

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

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**1                   Abstract**

**2** Sex-specific response to rising temperature and drought raises the questions of whether  
**3** global change could lead to a drastic change in the sex ratio and whether that change  
**4** in the sex ratio could drive population extinction or population range shift in dioecious  
**5** species. Answering these questions requires an understanding of the mechanism by  
**6** which a change in vital rates under future climate conditions for both male and female,  
**7** could be translated into a significant change in population dynamics. We forecast range  
**8** shift for a dioecious species using matrix models.

**9                   Keywords**

**10** climate change, demography, forecasting, matrix projection model, mechanistic models,  
**11** sex ratio, range limits

12

## Introduction

13 Rising temperatures and extreme drought events associated with global climate change  
14 are leading to increased concern about how species will become redistributed across the  
15 globe under future climate conditions (Bertrand et al., 2011; Gamelon et al., 2017; Smith  
16 et al., 2024). Dioecious species might be particularly vulnerable to the influence of climate  
17 change because they often display skewed sex ratios that are generated or reinforced by  
18 sexual niche differentiation (distinct responses of females and males to shared climate  
19 drivers) (Tognetti, 2012). Accounting for such a niche differentiation between male and  
20 female within a population is a long-standing challenge in accurately predicting which  
21 sex will successfully track environmental change and how this will impact population  
22 dynamics (Jones et al., 1999; Gissi et al., 2023a). The vast majority of theory and models  
23 in population biology, including those used to forecast biodiversity responses to climate  
24 change, ignore the complication of sex structure (Pottier et al., 2021; Ellis et al., 2017).  
25 As a result, accurate forecasts of colonization-extinction dynamics for dioecious species  
26 under future climate scenarios are limited.

27 Climate change can influence dioecious populations via shifts in sex ratio. Females  
28 and males respond differently to climate change, especially in species where there is  
29 sexual niche differentiation (Gissi et al., 2023a,b; Hultine et al., 2016). This sex-specific  
30 response to climate change may help one sex to succeed in extreme climatic conditions  
31 more than the other sex leading to a skewness in the operational sex ratio (relative num-  
32 ber of males and females who are ready to mate) (Eberhart-Phillips et al., 2017; Zhao  
33 et al., 2012; Bürli et al., 2022) . Experimentation manipulation revealed that when ex-  
34 posed to increasing temperatures, for example, in two populations of Atlantic marine  
35 copepods (*Acartia tonsa*), males showed significantly lower survival than females (Sasaki

36 et al., 2019). However, in some species, such as *Pteropus poliocephalus* or *Populus cathayana*,  
37 females showed lower survival than males in response to high temperature (Welbergen  
38 et al., 2008; Zhao et al., 2012).

39 Species's range limits, when not driven by dispersal limitation, should generally re-  
40 flect the limits of the ecological niche. For most species, niches and geographic ranges  
41 are often limited by climatic factors including temperature, precipitation (Sexton et al.,  
42 2009). Therefore, any substantial changes in the magnitude of these climatic factors in a  
43 given location across the range could impact population viability with potential implica-  
44 tion on range shift (Davis and Shaw, 2001; Pease et al., 1989). This is particularly true for  
45 dioecious species in which each sex has a different sensitivity to climate variation(Pottier  
46 et al., 2021; Morrison et al., 2016). Populations in which males are rare under current  
47 climatic conditions could experience low reproductive success due to sperm or pollen  
48 limitation that may lead to population decline in response to climate change (Eberhart-  
49 Phillips et al., 2017). In contrast, climate change could lead to male moving to more  
50 suitable areas (e.g. upslope), which might favor range expansion (Petry et al., 2016).  
51 Although the response of species to warming is generally understood, it is difficult to  
52 disentangle the interaction between sex and climate drivers to understand their relative  
53 contribution and effect on population dynamics and the consequence of such effect on  
54 range shift.

55 Our ability to track the impact of climate change on the population dynamics of  
56 dioecious plants and the implication of such impact on range shift depends on our ability  
57 to build mechanistic models that take into account the spatial and temporal context in  
58 which sex specific response to climate change affects population viability (Davis and  
59 Shaw, 2001; Evans et al., 2016; Czachura and Miller, 2020). At their range edge where  
60 climatic conditions are expected to be less favorable, if dioecious species populations are

61 non-viable in response to climate change, global warming will induce range contraction  
62 in dioecious species. In reverse, if populations at the edge are viable habitats in response  
63 to global warming, dioecious species populations could shift their range and relocate to  
64 more favorable and thereby favored range expansion.

