

Both life-history plasticity and local adaptation will shape range-wide responses to climate warming in the tundra plant *Silene acaulis*

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Abstract

Many predictions of how climate change will impact biodiversity have focused on range shifts using species-wide climate tolerances, an approach that ignores the demographic mechanisms that enable species to attain broad geographic distributions. But these mechanisms matter, as responses to climate change could fundamentally differ depending on the contributions of life-history plasticity vs. local adaptation to species-wide climate tolerances. In particular, if local adaptation to climate is strong, populations across a species' range—not only those at the trailing range edge—could decline sharply with global climate change. Indeed, faster rates of climate change in many high latitude regions could combine with local adaptation to generate sharper declines well away from trailing edges. Combining 15 years of demographic data from field populations across North America with growth chamber warming experiments, we show that growth and survival in a widespread tundra plant show compensatory responses to warming throughout the species' latitudinal range, buffering overall performance across a range of temperatures. However, populations also differ in their temperature responses, consistent with adaptation to local climate, especially growing season temperature. In particular, warming begins to negatively impact plant growth at cooler temperatures for plants from colder, northern populations than for those from warmer, southern populations, both in the field and in growth chambers. Furthermore, the individuals and maternal families with the fastest growth also have the lowest water use efficiency at all temperatures, suggesting that a trade-off between growth and water use efficiency could further constrain responses to forecasted warming and drying. Taken together, these results suggest that populations throughout species' ranges could be at risk of decline with continued climate change, and that the focus on trailing edge populations risks overlooking the largest potential impacts of climate change on species' abundance and distribution.

KEYWORDS

climate change, demographic compensation, geographical distribution, local adaptation, plasticity

1 | INTRODUCTION

One of the greatest challenges in ecology and evolutionary biology is to credibly predict how the abundances and geographic distributions of species will change as Earth's climate warms. Understanding shifts in both abundance and distribution is critical to assess extinction risk as well as changes in the roles species play in communities and ecosystems (Ehrlén & Morris, 2015). Presence/absence data have shown that many species' ranges have shifted either poleward (Parmesan et al., 1999; Thomas & Lennon, 1999) or upward in elevation (Grabherr, Gottfried, & Pauli, 1994; Klanderud & Birks, 2003; Lenoir, Gégout, Marquet, de Ruffray, & Brisse, 2008; Moritz et al., 2008; Wipf, Stöckli, Herz, & Rixen, 2013) over historical time. Frequently, these range shifts include both contraction near the warm edge of the range and expansion beyond the historical cool edge, just as we would expect if warm- and cool-edge populations experience climates near the respective thermal limits for the species. However, range edge shifts have frequently not followed these simple expectations (Moritz et al., 2008; Parmesan et al., 1999), calling into question their generality. In addition, the focus on range edges has left us largely in the dark about how populations in the interior of species' ranges have or will respond to warming. Climate change effects may be as strong or stronger away from historic range edges, which also comprise only a small fraction of the geographic extent of widespread species.

Disproportionate focus on range-edge dynamics has resulted in part from widespread use of species distribution models (SDMs; Franklin, 2009) to predict ecological consequences of climate change (Thuiller et al., 2008). SDMs draw attention to the edge of the range, as they are largely focused on predictions of probability of occurrence, which are assumed to fall as a species' overall climatic limits are approached. Although SDMs only require occurrence data, and thus can be easily applied to many species, detailed studies of climate responses for particular species are needed to test the assumptions of SDMs and clarify whether and why predictions from these simpler models may be inaccurate. For example, abundance in interior populations may respond to warming in ways that bear little resemblance to predicted changes in occurrence near range limits. For widespread species, longstanding climatic differences across the range are likely to have selected for different environmental tolerances, as supported by myriad demonstrations of strong local adaptation (Franks, Weber, & Aitken, 2014; Hereford, 2009; Jump & Peñuelas, 2005; Leimu & Fischer, 2008). However, intraspecific variation is largely ignored in SDMs, which rely on species-level estimates of environmental tolerances and also assume niche conservatism over time (but see Hällfors et al., 2016; Oney, Reineking, O'Neill, & Kreyling, 2013; Pearman, D'Amen, Graham, Thuiller, & Zimmermann, 2010). If local adaptation is strong, the breadth of environmental tolerances in local populations (including those at range edges) may be much narrower than for a species as a whole (Holt, 2009). If so, locally adapted populations could be highly susceptible to climate change regardless of their position within the

range, especially where the velocity of climate change (sensu Loarie et al., 2009) surpasses the species' dispersal ability and gene flow is limited by natural or artificial habitat fragmentation.

Moreover, the magnitude of climate change will likely differ across most species' ranges. If local populations have a narrower climatic tolerance than the species as a whole, we could see stronger population declines where climate change is greatest. In the Northern hemisphere, warming is predicted to be greatest at high latitudes (IPCC 2014), raising the paradoxical possibility that populations may be most vulnerable not at the southern range limit, where temperature is already warmer, but at the northern limit, where change has been and will be faster. The breadth of a population's climatic tolerance may also reflect past selection imposed by more or less variable environments, in which case the detrimental effects of climate change will depend on the balance between local climatic tolerances and the magnitude of climate change (Deutsch et al., 2008), both of which could vary throughout a species' range (Angert, Sheth, & Paul, 2011).

Several lines of evidence suggest that such variation in local climate tolerances is common in widespread species. First, reciprocal transplant experiments across species' latitudinal ranges often show that local populations outperform foreign populations under natural field conditions (Ågren & Schemske, 2012; Griffith & Watson, 2005; Joshi et al., 2001). Second, comparisons of populations from across latitudinal gradients have frequently demonstrated faster development of high-latitude individuals across a range of environmental conditions in lab studies (Conover, Duffy, & Hice, 2009; Laugen, Laurila, Räsänen, & Merilä, 2003; Paccard, Fruleux, & Willi, 2014). This "countergradient variation," in which the genetic differences among populations act to minimize trait variation along an environmental gradient, is thought to reflect adaptation to colder, shorter growing seasons at high latitudes (Conover & Schultz, 1995; Levins, 1969). Finally, comparisons of thermal performance curves often find that individuals differ in their thermal optima and/or breadth, and that these differences are correlated with local temperature regimes (Angert et al., 2011; Deutsch et al., 2008; Hoffman, Anderson, & Hallas, 2002; Kelly, Sanford, & Grosberg, 2012). Although local adaptation is most narrowly defined as a pattern of reciprocal advantage of local vs. foreign individuals (Kawecki & Ebert, 2004), patterns of countergradient variation or differences in thermal performance curves among populations are also interpreted as evidence of adaptation to local climate conditions (e.g. Conover et al., 2009; Hoffman et al., 2002; Kelly et al., 2012; Laugen et al., 2003), and could influence local responses to climate change.

