AN ABSTRACT OF THE THESIS OF

Ian A. Pfingsten for the degree of Master of Science in Botany & Plant Pathology

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Abstract approved: _____

Thomas N. Kaye

Increased temperatures due to anthropogenic-induced climate change may raise the threat of extinction for taxa with sessile life histories (*e.g.*, plants) in the near future. Linking climate change models to demographic models may provide useful insights into the potential effects of environmental changes on rare plants, and therefore aid in their current and future conservation. Population demographers generally agree that mechanistic models from a reductionist perspective are necessary to test assumptions in population drivers.

For the first study, I assessed the climate vulnerability of a rare plant species, *Pyrrocoma radiata*, with a mechanistic model of four climatically-similar populations. I used environmentally-driven demographic models to estimate vital rates and population sizes from a nonlinear, nonparametric regression with local climate variables. I assessed the utility of this environmentally-correlated, stage-structured population matrix model compared to a stationary model of independent and

identically-distributed environmental stochasticity. I then simulated future population projections based on climate conditions predicted by General Circulation Models (GCMs) under opposing emission scenarios.

The second study hopes to answer population-level questions using a traditionally community-level method, non-metric multidimensional scaling, which considers correlation structure between response variables and can be used to find environmental correlates of the ordination axes. Demographic data on a threatened perennial, *Astragalus tyghensis,* were collected from five sites in the Tygh Valley, OR. I considered correlation structure between demographic vital rates to find environmental correlates of the ordination axes.

The search for an environmental driver of population vital rates was successful for the two study species. Previous year dry dormant season precipitation likely affects the fertility rates a year later in *P. radiata* populations, and dry growing season reference evapotranspiration rates positively correlated with a growth gradient in *A. tyghensis*. Based on predicted precipitation, *P. radiata* is expected to rapidly decline by 2050, but this may be due to biases in the two GCMs and reliance on only one environmental factor. The NMS ordination adequately captured most of the variation in transition elements for the years and populations from *A. tyghensis* demographi*cs.* I provided support to the claim that model predictions can improve with the inclusion of mechanistic relationships. The inclusion of abiotic drivers in models used to predict population trends is supported by our study and may enhance predictive power in population viability assessments under changing climates.

Using Local Climate to Explain Temporal Variation in Rare Plant Populations

by

Ian A. Pfingsten

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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Ian A. Pfingsten, Author

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CONTRIBUTION OF AUTHORS

For Chapters 2 and 3, Thomas N. Kaye provided the demographic plant data and funding, and Ian A. Pfingsten provided the climate data, analysis, and writing.

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CHAPTER 1

General introduction

Increased temperatures due to anthropogenic-induced climate change may
increase the threat of extinction for taxa with sessile life histories (*e.g.*, plants) in the
near future (Parmesan 2003). The Intergovernmental Panel on Climate Change (2007)
predicts drastic shifts in global temperatures, potentially cascading to increases in
extreme weather events like hurricanes, droughts, and wildfires. Not only do we
expect shifts in mean temperatures and precipitation, but also increased variability in
climate and increased frequency of extreme weather (Easterling *et al.* 2000), which we
currently witness on a global scale. Effects of shifting climates on species distributions
is actively being studied to determine beneficial mitigation strategies for at risk
species, such as relocation to new habitats with suitable microclimate conditions
(Kreyling *et al.* 2011). Some species may have wide plasticity in traits, phenology, or
migration to buffer these changes (Tingley *et al.* 2009), but others may need assistance
through conservation efforts.

Previous attempts to predict species spatial distributions in changing climates
utilized presence/absence data in bioclimatic envelope models (Pearson *et al.* 2002,
Thuiller 2003). Originally, these habitat suitability models assumed species were
limited by all factors in their historic, Hutchinsonian niche, and that their future

survival depends on maintaining all aspects of that niche (Hutchinson 1957). Some

criticized this assumption in envelope models due to the reliance on correlations

between species observations and habitat conditions to predict future occurrences

without physiological mechanisms in the model (Pearson and Dawson 2003). Newer

models now use combinations of life history, biotic interactions, and habitat (Jiguet *et

al.* 2007, Keith *et al.* 2008), which may be a necessary complexity as some species

have wider resiliency than predicted and could be limited by a few biotic or abiotic

factors.

Demographers generally agree that mechanistic models from a reductionist

perspective are necessary to test assumptions in population drivers (Crone *et al.* 2012).

These drivers hopefully explain variation in life history stages, specifically in temporal

variability. Traditionally, this variability was attributed to environmental stochasticity,

and modeled through randomization of all deterministic population growth rates

calculated from age- or stage-structured population matrices throughout the sampling

period (Menges 2000, Caswell 2001). However, correlations among measured vital

rates (growth, survival, fertility) may explain variation in population dynamics

attributed to environmental stochasticity (Horvitz and Schemske 1995). We need more

mechanisms to explain these correlations among population vital rates, such as density

dependence, and correlations with time, such as disturbances. Fortunately many

studies provide evidence to support population models driven by herbivory (Ehrlén

1995), fire (Kaye *et al.* 2001, Quintana-Ascencio *et al.* 2003), hurricanes (Pascarella

and Horvitz 1998), genetics (Picó *et al.* 2008), and climate (Saltz *et al.* 2006, Doak

and Morris 2011).

Here, I explain two studies that use climate drivers explicitly in demographic population matrix models of two rare plant species found in Oregon and Idaho. I used long-term (N ≥ 9) demographic data from multiple populations of two herbaceous perennials to find the best climate covariate of each species, and I then developed a mechanistic model that is applicable across populations in the species' range. I selected a single, parsimonious climate driver through two relatively novel variable selection methods. I then projected future population sizes for one species using climate predictions from two general circulation models in the IPCC fourth assessment report (2007).

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CHAPTER 2

Forecasting the effects of climate change on rare plant populations

Ian A. Pfingsten & Thomas N. Kaye

Abstract

Rare plants that are strongly limited by environmental factors may increase in extinction risk due to local climate shifts. Linking climate change models to demographic models may provide useful insights into the potential effects of environmental changes on rare plants, and therefore aid in their current and future conservation. Here, I assessed the climate vulnerability of a rare plant species, *Pyrrocoma radiata*, with a mechanistic model of four climatically-similar populations. I used environmentally-driven demographic models to estimate vital rates and population sizes from a non-linear, nonparametric regression with local climate variables. I assessed the utility of this environmentally-correlated, stage-structured population matrix model compared to a stationary model of independent and identically-distributed environmental stochasticity. I then simulated future population projections based on climate conditions predicted by General Circulation Models (GCMs) under opposing emission scenarios. Previous year dry dormant season was the best predictor of *P. radiata* population growth, suggesting a strong unimodal relationship. However, this relationship was not equally strong across all four study sites. Still, the climate-driven model more accurately and precisely matched the observed population trend compared to the null model (without climate drivers). Based on predicted precipitation for the four sites, *P. radiata* is not expected to rapidly decline by 2050, but this may be due to biases in the two GCMs and reliance on only one environmental factor. The inclusion of abiotic drivers in models used to predict

population trends is supported by our study and may enhance predictive power in population viability assessments under changing climates.

Introduction

Changes in global climate may cause shifts in species distributions by affecting vital rates and increasing extinction risk for locally adapted, rare and endangered plant populations (Parmesan 2006, Ohlemüller *et al.* 2008, Vitt *et al.* 2010). Climate forecasts for the next century predict increases in average temperature as well as extreme temperature events for most of the planet (Salinger 2005). Rare plants that are strongly limited by certain abiotic factors will be most at risk to local climate shifts. This may not be the case if phenotypically plastic species have wide niches and can buffer effects of the altered climate. Climate envelope models generally assume that abiotic conditions must remain within historic limits for continued species viability, while few have addressed the more mechanistic links between environments and population vital rates (Keith *et al.* 2008). Keith *et al.* (2008) coupled spatial stochastic population models to bioclimatic habitat models. Their results indicated complex interactions among life histories, disturbance, and distribution regulate the extinction risk for three plant species under climate change scenarios. Linking local climate to demographic population models may provide useful insights into potential effects of environmental changes on rare plants, and therefore aid in their current and future conservation.

A useful and widely accepted method of assessing a population's viability is through its vital rates (survival, growth, and fertility) in demographic population projection models (Caswell 2001). These models have generally improved through long-term sampling, manipulative studies, and correlations to biotic and abiotic factors driving the population demographics (Menges 2000, Bakker *et al.* 2008, Crone *et al.* 2011). Simulating population projections using stochastic processes adds uncertainty caused by environmental variation and tends to produce a wide estimate of population viability (Tuljapurkar 1990, Boyce *et al.* 2006). Recent studies have shown the importance of temporal correlations with population vital rates, indicating improvements in accuracy and precision of population predictions (Tuljapurkar and Haridas 2006). These typically mechanistic approaches link environmental factors such as nitrogen (Gotelli and Ellison 2006), disturbance (Evans *et al.* 2010), and soil moisture (Machinski *et al.* 2006) to population vital rates. The number of studies linking climate to demographic population models is increasing (Saltz *et al.* 2006, Jenouvrier *et al.* 2009, Dalgleish *et al.* 2011, Davison *et al.* 2010, Hunter *et al.* 2010, Doak and Morris 2011, Nicolè *et al.* 2011). However, to make strong inferences on the relationship to climate covariances, these reductionist models require wide time-series data on a species throughout its distribution.

Here, I assess correlations between observed seasonal weather patterns and population growth rates with eleven years of demographic data on a rare, endemic, herbaceous perennial. I developed a mechanistic model of population growth response

to climate with measurements obtained from local weather stations. I then simulate four plant populations for one focal species using the demographic and climate data to compare two hypothetical models. The relative difference among simulation outputs from these models gives an idea of the impact on these populations due to climate conditions. Our proposed model includes two levels of sophistication over traditional population projection models: a density dependent function based on an empirically-supported relationship of seedling survival and adult fertility, and an environmentally-driven population growth rate through a nonlinear regression model, backed by theory and statistically validated in this study.