65 In this study, we used a mechanistic approach by combining field experiment and ma-  
66 trix projection modelling, to understand the demographic response of dioecious species  
67 to climate change and its implications for future range dynamics. Our study system  
68 is a dioecious plant species (*Poa arachnifera*) distributed along environmental gradients  
69 in the south-central US corresponding to variation in temperature across latitude and  
70 precipitation across longitude (MAP). Here, we asked three questions: (1) What is the  
71 sex-specific demographic response to rising temperature and precipitation ? (2) How  
72 that sex-specific demographic response affects populations dynamics under current and  
73 future climatic conditions ? (3) What are the implications of population dynamics on  
74 range dynamics ?

## 75 Materials and methods

### 76 *Study species*

77 Texas bluegrass (*Poa arachnifera*) is a perennial, summer-dormant cool-season (C3) grass.  
78 The species occurs in Texas, Oklahoma, and southern Kansas, USA (Hitchcock, 1971).  
79 Texas bluegrass grows during cool months between October and May, with onset of  
80 dormancy often from June to September (Kindiger, 2004). Flowering occurs in May and  
81 the species is pollinated by wind (Hitchcock, 1971).

82

### *Common garden experiment*

83 We set up a common garden experiment to manipulate climatic factors (e.g., temperature  
84 and precipitation) to detect mechanisms underlying sex-specific demographic response  
85 to climate and the implication of such a response on range limitation (Merow et al.,  
86 2017; Schwinnning et al., 2022). At this end, we collected vegetative tillers from flower-  
87 ing individuals of each sex in eight natural (sources) populations of the focal species.  
88 We then propagated these tillers in ProMix plotting soil and supplemented them with  
89 Osmocote slow-release fertilizer at 75°F to 85°F under natural climatic conditions at the  
90 Rice University Greenhouse. The common experiment was installed on 14 sites across  
91 a precipitation gradient (FigX). At each site, we established 14 blocks. Each block was  
92 selected so that they resemble the natural environment of the species. For each block we  
93 planted three females and three males individuals. We spared the individuals, provided  
94 ~1 L of water, and removed surrounding vegetation to avoid competition and promote  
95 establishment.

96

### *Demographic and climatic data collection*

97 To parametrize the demographic models, we first collected individual demographic data  
98 including survival (alive or dead), growth (number of tillers), flowers (reproductive or  
99 vegetative), and fertility (number of panicles) in each site for two censuses (2015 and  
100 2016). Secondly, we downloaded monthly temperature and precipitation from Chelsa to  
101 describe observed climate conditions (Karger et al., 2017). These climate data were used  
102 as covariates in vital rate regressions, which allowed us to forecast and back-cast the  
103 effect of climate change on population dynamics and map species' niche and distribution  
104 under future and past climate change. We prefer temperature and precipitation because

they capture the most the climate in the study region [Source](#). Since our experiment was installed in November, we aligned the climatic years to match demographic transition years rather than calendar years. Then we used the monthly data to estimate seasonal data (dormant and growing season), since our study species is a seasonal cool grass. We define June to September as the dormant season of the year and the rest of the year as the growing season. To back-cast and forecast the effect of future climate on species population dynamics, we downloaded climatic projection data for past climatic conditions (901-1930), current conditions (1990-2019) and future conditions (2070-2100). These climatic conditions (past, present and future) were downloaded from four general circulation models (GCMs) selected from the Coupled Model Intercomparison Project Phase 5 (CMIP5). The GCMs are MIROC5, ACCESS1-3, CESM1-BGC, CMCC-CM and were downloaded from chelsa (Sanderson et al., 2015). We evaluated future climate projections from two scenarios of representative concentration pathways (RCPs): RCP4.5, an intermediate-to-pessimistic scenario assuming a radiative forcing to amount to  $4.5 \text{ Wm}^{-2}$  by 2100, and RCP8.5, a pessimistic emission scenario which project a radiative forcing to amount to  $8.5 \text{ Wm}^{-2}$  by 2100 (Thomson et al., 2011; Schwalm et al., 2020).

