

Forecasting range shifts of a dioecious plant species under climate change

Jacob K. Moutouama 0000-0003-1599-1671^{*1}, Aldo Compagnoni 0000-0001-8302-7492², and Tom E.X. Miller 0000-0003-3208-6067¹

¹Program in Ecology and Evolutionary Biology, Department of BioSciences, Rice University, Houston, TX USA

²Institute

of Biology, Martin Luther University Halle-Wittenberg, Halle, Germany; and German Centre for Integrative Biodiversity Research (iDiv), Leipzig, Germany

Running header: Forecasting range shifts

Keywords: demography, forecasting, global warming, matrix projection model, population dynamics, sex ratio, range limits

Submitted to: *Ecology letters* (Letter)

Data accessibility statement: All data used in this paper are publicly available and cited appropriately (Miller and Compagnoni, 2022a). Should the paper be accepted, all computer scripts supporting the results will be archived in a Zenodo package, with the DOI included at the end of the article. During peer review, our code (Stan, Bash and R) is available at <https://github.com/jmoutouama/POAR-Forecasting>.

Conflict of interest statement: None.

Authorship statement: J.K.M., A.C. and T.E.X.M. designed the study. A.C. and T.E.X.M. collected the data. All authors conducted the statistical analyses and modeling. J.K.M. drafted the manuscript, and T.E.X.M contributed to revisions.

Abstract:

Main Text:

Figures: 6

Tables: 0

References: 106

*Corresponding author: jmoutouama@gmail.com

¹ Abstract

² Global climate change has triggered an urgent need for predicting the reorganization of Earth's
³ biodiversity. Currently, the vast majority of models used to forecast population viability and
⁴ range shifts in response to climate change ignore the complication of sex structure, and thus
⁵ the potential for females and males to differ in their sensitivity to climate drivers. We developed
⁶ demographic models of range limitation, parameterized from geographically distributed com-
⁷ mon garden experiments, with females and males of a dioecious grass species (*Poa arachnifera*)
⁸ throughout and beyond its range in the south-central U.S. Female-dominant and two-sex
⁹ model versions both predict that future climate change will alter population viability and
¹⁰ will induce a poleward niche shift beyond current northern limits. However, the magnitude of
¹¹ niche shift was underestimated by the female-dominant model, because females have broader
¹² temperature tolerance than males and become mate-limited under female-biased sex ratios.
¹³ Our result illustrate how explicit accounting for both sexes could enhance population viability
¹⁴ forecasts and conservation planning for dioecious species in response to climate change.

¹⁵ Introduction

¹⁶ Rising temperatures and extreme drought events associated with global climate change are
¹⁷ leading to increased concern about how species will become redistributed across the globe
¹⁸ under future climate conditions (Bertrand et al., 2011; Gamelon et al., 2017; Smith et al., 2024).
¹⁹ Species' range limits, when not driven by dispersal limitation, should generally reflect the limits
²⁰ of the ecological niche (Lee-Yaw et al., 2016). Niches and geographic ranges are often limited
²¹ by climatic factors including temperature and precipitation (Sexton et al., 2009). Therefore,
²² any substantial changes in the magnitude of these climatic factors could impact population
²³ viability, with implications for range expansions or contractions based on which regions of
²⁴ a species' range become more or less suitable (Davis and Shaw, 2001; Pease et al., 1989).

²⁵ Forecasting range shifts for dioecious species (most animals and ca. 7% of plant species)
²⁶ is complicated by the potential for sexual niche differentiation, i.e. distinct responses of
²⁷ females and males to shared climate drivers (Hultine et al., 2016; Morrison et al., 2016; Pottier
²⁸ et al., 2021; Tognetti, 2012). ¹ Accounting for sexual niche differentiation is a long-standing
²⁹ challenge in accurately predicting which sex will successfully track environmental change
³⁰ and how this will impact population viability and range shifts (Gissi et al., 2023; Jones et al.,
³¹ 1999). Populations in which males are rare under current climatic conditions could experience
³² low reproductive success due to sperm or pollen limitation that may lead to population
³³ decline in response to climate change that disproportionately favors females (Eberhart-Phillips
³⁴ et al., 2017). In contrast, climate change could expand male habitat suitability (e.g. upslope
³⁵ movement), which might increase seed set for mate-limited females and favor range expansion
³⁶ (Petry et al., 2016). Across dioecious plants, for example, studies suggest that future climate
³⁷ change toward hotter and drier conditions may favor male-biased sex ratios (Field et al.,
³⁸ 2013; Hultine et al., 2016). ² Although the response of species to climate warming is an urgent
³⁹ and active area of research, few studies have disentangled the interaction between sex and
⁴⁰ climate drivers to understand their combined effects on population dynamics and range shifts,
⁴¹ despite calls for such an approach (Gissi et al., 2023; Hultine et al., 2016).

⁴² The vast majority of theory and models in population biology, including those used
⁴³ to forecast biodiversity responses to climate change, ignore the complication of sex structure
⁴⁴ (but see Ellis et al., 2017; Gissi et al., 2024; Pottier et al., 2021). Traditional approaches instead
⁴⁵ focus exclusively on females, assuming that males are in sufficient supply as to never limit
⁴⁶ female fertility. In contrast, "two-sex" models are required to fully account for demographic

¹ Something this paragraph is missing is a mechanistic explanation for why females and males may have different climate sensitivity, likely something about costs of reproduction. This would be a good place for a sentence or two that addresses this.

² I am not sure if this is the best spot for it, but I think this prediction from the literature is relevant to bring up in the Intro.

47 differences between females and males and sex-specific responses to shared climate drivers
48 (Gerber and White, 2014; Miller et al., 2011). Sex differences in maturation, reproduction,
49 and mortality schedules can generate skew in the operational sex ratio (OSR; sex ratio of
50 individuals available for mating) even if the birth sex ratio is 1:1 (Eberhart-Phillips et al., 2017;
51 Shelton, 2010). Climate and other environmental drivers can therefore influence the OSR
52 via their influence on sex-specific demographic rates. In a two-sex framework, demographic
53 rates both influence and respond to the OSR in a feedback loop that makes two-sex models
54 inherently nonlinear and more data-hungry than corresponding female-dominant models.
55 Given the additional complexity and data needs, forecasts of range dynamics for dioecious
56 species under future climate change that explicitly account for females, males, and their
57 inter-dependence are limited (Lynch et al., 2014; Petry et al., 2016).

58 Tracking the impact of climate change on population viability (λ) and distributional
59 limits of dioecious taxa depends on our ability to build mechanistic models that take into
60 account the spatial and temporal context of sex specific response to climate change, while
61 accounting for sources of uncertainty (Davis and Shaw, 2001; Evans et al., 2016). Structured
62 population models built from demographic data collected from geographically distributed
63 observations or common garden experiments provide several advantages for studying
64 the impact of climate change on species' range shifts (Merow et al., 2017; Schultz et al.,
65 2022; Schwinning et al., 2022). First, demographic models link individual-level life history
66 events (mortality, development, and regeneration) to population demography, allowing the
67 investigation of factors explaining vital rate responses to environmental drivers (Dahlgren
68 et al., 2016; Ehrlén and Morris, 2015; Louthan et al., 2022). Second, demographic models
69 have a natural interface with statistical estimation of individual-level vital rates that provide
70 quantitative measures of uncertainty and isolate different sources of variation, features that
71 can be propagated to population-level predictions (Elderd and Miller, 2016; Ellner et al.,
72 2022).³ Finally, structured demographic models can be used to identify which aspects of
73 climate are the most important drivers of population dynamics. For example, Life Table
74 Response Experiments (LTRE) built from structured models have become widely used to
75 understand the relative importance of covariates in explaining variation in population growth
76 rate (Czachura and Miller, 2020; Ellner et al., 2016; Hernández et al., 2023).⁴

77 In this study, we combine geographically-distributed common garden experiments,
78 hierarchical Bayesian statistical modeling, two-sex population projection modeling, and climate
79 back-casting and forecasting to understand demographic responses to climate change and

³I cut the sentence about experiments because I don't think our data really exemplify this. While we did do an experiment, we did not manipulate climate, so we are subject to the same correlations as observational studies.

⁴I think LTRE is a relatively small part of the paper so I suggested reducing the amount of text on it here.

their implications for past, present, and future range dynamics. Our work focused on the dioecious plant Texas bluegrass (*Poa arachnifera*), which is distributed along environmental gradients in the south-central U.S. corresponding to variation in temperature across latitude and precipitation across longitude (Fig. 1). This region has experienced rapid climate warming since 1900 and this is projected to continue through the end of the century (Fig. S-1). Our previous study showed that, despite evidence for differentiation of climatic niche between sexes, the female niche mattered the most in driving longitudinal range limits of Texas bluegrass (Miller and Compagnoni, 2022b). However, that study used a single proxy variable (longitude) to represent environmental variation related to aridity and did not consider variation in temperature, which is the much stronger dimension of forecasted climate change in this region (Fig. S-1,S-2⁵). Developing a rigorous forecast for the implications of future climate change requires that we transition from implicit to explicit treatment of multiple climate drivers, as we do here. Leveraging the power of Bayesian inference, we take a probabilistic view of past, present, and future range limits by quantifying the probability of population viability ($Pr(\lambda \geq 1)$) in relation to climate drivers of demography, an approach that fully accounts for uncertainty arising from multiple sources of estimation and process error. Specifically, we asked:

1. What are the sex-specific vital rate responses to variation in temperature and precipitation across the species' range?
2. How do sex-specific vital rates combine to determine the influence of climate variation on population growth rate (λ)?
3. What is the impact of climate change on operational sex ratio throughout the range?
4. What are the likely historical and projected dynamics of the Texas bluegrass geographic niche and how does accounting for sex structure modify these predictions?

Materials and methods

Study species and climate context

Texas bluegrass (*Poa arachnifera*) is a dioecious perennial, summer-dormant cool-season (C3) grass that occurs in the south-central U.S. (Texas, Oklahoma, and southern Kansas) (Figure 1) (Hitchcock, 1971). Texas bluegrass grows between October and May, flowers in spring, and goes dormant during the hot summer months of June to September (Kindiger, 2004). Following this life history, we divide the calendar year into growing (October 1 - May 31) and dormant (June 1 - September 30) seasons. Biological sex is genetically based

⁵Please improve the legend for these figures.

and the birth (seed) sex ratio is 1:1 (Renganayaki et al., 2005). Females and males are morphologically indistinguishable except for their inflorescences. Like all grasses, this species is wind pollinated (Hitchcock, 1971) and most male-female pollen transfer occurs within 10-15m (Compagnoni et al., 2017). Surveys of 22 natural populations throughout the species' distribution indicated that operational sex ratio (the female fraction of inflorescences) ranged from 0.007 to 0.986 with a mean of 0.404 (Miller and Compagnoni, 2022b).

Latitudinal limits of the Texas bluegrass distribution span 7.74 °C to 16.94 °C of temperature during the dormant season and 24.38 °C to 28.80 °C during the dormant season. Longitudinal limits span 244.9 mm to 901.5 mm of precipitation during the growing season and 156.3 mm to 373.3 mm. This region has experienced *ca.* 0.5 °C of climate warming since 1900, with somewhat faster warming during the cool-season months (0.0055°C/yr) than the hot summers (0.0046°C/yr) (Fig. ??), with no consistent changes in precipitation (time series figure). Future warming is projected to accelerate to 0.03 – 0.06°C/yr depending on the season and forecast model (time series figure).⁶

Common garden experiment

Experimental design

We conducted a range-wide common garden experiment to quantify sex-specific demographic responses to climate variation. Details of the experimental design are provided in Miller and Compagnoni (2022b); we provide a brief overview here. The experiment was installed at 14 sites throughout and, in some cases, beyond the natural range of Texas bluegrass that sampled a broad range of temperature and precipitation (Figure 1).⁷ At each site, we established 14 blocks. For each block we planted three female and three male individuals that were clonally propagated from females and males from eight natural source populations (Figure 1); because sex is genetically-based, clones never deviated from their expected sex. The experiment was established in November 2013 with a total of # female and # male plants⁸, and was censused in May of 2014, 2015, and 2016. At each census, we collected data on survival, size (number of tillers), and number of panicles (reproductive inflorescences). For the analyses that follow, we focus on the 2014-15 and 2015-16 transitions years, since the start of the experiment did not include the full 2013-14 transition year.

⁶Rather than just describe climate, this would be a good place to say more about climate change, which I have added. All of this sets the stage for why this is an important system to forecast climate change responses.

⁷A few comments about figure 1 (I cannot comment in the legend). Please update the gray diamonds as GBIF occurrences, not natural population surveys. Please add "mm" and "°C" to the titles. It would also be good to spell out "growing" and "dormant" seasons.

⁸Add numbers.

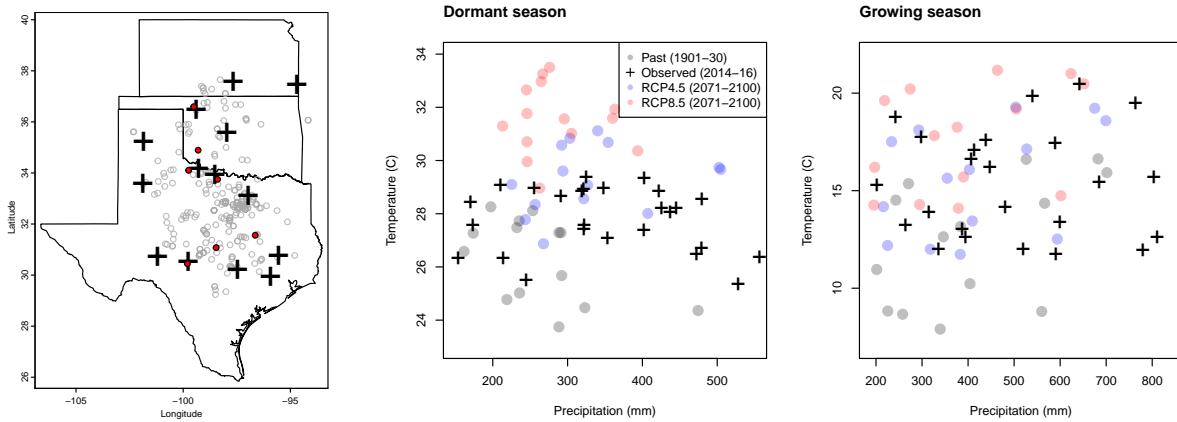


Figure 1: Maps of 30-year (1990-2019) climate normals and study sites used for demographic monitoring of *Poa arachnifera* in Texas, Kansas and Oklahoma in the United States. Precipitation is in mm and temperature is in °C. We surveyed 22 natural populations (grey diamond). The common garden sites were installed on 14 sites (black circle) collected from 7 sources populations (red circle). See also (Figure S-1, Figure S-2) for more details about climate variation across the study sites since the beginning of last century.

140 Climatic data collection

141 We gathered downscaled monthly temperature and precipitation for each site from Chelsa
 142 to describe observed climate conditions during our study period (Karger et al., 2017). These
 143 climate data were used as covariates in vital rate regressions. We aligned the climatic years
 144 to match demographic transition years (June 1 – May 31) and growing and dormant seasons
 145 within each year. To back-cast and forecast demographic responses to changes in climate
 146 throughout the study region, we also gathered projection data for three 30-year periods:
 147 “past” (1901-1930), “current” (1990-2019) and “future” (2070-2100). Data for future climatic
 148 periods were downloaded from four general circulation models (GCMs) selected from
 149 the Coupled Model Intercomparison Project Phase 5 (CMIP5): Model for Interdisciplinary
 150 Research on Climate (MIROC5), Australian Community Climate and Earth System Simulator
 151 (ACCESS1-3), Community Earth System Model (CESM1-BGC), Centro Euro-Mediterraneo sui
 152 Cambiamenti Climatici Climate Model (CMCC-CM). All the GCMs were downloaded from
 153 Chelsa (Sanderson et al., 2015). We evaluated future climate projections from two scenarios of
 154 representative concentration pathways (RCPs): RCP4.5, an intermediate-to-pessimistic scenario
 155 assuming a radiative forcing amounting to 4.5 Wm^{-2} by 2100, and RCP8.5, a pessimistic
 156 emission scenario which projects a radiative forcing of 8.5 Wm^{-2} by 2100 (Schwalm et al.,
 157 2020; Thomson et al., 2011).

158 Projection data for the three 30-year periods included warmer or colder conditions than
 159 observed in our experiment, so extending our inferences to these conditions required some

160 extrapolation, as we describe below. However, across all sites, both study years were 2–3°C
 161 warmer than their corresponding 1990–2019 temperature normals (Fig. S-8). Additionally,
 162 the 2014–15 growing season was substantially wetter and cooler across the study region than
 163 2015–16 (Fig. S-7). Thus, the geographic and inter-annual replication of the common garden
 164 experiment provided good coverage of most past, present, and future conditions throughout
 165 the study region (Fig. S-3, Fig. S-4, Fig. S-5, Fig. S-6).

166 **Sex-specific demographic responses to climatic variation across common garden sites**

We used individual-level measurements of survival, growth (change in number of tillers), flowering, and number of panicles (conditional on flowering) to develop Bayesian mixed effect models describing how each vital rate varies as a function of sex, size, and four climate covariates (precipitation and temperature of growing and dormant season). These vital rate models included main effects of size (the natural log of tiller number), sex, and seasonal climate covariates. Climate variables were fit with second-degree polynomial functions to accommodate the possibility of hump-shaped relationships (reduced demographic performance at both extremes). We also included two-way interactions between sex and each climate driver and between temperature and precipitation within each season, and a three-way interaction between sex, temperature, and precipitation within each season. Vital rate models were fit with the same linear predictors for the expected value (μ) (Eq. 1):

$$\begin{aligned}
 \mu = & \beta_0 + \beta_1 \text{size} + \beta_2 \text{sex} + \beta_3 \text{pptgrow} + \beta_4 \text{pptdorm} + \beta_5 \text{tempgrow} + \beta_6 \text{tempdorm} \\
 & + \beta_7 \text{pptgrow*sex} + \beta_8 \text{pptdorm*sex} + \beta_9 \text{tempgrow*sex} + \beta_{10} \text{tempdorm*sex} \\
 & + \beta_{11} \text{size*sex} + \beta_{12} \text{pptgrow*tempgrow} + \beta_{13} \text{pptdorm*tempdorm} \\
 & + \beta_{14} \text{pptgrow*tempgrow*sex} + \beta_{15} \text{pptdorm*tempdorm*sex} + \beta_{16} \text{pptgrow}^2 \\
 & + \beta_{17} \text{pptdorm}^2 + \beta_{18} \text{tempgrow}^2 + \beta_{19} \text{tempdorm}^2 + \beta_{20} \text{pptgrow}^2 * \text{sex} \\
 & + \beta_{21} \text{pptdorm}^2 * \text{sex} + \beta_{22} \text{tempgrow}^2 * \text{sex} + \beta_{23} \text{tempdorm}^2 * \text{sex} + \phi + \rho + \nu
 \end{aligned} \tag{1}$$

167 The linear predictor includes normally distributed random effects for block-to-block variation
 168 ($\phi \sim N(0, \sigma_{block})$), site to site variation ($\nu \sim N(0, \sigma_{site})$), and source-to-source variation that
 169 is related to the genetic provenance of the transplants used to establish the common garden
 170 ($\rho \sim N(0, \sigma_{source})$).

171 A different link function ($f(\mu)$) was applied depending on the the vital rate distributions.
 172 We modeled survival and flowering data with a Bernoulli distribution. We modeled the
 173 growth (tiller number) with a zero-truncated Poisson inverse Gaussian distribution. Fertility
 174 (panicle count conditional on flowering) was modeled as zero-truncated negative binomial.

