

Forecasting range shifts of a dioecious plant species under climate change

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1 Abstract

2 Rising temperatures and extreme drought events associated with global climate change has
3 triggered an urgent need for predicting species response to climate change. Currently, the
4 vast majority of theory and models in population biology, including those used to forecast
5 biodiversity responses to climate change, ignore the complication of sex structure. To address
6 this issue, we developed a climate-driven population matrix model using demographic data of
7 dioecious species (Texas bluegrass), past and future climate (different gas emission scenarios)
8 to forecast and backcast the effect of climate change on range shifts. Our results show a sex
9 specific demographic response to climate change. Female individuals have a demographic
10 advantage (higher vital rate) over males. Female demographic advantage led to a slight
11 decline in population viability under future climate assuming moderate gas emission and
12 a drastic reduction in population viability under future climate assuming high gas emission.
13 Despite a change in species range, climate change can alter population viability in dioecious
14 species. Overall, our work provides a framework for predicting the impact of climate on
15 dioecious species using population demography.

¹⁶ Introduction

¹⁷ Rising temperatures and extreme drought events associated with global climate change are
¹⁸ leading to increased concern about how species will become redistributed across the globe
¹⁹ under future climate conditions (Bertrand et al., 2011; Gamelon et al., 2017; Smith et al., 2024).
²⁰ Dioecious species (most animals and many plants) might be particularly vulnerable to the
²¹ influence of climate change because they often display skewed sex ratios that are generated or
²² reinforced by sexual niche differentiation (distinct responses of females and males to shared cli-
mate drivers) (Tognetti, 2012). Accounting for such a niche differentiation within a population
²⁴ is a long-standing challenge in accurately predicting which sex will successfully track envi-
ronmental change and how this will impact population viability and range shifts (Gissi et al.,
²⁵ 2023a; Jones et al., 1999). The vast majority of theory and models in population biology, includ-
²⁶ ing those used to forecast biodiversity responses to climate change, ignore the complication of
²⁷ sex structure (Ellis et al., 2017; Pottier et al., 2021). As a result, accurate forecasts of colonization-
²⁸ extinction dynamics for dioecious species under future climate scenarios are limited.
²⁹

³⁰ Climate change can influence dioecious populations via shifts in sex ratio.¹ Females and
³¹ males may respond differently to climate change, especially in species where there is sexual
³² niche differentiation (Gissi et al., 2023a,b; Hultine et al., 2016). This sex-specific response to
³³ climate change may help one sex to succeed in extreme climatic conditions rather than the
³⁴ other sex (Bürli et al., 2022; Zhao et al., 2012) leading to a skewness in the operational sex ratio
³⁵ (relative number of males and females as available mates) (Eberhart-Phillips et al., 2017). For
³⁶ example, experiments in two populations of Atlantic marine copepods (*Acartia tonsa*) revealed
³⁷ that male survival was more sensitive to increasing temperatures than female survival (Sasaki
³⁸ et al., 2019). In other species, such as *Pteropus poliocephalus* or *Populus cathayana*, females
³⁹ showed lower survival than males in response to high temperature (Welbergen et al., 2008;
⁴⁰ Zhao et al., 2012). Sex-specific responses to climate drivers have the potential to influence
⁴¹ population viability under global change because skew in the operational sex ratio can limit
⁴² reproduction through mate scarcity (Petry et al., 2016).

⁴³ Species's range limits, when not driven by dispersal limitation, should generally reflect
⁴⁴ the limits of the ecological niche (Lee-Yaw et al., 2016). For most species, niches and geographic
⁴⁵ ranges are often limited by climatic factors including temperature and precipitation (Sexton
⁴⁶ et al., 2009). Therefore, any substantial changes in the magnitude of these climatic factors in a
⁴⁷ given location across the range could impact population viability, with implications for range
⁴⁸ shifts based on which regions become more or less suitable (Davis and Shaw, 2001; Pease

¹This paragraph is really good but notice that the topic sentence (and much that follows) is largely redundant with the first paragraph. I would suggest creating clearer distinction between paragraphs.

49 et al., 1989). Forecasting range shifts for dioecious species is complicated by the potential for
50 each sex to respond differently to climate variation (Morrison et al., 2016; Pottier et al., 2021).
51 Populations in which males are rare under current climatic conditions could experience low
52 reproductive success due to sperm or pollen limitation that may lead to population decline in
53 response to climate change that disproportionately favors females (Eberhart-Phillips et al., 2017).
54 In contrast, climate change could expand male habitat suitability (e.g. upslope movement),
55 which might increase seed set for pollen-limited females and favor range expansion (Petry
56 et al., 2016). Although the response of species to climate warming is an urgent and active area
57 of research, few studies have disentangled the interaction between sex and climate drivers
58 to understand their combined effects on population dynamics and range shifts.

59 Our ability to track the impact of climate change on the population dynamics of
60 dioecious plants and the implication of such impact on range shift depends on our ability
61 to build mechanistic models that take into account the spatial and temporal context in which
62 sex specific response to climate change affects population viability (Czachura and Miller, 2020;
63 Davis and Shaw, 2001; Evans et al., 2016). For example, structured models that are built from
64 long-term demographic data collected from common garden experiments have emerged as
65 powerful technic to study the impact of climate change on species range shift (Merow et al.,
66 2017; Schwinning et al., 2022). These structured models are increasingly utilized for two
67 reasons. First, they enable the manipulation of climatic factors (temperature, precipitation)
68 and the measurement of species response to such a manipulation (Leicht-Young et al., 2007).
69 Second, they link individual-level demographic trait to population dynamics in response
70 to climate variation (Dahlgren et al., 2016; Louthan et al., 2022).

