable), watering (0 contracting, 4 expanding, 5 stable), and the combination of heating and watering (2 contracting, 2 expanding, 5 stable) (Table 3). Across all populations, experimental heating had a significant 1.8% reduction in population growth rate when averaged across the watering treatment (χ^2 = 5.553, df =1, p = 0.018). Experimental watering had no range-wide effect on population growth (χ^2 = 2.970, df = 1, p = 0.085), and there was no significant effect of heating and watering in all population across the species range (χ^2 = 3.272, df = 1, p = 0.070). Examining the treatment contrasts, I found significant differences in population growth between ambient, watering and the combination of heating and watering ($\mu_{ambient}$ = 1.045 [0.999-1.091], μ_{water} = 1.043 [0.997-1.09], $\mu_{heat*water}$ = 1.012 [0.966 - 1.059] df = 24, $p_{ambient-heat*water}$ = 0.0309, $p_{water-heat*water}$ = 0.0413), and no significant difference between heating and the combination of heating and watering (μ_{heat} = 1.040 [0.993 - 1.086], df =24, $p_{heat-heat*water}$ = 0.086) (Figure 5). These results taken together support the conclusion that although the greatest reduction in population growth was observed for combined heating and watering treatment, this reduction was primarily driven by the experimental heating (Figure 5).

I explored how population growth and its response to the manipulations varied across geographic (elevation) and climatic gradients (average accumulated degree-days, soil moisture, and snow persistence). Population growth rates decreased with elevation with expanding

population growth ($\lambda > 1$) in the lowest elevation populations and predominantly contracting ($\lambda < 1$) or stable population growth ($\lambda \sim 1$) at higher elevations ($\beta_{elevation} = -0.001$, $p = 0.026$) (Figure 6). Population growth increased with average soil moisture ($\beta_{soil.moisture} = 0.006$, $p < 0.001$) and number of days of snow-cover ($\beta_{snow.cover} = 0.002$, $p = 0.001$) with increasing population growth rates at the wettest sites with the most persistent snowpack. There was no relationship between population growth rate and accumulated degree-days ($\beta_{degree.days} = -0.001$, $p = 0.793$) (Figure 6). Differences in the effect of the climate manipulations across the geographic and climatic gradients would be represented by significant interactions between the gradients and the manipulations. I found a significant negative interaction between a population's number of snow-covered days and experimental heating ($\beta_{snow.cover*heat} = -0.001$, $p = 0.025$). Heating had a larger negative effect on population growth in population with more persistent snow-pack (Figure 6). No effect was found for watering or a watering by heating interaction across this snow-days gradient ($\chi^2_{water} = 2.436$, df = 1, $p = 0.119$; $\chi^2_{heat*water} = 0.065$, df = 1, $p = 0.798$). Also, there was no significant interaction between the elevation gradient and experimental heating ($\chi^2_{heat} = 1.245$, df = 1, $p = 0.264$), watering ($\chi^2_{water} = 0.958$, df = 1, $p = 0.328$), or heating and watering ($\chi^2_{heat*water} = 0.562$, df = 1, $p = 0.453$). There was also no significant interaction between the experimental manipulations and the population's average accumulated degree-days ($\chi^2_{heat} = 1.245$, df = 1, $p = 0.264$; $\chi^2_{water} = 0.958$, df = 1, $p = 0.328$; $\chi^2_{heat*water} = 0.562$, df = 1, $p = 0.453$) or soil moisture ($\chi^2_{heat} = 1.291$, df = 1, $p = 0.256$; $\chi^2_{water} = 1.9$, df = 1, $p = 0.275$; $\chi^2_{heat*water} = 1.069$, df = 1, $p = 0.301$).

Elasticity Analysis

The pattern of elasticity for demographic transitions varied across the populations. Across all populations survival and growth had a larger proportional influence on population growth rates than regeneration (Figure 7). However, for low elevation population with higher soil moisture and more persistent snow-pack, regeneration had higher elasticity values relative to high elevation populations (Figure 7). In these wetter, snowier sites, there was a greater influence of regeneration on population growth.

DISCUSSION

I investigated the role of changing climatic conditions on the range dynamics of *I. lycopodioides* by incorporating demographic responses to experimental heating and watering manipulations into integral projection modeling for nine populations across the species' entire elevational range. This approach brought together 1) range-wide spatial replication of demography and microclimate measurements, 2) experimental climate manipulations, and 3) quantification of all demographic rate response to manipulation across all populations, allowing us to attribute range shift predictions through population contraction and expansion to changes in temperature and precipitation (Gotelli & Ellison 2006; Merow *et al.* 2016). I hypothesized that experimental heating would have a negative effect on population dynamics at the hotter, drier populations and a positive effect at the cooler, wetter sites, and that manipulated precipitation would ameliorate the negative impacts of heating in the driest populations. The effect of experimental manipulation on demographic components was partially consistent with our predictions that heating would have a negative effect and watering would have a positive effect on populations in hotter, drier, and more exposed sites. However, these responses did not result in changes in population growth rates that would predict range expansion at the cool, wet leading

range edge and a contraction at the hot, dry trailing range edge. I instead observed a de-coupling of the temperature and soil moisture gradients and a negative effect of heating on population growth rate for all populations across this species range. I proposed that these unexpected impacts of climate manipulations on population growth are due to interactive effects of the variable size-dependent relationships between the manipulations and demographic components, changes in the effect of the climate manipulations across climatic gradients for each demographic component, and spatial variation in the proportional influence of each demographic component across the species range (Doak & Morris 2010; Pironon *et al.* 2017). I explore how these complexities drove our unexpected finding of range-wide reduction of population growth due to heating across this species entire range.

Demographic Responses to Manipulations

I found variable and size-dependent responses of the demographic components to both the temperature and precipitation manipulations, as well as their interaction. Climate manipulations varied in the direction of the effect on demographic components. Across all populations the combined effect of heating and watering increased the number of flowering stalks per large individual, but decreased germination. Many of the effects of the manipulations on demographic components also shifted across the geographic or climate gradients of this species range, and often, but not always, in line with our predictions based on the species range represented the species climatic niche (Sexton *et al.* 2009; Lee-Yaw *et al.* 2016; Pironon *et al.* 2017). For example, heating most positively influenced individual growth in the coolest sites, but the largest reductions in germination with heating and watering was in the snowiest sites. Often the manipulations only influenced demographic components in one part of the species range (*e.g.,* dry sites), but had minimal effects in other parts of the species range (*e.g.,* wet sites), suggesting that other factors besides our measured climate variables limit the demographic rate, including disturbance or biotic competition or facilitation (MacArthur 1972; Callaway *et al.* 2002; Alexander *et al.* 2017). Survival, for example, was not highly influenced in wetter sites by any of the climate manipulations, but heating caused a sharp decrease in survival rates in dry sites.

The influence of these manipulations on demography was further complicated by three-way interactions between size, treatment, and the geographic/climatic gradient found for most demographic components. Most often these three-way interactions exacerbated the negative effect of the treatments for small individuals and the exaggerated the positive effect for large individuals. This latter result is in line with other work that has found that smaller individuals may be the most sensitive to changes in climate (spatial or temporal) in montane systems (Forbis 2003; Wenk & Dawson 2007; Ettinger & Hille Ris Lambers 2013; Dobrowski *et al.* 2015; Máliš *et al.* 2016). Size-mediated responses are of particular interest because complex relationships between climate and different parts of species life-history can influence range dynamics causing species ranges to be in disequilibrium with their climatic niche (Pulliam 2000; Veloz *et al.* 2012). For example a "standing dead" population may be suitable for adult survival but unsuitable for recruitment and growth of new individuals and therefore without future change is slated for eventual extinction (Svenning & Sandel 2013; Bell, Bradford & Lauenroth 2014).

Population Growth Response to Manipulations

With IPMs I examined the overall effect on population growth of these complex interactions between the manipulations, individual size, demographic rates, and climatic

gradients. For non-manipulated conditions, population growth was primarily stable (λ ~ 1) or contracting (λ < 1) in the species range center and upper edge with dry conditions and less persistent snowpack. Populations in sites with higher soil moisture and number of snow-covered days at the lower range edge were expanding (λ > 1). In all populations across the range of *I. lycopodioides* experimental heating reduced population growth. In addition, this negative effect was the greatest in sites with the most persistent snowpack. Again, these results are counter to predictions of an opposite influence of heating for the leading or trailing geographic or climatic edge of the species range, and suggest that none of these populations are temperature-limited (Hampe & Petit 2005; Angert *et al.* 2018; Sheth & Angert 2018).

The elasticity analysis offers some clues about this counterintuitive response to manipulations across this species range. An underappreciated point in range shift predictions is that elasticity itself can vary across geographic and/or climatic gradients (Doak & Morris 2010; Villellas *et al.* 2015). Only when a change in climate influences a demographic rate with high proportional influence on population growth would we predict a change in population growth (Mclean *et al.* 2016; Amburgey *et al.* 2018). As expected for a slow-growing, long-lived plant species, survival of individuals had a large proportional influence and reproduction had a minimal proportional influence on population growth across most populations (Morris, Pfister & Tuljapurkar 2008). I observed this pattern in higher elevation, drier populations, but in the wetter, snowier populations at lower elevations, population growth was also dependent on the influence of reproduction. This change in elasticity may be due to a shorter growing season in these sites with more persistent snowpack that limits individual size in these populations (Bell & Bliss 1979), or due to community interactions (Alexander *et al.* 2017). The wetter, snowier sites had much higher overall vegetation density, potentially leading to limitation of demographic rates due to competition as opposed to climate directly (Rumpf *et al.* 2017).

I argue that different components of *I. lycopodioides*' life history was driving the decrease in population in different parts of the species range. The negative response to heating in center and upper edge populations was most likely due to reduced survival in drier conditions (Figure 4B) and the higher proportional influence of survival in those populations (Figure 7). In contrast, the negative response of population growth for lower edge populations was due to decreased emergence of new seedling with heating in sites with more persistent snowpack (Figure 4C) and the relatively greater proportional influence of regeneration in the populations (Figure 7). These results indicate that there are multiple demographic pathways in which climate change can decrease population stability, and that multiple demographic rates responses to climate change need to considered when trying to predict range shifts (Csergő *et al.* 2017; Amburgey *et al.* 2018). Also unexpected, was the finding that the largest negative effect of the climate manipulations was for populations in sites with the most persistent snow-pack. However, the negative effect of heating on multiple demographic components was greatest for smaller individuals (indicated by size by treatment interactions), potentially exacerbating the population growth responses in snowy sites where population growth was most strongly influenced by changes in small-individual establishment. Taken together these results reiterate the importance of mechanistic models for range shifts to include exposure, environmental sensitivity of multiple demographic rates as comparative metrics across a species range (Figure 1).

Range Shift Predictions

The negative effect of experimental heating leads to predictions of population contractions at mid elevations of the *I. lycopodioides* range in the driest conditions (Figure 6). In

these dry populations, the reduction in population growth and the lower ambient population growth relative to populations in wetter conditions caused population growth to drop below one forecasting potential extinction with warmer conditions in at least two populations (Table 3). Although alpine systems are considered heat-limited systems (Körner 2003), water balance is thought to be one of the most important drivers of vegetation changes due to climate change, especially for dry high elevation systems (Franklin *et al.* 2016; McCullough *et al.* 2016; Winkler *et al.* 2016a). Contractions of populations at climatic extremes are expected with climate change and this contraction playing out in the center of species range is not a recognized range shift pattern (Lenoir & Svenning 2014). Only one other study that I know of has shown a similar pattern of range-center population extirpations (Stewart, Wright & Heckman 2017). Other studies that failed to find decreased population growth in range edges have proposed that this is due to the climate variation being de-coupled from the geographic gradient (Aikens & Roach 2014; Pironon *et al.* 2015). Here I show clear evidence of this being the case, with lower population growth rates in range center due to drier conditions, and that this will in fact influence range shifts with climate change. One caveat to these range shift predictions is that population growth values are based on stable age structures of the populations, which are slow to converge for a long-lived alpine plant; Therefore, these are predictions for long-term dynamics of this species range in response to climate change.

Conclusions

A population biology approach can refine our understanding of the rate and magnitude of species range shifts with changing climate (Gaston 2009; Schurr *et al.* 2012; Mclean *et al.* 2016). Quantifying the exposure, response of each demographic rate, and the proportional influence of each demographic rate in each population across a species range can lead to an understanding of the mechanisms driving range shifts that may appear counterintuitive (Normand *et al.* 2014). Although studying demography and fine-scale climate for all species across their entire geographic ranges is not practical, there is still a need to understand when our assumptions that presence, abundance, or a subset of demographic rates represent approximate long-term population growth across the geographic and climatic gradients encompassed in a species ranges holds (Diez *et al.* 2014; Ehrlen & Morris 2015). Our results suggests that future range shifts studies need to consider the potential for life-history components to interact with changing climatic conditions in different ways when considering the vulnerability of populations across a species range (Doak & Morris 2010; Csergő *et al.* 2017; Pironon *et al.* 2017).

TABLES & FIGURES

Table 1. Parameters from regressions used in IPMs for population treatment combinations for survival, growth, probability of flowering, and the number of flowering stalks. Parameter estimates given for the intercept (β_0), and the effect of individual size (β_{Size}), heating treatment (β_H), watering treatment (β_W), size by heating treatment interaction (β_{Size*H}), size by watering treatment interaction (β_{Size*W}), heating by watering treatment interaction (β_{H*W}), interaction between size, heating treatment and watering treatments($\beta_{Size*H*W}$), and the standard deviation of model residuals (growth model only; Std(X). Parameters ordered from low to high elevation populations for each demographic component when parameter varies across populations.

Survival Probability

	β_0	β_{Size}	β_H	β_W	β_{Size*H}	β_{Size*W}	β_{H*W}	$\beta_{Size*H*W}$	Std(X)
	2.236		-0.936	-0.081			-0.060		
	4.431		0.148	-0.008			0.121		
	3.958		-0.070	-0.011			0.079		
	2.960		-0.521	-0.011			-0.012		
Survival Probability	3.359	2.823	-0.302	0.021	-0.476	-0.551	0.017	0.634	–
	1.502		-1.195	-0.022			-0.141		
	1.580		-1.172	-0.032			-0.132		
	2.805		-0.630	-0.042			-0.018		
	2.776		-0.642	-0.041			-0.021		

Growth

	β_0	β_{Size}	β_H	β_W	β_{Size*H}	β_{Size*W}	β_{H*W}	$\beta_{Size*H*W}$	Std(X)
	0.083		-0.012	-0.003			0.031		
	0.049		0.009	-0.010			-0.007		
	0.044		0.000	-0.017			0.011		
	-0.011		0.042	-0.026			-0.064		
Growth	0.059	0.971	-0.012	-0.015	-0.004	0.031	0.033	-0.021	0.357
	0.020		0.028	-0.017			-0.039		
	0.055		0.030	0.002			-0.049		
	0.077		-0.022	-0.011			0.052		
	0.115		0.038	0.038			-0.073		

Flowering Probability

	β_0	β_{Size}	β_H	β_W	β_{Size*H}	β_{Size*W}	β_{H*W}	$\beta_{Size*H*W}$	Std(X)
	-1.459		-0.108	0.064			0.111		
	-1.767		0.160	0.352			-0.363		
	-2.066		0.004	0.180			-0.232		
Flowering Probability	-1.408	1.976	-0.390	-0.240	-0.338	0.196	0.525	-0.410	–
	-0.051		-0.286	-0.115			0.788		
	-0.512		-0.333	-0.170			0.715		
	-0.238		-0.072	0.114			0.429		
	0.243		-0.403	-0.239			1.044		
	0.535		-0.602	-0.451			1.413		

Number of Flowering Stalks

	β_0	β_{Size}	β_H	β_W	β_{Size*H}	β_{Size*W}	β_{H*W}	$\beta_{Size*H*W}$	Std(X)
	2.263		0.253	0.083			-0.026		
	2.082		0.005	-0.011			-0.005		
	1.972		0.090	0.025			0.011		
Number of Flowering Stalks	2.566	0.224	-0.073	-0.167	-0.151	0.000	0.120	0.127	–
	2.771		0.078	-0.035			-0.036		
	2.872		-0.009	-0.365			0.445		
	2.897		0.182	0.170			-0.332		
	2.708		0.243	0.043			-0.044		
	3.181		0.253	-0.053			0.042		

Table 2. Germination rates used in IPMs with each row representing a population ordered from low to high elevation. μ_A is the establishment probability under ambient conditions, μ_H is the establishment probability under heated conditions, μ_W is the establishment probability under watering conditions, μ_{H*W} is the establishment probability under heating and watering conditions.

