

Forecasting range shifts of a dioecious plant species under climate change

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1 Abstract

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

9 Keywords

10climate change, demography, forecasting, matrix projection model, mechanistic models,
11sex 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.¹

27 Climate change can influence dioecious populations via shifts in sex ratio.² 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; Bürl 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

¹This is a great opening paragraph!

²This 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 niche³. 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.

³cite – 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).⁴ 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).⁵ 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 (λ)?

⁴This 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.

⁵I 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).⁶

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).⁷ 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 gradient⁸

⁶I 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.

⁷I 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.

⁸While 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 Each May (2014-2016), we collected individual demographic data including survival
102 (alive or dead), growth (number of tillers), flowering status (reproductive or vegetative),
103 and fertility (number of panicles, conditional on flowering). For the analyses that follow,
104 we focus on the 2014-15 and 2015-16 transitions years.

105 *Climatic data collection*

106 We downloaded monthly temperature and precipitation from Chelsa to describe ob-
107 served climate conditions during our study period (Karger et al., 2017). These climate
108 data were used as covariates in vital rate regressions, which allowed us to forecast and
109 back-cast demographic responses to climate change based on observations across the
110 common garden experiment. We aligned the climatic years to match demographic tran-
111 sition years (**May 1 – April 30**)⁹ rather than calendar years. Based on the natural history
112 of this summer-dormant cool-season species, we divided each transition year into grow-
113 ing and dormant seasons. We define June through September as the dormant season
114 and the rest of the year as the growing season. Across years and sites, the experiment
115 included substantial variation in growing and dormant season temperature and precipi-
116 tation (Figure¹⁰).

117 To back-cast and forecast changes in climate, we downloaded projection data for three

so the distinction should be made clear.

⁹I am not sure if these are actually the right dates.

¹⁰I think we should have a figure, maybe just for the appendix, that visualizes this.

118 30-year periods: past (1901-1930), current (1990-2019) and future (2070-2100). Data for
119 these climatic periods were downloaded from four general circulation models (GCMs)
120 selected from the Coupled Model Intercomparison Project Phase 5 (CMIP5). The GCMs
121 are MIROC5, ACCESS1-3, CESM1-BGC, CMCC-CM and were downloaded from chelsa
122 (Sanderson et al., 2015). We evaluated future climate projections from two scenarios of
123 representative concentration pathways (RCPs): RCP4.5, an intermediate-to-pessimistic
124 scenario assuming a radiative forcing to amount to 4.5 Wm^{-2} by 2100, and RCP8.5, a
125 pessimistic emission scenario which project a radiative forcing to amount to 8.5 Wm^{-2}
126 by 2100 (Thomson et al., 2011; Schwalm et al., 2020).

127 Tom stopped here Monday evening. Generall impressions: really good! Need more
128 hypotheses regarding sex-specific responses. Also need to say a little more about prev
129 study (including what is known about sex-specific niches), and lean into the natural
130 history at the end of intro and start of methods.¹¹

131 *Sex ratio experiment*

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

11

141 of females in each plot and collected the number of seeds in each panicle. Since the
142 number of panicles (proxy of reproduction effort) does not necessarily reflect reproduc-
143 tion success in *Poar arachnifera*, we accessed reproduction success (seed fertilized) using
144 greenhouse-based germination and trazolium-based seed viability assays.

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

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

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

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

154 *Sex specific demographic responses to climate*

155 We used individual level measurements of survival, growth (number of tillers), flow-
156 ering, number of panicles to independently develop Bayesian mixed effect models de-
157 scribing how each vital rate varies as a function of sex, size, precipitation of growing
158 and dormant season and temperature of of growing and dormant season. We fit vital

159 rate models with second-degree polynomial functions for the influence of climate. We
 160 included a second-degree polynomial because we expected that climate variables would
 161 affect vital rates through a hump-shaped relationship.