71 In this study, we used a mechanistic approach by combining geographically-distributed
72 field experiments, hierarchical statistical modeling, and two-sex population projection
73 modeling to understand the demographic response of dioecious species to climate change and
74 its implications for future range dynamics. Our study system is a dioecious plant species (*Poa*
75 *arachnifera*) distributed along environmental gradients in the south-central US corresponding
76 to variation in temperature across latitude and precipitation across longitude. A previous
77 study on the same system showed that, despite a differentiation of climatic niche between
78 sexes, the female niche mattered the most in driving the environmental limits of population
79 viability (Miller and Compagnoni, 2022b). However that study did not use climate variables
80 preventing us from backcasting and forecasting the impact of climate change on dioecious
81 species. Here, we asked four questions:

- 82 1. What are the sex-specific vital rate responses to variation in temperature and precipitation
83 across the species' range?

- 84 2. How sex-specific vital rates combine to determine the influence of climate variation on
85 population viability (λ)?
86 3. What are the historical and projected changes in climate across the species range?
87 4. What are the back-casted and fore-casted dynamics of this species' geographic niche
88 ($\lambda \geq 1$) and how does accountind for sex structure modify these predictions?

89 **Materials and methods**

90 **Study species**

91 Texas bluegrass (*Poa arachnifera*) is a perennial, summer-dormant cool-season (C3) grass that oc-
92 curs in Texas, Oklahoma, and southern Kansas, USA (Hitchcock, 1971). Texas bluegrass grows
93 between October and May, with onset of dormancy often from June to September (Kindiger,
94 2004). Flowering occurs in May and the species is pollinated by wind (Hitchcock, 1971).²

95 **Common garden experiment**

96 We set up a common garden experiment throughout and beyond the range of Texas bluegrass
97 to enable study of sex-specific demographic responses to climate and the implications for
98 range shifts. Details of the experimental design are provided in Miller and Compagnoni
99 (2022b); we provide a brief overview here.

100 The common experiment was installed at 14 sites across a **precipitation gradient**³ (FigX).
101 At each site, we established 14 blocks. For each block we planted three female and three
102 male individuals that were clonally propagated from eight natural source populations of
103 Texas bluegrass. The experiment was established in November 2013 and was census annually
104 through 2016, providing both spatial and inter-annual variation in climate.

105 Each May (2014-2016), we collected individual demographic data including survival
106 (alive or dead), growth (number of tillers), flowering status (reproductive or vegetative), and
107 fertility (number of panicles, conditional on flowering). For the analyses that follow, we focus
108 on the 2014-15 and 2015-16 transitions years.

²I think you need to say more about the geographic region and its climate. It will be important to motivate the split of growing and dormant seasons based on the natural history. You also need to describe the reproductive biology including dioecy and wind-pollination.

³While the Am Nat paper focused on precipitation, the actual design spans both temperature and precip, which is a feature you can exploit for your analysis, and would be worth highlighting as a source of novelty of this paper relative to the previous one. Some reviewers will be skeptical that we are publishing another paper from the same experiment, so the distinction should be made clear.

109 **Climatic data collection**

110 We downloaded monthly temperature and precipitation from Chelsa to describe observed
111 climate conditions during our study period (Karger et al., 2017). These climate data were used
112 as covariates in vital rate regressions, which allowed us to forecast and back-cast demographic
113 responses to climate change based on observations across the common garden experiment.
114 We aligned the climatic years to match demographic transition years (**May 1 – April 30**)⁴
115 rather than calendar years. Based on the natural history of this summer-dormant cool-season
116 species, we divided each transition year into growing and dormant seasons. We define June
117 through September as the dormant season and the rest of the year as the growing season.
118 Across years and sites, the experiment included substantial variation in growing and dormant
119 season temperature and precipitation (**Figure**⁵).

120 To back-cast and forecast changes in climate, we downloaded projection data for three
121 30-year periods: past (1901-1930), current (1990-2019) and future (2070-2100). Data for these
122 climatic periods were downloaded from four general circulation models (GCMs) selected
123 from the Coupled Model Intercomparison Project Phase 5 (CMIP5). The GCMs are MIROC5,
124 ACCESS1-3, CESM1-BGC, CMCC-CM and were downloaded from chelsa (Sanderson
125 et al., 2015). We evaluated future climate projections from two scenarios of representative
126 concentration pathways (RCPs): RCP4.5, an intermediate-to-pessimistic scenario assuming
127 a radiative forcing to amount to 4.5 Wm^{-2} by 2100, and RCP8.5, a pessimistic emission
128 scenario which project a radiative forcing to amount to 8.5 Wm^{-2} by 2100 (Schwalm et al.,
129 2020; Thomson et al., 2011).

130 Tom stopped here Monday evening. Generall impressions: really good! Need more
131 hypotheses regarding sex-specific responses. Also need to say a little more about prev study
132 (including what is known about sex-specific niches), and lean into the natural history at the
133 end of intro and start of methods. ⁶

134 **Sex ratio experiment**

135 We conducted a sex-ratio experiment on a site close (1 km) to a natural population of the
136 focal species at the center of the range to estimate the effect of sex-ratio variation on female
137 reproductive success. Details of the experiment are provided in Compagnoni et al. (2017) and
138 Miller and Compagnoni (2022b). In short, we established 124 experimental populations on
139 plots measuring 0.4 x 0.4m and separated by at least 15m from each other at that site. We chose

⁴I am not sure if these are actually the right dates.

⁵I think we should have a figure, maybe just for the appendix, that visualizes this.

⁶

¹⁴⁰ 15m because our pilot data show that more than 90% of wind pollination occurred within 13m.
¹⁴¹ We varied population density (1-48 plants/plot) and sex ratio (0%-100% female) across the ex-
¹⁴² perimental populations, and we replicated 34 combinations of density-sex ratios. We collected
¹⁴³ the number of panicles from a subset of females in each plot and collected the number of
¹⁴⁴ seeds in each panicle. Since the number of panicles (proxy of reproduction effort) does not nec-
¹⁴⁵ essarily reflect reproduction success in *Poar arachnifera*, we accessed reproduction success (seed
¹⁴⁶ fertilized) using greenhouse-based germination and trazolium-based seed viability assays.

