

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 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). **For ex-**
83 **ample,**⁵ Our previous study showed that, despite evidence for differentiation of climatic niche
84 between 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 vari-
87 ation in temperature, which is the much stronger dimension of forecasted climate change in
88 this region (Fig. S-1,S-2⁶). Developing a rigorous forecast for the implications of future climate
89 change requires that we transition from climate-implicit to climate-explicit treatment of multi-
90 ple environmental drivers as we do here. Leveraging the power of Bayesian inference, we take
91 a probabilistic view of past, present, and future range limits by quantifying the probability of
92 population viability ($Pr(\lambda \geq 1)$) 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 operational sex ratio throughout the range?
- 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
105 1) (Hitchcock, 1971)⁷.⁸ Texas bluegrass grows between October and May, flowers in spring,
106 and goes dormant during the hot summer months of June to September (Kindiger, 2004).

⁵Provide a more quantitative summary of how the climate is changing, i.e. For example, summer temperatures have increased by XX-XX degrees C since 1900, and climate models predict another XX-XX degrees of warming by 2100.

⁶Please improve the legend for these figures.

⁷I have updated the map

⁸If you are showing all these maps here is no need to report the climate values in the text.

¹⁰⁷ Following this life history, we divide the calendar year into growing (October 1 - May 31)
¹⁰⁸ and dormant seasons (June 1 - September 30).

¹⁰⁹ Biological sex in Texas bluegrass is genetically based and the birth (seed) sex ratio is
¹¹⁰ 1:1 (Renganayaki et al., 2005). Females and males are morphologically indistinguishable
¹¹¹ except for their inflorescences. Like all grasses, the species is wind pollinated (Hitchcock,
¹¹² 1971). Surveys of 22 natural populations throughout the species' distribution indicated that
¹¹³ operational sex ratio (the female fraction of inflorescnces) ranged from 0.007 to 0.986 with
¹¹⁴ a mean of 0.404 (Miller and Compagnoni, 2022b).

¹¹⁵ Common garden experiment

¹¹⁶ Experimental design

¹¹⁷ We conducted a common garden experiment to quantify sex-specific demographic responses
¹¹⁸ to climate variation. Details of the experimental design are provided in Miller and
¹¹⁹ Compagnoni (2022b); we provide a brief overview here. The experiment was installed at 14
¹²⁰ sites throughout and, in some cases, beyond the natural range of Texas bluegrass that sampled
¹²¹ a broad range of temperature and precipitation (Figure 1).⁹ At each site, we established 14
¹²² blocks. For each block we planted three female and three male individuals that were clonally
¹²³ propagated from females and males from eight natural source populations (Figure 1); because
¹²⁴ sex is genetically-based, clones never deviated from their expected sex. The experiment was
¹²⁵ established in November 2013 and was censused in May of 2014, 2015, and 2016. At each
¹²⁶ census, we collected individual demographic data including survival (alive or dead), size
¹²⁷ (number of tillers), and number of panicles (reproductive inflorescences). For the analyses that
¹²⁸ follow, we focus on the 2014-15 and 2015-16 transitions years, since the start of the experiment
¹²⁹ did not include the full 2013-14 transition year.

⁹ *A few comments about figure 1 (I cannot comment in the legend). Please update the gray diamonds as GBIF occurrences, not natural population surveys. Please add "mm" and "°C" to the titles. It would also be good to spell out "growing" and "dormant" seasons.*

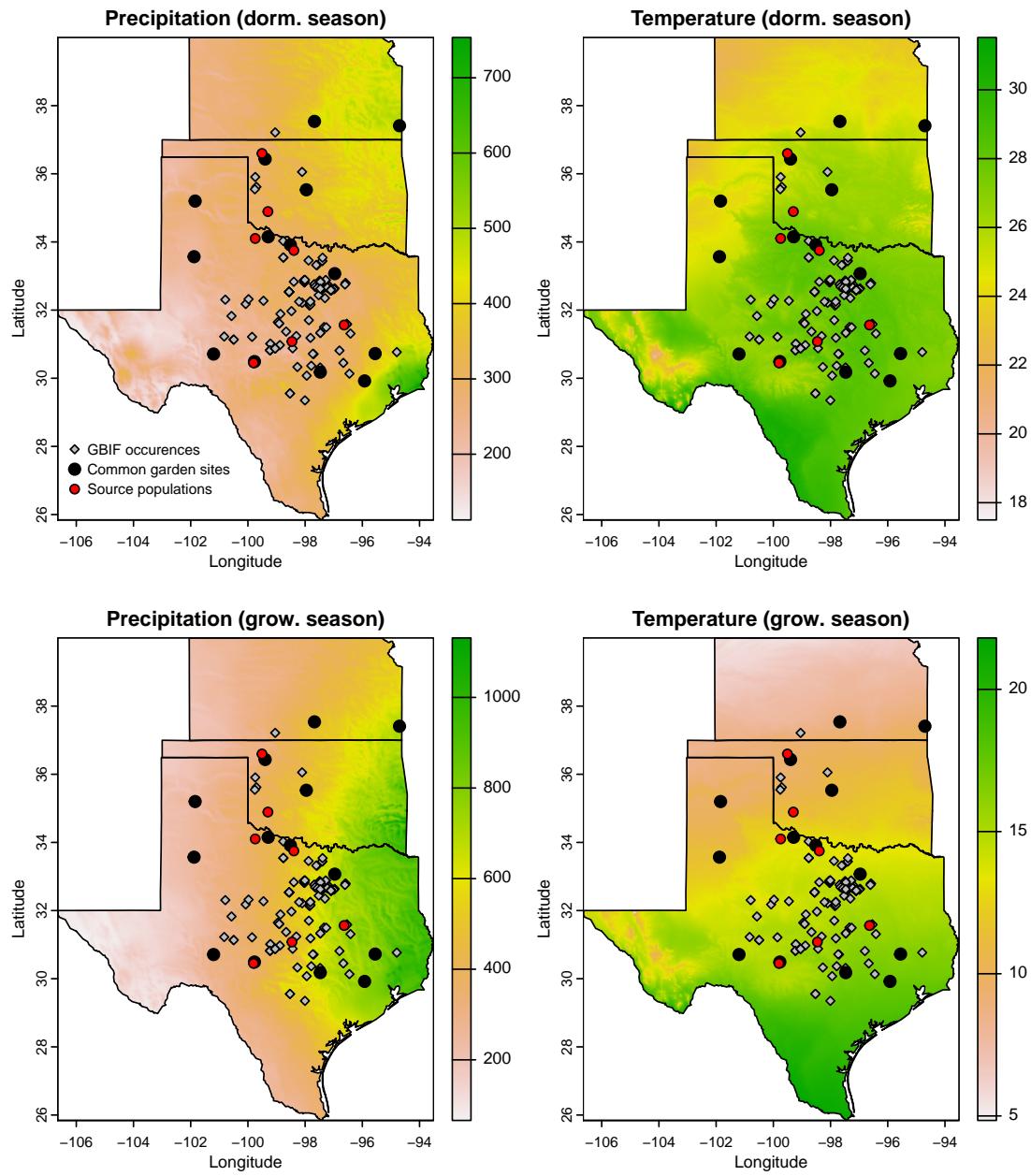


Figure 1: Maps of 30-year (1990-2019) climate normals and study sites used for demographic monitoring of *Poa arachnifera* in Texas, Kansas and Oklahoma in the United States. Precipitation is in mm and temperature is in °C. We surveyed 22 natural populations (grey diamond). The common garden sites were 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
134 years to match demographic transition years (June 1 – May 31) and growing and dormant
135 seasons within each year. To back-cast and forecast demographic responses to changes
136 in climate throughout the study region, we also downloaded projection data for three
137 30-year periods: “past” (1901-1930), “current” (1990-2019) and “future” (2070-2100). Data
138 for future climatic periods were downloaded from four general circulation models (GCMs)
139 selected from the Coupled Model Intercomparison Project Phase 5 (CMIP5): Model for
140 Interdisciplinary Research on Climate (MIROC5), Australian Community Climate and Earth
141 System Simulator (ACCESS1-3), Community Earth System Model (CESM1-BGC), Centro
142 Euro-Mediterraneo sui Cambiamenti Climatici Climate Model (CMCC-CM). All the GCMs
143 were also downloaded from chelsa (Sanderson et al., 2015). We evaluated future climate
144 projections from two scenarios of representative concentration pathways (RCPs): RCP4.5, an
145 intermediate-to-pessimistic scenario assuming a radiative forcing amounting to 4.5 Wm^{-2}
146 by 2100, and RCP8.5, a pessimistic emission scenario which projects a radiative forcing of
147 8.5 Wm^{-2} by 2100 (Schwalm et al., 2020; Thomson et al., 2011).

148 Projection data for the three 30-year periods included warmer or colder conditions than
149 observed in our experiment (Figure S-3, Figure S-4, Figure S-5, Figure S-6), so extending our
150 inferences to these conditions required extrapolation, as we describe below. However, the
151 observed period was substantially wetter and cooler across the study region than 2015-16,
152 especially during the growing season (Figure S-7), so our study design provides both spatial
153 and inter-annual coverage of climate variables.¹⁰

154 Sex-specific demographic responses to climatic variation across common garden sites

We used individual-level measurements of survival, growth (change in number of tillers), flowering, and number of panicles (conditional on flowering) to develop Bayesian 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). These vital rate models included main effects of size (the natural log of tiller number), sex, and seasonal climate covariates. Climate variables were fit with second-degree polynomial functions to accommodate the possibility of hump-shaped relationships (reduced demographic performance at both extremes). We also included two-way interactions between sex and each climate driver and between temperature and precipitation within each season, and a three-way interaction between sex, temperature, and precipitation within each season. Vital

¹⁰I struggle to follow this sentence. I know one of the years was very different from the 30-year normal, which is good because it gives more climate coverage, but I think this can be explained more directly.

rate models were fit with the same linear predictors for the expected value (μ)(Eq.1):

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

155 The linear predictor includes normally distributed random effects for block-to-block variation
 156 ($\phi \sim N(0, \sigma_{block})$), site to site variation ($\nu \sim N(0, \sigma_{site})$), and source-to-source variation that
 157 is related to the genetic provenance of the transplants used to establish the common garden
 158 ($\rho \sim N(0, \sigma_{source})$).

159 A different link function ($f(\mu)$) was applied depending on the the vital rate distributions.
 160 We modeled survival and flowering data with a Bernoulli distribution. We modeled the
 161 growth (tiller number) with a zero-truncated Poisson inverse Gaussian distribution. Fertility
 162 (panicle count conditional on flowering) was modeled as zero-truncated negative binomial.
 163 We used generic weakly informative priors to fit coefficients for survival, growth, flowering
 164 models ($\mu = 0, \sigma = 1.5$) and random effect variances ($\gamma[0.1, 0.1]$). **We fit fertility model with**
 165 **regularizing priors for coefficients ($\mu = 0, \sigma = 0.15$)**.¹¹

166 Sex ratio responses to climatic variation across common garden sites

We also used the experimental data to investigate how climatic variation across the range influenced sex ratio and operational sex ratio of the common garden populations. 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.2).

$$SR = \omega_0 + \omega_1 climate + \omega_2 climate * climate + \epsilon \quad (2)$$

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

¹¹I think you need to explain a little more about why fertility was handled differently and what you mean by regularizing.

170 **Model-fitting procedures**

171 All models were fit using Stan (Stan Development Team, 2023) in R 4.3.1 (R Core Team,
172 2023). We centered and standardized all climatic predictors to mean zero, variance one, which
173 facilitated model convergence. We ran three chains for 1000 samples for warmup and 4000
174 for sampling, with a thinning rate of 3. We assessed the quality of the models using the
175 predictive check graphs (Piironen and Vehtari, 2017) (Figure S-8).

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

177 To estimate population viability and sex ratio, we used the climate-dependent vital rate
178 regressions estimated above, combined with additional data sources, to build female-dominant
179 and two-sex versions of a climate-explicit matrix projection model (MPMs) structured by the
180 discrete state variables size (number of tillers) and sex. The female-dominant and two-sex
181 versions of the model both allow for sex-specific response to climate and differ only in the
182 feedback between operational sex ratio and seed fertilization. For clarity of presentation we
183 do not explicitly include climate-dependence in the notation below, but the following model
184 was evaluated over variation in seasonal temperature and precipitation.

Let $F_{x,t}$ and $M_{x,t}$ be the number of female and male plants of size x in year t , where $x \in [1, \dots, U]$. The minimum possible size is one tiller and U is the 95th percentile of observed maximum size (# tillers)¹². Let F_t^R and M_t^R be new female and male recruits in year t , which we treat as distinct from the rest of the size distribution because we assume they do not reproduce in their first year, consistent with our observations. For a pre-breeding census, the expected numbers of recruits in year $t+1$ is given by:

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

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

185 where p^F and c^F are flowering probability and panicle production for females of size x , d
186 is the number of seeds per female panicle, v is the probability that a seed is fertilized, m is
187 the probability that a fertilized seed germinates, and ρ is the primary sex ratio (proportion
188 of recruits that are female), which we assume to be 0.5.

In the two-sex model, seed fertilization is a function of population structure, allowing for feedback between vital rates and operational sex ratio (OSR). In the context of the model, OSR

¹²Give this number.

is defined as the fraction of panicles that are female and is derived from the $U \times 1$ vectors \mathbf{F}_t and \mathbf{M}_t :

$$v(\mathbf{F}_t, \mathbf{M}_t) = v_0 * \left[1 - \left(\frac{\sum_1^U p^F(x, z) c^F(x, z) F_{x,t}}{\sum_1^U p^F(x, z) c^F(x, z) F_{x,t} + p^M(x, z) c^M(x, z) M_{x,t}} \right)^\alpha \right] \quad (5)$$

The summations tally the total number of female and male panicles over the size distribution, giving the fraction female. This function has the properties that seed fertilization is maximized at v_0 as OSR approaches 100% male, goes to zero as OSR approaches 100% female, and parameter α controls how female seed viability declines as male panicles become rare. We estimated these parameters using data from a sex ratio manipulation experiment, conducted in the center of the range, in which seed fertilization was measured in plots of varying OSR; this experiment is described elsewhere (Compagnoni et al., 2017) and is summarized in [Supplementary Method S.2](#)¹³. This experiment also provided estimates for seed number per panicle (d) and germination rate (m). Lacking data on climate-dependence, we assume that seed fertilization, seed number, and germination do not vary with climate.

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

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

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

In the equations above, the first terms indicate recruits 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 estimated the seedling survival probability σ using demographic data from the congeneric species *Poa autumnalis* in east Texas (T.E.X. Miller and J.A. Rudgers, *unpublished data*), and we assume that σ is the same across sexes and climatic variables. We did this because we had little information on the early life cycle transitions of greenhouse-raised transplants. We used g ($y, x = 1$) (the future size distribution of one-tiller plants from the transplant experiment) to give the probability that a surviving recruit reaches size y . 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 indicate that these functions may be unique to females (F) and males (M).

¹³I think the supplement should also include a data figure showing the fit of the model to the experimental data.

