

Forecasting range shifts of a dioecious plant species under climate change

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Running header: Forecasting range shifts

Keywords: demography, forecasting, global warming, matrix projection model, population dynamics, sex ratio, range limits

Submitted to: *Ecology letters* (Letter)

Data accessibility statement: All data used in this paper are publicly available and cited appropriately (Miller and Compagnoni, 2022a). Should the paper be accepted, all computer scripts supporting the results will be archived in a Zenodo package, with the DOI included at the end of the article. During peer review, our code (Stan, Bash and R) is available at <https://github.com/jmoutouama/POAR-Forecasting>.

Conflict of interest statement: None.

Authorship statement: J.K.M., A.C. and T.E.X.M. designed the study. A.C. and T.E.X.M. collected the data. All authors conducted the statistical analyses and modeling. J.K.M. drafted the manuscript, and T.E.X.M contributed to revisions.

Abstract:

Main Text:

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¹ Abstract

² Global climate change has triggered an urgent need for predicting the reorganization of Earth's
³ biodiversity. Currently, the vast majority of models used to forecast population viability and
⁴ range shifts in response to climate change ignore the complication of sex structure, and thus
⁵ the potential for females and males to differ in their sensitivity to climate drivers. We developed
⁶ demographic models of range limitation, parameterized from geographically distributed com-
⁷ mon garden experiments, with females and males of a dioecious grass species (*Poa arachnifera*)
⁸ throughout and beyond its range in the south-central U.S. Female-dominant and two-sex
⁹ model versions both predict that future climate change will alter population viability and
¹⁰ will induce a poleward niche shift beyond current northern limits. However, the magnitude of
¹¹ niche shift was underestimated by the female-dominant model, because females have broader
¹² temperature tolerance than males and become mate-limited under female-biased sex ratios.
¹³ Our result illustrate how explicit accounting for both sexes could enhance population viability
¹⁴ forecasts and 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 Species' range limits, when not driven by dispersal limitation, should generally reflect the limits
20 of the ecological niche (Lee-Yaw et al., 2016). Niches and geographic ranges are often limited
21 by climatic factors including temperature and precipitation (Sexton et al., 2009). Therefore,
22 any substantial changes in the magnitude of these climatic factors could impact population
23 viability, with implications for range expansions or contractions based on which regions of
24 a species' range become more or less suitable (Davis and Shaw, 2001; Pease et al., 1989).

25 Forecasting range shifts for dioecious species (most animals and ca. 7% of plant species)
26 is complicated by the potential for each sex to respond differently to climate variation (Hultine
27 et al., 2016; Morrison et al., 2016; Pottier et al., 2021; Tognetti, 2012). ¹ Accounting for sexual
28 niche differentiation is a long-standing challenge in accurately predicting which sex will suc-
29 cessfully track environmental change and how this will impact population viability and range
30 shifts (Gissi et al., 2023; Jones et al., 1999). Populations in which males are rare under current
31 climatic conditions could experience low reproductive success due to sperm or pollen limita-
32 tion that may lead to population decline in response to climate change that disproportionately
33 favors females (Eberhart-Phillips et al., 2017). In contrast, climate change could expand male
34 habitat suitability (e.g. upslope movement), which might increases seed set for pollen-limited
35 females and favor range expansion (Petry et al., 2016). **Across dioecious plants, studies suggest**
36 **that future climate change toward hotter and drier conditions may favor male-biased sex ratios**
37 **(Field et al., 2013; Hultine et al., 2016).** ² Although the response of species to climate warming
38 is an urgent and active area of research, few studies have disentangled the interaction between
39 sex and climate drivers to understand their combined effects on population dynamics and
40 range shifts, despite calls for such an approach (Gissi et al., 2023; Hultine et al., 2016).

41 The vast majority of theory and models in population biology, including those used
42 to forecast biodiversity responses to climate change, ignore the complication of sex structure
43 (but see Ellis et al., 2017; Gissi et al., 2024; Pottier et al., 2021). Traditional approaches instead
44 focus exclusively on females, assuming that males are in sufficient supply as to never limit
45 female fertility. In contrast, "two-sex" models are required to fully account for demographic
46 differences between females and males and sex-specific responses to shared climate drivers

¹Something this paragraph is missing is a mechanistic explanation for why females and males may have different climate sensitivity, likely something about costs of reproduction. This would be a good place for a sentence or two that addresses this.

²I am not sure if this is the best spot for it, but I think this prediction from the literature is relevant to bring up in the Intro.

(Gerber and White, 2014; Miller et al., 2011). Sex differences in maturation, reproduction, and mortality schedules can generate skew in the operational sex ratio (OSR; sex ratio of individuals available for mating) even if the birth sex ratio is 1:1 (Eberhart-Phillips et al., 2017; Shelton, 2010). Climate and other environmental drivers can therefore influence the OSR via their influence on sex-specific demographic rates. In a two-sex framework, demographic rates both influence and respond to the OSR in a feedback loop that makes two-sex models inherently nonlinear and more data-hungry than corresponding female-dominant models. Given the additional complexity and data needs, forecasts of range dynamics for dioecious species under future climate change that explicitly account for females, males, and their inter-dependence are limited (Lynch et al., 2014; Petry et al., 2016).

Tracking the impact of climate change on population viability (λ) and distributional limits of dioecious taxa depends on our ability to build mechanistic models that take into account the spatial and temporal context of sex specific response to climate change, while accounting for sources of uncertainty (Czachura and Miller, 2020; Davis and Shaw, 2001; Evans et al., 2016). Structured population models built from demographic data collected from geographically distributed observations or common garden experiments provide several advantages for studying the impact of climate change on species' range shifts (Merow et al., 2017; Schultz et al., 2022; Schwinning et al., 2022). First, demographic models link individual-level life history events (mortality, development, and regeneration) to population demography, allowing the investigation of factors explaining vital rate responses to environmental drivers (Dahlgren et al., 2016; Ehrlén and Morris, 2015; Louthan et al., 2022). Second, demographic models have a natural interface with statistical estimation individual-level vital rates that provide quantitative measures of uncertainty and isolate different sources of variation, features that can be propagated to population-level predictions (Elderd and Miller, 2016).³ Finally, structured demographic models can be used to identify which aspects of climate are the most important drivers of population dynamics. For example, Life Table Response Experiments (LTRE) built from structured models have become widely used to understand the relative importance of covariates in explaining variation in population growth rate (Ellner et al., 2016; Hernández et al., 2023).⁴

In this study, we combine geographically-distributed common garden experiments, hierarchical Bayesian statistical modeling, two-sex population projection modeling, and climate back-casting and forecasting to understand demographic responses to climate change and their implications for past, present, and future range dynamics. Our work focused on the dioecious plant Texas bluegrass (*Poa arachnifera*), which is distributed along environmental

³I cut the sentence about experiments because I don't think our data really exemplify this. While we did do an experiment, we did not manipulate climate, so we are subject to the same correlations as observational studies.

⁴I think LTRE is a relatively small part of the paper so I suggested reducing the amount of text on it here.

80 gradients in the south-central U.S. corresponding to variation in temperature across latitude
81 and precipitation across longitude (Fig. 1). This region has experienced rapid climate warming
82 since 1900 and this is projected to continue through the end of the century (Fig. S-1). Our
83 previous study showed that, despite evidence for differentiation of climatic niche between
84 sexes, the female niche mattered the most in driving longitudinal range limits of Texas
85 bluegrass (Miller and Compagnoni, 2022b). However, that study used a single proxy variable
86 (longitude) to represent environmental variation related to aridity and did not consider
87 variation in temperature, which is the much stronger dimension of forecasted climate change
88 in this region (Fig. S-1,S-2). Developing a rigorous forecast for the implications of future
89 climate change requires that we transition from climate-implicit to climate-explicit treatment of
90 multiple environmental drivers as we do here. Leveraging the power of Bayesian inference, we
91 take a probabilistic view of past, present, and future range limits by quantifying the probability
92 of population viability ($Pr(\lambda_1)$) in relation to climate drivers of demography, given uncertainty
93 arising from multiple sources of estimation and process error. Specifically, we asked:

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

101 Materials and methods

102 Study species

103 Texas bluegrass (*Poa arachnifera*) is a dioecious perennial, summer-dormant cool-season (C3)
104 grass that occurs in the south-central U.S. (Texas, Oklahoma, and southern Kansas) (Figure 1)
105 (Hitchcock, 1971)⁵. Latitudinal limits of the Texas bluegrass distribution span 7.74 °C to 16.94
106 °C of temperature during the dormant season and 24.38 °C to 28.80 °C during the dormant sea-
107 son. Longitudinal limits span 244.9 mm to 901.5 mm of precipitation during the growing sea-
108 son and 156.3 mm to 373.3 mm. Texas bluegrass grows between October and May (growing sea-
109 son), with onset of dormancy often from June to September (dormant season) (Kindiger, 2004).

⁵I have updated the map

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

116 **Common garden experiment**

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

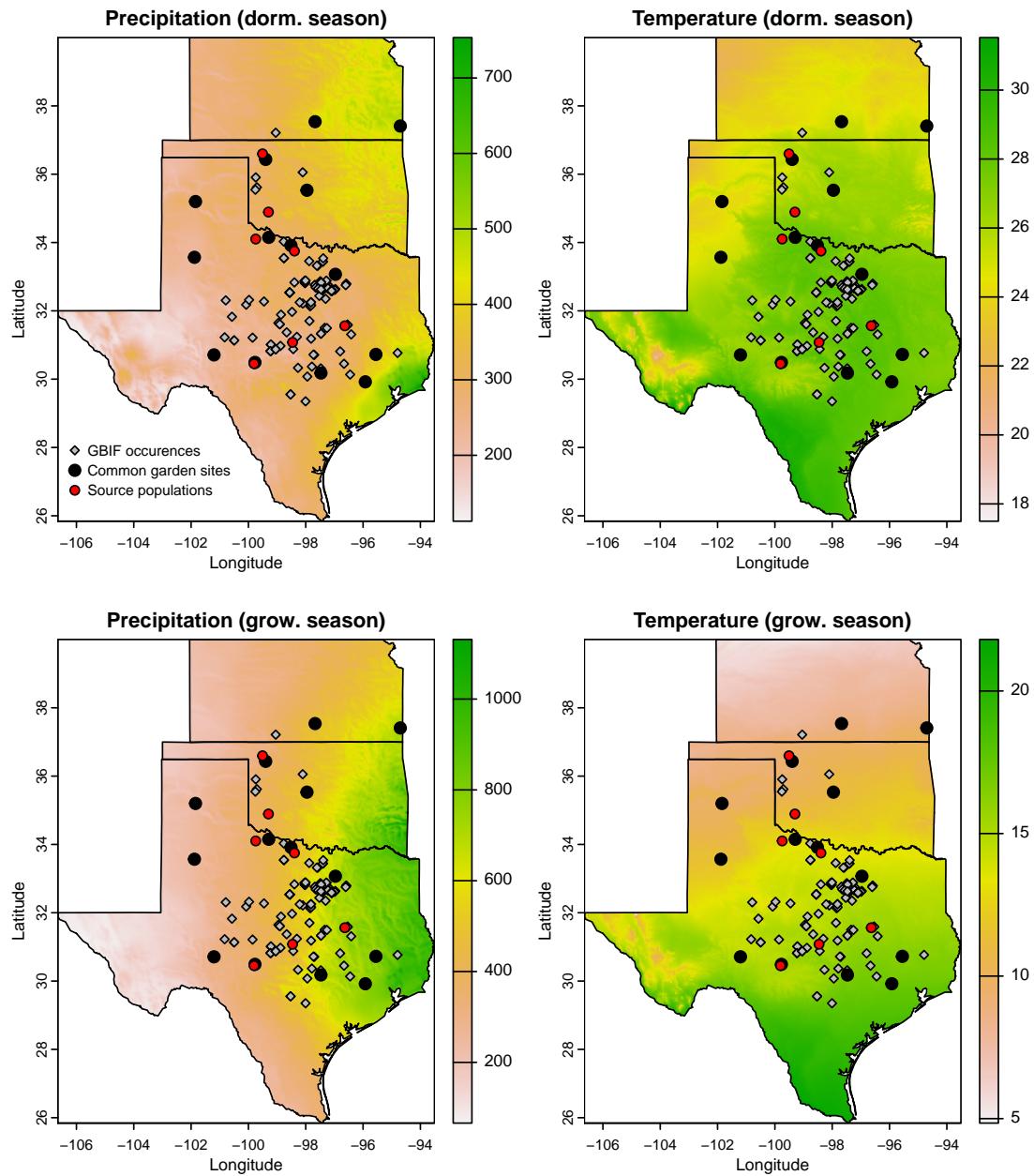


Figure 1: Maps of 30-year (1990-2019) normal climate and study sites used for demographic monitoring of *Poa arachnifera* in Texas, Kansas and Oklahoma in the United States. Precipitation of growing and precipitation of dormant season are in mm, temperature of the dormant and temperature of growing season 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.

130 **Climatic data collection**

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

137 To back-cast and forecast demographic responses to changes in climate throughout the
138 study region, we downloaded projection data for three 30-year periods: “past” (1901-1930),
139 “current” (1990-2019) and “future” (2070-2100). Data for future climatic periods were
140 downloaded from four general circulation models (GCMs) selected from the Coupled Model
141 Intercomparison Project Phase 5 (CMIP5). The GCMs are: Model for Interdisciplinary
142 Research on Climate (MIROC5), Australian Community Climate and Earth System Simulator
143 (ACCESS1-3), Community Earth System Model (CESM1-BGC), Centro Euro-Mediterraneo sui
144 Cambiamenti Climatici Climate Model (CMCC-CM). All the GCMs were also downloaded
145 from chelsa (Sanderson et al., 2015). We evaluated future climate projections from two
146 scenarios of representative concentration pathways (RCPs): RCP4.5, an intermediate-to-
147 pessimistic scenario assuming a radiative forcing amounting to 4.5 Wm^{-2} by 2100, and
148 RCP8.5, a pessimistic emission scenario which projects a radiative forcing of 8.5 Wm^{-2} by
149 2100 (Schwalm et al., 2020; Thomson et al., 2011).

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

155 **Sex specific demographic responses to climate**

⁶ We used individual level measurements of survival, growth (number of tillers), flowering, number of panicles to develop Bayesian linear mixed effect models describing how each vital rate varies as a function of sex, size, and four climate covariates (precipitation and temperature of growing and dormant season). We kept the four climate covariates in the mixed effect models because each climatic variable describes different aspect of climate that could be important for the species persistence across its range. Vital rate models were

⁶ 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.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Since the climate-dependent vital rate regressions were built using MCMC, we were able to propagate the uncertainty in vital rate parameters to uncertainty in predicted population growth rates (λ). We estimated population growth rate for the female dominant MPM using the function lambda in the package popbio (Stubben and Milligan, 2007). Since the two-sex MPM is nonlinear (vital rates affect and are affected by population structure) we estimated the asymptotic geometric growth rate (λ) by numerical simulation, and repeated this across a range of climate⁷.

Life Table Response Experiments

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

⁷I 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

⁸I 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.

