Astragalus mulfordiae (Mulford's milkvetch): modeling population growth rates and the effects of climate.

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PREFACE

IAE is a non-profit organization whose mission is the conservation of native ecosystems through restoration, research, and education. IAE provides services to public and private agencies and individuals through development and communication of information on ecosystems, species, and effective management strategies. Restoration of habitats, with a concentration on rare and invasive species, is a primary focus. IAE conducts its work through partnerships with a diverse group of agencies, organizations, and the private sector. IAE aims to link its community with native habitats through education and outreach.

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Cover photographs: Mulford's milkvetch (*Astragalus mulfordiae*). Photo by the Institute for Applied Ecology.

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1. EXECUTIVE SUMMARY

This study aims to identify relationships between Mulford's milkvetch (*Astragalus mulforidae)* demographic trends and climatic variables over multiple years, based on data collected both in Idaho and Oregon. Overall, populations are decreasing in both states, more accentuated in Idaho than Oregon. Count-based extinction probability was somewhat slower for Oregon populations, even though the tendency is for a collapse of the populations. Detailed data from Oregon populations allowed for a more thorough demographic analysis, arriving to the same conclusions of the species being under imminent risk. Compared to other climate variables, years with extreme hot and dry conditions showed less of a negative effect on simulated stochastic growth, and a deacceleration on quasi-extinction probability. Climate projections for the area indicate an increase in the number of dry hot years, which potentially could delay the forthcoming collapse of the species, but not avoid it. While the projected increase in drought conditions will likely alter community composition and productivity, disturbance requirements, and erosion; Mulford's milkvetch adaptation to new climate regimes is unknown.

2. INTRODUCTION

Climate change impacts on endemic plant species have been broadly studied worldwide (Manes et al. 2021), highlighting that greater extinction rates are associated with the restricted range of rare and/or endemic species (Staude et al. 2020) . Predicting the impact of climate change on these species is critical for their future conservation. Longitudinal studies of individual species has been shown to be more effective at assessing climate impacts as opposed to using climatic means (Germain and Lutz 2020).

Mulford's milkvetch (*Astragalus mulfordiae)* is an endemic species in the Pacific Northwest, specifically south-eastern Oregon and western Idaho. It is considered as endangered in Oregon, as an imperiled and sensitive species in Idaho, and as a species of concern under federal listings (Center for Plant Conservation 2009, Idaho Fish and Game 2022). Idaho populations have been monitored since 1989 and demographic studies of Oregon populations started in 2007 (Moseley 1989, Thorpe 2007). Mulford's milkvetch has shown variable demographic patterns over the years, with no clear relationship to cattle presence and an inverse relationship with the density of the invasive and highly competitive *Bromus tectorum*. It has shown an overall decrease in population size across all studied sites with very low to non-existent recruitment (Mancuso and Brabec 2019, Pyramid Botanical Consultants 2019, Diaz and Harris 2022). Particularly in Oregon, plant size has declined and the mortality of older, established plants has been recorded (Diaz and Harris 2022). Although reproductive effort (assessed by flower counts) has varied over time, the lack of recruitment and reduction of plant size indicate a severe risk for the species.

This study aims to identify relationships between demographic trends and climatic variables over multiple years, based on data collected both in Idaho and Oregon. This analysis uses stage-based transition matrix models to describe the population dynamics of Mulford's milkvetch over sixteen transition periods, spanning 22 years (Table 1). Using population surveys from both Idaho and Oregon, population growth rate (λ) and elasticity - the proportional contribution each life cycle transition has on λ- are estimated using transition matrix models (de Kroon et al. 1986, Caswell 2001). Elasticity is a particularly useful calculation that can be summed by the contribution of each vital rate to assess the impact of change on population growth rates, or λ (Silvertown et al. 1993).

Table 1. Mulford's milkvetch surveyed populations in Idaho and Oregon between 1999-2021.

State	Surveyed Periods	Surveyed Sites
Idaho	1999-2002	Varied between years: 34 element occurrences (1999), 7 (2000), 8 (2001), 5 (2003), 10 (2004), 25 (2005), 21 (2006), 20 (2007), 2 (2009), 8 in Boise Foothills and 12 in BLM lands (2019).
	2005-2008	
	2019	
Oregon	2009-2010	Five different populations: South Alkali, Brown Butte, Sniverly, Double Mountain and North Harper
	2012-2021	

3. GOALS AND OBJECTIVES

Objectives of this analysis:

1. determine population growth of Mulford's milkvetch throughout its distribution,
2. assess the spatial and temporal variability of population growth rate and elasticity,
3. determine if demographic parameters differ between years, accounting for differences in climate.

4. METHODS

4.1. Objective 1: Population growth

Data were collected in Idaho and Oregon sites using similar protocols (Mancuso 2002) for the period 1999-2021 (Table 1). The Idaho monitoring protocol did not track individual plants over time. Therefore, the Idaho sites were only used for a generalized analysis of the species, as well as for a comparative analysis between Oregon and Idaho sites (Objective 1). Data comprised sample-based estimates of population size for each site-year, divided in "stages". First year plants and all plants less than 4 cm tall (and at least 3 cm apart from another plant) were classified as *seedlings* and included in their own stage. The other stages were *non-reproductive* (plants taller than 4 cm and without flowers or seeds), *reproductive* (plants taller than 4 cm and with flowers or seeds), *dormant* (only for Oregon sites, plants that did not show up on the surveyed plots for at least one season and "re-appeared" a year or more later) and *dead* (Figure 1). Data were pooled by state, and all analyses in this section were performed for two "main sites": Idaho and Oregon.

We used a count-based projection model (CPM) for this dataset, where population samples were used to estimate log λ for each year and site. When demographic data on vital rates were not available (e.g., 2011) we used CPMs to calculate population growth rates, log λ, for both sites (Morris and Doak 2002). We also calculated quasi-extinction probabilities for both Idaho and Oregon populations over a 60-year period into the future, by using the function countCDFxt of the popbio package(Stubben and Milligan 2007) in R. This function takes parameters derived from population counts and calculates the probability of extinction with bootstrap confidence intervals for a density-independent model, using a diffusion approximation. The function plots the cumulative probabilities of quasi-extinction through time.

4.2. Objective 2 and 3: Spatial and temporal variability

The Oregon dataset is a comprehensive survey of all plants found on the five surveyed sites and their life history, allowing for a more detailed demographic analysis. Data collected were the same as for Objective 1 above, with the addition of detailed data for each plant: identity, stage, number of inflorescences and volume ("canopy" diameter by length).

We used stage-based transition matrix models to assess the spatial and temporal variability of population growth rate (λ) and elasticity. Elasticity is a measure of the effect that a change in a given matrix element ("stages" in our model) has as proportional to the change in that element. Fecundity was calculated as # seedlings year t /(mean number of inflorescences of t-1).