211 The model described above yields a $2(U+1) \times 2(U+1)$ transition matrix. We estimated
 212 the population growth rate λ of the female dominant model as the leading eigenvalue of
 213 the transition matrix. Since the two-sex MPM is nonlinear (matrix elements affect and are
 214 affected by population structure) we estimated λ and stable sex ratio (female fraction of all
 215 individuals) and operational sex ratio (female fraction of panicles) by numerical simulation.
 216 Since all parameters were estimated using MCMC sampling, we were able to propagate the
 217 uncertainty in our estimates of the vital rate parameters to uncertainty in λ . Furthermore,
 218 by sampling over distributions associated with site, block, and source population variance
 219 terms, we are able to additionally incorporate process error into the total uncertainty in λ .¹⁴

220 Life Table Response Experiments

221 We conducted two types of Life Table Response Experiments (LTRE) to isolate contributions
 222 of climate variables and sex-specific vital rates to variation in λ . First, to identify which
 223 aspect of climate is most important for population viability, we used an LTRE based on
 224 a nonparametric model for the dependence of λ on parameters associated with seasonal
 225 temperature and precipitation (Ellner et al., 2016). To do so, we used the RandomForest
 226 package to fit a regression model with four climatic variables (temperature of growing season,
 227 precipitation of growing season, temperature of the dormant season and precipitation of
 228 the dormant season) as predictors and λ ¹⁵ as response (Liaw et al., 2002). The regression
 229 model allowed the estimation of the relative importance of each predictor. The importance
 230 is measured by asking: how wrongly is λ predicted if we replaced the focal predictor (e.g.,
 231 temperature of growing season) by a random value of the other predictors.¹⁶

Second, to understand how climate drivers influence λ via sex-specific demography, we decomposed the effect of each climate variable on population growth rate (λ) into contribution arising from the effect on each female and male vital rate using a “regression design” LTRE (Caswell, 1989, 2000). This LTRE decomposes the sensitivity of λ to climate according to:

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

¹⁴I just want to confirm that this is actually what you did.

¹⁵Is this lambda from the female-dominant or two-sex model? Does it matter?

¹⁶I do not understand this.

232 where, θ_i^F and θ_i^M represent sex-specific parameters (the regression coefficients of the vital
233 rate functions). Because LTRE contributions are additive, we summed across vital rates to
234 compare the total contributions of female and male parameters.¹⁷¹⁸

235 Population viability across the climatic niche and geographic range

236 To understand the impact of climate change on species niche shifts, we estimated the probability
237 of self-sustaining populations, which is $\Pr(\lambda \geq 1)$ conditional to temperature and precipitation
238 of the dormant and growing seasons. $\Pr(\lambda > 1)$ was calculated for the two-sex model and
239 the female dominant MPMs using the proportion of the 300 MCMC samples that lead to a $\lambda \geq 1$
240 (Diez et al., 2014). Population viability in climate niche space was then represented as a contour
241 plot with values of $\Pr(\lambda > 1)$ at given temperature and precipitation for the growing season,
242 holding dormant season climate constant, and vice versa. We also visualized how our common
243 garden sites have “moved” through climate space through time due to climate change.

244 $\Pr(\lambda > 1)$ was also mapped onto geographic layers of three US states (Texas, Oklahoma
245 and Kansas) to delineate past, current and future potential geographic distribution of the
246 species. To do so, we estimated $\Pr(\lambda > 1)$ conditional to all climate covariates for each
247 pixel ($\sim 25 \text{ km}^2$) for each time period (past, present, future). Because of the amount of the
248 computation involved in the Markov chain Monte Carlo iterations, use only 100 posterior
249 samples to estimate $\Pr(\lambda > 1)$ across the study area (Texas, Oklahoma and Kansas).

250 To compare the probability of self-sustaining populations between the female dominant
251 and the two-sex model, we used a zero-inflated beta model in brms (Bürkner, 2017).¹⁹

252 Results

253 Sex specific demographic response to climatic gradient

254 We found a sex specific demographic response to climatic gradient in *Poa arachnifera*
255 populations. Specifically, female individuals had higher survival and flowering rate than male
256 across species range during the dormant and growing season (Figure 2A-3D, 3I-3L). Male
257 individuals produce more panicles than female across species range (Figure 2M-3P). On the
258 contrary, female had a size advantage for low value values of climate during the growing

¹⁷ θ_i^F and θ_i^M include the interaction and second order effect. I think we are good with this formula

¹⁸I do not agree. It is true that you can compute this, but only by “turning off” the interaction by holding the interacting variable constant. I still think this needs to be better addressed in both LTRE analyses.

¹⁹This just floats here without much context. Not sure we need it, but I am flagging for now and will come back to this after reading the results.

259 season and for high values of climate during the dormant season (Figure 2E-3H). We also
260 found opposite patterns in the direction of the effect on climate on the probability of survival
261 and flowering. If temperature of the growing seasons and dormant season are constant, then
262 precipitation of the growing season has a negative effect on the probability of survival, the
263 number of tillers, and the probability of flowering (Figure 2). In contrast, if temperature of
264 the growing and dormant season are constant, then the precipitation of dormant season has
265 a positive effect on these vital rates (Figure 2E-3H). If precipitation of growing and dormant
266 season are constant, then temperature of the growing season has a positive effect of the
267 probability of survival, a negative effect on the probability of flowering, and the number of
268 tillers, but no significant effect on the number of panicles (Figure 2).²⁰

²⁰I tried to add the conditionality here. I hope it makes sense

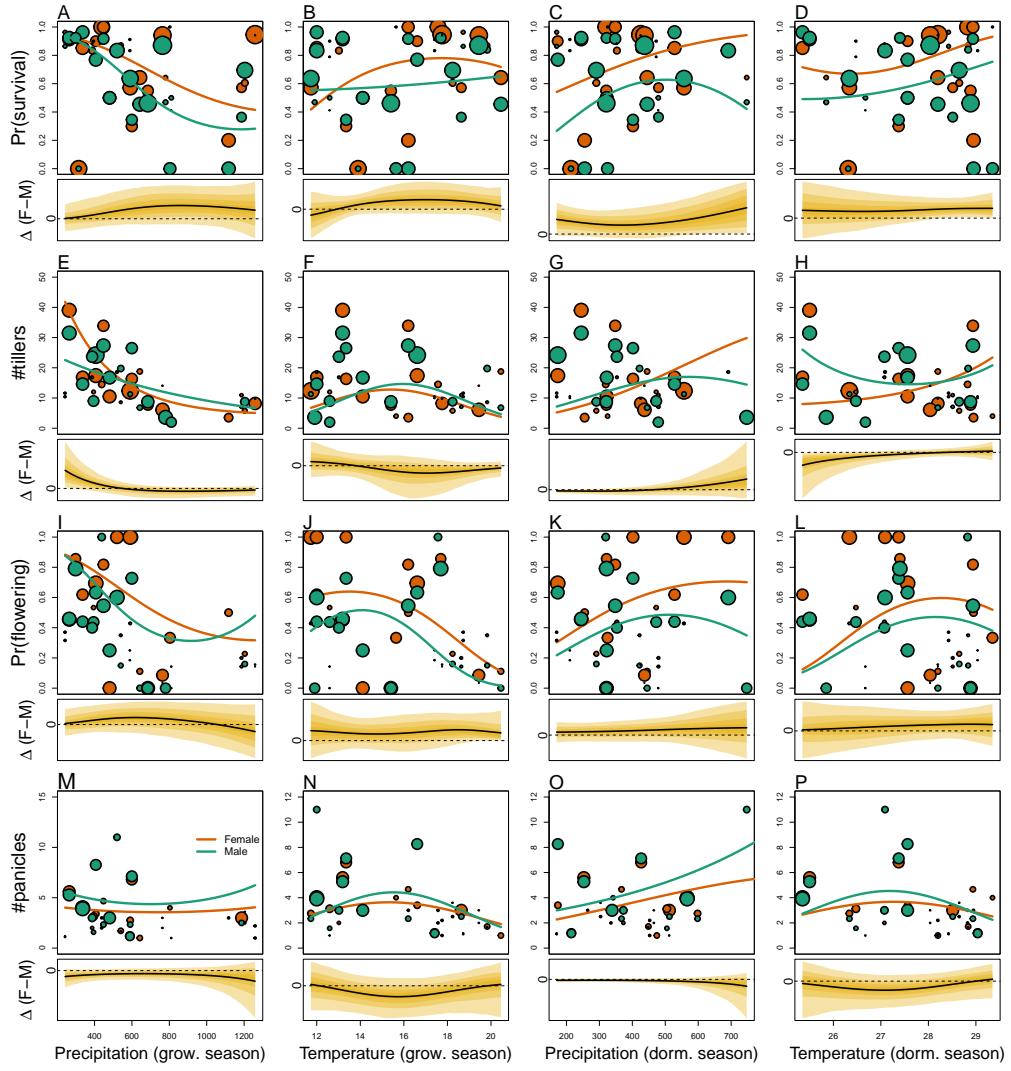


Figure 2: Sex specific demographic response to climate across species range. (A, B, C, D) Probability of survival as a function of precipitation and temperature of the growing and dormant season. (E, F, G, H) Change in number of tillers as a function of precipitation and temperature of the growing and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

269 Female bias in sex-ratio in response to climate change

270 Operational-Sex Ratio (proportion of females panicles) increased significantly with an increase
 271 of precipitation and temperature of the growing season and precipitation and temperature
 272 of dormant season (Figure S-10, Figure S-11). Similarly, the proportion of female plants

increased with an increase of temperature of growing season and temperature of dormant season (Figure S-12 B, D, Figure S-13). However, the proportion of female plants did not vary significantly with precipitation of dormant and growing season (Figure S-12 A, C). Future climate drive to extreme female-biased in *Poa arachnifera* populations (Figure 3, Figure S-14).

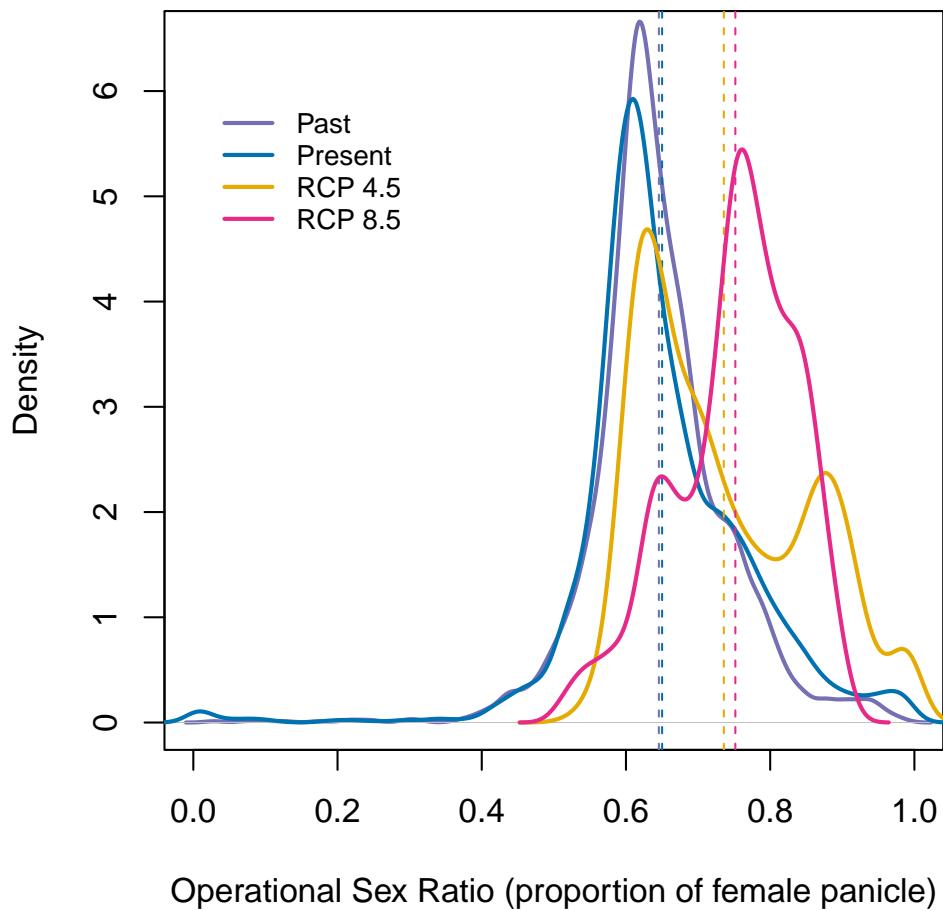


Figure 3: Change in Operational Sex Ratio (proportion of female panicule) over time (past, present, future). Future projections were based on the CMCC-CM model. The mean sex ratio for each time period is shown as vertical dashed line.

Climate change alters population viability

We estimated population growth rate variation across species range as a function of each climatic variable given the average of the three other climatic variables using two models: a female dominant model and a two-sex model²¹. For both models, population growth rate

²¹ I have now provided the methods for this contrast.

decreased toward high precipitation of growing season (Figure 4A). In contrast population growth rate increased with an increase in precipitation of the dormant season (Figure 4C). Furthermore, population growth rate was maximized between 14 and 17 °C and decreased below zero beyond 18 °C during the growing season (Figure 4B). Similarly population fitness was maximized between 27 and 31 °C and decreased below zero just beyond 20 °C during the dormant season (Figure 4D).²²

We have also detected a strong association between predicted lambda and different ranges of climate (past, present and future). Under past climate conditions, population growth rate decreased below one for temperature of the growing season. Populations will still be viable under moderate gas emission (RCP4.5). However high gas emission (RCP8.5) will alter population viability (Figure 4B, D).²³

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

²²I 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 better 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.

²³I changed how I write the first sentence to remove the "effect of climate on". Again I don't mind removing the Figure.

