

Nowcasting the distribution of *Valeriana edulis* using climate driven population models

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Abstract

Climate change poses a unique problem for sessile species because individuals are unable to move to track their optimal habitat. Instead, population turnover governed by population processes must occur in order for the species distribution to change. Current methods to predict current and future species distributions are limited in that they are based on presence vs. absence data and use only currently observable climate regimes that may not reflect novel future climates. The first step towards improving our framework for predicting future species distributions is to develop a mechanistic model of species performance that uses contemporary data to predict the current spatial distribution of a specific species, then validate the model against field observations. Here we develop a Demographic Distribution Model (DDM) for *Valeriana edulis*, a long-lived species with a broad climatic niche, that uses an Integral Projection Model (IPM) to predict the individual- and population-level impacts of climate drivers (snowmelt timing and growing season temperature and precipitation) on population growth and fate. The complex interactions of the differing effects of the climate drivers were found to impact the vital rates of individual plants, which resulted in a range of predicted population growth rates across a landscape with varying climatic conditions. This proved to be an important tool for creating informed predictions about how species distributions respond to dynamically changing climate variables.

Introduction

The future of population performance and species' distributions is being altered by the effects of climate change (Walther et al. 2002). Some species will be able to cope with shifting climates through immediate migration, but population turnover is expected to play an equally if not more important role for many species (Parmesan 1999). Although mobile organisms may be able to track shifting habitats by moving to newly suitable areas, sessile species, including plants, may be more strongly impacted due to their immobility. Instead of having the ability to individually migrate to new habitats with ideal climatic conditions, sessile species must rely on population turnover in order for this crucial movement to take place (Körner 1999). Demography therefore plays a foundational role in controlling species distributions. Current methods to predict current and future species distributions largely put the demographic processes that determine performance in a 'black box.' They (i) are based only on associating species' presence vs. absence with putative climate drivers, precluding understanding of the demographic mechanisms that determine population persistence, and (ii) rely on currently observable combinations of climate variables that may not capture the consequences of novel climate regimes (Elith 2009; Ehrlén and Morris 2015). The limitations of the current phenomenological

approach present a major obstacle to our ability to accurately and mechanistically forecast future changes in plant population distributions, limiting effective responses to a wide range of emerging ecological problems from pest management to the conservation of ecosystem functions.

The ability of a population to persist at a given place, under a given climatic regime depends on individuals being able to successfully complete their life cycle. What may be the optimal conditions for one life stage may be suboptimal or even intolerable for another stage (Johnson et al. 2016). Therefore, we should expect that a change in any single climate variable can impact varying parts of a species' life cycle with different directions and magnitudes (Petty 2016). For example, in the short-lived perennial *Ipomopsis aggregata*, snowmelt timing strongly affected seed production and seedling establishment while the plants' growth and survival rates were relatively unaffected (Campbell 2019). Moreover, the effect of snowmelt varied with the composition of the populations, such as individual size and age. In the context of modern climate change, the reality is that there is not only one climate driver- such as snowmelt timing- that is rapidly changing, but a plethora of them. In combination with each other, these variables compound their already complex individual effects.

In order to make predictions about the impacts of compounding climate variables, a tool that considers their unique effects is necessary. An Integral Projection Model (IPM) is the ideal solution for this daunting task of integrating individual-level performance impacts of climate drivers in the context of an entire life cycle (Easterling 2000; Ellner 2016). IPMs are built on individual-level demographic vital rates of growth, survival, reproduction, and recruitment. These vital rates are estimated as continuous functions by regressing observational census data against predictors that describe the individual's state (e.g., age, size, stage, and/or sex). Climate drivers can be added as covariates to the regression models in a way that alters the individual's state-specific vital rates. An appropriate analogy for an IPM is a continuous "lookup table" where an individual's demographics combined with specific climate drivers can be used to determine an individual's likelihood of survival. The IPM kernel can be used to project the future population size and state composition for any starting population, and the expected long-term behavior of the population can be determined by the equilibrium per-capita population growth rate (Merow et al. 2014a):

$$\lambda = \lim_{t \rightarrow \infty} \frac{N_{t+1}}{N_t},$$

where N_t is the number of individuals in the population at time t . When λ is less than one, each individual is expected to produce less than one offspring over the course of its lifetime; the population is expected to go extinct. When λ is greater than or equal to one, the population is expected to persist. The relationship between λ and climate therefore reveals the net effect of climate drivers at the population scale (Campbell 2019).

Although IPMs fundamentally make projections of dynamics at the population-level, they can be scaled up to whole species ranges by driving them using spatially-explicit data on climate variables. The result is known as a Demographic Distribution Model (DDM; Merow et al.

2014b), which allows individual-level demographic rates and whole population dynamics to be simulated even in locations where no population is present. Moreover, when the species is predicted to be absent under the climate conditions of a given location ($\lambda < 1$), the DDM can be used to determine which components of the life cycle prevent the species from actually existing under the climate regime of a given location. This method uses information from an individual level, and expands this knowledge to make inferences on a population level (Merow 2014).