¹⁴⁷ We used the sex-ratio to estimate the probability of viability and the germination rate.
¹⁴⁸ Seed viability was modeled with a binomial distribution where the probability of viability
¹⁴⁹ (v) was given by:

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

¹⁵⁰ where OSR is the operational sex ratio (proportion of panicles that were female) in the
¹⁵¹ experimental populations. The properties of the above function is supported by our previous
¹⁵² work (Compagnoni et al., 2017). Here, seed viability is maximized at v_0 as OSR approaches
¹⁵³ zero (strongly male-biased) and goes to zero as OSR approaches 1 (strongly female-biased).
¹⁵⁴ Parameter α controls how viability declines with increasing female bias.
¹⁵⁵ Parameter α controls how viability declines with increasing female bias.

¹⁵⁶ We used a binomial distribution to model the germination data from greenhouse trials.
¹⁵⁷ Given that germination was conditional on seed viability, the probability of success was given
¹⁵⁸ by the product $v * g$, where v is a function of OSR (Eq. 1) and g is assumed to be constant.

¹⁵⁹ Sex specific demographic responses to climate

¹⁶⁰ We used individual level measurements of survival, growth (number of tillers), flowering, num-
¹⁶¹ ber of panicles to independently develop Bayesian mixed effect models describing how each
¹⁶² vital rate varies as a function of sex, size, precipitation of growing and dormant season and tem-
¹⁶³ perature of of growing and dormant season. We fit vital rate models with second-degree poly-
¹⁶⁴ nomial functions for the influence of climate. We included a second-degree polynomial because
¹⁶⁵ we expected that climate variables would affect vital rates through a hump-shaped relationship.

¹⁶⁶ We centered and standardized all predictors to facilitate model convergence. We included
¹⁶⁷ site, source, and block as random effect. All the vital rate models used the same linear and
¹⁶⁸ quadratic predictor for the expected value (μ) (Eq. 2). However, we applied a different
¹⁶⁹ link function ($f(\mu)$) depending on the distribution the vital rate. We modeled survival and
¹⁷⁰ flowering data with a Bernoulli distribution. We modeled the growth (tiller number) with
¹⁷¹ a zero-truncated Poisson inverse Gaussian distribution. Fertility (panicle count) was model

172 as zero-truncated negative binomial.

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

174 where β_0 is the grand mean intercept, $\beta_1 \dots \beta_{13}$ represent the size and climate dependent slopes.
175 size was on a natural logarithm scale. pptgrow is the precipitation of the growing season
176 (standardized to mean zero and unit variance), tempgrow is the temperature of the growing
177 season (standardized to mean zero and unit variance), pptdorm is the precipitation of the
178 dormant season (standardized to mean zero and unit variance), tempdorm is the temperature
179 of the dormant season (standardized to mean zero and unit variance). The model also
180 includes normally distributed random effects for block-to-block variation ($\phi \sim N(0, \sigma_{\text{block}})$)
181 and source-to-source variation that is related to the provenence of the seeds used to establish
182 the common garden ($\rho \sim N(0, \sigma_{\text{source}})$), site to site variation ($\nu \sim N(0, \sigma_{\text{site}})$)

183 We fit all models in Stan (Stan Development Team, 2023), with weakly informative priors
184 for coefficients ($\mu = 0, \sigma = 100$) and variances ($\gamma[0.001, 0.001]$). We ran three chains for 1000
185 samples for warmup and 4000 for interactions, with a thinning rate of 3. We accessed the
186 quality of the models using trace plots and predictive check graphs (Piironen and Vehtari,
187 2017) (Supporting Information S-2).

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

192 Population growth rate responses to climate

193 To understand the effect of climate on population growth rate, we used the vital rate estimated
194 earlier to build a matrix projection model (MPM) structured by size (number of tillers), sex
195 and climate as covariate. Let $F_{x,z,t}$ and $M_{x,z,t}$ be the number of female and male plants of
196 size x in year t present at a location that has z as climate, where $x \in \{1, 2, \dots, U\}$ and U is the
197 maximum number of tillers a plant can reach (here 95th percentile of observed maximum
198 size). Let F_t^R and M_t^R be the new recruits, which we assume do not reproduce in their first

¹⁹⁹ year. We assume that the parameters of sex ratio-dependent mating (Eq. 1) do not vary with
²⁰⁰ climate. For a pre-breeding census, the expected numbers of recruits in year $t+1$ is given by:

$$\text{201} \quad F_{t+1}^R = \sum_{x=1}^U [p^F(x,z) \cdot c^F(x,z) \cdot d \cdot v(\mathbf{F}_t, \mathbf{M}_t) \cdot m \cdot \rho] F_{x,z,t} \quad (3)$$

$$\text{202} \quad M_{t+1}^R = \sum_{x=1}^U [p^F(x,z) \cdot c^F(x,z) \cdot d \cdot v(\mathbf{F}_t, \mathbf{M}_t) \cdot m \cdot (1-\rho)] F_{x,z,t} \quad (4)$$

²⁰³ where p^F and c^F are flowering probability and panicle production for females of size x , d
²⁰⁴ is the number of seeds per female panicle, v is the probability that a seed is fertilized, m is
²⁰⁵ the probability that a fertilized seed germinates, and ρ is the primary sex ratio (proportion
²⁰⁶ of recruits that are female), z is the climate. Seed fertilization depends on the OSR of panicles
²⁰⁷ (following Eq. 1) which was derived from the $U \times 1$ vectors of population structure \mathbf{F}_t and \mathbf{M}_t :

$$\text{208} \quad v(\mathbf{F}_t, \mathbf{M}_t) = v_0 * \left[1 - \left(\frac{\sum_{x=1}^U p^F(x,z) c^F(x,z) F_{x,z,t}}{\sum_{x=1}^U p^F(x,z) c^F(x,z) F_{x,z,t} + p^M(x,z) c^M(x,z) M_{x,z,t}} \right)^\alpha \right] \quad (5)$$

