

Variation in impacts of climate change across a species' range arise from idiosyncratic responses of populations to temperature and variation in warming rates

Final report on work in Alaska National Park system

Introduction

Effects of climate change on species range shifts are well-documented and widespread (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Parmesan, 2006). In order for a species to shift its range with climate change, the impacts of climate change must differ systematically across populations: the negative impact of climate change on populations must be stronger in hotter locations, with muted or even positive effects at cooler locations. Namely, populations located in hotter locations (e.g., low latitude or elevation) must experience substantial reductions in population growth rates due to the deleterious effects of high temperatures, resulting in eventual extinction. By contrast, population growth rate in cooler locations must be maintained at or above unity, leading to persistence of populations at these cooler populations, as well as colonization of newly suitable habitat in formerly too-cold locations. Presumably, when range shifts occur, high elevation or high latitude populations are more able to maintain population growth rate greater than unity in the face of increasing temperatures because they are not pushed outside of their physiological limits (e.g., Doak & Morris, 2010; Sheth & Angert, 2018). Conversely, low elevation or low latitude populations suffer because increasing temperatures at these populations, where temperatures are already relatively high, push them outside of their physiological limits (Bernardo & Spotila, 2006).

The sum impact of climate change on population growth rate at any given population is a product of the magnitude of climate change at that location and the population's sensitivity to climate change (Deutsch et al., 2008), both of which can differ across a species' range. For some species, not all populations across their range experience equivalent rates of warming. For example, very wide ranging species are likely to experience faster rates of warming at their poleward limits and slower rates at their equatorward limits. These latitudinal patterns in rates of warming can be complicated by topography, elevation, or buffering impacts of the ocean (Ashcroft, Chisholm, & French, 2009). At the same time, sensitivity to unit changes in climate can vary across the range of a species (Crozier, Zabel, & Hamlet, 2007; Ettinger & HilleRisLambers, 2013; Jarema, Samson, McGill, & Humphries, 2009), such that a given amount of temperature increase at one population will result in much more deleterious effects than the same amount of temperature increase at another population, simply due to life history differences across populations. Differential rates of warming across populations, combined with variation in sensitivity to warming, mean that it is hard to predict how the sum impact of climate change on population growth rate varies across a species' range. The combination of these two factors could explain some of the idiosyncratic responses of species' range shifts to climate change, where many species do not show a net range shift with climate change (Moritz et al., 2008; Parmesan, 2006; Tingley, Monahan, Beissinger, & Moritz, 2009).

Populations may also differ in their sensitivity to individual aspects of climate (e.g., winter temperature v. summer temperature), which can result in different effects of climate change at different populations. In Chinook salmon, juvenile survival depends on different aspects of climate in different populations (Crozier et al., 2007), meaning that climate drivers to which populations respond in one population may have no effect at all in other populations. If different aspects of climate are changing at different rates, this can further complicate predictions of climate change impacts. For example, if too-hot summers decrease survival of recruits, but

warmer winters increase adult survival, increases in temperatures with climate change will lead to lower recruit survival but higher adult survival. If summers are warming faster than winters in some populations, climate change impacts will be more detrimental at those populations. As another potential complication, if populations across a species' range differ in their sensitivity to recruitment failure (Louthan et al., 2018; Sheth & Angert, 2018), climate change will have very divergent impacts at populations across a species' range.

The role of sensitivity to climate change v. magnitude of climate change, and understanding which vital rates drive the responses, is particularly important to consider for rare species. Rare species are likely to be more strongly affected by climate change impacts at a distributional (Payne & Bro-Jørgensen, 2016) and individual scale (Sheth & Angert, 2014). For species that have a small geographic range, high habitat specificity, and small population sizes (the most extreme form of rarity; Rabinowitz, 1981), extirpation of one or a few populations is likely to dramatically increase extinction risk. If extirpation of a population occurs due to a high magnitude of climate change at that population (i.e., substantial increases in temperature), a viable conservation strategy could be to facilitate colonization in appropriate habitat in which predicted temperature increases are smaller (Ashcroft et al., 2009). If extirpation occurs because populations are very sensitive to particular vital rates on which climate has small (but nonzero) effects, perhaps conservation efforts could focus on improving those vital rates. For example, if a population is very sensitive to nesting success, and temperature has weak negative effects on this vital rate, conservation efforts could work to improve nesting success, either by ameliorating the minimal climate impacts on that vital rate (e.g., erecting nest boxes in locations sheltered from wind chill) or by working to improve baseline levels of nesting success, such that a reduction in nesting success due to climate becomes less important (e.g. by reducing densities of nest predators).

Here, we use a rare Arctic plant species, *Douglasia alaskana*, to test how sensitivity to climate variables and rates of warming combine to influence population growth rate across much of a species' range. *Douglasia alaskana* has a small geographic range (South Alaska), high habitat specificity (alpine scree fields), and small population sizes (4-300), and occurs in one of the fastest- warming locations in the world (the Arctic). Populations included in our study differ substantially in their rates of warming due to differences in latitude and proximity to the ocean. We construct climate-driven integral projection models for five populations using observed climate responses and realistic predictions of future climate. We then ask how the magnitude of temperature increase correlates with the impact of climate change on population growth rate, and whether these impacts are driven by the magnitude of temperature increase v. change in sensitivity to particular aspects of climate across populations.

