Modeling demographic impacts of snowmelt variability on *Valeriana edulis* population dynamics

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ABSTRACT

Snowmelt timing is crucial for many aspects of ecosystem function; for plants it determines the onset and length of the growing season. This can mean more time for growth with an earlier germination date, but can also expose plants to spring freezes overnight and increases in drought stress. Climate change is causing snow to melt earlier, while also increasing the variability of snowmelt timing from year-to-year. To determine the impacts of this variability on specific plant populations, demographic theory suggests this is connected to the species' location on the fast-slow continuum. Populations with a faster life history are better able to adjust to variation, while those of slow life history have increased ability to buffer against its impact. Here, I investigated whether the fast-slow continuum applies to population-level variation across the elevation range of the plant species *Valeriana edulis*. I combined long-term census data, remotely-sensed snowmelt data, and demographic models to test the impact of changing snowmelt trends on longevity and population growth. Snowmelt timing impacted survival and flowering probabilities: late snowmelt was negative for survival and positive for flowering. The impact of snowmelt variability on population growth varied ideosyncratically across sites, while longevity values saw a standard increase with an increase in variability.

INTRODUCTION

The timing of snowmelt in montane ecosystems can have substantial impacts on plant survival, growth, and reproduction. Earlier germination, leaf emergence, and flowering associated with earlier snowmelt can result in longer growing periods, and bigger, stronger, plants. However, this also means more exposure to varying temperatures and climatic conditions occurring earlier in the spring (Iler *et al.* 2021). With earlier season flowering, there is a greater risk of mismatch between flowering onset and pollinator emergence due to the differing warming periods of surface and soil temperatures. Although this mismatch and increased spring frost damage in flowers reduces reproductive success, a decrease in survival rates have been found to be the primary connection to threats of population extinction due to early snowmelt. The earlier the snow melts, the longer the growing season and extended dry period becomes. This increases water stress for plant populations, as found in a study on *Helianthella quinquenervis,* a long-lived alpine sunflower species (Iler *et al.* 2019). However, delayed snowmelt, as opposed to early snowmelt, has been found to decrease plant productivity and growth by 13.1% due to a shorter growing period (Wipf & Rixen 2010).

Globally, variation in snow cover duration is increasing, with some studies predicting a 6.6% to 42.2% increase in frequency of consecutive snow drought years (Franzke *et al.* 2015; Roessler & Dietz 2023). Snowmelt timing has advanced significantly in montane environments due to warming temperatures and an increase in spring snow density. Denser snow has a lower albedo and lower insulating capacity than lighter, fluffier snow, so is able to absorb more solar energy. There has also been an increase in "dust-on-snow" events adding darker materials like dust and dirt to snow, exacerbating this decline in albedo. With more solar energy absorbed, the snow melts faster, resulting in earlier overall snowmelt. Additionally, more variability in average

daily precipitation across the seasons has been observed in alpine environments, thus leading to an increase in snowmelt variability as the amounts and types of snow vary across the snow season (Inouye *et al.* 2025).

Life history theory predicts that a species' position along the fast-slow continuum will help determine how populations respond to environmental mean and variability changes. Fast growing, shorter-lived species with high individual turnover are present at one end of the continuum, and slower-maturing, longer lived species are at the other (Salguero-Gómez et al. 2016). To maintain a stable population size and population growth rate from one year to the next, "fast" species depend on the production of new individuals whereas "slow" species depend on the persistence of established individuals. When faced with environmental fluctuations such as a change in snowmelt date, the high individual turnover makes "fast" species populations very sensitive to year-to-year variation, but allows for rapid recovery after a period of adverse conditions. Alternatively, the populations of "slow" life history species have high resistance to environmental changes, but low resilience (Laiolo & Obeso 2017). The Demographic Buffering Hypothesis further argues that selection should favor the evolution of strategies that reduce variation in the life cycle process rates that most strongly influence the population growth rate. In species with "fast" life history strategies these sensitive traits are fecundity and juvenile survival, as compared to adult survival rates in "slow" life history species' (Hilde *et al.* 2020).

Longevity, as a demographic measure of how long an individual can live, varies across the fast-slow continuum and across populations of the same species themselves. Population stability increases with increased longevity, and since populations with lower temporal stability are more likely to experience low abundance and eventual extinction, longevity is a key demographic measure for understanding the risk of species extinction. Longevity is higher in individuals who follow "slow" life history strategies (Roeder *et al.* 2021). Higher elevations with cooler temperatures and greater snow also see plants with increasingly greater longevity, highlighting a potential variable contributing to the stability of these populations (Von Arx *et al.* 2006).

There is no present stochastic analysis of snow cover duration variability's impact on the longevity and population growth, and therefore stability of these populations. Environmental variations that increase vital rate fluctuation have been found to decrease stochastic population growth rate (Hilde *et al.* 2020). We expect to see lower longevity and population growth in populations that experience higher snowmelt variation. By using a stochastic model rather than a mean climate metric, we can accurately predict climate variability using a continuous climate data series with the goals of predicting future population dynamics and reducing model bias (Franzke *et al.* 2015; Williams *et al.* 2025).

Here I used long-term demographic data across the elevation range of a medium-to-long-lived montane plant species to test for the impact of changing snowmelt timing on plant longevity. I combined data from a long-term demographic census with remotely-sensed snowmelt dates. I parameterized a demographic model that matches the responses of

individual-level performance across the life cycle to change in snowmelt, to population-level ramifications. This study sought to answer the following questions:

1. How does snowmelt timing impact individual demographic rates across the life cycle?
2. How does year to year variability in snowmelt timing impact the population growth rate?
3. How does year to year variability in snowmelt timing impact population longevity?

METHODS

Study Organism

Valeriana edulis is a medium-to-long-lived perennial herb native to western North America. This species has a broad elevation range in western Colorado where populations are found from 2000m above sea level in dry shrublands and woodlands up to the subalpine-alpine ecotone at nearly 3800m. As elevation increases across this range, there is a delay in snowmelt, resulting in a decreased growing season length.