²⁰⁹ Thus, the dynamics of the size-structured component of the population are given by:

$$\text{210} \quad F_{y,t+1} = [\sigma \cdot g^F(y, x=1, z)] F_t^R + \sum_{x=1}^U [s^F(x,z) \cdot g^F(y, x, z)] F_{x,z,t} \quad (6)$$

$$\text{211} \quad M_{y,t+1} = [\sigma \cdot g^M(y, x=1, z)] M_t^R + \sum_{x=1}^U [s^M(x,z) \cdot g^M(y, x, z)] M_{x,z,t} \quad (7)$$

²¹² In the two formula above, the first term represents seedlings that survived their first year
²¹³ and enter the size distribution of established plants. Instead of using *P. arachnifera* survival
²¹⁴ probability, we used the seedling survival probability (σ) from demographic studies of the
²¹⁵ hermaphroditic congener *Poa autumnalis* in east Texas (T.E.X. Miller and J.A. Rudgers, *unpub-*
²¹⁶ *lished data*), and we assume this probability was constant across sexes and climatic variables. We
²¹⁷ did this because we had little information on the early life cycle transitions of greenhouse-raised
²¹⁸ transplants. We also assume that $g(y, x=1)$ is the probability that a surviving seedlings reach
²¹⁹ size y , the expected future size of 1-tiller plants from the transplant experiment. The second
²²⁰ term represents survival and size transition of established plants from the previous year, where
²²¹ s and g give the probabilities of surviving at size x and growing from sizes x to y , respectively,
²²² and superscripts indicate that these functions may be unique to females (F) and males (M).

²²³ Because the two-sex MPM is nonlinear (vital rates affect and are affected by population
²²⁴ structure) we estimated the asymptotic geometric growth rate (λ) by numerical simulation,
²²⁵ and repeated this across a range of climate.

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

227 ⁷ To identify which aspect of climate is most important for population viability, we use
228 a "random design" Life Table Response Experiment (LTRE). We used the RandomForest
229 package to fit a regression model with θ as predictors and λ_c as response (Ellner et al., 2016;
230 Liaw et al., 2002). The LTRE approximates the variation in λ in response to climate covariates
231 and their interaction (Caswell, 2000; Hernández et al., 2023):

232

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

233 where, θ_i , θ_j , θ_{ij} represent respectively the fitted regression slope for the covariate of the
234 dormant season, j the covariate of the growing season and ij the covariate of their interactions.

235 Because LTRE contributions are additive, we summed across vital rates to compare the
236 total contributions of female and male parameters.

237 **Implication on range shifts**

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

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

243 **Results**

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

245 Most vital rates were strongly climate dependent, but the magnitude of their response differed
246 between sexes suggesting a sex-specific demographic response to climate. Survival and
247 flowering were strongly more dependent on climate than growth (number of tillers) and
248 reproduction (number of panicles) (Fig.1; Supporting Information S-3). We found opposite
249 patterns in the direction of the effect on seasonal climate on the probability of survival and
250 flowering. The growing season (precipitation) has a negative effect on the probability of
251 survival, number of tillers, and the probability of flowering, whereas the dormant season has a
252 positive effect on these vital rates. Unlike the other seasonal variables, temperature had differ-

⁷I don't think the LTRE analysis is adequately motivated by the Intro.

ent effects on different vital rates. The growing season has a positive effect of the probability of survival, a negative effect of the probability of flowering, and the number of tillers, but no significant effect on the number of panicles. Further, there was a female survival and flowering advantage across both climatic seasons (Figures. 3A-3D, 3I-3K). On the contrary, there was a male panicle advantage across all climatic variables (Figure3X-Y). Counter-intuitively, there was no significant sex growth advantage in all season climatic variables (Figures. 3E-3H).

Population growth rate response to climate change

We estimated the predicted response to population fitness to seasonal climate gradients using a model assuming a female dominant model and another model using the two sexes. Consistent with the effect of climate on the individual vital rate, we found a strong effect of seasonal climate on population fitness. For both models (female dominant and two sexes), population fitness decreases with an increase of precipitation of growing season. Furthermore, population fitness was maximized between 23 and 17 degrees Celsius and decreases to zero just beyond 20 degrees Celsius during the growing season. Population fitness increases with temperature and precipitation of the dormant season.

Climatic niches and range predictions

We detected a strong effect of the past and future climate on population growth rate. However, for future climate, the magnitude of that effect was different between gas-scenario emissions. A moderate emission gas scenario (RCP4.5) has a moderate effect on the population growth rate, while a high emission scenario (RCP8.5) has a strong effect on the population growth rate. High-emission scenario (RCP8.5) will lead to an alteration of population viability. Under past climate conditions, population growth rate decreased below one for temperature of the growing season and the dormant season. Our demographically based range predictions broadly captured the known distribution of the species (Fig. 1). More specifically, the predicted population viable ($\lambda > 1$) matches the presence and absence of the species. Furthermore, viable populations of *P. arichnifera* were only predicted at the center of the range for current climatic conditions (Fig1). Future and past projections of climate change showed a north-west range shift compared to current distributions. Although *P. arichnifera* was predicted to have suitable habitat in the center of the range under the current climate, future warming is predicted to reduce much of the suitable habitat in the southern part (Figure).

