

# Forecasting range shifts of a dioecious plant species under climate change

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**Data accessibility statement:** All data used in this paper are publicly available and cited appropriately (?). 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>.

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**Abstract:**

**Main Text:**

**Figures:** 6

**Tables:** 0

**References:** 106

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## <sup>1</sup> Abstract

<sup>2</sup> Global warming has triggered an urgent need for predicting the reorganization of Earth's  
<sup>3</sup> biodiversity under climate change. Currently, the vast majority of theory and models in  
<sup>4</sup> population biology, including those used to forecast biodiversity responses to climate change,  
<sup>5</sup> ignore the complication of sex structure. We developed demographic models of range  
<sup>6</sup> limitation, parameterized from geographically distributed common garden experiments  
<sup>7</sup> with females and males of a dioecious grass species (*Poa arachnifera*) throughout and beyond  
<sup>8</sup> its range in the south-central U.S. Female-dominant and two-sex model versions of the  
<sup>9</sup> demographic model both predict that future climate change will alter population viability  
<sup>10</sup> and will induce latitudinal niche extension beyond current northern limits. However, the  
<sup>11</sup> magnitude of niche shift was underestimated by the female-dominant model, because females  
<sup>12</sup> have broader temperature tolerance than males and become mate-limited under female-biased  
<sup>13</sup> sex ratios. Explicitly account for both sexes could enhance population viability forecasts and  
<sup>14</sup> 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 (??). Dioecious species (most animals and ca. 7% of plant  
19 species) might be particularly vulnerable to the influence of climate change because they often  
20 display skewed sex ratios that are generated or reinforced by sexual niche differentiation (dis-  
21 tinct responses of females and males to shared climate drivers) (?). Accounting for such a niche  
22 differentiation within a population is a long-standing challenge in accurately predicting which  
23 sex will successfully track environmental change and how this will impact population viability  
24 and range shifts (??). The vast majority of theory and models in population biology, including  
25 those used to forecast biodiversity responses to climate change, **ignore the complication of sex**  
26 **structure**<sup>1</sup> (but ???). Traditional approaches in population biology instead focus exclusively on  
27 females, assuming that males are in sufficient supply as to never limit female fertility (?). As a  
28 result, forecasts of colonization-extinction dynamics for dioecious species under future climate  
29 change that explicitly account for females, males, and their inter-dependence are limited.

30 Species's range limits, when not driven by dispersal limitation, should generally reflect  
31 the limits of the ecological niche (?). Niches and geographic ranges are often limited by climatic  
32 factors including temperature and precipitation (?). Therefore, any substantial changes in the  
33 magnitude of these climatic factors in a given location across the range could impact population  
34 viability, with implications for range expansions or contractions based on which regions be-  
35 come more or less suitable (??). Forecasting range shifts for dioecious species is complicated by  
36 the potential for each sex to respond differently to climate variation (??). Populations in which  
37 males are rare under current climatic conditions could experience low reproductive success  
38 due to sperm or pollen limitation that may lead to population decline in response to climate  
39 change that disproportionately favors females (?). In contrast, climate change could expand  
40 male habitat suitability (e.g. upslope movement), which might increases seed set for pollen-  
41 limited females and favor range expansion (?). Although the response of species to climate  
42 warming is an urgent and active area of research, few studies have disentangled the interaction  
43 between sex and climate drivers to understand their combined effects on population dynamics  
44 and range shifts, despite calls for such an approach (hultine2016climate,gissi2023exploring).

45 Tracking the impact of climate change on population growth rate ( $\lambda$ ) and range or niche  
46 limits of dioecious taxa depends on our ability to build mechanistic models that take into  
47 account the spatial and temporal context in which sex specific response to climate change

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

48 affects population viability (???). Structured population models built from demographic data  
49 collected from geographically distributed observations or common garden experiments pro-  
50 vide several advantages for studying the impact of climate change on species' range shifts (???).  
51 First, demographic models link individual-level life history events (mortality, development,  
52 and regeneration) to population demography, allowing the investigation of factors explaining  
53 vital rate responses to environmental drivers (???). Second, demographic models have a nat-  
54 ural interface with experimental treatments that can isolate spatial and temporal correlations  
55 between environmental factors, thus overcoming a main disadvantage with many types of  
56 correlative studies (?). Third, demographic models using Markov Chain Monte Carlo (MCMC)  
57 can be utilized to infer species niche which is defined as the range of resources and conditions  
58 allowing its populations of self-sustaining populations, conditional on different factors of the  
59 environment (???)<sup>2</sup>. Finally, structured demographic models can be used to identify which as-  
60 pect of climate is more important for population dynamics. For example, Life Table Response  
61 Experiments (LTRE) built from structured models have become widely used to understand the  
62 relative importance of covariates in explaining variation in population growth rate (??). LTRE  
63 is also used to get a mechanistic understanding of how a given treatment (eg. temperature or  
64 precipitation) could affect population dynamics through unique vital rate responses (????).<sup>3</sup>

65 In this study, we used a mechanistic approach, combining geographically-distributed field  
66 experiments, Bayesian statistical modeling, and two-sex population projection modeling, to un-  
67 derstand the demographic response of dioecious species to climate change and its implications  
68 for past, present, and future range dynamics. Our work focused on the dioecious grass species  
69 Texas bluegrass (*Poa arachnifera*), which is distributed along environmental gradients in the  
70 south-central U.S. corresponding to variation in temperature across latitude and precipitation  
71 across longitude. Moreover, the south-central U.S. has experienced an increase of temperature  
72 since the 20th century and this is very likely to continue over the next years (Figure ??).<sup>4</sup>  
73 Our previous study showed that, despite a differentiation of climatic niche between sexes,  
74 the female niche mattered the most in driving the environmental limits of population viability  
75 across longitude (?). However, that study used a single proxy variable (longitude) to represent  
76 environmental variation related to aridity. Developing a rigorous forecast for the implications  
77 of future climate change requires that we transition from climate-implicit to climate-explicit  
78 treatment of environmental drivers as we do here. Here, we asked four questions<sup>5</sup>:

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<sup>2</sup>I added the niche part in the introduction as you suggested

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

<sup>4</sup>I added some context about climate change in this study region

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

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

## 86 Materials and methods

### 87 Study species

88 Texas bluegrass (*Poa arachnifera*) is a dioecious perennial, summer-dormant cool-season (C3)  
89 grass that occurs in the south-central U.S. (Texas, Oklahoma, and southern Kansas) (Figure  
90 ??) (?)<sup>6</sup>. Latitudinal limits of the Texas bluegrass distribution span 7.74 °C to 16.94 °C of  
91 temperature during the dormant season and 24.38 °C to 28.80 °C during the dormant season.  
92 Longitudinal limits span 244.9 mm to 901.5 mm of precipitation during the growing season  
93 and 156.3 mm to 373.3 mm. Texas bluegrass grows between October and May (growing  
94 season), with onset of dormancy often from June to September (dormant season) (?).

95 Biological sex in Texas bluegrass is genetically based and the birth (seed) sex ratio is 1:1  
96 (?). Females and males are morphologically indistinguishable except for their inflorescences.  
97 Flowering occurs in May and the species is wind pollinated (?). Surveys of 22 natural  
98 populations throughout the species' distribution indicated that operational sex ratio (the  
99 female fraction of flowering plants) ranged from 0.007 to 0.986 with a mean of 0.404 (?).

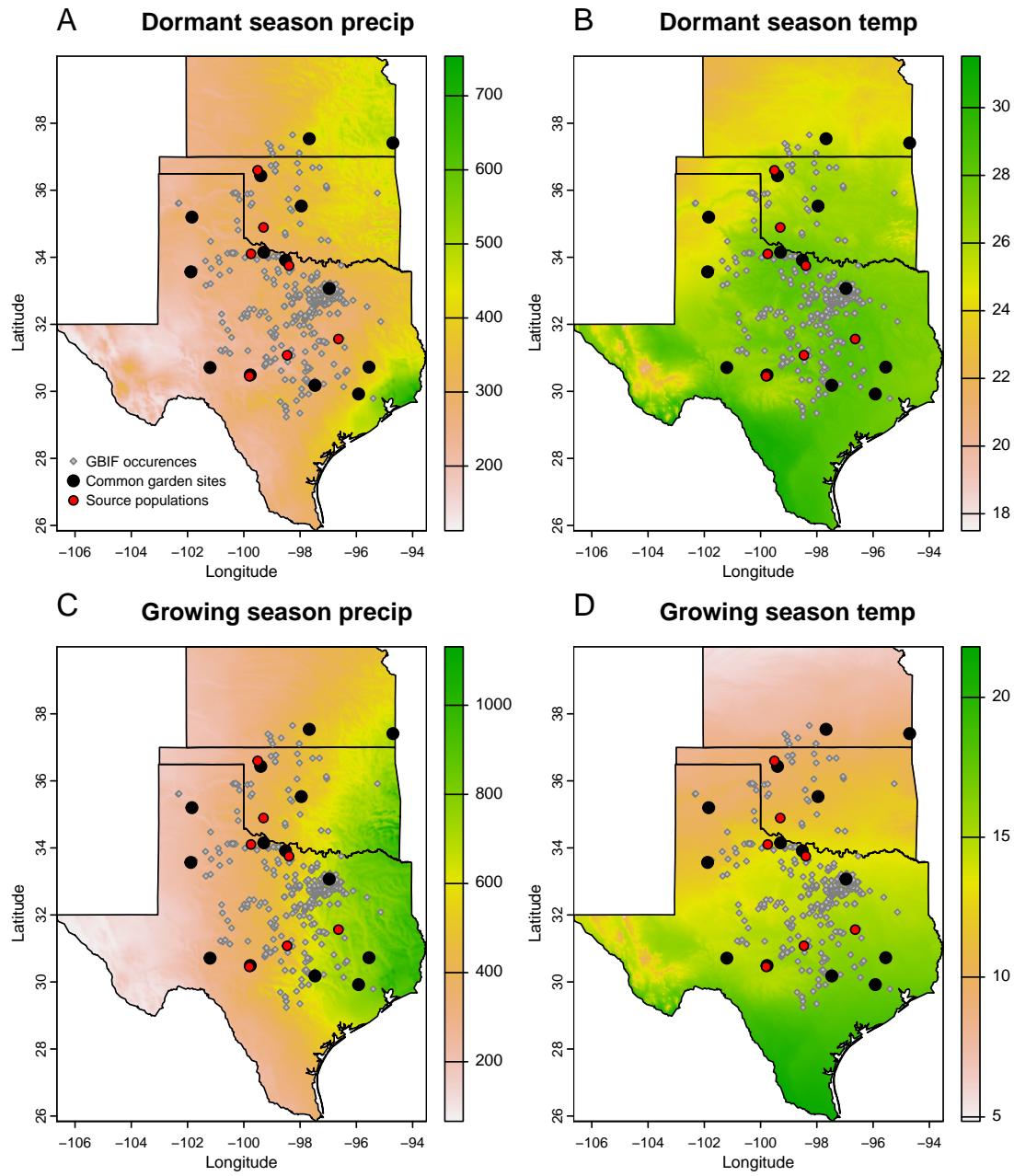
### 100 Common garden experiment

101 We set up a common garden experiment throughout and beyond the range of Texas bluegrass  
102 to quantify sex-specific demographic responses to climate. Details of the experimental design  
103 are provided in ?; we provide a brief overview here. The experiment was installed at 14 sites  
104 throughout and, in some cases, beyond the species' natural range (Figure ??). At each site, we  
105 established 14 blocks. For each block we planted the same number of plant from each sex (three  
106 female and three male individuals) that were clonally propagated from females and males  
107 from eight natural source populations (Figure ??); because sex is genetically-based, clones never  
108 deviated from their expected sex. The experiment was established in November 2013 and was

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<sup>6</sup>I have updated the map

<sup>109</sup> censused in May of 2014, 2015, and 2016. At each census, we collected individual demographic  
<sup>110</sup> data including survival (alive or dead), size (number of tillers), and number of panicles (repro-  
<sup>111</sup> ductive inflorescences). For the analyses that follow, we focus on the 2014-15 and 2015-16 tran-  
<sup>112</sup> sitions years, since the start 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 source populations (red circle). See also (Figure ??, Figure ??) for more details about climate variation across the study sites since the beginning of last century.

113 **Climatic data collection**

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

120 To back-cast and forecast demographic responses to changes in climate throughout the  
121 study region, we downloaded projection data for three 30-year periods: “past” (1901-1930),  
122 “current” (1990-2019) and “future” (2070-2100). Data for future climatic periods were  
123 downloaded from four general circulation models (GCMs) selected from the Coupled Model  
124 Intercomparison Project Phase 5 (CMIP5). The GCMs are: Model for Interdisciplinary  
125 Research on Climate (MIROC5), Australian Community Climate and Earth System Simulator  
126 (ACCESS1-3), Community Earth System Model (CESM1-BGC), Centro Euro-Mediterraneo sui  
127 Cambiamenti Climatici Climate Model (CMCC-CM). All the GCMs were also downloaded  
128 from chelsa (?). We evaluated future climate projections from two scenarios of representative  
129 concentration pathways (RCPs): RCP4.5, an intermediate-to-pessimistic scenario assuming  
130 a radiative forcing amounting to  $4.5 \text{ Wm}^{-2}$  by 2100, and RCP8.5, a pessimistic emission  
131 scenario which projects a radiative forcing of  $8.5 \text{ Wm}^{-2}$  by 2100 (??).

132 Projection data for the three 30-year periods had warmer or colder conditions than  
133 observed in our experiment (Figure ??, Figure ??, Figure ??, Figure ??). However, the observed  
134 period was substantially wetter and cooler across the study region than 2015-16, especially  
135 during the growing season (Figure ??), so our study design provides both spatial and  
136 inter-annual coverage of climate variables.

137 **Sex specific demographic responses to climate**

138 <sup>7</sup> We used individual level measurements of survival, growth (number of tillers), flowering,  
139 number of panicles to develop Bayesian linear mixed effect models describing how each  
140 vital rate varies as a function of sex, size, and four climate covariates (precipitation and  
141 temperature of growing and dormant season). We kept the four climate covariates in the  
142 mixed effect models because each climatic variable describes different aspect of climate that  
143 could be important for the species persistence across its range. Vital rate models were fit with  
144 second-degree polynomial functions and with the same linear predictors for the expected

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<sup>7</sup> 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.

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

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

152 where  $\beta_0$  is the grand mean intercept,  $\beta_1$  is the size dependent slopes. *size* was on a natural  
 153 logarithm scale.  $\beta_2 \dots \beta_{13}$  represent the climate dependent slopes.  $\beta_{14} \dots \beta_{23}$  represent the  
 154 sex-climate interaction slopes. *pptgrow* is the precipitation of the growing season, *tempgrow*  
 155 is the temperature of the growing season, *pptdorm* is the precipitation of the dormant season,  
 156 *tempdorm* is the temperature of the dormant season.

