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E-ARTICLE

A Long-Lived Alpine Perennial Advances Flowering under Warmer Conditions but Not Enough to Maintain Reproductive Success

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ABSTRACT: Assessing whether phenological shifts in response to climate change confer a fitness advantage requires investigating the relationships among phenology, fitness, and environmental drivers of selection. Despite widely documented advancements in phenology with warming climate, we lack empirical estimates of how selection on phenology varies in response to continuous climate drivers or how phenological shifts in response to warming conditions affect fitness. We leverage an unusual long-term dataset with repeated, individual measurements of phenology and reproduction in a long-lived alpine plant. We analyze phenotypic plasticity in flowering phenology in relation to two climate drivers, snowmelt timing and growing degree days (GDDs). Plants flower earlier with increased GDDs and earlier snowmelt, and directional selection also favors earlier flowering under these conditions. However, reproduction still declines with warming and early snowmelt, even when flowering is early. Furthermore, the steepness of this reproductive decline increases dramatically with warming conditions, resulting in very little fruit production regardless of flowering time once GDDs exceed approximately 225 degree days or snowmelt occurs before May 15. Even though advancing phenology confers a fitness advantage relative to stasis, these shifts are insufficient to maintain reproduction under warming, highlighting limits to the potential benefits of phenological plasticity under climate change.

Keywords: plasticity, climate change, fitness landscape, phenology, selection.

Introduction

Changes in the timing of life history events (i.e., phenology) are an important response to climate change that can impact individual fitness, species' extinction risk, and geographic range shifts (Matesanz et al. 2010; Merilä and Hendry 2014; Münzbergová et al. 2017; Ensing and Eckert 2019; Iler et al. 2021; Zettlemoyer and DeMarche 2021*a*, 2021*b*). Despite the common assumption that phenological shifts should benefit population persistence under climate change, we still have limited evidence linking climate-induced phenological shifts to vital rates (e.g., survival and reproduction) or population dynamics (Iler et al. 2021). Of the surprisingly few studies directly correlating changes in vital rates and reproductive phenology with changes in climate, most associate earlier reproduction with increased fecundity (Iler et al. 2021). In contrast, species that are unable to track climate change by shifting their phenology, via either plasticity or rapid evolution, are at greater risk of decline (Willis et al. 2008; Zettlemoyer et al. 2021). Therefore, phenological shifts could contribute to population persistence under novel environmental conditions (Vedder et al. 2013; Urban et al. 2016), and we need to evaluate the fitness consequences of phenological shifts in response to climate change (Wadgymar et al. 2018).

Plasticity may play a critical role in allowing populations to persist under rapid environmental change, particularly for long-lived organisms (Chevin et al. 2010, 2013; Ashander et al. 2016; Hendry 2016; Arnold et al. 2019*a*, 2019*b*; Fox et al. 2019). Specifically, plasticity can allow a population's mean phenotype to track an environmentally determined "optimal" phenotype, minimizing the effects of environmental change on mean fitness and possibly facilitating longer-term population persistence and adaptation (Kelly 2019; Bonamour et al. 2020; Gauzere et al. 2020). However, plasticity can also cause species

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to express traits that are mismatched with their new environment (Ghalambor et al. 2007). For instance, species that advance reproduction may experience frost damage or mismatches with food resources (Inouye 2008; Reed et al. 2013; Ramakers et al. 2018; Pardee et al. 2019). Although phenological plasticity can be either beneficial or detrimental, distinguishing its effects on fitness requires investigating how selection on phenotypes (here, phenology) varies across environments (Merilä and Hendry 2014; Caruso et al. 2017; Siepielski et al. 2017; Fox et al. 2019). Specifically, for phenological plasticity to increase fitness (i.e., shifts in an adaptive direction; Ghalambor et al. 2007) there must be natural selection on phenology, and selection must be in the same direction as the phenological shift (Navarro et al. 2022). Alternatively, plasticity can have no effect or decrease fitness (i.e., shifts in a nonadaptive or maladaptive direction, respectively; Arnold et al. 2019*a*). Therefore, an important first step in understanding the fitness consequences of plastic phenological shifts is testing whether such shifts are in a direction favored by selection under climate change (although we note that rigorously testing whether plasticity is adaptive requires quantifying selection on individual reaction norms; Arnold et al. 2019*b*).

Most studies of effects of climate change on selection rely on discrete environmental contrasts, such as ambient versus warming treatments (Collins et al. 2022). Yet we have little understanding of how continuous environmental drivers alter patterns of selection (i.e., fitness landscapes; Chevin et al. 2015). Indeed, the rate of change in an optimal phenotype, such as phenology, with environmental change (i.e., the environmental sensitivity of selection) is a critical parameter in theoretical models for predicting population persistence under climate change (Chevin et al. 2010; Vinton et al. 2022). However, we have virtually no empirical estimates of how selective landscapes shift with continuous environmental drivers in wild populations (Chevin et al. 2015; Gamelon et al. 2018).

Here, we conduct a rare quantitative assessment of the potential benefits of plastic phenological shifts under warming (Kingsolver and Buckley 2017; Gauzere et al. 2020) in a long-lived alpine plant (*Silene acaulis* [L.] Jacq., Caryophyllaceae). A previous analysis of 149 years (1872–2021) of herbarium records documented that *S. acaulis* flowering has advanced on average by 0.06 ± 0.02 days per year (Zettlemoyer et al. 2022). Here, we leverage a 6-year observational dataset recording individual-level flowering phenology and reproductive success to investigate the following questions.

Question 1 (Q1). Is there temporal variation among years in individuals' phenology, indicating phenological plasticity? If so, how much of that temporal variation in phenology is in response to changing climatic conditions (advancing snowmelt and warming temperatures)?

Question 2 (Q2). Do climate-relevant measures of phenology, such as growing degree days accumulated at flowering or days since snowmelt at flowering, remain constant across changing climatic conditions?

Question 3 (Q3). Is there selection on phenology? If so, how does optimal phenology shift with climate drivers?

Question 4 (Q4). How much temporal variation in selection (i.e., variation among years) is explained by climatic drivers?

Material and Methods

Study System

Silene acaulis (Caryophyllaceae), or moss campion, is an arctic-alpine cushion plant common in circumboreal tundra habitats. Moss campion does not spread clonally and reproduces solely through seeds. It has a gynodioecious mating system; plants are either hermaphroditic (producing perfect flowers) or female (producing pollen-sterile flowers). Moss campion is primarily fly and bee pollinated (Hall et al. 2018) and is slow growing and long lived; the age of first reproduction is estimated at >24 years, and the vast majority of seeds are produced by large plants >100 years old (Morris and Doak 1998).

Phenology and Reproductive Success

Each year from 2016 to 2021, we monitored the flowering phenology and reproductive success of permanently marked and mapped individual plants of *S. acaulis* along transects in each of four plots (SN1–SN4) at Niwot Ridge Long-Term Ecological Research (LTER) Program in Colorado (40°3′318.48″N, 105°35′50.33″W, 3,574 m asl; fig. S1.1; table S1.1 [figs. S1.1–S1.12, S2.1–S2.3, S3.1–S3.5 and tables S1.1–S1.8, S3.1–S3.5 are available online]; the first years of phenology surveys are described in Hall et al. 2018 and Waddle et al. 2019). Individuals were originally tagged and mapped in four plots, selected to capture a representative sample of the larger population at Niwot Ridge, in 2001 as part of an ongoing, long-term demographic study (Doak and Morris 2010). Since 2016, we have measured size, flowering phenology, and fruit production (a proxy for reproductive success) on all plants along each of two parallel transects (>15 m long, 0.5 m wide, separated by at least 2 m) per plot (fig. S1.1). Within any given year, 495–636 individuals were monitored for flowering phenology, with 172–383 individuals observed to flower. Year-to-year variation in sample sizes is largely due to young plants reproducing for the first time, older plants senescing, and some plants failing to flower in some years (supplement S2; supplements S1–S3 are available online). Thus, although we have collected phenology data for 649 individual plants during at least one year of the study, there is wide variation in the number of years for which we have data for a given individual (mean = 3.7 years, SD = 1.8; fig. S2.1).

