

Subtle dimensions of climate change have strong
demographic effects on a cactus population in
extinction debt

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Abstract

- 1 1. The effects of climate change on population viability reflect the net influ-
2 ence of potentially diverse responses of individual-level demographic pro-
3 cesses (growth, survival, regeneration) to multiple components of climate.
4 Articulating climate-demography connections can facilitate forecasts of re-
5 sponses to future climate change as well as back-casts that may reveal how
6 populations responded to historical climate change.
- 7 2. We studied climate-demography relationships in the cactus *Cyclindriopun-*
8 *tia imbricata*; previous work indicated that our focal population has high
9 abundance but a negative population growth rate, where deaths exceed
10 births, suggesting that it persists under extinction debt. We parameter-
11 ized a climate-dependent integral projection model with data from a 14-year
12 field study, then back-casted expected population growth rates since 1900
13 to test the hypothesis that recent climate change has driven this population
14 into extinction debt.
- 15 3. We found clear patterns of climate change in our central New Mexico study
16 region but, contrary to our hypothesis, *C. imbricata* has most likely bene-
17 fitted from recent climate change and is on track to reach replacement-level
18 population growth within 38 years, or sooner if climate change accelerates.
19 Furthermore, the strongest feature of climate change (a trend toward years
20 that are overall warmer and drier, captured by the first principal component
21 of inter-annual variation) was not the main driver of population responses.
22 Instead, temporal trends in population growth were dominated by more sub-

23 tle, seasonal climatic factors with relatively weak signals of recent change
24 (wetter and milder cool seasons, captured by the second and third principal
25 components).

26 4. *Synthesis*. Our results highlight the challenges of forecasting population dy-
27 namics under climate change, since the most apparent features of climate
28 change may not be the most important drivers of ecological responses. Envi-
29 ronmentally explicit demographic models can help meet this challenge, but
30 they must consider the magnitudes of different aspects of climate change
31 alongside the magnitudes of demographic responses to those changes.

32 **Keywords**

33 Cactaceae; Climate change; Demography; Extinction debt; Integral Projection
34 Model; Long-term ecological research

Introduction

Population extinction debt is likely to increase in frequency as a fingerprint of global change, including climate change (Dullinger *et al.*, 2012; Urban, 2015). Extinction debt is a form of transient dynamics whereby populations persist despite having population growth rates that fall below replacement level ($\lambda < 1$), suggesting a long-term trajectory toward local extinction but with potentially long time lags (Hastings *et al.*, 2018; Kuussaari *et al.*, 2009). While extinction debt is often studied through species richness patterns at the community level (e.g., Vellend *et al.* 2006), there is recent emphasis on the underlying single-species dynamics whereby populations transition from positive to negative growth rates (Lehtilä *et al.*, 2016; Hylander & Ehrlén, 2013). In the absence of significant migration (which can maintain populations in sink habitats), extinction debt suggests that the environment was more favorable for population growth at some time in the past. However, the mechanisms that cause populations to tip from positive to negative growth rates are rarely known, and this information may be critical for effective conservation planning (Hylander & Ehrlén, 2013).

Structured population models built from individual-level demographic rates provide a powerful framework for studying drivers of extinction debt (Lehtilä *et al.*, 2016) and environment-dependent population dynamics more generally (Ehrlén & Morris, 2015). By incorporating climatic factors as statistical covariates, previous studies have identified climatic limits of population viability and forecasted responses to particular types of climate change (e.g., Adler *et al.* 2013; Maschinski *et al.* 2006; Jenouvrier *et al.* 2014). Additionally, articulating the connections between environment and demography can allow for ‘back-casting’ popu-

59 lation dynamics into historical environmental regimes; while rarely done (Smith
60 *et al.*, 2005), this approach may provide valuable insight regarding when and why
61 populations fell into extinction debt.

62 Many studies of climate-demography relationships focus on single climate vari-
63 ables that are known to be a dominant component of climate change and / or
64 known to have a strong influence on the focal species (e.g., Van de Pol *et al.* 2010;
65 Iler *et al.* 2019; Jenouvrier *et al.* 2009). However, for many species, it is not always
66 apparent *a priori* which dimensions of climate are most important, and this poses
67 challenges for predicting population responses to climate change. Previous studies
68 have shown that different components of climate change may have independent
69 effects on different aspects of demography or physiology (Buckley & Kingsolver,
70 2012; Frederiksen *et al.*, 2008; Van de Pol *et al.*, 2010; Lynch *et al.*, 2014). Fur-
71 thermore, different life stages (e.g., young vs old) and different vital rate processes
72 (e.g., growth, survival, reproduction) may differ in the magnitude and even di-
73 rection of their responses to single climate drivers (Doak & Morris, 2010; Dybala
74 *et al.*, 2013; Morrison & Hik, 2007; Tenhumberg *et al.*, 2018), and single life stages
75 or vital rates may be affected by multiple drivers (Dalglish *et al.*, 2011; Williams
76 *et al.*, 2015; Frederiksen *et al.*, 2008; Sletvold *et al.*, 2013). Ultimately, the influ-
77 ence of climate on population growth depends on the sensitivities of vital rates
78 to climate drivers and the sensitivities of λ to the vital rates, integrated across the
79 life cycle (McLean *et al.*, 2016; Ådahl *et al.*, 2006). These complications, common
80 to environmentally explicit demographic studies (Ehrlén *et al.*, 2016), highlight
81 the value of leveraging long-term data to gain resolution of climate drivers and the
82 importance of accounting for demographic complexity across the life cycle.

83 We used long-term demographic data to study climate-dependent population

84 dynamics of a long-lived Chihuahuan desert cactus persisting under extinction
 85 debt. Our previous work with the tree cholla cactus (*Cylindriopuntia imbricata*
 86 Haw. D.C.) (Cactaceae) indicated, with >95% certainty, that our focal population
 87 in the northern Chihuahuan Desert (New Mexico, USA) is in decline (stochastic
 88 population growth rate $\lambda_S < 1$) despite current densities that are reasonably high
 89 (Ohm & Miller, 2014; Miller *et al.*, 2009; Elderd & Miller, 2016). Our study region
 90 has experienced strong climatic fluctuations over the past century, including several
 91 decadal-scale droughts interrupted by relatively wet periods (Peters *et al.*, 2015).
 92 Recent and projected climate change in our study region includes increases in
 93 temperature and shifts in the seasonal timing of precipitation (Petrie *et al.*, 2014;
 94 Cook & Seager, 2013; Cook *et al.*, 2015). Our study was designed to reconstruct
 95 how historical climate patterns affected population viability in *C. imbricata* and
 96 to test the hypothesis that recent climate change has driven this population into
 97 extinction debt. We also sought to identify which aspects of climate are changing
 98 most strongly, and then ask whether the strongest features of climate change are
 99 the most important determinants of population responses. Our specific aims were
 100 to:

- 101 • Characterize climate variation and change in our northern Chihuahuan desert
 102 study region over the past century
- 103 • Quantify cactus vital rate responses to inter-annual climate variation during
 104 the demographic study period (2004–2017)
- 105 • Back-cast climate-dependent demography to determine whether the past cen-
 106 tury included periods that were favorable for population growth

- Identify which aspects of climate (cool and warm season temperature and precipitation) are changing most strongly, and which demographic responses to climate (growth, survival, reproduction) most strongly determine temporal trends in population growth

Materials and methods

Focal species, study site, and demographic data collection

Tree cholla cactus is widely distributed throughout desert and grassland habitats of the southwest U.S. and northern Mexico. These long-lived plants (40-plus years) grow through the production and elongation of cylindrical stem segments. These vegetative structures as well as flowerbuds are initiated in late spring. Flowering occurs in early summer and stem segment elongation takes place during the remainder of the growing season. For climate analyses, we divide the calendar year into warm-season months (May through September), when stem elongation, flowering, and seed production occur, and cool-season months (October through April).

This study was conducted at the Sevilleta National Wildlife Refuge (SNWR), a Long-Term Ecological Research site (SEV-LTER) in central New Mexico and near the center of this species' geographic distribution. Our study population occurs in the Los Piños mountains at an elevation of 1790 m. Tree cholla are a dominant component of the vegetation in this area (0.1 m⁻²: Miller *et al.* 2009), along with oaks, yucca, Piñon pine, and the grasses *Bouteloua gracilis* and *B. eriopoda*.

The present study relies on long-term (2004–2017) demographic data on individual-

level measures of growth, survival, and reproduction recorded from tagged plants in the Los Piños population that were censused in late May each year. This was a pre-breeding census that corresponds to the initiation of vegetative and reproductive structures (Fig. C1). We treat May 1 as the start of the transition year (coincident with the start of the warm-season months). There were a total of 1172 unique individuals in the data set and 7442 transition-year observations from 4–8 plots or spatial blocks depending on the year. Full details of the study design and data collection are given elsewhere (Miller *et al.*, 2009; Ohm & Miller, 2014; Elderder & Miller, 2016).

Climate data

Our goal was to connect inter-annual variation in demography to corresponding variation in temperature and precipitation. SEV-LTER collects climate data from a network of meteorological stations throughout SNWR, with the oldest records coming from the late 1980s. While the SEV-LTER climate data cover years of our demographic data collection, our intention was to back-cast demographic performance farther back into the 20th century. We therefore gathered climate data from ClimateWNA v5.60 (Wang *et al.*, 2016), a software package that uses PRISM (Daly *et al.*, 2008) and WorldClim (Hijmans *et al.*, 2005) data to calculate downscaled data for western North America based on location and elevation, going as far back as 1900. By relying on downscaled, interpolated climate data instead of direct observations from meteorological stations we are trading off local resolution in favor of more historical years of data. We quantified this loss of resolution by comparing predictions from ClimateWNA to SEV-LTER data for years that they over-lapped,

152 using the SEV-LTER meteorological station that was nearest our study popula-
153 tion (Appendix A). We found that the two data sets were highly correlated (Table
154 A1, Figure A1), which bolstered our confidence that ClimateWNA provided lo-
155 cally accurate climate data for both the demographic observation period as well
156 as historical years that preceded our study. We derived seasonal estimates (warm-
157 and cool-season) of total precipitation and mean, minimum, and maximum tem-
158 perature from monthly climate data, for a total of eight variables. Months were
159 aligned to correspond to demographic transition years rather than calendar years,
160 which means the cool-season climate for a transition year beginning in May of year
161 t spans October of year t through April of year $t + 1$ (Fig. C1).

