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LETTER

Climate change disrupts local adaptation and favours upslope migration

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Abstract

Contemporary climate change is proceeding at an unprecedented rate. The question remains whether populations adapted to historical conditions can persist under rapid environmental change. We tested whether climate change will disrupt local adaptation and reduce population growth rates using the perennial plant *Boechera stricta* (Brassicaceae). In a large-scale field experiment conducted over five years, we exposed > 106 000 transplants to historical, current, or future climates and quantified fitness components. Low-elevation populations outperformed local populations under simulated climate change (snow removal) across all five experimental gardens. Local maladaptation also emerged in control treatments, but it was less pronounced than under snow removal. We recovered local adaptation under snow addition treatments, which reflect historical conditions. Our results revealed that low elevation populations risk rapid decline, whereas upslope migration could enable population persistence and expansion at higher elevation locales. Local adaptation to historical conditions could increase vulnerability to climate change, even for geographically widespread species.

Keywords

Common garden, elevational gradient, integral projection model, local adaptation, population growth rate, reciprocal transplant.

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INTRODUCTION

Climate change is rapidly altering the suite of abiotic and biotic conditions that populations experience (Diffenbaugh *et al.* 2018). As thermal climate envelopes move poleward, or upslope in mountainous regions, populations that were locally adapted historically may no longer perform optimally in the new conditions at their home sites. Instead, individuals from populations adapted to hotter and drier climates could have a fitness advantage, resulting in widespread local maladaptation (Wang *et al.* 2010; Wilczek *et al.* 2014). The strong novel selection regime imposed by climate change may outpace the adaptive potential of many species (Wilczek *et al.* 2014), thereby reducing population growth rates (Morris *et al.* 2008) and increasing the risk of local extinction (Willis *et al.* 2008). Contracting local populations likely have diminished genetic variation, which restricts the capacity to adapt to further environmental change. Additionally, reduced offspring production shrinks the pool of potential emigrants to newly suitable upslope or poleward sites (Anderson 2016). Thus, population declines due to climate change could weaken both the potential for populations to adapt *in situ* in the short-term and to migrate to areas with favourable climates.

Variable selection across the landscape often results in the evolution of local adaptation, such that populations perform best in the environment in which they evolved (Kawecki 2008; Hereford 2009; Lowry *et al.* 2019). Climate change is decoupling historically correlated conditions, like photoperiod and temperature, but we know little about how climate change shifts fitness landscapes (Etterson & Shaw 2001; Kingsolver *et al.* 2013; Logan *et al.* 2014; Wadgymar *et al.* 2018b). To predict the eco-evolutionary consequences of climate change, we must dissect the extent to which novel climates disrupt long-standing patterns of local adaptation (Wang *et al.* 2010; Wilczek *et al.* 2014) and diminish population growth rates (Panetta *et al.* 2018; Campbell 2019). Here, we address these crucial issues by manipulating the timing of snowmelt and depth of snowpack in temporally and spatially replicated field experiments conducted across an elevational gradient. Climate change has brought elevated temperatures and disrupted snow dynamics to high-elevation ecosystems, altering physiology, phenology and community composition (Harte & Shaw 1995; Lambrecht *et al.* 2007; Pederson *et al.* 2011; CaraDonna *et al.* 2014). Observational data and simulation models point to increased warming at higher elevations such as the Rocky Mountains (Mountain Research Initiative 2015). Additionally, models predict extensive habitat loss (> 80%) for montane ecosystems before 2100 (Engler *et al.* 2011), and severe reductions in range size of plant species in these systems (Dullinger *et al.* 2012).

To evaluate local adaptation under climate change, we combined several powerful approaches: provenance experiments (Wang *et al.* 2010; Wilczek *et al.* 2014), space-for-time substitutions and reciprocal transplant experiments (Etterson & Shaw 2001) and *in situ* climatic manipulations (Liancourt *et al.* 2013; Harte *et al.* 2015). In provenance trials, researchers expose genotypes from numerous populations across the range of a species to multiple common gardens, thereby interrogating the fitness consequences of environmental variation for genotypes that evolved under disparate conditions (e.g. Wang *et al.* 2010; Wilczek *et al.* 2014). Transplanting genotypes into sites that mimic climate projections (e.g. warmer

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lower elevations) in a space-for-time framework can reveal how climate change could alter fitness (Etterson & Shaw 2001). However, non-climatic agents of selection also vary spatially, potentially distorting conclusions about adaptation to climate change (Shaw & Etterson 2012). By manipulating a key climatic factor (snowmelt dynamics) in five common gardens, our field experiments directly test whether local maladaptation results from novel climates while accounting for spatial variation in other environmental conditions. We examined fitness in three situations relevant to climate change: (1) populations transplanted into lower elevation sites, which reflect future climatic conditions, but differ in non-climatic factors; (2) local populations experiencing simulated climate change in their home sites and (3) populations transplanted into higher elevation sites in climatic manipulations, which indicates how upslope migrants fare in novel locales. Field manipulations of abiotic factors have rarely been applied in an evolutionary context (De Frenne *et al*. 2011; Pfeifer-Meister *et al*. 2013; Hargreaves & Eckert 2019) despite their potential for illuminating the eco-evolutionary consequences of climate change.

Into five common gardens, we transplanted > 100 000 experimental individuals of the ecological model species *Boechera stricta* (A. Gray) A. Löve & D. Löve (Brassicaceae), a montane perennial forb that is widely distributed across broad climatic gradients in regions where the climate is changing rapidly. In each garden, we exposed experimental individuals to historical, contemporary and simulated future climates to test three key hypotheses: (1) Climate change disrupts local adaptation. (2) Low-elevation sites will become less hospitable under arid conditions associated with climate change. (3) Upslope migration will enhance population growth rates in higher elevation locations. We predict that future climatic conditions will favour low-elevation genotypes whose current climates are similar to projections for higher elevations, and that climate change will depress fitness of local populations that are adapted to historical conditions.

