

Forecasting range shifts of a dioecious plant species under climate change

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Abstract:

Main Text:

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¹ Abstract

² Global warming has triggered an urgent need for predicting the reorganization of Earth's
³ biodiversity under climate change. Currently, the vast majority of theory and models in
⁴ population biology, including those used to forecast biodiversity responses to climate change,
⁵ ignore the complication of sex structure. We developed demographic models of range
⁶ limitation, parameterized from geographically distributed common garden experiments
⁷ with females and males of a dioecious grass species (*Poa arachnifera*) throughout and beyond
⁸ its range in the south-central U.S. Female-dominant and two-sex model versions of the
⁹ demographic model both predict that future climate change will alter population viability
¹⁰ and will induce latitudinal niche extension beyond current northern limits. However, the
¹¹ magnitude of niche shift was underestimated by the female-dominant model, because females
¹² have broader temperature tolerance than males and become mate-limited under female-biased
¹³ sex ratios. Explicitly account for both sexes could enhance population viability forecasts and
¹⁴ conservation planning for dioecious species in response to climate change.

¹⁵ Introduction

¹⁶ Rising temperatures and extreme drought events associated with global climate change are
¹⁷ leading to increased concern about how species will become redistributed across the globe
¹⁸ under future climate conditions (Bertrand et al., 2011; Gamelon et al., 2017; Smith et al., 2024).
¹⁹ Dioecious species (most animals and ca. 7% of plant species) might be particularly vulnerable
²⁰ to the influence of climate change because they often display skewed sex ratios that are gen-
²¹ erated or reinforced by sexual niche differentiation (distinct responses of females and males
²² to shared climate drivers) (Tognetti, 2012). Accounting for such a niche differentiation within
²³ a population is a long-standing challenge in accurately predicting which sex will successfully
²⁴ track environmental change and how this will impact population viability and range shifts
²⁵ (Gissi et al., 2023; Jones et al., 1999). The vast majority of theory and models in population
²⁶ biology, including those used to forecast biodiversity responses to climate change, **ignore the**
²⁷ **complication of sex structure**¹ (but Ellis et al., 2017; Gissi et al., 2024; Pottier et al., 2021). Tra-
²⁸ ditional approaches in population biology instead focus exclusively on females, assuming that
²⁹ males are in sufficient supply as to never limit female fertility (Miller and Inouye, 2011). As a
³⁰ result, forecasts of colonization-extinction dynamics for dioecious species under future climate
³¹ change that explicitly account for females, males, and their inter-dependence are limited.

³² Species's range limits, when not driven by dispersal limitation, should generally reflect
³³ the limits of the ecological niche (Lee-Yaw et al., 2016). Niches and geographic ranges are
³⁴ often limited by climatic factors including temperature and precipitation (Sexton et al., 2009).
³⁵ Therefore, any substantial changes in the magnitude of these climatic factors in a given location
³⁶ across the range could impact population viability, with implications for range expansions
³⁷ or contractions based on which regions become more or less suitable (Davis and Shaw,
³⁸ 2001; Pease et al., 1989). Forecasting range shifts for dioecious species is complicated by the
³⁹ potential for each sex to respond differently to climate variation (Hultine et al., 2016; Morrison
⁴⁰ et al., 2016; Pottier et al., 2021). Populations in which males are rare under current climatic
⁴¹ conditions could experience low reproductive success due to sperm or pollen limitation that
⁴² may lead to population decline in response to climate change that disproportionately favors
⁴³ females (Eberhart-Phillips et al., 2017). In contrast, climate change could expand male habitat
⁴⁴ suitability (e.g. upslope movement), which might increases seed set for pollen-limited females
⁴⁵ and favor range expansion (Petry et al., 2016). Although the response of species to climate
⁴⁶ warming is an urgent and active area of research, few studies have disentangled the interaction

¹*These are examples of studies accounting for sex structure. I added "but" before the citation*

47 between sex and climate drivers to understand their combined effects on population dynamics
48 and range shifts, despite calls for such an approach (hultine2016climate,gissi2023exploring).

49 Tracking the impact of climate change on population growth rate (λ) and range or niche
50 limits of dioecious taxa depends on our ability to build mechanistic models that take into ac-
51 count the spatial and temporal context in which sex specific response to climate change affects
52 population viability (Czachura and Miller, 2020; Davis and Shaw, 2001; Evans et al., 2016).
53 Structured population models built from demographic data collected from geographically dis-
54 tributed observations or common garden experiments provide several advantages for studying
55 the impact of climate change on species' range shifts (Merow et al., 2017; Schultz et al., 2022;
56 Schwinnning et al., 2022). First, demographic models link individual-level life history events
57 (mortality, development, and regeneration) to population demography, allowing the investiga-
58 tion of factors explaining vital rate responses to environmental drivers (Dahlgren et al., 2016;
59 Ehrlén and Morris, 2015; Louthan et al., 2022). Second, demographic models have a natural in-
60 terface with experimental treatments that can isolate spatial and temporal correlations between
61 environmental factors, thus overcoming a main disadvantage with many types of correlative
62 studies (Leicht-Young et al., 2007). Third, demographic models using Markov Chain Monte
63 Carlo (MCMC) can be utilized to infer species niche which is defined as the range of resources
64 and conditions allowing its populations of self-sustaining populations, conditional on different
65 factors of the environment (Diez et al., 2014; Hutchinson et al., 1978; Maguire Jr, 1973)². Finally,
66 structured demographic models can be used to identify which aspect of climate is more
67 important for population dynamics. For example, Life Table Response Experiments (LTRE)
68 built from structured models have become widely used to understand the relative importance
69 of covariates in explaining variation in population growth rate (Ellner et al., 2016; Hernández
70 et al., 2023). LTRE is also used to get a mechanistic understanding of how a given treatment
71 (eg, temperature or precipitation) could affect population dynamics through unique vital rate
72 responses (Caswell, 1989; Iler et al., 2019; Morrison and Hik, 2007; O'Connell et al., 2024).³

73 In this study, we used a mechanistic approach, combining geographically-distributed
74 field experiments, Bayesian statistical modeling, and two-sex population projection modeling,
75 to understand the demographic response of dioecious species to climate change and its
76 implications for past, present, and future range dynamics. Our work focused on the dioecious
77 grass species Texas bluegrass (*Poa arachnifera*), which is distributed along environmental
78 gradients in the south-central U.S. corresponding to variation in temperature across latitude
79 and precipitation across longitude. Moreover, the south-central U.S. has experienced an

²I added the niche part in the introduction as you suggested

³Yes I don't want to get distracted by SDMs. The story is still interesting without bashing the SDMs studies. That being said, I showed the advantage of using demographic models over traditional correlative approaches. Line 59-62)

increase of temperature since the 20th century and this is very likely to continue over the next years (Figure S-1). ⁴ Our previous study showed that, despite a differentiation of climatic niche between sexes, the female niche mattered the most in driving the environmental limits of population viability across longitude (Miller and Compagnoni, 2022b). However, that study used a single proxy variable (longitude) to represent environmental variation related to aridity. Developing a rigorous forecast for the implications of future climate change requires that we transition from climate-implicit to climate-explicit treatment of environmental drivers as we do here. Here, we asked four **questions**⁵:

1. What are the sex-specific vital rate responses to variation in temperature and precipitation across the species' range ?
2. How do sex-specific vital rates combine to determine the influence of climate variation on population growth rate (λ) ?
3. What is the impact of climate change on sex ratio ?
4. What are the historical and projected dynamics of the Texas bluegrass geographic niche and how does accounting for sex structure modify these predictions?

Materials and methods

Study species

Texas bluegrass (*Poa arachnifera*) is a dioecious perennial, summer-dormant cool-season (C3) grass that occurs in the south-central U.S. (Texas, Oklahoma, and southern Kansas) (Figure 1) (Hitchcock, 1971)⁶. Latitudinal limits of the Texas bluegrass distribution span 7.74 °C to 16.94 °C of temperature during the dormant season and 24.38 °C to 28.80 °C during the dormant season. Longitudinal limits span 244.9 mm to 901.5 mm of precipitation during the growing season and 156.3 mm to 373.3 mm. Texas bluegrass grows between October and May (growing season), with onset of dormancy often from June to September (dormant season) (Kindiger, 2004).

Biological sex in Texas bluegrass is genetically based and the birth (seed) sex ratio is 1:1 (Renganayaki et al., 2005). Females and males are morphologically indistinguishable except for their inflorescences. Flowering occurs in May and the species is wind pollinated (Hitchcock, 1971). Surveys of 22 natural populations throughout the species' distribution indicated that operational sex ratio (the female fraction of flowering plants) ranged from 0.007 to 0.986 with a mean of 0.404 (Miller and Compagnoni, 2022b).

⁴I added some context about climate change in this study region

⁵I changed the order of the questions and added a new question that will add value to our paper.

⁶I have updated the map

110 **Common garden experiment**

111 We set up a common garden experiment throughout and beyond the range of Texas bluegrass
112 to quantify sex-specific demographic responses to climate. Details of the experimental design
113 are provided in Miller and Compagnoni (2022b); we provide a brief overview here. The
114 experiment was installed at 14 sites throughout and, in some cases, beyond the species'
115 natural range (Figure 1). At each site, we established 14 blocks. For each block we planted
116 the same number of plant from each sex (three female and three male individuals) that
117 were clonally propagated from females and males from eight natural source populations
118 (Figure 1); because sex is genetically-based, clones never deviated from their expected sex.
119 The experiment was established in November 2013 and was censused in May of 2014, 2015,
120 and 2016. At each census, we collected individual demographic data including survival (alive
121 or dead), size (number of tillers), and number of panicles (reproductive inflorescences). For
122 the analyses that follow, we focus on the 2014-15 and 2015-16 transitions years, since the start
123 of the experiment did not include the full 2013-14 transition year.

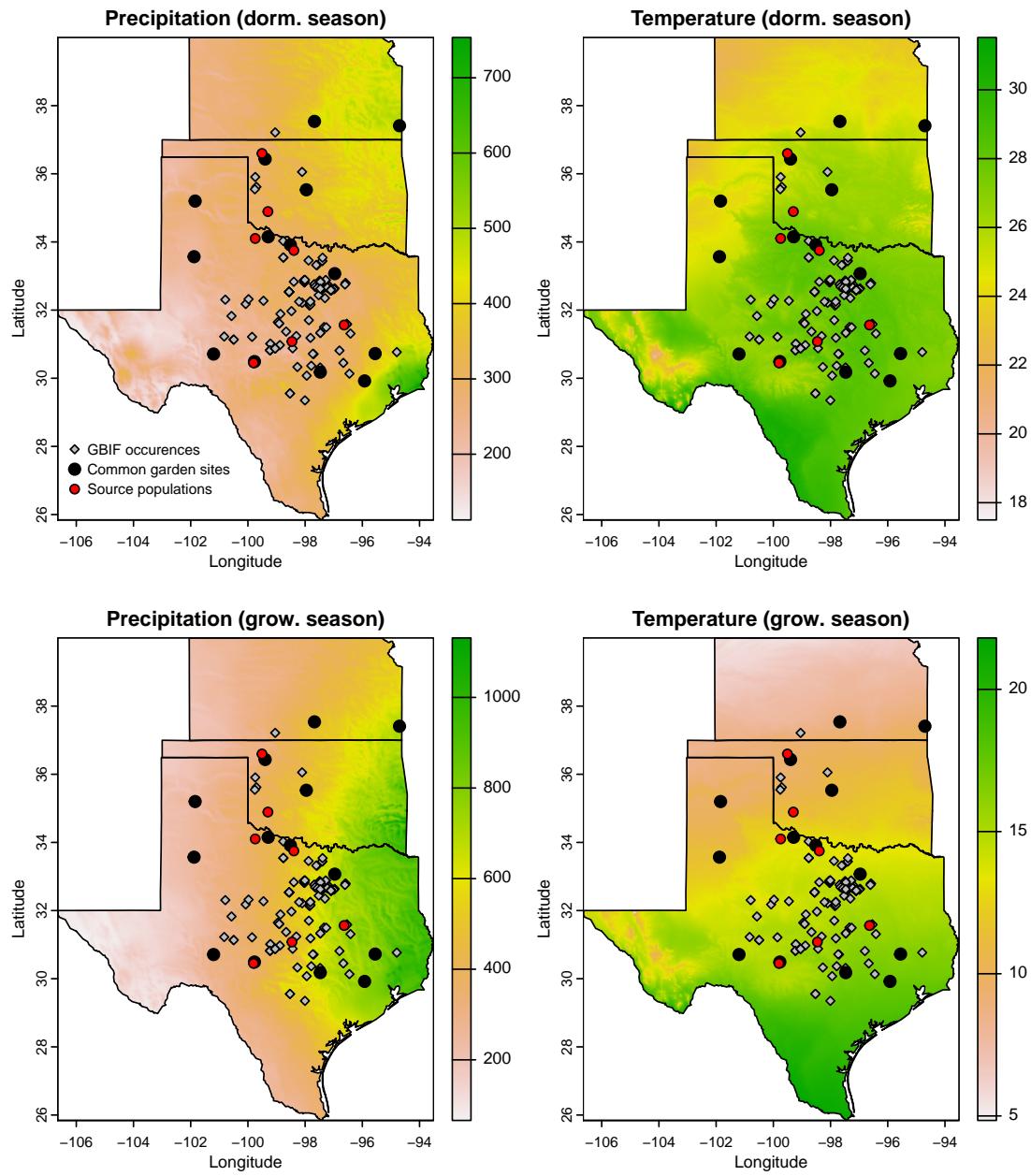


Figure 1: Maps of 30-year (1990-2019) normal climate and study sites used for demographic monitoring of *Poa arachnifera* in Texas, Kansas and Oklahoma in the United States. Precipitation of growing and precipitation of dormant season are in mm, temperature of the dormant and temperature of growing season are 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). See also (Figure S-1, Figure S-2) for more details about climate variation across the study sites since the beginning of last century.

¹²⁴ **Climatic data collection**

¹²⁵ We gathered downscaled monthly temperature and precipitation for each site from Chelsa
¹²⁶ to describe observed climate conditions during our study period (Karger et al., 2017). These
¹²⁷ climate data were used as covariates in vital rate regressions. We aligned the climatic years to
¹²⁸ match demographic transition years (June 1 – May 31) rather than calendar years. Based on the
¹²⁹ natural history of this summer-dormant cool-season species, we divided each transition year
¹³⁰ into dormant (June 1 through September 30) and growing (October 1 through May 31) seasons.

¹³¹ To back-cast and forecast demographic responses to changes in climate throughout the
¹³² study region, we downloaded projection data for three 30-year periods: “past” (1901-1930),
¹³³ “current” (1990-2019) and “future” (2070-2100). Data for future climatic periods were
¹³⁴ downloaded from four general circulation models (GCMs) selected from the Coupled Model
¹³⁵ Intercomparison Project Phase 5 (CMIP5). The GCMs are: Model for Interdisciplinary
¹³⁶ Research on Climate (MIROC5), Australian Community Climate and Earth System Simulator
¹³⁷ (ACCESS1-3), Community Earth System Model (CESM1-BGC), Centro Euro-Mediterraneo sui
¹³⁸ Cambiamenti Climatici Climate Model (CMCC-CM). All the GCMs were also downloaded
¹³⁹ from chelsa (Sanderson et al., 2015). We evaluated future climate projections from two
¹⁴⁰ scenarios of representative concentration pathways (RCPs): RCP4.5, an intermediate-to-
¹⁴¹ pessimistic scenario assuming a radiative forcing amounting to 4.5 Wm^{-2} by 2100, and
¹⁴² RCP8.5, a pessimistic emission scenario which projects a radiative forcing of 8.5 Wm^{-2} by
¹⁴³ 2100 (Schwalm et al., 2020; Thomson et al., 2011).

¹⁴⁴ Projection data for the three 30-year periods had warmer or colder conditions than
¹⁴⁵ observed in our experiment (Figure S-3, Figure S-4, Figure S-5, Figure S-6). However, the
¹⁴⁶ observed period was substantially wetter and cooler across the study region than 2015-16,
¹⁴⁷ especially during the growing season (Figure S-7), so our study design provides both spatial
¹⁴⁸ and inter-annual coverage of climate variables.

¹⁴⁹ **Sex specific demographic responses to climate**

¹⁵⁰ ⁷ We used individual level measurements of survival, growth (number of tillers), flowering,
¹⁵¹ number of panicles to develop Bayesian linear mixed effect models describing how each
¹⁵² vital rate varies as a function of sex, size, and four climate covariates (precipitation and
¹⁵³ temperature of growing and dormant season). We kept the four climate covariates in the
¹⁵⁴ mixed effect models because each climatic variable describes different aspect of climate
¹⁵⁵ that could be important for the species persistence across its range. Vital rate models were

⁷ I have reduced the redundancy between the two paragraphs and added the biological rationale for the model. I hope that the explanation I added provided a clarification about why I did not use model selection.