Methods

Douglasia alaskana is a perennial alpine plant with leaves occurring in a 1-3 rosettes with fruits presented on short (<15 cm) peduncles, occurring in alpine scree on ridgelines and mountaintops in South Alaska, USA. Populations are small, ranging from 4-300 individuals in our study. The species is uncommon, with a very small fraction of seemingly suitable habitat occupied. Seeds are dropped within 15 cm of the parent plant into unvegetated scree fields. The species is weakly semelparous, with most (775/987) individuals dying after reproducing.

To quantify response of *D. alaskana* to climate, we conducted a demographic survey at five populations over one transition interval (Figure 1). In 2016, we marked and mapped 56-196 individuals at 2 populations, measuring size and number of fruits of each individual. We returned in 2017 to score survival and measure size and number of fruits. In 2017-2018, we repeated this

procedure on 3 additional populations, with 218-383 individuals marked and mapped at each population in 2017. From the 2016-2018 interval, we obtained five population x years of data with 1162 individual x years of data. We derived 6 vital rates from these data: annual survival, mean size after one year of growth, variance in size after one year of growth, probability of fruiting, and number of fruits given fruiting. We also estimated seedlings per fruit in the prior year by counting all seedlings within a 15 cm radius the year after an individual fruited at four of these five populations. At each population, we deployed 1-2 temperature loggers (iButtons) to measure local temperature variation over the period of our study. We buried these temperature loggers ~5 cm underground, using the resulting data to obtain mean monthly temperature for every month (besides July, for which we were missing data from some populations).

To estimate the timing of snow-free periods at each of these populations, we combined projections of temperature and precipitation with satellite images of daily snow cover at each of these populations from the Moderate Resolution Imaging Spectroradiometer Dataset (MODIS; Hall and Riggs 2016). Specifically, we estimated months of snowmelt and snowfall using the Daily Snow Cover MODIS dataset for 2007-2018. We used the month of the first observation of zero daily snow cover to estimate month of snowmelt, and the month of the last such observation to estimate month of snowfall. We then obtained downscaled projections of monthly average, minimum, and maximum temperatures for 5 global circulation models (GCMs) from the CMIP5/AR5 models from the Scenarios Network for Alaska and Arctic Planning group (SNAP). Delta downscaling used CRU CL v. 2.1 climatological datasets from 1961-1990 as the baseline, generating 2km x 2km spatial resolution climate projections from 2006-2099 (Scenarios Network for Alaska and Arctic Planning, University of Alaska). We then determined the relationship between timing of snowmelt and snowfall and climate using a model selection approach. We regressed 2007-2018 month of snowfall and 2007-2018 month of snowmelt on total annual precipitation, mean annual monthly temperature, and their interaction, using a model selection approach to select a best-fit model (temperature and precipitation projections were averaged across the 5 GCMs). We then used this best-fit model to predict snowmelt dates and snowfall dates for all subsequent analyses. For all analyses, each year was defined by the August 1 to July 31 interval; for example, to estimate precipitation in 2018, we calculated cumulative precipitation from August 1 2017- July 31 2018.

We synthesized our iButton temperature and SNAP temperature and precipitation data into six metrics of 2015-2018 climate at each population: 1. average annual temperature; 2. average snow-free season temperature; 3. average snow-covered season temperature; 4. coldest month temperature; 5. hottest month temperature; and 6. annual precipitation. We determined the identity of the coldest and hottest month from the average monthly temperature across the 5 GCMs, and determined the identity of the snow-free months and snow-covered months using the MODIS regression described above. Recall that we were missing iButton data for July, which was often the hottest month; thus, we used the predictions of the SNAP data for the temperature of the hottest month (averaged across GCMs). We calculated cumulative annual precipitation using the mean predicted annual precipitation across the five GCM's. We determined the identity of the coldest and hottest month from the average monthly temperature across the 5 GCMs, and determined the identity of the snow-free months and snow-covered months using the MODIS regression described above.

We assessed the impact of these climate metrics on vital rates using a model selection approach. For mean log size after one year of growth, log variance in size after one year of growth, probability of fruiting, and log number of fruits per size, we tested all possible subsets of

a global model with log size in previous time step, average annual temperature, cumulative annual precipitation, and the interaction of average annual temperature and cumulative annual precipitation as predictor variables. We used AICc to select a best-fit model, correcting for collinearity as described in the next paragraph. We repeated this process for four other global models: 1) snow-covered season temperature and precipitation, 2) snow-free season temperature and precipitation, and 3) coldest and 4) hottest month temperatures and precipitation, testing the best fit model from each of these five comparisons against each other using AICc. We used the resulting best fit model in subsequent analyses. We used a linear model for all vital rates besides probability of fruiting, for which we used a general linear model with a binomial distribution. We modified our model selection approach for probability of survival, which likely depends on both climate variables over the year of interest, as well as the probability of fruiting in the year prior (which itself depends on the climate conditions the year before the year of interest). Specifically, we tested the same 5 global models as described above, but also allowed these models to include terms for coldest month temperature and precipitation in the year prior, as well as an interaction between log size in the year prior and coldest month temperature, and between log size in the year prior and coldest month precipitation. We included these terms because coldest month conditions affected the probability of fruiting. The SNAP temperature data could differ from the iButton temperature data due to elevation of the population, insolation, or other microsite characteristics; thus, in all analyses, climate variables from SNAP data were transformed into population-specific climate variables using the differences between SNAP and iButton data at each population.