We centered and standardized all predictors to facilitate model convergence. We included site, source, and block as random effect. All the vital rate models used the same linear and quadratic predictor for the expected value (μ) (Eq. 2). However, we applied a different link function ($f(\mu)$) depending on the distribution the vital rate. We modeled survival and flowering data with a Bernoulli distribution. We modeled the growth (tiller number) with a zero-truncated Poisson inverse Gaussian distribution. Fertility (panicle 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 β_0 is the grand mean intercept, $\beta_1 \dots \beta_{13}$ 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 provenence 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*

To understand the effect of climate on population growth rate, we used the vital rate estimated earlier to build a matrix projection model (MPM) structured by size (number of tillers), sex and climate as covariate. Let $F_{x,z,t}$ and $M_{x,z,t}$ be the number of female and male plants of 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 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 new recruits, which we assume do not reproduce in their first year. We assume that the parameters of sex ratio-dependent mating (Eq. 1) do not vary with climate. For a pre-breeding census, the

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

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

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

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 ρ 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 :

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

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

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

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

¹⁸² In the two formula above, the first term represents seedlings that survived their first
¹⁸³ year and enter the size distribution of established plants. Instead of using *P. arachnifera*
¹⁸⁴ survival probability, we used the seedling survival probability (σ) from demographic
¹⁸⁵ studies of the hermaphroditic congener *Poa autumnalis* in east Texas (T.E.X. Miller and
¹⁸⁶ J.A. Rudgers, *unpublished data*), and we assume this probability was constant across sexes
¹⁸⁷ and climatic variables. We did this because we had little information on the early life

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

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

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

¹² 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 (λ)
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 λ with climate as the product of the sensitivity of
 λ to the parameters times the sensitivity of the parameters to climate, summed over all
parameters (Caswell, 1989):

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

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

¹²I don't think the LTRE analysis is adequately motivated by the Intro.

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

203 *Implication on range shifts*

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

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

209 **Results**

210 *Sex specific demographic response to climate change*

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

218 Precipitation of the growing season decreased seasonal survival, whereas tempera-
219 ture of the growing season, precipitation of the dormant season, and temperature of the
220 dormant season increased seasonal survival. Unlike the probability of survival, the prob-
221 ability of flowering increased with precipitation of the growing season and decreased
222 with precipitation of the growing season and increased with temperature of the growing

223 season, precipitation of the dormant season, and temperature of the dormant season.
224 This trade-off between survival and flowering provides an insight into the persistence
225 of the species. In addition, the number of panicles decreased with precipitation for
226 the growing season and the temperature of the dormant season and increased with the
227 temperature of the growing season and precipitation. Finally, the precipitation and tem-
228 perature of the growing season decreased seasonal growth, whereas the precipitation
229 and temperature of the dormant season increased seasonal growth.