Studies with mechanistic models of climate driven populations are increasing (Maschinski *et al.* 2006, Saltz *et al.* 2006, Dalgleish *et al.* 2011, Davison *et al.* 2010, Hunter *et al.* 2010, Nicolè *et al.* 2011), but non-linear relationships of vital rates and environments are rarely documented (Doak and Morris 2011, Jenouvrier 2012). Early attempts to explain plant demographics with climate covariates used a matrix selection method by associating matrices with extreme weather (Maschinski *et al.* 2006, Marrero-Gómez *et al.* 2007, Jenouvrier *et al.* 2009, Hunter *et al.* 2010). Studies using regression models found convincing relationships with vital rates and local climate factors (Saltz *et al.* 2006, Dalgleish *et al.* 2011, Nicolè *et al.* 2011). Dalgleish *et al.* (2011) and Nicolè *et al.* (2011) utilized stage-less, integral projection models (Easterling *et al.* 2000), a potentially more appropriate technique than stage-structured matrix models to demonstrate climate effects on plant population dynamics. Support

for non-linear effects on plant population growth may be increasing. A recent study by Doak and Morris (2011) found a non-linear trend between snow cover and two North American tundra plant populations, and Jenouvrier *et al.* (2012) found emperor penguins are at risk to anomalies in sea ice cover at both extremes.

For our assessment, I used a data set for a plant species with more than five years of demographic data to observe population trends due to environmental variation (Kaye and Pyke 2003, Ellis *et al.* 2012). I chose a rare, native herbaceous perennial, Snake River goldenweed (*Pyrrocoma radiata*) Nutt., Asteraceae, a narrow endemic found in the Snake River Canyon of eastern Oregon and adjoining Idaho, USA. *P. radiata* is listed as Endangered by the Oregon Department of Agriculture, as a Species of Concern by the U.S. Fish and Wildlife Service, and a Bureau of Land Management Special Status Species (Oregon Natural Heritage Program 2001). Population growth and reproduction are impacted negatively by livestock grazing and insect herbivory (Kaye 2002), while competition from exotic, annual forbs and grasses poses additional threats to population viability (Mancuso and Moseley 1993).

I asked three main questions:

1.) Are *P. radiata* population growth rates predictable from weather conditions? I expect plant population growth to have a nonlinear relationship to local, seasonal weather, as theorized by unimodal distributions along environmental gradients (Whittaker 1956).

2.) Do models with climate drivers fit observed *P. radiata* population trends? I consider two population projection algorithms: one without climate variables (null model) and one with climate variables explicitly linked to population growth rates.

3.) How will climate change affect *P. radiata* population viability in the near future? I simulated 10,000 iterations of the climate-driven population algorithm using two opposing emissions scenarios to assess population viability while considering uncertainty in climate predictions.

Methods

Study species and demographic data

Growing seasons range from May to August with flowering from June to July, seldom to September. Seed production is vital to this species as plants do not reproduce vegetatively. Seedlings will germinate as early as May (Kaye and Meinke 1992). This species is non-dormant, and seed does not survive over one year in seed banks (Kaye *et al.* 1990). Plants are herbaceous, with the exception of a woody taproot, and heights of erect flowering stems are mostly above 40 cm.

Populations are usually found in rocky, open soil, on south to west-facing, gentle to steep (> 50%) slopes, with elevations from 640 to 1830 m. Soil is slightly to very calcareous, often overlaying a shale formation. *P. radiata* occurs within a grazing-modified version of a sagebrush/grassland community consisting of *Artemisia tridentata*, *Agropyron spicatum*, and *Poa sandbergii*. The regional climate tends

toward mild, warm winters due to the Pacific Maritime air mass, and dry, hot

summers.

Table 1. *P. radiata* population slope aspect, elevation, and geographic location.

Population	Aspect	Elevation (m)	Location
Site 1	south-facing slope	610	Lat: 44.412 Lon: -117.322
Site 2	gentle, east-facing slope	756	Lat: 44.412 Lon: -117.313
Site 3	gentle, west-facing slope	902	Lat: 44.479 Lon: -117.327
Site 4	west-facing slope	829	Lat: 44.476 Lon: -117.333

Four populations were monitored for eleven years (Table 1), and ten stage-

structured demographic transition matrices (Leftkovitch 1965) (Eq. 1) were created for

each year t to t +1 of study and for each population based on four life history stages :

seedling, juvenile ($\leq$ three leaves), vegetative ($\geq$ four leaves), and reproductive (Kaye

2002, Kaye and Pyke 2003, Ellis *et al.* 2012) (see appendix for matrices). Individual

plant survival, leaf number, and flowering head number were recorded annually to

calculate three types of life history vital rates: survival (**S**), growth (**G**), and fertility

(**F**), where $\mathbf{A}_{ij} = f(\mathbf{F}, \mathbf{S}, \mathbf{G})$ (Eq. 1). The intrinsic population growth rate, λ, was

calculated from the maximum eigenvalue of each transition matrix (Caswell 2001).

$$A_{ij} = \begin{bmatrix} 0 & 0 & 0 & F_4 \\ S_1 * G_{1,2} & S_2 * G_{2,2} & S_3 * G_{3,2} & S_4 * G_{4,2} \\ S_1 * G_{1,3} & S_2 * G_{2,3} & S_3 * G_{3,3} & S_4 * G_{4,3} \\ S_1 * G_{1,4} & S_2 * G_{2,4} & S_3 * G_{3,4} & S_4 * G_{4,4} \end{bmatrix} \qquad \text{Eq. 1}$$

Climate drivers

Climate predictor estimates were calculated from PRISM (Parameter-elevation Regressions on Independent Slopes Model), a climate mapping system that uses measurements from weather stations, a digital elevation model, and expert knowledge of complex climatic extremes to produce continuous grid estimates of weather parameters (Daly *et al.* 1994). Our predictors included seasonal precipitation and maximum temperature estimated from monthly PRISM estimates at 30 arc-second (~800m) grid resolution, which was small enough to differentiate conditions at all four populations. Monthly precipitation and maximum temperature were totaled and averaged, respectively, across four life history seasons specific to *P. radiata* and its habitat: wet growing season (May-Jun), dry growing season (Jul-Aug),wet dormant season (Nov-Apr), and dry dormant season (Sep-Oct). Wet seasons were those months with higher than mean annual precipitation, while growing seasons were those during which the species typically has green leaves (Kaye 2002). The climate predictors were then grouped into two time lags according to the current and next year's demographic monitoring, assuming there are instant and delayed effects from climate on the population (*e.g.*, warm months might decrease seedling survival through increased evapotranspiration rates in the current year, while a drought the previous year might cause reproductive adults to allocate resources to survival and decrease fertility in the current year). Climate predictors used in variable selection totaled sixteen (2 climate drivers x 4 seasons x 2 time lags).

Predictor selection

Analyses were conducted in R, version 2.15.1 (R Development Core Team 2012), using scripts developed for this study and adapted from a similar study (Quintana-Ascencio *et al. unpublished*).

I used nonparametric regression with a local mean Gaussian weighting kernel to assess the best one-predictor, nonlinear model of population growth (McCune 2006). A nonlinear regression was preferred over an ordinary least-squares regression due to an expected unimodal population growth across an environmental gradient. There are no coefficients in this nonparametric regression, which instead uses the predictor values and a tolerance level, or proportion of the predictor range, to produce nonlinear regressions. Because the data are fixed, tolerances are incrementally adjusted to find the best fit to the data, with constraints on over-fitting.

I chose the model with the highest cross-validated R^2 (xR^2) from a single climate predictor of λ averaged across all study populations for each year. Cross-validation used a jackknife approach to calculate the $\hat{y}$ values by excluding the *i*th data point in estimating $\hat{y}_i$ (Antoine & McCune 2004). For weak models, xR^2 values can be negative when the residual sum of squares is larger than the total sum of squares. A maximum of one variable was chosen for each model due to limited λ values collected for each site (N = 10). I constrained models by a minimum average neighborhood size (the average predictor kernel width) of 25% of the sample size (10 x 0.25 = 2.5 data

points in a local regression). This was a second overfitting protection applied to find the optimum tolerance in the local model kernel.

After I chose the best climate predictor for the species, population models with the chosen predictor of λ were assessed for each of the four populations. Each population model was determined by the same minimum average neighborhood size (25% of N) as in the site-averaged population model. Model significance was checked with a randomization test to calculate an empirically-derived p-value (Manly 1997), although the small sample size limited the power of significance tests.

Simulations: External validation

To assess the validity of our climate-driven population assumption, I compared simulations of each population's sizes through time with two population projections: our environmentally-driven population growth (ED) model and an independent and identically-distributed environment (IID) model. The ED model assumes that vital rates are correlated with the environment, while the IID (or null) model assumes that each year's environment is unrelated to the previous year's environment, and all environments are equally likely in a given year (*i.e.*, entire matrices are selected at random per iteration) (Caswell 2001, Kaye and Pyke 2003). Both models incorporated density dependence on population size by an exponential decay function (Eq. 2) of the previous year's fertility rate times the current year's seedling death rate, to estimate current year seedling survival rates. This is biologically reasonable assuming the

proportion of surviving seedlings increases when seed production is low the previous

year, and *vice-versa*, which is supported by an observed negative correlation between

the two vital rates for each population (Spearman rank correlations = -0.45, -0.72,

-0.26, -0.35 for sites 1-4 respectively). The density dependent function was applied

after vital rates were estimated or matrices were selected. Each population projection

algorithm was run for 1,000 iterations to estimate the trajectory's 95% confidence

intervals.

$$S_{t+1,1} = e^{-(1-S_{t+1,1})\,F_{t,4}}$$

Eq. 2

To assess the utility of the ED model over the IID model, I calculated three

measures of the difference between observed and estimated population sizes: accuracy,

precision, and correlation. Accuracy was calculated as the ratio of change in observed

population size due to the absolute difference between median estimated population

size and observed size (Eq. 3). I similarly calculated precision as the ratio of change in

the observed population size range due to the difference in the 97.5th and 2.5th

quantiles of the estimated population sizes (Eq. 4). I measured correlation as the

Spearman's rank correlation coefficient between observed and estimated population

sizes for the period of observation (Eq. 5). I then calculated the means and standard

errors among all iterations of accuracies, precisions, and correlations across all

projected years (Table 3).

$$Accuracy = \frac{N_{obs}}{N_{obs} + |N_{est} - N_{obs}|}$$

Eq. 3

$$Precision = \frac{N_{obsMAX} - N_{obsMIN}}{N_{obsMAX} - N_{obsMIN} + \left| N_{est\,97.5th} - N_{est\,2.5th} \right|} \qquad \text{Eq. 4}$$

$$Correlation = \text{Spearman's rank corr}\left(N_{obs}, N_{est}\right) = \rho_{N_{obs}, N_{est}} \qquad \text{Eq. 5}$$

I constructed three vital rate matrices by individual plant survival (S_{tj}), fertility (F_{tj}), and growth (G_{tji}) for each of the four stages at year t, because these vital rates, more than the transition matrix elements, represent the population measurements in the field. For each column (j) of the three vital rate matrices, I used the same climate variable in nonlinear, nonparametric regression models as above to estimate a new set of vital rates ($\hat{y}$). I then calculated a new transition matrix from each iterated bootstrapped vital rate estimate (Eq. 1) and cross-multiplied it by the previous year's stage structure vector, starting with the initial stage structure from year t, to produce the next year's stage structure (Caswell 2001). Uncertainty in model estimates was due to confidence around vital rates estimates predicted from 1,000 bootstrapped regressions of each vital rate and the climate driver.