METHODS

Study system

Boechera stricta (Brassicaceae) is a perennial forb native to the Rocky Mountains, where it inhabits elevations from 700 to 3900 m and latitudes from Utah to Alaska (Al-Shehbaz & Windham 2010). Climatic variation across mountains often results in local adaptation to elevation (e.g. Clausen et al. 1940; Kim & Donohue 2013). Indeed, populations of *B. stricta* have adapted to local environments over short geographic distances (Lee & Mitchell-Olds 2011; Anderson *et al*. 2014; Anderson *et al*. 2015) and rapidly recolonised high latitudes and elevations after the Pleistocene glacial retreat (Song *et al*. 2006; Kiefer *et al*. 2009). Our study occurred in the centre of genetic diversity of *B. stricta* (Kiefer *et al*. 2009), where genetic variation could potentially enable adaptation to progressively changing climates. As with 10–15% of plants (Goodwillie *et al*. 2005), *B. stricta* primarily self-pollinates (F_{IS}: 0.74–0.97) (Song *et al*. 2006), facilitating studies of genotype-by-environment interactions.

In fall 2013, we established five common gardens (elevations: 2530, 2710, 2890, 3133, 3340 m) near the Rocky Mountain Biological Lab (Gothic, Colorado). In this region, increasing elevation is associated with longer winters with deeper snowpack, reduced temperatures and increased soil moisture availability; therefore, elevation is a reliable proxy for climate (Fig. 1, Table S1 and S2, Supplemental Methods). We have identified natural *B. stricta* populations in elevations ranging from 2500 to 3600 m in this region; therefore, our experimental gardens reflect the local elevational distribution of this species (see Tables S1 and S2).

Experimental design

We performed two types of manipulative experiments that together yield a comprehensive view of how climate change will influence *B. stricta* populations (Table 1). First, we conducted provenance trials to evaluate local adaptation under climate change at a regional level using genotypes from source populations distributed across a broad elevational gradient (Fig. 1d). The inclusion of many populations sampled evenly across an elevational gradient enabled us to examine how climate change alters the spatial scale of local adaptation. We also conducted reciprocal transplant experiments, which differ from the provenance trials because the transplants originated exclusively from natural populations adjacent to the five gardens. This experimental design included sufficient replication of families local to each of the five gardens for modelling demographic parameters with precision, evaluating population growth rates and predicting how climate change will influence population persistence in the future (Table 1). With these approaches, we assessed local adaptation by comparing local vs. foreign population performance in each garden and by contrasting population growth rates in home vs. non-native sites (Kawecki & Ebert 2004).

Prior to all experiments, we collected seeds from naturally recruiting plants separated by at least 1.5 m in source populations and grew these seeds in the greenhouse for one generation to minimise variation in maternal effects (Wadgymar *et al*. 2018a) and to generate full-sibling families via self-fertilisation. From 2013 to 2017, we transplanted a total of $N = 106\,524$ seeds and 3-month-old juvenile rosettes into the matrix of natural vegetation in ambient and snow manipulation treatments in the five common gardens ($N = 434$ maternal families from 102 source populations, ranging in elevation from 2499 to 3690 m, Table 1). Seeds provide essential data on early life history, whereas juvenile rosettes afford timely measurements of fecundity for the same families. Planting in the autumn exposes experimental individuals to winter conditions necessary for germination and flowering. We randomized seeds into grids containing 1 cm^3 cells of potting soil. We only included seedlings in our study that germinated in the spring immediately after planting to eliminate potential contamination from natural seed sources that could compound over many growing seasons (Supplemental Methods). We transplanted greenhouse-reared rosettes into 60 × 120 cm blocks with minimal disturbance of natural communities, with experimental individuals separated by 10 cm. In subsequent growing seasons, we monitored the germination

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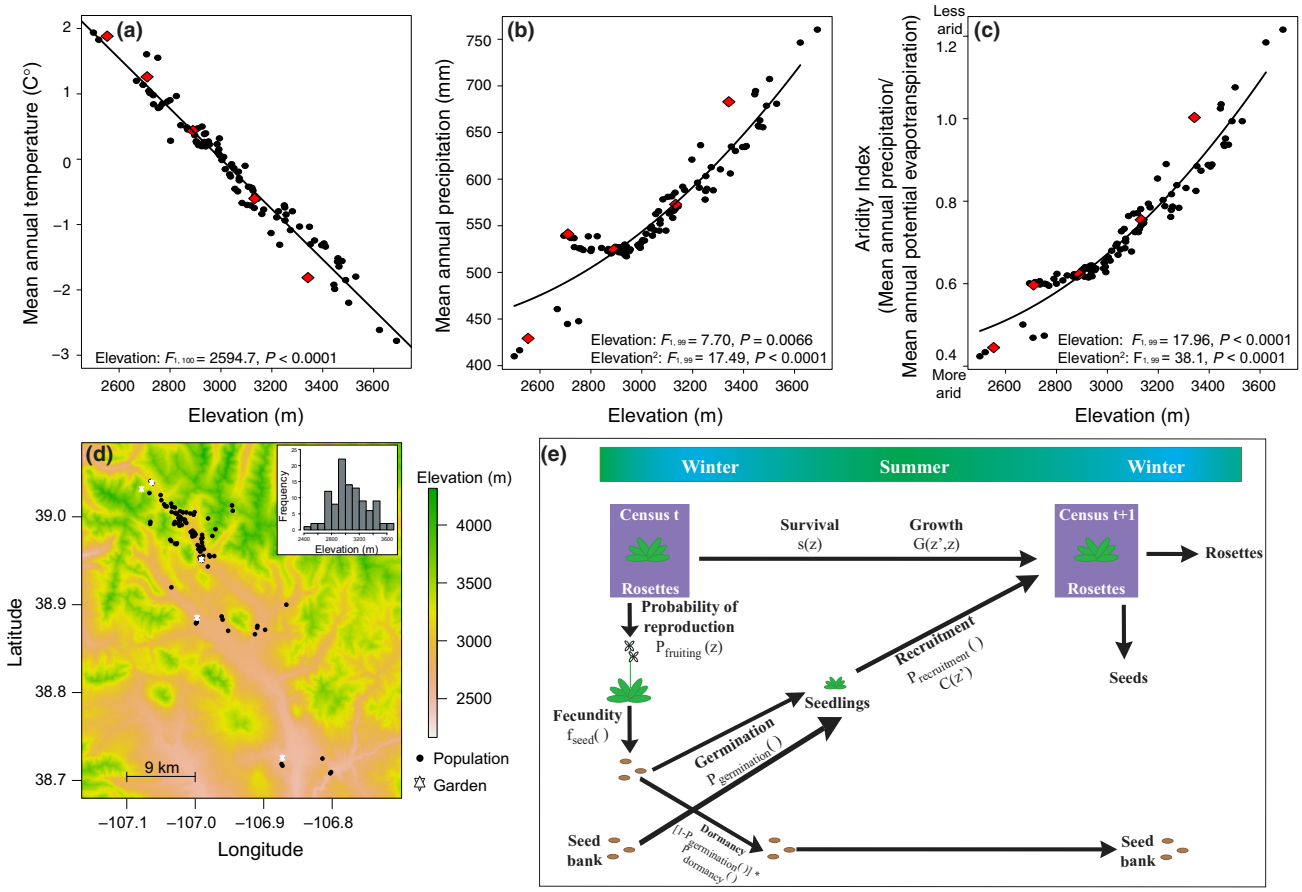

