

Elevation Does Not Predict Density Dependent Population Dynamics in *Valeriana edulis*

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Abstract:

Density dependence—the impact of neighbors on the survival, growth, or reproduction of individuals—strongly impacts the size and dynamics of populations. However, it is unknown how the effects of density dependence vary across species ranges, which will be integral knowledge in the face of climate change and shifting populations. We sought to determine whether density dependence varies systematically across a species elevation range in the long-lived perennial plant *Valeriana edulis* (valerian). We assessed density dependence three ways across the species elevation range. First, we measured natural population density. Second, we quantified the impact of neighbor density on individuals survival, growth, flowering, and seed production. Third, we combined the measures of density dependent individual performance into a demographic model and projected the population's carrying capacity. There was no significant relationship between observed population density and elevation. However, density dependence impacted multiple parts of the plant life cycle: size-specific survival and flowering probabilities of individual plants decreased with increasing numbers of neighbors. Finally, integrating the impacts of density across the full life cycle revealed that there was no significant relationship between elevation and model-projected carrying capacity. Taken together, these results suggest that density dependence has idiosyncratic effects on population dynamics across a species' range.

Introduction:

Across all biological taxa, population dynamics are affected by both external and internal variables. External factors such as climate, topography, interactions with other species, resource availability, and physical space all play important roles in determining whether a population persists or declines (Chang et al, 2015; Fu et al, 2010; Ibrahim et al, 2022). Internal factors such as resource competition, mating dynamics and shelter against extreme conditions can have similar, concurrent impacts on population dynamics (Bennion and Ward, 2023; Callaghan and Emanuelson, 1985). These combined external and internal drivers of performance dictate the dynamics and mortality rates of populations, yet we still don't understand under what conditions populations will be significantly affected by specific drivers at specific times.

Population density mediates how individuals experience their environment and can profoundly impact individual performance. Individual performance may be negatively impacted by the presence and abundance of neighbors of the same species. For example, competition for resources (Craine, Dybzinski 2013) and spillover of diseases or parasitic outbreaks (Ebert et al. 2000; Parker, Gilbert 2013) will tend to negatively impact the performance of a focal individual as neighbor density increases. But the effects of neighbors can also be positive. For example, higher neighbor density could increase the attraction of mutualists (Wolin, Lawlor 1984) or increase the availability of mates (Mustajärvi et al. 2001). As such, population density can affect multiple life stages simultaneously with differing signs and magnitudes. Density dependent performance is widespread in nature, having been detected in the majority of population abundance time series data across 1198 species (66.2-93.9%, depending on the way density dependence was assessed; Brook et al. 2006). A larger and denser population can have positive effects, such as increased pollination/genetic diversity, or negative effects such as over-consumption of resources.

The net effects of density dependence acting on different parts of the life cycle will determine the carrying capacity of a population. In plant populations, increasing density increases competition for resources, space, and sunlight are expected to decrease probabilities of survival, growth, and flowering. All these processes require resource investment, and with neighbors competing for the same resource, there would be less to go around to facilitate survival, growth and flowering. In contrast, a higher density may aid in pollination and seed production. A dense patch of flowering plants may attract more pollinators and lead to cross pollination at a higher frequency than observed in a sparsely populated area.

We understand very little about how the sign and strength of density dependence changes across a species' range. From a theoretical standpoint, the most relevant hypothesis—the Abundant Center Hypothesis—posits that population density will be higher in more central populations compared to populations at the range margin (Dallas et al. 2020). Low density could be observed because density dependence is very strong or because of density independent factors. Likewise, density might only be high enough to substantively impact individual performance in populations at the range center. Empirically, there have been few explicit

measurements of density dependence across a species range. The studies conducted to observe the effects of elevation on density dependence have only been in tropical and subtropical forests, and the species studied have been trees at the seedling stage (Xu and Yu, 2014), and trees with >1cm diameter at breast height (LeManna et. al 2022). According to these studies, negative density dependence becomes stronger as elevation decreases. Furthermore, we know of no studies that have projected the impact of measured density dependence on the population carrying capacity across a species' range.

Here we study the impacts of density dependence on populations of the perennial plant *Valeriana edulis* using observational data and demographic modeling. We seek to answer the following questions:

1) Is there a relationship between population density and elevation?

An elevational pattern in the strength and sign of density dependence could cause a detectable change in population density over the species' elevation range. This pattern may reflect underlying patterns in density dependence, but is also subject to confounding impacts from density-independent effects on density.

