

Forecasting range shifts of a dioecious plant species under climate change

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Abstract:

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1 Abstract

2 Global warming has triggered an urgent need for predicting species response to climate
3 change. Currently, the vast majority of theory and models in population biology, including
4 those used to forecast biodiversity responses to climate change ignore the complication of
5 sex structure. To address this issue, we developed two contrasting climate-driven matrix
6 projection models (MPMs), a female dominant model and a two-sex model. The MPMs were
7 built from demographic data of a dioecious plant species (Texas bluegrass), past and future
8 climate. Both models predict that future climate will alter population viability and will induce
9 niche shift with a cascading effect on range shift toward the Northern edge of the current
10 range. However, the magnitude of niche and range shift was overestimated by the female
11 dominant. Tracking only one sex to forecast dioecious species response to climate change
12 could lead to ineffective conservation strategies.

¹³ Introduction

¹⁴ Rising temperatures and extreme drought events associated with global climate change are
¹⁵ leading to increased concern about how species will become redistributed across the globe
¹⁶ under future climate conditions (Bertrand et al., 2011; Gamelon et al., 2017; Smith et al., 2024).
¹⁷ Dioecious species (most animals and 7% of plants) might be particularly vulnerable to the
¹⁸ influence of climate change because they often display skewed sex ratios that are generated
¹⁹ or reinforced by sexual niche differentiation (distinct responses of females and males to
²⁰ shared climate drivers) (Tognetti, 2012). Accounting for such a niche differentiation within
²¹ a population is a long-standing challenge in accurately predicting which sex will successfully
²² track environmental change and how this will impact population viability and range shifts
²³ (Gissi et al., 2023; Jones et al., 1999). The vast majority of theory and models in population
²⁴ biology, including those used to forecast biodiversity responses to climate change, ignore
²⁵ the complication of sex structure (Ellis et al., 2017; Gissi et al., 2024; Pottier et al., 2021). As
²⁶ a result, accurate forecasts of colonization-extinction dynamics for dioecious species under
²⁷ future climate scenarios are limited.

²⁸ Species's range limits, when not driven by dispersal limitation, should generally reflect
²⁹ the limits of the ecological niche (Lee-Yaw et al., 2016). For most species, niches and geographic
³⁰ ranges are often limited by climatic factors including temperature and precipitation (Sexton
³¹ et al., 2009). Therefore, any substantial changes in the magnitude of these climatic factors in a
³² given location across the range could impact population viability, with implications for range
³³ shifts based on which regions become more or less suitable (Davis and Shaw, 2001; Pease
³⁴ et al., 1989). Forecasting range shifts for dioecious species is complicated by the potential for
³⁵ each sex to respond differently to climate variation (Morrison et al., 2016; Pottier et al., 2021).
³⁶ Populations in which males are rare under current climatic conditions could experience low
³⁷ reproductive success due to sperm or pollen limitation that may lead to population decline in
³⁸ response to climate change that disproportionately favors females (Eberhart-Phillips et al., 2017).
³⁹ In contrast, climate change could expand male habitat suitability (e.g. upslope movement),
⁴⁰ which might increases seed set for pollen-limited females and favor range expansion (Petry
⁴¹ et al., 2016). Although the response of species to climate warming is an urgent and active area
⁴² of research, few studies have disentangled the interaction between sex and climate drivers
⁴³ to understand their combined effects on population dynamics and range shifts.

⁴⁴ Our ability to track the impact of climate change on the population dynamics of dioecious
⁴⁵ plants and the implication of such impact on range shift depends on our ability to build mech-
⁴⁶ anistic models that take into account the spatial and temporal context in which sex specific
⁴⁷ response to climate change affects population viability (Czachura and Miller, 2020; Davis and

48 Shaw, 2001; Evans et al., 2016). Structured models that are built from long-term demographic
49 data collected from common garden experiments have emerged as powerful tool to study
50 the impact of climate change on species range shift (Merow et al., 2017; Schwinnig et al.,
51 2022). These structured models are increasingly utilized for several reasons. First, structured
52 models enable the manipulation of treatments that can isolate spatial and temporal correlations
53 between environmental factors, thus overcoming a main disadvantage with many types of
54 correlative studies (Leicht-Young et al., 2007). Second, structured models link individual-level
55 demographic trait to population demography allowing the investigation of factors explaining
56 vital rates (e.g. survival, fertility, growth and seed germination) response to environmental
57 variation (Dahlgren et al., 2016; Louthan et al., 2022). Third, structured models can be used to
58 identify which aspect of climate is more important for population dynamics. For example, Life
59 Table Response Experiment (LTRE) build from structured models is an approach that has be-
60 come widely used to understand the relative importance of covariates in explaining population
61 growth rate variation (Ellner et al., 2016). LTRE is also used to get a mechanistic understanding
62 of how a given treatment (eg. temperature or precipitation) could affect population dynamics
63 (Caswell, 1989; Iler et al., 2019; Morrison and Hik, 2007; O'Connell et al., 2024).

64 In this study, we used a mechanistic approach by combining geographically-distributed
65 field experiments, bayesian statistical modeling, and two-sex population projection modeling
66 and LTRE to understand the demographic response of dioecious species to climate change
67 and its implications for future range dynamics. Our study system is a dioecious plant
68 species (*Poa arachnifera*) distributed along environmental gradients in the south-central US
69 corresponding to variation in temperature across latitude and precipitation across longitude.
70 A previous study on the same system showed that, despite a differentiation of climatic niche
71 between sexes, the female niche mattered the most in driving the environmental limits of
72 population viability (Miller and Compagnoni, 2022b). However that study did not use climate
73 variables preventing us from backcasting and forecasting the impact of climate change on
74 dioecious species. Here, we asked four questions:

- 75 1. What are the sex-specific vital rate responses to variation in temperature and precipitation
76 across the species' range ?
- 77 2. How sex-specific vital rates combine to determine the influence of climate variation on
78 population growth rate (λ) ?
- 79 3. What are the historical and projected changes in climate across the species range ?
- 80 4. What are the back-casted and fore-casted dynamics of this species' geographic niche and
81 how does accounting for sex structure modify these predictions ?

82 **Materials and methods**

83 **Study species**

84 Texas bluegrass (*Poa arachnifera*) is a dioecious perennial, summer-dormant cool-season (C3)
85 grass that occurs in the south-central U.S. (Texas, Oklahoma, and southern Kansas) (Hitchcock,
86 1971). Texas bluegrass grows between October and May (growing season), with onset of
87 dormancy often from June to September (dormant season) (Kindiger, 2004). Flowering occurs
88 in May and the species is wind pollinated (Hitchcock, 1971). Average temperatures along the
89 distribution of the species tend to decrease northward as a result of the influence of latitude:
90 lower latitudes receive more heat from the sun over the course of a year. Similarly the average
91 precipitation decrease eastward as a result of the influence of longitude: lower longitudes
92 receive less precipitation over the year.

93 **Common garden experiment**

94 We set up a common garden experiment throughout and beyond the range of Texas bluegrass
95 to enable study of sex-specific demographic responses to climate and the implications for range
96 shifts. The novelty of this study lies in the fact that we use a precise climate variable to build
97 a mechanistic model to forecast the response of species to climate change. Details of the exper-
98 imental design are provided in Miller and Compagnoni (2022b); we provide a brief overview
99 here. The common experiment was installed at 14 sites across a climatic gradient (Fig.1). At
100 each site, we established 14 blocks. For each block we planted three female and three male indi-
101 viduals that were clonally propagated from eight natural source populations of Texas bluegrass.
102 The experiment was established in November 2013 and was census annually through 2016, pro-
103 viding both spatial and inter-annual variation in climate. Each May (2014-2016), we collected
104 individual demographic data including survival (alive or dead), growth (number of tillers),
105 flowering status (reproductive or vegetative), and fertility (number of panicles conditional on
106 flowering). For the analyses that follow, we focus on the 2014-15 and 2015-16 transitions years.

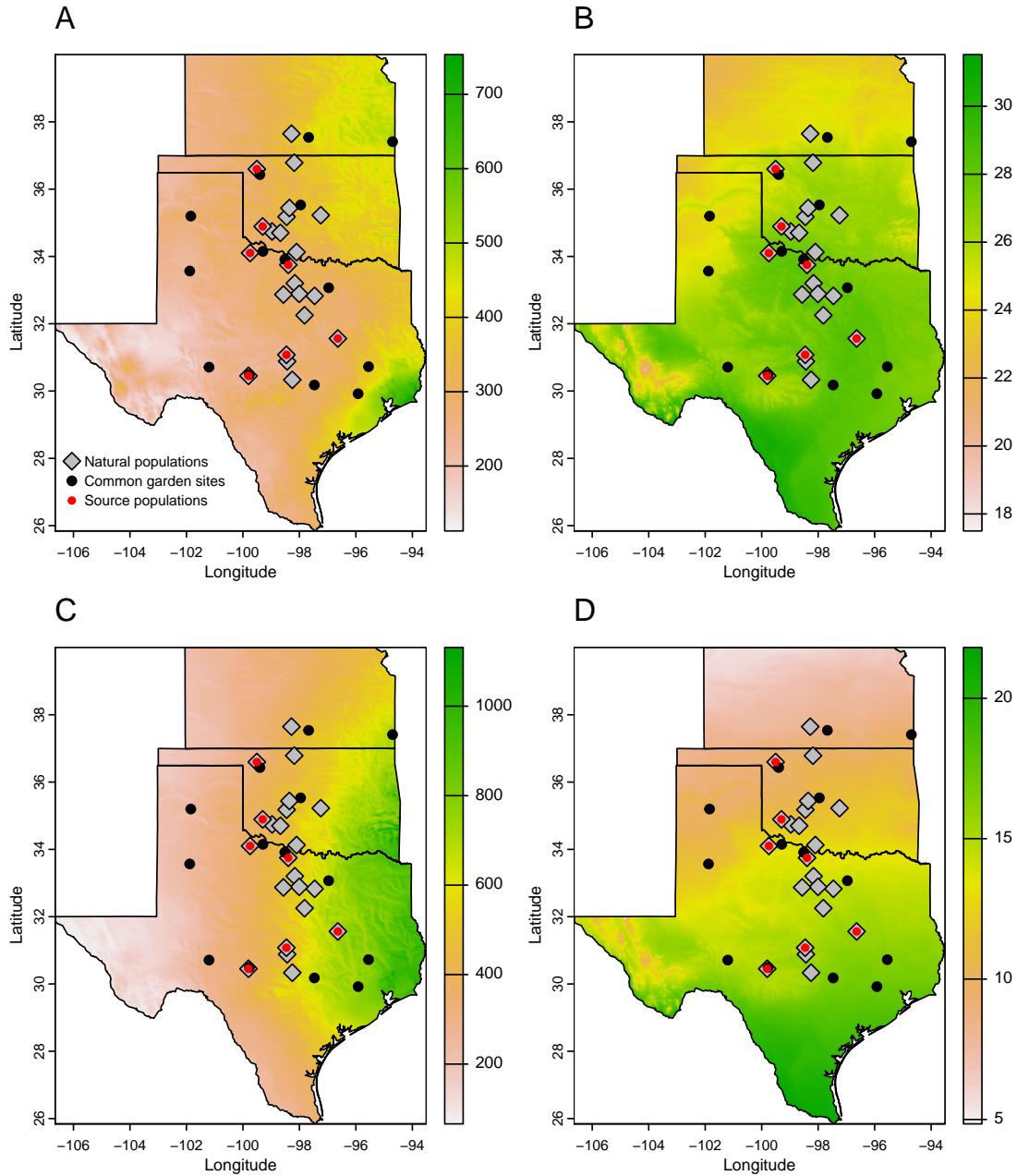


Figure 1: Maps of 30-year (1990-2019) normal climate and study sites used for demographic monitoring of *Poa arachnifera* in Texas, Kansas and Oklahoma in the United States. (A) Precipitation of the dormant season in mm , (B) temperature of the dormant season in °C , (C) precipitation of the growing season in mm , (D) temperature of the growing season in °C . We surveyed 22 natural populations (grey diamond). The common garden sites were installed on 14 sites (black circle) collected from 7 sources populations (red circle). Average temperatures along the distribution of the species tend to decrease northward as a result of the influence of latitude: lower latitudes receive more heat from the sun over the course of a year. Similarly, the average precipitation decreases eastward as a result of the influence of longitude: lower longitudes receive less precipitation over the year. See also Fig.S-1, Fig.S-2.

107 **Climatic data collection**

108 We downloaded monthly temperature and precipitation from Chelsa to describe observed
109 climate conditions during our study period (Karger et al., 2017). These climate data were used
110 as covariates in vital rate regressions, which allowed us to forecast and back-cast demographic
111 responses to climate change based on observations across the common garden experiment.
112 We aligned the climatic years to match demographic transition years ([May 1 – April 30](#)) rather
113 than calendar years. Based on the natural history of this summer-dormant cool-season species,
114 we divided each transition year into growing and dormant seasons. We define June through
115 September as the dormant season and the rest of the year as the growing season. Across
116 years and sites, the experiment included substantial variation in growing and dormant season
117 temperature and precipitation (Fig. S-1, S-2).

