**Title**

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**Abstract**

**Introduction**

Environmental and biotic filtering can act at the community level by affecting vital rates across multiple species. But these filtering processes also act on the species level to affect growth, survival, and reproduction. These fine-scale filtering processes are of particular interest in populations that are small, either because they are naturally rare, or because they are adversely impacted by anthropogenic change. Both positive and negative impacts of both biotic and abiotic filtering on rates of birth, death, growth, or survival can have major implications for a population’s existence, particularly when it is already small.

There are five main processes by which abiotic and biotic variation can impact vital rates to maintain rare populations: negative density dependence, opposing response of demographic rates to the same environmental factors, vital rate buffering, asynchronous responses between subpopulations, and source-sink dynamics (Dibner et al. 2019). Determining which of these factors contribute to persistence or decline in populations of rare species is critical for informed conservation and management. I will use size-based Integral Population Models (IPMs) that incorporate a seed bank stage to identify which factors are contributing to the persistence and in some cases population growth of a rare plant species, *Oenothera coloradensis* (Onagraceae).

Oenothera coloradensis is monocarpic perennial forb that occurs in riparian habitats in southeastern Wyoming, northern Colorado, and western Nebraska. It was listed as ‘threatened’ under the Endangered Species Act from 2000 until 2019, when it was delisted due to recovery. The largest known populations exists on the FE Warren Airforce Base (FEWAFB) near Cheyenne, WY, and the Soapstone Prairie Natural Area in Larimer County, CO. A three-year demographic study of O. coloradensis was established at the FEWAFB in the 1990s. The results from this study were used to create a matrix population model for this species, which indicated overall population growth with spatial variability in population growth rates across measured subpopulations, and identified the transitions from large rosette to reproductive, and from seedling to small rosette as the most important for population growth (Floyd and Ranker 1998). Our study will evaluate the current population growth rates of O. coloradensis in three FEWAFB subpopulations, and three subpopulations at Soapstone. I will use IPMs in place of transition matrix models, which allow us to model transition probabilities across a continuous spectrum of plant size, as opposed to discrete life stages (Easterling et al. 2000). The updated model of vital rates for these populations, combined with measurements of environmental variation, will allow us to identify mechanisms by which biotic and abiotic filtering are driving subpopulation persistence or decline. Even though O. coloradensis is no longer managed under the Endangered Species Act, it is critical that we understand the forces shaping population size and fitness in order to effectively keep this species on a trajectory of recovery.

Hypothesis 1: Density dependence, small-scale source-sink dynamics and asynchronous responses between subpopulations are important mechanisms for the persistence of O. coloradensis populations. This species occurs in habitats that naturally experience frequent, highly-localized disturbance, which means that some subpopulations of O. coloradensis might be negatively affected by flood, for example, while other nearby populations are simultaneously thriving due to lack of disturbance. This population-wide pattern of asynchronous disturbance also could make source-sink dynamics important. We also have anecdotal evidence of large fluctuations in the number of plants within subpopulations, indicating that density dependence might be important.

* Motivation for the study
  + Importance of demographic information for conservation
  + Of particular importance for rare plants
    - Important to identify life stages most relevant to population growth/persistence—considering *every* life stage
      * Talk about seedbanks here
    - Also important to identify other processes that affect population growth/persistence, and may allow rare populations to persist
* Introduce study species
  + Basic intro
    - *O. coloradesis* is "weakly conserved", and has a "protection status score" of 1.7 out of 10 (Rondeau et al. 2011)—primarily due to lack of conservation of its habitat, and likelihood of development impact (particularly oil and gas)
    - ESA listing rule: (Jennings 2000)
    - Delisting proposal: (Kurth 2018)
    - Final desilting rule: (Everson 2019)
    - 2021 WYNDD monitoring report (Heidel et al. 2021) (incorporates census data through 2020)
  + Previous work
    - Floyd and Ranker; Burgess; WYNDD monitoring; Soapstone counts?
    - Floyd and Ranker identified size as the more important for lambda than age
* Brief synopsis of what we did