157 Different link function ( $f(\mu)$ ) was applied depending on the the vital rate distributions.  
 158 We modeled survival and flowering data with a Bernoulli distribution. We modeled the  
 159 growth (tiller number) with a zero-truncated Poisson inverse Gaussian distribution. Fertility  
 160 (panicle count) was model as zero-truncated negative binomial. Each vital rate model  
 161 includes normally distributed random effects for block-to-block variation ( $\phi \sim N(0, \sigma_{block})$ )  
 162 and source-to-source variation that is related to the provenence of the seeds used to  
 163 establish the common garden ( $\rho \sim N(0, \sigma_{source})$ ), site to site variation ( $\nu \sim N(0, \sigma_{site})$ ). We fit  
 164 survival, growth, flowering models with generic weakly informative priors for coefficients  
 165 ( $\mu = 0, \sigma = 1.5$ ) and variances ( $\gamma[0.1, 0.1]$ ). We fit fertility model with regularizing priors for  
 166 coefficients ( $\mu = 0, \sigma = 0.15$ ). We ran three chains for 1000 samples for warmup and 4000  
 167 for sampling, with a thinning rate of 3. We accessed the quality of the models using the  
 168 predictive check graphs (?) (Figure ??). To understand the effect of climate on vital rates, we  
 169 got the 95 % credible interval of the posterior distribution. Then we assumed that there is  
 170 95 % probability that the true (unknown) estimates would lie within that interval, given the  
 171 evidence provided by the observed data for each vital rate. All models were fit in Stan (?).

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

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

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

185 
$$v = v_0 * (1 - OSR^\alpha) \quad (2)$$

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

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

193 
$$F_{t+1}^R = \sum_L^U [p^F(x, z) \cdot c^F(x, z) \cdot d \cdot v(\mathbf{F}_t, \mathbf{M}_t) \cdot m \cdot \rho] F_{x,t} \quad (3)$$

194 
$$M_{t+1}^R = \sum_L^U [p^F(x, z) \cdot c^F(x, z) \cdot d \cdot v(\mathbf{F}_t, \mathbf{M}_t) \cdot m \cdot (1 - \rho)] F_{x,t} \quad (4)$$

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

200 
$$v(\mathbf{F}_t, \mathbf{M}_t) = v_0 * \left[ 1 - \left( \frac{\sum_L^U p^F(x, z) c^F(x, z) F_{x,t}}{\sum_L^U p^F(x, z) c^F(x, z) F_{x,t} + p^M(x, z) c^M(x, z) M_{x,t}} \right)^\alpha \right] \quad (5)$$

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

202

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

203

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

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

215 Since the climate-dependent vital rate regressions were built using MCMC, we were able  
216 to propagate the uncertainty in vital rate parameters to uncertainty in predicted population  
217 growth rates ( $\lambda$ ). We estimated population growth rate for the female dominant MPM using  
218 the function lambda in the package popbio (?). Since the two-sex MPM is nonlinear (vital  
219 rates affect and are affected by population structure) we estimated the asymptotic geometric  
220 growth rate ( $\lambda$ ) by numerical simulation, and repeated this across a range of climate<sup>8</sup>.

## 221 Life Table Response Experiments

222 To identify which aspect of climate is most important for population viability, we used a Life  
223 Table Response Experiments (LTRE) based on a non parametric model for the dependence  
224 of  $\lambda$  on time-varying parameters (?). To do so, we used the RandomForest package to fit  
225 a regression model with four climatic variable (temperature of growing season, precipitation  
226 of growing season, temperature of the dormant season and precipitation of the dormant  
227 season) as predictors and  $\lambda$  as response (?). The regression model allowed the estimation

<sup>8</sup>I 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

<sup>9</sup>I 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.

228 of the relative importance of each predictor. The importance is measured by asking: how  
 229 wrongly is  $\lambda$  predicted if we replaced the focal predictor (e.g., temperature of growing season)  
 230 by a random value of the other predictors.

231 To estimate the contribution of each sex to population growth rate variation, we decom-  
 232 posed the effect of each climate variable on population growth rate ( $\lambda$ ) into contribution arising  
 233 from the effect on each vital rate (?). At this end we used another LTRE with a "regression  
 234 design"(?). The LTRE with a "regression design" estimates the contribution of each sex (Eq. ??).

$$235 \quad \frac{\partial \lambda}{\partial \text{climate}} \approx \sum_i \frac{\partial \lambda}{\partial \theta_i^F} \frac{\partial \theta_i^F}{\partial \text{climate}} + \frac{\partial \lambda}{\partial \theta_i^M} \frac{\partial \theta_i^M}{\partial \text{climate}} \quad (8)$$

236 where,  $\theta_i^F$  and  $\theta_i^M$  represent sex-specific parameters: the regression coefficients for the  
 237 intercepts and slopes of size-dependent vital rate functions. Because LTRE contributions are  
 238 additive, we summed across vital rates to compare the total contributions of female and male  
 239 parameters.<sup>10</sup>

## 240 Climate change impacts on sex ratio

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

$$244 \quad SR = \omega_0 + \omega_1 \text{climate} + \omega_2 \text{climate} * \text{climate} + \epsilon \quad (9)$$

245 where  $SR$  is the proportion of panicles that were female or proportion of female individuals  
 246 in the experimental populations.  $\omega_0$  is the intercept,  $\omega_1$  and  $\omega_2$  are the climate dependent  
 247 slopes.  $\epsilon$  is error term.

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

## 252 Climate change impacts on niche and range shifts

253 To understand the impact of climate change on species niche shifts, we estimated the  
 254 probability of self- sustaining populations, which is  $\Pr(\lambda > 1)$  conditional to (i) temperature  
 255 and precipitation of the dormant season or to (ii) temperature and precipitation of the

---

<sup>10</sup> $\theta_i^F$  and  $\theta_i^M$  include the interaction and second order effect. I think we are good with this formula

256 growing season.  $\Pr(\lambda > 1)$  was calculated for the two-sex model and the female dominant  
257 MPMs using the proportion of the 300 Markov chain Monte Carlo iterations that lead to a  
258  $\lambda > 1$  (?). The probability of self- sustaining populations was then represented as a contour  
259 plot with values of  $\Pr(\lambda > 1)$  at given temperature and precipitation for the growing and  
260 dormant season across time (past, present and future).

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

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

269 All the analyses were performed in R 4.3.1 (?)

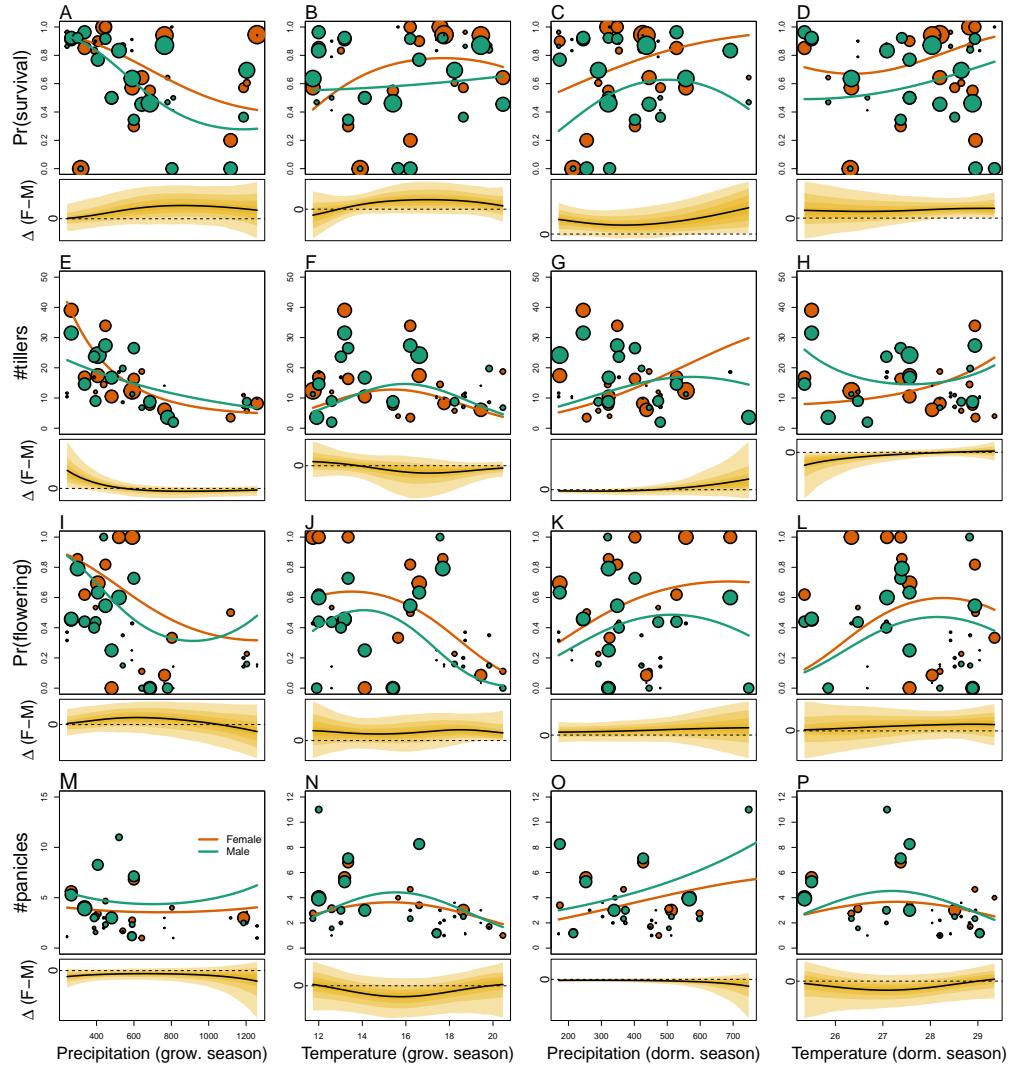
## 270 Results

### 271 Sex specific demographic response to climatic gradient

272 We found a sex specific demographic response to climatic gradient in *Poa arachnifera*  
273 populations. Specifically, female individuals had higher survival and flowering rate than  
274 male across species range during the dormant and growing season (Figure ??A-3D, 3I-3L).  
275 Male individuals produce more panicles than female across species range (Figure ??M-3P).  
276 On the contrary, female had a size advantage for low value values of climate during the  
277 growing season and for high values of climate during the dormant season (Figure ??E-3H).  
278 We also found opposite patterns in the direction of the effect on climate on the probability  
279 of survival and flowering. If temperature of the growing seasons and dormant season are  
280 constant, then precipitation of the growing season has a negative effect on the probability  
281 of survival, the number of tillers, and the probability of flowering (Figure ??). In contrast,  
282 if temperature of the growing and dormant season are constant, then the precipitation of  
283 dormant season has a positive effect on these vital rates (Figure ??E-3H). If precipitation of  
284 growing and dormant season are constant, then temperature of the growing season has a  
285 positive effect of the probability of survival, a negative effect on the probability of flowering,  
286 and the number of tillers, but no significant effect on the number of panicles (Figure ??).<sup>11</sup>

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<sup>11</sup>I tried to add the conditionality here. I hope it makes sense

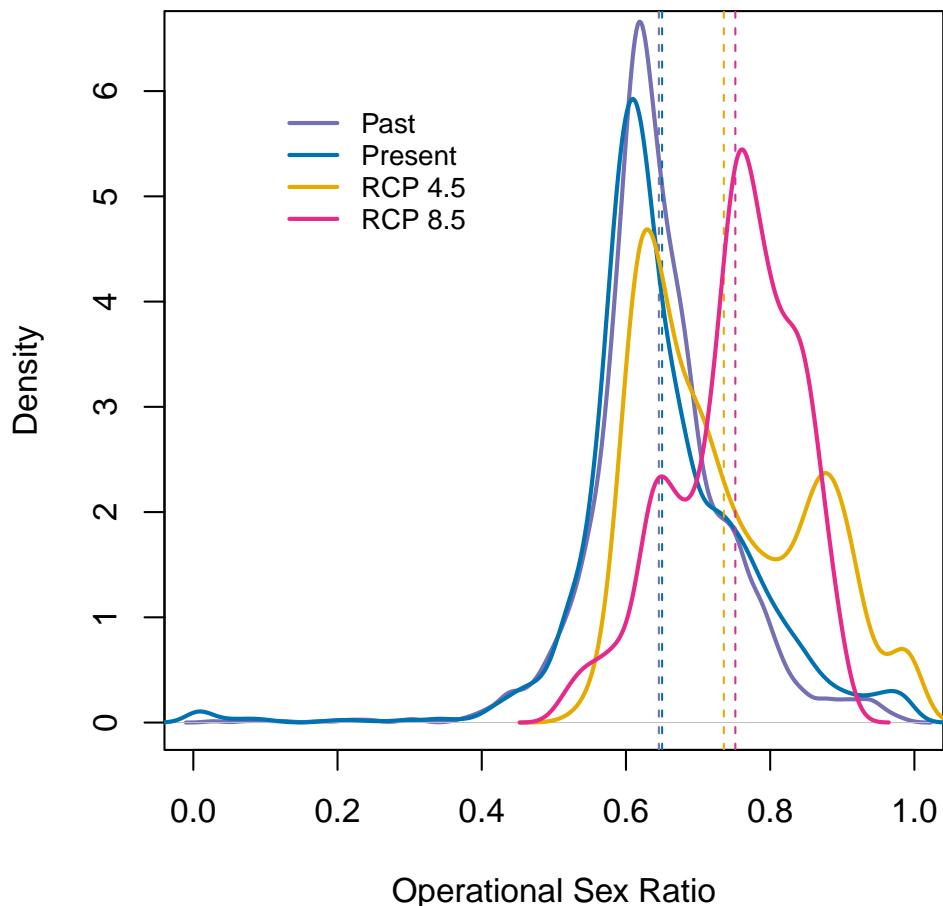


**Figure 2: Sex specific demographic response to climate across species range.** (A, B, C, D) Probability of survival as a function of precipitation and temperature of the growing and dormant season. (E, F, G, H) Change in number of tillers as a function of precipitation and temperature of the growing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

## 287 Female bias in sex-ratio in response to climate change

288 Operational-Sex Ratio (proportion of females panicles) increased significantly with an increase  
 289 of precipitation and temperature of the growing season and precipitation and temperature  
 290 of dormant season (Figure ??, Figure ??). Similarly, the proportion of female plants increased

291 with an increase of temperature of growing season and temperature of dormant season  
 292 (Figure ?? B, D, Figure ??). However, the proportion of female plants did not vary significantly  
 293 with precipitation of dormant and growing season (Figure ?? A, C). Future climate drive to  
 294 extreme female-biased in *Poa arachnifera* populations (Figure ??, Figure ??).