Simulations: Climate predictions

To assess population viabilities under climate change scenarios, I extrapolated vital rates from climate predictions using the previous nonparametric regressions, and thus uncertainty was applied as in the external validation simulations. Climate predictions were from two General Circulation Models (GCMs), Hadley CM3 (Gordon *et al.* 2000, Pope *et al.* 2000) and CSIRO Mk3 (Gordon *et al.* 2002), both

used in the fourth IPCC climate change assessment (IPCC 2007) and down-scaled to a

30 arc-second resolution. Special report on emissions scenarios (SRES) A2 (increasing

emissions) and B1 (reduced emissions) were chosen for the two GCMs, respectively,

to represent the most pessimistic and optimistic forecasts for the region (*i.e.*, the

pessimistic forecast is Hadley CM3 SRES A2, and the optimistic forecast is CSIRO

Mk3 SRES B1). Monthly climate predictions were averaged or totaled as mention

above to match the chosen climate driver season interval.

I ran simulations using the ED population projection algorithm to compare

outcomes in population size estimates among the two climate scenarios. The ED

model used the same predictor chosen in the population models. Vital rates were

estimated with the nonparametric regression models as in the external validation.

These simulations were projected to the year 2050 and iterated 10,000 times to

empirically estimate the population size trajectory's 95% confidence intervals.

To calculate the stochastic population growth rate $\log(\lambda_s)$, I took the log ratio of

subsequent pairs of population sizes, $\log[N(t + 1) / N(t)]$, and calculated the arithmetic

mean of all log ratios along the climate scenario time series. The mean $\log(\lambda_s)$ was

calculated from the average of 1,000 iterations of $\log(\lambda_s)$, where each $\log(\lambda_s)$ was

simulated from a bootstrapped regression of the vital rates. A 95% confidence interval

around the mean $\log(\lambda_s)$ was empirically calculated from the iterations of $\log(\lambda_s)$. A

$\log(\lambda_s)$ value of less than zero, or λ_s less than one, indicates a decreasing population.

Results

Climate driver

Total precipitation in the previous year's dry dormant season had the highest xR^2 (-0.13, R^2 = 0.35) with site-averaged λ (Table 2). Mean maximum temperature in the previous year's dry growing season was the next best predictor of λ (xR2 = -0.14, R2 = 0.39) (*see Appendix Table S6*). Total precipitation for this season during all years of population monitoring ranged from 14.0 (driest year) to 66.7 (wettest year) mm across all sites.

The nonlinear regression of total dry dormant season precipitation on the site-averaged deterministic population growth rate had a noticeable unimodal curve (Figure 1). Even the 95% bootstrapped variability bands retained a unimodal shape. The peak of the curve is around 34 mm of total precipitation, although the highest λ seems to correspond to around 32 mm. The nonlinear regressions of dry dormant season precipitation against each of the 17 vital rates showed that the fertility rate of reproductive adults was the only vital rate with a similar unimodal curve (Figure 2).

Table 2. Cross-validated R^2 (xR^2), R^2, and p-values for each nonparametric model of *P. radiata* population growth rate from total precipitation in the previous year's dry dormant season. The site-averaged model statistics are on the first row.

Population	N (plants)	xR²	R²	p-value
Average	17861	-0.13	0.35	0.130
Site 1	8164	0.07	0.47	0.051
Site 2	3194	-0.09	0.40	0.170
Site 3	4913	-0.26	0.00	0.757
Site 4	1590	-0.25	0.01	0.505

Figure 1. Nonlinear regression of seasonal precipitation on site-averaged population growth rates. 95% variability bands are estimated with 100 bootstrap regressions.

Simulations: External validation

All population size estimates were improved in the three metrics under the ED model over the IID model, with the exception of accuracy in the Site 3 model (Table 3). The largest improvement in accuracy (5.12%) and precision (39.46%) was the in Site 1 model. ED models for sites 2 and 4 (0.608 and 0.824, respectively) had the largest improvement in correlation coefficients than those of IID models.

The ED model is better than the IID model at matching peaks and troughs of the observed population size (Figure 3). The lagged effect of precipitation on the population is apparent on years 1993 and 1998 where the population size estimation rises the following year in response to the previous year's precipitation around 30 mm.

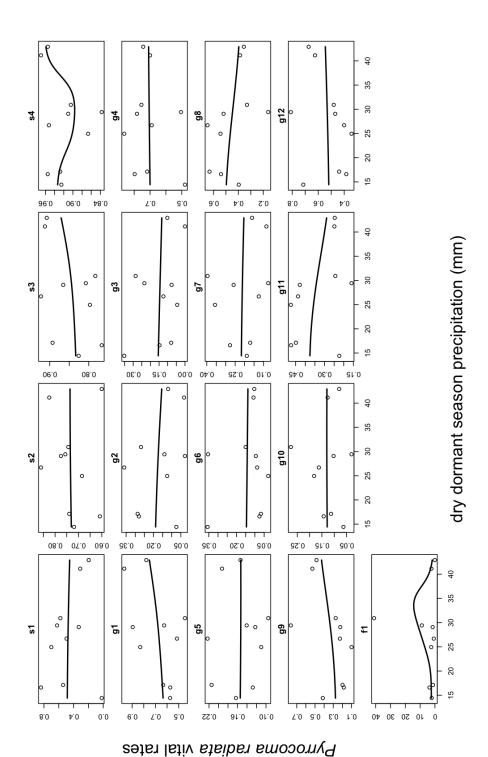**Figure 2.** Non-linear regression of seasonal precipitation on site-averaged population vital rates. Survival (s1-s4) and growth rates (g12-g44) are in units of probabilities. Fertility rates (f4) are in units of seedlings per reproductive adult.

Table 3. Validation metric means (SE) of observed to estimated population sizes for ED and IID models of *P. radiata* populations. Accuracy and precision range from 0 to 1; correlation ranges from -1 to 1. Improvement is the difference in a measure between ED and IID models.

Population	Accuracy			Precision			Correlation	
	ED	IID	Improvement	ED	IID	Improvement	ED	IID
Site 1	0.641 (0.053)	0.590 (0.011)	5.12%	0.602 (0.048)	0.207 (0.021)	39.46%	0.134 (0.006)	0.067 (0.011)
Site 2	0.526 (0.070)	0.492 (0.032)	3.35%	0.556 (0.057)	0.168 (0.018)	38.78%	0.608 (0.008)	0.009 (0.013)
Site 3	0.657 (0.025)	0.652 (0.022)	0.56%	0.835 (0.011)	0.645 (0.023)	19.03%	0.173 (0.006)	0.008 (0.010)
Site 4	0.696 (0.023)	0.700 (0.024)	-0.41%	0.676 (0.017)	0.389 (0.025)	28.70%	0.824 (0.006)	0.446 (0.014)
Average	0.685 (0.040)	0.673 (0.014)	1.27%	0.694 (0.044)	0.391 (0.009)	30.25%	0.226 (0.007)	-0.032 (0.010)

Figure 3. Site-averaged *P. radiata* log population size projections estimated with the ED and IID algorithms. The blue and red solid and dashed lines are the population size medians and 95% quantiles under the ED and IID algorithms, respectively. The black dotted line is the total dry dormant season precipitation for the site-averaged population. Population sizes are log base 10 transformed.

Simulations: Climate predictions

All population models projected slight population decreases by 2050 under the two emission scenarios. Population projections were similar across different GCMs under opposing emission scenarios. Median projection estimates decreased under the B1 than the A2 scenarios by 2050 for the site-averaged population (Figure 4). I estimated the mean λ_s to be below one for the SRES B1 and A2 scenarios, except for Site 1 under the A2 scenario (Table 4). The 95% confidence interval around mean λ_s overlapped one, except for Site 4 with an interval below one for both scenarios. The Site 3 model estimated the fastest decrease in population, with at least a 14% decrease under the A2 scenario, while the Site 1 model estimated at most a 13% increase in population size per year.

Table 4. Mean stochastic population growth rates (λ_s) with 95% confidence intervals of the mean, calculated from 1,000 iterations of *P. radiata* population projections under the ED algorithm. The average population λ_s is calculated from the average vital rates and climates across study populations. B1 is the optimistic emissions scenario and A2 is the pessimistic emissions scenario.

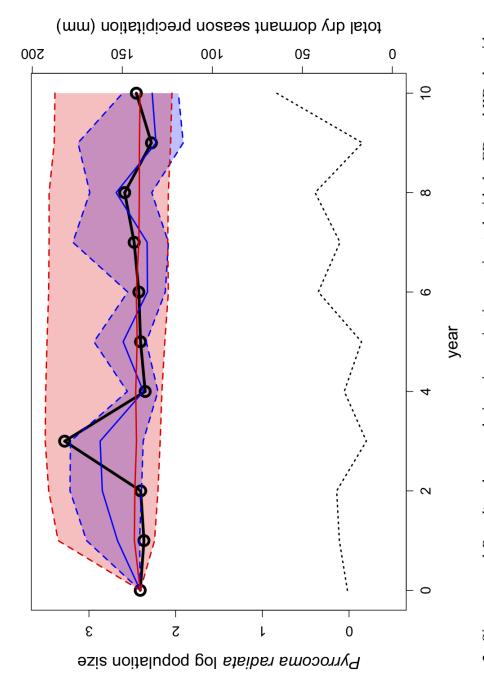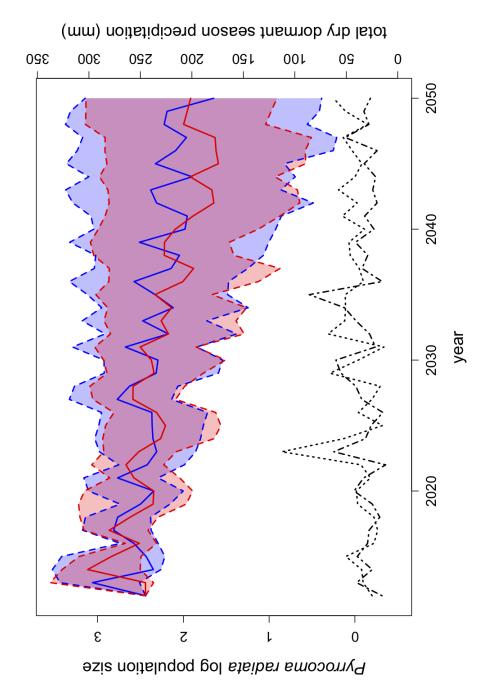|	Mean λ_s		95% C.I.	
Population	B1	A2	B1	A2
Site 1	0.98	1.03	0.89, 1.09	0.94, 1.13
Site 2	0.97	0.99	0.85, 1.08	0.89, 1.09
Site 3	0.93	0.92	0.84, 1.05	0.83, 1.07
Site 4	0.94	0.92	0.87, 0.99	0.86, 0.98
Average	0.95	0.97	0.87, 1.04	0.91, 1.04

Figure 4. Site-averaged *P. radiata* log population size projections estimated with the ED algorithm. The blue and red solid and dashed lines are the population size medians and 95% quantiles under the B1 and A2 emission scenarios, respectively. The black dotted and dash-dotted lines are the total dry dormant season precipitation estimated from the B1 and A2 emission scenarios, respectively. Population sizes are log base 10 transformed.