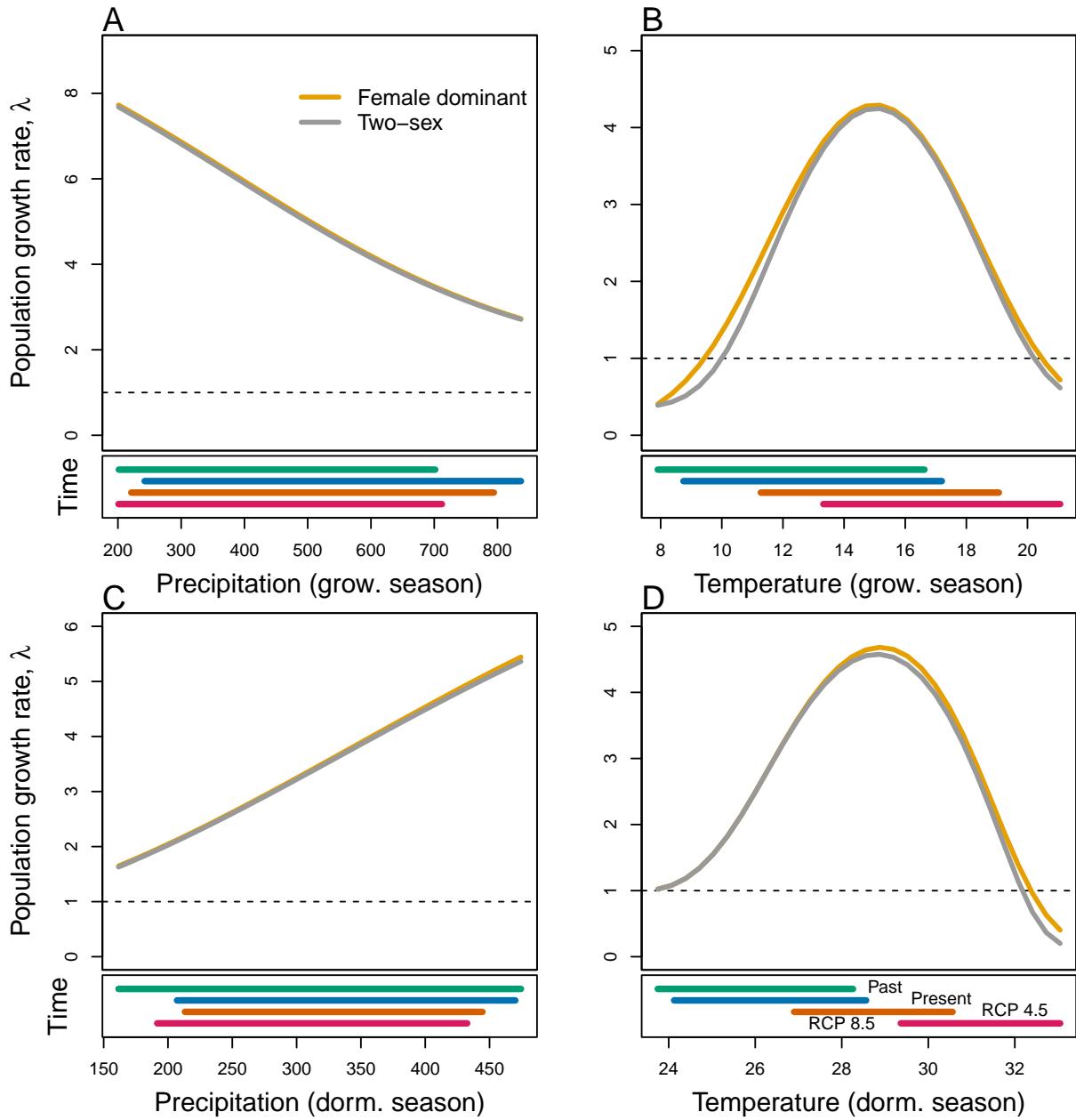


Figure 4: Predicted population growth rate (λ) in different ranges of climate. (A) Precipitation of the growing season, (B) Temperature of the growing season, (C) Precipitation of the dormant season, (D) Temperature of the dormant season. The grey curve shows prediction by the two-sex matrix projection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

²⁹⁹ **Climatic change induces niche and range shifts**

³⁰⁰ Female dominant model and two-sex models predicts a niche shift in *Poa arachnifera*
³⁰¹ populations (Figure 5). However, the female dominant model underestimated the magnitude
³⁰² of niche shifts (Figure 5E, F; -0.16[-0.29,-0.03]). Female dominant model and the two-sex
³⁰³ models agree that viable populations of *P. arichnifera* were only predicted at the center of the
³⁰⁴ range for current climatic conditions (Figure 6). Although *P. arichnifera* was predicted to have
³⁰⁵ suitable habitats in the center of the range under current climate, global warming is projected
³⁰⁶ to reduce much of these suitable habitats (Figure 6). If the species is able to disperse far and
³⁰⁷ if there is no physical barriers, most of the current suitable habitats will move toward the
³⁰⁸ Northern range edge as a results of niche shifts. Niche shift underestimation by the female
³⁰⁹ dominant model led to a geographic range underestimation by the female dominant model.

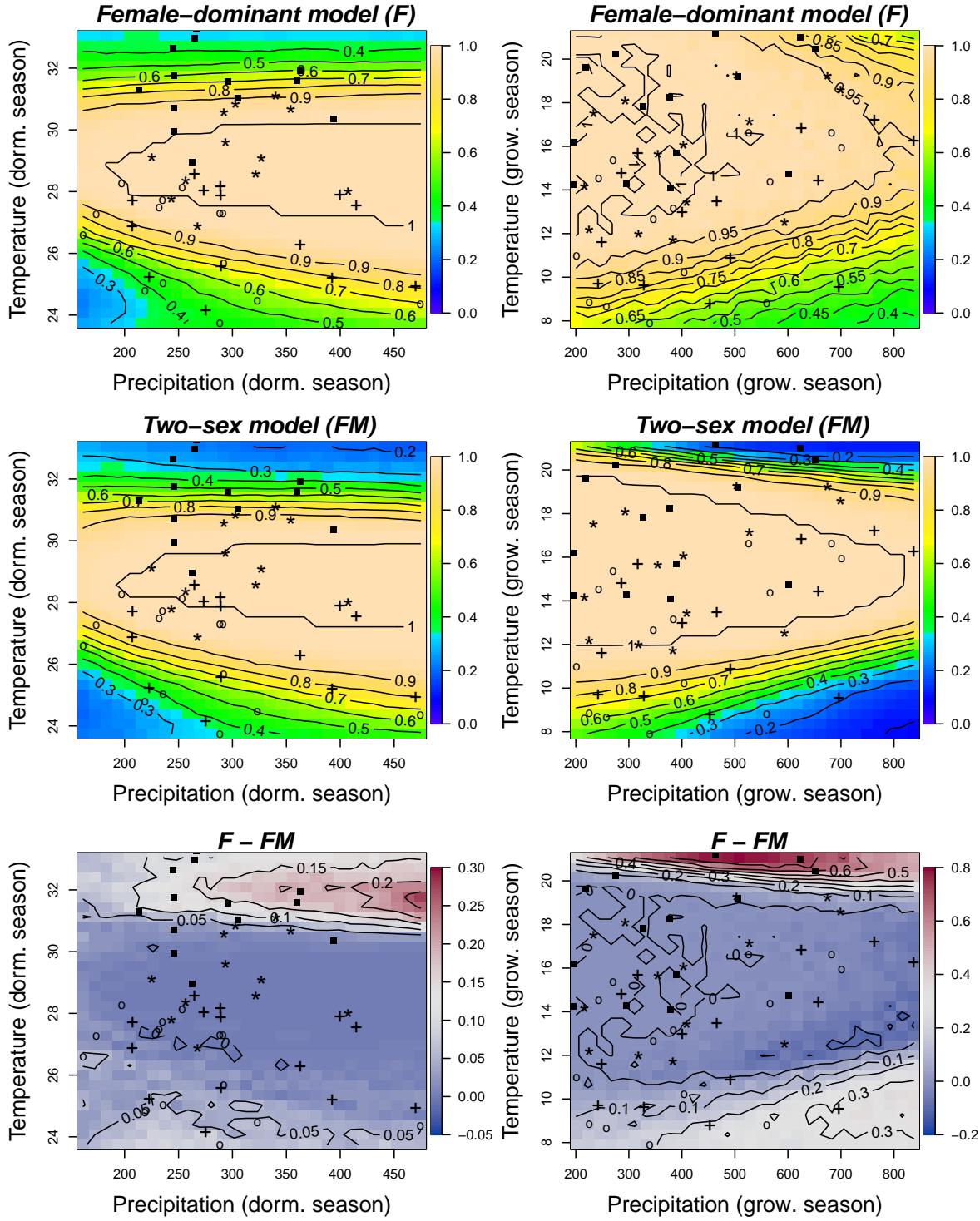


Figure 5: A two-dimensional representation of the predicted niche shift over time (past, present and future climate conditions). Contours on the first four panels show predicted probabilities of self-sustaining populations, $\Pr(\lambda > 1)$ conditional on precipitation and temperature of the dormant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

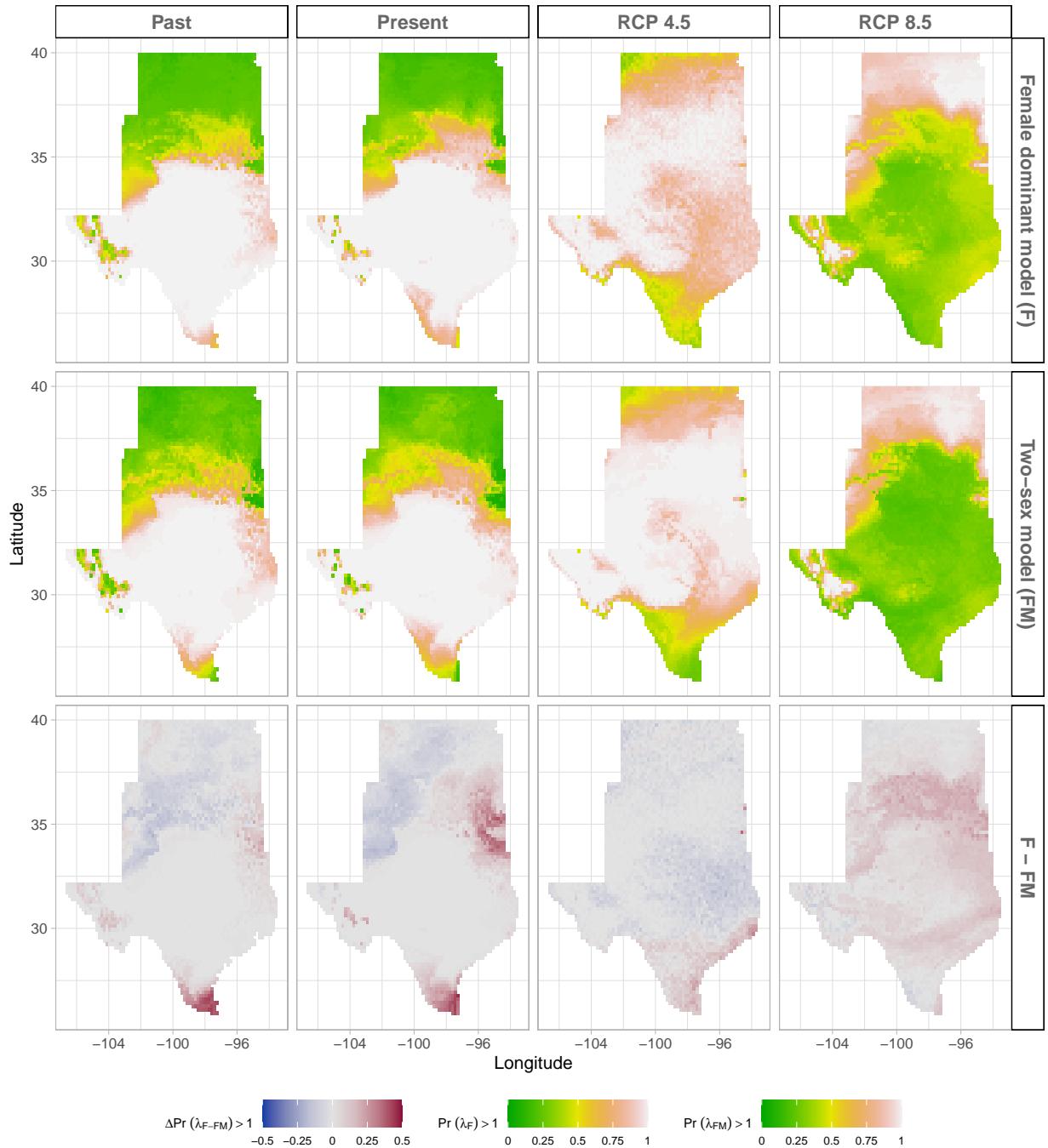


Figure 6: Climate change favors range shift towards north edge. (A) Past, (B) Current, (C and D) Future predicted range shift based on the predicted probabilities of self- sustaining populations, $\Pr(\lambda > 1)$, using the two-sex model that incorporates sex- specific demographic responses to climate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

310 **Discussion**

311 ²⁴Dioecious species make up a large fraction of Earth's biodiversity – most animals and
312 many plants – yet we have little knowledge about how skewness in sex ratio will affect
313 population viability and range shifts of dioecious species under climate change. We used
314 three years of demographic data collected from common garden experiments across climatic
315 gradient to forecast for the first time the impact of climate change on dioecious species. Our
316 future projections require extrapolation to warmer or colder conditions than observed in
317 our experiment and subsequently should be interpreted with caution (Chen et al., 2024).
318 Despite all these limitations, the qualitative implications of the response of our study species
319 to increase temperature (dormant and growing season) seems consistent across all GCMs
320 (Figure S-19, Figure S-20, Figure S-21). Three general patterns emerged from our analysis
321 of range-wide common garden experiments and sex-structured, climate-explicit demographic
322 models. First, our Bayesian mixed effect model suggests a sex specific demographic response
323 to climate change that lead to higher proportion of female as climate increase. Second, climate
324 change favors a northern range shifts in suitable habitats. Third, the female dominant model
325 (model that does not account for sex structure) overestimates species niche and range shifts.

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

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

²⁴This is my new proposition regarding the discussion

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

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

³⁷⁶ **Conclusion**

³⁷⁷ We have investigated the potential consequence of skewness in sex ratio on population
³⁷⁸ dynamics and range shift in the context of climate change using the Texas bluegrass. We
³⁷⁹ found extreme female -biased in response to climate change. The effect of female biased
³⁸⁰ will induce range shifts to the northern edge of the species current range by limiting mate
³⁸¹ availability. Beyond, our study case, our results also suggest that tracking only one sex could
³⁸² lead to an underestimation of the effect of climate change on population dynamics. Our
³⁸³ work provides also a framework for predicting the impact of global warming on population
³⁸⁴ dynamics using the probability of population to self-sustain.

³⁸⁵ **Acknowledgements**

³⁸⁶ This research was supported by National Science Foundation Division of Environmental
³⁸⁷ Biology awards 1543651 and 1754468 and by the Rice University Faculty Initiatives Fund.