Figure 1 Background for provenance trial and reciprocal transplant experiments. Climate varies predictably with elevation in this region. We extracted climatic data from WorldClim for source populations (filled circles) and garden sites (red diamonds). Mean annual temperature (panel a) declines significantly with elevation whereas mean annual precipitation increases (panel b). The unitless Aridity Index (mean annual precipitation/ mean annual potential evapotranspiration) is the inverse of aridity, with low values indicating more arid locations. In this system (panel c), the aridity index increases with elevation, indicating that low elevation sites are more arid. Panel d displays a map of the source populations (filled circles) and garden sites (open stars) on the landscape, with an inset histogram indicating the elevations of the source populations used in our experiments. Panel e shows the lifecycle diagram that we used to model population growth rates using pre-reproductive censuses. Population growth rates depend on growth and survival of existing plants, as well as seedling recruitment either from seeds produced within a year or from dormant seeds in the seed bank. We assume the soil seedbank is short-lived; relaxing this assumption increases our population growth rate estimates negligibly.

of seeds and survival of seedlings 2–4 times per week beginning just after snowmelt, the survival of rosettes at the beginning and end of the growing season and the growth and fecundity of rosettes mid- to late-season.

Climatic manipulations

Climate change reduces winter snowpack, diminishes snow-water equivalent and hastens spring snowmelt (IPCC 2014; Fyfe *et al.* 2017). Increased evapotranspiration from warming in concert with declining snowpack heightens drought during the growing season (Rangwala *et al.* 2012). Experimental snow removal reduces snowpack, accelerates snowmelt and decreases soil moisture, accurately altering the suite of environmental variables predicted to shift with climate change (Tables S2 and S3) (Anderson & Gezon 2015; Wadgymar *et al.* 2018b). By the same logic, snow addition simulates historical conditions preceding current climate warming.

From spring 2014–2018, we exposed half of experimental individuals to ambient (control) snow dynamics and half to early snow removal (Supplemental Methods). We imposed early snow removal by shovelling snow to a depth of 10 cm (to avoid damaging underlying vegetation) when ambient snowpack receded to 1 m in late winter (March–June). We maintained a 0.5 m buffer around each control and snow removal block (Video S1). Our protocol advanced snowmelt by an average of 5.7–19.1 days across this multiyear experiment (Table S3), simulating projections for the mid-21st century (Cayan *et al.* 2016). Snowmelt in this area has been advancing by 7.4 days/decade since 1991 (Harte *et al.* 2015), similar to observed changes in other parts of the region (Clow 2010; McGuire *et al.* 2012). Although the timing of snowmelt is accelerating and snowpack depths are decreasing over time in this region (Wadgymar *et al.* 2018b), the conditions experienced by plants in control treatments were within the range of annual variation from 1975 to the present (Fig. S1). Additionally, snow dynamics in the snow removal blocks reflected historical climates from lower elevation locations (Fig. S1).

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Table 1 Study parameters. We conducted two types of experiments: provenance trials using 43–56 populations to test for local adaptation regionally and reciprocal transplants of five populations to collect vital rate data for testing the effects of climate change on population growth rates

Experiment	Life-history stage	Cohort	Number of gardens	Treatments applied	Data collected	Study duration (years)	Total Sample size	Number of maternal families	Number of source populations
Provenance	Rosettes	2013	5	C, R	S, G, F	5	6019	104	43
Provenance	Rosettes	2014	5	C, R	S, G, F	4	7246	166	50
Provenance	Seeds	2013	4	C, R	GS	1	7058	154	45
Provenance	Seeds	2014	5	C, R	GS	1	19 154	205	56
Provenance	Seeds	2016	5	C, R, A	GS	1	29 153	100	50
Provenance	Seeds	2017	4	C, R, A, W	GS	1	19 200	75	54
Reciprocal transplant	Seeds	2015	5	C, R	GS	2	11 850	124	5
Reciprocal transplant	Rosettes	2016	5	C, R	S, G, F	2	6844	123	5

We named the cohorts according to the year in which we transplanted experimental individuals. In cases in which only four experimental gardens were included in a study, the excluded garden was the lowest elevation Estess garden (elevation: 2553 m). Treatments applied include controls (C), early snow removal (R), snow addition (A) and snow addition plus supplemental watering (W). We collected data on survival (S), growth (G) and fecundity for rosettes and germination success (GS) and seedling survival for seeds.

In fall 2016, we implemented a snow addition treatment to evaluate fitness under historical conditions. Environmental conditions are a strong filter against maladapted genotypes early in life history; therefore, we focused snow addition manipulations on the seed to seedling transition. To add snow, we inverted 75.7 L cylinders over the seed grids immediately after planting, and left them in place throughout the winter (Fig. S2). These cylinders accumulated snow during the winter and were supplemented with snow before natural snowmelt. After snowmelt in the spring, we removed the cylinders. Our snow addition treatment delayed snowmelt by 2–7.7 days (average: 4.5 days; Table S3), reflecting snow dynamics in the recent past. In fall 2017, we included a fourth treatment: snow addition plus supplemental watering during the growing season. We watered blocks in the snow addition and watering treatment every 2–3 days across the growing season. This fourth treatment better reflects the longer winters, delayed snowmelt, and reduced evapotranspiration of historical climates. We maintained treatment effects from planting through the fall of 2018.

Provenance trial analyses

To evaluate local adaptation in a regional context, we first calculated elevational difference for every population, which is the difference in elevation between the source population and the common garden. Elevational difference < 0 indicate that an individual was transplanted into a higher elevation garden. We predicted local adaptation in the control treatment, with negative quadratic functions and the maximum fitness at 0 m elevational difference. In contrast, we predicted that low-elevation populations would have a fitness advantage under snow removal, which simulates conditions to which these populations were locally adapted in their arid home sites. These predictions would manifest as interactions between treatment and (linear or quadratic) elevational difference. We examined local adaptation via germination success, seedling establishment, the probability of producing fruit and the total length of all mature fruits (a reliable proxy for seed count, Wadgymar *et al*. 2017).