We ensured our best-fit model was robust to collinearity among predictor variables. Freckleton (2011) shows that information theoretic approaches are largely robust to collinearity, with the exception of correlated variables that have quite different effect sizes. For all best-fit models with linear predictor variables correlated at $|R| > 0.6$, we ensured that the absolute value of the coefficient estimates of correlated predictor values (a rough estimate of their true effect size) were similar to one another (ratios of coefficients were ≤ 3). If ratios of coefficients differed by more than a factor of three, we replaced the best fit model with the next best model with a coefficient ratio ≤ 3 (or with no correlated predictor variables). Note that the approach outlined here uses very conservative cutoffs, according to Freckleton's analysis of simulated data.

We used these vital rates to construct climate-driven population-specific integral projection models (IPMs). Because some of the vital rates predicted unrealistic values for novel climate conditions, we limited all vital rates to $\pm 30\%$ of their observed maxima or minima (for binomial vital rates, $\pm 45\%$ of their fitted size-specific values). Our kernels used log size as a size variable, and had an additional class for seedlings. We used the population-specific estimates of seedlings per fruit in the year prior as an estimate of recruitment, and seedling survival and seedling size distribution were reflective of the across-population means. To project population growth rates, we used the SNAP temperature data that was transformed into iButton temperature data, but did this for each of the 5 GCMs. Identity of hottest and coldest month could vary across years, sites, and GCMs. We obtained mean monthly temperature of snow-covered and snow-free months (these months were predicted using our MODIS regression, so could vary across years, sites, and GCMs). We then used these climate variables in IPM kernels to project population sizes from 2018-2099, initializing the projections with the size distribution from the mean 2018-2099 kernel. To obtain estimates of population growth rate for the 2016-2017 or 2017-2018 intervals, we constructed kernels as described, but simply obtained

population growth rate (dominant eigenvalue) from the 2016-2017 or 2017-2018 kernel. We included parameter uncertainty in our predictions by sampling 500 parameter estimates from the parameters' covariance matrix and recalculating population growth rate (both current and future) for each set of parameter estimates. Finally, we assessed the impact of climate variables on population growth rate using a perturbation approach, perturbing each climate variable by 5% each year and quantifying the impact on population growth rate.

Results

We found climate effects on every vital rate in which we tested for them, besides variance in size after one year of growth (Table 1). Annual climate conditions affected mean size after one year of growth, and coldest month climate conditions affected probability of fruiting and number of fruits given fruiting (Figure 2). Coldest month climate conditions over the census interval and in the year prior affected probability of survival. Interactions among climate variables and between climate variables and size were also present, leading to complex effects of some climate variables on some vital rates (Table 1). For example, the positive effect of temperature on mean size after one year of growth was dampened by high precipitation, perhaps due to increased competition in wet conditions limiting the positive effects of temperature (Figure 2). Similarly, for probability of survival, the positive interaction between size in the previous time step and the coldest month's temperatures in the year prior suggests that larger plants are more buffered from negative effects of high temperatures (Table 1).

Climate is predicted to be warmer at all populations, with variability in the magnitude of temperature increases across populations, with more variable predictions for precipitation. Projections of relevant climate variables indicate large increases in mean annual temperature at all populations (ranging from 2.24- 3.01° C, Figure 3). Our Northern population (in Denali National Park) will likely experience the most substantial increases in temperature over the 2018-2099 period, and Southern populations will likely experience only moderate increases in temperature (Figure 3B). Coldest month temperatures follow a similar pattern (Figure 4B). While precipitation is predicted to increase on average (even more so than temperature), the magnitude and timing of precipitation changes differs across populations (Figure 4B). The magnitude of changes in precipitation does not differ systematically with latitude, perhaps reflecting higher snow loads at coastal v. inland sites, or buffering effects of the ocean (Supplemental Table 1).

Consistent with increases in temperature across our populations, for most populations our projections show declines in population growth rate in a future climate (Figure 3). Current population growth rates, over the 2016-2107 or 2017-2018 interval, were below unity (Figure 3). Current population growth rates below unity are not surprising, given current climate conditions in this area (warmer than historical conditions), the rarity of this species (suggesting the possibility of very specific temperature requirements; Hultén, 1968) and possible extirpation from some historically occupied locations (A. Louthan, personal observation). Declines in future population growth rates could be quite substantial, with our projections indicating up to a 22% decrease in population growth rate. Consistent with more substantial increases in temperature at our Northern and Eastern populations (Eastern populations are in Wrangell-St. Elias National Park and Preserve), we see more substantial declines in population growth rate under future climate conditions in Northern and Eastern sites (Figure 3). Namely, the magnitude of the change in population growth rate correlates with the magnitude of the change in mean annual temperature at each population (Pearson's correlation coefficient = -0.648; note that $P > 0.05$). Reductions in population growth rate in a future climate appear to be driven in part by a moderate sensitivity to increases in coldest month temperature coupled with substantial increases