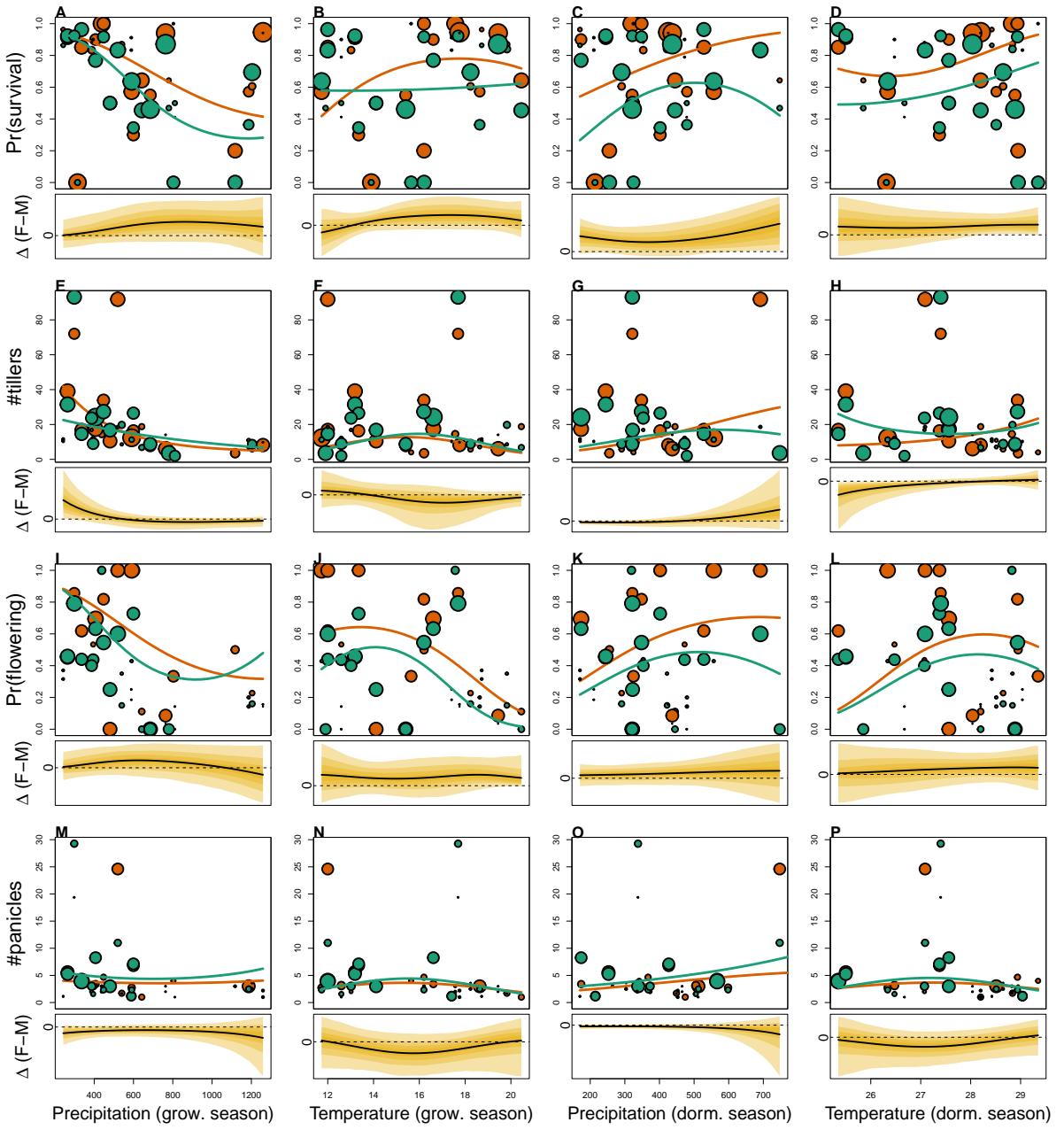


Figure 1: Sex specific demographic response to climate across species range: A–D, inter-annual probability of survival; E–H, inter-annual growth (change in number of tillers); I–L, probability of flowering; M–P, number of panicles produced given flowering. Points show means by site for females (orange)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

