

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

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February 26, 2024

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Submitted to *Ecology letters*

Manuscript type: Article

Open Research statement: All of our data and code are available during peer review at <https://github.com/jmoutouama/POAR-Forecasting>. This manuscript and its contents can be reproduced from this file: <https://github.com/jmoutouama/POAR-Forecasting/Manuscript/Forescasting.Rnw>. All data are provided at <https://github.com/jmoutouama/POAR-Forecasting/tree/main/data>.

**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

## 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 (most animals and many plants) might be particularly  
17 vulnerable to the influence of climate change because they often display skewed sex ra-  
18 tios that are generated or reinforced by sexual niche differentiation (distinct responses  
19 of females and males to shared climate drivers) (Tognetti, 2012). Accounting for such a  
20 niche differentiation within a population is a long-standing challenge in accurately pre-  
21 dicting which sex will successfully track environmental change and how this will impact  
22 population viability and range shifts (Jones et al., 1999; Gissi et al., 2023a). The vast  
23 majority of theory and models in population biology, including those used to forecast  
24 biodiversity responses to climate change, ignore the complication of sex structure (Pot-  
25 tier et al., 2021; Ellis et al., 2017). As a result, accurate forecasts of colonization-extinction  
26 dynamics for dioecious species under future climate scenarios are limited.<sup>1</sup>

27 Climate change can influence dioecious populations via shifts in sex ratio.<sup>2</sup> Females  
28 and males may respond differently to climate change, especially in species where there  
29 is 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 rather than the other sex (Zhao et al., 2012; Bürli et al., 2022) leading to a skewness in the  
32 operational sex ratio (relative number of males and females as available mates) (Eberhart-  
33 Phillips et al., 2017). For example, experiments in two populations of Atlantic marine

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<sup>1</sup>This is a great opening paragraph!

<sup>2</sup>This 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.

34 copepods (*Acartia tonsa*) revealed that male survival was more sensitive to increasing  
35 temperatures than female survival (Sasaki et al., 2019). In other species, such as *Pteropus*  
36 *poliocephalus* or *Populus cathayana*, females showed lower survival than males in response  
37 to high temperature (Welbergen et al., 2008; Zhao et al., 2012). Sex-specific responses to  
38 climate drivers have the potential to influence population viability under global change  
39 because skew in the operational sex ratio can limit reproduction through mate scarcity  
40 (Petry et al., 2016).

41 Species's range limits, when not driven by dispersal limitation, should generally re-  
42 flect the limits of the ecological niche<sup>3</sup>. For most species, niches and geographic ranges  
43 are often limited by climatic factors including temperature and precipitation (Sexton  
44 et al., 2009). Therefore, any substantial changes in the magnitude of these climatic factors  
45 in a given location across the range could impact population viability, with implications  
46 for range shifts based on which regions become more or less suitable (Davis and Shaw,  
47 2001; Pease et al., 1989). Forecasting range shifts for dioecious species is complicated  
48 by the potential for each sex to respond differently to climate variation (Pottier et al.,  
49 2021; Morrison et al., 2016). Populations in which males are rare under current climatic  
50 conditions could experience low reproductive success due to sperm or pollen limitation  
51 that may lead to population decline in response to climate change that disproportionately  
52 favors females (Eberhart-Phillips et al., 2017). In contrast, climate change could  
53 expand male habitat suitability (e.g. upslope movement), which might increase seed  
54 set for pollen-limited females and favor range expansion (Petry et al., 2016). Although  
55 the response of species to climate warming is an urgent and active area of research, few  
56 studies have disentangled the interaction between sex and climate drivers to understand  
57 their combined effects on population dynamics and range shifts.

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<sup>3</sup>cite – there is a relevant paper by Julie Lee-Yaw and Amy Angert, and lots of related literature

58 Our ability to track the impact of climate change on the population dynamics of  
59 dioecious plants and the implication of such impact on range shift depends on our ability  
60 to build mechanistic models that take into account the spatial and temporal context in  
61 which sex specific response to climate change affects population viability (Davis and  
62 Shaw, 2001; Evans et al., 2016; Czachura and Miller, 2020).<sup>4</sup> At their range edge where  
63 climatic conditions are expected to be less favorable, if dioecious species populations are  
64 non-viable in response to climate change, global warming will induce range contraction  
65 in dioecious species. In reverse, if populations at the edge are viable habitats in response  
66 to global warming, dioecious species populations could shift their range and relocate to  
67 more favorable and thereby favored range expansion.