**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.

## 295 Climate change alters population viability

296 We estimated population growth rate variation across species range as a function of each  
 297 climatic variable given the average of the three other climatic variables using two models:  
 298 a female dominant model and a two-sex model<sup>12</sup>. For both models, population growth rate

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<sup>12</sup>I have now provided the methods for this contrast.

decreased toward high precipitation of growing season (Figure ??A). In contrast population growth rate increased with an increase in precipitation of the dormant season (Figure ??C). Furthermore, population growth rate was maximized between 14 and 17 °C and decreased below zero beyond 18 °C during the growing season (Figure ??B). Similarly population fitness was maximized between 27 and 31 °C and decreased below zero just beyond 20 °C during the dormant season (Figure ??D).<sup>13</sup>

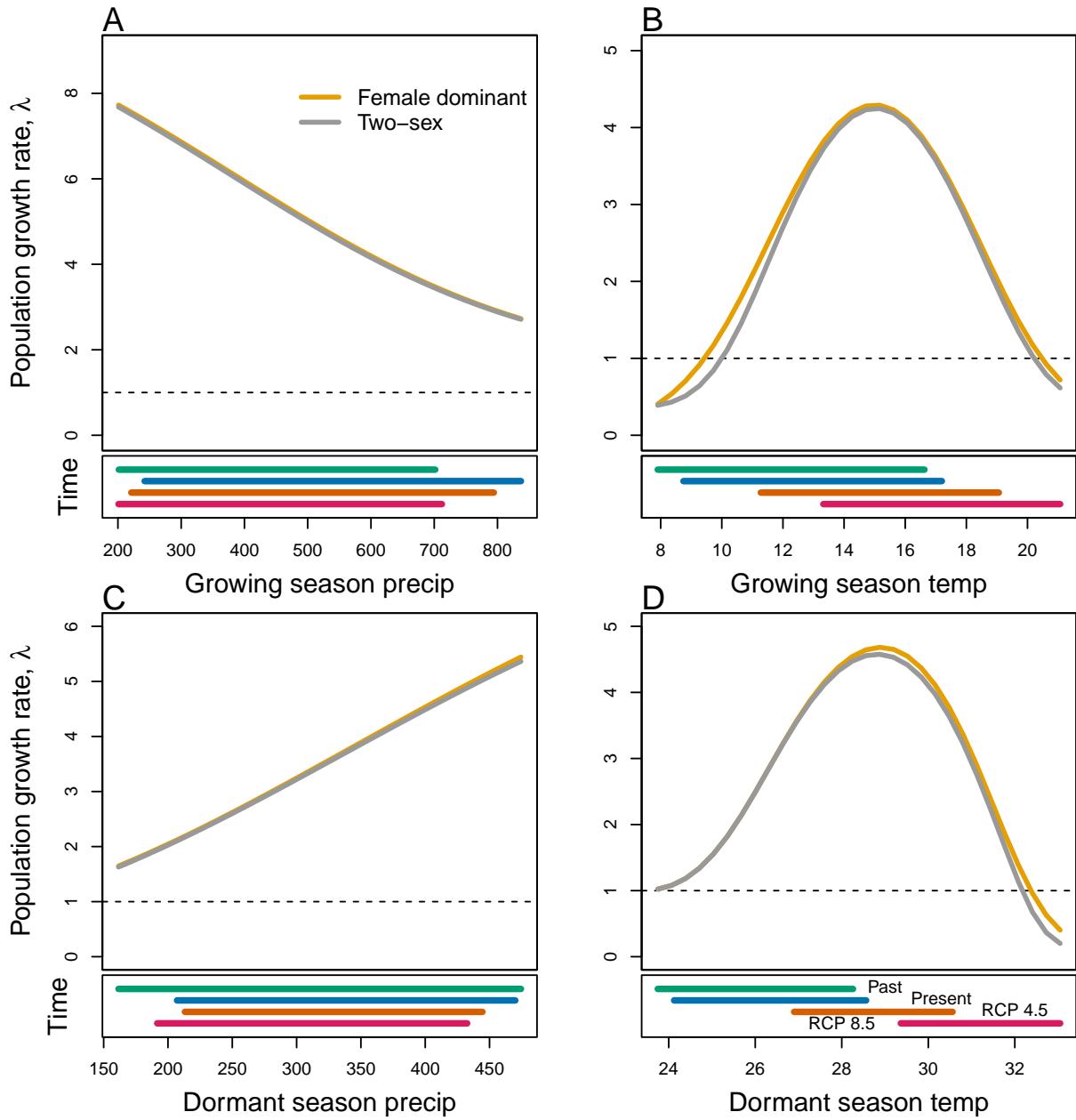
We have also detected a strong association between predicted lambda and different ranges of climate (past, present and future). Under past climate conditions, population growth rate decreased below one for temperature of the growing season. Populations will still be viable under moderate gas emission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

Population growth rate was most sensitive to change in temperature of the growing season and temperature of the dormant season (Figure ??). Despite contribution for both sexes, females have a higher contribution to population dynamics than males (Figure ??; Figure ??). For both sexes, the reduction of  $\lambda$  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 ??F, H, G, L). However, the change of population growth rate for high value of precipitation was not driven by change in vital rates.

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<sup>13</sup>I 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.

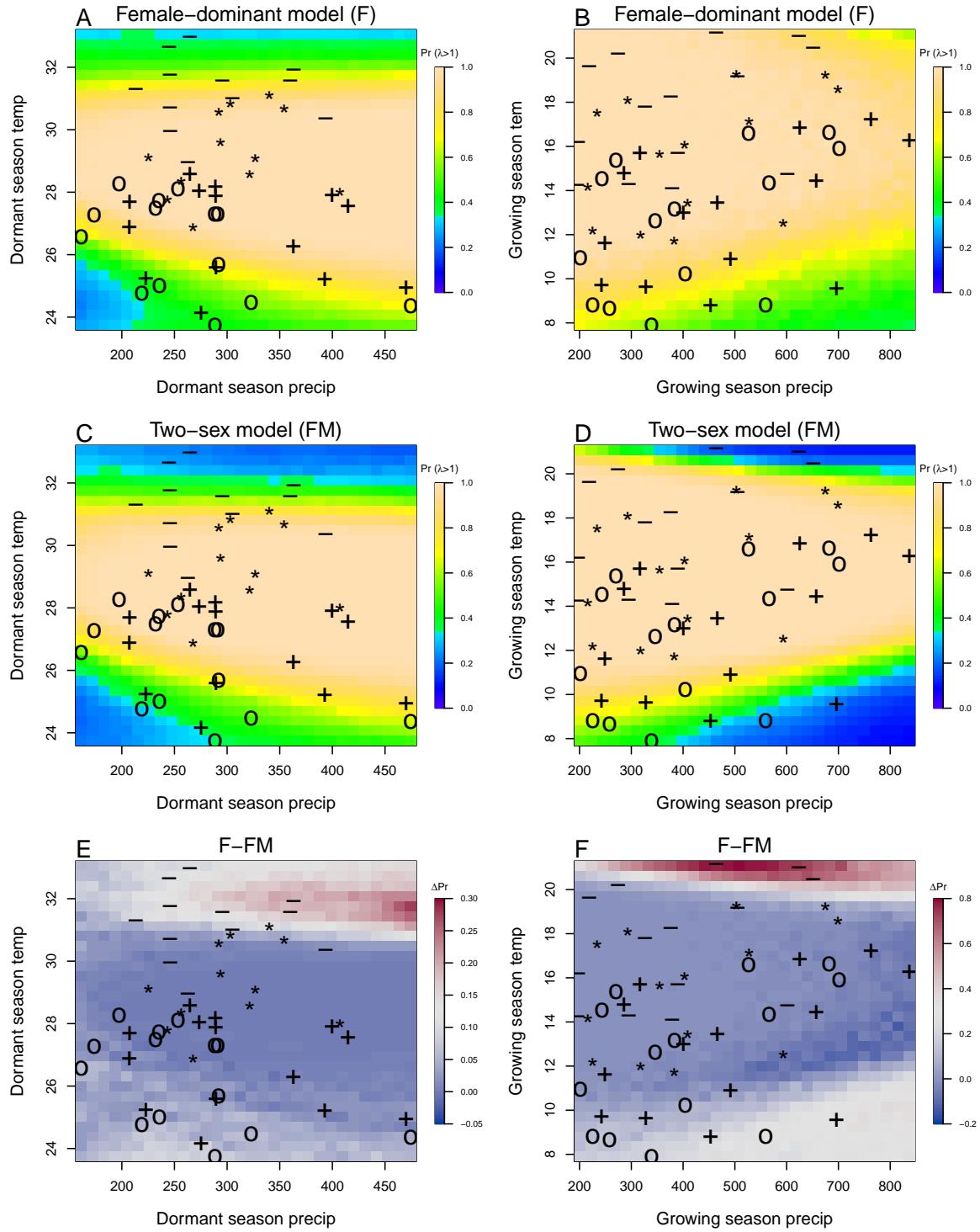
<sup>14</sup>I changed how I write the first sentence to remove the "effect of climate on". Again I don't mind removing the Figure.



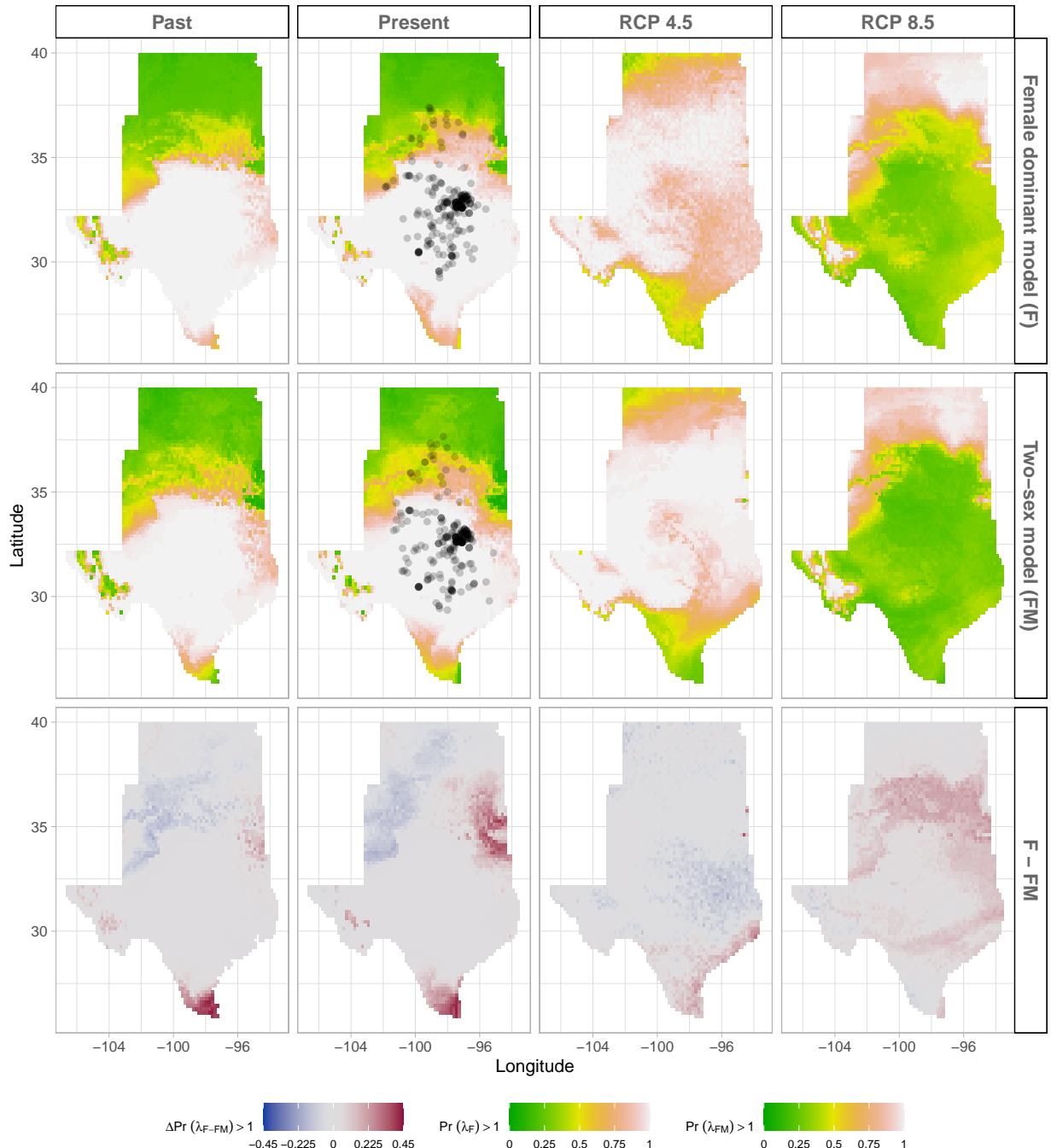
**Figure 4: Predicted population growth rate ( $\lambda$ ) in different ranges of climate.** (A) Precipitation of the growing season, (B) Temperature of the growing season, (C) Precipitation of the dormant season, (D) Temperature of the dormant season. The grey curve shows prediction by the two-sex matrix 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 ( $\lambda$ ) are derived from the mean climate variables across 4 GCMs (MIROC5, ACCESS1-3, CESM1-BGC, CMCC-CM).

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

318 Female dominant model and two-sex models predicts a niche shift in *Poa arachnifera*  
319 populations (Figure ??). However, the female dominant model underestimated the magnitude  
320 of niche shifts (Figure ??E, F; -0.16[-0.29,-0.03]). Female dominant model and the two-sex  
321 models agree that viable populations of *P. arichnifera* were only predicted at the center of the  
322 range for current climatic conditions (Figure ??). Although *P. arichnifera* was predicted to have  
323 suitable habitats in the center of the range under current climate, global warming is projected  
324 to reduce much of these suitable habitats (Figure ??). If the species is able to disperse far and  
325 if there is no physical barriers, most of the current suitable habitats will move toward the  
326 Northern range edge as a results of niche shifts. Niche shift underestimation by the female  
327 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,  $\text{Pr}(\lambda > 1)$ , using the two-sex model that incorporates sex- specific demographic responses to climate with sex ratio dependent seed fertilization. (E) Past, (F) Current, (G and H) Future predicted range shift based on the predicted probabilities of self- sustaining populations,  $\text{Pr}(\lambda > 1)$ , using the female dominant model. Future projections were based on the CMCC-CM model. The black dots on panel B and F indicate all known presence points collected from GBIF from 1990 to 2019, which corresponds to the current condition in our prediction. The occurrences of GBIFs are distributed in with higher population fitness habitat  $\text{Pr}(\lambda > 1)$ , confirming that our study approach can reasonably predict range shifts.

328 **Discussion**

329 <sup>15</sup>Dioecious species make up a large fraction of Earth's biodiversity – most animals and many  
330 plants – yet we have little knowledge about how skewness in sex ratio will affect population  
331 viability and range shifts of dioecious species under climate change. We used three years of  
332 demographic data collected from common garden experiments across climatic gradient to forecast  
333 for the first time the impact of climate change on dioecious species. Our future projections  
334 require extrapolation to warmer or colder conditions than observed in our experiment  
335 and subsequently should be interpreted with caution (?). Despite all these limitations, the  
336 qualitative implications of the response of our study species to increase temperature (dormant  
337 and growing season) seems consistent across all GCMs (Figure ??, Figure ??, Figure ??). Three  
338 general patterns emerged from our analysis of range-wide common garden experiments and  
339 sex-structured, climate-explicit demographic models. First, our Bayesian mixed effect model  
340 suggests a sex specific demographic response to climate change that lead to higher proportion  
341 of female as climate increase. Second, climate change favors a northern range shifts in suitable  
342 habitats. Third, the female dominant model (model that does not account for sex structure)  
343 overestimates species niche and range shifts.

344 There was a female demographic advantage leading to a female biased in response  
345 to climate change in *Poa arachnifera* populations. The extreme female-bias in response to  
346 climate change contrast with previous studies suggesting that an increase in male frequency  
347 in response to climate change (??). Two mechanisms could explain the observed demographic  
348 advantage of females over males for survival and flowering and the opposite for growth  
349 and number of panicles. The trade-off between fitness traits (survival, growth and fertility)  
350 due to resource limitation and the pollination mode of our study species (wind pollinated)  
351 could explain such a result (??). For most species, the cost of reproduction is often higher for  
352 females than males due to the requirement to develop seeds and fruits (?). However, several  
353 studies reported a higher cost of reproduction for males in wind pollinated species due to  
354 the larger amounts of pollen they produce (????).