**Methods**

*Species description*

*Oenothera coloradensis*, formerly *Gaura neomexicana spp. coloradensis* (Wagner et al. 2007), is an herbaceous, monocarpic perennial plant in the Onagraceae family. Non-reproductive plants consist of a rosette of basal leaves with a fleshy taproot. Flowering typically occurs around four years of age, when plants send up a stalk between 10 and 30 cm tall that bears flowers and fruits. Plants almost always die after flowering. Seeds are contained within small, woody, indehiscent capsules that contain two to five seeds each (Burgess et al. 2005). A single adult plant can produce more than 500 capsules. This species does not reproduce vegetatively, although seeds typically germinate near the base of the parent plant, which often results in dense clumps of mature individuals (Heidel et al. 2021). *O. coloradensis* has no known specialist pollinators or seed dispersers.

Previous work established that *O. coloradensis* population growth rate is particularly impacted by recruitment of individuals to the small rosette, or seedling, stage (Floyd and Ranker 1998). Seedling recruitment increases when non-*O. coloradensis* biomass is removed, indicating that surrounding grasses and forbs outcompete or shade-out seedlings (Munk et al. 2002). Previous work also suggests that seedbanks are important for this species, since years of high seedling density are not necessarily preceded by years of high rates of flowering and seed production (Munk et al. 2002). The *O. coloradensis* seedbank has not been studied directly, but a greenhouse seed viability and germination study showed that an average of 58% of seeds produced by a parent plant are viable, and that a viable seed has a 20% mean probability of germinating (Burgess et al. 2005). Neither seed viability nor germination rate changed meaningfully over the five years of the study. These results also showed that two-months of cold-moist stratification triggered germination.

This species primarily occurs in open, frequently disturbed habitats with sub-irrigated, alluvial soils (Jennings 2000). Populations typically occur within the floodplain of ephemeral or perennial streams, but also exist in wet meadows, drainage bottoms, and spring-fed wetlands (Munk 1999). *O*. *coloradensis* commonly co-occurs with ﻿*Agrostis stolonifera*, *Pascopyrum smithii*, *Poa pratensis*, *Glycyrrhiza lepidota*, *Iris missouriensis*, *Cirsium flodmanii*, and *Grindelia squarrosa* (Jennings 2000, Munk et al. 2002). Encroachment of woody shrubs such as *Salix exigua* has been correlated with declining numbers in some populations (Heidel et al. 2021). Relatively frequent disturbance such as flooding that reduces growth of both woody and herbaceous species and removes litter is important for this species, especially for successful seedling recruitment (Jennings 2000, Burgess 2003).

All historical and extant known *O. coloradensis* populations lie within a ﻿17,000 acre area that includes southeast Wyoming, northern Colorado, and a small part of southwest Nebraska. Range-wide survey efforts between 1984 and 1986 identified more than 20 populations. The largest population on Federal land occurs on the F. E. Warren Airforce Base near Cheyenne, WY. The Wyoming Natural Diversity Database (WYNDD) began a base-wide census of reproductive individuals in this population in 1986, and has repeated this census annually since 1988 (Heidel et al. 2021). The Soapstone Prairie Natural Area, a public property owned by the city of Fort Collins, CO, has the largest documented number of *O. coloradensis* individuals, but this population has not been routinely monitored. The first estimate of species size after its full geographic range was identified occurred in 1998, when it was approximated that the entire species consisted of 47,300 to 50,300 reproductive individuals (Jennings 2000). Although an older estimate of total species numbers or geographic range does not exist to serve as a reference, decline in a majority of the known populations between the mid-1980s and 2000 lead the U.S. Fish and Wildlife Service (USFWS) to designate *O. coloradensis* as a “threatened” species protected under the Endangered Species Act (Jennings 2000). Although this species appears to be naturally rare, mangers were concerned that, without protection, *O. coloradensis* had the potential for extinction because of habitat loss due to ranching, natural resource extraction, and shrub encroachment resulting from altered disturbance regimes.