2) Where in the life cycle of *Valeriana edulis* does local density affect individual performance?

In order to isolate the effects of density dependence on the population level, we must first find the effects of density dependence on individual performance. The life cycle is split up into survival probability, growth, flowering probability, and seed production.

3) Do the impacts of density dependence across the life cycle produce an elevation gradient in the carrying capacity of the population?

With our vital rate data from the previous question, we are able to project individual performance on a population level. We can project the population demographic rates until equilibrium, at which the population size will stabilize at carrying capacity (K). This isolates density dependence in our model and allows us to observe the potential effects that elevation has on carrying capacity.

By answering these questions, the effects of density dependence on the life cycle of plants in alpine ecosystems can be better understood, in order to secure the survival of healthy populations in the face of climate change, deforestation, and recovering ecosystems.

Methods:

Study system & sites

Valeriana edulis (valerian) is a long-lived, slow-growing, dioecious perennial plant found across the western United States in the Rocky Mountains. This species most commonly grows in wet alpine meadows, and is pollinated by generalist species such as flies and solitary bees (Petry et al. 2016).

We studied a total of 20 populations of *V. edulis* in western Colorado: we collected natural density data in 20 populations and demographic census data from 18 populations (Table 1).

Table 1. Study populations and their GPS coordinates. Natural density is quantified in plant per meter²

<u>Site Name</u>	<u>Elevation (m)</u>	<u>Coordinates</u>	<u>Natural density</u>	<u>Demographic census</u>
Bellview 1	3440 m	39.0124, -107.0349	2.333	352
Bellview 2	3429 m	39.01763, -107.04102	5.8407	50
Burro Park	3082 m	38.122988, -106.79134	2.5144	50
Cement Creek	3195 m	38.92582, -106.77765	2.0446	57
Cottonwood Pass	3450 m	38.84618, -106.42587	6.3237	50
Gothic/Baldy Saddle	3266 m	38.97699, -107.02518	2.2725	50
Judd Falls Trailhead	2918 m	38.96649, -106.99473	0.2015	60
Lily Lake	3075 m	38.84271, -107.06286	2.2890	61
Mexican Cut	3440 m	39.02656, -107.06679	9.1457	52
Mount Crested Butte	2756 m	38.87534, -106.90848	0.9625	62
North Rustler's Gulch	2989 m	38.99451, -107.01538	2.0523	138
Ohio Creek Meadow	2730 m	38.79676, -107.08731	1.9098	54
Paonia Meadow	1967 m	38.923873, -107.33737	1.9014	62
Rocky Brook	3219 m	38.86939, -106.6633	6.5435	56
Spring Creek	2668 m	38.77058, -106.76467	3.3107	69
Thalictrum Hill (Research Meadow)	2897 m	38.95747, -106.98709	0.2361	280
Triangle High Meadow	3675 m	39.0008439, -106.925	9.8244	49
Virginia Basin	3350 m	38.97594, -106.97809	1.1610	51
Yule Pass East	3502 m	38.99706, -107.08272	1.4715	55

Q1: Determining natural patterns of population density across the elevation range

Field methods: At each of the 20 sites, a rectangular area in the core of each population was selected. Sizes of these plots ranged from 5.69 m² to 297.77 m². Individuals were mapped with an Emlid Reach RS2 GNSS receiver with centimeter level precision. Using these map points, we can ascertain the density of each plot and the number of neighbors each plant has (any plants within 1 meter of each other are neighbors). We can then calculate the population density (plants/m²) of each site and plot these data against the elevation (in meters) in order to determine if there is a relationship between elevation and population density.

Analysis: We log-transformed the density data and used a linear regression to test for an effect of elevation on population density.

Q2: Quantifying the impact of density on plant performance across the life cycle

Field methods: We conducted an annual demographic census of uniquely tagged plants across the species' elevation range. At each census we recorded plant survival (or death), the perimeter of the rosette where the plant's leaves enter the ground, whether the plant was flowering, plant sex, and the number of seeds produced. All quantitative measurements were recorded to the nearest half centimeter. For individuals producing >200 seeds, a portion of the inflorescence's seeds was counted then multiplied by the number of similarly-sized portions needed to make up the full inflorescence.

The same precision mapping methods were used to determine the location of each tagged plant in the demographic census as well as each plant's neighborhood density. We drew a 1m radius around each individual, counted the number of conspecific individuals within the radius, then divided that by the area of the neighborhood ($\pi \text{ m}^2$).