162 To reduce the dimensionality of the climate data, we conducted Principal Com-
163 ponents Analysis (PCA) on the eight climate variables for the years 1900-2017,
164 with climate values scaled to unit variance. We estimated the variance in the raw
165 climate data explained by each PC and the variable loadings, which give the cor-
166 relations between original variables and PC values. PCA allowed us to rank the
167 magnitudes of multiple aspects of climate variation and change by examining how
168 warm- and cool-season variables loaded onto the ranked PC axes.

169 **Statistical estimation of climate-dependence**

170 We fit generalized linear mixed effects models in a hierarchical Bayesian framework
171 to quantify climate dependence in demographic vital rates, as captured by three
172 principal components of climatic variability. The choice of three PCs was based
173 on results of parallel analysis (Fig. A2), a statistical method for determining how
174 many components to retain (Franklin *et al.*, 1995). There were four vital rates

175 measured in the long-term study for which we could estimate climate dependence:
 176 survival from year t to year $t+1$, individual growth (change in size from year
 177 t to year $t+1$), probability of flowering in year t , and the number of flowerbuds
 178 produced year in t , given that a plant flowered. Survival and growth from year $t-1$
 179 to t were dependent on size in year $t-1$, and the climate covariate corresponded
 180 to the climate year $t-1$ to t . Reproductive status and fertility in year t were
 181 dependent on size in year t and on climate from $t-1$ to t . This timing of size
 182 and climate effects was intended to match processes in the population model (Fig.
 183 C1). We did not quantify climate-dependence in seedling recruitment. While we
 184 searched plots each year and added newly detected plants to the census, we could
 185 not confidently assign a birth year to these new additions (seedlings require several
 186 years of growth before they are consistently detectable in our census) so we do not
 187 know the climatic conditions under which they recruited.

188 All of the models for climate-dependent vital rates used the same linear predic-
 189 tor for the expected value (μ) but applied a different link function ($f(\mu)$) depending
 190 on the distribution of the observations:

$$\begin{aligned}
 f(\mu) = & \beta_0 + \beta_1 x + \\
 & \rho_1^1 PC1 + \rho_2^1 PC1^2 + \rho_3^1 x PC1 + \\
 & \rho_1^2 PC2 + \rho_2^2 PC2^2 + \rho_3^2 x PC2 + \\
 & \rho_1^3 PC3 + \rho_2^3 PC3^2 + \rho_3^3 x PC3 + \\
 & \gamma + \tau
 \end{aligned} \tag{1}$$

191 The linear predictor includes a grand mean intercept (β_0) and size-dependent

192 slope (β_1). The size variable x is the natural logarithm of plant volume ($\log_e(cm^3)$),
 193 which was standardized to mean zero and unit variance for analysis. Other fixed-
 194 effect coefficients (ρ) correspond to climate variables and climate \times size inter-
 195 actions. We include quadratic terms for climate to account for the possibility of
 196 non-monotonic climate responses. Climate coefficient (ρ) superscripts correspond
 197 to each PC, and subscripts correspond to linear, quadratic, and size-interaction ef-
 198 fects. Finally, the linear predictor includes normally distributed random effects for
 199 plot-to-plot variation ($\gamma \sim N(0, \sigma_{plot})$) and year-to-year variation that is unrelated
 200 to climate effects captured by PCs 1-3 ($\tau \sim N(0, \sigma_{year})$). The year random-effect
 201 can be interpreted as inter-annual variability in demography that cannot be ex-
 202 plained by the climate PCs. We used stochastic variable selection in a Bayesian
 203 framework to reduce model complexity, dropping coefficients that were effectively
 204 zero with $\geq 90\%$ certainty. Complete methods for variable selection are provided
 205 in Appendix B.

206 The growth data were normally distributed; this model applied the identity
 207 link and included an additional parameter for residual variance. We explored size-
 208 dependence in the residual variance of growth (which determines how individuals
 209 are distributed around their expected future size) but found that this led to poorer
 210 model fits, so we proceeded to assume a constant value. The survival and flower-
 211 ing data were Bernoulli distributed, and these models applied the logit link func-
 212 tion. The fertility data (flowerbud counts) were modeled as Poisson-distributed,
 213 including an individual-level random effect to account for overdispersion. All co-
 214 efficients were given vague priors. We evaluated model fits using posterior predic-
 215 tive checks (Elder & Miller, 2016). All models were fit using JAGS (Plummer
 216 *et al.*, 2003) and R2JAGS (Su & Yajima, 2012). Analysis code is available at

217 https://github.com/texmiller/cholla_climate_IPM.

218 Demographic modeling

219 Model description

220 The statistical models described above formed the backbone of the integral projec-
221 tion model (IPM) that we used to estimate population growth in variable climate
222 environments. Following previous studies (Compagnoni *et al.*, 2016; Ohm & Miller,
223 2014; Elderd & Miller, 2016), we modeled the life cycle of *C. imbricata* using con-
224 tinuously size-structured plants, $n(x)$, and two discrete seed banks ($B_{1,t}$ and $B_{2,t}$)
225 corresponding to 1 and 2-year old seeds:

$$B_{1,t+1} = \kappa \delta \int_L^U P(x, \mathbf{c}_{t-1}; \alpha_t^P) F(x, \mathbf{c}_{t-1}; \alpha_t^F) n(x)_t dx \quad (2)$$

$$B_{2,t+1} = (1 - \gamma_1 B_{1,t}) \quad (3)$$

226 Functions P and F give the probability of flowering and the number of flower-
227 buds produced, respectively, for an x -sized plant. The vector \mathbf{c}_{t-1} contains the
228 climate PC values for climate-year $t - 1$, which affects flowering and fertility in
229 year t , and hence the 1-year old seed bank in year $t + 1$. Parameters α_t^P and α_t^F are
230 random year effects estimated from the statistical models. The integral is multi-
231 plied by the number of seeds per fruit (κ) and probability of seed dispersal/survival
232 (δ) to give the number of seeds that enter the 1-year old seed bank. Parameters L
233 and U are the lower and upper bounds, respectively, of the plant size distribution.
234 Plants can recruit out of the 1-year old seed bank with probability γ_1 or transition

235 to the 2-year old seed bank with probability $(1 - \gamma_1)$. Seeds in the 2-year old seed
 236 bank are assumed to either germinate (probability γ_2) or die.

237 Continuous-size dynamics were given by:

$$n(y)_{t+1} = (\gamma_1 B_{1,t} + \gamma_2 B_{2,t}) \eta(y) \omega + \int_L^U S(x, \mathbf{c}_t; \alpha_t^S) G(y, x, \mathbf{c}_t; \alpha_t^G) n(x)_t dx \quad (4)$$

238 The first term indicates recruitment from the seed banks to size y , where $\eta(y)$
 239 gives the seedling size distribution, assumed normal with mean μ_s and standard
 240 deviation σ_s . Mortality between germination (late summer) and the yearly demo-
 241 graphic census (May) is accounted for with survival probability ω . In the second
 242 term, functions S and G give the probabilities of surviving to year $t + 1$ and grow-
 243 ing to size y , respectively, for an x -sized plant in year t . Climate-dependence and
 244 random year effects are included as in Eq. 2, except the timing of climate effects
 245 is shifted such that growth and survival from t to $t + 1$ are affected by climate over
 246 the same interval (Fig. C1). As above, survival and growth functions also take
 247 time-varying random intercepts. Field data used to estimate seed and seed bank
 248 parameters are described elsewhere (Compagnoni *et al.*, 2016; Elderd & Miller,
 249 2016). All parameter estimates are provided in Table C1.

250 Model analysis

251 For analysis, we discretized x into n bins, replacing the continuous kernel with an
 252 n -by- n matrix (because our model also included two additional discrete states, the
 253 final projection matrix had dimensions $n + 2$ -by- $n + 2$). We used $n = 200$ bins. We
 254 extended integration limits L and U to avoid unintentional “eviction” (Williams

255 *et al.*, 2012).

256 We estimated the asymptotic population growth rate λ as the dominant eigen-
257 value of the discretized IPM kernel. We compared the observed size distribution
258 and the predicted distribution at the long-term mean climate ($PC_1 = PC_2 =$
259 $PC_3 = 0$) and found generally good agreement (Fig. C2). We then evaluated how
260 λ responded to climate variation by first varying each climate PC independently,
261 holding the other two fixed at their long-term mean. Second, we back-casted λ
262 over the entire climatological record that we had available (1900–2017), which gen-
263 erated a time series of λ_t . We used linear regression to test for temporal trends
264 in λ over this period. We incorporated two types of uncertainty into back-casted
265 values of λ : imperfect knowledge of the parameter values (“estimation error”) and
266 year-to-year fluctuations that were not related to climate (“process error”); the
267 latter was estimated from the variances of random year effects. For the years of
268 demographic data collection (2004–2017), we could additionally quantify the devi-
269 ations between predicted λ based solely on climate and “observed” λ that reflects
270 climate and non-climate year effects (quotations indicate that these are the asymp-
271 totic predictions given the vital rates observed in that year). We also conducted a
272 similar analysis of λ_S using a 10-year sliding window, as described in Appendix C.