Silene acaulis grows horizontally as flat "cushions" composed of many leaf rosettes; size is estimated as cushion area for plants with ≥20 rosettes (Doak and Morris 2010). Small plants with <20 rosettes almost never flower and were excluded from analyses.

We recorded the number of open flowers on each plant every 2–5 days throughout the growing season (approximately June 10–July 30). Each year, we visited plots early in the growing season to time our first census with the onset of flowering. We continued censuses until most individuals had ceased flowering, with the exception of 2018, when early snowmelt conditions meant that ~32% of individuals had begun flowering by our first census (supplement S2). We summarized individual-level flowering phenology by fitting quadratic curves to the proportion of open flowers on each census day and extracting the day of first flower, peak flower, and flowering duration for each individual in a given year (fig. S2.2). Because flowering was not recorded daily, this method allows us to interpolate an estimate of every phenological value for every individual; interpolated estimates are highly correlated with empirical estimates based on census dates ($r \geq 0.9$; fig. S2.3).

We counted mature fruits and estimated plant size for each individual at the end of each growing season (last week of July, consistent with the timing of demographic censuses in the long-term demographic study; Doak and Morris 2010). *Silene acaulis* fruits with mature seeds are hard capsules easily distinguished from immature or aborted fruits (Hall et al. 2018), and an individual's fruit production is highly correlated with subsequent seedling recruitment (see table S2 in Doak and Morris 2010). Similar to other long-lived species, mean reproductive rates have a smaller effect on population growth of *S. acaulis* than other vital rates, such as adult survival and growth (Morris and Doak 2005). However, reproduction is one of the most variable vital rates in this species over time, and stochastic population growth is similarly elastic to variability in reproduction as to variability in other vital rates (Morris and Doak 2005). Furthermore, reproductive failure is an increasingly critical limitation to population persistence of *S. acaulis* toward its southern range edge, including Niwot Ridge (Doak and Morris 2010).

Environmental Data

Local soil surface temperature was recorded every 2–4 h using three to eight temperature sensors in each plot (2008–2020: Thermochron iButtons; 2020–2021: Onset HOBO pendants). We summarized temperature data across sensors within each plot and year to estimate two climatic drivers commonly found to affect phenology in alpine plants: snowmelt timing and temperature (Wipf and Rixen 2010; Iler et al. 2013; Oberbauer et al. 2013; Wielgolaski and Inouye 2013; Jerome et al. 2021; note that these studies use weather station climate data). We averaged temperature data across sensors within a given plot to estimate mean conditions in that plot (Ensing and Eckert 2019; Czachura and Miller 2020; Miller-Struttmann et al. 2022). We estimated snowmelt timing as the first spring day with mean temperature ≥2°C and ≥1°C difference between maximum and minimum daily temperatures, indicating that a sensor is no longer insulated by snowpack (hereafter, "estimated day of snowmelt"; fig. S1.2). Snowmelt timing also depends on winter precipitation and soil moisture; however, we were unable to quantify those variables at the plot level in each year. We also calculated growing degree days (GDDs; a measure of heat accumulation) as the sum of daily average temperatures exceeding a baseline temperature of 2°C (threshold chosen during preliminary analyses). Measures of GDDs incorporate information on both the timing of snowmelt (days with snow cover contribute nothing to GDD accumulation) and temperature following snowmelt (warmer days contribute more to GDDs; fig. S1.2). We aggregated GDD and temperature data into six potential temperature metrics that we predicted could be informative for phenology: (1) average daily temperature in May; (2) average daily temperature from April 1 to June 15 (hereafter, "average seasonal temperature"; April 1 represents a date before snowmelt in any year, and June 15 represents a date close to the start of flowering in most years); (3) GDDs accumulated in April; (4) GDDs accumulated in May; (5) GDDs accumulated from June 1 to June 15; and (6) GDDs accumulated from April 1 to June 15 ("seasonal GDDs"). These metrics represent the abiotic environment over a fixed window of time within a given year (fig. S1.3), providing a measure of the climate conditions in a given plot and year that is independent of phenology. Photoperiod does not vary substantially across the range of flowering phenologies observed in this study (range: 14.8–15.0 h of day length at first flower), and preliminary analyses indicated little predictive power of photoperiod for flowering time.

Statistical Analyses

All statistical analyses were conducted in R version 4.1.0 (R Core Team 2021). Our overall approach was to fit a series of generalized linear mixed models (GLMMs; Bolker et al. 2009; Harrison 2014; Bolker 2015) to address each of our questions using the lme4 package (Bates et al. 2015). We modeled flowering phenology response variables as normally distributed (i.e., linear mixed models) and modeled reproductive success (number of fruits) using a Poisson distribution and an observation-level random effect to account for overdispersion (Elston et al. 2001; Harrison 2014). In all models, we included fixed effects of plant size (area; log transformed to meet assumptions of normality in the residuals) and sex (female or hermaphrodite) to account for size- or sex-specific effects on phenology or reproductive success. Interactions of size and sex with year and climate drivers were not significant ($P > .1$) and thus were excluded from analyses. In all models, we included random effects of individual plants (PlantID, to control for repeated measures; Elston et al. 2001; Wadgymar et al. 2018) nested within plot (SN1–SN4, to control for spatial structure in the data and other unaccounted-for environmental covariates at the plot level). We included plot as a random effect because plots were selected to capture representative variation in environmental conditions experienced by the larger *S. acaulis* population at Niwot Ridge (fig. S1.1). We used the Akaike information criterion with a sample size correction (AICc; Burnham and Anderson 2004) to evaluate the relative predictive power of alternative explanatory variables, such as climate variables, for a given response variable. We also report conditional and marginal R^2 values for each model using the r.squaredGLMM command in the MuMIn package (Barton 2009; Nakagawa and Schielzeth 2013). For some questions, we supplement these GLMMs with additional analyses that provide complementary tests or interrogation of patterns. We further describe the specific analyses used to answer each question below.

Q1: Temporal variation in absolute phenology. We tested for temporal variation in absolute phenology by including the effect of year (2016–2021) as a categorical fixed effect in LMMs using each of the three measures of flowering phenology (first flower [day of year (doy)], peak flower [doy], and flowering duration [number of days between first and last flower]) as response variables. LMMs allow us to test for variation in phenology at the individual level, including testing for effects of individual-level covariates, such as plant size and sex. However, we also explored variation in phenology aggregated at the plot level by fitting linear models using means for every combination of plot and year ($n = 24$ data points/model) for absolute first flower, peak flower, and flower duration, mimicking other studies in which phenology data are collected at the population level and individual plant ID is not known (table S3.1). These additional analyses allowed us to check the sensitivity of our findings to complex model structure but ignore individual variation in phenology within plots.

Climate effects on absolute phenology. We next tested whether annual climate conditions are associated with shifts in absolute phenology by including climate drivers as fixed effects in LMMs of phenology. We tested the effects of (1) estimated day of snowmelt and (2) six potential temperature metrics (GDDs in April, GDDs in May, GDDs in early June, seasonal GDDs, average May temperature, and average seasonal temperature) on each measure of absolute flowering phenology (doy). Climate drivers were highly correlated, potentially because of estimation from the same temperature sensor datasets (fig. S1.5), so we fitted a series of LMMs with each climate driver as separate fixed effects and absolute first flower, peak flower, and flowering duration as separate response variables ($n = 7$ models/phenological variable). Likewise, because estimated day of snowmelt was significantly correlated with all temperature metrics (fig. S1.5), we did not include estimated day of snowmelt × temperature interactions despite the fact that temperature and snowmelt can have either separate or combined effects on plant phenology (e.g., greater winter precipitation can increase snowpack, while greater winter temperatures can decrease snowpack; Dunne et al. 2003; Sherwood et al. 2017). We tested for nonlinear climate effects by comparing linear climate models to models including quadratic climate effects using AICc; including quadratic effects was supported ($\Delta\text{AICc} > 2$) in most cases. We also used AICc to determine which climate variables best explained variation in each of our three measures of phenology. We compared R^2 values for models with year as a categorical fixed effect versus models with continuous climate variables to test how much of the temporal variation in phenology is accounted for by changing climatic conditions. We again supplemented these LMMs with a complementary plot-level analysis as a valuable check for effects of model structure (linear models with mean phenology for every plot/year combination as response variables; table S3.2).