230 *Population growth rate response to climate change*

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

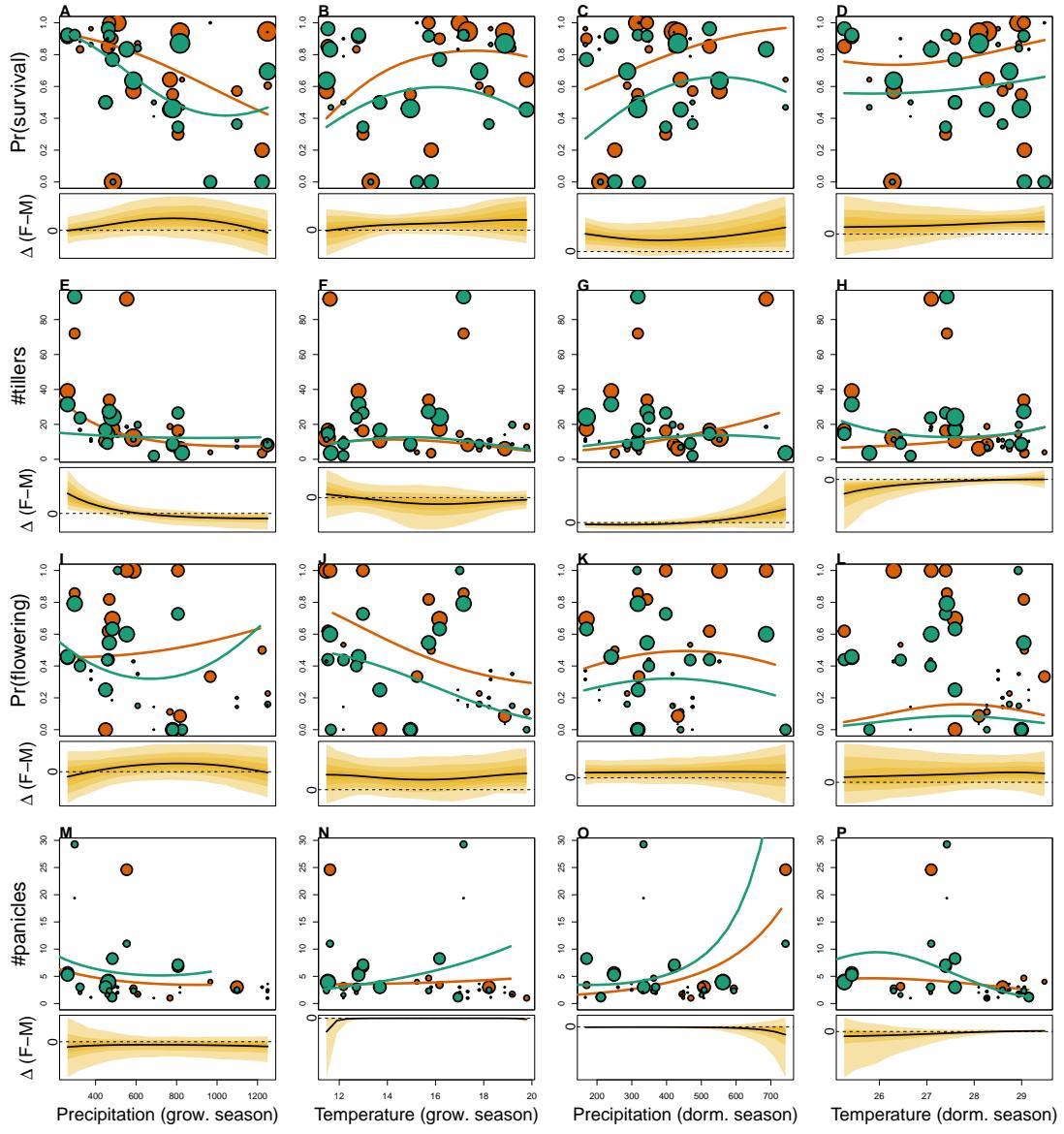
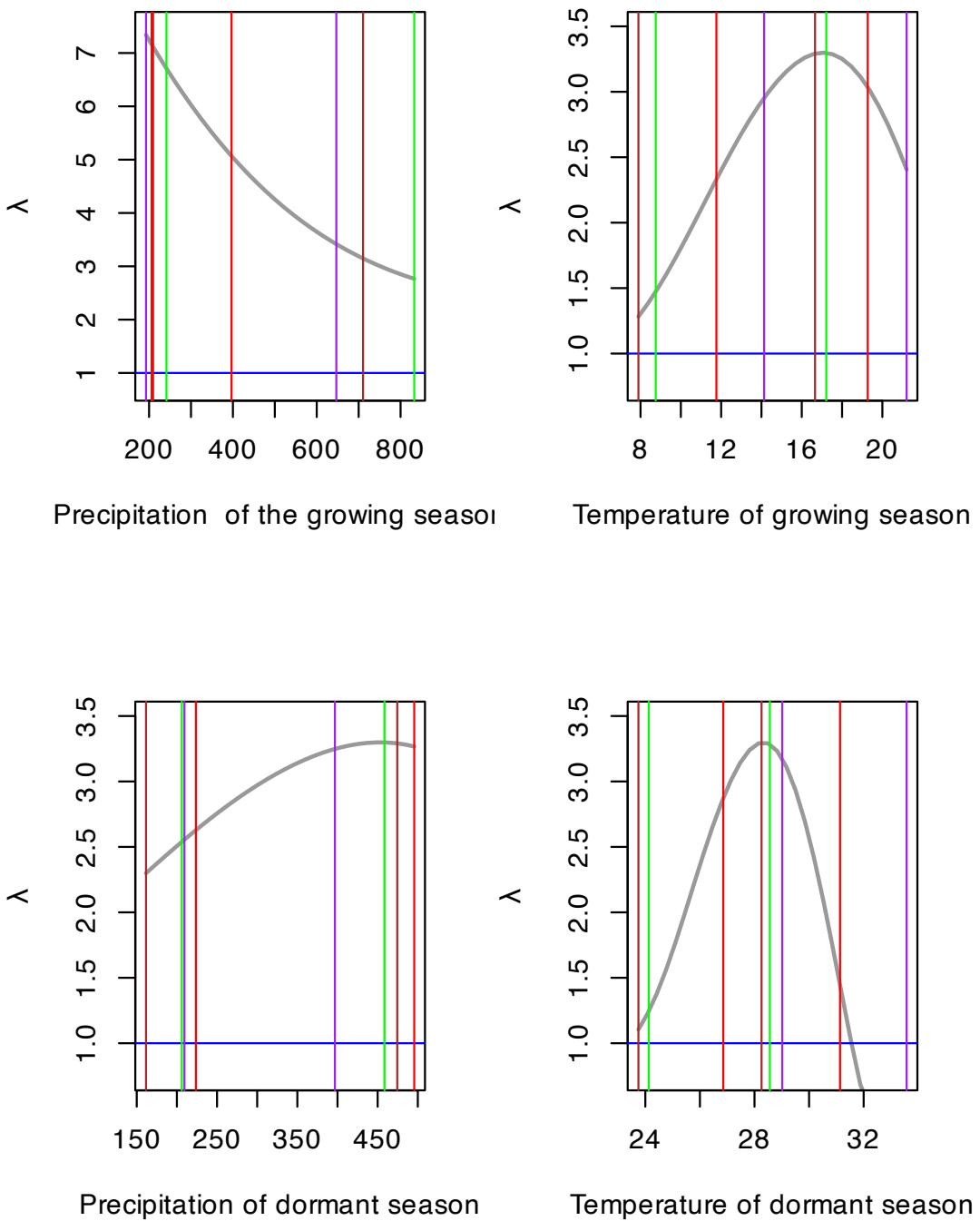