156 fit with second-degree polynomial functions and with the same linear predictors for the
 157 expected value (μ)(Eq.1). The second-degree polynomial was included because we expected
 158 that climate would affect vital rates through a hump-shaped relationship assuming that (i)
 159 the center of the range is the optimum range for the species (ii) and climate sets limits on
 160 whether habitats will be suitable for the study species. We also included the interaction effect
 161 of temperature and precipitation for each season to understand the synergistic effect of both
 162 variables on population demography. We centered and standardized all climatic predictors
 163 to facilitate model convergence. Size (number of tillers) was on a natural logarithm scale.
 164

$$\begin{aligned}
 \mu = & \beta_0 + \beta_1 size + \beta_2 sex + \beta_3 pptgrow + \beta_4 pptdorm + \beta_5 tempgrow + \beta_6 tempdorm \\
 & + \beta_7 pptgrow * sex + \beta_8 pptdorm * sex + \beta_9 tempgrow * sex + \beta_{10} tempdorm * sex \\
 & + \beta_{11} size * sex + \beta_{12} pptgrow * tempgrow + \beta_{13} pptdorm * tempdorm \\
 & + \beta_{14} pptgrow * tempgrow * sex + \beta_{15} pptdorm * tempdorm * sex + \beta_{16} pptgrow^2 \\
 & + \beta_{17} pptdorm^2 + \beta_{18} tempgrow^2 + \beta_{19} tempdorm^2 + \beta_{20} pptgrow^2 * sex \\
 & + \beta_{21} pptdorm^2 * sex + \beta_{22} tempgrow^2 * sex + \beta_{23} tempdorm^2 * sex + \phi + \rho + \nu
 \end{aligned} \tag{1}$$

165 where β_0 is the grand mean intercept, β_1 is the size dependent slopes. *size* was on a natural
 166 logarithm scale. $\beta_2 \dots \beta_{13}$ represent the climate dependent slopes. $\beta_{14} \dots \beta_{23}$ represent the
 167 sex-climate interaction slopes. *pptgrow* is the precipitation of the growing season, *tempgrow*
 168 is the temperature of the growing season, *pptdorm* is the precipitation of the dormant season,
 169 *tempdorm* is the temperature of the dormant season.
 170

Different link function ($f(\mu)$) was applied depending on the the vital rate distributions.
 171 We modeled survival and flowering data with a Bernoulli distribution. We modeled the growth
 172 (tiller number) with a zero-truncated Poisson inverse Gaussian distribution. Fertility (panicle
 173 count) was model as zero-truncated negative binomial. Each vital rate model includes normally
 174 distributed random effects for block-to-block variation ($\phi \sim N(0, \sigma_{block})$) and source-to-source
 175 variation that is related to the provenence of the seeds used to establish the common garden
 176 ($\rho \sim N(0, \sigma_{source})$), site to site variation ($\nu \sim N(0, \sigma_{site})$). We fit survival, growth, flowering
 177 models with generic weakly informative priors for coefficients ($\mu = 0, \sigma = 1.5$) and variances
 178 ($\gamma[0.1, 0.1]$). We fit fertility model with regularizing priors for coefficients ($\mu = 0, \sigma = 0.15$). We
 179 ran three chains for 1000 samples for warmup and 4000 for sampling, with a thinning rate of 3.
 180 We accessed the quality of the models using the predictive check graphs (Piironen and Vehtari,
 181 2017) (Figure S-8). To understand the effect of climate on vital rates, we got the 95 % credible
 182 interval of the posterior distribution. Then we assumed that there is 95 % probability that the
 183 true (unknown) estimates would lie within that interval, given the evidence provided by the
 184 observed data for each vital rate. All models were fit in Stan (Stan Development Team, 2023).

185 **Two-sex and female dominant climate-dependent matrix projection models**

186 To estimate population growth rate and sex ratio, we used the climate-dependent vital rate
 187 regressions estimated above and the number of new recruit per year to build two matrix
 188 projection models (MPMs) structured by size (number of tillers) and sex. The first MPM
 189 assumes that climate affects population growth rate through the female alone (female dom-
 190 inant model). The second MPM assumes that climate affects population growth rate through
 191 a sex-specific response to climate which may lead to skewness in sex ratio that will affect
 192 female vital rates (two-sex model). Below we describe how the number of new recruit per
 193 year, the probability of seed viability, the female dominant and the two-sex models were built.

194 Let v be the probability of seed viability (Eq. 2). We modeled v using data collected
 195 from a sex-ratio experiment (Supplementary Method S.2). We assume that v does not vary
 196 with climate.

197
$$v = v_0 * (1 - OSR^\alpha) \quad (2)$$

198 where OSR is the (proportion of panicles that were female) in the experimental populations.
 199 α is the parameter that controls how seed viability declines with increasing female bias.

200 Let $F_{x,t}$ and $M_{x,t}$ be the number of female and male plants of size x in year t present
 201 at a location that has z as climate, where $x \in [L, U]$. L is the minimum possible sizes and U
 202 is the 95th percentile of observed maximum size. Let F_t^R and M_t^R be new recruits, which we
 203 assume do not reproduce in their first year. For a pre-breeding census, the expected numbers
 204 of recruits in year $t+1$ is given by:

205
$$F_{t+1}^R = \sum_L^U [p^F(x, z) \cdot c^F(x, z) \cdot d \cdot v(\mathbf{F}_t, \mathbf{M}_t) \cdot m \cdot \rho] F_{x,t} \quad (3)$$

206
$$M_{t+1}^R = \sum_L^U [p^F(x, z) \cdot c^F(x, z) \cdot d \cdot v(\mathbf{F}_t, \mathbf{M}_t) \cdot m \cdot (1 - \rho)] F_{x,t} \quad (4)$$

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

212
$$v(\mathbf{F}_t, \mathbf{M}_t) = v_0 * \left[1 - \left(\frac{\sum_L^U p^F(x, z) c^F(x, z) F_{x,t}}{\sum_L^U p^F(x, z) c^F(x, z) F_{x,t} + p^M(x, z) c^M(x, z) M_{x,t}} \right)^\alpha \right] \quad (5)$$

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

214

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

215

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

216 In the two equations above, the first component indicates seedlings that survived their first
217 year and enter the size distribution of established plants. Here, we assume that seedling
218 survival probability (σ) is the same across sexes and climatic variables. We used σ from a sister
219 species *Poa autumnalis* in east Texas (T.E.X. Miller and J.A. Rudgers, *unpublished data*). We did
220 this because we had little information on the early life cycle transitions of greenhouse-raised
221 transplants. We also assume that $g(y, x=1)$ is the probability that a surviving seedlings
222 reach size y , the expected future size of L-tiller plants from the transplant experiment. The
223 second component of the equations indicates survival and size transition of established
224 plants from the previous year, where s and g give the probabilities of surviving at size x and
225 growing from sizes x to y , respectively, and superscripts suggest that these functions may
226 be unique to females (F) and males (M).

227 Since the climate-dependent vital rate regressions were built using MCMC, we were able
228 to propagate the uncertainty in vital rate parameters to uncertainty in predicted population
229 growth rates (λ). We estimated population growth rate for the female dominant MPM using
230 the function lambda in the package popbio (Stubben and Milligan, 2007). Since the two-sex
231 MPM is nonlinear (vital rates affect and are affected by population structure) we estimated
232 the asymptotic geometric growth rate (λ) by numerical simulation, and repeated this across
233 a range of climate⁸.

234 **Life Table Response Experiments**

235 ⁹To identify which aspect of climate is most important for population viability, we used a Life
236 Table Response Experiments (LTRE) based on a non parametric model for the dependence
237 of λ on time-varying parameters (Ellner et al., 2016). To do so, we used the RandomForest
238 package to fit a regression model with four climatic variable (temperature of growing season,
239 precipitation of growing season, temperature of the dormant season and precipitation of

⁸I think the key thing here is that the estimation of lambda was not from an eigen value as opposed to the female dominant.I added an explanation of "vital rates affect and are affected by population structure" in the first paragraph

⁹I modified this section. I understand your concern about accounting for the second order term in the first LTRE but I don't think we should be worry about that here. I am saying that because the technic here is similar to an ANOVA-we dropped one predictor to see how much the error goes up. That's why we don't account for sex or size because lambda account for them already.

240 the dormant season) as predictors and λ as response (Liaw et al., 2002). The regression
 241 model allowed the estimation of the relative importance of each predictor. The importance
 242 is measured by asking: how wrongly is λ predicted if we replaced the focal predictor (e.g.,
 243 temperature of growing season) by a random value of the other predictors.

244 To estimate the contribution of each sex to population growth rate variation, we
 245 decomposed the effect of each climate variable on population growth rate (λ) into contribution
 246 arising from the effect on each vital rate (Caswell, 2000). At this end we used another LTRE
 247 with a "regression design"(Caswell, 1989). The LTRE with a "regression design" estimates
 248 the contribution of each sex (Eq. 8).

$$249 \quad \frac{\partial \lambda}{\partial \text{climate}} \approx \sum_i \frac{\partial \lambda}{\partial \theta_i^F} \frac{\partial \theta_i^F}{\partial \text{climate}} + \frac{\partial \lambda}{\partial \theta_i^M} \frac{\partial \theta_i^M}{\partial \text{climate}} \quad (8)$$

250 where, θ_i^F and θ_i^M represent sex-specific parameters: the regression coefficients for the
 251 intercepts and slopes of size-dependent vital rate functions. Because LTRE contributions are
 252 additive, we summed across vital rates to compare the total contributions of female and male
 253 parameters.¹⁰

254 Climate change impacts on sex ratio

255 To understand the impact of climate change on sex ratio, we used two methods. First, we
 256 developed eight Bayesian linear models using data collected during three years. Each model
 257 had OSR or SR as response variable and a climate variable as predictor (Eq.9).

$$258 \quad SR = \omega_0 + \omega_1 \text{climate} + \omega_2 \text{climate} * \text{climate} + \epsilon \quad (9)$$

259 where SR is the proportion of panicles that were female or proportion of female individuals
 260 in the experimental populations. ω_0 is the intercept, ω_1 and ω_2 are the climate dependent
 261 slopes. ϵ is error term.

262 Second, we used the two-sex model to estimate sex-ratio by numerical simulation and
 263 repeated this across a range of climate. This allow us to have the sex-ratio that account for
 264 all climate covariates. We then compare sex ratio across time (past, present and future) using
 265 density plots.

¹⁰ θ_i^F and θ_i^M include the interaction and second order effect. I think we are good with this formula

266 **Climate change impacts on niche and range shifts**

267 To understand the impact of climate change on species niche shifts, we estimated the
268 probability of self- sustaining populations, which is $\Pr(\lambda > 1)$ conditional to (i) temperature
269 and precipitation of the dormant season or to (ii) temperature and precipitation of the
270 growing season. $\Pr(\lambda > 1)$ was calculated for the two-sex model and the female dominant
271 MPMs using the proportion of the 300 Markov chain Monte Carlo iterations that lead to a
272 $\lambda > 1$ (Diez et al., 2014). The probability of self- sustaining populations was then represented
273 as a contour plot with values of $\Pr(\lambda > 1)$ at given temperature and precipitation for the
274 growing and dormant season across time (past, present and future).

275 $\Pr(\lambda > 1)$ was also mapped onto geographic layers of three state (Texas, Oklahoma and
276 Kansas) to delineate past, current and future potential distribution of the species. To do so,
277 we estimated $\Pr(\lambda > 1)$ conditional to all climate covariates for each pixel ($\sim 25 \text{ km}^2$) across
278 the species range for each time period (past, present, future). Because of the amount of the
279 computation involved in the Markov chain Monte Carlo iterations, use only 100 posterior
280 samples to estimate $\Pr(\lambda > 1)$ across the study area (Texas, Oklahoma and Kansas).

281 To compare the probability of self-sustaining populations between the female dominant
282 and the two-sex model, we used a zero-inflated beta model in brms (Bürkner, 2017).

283 All the analyses were performed in R 4.3.1 (R Core Team, 2023)

284 **Results**

285 **Sex specific demographic response to climatic gradient**

286 We found a sex specific demographic response to climatic gradient in *Poa arachnifera*
287 populations. Specifically, female individuals had higher survival and flowering rate than male
288 across species range during the dormant and growing season (Figure 2A-3D, 3I-3L). Male
289 individuals produce more panicles than female across species range (Figure 2M-3P). On the
290 contrary, female had a size advantage for low value values of climate during the growing
291 season and for high values of climate during the dormant season (Figure 2E-3H). We also
292 found opposite patterns in the direction of the effect on climate on the probability of survival
293 and flowering. If temperature of the growing seasons and dormant season are constant, then
294 precipitation of the growing season has a negative effect on the probability of survival, the
295 number of tillers, and the probability of flowering (Figure 2). In contrast, if temperature of
296 the growing and dormant season are constant, then the precipitation of dormant season has
297 a positive effect on these vital rates (Figure 2E-3H). If precipitation of growing and dormant

298 season are constant, then temperature of the growing season has a positive effect of the
 299 probability of survival, a negative effect on the probability of flowering, and the number of
 300 tillers, but no significant effect on the number of panicles (Figure 2).¹¹

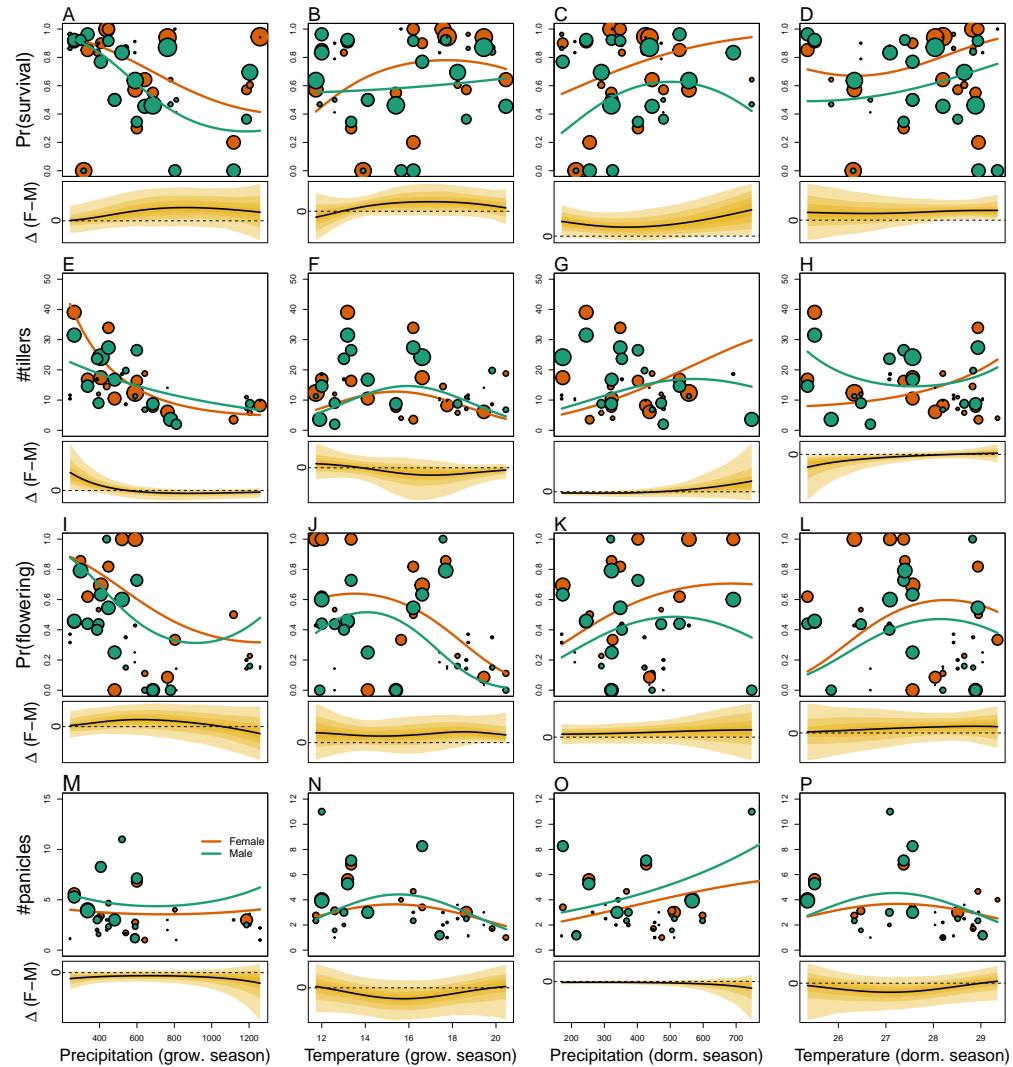


Figure 2: Sex specific demographic response to climate across species range. (A, B, C, D) Probability of survival as a function of precipitation and temperature of the growing and dormant season. (E, F, G, H) Change in number of tillers as a function of precipitation and temperature of the growing and dormant season. (I, J, K, L) Probability of flowering as a function of precipitation and temperature of growing and dormant season. (M, N, O, P) Change in number of panicles as a function of precipitation and temperature of the growing and 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.

¹¹I tried to add the conditionality here. I hope it makes sense

301 **Female bias in sex-ratio in response to climate climate change**

302 Operational-Sex Ratio (proportion of females panicles) increased significantly with an increase
303 of precipitation and temperature of the growing season and precipitation and temperature
304 of dormant season (Figure S-10, Figure S-11). Similarly, the proportion of female plants
305 increased with an increase of temperature of growing season and temperature of dormant
306 season (Figure S-12 B, D, Figure S-13). However, the proportion of female plants did not vary
307 significantly with precipitation of dormant and growing season (Figure S-12 A, C). Future
308 climate drive to extreme female-biased in *Poa arachnifera* populations (Figure 3, Figure S-14).