68 In this study, we used a mechanistic approach by combining geographically-distributed  
69 field experiments, hierarchical statistical modeling, and two-sex population projection  
70 modeling to understand the demographic response of dioecious species to climate change  
71 and its implications for future range dynamics. Our study system is a dioecious plant  
72 species (*Poa arachnifera*) distributed along environmental gradients in the south-central  
73 US corresponding to variation in temperature across latitude and precipitation across  
74 longitude (MAP).<sup>5</sup> Here, we asked four questions:

- 75 1. What are the sex-specific vital rate responses to variation in temperature and pre-  
76 cipitation across the species' range?
- 77 2. How sex-specific vital rates combine to determine the influence of climate variation  
78 on population viability ( $\lambda$ )?

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<sup>4</sup>This is a great topic sentence and an important point, but the paragraph does not really expand upon this point about mechanistic models. The next few sentences do not really say anything new. I think it would be stronger to discuss the value and challenges of mechanistic models for species' range shifts.

<sup>5</sup>I would include a few more sentences of context about the study before jumping to the questions. For example it seems relevant to acknowledge the previous study and highlight that our previous approach used proxy variables, so could not be used to forecast responses to environmental change.

- 79      3. What are the historical and projected changes in climate across the species range?
- 80      4. What are the back-casted and fore-casted dynamics of this species' geographic
- 81      niche ( $\lambda \geq 1$ ) and how does accountind for sex structure modify these predictions?

82                         **Materials and methods**

83                         *Study species*

84      Texas bluegrass (*Poa arachnifera*) is a perenniel, summer-dormant cool-season (C3) grass  
85      that occurs in Texas, Oklahoma, and southern Kansas, USA (Hitchcock, 1971). Texas  
86      bluegrass grows between October and May, with onset of dormancy often from June to  
87      September (Kindiger, 2004). Flowering occurs in May and the species is pollinated by  
88      wind (Hitchcock, 1971).<sup>6</sup>

89                         *Common garden experiment*

90      We set up a common garden experiment throughout and beyond the range of Texas  
91      bluegrass to enable study of sex-specific demographic responses to climate and the im-  
92      plications for range shifts (Merow et al., 2017; Schwinning et al., 2022).<sup>7</sup> Details of the  
93      experimental design are provided in Miller and Compagnoni (2022); we provide a brief  
94      overview here.

95      The common experiment was installed at 14 sites across a precipitation gradient<sup>8</sup>

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<sup>6</sup>I 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.

<sup>7</sup>I am not sure why you cite these studies here. They would be more appropriate for the Intro if you expand the paragraph about mechanistic modeling.

<sup>8</sup>While the Am Nat paper focused on precipitation, the actual design spans both temperature and precip, whch 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,

96 (FigX). At each site, we established 14 blocks. For each block we planted three female  
97 and three male individuals that were clonally propagated from eight natural source pop-  
98 ulations of Texas bluegrass. The experiment was established in November 2013 and  
99 was census annually through 2016, providing both spatial and inter-annual variation in  
100 climate.

101 In mid-May of each year (2014-2016), we collected individual demographic data in-  
102 cluding survival (alive or dead), growth (number of tillers), flowering status (reproduc-  
103 tive or vegetative), and fertility (number of panicles, conditional on flowering). For the  
104 analyses that follow, we focus on the 2014-15 and 2015-16 transitions years, since 2013-14  
105 was not a complete (12-month) transition year. The data set included # unique individu-  
106 als (# and # females) and # plant-year observations.

### 107 *Climatic data collection*

108 We downloaded monthly temperature and precipitation from Chelsa to describe ob-  
109 served climate conditions during our study period (Karger et al., 2017). These climate  
110 data were used as covariates in vital rate regressions, which allowed us to forecast and  
111 back-cast demographic responses to climate change based on observations across the  
112 common garden experiment. We aligned the climatic years to match demographic tran-  
113 sition years (**June 1 – May 31**)<sup>9</sup> rather than calendar years. Based on the natural history of  
114 this summer-dormant cool-season species, we divided each transition year into growing  
115 and dormant seasons. We define June 1 through September 30 as the dormant season  
116 and the rest of the transition year (October 1 – May 31) as the growing season. Across  
117 years and sites, the experiment included substantial variation in growing and dormant  
118 season temperature and precipitation (Figure A4).

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so the distinction should be made clear.

<sup>9</sup>Updated with new approach.