355 Our results suggest that climate change will alter population at the center of the range and  
356 drive a northern range shifts. This impact of climate change on the species current niche could  
357 be explained by the increase of temperature over the next years. Small change in temperature  
358 of the growing and dormant season have a larger impact on population viability. Temperature  
359 can impact plant populations through different mechanisms. Increasing temperature could  
360 increase evaporative demand, affect plant phenology (??), and germination rate (?). The poten-

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<sup>15</sup>This is my new proposition regarding the discussion

tial for temperature to influence these different processes changes seasonally (?). For example, studies suggested that species that are active during the growing season such as cool grass species can have delayed phenology in response to global warming, particularly if temperatures rise above their physiological tolerances (??). In addition, high temperature during the growing season by affecting pollen viability, fertilization could affect seed formation and germination (??). Pollen dispersal may allow plants to resist climate change because pollen dispersal may provide the local genetic diversity necessary to adapt at the leading edge of the population (???). Since wind pollination is most effective at short distances, it is most often found in plant species growing at high density such as our study species, it is less likely that dispersal limitation affect niche shift in our study system. Difference in non-climatic factors such as soil, or biotic interactions could also explain decline in population growth rate as an indirect effects of increase in temperature (??). For example, climate change could increase the strength of species competition and thereby constrain our study species to a narrower realized niche (??).

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

## Conclusion

We have investigated the potential consequence of skewness in sex ratio on population dynamics and range shift in the context of climate change using the Texas bluegrass. We found extreme female -biased in response to climate change. The effect of female biased will induce range shifts to the northern edge of the species current range by limiting mate availability. Beyond, our study case, our results also suggest that tracking only one sex could lead to an underestimation of the effect of climate change on population dynamics. Our

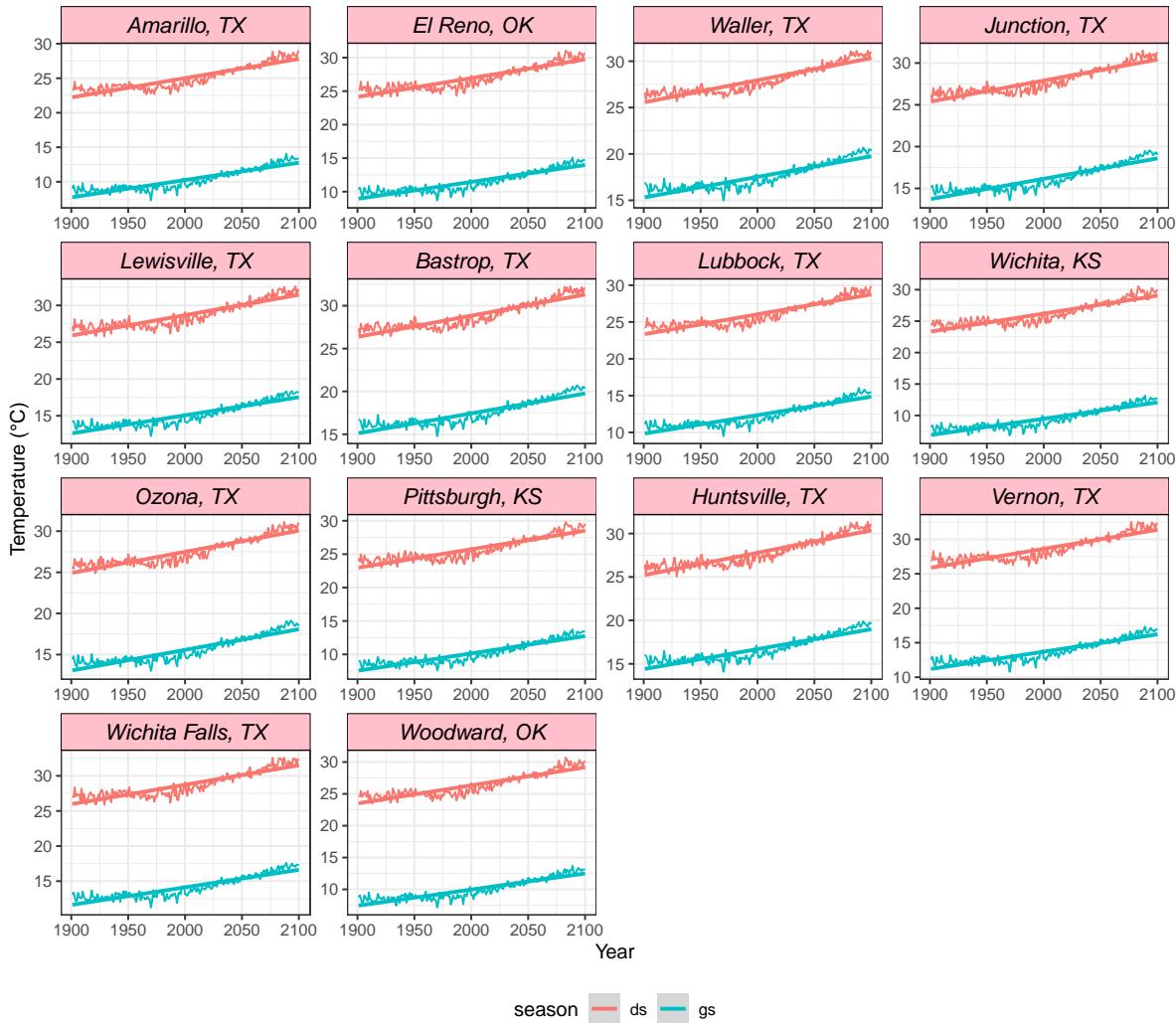
<sup>394</sup> work provides also a framework for predicting the impact of global warming on population  
<sup>395</sup> dynamics using the probability of population to self-sustain.

<sup>396</sup> **Acknowledgements**

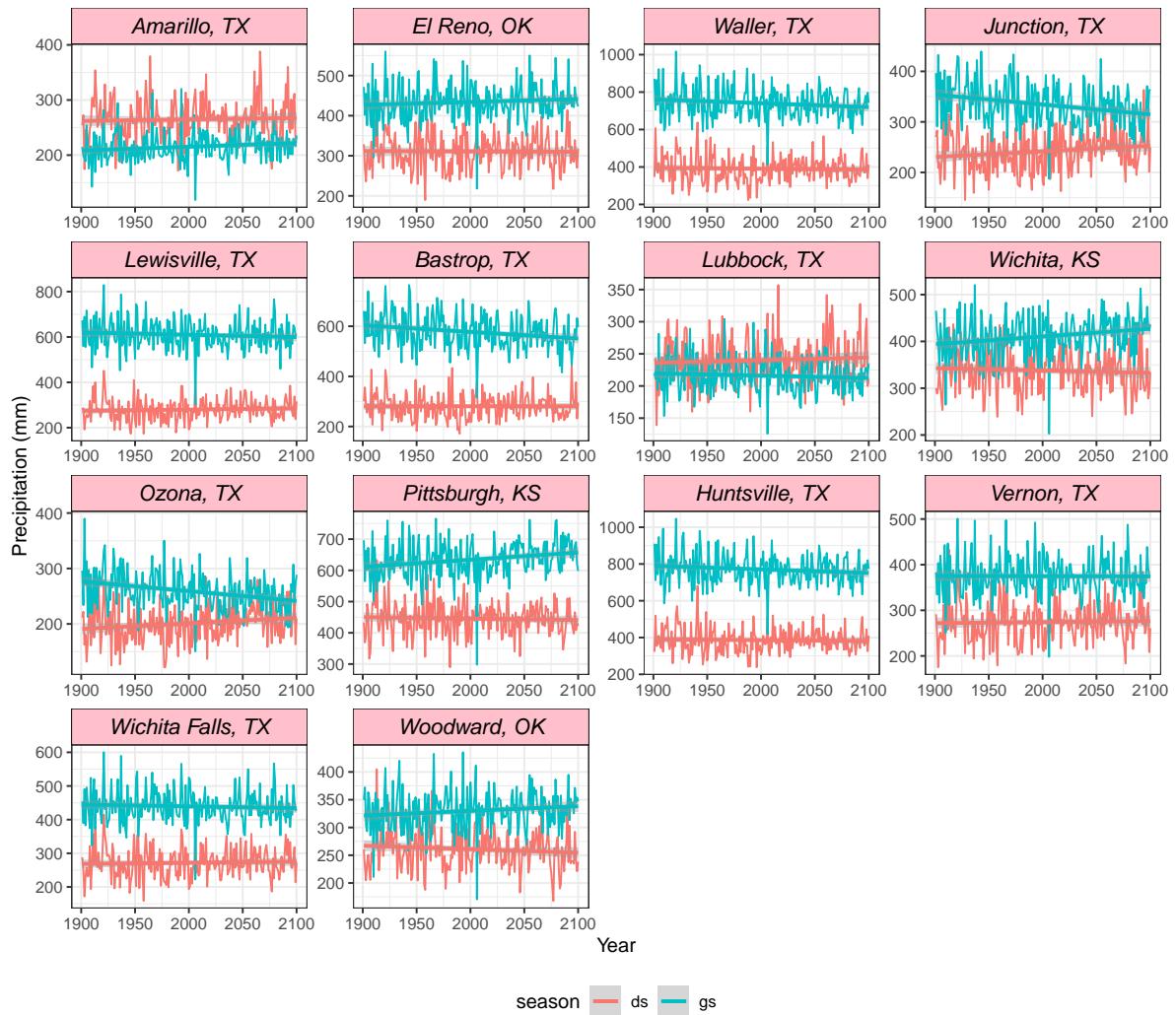
<sup>397</sup> This research was supported by National Science Foundation Division of Environmental  
<sup>398</sup> Biology awards 1543651 and 1754468 and by the Rice University Faculty Initiatives Fund.

# Supporting Information

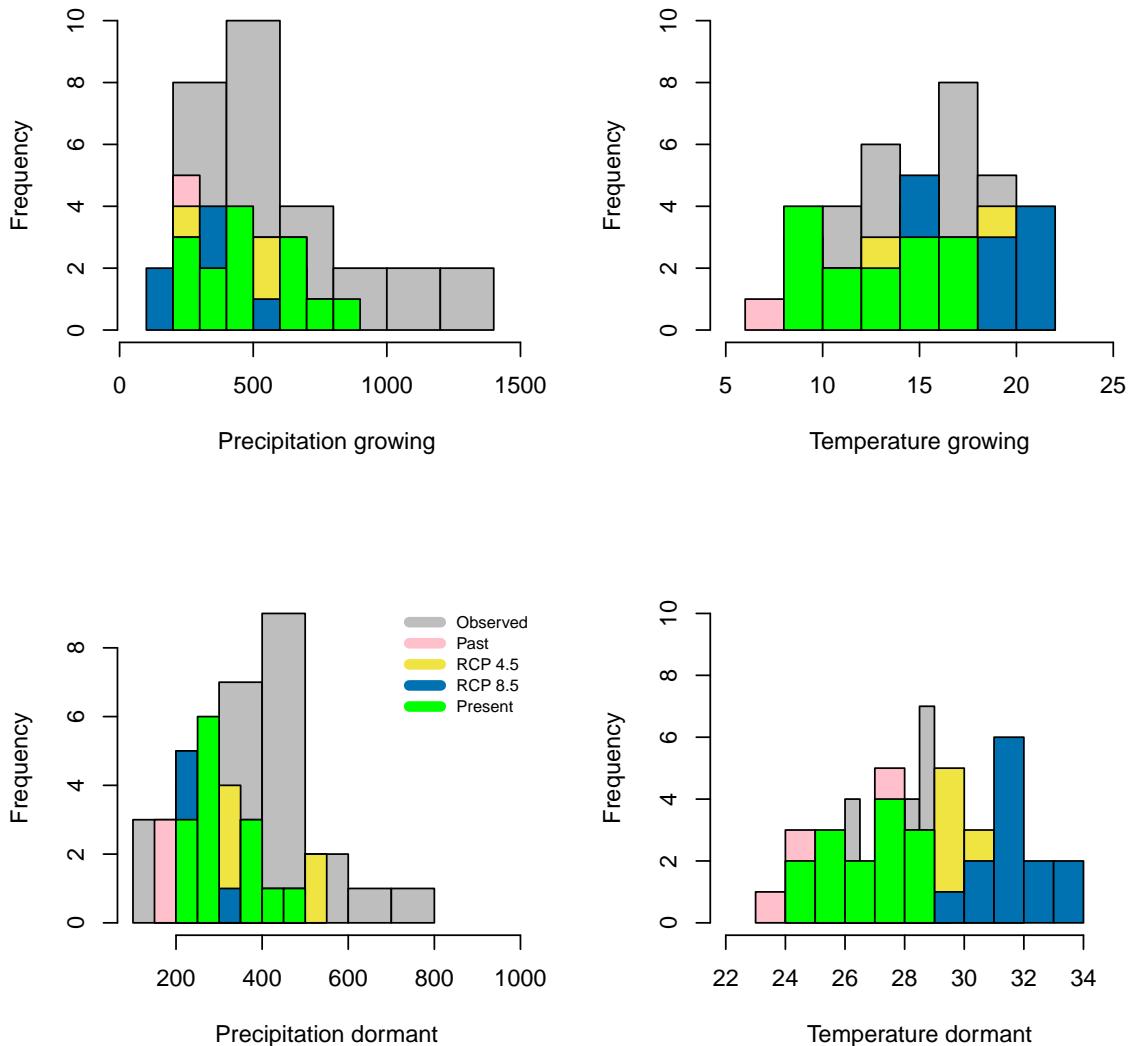
## 399 S.1 Supporting Figures



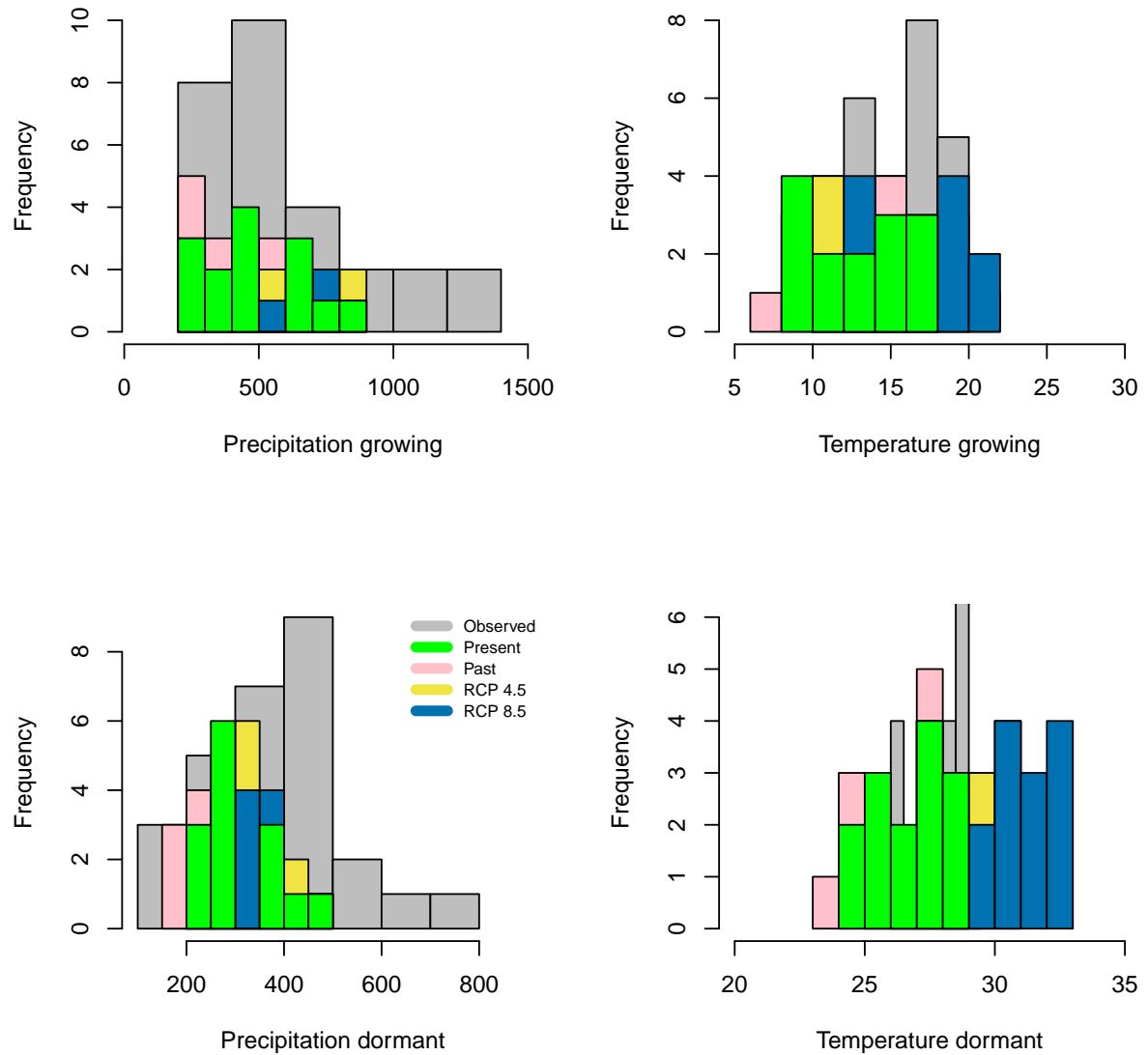
**Figure S-1:** Temperature variation across the study sites from 1990 to 2100, ds: Dormant season, dg: Growing season.