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Supporting Information

577 S.1 Supporting Figures

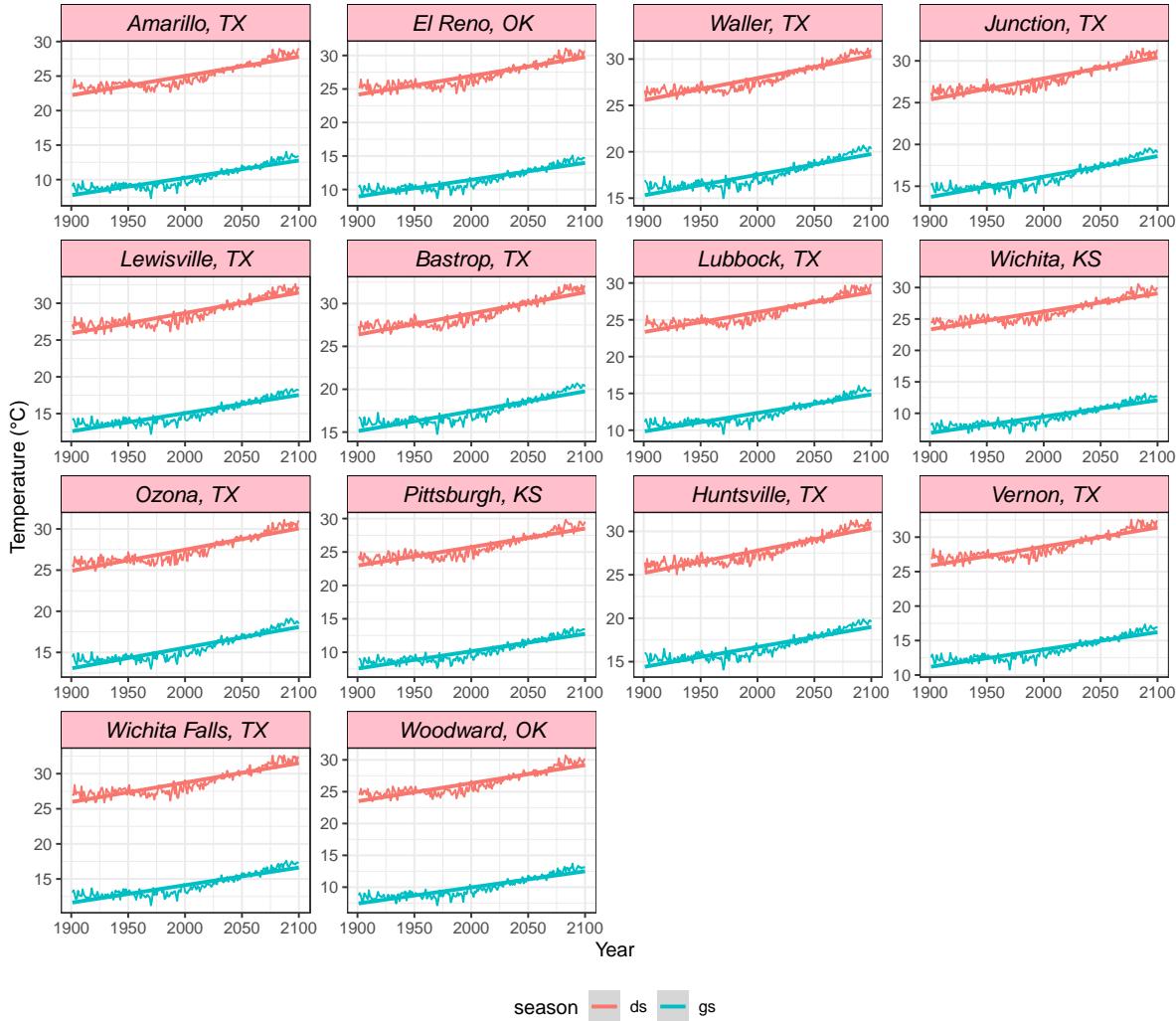


Figure S-1: Temperature variation across the study sites from 1990 to 2100, ds: Dormant season, dg: Growing season.

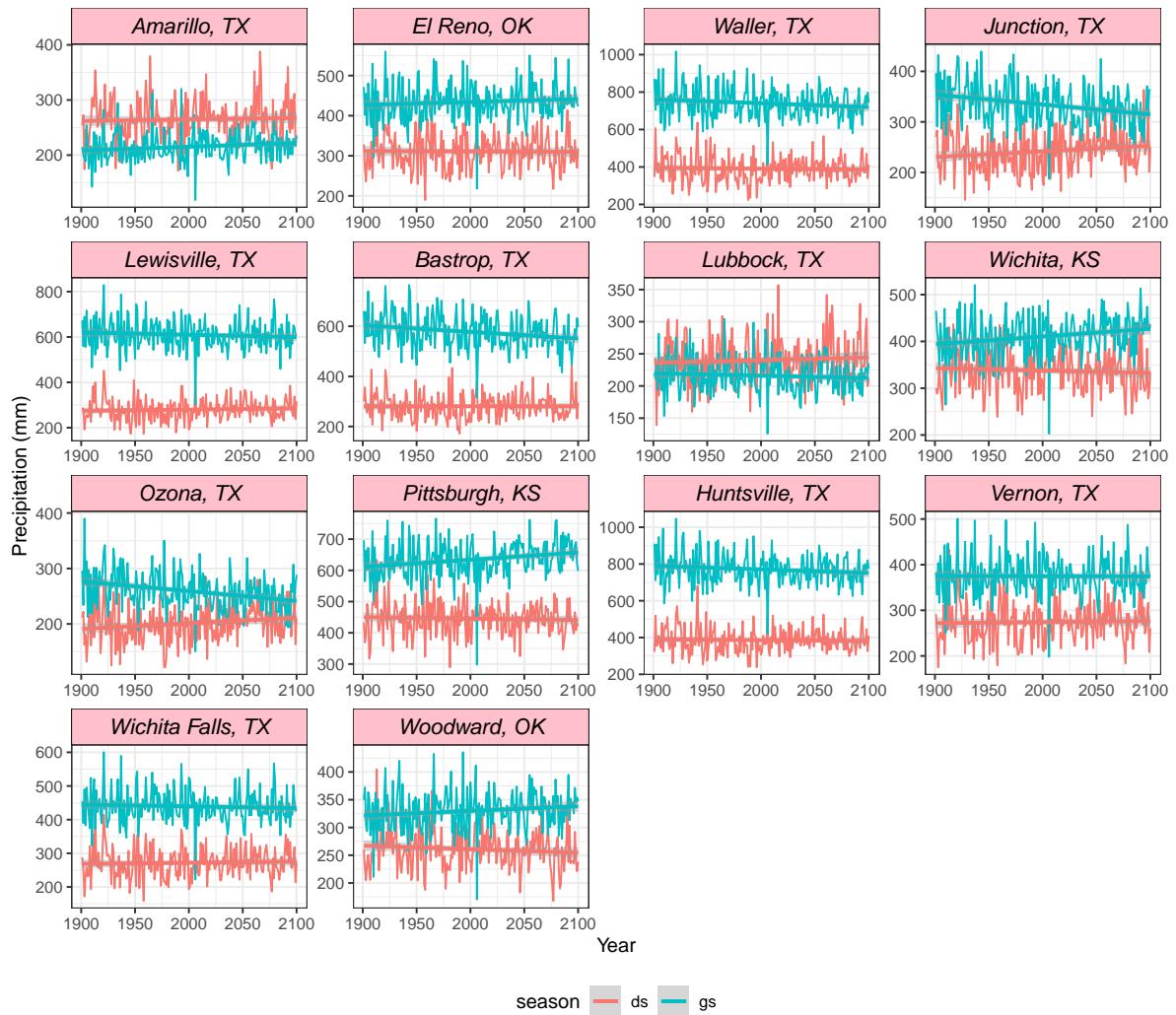


Figure S-2: Precipitation variation across the study sites from 1990 to 2100. ds: Dormant season, dg: Growing season.

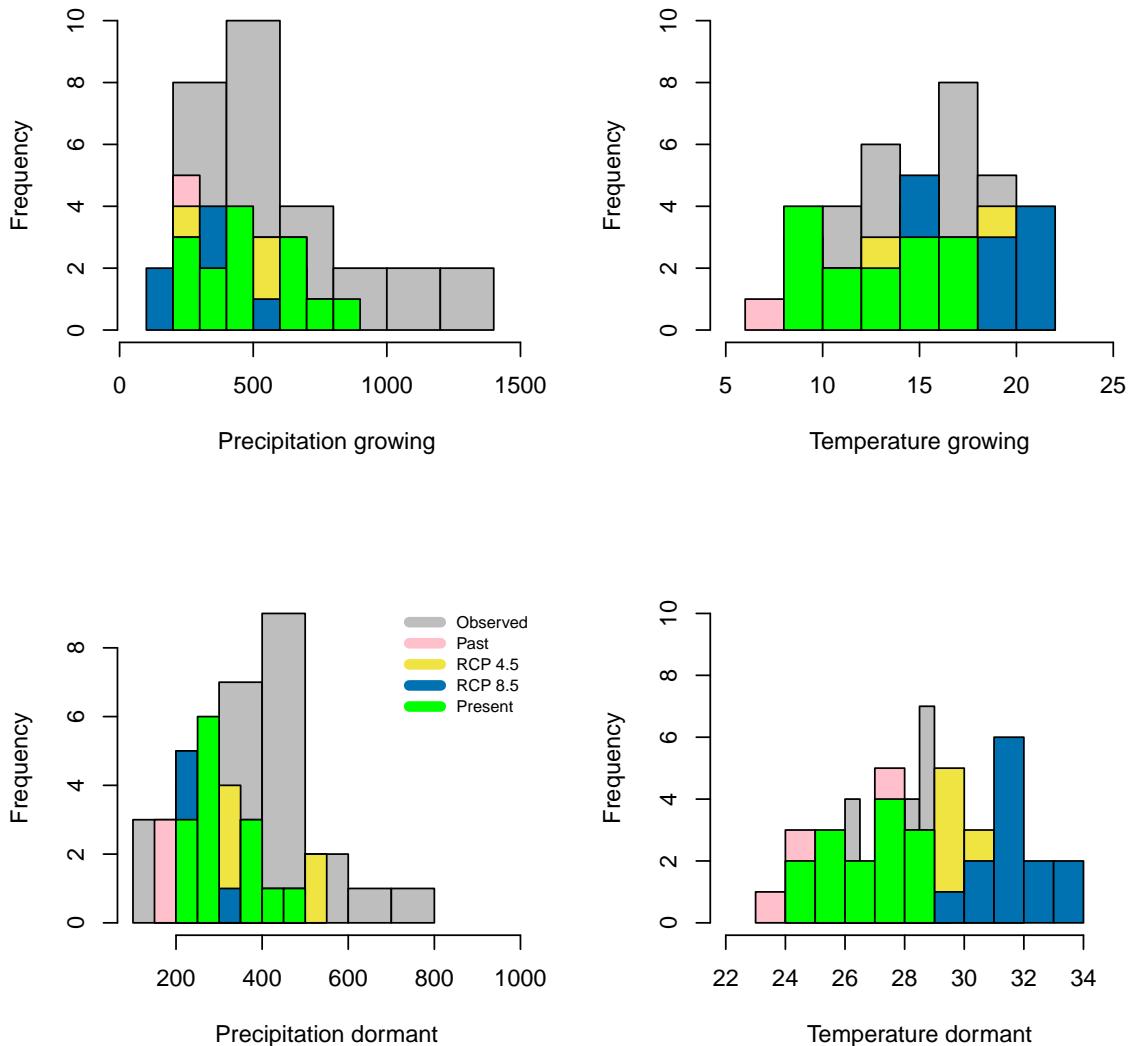


Figure S-3: Past, Observed, present and future (MIROC Model) climate data across the study area.

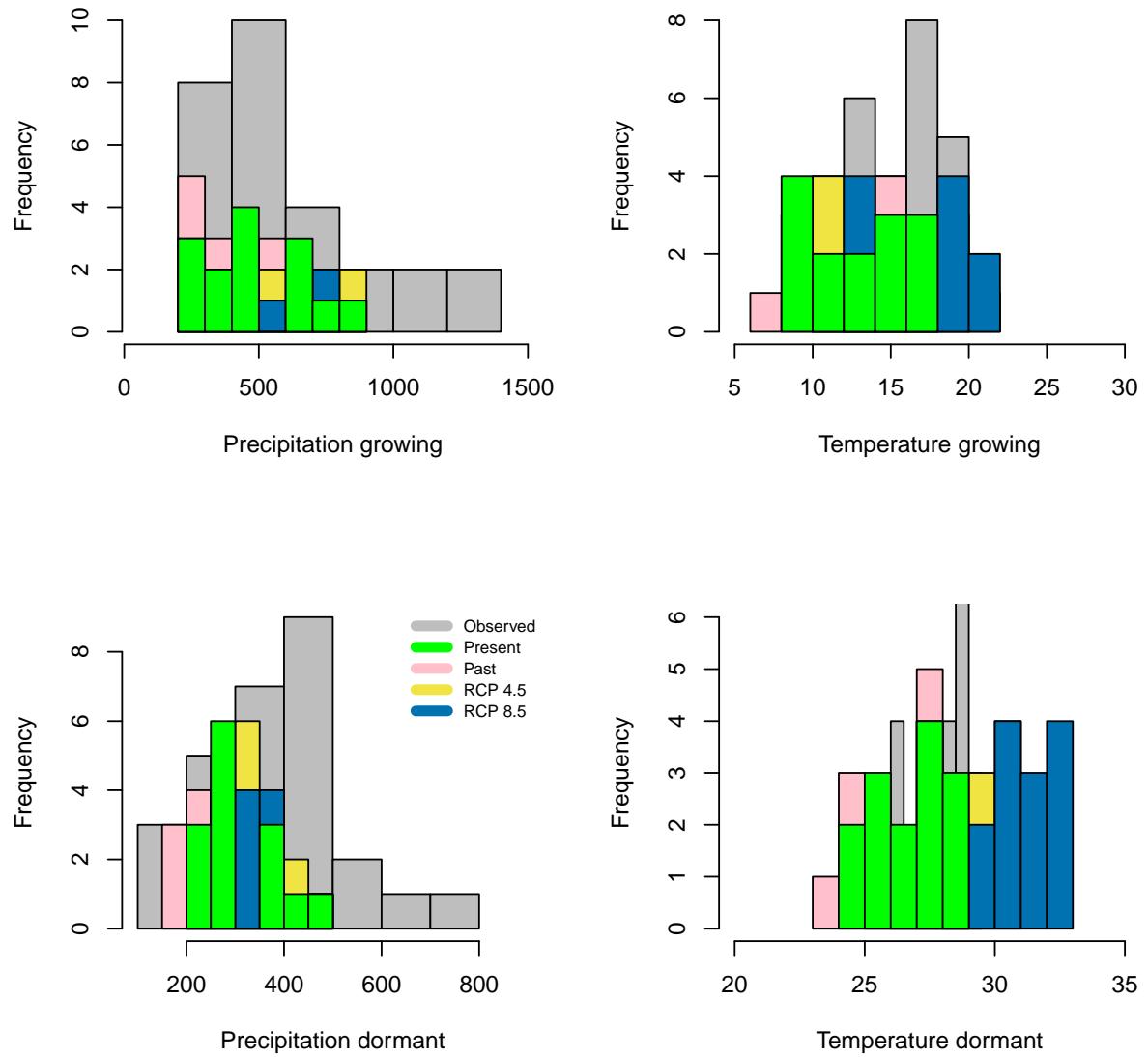


Figure S-4: Past, Observed, present and future (ACCESS Model) climate data across the study area.