118 To back-cast and forecast changes in climate, we downloaded projection data for three
119 30-year periods: past (1901-1930), current (1990-2019) and future (2070-2100). Data for these
120 climatic periods were downloaded from four general circulation models (GCMs) selected
121 from the Coupled Model Intercomparison Project Phase 5 (CMIP5). The GCMs are: Model
122 for Interdisciplinary Research on Climate (MIROC5), Australian Community Climate and
123 Earth System Simulator (ACCESS1-3), Community Earth System Model (CESM1-BGC),
124 Centro Euro-Mediterraneo sui Cambiamenti Climatici Climate Model (CMCC-CM). All the
125 GCMs were downloaded from chelsa (Sanderson et al., 2015). We evaluated future climate
126 projections from two scenarios of representative concentration pathways (RCPs): RCP4.5, an
127 intermediate-to-pessimistic scenario assuming a radiative forcing to amount to 4.5 W m^{-2} by
128 2100, and RCP8.5, a pessimistic emission scenario which project a radiative forcing to amount
129 to 8.5 W m^{-2} by 2100 (Schwalm et al., 2020; Thomson et al., 2011).

130 **Sex ratio experiment**

131 We conducted a sex-ratio experiment on a site close (1 km) to a natural population of the
132 focal species at the center of the range to estimate the effect of sex-ratio variation on female
133 reproductive success. Details of the experiment are provided in Compagnoni et al. (2017) and
134 Miller and Compagnoni (2022b). In short, we established 124 experimental populations on
135 plots measuring $0.4 \times 0.4\text{m}$ and separated by at least 15m from each other at that site. We chose
136 15m because our pilot data show that more than 90% of wind pollination occurred within 13m.
137 We varied population density (1-48 plants/plot) and sex ratio (0%-100% female) across the ex-
138 perimental populations, and we replicated 34 combinations of density-sex ratios. We collected
139 the number of panicles from a subset of females in each plot and collected the number of
140 seeds in each panicle. Since the number of panicles (proxy of reproduction effort) does not nec-

¹⁴¹ essarily reflect reproduction success in *Poar arachnifera*, we accessed reproduction success (seed
¹⁴² fertilized) using greenhouse-based germination and trazolium-based seed viability assays.

¹⁴³ We used the sex-ratio to estimate the probability of viability and the germination rate.

¹⁴⁴ Seed viability was modeled with a binomial distribution where the probability of viability

¹⁴⁵ (v) was given by:

$$\text{146} \quad v = v_0 * (1 - OSR^\alpha) \quad (1)$$

¹⁴⁷ where OSR is the operational sex ratio (proportion of panicles that were female) in the
¹⁴⁸ experimental populations. The properties of the above function is supported by our previous
¹⁴⁹ work (Compagnoni et al., 2017). Here, seed viability is maximized at v_0 as OSR approaches
¹⁵⁰ zero (strongly male-biased) and goes to zero as OSR approaches 1 (strongly female-biased).
¹⁵¹ Parameter α controls how viability declines with increasing female bias.

¹⁵² We used a binomial distribution to model the germination data from greenhouse trials.

¹⁵³ Given that germination was conditional on seed viability, the probability of success was given
¹⁵⁴ by the product $v * g$, where v is a function of OSR (Eq. 1) and g is assumed to be constant.

¹⁵⁵ Sex specific demographic responses to climate

¹⁵⁶ We used individual level measurements of survival, growth (number of tillers), flowering, num-
¹⁵⁷ ber of panicles to independently develop Bayesian mixed effect models describing how each
¹⁵⁸ vital rate varies as a function of sex, size, precipitation of growing and dormant season and tem-
¹⁵⁹ perature of of growing and dormant season. We fit vital rate models with second-degree poly-
¹⁶⁰ nomial functions for the influence of climate. We included a second-degree polynomial because
¹⁶¹ we expected that climate variables would affect vital rates through a hump-shaped relationship.

¹⁶² We centered and standardized all climatic predictors to facilitate model convergence.

¹⁶³ However, Size was on a natural logarithm scale. We included site,source, and block as
¹⁶⁴ random effect. All the vital rate models used the same linear and quadratic predictor for
¹⁶⁵ the expected value (μ)(Eq.2) . However, we applied a different link function ($f(\mu)$) depending
¹⁶⁶ on the distribution the vital rate. We modeled survival and flowering data with a Bernoulli
¹⁶⁷ distribution. We modeled the growth (tiller number) with a zero-truncated Poisson inverse

168 Gaussian distribution. Fertility (panicle count) was model as zero-truncated negative binomial.

$$\begin{aligned} \mu = & \beta_0 + \beta_1 size + \beta_2 sex + \beta_3 pptgrow + \beta_4 pptdorm + \beta_5 tempgrow + \beta_6 tempdorm \\ & + \beta_7 pptgrow * sex + \beta_8 pptdorm * sex + \beta_9 tempgrow * sex + \beta_{10} tempdorm * sex \\ & + \beta_{11} size * sex + \beta_{12} pptgrow * tempgrow + \beta_{13} pptdorm * tempdorm \\ & + \beta_{14} pptgrow * tempgrow * sex + \beta_{15} pptdorm * tempdorm * sex + \beta_{16} pptgrow^2 \\ & + \beta_{17} pptdorm^2 + \beta_{18} tempgrow^2 + \beta_{19} tempdorm^2 + \beta_{20} pptgrow^2 * sex \\ & + \beta_{21} pptdorm^2 * sex + \beta_{22} tempgrow^2 * sex + \beta_{23} tempdorm^2 * sex + \phi + \rho + \nu \end{aligned} \quad (2)$$

170 where β_0 is the grand mean intercept, β_1 is the size dependent slopes. *size* was on a natural log-
171 arithm scale. $\beta_2 \dots \beta_{13}$ represent the climate dependent slopes. $\beta_{14} \dots \beta_{23}$ represent the sex-climate
172 interaction slopes. *pptgrow* is the precipitation of the growing season (standardized to mean
173 zero and unit variance), *tempgrow* is the temperature of the growing season (standardized to
174 mean zero and unit variance), *pptdorm* is the precipitation of the dormant season (standardized
175 to mean zero and unit variance), *tempdorm* is the temperature of the dormant season (standard-
176 ized to mean zero and unit variance). The model also includes normally distributed random
177 effects for block-to-block variation ($\phi \sim N(0, \sigma_{block})$) and source-to-source variation that is
178 related to the provenence of the seeds used to establish the common garden ($\rho \sim N(0, \sigma_{source})$),
179 site to site variation ($\nu \sim N(0, \sigma_{site})$). We fit survival, growth, flowering models with generic
180 weakly informative priors for coefficients ($\mu = 0, \sigma = 1.5$) and variances ($\gamma[0.1, 0.1]$). We fit
181 fertility model with regularizing priors for coefficients ($\mu = 0, \sigma = 0.15$). We ran three chains
182 for 1000 samples for warmup and 4000 for interactions, with a thinning rate of 3. We accessed
183 the quality of the models using trace plots and predictive check graphs (Piironen and Vehtari,
184 2017) (Fig. S-4). To understand the effect of climate on vital rates, we got the 95 % credible
185 interval of the posterior distribution. Then we assumed that there is 95 % probability that the
186 true (unknown) estimates would lie within that interval, given the evidence provided by the
187 observed data for each vital rate. All models were fit in Stan (Stan Development Team, 2023).

188 Influence of climate variation on population growth rate

189 To understand the effect of climate on population growth rate, we used the vital rate estimated
190 earlier to build a matrix projection model (MPM) structured by size (number of tillers),
191 sex and climate (dormant and growing) as covariate. Let $F_{x,z,t}$ and $M_{x,z,t}$ be the number of
192 female and male plants of size x in year t present at a location that has z as climate, where
193 $x \in \{1, 2, \dots, U\}$ and U is the maximum number of tillers a plant can reach (here 95th percentile
194 of observed maximum size). Let F_t^R and M_t^R be the new recruits, which we assume do not

195 reproduce in their first year. We assume that the parameters of sex ratio-dependent mating
 196 (Eq. 1) do not vary with climate. For a pre-breeding census, the expected numbers of recruits
 197 in year $t+1$ is given by:

$$198 \quad F_{t+1}^R = \sum_{x=1}^U [p^F(x,z) \cdot c^F(x,z) \cdot d \cdot v(\mathbf{F}_t, \mathbf{M}_t) \cdot m \cdot \rho] F_{x,z,t} \quad (3)$$

$$199 \quad M_{t+1}^R = \sum_{x=1}^U [p^F(x,z) \cdot c^F(x,z) \cdot d \cdot v(\mathbf{F}_t, \mathbf{M}_t) \cdot m \cdot (1-\rho)] F_{x,z,t} \quad (4)$$

200 where p^F and c^F are flowering probability and panicle production for females of size x , d
 201 is the number of seeds per female panicle, v is the probability that a seed is fertilized, m is
 202 the probability that a fertilized seed germinates, and ρ is the primary sex ratio (proportion
 203 of recruits that are female), z is the climate. Seed fertilization depends on the OSR of panicles
 204 (following Eq. 1) which was derived from the $U \times 1$ vectors of population structure \mathbf{F}_t and \mathbf{M}_t :

$$205 \quad v(\mathbf{F}_t, \mathbf{M}_t) = v_0 * \left[1 - \left(\frac{\sum_{x=1}^U p^F(x,z) c^F(x,z) F_{x,z,t}}{\sum_{x=1}^U p^F(x,z) c^F(x,z) F_{x,z,t} + p^M(x,z) c^M(x,z) M_{x,z,t}} \right)^\alpha \right] \quad (5)$$

206 Thus, the dynamics of the size-structured component of the population are given by:

$$207 \quad F_{y,t+1} = [\sigma \cdot g^F(y, x=1, z)] F_t^R + \sum_{x=1}^U [s^F(x,z) \cdot g^F(y, x, z)] F_{x,z,t} \quad (6)$$

$$208 \quad M_{y,t+1} = [\sigma \cdot g^M(y, x=1, z)] M_t^R + \sum_{x=1}^U [s^M(x,z) \cdot g^M(y, x, z)] M_{x,z,t} \quad (7)$$

209 In the two formula above, the first term indicates seedlings that survived their first year and en-
 210 ter the size distribution of established plants. Instead of using *P. arachnifera* survival probability,
 211 we used the seedling survival probability (σ) from demographic studies of the hermaphroditic
 212 congener *Poa autumnalis* in east Texas (T.E.X. Miller and J.A. Rudgers, *unpublished data*), and we
 213 assume this probability was constant across sexes and climatic variables. We did this because
 214 we had little information on the early life cycle transitions of greenhouse-raised transplants.
 215 We also assume that $g(y, x=1)$ is the probability that a surviving seedlings reach size y ,
 216 the expected future size of 1-tiller plants from the transplant experiment. The second term
 217 represents survival and size transition of established plants from the previous year, where
 218 s and g give the probabilities of surviving at size x and growing from sizes x to y , respectively,
 219 and superscripts indicate that these functions may be unique to females (F) and males (M).

220 Since the two-sex MPM is nonlinear (vital rates affect and are affected by population
 221 structure) we estimated the asymptotic geometric growth rate (λ) by numerical simulation,
 222 and repeated this across a range of climate.

223 Identifying the mechanisms of population growth rate sensitivity to climate

224 To identify which aspect of climate is most important for population viability, we used a
 225 "random design" Life Table Response Experiment (LTRE). We used the RandomForest package
 226 to fit a regression model with seasonal climate (here θ) as predictors and λ as response
 227 (Ellner et al., 2016; Liaw et al., 2002). The LTRE approximates the variation in λ in response
 228 to seasonal climate covariates and their interaction (Caswell, 2000; Hernández et al., 2023):

$$229 \quad Var(\lambda_c) \approx \sum_{i=-1}^n \sum_{j=1}^n Cov(\theta_i, \theta_j, \theta_{ij}) + Var(\epsilon) \quad (8)$$

230 where, θ_i , θ_j , θ_{ij} represent respectively the fitted regression slope for the covariates of the
 231 dormant season, j the covariates of the growing season and ij the covariates of their interactions.

232 To identify the mechanism by which climate affects population growth rate for each sex,
 233 we decomposed the effect of each climate variable on population growth rate (λ) into contribu-
 234 tion arising from the effect on each stage-specific vital rate (Caswell, 2000). At this end we used
 235 another LTRE with a "regression design". The LTRE with a "regression design" approximates
 236 the change in λ with climate as the product of the sensitivity of λ to the parameters times
 237 the sensitivity of the parameters to climate, summed over all parameters (Caswell, 1989):

$$238 \quad \frac{\partial \lambda}{\partial \text{climate}} \approx \sum_i \frac{\partial \lambda}{\partial \theta_i^F} \frac{\partial \theta_i^F}{\partial \text{climate}} + \frac{\partial \lambda}{\partial \theta_i^M} \frac{\partial \theta_i^M}{\partial \text{climate}} \quad (9)$$

239 where, θ_i^F and θ_i^M represent sex-specific parameters: the regression coefficients for the
 240 intercepts and slopes of size-dependent vital rate functions. Because LTRE contributions are
 241 additive, we summed across vital rates to compare the total contributions of female and male
 242 parameters.