Here, we investigate how climate responses can vary across a species' range, using experimental and long-term observational data on the tundra plant *Silene acaulis* arrayed across its ~35° latitudinal range in western North America (Figure 1a). We have previously shown that mean annual values of several vital rates show compensatory changes across latitudes and corresponding climate regimes (Doak & Morris, 2010). Decreasing survival and reproduction toward the southern range limit are compensated by increasing growth

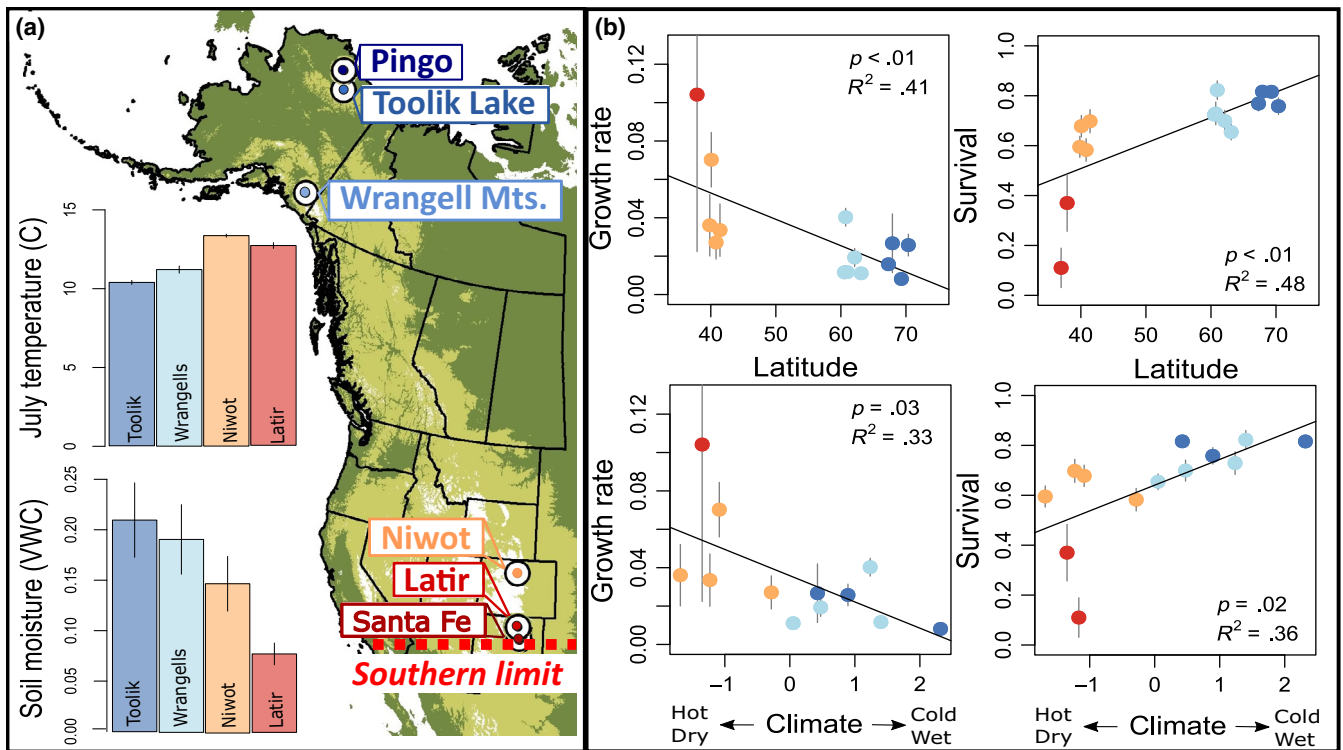


FIGURE 1 Local climate and demographic rates of *Silene acaulis* throughout its western North American latitudinal range. (a) Study populations span arctic Alaska to the southern range limit in the Sangre de Cristo mountains of New Mexico. Inset: Conditions during the growing season are warmer and drier on average toward the southern range limit. Average July soil temperature from 2009 to 2016 and average soil moisture in June and July from 2014 to 2016 (± 1 SEM). Elevations: green, ≤ 500 m; tan, > 500 m and $\leq 2,000$ m; white, $> 2,000$ m. (b) Demographic compensation in average small plant survival and growth rates across latitude (top) and climate (bottom). Points show the mean growth rate (left) and survival rates for small plants (right) for each demographic study population (± 1 SEM) from Latir NM (red), Niwot CO (orange), Wrangell Mts. AK (light blue), and Toolik Lake AK (dark blue). Growth rates decrease and survival rates increase with latitude (top) and along a climate principal component axis, which explains 78.6% of the total variation in mean July soil temperature and soil moisture across populations. Note: points are jittered slightly along the x-axis in the top panels for clarity. For an explanation of missing points, see the Supporting Information

rates, resulting in stable populations; we also found evidence for this same pattern across years within regions. We termed these opposing trends, which are particularly pronounced for growth and survival of small plants, “demographic compensation” (Doak & Morris, 2010; Vilellas, Doak, García, & Morris, 2015).

Demographic compensation across climate gradients has now been documented in multiple plant species (Vilellas et al., 2015), but could be produced by several potential mechanisms with differing implications for climate change effects. For example, demographic compensation could reflect species-wide plasticity in vital rates. If all populations share the same plastic response to temperature for a given vital rate, with opposing trends for different vital rates (Figure 2a), then most populations across the range would be buffered against a limited degree of warming, with only the warmest, southernmost populations expected to immediately exceed a climatic tipping point. In contrast, demographic compensation could also arise if populations are adapted to local climate, but the means of different vital rates within populations show opposing trends to climate across populations (Figure 2b). In this case, populations would have little ability to cope with in situ climate change despite a broad species-

wide climatic tolerance, with all populations likely to exceed local tipping points with moderate warming. Thus, understanding the mechanism responsible for demographic compensation has important implications for predicting changes in a species' abundance and geographic range with climate change, and would tell us whether the past emphasis on the responses of range edges to climate change will underestimate the magnitude of ecological disruption we should expect with continued warming.