in coldest month temperature (Figure 3). Increases in mean annual temperature actually act in the opposite direction, increasing population growth rate in a future climate, and while populations are quite sensitive to these changes, increases in mean annual temperature are only moderate (Figure 3). Negative impacts of coldest month temperature increases are stronger than positive impacts of annual mean temperature: while increases in annual mean temperature act to increase population growth rate, and populations are very sensitive to this temperature variable, increases in annual mean temperature are very small. A low correlation between the sum of the sensitivities (averaged across 500 replicates) to each climate variable, and the predicted overall change in population growth rate (averaged across 500 replicates) in a future climate, (correlation = 0.540) suggest that covariance among climate variables' contributions also play a major role.

Discussion

We see a mix of positive and negative effects of temperature and precipitation on *D. alaskana* vital rates, and the climate variables predicted to increase in the future generally reduce performance. Higher temperatures decrease most vital rates, though higher mean annual temperatures do increase mean size after one year of growth; this finding is similar to work done by Doak and Morris (2010), who found that higher temperatures decrease survival and reproduction in the wide-ranging alpine plant *Silene acaulis*, but increase growth rates, perhaps due to longer and warmer growing seasons. Temperature, particularly coldest month temperature, is slated to increase in the future (Supplemental Table 1). Because coldest month temperatures, which reduce performance, are increasing more quickly than mean annual temperature, which increases performance, we see sum negative impacts of increases in temperature on vital rates. Precipitation also impacts vital rates, and most of these impacts are negative. Negative effects of precipitation could reflect higher snowload and thus a shorter growing season, though increasing temperature could accelerate melt-out and negate this negative impact of precipitation (Jonas, Rixen, Sturm, & Stoeckli, 2008). Positive impacts of precipitation, which we find for survival, appear to be mediated entirely by their negative impact on probability of fruiting; we see a lagged positive effect of precipitation on survival, likely because precipitation reduces the probability of fruiting, which in turn increases survival. These effects are similar to other work showing a mix of positive and negative effects of precipitation on different vital rates (Shriver, 2016). Similar to temperature, precipitation is also slated to increase in the future, at most populations, meaning increases in precipitation are likely to decrease plant performance in the future.

Consistent with these impacts of temperature and precipitation on individual vital rates, future population growth rates are likely to decline substantially at most populations, and the magnitude of changes in climate is largely consistent with the impact on population growth rate. While current population growth rate is less than unity at all populations, most populations will experience substantial declines (up to 22%) in population growth rate and thus are quite likely to go extinct in a future climate. These declines appear to be driven by large increases in coldest month temperatures. Namely, we see positive effects of mean annual temperature increases on population growth rate and negative impacts of increases in coldest month temperatures (Figure 4C). Coldest month temperatures are warming more quickly than are average temperatures, and populations are sufficiently sensitive to coldest month temperatures to elicit a decrease in population growth rate. No aspect of precipitation has substantial impacts on population growth rate (Figure 4C), in spite of large changes in precipitation (Figure 4B). In populations where the magnitude of climate change (defined as the increase in average annual temperature) is higher,

declines in population growth rate are more severe (Figure 3B). Our findings are consistent with prior work showing that population abundances decline more rapidly in areas where mean temperature is increasing the most rapidly (Spooner, Pearson, & Freeman, 2018). There is evidence that higher rates of population decline under higher rates of warming translates to the distributional level, with faster range shifts under more substantial changes in climate (Chen et al., 2011; Ordonez & Williams, 2013).

While we know that climate change impacts on population growth rate vary across species' ranges (Spooner et al., 2018), few studies ask whether variation in sensitivity to climate variables or the magnitude of climate change are driving these effects. Our work shows that both differences in the magnitude of climate change and the sensitivity to climate change across populations mediates differential responses to climate change across *D. alaskana*'s range. Namely, the sum impact of climate change at most populations is a function of the relative strength of positive impacts of annual mean temperature and negative impacts of coldest month temperature, and the strength of these two climate impacts is mediated by sensitivity differences at some populations and climate change magnitude at others. At S2, we see relatively weak effects of both temperature variables due to low sensitivity to and small magnitude of change in these variables, but the negative impacts of coldest month temperature (and to a lesser extent, annual precipitation) outweigh the positive impacts of annual mean temperature. At N (in Denali National Park), the negative impact of coldest month temperature is larger than the positive impacts of mean annual temperature, because coldest month temperature increases dramatically and this population is quite sensitive to coldest month temperatures. By contrast, S1 is relatively insensitive to coldest- month temperatures, such that the negative impact of coldest month temperatures is weaker than the positive impact of annual mean temperature. Finally, E1 and E2 (in Wrangell-St. Elias National Park and Preserve) are quite sensitive to both annual mean temperature and temperature in the coldest month (A), leading to large impacts of these variables on population growth rate (C). E1 and E2 will also experience large increases in precipitation in the coldest month (B), which further increases population growth rate (C). However, because the sum of the contributions does not correspond with the sum impact of climate change for E1 and E2, these two populations are likely affected by the covariance among climate variables as well. In sum, divergent responses to climate change across populations are sometimes driven by sensitivity differences (including interactions among sensitivities), sometimes by magnitude of climate change at that population, and sometimes by both.