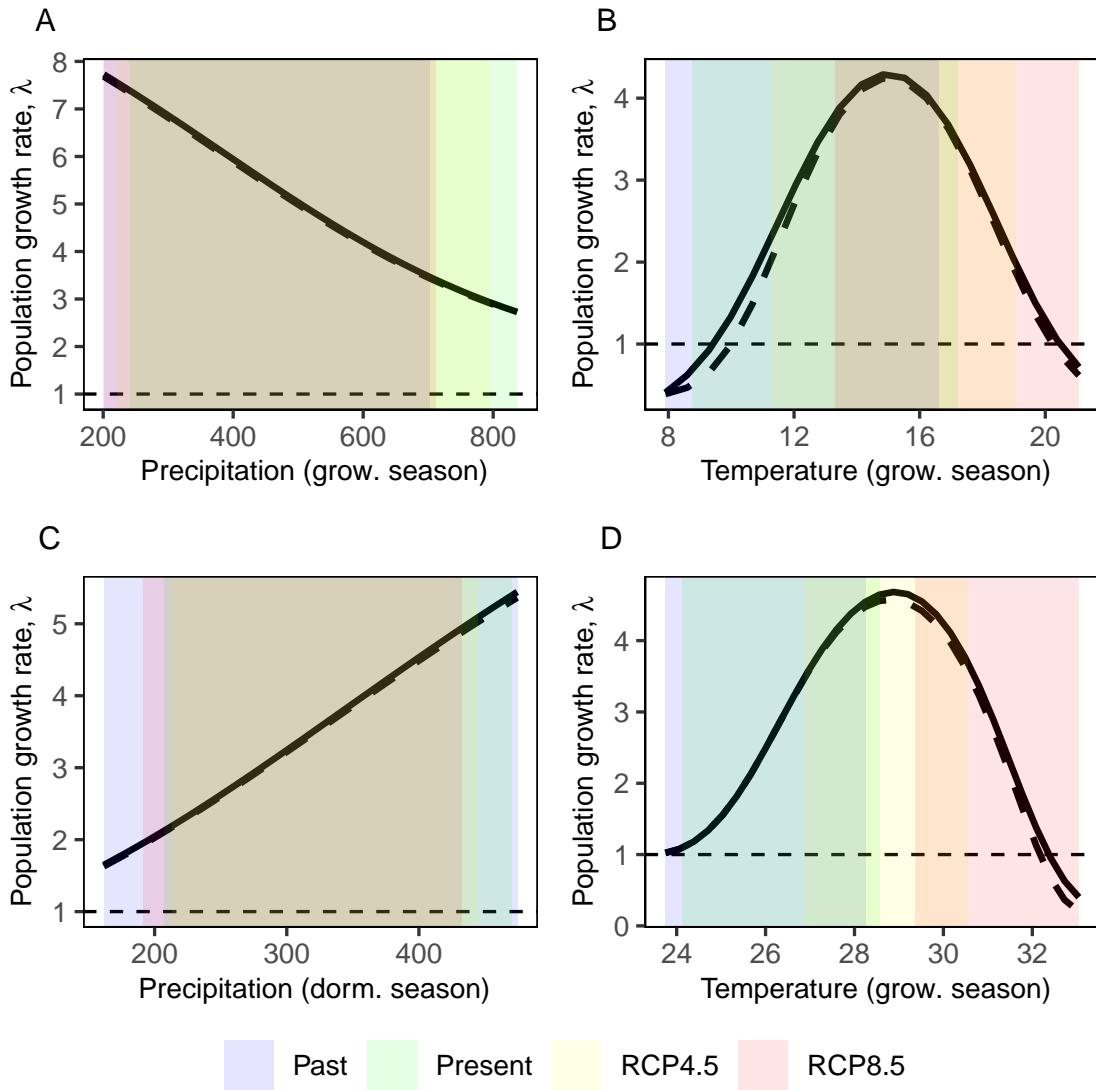


Figure 2: Population growth rate (λ) as a function of climate (past climate, present and predicted future climates). For future climate, we show a Representation Concentration Pathways 4.5 and 8.5. Values of (λ) are derived from the mean climate variables across 4 GCMs. The solid bold curve shows prediction by the two-sex matrix projection model that incorporates sex- specific demographic responses to climate with sex ratio dependent seed fertilization. The bold dashed curve represents the prediction by the female dominant matrix projection model. The dashed horizontal line indicates the limit of population viability ($\lambda = 1$)

