

Forecasting range shifts of a dioecious plant species under climate change

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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>.

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Abstract:

Main Text:

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Figures:

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¹ Abstract

² Global warming has triggered an urgent need for predicting the reorganization of Earth's
³ biodiversity under climate change. Currently, the vast majority of theory and models
⁴ in population biology, including those used to forecast biodiversity responses to climate
⁵ change, ignore the complication of sex structure. For dioecious species, it is unclear how
⁶ commonly unique climate sensitivities of females and males could influence projections
⁷ for species-level responses to climate change. We developed demographic models of range
⁸ limitation, parameterized from geographically distributed common garden experiments
⁹ with females and males of a dioecious grass species (*Poa arachnifera*) throughout and beyond
¹⁰ its range in the south-central U.S. Female-dominant and two-sex model versions of the
¹¹ demographic model both predict that future climate change will alter population viability
¹² and will induce latitudinal niche extension beyond current northern limits. However, the
¹³ magnitude of niche shift was overestimated by the female-dominant model, because females
¹⁴ have broader temperature tolerance than males and become mate-limited under female-biased
¹⁵ sex ratios¹. Explicitly account for both sexes could enhance population viability forecasts
¹⁶ and conservation planning for dioecious species in response to climate change.

¹Not sure yet if this is true but we need some sort of biological rationale to accompany this result.

¹⁷ Introduction

¹⁸ Rising temperatures and extreme drought events associated with global climate change are
¹⁹ leading to increased concern about how species will become redistributed across the globe
²⁰ under future climate conditions (Bertrand et al., 2011; Gamelon et al., 2017; Smith et al., 2024).
²¹ Dioecious species (most animals and ca. 7% of plant species) might be particularly vulnerable
²² to the influence of climate change because they often display skewed sex ratios that are
²³ generated or reinforced by sexual niche differentiation (distinct responses of females and males
²⁴ to shared climate drivers) (Tognetti, 2012). Accounting for such a niche differentiation within
²⁵ a population is a long-standing challenge in accurately predicting which sex will successfully
²⁶ track environmental change and how this will impact population viability and range shifts
²⁷ (Gissi et al., 2023; Jones et al., 1999). The vast majority of theory and models in population
²⁸ biology, including those used to forecast biodiversity responses to climate change, **ignore the**
²⁹ **complication of sex structure**² (Ellis et al., 2017; Gissi et al., 2024; Pottier et al., 2021). Traditional
³⁰ approaches in population biology instead focus exclusively on females, assuming that males
³¹ are in sufficient supply as to never limit female fertility (Miller and Inouye, 2011). As a
³² result, forecasts of colonization-extinction dynamics for dioecious species under future climate
³³ change that explicitly account for females, males, and their inter-dependence are limited.

³⁴ Species's range limits, when not driven by dispersal limitation, should generally reflect
³⁵ the limits of the ecological niche (Lee-Yaw et al., 2016). Niches and geographic ranges are
³⁶ often limited by climatic factors including temperature and precipitation (Sexton et al., 2009).
³⁷ Therefore, any substantial changes in the magnitude of these climatic factors in a given location
³⁸ across the range could impact population viability, with implications for range expansions
³⁹ or contractions based on which regions become more or less suitable (Davis and Shaw,
⁴⁰ 2001; Pease et al., 1989). Forecasting range shifts for dioecious species is complicated by the
⁴¹ potential for each sex to respond differently to climate variation (Hultine et al., 2016; Morrison
⁴² et al., 2016; Pottier et al., 2021). Populations in which males are rare under current climatic
⁴³ conditions could experience low reproductive success due to sperm or pollen limitation that
⁴⁴ may lead to population decline in response to climate change that disproportionately favors
⁴⁵ females (Eberhart-Phillips et al., 2017). In contrast, climate change could expand male habitat
⁴⁶ suitability (e.g. upslope movement), which might increases seed set for pollen-limited females
⁴⁷ and favor range expansion (Petry et al., 2016). Although the response of species to climate
⁴⁸ warming is an urgent and active area of research, few studies have disentangled the interaction

²*It is unclear how you are citing these studies. Are they examples of ignoring sex structure? Or examples of accounting for sex structure?*

49 between sex and climate drivers to understand their combined effects on population dynamics
50 and range shifts, despite calls for such an approach (hultine2016climate,gissi2023exploring).