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

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

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

215 where, θ_i^F and θ_i^M represent sex-specific parameters: the regression coefficients for the
 216 intercepts and slopes of size-dependent vital rate functions. Because LTRE contributions are
 217 additive, we summed across vital rates to compare the total contributions of female and male
 218 parameters.⁹

219 Climate change impacts on sex ratio

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

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

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

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

⁹ θ_i^F and θ_i^M include the interaction and second order effect. I think we are good with this formula

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

228 To understand the impact of climate change on species niche shifts, we estimated the
229 probability of self- sustaining populations, which is $\Pr(\lambda > 1)$ conditional to (i) temperature
230 and precipitation of the dormant season or to (ii) temperature and precipitation of the
231 growing season. $\Pr(\lambda > 1)$ was calculated for the two-sex model and the female dominant
232 MPMs using the proportion of the 300 Markov chain Monte Carlo iterations that lead to a
233 $\lambda > 1$ (Diez et al., 2014). The probability of self- sustaining populations was then represented
234 as a contour plot with values of $\Pr(\lambda > 1)$ at given temperature and precipitation for the
235 growing and dormant season across time (past, present and future).

236 $\Pr(\lambda > 1)$ was also mapped onto geographic layers of three state (Texas, Oklahoma and
237 Kansas) to delineate past, current and future potential distribution of the species. To do so,
238 we estimated $\Pr(\lambda > 1)$ conditional to all climate covariates for each pixel ($\sim 25 \text{ km}^2$) across
239 the species range for each time period (past, present, future). Because of the amount of the
240 computation involved in the Markov chain Monte Carlo iterations, use only 100 posterior
241 samples to estimate $\Pr(\lambda > 1)$ across the study area (Texas, Oklahoma and Kansas).

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

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

245 **Results**

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

247 We found a sex specific demographic response to climatic gradient in *Poa arachnifera*
248 populations. Specifically, female individuals had higher survival and flowering rate than male
249 across species range during the dormant and growing season (Figure 2A-3D, 3I-3L). Male
250 individuals produce more panicles than female across species range (Figure 2M-3P). On the
251 contrary, female had a size advantage for low value values of climate during the growing
252 season and for high values of climate during the dormant season (Figure 2E-3H). We also
253 found opposite patterns in the direction of the effect on climate on the probability of survival
254 and flowering. If temperature of the growing seasons and dormant season are constant, then
255 precipitation of the growing season has a negative effect on the probability of survival, the
256 number of tillers, and the probability of flowering (Figure 2). In contrast, if temperature of
257 the growing and dormant season are constant, then the precipitation of dormant season has
258 a positive effect on these vital rates (Figure 2E-3H). If precipitation of growing and dormant

259 season are constant, then temperature of the growing season has a positive effect of the
 260 probability of survival, a negative effect on the probability of flowering, and the number of
 261 tillers, but no significant effect on the number of panicles (Figure 2).¹⁰

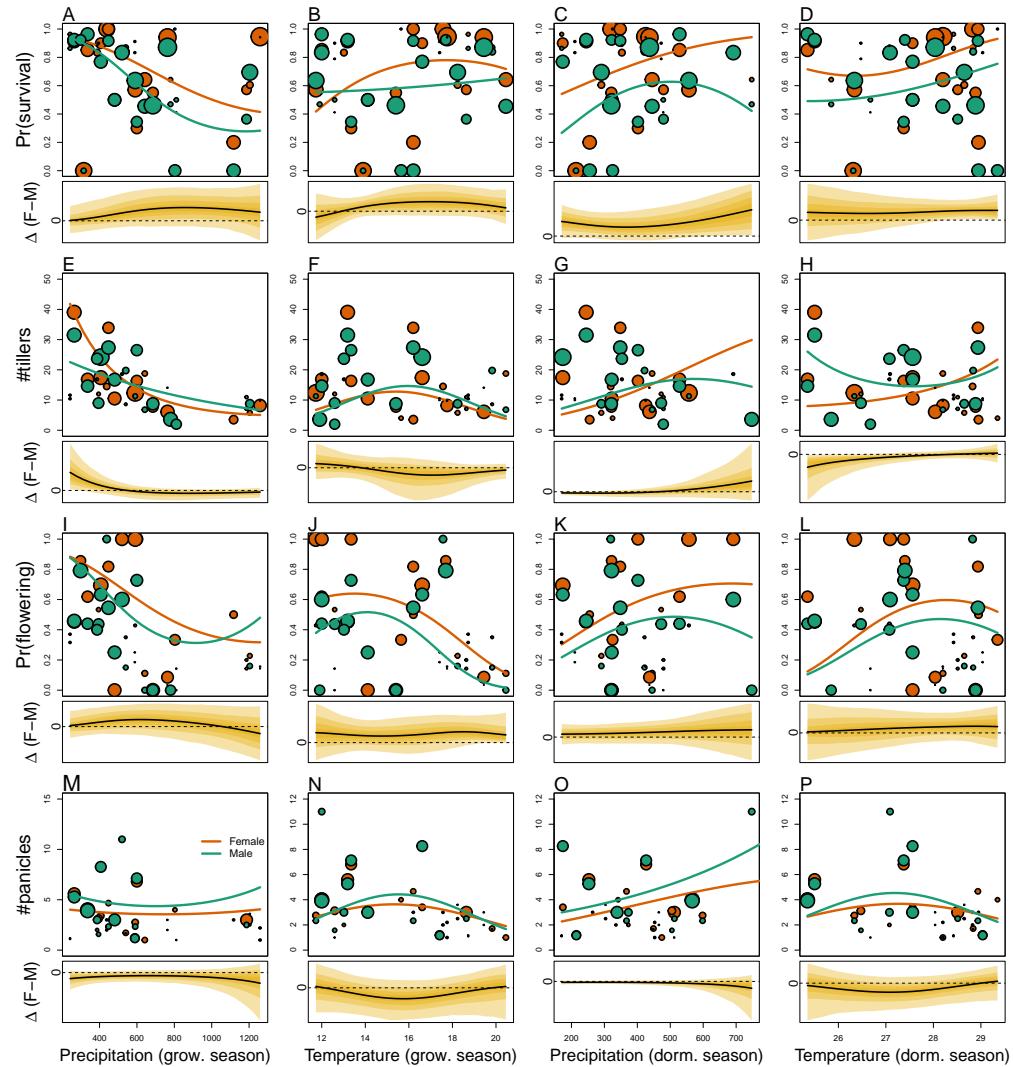


Figure 2: Sex specific demographic response to climate across species range. (A, B, C, D) Probability of survival as a function of precipitation and temperature of the growing and dormant season. (E, F, G, H) Change in number of tillers as a function of precipitation and temperature of the growing and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

¹⁰I tried to add the conditionality here. I hope it makes sense

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

263 Operational-Sex Ratio (proportion of females panicles) increased significantly with an increase
264 of precipitation and temperature of the growing season and precipitation and temperature
265 of dormant season (Figure S-10, Figure S-11). Similarly, the proportion of female plants
266 increased with an increase of temperature of growing season and temperature of dormant
267 season (Figure S-12 B, D, Figure S-13). However, the proportion of female plants did not vary
268 significantly with precipitation of dormant and growing season (Figure S-12 A, C). Future
269 climate drive to extreme female-biased in *Poa arachnifera* populations (Figure 3, Figure S-14).

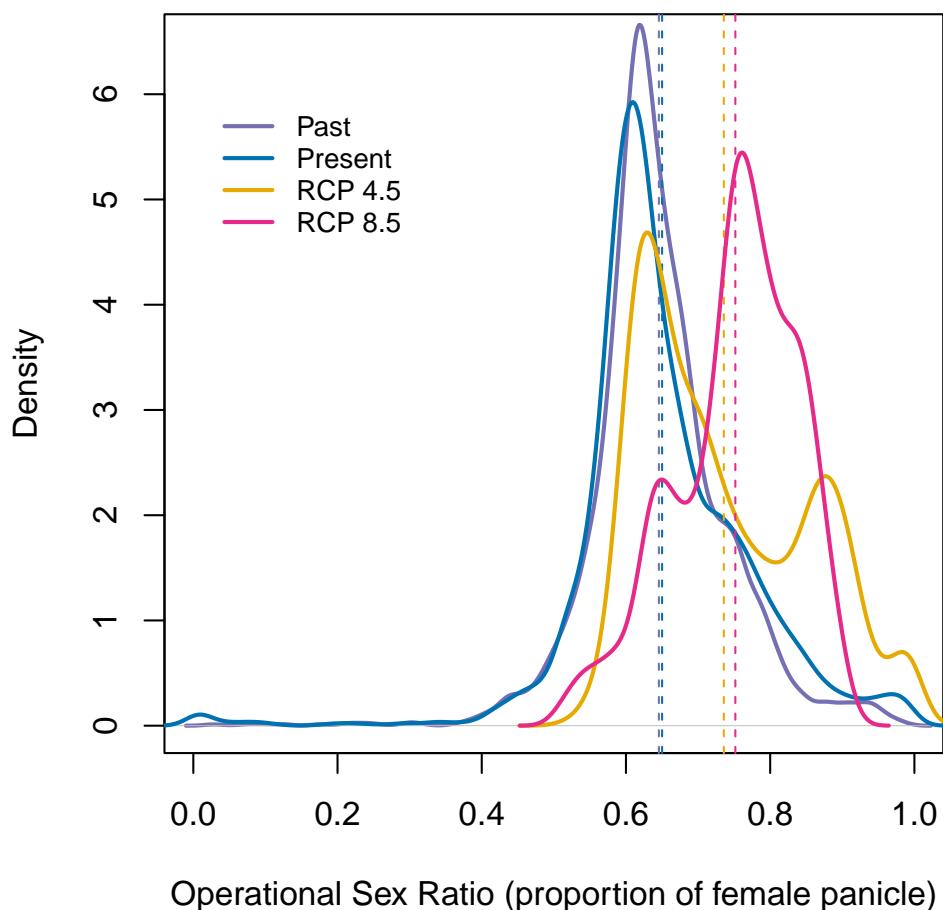


Figure 3: Change in Operational Sex Ratio (proportion of female panicule) over time (past, present, future). Future projections were based on the CMCC-CM model. The mean sex ratio for each time period is shown as vertical dashed line.

270 **Climate change alters population viability**

271 We estimated population growth rate variation across species range as a function of each
272 climatic variable given the average of the three other climatic variables using two models:
273 a female dominant model and a two-sex model¹¹. For both models, population growth rate
274 decreased toward high precipitation of growing season (Figure 4A). In contrast population
275 growth rate increased with an increase in precipitation of the dormant season (Figure 4C).
276 Furthermore, population growth rate was maximized between 14 and 17 °C and decreased
277 bellow zero beyond 18 °C during the growing season (Figure 4B). Similarly population fitness
278 was maximized between 27 and 31 °C and decreased bellow zero just beyond 20 °C during
279 the dormant season (Figure 4D).¹²

280 We have also detected a strong association between predicted lambda and different
281 ranges of climate (past, present and future). Under past climate conditions, population growth
282 rate decreased below one for temperature of the growing season. Populations will still be
283 viable under moderate gas emission (RCP4.5). However high gas emission (RCP8.5) will alter
284 population viability (Figure 4B, D).¹³

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

¹¹I have now provided the methods for this contrast.

¹²I 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.

¹³I changed how I write the first sentence to remove the "effect of climate on". Again I don't mind removeing the Figure.

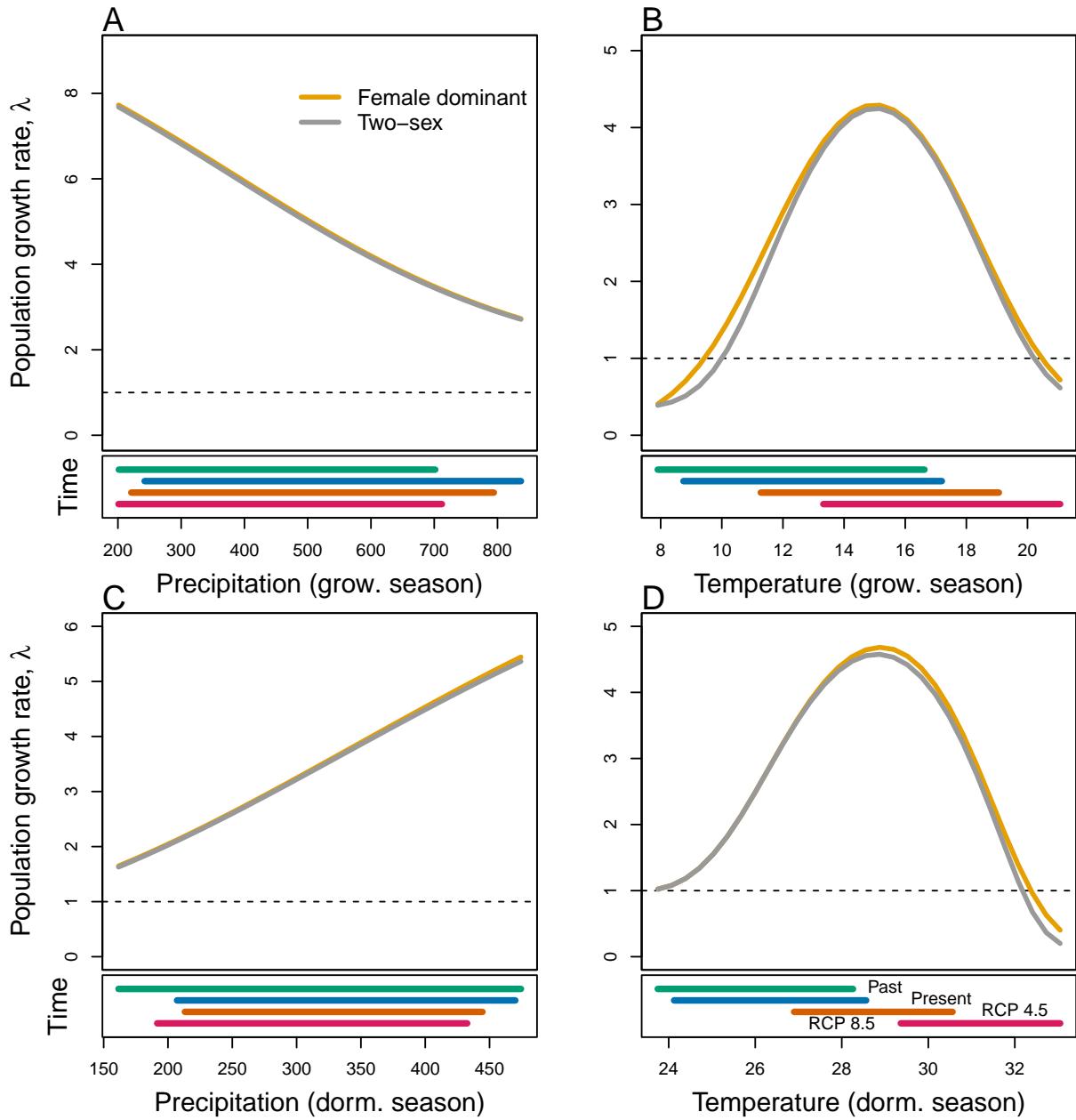


Figure 4: Predicted population growth rate (λ) in different ranges of climate. (A) Precipitation of the growing season, (B) Temperature of the growing season, (C) Precipitation of the dormant season, (D) Temperature of the dormant season. The grey curve shows prediction by the two-sex matrix projection 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).