243 Impact of climate change on niche and range shifts

244 A species' ecological niche can be defined as the range of resources and conditions allowing
 245 its populations to self-sustained ($\lambda > 1$) (Hutchinson et al., 1978; Maguire Jr, 1973). To
 246 understand the impact of climate change on species niche shifts, we estimated the probability
 247 of self-sustaining populations, which is $\Pr(\lambda > 1)$ conditional to two environmental axes:
 248 (i) temperature and precipitation of the dormant season and (ii) temperature and precipitation

249 of the growing season. $\text{Pr}(\lambda > 1)$ was calculated using the proportion of the 300 Markov
250 chain Monte Carlo iterations that lead to a $\lambda > 1$ (Diez et al., 2014).

251 $\text{Pr}(\lambda > 1)$ was also mapped onto geographic layers of three state (Texas, Oklahoma and
252 Kansas) to delineate past, current and future potential distribution of the species. To do so,
253 we estimated $\text{Pr}(\lambda > 1)$ conditional to all climate covariates for each pixel ($\sim 340 \text{ km}^2$) across
254 the species range. Then we add the current occurrences record of the species (1990-2019) from
255 Global Biodiversity Information Facility (GBIF) to validate the accuracy of our prediction
256 Because of the amount of the computation involve in the Markov chain Monte Carlo iterations,
257 use only 100 posterior samples to estimate $\text{Pr}(\lambda > 1)$ across the Texas, Oklahoma and Kansas.

258 All the analysis were performed in R 4.3.1 (R Core Team, 2023) However the estimation
259 of the impact of climate change on niche and range shifts were processed in parallel using
260 open-source software on the Rice Super computer (NOTS) and the German Centre for
261 Integrative Biodiversity Research (iDiv) High-Performance Computing Cluster.

262 Results

263 Sex specific demographic response to climate change

264 Most vital rates were strongly climate dependent, but the magnitude of their response were sim-
265 ilar between sexes suggesting no sex-specific demographic response to climate. Survival and
266 flowering were strongly more dependent on climate than growth (number of tillers) and repro-
267 duction (number of panicles) (Fig.2; Fig. S-5). In addition, we found opposite patterns in the di-
268 rection of the effect on seasonal climate on the probability of survival and flowering. The grow-
269 ing season (precipitation) has a negative effect on the probability of survival, number of tillers,
270 and the probability of flowering, whereas the dormant season has a positive effect on these vital
271 rates. Unlike precipitation, temperature of the growing season has a positive effect of the proba-
272 bility of survival, a negative effect of the probability of flowering, and the number of tillers, but
273 no significant effect on the number of panicles. Further, there was a female survival and flow-
274 ering advantage across both climatic seasons (Figures. 3A-3D, 3I-3L). On the contrary, there
275 was a male panicle advantage across all climatic variables (Figure3M-3P). Counter-intuitively,
276 there was no significant sex growth advantage in all season climatic variables (Figures. 3E-3H).

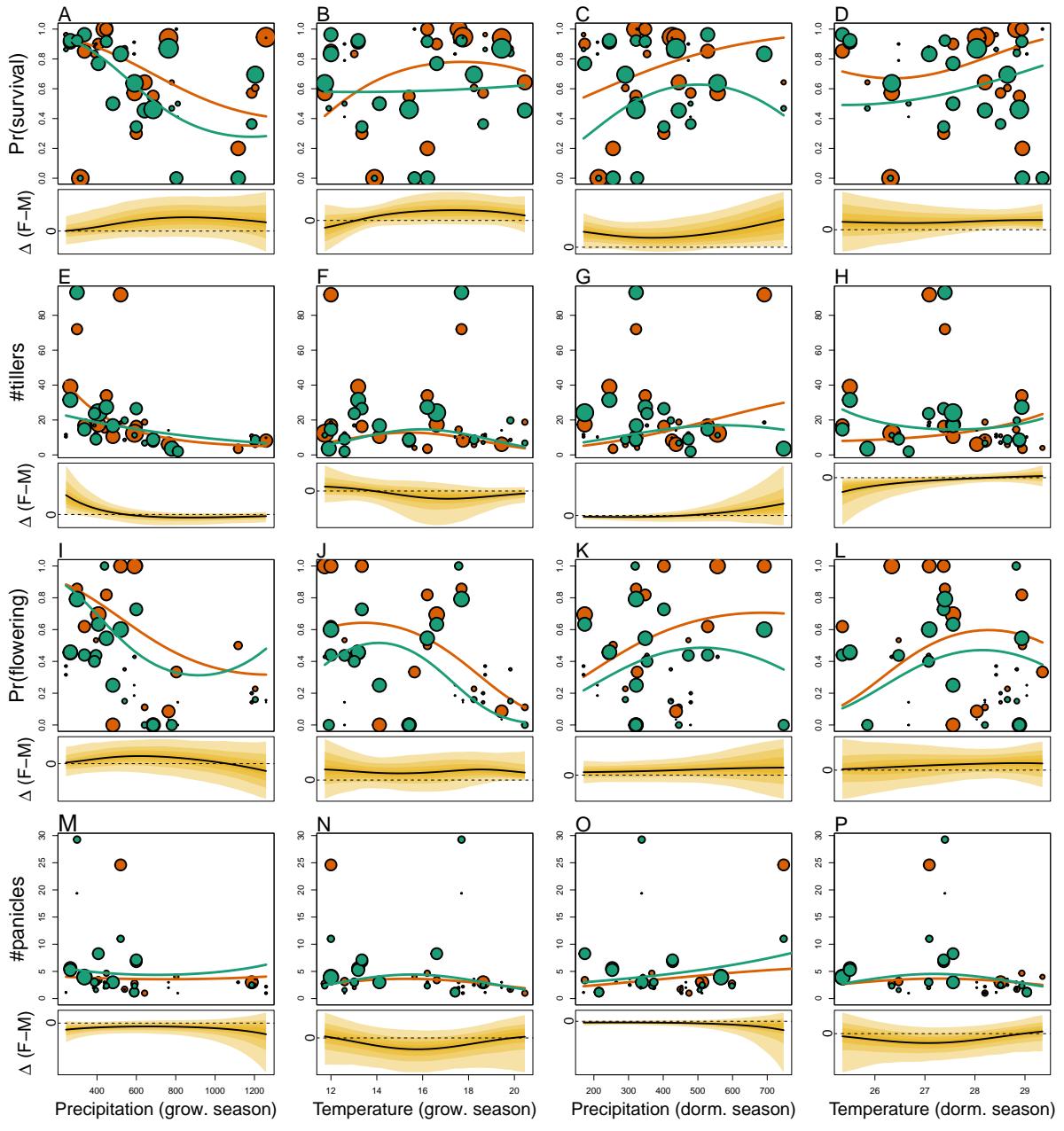


Figure 2: Sex specific demographic response to climate across species range. (A, B) Probability of survival during the growing season; (C, D) Probability of survival during the dormant season (E, F) Change in number of tillers during the growing season; (F, G) Change in number of tillers during the dormant season (I, J), Probability of flowering during the growing season; (K, L) Probability of flowering during the dormant season (M, N), Change in number of panicles produced given flowering during the growing season; (O, P) Change in number of panicles produced given flowering during the dormant season. Points show means by site for females (orange) and males (green). Points sizes are proportional to the sample sizes of the mean and are jittered. Lines show fitted statistical models for females (orange) and males (green) based on posterior mean parameter values. Lower panels below each data panel show the posterior distribution of the difference between females and males as a function of climate (positive and negative values indicate female and male advantage, respectively); dashed horizontal line shows zero difference. Statistical results are shown in Fig. S-5.

²⁷⁷ **Climate change alters population viability**

²⁷⁸ We estimated population growth rate response to seasonal climate gradients using two
²⁷⁹ models: a female dominant model and a two-sex model. Consistent with the effect of climate
²⁸⁰ on the individual vital rate, we found a strong effect of seasonal climate on population fitness
²⁸¹ (Fig.3). For both models, population growth rate decreased toward high precipitation of
²⁸² growing season (Fig.3 A, C). In contrast population growth rate increased with an increase
²⁸³ in precipitation of the dormant season. Furthermore, population growth rate was maximized
²⁸⁴ between 14 and 17 °C and decreased below zero beyond 18 °C during the growing season
²⁸⁵ (Fig.3 B). Similarly population fitness was maximized between 27 and 31 °C and decreasesd
²⁸⁶ below zero just beyond 20 °C during the dormant season (Fig.3 D). We have also detected
²⁸⁷ a strong effect of the past and future climate on population growth rate. However, the
²⁸⁸ magnitude of the effect of future climate on population growth rate was different between
²⁸⁹ gas-scenario emissions. Under past climate conditions, population growth rate decreased
²⁹⁰ below one for temperature of the growing season. A moderate emission gas scenario (RCP4.5)
²⁹¹ has a no effect on the population growth rate while a high emission scenario (RCP8.5) has
²⁹² a strong negative effect on population growth rate (Fig.3 B, D).

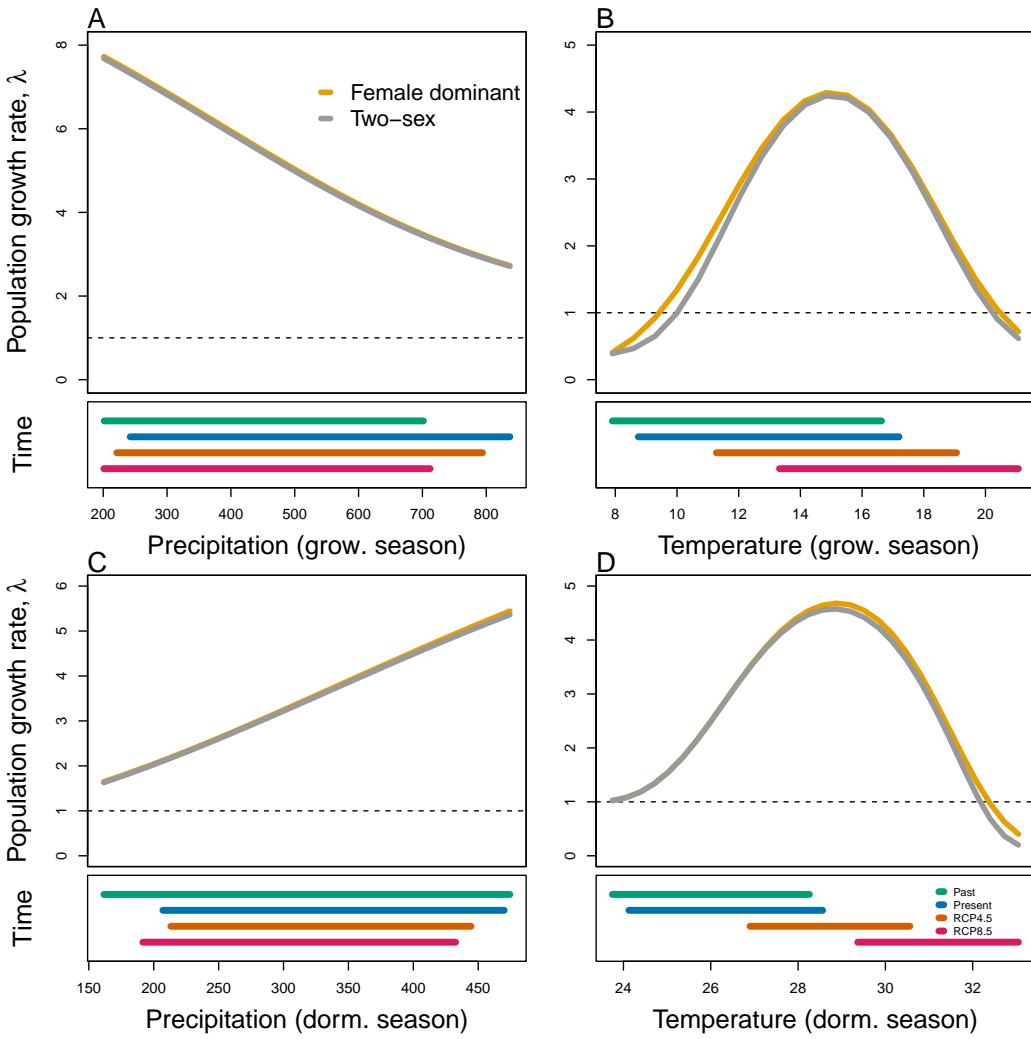


Figure 3: Population growth rate (λ) as a function of seasonal climate. (A) Precipitation of the growing season, (B) Temperature of the growing season, (C) Precipitation of the dormant season, (D) Temperature of the dormant season. The grey curve shows prediction by the two-sex matrix projection model that incorporates sex-specific demographic responses to climate with sex ratio dependent seed fertilization. The orange curve represents the prediction by the female dominant matrix projection model. The dashed horizontal line indicates the limit of population viability ($\lambda = 1$). Lower panels below each data panel show climate values at different time periods (past climate, present and future climates). For future climate, we show a Representative Concentration Pathways (RCP) 4.5 and 8.5. Values of (λ) are derived from the mean climate variables across 4 GCMs (MIROC5, ACCESS1-3, CESM1-BGC, CMCC-CM).