Population	Elevation (m)	μ_A	μ_H	μ_W	μ_{H*W}
1	3494	0.149	0.283	0.134	0.369
2	3562	0.36	0.183	0.232	0.103
3	3573	0.271	0.288	0.17	0.121
4	3735	0.024	0.071	0.005	0.017
5	3789	0.014	0.03	0.03	0.0004
6	3815	0.009	0.011	0.001	0.011
7	3974	0.002	0.031	0.003	0.022
8	4005	0.001	0.007	0.004	0.004
9	4028	0.006	0.012	0.011	0.001

Table 3. 95% confidence intervals for population growth for each treatment status in each population by bootstrapping the data 1,000 times keeping the total number of observation within each population, treatment combination constant. Each row represents a population ordered from low to high elevation

Population	Elevation (m)	$CI_{Ambient}$	CI_{Water}	CI_{Heat}	$CI_{Heat+Water}$
1	3494	1.23 – 1.26	1.13 – 1.28	0.72 – 1.06	0.94 – 1.60
2	3562	1.13 – 1.24	1.21 – 1.28	1.09 – 1.20	1.04 – 1.15
3	3573	1.02 – 1.12	1.16 – 1.22	1.11 – 1.26	1.12 – 1.23
4	3735	0.92 – 1.01	0.80 – 0.97	1.00 – 1.12	0.77 – 0.94
5	3789	0.99 – 1.06	0.95 – 1.03	1.04 – 1.20	0.87 – 1.00
6	3815	0.90 – 0.99	0.79 – 0.93	0.81 – 1.00	0.62 – 0.99
7	3974	0.92 – 0.99	0.67 – 0.99	0.95 – 1.04	0.89 – 1.00
8	4005	0.98 – 1.01	1.00 – 1.29	0.86 – 1.00	0.96 – 1.04
9	4028	1.03 – 1.14	1.03 – 1.14	1.23 – 1.58	0.92 – 1.02
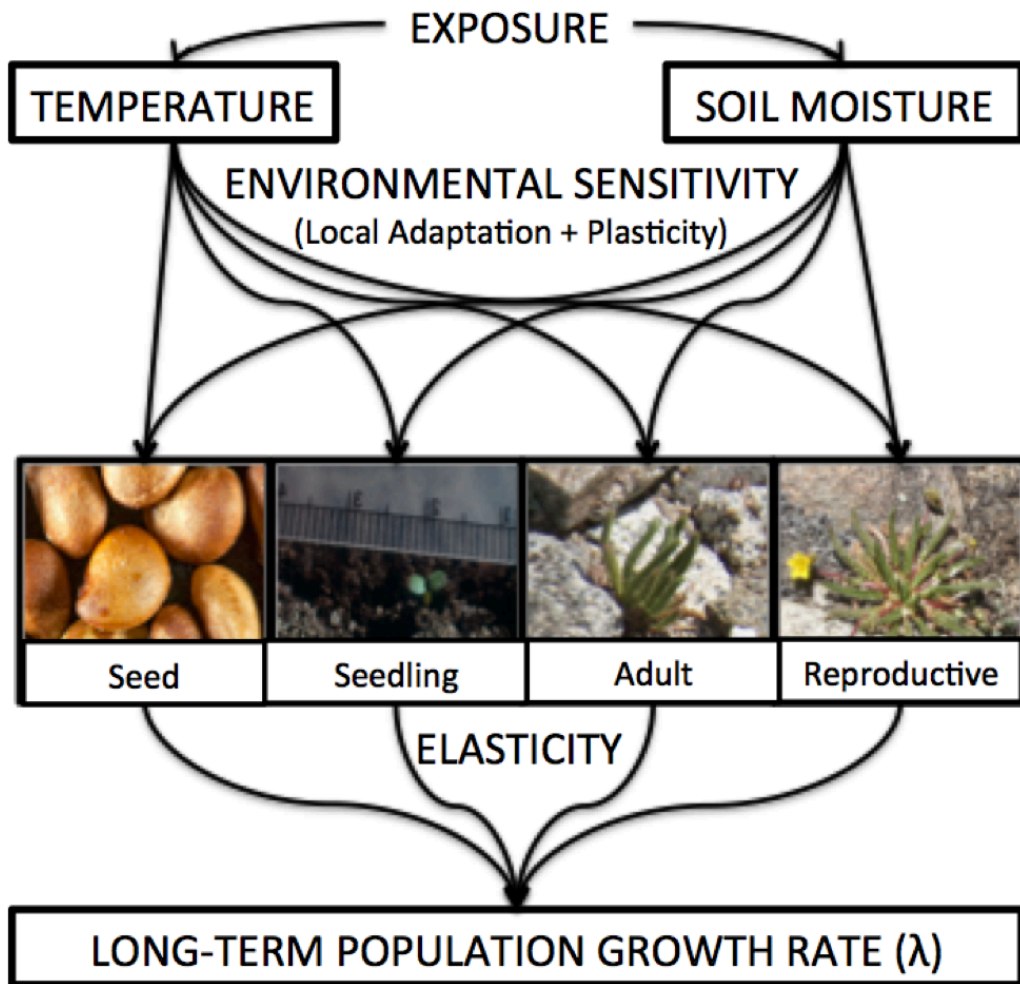
Figure 1. The images of the focal species *I. lycopodioides* represent its different demographic rates. Population response to a change in climate will be shaped by exposure, environmental sensitivity and demographic elasticity.
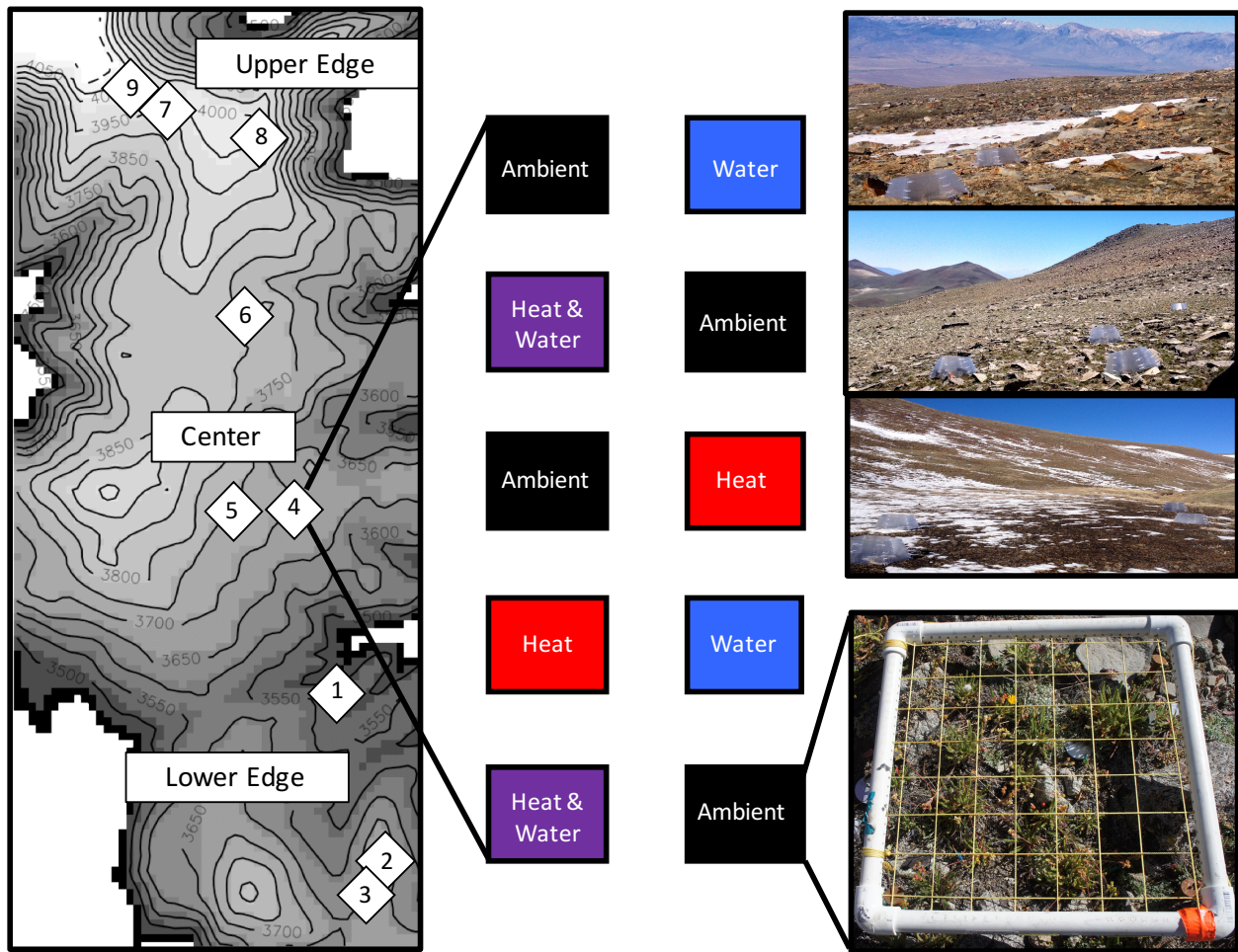
Figure 2. Schematic of study design across elevational range of *I. lycopodioides*. In each experimental population (white diamonds), 30x30 m plots were randomly assigned to one of four treatments (ambient, heated, watered, heated and watered) with a replication of at least two plots per treatment. In each plot individual's demographic rates were followed through time and climatic conditions were quantified annually. The heating treatment was performed using passive warming chambers (shown in top right in populations across the species range). Populations numbered from low to high elevation.
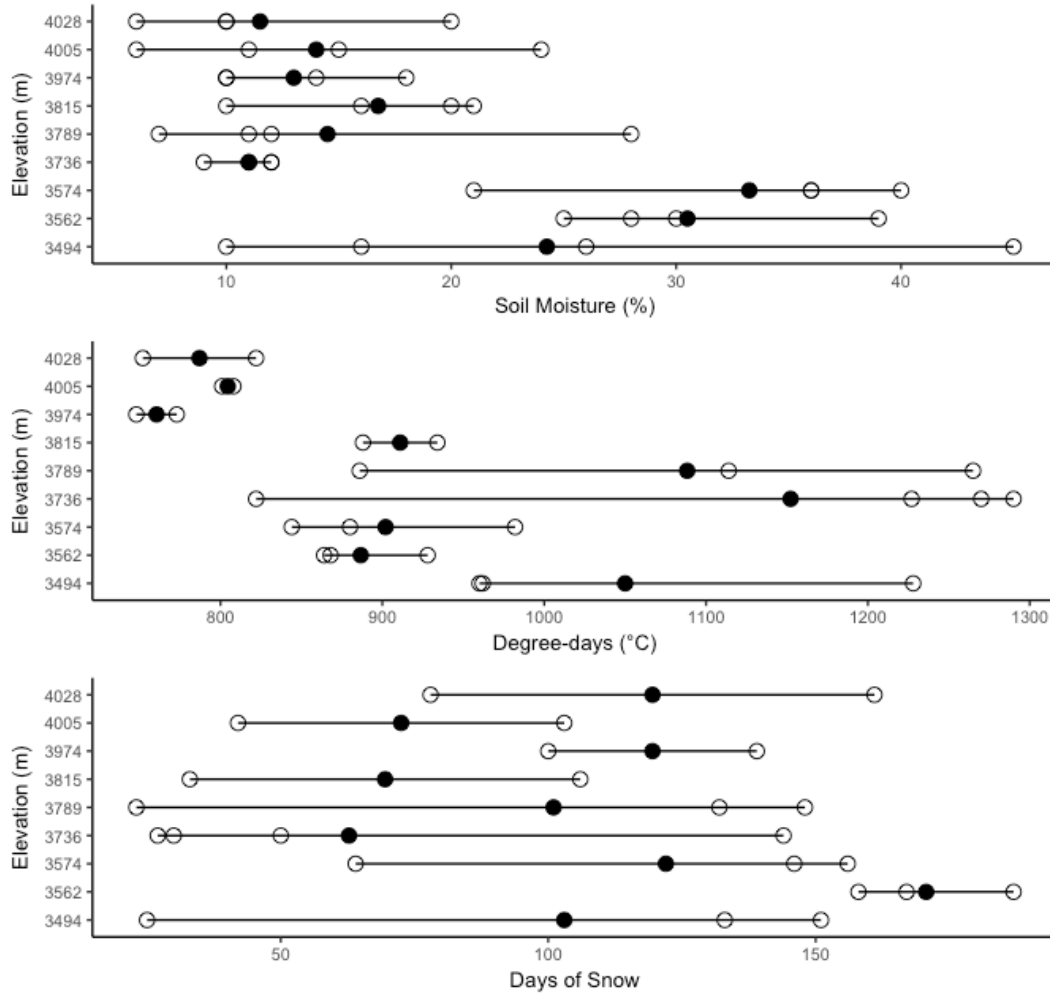
Figure 3. Variation in soil moisture and accumulation of degree-days for the 2014 – 2017 summer growing seasons (top, center) across the elevation gradient. Variation in the days of snow cover for 2015, 2016, and 2017 winters across the elevation gradient (bottom). Both site means for each year (open circles) and means across all years (filled circles) for all nine populations shown.
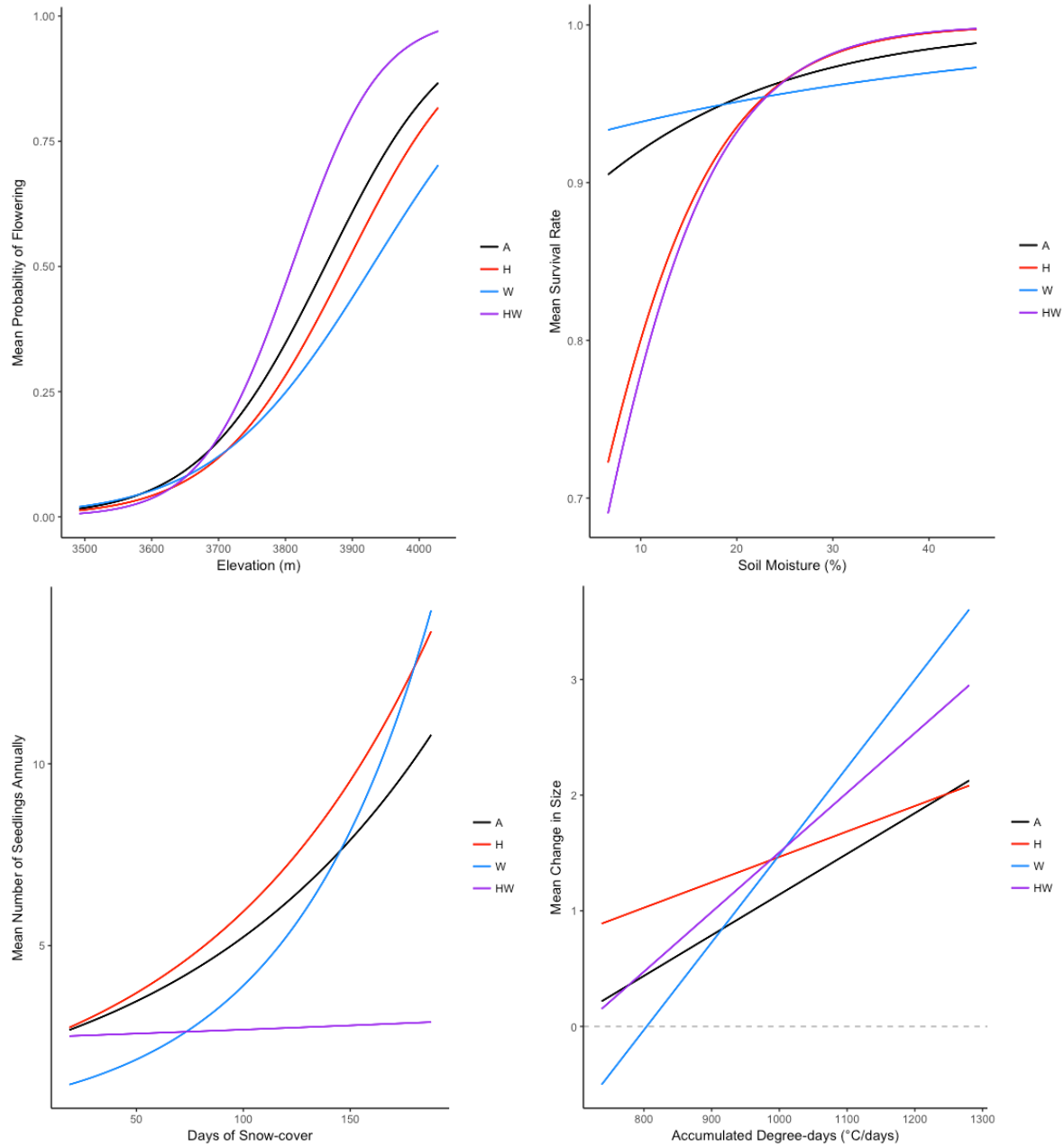
Figure 4. Subset of demographic component responses to experimental heating and watering across geographic or climatic gradients that highlight interactions between treatment effects and the gradients. Lines represent model fits of the effect of manipulations on demographic components.
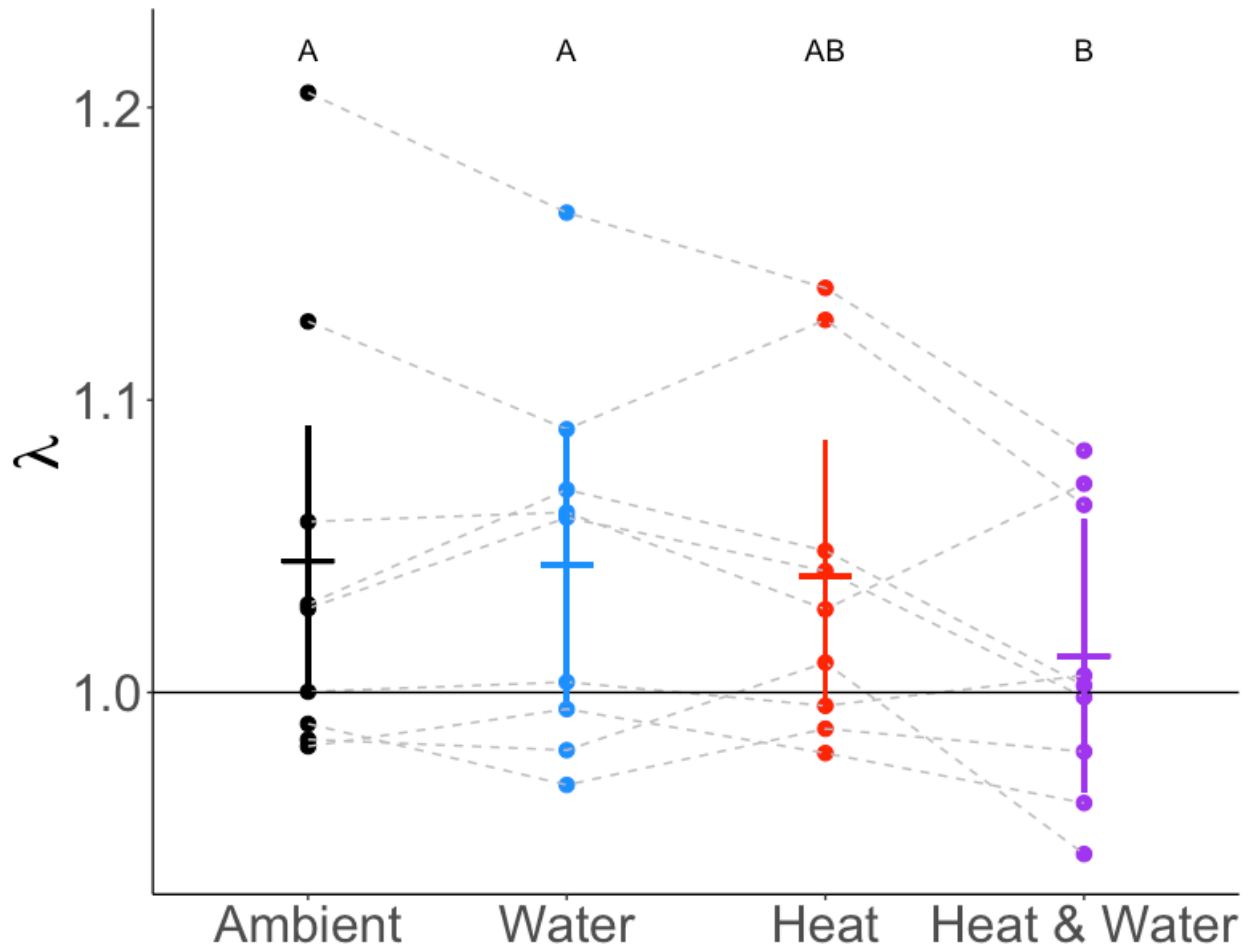
Figure 5. Population growth rate for each treatment group across all population. Mean and 95% confidence intervals of population growth rate in each treatment group shown with solid lines. Dashed lines connect populations (filled circles). Letters indicate significantly different groups. Color represent treatment status: ambient (black), heating (red), watering (blue), heating and watering (purple).
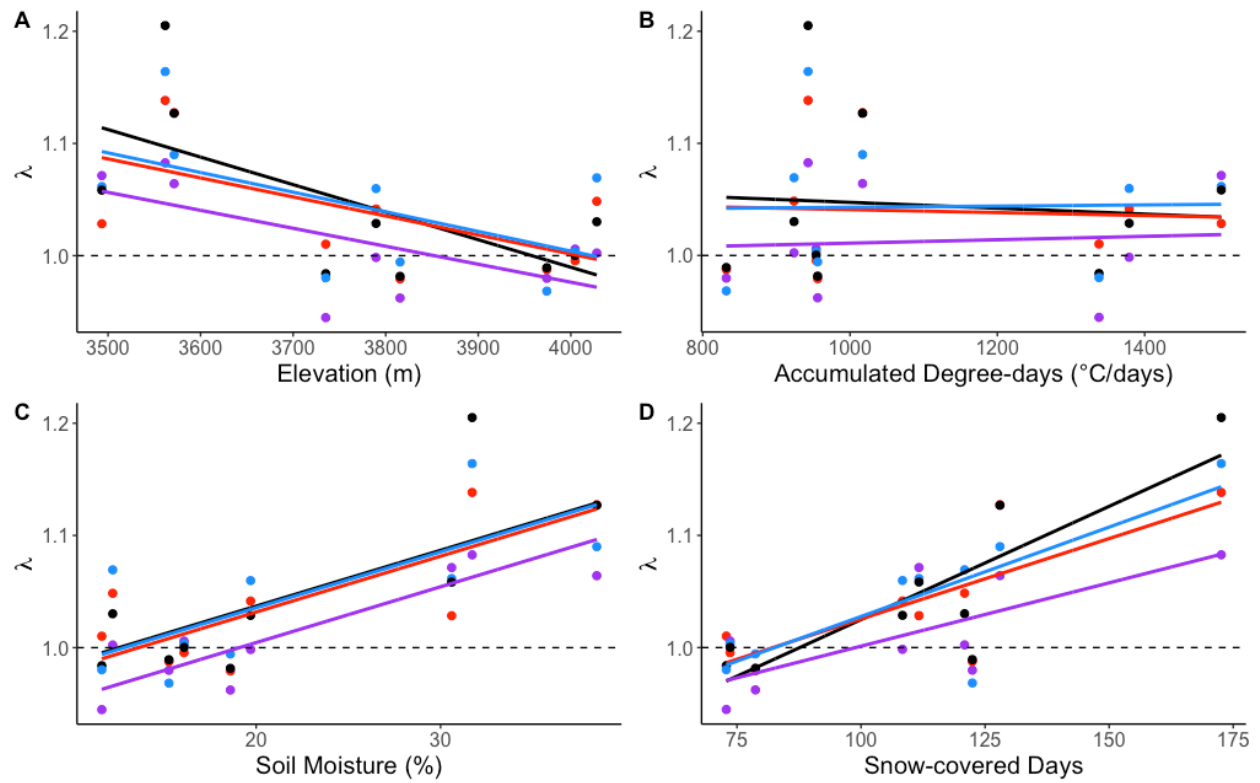
Figure 6. Population growth rate (λ) across geographic (A – elevation) and climatic gradients (B – Accumulated degree-day, C – Soil moisture, D – Snow-covered days) for different treatments. Line represents model fits for population growth under ambient (black), heating (red), watering (blue), heating and watering (purple) across these gradients. Colors of points also represent experimental status for each population growth value.
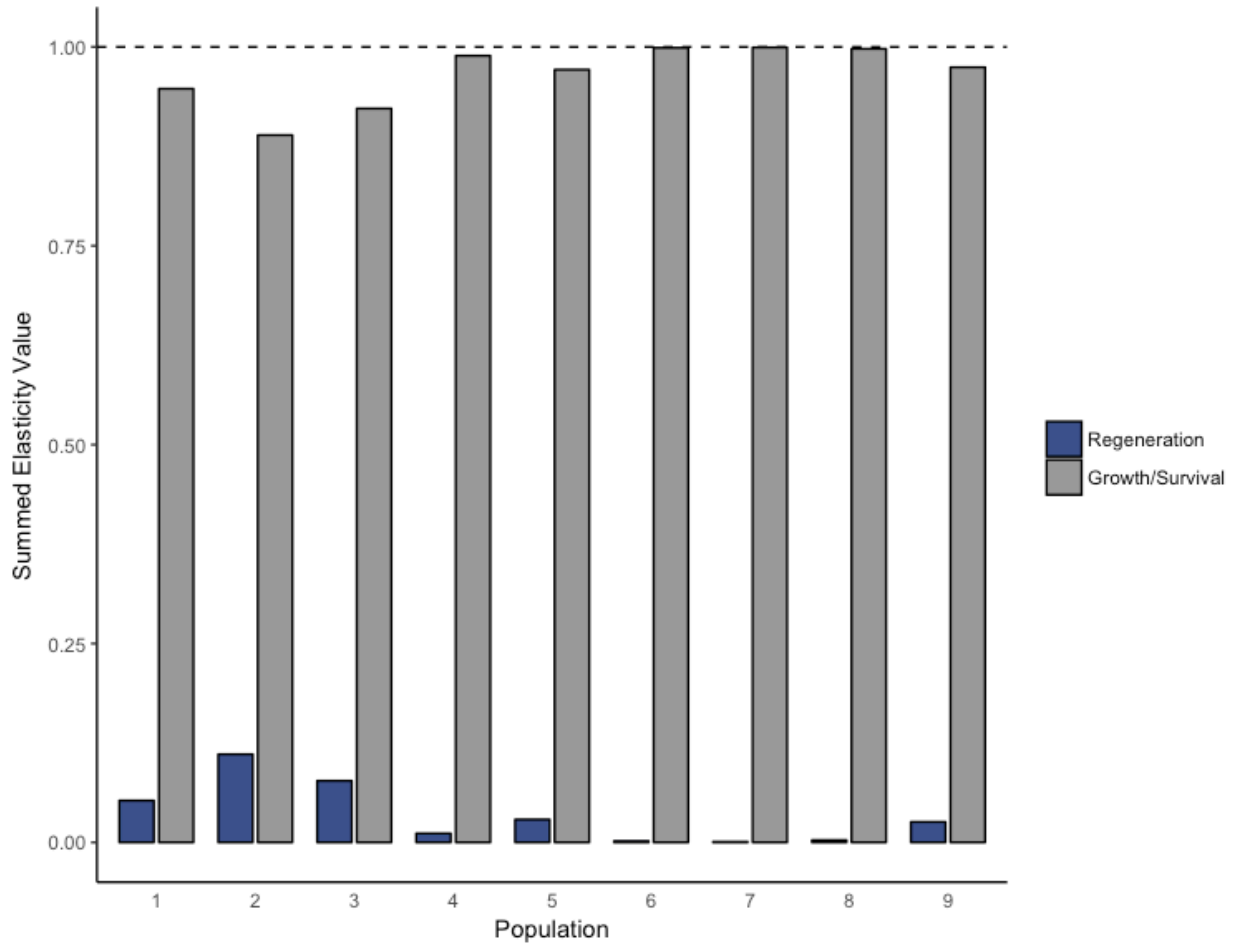
Figure 7. Elasticity values for reproduction/recruitment and growth/survival based on non-manipulated conditions for each population ordered by increasing elevation. Due to the summed elasticity being proportional (sums to 1) the values can be compared across populations.