51 Tracking the impact of climate change on the population dynamics and range limits
52 of dioecious taxa depends on our ability to build mechanistic models that take into account
53 the spatial and temporal context in which sex specific response to climate change affects
54 population viability (Czachura and Miller, 2020; Davis and Shaw, 2001; Evans et al., 2016).
55 Structured population models built from demographic data collected from geographically
56 distributed observations or common garden experiments provide several advantages for
57 studying the impact of climate change on species' range shifts (Merow et al., 2017; Schultz
58 et al., 2022; Schwinnning et al., 2022). First, demographic models link individual-level life
59 history events (mortality, development, and regeneration) to population demography, allowing
60 the investigation of factors explaining vital rate responses to environmental drivers (Dahlgren
61 et al., 2016; Ehrlén and Morris, 2015; Louthan et al., 2022). Second, demographic models
62 have a natural interface with experimental treatments that can isolate spatial and temporal
63 correlations between environmental factors, thus overcoming a main disadvantage with many
64 types of correlative studies (Leicht-Young et al., 2007). Third, structured demographic models
65 can be used to identify which aspect of climate is more important for population dynamics.
66 For example, Life Table Response Experiments (LTRE) built from structured models have
67 become widely used to understand the relative importance of covariates in explaining
68 variation in population growth rate (Ellner et al., 2016; Hernández et al., 2023). LTRE is
69 also used to get a mechanistic understanding of how a given treatment (eg. temperature or
70 precipitation) could affect population dynamics through unique vital rate responses (Caswell,
71 1989; Iler et al., 2019; Morrison and Hik, 2007; O'Connell et al., 2024).³

72 In this study, we used a mechanistic approach, combining geographically-distributed
73 field experiments, Bayesian statistical modeling, and two-sex population projection modeling,
74 to understand the demographic response of dioecious species to climate change and its
75 implications for past, present, and future range dynamics. Our work focused on the dioecious
76 grass species Texas bluegrass (*Poa arachnifera*), which is distributed along environmental
77 gradients in the south-central U.S. corresponding to variation in temperature across latitude
78 and precipitation across longitude.⁴ Our previous study showed that, despite a differentiation
79 of climatic niche between sexes, the female niche mattered the most in driving the
80 environmental limits of population viability across longitude (Miller and Compagnoni, 2022b).
81 However, that study used a single proxy variable (longitude) to represent environmental

³It is noticeable that you never mention SDMs as a point of contrast with demographic models. Are you intentionally avoiding that?

⁴I think it would be good to add some context about climate change in this study region – what has already occurred and what is projected.

82 variation related to aridity. Developing a rigorous forecast for the implications of future
83 climate change requires that we transition from climate-implicit to climate-explicit treatment
84 of environmental drivers as we do here. Here, we asked four questions:

- 85 1. What are the sex-specific vital rate responses to variation in temperature and precipitation
86 across the species' range ?
- 87 2. How do sex-specific vital rates combine to determine the influence of climate variation
88 on population growth rate (λ) ?
- 89 3. What are the historical and projected dynamics of the Texas bluegrass geographic niche
90 and how does accounting for sex structure modify these predictions?
- 91 4. Which vital rates and climate covariates most strongly determine past and future changes
92 in the geographic niche?

93 Materials and methods

94 Study species

95 Texas bluegrass (*Poa arachnifera*) is a dioecious perennial, summer-dormant cool-season (C3)
96 grass that occurs in the south-central U.S. (Texas, Oklahoma, and southern Kansas) (Hitchcock,
97 1971)⁵. Latitudinal limits of the Texas bluegrass distribution span # to # in mean annual
98 temperature, and longitudinal limits span # to # in annual precipitation. Texas bluegrass
99 grows between October and May (growing season), with onset of dormancy often from June
100 to September (dormant season) (Kindiger, 2004).