Here we use *Valeriana edulis* as a model species to determine how climate shapes the current species distribution in a highly heterogeneous environment and how well species distribution models based on climate-demography relationships can predict these distributions. Several attributes of *V. edulis*' natural history make it an ideal candidate species for evaluating a DDM-based range prediction. This plant grows across a wide climatic range, which is beneficial for modeling because vital rates can readily be measured under many different combinations of climatic variables. Its complex life history is also advantageous because it allows us to investigate the effect that climate has on individual performance at many points of its life cycle. *Valeriana edulis* also has extensive historic data available regarding its life history and demographics (Petry et al. 2016; Soule 1981). A previous climate manipulation study revealed that snowmelt date and growing season precipitation drive demographic rates and population growth for *V. edulis* (Petry et al., *unpublished data*). Growing season precipitation is associated with changes in population composition across the species elevation range (Petry et al. 2016).

Population models that accurately predict future distributions are a necessary tool in confronting questions related to the implications of climate change. The first step in accurately generating these models is ensuring that they have the ability to 'nowcast' the current species distribution. To this end, I sought to answer three questions that use demography to scale up responses to climate from individuals to populations to the whole species distribution:

1. How are individual demographic rates in *Valeriana edulis* influenced by changes in snowmelt date, growing season temperature, and growing season precipitation?
2. How does the per-capita population growth rate (λ) of *Valeriana edulis* respond to changes in snowmelt date, growing season temperature, and growing season precipitation?
3. Can we accurately predict the current distribution of *Valeriana edulis* populations using demographic models driven by climate-demography relationships?

Methods

The primary goal of this study was to use climate-demography relationships to predict the current spatial distribution of *Valeriana edulis*. To do this, we used long-term census data from study populations growing across a large elevational, and therefore climatic, gradient. We parameterized a size-structured IPM where vital rate functions could be moderated by snowmelt date, growing season temperature, and growing season precipitation, then paired it with gridded climate data to build a DDM that predicted where populations could persist. The three climate

variables were chosen based on their observed effect on the demographics of *V. edulis* in previous studies. Finally, we calibrated and scored the predictive performance of the DDM against field observations of the presence/absence of *V. edulis* (Merow et al. 2014b).

Demographic data collection protocol

Demographic data for *V. edulis* was collected from seven core populations: Paonia B, Brush Creek Range, Judd Falls Trailhead, North Rustlers Gulch, Emerald Lake, Belleview I, and Frigid Air Pass (Figure 1). At each core population, ca. 250 individuals were permanently marked with metal tags in 2013 and have been censused annually ever since, with new plants tagged each year to replace individuals that died. The census consisted of determining whether or not the plant was still present (survival), its current size (rosette perimeter; growth), and flowering status plus estimated seed production (reproduction; Petry et al. 2016). Germination and recruitment were measured by dispersing 250 seeds into 50x50cm plots and counting germinants the following growing season.

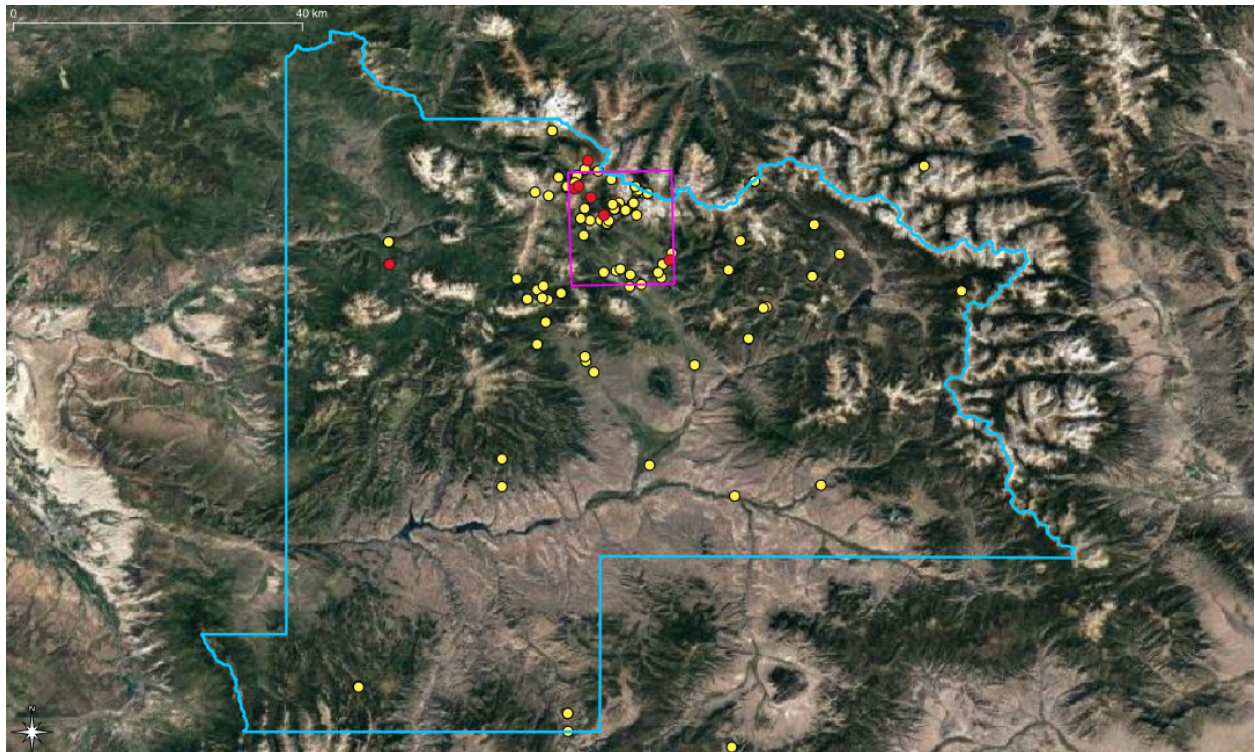


Figure 1. Map of *Valeriana edulis* populations: Core demography populations are represented by red dots and other occurrences are represented by yellow dots. The purple rectangle marks the Upper East River Domain, which was the area of interest for the DDM. Gunnison County is outlined in light blue.

