

The role of soil in regulating plant performance in *Valeriana edulis*

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ABSTRACT

Climate change is currently shifting the ranges of plant species, and while climate-based variables trigger migration, sessile plants may reach an expansion limit due to variations in the characteristics of local soils. To better understand the effects of soil on plant performance, we paired 13 years of demographic data on *Valeriana edulis* with gridded and field-collected soil data, then built vital rate models with these soil covariates to determine their impact on plants across the life cycle. We found that average grain size was highly influential on the survival, flowering, and seed production rates of *Valeriana edulis*. Water holding capacity and pH had moderate effects on flowering, and nitrogen had no meaningful impact. By analyzing how individual soil characteristics the performance of *Valeriana edulis* across its life cycle, we can make informed predictions about the eventual fate of the species under new environmental regimes.

1 | INTRODUCTION

As the effects of climate change become increasingly extreme, shifts in abiotic factors such as rainfall amounts or average temperatures will determine plant performance. Abiotic changes shift the climate envelope, and in some cases, push plants out of their native habitats faster than they can adapt (Cang et al., 2016; Walther et al., 2002). Even for species that are adapting, the landscape they traverse is not uniform, as soil properties—another major abiotic driver of plant performance—vary over space but do not move in concert with shifting climate envelopes. If this disparity between climate and soil is too extreme, species' ranges may not merely shift but instead narrow as plants reach inhospitable boundaries. Depending on the severity of this mismatch, we may have a shorter amount of time to slow the effects of climate change and ensure that wild and native plants don't go extinct.

The life cycles of sessile plants comprise many distinct stages, each of which must be able to withstand a variety of abiotic stresses to produce the next generation of recruits. Furthermore, while a set of climate and soil variables might be beneficial for one stage, it could

be negligible or even detrimental to another. For example, while a mature plant may benefit from high rainfall during the growing season due to the water demand of seed production, small seedlings could be more susceptible to fungal infection or even be uprooted by heavy rainfall. These abiotic stresses affect an individual plant's vital rates, and an individual factor can have varied impacts across different components of the life cycle, influencing everything from survival and fecundity to size and flowering probability. We aggregate each of these responses in the context of the full lifecycle in order to meaningfully understand the net impact of each factor and ultimately understand the broader consequences for population dynamics and fate.

The importance of soil has been extensively studied in relation to agricultural cash crops, but this knowledge is not directly transferable to the more complex soil environments and broader ecological ranges found in nature (He et al., 2013). Soil has a profound impact on organism performance, but has largely been ignored in favor of the more dramatic effects of climate variables (Ford & Hille Ris Lambers, 2020; Zeh, 2021). A study on Mt. Rainier sought to fill this knowledge gap, and discovered that meadow soils alleviated water stress due to their higher water-holding capacity over more barren regions (Ford & Hille Ris Lambers, 2020). While the study was limited to “meadow” and “bare” soils, it hypothesized that plants in the meadow could grow larger because of the higher levels of nitrogen in the meadow system (Ford & Hille Ris Lambers, 2020). These differences can be attributed to the parent material from which the soil originated, as metasedimentary, sedimentary, and mixed soils often have a higher mineralized nitrogen content than soils from plutonic and volcanic origins (Moore et al., 2022). Parent rock material also strongly determines the baseline pH, as the calcium carbonate in limestone produces alkaline soils, while granite and sandstone are more acidic (Yaulilahua-Huacho et al., 2024). When observed comprehensively, it is clear that climate and soil are not isolated variables but instead work in conjunction to alter the life history and vital rates of every single plant species.

In this study, we used *Valeriana edulis*—a montane plant native to the meadows of the North American Rocky Mountains—as a model species to investigate the dual effects of climate and soil on species demography. *Valeriana* was an ideal species for this study due to its long lifespan and extensive historical data that allowed us to simulate its population dynamics under a wide range of climate and soil conditions throughout its life cycle (Pettry et al., 2016; Soule, 1981). Previous models revealed that climate has a significant effect on *Valeriana*, as individual

growth rate and survival increase with later snowmelt and higher mean temperatures (Zeh, 2021). Flowering probability and seed production decreased with higher temperatures and increased precipitation, respectively, while the germination rate responded negatively to both (Zeh, 2021). While the effects of climate on plant demography are extensively documented, most studies simply recognize the potential effects of soil data and stop short of doing a focused geological analysis (Jerome et al., 2021). Ultimately, we expanded on the existing and extensive research done on climate data by incorporating a novel soil analysis to build a comprehensive understanding of population dynamics. To accomplish this, we attempted to answer one main question: how is the performance of *Valeriana edulis* across its life cycle affected by variations in water holding capacity, average grain size, availability of nitrogen, and the pH of the soil?