²⁹² **Climatic change induces niche and range shifts**

²⁹³ Female dominant model and two-sex models predicts a niche shift in *Poa arachnifera*
²⁹⁴ populations (Figure 5). However, the female dominant model underestimated the magnitude
²⁹⁵ of niche shifts (Figure 5E, F; -0.16[-0.29,-0.03]). Female dominant model and the two-sex
²⁹⁶ models agree that viable populations of *P. arichnifera* were only predicted at the center of the
²⁹⁷ range for current climatic conditions (Figure 6). Although *P. arichnifera* was predicted to have
²⁹⁸ suitable habitats in the center of the range under current climate, global warming is projected
²⁹⁹ to reduce much of these suitable habitats (Figure 6). If the species is able to disperse far and
³⁰⁰ if there is no physical barriers, most of the current suitable habitats will move toward the
³⁰¹ Northern range edge as a results of niche shifts. Niche shift underestimation by the female
³⁰² dominant model led to a geographic range underestimation by the female dominant model.

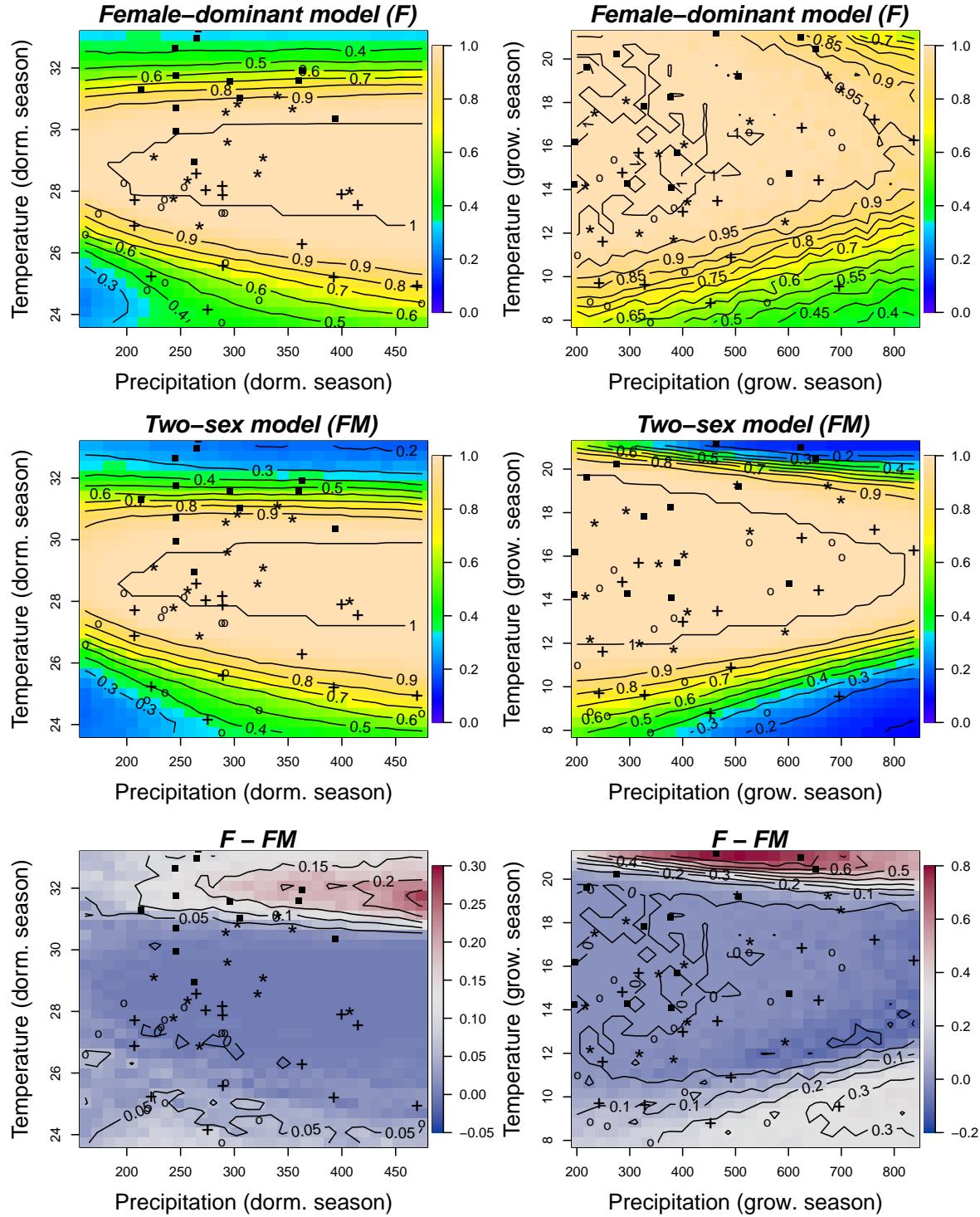


Figure 5: A two-dimensional representation of the predicted niche shift over time (past, present and future climate conditions). Contours on the first four panels show predicted probabilities of self-sustaining populations, $\text{Pr}(\lambda > 1)$ conditional on precipitation and temperature of the 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.

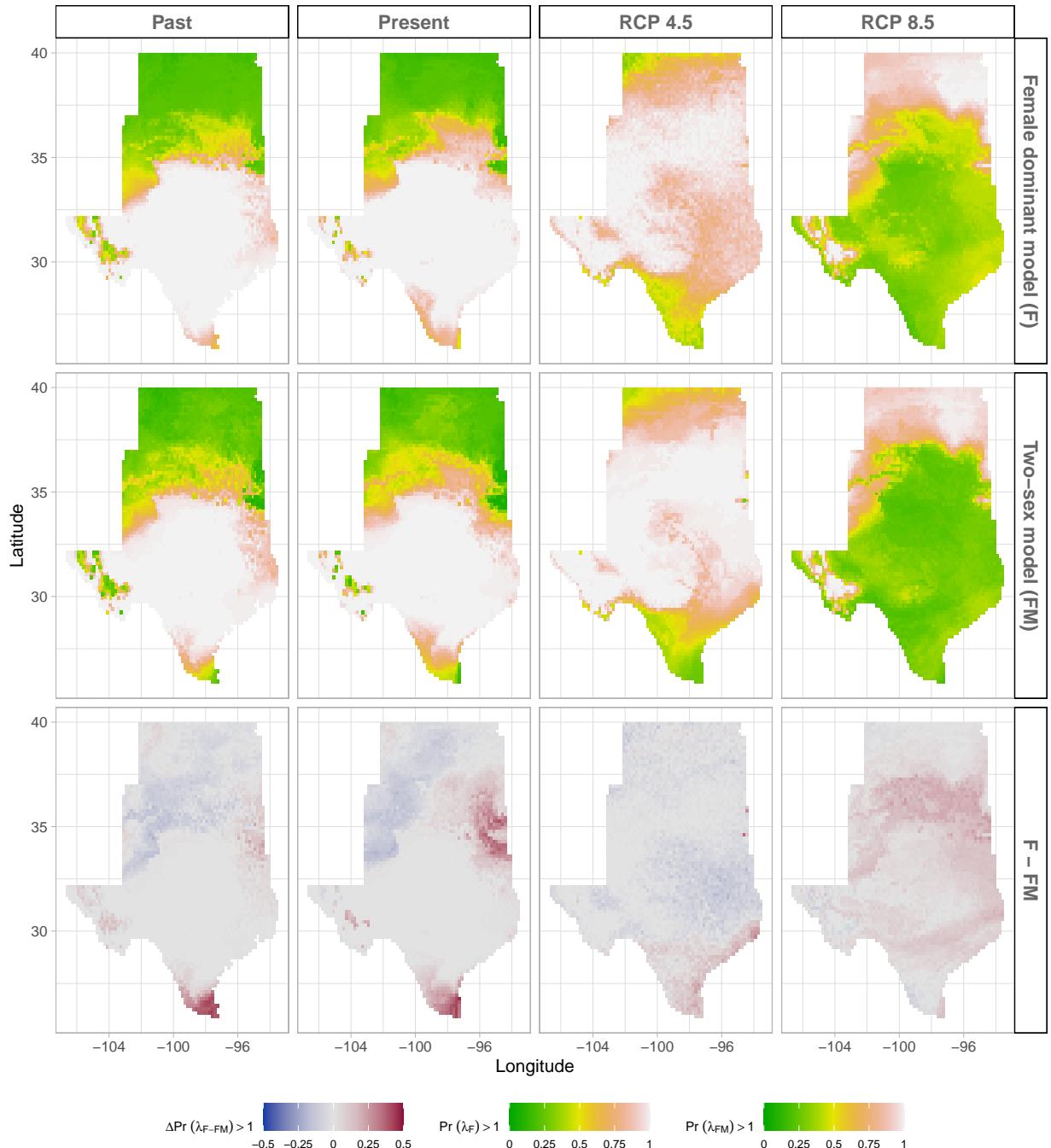


Figure 6: Climate change favors range shift towards north edge. (A) Past, (B) Current, (C and D) Future predicted range shift based on the predicted probabilities of self- sustaining populations, $\Pr(\lambda > 1)$, using the two-sex model that incorporates sex- specific demographic responses to climate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

303 **Discussion**

304 ¹⁴Dioecious species make up a large fraction of Earth's biodiversity – most animals and
305 many plants – yet we have little knowledge about how skewness in sex ratio will affect
306 population viability and range shifts of dioecious species under climate change. We used
307 three years of demographic data collected from common garden experiments across climatic
308 gradient to forecast for the first time the impact of climate change on dioecious species. Our
309 future projections require extrapolation to warmer or colder conditions than observed in
310 our experiment and subsequently should be interpreted with caution (Chen et al., 2024).
311 Despite all these limitations, the qualitative implications of the response of our study species
312 to increase temperature (dormant and growing season) seems consistent across all GCMs
313 (Figure S-19, Figure S-20, Figure S-21). Three general patterns emerged from our analysis
314 of range-wide common garden experiments and sex-structured, climate-explicit demographic
315 models. First, our Bayesian mixed effect model suggests a sex specific demographic response
316 to climate change that lead to higher proportion of female as climate increase. Second, climate
317 change favors a northern range shifts in suitable habitats. Third, the female dominant model
318 (model that does not account for sex structure) overestimates species niche and range shifts.

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

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

¹⁴This is my new proposition regarding the discussion

336 viability. Temperature can impact plant populations through different mechanisms. Increasing
337 temperature could increase evaporative demand, affect plant phenology (Iler et al., 2019;
338 McLean et al., 2016; Sherry et al., 2007), and germination rate (Reed et al., 2021). The potential
339 for temperature to influence these different processes changes seasonally (Konapala et al.,
340 2020). For example, studies suggested that species that are active during the growing season
341 such as cool grass species can have delayed phenology in response to global warming,
342 particularly if temperatures rise above their physiological tolerances (Cleland et al., 2007;
343 Williams et al., 2015). In addition, high temperature during the growing season by affecting
344 pollen viability, fertilization could affect seed formation and germination (Hatfield and
345 Prueger, 2015; Sletvold and Ågren, 2015). Pollen dispersal may allow plants to resist climate
346 change because pollen dispersal may provide the local genetic diversity necessary to adapt
347 at the leading edge of the population (Corlett and Westcott, 2013; Duputié et al., 2012; Kremer
348 et al., 2012). Since wind pollination is most effective at short distances, it is most often
349 found in plant species growing at high density such as our study species, it is less likely
350 that dispersal limitation affect niche shift in our study system. Difference in non-climatic
351 factors such as soil, or biotic interactions could also explain decline in population growth rate
352 as an indirect effects of increase in temperature (Alexander et al., 2015; Schultz et al., 2022).
353 For example, climate change could increase the strength of species competition and thereby
354 constrain our study species to a narrower realized niche (Aguilée et al., 2016; Pulliam, 2000).

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

³⁶⁹ **Conclusion**

³⁷⁰ We have investigated the potential consequence of skewness in sex ratio on population
³⁷¹ dynamics and range shift in the context of climate change using the Texas bluegrass. We
³⁷² found extreme female -biased in response to climate change. The effect of female biased
³⁷³ will induce range shifts to the northern edge of the species current range by limiting mate
³⁷⁴ availability. Beyond, our study case, our results also suggest that tracking only one sex could
³⁷⁵ lead to an underestimation of the effect of climate change on population dynamics. Our
³⁷⁶ work provides also a framework for predicting the impact of global warming on population
³⁷⁷ dynamics using the probability of population to self-sustain.

³⁷⁸ **Acknowledgements**

³⁷⁹ This research was supported by National Science Foundation Division of Environmental
³⁸⁰ Biology awards 1543651 and 1754468 and by the Rice University Faculty Initiatives Fund.

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Supporting Information

570 S.1 Supporting Figures

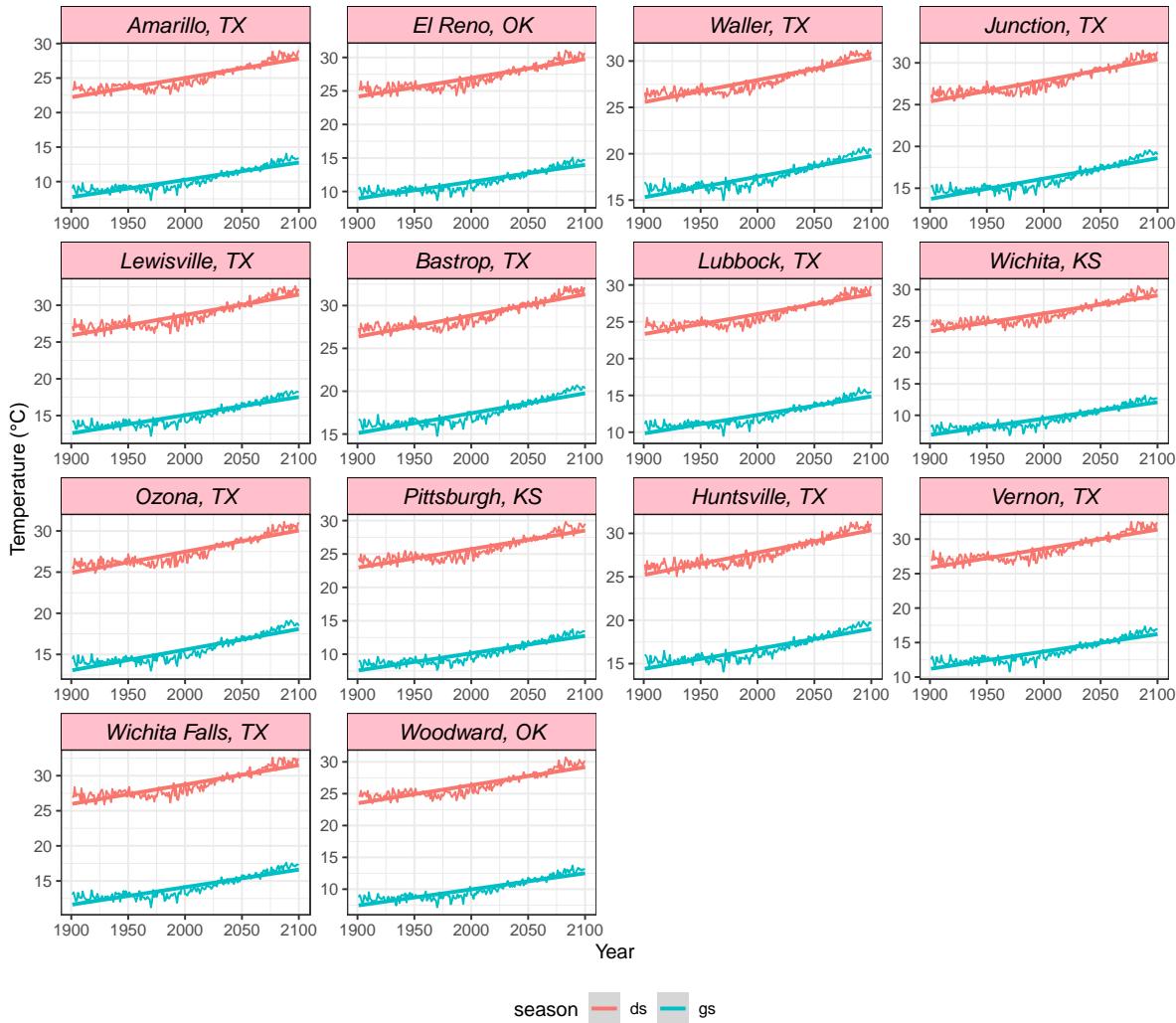


Figure S-1: Temperature variation across the study sites from 1990 to 2100, ds: Dormant season, dg: Growing season.