Valeriana edulis recruits live for up to a decade before reaching reproductive maturity. As these individuals grow larger, they increase frequency of and effort towards reproduction. This species is dioecious, meaning that it has male and female individuals. The frequency of males to females has been found to decrease with elevation (Petry *et al.* 2016; Soule 1981).

Demographic Census

Since 2013, we have conducted an annual demographic census of ca. 250 tagged individual plants at each of 7 populations across the elevation range of *V. edulis*. In 2021, the census was expanded to an additional 16 populations with ca. 50 tagged individuals each. These populations extend across much of Gunnison County and into northern Saguache County, Colorado (Fig 1). Each year in each population, we assess persistence variables: survival (Yes/No) and growth (perimeter of the basal rosette), and reproduction variables: sex (male/female), flowering (Yes/No), and seed count (number of seeds). We measure the probability of germination and germinant size from a seed plot consisting of 250 seeds sown into a 50x50 cm plot at each population.

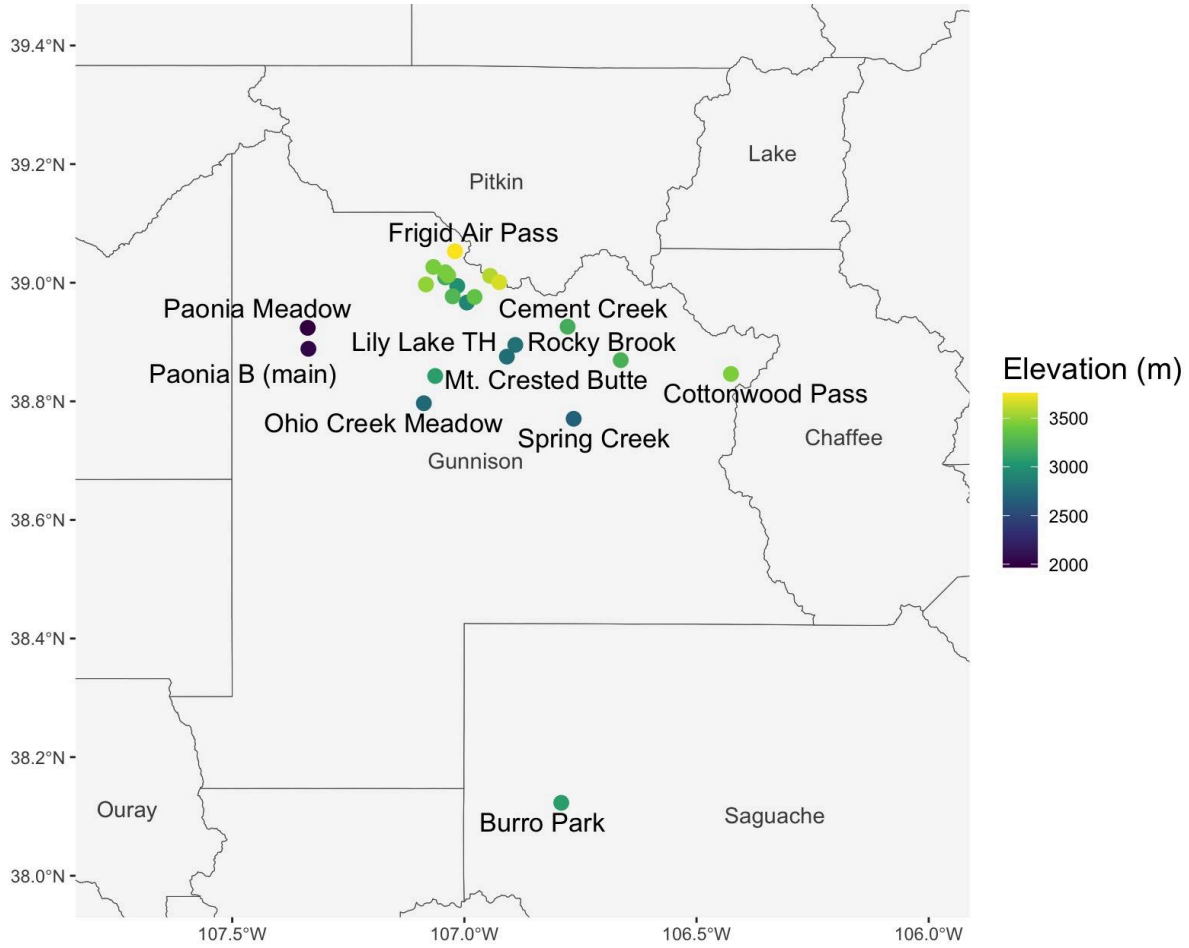

Figure 1. Map of the *Valeriana edulis* study sites, color coded by elevation. Dark colors are lower elevation sites, and lighter colors are higher elevation sites. Most sites are present inside the Gunnison county polygon. The cluster of sites unnamed are up the East River Valley from Gothic, Colorado.

Snowmelt Data

Data for the day of snowmelt across the study area was taken from the RMBL spatial data platform, utilizing the "Spring Snowpack Persistence Annual Time Series for the Upper Gunnison Domain Derived from Landsat Data, version 2" dataset (RMBL Spatial Data Platform n.d.). This dataset provides annual assessments of the first day of bare ground from 1985 to 2024, by combining monthly ground snow cover fraction maps from the USGS Landsat Collection 2 Level 3 fSCA Statistics (https://doi.org/10.5066/F7VQ31ZQ) with a time-series analysis of a spectral snow index (NDSI).

In addition, two HOBO loggers were deployed to each study site with tagged plants to measure temperature and light data. These provide an indication for the type of temperatures plants are experiencing, and since the under the snow temperature over the winter is held at a constant 0°C, temperature fluctuations indicate snowmelt date. This snowmelt data was used to supplement the spatial data set, and fill in data for populations outside of its coverage area. We

filled gaps in these logger records due to logger failure and prior to census start using MODIS (Hall & Riggs 2021).