We analysed fitness as a function of elevational transfer distance instead of climatic transfer distance for three reasons. First, we directly measured elevation in the field at all source populations and garden sites. At the five garden sites, we have collected data on soil temperature, soil volumetric water content and the timing of snowmelt (Table S2 and S3), but we do not have these climatic data from the 102 source populations included in our experiments. Therefore, to model fitness as a function of climatic variables, we would need to use interpolated climatic data. Second, many species have already shifted their distributions upward in elevation in response to changing climate (e.g., Kelly & Goulden 2008; Lenoir *et al*. 2008; Chen *et al*. 2011; Morueta-Holme *et al*. 2015; Fadrique *et al*. 2018), which motivated our prediction that low-elevation genotypes should express greater fitness than local genotypes under conditions that model climate change. Finally, given that climate is multivariate, any climatic predictor would need to integrate across various aspects of the climate, including temperature, snow dynamics and growing season precipitation. In this region, elevation provides a readily accessible mechanism for describing the multivariate nature of climate, as elevation is tightly correlated with multiple climatic factors (Fig. 1, Tables S1–S3). In addition to the models that we present in the main text, we conducted complementary analyses with transfer distances in mean annual temperature and aridity index as the predictor variables instead of elevational difference. The results of all analyses are highly congruent; thus, modelling interpolated climatic factors instead of elevation did not alter the inferences that can be drawn from this study (Figs S4–S7; Tables S9–S12).

We analysed data at the family level, although individual-level analyses generated similar results. In generalised linear mixed models, we analysed fitness as a function of treatment-by-linear and -quadratic effects of elevational difference in models with random intercept effect for maternal family and random slope and intercept for transplant garden by elevational difference. These models evaluate local adaptation in a regional context, while accounting for variation in the slope of elevational difference across gardens. Analyses with fixed effects for garden produced nearly identical results (Tables

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S4–S7B). We determined significance using Type III Sums of Squares (car package in R) and used bootstrap resampling to generate 95% bias-corrected confidence intervals around predicted slopes (Puth *et al*. 2015).

Rosette reproductive success

We assessed local adaptation by examining the influence of elevation and treatment on fecundity of experimental rosettes. We tested for local adaptation separately for the 2013 and 2014 cohorts because we have 5 and 4 years of fitness data for these plants respectively. We adjusted our α to 0.025 (=0.05/2 cohorts) to account for the separate analyses. As with most data sets of fitness under field conditions, fecundity was zero-inflated because many individuals died or failed to reproduce. We adopted a hurdle model approach to evaluate lifetime fitness while accounting for zero-inflation. We first analysed the probability of fruiting as a function of the aforementioned fixed and random effects in a logistic regression framework with a binomial distribution and logit link (glmer package in R; Table S4) and then modelled mature fruit length among families that fruited using a gamma distribution and a log link (Table S5). To generate family level fitness, we summarised the number of individuals planted and the number of individuals that successfully reproduced to use as a binomial fitness component. Among plants that produced fruits, we extracted LSMEAN values from a generalised linear mixed model that evaluated total fruit length as a function of family-by-garden-by-treatment with a random effect for block (SAS ver. 9.4, proc Glimmix, Gamma distribution).

Seed germination and survival

We modelled germination success at the family level (# seedlings germinated/# seeds planted) in mixed model logistic regressions (glmer package of R). As the 2013 and 2014 seed cohorts experienced the same treatments (control vs. snow removal), we analysed these cohorts together, including a fixed effect for cohort (Table S7). We analysed the 2016 and 2017 seed cohorts separately because of the different treatments applied each year (Table 1). We present raw p-values, but we adjusted our α to 0.017 (=0.05/3 because we had three separate analyses of seed germination). For the 2013 and 2014 cohorts, we also modelled seedling survival through the first growing season (# surviving seedlings/ # seeds planted) using the same predictors as above (Table S6). As few seedlings in the 2016 and 2017 cohorts successfully survived their first growing seasons (9% and 2% respectively), we conducted Cox proportional hazards models to test local adaptation in longevity (elapsed days from germination to death, Table S8) in the coxme package in R (Therneau 2018), with random effects for family, garden and block.

Reciprocal transplant analyses

To test whether climate change depresses population growth rates (λ), especially in low-elevation locations, and whether upslope migration could rescue local populations demographically, we conducted reciprocal transplant experiments across all common gardens, exposing experimental individuals to snow removal and control conditions (Table 1). From planting through September 2018, we monitored plant size (number of leaves), survival and seed production on transplanted rosettes. In 2016, snowpack in our lowest elevation site was so low that we could not successfully remove snow without damaging the vegetation. Seeds from the 2015 cohort completely failed to germinate there, which likely accounts for the low population growth rate (λ) estimates in that site. Seed germination for the 2013, 2014 and 2016 cohorts at that site was also very low (1.7, 2.6 and 1.8% respectively), and we observed complete failure to germinate among $N = 1216$ seeds from 19 local families planted into control and snow removal treatments in another experiment at that site in 2017.

Integral projection models

We estimated population growth rates (λ) of local and foreign populations under different environments using integral projection models (IPM), parameterised with vital rates from our reciprocal transplant experiments (Ellner *et al*. 2016; Sheth & Angert 2018). IPMs evaluate demographic transitions based on individual size and discrete age classes (Ellner *et al*. 2016; Sheth & Angert 2018). We used generalised linear mixed models to model seven vital rates at the individual-level: survival, growth, probability of producing mature seeds, total number of seeds produced, germination success in the first growing season after planting, seedling survival into the end of the first year and seedling recruit size (Fig. 1e, Table S13, Supplemental Methods). We modelled an average probability of seed dormancy (0.032, Supplemental Methods, Table S14). We implemented IPMs using the midpoint rule (Ellner *et al*. 2016). We based the size of the iteration matrix on the number of rows in the data set for each of the 50 garden-by-source population-by-treatment categories, and calculated λ as the dominant eigenvalue of the discretised matrix (Supplemental Methods). We estimated bias-corrected 95% confidence intervals (Puth *et al*. 2015) around λ by bootstrapping the data 2000 times.