### *Sex ratio experiment*

We conducted a sex-ratio experiment on a site close (1 km) to a natural population of the focal species at the center of the range to estimate the effect of sex-ratio variation on female reproductive success. Details of the experiment are provided in Compagnoni et al. (2017) and Miller and Compagnoni (2022). In short, we established 124 experimental populations on plots measuring  $0.4 \times 0.4\text{m}$  and separated by at least 15m from each other at that site. We chose 15m because our pilot data show that more than 90% of wind pollination occurred within 13m. We varied population density (1-48 plants/plot)

129 and sex ratio (0%-100% female) across the experimental populations, and we replicated  
130 34 combinations of density-sex ratios. We collected the number of panicles from a subset  
131 of females in each plot and collected the number of seeds in each panicle. Since the  
132 number of panicles (proxy of reproduction effort) does not necessarily reflect reproduc-  
133 tion success in *Poar arachnifera*, we accessed reproduction success (seed fertilized) using  
134 greenhouse-based germination and trazolium-based seed viability assays.

135 We used the sex-ratio to estimate the probability of viability and the germination  
136 rate. Seed viability was modeled with a binomial distribution where the probability of  
137 viability ( $v$ ) was given by:

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

138 where  $OSR$  is the operational sex ratio (proportion of panicles that were female) in the  
139 experimental populations. The properties of the above function is supported by our  
140 previous work (Compagnoni et al., 2017). Here, seed viability is maximized at  $v_0$  as  $OSR$   
141 approaches zero (strongly male-biased) and goes to zero as  $OSR$  approaches 1 (strongly  
142 female-biased). Parameter  $\alpha$  controls how viability declines with increasing female bias.

143 We used a binomial distribution to model the germination data from greenhouse  
144 trials. Given that germination was conditional on seed viability, the probability of success  
145 was given by the product  $v * g$ , where  $v$  is a function of  $OSR$  (Eq. 1) and  $g$  is assumed to  
146 be constant.

### 147 *Sex specific demographic responses to climate*

148 We used individual level measurements of survival, growth (number of tillers), flow-  
149 ering, number of panicles to independently develop Bayesian mixed effect models de-

150 scribing how each vital rate varies as a function of sex, size, precipitation of growing  
 151 and dormant season and temperature of of growing and dormant season. We fit vital  
 152 rate models with second-degree polynomial functions for the influence of climate. We  
 153 included a second-degree polynomial because we expected that climate variables would  
 154 affect vital rates through a hump-shaped relationship.

155 We centered and standardized all predictors to facilitate model convergence. We  
 156 included site,source, and block as random effect. All the vital rate models used the same  
 157 linear and quadratic predictor for the expected value ( $\mu$ )(Eq. 2) . However, we applied a  
 158 different link function ( $f(\mu)$ ) depending on the distribution the vital rate. We modeled  
 159 survival and flowering data with a Bernoulli distribution. We modeled the growth (tiller  
 160 number) with a zero-truncated Poisson inverse Gaussian distribution. Fertility (panicle  
 161 count) was model as zero-truncated negative binomial.

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

162 where  $\beta_0$  is the grand mean intercept,  $\beta_1...\beta_{13}$  represent the size and climate dependent  
 163 slopes. *size* was on a natural logarithm scale. *pptgrow* is the precipitation of the growing  
 164 season (standardized to mean zero and unit variance), *tempgrow* is the temperature of  
 165 the growing season (standardized to mean zero and unit variance), *pptdorm* is the precip-  
 166 itation of the dormant season (standardized to mean zero and unit variance), *tempdorm*

167 is the temperature of the dormant season (standardized to mean zero and unit variance).  
168 The model also includes normally distributed random effects for block-to-block varia-  
169 tion ( $\phi \sim N(0, \sigma_{block})$ ) and source-to-source variation that is related to the provenance of  
170 the seeds used to establish the common garden ( $\rho \sim N(0, \sigma_{source})$ ), site to site variation  
171 ( $\nu \sim N(0, \sigma_{site})$ )

172 We fit all models in Stan (Stan Development Team, 2023), with weakly informative  
173 priors for coefficients ( $\mu = 0, \sigma = 100$ ) and variances ( $\gamma[0.001, 0.001]$ ). We ran three  
174 chains for 1000 samples for warmup and 4000 for interactions, with a thinning rate of  
175 3. We accessed the quality of the models using trace plots and predictive check graphs  
176 (Piironen and Vehtari, 2017) (Appendix S1: Figure S1).

177 To understand the effect of climate on vital rates, we got the 95 % credible interval of  
178 the posterior distribution. Then we assumed that there is 95 % probability that the true  
179 (unknown) estimates would lie within that interval, given the evidence provided by the  
180 observed data for each vital rate.