CHAPTER 3: THERMOPHILIZATION OF AN ALPINE PLANT COMMUNITY IN RESPONSE TO EXPERIMENTAL WARMING IN A XERIC MOUNTAIN RANGE

ABSTRACT

A warming climate has been shown to drive thermophilization – a shift from communities dominated by cool-adapted species to communities dominated by warm-adapted species. Studies of alpine plant community responses to climate change have predominantly focused on temperature-limited systems. However, mountain ranges in semi-arid regions, such as western North America, where temperature and moisture both play strong roles in the determination of the distribution of alpine communities, require more research. I surveyed community composition in nine sites that ranged in elevation across the alpine zone in the xeric White Mountains, CA USA. In each site, I experimentally increased summertime temperature and precipitation from 2015 to 2017 and quantified community responses with both a community dissimilarity and a climate niche analysis. I investigated if thermophilization occurred in response to experimental heating, and if this effect was ameliorated by experimental watering. Under experimentally warmer climatic conditions, thermophilization of this community was supported by two lines of evidence: 1) an increase in the 75th percentile community-weighted climatic niche indicating an increase of hot, dry adapted species within each site and 2) and higher proportional abundance of species that are hot, dry adapted relative to their surrounding community. Experimental watering did not ameliorate this effect of heating. Concordantly, I found that overall abundance increased and species richness decreased with experimental heating. Together, these results indicate that with warmer conditions the White Mountain alpine zone will be made up of less diverse plant communities dominated by species associated with hotter, drier conditions. This finding is in line with other work that has predicted larger montane habitat loss with climate change under water-limited scenarios.

INTRODUCTION

Montane systems provide important early indicators of plant community responses to changing climate (Körner 2003; Grabherr *et al.* 2010; Rixen & Wipf 2017; Steinbauer *et al.* 2018); climate warming is more pronounced at higher elevations (Pepin *et al.* 2015), and exposure to climate change is exacerbated in xeric mountain ranges due to shifts from snow-dominated to rain-dominated precipitation (McCullough *et al.* 2016). Alpine species, often cool-adapted and long-lived, are particularly sensitive to temperature change mediated either directly via their physiology and demography or indirectly via competitive exclusion by faster growing species that recruit from lower elevations (Cranston *et al.* 2015; Graae *et al.* 2017; Rumpf *et al.* 2017). Moreover, the physical isolation of mountain ranges creates large geographic barriers to species movement at regional scales (Dirnbock, Essle & Rabitsch 2011). However, the topographic complexity of mountains creates a variety of potentially suitable microrefugia that may allow alpine species to track their climate niche at local scales (Scherrer & Korner 2011; Winkler *et al.* 2016b). Understanding how changing climate drives community shifts across these isolated, topographically heterogeneous landscapes can facilitate predictions of the potential vulnerability of these socio-ecologically important montane systems (Pecl *et al.* 2017).

Observational and experimental studies of montane species reveal distributional and community shifts in response to warming conditions (Walther, Beibner & Burga 2005; Walker *et al.* 2006; Gottfried *et al.* 2012; Morueta-Holme *et al.* 2015; Suding *et al.* 2015; Lesica & Crone 2016). Recent work using resurveys of mountaintops spanning over 100 years has linked accelerating increases in alpine plant diversity to accelerating increases in temperature (Steinbauer *et al.* 2018). A warming climate has been specifically shown to drive thermophilization – a shift from communities dominated by cool-adapted species to communities dominated by warm-adapted species (Gottfried *et al.* 2012; Savage & Vellend 2015; Vanneste *et al.* 2017). This process is shaped by the loss of or decrease in abundance of cryophilic species, and/or a gain or increase in abundance of thermophilic species (Gottfried *et al.* 2012). The lack of microclimatic buffering by over-story canopies is likely to make thermophilization more evident in alpine systems (De Frenne *et al.* 2013; Stevens *et al.* 2015). Although fine-scale microclimatic gradients driven by topography may buffer species loss in response to warmer montane conditions (Scherrer & Korner 2011), community shifts are likely to occur as competition and facilitation dynamics play out at fine spatial scales (Alexander, Diez & Levine 2015; Alexander *et al.* 2017; Kulonen *et al.* 2018).

Interactions between temperature and other climate variables (*e.g.,* precipitation) influence how plant communities respond to changing climatic conditions (Rapacciuolo *et al.* 2014; Harsch & Hille Ris Lambers 2016). Trends in distributional shifts of alpine plants in response to recent warming in water-limited Mediterranean mountains differ from shifts in temperature-limited boreal-temperate mountains (Pauli *et al.* 2012). The impact of warming on alpine community dynamics can be dependent on soil moisture availability, with the potential for positive effects on abundance and productivity under wetter conditions and negative effects under drier conditions (Elmendorf *et al.* 2012; Winkler *et al.* 2016a). Changes in snow-melt timing due to the interactive effects of snow persistence on temperature exposure (i.e. snow protection from winter cold) and soil moisture availability also have variable species-specific effects on alpine plants (Wipf, Stoeckli & Bebi 2009). Studies of alpine plant responses to climate change have predominantly focused on temperature-limited systems (Körner 2003; Gottfried *et al.* 2012). However, mountain ranges in semi-arid regions, such as western North America, where temperature and moisture both play strong roles in the determination of the

distribution of alpine communities, require more research (Isard 1986; Cavieres *et al.* 2006; Lesica & Crone 2016; Winkler *et al.* 2016a).

This study was conducted in the White Mountains (California, USA), a semi-arid mountain range which has experienced marked change in water balance with 20th century climate change (Rundel *et al.* 2008; Rapacciuolo *et al.* 2014). Climatic water deficit (CWD), an integrative measure of the relationship between temperature and precipitation availability, has increased by approximately 20 mm (hotter, drier conditions) in this region (Flint *et al.* 2013; Rapacciuolo *et al.* 2014). Historical resurveys indicate that there have already been shifts in the alpine communities in this mountain range with a changing climate (Kopp & Cleland 2014). Between 1961 - 2010 there was an upward shift of the sub-alpine shrub *Artemesia* and a decrease in the abundance of multiple alpine cushion plants at the subalpine – alpine ecotone attributed to a concurrent decrease in mean annual precipitation and an increase in summer minimum temperature (Kopp & Cleland 2014). With projected future climate change, many species in the White Mountains are predicted to become locally extinct (Van de Ven *et al.* 2007). I have built on this observational research with field experiments manipulating both temperature and moisture availability in multiple locations across the alpine zone of this xeric mountain range.

I surveyed community composition in nine sites that ranged in elevation across the alpine zone in the White Mountains. In each site, I experimentally increased summertime temperature and precipitation from 2015 to 2017 and quantified shifts in the alpine plant community in response to the manipulations. I asked whether thermophilization of the communities occurs in response to experimental heating, and if this effect is ameliorated by experimental watering. This question was addressed with both a community dissimilarity analysis and community-weighted climatic niche analysis. Due to potential community lags shaped by the physical and biological characteristics of the alpine zone (rugged topography, long-lived species, limited dispersal) (Alexander *et al.* 2017), I hypothesize that thermophilization will be primarily driven by the shifts in species proportional abundances rather than species immigration or local extinction. I expect to observe an increase in the abundance of species with higher climatic niche values – more hot, dry adapted – relative to aggregate community climate niches.

METHODS

Study Site & Design

The White Mountain range is a narrow, steep range that spans the California-Nevada border in the Western US. The alpine zone in the White Mountains extends from 3500 – 4344m (White Mountain peak) and is unusually xeric and depauperate in plant diversity relative to alpine areas worldwide (Körner 2003). The rain shadow of the nearby Sierra Nevada reduces the precipitation delivered to the White Mountains, particularly for wintertime snow (Lloyd & Mitchell 1973; Rundel *et al.* 2008). Sitting at an intersection between multiple floristic regions, the White Mountain alpine flora originates from the Sierra Nevada, Great Basin/Mojave desert, and Rocky Mountain floras (Billings 1978; Morefield 1992) and is predominantly made up of long-lived, slow-growing perennials including chamaetophytes, cushion plants, herbaceous dicots and graminoids (Table 1) (Spira 1987; Rundel *et al.* 2008; Kopp & Cleland 2014). Many common alpine species of the White Mountains can also be found in the Sierra Nevada alpine, as well as in surrounding lower montane and cold desert landscapes (Rundel *et al.* 2008).

