

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

Jacob K. Moutouama 0000-0003-1599-1671<sup>\*1</sup>, Aldo Compagnoni 0000-0001-8302-7492<sup>2</sup>, and Tom E.X. Miller 0000-0003-3208-6067<sup>1</sup>

<sup>1</sup>Program in Ecology and Evolutionary Biology, Department of BioSciences, Rice University, Houston, TX USA

<sup>2</sup>Institute

of Biology, Martin Luther University Halle-Wittenberg, Halle, Germany; and German Centre for Integrative Biodiversity Research (iDiv), Leipzig, Germany

**Running header:** Forecasting range shifts

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

**Submitted to:** *Ecology letters* (Letter)

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

**Conflict of interest statement:** None.

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

**Abstract:**

**Main Text:**

**Figures:**

**Tables:**

**References:**

---

\*Corresponding author: jmoutouama@gmail.com

## <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.

## <sup>15</sup> Introduction

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

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

---

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

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

49 Tracking the impact of climate change on population growth rate ( $\lambda$ ) and range or  
50 niche limits of dioecious taxa depends on our ability to build mechanistic models that take  
51 into account the spatial and temporal context in which sex specific response to climate  
52 change affects population viability (Czachura and Miller, 2020; Davis and Shaw, 2001;  
53 Evans et al., 2016). Structured population models built from demographic data collected  
54 from geographically distributed observations or common garden experiments provide  
55 several advantages for studying the impact of climate change on species' range shifts  
56 (Merow et al., 2017; Schultz et al., 2022; Schwinning et al., 2022). First, demographic  
57 models link individual-level life history events (mortality, development, and regeneration) to  
58 population demography, allowing the investigation of factors explaining vital rate responses  
59 to environmental drivers (Dahlgren et al., 2016; Ehrlén and Morris, 2015; Louthan et al., 2022).  
60 Second, demographic models have a natural interface with experimental treatments that can  
61 isolate spatial and temporal correlations between environmental factors, thus overcoming  
62 a main disadvantage with many types of correlative studies (Leicht-Young et al., 2007).  
63 Third, demographic models using Markov Chain Monte Carlo (MCMC) can be utilized to  
64 infer species niche which is defined as the range of resources and conditions allowing its  
65 populations to self-sustained,  $\Pr(\lambda > 1)$  (Hutchinson et al., 1978; Maguire Jr, 1973)<sup>2</sup>. Finally,  
66 structured demographic models can be used to identify which aspect of climate is more  
67 important for population dynamics. For example, Life Table Response Experiments (LTRE)  
68 built from structured models have become widely used to understand the relative importance  
69 of covariates in explaining variation in population growth rate (Ellner et al., 2016; Hernández  
70 et al., 2023). LTRE is also used to get a mechanistic understanding of how a given treatment  
71 (e.g. temperature or precipitation) could affect population dynamics through unique vital rate  
72 responses (Caswell, 1989; Iler et al., 2019; Morrison and Hik, 2007; O'Connell et al., 2024).<sup>3</sup>

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

---

<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)

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

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

## Materials and methods

### Study species

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

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

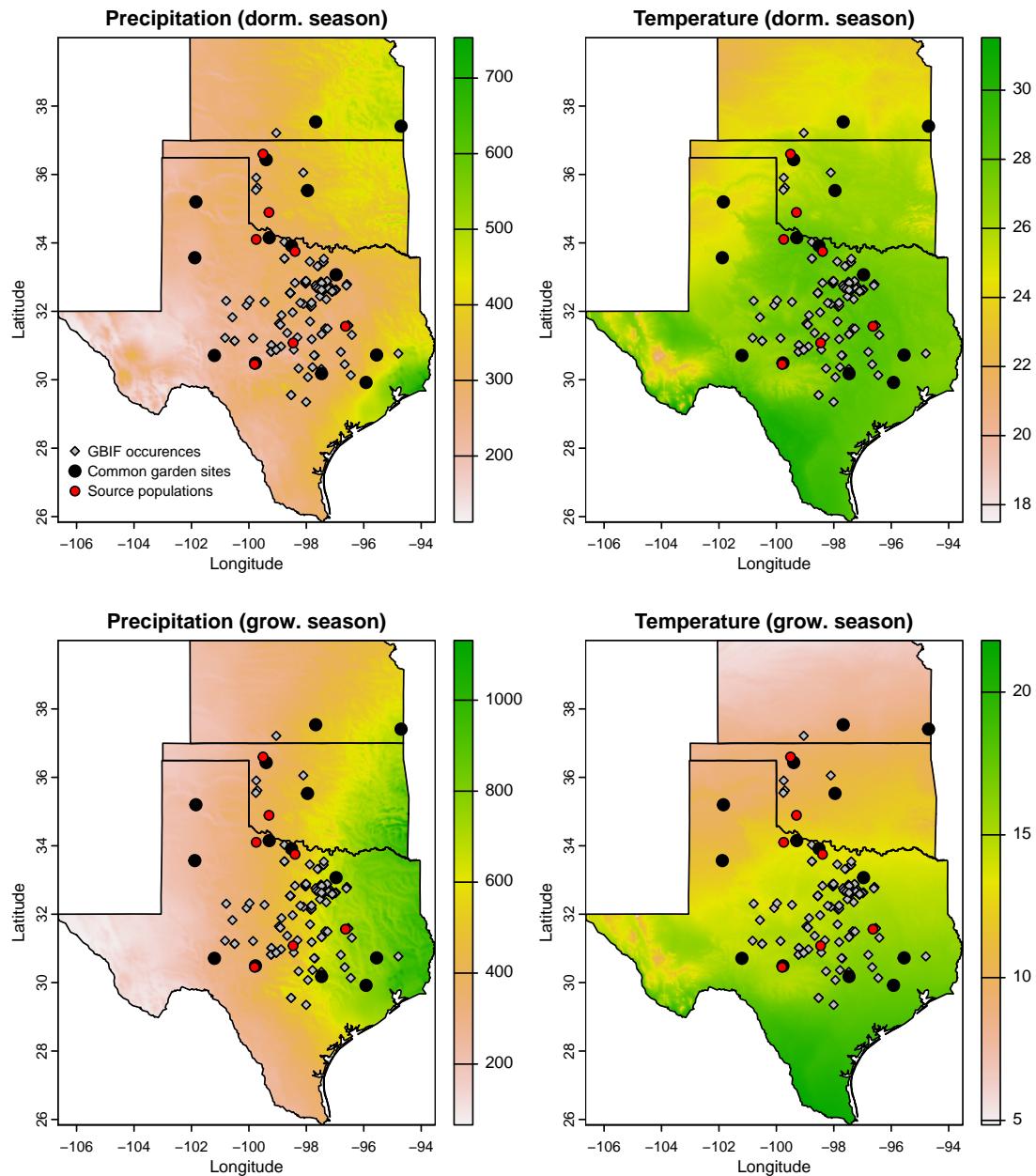
<sup>4</sup>I added some context about climate change in this study region

<sup>5</sup>I changed the order of the questions. What was Q4 is now Q3

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

<sup>110</sup> **Common garden experiment**

<sup>111</sup> We set up a common garden experiment throughout and beyond the range of Texas bluegrass  
<sup>112</sup> to quantify sex-specific demographic responses to climate. Details of the experimental design  
<sup>113</sup> are provided in Miller and Compagnoni (2022b); we provide a brief overview here. The  
<sup>114</sup> experiment was installed at 14 sites throughout and, in some cases, beyond the species'  
<sup>115</sup> natural range (Fig.1). At each site, we established 14 blocks. For each block we planted  
<sup>116</sup> the same number of plant from each sex (three female and three male individuals) that  
<sup>117</sup> were clonally propagated from females and males from eight natural source populations  
<sup>118</sup> (Fig.1); because sex is genetically-based, clones never deviated from their expected sex. The  
<sup>119</sup> experiment was established in November 2013 and was censused in May of 2014, 2015, and  
<sup>120</sup> 2016. At each census, we collected individual demographic data including survival (alive  
<sup>121</sup> or dead), size (number of tillers), and number of panicles (reproductive inflorescences). For  
<sup>122</sup> the analyses that follow, we focus on the 2014-15 and 2015-16 transitions years, since the start  
<sup>123</sup> 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 (Fig. S-1, Fig. S-2) for more details about climate variation across the study sites since the beginning of last century.

<sup>124</sup> **Climatic data collection**

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

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

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

<sup>149</sup> **Sex specific demographic responses to climate**

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

---

<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.

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

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

165 where  $\beta_0$  is the grand mean intercept,  $\beta_1$  is the size dependent slopes. *size* was on a natural  
 166 logarithm scale.  $\beta_2 \dots \beta_{13}$  represent the climate dependent slopes.  $\beta_{14} \dots \beta_{23}$  represent the  
 167 sex-climate interaction slopes. *pptgrow* is the precipitation of the growing season, *tempgrow*  
 168 is the temperature of the growing season, *pptdorm* is the precipitation of the dormant season,  
 169 *tempdorm* is the temperature of the dormant season.  
 170

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

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

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

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

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

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

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

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

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

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

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

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

214

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

215

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

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

227 We estimated population growth rate for the female dominant MPM using the function  
228 `lambda` in the package `popbio` (Stubben and Milligan, 2007). Since the two-sex MPM is non-  
229 linear (vital rates affect and are affected by population structure) we estimated the asymptotic  
230 geometric growth rate ( $\lambda$ ) by numerical simulation, [and repeated this across a range of climate](#)<sup>8</sup>.

## 231 Life Table Response Experiments

232 To identify which aspect of climate is most important for population viability, we used a non  
233 parametric model for the dependence of  $\lambda$  on time-varying parameters. To do so, we used  
234 the `RandomForest` package to fit a regression model with four climatic variable (temperature  
235 of growing season, precipitation of growing season, temperature of the dormant season and  
236 precipitation of the dormant season) as predictors and  $\lambda$  as response (Ellner et al., 2016; Liaw  
237 et al., 2002). The regression model allowed the estimation of the relative importance of each pre-  
238 dictors. The importance is measured by asking: how wrongly is  $\lambda$  predicted if we replaced the  
239 focal predictor (e.g., temperature of growing season) by a random value of the other predictors.

<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. I will say this is an independent test.

240 To estimate the contribution of each sex to population growth rate variation, we  
 241 decomposed the effect of each climate variable on population growth rate ( $\lambda$ ) into contribution  
 242 arising from the effect on each vital rate (Caswell, 2000). At this end we used a LTRE with a  
 243 "regression design". The LTRE with a "regression design" approximates the change in  $\lambda$  with  
 244 a slight climate as the product of the sensitivity of  $\lambda$  to the parameters times the sensitivity  
 245 of the parameters to climate, summed over all parameters (Caswell, 1989):

$$246 \quad \frac{\partial \lambda}{\partial \text{climate}} \approx \sum_i \frac{\partial \lambda}{\partial \theta_i^F} \frac{\partial \theta_i^F}{\partial \text{climate}} + \frac{\partial \lambda}{\partial \theta_i^M} \frac{\partial \theta_i^M}{\partial \text{climate}} \quad (8)$$

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

## 251 Climate change impacts on sex ratio

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

$$255 \quad SR = \omega_0 + \omega_1 \text{climate} + \omega_2 \text{climate} * \text{climate} + \epsilon \quad (9)$$

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

259 Second, we used the two-sex model to estimate sex-ratio by numerical simulation and  
 260 repeated this across a range of climate. This allow us to have the sex-ratio that account for  
 261 all climates covariates. We then projected sex ratio across time and space.

## 262 Impact of climate change on niche and range shifts

263 To understand the impact of climate change on species niche shifts, we estimated the  
 264 probability of self-sustaining populations, which is  $\Pr(\lambda > 1)$  conditional (i) temperature  
 265 and precipitation of the dormant season and (ii) temperature and precipitation of the growing  
 266 season.  $\Pr(\lambda > 1)$  was calculated for the two-sex model and the female dominant MPMs  
 267 using the proportion of the 300 Markov chain Monte Carlo iterations that lead to a  $\lambda > 1$  (Diez

---

<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

et al., 2014). The probability of self- sustaining populations was then represented as a contour plot with values of  $\text{Pr}(\lambda > 1)$  at given temperature and precipitation for the growing and dormant season across time (past, present and future).

$\text{Pr}(\lambda > 1)$  was also mapped onto geographic layers of three state (Texas, Oklahoma and Kansas) to delineate past, current and future potential distribution of the species. To do so, we estimated  $\text{Pr}(\lambda > 1)$  conditional to all climate covariates for each pixel ( $\sim 340 \text{ km}^2$ ) across the species range for each time period (past, present, future). Because of the amount of the computation involved in the Markov chain Monte Carlo iterations, use only 100 posterior samples to estimate  $\text{Pr}(\lambda > 1)$  across the study area (Texas, Oklahoma and Kansas).

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

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

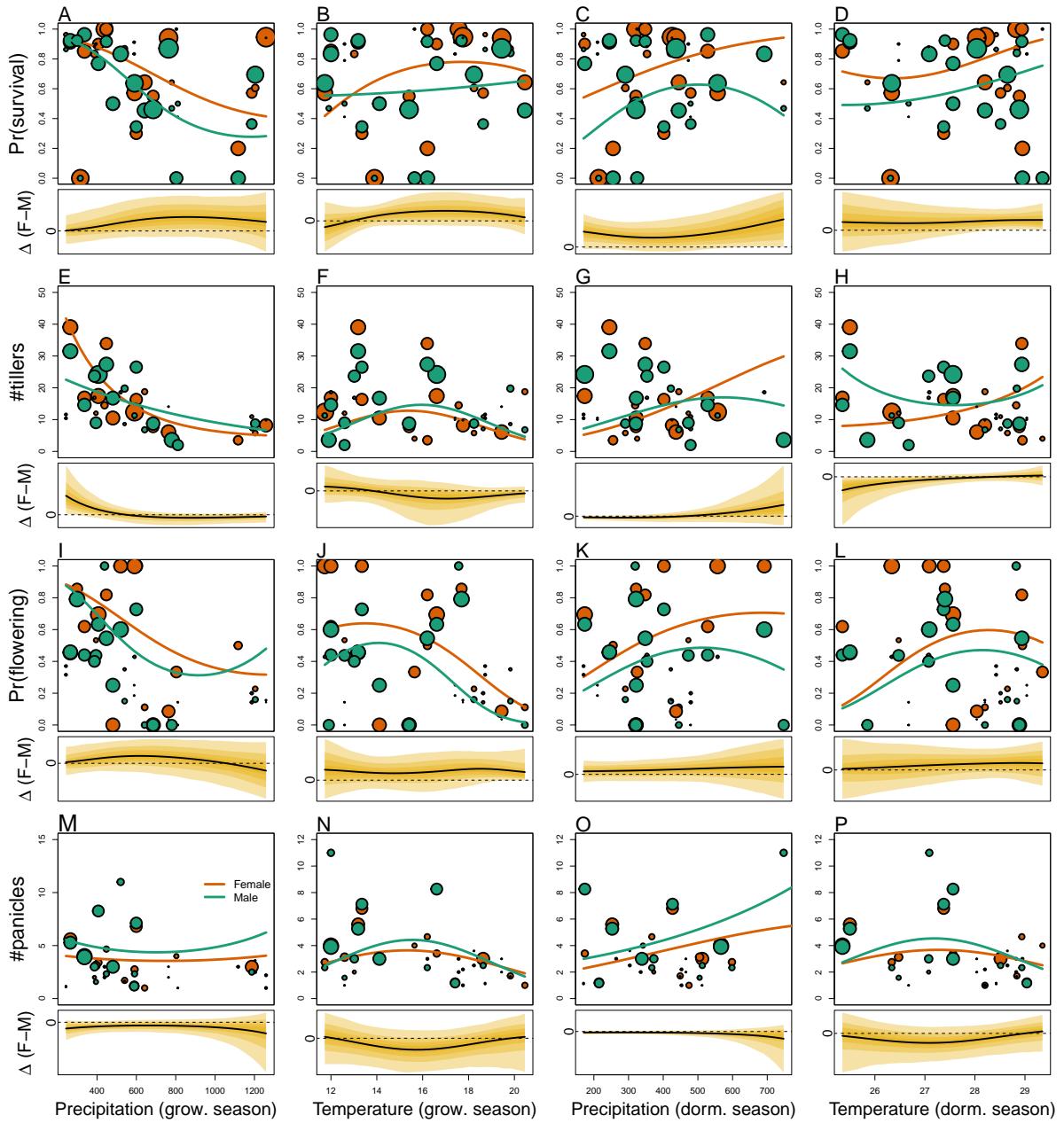
## Results

### Sex specific demographic response to climatic gradient

We found a sex specific demographic response to climatic gradient in *Poa arachnifera* populations. Specifically, female individuals had survival and flowering advantage over male across species range during the dormant and growing season (Fig.2A-3D, 3I-3L). Male individuals produce more panicles than female across species range (Fig.2M-3P). On the contrary, female had a size advantage for low value values of climate during the growing season and for high values of climate during the dormant season (Fig.2E-3H). We also found opposite patterns in the direction of the effect on climate on the probability of survival and flowering. If temperature of the growing seasons and dormant season are constant, then precipitation of the growing season has a negative effect on the probability of survival, the number of tillers, and the probability of flowering (Fig.2). In contrast, if temperature of the growing and dormant season are constant, then the precipitation of dormant season has a positive effect on these vital rates (Fig.2E-3H). If precipitation of growing and dormant season are constant, then temperature of the growing season has a positive effect of the probability of survival, a negative effect on the probability of flowering, and the number of tillers, but no significant effect on the number of panicles(Fig.2).<sup>11</sup>

---

<sup>11</sup>I tried to add the conditionality here



**Figure 2: Sex specific demographic response to climate across species range.** All vital rates as a function of one climatic variable given 3 others climate variables. (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. Statistical results are shown in Fig. S-9.