101 Biological sex in Texas bluegrass is genetically based and the birth (seed) sex ratio
102 is 1:1 (CITE). Females and males are morphologically indistinguishable except for their
103 inflorescences. Flowering occurs in May and the species is wind pollinated (Hitchcock,
104 1971). Surveys of # natural populations throughout the species' distribution indicated that
105 operational sex ratio (the female fraction of flowering plants) ranged from # to # with a mean
106 of # (Miller and Compagnoni, 2022b).

⁵I would reference the map figure (current Fig. 1) here. I also suggest either adding the GBIF records to this figure or adding the county occurrences as in the Am Nat paper, because it is important for readers to see the natural distribution early in the paper. The natural population surveys can be cut from this figure because you don't say anything about them and you do not use the data here. Alternatively, there may be value in re-analyzing the sex ratio surveys with your climate covariates. Fig 1 also needs to be updated with labels and units on the climate variable color bars. I recommend putting panels A-C and B-D on the same climate scale.

107 **Common garden experiment**

108 We set up a common garden experiment throughout and beyond the range of Texas bluegrass
109 to quantify sex-specific demographic responses to climate. **The novelty of this study lies**
110 **in the fact that we use a precise climate variable to build a mechanistic model to forecast**
111 **the response of species to climate change.**⁶ Details of the experimental design are provided
112 in Miller and Compagnoni (2022b); we provide a brief overview here. The experiment was
113 installed at 14 sites throughout and, in some cases, beyond the species' natural range (Fig.1).
114 At each site, we established 14 blocks. For each block we planted three female and three male
115 individuals that were clonally propagated from females and males from eight natural source
116 populations (Fig.1); because sex is genetically-based, clones never deviated from their expected
117 sex. The experiment was established in November 2013 and was censused in May of 2014,
118 2015, and 2016. At each census, we collected individual demographic data including survival
119 (alive or dead), size (number of tillers), and number of panicles (reproductive inflorescences).
120 For the analyses that follow, we focus on the 2014-15 and 2015-16 transitions years, since the
121 start of the experiment did not include the full 2013-14 transition year.