Our reasoning behind this research question was as follows; we expected that small-grained soils such as clay would have a higher water-holding capacity than coarser soils due to their smaller surface area and greater ability to attract water (Nelson et al., 2024; Yang et al., 2023; Y. Zhang et al., 2021). We predicted that increased water availability associated with finer soils would lead to enhanced flowering, seed production, germination, and survival, particularly during periods of drought. Fine-grained sedimentary-based soils would also retain more nutrients, such as nitrogen, further benefiting overall survival and reproductive-based vital rates (Chen et al., 2025; Moore et al., 2022). We were unsure how exactly *Valeriana edulis* would respond to variations in pH, as little research had been conducted on the subject; however, we expected that the ability for parent material to influence pH over a broad geographic range would promote a specific geological preference (Yaulilahua-Huacho et al., 2024).

2 | METHODS

2.1 | Study species

Valeriana edulis (Caprifoliaceae) is a perennial, dioecious herb with a fixed sex expression (Petry et al., 2016; Soule, 1981). *Valeriana edulis* is native to the Rocky Mountains of Colorado and grows from low-elevation, arid scrublands to alpine tundras (ca. 2000-3790 m) (Petry et al., 2016). There are 13 years of demographic records on *Valeriana*, which is useful for modeling life history, as the plant can reach >200 years old (W. Petry, pers. comm.).

2.2 | Study sites

We collected demographic data for *Valeriana edulis* from 6 “core” populations within Gunnison County, Colorado: Belleview I, Brush Creek Range, Emerald Lake, Judd Falls Trailhead, North Rustlers Gulch, and Paonia B. We also censused 7 “satellite” populations. These sites were located throughout Gunnison and northern Saguache Counties, Colorado, and range in elevation from 2,040 to 3,440 meters above sea level (Figure 1). Soil parent material varied between populations, but the main lithologies included the Mesa Verde formation, Mancos shale, San Juan volcanics, Maroon formation, and the Dakota formation.

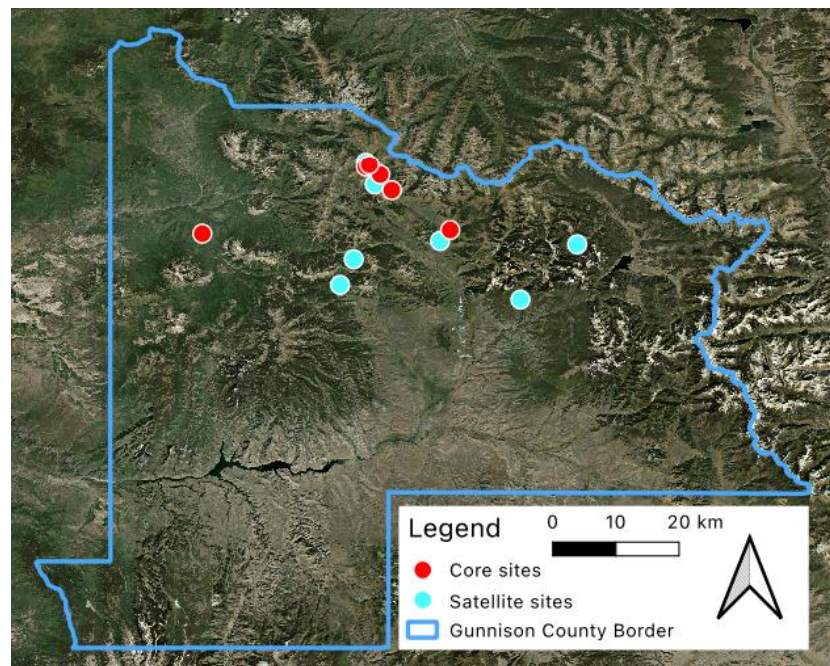


Figure 1. Map of *Valeriana edulis* populations where in-situ soil data (Table S3) was obtained within Gunnison County, Colorado. Core sites contain approximately 250 tagged *Valeriana*, while satellite sites have roughly 50.