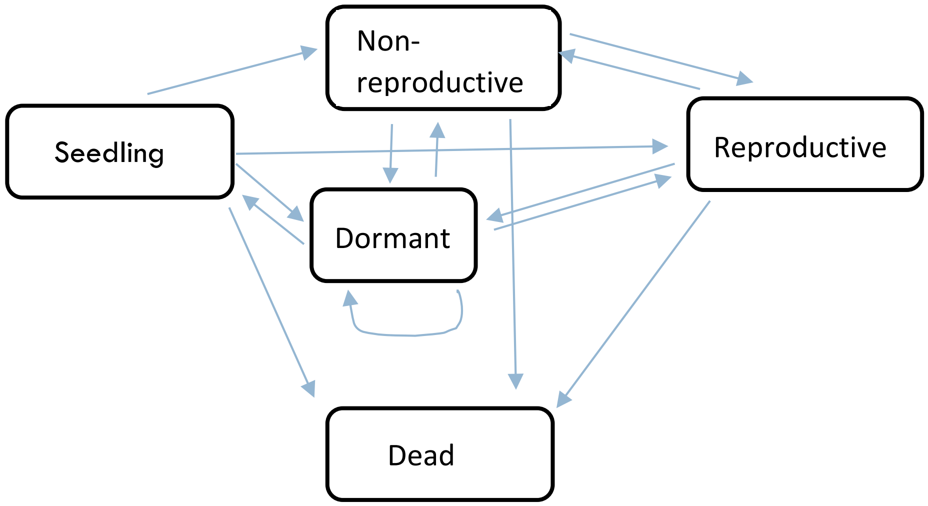

Figure 1. Mulford's milkvetch stages.

TEMPORAL VARIATION OF DEMOGRAPHIC PARAMETERS:

Due to the small number of observations per site in many years, only one main pooled matrix (with all sites) was constructed. Population growth rate (λ) was calculated for Mulford's milkvetch by year. All matrix calculations were made using the popbio package in R (Stubben and Milligan 2007).

Elasticity was computed for each element in all matrices. Individual elasticities were then summed by starting stage class to create grouped elasticity values for each site-by-year combination. Within the stage classes, elasticities were further divided into those that contribute to reproduction (fecundity transitions to seedling stage class) and those that contribute to survival or growth. Ninety-five percent confidence intervals were computed for λ and each elasticity estimate using 2000 runs of bootstrapped data (Caswell 2001).

CLIMATE EFFECT ON OREGON POPULATIONS

Because the Oregon dataset also contained information about each individual plant, we evaluated the relationship between climate, demographic variables, and reproduction. Climate data was sourced from the PRISM dataset from a centralized location (North Harper). Yearly and monthly general climatic patterns were identified for the study period (Table 2). We built a correlation matrix with all the climatic variables at time 0, the year before (t-1) and two years before (t-2) (see APPENDIX I for correlation values). The retained variables were used to construct models for each variable and its relationship with climate at time 0, 1 (t-1) and 2 (t-2) for all Oregon populations.

We used the variation of inflation factors (VIF, R package car) to assess for multicollinearity each time a model was run, eliminating variables with high VIF (>5, severe correlation) and retaining the ones with medium (1<VIF<5, moderate correlation) or small (=1, no correlation), as multicollinearity does not provide unique or independent information. The VIF measures the correlation and strength of correlation between the predictor variables in a model. After eliminating variables with high VIF (using R package effectsize) and/or without biological meaning, we ran the models again until obtaining low and moderate VIFs for all retained variables.

Generalized linear models were used to test the hypothesis that number of plants (reproductive, non-reproductive, seedlings and total), and number of flowers are related with climatic periods. Flower set was cube root-transformed in order to meet the assumption of normal distribution of the residuals. We expect that a combination of these climatic factors will provide a better understanding of Mulford's milkvetch population dynamics over the study period.

Table 2. Climatic variables identified by considering how precipitation (Ppt), temperature (Temp), mean dew point temperature (TD) and vapor pressure deficit (VP) affect vital rates.

Variable	Explanation of Variable	Phenology relationship
MayPpt	May precipitation	Growing period/ blooming
WetMonths	Wet months: precipitation in May and December to February period	Dec-Feb: vegetative state & May: growing period/blooming
AugPpt	August precipitation	Seeds dispersion/establishment
DryMonths	Dry months: precipitation in August to September period	Seeds dispersion/establishment
JulyMaxTemp	July max temperature	Seeds dispersion/establishment
coldMonths	Cold months: December and January	Dec-Jan: vegetative state
JulyAugTDmax	July and August mean dew point max temperature	Seeds dispersion/establishment
DecFebTDmin	December to February mean dew point min temperature	Dec-Feb: vegetative state
JulyVPmax	July max vapor pressure	Seeds dispersion/establishment
JulAugVPmax	July and August max vapor pressure	Seeds dispersion/establishment
NovMarchVP	November to March vapor pressure	Nov-March: vegetative state

5. RESULTS

5.1. Idaho and Oregon Populations

Populations were surveyed between 1999 and 2021 in both states, showing different patterns over time (Figure 2), with a common downward trend in both sets of populations. Idaho populations had an average total of plants of 24 ± 14 in 1999 that went down to 3 ± 7 in 2021; while Oregon populations had an average total of plants of 26 ± 18 in 2009 that went down to 11 ± 15 in 2021.