Climate had weak and variable effects on flowering duration (fig. 1), potentially due to higher variation in day of last flower responses to climate (fig. S1.6) and limited year-to-year variation in flowering duration (fig. S1.7), so hereafter we focus on first and peak flowering time. Seasonal GDDs was the best predictor of both first and peak flowering time (table S1.2), so we used seasonal GDDs as the most relevant climate metric. However, because many studies of alpine plant phenology focus on snowmelt timing (see above), we also present results from models with estimated day of snowmelt as a climate driver.

Individual variation in climate responses. Because individuals can vary in their responses to climate (individual × environment [I×E] interactions; Nussey et al. 2007), we quantified the shape of individual reaction norms by refitting the LMMs described above to include random slopes for individual responses to climate. We tested the significance of I×E interactions using likelihood ratio tests comparing models with and without random slopes (Arnold et al. 2019*a*). We also tested for quadratic individual responses to climate; quadratic reaction norms were never supported by likelihood ratio tests (table S1.3).

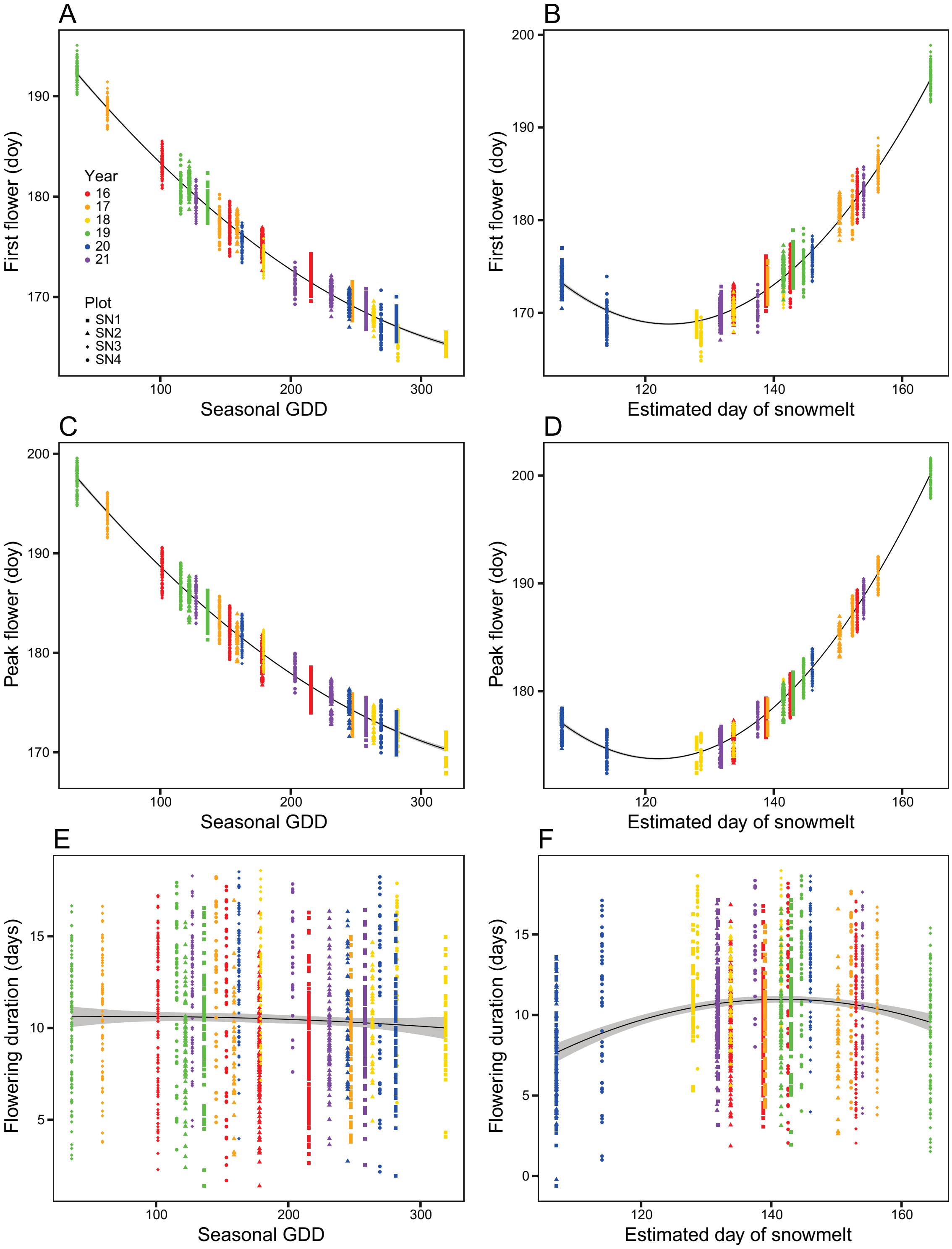

Figure 1: Absolute flowering phenology shifts in response to climate. Shown are the effects of seasonal GDDs (growing degree days accumulated from April 1 to June 15; *left*) and estimated day of snowmelt (*right*) on absolute first flower (day of year [doy]; *A*, *B*), absolute peak flower (doy; *C*, *D*), and flowering duration (number of days between first and last flower; *E*, *F*) for individuals of *Silene acaulis*. Colors represent years (2016–2021; ROYGBV), and symbols represent plots (squares, triangles, diamonds, and circles indicate SN1–SN4, respectively). Lines represent quadratic fit after accounting for all model terms; gray areas represent 95% confidence intervals.

Q2: Shifts in climate-relevant phenology. Ecological and evolutionary studies often report phenology as day of year, but measuring phenology on a biologically relevant scale may reveal the environmental factors that contribute to variation in phenological shifts. By examining phenology relative to climate drivers, we can test whether climate change might outpace phenological shifts (Wadgymar et al. 2018). Specifically, despite flowering earlier in the season (shifts in absolute phenology [doy]; Q1), individuals might still flower under similar climate conditions (i.e., the same accumulated GDDs or a similar number of days after snowmelt). In this case, absolute phenology perfectly accelerates with changing climate conditions such that flowering occurs 1 day earlier for every 1 day advance in the timing of spring. Alternatively, if individuals flower under warmer conditions, then phenological shifts are occurring more slowly than climate change. If individuals shift phenology more rapidly than conditions are shifting, then earlier flowering might reflect accelerated rates of growth and development due to reasons beyond the studied climate variables (Wadgymar et al. 2018).

We therefore tested for shifts in several climate-relevant measures of phenology. We quantified first and peak flowering time relative to seasonal GDDs (the best climate metric following table S1.2) and estimated day of snowmelt, resulting in four climate-relevant phenology metrics. For each individual, we estimated the number of GDDs accumulated from April 1 to the date of first or peak flower ("GDDs accumulated from April 1 to first or peak flower") and the number of days between estimated day of snowmelt and the date of first or peak flower ("number of days between snowmelt and first or peak flower"). These measures represent the abiotic environment over a biological window of time that is dependent on an individual's phenology and essentially rescale what is considered early versus late flowering relative to the climate conditions of a particular year (fig. S1.3).

We tested for shifts in climate-relevant phenology by repeating our analyses described above but using each of the four climate-relevant phenology metrics as separate response variables. We included seasonal GDDs and seasonal GDDs^2 as climate predictors in LMMs examining GDDs accumulated from April 1 to first or peak flower. We included estimated day of snowmelt and estimated day of snowmelt^2 as climate predictors in LMMs examining the number of days between snowmelt and first or peak flower. If shifts in absolute phenology (doy) perfectly track the same climate conditions during flowering, we would predict that climate-relevant phenology remains constant over time (i.e., no effects of seasonal GDDs or estimated day of snowmelt as predictors). If we detect an effect of climate conditions on climate-relevant phenology, this would indicate that despite flowering occurring earlier in the year, phenology is shifting either (*a*) more slowly (if plants flower with more accumulated GDDs or later after snowmelt) or (*b*) more rapidly (if plants flower with fewer accumulated GDDs or more rapidly after snowmelt) than climate change in this system. We also fitted complementary linear models using plot/year means (table S3.3).