Climate data

Climate data was obtained from two different sources at the finest spatial resolution available for the time period overlapping our census data (Table 1). We extracted climate data at the finest resolution available to pair with the census data, but were limited to the time period when data for all variables was available (2013-2018). Before projecting the DDM, the mismatched spatial resolutions were reconciled by reprojecting the snowmelt date map to the coarser, 1km grid used by the other two variables.

Table 1. The spatial resolution, temporal coverage, and temporal resolution for each of the three focal climate variables, and the sources of the datasets used to associate climate with demographic census data and to project the Integral Projection and Demographic Distribution Models.

Climate variable	Spatial resolution	Temporal coverage & resolution	Source
Snowmelt date (doy)	10m	2013-2019 (annual)	LS Sentinel Snow Departure DOY, Snow ML Kriging v.May2021 (I. Breckheimer, pers. comm.)
Mean temperature (Jun-Aug, °C)	1km	2013-2019 (monthly)	CHELSEA v.2.1 (Karger et al. 2017)
Total precipitation (Jun-Aug, mm)	1km	2013-2018 (monthly)	CHELSEA v.2.1 (Karger et al. 2017)

Q1: Determining the impact of climate on individual-level demographic rates

_____ Vital rate functions were estimated from field data on female and non-flowering plants by using generalized linear mixed models (GLMMs) where the natural logarithm of a plant's size (rosette perimeter) was the independent variable with random intercepts for year and population to account for spatiotemporal non-independence. Gaussian error was used for growth, binomial error for survival (alive/dead), flowering status (yes/no), and germination (yes/no), and negative binomial error for seed production.

To understand how climate covariates moderated these vital rate functions, multiple candidate models were fit for each vital rate wherein climate could affect the function in different ways (Table S1). The simplest candidate model excluded all climate covariates. The next set of models included only additive effects of all combinations of the three climate variables (Table 1), such that climate altered the intercept of the vital rate function. That is, the effect of climate on performance was equivalent across all plant sizes with no interactions among the climate variables. In the final set of candidate models, size-by-climate interactions were added for all combinations of climate variables while still omitting all interactions among climate variables. Germination rate was assumed to be independent of maternal size, therefore the main and

interactive effects of $\ln(\text{size})$ were omitted from the candidate models for this vital rate function. The best fitting model for each vital rate function was chosen as the candidate with the lowest AIC, using a ΔAIC threshold of 2 to rank candidate models and selecting the model with the fewest parameters in the event of ties (Burnham & Anderson 2002).

Q2: Scaling up individual-level climate impacts to population-level persistence potential

The selected candidate model for each vital rate was used to construct and parameterize the IPM kernel. The projection equation for the size-structured, climate-driven IPM is given as,

$$n(z')_{t+1} = \int_L^U [S(z, E)G(z', z, E) + F(z, E)P(z, E)R(z', E)]n(z)_t dz,$$

where $n(z)_t$ is the number of z -sized individuals at time t growing in the environmental conditions E . The first term captures persistence of previously-established plants and is composed of the size- and environment-specific survival and growth rates, $S(z, E)$ and $G(z', z, E)$. The second term captures the recruitment of new plants into the population, which happens when plants flower, $F(z, E)$, produce seeds, $P(z, E)$, and those seeds successfully germinate, $R(z', E)$. L and U are the size limits of the integration, and dz is the integration constant.

To perform the integration and project the IPM, the kernel was discretized into 200 equally-sized bins using the midpoint rule (Ellner et al. 2016). The integration limits were set to $L = -1$ and $U = 5$, corresponding to rosette perimeters of 0.36-148.41 cm and which extend beyond the smallest and largest observed plant sizes in the field, respectively. We corrected for eviction (plants growing or shrinking to sizes outside of the integration limits) by using truncated Gaussian distributions when distributing individual sizes in the next timestep (z') around their expected values (Williams et al. 2012). Projecting the IPM to equilibrium allowed λ , the long-run population growth rate, to be calculated as,

$$\lambda = \lim_{t \rightarrow \infty} \int_L^U n(z')_{t+1} / n(z)_t dz.$$

The IPM was constructed and projected using the R package `ipmr` v.0.0.3 (Levin et al. 2021).

The relationship between λ and climate was determined by fitting a linear model with a global intercept and an additive term for each climate variable. The marginal effect of each climate variable on λ was calculated by holding all other variables at their mean value.

Q3: Nowcasting the spatial distribution of *Valeriana edulis* populations

The IPM was projected to equilibrium and λ was calculated for each 1x1 km grid cell in the focal area (Fig. 1) using the time-averaged mean climate values in each grid cell. Each cell was started with 10 individual plants in each size bin and iterated for 100 years, ensuring enough time for λ to reach equilibrium.