2.3 | Experimental design

2.3.1 | Demographic census

At each “core” site, we censused approximately 250 individually tagged *Valeriana* plants that have been censused each year since 2013. At each of the additional 7 “satellite” populations, there were approximately 50 tagged individuals that have been censused since 2021. We tagged the plants with plastic stakes and metal ID disks to ensure that the same plant is measured over subsequent years, allowing us to determine if a plant dies. The census assessed survival, the current size of the plant (rosette perimeter, crown diameter, and stem length), and estimated seed

production by tallying the seeds on 1/5th of a flowering stem and multiplying that by the total number of floral units for the plant. Germination was assessed by adding 250 seeds to a 0.5 by 0.5-meter plot and counting the number of recruits the following year.

2.3.2 | *Abiotic data*

Data for water holding capacity and grain size were obtained from SoilGrids and Web Soil Survey and validated using soil samples from the “core” and “satellite” sites (Table 1). Gridded pH and nitrogen concentration data were obtained from SoilGrids but not ground-truthed due to study limitations. At each study population, we collected approximately five liters of soil by digging out a 22x22x13 cm plot from a location among the tagged *Valeriana* plants. We then air-dried the soil before blending and sieving it to <2 mm prior to performing the following analyses.

Abiotic variable	Spatial resolution	Temporal coverage & resolution	Source
Water holding capacity (g of water per g of dry soil)	Localized point	Present	In-situ sample collection
Grain size (sand, silt, and clay percentages)	Localized point	Present	In-situ sample collection
pH	250m	Present	Soil Grids
Nitrogen concentration (cg/kg)	250m	Present	Soil Grids

Table 1. The spatial resolution, temporal coverage, and temporal resolution of the soil variables used, as well as the sources of the datasets.

We measured water carrying capacity using the MWHC_{FFPD} (maximum water holding capacity - funnel, filter paper, and drainage) method, as described by (Nelson et al., 2024). First, we placed a BUNN brand coffee filter in a 100 mL conical funnel and saturated it with deionized

(DI) water. After adding 10 g of air-dried and sieved soil to the filter, we gently watered the dirt until a thin layer of DI water sat on top of the soil, indicating that it couldn't hold anymore. The soil was then allowed to drain for 6 hours, after which we weighed the damp soil and the filter and then oven-dried both at 105°C for 24 hours to obtain the dry weight and the $MWHC_{FFPD}$ value via the equation:

$$MWHC_{FFPD} = \frac{[SF_6 + (BF_{dry} - BF_6)] - SF_{dry}}{SF_{dry}}$$

Where SF_6 https://www.codecogs.com/eqnedit.php?latex=SF_6#0 is the mass in grams of the saturated and drained soil and filter paper after 6 hours of drainage. BF_{dry} https://www.codecogs.com/eqnedit.php?latex=BF_{dry}#0 and BF_6 https://www.codecogs.com/eqnedit.php?latex=BF_6#0 are the weight of the dry filter and of an unfilled but saturated filter, thus accounting for evaporation. SF_{dry} https://www.codecogs.com/eqnedit.php?latex=SF_{dry}#0 is the mass of the soil and filter after being oven dried.

Grain size was estimated using the jar method, as described by the Clemson College of Agriculture, Forestry, and Life Sciences (Jeffers, 2023). We filled a 1 L jar with 10 oz of soil and then shook it vigorously until the soil turned into a slurry. We let the slurry sit for 48 hours before marking the visible transitions between the deposited sand, silt and clay. We then measured the depth of each layer before using R to find the overall bulk percentage of each grain size.

2.3.3 | Vital rate modeling

Individual vital rates of *Valeriana* were assessed using generalized linear mixed models (GLMMs), where the natural log of the plant's size is plotted as the independent variable against survival, probability of flowering, number of seeds produced, and germination. For example, we used the equation $P(z'|z, \mathbf{x}) = s(z, \mathbf{x})g(z'|z, \mathbf{x})$ [https://www.codecogs.com/eqnedit.php?latex=P\(z'%7Cz%2C%5Ctextbf%7Bx%7D\)%20%3D%20s\(z%2C%5Ctextbf%7Bx%7D\)g\(z'%7Cz%2C%5Ctextbf%7Bx%7D\)#0](https://www.codecogs.com/eqnedit.php?latex=P(z'%7Cz%2C%5Ctextbf%7Bx%7D)%20%3D%20s(z%2C%5Ctextbf%7Bx%7D)g(z'%7Cz%2C%5Ctextbf%7Bx%7D)#0) to model the probability of persistence based on the size of the plant and environmental factors (Merow et al., 2014). $P(z'|z, \mathbf{x})$ [https://www.codecogs.com/eqnedit.php?latex=P\(z'%7Cz%2C%5Ctextbf%7Bx%7D\)#0](https://www.codecogs.com/eqnedit.php?latex=P(z'%7Cz%2C%5Ctextbf%7Bx%7D)#0) is a growth “kernel” that acts like a lookup table, while z'