Q3: Selection on phenology. To assess whether selection on phenology mirrors phenological shifts in this system, we ask the following questions: (Q3a) How does fruit production vary with climate conditions (advancing snowmelt and warming temperatures)? (Q3b) Is phenology under selection? (Q3c) How does optimal phenology (i.e., flowering time where fitness is maximized) shift with respect to climate, and is this shift consistent with observed phenological responses from Q1 and Q2?

We used the number of mature fruits produced (hereafter, "fruit production") as a proxy for an individual's yearly absolute fitness. For each question below, we fit both Poisson GLMMs and complementary linear models using plot/year means (supplement S3).

Q3a: Shifts in reproductive success. We first examined the effects of climate on fruit production using two models that included fruit production as the response variable and either seasonal GDDs or estimated day of snowmelt as two separate predictors.

Q3b: Selection on climate-relevant phenology. We then tested for selection on climate-relevant measures of phenology. We fit separate GLMMs testing the effects of each of the four metrics of climate-relevant phenology (described in Q2) on fruit production. We included quadratic terms for climate-relevant phenology in each model to test for nonlinear selection (Lande and Arnold 1983; Brodie et al. 1995). We then used AICc to determine which metric of phenology best explained variation in fruit production. First flowering time metrics were better predictors of fruit production than peak flowering time metrics (table S1.4), so we used first flowering time metrics to build fitness landscapes (Q3c).

Q3c: Optimal phenology as a function of climate. The GLMMs described above provide robust statistical tests for selection but impose constraints on the form of the fitness function (e.g., linear or quadratic; Schluter 1988; Calsbeek 2012; Martin and Wainwright 2013). To visualize the shape of continuous fitness landscapes, we next fit nonparametric loess models to fruit production as functions of climate and both absolute and climate-relevant phenology. This allowed us to interpolate a smooth fitness surface for flowering phenology across climate conditions without the constraints of a quadratic fitness function (Schluter 1988; Calsbeek 2012; Martin and Wainwright 2013). We created fitness landscapes for (1) absolute first flower (doy) and seasonal GDDs, (2) absolute first flower and estimated day of snowmelt, (3) GDDs accumulated from April 1 to first flower and seasonal GDDs, and (4) number of days between snowmelt and first flower and estimated day of snowmelt. This allowed us to explore how optimal phenology, in terms of both day of year and climate-relevant phenology, may shift with warming.

Q4: Climate drivers of temporal variation in selection on absolute phenology. Finally, we asked how well climate drivers explain temporal variation in selection on phenology. To do this, we fit GLMMs of fruit production that included year as a factor (2016–2021), absolute first (or peak) flower (doy), and their interaction as fixed effects. In all models, we also included random slopes for each year in each plot to control for spatial variability in temporal patterns of selection, as well as first (or peak) flower^2 as a fixed effect to test for nonlinear selection. We then compared conditional and marginal R^2 of these models to those of GLMMs that substitute climate drivers (seasonal GDDs and estimated day of snowmelt) for year effects.

Results

Q1: Is There Temporal Variation in Phenology, and How Much of That Temporal Variation in Phenology Is in Response to Changing Climatic Conditions?

We detected significant temporal variation in absolute flowering phenology (doy; tables S1.5, S3.1; figs. S1.7, S3.1). Absolute first and peak flowering time advanced nonlinearly in response to more accumulated seasonal GDDs and earlier snowmelt (tables S1.2, S.1.5; fig. 1*A*–1*D*). Flowering duration extended slightly with increasing seasonal GDDs and later snowmelt. However, climate effects on duration were weak (table S1.2; fig. 1*E*, 1*F*). The strong nonlinear responses to snowmelt may be largely driven by 2020, a year with normal seasonal GDDs but extremely early snowmelt relative to other years (i.e., early snowmelt followed by cool spring temperatures). Climate drivers explained slightly more of the variation in absolute phenology than year effects (compare R^2 values of year vs. climate models in table S1.2), indicating that climate explains temporal variation in phenology (marginal R^2 values for first flower: year $= 0.49$, snowmelt $= 0.53$, seasonal GDDs $= 0.57$; marginal R^2 values for peak flower: year $= 0.52$, snowmelt $= 0.57$, seasonal GDDs $= 0.63$). Results using plot/year means were qualitatively similar (table S3.2; fig. S3.2).

We also uncovered size- and sex-specific differences in absolute phenology (table S1.2). Females flowered slightly earlier than hermaphrodites on average (absolute first flower: female $=$ day 175 ± 1.11 vs. hermaphrodite $=$ day 176 ± 1.09; absolute peak flower: female $=$ day 180 ± 1.35 vs. hermaphrodite $=$ day 182 ± 1.34). Larger plants produced first flowers earlier, peaked later, and flowered for a longer duration than smaller plants (fig. S1.8). This effect was not due to sex-specific size differences (size did not differ between sexes [$P = .29$], and size × sex interactions were nonsignificant [$P > .4$]).

We detected significant I×E interactions for both absolute first and peak flowering time in response to seasonal GDDs (table S1.3; fig. S1.9). Generally, individuals advanced first and peak flower with increasing seasonal GDDs, primarily differing in the magnitude rather than the direction of phenological shifts. Individuals also demonstrated variation in the magnitude of their reaction norms in response to estimated day of snowmelt, although I×E interactions in first flower response to snowmelt were weak (table S1.3; fig. S1.9).

Q2: Do Climate-Relevant Measures of Phenology Shift in Response to Warming Conditions?

Climate-relevant plant phenology shifted with warming. Specifically, climate-relevant phenology was not constant over time, as predicted if phenological shifts track changing climate perfectly (table S1.6). Generally, plants flowered with more accumulated GDDs in years with higher seasonal GDDs and later after snowmelt in years with earlier snowmelt. Specifically, GDDs accumulated from April 1 to first and peak flower increased nonlinearly with seasonal GDDs, indicating that flowering occurs under much warmer conditions in years with high seasonal GDDs, despite flowering earlier in the growing season (table S1.6, pts. A, B; fig. 2*A*, 2*B*). The number of days between snowmelt and first and peak flower decreased nonlinearly with estimated day of snowmelt, indicating that flowering is increasingly delayed relative to snowmelt when snowmelt occurs earlier in the season, again despite flowering earlier in the year (table S1.6, pts. C, D; fig. 2*C*, 2*D*). Results using plot/year means were qualitatively similar (although nonsignificant for GDDs accumulated from April 1 to first and peak flower; table S3.3; fig. S3.3).

Q3: Is Phenology under Selection, and How Does Optimal Phenology Shift with Respect to Climatic Drivers?

Shifts in reproductive success. Fruit production declined with higher seasonal GDDs and earlier estimated day of snowmelt (tables S1.7, S3.4; seasonal GDDs: $-9.8\mathrm{e}^{-03} \pm 8.7\mathrm{e}^{-04}$ fruits/GDD, $\chi^2_{1,\,1{,}516} = 126.17$, $P < .0001$; snowmelt: 0.06 ± 0.01 fruits/day, $\chi^2_{1,\,1{,}516} = 142.04$, $P < .0001$; figs. 3, S3.4).

Selection on climate-relevant phenology. We found strong effects of climate-relevant phenology on reproductive success (fig. 4; table S1.4). GDDs accumulated from April 1 to first flower was the best predictor of reproductive success, although patterns of selection were similar across