296 **Climate change alters population viability**

297 We estimated population growth rate variation across species range as a function of each cli-  
298 matic variable given the average of the three other climatic variables using two models: **a female**  
299 **dominant model and a two-sex model**<sup>12</sup>. For both models, population growth rate decreased  
300 toward high precipitation of growing season (Fig.3A). In contrast population growth rate  
301 increased with an increase in precipitation of the dormant season (Fig.3 C). Furthermore, popu-  
302 lation growth rate was maximized between 14 and 17 °C and decreased bellow zero beyond 18  
303 °C during the growing season (Fig.3B). Similarly population fitness was maximized between 27  
304 and 31 °C and decreased bellow zero just beyond 20 °C during the dormant season (Fig.3D). <sup>13</sup>

305 We have also detected a strong association between predicted lambda and different  
306 ranges of climate (past, present and future). Under past climate conditions, population growth  
307 rate decreased below one for temperature of the growing season. Assuming a moderate gas  
308 emission (RCP4.5), population growth rate will still be viable. However high gas emission  
309 (RCP8.5) will alter population viability (Fig.3B, D).<sup>14</sup>

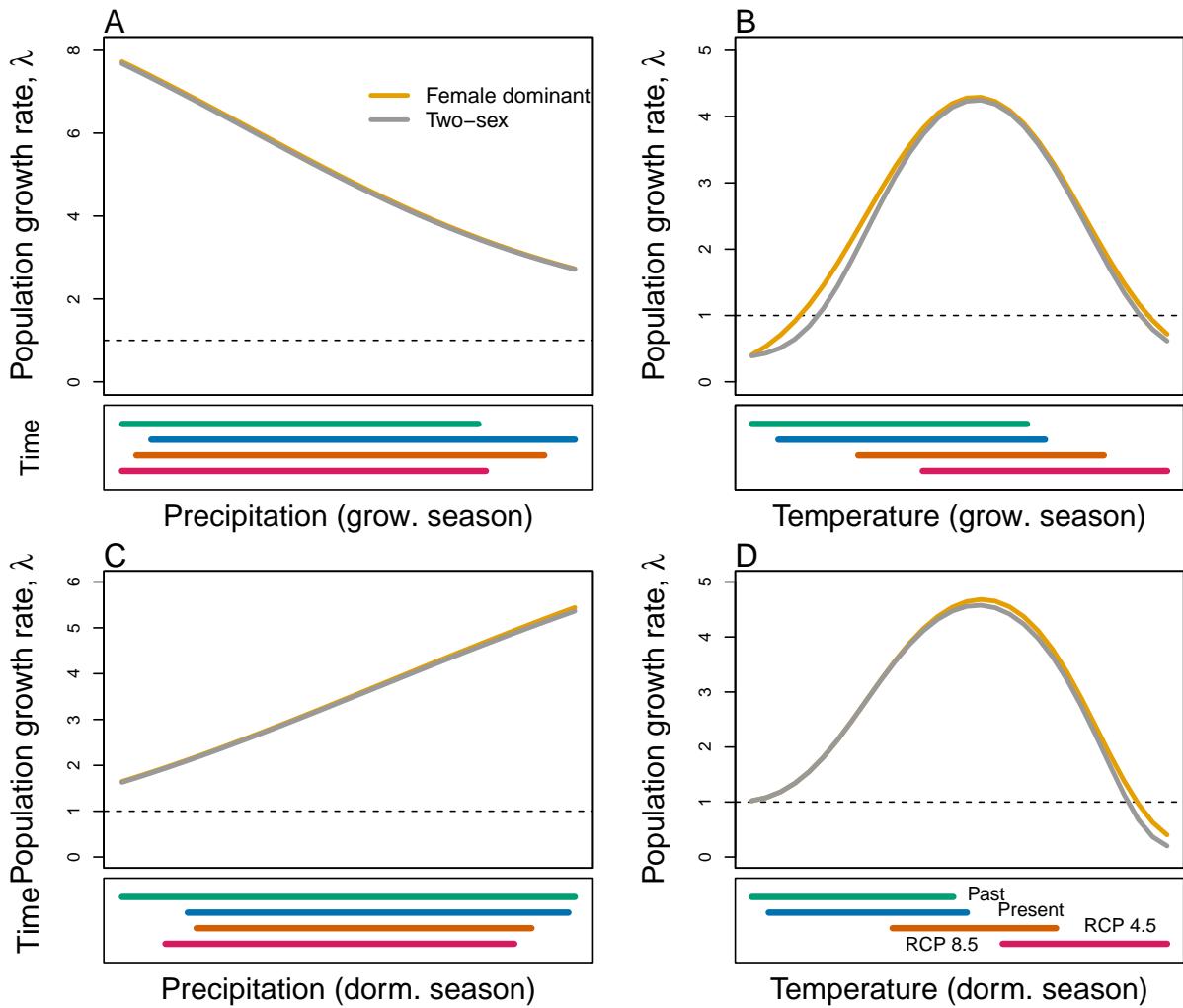
310 Population growth rate was most sensitive to change in temperature of the growing  
311 season and temperature of the dormant season (Fig. S-10). Despite contribution for both sexes,  
312 females have a higher contribution to population dynamics than males (Fig.S-11;Fig.S-12). For  
313 both sexes, the reduction of  $\lambda$  for high value of temperature (dormant and growing season)  
314 was driven by a reduction of survival rate, growth rate, and a reduction in number of panicles  
315 (Fig.3F, H, G, L). However, the change of  $\lambda$  for high value of precipitation was not driven  
316 by change in vital rates.

---

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

<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 beter approximation of lambda than the 2D. I added the conditional part in the description of the results. I see the 2D as a way of showing the difference in niche. That said if you really want to remove this I am down you have more experience than me.

<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.

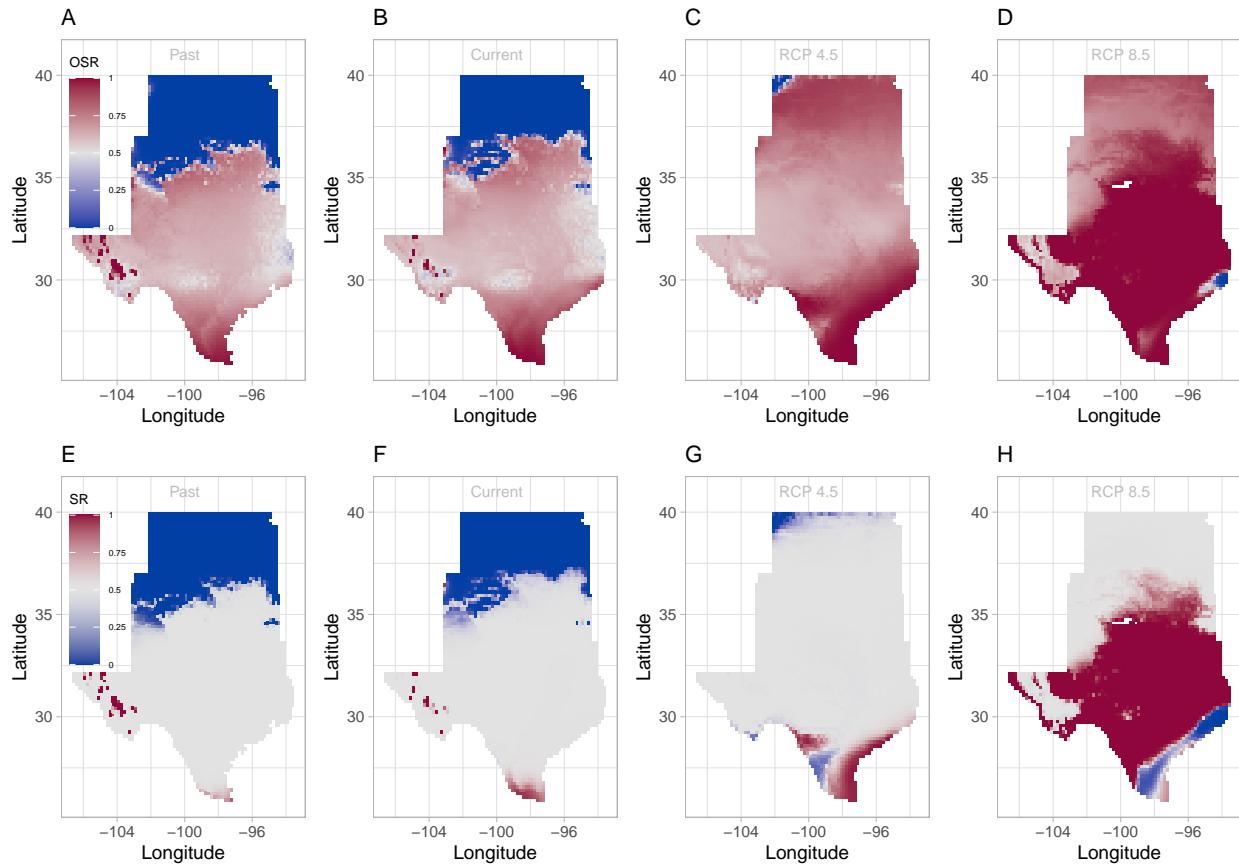


**Figure 3: Predicted population growth rate ( $\lambda$ ) in different ranges of climate.** (A) Precipitation of the growing season, (B) Temperature of the growing season, (C) Precipitation of the dormant season, (D) Temperature of the dormant season. The grey curve shows prediction by the two-sex matrix 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 Female bias in sex-ratio in response to climate change

318 There was a significant association between female bias sex-ratio and climate increase.  
 319 Operational-Sex Ratio (proportion of females panicles) increased significantly with an increase  
 320 of precipitation and temperature of the growing season and precipitation and temperature of

321 dormant season (Fig.S-20, Fig. S-18). Similarly, the proportion of female plants increased with  
 322 an increase of temperature of growing season and temperature of dormant season (Fig.S-17  
 323 B, D, Fig. S-19). However, the proportion of female plants did not vary significantly with  
 324 precipitation of dormant and growing season (Fig.S-17 A, C). Future climate drive to extreme  
 325 female-biased in *Poa arachnifera* populations (Fig.4).

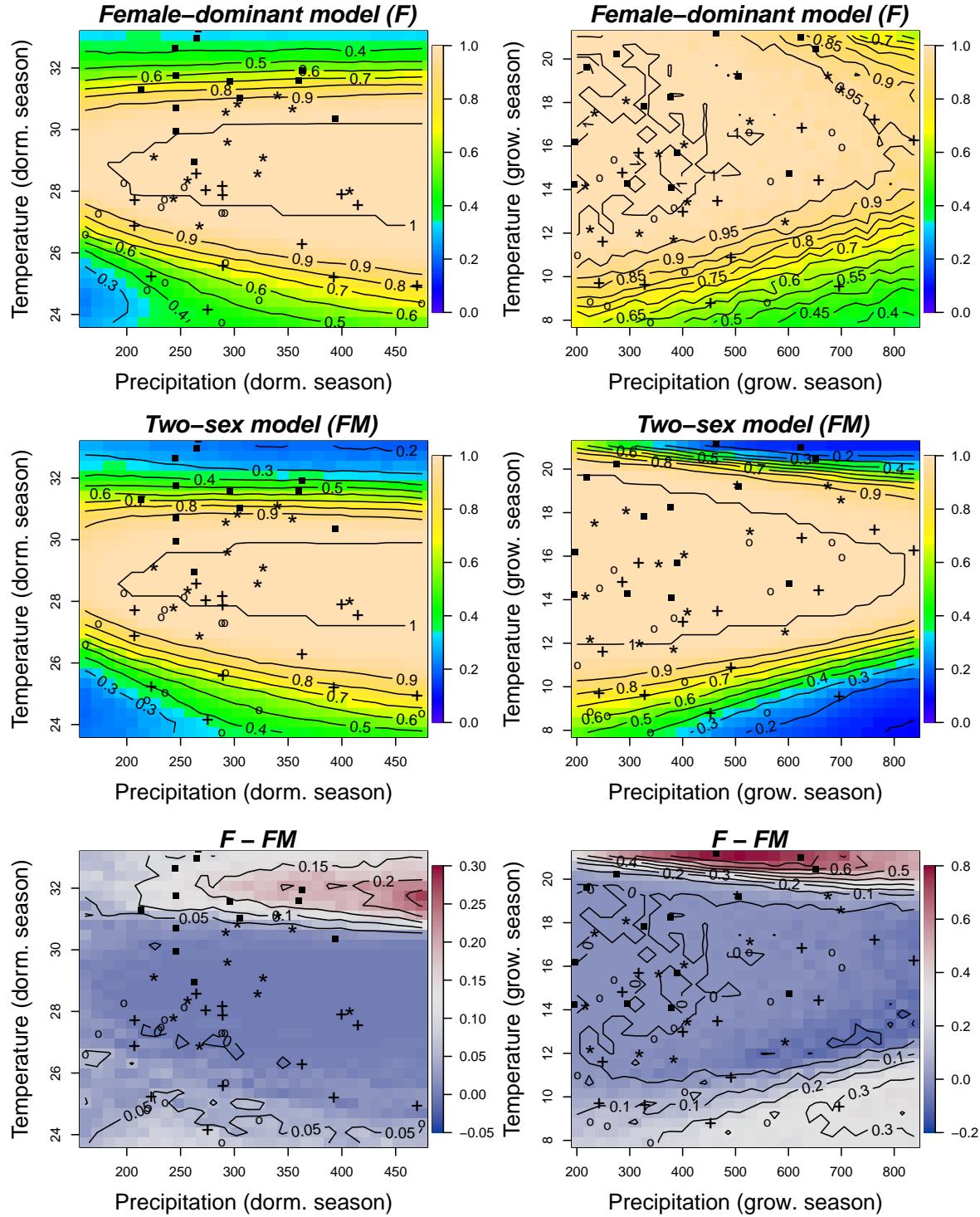


**Figure 4:** Sex ratio and climate change. (A) Past, (B) Current, (C and D) Future predicted operational sex ratio using the two-sex model that incorporates sex- specific demographic responses to climate with sex ratio dependent seed fertilization. (E) Past, (F) Current, (G and H) Future predicted operational sex ratio using the two-sex model that incorporates sex- specific demographic responses to climate with sex ratio dependent seed fertilization. Future projections were based on the CMCC-CM model.

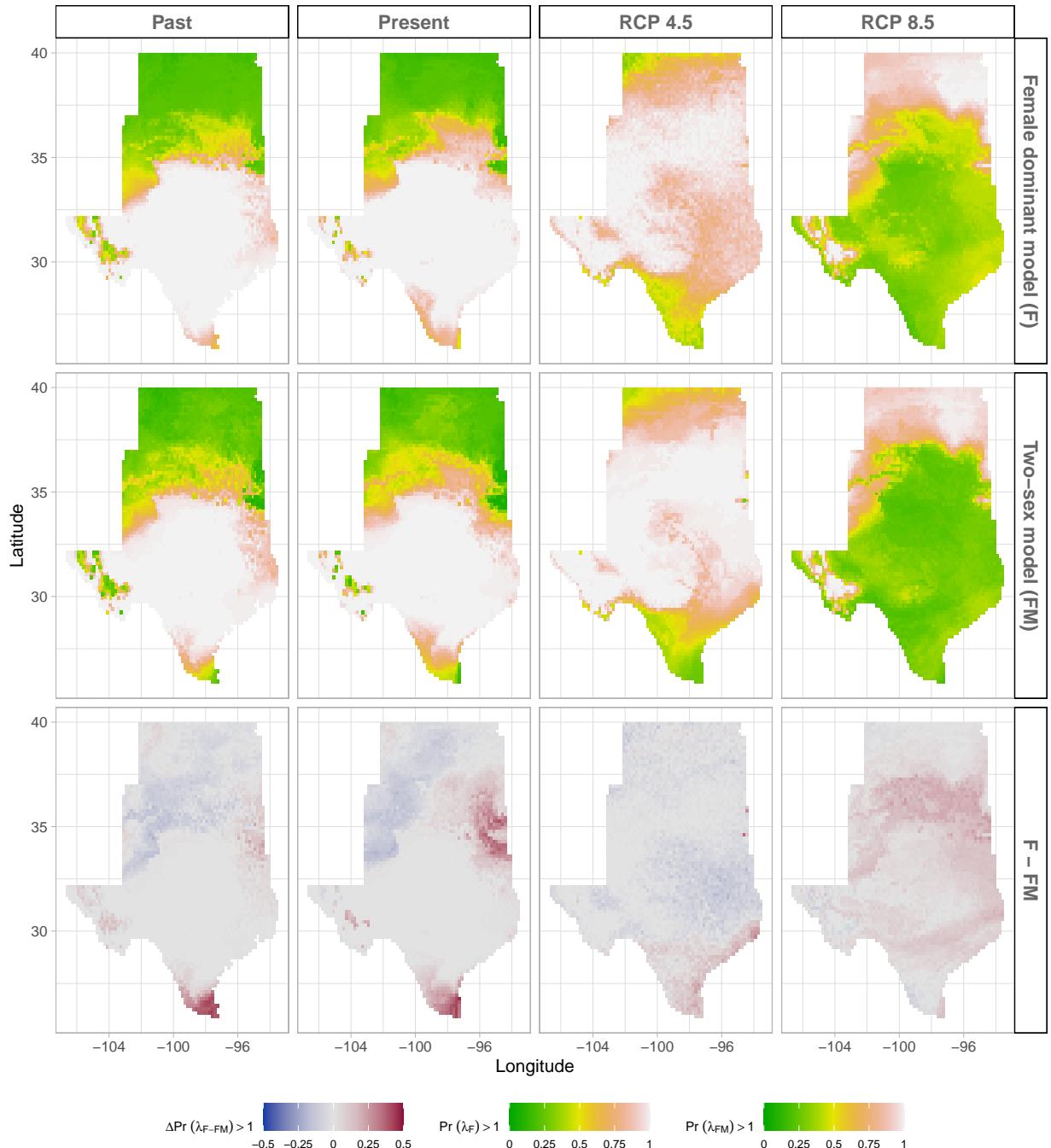
### 326 Climatic change induces niche and range shifts

327 Female dominant model and two-sex models predicts a niche shift in *Poa arachnifera*  
 328 populations (Fig. 5). However, the female dominant model underestimated the magnitude  
 329 of niche shifts (Fig. 5E, F;-0.16[-0.29,-0.03]). Female dominant model and the two-sex models  
 330 agree that viable populations of *P. arichnifera* were only predicted at the center of the range  
 331 for current climatic conditions (Fig. 6). Although *P. arichnifera* was predicted to have suitable

<sup>332</sup> habitats in the center of the range under current climate, global warming is projected to  
<sup>333</sup> reduce much of these suitable habitats (Fig. 6). If the species is able to disperse far and if there  
<sup>334</sup> is no physical barriers, most of the current suitable habitats will move toward the Northern  
<sup>335</sup> range edge as a results of niche shifts. Niche shift underestimation by the female dominant  
<sup>336</sup> model led to a geographic range underestimation by the female dominant model.



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



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

337 **Discussion**

338 Dioecious species make up a large fraction of Earth's biodiversity – most animals and many  
339 plants – yet we have little knowledge about how skewness in sex ratio will affect population  
340 viability and range shifts of dioecious species under climate change. Three general patterns  
341 emerged from our analysis of range-wide common garden experiments and sex-structured,  
342 climate-explicit demographic models. First, our Bayesian a sex specific demographic response  
343 to climate change. Second, climate change favors range shifts. Third, using only one sex to  
344 forecast range shifts of dioecious under climate change could lead to an underestimation  
345 of the impact of climate change on species.

346 There was a sex-specific demographic response to climate change in *Poa arachnifera*  
347 populations. This result is not unique to our study system and has been observed in several  
348 dioecious species (Sasaki et al., 2019; Welbergen et al., 2008; Zhao et al., 2012). Several  
349 hypotheses could explain the observed demographic advantage of females over males for  
350 survival and flowering and the opposite for growth and number of panicles. The trade-off  
351 between fitness traits (survival, growth fertility) due to resource limitation and the pollination  
352 mode of our study species (wind pollinated) could explain such a result (Cipollini and  
353 Whigham, 1994; Freeman et al., 1976). For most species, the cost of reproduction is often  
354 higher for females than males due to the requirement to develop seeds and fruits (Hultine  
355 et al., 2016). However, several studies reported a higher cost of reproduction for males in  
356 wind pollinated species due to the larger amounts of pollen they produce (Bruijning et al.,  
357 2017; Bürl et al., 2022; Cipollini and Whigham, 1994; Field et al., 2013).