⁶*This is not relevant to the description of the experiment.*

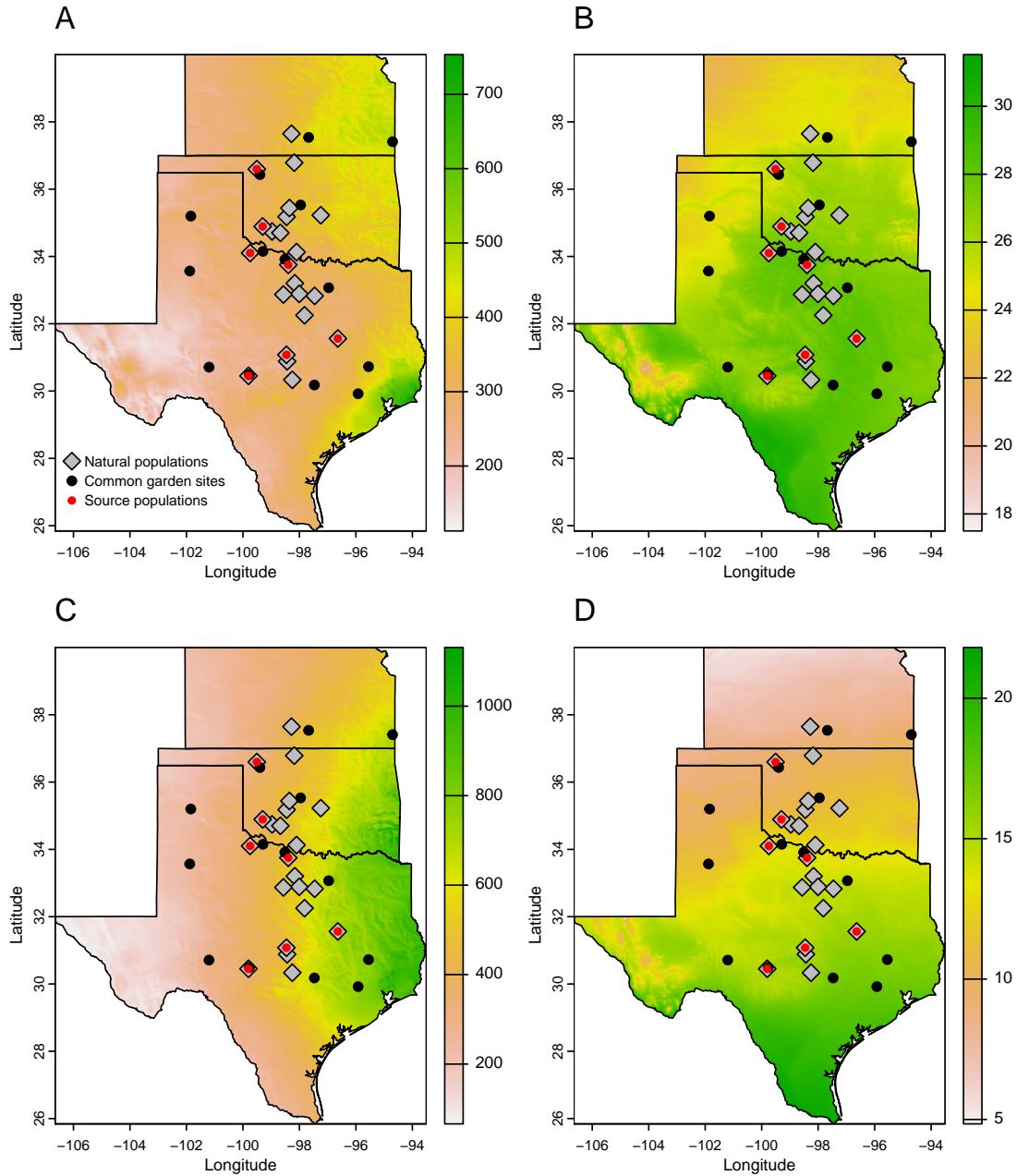


Figure 1: Maps of 30-year (1990-2019) normal climate and study sites used for demographic monitoring of *Poa arachnifera* in Texas, Kansas and Oklahoma in the United States. (A) Precipitation of the dormant season in mm , (B) temperature of the dormant season in °C , (C) precipitation of the growing season in mm , (D) temperature of the growing season 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). Average temperatures along the distribution of the species tend to decrease northward as a result of the influence of latitude: lower latitudes receive more heat from the sun over the course of a year. Similarly, the average precipitation decreases eastward as a result of the influence of longitude: lower longitudes receive less precipitation over the year. See also Fig.S-1, Fig.S-2.

122 **Climatic data collection**

123 We gathered downscaled monthly temperature⁷ and precipitation⁸ for each site from Chelsa
124 to describe observed climate conditions during our study period (Karger et al., 2017). These
125 climate data were used as covariates in vital rate regressions. We aligned the climatic years to
126 match demographic transition years (May 1 – April 30)⁹ rather than calendar years. Based on
127 the natural history of this summer-dormant cool-season species, we divided each transition
128 year into dormant (June 1 through September 30) and growing (October 1 through May 31)
129 seasons. The 2014-15 transition year was substantially wetter and cooler across the study
130 region than 2015-16, especially during the growing season (figure¹⁰), so our study design
131 provides both spatial and inter-annual coverage of climate variables.

132 To back-cast and forecast demographic responses to changes in climate throughout the
133 study region, we downloaded projection data for three 30-year periods: “past” (1901-1930),
134 “current” (1990-2019) and “future” (2070-2100). Data for these climatic periods¹¹ were
135 downloaded from four general circulation models (GCMs) selected from the Coupled Model
136 Intercomparison Project Phase 5 (CMIP5). The GCMs are: Model for Interdisciplinary
137 Research on Climate (MIROC5), Australian Community Climate and Earth System Simulator
138 (ACCESS1-3), Community Earth System Model (CESM1-BGC), Centro Euro-Mediterraneo sui
139 Cambiamenti Climatici Climate Model (CMCC-CM). All the GCMs were downloaded from
140 chelsa (Sanderson et al., 2015). We evaluated future climate projections from two scenarios of
141 representative concentration pathways (RCPs): RCP4.5, an intermediate-to-pessimistic scenario
142 assuming a radiative forcing amounting to 4.5 W m^{-2} by 2100, and RCP8.5, a pessimistic
143 emission scenario which projects a radiative forcing of 8.5 W m^{-2} by 2100 (Schwalm et al.,
144 2020; Thomson et al., 2011).