293 Temperature as a driver of population growth rate decline

294 Population growth rate was most sensitive to change in temperature of the growing season
 295 and temperature of the dormant season (Supporting Information S-6). LTRE decomposition
 296 revealed that, for each sex, the reduction of λ for high value of temperature of the growing
 297 season was driven by a reduction of survival rate, growth rate, and a reduction in number

298 of panicles (Fig.4 A, B). However, the reduction of population growth rate for higher value
 299 of temperature of the dormant season was driven by only female individuals(Fig.4 C, D).
 300 The increase of the probability of flowering was sufficient to prevent population growth rate
 301 from declining for high tmeprature of the dormant season (Fig.4 C).

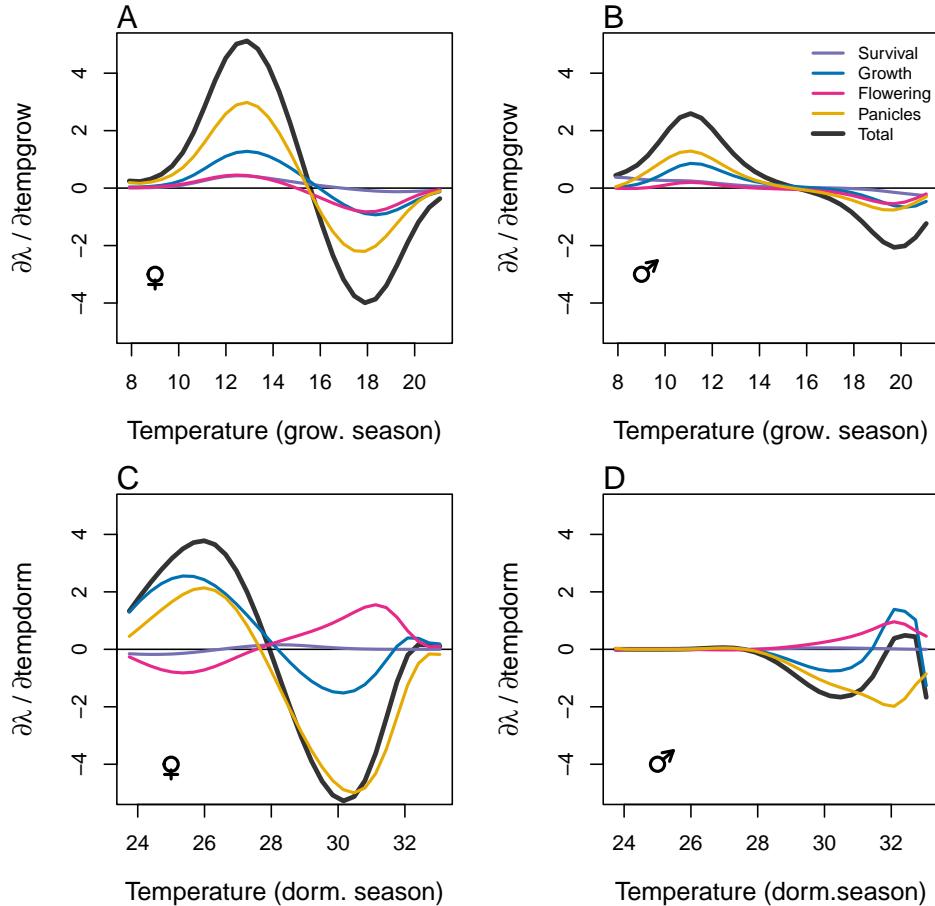


Figure 4: Life table response experiment decomposition of the sensitivity of λ to seasonal climate into additive vital rate contributions of males and females based on posterior mean parameter estimates. (A) Temperature of growing season (contribution of female), (B) Temperature of growing season (contribution of male), (C) Temperature of dormant season (contribution of female) and (D) Temperature of dormant season (contribution of male).

302 Climatic change induce niche and range shifts

303 Our results suggested niche sifts for both models (female dominant and two-sex) during the
 304 dormant and growing season (Fig. 5). However, the female dominant model overestimated

305 the magnitude of niche shifts (Fig. 5 D). Further, our demographically based range predictions
 306 broadly captured the known distribution of the species. More specifically, the predicted
 307 probabilities of self-sustaining ($\lambda > 1$) matches the presence and absence of the species (Fig. 6
 308 B, Fig. 6 F). Furthermore, viable populations of *P. arichnifera* were only predicted at the center
 309 of the range for current climatic conditions (Fig. 6 B). Although *P. arichnifera* was predicted
 310 to have suitable habitats in the center of the range under current climate, global warming
 311 (regardless of the future scenario of carbon emission used) is predicted to reduce much of
 312 these suitable habitats (Fig. 6 C, D). Most of the current suitable habitats will move toward
 313 the Northern range edge.

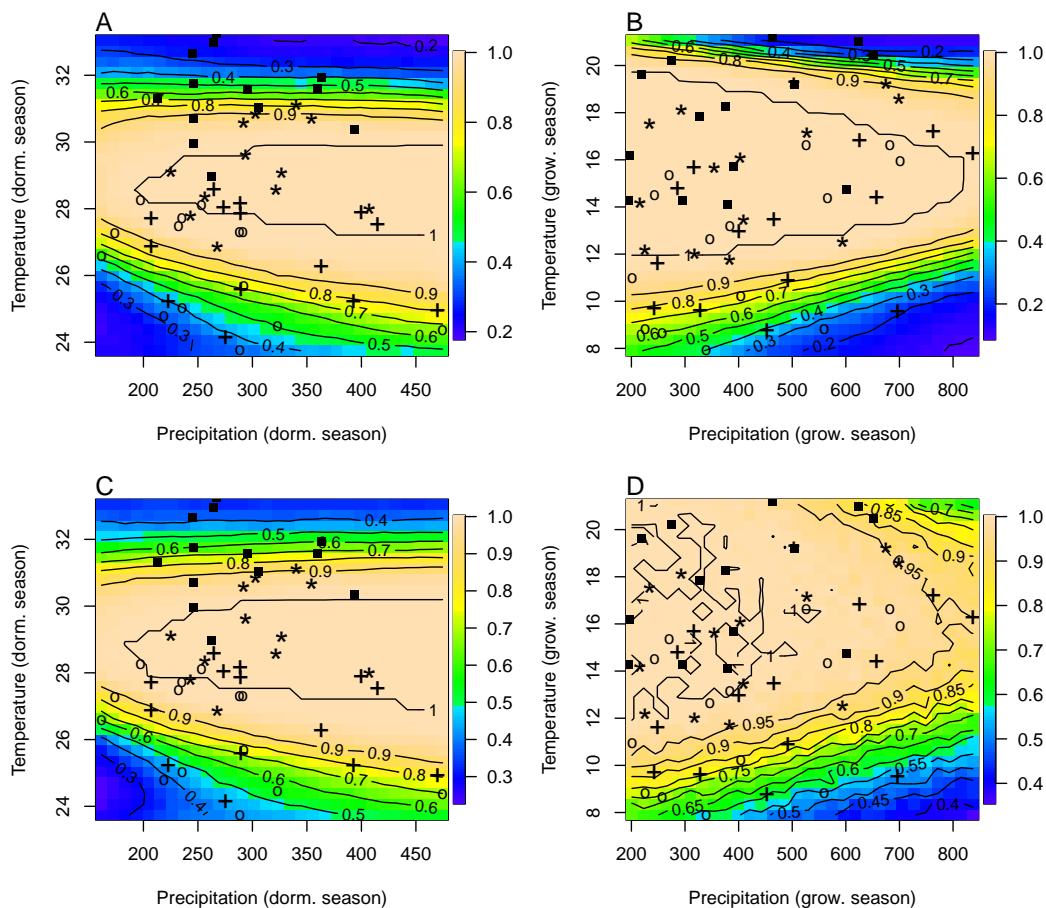


Figure 5: A two-dimensional representation of the predicted niche shift over time (past, present and future climate conditions). Contours show predicted probabilities of self-sustaining populations, $\text{Pr}(\lambda > 1)$ conditional on precipitation and temperature of the dormant and growing season. (A) Niche of dormant season for the two sex model, (B) Niche of growing season for the two sex model, (C) Niche of dormant season for female dominant model, (D) Niche of growing season for female dominant model. "o": Past, "+" Current, "*": RCP 4.5, "■": RCP 8.5.

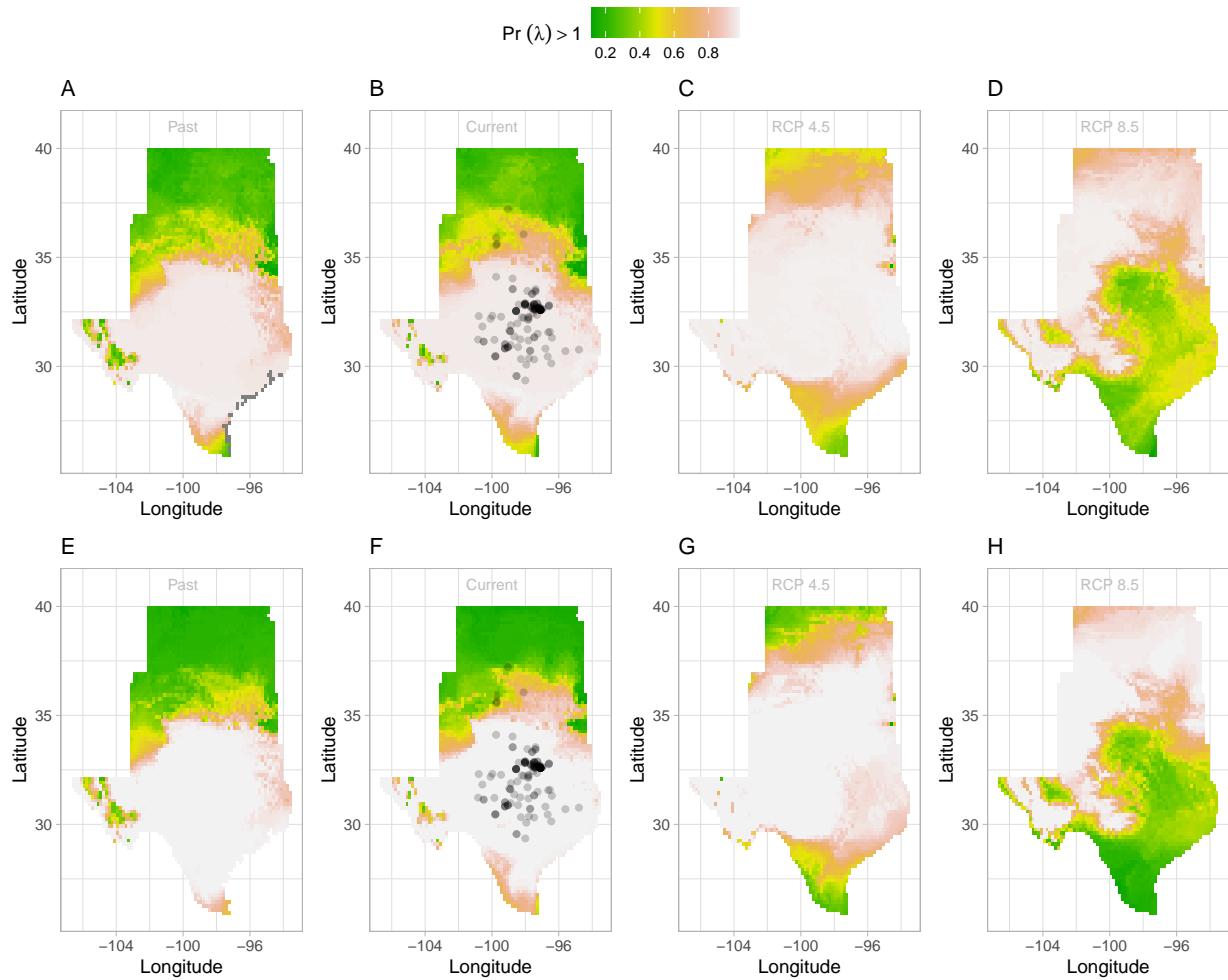


Figure 6: Climate change favors range shift toward the North edge of the current range. (A) Past, (B) Current, (C and D) Future predicted range shift based on the predicted probabilities of self-sustaining populations, $\text{Pr}(\lambda > 1)$, using the two-sex model that incorporates sex-specific demographic responses to climate with sex ratio dependent seed fertilization. (E) Past, (F) Current, (G and H) Future predicted range shift based on the predicted probabilities of self-sustaining populations, $\text{Pr}(\lambda > 1)$, using the female dominant model. Future projections were based on the ACCESS model. The black dots on panel B and F indicate all known presence points collected from GBIF from 1990 to 2019, which corresponds to the current condition in our prediction. The occurrences of GBIFs are distributed in with higher population fitness habitat $\text{Pr}(\lambda > 1)$, confirming that our study approach can reasonably predict range shifts.