Demographic Vital Rate Modeling

I estimated the impact of snowmelt timing on individual growth rates across the life cycle using Generalized Linear Mixed Models and the "lme4" package in R (version 2.0.6; Douglas Bates *et al.* 2015). I built these models using plant size (rosette perimeter) as the independent variable and the vital rates (survival, growth, and reproduction: flowering probability and seed count) as the dependent variables. The current year's snowmelt informed the survival and growth models, while flowering and seed count used data from the previous year's snowmelt. This analysis used a binomial GLMM to evaluate survival probability, Gaussian for growth rate, binomial for flowering probability, and negative binomial for seed count. I included varying group-level intercepts and size slopes for each population (i.e., "random effects") to account for other sources of population-level vital rate differences beyond snowmelt date. Candidate models estimated regression model coefficients under different circumstances of snowmelt timing's impact for each vital rate. I chose the best fit model for each using AIC values, and a tie breaker using analysis of previous data and literature for flowering probability.

Characterizing Snowmelt Using ARIMA Time Series Modeling

I fit an ARIMA time series model to the observed sequence of snowmelt dates at each population to estimate the mean, variance, and temporal autocorrelation of climatic variation using the R package "fable" (version 0.5.0; M O'Hara-Wild *et al.* 2026). The autocorrelation function (ACF) and the partial autocorrelation function (PACF) for each site informed the chosen orders of p, d, and q for the ARIMA models. I took the most common "best" values for both p and q across the sites, and applied one degree of differencing (d) to convert the snowmelt date data to stationary data. This resulted in an ARIMA model with order (2, 1, 1). Using the parameters of the fitted ARIMA model for each population, I then simulated a time series of snowmelt dates using the generate() function from "fable". For each population, I simulated a snowmelt sequence for which I manipulated the standard deviation while leaving the mean, autoregressive, and moving average coefficients at the values estimated from the empirical snowmelt data. Specifically, I simulated sequences with standard deviation values at 0%, 50%, 150%, and 200% of the fitted empirical variation in order to incorporate analyses for changes in snowmelt date variation. I used this collection of snowmelt timing sequences to drive the environmental stochasticity of a demographic model.

Stochastic Snowmelt-driven Model of the Life Cycle

I constructed a demographic model that describes the rates at which individual plants within a population move through the life cycle, from seedlings to mature adults, and how their lives are affected by snowmelt timing. The size-specific vital rates were combined and added to a climactically driven Integral Projection Model. The kernel is defined as:

$$n(z')_{t+1} = \int_{L}^{U} [s(z, M_{t1}) g(z', z, M_{t1}) + f(z, M_t) b(z, M_t) p_e(M_t) d(z')]\, n(z)_t\, dz,$$

where $n(z)_t$ is the number of individuals of size z at time t under current environmental snowmelt conditions M_{t1} and the year before M_t. The first term describes the persistence of previously established individuals with established size and environmental conditions and is made up of survival probability, $s(z, M)$, and growth, $g(z', z, M)$, that redistributes surviving individuals across the size distribution. The second term describes the production of new recruits by established individuals: probability of flowering, $f(z, M)$, number of seeds produced, $b(z, M)$, probability of recruit establishment, $p_e(M)$, and the recruit distribution, $d(z')$.

I constructed the model using the R package "ipmr" (version 0.0.7; (Sam C. Levin *et al.* 2021). I parameterized the model using the estimated regression coefficients from our vital rate models, then calculated the transition kernel for a typical population across the full range of observed snow melt dates. For computer analysis this was discretized into a large transformation matrix by the midpoint rule and 200 bins to be used in simulating for demographic metric conclusions (Ellner *et al.* 2016).

Simulating Snowmelt Variation Impacts on Longevity and Population Growth

Starting with a cohort of individuals at typical seedling size, I ran the IPM simulation for each site at each variation level, extracting each year's snowmelt date condition from the generated ARIMA time series. I calculated the equilibrium per-capita population growth rate (λ) as the dominant eigenvalue of the discretized IPM kernel using the lambda() function in "ipmr." Then, I isolated the persistence subkernels, and used them to simulate a cohort of individuals under a stochastic sequence of snowmelt times. I checked the total number of individuals alive at each time step. I continued this process until less than 1% of individuals were still alive or until I had hit the maximum length of the simulation (number of IPM iterations). The longevity of the population was considered to be the number of time steps taken before reaching the 1% remaining threshold. This was done for each combination of population and snowmelt standard deviation.

Then I plotted population growth and longevity values against the percent of variation, separated by site, and fit a linear model to each plot to see the relationship present.

RESULTS

Stochasticity of Snowmelt Date

This study's ARIMA model order, (2, 1, 1) represents an autocorrelation value (ACF) of 2, and a moving average (PACF) of 1. This model used 2 previous time steps to generate snowmelt timing conditions in the current timestep, and used the lagged forecast error of the previous time step to help correct current timestep values. This model calculated the standard deviation of empirical snowmelt time series data for each site (Table 1). Populations differ in the amount of variability (standard deviation value), and are largely independent of their elevations

(Fig 2). The highest variation (standard deviation of time series data) was 0.21664149 at Burro Park (3082), and the lowest was 0.06272380 at Lily Lake (3075m).

