**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 population on federal land 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 subpopulations, 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*: 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 temperature of 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*. We first created a density-independent IPM using data from both populations that had a single continuous, size-based population state, and did not include a seedbank state (Table 2: IPM “OO”). Then, we created a suite of IPMs that included both a discrete seedbank state, and a continuous, size-based stage for above-ground plants (Table 2: IPMs “A” – “NN”) (Ellner and Rees 2006, Rees et al. 2006, Paniw et al. 2017). Each of these IPMs used a different subset of data, and 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 any combination of the following: population size in the previous year (density dependence), environmental variation (water year precipitation, mean annual growing season temperature, and mean annual winter temperature), and a random intercept of subpopulation to approximate effects of demographic stochasticity.

**Table 2.** A description of the data used to create each IPM, as well as the covariates included in the vital rate models used in that IPM. Log(λ) estimates and 95% bootstrap confidence intervals of log(λ) are also shown for each IPM. log(λ) is not given for IPMs that were constructed with random effects or continuous environmental covariates, since those models were implemented stochastically. For those models, λs is given instead.

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **IPM name** | **Data Included** | | | | | | | | | | | **Transitions included** | | | **Covariates included** | | | **log(λ) (95% CI)** | **λs** |
| **Continuous state only** | **Continuous + seedbank states** | **All subpopulations** | **Each population** | | **Each subpopulation** | | | | | | **All transitions** | **Each transition** | | **Density dependence** | **Environmental covariates** | **subpopulation random intercept** |
| **Soapstone** | **FEWAFB** | **Unnamed Creek** | **Diamond Creek** | **Crow Creek** | **Meadow** | **HQ3** | **HQ5** | **2018-2019** | **2019-2020** |
| OO | x |  | x |  |  |  |  |  |  |  |  | x |  |  |  |  |  | 0.41 (0.408, 0.411) | N/A |
| A |  | x | x |  |  |  |  |  |  |  |  | x |  |  |  |  |  | 0.39 (0.393, 0.395) | N/A |
| B |  | x | x |  |  |  |  |  |  |  |  | x |  |  | x |  |  | 0.35 | N/A |
| C |  | x |  |  |  | x |  |  |  |  |  | x |  |  |  |  |  | 0.24 (0.241, 0.244) | N/A |
| D |  | x |  |  |  |  | x |  |  |  |  | x |  |  |  |  |  | 0.81 (0.814, 0.819) | N/A |
| E |  | x |  |  |  |  |  | x |  |  |  | x |  |  |  |  |  | 0.46 (0.462, 0.468) | N/A |
| F |  | x |  |  |  |  |  |  | x |  |  | x |  |  |  |  |  | 0.31 (0.306, 0.310) | N/A |
| G |  | x |  |  |  |  |  |  |  | x |  | x |  |  |  |  |  | 0.19 (0.184, 0.189) | N/A |
| H |  | x |  |  |  |  |  |  |  |  | x | x |  |  |  |  |  | 0.29 (0.291, 0.295) | N/A |
| I |  | x |  |  |  | x |  |  |  |  |  | x |  |  | x |  |  | 0.34 | N/A |
| J |  | x |  |  |  |  | x |  |  |  |  | x |  |  | x |  |  | 0.53 | N/A |
| K |  | x |  |  |  |  |  | x |  |  |  | x |  |  | x |  |  | 0.65 | N/A |
| L |  | x |  |  |  |  |  |  | x |  |  | x |  |  | x |  |  | -0.28 | N/A |
| M |  | x |  |  |  |  |  |  |  | x |  | x |  |  | x |  |  | -0.24 | N/A |
| N |  | x |  |  |  |  |  |  |  |  | x | x |  |  | x |  |  | 0.32 | N/A |
| O |  | x |  | x |  |  |  |  |  |  |  | x |  |  | x | x | x | N/A | 0.044 |
| P (hot+dry) |  | x |  |  | x |  |  |  |  |  |  | x |  |  | x | x | x | N/A | 0.022 |
| Q |  | x |  | x |  |  |  |  |  |  |  | x |  |  | x | x | x | N/A | 0.067 |
| R (hot+ dry) |  | x |  |  | x |  |  |  |  |  |  | x |  |  | x | x | x | N/A | 0.069 |
| S |  | x |  |  |  | x |  |  |  |  |  | x |  |  | x | x |  | 0.33 | N/A |
| T |  | x |  |  |  |  | x |  |  |  |  | x |  |  | x | x |  | 0.39 | N/A |
| U |  | x |  |  |  |  |  | x |  |  |  | x |  |  | x | x |  | 0.61 | N/A |
| V |  | x |  |  |  |  |  |  | x |  |  | x |  |  | x | x |  | -0.27 | N/A |
| W |  | x |  |  |  |  |  |  |  | x |  | x |  |  | x | x |  | -0.21 | N/A |
| X |  | x |  |  |  |  |  |  |  |  | x | x |  |  | x | x |  | 0.50 | N/A |
| Y |  | x | x |  |  |  |  |  |  |  |  |  | x |  |  |  |  | 0.61 | N/A |
| Z |  | x | x |  |  |  |  |  |  |  |  |  |  | x |  |  |  | 0.15 | N/A |
| AA |  | x |  | x |  |  |  |  |  |  |  | x |  |  |  |  |  | 0.27 | N/A |
| BB |  | x |  |  | x |  |  |  |  |  |  | x |  |  |  |  |  | 0.458 (0.457, 0.459) | N/A |
| CC |  | x |  |  |  | x |  |  |  |  |  |  | x |  |  |  |  | 0.16 | N/A |
| DD |  | x |  |  |  |  | x |  |  |  |  |  | x |  |  |  |  | 1.21 | N/A |
| EE |  | x |  |  |  |  |  | x |  |  |  |  | x |  |  |  |  | 0.62 | N/A |
| FF |  | x |  |  |  |  |  |  | x |  |  |  | x |  |  |  |  | 0.38 | N/A |
| GG |  | x |  |  |  |  |  |  |  | x |  |  | x |  |  |  |  | 0.51 | N/A |
| HH |  | x |  |  |  |  |  |  |  |  | x |  | x |  |  |  |  | 0.82 | N/A |
| II |  | x |  |  |  | x |  |  |  |  |  |  |  | x |  |  |  | 0.26 | N/A |
| JJ |  | x |  |  |  |  | x |  |  |  |  |  |  | x |  |  |  | 0.48 | N/A |
| KK |  | x |  |  |  |  |  | x |  |  |  |  |  | x |  |  |  | 0.46 | N/A |
| LL |  | x |  |  |  |  |  |  | x |  |  |  |  | x |  |  |  | 0.20 | N/A |
| MM |  | x |  |  |  |  |  |  |  | x |  |  |  | x |  |  |  | -0.10 | N/A |
| NN |  | x |  |  |  |  |  |  |  |  | x |  |  | x |  |  |  | -0.19 | N/A |