<https://www.codecogs.com/eqnedit.php?latex=z'#0> represents the size at time $t + 1$

<https://www.codecogs.com/eqnedit.php?latex=t%20%2B%201#0>, z

<https://www.codecogs.com/eqnedit.php?latex=z#0> indicates the size at time t

<https://www.codecogs.com/eqnedit.php?latex=t#0>, and x

<https://www.codecogs.com/eqnedit.php?latex=%5Ctextbf%7Bx%7D#0> acts as an environmental covariate. Plugging in known values for size and soil revealed how the probability of survival changes throughout the entire life cycle. To better understand how soil affects vital rates, we ran models for each environmental co-variate to see how they would affect each individual vital rate. These models included the additive impact of the environment on the intercept while also allowing covariates to interact with size, simulating different effects across various life stages.

We used this same framework to also create a kernel $F(z'|z, \mathbf{x}) = f(z, \mathbf{x})p(z, \mathbf{x})r(z', \mathbf{x})$

[https://www.codecogs.com/eqnedit.php?latex=F\(z'%7Cz%2C%5Ctextbf%7Bx%7D\)%20%3D%20f\(z%2C%5Ctextbf%7Bx%7D\)p\(z%2C%5Ctextbf%7Bx%7D\)r\(z'%7Cz%2C%5Ctextbf%7Bx%7D\)#0](https://www.codecogs.com/eqnedit.php?latex=F(z'%7Cz%2C%5Ctextbf%7Bx%7D)%20%3D%20f(z%2C%5Ctextbf%7Bx%7D)p(z%2C%5Ctextbf%7Bx%7D)r(z'%7Cz%2C%5Ctextbf%7Bx%7D)#0) to model the probability of reproduction. $F(z'|z, \mathbf{x})$

[https://www.codecogs.com/eqnedit.php?latex=F\(z'%7Cz%2C%5Ctextbf%7Bx%7D\)#0](https://www.codecogs.com/eqnedit.php?latex=F(z'%7Cz%2C%5Ctextbf%7Bx%7D)#0) is the reproduction kernel itself, and is composed of the flowering $f(z, \mathbf{x})$

[https://www.codecogs.com/eqnedit.php?latex=f\(z%2C%5Ctextbf%7Bx%7D\)#0](https://www.codecogs.com/eqnedit.php?latex=f(z%2C%5Ctextbf%7Bx%7D)#0), seed production $p(z, \mathbf{x})$ [https://www.codecogs.com/eqnedit.php?latex=p\(z%2C%5Ctextbf%7Bx%7D\)#0](https://www.codecogs.com/eqnedit.php?latex=p(z%2C%5Ctextbf%7Bx%7D)#0), and germination $r(z', \mathbf{x})$

[https://www.codecogs.com/eqnedit.php?latex=r\(z'%7Cz%2C%5Ctextbf%7Bx%7D\)#0](https://www.codecogs.com/eqnedit.php?latex=r(z'%7Cz%2C%5Ctextbf%7Bx%7D)#0) kernels.

Each vital rate function, except for germination, was predicted by a variety of model terms, fixed effects and random intercepts. Survival, growth, flowering, and seed production all used $\log(\text{size})$, t as one of their fixed effects. Survival and growth had $\log(\text{size})$, t interact with sex. Flowering and seed production did not include sex as we assumed that populations of *Valeriana edulis* are generally female limited, and were therefore deemed the more important sex to model for reproductive traits. We fit separate models for each soil variable (as shown in Tables S1 & S2), meaning that the fixed effects of each vital rate were able to interact with water holding capacity, grain size, pH, and nitrogen independently. Finally, each model included year and population as random intercepts. We used a Gaussian response distribution for growth, binomial for survival and flowering, and a negative binomial distribution for seed production. Germination was also predicted using separate models, where each soil variable acted as an

independent fixed effect. Once again, we used year and population as random effects with a binomial response distribution. All vital rate models were fitted using the “merTools” (version 1.14-4) and “glmmTMB” (version 1.1.11) R packages.