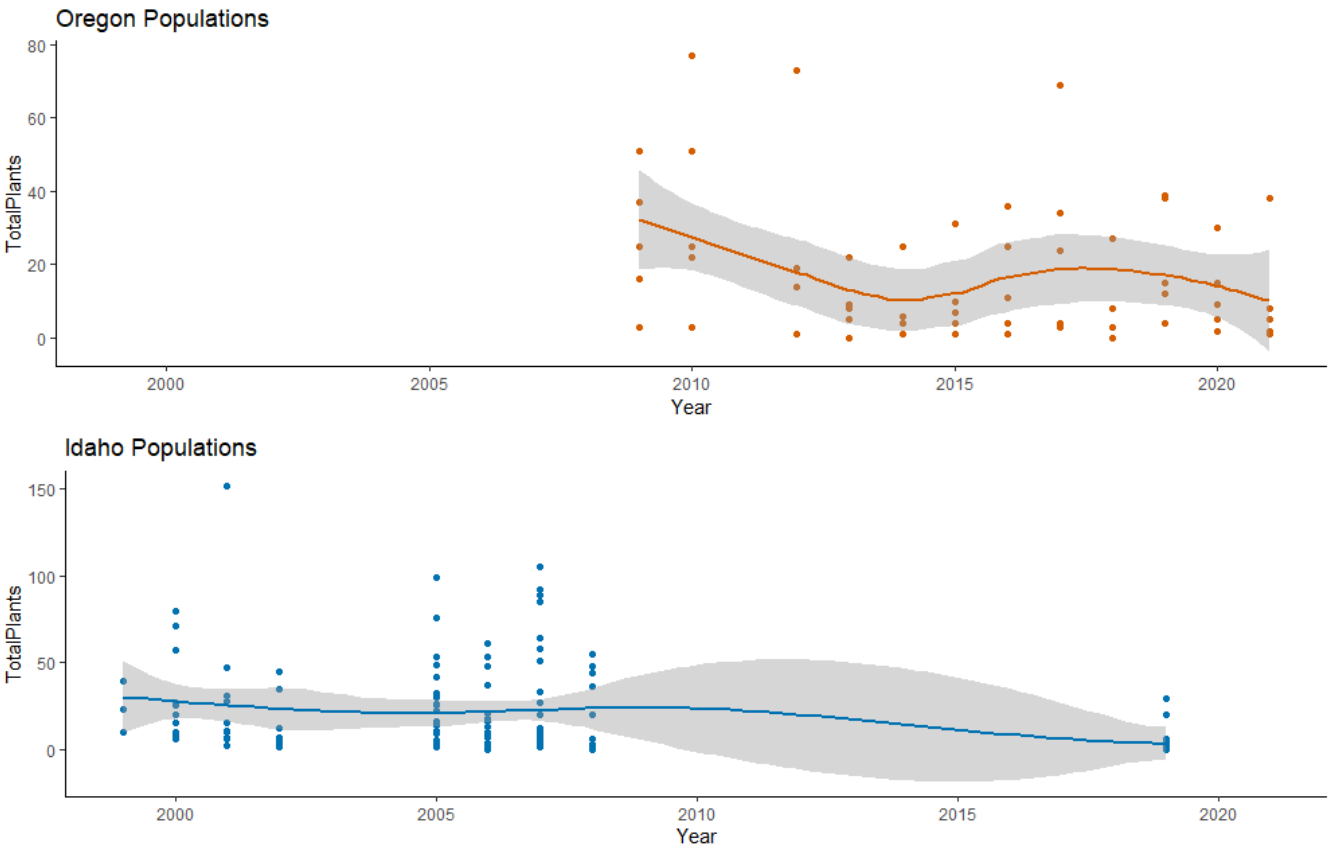

Figure 2. Total plants surveyed in Idaho and Oregon during the 1999-2021 period, represented by a loess smoothed line and 95% confidence intervals in grey.

Two count-based matrices were developed, one for the Idaho populations and the other for the Oregon populations (Table 3). In both cases, the estimated growth rates were negative, reflecting the decline of the species, although in Idaho is more accentuated.

Table 3. Estimated population parameters for the Mulford's milkvetch Idaho and Oregon populations.

	Period	Population growth rate	Estimated σ^2
Idaho	1999-2007	-0.4338	1.1345
Oregon	2009-2021	-0.2111	1.0079

We calculated the count-based extinction probability for both populations (Figure 3), which resulted in high probability of quasi-extinction for both sets of populations, although at a different rate. Idaho populations showed a steeper and higher probability of quasi- extinction, while in Oregon the rate is somewhat slower to reach a quasi-extinction threshold of 20 individuals.

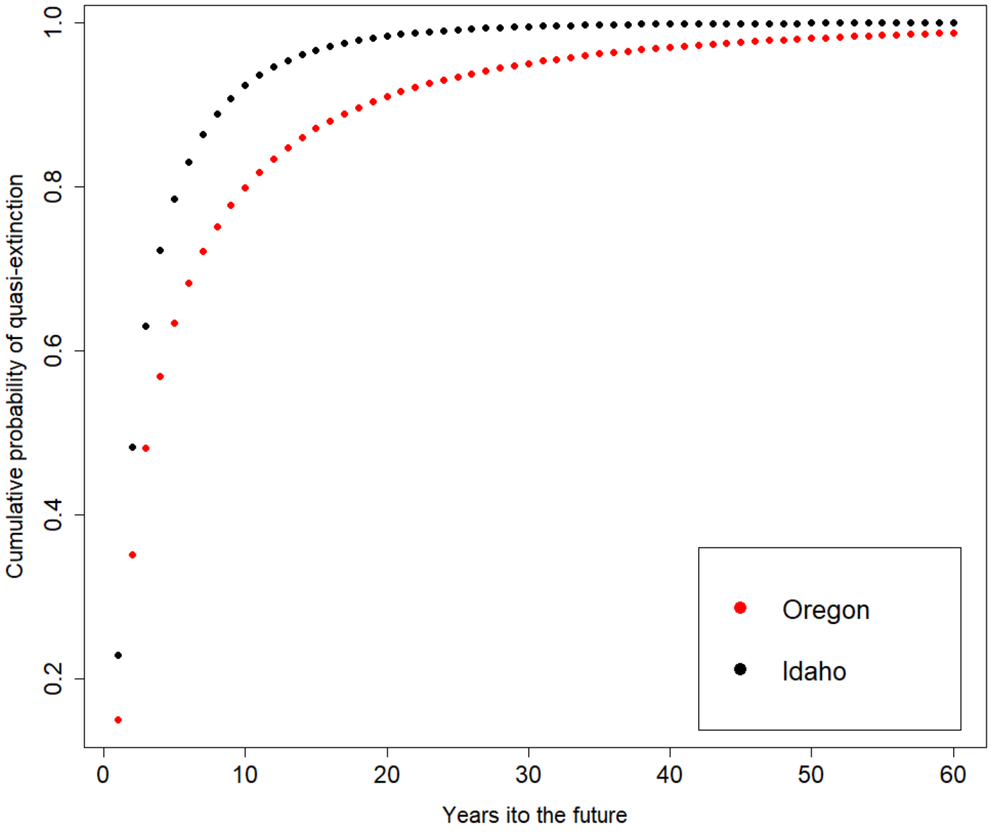

Figure 3. Quasi-extinction probability for Oregon and Idaho populations over a 60-year period.

5.2. Oregon Populations

Oregon populations showed a decreasing trend over the period 2012-2020 (Figure 4). The projected growth rate of the stochastic model was λ =0.837, showing that these populations are declining in Oregon, as most years within the study period had a λ<0.89 (range 0.712-0.886).

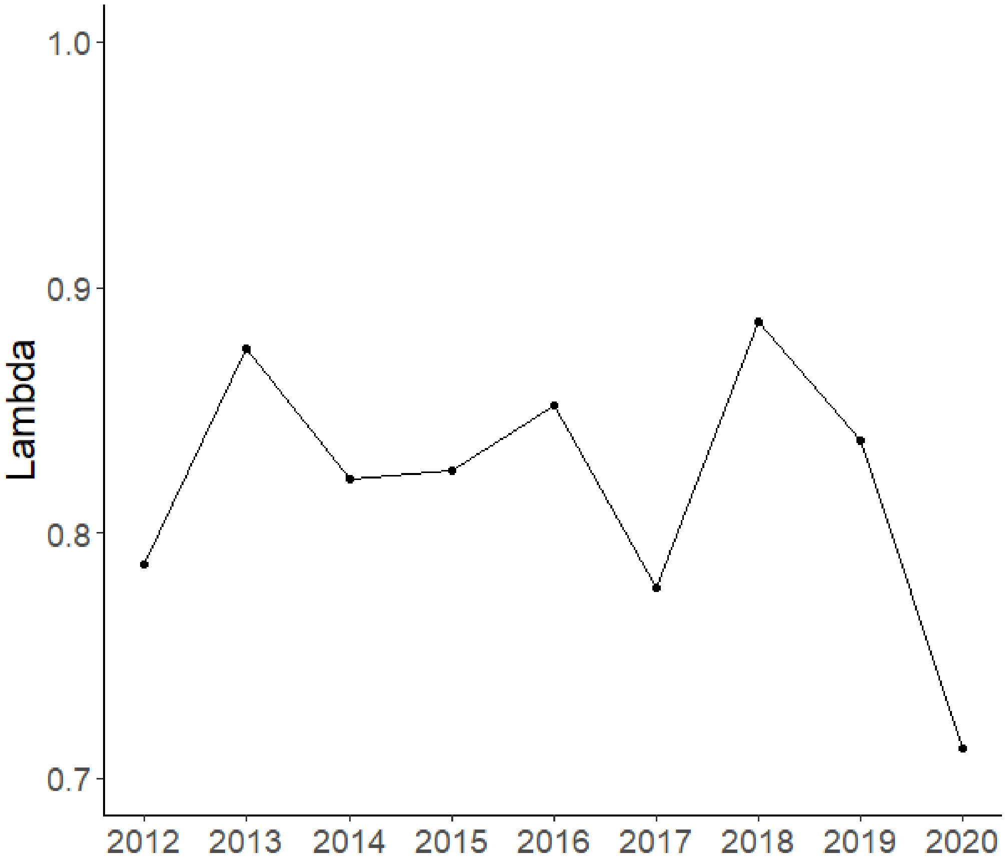

Figure 4. Population growth (lambda) for Mulford's milkvetch in Oregon.