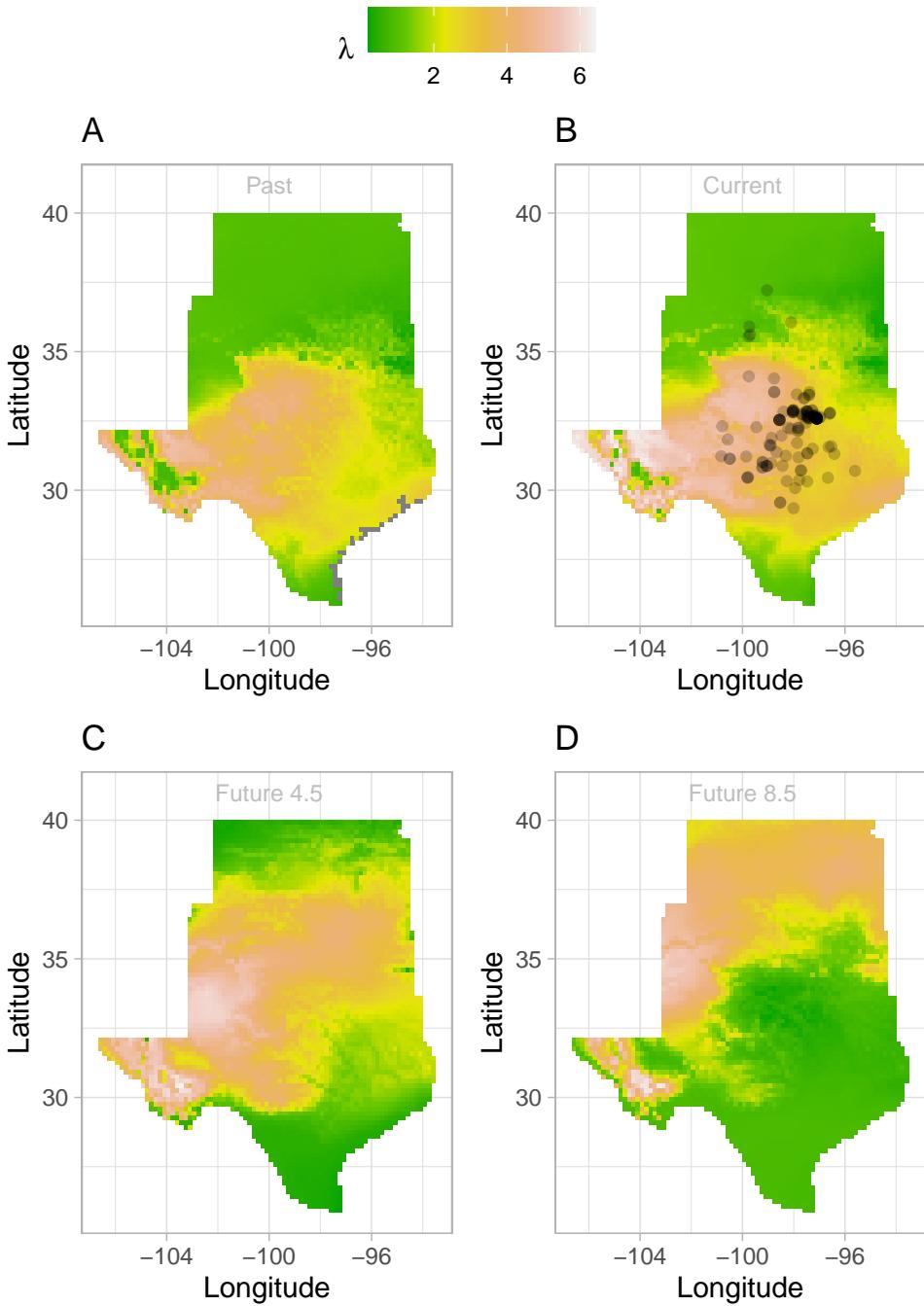


Figure 3: Past (A), Current (B), Future (2070–20100) (C and D) predicted range shift based on population growth rate. Future projections were based on the average population growth rate in four GCMs. The black circles on panel B indicate all known presence points collected from GBIF from 1990 to 2019, which corresponds to the current condition in our prediction. The occurrences of GBIFs are distributed inwith higher population fitness habitat ($\lambda > 1$) , confirming that our study approach can reasonably predict range shifts.

²⁸³ **Discussion**

284 **References**

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Supporting Information

396 S.1 XX

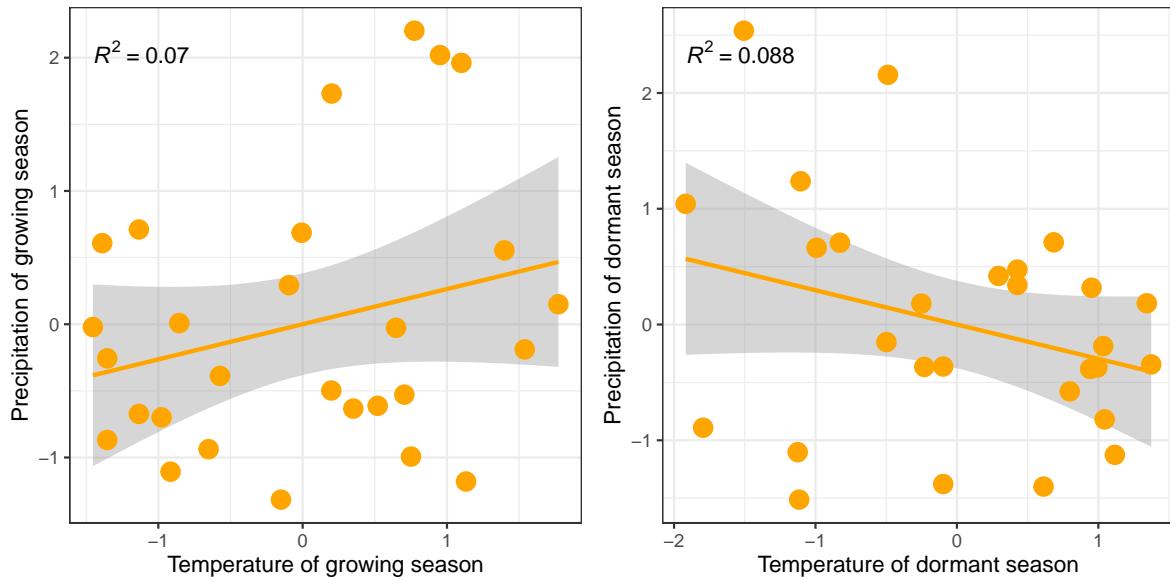


Figure S-1: Relation between precipitation and temperature for each season (growing and dormant). R^2 indicates the value of proportion of explained variance between the temperature and precipitation