### 181 *Population growth rate responses to climate*

182 To understand the effect of climate on population growth rate, we used the vital rate  
183 estimated earlier to build a matrix projection model (MPM) structured by size (number  
184 of tillers), sex and climate as covariate. Let  $F_{x,z,t}$  and  $M_{x,z,t}$  be the number of female  
185 and male plants of size  $x$  in year  $t$  present at a location that has  $z$  as climate, where  
186  $x \in \{1, 2, \dots, U\}$  and  $U$  is the maximum number of tillers a plant can reach (here 95th  
187 percentile of observed maximum size). Let  $F_t^R$  and  $M_t^R$  be the new recruits, which we  
188 assume do not reproduce in their first year. We assume that the parameters of sex ratio-  
189 dependent mating (Eq. 1) do not vary with climate. For a pre-breeding census, the

190 expected numbers of recruits in year  $t + 1$  is given by:

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

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

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

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

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

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

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

198 In the two formula above, the first term represents seedlings that survived their first  
 199 year and enter the size distribution of established plants. Instead of using *P. arachnifera*  
 200 survival probability, we used the seedling survival probability ( $\sigma$ ) from demographic  
 201 studies of the hermaphroditic congener *Poa autumnalis* in east Texas (T.E.X. Miller and  
 202 J.A. Rudgers, *unpublished data*), and we assume this probability was constant across sexes  
 203 and climatic variables. We did this because we had little information on the early life

cycle transitions of greenhouse-raised transplants. We also assume that  $g(y, x = 1)$  is the probability that a surviving seedlings reach size  $y$ , the expected future size of 1-tiller plants from the transplant experiment. The second term represents survival and size transition of established plants from the previous year, where  $s$  and  $g$  give the probabilities of surviving at size  $x$  and growing from sizes  $x$  to  $y$ , respectively, and superscripts indicate that these functions may be unique to females ( $F$ ) and males ( $M$ ).

Because the two-sex MPM is nonlinear (vital rates affect and are affected by population structure) we estimated the asymptotic geometric growth rate ( $\lambda$ ) by numerical simulation, and repeated this across a range of climate.

*Identifying the mechanisms of population growth rate sensitivity to climate*

<sup>1</sup> To identify the mechanism by which climate affects population growth rate, we decomposed the effect of each climate variable (here Climate) on population growth rate ( $\lambda$ ) into contribution arising from the effect on each stage-specific vital rate (Caswell, 2000). At this end we used a life table response experiment (LTRE) with a regression designs. The LTRE approximates the change in  $\lambda$  with climate as the product of the sensitivity of  $\lambda$  to the parameters times the sensitivity of the parameters to climate, summed over all parameters (Caswell, 1989):

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

where,  $\theta_i^F$  and  $\theta_i^M$  represent sex-specific parameters: the regression coefficients for the intercepts and slopes of size-dependent vital rate functions. Because LTRE contributions

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<sup>1</sup>I don't think the LTRE analysis is adequately motivated by the Intro.

224 are additive, we summed across vital rates to compare the total contributions of female  
225 and male parameters.

226 *Implication on range shifts*

227 To understand the implication of our study on range, we extrapolate population growth  
228 using past, current and future climatic data across the range to map species distributions.  
229 Averaging projection of population growth rates was used to reduce uncertainty across  
230 climate projections (general circulation models).

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

232 **Results**

233 *Sex specific demographic response to climate change*

234 Most vital rates were strongly climate dependent, but the magnitude of their response  
235 differed between sexes suggesting a sex-specific demographic response to climate. Sur-  
236 vival and growth were strongly more dependent on climate than flowering and panicles  
237 Fig.2. There was a female survival and flowering advantage across all climatic seasons  
238 (Figs. 3A-3D, 3I-3K). On the contrary, there was a male panicle advantage across all cli-  
239 matic variables (Fig3X-Y). Counter-intuitively, there was no sex growth advantage in all  
240 season climatic variables (Fig 3E-3H).

241 Precipitation of the growing season decreased seasonal survival, whereas tempera-  
242 ture of the growing season, precipitation of the dormant season, and temperature of the  
243 dormant season increased seasonal survival. Unlike the probability of survival, the prob-  
244 ability of flowering increased with precipitation of the growing season and decreased  
245 with precipitation of the growing season and increased with temperature of the growing

246 season, precipitation of the dormant season, and temperature of the dormant season.  
247 This trade-off between survival and flowering provides an insight into the persistence  
248 of the species. In addition, the number of panicles decreased with precipitation for  
249 the growing season and the temperature of the dormant season and increased with the  
250 temperature of the growing season and precipitation. Finally, the precipitation and tem-  
251 perature of the growing season decreased seasonal growth, whereas the precipitation  
252 and temperature of the dormant season increased seasonal growth.