Finally, we used Life Table Response Experiments (LTREs) to decompose which combinations of climate PCs and vital rate responses were most strongly responsible for temporal fluctuations in the back-casted time series λ_t . We used a fixed-design LTRE (Caswell, 2001) where λ_t was defined as a linear function of

climate predictors:

$$\lambda_t = \bar{\lambda} + \sum_{i=1}^3 \beta_i PC_{i,t} \quad (5)$$

There is no error term because, in this analysis, climate PCs are assumed to be the sole drivers of fluctuations in λ_t . The coefficient for each climate PC was approximated as:

$$\beta_i \approx \sum_{j=1}^n \frac{\partial \bar{\lambda}}{\partial \theta_j} \frac{\partial \theta_j}{\partial PC_i} \quad (6)$$

273 The LTRE approximation is based on the product of the sensitivity of λ to the vital
274 rates (θ), evaluated at the long-term mean climate ($PC_1 = PC_2 = PC_3 = 0$), and
275 the sensitivity of the vital rates to climate, summed over all vital rates n . Because
276 LTRE components are additive, we summed LTRE estimates over the intercept
277 and slope of each vital rate function so that we could interpret the results in terms
278 of vital rate contributions.

279 Results

280 Climate trends

281 Three principal components cumulatively explained 73.3% of the inter-annual vari-
282 ation in climate (Figure 1A). PC1 was dominated by inter-annual differences in
283 temperature and precipitation, regardless of season, and the three components of
284 temperature (mean, min, max) loaded similarly onto this component (Figure 1B).
285 Over the last century, PC1 trends have fluctuated, with prolonged stretches of

286 warm and dry years (the 1950s and early 2000s) and other periods of cool and
287 wet years (early 1900s and 1970s-80s), though the overall temporal trend for PC1
288 is negative. The decline per-year is nearly five times stronger since 1970 com-
289 pared to the long-term average (Fig. 1C), suggesting an accelerating trajectory
290 of warmer and drier years. PC2 was strongly driven by cool-season climate, espe-
291 cially precipitation, such that greater values corresponded to wetter winters with
292 low temperature maxima and high temperature minima (Figure 1B). Warm-season
293 temperatures also loaded positively onto this axis to a lesser degree (Figure 1B).
294 PC2 has increased since 1900 and the change per-year is nearly four times stronger
295 since 1970 (Figure 1D), indicating an accelerating trend of wetter cool seasons with
296 moderate winter temperatures. Lastly, PC3 was correlated with a combination of
297 warm- and cool-season climate variables. The strongest variable loadings on this
298 component were minimum and mean temperatures in the cool season and warm-
299 season precipitation. Temporal trends for PC3 showed weak declines since 1900,
300 corresponding to milder winters with higher minimum and mean temperatures and
301 wetter warm seasons; this trend has been slightly stronger since 1970 (Figure 1E).

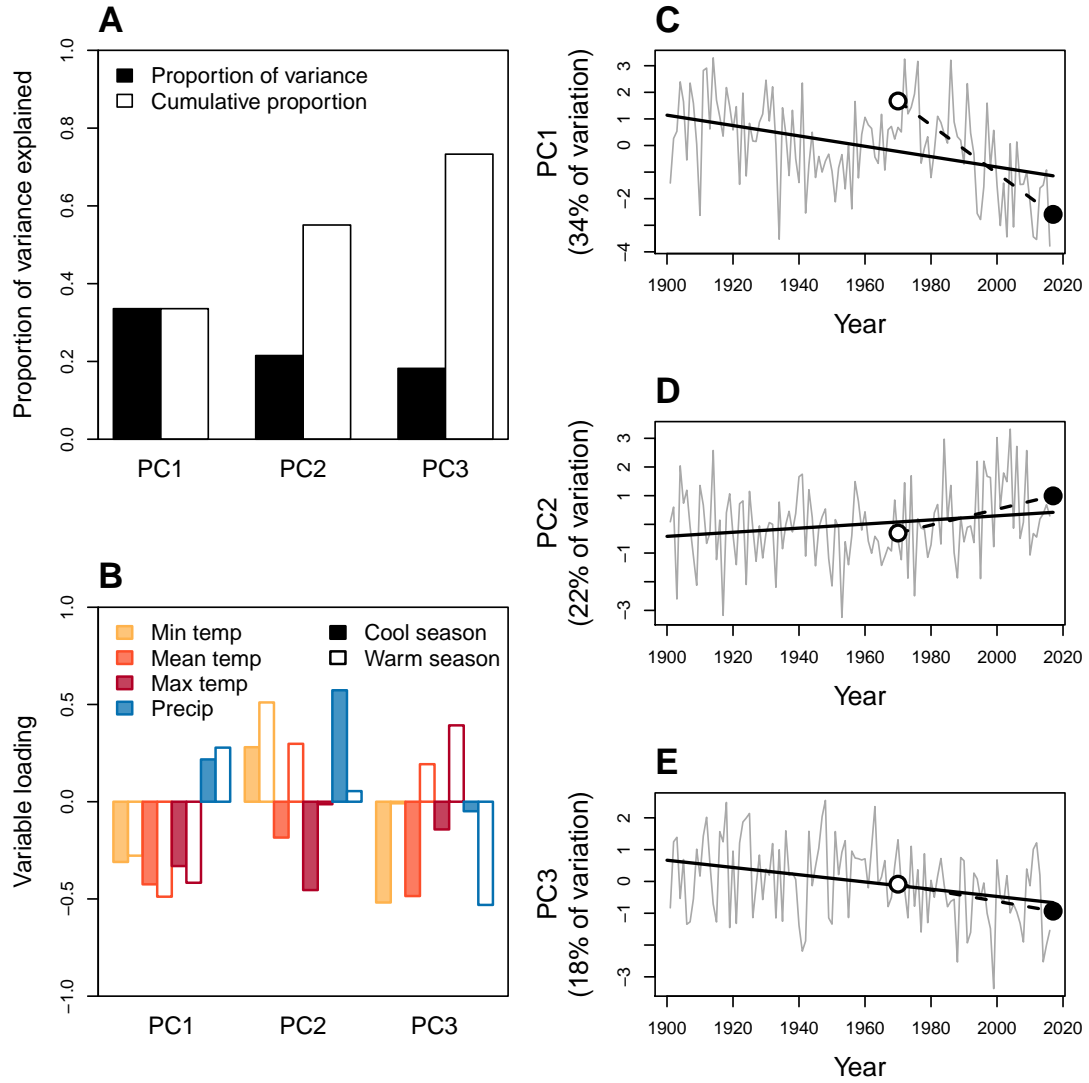


Figure 1: Principal components analysis (PCA) of inter-annual climate variability at SNWR, 1901–2017. **A**, Proportion and cumulative proportion of variation in seasonal temperatures (minimum, mean, maximum) and precipitation explained by the first three PCs. **B**, Loadings of seasonal climate variables onto PC1-3. Because climate data were standardized to mean zero and unit variance, loadings can be interpreted as the correlation between the climate variable and the PC. **C–E**, Time series of PC values, with regression lines showing long-term trends since 1901 (solid lines) or 1970 (dashed lines); open and filled points indicate the years 1970 and 2017, respectively, and correspond to the same shapes in Fig. 3

Vital rate responses to climate

Demographic vital rates estimated from long-term data (survival, growth, reproductive status, and fertility of flowering plants) were least responsive to PC1, the dominant axis of climate variability and change. All of the vital rates were strongly, positively size-dependent but there was heterogeneity in the magnitude and sign of responses to different dimensions of climate variability. Figure 2 shows vital rate data and fitted statistical models following variable selection procedures that eliminated coefficients that were weakly supported (Table B1). There was very little support for coefficients of quadratic climate effects (Table B1), indicating that responses to climate were monotonic over the range of variation we observed.

For PC1, there was a weak reduction in survival probability (especially for smaller plants; Fig. 2A) and a moderate reduction in flowering probability (especially for larger plants; Fig. 2G) at higher PC values, i.e., in cooler and wetter years. Fertility of flowering plants was not responsive to PC1 variation (Fig. 2J) and growth was not responsive to any of the climate PCs (Fig. 2D,E,F). There were positive responses to PC2 in survival (Fig. 2B), flowering probability (Fig. 2H), and fertility of flowering plants (Fig. 2K), indicating that these vital rates benefitted from years with wetter cool seasons. Responses to PC3 varied in sign, with survival increasing with decreasing PC values (years with mild winter temperature minima and wet summers) and reproductive rates increasing with increasing PC values (years with low winter minima and dry summers) (Fig. 2C,I,L).