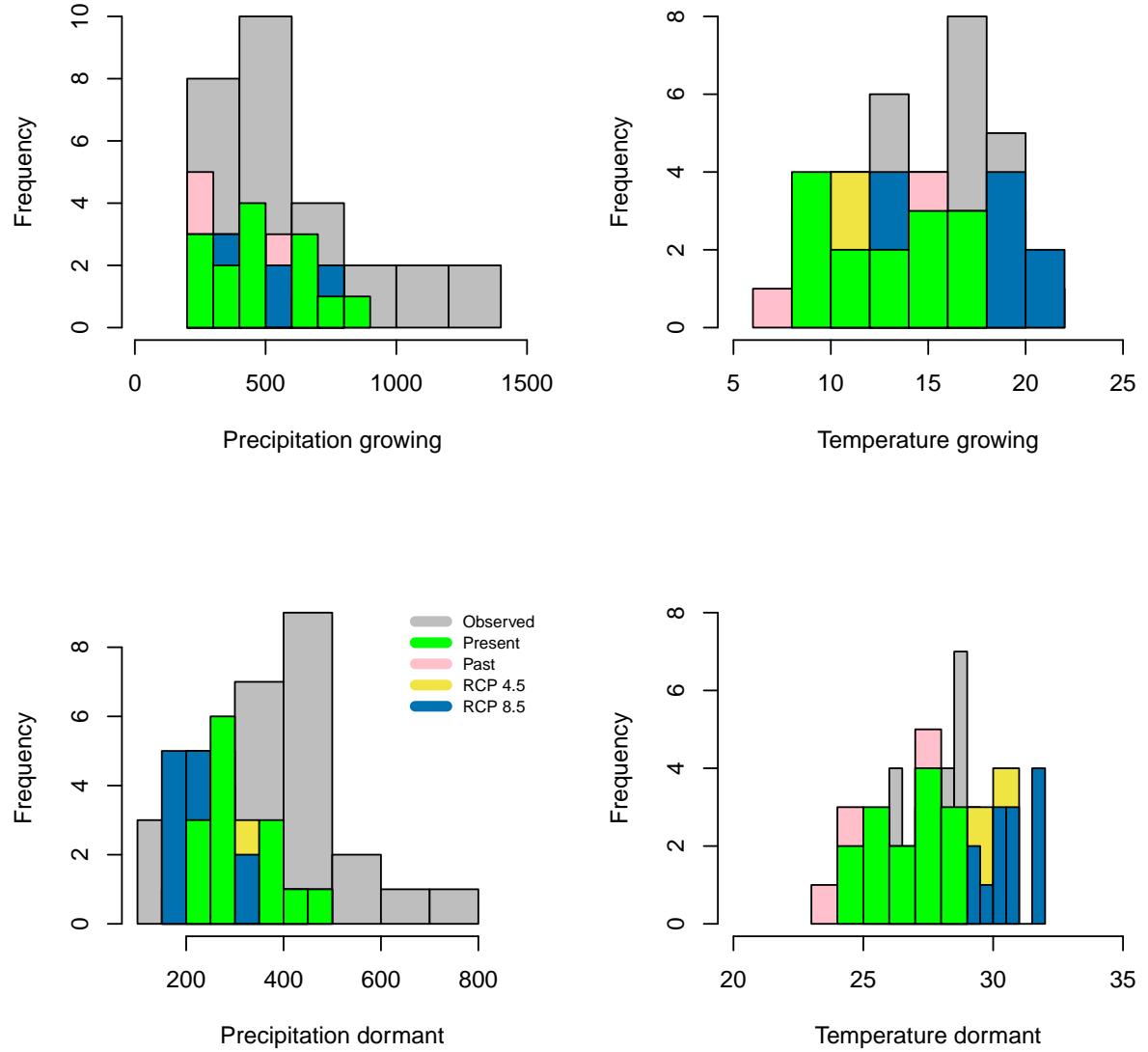
**Figure S-2:** Precipitation variation across the study sites from 1990 to 2100. ds: Dormant season, dg: Growing season.



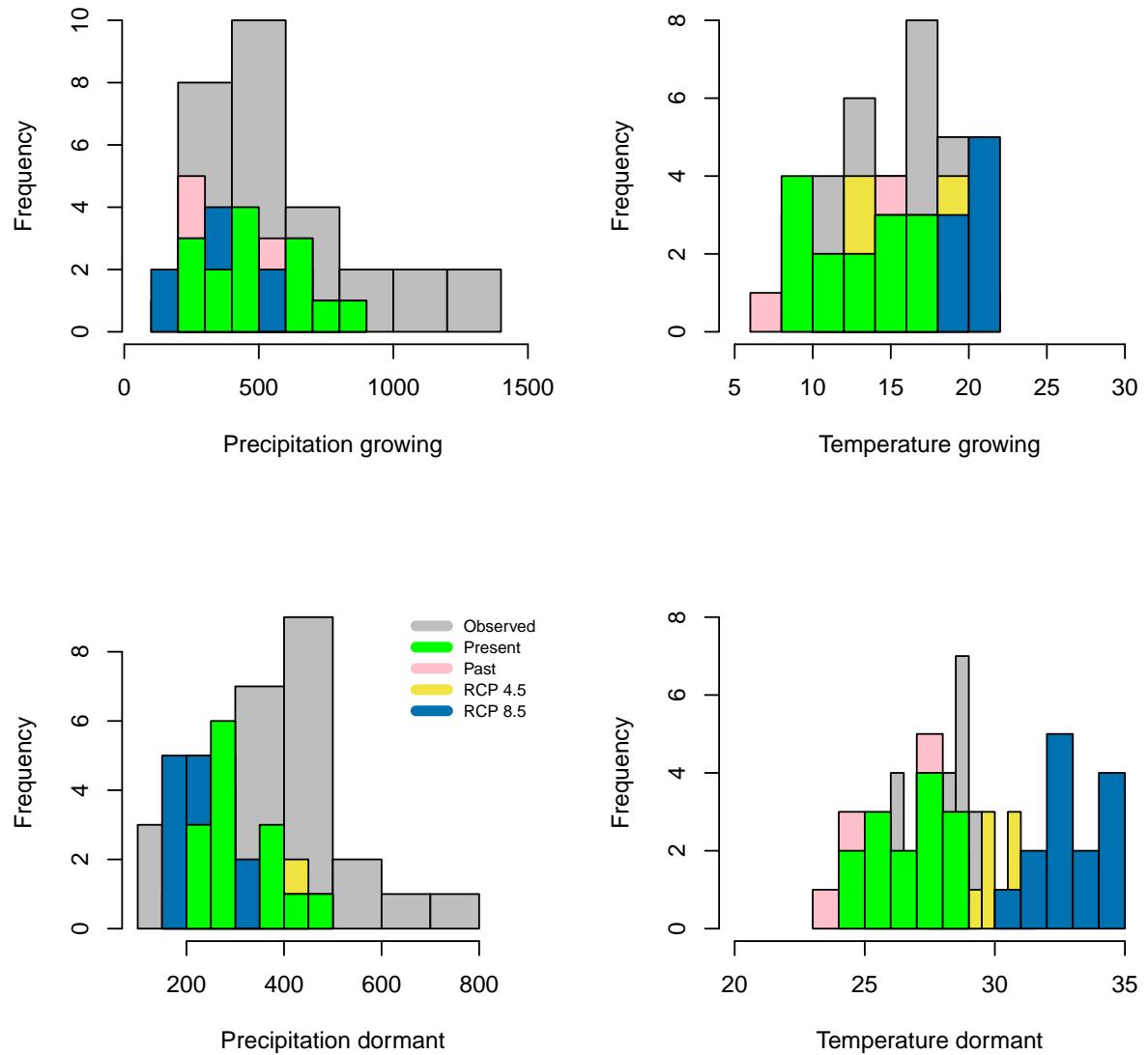
**Figure S-3:** Past, Observed, present and future (MIROC Model) climate data across the study area.



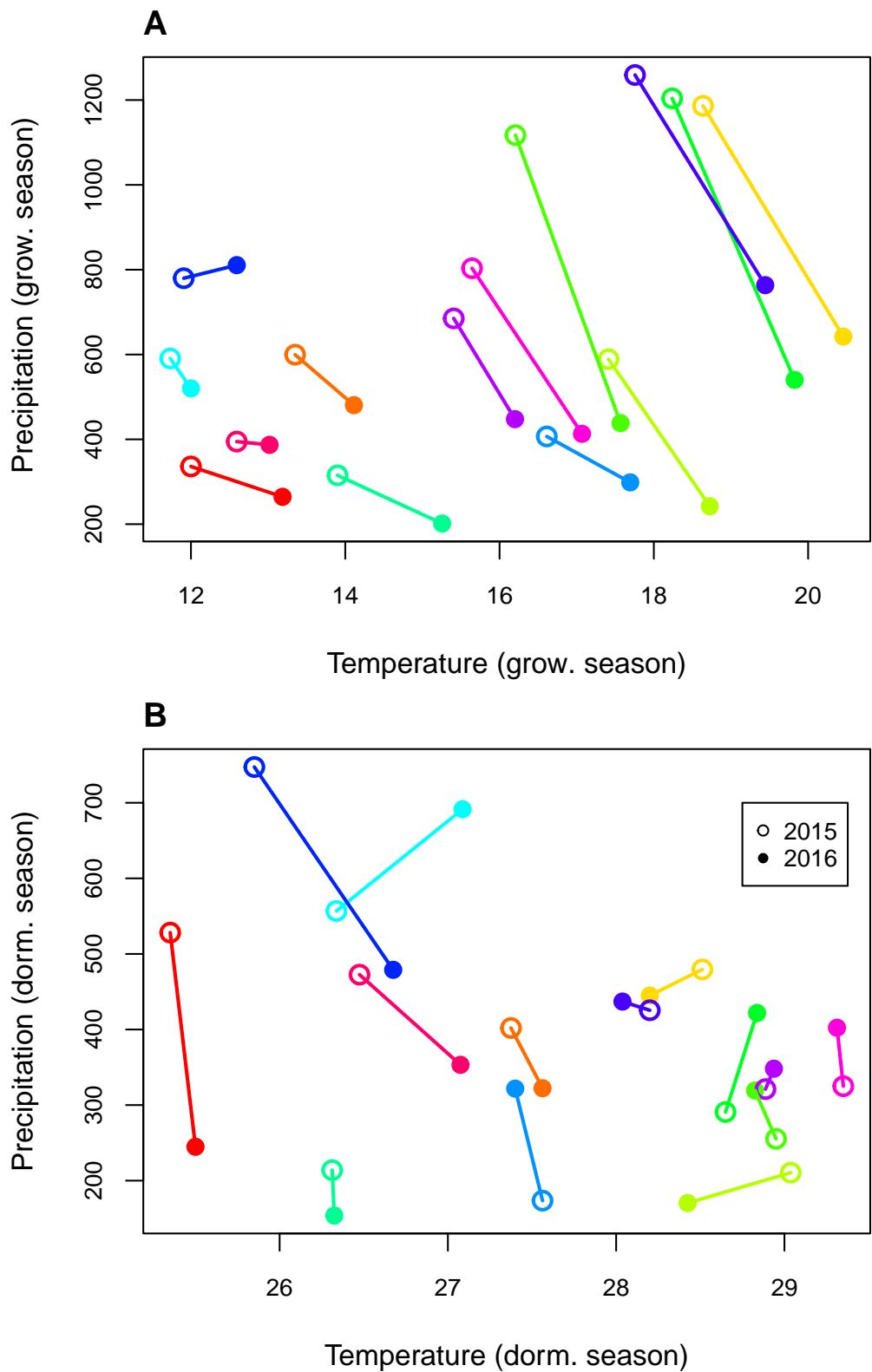
**Figure S-4:** Past, Observed, present and future (ACCESS Model) climate data across the study area.