358 Our results suggest that climate change will drive range shifts and the magnitude and  
359 rate of that range shift could be underestimated when tracking only one sex (Fig. S-14, Fig.  
360 S-15, Fig. S-16). This underestimation of the impact of climate change using a female dominant  
361 model could be due to several factors. First, small change in temperature of the growing and  
362 dormant season could have a larger impact on population viability. Temperature can impact  
363 plant populations through different mechanisms. Increasing temperature could increase  
364 evaporative demand, affect plant phenology (Iler et al., 2019; McLean et al., 2016; Sherry et al.,  
365 2007), and germination rate (Reed et al., 2021). The potential for temperature to influence  
366 these different processes changes seasonally (Konapala et al., 2020). For example, studies  
367 suggested that species that are active during the growing season such as cool grass species  
368 can have delayed phenology in response to global warming, particularly if temperatures rise  
369 above their physiological tolerances (Cleland et al., 2007; Williams et al., 2015). In addition,  
370 high temperature during the growing season by affecting pollen viability, fertilization could  
371 affect seed formation and germination (Hatfield and Prueger, 2015; Sletvold and Ågren,

<sup>372</sup> 2015). Second, temperature (aridity gradient) also affected sex ratio (Hultine et al., 2016). *Poa*  
<sup>373</sup> *arachnifera* populations will be female biased in response to climate change (Fig. S-21; Fig.  
<sup>374</sup> S-22; Fig. S-23). That extreme female-bias could affect population growth rate by altering  
<sup>375</sup> males' fitness with reduction on mate availability given that females individuals have a  
<sup>376</sup> demographic advantage over males (Haridas et al., 2014; Knight et al., 2005).

<sup>377</sup> We used three years of demographic data collected common garden experiments across  
<sup>378</sup> climatic gradient to forecast the impact of climate change on dioecious species. Thus our  
<sup>379</sup> models can only capture a certain range of demographic and environmental variability (Fig.  
<sup>380</sup> S-24). Moreover, our future projections require extrapolation to warmer or colder conditions  
<sup>381</sup> than observed in our experiment and subsequently should be interpreted with caution (Chen  
<sup>382</sup> et al., 2024). Despite all these limitations, the qualitative implications of the response of species  
<sup>383</sup> to increase temperature (dormant and growing season seems consistent across all GCMs.  
<sup>384</sup> Most of the suitable areas move toward the North, beyond the current range in response  
<sup>385</sup> to climate change. Our work suggest that population viability is sensitive to climate under  
<sup>386</sup> current and future conditions. Management strategies that focus on both sexes would be  
<sup>387</sup> effective and will enhance population growth rate in response to global warming.

## <sup>388</sup> Conclusion

<sup>389</sup> We have investigated the potential consequence of skewness in sex ratio on population  
<sup>390</sup> dynamics and range shift in the context of climate change. We found extreme female -biased  
<sup>391</sup> in response to climate change. The effect of female biased will induce range shifts to the  
<sup>392</sup> northern edge of the species current range by limiting mate availability. Our results also  
<sup>393</sup> suggest that tracking only one sex could lead to an overestimation of the effect of climate  
<sup>394</sup> change on population dynamics. Our work provides a framework for predicting the impact  
<sup>395</sup> of global warming on species using population demography.

## <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.

399 **References**

- 400 Bertrand, R., Lenoir, J., Piedallu, C., Riofrío-Dillon, G., De Ruffray, P., Vidal, C., Pierrat, J.-C.,  
401 and Gégout, J.-C. (2011). Changes in plant community composition lag behind climate  
402 warming in lowland forests. *Nature*, 479(7374):517–520.
- 403 Bruijning, M., Visser, M. D., Muller-Landau, H. C., Wright, S. J., Comita, L. S., Hubbell, S. P.,  
404 de Kroon, H., and Jongejans, E. (2017). Surviving in a cosexual world: A cost-benefit  
405 analysis of dioecy in tropical trees. *The American Naturalist*, 189(3):297–314.
- 406 Bürli, S., Pannell, J. R., and Tonnabel, J. (2022). Environmental variation in sex ratios and  
407 sexual dimorphism in three wind-pollinated dioecious plant species. *Oikos*, 2022(6):e08651.
- 408 Bürkner, P.-C. (2017). brms: An R package for Bayesian multilevel models using Stan. *Journal*  
409 *of Statistical Software*, 80(1):1–28.
- 410 Caswell, H. (1989). Analysis of life table response experiments i. decomposition of effects  
411 on population growth rate. *Ecological Modelling*, 46(3-4):221–237.
- 412 Caswell, H. (2000). *Matrix population models*, volume 1. Sinauer Sunderland, MA.
- 413 Chen, X., Liang, Y., and Feng, X. (2024). Influence of model complexity, training collinearity,  
414 collinearity shift, predictor novelty and their interactions on ecological forecasting. *Global*  
415 *Ecology and Biogeography*, 33(3):371–384.
- 416 Cipollini, M. L. and Whigham, D. F. (1994). Sexual dimorphism and cost of reproduction  
417 in the dioecious shrub *lindera benzoin* (lauraceae). *American Journal of Botany*, 81(1):65–75.
- 418 Cleland, E. E., Chuine, I., Menzel, A., Mooney, H. A., and Schwartz, M. D. (2007). Shifting  
419 plant phenology in response to global change. *Trends in ecology & evolution*, 22(7):357–365.
- 420 Compagnoni, A., Steigman, K., and Miller, T. E. (2017). Can't live with them, can't live  
421 without them? balancing mating and competition in two-sex populations. *Proceedings of*  
422 *the Royal Society B: Biological Sciences*, 284(1865):20171999.
- 423 Czachura, K. and Miller, T. E. (2020). Demographic back-casting reveals that subtle  
424 dimensions of climate change have strong effects on population viability. *Journal of Ecology*,  
425 108(6):2557–2570.
- 426 Dahlgren, J. P., Bengtsson, K., and Ehrlén, J. (2016). The demography of climate-driven and  
427 density-regulated population dynamics in a perennial plant. *Ecology*, 97(4):899–907.

- 428 Davis, M. B. and Shaw, R. G. (2001). Range shifts and adaptive responses to quaternary  
429 climate change. *Science*, 292(5517):673–679.
- 430 Diez, J. M., Giladi, I., Warren, R., and Pulliam, H. R. (2014). Probabilistic and spatially variable  
431 niches inferred from demography. *Journal of ecology*, 102(2):544–554.
- 432 Eberhart-Phillips, L. J., Küpper, C., Miller, T. E., Cruz-López, M., Maher, K. H., Dos Remedios,  
433 N., Stoffel, M. A., Hoffman, J. I., Krüger, O., and Székely, T. (2017). Sex-specific early  
434 survival drives adult sex ratio bias in snowy plovers and impacts mating system and  
435 population growth. *Proceedings of the National Academy of Sciences*, 114(27):E5474–E5481.
- 436 Ehrlén, J. and Morris, W. F. (2015). Predicting changes in the distribution and abundance  
437 of species under environmental change. *Ecology letters*, 18(3):303–314.
- 438 Ellis, R. P., Davison, W., Queirós, A. M., Kroeker, K. J., Calosi, P., Dupont, S., Spicer, J. I.,  
439 Wilson, R. W., Widdicombe, S., and Urbina, M. A. (2017). Does sex really matter? explaining  
440 intraspecies variation in ocean acidification responses. *Biology letters*, 13(2):20160761.
- 441 Ellner, S. P., Childs, D. Z., Rees, M., et al. (2016). Data-driven modelling of structured  
442 populations. *A practical guide to the Integral Projection Model*. Cham: Springer.
- 443 Evans, M. E., Merow, C., Record, S., McMahon, S. M., and Enquist, B. J. (2016). Towards  
444 process-based range modeling of many species. *Trends in Ecology & Evolution*, 31(11):860–871.
- 445 Field, D. L., Pickup, M., and Barrett, S. C. (2013). Comparative analyses of sex-ratio variation  
446 in dioecious flowering plants. *Evolution*, 67(3):661–672.
- 447 Freeman, D. C., Klikoff, L. G., and Harper, K. T. (1976). Differential resource utilization by  
448 the sexes of dioecious plants. *Science*, 193(4253):597–599.
- 449 Gamelon, M., Grøtan, V., Nilsson, A. L., Engen, S., Hurrell, J. W., Jerstad, K., Phillips, A. S.,  
450 Røstad, O. W., Slagsvold, T., Walseng, B., et al. (2017). Interactions between demography  
451 and environmental effects are important determinants of population dynamics. *Science  
452 Advances*, 3(2):e1602298.
- 453 Gissi, E., Bowyer, R. T., and Bleich, V. C. (2024). Sex-based differences affect conservation.  
454 *Science*, 384(6702):1309–1310.
- 455 Gissi, E., Schiebinger, L., Hadly, E. A., Crowder, L. B., Santoleri, R., and Micheli, F. (2023).  
456 Exploring climate-induced sex-based differences in aquatic and terrestrial ecosystems to  
457 mitigate biodiversity loss. *nature communications*, 14(1):4787.

- 458 Haridas, C., Eager, E. A., Rebarber, R., and Tenhumberg, B. (2014). Frequency-dependent  
459 population dynamics: Effect of sex ratio and mating system on the elasticity of population  
460 growth rate. *Theoretical Population Biology*, 97:49–56.
- 461 Hatfield, J. and Prueger, J. (2015). Temperature extremes: effect on plant growth and  
462 development. *weather clim extrem* 10: 4–10.
- 463 Hernández, C. M., Ellner, S. P., Adler, P. B., Hooker, G., and Snyder, R. E. (2023). An exact  
464 version of life table response experiment analysis, and the r package exactltre. *Methods*  
465 in Ecology and Evolution
- 466 Hitchcock, A. S. (1971). *Manual of the grasses of the United States*, volume 2. Courier Corporation.
- 467 Hultine, K. R., Grady, K. C., Wood, T. E., Shuster, S. M., Stella, J. C., and Whitham, T. G. (2016).  
468 Climate change perils for dioecious plant species. *Nature Plants*, 2(8):1–8.
- 469 Hutchinson, G. E. et al. (1978). *Introduction to population ecology*.
- 470 Iler, A. M., Compagnoni, A., Inouye, D. W., Williams, J. L., CaraDonna, P. J., Anderson, A., and  
471 Miller, T. E. (2019). Reproductive losses due to climate change-induced earlier flowering are  
472 not the primary threat to plant population viability in a perennial herb. *Journal of Ecology*,  
473 107(4):1931–1943.
- 474 Jones, M. H., Macdonald, S. E., and Henry, G. H. (1999). Sex-and habitat-specific responses  
475 of a high arctic willow, *salix arctica*, to experimental climate change. *Oikos*, pages 129–138.
- 476 Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann,  
477 N. E., Linder, H. P., and Kessler, M. (2017). Climatologies at high resolution for the earth's  
478 land surface areas. *Scientific data*, 4(1):1–20.
- 479 Kindiger, B. (2004). Interspecific hybrids of *poa arachnifera* × *poa secunda*. *Journal of New*  
480 *Seeds*, 6(1):1–26.
- 481 Knight, T. M., Steets, J. A., Vamosi, J. C., Mazer, S. J., Burd, M., Campbell, D. R., Dudash,  
482 M. R., Johnston, M. O., Mitchell, R. J., and Ashman, T.-L. (2005). Pollen limitation of plant  
483 reproduction: pattern and process. *Annu. Rev. Ecol. Evol. Syst.*, 36:467–497.
- 484 Konapala, G., Mishra, A. K., Wada, Y., and Mann, M. E. (2020). Climate change will affect  
485 global water availability through compounding changes in seasonal precipitation and  
486 evaporation. *Nature communications*, 11(1):3044.

- 487 Lee-Yaw, J. A., Kharouba, H. M., Bontrager, M., Mahony, C., Csergő, A. M., Noreen, A. M.,  
488 Li, Q., Schuster, R., and Angert, A. L. (2016). A synthesis of transplant experiments and  
489 ecological niche models suggests that range limits are often niche limits. *Ecology letters*,  
490 19(6):710–722.
- 491 Leicht-Young, S. A., Silander, J. A., and Latimer, A. M. (2007). Comparative performance of  
492 invasive and native celastrus species across environmental gradients. *Oecologia*, 154:273–282.
- 493 Liaw, A., Wiener, M., et al. (2002). Classification and regression by randomforest. *R news*,  
494 2(3):18–22.
- 495 Louthan, A. M., Keighron, M., Kiekebusch, E., Cayton, H., Terando, A., and Morris, W. F.  
496 (2022). Climate change weakens the impact of disturbance interval on the growth rate of  
497 natural populations of venus flytrap. *Ecological Monographs*, 92(4):e1528.
- 498 Maguire Jr, B. (1973). Niche response structure and the analytical potentials of its relationship  
499 to the habitat. *The American Naturalist*, 107(954):213–246.
- 500 McLean, N., Lawson, C. R., Leech, D. I., and van de Pol, M. (2016). Predicting when climate-  
501 driven phenotypic change affects population dynamics. *Ecology Letters*, 19(6):595–608.
- 502 Merow, C., Bois, S. T., Allen, J. M., Xie, Y., and Silander Jr, J. A. (2017). Climate change both  
503 facilitates and inhibits invasive plant ranges in new england. *Proceedings of the National  
504 Academy of Sciences*, 114(16):E3276–E3284.
- 505 Miller, T. and Compagnoni, A. (2022a). Data from: Two-sex demography, sexual niche  
506 differentiation, and the geographic range limits of texas bluegrass (*Poa arachnifera*). *American  
507 Naturalist, Dryad Digital Repository*. <https://doi.org/10.5061/dryad.kkwh70s5x>.
- 508 Miller, T. E. and Compagnoni, A. (2022b). Two-sex demography, sexual niche differentiation,  
509 and the geographic range limits of texas bluegrass (*poa arachnifera*). *The American  
510 Naturalist*, 200(1):17–31.
- 511 Miller, T. E. and Inouye, B. D. (2011). Confronting two-sex demographic models with data.  
512 *Ecology*, 92(11):2141–2151.
- 513 Morrison, C. A., Robinson, R. A., Clark, J. A., and Gill, J. A. (2016). Causes and consequences  
514 of spatial variation in sex ratios in a declining bird species. *Journal of Animal Ecology*,  
515 85(5):1298–1306.

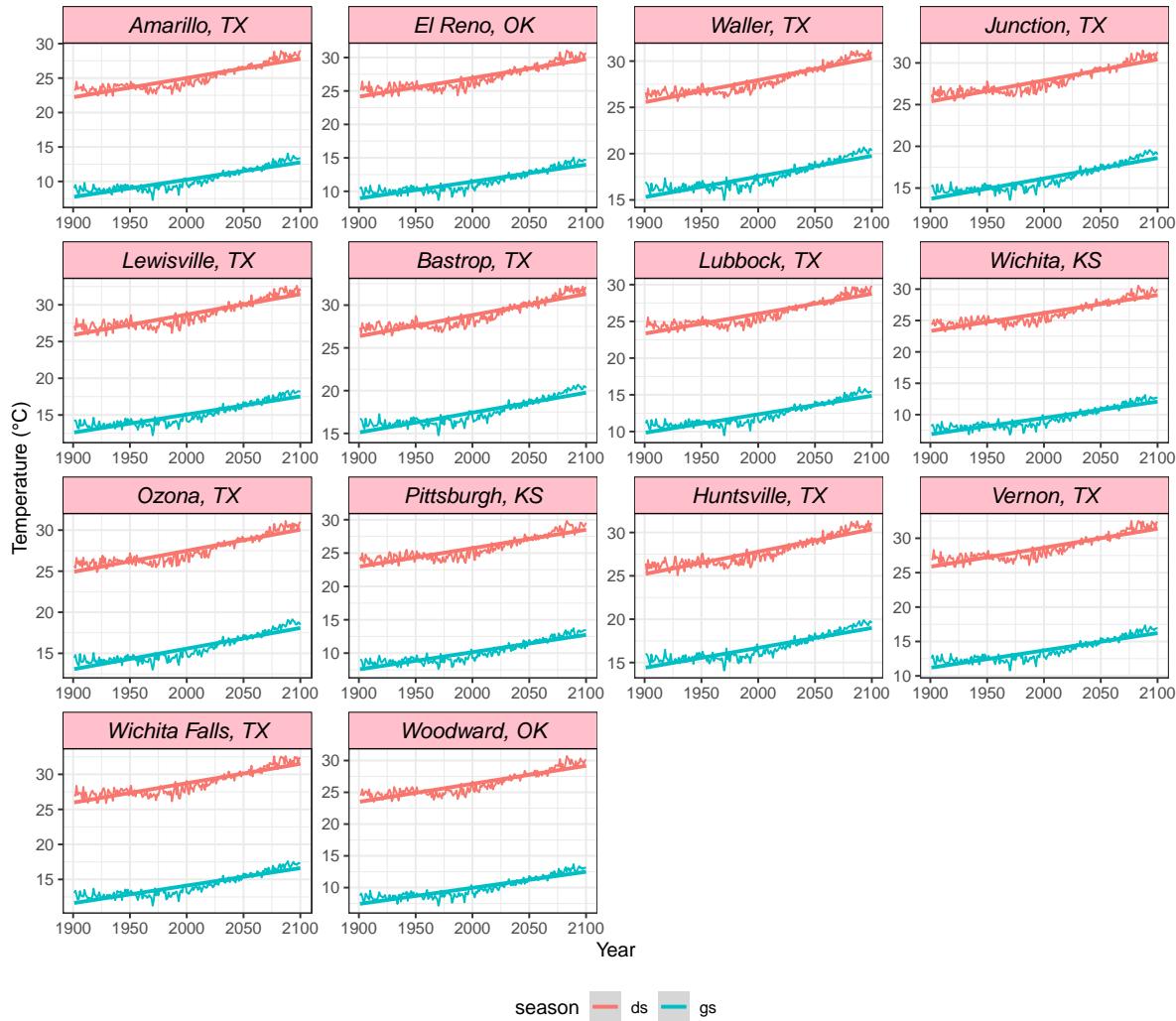
- 516 Morrison, S. F. and Hik, D. S. (2007). Demographic analysis of a declining pika *ochotona*  
517 *collaris* population: linking survival to broad-scale climate patterns via spring snowmelt  
518 patterns. *Journal of Animal ecology*, pages 899–907.
- 519 O'Connell, R. D., Doak, D. F., Horvitz, C. C., Pascarella, J. B., and Morris, W. F. (2024). Nonlinear  
520 life table response experiment analysis: Decomposing nonlinear and nonadditive population  
521 growth responses to changes in environmental drivers. *Ecology Letters*, 27(3):e14417.
- 522 Pease, C. M., Lande, R., and Bull, J. (1989). A model of population growth, dispersal and  
523 evolution in a changing environment. *Ecology*, 70(6):1657–1664.
- 524 Petry, W. K., Soule, J. D., Iler, A. M., Chicas-Mosier, A., Inouye, D. W., Miller, T. E., and  
525 Mooney, K. A. (2016). Sex-specific responses to climate change in plants alter population  
526 sex ratio and performance. *Science*, 353(6294):69–71.
- 527 Piironen, J. and Vehtari, A. (2017). Comparison of bayesian predictive methods for model  
528 selection. *Statistics and Computing*, 27:711–735.
- 529 Pottier, P., Burke, S., Drobniak, S. M., Lagisz, M., and Nakagawa, S. (2021). Sexual (in) equality?  
530 a meta-analysis of sex differences in thermal acclimation capacity across ectotherms.  
531 *Functional Ecology*, 35(12):2663–2678.
- 532 R Core Team (2023). *R: A Language and Environment for Statistical Computing*. R Foundation  
533 for Statistical Computing, Vienna, Austria.
- 534 Reed, P. B., Peterson, M. L., Pfeifer-Meister, L. E., Morris, W. F., Doak, D. F., Roy, B. A., Johnson,  
535 B. R., Bailes, G. T., Nelson, A. A., and Bridgham, S. D. (2021). Climate manipulations  
536 differentially affect plant population dynamics within versus beyond northern range limits.  
537 *Journal of Ecology*, 109(2):664–675.
- 538 Renganayaki, K., Jessup, R., Burson, B., Hussey, M., and Read, J. (2005). Identification of  
539 male-specific aflu markers in dioecious texas bluegrass. *Crop science*, 45(6):2529–2539.
- 540 Sanderson, B. M., Knutti, R., and Caldwell, P. (2015). A representative democracy to reduce  
541 interdependency in a multimodel ensemble. *Journal of Climate*, 28(13):5171–5194.
- 542 Sasaki, M., Hedberg, S., Richardson, K., and Dam, H. G. (2019). Complex interactions  
543 between local adaptation, phenotypic plasticity and sex affect vulnerability to warming  
544 in a widespread marine copepod. *Royal Society open science*, 6(3):182115.