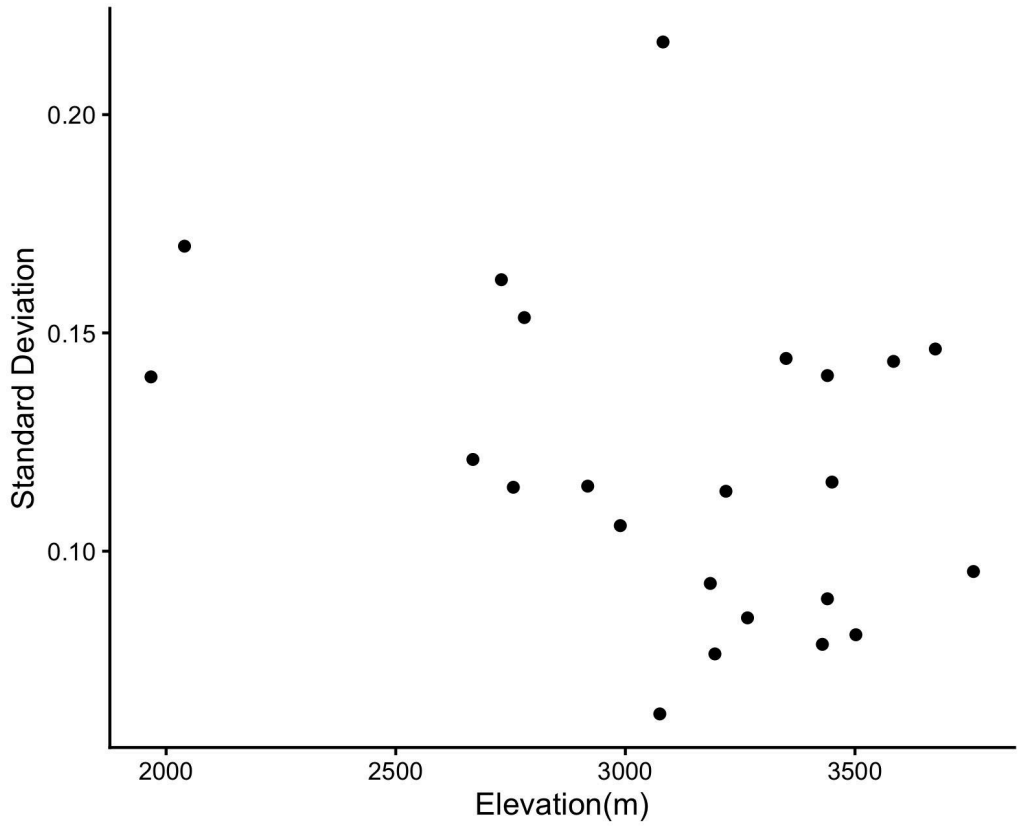

Figure 2. Elevation (m) plotted against the standard deviation of each site's empirical snowmelt time series data, showing that empirical variation is independent of elevation, and varies across sites.

Effects of Snowmelt Timing on Demographic Vital Rates

The timing of snowmelt impacted only the survival and flowering functions. For survival, the best fit model included snowmelt date as a covariate, but not the interaction between snowmelt date and log(size). Early snowmelt increased the probability of survival, and the impact was equal (on the log-odds scale) across the life cycle (Fig. 3). Similarly, snowmelt timing altered the probability of flowering, but here late snowmelt was associated with an increase in the likelihood of attempting to reproduce. Like the survival function, the impact of snowmelt timing on the log-odds for flowering was independent of size (Fig. 4).

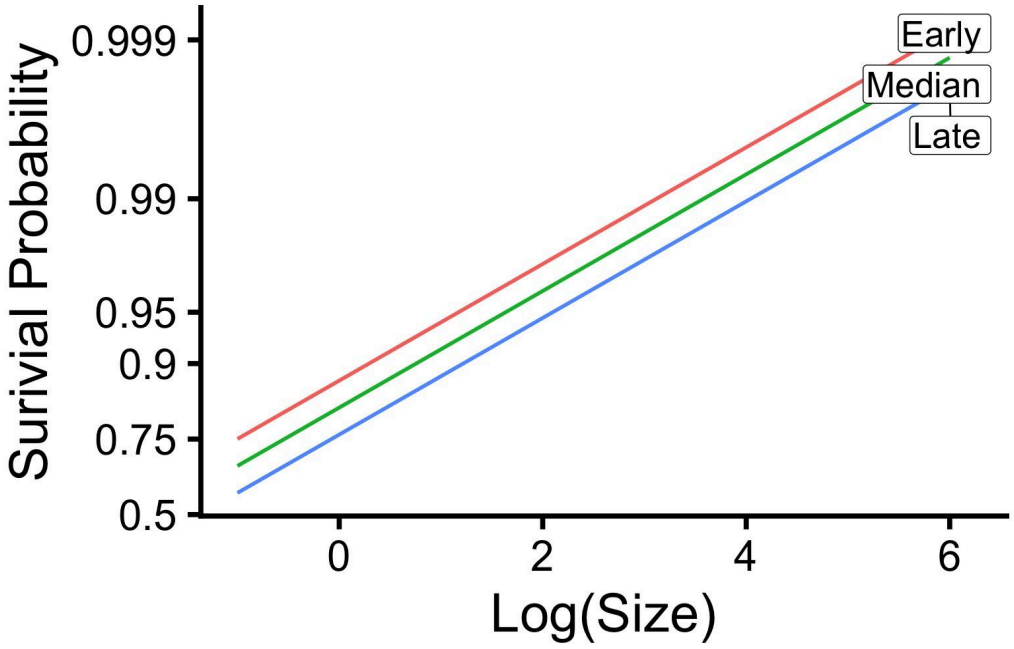

Figure 3. Early snowmelt increases the survival probability of *Valeriana edulis* across the size distribution. The three lines show a logistic generalized linear mixed model fits for the average population under early (red), median (green), and late (blue) snowmelt dates.The state variable (plant size, x-axis) has been log-transformed. The survival probability (y-axis) is shown on the log-odds scale. The parallel slopes of the fitted regression lines indicate that the effect of snowmelt date on survival is equivalent across the life cycle.