The plant community was surveyed in nine sites in the alpine zone in the White Mountains during the 2015, 2016, and 2017 summer growing seasons. These sites spanned elevational, as well as temperature, soil moisture, and snow persistence gradients. The

elevational range of the sites was 3494 – 4028 m. Mean accumulated degree-days (sum of daily temperature above 0ºC) ranged from 732-1289 ºC/days, mean summertime soil moisture ranged from 9 – 33 %, and mean numbers of days with cover ranged from 62 – 171 days (for microclimate methods see Chapter 1). Geologic type has a large effect on plant community composition in the White Mountains (Van de Ven *et al.* 2007). Our study targeted a single geologic type (granite) in order to focus on the spatial and temporal effects of warming and soil moisture, and avoiding additional interactions with soil type. Restricting our sites to this geologic type precluded covering the highest elevation plant communities in the White Mountains. This study was part of a larger project examining demography of a target species (Chapter 1, Chapter 2). As a result, the communities are those found in locations where this species occurs, and tend to be on somewhat deeper soils and flatter slopes compared to the landscape overall (Pollak 1997).

Between August 1 – 15th in each of three years (2015-2017),I quantified presence and frequency of all alpine plants in 8–10 30x30 cm plots within each site. Each square plot was divided into 49 4x4 cm sub-squares with a 1 cm buffer on all sides of the plot. Frequency of each species was counted as the number of cells in which live tissue was present in a plot and served as our metric for species abundance. In each plot, I also performed ocular estimate of percent cover of live vegetation, rock, scree, bare ground and litter.

In each of these nine sites, I manipulated climatic conditions with a fully-factorial experiment augmenting growing season temperature and precipitation for three summers (2015, 2016, 2017). Summertime temperature was increased with passive warming chambers placed on plots annually within a week after snow melt-out. The chambers were constructed of double-walled poly-carbonate and were hexagonal with a height of 30.5 cm and a width of 60 cm at the widest point. Summer precipitation was manipulated by the evenly spaced addition of 1 liter of water applied five times per plot throughout the summer growing season. Impacts of the treatments were assessed with iButton Thermochrons (Maxim, San Jose USA) in each plot and manual measurements of soil moisture with a Hydrosense TDR (Campbell Scientific, Logan USA) conducted at intervals of 2 days after application of additional water (Chapter 2). The chambers significantly increased the daily minimum temperatures by 0.8°C and the accumulated degree-days by 53°C/days (5% increase of the mean accumulated degree-days under ambient conditions) (Chapter 2). The heating treatment did not have a measurable drying effect and there was no measurable effect of the watering treatment on the soil moisture (Chapter 2).

Community Composition Analyses

I performed a non-metric dimensional scaling ordination of the community composition data in order to visualize how changes in the presence and abundance of individual species influenced the overall community turnover across our study sites (Anderson *et al.* 2011). Using a permutational multivariate analysis of variance (MANOVA), I quantified the influence of elevation as well as the microclimatic gradients (soil moisture, temperature, and snowpack) on the variation in community composition (Anderson *et al.* 2011). I also used a MANOVA to quantify the effects of the experimental manipulations and their interactions on the community variation within each site for each separate year. All multivariate analyses used Bray-Curtis community dissimilarity based on species abundance and were performed with the VEGAN package in R (Dixon 2003). Significance of model parameters was determined with 10,000 permutations. I also examined changes in species richness and vegetation percent cover in

response to the climate manipulations with separate linear mixed effects models including fixed effects of heating, watering, as well as their interaction, and random effects of site and year.

Climatic Niche Analysis

I quantified thermophilization as a shift in a community-weighted climatic niche (CCN) for each site. A CCN is an abundance-weighted metric of a community (similar to weighted trait mean values) derived from the component species' niches, and can be based on any climate variable or indicator variable of interest (Gottfried *et al.* 2012; De Frenne *et al.* 2013). The weighting gives abundant species a larger effect on the community's CCN. I based our CCN on climatic water deficit (CWD), an important climatic determinant of vegetation distributions that takes into account the influence of both temperature and soil moisture, as well as their combined seasonality (Stephenson *et al.* 1990). CWD is an integrative measure of when energy availability (temperature) exceeds water supply (precipitation), with higher values indicating hotter, drier conditions, and lower values indicating cooler, wetter conditions (Stephenson *et al.* 1990; Flint *et al.* 2013).

The niches of the component species were calculated based on their current regional distributions across California (Lee-Yaw *et al.* 2016). Specimen localities of all species present in our study were compiled from a recently published extract from the Consortium of California Herbaria specimen database filtered for taxonomic and geographic accuracy (Baldwin *et al.* 2017). Using a 270m raster of average CWD (1981 - 2010) for California, I extracted CWD values for each specimen locality (Flint *et al.* 2013). The species-specific climatic niche was calculated as the average of the extracted CWD value across all localities for each species. The mean, 25th, and 75th percentile CCN for each plot in each site was calculated using these species-specific climate niches and weighted by the frequency of each species in each plot.

I first examined how the mean CCN across our study sites related to the elevational and microclimatic gradients with linear mixed effects models using only data from non-manipulated (ambient) plots. For the elevation gradient, the ambient CCN of each plot was regressed against the elevation (linear and quadratic) with random effects of year and plot. For the microclimatic gradients, the ambient CNN was regressed against the site-specific summertime accumulated degree-days, summertime soil moisture, and days of persistent snow-pack averaged across years (random effects of year and plot). To assess thermophilization with the experimental warming and watering, I compared the mean, 25th and 75th percentiles of the CCN in experimental plots relative to ambient plots. Shifts in the mean CCN represent mean changes in the community climatic niche and shifts in the upper and lower percentiles represent changes in presence or abundance of the hottest and coolest adapted species respectively (De Frenne *et al.* 2013). I built linear mixed-effects models with CCN (mean and percentiles) as the response variable with fixed additive and multiplicative effects of the experimental manipulations and random effects of site, plot, and year.

Finally, I examined whether the proportional abundance of each species was dependent on the species (*i*) having a lower or higher climatic niche relative to the aggregated ambient CCN for each site (*j*) ($\Delta_{niche\ (i,j)}$ = specific-species climatic niche$_i$ – CCN$_j$). Negative Δ_{niche} values indicate that a species has a low climatic niche (more cool, wet adapted) relative to dominant species in that site, and positive Δ_{niche} values indicate that a species has a high climatic niche (more hot, dry adapted) relative to dominant species in that site. To test if the experimental manipulations interacted with Δ_{niche} to shape species' proportional abundance I built a linear mixed-effects model with species-specific abundance as a response variable, fixed effects of

Δ_{niche}, heating, watering, and their three-way interaction, and random effects of site, plot, year, and species. Significance of each parameter from all models was estimated using Type II Wald χ^2 tests and the differences between treatment groups was determined by contrast tests with Tukey adjustments to account for multiple comparisons. All mixed-effects modeling was performed in R 3.4.3 with the lme4 package (Bates *et al.* 2013; R Core Team 2017).

RESULTS

Community Composition Analyses

Our analysis revealed that variation in community structure as measured by Bray-Curtis dissimilarity was significantly explained by elevation and additionally by each of the microclimatic gradients. The first axis of community variation was explained by changes in both elevation and soil moisture with species associated with wetter conditions more likely found at lower elevations (Figure 1). The second axis of community variation was explained by changes in accumulated degree-days and snow-pack persistence (Figure 1). Just under 50% of the community variation is explained by this combination of geographic and microclimatic gradients (Table 2). Elevation explains the largest amount of the community variation (22%), followed by accumulated degree-days (14%), soil moisture (6%), and days of snow-pack (5%) (Table 2).

Despite this evident sensitivity of the community variation to the microclimate gradients there was limited response of the community composition to the experimental manipulations. In 2017, the interaction between heating and watering significantly explained 0.1% of the community variation (p = 0.029 based on 10,000 permutations). However, no effect was apparent in any of the prior years of the experiment. Across all years both heating and watering decreased richness (β_{heat} = -0.467, p = 0.013; β_{water} = -0.523, p = 0.006; $\beta_{heat*water}$ = -0.162, p = 0.710) (Figure 4D). Ambient conditions had a mean of 9 species per plot and heating and watering reduced richness by approximately 1 species ($\mu_{ambient}$ = 8.986, μ_{heat} = 8.518, μ_{water} = 8.463, $\mu_{heat*water}$ = 7.833, df = 244, $p_{ambient-heat*water}$ = 0.001) (Figure 4A). Mean vegetation cover was 54% across all sites and significantly increased to 57% with experimental heating (β_{heat} = 2.681, p = 0.0268). The percent cover of vegetation was not impacted by experimental watering (χ^2_{water} = 0.016, df = 1, p = 0.898; $\chi^2_{heat*water}$ = 0.940, df = 1, p = 0.332).

Climatic Niche Analysis

Climatic niche values for the species found across these sites ranged widely (CWD = 176 mm – 710 mm) and species with distributions associated with both high CWD (hot, dry adapted) and low CWD (cool, wet adapted) conditions were abundant (Table 1; Figure 2). The mean CCN across all sites ranged from 196 – 498 mm, the CCN 25th percentile ranged from 167 – 308 mm, and the CCN 75th percentile ranged from 216 – 764 mm. CCN increased with accumulated degree-days (Figure 3B; $\beta_{Degree-days}$ = 0.246, p = 0.001) and decreased with available soil moisture (Figure 3C; $\beta_{Soil-moisture}$ = -4.624, p = 0.003). In contrast, the mean CCN did not vary predictably across the snow persistence gradient (Figure 3D; $\beta_{Snow-days}$ = 0.474, p = 0.174). Across the geographic gradient (elevation), the mean ambient CCN was highest at mid elevations (Figure 3A; $\beta_{Elevation}$ = 7.571, p = 0.001; $\beta_{Elevation}^2$ = -0.001, p = 0.001).

The CCN 75th percentile increased with experimental heating (β_{heat} = 39.978, p = 0.013) (Figure 4B). When averaged across the watering treatment, there was a significant difference between the ambient and heated plots across all sites ($p_{ambient-heat}$ = 0.014); under ambient conditions the mean 75th percentile CCN was 366 and under heated conditions the mean 75th

percentile was 413mm (an increase of 12.8%). This increase in the upper percentile of the CCN indicates that heating drove an increase in the presence and/or abundance of the species adapted to the hottest, driest conditions — evidence of thermophilization. This effect was not mediated by the watering treatment (χ^2_{water} = 0.246, df = 1, p = 0.620; $\chi^2_{heat*water}$ = 0.164, df = 1, p = 0.645). Also, despite a general trend of the mean CCN increasing with heating and an amelioration of this effect with watering (Figure 4C), the experimental manipulations had no significant effect on the mean CCN (χ^2_{heat} = 0.930, df = 1, p = 0.335; χ^2_{water} = 0.0001, df = 1, p = 0.995; $\chi^2_{heat*water}$ = 0.086, df = 1, p = 0.769) or the 25th percentile CCN (χ^2_{heat} = 0.866, df = 1, p = 0.352; χ^2_{water} = 0.310, df = 1, p = 0.578; $\chi^2_{heat*water}$ = 0.985, df = 1, p = 0.321) (Figure 4D).

Experimental heating drove an increase in the proportional abundance for species that were hot, dry adapted relative to their surrounding community ($+\Delta_{niche}$) and a decrease in proportional abundance for species that were cool, wet adapted relative to their surrounding community ($-\Delta_{niche}$) (Figure 5; $\beta_{heat*\Delta_{niche}}$ = 4.426e-05, p = 0.040). There were no additional significant additive or interaction effects of Δ_{niche}, heating, or watering on proportional abundance ($\chi^2_{\Delta_{niche}}$ = 1.237, df = 1, p = 0.266; χ^2_{heat} = 0.170, df = 1, p = 0.680; χ^2_{water} = 1.970, df = 1, p = 0.160; $\chi^2_{heat*water}$ = 0.025, df = 1, p = 0.873; $\chi^2_{water*\Delta_{niche}}$ = 1.349, df = 1, p = 0.245; $\chi^2_{heat*water*\Delta_{niche}}$ = 0.627, df = 1, p = 0.428).

DISCUSSION

I examined effects of experimental warming and watering on plant communities in a xeric high-elevation alpine zone. Under warmer climatic conditions, thermophilization of this community was supported by two lines of evidence: 1) an increase in the 75th percentile CCN indicating an increase of hot, dry adapted species within each site and 2) a positive interaction between experimental heating and Δ_{niche} representing species with higher climatic niche values relative to their community increasing in proportional abundance. Additionally, a small amount of the overall community variation was explained by the combination of heating and watering in the final year of the experiment. However, despite both community composition and CCNs varying across both temperature and soil moisture gradients, experimental watering did not ameliorate the effect of heating in the climate niche analysis. Concordant with evidence of thermophilization, I also found that overall abundance increased and species richness decreased with experimental heating. Together, these results indicate that with warmer conditions the White Mountain's alpine zone will be made up of less diverse plant communities dominated by species associated with hotter, drier conditions.

Consistent with most high-elevation montane systems, most species in this alpine community were regionally associated with cool, wet conditions (Körner 2003). Although our sites span a limited elevation gradient, I still saw a large variation in both the climatic niche means of the species present and in the aggregated ambient CCNs. This variation was due to the microclimatic gradients; CCN increased with accumulated degree-days and decreased with soil moisture. These significant relationships indicate that our CCN metric based on species regional distributions is representative of species local distributions across fine-scale climatic gradients (Scherrer & Korner 2011). In conjunction with the significant community variation explained by the temperature, soil moisture, and snow-pack gradients, this supports the use of a CCN metric that encompasses both temperature and moisture availability and strengths our conclusions concerning positive shifts in the CCN with the experimental heating. Cooler, drier conditions at higher elevations, and wetter, warmer conditions at low elevations resulted in the highest CCN values occurring at mid elevations. Therefore, with thermophilization we may predict a

contraction in both the upper and lower ecotone of the alpine communities due to differing climate limitations (temperature versus soil moisture) (Tingley *et al.* 2012; Suding *et al.* 2015), as opposed to shifts to higher elevation as observed in many other alpine systems (Rixen & Wipf 2017; Rumpf *et al.* 2017).

In this temperature and soil moisture limited alpine system, I show that minimally warmer conditions may drive a community shift towards relatively hotter, drier adapted species within a short timeframe (3 years). This work is in agreement with others that found an increase in hot-adapted species, but a lesser subsequent decrease in cool-adapted species (Gottfried *et al.* 2012; Alexander *et al.* 2017; Kulonen *et al.* 2018). I observed no response to the experimental heating in the mean CCN or for the coolest, wettest adapted species (25th percentile CCN). This result may testify to the resistance of alpine plant communities where community inertia resists changing climate conditions and leads to disequilibrium dynamics where species can be distributed in areas with unsuitable climate (Körner 2003; Svenning & Sandel 2013). This lack of response of cool-adapted plant species has been termed *extinction debt* and is hypothesized to be driven by lags in both population and community dynamics (Dullinger *et al.* 2012; Hylander & Ehrlén 2013). Loss of cool adapted alpine endemics through species interactions rather than by direct effects is predicted to be a slower process due to lags in dispersal, establishment, and local extinction of alpine species (Alexander *et al.* 2017; Rixen & Wipf 2017).

However, flora in an arid alpine system may be especially vulnerable to climate change (Engler *et al.* 2011). In contrast to Rumpf *et al.* (2017) and Steinbauer *et al.* (2018) who found an increase in richness and overall vegetation cover with a warmer climate, I found that richness decreased with experimental heating. This pattern of decreased richness with warming conditions in more water-limited systems was also found in Mediterranean mountains and on the driest aspect of single mountaintops (Pauli *et al.* 2012; Winkler *et al.* 2016b). However, I did find an increase overall vegetation cover with warming (infilling). Warming conditions may have allowed for more growth of the dominant species initially by reducing temperature limitation (Gilman *et al.* 2010), despite the possibility of system's productivity being also limited by soil moisture conditions (Winkler *et al.* 2016a). The increase in overall abundance may be driven by an encroachment of competitors that will eventually drive loss of cool, wet adapted species (Graae *et al.* 2011; Lembrechts *et al.* 2017; Steinbauer *et al.* 2018).

Alpine plants are long-lived, have extensive carbohydrate storage, and are adapted to dramatic fluctuation in environmental conditions (Körner 2003; Graae *et al.* 2017). Consequently these alpine species may be less likely to be locally extirpated by the direct effect of changing climate on their physiology and demography, but more likely to be displaced by competition with faster-growing species associated with hotter climatic conditions (Alexander *et al.* 2015; Kopp & Cleland 2015; Rumpf *et al.* 2017). Although high climate heterogeneity in alpine zones may allow species to more easily track their suitable climatic conditions, these fine-scale climate gradients may also reduce the amount suitable habitat for each species, as well as facilitate uphill movement of potential dominant competitors, increasing competitive pressures (Scherrer & Korner 2011; Graae *et al.* 2017; Kulonen *et al.* 2018). On the other hand, the influence of positive interactions are thought to have a large effect in sparse, xeric habitats like our study system (Michalet *et al.* 2014; Alexander *et al.* 2017). Increases in abundance may increase the possibility for facilitative interactions between or within species, reducing additional species loss (Callaway *et al.* 2002; Cavieres *et al.* 2014).