314 Discussion

315 Although much emphasis has been placed in the response of monoecious species to climate, we
 316 have little knowledge about how skewness in sex ratio will affect dioecious species population
 317 dynamics and dioecious range shifts. We forecasted range shifts in dioecious species using
 318 climate-demographic models. Three general patterns emerged from our analysis. First, our
 319 Bayesian mixed effect model predicts that seasonal climate (temperature and precipitation)

320 affects sex-demographic processes in distinctive and contrasting ways. While climate has a
321 significant effect on the probability of survival and growth, it has no effect on the number
322 of panicles. Second, future climate, by increasing seasonal temperature, will reduce survival
323 rate, growth rate and reproduction and thereby alter population viability. In addition, climate
324 change favors range shifts. Third, using only one sex to forecast range shifts of dioecious under
325 climate change could lead to an overestimation of the impact of climate change on species.

326 Our results indicate no sex-specific demographic response to climate change. However,
327 females have higher survival rate and fertility rate than males. This result is not unique to
328 our study system and has been observed in a range of pollen dispersal species across climatic
329 gradients (Sasaki et al., 2019; Welbergen et al., 2008; Zhao et al., 2012). Several hypotheses
330 could explain the observed demographic advantage of females over males for survival and
331 flowering and the opposite for growth and number of panicles. The trade-off between fitness
332 traits (survival, growth, fertility) due to resource limitation and the pollination mode of our
333 study species (wind pollinated) could explain such a result (Cipollini and Whigham, 1994;
334 Freeman et al., 1976). For most species, the cost of reproduction is often higher for females
335 than males due to the requirement to develop seeds and fruits (Hultine et al., 2016). However,
336 several studies reported a higher cost of reproduction for males in wind pollinated species
337 due to the larger amounts of pollen they produce (Bruijning et al., 2017; Bürl et al., 2022;
338 Cipollini and Whigham, 1994; Field et al., 2013). In addition to life history trade-off, difference
339 in non-climatic factors such as soil, or biotic interactions could explain decline in vital rate
340 as an indirect effects of increase in temperature (Alexander et al., 2015; Schultz et al., 2022).

341 Under current conditions, most populations across the range are viable. This result could
342 be explained by two hypotheses. First, demographic compensation whereby an increase of
343 one vital rate is coupled with a decrease of another vital rate could explain viable populations
344 in harsh conditions at the range edge (Doak and Morris, 2010; Nomoto and Alexander, 2021;
345 Villegas et al., 2015). In our system, a decrease in fertility and survival rate was counterbalanced
346 by an increase in flowering rate, preventing the population growth rate from declining even at
347 range edge during the dormant season. Second, local adaptation at the edge of the range could
348 explain the viable populations throughout the range (Miller and Compagnoni, 2022b). Our
349 study was based on a common garden experiment; therefore, individuals planted in climatic
350 conditions that are similar to their source populations climatic conditions were less impacted
351 by stressful environmental conditions. An important question to ask is: what is the role of
352 local adaptation in buffering species response against climate change. Unfortunately, our
353 model does not shed light on that question. Adding another predictor to our complex model
354 would have lead to overfitting. Therefore, the role of local adaptation in mitigating population
355 response to climate should be the next step in forecasting species response to climate.

Our LTRE analysis reveals that a small change in temperature of the growing and dormant season could have a larger impact on population viability. Temperature can impact plant populations through different mechanisms. Increasing temperature could increase evaporative demand, affect plant phenology (Iler et al., 2019; McLean et al., 2016; Sherry et al., 2007), and germination rate (Reed et al., 2021). The potential for temperature to influence these different processes changes seasonally (Konapala et al., 2020). For example, studies suggested that species that are active during the growing season such as cool grass species can have delayed phenology in response to global warming, particularly if temperatures rise above their physiological tolerances (Cleland et al., 2007; Williams et al., 2015). In addition, high temperature during the growing season by affecting pollen viability, fertilization could affect seed formation and germination (Hatfield and Prueger, 2015; Sletvold and Ågren, 2015). Temperature also affected operational sex ratio (OSR) (Fig.S-12). That variation in OSR could affect population growth rate by altering females' fitness (Haridas et al., 2014; Knight et al., 2005; Petry et al., 2016).

We found evidence of climatic niche shifts for the female dominant model and the two-sex model. However the female dominant model overestimated species niche, suggesting that using one sex to predict niche shifts could be misleading. Despite that overestimation for the female dominant model, both models agree on the fact that climatic conditions that are not optimal under current conditions will be optimal for the species over the next years particularly at the edge of species. Further, pollen dispersal may allow plants to resist climate change because pollen dispersal may provide the local genetic diversity necessary to adapt at the leading edge of the population (Corlett and Westcott, 2013; Duputié et al., 2012; Kremer et al., 2012). Since wind pollination is most effective at short distances, it is most often found in plant species growing at high density such as our study species, it is less likely that dispersal limitation affect niche shift in our study system. However, others biotic factors such as species competition might constrain the species to a narrower realized niche (Aguilée et al., 2016; Pulliam, 2000).

Our results suggest that climate change will drive range shifts and the magnitude and rate of that range shift could be overestimated when tracking only one sex (Fig. S-9, Fig. S-10, Fig. S-11). This overestimation of the impact of climate change using a female dominant model could be due to several factors. First, small change in seasonal temperature affects population viability for both sexes. Second, operational sex ratio in *Poa arachnifera* become female biased in area with lower temperature of growing season such as Northern range edge (Fig.S-12 B). Our results converge with previous studies that have found the same pattern for other dioecious species (Varga and Soulsbury, 2020; Woldemelak et al., 2021). Our funding also contrast with a previous study suggesting that an increase in male frequency induce range shifts by reducing pollen limitation in conditions that were not suitable (Petry et al., 2016).

Three years represent a relatively decent time for demographic study for common garden experiments across climatic gradient. Thus our models can only capture a certain range of demographic and environmental variability (Fig. S-8). Moreover, our future projections require extrapolation to warmer or colder conditions than observed in our experiment and subsequently should be interpreted with caution (Chen et al., 2024). Despite all these limitations, the qualitative implications of a negative response of species to increase temperature (dormant and growing season) seems consistent across all GCMs. Most of the suitable areas move toward the North of the current range in response to climate change. Climate change will affect population growth rate primarily through the response of female which is more sensitive to climate change (Miller and Compagnoni, 2022b). Males also have a significant contribution to population growth rate particularly for temperature. Our work suggest that current climate may not affect population viability, but populations may be impacted negatively over the next decades in response to a climate change. This is key because most conservation actions are design from data on current responses to climate, rather than future response to climate (Sletvold et al., 2013). Moreover, management strategies that focus on both sex would be effective and will enhance population growth rate in response to global warming.

Conclusion

We have investigated the potential consequence of skewness in sex ratio on population dynamics and range shift in the context of climate change. We found that future climate will affect population growth rate at the center of species range. This reduction in population growth rate will induce a range shift to the northern edge of the species current range. Our results also suggest that tracking only one sex could lead to an overestimation of the effect of climate change on population dynamics. Our work provides a framework for predicting the impact of global warming on species using population demography.

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Supporting Information

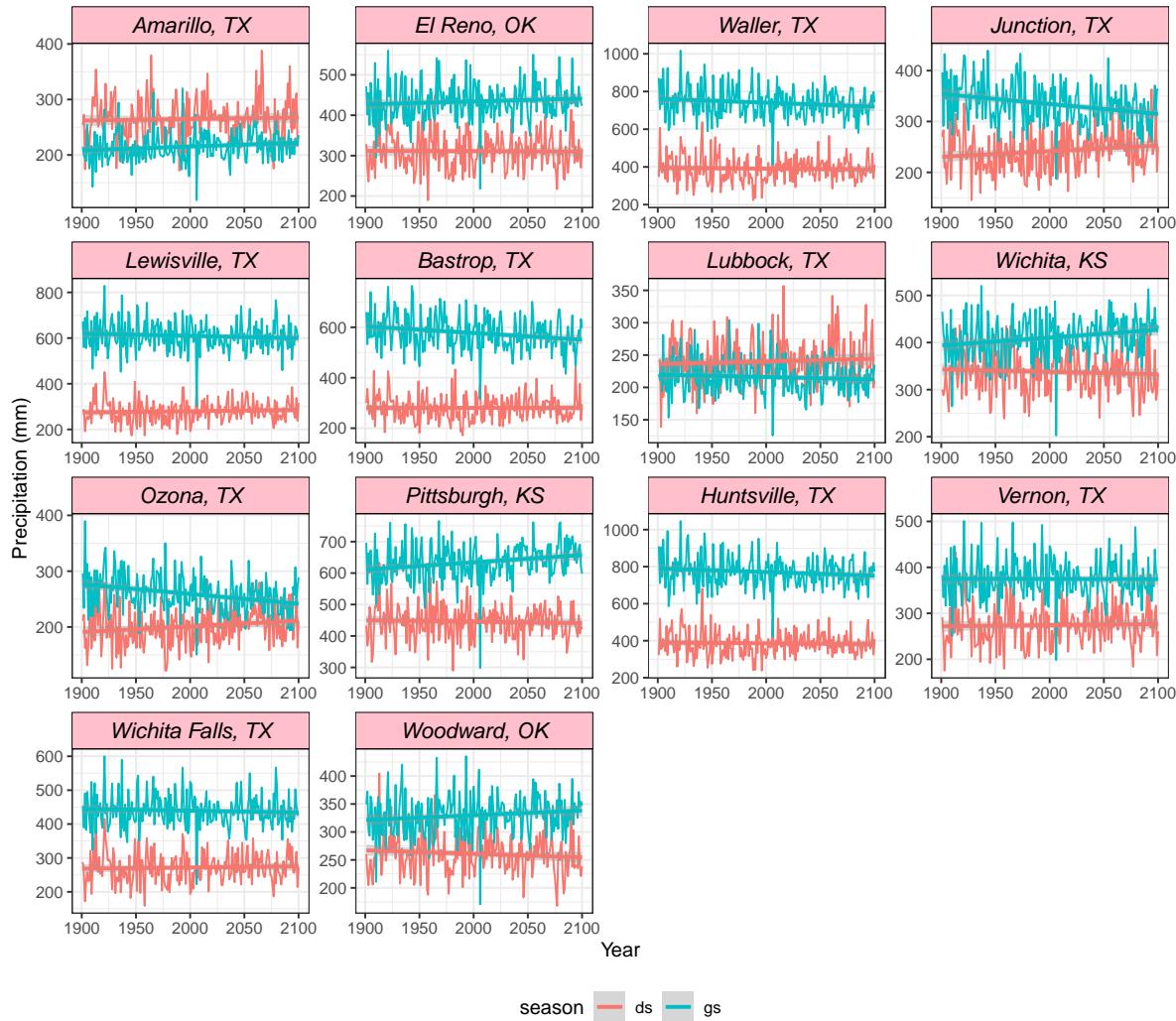


Figure S-1: Precipitation variation across the study sites from 1990 to 2100. ds:Dormant season, dg:Growing season.

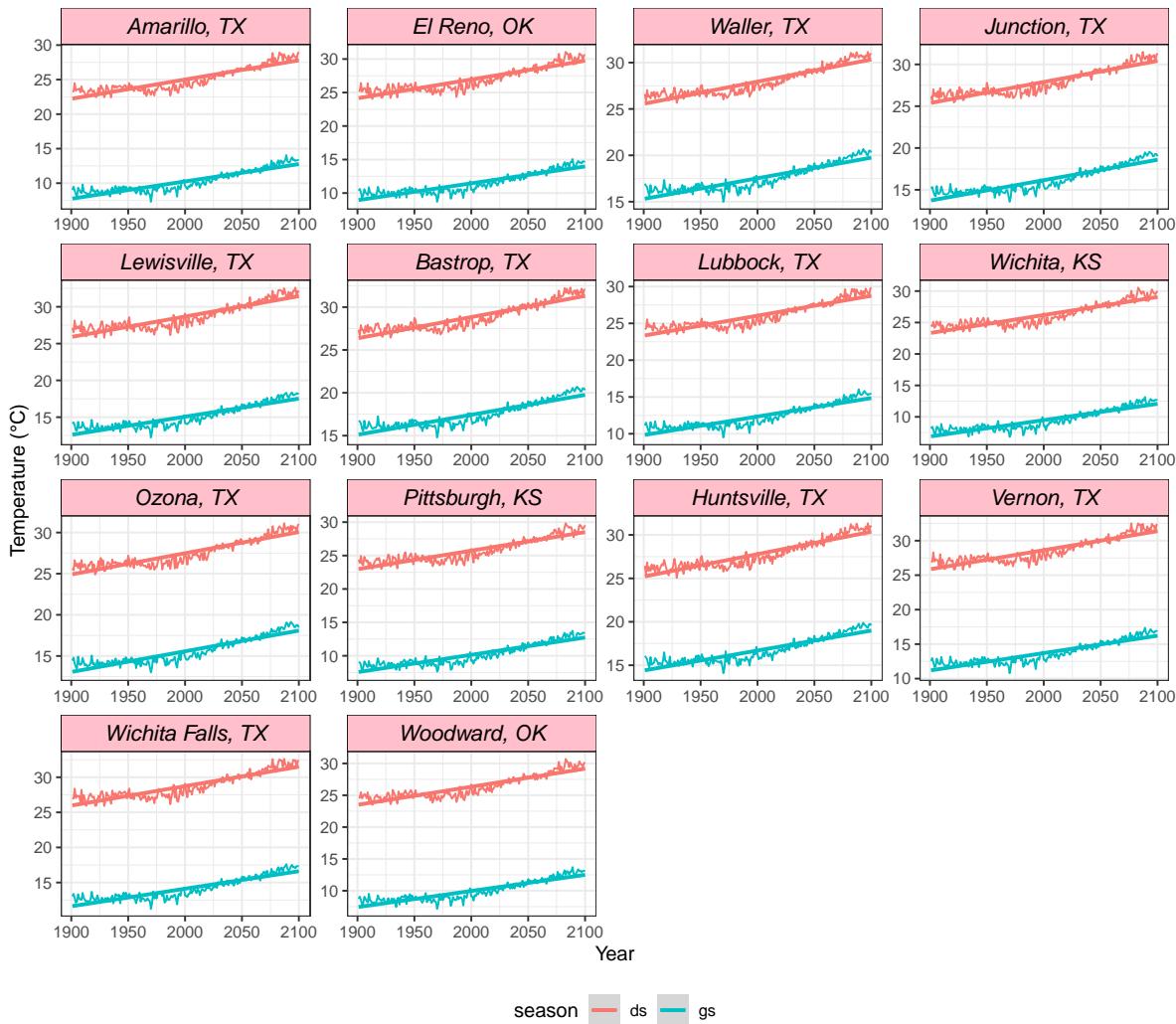


Figure S-2: Temperature variation accross the study sites from 1990 to 2100, ds: Dormant season, dg: Growing season.