145 **Sex ratio experiment**

146 ¹² We conducted a sex-ratio experiment at one site near the center of the range to estimate
147 the effect of sex-ratio variation on female reproductive success. Details of the experiment
148 are provided in Compagnoni et al. (2017) and Miller and Compagnoni (2022b). In short, we

⁷Give units

⁸Give units

⁹I think this is not right. I think we updated the transition year to be June 1 – May 31.

¹⁰I would like to use the figure I made called site-year-weather. However, I cannot tell from this figure whether the first year was unusually wet or the second year was unusually dry – this will take looking at the climate data more broadly. I am also not sure if this figure was made before or after we changed the dates of the transition year, so it may need to be updated

¹¹The four GCMs only refers to the future data, right?

¹²You say nothing about this experiment in the Results or Discussion, so in its current state this section serves no purpose in this paper.

149 established 124 experimental populations in plots measuring 0.4 x 0.4m and separated by at
150 least 15m from each other. We chose 15m because our pilot data showed that more than 90%
151 of wind pollination occurred within 13m. We varied population density (1-48 plants/plot)
152 and sex ratio (0%-100% female) across the experimental populations, and we replicated 34
153 combinations of density and sex ratio. We collected panicles from a subset of females in each
154 plot and recorded the number of seeds in each panicle. We assessed reproductive success (seeds
155 fertilized) using greenhouse-based germination and trazolium-based seed viability assays.

¹³We used data from the sex-ratio experiment to estimate the probability of seed viability
and the germination rate. Seed viability was modeled with a binomial distribution where
the probability of viability (v) was given by:

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

156 where OSR is the **operational sex ratio**¹⁴ (proportion of panicles that were female) in the
157 experimental populations. The properties of the above function is supported by our previous
158 work (Compagnoni et al., 2017). Here, seed viability is maximized at v_0 as OSR approaches
159 zero (strongly male-biased) and goes to zero as OSR approaches 1 (strongly female-biased).
160 Parameter α controls how viability declines with increasing female bias.¹⁵

161 We used a binomial distribution to model the germination data from greenhouse trials.
162 Given that germination was conditional on seed viability, the probability of success was given
163 by the product $v * g$, where v is a function of OSR (Eq. 1) and g is assumed to be constant.¹⁶

164 Sex specific demographic responses to climate

165 ¹⁷ We used individual level measurements of survival, growth (number of tillers), flowering,
166 number of panicles to independently develop Bayesian mixed effect models describing how

¹³I think the data analysis methods could be better organized. Here you describe the experimental methods and data analysis in the same section, but for the common garden experiment you split them.

¹⁴I tried to add a little about this, but generally I think the concept of the operational sex ratio is under-developed throughout the manuscript. It is the main way through which sex-specific climate responses can feed back to influence lambda, so it warrants greater attention.

¹⁵Throughout the methods I recognize a lot of the text as coming directly from the Am Nat paper. I strongly recommend that you diversify your language and never use published text verbatim. Many journals use plagiarism detection software and this will raise a red flag, even if we are plagiarizing ourselves.

¹⁶You provide no information about how this model was fit. This echoes my previous comment that the data analysis should be better organized.

¹⁷This section needs to be more carefully edited, which I have not done. There is redundancy between the two paragraphs and most importantly, there is not enough biological rationale for the model that you fit. You do not describe which interactions you include, which you do not include, and why. This is a very complex model – 24 fixed-effect coefficients! – and it will get skepticism from reviewers. You need to justify why this is the right model, especially since you do not have any model selection or variable selection.

167 each vital rate varies as a function of sex, size, and four climate covariates (precipitation and
 168 temperature of growing and dormant seasons). We fit vital rate models with second-degree
 169 polynomial functions for the influence of climate. We included a second-degree polynomial
 170 because we expected that climate variables would affect vital rates through a hump-shaped
 171 relationship.