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

129 10

### 130 *Sex ratio experiment*

131 We conducted an experiment at a site near the center of the range to estimate the effect  
132 of sex ratio variation on female reproductive success. Details of the experiment are  
133 provided in Compagnoni et al. (2017) and Miller and Compagnoni (2022). In short, we  
134 established 124 experimental populations on plots measuring  $0.4 \times 0.4\text{m}$  and separated  
135 by at least 15m from each other. We chose 15m because our pilot data show that more  
136 than 90% of wind pollination occurred within 13m. We varied population density (1-48  
137 plants/plot) and sex ratio (0%-100% female) across the experimental populations, and  
138 we replicated 34 combinations of density and sex ratio. We collected the number of  
139 panicles from a subset of females in each plot and recorded the number of seeds in each  
140 panicle. The raw seed count included both fertilized and unfertilized seeds. We further

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<sup>10</sup>*Tom stopped here during the first round of edits. Generall impressions so far: really good! Need more hypotheses regarding sex-specific responses. Also need to say a little more about prev study (including what is known about sex-specific niches), and lean into the natural history at the end of intro and start of methods.*

<sup>141</sup> assessed reproductive success (seeds fertilized) using greenhouse-based germination and  
<sup>142</sup> trazolium-based seed viability assays.

Using these data, seed viability was modeled as a function of local sex ratio with a binomial distribution where the probability of viability ( $v$ ) was given by:

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

<sup>143</sup>  $OSR$  is the operational sex ratio (proportion of panicles that were female) in the experimental populations. The properties of this function are supported by our previous work  
<sup>144</sup> (Compagnoni et al., 2017): seed viability is maximized at  $v_0$  as  $OSR$  approaches zero  
<sup>145</sup> (strongly male-biased) and goes to zero as  $OSR$  approaches 1 (strongly female-biased).  
<sup>146</sup> Parameter  $\alpha$  controls how viability declines with increasing female bias.  
<sup>147</sup>

<sup>148</sup> We used a binomial distribution to model the germination data from greenhouse trials. Given that germination was conditional on seed viability, the probability of success  
<sup>149</sup> was given by the product  $v * g$ , where  $v$  is given by Eq. 1 and  $g$  is assumed to be constant.  
<sup>150</sup>

### <sup>151</sup> *Sex specific demographic responses to climate*

<sup>152</sup> We used individual-level measurements of survival, growth (number of tillers), flower-  
<sup>153</sup> ing, and number of panicles to develop Bayesian mixed effect models describing how  
<sup>154</sup> each vital rate varies as a function of sex, size, and temperature and precipitation of  
<sup>155</sup> growing and dormant seasons. To allow for non-monotonic climate responses (e.g., in-  
<sup>156</sup> termediate optima), we fit vital rate models with second-degree polynomial functions  
<sup>157</sup> for the influence of climate variables. We account for background heterogeneity asso-  
<sup>158</sup> ciated with site, block, and source population of the transplants, which are modeled as  
<sup>159</sup> statistical random effects.

All the vital rate models used the same linear predictor for the expected value ( $\mu$ )(Eq. 2) that included main effects of size, sex, and four climate variables as well as two-way and three-way interactions that allow for interaction between temperature and precipitation (within season) and sex-specific size-dependence and climate-sensitivity:

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

When used as a covariate, *size* was on a natural logarithm scale ( $\log(tillers)$ ). We centered and standardized (mean zero, unit variance) all predictors to facilitate model convergence. *pptgrow* is the precipitation of the growing season, *tempgrow* is the temperature of the growing season, *pptdorm* is the precipitation of the dormant season, *tempdorm* is the temperature of the dormant season. The model also includes normally distributed random effects for site to site variation ( $\nu \sim N(0, \sigma_{site})$ ), block-to-block variation ( $\phi \sim N(0, \sigma_{block})$ ), and variation among source populations related to the provenience of the plants used to establish the common garden ( $\rho \sim N(0, \sigma_{source})$ ),

We applied a different link function ( $f(\mu)$ ) and error distribution depending on the vital rate. We modeled survival and flowering data with a Bernoulli distribution (logit link). We modeled the growth (tiller number) with a zero-truncated Poisson inverse Gaussian distribution and fertility (panicle count) as zero-truncated negative binomial (log link). For growth and survival the size covariate was  $\log(tillers)$  in the previous

173 census. For flowering and panicle production the size covariate was log(tillers) in the  
174 current census. Note that the growth model uses raw tiller count as the discrete response  
175 variable, which allows us to populate a transition matrix for expected tiller number  
176 conditional on previous tiller number. We found that the mean-variance flexibility of the  
177 Poisson inverse Gaussian was necessary for capturing patterns of size transition in the  
178 data.