*Demographic Data Collection*

We conducted a three-year demographic study of *O. coloradensis* across six subpopulation, three at the F.E. Warren Airforce Base (FEWAFB) and three at the Soapstone Prairie Natural Area. In early summer 2018 we established three 2x2 m quadrats in each of these subpopulations, resulting in 18 plots (Table 1). We tagged and mapped every unique individual in each of these plots that had a maximum leaf length greater than 3 cm, and recorded their longest leaf length, reproductive status, reproductive output, and presence and character of herbivory damage. In 2019 and 2020 censuses, we mapped and tagged new plants larger than 3 cm and re-measured all surviving plants from previous years. There were too many *O. coloradensis* plants smaller than 3 cm in longest leaf length to map and tag each year, so instead we recorded a tally of these in each plot in each year. We will refer to these plants smaller than 3 cm as “seedlings,” and plants larger that 3 cm as “mature plants.” All censuses took place between late May and early July, during the peak of the *O. coloradensis* growing season.

It was not possible to measure exact reproductive output for flowering mature individuals, since *O. coloradensis* seeds are contained in indehiscent capsules. Additionally, buds on the same plant flower and set seed with a time lag, such that mature seed capsules often exist at the tip of a stem while un-opened buds lower down on that same stem have not yet flowered. This makes it difficult to count the total number of capsules produced by a plant. However, seed capsules leave a noticeable scar on the stem, so we used the number of seed capsule scars on reproductive stems as an estimate of capsule production. Counting scars is extremely time-intensive since a single plant can produce several hundred capsules, so we used linear regression to estimate the relationship between the length of stem bearing capsule scars and the number of capsules produced by that stem. Linear regression using stem measurements and capsule counts from 106 individuals indicates that number of capsules produced = 2.95 + 2.0\*(stem length in cm) (multiple R-squared = 0.67, P = < 0.01, F-statistic = 212.5, df = 104). We used this relationship to estimate capsule production for each reproductive individual. Previous work indicated that each capsule contained an average of 1.7 seeds, so we multiplied the estimated number of capsules produced by an adult plant by 1.7 to estimate seed production (Burgess et al. 2005).

**Table 1**: Permanent Plot Locations. GPS coordinates listed in decimal degrees, map datum and spheroid: WGS 84.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Site** | **Subpopulation** | **Plot Name** | **N Coordinate** | **W Coordinate** |
| FEWAFB | Unnamed Creek | U3 | 41.13642 | -104.87209 |
| FEWAFB | Unnamed Creek | U4 | 41.13634 | -104.87183 |
| FEWAFB | Unnamed Creek | U6 | 41.13647 | -104.87132 |
| FEWAFB | Diamond Creek | D7 | 41.14340 | -104.88380 |
| FEWAFB | Diamond Creek | D10 | 41.14441 | -104.88303 |
| FEWAFB | Diamond Creek | D11 | 41.14431 | -104.88094 |
| FEWAFB | Crow Creek | C4 | 41.15540 | -104.87497 |
| FEWAFB | Crow Creek | C5 | 41.15477 | -104.87474 |
| FEWAFB | Crow Creek | C8 | 41.15534 | -104.87487 |
| Soapstone | Pasture HQ5 | S1 | 40.99297 | -105.00925 |
| Soapstone | Pasture HQ5 | S2 | 40.99318 | -105.00935 |
| Soapstone | Pasture HQ5 | S3 | 40.99342 | -105.00937 |
| Soapstone | Pasture HQ3 | S4 | 40.98623 | -105.01691 |
| Soapstone | Pasture HQ3 | S5 | 40.98639 | -105.01671 |
| Soapstone | Pasture HQ3 | S6 | 40.98650 | -105.01656 |
| Soapstone | Meadow | S7 | 40.98753 | -105.02148 |
| Soapstone | Meadow | S8 | 40.98747 | -105.02179 |
| Soapstone | Meadow | S9 | 40.98724 | -105.02145 |

*Environmental Measurements*: We measured growing season soil temperature and soil moisture at each plot to quantify variation in average abiotic conditions across subpopulations. To measure soil temperature, we buried an iButton temperature logger (model SD19216-F5# Thermocron) approximately 2 cm below the soil surface immediately outside the perimeter of each plot (Brabyn et al. 2014). These iButtons were in place from June 2019 through May 2020, and recorded temperature every two hours over that period. From this data we calculated average and standard deviation of soil temperature during the growing season (April-September) and winter (October-May). Several iButtons were damaged or removed by animals, so soil temperature values were averaged across plots in the same subpopulation. We measured soil moisture using (insert soil moisture meter details here) at each plot on the same day in September, 2019. These soil temperature and moisture values were not used to predict changes in population dynamics over time, but instead were used to test the effect of subpopulation-level differences in abiotic conditions on population dynamics. These variables are referred to as “soil characteristics.”