The model was validated by comparing DDM-predicted occurrence to a combination of previously known presences and field searches of grid cells in the focal area. Known presences were assembled from previous field observations (W. Petry, *personal communication*) and georeferenced, ‘Research Grade’ observations from iNaturalist (queried 10 August 2021). These

presence observations were supplemented by going into the field and checking whether or not *V. edulis* was present at a subset of the remaining grid cells. For each cell that was searched, only the area where *V. edulis* is able to grow (meadows) was visited. Cells were sampled by walking in transects 10 meters apart until (i) *V. edulis* was observed (determined to be present) or (ii) all meadows in the cell were searched without finding any *V. edulis* (determined to be absent). Grid cell sampling was targeted towards cells where the DDM predicted absences because occurrence data from other sources was biased towards cells where the DDM predicted presence. In total, presence/absence data were collected for 66 (of 420) grid cells.

The 66 grid cells with presence/absence data were categorized into a confusion matrix that compared qualitative model predictions against observed outcomes. The True Skill Statistic (TSS; Allouche et al. 2006) was used to score the predictive skill of the DDM where:

$$TSS = Sensitivity + Specificity - 1$$

$$= \frac{True\ Positives}{True\ Positives + False\ Negatives} + \frac{True\ Negatives}{False\ Positives + True\ Negatives} - 1.$$

The TSS is on a scale of [-1, 1], where -1 is the worst score (all model predictions are either false negatives or false positives) and 1 is a perfect score (all model predictions are either true positives or true negatives).

In order to calibrate the model and calculate the optimal cutoff value for λ , a sequence of λ cutoff values at increments of 0.000001 was generated across the total range that was predicted by the DDM. The confusion matrix and TSS score was recalculated at each cutoff value. The λ cutoff value that maximized the TSS score was chosen and used to determine the presence and absence predictions (Figure S1).

Results

Q1: The impact of climate on individual-level demographic rates

All climate variables affected at least one vital rate function and all vital rate functions were affected by at least one climate variable as determined by AIC model selection (Figures 2 & 3; Tables S2-S7). Individual growth rate was increased with later snowmelt date and higher mean temperatures during the growing season equally across all plant sizes. For survival, these same two climate drivers interacted with plant size such that later snowmelt and higher temperatures increased survival of small plants, but decreased survival of large plants. Flowering probability decreased with higher mean growing season temperatures equally across all plant sizes. Higher growing season precipitation decreased the amount of seeds produced equally across all plant sizes. The germination rate for plants of all sizes were negatively impacted by the additive effects of growing season temperature and growing season precipitation.

Although the effects of the climate drivers on vital rates appear to be idiosyncratic, several patterns emerged. Climate tended to affect individual demographic rates equally across plant sizes; the only instance where climate had differing impacts based on individual size was the effect of snowmelt date and growing season temperature on the survival rate. Growing season precipitation always had a positive additive effect on the vital rates. Snowmelt date always had a

positive impact on the intercept of the functions and a negative impact on the size-by climate effects. Temperature had a mixture of both positive and negative effects on the intercepts of the vital rate functions.

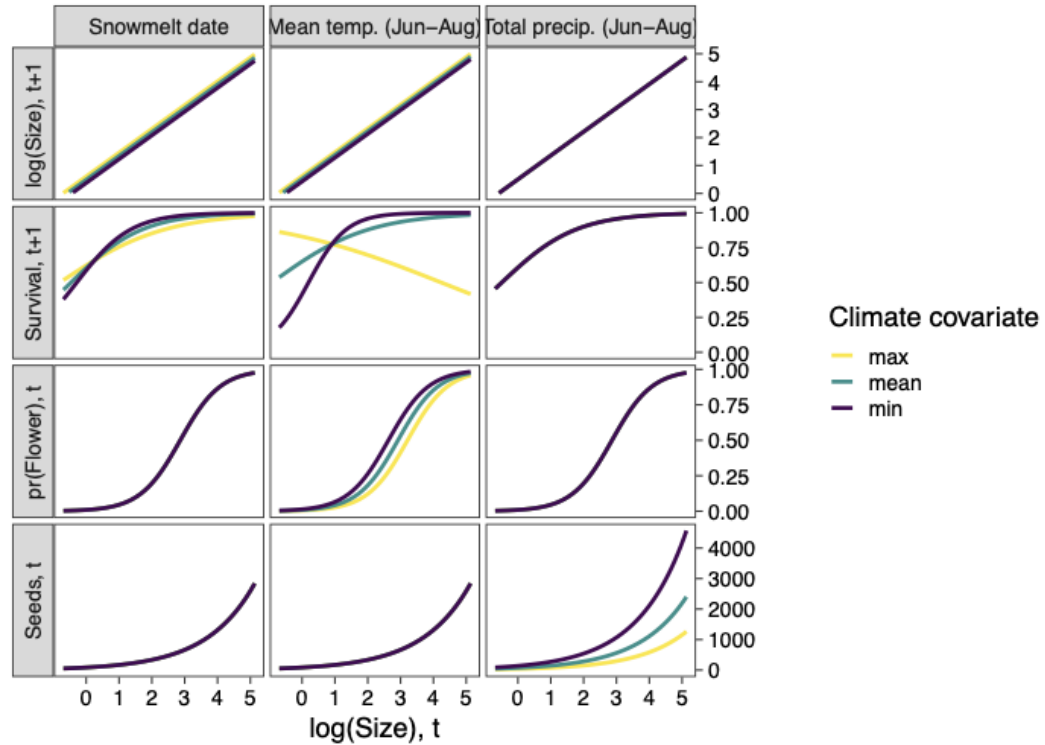


Figure 2. The individual effects that each climate covariate had on the growth, survival, flowering, and seed production of *Valeriana edulis*. The minimum, mean, and maximum values for each climate covariate are represented by purple, green, and yellow lines, respectively. Each climate covariate affected at least one vital rate and each vital rate was affected by at least one climate covariate.