Discussion

Climate driver

I found relatively strong relationships between population growth rate and a climate driver (Table 2). Kaye (2002) found *P. radiata* population growth linearly increased with fall precipitation in the same year, but flower and seed production positively correlated with winter and summer precipitation, respectively. This supports our findings that previous year precipitation may affect flowers production, followed by seedling recruitment the following year. Dalgleish *et al.* (2011) also showed a lagged climate effect on a sagebrush steppe, perennial bunchgrass population that was positively associated with previous year precipitation, yet this was a linear trend. Other studies indicating a unimodal pattern with precipitation are rare, but a few note unimodal relationships between mean annual precipitation and rain use efficiency (Paruelo et al 1999, Yang et al 2010).

Fertility rates of reproductive adult plants had the strongest nonlinear relationship with precipitation in the previous year's dry dormant season or a late into the dry growing season. The inherent properties of the nonparametric regression local mean weighting kernel constrained other vital rates from extrapolation past their observed range, where weaker regression estimations approached the mean of observed vital rates. Hence, our ED model is mostly driven by changes in fertility originating from changes in precipitation. Precipitation appears to have a lagged effect on fertility through resource allocation by reproductive adults.

A manipulative study is needed to determine if precipitation has a direct or

indirect effect on next year's fertility. Reproductive adult plants could be allocating resources directly from early dormant season rainfall, or rainfall could be affecting herbivory rates on *P. radiata* and thus indirectly affecting populations (Kaye 2002). Likewise, runoff from intense rain events could also increase soil, litter, and seed loss (Descheemaeker *et al.* 2006, Cerdà and García-Fayos 2002) causing negative effects on fecundity from high precipitation.

A potential predictor not considered in this study is the variability within the seasonal climate drivers. The assumption here is that plant populations are more affected by extreme than average climatic events (Boyce *et al.* 2006, Verboom *et al.* 2010). Extreme cold periods, for example, even if a rare event in the growing season, may be enough to decimate seed production or seedling recruitment. Precipitation in the dry dormant season was mostly attributed to intense rainfall over 10 mm during one or two days for eight of the ten study years according to measurements collected from two local remote automated weather stations at Dead Indian Ridge, ID and Morgan Mountain, OR. These events may be obscured in averages and totals, yet this daily variance may serve as climatic driver in some species.

Microclimate may also play an important role in determining the viability of plant populations. Topographic aspect and tree or shrub canopy shade will have direct effects on plants by altering solar exposure, with potentially larger temperature variation than expected from anthropogenic climate change (Suggitt *et al.* 2011). Larger shrubs and trees may ameliorate the detrimental effects of localized climate on smaller herbs through facilitation by insulation, litter, or protection from herbivores.

Simulations: External validation

Accuracy, precision, or trend match all improved under the ED model compared to the IID model (Table 3). The validation procedure indicates a robust estimate of *P. radiata* population sizes and provides support for models that include temporal covariates rather than considering all years independent and identically-distributed. Quintana-Ascencio *et al.* (*unpub.*) found similar results using nine different plant species under a linear regression ED model. To our knowledge, no other study has explicitly compared population projections between these two environmental stochasticity models. Gotelli and Ellison (2006) related the two approaches, deemed stationary for the IID model and non-stationary for the ED model, by their determinants of extinction risk. They summarized that for the stationary stochastic model (IID), extinction risk is affected by variances and covariances of matrix elements, and for the non-stationary stochastic model (ED), extinction risk is affected by the initial population structure and the coefficient or linking function of the time-series model to population vital rates.

Simulations: Climate predictions

Rainfall is more difficult to predict than temperature, yet global water vapor is expected to increase by 7% for each degree centigrade increase, leading to around 1-2% increase in precipitation volume (IPCC 2007). The Pacific Northwest might see more rainfall from higher water vapor as well as melted snow from higher

temperatures. The predicted response of *P. radiata* populations to precipitation in the prior year's dry dormant season was very similar by 2050 for both forecast scenarios. Dry growing season rainfall predictions under the two GCMs and their opposing emissions scenarios ranged from 8.4 to 87.8 mm and 6.6 to 117.1 mm and averaged 34.0 and 38.8 mm for the A2 and B1 scenarios, respectively. These scenarios predict a slight decrease (-0.05 mm) under the optimistic B1 and a slight increase (0.01 mm) under the pessimistic A2 in dry dormant season rainfall for these four populations, which may explain the greater decline of the B1 over the A2 scenario (Figure 4).

Even with slightly higher predicted precipitation for the optimistic scenario, the population projections generally overlapped. This trend was consistent across all the populations due to the small differences in precipitation in the downscaled predictions, therefore a site-averaged population model was deemed more conservative for the relatively small spatial differences. The mean stochastic population growth rates indicated a decreasing population size in the near future (Table 4), suggesting that average seasonal changes in precipitation in the dry dormant season alone may cause a rapid decline or extinction in *P. radiata* in the short-term. It also suggests that the worst-case scenario of greenhouse gas emissions has higher uncertainty than the best-case scenario in the next 30-40 years, but comparable median projections.

Conclusion

Future management of *P. radiata* may need to track the frequency of high and

low precipitation events during the dry season, and, more importantly, track the years when fertility rates are higher than average for each population. The four populations evaluated here all had higher than average fertility rates during the same years, despite their differences in elevation, slope, aspect, and plant density.

The inclusion of abiotic drivers in models used to predict population trends is supported by our study. I incorporated multiple validations of each model to protect from over-fitting observed data, and I chose one environmental driver as a simple and parsimonious predictor of population vital rates. This is one of the first studies (Doak and Morris 2011) to utilize nonlinear, nonparametric regression to predict population vital rates by fitting trends to data instead of data to an assumed trend. Our results from the climate predictions under our ED model suggest that *P. radiata* population sizes will not drastically differ among forecast emission scenarios, and it supports including biotic or abiotic environmental covariates in population projection models to improve their predictive power (Crone *et al.* 2011).

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CHAPTER 3

Assessing climate drivers through demographic ordination of a rare plant species

Ian A. Pfingsten & Thomas N. Kaye

Abstract

The threat to plant populations by changes in climate is expected to increase as global temperatures rise. However, populations may not be driven by all abiotic factors in their current range, which is the assumption of most climate envelope models. Determining which abiotic factors are correlated with population vital rates is a more reductionist approach to predicting species ranges and extinction risk under future climates. This study hopes to answer population-level questions using a traditionally community-level method, non-metric multidimensional scaling, which considers correlation structure between response variables and can be used to find environmental correlates of the ordination axes. I modeled plant population growth using annual, demographic measurements to track individual survival, growth, and fertility (vital rates) as a differential change in those measurements. Demographic data on a threatened perennial, *Astragalus tyghensis,* were collected from five sites in the Tygh Valley, OR from 1991 to 2000, and climate data was spatially and temporally interpolated from weather station data as total precipitation, mean temperature (dew point, minimum, and maximum), and mean reference evapotranspiration rates across eight biologically relevant seasons. Two axes that were highly correlated with population growth and fertility explained 75.2% and 15.2% of the variation, respectively, in individual transition rates in a non-metric multidimensional scaling ordination. The asymptotic population growth rates for each transition matrix covaried along both axes, towards increasing growth ($R^2 = 74.2\%$) and fertility ($R^2 = 1.4\%$), and average reference evapotranspiration rates during the dry-growing season had the

strongest association with both axes combined ($R^2 = 32.8\%$). This ordination approach gives demographers the ability to analyze multiple transition rates at once and to further overlay environmental or biotic gradients in the ordination space to assess their linear relationships. Climate may explain a large portion of the variation in *A. tyghensis* population growth, specifically in transitions to larger and smaller-sized plants. By identifying important environmental drivers of population growth, this represents a mechanistic improvement over previous approaches, with emphasis on biological realism necessary to project population risk given severe, predicted climate change.

Introduction

The threat to plant populations by changes in climate is expected to increase as global temperatures rise (Parmesan 2006, Ohlemüller *et al.* 2008). The Intergovernmental Panel on Climate Change (2007) predicts a global temperature increase by about 0.2°C per decade, and a likely increase in the frequency of extreme heat and precipitation. Some argue that plants already threatened with extinction may need to be moved to more suitable environments (McLachlan *et al.* 2007). However, populations may not be driven by all abiotic factors in their current range, which is the assumption of most climate envelope models (Keith *et al.* 2008). One or two environmental factors could largely drive population persistence, while others are relatively negligible. Determining which abiotic factors are correlated with population vital rates is a more reductionist approach to predicting species ranges and extinction

risk under future climates, but long-term time series of abiotic conditions and population demographics are needed for accurate predictions.

Previous studies explicitly modeled environmental effects on plant populations in hopes to increase accuracy in projection estimates of population risk (Menges and Dolan 1998, Menges 2000, Kaye *et al.* 2001). In a five year experimental study, Kaye *et al.* (2001) found that populations of a wetland perennial, *Lomatium bradshawii*, were positively effected by fire disturbance. Longer studies rarely have experimental designs to determine environmental effects on populations. Environments in these studies are thus assumed completely stochastic or based on a reasonable correlate to explain the temporal variation, yet few have assessed if plant populations correlate with environments (Maschinski *et al.* 2006, Dalgleish *et al.* 2010, Davison *et al.* 2010, Doak and Morris 2011, Nicolè *et al.* 2011) because sample years are generally much fewer than the number of predictors. The mean vital rates of the population (response variables) also tend to exhibit an inherent correlation structure (*e.g.*, the transition rate of a stage to a larger plant is negatively correlated to the rate of the same stage to a smaller plant).