To determine the effect of temporal variation in climate on *O. coloradensis* populations, we used modeled, population-level temperature and precipitation data from PRISM (PRISM Climate Group, Oregon State University, https://prism.oregonstate.edu, accessed 30 November 2021). We calculated the mean and standard deviation of temperature for both the growing season and preceding winter season for each year of demographic data collection at FEWAFB and Soapstone Prairie. We also calculated total precipitation for each water-year, which we defined as the period from October of the previous year to September of the current year. These variables are referred to as “environmental covariates.”

*Population Models:* We used data from the demographic study detailed above in combination with results from greenhouse and field seedbank studies, to parameterize integral projection models (IPMs) for *O. coloradensis*. These IPMs each have a discrete seedbank stage, and a continuous, size-based stage for above-ground plants (Ellner and Rees 2006, Rees et al. 2006, Paniw et al. 2017). We created a suite of IPMs that each used a different subset of data, or included different covariates in vital rate models. First, the data used to fit vital rate models came either from a single subpopulation, a population (FEWAFB or Soapstone prairie), or from all locations, and included data for all transitions, or only one transition (2018-2019 or 2019-2020). Second, while all vital rate models included size­*t*(or (size*t*)2) as a predictor of vital rates, these models could also include predictor terms for one or both of the following: population size in the previous year (density dependence), and environmental variation (water year precipitation, mean and standard deviation of annual growing season temperature, and mean and standard deviation of annual winter temperature). Table 2 indicates the data and covariates included in each of the IPMs we constructed.

All of the IPMs used the same kernel structure, where the continuous, above-ground population size (*n(z’, t+*1*)*) and the seedbank (*B(t+*1*)*) at time *t+*1were described by the following equations:

where *z* is the distribution of plant size in the current year (“size*t*”), *z’* is the distribution of plant size in the next year (“size*t*+1”), and *U* and *L* are the upper and lower boundaries of plant size. *G*(*z’, z*) is the vital rate function describing size*t*+1 as a function of size*t*. The vital rate functions *s*(*z*), *Pb*(*z*), and *b*(*z*) describe the relationship between size*t* and survival probability of non-flowering plants, flowering probability, and seed production of flowering plants. *co*(*z’*) is the distribution of above-ground recruit size*t*+1. *goCont*, *outSB*, *goSB*, and *staySB* are discrete parameters indicating the probability of a seed produced in year *t* germinating as a seedling in year *t*+1, a seed from the seedbank in year *t* germinating as a seedling in year *t*+1, a seed produced in year *t* going into the seedbank in year *t*+1, and a seed from the seedbank in year *t* persisting in the seedbank in year *t*+1 (Paniw et al. 2017) (Table 2).

We used data from the three-year demographic monitoring study to parameterize the vital rates used in the IPMs. Vital rate functions for the continuous, size-based above-ground stage were parameterized using data from “mature plants” as well as seedlings. Although seedlings (above-ground plants < 3 cm in leaf length) were only tallied in each quadrat and year instead of tagged and measured, we incorporated them into the dataset for continuous, above-ground plants by assigning them a random size drawn from a continuous, uniform probability distribution (seedling size ~ *U*(0.1, 3)). Each new recruit to the > 3 cm stage in year *t*+1 was randomly assigned to a seedling in year *t*. Seedlings in year *t* that were assigned a recruit in year *t*+1 survived, while those without an assigned recruit died. Incorporating seedlings into the continuous dataset in this fashion allowed us to create IPMs using only one discrete stage.