Figure 1: Sex specific demographic response to climate across species range: A–D, inter-annual probability of survival; E–H, inter-annual growth (change in number of tillers); I–L, probability of flowering; M–P, number of panicles produced given flowering. Points show means by site for females (orange)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



Figure¹⁷: XXX

Appendix S1: Correspondence

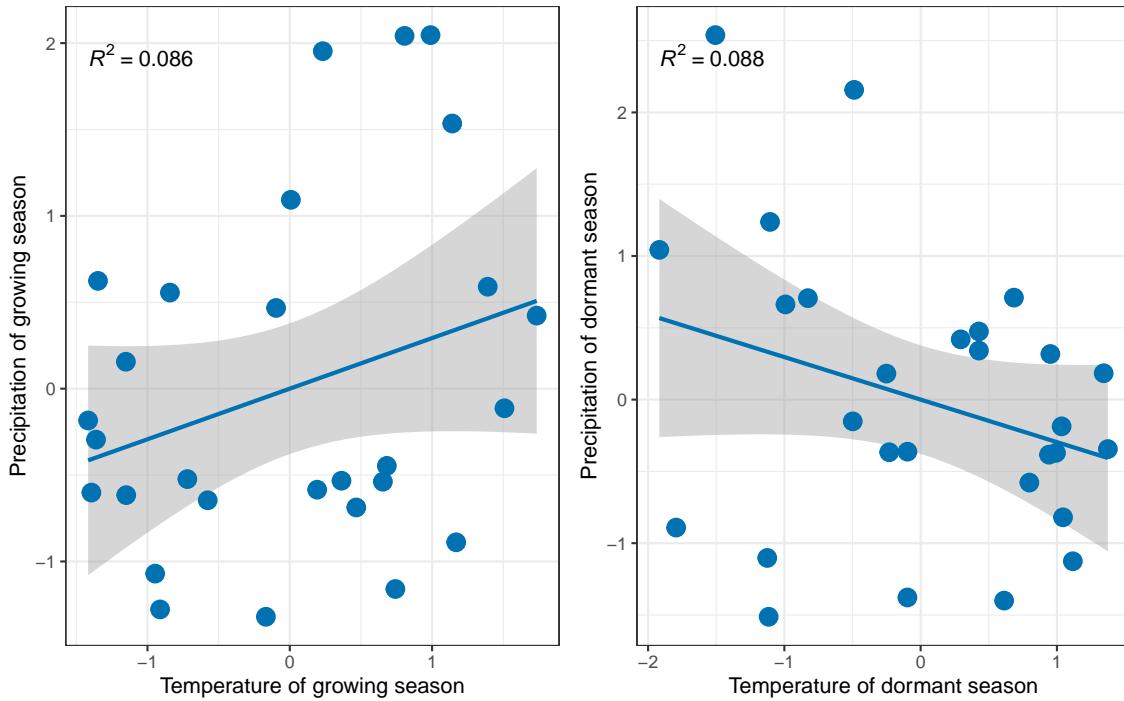


Figure A1: Relation between precipitation and temperature for each season (growing and dormant). R^2 indicates the value of proportion of explained variance between the temperature and precipitation

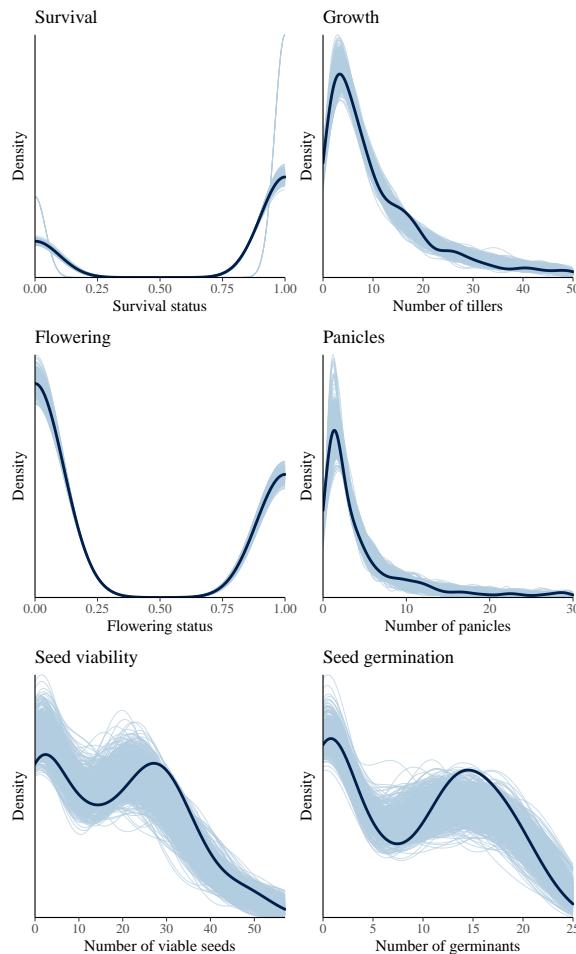


Figure A2: Consistency between real data and simulated values suggests that the fitted model accurately describes the data. Graph shows density curves for the observed data (light blue) along with the simulated values (dark blue). The first column shows the linear models and the second column shows the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

238

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tempgrow² : sex
tempdorm² : sex
pptdorm² : sex
pptdorm²
pptgrow² : sex
tempgrow²
pptgrow²
tempdorm:pptdorm:sex
tempgrow: pptgrow: sex
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tempgrow: sex
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