Elasticity:

Elasticity with respect to growth and survival showed reproductive plants having the highest values similar to 1 (meaning that the absolute and relative contribution of reproductive plants to population growth rate (PGR) is similar to 1), while, non-reproductive and dormant plants had very small values and seedlings were close to zero, with a very low absolute and relative contribution to PGR (Figure 5).

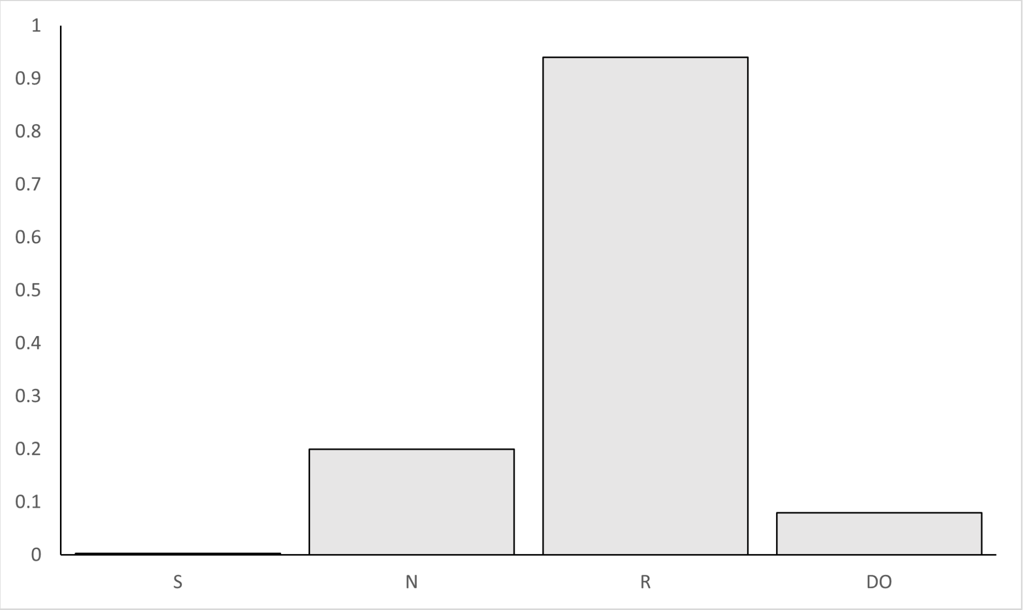

Figure 5. Elasticity of each life stage with respect to growth and survival. S: seedlings, N: non-reproductive plants, R: reproductive plants, DO: dormant plants.

Climate and Population dynamics

Population data were analyzed by pooling by main climatic events (Figure 6, Table 4). Only years with sharp deviations from the normal were analyzed (e.g., 2013 had drought conditions and low mean annual temperatures, Table 4).

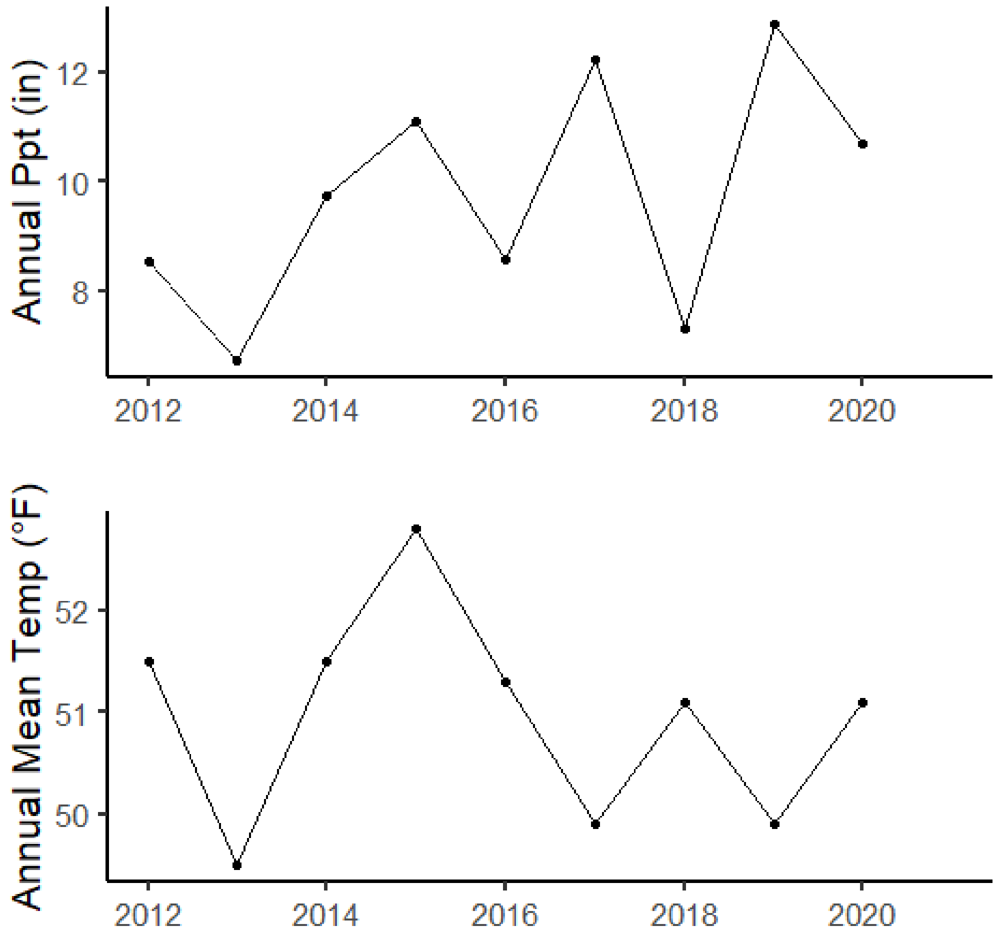

Figure 6. Annual mean temperature and precipitation for Mulford's milkvetch Oregon sites (source: PRISM, using North Harper as representative site because of its centralized location).

Table 4. Extreme climatic events during the 2012-2021 study period.

Period	Precipitation	Temperature
2013	Drought	Cold
2015	Wet	Hot
2017	Wet	Cold
2018	Drought	Hot
2019	Wet	Cold

Population data was projected accounting for years with severe drought (2013 and 2018) and high precipitation years (2017, 2018, and 2019) and compared with stochastic projections without weighing any year by climatic variables ("equal", Figure 7). Stochastic growth projections of wet years behaved similarly to the one without weights, with higher mean than the projection for drought. When analyzing only extreme temperature events as a factor ("hot" in 2015 and 2018, "cold": 2013, 2017 and 2019) and compared with the projection of stochastic growth without assigning weights to years, we found that colder years drove the frequency distribution towards more negative numbers, indicating a major effect on the populations stochastic growth (Figure 8). While hot temperatures did also have a negative effect on the frequency distribution, it was less accentuated than for cold temperatures. Both projections showed a negative effect on the frequency distribution while the equal probabilities projection remained closer to minus one.