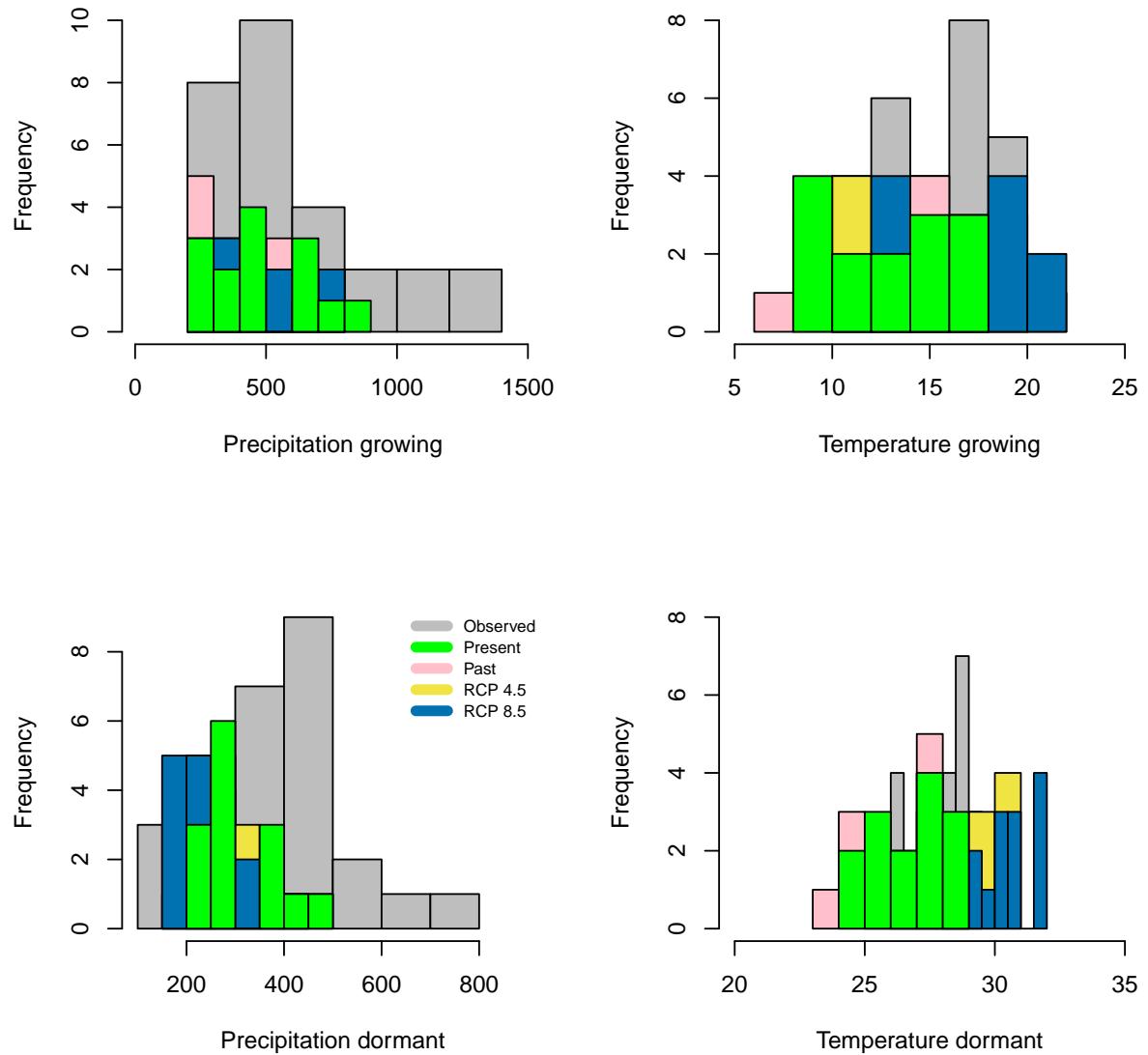


Figure S-5: Past, Observed, present and future (CESM1 Model) climate data across the study area.

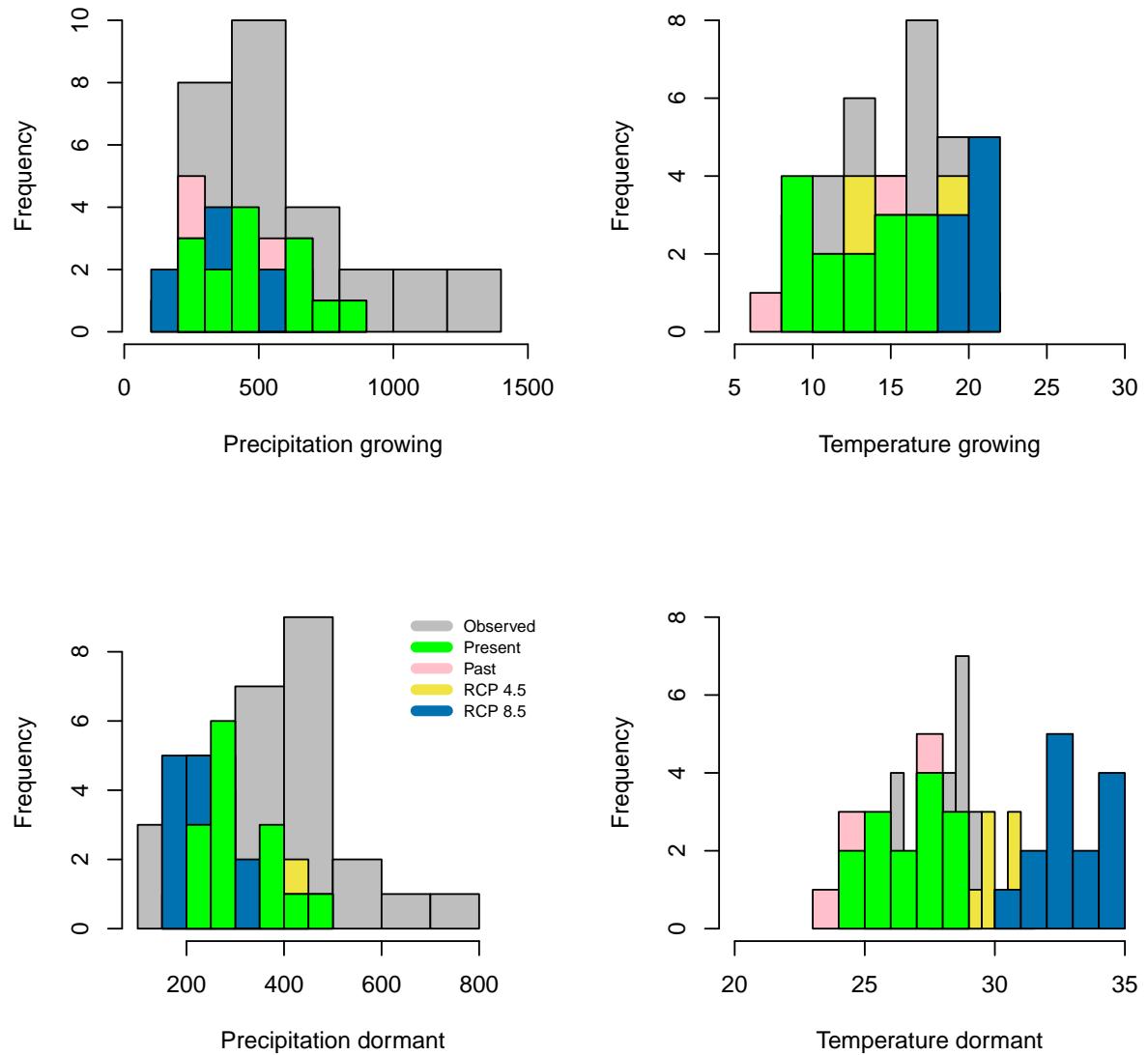


Figure S-6: Past, Observed, present and future (CMCC Model) climate data across the study area.

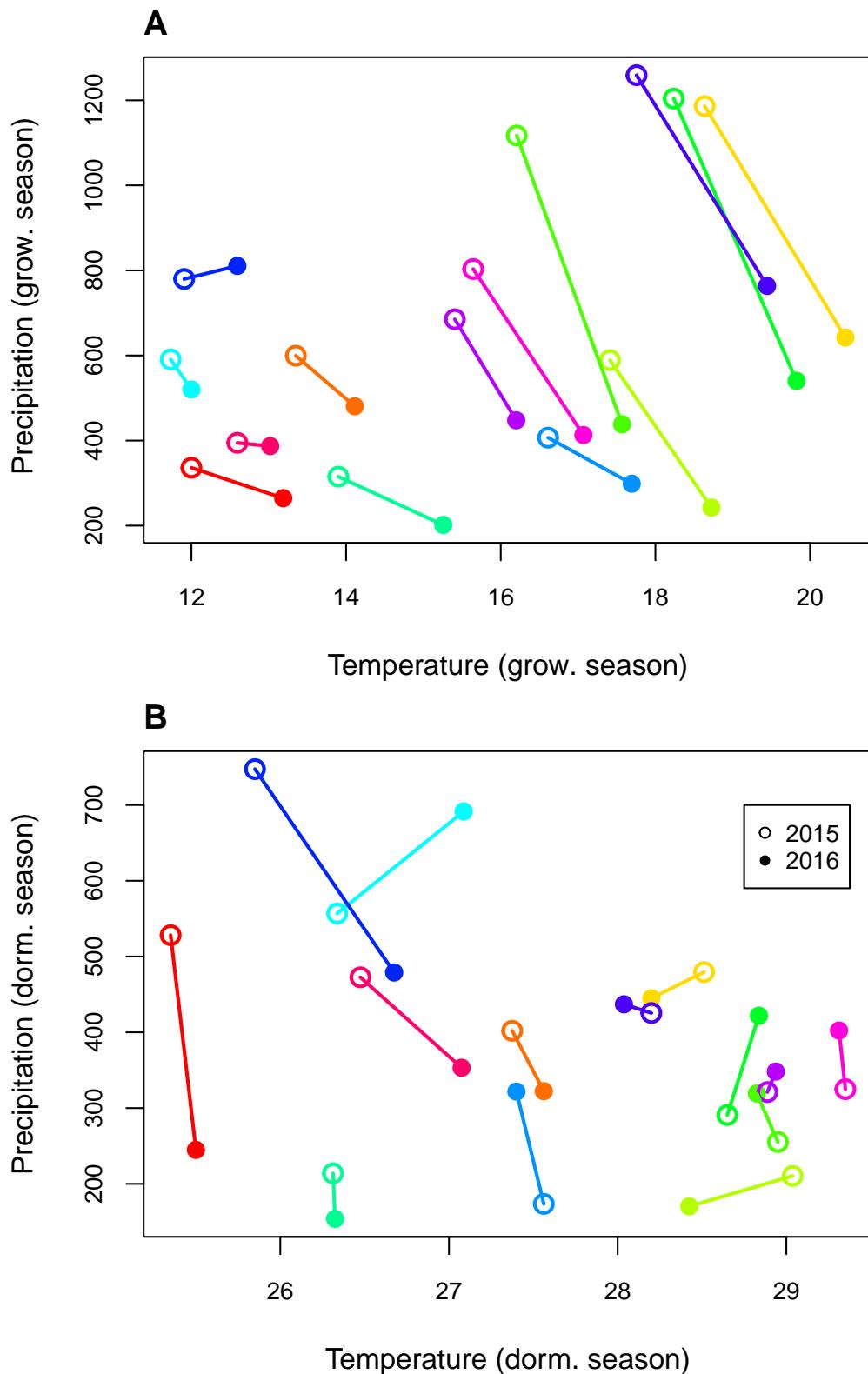


Figure S-7: Climate variation across the study sites during the monitoring period.

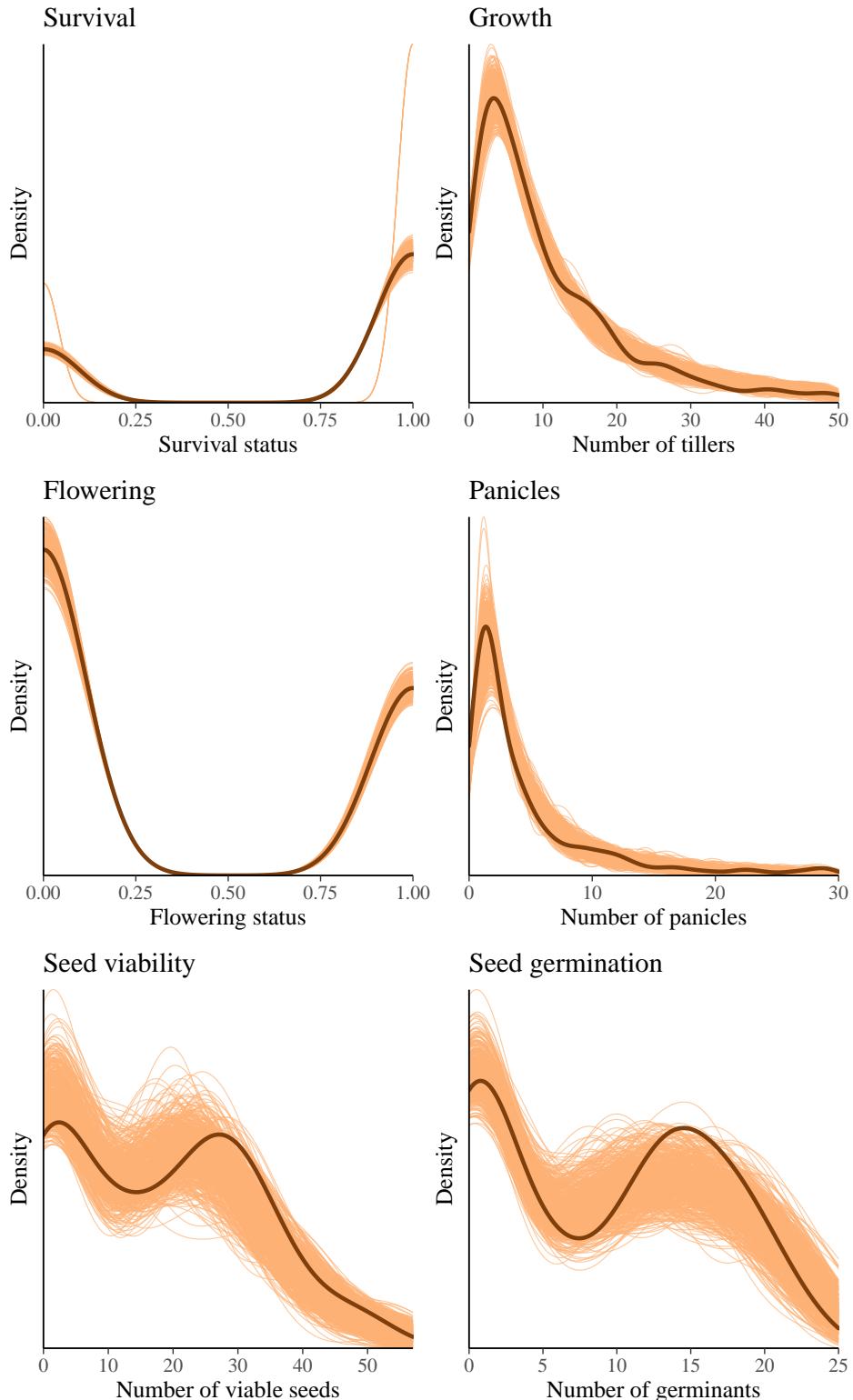


Figure S-8: Posterior predictive checks. Consistency between real data and simulated values suggests that the fitted vital rate models accurately describes the data. Graph shows density curves for the observed data (light orange) along with the simulated values (dark orange).