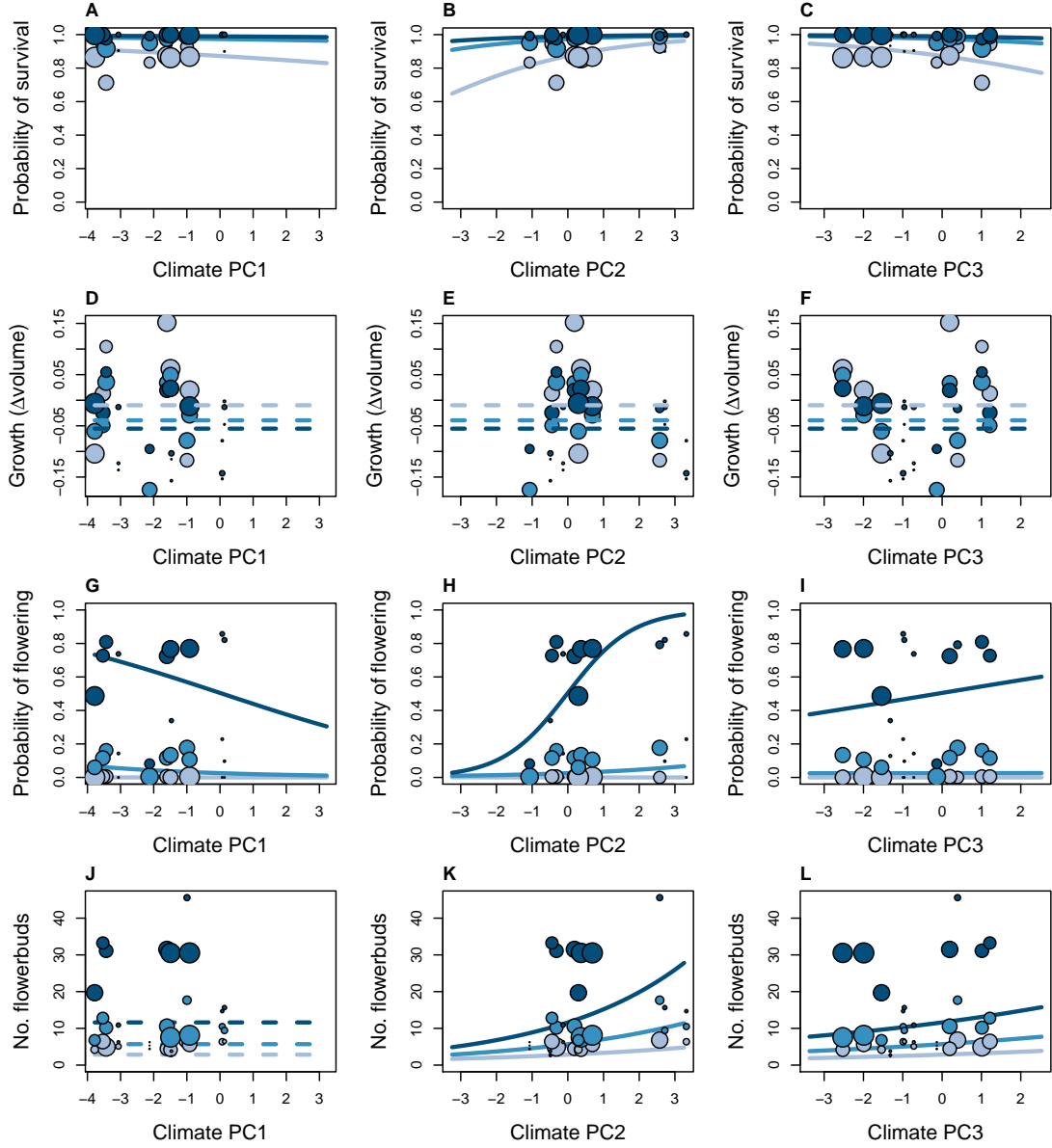


Figure 2: Climate- and size-dependent variation in survival (A-C), growth (D-F), flowering (G-I), and fertility of flowering plants (J-L) in relation to three principal components of seasonal climate variation (columns). For visualization only, the plant size distribution was discretized into three groups (small, medium, and large, corresponding to increasingly dark shading). Points show means for each size group in each year, where different years have unique PC values and point size is proportional to sample size for each size group in each year. Lines show fitted statistical models using posterior mean parameter values, with shading corresponding to size groups. Dashed lines indicate that the climate predictor was not statistically supported. Ranges of x -axes show the climate extrapolation that was required for back-casting.

Climate-dependent population growth

The population growth rate λ was predicted to increase with decreasing values of PC1 (hotter, drier years), holding other PCs fixed at their long-term average (Fig. 3A). Population growth was also predicted to increase with increasing values of PC2 (wetter cool seasons; Fig. 3B). Population growth was more sensitive to PC2 than PC1, such that the predicted change in λ from 1970 to 2017 was slightly greater for PC2 even though PC1 exhibited much greater change than PC2 over this period. Finally, greater values of PC3 (colder winters and drier summers) were predicted to cause declines in population growth, indicating that negative effects on cactus survival outweighed positive effects of PC3 on reproduction (Fig. 2). PC3 has changed relatively little since 1970 but this was associated with a change in λ of about half the magnitude to the response to relatively large change in PC1. Overall, recent climate change in each of the principal components, in isolation, has been in the direction that favors increased population growth (Fig. 1, 3). However, mean estimates for population growth rates were consistently below replacement level for all climate PC values, and the posterior probability densities rarely met or exceeded $\lambda = 1$.

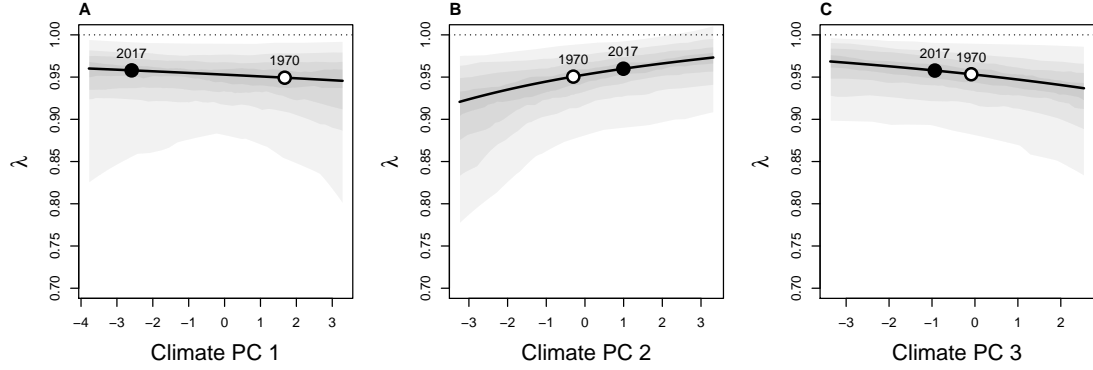


Figure 3: Predicted asymptotic population growth rate (λ) in response to three principal components of inter-annual climatic variation (A-C). For each panel, the indicated principal component is varying while the others are held at zero (the average value). Lines show the expected relationships based on posterior mean parameter values and shaded contours show the 25,50,75, and 95% credible intervals, representing uncertainty in demographic parameters. Points highlight the change the PC value (on the x -axis) between 1970 and 2017, based on the regression lines shown in Fig. 1, and the predicted corresponding change in λ (y -axis).

Back-casting population growth

Figure 4A shows the back-casted time series of λ accounting for inter-annual variation in all three PC components. For the observation years (2004-2017), the three climate PCs explained 57% of the inter-annual variation in λ (points in Fig. 4A). Thus, even with relatively strong climate-demography associations (Fig. 2), there was substantial uncertainty in our back-casted estimates of λ due to process error, i.e., heterogeneity in vital rates across years that could not be attributed to the climate PCs. This uncertainty, combined with uncertainty arising from imperfect knowledge of the underlying parameters, is shown in the shaded regions of Fig. Figure 4A.

350 Despite uncertainty in our back-cast, the results indicated that λ has likely
 351 remained below replacement levels for more than a century; there was no evidence
 352 that climate change drove this population into extinction debt. To the contrary,
 353 there was a positive temporal trend ($\frac{\Delta\lambda}{\Delta Year} > 0$), suggesting a trajectory of increas-
 354 ing population growth rates through time (Fig. 4B). There was wide uncertainty
 355 in the rate of change but the posterior probability distribution indicated that it
 356 was 2.27 times more likely that λ has increased than decreased. Furthermore, the
 357 median rate of increase was 2.76 times greater since 1970 compared to the overall
 358 trend since 1900 (Fig. 4B), corresponding to the acceleration of climate change
 359 (Fig. 1). There was greater uncertainty in $\frac{\Delta\lambda}{\Delta Year}$ since 1970 because this estimate
 360 was based on fewer years. Under the trajectory since 1970, population growth
 361 was expected to reach the threshold of positive population growth ($\lambda = 1$) in the
 362 year 2057 (Fig. 4C); accelerating climate change would advance this transition to
 363 viable growth rates.

364 The stochastic population growth rate (λ_S) showed a similar trend of $\lambda_S < 1$
 365 but increasing population growth rates over the past 120 years (Fig. C3). The
 366 stochastic growth rate reveals the effects of multi-year climate events, such as the
 367 runs of good years in the 1940s and 2000s.

368 Life Table Response Experiment

369 Life Table Response Experiments (LTRE) provided a decomposition of how λ
 370 responded to long-term climate trends (1900-2017), allowing us to understand the
 371 relative importance of different dimensions of climate variability and vital rate
 372 responses to them. LTRE results indicated that survival responses to climate

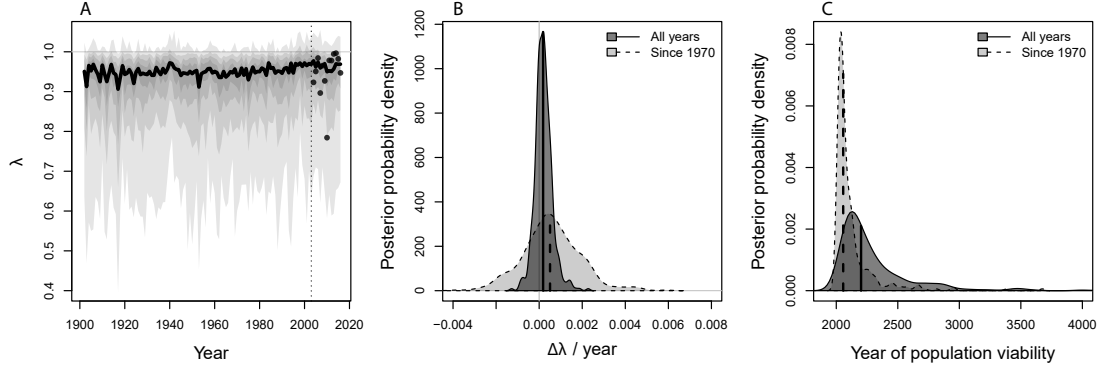


Figure 4: **A**, Posterior probability distribution for the time series of asymptotic population growth rates (λ) predicted based on inter-annual variation in three climate PCs. Thick black line shows the mean prediction and shaded regions show the 25, 50, 75, and 95% credible regions accounting for both parameter uncertainty and process error (year-to-year variation in vital rates that was unrelated to climate). Dashed vertical line separates years that were back-casted versus years that were directly observed. The observation years (2004 and later) include estimates for year-specific population growth rates (points), captured statistically as year-specific random effects in the vital rates. **B**, Posterior distributions for the rate of temporal change in population growth ($\frac{\Delta\lambda}{\Delta Y_{\text{year}}}$). Dark grey shows the rate of change across all years shown in **A** and light grey shows the rate of change since 1970. Vertical lines show median values. **C**, Posterior distributions for the year of population viability ($\lambda = 1$) for the subset of posterior samples for which $\frac{\Delta\lambda}{\Delta Y_{\text{year}}} > 0$. Shading and lines as in **B**.