179 We fit all models in Stan (Stan Development Team, 2023), with weakly informative  
180 priors for all  $\beta$  coefficients ( $\mu = 0, \sigma = 100$ ) and variances ( $\gamma[0.001, 0.001]$ ). We ran three  
181 chains for 1000 samples for warmup and 4000 for interactions, with a thinning rate of  
182 3. We used trace plots to assess model convergence and predictive checks to compare  
183 real data against data simulated from the fitted models (Piironen and Vehtari, 2017)  
184 (Appendix S1: Figure S1). To understand the effect of climate on vital rates, we got the  
185 95 % credible interval of the posterior distribution.<sup>11</sup>

186 *Population growth rate responses to climate*

To understand the effect of climate on population growth rate, we used the fitted vital rates to build a matrix projection model (MPM) structured by size (number of tillers) and sex, with climate variables as covariates to the vital rate functions. Following parameter estimation from the common garden experiment, we assume that demographic sensitivity to climate is limited to survival, growth, the probability of flowering, and panicle production of flowering plants. Let  $F_{x,t}$  and  $M_{x,t}$  be the number of female and male plants of size  $x$  in year  $t$ , where  $x \in \{1, 2, \dots, U\}$  and  $U$  is the maximum number of tillers a plant can reach (here 95th percentile of observed maximum size). Let  $F_t^R$  and  $M_t^R$  be the

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<sup>11</sup>Because there are quadratic terms in the model I don't think the coefficients really tell the story of climate effects. It's much more effective to look at your plots of the functions, though it could still be fine to include the coefficient plot in the appendix. One concern: there are 24 coefficients in the model you have written above but only 21 in the Posterior\_mean.pdf coefficient plot.

new recruits, which we assume do not reproduce in their first year, and let  $\mathbf{z}$  be a vector of climate covariates (growing and dormant season temperature and precipitation). For a pre-breeding census, the expected numbers of recruits in year  $t + 1$  is given by:

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

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

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

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

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

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

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

<sup>187</sup> In Eq. 6, the first term represents seedlings that survived their first year (survival probability  $\sigma$ ) and enter the size distribution of established plants. Because we did not measure  
<sup>188</sup> *P. arachnifera* seedling survival in our common garden experiment, we used the seedling  
<sup>189</sup> survival probability from our demographic studies of the hermaphroditic congener *Poa*  
<sup>190</sup>

191 *autumnalis* in east Texas (*unpublished data*), and we assume this probability was constant  
192 across sexes and climatic variables. We also assume that surviving seedlings reach size  
193  $y$  in year  $t + 1$  according to  $g(y, x = 1; \mathbf{z})$ , the expected future size of 1-tiller plants from  
194 the common garden experiment. The second term represents survival and size transi-  
195 tion of established plants from the previous year, where  $s$  and  $g$  give the probabilities of  
196 surviving at size  $x$  and growing from sizes  $x$  to  $y$ , respectively, and superscripts indicate  
197 that these functions may be unique to females ( $F$ ) and males ( $M$ ).

198 Because the two-sex MPM is nonlinear (vital rates affect and are affected by popu-  
199 lation structure) we estimated the asymptotic geometric growth rate ( $\lambda$ ) by numerical  
200 simulation, and repeated this across a range of climate.<sup>12</sup>

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

<sup>13</sup> To identify the mechanism by which climate affects population growth rate, we de-  
composed 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

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<sup>12</sup>I think methods for projecting across a range of climate need to be described in greater detail. Also you say here at you analyzed the two-sex IPM through simulation but the female-dominant version can be analyzed through eigenanalysis, and I think you are presenting both, so this should be explained.

<sup>13</sup>I don't think the LTRE analysis is adequately motivated by the Intro. I have not edited much here but we can talk about it.

parameters (Caswell, 1989):

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

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

### *Implication on range shifts*

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

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

## Results

15

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

Most vital rates were strongly climate dependent, but the magnitude of their response differed between sexes suggesting a sex-specific demographic response to climate. Survival and growth were strongly more dependent on climate than flowering and panicles

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<sup>14</sup>I think this section should be expanded. In general, you did a great job of presenting the model but you have not effectively communicated how you are using the model to answer your questions.

<sup>15</sup>Since the vital rate results will be updated with the new seasonal covariates I will wait to edit an updated version.

219 Fig.2. There was a female survival and flowering advantage across all climatic seasons  
220 (Figs. 3A-3D, 3I-3K). On the contrary, there was a male panicle advantage across all cli-  
221 matic variables (Fig3X-Y). Counter-intuitively, there was no sex growth advantage in all  
222 season climatic variables (Fig 3E-3H).