¹⁷⁵ We used generic, weakly informative priors to fit coefficients for survival, growth, flowering
¹⁷⁶ models ($\beta \sim N(0,1.5)$) and random effect variances ($\sigma \sim Gamma(\gamma(0.1,0.1))$). **We fit fertility**
¹⁷⁷ **model with regularizing priors for coefficients ($\mu=0, \sigma=0.15$)**.⁹

¹⁷⁸ **Sex ratio responses to climatic variation across common garden sites**

¹⁰ We also used the experimental data to investigate how climatic variation across the range influenced sex ratio and operational sex ratio of the common garden populations. To understand the impact of climate change on sex ratio, we used two methods. First, we developed eight Bayesian linear models using data collected during three years. Each model had OSR or SR as response variable and a climate variable as predictor (Eq.2).

$$SR = \omega_0 + \omega_1 climate + \omega_2 climate * climate + \epsilon \quad (2)$$

¹⁷⁹ where SR is the proportion of panicles that were female or proportion of female individuals
¹⁸⁰ in the experimental populations. ω_0 is the intercept, ω_1 and ω_2 are the climate dependent
¹⁸¹ slopes. ϵ is error term.

¹⁸² **Model-fitting procedures**

¹⁸³ All models were fit using Stan (Stan Development Team, 2023) in R 4.3.1 (R Core Team,
¹⁸⁴ 2023). We centered and standardized all climatic predictors to mean zero, variance one, which
¹⁸⁵ facilitated model convergence. We ran three chains for 1000 samples for warmup and 4000
¹⁸⁶ for sampling, with a thinning rate of 3. We assessed the quality of the models using posterior
¹⁸⁷ predictive checks (Piironen and Vehtari, 2017) (Figure S-9).

¹⁸⁸ **Two-sex and female-dominant matrix projection models**

¹⁸⁹ We used the climate-dependent vital rate regressions estimated above, combined with
¹⁹⁰ additional data sources, to build female-dominant and two-sex versions of a climate-explicit
¹⁹¹ matrix projection model (MPMs) structured by the discrete state variables size (number
¹⁹² of tillers) and sex. The female-dominant and two-sex versions of the model both allow
¹⁹³ for sex-specific response to climate and differ only in the feedback between operational
¹⁹⁴ sex ratio and seed fertilization. For clarity of presentation we do not explicitly include
¹⁹⁵ climate-dependence in the notation below, but the following model was evaluated over
¹⁹⁶ variation in seasonal temperature and precipitation.

⁹ I think you need to explain a little more about why fertility was handled differently and what you mean by regularizing.

¹⁰ This section will need to be updated with the new model.

Let $F_{x,t}$ and $M_{x,t}$ be the number of female and male plants of size x in year t , where $x \in [1, \dots, U]$. The minimum possible size is one tiller and U is the 95th percentile of observed maximum size (# tillers)¹¹. Let F_t^R and M_t^R be new female and male recruits in year t , which we treat as distinct from the rest of the size distribution because we assume they do not reproduce in their first year, consistent with our observations. For a pre-breeding census, the expected numbers of recruits in year $t+1$ is given by:

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

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

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 ρ is the primary sex ratio (proportion of recruits that are female), which we assume to be 0.5¹².

In the two-sex model, seed fertilization is a function of population structure, allowing for feedback between vital rates and operational sex ratio (OSR). In the context of the model, OSR is defined as the fraction of panicles that are female and is derived from the $U \times 1$ vectors \mathbf{F}_t and \mathbf{M}_t :

$$v(\mathbf{F}_t, \mathbf{M}_t) = v_0 * \left[1 - \left(\frac{\sum_1^U p^F(x, z) c^F(x, z) F_{x,t}}{\sum_1^U p^F(x, z) c^F(x, z) F_{x,t} + p^M(x, z) c^M(x, z) M_{x,t}} \right)^\alpha \right] \quad (5)$$

The summations tally the total number of female and male panicles over the size distribution, giving the fraction of total panicles that are female. We focus on the female fraction of panicles and not female fraction of reproductive individuals because panicle number can vary widely depending on size; we assume that few males with many panicles vs. many males with few panicles are interchangeable pollination environments. Eq. 5 has the properties that seed fertilization is maximized at v_0 as OSR approaches 100% male, goes to zero as OSR approaches 100% female, and parameter α controls how female seed viability declines as male panicles become rare. We estimated these parameters using data from a sex ratio manipulation experiment, conducted in the center of the range, in which seed fertilization was measured in plots of varying OSR; this experiment is described elsewhere (Compagnoni et al., 2017) and is summarized in Supplementary Method S.2¹³. This experiment also provided estimates for

¹¹Give this number.

¹²I believe we can cite this - check the Am Nat paper.

¹³I think the supplement should also include a data figure showing the fit of the model to the experimental data.

212 seed number per panicle (d) and germination rate (m). Lacking data on climate-dependence,
 213 we assume that seed fertilization, seed number, and germination rate do not vary with climate.

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

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

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

214 The first terms indicate recruits that survived their first year and enter the size distribution
 215 of established plants. We estimated the seedling survival probability σ using demographic
 216 data from the congeneric species *Poa autumnalis* in east Texas (T.E.X. Miller and J.A. Rudgers,
 217 *unpublished data*), and we assume that σ is the same across sexes and climatic variables. We did
 218 this because we had little information on the early life cycle transitions of greenhouse-raised
 219 transplants. We used $g(y, x=1)$ (the future size distribution of one-tiller plants from the
 220 transplant experiment) to give the probability that a surviving recruit reaches size y . The
 221 second component of the equations indicates survival and size transition of established
 222 plants from the previous year, where s and g give the probabilities of surviving at size x and
 223 growing from sizes x to y , respectively, and superscripts indicate that these functions may
 224 be unique to females (F) and males (M).

225 The model described above yields a $2(U+1) \times 2(U+1)$ transition matrix. We estimated
 226 the population growth rate λ of the female dominant model as the leading eigenvalue of
 227 the transition matrix. Since the two-sex MPM is nonlinear (matrix elements affect and are
 228 affected by population structure) we estimated λ and stable sex ratio (female fraction of all
 229 individuals) and operational sex ratio (female fraction of panicles) by numerical simulation.
 230 Since all parameters were estimated using MCMC sampling, we were able to propagate the
 231 uncertainty in our estimates of the vital rate parameters to uncertainty in λ . Furthermore,
 232 by sampling over distributions associated with site, block, and source population variance
 233 terms, we are able to incorporate process error into the total uncertainty in λ , in addition
 234 to the uncertainty that arises from imperfect knowledge of the parameter values. For example,
 235 sampling over site and block variances accounts for regional and local spatial heterogeneity
 236 that is not explained by climate, and sampling over source population variance accounts for
 237 genetically-based demographic differences across the species' range.¹⁴

¹⁴I just want to confirm that this is actually what you did.

238 **Life Table Response Experiments**

239 We conducted two types of Life Table Response Experiments (LTRE) to isolate contributions
240 of climate variables and sex-specific vital rates to variation in λ . First, to identify which
241 aspect of climate is most important for population viability, we used an LTRE based on
242 a nonparametric model for the dependence of λ on parameters associated with seasonal
243 temperature and precipitation (Ellner et al., 2016). To do so, we used the RandomForest
244 package to fit a regression model with four climatic variables (temperature of growing season,
245 precipitation of growing season, temperature of the dormant season and precipitation of
246 the dormant season) as predictors and λ^{15} as response (Liaw et al., 2002). The regression
247 model allowed the estimation of the relative importance of each predictor. **The importance**
248 **is measured by asking: how wrongly is λ predicted if we replaced the focal predictor (e.g.,**
249 **temperature of growing season) by a random value of the other predictors.**¹⁶

Second, to understand how climate drivers influence λ via sex-specific demography, we decomposed the effect of each climate variable on population growth rate (λ) into contribution arising from the effect on each female and male vital rate using a “regression design” LTRE (Caswell, 1989, 2000). This LTRE decomposes the sensitivity of λ to climate according to:

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

250 where, θ_i^F and θ_i^M represent sex-specific parameters (the regression coefficients of the vital
251 rate functions). Because LTRE contributions are additive, we summed across vital rates to
252 compare the total contributions of female and male parameters.¹⁷¹⁸

253 **Population viability across the climatic niche and geographic range**

254 To understand how climate shapes the niche and geographic range of Texas bluegrass, we
255 estimated the probability of self-sustaining populations, which is $\Pr(\lambda \geq 1)$ conditional to
256 temperature and precipitation of the dormant and growing seasons. $\Pr(\lambda > 1)$ was calculated
257 for the two-sex model and the female dominant MPMs using the proportion of the 300
258 posterior samples that lead to a $\lambda \geq 1$ (Diez et al., 2014). Population viability in climate niche
259 space was then represented as a contour plot with values of $\Pr(\lambda > 1)$ at given temperature
260 and precipitation for the growing season, holding dormant season climate constant, and vice

¹⁵Is this lambda from the female-dominant or two-sex model? Does it matter?

¹⁶I do not understand this.

¹⁷ θ_i^F and θ_i^M include the interaction and second order effect. I think we are good with this formula

¹⁸I do not agree. It is true that you can compute this, but only by “turning off” the interaction by holding the interacting variable constant. I still think this needs to be better addressed in both LTRE analyses.

²⁶¹ versa. We also visualized how our common garden sites have moved and are expected to
²⁶² move through climate space through time due to climate change.

²⁶³ $\Pr(\lambda > 1)$ was also mapped onto geographic layers of three US states (Texas, Oklahoma
²⁶⁴ and Kansas) to delineate past, current and future potential geographic distribution of the
²⁶⁵ species. To do so, we estimated $\Pr(\lambda > 1)$ conditional to all climate covariates for each
²⁶⁶ pixel ($\sim 25 \text{ km}^2$) for each time period (past, present, future). Because of the amount of the
²⁶⁷ computation involved, we use 100 posterior samples to estimate $\Pr(\lambda > 1)$ across the study
²⁶⁸ area (Texas, Oklahoma and Kansas).

²⁶⁹ To compare the probability of self-sustaining populations between the female dominant
²⁷⁰ and the two-sex model, we used a zero-inflated beta model in brms (Bürkner, 2017). ¹⁹

²⁷¹ Results

²⁷² Sex specific demographic response to climatic gradient

²⁷³ We found strong demographic responses to climate drivers across our Texas bluegrass
²⁷⁴ common garden sites and evidence for demographic differences between the sexes. ²⁰

¹⁹ *This just floats here without much context. Not sure we need it, but I am flagging for now and will come back to this after reading the results.*

²⁰ *I am skipping the rest of this section for now because I think the figure needs to be re-worked and that will change the rest of this paragraph. I also think this section should include the common garden sex ratio results, since they are connected to the vital rate responses.*

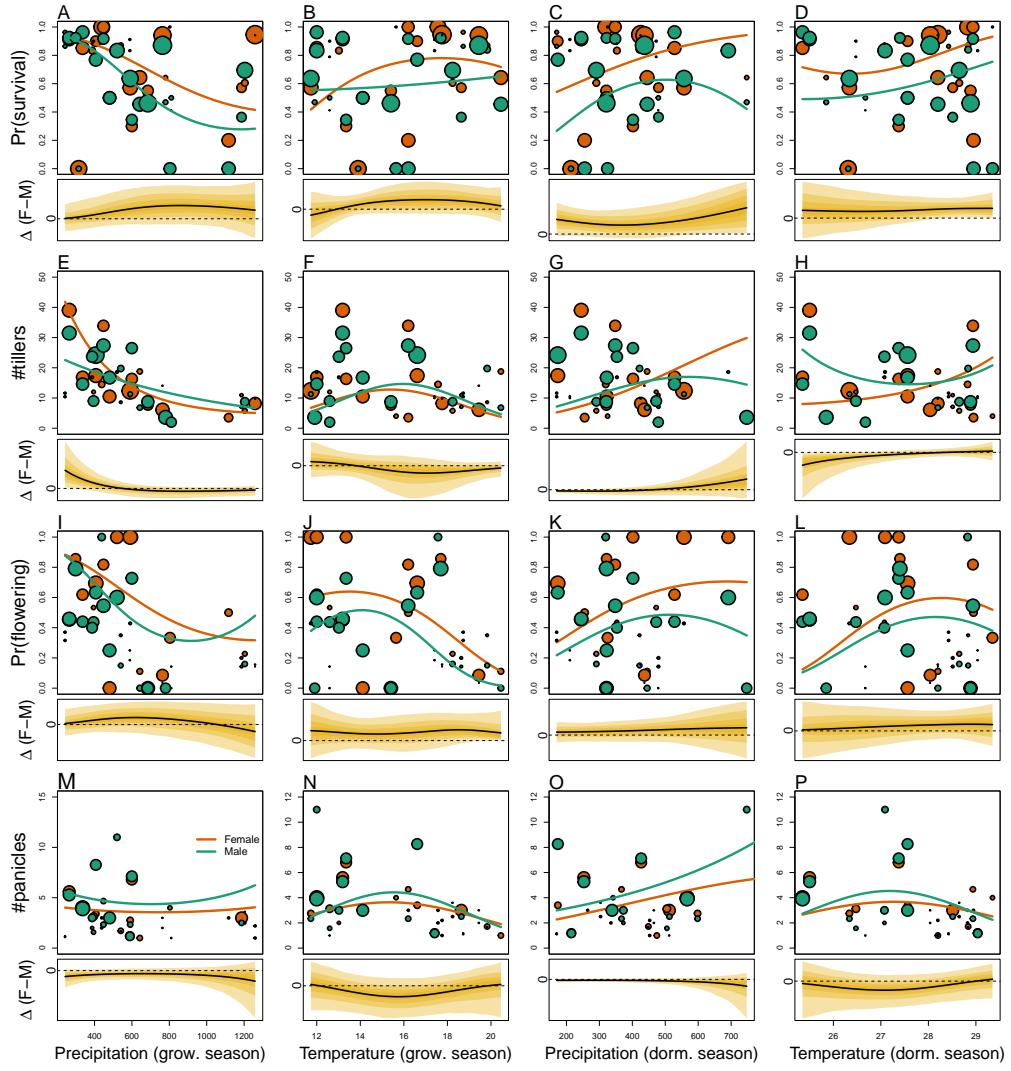


Figure 2: Sex specific demographic response to climate across species range. (A, B, C, D) Probability of survival as a function of precipitation and temperature of the growing and dormant season. (E, F, G, H) Change in number of tillers as a function of precipitation and temperature of the growing and dormant season. (I, J, K, L) Probability of flowering as a function of precipitation and temperature of growing and dormant season. (M, N, O, P) Change in number of panicles as a function of precipitation and temperature of the growing and dormant season. Points show means by site for females (orange) and males (green). Points sizes are proportional to the sample sizes of the mean and are jittered. Lines show fitted statistical models for females (orange) and males (green) based on posterior mean parameter values. Lower panels below each data panel show the posterior distribution of the difference between females and males as a function of climate (positive and negative values indicate female and male advantage, respectively); dashed horizontal line shows zero difference.

275 Climate change alters population viability

276 We estimated population growth rate variation across species range as a function of each
 277 climatic variable given the average of the three other climatic variables using two models:

278 a female dominant model and a two-sex model²¹. For both models, population growth rate
279 decreased toward high precipitation of growing season (Figure 3A). In contrast population
280 growth rate increased with an increase in precipitation of the dormant season (Figure 3C).
281 Furthermore, population growth rate was maximized between 14 and 17 °C and decreased
282 bellow zero beyond 18 °C during the growing season (Figure 3B). Similarly population fitness
283 was maximized between 27 and 31 °C and decreased bellow zero just beyond 20 °C during
284 the dormant season (Figure 3D). ²²

285 We have also detected a strong association between predicted lambda and different
286 ranges of climate (past, present and future). Under past climate conditions, population growth
287 rate decreased below one for temperature of the growing season. Populations will still be
288 viable under moderate gas emission (RCP4.5). However high gas emission (RCP8.5) will alter
289 population viability (Figure 3B, D).²³

290 Population growth rate was most sensitive to change in temperature of the growing
291 season and temperature of the dormant season (Figure S-15). Despite contribution for both
292 sexes, females have a higher contribution to population dynamics than males (Figure S-16;
293 Figure S-17). For both sexes, the reduction of λ for high value of temperature (dormant and
294 growing season) was driven by a reduction of survival rate, growth rate, and a reduction
295 in number of panicles (Figure 3F, H, G, L). However, the change of population growth rate
296 for high value of precipitation was not driven by change in vital rates.

²¹I have now provided the methods for this contrast.

²²I think we should keep this figure. The 2-D niche plots are the better representation of these results, because there are temp*precip interactions that we cannot see here but you can see in the 2-D niche plot. However a model with the 4 predictors together will also give a better approximation of lambda than the 2D. I added the conditional part in the description of the results. I see the 2D as a way of showing the difference in niche. That said if you really want to remove this I am down you have more experience than me.

²³I changed how I write the first sentence to remove the "effect of climate on". Again I don't mind removing the Figure.

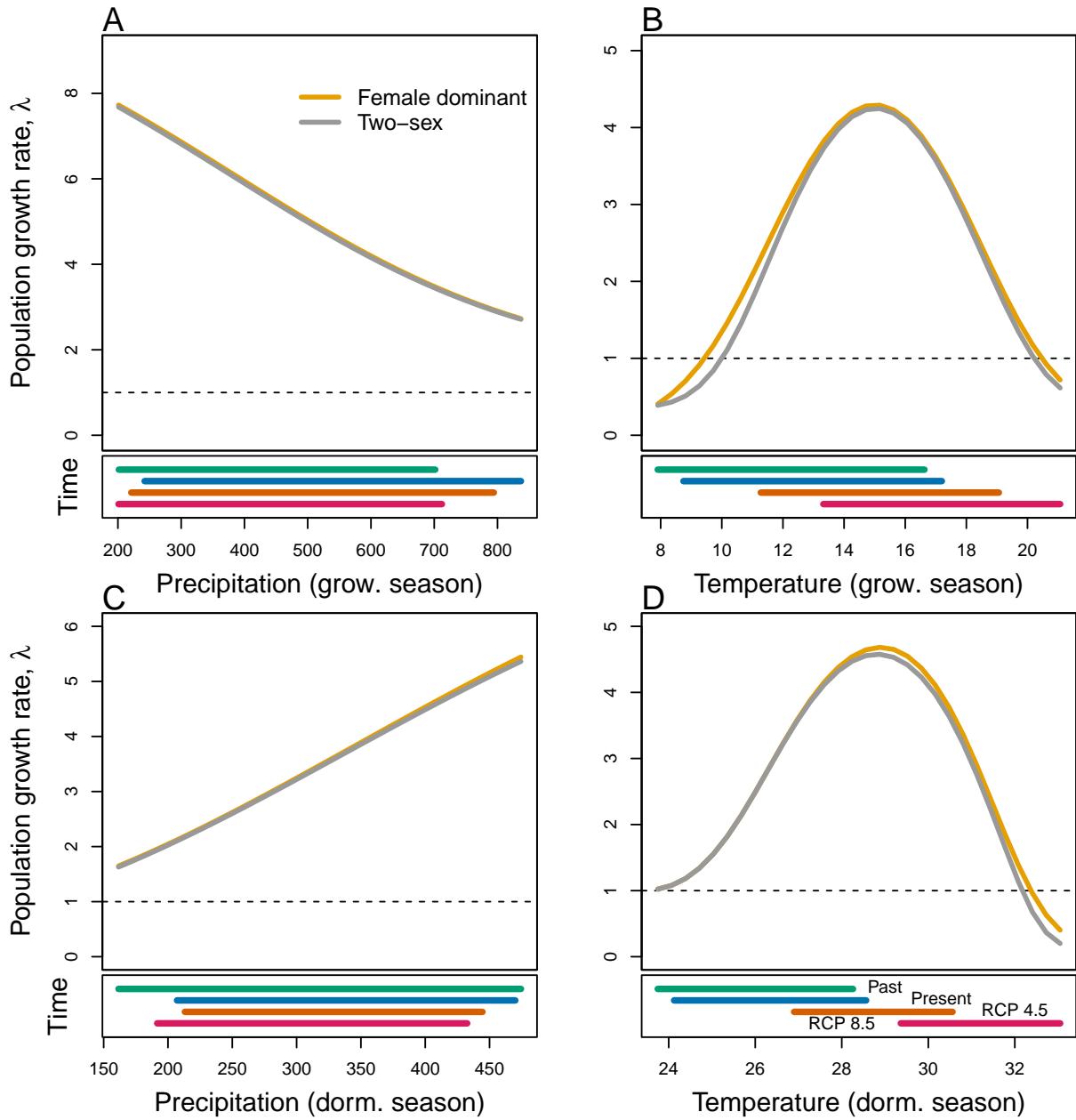


Figure 3: Predicted population growth rate (λ) in different ranges of climate. (A) Precipitation of the growing season, (B) Temperature of the growing season, (C) Precipitation of the dormant season, (D) Temperature of the dormant season. The grey curve shows prediction by the two-sex matrix projection model that incorporates sex-specific demographic responses to climate with sex ratio dependent seed fertilization. The orange curve represents the prediction by the female dominant matrix projection model. The dashed horizontal line indicates the limit of population viability ($\lambda = 1$). Lower panels below each data panel show ranges of climate values for different time period (past climate, present and future climates). For future climate, we show a Representation Concentration Pathways (RCP) 4.5 and 8.5. Values of (λ) are derived from the mean climate variables across 4 GCMs (MIROC5, ACCESS1-3, CESM1-BGC, CMCC-CM).