3 | RESULTS

Soil variables impacted plant performance across the life cycle: each soil variable affected at least one vital rate, and each vital rate was affected by at least one soil variable (Figure. 2). Individual growth rate for smaller males increased as average grain size decreased, and diminished as the average grain size grew larger. Growth rate also changed in response to pH, where more acidic soils were detrimental to smaller male plants and beneficial to larger ones. Survival was only affected by the average grain size, as larger grain sizes reduced the chance of living another year when plants were small. Flowering probability decreased slightly as the maximum water holding capacity increased. Interactions between grain sizes and flowering resulted in plateaus at zero and one for maximum and minimum grain sizes respectively. More acidic pH values resulted in higher flowering probabilities for smaller *Valeriana*, lower probabilities for larger *Valeriana*, and vice versa for more basic pH values. Larger average grain size caused *Valeriana* to produce more seeds than the other soil variables, and to do so at a smaller size. Finally, the germination rate for plants was positively affected by average grain size and water holding capacity, and negatively affected by more basic pH and increases in nitrogen.

Although the effects of soil varied in intensity across vital rates, there were several consistent patterns. Germination was the only vital rate to be affected by all of the soil variables, albeit to varying degrees of intensity. As for the soil variables, average grain size was the only one to affect all the vital rates, with smaller grain sizes generally being better for tinier plants and larger grain sizes better for bigger plants. Water holding capacity and pH were the only other two soil variables that affected a non-germination vital rate, and both affected flowering, with pH also having a marginal effect on growth.

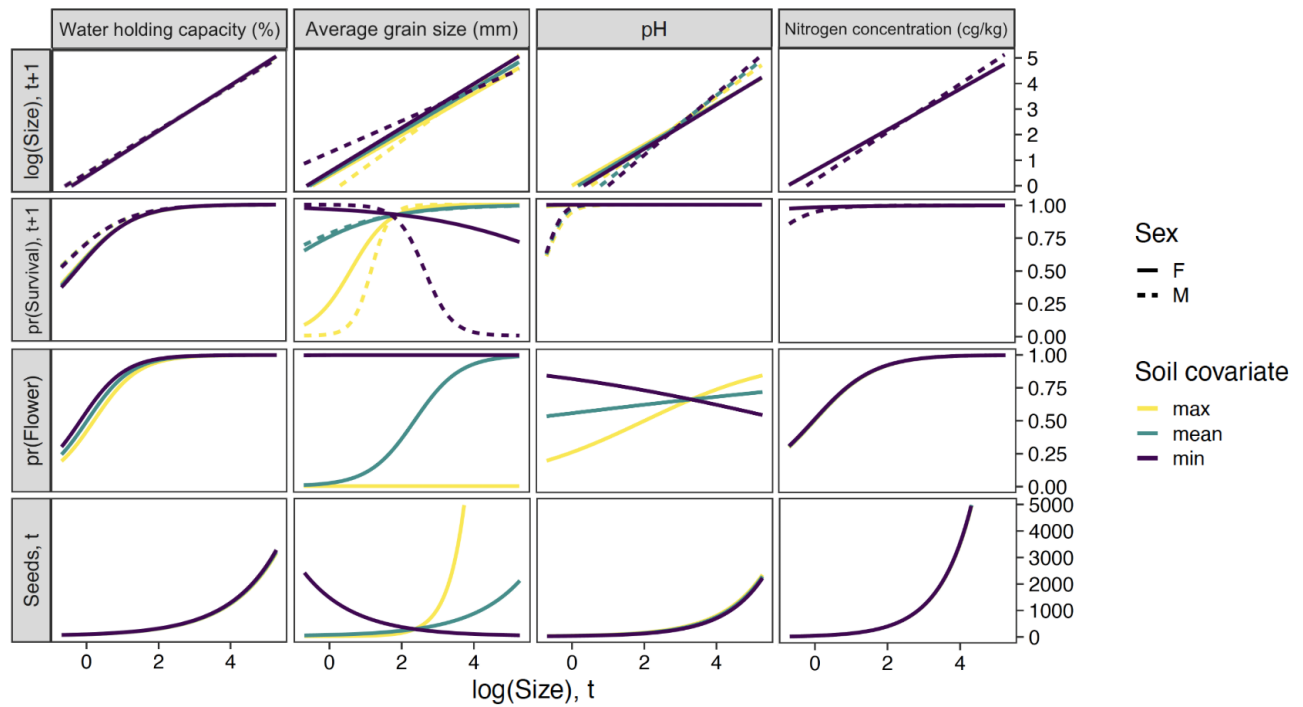


Figure 2. The individual effects of each soil variable on the growth, survival, flowering, and seed production of *Valeriana edulis*. The maximum, mean, and minimum values for each soil covariate are represented by the yellow, green, and purple lines, respectively (Table S3). Female plants are represented with solid lines and males are indicated with dashed lines. Water holding capacity is shown as a percentage of grams of water per gram of dry soil. Average grain size is shown in millimeters, and nitrogen concentration in centigrams per kilogram of dirt.

