

# 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 (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>.

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**Abstract:**

**Main Text:**

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**Figures:**

**Tables:**

**References:**

## <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  
<sup>4</sup> in population biology, including those used to forecast biodiversity responses to climate  
<sup>5</sup> change, ignore the complication of sex structure. For dioecious species, it is unclear how  
<sup>6</sup> commonly unique climate sensitivities of females and males could influence projections  
<sup>7</sup> for species-level responses to climate change. We developed demographic models of range  
<sup>8</sup> limitation, parameterized from geographically distributed common garden experiments  
<sup>9</sup> with females and males of a dioecious grass species (*Poa arachnifera*) throughout and beyond  
<sup>10</sup> its range in the south-central U.S. Female-dominant and two-sex model versions of the  
<sup>11</sup> demographic model both predict that future climate change will alter population viability  
<sup>12</sup> and will induce latitudinal niche extension beyond current northern limits. However, the  
<sup>13</sup> magnitude of niche shift was overestimated by the female-dominant model, because females  
<sup>14</sup> have broader temperature tolerance than males and become mate-limited under female-biased  
<sup>15</sup> sex ratios<sup>1</sup>. Explicitly account for both sexes could enhance population viability forecasts  
<sup>16</sup> and conservation planning for dioecious species in response to climate change.

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<sup>1</sup>Not sure yet if this is true but we need some sort of biological rationale to accompany this result.

## <sup>17</sup> Introduction

<sup>18</sup> Rising temperatures and extreme drought events associated with global climate change are  
<sup>19</sup> leading to increased concern about how species will become redistributed across the globe  
<sup>20</sup> under future climate conditions (Bertrand et al., 2011; Gamelon et al., 2017; Smith et al., 2024).  
<sup>21</sup> Dioecious species (most animals and ca. 7% of plant species) might be particularly vulnerable  
<sup>22</sup> to the influence of climate change because they often display skewed sex ratios that are  
<sup>23</sup> generated or reinforced by sexual niche differentiation (distinct responses of females and males  
<sup>24</sup> to shared climate drivers) (Tognetti, 2012). Accounting for such a niche differentiation within  
<sup>25</sup> a population is a long-standing challenge in accurately predicting which sex will successfully  
<sup>26</sup> track environmental change and how this will impact population viability and range shifts  
<sup>27</sup> (Gissi et al., 2023; Jones et al., 1999). The vast majority of theory and models in population  
<sup>28</sup> biology, including those used to forecast biodiversity responses to climate change, **ignore the**  
<sup>29</sup> **complication of sex structure**<sup>2</sup> (Ellis et al., 2017; Gissi et al., 2024; Pottier et al., 2021). Traditional  
<sup>30</sup> approaches in population biology instead focus exclusively on females, assuming that males  
<sup>31</sup> are in sufficient supply as to never limit female fertility (Miller and Inouye, 2011). As a  
<sup>32</sup> result, forecasts of colonization-extinction dynamics for dioecious species under future climate  
<sup>33</sup> change that explicitly account for females, males, and their inter-dependence are limited.

<sup>34</sup> Species's range limits, when not driven by dispersal limitation, should generally reflect  
<sup>35</sup> the limits of the ecological niche (Lee-Yaw et al., 2016). Niches and geographic ranges are  
<sup>36</sup> often limited by climatic factors including temperature and precipitation (Sexton et al., 2009).  
<sup>37</sup> Therefore, any substantial changes in the magnitude of these climatic factors in a given location  
<sup>38</sup> across the range could impact population viability, with implications for range expansions  
<sup>39</sup> or contractions based on which regions become more or less suitable (Davis and Shaw,  
<sup>40</sup> 2001; Pease et al., 1989). Forecasting range shifts for dioecious species is complicated by the  
<sup>41</sup> potential for each sex to respond differently to climate variation (Hultine et al., 2016; Morrison  
<sup>42</sup> et al., 2016; Pottier et al., 2021). Populations in which males are rare under current climatic  
<sup>43</sup> conditions could experience low reproductive success due to sperm or pollen limitation that  
<sup>44</sup> may lead to population decline in response to climate change that disproportionately favors  
<sup>45</sup> females (Eberhart-Phillips et al., 2017). In contrast, climate change could expand male habitat  
<sup>46</sup> suitability (e.g. upslope movement), which might increases seed set for pollen-limited females  
<sup>47</sup> and favor range expansion (Petry et al., 2016). Although the response of species to climate  
<sup>48</sup> warming is an urgent and active area of research, few studies have disentangled the interaction

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<sup>2</sup>*It is unclear how you are citing these studies. Are they examples of ignoring sex structure? Or examples of accounting for sex structure?*

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

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

72 In this study, we used a mechanistic approach, combining geographically-distributed  
73 field experiments, Bayesian statistical modeling, and two-sex population projection modeling,  
74 to understand the demographic response of dioecious species to climate change and its  
75 implications for past, present, and future range dynamics. Our work focused on the dioecious  
76 grass species Texas bluegrass (*Poa arachnifera*), which is distributed along environmental  
77 gradients in the south-central U.S. corresponding to variation in temperature across latitude  
78 and precipitation across longitude.<sup>4</sup> Our previous study showed that, despite a differentiation  
79 of climatic niche between sexes, the female niche mattered the most in driving the  
80 environmental limits of population viability across longitude (Miller and Compagnoni, 2022b).  
81 However, that study used a single proxy variable (longitude) to represent environmental

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<sup>3</sup>It is noticeable that you never mention SDMs as a point of contrast with demographic models. Are you intentionally avoiding that?

<sup>4</sup>I think it would be good to add some context about climate change in this study region – what has already occurred and what is projected.

82 variation related to aridity. Developing a rigorous forecast for the implications of future  
83 climate change requires that we transition from climate-implicit to climate-explicit treatment  
84 of environmental drivers as we do here. Here, we asked four questions:

- 85 1. What are the sex-specific vital rate responses to variation in temperature and precipitation  
86 across the species' range ?
- 87 2. How do sex-specific vital rates combine to determine the influence of climate variation  
88 on population growth rate ( $\lambda$ ) ?
- 89 3. What are the historical and projected dynamics of the Texas bluegrass geographic niche  
90 and how does accounting for sex structure modify these predictions?
- 91 4. Which vital rates and climate covariates most strongly determine past and future changes  
92 in the geographic niche?

## 93 Materials and methods

### 94 Study species

95 Texas bluegrass (*Poa arachnifera*) is a dioecious perennial, summer-dormant cool-season (C3)  
96 grass that occurs in the south-central U.S. (Texas, Oklahoma, and southern Kansas) (Hitchcock,  
97 1971)<sup>5</sup>. Latitudinal limits of the Texas bluegrass distribution span # to # in mean annual  
98 temperature, and longitudinal limits span # to # in annual precipitation. Texas bluegrass  
99 grows between October and May (growing season), with onset of dormancy often from June  
100 to September (dormant season) (Kindiger, 2004).

101 Biological sex in Texas bluegrass is genetically based and the birth (seed) sex ratio  
102 is 1:1 (CITE). Females and males are morphologically indistinguishable except for their  
103 inflorescences. Flowering occurs in May and the species is wind pollinated (Hitchcock,  
104 1971). Surveys of # natural populations throughout the species' distribution indicated that  
105 operational sex ratio (the female fraction of flowering plants) ranged from # to # with a mean  
106 of # (Miller and Compagnoni, 2022b).

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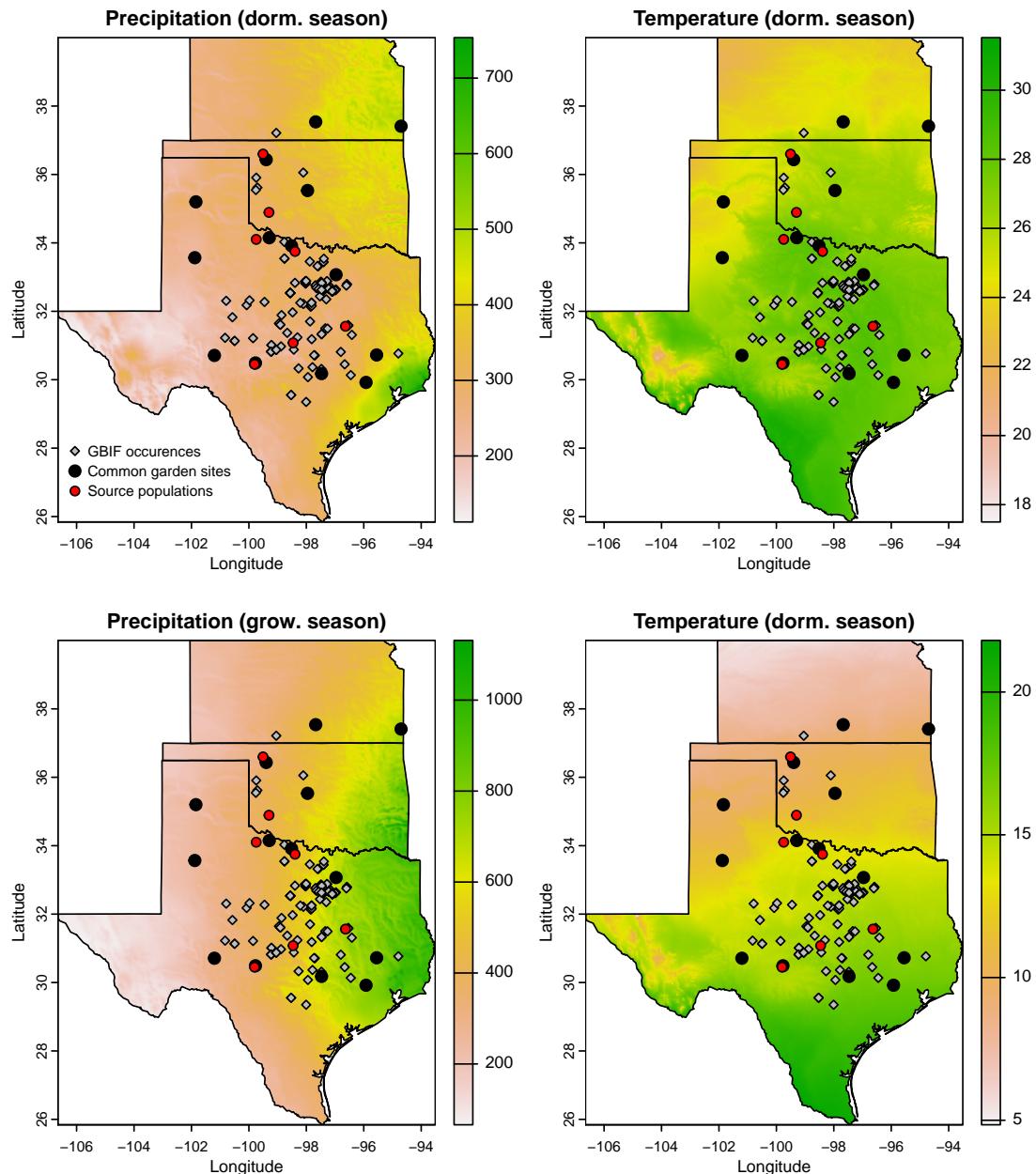
<sup>5</sup>I would reference the map figure (current Fig. 1) here. I also suggest either adding the GBIF records to this figure or adding the county occurrences as in the Am Nat paper, because it is important for readers to see the natural distribution early in the paper. The natural population surveys can be cut from this figure because you don't say anything about them and you do not use the data here. Alternatively, there may be value in re-analyzing the sex ratio surveys with your climate covariates. Fig 1 also needs to be updated with labels and units on the climate variable color bars. I recommend putting panels A-C and B-D on the same climate scale.

107 **Common garden experiment**

108 We set up a common garden experiment throughout and beyond the range of Texas bluegrass  
109 to quantify sex-specific demographic responses to climate. **The novelty of this study lies**  
110 **in the fact that we use a precise climate variable to build a mechanistic model to forecast**  
111 **the response of species to climate change.**<sup>6</sup> Details of the experimental design are provided  
112 in Miller and Compagnoni (2022b); we provide a brief overview here. The experiment was  
113 installed at 14 sites throughout and, in some cases, beyond the species' natural range (Fig.1).  
114 At each site, we established 14 blocks. For each block we planted three female and three male  
115 individuals that were clonally propagated from females and males from eight natural source  
116 populations (Fig.1); because sex is genetically-based, clones never deviated from their expected  
117 sex. The experiment was established in November 2013 and was censused in May of 2014,  
118 2015, and 2016. At each census, we collected individual demographic data including survival  
119 (alive or dead), size (number of tillers), and number of panicles (reproductive inflorescences).  
120 For the analyses that follow, we focus on the 2014-15 and 2015-16 transitions years, since the  
121 start of the experiment did not include the full 2013-14 transition year.

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<sup>6</sup>*This is not relevant to the description of the experiment.*



**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.** (A) Precipitation of the dormant season in mm , (B) temperature of the dormant season in °C , (C) precipitation of the growing season in mm , (D) temperature of the growing season in °C . We surveyed 22 natural populations (grey diamond). The common garden sites were installed on 14 sites (black circle) collected from 7 sources populations (red circle). Average temperatures along the distribution of the species tend to decrease northward as a result of the influence of latitude: lower latitudes receive more heat from the sun over the course of a year. Similarly, the average precipitation decreases eastward as a result of the influence of longitude: lower longitudes receive less precipitation over the year. See also Fig.S-1, Fig.S-2.

122 **Climatic data collection**

123 We gathered downscaled monthly temperature<sup>7</sup> and precipitation<sup>8</sup> for each site from Chelsa  
124 to describe observed climate conditions during our study period (Karger et al., 2017). These  
125 climate data were used as covariates in vital rate regressions. We aligned the climatic years to  
126 match demographic transition years (May 1 – April 30)<sup>9</sup> rather than calendar years. Based on  
127 the natural history of this summer-dormant cool-season species, we divided each transition  
128 year into dormant (June 1 through September 30) and growing (October 1 through May 31)  
129 seasons. The 2014-15 transition year was substantially wetter and cooler across the study  
130 region than 2015-16, especially during the growing season (figure<sup>10</sup>), so our study design  
131 provides both spatial and inter-annual coverage of climate variables.