When relating both approaches, we tested for effects of both climatic variables combined as shown on Table 4. Figure 9 shows the 5 different projections, with the combination of dry/wet, cold/hot conditions for particular years within the study period. Again, the projection with equal probabilities for all years shows no change, while the projection for dry and hot years is somewhat better to similar to the projection for wet and hot years. The projection for wet and cold years is more negative and the projection for dry and cold years shows the most negative values.

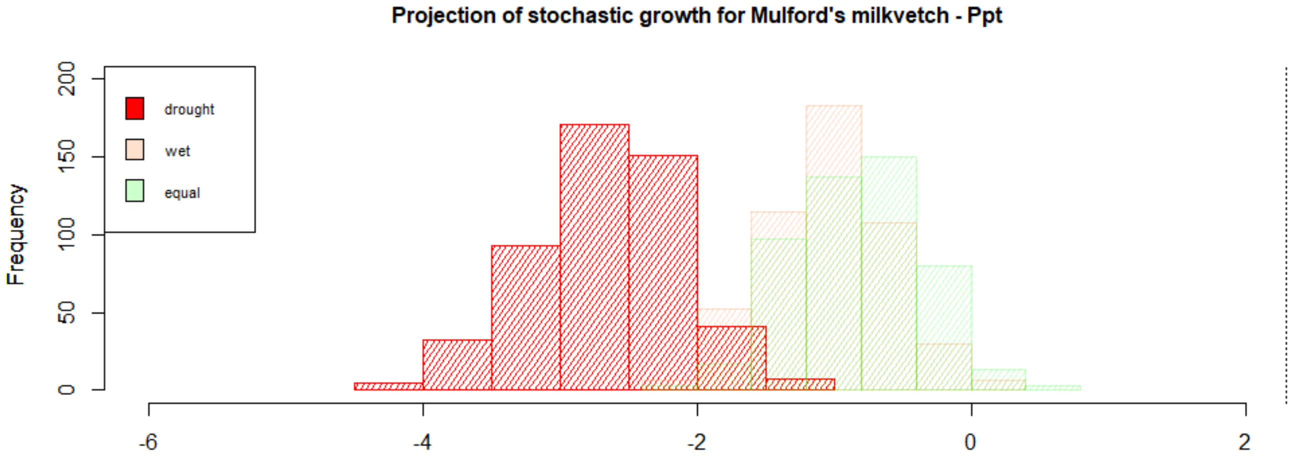

Figure 7. Drought, wet and equal conditions frequency distributions of projections of stochastic growth for Mulford's milkvetch. Dotted line (right) indicates starting population size for reference, y-axis is the frequency of final population size at tmax.

Figure 8: Cold, hot and equal conditions frequency distributions of projections of stochastic growth for Mulford's milkvetch. Dotted line (right) indicates starting population size for reference.

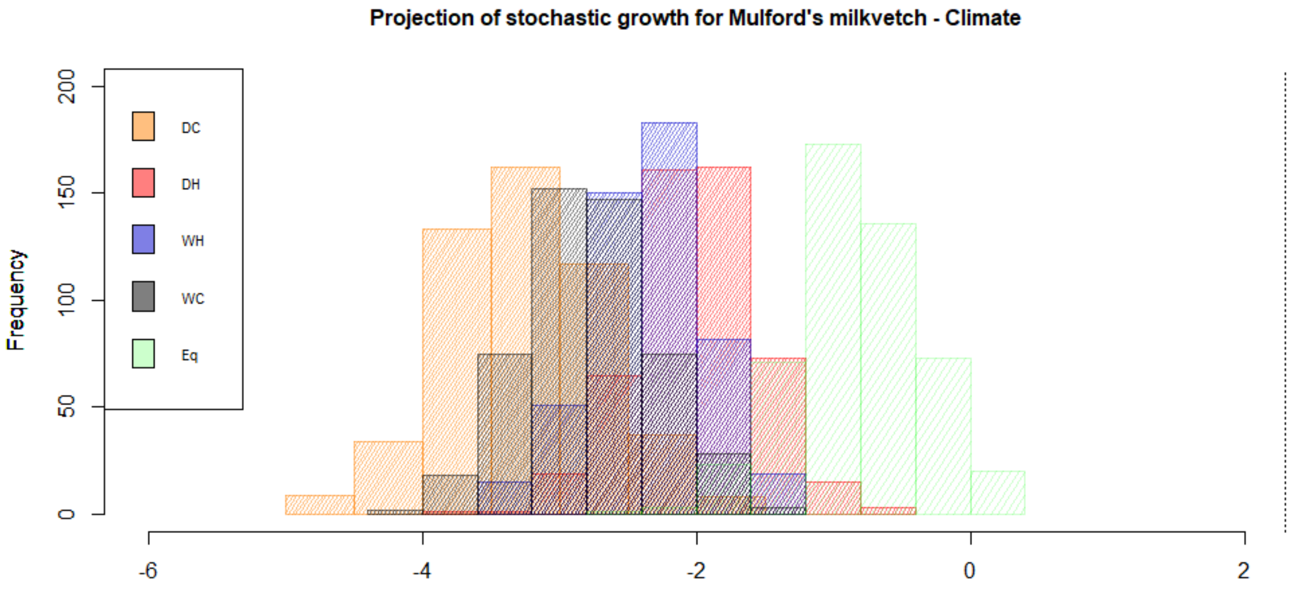

Figure 9. Projection of stochastic growth of the combination of precipitation and mean annual temperature. DC (drought cold), DH (drought hot), WH (wet cold), WC (wet cold) and EQ (equal probabilities for all years).

Quasi extinction analysis:

Simulations of populations under drought with hot or cold conditions, showing the time to reach a quasi-extinction threshold of 20 individuals are shown on the left side of Figure 10. The stable condition (black) is reaching the collapse of the population faster than the ones under drought and cold conditions (gray), while the populations under drought and hot conditions (red) are showing to be more resilient but reaching collapse with a few years of delay. When simulated populations based on wet years (right side) also with hot or cold conditions, both scenarios showed populations collapsing much faster than under hot drought conditions, with populations under wet cold conditions collapsing even earlier than any other simulated scenarios.