We used data from the demographic study to estimate continuous vital rate functions describing survival, growth, probability of flowering, seed production, and recruit size. For each of these vital rates, we fit subpopulation-level models as well as models using data across all sites. We additionally fit models with and without density dependence, with and without environmental covariates, and using data either from all years or from each unique annual transition. The basic model structure was the same for each vital rate (Table 2). Additional covariates indicating population size and environmental conditions were added to these basic models. We modeled survival probability (*s(z)*) as a function of log-transformed leaf size*t* using generalized linear models with binomial error distributions. Flowering individuals were excluded from the data used to fit survival models, since *O. coloradensis* is a monocarpic perennial that nearly always dies after flowering. Probability of flowering (*Pb(z))* was also modeled using generalized linear models with binomial error distributions, and was predicted by log-transformed leaf size*t* plus log-transformed leaf size*t* squared. We estimated seed production (*b(z)*) as a function of size*t* using negative binomial models, which are ideal for overdispersed count data. We only used data from flowering plants in this analysis, and fit these models using the “glm.nb” function from the “MASS” R package (Venables and Ripley 2002). Plant size*t+1* (*G(z’,z)*) was described as a series of Normal distributions with mean = μs and standard deviation = σs. Mean plant size­*t+1* (μs) was modeled as a function ofsize­*t* using linear models with Gaussian error. The standard deviation of plant size­*t+1* (σs) was the residual standard error of these linear models. The distributions of recruit size in the next year (*co*(*z’*)) were described by Normal distributions with the mean μr, and the standard deviation σr. μr and σr were the mean and standard deviation of observed plant size in the next year.

**Table 2**. Description of vital rates used in *O. coloradensis* IPMs

|  |  |  |
| --- | --- | --- |
| **Vital rate** | **Description** | **Model** |
| *goCont* | *P*(seed produced in *t* germinates in *t*+1) | *goCont* = viab. rate (germ. rate) |
| *outSB* | *P*(seedbank seed in *t* germinates in *t*+1) | *outSB* = germ. rate (1 - death rate) |
| *goSB* | *P*(seed produced in *t* goes to the seedbank in *t*+1) | *goSB* = viab.rate (1 - germ. rate) |
| *staySB* | *P*(seedbank seed in *t* stays in the seedbank in *t*+1) | *staySB =* (1 - germ. rate) (1 - death rate) |
| *s*(*z*) | *P*(survival from *t* to *t+1*) | logit(survival) ~ β0 + β1 (log(size*t*)) + ε |
| *Pb*(*z*) | *P*(flowering in *t*) | logit(flowering) ~ β0 + β1 (log(size*t*)) + β2 (log(size*t*)2) + ε |
| *b*(*z*) | Seed production in *t* | exp(seed number) ~ β0 + β1 (log(size*t*))+ ε |
| *G*(*z’,z*) | Distribution of plant size in year *t* | *G*(*z’,z*) = *N* (μs, σs); μs ~ β0 + β1 (log(size*t*)) + ε ; σs~ RSE (β0 + β1 (log(size*t*)) + ε) |
| *co*(*z’*) | Distribution of new recruit size in year *t* | *co*(*z’*) = *N*(μr, σr); μr = mean (size of recruits in *t*) σr = stnd. dev. (size of recruits in *t*) |

\* RSE = residual standard error

We estimated discrete vital rates for seeds using data from both greenhouse and field-based germination and seed viability studies. Previously-published data from a greenhouse experiment using *O. coloradensis* seed capsules collected from the FEWAFB populations determined that viable seeds had an average germination rate of 20.3% after cold-stratification, and did not identify a consistent decline in germination rate over five years (Burgess et al. 2005). This study also found that a seed capsule contained an average of 1.7 seeds, and that 58.5% of seeds produced were viable. We conducted an additional seed study to determine if overwintering in natural conditions lead to a lower germination rate than was identified in the previous greenhouse study. We buried 60 field-collected seed capsules in mesh bags at 6 locations near our demographic study plots at FEWAFB, and then recovered the seed bags after one winter. An average of 10% of seed capsules were not recoverable, likely because they were non-viable and withered away or were eaten. We planted the recovered capsules in standard greenhouse conditions, and found a mean germination rate of 6.8%. This germination rate was much lower than that identified by Burgess et al., however our seed study had a much smaller sample size, which reduces the credibility of our result. However, it is still likely that true germination rates are much lower than those identified in greenhouse conditions, so we reduced the germination rate identified in Burgess, et al. by 20%. These were the parameters we used to estimate the discrete seed vital rate parameters: viable seed germination rate (germ. rate) = 0.16, viability rate of seeds produced by a parent plant (viab. rate) = 0.58, rate of natural seed death in the seedbank (death rate) = 0.10. We did not have the data required to determine how these rates changed across subpopulations or in response to abiotic variation, so we used the same seed vital rates for all IPM models (Table 2).