To overcome the limitation of multiple, correlated response variables, I utilized multivariate ordination to find the best explanatory variable of stage-structured population transition matrices from ten years of demographic data across five populations of a rare, endemic, native perennial. A similar approach was previously used by Silvertown *et al.* (1992, 1996), where elasticities of population mean stasis, growth, and fertility rates are axes on a two-dimensional, triangular ordination, each

scaled to one. Silvertown *et al.*'s mechanistic, reductionist method is analogous to Grime's descriptive CSR theory (Grime 1977), but results from the two ordinations do not correlate well, although their populations were not at equilibrium (*i.e.*, at stable stage distributions) and from different regions (Silvertown et al. 1992). The larger issue with the triangular ordination is the inherent negative association between stasis and growth that is inherent in the transition rate calculations (Caswell 2001). This study hopes to answer population-level questions using a traditionally community-level method, non-metric multidimensional scaling, which considers correlation structure between response variables and can be used to find environmental correlates of the ordination axes.

Demographic data on a threatened herbaceous perennial, *Astragalus tyghensis,* were collected from five populations in the Tygh Valley, OR from 1991 to 2000 (Carlson and Kaye 2001).

This study intends to answer two questions:

- Can I simplify the correlation structure in a stage-structured matrix model of *Astragalus tyghensis*?
- Do *Astragalus tyghensis* stage-structured matrices strongly covary with climate?

Methods

I modeled plant population growth using annual, demographic measurements to track individual survival, growth, and fertility (vital rates) as a differential change in

those measurements. Mean vital rates of each year constitute the elements in a square transition matrix based on the species' life history, where the matrix dimensions depend on the number of age (Leslie 1945) or size (Lefkovitch 1965) classes assumed in the life history; the latter formally called a stage-structured matrix. These matrices can then be used in forecasts of population extinction risk, and have relevant attributes of typical square matrices, such as left eigenvectors representing reproductive values and dominant eigenvalues representing asymptotic growth rates.

Annual measurements were taken of individual plant diameters (cm), longest stem lengths (cm), inflorescence counts, and apparent herbivory (binary) within 15 permanent, 5 x 5m plots. Fruit and seed counts were estimated from a sub-sample of plants each year per site. Plant longest stem length from previous to subsequent years determined growth to five successive, arbitrary stages (seedlings and four reproductive sizes) (Carlson and Kaye 2001). The probabilities of individuals surviving and transitioning among stages parametrized the vital rate transition matrix. Inflorescence counts and first year germinants determined the average, individual fertility for each stage within the matrix. Three transitions (seedlings remaining seedlings, seedlings becoming stage four plants, and seedlings becoming stage five plants) were excluded from analysis due to their impossible or improbable chance of occurrence. There were 45 total transition matrices for the study (9 year-to-year transitions x 5 sites). The dominant eigenvalue, or asymptotic population growth rate, was calculated for each matrix (Caswell 2001).

Climate data was provided through PRISM (Daly *et al.* 1994) as an 800 x 800

m grid of modeled, total monthly precipitation (mm), and mean monthly temperature (°C) (dew point, minimum, and maximum). Monthly precipitation and temperature estimates were totaled and averaged, respectively, across wet and dry, and growing and dormant seasons, as well as the four combinations of these biological seasons (wet-growing, dry-growing, wet-dormant, and dry-dormant). A synthetic climate factor, reference (without specific plant coefficients) evapotranspiration (ET) (mm/month), was calculated using the FAO 56 Penman-Monteith equation (Penman 1948, Monteith 1965, Allen *et al.* 1998) with environmental variables from PRISM temperatures, Remote Automated Weather Stations (Wamic Mill, OR station) mean wind speed (m/s), and University of Oregon Solar Radiation Monitoring Laboratory (Madras, OR station) global solar radiation (MJ/m^2). ET rates were also averaged across the eight biological seasons.

To answer the study questions, the demographic data were arranged in a 45 x 22 matrix (P) of interannual transitions for each plant stage (Table 5). The climate data were structured in a 45 x 46 matrix (CF) of mean and total, seasonal climate measures, year and site groupings, asymptotic population growth rates, and first difference (year [t + 1] - year [t]) total seedling plant counts and herbivory rates. Before analysis, the P matrix was relativized by maximum values of population variables (columns) respectively. This was done in order to remove the strong bias of fertility rates (generally greater than one) compared to survival and growth rates (between zero and one). Also this retained the interannual (row) variation by not altering the population variable ranks across years. Outlier analysis confirmed that no interannual mean vital

rate Euclidean distances fell outside of three standard deviations of the mean vital rate

distance in all years, which supported the use of Euclidean distances in the ordination.

All analyses were conducted in PC-ORD v6.02 (McCune and Mefford 2011).

A blocked multi-response permutation procedure (MRBP) (Mielke 1984) using

median alignment and Euclidean distance was conducted to test the null hypothesis of

no difference in population variables between years within sites (blocks) for the P

matrix.

Table 5. Transition matrix structure for *A. tyghensis*.

		Year N				
		1	2	3	4	5
Year N+1	1	-	2,1	3,1	4,1	5,1
	2	1,2	2,2	3,2	4,2	5,2
	3	1,3	2,3	3,3	4,3	5,3
	4	-	2,4	3,4	4,4	5,4
	5	-	2,5	3,5	4,5	5,5

Nonmetric multidimensional scaling (NMS) (Kruskal 1964, Mather 1976) was

used to ordinate the P matrix because of the method's versatility in handling nonlinear

relationships. Euclidean distance measure was used based on its emphasis of variation.

The NMS was first run on autopilot mode under the thorough setting with ties

penalized. The axis scores were saved and used as starting coordinates to rerun the

NMS using 100 runs with real data, each with 500 iterative steps, rotation to

orthogonal principal axes, and the number of axes determined by the autopilot NMS.

Climate factors were checked for covariance with ordination scores by vector overlays of each climate factor in the ordination space. Factors were considered biologically relevant if they explained at least 25% of the variation in all ordination axes combined using the Pythagorean theorem (hypotenuse length of R^2 values between the variable and axes). Statistical significance of environmental factor regressions was disregarded in this case due to the focus on biological significance and the small likelihood of non-significance at $R^2 \geq 0.25$.

Results

Vital rates differed strongly between years while controlling for sites in P (A = 0.18, $p < 0.001$). The final NMS on P, using the autopilot axis scores as starting coordinates, cumulatively explained 90.4% of the variation in the transition rates, with 75.2% attributed to axis one and 15.2% to axis two. The NMS on autopilot produced a two-dimensional ordination of the P matrix, supported by a randomization test using 250 iterations (p = 0.004), with a final stress of 13.59 and a final instability of 0 based on the standard deviations in stress over the last ten iterations.

Individual transition rates were strongly associated with both axes in the NMS on P (Table 6). The strongest was growth from stage four to five plants ($R^2 = 66.8\%$), which was positively correlated with axis one, but barely noticed on axis two. Retrogression of plants from stage three to two had the strongest negative correlation ($R^2 = 61.3\%$) with axis one. This was a general trend for growth and retrogression transitions along axis one, dubbed the growth axis (Figure 5). Fertility of stage five

plants had the strongest positive correlation ($R^2 = 36.8\%$) with axis two, while growth from stage two to five plants had the strongest negative correlation ($R^2 = 15.4\%$) with axis two. Fertility transitions were generally associated with axis two, with a few exceptions. The asymptotic population growth rate, lambda, correlates along both axes ($R^2 = 74.2\%$), towards increasing growth ($R^2 = 74.2\%$) and fertility ($R^2 = 1.4\%$) (Figure 5). First difference seedling counts correlated with the combined axes ($R^2 = 26.8\%$), which was positively associated to axis one ($R^2 = 24.4\%$) and axis two ($R^2 = 11.0\%$).

According to the final, two-dimensional NMS ordination on P (Figure 5), average ET during the dry-growing season had the strongest association with both axes combined ($R^2 = 32.8\%$), with most of its correlation on axis one ($R^2 = 32.7\%$); other factors were not visible due to R^2 values below the 25% criteria. The second strongest association with the combined axes was average ET during the dry season ($R^2 = 24.1\%$). These two ET variables were positively correlated with axis one and slightly negatively correlated with axis two. Total precipitation during the dry-dormant season and average dew point temperature during the wet-growing season had the strongest negative associations with axes one ($R^2 = 7.3\%$) and two ($R^2 = 7.6\%$) respectively. First difference, average herbivory had the strongest, positive correlation with axis two ($R^2 = 7.3\%$).
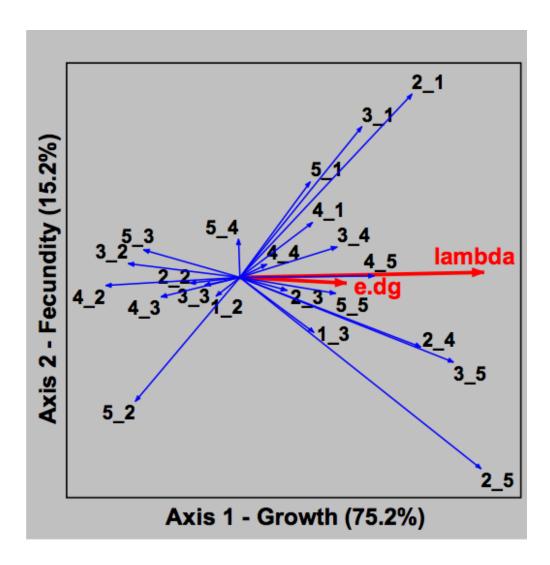
Figure 5. NMS ordinations of matrix transition rates in vital rate space, with population growth (lambda) and evapotranspiration in dry-growing season (e.dg) vector overlays. Transition rates are in reference to Table 5.

Table 6. Correlations of transitions rates with the first and second axes of the population transition rates ordination. Bold values are biologically relevant based on $R^2 > 0.25$.