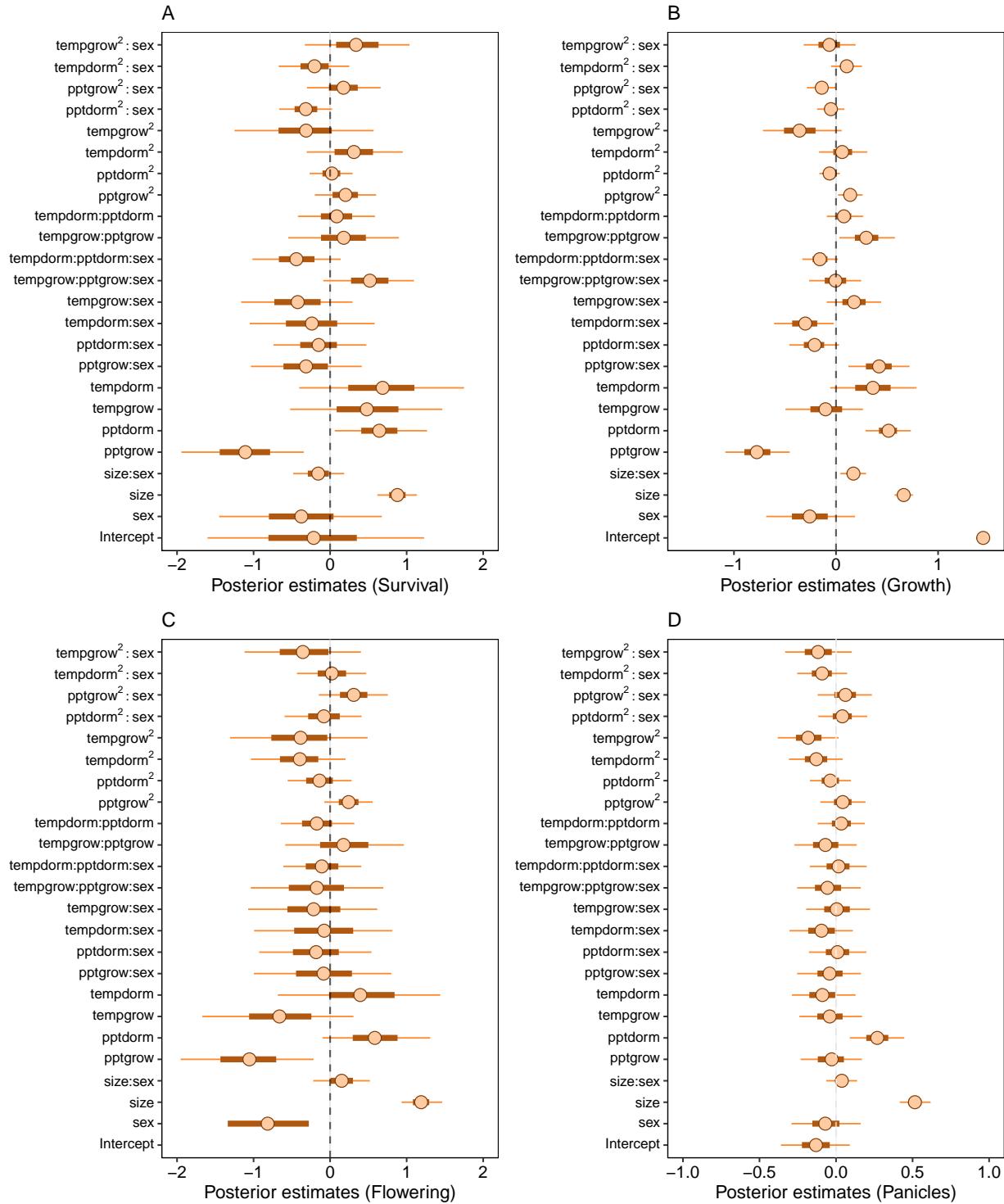


Figure S-9: Mean parameter values and 95% credible intervals of the posterior probability distributions. pptgrow is the precipitation of growing season, Tempgrow is the temperature of growing season, pptdorm is the temperature of dormant season, Tempdorm is the temperature of dormant season.

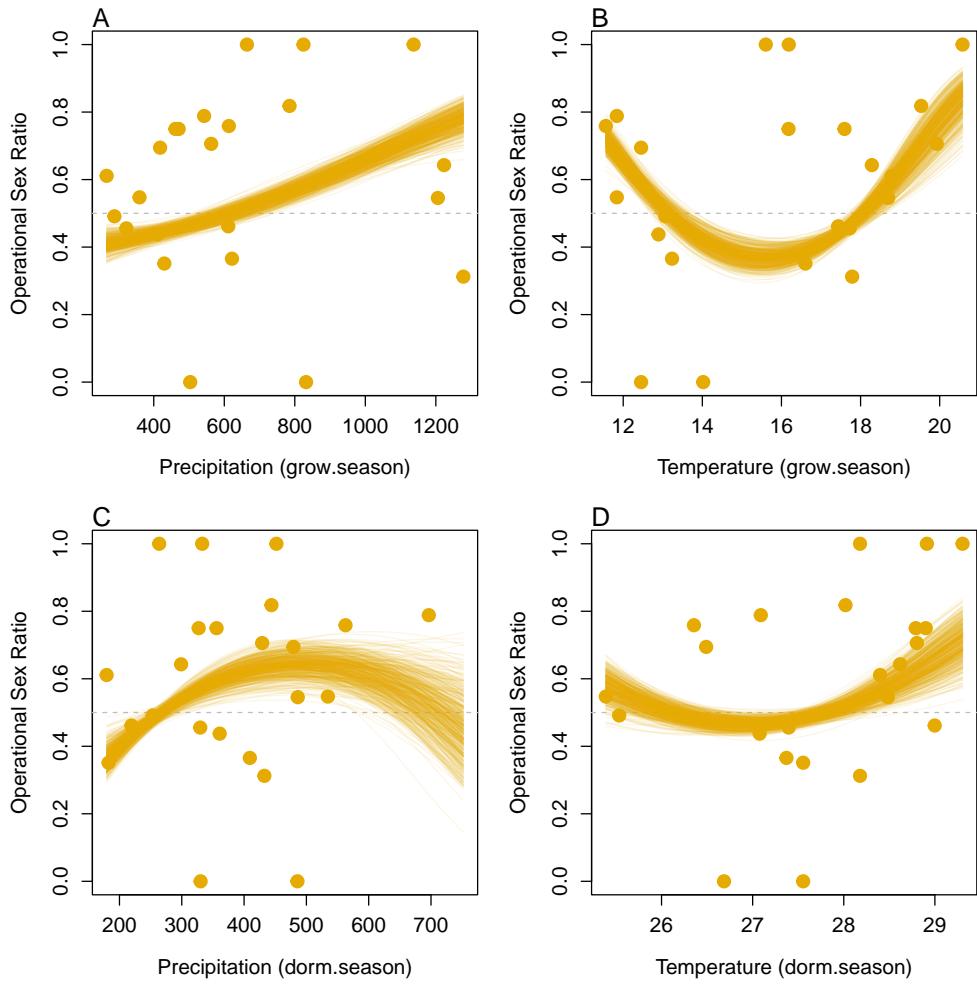


Figure S-10: Significant Operational Sex Ratio response across climate gradient. (A, B) Proportion of panicles that were females across precipitation and temperature of the growing season; (C, D) Proportion of panicles that were females across precipitation and temperature of the dormant season.

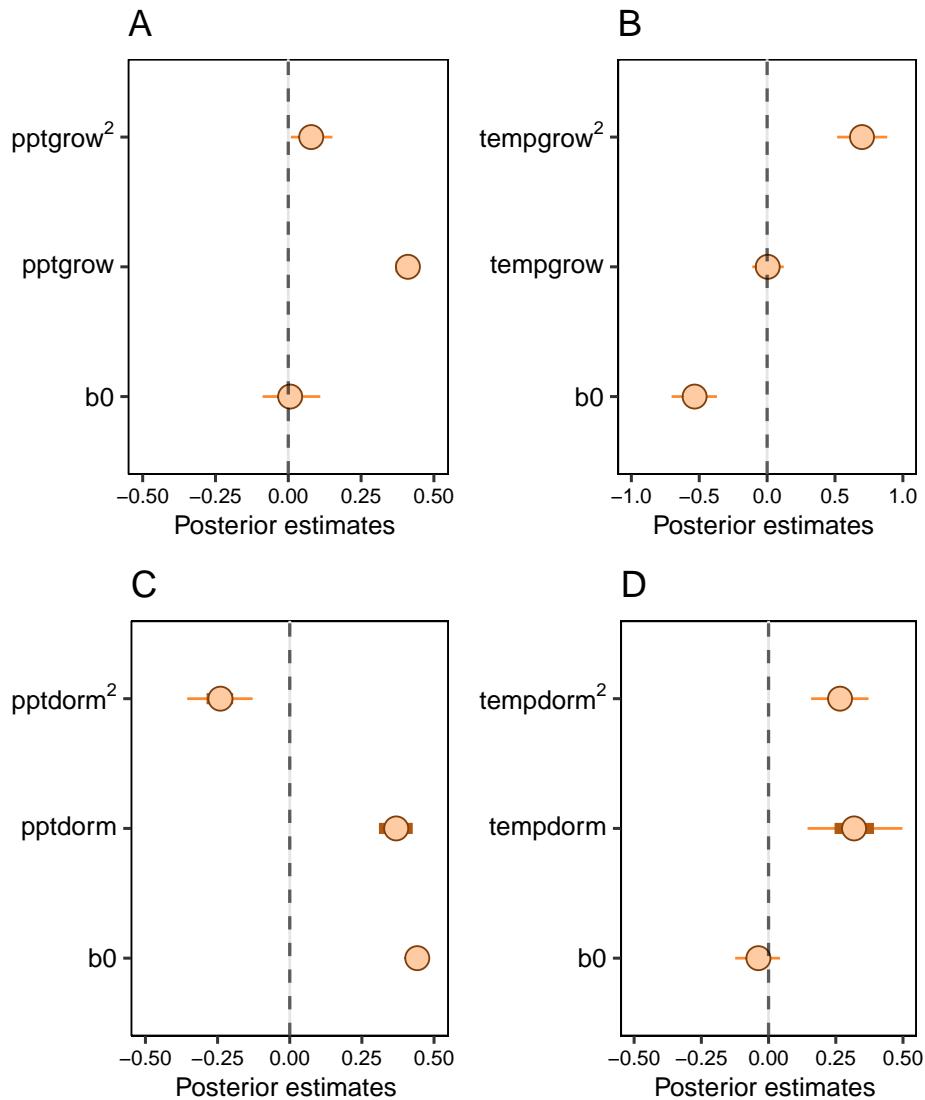


Figure S-11: Mean parameter values and 95% credible intervals of the posterior probability distributions. pptgrow is the precipitation of growing season, Tempgrow is the temperature of growing season, pptdorm is the temperature of dormant season, Tempdorm is the temperature of dormant season.

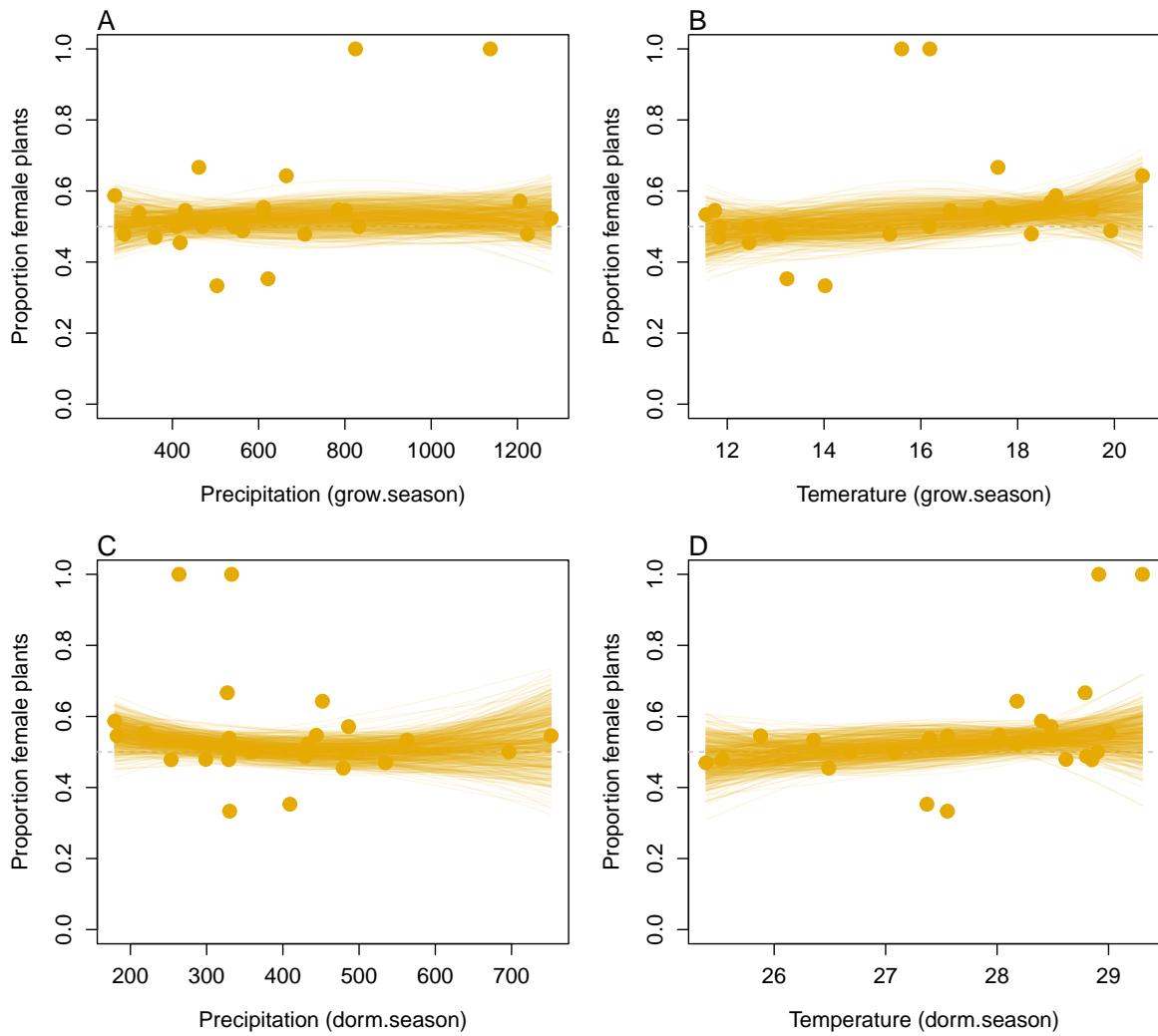


Figure S-12: Variation in sex-ratio accross climate gradient. (A, B) Proportion of plants that were females across precipitation and temperature of the growing season; (C, D) Proportion of plants that were females across precipitation and temperature of the dormant season.