Distinguishing among alternative mechanisms for demographic compensation is easier if individuals from different populations are all exposed to the same broad range of temperatures experienced by the species as a whole. Differences among populations under common environmental conditions are then likely due to genetic divergence. However, as for most widely distributed species, populations of *S. acaulis* in the field experience only partially overlapping climatic conditions (Figure 1, Figure S10). Here, we report results from two common garden growth chamber experiments in which we grew plants from across the latitudinal range of *S. acaulis* under the same broad range of temperatures, crossed with a watering treatment. With these experiments, we evaluate whether plants from different

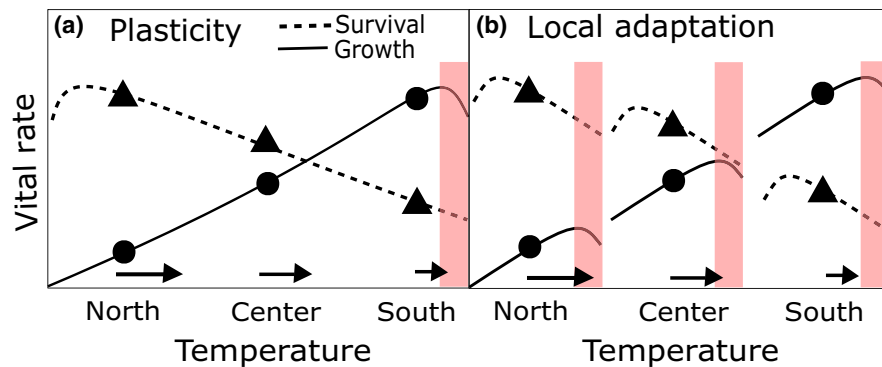


FIGURE 2 Different mechanisms could drive demographic compensation across a species' range. Survival (triangles, dashed lines) increases with latitude, whereas growth (circles, solid lines) decreases. (a) If this pattern is caused entirely by life-history plasticity, compensatory changes in survival and growth with temperature will buffer populations to climate change (arrows at the bottom show the magnitude of warming, assumed to be greatest in the north), up to a threshold beyond which both vital rates decline (shown in pink). Southern-edge populations are closest to this threshold and most susceptible to climate change. (b) Alternatively, if populations are locally adapted, then compensatory changes will buffer populations up to a population-specific threshold. In this case, populations that experience the greatest increases in temperature (i.e., in the northern portion of the range) are more likely to exceed population-specific thresholds and are thus most susceptible

populations show the same plastic responses in survival and growth rates to temperature, or whether there is evidence of adaptation to local temperatures in either vital rate. In particular, we compare patterns of absolute performance among populations to test for countergradient variation or reciprocal local advantage, as well as temperature responses within populations to look for evidence of population-specific optima. We also verify patterns of demographic compensation within and between natural populations and look for evidence of population differences in climate responses, using 15 years of field data, new local climate data, and new populations closer to the southern range limit.

Finally, we evaluate the potential for populations to persist in the face of warming through rapid evolution of thermal tolerances. Genetic variation in underlying vital rate responses could allow evolutionary rescue, in which populations adapt to changing climate sufficiently quickly to prevent local extinction (Chevin & Lande, 2010; Chevin, Lande, & Mace, 2010). However, because plants must lose water to acquire carbon, they face a fundamental trade-off in climate adaptation (Arntz & Delph, 2001; Dudley, 1996; Geber & Dawson, 1997) which on short time-scales is likely to be an important constraint on the evolution of thermal tolerances (Long & Ort, 2010; Sage & Kubien, 2007). To explore this idea, we tested whether fast growth trades off with intrinsic water use efficiency (WUE), particularly at high temperature, within and among maternal seed families in our growth chamber experiments. Functional or genetic constraints among climate-related phenotypes, such as growth rate and WUE, can prevent rapid adaptation to climate change (Chevin, 2013; Etterson & Shaw, 2001).

2 | MATERIALS AND METHODS

2.1 | Study populations

Silene acaulis (Caryophyllaceae) is a long-lived cushion plant that is broadly distributed in arctic and alpine tundra. In western North

America, its latitudinal range extends from arctic Alaska to the Sangre de Cristo mountains of northern New Mexico. The local distribution of *S. acaulis* ranges from patchy to more or less continuous within alpine habitats, whereas on larger scales alpine habitats are virtually always extremely patchy within a matrix of intervening, unsuitable habitat. At local scales, populations show genetic structure consistent with limited seed dispersal (Gehring & Delph, 1999) and, at the continental scale, the southern Rocky Mountains show substantial genetic divergence from arctic Alaskan populations, suggesting vicariance during periods of glaciation (Gussarova et al., 2015). Individual cushions have a single taproot and grow by adding branch tips ("rosettes"). *Silene acaulis* demographic rates were monitored from 2001 to 2016 in 13 populations across three regions (Niwot Ridge Long-Term Ecological Research Site [Colorado], the Wrangell Mountains [south-central Alaska], and the Toolik Lake Long-Term Ecological Research Site [northern Alaska]) and from 2007 to 2016 in two populations in the Latir Peak Wilderness (Sangre de Cristo Mountains, New Mexico). We tracked survival, growth (in number of rosettes), and recruitment of small plants (seedlings or one-rosette plants past the seedling stage; $N = 211\text{--}13,707$ plant-years per region). While larger *Silene acaulis* can have hundreds of rosettes, we focus here on these small plants, which are more responsive to climate (Doak & Morris, 2010) and that are similar in size to the seedlings in our growth chamber experiments. At all field sites, we also recorded local soil temperature from 2009 to 2016 with shallowly buried (<1 cm) microthermistors (iButtons, 2–8 per population) and volumetric soil moisture from 2012 to 2016 (Decadon EC-5 sensors, 2 per population). Details of the demographic study populations and methods are described in Doak and Morris (2010). We also downloaded daily climate data from 2000 to 2016 from US National Oceanic and Atmospheric Administration weather stations in two regions (Santa Fe NM, Pingo AK), from Prism Climate Group (Latir NM, Niwot CO), from Toolik Field Station (Toolik AK), and from the Western Regional Climate Center network (Wrangell Mts. AK) to

generate estimated local soil temperatures for years prior to iButton deployment (see Supporting Information Methods).