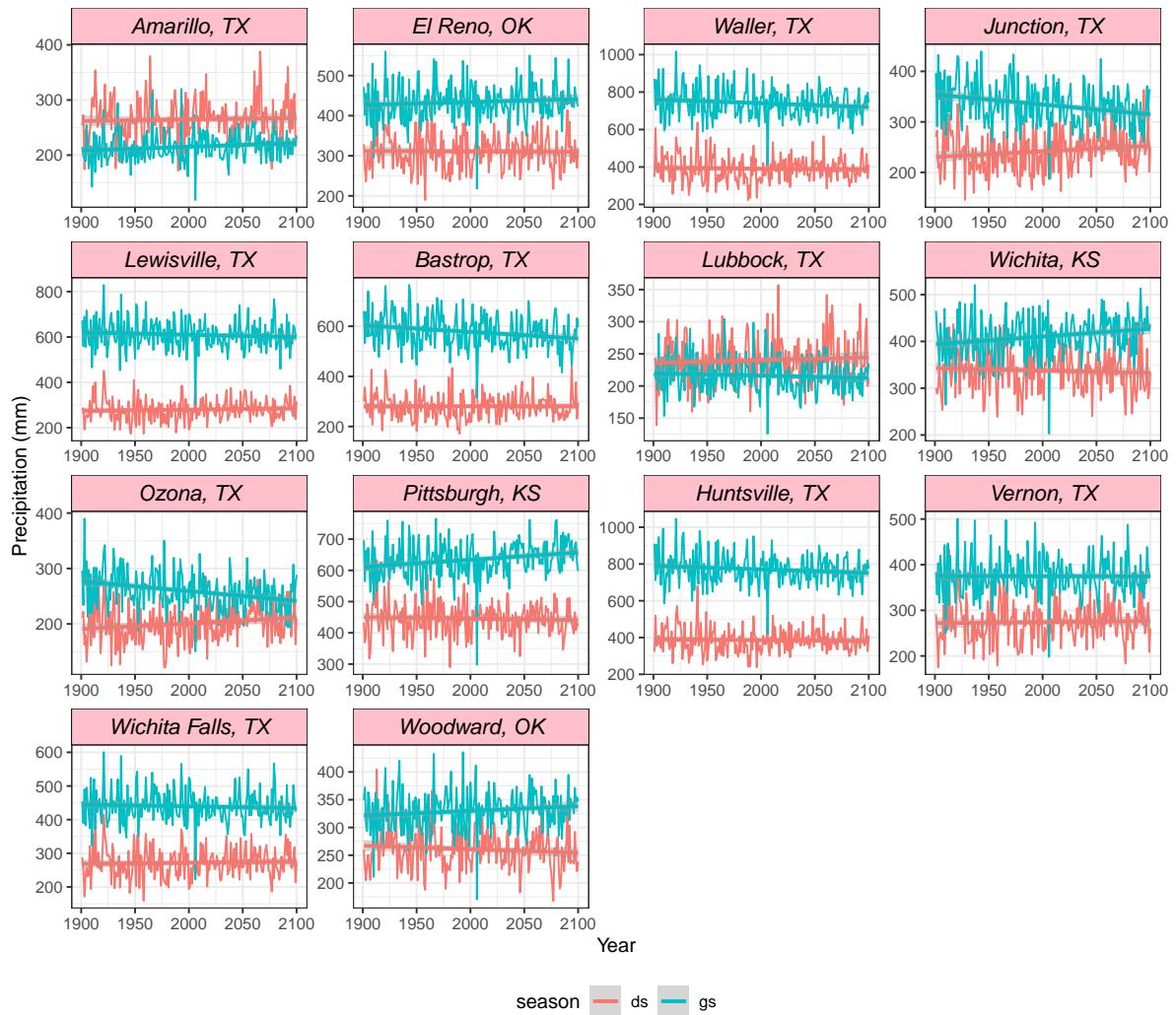


Figure S-2: Precipitation variation across the study sites from 1990 to 2100. ds: Dormant season, dg: Growing season.

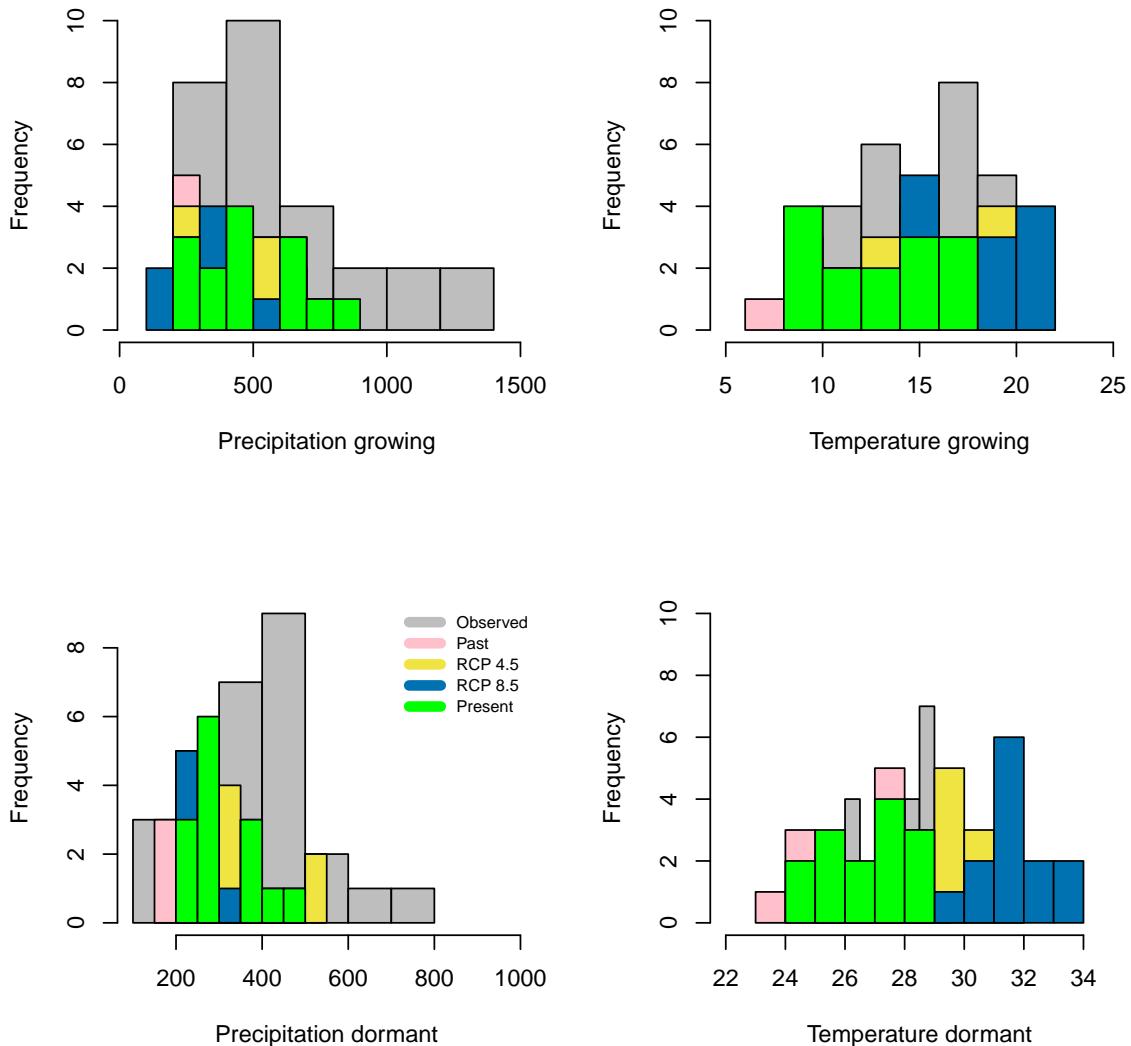


Figure S-3: Past, Observed, present and future (MIROC Model) climate data across the study area.

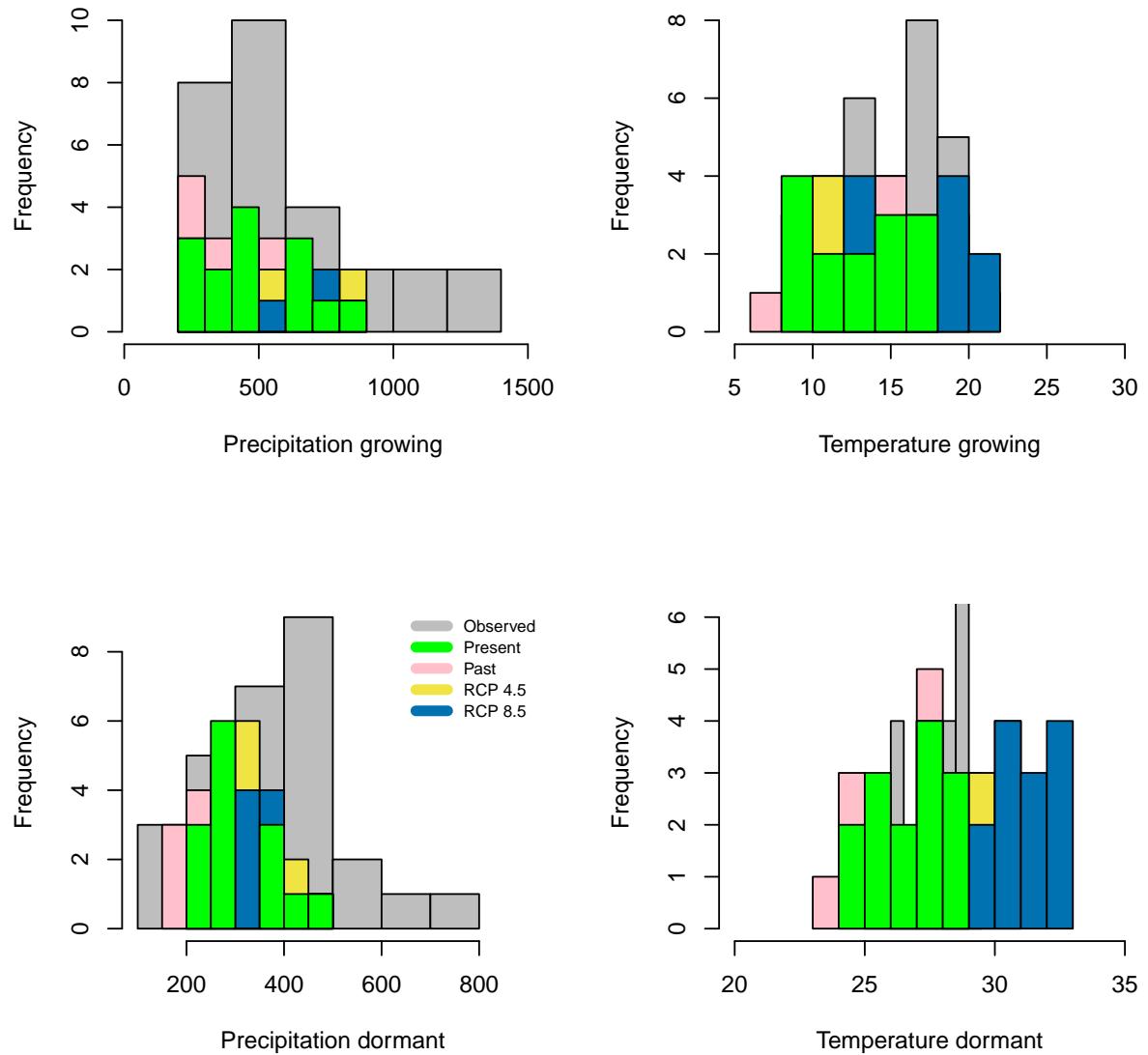


Figure S-4: Past, Observed, present and future (ACCESS Model) climate data across the study area.