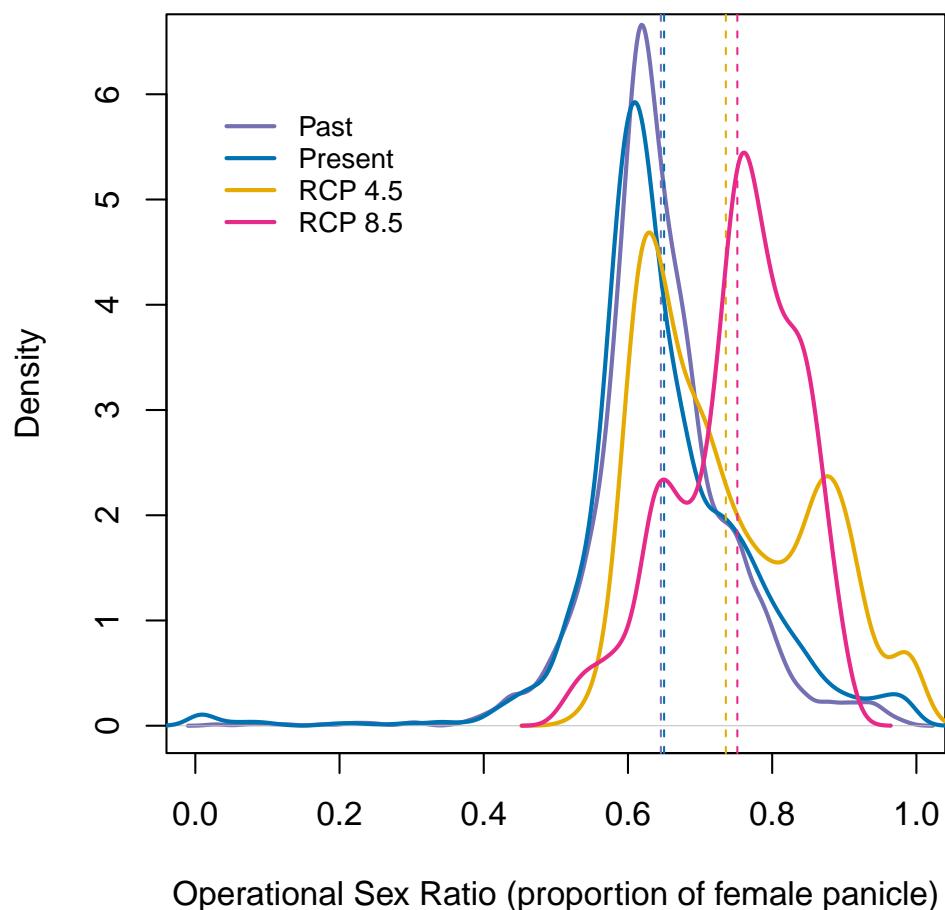


Figure 3: Change in Operational Sex Ratio (proportion of female panicule) over time (past, present, future). Future projections were based on the CMCC-CM model. The mean sex ratio for each time period is shown as vertical dashed line.

309 **Climate change alters population viability**

310 We estimated population growth rate variation across species range as a function of each
311 climatic variable given the average of the three other climatic variables using two models:
312 a female dominant model and a two-sex model¹². For both models, population growth rate
313 decreased toward high precipitation of growing season (Figure 4A). In contrast population
314 growth rate increased with an increase in precipitation of the dormant season (Figure 4C).
315 Furthermore, population growth rate was maximized between 14 and 17 °C and decreased
316 bellow zero beyond 18 °C during the growing season (Figure 4B). Similarly population fitness
317 was maximized between 27 and 31 °C and decreased bellow zero just beyond 20 °C during
318 the dormant season (Figure 4D).¹³

319 We have also detected a strong association between predicted lambda and different
320 ranges of climate (past, present and future). Under past climate conditions, population growth
321 rate decreased below one for temperature of the growing season. Populations will still be
322 viable under moderate gas emission (RCP4.5). However high gas emission (RCP8.5) will alter
323 population viability (Figure 4B, D).¹⁴

324 Population growth rate was most sensitive to change in temperature of the growing
325 season and temperature of the dormant season (Figure S-15). Despite contribution for both
326 sexes, females have a higher contribution to population dynamics than males (Figure S-16;
327 Figure S-17). For both sexes, the reduction of λ for high value of temperature (dormant and
328 growing season) was driven by a reduction of survival rate, growth rate, and a reduction
329 in number of panicles (Figure 4F, H, G, L). However, the change of population growth rate
330 for high value of precipitation was not driven by change in vital rates.

¹²I have now provided the methods for this contrast.

¹³I think we should keep this figure. The 2-D niche plots are the better representation of these results, because there are temp*precip interactions that we cannot see here but you can see in the 2-D niche plot. However a model with the 4 predictors together will also give a beter approximation of lambda than the 2D. I added the conditional part in the description of the results. I see the 2D as a way of showing the difference in niche. That said if you really want to remove this I am down you have more experience than me.

¹⁴I changed how I write the first sentence to remove the "effect of climate on". Again I don't mind removeing the Figure.

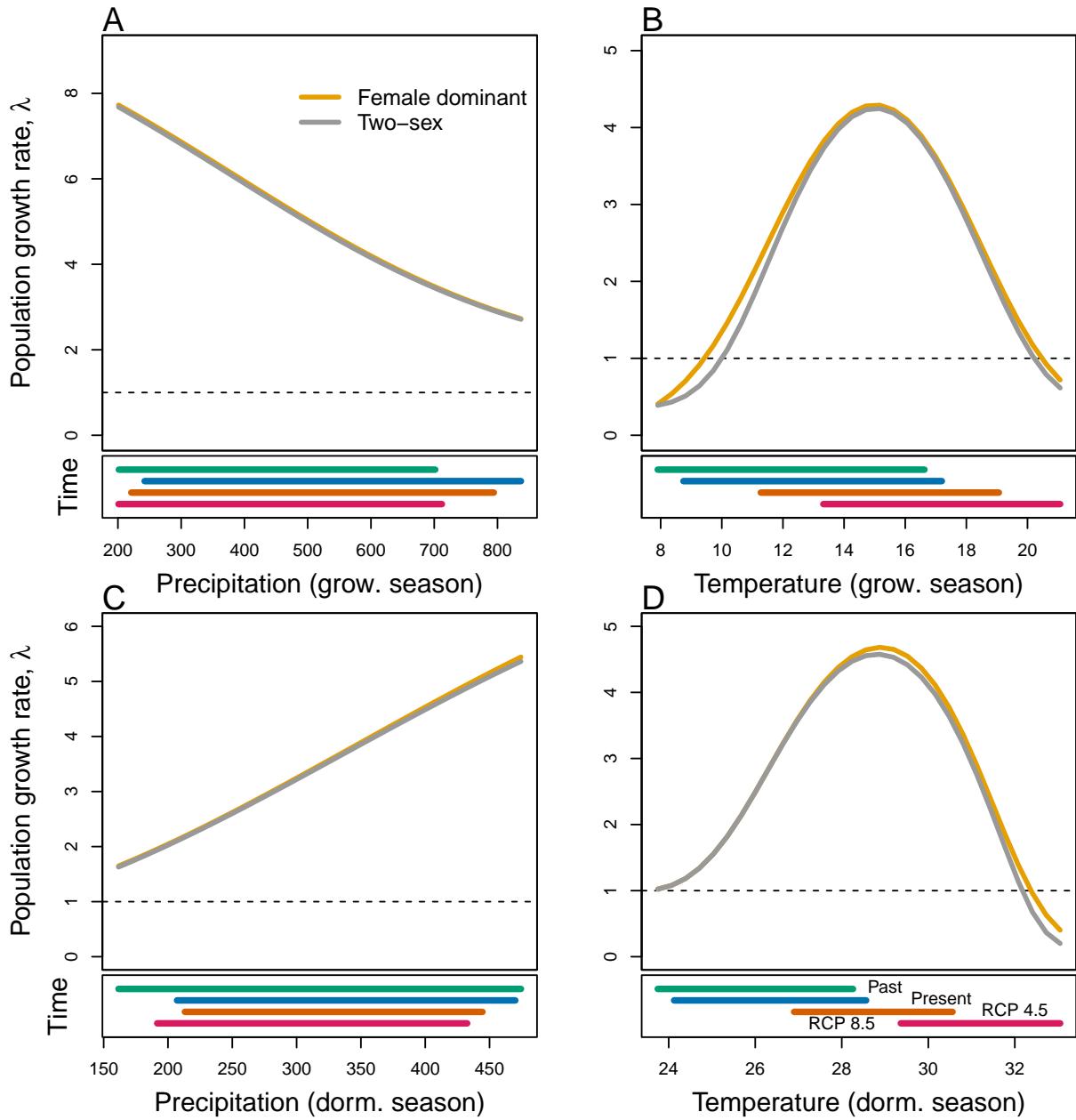


Figure 4: Predicted population growth rate (λ) in different ranges of climate. (A) Precipitation of the growing season, (B) Temperature of the growing season, (C) Precipitation of the dormant season, (D) Temperature of the dormant season. The grey curve shows prediction by the two-sex matrix projection 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 ranges of climate values for different time period (past climate, present and future climates). For future climate, we show a Representation 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).

331 Climatic change induces niche and range shifts

332 Female dominant model and two-sex models predicts a niche shift in *Poa arachnifera*
333 populations (Figure 5). However, the female dominant model underestimated the magnitude
334 of niche shifts (Figure 5E, F; -0.16[-0.29,-0.03]). Female dominant model and the two-sex
335 models agree that viable populations of *P. arichnifera* were only predicted at the center of the
336 range for current climatic conditions (Figure 6). Although *P. arichnifera* was predicted to have
337 suitable habitats in the center of the range under current climate, global warming is projected
338 to reduce much of these suitable habitats (Figure 6). If the species is able to disperse far and
339 if there is no physical barriers, most of the current suitable habitats will move toward the
340 Northern range edge as a results of niche shifts. Niche shift underestimation by the female
341 dominant model led to a geographic range underestimation by the female dominant model.

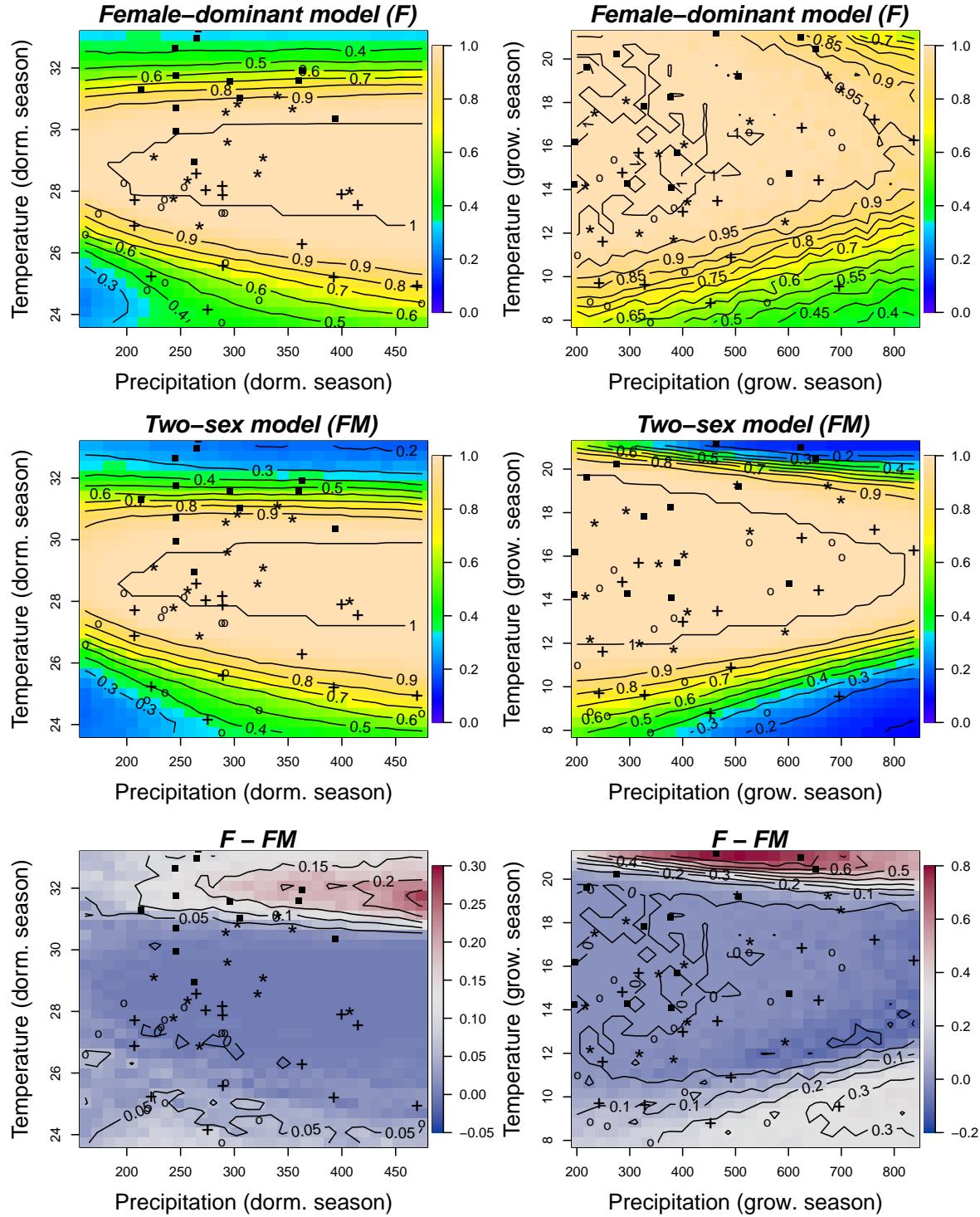


Figure 5: A two-dimensional representation of the predicted niche shift over time (past, present and future climate conditions). Contours on the first four panels show predicted probabilities of self-sustaining populations, $\Pr(\lambda > 1)$ conditional on precipitation and temperature of the dormant and growing season. The last two panels show difference in niche estimation between the female dominant model and the two-sex model for each season. "o": Past, "+": Current, "*": RCP 4.5, "■": RCP 8.5.

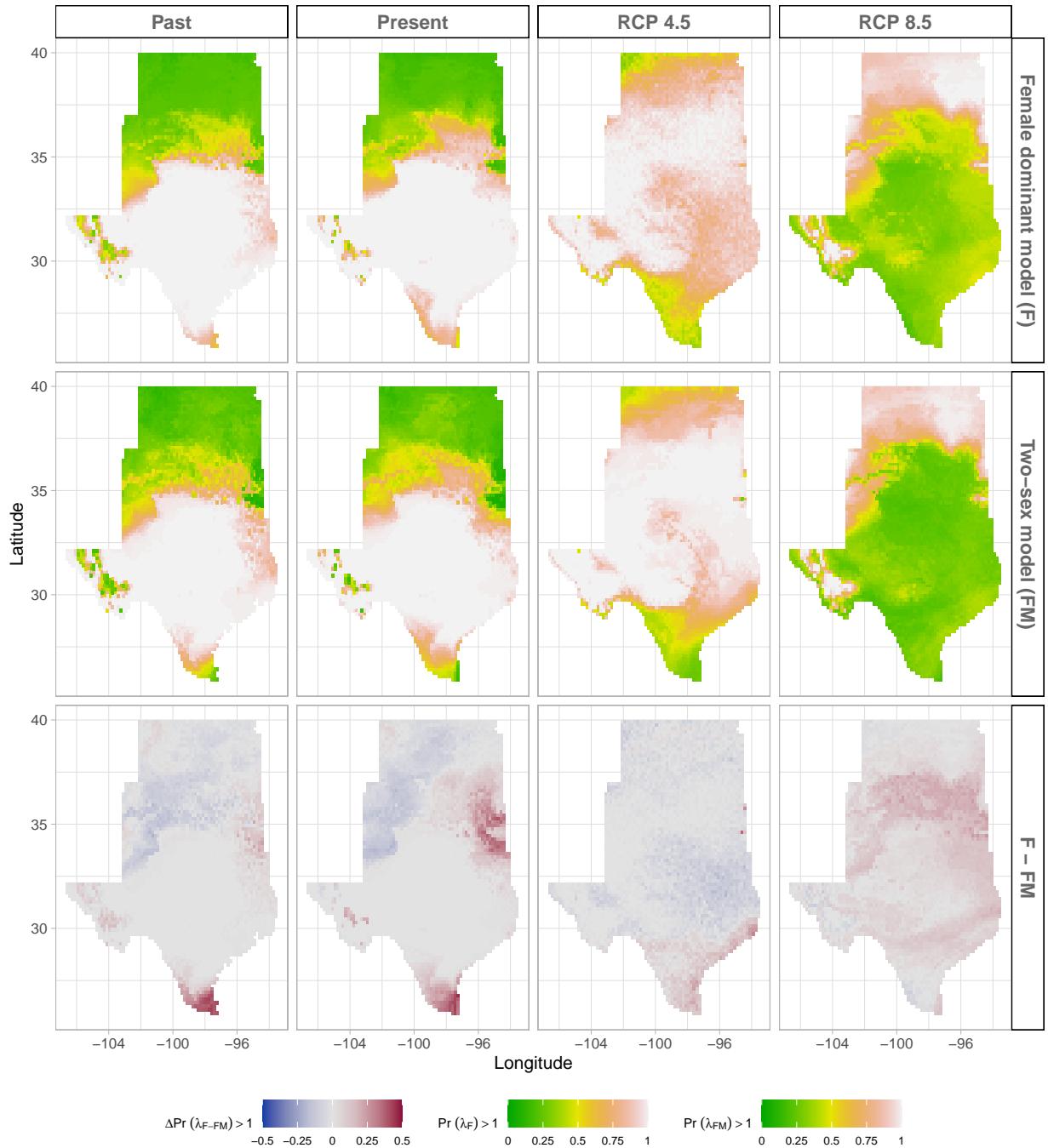


Figure 6: Climate change favors range shift towards north edge. (A) Past, (B) Current, (C and D) Future predicted range shift based on the predicted probabilities of self- sustaining populations, $\Pr(\lambda > 1)$, using the two-sex model that incorporates sex- specific demographic responses to climate 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, $\Pr(\lambda > 1)$, 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 $\Pr(\lambda > 1)$, confirming that our study approach can reasonably predict range shifts.