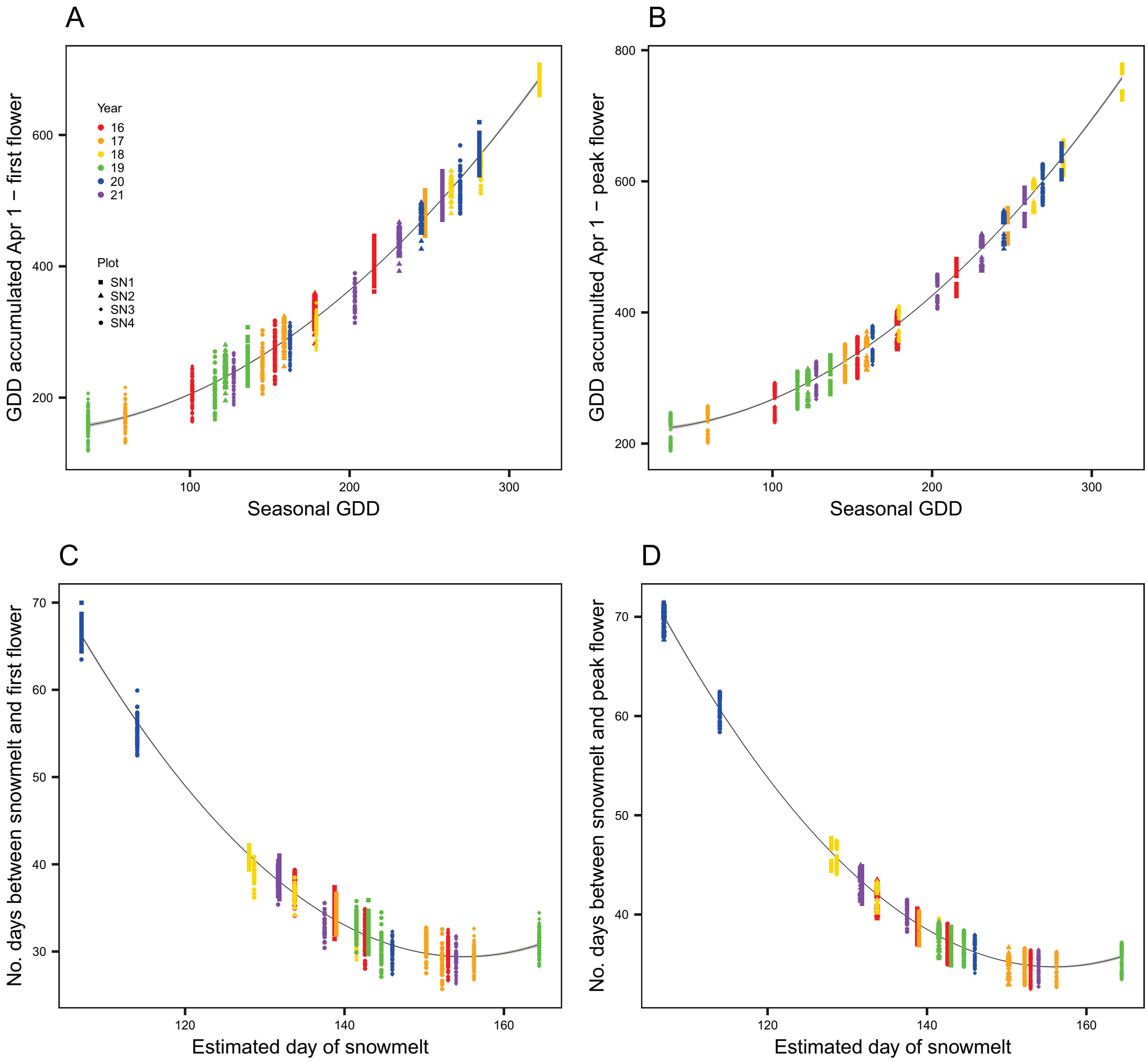

Figure 2: Shifts in climate-relevant phenology in response to climate. *Top*, effect of growing degree days accumulated from April 1 to June 15 (seasonal GDDs) on predicted GDDs accumulated from April 1 to day of first flower (*A*) and GDDs accumulated from April 1 to day of peak flower (*B*) of individual *Silene acaulis*. *Bottom*, effect of estimated day of snowmelt on predicted number of days between estimated day of snowmelt and day of first flower (*C*) and number of days between estimated day of snowmelt and day of peak flower (*D*) of individual *S. acaulis*. Lower values indicate flowering under cooler conditions, which could occur either via earlier flowering within a growing season (i.e., with fewer accumulated GDDs or more rapidly following snowmelt) or flowering in a year with lower seasonal GDDs or later snowmelt. Colors represent years (2016–2021; ROYGBV), and symbols represent plots (squares, triangles, diamonds, and circles indicate SN1–SN4, respectively). Lines represent quadratic fit after controlling for all model terms; gray areas represent 95% confidence intervals (too narrow to visualize).

all four measures of climate-relevant phenology (table S1.4; fig. S1.10).

Climate-relevant phenology was under directional selection, with greater fruit production when individuals flower with fewer accumulated GDDs from April 1 to first flower (-1.18 ± 0.10 fruits/GDD, $\chi^2_{1,\,1,515} = 139.73$, $P < .0001$; fig. 4*A*) and sooner after snowmelt (-0.15 ± 0.02 fruits/day between snowmelt and first flower, $\chi^2_{1,\,1,515} = 45.40$, $P < .0001$; fig. 4*B*). We also detected significant quadratic effects of climate-relevant phenology, with coefficients indicating nonlinear directional selection rather than stabilizing selection (table S1.4). This suggests that fruit production is

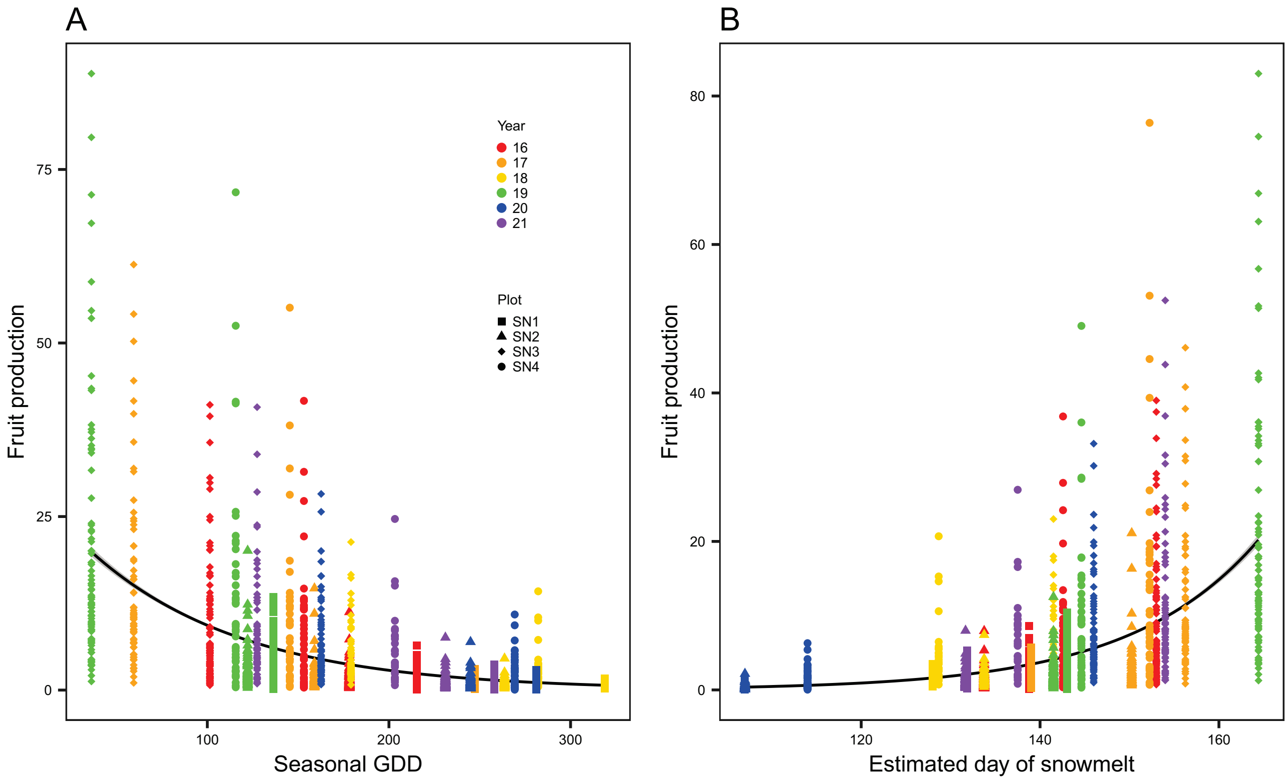

Figure 3: Fruit production (a proxy for yearly fitness) decreases with greater growing degree days (GDDs) or earlier snowmelt. Shown are the effects of seasonal GDDs (GDDs accumulated from April 1 to June 15; *A*) and estimated day of snowmelt (*B*) on the predicted number of mature fruits produced by individual *Silene acaulis* after accounting for all model terms, including log(plant size). Colors represent years (2016–2021; ROYGBV), and symbols represent plots (squares, triangles, diamonds, and circles indicate SN1–SN4, respectively). Lines represent Poisson generalized linear model fit after controlling for all model terms; gray areas represent 95% confidence intervals.

low across a wide range of observed climate-relevant phenologies and increases dramatically for the earliest flowering individuals relative to seasonal GDDs or estimated day of snowmelt (fig. 4). Effects were qualitatively similar but nonsignificant when using plot/year means (table S3.5; fig. S3.5).