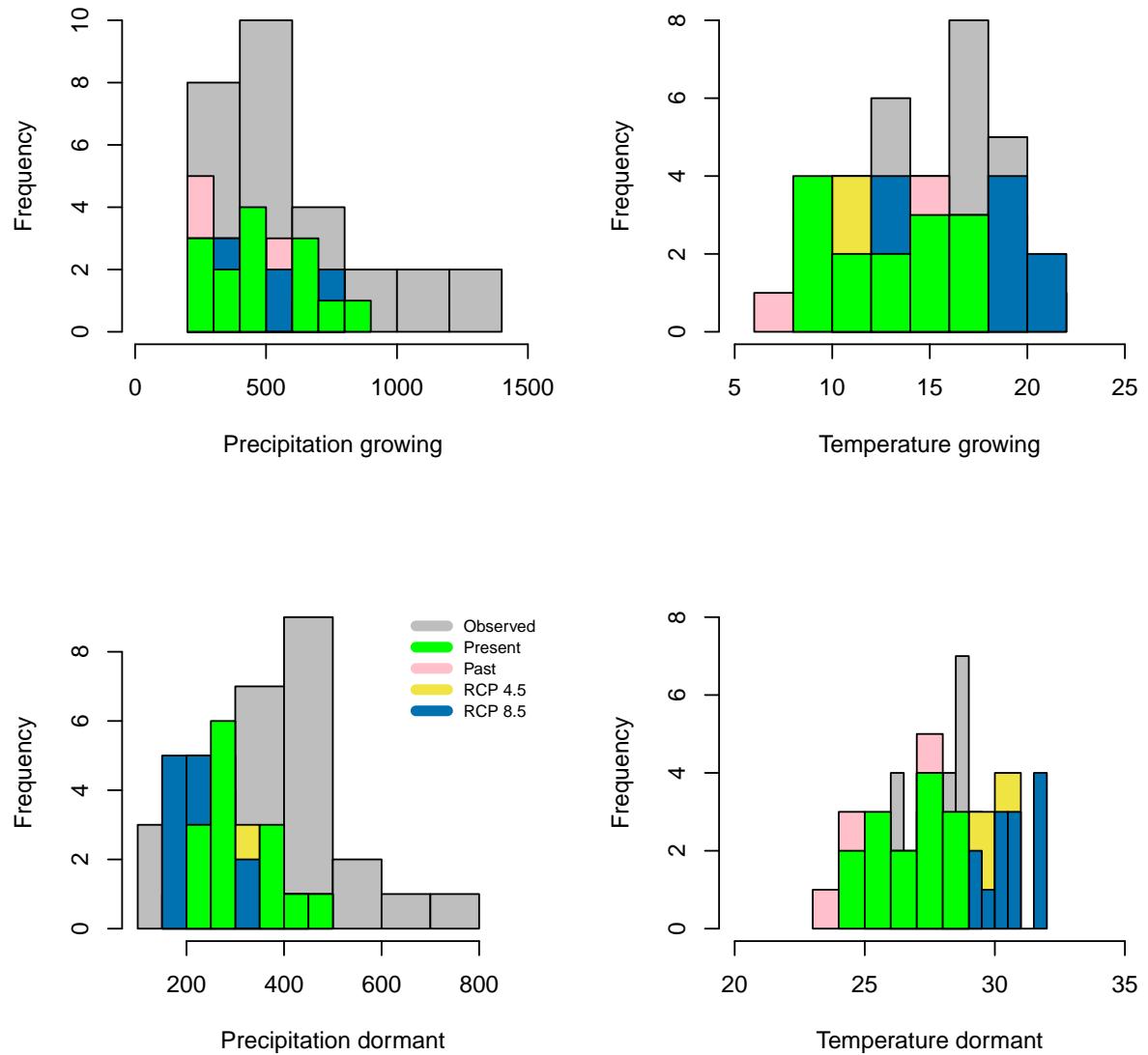


Figure S-5: Past, Observed, present and future (CESM1 Model) climate data across the study area.

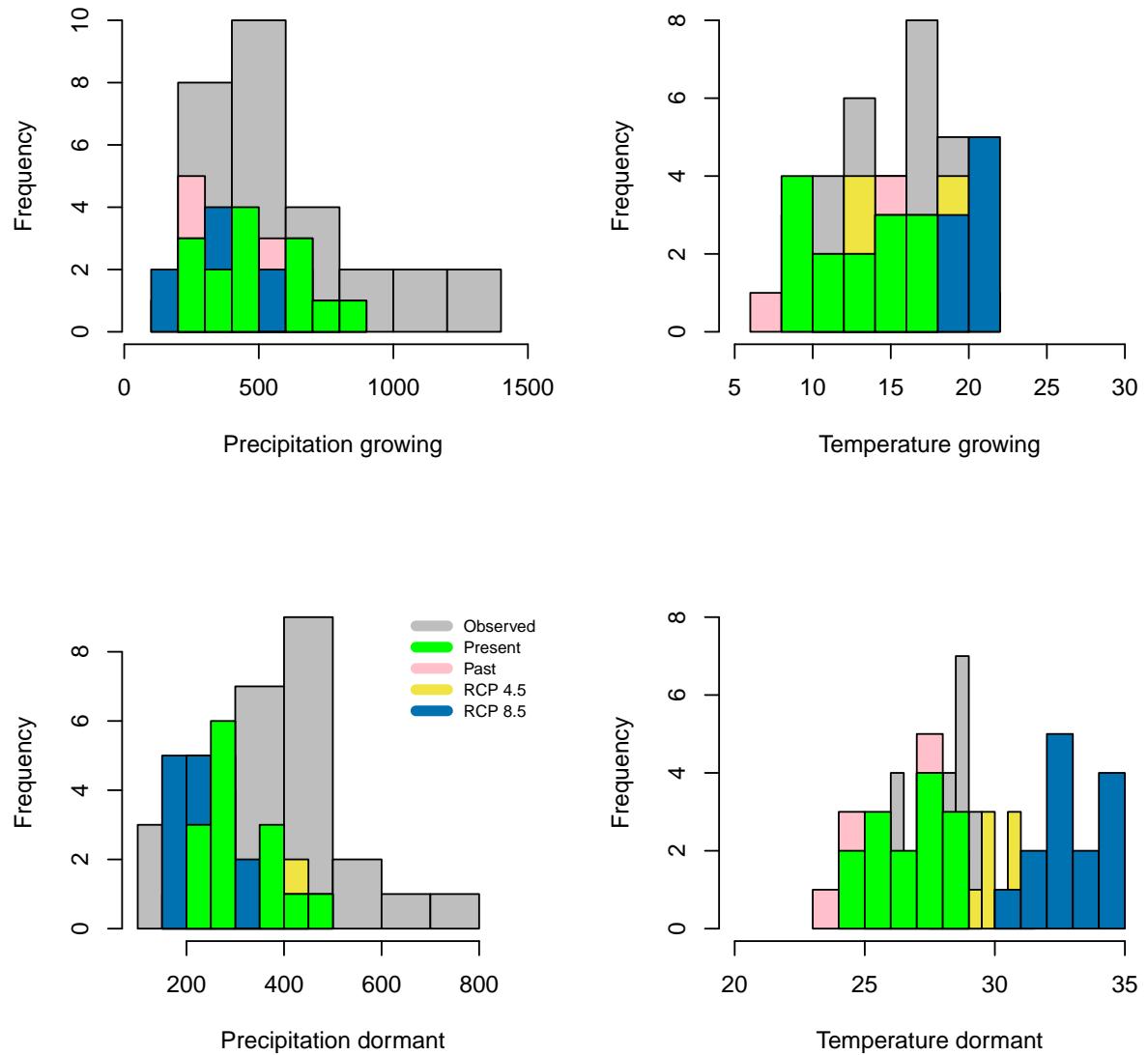


Figure S-6: Past, Observed, present and future (CMCC Model) climate data across the study area.

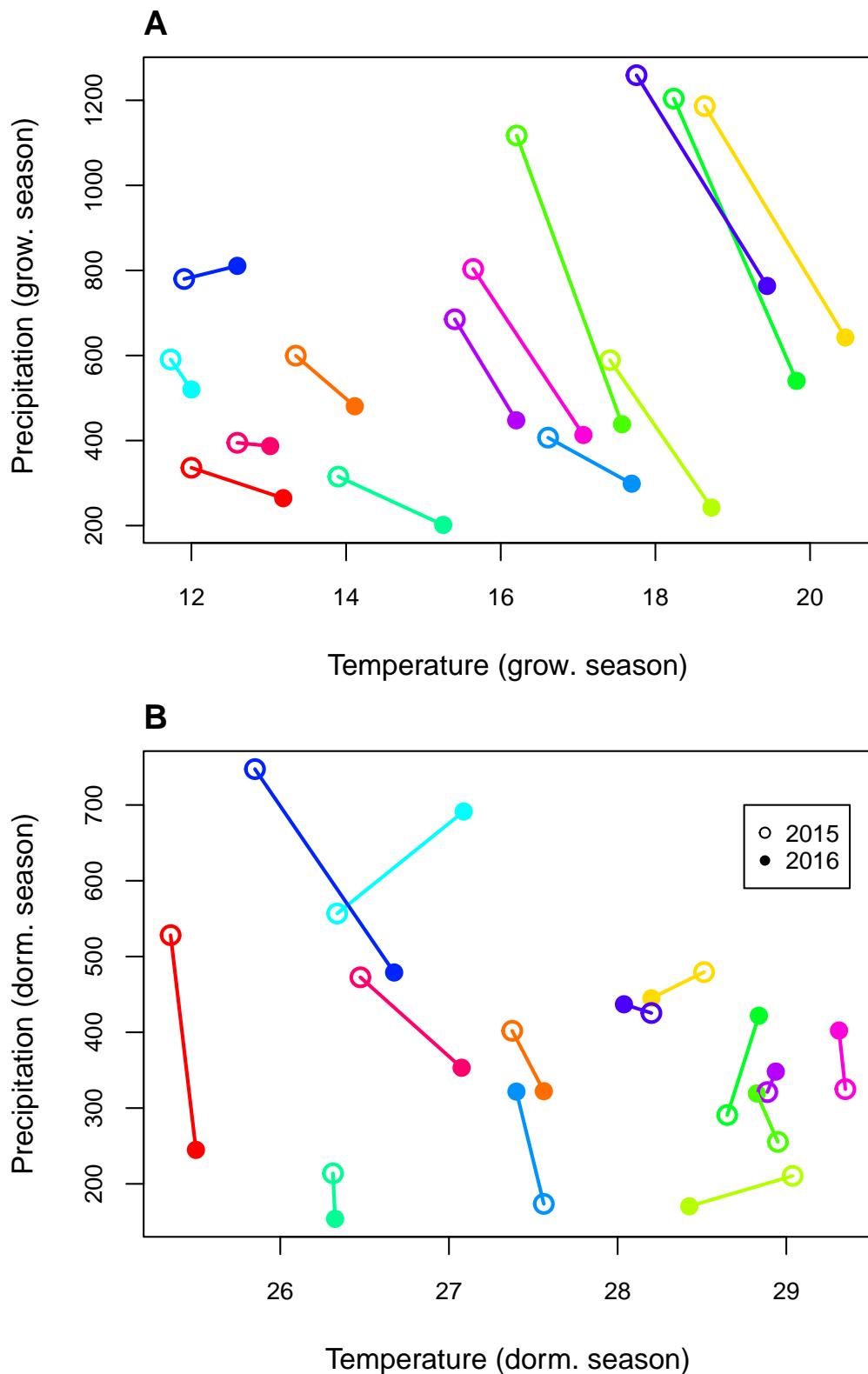


Figure S-7: Climate variation across the study sites during the monitoring period.

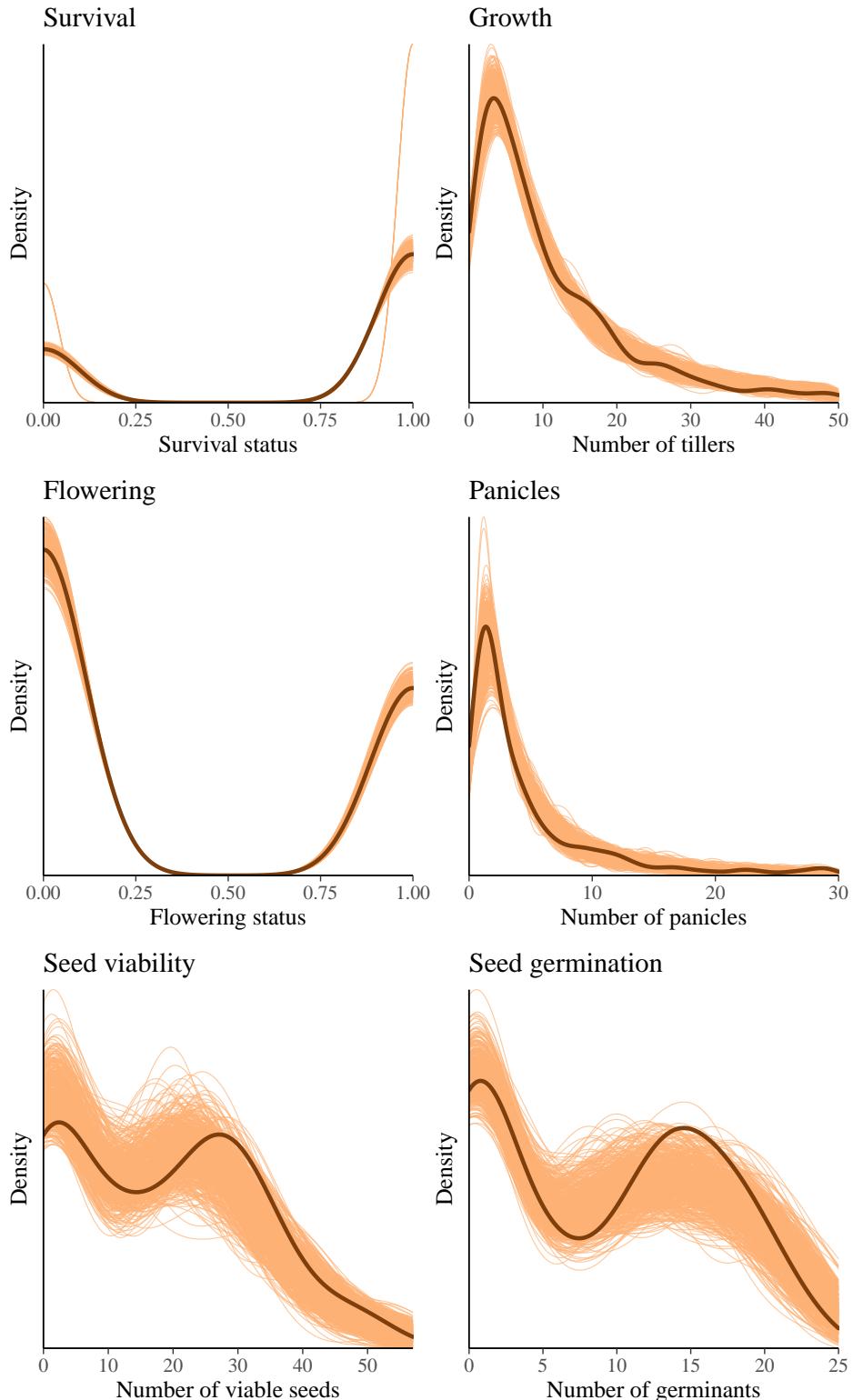


Figure S-8: Posterior predictive checks. Consistency between real data and simulated values suggests that the fitted vital rate models accurately describes the data. Graph shows density curves for the observed data (light orange) along with the simulated values (dark orange).