Analysis: We fit three candidate Generalized Linear Mixed Models (GLMMs) for each of the four components of the plant life cycle: survival, growth, flowering probability, and seed production. The first model's fixed effect predictors were an intercept and a slope for the plant's log-transformed current size with a random intercept and size slope by population and a random intercept for year. The second candidate model added a fixed effect slope for local density around the focal individual independent of plant size. Finally, the third candidate model added a fixed effect interaction between local density and focal plant size, allowing big and small plants to differ in the sign or magnitude of their response to neighbors. We chose an appropriate response distribution for each component of the life cycle. Survival probability was analyzed using a binomial distribution, growth was analyzed using a Gaussian distribution, flowering probability was analyzed using a binomial distribution, and seed production was analyzed using a zero-inflated negative binomial distribution. We used the following R packages to fit the

GLMMs: ‘tidyverse’, ‘lme4’, ‘glmmTMB’, and ‘modelr’ (Wickham et al. 2019; Bates et al. 2015; Brooks et al. 2017; Wickham 2023).

We used a model comparison approach to select the best fitting candidate model using AIC. If the difference between AIC scores was less than 2 or tied, the model with the lower degree of freedom was selected.

Q3: Predicting the effects of density-dependence on population carrying capacity across the elevation range

Field Methods: This process is entirely data processing and analysis.

Analysis: For each of the components of the life cycle, we used the best model fit from Q2 to parameterize a density-dependent, size-structured Integral Projection Model (IPM; Ellner, Rees 2006). These vital rate functions allowed us to build a representation of the complete life cycle and to determine the performance of any individual in any population at any density.

The iteration equation for our IPM was,

$$n(z', t + 1) = \int_{L_z}^{U_z} [P(z', z, N) + F(z', z), N] n(z, t) dz \quad (\text{eq. 1})$$

where n is a vector containing the number of individuals of size z at time t . P describes the persistence of established plants, which is the product of size- (z) and density-specific (N) probability of survival (s) and size-specific growth (g),

$$P(z', z) = s(z, N) * g(z', z). \quad (\text{eq. 2})$$

The equation for survival probability was,

$$s(z', z, N) = \text{plogis}(s_{int} + s_z * z + s_N * \text{sum}(n(z, t)) + s_{zN} * z * \text{sum}(n(z, t))) \quad (\text{eq. 3})$$

The equation for growth was,

$$g(z', z) = \text{Norm}(z' | g_{int} + g_z * z, sd_g). \quad (\text{eq. 4})$$

F describes the production of new individuals as the product of size- and density-specific probability of flowering (f), the probability of breeding success (p_b), the number of seeds produced (b), the probability of seedling establishment (p_{est}), and a distribution of seedlings across the range of possible seedling size (r_d),

$$F(z', z) = f(z', z, N) * p_b * b(z', z) * p_{est} * r_d. \quad (\text{eq. 5})$$

The equation for flowering probability was,

$$f(z', z, N) = \text{plogis}(fl_{int} + fl_z * z + fl_N * \text{sum}(n(z, t)) + fl_{zN} * z * \text{sum}(n(z, t))) \quad (\text{eq. 6})$$

The equation for seed production was,

$$b(z', z) = e^{se_{int} + se_z * z + se_N * \text{sum}(n(z, t)) + se_{zN} * z * \text{sum}(n(z, t))} \quad (\text{eq. 7})$$

The estimated parameter values for these vital rate equations are provided for each population in Table 2.

We constructed and projected the IPM using the R package ‘ipmr’ (Levin et al. 2021). We then projected the IPM until equilibrium and extracted the stable population size, also known as carrying capacity. We then used a linear regression to test for an effect of elevation on the carrying capacity of each population across the species’ elevation range.

Results

Q1: Elevation does not influence natural population density

There was a trend for increasing population density at higher elevation, but the relationship was not significant ($t = 2.023$, d.f. = 1, $p\text{-value} = 0.058$, $R^2 = 0.1853$; Fig. 1).