- 545 Schultz, E. L., Hülsmann, L., Pillet, M. D., Hartig, F., Breshears, D. D., Record, S., Shaw, J. D.,  
546 DeRose, R. J., Zuidema, P. A., and Evans, M. E. (2022). Climate-driven, but dynamic and  
547 complex? a reconciliation of competing hypotheses for species' distributions. *Ecology letters*,  
548 25(1):38–51.
- 549 Schwalm, C. R., Glendon, S., and Duffy, P. B. (2020). Rcp8. 5 tracks cumulative co2 emissions.  
550 *Proceedings of the National Academy of Sciences*, 117(33):19656–19657.
- 551 Schwinning, S., Lortie, C. J., Esque, T. C., and DeFalco, L. A. (2022). What common-garden  
552 experiments tell us about climate responses in plants.
- 553 Sexton, J. P., McIntyre, P. J., Angert, A. L., and Rice, K. J. (2009). Evolution and ecology of  
554 species range limits. *Annu. Rev. Ecol. Evol. Syst.*, 40:415–436.
- 555 Sherry, R. A., Zhou, X., Gu, S., Arnone III, J. A., Schimel, D. S., Verburg, P. S., Wallace,  
556 L. L., and Luo, Y. (2007). Divergence of reproductive phenology under climate warming.  
557 *Proceedings of the National Academy of Sciences*, 104(1):198–202.
- 558 Sletvold, N. and Ågren, J. (2015). Climate-dependent costs of reproduction: Survival and  
559 fecundity costs decline with length of the growing season and summer temperature.  
560 *Ecology Letters*, 18(4):357–364.
- 561 Smith, M. D., Wilkins, K. D., Holdrege, M. C., Wilfahrt, P., Collins, S. L., Knapp, A. K., Sala,  
562 O. E., Dukes, J. S., Phillips, R. P., Yahdjian, L., et al. (2024). Extreme drought impacts have  
563 been underestimated in grasslands and shrublands globally. *Proceedings of the National  
564 Academy of Sciences*, 121(4):e2309881120.
- 565 Stan Development Team (2023). RStan: the R interface to Stan. R package version 2.21.8.
- 566 Stubben, C. J. and Milligan, B. G. (2007). Estimating and analyzing demographic models  
567 using the popbio package in r. *Journal of Statistical Software*, 22(11).
- 568 Thomson, A. M., Calvin, K. V., Smith, S. J., Kyle, G. P., Volke, A., Patel, P., Delgado-Arias,  
569 S., Bond-Lamberty, B., Wise, M. A., Clarke, L. E., et al. (2011). Rcp4. 5: a pathway for  
570 stabilization of radiative forcing by 2100. *Climatic change*, 109:77–94.
- 571 Tognetti, R. (2012). Adaptation to climate change of dioecious plants: does gender balance  
572 matter? *Tree Physiology*, 32(11):1321–1324.
- 573 Welbergen, J. A., Klose, S. M., Markus, N., and Eby, P. (2008). Climate change and the  
574 effects of temperature extremes on australian flying-foxes. *Proceedings of the Royal Society  
575 B: Biological Sciences*, 275(1633):419–425.

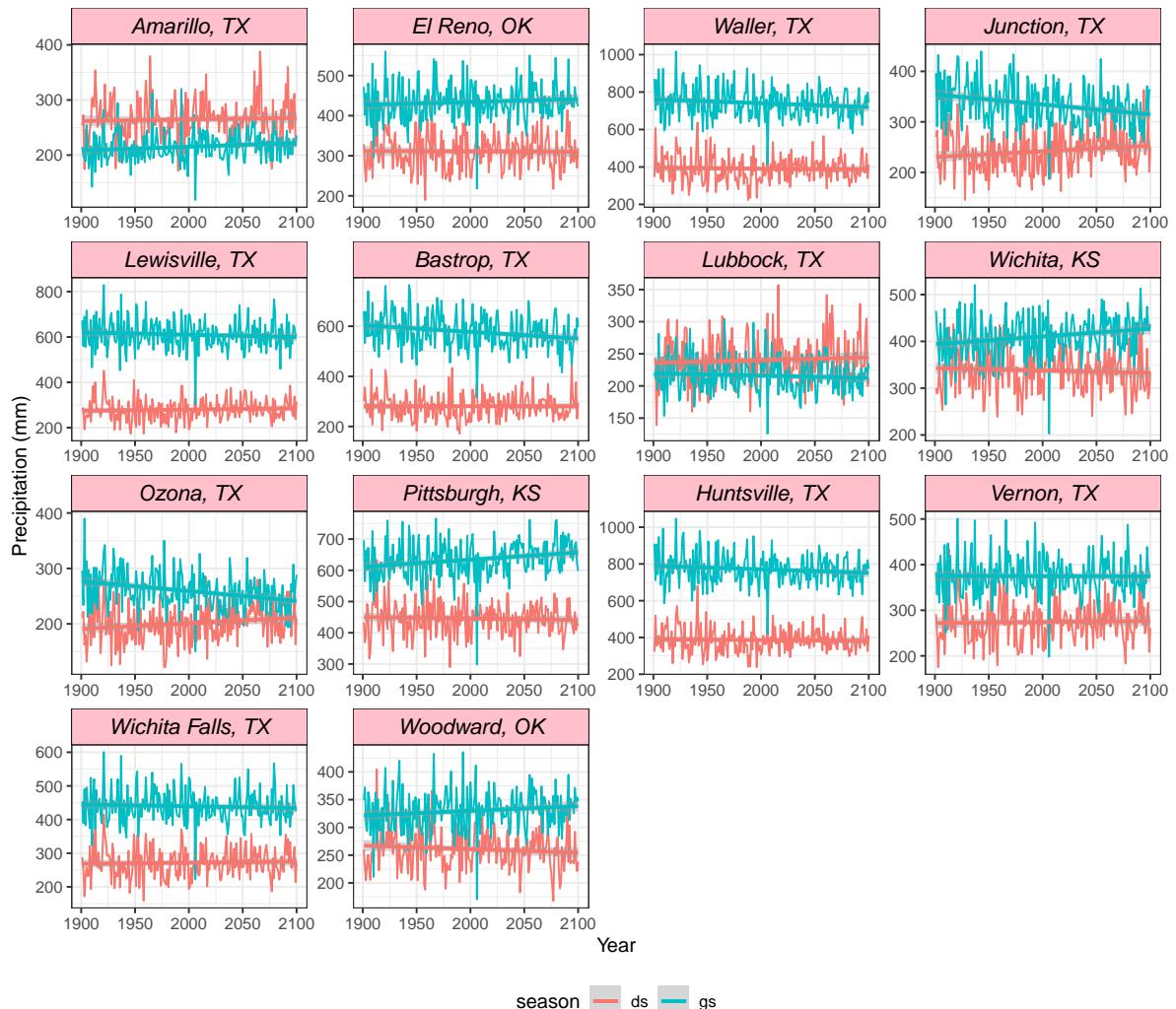
- 576 Williams, J. L., Jacquemyn, H., Ochocki, B. M., Brys, R., and Miller, T. E. (2015). Life  
577 history evolution under climate change and its influence on the population dynamics of  
578 a long-lived plant. *Journal of Ecology*, 103(4):798–808.
- 579 Zhao, H., Li, Y., Zhang, X., Korpelainen, H., and Li, C. (2012). Sex-related and stage-dependent  
580 source-to-sink transition in *populus cathayana* grown at elevated co 2 and elevated  
581 temperature. *Tree Physiology*, 32(11):1325–1338.

# Supporting Information

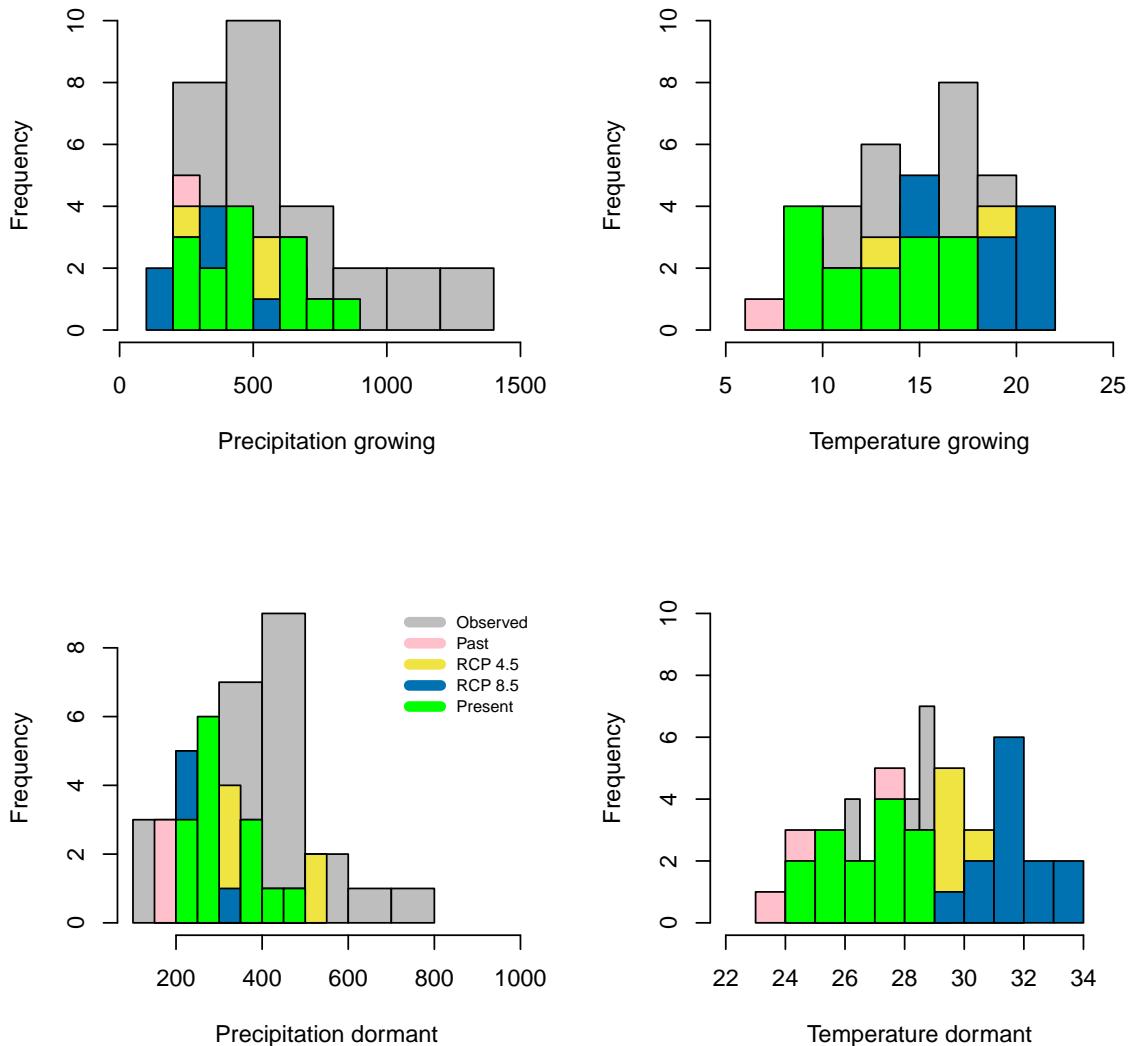
## 582 S.1 Supporting Figures



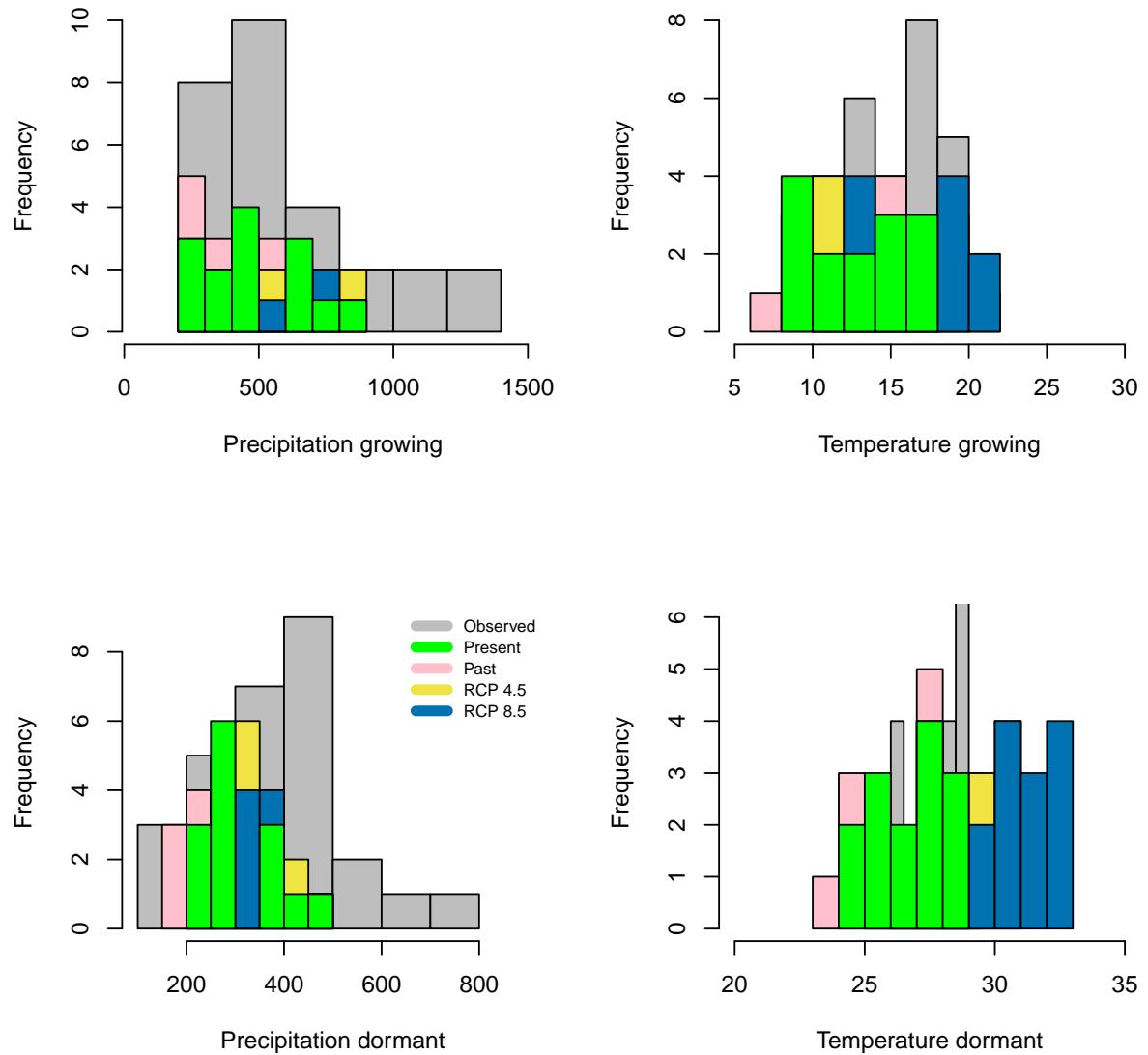
**Figure S-1:** Temperature variation across the study sites from 1990 to 2100, ds: Dormant season, dg: Growing season.