2.2 | Growth chamber experiments

We collected seeds from the four demography study regions and from two other populations closer to the edges of the species' latitudinal range (Santa Fe National Forest, New Mexico and Pingo near Deadhorse, Alaska) in the 1–2 years prior to each experiment. We collected at least 10 mature fruits from 16 to 31 maternal plants, located at least 1 m apart, within each region and tracked responses of seeds and seedlings from each of these maternal families. *Silene acaulis* is gynodioecious and insect-pollinated, and seeds from the same maternal plant most likely represent half-sibships. Relatively slow maturation to flowering in the greenhouse and a small number of seeds per fruit precluded performing controlled crosses in the greenhouse which would be needed to generate a sufficient number of seeds for the experiments in a balanced half-sib design.

For each experiment, we germinated seeds on moist filter paper and transplanted seedlings into separate cells of 288-cell plug trays filled with a mixture of 50% sand and 50% germination mix. We initially tested small plant survival and growth rates in response to three temperatures (1, 10, and 19°C; experiment 1). Then, to better identify the optimum temperatures for growth, we grew plants at 10, 20, and 30°C, and crossed the temperature treatment with two watering frequencies (daily vs. every 3rd day) to vary soil moisture (hereafter wet and dry; experiment 2). Trays were randomly assigned to growth chambers with a 16/8 hr light/dark schedule, and maintained at either 1, 10, or 19°C for 21–62 days at Uppsala University in 2014, or at 10, 20, or 30°C for 36–65 days across two temporal replicates at Duke University in 2015–16. In this second experiment, half of the trays were maintained with a 20 mm water table (wet treatment) and half experienced two 3-day dry down periods per week (dry treatment) (Figure S7; Snow & Tingey, 1985). Trays were rotated weekly to reduce position effects.

At the end of each experiment, we scored survival and all survivors were washed, dried at 40°C for at least 24 hr, and weighed for above-ground biomass (both experiments) and below-ground biomass (experiment 2 only). We selected the best-represented maternal families from two regions, Niwot CO and Wrangell Mts. AK, for carbon isotope analysis ($N = 10$ and 11 families from Niwot and Wrangell Mts., respectively). For each family, we included all surviving individuals across all experimental treatments ($N = 20$ – 29 individuals per family [mean = 23.8]) and homogenized dried above-ground biomass by grinding with a mortar and pestle. For approximately 6% of individuals, we included two replicate samples; replicates were highly correlated ($\rho = .955$, $t = 17.86$, $N = 31$, $p < .001$) and averaged in subsequent analyses. Isotope analysis was conducted by the University of California Santa Cruz Stable Isotope Lab. We converted $\delta^{13}\text{C}$ ratios to discrimination as $\Delta^{13}\text{C} = (\delta^{13}\text{C}_{\text{air}} - \delta^{13}\text{C}_{\text{plant}})/(1 + \delta^{13}\text{C}_{\text{plant}}/1000)$ and setting $\delta^{13}\text{C}_{\text{air}} = -8$. Carbon discrimination ($\Delta^{13}\text{C}$) reflects the average concentration of CO_2 within the leaf relative to the atmosphere over time, which is determined by the

balance of CO_2 entering the leaf through stomatal conductance and carbon fixation through photosynthesis. Under common environmental conditions, $\Delta^{13}\text{C}$ is negatively related to the intrinsic water use efficiency (hereafter “WUE”). For this reason, we used the negative of discrimination ($-\Delta^{13}\text{C}$) as an estimate of WUE in all analyses (following Angert, Kimball, DeMarche, Huxman, & Venable, 2014), so that a negative relationship between $-\Delta^{13}\text{C}$ and growth rate would indicate the expected trade-off between WUE and growth.

2.3 | Analysis

We compared the growth and survival rates of seedlings and 1-rosette plants in demographic study populations. We tested for demographic compensation by regressing mean growth or survival rates for each study population against latitude or a time-averaged climate measure. As a univariate measure of climate, we used the first principal component, explaining 78.6% of the variation, from an analysis of mean July temperature from iButtons and mean soil moisture (VWC) of each population, both standardized to mean 0 and unit variance. We next tested whether the probabilities of a 1-rosette plant surviving and, if so, growing to a larger size class (≥ 2 rosettes) depended on annual climate within each of our longest-running demographic study populations at Toolik Lake AK, Wrangell Mts. AK, and Niwot CO from 2001 to 2016. We fit generalized linear models using a binomial family and considered linear and quadratic terms for mean July temperature from weather stations, adjusted to match local microthermistor data (see Supporting Information), fixed effects of region and population within region, and interactions between temperature and region. For survival, we used data for both seedlings and 1-rosette plants and all models also included a factor indexing whether a plant was a seedling or 1-rosette plant past the seedling stage; results in Figure 5 are for 1-rosette plants as predicted by the best-supported model. We compared full and simplified models with AICc to determine support for different explanatory factors and alternative function forms of these effects (Burnham & Anderson, 2004).

We next compared how survival, growth rates, and WUE from the growth chamber experiments differed among treatments and seed source regions. We fit linear mixed models to growth rate and WUE data and generalized linear mixed models with binomial errors and bobyqa optimizer to binary survival data, and including maternal seed family and tray as random effects where supported by likelihood ratio tests. All mixed models were fit with the lme4 package in R v. 3.2.3 (Bates, Mächler, Bolker, & Walker, 2015; R Core Development Team 2015). The total number of days between planting and harvest for each plant was included as a covariate in models of survival and in the denominator of the growth rate, which was estimated as $\log(\text{final biomass mg} + 1)/\text{days}$. For analyses of data from the second experiment, we considered fixed effects for temporal replicate and chamber identity to account for uncontrolled differences in growing conditions, and used the sum of above-ground and below-ground biomass in estimates of growth rates. We used an information-theoretic approach to infer the drivers of survival and

growth rate variation in our experiments by comparing full and simplified models with AICc; there was mixed support for some interactions in the second experiment, so we show weighted-average predictions across all models with $\Delta\text{AICc} \leq 2$. We also compared models with linear plus quadratic temperature terms to models with linear plus natural log of temperature effects to allow asymmetry in temperature responses; both approaches produced very similar predictions (Pearson's $\rho > .999$, $p < .001$) and models with quadratic temperature responses had slightly greater support ($\Delta\text{AICc} = 0.3$), so we present quadratic models here.