²⁹⁷ **Climatic change induces niche and range shifts**

²⁹⁸ Female dominant model and two-sex models predicts a niche shift in *Poa arachnifera*
²⁹⁹ populations (Figure 4). However, the female dominant model underestimated the magnitude
³⁰⁰ of niche shifts (Figure 4E, F; -0.16[-0.29,-0.03]). Female dominant model and the two-sex
³⁰¹ models agree that viable populations of *P. arichnifera* were only predicted at the center of the
³⁰² range for current climatic conditions (Figure 5). Although *P. arichnifera* was predicted to have
³⁰³ suitable habitats in the center of the range under current climate, global warming is projected
³⁰⁴ to reduce much of these suitable habitats (Figure 5). If the species is able to disperse far and
³⁰⁵ if there is no physical barriers, most of the current suitable habitats will move toward the
³⁰⁶ Northern range edge as a results of niche shifts. Niche shift underestimation by the female
³⁰⁷ dominant model led to a geographic range underestimation by the female dominant model.

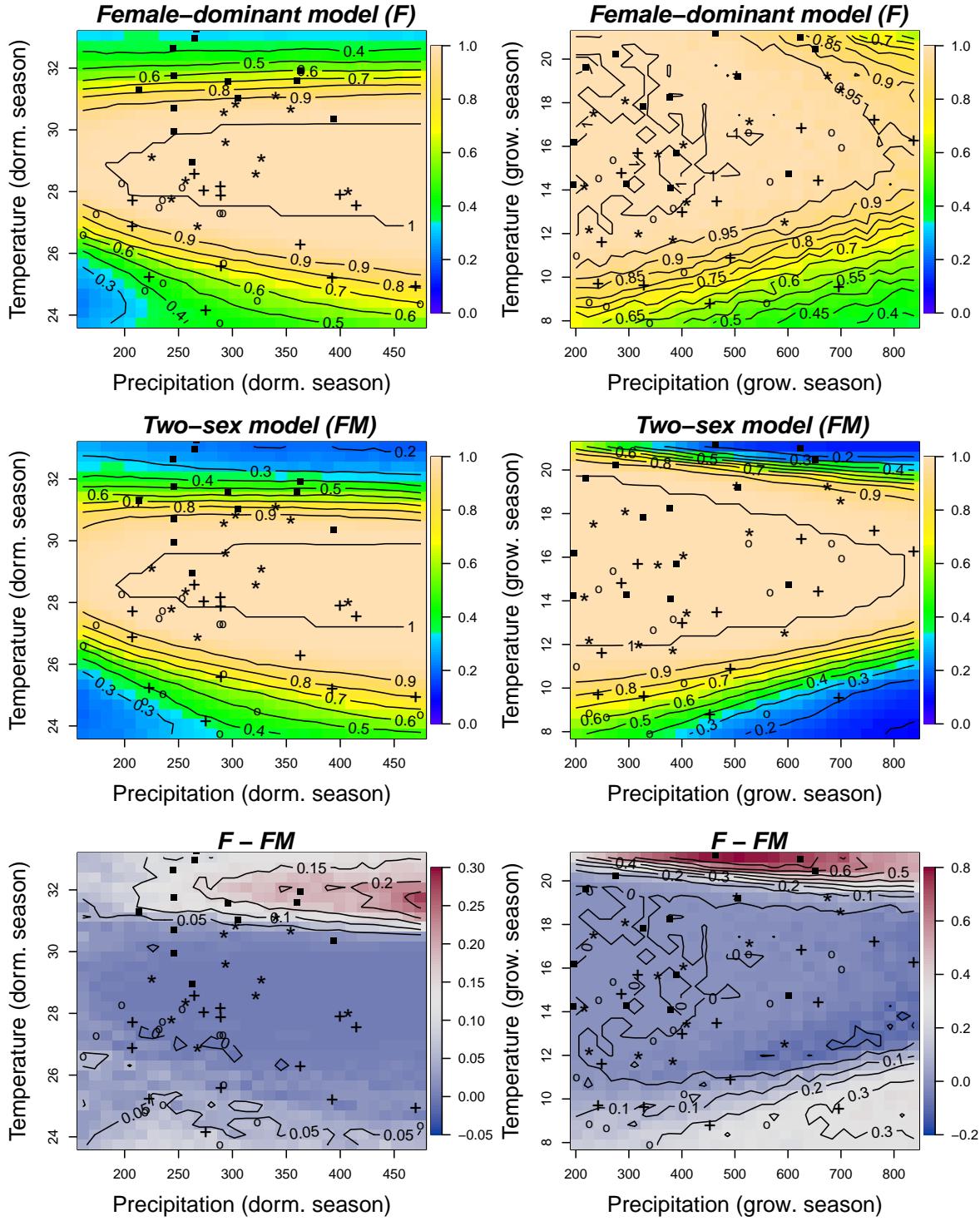


Figure 4: A two-dimensional representation of the predicted niche shift over time (past, present and future climate conditions). Contours on the first four panels show predicted probabilities of self-sustaining populations, $\Pr(\lambda > 1)$ conditional on precipitation and temperature of the dormant and growing season. The last two panels show difference in niche estimation between the female dominant model and the two-sex model for each season. "o": Past, "+": Current, "*": RCP 4.5, "■": RCP 8.5.

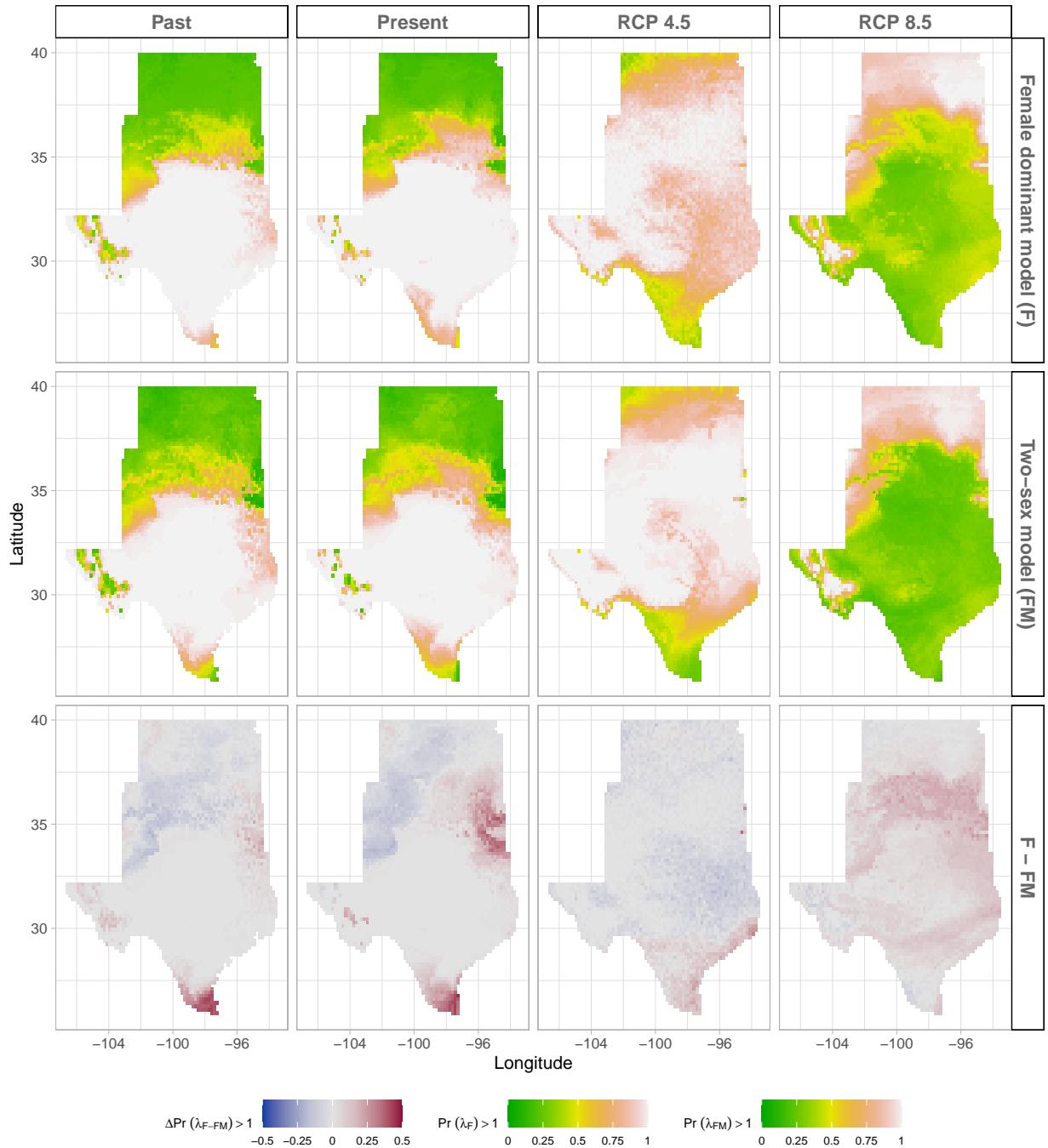


Figure 5: Climate change favors range shift towards north edge. (A) Past, (B) Current, (C and D) Future predicted range shift based on the predicted probabilities of self- sustaining populations, $\Pr(\lambda > 1)$, using the two-sex model that incorporates sex- specific demographic responses to climate with sex ratio dependent seed fertilization. (E) Past, (F) Current, (G and H) Future predicted range shift based on the predicted probabilities of self- sustaining populations, $\Pr(\lambda > 1)$, using the female dominant model. Future projections were based on the CMCC-CM model. The black dots on panel B and F indicate all known presence points collected from GBIF from 1990 to 2019, which corresponds to the current condition in our prediction. The occurrences of GBIFs are distributed in with higher population fitness habitat $\Pr(\lambda > 1)$, confirming that our study approach can reasonably predict range shifts.

308 **Female bias in sex-ratio in response to climate climate change**

309 ²⁴ Operational-Sex Ratio (proportion of females panicles) increased significantly with an
310 increase of precipitation and temperature of the growing season and precipitation and tem-
311 perature of dormant season (Figure S-11, Figure ??). Similarly, the proportion of female plants
312 increased with an increase of temperature of growing season and temperature of dormant
313 season (Figure S-12 B, D, Figure S-13). However, the proportion of female plants did not vary
314 significantly with precipitation of dormant and growing season (Figure S-12 A, C). Future
315 climate drive to extreme female-biased in *Poa arachnifera* populations (Figure 6, Figure S-14).

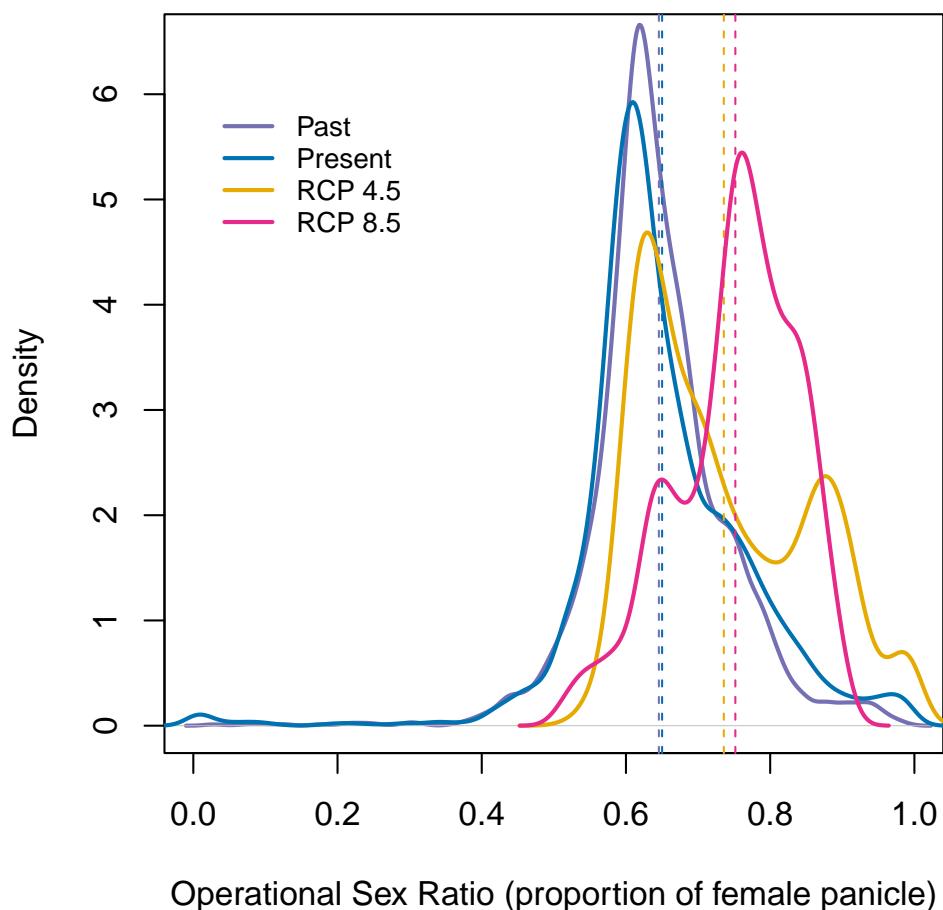


Figure 6: Change in Operational Sex Ratio (proportion of female panicule) over time (past, present, future). Future projections were based on the CMCC-CM model. The mean sex ratio for each time period is shown as vertical dashed line.

²⁴I moved this section because it only makes sense with respect to the geographic projections, because the histograms are showing distributions across the study region. Are these locations conditional on lambda greater than 1 or Pr lambda greater than some value?

316 **Discussion**

317 25 Dioecious species make up a large fraction of Earth's biodiversity – most animals and
318 many plants – yet we have little knowledge about how sex-specific demography and
319 responses to climate drivers may affect population viability and range shifts of dioecious
320 species under climate change.²⁶ We used three years of demographic data collected common
321 garden experiments across climatic gradient to forecast for the first time the impact of climate
322 change on dioecious species. Our future projections require extrapolation to warmer or colder
323 conditions than observed in our experiment and subsequently should be interpreted with
324 caution (Chen et al., 2024). Despite all these limitations, the qualitative implications of the
325 response of our study species to increase temperature (dormant and growing season) seems
326 consistent across all GCMs (Figure S-19, Figure S-20, Figure S-21). Three general patterns
327 emerged from our analysis of range-wide common garden experiments and sex-structured,
328 climate-explicit demographic models. First, our Bayesian mixed effect model suggests a
329 sex specific demographic response to climate change that lead to higher proportion of
330 female as climate increase. Second, climate change favors a northern range shifts in suitable
331 habitats. Third, the female dominant model (model that does not account for sex structure)
332 overestimates species niche and range shifts.

333 There was a female demographic advantage leading to a female biased in response
334 to climate change in *Poa arachnifera* populations. The extreme female-bias in response to
335 climate change contrast with previous studies suggesting that an increase in male frequency
336 in response to climate change (Hultine et al., 2016; Petry et al., 2016). Two mechanisms
337 could explain the observed demographic advantage of females over males for survival and
338 flowering and the opposite for growth and number of panicles. The trade-off between fitness
339 traits (survival, growth and fertility) due to resource limitation and the pollination mode of
340 our study species (wind pollinated) could explain such a result (Cipollini and Whigham, 1994;
341 Freeman et al., 1976). For most species, the cost of reproduction is often higher for females
342 than males due to the requirement to develop seeds and fruits (Hultine et al., 2016). However,
343 several studies reported a higher cost of reproduction for males in wind pollinated species
344 due to the larger amounts of pollen they produce (Bruijning et al., 2017; Bürli et al., 2022;
345 Cipollini and Whigham, 1994; Field et al., 2013).

346 Our results suggest that climate change will alter population at the center of the range
347 and drive a northern range shifts. This impact of climate change on the species current
348 niche could be explained by the increase of temperature over the next years. Small change

25 *This is my new proposition regarding the discussion*

26 *Love this opening sentence.*

349 in temperature of the growing and dormant season have a larger impact on population
350 viability. Temperature can impact plant populations through different mechanisms. Increasing
351 temperature could increase evaporative demand, affect plant phenology (Iler et al., 2019;
352 McLean et al., 2016; Sherry et al., 2007), and germination rate (Reed et al., 2021). The potential
353 for temperature to influence these different processes changes seasonally (Konapala et al.,
354 2020). For example, studies suggested that species that are active during the growing season
355 such as cool grass species can have delayed phenology in response to global warming,
356 particularly if temperatures rise above their physiological tolerances (Cleland et al., 2007;
357 Williams et al., 2015). In addition, high temperature during the growing season by affecting
358 pollen viability, fertilization could affect seed formation and germination (Hatfield and
359 Prueger, 2015; Sletvold and Ågren, 2015). Pollen dispersal may allow plants to resist climate
360 change because pollen dispersal may provide the local genetic diversity necessary to adapt
361 at the leading edge of the population (Corlett and Westcott, 2013; Duputié et al., 2012; Kremer
362 et al., 2012). Since wind pollination is most effective at short distances, it is most often
363 found in plant species growing at high density such as our study species, it is less likely
364 that dispersal limitation affect niche shift in our study system. Difference in non-climatic
365 factors such as soil, or biotic interactions could also explain decline in population growth rate
366 as an indirect effects of increase in temperature (Alexander et al., 2015; Schultz et al., 2022).
367 For example, climate change could increase the strength of species competition and thereby
368 constrain our study species to a narrower realized niche (Aguilée et al., 2016; Pulliam, 2000).

369 We found evidence of underestimation of the impact of climatic change on population
370 dynamics by the female dominant model and implication for such an underestimation on
371 conservation actions for dioecious species. The underestimation of the impact of climatic
372 change on population dynamics by the female dominant model makes sense given the sex
373 specific response to climatic change. *Poa arachnifera* populations will be female biased in
374 response to climate change. That extreme female-bias could affect population growth rate
375 by altering males' fitness with reduction on mate availability given that females individuals
376 have a demographic advantage over males (Haridas et al., 2014; Knight et al., 2005). Further,
377 our work suggest that population viability is sensitive to climate under current and future
378 conditions. This is key because most conservation actions are design from data on current
379 responses to climate, rather than future response to climate (Sletvold et al., 2013). Since the
380 role of male is not negligible in accurately predicting dioecious species response to climate
381 change, management strategies that focus on both sexes would be effective and will enhance
382 our understanding of dioecious species response to global warming.