342 **Discussion**

343 ¹⁵Dioecious species make up a large fraction of Earth's biodiversity – most animals and
344 many plants – yet we have little knowledge about how skewness in sex ratio will affect
345 population viability and range shifts of dioecious species under climate change. We used
346 three years of demographic data collected from common garden experiments across climatic
347 gradient to forecast for the first time the impact of climate change on dioecious species. Our
348 future projections require extrapolation to warmer or colder conditions than observed in
349 our experiment and subsequently should be interpreted with caution (Chen et al., 2024).
350 Despite all these limitations, the qualitative implications of the response of our study species
351 to increase temperature (dormant and growing season) seems consistent across all GCMs
352 (Figure S-19, Figure S-20, Figure S-21). Three general patterns emerged from our analysis
353 of range-wide common garden experiments and sex-structured, climate-explicit demographic
354 models. First, our Bayesian mixed effect model suggests a sex specific demographic response
355 to climate change that lead to higher proportion of female as climate increase. Second, climate
356 change favors a northern range shifts in suitable habitats. Third, the female dominant model
357 (model that does not account for sex structure) overestimates species niche and range shifts.

358 There was a female demographic advantage leading to a female biased in response
359 to climate change in *Poa arachnifera* populations. The extreme female-bias in response to
360 climate change contrast with previous studies suggesting that an increase in male frequency
361 in response to climate change (Hultine et al., 2016; Petry et al., 2016). Two mechanisms
362 could explain the observed demographic advantage of females over males for survival and
363 flowering and the opposite for growth and number of panicles. The trade-off between fitness
364 traits (survival, growth and fertility) due to resource limitation and the pollination mode of
365 our study species (wind pollinated) could explain such a result (Cipollini and Whigham, 1994;
366 Freeman et al., 1976). For most species, the cost of reproduction is often higher for females
367 than males due to the requirement to develop seeds and fruits (Hultine et al., 2016). However,
368 several studies reported a higher cost of reproduction for males in wind pollinated species
369 due to the larger amounts of pollen they produce (Bruijning et al., 2017; Bürli et al., 2022;
370 Cipollini and Whigham, 1994; Field et al., 2013).

371 Our results suggest that climate change will alter population at the center of the range
372 and drive a northern range shifts. This impact of climate change on the species current
373 niche could be explained by the increase of temperature over the next years. Small change
374 in temperature of the growing and dormant season have a larger impact on population

¹⁵This is my new proposition regarding the discussion

375 viability. Temperature can impact plant populations through different mechanisms. Increasing
376 temperature could increase evaporative demand, affect plant phenology (Iler et al., 2019;
377 McLean et al., 2016; Sherry et al., 2007), and germination rate (Reed et al., 2021). The potential
378 for temperature to influence these different processes changes seasonally (Konapala et al.,
379 2020). For example, studies suggested that species that are active during the growing season
380 such as cool grass species can have delayed phenology in response to global warming,
381 particularly if temperatures rise above their physiological tolerances (Cleland et al., 2007;
382 Williams et al., 2015). In addition, high temperature during the growing season by affecting
383 pollen viability, fertilization could affect seed formation and germination (Hatfield and
384 Prueger, 2015; Sletvold and Ågren, 2015). Pollen dispersal may allow plants to resist climate
385 change because pollen dispersal may provide the local genetic diversity necessary to adapt
386 at the leading edge of the population (Corlett and Westcott, 2013; Duputié et al., 2012; Kremer
387 et al., 2012). Since wind pollination is most effective at short distances, it is most often
388 found in plant species growing at high density such as our study species, it is less likely
389 that dispersal limitation affect niche shift in our study system. Difference in non-climatic
390 factors such as soil, or biotic interactions could also explain decline in population growth rate
391 as an indirect effects of increase in temperature (Alexander et al., 2015; Schultz et al., 2022).
392 For example, climate change could increase the strength of species competition and thereby
393 constrain our study species to a narrower realized niche (Aguilée et al., 2016; Pulliam, 2000).

394 We found evidence of underestimation of the impact of climatic change on population
395 dynamics by the female dominant model and implication for such an underestimation on
396 conservation actions for dioecious species. The underestimation of the impact of climatic
397 change on population dynamics by the female dominant model makes sense given the sex
398 specific response to climatic change. *Poa arachnifera* populations will be female biased in
399 response to climate change. That extreme female-bias could affect population growth rate
400 by altering males' fitness with reduction on mate availability given that females individuals
401 have a demographic advantage over males (Haridas et al., 2014; Knight et al., 2005). Further,
402 our work suggest that population viability is sensitive to climate under current and future
403 conditions. This is key because most conservation actions are design from data on current
404 responses to climate, rather than future response to climate (Sletvold et al., 2013). Since the
405 role of male is not negligible in accurately predicting dioecious species response to climate
406 change, management strategies that focus on both sexes would be effective and will enhance
407 our understanding of dioecious species response to global warming.

⁴⁰⁸ **Conclusion**

⁴⁰⁹ We have investigated the potential consequence of skewness in sex ratio on population
⁴¹⁰ dynamics and range shift in the context of climate change using the Texas bluegrass. We
⁴¹¹ found extreme female -biased in response to climate change. The effect of female biased
⁴¹² will induce range shifts to the northern edge of the species current range by limiting mate
⁴¹³ availability. Beyond, our study case, our results also suggest that tracking only one sex could
⁴¹⁴ lead to an underestimation of the effect of climate change on population dynamics. Our
⁴¹⁵ work provides also a framework for predicting the impact of global warming on population
⁴¹⁶ dynamics using the probability of population to self-sustain.

⁴¹⁷ **Acknowledgements**

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Supporting Information

611 S.1 Supporting Figures

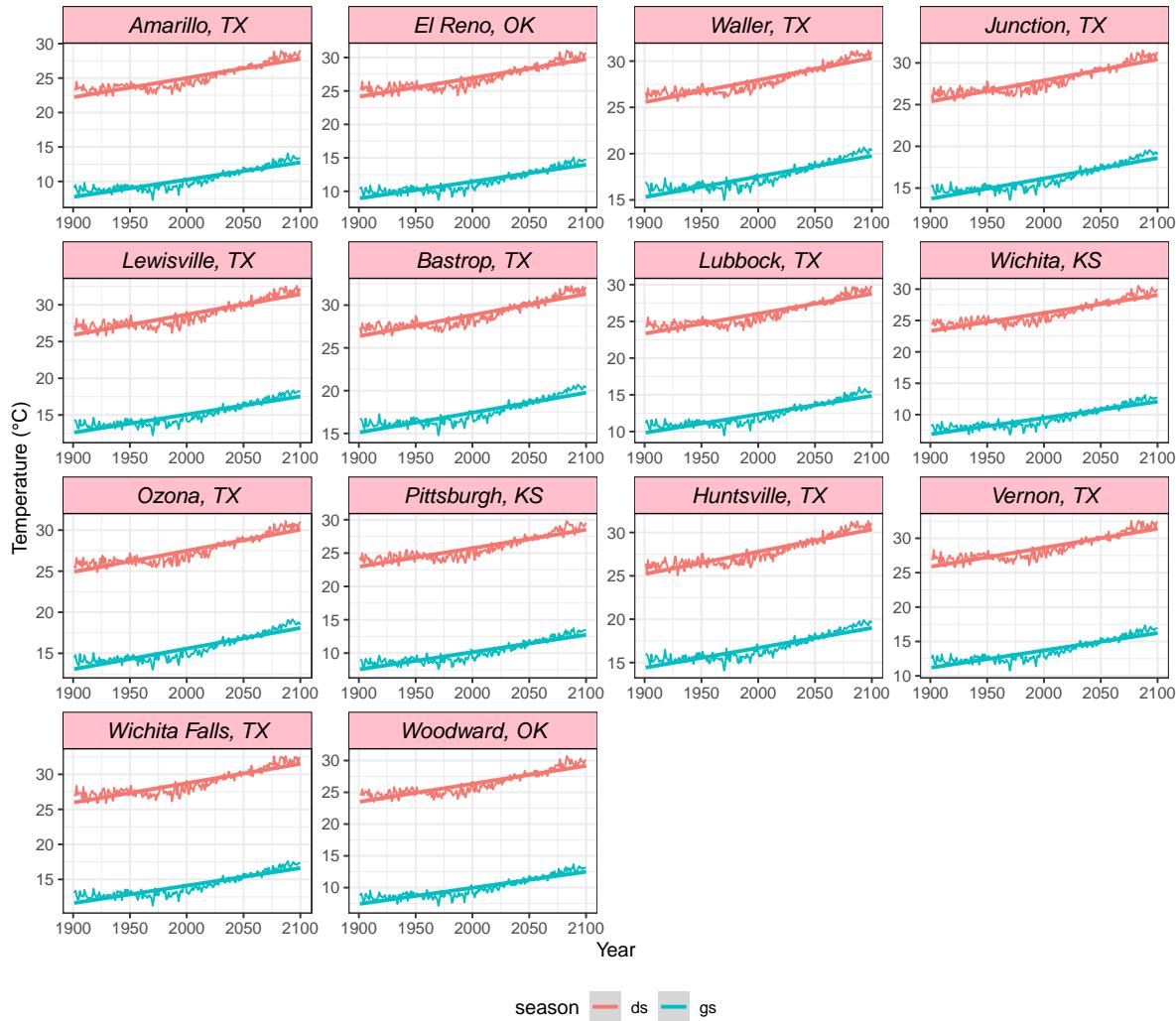


Figure S-1: Temperature variation across the study sites from 1990 to 2100, ds: Dormant season, dg: Growing season.

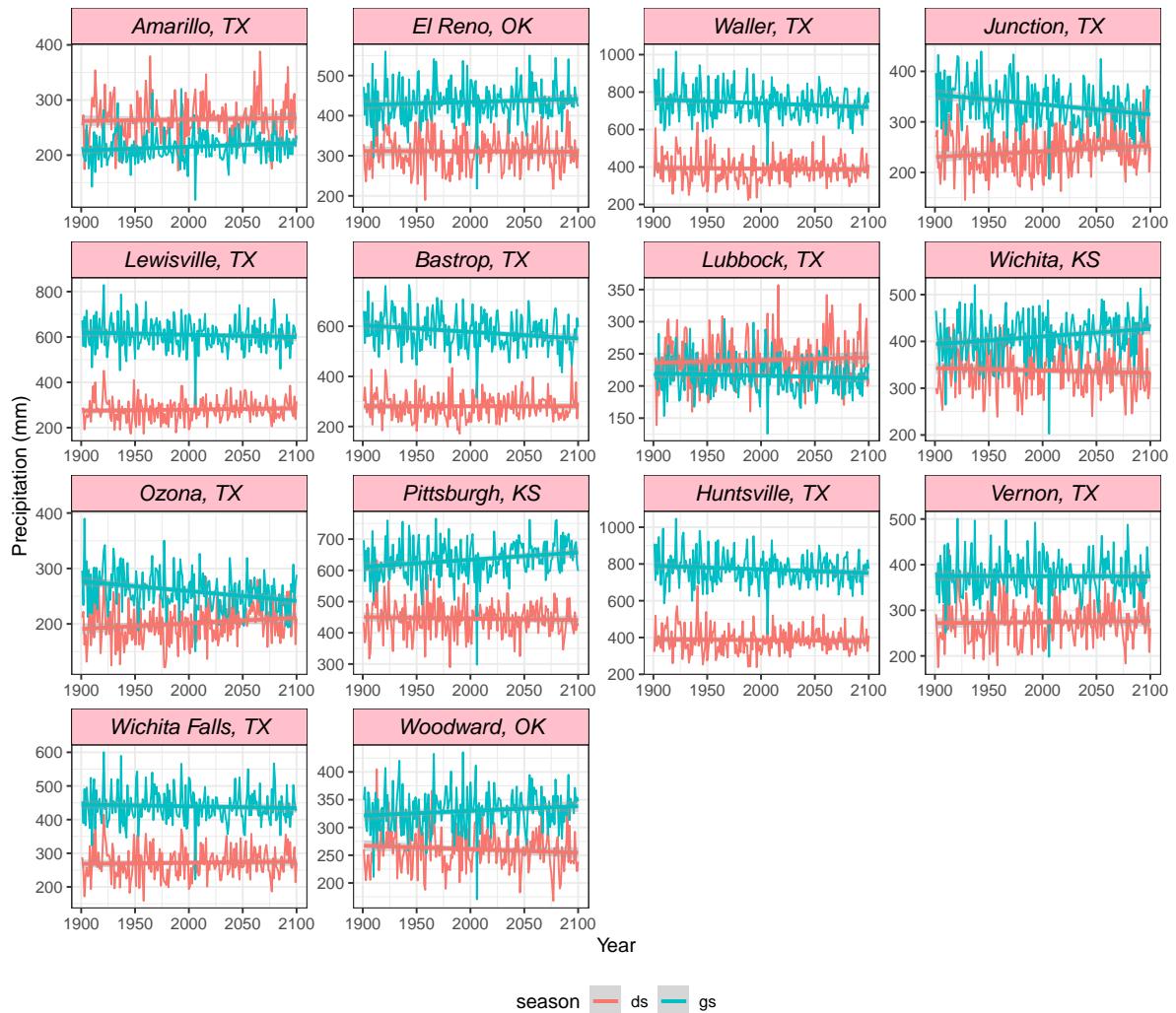


Figure S-2: Precipitation variation across the study sites from 1990 to 2100. ds: Dormant season, dg: Growing season.

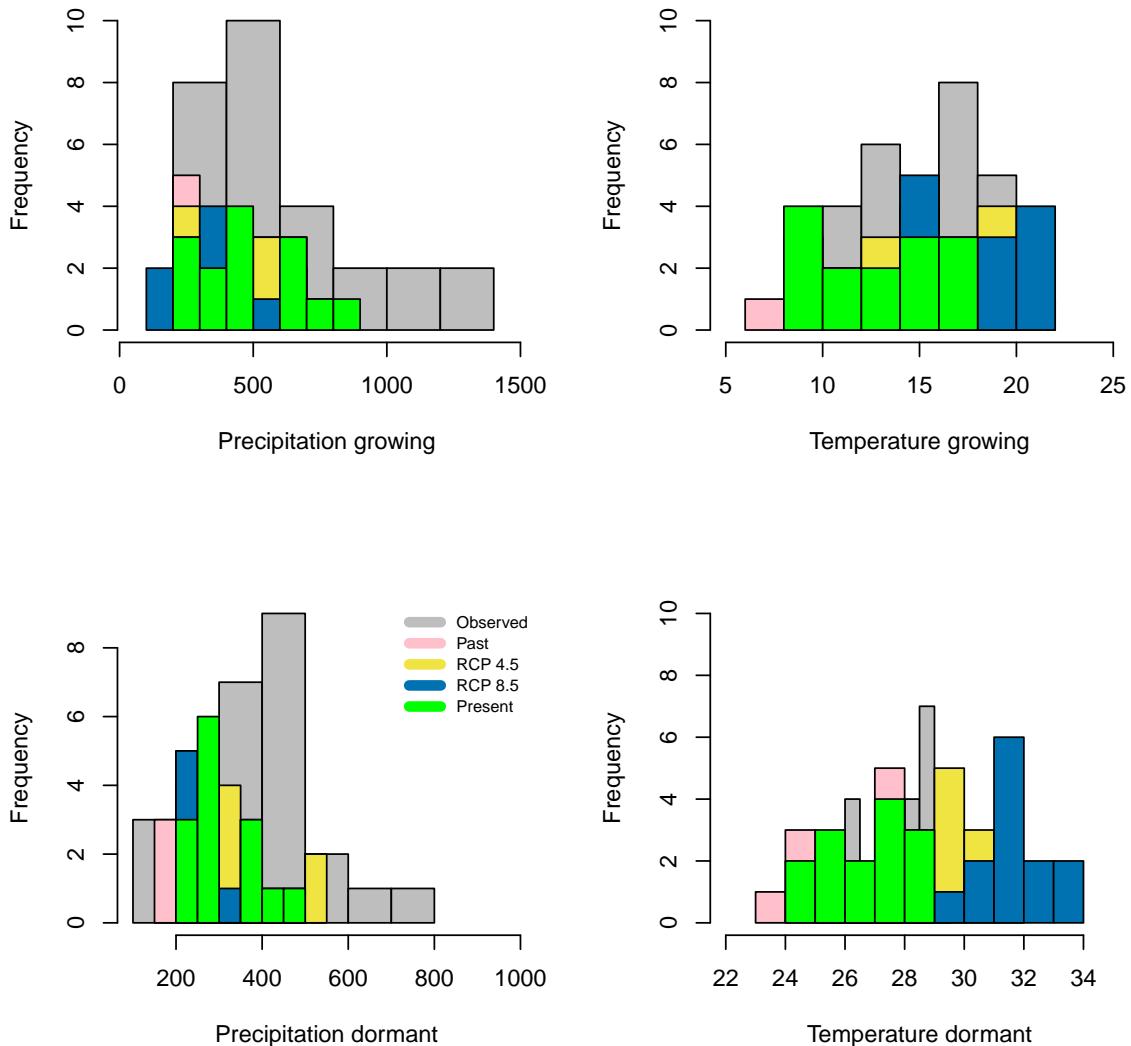


Figure S-3: Past, Observed, present and future (MIROC Model) climate data across the study area.