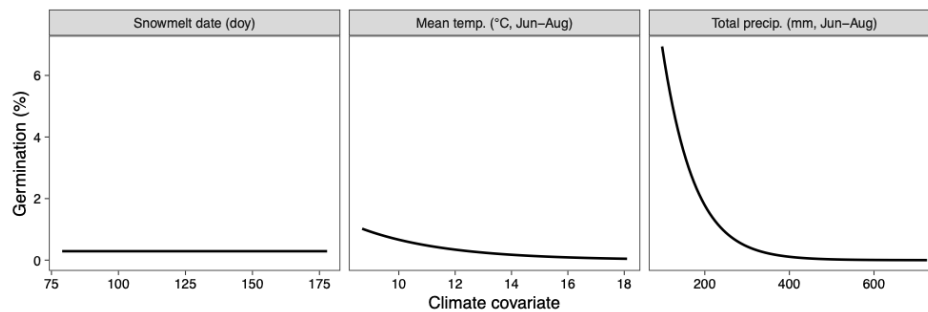


Figure 3. Relationships between germination rate and snowmelt date, mean temperature during the growing season, and total precipitation during the growing season. The germination rate was low and decreased gradually with increasing temperature and sharply with increasing precipitation.

Q2: Scaling up individual-level climate impacts to population-level persistence potential

Each of the three climate variables that was analyzed had a different effect on λ (Figure 4). Later snowmelt date increased λ , and thus the likelihood of population growth and presence. Growing season temperature and growing season precipitation both had negative effects on λ , although the slope for precipitation was much stronger.

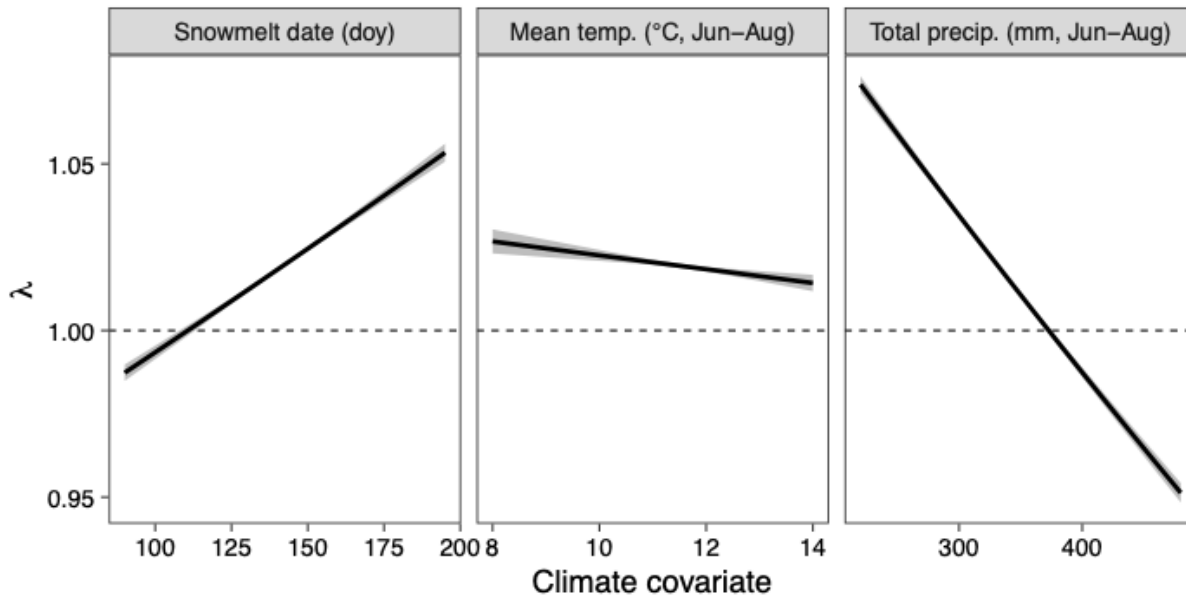


Figure 4. Relationships between λ and snowmelt date, mean temperature during the growing season, and total growing season precipitation. Climate effects on λ varied in strength and direction among these three drivers.

Q3: Nowcasting the spatial distribution of *Valeriana edulis* populations

The DDM predicted population growth rates ranging from 0.984 to 1.072 across the study area (Figure 4A). The DDM was calibrated with a λ cutoff value of 1.011 (Figure S1), resulting in a total of 244 predicted presences and 176 predicted absences (Figure 4B).