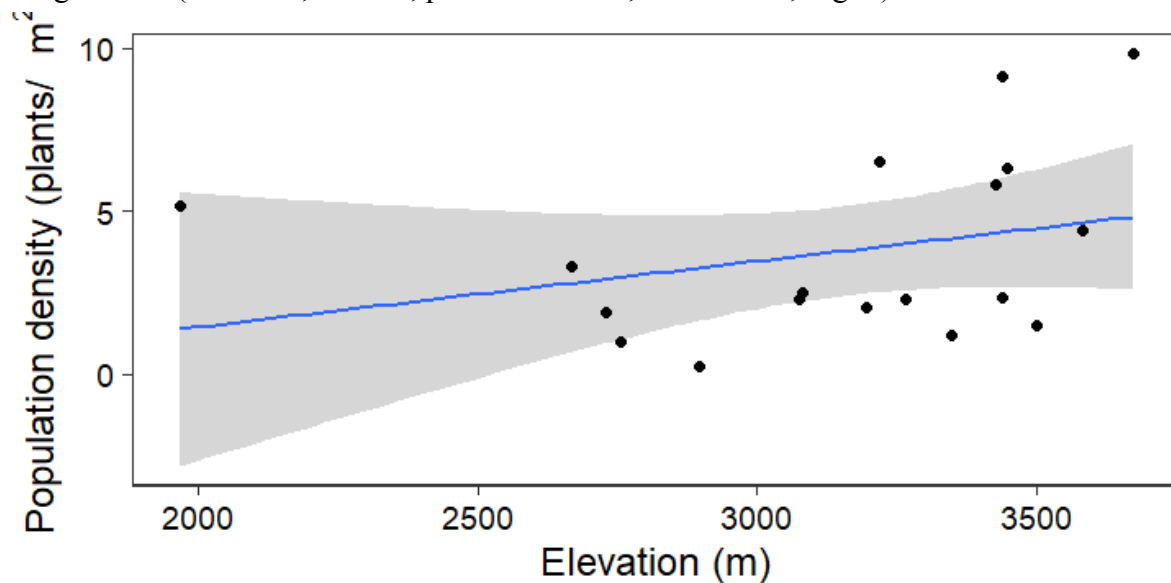


Figure 1: Observed population density of *Valeriana edulis* (plants/m²) across the species’ elevation range.

Q2: Survival and flowering probabilities were density dependent, growth and seed production were density independent.

Survival probability was analyzed using a binomial logistic regression. The model included main effects of plant size and local density (Table 2). As plant size increased, so too did

the probability of survival. However, as the number of neighbors increased, the probability of survival decreased, and this was true for all plants regardless of size.

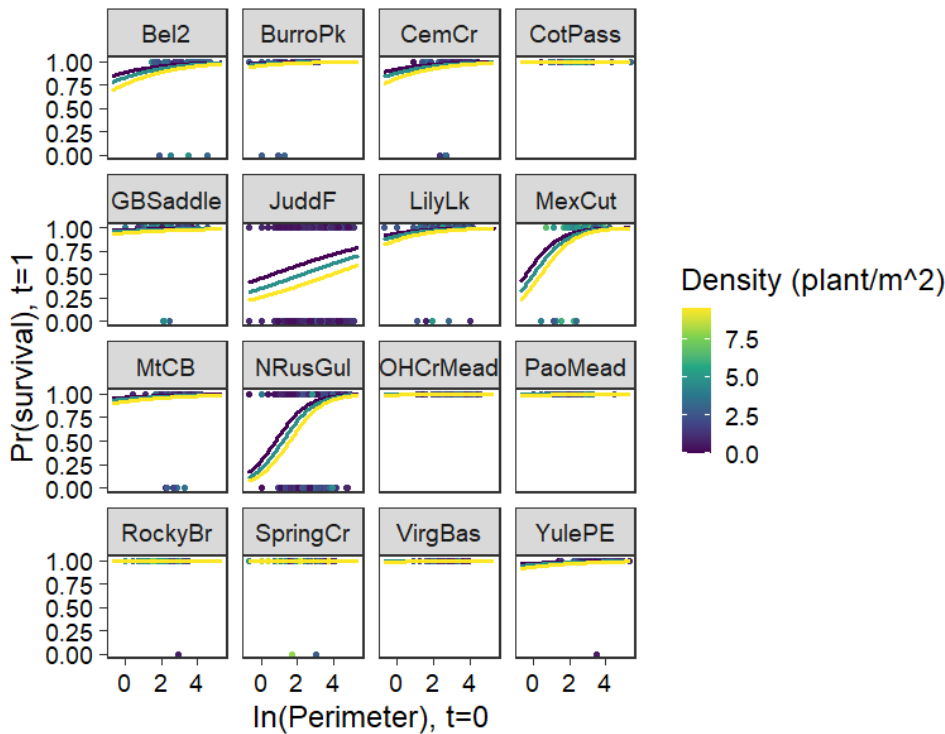
Growth was analyzed using a Gaussian distribution. The model of best fit was density independent, with only a main effect of plant size. Large plants grew larger year to year than smaller plants, who experienced less growth each year.