132 To back-cast and forecast demographic responses to changes in climate throughout the  
133 study region, we downloaded projection data for three 30-year periods: “past” (1901-1930),  
134 “current” (1990-2019) and “future” (2070-2100). Data for these climatic periods<sup>11</sup> were  
135 downloaded from four general circulation models (GCMs) selected from the Coupled Model  
136 Intercomparison Project Phase 5 (CMIP5). The GCMs are: Model for Interdisciplinary  
137 Research on Climate (MIROC5), Australian Community Climate and Earth System Simulator  
138 (ACCESS1-3), Community Earth System Model (CESM1-BGC), Centro Euro-Mediterraneo sui  
139 Cambiamenti Climatici Climate Model (CMCC-CM). All the GCMs were downloaded from  
140 chelsa (Sanderson et al., 2015). We evaluated future climate projections from two scenarios of  
141 representative concentration pathways (RCPs): RCP4.5, an intermediate-to-pessimistic scenario  
142 assuming a radiative forcing amounting to  $4.5 \text{ W m}^{-2}$  by 2100, and RCP8.5, a pessimistic  
143 emission scenario which projects a radiative forcing of  $8.5 \text{ W m}^{-2}$  by 2100 (Schwalm et al.,  
144 2020; Thomson et al., 2011).

145 **Sex ratio experiment**

146 <sup>12</sup> We conducted a sex-ratio experiment at one site near the center of the range to estimate  
147 the effect of sex-ratio variation on female reproductive success. Details of the experiment  
148 are provided in Compagnoni et al. (2017) and Miller and Compagnoni (2022b). In short, we

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<sup>7</sup>Give units

<sup>8</sup>Give units

<sup>9</sup>I think this is not right. I think we updated the transition year to be June 1 – May 31.

<sup>10</sup>I would like to use the figure I made called site-year-weather. However, I cannot tell from this figure whether the first year was unusually wet or the second year was unusually dry – this will take looking at the climate data more broadly. I am also not sure if this figure was made before or after we changed the dates of the transition year, so it may need to be updated

<sup>11</sup>The four GCMs only refers to the future data, right?

<sup>12</sup>You say nothing about this experiment in the Results or Discussion, so in its current state this section serves no purpose in this paper.

149 established 124 experimental populations in plots measuring 0.4 x 0.4m and separated by at  
150 least 15m from each other. We chose 15m because our pilot data showed that more than 90%  
151 of wind pollination occurred within 13m. We varied population density (1-48 plants/plot)  
152 and sex ratio (0%-100% female) across the experimental populations, and we replicated 34  
153 combinations of density and sex ratio. We collected panicles from a subset of females in each  
154 plot and recorded the number of seeds in each panicle. We assessed reproductive success (seeds  
155 fertilized) using greenhouse-based germination and trazolium-based seed viability assays.

156 <sup>13</sup>We used data from the sex-ratio experiment to estimate the probability of seed viability  
157 and the germination rate. Seed viability was modeled with a binomial distribution where  
158 the probability of viability ( $v$ ) was given by:

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

160 where  $OSR$  is the **operational sex ratio**<sup>14</sup> (proportion of panicles that were female) in the  
161 experimental populations. The properties of the above function is supported by our previous  
162 work (Compagnoni et al., 2017). Here, seed viability is maximized at  $v_0$  as  $OSR$  approaches  
163 zero (strongly male-biased) and goes to zero as  $OSR$  approaches 1 (strongly female-biased).  
164 Parameter  $\alpha$  controls how viability declines with increasing female bias. <sup>15</sup>

165 We used a binomial distribution to model the germination data from greenhouse trials.  
166 Given that germination was conditional on seed viability, the probability of success was given  
167 by the product  $v * g$ , where  $v$  is a function of  $OSR$  (Eq. 1) and  $g$  is assumed to be constant.<sup>16</sup>

## 168 Sex specific demographic responses to climate

169 <sup>17</sup> We used individual level measurements of survival, growth (number of tillers), flowering,  
170 number of panicles to independently develop Bayesian mixed effect models describing how

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<sup>13</sup>I think the data analysis methods could be better organized. Here you describe the experimental methods and data analysis in the same section, but for the common garden experiment you split them.

<sup>14</sup>I tried to add a little about this, but generally I think the concept of the operational sex ratio is under-developed throughout the manuscript. It is the main way through which sex-specific climate responses can feed back to influence lambda, so it warrants greater attention.

<sup>15</sup>Throughout the methods I recognize a lot of the text as coming directly from the Am Nat paper. I strongly recommend that you diversify your language and never use published text verbatim. Many journals use plagiarism detection software and this will raise a red flag, even if we are plagiarizing ourselves.

<sup>16</sup>You provide no information about how this model was fit. This echoes my previous comment that the data analysis should be better organized.

<sup>17</sup>This section needs to be more carefully edited, which I have not done. There is redundancy between the two paragraphs and most importantly, there is not enough biological rationale for the model that you fit. You do not describe which interactions you include, which you do not include, and why. This is a very complex model – 24 fixed-effect coefficients! – and it will get skepticism from reviewers. You need to justify why this is the right model, especially since you do not have any model selection or variable selection.

171 each vital rate varies as a function of sex, size, and four climate covariates (precipitation and  
 172 temperature of growing and dormant seasons). We fit vital rate models with second-degree  
 173 polynomial functions for the influence of climate. We included a second-degree polynomial  
 174 because we expected that climate variables would affect vital rates through a hump-shaped  
 175 relationship.

176 We centered and standardized all climatic predictors to facilitate model convergence.  
 177 Size (number of tillers) was on a natural logarithm scale. We included site, source, and  
 178 block as random effects. All the vital rate models used the same **linear predictor**<sup>18</sup> for the  
 179 expected value ( $\mu$ ) (Eq. 2). However, we applied a different link function ( $f(\mu)$ ) depending  
 180 on the distribution the vital rate. We modeled survival and flowering data with a Bernoulli  
 181 distribution. We modeled the growth (tiller number) with a zero-truncated Poisson inverse  
 182 Gaussian distribution. Fertility (panicle count) was model as zero-truncated negative binomial.

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

183 where  $\beta_0$  is the grand mean intercept,  $\beta_1$  is the size dependent slopes. *size* was on a natural log-  
 184 arithm scale.  $\beta_2 \dots \beta_{13}$  represent the climate dependent slopes.  $\beta_{14} \dots \beta_{23}$  represent the sex-climate  
 185 interaction slopes. *pptgrow* is the precipitation of the growing season (standardized to mean  
 186 zero and unit variance), *tempgrow* is the temperature of the growing season (standardized to  
 187 mean zero and unit variance), *pptdorm* is the precipitation of the dormant season (standardized  
 188 to mean zero and unit variance), *tempdorm* is the temperature of the dormant season (standard-  
 189 ized to mean zero and unit variance). The model also includes normally distributed random  
 190 effects for block-to-block variation ( $\phi \sim N(0, \sigma_{block})$ ) and source-to-source variation that is  
 191 related to the provenence of the seeds used to establish the common garden ( $\rho \sim N(0, \sigma_{source})$ ),  
 192 site to site variation ( $\nu \sim N(0, \sigma_{site})$ ). We fit survival, growth, flowering models with generic  
 193 weakly informative priors for coefficients ( $\mu = 0, \sigma = 1.5$ ) and variances ( $\gamma[0.1, 0.1]$ ). We fit  
 194 fertility model with regularizing priors for coefficients ( $\mu = 0, \sigma = 0.15$ ). We ran three chains  
 195 for 1000 samples for warmup and 4000 for interactions, with a thinning rate of 3. We accessed  
 196 the quality of the models using trace plots and predictive check graphs (Piironen and Vehtari,  
 197 2017) (Fig. S-4). To understand the effect of climate on vital rates, we got the 95 % credible

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<sup>18</sup>It is still a “linear predictor” even if it has quadratic terms.

<sup>199</sup> interval of the posterior distribution. Then we assumed that there is 95 % probability that the  
<sup>200</sup> true (unknown) estimates would lie within that interval, given the evidence provided by the  
<sup>201</sup> observed data for each vital rate. All models were fit in Stan (Stan Development Team, 2023).

## <sup>202</sup> Two-sex and climate-dependent matrix projection model

<sup>203</sup> To understand the effect of climate on population growth rate incorporating both female  
<sup>204</sup> and male climate responses, we used the climate-dependent vital rate regressions to build  
<sup>205</sup> a matrix projection model (MPM) structured by size (number of tillers) and sex Let  $F_{x,z,t}$  and  
<sup>206</sup>  $M_{x,z,t}$  be the number of female and male plants of size  $x$  in year  $t$  present at a location that  
<sup>207</sup> has  $z$  as climate<sup>19</sup>, where  $x \in \{1, 2, \dots, U\}$  and  $U$  is the maximum number of tillers a plant can  
<sup>208</sup> reach (here 95th percentile<sup>20</sup> of observed maximum size). Let  $F_t^R$  and  $M_t^R$  be new recruits,  
<sup>209</sup> which we assume do not reproduce in their first year. We assume that the parameters of  
<sup>210</sup> sex ratio-dependent mating (Eq. 1) do not vary with climate. For a pre-breeding census, the  
<sup>211</sup> expected numbers of recruits in year  $t+1$  is given by:

$$\text{212} \quad F_{t+1}^R = \sum_{x=1}^U [p^F(x,z) \cdot c^F(x,z) \cdot d \cdot v(\mathbf{F}_t, \mathbf{M}_t) \cdot m \cdot \rho] F_{x,z,t} \quad (3)$$

$$\text{213} \quad M_{t+1}^R = \sum_{x=1}^U [p^F(x,z) \cdot c^F(x,z) \cdot d \cdot v(\mathbf{F}_t, \mathbf{M}_t) \cdot m \cdot (1-\rho)] F_{x,z,t} \quad (4)$$

<sup>214</sup> where  $p^F$  and  $c^F$  are flowering probability and panicle production for females of size  $x$ ,  $d$   
<sup>215</sup> is the number of seeds per female panicle,  $v$  is the probability that a seed is fertilized,  $m$  is  
<sup>216</sup> the probability that a fertilized seed germinates, and  $\rho$  is the primary sex ratio (proportion  
<sup>217</sup> of recruits that are female),  $z$  is the climate. Seed fertilization depends on the OSR of panicles  
<sup>218</sup> (following Eq. 1) which was derived from the  $U \times 1$  vectors of population structure  $\mathbf{F}_t$  and  $\mathbf{M}_t$ :

$$\text{219} \quad v(\mathbf{F}_t, \mathbf{M}_t) = v_0 * \left[ 1 - \left( \frac{\sum_{x=1}^U p^F(x,z) c^F(x,z) F_{x,z,t}}{\sum_{x=1}^U p^F(x,z) c^F(x,z) F_{x,z,t} + p^M(x,z) c^M(x,z) M_{x,z,t}} \right)^\alpha \right] \quad (5)$$

<sup>220</sup> Thus, the dynamics of the size-structured component of the population are given by:

$$\text{221} \quad F_{y,t+1} = [\sigma \cdot g^F(y, x=1, z)] F_t^R + \sum_{x=1}^U [s^F(x,z) \cdot g^F(y, x, z)] F_{x,z,t} \quad (6)$$

$$\text{222} \quad M_{y,t+1} = [\sigma \cdot g^M(y, x=1, z)] M_t^R + \sum_{x=1}^U [s^M(x,z) \cdot g^M(y, x, z)] M_{x,z,t} \quad (7)$$

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<sup>19</sup>The variable  $z$  is not used consistently or correctly. Notice in eq:viabMPM and eq:dynamics you use  $z$  in the RHS but not the LHS. CLimate is not a state variable.

<sup>20</sup>I remember you experimented with this. Is this the actual percentile you used or was this text from the Am Nat paper?

223 In the two formula above, the first term indicates seedlings that survived their first year and en-  
 224 ter the size distribution of established plants. Instead of using *P. arachnifera* survival probability,  
 225 we used the seedling survival probability ( $\sigma$ ) from demographic studies of the hermaphroditic  
 226 congener *Poa autumnalis* in east Texas (T.E.X. Miller and J.A. Rudgers, *unpublished data*), and we  
 227 assume this probability was constant across sexes and climatic variables. We did this because  
 228 we had little information on the early life cycle transitions of greenhouse-raised transplants.  
 229 We also assume that  $g(y, x = 1)$  is the probability that a surviving seedlings reach size  $y$ ,  
 230 the expected future size of 1-tiller plants from the transplant experiment. The second term  
 231 represents survival and size transition of established plants from the previous year, where  
 232  $s$  and  $g$  give the probabilities of surviving at size  $x$  and growing from sizes  $x$  to  $y$ , respectively,  
 233 and superscripts indicate that these functions may be unique to females ( $F$ ) and males ( $M$ ).

234 Since the two-sex MPM is nonlinear (vital rates affect and are affected by population  
 235 structure) we estimated the asymptotic geometric growth rate ( $\lambda$ ) by numerical simulation,  
 236 and repeated this across a range of climate<sup>21</sup>.<sup>22</sup>

## 237 Life Table Response Experiments

238 To identify which aspect of climate is most important for population viability, we used a  
 239 "random design" Life Table Response Experiment (LTRE). We used the RandomForest package  
 240 to fit a regression model with seasonal climate<sup>23</sup> (here  $\theta$ ) as predictors and  $\lambda$  as response  
 241 (Ellner et al., 2016; Liaw et al., 2002). The LTRE approximates the variation in  $\lambda$  in response  
 242 to seasonal climate covariates and their interaction (Caswell, 2000; Hernández et al., 2023):

$$243 \quad Var(\lambda_c) \approx \sum_{i=-1}^n \sum_{j=1}^n Cov(\theta_i, \theta_j, \theta_{ij}) + Var(\epsilon) \quad (8)$$

244 where,  $\theta_i$ ,  $\theta_j$ ,  $\theta_{ij}$  represent respectively the fitted regression slope for the covariates of the dor-  
 245 mant season, j the covariates of the growing season and ij the covariates of their interactions.<sup>24</sup>

246 To identify the mechanism by which climate affects population growth rate for each sex,  
 247 we decomposed the effect of each climate variable on population growth rate ( $\lambda$ ) into contri-  
 248 bution arising from the effect on each stage-specific vital rate<sup>25</sup> (Caswell, 2000). At this end we

<sup>21</sup>Vague - needs more detail.

<sup>22</sup>Too much of this section is familiar to me from the Am Nat paper. I suggest you write this in your own voice. You also should provide an explanation for the female-dominant model.