373 were the overwhelming driver of temporal trends in λ (Fig. 5). Individual growth
 374 made no contribution to these trends because it was unresponsive to climate (Fig.
 375 D,E,F), whereas flowering and fertility were responsive to climate but their role
 376 was relatively small and imperceptible in Fig. 5. Furthermore, survival responses
 377 to climate PC2 were the dominant driver of temporal trends, followed by PC3
 378 and then PC1. Collectively, responses to PC2 and PC3 accounted for 91% of the
 379 overall climate effect in back-casted values of λ .

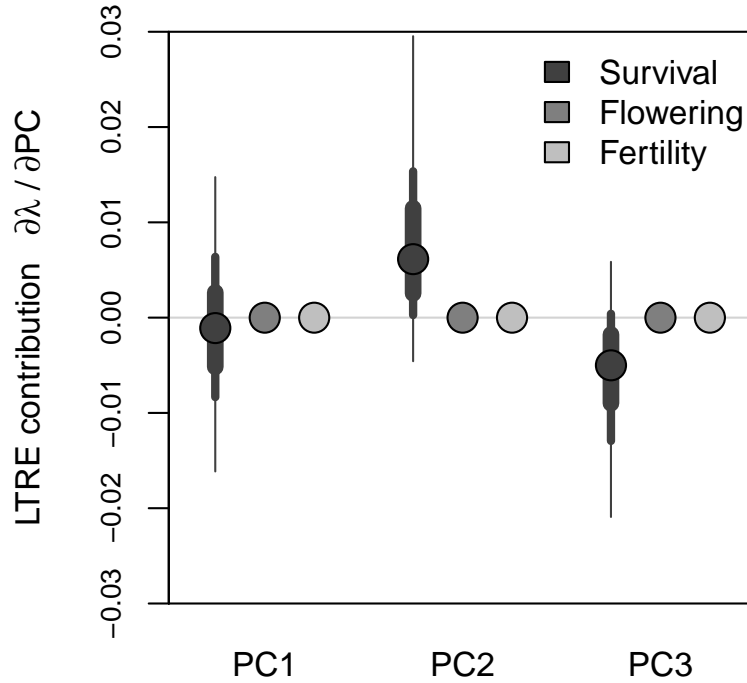


Figure 5: LTR decomposition of climate-driven inter-annual variability in population growth rates. Lines of decreasing thickness show the 50, 75 and 95 percentiles of the posterior distributions of the vital rate parameters, and points show the median. Shading corresponds to different vital rates (survival, flowering, and fertility) Posterior distributions for flowering and fertility are imperceptible on this scale.

Discussion

Understanding and predicting the effects of environmental change on plant demography and population dynamics are urgent challenges. The integration of long-term data with environmentally explicit demographic models provides a powerful vehicle

384 for meeting these challenges and may aid in identifying processes that drive some
385 populations into decline. By reconstructing 117 years of climate-dependent demog-
386 raphy, we tested the hypothesis that the extinction debt of our study population
387 was a consequence of recent climate change. Our results suggest the opposite: *C.*
388 *imbricata* is likely a climate change “winner”, on an accelerating trajectory toward
389 replacement-level within 38 years if current climate change trends persist, and
390 sooner if they accelerate. We further show that the strongest feature of climate
391 change in this system was not the main driver of population responses. Instead,
392 temporal trends in population viability were dominated by more subtle climatic
393 factors with relatively weak signals of recent change. Below, we interpret these
394 results in greater detail and discuss their broader significance.

395 Until recently, few plant demographic studies explicitly considered climatic
396 drivers of inter-annual variation (Ehrlén *et al.*, 2016; Crone *et al.*, 2011), though
397 this is rapidly changing. We are aware of no previous studies that have compared
398 the magnitudes of different aspects of climate change alongside the magnitudes of
399 demographic responses to those changes. However, we suspect that our key finding
400 – that the strongest dimension of climate change was not the strongest driver of
401 demography – may be common, since at the heart of this result lies the difference
402 between annual climate trends (captured by PC1) versus seasonal trends (PCs 2
403 and 3). Annual rainfall totals in our region have been decreasing but more of the
404 annual rainfall has been falling in the cool season, consistent with previous climata-
405 logical studies that suggest a shift from warm- to cool-season precipitation (Cook &
406 Seager, 2013; Cook *et al.*, 2015; Petrie *et al.*, 2014). Similarly, annual temperatures
407 have been increasing in our study region but it was cool-season warming, specif-
408 ically, that was most important for *C. imbricata* demography. Many plant and

409 animal life histories operate on seasonal schedules and may therefore be more sen-
410 sitive to seasonal redistribution of rainfall and temperature than to climate effects
411 that manifest over an entire year. Our results are consistent with previous studies
412 that demonstrate the importance of considering seasonal, not annual, drivers of
413 plant demographic responses (Selwood *et al.*, 2015; Williams *et al.*, 2015; Dahlgren
414 *et al.*, 2016). Some recent studies have taken a finer-grained approach, connecting
415 plant responses to weather events on monthly, weekly, or even daily time scales
416 (Teller *et al.*, 2016; Tenhumberg *et al.*, 2018; Shriver, 2016). For tractability, we
417 did not explore lagged climate effects beyond one year, though methods for doing
418 so are rapidly developing (Teller *et al.*, 2016; Tenhumberg *et al.*, 2018; Ogle *et al.*,
419 2015). Finding the appropriate timing and resolution of climate covariates is an
420 important area for future work in this system and more generally.

421 Rigorously accounting for various types of uncertainty is another an important
422 area in the development of environmentally explicit models for forecasting or back-
423 casting. Even with strong climate-demography relationships detected with our
424 unusually long-term data set, climate drivers accounted for little over half of the
425 inter-annual variation in λ during the study years. It was therefore important to
426 place our predictions for historical growth rates in the context of the substantial
427 uncertainty that arose from process error: all the additional, unspecified ways
428 that years may differ. We have emphasized the positive trajectory of population
429 viability as the most likely trend in λ , but this should be interpreted in light
430 of the probability distributions that we provide (Fig. 4) – that is, with nuance
431 and appropriate caution¹. As ecologists are increasingly called upon to forecast

¹The odds that λ is increasing were slightly lower than the odds of a Clinton victory in the 2016 U.S. presidential election: <https://projects.fivethirtyeight.com/2016-election-forecast/>

432 responses to change in climate drivers, it will be essential to do so in a probabilistic
433 framework that accommodates process error, i.e., the variability *not* explained by
434 climate drivers.

435 Different aspects of a species' life cycle may respond in diverse ways to environ-
436 mental drivers (Doak & Morris, 2010; Villellas *et al.*, 2015), highlighting the addi-
437 tional importance of considering multiple vital rates for understanding responses
438 to global change. Our work was able to pinpoint which responses throughout the
439 life cycle were most important for the overall population response to climate. Our
440 results are consistent with previous findings that high-sensitivity vital rates (those
441 that strongly influence λ , in this case survival and growth) are buffered against en-
442 vironmental variability while low-sensitivity vital rates (flowering and fertility) may
443 exhibit wide fluctuations (Pfister, 1998). However, incomplete buffering of survival
444 led to greater mortality in years with cold and dry cool-seasons – years that are be-
445 coming less frequent under climate change (Fig. 1) – and these survival responses
446 dominated the overall increase in population viability over the past 120 years
447 (Fig. 5). These results mirror a recent study of another long-lived perennial plant,
448 the alpine sunflower *Helianthella quinquinervis*, where reproductive responses to
449 climate drivers were strong but ultimately overwhelmed by weaker responses in
450 survival that more strongly affected population growth (Iler *et al.*, 2019). It is
451 commonly observed that demographic transitions related to growth and survival
452 are the most important determinants of population viability in species with long-
453 lived perennial life histories (Franco & Silvertown, 2004). It may therefore be a
454 general result that climate effects on growth and survival will be more consequen-
455 tial in long-lived perennials than effects on reproductive processes, even as the
456 latter exhibit greater sensitivity to climate, since perennials have many reproduc-

457 tive opportunities over potentially long lifespans (Dalglish *et al.*, 2010; Morris
458 *et al.*, 2008).