	Axis 1		Axis 2		Combined
	R	R^2	R	R^2	R^2
1,2	-0.334	0.112	-0.255	0.065	0.129
1,3	0.444	0.197	-0.320	0.103	0.222
2,1	0.406	0.165	0.421	0.177	0.242
2,2	-0.668	0.447	-0.074	0.005	**0.447**
2,3	0.622	0.386	-0.161	0.026	**0.387**
2,4	0.687	0.472	-0.256	0.065	**0.476**
2,5	0.509	0.259	-0.392	0.154	**0.301**
3,1	0.320	0.102	0.385	0.148	0.180
3,2	-0.783	0.613	0.096	0.009	**0.613**
3,3	-0.556	0.309	-0.113	0.013	**0.309**
3,4	0.792	0.626	0.241	0.058	**0.629**
3,5	0.727	0.529	-0.279	0.078	**0.535**
4,1	0.547	0.299	0.403	0.163	**0.341**
4,2	-0.647	0.419	-0.037	0.001	**0.419**
4,3	-0.722	0.522	-0.170	0.029	**0.523**
4,4	0.305	0.093	0.149	0.022	0.096
4,5	0.818	0.668	0.008	0.000	**0.668**
5,1	0.459	0.210	0.607	0.368	**0.424**
5,2	-0.317	0.101	-0.367	0.135	0.169
5,3	-0.656	0.430	0.185	0.034	**0.431**
5,4	-0.007	0.000	0.320	0.102	0.102
5,5	0.796	0.633	-0.126	0.016	**0.633**

Discussion

Climate may explain a large portion of the variation in *Astragalus tyghensis* population growth, specifically in transitions to larger and smaller-sized plants. Nearly 33% of the variation in population stage transitions was explained by dry-growing season evapotranspiration alone. This is reasonable given the nature of the synthetic variable, which uses three temperature variables from the CF matrix, and mechanistically, given the physiological relevance of water loss from plant surfaces. The IPCC (2007) predicts increased ET rates in the geographic range of *A. tyghensis* during its growing season. Therefore this species may persist well in its current locations as climate changes, due to the positive correlation between the climate driver and the population vital rates.

Extremely dry years could negatively affect *A. tyghensis* vital rates, but I found no strong relationships with rainfall and instead observed a positive correlation with reference ET, a function of temperature, humidity, wind speed, and solar radiation, and population vital rates. This was supported by the strong correlation between the growth axis scores and the lambda vector, which had a similar vector angle to the climate factor. Our calculation of reference ET, by definition, did not include a vegetation component. Actual (*here I mean vegetative*) ET is measured at the plant stomata where gas exchange occurs. Sumner and Jacobs (2005) showed that reference ET was about 1.5 to 2 times higher than actual ET in low rainfall months, which was explained by a strong positive linear relationship to leaf-area-index (LAI). Thus plant

LAI and abundance should directly affect vegetative ET rates, not necessarily the reverse. The dry-growing season for *A. tyghensis* occurs during June and July when the population LAI might be lower than in the wet season, causing an overestimation of ET rates. I did not measure LAI in our study, although reference ET calculations were consistent for all seasons and years, potentially alleviating any overestimation bias on annual variation. Still, the question of what might explain a positive relationship between reference ET and population growth is unanswered. There could be direct effects on photosynthesis by solar radiation or indirect effects through suppression of competing plants, especially invasives that may not tolerate extreme abiotic conditions.

A high proportion of the variation in the P matrix was explained in the two axes. The strength of the second axis to describe a fertility pattern was weak compared to the growth pattern in the first axis. Even though the population transition rates were removed from the demographic matrix structure and rescaled to new values, they maintained information about the population as interpreted in the ordination scores. This ordination approach gives demographers the ability to analyze multiple transition rates at once and to further overlay environmental or biotic gradients in the ordination space to assess their linear relationships. It also addresses the correlated axes criticism towards Silvertown *et al.*'s (1992) elasticity ordination triangle (Caswell 2001). This method however does not account for interacting or nonlinear relationships among environmental factors, which may be behind the mechanisms involved in regulating population fluctuations. One could, however, use axis scores as dependent variables in

population models with interacting factors.

Identifying important drivers of population growth through population transition or vital rate ordinations may improve efforts to prioritize conservation of many threatened and endangered populations, either through *in situ* protections or identification of appropriate sites for assisted migration. The transition rates that have the strongest positive and negative covariance with either population growth or fertility ordination scores may indicate the transitions in the plant's life history that have the strongest effect on population growth or fertility. Likewise, environmental drivers with strong positive or negative covariance with the ordination scores may describe which factors affect or are affected by plant growth or fertility. By identifying important environmental drivers of population growth, this represents a mechanistic improvement over previous approaches, with emphasis on biological realism necessary to project population risk given severe, predicted climate change.

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CHAPTER 4

General conclusions

The search for an environmental driver of population vital rates was successful for the two study species. Previous year dry dormant season precipitation likely affects the fertility rates the following year in *Pyrrocoma radiata* populations, and the relationship was strongly unimodal. Dry growing season reference evapotranspiration rates were positively correlated with a vital rate gradient representing population growth in *Astragalus tyghensis*, possibly due to solar radiation increasing stomatal function or stressful conditions negatively affecting interspecific plant competitors. In both studies a single climate driver explained > 30% of the variation in population growth, and, with the exception of one moderately-associated competing driver of *A. tyghensis*, all other climate variables had weak relationships with the species. Our variable selection process benefited from the long-term data sets across multiple sites. The combined models for population growth, with population as a blocking factor, gave us more power when selecting the best climate driver than if I used one site alone; not many demographers have this luxury (Dalgleish *et al.* 2011). However, these populations were spatially located in a small enough geographic area that climate did not vary much among sites, which meant regressions were idiosyncratic when vital rates varied among sites.

For choosing a climate driver, our demographic ordination produced two gradients from transition element space, which simplified the variable selection step as

both response gradients (growth and fertility) were orthogonal, and thus uncorrelated. The NMS ordination adequately captured most of the variation in transition elements for the years and populations from the *A. tyghensis* data set. Still, I have two concerns with the ordination approach: 1) I should have used vital rates instead of transition elements from the population matrices because they represent actual field measurements, and 2) I wanted the ability to consider nonlinear relationships with environmental factors and ordination gradients. The first concern can be addressed through algebraic manipulation, but the second concern needs a different approach that might combine the two studies in this thesis to produce new estimates of population vital rates or sizes.

I provided support to the claim that model predictions can improve with the inclusion of mechanistic relationships (Crone *et al.* 2011) (Table 2). Stationary stochastic models (IID) still have potential given their simplicity (Gotelli and Ellison 2006), but as demographic data sets increase with more sample years, I expect non-stationary stochastic models (ED) to increase for predictive purposes due to higher accuracy and precision than stationary stochastic models. I also expect to see more comparisons of competing model approaches as long-term data sets become more common and accessible. With computer-intensive simulations rarely a limitation in current studies, a comparison of recent advances in population projection models is now possible. A comparison of Bayesian (Evans *et al.* 2010), integral projection (Ellner and Rees 2006), diffusion approximation (Varughese 2009), and structured matrix models (Caswell 2001), either through direct simulations on a set of species or

through a meta-analysis, would be interesting, although sufficient comprehension of

all modeling approaches by even a few authors seems to be the limiting factor.

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APPENDIX

Table S1. *Pyrrocoma radiata* stage transition matrices for the study populations. S – seedlings, J – juveniles, V – vegetatives, R – reproductives.

Site 1	Transition	1991-1992	1992-1993	1993-1994	1994-1995	1995-1996	1996-1997	1997-1998	1998-1999	1999-2000	2000-2001
	S->S	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	S->J	0.565	0.254	0.202	0.010	0.315	0.554	0.430	0.389	0.064	0.500
	S->V	0.174	0.075	0.250	0.003	0.258	0.256	0.000	0.028	0.007	0.500
	S->R	0.000	0.179	0.190	0.012	0.169	0.030	0.000	0.111	0.002	0.000
	J->S	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	J->J	0.753	0.374	0.514	0.440	0.580	0.596	0.700	0.608	0.701	0.627
	J->V	0.198	0.096	0.122	0.143	0.198	0.275	0.126	0.166	0.136	0.149
	J->R	0.000	0.374	0.068	0.242	0.136	0.064	0.132	0.041	0.045	0.015
	V->S	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	V->J	0.270	0.107	0.281	0.088	0.153	0.109	0.112	0.148	0.147	0.239
	V->V	0.629	0.131	0.313	0.490	0.482	0.706	0.451	0.625	0.497	0.679
	V->R	0.045	0.721	0.094	0.343	0.294	0.151	0.417	0.180	0.309	0.006
	R->S	3.268	18.667	67.497	5.933	1.302	1.174	0.474	3.543	0.034	0.360
	R->J	0.207	0.056	0.170	0.067	0.163	0.165	0.039	0.069	0.085	0.176
	R->V	0.561	0.000	0.390	0.217	0.302	0.426	0.145	0.428	0.308	0.684
	R->R	0.171	0.889	0.226	0.683	0.496	0.400	0.816	0.468	0.581	0.110

Site 2	Transition	1991-1992	1992-1993	1993-1994	1994-1995	1995-1996	1996-1997	1997-1998	1998-1999	1999-2000	2000-2001
	S->S	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	S->J	0.500	0.353	0.106	0.002	0.095	0.200	0.333	0.059	0.037	0.500
	S->V	0.096	0.088	0.022	0.000	0.286	0.400	0.000	0.004	0.019	0.000
	S->R	0.096	0.118	0.067	0.006	0.143	0.150	0.000	0.000	0.019	0.500
	J->S	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	J->J	0.423	0.358	0.348	0.109	0.417	0.357	0.333	0.364	0.160	0.364
	J->V	0.057	0.063	0.045	0.063	0.250	0.143	0.278	0.000	0.120	0.000
	J->R	0.033	0.263	0.106	0.297	0.083	0.071	0.111	0.182	0.120	0.091
	V->S	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	V->J	0.263	0.102	0.235	0.095	0.063	0.109	0.024	0.152	0.033	0.125
	V->V	0.474	0.061	0.176	0.143	0.563	0.391	0.366	0.394	0.167	0.313
	V->R	0.211	0.673	0.118	0.429	0.188	0.326	0.488	0.273	0.633	0.375
	R->S	2.894	13.333	41.158	0.894	0.204	0.145	4.322	0.818	0.035	0.453
	R->J	0.128	0.056	0.158	0.011	0.061	0.065	0.017	0.015	0.070	0.000
	R->V	0.298	0.037	0.096	0.096	0.286	0.210	0.220	0.242	0.123	0.234
	R->R	0.436	0.889	0.640	0.670	0.561	0.645	0.746	0.697	0.719	0.688

Table S1. (Continued)