<sup>23</sup>It is unclear what variation in climate you are sampling over.

<sup>24</sup>But you also have second-order terms, and I am not sure whether and how this LTRE accounts for that. Also, what is n here? Why does the summation over i start at -1? And why do you show only two variables, since you have four?

<sup>25</sup>I don't know what you mean by "stage-specific"

249 used another LTRE with a "regression design".<sup>26</sup> The LTRE with a "regression design" approx-  
250 imates the change in  $\lambda$  with climate as the product of the sensitivity of  $\lambda$  to the parameters  
251 times the sensitivity of the parameters to climate, summed over all parameters (Caswell, 1989):

252

$$\frac{\partial \lambda}{\partial \text{climate}} \approx \sum_i \frac{\partial \lambda}{\partial \theta_i^F} \frac{\partial \theta_i^F}{\partial \text{climate}} + \frac{\partial \lambda}{\partial \theta_i^M} \frac{\partial \theta_i^M}{\partial \text{climate}} \quad (9)$$

253 where,  $\theta_i^F$  and  $\theta_i^M$  represent sex-specific parameters: the regression coefficients for the  
254 intercepts and slopes of size-dependent vital rate functions. Because LTRE contributions are  
255 additive, we summed across vital rates to compare the total contributions of female and male  
256 parameters.<sup>27</sup>

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

258 A species' ecological niche can be defined as the range of resources and conditions allowing  
259 its populations to self-sustained ( $\lambda > 1$ ) (Hutchinson et al., 1978; Maguire Jr, 1973). To  
260 understand the impact of climate change on species niche shifts, we estimated the probability  
261 of self-sustaining populations, which is  $\Pr(\lambda > 1)$  conditional to two environmental axes:  
262 (i) temperature and precipitation of the dormant season and (ii) temperature and precipitation  
263 of the growing season.<sup>28</sup>  $\Pr(\lambda > 1)$  was calculated using the proportion of the 300 Markov  
264 chain Monte Carlo iterations that lead to a  $\lambda > 1$  (Diez et al., 2014).<sup>29</sup>

265  $\Pr(\lambda > 1)$  was also mapped onto geographic layers of three state (Texas, Oklahoma and  
266 Kansas) to delineate past, current and future potential distribution of the species. To do so, we  
267 estimated  $\Pr(\lambda > 1)$  conditional to all climate covariates for each pixel ( $\sim 340 \text{ km}^2$ ) across the  
268 species range.<sup>30</sup> Then we add the current occurrences record of the species (1990-2019) from  
269 Global Biodiversity Information Facility (GBIF) to validate the accuracy of our prediction<sup>31</sup>  
270 Because of the amount of the computation involved in the Markov chain Monte Carlo iterations,  
271 use only 100 posterior samples to estimate  $\Pr(\lambda > 1)$  across the Texas, Oklahoma and Kansas.

<sup>26</sup>I think you need greater clarification about what different information you get out of the two LTREs, and how they relate to the motivating biological questions. I understand this, of course, but I think readers will be confused.

<sup>27</sup>I don't really understand how this LTRE works because your climate variables interact. So this should not decompose as cleanly as the equation implies.

<sup>28</sup>As a general comment, I find it difficult to follow which analyses are explicitly spatial (i.e., mapping quantities as rasters) and which are not – I think the methods can be sharpened around this.

<sup>29</sup>I suggest you bring this up much earlier, in the Intro probably. I think you under-sell the value of this approach, particularly related to accounting for uncertainty. You also need to describe which types of uncertainty are accounted for here, i.e., process error and estimation error.

<sup>30</sup>I think you did this separately for past, present, and future, and for multiple futures? Needs to be explained.

<sup>31</sup>If you actually intend this as model validation then it needs to be presented more thoroughly and analyzed more rigorously.

272 All the analyses were performed in R 4.3.1 (R Core Team, 2023) However the estimation  
273 of the impact of climate change on niche and range shifts were processed in parallel using  
274 open-source software on the Rice Super computer (NOTS) and the German Centre for  
275 Integrative Biodiversity Research (iDiv) High-Performance Computing Cluster.<sup>32</sup>

276 **Results**

277 **Sex specific demographic response to climate change**

278 Most vital rates were strongly climate dependent, but the magnitude of their response were sim-  
279 ilar between sexes suggesting no sex-specific demographic response to climate<sup>33</sup>. Survival and  
280 flowering were strongly more dependent on climate than growth (number of tillers) and pan-  
281icle production (Fig.2; Fig. S-5).<sup>34</sup> In addition, we found opposite patterns in the direction of the  
282 effect on seasonal climate on the probability of survival and flowering. Growing season precip-  
283 itation has a negative effect on the probability of survival, number of tillers, and the probability  
284 of flowering, whereas dormant season precipitation has a positive effect on these vital rates.<sup>35</sup>  
285 Unlike precipitation, temperature of the growing season has a positive effect of the probability  
286 of survival, a negative effect of the probability of flowering, and the number of tillers, but no  
287 significant effect on the number of panicles. Further, there was a female survival and flowering  
288 advantage across both climatic seasons<sup>36</sup> (Figures. 3A-3D, 3I-3L). On the contrary, there was a  
289 male panicle advantage across all climatic variables (Figure3M-3P).<sup>37</sup> Counter-intuitively, there  
290 was no significant sex growth advantage in all season climatic variables (Figures. 3E-3H).<sup>38 39</sup>

---

<sup>32</sup>I am not sure you need this – it was still done in R.

<sup>33</sup>A few comments here: 1-This undermines the entire premise of the paper! If that's the result, it is what it is, but it suggests that the current Introduction does not serve the Results very well. 2-Your figure masks a lot of variation and interactions, and I think these are worth looking into more deeply. 3-This result is inconsistent with what we found in the Am Nat paper, and that concerns me, and will concern reviewers. 4-The niche plot indicates differences between two-sex and female dominant, which could only happen if there were sex-specific responses in the vital rates.

<sup>34</sup>I am not sure this is true. The scales are very different.

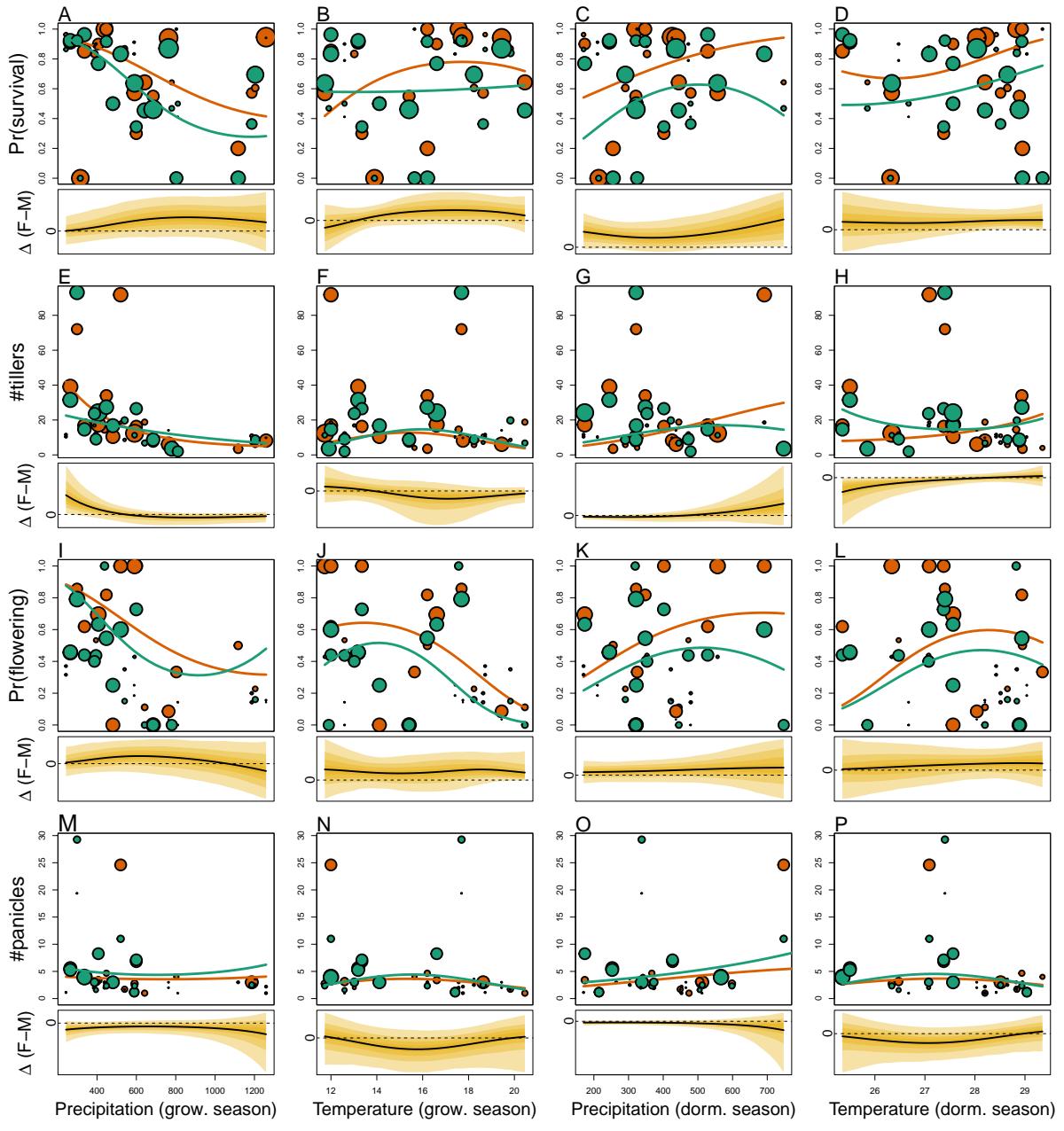
<sup>35</sup>I think these trends are conditional on temperature - see other comments.

<sup>36</sup>I am not sure what you mean by "climatic seasons". More precise language will help.

<sup>37</sup>The points and lines look very similar

<sup>38</sup>I cannot follow what this sentence is saying or why it is counter-intuitive.

<sup>39</sup>I found this paragraph difficult to read, and obviously there are a lot of results to explain. I suggest you put some thought into how to organize these results in a way that communicates what you think are the most important points and makes it easier to digest. I think you also need to be careful about providing statistical support for your assertions.



**Figure 2: Sex specific demographic response to climate across species range.** (A, B) Probability of survival during the growing season; (C, D) Probability of survival during the dormant season (E, F) Change in number of tillers during the growing season; (F, G) Change in number of tillers during the dormant season (I, J), Probability of flowering during the growing season; (K, L) Probability of flowering during the dormant season (M, N), Change in number of panicles produced given flowering during the growing season; (O, P) Change in number of panicles produced given flowering during the 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-5.

291 **Climate change alters population viability**

292 We estimated population growth rate response to seasonal climate gradients using two  
293 models: a female dominant model and a two-sex model<sup>40</sup>. Consistent with the effect of  
294 climate on the individual vital rate, we found a strong effect of seasonal climate on population  
295 fitness (Fig.3).<sup>41</sup> For both models, population growth rate decreased toward high precipitation  
296 of growing season (Fig.3 A, C). In contrast population growth rate increased with an increase  
297 in precipitation of the dormant season. Furthermore, population growth rate was maximized  
298 between 14 and 17 °C and decreased below zero beyond 18 °C during the growing season  
299 (Fig.3 B). Similarly population fitness was maximized between 27 and 31 °C and decreasesd  
300 bellow zero just beyond 20 °C during the dormant season (Fig.3 D).<sup>42</sup>

301 We have also detected a strong effect of the past and future climate on population growth  
302 rate. However, the magnitude of the effect of future climate on population growth rate was  
303 different between emissions scenarios. Under past climate conditions, population growth  
304 rate decreased below one for temperature of the growing season. A moderate emission gas  
305 scenario (RCP4.5) has a no effect on the population growth rate while a high emission scenario  
306 (RCP8.5) has a strong negative effect on population growth rate (Fig.3 B, D).<sup>43 44</sup>

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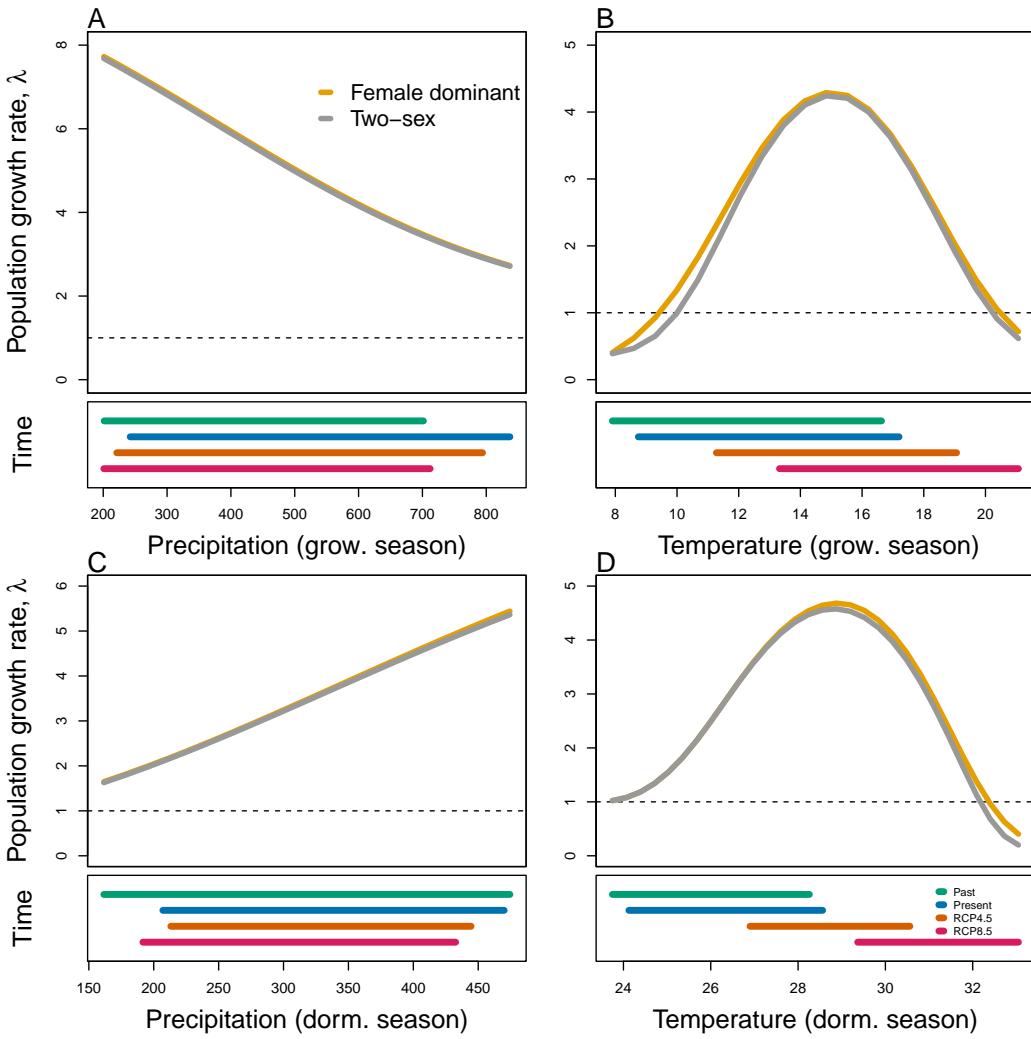
<sup>40</sup>You do not provide any methods for this contrast.