Optimal phenology as a function of climate. This pattern is also supported by nonparametric fitness landscapes (fig. 5). Optimal first flowering time (i.e., absolute first flowering time [doy] associated with maximum fruit production) occurred under lower seasonal GDDs and later estimated day of snowmelt. Maximum fruit production was high under both lower seasonal GDDs and later estimated day of snowmelt across a range of early to intermediate absolute first flowering times, declining when flowering is later in the season (fig. 5*A*, 5*B*). This suggests that advancing first flowering time in response to increasing seasonal GDDs and earlier snowmelt is tracking a climate-driven phenotypic optimum. However, these fitness landscapes also highlight that although earlier absolute flowering increased fruit production, maximum reproductive success declined under higher seasonal GDDs and earlier estimated day of snowmelt. For example, even the earliest-flowering individuals were in lower fitness isoclines (blue areas in fig. 5*A*, 5*B*) in years with seasonal GDDs above 225 or when snow melts before day 135, whereas most individuals were in higher fitness isoclines (orange areas in fig. 5*A*, 5*B*) in years below these warming thresholds. Thus, although populations flower earlier in years with higher seasonal GDDs and earlier estimated day of snowmelt, this is insufficient to maintain constant fitness isoclines and instead population mean fitness drops into lower fitness isoclines (large black symbols [indicating plot/year means] with increasing GDDs or earlier snowmelt in fig. 5).

Fitness landscapes for climate-relevant phenology similarly indicated that optimal flowering occurred with fewer GDDs accumulated from April 1 to first flower or sooner after snowmelt (fewer days between snowmelt and first flower; fig. 5*C*, 5*D*). However, we still observed a decline in fruit production under higher seasonal GDDs and earlier estimated day of snowmelt even for a constant climate-relevant phenology. For example, individuals that flowered after accumulating approximately 200 GDDs or ~20 days after snowmelt enjoyed relatively high reproductive success

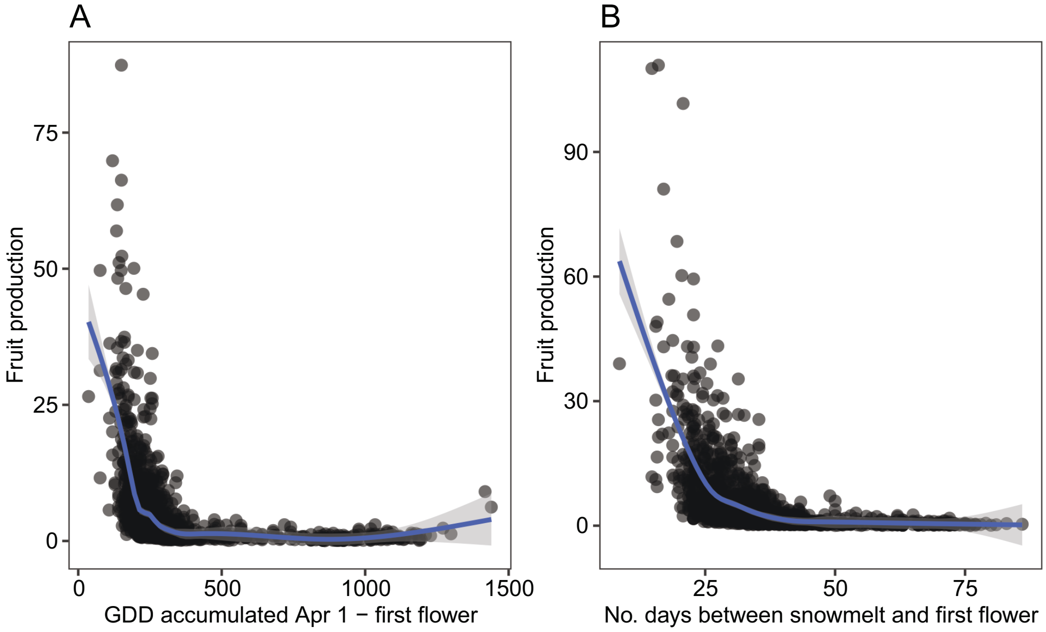

Figure 4: Directional selection on first flowering time relative to seasonal GDDs (growing degree days accumulated from April 1 to June 15; *A*) and estimated day of snowmelt (*B*). Predictors represent climate-relevant measures of phenology: GDDs accumulated from April 1 to day of first flower (*A*) and number of days between estimated day of snowmelt and day of first flower (*B*). In both cases, lower values indicate flowering under cooler conditions, which could occur either via earlier flowering within a growing season (i.e., with fewer accumulated GDDs or more rapidly following snowmelt) or via flowering in a year with lower seasonal GDDs or later snowmelt. Points represent predicted fruit production (a proxy for yearly fitness) for individual *Silene acaulis* after accounting for all model terms, including log(plant size). Blue lines represent nonparametric loess fit, and gray areas represent 95% confidence intervals.

in years with lower seasonal GDDs and later estimated day of snowmelt but drop to low fitness isoclines in years with higher seasonal GDDs and earlier estimated day of snowmelt. This suggests that even if populations were able to maintain a consistent climate-relevant phenology, it would not be sufficient to avoid decreases in reproductive success associated with warming.

Q4: How Much Temporal Variation in Selection Is Explained by Climatic Drivers versus Year Effects?

The strength of selection on absolute first flowering time (doy) varied strongly among years, consistent with important effects of interannual climate variation (fig. S1.11; table S1.8). However, earlier absolute flowering generally correlated with higher fruit production, even in cases where fruit production also demonstrated an intermediate hump (e.g., SN4). In these models, we detected significant quadratic effects of phenology that varied among years, consistent with both stabilizing and nonlinear directional selection (figs. S1.11, S1.12; table S1.8). Climate drivers captured roughly three-fourths of the temporal variation in selection explained by models with a fixed effect of year (marginal R^2 values: year model = 0.47, GDD model = 0.36, snowmelt model = 0.38). We did not detect significant selection on absolute peak flowering time (table S1.8).

Discussion

We assessed the fitness consequences of climate-driven shifts in flowering phenology for a long-lived alpine plant. We find that individuals flower earlier in years with a high number of seasonal GDDs or earlier snowmelt, indicating phenotypic plasticity for flowering phenology. However, this phenological plasticity is unable to track consistent climate conditions during flowering; in years with high seasonal GDDs and early snowmelt, flowering is increasingly delayed relative to snowmelt and occurs after more accumulated GDDs. Furthermore, mean reproductive success declines precipitously with higher seasonal GDDs and earlier snowmelt, while nonlinear directional selection strongly favors flowering sooner after snowmelt and with fewer accumulated GDDs. Although phenological plasticity is in the direction favored by selection, earlier flowering is unable to prevent fitness declines as climates warm. By testing how climate influences both phenological shifts and fitness landscapes, our dataset provides unique insight into