We centered and standardized all climatic predictors to facilitate model convergence. Size (number of tillers) was on a natural logarithm scale. We included site, source, and block as random effects. All the vital rate models used the same **linear predictor**¹⁸ 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.

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

172 where β_0 is the grand mean intercept, β_1 is the size dependent slopes. *size* was on a natural log-
 173 arithm scale. $\beta_2 \dots \beta_{13}$ represent the climate dependent slopes. $\beta_{14} \dots \beta_{23}$ represent the sex-climate
 174 interaction slopes. *pptgrow* is the precipitation of the growing season (standardized to mean
 175 zero and unit variance), *tempgrow* is the temperature of the growing season (standardized to
 176 mean zero and unit variance), *pptdorm* is the precipitation of the dormant season (standardized
 177 to mean zero and unit variance), *tempdorm* is the temperature of the dormant season (standard-
 178 ized to mean zero and unit variance). The model also includes normally distributed random
 179 effects for block-to-block variation ($\phi \sim N(0, \sigma_{block})$) and source-to-source variation that is
 180 related to the provenence of the seeds used to establish the common garden ($\rho \sim N(0, \sigma_{source})$),
 181 site to site variation ($\nu \sim N(0, \sigma_{site})$). We fit survival, growth, flowering models with generic
 182 weakly informative priors for coefficients ($\mu = 0, \sigma = 1.5$) and variances ($\gamma[0.1, 0.1]$). We fit
 183 fertility model with regularizing priors for coefficients ($\mu = 0, \sigma = 0.15$). We ran three chains
 184 for 1000 samples for warmup and 4000 for interactions, with a thinning rate of 3. We accessed
 185 the quality of the models using trace plots and predictive check graphs (Piironen and Vehtari,
 186 2017) (Fig. S-4). To understand the effect of climate on vital rates, we got the 95 % credible

¹⁸It is still a “linear predictor” even if it has quadratic terms.

¹⁸⁷ interval of the posterior distribution. Then we assumed that there is 95 % probability that the
¹⁸⁸ true (unknown) estimates would lie within that interval, given the evidence provided by the
¹⁸⁹ observed data for each vital rate. All models were fit in Stan (Stan Development Team, 2023).

¹⁹⁰ **Two-sex and climate-dependent matrix projection model**

To understand the effect of climate on population growth rate incorporating both female and male climate responses, we used the climate-dependent vital rate regressions to build a matrix projection model (MPM) structured by size (number of tillers) and sex. 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 climate¹⁹, where $x \in \{1, 2, \dots, U\}$ and U is the maximum number of tillers a plant can reach (here 95th percentile²⁰ of observed maximum size). Let F_t^R and M_t^R be 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 :

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

¹⁹The variable z is not used consistently or correctly. Notice in eq:viabMPM and eq:dynamics you use z in the RHS but not the LHS. CLimate is not a state variable.

²⁰I remember you experimented with this. Is this the actual percentile you used or was this text from the Am Nat paper?

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

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

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

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

Since the two-sex MPM is nonlinear (vital rates affect and are affected by population structure) we estimated the asymptotic geometric growth rate (λ) by numerical simulation, and repeated this across a range of climate²¹. ²²

Life Table Response Experiments

To identify which aspect of climate is most important for population viability, we used a "random design" Life Table Response Experiment (LTRE). We used the RandomForest package to fit a regression model with seasonal climate²³ (here θ) as predictors and λ as response (Ellner et al., 2016; Liaw et al., 2002). The LTRE approximates the variation in λ in response to seasonal climate covariates and their interaction (Caswell, 2000; Hernández et al., 2023):

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

²¹Vague - needs more detail.

²²Too much of this section is familiar to me from the Am Nat paper. I suggest you write this in your own voice. You also should provide an explanation for the female-dominant model.

²³It is unclear what variation in climate you are sampling over.