<sup>41</sup>Here and in the preceding figure, I think we need to be more transparent about at what climate values we are purely extrapolating. If I recall correctly, the "present" ranges shown in the lambda figure are not the actual range you fit the models over.

<sup>42</sup>I would like to discuss possibly not using this figure. I actually think the 2-D niche plots are the better representation of these results, because there are temp\*precip interactions that you cannot see here but you can see in the 2-D niche plot. For example, the result that lambda increases with lower temperature is kind of weird, but you can see in the 2-D plot that this is only true at low temperature, and it reverses at high temperature. There are probably important interactions that we should try to visualize in the vital rates.

<sup>43</sup>I understand what you are describing here, but I would not say that this shows "effects of climate change on population growth". Rather it shows what we predict lambda would be in different ranges of climate. That is a subtle distinction but I think it is important because "effects of climate change" depend on where in the range you are. All this might be moot if we don't use figure, although I love the way you show changes in climate from past to future, so we should find a way to keep that.

<sup>44</sup>I cannot write comments in the figure captions, so this comment applies to "Lower panels below each data panel".THis is not an adequate explanation of what is shown here. These are the ranges (min-max) of monthly climate values for the entire set of experimental sites over specific years, which need to be identified here.



**Figure 3: Population growth rate ( $\lambda$ ) as a function of seasonal 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 climate values at different time periods (past climate, present and future climates). For future climate, we show a Representative 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).

### 307 Temperature as a driver of population growth rate decline

308 Population growth rate was most sensitive to change in temperature of the growing season  
 309 and temperature of the dormant season (Supporting Information S-6). LTRE decomposition  
 310 revealed that, for each sex, the reduction of  $\lambda$  for high value of temperature of the growing  
 311 season was driven by a reduction of survival rate, growth rate, and a reduction in number

312 of panicles (Fig.4 A, B). However, the reduction of population growth rate for higher value  
 313 of temperature of the dormant season was driven by only female individuals(Fig.4 C, D).  
 314 45 The increase of the probability of flowering was sufficient to prevent population growth  
 315 rate from declining for high tmeprature of the dormant season (Fig.4 C). 46

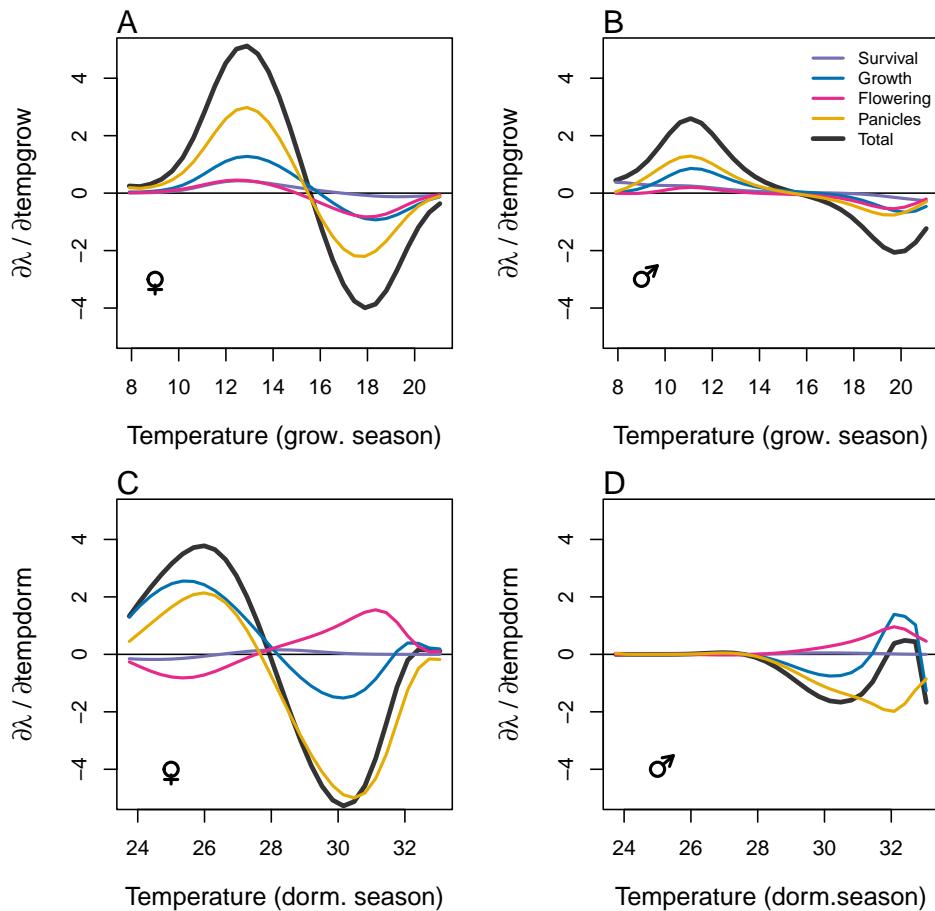


Figure 4: Life table response experiment decomposition of the sensitivity of  $\lambda$  to seasonal climate into additive vital rate contributions of males and females based on posterior mean parameter estimates. (A) Temperature of growing season (contribution of female), (B) Temperature of growing season (contribution of male), (C) Temperature of dormant season (contribution of female) and (D) Temperature of dormant season (contribution of male).

### 316 Climatic change induce niche and range shifts

45 This is not how I interpret the figure.

46 I don't think readers will understand how to process these results, or what they mean with respect to the motivating questions. I think this can be presented in a more reader-friendly way that connects more clearly to the conceptual aims of the study.

317 <sup>47</sup> Our results suggested niche sifts for both models (female dominant and two-sex) during the  
318 dormant and growing season (Fig. 5). <sup>48</sup> However, the female dominant model overestimated  
319 the magnitude of niche shifts (Fig. 5 D). <sup>49</sup> Further, our demographically based range  
320 predictions broadly captured the known distribution of the species. More specifically, the  
321 predicted probabilities of self-sustaining ( $\lambda > 1$ ) matches the presence and absence of the  
322 species (Fig. 6 B, Fig. 6 F). <sup>50</sup> Furthermore, viable populations of *P. arichnifera* were only  
323 predicted at the center of the range for current climatic conditions (Fig. 6 B). Although *P.*  
324 *arichnifera* was predicted to have suitable habitats in the center of the range under current  
325 climate, global warming (regardless of the future scenario of carbon emission used) is  
326 predicted to reduce much of these suitable habitats (Fig. 6 C, D). Most of the current suitable  
327 habitats will move toward the Northern range edge.

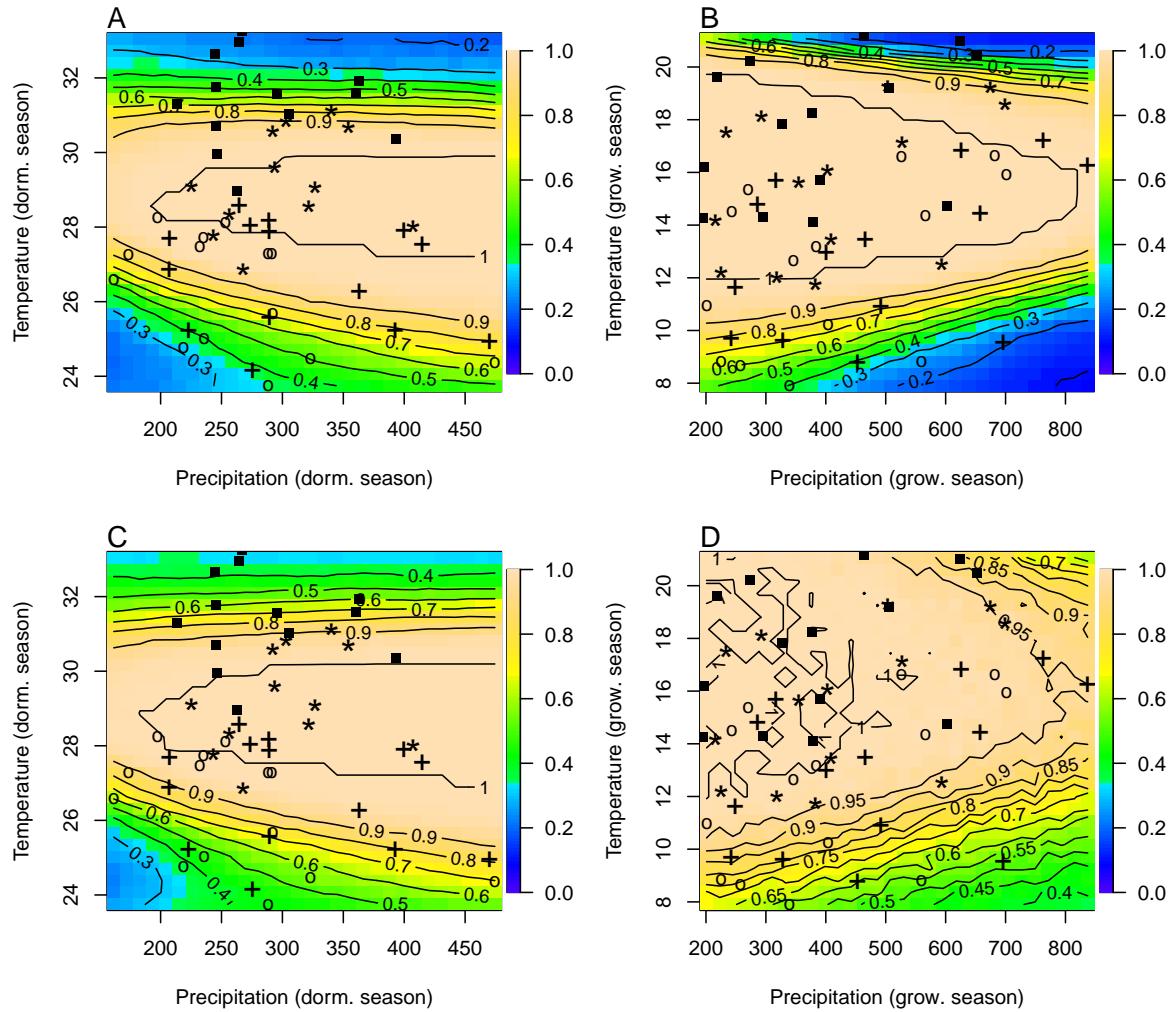
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<sup>47</sup> General comment on this section: these are the most important results of the paper but they are described only briefly and without much statistical support. That is true for much of the Results section. I think this could be strengthened. I also think for both the niche and the map figures we need a more visually intuitive way to contrast the two-sex and female-dominant models.

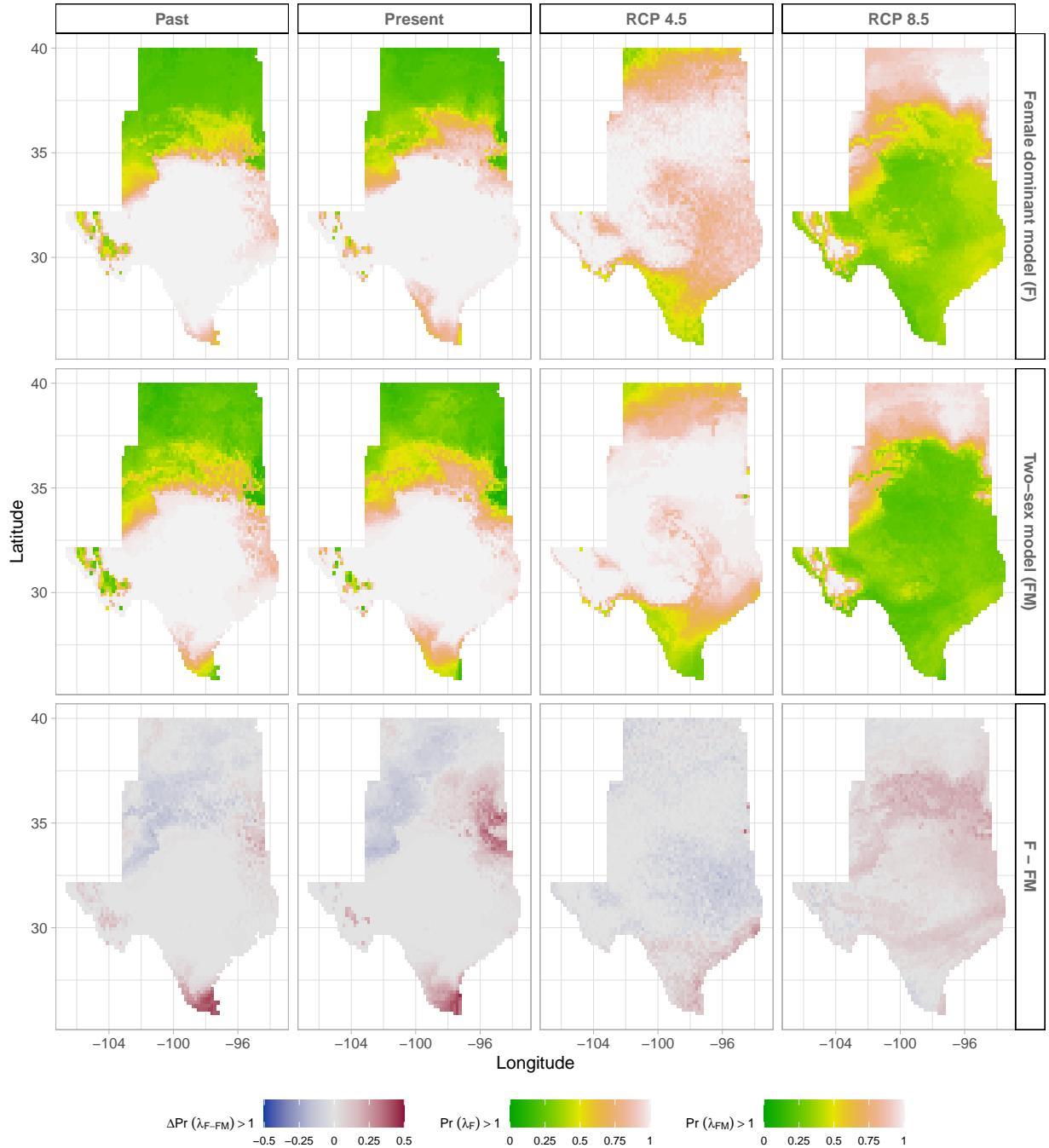
<sup>48</sup> I do not understand this statement.