The IPM with one state variable corresponding to continuous plant size (IPM “OO”) used a kernel structure where the continuous, above-ground population state ((*n(z’, t+*1*)*) at time *t*+1 was described by the following equation:

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

In both sets of equations, *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 3). *pEstab* is the probability of a seed produced in year *t* establishing as a seedling in year *t*+1.

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 3). 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 over-dispersed 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 3**. Description of vital rates used in *O. coloradensis* IPMs

|  |  |  |
| --- | --- | --- |
| **Vital rate** | **Description** | **Model** |
| *pEstab* | *P*(seed produced in *t* establishes as a seedling in *t*+1) | *pEstab* = |
| *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 3).

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 (IPM “A”) 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.

*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 compared the difference between density-dependent and density-independent log(λ) in each subpopulation with the mean population size of that subpopulation.

*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 each subpopulation and both transitions, and that included covariates for density dependence and all environmental covariates (vital rate models from IPMs “S”-“X”). 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 (Table 2: IPM “A”) to calculate elasticity values for each discrete vital rate and each parameter in each continuous vital rate function (Morris and Doak 2002). We calculated the CV for each 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 (Table 2: IPMs “CC”-“NN”). Because we did not have site-level information about discrete seedbank vital rates, we calculated CV for them differently. We calculated the mean and standard deviation of germination and viability rates from data reported by Burgess, et al. (2005). We did not have information about the variation seed survival rate, so we simulated its mean and standard deviation values. Because it is a probability bounded by 0 and 1, we used a mean of 0.5 and a standard deviation of 0.175 to allow seed survival to vary as much as is biologically possible. We then evaluated the correlation between CV and elasticity of vital rate parameters (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 log(λ) across each transition was correlated across each subpopulation, using values of log(λ) derived from IPMs for each subpopulation (Table 2: IPMs “C”-“H”). We used the “mantel()” function from the “vegan” R package to perform a Mantel test, which determined if the Spearman correlation of log(λ) across subpopulations was significantly related to the Euclidian distance between each subpopulation (Oksanen et al. 2020). A positive relationship between subpopulation proximity and degree of correlation of log(λ) was evidence for spatial asynchrony between subpopulations.