³⁸³ **Conclusion**

³⁸⁴ We have investigated the potential consequence of skewness in sex ratio on population
³⁸⁵ dynamics and range shift in the context of climate change using the Texas bluegrass. We
³⁸⁶ found extreme female -biased in response to climate change. The effect of female biased
³⁸⁷ will induce range shifts to the northern edge of the species current range by limiting mate
³⁸⁸ availability. Beyond, our study case, our results also suggest that tracking only one sex could
³⁸⁹ lead to an underestimation of the effect of climate change on population dynamics. Our
³⁹⁰ work provides also a framework for predicting the impact of global warming on population
³⁹¹ dynamics using the probability of population to self-sustain.

³⁹² **Acknowledgements**

³⁹³ This research was supported by National Science Foundation Division of Environmental
³⁹⁴ Biology awards 1543651 and 1754468 and by the Rice University Faculty Initiatives Fund.

395 **References**

- 396 Aguilée, R., Raoul, G., Rousset, F., and Ronce, O. (2016). Pollen dispersal slows geographical
397 range shift and accelerates ecological niche shift under climate change. *Proceedings of the*
398 *National Academy of Sciences*, 113(39):E5741–E5748.
- 399 Alexander, J. M., Diez, J. M., and Levine, J. M. (2015). Novel competitors shape species'
400 responses to climate change. *Nature*, 525(7570):515–518.
- 401 Bertrand, R., Lenoir, J., Piedallu, C., Riofrío-Dillon, G., De Ruffray, P., Vidal, C., Pierrat, J.-C.,
402 and Gégout, J.-C. (2011). Changes in plant community composition lag behind climate
403 warming in lowland forests. *Nature*, 479(7374):517–520.
- 404 Bürkner, P.-C. (2017). brms: An R package for Bayesian multilevel models using Stan. *Journal*
405 *of Statistical Software*, 80(1):1–28.
- 406 Bruijning, M., Visser, M. D., Muller-Landau, H. C., Wright, S. J., Comita, L. S., Hubbell, S. P.,
407 de Kroon, H., and Jongejans, E. (2017). Surviving in a cosexual world: A cost-benefit
408 analysis of dioecy in tropical trees. *The American Naturalist*, 189(3):297–314.
- 409 Bürli, S., Pannell, J. R., and Tonnabel, J. (2022). Environmental variation in sex ratios and
410 sexual dimorphism in three wind-pollinated dioecious plant species. *Oikos*, 2022(6):e08651.
- 411 Caswell, H. (1989). Analysis of life table response experiments i. decomposition of effects
412 on population growth rate. *Ecological Modelling*, 46(3-4):221–237.
- 413 Caswell, H. (2000). *Matrix population models*, volume 1. Sinauer Sunderland, MA.
- 414 Chen, X., Liang, Y., and Feng, X. (2024). Influence of model complexity, training collinearity,
415 collinearity shift, predictor novelty and their interactions on ecological forecasting. *Global*
416 *Ecology and Biogeography*, 33(3):371–384.
- 417 Cipollini, M. L. and Whigham, D. F. (1994). Sexual dimorphism and cost of reproduction
418 in the dioecious shrub *lindera benzoin* (lauraceae). *American Journal of Botany*, 81(1):65–75.
- 419 Cleland, E. E., Chuine, I., Menzel, A., Mooney, H. A., and Schwartz, M. D. (2007). Shifting
420 plant phenology in response to global change. *Trends in ecology & evolution*, 22(7):357–365.
- 421 Compagnoni, A., Steigman, K., and Miller, T. E. (2017). Can't live with them, can't live
422 without them? balancing mating and competition in two-sex populations. *Proceedings of*
423 *the Royal Society B: Biological Sciences*, 284(1865):20171999.

- ⁴²⁴ Corlett, R. T. and Westcott, D. A. (2013). Will plant movements keep up with climate change?
⁴²⁵ *Trends in ecology & evolution*, 28(8):482–488.
- ⁴²⁶ Czachura, K. and Miller, T. E. (2020). Demographic back-casting reveals that subtle
⁴²⁷ dimensions of climate change have strong effects on population viability. *Journal of Ecology*,
⁴²⁸ 108(6):2557–2570.
- ⁴²⁹ Dahlgren, J. P., Bengtsson, K., and Ehrlén, J. (2016). The demography of climate-driven and
⁴³⁰ density-regulated population dynamics in a perennial plant. *Ecology*, 97(4):899–907.
- ⁴³¹ Davis, M. B. and Shaw, R. G. (2001). Range shifts and adaptive responses to quaternary
⁴³² climate change. *Science*, 292(5517):673–679.
- ⁴³³ Diez, J. M., Giladi, I., Warren, R., and Pulliam, H. R. (2014). Probabilistic and spatially variable
⁴³⁴ niches inferred from demography. *Journal of ecology*, 102(2):544–554.
- ⁴³⁵ Duputié, A., Massol, F., Chuine, I., Kirkpatrick, M., and Ronce, O. (2012). How do genetic cor-
⁴³⁶ relations affect species range shifts in a changing environment? *Ecology letters*, 15(3):251–259.
- ⁴³⁷ Eberhart-Phillips, L. J., Küpper, C., Miller, T. E., Cruz-López, M., Maher, K. H., Dos Remedios,
⁴³⁸ N., Stoffel, M. A., Hoffman, J. I., Krüger, O., and Székely, T. (2017). Sex-specific early
⁴³⁹ survival drives adult sex ratio bias in snowy plovers and impacts mating system and
⁴⁴⁰ population growth. *Proceedings of the National Academy of Sciences*, 114(27):E5474–E5481.
- ⁴⁴¹ Ehrlén, J. and Morris, W. F. (2015). Predicting changes in the distribution and abundance
⁴⁴² of species under environmental change. *Ecology letters*, 18(3):303–314.
- ⁴⁴³ Elderd, B. D. and Miller, T. E. (2016). Quantifying demographic uncertainty: Bayesian methods
⁴⁴⁴ for integral projection models. *Ecological Monographs*, 86(1):125–144.
- ⁴⁴⁵ Ellis, R. P., Davison, W., Queirós, A. M., Kroeker, K. J., Calosi, P., Dupont, S., Spicer, J. I.,
⁴⁴⁶ Wilson, R. W., Widdicombe, S., and Urbina, M. A. (2017). Does sex really matter? explaining
⁴⁴⁷ intraspecies variation in ocean acidification responses. *Biology letters*, 13(2):20160761.
- ⁴⁴⁸ Ellner, S. P., Adler, P. B., Childs, D. Z., Hooker, G., Miller, T. E., and Rees, M. (2022). A critical
⁴⁴⁹ comparison of integral projection and matrix projection models for demographic analysis:
⁴⁵⁰ Comment. *Ecology*.
- ⁴⁵¹ Ellner, S. P., Childs, D. Z., Rees, M., et al. (2016). Data-driven modelling of structured
⁴⁵² populations. *A practical guide to the Integral Projection Model*. Cham: Springer.

- 453 Evans, M. E., Merow, C., Record, S., McMahon, S. M., and Enquist, B. J. (2016). Towards
454 process-based range modeling of many species. *Trends in Ecology & Evolution*, 31(11):860–871.
- 455 Field, D. L., Pickup, M., and Barrett, S. C. (2013). Comparative analyses of sex-ratio variation
456 in dioecious flowering plants. *Evolution*, 67(3):661–672.
- 457 Freeman, D. C., Klikoff, L. G., and Harper, K. T. (1976). Differential resource utilization by
458 the sexes of dioecious plants. *Science*, 193(4253):597–599.
- 459 Gamelon, M., Grøtan, V., Nilsson, A. L., Engen, S., Hurrell, J. W., Jerstad, K., Phillips, A. S.,
460 Røstad, O. W., Slagsvold, T., Walseng, B., et al. (2017). Interactions between demography
461 and environmental effects are important determinants of population dynamics. *Science
462 Advances*, 3(2):e1602298.
- 463 Gerber, L. R. and White, E. R. (2014). Two-sex matrix models in assessing population viability:
464 when do male dynamics matter? *Journal of Applied Ecology*, 51(1):270–278.
- 465 Gissi, E., Bowyer, R. T., and Bleich, V. C. (2024). Sex-based differences affect conservation.
466 *Science*, 384(6702):1309–1310.
- 467 Gissi, E., Schiebinger, L., Hadly, E. A., Crowder, L. B., Santoleri, R., and Micheli, F. (2023).
468 Exploring climate-induced sex-based differences in aquatic and terrestrial ecosystems to
469 mitigate biodiversity loss. *nature communications*, 14(1):4787.
- 470 Haridas, C., Eager, E. A., Rebarber, R., and Tenhumberg, B. (2014). Frequency-dependent
471 population dynamics: Effect of sex ratio and mating system on the elasticity of population
472 growth rate. *Theoretical Population Biology*, 97:49–56.
- 473 Hatfield, J. and Prueger, J. (2015). Temperature extremes: effect on plant growth and
474 development. *weather clim extrem* 10: 4–10.
- 475 Hernández, C. M., Ellner, S. P., Adler, P. B., Hooker, G., and Snyder, R. E. (2023). An exact
476 version of life table response experiment analysis, and the r package exactltre. *Methods
477 in Ecology and Evolution*, 14(3):939–951.
- 478 Hitchcock, A. S. (1971). *Manual of the grasses of the United States*, volume 2. Courier Corporation.
- 479 Hultine, K. R., Grady, K. C., Wood, T. E., Shuster, S. M., Stella, J. C., and Whitham, T. G. (2016).
480 Climate change perils for dioecious plant species. *Nature Plants*, 2(8):1–8.

- 481 Iler, A. M., Compagnoni, A., Inouye, D. W., Williams, J. L., CaraDonna, P. J., Anderson, A., and
482 Miller, T. E. (2019). Reproductive losses due to climate change-induced earlier flowering are
483 not the primary threat to plant population viability in a perennial herb. *Journal of Ecology*,
484 107(4):1931–1943.
- 485 Jones, M. H., Macdonald, S. E., and Henry, G. H. (1999). Sex-and habitat-specific responses
486 of a high arctic willow, *salix arctica*, to experimental climate change. *Oikos*, pages 129–138.
- 487 Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann,
488 N. E., Linder, H. P., and Kessler, M. (2017). Climatologies at high resolution for the earth's
489 land surface areas. *Scientific data*, 4(1):1–20.
- 490 Kindiger, B. (2004). Interspecific hybrids of *poa arachnifera* × *poa secunda*. *Journal of New
491 Seeds*, 6(1):1–26.
- 492 Knight, T. M., Steets, J. A., Vamosi, J. C., Mazer, S. J., Burd, M., Campbell, D. R., Dudash,
493 M. R., Johnston, M. O., Mitchell, R. J., and Ashman, T.-L. (2005). Pollen limitation of plant
494 reproduction: pattern and process. *Annu. Rev. Ecol. Evol. Syst.*, 36:467–497.
- 495 Konapala, G., Mishra, A. K., Wada, Y., and Mann, M. E. (2020). Climate change will affect
496 global water availability through compounding changes in seasonal precipitation and
497 evaporation. *Nature communications*, 11(1):3044.
- 498 Kremer, A., Ronce, O., Robledo-Arnuncio, J. J., Guillaume, F., Bohrer, G., Nathan, R., Bridle,
499 J. R., Gomulkiewicz, R., Klein, E. K., Ritland, K., et al. (2012). Long-distance gene flow and
500 adaptation of forest trees to rapid climate change. *Ecology letters*, 15(4):378–392.
- 501 Lee-Yaw, J. A., Kharouba, H. M., Bontrager, M., Mahony, C., Csergő, A. M., Noreen, A. M.,
502 Li, Q., Schuster, R., and Angert, A. L. (2016). A synthesis of transplant experiments and
503 ecological niche models suggests that range limits are often niche limits. *Ecology letters*,
504 19(6):710–722.
- 505 Liaw, A., Wiener, M., et al. (2002). Classification and regression by randomforest. *R news*,
506 2(3):18–22.
- 507 Louthan, A. M., Keighron, M., Kiekebusch, E., Cayton, H., Terando, A., and Morris, W. F.
508 (2022). Climate change weakens the impact of disturbance interval on the growth rate of
509 natural populations of venus flytrap. *Ecological Monographs*, 92(4):e1528.

- 510 Lynch, H. J., Rhainds, M., Calabrese, J. M., Cantrell, S., Cosner, C., and Fagan, W. F. (2014).
511 How climate extremes—not means—define a species' geographic range boundary via a
512 demographic tipping point. *Ecological Monographs*, 84(1):131–149.
- 513 McLean, N., Lawson, C. R., Leech, D. I., and van de Pol, M. (2016). Predicting when climate-
514 driven phenotypic change affects population dynamics. *Ecology Letters*, 19(6):595–608.
- 515 Merow, C., Bois, S. T., Allen, J. M., Xie, Y., and Silander Jr, J. A. (2017). Climate change both
516 facilitates and inhibits invasive plant ranges in new england. *Proceedings of the National
517 Academy of Sciences*, 114(16):E3276–E3284.
- 518 Miller, T. and Compagnoni, A. (2022a). Data from: Two-sex demography, sexual niche
519 differentiation, and the geographic range limits of texas bluegrass (*Poa arachnifera*). *American
520 Naturalist, Dryad Digital Repository*,. <https://doi.org/10.5061/dryad.kkwh70s5x>.
- 521 Miller, T. E. and Compagnoni, A. (2022b). Two-sex demography, sexual niche differentiation,
522 and the geographic range limits of texas bluegrass (*poa arachnifera*). *The American
523 Naturalist*, 200(1):17–31.
- 524 Miller, T. E., Shaw, A. K., Inouye, B. D., and Neubert, M. G. (2011). Sex-biased dispersal and
525 the speed of two-sex invasions. *The American Naturalist*, 177(5):549–561.
- 526 Morrison, C. A., Robinson, R. A., Clark, J. A., and Gill, J. A. (2016). Causes and consequences
527 of spatial variation in sex ratios in a declining bird species. *Journal of Animal Ecology*,
528 85(5):1298–1306.
- 529 Pease, C. M., Lande, R., and Bull, J. (1989). A model of population growth, dispersal and
530 evolution in a changing environment. *Ecology*, 70(6):1657–1664.
- 531 Petry, W. K., Soule, J. D., Iler, A. M., Chicas-Mosier, A., Inouye, D. W., Miller, T. E., and
532 Mooney, K. A. (2016). Sex-specific responses to climate change in plants alter population
533 sex ratio and performance. *Science*, 353(6294):69–71.
- 534 Piironen, J. and Vehtari, A. (2017). Comparison of bayesian predictive methods for model
535 selection. *Statistics and Computing*, 27:711–735.
- 536 Pottier, P., Burke, S., Drobniak, S. M., Lagisz, M., and Nakagawa, S. (2021). Sexual (in) equality?
537 a meta-analysis of sex differences in thermal acclimation capacity across ectotherms.
538 *Functional Ecology*, 35(12):2663–2678.

- 539 Pulliam, H. R. (2000). On the relationship between niche and distribution. *Ecology letters*,
540 3(4):349–361.
- 541 R Core Team (2023). *R: A Language and Environment for Statistical Computing*. R Foundation
542 for Statistical Computing, Vienna, Austria.
- 543 Reed, P. B., Peterson, M. L., Pfeifer-Meister, L. E., Morris, W. F., Doak, D. F., Roy, B. A., Johnson,
544 B. R., Bailes, G. T., Nelson, A. A., and Bridgman, S. D. (2021). Climate manipulations
545 differentially affect plant population dynamics within versus beyond northern range limits.
546 *Journal of Ecology*, 109(2):664–675.
- 547 Renganayaki, K., Jessup, R., Burson, B., Hussey, M., and Read, J. (2005). Identification of
548 male-specific AFLP markers in dioecious Texas bluegrass. *Crop science*, 45(6):2529–2539.
- 549 Sanderson, B. M., Knutti, R., and Caldwell, P. (2015). A representative democracy to reduce
550 interdependency in a multimodel ensemble. *Journal of Climate*, 28(13):5171–5194.
- 551 Schultz, E. L., Hülsmann, L., Pillet, M. D., Hartig, F., Breshears, D. D., Record, S., Shaw, J. D.,
552 DeRose, R. J., Zuidema, P. A., and Evans, M. E. (2022). Climate-driven, but dynamic and
553 complex? a reconciliation of competing hypotheses for species' distributions. *Ecology letters*,
554 25(1):38–51.
- 555 Schwalm, C. R., Glendon, S., and Duffy, P. B. (2020). Rcp8.5 tracks cumulative CO₂ emissions.
556 *Proceedings of the National Academy of Sciences*, 117(33):19656–19657.
- 557 Schwinning, S., Lortie, C. J., Esque, T. C., and DeFalco, L. A. (2022). What common-garden
558 experiments tell us about climate responses in plants.
- 559 Sexton, J. P., McIntyre, P. J., Angert, A. L., and Rice, K. J. (2009). Evolution and ecology of
560 species range limits. *Annu. Rev. Ecol. Evol. Syst.*, 40:415–436.
- 561 Shelton, A. O. (2010). The ecological and evolutionary drivers of female-biased sex ratios:
562 two-sex models of perennial seagrasses. *The American Naturalist*, 175(3):302–315.
- 563 Sherry, R. A., Zhou, X., Gu, S., Arnone III, J. A., Schimel, D. S., Verburg, P. S., Wallace,
564 L. L., and Luo, Y. (2007). Divergence of reproductive phenology under climate warming.
565 *Proceedings of the National Academy of Sciences*, 104(1):198–202.
- 566 Sletvold, N. and Ågren, J. (2015). Climate-dependent costs of reproduction: Survival and
567 fecundity costs decline with length of the growing season and summer temperature.
568 *Ecology Letters*, 18(4):357–364.

- 569 Sletvold, N., Dahlgren, J. P., Øien, D.-I., Moen, A., and Ehrlén, J. (2013). Climate warming
570 alters effects of management on population viability of threatened species: results from
571 a 30-year experimental study on a rare orchid. *Global Change Biology*, 19(9):2729–2738.
- 572 Smith, M. D., Wilkins, K. D., Holdrege, M. C., Wilfahrt, P., Collins, S. L., Knapp, A. K., Sala,
573 O. E., Dukes, J. S., Phillips, R. P., Yahdjian, L., et al. (2024). Extreme drought impacts have
574 been underestimated in grasslands and shrublands globally. *Proceedings of the National
575 Academy of Sciences*, 121(4):e2309881120.
- 576 Stan Development Team (2023). RStan: the R interface to Stan. R package version 2.21.8.
- 577 Thomson, A. M., Calvin, K. V., Smith, S. J., Kyle, G. P., Volke, A., Patel, P., Delgado-Arias,
578 S., Bond-Lamberty, B., Wise, M. A., Clarke, L. E., et al. (2011). Rcp4. 5: a pathway for
579 stabilization of radiative forcing by 2100. *Climatic change*, 109:77–94.
- 580 Tognetti, R. (2012). Adaptation to climate change of dioecious plants: does gender balance
581 matter? *Tree Physiology*, 32(11):1321–1324.
- 582 Williams, J. L., Jacquemyn, H., Ochocki, B. M., Brys, R., and Miller, T. E. (2015). Life
583 history evolution under climate change and its influence on the population dynamics of
584 a long-lived plant. *Journal of Ecology*, 103(4):798–808.