Flowering probability was analyzed using a binomial logistic regression. The model of best fit included main effects of plant size and local density. As plants grew larger, the probability of flowering increased. However, as the number of neighbors increased, the probability of flowering decreased, and this was true for all plants regardless of size.

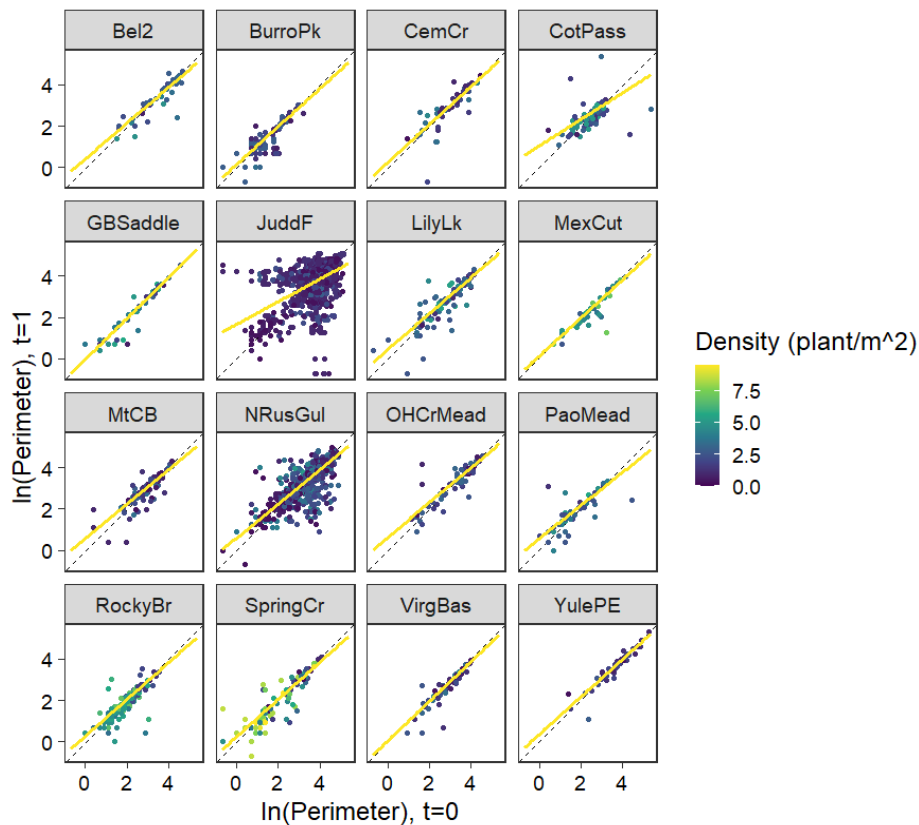
Seed production was analyzed using a zero-inflated negative binomial regression. The model of best fit was found to be density independent with only a main effect of plant size. As plant size increased, the number of seeds produced increased as well. The runner-up model also included a main effect of local density, with a positive effect of density on seed production.

Table 2. Candidate model comparison with AIC to identify where local density impacts performance across the plant life cycle. The AIC score in bold indicates the best model (rows) for each vital rate function (columns).

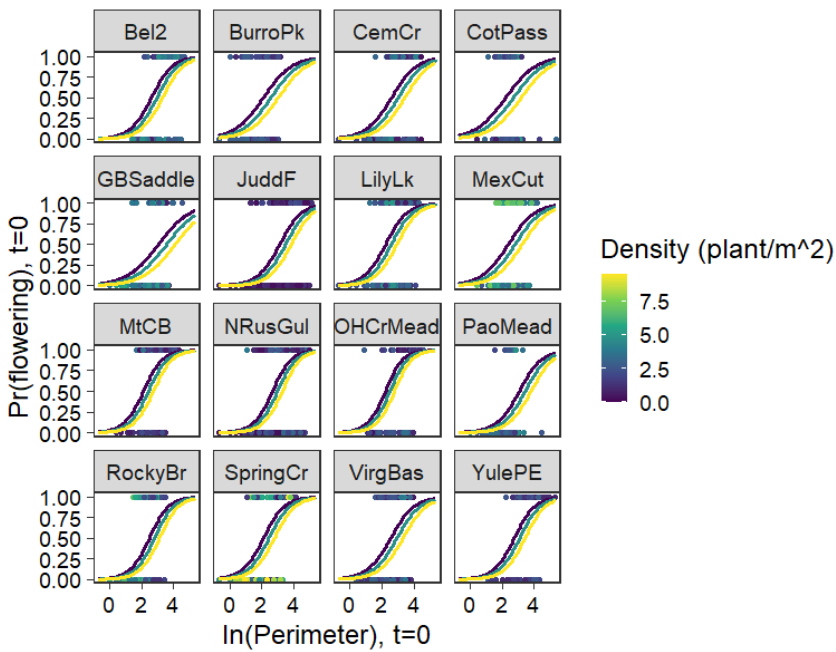
Candidate Model	Survival AICs	Growth AICs	Flowering AICs	Seed production AICs
DI	3552.724	7126.195	6091.294	21255.59 (best fit due to lowest degree of freedom)
DD (equal across size)	3551.264	7126.367	6078.383	21256.88
DD (size dependent)	3552.124	7132.414	6079.635	21254.94