While few studies quantify the impact of differences in sensitivity to climate change v. climate change magnitude across populations, there are numerous studies looking at these effects in isolation. We know that interspecific variation in life history characteristics can modulate the impact of a given amount of climate change; for example, species that are shorter lived (Morris et al., 2008) or have shorter generation times (Saether et al., 2013) tend to be more impacted by variation in environmental conditions, such as climate change. Because life history characteristics (including generation time) can vary substantially across populations (Louthan et al., 2018), sensitivity to climate variables could also vary. Supporting this prediction, Crozier et al. (2007) found that populations of spring Chinook salmon responded differently to climate change impacts, likely due to differences in sensitivity of juvenile survival to climate change impacts across populations. At the same time, we know that different populations can experience different rates of warming, with high-latitude, inland, or wind-protected populations experiencing higher rates of warming (Ashcroft et al., 2009). In our study, E1 and E2 experienced much higher rates of warming than did S1, even though these populations were at

the same latitude, likely due to their inland location. Higher rates of warming at E1 and E2 contributed to larger climate change impacts. Our work shows that both sensitivity to climate change and the magnitude of climate change are important to consider when predicting the sum impact of climate change at populations across a species range.

The fate of *Douglasia alaskana* is likely representative of a suite of uncommon Alaskan alpine plant species, about which we know very little, but that have similar distribution patterns and population sizes. In general, we know little about plant extinction risk; the status of less than 5% of plant species worldwide has been assessed using IUCN criteria (Nic Lughadha et al., 2005), and the rate of description of new species matches the rate of new assessments of extinction risk (Brummitt et al., 2015). We do know that uncommon species are more likely to go extinct than more common species (Lavergne, Molina, and Debussche, 2006), meaning that uncommon plants such as *D. alaskana* (and its uncommon alpine heterospecifics) are more at risk. Further, alpine species are experiencing even more rapid warming than their low elevation counterparts. In the rapidly-warming Arctic, it is likely that many uncommon species, particularly alpine species, are at quite high risk for extinction, as is *Douglasia alaskana*.

Our work has important implications for predicting range shifts with climate change. To elicit latitudinal range shifts in response to climate change, low latitude populations must be negatively impacted by climate change, eventually declining to extinction, and high latitude populations must persist and colonize higher latitudes. In our study, we see the largest impacts of climate change not at the low latitude populations, but at the high-latitude and inland populations. In fact, some of our low-latitude populations actually do better in a future climate. Some of these effects are mediated by unequal rates of warming across populations (that do not vary predictably with latitude), but variation in sensitivity to climate change also mediates this unexpected response. Thus, our work highlights the need to consider both of these classes of factors in predicting species' range shifts, and may provide a framework for understanding why many species do not show predictable shifts in their geographic range with climate change (Moritz et al., 2008; Parmesan, 2006; Tingley, Monahan, Beissinger, & Moritz, 2009).

Citations:

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Table 1. Coefficient estimates (first row) and standard error (second row) of coefficient estimates for each vital rate and each climate variable used in this study. Coefficients significant at the 0.05 level are shown in bold. We also show estimates of seedlings per fruit (recruitment) for each population.

vital rate	intercept	ln(size in previous time step)	annual precipitation	average annual temperature	annual precipaiton x average annual temperature	precipitation in coldest month	temperature in coldest month	precipitation in coldest month (year prior)	temperature in coldest month (year prior)	precipitation in coldest month (year prior) x ln (size in the	temperature in coldest month (year prior) x ln (size in the previous time step)
p(survival)	- 19.8227 4.0273	- 0.4358 0.1051				- 1.0350 0.2041		1.2249 0.2411	- 1.1961 0.2425	0.0045 0.0012	0.0357 0.0147
mean size	2.0511 0.4793	0.7258 0.0206	- 0.0011 0.0004	1.2916 0.4309	- 0.0008 0.0004						
variance in size	-1.9127 0.1065	- 0.1012 0.0518									
p(fruiting)	-2.6286 0.4043	2.0670 0.2265				- 0.0166 0.0042	- 0.2513 0.0655				
number of fruits given fruiting	0.5191 0.1657	- 0.2180 0.0720					- 0.2076 0.0234				
	S1	E1	E2	N	S2						
seedlings per fruit	0.1925	0.3333	0.1600	0.0974	0.1958						