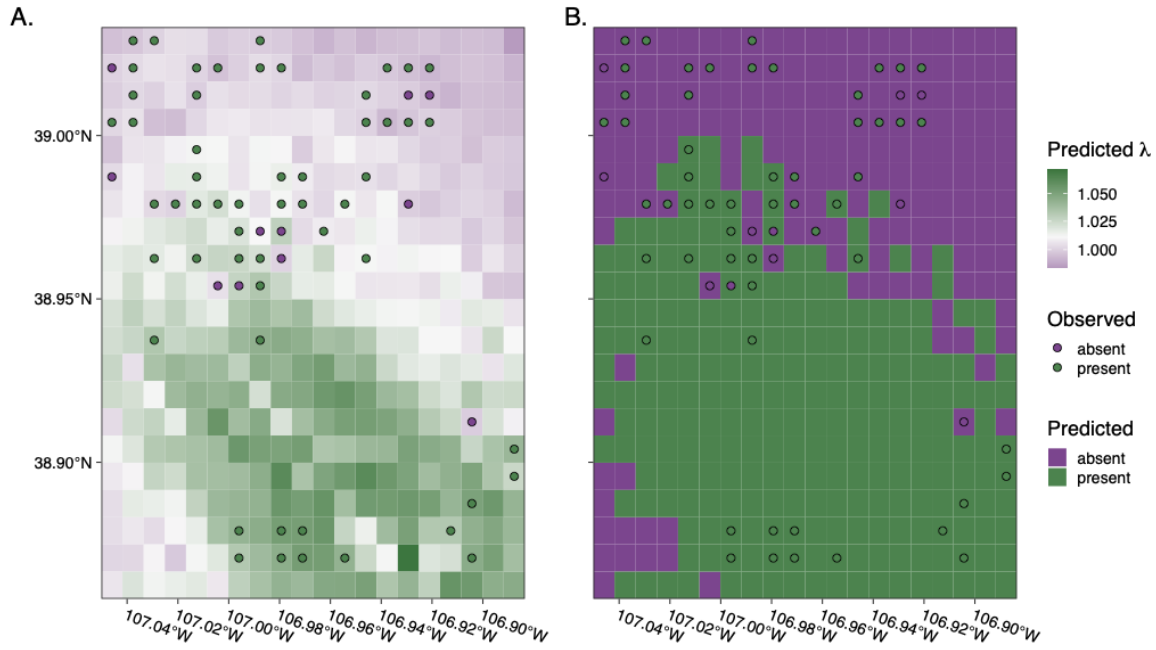


Figure 4. Demographic Distribution Model (DDM) for *Valeriana edulis* across the study area. **(A)** The predicted value of λ for each grid cell. Purple represents predicted absence ($\lambda < 1.011$) while green represents predicted presence ($\lambda \geq 1.011$). **(B)** The discretized DDM predicted presences and absences using a threshold of $\lambda = 1.011$. Overlaying both panels are observed presences (green dots) and observed absences (purple dots).

A total of 66 grid cells were observed for the presence or absence of *Valeriana edulis* (Figure 4). The calibrated DDM correctly predicted 57% (37 of 66) of the observed presences and absences, with the majority of incorrect predictions as false negatives (26 of 28; Table 2). Using the optimal λ cutoff, the sensitivity of the DDM was 0.527, the specificity was 0.818, and the TSS was 0.345.

Table 2. Confusion matrix comparing observations against model predictions for the calibrated Demographic Distribution Model.

	Observed presence	Observed absence
Predicted presence ($\lambda \geq 1.011$)	29 (true positives)	2 (false positives)
Predicted absence ($\lambda < 1.011$)	26 (false negatives)	9 (true negatives)

Discussion

The combined effects of snowmelt timing and growing season temperature and precipitation had a strong impact on the performance of *V. edulis* from the individual to range-wide scale. On the individual-level, the impacts of the climate variables were widespread across the life cycle of *V. edulis* and tended to affect vital rates across all sizes equally. The effect of climate variables on the population growth rate of *V. edulis* varied in both strength and direction: it was positive and strong for snowmelt timing, while it was negative for growing season temperature and precipitation, with a stronger effect on the latter. The DDM had a moderately positive TSS, with modest sensitivity and high specificity. Demographically-based distribution models hold great potential for nowcasting and forecasting species occurrence in a changing world.

Important patterns across the vital rate models that were generated reveal certain similarities about the effect of the climate drivers. Overall, there were very few interactions between plant size and climate (Table S2). Instead, these climate variables tended to raise or lower the demographic vital rate across all sizes equally (additive effects). This suggests that relatively simple models may be more effective at predicting the consequences of climate change because unnecessary complexity (such as size-dependent effects) could make it more difficult to produce accurate results. Climate variables that impacted multiple vital rate functions tended to do so in the same direction across all affected vital rates. Growing season temperature had the broadest range of effects across vital rate functions, whereas the impacts of snowmelt timing were limited to persistence (growth and survival) and precipitation only affected reproductive components of the plant life cycle. These relatively simplified climate effects on vital rates imply that demographics tend to be impacted similarly across all life cycle stages, which allows researchers to avoid creating models that are convoluted with unnecessary considerations. This outcome differs from previous studies (Merow et al. 2014 & Campbell 2019), where more of the effects of climate on vital rates were size-dependent. These patterns imply that although the climate covariates had varying effects, there are still similarities that can be used to make informed predictions about the performance of individual plants. Future studies could build upon this observation and investigate if the effect of climate on vital rates, independent of size, is consistent across species.

The relationships between λ and each of the climate variables underscored the importance of combining climate impacts across the life cycle to determine their net impact on performance. Snowmelt date is predicted to become earlier in the future as climate change progresses (Clow 2010). Since this variable had a positive relationship with λ , it can be inferred that populations of *V. edulis* are expected to decline and ultimately go extinct. However, the growing season temperature is expected to increase (Walther et al. 2002). Due to the positive relationship between temperature and λ , this indicates that its effect on populations of *V. edulis* will cause them to increase and persist. Growing season precipitation is expected to decrease (Alexander et al. 2013). Therefore, the positive relationship between precipitation with λ indicates that climate

change may cause populations of *V. edulis* to decline or even go extinct. Since snowmelt date and growing season precipitation had stronger relationships with λ , it can be inferred that the net effect of these changing variables will have negative impacts on the population growth and distribution of *V. edulis*. The opposing effects of climate on λ are complex, however not unexpected. Similar outcomes of simultaneous aspects of climate impacting population-level performance in opposite directions have been observed in previous studies using demographically-based distribution models (Merow et al. 2014b).