We used these vital rate functions and discrete parameters described above to construct discretized IPM kernels. All kernels were numerically implemented using the “midpoint rule” method (Easterling et al. 2000) with 500 bins, an upper size limit corresponding to 120% of the maximum observed plant size and a lower size limit corresponding to 80% of the minimum observed plant size. We then used eigen analysis of these kernels to estimate asymptotic population growth rate, λ, damping ratio, stable size distribution, and reproductive value (Caswell 2001, Ellner et al. 2016). We used 1000 iterations of bootstrap resampling to estimate 95% bootstrap confidence intervals (95% CIs) for each continuous vital rate parameter included in each IPM, as well each estimate of λ (Merow et al. 2014, Fieberg et al. 2020). We were unable to estimate CIs for discrete seedbank parameters because they were from a previous publication. We used perturbation analysis to determine the sensitivity and elasticity of λ to changes in germination rate, viability rate, seed survival rate, and each parameter in each continuous vital rate model (Morris and Doak 2002). We used the IPM with all data and no density dependence or environmental covariates for this analysis. These vital rates and IPMs, as well as the information derived from them, were used to evaluate the importance of negative density dependence, demographic compensation, vital rate buffering, asynchronous responses, and source-sink dynamics for persistence of *O. coloradensis* populations.

**Table 3:** A key to the data and covariates included in each integral projection model.

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **IPM name** | **Data Included** | | | | | | | | | **Transitions included** | | | **Covariates included** | |
| **All subpopulations** | **Each population** | | **Each subpopulation** | | | | | | **All transitions** | **Each transition** | | **Density dependence** | **Environmental covariates** |
| **Soapstone prairie** | **FEWAFB** | **Unnamed Creek** | **Diamond Creek** | **Crow Creek** | **Meadow** | **HQ3** | **HQ5** | **2018-2019** | **2019-2020** |
| A | x |  |  |  |  |  |  |  |  | x |  |  |  |  |
| B | x |  |  |  |  |  |  |  |  | x |  |  | x |  |
| C, D, E, F, G, H |  |  |  | x | x | x | x | x | x | x |  |  |  |  |
| I, J, K, L, M, N |  |  |  | x | x | x | x | x | x | x |  |  | x |  |
| first\_DI/ second\_DI | x |  |  |  |  |  |  |  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |

*Evaluating Persistence Mechanisms: Negative Density Dependence*

In order to determine the importance of density dependence in *O. coloradensis* populations, we compared subpopulation-level, all-transition IPMs and vital rate functions that did and did not include population size in the current year as a covariate in vital rate models (density-independent IPMs: C-H; density-dependent IPMs: I-N). We compared the 95% CIs of asymptotic λ values to identify significant differences between density-dependent and density-independent IPMs. We also used AIC to identify significant differences between vital rate models with and without density dependence. Finally, we used the “ipmr” R package to project each subpopulation forward 100 time-steps, either with or without density dependence (Levin et al. 2021). Each projection incorporated demographic stochasticity, was initiated with the stable size distribution derived from the respective IPM, and was repeated 1000 times. We used these projections to estimate the distribution of stochastic lambda (λs) for each subpopulation, which we then compared to identify the importance of density dependence for determining long-term population dynamics.