On the basis of evidence that regions differed in their temperature responses (see Results), we next tested whether the optimum temperatures inferred from fitted response curves were correlated with mean temperatures in the field. We estimated temperature optima (hereafter " T_{opt} ") as the local maxima from fitted temperature response curves of survival and growth for each region from the best-supported models. We focused on survival rates across the lower temperature range in experiment 1 and growth rates across the higher temperature range in experiment 2; differences in the designs of these experiments precluded an analysis combining across the full temperature range, and these datasets yielded the strongest support for region \times temperature² interactions for survival and growth rate, respectively (Tables S1–S8, see Supporting Information). We estimated T_{opt} using the fitted coefficients for each region from the best-supported models (Tables S2 and S8) and solving for the local maximum by finding the temperature at which the first derivative of the vital rate function is equal to zero. In two cases, this approach produced extreme values (e.g., $>60^\circ\text{C}$), reflecting fitted vital rate functions that were insufficiently unimodal within our range of experimental temperatures. In these cases, we inferred that the optimum occurs at some higher temperature than estimates for other regions, so we set these values equal to the highest estimate in Figure 5. We tested for the significance of the correlations of T_{opt} values with local mean July temperature (C) using Spearman rank correlations and computed 95% nonparametric bootstrap confidence intervals by re-sampling the dataset with replacement, stratified by population and treatment to preserve the sample sizes of the original dataset, to generate a distribution of correlation coefficients from 500 samples. In cases where fitted vital rate functions, either from the original or bootstrapped datasets, were insufficiently unimodal to estimate T_{opt} , we inferred that the optimum occurs at some higher temperature than estimates for other regions, and ranked this value first to calculate Spearman rank correlations. All analyses were conducted in R v. 3.2.3 (R Core Development Team 2015).

3 | RESULTS

By following the fates of small plants over 8–15 annual transitions in 2–5 populations in each of 4 geographic regions (Figure 1a), we found that the opposing latitudinal trends in small plant growth and survival previously reported (Doak & Morris, 2010) were strongly corroborated. In particular, mean annual survival was lowest and

growth rate highest at the new southernmost study region, and growth falls, whereas survival rises with increasing latitude (Figure 1b). The same pattern is recovered with a climate principal component combining local mean July temperature and soil moisture rather than latitude (Figure 1b). These results are robust to potential outliers (i.e., excluding Latir; Latitude: $p < .01$, $R^2 = .48$ and $p = .03$, $R^2 = .33$; Climate: $p < .01$, $R^2 = .51$ and $p = .05$, $R^2 = .28$, for survival and growth rates, respectively).

Plants originating from all regions showed similar compensatory responses in survival and growth across a broad range of temperatures in growth chamber experiments (Figure 3, model selection tables and coefficients of the best-supported models given in Tables S1–S8, model fit to the data shown in Figures S1–S4). In general, the best-fit growth rate curves first increase with warming but then plateau or decline at the highest temperatures tested (Figure 3e,f,g, ΔAICc for models without a temperature² effect >4). In contrast, the best-fit survival curves increase at the lowest temperatures tested (experiment 1, Figure 3a) but decrease over a broad range of intermediate to high temperatures (experiment 2, Figure 3b,c). Drier conditions increased performance at low temperatures and decreased performance at high temperatures, with stronger effects on growth than survival (Tables S5–S8, ΔAICc for models without water \times temperature effects <1). However, watering had less effect on both rates than did temperature (Figure 3b,c,f,g, Tables S5–S8). In contrast to mean growth in the field, growth in the experiments was higher for plants originating from northern populations (Figure 3e,f,g, ΔAICc for models without a region effect >4), likely due to the higher mean mass of seeds from northern populations (Figure S5). Plants from northern populations also had higher survival across temperatures in experiment 2 (Figure 3b,c, ΔAICc for models without a region effect >4).

Although the compensatory changes in survival and growth with experimental warming are broadly similar for plants originating from each region, we also find strong evidence of adaptation to local temperature conditions. Plants originating from northern populations showed more rapid development under common environmental conditions (Figure 3e,f,g, ΔAICc for models without a region effect >4 , Tables S3, S4, S7 and S8), consistent with countergradient variation and adaptation to shorter, colder growing seasons. Relative changes in performance with temperature, or the locations of thermal performance curves, were also consistent with adaptation to local climate conditions. In particular, T_{opt} values were lower for northern populations and higher for southern populations, reflecting local mean growing season temperatures in the field (Figure 3d,h; Survival: $\rho = .7$ (95% CI: 0.30–0.97), Growth: $\rho = .5$ (95% CI: 0.03–0.81)).

Within populations, maternal seed families varied significantly in survival, growth, and WUE (likelihood ratio tests; experiment 1: survival: $\chi^2 = 42.36$, $p < .01$, growth: $\chi^2 = 89.25$, $p < .01$; experiment 2: survival: $\chi^2 = 47.55$, $p < .01$, growth: $\chi^2 = 12.45$, $p < .01$, WUE: $\chi^2 = 12.16$, $p < .01$; Tables S9 and S10). However, at all temperatures, growth rate was negatively correlated with WUE across individuals (Figure 4). This phenotypic trade-off was stronger at higher temperatures (Figure 4; Temperature \times WUE interaction for growth