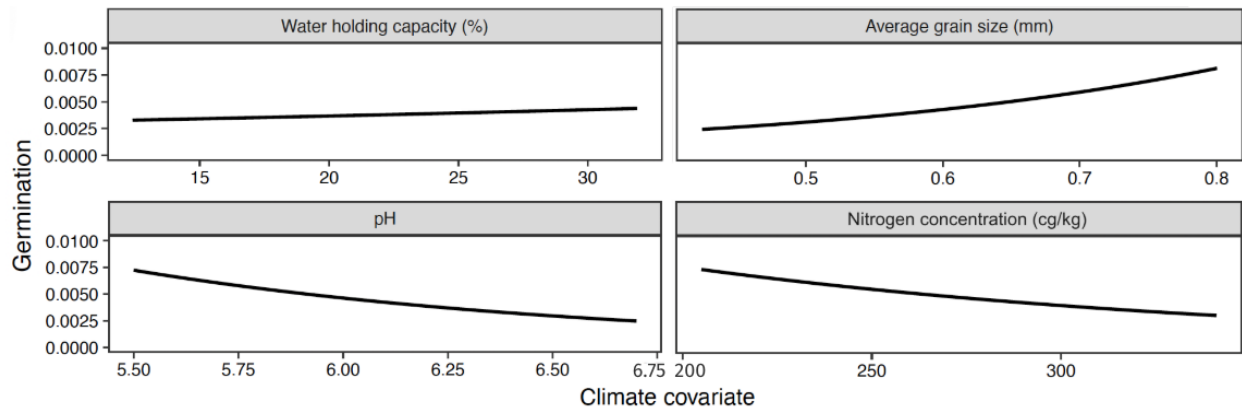


Figure 3. The effects of water holding capacity, average grain size, pH, and nitrogen concentration on germination. The germination rate increased slightly with more water holding capacity, increased substantially for larger average grain sizes, and decreased as pH got more basic and nitrogen concentration increased. However, the overall germination rate remained

incredibly low, reaching a maximum proportion of around 0.01. Water holding capacity is shown as a percentage of grams of water per gram of dry soil. Average grain size is shown in millimeters, and nitrogen concentration in centigrams per kilogram of dirt.

4 | DISCUSSION

The effects of average grain size and pH had strong impacts on the performance of *Valeriana edulis* across its life cycle. As these environmental controls varied in strength and intensity across different vital rates, they provided valuable insight into the potential future population fate, especially as climate change continues to shift habitable zones. At an individual level, soil variables had a minimal effect on the amount of growth, but were more influential when affecting survival, flowering probability, and seed production. Out of the four variables we studied, average grain size was by far the most important, as it was the only soil variable to affect all the vital rates, including germination (Figures 2 & 3). The impacts of other variables were much more limited. The pH of the soil only affected growth, flowering probability, and germination. Water holding capacity had very marginal effects on flowering probability and germination. Finally, variations in nitrogen only affected germination. While simplified, these results indicate that soil has a meaningful effect on plant performance, but the full picture is only revealed when looking at the whole suite of environmental effects.

Our modeling approach differed from Zeh (2021) in respect to the fact that we analyzed how each soil variable directly affected the intercept and interaction for a given vital rate, whereas Zeh found the optimal set of interacting climate variables for each vital rate. However, we are still able to make several comparisons between the two. In our models, average soil grain size proved to have a broader effect than any of the climatic variables, and had more drastic effects, especially for survival and flowering. In contrast, climate variables were more consistent with snowmelt date, mean temperature, and mean precipitation, each affecting at least one vital rate, unlike nitrogen (Zeh, 2021). By comprehensively comparing climate and soil, we can begin to make predictions about what type of environments would be beneficial for future *Valeriana* populations, and what conditions would lead to extinction. To do this, we look at survival, which exerts a disproportionate amount of leverage on plant fitness compared to other vital rates. This is because perennials like *Valeriana* can produce thousands of seeds for over a hundred years.

The ramifications of a small decrease in germination rate are far less important than an equally negative shift in survival chance. By focusing on survival as the most important factor, we can assume that *Valeriana* will prefer silty and sandy environments with low temperatures, later snowmelt dates, and less total precipitation (Zeh, 2021).