*Evaluating Persistence Mechanisms: Demographic Compensation*

To test for demographic compensation, we calculated the correlation between environmental covariate coefficients in different vital rate models. A negative correlation between coefficients of the same covariate in different vital rate models indicated demographic compensation was taking place (Villellas et al. 2015, Dibner et al. 2019). For example, if soil moisture had a positive effect on growth but a negative effect on survival, this would be evidence for demographic compensation. For this correlation analysis we used vital rate models that were fit using data from all subpopulations and both transitions, and that included covariates for density dependence and all environmental covariates (water year precipitation, mean and standard deviation of growing season temperature, and mean and standard deviation of winter temperature). We tested the significance of negative correlations between environmental covariate coefficients using a randomization procedure similar to that used by Villellas et al. (2015), where we randomly assigned an environmental covariate coefficient drawn from the observed distribution of values for that coefficient to each vital rate function, calculated a correlation matrix between those coefficients in each vital rate function, and counted the number of negative correlations in that matrix. This procedure was repeated 10,000 times to generate a null distribution of the expected number of negative correlations between environmental coefficients that would occur randomly. We compared the observed number of negative correlations between each environmental covariate coefficient to these expected distributions of random correlations to determine statistical significance. We could not test for demographic compensation in discrete seedbank vital rate parameters because we did not know how they varied according to environmental conditions.

*Evaluating Persistence Mechanisms: Vital Rate Buffering*

We tested for the presence of vital rate buffering in *O. coloradensis* populations by comparing the coefficient of variation (CV) of each vital rate parameter to its elasticity (Pfister 1998, Morris and Doak 2004). We used the IPM that was fit across all subpopulations using data from both transitions to calculate elasticity values for each parameter in each continuous vital rate function (Morris and Doak 2002). We calculated the CV for each seedbank rate and vital rate function parameter using the equation ﻿CV = (σ / μ)\*100, where μ and σ represent the mean and standard deviation of observed values of each vital rate, respectively. These “observed values” were 12 parameter estimates for each vital rate parameter which were taken from the vital rate functions that were fit uniquely for each subpopulation and each transition. We used Spearman correlations to identify significant correlation between the CV and elasticity of each vital rate parameter (Pfister 1998). A significant negative correlation indicated that vital rate buffering was present. We were unable to estimate CV values for discrete, seedbank vital rates and so could not determine whether they were contributing to vital rate buffering.

*Evaluating Persistence Mechanisms: Asynchronous Responses and Source-Sink Dynamics*

We conducted two tests to determine whether *O. coloradensis* subpopulations showed asynchronous responses to environmental variation. First, we made a correlation matrix to determine how change in λ across each transition was correlated across each subpopulation, using values of λ derived from IPMs for each subpopulation in each transition. We used Mantel tests to determine if the correlation of λ across subpopulations was significantly related to the Euclidian distance between each subpopulation. A positive relationship between subpopulation proximity and degree of correlation of λ was evidence for spatial asynchrony between subpopulations. We also used the “ipmr” R package to project each population (Soapstone prairie and FEWAFB) forward 100 years. Once set of projections included a random effect of subpopulation in vital rate functions to account for spatial asynchrony in demographic processes, and the other set did not. Each projection was repeated 1000 times, and icluded the effects of density dependence and demographic stochasticity. A difference in stochastic λ (λs) between projections with and without a random effect of subpopulation would indicate that spatial asynchrony was important for demographic processes in these populations.

Because we did not have information about gene flow between subpopulations of *O. coloradensis* via pollination or seed dispersal, it was not possible to directly measure whether fine-scale source-sink dynamics were acting in these populations. However, because variation in population growth rate across space is a pre-requisite for source-sink dynamics, the previously described tests for spatial asynchrony in subpopulations can also provide some evidence for the existence of source-sink dynamics.

*Determining population stability over time*

To determine the likelihood that each population (Soapstone prairie and FEWAFB) would persist, we used the “ipmr” R package to project each population forward 100 years, incorporating the effects of density dependence and demographic and environmental stochasticity. Each projection was repeated 1000 times. We did one set of projections using climate values that were randomly drawn from the distribution of observed climate values at each population site. A second set of projections drew climate values from distributions that were 10 % warmer and 10 % drier than the observed climate, which provided a rough estimate of how *O. coloradensis* populations may fare under the generally hotter and drier conditions that will be brought on by climate change (Vicente-Serrano et al. 2020).