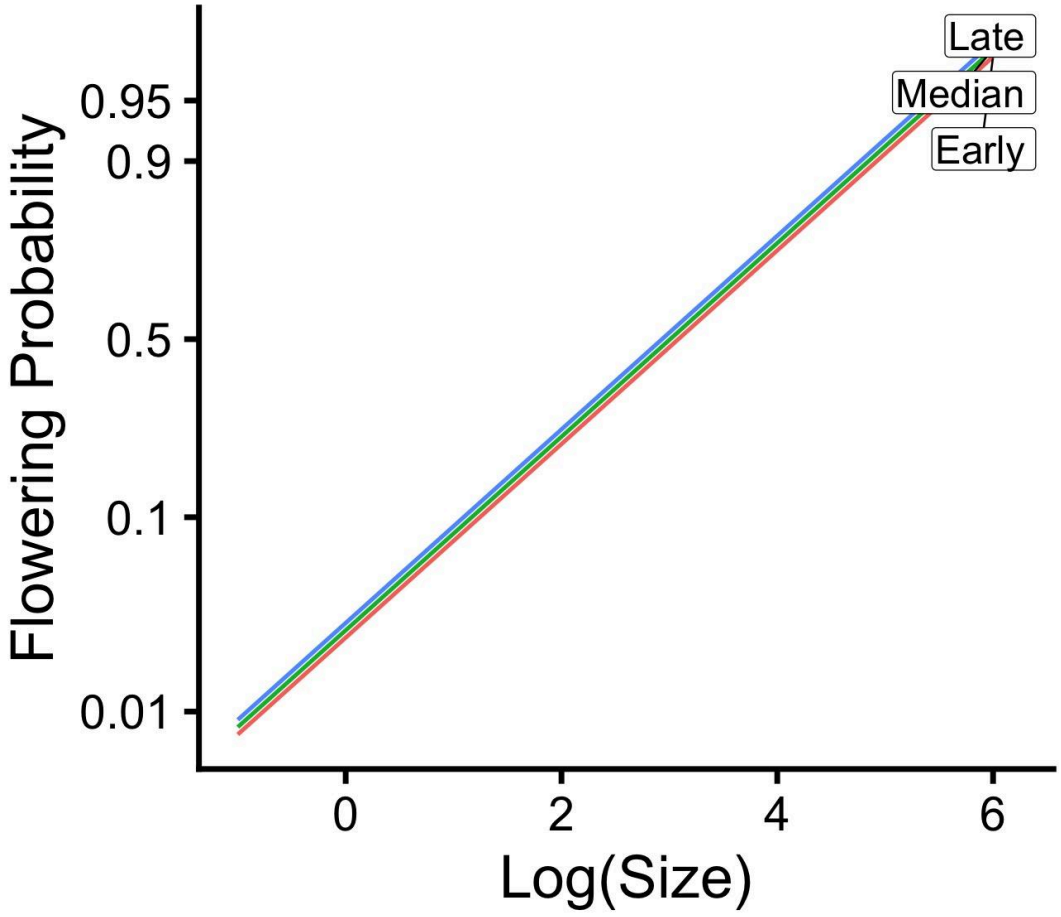

Figure 4. Later snowmelt increases the flowering probability of *Valeriana edulis* across the size distribution. The three lines show a logistic generalized linear mixed model fit for the average population under early (red), median (green), and late (blue) snowmelt dates. The state variable (plant size, x-axis) has been log-transformed. The flowering probability (y-axis) is shown on the log-odds scale. The parallel slopes of the fitted regression lines indicate that the effect of snowmelt date on flowering is equivalent across the life cycle.

Snowmelt timing affected neither growth or seed count, as the best fit model included neither snowmelt date as a covariate or the interaction between snowmelt date and log(size). The figures and general conclusions concern the mean population, as each vital rate incorporates site specific variation. Table S1 shows the regression equation components for each vital rate. As a result of the regression, site specific intercepts and coefficients are returned for each vital rate. The survival intercept and slope values vary the most out of all the vital rates. Emerald Lake and Frigid Air have the lowest intercepts, representing much lower survival rates for small plants than at sites with higher intercept values such as Lily Lake and Spring Creek. Sites like Paonia and Judd Falls have much lower slope values (how fast the survival probability changes across life stages) than the rest of the sites (Table S2). The other vital rates see similar variation across

sites, with some similar patterns: Frigid Air consistently has one of the lowest intercept values across the vital rates (Table S3, Table S4, Table S5).

Effects of Snowmelt timing's variation on population growth and longevity

Variation in snowmelt timing had an impact on population growth, although the sign of the impact varied by site with no apparent pattern. For most populations, an increase in the variation of snowmelt timing either consistently increased or decreased λ (Fig. 5). There was no elevational trend in the sign or magnitude of the sensitivity of λ to variation in snowmelt timing. Moreover, some pairs of adjacent populations showed similar sensitivities (e.g., Bel1 and Bel2), whereas others did not (e.g., Pao and PaoMead).