459 Our historical reconstruction of climate-dependent population growth indicated
460 that the climate has likely never been better for *C. imbricata* than it is now. This
461 result begs the question of how these plants have reached their current, relatively
462 high abundance, given over a century of population growth rates that were inferred
463 to fall well below replacement levels. Land use history – which is not incorporated
464 into our back-casted estimates – may have played a role. The Sevilleta NWR
465 was exposed to grazing for much of the 20th century until 1973. Previous work
466 suggests that cacti, and *C. imbricata* in particular, can increase in abundance
467 in response to grazing, due to livestock dispersing detached stem segment and
468 thus promoting asexual regeneration (Allen *et al.*, 1991). During our study, we
469 observed recruitment to be almost exclusively from seed (sexual and asexual re-
470 cruits are easily distinguishable), though it is possible that regeneration dynamics
471 were different under historical grazing regimes. Grazing may have also promoted
472 cactus populations through release of competitive interactions with grasses (Yu
473 *et al.*, 2019). Thus, one hypothesis is that *C. imbricata* achieved current densities
474 under the historical land use regime, and cannot maintain these densities in the
475 absence of cattle grazing. For long-lived plants, it may take decades to centuries
476 for full payment of extinction debt driven by land use changes (Lehtilä *et al.*,
477 2016; González-Varo *et al.*, 2015). An alternative hypothesis is that, independent
478 of grazing or other land use history, our study population may be located in sink
479 habitat and maintained by dispersal from nearby populations that are more vi-
480 able. Indeed, previous work showed that *C. imbricata* at lower elevations had
481 positive population growth rates (Miller *et al.*, 2009) and may therefore act as

source populations. Regardless of which process or processes best account for the persistence of a population that is currently inviable, our results indicate that it will likely be ‘rescued’ by ongoing climate change. One caveat to this conclusion is that, beyond the mean climate trends we have described, future climate (and especially monsoon precipitation) in our region is expected to be more variable (Rudgers *et al.*, 2018; Cook *et al.*, 2015) and this may dampen population growth independently of mean conditions (Boyce *et al.*, 2006). However, our stochastic demographic analysis, which accounts for increasing climate variability during the 20th century, also showed a positive trajectory of λ_S (Fig. C3).

Previous studies of cacti have emphasized their sensitivity to freezing as a constraint on physiological performance and geographic distribution (Flores & Yeaton, 2003; Kinraide, 1978; Nobel, 1984). In our study, we detected an important role for winter minimum temperature and observed high mortality following record low winter temperatures over a multi-day deep-freeze in 2011 (this is the low outlier in Fig. 4A). As these freezing events become less frequent under climate change, we expect an increase in regional abundance and perhaps northern expansion of *C. imbricata*’s range, which currently extends to southern Colorado and is likely limited by winter minimum temperatures. This may be an issue of applied concern in the region since *C. imbricata* is considered undesirable, particularly on rangelands (Allen *et al.*, 1991). The role of cool-season precipitation that we detected was more surprising. A majority of annual precipitation in the Southwest US comes from warm-season monsoon events (Adams & Comrie, 1997) and these events play a critical role in vegetation dynamics (Notaro & Gutzler, 2012; Petrie *et al.*, 2014), especially for plants with C4 and CAM photosynthesis that are physiologically most active during the warm summer months. Previous cactus demographic

507 studies have emphasized the role of summer monsoon precipitation (Winkler *et al.*,
508 2018; Bowers, 2005). Our results suggest that, despite its summer-adapted CAM
509 photosynthetic pathway, *C. imbricata* is able to capitalize on cool-season mois-
510 ture, and this was an important component of the positive demographic effects
511 of recent climate change. Similarly, Salguero-Gomez *et al.* (2012) identified the
512 desert species *Cryptantha flava* as a climate change winner due in part to seasonal
513 redistribution of rainfall that will lengthen its growing season.

514 Several limitations of our study warrant consideration in the interpretation of
515 our results. First, our consideration of climate dependence was limited to four
516 vital rate processes of established plants. Because we could not reliably assign a
517 birth year to new recruits, we did not incorporate climate dependence in seedling
518 recruitment. Previous studies of cactus demography suggest that seedling recruit-
519 ment may be highly sensitive to climate, especially monsoon precipitation (e.g.,
520 Bowers 2005; Winkler *et al.* 2018). We suspect this is the case for *C. imbricata*,
521 since germination usually coincides with late-summer rains (*T.E.X. Miller, un-*
522 *publ. data*). Because we did not model this process as climate-dependent, our
523 results for climate effects on population growth are conservative. However, con-
524 sistent with expectations for long-lived perennials, we know seedling recruitment
525 to have very low eigenvalue sensitivities (Elder & Miller, 2016), which suggests
526 that even large climate effects on this process may not strongly register in terms
527 of population growth, as we observed for the reproductive functions of established
528 plants (Fig. 4B).

529 A second limitation is that our approach to quantifying climate drivers know-
530 ingly forfeits some information, and in two ways. First, in order to gain deep
531 temporal coverage, we relied on downscaled climate projections rather than di-

rect climatological observations. While we know these two types of data to be highly correlated (Fig. A1), they are not perfectly so; this is especially true for temperature minima and maxima (Table A1), where downscaled data likely misestimate localized extremes. It is noteworthy that the downscaled climate data poorly captured the extreme deep-freeze of winter 2011 (Fig. A1). Poor demographic performance in this year was consequently attributed to a statistical random effect (Fig. 4A), though this was almost certainly a true climate effect. Second, we limited our consideration of climate drivers to the first three principal components of inter-annual variation. While these three components explained a large majority of the variation (Fig. 1A), we are disregarding some of the more subtle dimensions of climate variability and change. Given our main finding that the strongest features of climate change are not the main determinants of population responses, these neglected dimensions may include important demographic drivers. These two factors mean that our conclusions for climate-dependence err on the conservative side.

To conclude, this study illustrates how long-term patterns of population viability can be reconstructed through climate-demography relationships observed on relatively short time scales. This allowed us to evaluate the hypothesis that recent climate change has driven *C. imbricata* in our region into extinction debt, a hypothesis that we soundly reject. Instead, this species is most likely a climate change winner, largely due to its positive responses, especially in survival, to recent and ongoing shifts in cool-season temperature and precipitation. Interestingly, changes in cool-season climate were not the strongest features of climate change, but they were nonetheless the most important determinants of population responses. The more general lesson for global change biologists is that relatively

557 subtle dimensions of climate change may trigger strong ecological responses.

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565 **Author contributions**

566 TEXM initiated and maintains the long-term study. KC collected and analyzed
567 data and prepared a manuscript draft. TEXM finalized text and analyses. Both
568 coauthors approve this submission.

569 **Data accessibility**

570 All of the code for our statistical and demographic modeling is available at **https:**
571 **//github.com/texmiller/cholla_climate_IPM** and raw data will be published
572 in parallel with this manuscript.

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765 Appendix A: Correspondence between downscaled 766 and locally measured climate variables

767 We compared warm- and cool-season values of four climate variables (total pre-
768 cipitation and minimum, mean, and maximum temperature) between two data
769 sources: the SEV-LTER meteorological station nearest our study site (station 50 in
770 the SEV-LTER meteorological network) and downscaled data from ClimateWNA
771 corresponding to the same latitude, longitude, and elevation as station 50. Our
772 goal was to determine how well the downscaled data captured conditions ‘on the
773 ground’ as measured directly by the meteorological station. We compared the
774 years 2001 through 2017, which are the years of overlap between the two data
775 sources.

776 There was generally strong agreement between the two data sources (Table A1,
777 Figure A1). Temperature extrema were less strongly correlated between the two
778 data sets than temperature means, which is unsurprising given that extreme values
779 may be sensitive to local micro-environmental conditions that the relatively coarse
780 downscaled data would miss. The weakest correlation was that of warm-season
781 maximum temperature (Spearman’s $r = 0.41$, $P = 0.11$).

Table A1: Correlations between seasonal climate values measured by an on-site meteorological station versus downscaled data from ClimateWNA corresponding to the same years and location. Correlation values show Pearson correlations and P-values come from t -tests with 14 degrees of freedom.

Season	Variable	Correlation	P-value
Warm	Min temperature	0.59	0.0153
Warm	Mean temperature	0.84	10^{-4}
Warm	Max temperature	0.41	0.1135
Warm	Precipitation	0.49	0.0544
Cool	Min temperature	0.51	0.0622
Cool	Mean temperature	0.94	3.6×10^{-7}
Cool	Max temperature	0.69	0.0069
Cool	Precipitation	0.87	4.6×10^{-5}

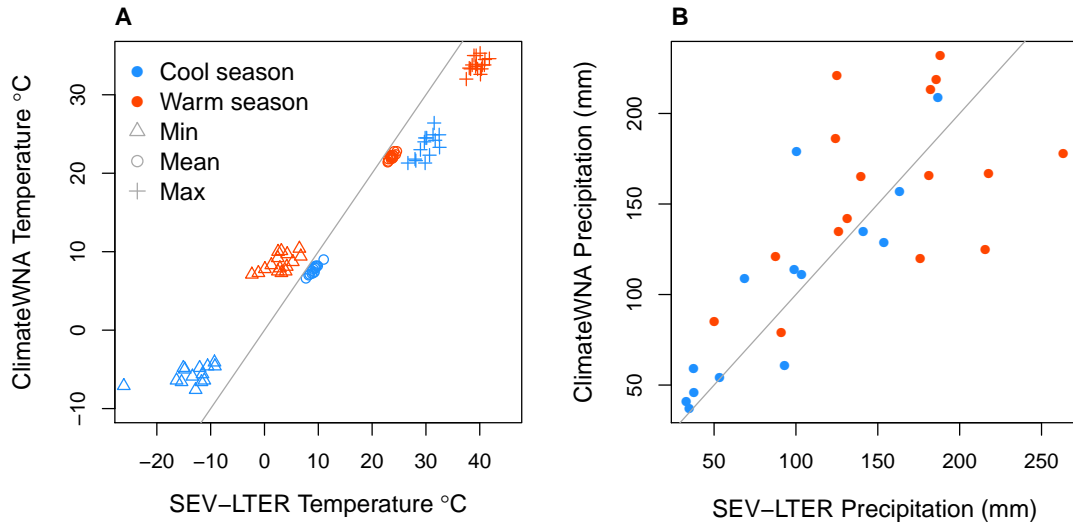


Figure A1: Correlations between seasonal climate values (**A**: temperature; **B**: precipitation) between SEV-LTER meteorological data and downscaled estimates from ClimateWNA for years 2001–2017. Gray lines show $y = x$.