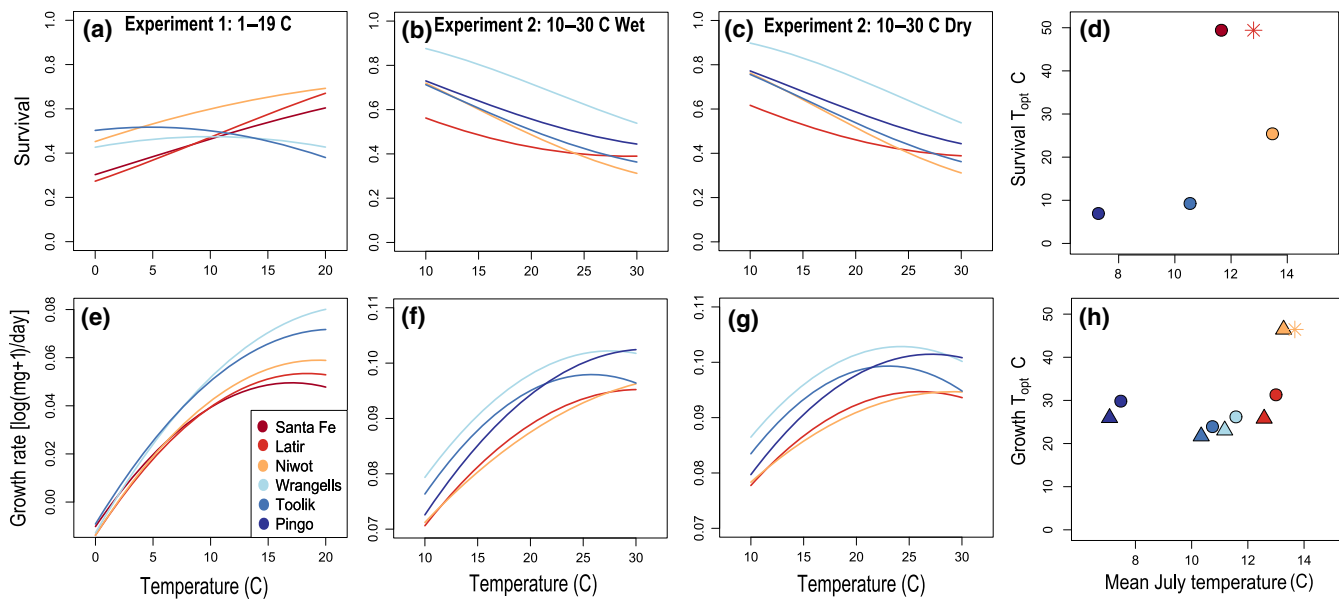


FIGURE 3 Effects of temperature and watering on survival (top) and growth (bottom) of small plants in the two experiments. (a–f) Lines are best-fit relationships for each region from generalized linear mixed models (Tables S1–S8). Growth rates reflect above-ground biomass only in experiment 1 but total (above- and below-ground) biomass in experiment 2. Note that panels have differing axis ranges depending on experiment and response variable. (g, h) Optimum temperatures (T_{opt}) for survival and growth, estimated for each region from experiments, are correlated with local mean July temperatures in the field. T_{opt} were estimated from the first experiment for survival and the second experiment for growth, since these datasets had the strongest support for differing T_{opt} among regions for each vital rate (i.e., region \times temperature² interactions, Tables S1–S8, Supporting Information Methods). Asterisks indicate populations for which T_{opt} was not estimable and are shown at the largest estimated T_{opt} . Triangles indicate estimates from the dry treatment. Mean temperatures based on microthermistors, except for Santa Fe NM and Pingo AK, for which we did not have microthermistor data and used data from nearby climate stations. Experiment 1: 16–22 families per region, 1–70 (mean = 23.6) plants per family. Experiment 2: 30–31 families per region, 1–41 (mean = 20.2) plants per family

rate: $F_{2,243} = 3.53$, $p = .03$ and $F_{2,244} = 5.89$, $p < .01$ for plants from Niwot and Wrangell Mts., respectively) and at least partially due to a genetic trade-off among maternal families (Pearson correlation coefficients given in Figure 4). Thus, the individuals and families with the fastest growth at high temperature also have the lowest WUE.

Our experiments suggested that populations throughout the range of *S. acaulis* should eventually see both survival and growth of small plants decline with continued warming, even when locally “hot” temperatures are well within the range of temperatures seen across the species’ entire range. By pairing demographic data with annual mean July soil temperature for our longest-monitored populations, we found evidence of demographic compensation over at least some naturally experienced temperatures (Figure 5, Tables S11–S14, Figures S9 and S10, $\Delta AICc$ for models without region \times temperature and region \times temperature² effects >4). For example, at the southernmost region, there is a simple increase in growth and decline in survival across virtually the whole range of temperatures observed in the past 15 years. However, in the two northern regions, both survival and growth are unimodal (temperature² coefficients; growth: -0.0169 and -0.1148 ; survival: -0.0126 , and -0.0038 , for Wrangell Mts. and Toolik Lake, respectively, Tables S12 and S14), and both decline at the warmest temperatures observed locally in our study, including temperatures over which Niwot growth rates were still increasing. The Wrangell Mts. site experiences much greater variability in growing season temperatures (Figure 5a, Figure S10;

mean July temperature range: 5.61–16.57, 7.50–13.28, and 11.33–15.30 for Wrangell Mts., Toolik Lake, and Niwot, respectively), but less variability in both growth and survival rates across this range (range of predicted vital rates for Wrangell Mts., Toolik Lake, and Niwot, respectively; growth: 0.007–0.019, 0.003–0.018, and 0.022–0.095; survival: 0.716–0.804, 0.721–0.870, 0.632–0.889), potentially suggesting a relationship between higher temperature variability and lower responsiveness of vital rates.

4 | DISCUSSION

Accurately predicting how climate change will alter the abundance and distribution of even a single species is a substantial challenge. While populations are often buffered against some degree of environmental variation by compensatory vital rate responses (Villemas et al., 2015) or by low sensitivity of key demographic processes (Pfister, 1998), the mechanisms that contribute to these effects, and thus population persistence, are difficult to extrapolate and could quickly erode once climate change thresholds are reached (Doak & Morris, 2010). An even greater challenge is to predict how multiple species will shift in distribution and abundance across a landscape, with implications both for conservation and for the quality of ecosystem services provided to humans (Cardinale et al., 2012). Recent predictions of the impacts of climate warming on biodiversity