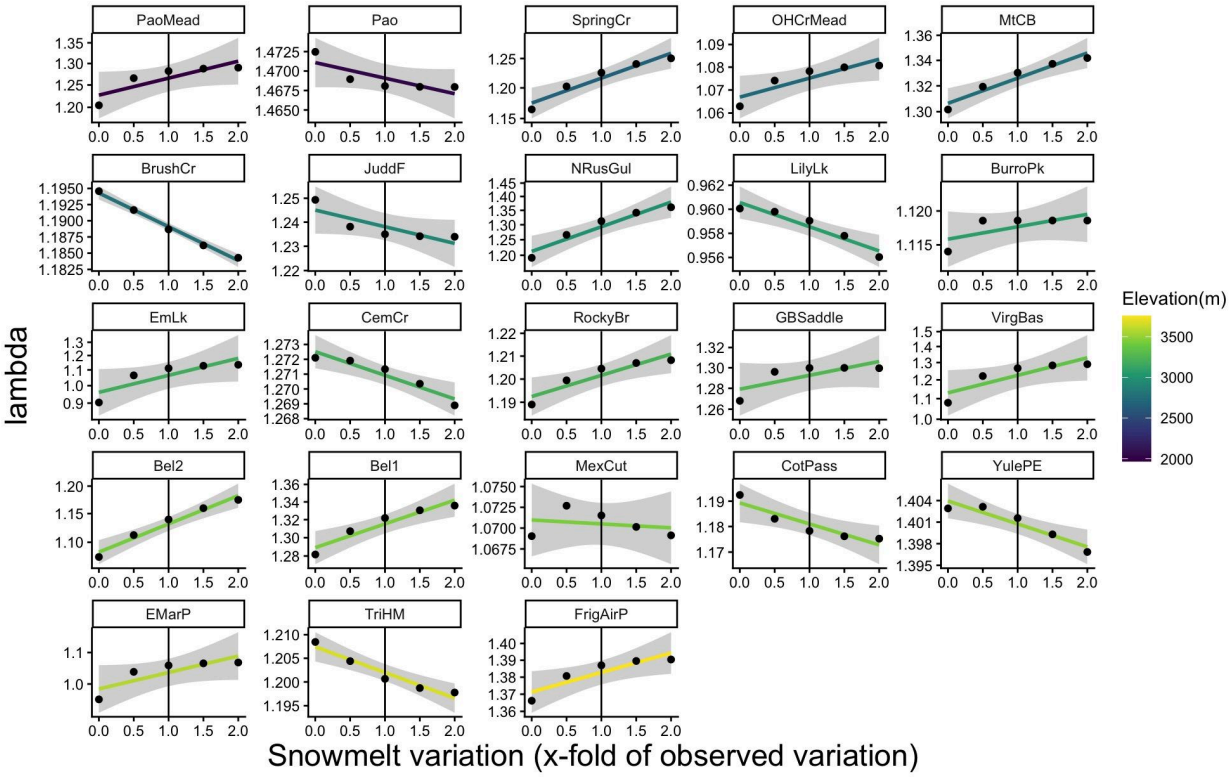

Figure 5. The asymptomatic population growth rate (λ) was sensitive to changes in the standard deviation in snowmelt timing, but varied ideosyncratically in sign and magnitude between populations of *Valeriana edulis*. The x-axis represents the x-fold of observed standard deviation with empirical variation represented by the value 1. The y-axis, lambda, is the asymptomatic population growth rate, with each site on a different scale due to their individual values. Panels are arranged by elevation, with lowest elevation sites represented by darker colors starting at the top left of the graph, working to higher elevations with lighter coloring in the bottom right.

Variation in snowmelt timing had a positive impact on longevity. As variation increased, longevity increased, with the exception of a couple sites (Lily Lake and Cement Creek). Three sites were removed due to their inability to hit the critical value for longevity conclusions using 5000 IPM iterations: Judd Falls, Cottonwood Pass, and Triangle High Meadow.

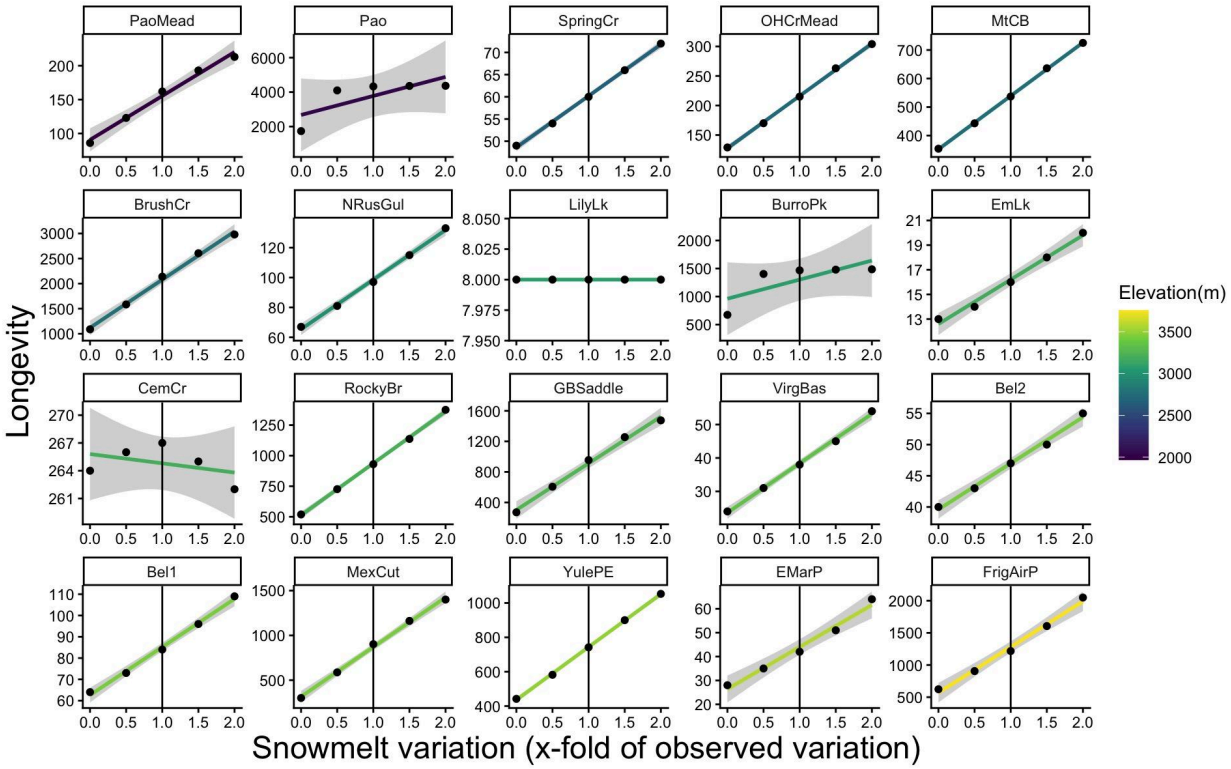

Figure 6. Values of longevity with changes in snowmelt timing variation levels. The x-axis represents the x-fold of observed variation with empirical variation represented by the value 1. The y-axis, longevity, is the expected life span of an individual, with each site on a different scale due to their individual values. Sites are sorted by elevation, with lowest elevation sites represented by darker colors starting at the top left of the graph, working to higher elevations with lighter coloring in the bottom right.