Although previous work found that alpine community responses to warming conditions is mediated by water availability (Engler *et al.* 2011; Elmendorf *et al.* 2012; Winkler *et al.* 2016a),

I observed minimal influences of the watering treatment, both additively and in interaction with the experimental heating. This lack of a response may be due to the addition of water being too limited to influence community dynamics. Although the aim was to increase the amount of historical summertime precipitation by 55%, this amount may not have been relevant within the duration of this experiment. In addition, although I manipulated summertime precipitation I did not modify wintertime precipitation (*e.g.,* snow), an important driver of community composition in many alpine systems (Stanton *et al.* 1994; Körner 2003; Jonas *et al.* 2008; Mark *et al.* 2015). Despite large variability in snowpack spatially and temporally (Chapter 1), it remained a consistent predictor of community composition, albeit not CCN, across our study sites. The patterning of snowpack across the landscape has a strong influence on soil moisture availability throughout the growing season (Isard 1986; Jonas *et al.* 2008; Litaor, Williams & Seastedt 2008). Our lack of a quantifiable change in soil moisture with the watering treatment or heating treatment (due to soil drying) indicates that snowpack persistence and timing of melt-out had a larger effect on the soil moisture gradient and the plant community composition than our manipulations (Wipf *et al.* 2009). Lastly, the low water holding capacity of granitic soils and the reduced amount of organic soil in alpine systems may also have reduced residence time of any experimental precipitation inputs, limiting their impact on community dynamics (Wenk & Dawson 2007; Kulonen *et al.* 2018).

Conclusions

Understanding how species and communities shift locally and regionally poses a great challenge as we manage for resilience in the face of a changing climate (Pecl *et al.*, 2017). This study helps inform how alpine plant communities are responding to climate change at local scales in a xeric mountain range. As predicted, I observed thermophilization of the alpine plant communities in the White Mountains with experimental warming adding to the short list of examples of thermophilization in xeric mountain ranges (Pauli *et al.* 2012). These community-weighted climatic niche responses to only three years of heating of less than 1ºC, paired with an overall reduction in richness and increase in vegetation cover indicate that the alpine plant community in more xeric alpine systems may be highly sensitive to changing climatic conditions. This is in line with other work that predicted larger montane habitat loss with climate change under water-limited scenarios (Engler *et al.* 2011; Rixen & Wipf 2017). Future work will investigate responses of traits besides the community-weighted climate niche, such as those signifying competitive, facilitative, or dispersal abilities, to better understand how species interactions with novel climate will further illuminate how we expect alpine vegetation to respond to a changing climate (Alexander *et al.* 2017).

TABLES & FIGURES

Table 1. Study species with associated codes used in Figure 1, number of sites that the species were present in, mean frequency within a plot for sites in which the species were present, and species-specific climatic niche means (CNM) based on the species regional distribution.

Species	Code	Number of Sites Present	Mean Frequency	CNM (mm)
Antennaria media	A.med	9	25	257
Ivesia lycopodioides	I.lyc	9	25	256
Lewisia pygmaea	Lepy	9	17	269
Carex duriuscula	C.dur	8	24	176
Pyrrocoma apargioides	Pyro	8	5	319
Rumex paucifolius	R.pau	8	3	353
Koelaria macrantha	K.mac	7	11	710
Festuca brachyphylla	F.brach	6	6	263
Trifolium andersonii	T.and	6	22	588
Carex vernacula	C.ven	5	8	264
Phlox condensata	P.con	5	6	314
Poa glauca subsp. rupicola	P.gla	5	14	226
Androsace septentrionalis	A.sep	4	5	222
Castilleja nana	C.nan	4	2	282
Erigeron pygmaeus	E.pyg	4	2	268
Mimulus suksdorfii	M.suk	4	9	424
Penstemon heterodoxus	P.het	4	12	322
Selaginella watsonii	S.wat	4	9	390
Eriogonum ovalifolium	E.oval	3	6	405
Gentiana newberryi	G.new	3	23	340
Mimulus primuloides	M.prim	3	25	402
Muhlenbergia richardsonis	M.ric	3	1	477
Pedicularis attollens	P.att	3	12	355
Trisetum spicatum	T.spic	3	14	309
Lupinus lepidus	L.lep	2	9	431
Eremogone kingii var. glabrescens	A.kin	2	3	344
Boechera lemmonii	B.lem	1	6	234
Carex breweri	C.bre	1	7	220
Comastoma tenellum	C.ten	1	7	311
Elymus elymoides var. californicus	E.ely	1	2	388
Erigeron clokeyi	E.clok	1	1	420
Sagina saginoides	S.sag	1	1	488
Solidago multiradiata	S.mul	1	5	326
Townsendia condensata	T.con	1	1	202
Draba sp.	Draba sp.	7	4	-
Poa sp.	Poa sp.	4	4	-
Potentilla sp.	Potentilla sp.	3	1	-

Table 2. MANOVA output from the multivariate model estimating the effect of the geographic and microclimatic gradients on the community Bray-Curtis dissimilarity. Significance of the variation explained by each parameter determined by permutation analysis (10,000 permutations).

	Degrees of Freedom	Sums of Squares	Mean Squares	F Model	R^2	Probability (>F)
Elevation	1	3.748	3.748	32.494	0.215	0.001
Degree-days	1	2.504	2.504	21.708	0.144	0.001
Days of Snow	1	0.835	0.835	7.240	0.048	0.001
Soil Moisture	1	0.967	0.967	8.383	0.056	0.001
Residuals	81	9.342	0.115		0.537	
Total	85	17.396			1	
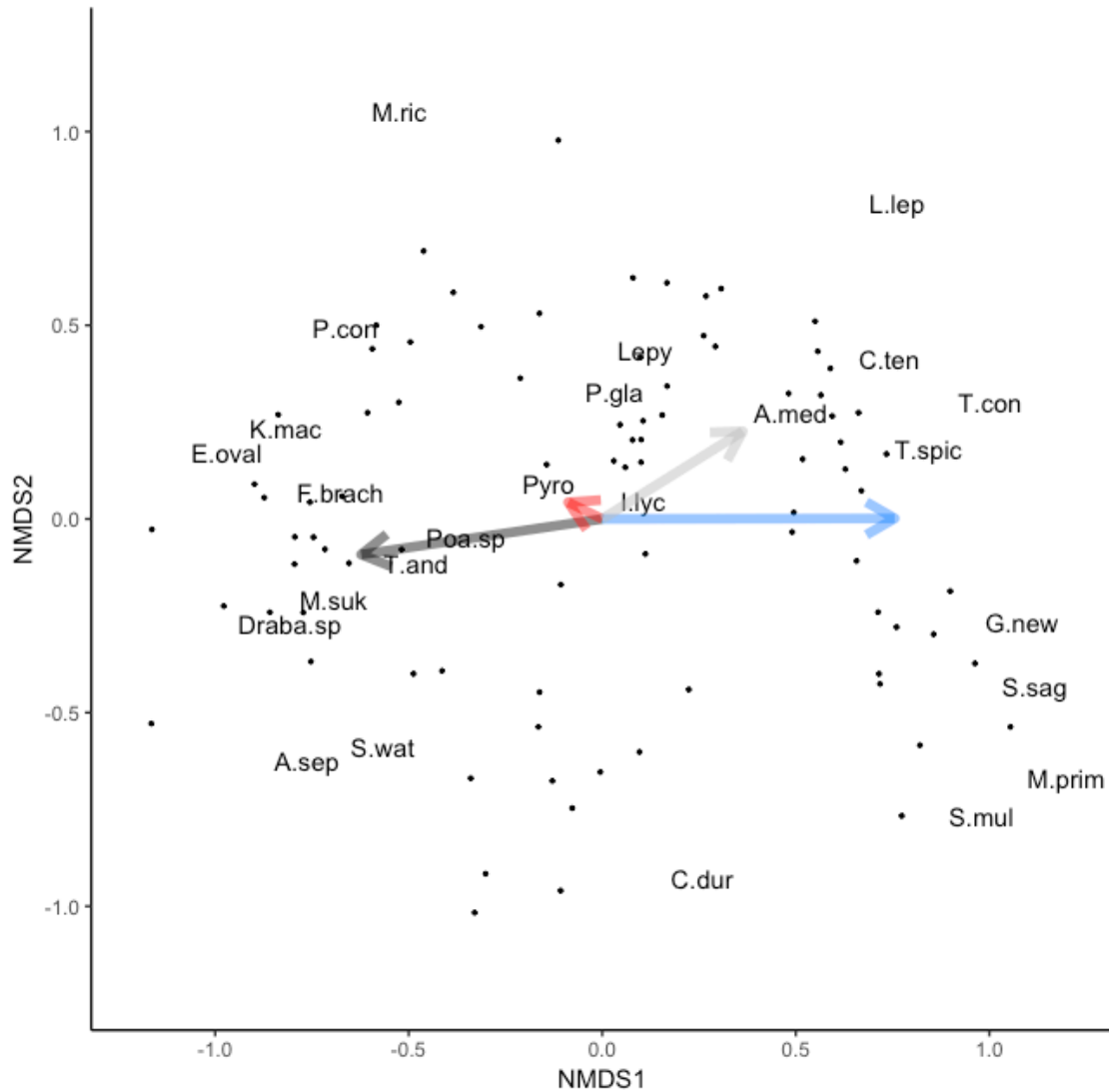
Figure 1. Non-metric dimensional scaling ordination of the communities across all sites. Arrows represent axis (direction) and magnitude (length) of variation explained by elevation (black, m), accumulated degree-days (red, ºC), snow-cover (grey, days) and soil moisture (blue, %) within the bi-dimensional space. Species codes from Table 1. Variation explained in multivariate space by each component in Table 2.
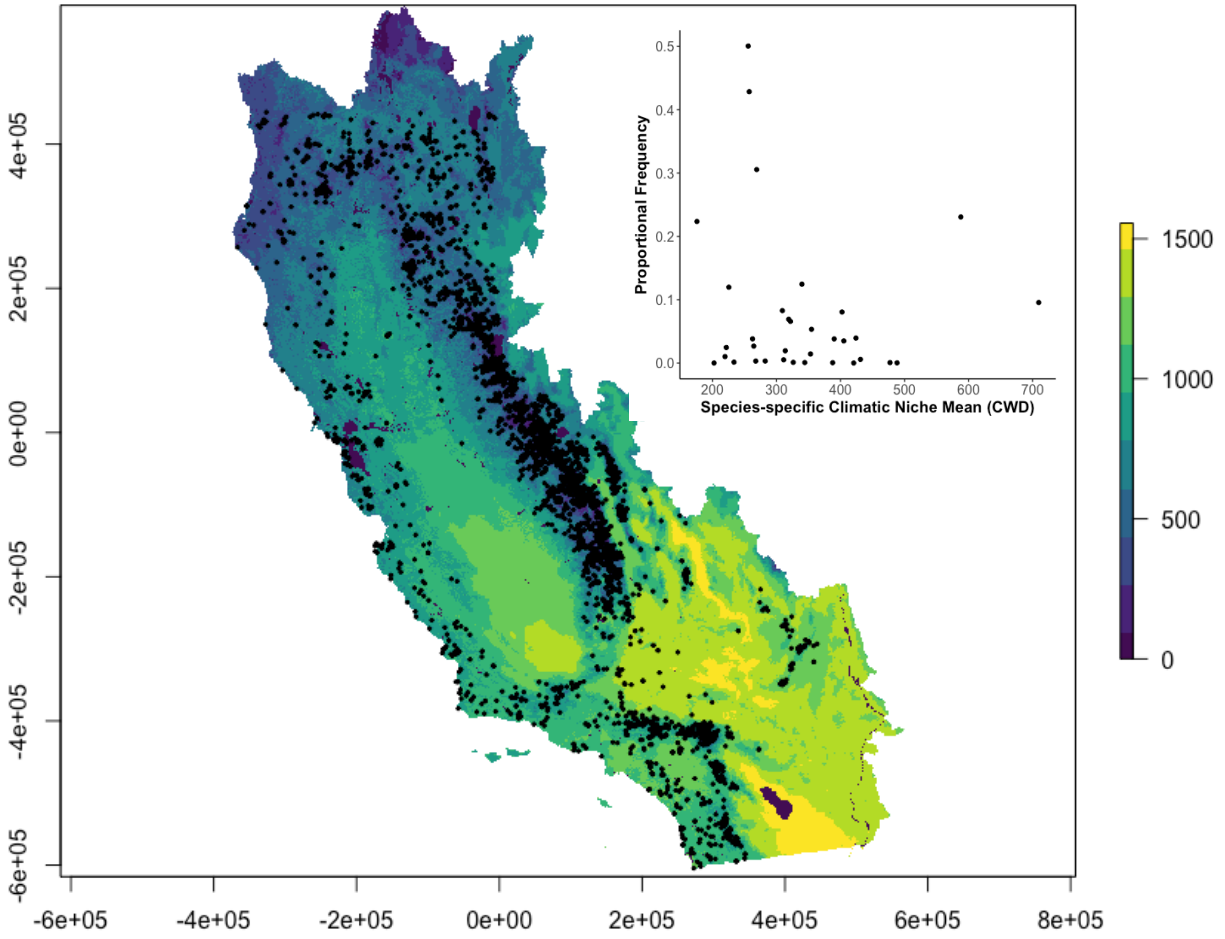
Figure 2. Map of CWD (mm) for California with points representing the locality data for all study species used to calculate the species climatic niche means. In subset, the relationship between the proportional frequency averaged across all sites for each species and the species climatic niche mean.
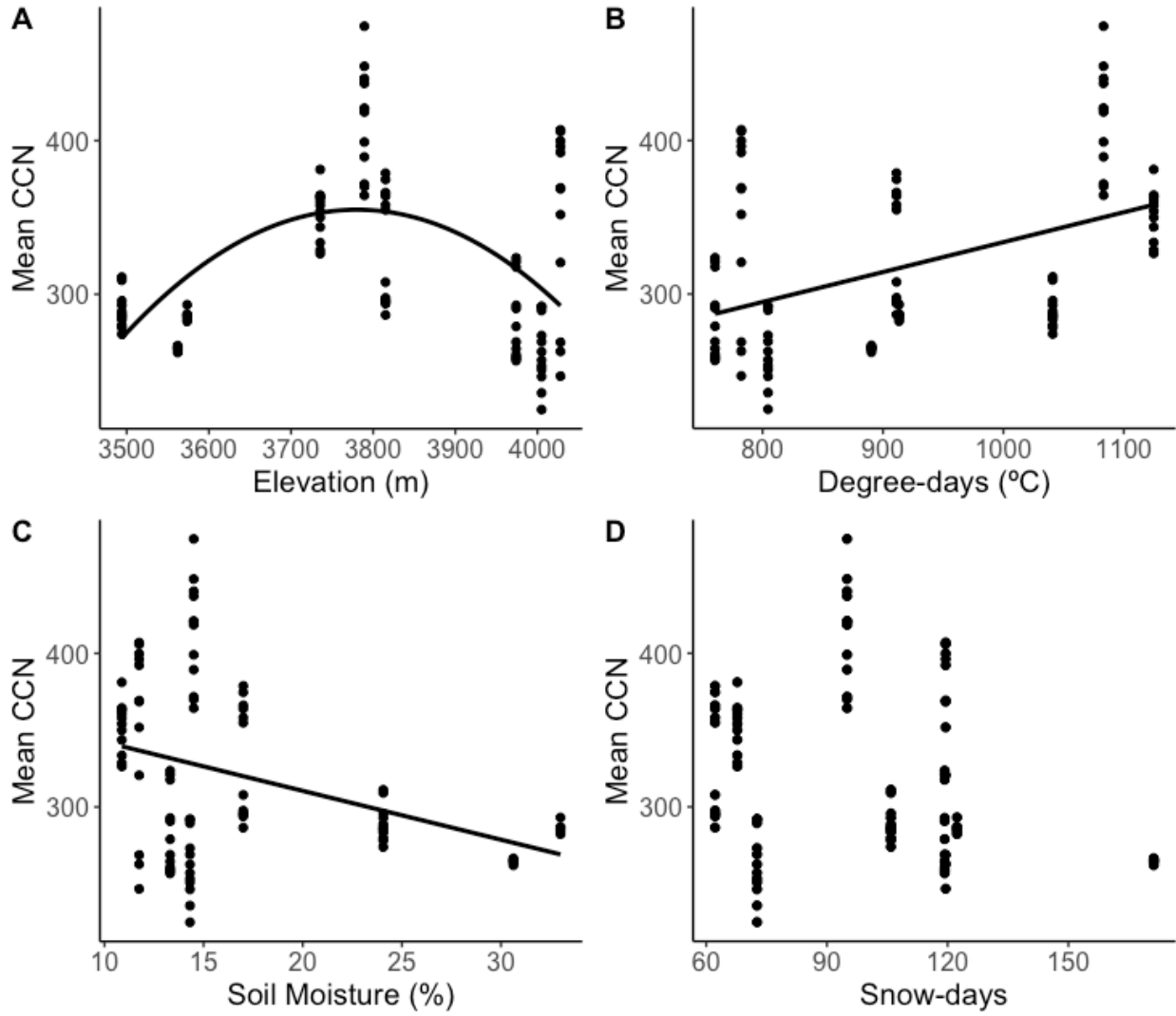
Figure 3. Mean ambient community-weighted climatic niche (CCN) across the A) elevational and climatic gradients (B-D). Lines represent significant model fits.
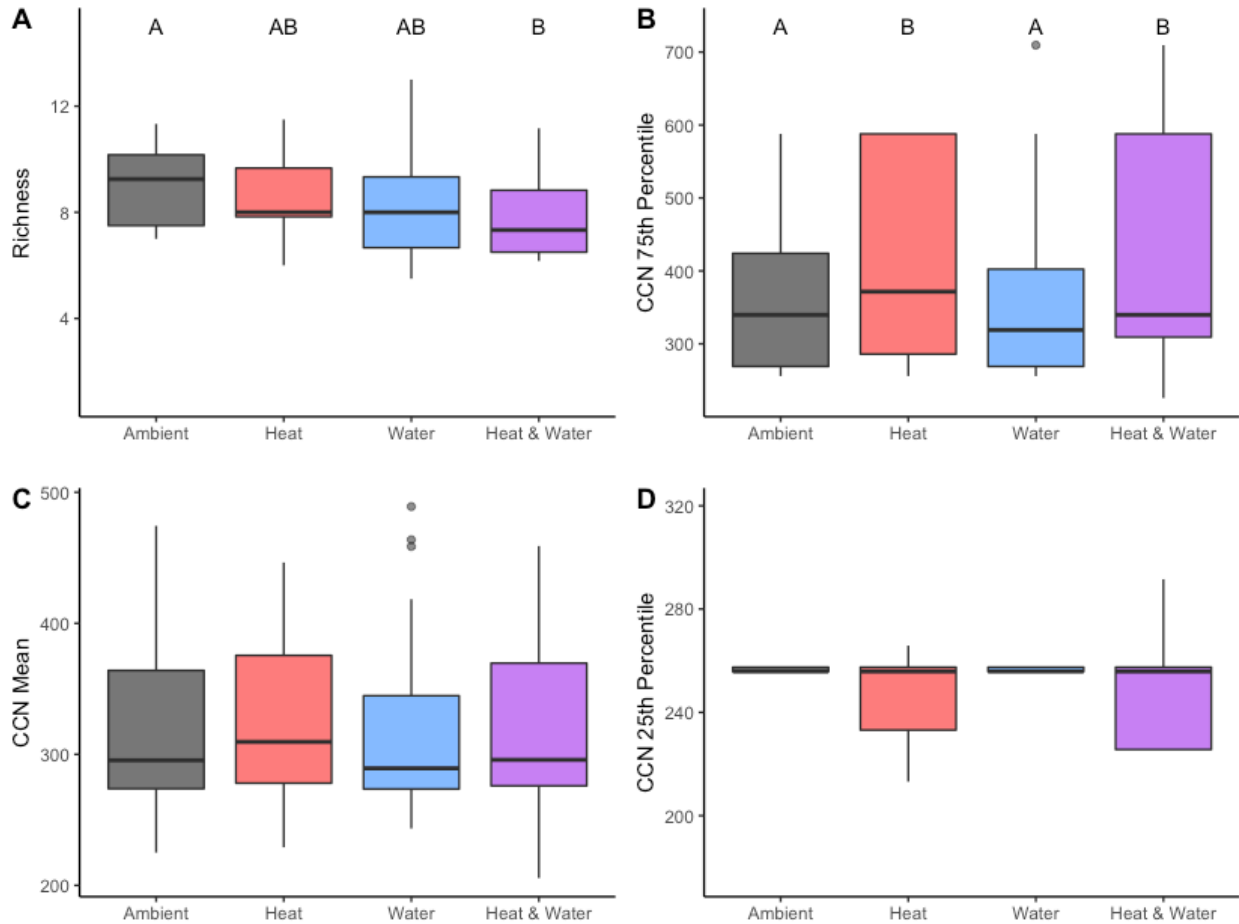
Figure 4. A) Mean CCN responses to the climate manipulations shows a non-significant trend of higher mean CCN with heating, and a lessening of this effect when heating is in combination with experimental watering. There are no significant differences between any of the treatment groups. B) The CCN 75th percentile significantly increased with the experimental heating. C) The CCN 25th percentile had no significant response to the treatments. D) Species richness deceased with experimental heating and watering. Letters indicate significantly different groups.
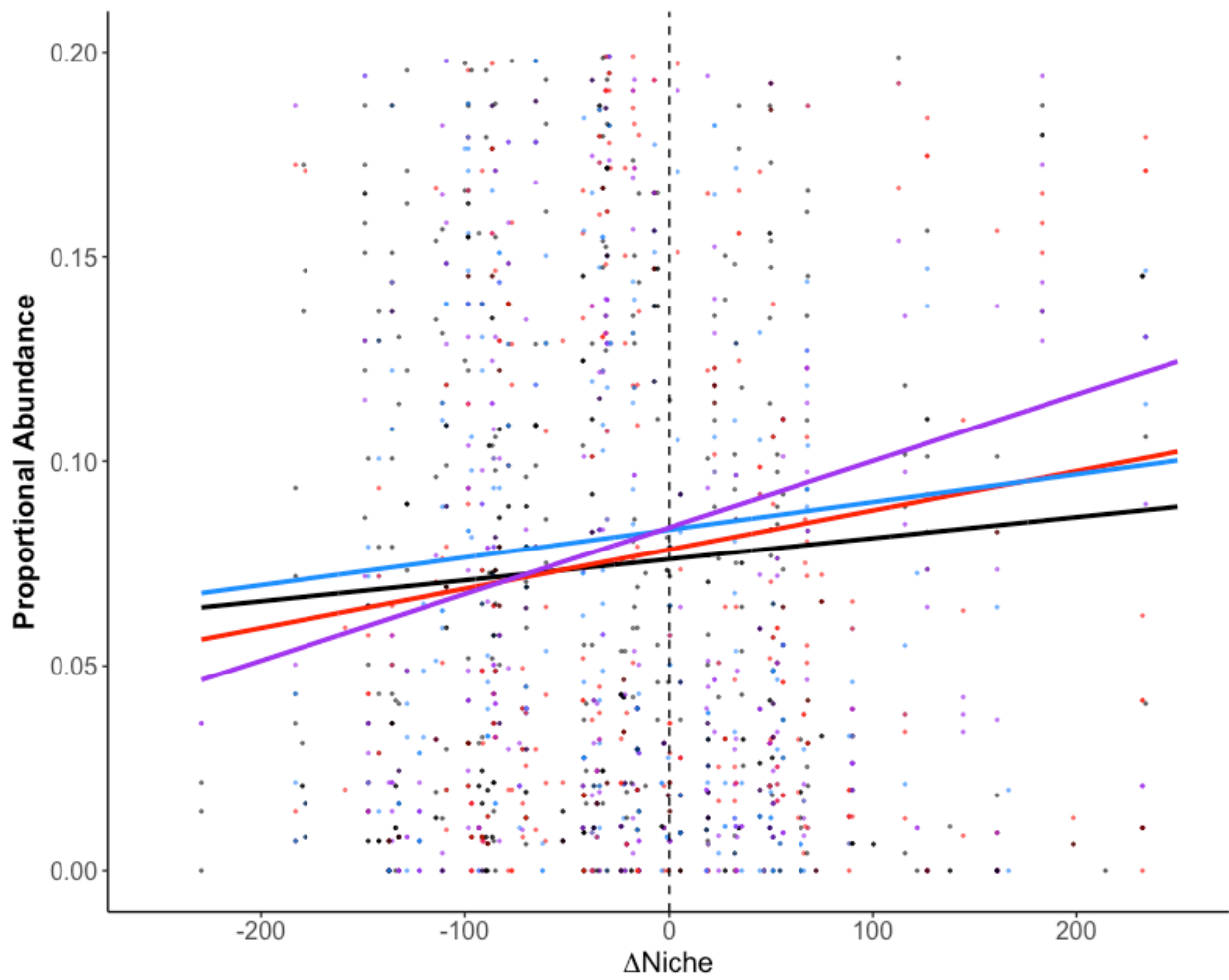
Figure 5. The proportional abundance of species relative to the difference between the species climatic niche mean and the aggregated ambient site CCN mean (Δ_{niche}). Each point represents a species by site combination. The lines represent model fits for each treatment group (ambient (black), heating (red), watering (blue), heating and watering (purple)).