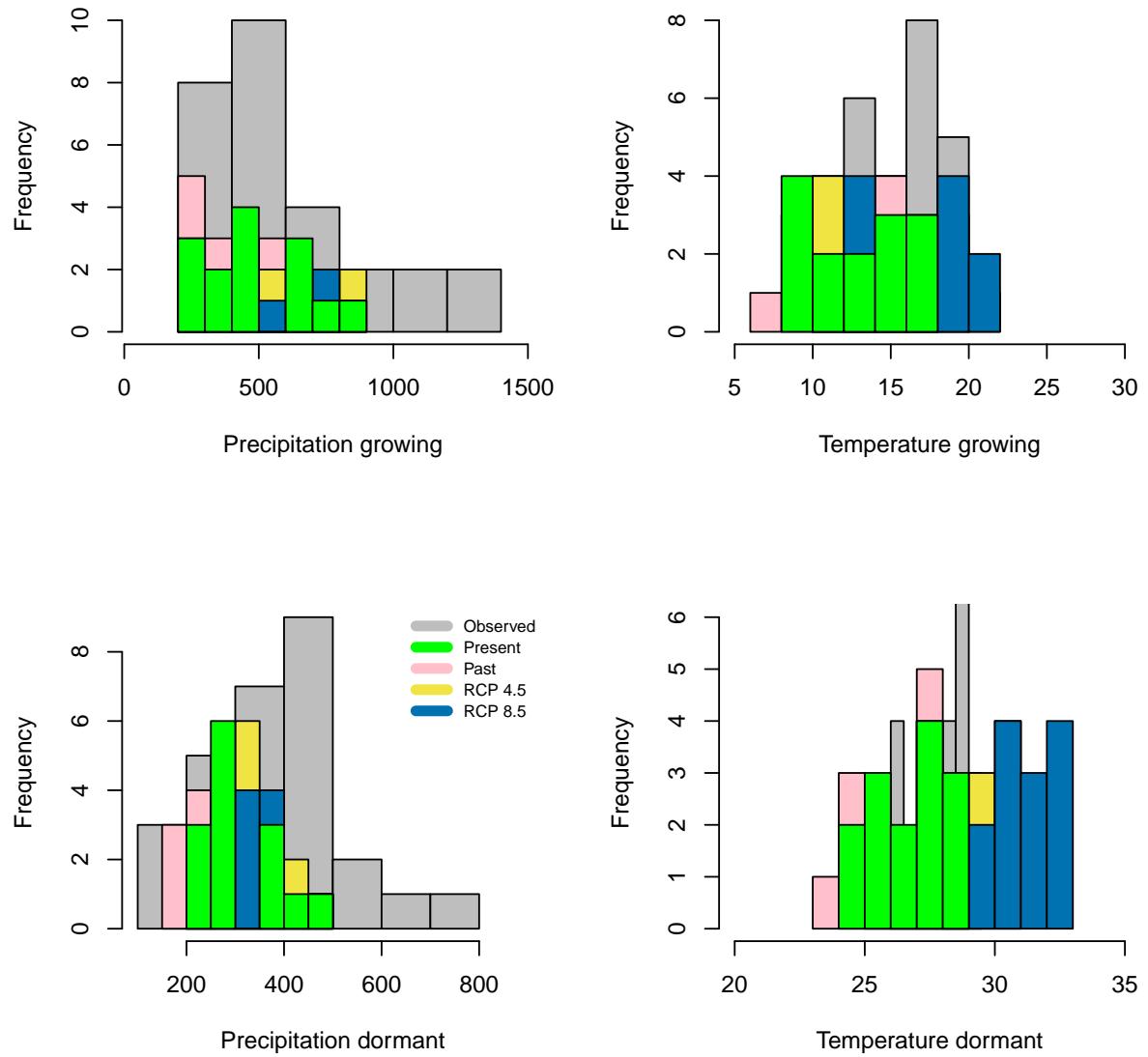


Figure S-4: Past, Observed, present and future (ACCESS Model) climate data across the study area.

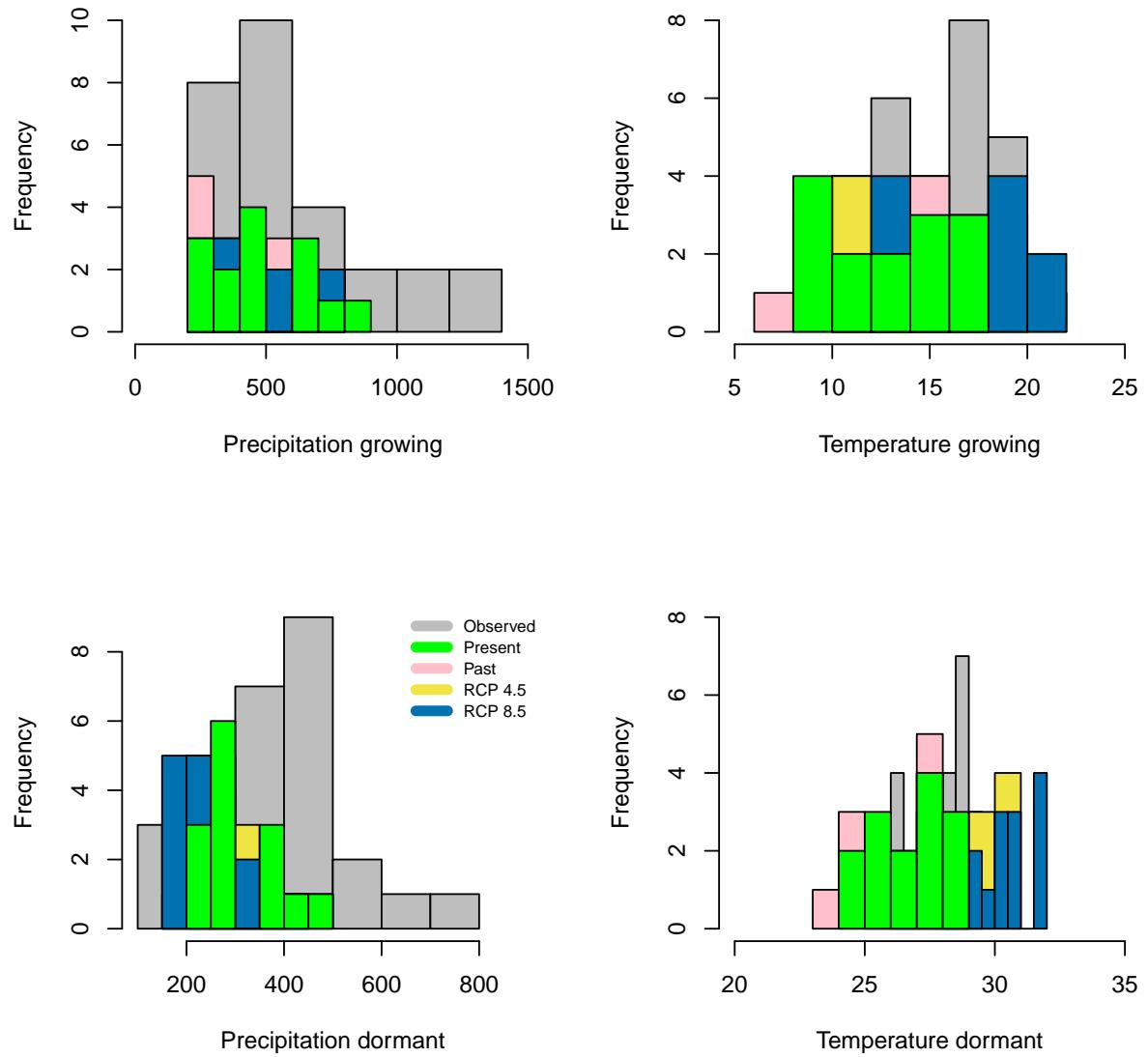


Figure S-5: Past, Observed, present and future (CESM1 Model) climate data across the study area.

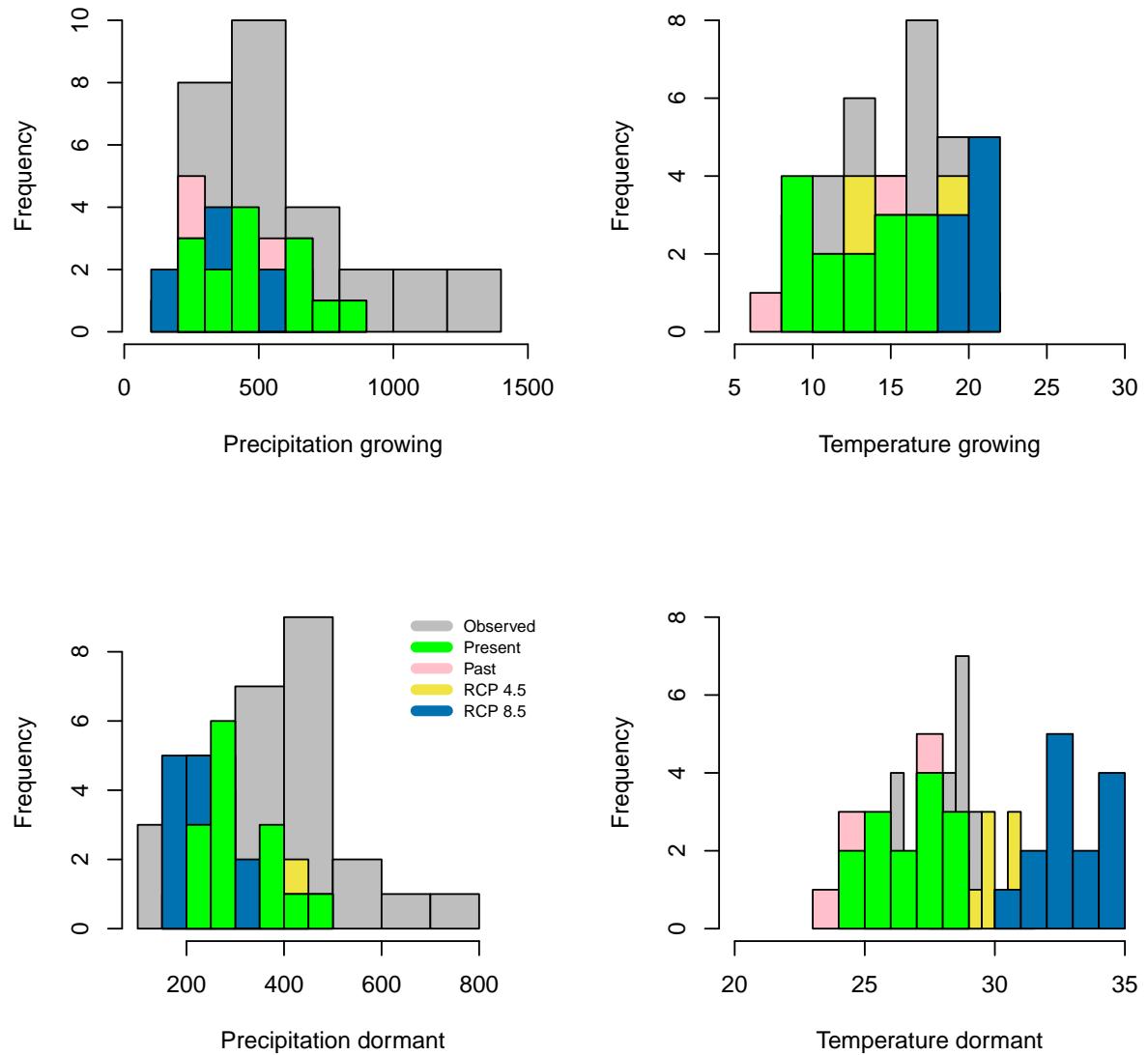


Figure S-6: Past, Observed, present and future (CMCC Model) climate data across the study area.

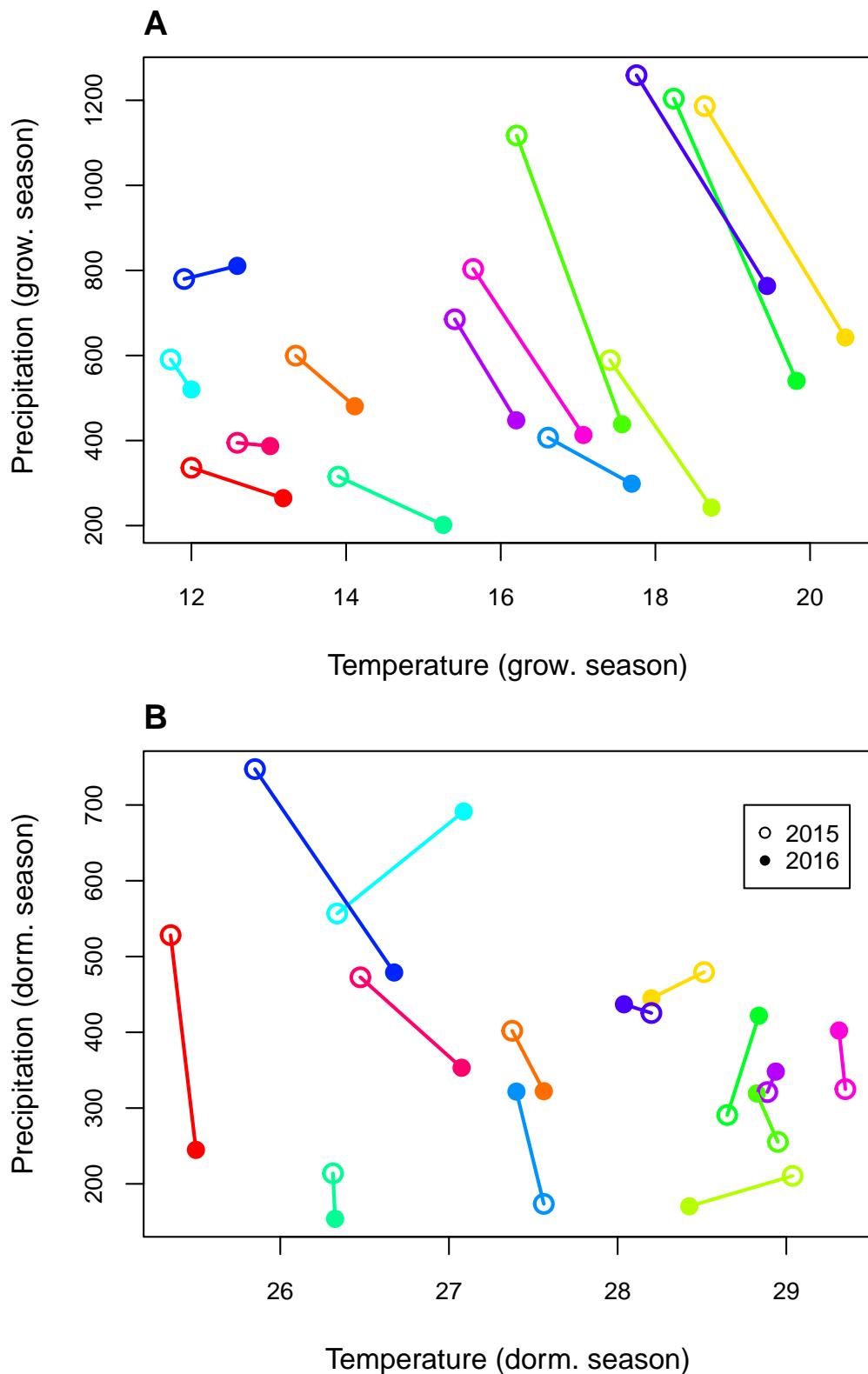


Figure S-7: Climate variation across the study sites during the monitoring period.