Table 1. The empirical variation in snowmelt time series data (standard deviation), elevation (m), equilibrium per-capita population growth rate (λ), and longevity (years) values for each site across the elevational gradient.

Site	Variation (SD)	Elevation(m)	Population Growth	Longevity
PaoMead	0.13992855	1967	1.2821015	162
Pao	0.16986783	2040	1.4680724	4329
SpringCr	0.12101151	2668	1.2256619	60
OHCrMead	0.16218580	2730	1.0782146	215
MtCB	0.11464087	2756	1.3302577	537
BrushCr	0.15351068	2780	1.1886588	2139
JuddF	0.11489892	2918	1.2349876	NA
NRusGul	0.10585393	2989	1.3123826	97
LilyLk	0.06272380	3075	0.9590456	8
BurroPk	0.21664149	3082	1.1185891	1467
EmLk	0.09261579	3185	1.1108731	16
CemCr	0.07646682	3195	1.2713371	267
RockyBr	0.11372841	3219	1.2045202	930
GBSaddle	0.08472951	3266	1.2997787	955
VirgBas	0.14414836	3350	1.2662219	38
Bel2	0.07865954	3429	1.1395519	47
Bel1	0.08909510	3440	1.3218319	84
MexCut	0.14022828	3440	1.0715210	902
CotPass	0.11583067	3450	1.1782874	NA
YulePE	0.08085901	3502	1.4015608	742
EMarP	0.14347554	3584	1.0578306	42
TriHM	0.14631434	3675	1.2006456	NA
FrigAirP	0.09534313	3758	1.3870011	1217

DISCUSSION

Snowmelt timing impacts multiple vital rates with opposing signs. Early snowmelt timing had a positive effect on survival among *V. edulis* populations. An earlier day of melt leads to a longer growing season due to earlier plant emergence, while simultaneously increasing the length of the summer drought period. It was expected that this would lead to negative impacts on survival (Campbell 2019; Oldfather & Ackerly 2019), but the chosen vital rate model instead predicted higher probabilities of survival under earlier snowmelt conditions consistently across all life stages. Based on life history theory and the Demographic Buffering Hypothesis, the population growth of a long-lived species like *V. edulis* would demonstrate the most sensitivity to changes in adult survival. Thus the population should buffer this demographic component (Hilde *et al.* 2020). This indicates that survival rates for "mature" larger individuals should be higher than other size classes, which was not supported by the survival model. Other studies suggest that survival rates are dependent on the year before's snow melt conditions, different from this study's model which was based on the current year's snowmelt (Campbell 2019). This could lead to the discrepancy in snowmelt timing's impact on survival observed between this study and previous literature. Contrarily, early snowmelt had a negative impact on flowering. Previous literature states that early snowmelt causes early plant and flower emergence. Not only does this increase risk for frost events and reproductive damage, but also reduces flowering volume (Campbell 2019; Pardee *et al.* 2019). Thus, it was expected that later snowmelt would increase the probability of flowering, as supported in the results of this study.

The best fit vital rate models for growth and seed count indicated no snowmelt timing impact. Frost events have been observed to generate suboptimal temperatures for growth and provide similar damage to growth rates as flowering probabilities (Iler *et al.* 2021; Wipf & Rixen 2010). Thus, years of early snowmelt can be harmful for plant growth rates. Other studies argue that nighttime warming can mitigate frost damage and neutralize snow melt's impact on growth (Frei & Henry 2022; Sherwood *et al.* 2017). This might provide an explanation for this study's result of no impact on growth from snowmelt timing. Similarly, frost damage also causes declines in seed production with reduced flower success (Campbell 2019; Iler *et al.* 2021). However, early plant and flowering emergence leads to frost damage that can drive increased seed production (Nordstrom *et al.* 2026). Perhaps seed count experiences a similar neutral impact as growth, with mechanisms that both increase and decrease seed production for a net indifferent impact from snowmelt timing.

Incorporating increases and decreases in empirical variation at each site, population growth had a variable impact per site, while longevity saw a standard growth with increase in variability. Environmental fluctuations that lead to increased vital rate variance usually decrease the stochastic population growth rate due to the higher likelihood of singular or accumulative "bad" years (Hilde *et al.* 2020; Pardee *et al.* 2019; Morris *et al.* 2008). Conversely, a manipulative precipitation experiment found decreased precipitation predictability led to earlier flowering and higher reproductive success, resulting in higher population growth (March-Salas *et*

al. 2019). The mix of population growth responses, and the positive longevity trend indicate a potential distribution of sensitivities to individual vital rates and site environmental differences (Iler *et al.* 2021). Life history theory, and parts of the literature argue that long-lived species are most sensitive to growth and survival rates (Iler *et al.* 2019, 2021; Oldfather & Ackerly 2019). Other studies found that seed production and flowering carry the biggest influence on population growth outcomes (Campbell 2019; Nordstrom *et al.* 2026). Although snowmelt might have impacts across the vital rates, snowmelt timing conditions cannot necessarily capture the entire complexity of the environmental conditions of each plant population. Soil moisture and air temperatures are additional indicators for population demographic responses (Gehrmann *et al.* 2017). Additionally, plants are able to adjust allocation of resources to survival, growth, and reproduction continuously as environmental conditions change (Iler *et al.* 2026; Salguero-Gómez *et al.* 2016). The sites in this study contain various soil types across a range of elevational and temperature conditions. This could indicate mixed reactions to changing variabilities in snow melt, as populations could have different sensitivities to vital rates and environmental conditions beside snowmelt timing, as well as different allocation reactions. Additionally, low sensitivities to demographic variability often indicate higher longevity values (Morris *et al.* 2008).