253 *Population growth rate response to climate change*

254 Consistent with the effect of climate on individual vital rate, we also found an effect  
255 of seasonal climate on population growth rate. Precipitation and temperature of the  
256 growing season decreased the population growth rate, whereas precipitation and tem-  
257 perature of the dormant season increased the population growth rate. Across all sites,  
258 the population growth rate was higher than one, suggesting an increase of population  
259 over time.

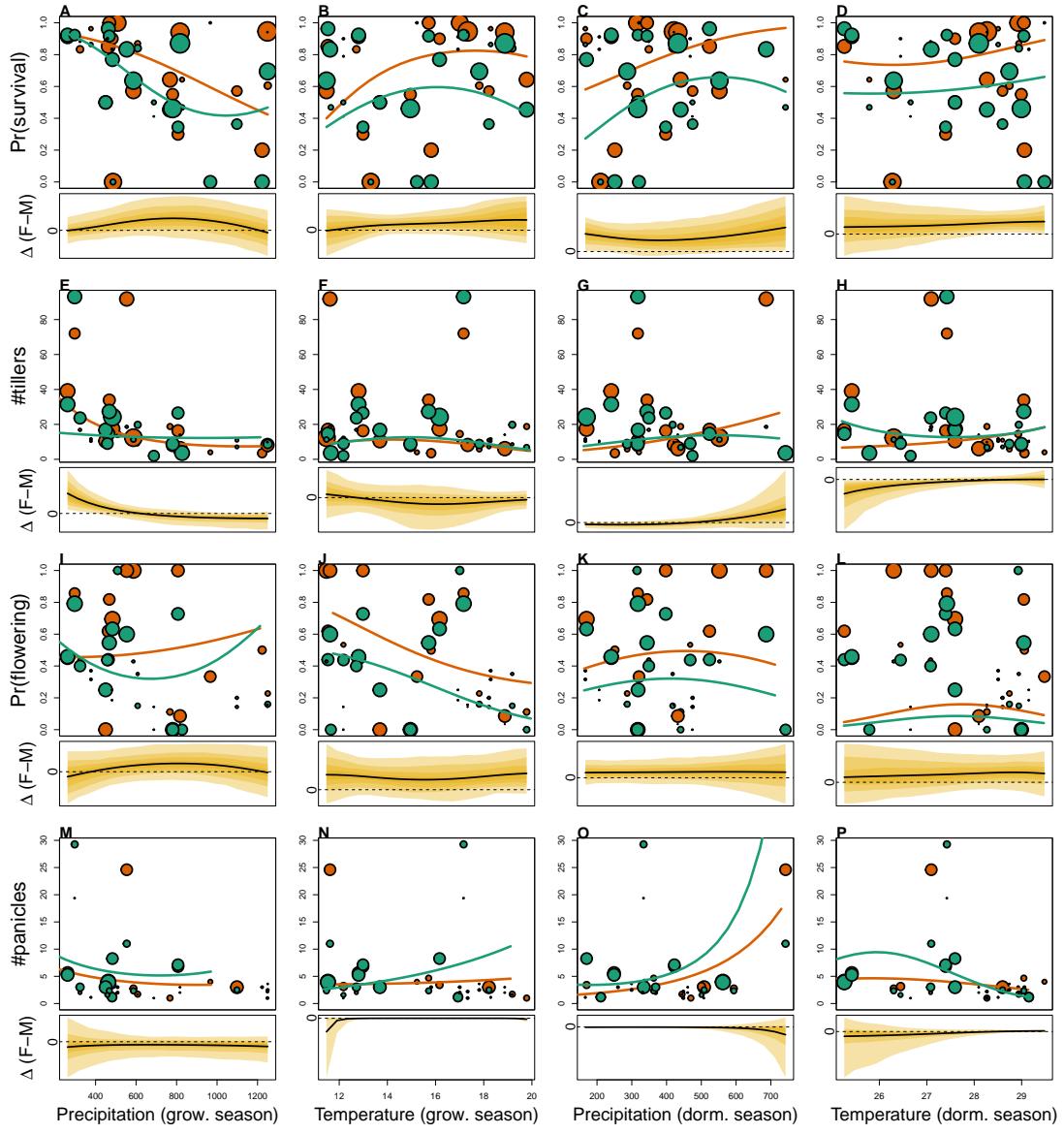
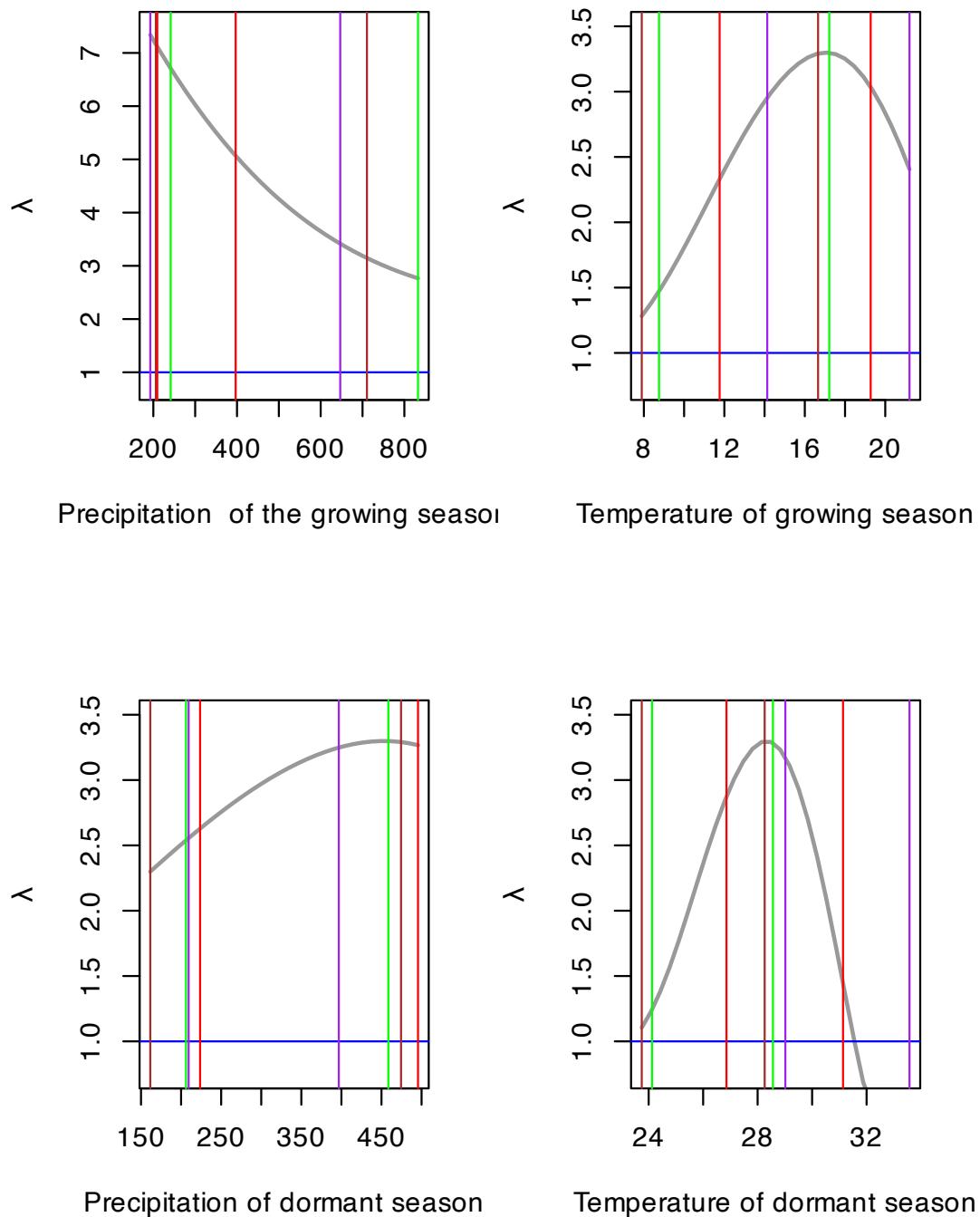