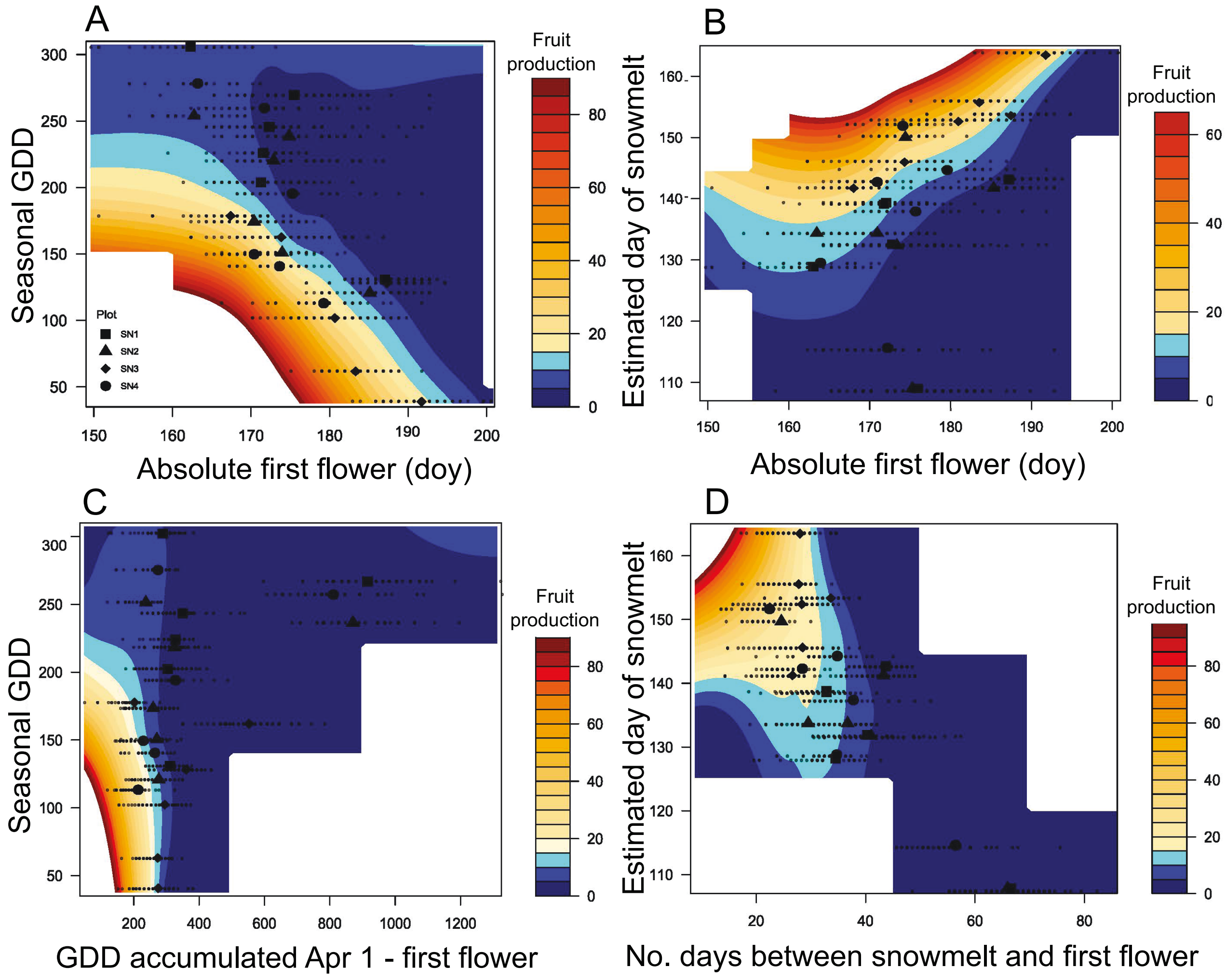

Figure 5: Fitness landscapes for the effects of seasonal GDDs (growing degree days accumulated from April 1 to June 15; *left*) and estimated day of snowmelt (*right*) on absolute first flowering time (day of year [doy]; *A*, *B*) and climate-relevant first flowering time (*C*, GDDs accumulated from April 1 to day of first flower; *D*, number of days between estimated day of snowmelt and day of first flower) on fruit production (a proxy for yearly fitness) of individual *Silene acaulis*. Lower values of GDDs accumulated from April 1 to day of first flower and fewer days between snowmelt and day of first flower indicate flowering under cooler conditions, which could occur via either earlier flowering within a growing season or flowering in a year with lower seasonal GDDs or later snowmelt. Small points represent individual plants, and large shapes represent plot means (squares, triangles, diamonds, and circles indicate SN1–SN4, respectively). Blue shades represent lower fitness isoclines with lower fruit production; red represents the highest fitness isoclines with the greatest fruit production. The optimal phenotype occurs where fruit production is maximized (here, under earlier flowering and either fewer seasonal GDDs or later snowmelt). Some regions of each panel have been set to white to avoid extrapolation of fitness landscapes beyond the range of available data.

the potential role of phenology in maintaining population fitness under warming or, alternatively, leading to maladaptation under warming.

Phenology Advances with Warming but Fails to Track Climate Conditions

Many studies document advancing phenology in response to climate warming (Parmesan 2006, 2007; Calinger et al. 2013; CaraDonna et al. 2014; Thackeray et al. 2016; Piao et al. 2019). Consistent with these studies as well as with an analysis based on herbarium records of *Silene acaulis* (Zettlemoyer et al. 2022), we find that individuals' flowering phenology is highly responsive to climate conditions from year to year, with individuals flowering up to 3 weeks earlier in the warmest years. However, by examining phenology relative to climate conditions during flowering, we find that even these strong phenological shifts do not result in consistent climate conditions during flowering. Instead, individuals are flowering later following snowmelt and with more accumulated GDDs with climate warming. In other words, climate change is occurring more rapidly than phenology can shift in this system. This imperfect tracking could be due to constraints on flowering time plasticity (e.g., physiological constraints [Preston and Fjellheim 2020]; other environmental cues, such as photoperiod [Meng et al. 2021] or winter temperatures [Cook et al. 2012]); or a need to match pollinator phenology [Rafferty and Ives 2012]). In contrast, Wadgymar et al. (2018) found that flowering time relative to snowmelt and GDDs is relatively constant in an alpine community, with most species tracking climate to flower at a fixed time after snowmelt (i.e., perfect tracking). Since *S. acaulis* can survive for centuries (Morris and Doak 1998), it may be unlikely to track climate as precisely as shorter-lived alpine perennials (Wadgymar et al. 2018), indicating a need to examine how closely phenology tracks climate in longer-lived species. For example, shorter-lived species may exhibit phenological shifts that are a product of both phenotypic plasticity and rapid adaptive evolution (Franks et al. 2007; Anderson et al. 2012), resulting in better climate tracking, whereas long-lived species are more buffered to climate variability (Morris et al. 2008; Compagnoni et al. 2021), which could weaken selection for precise climate tracking via phenological plasticity.

Climate Drives Selection on Phenology

Selection on flowering phenology is strongly influenced by climate, with climate variables explaining much of the temporal variation in selection. Phenology relative to climate conditions is under nonlinear directional selection whereby reproductive success increases sharply when individuals flower under fewer accumulated GDDs or sooner following snowmelt. Selection for earlier flowering in response to climate change (warming, snowmelt, or drought) has been detected in numerous species, including *Brassica rapa* (Franks et al. 2007), *Boechera stricta* (Anderson et al. 2011, 2012; Bemmels and Anderson 2019), *Lathyrus vernus* (Ehrlén and Münzbergová 2009; Ehrlén and Valdes 2020), and across meta-analyses of selection on flowering time (Munguía-Rosas et al. 2011; Caruso et al. 2020). This has often been interpreted as evidence that climate change shifts fitness landscapes and thus optimal flowering times, yet few studies have directly estimated the environmental sensitivity of selection in wild populations (Chevin et al. 2015; Gauzere et al. 2020). Indeed, many studies implicitly assume that selection favors phenological shifts that are exactly equal to the rate of environmental change (i.e., flowering one day earlier for each day of advancing snowmelt) and that maximum fitness will remain constant if perfect phenological tracking is achieved. Here, we show that fitness landscapes for flowering time change dramatically with continuous annual climate drivers such as seasonal GDDs and snowmelt timing. Specifically, we find changes not only in the optimal phenology but also in the steepness of the fitness landscape and maximum detected reproductive success with warming. This results in very low reproductive success under extremely warm conditions (GDDs >225 or snowmelt before doy 135), regardless of flowering time. Together, these landscapes indicate a fitness peak maximizing fruit production under a combination of early flowering and cold conditions, with populations increasingly displaced from this optimum with warming (see also fig. 1 in Anderson et al. 2012). If frost damage were to cause reproductive failure (Iler et al. 2019), the fitness landscapes could change dramatically; future work will investigate how freezing degree days influence phenology.