As we extend the implications of this study into the near future, we can begin to interpolate how the responses of *Valeriana edulis* to climate change might be more sporadic than previously thought. *Valeriana* has been proven to survive in a variety of soil conditions, but if global warming persists, we may start to see populations forced into less hospitable environments. At one end of the spectrum, there may eventually be small clusters of hundreds of tiny *Valeriana* in areas with more clay-based substrate. At the other extreme, there may also be regions with a few large but solitary plants that were able to survive for long enough in harsh, sandy soils. The high elevations of Gunnison County are incredibly varied in their grain size, ability to hold water, pH, and nitrogen, so the most likely reality is that existing *Valeriana* populations will eventually be pushed to their extremes and localized extinction via a combination of shifting climate and poor soil conditions (Table S3).

While our analysis of the effects of soil on the vital rates provided additional insight into the performance of *Valeriana edulis*, it also furthered our understanding of how soil can be used to track the range shifts of wildflower species as a whole. More specifically, our vital rates highlight what variables should be considered when predicting multi-generational migrations of long-lived perennials. Most interestingly, we found that average soil grain size was the best predictor of plant performance, but didn't have the effect on germination that we had first expected. We originally hypothesized that smaller grain sizes—like clay—would universally support vital rates, due to their water retention abilities (Nelson et al., 2024; Yang et al., 2023; Y. Zhang et al., 2021). While this was generally true for smaller plants, we expect that larger grain sizes were beneficial for germination due to the more compact nature of clays, which makes it harder for seeds to emerge effectively (Benvenuti & Mazzoncini, 2021). In contrast to grain size, all of the other soil variables that we expected to have substantial impacts on plant performance failed to do so. Our nitrogen analysis found no meaningful evidence to support Ford and Hille Ris Lambers' hypothesis that increased nitrogen in meadow soils could promote the growth of larger plants (Ford & Hille Ris Lambers, 2020). In fact, we observed that meadows tended to have extremely varied nitrogen concentrations, as seen when comparing Brush Creek and North

Rustlers Gulch, which had the highest and lowest nitrogen content values across all sites, respectively (Table S3). Both sites were composed of the same parent material, suggesting that future studies should also account for local topography, which can influence both climate and soil variables (S. Zhang et al., 2016). Finally, while we had no major predictions for how pH would affect plant success, we did not expect water holding capacity to only affect flowering probability and germination as opposed to all the vital rates. This response was likely specific to *Valeriana edulis*, as previous studies show increases in water holding capacity to strongly improve growth, flowering probability, and seed production (Dai et al., 2022). While soil variables have been proven to affect species' ranges, fully understanding the exact variables that either promote or inhibit plant success is crucial to predicting exactly where those plants will move to under new climatic regimes (Ford & Hille Ris Lambers, 2020; He et al., 2013; Ni & Vellend, 2024). The vital rate responses we observed in this study are specific to *Valeriana edulis*, but they still indicate the need for broad-scale demographic research across multiple ecosystems and geological boundaries.

Vital rates give us valuable insight into how individual plants will respond to climate change, but future studies may expand on this framework by creating demographic distribution models to spatially overlap optimal conditions and pinpoint where exactly the future of *Valeriana* lies. Ultimately, if more research uses this combined climate-soil modeling approach, we will gain a better understanding of population dynamics as a whole and how best to structure policy-based conservation decisions.

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SUPPLEMENTAL MATERIALS

Table S1. Candidate models for vital rate functions and their various included terms as indicated by a • symbol. Soil models use a pattern of water holding capacity (W), average soil grain size (G), pH (A), and nitrogen concentration (N). The uppercase letters indicate additive effects and an interaction with ln(size), and a 0 indicates that there are no terms in the model for that variable.

Candidate model	<u>Fixed effects</u>								<u>Random intercepts</u>			
	Intercept	ln(size)	Water	Grain	Acidity	Nitrogen	ln(size) * Water	ln(size) * Grain	ln(size) * Acidity	ln(size) * Nitrogen	Year	Population
W000	•	•	•				•				•	•
0G00	•	•		•				•			•	•
00A0	•	•			•				•		•	•
000N	•	•				•				•	•	•

Table S2. Parameter values for each environmental co-variate as it relates to each vital rate function. A dash (-) indicates that the term was not included in the model. A dash with an asterisk (-*) means that the term was not generated by the model.