RESULTS

Local adaptation

Rosette reproductive success

Hurdle models first evaluated the cumulative probability of reproduction across the duration of the experiment, accounting for both mortality and failure to reproduce. For both cohorts, we found significant interactions between elevational difference and treatment in the probability of reproduction, indicating that the extent of local adaptation differed between snow removal and control environments (2013 cohort: $\chi^2 = 6.84$, $P = 0.0089$; 2014 cohort: $\chi^2 = 5.09$, $P = 0.024$, Table S4). In both treatments, low-elevation families outperformed local families, suggesting that local maladaptation has already arisen in this system. However, local maladaptation was more pronounced under snow removal. The odds of reproduction declined by nearly 80% with every 1 km increase in elevational difference under snow removal in the 2013 rosette cohort (odds ratio: 0.21; 95% CI: 0.12, 0.36; Fig. 2b, Table S4) and by 75% in the 2014 rosette cohort (odds ratio: 0.25; 95% CI: 0.12, 0.33; Fig. 2d, Table S4). In the 2013

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cohort, the probability of reproduction declined with elevational difference in the control treatment, at a much lower rate than under snow removal (55% decline in odds of reproduction with every 1 km increase in elevational difference; odds ratio: 0.45; 95% CI: 0.26, 0.82; Fig. 2b, Table S4). Local adaptation was more evident in the probability of reproduction for the 2014 rosette cohort, as a negative quadratic function demonstrated that families from 277 m below local achieved peak fitness under control conditions (95% CI in optimal probability of reproduction: −294 m to −196 m; Fig. 2d).

Among individuals that reproduced, families from 510 m elevational difference (95% CI: 213 m-1420 m) reached optimal fecundity in the control treatment of the 2013 cohort (treatment by linear elevational difference: $\chi^2 = 10.6$, $P = 0.0011$; treatment-by-quadratic elevational difference: $\chi^2 = 9.8$, $P = 0.00176$, Table S5, Fig. 3a). Thus, higher elevation families outperform local and lower elevation families, which may offset any fitness gain that low-elevation families experience in the probability of reproduction. We found no relationship between elevational difference and fecundity under snow removal (Fig. 3b); integrated across the probability of reproduction and fruit length, low-elevation families have a fitness advantage under snow removal. Fecundity did not vary with elevational difference for either treatment in the 2014 cohort (Table S7).

Seed germination and survival

We found a significant interaction between treatment and elevational difference for seedling establishment to the end of the first growing season amongst all seeds planted in the 2013 and 2014 cohorts ($\chi^2 = 49.9$, $P < 0.0001$, Table S6). Severe local maladaptation emerged under snow removal, as families from 537 m below local (95% CI: −820 m, −454 m) displayed maximum establishment (Table S5, Fig. 4a). In contrast, the control treatment showed clear evidence for local adaptation, as peak establishment occurred for local families (31 m; 95% CI: −107 m, 586 m; Fig. 3a). We found similar patterns for germination success for these cohorts (Fig. S3, Table S7).

The degree of local adaptation also varied with treatment in the snow addition experiment (Table S7). Local maladaptation emerged in both snow removal and control treatments across all gardens in the 2016 cohort. Under snow removal, germination success was highest for populations from 346 m

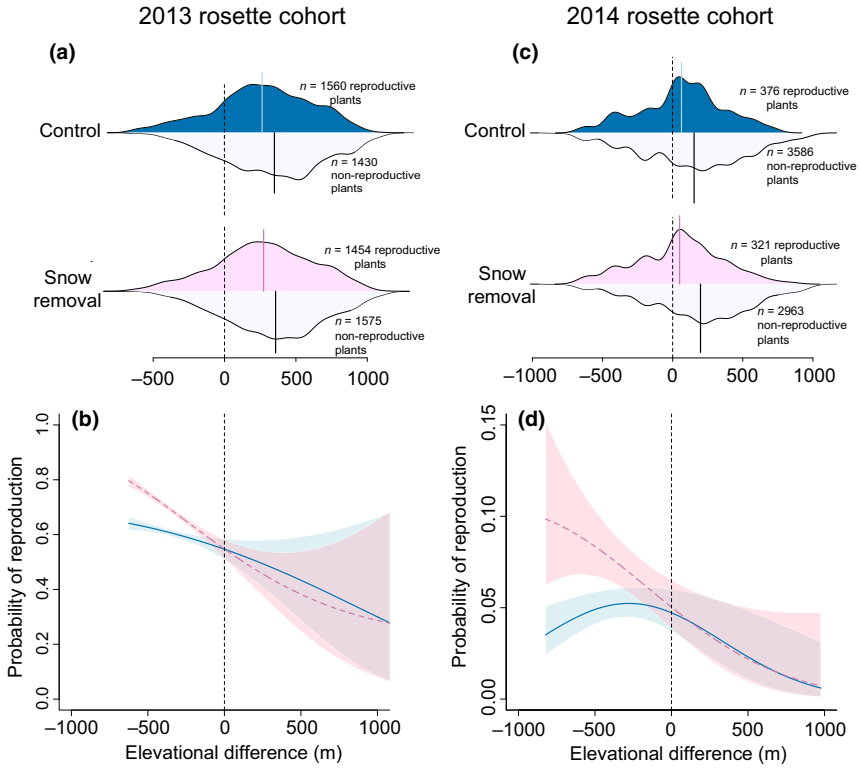

Figure 2 The probability of reproduction varied as a function of treatment by elevational difference for the 2013 cohort (panels a and b) and the 2014 cohort (panels c and d) across growing seasons. The top two panels (a and c) present the smoothed density distributions of data points in both treatments for individuals that produced at least one mature fruit (blue for control; pink for snow removal). Density distributions for individuals of each treatment that failed to reproduce because they remained vegetative or died are mirrored below in light grey. Average elevational differences are highlighted with vertical lines within each distribution. The bottom panels (b and d) show the corresponding predicted regression relationships from mixed effects logistic regressions, with 95% confidence intervals derived from $N = 2000$ bootstraps. A negative quadratic fitness function with the optimum at 0 elevational difference would reflect perfect local adaptation to elevation. Negative elevational difference represents low elevation populations planted into a higher elevation garden. Local maladaptation emerged under snow removal (dashed pink line) in both cohorts. In the control treatment (blue solid line), local maladaptation was less pronounced than under snow removal in the 2013 cohort. We detected patterns consistent with local adaptation in the 2014 cohort exposed to control conditions.