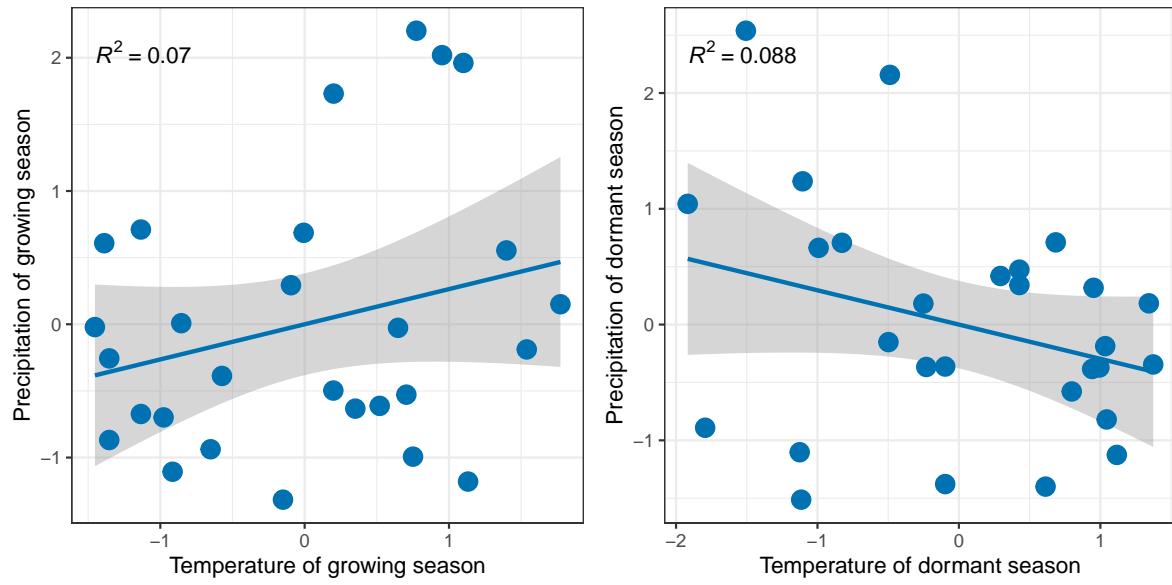


Figure S-3: Relation between precipitation and temperature for each season (growing and dormant). R^2 indicates the value of proportion of explained variance between the temperature and precipitation

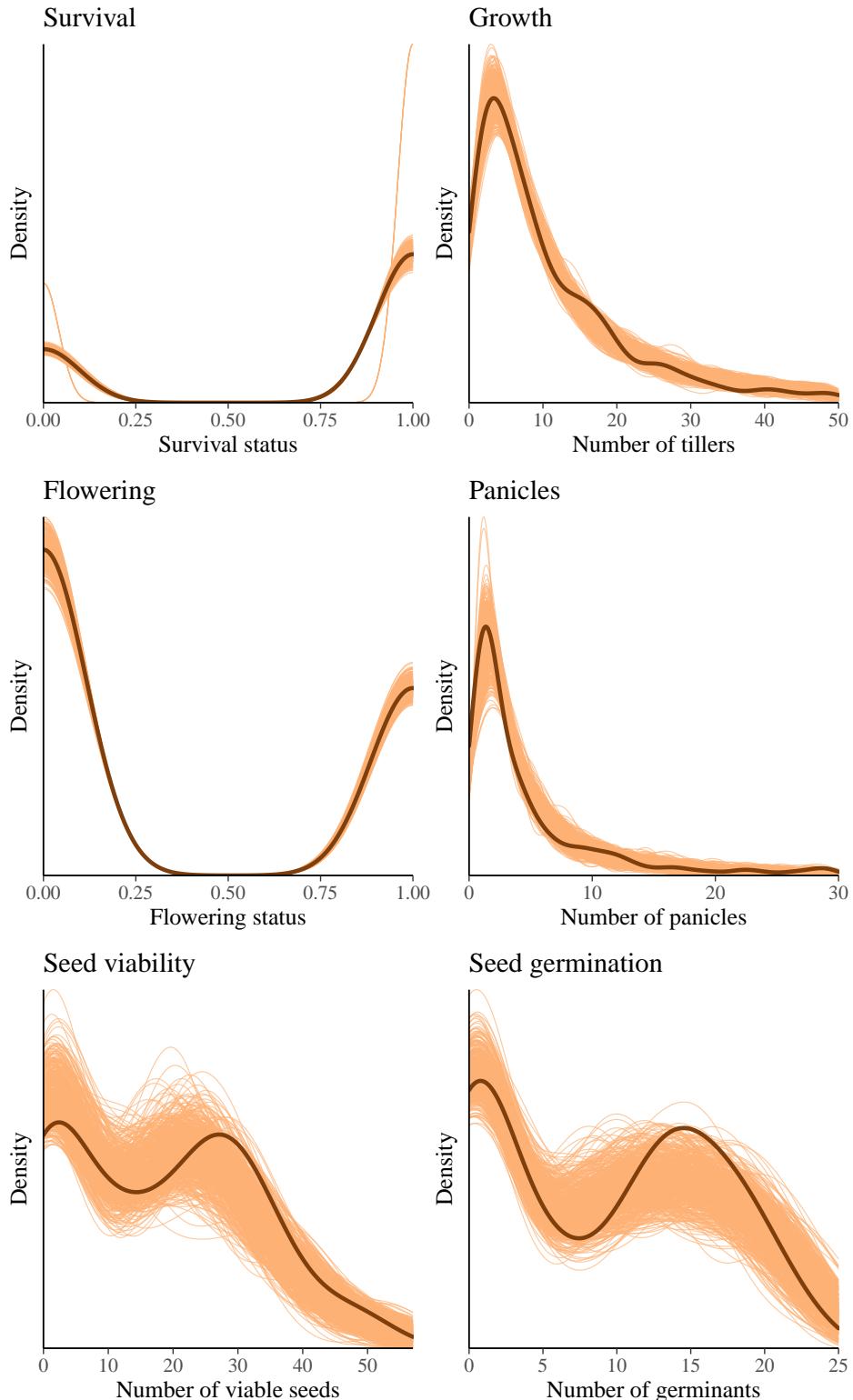


Figure S-4: Posterior predictive checks. Consistency between real data and simulated values suggests that the fitted model accurately describes the data. Graph shows density curves for the observed data (light blue) along with the simulated values (dark blue). The first column shows the linear models and the second column shows the 2 degree polynomial models.

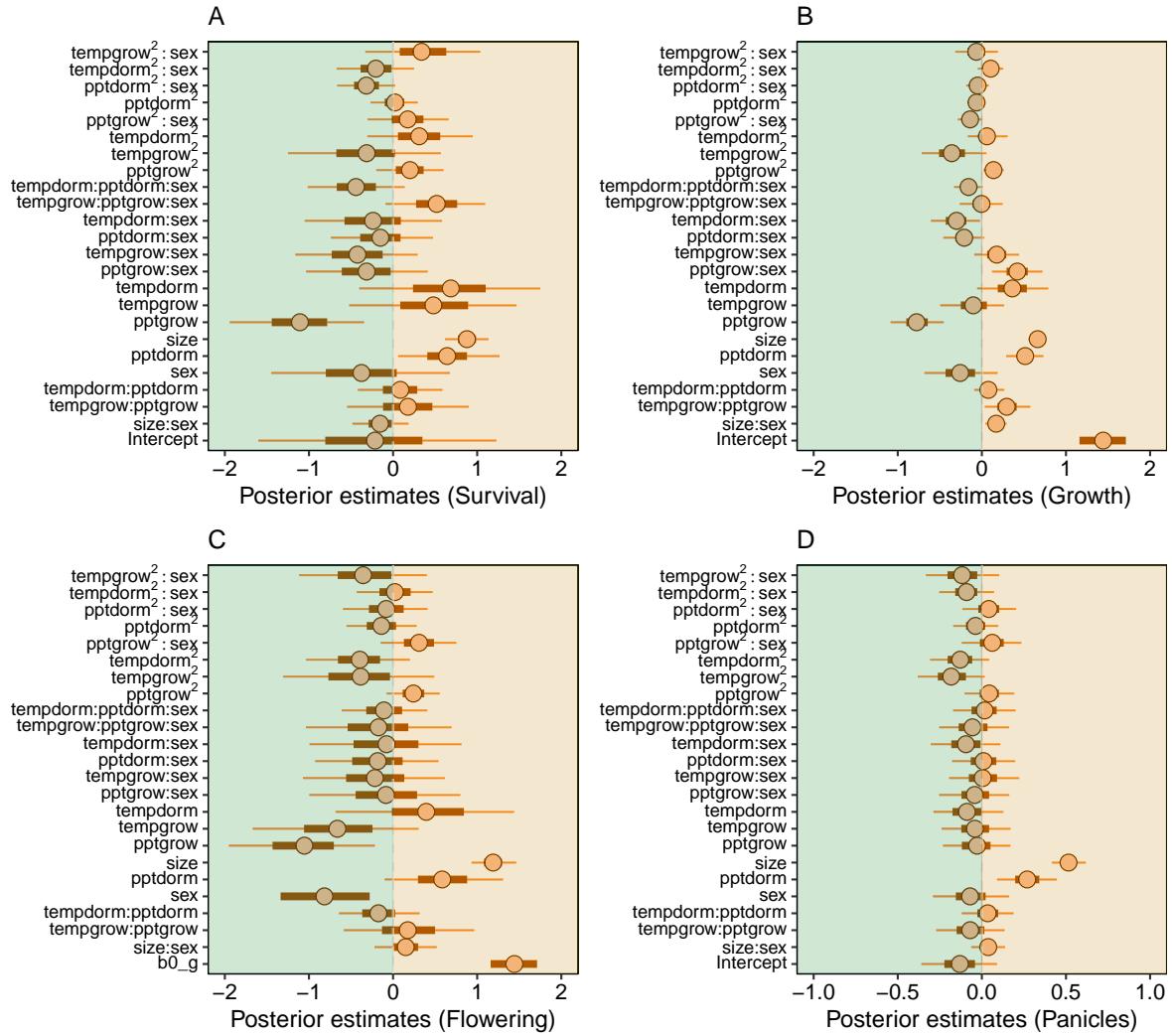


Figure S-5: Mean parameter values and 95% credible intervals for all vital rates. pptgrow is the precipitation of growing season, Tempgrow is the temperature of growing season, pptdorm is the temperature of dormant season, Tempdorm is the temperature of dormant season.