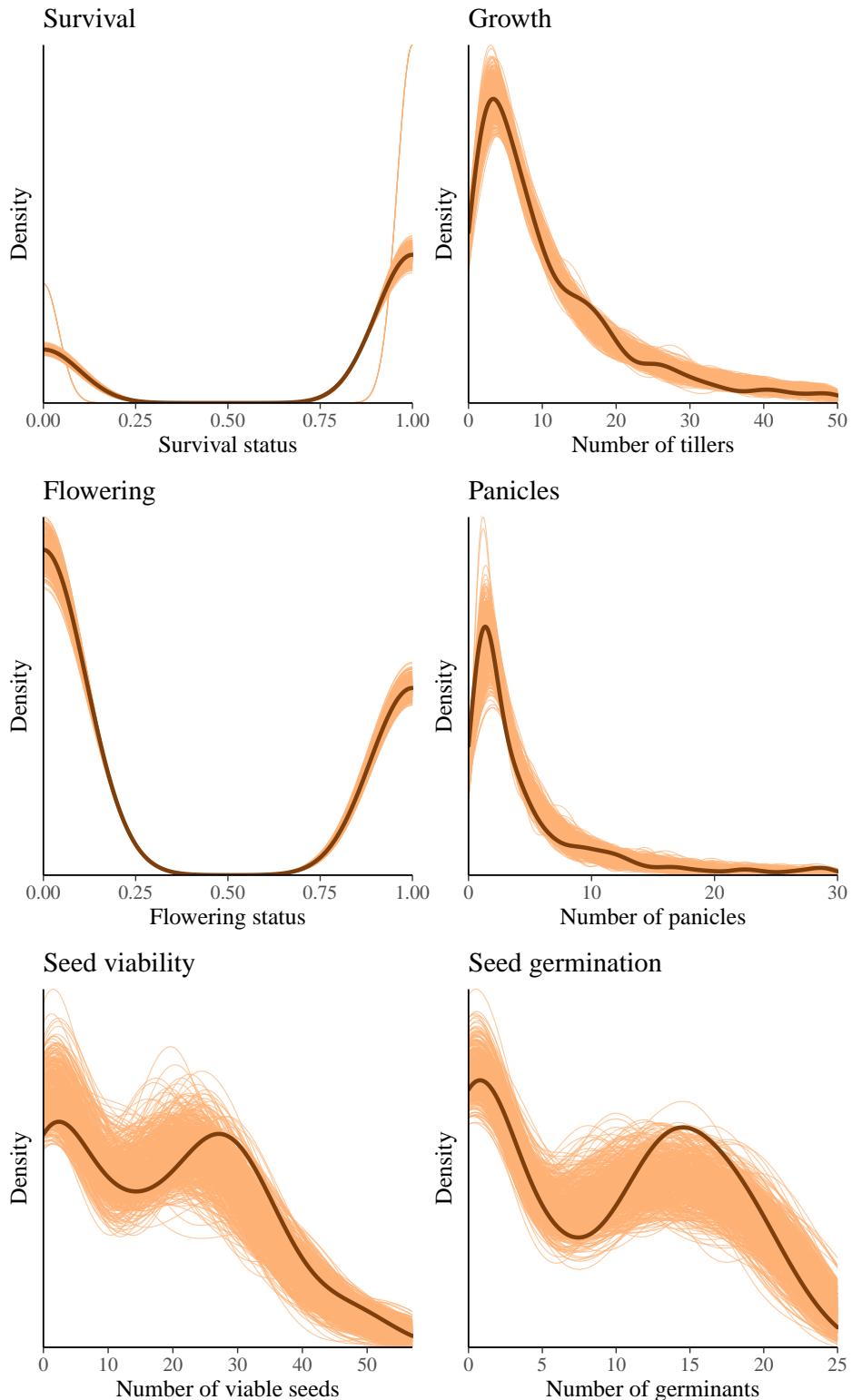


Figure S-2: Consistency between real data and simulated values suggests that the fitted model accurately describes the data. Graph shows density curves for the observed data (light blue) along with the simulated values (dark blue). The first column shows the linear models and the second column shows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

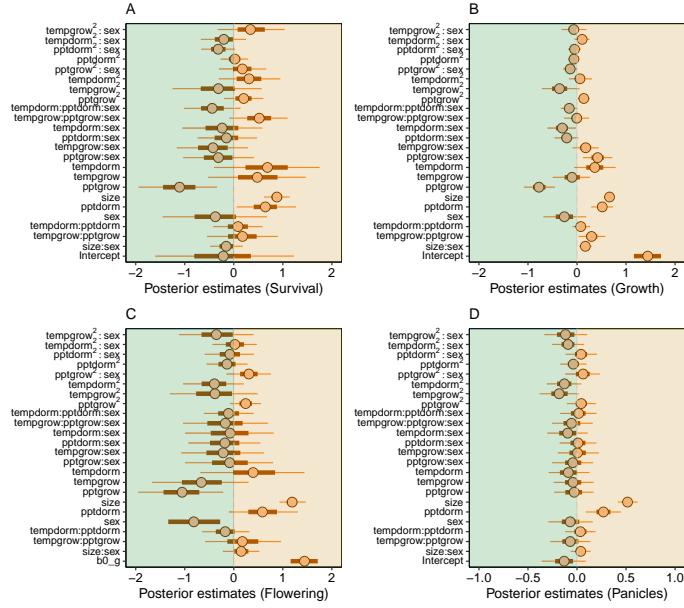


Figure S-3: Mean parameter values and 95% credible intervals for all vital rates.

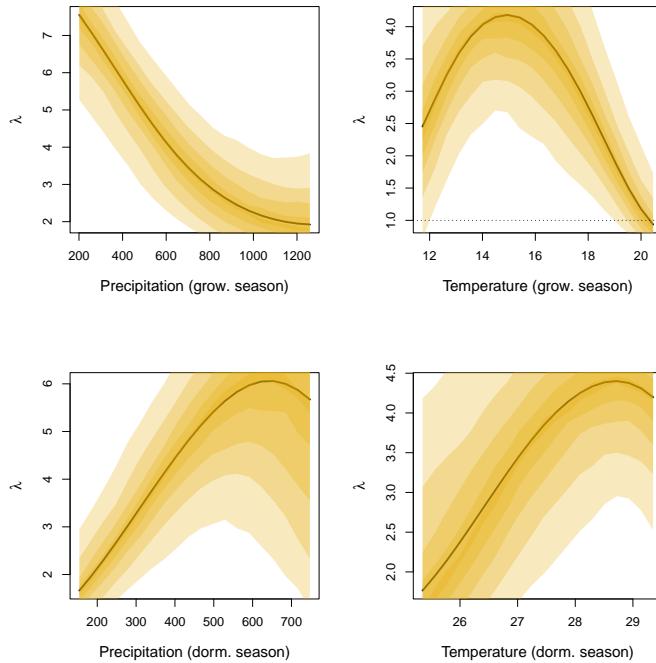


Figure S-4: Population growth rate (λ) as a function of seasonal climate (2016-2017), predicted by the two-sex matrix projection model that incorporates sex-specific demographic responses to climate with sex ratio-dependent seed fertilization. We show the mean posterior distribution of λ in solid lines, 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 ($\lambda = 1$)

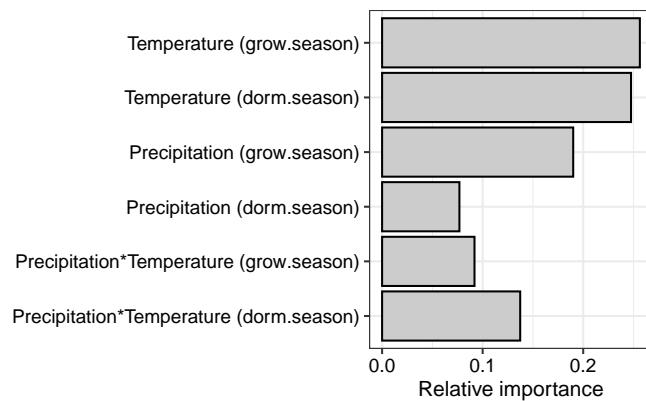


Figure S-5: XXX