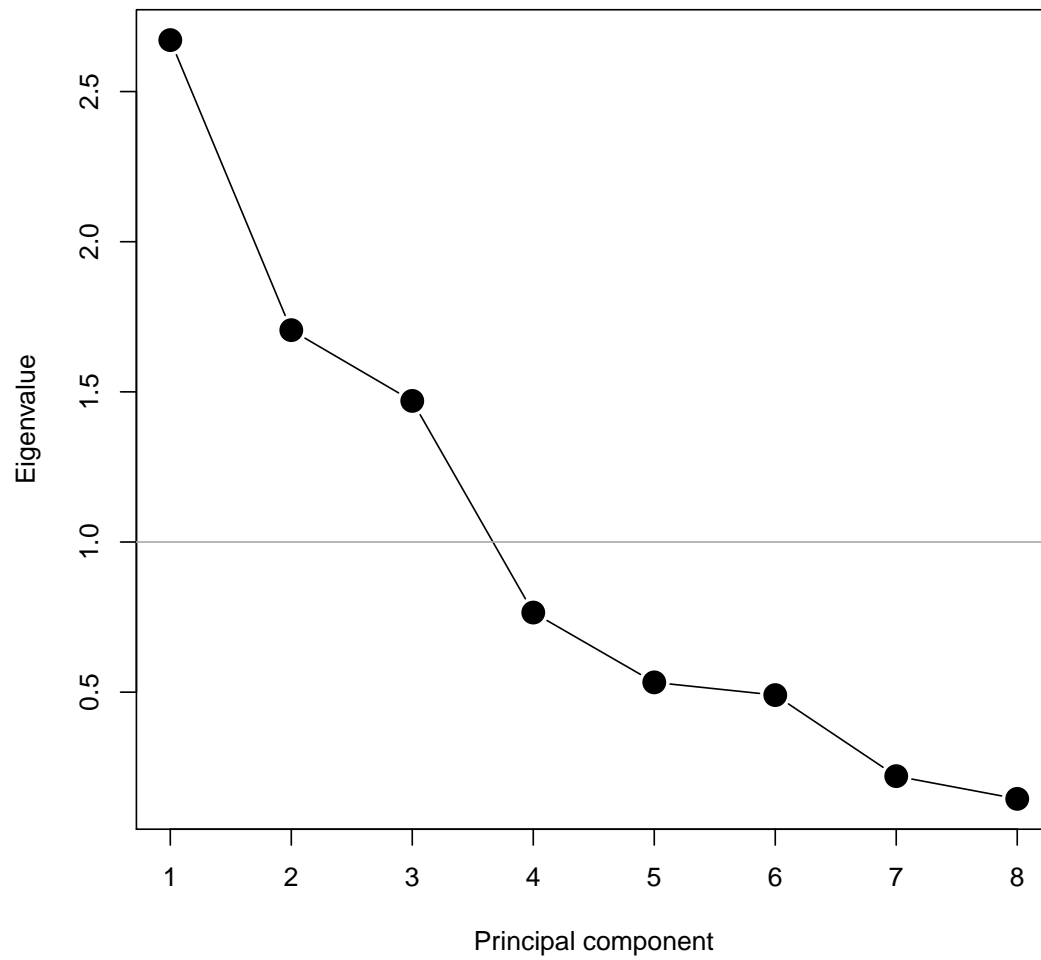


Figure A2: Results of parallel analysis conducted using the R package ‘paran’ (Dinno, 2018). Components with eigenvalues greater than 1 are retained.

Appendix B: Stochastic variable selection

Because we intended to extrapolate the vital rate models into past climate environments that were not well represented during the long-term study, it was important that we simplify the vital rate models to exclude unnecessary coefficients (which, even if small in absolute value, could generate unrealistic predictions when extrapolated over a greater range of climate than the models were fitted to). To do this, we used stochastic variable selection, a ‘model-based model selection’ approach (Hooten & Hobbs, 2015) that generates weightings for each fixed-effect coefficient, indicating the probability that the coefficient is non-zero. We employed an approach based on George and McCulloch (1993) where each coefficient (C_i) is modeled as a mixture distribution with zero and non-zero modes, where modal frequency is determined by an indicator variable (z_i). The coefficient prior was:

$$C_i \sim (1 - z_i) * N(0, 0.1) + z_i * N(0, 1000) \quad (\text{B1})$$

$$z_i \sim \text{Bernoulli}(0.5) \quad (\text{B2})$$

The first term of the mixture distribution assigns, with probability $(1 - z_i)$, a prior with mean zero and arbitrarily small variance, effectively forcing the posterior estimate to equal zero. The second term assigns, with probability z_i , a prior with mean zero and arbitrarily large variance, which allows for a non-zero posterior estimate. The posterior distribution of the indicator variable z_i gives the probability that the coefficient is non-zero. We estimated this probability for each coefficient in Eq. B1 and retained in the final model all coefficients with a posterior

mean $\hat{z}_i > 0.1$, meaning that the model term is determined to be non-zero with
90% confidence. All z_i values from the full model are shown in Table B1.

Climate PC	Model term	Survival	Growth	Flowering	Fertility
	Size	1	0.53	1	1
1	PC	0.13	0.04	0.12	0.05
1	PC*PC	0.03	0.01	0.03	0.01
1	PC*size	0.06	0.01	0.08	0.07
2	PC	0.18	0.03	0.11	0.14
2	PC*PC	0.06	0.01	0.06	0.03
2	PC*size	0.04	0.02	1	0.27
3	PC	0.18	0.02	0.12	0.18
3	PC*PC	0.09	0.01	0.09	0.06
3	PC*size	0.06	0.01	0.13	0.03

Table B1: Stochastic variable selection results. Values (z) can be interpreted as the probability that a model coefficient is non-zero. Bolded values indicate terms retained in the final model.

803 Appendix C: Additional demographic modeling meth- 804 ods and results

805 We estimated a time series for the stochastic population growth rate (λ_S) over
806 the period 1900-2017 using a moving window approach. While the determinis-
807 tic growth rate for each year estimates the long-run growth rate expected if the
808 conditions of that year remained constant, the stochastic growth rate integrated
809 over a broader range of conditions, incorporating year-to-year fluctuations and
810 auto-correlation of climate variables.

We simulated population dynamics according to Equations 4–2 to estimate the stochastic population growth rate λ_S . We estimated λ_S for 10-year windows spanning the time series 1901–2017, such that the value of λ_S for year t reflects the stochastic growth rate for a climate environment defined by years t through $t + 9$. For each 10-year window, we simulated 1000 years of population dynamics, each year randomly drawing one of the 10 climate-years. For each year of the simulation, we calculated total population size as:

$$N_t = \int n(x)_t dx + B_{1,t} + B_{2,t} \quad (\text{C1})$$

and estimated the stochastic growth rate for that window as the expected value of the one-year growth rate:

$$\log(\lambda_S) = \mathbb{E}[\log(\frac{N_{t+1}}{N_t})] \quad (\text{C2})$$

Table C1: Parameter values of tree cholla IPM.

Parameter description	Symbol	Mean	95%CI
Survival coefficients	β_0	3.33	(1.4 – 5.25)
	β_1	1.31	(1.18 – 1.44)
	ρ_1^1	-0.11	(-0.82 – 0.61)
	ρ_1^2	0.41	(-0.25 – 1.13)
	ρ_1^3	-0.28	(-0.84 – 0.3)
Growth coefficients	β_0	-0.03	(-0.08 – 0.02)
	β_1	-0.02	(-0.03 – -0.02)
Growth standard deviation	σ	0.25	(0.25 – 0.26)
Flowering coefficients	β_0	-4.76	(-7.37 – -2.22)
	β_1	5.17	(4.78 – 5.54)
	ρ_1^1	-0.26	(-1.27 – 0.7)
	ρ_1^2	0.07	(-0.85 – 1.01)
	ρ_3^2	1.11	(0.65 – 1.61)
	ρ_1^3	-0.04	(-0.79 – 0.77)
	ρ_3^3	0.21	(-0.06 – 0.47)
Fertility coefficients	β_0	-0.25	(-0.6 – 0.1)
	β_1	2.22	(2.01 – 2.42)
	ρ_1^2	0.06	(-0.15 – 0.28)
	ρ_3^2	0.17	(-0.01 – 0.35)
	ρ_1^3	0.12	(-0.04 – 0.29)
Seeds per fruit	κ	113.46	(93.47 – 132.59)
Recruitment into seed bank	δ	0.03	(0.02 – 0.05)
Germination rates	γ_1	0.0059	(0.0047 – 0.0073)
	γ_2	0.0044	(0.0033 – 0.0056)
Seedling size distribution	μ_s	-3.49	(-3.62 – -3.37)
	σ_s	0.23	(0.15 – 0.35)
Seedling survival	ω	0.5	(0.002 – 0.998)
Size bounds	L	-3.94	
	U	1.89	