REFERENCES

Abeli, T., Gentili, R., Mondoni, A., Orsenigo, S. & Rossi, G. (2014) Effects of marginality on plant population performance. *Journal of Biogeography*, **41**, 239–249.

Adler, P.B., Dalgleish, H.J. & Ellner, S.P. (2012) Forecasting plant community impacts of climate variability and change: When do competitive interactions matter? *Journal of Ecology*, **100**, 478–487.

Aikens, M.L. & Roach, D. a. (2014) Population dynamics in central and edge populations of a narrowly endemic plant. *Ecology*, **95**, 1850–1860.

Alexander, J.M., Burgess, I., Essl, F., Haider, S., Kueffer, C., Mcdougall, K., Milbau, A., Rabitsch, W., Rew, L.J. & Sanders, N.J. (2017) Lags in the response of mountain plant communities to climate change. *Global Change Biology*, **0**, 1–17.

Alexander, J.M., Diez, J.M. & Levine, J.M. (2015) Novel competitors shape species' responses to climate change. *Nature*, **525**, 515–518.

Amburgey, S.M., Miller, D.A.W., Campbell, E.H., Tracy, G., Michael, G.R., Jonathan, F.B., Mark, L.R., Hughson, W., Brand, A.B., Davis, C.J., Hardin, C.R., Paton, P.W.C., Raithel, C.J., Relyea, R.A., Scott, A.F., Skelly, D.K., Skidds, D.E., Smith, C.K. & Werner, E.E. (2018) Range position and climate sensitivity : The structure of among-population demographic responses to climatic variation. *Global Change Biology*, **24**, 439–454.

Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L., Sanders, N.J., Cornell, H. V, Comita, L.S., Davies, K.F., Harrison, S.P., Kraft, N.J.B., Stegen, J.C. & Swenson, N.G. (2011) Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecology letters*, **14**, 19–28.

Angert, A.L. (2009) The niche , limits to species ' distributions , and spatiotemporal variation in demography across the elevation ranges of two monkeyflowers. , **106**.

Angert, A.L., Bayly, M., Sheth, S.N. & Paul, J.R. (2018) Testing Range-Limit Hypotheses Using Range-Wide Habitat Suitability and Occupancy for the Scarlet Monkey flower (Erythranthe cardinalis). *The American Naturalist*, **191**, 1–14.

Ashcroft, M.B. & Gollan, J.R. (2013) Moisture, thermal inertia, and the spatial distributions of near-surface soil and air temperatures: Understanding factors that promote microrefugia. *Agricultural and Forest Meteorology*, **176**, 77–89.

Baldwin, B.G., Thornhill, A.H., Freyman, W.A., Ackerly, D.D., Kling, M.M., Morueta-holme, N. & Mishler, B.D. (2017) Species richness and endemism in the native flora. *American Journal of Botany*, **104**, 487–501.

Barrett, R.T.S., Hollister, R.D., Oberbauer, S.F. & Tweedie, C.E. (2015) Arctic plant responses to changing abiotic factors in northern Alaska. *American Journal of Botany*, **102**, 2020–2031.

Bates, D., Bolker, B., Maechler, M. & Walker, S. (2013) Package "lme4." , 1–113.

Bell, K.L. & Bliss, L.C. (1979) Autecology of Kobresia bellardii : Why Winter Snow Accumulation Limits Local Distribution. *Ecological Monographs*, **49**, 377–402.

Bell, D.M., Bradford, J.B. & Lauenroth, W.K. (2014) Early indicators of change: divergent climate envelopes between tree life stages imply range shifts in the western United States. *Global Ecology and Biogeography*, **23**, 168–180.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. (2012) Impacts of climate change on the future of biodiversity. *Ecology Letters*, **15**, 365–377.

Benton, T.G. & Grant, A. (1999) Elasticity analysis as an importanct tool in evolutionary and population ecology. *Trends in ecology & evolution*, **14**, 467–471.

Billings, W.D. (1978) Alpine Pytogeography Across the Great Basin. *Intermountain Biogeography*, **2**, 105–117.

Boggs, C.L. & Inouye, D.W. (2012) A single climate driver has direct and indirect effects on insect population dynamics. *Ecology Letters*, **15**, 502–508.

Boyce, M.S., Haridas, C.V, Lee, C.T. & The Nceas Stochastic Demography Working Group. (2006) Demography in an increasingly variable world. *Trends in Ecology and Evolution*, **21**, 141–148.

Buckley, Y.M., Ramula, S., Blomberg, S.P., Burns, J.H., Crone, E.E., Ehrlén, J., Knight, T.M., Pichancourt, J.B., Quested, H. & Wardle, G.M. (2010a) Causes and consequences of variation in plant population growth rate: a synthesis of matrix population models in a phylogenetic context. *Ecology Letters*, **13**, 1182–1197.

Buckley, L.B., Urban, M.C., Angilletta, M.J., Crozier, L.G., Rissler, L.J. & Sears, M.W. (2010b) Can mechanism inform species' distribution models? *Ecology Letters*, **13**, 1041–1054.

Buizer, B., Weijers, S., Bodegom, P.M. van, Greve Alsos, I., Eidesen, P.B., Van Breda, J., De Korte, M., Van Rijckevorsel, J. & Rozema, J. (2012) Range shifts and global warming: ecological responses of Empetrum nigrum L. to experimental warming at its northern (high Arctic) and southern (Atlantic) geographical range margin. *Environmental Research Letters*, **7**, 1–10.

Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Pugnaire, F.I., Newingham, B. & Aschehoug, E.T. (2002) Positive interactions among alpine plants increase with stress. *Nature*, **417**, 844–848.

Caswell, H. (2001) *Matrix Population Models: Construction, Analysis, and Interpretation*, 2nd ed. Sinauer Associates, Sunderland, MA.

Cavieres, L.A., Badano, E.I., Sierra-Almeida, A., Gómez-González, S. & Molina-Montenegro, M.A. (2006) Positive interactions between alpine plant species and the nurse cushion plant Laretia acaulis do not increase with elevation in the Andes of central Chile. *New Phytologist*, **169**, 59–69.

Cavieres, L.A., Brooker, R.W., Butterfield, B.J., Cook, B.J., Kikvidze, Z., Lortie, C.J., Michalet, R., Pugnaire, F.I., Schöb, C., Xiao, S., Anthelme, F., Björk, R.G., Dickinson, K.J.M., Cranston, B.H., Gavilán, R., Gutiérrez-Girón, A., Kanka, R., Maalouf, J.P., Mark, A.F., Noroozi, J., Parajuli, R., Phoenix, G.K., Reid, A.M., Ridenour, W.M., Rixen, C., Wipf, S., Zhao, L., Escudero, A., Zaitchik, B.F., Lingua, E., Aschehoug, E.T. & Callaway, R.M. (2014) Facilitative plant interactions and climate simultaneously drive alpine plant diversity. *Ecology Letters*, **17**, 193–202.

Chardon, N.I., Cornwell, W.K., Flint, L.E., Flint, A.L. & Ackerly, D.D. (2015) Topographic, latitudinal and climatic distribution of Pinus coulteri : geographic range limits are not at the edge of the climate envelope. *Ecography*, **38**, 590–601.

Chen, I., Hill, J.K., Ohlemüller, R., Roy, D.B. & Thomas, C.D. (2011) Rapid range shifts of species of climate warming. *Science*, **333**, 1024–1026.

Compagnoni, A., Bibian, A.J., Ochocki, B.M., Rogers, H.S., Schultz, E.L., Sneck, M.E., Elderd, B.D., Iler, A.M., Inouye, D.W., Jacquemyn, H. & Miller, T.E.X. (2016) The effect of demographic correlations on the stochastic population dynamics of perennial plants. *Ecological Monographs*, **86**, 480–494.

Coutts, S.R., Salguero-Gómez, R., Csergo, A.M. & Buckley, Y.M. (2016) Extrapolating demography with climate, proximity and phylogeny: approach with caution. *Ecology Letters*, **19**, 1429–1438.

Cranston, B.H., Monks, A., Whigham, P.A. & Dickinson, K.J.M. (2015) Variation and response to experimental warming in a New Zealand cushion plant species. *Austral Ecology*, **40**, 642–650.

Crimmins, S.M., Dobrowski, S.Z., Greenberg, J.A., Abatzoglou, J.T. & Mynsberge, A.R. (2011) Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. *Science*, **331**, 324–7.

Crone, E.E., Ellis, M.M., Morris, W.F., Stanley, A., Bell, T., Bierzychudek, P., Ehrlén, J., Kaye, T.N., Knight, T.M., Lesica, P., Oostermeijer, G., Quintana-Ascencio, P.F., Ticktin, T., Valverde, T., Williams, J.L., Doak, D.F., Ganesan, R., McEachern, K., Thorpe, A.S. & Menges, E.S. (2013) Ability of matrix models to explain the past and predict the future of plant populations. *Conservation Biology*, **27**, 968–978.

Csergő, A.M., Salguero-gomez, R., Broennimmann, O., Coutts, S.R., Guisan, A., Angert, A.L., Welk, E., Stott, I., Enquist, B.J., McGill, B., Svenning, J.-C., Violle, C. & Buckley, Y.M. (2017) Less favourable climates constrain demographic strategies in plants. *Ecology Letters*, **0**, 1–12.

Dahlgren, J.P., Bengtsson, K. & Ehrlen, J. (2016) The demography of climate-driven and density-regulated population dynamics in a perennial plant. *Ecology*, **97**, 899–907.

Dalgleish, H.J., Koons, D.N., Hooten, M.B., Moffet, C.A. & Adler, P.B. (2011) Climate influences the demography of three dominant sagebrush steppe plants. *Ecology*, **92**, 75–85.

Dallas, T., Decker, R. & Hastings, A. (2017) Species are not most abundant in the centre of their geographic range or climatic niche. *Ecology Letters*, **20**, 1526–1533.

Diez, J.M., Giladi, I., Warren, R. & Pulliam, H.R. (2014) Probabilistic and spatially variable niches inferred from demography (ed E Jongejans). *Journal of Ecology*, **102**, 544–554.

Dirnbock, T., Essle, F. & Rabitsch, W. (2011) Disproportional risk for habitat loss of high-altitude endemic species under climate change. *Global Change Biology*, **17**, 990–996.

Dixon, P.M. (2003) VEGAN, a package of R functions for community ecology. *Journal of Vegetation Science*, **14**, 927–930.

Doak, D.F. & Morris, W.F. (2010) Demographic compensation and tipping points in climate-induced range shifts. *Nature*, **467**, 959–962.