In contrast to absolute early and peak flowering, we do not find strong effects of climate on flowering duration. Flowering duration may show weaker responses to climate than first or peak flower for several reasons. First, the decision to initiate flowering exposes plants to the risk of losing energetically expensive reproductive structures (e.g., to frost damage; Pardee et al. 2019), while the timing of peak flowering is important for flowering synchronously with mates and to attract pollinators (Parra-Table and Vargas 2004; Elzinga et al. 2007; Dai et al. 2023). Thus, first or peak flower is more likely to be the target of selection to respond appropriately to environmental cues. Selection for earlier flowering has been suggested to be driven, at least in part, by selection for longer flowering duration (Austen et al. 2017). Although we do see the predicted pattern of increasing fruit production with longer flowering duration (table S1.8; fig. S1.12), the relationship between first flower and flowering duration in this study is relatively weak ($r = -0.4$; fig. S2.3). Second, the duration of flowering may be constrained by the availability of soil moisture in warm or early-melting years (Sethi et al. 2020), by the onset of fall in cool or late-melting years, or by cascading effects of previous phenological transitions (Ettinger et al. 2018), making it more consistent across years, as is true in our study (fig. S1.7).

Phenological Shifts Are Insufficient to Maintain Reproductive Success

By advancing flowering in years with higher seasonal GDDs or earlier snowmelt, individuals can shift their phenology in the direction favored by selection (i.e., fewer GDDs accumulated at flowering), suggesting that advancing phenology could be adaptive in this system (Caruso et al. 2006; Merilä and Hendry 2014; Navarro et al. 2022). Data from wild populations cannot test causal links between the environment and phenology or distinguish between plastic and genetic responses to environmental change (Wadgymar et al. 2018). However, our results are consistent with experimental warming studies that have established effects of earlier snowmelt or warmer temperatures on advancing phenology (Wipf and Rixen 2010; Oberbauer et al. 2013; Knapp et al. 2018; Zettlemoyer et al. 2019; Collins et al. 2021; Stuble et al. 2021). Furthermore, by monitoring phenology of the same set of long-lived individuals over 6 years, the phenological shifts observed here can be attributed to plasticity rather than evolutionary change.

Despite phenology shifting in an appropriate direction, fruit production still declines under both higher seasonal GDDs and earlier snowmelt, indicating that advancing phenology is insufficient to maintain reproductive success under warming. Indeed, most individuals in our observational dataset flowered much later than the narrow optimal climate-relevant flowering time, resulting in low reproductive success (e.g., long right tail in fig. 4). This indicates that as climates warm, even substantial phenological plasticity in the appropriate direction to increase fitness may not be sufficient to maintain high fitness.

Interestingly, even when phenology is assessed relative to climatic drivers, we still observe steep declines in fruit production with warming. This suggests that reproductive declines in this system under warming cannot be solely attributed to lagging phenology but can also be attributed to changing environmental conditions. In other words, even if populations were able to shift their phenology sufficiently early to maintain consistent climate conditions during flowering (i.e., constant GDDs accumulated at flowering or constant flowering time relative to snowmelt), we would still observe decreases in reproductive success with warming. Such reproductive declines, regardless of phenology, could be driven by novel climate combinations under warming (e.g., earlier flowering under warming resulting in frost damage; Pardee et al. 2019) or mismatches with pollinators (e.g., earlier flowering resulting in low pollination success under warm conditions; Rafferty and Ives 2012). Regardless of the mechanism, this suggests that populations may struggle to maintain high fitness under climate warming by shifting their phenology to track historical climate conditions in time.

Our findings have important implications for models of population persistence under environmental change, which have largely focused on phenotypic lag—the extent to which a populations' mean phenotype fails to track a shifting optimal phenotype either via evolution or plasticity—in driving fitness declines (Chevin et al. 2010; Gienapp et al. 2013; Vedder et al. 2013; Chevin et al. 2015). By examining continuous fitness landscapes across climate conditions, we show that decreasing reproductive success in this system is due to a combination of phenological lag and decreasing maximum reproduction with warming. Few studies have considered the potential for changes in maximum fitness of fitness landscapes with environmental change. Gauzere et al. (2020) used a phenological model to simulate fitness landscapes for tree phenology along elevation gradients and found that maximum fitness at the optimum phenology, as well as the range of phenologies resulting in high fitness, decreased with elevation. Together with our study, this highlights the importance of considering variation in the overall shape of fitness landscapes for understanding population persistence under environmental change. Other studies have concluded that plastic responses in general are likely insufficient to keep pace with climate change (Etterson 2004; Savolainen et al. 2004; Kim and Donohue 2011; Anderson et al. 2012; Franks et al. 2013; Pratt and Mooney 2013; Gienapp et al. 2014; Morgan et al. 2020; but see Vedder et al. 2013; Richardson et al. 2017; Helm et al. 2019). Understanding whether phenotypic change is enough to maintain fitness under future climates requires quantifying how the relationship among phenotype, fitness, and potential drivers of selection shifts with directional climate change (Duputié et al. 2015; Gauzere et al. 2020). Additionally, phenological plasticity itself could be under selection (Scheiner and Callahan 1999; Arnold et al. 2019*b*). The individuals tracked here demonstrated significant variation in the degree of their phenological responses to both GDDs and snowmelt. Ongoing work in this system aims to quantify whether individual plasticity (i.e., individual reaction norms) covaries with fitness.

Are There Costs to Early Flowering?

Interestingly, we did not detect clear stabilizing selection on flowering time, despite the potential costs of flowering too early (e.g., mismatched photoperiods [McNamara et al. 2011; Meng et al. 2021], exposure to frost [Inouye 2008; Pardee et al. 2019; Cooper et al. 2019], drought [Gugger et al. 2015], or pollinator limitation [Elzinga et al. 2007; Renner and Zohner 2018; Kharouba and Wolkovich 2020]). We propose four potential explanations for this result. First, populations may be far from the phenotypic optimum, potentially explaining why we see nonlinear directional selection rather than stabilizing or weakly directional selection (Anderson et al. 2012; Austen et al. 2017). Second, selection on other fitness components (e.g., plant size [Kulpa and Leger 2013], survival [Fournier-Level et al. 2013], or seed viability [Wadgymar et al. 2017]) could balance or weaken directional selection on fecundity (McGlothin 2010; Ehrlén 2015). This species is extremely long lived with high adult survival rates (Morris and Doak 1998); there has not yet been sufficient adult mortality of the individuals in this study in the 6 years that we have collected phenological data to test for trade-offs between flowering time and survival. However, future work in this system could test for effects of flowering phenology on plant size and seed and seedling viability. Third, the relationship between flowering time and fitness was asymmetrical, where later flowering under warm conditions correlated with low fruit production. Such patterns can bias the net pattern of selection by imposing stronger penalties when flowering is later than the optimum (Weis et al. 2014). Indeed, we find some evidence for stabilizing selection on flowering phenology in particular plots and years (fig. S2.5; table S2.6), suggesting that we may detect a stronger signal of costs to extremely early flowering as climate change progresses. Finally, while we assess environmental covariance between flowering time and fruit production, there could also be genetic covariance between flowering time and fecundity. Quantifying genetic versus environmental covariance will require experimentally disassociating flowering time and seasonal conditions (i.e., artificial selection experiments; Galloway and Burgess 2012; Austen and Weis 2015; Bonduriansky et al. 2015; Austen et al. 2017).

Conclusions

In sessile and long-lived species, phenotypic plasticity is likely to be the most effective mechanism for adjusting to warming climates. Here, we demonstrate that phenological shifts in response to warming are in the direction favored by selection, tracking a climate-driven optimum of flowering earlier after snowmelt and with fewer accumulated GDDs. Yet these phenological shifts appear insufficient to maintain fitness, and populations are suffering declining reproductive success under climate warming. Our findings suggest that the negative fitness effects of climate change might outpace the potential benefits of phenological shifts, highlighting a need to consider the limits of phenological responses in maintaining fitness under climate change.

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Statement of Authorship

M.L.D. conceived the study, M.L.D. and M.A.Z. analyzed the data, and M.A.Z. wrote the manuscript. All authors contributed to data collection and revisions.

Data and Code Availability

Data and code for this study are available in Figshare (https://doi.org/10.6084/m9.figshare.24512944; Zettlemoyer and DeMarche 2023).

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Silene acaulis at Niwot Ridge, Colorado. Photo credit: Meredith Zettlemoyer.