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 (using IPMs “O”-“R”). Each projection was repeated 1000 times, and stochastic log(λ) (or λs) was calculated with a “burn-in” of 15. 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).

**Results**

*Vital Rate Models*

We measured growth, survival, and reproduction for 3,150 unique individuals during demographic monitoring. We used this information to estimate continuous vital rate functions that explained the effect of current year plant size (log(size*t*)) on survival probability, size in the next year (log(size*t*+1)), flowering probability, and seed production. We constructed multiple versions of each vital rate function, each of which included a unique combination of covariates (Table 2). Every vital rate function included log(size*t*) as a fixed effect. In vital rate models parameterized for each population using data from both transitions, we found that larger plants non-reproductive plants are more likely to survive to year *t+*1 than smaller plants (Fig.1: A). However, plants tend to become smaller in the next year (Fig 1. B). Flowering only occurs once a plant reaches a certain size, when log(size*t*) is around 2.5, but then declines again at the upper end of observed plant size (Fig. 1 C). The number of seeds that a reproductive plant produces increases sharply with log(size*t*) (Fig 1. D). The inclusion of additional covariates did not alter the overall shape or sign of the relationships between log(size*t*) and vital rates, so models shown in figure 1 did not include any additional covariates beyond log(size­*­t*).

![Diagram, line chart

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**Figure 1**. The effect of current year size (log(size*t*)) on vital rates in monitored *O. coloradensis* populations. Data for from all sites and all transitions is shown. Lines indicate vital rate functions for each population, and include only log(size*t*) as a predictor. The dashed line in panel **B** shows a 1:1 line.

*Integral Projection Models*: We found that including a discrete state that represents the seedbank in IPMs for *O. coloradensis* significantly lowered the asymptotic population growth rate. The continuous state-only IPM (Table 2: IPM “OO”) predicted an asymptotic log(λ) of 0.41 for all populations, while the continuous + discrete state IPM (Table 2: IPM “A”) predicted an asymptotic log(λ) of 0.39. The 95% bootstrap confidence intervals for these asymptotic growth rates did not overlap (Table 2). All subsequent IPM results refer to models that included a discrete seedbank state. The simplest two-state IPMs that excluded density dependence and environmental variation indicated that both the Soapstone prairie and FEWAFB populations had positive population growth rates (Table 2: Soapstone prairie- IPM “AA”, log(λ) = 0.27**;**  FEWAFB – IPM “BB”, log(λ) **=**  0.46). The Diamond Creek subpopulation at FEWAFB had the highest population growth rate from 2018 to 2020 (Table 2: IPM “D”, log(λ) = 0.81), while the HQ3 subpopulation at Soapstone prairie had the lowest growth rate (Table 2: IPM “G”, log(λ) = 0.19). Including the effect of density dependence decreased the population growth rate from log(λ) = 0.39 to log(λ) = 0.35 when all subpopulations were considered together (Table 2: density-independent IPM “A”, log(λ) = 0.39, density-dependent IPM “B”, log(λ) =0.35). However, when considering each subpopulation independently, incorporating density-dependence did not have a uniformly positive or negative impact of population growth rate (Table 2: density-independent IPMs “C”-“H”, density-dependent IPMs “I”-“N”). For example, including density-dependence increased the growth rate of the Unnamed creek subpopulation from 0.24 to 0.34, but decreased the growth rate of the Meadow subpopulation from 0.31 to -0.28. We parameterized multiple other sets of IPMs that used different combinations of covariates in their vital rate models, and almost all identified a positive population growth rate (Table 2).