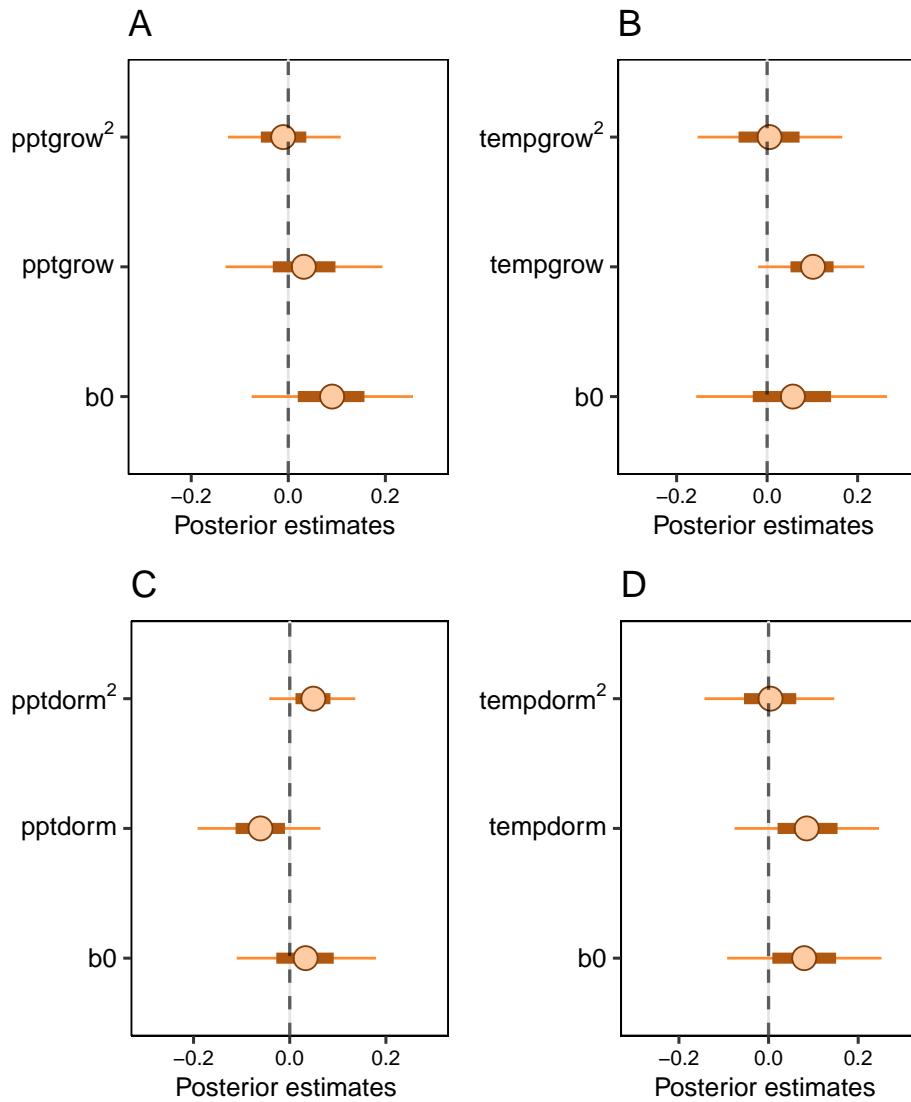


Figure S-13: Mean parameter values and 95% credible intervals of the posterior probability distributions. pptgrow is the precipitation of growing season, Tempgrow is the temperature of growing season, pptdorm is the temperature of dormant season, Tempdorm is the temperature of dormant season.

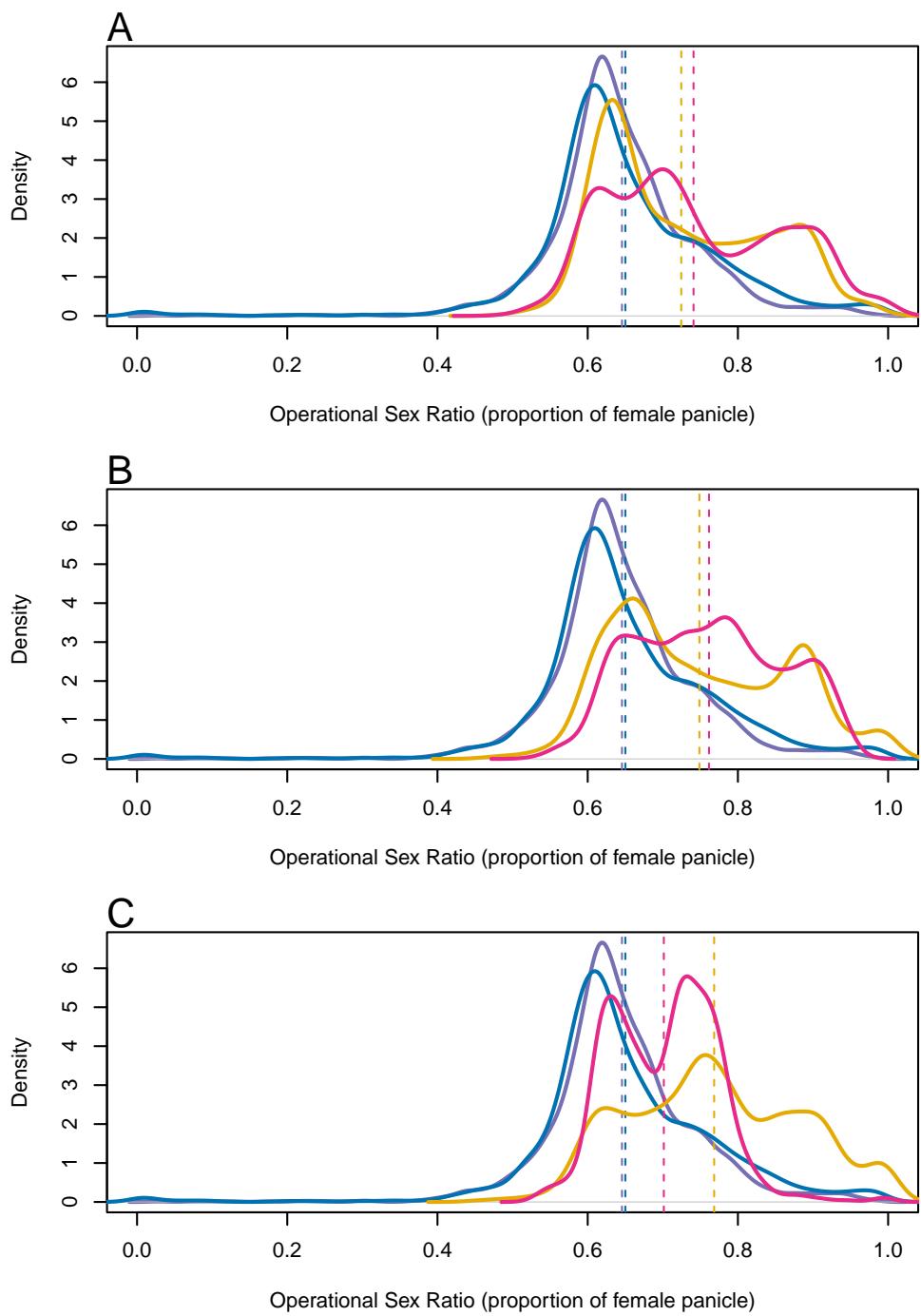


Figure S-14: Change in Operational Sex Ratio (proportion of female) over time (past, present, future). Future projections were based on A) MIROC 5, B) CES, C) ACC. The means for each model are shown as vertical dashed lines.

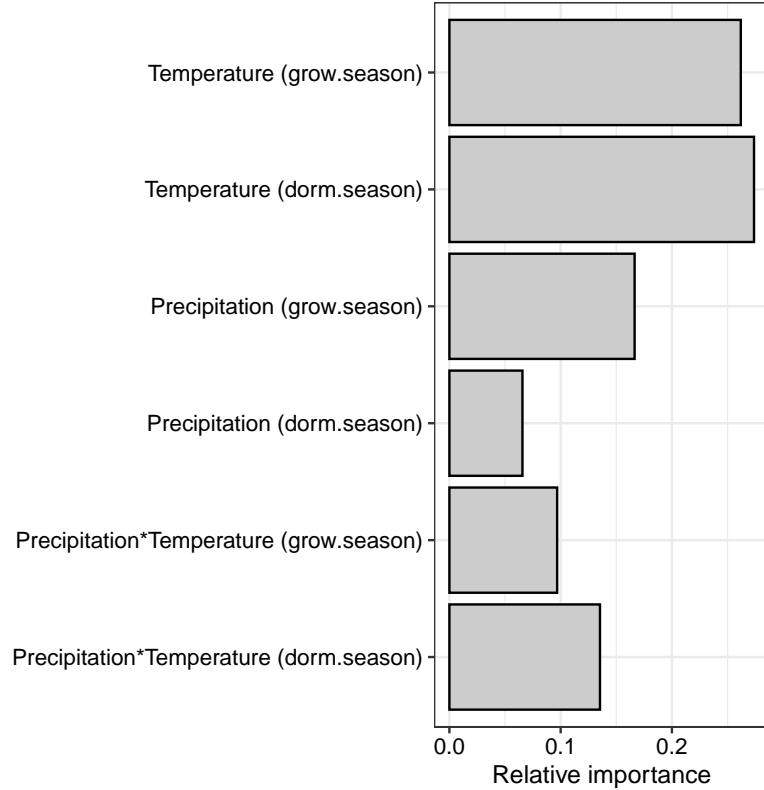


Figure S-15: Life Table Response Experiment: The bar represent the relative importance of each predictors.

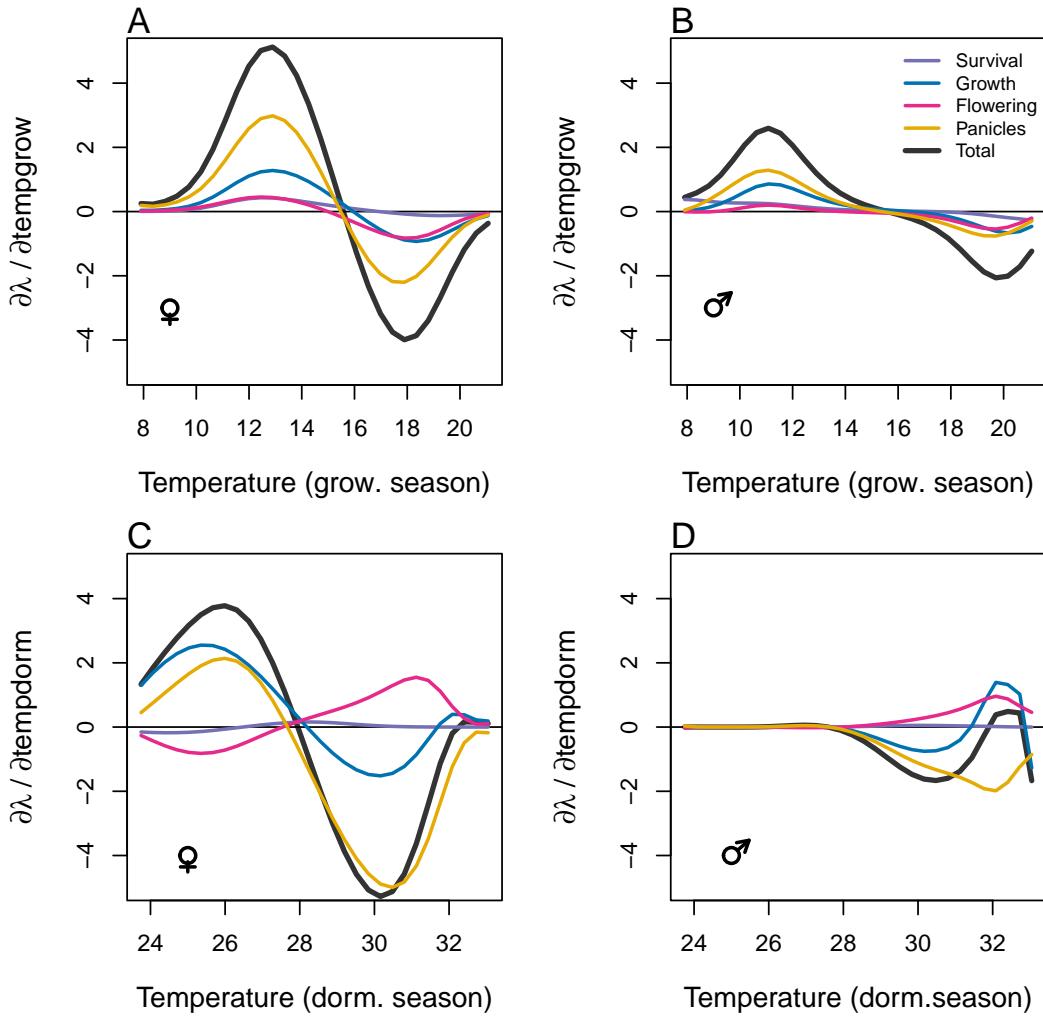


Figure S-16: Life table response experiment decomposition of the sensitivity of λ to seasonal climate into additive vital rate contributions of males and females based on posterior mean parameter estimates. (A) Temperature of growing season (contribution of female), (B) Temperature of growing season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

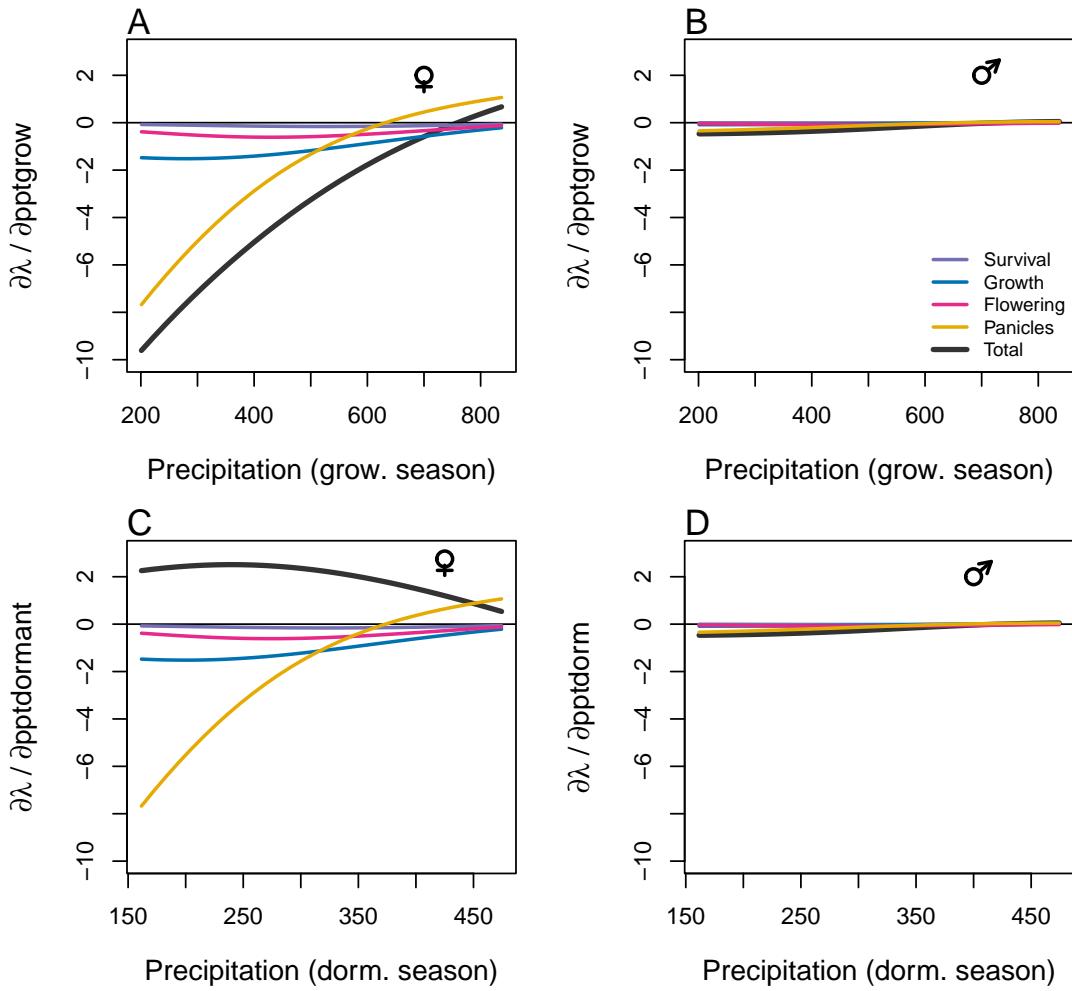


Figure S-17: Life table response experiment decomposition of the sensitivity of λ to seasonal climate into additive vital rate contributions of males and females based on posterior mean parameter estimates. (A) Precipitation of growing season (contribution of female), (B) Precipitation of growing season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