223 Precipitation of the growing season decreased seasonal survival, whereas tempera-  
224 ture of the growing season, precipitation of the dormant season, and temperature of the  
225 dormant season increased seasonal survival. Unlike the probability of survival, the prob-  
226 ability of flowering increased with precipitation of the growing season and decreased  
227 with precipitation of the growing season and increased with temperature of the growing  
228 season, precipitation of the dormant season, and temperature of the dormant season.  
229 This trade-off between survival and flowering provides an insight into the persistence  
230 of the species. In addition, the number of panicles decreased with precipitation for  
231 the growing season and the temperature of the dormant season and increased with the  
232 temperature of the growing season and precipitation. Finally, the precipitation and tem-  
233 perature of the growing season decreased seasonal growth, whereas the precipitation  
234 and temperature of the dormant season increased seasonal growth.

235 *Population growth rate response to climate change*

236 Consistent with the effect of climate on individual vital rate, we also found an effect  
237 of seasonal climate on population growth rate. Precipitation and temperature of the  
238 growing season decreased the population growth rate, whereas precipitation and tem-  
239 perature of the dormant season increased the population growth rate. Across all sites,  
240 the population growth rate was higher than one, suggesting an increase of population  
241 over time.

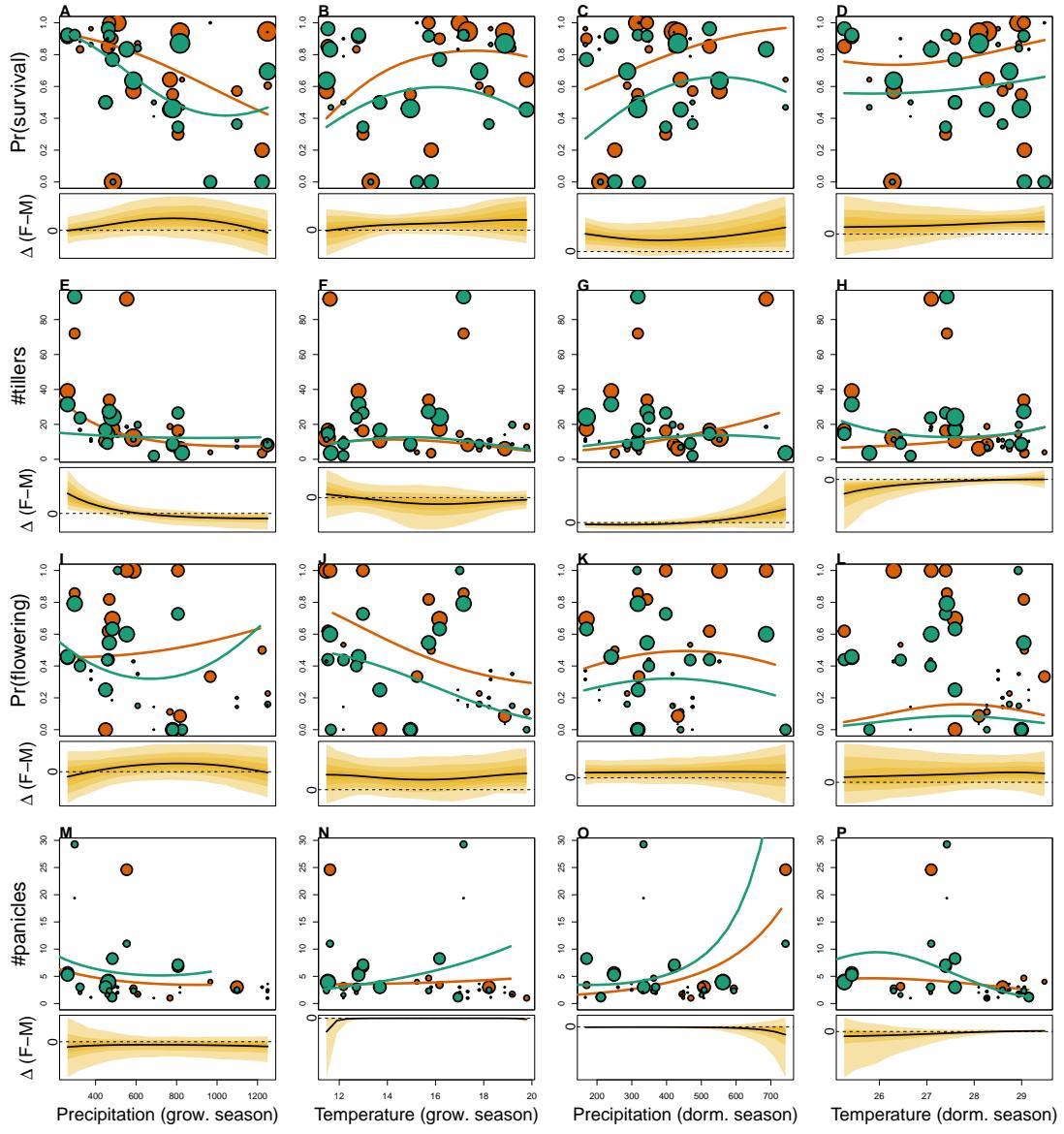
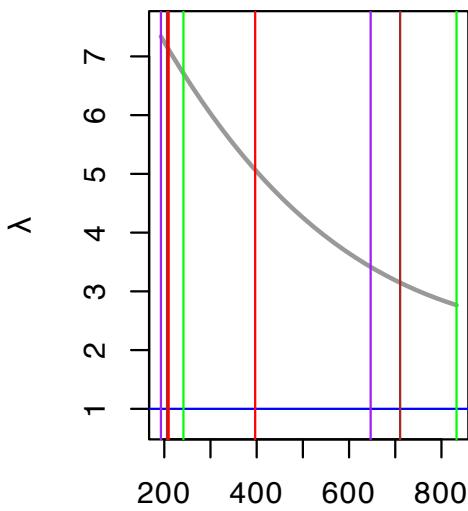
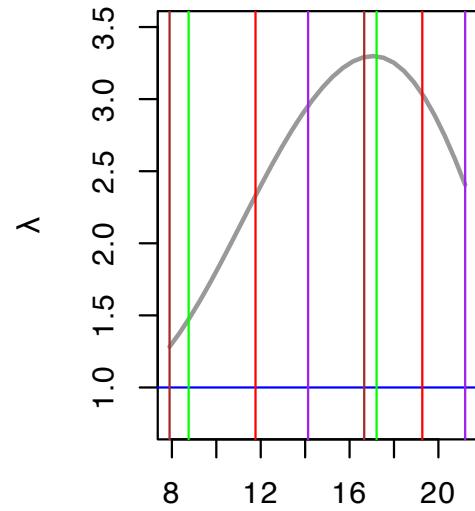