A density-independent, discretized IPM kernel (made using IPM “A”) shows transition probabilities within and between the discrete and continuous stages of the *O. coloradensis* lifecycle when all populations and transitions are considered together (Fig. 2: A). Relative to the rest of the kernel, there is a very high probability that seeds stay in the seedbank, as well as high contribution of adult plants to the size of the seedbank in the next year. The rates at which seeds are produced by adult plants and stay in the seedbank have the most impact on population growth rate (Fig. 2: C). 

**Figure 2**. Visualizations of the *O. coloradensis* IPM. (**A**) The IPM kernel for *O. coloradensis*. This kernel shows a density-independent IPM constructed using all data from all transitions (IPM A). (**B**) Sensitivity of the IPM kernel. (**C**) Elasticity of the IPM kernel. In all panels, color indicates probability, with darker colors corresponding to higher probability, and lighter colors corresponding to lower probability. The dashed line shows a 1:1 line.

*Evaluating Persistence Mechanisms: Negative Density Dependence*: AIC comparison of continuous vital rate models indicate that density-dependent models are better predictors of most vital rates than density-independent models in most subpopulations (Table 4). Models that included population size in the previous year as a covariate were better predictors of growth in five of six subpopulations. Density dependent models were better predictors of survival and seed production than density independent models in four out of six subpopulations, and density dependent models of flowering were better in one subpopulation. Recruit size distribution was not affected by density dependence—AIC model comparison did not indicate substantial differences, either negative or positive, between recruit size models for any subpopulation. The vital rate models for the Meadow population at Soapstone Prairie were least affected by density dependence. Only the growth model was improved by including a density dependence term. Just as including density-dependence affected vital rate models differently for each subpopulation, including density-dependence had a different effect on population growth rate for each subpopulation (Table 2: density-independent IPMs “C”-“H”, density-dependent IPMs “I”-“N”). As the mean number of individuals in a subpopulation increased, the negative impact of including density dependence on population growth rate became more pronounced, although this effect is not significant in a linear model (β = -0.0004, *P* = 0.17, df = 4)(Fig. 3).

**Table 4**. Comparison of vital rate models that do and do not include density dependence. The “DI” and “DD” rows contain AIC values for each vital rate model in each subpopulation for models that are density-independent (DI) and density-dependent (DD). The difference between the AIC of DI and DD models is shown in the Δ AIC column. **Bold text** indicates that the |ΔAIC| value is > 3, which means that including a term for density dependence substantially changed that vital rate model. A positive ΔAIC indicates that including density dependence improved the model, while a negative value indicates that including density dependence made model fit worse.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Vital Rate Model | | Subpopulation | | | | | |
| Crow Creek | Diamond Creek | Unnamed Creek | HQ5 | HQ3 | Meadow |
| Survival | DI | 776.79 | 1012.69 | 2678.99 | 3247.02 | 716.77 | 164.69 |
| DD | 757.98 | 905.76 | 2679.41 | 2927.47 | 637.98 | 169.69 |
| Δ AIC | **18.79** | **106.93** | -0.41 | **319.55** | **78.80** | 0 |
| Growth | DI | 511.97 | 951.59 | 1100.00 | 1570.03 | 291.46 | 113.16 |
| DD | 508.07 | 935.49 | 1070.15 | 1109.27 | 259.15 | 113.16 |
| Δ AIC | **3.89** | **16.10** | **29.85** | **460.76** | **32.31** | 0 |
| Flowering | DI | 371.68 | 523.30 | 1087.93 | 538.55 | 191.46 | 104.24 |
| DD | 373.31 | 523.73 | 1087.48 | 483.99 | 193.22 | 106.05 |
| Δ AIC | -1.63 | -0.44 | 0.45 | **54.52** | -1.76 | -1.81 |
| Seed production | DI | 737.74 | 1397.76 | 2459.80 | 1248.52 | 521.81 | 242.26 |
| DD | 731.30 | 1383.77 | 2461.10 | 1244.70 | 517.66 | 243.79 |
| Δ AIC | **6.45** | **13.99** | -1.30 | **3.81** | **4.15** | -1.53 |
| Recruit Size | DI | 920.42 | 1015.31 | 3365.29 | 4655.41 | 973.09 | 159.41 |
| DD | 922.25 | 1016.49 | 3367.29 | 4657.33 | 974.34 | 161.21 |
| Δ AIC | -1.82 | -1.18 | -1.99 | -1.92 | -1.25 | -1.81 |

**![Chart, scatter chart

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**Figure 3**. The difference between subpopulation-level, density-independent log(λ) and density-dependent log(λ) is more negative as mean subpopulation size increases. There is an insignificant negative effect of population size on the difference in log(λ) (β = -0.0004, *P* = 0.17, df = 4).