Dobrowski, S.Z. (2011) A climatic basis for microrefugia: The influence of terrain on climate. *Global Change Biology*, **17**, 1022–1035.

Dobrowski, S.Z., Swanson, A.K., Abatzoglou, J.T., Holden, Z. a., Safford, H.D., Schwartz, M.K. & Gavin, D.G. (2015) Forest structure and species traits mediate projected recruitment declines in western US tree species. *Global Ecology and Biogeography*, **24**, 917–927.

Dullinger, S., Gattringer, A., Thuiller, W., Moser, D., Zimmermann, N.E., Guisan, A., Willner, W., Plutzar, C., Leitner, M., Mang, T., Caccianiga, M., Dirnböck, T., Ertl, S., Fischer, A., Lenoir, J., Svenning, J.C., Psomas, A., Schmatz, D.R., Silc, U., Vittoz, P. & Hülber, K. (2012) Extinction debt of high-mountain plants under twenty-first-century climate change. *Nature Climate Change*, **2**, 619–622.

Easterling, M.R., Ellner, S.P. & Dixon, P.M. (2000) Size-specific sensitivity: Applying a new structured population model. *Ecology*, **81**, 694–708.

Ehrlen, J. & Morris, W.F. (2015) Predicting changes in the distribution and abundance of species under environmental change. *Ecology Letters*, **18**, 303–314.

Ehrlen, J., Morris, W.F., Euler, T. Von & Dahlgren, J.P. (2016) Advancing environmentally explicit structured population models of plants. *Journal of Ecology*, **104**, 292–305.

Ellner, S.P., Childs, D.Z. & Rees, M. (2016) *Data-Driven Modelling of Structured Populations:*

A Practical Guide to the Integral Projection Model. Springer, Basel, Switzerland.

Elmendorf, S.C., Henry, G.H.R., Hollister, R.D., Bjork, R.G., Bjorkman, A.D., Callaghan, T. V., Collier, L.S., Cooper, E.J., Cornelissen, J.H.C., Day, T.A., Fosaa, A.M., Gould, W.A., Gretarsdottir, J., Harte, J., Hermanutz, L., Hik, D.S., Hofgaard, A., Jarrad, F., Jonsdottir, I.S., Keuper, F., Klanderud, K., Klein, J.A., Koh, S., Kudo, G., Lang, S.I., Loewen, V., May, J.L., Mercado, J., Michelsen, A., Molau, U., Myers-Smith, I.H., Oberbauer, S.F., Pieper, S., Post, E., Rixen, C., Robinson, C.H., Schmidt, N.M., Shaver, G.R., Stenstrom, A., Tolvanen, A., Totland, Ø., Troxler, T., Wahren, C.-H., Webber, P.J. & Welker, J.M.P.A.W. (2012) Global assessment of experimental climate warming on tundra vegetation : heterogeneity over space and time. *Ecology Letters*, **15**, 164–175.

Engler, R., Randin, C.F., Thuiller, W., Dullinger, S., Zimmermann, N.E., Araújo, M.B., Pearman, P.B., Le Lay, G., Piedallu, C., Albert, C.H., Choler, P., Coldea, G., De Lamo, X., Dirnböck, T., Gégout, J.C., Gómez-García, D., Grytnes, J.A., Heegaard, E., Høistad, F., Nogués-Bravo, D., Normand, S., Puşcaş, M., Sebastià, M.T., Stanisci, A., Theurillat, J.P., Trivedi, M.R., Vittoz, P. & Guisan, A. (2011) 21st century climate change threatens mountain flora unequally across Europe. *Global Change Biology*, **17**, 2330–2341.

Ertter, B. (1989) Revisionary studies in *Ivesia* (Rosaceae: Potentilleae). *Systematic Botany*, **14**, 231–244.

Ettinger, A.K., Ford, K.R. & Hille Ris Lambers, J. (2011) Climate determines upper, but not lower, altitudinal range limits of Pacific Northwest conifers. *Ecology*, **92**, 1323–1331.

Ettinger, A.K. & Hille Ris Lambers, J. (2013) Climate isn't everything: Competitive interactions and variation by life stage will also affect range shifts in a warming world. *American journal of botany*, **100**, 1344–55.

Evans, M., Merow, C., Record, S., McMahon, S.M. & Enquist, B.J. (2016) Towards Process-based Range Modeling of Many Species. *Trends in Ecology & Evolution*, **31**, 860–871.

Ezard, T.H.G., Bullock, J.M., Dalgleish, H.J., Millon, A., Pelletier, F., Ozgul, A. & Koons, D.N. (2010) Matrix models for a changeable world: the importance of transient dynamics in population management. *Journal of Applied Ecology*, **47**, 515–523.

Fisk, M.C., Schmidt, S.K. & Seastedt, T.R. (1998) Topographic patterns of above- and belowground production and nitrogen cycling in alpine tundra. *Ecology*, **79**, 2253–2266.

Flint, L.E., Flint, A.L., Thorne, J.H. & Boynton, R. (2013) Fine-scale hydrologic modeling for regional landscape applications : the California Basin Characterization Model development and performance. *Ecologial Processes*, **2**, 1–21.

Forbis, T. (2003) Seedling Demography in an Alpine Ecosystem. *American Journal of Botany*, **90**, 1197–1206.

Fordham, D.A., Bertelsmeier, C., Brook, B.W., Early, R., Ara, M.B., Neto, D. & Brown, S.C. (2018) How complex should models be ? Comparing correlative and mechanistic range dynamics models. *Global Change Biology*, **24**, 1357–1370.

Franklin, J., Davis, F.W., Ikegami, M., Syphard, A.D., Flint, L.E., Flint, A.L. & Hannah, L. (2013) Modeling plant species distributions under future climates: How fine scale do climate projections need to be? *Global Change Biology*, **19**, 473–483.

Franklin, J., Serra-Diaz, J.M., Syphard, A.D. & Regan, H.M. (2016) Global change and terrestrial plant community dynamics. *Proceedings of the National Academy of Sciences*, **113**, 3725–3734.

De Frenne, P., Rodríguez-Sánchez, F., Coomes, D.A., Baeten, L., Verstraeten, G., Vellend, M., Bernhardt-Römermann, M., Brown, C.D., Brunet, J., Cornelis, J., Decocq, G.M., Dierschke,

H., Eriksson, O., Gilliam, F.S., Hédl, R., Heinken, T., Hermy, M., Hommel, P., Jenkins, M. a, Kelly, D.L., Kirby, K.J., Mitchell, F.J.G., Naaf, T., Newman, M., Peterken, G., Petrík, P., Schultz, J., Sonnier, G., Van Calster, H., Waller, D.M., Walther, G.-R., White, P.S., Woods, K.D., Wulf, M., Graae, B.J. & Verheyen, K. (2013) Microclimate moderates plant responses to macroclimate warming. *Proceedings of the National Academy of Sciences of the United States of America*, **110**, 18561–18565.

Fridley, J.D. (2009) Downscaling climate over complex terrain: High finescale (<1000 m) spatial variation of near-ground temperatures in a montane forested landscape (Great Smoky Mountains). *Journal of Applied Meteorology and Climatology*, **48**, 1033–1049.

Galen, C. & Stanton, M.L. (1991) Consequences of Emergence Phenology for Reproductive Success in Ranunculus adoneus. *American Journal of Botany*, **78**, 978–988.

Gaston, K.J. (2009) Geographic range limits: achieving synthesis. *Proceedings of the Royal Society B Biological Sciences*, **276**, 1395–1406.

Geiger, R., Aron, R.H. & Todhunter, P. (2009) *The Climate Near the Ground*, 7th ed. Rowman & Littlefield.

Gerst, K.L., Angert, A.L. & Venable, D.L. (2011) The effect of geographic range position on demographic variability in annual plants. *Journal of Ecology*, **99**, 591–599.

Gilman, S.E., Urban, M.C., Tewksbury, J., Gilchrist, G.W. & Holt, R.D. (2010) A framework for community interactions under climate change. *Trends in ecology & evolution*, **25**, 325–31.

Gotelli, N.J. & Ellison, A.M. (2006) Forecasting extiction risk with nonstationary matrix models. *Contemporary Statistics and Ecology*, **16**, 51–61.

Gottfried, M., Pauli, H., Futschik, A., Akhalkatsi, M., Barančok, P., Alonso, B., Luis, J., Coldea, G., Dick, J., Erschbamer, B., Calzado, F., Rosa, M., Kazakis, G., Krajči, J., Larsson, P., Mallaun, M., Michelsen, O., Moiseev, D., Moiseev, P., Molau, U., Merzouki, A., Nagy, L., Nakhutsrishvili, G., Pedersen, B., Pelino, G., Puscas, M., Rossi, G., Stanisci, A., Theurillat, J.-P., Tomaselli, M., Villar, L., Vittoz, P., Vogiatzakis, I. & Grabherr, G. (2012) Continent-wide response of mountain vegetation to climate change. *Nature Climate Change*, **2**, 111–115.

Graae, B.J., Ejrnæs, R., Lang, S.I., Meineri, E., Ibarra, P.T. & Bruun, H.H. (2011) Strong microsite control of seedling recruitment in tundra. *Oecologia*, **166**, 565–576.

Graae, B.J., Vandvik, V., Armbruster, W.S., Eiserhardt, W.L., Svenning, J.C., Hylander, K., Ehrlén, J., Speed, J.D.M., Klanderud, K., Bråthen, K.A., Milbau, A., Opedal, Ø.H., Alsos, I.G., Ejrnæs, R., Bruun, H.H., Birks, H.J.B., Westergaard, K.B., Birks, H.H. & Lenoir, J. (2017) Stay or go - how topographic complexity influences alpine plant population and community responses to climate change. *Perspectives in Plant Ecology, Evolution and Systematics*, **30**, 41–50.

Grabherr, G., Gottfried, M. & Pauli, H. (2010) Climate Change Impacts in Alpine Environments. *Geography Compass*, **4**, 1133–1153.

Griffith, A.B. (2017) Perturbation approaches for integral projection models. *Oikos*, **126**, 1675–1686.

Grubb, P.J. (1977) The Maintenance of Species-Richness in Plant Communities: the Importance of the Regeneration Niche. *Biol. Rev*, **52**, 107–145.

Halbritter, A.H., Billeter, R., Edwards, P.J. & Alexander, J.M. (2015) Local adaptation at range edges: Comparing elevation and latitudinal gradients. *Journal of Evolutionary Biology*, **28**, 1849–1860.

Hampe, A. & Petit, R.J. (2005) Conserving biodiversity under climate change: the rear edge

matters. *Ecology Letters*, **8**, 461–467.

Hargreaves, A.L., Samis, K.E. & Eckert, C.G. (2014) Are species' range limits simply niche limits writ large? A review of transplant experiments beyond the range. *The American naturalist*, **183**, 157–73.

Harrison, S., Damschen, E.I. & Grace, J.B. (2010) Ecological contingency in the effects of climatic warming on forest herb communities. *Proceedings of the National Academy of Sciences*, **107**, 19362–19367.

Harsch, M.A. & Hille Ris Lambers, J. (2016) Climate Warming and Seasonal Precipitation Change Interact to Limit Species Distribution Shifts across Western North America. *PloS one*, **0**, 1–17.

Harte, J. & Shaw, R. (1995) Shifting Dominance Within a Montane Vegetation Community : Results of a Climate-Warming Experiment. *Science*, **267**, 876–880.

Hijmans, R., Etten, J. van & Mattiuzzi, M. (2015) R Package "raster."

Holt, R.D. (2003) On the evolutionary ecology of species' ranges. *Evolutionary Ecology Research*, **5**, 159–178.

Hurvich, C.M. & Tsai, C. (1991) A Corrected Akaine Information Criterion for Vector Autoregressive Model Selection. *Journal of Time Series Analysis*, **14**, 271–279.

Hylander, K. & Ehrlén, J. (2013) The mechanisms causing extinction debts. *Trends in Ecology and Evolution*, **28**, 341–346.

Isard, a. (1986) Factors Influencing Soil Moisture and Plant Community. *Arctic, Antarctic, and Alpine Research*, **18**, 83–96.

Jackson, S.T., Betancourt, J.L., Booth, R.K. & Gray, S.T. (2009) Ecology and the ratchet of events : Climate variability , niche dimensions , and species distributions. *Proceedings of the National Academy of Sciences*, **106**, 19685–19692.

Jonas, T., Rixen, C., Sturm, M. & Stoeckli, V. (2008) How alpine plant growth is linked to snow cover and climate variability. *Journal of Geophysical Research: Biogeosciences*, **113**, 1–10.

Jongejans, E. & De Kroon, H. (2005) Space versus time variation in the population dynamics of three co-occurring perennial herbs. *Journal of Ecology*, **93**, 681–692.

Jongejans, E., de Kroon, H., Tuljapurkar, S. & Shea, K. (2010) Plant populations track rather than buffer climate fluctuations. *Ecology Letters*, **13**, 736–743.

Kirkpatrick, M. & Barton, N.H. (1997) Evolution of a species' range. *The American Naturalist*, **150**, 1–23.

Kopp, C.W. & Cleland, E.E. (2014) Shifts in plant species elevational range limits and abundances observed over nearly five decades in a western North America mountain range (ed P Adler). *Journal of Vegetation Science*, **25**, 135–146.

Kopp, C.W. & Cleland, E.E. (2015) A Range-Expanding Shrub Species Alters Plant Phenological Response to Experimental Warming. *Plos One*, **10**, 1–9.

Körner, C. (2003) *Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems* (ed Springer). Heidelberg, Germany.

Kueppers, L.M., Conlisk, E., Castanha, C. & Andrew, B. (2017) Warming and provenance limit tree recruitment across and beyond the elevation range of subalpine forest. *Global Change Biology*, **23**, 2383–2395.

Kulonen, A., Imboden, R.A., Rixen, C., Maier, S.B. & Wipf, S. (2018) Enough space in a warmer world? Microhabitat diversity and small-scale distribution of alpine plants on mountain summits. *Diversity and Distributions*, **24**, 252–261.

Lawson, C.R., Vindenes, Y., Bailey, L. & van de Pol, M. (2015) Environmental variation and

population responses to global change. *Ecology Letters*, **18**, 724–736.

Lee-Yaw, J.A., Kharouba, H.M., Bontrager, M., Mahony, C., Csergo, A.M., Noreen, A.M.E., Li, Q., Schuster, R. & Angert, A.L. (2016) A synthesis of transplant experiments and ecological niche models suggests that range limits are often niche limits. *Ecology Letters*, **0**, 1–13.

Lembrechts, J.J., Lenoir, J., Nu, M.A., Geron, C., Buss, G., Milbau, A. & Nijs, I. (2017) Microclimate variability in alpine ecosystems as stepping stones for non-native plant establishment above their current elevational limit. *Ecography*, **40**, 1–9.

Lenoir, J., Gégout, J.C., Marquet, P.A., de Ruffray, P. & Brisse, H. (2008) A significant upward shift in plant species optimum elevation during the 20th century. *Science*, **320**, 1768–71.

Lenoir, J., Graae, B.J., Aarrestad, P.A., Alsos, I.G., Armbruster, W.S., Austrheim, G., Bergendorff, C., Birks, H.J.B., Bråthen, K.A., Brunet, J., Bruun, H.H., Dahlberg, C.J., Decocq, G., Diekmann, M., Dynesius, M., Ejrnaes, R., Grytnes, J.-A., Hylander, K., Klanderud, K., Luoto, M., Milbau, A., Moora, M., Nygaard, B., Odland, A., Ravolainen, V.T., Reinhardt, S., Sandvik, S.M., Schei, F.H., Speed, J.D.M., Tveraabak, L.U., Vandvik, V., Velle, L.G., Virtanen, R., Zobel, M. & Svenning, J.-C. (2013) Local temperatures inferred from plant communities suggest strong spatial buffering of climate warming across Northern Europe. *Global Change Biology*, **19**, 1470–1481.

Lenoir, J. & Svenning, J.C. (2014) Climate-related range shifts - a global multidimensional synthesis and new research directions. *Ecography*, **38**, 15–28.

Lesica, P. & Crone, E.E. (2016) Arctic and boreal plant species decline at their southern range limits in the Rocky Mountains. *Ecology Letters*, **0**, 1–9.

Litaor, M.I., Williams, M. & Seastedt, T.R. (2008) Topographic controls on snow distribution, soil moisture, and species diversity of herbaceous alpine Vegetation, Netwot Ridge, Colorado. *Journal of Geophysical Research: Biogeosciences*, **113**, 1–10.

Lloyd, R. & Mitchell, R. (1973) *A Flora of the White Mountains, California and Nevada*. University of California Press, Berkeley.

MacArthur, R. (1972) *Geographical Ecology*. Harper and Row, New York.

Máliš, F., Kopecký, M., Petřík, P., Vladovič, J., Merganič, J. & Vida, T. (2016) Life-stage, not climate change, explains observed tree range shifts. *Global Change Biology*, **22**, 1904–1914.

Mark, A.F., Korsten, A.C., Guevara, D.U., Dickinson, K.J.M., Michel, P., Halloy, S.R.P., Lord, J.M., Venn, S.E., John, W., Whigham, P.A. & Nielsen, J.A. (2015) Ecological Responses to 52 Years of Experimental Snow Manipulation in High-alpine Cushionfield , Old Man Range, South-central New Zealand. *Arctic, Antarctic, and Alpine Research*, **47**, 751–772.

McCullough, I.M., Davis, F.W., Dingman, J.R., Flint, L.E., Flint, A.L., Serra-Diaz, J.M., Syphard, A.D., Moritz, M.A., Hannah, L. & Franklin, J. (2016) High and dry: high elevations disproportionately exposed to regional climate change in Mediterranean-climate landscapes. *Landscape Ecology*, **31**, 1063–1075.