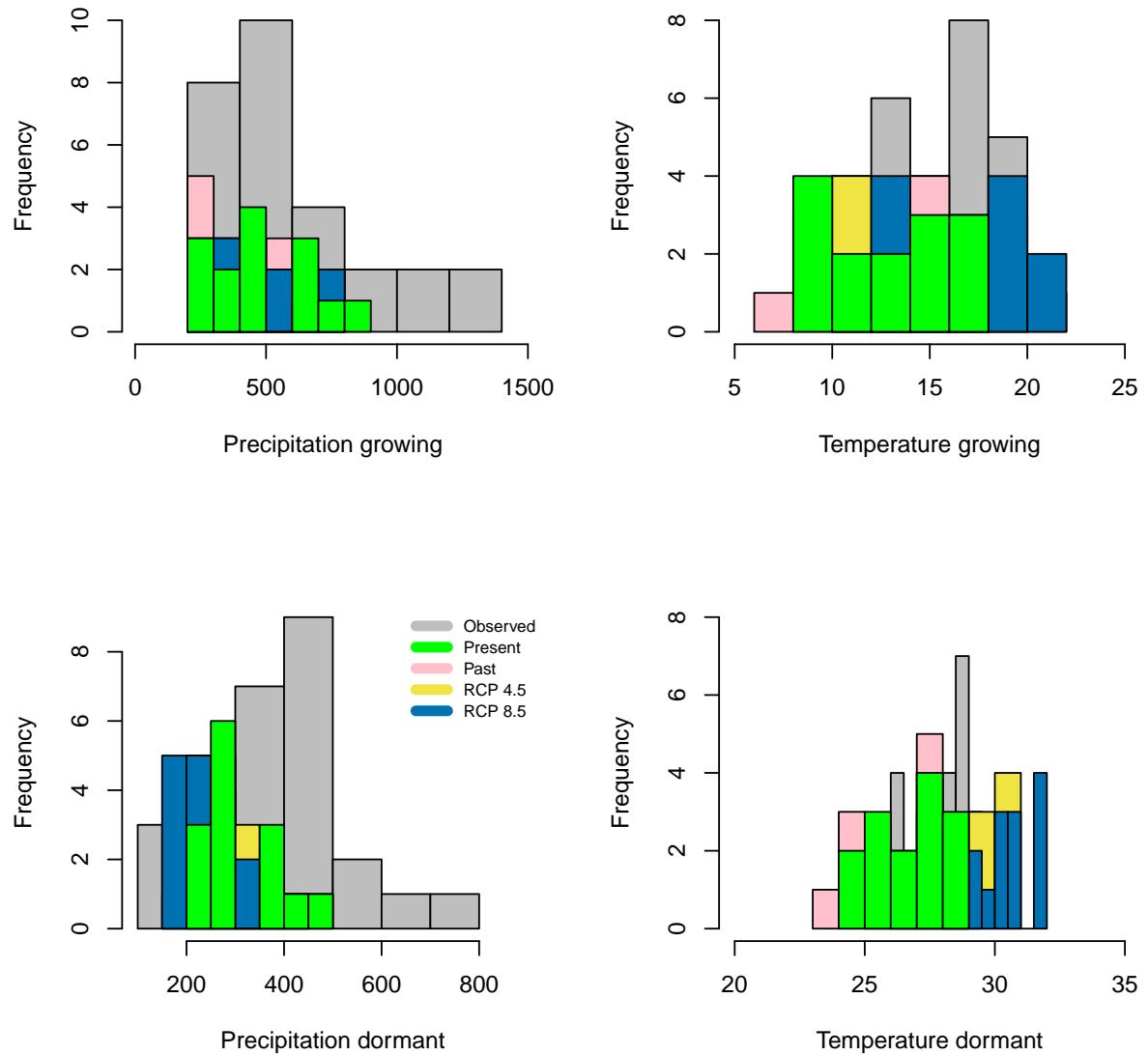
**Figure S-2:** Precipitation variation across the study sites from 1990 to 2100. ds:Dormant season, dg:Growing season.



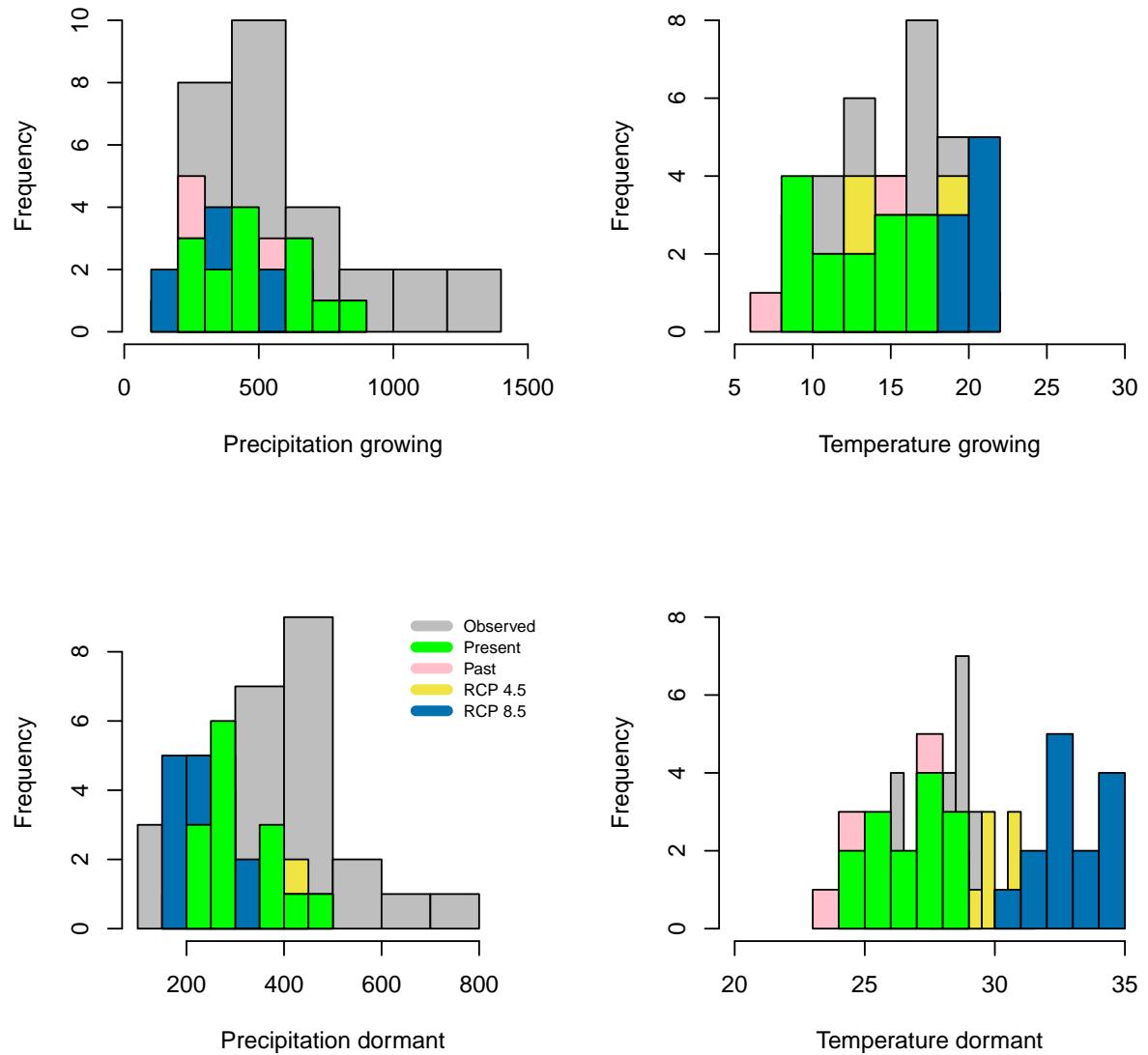
**Figure S-3:** Past, Observed, present and future (MIROC Model) climate data across the study area.



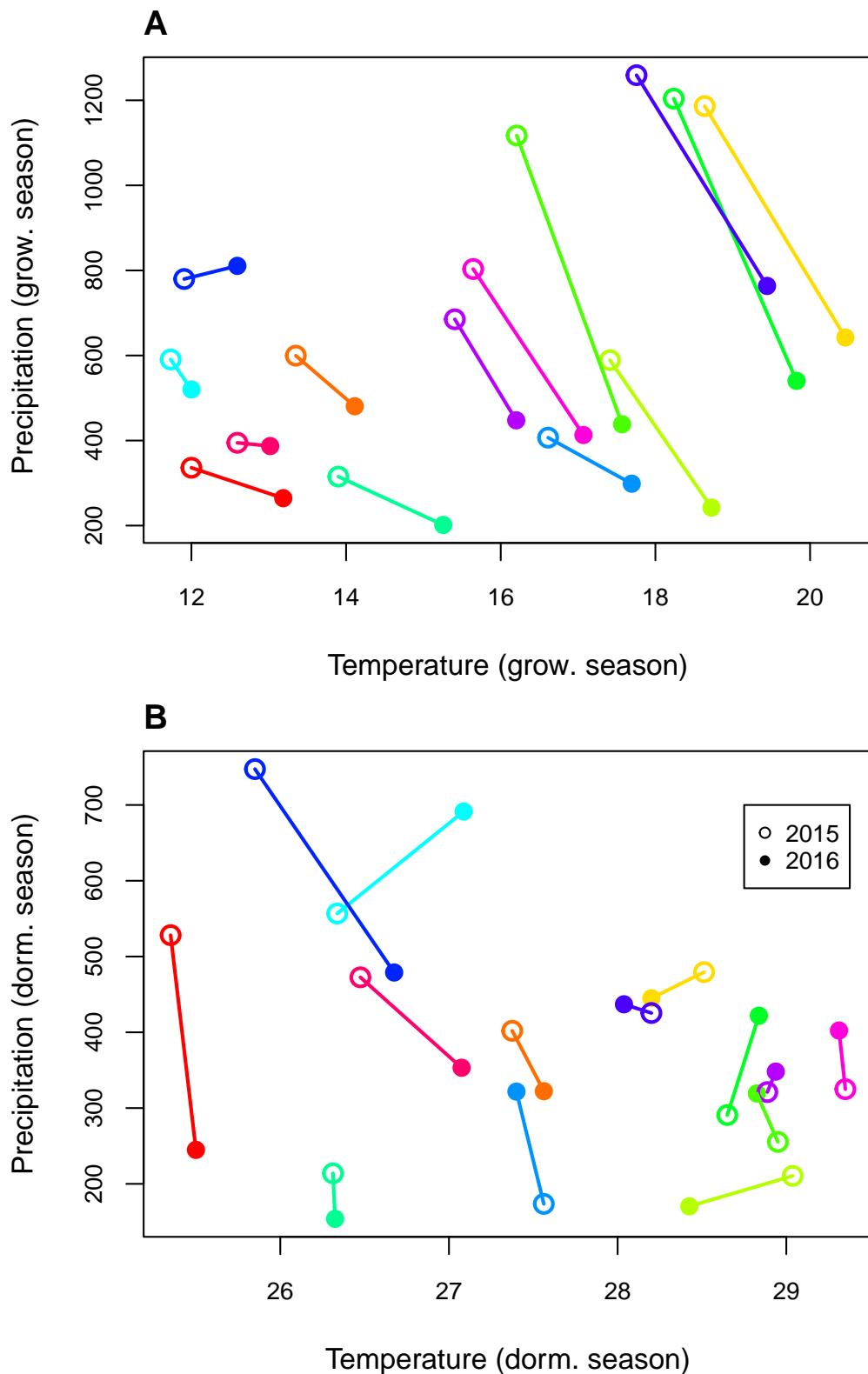
**Figure S-4:** Past, Observed, present and future (ACCESS Model) climate data across the study area.



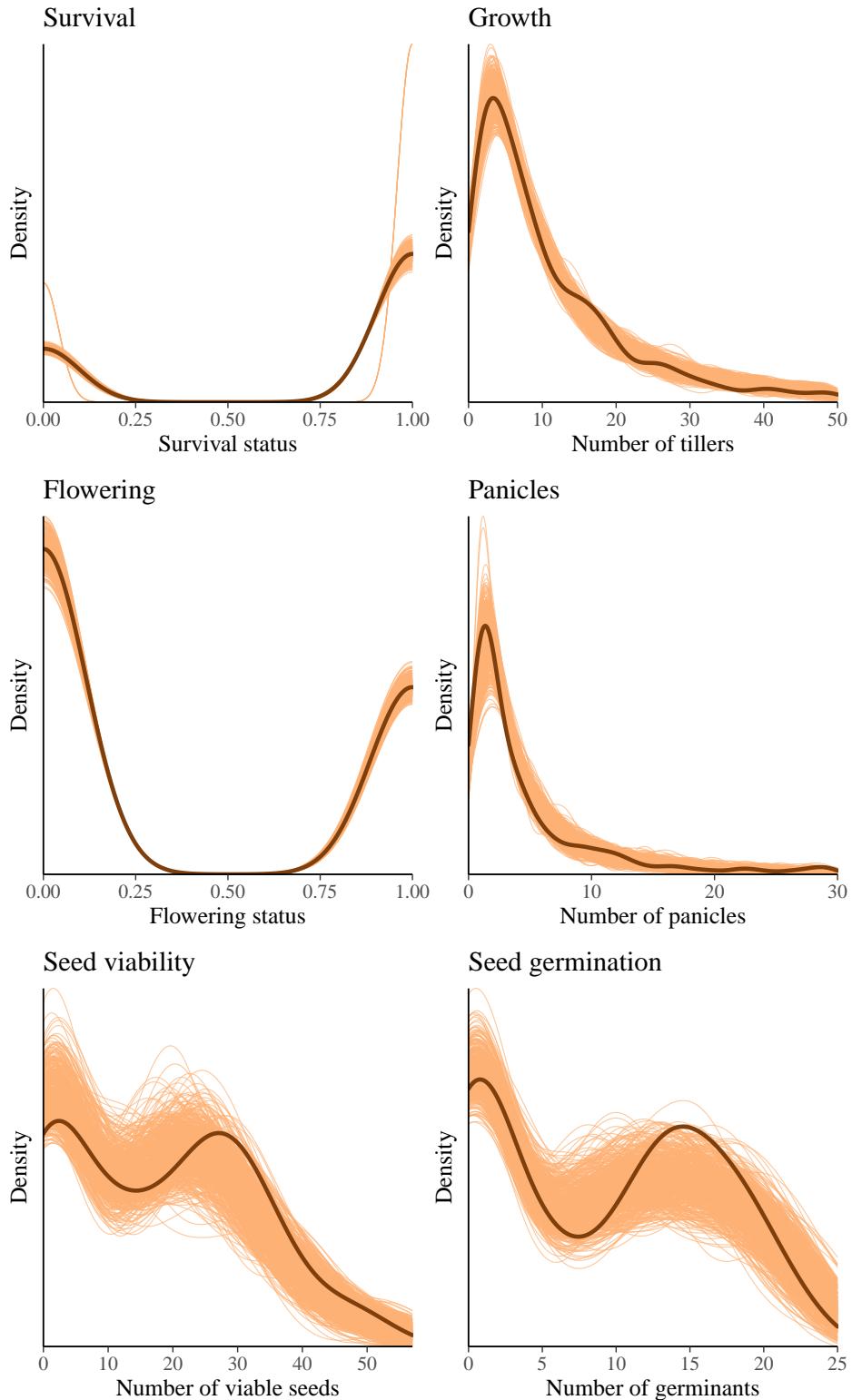
**Figure S-5:** Past, Observed, present and future (CESM1 Model) climate data across the study area.



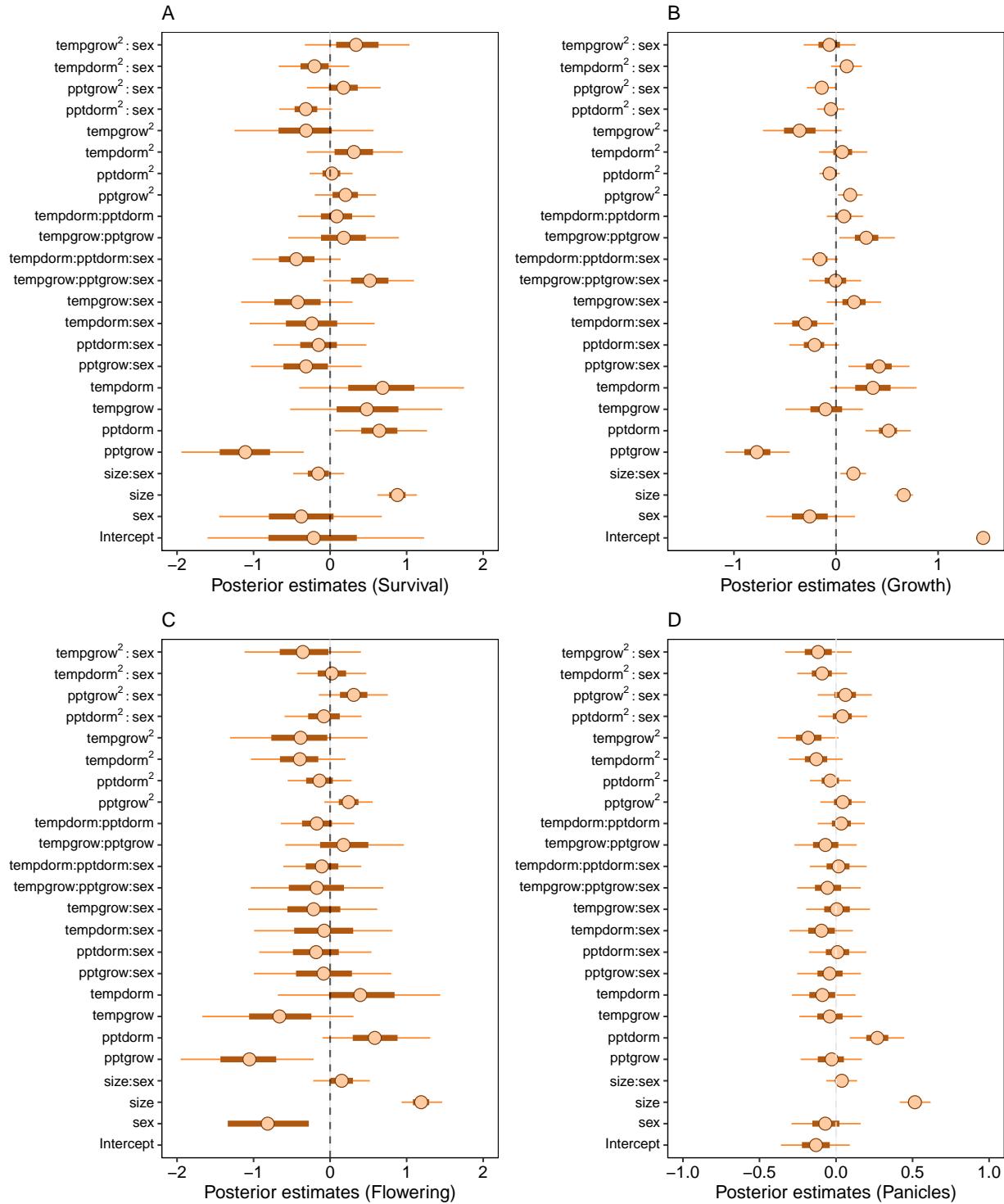
**Figure S-6:** Past, Observed, present and future (CMCC Model) climate data across the study area.