*Evaluating Persistence Mechanisms: Demographic Compensation:* Our analyses did not identify signatures of demographic compensation in *O. coloradensis* populations. While there were negative correlations between the effect of mean growing season temperature on vital rates for five combinations of vital rates, none of these correlations were significant (Table 5). 10,000 correlations of randomly assigned coefficients found that the number of negative correlations in a matrix can be described by a normal distribution with a mean of 5.01 and a standard deviation of 1.58. Using this distribution as a null model, there is a 49.8 % probability of observing five negative correlations. Although there is no significant evidence for demographic compensation, it is notable that the effect of mean growing season temperature on distribution of recruit size was negatively correlated with the effect of growing season temp on all other vital rates. We were only able to compare coefficients across vital rate models for mean growing season temperature, because including precipitation and mean winter temperature as covariates resulted in overfitting in some cases.

**Table 5.** Pearson correlations between mean growing season temperature coefficients in each continuous vital rate function. Below each correlation value is the *P* value for that correlation.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  | | Vital Rate | | | | |
| Flowering | Survival | Growth | Seeds | Recruit Size |
| Vital Rate | Flowering | 1.00 0 | 0.415 0.413 | 0.163 0.773 | -0.073 0.891 | -0.381 0.456 |
| Survival | | 1.00 0 | 0.822 0.045 | 0.708 0.115 | -0.300 0.568 |
| Growth | | | 1.00 0 | 0.683 0.135 | -0.091 0.863 |
| Seeds | | | | 1.00 0 | -0.604 0.204 |
| Recruit Size | | | | | 1.00 0 |

*Evaluating Persistence Mechanisms: Vital Rate Buffering:* We did not identify evidence of vital rate buffering in the *O. coloradensis* populations we observed. The coefficients of variation and elasticities of discrete vital rates and continuous vital rate parameters were positively correlated, albeit weakly (Fig. 4, r = 0.11, *P*=0.68). As a vital rate became more important for determining population growth rate, it also was more variable, which is the inverse of what is expected when vital rate buffering is taking place.



**Figure 4**. The coefficient of variation of each vital rate parameter is positively correlated to its elasticity. This indicates that vital rate buffering is not acting in *O. coloradensis* populations we studied.

*Evaluating Persistence Mechanisms: Asynchronous Responses and Source-Sink Dynamics:* We did not identify a significant relationship between the Spearman correlation of log(λ) between subpopulations and their spatial proximity (Mantel statistic = 0.08, *P* = 0.37). We also performed Mantel tests using log(λ) correlation and distance matrices calculated uniquely for each population, and while the tests did not identify significant relationships, we did find a positive relationship between correlation of log(λ) and distance between subpopulations at Soapstone prairie, and a negative relationship between correlation of log(λ) and distance between subpopulations at FEWAFB. These insignificant Mantel tests also indicate that fine-scale source-sink dynamics are not important for these *O. coloradensis* populations.

*Determining population stability over time:* Simulations that incorporate demographic and environmental stochasticity indicate that, if the demographic patterns observed during our monitoring study persist, both the Soapstone prairie and FEWAFB populations of *O. coloradensis* will hover around their current population size for the next decade (Figure 5: A). Over a span of 100 years, however, the simulations suggest that the Soapstone population will grow considerably to reach an equilibrium size that is an order of magnitude larger than it is currently, and the FEWAFB population will grow exponentially and then decline steadily through the end of the simulation period. By the end of the simulations, the population growth rate of the Soapstone population stabilizes slightly above zero, while the growth rate of the FEWAFB population stabilizes slightly below zero (Figure 5: B). Even though the FEWAFB population is in decline at the end of the simulation period, the mean stochastic log(λ) (or log(λs), which is the mean of the log(λ) values of the 15th through 100th simulated transitions, is positive. This is driven by the very high log(λ) values in the first 30 years of the simulations (Figure 5: C). The mean log(λs) for the Soapstone population is lower than the FEWAFB log(λs), but is still positive. The climate scenario used for the simulation did not substantially affect the outcome for the FEWAFB populations. Mean population size, mean log(λ) and log(λs) of the FEWAFB population are very similar both in simulations using a scenario based on current observed climate and a scenario with higher mean temperature and lower precipitation. However, climate scenario did affect the outcome of simulations of the Soapstone prairie population. In the hotter and drier scenario, population size grew faster initially, but stabilized at a smaller size than in the current climate scenario (Figure 5: B). Mean log(λs) was also lower in the hotter and drier climate scenario (Figure 5: C).