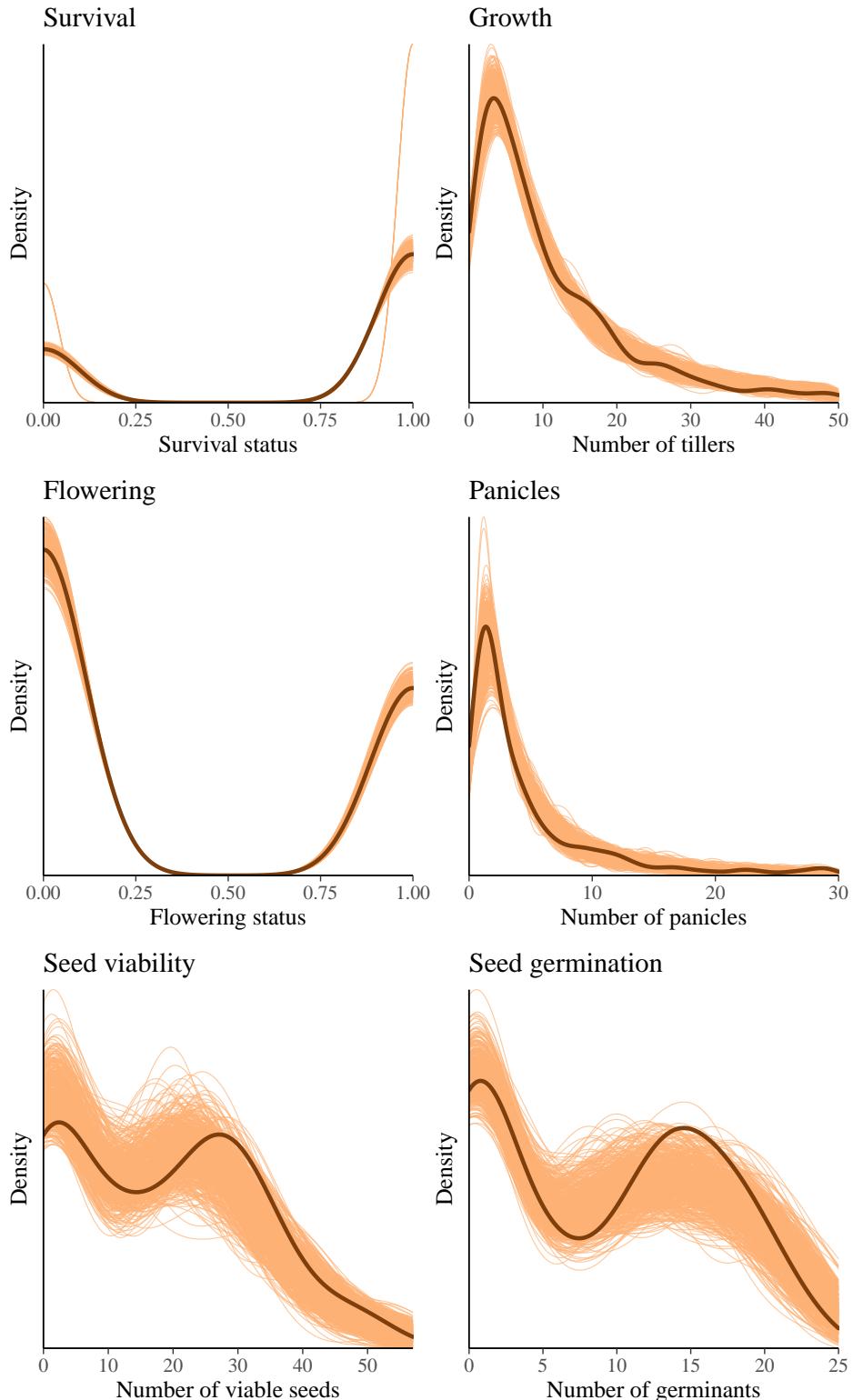


Figure S-8: Posterior predictive checks. Consistency between real data and simulated values suggests that the fitted vital rate models accurately describes the data. Graph shows density curves for the observed data (light orange) along with the simulated values (dark orange).

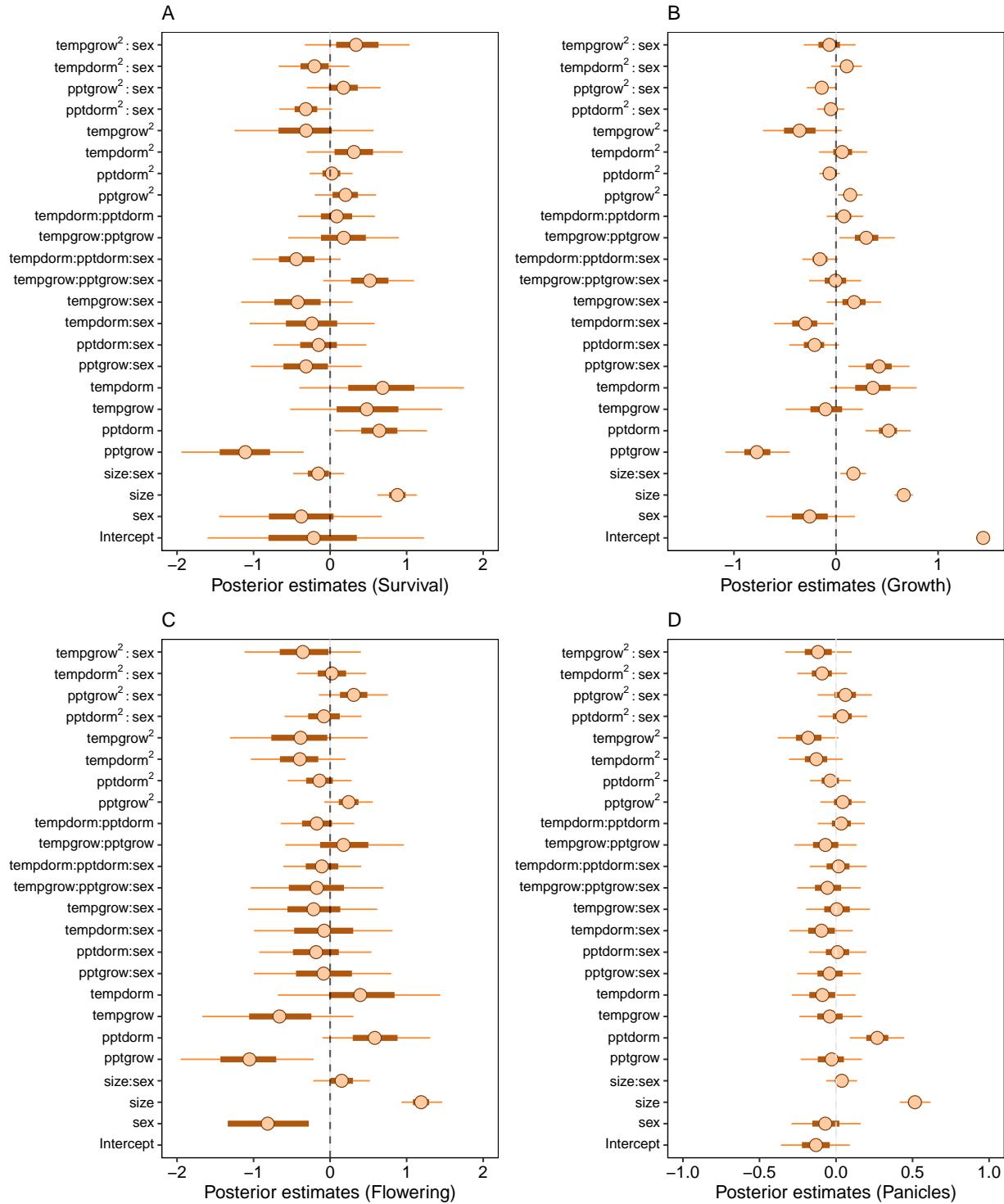


Figure S-9: Mean parameter values and 95% credible intervals of the posterior probability distributions. pptgrow is the precipitation of growing season, Tempgrow is the temperature of growing season, pptdorm is the temperature of dormant season, Tempdorm is the temperature of dormant season.

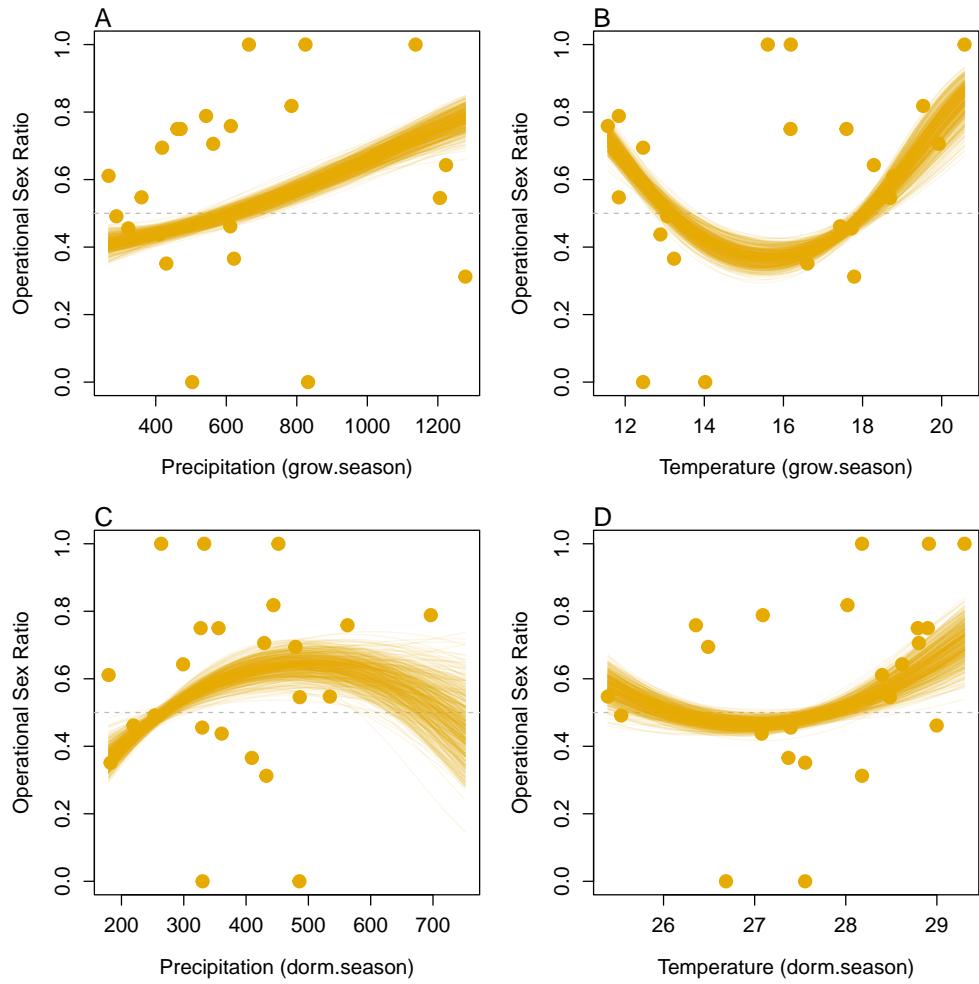


Figure S-10: Significant Operational Sex Ratio response across climate gradient. (A, B) Proportion of panicles that were females across precipitation and temperature of the growing season; (C, D) Proportion of panicles that were females across precipitation and temperature of the dormant season.

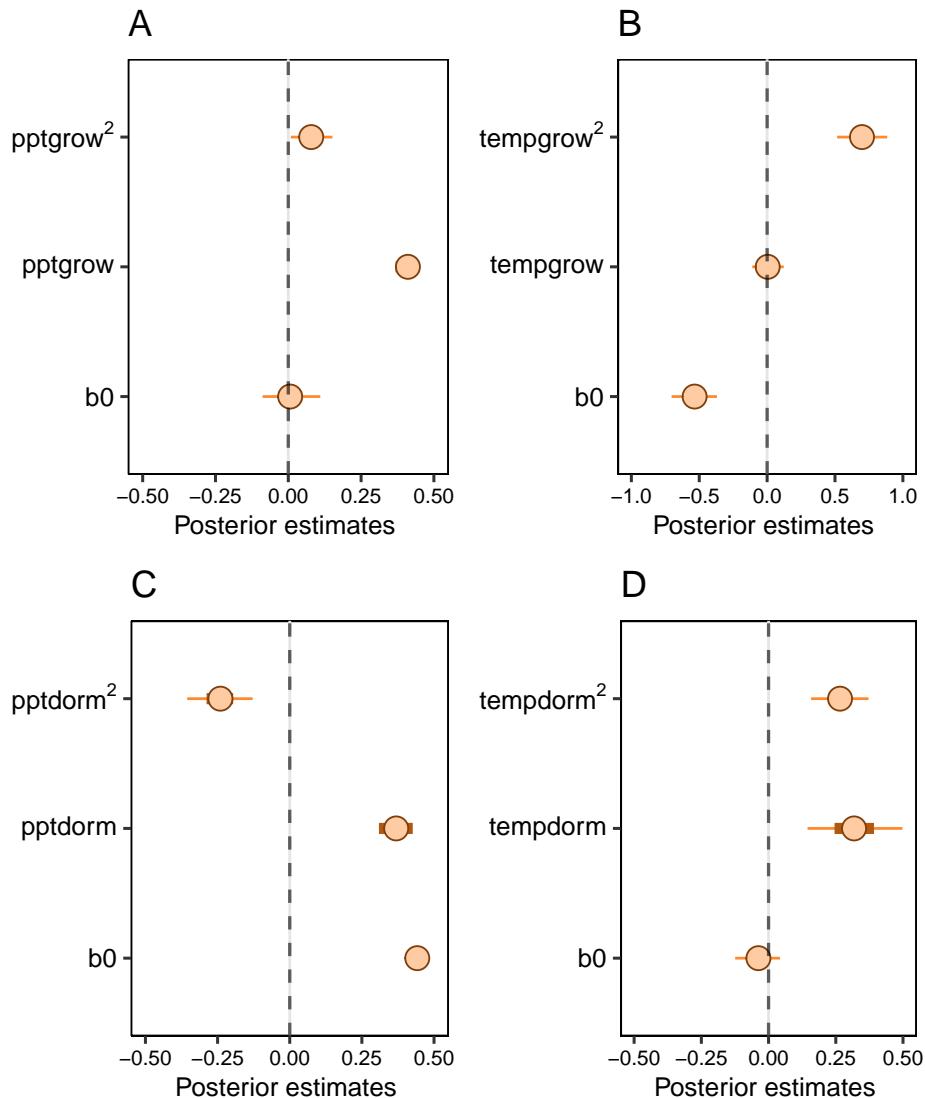


Figure S-11: Mean parameter values and 95% credible intervals of the posterior probability distributions. pptgrow is the precipitation of growing season, Tempgrow is the temperature of growing season, pptdorm is the temperature of dormant season, Tempdorm is the temperature of dormant season.

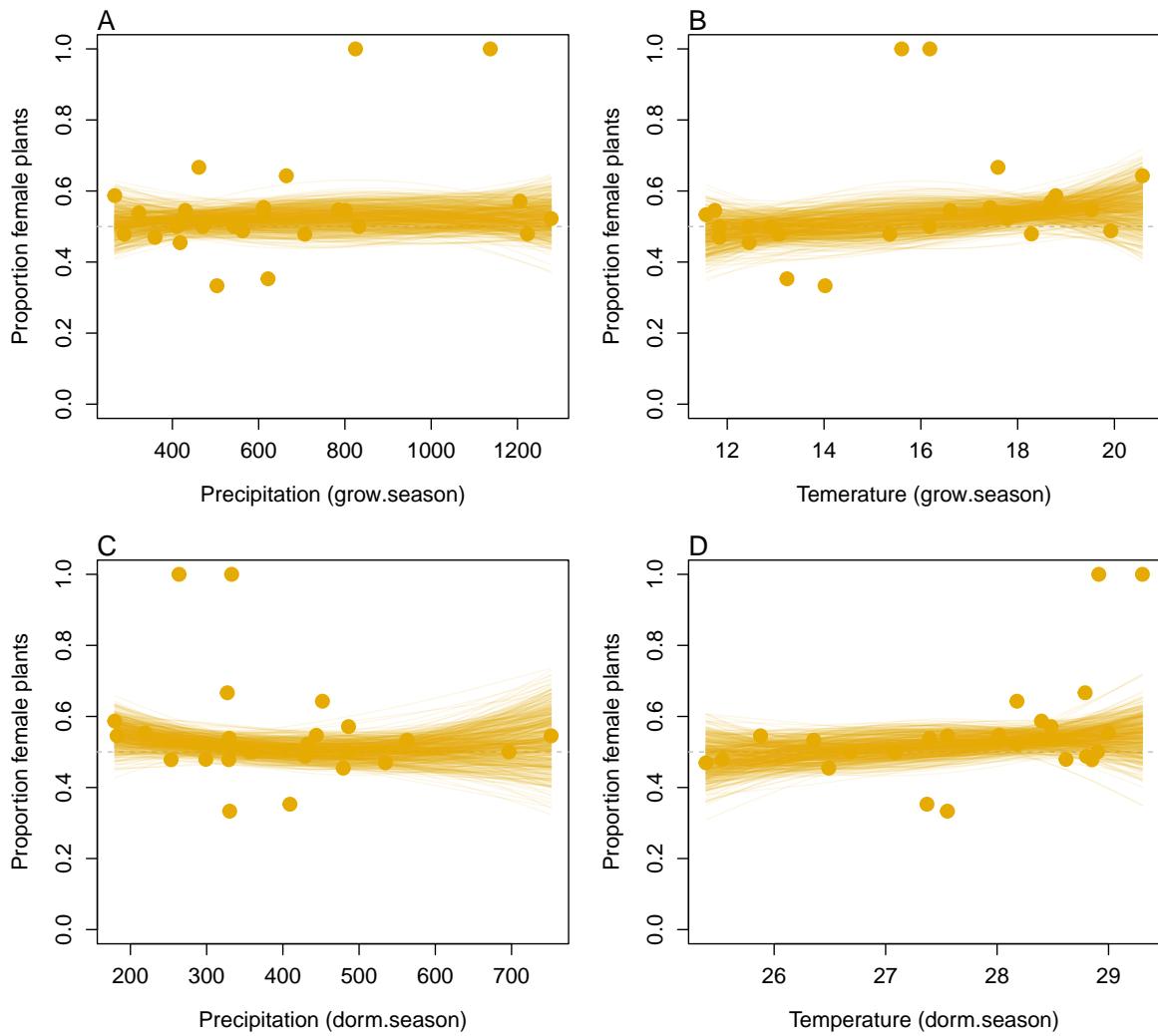


Figure S-12: Variation in sex-ratio accross climate gradient. (A, B) Proportion of plants that were females across precipitation and temperature of the growing season; (C, D) Proportion of plants that were females across precipitation and temperature of the dormant season.