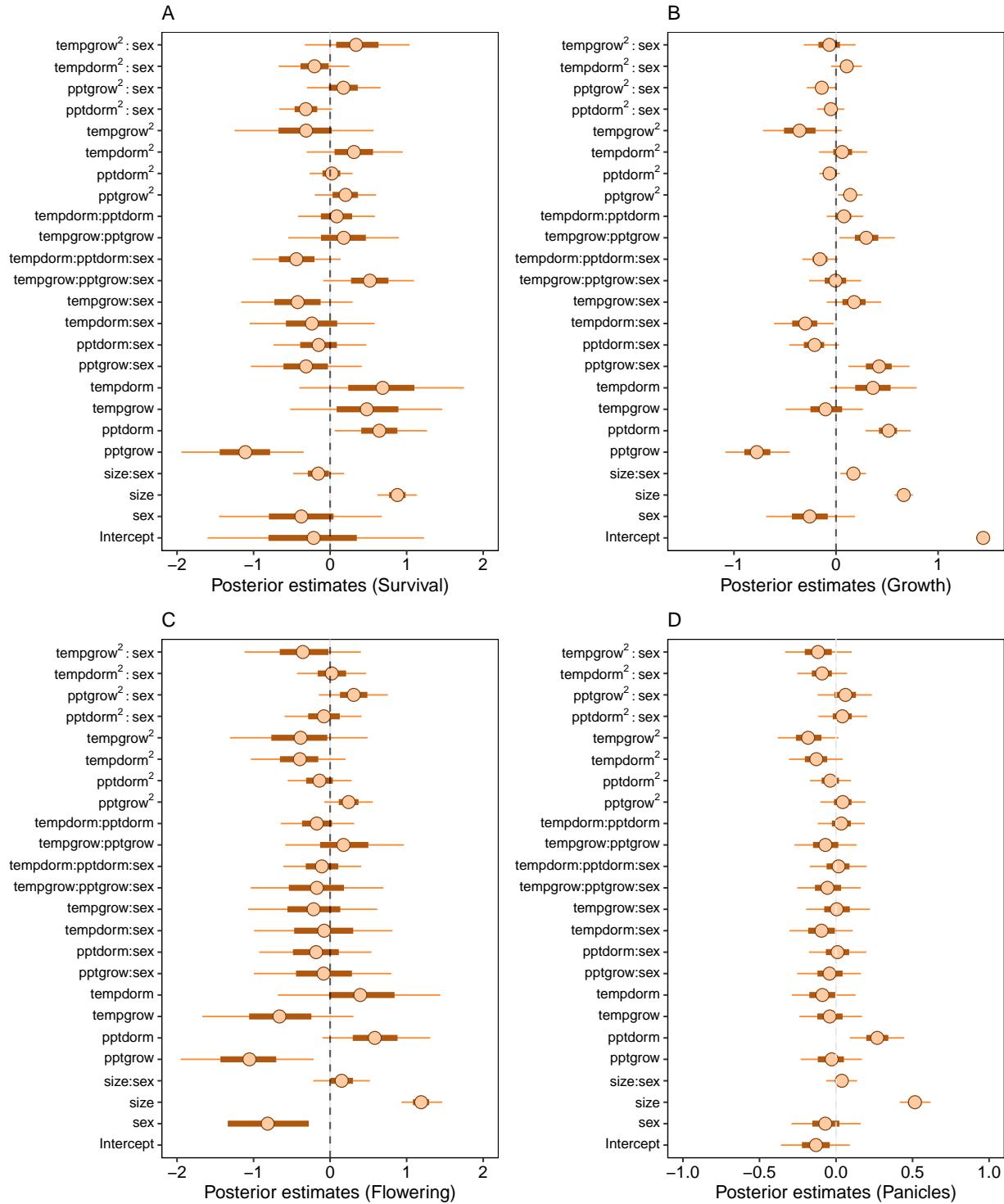


Figure S-9: Mean parameter values and 95% credible intervals of the posterior probability distributions. pptgrow is the precipitation of growing season, Tempgrow is the temperature of growing season, pptdorm is the temperature of dormant season, Tempdorm is the temperature of dormant season.

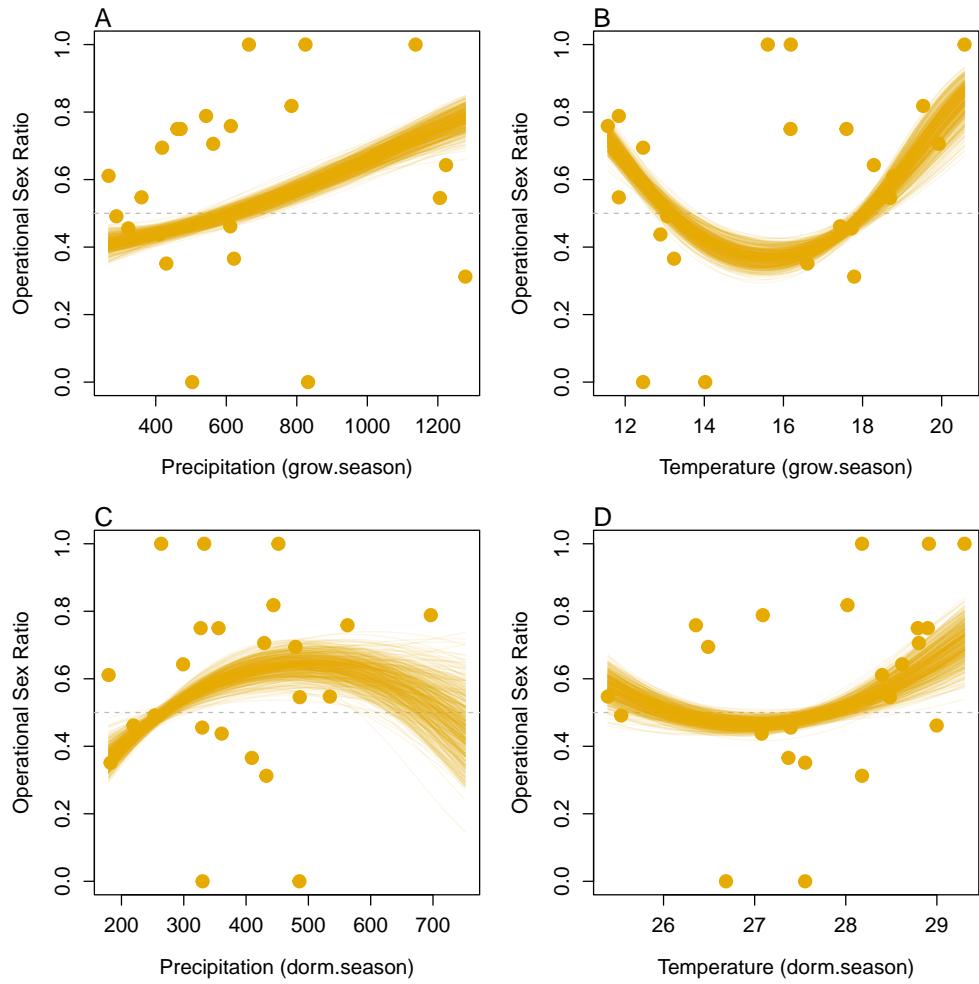


Figure S-10: Significant Operational Sex Ratio response across climate gradient. (A, B) Proportion of panicles that were females across precipitation and temperature of the growing season; (C, D) Proportion of panicles that were females across precipitation and temperature of the dormant season.

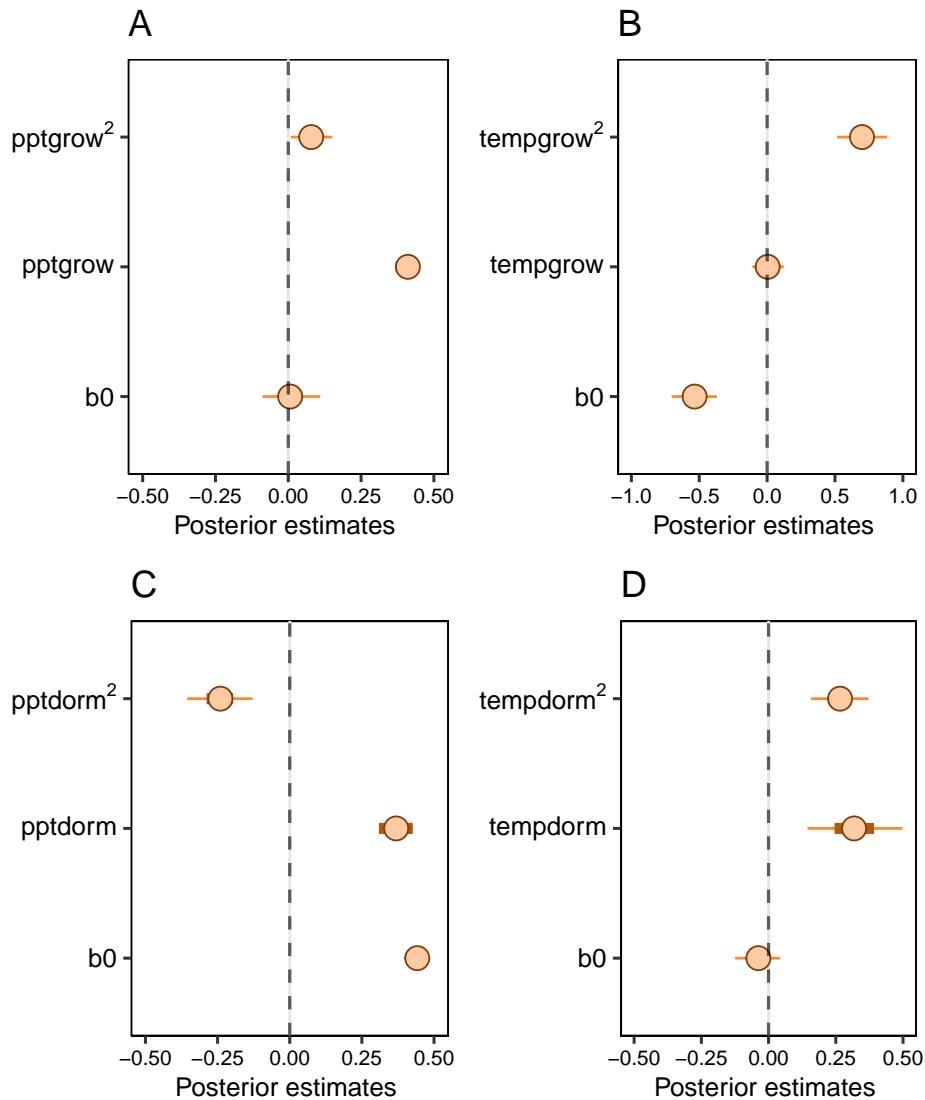


Figure S-11: Mean parameter values and 95% credible intervals of the posterior probability distributions. pptgrow is the precipitation of growing season, Tempgrow is the temperature of growing season, pptdorm is the temperature of dormant season, Tempdorm is the temperature of dormant season.

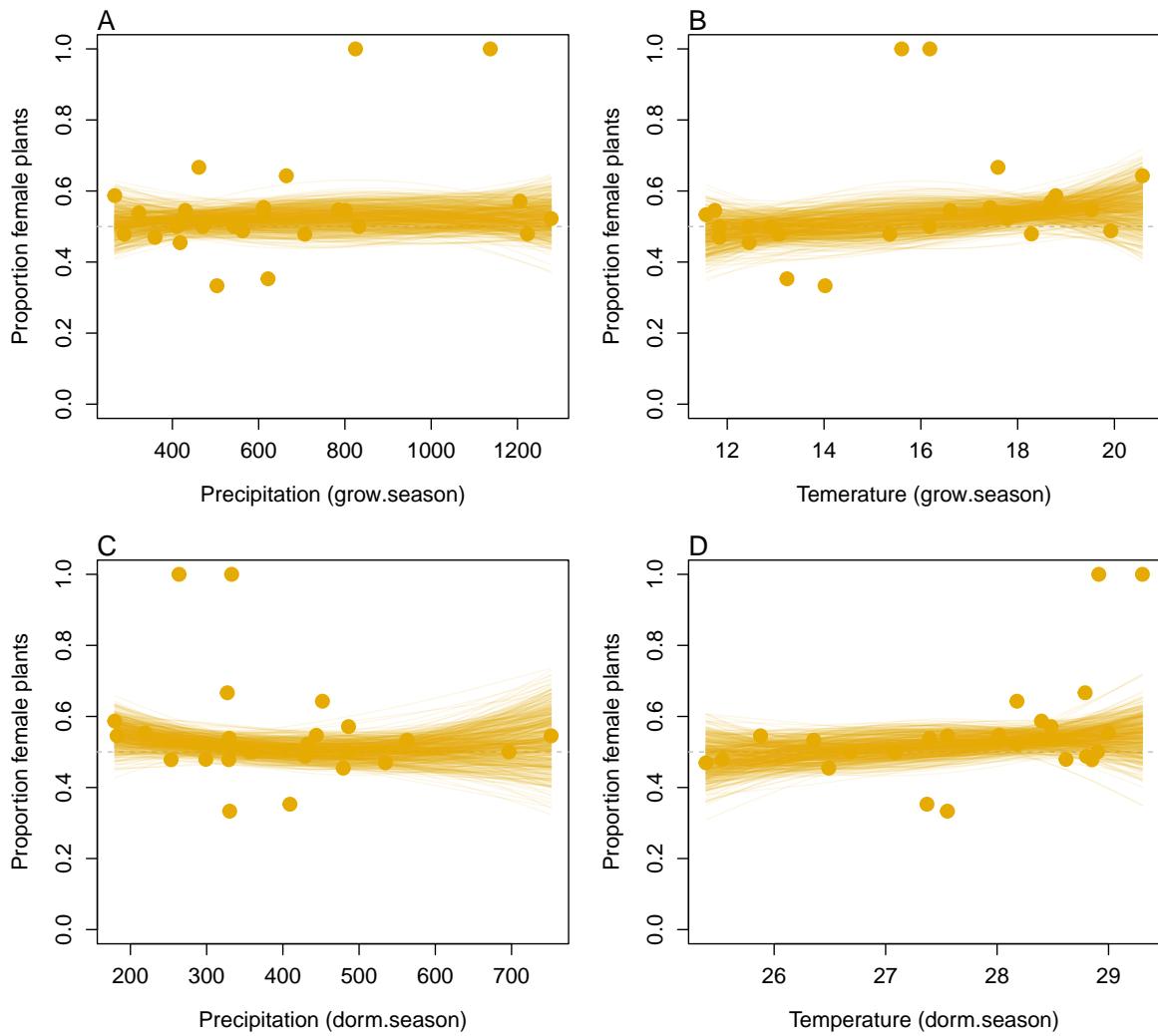


Figure S-12: Variation in sex-ratio accross climate gradient. (A, B) Proportion of plants that were females across precipitation and temperature of the growing season; (C, D) Proportion of plants that were females across precipitation and temperature of the dormant season.