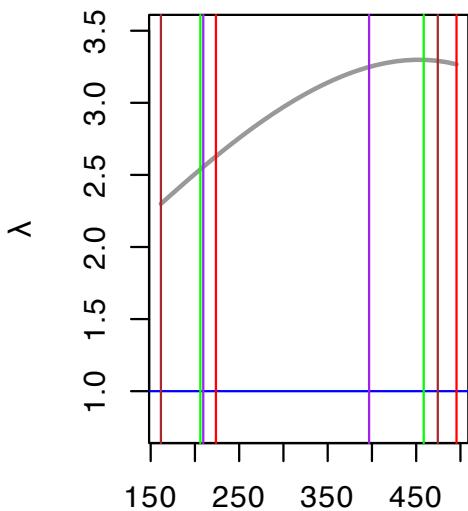
Figure 1: Sex specific demographic response to climate across species range: A–D, inter-annual probability of survival; E–H, inter-annual growth (change in number of tillers); I–L, probability of flowering; M–P, number of panicles produced given flowering. Points show means by site for females (orange)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



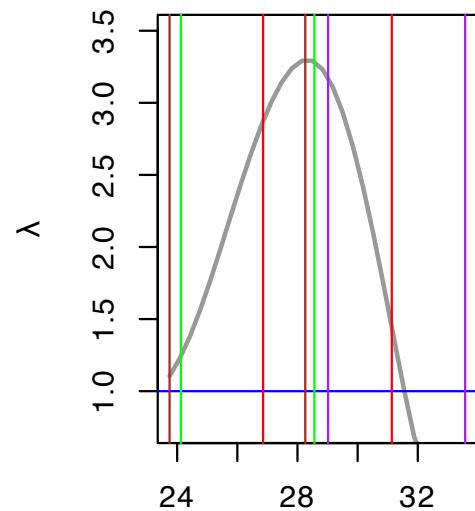
Precipitation of the growing season



Temperature of growing season



Precipitation of dormant season



Temperature of dormant season

Figure<sup>17</sup>: XXX

## Appendix S1: Correspondence

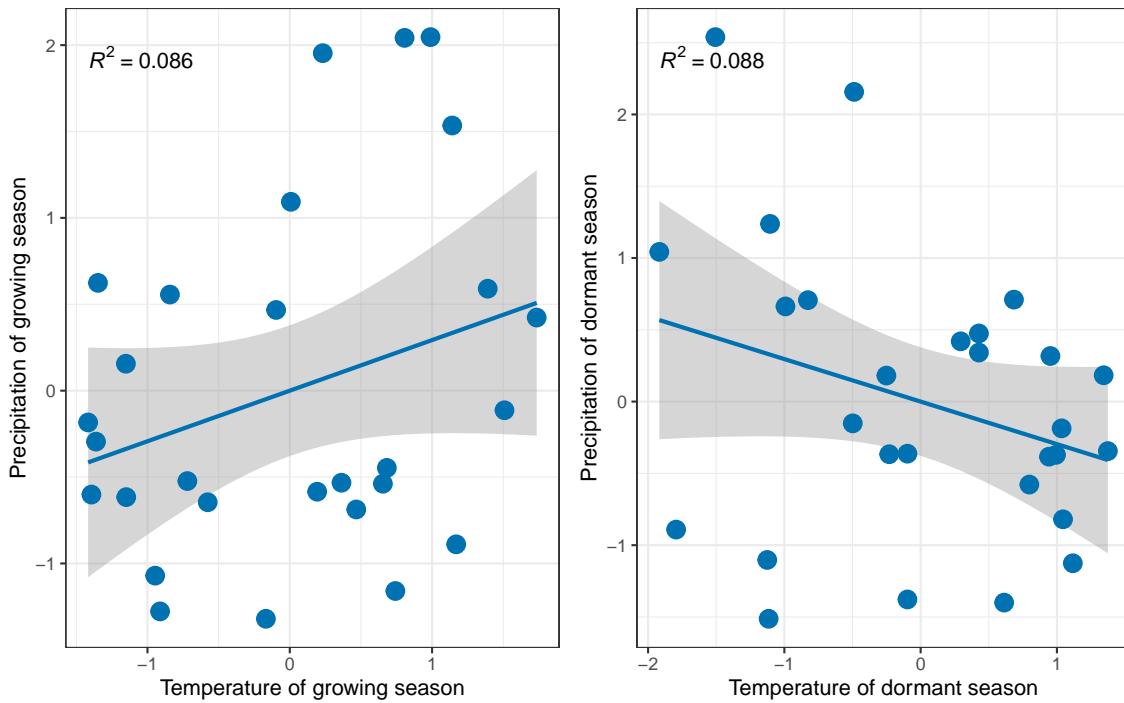
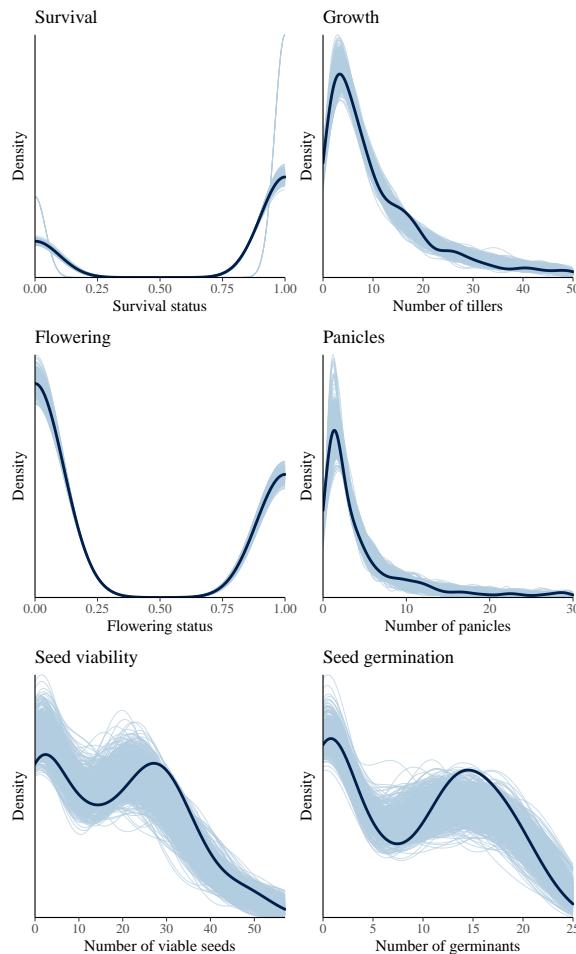


Figure A1: Relation between precipitation and temperature for each season (growing and dormant).  $R^2$  indicates the value of proportion of explained variance between the temperature and precipitation