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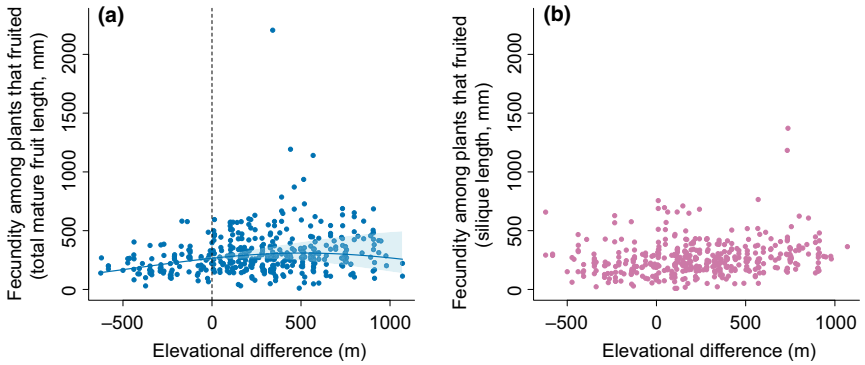

Figure 3 (a) Among families that successfully fruited, high elevation families had a fecundity advantage under control conditions in the 2013 cohort, with optimal fitness for families from 514 m above local (95% CI: 229m-1, 140m). (b) We found no relationship between fecundity and elevational difference under snow removal for this cohort.

below local (95% CI: −326, −345). We found even more severe local maladaptation in the control, such that the odds of germinating decreased by 60% for every 1 km increase in elevational difference (odds ratio: 0.40; 95% CI: 0.26, 0.69). However, local populations had a fitness advantage under snow addition across gardens (optimum: 93 m; 95% CI: −28, 568 m). By simulating historical conditions, we recovered local adaptation.

These results were even more evident when we replicated this experiment in 2017, implementing snow addition &

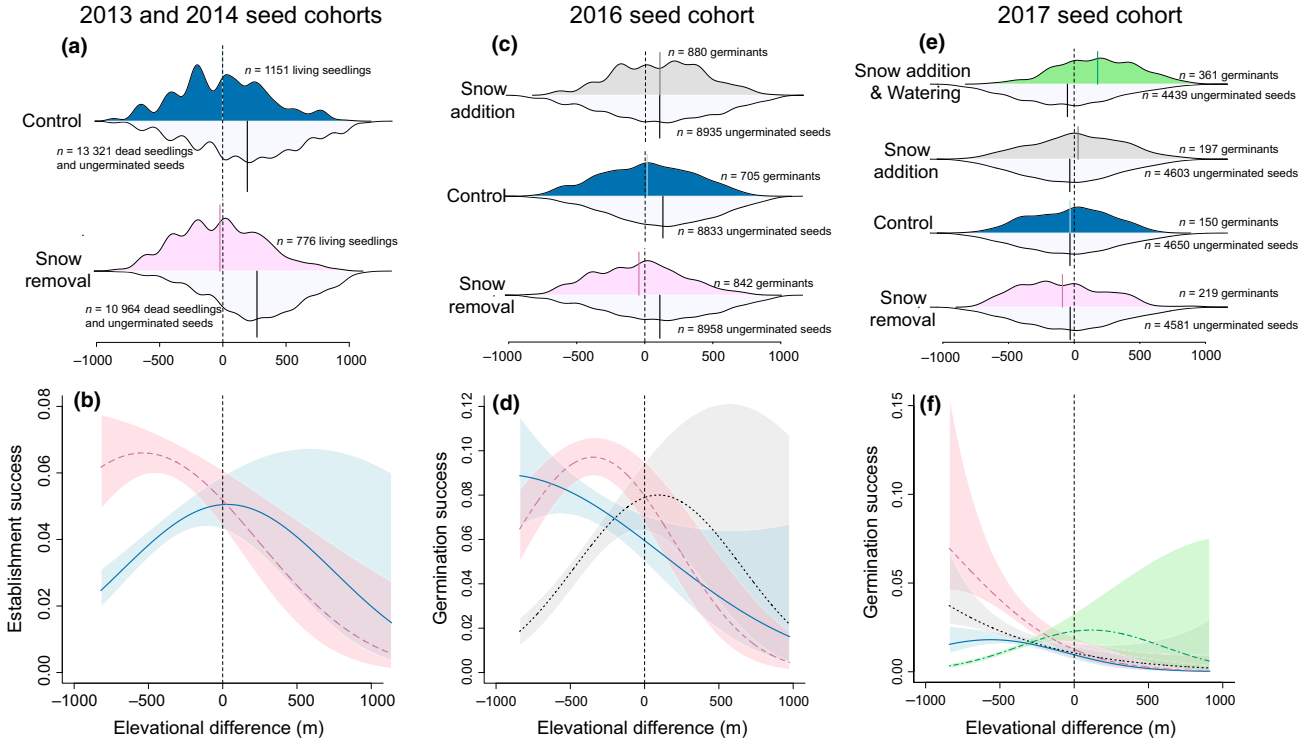

Figure 4 Seedling establishment success varied as a function of elevational difference across treatments for the 2013 and 2014 cohorts (panels a and b), as did seed germination success the 2016 cohort (panels c and d) and the 2017 cohort (panels e and f). Seedling survival was too low in the 2016 and 2017 cohorts to analyse seedling establishment; therefore, we display germination success for those cohorts here (see Table S9 for longevity analyses; seed germination results for the 2013/2014 cohort are presented in Fig. S3). The top three panels (a, c and e) present the smoothed density distributions of data points for seeds that germinated or seedlings that survived (blue for control; pink for snow removal; dark grey for snow addition; green for snow addition and supplementary watering). Density distributions for individuals of each treatment that failed to germinate or died are mirrored below in light grey. Average elevational differences are highlighted with vertical lines within each distribution. The bottom panels (b, d and f) show the corresponding predicted regression relationships from mixed effects logistic regressions, with 95% confidence intervals derived from $N = 2000$ bootstraps. A negative quadratic fitness function with the optimum at 0 elevational difference would reflect perfect local adaptation to elevation. In all cohorts, snow removal induced local maladaptation. Under control conditions, patterns were consistent with local adaptation in the 2013 and 2014 cohort and local maladaptation in the 2016 and 2017 cohorts. We recovered local adaptation when we simulated benign historical conditions with snow addition in the 2016 cohort and with snow addition plus supplemental watering in the 2017 cohort.