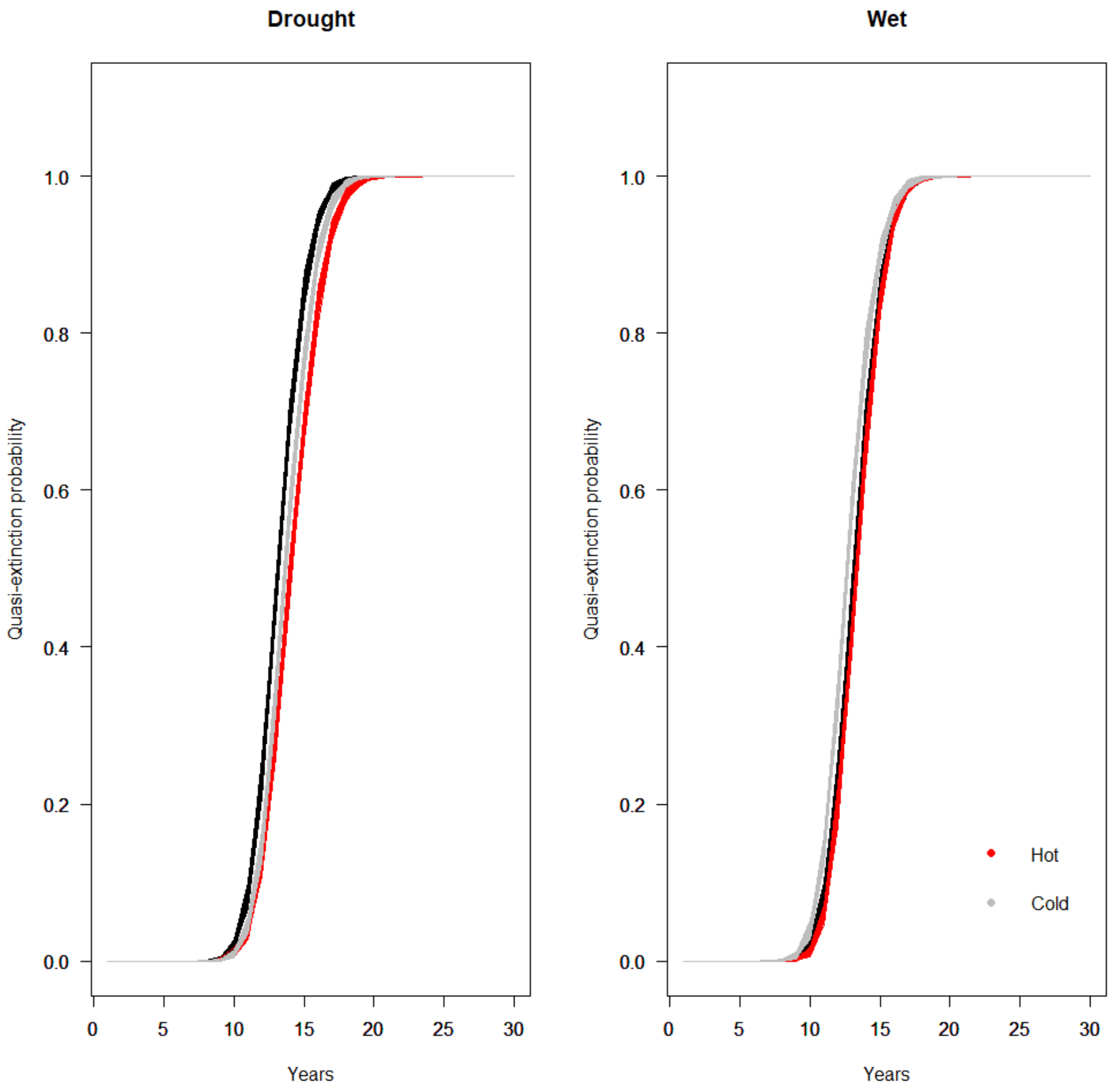

Figure 10. Quasi extinction probability for populations assuming equilibrium at stable stage (black), in comparison with stochastic simulation under drought (left) and higher (red) and lower (gray) than average mean temperatures, and wet conditions (right) and higher (red) and lower (gray) than average mean temperatures. X axis is years in the future.

Models between demographic and climate variables for Oregon Populations

Final models and estimated parameters for each demographic variable modeled against climatic variables are shown in APPENDIX II and APPENDIX III.

The total number of plants on a given year was directly related with the amount of precipitation during August from one and two years before, one of the driest months (see Table 2 for explanation of variables), as well as the vapor pressure (VP) during the November-March period of two years before and inversely related to the maximum vapor pressure of the period July-August of two years before.

The total number of reproductive plants on a given year was directly related to the precipitation during the wet months, the vapor pressure during November-March period, precipitation levels during August of the year before, as well during wet months of two years before, maximum vapor pressure during July of the year before-and the vapor pressure during November-March period of two years before. The total of reproductive plants was inversely related to maximum TD during July and August of the previous year, and the vapor pressure of the period November-March of the previous year.

The total number of non-reproductive plants on a given year was directly related to the conditions of two years before: directly related to the amount of precipitation during the dry months, in particular in August, the maximum temperature during July, the temperature during the cold months and the vapor pressure during the period November-March; and it was inversely related to the maximum vapor pressure during July and August.

POPULATION GROWTH (LAMBDA)

Population growth (lambda) showed a direct relationship with the maximum vapor pressure in July and August of two years before, and it was inversely related with the vapor pressure of the period November-March of the same year and from two years before.

INFLORESCENCES

The number of inflorescences showed a direct relationship with the amount of precipitation during the wet months, and a negative relationship with the amount of precipitation in August and the temperature during the cold months of the year before.

6. DISCUSSION

Mulford's milkvetch populations are in clear decline throughout its range, and projections for the near future suggest a collapse of the species in the near future. Climate projections for the area (Chambers et al. 2008) indicate an increase in dry hot years, which potentially could delay the forthcoming collapse of the species, but not avoid it. While the projected increase in drought conditions will likely alter community composition and productivity, disturbance requirements, and erosion (Clark et al. 2002); the ability of Mulford's milkvetch to adapt to new climate regimes is unknown.

Additionally, drought could have a more negative effect on the plants than changes in temperatures (Lipiec et al. 2013, Kumawat and Sharma 2018), due to the endemic nature of the species, with limited abundance and distribution. Drought and changes in temperature can have additive effects on plants, so they could be hard to distinguish. Even though this study did not address the effects of climate change on phenology, the research literature provides ample evidence about detrimental effect of climate change on phenology and distribution (Munson and Sher 2015, Kidane et al. 2019).

Higher temperatures and changes in precipitation may increase the frequency and severity of disease outbreaks (Harvell et al. 2002). Due to the restricted range, low and decreasing population sizes, and sensitivity to climate change, a pathogen or disease outbreak could mean the ultimate collapse of the species.

Future steps

- **Seed collection** is recommended for seed banking, propagation, and replanting. Research should be conducted to assess the viability of long-term seed storage. There is evidence that seed collection and propagation could be successful with no specific requirements for this species (Center for Plant Conservation, *Astragalus mulfordiae* plant profile, website accessed 10/15/2022). Seeds, plugs, and/or seedlings should be planted in areas where the species shows more stable populations (Diaz and Harris 2022) (Mancuso and Brabec 2019, Pyramid Botanical Consultants 2019, for site specific details).

- **Habitat Suitability modeling and climate projections.** A suitability model for Mulford's milkvetch under different climatic projections would help to determine potential new areas where the species could be established in the future. The geographic region where temperature and precipitation patterns are suitable for a species to persist is called its climate niche (Pearson and Dawson 2003). While a climatic niche describes "suitable" habitat, it does not mean that a species will not be able to inhabit an area that is considered climatically unsuitable in the future. Modeled shifts in a species climatic niche are not necessarily a perfect representation of the species future distribution. Changes in climate may expand, contract, or shift the climate niches of species (Parmesan and Yohe 2003). Furthermore, climate variables alone do not sufficiently describe the distribution of a species. Using both dynamic and static variables improve accuracy of models, providing a more realistic prediction of species distribution under influence of climate change (Zangiabadi et al. 2021). Contrasting our findings against climate projections for the coming decades will bring light to potential trends for this declining species.