Site 3	Transition	1991-1992	1992-1993	1993-1994	1994-1995	1995-1996	1996-1997	1997-1998	1998-1999	1999-2000	2000-2001
	S->S	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	S->J	0.339	0.375	0.636	0.019	0.355	0.286	0.150	0.174	0.227	0.285
	S->V	0.048	0.208	0.045	0.000	0.016	0.057	0.000	0.000	0.000	0.042
	S->R	0.016	0.250	0.000	0.000	0.000	0.029	0.000	0.000	0.000	0.033
	J->S	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	J->J	0.602	0.247	0.667	0.394	0.761	0.726	0.735	0.795	0.281	0.526
	J->V	0.068	0.186	0.056	0.169	0.120	0.038	0.078	0.034	0.045	0.053
	J->R	0.034	0.402	0.139	0.197	0.011	0.028	0.049	0.000	0.011	0.053
	V->S	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	V->J	0.235	0.063	0.400	0.063	0.146	0.173	0.103	0.267	0.077	0.211
	V->V	0.388	0.229	0.286	0.563	0.732	0.556	0.293	0.467	0.385	0.368
	V->R	0.035	0.583	0.314	0.281	0.073	0.160	0.517	0.067	0.436	0.053
	R->S	1.412	2.000	33.268	1.069	0.565	2.353	0.920	0.863	0.074	12.344
	R->J	0.176	0.000	0.232	0.172	0.129	0.059	0.040	0.137	0.000	0.031
	R->V	0.353	0.091	0.232	0.172	0.629	0.412	0.200	0.431	0.000	0.406
	R->R	0.235	0.818	0.512	0.655	0.210	0.471	0.640	0.255	0.933	0.500

Site 4	Transition	1991-1992	1992-1993	1993-1994	1994-1995	1995-1996	1996-1997	1997-1998	1998-1999	1999-2000	2000-2001
	S->S	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	S->J	0.966	0.545	0.000	0.011	0.176	0.167	0.292	0.500	0.300	0.500
	S->V	0.000	0.000	0.400	0.003	0.176	0.033	0.042	0.000	0.050	0.500
	S->R	0.000	0.045	0.400	0.003	0.000	0.000	0.000	0.056	0.050	0.000
	J->S	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	J->J	0.570	0.508	0.740	0.523	0.643	0.450	0.576	0.677	0.744	0.422
	J->V	0.013	0.092	0.055	0.108	0.190	0.175	0.121	0.226	0.026	0.133
	J->R	0.000	0.075	0.123	0.200	0.071	0.025	0.061	0.000	0.026	0.000
	V->S	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	V->J	0.316	0.000	0.308	0.364	0.111	0.222	0.077	0.316	0.348	0.267
	V->V	0.263	0.091	0.231	0.182	0.611	0.611	0.308	0.316	0.261	0.333
	V->R	0.053	0.455	0.385	0.273	0.278	0.056	0.487	0.263	0.348	0.133
	R->S	2.444	1.250	22.438	0.773	1.000	1.600	3.600	0.909	0.154	1.500
	R->J	0.111	0.000	0.438	0.000	0.267	0.133	0.400	0.136	0.154	0.357
	R->V	0.444	0.250	0.125	0.364	0.467	0.600	0.400	0.455	0.538	0.500
	R->R	0.333	0.250	0.375	0.591	0.233	0.133	0.200	0.318	0.308	0.143

Table S2. *Pyrrocoma radiata* population sizes for the study populations.

Year	Site 1	Site 2	Site 3	Site 4
1991	275	288	252	206
1992	322	266	180	157
1993	349	377	175	107
1994	2936	1352	2889	457
1995	384	147	257	107
1996	511	142	239	121
1997	607	127	225	101
1998	554	365	192	90
1999	1098	166	187	95
2000	500	93	89	76
2001	491	108	461	73

Table S3. *Pyrrocoma radiata* initial population stage counts. S – seedlings, J – juveniles, V – vegetatives, R – reproductives.

Stage	Site 1	Site 2	Site 3	Site 4
S	23	52	62	29
J	81	123	88	149
V	89	19	85	19
R	82	94	17	9

Table S4. *Pyrrocoma radiata* deterministic population growth rates.

Transition	Site 1	Site 2	Site 3	Site 4
1991-1992	1.00	1.06	0.75	0.62
1992-1993	2.64	2.16	1.51	0.82
1993-1994	3.81	2.12	1.98	3.39
1994-1995	1.01	0.76	0.93	0.89
1995-1996	1.18	0.88	0.94	1.03
1996-1997	1.09	0.90	0.96	0.81
1997-1998	1.07	1.23	0.93	1.03
1998-1999	1.19	0.88	0.83	0.97
1999-2000	0.94	0.86	0.93	0.86
2000-2001	0.86	1.05	1.18	0.80

Table S5. *Pyrrocoma radiata* local climate for the study populations. One-year-lagged variables contain weather during 1990-1999. Non-lagged variables are from 1991-2000.

	Year	Total Precipitation (mm)				Mean Maximum Temperature (°C)			
		Wet-growing	Dry-growing	Dry-dormant	Wet-dormant	Wet-growing	Dry-growing	Dry-dormant	Wet-dormant
Site 1	1990	109.20	46.70	25.50	172.40	19.82	31.08	21.83	6.03
	1991	58.60	24.90	31.20	183.30	25.93	30.74	22.20	8.65
	1992	85.20	29.30	31.90	345.80	22.06	27.90	21.37	4.13
	1993	53.20	28.60	15.20	171.00	23.54	30.09	21.31	7.67
	1994	81.00	49.10	27.60	358.50	21.24	30.92	22.10	6.63
	1995	78.90	38.30	17.40	288.20	21.35	30.62	20.71	7.52
	1996	52.00	60.90	42.40	309.10	23.63	29.84	19.51	7.64
	1997	172.10	39.20	30.10	279.20	20.57	32.29	21.05	7.70
	1998	45.00	5.90	42.80	323.40	21.91	31.76	21.62	6.79
	1999	32.50	13.40	17.50	298.50	24.06	31.64	21.50	8.53
	2000	29.20	19.70	64.90	153.00	23.79	31.80	19.39	6.02
Site 2	1990	103.40	46.30	23.10	166.90	21.06	32.24	23.06	6.90
	1991	55.40	21.80	31.60	176.00	27.12	31.85	23.44	9.57
	1992	81.30	27.80	30.70	337.30	23.28	29.04	22.57	4.75
	1993	51.30	25.60	14.00	164.60	24.76	31.22	22.55	8.48
	1994	79.60	47.60	27.40	346.80	22.46	32.04	23.31	7.50
	1995	75.50	36.80	15.70	274.30	22.59	31.76	21.97	8.40
	1996	49.10	57.70	41.50	293.70	24.87	30.98	20.75	8.59
	1997	167.90	36.10	29.00	270.30	21.80	33.43	22.32	8.69
	1998	43.70	5.80	42.20	310.30	23.15	32.90	22.85	7.84
	1999	29.90	10.80	16.20	287.90	25.33	32.80	22.73	9.37
	2000	26.50	17.30	63.20	148.20	25.03	32.96	20.64	6.57

Table S5. (Continued)

Site	Year	Total Precipitation (mm)				Mean Maximum Temperature (°C)			
		Wet-growing	Dry-growing	Dry-dormant	Wet-dormant	Wet-growing	Dry-growing	Dry-dormant	Wet-dormant
Site 3	1990	108.00	41.90	26.30	162.30	18.82	30.22	21.13	5.63
	1991	62.10	22.80	27.40	183.20	25.06	29.86	21.56	8.17
	1992	96.20	28.90	31.10	327.30	21.16	26.99	20.59	3.94
	1993	51.00	27.60	14.30	164.20	22.61	29.26	20.55	7.30
	1994	86.10	44.40	25.80	326.60	20.30	30.23	21.12	6.05
	1995	76.40	35.40	17.90	282.10	20.31	29.89	19.75	7.04
	1996	56.50	57.30	40.70	290.90	22.53	29.09	18.82	6.93
	1997	170.30	36.90	29.60	264.90	19.49	31.50	20.12	7.00
	1998	45.00	5.10	44.80	308.10	20.73	30.91	20.91	6.04
	1999	33.80	14.60	16.70	281.30	22.85	30.74	20.89	8.07
	2000	32.40	17.50	66.70	149.50	22.82	30.86	18.71	5.67
Site 4	1990	106.40	42.70	24.90	150.40	20.33	31.69	22.62	6.75
	1991	57.60	22.40	27.50	166.50	26.53	31.35	23.04	9.40
	1992	90.50	29.40	30.00	309.80	22.62	28.46	22.09	4.68
	1993	50.60	27.30	14.20	149.30	24.09	30.74	22.04	8.20
	1994	82.50	43.90	26.00	302.30	21.80	31.63	22.64	7.22
	1995	77.80	36.60	17.50	255.70	21.79	31.37	21.28	8.14
	1996	52.50	57.10	40.00	265.70	24.04	30.53	20.30	8.28
	1997	170.30	36.20	27.60	245.80	20.97	32.95	21.64	8.30
	1998	46.60	5.20	41.90	274.40	22.23	32.35	22.40	7.47
	1999	31.70	14.40	16.00	257.40	24.36	32.16	22.34	9.08
	2000	31.30	17.70	62.30	140.10	24.31	32.31	20.20	6.35

Table S6. Climate variable model selection results. The highest cross-validated R^2 (xR^2) was the selection criterion.

year	climate driver	season	xR^2
t - 1	Precipitation	dry growing	-0.16
		dry dormant	*-0.12*
		wet growing	-0.26
		wet dormant	-0.28
	Maximum Temperature	dry growing	-0.14
		dry dormant	-0.25
		wet growing	-0.24
		wet dormant	-0.14
t	Precipitation	dry growing	-0.18
		dry dormant	-0.25
		wet growing	-0.25
		wet dormant	-0.26
	Maximum Temperature	dry growing	-0.16
		dry dormant	-0.26
		wet growing	-0.26
		wet dormant	-0.25

Table S7. *Astragalus tyghensis* stage transitions for the study populations, which are noted by letters a-e in the year transition labels. Each transition is relativized by its maximum column value.