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watering to simulate historically cool and moist conditions. The region experienced the most severe winter drought on record that year since 1976–1977, with extremely low snowpack and accelerated snowmelt (Fig. S1) (Barr 2019). Total snowfall in the winter of 2017 to 2018 (490 cm) was only 46% of the average winter snowfall recorded at the research station from 1974 to 2018 (1064.6 cm) (Barr 2019). We detected local maladaptation in snow removal, control and snow addition conditions, such that low elevation seeds had a germination advantage (Fig. 4f; Table S7). For every 1km increase in elevational difference, the odds of germination declined by 94% under snow removal (odds ratio: 0.06, 95% CI: 0.017, 0.17), 90% in control conditions (odds ratio: 0.10, 95% CI: 0.03, 0.33) and 81% with snow addition (odds ratio: 0.21, 95% CI: 0.06, 0.55). The only treatment that reflected local adaptation was snow addition and watering, for which the elevational difference conferring enhanced germination success occurred at 113.7 m (95% CI: −77 m, 1054 m). This severe drought caused even control and snow addition blocks to experience warmer and drier conditions than historical climates, resulting in maladaptation under multiple treatments.

In the 2016 and 2017 seed cohorts, seedling longevity was significantly greater in control (2016 cohort) and snow addition (both cohorts) treatments than in the snow removal (Table S8). In the 2016 cohort, seedlings from 148m above local (95% CI: −16.6, 429 m) achieved maximum longevity across treatments and gardens. In the 2017 cohort, seedling longevity increased with elevational difference across environments (Table S8). Thus, historical and contemporary conditions enhance seedling fitness, with high-elevation families having a longevity advantage.

Population growth rates

Population growth rates (λ) were significantly below replacement in the three lowest gardens over the course of this experiment (Fig. 5a, Table S13). Indeed, λ estimates only approached or exceeded the replacement values of 1 in the two higher elevation gardens. The intense winter drought during 2018 likely reduced λ estimates below what would be observed in natural populations during an average year. Indeed, during the more benign years of 2010–2012, we modelled stable population dynamics in natural populations at a mid-elevation site ($\lambda = 1.03$, 95% CI: 0.98, 1.08, Table S15). Our experiment suggests that low-elevation populations risk declines in years that reflect climatic projections for reduced winter snowpack.

DISCUSSION

Our study revealed strong eco-evolutionary and demographic consequences of climate change for a widely distributed native plant species. Snow removal, simulating future conditions, induced local maladaptation across life-history stages. Additionally, lower elevation families outperformed local families even under control conditions in some cases, suggesting that climate warming may have already disrupted local adaptation. By modelling historical conditions, our snow addition experiments restored local adaptation, strengthening our conclusion that climate change has generated maladaptation. Across all experiments, we found more pronounced differences between snow addition treatments and control than we found between control and snow removal treatments, signifying that populations are adapted to historical climates that may no longer exist locally. Finally, our demographic models predict severe risks of local extinction for low-elevation populations, along with population expansion in higher elevation locales, especially during a severe winter drought that reflects climatic projections for this region.

Integral projection models documented pervasive local maladaptation via both the home vs. away and local vs. foreign criteria of local adaptation (Kawecki & Ebert 2004) in one or both treatments in all gardens (Fig. 5, Table S13). The home-away criterion indicates that locally adapted populations have enhanced fitness in their home sites and depressed fitness in alternative sites. This criterion holds only for the highest elevation population, which had greater λ estimates in its home site than in all other locations. For all other populations, λ estimates were significantly greater in both control and snow removal treatments in higher elevation gardens (local maladaptation via the home-away criterion). The local-foreign criterion states that locally-adapted populations outperform foreign populations at their home site. In our experiment, that criterion only applies in the second highest elevation garden, where local populations under snow removal may have greater λ estimates than other populations; however, we caution that 95% confidence intervals are highly overlapping across source populations. In other gardens, local populations either underperformed relative to foreign populations (gardens at 2710 m and 3340 m) or had λ values very similar to those of foreign populations (gardens at 2553 m and 2890 m), indicative of local maladaptation via the local-foreign criterion. In conjunction with our provenance trial experiments, these results indicate that local populations may no longer be best adapted to the changing environments they are experiencing (Wang *et al*. 2010; Wilczek *et al*. 2014).

Notably, all source populations had λ values lower than replacement in both treatments in the three lowest elevation gardens. We planted seeds into the reciprocal transplant experiment in the fall of 2015, such that they germinated and established after the relatively early snowmelt of 2016 (Fig. S1). We planted the juvenile rosettes in the fall of 2016, such that their first growing season for reproduction (2017) was relatively benign climatically. However, they experienced a severe winter drought prior to the onset of the 2018 growing season (Fig. S1). Thus, across years, plants included in this experiment were subjected to reduced snowpack and early snowmelt similar to climatic projections for the region (Cayan *et al*. 2016). Climate change has likely already jeopardised the persistence of local populations in arid low elevation sites, and will continue to do so as aridity and temperatures increases. In this region, we have not identified populations below 2500 m in elevation; therefore, demographic or evolutionary rescue from warm-adapted, lower elevation populations seems improbable. This result is consistent with other studies that document local extinctions in trailing edge populations at the warm edge of the range (Sheth & Angert 2018). Indeed, montane plants are vulnerable to extreme reductions