**Figure 2:**

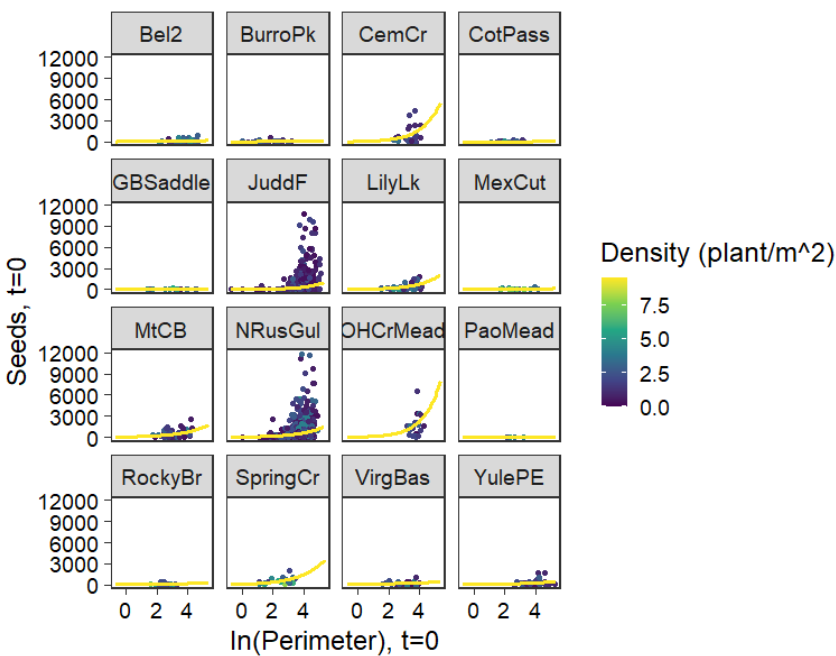
Plant survival probability increased with plant size and decreased with local density for all sizes. Panels depict the best model fit (lines) to census data (points) for each population. For simplicity, three density levels are plotted spanning the observed range.

**Figure 3.**

Growth from year to year was found to have no relationship with density. Larger plants were able to grow larger year to year compared to smaller plants, who had a slower growth rate. Panels depict the best model fit (lines) to census data (points) for each population. For simplicity, three density levels are plotted spanning the observed range.

**Figure 4.**

Flowering probability increased with plant size and decreased with local density for all sizes. Panels depict the best model fit (lines) to census data (points) for each population. For simplicity, three density levels are plotted spanning the observed range.

**Figure 5.**

Seed production was found to have no relationship with density. Panels depict the best model fit (lines) to census data (points) for each population. For simplicity, three density levels are plotted spanning the observed range.

Q3: Elevation had no effect on model-projected carrying capacity

Table 3. Estimated parameters for vital rate regressions in each study population.