In this study, I made several important modeling assumptions that have ramifications for the perception of the results, as well as opportunities for future model extensions. *Valeriana edulis* is dioecious, with a higher frequency of females at higher elevations than males. This indicates a difference in resource use and endurance of environmental conditions (Petry *et al.* 2016). This analysis combined all plants in one model, which could dampen the individual impacts on population dynamics between the two sexes. Future analysis could divide individuals into two separate groups and complete analyses to investigate snowmelt variation's impact on the sexes separately. To examine the resulting dynamics of population growth and longevity, one could perform a sensitivity analysis to find which vital rates are most influential on the resulting demographic metric values. This could indicate underlying causes for increases or decreases in population growth and longevity with variation, while examining potential tradeoff relationships. Years that are highly beneficial for one vital rate can be detrimental to another, and depending on the sensitivity to each vital rate, can be highly or rarely influential on population dynamics (Compagnoni *et al.* 2016). In the longevity analysis, some of the values seem unrealistically large, reaching values upwards of 2000 years. This could potentially be caused by the data's inability to capture the full complexity of vital rate patterns over time in the long lived species *V. edulis*. This could indicate an unrealistically high survival rate in larger, older individuals and lead to an overestimate in life span.

Snowmelt timing impacts the survival and flowering probabilities of *V. edulis* populations in opposing ways, and leads to variable population growth values with increases in variation, and increasing longevity values.

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SUPPLEMENTAL INFORMATION

Table S1. The intercept, log(size) slope, and snowmelt coefficient of the regression for each vital rate.

Vital Rate	**Intercept**	**log(size) slope**	**Snowmelt coefficient**
Survival	3.28950	0.84850	-0.01271
Growth	0.4765	0.8394	NA
Flowering	-4.033841	1.194536	0.003172
Seed Production	4.1645	0.5072	NA

Table S2. The intercept and log(size) site specific coefficients for the **survival** regression.

Site	**Intercept**	**log(size)**
Bel1	1.995652	0.8007803
Bel2	3.681872	0.8608358
Brush Cr	2.023619	0.7402649
BurroPk	3.708793	0.8258509
CemCr	2.544498	1.1158438
CotPass	4.172315	1.0158311
EMarP	5.179344	1.0046435
EmLk	1.236410	1.1056530
FrigAirP	1.237667	1.0210132
GBSaddle	3.233962	0.9193745
JuddF	2.124469	0.2939535
LilyLk	4.005995	0.6641996
MexCut	3.314062	1.1077570
MtCB	3.692348	0.7392453
NRusGul	1.201603	0.8777668
OHCrMead	2.404315	0.7504115
Pao	3.639418	0.3769567
PaoMead	4.185594	1.1930318
RockyBr	5.377102	0.8645862
SpringCr	4.912246	0.7270306
TriHM	2.430480	0.6193199
VirgBas	4.887995	0.8978393
YulePE	3.565718	0.9379180

Table S3. The intercept and log(size) site specific coefficients for the **growth** regression.

Site	**Intercept**	**log(size)**
Bel1	0.5447377	0.8324294
Bel2	0.5210283	0.8726504
Brush Cr	0.4819078	0.8264012
BurroPk	0.1813071	0.8733977
CemCr	0.5206406	0.8490856
CotPass	0.8750089	0.6875998
EMarP	0.3381233	0.9026507
EmLk	0.5331250	0.8591733
FrigAirP	0.3063221	0.9028347
GBSaddle	0.3129332	0.9053385
JuddF	0.3867014	0.8706596
LilyLk	0.4682886	0.8563992
MexCut	0.5613584	0.8286093
MtCB	0.5046072	0.8571622
NRusGul	0.5239522	0.8461935
OHCrMead	0.3537944	0.8982776
Pao	0.3715790	0.8771547
PaoMead	0.4541519	0.7543891
RockyBr	0.5162507	0.8050871
SpringCr	0.3978620	0.8514144
TriHM	0.8140467	0.6242709
VirgBas	0.4288313	0.8650371
YulePE	0.5633633	0.8606228

Table S4. The intercept and log(size) site specific coefficients for the **flowering** regression.

Site	**Intercept**	**log(size)**
Bel1	-3.715168	1.1154390
Bel2	-3.869959	1.3161373
Brush Cr	-3.698294	1.2031174
BurroPk	-3.391163	1.1621315
CemCr	-3.760214	1.2405361
CotPass	-4.126377	1.0547833
EMarP	-3.678369	1.0419357
EmLk	-3.873682	1.3190317
FrigAirP	-4.004156	1.2744605
GBSaddle	-4.815168	1.0444904
JuddF	-4.369230	1.2007967
LilyLk	-3.844095	1.1956809
MexCut	-3.851115	1.1714592
MtCB	-3.306883	1.2056126
NRusGul	-3.673882	1.1905292
OHCrMead	-3.849428	1.2449738
Pao	-4.533295	1.3589787
PaoMead	-4.924786	1.1372977
RockyBr	-4.218078	1.2649871
SpringCr	-4.139365	1.3366036
TriHM	-4.752753	0.9771482
VirgBas	-3.722879	1.2211759
YulePE	-4.552799	1.1673651

Table S5. The intercept and log(size) site specific coefficients for the **seed count** regression.

Site	**Intercept**	**log(size)**
Bel1	4.952098	0.3124223
Bel2	4.727425	0.5200142
Brush Cr	4.081625	0.6877603
BurroPk	3.592392	0.4113047
CemCr	4.286216	0.5657289
CotPass	3.679468	0.4329605
EMarP	4.224071	0.4417307
EmLk	4.666793	0.6133264
FrigAirP	3.709658	0.6859468
GBSaddle	4.021420	0.3750089
JuddF	3.606646	0.6705497
LilyLk	4.090196	0.5302644
MexCut	3.849836	0.3563924
MtCB	3.916846	0.4678503
NRusGul	4.430184	0.5806935
OHCrMead	4.059818	0.5257632
Pao	5.055496	0.5477389
PaoMead	3.912850	0.4538181
RockyBr	3.784360	0.4132159
SpringCr	4.770557	0.6491451
TriHM	4.062179	0.4830666
VirgBas	3.915724	0.3159836
YulePE	4.389613	0.6257945