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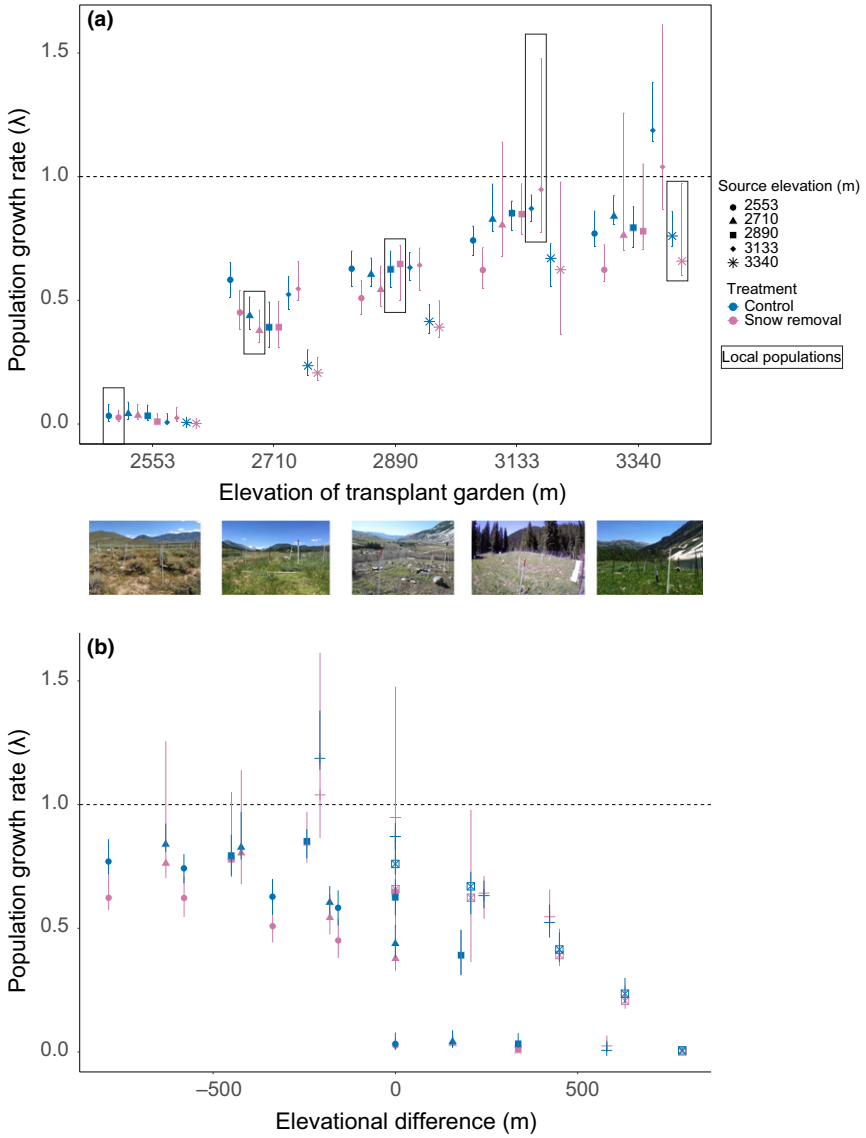

Figure 5 Estimates of population growth rates (λ ± 95% confidence intervals, derived from bootstrap resampling) from integral projection models (IPMs) under snow removal and control conditions in five experimental gardens. We display (a) λ estimates against the elevation of the transplant garden and (b) λ estimates as a function of elevational difference (source elevation − transplant garden). The dashed horizontal line in both panels represents the replacement value (λ = 1), above which populations are growing and below which populations are declining. For panel (a), local populations in each transplant garden are highlighted within black boxes.

in range size as climate change causes many sites to become unsuitable (Dullinger *et al*. 2012; Hülber *et al*. 2016; Panetta *et al*. 2018; Campbell 2019).

Poleward and upslope migration could enable populations to escape the negative consequences of climate change, and many species have already shifted their distributions upward in elevation in response to changing conditions (e.g Kelly & Goulden 2008; Lenoir *et al*. 2008; Chen *et al*. 2011; Fadrique *et al*. 2018). In our study, all four source populations transplanted into higher elevation gardens exhibited greater λ values in those higher sites than in their home locales. However, our results suggest that there is a limit to the extent to which upslope migration will conserve vulnerable low-elevation populations, likely because populations have adapted to a complex suite of abiotic and biotic conditions that can vary across the landscape. For example the lowest elevation source population only attained λ near replacement in control treatments of the two highest elevation gardens (*c*. 600–800 m above the local site). Migration of this elevational distance is likely to be quite slow in species like *B. stricta* that have spatially limited pollen and seed dispersal. Additionally, geographic barriers can further restrict migration of montane species (Dullinger *et al*. 2012; Hülber *et al*. 2016). Nevertheless, source populations from 3133 m achieved λ values > 1, indicative of population expansion, in both snow removal and control treatments in the garden at 3340 m. Migration over such a short distance is likely feasible even in this system. Thus, migration from lower sites could offset fitness losses from climate change and contribute to population expansion at the leading edge of the elevational range.

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Somewhat surprisingly, we found that downslope migration could potentially enhance population growth rates in some cases: the population from 3133 m outperformed the local population in both treatments in the garden at 2710 m. We hypothesise that climate change will favour novel suites of trait combinations that do not currently exist, such as the rapid development of high elevation genotypes combined with the drought tolerance and insect herbivore resistance of low elevational genotypes (Anderson *et al*. 2012; Wadgymar *et al*. 2017). Multi-directional migration could generate novel gene complexes that will enhance fitness under climate change, potentially facilitating adaptation and population persistence (Bontrager & Angert 2019).

We focused our studies on snow dynamics, a key abiotic agent of selection that is rapidly shifting due to increasing global temperatures and novel precipitation regimes (Fyfe *et al*. 2017). Field manipulations restored local adaptation under benign conditions, thereby demonstrating that climate change has already disrupted local adaptation. We hypothesise that populations will experience more severe local maladaptation as climate change continues to elevate temperature, atmospheric CO_2 concentrations and drought stress. Altered biotic communities could exacerbate adaptational lag (Alexander *et al*. 2015). For example in the geological record, herbivory often increases under elevated CO_2 concentrations, as plant C:N ratios decline and herbivores consume additional plant tissue to meet their nutritional needs (Currano *et al*. 2008). Similar to other systems (Pellissier *et al*. 2014), *B. stricta*'s resistance to insect herbivory declines with elevation (Anderson *et al*. 2015), likely because plants have limited exposure to insect herbivores in high elevation locations (Rasmann *et al*. 2014) and because selection for rapid flowering under short growing seasons may preclude the evolution of defensive traits (Anderson *et al*. 2015; Wadgymar *et al*. 2017). We postulate that the direct abiotic consequences of climate change could drive local extinctions in arid low-elevation sites, whereas the indirect effects of increasing herbivory could put high elevation populations at risk of decline.

Local adaptation to historical conditions may come at an acute fitness cost in a rapidly changing climate. Researchers must take care in drawing inferences about the extent of local adaptation in contemporary field experiments, as local populations may no longer have enhanced fitness in their home sites. Poor performance of high-elevation populations at lower sites and reduced fitness of local populations under snow removal foreshadow future maladaptation as climate change progresses. If gene flow is insufficient to maintain historical allele-climate matches, shifting fitness functions and widespread maladaptation could reduce population growth rates and increase the risk of extinction.

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AUTHOR CONTRIBUTIONS

JTA designed the experiments and acquired funding. JTA and SMW collected data, which JTA analysed after preliminary analysis by SMW. JTA wrote the first draft of the manuscript, which both JTA and SMW subsequently edited.

DATA AVAILABILITY STATEMENT

We have deposited all data and code in FigShare (https://doi.org/10.6084/m9.figshare.10010138.v1; https://doi.org/10.6084/m9.figshare.10010168.v1; https://doi.org/10.6084/m9.figshare.10010141.v1)

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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