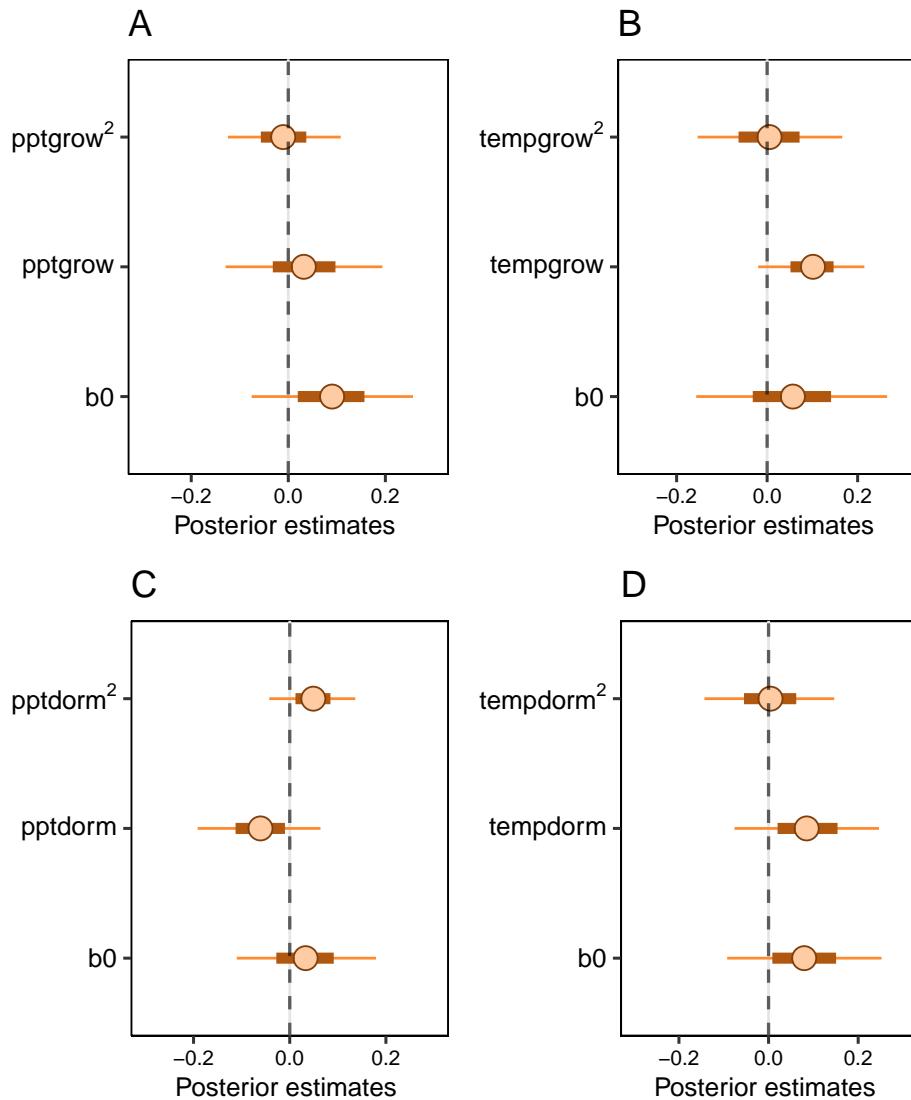


Figure S-13: Mean parameter values and 95% credible intervals of the posterior probability distributions. pptgrow is the precipitation of growing season, Tempgrow is the temperature of growing season, pptdorm is the temperature of dormant season, Tempdorm is the temperature of dormant season.

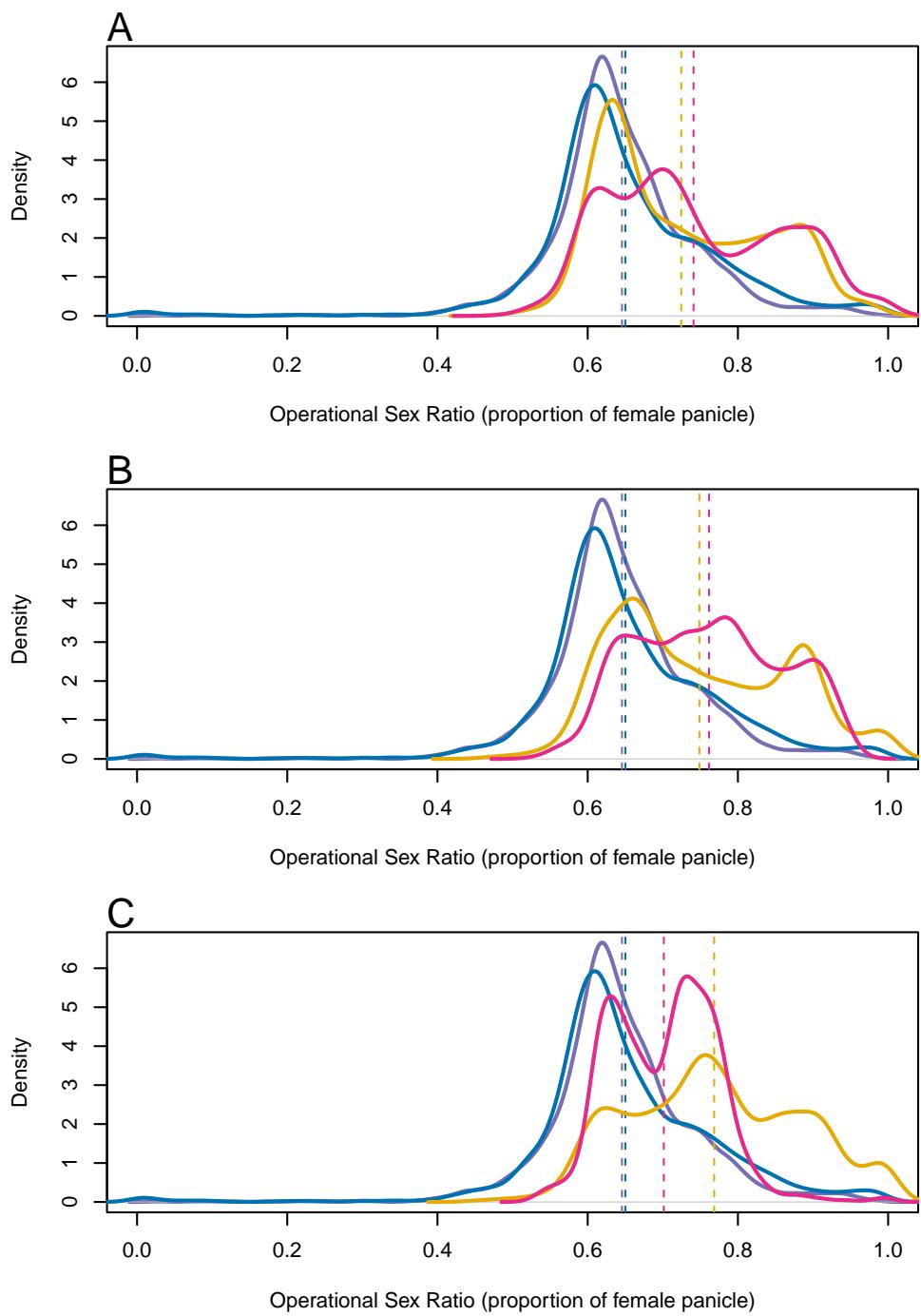


Figure S-14: Change in Operational Sex Ratio (proportion of female) over time (past, present, future). Future projections were based on A) MIROC 5, B) CES, C) ACC. The means for each model are shown as vertical dashed lines.

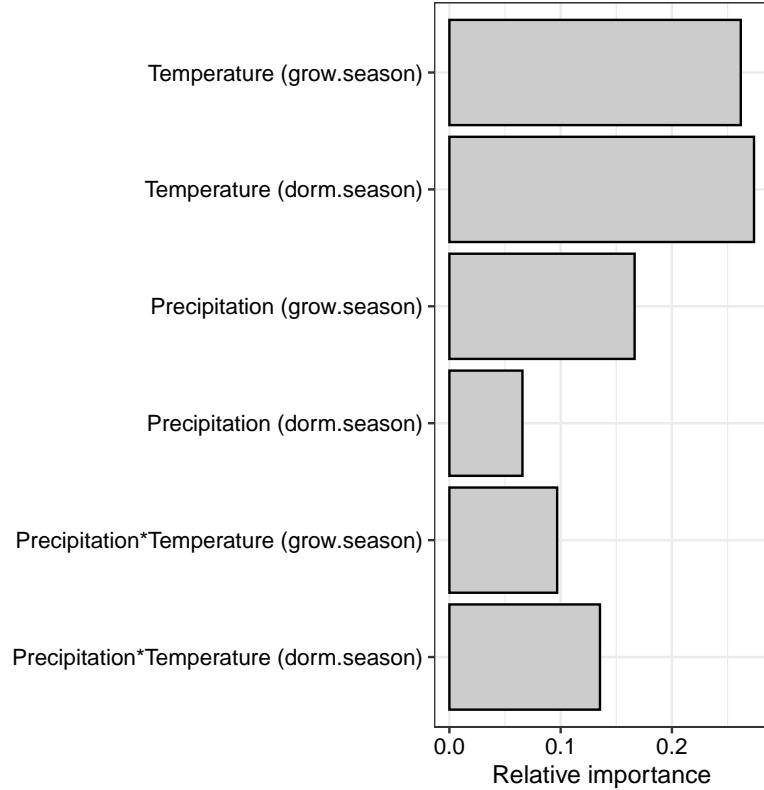


Figure S-15: Life Table Response Experiment: The bar represent the relative importance of each predictors.

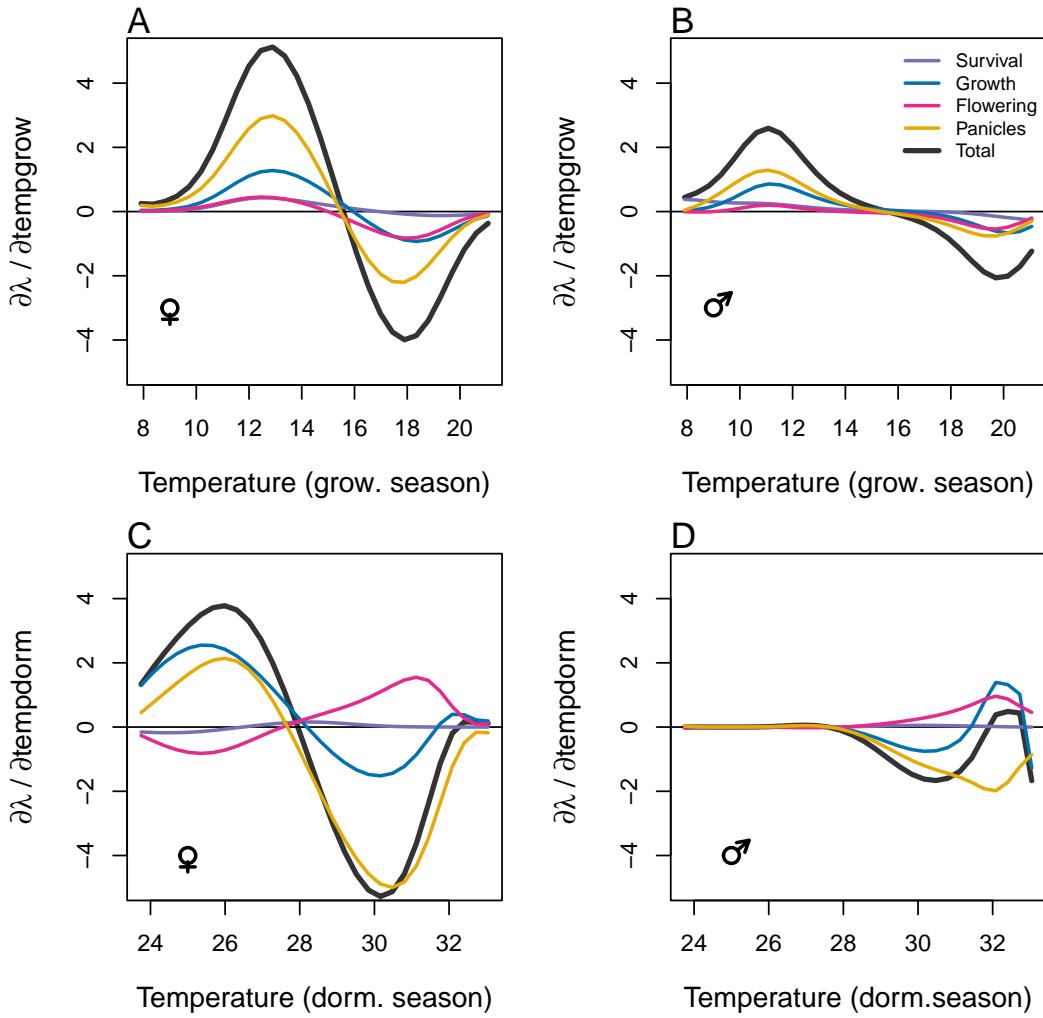


Figure S-16: Life table response experiment decomposition of the sensitivity of λ to seasonal climate into additive vital rate contributions of males and females based on posterior mean parameter estimates. (A) Temperature of growing season (contribution of female), (B) Temperature of growing season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

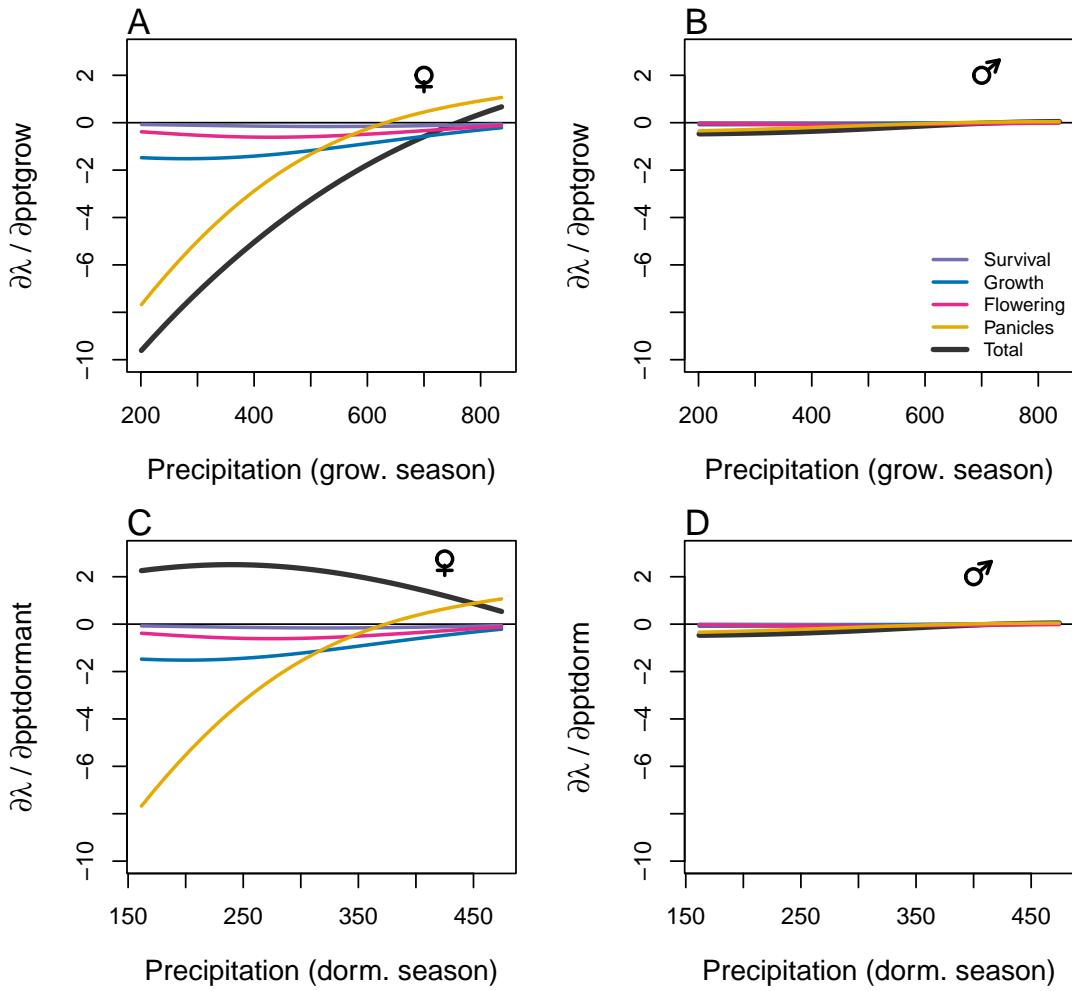


Figure S-17: Life table response experiment decomposition of the sensitivity of λ to seasonal climate into additive vital rate contributions of males and females based on posterior mean parameter estimates. (A) Precipitation of growing season (contribution of female), (B) Precipitation of growing season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