The DDM performed quite well in terms of predicting occurrences of *V. edulis* in the study area. The positive TSS score (0.345, on a scale of [-1 to 1]) indicates that the climate variables did have a significant effect on the growth, survival, flowering, seed production, and germination of *V. edulis*. Running the model without climate drivers yielded a TSS = 0 (results not shown). However, there is still room for improvement in order to create a model that produces better predictions of occurrence. The specificity of the model scored higher than the sensitivity did. This means that the model was more accurate at predicting absences than presences. One reason for this is because it is more difficult to confirm an observed absence than presence. This could also account for the false positives. Another likely reason why the TSS was below a perfect score of 1 is because there could be other climate variables that have more significant impacts on the distribution of *V. edulis* than the three that were chosen. Future studies could experiment with the effect of additional climate variables on the TSS score. Additionally, the DDM did not take into account other factors that may impact the distribution of *V. edulis*, such as terrain and substrate. A cell could have ideal climatic conditions for the plant to grow, however if it is entirely rocky terrain then it will not be found there. Finally, the λ cutoff used to calibrate the DDM was greater than 1, indicating that the model predicted population growth rates that were too high. These overly optimistic predictions may be caused by the model's use of time-averaged climate conditions. We expect that year-to-year variance in climate drivers ought to lower λ (Kendall 1949; Caswell 2001), and a stochastic DDM might better account for the negative effect of vital rate variation on population growth rate.

Demographically-based distribution models offer a powerful tool for learning how climate impacts species distributions. Although we have demonstrated the ability of DDMs to nowcast the distribution of a plant species, future studies should assess their performance for forecasting distribution shifts under future and changing climates. This is an important next step in the effort to gain an informed perspective about the various impacts that climate change is having on species. If DDMs can be validated in this forward-looking context, we will gain valuable, mechanistic insight into the fundamental processes that shape species distributions as well as a tool for making principled population management decisions.

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Supplemental materials

Table S1. Candidate models for vital rate functions with included terms indicated by a •. Model names follow a pattern of snowmelt date (s or S), growing season temperature (t or T), and growing season precipitation (p or P). Lower case letters indicate an additive effect, upper case indicates an additive effect and interaction with ln(size), and 0 indicates no terms in the model for that variable.

Candidate model	Fixed effects						Random intercepts			
	Intercept	ln(size)	Snowmelt	Temp.	Precip.	ln(size) × Snowmelt	ln(size) × Temp.	ln(size) × Precip.	Year	Population
000	•	•							•	•
s00	•	•	•						•	•
0t0	•	•		•					•	•
00p	•	•			•				•	•
st0	•	•	•	•					•	•
s0p	•	•	•		•				•	•
0tp	•	•		•	•				•	•
stp	•	•	•	•	•				•	•
S00	•	•	•			•			•	•
0T0	•	•		•			•		•	•
00P	•	•			•			•	•	•
ST0	•	•	•	•		•	•		•	•
S0P	•	•	•		•	•		•	•	•
0TP	•	•		•	•		•	•	•	•
STP	•	•	•	•	•	•	•	•	•	•

Table S2. Parameter values for the candidate model selected by AIC for each vital rate function and used to construct the Integral Projection Model. A dash (—) indicates that the term was not included in the best-fitting model (see Tables S3-S7 for AIC model comparisons).

Vital rate function (link)	<u>Fixed effects</u>								<u>Random intercepts</u>		<u>Residuals</u>
	Intercept	ln(size)	Snowmelt	Temp.	Precip.	ln(size) × Snowmelt	ln(size) × Temp.	ln(size) × Precip.	Year (sd)	Population (sd)	sd
Survival (logit)	-2.319	4.480	0.002	0.204	—	-0.006	-0.224	—	0.024	1.016	0.213
Growth (identity)	-0.074	0.852	0.002	0.021	—	—	—	—	0.038	0.007	0.416
Flowering (logit)	-3.413	1.632	—	-0.101	—	—	—	—	0.193	0.171	0.389
Seed production (exponential)	5.133	0.681	—	—	-0.002	—	—	—	0.487	0.172	1645.358
Germination (logit)	2.960	—*	—	-0.334	-0.014	—*	—*	—*	0.274	0.350	0.008

*Term omitted from candidate models.

Table S3. Candidate models for the growth function, ranked by AIC. The best-performing model (st0) is in bold text and was used in the construction of the Integral Projection Model. See Table S1 for model naming convention and included predictors.

Candidate model	Degrees of freedom	AIC	Δ AIC
ST0	9	6192.027	0
st0	7	6192.844	0.817
stp	8	6194.405	2.378
STP	11	6195.412	3.385
S00	7	6198.503	6.476
s00	6	6200.555	8.528
S0P	9	6202.310	10.283
s0p	7	6202.379	10.351
00p	6	6208.014	15.987
0T0	7	6208.097	16.070
0TP	9	6208.305	16.277
00P	7	6209.784	17.757
0tp	7	6209.931	17.904
000	5	6210.259	18.231
0t0	6	6211.337	19.309

Table S4. Candidate models for the survival function, ranked by AIC. The best-performing model (ST0) is in bold text and was used in the construction of the Integral Projection Model. See Table S1 for model naming convention and included predictors.

