**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 Covariates*: 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.

To determine the effect of temporal variation in climate on *O. coloradensis* populations, we used modeled, site-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.

*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 IPMs for each subpopulation, for each site, and then using data from all sites. We made three versions of each IPM: The first had only size in the current year as the predictor in vital rate models; the second incorporated density dependence by including population size in the current year as a covariate in vital rate models; and the third incorporated density dependence as well as environmental variation by including covariates for both population size and abiotic conditions in vital rate models.

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+*1are described by the following equations:

where *z* is the distribution of plant size in year *t*, *z’* is the distribution of plant size in year *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 in year *t*+1 as a function of size in year *t*. The vital rate functions *s*(*z*), *Pb*(*z*), and *b*(*z*) describe the relationship between size in year *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 in year *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). Vital rate parameters

(table of vital rate parameters, their functions/distributions, etc., maybe parameter values?—if so would put in the results section? )

We used data from the three-year demographic monitoring study to parameterize the vital rate functions 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 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).

**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) |

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|  |  |  |
| --- | --- | --- |
| *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

# describe general vital rate model formats (i.e. types of model error, basic model structure, etct. )

* vital rate models
  + plot-level models
    - w/ and w/out density dependence
  + global models
    - w and w/out density dependence
* Actually modeling the IPM (equations, ipmr package vs. by-hand, etc.)
* count-based PVA
  + using previously-published data from WYNDD report
* calculations using IPMs
  + lambdas
  + elasticities
  + stable size dist., reproductive value, etc.
* 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**

**References**

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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