Supporting Information

585 S.1 Supporting Figures

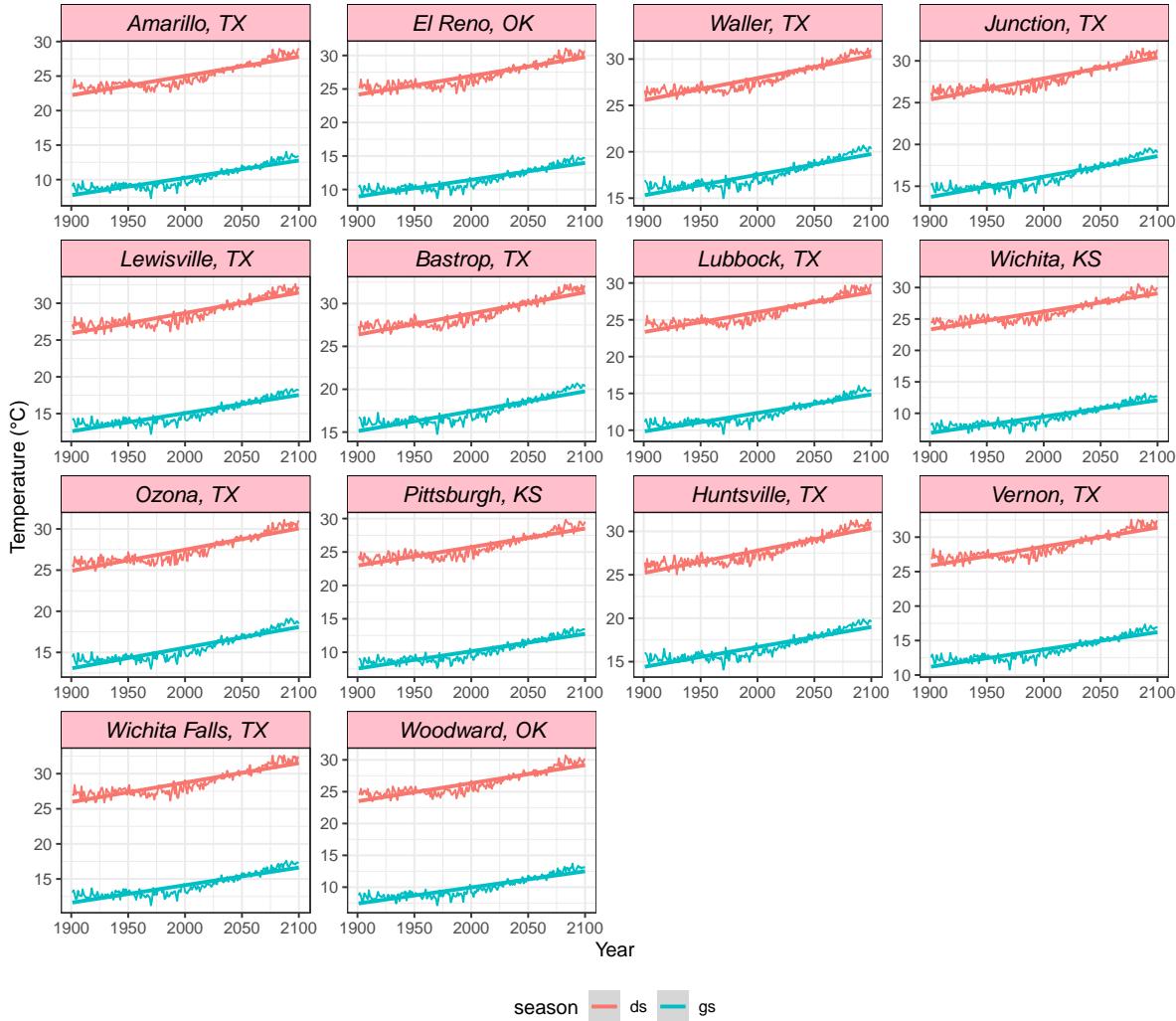


Figure S-1: Temperature variation across the study sites from 1990 to 2100, ds: Dormant season, dg: Growing season.

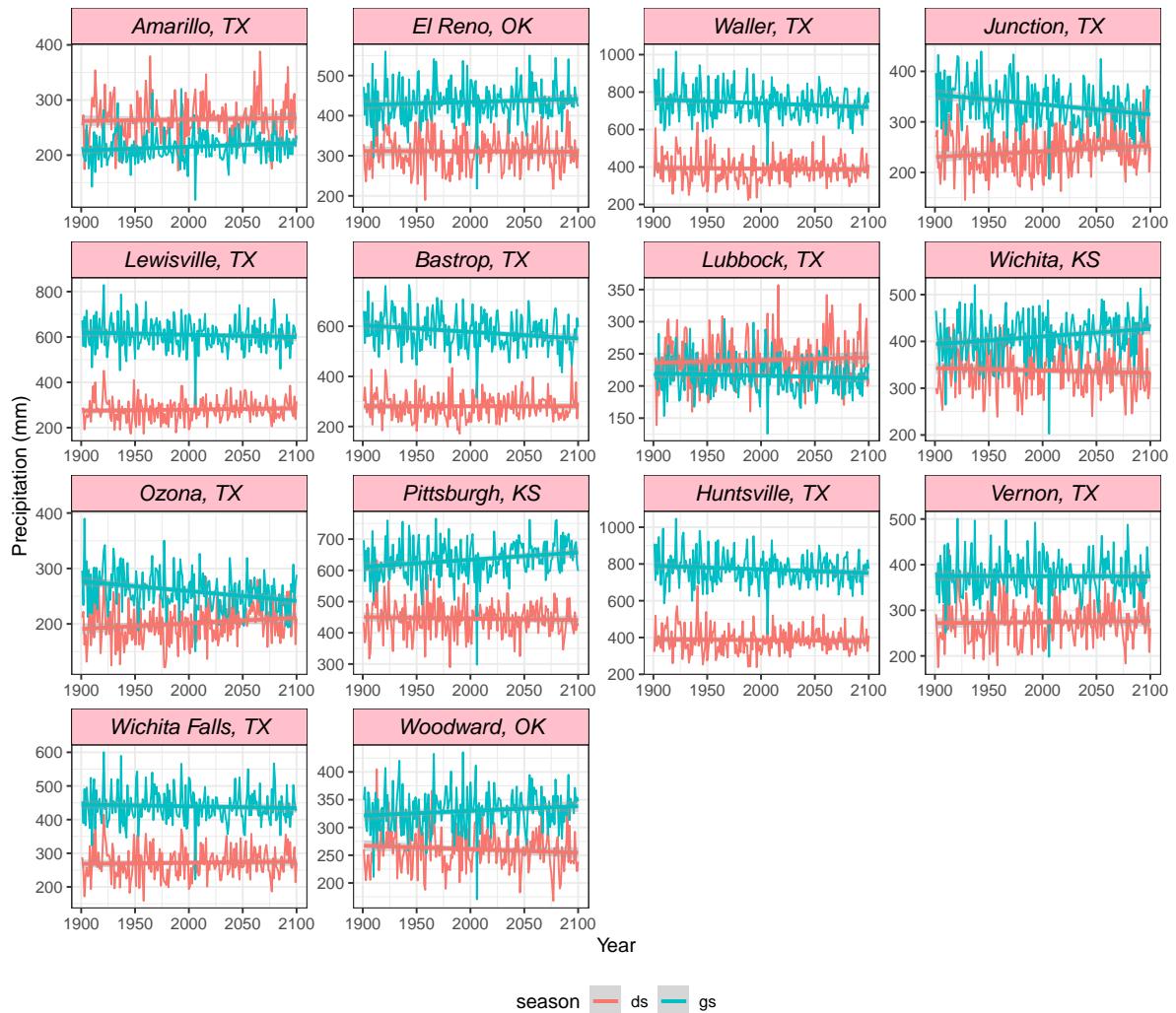


Figure S-2: Precipitation variation across the study sites from 1990 to 2100. ds: Dormant season, dg: Growing season.

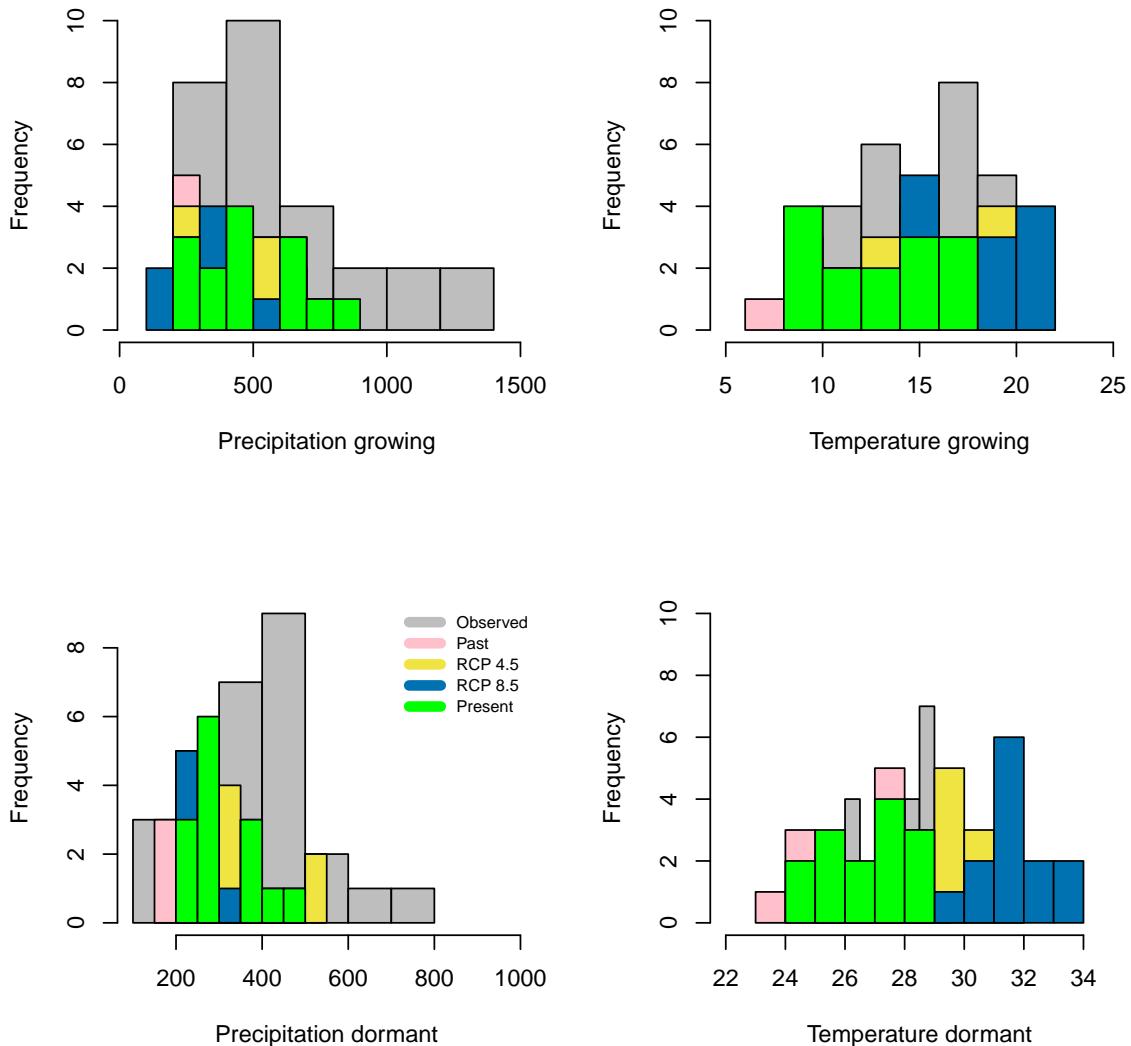


Figure S-3: Past, Observed, present and future (MIROC Model) climate data across the study area.

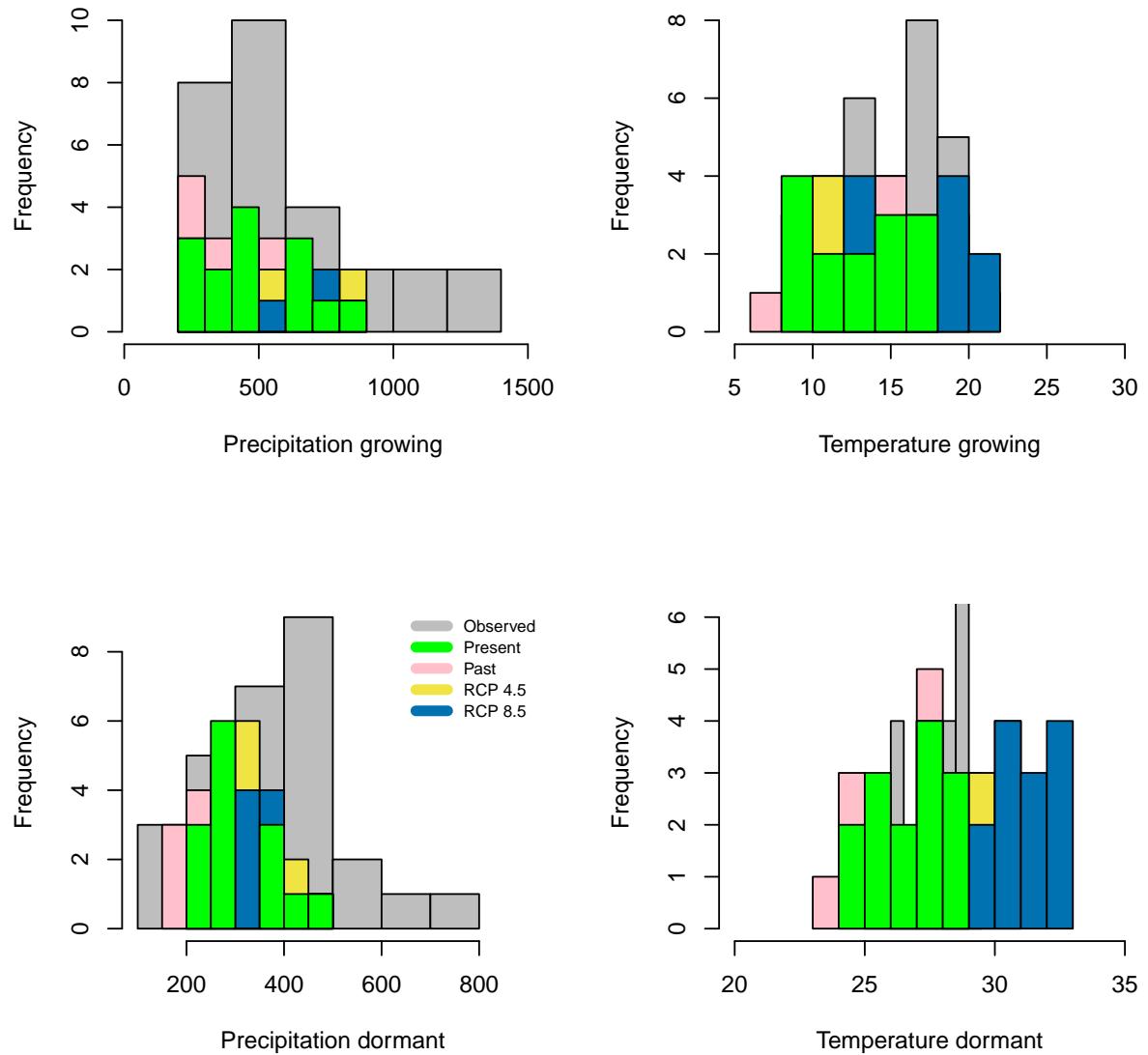


Figure S-4: Past, Observed, present and future (ACCESS Model) climate data across the study area.

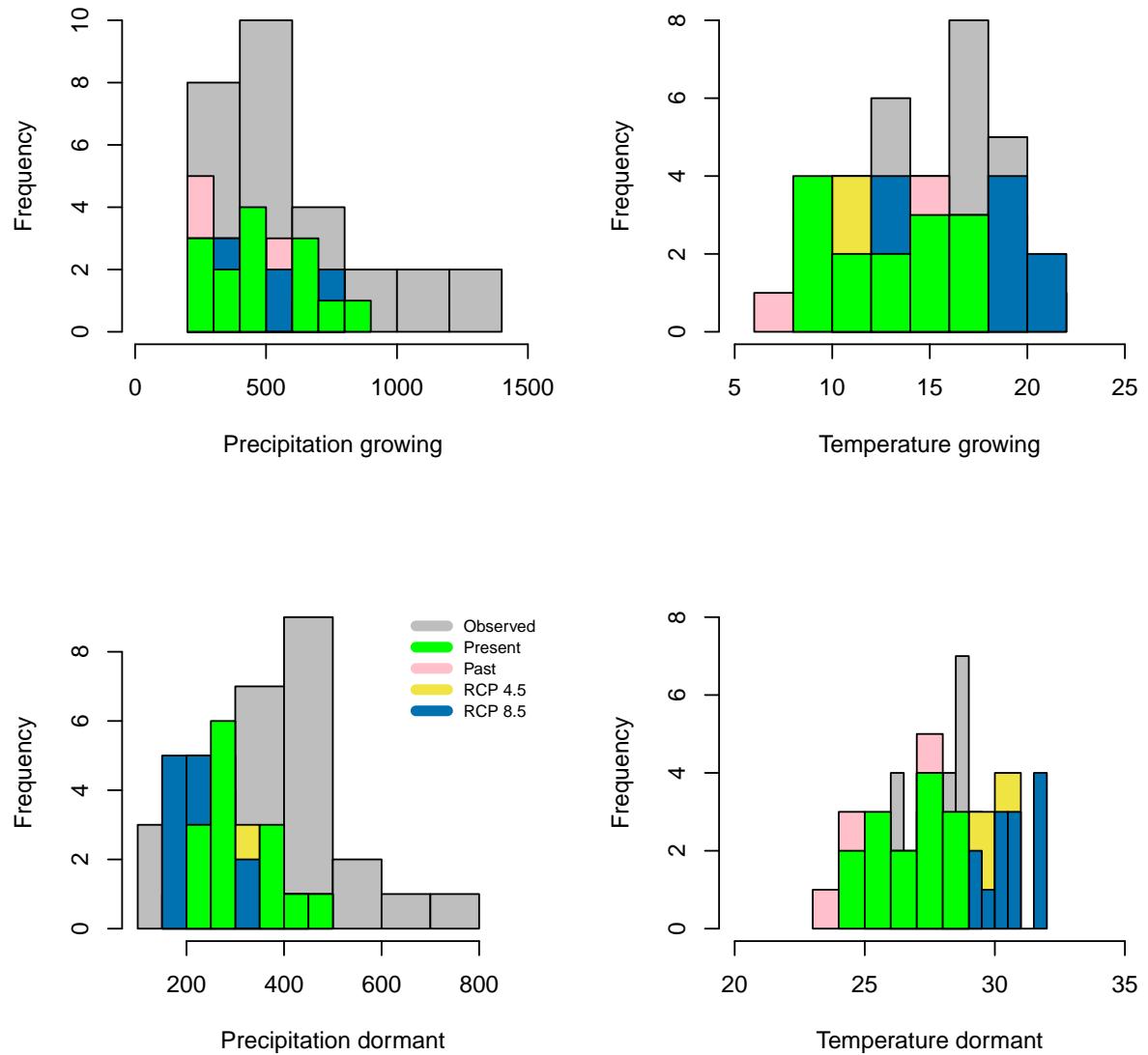


Figure S-5: Past, Observed, present and future (CESM1 Model) climate data across the study area.