Figure 1: Sex specific demographic response to climate across species range: A–D, inter-annual probability of survival; E–H, inter-annual growth (change in number of tillers); I–L, probability of flowering; M–P, number of panicles produced given flowering. Points show means by site for females (orange) and males (green). Point size is proportional to the sample size of the mean. 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.



Figure<sup>16</sup> 2: XXX

## Appendix S1: Correspondence

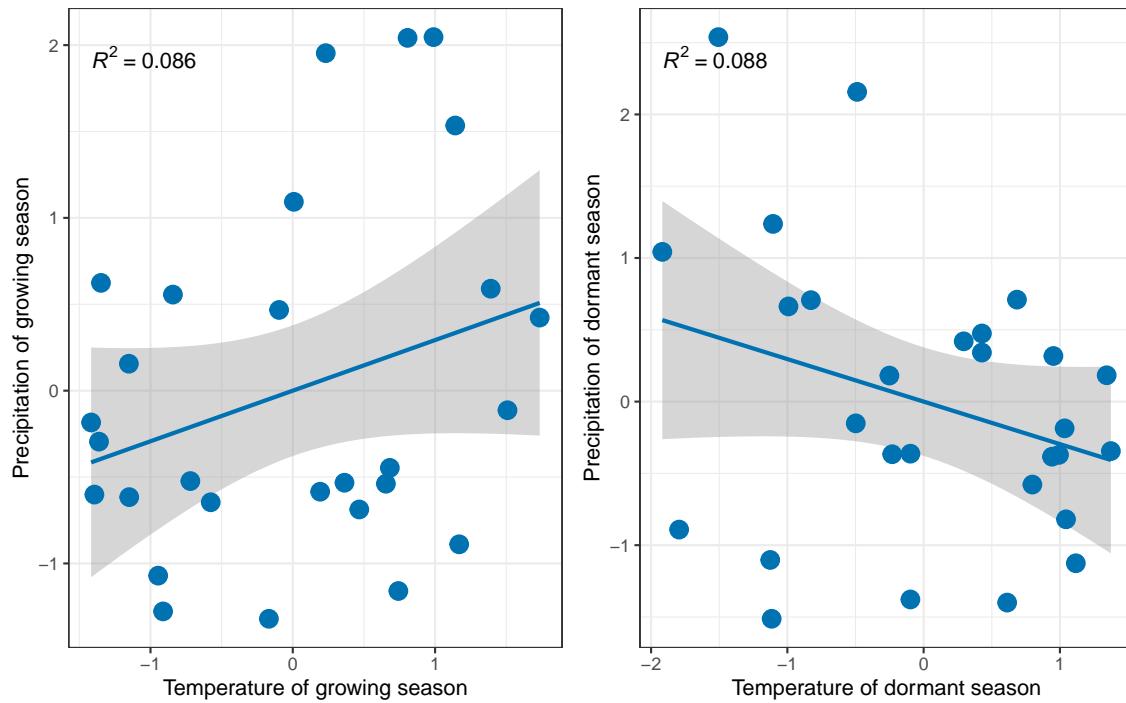


Figure A1: Relation between precipitation and temperature for each season (growing and dormant).  $R^2$  indicates the value of proportion of explained variance between the temperature and precipitation