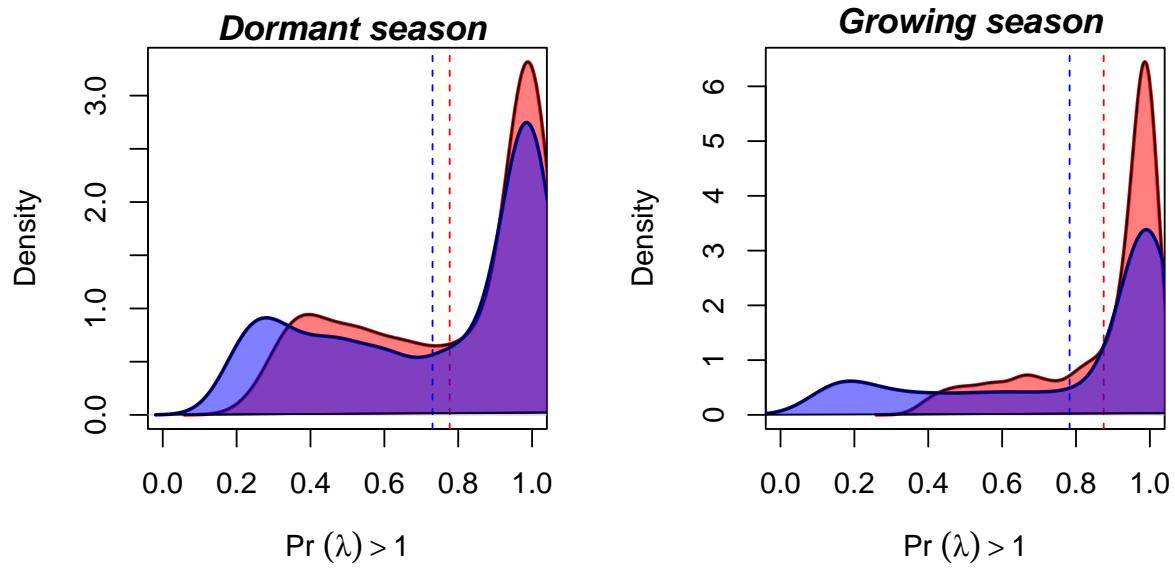


Figure S-18: Assessment of the statistical difference between the two-sex models and the female dominant model for the dormant and growing season. Plots show the density of $\Pr(\lambda) > 1$ values for female dominant (pink) and two-sex models (violet) for each season. The means for each model are shown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

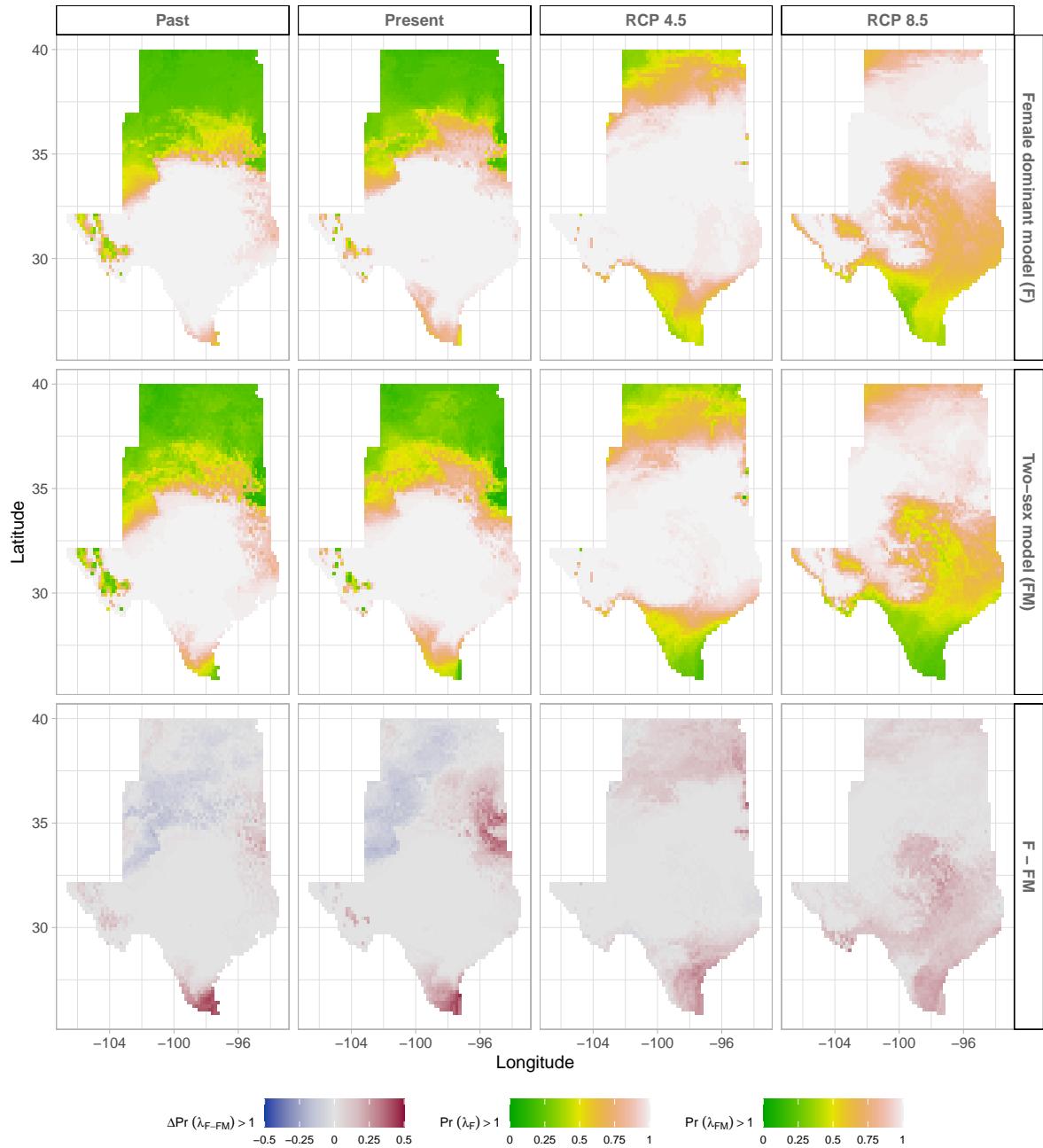


Figure S-19: Climate change favors range shift toward the North edge of the current range. (A) Past, (B) Current, (C and D) Future predicted range shift based on the predicted probabilities of self- sustaining populations, $\Pr(\lambda > 1)$, using the two-sex model that incorporates sex- specific demographic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

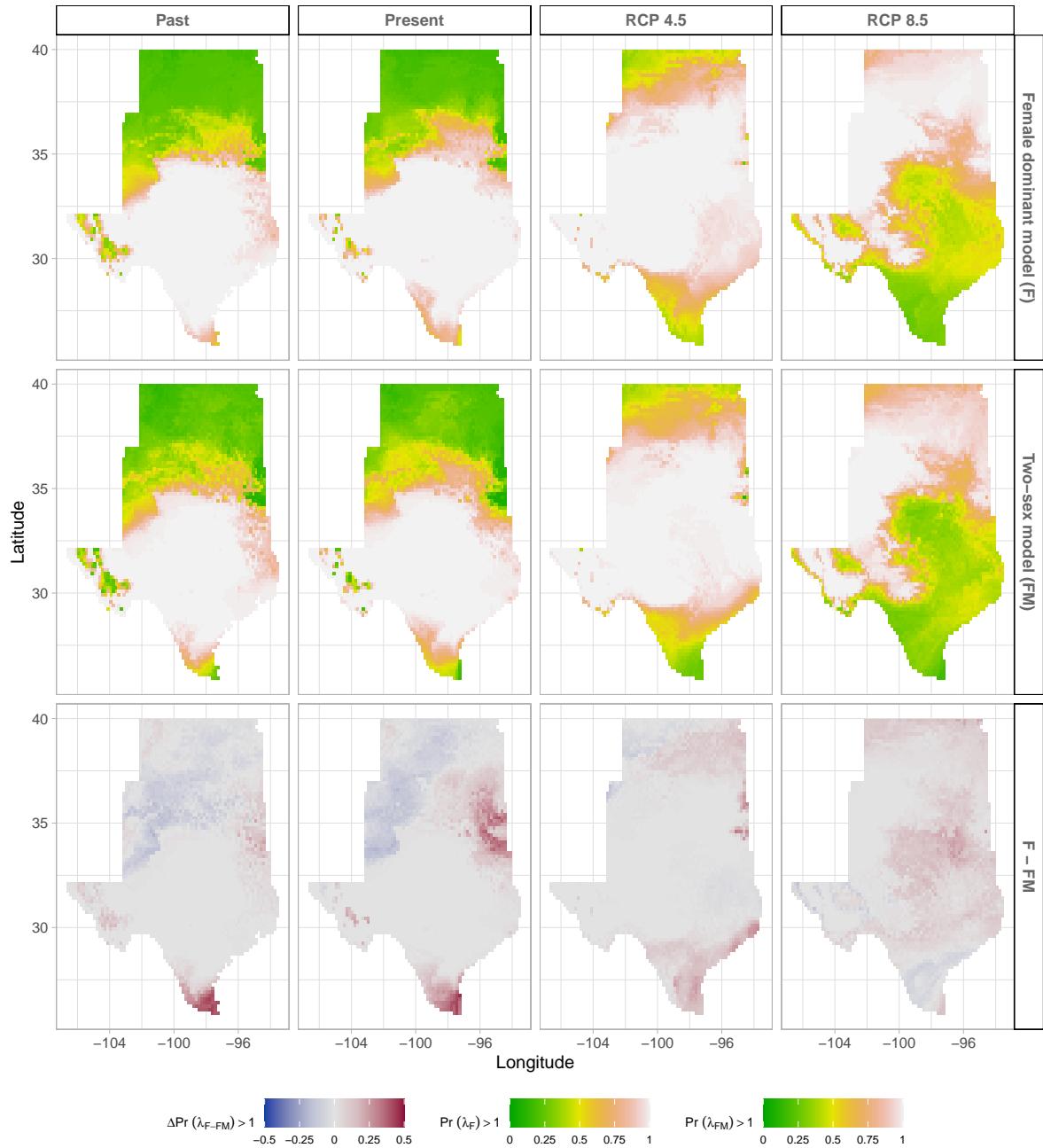


Figure S-20: Climate change favors range shift toward the North edge of the current range. (A) Past, (B) Current, (C and D) Future predicted range shift based on the predicted probabilities of self-sustaining populations, $\Pr(\lambda > 1)$, using the two-sex model that incorporates sex-specific demographic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

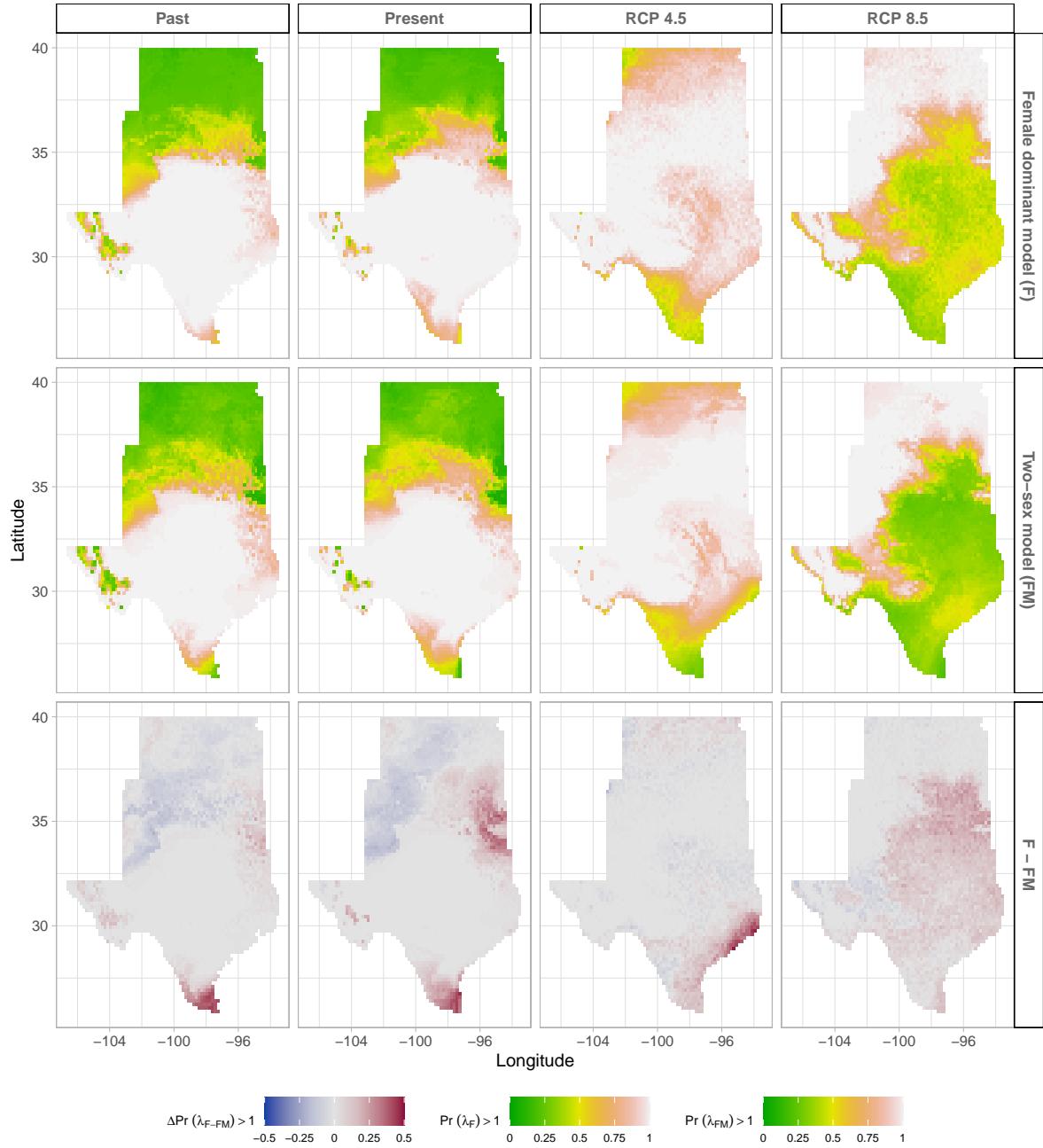


Figure S-21: Climate change favors range shift toward the North edge of the current range. (A) Past, (B) Current, (C and D) Future predicted range shift based on the predicted probabilities of self- sustaining populations, $\Pr(\lambda > 1)$, using the two-sex model that incorporates sex- specific demographic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

578 **S.2 Supporting Methods**

579 **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 x 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:

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

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