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APPENDIX I. CORRELATION VALUES BETWEEN CLIMATIC VARIABLES

	MayPpt	WetMonths	AugPpt	DryMonths	JulyMaxTemp	coldMonths	JulyAugTDmax	DecFebTDmin	JulyVPmax	JulAugVPmax	NovMarchVP	MayPpt1	WetMonths1	AugPpt1	DryMonths1	JulyMaxTemp1	coldMonths1	JulyAugTDmax1	DecFebTDmin1	JulyVPmax1	JulAugVPmax1	NovMarchVP1	MayPpt2	WetMonths2	AugPpt2	DryMonths2	JulyMaxTemp2	coldMonths2	JulyAugTDmax2
MayPpt	1.00	0.69	-0.21	0.26	-0.72	0.29	0.33	0.32	-0.74	-0.65	-0.18	0.28	-0.20	0.19	-0.11	-0.06	-0.28	-0.17	-0.08	-0.10	0.55	0.50	-0.37	0.19	0.03	0.47	-0.34	-0.10	0.54
WetMonths	0.69	1.00	0.11	-0.02	-0.49	0.38	0.60	0.45	-0.58	-0.66	-0.20	0.03	-0.09	-0.15	-0.03	-0.07	-0.43	0.00	-0.37	-0.12	0.40	0.12	-0.38	-0.17	0.28	0.16	-0.39	-0.01	0.30
AugPpt	-0.21	0.11	1.00	0.17	0.52	0.26	0.47	0.27	0.47	0.04	0.43	0.25	0.73	-0.42	0.56	-0.30	-0.22	0.47	-0.28	0.01	-0.24	-0.20	0.31	-0.16	0.41	-0.32	0.26	0.09	-0.35
DryMonths	0.26	-0.02	0.17	1.00	0.02	0.06	0.14	-0.01	0.07	-0.05	0.25	0.78	0.20	0.36	0.09	-0.23	-0.43	-0.12	-0.23	-0.28	-0.18	-0.04	0.48	0.37	-0.27	-0.08	0.46	-0.33	-0.11
JulyMaxTemp	-0.72	-0.49	0.52	0.02	1.00	-0.24	0.02	-0.32	0.98	0.83	0.28	-0.05	0.62	-0.30	0.49	-0.22	0.12	0.34	0.04	0.07	-0.70	-0.37	0.45	-0.33	0.09	-0.40	0.46	0.13	-0.72
coldMonths	0.29	0.38	0.26	0.06	-0.24	1.00	0.35	0.96	-0.28	-0.40	0.27	0.15	0.21	0.18	-0.38	0.40	-0.31	0.57	-0.27	0.12	0.33	-0.12	-0.42	0.25	0.07	-0.08	-0.54	0.15	0.32
JulyAugTDmax	0.33	0.60	0.47	0.14	0.02	0.35	1.00	0.40	-0.15	-0.37	-0.10	0.00	0.27	-0.41	0.07	-0.05	-0.38	0.17	-0.26	0.11	0.23	-0.12	-0.08	-0.01	0.42	-0.11	-0.14	0.19	0.09
DecFebTDmin	0.32	0.45	0.27	-0.01	-0.32	0.96	0.40	1.00	-0.36	-0.51	0.16	0.11	0.13	0.05	-0.41	0.32	-0.40	0.44	-0.41	0.17	0.49	-0.12	-0.42	0.30	0.16	-0.08	-0.52	0.20	0.44
JulyVPmax	-0.74	-0.58	0.47	0.07	0.98	-0.28	-0.15	-0.36	1.00	0.86	0.31	0.02	0.58	-0.22	0.50	-0.28	0.11	0.28	0.02	0.06	-0.72	-0.35	0.50	-0.29	0.02	-0.40	0.53	0.10	-0.71
JulAugVPmax	-0.65	-0.66	0.04	-0.05	0.83	-0.40	-0.37	-0.51	0.86	1.00	0.23	-0.09	0.33	-0.01	0.23	-0.04	0.32	0.16	0.26	0.01	-0.60	-0.12	0.32	-0.22	-0.15	-0.10	0.36	0.03	-0.53
NovMarchVP	-0.18	-0.20	0.43	0.25	0.28	0.27	-0.10	0.16	0.31	0.23	1.00	0.45	0.58	0.38	0.17	0.33	0.24	0.66	0.24	-0.40	-0.30	0.32	0.11	0.21	0.06	0.27	-0.01	-0.41	-0.27
MayPpt1	0.28	0.03	0.25	0.78	-0.05	0.15	0.00	0.11	0.02	-0.09	0.45	1.00	0.39	0.56	0.22	-0.24	-0.18	0.13	-0.19	-0.65	-0.13	0.30	0.55	0.38	0.17	0.30	0.51	-0.69	-0.12
WetMonths1	-0.20	0.09	0.73	0.20	0.62	0.21	0.27	0.13	0.58	0.33	0.58	0.39	1.00	0.03	0.61	-0.18	-0.06	0.67	-0.15	-0.37	-0.59	0.01	0.25	-0.12	0.41	-0.01	0.25	-0.28	-0.65
AugPpt1	0.19	-0.15	-0.42	0.36	-0.30	0.18	-0.41	0.05	-0.22	-0.01	0.38	0.56	0.03	1.00	-0.20	0.37	0.30	0.26	0.31	-0.64	-0.18	0.42	0.05	0.44	-0.09	0.51	-0.01	-0.72	-0.08
DryMonths1	-0.11	-0.03	0.56	0.09	0.49	-0.38	0.07	-0.41	0.50	0.23	0.17	0.22	0.61	-0.20	1.00	-0.65	0.12	0.18	0.07	-0.26	-0.62	0.13	0.43	-0.36	0.42	-0.02	0.54	-0.20	-0.69
JulyMaxTemp1	-0.06	-0.07	-0.30	-0.23	-0.22	0.40	-0.05	0.32	-0.28	-0.04	0.33	-0.24	-0.18	0.37	-0.65	1.00	0.40	0.44	0.48	-0.04	0.23	0.18	-0.48	0.21	-0.19	0.28	-0.68	-0.06	0.28