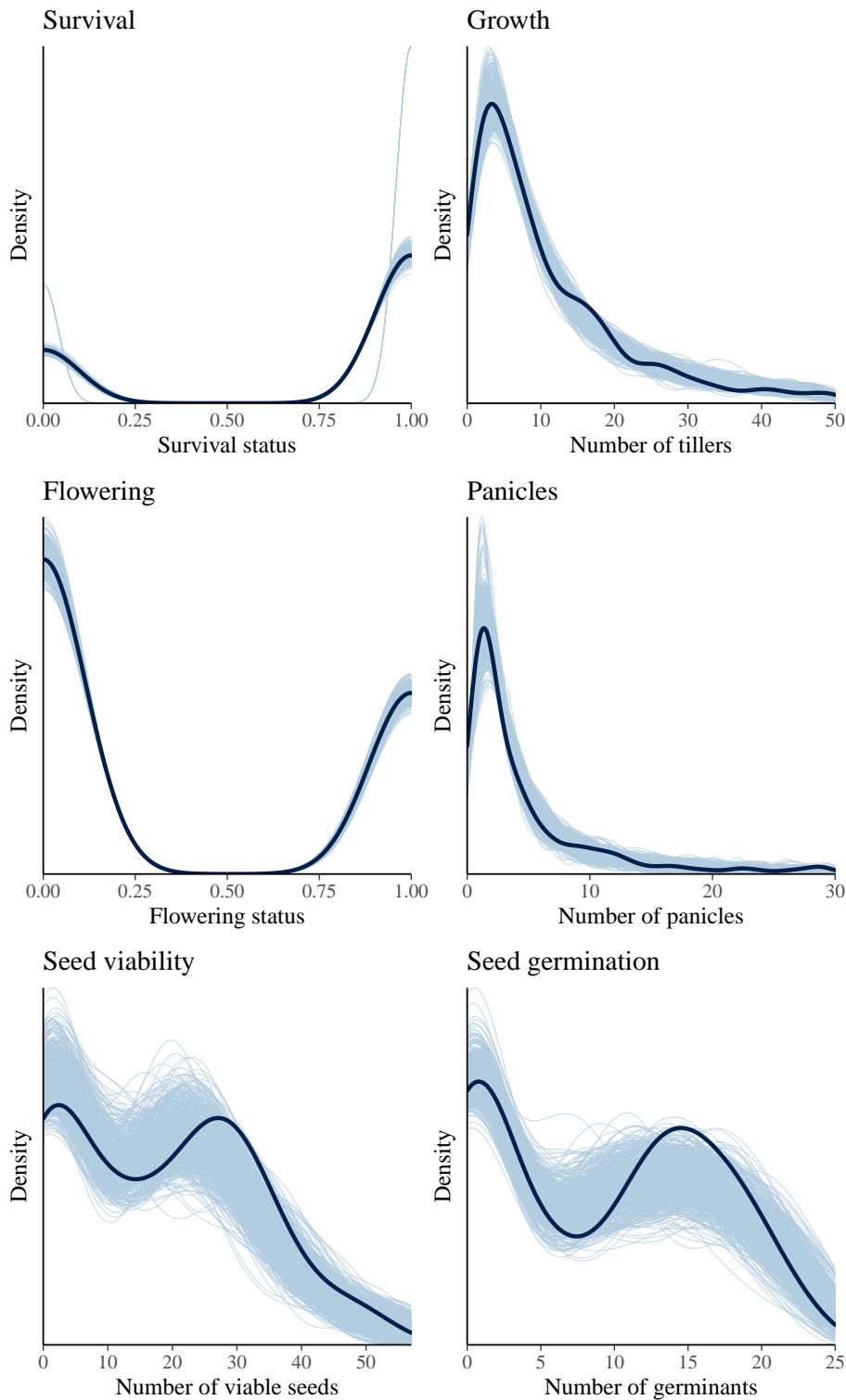


Figure A2: Consistency between real data and simulated values suggests that the fitted model accurately describes the data. Graph shows density curves for the observed data (light blue) along with the simulated values (dark blue). The first column shows the linear models and the second column shows the 2 degree polynomial models.

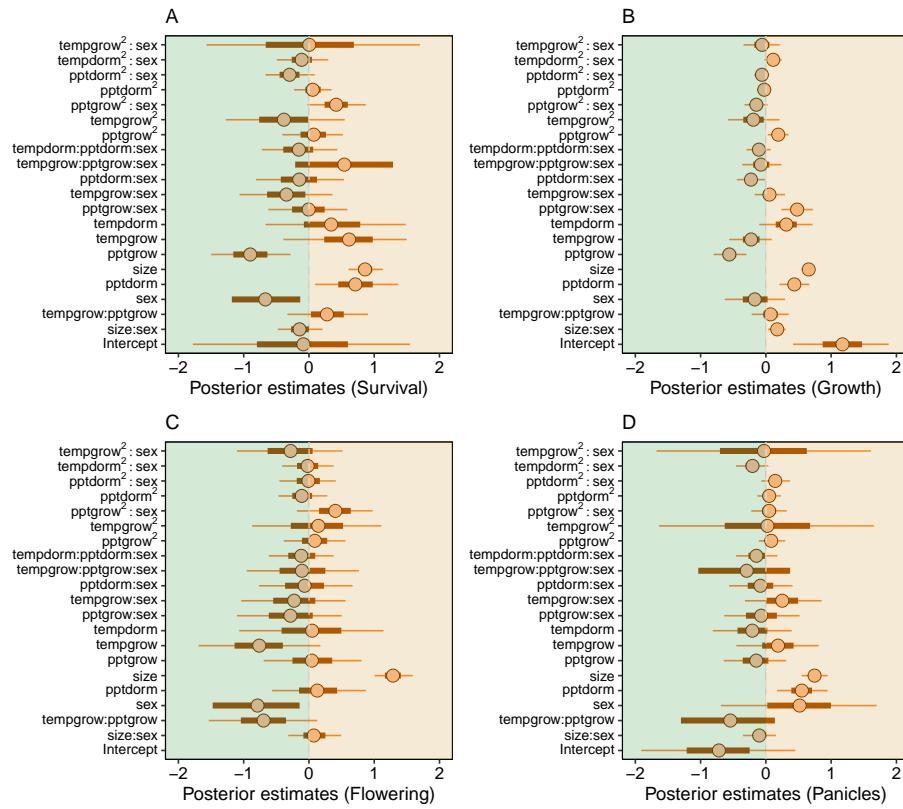


Figure A3: Posterior mean for each vital rate.

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