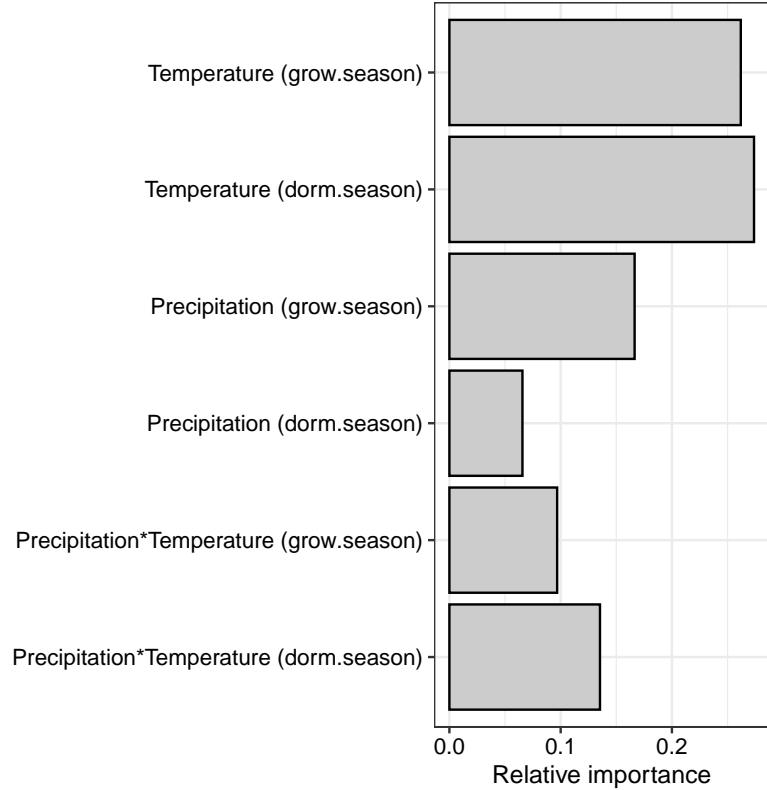


Figure S-6: Life Table Response Experiment: The bar represent the relative importance of each predictors

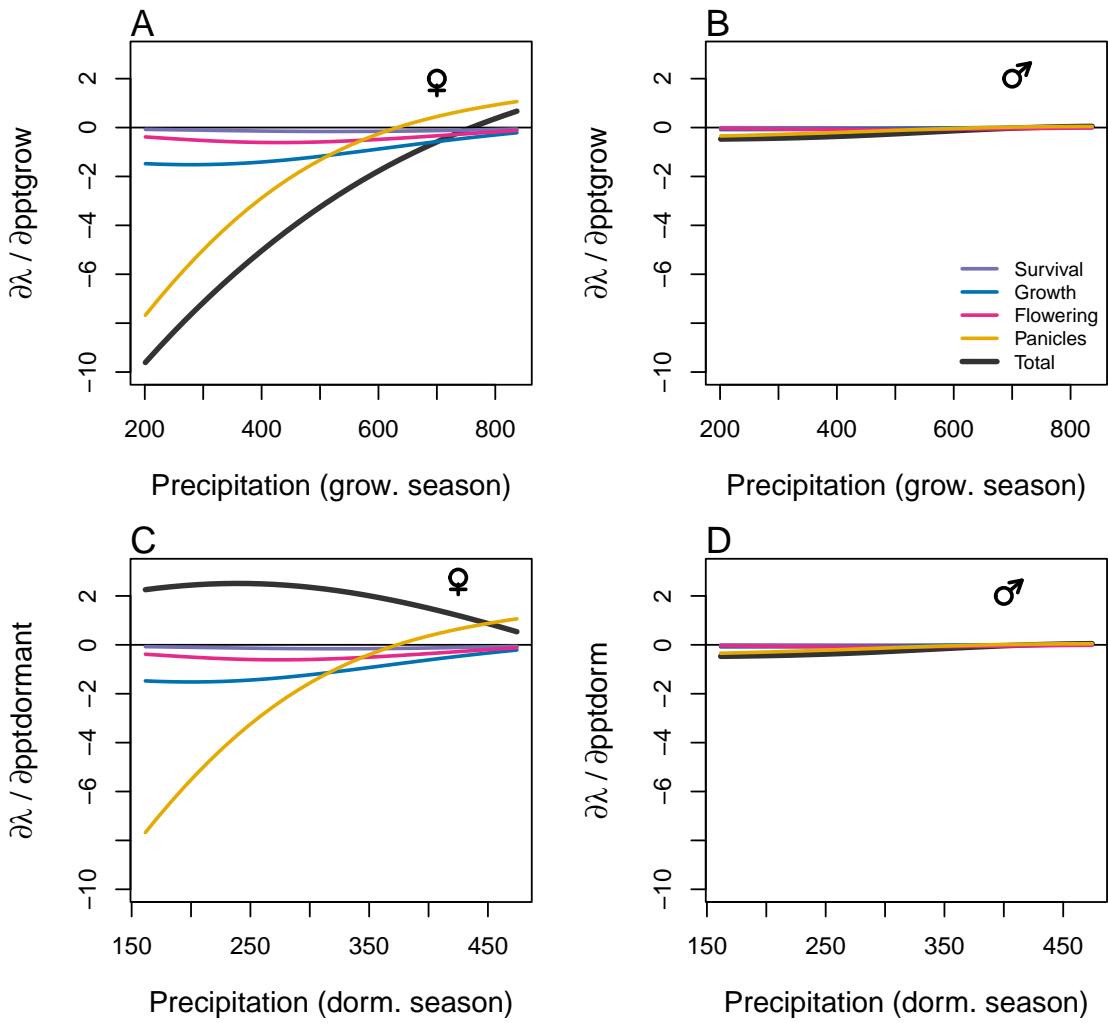


Figure S-7: Life table response experiment decomposition of the sensitivity of λ to seasonal climate into additive vital rate contributions of males and females based on posterior mean parameter estimates. (A) Precipitation of growing season (contribution of female), (B) Precipitation of growing season (contribution of male), (C) Precipitation of dormant season (contribution of female) and (D) Precipitation of dormant season (contribution of male).

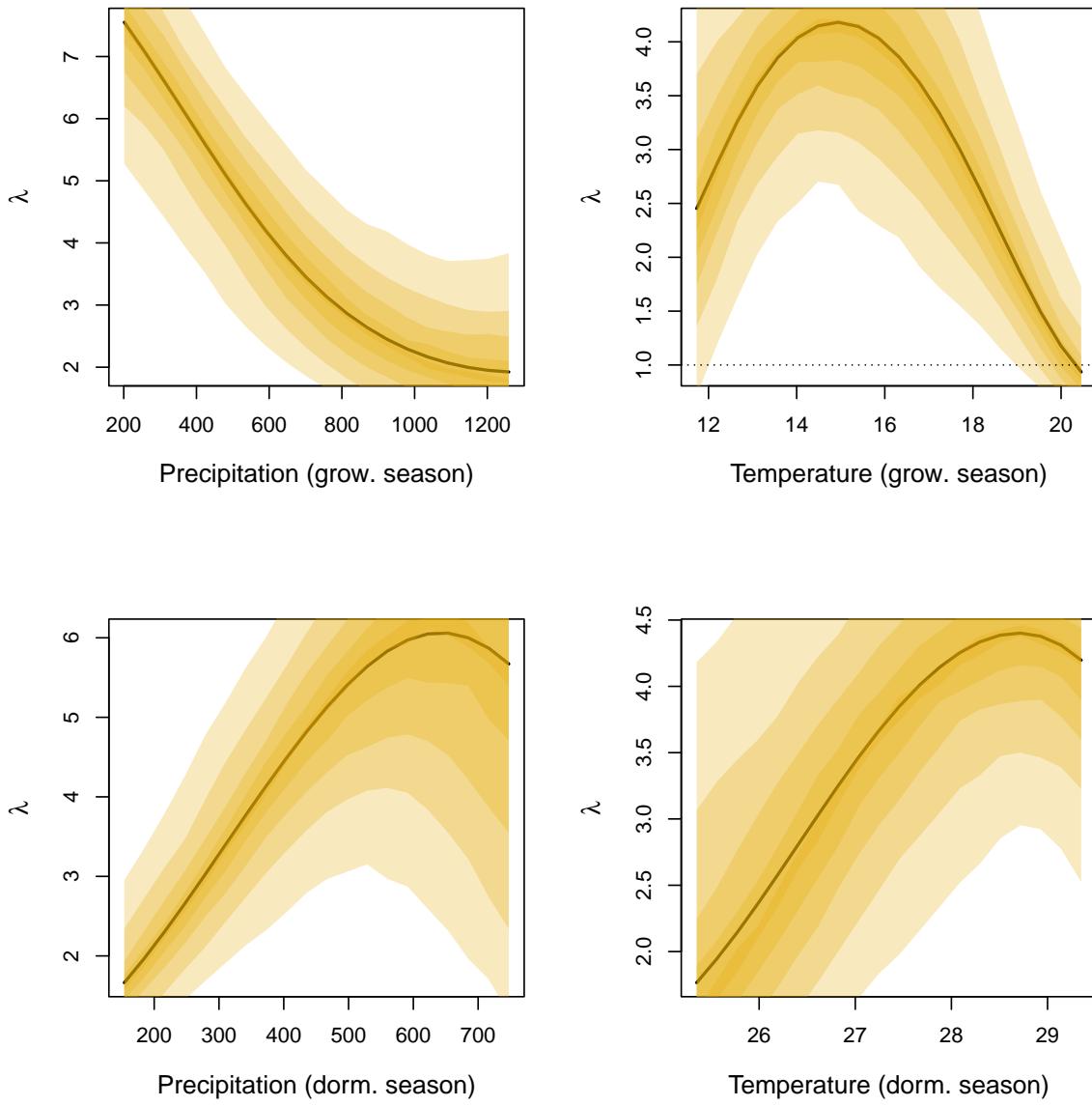


Figure S-8: Population growth rate (λ) as a function of seasonal climate (2015-2017), predicted by the two-sex matrix projection model that incorporates sex-specific demographic responses to climate with sex ratio-dependent seed fertilization. We show the mean posterior distribution of λ in solid lines, and the 5, 25, 50, 75, and 95% percentiles of parameter uncertainty in shaded gold color. The dashed horizontal line indicates the limit of population viability ($\lambda = 1$)

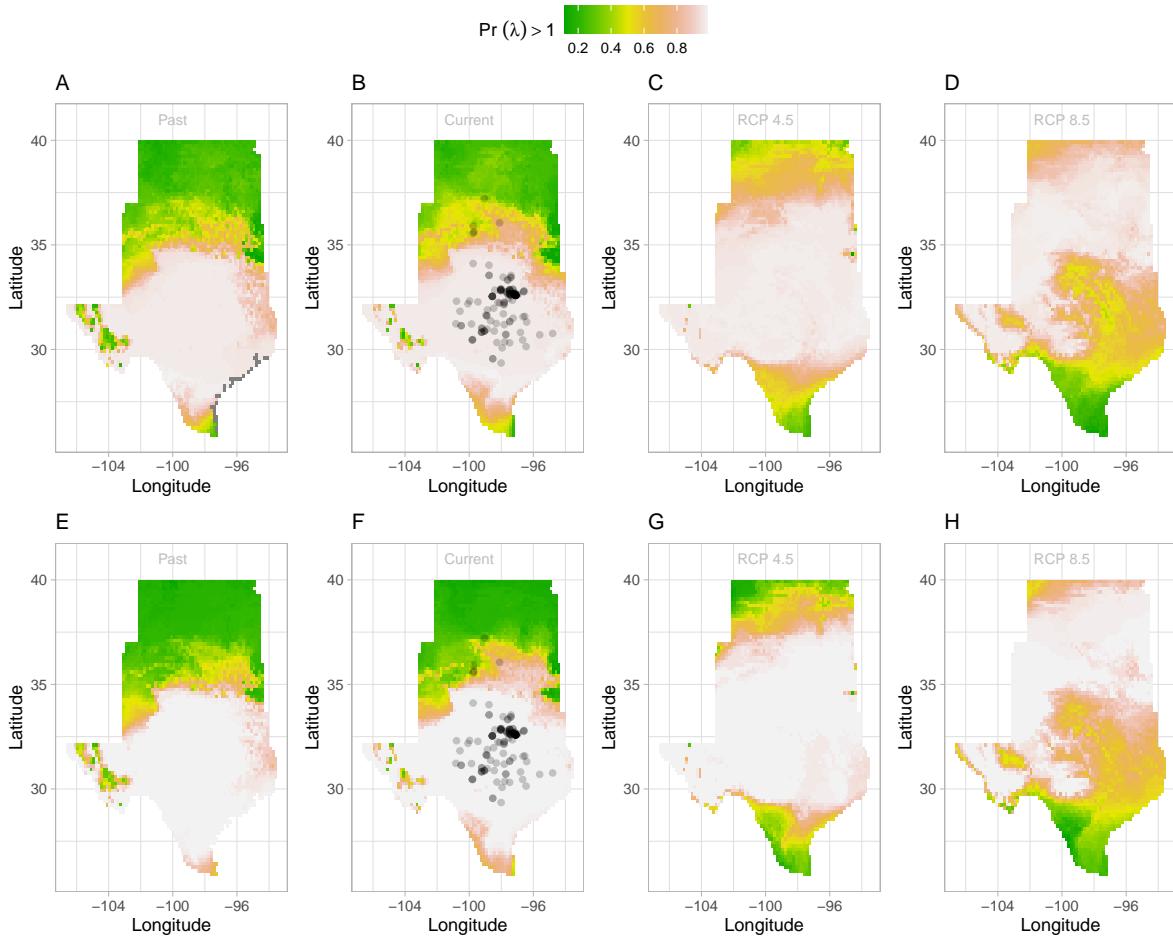


Figure S-9: Climate change favors range shift toward the North edge of the current range. (A) Past, (B) Current, (C and D) Future predicted range shift based on the predicted probabilities of self-sustaining populations, $\text{Pr}(\lambda > 1)$, using the two-sex model that incorporates sex-specific demographic responses to climate with sex ratio dependent seed fertilization. (E) Past, (F) Current, (G and H) Future predicted range shift based on the predicted probabilities of self-sustaining populations, $\text{Pr}(\lambda > 1)$, using the female dominant model. Future projections were based on the CESM1-BGC model. The black dots on panel B and F indicate all known presence points collected from GBIF from 1990 to 2019, which corresponds to the current condition in our prediction. The occurrences of GBIFs are distributed in with higher population fitness habitat $\text{Pr}(\lambda > 1)$, confirming that our study approach can reasonably predict range shifts.