<sup>49</sup> This needs to be quantified more rigorously and statistically better supported. This also is inconsistent with the result that there were no sex-specific climate responses, because that is the only way the predictions could differ.

<sup>50</sup> Again, these results need to be reported in a more quantitatively rigorous way. I also do not agree that the model captures the known distribution. I think it drastically over-predicts known occurrence, and that warrants some attention.



**Figure 5: A two-dimensional representation of the predicted niche shift over time (past, present and future climate conditions).** Contours show predicted probabilities of self-sustaining populations,  $\text{Pr}(\lambda > 1)$  conditional on precipitation and temperature of the dormant and growing season. (A) Niche of dormant season for the two sex model, (B) Niche of growing season for the two sex model, (C) Niche of dormant season for female dominant model, (D) Niche of growing season for female dominant model. "o": Past, "+": Current, "\*": RCP 4.5, ■: RCP 8.5.



**Figure 6: 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 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.

328 **Discussion**

329 Dioecious species make up a large fraction of Earth's biodiversity – most animals and  
330 many plants – yet we have little knowledge about how **skewness in sex ratio**<sup>51</sup> will affect  
331 population viability and range shifts of dioecious species under climate change. Three  
332 general patterns emerged from our analysis of range-wide common garden experiments  
333 and sex-structured, climate-explicit demographic models. First, our Bayesian mixed effect  
334 model predicts that seasonal climate (temperature and precipitation) affects sex-demographic  
335 processes in **distinctive and contrasting ways**<sup>52</sup>. While climate has a significant effect on  
336 the probability of survival and growth, it has no effect on the number of panicles. Second,  
337 future climate, by increasing **seasonal temperature**<sup>53</sup>, **will reduce survival rate, growth rate**  
338 **and reproduction and thereby alter population viability.**<sup>54</sup> In addition, climate change favors  
339 range shifts. Third, **using only one sex to forecast range shifts of dioecious under climate**  
340 **change could lead to an overestimation of the impact of climate change on species.**<sup>55</sup>

341 Our results indicate no sex-specific demographic response to climate change.<sup>56</sup> However,  
342 females have higher survival rate and fertility rate than males. **This result**<sup>57</sup> is not unique to  
343 our study system and has been observed in **a range of pollen dispersal species across climatic**  
344 **gradients**<sup>58</sup> (Sasaki et al., 2019; Welbergen et al., 2008; Zhao et al., 2012). Several hypotheses  
345 could explain the observed demographic advantage of females over males for survival and  
346 flowering and the opposite for growth and number of panicles. The trade-off between fitness  
347 traits (survival, growth, fertility) due to resource limitation and the pollination mode of our  
348 study species (wind pollinated) could explain such a result (Cipollini and Whigham, 1994;  
349 Freeman et al., 1976). For most species, the cost of reproduction is often higher for females  
350 than males due to the requirement to develop seeds and fruits (Hultine et al., 2016). However,  
351 several studies reported a higher cost of reproduction for males in wind pollinated species  
352 due to the larger amounts of pollen they produce (Bruijning et al., 2017; Bürli et al., 2022;  
353 Cipollini and Whigham, 1994; Field et al., 2013). **In addition to life history trade-off, difference**

<sup>51</sup> You have not described anything about skewness in sex ratio, either from the model or in the data, and this is a glaring omission because as you correctly observe here, it is the way that sex structure matters for population viability

<sup>52</sup> I am not sure whether this is referring to distinct and contrasting climate variables or sex differences.

<sup>53</sup> I don't know what you mean by "seasonal temperature" – be more specific

<sup>54</sup> It will not do so everywhere – in some places these metrics will increase in others they will decrease, hence the range shifts.

<sup>55</sup> This result needs a clearer biological mechanism.

<sup>56</sup> Again, if this is true then there should be no difference between the female-dominant and two-sex models.

<sup>57</sup> Which result are you referring to?

<sup>58</sup> Not sure what this means.

354 in non-climatic factors such as soil, or biotic interactions could explain decline in vital rate as  
355 an indirect effects of increase in temperature (Alexander et al., 2015; Schultz et al., 2022).<sup>59</sup>

356 Under current conditions, most populations across the range are viable.<sup>60</sup> This result could  
357 be explained by two hypotheses. First, demographic compensation whereby an increase of  
358 one vital rate is coupled with a decrease of another vital rate could explain viable populations  
359 in harsh conditions at the range edge (Doak and Morris, 2010; Nomoto and Alexander, 2021;  
360 Villegas et al., 2015). In our system, a decrease in fertility and survival rate was counterbalanced  
361 by an increase in flowering rate, preventing the population growth rate from declining even  
362 at range edge<sup>61</sup> during the dormant season<sup>62</sup>. Second, local adaptation at the edge of the  
363 range could explain the viable populations throughout the range (Miller and Compagnoni,  
364 2022b). Our study was based on a common garden experiment; therefore, individuals planted  
365 in climatic conditions that are similar to their source populations climatic conditions were less  
366 impacted by stressful environmental conditions.<sup>63</sup> An important question to ask is: what is the  
367 role of local adaptation in buffering species response against climate change. Unfortunately,  
368 our model does not shed light on that question. Adding another predictor to our complex  
369 model would have lead to overfitting. Therefore, the role of local adaptation in mitigating  
370 population response to climate should be the next step in forecasting species response to  
371 climate.<sup>64</sup>

372 Our LTRE analysis reveals that a small change in temperature of the growing and dor-  
373 mant season could have a larger impact on population viability. Temperature can impact plant  
374 populations through different mechanisms. Increasing temperature could increase evaporative  
375 demand, affect plant phenology (Iler et al., 2019; McLean et al., 2016; Sherry et al., 2007), and  
376 germination rate (Reed et al., 2021). The potential for temperature to influence these different  
377 processes changes seasonally (Konapala et al., 2020). For example, studies suggested that  
378 species that are active during the growing season such as cool grass species can have delayed  
379 phenology in response to global warming, particularly if temperatures rise above their physio-  
380 logical tolerances (Cleland et al., 2007; Williams et al., 2015). In addition, high temperature dur-  
381 ing the growing season by affecting pollen viability, fertilization could affect seed formation and  
382 germination (Hatfield and Prueger, 2015; Sletvold and Ågren, 2015). Temperature also affected

<sup>59</sup>This seems like a general comment about climate effects whereas I thought the paragraph was focused on sex differences.

<sup>60</sup>I don't think this statement is well-supported. We don't have any data from natural populations.

<sup>61</sup>Not sure I follow this - if lambda was not declining it would not be a range edge

<sup>62</sup>Population growth rate is an annual measure, it does not refer to any season. I think what you mean here is that dormant season weather can affect population growth rate.

<sup>63</sup>This statement lacks evidence.

<sup>64</sup>I don't think this is a very effective use of the Discussion. If you want to address local adaptation maybe that can go in an appendix. I don't actually understand the point of this paragraph but maybe I am not understanding something.

383 operational sex ratio (OSR) (Fig.S-12). That variation in OSR could affect population growth  
384 rate by altering females' fitness (Haridas et al., 2014; Knight et al., 2005; Petry et al., 2016).<sup>65</sup>

385 We found evidence of climatic niche shifts for the female dominant model and the  
386 two-sex model. However the female dominant model overestimated species niche, suggesting  
387 that using one sex to predict niche shifts could be misleading.<sup>66</sup> Despite that overestimation for  
388 the female dominant model, both models agree on the fact that climatic conditions that are not  
389 optimal under current conditions will be optimal for the species over the next years particularly  
390 at the edge of species<sup>67</sup>. Further, pollen dispersal may allow plants to resist climate change be-  
391 cause pollen dispersal may provide the local genetic diversity necessary to adapt at the leading  
392 edge of the population (Corlett and Westcott, 2013; Duputié et al., 2012; Kremer et al., 2012).  
393 Since wind pollination is most effective at short distances, it is most often found in plant species  
394 growing at high density such as our study species, it is less likely that dispersal limitation affect  
395 niche shift in our study system.<sup>68</sup> However, others biotic factors such as species competition  
396 might constrain the species to a narrower realized niche (Aguilée et al., 2016; Pulliam, 2000).

397 Our results suggest that climate change will drive range shifts and the magnitude and  
398 rate of that range shift could be overestimated when tracking only one sex (Fig. S-9, Fig.  
399 S-10, Fig. S-11). This overestimation of the impact of climate change using a female dominant  
400 model could be due to several factors.<sup>69</sup> First, small change in seasonal temperature affects  
401 population viability for both sexes<sup>70</sup>. Second, operational sex ratio in *Poa arachnifera* become  
402 female biased in areas with lower temperature of growing season such as Northern range edge  
403 (Fig.S-12 B). Our results converge with previous studies that have found the same pattern<sup>71</sup> for  
404 other dioecious species (Varga and Soulsbury, 2020; Woldemelak et al., 2021). Our finding also  
405 contrast with a previous study suggesting that an increase in male frequency induce range  
406 shifts by reducing pollen limitation in conditions that were not suitable (Petry et al., 2016).

407 Three years represent a relatively decent time for demographic study for common garden  
408 experiments across climatic gradient.<sup>72</sup> Thus our models can only capture a certain range  
409 of demographic and environmental variability (Fig. S-8). Moreover, our future projections  
410 require extrapolation to warmer or colder conditions than observed in our experiment

<sup>65</sup>These results need to be better developed because they underlie all the other results. And again, the only way you can get an effect on temperature on OSR is if there were sex-specific responses to climate, but you say there were none.

<sup>66</sup>Again – what is the biological explanation for this result?

<sup>67</sup>Which edge? I am not sure which specific results you are referring to here.

<sup>68</sup>I do not find this particularly relevant for interpreting the result that opens this paragraph.

<sup>69</sup>OK I was expecting this earlier.

<sup>70</sup>Population viability is a property of the entire population, so females and males cannot have their own population viability.

<sup>71</sup>Unclear what pattern you are referring to

<sup>72</sup>I am not sure whether this is intended to mean that three years is short or long – can you sharpen this?

411 and subsequently should be interpreted with caution (Chen et al., 2024). <sup>73</sup> Despite all  
412 these limitations, the qualitative implications of a negative response of species to increase  
413 temperature (dormant and growing season)<sup>74</sup> seems consistent across all GCMs. Most of the  
414 suitable areas move toward the North of the current range in response to climate change.  
415 Climate change will affect population growth rate primarily through the response of female  
416 which is more sensitive to climate change (Miller and Compagnoni, 2022b).<sup>75</sup> Males also have  
417 a significant contribution to population growth rate particularly for temperature.<sup>76</sup> Our work  
418 suggest that current climate may not affect population viability<sup>77</sup>, but populations may be  
419 impacted negatively over the next decades in response to a climate change. This is key because  
420 most conservation actions are design from data on current responses to climate, rather than  
421 future response to climate (Sletvold et al., 2013). Moreover, management strategies that focus  
422 on both sexes would be effective and will enhance population growth rate in response to  
423 global warming.

## 424 Conclusion

425 We have investigated the potential consequence of skewness in sex ratio on population  
426 dynamics and range shift in the context of climate change. We found that future climate will  
427 affect population growth rate at the center of species range.<sup>78</sup> This reduction in population  
428 growth rate will induce a range shift to the northern edge of the species current range. Our  
429 results also suggest that tracking only one sex could lead to an overestimation of the effect  
430 of climate change on population dynamics. Our work provides a framework for predicting  
431 the impact of global warming on species using population demography.