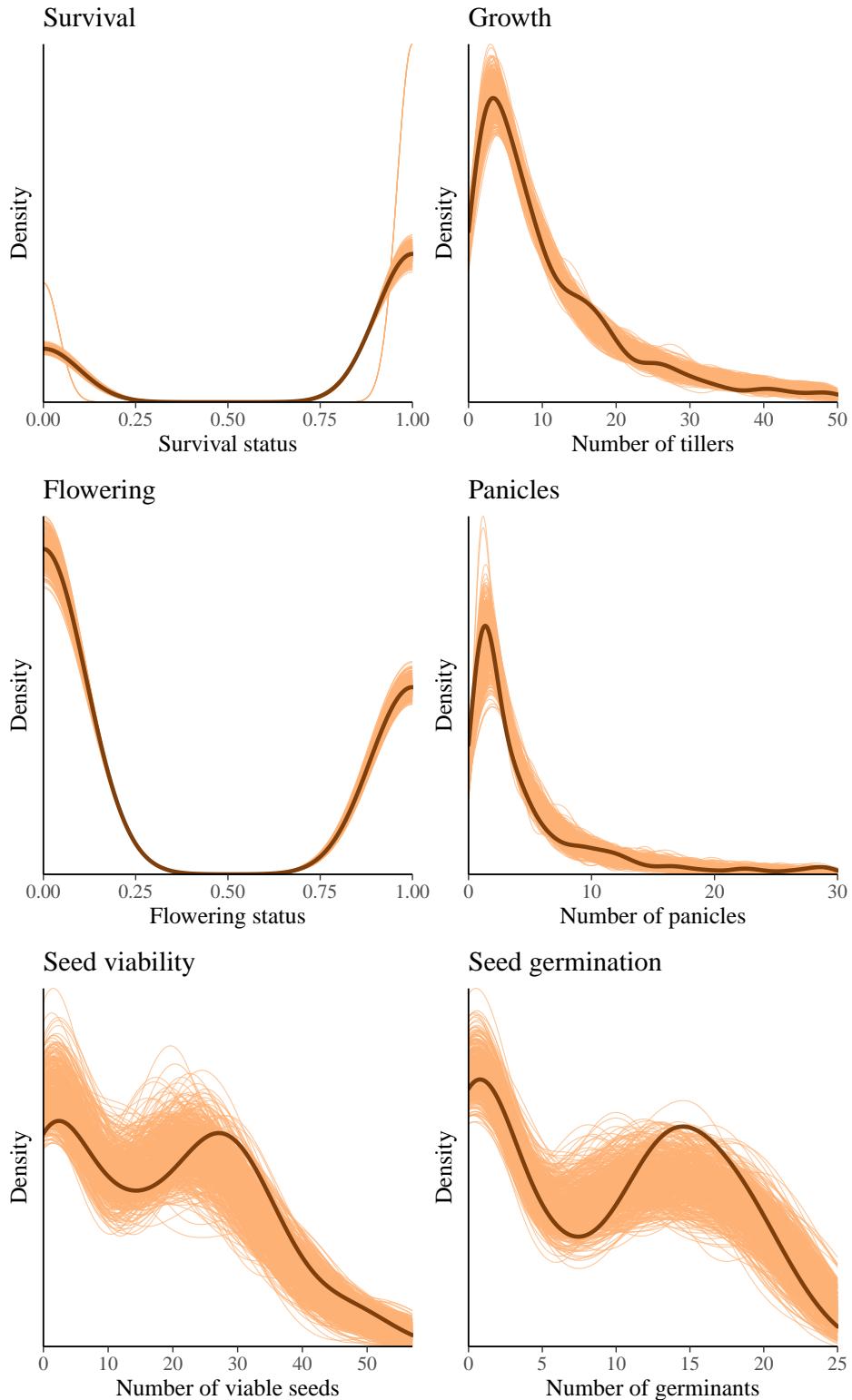
**Figure S-5:** Past, Observed, present and future (CESM1 Model) climate data across the study area.



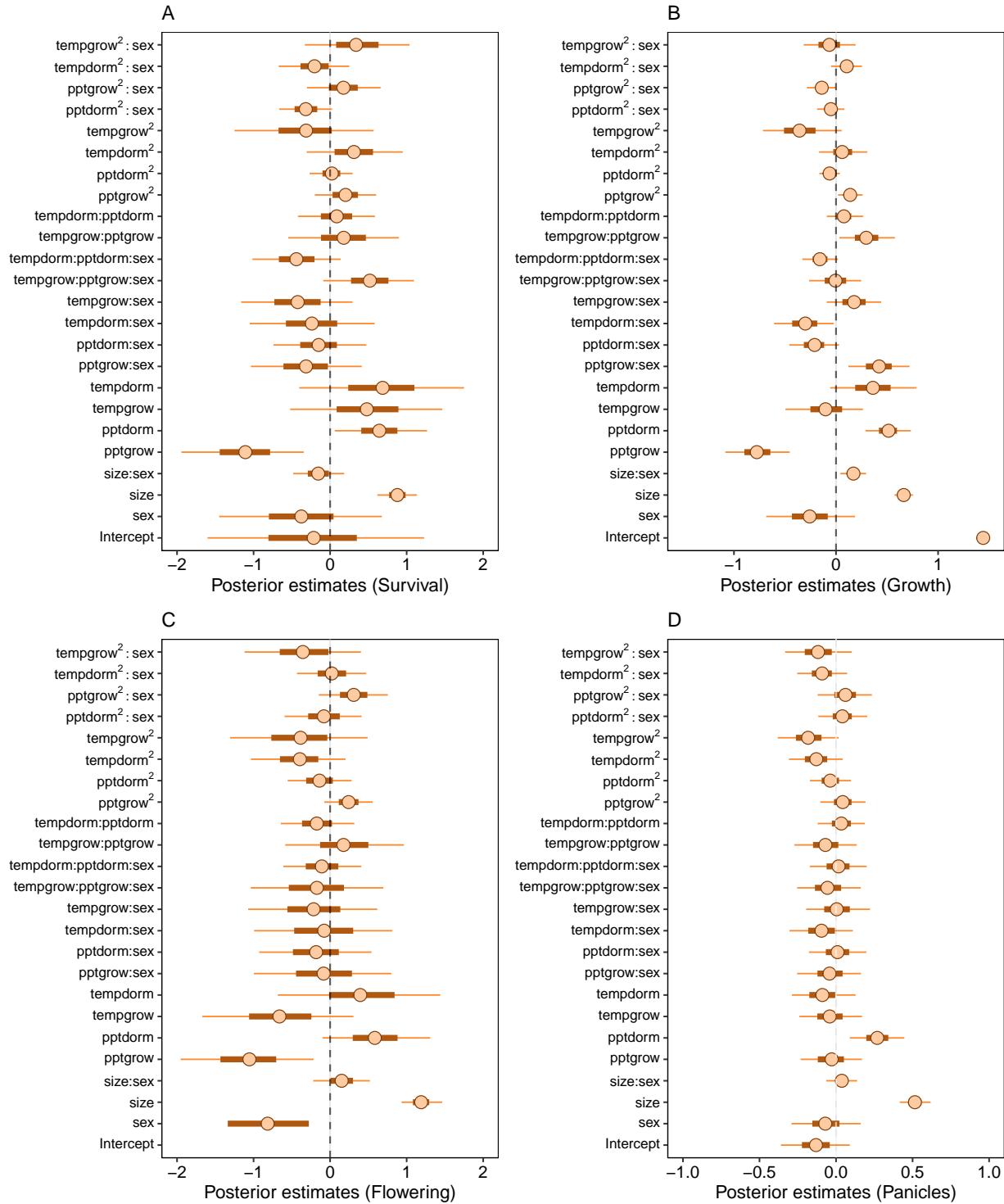
**Figure S-6:** Past, Observed, present and future (CMCC Model) climate data across the study area.



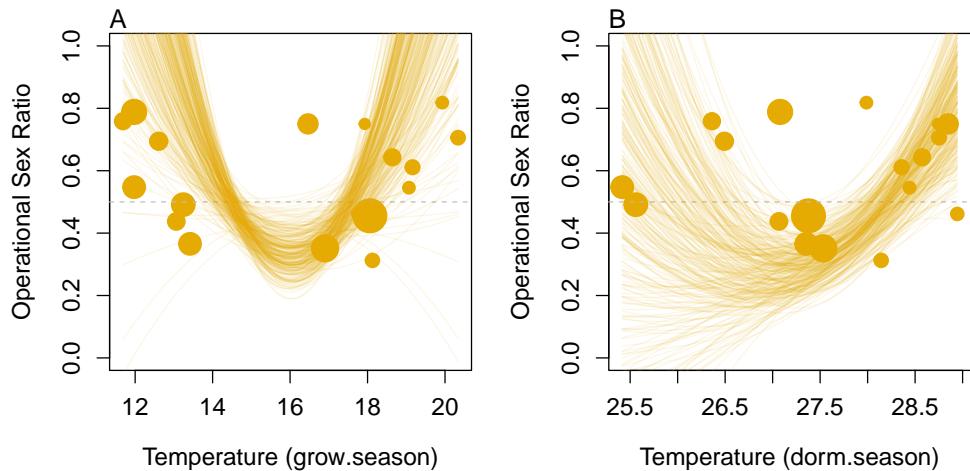
**Figure S-7:** Climate variation across the study sites during the monitoring period.



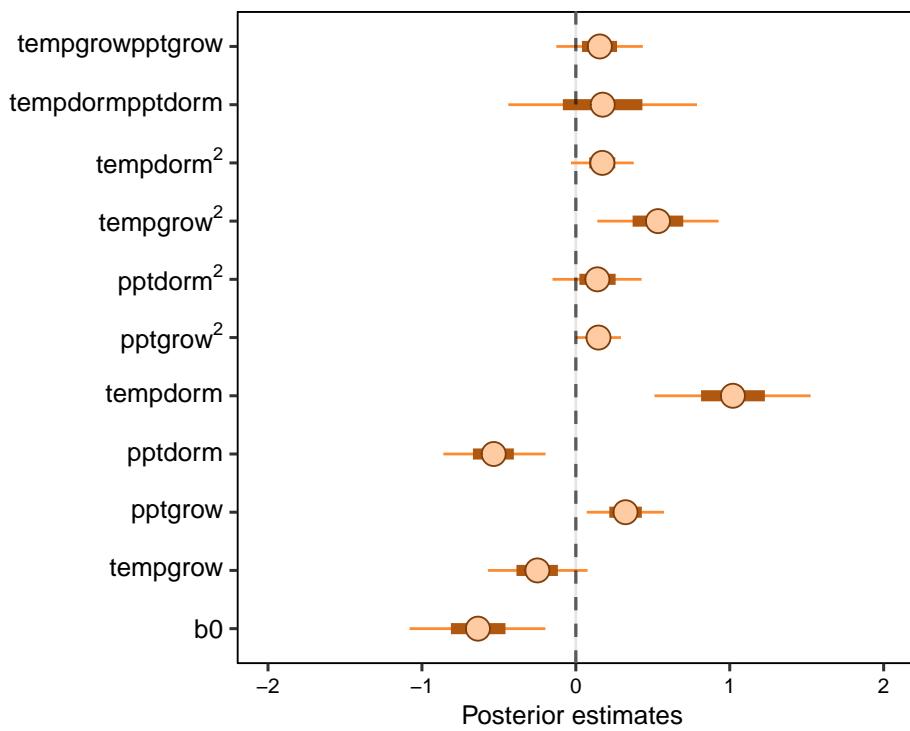
**Figure S-8:** Posterior predictive checks. Consistency between real data and simulated values suggests that the fitted vital rate models accurately describes the data. Graph shows density curves for the observed data (light orange) along with the simulated values (dark orange).



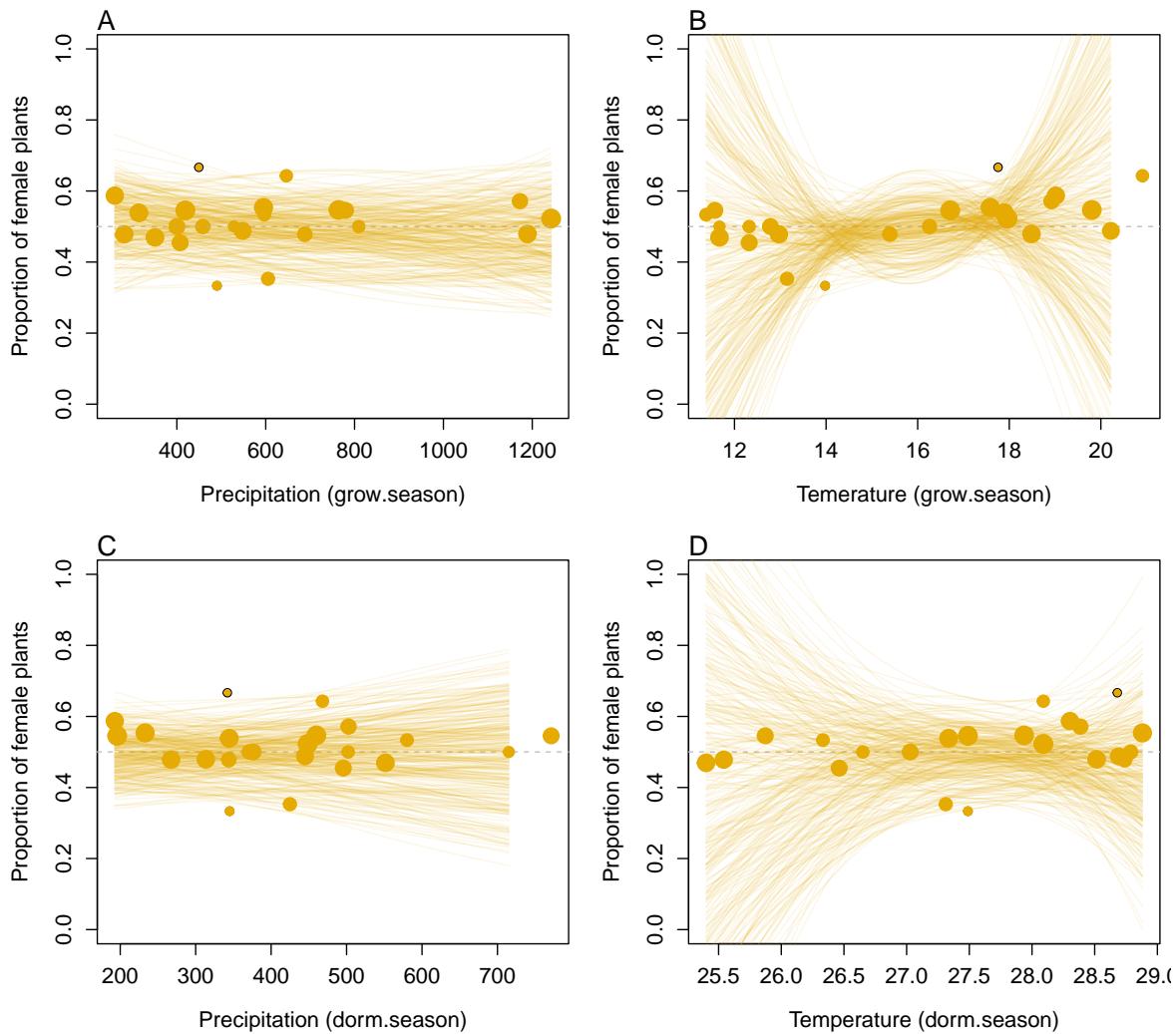
**Figure S-9:** Mean parameter values and 95% credible intervals of the posterior probability distributions. pptgrow is the precipitation of growing season, Tempgrow is the temperature of growing season, pptdorm is the temperature of dormant season, Tempdorm is the temperature of dormant season.