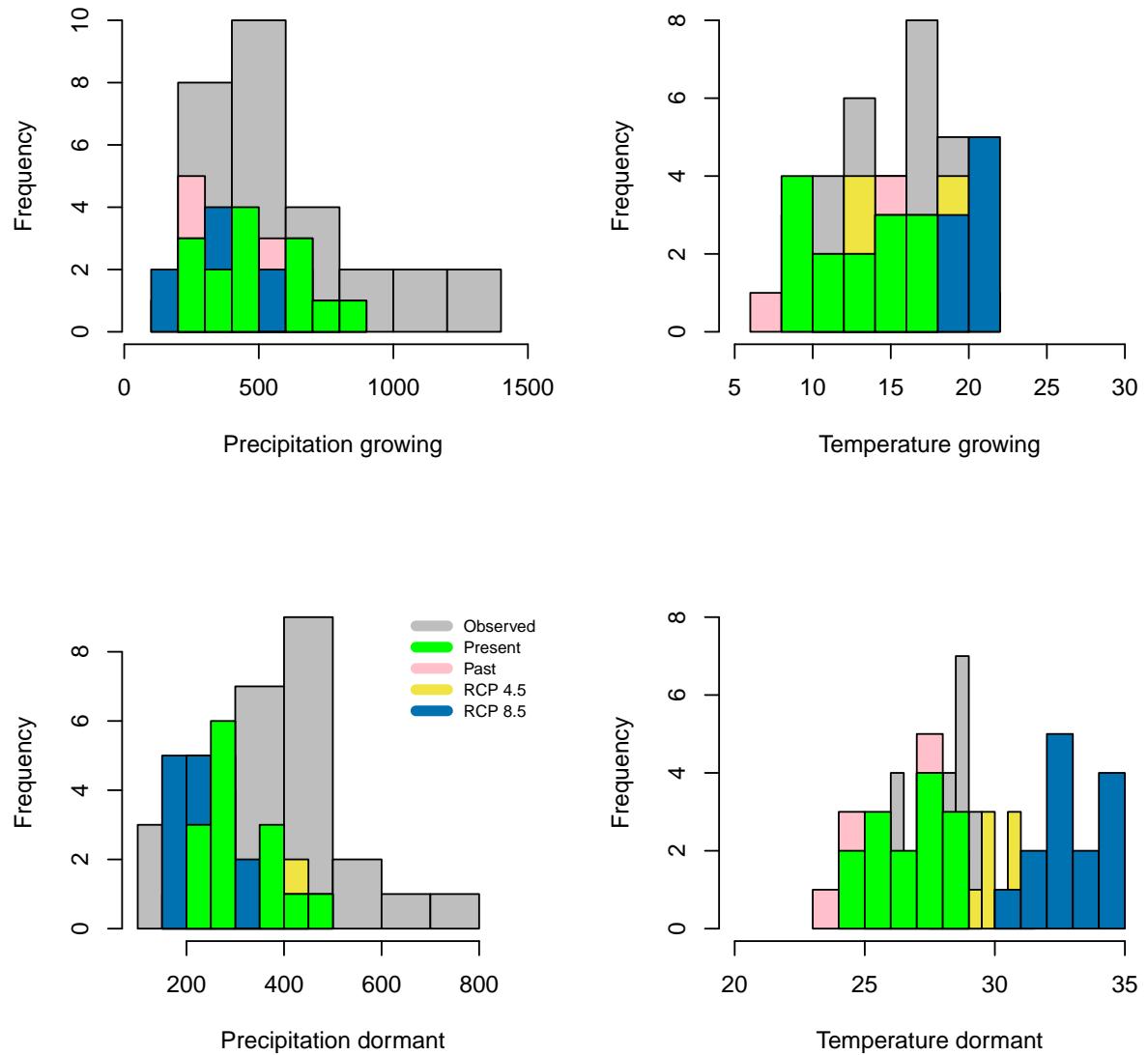


Figure S-6: Past, Observed, present and future (CMCC Model) climate data across the study area.

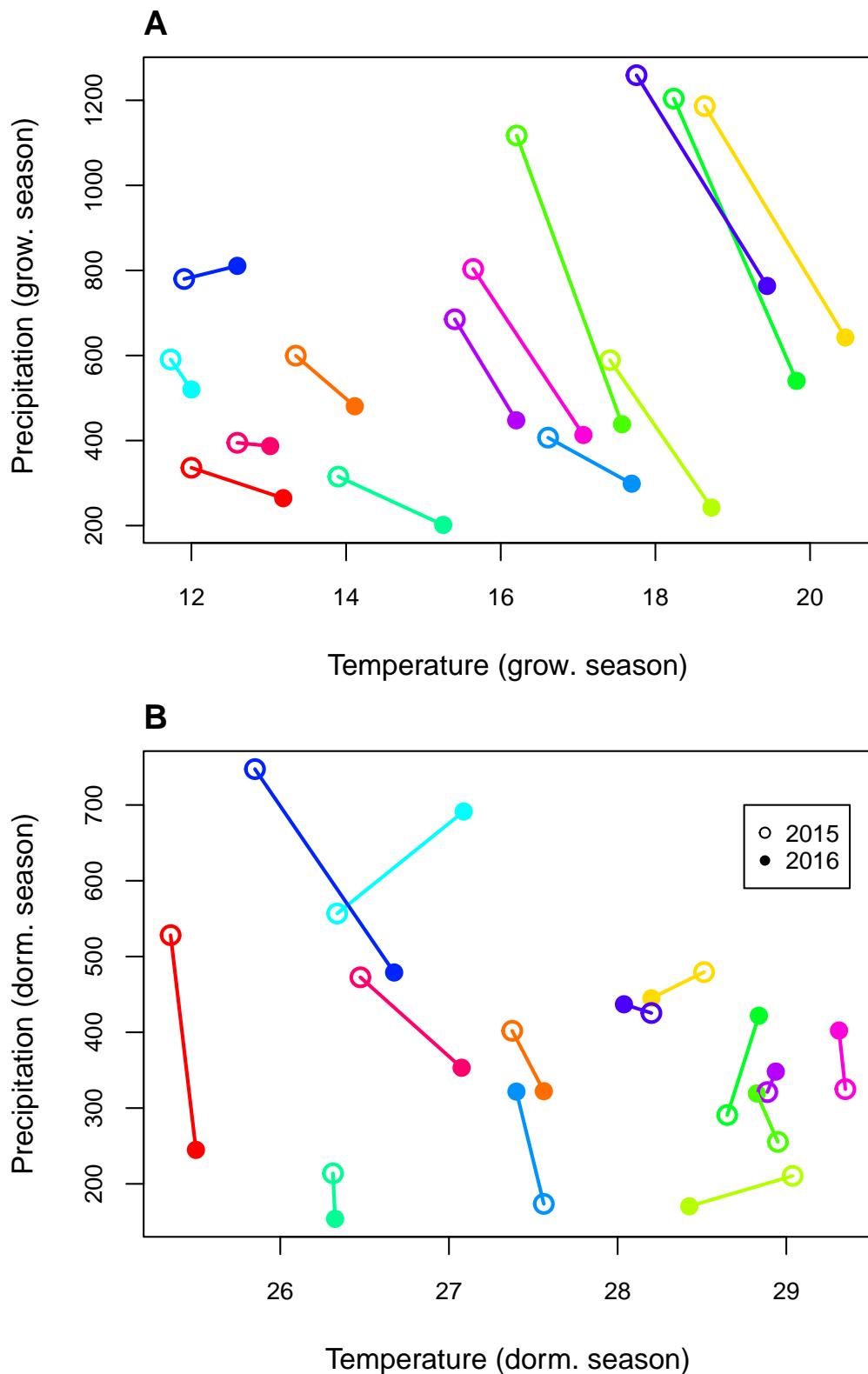


Figure S-7: Seasonal climate variation (temperature in °C and precipitation in mm) across the common garden sites during the 2014–15 and 2015–16 census periods. Each color represents a site and lines connect the same site between years.

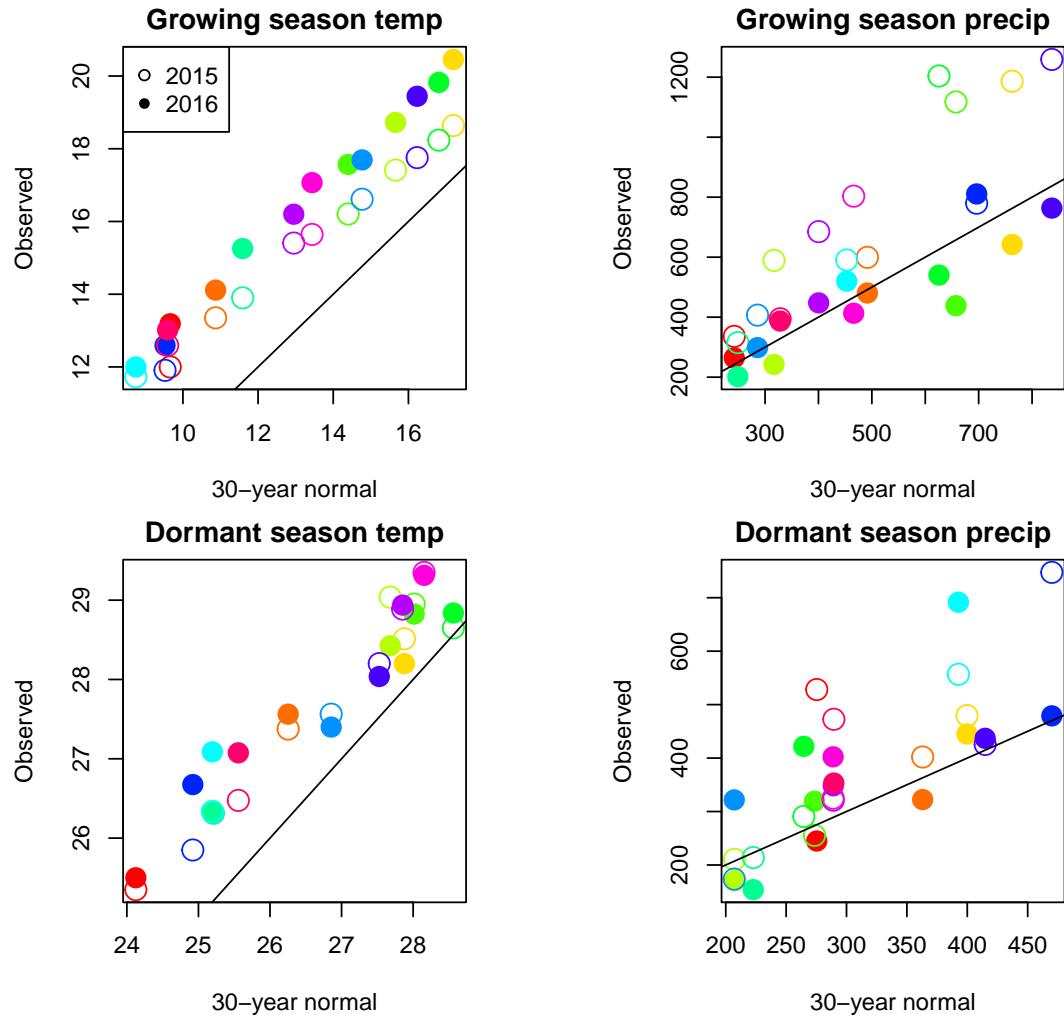


Figure S-8: Comparison of 30-year (1990-2019) climate normals and observed weather conditions at common garden sites during the 2014-15 and 2015-16 census periods. Temperature is in $^{\circ}\text{C}$ and precipitation is in mm . Colors represent sites and lines show the $y=x$ relationship.

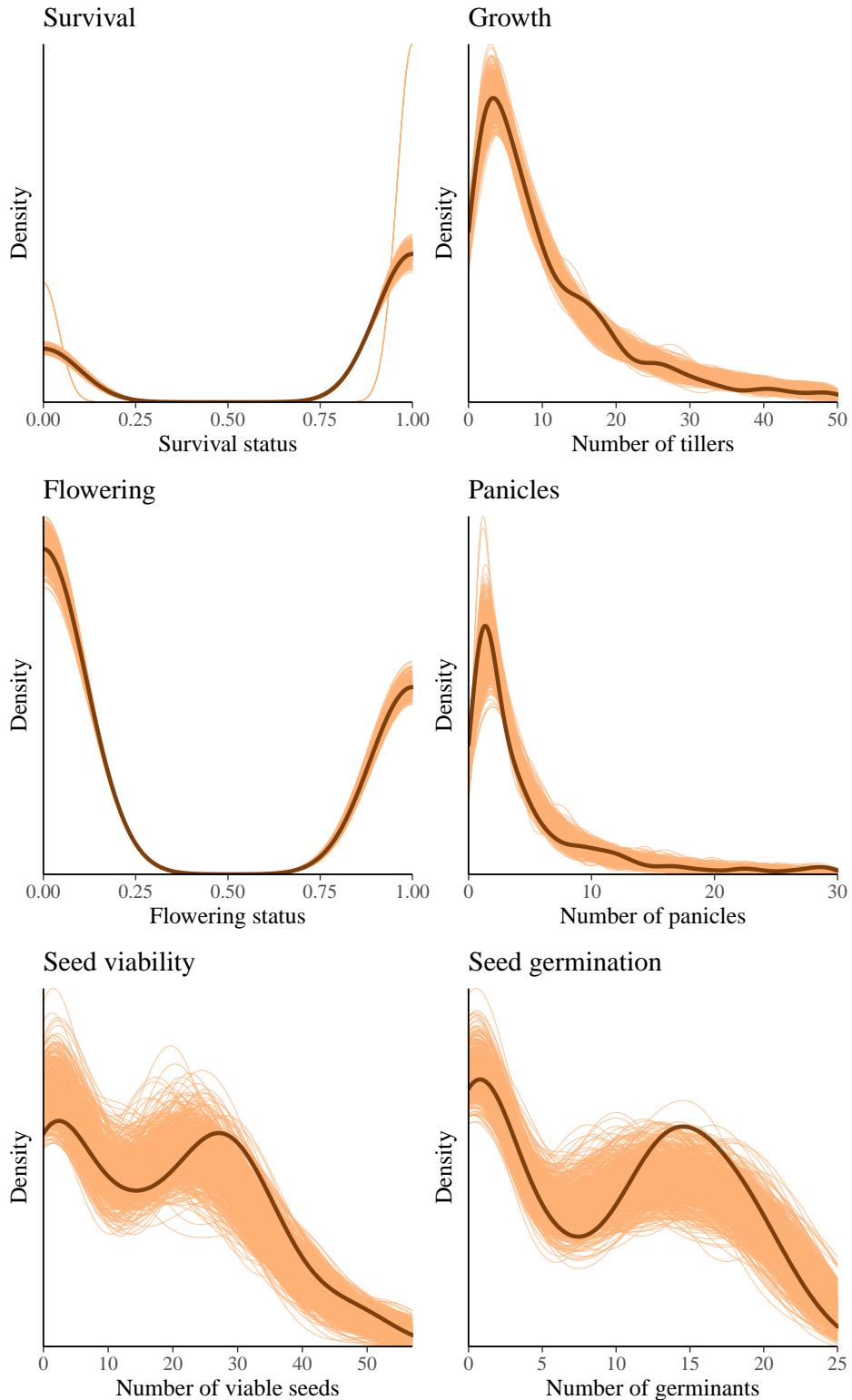


Figure S-9: Posterior predictive checks. Consistency between real data and simulated values suggests that the fitted vital rate models accurately describes the data. Graph shows density curves for the observed data (light orange) along with the simulated values (dark orange).

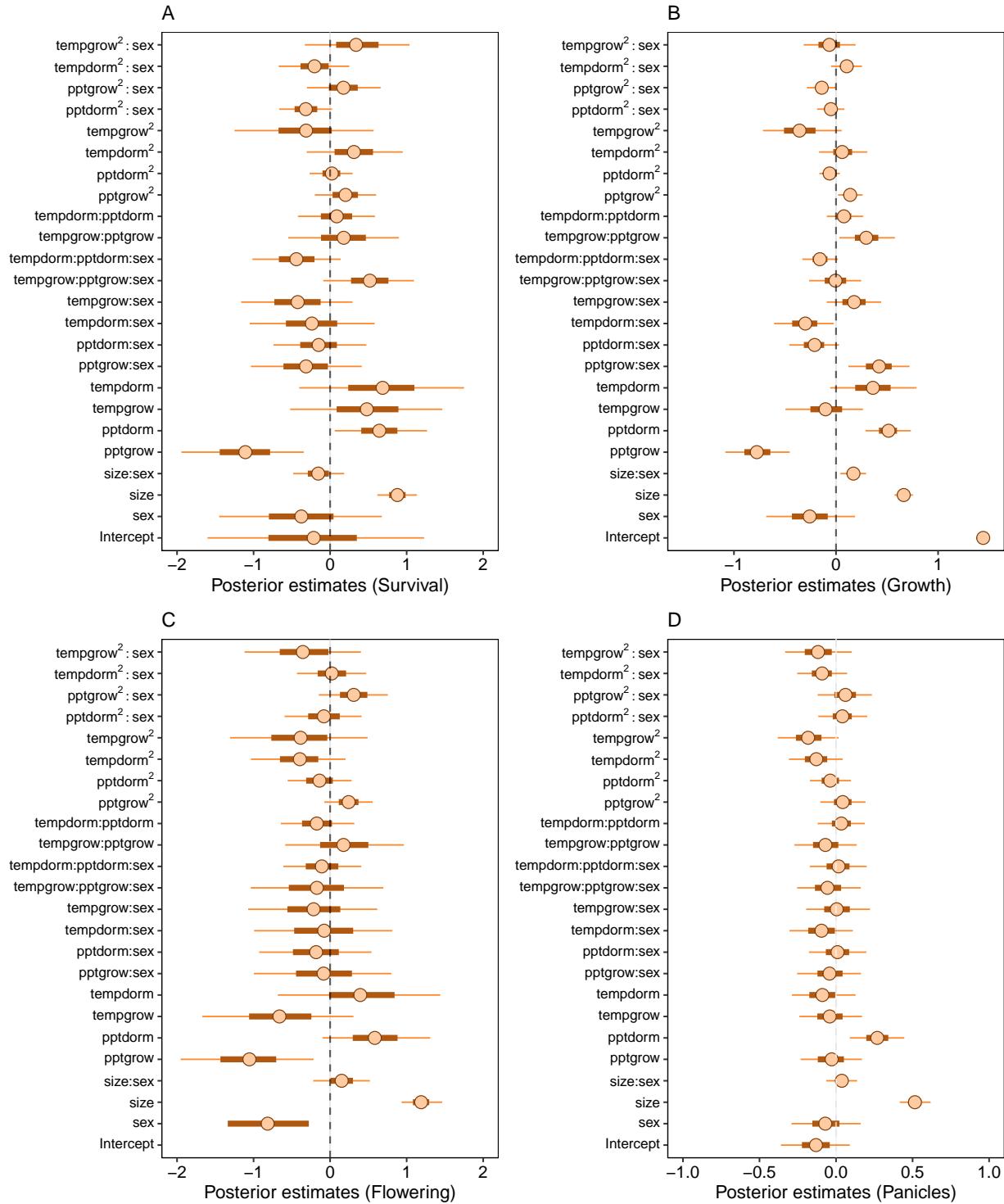


Figure S-10: Mean parameter values and 95% credible intervals of the posterior probability distributions. pptgrow is the precipitation of growing season, Tempgrow is the temperature of growing season, pptdorm is the temperature of dormant season, Tempdorm is the temperature of dormant season.