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<sup>73</sup>*This is a good point, and it needs to be shown more clearly in methods and results.*

<sup>74</sup>*Again, it is not negative everywhere. Northern populations with benefit from warming, so these results need to be described with greater nuance.*

<sup>75</sup>*This paper says the opposite.*

<sup>76</sup>*I do not know what this is saying.*

<sup>77</sup>*This statement does not make sense to me. Our data show that population viability is sensitive to climate under current (observed) conditions.*

<sup>78</sup>*I do not follow what this is referring to.*

<sup>79</sup>*Much of this looks like it is copied from the Am Nat paper.*

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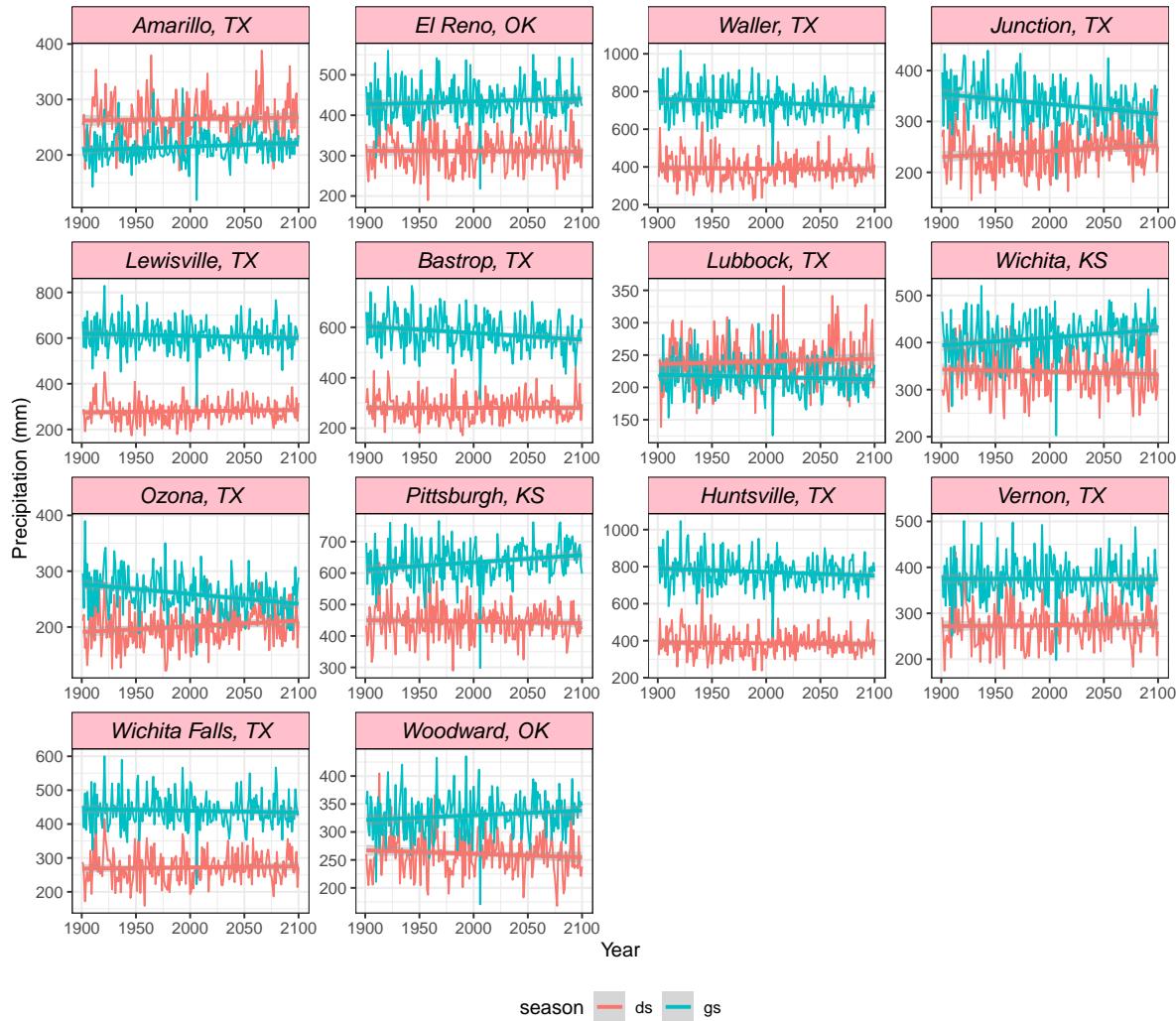
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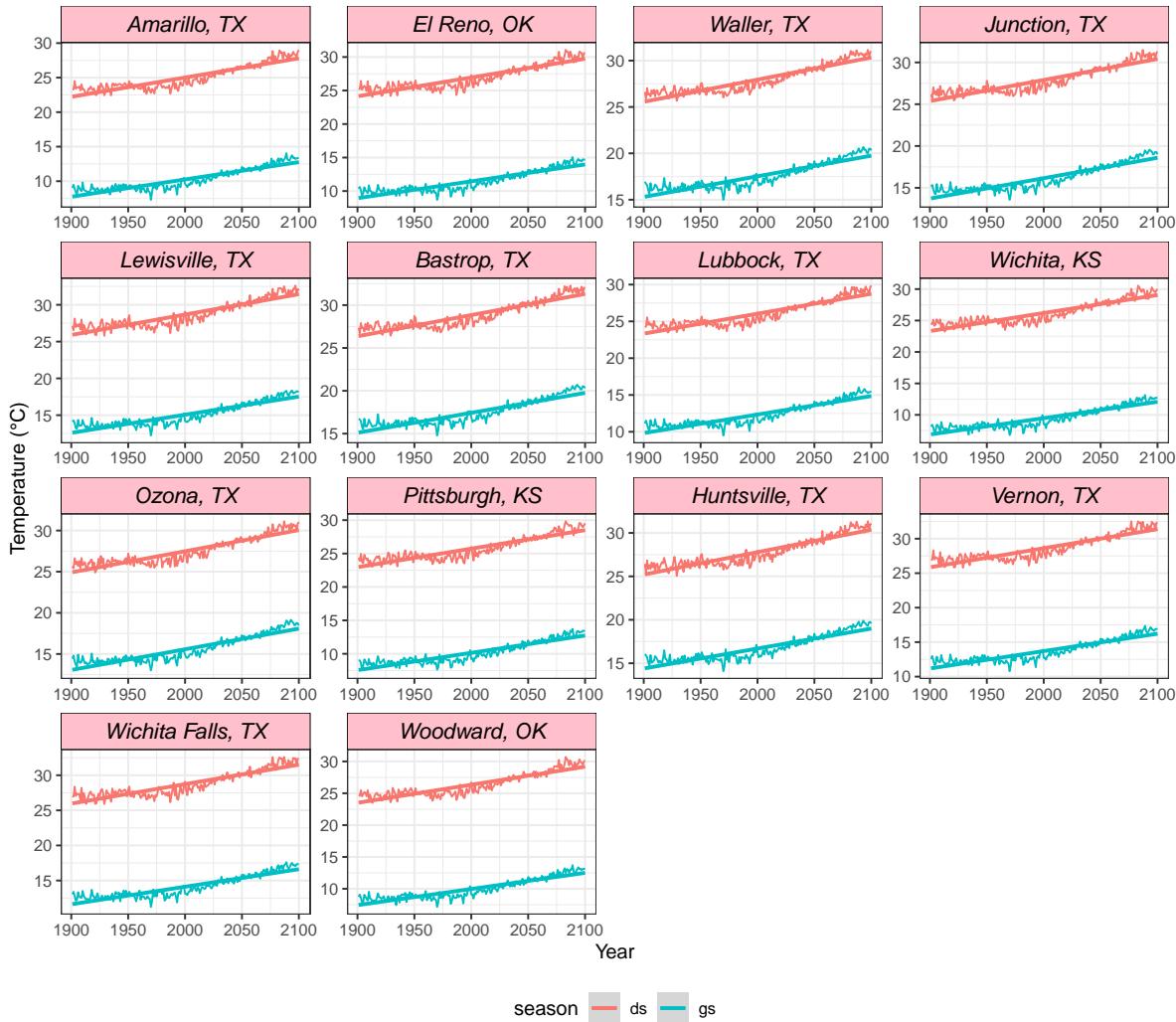
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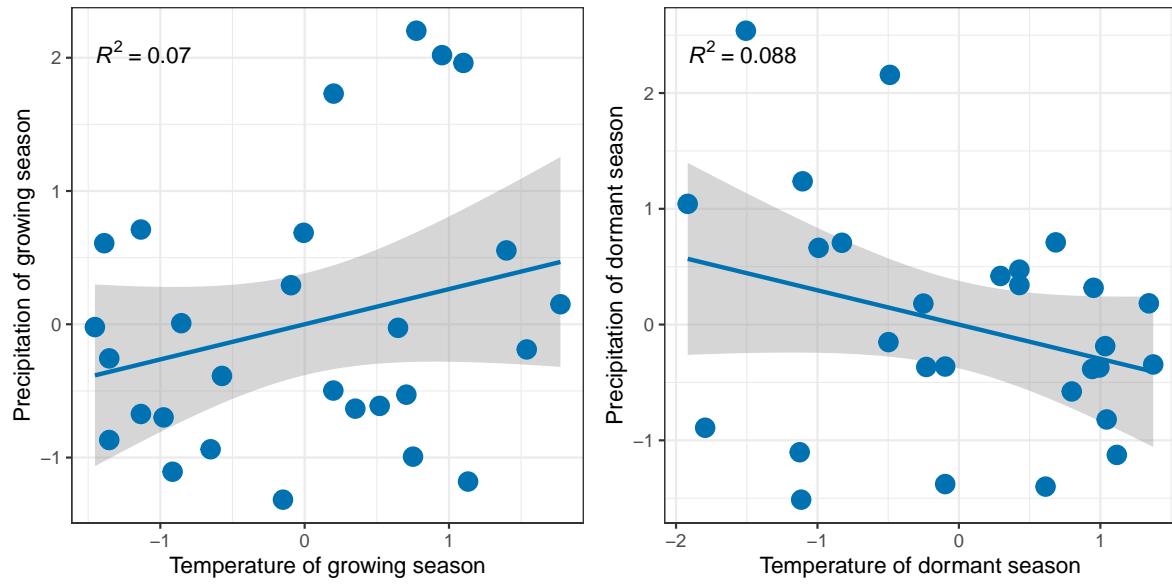
## Supporting Information



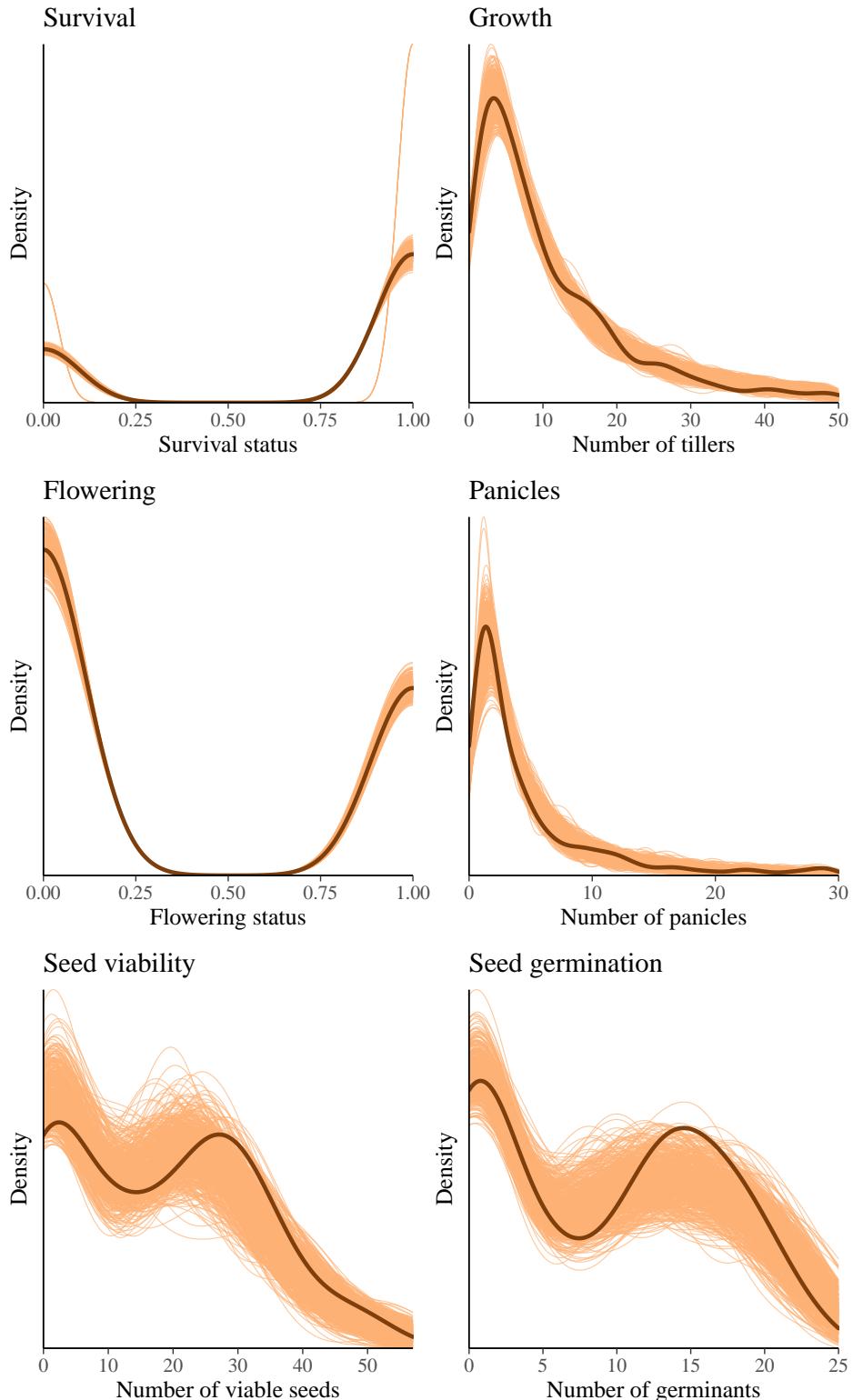
**Figure S-1:** Precipitation variation accross the study sites from 1990 to 2100. ds:Dormant season, dg:Growing season.