**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.

243

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tempgrow<sup>2</sup> : sex  
tempdorm<sup>2</sup> : sex  
pptdorm<sup>2</sup> : sex  
pptdorm<sup>2</sup>  
pptgrow<sup>2</sup> : sex  
tempgrow<sup>2</sup>  
pptgrow<sup>2</sup>  
tempdorm:pptdorm:sex  
tempgrow: pptgrow: sex  
20 pptdorm: sex  
tempgrow: sex  
pptgrow: sex

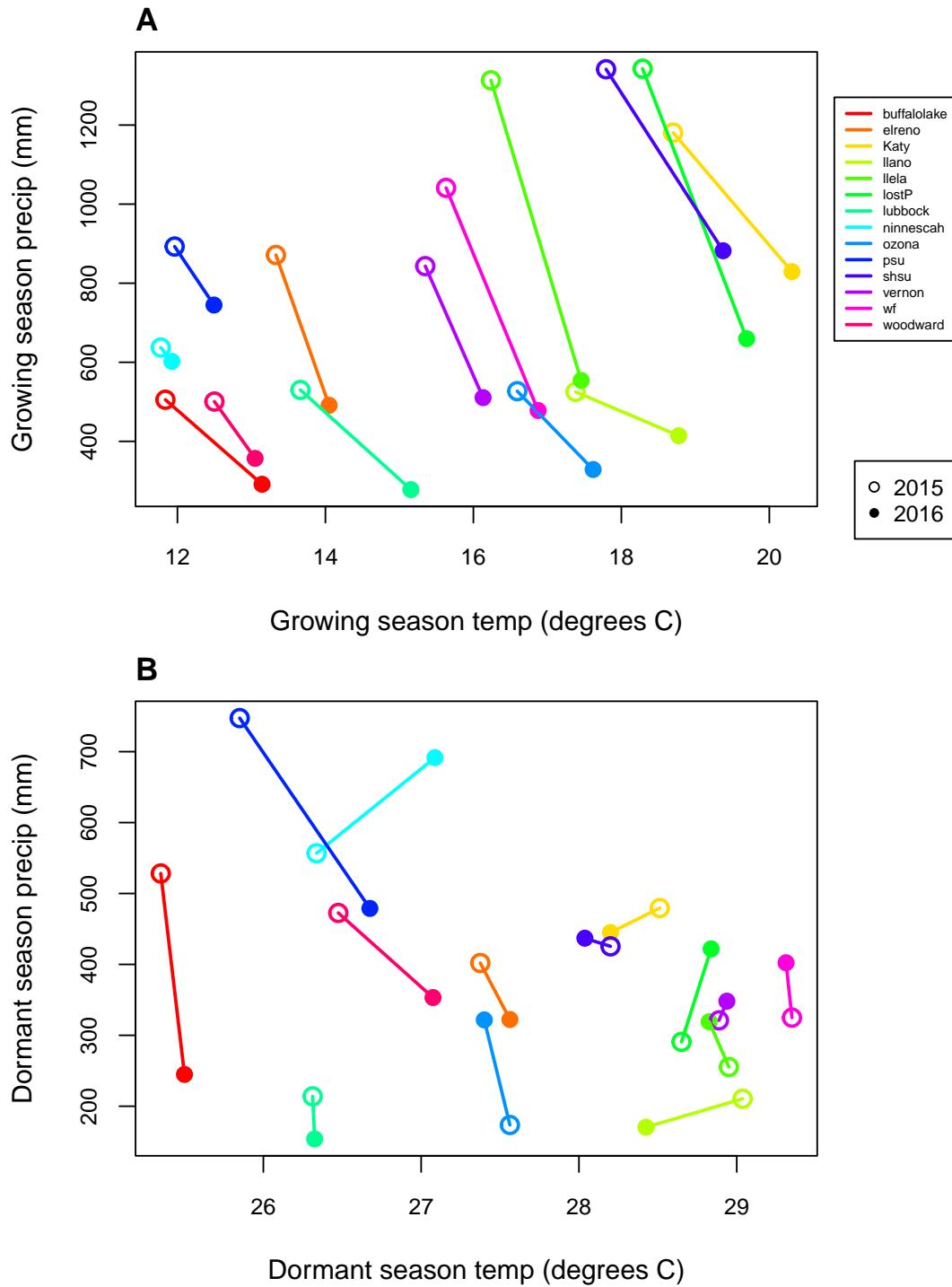


Figure A4: XXX

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