Candidate model	Degrees of freedom	AIC	Δ AIC
ST0	8	2111.646	0.000
STP	10	2112.392	0.746
OT0	6	2114.350	2.704
OTP	8	2115.428	3.782
S00	6	2139.348	27.702
stp	7	2141.733	30.087
st0	6	2142.463	30.818
S0P	8	2142.703	31.057
0tp	6	2144.052	32.406
0t0	5	2144.695	33.049
00P	6	2146.904	35.258
000	4	2146.972	35.326
s00	5	2148.612	36.966
00p	5	2148.740	37.094
s0p	6	2150.509	38.863

Table S5. Candidate models for the flowering function, ranked by AIC. The best-performing model (0t0) is in bold text and was used in the construction of the Integral Projection Model. See Table S1 for model naming convention and included predictors.

Candidate model	Degrees of freedom	AIC	Δ AIC
0t0	5	5716.804	0.000
S00	6	5717.464	0.660
s00	5	5717.484	0.679
st0	6	5717.955	1.150
0tp	6	5718.299	1.495
ST0	8	5718.539	1.734
OT0	6	5718.665	1.860
000	4	5718.918	2.113
s0p	6	5719.118	2.314
stp	7	5719.716	2.912
00p	5	5720.287	3.483
S0P	8	5721.077	4.272
0TP	8	5721.861	5.056
00P	6	5722.002	5.198
STP	10	5722.285	5.481

Table S6. Candidate models for the seed production function, ranked by AIC. The best-performing model (00p) is in bold text and was used in the construction of the Integral Projection Model. See Table S1 for model naming convention and included predictors.

Candidate model	Degrees of freedom	AIC	Δ AIC
00p	6	34561.08	0.000
s0p	7	34563.02	1.937
00P	7	34563.07	1.990
0tp	7	34563.08	1.993
stp	8	34565.01	3.922
0TP	9	34565.15	4.066
S0P	9	34566.32	5.237
STP	11	34568.92	7.833
s00	6	34570.29	9.204
0t0	6	34571.09	10.007
S00	7	34571.63	10.549
0T0	7	34571.75	10.663
st0	7	34571.88	10.799
000	5	34574.46	13.376
ST0	9	34574.47	13.388

Table S7. Candidate models for the germination function, ranked by AIC. The best-performing model (0tp) is in bold text and was used in the construction of the Integral Projection Model. See Table S1 for model naming convention and included predictors.

Candidate model	Degrees of freedom	AIC	Δ AIC
0tp	5	118.573	0.000
stp	6	120.573	2.000
s0p	5	122.482	3.910
00p	4	123.601	5.028
st0	5	127.276	8.703
000	3	127.302	8.729
s00	4	127.481	8.908
0t0	4	129.232	10.659

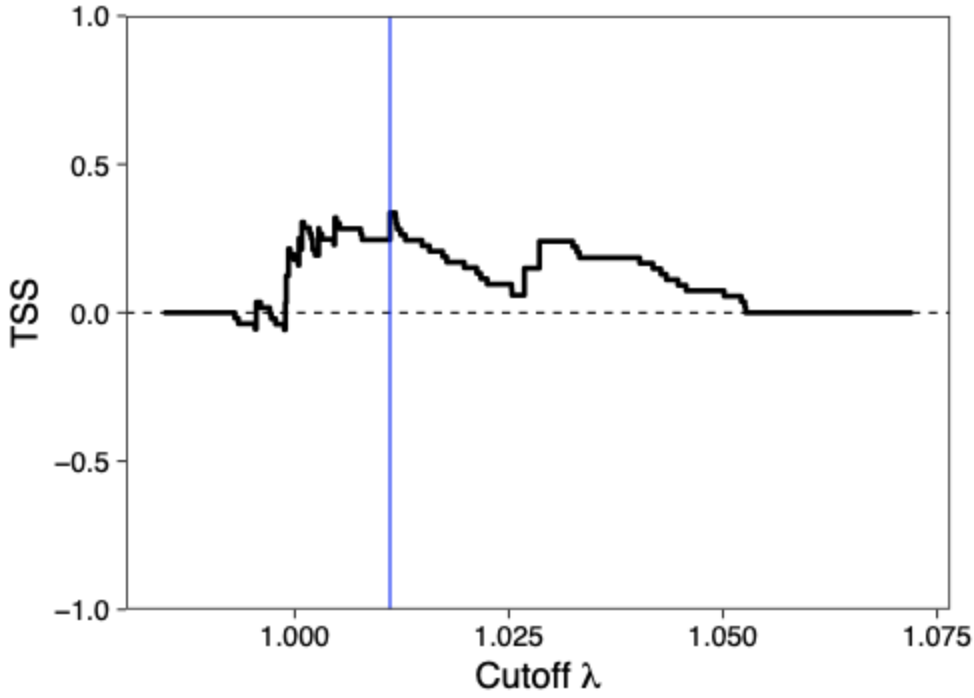


Figure S1. Profile plot of the True Skill Statistic (TSS) versus λ cutoff values spanning the range of λ values predicted by the Demographic Distribution Model (DDM). The TSS was maximized at a λ cutoff of 1.011, and the DDM was calibrated by scoring all grid cells with $\lambda \geq 1.011$ as ‘present’ and $\lambda < 1.011$ as ‘absent.’