* Testing for each of the population-maintenance forces: : calculations that use IPM results
  + Negative density dependence
    - fit both density-dependent and density-independent models to the census data—for each plot, as well as the entire population.
    - Compare models of lambda w/ and w/out density terms
    - **Model abundance at time *t + 1* (counts) as a negative binomial mixed model** (glmm) with an offset for log(Nt), following the general approach of Abbott et al. (2017) and Brown ﻿and Crone (2016). (for count data from FEWAFB)
    - **Compare Ricker models**, which include a fixed effect of abundance at time *t* (Ricker 1954), to density-independent models.
  + Demographic compensation (different vital rates have opposing responses to environmental variation)
    - Used correlations between the coefficients for year effects in each vital rate function (from the IPMs)(for vital rates that had significant temporal variation). Negative correlations indicate demographic compensation (Villellas et al. 2015)
    - comparing coefficients for plot effects for vital rate functions that had significant spatial variation.
    - Tested the importance of vital rate buffering and temporal demographic compensation (of each vital rate!) for pop. Growth using randomization procedures to simulate 500 stochastic growth trajectories over 100 yrs without one or both of these patterns. Compared these stochastic growth rate estimates (estimated for each transect) with point-estimates of long-term stochastic growth rates that include demographic compensation and vital rate buffering.
  + Vital rate buffering (variability of demographic rates is inversely related to their importance for determining pop. Growth rate)
    - Compare vital rate variability to their elasticity values (Pfister 1998; Morris and Doak 2004)
      * Variability: coefficient of variation (CV) for the mean and variance of each vital rate (Morris and Doak, 2004)
      * Used the ‘standard perturbation approach’ to estimate elasticity values (Caswell 2001, Morris and Doak 2002)
  + Asynchronous responses to environmental variation across subpopulations
    - To identify if the magnitude of correlations between plots in log(*t*) or log(N) was related to their spatial distance from one another, we used **Mantel tests**.
    - **population-level synchrony index** (Loreau and de Mazancourt 2008, Thibaut and Connolly 2013)
    - **mean-variance portfolio effect** (PE; Anderson et al. 2013).
    - We **tested whether each of these climate variables explained variation in log(*t*) among years by comparing negative binomial glmm Ricker models of population growth, as described above, that included one of the four climate variables with AICc**. In particular, we compared Ricker models with random variation in intercepts and slopes among plots, but that substituted fixed effects of climate in each year for randomly varying intercepts in each year. For each climate variable, we fit models that considered linear and quadratic effects of climate and their interactions with plot position along the north-south axis, capturing interactions between climate and the main spatial variation in habitat.
    - PVA-based simulation
  + Fine-scale source-sink dynamics
    - Can’t directly measure (no seed movement data), but plot-level population growth rates indicate whether or not there are consistent spatial differences in average population performance, a necessary pre-condition for source–sink dynamics.
* Simulations
  + **Multi-site, count-based PVA** for entire site based on long-term census data (Morris and Doak, 2002)
    - **Simulated population growth in each time step by estimating an expected log(*t*) for each plot based on it’s abundance of plants, climate variable, and the plot-specific coefficients from the best-supported Ricker model**. Then added to this log(*t*) a plot-specific correlated random value estimated from the covariance matrix of the model residuals among plots (following Abbot et al. 2017)—allows for stochasticity
    - Tested the accuracy of these models by starting them at the beginning of the census data, and then comparing modeled to actual data (compare correlation)
    - Then project into the future by using the last year of census data as the starting point and ﻿randomly drawing annual precipitation values from a normal distribution with mean and variance taken from the 99 complete observations of annual precip. From the Riverton NOAA station.
    - Did these simulations 10,000 times over 100-year time window
  + Ran **three additional simulations** to estimate the impact of density dependence and spatial asynchrony
    - Ran simulations based on an alternative model that removed effects of spatial asynchrony in climate responses
    - Ran simulations based on models that removed the stabilizing effects of density dependence while still imposing a density cap on numbers
    - Ran simulations based on models that excluded both of these effects

**Results**

**Discussion**

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\*\* change the Rondeau and Heidel citations to include the ‘Prepared for…” statements \*\* also maybe change the italicization of the species name, if required