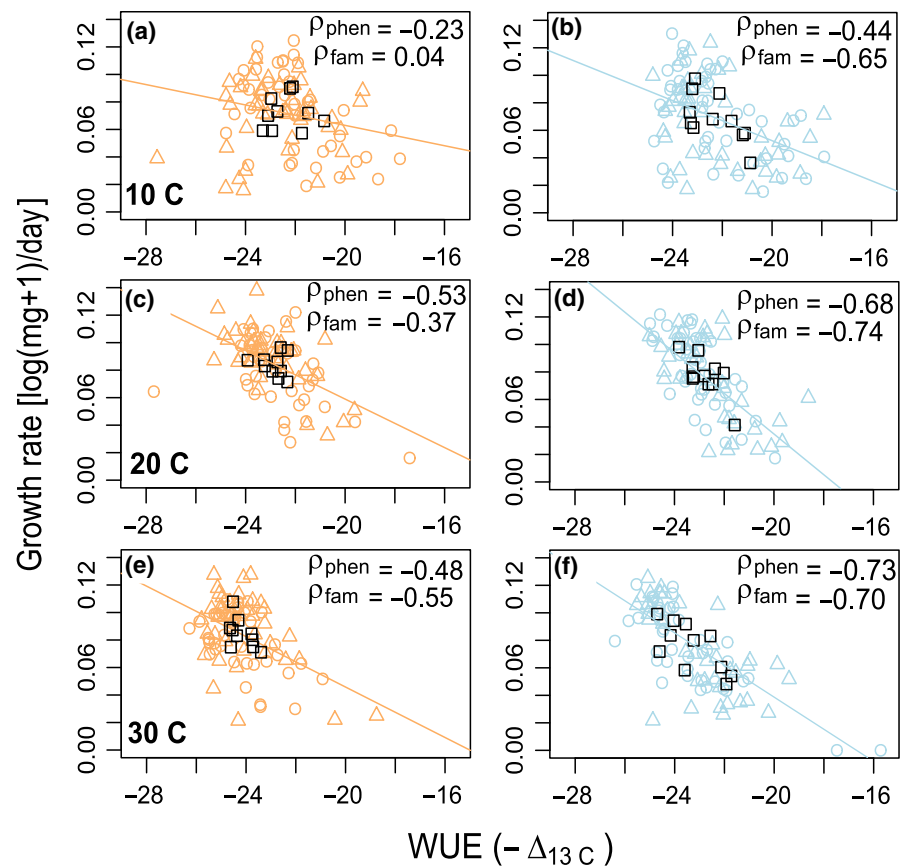


FIGURE 4 Growth rates are negatively correlated with water use efficiency. Each point is an individual plant from Niwot Ridge, CO (orange, left) or Wrangell Mountains, AK (blue, right) that was grown at either 10, 20, or 30°C in experiment 2 under wet (circle) or dry (triangle) conditions. Black squares show the maternal seed family means at each temperature. Lines show regressions of growth rate on WUE for each region and temperature. Phenotypic correlations among individuals and broad-sense genetic correlations among families are given in the upper right ($N = 10\text{--}11$ families, 20–29 plants per family)

are largely based on species distribution models (SDMs; e.g., Thomas et al., 2004; Thuiller, Lavorel, Araujo, Sykes, & Prentice, 2005), which do not consider the demographic mechanisms that dictate the geographical distributions and local abundances of species. Our work suggests that a more detailed consideration of the mechanisms that maintain populations, and in particular the role of local adaptation in climate responses, is needed to make accurate forecasts of responses—both in single species and entire communities—to climate change.

We find that demographic compensation (Doak & Morris, 2010; Villellas et al., 2015), both in mean vital rates across regions (Figure 1b) and in annual vital rates within regions (Figure 5), contributes to the ability of *S. acaulis* to persist across a broad latitudinal and climatic range. In particular, survival and growth of small plants from across the continent responded in opposite directions to warming in both controlled growth chamber experiments (Figure 3) and under field conditions (Figure 5). Previous analyses that documented this same pattern used cruder information from nearby weather stations to give regional measures of climate, and did not include region \times climate interactions (Doak & Morris, 2010). These opposing responses of small plant survival and growth to temperature should reduce the impact of environmental variability on the stochastic population growth rate (Doak, Morris, Pfister, Kendall, & Bruna, 2005; Tuljapurkar, 1990), and thus—to a point—buffer populations against variation in local climate.

While we see evidence of demographic compensation in plants from all regions (Figure 3), this compensation cannot be explained

simply as points along a single, species-wide response of each vital rate to temperature (as in Figure 2a). Instead, T_{opt} for growth and survival differed among regions as would be expected based on adaptation to local climate: T_{opt} was higher for plants originating in sites where the mean temperature is higher (Figure 3). These differences clearly indicate that species-wide environmental tolerances do not reflect the population-specific temperature responses for *S. acaulis*. Although we cannot rule out nongenetic effects of the maternal environment on seedling climate responses, such as epigenetic effects or other mechanisms of transgenerational plasticity, the most likely explanation given the substantial geographic, genetic, and environmental differences among these populations (Figure 1; Doak & Morris, 2010; Gussarova et al., 2015) is that the observed differences in climate responses under controlled conditions reflect genetically-based variation consistent with local adaptation. To our knowledge, this study is the first to experimentally distinguish between the roles of genetic divergence among populations vs. plasticity in generating range-wide demographic compensation.

Population-specific environmental tolerances will likely shape the response of *S. acaulis* to climate warming across its range. Because T_{opt} is lower in northern populations, they do not have to warm beyond the temperatures now experienced by southern populations before their vital rates begin to deteriorate (Figure 2a); far less warming could push them into a decline (Figure 2b). In particular, we see small plant growth declining in the warmest years in northern populations at temperatures at which growth is still increasing in southern populations (Figure 5). Combined with the potential for