![Graphical user interface, chart, histogram

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**Figure 5:** Simulated growth rates and sizes of each population under two climate scenarios. (**A**) Simulated log(λ) of the Soapstone prairie population stabilizes just above zero in both climate scenarios after ~30 years. Simulated log(λ) of the FEWAFB population stabilizes just below zero after ~40 years. Solid, dark-colored lines show the mean log(λ) at each simulated transition, while faint lines show log(λ) values for each iteration of the simulation. Horizontal dashed lines indicate log(λs) = 0. (**B**) Simulated size of the Soapstone prairie population grows until reaching an equilibrium size, which is smaller in the hotter and drier climate scenario. Simulated size of the FEWAFB population grows initially, but is still in decline at the end of the simulation period. (**C**) Climate scenario does not have a pronounced effect on the distribution of observed stochastic λ (λs) values in simulations of the FEWAFB population. In simulations of the Soapstone prairie population, mean λs is lower under the hotter and drier climate scenario. Vertical dashed lines indicate mean λs under each climate scenario.

**Table 6**: Coefficients from vital rate models that were used to create projection IPMs

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  |  | Coefficient (*P*-value) | | | | | | Variance (std. dev.) |
|  | Response Variable | Intercept | log(size*t*) | log(size*t*)2 | Plot-level plant density | mean growing season temp. | total water-year precip. | subpop. random-intercept |
| Soapstone Prairie | P(survival) | -0.21 (0.48) | 0.73 (< 0.01) | - | 0.002 (< 0.01) | 0.82 (< 0.01) | - | 0.24 (0.49) |
| log(size*t*+1) | 1.56 (0.001) | 0.17 (< 0.01) | - | -3.76x10-5 (0.39) | 0.21 (< 0.01) | - | 0.01 (0.10) |
| P(flowering) | -30.77 (< 0.01) | 23.13 (< 0.01) | -4.34 (< 0.01) | 0.0014 (0.007) | 0.50 (< 0.01) | -0.14 (0.47) | 0.24 (0.49) |
| Num. seeds | 3.89 (< 0.01) | 0.39 (0.07) | - | 0.0006 (0.0002) | 0.38 (< 0.01) | 0.83 (< 0.01) | - |
| recruit size | 0.23 (< 0.01) | - | - | -7.57x10-6 (0.90) | -4.51x10-3 (0.80) | -0.002 (0.45) | - |
| FEWAFB | P(survival) | -1.07 (0.08) | 0.27 (< 0.01) | - | 0.005 (< 0.01) | 0.20 (< 0.01) | - | 1.07 (1.03) |
| log(size*t*+1) | 1.62 (0.009) | 0.19 (< 0.01) | - | 5.08x10-4 (< 0.01) | -0.02 (0.14) | - | 0.09 (0.30) |
| P(flowering) | -30.12 (< 0.01) | 27.38 (< 0.01) | -5.88 (< 0.01) | 3.95x10-4 (0.45) | 0.11 (0.09) | 0.22 (0.0001) | 0.07 (0.26) |
| Num. seeds | 3.13 (< 0.01) | 0.90 (< 0.01) | - | -0.0001 (0.56) | 0.11 (0.008) | 0.11 (0.0008) | - |
| recruit size | 0.19 (< 0.02) | - | - | -1.22x10-5 (0.89) | 0.03 (0.10) | -0.006 (0.68) | - |

**Discussion**

-why was density dependence least important at the Meadow population? Maybe because it has the smallest population size?

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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