Population	s_{int}	s_z	s_N	g_{int}	g_z	sd_g	f_{int}	f_z	f_N	$-\text{logit}(p_b)$	b_{int}	b_z	p_{est}	r_d mean	r_d sd
Bel2	2.013	0.459	-0.094	0.395	0.866	0.544	-3.960	1.510	-0.109	-1.919	4.847	0.260	0.010	0.916	0.100
BurroPk	3.935	0.493	-0.094	0.136	0.916	0.544	-2.383	1.123	-0.109	-0.836	4.905	0.332	0.010	0.916	0.100
CemCr	2.410	0.480	-0.094	0.240	0.919	0.544	-3.293	1.262	-0.109	-5.014	4.480	0.852	0.010	0.916	0.100
CotPass	6.191	0.159	-0.094	1.037	0.641	0.544	-2.392	1.072	-0.109	-1.526	4.473	0.097	0.010	0.916	0.100
GBSaddle	3.742	0.283	-0.094	-0.040	0.991	0.544	-3.075	1.001	-0.109	-5.664	5.138	-0.137	0.010	0.916	0.100
JuddF	-0.162	0.274	-0.094	1.663	0.548	0.544	-4.562	1.459	-0.109	-1.915	3.840	0.734	0.010	0.916	0.100
LilyLk	2.788	0.568	-0.094	0.446	0.871	0.544	-3.315	1.487	-0.109	-5.659	4.213	0.716	0.010	0.916	0.100
MexCut	0.433	1.078	-0.094	0.126	0.923	0.544	-2.847	1.196	-0.109	-3.297	4.680	0.173	0.010	0.916	0.100
MtCB	3.331	0.351	-0.094	0.571	0.826	0.544	-3.575	1.684	-0.109	-2.762	4.769	0.620	0.010	0.916	0.100
NRusGul	-0.934	1.137	-0.094	0.580	0.824	0.544	-4.608	1.723	-0.109	-3.370	4.303	0.662	0.010	0.916	0.100
OHCrMead	5.751	0.254	-0.094	0.618	0.845	0.544	-4.021	1.822	-0.109	-5.131	4.404	0.934	0.010	0.916	0.100
PaoMead	5.623	0.165	-0.094	0.559	0.801	0.544	-4.402	1.433	-0.109	1.464	4.646	0.435	0.010	0.916	0.100
RockyBr	5.930	0.005	-0.094	0.248	0.891	0.544	-4.150	1.662	-0.109	-4.758	4.736	0.254	0.010	0.916	0.100
SpringCr	5.522	0.027	-0.094	0.231	0.901	0.544	-3.231	1.529	-0.109	-5.136	5.117	0.648	0.010	0.916	0.100
VirgBas	5.180	0.257	-0.094	0.038	0.958	0.544	-3.506	1.369	-0.109	-5.214	5.143	0.256	0.010	0.916	0.100
YulePE	3.470	0.364	-0.094	0.347	0.908	0.544	-4.297	1.558	-0.109	-4.221	4.650	0.377	0.010	0.916	0.100

Table 4. Shown is the model-projected carrying capacity for each site.

Sites	Model-Projected Carrying Capacity (K)
Bellview 2	1599.6462
Burro Park	2516.1143
Cement Creek	2663.4313
Cottonwood Pass	3245.7691
Gothic-Baldy Saddle	1247.0518
Judd Falls Trailhead	610.8084
Lily Lake	3259.4411
Mexican Cut	702.1936
Mt. Crested Butte	3439.2298
North Rustler's Gulch	1066.0545
Ohio Creek Meadow	4814.0413
Paonia Meadow	2410.6561
Rocky Brook	3266.8097
Spring Creek	4195.8011
Virginia Basin	2997.3476
Yule Pass East	2822.7642

Using the demographic rate data from the previous question (Table 2), our IPMs all converged on an equilibrium carrying capacity. While the data does suggest a negative trend in carrying capacity with increase in elevation, the relationship is not significant, so there is no observable effect of elevation on model-projected carrying capacity (t test statistic= 1.979, d.f.= 1, p-value: 0.3515, R^2 = 0.06221; Fig. 6)