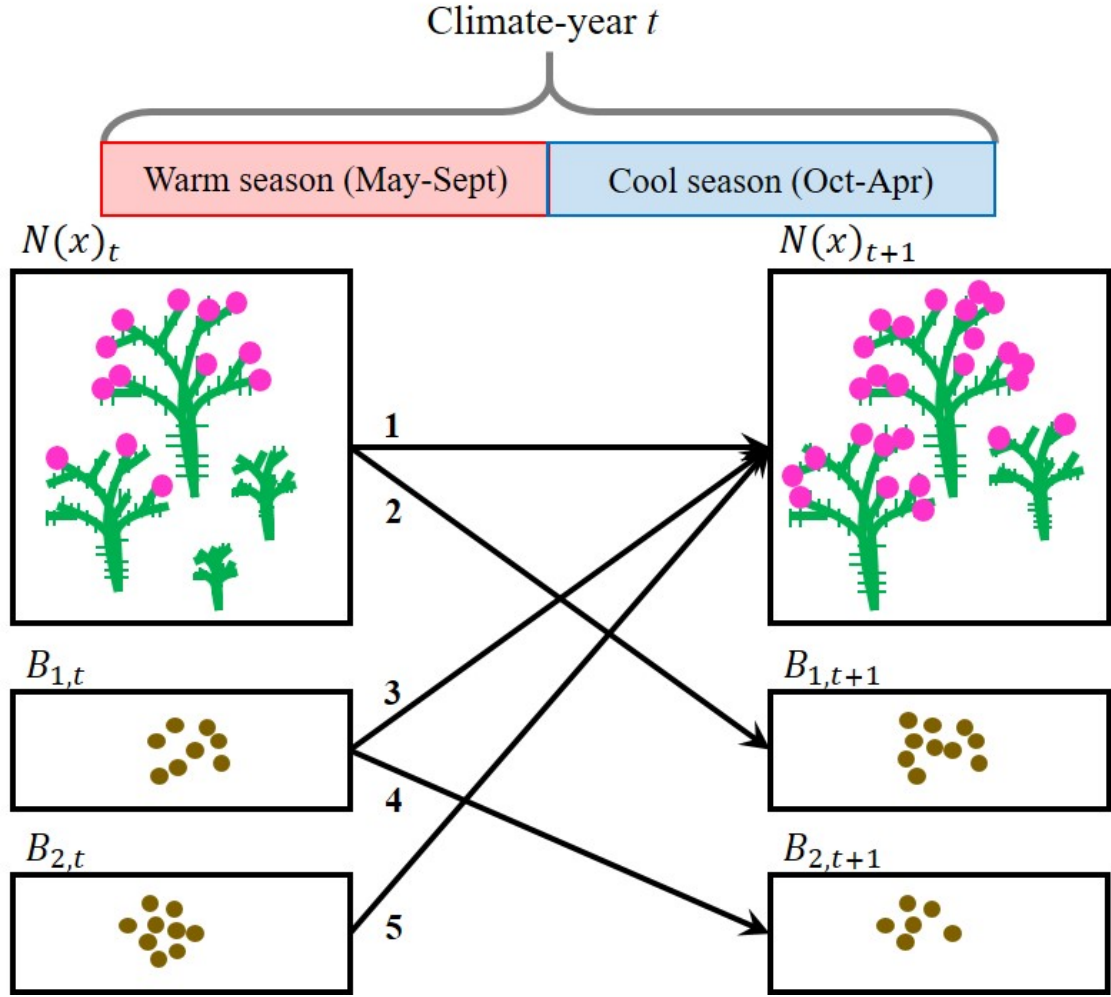


Figure C1: *C. imbricata* life cycle and census timing with respect to warm- and cool-season climate. Numbered arrows correspond to demographic events that occur during a transition year: (1) established plants survive and grow, (2) plants that are reproductive in year t contribute seeds that will make up the 1-yo seed bank in year $t+1$, (3) a fraction of seeds in the 1-yo seed bank survive and recruit into the plant population as seedlings in year $t+1$, (4) another fraction of seeds in the 1-yo seed bank survives and remains to form the 2-yo seed bank in year $t+1$, (5) a fraction of seeds in the 2-yo seed bank survive and recruit into the plant population as seedlings in year $t+1$. Survival and growth from year t to year $t+1$ (arrow 1) depended on climate year year t , whereas flowering and flowerbud production in year t (components of arrow 2) depended on climate in year $t-1$.

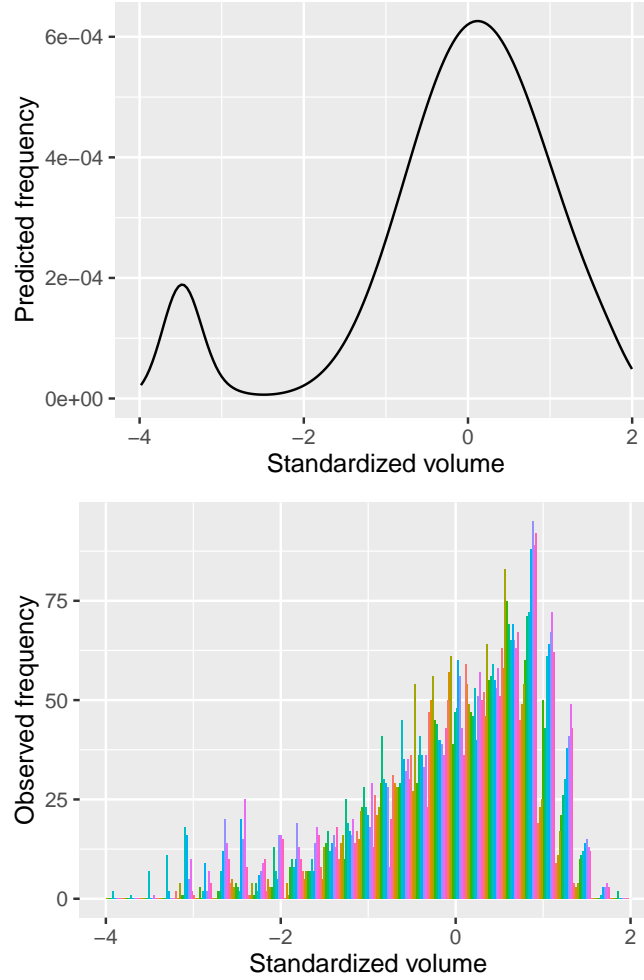


Figure C2: Comparison of predicted (top) and observed (bottom) size distributions, where size was the natural logarithm of plant volume standardized to mean zero. In the bottom panel, different colors represent different years. The predicted stable size distribution (evaluated at the average climate) corresponded well to the observed size distribution, though very large plants were over-represented in the observed distribution. This is consistent with the idea that the population may have recently transitioned into decline, whereby the persistence of large plants may reflect a legacy of positive growth rates. Also, the peak for new recruits was at a larger size in the observed distribution, but this was likely a consequence of the fact that we rarely detected new recruits. The “new” plants in our plots each year were likely several years old.

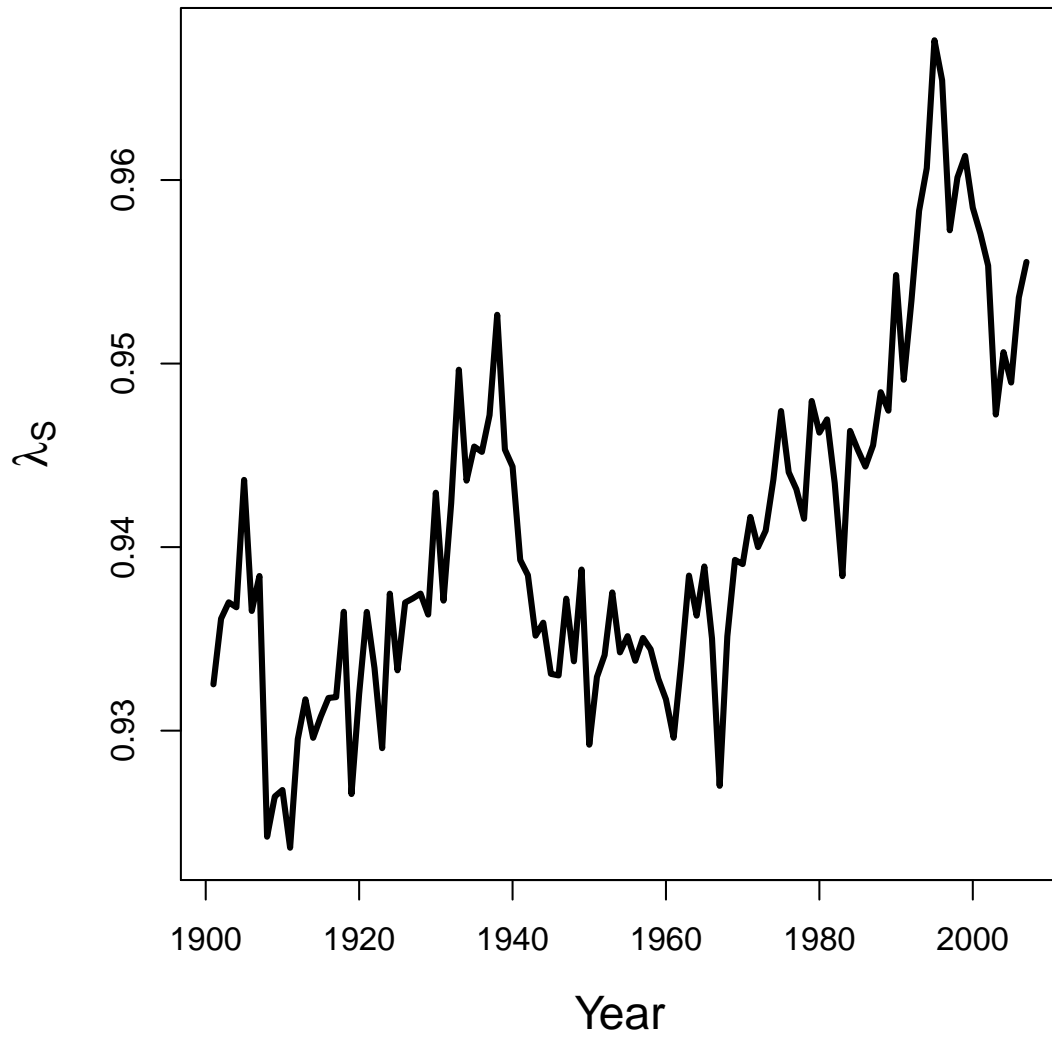


Figure C3: Time series of stochastic population growth rates (λ_S). Values are based on a 10-year sliding window such that λ_S is year t is based on the climate regime over the years t through $t + 9$