Mclean, N., Lawson, C.R., Leech, D.I. & van de Pol, M. (2016) Predicting when climate-driven phenotypic change affects population dynamics. *Ecology Letters*, **19**, 595–608.

Merow, C., Dahlgren, J., Metcalf, C.J., Childs, D., Evans, M., Jongejans, E., Record, S., Rees, M., Salguero-Gómez, R. & McMahon, S. (2014) Advancing population ecology with integral projection models: a practical guide. *Methods in Ecology and Evolution*, **5**, 99–110.

Merow, C., Mcmahon, S., Grif, A.B. & Salguero-g, R. (2016) Demography beyond the population. *Journal of Ec*, **104**, 271–280.

Michalet, R., Schöb, C., Lortie, C.J., Brooker, R.W. & Callaway, R.M. (2014) Partitioning net

interactions among plants along altitudinal gradients to study community responses to climate change. *Functional Ecology*, **28**, 75–86.

Millar, C.I., Westfall, R.D., Delany, D.L., Flint, A.L. & Flint, L.E. (2015) Recruitment patterns and growth of high-elevation pines in response to climatic variability (1883 – 2013), in the western Great Basin, USA. *Canadian Journal of Forest Research*, **45**, 1299–1312.

Morefield, J.D. (1992) Spatial and Ecologic Segregation of Phytogeographic Elements in the White Mountains of California and Nevada. *Journal of Biogeography*, **19**, 33–50.

Morris, W.F. & Doak, D.F. (2002) *Quantitative Conservation Biology*. Sinauer Associates, Sunderland, Massachusetts, USA.

Morris, W., Pfister, C. & Tuljapurkar, S. (2008) Longevity can buffer plant and animal populations against climate variability. *Ecology*, **89**, 19–25.

Morueta-Holme, N., Engemann, K., Sandoval-Acuña, P., Jonas, J.D., Segnitz, R.M. & Svenning, J.-C. (2015) Strong upslope shifts in Chimborazo's vegetation over two centuries since Humboldt. *Proceedings of the National Academy of Sciences*, **112**, 12741–12745.

Nakagawa, S. & Schielzeth, H. (2013) A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, **4**, 133–142.

Normand, S., Zimmermann, N.E., Schurr, F.M. & Lischke, H. (2014) Demography as the basis for understanding and predicting range dynamics. *Ecography*, **37**, 1149–1154.

Oberbauer, S.F. & Billings, W.D. (1981) Drought tolerance and water use by plants along an alpine topographic gradient. *Oecologia*, **50**, 325–331.

Oldfather, M.F., Britton, M.N., Papper, P.D., Koontz, M.J., Halbur, M.M., Dodge, C., Flint, A.L., Flint, L.E. & Ackerly, D.D. (2016) Effects of Topoclimatic Complexity on the Composition of Woody Plant Communities. *AoB Plants*, plw049.

Pauli, H., Gottfried, M., Dullinger, S., Abdaladze, O., Luis, J., Alonso, B., Coldea, G., Dick, J., Erschbamer, B., Calzado, R., Ghosn, D., Holten, J. & Kanka, R. (2012) Recent Plant Diversity Changes on Europe ' s Mountain Summits. *Science*, **336**, 353–355.

Pecl, G., Araújo, M., Bell, J., Blanchard, J., Bonebrake, T., Chen, I., Clark, T., Colwell, R., Danielsen, F., Evengård, B., Falconi, L., Ferrier, S., Frusher, S., Garcia, R., Griffis, R., Hobday, A., Janion-scheepers, C., Jarzyna, M., Jennings, S., Lenoir, J., Linnetved, H., Martin, V., Mccormack, P., Mcdonald, J., Mitchell, N., Mustonen, T., Pandolfi, J., Pettorelli, N., Popova, E., Robinson, S., Scheffers, B., Shaw, J., Sorte, C., Strugnell, J., Sunday, J. & Tuanmu, M. (2017) Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, **355**, 1–9.

Pepin, N., Bradley, S., Diaz, H.., Baraer, E.B., Caceres, N., Forsythe, H., Fowler, G., Greenwood, M.Z., Hashmi, X., Liu, J.R., Miller, L., Ning, A., Ohmura, E., Palazzi, I., Rangwala, W., Schöner, I., Severskiy, M., Shahgedanova, M., Wang, S.N., Williamson, S.N. & Yang, D.Q. (2015) Elevation-dependent warming in mountain regions of the world. *Nature Climate Change*, **5**, 424–430.

Pironon, S., Papuga, G., Villellas, J., Angert, A.L., García, M.B. & Thompson, J.D. (2016) Geographic variation in genetic and demographic performance: new insights from an old biogeographical paradigm. *Biological Reviews*, doi:10.1111/brv.12313.

Pironon, S., Villellas, J., Morris, W.F., Doak, D.F. & García, M.B. (2015) Do geographic, climatic or historical ranges differentiate the performance of central versus peripheral populations? *Global Ecology and Biogeography*, **24**, 611–620.

Pironon, S., Villellas, J., Thuiller, W., Eckhart, V.M., Geber, M.A., Moeller, D.A. & García, M.B. (2017) The "Hutchinsonian niche" as an assemblage of demographic niches:

implications for species geographic ranges. *Ecography*, **40**, 1–10.

Pollak, O. (1997) Morphlogy and dynamics of alpine populations of *Ivesia lycopodioides* ssp.*scandularis* from the White Mountains of California. *Plant Biology*, 97–116.

Potter, K.A., Arthur Woods, H. & Pincebourde, S. (2013) Microclimatic challenges in global change biology. *Global Change Biology*, **19**, 2932–2939.

Pulliam, H.R. (2000) On the relationship between niche and distribution. *Ecology Letters*, **3**, 349–361.

R Core Team. (2017) R: A language and environment for statistical computing.

Ramula, S., Rees, M. & Buckley, Y.M. (2009) Integral projection models perform better for small demographic data sets than matrix population models: a case study of two perennial herbs. *Journal of Applied Ecology*, **46**, 1048–1053.

Rapacciuolo, G., Maher, S.P., Schneider, A.C., Hammond, T.T., Jabis, M.D., Walsh, R.E., Iknayan, K.J., Walden, G.K., Oldfather, M.F., Ackerly, D.D. & Beissinger, S.R. (2014) Beyond a warming fingerprint: individualistic biogeographic responses to heterogeneous climate change in California. *Global Change Biology*, **20**, 2841–55.

Rixen, C. & Wipf, S. (2017) Non-equilibrium in Alpine Plant Assemblages: Shifts in Europe's Summit Floras. *High Mountain Conservation In A Changing World - Advances in Global Change Research*, p. Springer.

Rumpf, S.B., Hülber, K., Klonner, G., Moser, D., Schütz, M. & Wessely, J. (2017) Range dynamics of mountain plants decrease with elevation. *Proceedings of the National Academy of Sciences*, **115**, 1848–1853.

Rundel, P., Gibson, A. & Sharifi, M.R. (2005) Plant Functional Groups in Alpine Fellfield Habitats of the White Mountains , California. *Artice, Antarctic, and Alpine Research*, **37**, 358–365.

Rundel, P., Gibson, A.C. & Sharifi, M.R. (2008) the Alpine Flora of the White Mountains, California. *Madroño*, **55**, 202–215.

Sagarin, R., Gaines, S. & Gaylord, B. (2006) Moving beyond assumptions to understand abundance distributions across the ranges of species. *Trends in Ecology and Evolution*, **21**, 524–530.

Sage, T. & Sage, R. (2002) Microsite characteristics of Muhlenbergia richardsonis (Trin.) Rydb., an alpine C 4 grass from the White Mountains, California. *Oecologia*, **132**, 501–508.

Salguero-Gómez, R., Jones, O.R., Jongejans, E., Blomberg, S.P., Hodgson, D.J., Mbeau-Ache, C., Zuidema, P.A., De Kroon, H. & Buckley, Y.M. (2016) Fast–slow continuum and reproductive strategies structure plant life-history variation worldwide. *Proceedings of the National Academy of Sciences*, **113**, 230–235.

Savage, J. & Vellend, M. (2015) Elevational shifts, biotic homogenization and time lags in vegetation change during 40 years of climate warming. *Ecography*, **38**, 546–555.

Scherrer, D. & Korner, C. (2011) Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. *Journal of Biogeography*, **38**, 406–416.

Schurr, F.M., Pagel, J., Cabral, J.S., Groeneveld, J., Bykova, O., O'Hara, R.B., Hartig, F., Kissling, W.D., Linder, H.P., Midgley, G.F., Schröder, B., Singer, A. & Zimmermann, N.E. (2012) How to understand species' niches and range dynamics: A demographic research agenda for biogeography. *Journal of Biogeography*, **39**, 2146–2162.

Serra-Diaz, J.M., Franklin, J., Sweet, L.C., McCullough, I.M., Syphard, A.D., Regan, H.M., Flint, L.E., Flint, A.L., Dingman, J.R., Moritz, M.A., Redmond, K., Hannah, L. & Davis,

F.W. (2016) Averaged 30 year climate change projections mask opportunities for species establishment. *Ecography*, **39**, 844–845.

Sexton, J.P., McIntyre, P.J., Angert, A.L. & Rice, K.J. (2009) Evolution and ecology of species range limits. *Annual Review of Ecology, Evolution, and Systematics*, **40**, 415–436.

Sexton, J.P., Strauss, S.Y. & Rice, K.J. (2011) Gene flow increases fitness at the warm edge of a species' range. *Proceedings of the National Academy of Sciences*, **108**, 11704–11709.

Sheth, S.N. & Angert, A.L. (2018) Demographic compensation does not rescue populations at a trailing range edge. *Proceedings of the National Academy of Sciences*, **10**, 1–6.

Spira, T. (1987) Alpine Annual Plants Species in the White Mountains of Eastern California. *Madroño*, **34**, 315–323.

Stanton, A.M.L., Rejmánek, M. & Galen, C. (1994) Changes in vegetation and soil fertility along a predictable snowmelt gradient in the Mosquito Range, Colorado, U.S.A. *Arctic and Alpine Research*, **26**, 364–374.

Steinbauer, M.J., Grytnes, J.-A., Jurasinski, G., Kulonen, A., Lenoir, J., Pauli, H., Rixen, C., Winkler, M., Bardy-Durchhalter, M., Barni, E., Bjorkman, A.D., Breiner, F.T., Burg, S., Czortek, P., Dawes, M.A., Delimat, A., Dullinger, S., Erschbamer, B., Felde, V.A., Fernández-Arberas, O., Fossheim, K.F., Gómez-García, D., Georges, D., Grindrud, E., Haider, S., Haugum, S. V., Henriksen, H., Herreros, M.J., Jaroszewicz, B., Jaroszynska, F., Kanka, R., Kapfer, J., Klanderud, K., Kühn, I., Lamprecht, A., Matteodo, M., Morra di Cella, U., Normand, S., Odland, A., Olsen, S.L., Palacio, S., Pete, M., Piscová, V., Sedlakova, B., Steinbauer, K., Stöckli, V., Svenning, J.-C., Teppa, G., Theurillat, J.-P., Vittoz, P., Woodin, S.J., Zimmermann, N.E. & Wipf, S. (2018) Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature*, **In Press**.

Stephenson, N.L., The, S., Naturalist, A. & May, N. (1990) Climatic Control of Vegetation Distribution : The Role of the Water Balance. *The American Naturalist*, **135**, 649–670.

Stevens, J.T., Safford, H.D., Harrison, S. & Latimer, A.M. (2015) Forest disturbance accelerates thermophilization of understory plant communities. *Journal of Ecology*, **103**, 1253–1263.

Stewart, J.A.E., Wright, D.H. & Heckman, K.A. (2017) Apparent climate-mediated loss and fragmentation of core habitat of the American pika in the Northern Sierra Nevada, California, USA. *PLoS ONE*, **12**, 1–17.

Suding, K.N., Farrer, E.C., King, A.J., Kueppers, L., Suding, K.N., Farrer, E.C., King, A.J. & Kueppers, L. (2015) Plant Ecology & Diversity Vegetation change at high elevation : scale dependence and interactive effects on Niwot Ridge. *Plant Ecology & Diversity*, **8**, 713–725.

Sutherland, W.J., Freckleton, R.P., Godfray, H.C.J., Beissinger, S.R., Benton, T., Cameron, D.D., Carmel, Y., Coomes, D.A., Coulson, T., Emmerson, M.C., Hails, R.S., Hays, G.C., Hodgson, D.J., Hutchings, M.J., Johnson, D., Jones, J.P.G., Keeling, M.J., Kokko, H., Kunin, W.E., Lambin, X., Lewis, O.T., Malhi, Y., Mieszkowska, N., Milner-Gulland, E.J., Norris, K., Phillimore, A.B., Purves, D.W., Reid, J.M., Reuman, D.C., Thompson, K., Travis, J.M.J., Turnbull, L.A., Wardle, D.A. & Wiegand, T. (2013) Identification of 100 fundamental ecological questions. *Journal of Ecology*, **101**, 58–67.

Svenning, J.-C. & Sandel, B. (2013) Disequilibrium vegetation dynamics under future climate change. *American Journal of Botany*, **100**, 1–21.

Tingley, M.W., Koo, M.S., Moritz, C., Rush, A.C. & Beissinger, S.R. (2012) The push and pull of climate change causes heterogeneous shifts in avian elevational ranges. *Global Change Biology*, **18**, 3279–3290.

Tingley, M.W., Monahan, W.B., Beissinger, S.R. & Moritz, C. (2009) Birds track their

Grinnellian niche through a century of climate change. *Proceedings of the National Academy of Sciences*, **106**, 19637–19643.

Tredennick, A.T., Hooten, M.B. & Adler, P.B. (2016) Do we need demographic data to forecast population responses to climate change? *Methods in Ecology and Evolution*, doi: 10.1111/2041-210X.12686.

Vanneste, T., Michelsen, O., Graae, B.J., Kyrkjeeide, M.O., Holien, H., Hassel, K., Lindmo, S., Kapás, R.E. & De Frenne, P. (2017) Impact of climate change on alpine vegetation of mountain summits in Norway. *Ecological Research*, **32**, 579–593.

Veloz, S.D., Williams, J.W., Blois, J.L., He, F., Otto-Bliesner, B. & Liu, Z. (2012) No-analog climates and shifting realized niches during the late quaternary: implications for 21st-century predictions by species distribution models. *Global Change Biology*, **18**, 1698–1713.

Van de Ven, C.M., Weiss, S.B. & Ernst, W.G. (2007) Plant Species Distributions under Present Conditions and Forecasted for Warmer Climates in an Arid Mountain Range. *Earth Interactions*, **11**, 1–33.

Villellas, J., Doak, D.F., García, M.B. & Morris, W.F. (2015) Demographic compensation among populations: what is it, how does it arise and what are its implications? (ed J Hille Ris Lambers). *Ecology Letters*, **18**, 1139–1152.

Villellas, J., Morris, W.F. & Garcia, M.B. (2013) Variation in stochastic demography between and within central and peripheral regions in a widespread short-lived herb. *Ecology*, **94**, 1378–1388.

Walker, M.D., Ingersoll, R.C. & Webber, P.J. (1995) Effects of interannual climate variation on phenology and growth of two alpines forbs. *Ecology*, **76**, 1067–1083.

Walker, M.D., Wahren, C.H., Hollister, R.D., Henry, G.H.R., Ahlquist, L.E., Alatalo, J.M., Bret-harte, M.S., Calef, M.P., Callaghan, T. V, Carroll, A.B., Epstein, H.E., Jo, S., Robinson, C.H., Shaver, G.R., Suding, K.N., Thompson, C.C., Tolvanen, A., Totland, Ø., Turner, P.L., Tweedie, C.E., Webber, P.J. & Wookey, P.A. (2006) Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences*, **103**, 1342–1346.

Walther, G.-R., Beibner, S. & Burga, C. (2005) Trends in the Upward Shift of Alpine Plants Author. *Journal of Vegetation Science*, **16**, 541–548.

Wenk, E.H. & Dawson, T.E. (2007) Interspecific Differences in Seed Germination, Establishment, and Early Growth in Relation to Preferred Soil Type in an Alpine Community. *Arctic, Antarctic, and Alpine Research*, **39**, 165–176.

Winkler, D., Chapin, K. & Kueppers, L. (2016a) Soil moisture mediates alpine life form and community productivity responses to warming. *Ecology*, **97**, 1553–1563.

Winkler, M., Lamprecht, A., Steinbauer, K., Hulber, K., Theurillat, J.-P., Breiner, F., Choler, P., Ertl, S., Giron, A., Rossi, G., Vittoz, P., Akhalkatsi, M., Bay, C., Alonso, J.-L., Bergstreom, T., Carranza, M., Corcket, E., Dick, J., Erschbamer, B., Calzado, R., Fosaa, A.M., Gavilan, R., Ghosn, D., Gigauri, K., Huber, D., Kanka, R., Kazakis, G., Klipp, M., Kollar, J., Kudernatsch, T., Larsson, P., Mallaun, M., Michelsen, O., Moiseev, P., Moiseev, D., Molau, U., Mesa, J., Morra di Cella, U., Nagy, L., Petey, M., Pușcaș, M., Rixen, C., Stanisci, A., Suen, M., Anne, S., Tomaselli, M., Unterluggaue, P., Uru, T., Villar, L., Gottfried, M. & Pauli, H. (2016b) The rich sides of mountain summits – a pan-European view on aspect preferences of alpine plants. *Journal of Biogeography*, **43**, 2261–2273.

Wipf, S., Stoeckli, V. & Bebi, P. (2009) Winter climate change in alpine tundra: Plant responses to changes in snow depth and snowmelt timing. *Climatic Change*, **94**, 105–121.

Zhuoting, W., Dijksea, P., Kock, G., Penuelas, J. & Hungate, B. (2011) Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. *Global Change Biology*, **17**, 927–942.