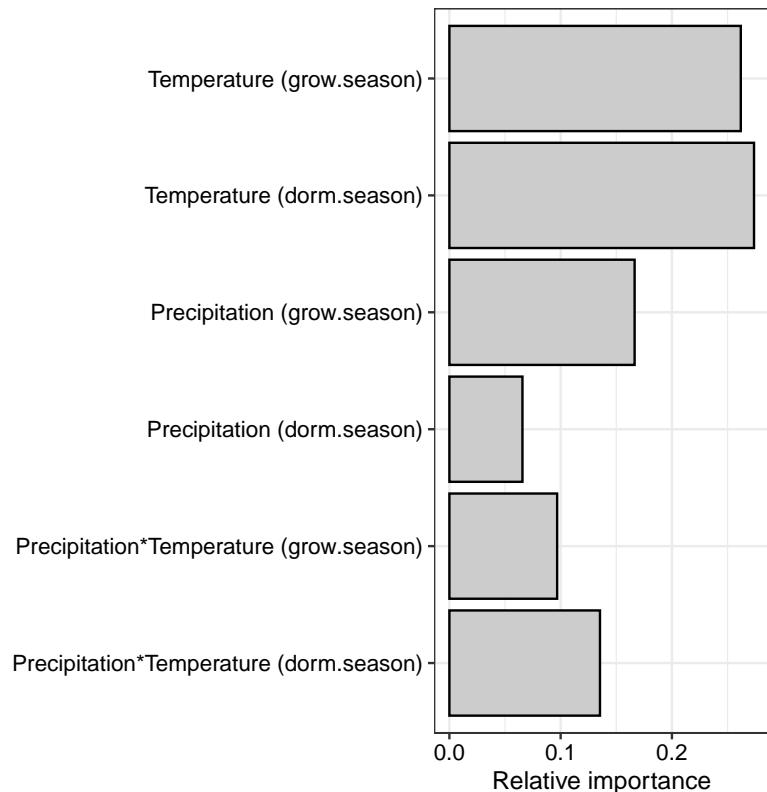
**Figure S-7:** Climate variation across the study sites during the monitoring period. ds:Dormant season, dg:Growing season.



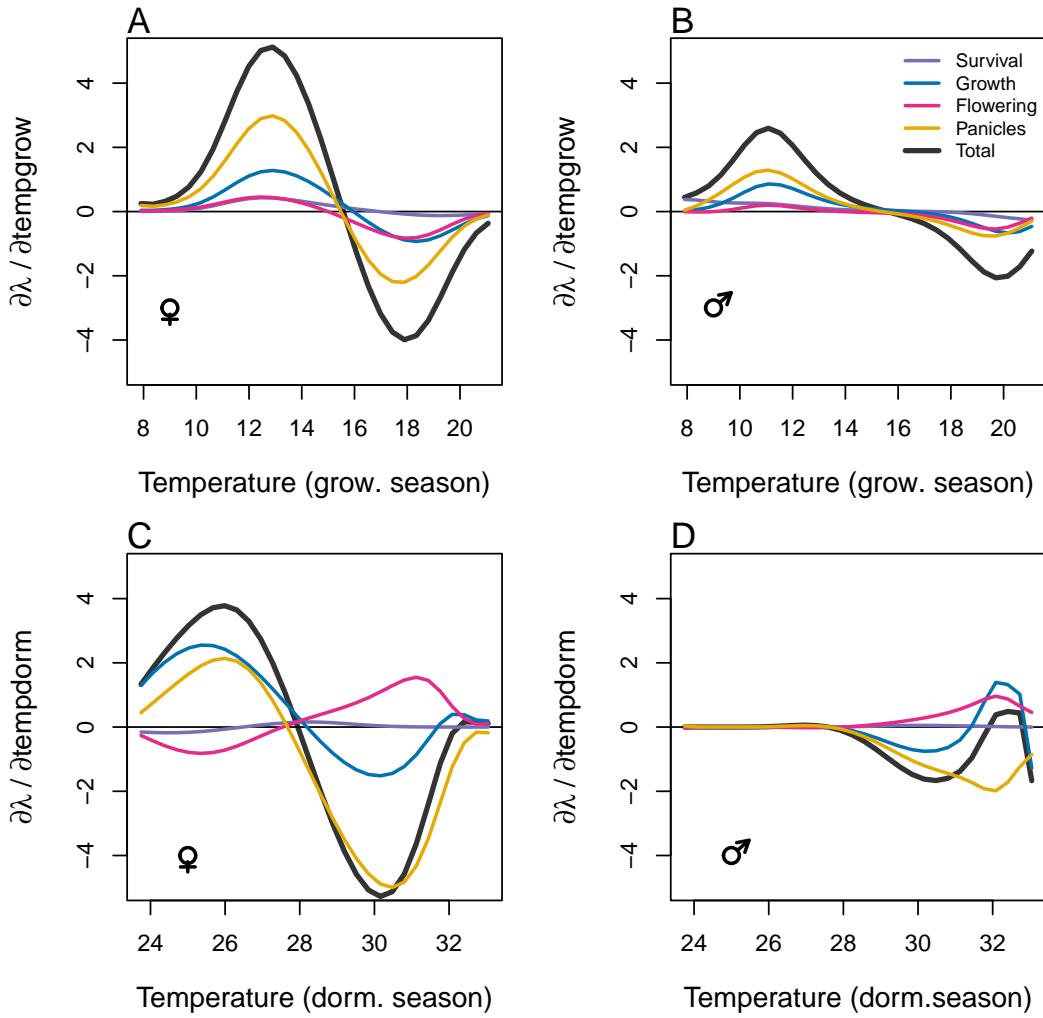
**Figure S-8:** Posterior predictive checks. Consistency between real data and simulated values suggests that the fitted model accurately describes the data. Graph shows density curves for the observed data (light blue) along with the simulated values (dark blue). The first column shows the linear models and the second column shows the 2 degree polynomial models.



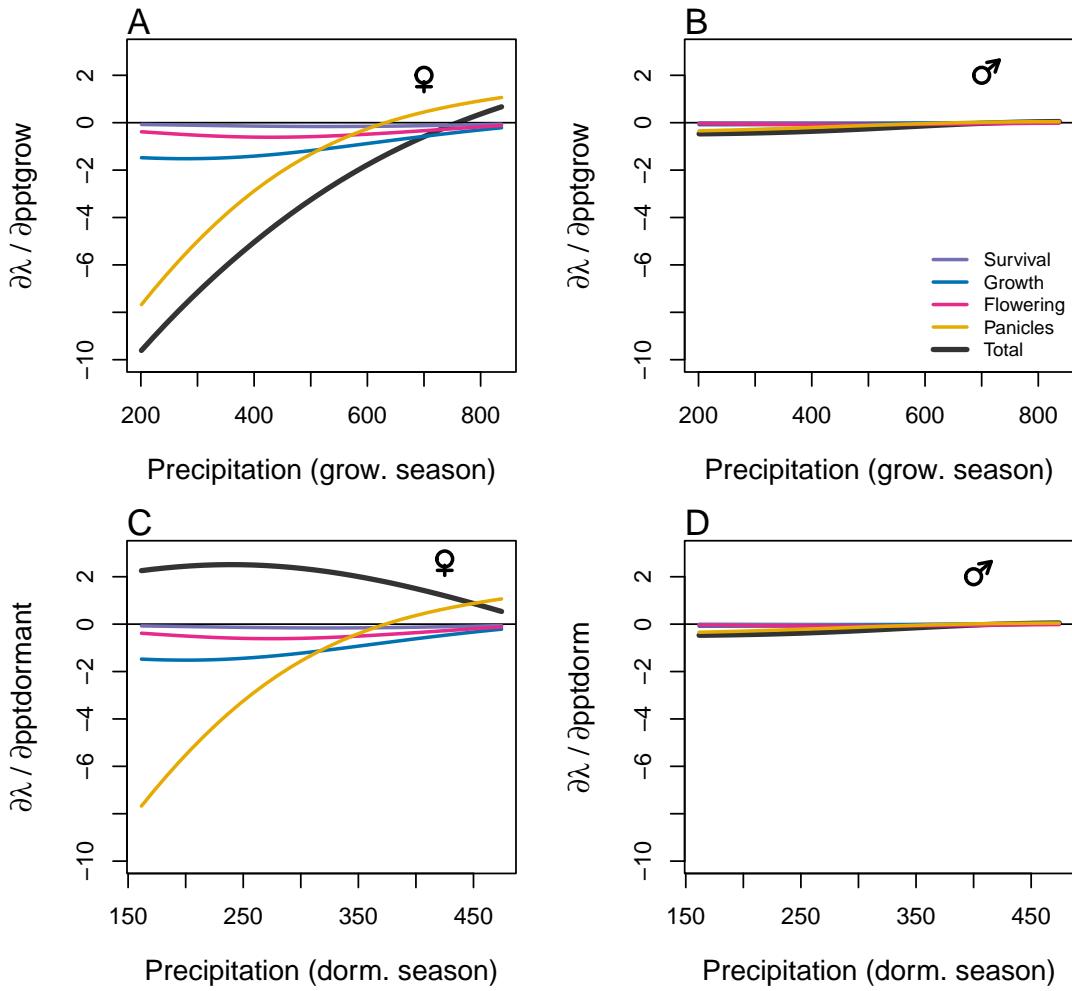
**Figure S-9:** Mean parameter values and 95% credible intervals of the posterior probability distributions. pptgrow is the precipitation of growing season, Tempgrow is the temperature of growing season, pptdorm is the temperature of dormant season, Tempdorm is the temperature of dormant season.



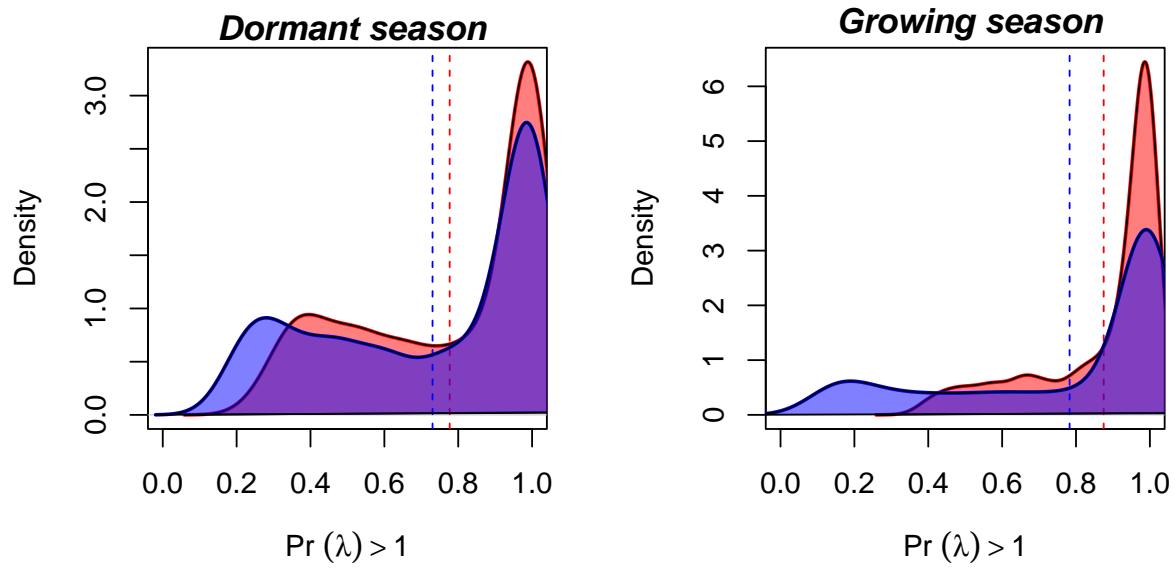
**Figure S-10:** Life Table Response Experiment: The bar represent the relative importance of each predictors



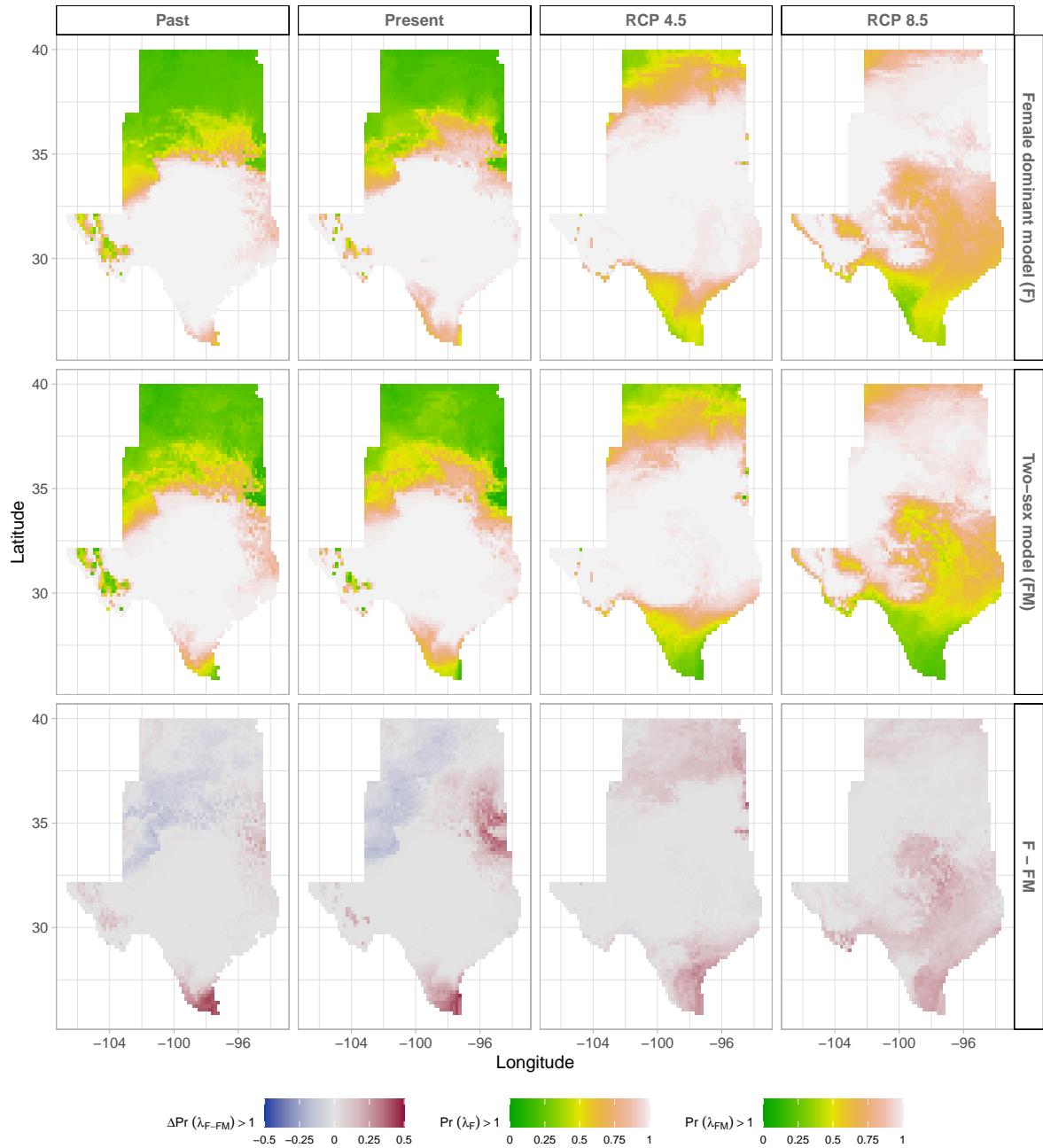
**Figure S-11:** Life table response experiment decomposition of the sensitivity of  $\lambda$  to seasonal climate into additive vital rate contributions of males and females based on posterior mean parameter estimates. (A) Temperature of growing season (contribution of female), (B) Temperature of growing season (contribution of male), (C) Temperature of dormant season (contribution of female) and (D) Temperature of dormant season (contribution of male)



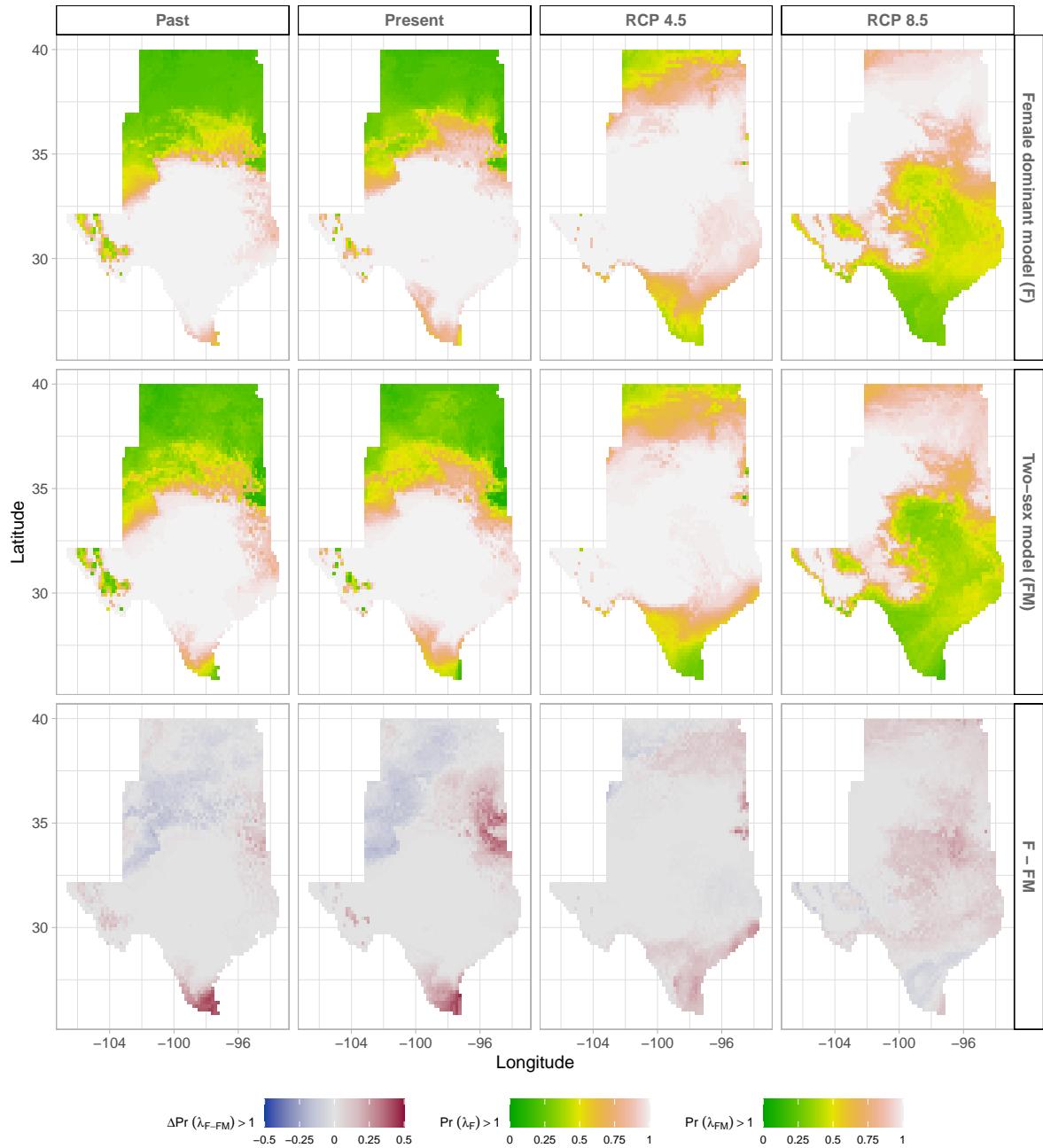
**Figure S-12:** Life table response experiment decomposition of the sensitivity of  $\lambda$  to seasonal climate into additive vital rate contributions of males and females based on posterior mean parameter estimates. (A) Precipitation of growing season (contribution of female), (B) Precipitation of growing season (contribution of male), (C) Precipitation of dormant season (contribution of female) and (D) Precipitation of dormant season (contribution of male)