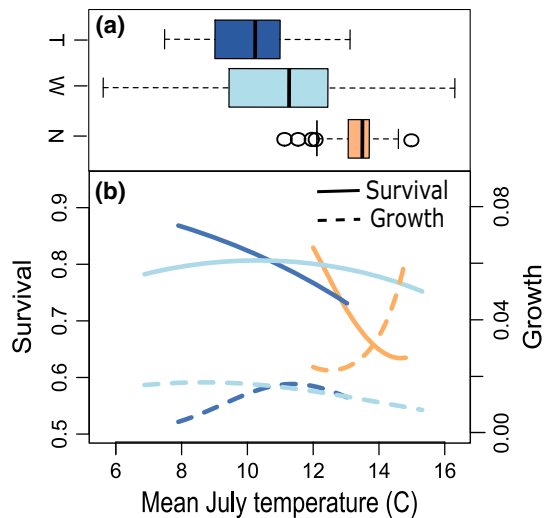


FIGURE 5 Temperature responses of survival and growth rates show temporal demographic compensation in natural populations. (a) The mean and range of temperatures in the field differ among regions (see also Figure S10). (b) Survival (solid line) and growth (dashed line) rates of 1-rosette plants as functions of mean July soil temperature (C) under field conditions in Niwtot CO (orange), Wrangell Mts. AK (light blue), and Toolik Lake AK (dark blue). Lines are best-fit relationships from generalized linear models (Tables S11–S14, $N = 25,955$ and $16,913$ plant-years for survival and growth, respectively) shown for the 95% quantiles of temperatures experienced in each region

greater absolute increases in temperature in northern populations (IPCC 2014), population-specific T_{opt} values imply that a shift in the geographic range of *S. acaulis* will not necessarily occur by “rolling back” the southern edge of the distribution where temperature is already warmer (Figure 1). Northern populations may even decline, whereas southern populations remain stable (we have not yet seen both survival and growth decline in the warmest years in the southern populations; Figure 5), an outcome not likely to be predicted by SDMs assuming uniform species-level environmental tolerances. We caution that our results only indicate likely adaptation to local climate in survival and growth of early life stages. These vital rates have only a small impact on population growth and fitness in *S. acaulis*, which is exceptionally long-lived (Morris & Doak, 2005), although as the average survival rates of small and large plants tend to be positively correlated, as do their growth rates (Villeras et al., 2015), we anticipate similar local adaptation in vital rates of larger plants that more strongly influence population growth.

We also found several differences between temperature responses in controlled environment experiments vs. under field conditions, shedding light on the potential forces shaping population-specific temperature responses (Angilletta, Wilson, Navas, & James, 2003). Specifically, the ranking of absolute growth rates was reversed between common environment experiments and natural populations, with northern populations growing fastest across all experimental temperatures. Plants from higher latitudes or altitudes may evolve higher rates of photosynthesis or development (Griffith

& Watson, 2005; Gurevitch, 1992; Paccard et al., 2014; Soolanayakanahally, Guy, Silim, Drewes, & Schroeder, 2009) to counteract the effects of colder, shorter growing seasons (“countergradient variation”; Conover & Schultz, 1995; sensu Levins, 1969). Interestingly, higher seed mass in northern populations could largely explain this faster growth (Figure S5), though whether differences in seed mass are genetically based remains unknown. Highly variable environments are also predicted to favor broader thermal tolerances (Deutsch et al., 2008), potentially at the cost of reduced maximal performance (Huey & Hertz, 1984). Although testing this hypothesis was not a focus of our study, we saw much broader temperature responses and lower maxima of both growth and survival under field conditions in the Wrangell Mts. site, which also experiences the most variable temperatures within and among years (Figure S10). Furthermore, although we found the same relative ranking of T_{opt} between field and experimental conditions, with performance beginning to decline at cooler temperatures in northern populations, these declines occurred at lower temperatures in the field than we would have expected from our experimental results (Figures 3 and 5). Acclimation to constant, controlled environments in our experiments may have allowed plants to achieve higher T_{opt} compared to more variable field conditions (Sage & Kubien, 2007) (Figure S10). Together, these patterns suggest that differences in the mean and variance of local temperatures and growing season length have shaped population-specific responses of growth and survival rates to temperature in *S. acaulis*. Indirect effects of climate mediated through biotic interactions (e.g., competition or facilitation with neighbors) may also have contributed to the altered temperature responses seen in the field.

Despite evidence that the vital rate responses of *S. acaulis* have been shaped by adaptation to local temperatures in the past, the potential for populations to rapidly adapt to new temperature regimes remains questionable. Models and laboratory tests of evolutionary rescue have focused on single traits and shifts in a single environmental driver (Carlson, Cunningham, & Westley, 2014; Chevin & Lande, 2010; Chevin et al., 2010), but the multivariate nature of both climate change and climate adaptation increases the risk that functional or genetic constraints will limit evolutionary responses to selection (Chevin, 2013; Ezzerson & Shaw, 2001). Despite significant variance among maternal families in growth responses, families with the highest growth rates under warming also have lower WUE, which has been shown in some plants to reduce survival under sustained drought conditions (Ehleringer, 1993; Knight et al., 2006). Although correlations among field-collected seed families are potentially due in part to maternal and dominance effects, the trade-off we observed between rapid growth and WUE is consistent with a general pattern in plant climate adaptation in which climatically stressful environments favor either stress-avoidant strategies that couple rapid development with low resource-use efficiency or stress-tolerant strategies that achieve high resource-use efficiency at the cost of slower growth (Arntz & Delph, 2001; Geber & Dawson, 1997). Climate change will likely alter both the temperature and soil moisture experienced by alpine plants during the growing season, as

both decreased snowpack and earlier snowmelt may combine to reduce water availability late in the growing season (IPCC 2014). The few examples of rapid adaptation in plants to changing climate have primarily involved shifts in phenology (e.g., Colautti & Barrett, 2013; Franks, Sim, & Weis, 2007), whereas there is evidence that climate change has outpaced adaptation in even short-lived organisms (Wilczek, Cooper, Korves, & Schmitt, 2014). In long-lived species such as *S. acaulis* (Morris & Doak, 1998), the need to tolerate increasingly warm and dry conditions throughout the growing season, coupled with the rapid pace of climate change relative to generation time, is likely to preclude evolutionary rescue.

Our results demonstrate that both life-history plasticity and local adaptation shape the responses of our study species to existing climate variation across the range, and are likely to continue to do so as climate warms. If, as seems likely, this combination of plasticity and local adaptation is common, accurate prediction of the responses of distribution and abundance to climate change will require us to take into account population-specific responses to temperature (and perhaps other climate variables). Moreover, potential limits to rapid evolutionary responses, such as long generation times and/or genetic constraints, mean we cannot assume that environmental tolerance is a species-level trait. Perhaps the most important implication of this work is that abundances of widespread species may well suffer as much or more at the range center or at the colder range boundary as at the warmer range boundary. Assessing the potential for range-wide declines will require careful studies of how individual populations will respond to the direct and indirect effects of warming, as well as the magnitude of climate change across the range.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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