coldMonths1	-0.28	-0.43	-0.22	-0.43	0.12	-0.31	-0.38	-0.40	0.11	0.32	0.24	-0.18	-0.06	0.30	0.12	0.40	1.00	0.36	0.89	-0.34	-0.21	0.46	0.06	-0.19	0.23	0.48	-0.05	-0.35	-0.21
JulyAugTDmax1	-0.17	0.00	0.47	-0.12	0.34	0.57	0.17	0.44	0.28	0.16	0.66	0.13	0.67	0.26	0.18	0.44	0.36	1.00	0.29	-0.26	-0.30	0.13	-0.12	-0.06	0.36	0.14	-0.27	-0.20	-0.34
DecFebTDmin1	-0.08	-0.37	-0.28	-0.23	0.04	-0.27	-0.26	-0.41	0.02	0.26	0.24	-0.19	-0.15	0.31	0.07	0.48	0.89	0.29	1.00	-0.22	-0.18	0.49	-0.07	-0.15	-0.01	0.46	-0.19	-0.23	-0.14
JulyVPmax1	-0.10	-0.12	0.01	-0.28	0.07	0.12	0.11	0.17	0.06	0.01	-0.40	-0.65	-0.37	-0.64	-0.26	-0.04	-0.34	-0.26	-0.22	1.00	0.31	-0.47	-0.44	0.00	-0.42	-0.57	-0.34	0.97	0.35
JulAugVPmax1	0.55	0.40	-0.24	-0.18	-0.70	0.33	0.23	0.49	-0.72	-0.60	-0.30	-0.13	-0.59	-0.18	-0.62	0.23	-0.21	-0.30	-0.18	0.31	1.00	0.19	-0.41	0.22	-0.01	0.22	-0.47	0.30	0.97
NovMarchVP1	0.50	0.12	-0.20	-0.04	-0.37	-0.12	-0.12	-0.12	-0.35	-0.12	0.32	0.30	0.01	0.42	0.13	0.18	0.46	0.13	0.49	-0.47	0.19	1.00	-0.19	0.25	0.26	0.96	-0.18	-0.50	0.21
MayPpt2	-0.37	-0.38	0.31	0.48	0.45	-0.42	-0.08	-0.42	0.50	0.32	0.11	0.55	0.25	0.05	0.43	-0.48	0.06	-0.12	-0.07	-0.44	-0.41	-0.19	1.00	-0.13	0.24	-0.20	0.94	-0.44	-0.45
WetMonths2	0.19	-0.17	-0.16	0.37	-0.33	0.25	-0.01	0.30	-0.29	-0.22	0.21	0.38	-0.12	0.44	-0.36	0.21	-0.19	-0.06	-0.15	0.00	0.22	0.25	-0.13	1.00	-0.08	0.27	-0.05	-0.19	0.28
AugPpt2	0.03	0.28	0.41	-0.27	0.09	0.07	0.42	0.16	0.02	-0.15	0.06	0.17	0.41	-0.09	0.42	-0.19	0.23	0.36	-0.01	-0.42	-0.01	0.26	0.24	-0.08	1.00	0.31	0.21	-0.37	-0.20
DryMonths2	0.47	0.16	-0.32	-0.08	-0.40	-0.08	-0.11	-0.08	-0.40	-0.10	0.27	0.30	-0.01	0.51	-0.02	0.28	0.48	0.14	0.46	-0.57	0.22	0.96	-0.20	0.27	0.31	1.00	-0.20	-0.60	0.23
JulyMaxTemp2	-0.34	-0.39	0.26	0.46	0.46	-0.54	-0.14	-0.52	0.53	0.36	-0.01	0.51	0.25	-0.01	0.54	-0.68	-0.05	-0.27	-0.19	-0.34	-0.47	-0.18	0.94	-0.05	0.21	-0.20	1.00	-0.37	-0.50
coldMonths2	-0.10	-0.01	0.09	-0.33	0.13	0.15	0.19	0.20	0.10	0.03	-0.41	-0.69	-0.28	-0.72	-0.20	-0.06	-0.35	-0.20	-0.23	0.97	0.30	-0.50	-0.44	-0.19	-0.37	-0.60	-0.37	1.00	0.31
JulyAugTDmax2	0.54	0.30	-0.35	-0.11	-0.72	0.32	0.09	0.44	-0.71	-0.53	-0.27	-0.12	-0.65	-0.08	-0.69	0.28	-0.21	-0.34	-0.14	0.35	0.97	0.21	-0.45	0.28	-0.20	0.23	-0.50	0.31	1.00

APPENDIX II. DEMOGRAPHIC AND CLIMATIC VARIABLES MODELS.

Variables in parenthesis displayed a moderate variance inflation factor

Demographic Variable	Climatic Variables at t0	Climatic Variables at t-1	Climatic Variables at t-2	Final model with Climatic Variables at all 3 times
Total Plants	WetMonths DryMonths NovMarchVP (MayPpt)	MayPpt1 JulyVPmax1 JulAugVPmax1 NovMarchVP1 (AugPpt1) (DryMonths1)	AugPpt2 JulAugVPmax2 (NovMarchVP2) (years) (DryMonths2)	TotalPlants ~ AugPpt1 + AugPpt2 + JulAugVPMax2 + NovMarchVP2
Reproductive Plants	WetMonths DryMonths NovMarchVP (MayPpt)	MayPpt1 (Wet Months1) (AugPpt1) (DryMonths1) (JulyAugTDmax1) JulyVPmax1 NovMarchVP1	(years) WetMonths2 JulAugVPmax2 (NovMarchVP2)	Reprod ~ WetMonths + NovMarchVP + AugPpt1 + DryMonths1 + JulyAugTDmax1 + JulyVPmax1 + NovMarchVP1 + WetMonths2 + JulAugVPmax2 + NovMarchVP2
Non-Reproductive Plants	(JulyMaxTemp) JulyAugTDmax (JulAugVPmax)	--	AugPpt2 DryMonths2 JulyMaxTemp2 coldMonths2 JulAugVPmax2 NovMarchVP2	nonReprod ~ AugPpt2 + DryMonths2 + JulyMaxTemp2 + coldMonths2 + JulAugVPmax2 +NovMarchVP2

Seedlings	years MayPpt DryMonths DecFebTDmin NovMarchVP	MayPpt1 AugPpt1 coldMonths1 (JulyAugTDmax1) (JulAugVPmax1) NovMarchVP1	AugPpt2 JulyVPmax2 JulAugVPmax2 NovMarchVP2	
Lambda				lambda ~ NovMarchVP + JulAugVPmax2 + NovMarchVP2
Inflorescences				infl ~ WetMonths + AugPpt + coldMonths1 + JulAugVPmax2

APPENDIX II. FINAL MODELS PARAMETER VALUES.

	Estimate	Std. Error	t value	Pr(>|t|)		McFadden R^2 (^)
			Total Plants			
(Intercept)	-164.18	45.88	-3.58	0.00	***	0.28
AugPpt1	7.13	4.51	1.58	0.12		
AugPpt2	3.73	1.02	3.65	0.00	***	
JulAugVPmax2	-45.69	30.39	-1.50	0.14		
NovMarchVP2	69.62	26.15	2.66	0.01	*	
			Reproductive Plants			
(Intercept)	-343.16	69.67	-4.93	0.00	***	**0.64**
WetMonths	23.94	3.31	7.23	0.00	***	
NovMarchVP	29.21	14.59	2.00	0.05	.	
AugPpt1	21.81	4.04	5.39	0.00	***	
DryMonths1	12.49	3.23	3.87	0.00	***	
JulyAugTDmax1	-12.50	3.30	-3.78	0.00	***	
JulyVPmax1	2.06	0.56	3.69	0.00	***	
NovMarchVP1	-0.85	0.24	-3.54	0.00	**	
WetMonths2	1.07	0.69	1.56	0.13		
JulAugVPmax2	90.14	20.48	4.40	0.00	***	
NovMarchVP2	43.14	16.69	2.58	0.01	*	
			Non-Reproductive Plants			
(Intercept)	-149.06	38.17	-3.91	0.00	***	**0.42**
AugPpt2	2.07	0.49	4.22	0.00	***	
DryMonths2	1.19	0.50	2.40	0.02	*	
JulyMaxTemp2	0.72	0.42	1.71	0.09	.	
coldMonths2	0.63	0.30	2.07	0.04	*	
JulAugVPmax2	-52.72	14.15	-3.73	0.00	***	
NovMarchVP2	31.31	12.60	2.48	0.017	*	

Lambda						
(Intercept)	0.82	0.04	20.79	<0.00	***	**0.46**
NovMarchVP	-0.25	0.08	-3.03	0.00	**	
JulAugVPmax2	0.45	0.09	4.93	0.00	***	
NovMarchVP2	-0.19	0.09	-2.06	0.05	*	
Inflorescences						
(Intercept)	-4775.7	1545.6	-3.09	0.003	**	0.32
WetMonths	1782.1	560.3	3.18	0.002	**	
coldMonths1	-606.0	875.0	-0.69	0.49		
JulAugVPmax2	9869.9	3247.5	3.04	0.004	**	

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(^) McFadden R2 was used to assess how well the selected model fits the data. In practice, values 0.4 indicate that a model fits the data very well.