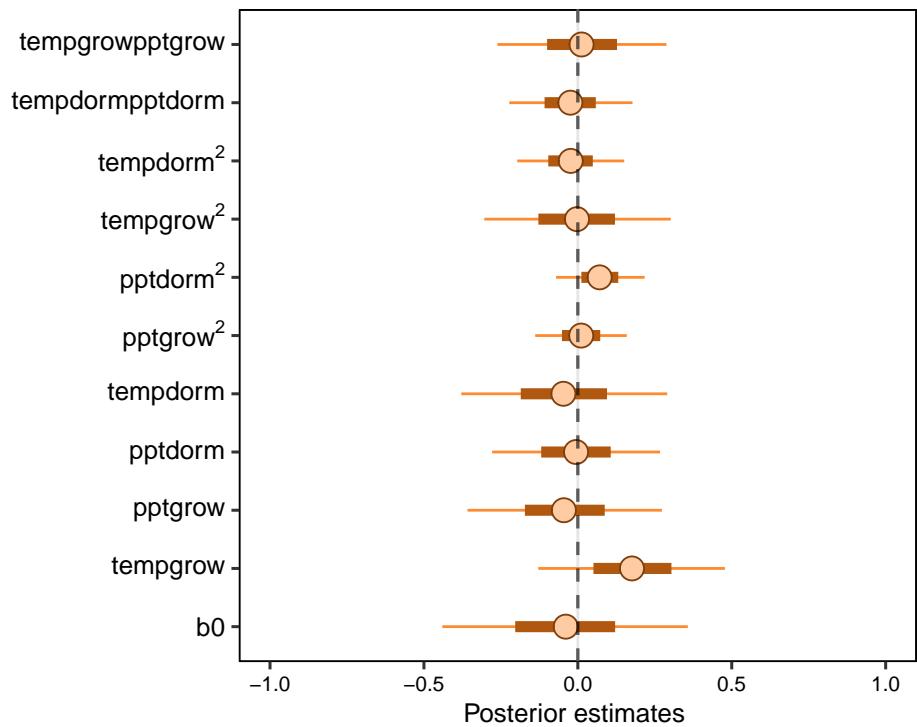
**Figure S-10: Significant Operational Sex Ratio response across climate gradient.** (A, B) Proportion of panicles that were females across precipitation and temperature of the growing season; (C, D) Proportion of panicles that were females across precipitation and temperature of the dormant season.



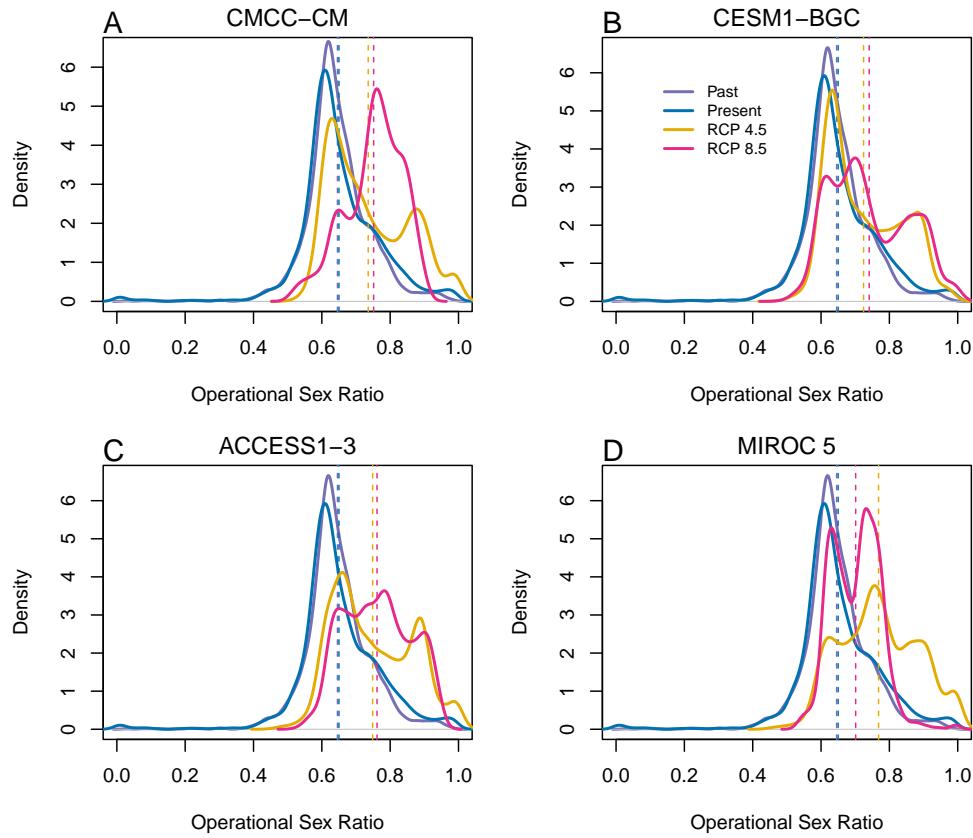
**Figure S-11:** Mean parameter values and 95% credible intervals of the posterior probability distributions. pptgrow is the precipitation of growing season, Tempgrow is the temperature of growing season, pptdorm is the temperature of dormant season, Tempdorm is the temperature of dormancy season.



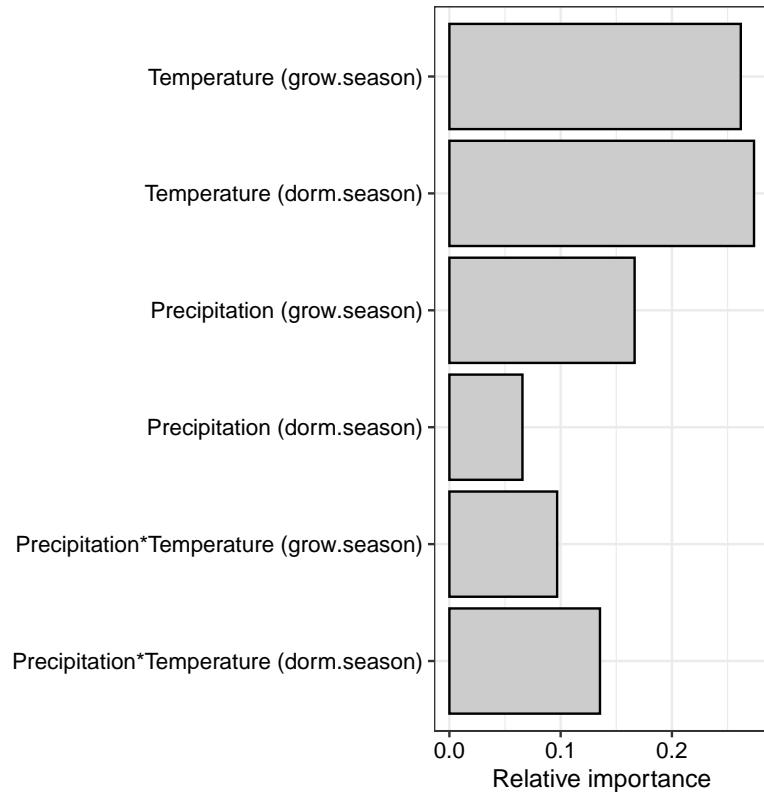
**Figure S-12: Variation in sex-ratio accross climate gradient.** (A, B) Proportion of plants that were females across precipitation and temperature of the growing season; (C, D) Proportion of plants that were females across precipitation and temperature of the dormant season.



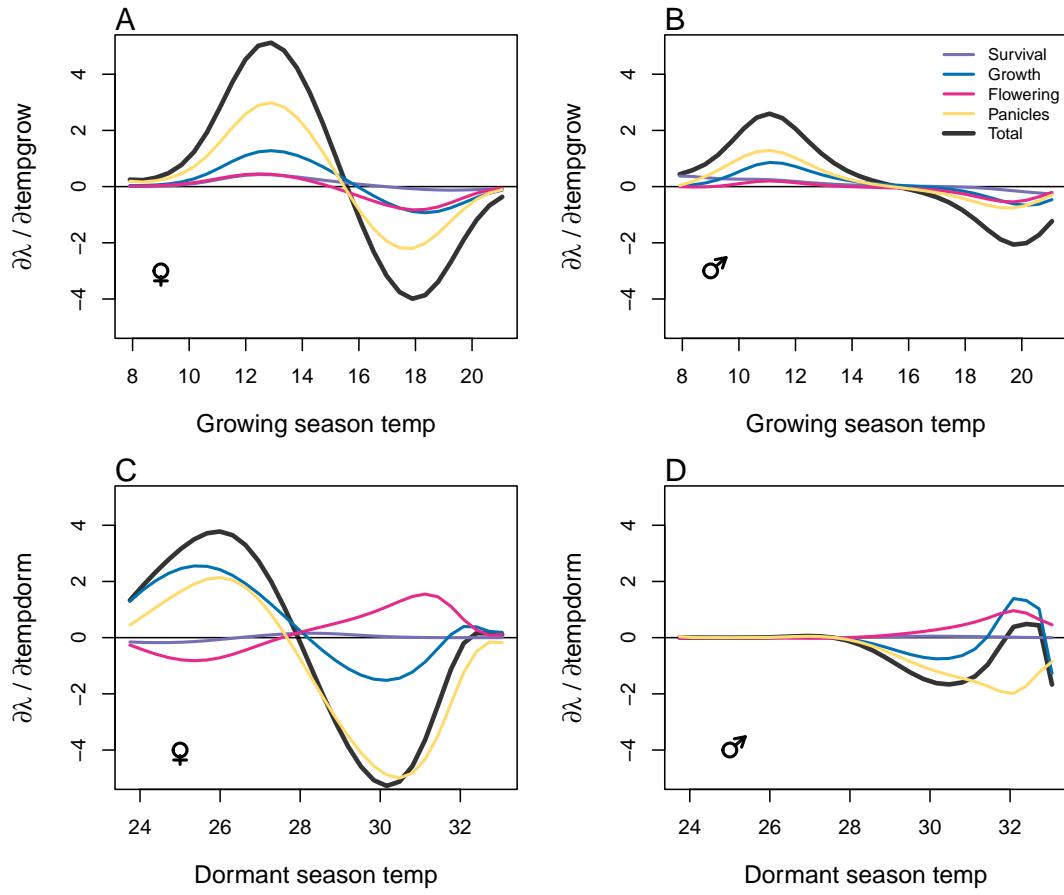
**Figure S-13:** Mean parameter values and 95% credible intervals of the posterior probability distributions. pptgrow is the precipitation of growing season, Tempgrow is the temperature of growing season, pptdorm is the temperature of dormant season, Tempdorm is the temperature of dormant season.



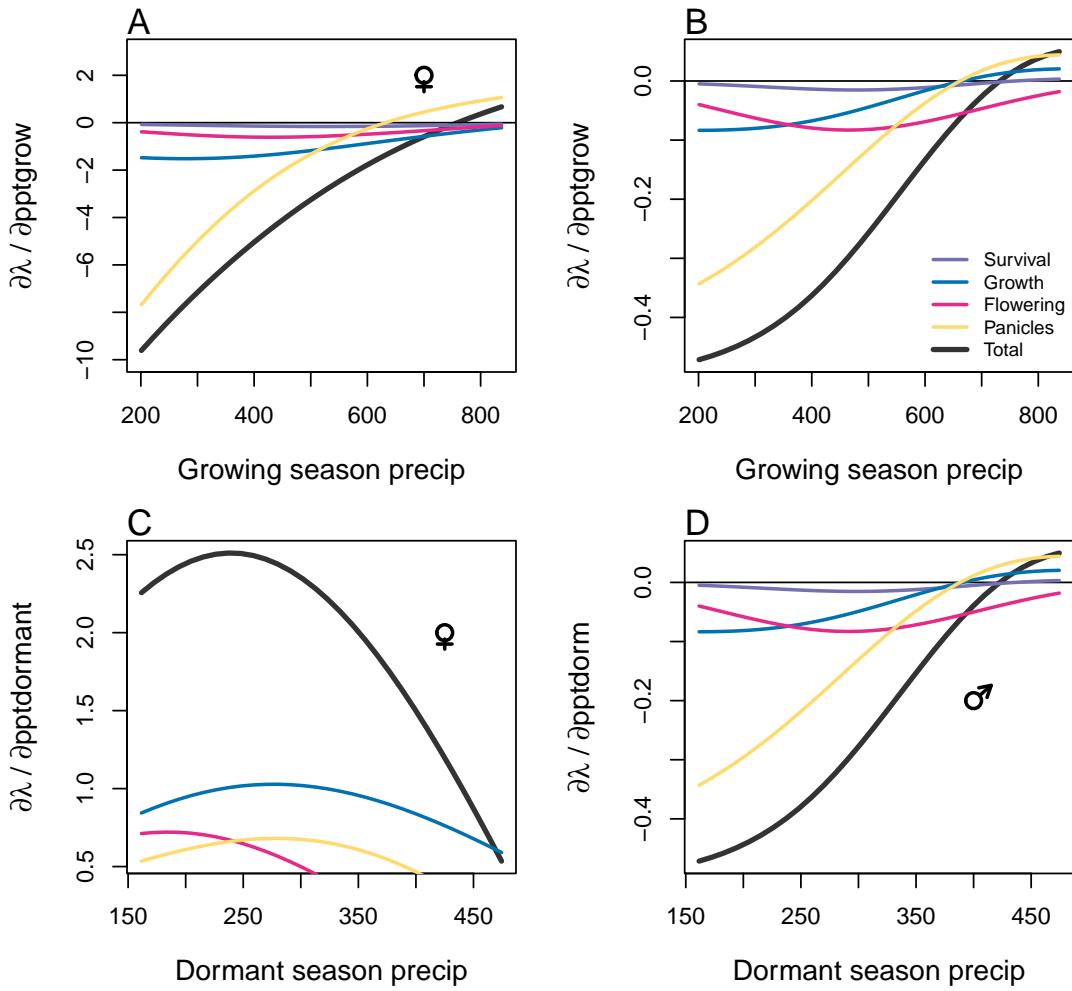
**Figure S-14:** Change in Operational Sex Ratio (proportion of female) over time (past, present, future). Future projections were based on A) MIROC 5, B) CES, C) ACC. The means for each model are shown as vertical dashed lines.



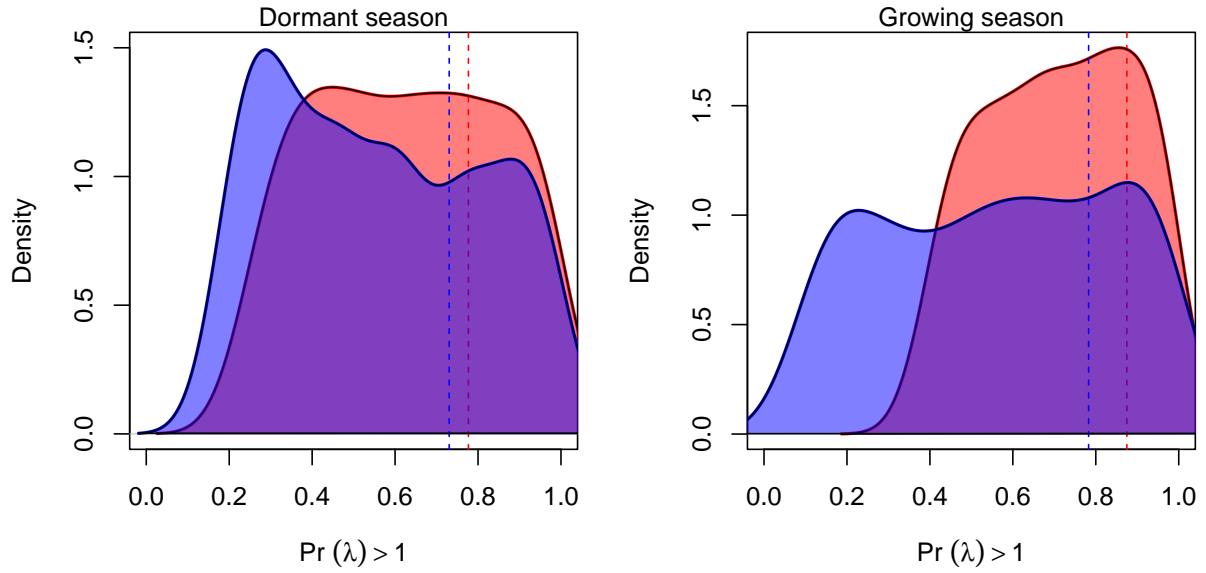
**Figure S-15:** Life Table Response Experiment: The bar represent the relative importance of each predictors.