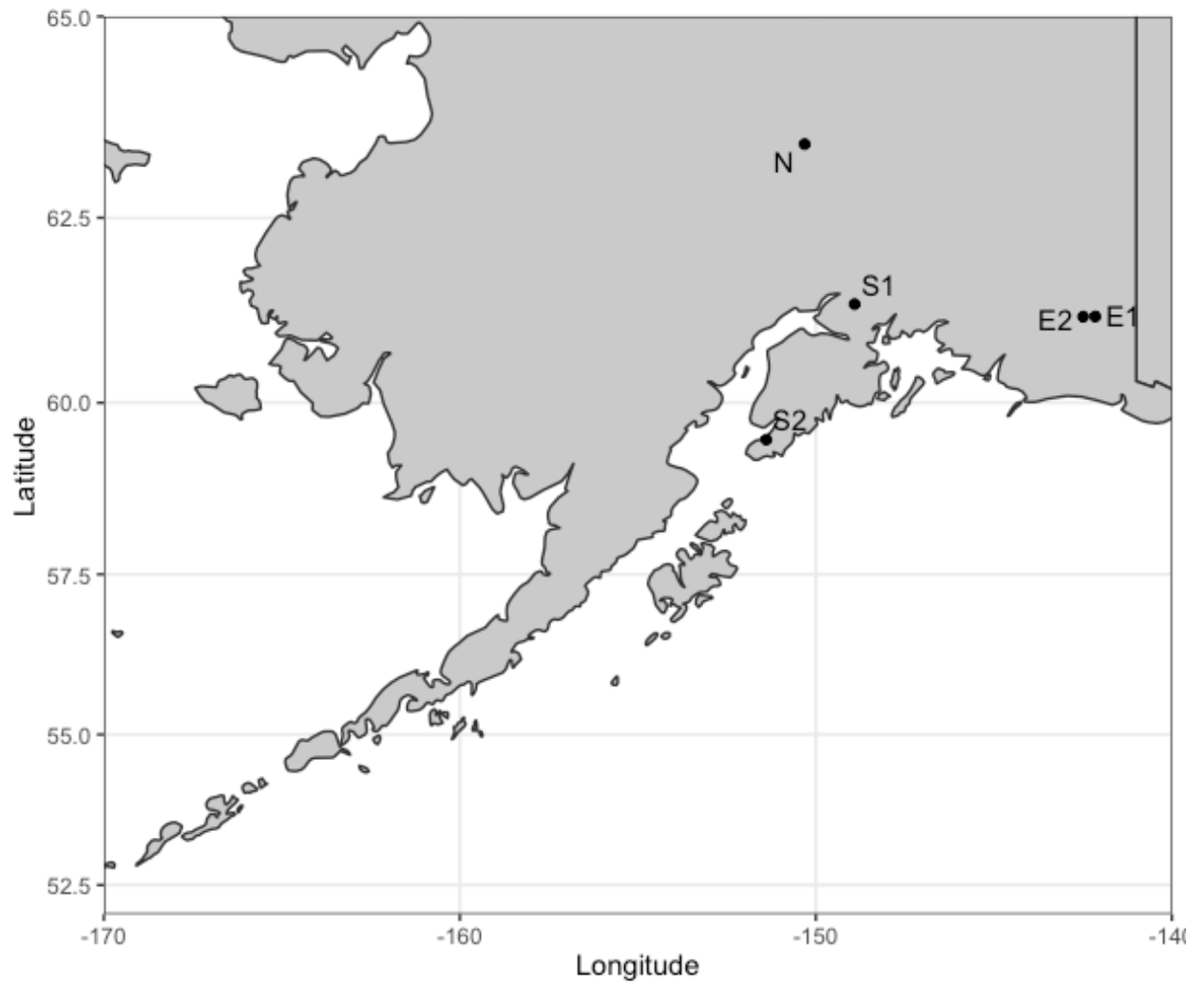


Figure 1. Populations used in this work. Labels of populations correspond to those of other figures. E2 and E1 are offset from one another to allow readability.