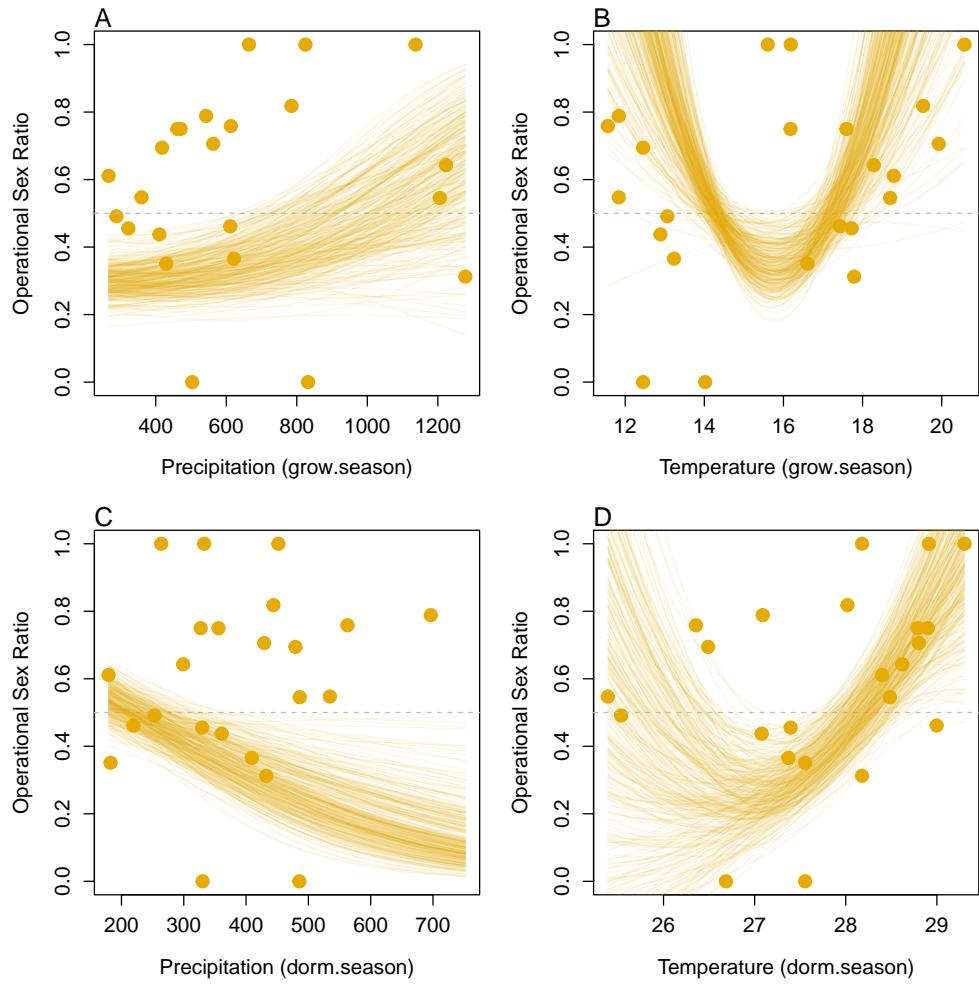


Figure S-11: Significant Operational Sex Ratio response accross climate gradient. (A, B) Proportion of panicles that were females across precipitation and temperature of the growing season; (C, D) Proportion of panicles that were females across precipitation and temperature of the dormant season.

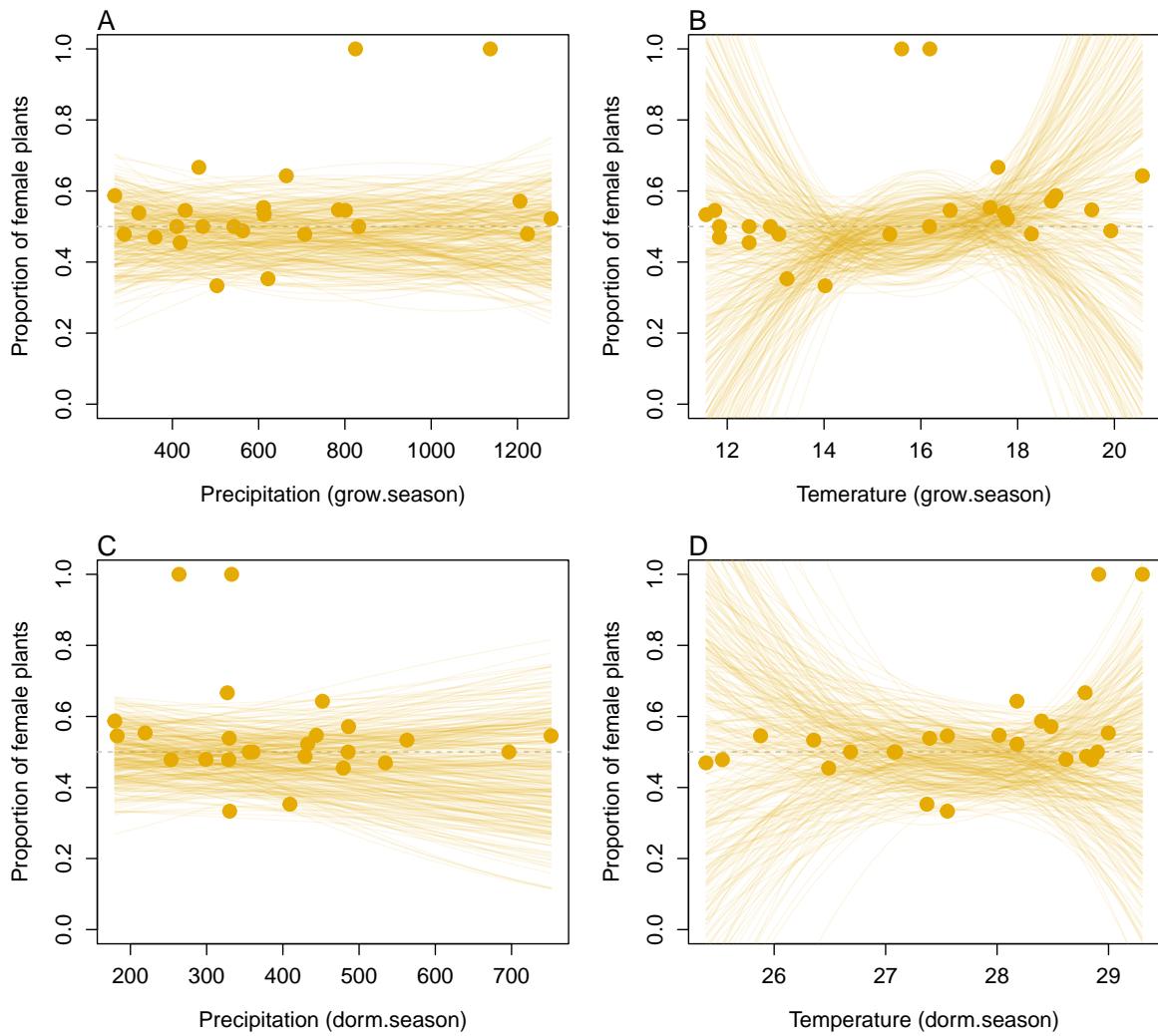


Figure S-12: Variation in sex-ratio accross climate gradient. (A, B) Proportion of plants that were females across precipitation and temperature of the growing season; (C, D) Proportion of plants that were females across precipitation and temperature of the dormant season.

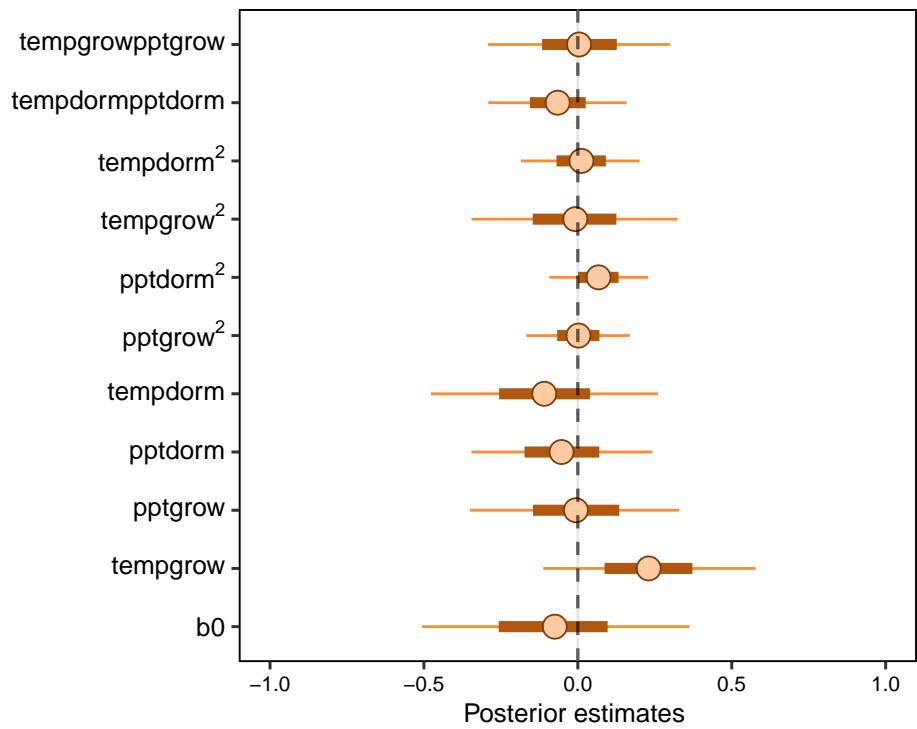


Figure S-13: Mean parameter values and 95% credible intervals of the posterior probability distributions. pptgrow is the precipitation of growing season, Tempgrow is the temperature of growing season, pptdorm is the temperature of dormant season, Tempdorm is the temperature of dormant season.

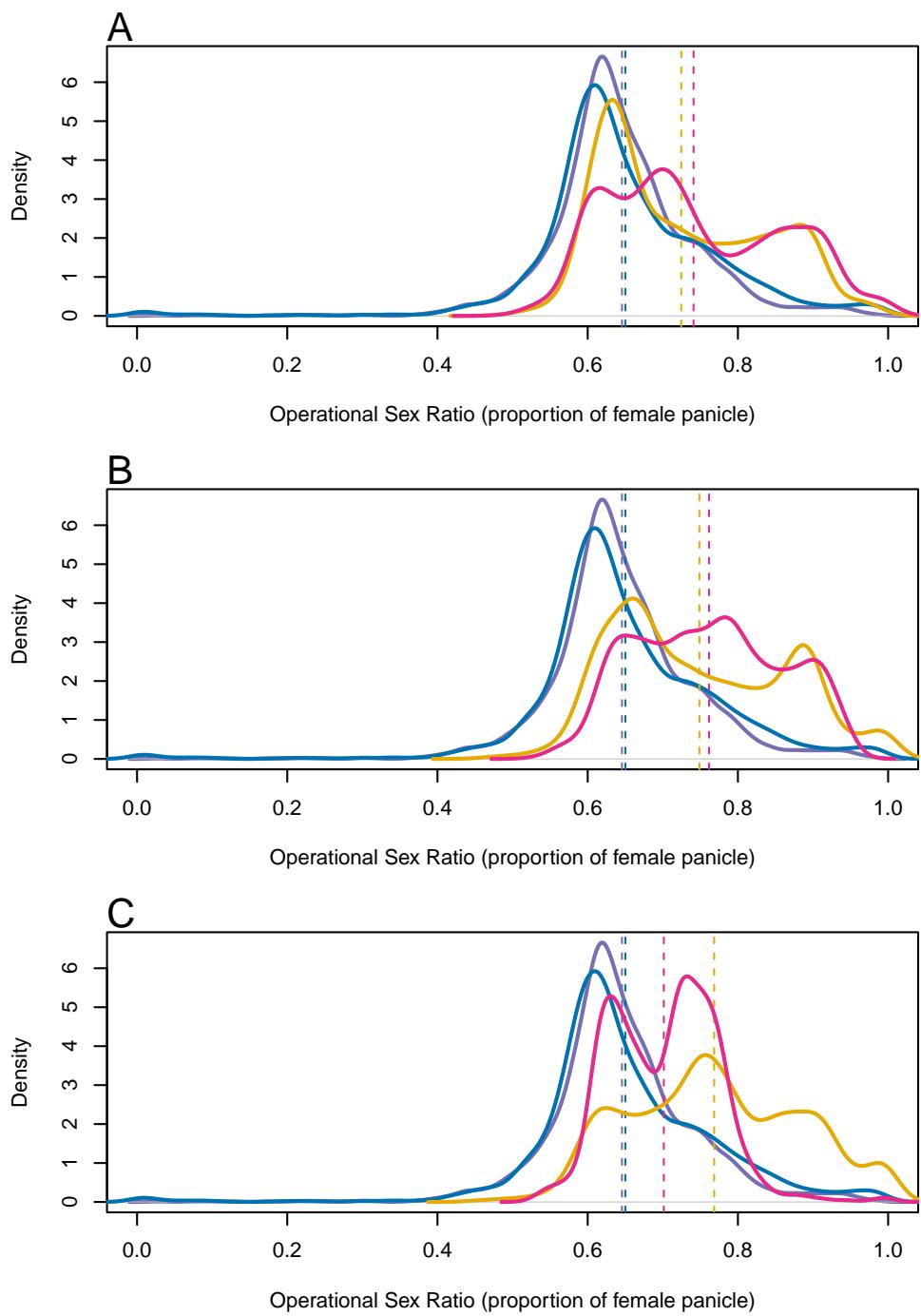


Figure S-14: Change in Operational Sex Ratio (proportion of female) over time (past, present, future). Future projections were based on A) MIROC 5, B) CES, C) ACC. The means for each model are shown as vertical dashed lines.

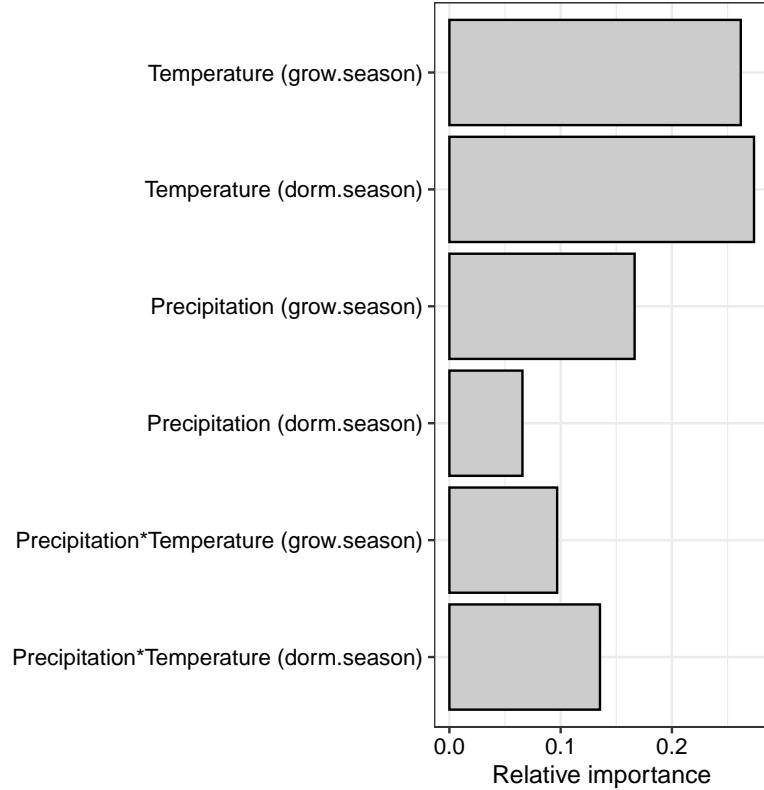


Figure S-15: Life Table Response Experiment: The bar represent the relative importance of each predictors.

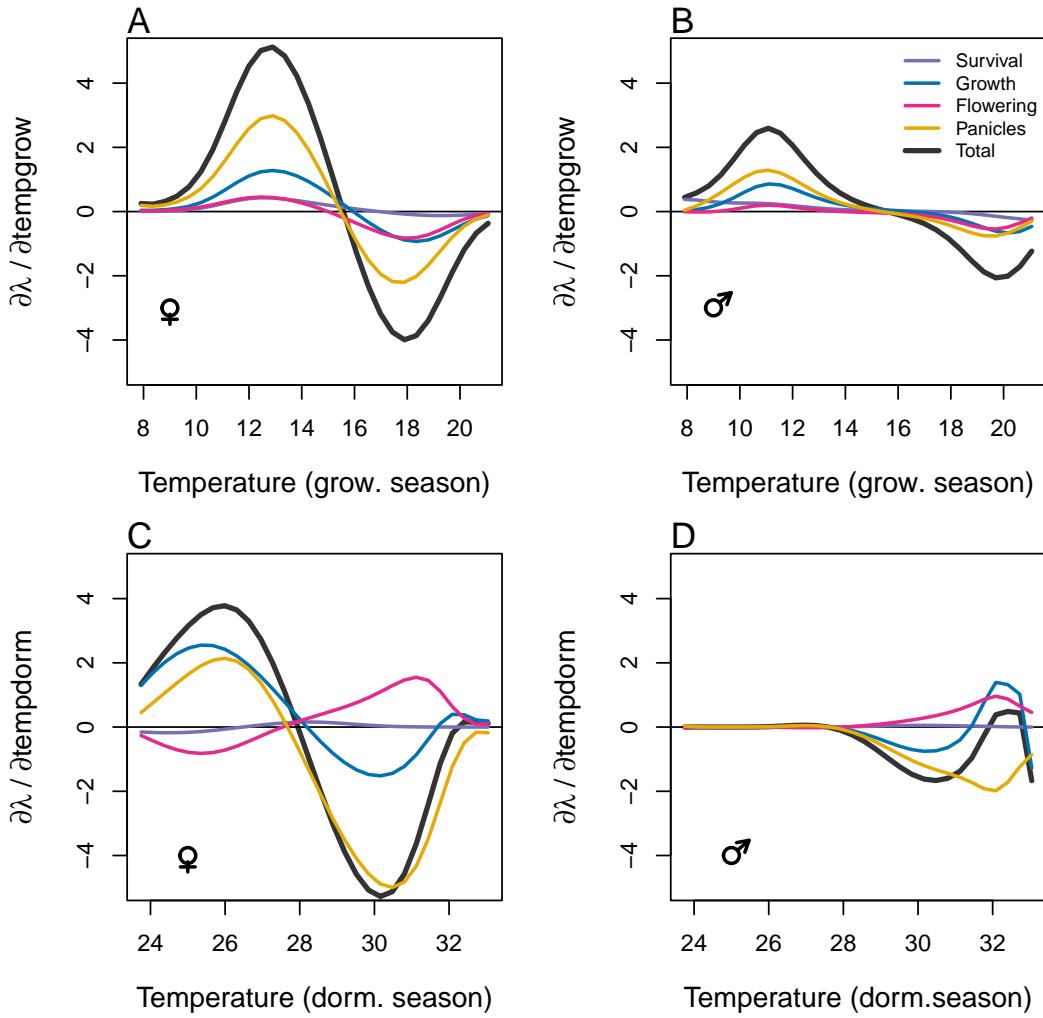


Figure S-16: Life table response experiment decomposition of the sensitivity of λ to seasonal climate into additive vital rate contributions of males and females based on posterior mean parameter estimates. (A) Temperature of growing season (contribution of female), (B) Temperature of growing season (contribution of male), (C) Temperature of dormant season (contribution of female) and (D) Temperature of dormant season (contribution of male).