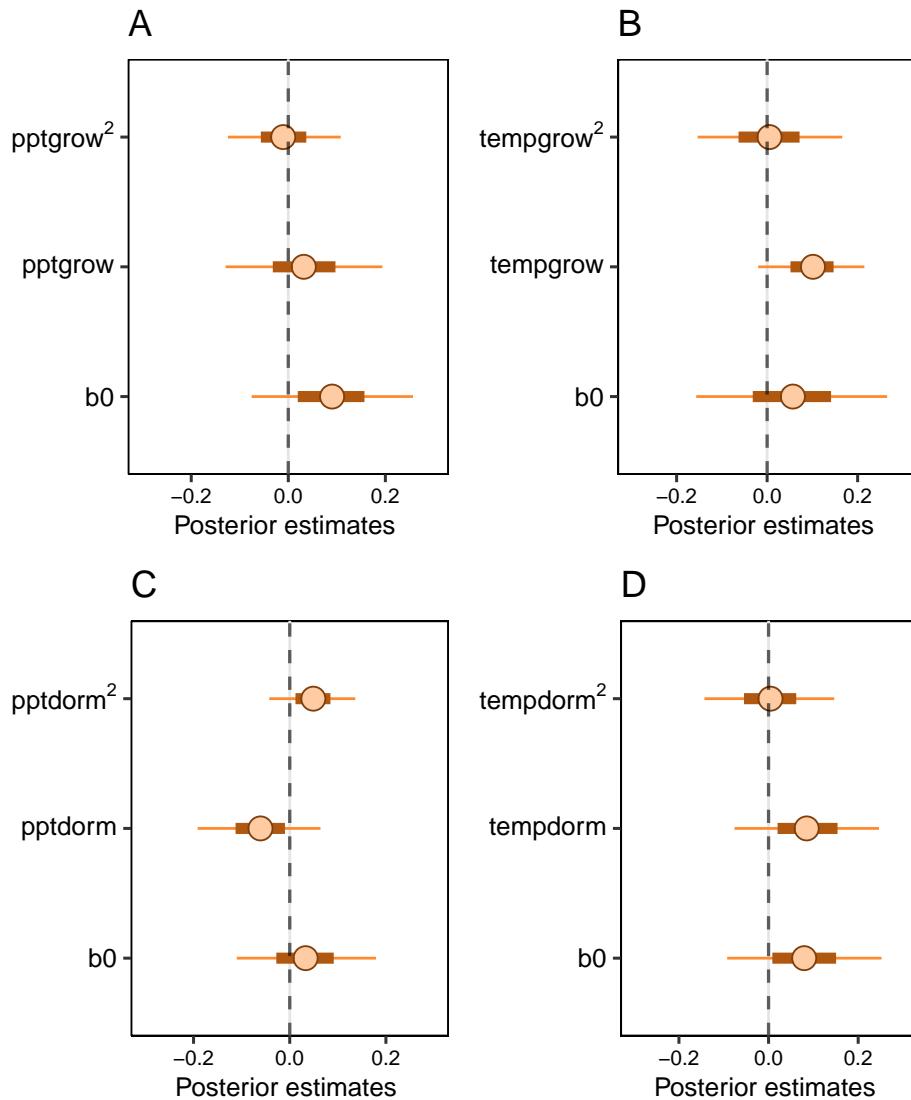


Figure S-13: Mean parameter values and 95% credible intervals of the posterior probability distributions. pptgrow is the precipitation of growing season, Tempgrow is the temperature of growing season, pptdorm is the temperature of dormant season, Tempdorm is the temperature of dormant season.

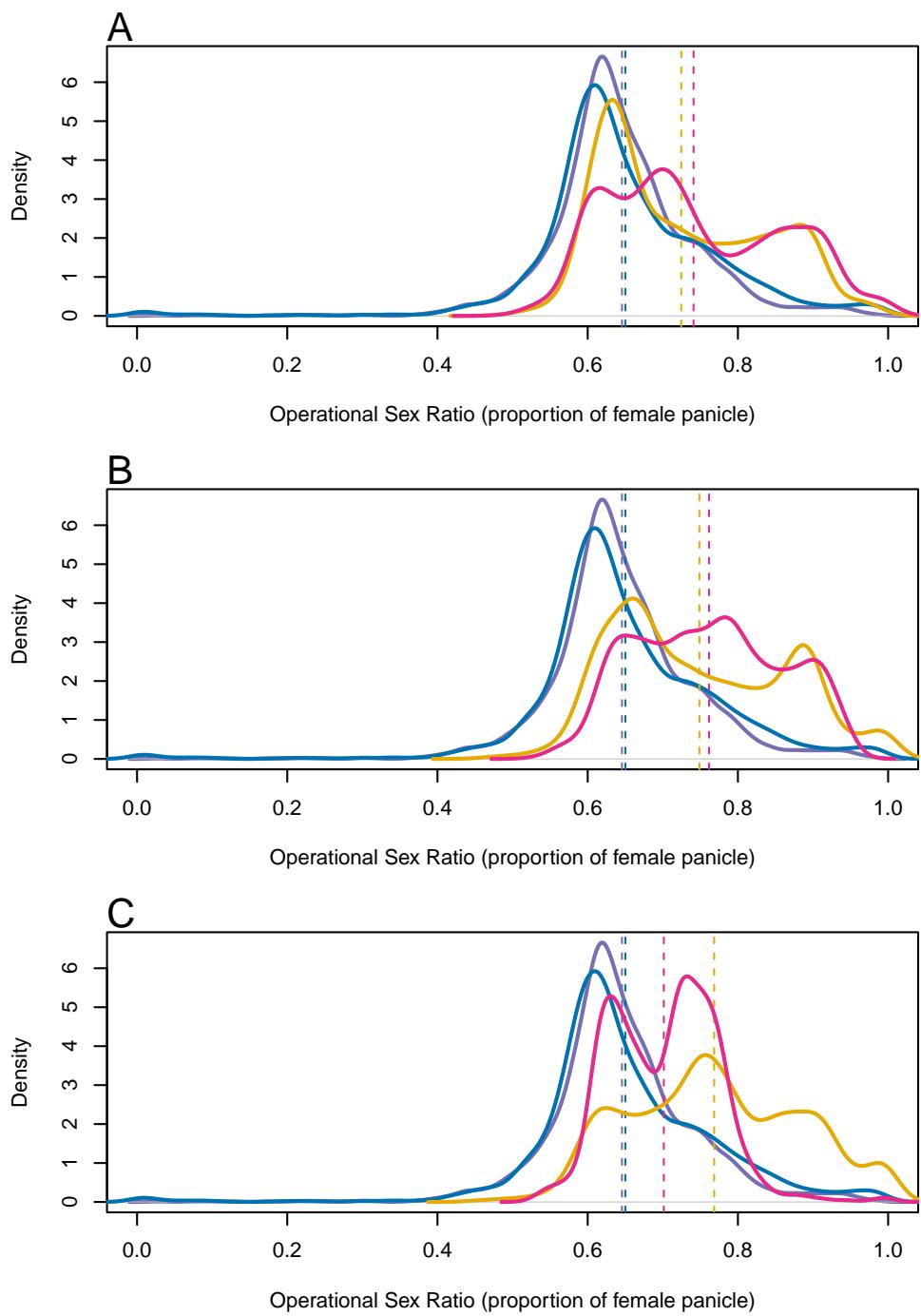


Figure S-14: Change in Operational Sex Ratio (proportion of female) over time (past, present, future). Future projections were based on A) MIROC 5, B) CES, C) ACC. The means for each model are shown as vertical dashed lines.

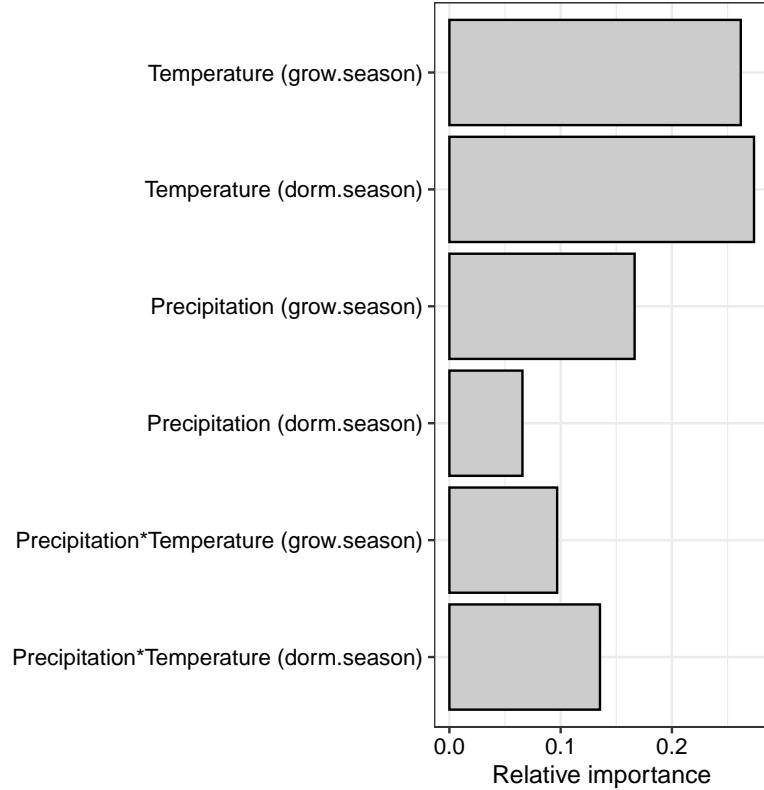


Figure S-15: Life Table Response Experiment: The bar represent the relative importance of each predictors.

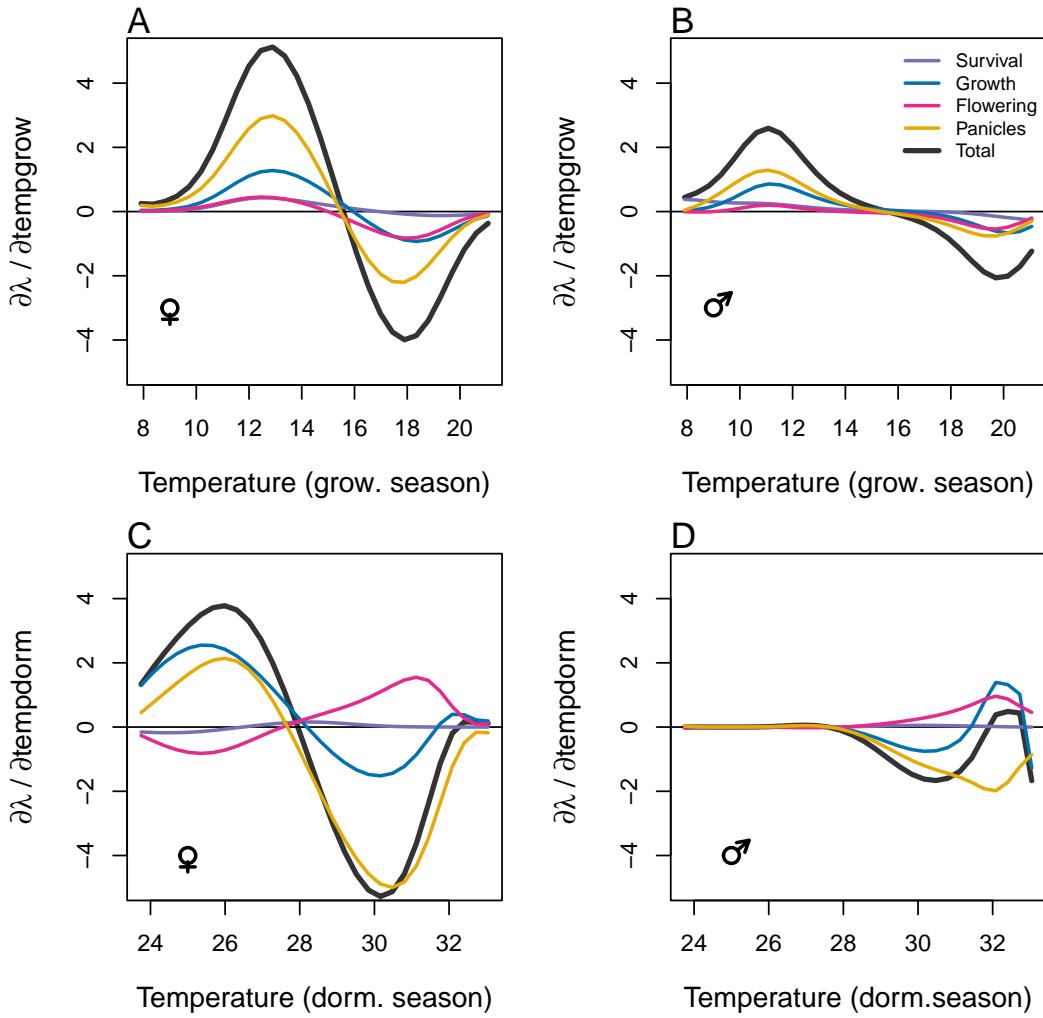


Figure S-16: Life table response experiment decomposition of the sensitivity of λ to seasonal climate into additive vital rate contributions of males and females based on posterior mean parameter estimates. (A) Temperature of growing season (contribution of female), (B) Temperature of growing season (contribution of male), (C) Temperature of dormant season (contribution of female) and (D) Temperature of dormant season (contribution of male).

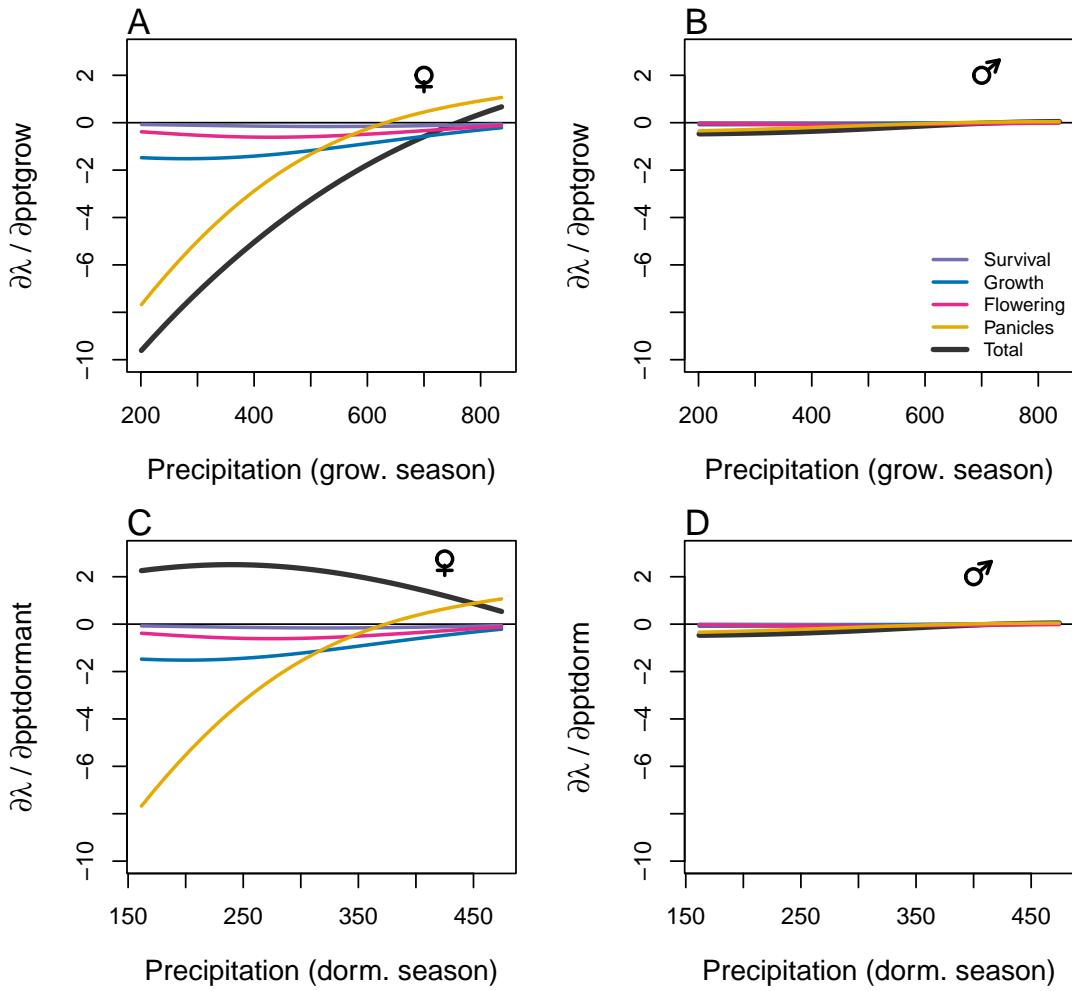


Figure S-17: Life table response experiment decomposition of the sensitivity of λ to seasonal climate into additive vital rate contributions of males and females based on posterior mean parameter estimates. (A) Precipitation of growing season (contribution of female), (B) Precipitation of growing season (contribution of male), (C) Precipitation of dormant season (contribution of female) and (D) Precipitation of dormant season (contribution of male).