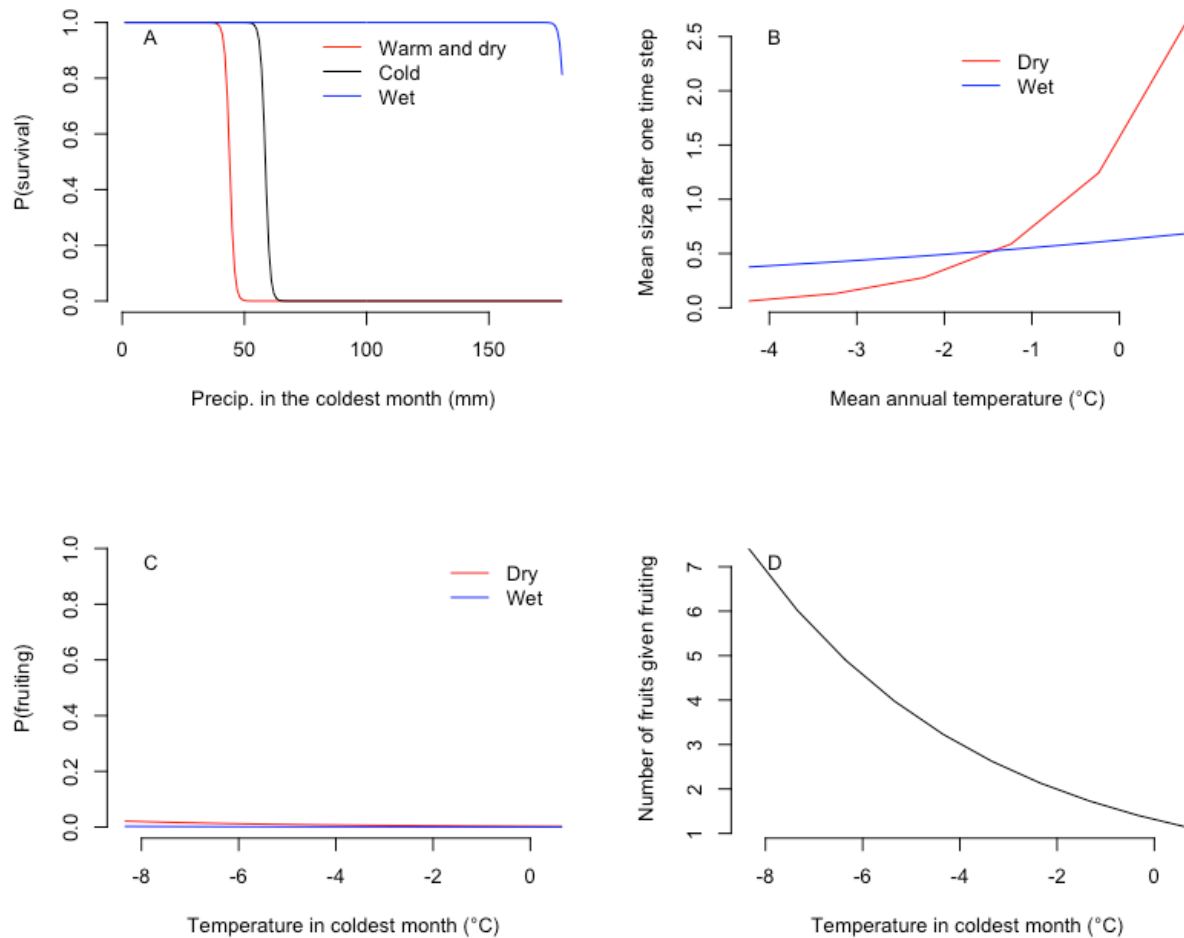


Figure 2. Vital rate functions for probability of survival (A), mean size after one year of growth (B), probability of fruiting (C), and number of fruits given fruiting (D). For A, we show how the impact of precipitation in the coldest month changes with coldest month conditions in the year prior. For example, if the coldest month in the year prior was warm and dry, then the probability of survival over a given year depends more strongly on precipitation in the coldest month of the given year. For B and C, we show how the impact of temperature varies with the associated precipitation during the same interval.

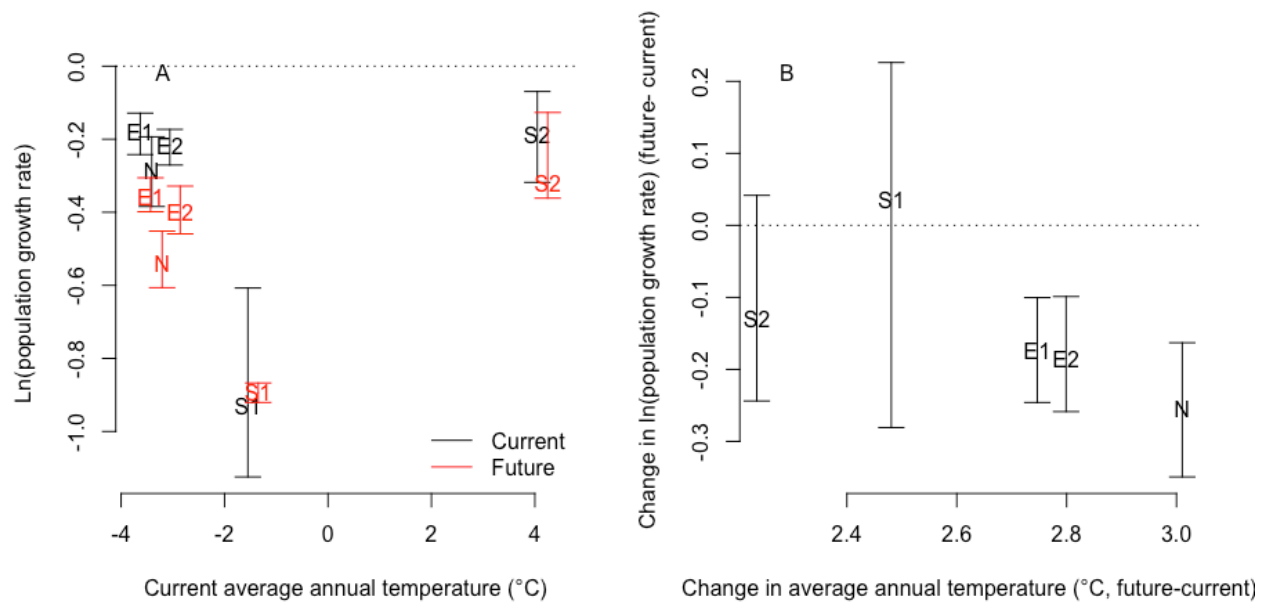


Figure 3. The impact of average annual temperature and changes in average annual temperature on population growth rates. In (A), we show the impact of current average annual temperatures over the 2016-2017 or 2017-2018 period on current and future population growth rate. In (B), we show the impact of changes in average annual temperature on the change in population growth rate. In A, points are jittered for readability.