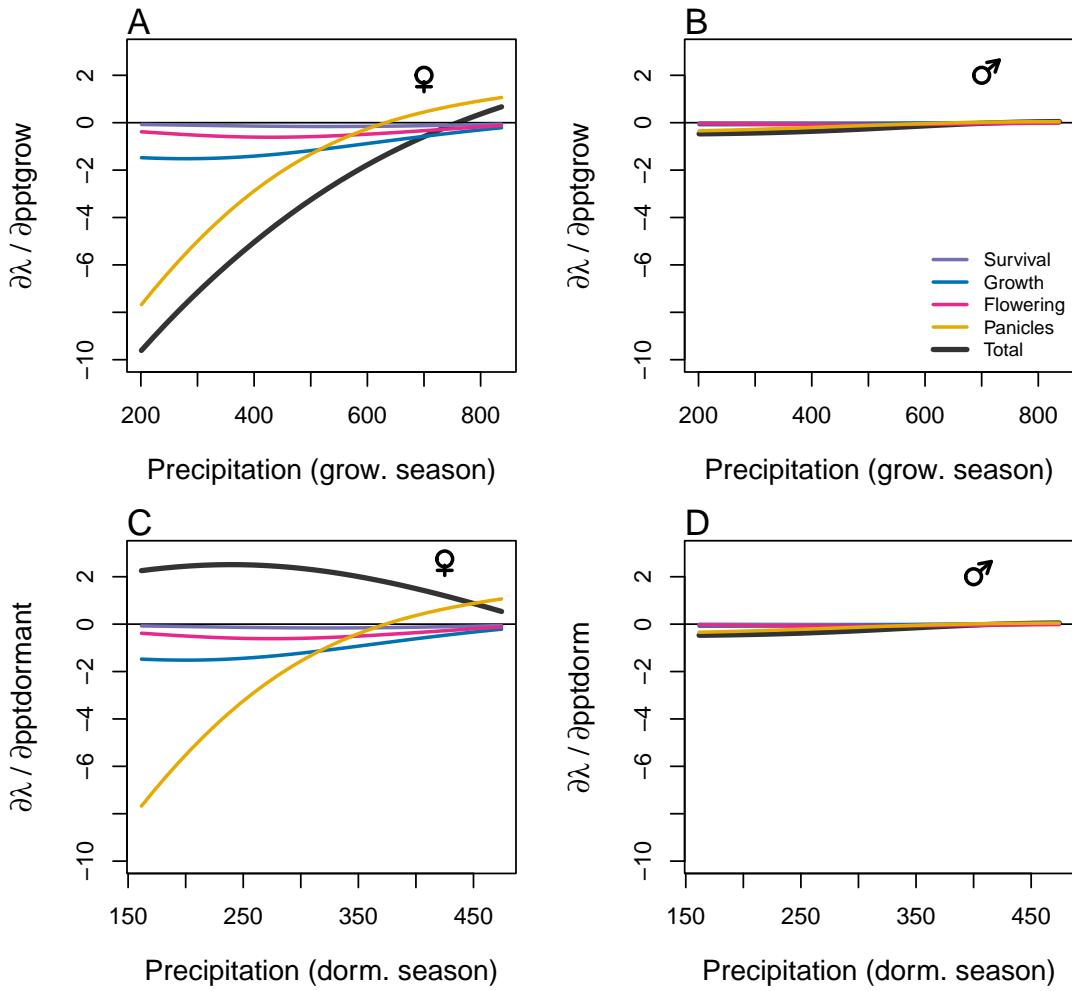


Figure S-17: Life table response experiment decomposition of the sensitivity of λ to seasonal climate into additive vital rate contributions of males and females based on posterior mean parameter estimates. (A) Precipitation of growing season (contribution of female), (B) Precipitation of growing season (contribution of male), (C) Precipitation of dormant season (contribution of female) and (D) Precipitation of dormant season (contribution of male).

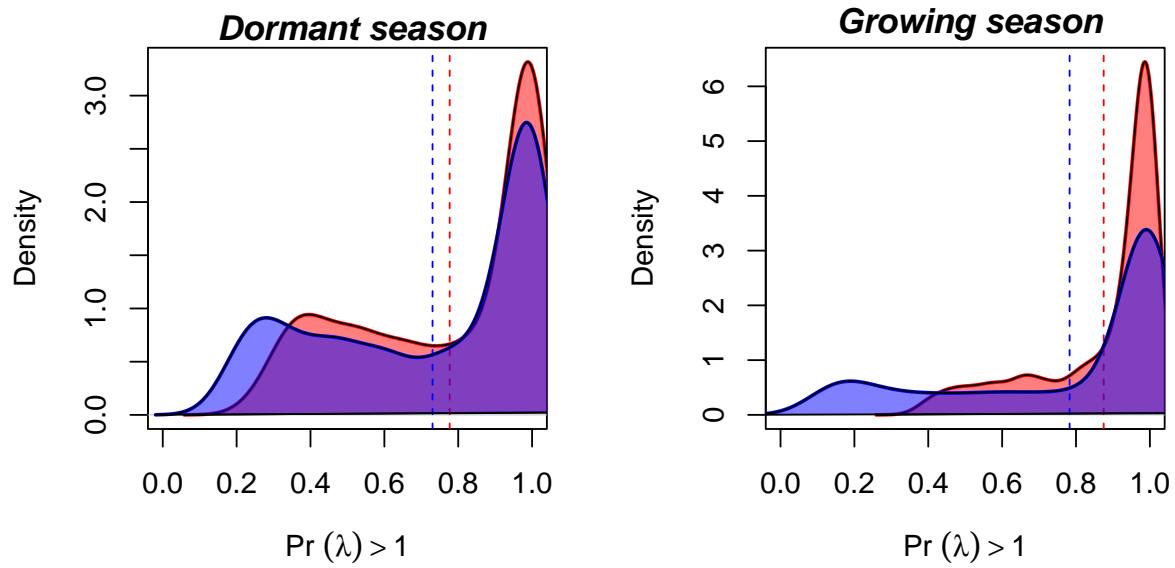


Figure S-18: Assessment of the statistical difference between the two-sex models and the female dominant model for the dormant and growing season. Plots show the density of $\Pr(\lambda) > 1$ values for female dominant (pink) and two-sex models (violet) for each season. The means for each model are shown as vertical dashed lines.

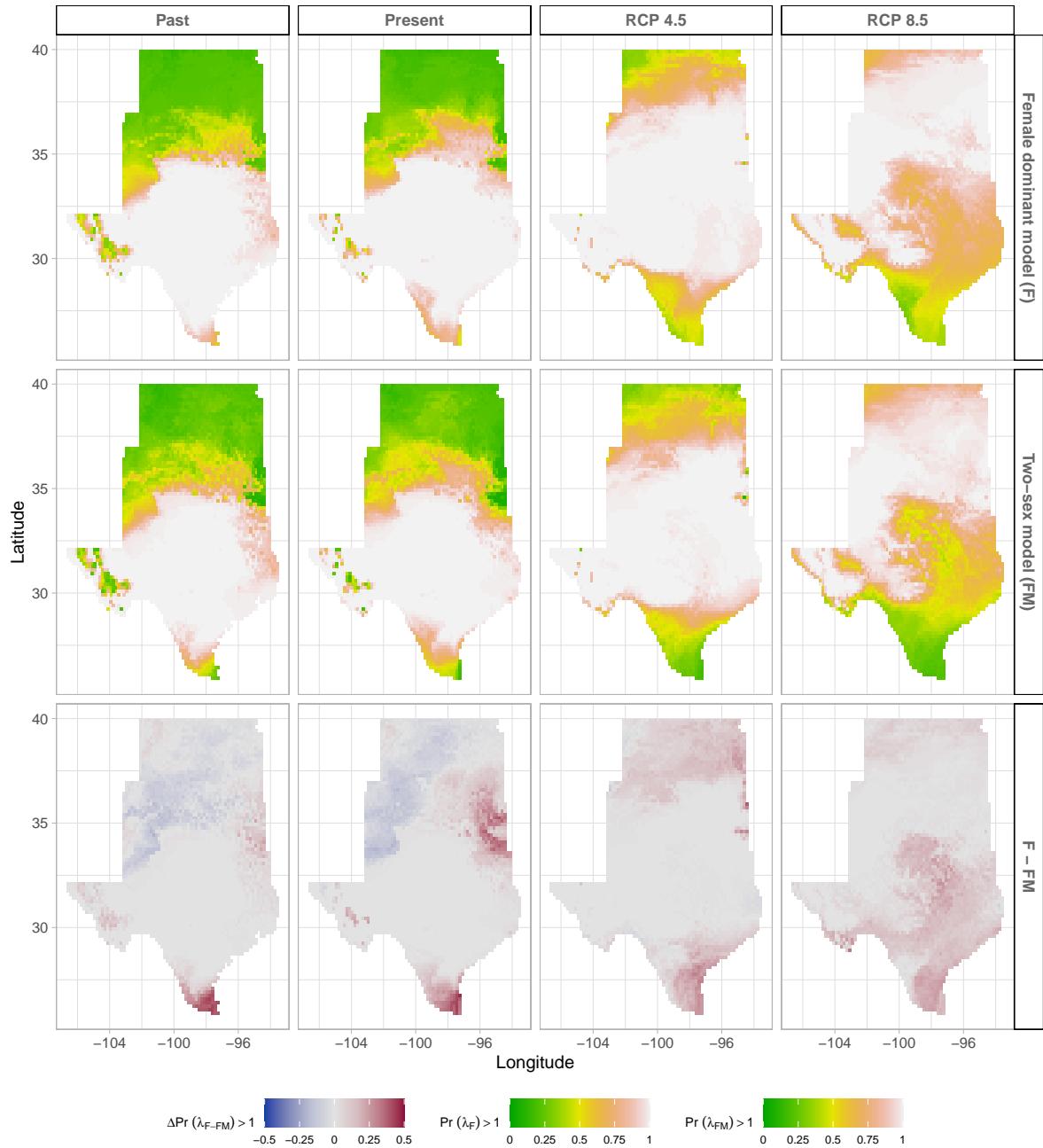


Figure S-19: Climate change favors range shift toward the North edge of the current range. (A) Past, (B) Current, (C and D) Future predicted range shift based on the predicted probabilities of self- sustaining populations, $\Pr(\lambda > 1)$, using the two-sex model that incorporates sex- specific demographic responses to climate with sex ratio dependent seed fertilization. (E) Past, (F) Current, (G and H) Future predicted range shift based on the predicted probabilities of self- sustaining populations, $\Pr(\lambda > 1)$, using the female dominant model. Future projections were based on the CESM1-BGC model. The black dots on panel B and F indicate all known presence points collected from GBIF from 1990 to 2019, which corresponds to the current condition in our prediction. The occurrences of GBIFs are distributed in with higher population fitness habitat $\Pr(\lambda > 1)$, confirming that our study approach can reasonably predict range shifts.

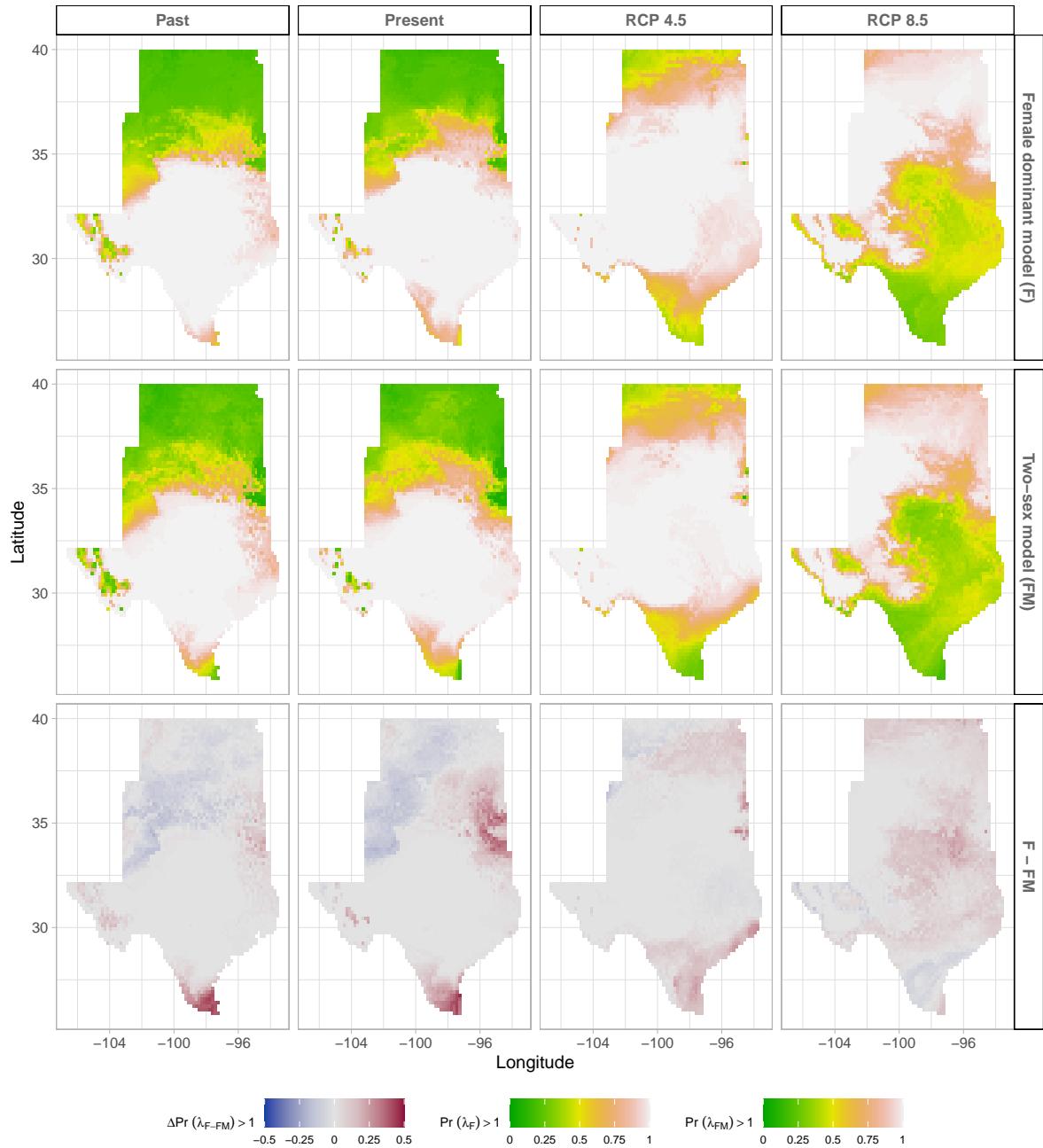


Figure S-20: Climate change favors range shift toward the North edge of the current range. (A) Past, (B) Current, (C and D) Future predicted range shift based on the predicted probabilities of self- sustaining populations, $\Pr(\lambda > 1)$, using the two-sex model that incorporates sex- specific demographic responses to climate with sex ratio dependent seed fertilization. (E) Past, (F) Current, (G and H) Future predicted range shift based on the predicted probabilities of self- sustaining populations, $\Pr(\lambda > 1)$, using the female dominant model. Future projections were based on the ACCESS model. The black dots on panel B and F indicate all known presence points collected from GBIF from 1990 to 2019, which corresponds to the current condition in our prediction. The occurrences of GBIFs are distributed in with higher population fitness habitat $\Pr(\lambda > 1)$, confirming that our study approach can reasonably predict range shifts.

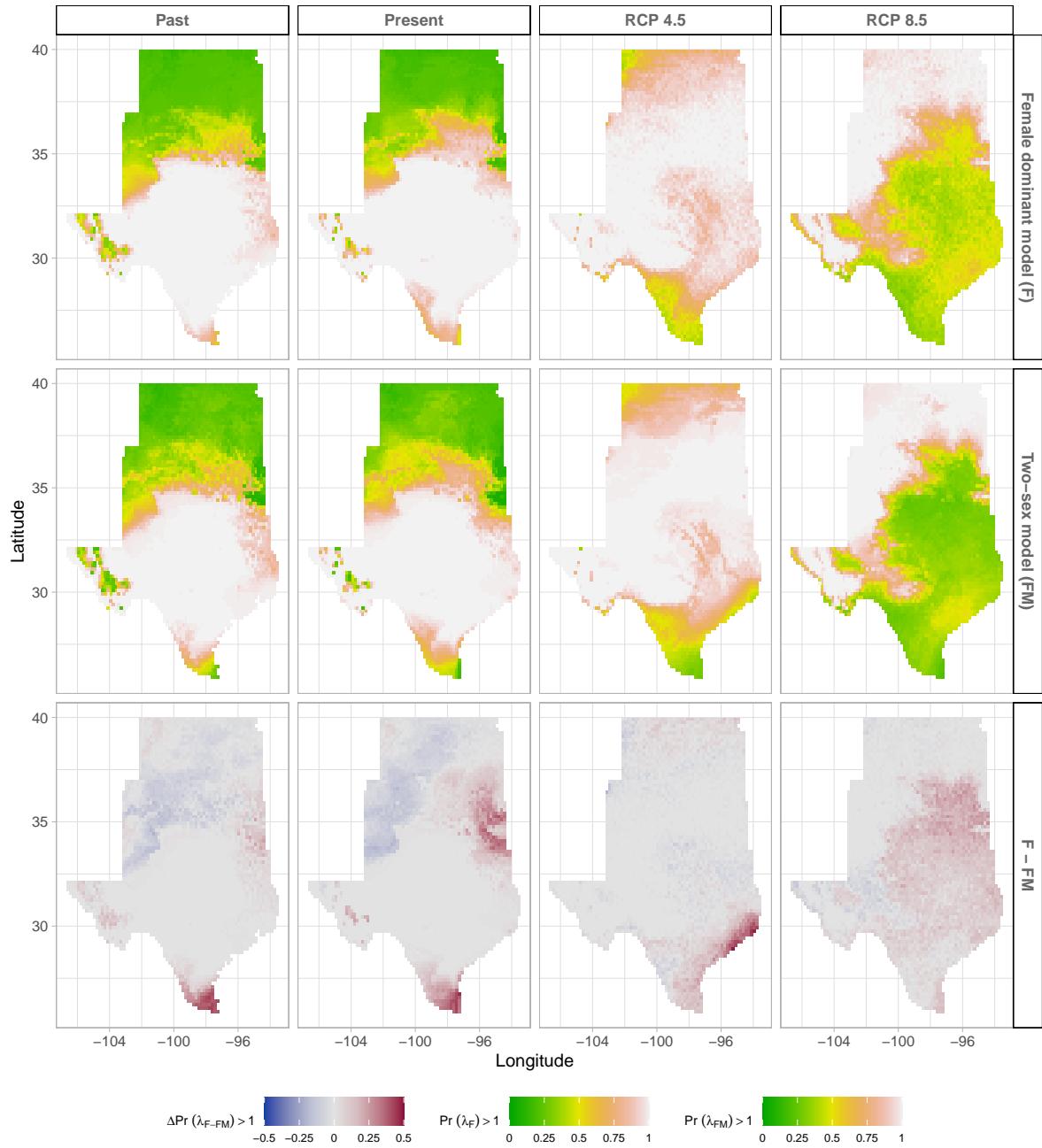


Figure S-21: Climate change favors range shift toward the North edge of the current range. (A) Past, (B) Current, (C and D) Future predicted range shift based on the predicted probabilities of self- sustaining populations, $\text{Pr}(\lambda > 1)$, using the two-sex model that incorporates sex- specific demographic responses to climate with sex ratio dependent seed fertilization. (E) Past, (F) Current, (G and H) Future predicted range shift based on the predicted probabilities of self- sustaining populations, $\text{Pr}(\lambda > 1)$, using the female dominant model. Future projections were based on the MIROC5 model. The black dots on panel B and F indicate all known presence points collected from GBIF from 1990 to 2019, which corresponds to the current condition in our prediction. The occurrences of GBIFs are distributed in with higher population fitness habitat $\text{Pr}(\lambda > 1)$, confirming that our study approach can reasonably predict range shifts.

586 **S.2 Supporting Methods**

587 **Sex ratio experiment**

To estimate the probability of seed viability, the germination rate and the effect of sex-ratio variation on female reproductive success, we conducted a sex-ratio experiment at one site near the center of the range to estimate the effect of sex-ratio variation on female reproductive success. The details of the experiment are provided in Compagnoni et al. (2017) and Miller and Compagnoni (2022b). Here we provide a summary of the experiment. We established 124 experimental populations in plots measuring 0.4 × 0.4m and separated by at least 15m from each other. We varied population density (1-48 plants/plot) and sex ratio (0%-100% female) across the experimental populations, and we replicated 34 combinations of density and sex ratio. We collected panicles from a subset of females in each plot and recorded the number of seeds in each panicle. We assessed reproductive success (seeds fertilized) using greenhouse-based germination and trazolium-based seed viability assays. Seed viability was modeled with a binomial distribution where the probability of viability (v) was given by:

$$v = v_0 * (1 - OSR^\alpha) \quad (\text{S.1})$$

588 where OSR is the proportion of panicles that were female in the experimental populations.
589 α is the parameter that control for how viability declines with increasing female bias. Further,
590 germination rate was modeled using a binomial distribution to model the germination
591 data from greenhouse trials. Given that germination was conditional on seed viability, the
592 probability of success was given by the product $v * g$, where v is a function of OSR (Eq. S.1)
593 and g is assumed to be constant.