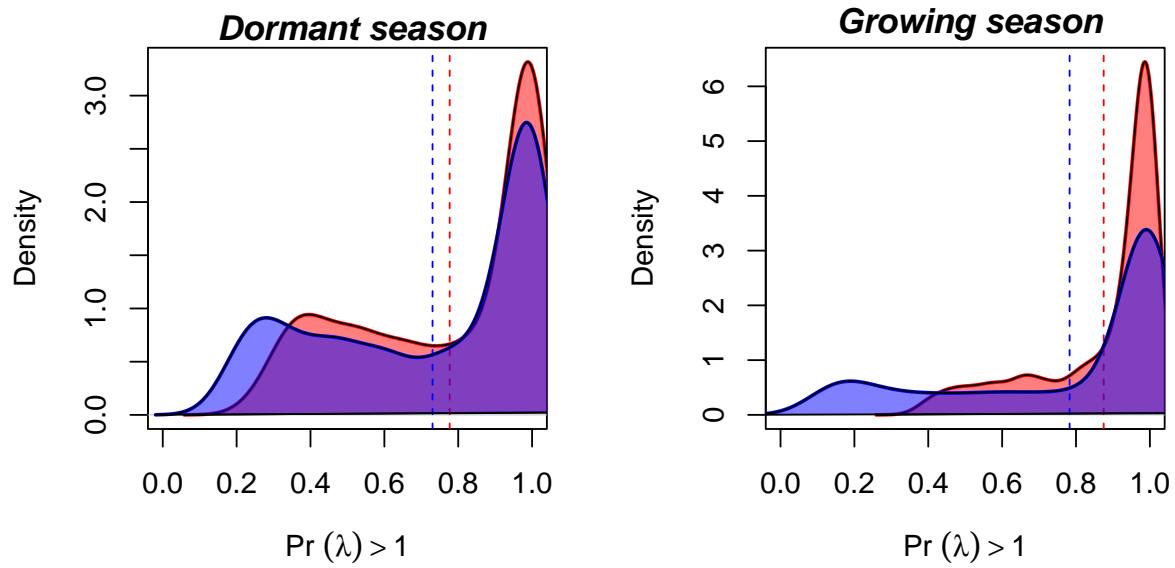


Figure S-18: Assessment of the statistical difference between the two-sex models and the female dominant model for the dormant and growing season. Plots show the density of $\Pr(\lambda) > 1$ values for female dominant (pink) and two-sex models (violet) for each season. The means for each model are shown as vertical dashed lines.

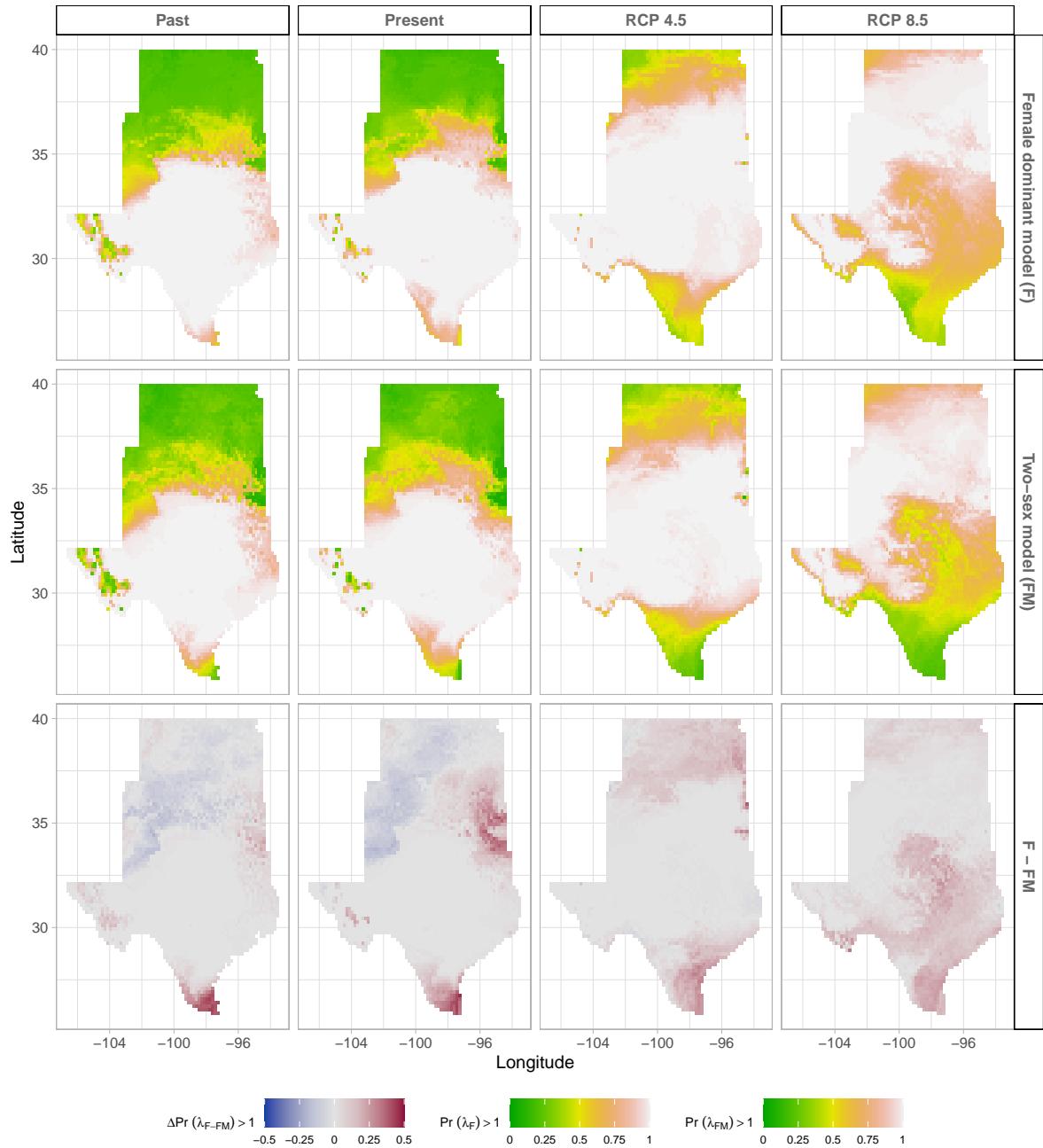


Figure S-19: Climate change favors range shift toward the North edge of the current range. (A) Past, (B) Current, (C and D) Future predicted range shift based on the predicted probabilities of self- sustaining populations, $\Pr(\lambda > 1)$, using the two-sex model that incorporates sex- specific demographic 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, $\Pr(\lambda > 1)$, 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 $\Pr(\lambda > 1)$, confirming that our study approach can reasonably predict range shifts.

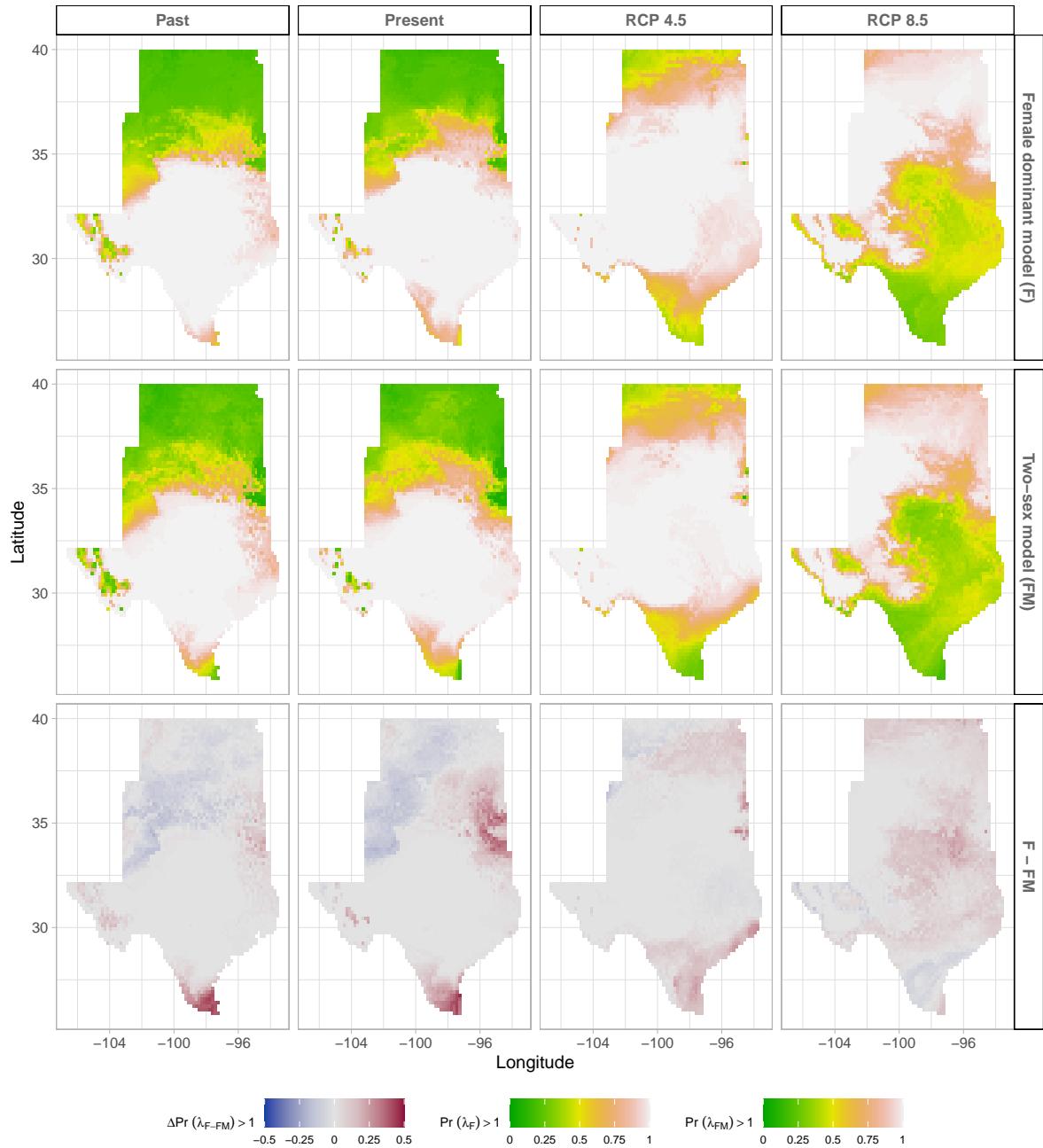


Figure S-20: Climate change favors range shift toward the North edge of the current range. (A) Past, (B) Current, (C and D) Future predicted range shift based on the predicted probabilities of self- sustaining populations, $\Pr(\lambda > 1)$, using the two-sex model that incorporates sex- specific demographic 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, $\Pr(\lambda > 1)$, 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 $\Pr(\lambda > 1)$, confirming that our study approach can reasonably predict range shifts.

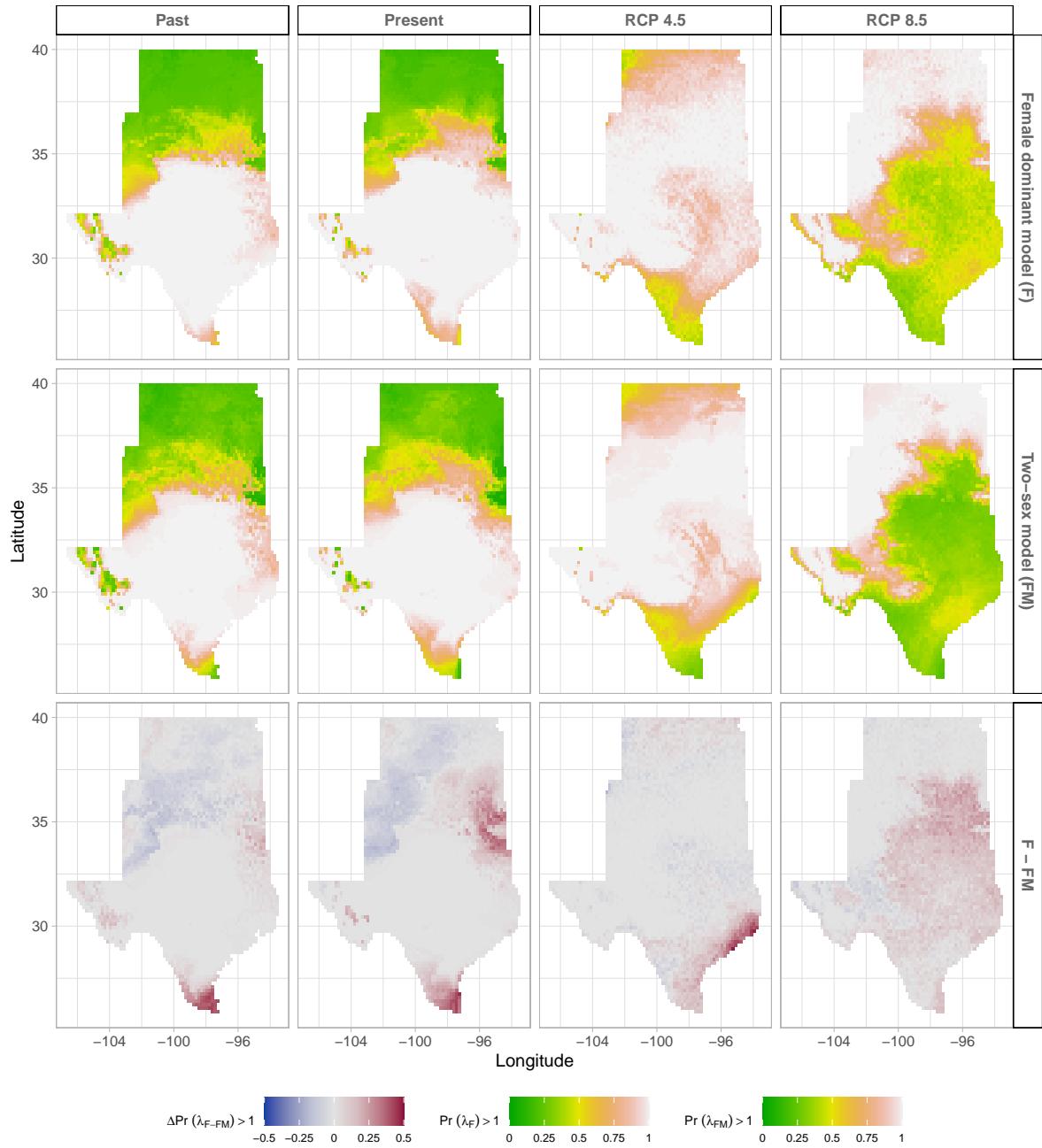


Figure S-21: Climate change favors range shift toward the North edge of the current range. (A) Past, (B) Current, (C and D) Future predicted range shift based on the predicted probabilities of self- sustaining populations, $\text{Pr}(\lambda > 1)$, using the two-sex model that incorporates sex- specific 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.

612 **S.2 Supporting Methods**

613 **Sex ratio experiment**

614 To estimate the probability of seed viability, the germination rate and the effect of sex-ratio
615 variation on female reproductive success, we conducted a sex-ratio experiment at one site
616 near the center of the range to estimate the effect of sex-ratio variation on female reproductive
617 success. The details of the experiment are provided in Compagnoni et al. (2017) and Miller
618 and Compagnoni (2022b). Here we provide a summary of the experiment. We established
619 124 experimental populations in plots measuring 0.4 × 0.4m and separated by at least 15m
620 from each other. We varied population density (1-48 plants/plot) and sex ratio (0%-100%
621 female) across the experimental populations, and we replicated 34 combinations of density
622 and sex ratio. We collected panicles from a subset of females in each plot and recorded the
623 number of seeds in each panicle. We assessed reproductive success (seeds fertilized) using
624 greenhouse-based germination and trazolium-based seed viability assays. Seed viability was
625 modeled with a binomial distribution where the probability of viability (v) was given by:

626
$$v = v_0 * (1 - OSR^\alpha) \quad (\text{S.1})$$

627 where OSR is the proportion of panicles that were female in the experimental populations.
628 α is the parameter that control for how viability declines with increasing female bias. Further,
629 germination rate was modeled using a binomial distribution to model the germination
630 data from greenhouse trials. Given that germination was conditional on seed viability, the
631 probability of success was given by the product $v * g$, where v is a function of OSR (Eq. S.1)
632 and g is assumed to be constant.