Transition	1->2	1->3	2->1	2->2	2->3	2->4	2->5	3->1	3->2	3->3	3->4	3->5	4->1	4->2	4->3	4->4	4->5	5->1	5->2	5->3	5->4	5->5
91_92a	0.41	0.02	0.00	0.51	0.18	0.01	0.00	0.18	0.16	0.37	0.26	0.05	2.18	0.00	0.19	0.81	0.00	3.33	0.00	0.20	0.40	0.40
92_93a	0.22	0.02	0.00	0.25	0.22	0.00	0.00	0.23	0.12	0.58	0.15	0.00	2.82	0.04	0.19	0.63	0.11	3.12	0.00	0.25	0.75	0.00
93_94a	0.48	0.01	0.00	0.44	0.08	0.00	0.00	0.06	0.19	0.46	0.00	0.00	0.62	0.16	0.24	0.52	0.00	2.32	0.33	0.00	0.00	0.33
94_95a	0.12	0.16	0.00	0.15	0.09	0.00	0.01	0.25	0.13	0.37	0.30	0.00	3.08	0.00	0.07	0.21	0.64	6.47	0.00	0.00	1.00	0.00
95_96a	0.63	0.04	0.00	0.26	0.13	0.00	0.00	0.05	0.28	0.56	0.00	0.00	0.79	0.15	0.62	0.23	0.00	1.56	0.00	0.10	0.60	0.10
96_97a	0.56	0.04	0.00	0.42	0.23	0.00	0.00	0.53	0.03	0.73	0.13	0.00	2.71	0.00	0.33	0.44	0.22	0.74	1.00	0.00	0.00	0.00
97_98a	0.68	0.00	0.00	0.35	0.30	0.00	0.00	0.32	0.18	0.37	0.24	0.03	1.54	0.00	0.38	0.25	0.25	2.31	0.00	0.00	0.50	0.50
98_99a	0.34	0.03	0.00	0.46	0.13	0.00	0.00	0.05	0.24	0.55	0.00	0.00	1.74	0.08	0.50	0.08	0.00	3.65	0.25	0.50	0.00	0.00
99_00a	0.51	0.00	0.00	0.22	0.25	0.02	0.00	0.21	0.13	0.34	0.19	0.00	1.93	0.00	0.00	1.00	0.00	2.94	0.20	0.13	0.45	0.17
91_92b	0.28	0.11	0.02	0.29	0.17	0.17	0.00	0.56	0.02	0.32	0.56	0.06	2.68	0.00	0.13	0.55	0.28	4.86	0.08	0.00	0.33	0.50
92_93b	0.06	0.02	0.00	0.22	0.13	0.04	0.00	0.19	0.03	0.53	0.20	0.03	1.02	0.06	0.34	0.39	0.10	2.36	0.00	0.15	0.50	0.25
93_94b	0.32	0.02	0.00	0.48	0.22	0.00	0.00	0.21	0.17	0.64	0.13	0.00	0.99	0.02	0.57	0.36	0.02	1.22	0.00	0.58	0.25	0.17
94_95b	0.22	0.03	0.00	0.16	0.27	0.05	0.02	0.56	0.03	0.19	0.41	0.26	2.69	0.00	0.04	0.24	0.64	3.18	0.00	0.00	0.00	1.00
95_96b	0.53	0.03	0.01	0.30	0.30	0.00	0.00	0.05	0.23	0.50	0.18	0.03	0.32	0.05	0.62	0.31	0.00	0.75	0.03	0.21	0.55	0.10
96_97b	0.51	0.05	0.01	0.46	0.23	0.00	0.00	0.44	0.16	0.53	0.19	0.02	2.15	0.05	0.31	0.41	0.10	4.38	0.00	0.60	0.00	0.40
97_98b	0.36	0.02	0.00	0.46	0.25	0.03	0.00	0.31	0.05	0.62	0.19	0.01	1.78	0.00	0.62	0.38	0.00	1.38	0.00	0.43	0.29	0.14
98_99b	0.20	0.02	0.01	0.33	0.16	0.00	0.00	1.02	0.25	0.44	0.07	0.01	3.59	0.21	0.45	0.14	0.00	3.75	0.00	0.50	0.50	0.00
99_00b	0.11	0.00	0.00	0.23	0.41	0.06	0.01	0.42	0.01	0.51	0.33	0.03	1.90	0.00	0.08	0.50	0.42	2.59	0.01	0.31	0.30	0.32
91_92c	0.37	0.03	0.09	0.42	0.19	0.08	0.01	1.43	0.07	0.28	0.42	0.16	5.55	0.06	0.06	0.44	0.38	14.57	0.00	0.14	0.14	0.64
92_93c	0.15	0.06	0.00	0.19	0.19	0.03	0.00	0.42	0.06	0.32	0.36	0.12	4.18	0.01	0.16	0.38	0.43	11.30	0.00	0.05	0.25	0.70
93_94c	0.29	0.01	0.00	0.44	0.06	0.00	0.00	0.07	0.54	0.29	0.00	0.00	0.73	0.38	0.51	0.00	0.00	1.84	0.22	0.69	0.00	0.00
94_95c	0.36	0.04	0.10	0.27	0.16	0.06	0.02	6.67	0.12	0.23	0.27	0.24	2.84	0.10	0.20	0.36	0.24	6.82	0.04	0.17	0.22	0.50
95_96c	0.28	0.05	0.00	0.36	0.18	0.01	0.04	0.23	0.17	0.32	0.12	0.04	1.25	0.07	0.17	0.35	0.23	3.00	0.00	0.08	0.35	0.50
96_97c	0.30	0.06	0.00	0.22	0.19	0.02	0.01	0.30	0.10	0.36	0.12	0.05	3.51	0.04	0.10	0.54	0.14	5.48	0.03	0.03	0.24	0.50
97_98c	0.38	0.09	0.00	0.34	0.34	0.02	0.00	0.09	0.06	0.56	0.19	0.04	1.93	0.02	0.22	0.46	0.27	5.09	0.00	0.06	0.31	0.63
98_99c	0.38	0.04	0.00	0.44	0.12	0.00	0.00	0.06	0.25	0.47	0.04	0.00	0.88	0.16	0.49	0.23	0.03	2.69	0.07	0.39	0.25	0.16
99_00c	0.19	0.03	0.00	0.26	0.17	0.01	0.00	0.11	0.12	0.35	0.20	0.00	1.23	0.03	0.14	0.36	0.28	2.54	0.00	0.11	0.33	0.56
91_92d	0.38	0.04	0.02	0.13	0.38	0.32	0.05	0.93	0.00	0.09	0.62	0.26	6.86	0.00	0.06	0.30	0.64	6.04	0.00	0.00	0.20	0.80
92_93d	0.18	0.07	0.00	0.12	0.23	0.00	0.00	0.26	0.02	0.59	0.28	0.02	1.69	0.02	0.29	0.45	0.18	3.40	0.00	0.11	0.41	0.46
93_94d	0.34	0.03	0.00	0.55	0.13	0.00	0.00	0.05	0.20	0.61	0.08	0.02	0.29	0.07	0.68	0.19	0.00	0.73	0.02	0.47	0.27	0.22
94_95d	0.24	0.27	0.00	0.13	0.35	0.09	0.05	0.16	0.02	0.05	0.20	0.67	2.21	0.12	0.03	0.05	0.87	5.58	0.01	0.00	0.00	1.00
95_96d	0.40	0.07	0.00	0.75	0.09	0.06	0.00	0.00	0.11	0.61	0.07	0.02	0.05	0.07	0.52	0.21	0.07	0.26	0.01	0.23	0.38	0.32
96_97d	0.24	0.02	0.00	0.31	0.27	0.02	0.01	0.03	0.09	0.53	0.20	0.08	0.34	0.02	0.17	0.48	0.27	0.72	0.00	0.09	0.25	0.54
97_98d	0.38	0.09	0.00	0.39	0.14	0.02	0.00	0.02	0.20	0.58	0.06	0.00	0.30	0.16	0.50	0.24	0.01	0.65	0.03	0.49	0.26	0.08
98_99d	0.42	0.06	0.00	0.37	0.05	0.00	0.00	0.07	0.32	0.31	0.01	0.06	0.70	0.23	0.33	0.06	0.60	1.39	0.14	0.57	0.00	0.00
99_00d	0.14	0.03	0.00	0.27	0.18	0.04	0.00	0.19	0.05	0.38	0.29	0.00	1.56	0.00	0.00	0.40	0.60	2.48	0.03	0.25	0.22	0.43
91_92e	0.59	0.06	0.00	0.69	0.23	0.01	0.00	0.00	0.23	0.77	0.00	0.00	1.88	0.10	0.20	0.29	0.32	0.68	0.13	0.14	0.19	0.47
92_93e	0.41	0.20	0.05	0.08	0.34	0.34	0.13	2.39	0.04	0.22	0.41	0.33	1.88	0.10	0.20	0.29	0.32	0.68	0.13	0.14	0.19	0.47
93_94e	0.46	0.03	0.00	0.63	0.03	0.00	0.00	0.08	0.56	0.19	0.00	0.00	0.33	0.42	0.30	0.29	0.00	0.54	0.50	0.33	0.00	0.00
94_95e	0.17	0.08	0.00	0.11	0.19	0.22	0.17	0.00	0.00	0.11	0.11	0.56	0.15	0.00	0.25	0.54	0.21	0.68	0.13	0.14	0.19	0.47
95_96e	0.37	0.17	0.00	0.37	0.05	0.10	0.00	0.04	0.00	0.56	0.22	0.15	0.22	0.00	0.21	0.52	0.24	0.57	0.00	0.00	0.18	0.76
96_97e	0.29	0.25	0.00	0.28	0.38	0.00	0.00	0.03	0.03	0.38	0.25	0.03	0.18	0.06	0.23	0.41	0.15	0.82	0.00	0.11	0.23	0.57
97_98e	0.33	0.08	0.00	0.39	0.28	0.06	0.00	0.01	0.17	0.34	0.22	0.00	0.18	0.18	0.41	0.03	0.00	0.92	0.00	0.11	0.36	0.54
98_99e	0.31	0.03	0.00	0.32	0.04	0.00	0.00	0.00	0.15	0.50	0.00	0.00	0.04	0.18	0.41	0.03	0.15	0.18	0.30	0.40	0.05	0.00
99_00e	0.00	0.00	0.01	0.05	0.30	0.13	0.00	0.02	0.05	0.26	0.41	0.05	0.15	0.00	0.00	0.50	0.50	0.71	0.16	0.19	0.16	0.37

Table S8. *Astragalus tyghensis* deterministic growth rates for the study populations.

Years	Site 4	Site 10	Site 13	Site 25	Site 41
1991	1.08	1.30	1.45	1.67	0.98
1992	0.96	0.84	1.26	1.04	1.45
1993	0.60	0.93	0.57	0.84	0.67
1994	1.18	1.19	1.34	1.63	1.00
1995	0.67	0.90	0.88	0.87	1.03
1996	1.08	1.06	0.97	0.94	0.97
1997	1.05	1.02	1.17	0.75	0.87
1998	0.70	0.78	0.69	0.49	0.53
1999	1.09	1.04	0.89	1.00	0.87

Table S9. *Astragalus tyghensis* dry growing season reference ET rates for the study populations.

Years	Site 4	Site 10	Site 13	Site 25	Site 41
1991	7.61	7.53	7.48	7.71	7.85
1992	6.93	6.85	6.76	7.16	7.37
1993	6.59	6.48	6.44	6.70	6.90
1994	7.37	7.32	7.26	7.51	7.64
1995	6.98	6.91	6.83	7.13	7.26
1996	7.08	7.04	6.97	7.28	7.38
1997	6.45	6.41	6.34	6.61	6.71
1998	6.53	6.51	6.44	6.71	6.80
1999	6.65	6.62	6.55	6.80	6.88