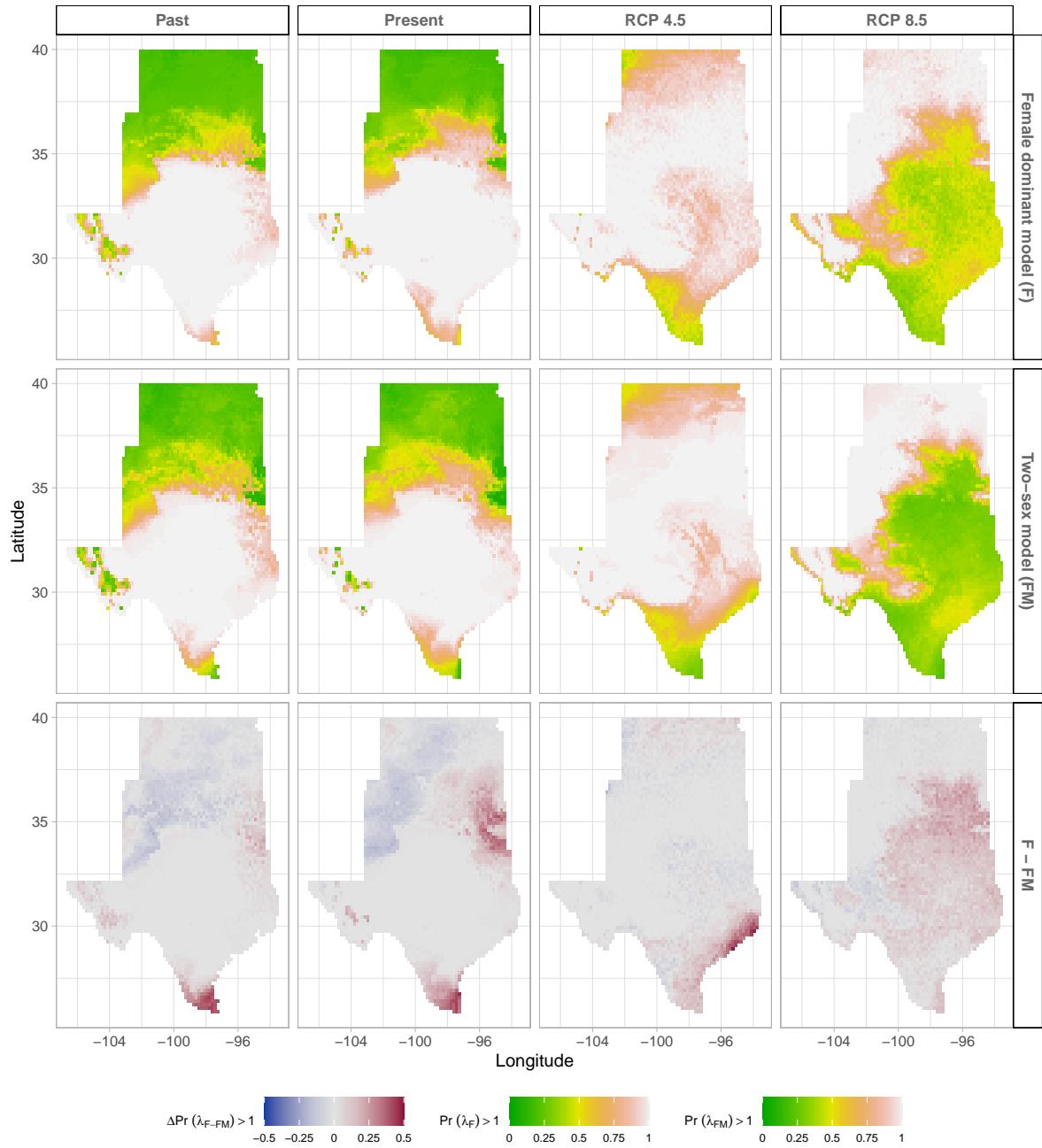
**Figure S-13:** Assessment of the statistical difference between the two-sex models and the female dominant model for the dormant and growing season. Plots show the density of  $\lambda$  values at presences (pink) and background locations (blue) for each species. The means for each model are shown as vertical dashed lines.



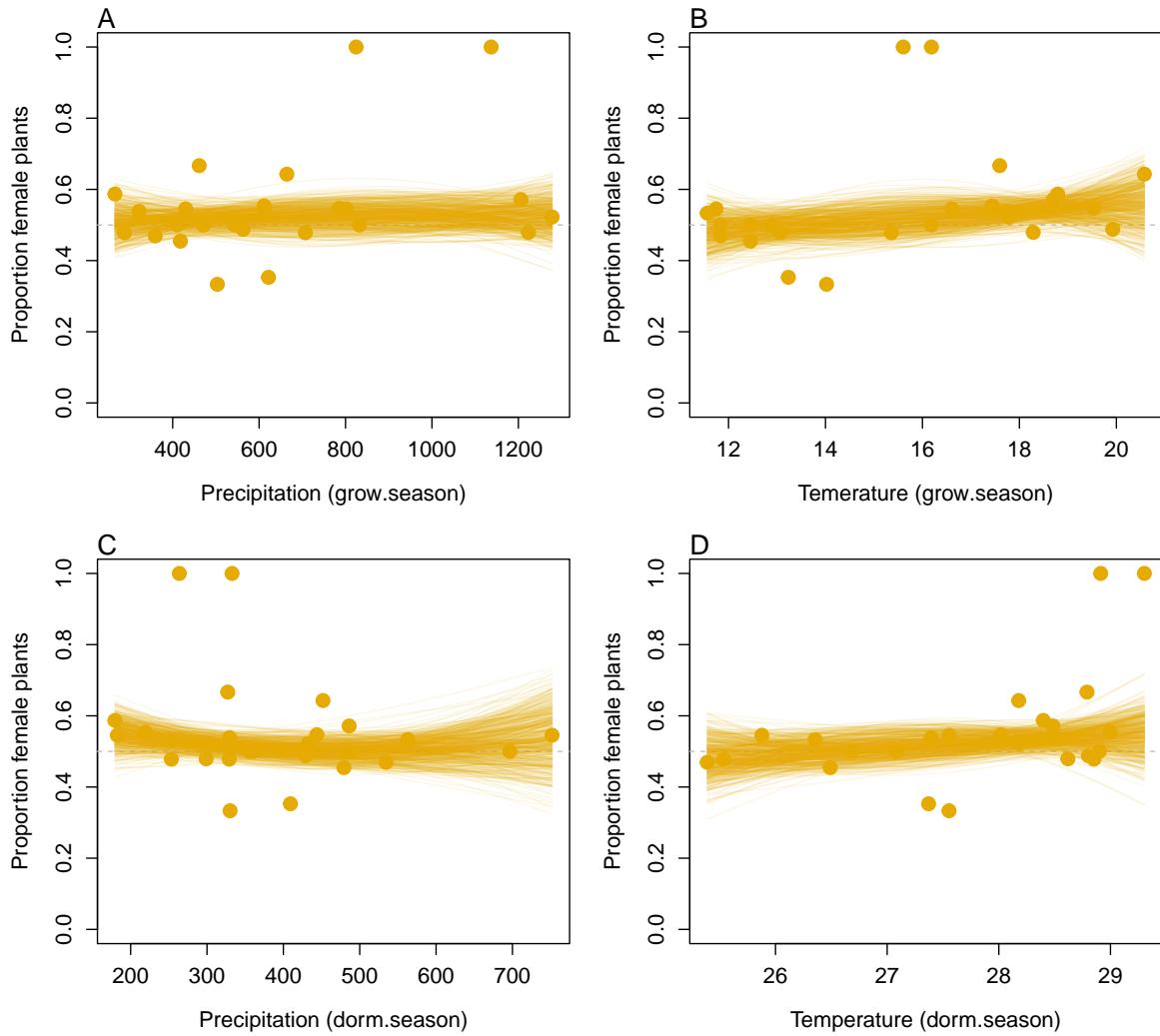
**Figure S-14:** Climate change favors range shift toward the North edge of the current range. (A) Past, (B) Current, (C and D) Future predicted range shift based on the predicted probabilities of self- sustaining populations,  $\Pr(\lambda > 1)$ , using the two-sex model that incorporates sex- specific 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.



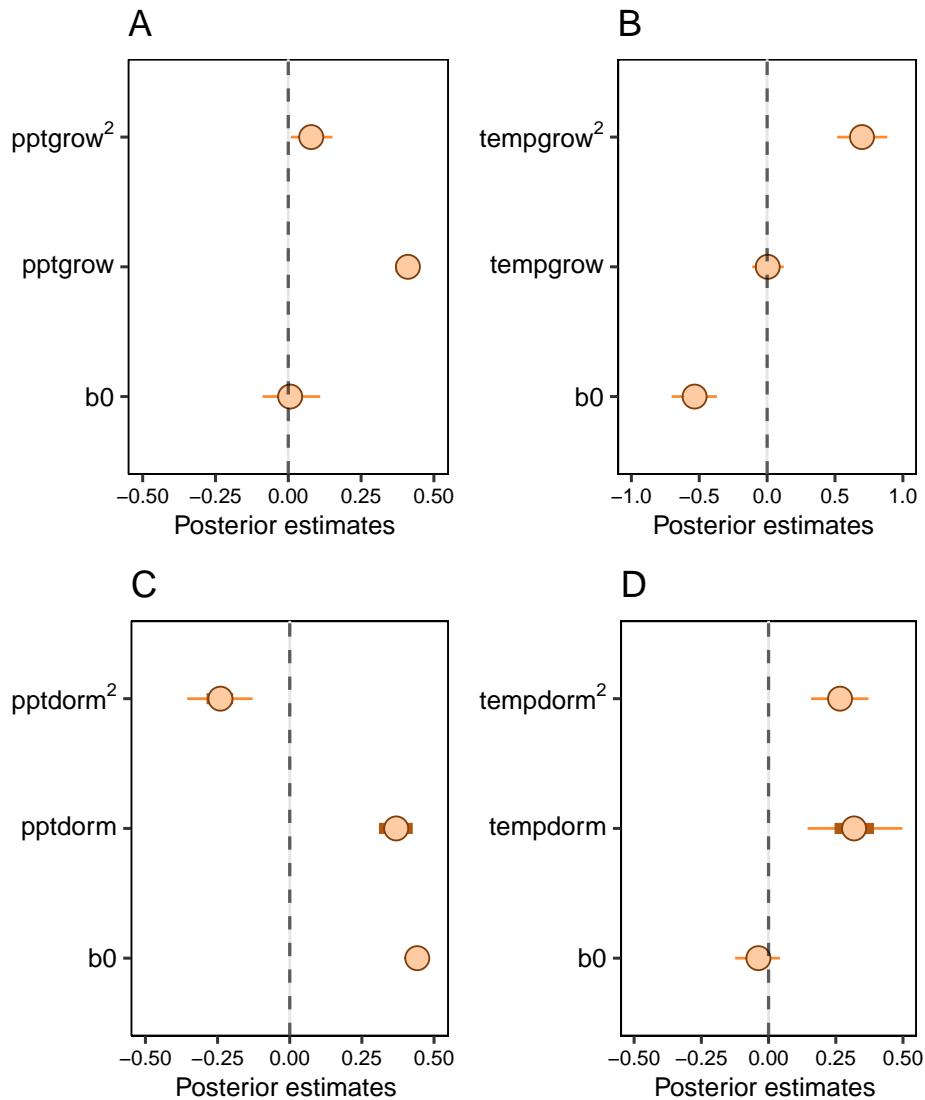
**Figure S-15:** Climate change favors range shift toward the North edge of the current range. (A) Past, (B) Current, (C and D) Future predicted range shift based on the predicted probabilities of self- sustaining populations,  $\text{Pr}(\lambda > 1)$ , using the two-sex model that incorporates sex- specific demographic responses to climate with sex ratio dependent seed fertilization. (E) Past, (F) Current, (G and H) Future predicted range shift based on the predicted probabilities of self- sustaining populations,  $\text{Pr}(\lambda > 1)$ , using the female dominant model. Future projections were based on the ACCESS model. The black dots on panel B and F indicate all known presence points collected from GBIF from 1990 to 2019, which corresponds to the current condition in our prediction. The occurrences of GBIFs are distributed in with higher population fitness habitat  $\text{Pr}(\lambda > 1)$ , confirming that our study approach can reasonably predict range shifts.



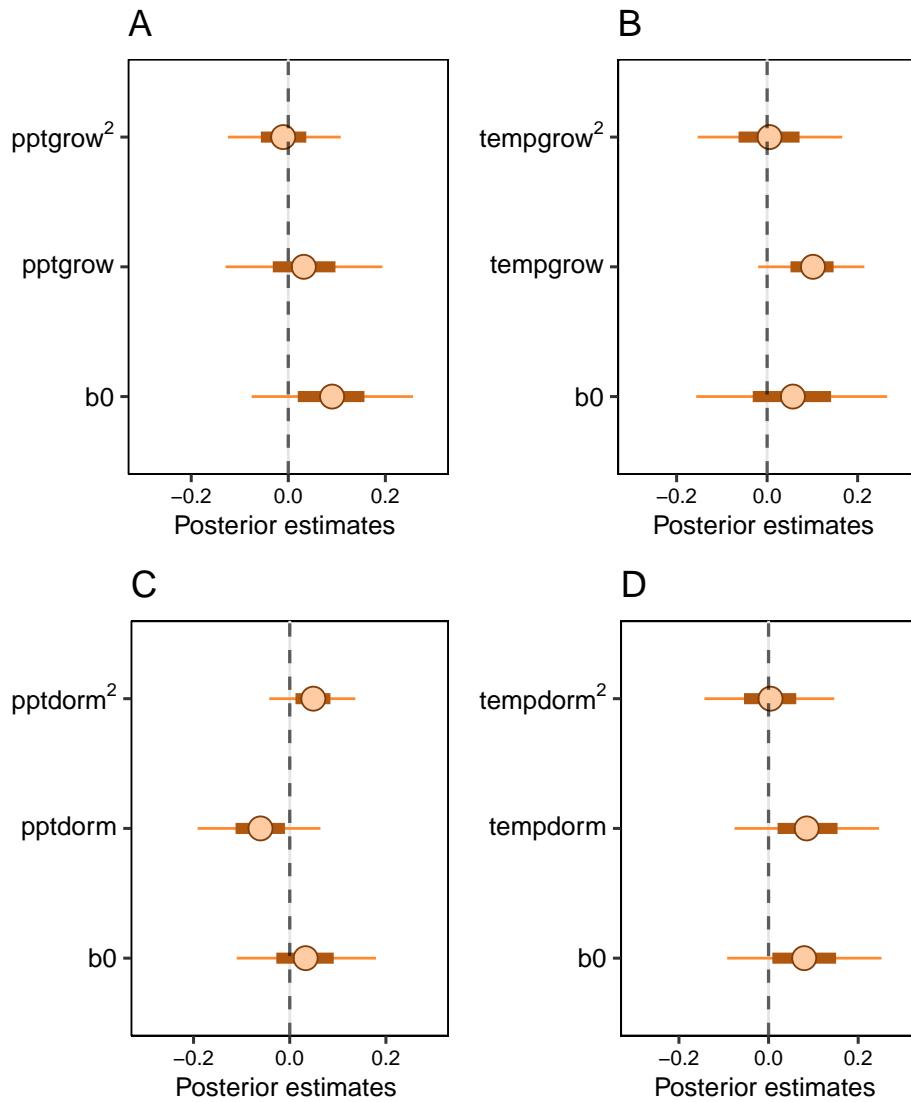
**Figure S-16:** Climate change favors range shift toward the North edge of the current range. (A) Past, (B) Current, (C and D) Future predicted range shift based on the predicted probabilities of self- sustaining populations,  $\Pr(\lambda > 1)$ , using the two-sex model that incorporates sex- specific demographic responses to climate with sex ratio dependent seed fertilization. (E) Past, (F) Current, (G and H) Future predicted range shift based on the predicted probabilities of self- sustaining populations,  $\Pr(\lambda > 1)$ , using the female dominant model. Future projections were based on the MIROC5 model. The black dots on panel B and F indicate all known presence points collected from GBIF from 1990 to 2019, which corresponds to the current condition in our prediction. The occurrences of GBIFs are distributed in with higher population fitness habitat  $\Pr(\lambda > 1)$ , confirming that our study approach can reasonably predict range shifts.



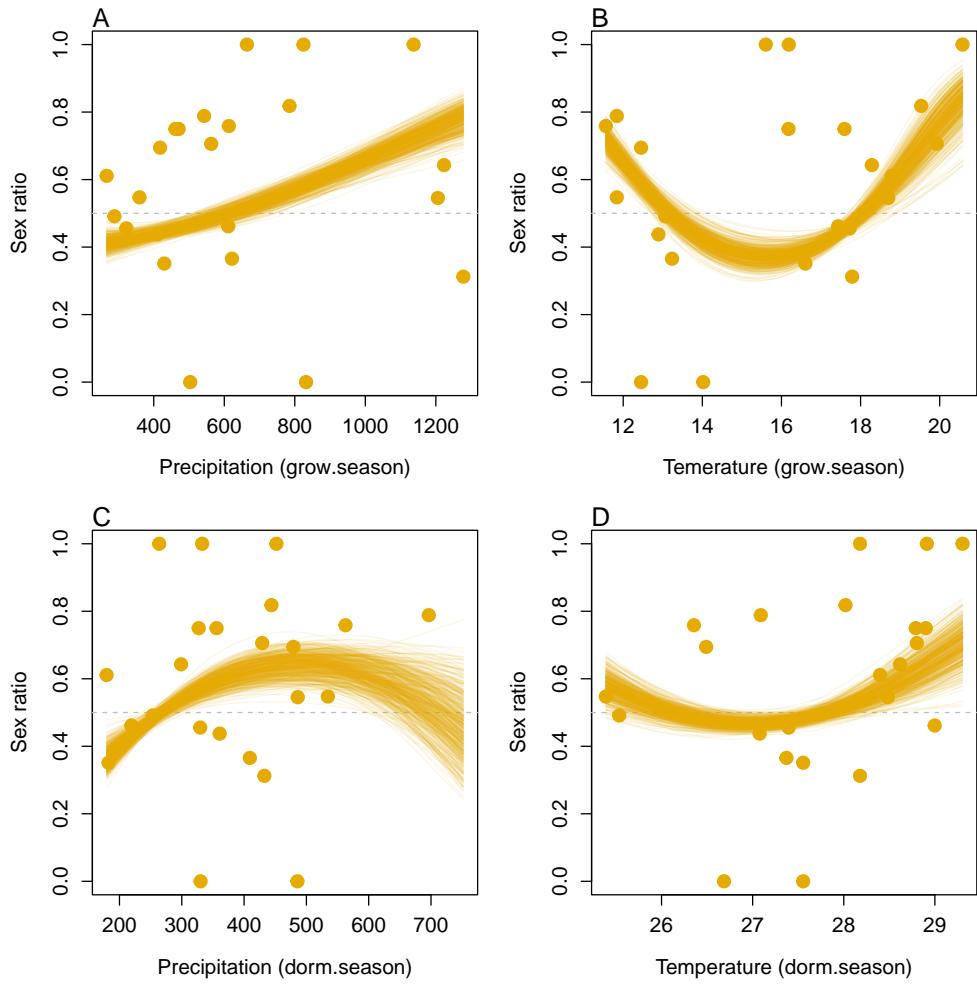
**Figure S-17: Variation in sex-ratio accross climate gradient.** (A, B) Proportion of plants that were females across precipitation and temperature of the growing season; (C, D) Proportion of plants that were females across precipitation and temperature of the dormant season. Statistical results are shown in Fig. S-19.