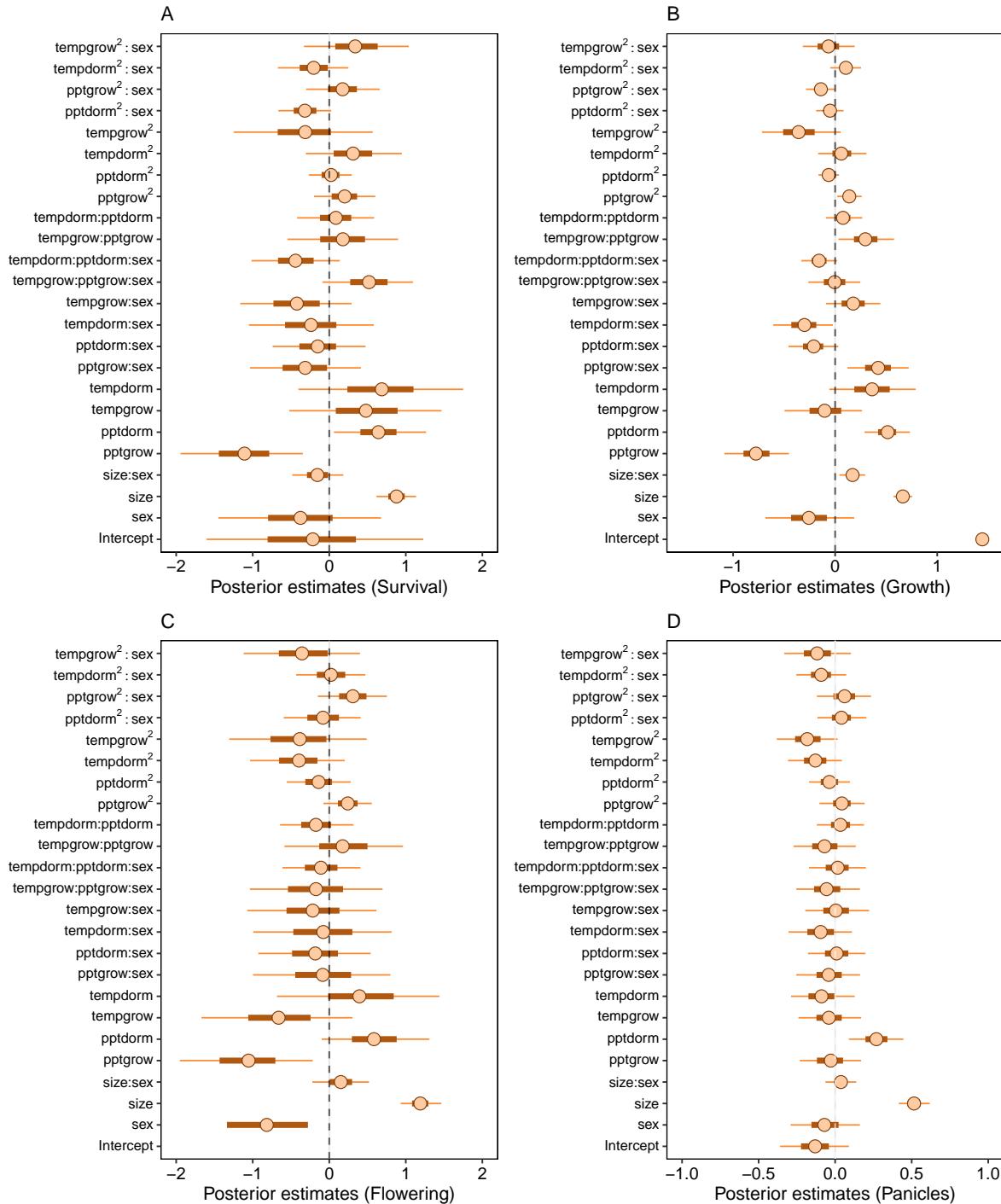
**Figure S-2:** Temperature variation accross the study sites from 1990 to 2100, ds: Dormant season, dg: Growing season.



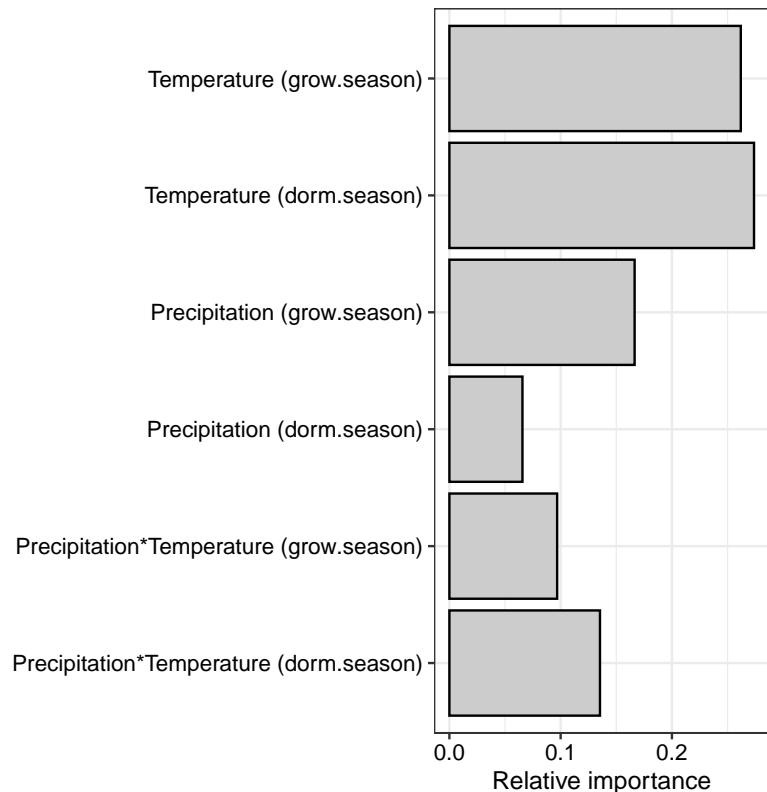
**Figure S-3:** Relation between precipitation and temperature for each season (growing and dormant).  $R^2$  indicates the value of proportion of explained variance between the temperature and precipitation



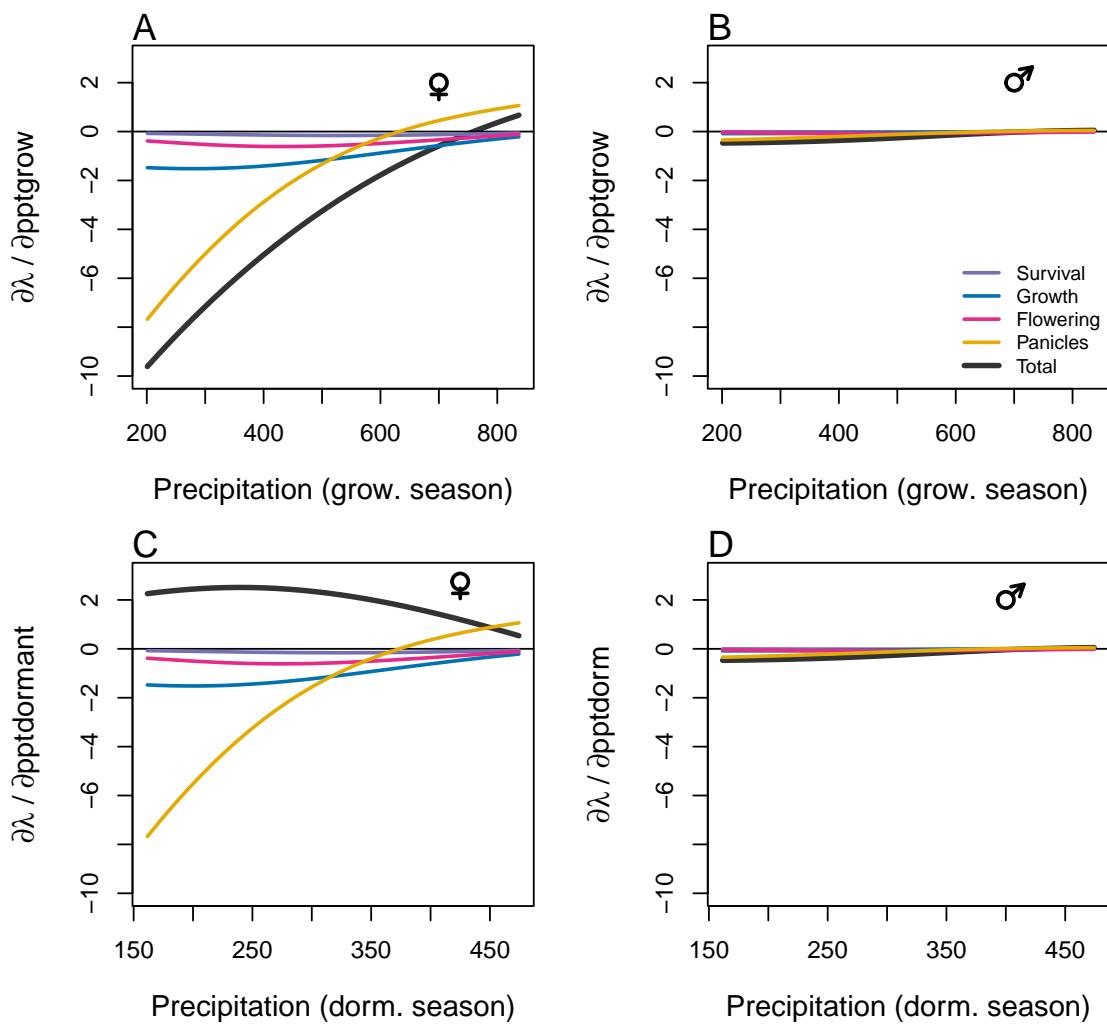
**Figure S-4:** Posterior predictive checks. Consistency between real data and simulated values suggests that the fitted model accurately describes the data. Graph shows density curves for the observed data (light blue) along with the simulated values (dark blue). The first column shows the linear models and the second column shows the 2 degree polynomial models.



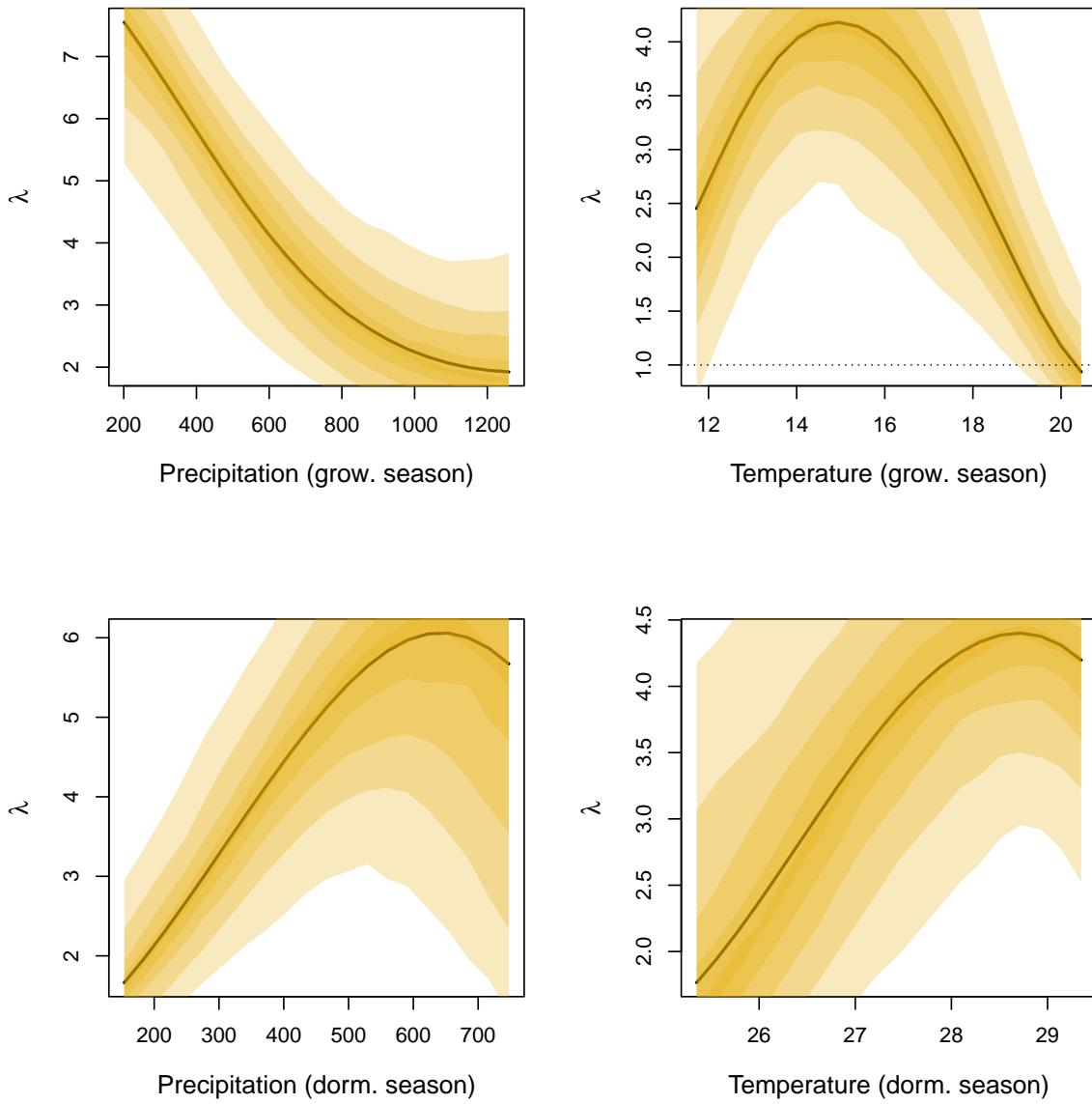
**Figure S-5:** Mean parameter values and 95% credible intervals for all vital rates. pptgrow is the precipitation of growing season, Tempgrow is the temperature of growing season, pptdorm is the temperature of dormant season, Tempdorm is the temperature of dormant season.