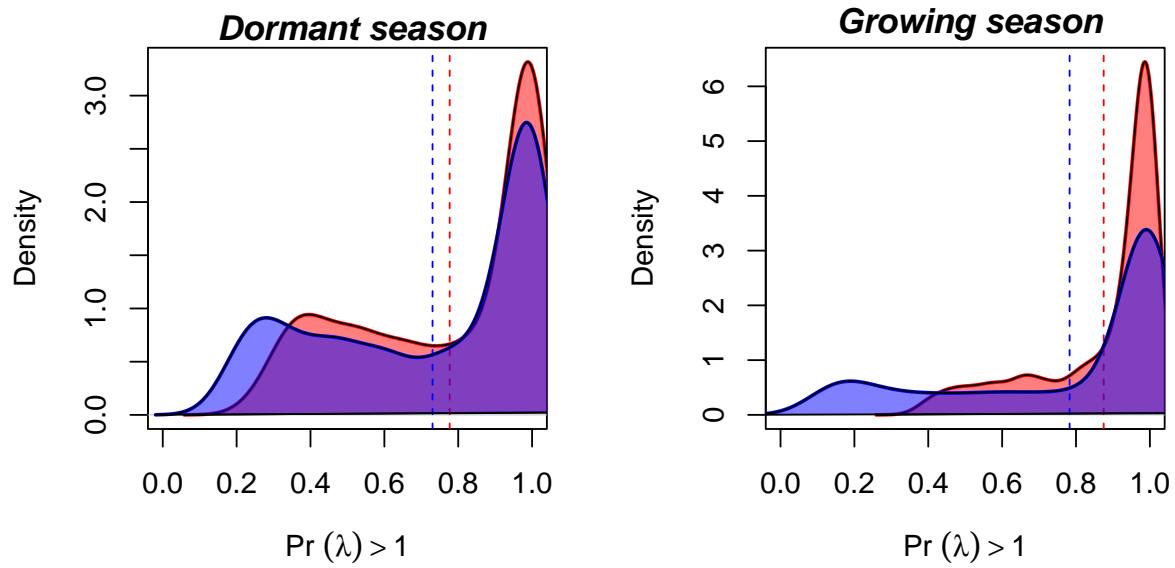


Figure S-18: Assessment of the statistical difference between the two-sex models and the female dominant model for the dormant and growing season. Plots show the density of $\Pr(\lambda) > 1$ values for female dominant (pink) and two-sex models (violet) for each season. The means for each model are shown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

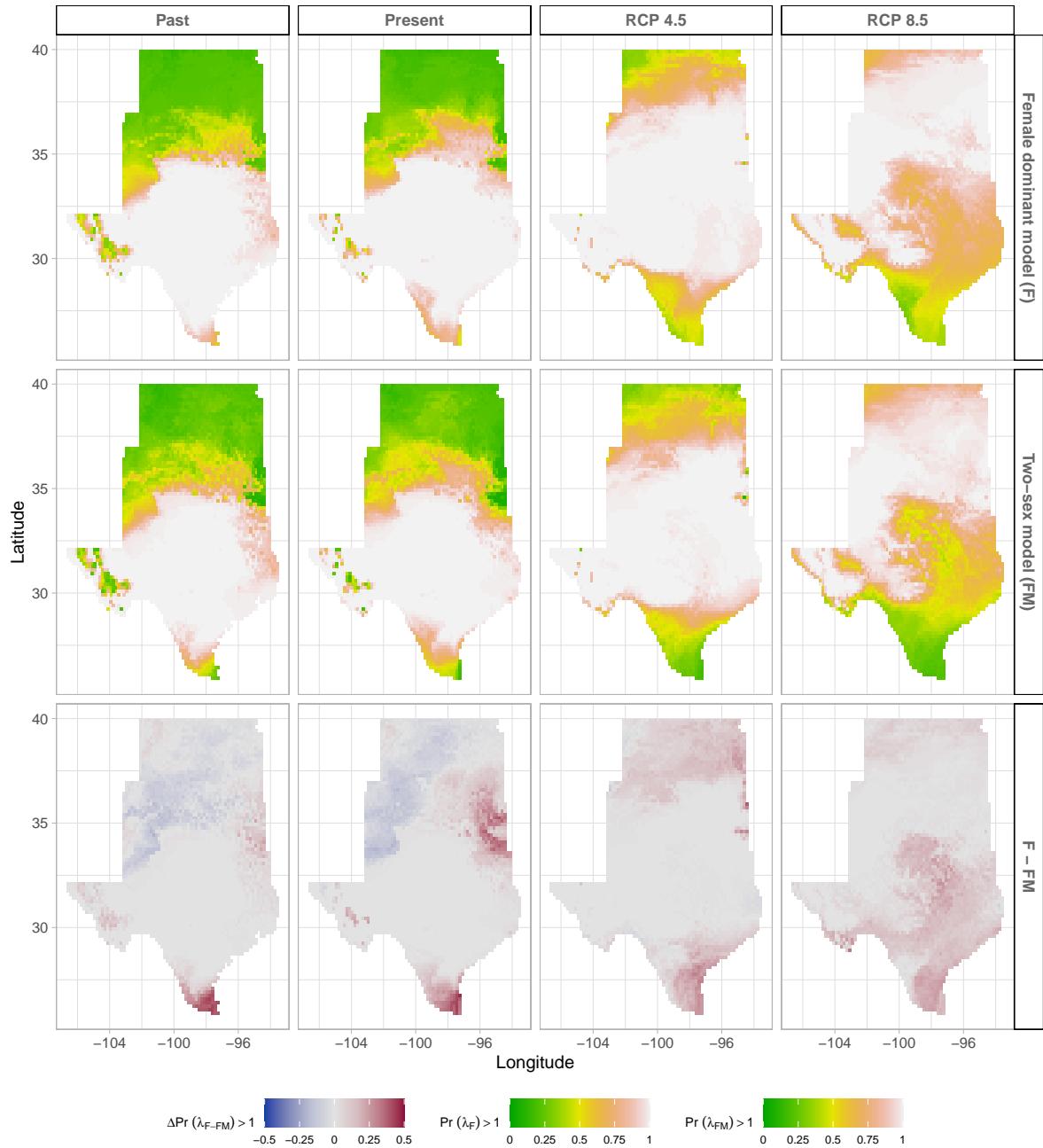


Figure S-19: Climate change favors range shift toward the North edge of the current range. (A) Past, (B) Current, (C and D) Future predicted range shift based on the predicted probabilities of self- sustaining populations, $\Pr(\lambda > 1)$, using the two-sex model that incorporates sex- specific demographic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

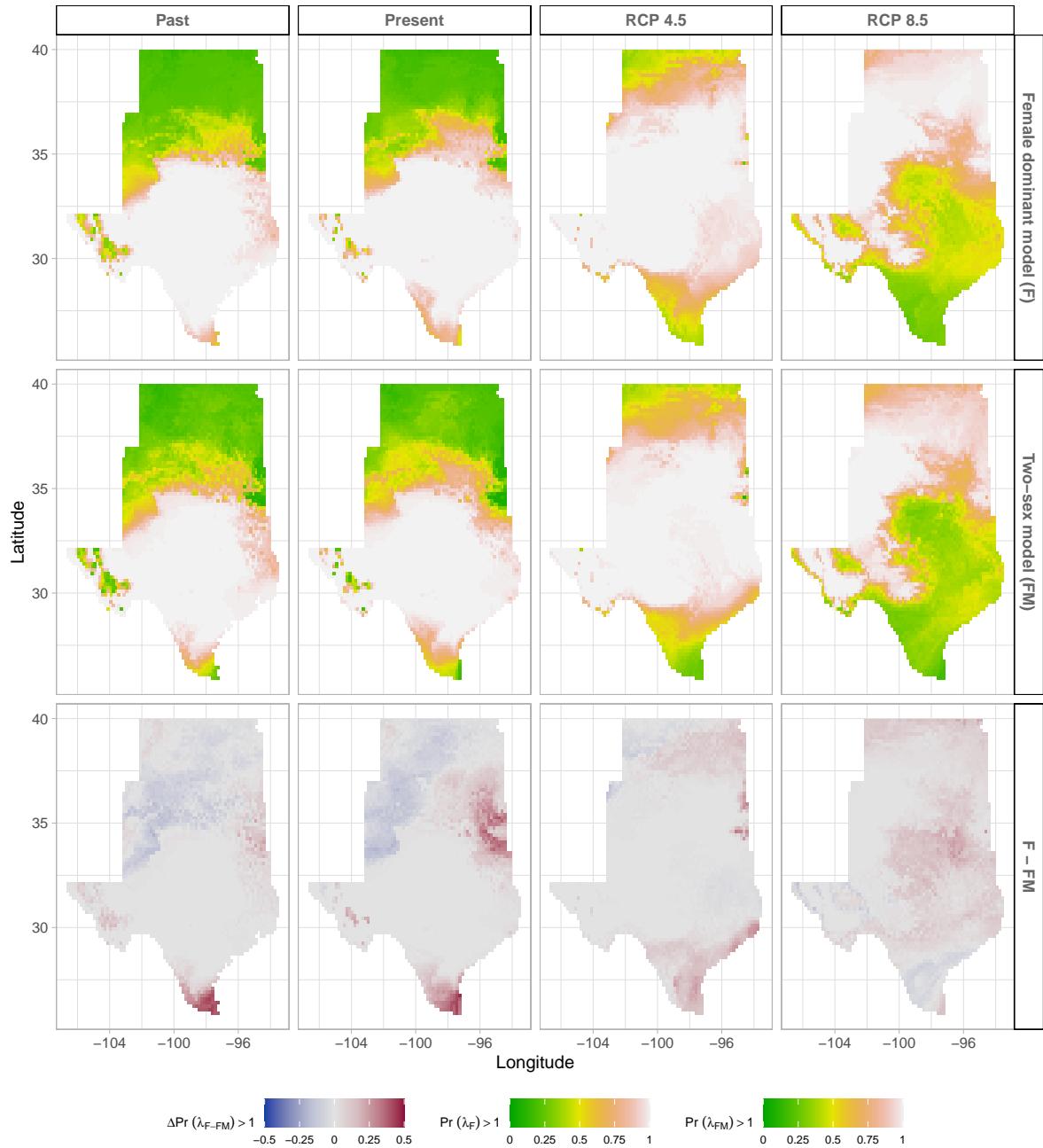


Figure S-20: Climate change favors range shift toward the North edge of the current range. (A) Past, (B) Current, (C and D) Future predicted range shift based on the predicted probabilities of self-sustaining populations, $\text{Pr}(\lambda > 1)$, using the two-sex model that incorporates sex-specific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

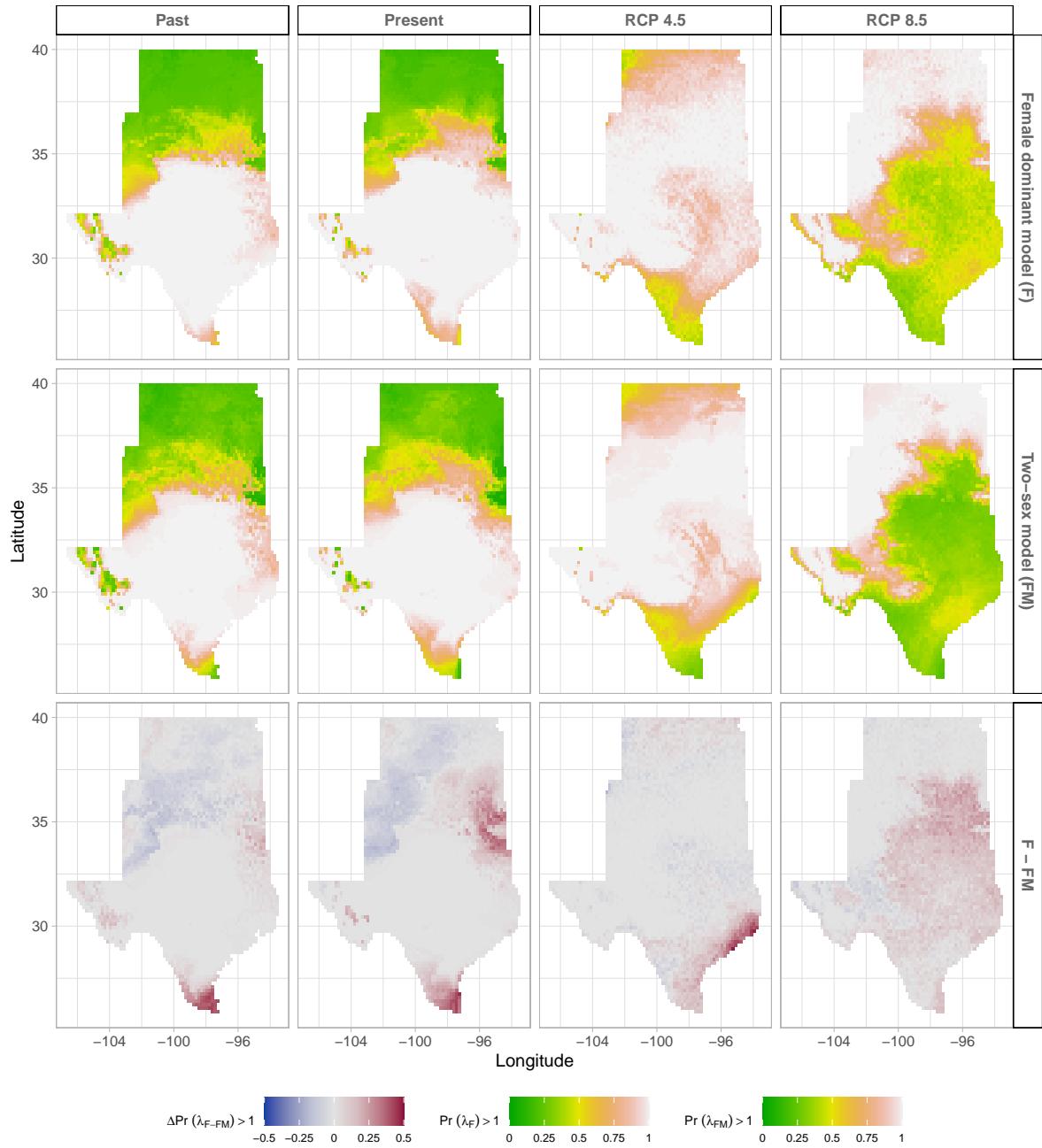


Figure S-21: Climate change favors range shift toward the North edge of the current range. (A) Past, (B) Current, (C and D) Future predicted range shift based on the predicted probabilities of self- sustaining populations, $\Pr(\lambda > 1)$, using the two-sex model that incorporates sex- specific demographic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

571 **S.2 Supporting Methods**

572 **Sex ratio experiment**

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

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

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