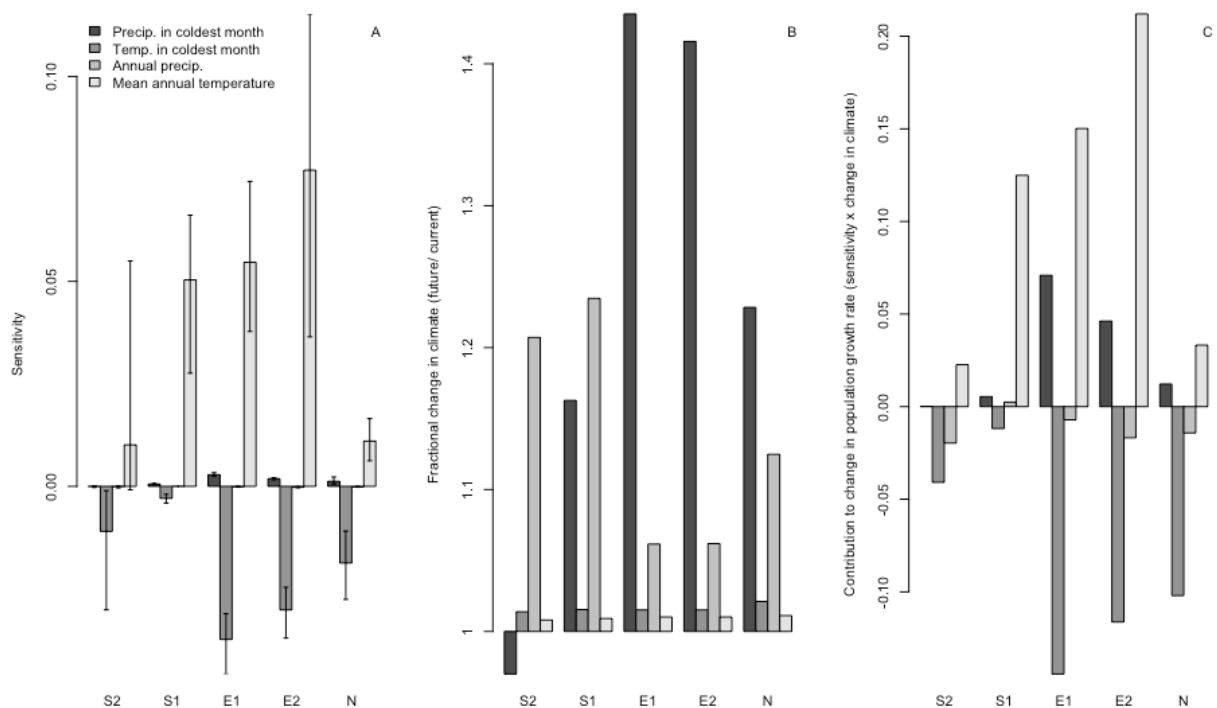


Figure 4. Sensitivity to (A) and fractional change in (B) climate conditions at each of our five populations for each climate variable present in our vital rate functions. The product of sensitivity to and differenced change in climate conditions (shown in C) estimates the population-specific contribution of each climate variable to the predicted change in population growth rate (future – current) at each population. Sensitivities were calculated using a perturbation approach using kernels from the future time period (2019-2099). In all panels, populations are arranged in order of increasing magnitude of climate change impacts on population growth rate. Note that there is a positive covariance between temperature in coldest month and annual mean temperature, meaning that the sum of each climate variable’s contribution to change in population growth rate does not sum to the overall change in population growth rate. We do not show the sensitivity to the covariance between these two climate variables, because we cannot calculate the change in covariance of these variables over time for each population, as each population x year only has one pair of these variables.

Supplemental Table 1. Current, future, and change in climate conditions at each population for each of the four climate variables used in vital rate functions.

	current				future				Change (future – current)			
population	temperature in coldest month (°C)	precipitation in coldest month (mm)	average annual temperature (° C)	annual precipitation (mm)	temperature in coldest month (°C)	precipitation in coldest month (mm)	average annual temperature (° C)	annual precipitation (mm)	temperature in coldest month (°C)	precipitation in coldest month (mm)	average annual temperature (° C)	annual precipitation (mm)
S1	-10.84	59.00	-1.55	662.80	-6.79	68.60	0.93	818.35	4.05	9.60	2.48	155.55
S2	-4.54	180.80	4.05	1431.00	-0.81	175.38	6.28	1727.45	3.73	-5.42	2.24	296.45
N	-15.28	43.20	-3.41	955.80	-9.82	53.06	-0.40	1075.09	5.46	9.86	3.01	119.29
E1	-18.24	57.20	-3.43	1184.20	-14.37	82.09	-0.68	1257.10	3.87	24.89	2.75	72.90
E2	-18.32	59.20	-3.26	1232.80	-14.46	83.81	-0.51	1309.14	3.86	24.61	2.75	76.34