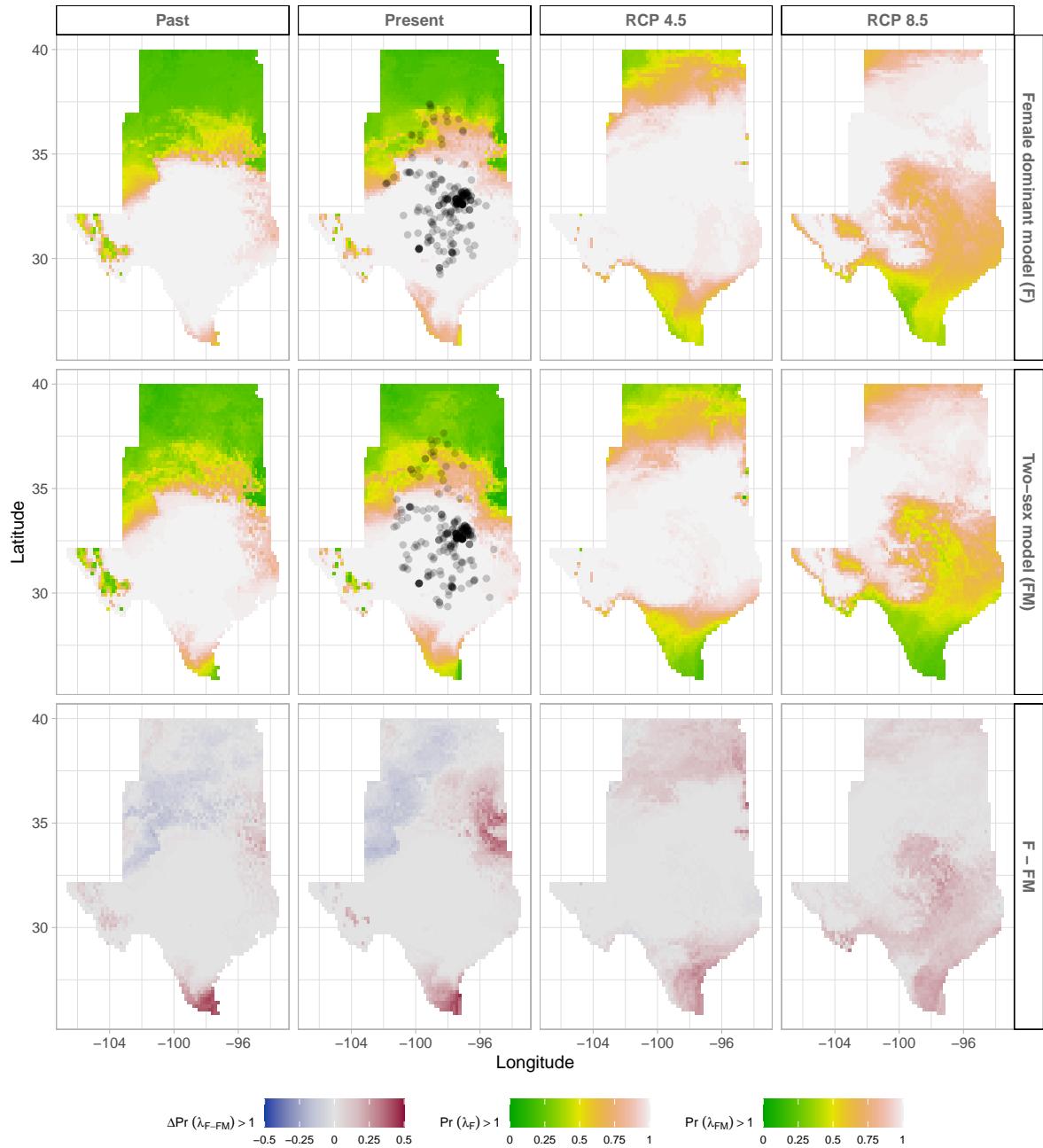
**Figure S-16:** Life table response experiment decomposition of the sensitivity of  $\lambda$  to seasonal climate into additive vital rate contributions of males and females based on posterior mean parameter estimates. (A) Temperature of growing season (contribution of female), (B) Temperature of growing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



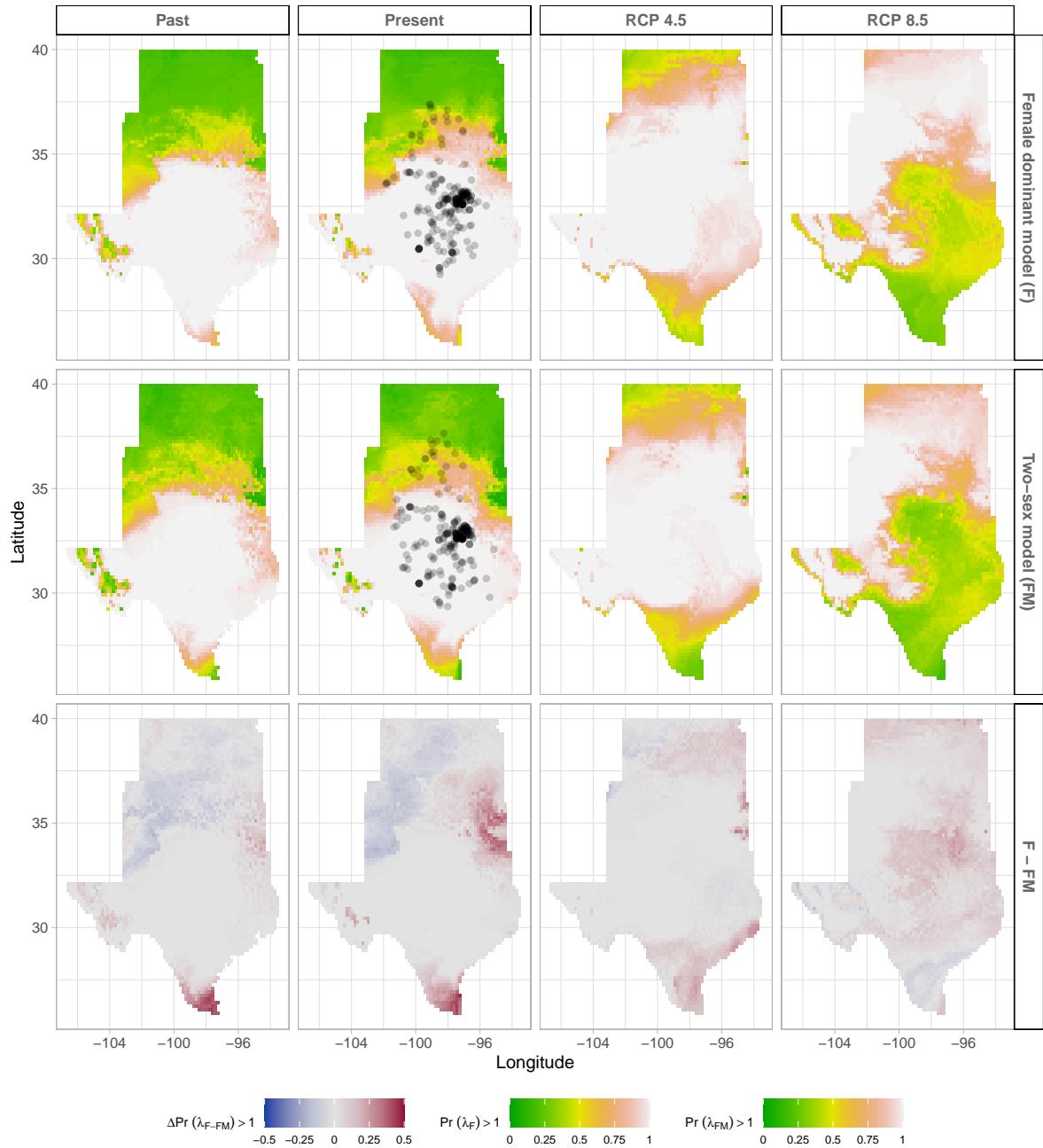
**Figure S-17:** Life table response experiment decomposition of the sensitivity of  $\lambda$  to seasonal climate into additive vital rate contributions of males and females based on posterior mean parameter estimates. (A) Precipitation of growing season (contribution of female), (B) Precipitation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



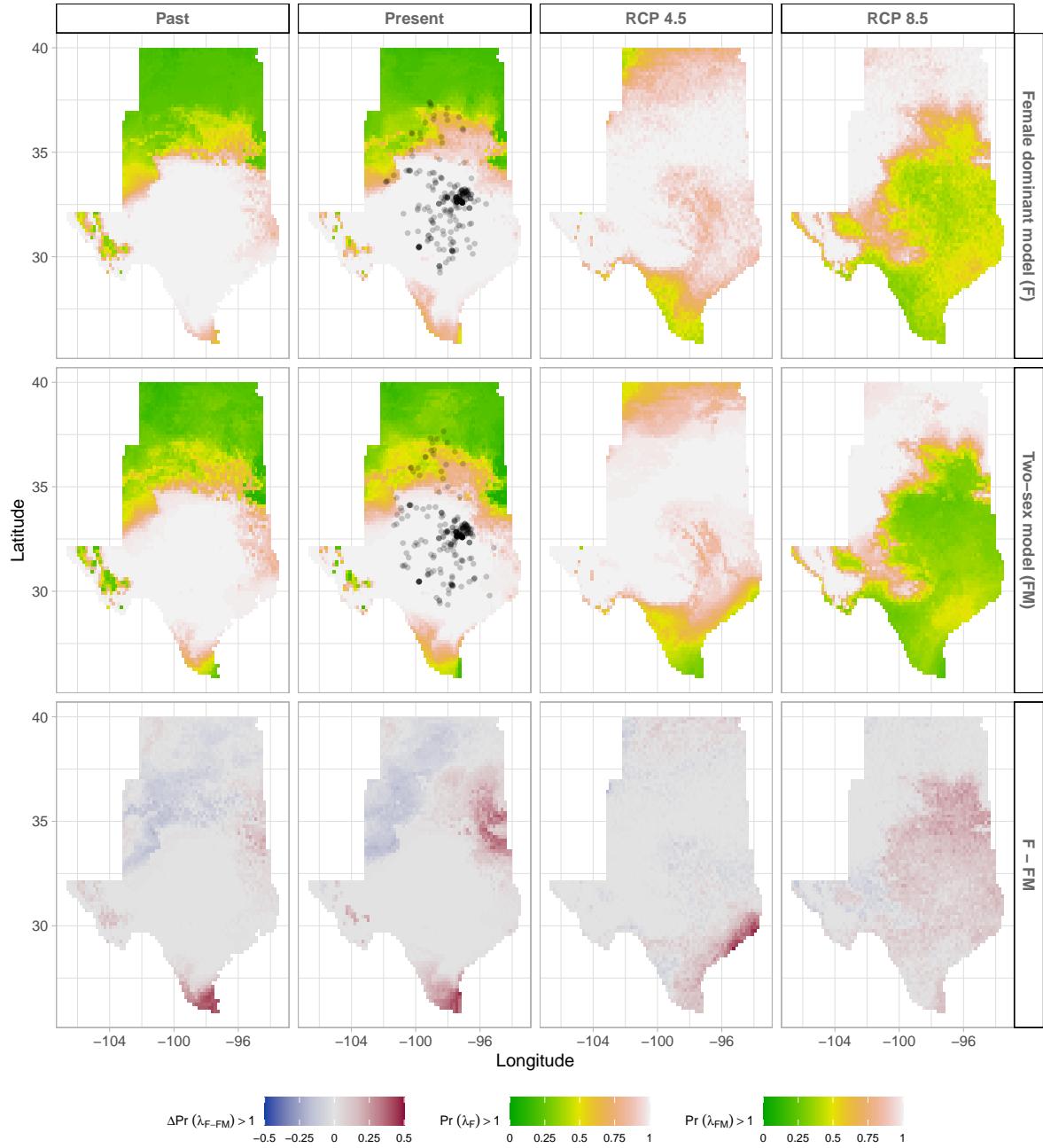
**Figure S-18:** Assessment of the statistical difference between the two-sex models and the female dominant model for the dormant and growing season. Plots show the density of  $\Pr(\lambda) > 1$  values for female dominant (pink) and two-sex models (violet) for each season. The means for each model 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,  $\text{Pr}(\lambda > 1)$ , using the two-sex model that incorporates sex- specific demographic responses to climate with sex ratio dependent seed fertilization. (E) Past, (F) Current, (G and H) Future predicted range shift based on the predicted probabilities of self- sustaining populations,  $\text{Pr}(\lambda > 1)$ , using the female dominant model. Future projections were based on the CESM1-BGC model. The black dots on panel B and F indicate all known presence points collected from GBIF from 1990 to 2019, which corresponds to the current condition in our prediction. The occurrences of GBIFs are distributed in with higher population fitness habitat  $\text{Pr}(\lambda > 1)$ , confirming that our study approach can reasonably predict range shifts.



**Figure S-20:** Climate change favors range shift toward the North edge of the current range. (A) Past, (B) Current, (C and D) Future predicted range shift based on the predicted probabilities of self-sustaining populations,  $\Pr(\lambda > 1)$ , using the two-sex model that incorporates sex-specific demographic responses to climate with sex ratio dependent seed fertilization. (E) Past, (F) Current, (G and H) Future predicted range shift based on the predicted probabilities of self-sustaining populations,  $\Pr(\lambda > 1)$ , using the female dominant model. Future projections were based on the ACCESS model. The black dots on panel B and F indicate all known presence points collected from GBIF from 1990 to 2019, which corresponds to the current condition in our prediction. The occurrences of GBIFs are distributed in with higher population fitness habitat  $\Pr(\lambda > 1)$ , confirming that our study approach can reasonably predict range shifts.



**Figure S-21:** Climate change favors range shift toward the North edge of the current range. (A) Past, (B) Current, (C and D) Future predicted range shift based on the predicted probabilities of self- sustaining populations,  $\text{Pr}(\lambda > 1)$ , using the two-sex model that incorporates sex- specific demographic responses to climate with sex ratio dependent seed fertilization. (E) Past, (F) Current, (G and H) Future predicted range shift based on the predicted probabilities of self- sustaining populations,  $\text{Pr}(\lambda > 1)$ , using the female dominant model. Future projections were based on the MIROC5 model. The black dots on panel B and F indicate all known presence points collected from GBIF from 1990 to 2019, which corresponds to the current condition in our prediction. The occurrences of GBIFs are distributed in with higher population fitness habitat  $\text{Pr}(\lambda > 1)$ , confirming that our study approach can reasonably predict range shifts.

400 **S.2 Supporting Methods**

401 **Sex ratio experiment**

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

414 
$$v = v_0 * (1 - OSR^\alpha) \quad (\text{S.1})$$

415 where  $OSR$  is the proportion of panicles that were female in the experimental populations.  
416  $\alpha$  is the parameter that control for how viability declines with increasing female bias. Further,  
417 germination rate was modeled using a binomial distribution to model the germination  
418 data from greenhouse trials. Given that germination was conditional on seed viability, the  
419 probability of success was given by the product  $v * g$ , where  $v$  is a function of  $OSR$  (Eq. ??)  
420 and  $g$  is assumed to be constant.