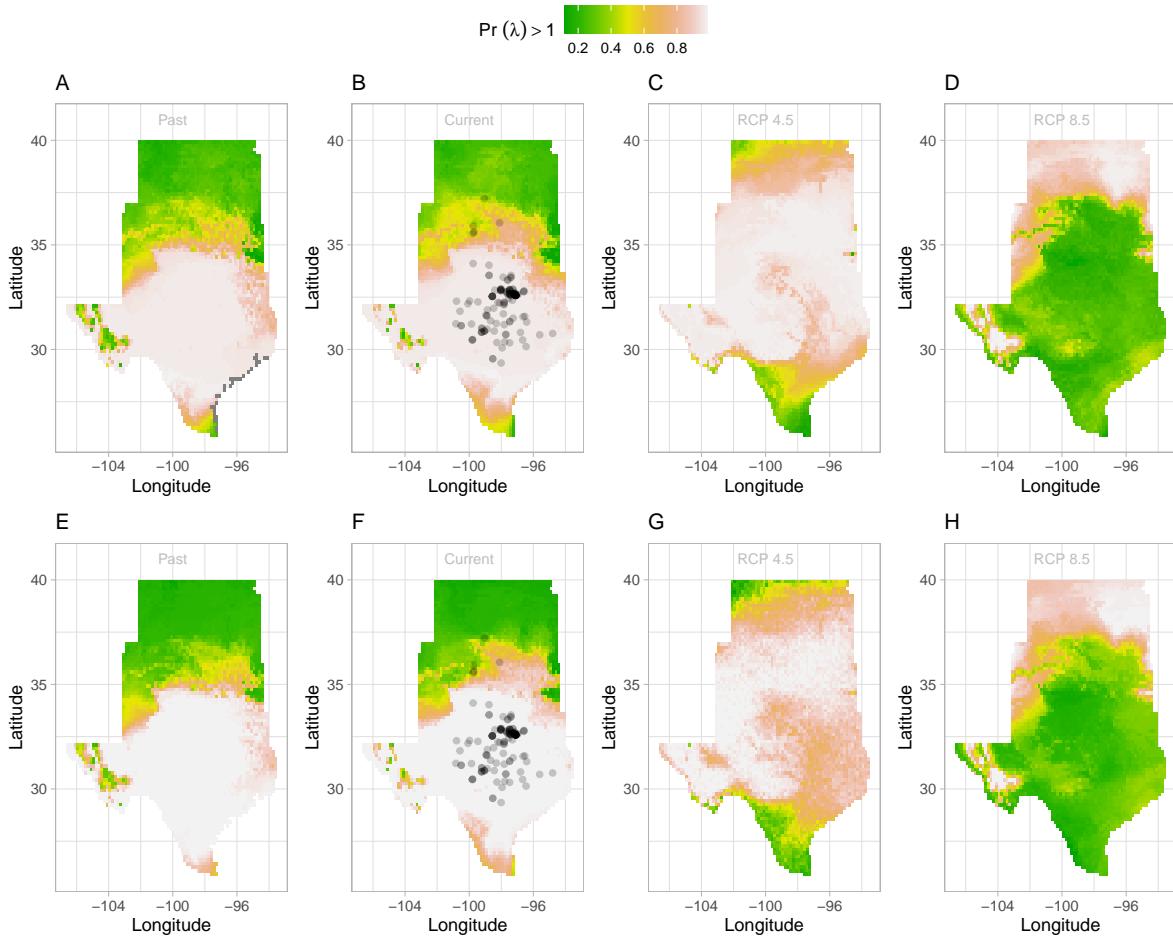


Figure S-10: Climate change favors range shift toward the North edge of the current range. (A) Past, (B) Current, (C and D) Future predicted range shift based on the predicted probabilities of self-sustaining populations, $\text{Pr}(\lambda > 1)$, using the two-sex model that incorporates sex-specific demographic responses to climate with sex ratio dependent seed fertilization. (E) Past, (F) Current, (G and H) Future predicted range shift based on the predicted probabilities of self-sustaining populations, $\text{Pr}(\lambda > 1)$, using the female dominant model. Future projections were based on the CMCC-CM model. The black dots on panel B and F indicate all known presence points collected from GBIF from 1990 to 2019, which corresponds to the current condition in our prediction. The occurrences of GBIFs are distributed in with higher population fitness habitat $\text{Pr}(\lambda > 1)$, confirming that our study approach can reasonably predict range shifts.

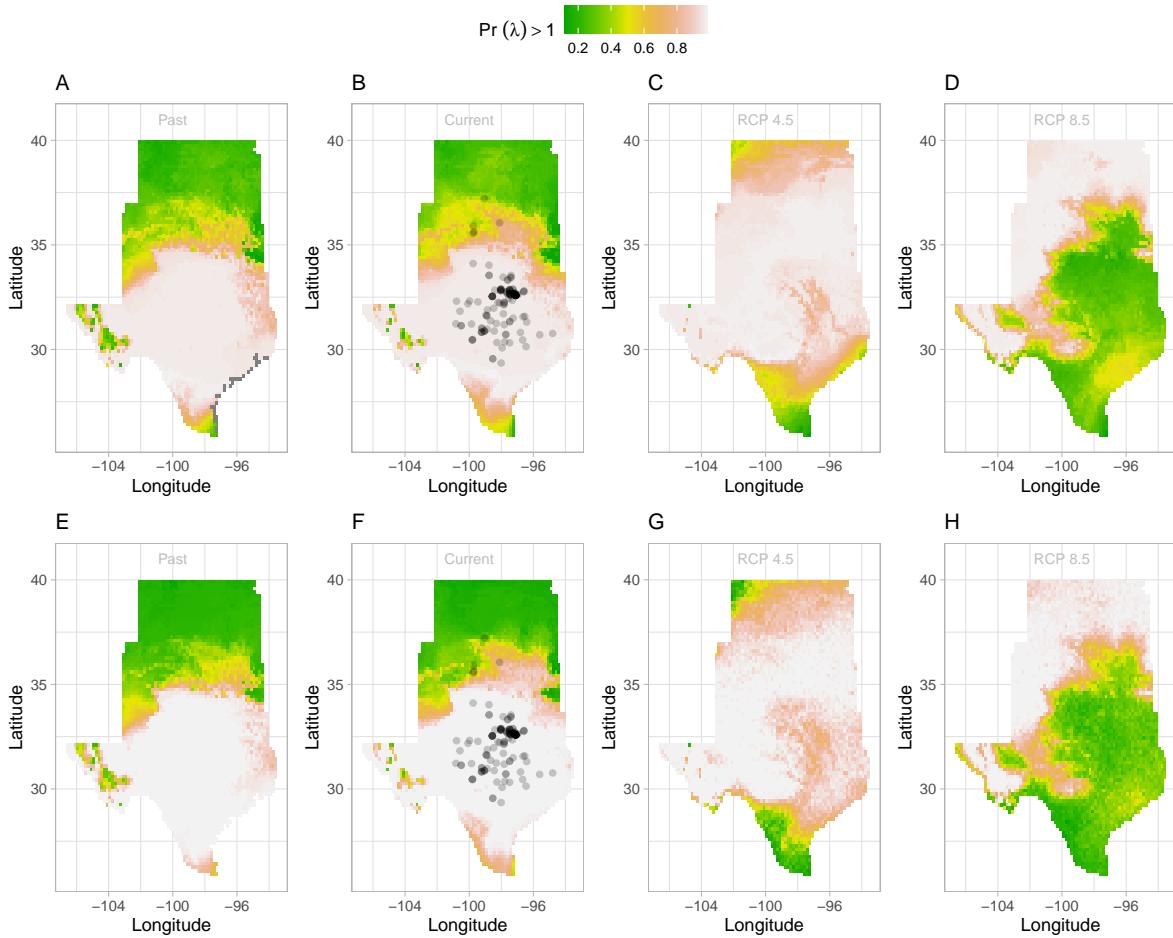


Figure S-11: Climate change favors range shift toward the North edge of the current range. (A) Past, (B) Current, (C and D) Future predicted range shift based on the predicted probabilities of self-sustaining populations, $\text{Pr}(\lambda > 1)$, using the two-sex model that incorporates sex-specific demographic responses to climate with sex ratio dependent seed fertilization. (E) Past, (F) Current, (G and H) Future predicted range shift based on the predicted probabilities of self-sustaining populations, $\text{Pr}(\lambda > 1)$, using the female dominant model. Future projections were based on the MIROC5 model. The black dots on panel B and F indicate all known presence points collected from GBIF from 1990 to 2019, which corresponds to the current condition in our prediction. The occurrences of GBIFs are distributed in with higher population fitness habitat $\text{Pr}(\lambda > 1)$, confirming that our study approach can reasonably predict range shifts.

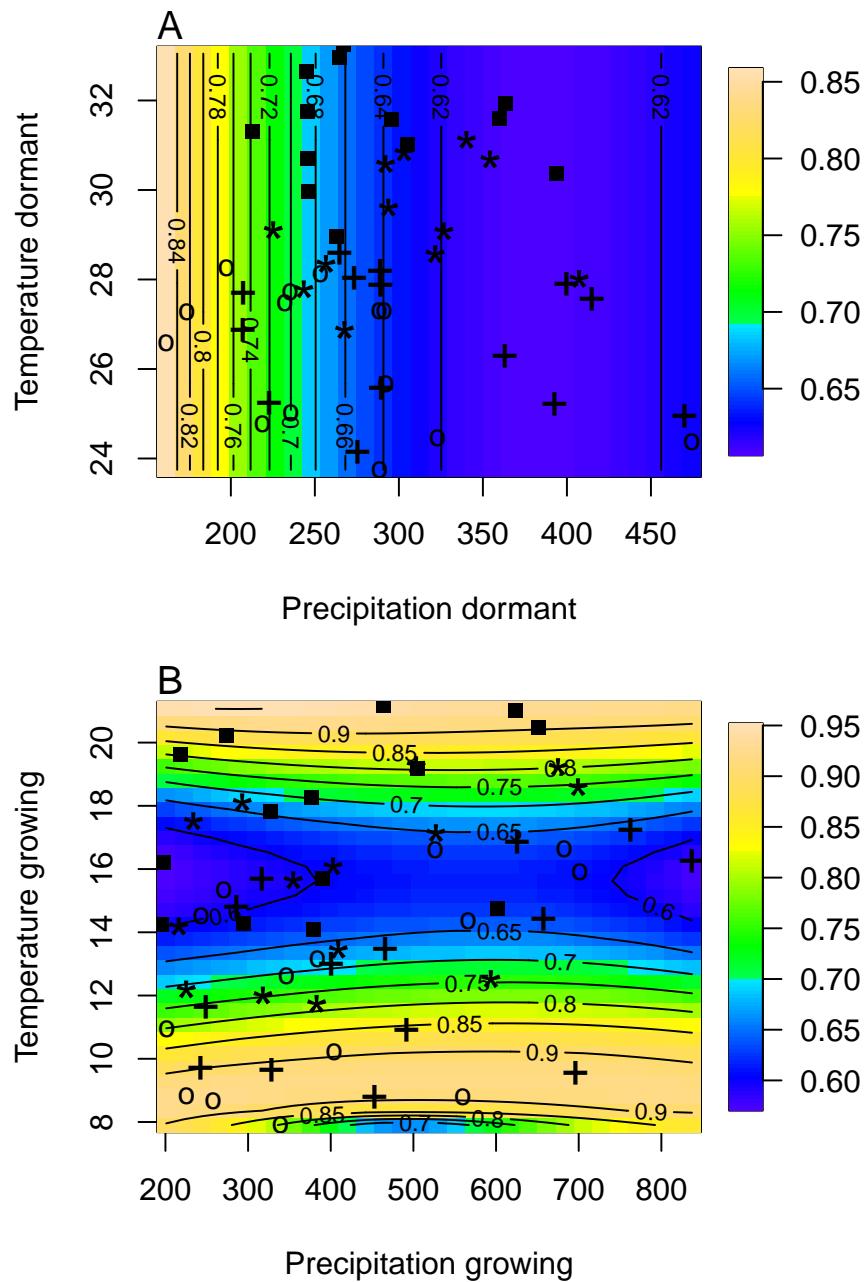


Figure S-12: A two-dimensional representation of the Operational Sex Ratio (OSR) over time (past, present and future climate conditions). OSR represents the proportion of females. Contours show predicted values of OSR conditional on precipitation and temperature of the dormant and growing season. Operational Sex Ratio during the dormant season for the two sex model (A), Operational Sex Ratio during the growing season for the two sex model (B). "o": Past, "+": Current, "*": RCP 4.5, "■": RCP 8.5.