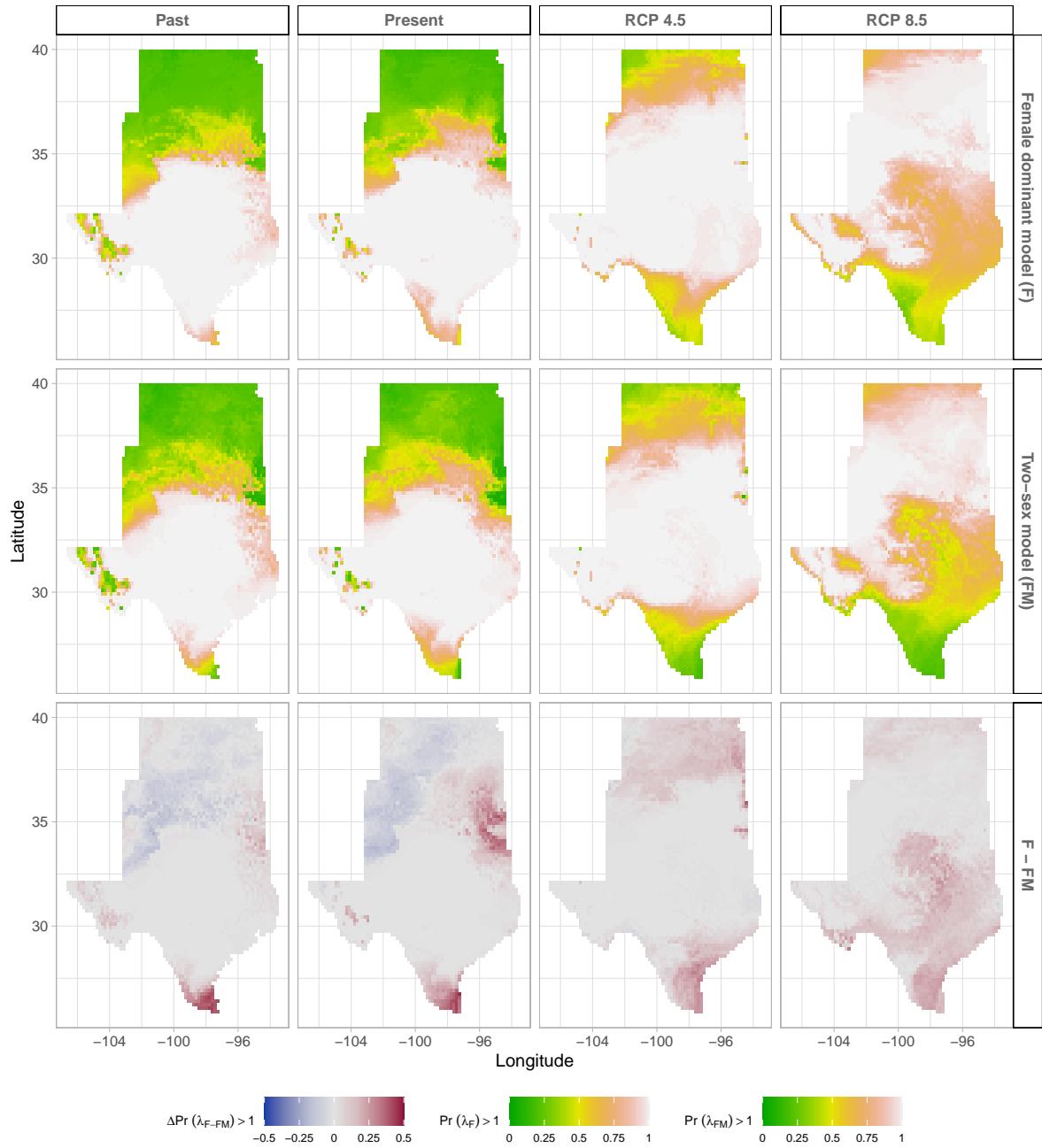
**Figure S-6:** Life Table Response Experiment: The bar represent the relative importance of each predictors



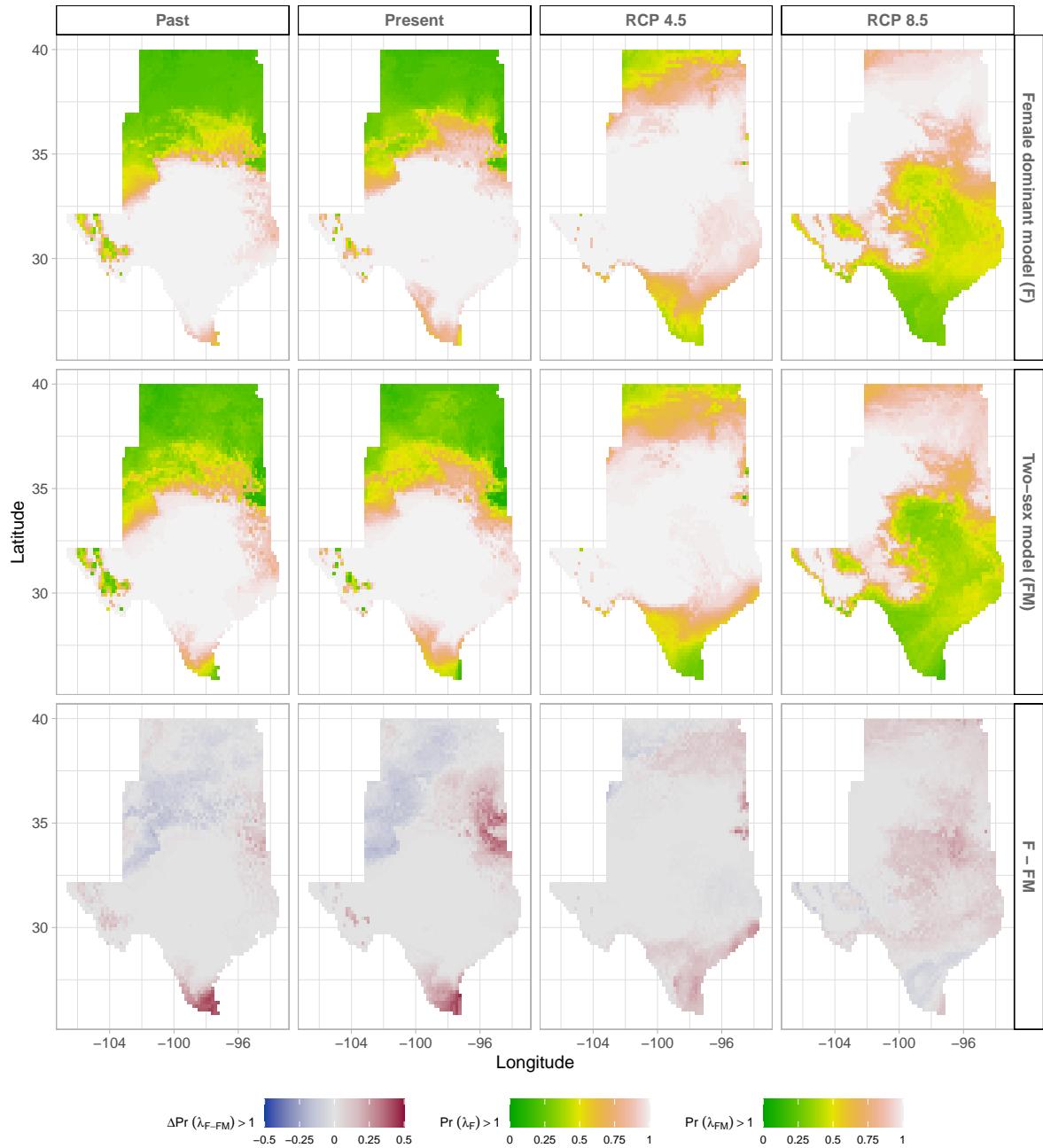
**Figure S-7:** Life table response experiment decomposition of the sensitivity of  $\lambda$  to seasonal climate into additive vital rate contributions of males and females based on posterior mean parameter estimates. (A) Precipitation of growing season (contribution of female), (B) Precipitation of growing season (contribution of male), (C) Precipitation of dormant season (contribution of female) and (D) Precipitation of dormant season (contribution of male).



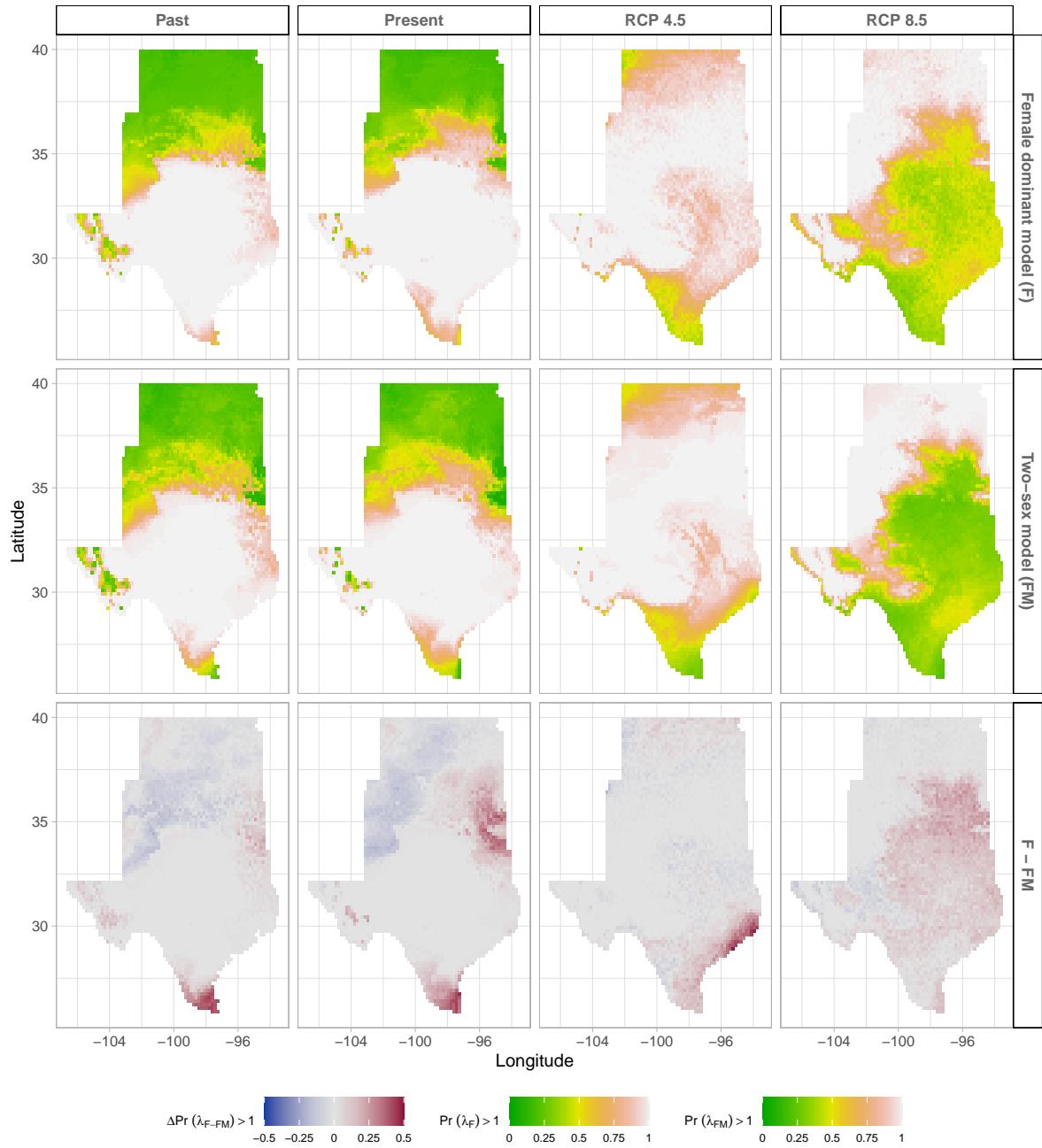
**Figure S-8:** Population growth rate ( $\lambda$ ) as a function of seasonal climate (2015-2017), predicted by the two-sex matrix projection model that incorporates sex-specific demographic responses to climate with sex ratio-dependent seed fertilization. We show the mean posterior distribution of  $\lambda$  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 ( $\lambda = 1$ )



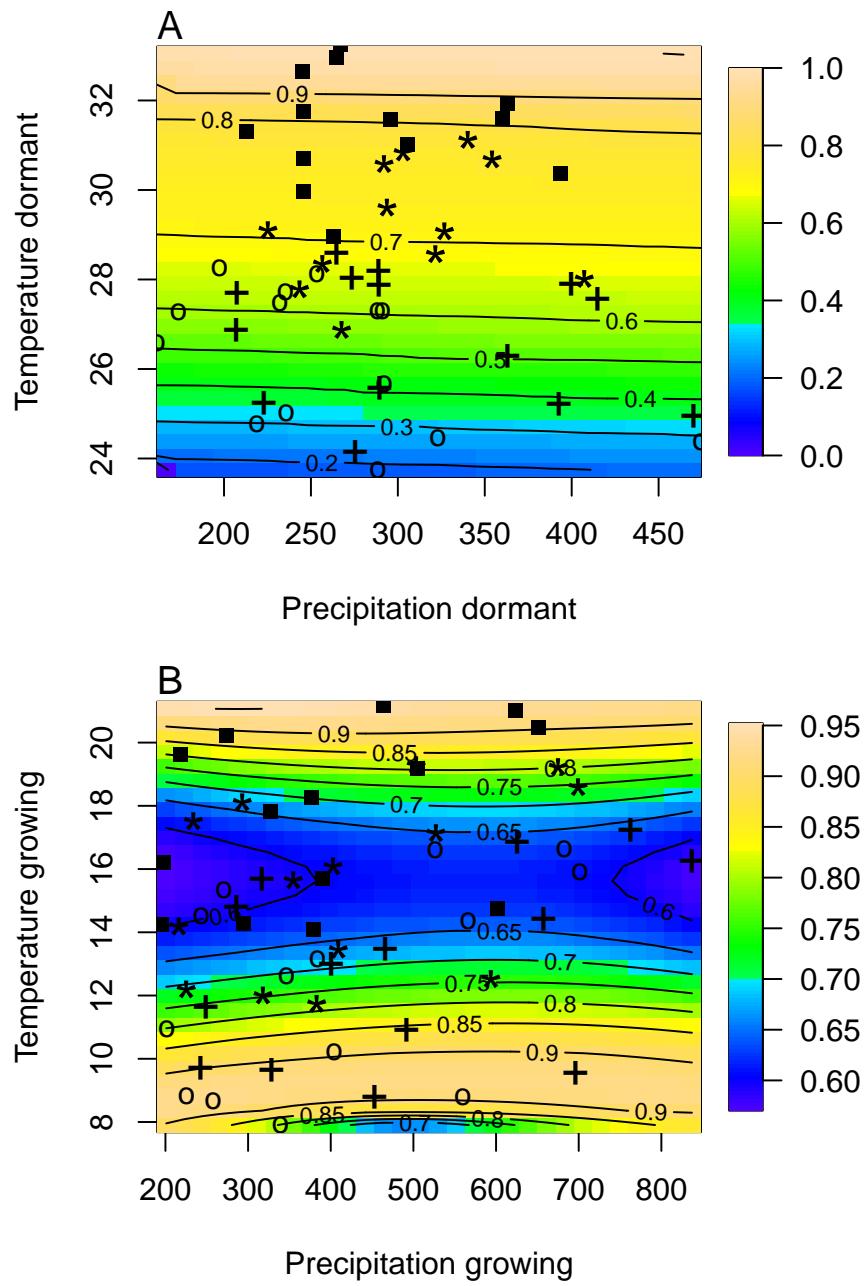
**Figure S-9:** Climate change favors range shift toward the North edge of the current range. (A) Past, (B) Current, (C and D) Future predicted range shift based on the predicted probabilities of self- sustaining populations,  $\Pr(\lambda > 1)$ , using the two-sex model that incorporates sex- specific 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-10:** 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-11:** 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.



**Figure S-12:** A two-dimensional representation of the Operational Sex Ratio (OSR) over time (past, present and future climate conditions). OSR represents the proportion of females. Contours show predicted values of OSR conditional on precipitation and temperature of the dormant and growing season. Operational Sex Ratio during the dormant season for the two sex model (A), Operational Sex Ratio during the growing season for the two sex model (B). "o": Past, "+": Current, "\*": RCP 4.5, "■": RCP 8.5.