<u>Fixed effects</u>												<u>Random intercepts</u>		<u>Residuals</u>
Vital rate function	Soil covariate	Intercept	ln(size)	Water	Grain	Acidity	Nitrogen	ln(size) * Water	ln(size) * Grain	ln(size) * Acidity	ln(size) * Nitrogen	Year	Population	sd
Survival	W	M: 0.870 F: 0.381	1.273	0.027	-	-	-	-0.023	-	-	-	0.66 6	1.162	1.000
	G	M: 3.263 F: 1.872	0.332	-	-1.552	-	-	-	0.814	-	-	0.69 5	1.141	1.000

Growth	A	M: 3.791 F: 7.310	2.239	-	-	-1.074	-	-	-	-0.235	-	0.68 1	1.027	1.000
	N	M: 2.941 F: 4.190	0.698	-	-	-	-0.011	-	-	-	0.000	0.67 4	0.991	1.000
	W	M: 0.532 F: 0.407	0.892	0.003	-	-	-	-0.002	-	-	-	0.04 5	0.076	0.419
	G	M: 0.782 F: 0.496	0.869	-	-0.057	-	-	-	-0.019	-	-	0.04 6	0.077	0.419
	A	M: - 0.962 F: -0.130	0.984	-	-	0.097	-	-	-	-0.020	-	0.04 5	0.070	0.418
	N	M: 0.193 F: 0.580	0.792	-	-	-	0.000	-	-	-	0.000	0.04 5	0.079	0.419
	W	-*	1.618	-0.203	-	-	-	-0.002	-	-	-	0.27 8	1.643	1.000
	G	-*	1.690	-	-7.763	-	-	-	-0.206	-	-	0.27 8	1.062	1.000
	A	-*	0.205	-	-	-0.737	-	-	-	-0.223	-	0.27 8	0.490	1.000
	N	-*	1.212	-	-	-	-0.015	-	-	-	-0.001	0.27 8	0.675	1.000
	W	4.134	0.748	-0.018	-	-	-	0.001	-	-	-	0.22 8	0.172	0.301
	G	5.042	0.234	-	-2.297	-	-	-	0.973	-	-	0.23 0	0.164	0.302
Seed production	A	3.086	0.882	-	-	0.111	-	-	-	-0.018	-	0.22 8	0.189	0.301
	N	3.808	1.089	-	-	-	0.000	-	-	-	-0.001	0.23 0	0.180	0.301
	w	-5.903	-*	0.015	-	-	-	-	-	-	-	1.74 0	0.191	-*
Germination	g	-7.363	-*	-	3.201	-	-	-	-	-	-	1.68 3	0.000	-*
	a	0.033	-*	-	-	-0.901	-	-	-	-	-	1.71 6	0.106	-*

n -3.581 -* - - - -0.006 - - - - 1.71
5 0.061 -*

Table S3. Soil properties at each site. Water holding capacity is shown as a percentage of grams of water per gram of dry soil. Average grain size is shown in millimeters, and nitrogen concentration in centigrams per kilogram of dirt. Bolded sites indicate locations that had a maximum and/or a minimum soil variable. Bolded terms with one asterisk (*) show the minimum value for that soil variable across all sites. Two asterisks (**) indicate the maximum value across all sites. Lithologies with a slash (/) separating two parent materials means that the site was located at a geological boundary.

Site	Lithology	Elevation	Water holding capacity (%)	Average grain size (mm)	pH	Nitrogen concentration (cg/kg)
Paonia B	Mesaverde (sandstone, shale)	2040	21.767	0.434	6.7 **	337
Spring Creek	Granitic Rock	2668	13.708	0.600	5.5 *	207
Ohio Creek Meadow	Ohio Creek (claystone, mudstone, sandstone, conglomerate)	2730	16.052	0.704	5.7	228
Mt. Crested Butte	Mancos Shale	2756	30.071	0.435	5.6	334
Brush Creek	Mancos Shale / Glacial drift	2780	31.904 **	0.800 **	5.7	205 *
Judd Falls	Mancos Shale	2918	22.632	0.496	6.2	327
North Rustlers Gulch	Mancos Shale	2989	12.404 *	0.573	6.2	341 **
Lily Lake	Intrusive Rock	3075	12.507	0.493	6	274
Emerald Lake	Mancos Shale	3185	13.570	0.582	6.4	338
Rocky Brook	Glacial drift	3219	22.681	0.015 *	5.9	254
Gothic/Baldy Saddle	Mancos Shale / Intrusive Rock	3266	13.702	0.631	5.7	330
Bellview II	Mancos Shale	3429	22.621	0.483	5.6	226
Bellview I	Dakota Sandstone	3440	24.573	0.424	6.2	315