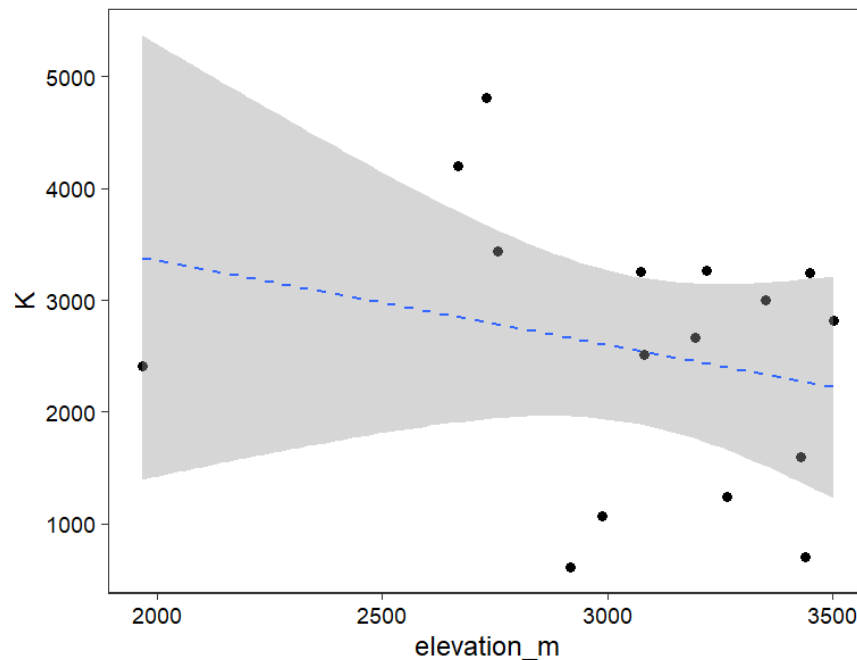


Figure 6.

The equilibrium carrying capacity (K) projected by an Integral Projection Model was not related to population elevation.

Discussion

We used three complementary approaches to identify the signatures of density-dependence across the elevation range of the plant *V. edulis*. We found (1) no elevational gradient in observed natural density of populations, (2) density dependence impacted survival and flowering probabilities, but not yearly growth rates or seed production, But (3) equilibrium carrying capacity projected by our IPM had no relationship with elevation.

Elevation had no significant relationship, positive or negative, with observed population density. Furthermore, our data did not support the Abundance Center Hypothesis was not fulfilled, since our population points were observed in a random pattern, instead of the predicted parabolic shape (Fig. 1; Dallas et al. 2020). Several ecological mechanisms could be responsible for the lack of a clear pattern in natural population density across the elevation range of *V. edulis*. First, it could be that no factor has a more significant positive or negative effect than other factors (resource availability, disturbance frequency, herbivory, etc). Second, natural densities are subject to the confounding effects of population differences in density-independent factors that nonetheless impact population density. For example, a recent avalanche at the Judd Falls Trailhead is believed to have caused heavy mortality across the entire population (W.K. Petry, pers. comm.). Even if local density had no impact on plant mortality rates following the avalanche, this disturbance reduced density only at this population and not consistently across the species elevation range. In short, there may be too many factors included with elevation. We observed no significant differences in natural population density in any of our sites across 2500 meters of elevation.

Individual plant performance tended to increase with plant size and—when detected—decrease with local density. An increased perimeter of individual plants projects a

higher chance of survival into the next year, and higher plant density is associated with a lower probability of survival, regardless of size. As the plants grew larger, their chance of survival increased relative to their size. Deeper roots, higher resource or energy reserves, and more leaves for photosynthesis all give larger plants a better probability of survival. However, regardless of how large the plants were, their probability of survival decreased with the number of neighbors they had competing for resources, light, and space.

Probability of flowering was also found to increase with plant size, and decrease with a high number of neighboring plants. Since flowering is a significant resource investment, the larger plants with more robust energy and resource storage had a higher probability of flowering year to year. Smaller plants, especially those that have just put up their first leaves, do not have the spare resources to invest into flowers. Flowering was found to be negatively affected by density, since the neighboring plants are competing for the same resources in attempts to make their own flowers.

Growth is not found to be impacted by density, which was surprising, since it could be assumed that resource competition would play a role in growth as well. Seed production was found to be density independent, followed very closely by a positive density dependent model. A potential explanation for this result is that there may be a positive relationship between density and seed production; a dense patch of flowering plants will attract pollinators, who will cross pollinate the plants and increase the chances of seed production. However, the resource and energy cost of seed production must be greater than any benefit that density can bring, since the density independent model best fit the data.

After projecting our IPM to equilibrium, we found no relationship between model-projected carrying capacity and elevation. Though there was no significant relationship, we did observe a generally negative *trend* in carrying capacity as elevation increased. There may be confounding factors across elevation (soil types, soil moisture, snowmelt date, herbivores, or precipitation rates) that led to this result, and these factors could be similar in their effects on carrying capacity across elevation. Unlike Xu and Yu, 2014, and LeManna et al., 2022, *Valeriana edulis* does not show the same relationship between elevation and density.

Further research could observe the effects of density dependence in other ways, by studying the mechanism by which DD acts upon populations. Environmental and sex ratio variation could play a part in dense population dynamics as well. Perhaps *Valeriana edulis* is not the species to study the effects of elevation on density dependence. Other species may be more suitable for this type of research and study. There may be some confounding factor that was not observed in this study.

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