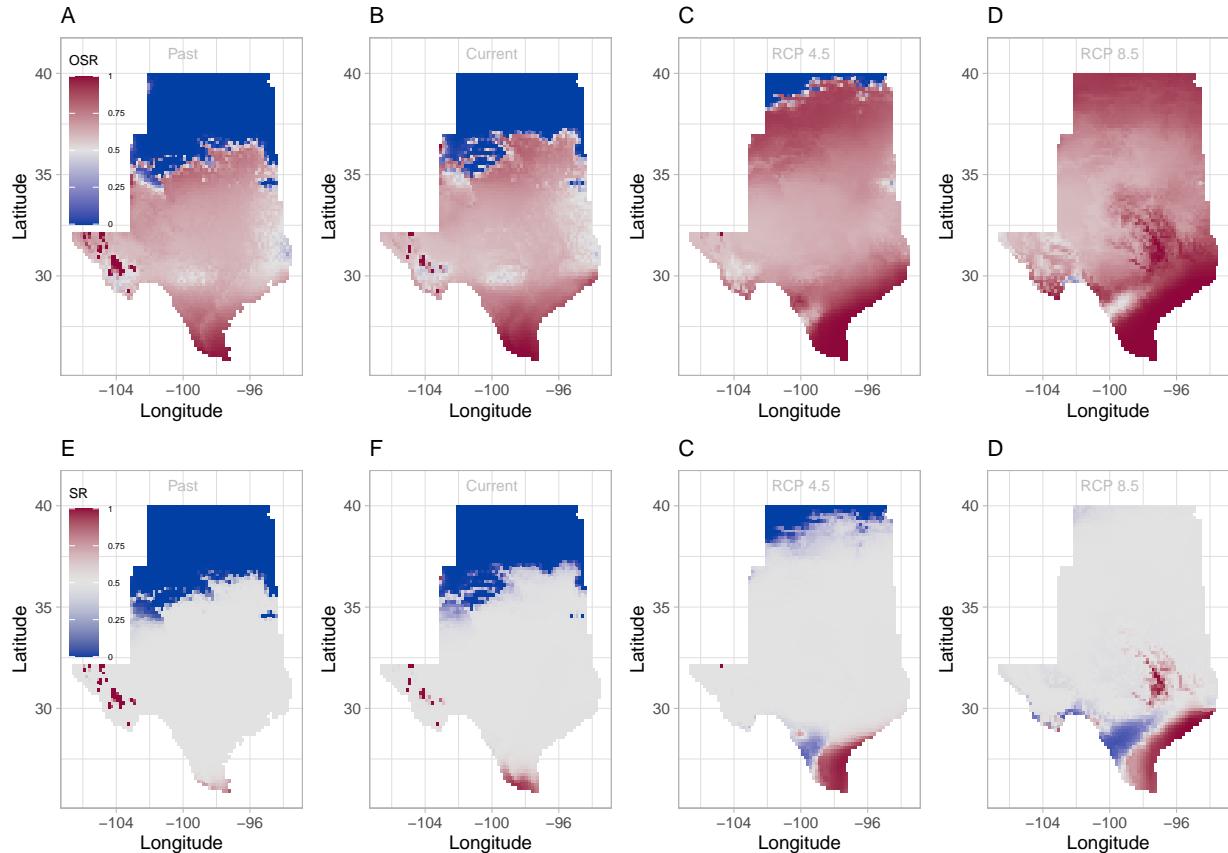
**Figure S-18:** Mean parameter values and 95% credible intervals of the posterior probability distributions. pptgrow is the precipitation of growing season, Tempgrow is the temperature of growing season, pptdorm is the temperature of dormant season, Tempdorm is the temperature of dormant season.



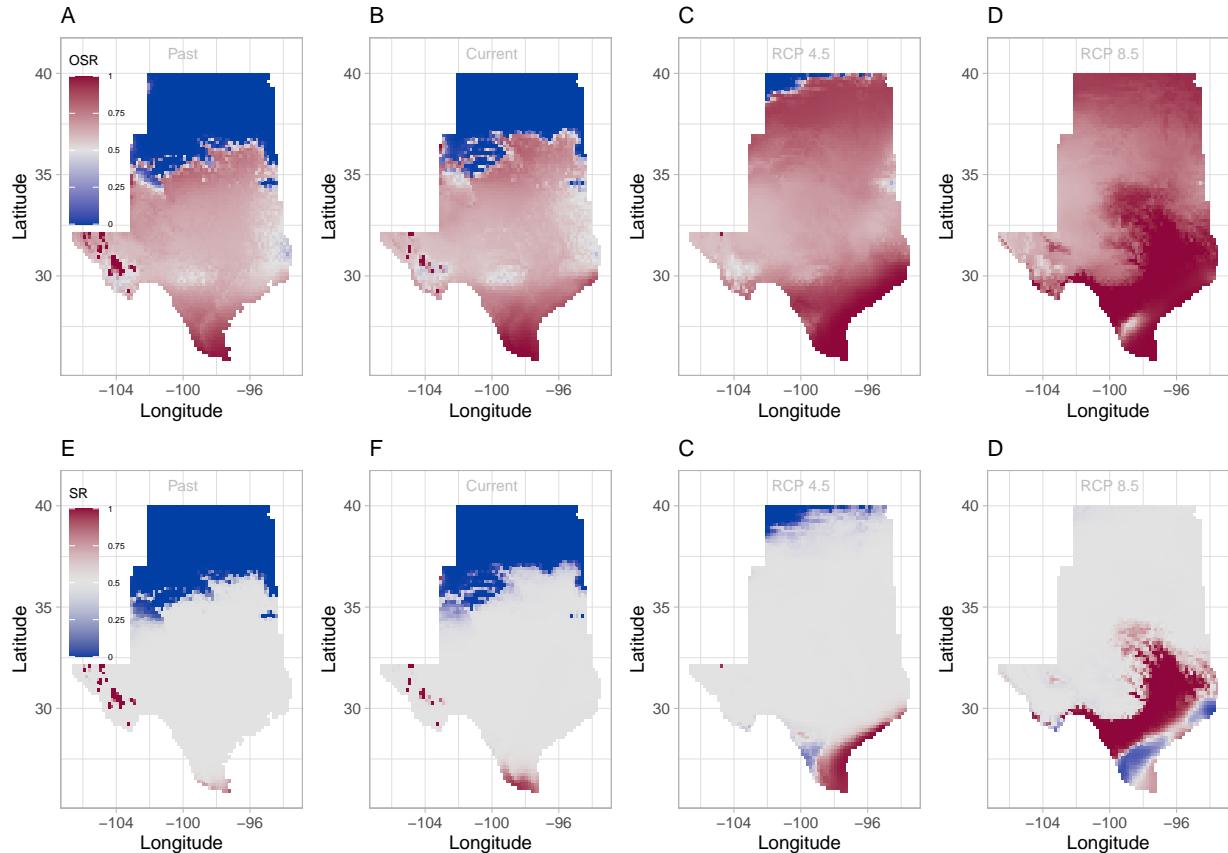
**Figure S-19:** Mean parameter values and 95% credible intervals of the posterior probability distributions. pptgrow is the precipitation of growing season, Tempgrow is the temperature of growing season, pptdorm is the temperature of dormant season, Tempdorm is the temperature of dormant season.



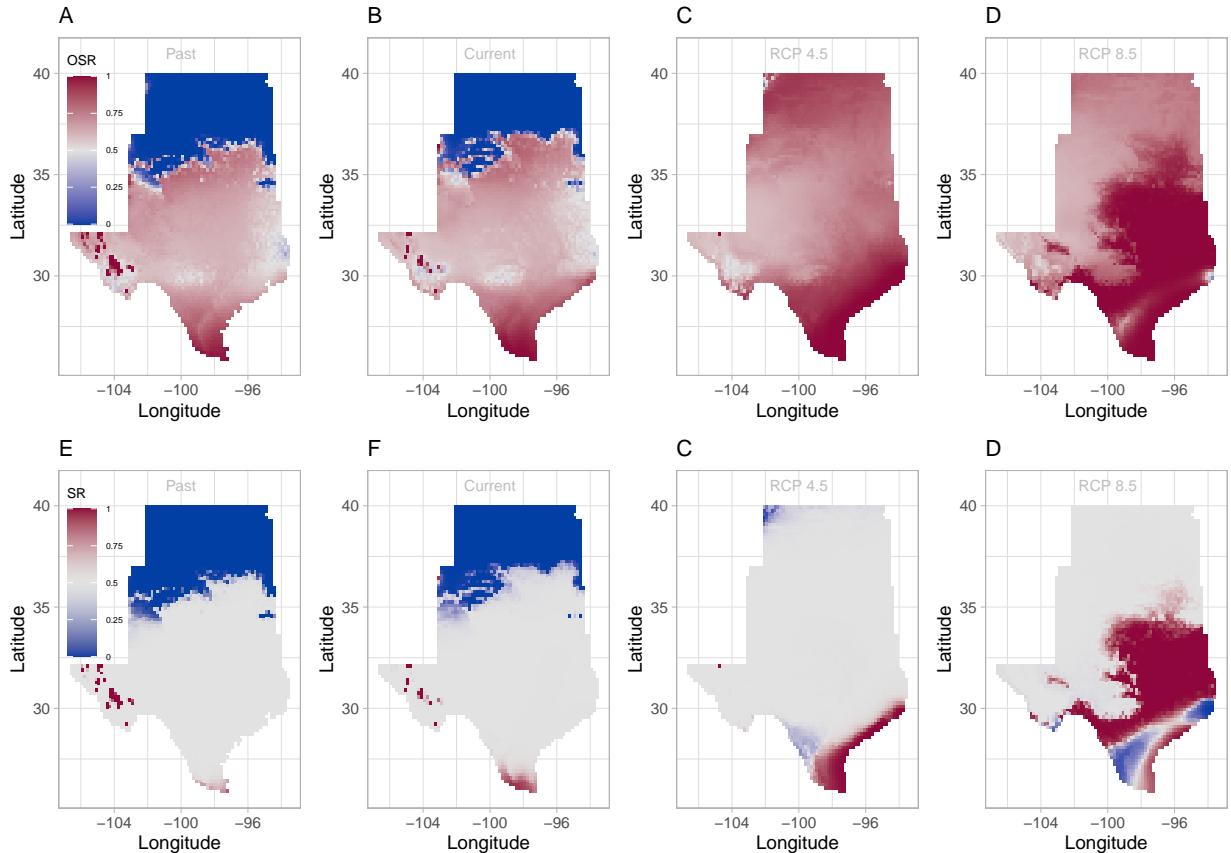
**Figure S-20: Significant sex ratio response across climate gradient.** (A, B) Proportion of panicles that were females across precipitation and temperature of the growing season; (C, D) Proportion of of panicles that were females across precipitation and temperature of the dormant season. Statistical results are shown in Fig. S-18.



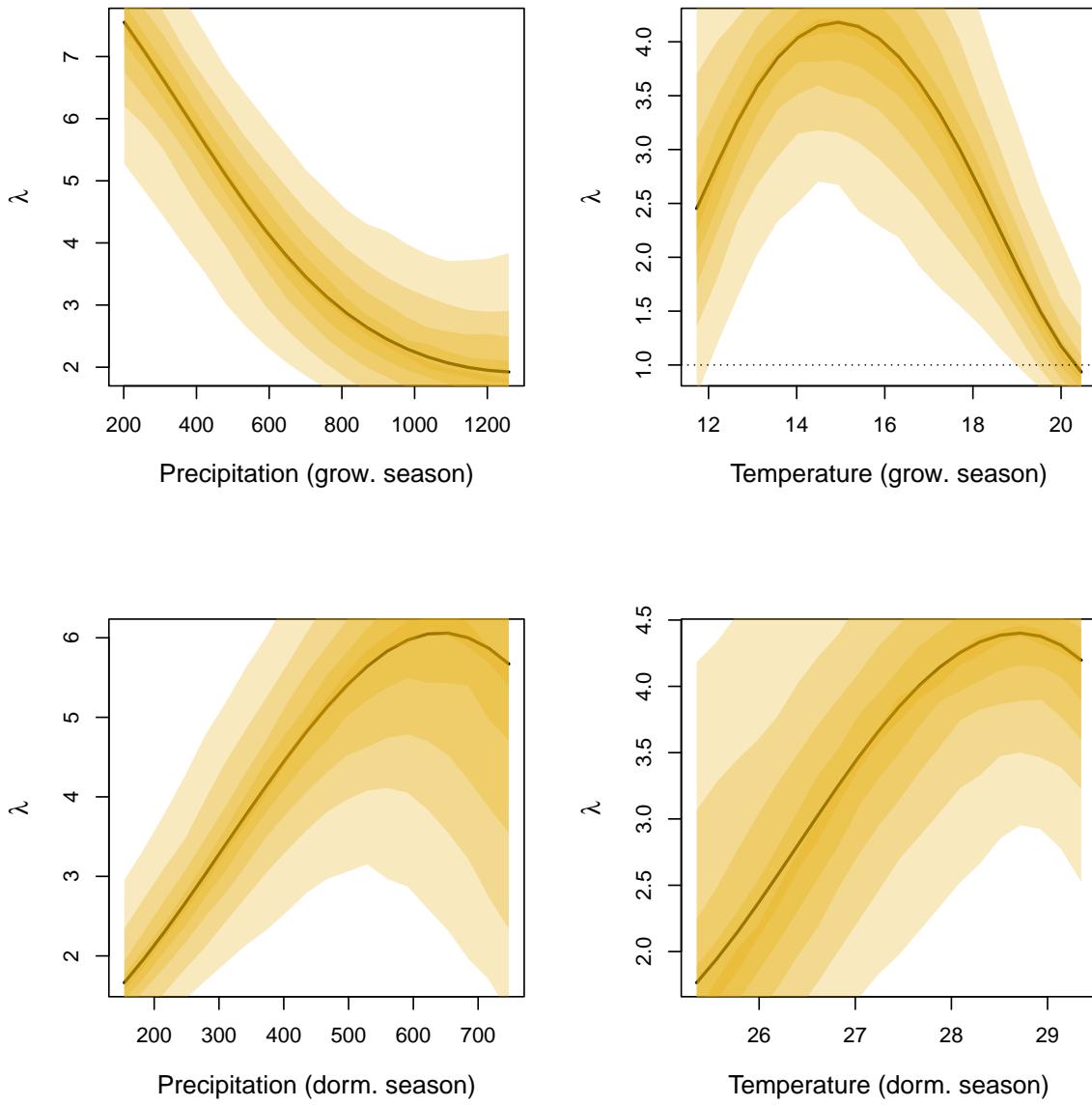
**Figure S-21:** Climate change favors range shift toward the North edge of the current range. (A) Past, (B) Current, (C and D) Future predicted range shift based on the predicted probabilities of self- sustaining populations,  $\Pr(\lambda > 1)$ , using the two-sex model that incorporates sex- specific 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 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-22:** Climate change favors range shift toward the North edge of the current range. (A) Past, (B) Current, (C and D) Future predicted range shift based on the predicted probabilities of self-sustaining populations,  $\text{Pr}(\lambda > 1)$ , using the two-sex model that incorporates sex-specific demographic responses to climate with sex ratio dependent seed fertilization. (E) Past, (F) Current, (G and H) Future predicted range shift based on the predicted probabilities of self-sustaining populations,  $\text{Pr}(\lambda > 1)$ , using the female dominant model. Future projections were based on the ACCESS model. The black dots on panel B and F indicate all known presence points collected from GBIF from 1990 to 2019, which corresponds to the current condition in our prediction. The occurrences of GBIFs are distributed in with higher population fitness habitat  $\text{Pr}(\lambda > 1)$ , confirming that our study approach can reasonably predict range shifts.



**Figure S-23:** Climate change favors range shift toward the North edge of the current range. (A) Past, (B) Current, (C and D) Future predicted range shift based on the predicted probabilities of self- sustaining populations,  $\Pr(\lambda > 1)$ , using the two-sex model that incorporates sex- specific demographic responses to climate with sex ratio dependent seed fertilization. (E) Past, (F) Current, (G and H) Future predicted range shift based on the predicted probabilities of self- sustaining populations,  $\Pr(\lambda > 1)$ , using the female dominant model. Future projections were based on the MIROC5 model. The black dots on panel B and F indicate all known presence points collected from GBIF from 1990 to 2019, which corresponds to the current condition in our prediction. The occurrences of GBIFs are distributed in with higher population fitness habitat  $\Pr(\lambda > 1)$  , confirming that our study approach can reasonably predict range shifts.



**Figure S-24:** Population growth rate ( $\lambda$ ) as a function of seasonal climate (2015-2017), predicted by the two-sex matrix projection model that incorporates sex-specific demographic responses to climate with sex ratio-dependent seed fertilization. We show the mean posterior distribution of  $\lambda$  in solid lines, and the 5, 25, 50, 75, and 95% percentiles of parameter uncertainty in shaded gold color. The dashed horizontal line indicates the limit of population viability ( $\lambda = 1$ )

583 **S.2 Supporting Methods**

584 **Sex ratio experiment**

585 To estimate the probability of seed viability, the germination rate and the effect of sex-ratio  
586 variation on female reproductive success, we conducted a sex-ratio experiment at one site  
587 near the center of the range to estimate the effect of sex-ratio variation on female reproductive  
588 success. The details of the experiment are provided in Compagnoni et al. (2017) and Miller  
589 and Compagnoni (2022b). Here we provide a summary of the experiment. We established  
590 124 experimental populations in plots measuring 0.4 × 0.4m and separated by at least 15m  
591 from each other. We varied population density (1-48 plants/plot) and sex ratio (0%-100%  
592 female) across the experimental populations, and we replicated 34 combinations of density  
593 and sex ratio. We collected panicles from a subset of females in each plot and recorded the  
594 number of seeds in each panicle. We assessed reproductive success (seeds fertilized) using  
595 greenhouse-based germination and trazolium-based seed viability assays. Seed viability was  
596 modeled with a binomial distribution where the probability of viability ( $v$ ) was given by:

597 
$$v = v_0 * (1 - OSR^\alpha) \quad (\text{S.1})$$

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