206 where, θ_i , θ_j , θ_{ij} represent respectively the fitted regression slope for the covariates of the dor-
207 mant season, j the covariates of the growing season and ij the covariates of their interactions.²⁴

To identify the mechanism by which climate affects population growth rate for each sex, we decomposed the effect of each climate variable on population growth rate (λ) into contribution arising from the effect on each stage-specific vital rate²⁵ (Caswell, 2000). At this end we used another LTRE with a "regression design".²⁶ The LTRE with a "regression design" 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):

$$\frac{\partial \lambda}{\partial \text{climate}} \approx \sum_i \frac{\partial \lambda}{\partial \theta_i^F} \frac{\partial \theta_i^F}{\partial \text{climate}} + \frac{\partial \lambda}{\partial \theta_i^M} \frac{\partial \theta_i^M}{\partial \text{climate}} \quad (9)$$

208 where, θ_i^F and θ_i^M represent sex-specific parameters: the regression coefficients for the
209 intercepts and slopes of size-dependent vital rate functions. Because LTRE contributions are
210 additive, we summed across vital rates to compare the total contributions of female and male
211 parameters.²⁷

212 Impact of climate change on niche and range shifts

213 A species' ecological niche can be defined as the range of resources and conditions allowing
214 its populations to self-sustained ($\lambda > 1$) (Hutchinson et al., 1978; Maguire Jr, 1973). To
215 understand the impact of climate change on species niche shifts, we estimated the probability
216 of self-sustaining populations, which is $\Pr(\lambda > 1)$ conditional to two environmental axes:
217 (i) temperature and precipitation of the dormant season and (ii) temperature and precipitation
218 of the growing season.²⁸ $\Pr(\lambda > 1)$ was calculated using the proportion of the 300 Markov
219 chain Monte Carlo iterations that lead to a $\lambda > 1$ (Diez et al., 2014).²⁹

220 $\Pr(\lambda > 1)$ was also mapped onto geographic layers of three state (Texas, Oklahoma and
221 Kansas) to delineate past, current and future potential distribution of the species. To do so, we
222 estimated $\Pr(\lambda > 1)$ conditional to all climate covariates for each pixel ($\sim 340 \text{ km}^2$) across the

²⁴But you also have second-order terms, and I am not sure whether and how this LTRE accounts for that. Also, what is n here? Why does the summation over i start at -1? And why do you show only two variables, since you have four?

²⁵I don't know what you mean by "stage-specific"

²⁶I think you need greater clarification about what different information you get out of the two LTREs, and how they relate to the motivating biological questions. I understand this, of course, but I think readers will be confused.

²⁷I don't really understand how this LTRE works because your climate variables interact. So this should not decompose as cleanly as the equation implies.

²⁸As a general comment, I find it difficult to follow which analyses are explicitly spatial (i.e., mapping quantities as rasters) and which are not – I think the methods can be sharpened around this.

²⁹I suggest you bring this up much earlier, in the Intro probably. I think you under-sell the value of this approach, particularly related to accounting for uncertainty. You also need to describe which types of uncertainty are accounted for here, i.e., process error and estimation error.

223 species range.³⁰ Then we add the current occurrences record of the species (1990-2019) from
224 Global Biodiversity Information Facility (GBIF) to validate the accuracy of our prediction³¹

225 Because of the amount of the computation involved in the Markov chain Monte Carlo iterations,
226 use only 100 posterior samples to estimate $\Pr(\lambda > 1)$ across the Texas, Oklahoma and Kansas.

227 All the analyses were performed in R 4.3.1 (R Core Team, 2023) However the estimation
228 of the impact of climate change on niche and range shifts were processed in parallel using
229 open-source software on the Rice Super computer (NOTS) and the German Centre for
230 Integrative Biodiversity Research (iDiv) High-Performance Computing Cluster.³²

231 Results

232 Sex specific demographic response to climate change

233 Most vital rates were strongly climate dependent, but the magnitude of their response were sim-
234 ilar between sexes suggesting no sex-specific demographic response to climate³³. Survival and
235 flowering were strongly more dependent on climate than growth (number of tillers) and pani-
236 cle production (Fig.2; Fig. S-5).³⁴ In addition, we found opposite patterns in the direction of the
237 effect on seasonal climate on the probability of survival and flowering. Growing season precip-
238 itation has a negative effect on the probability of survival, number of tillers, and the probability
239 of flowering, whereas dormant season precipitation has a positive effect on these vital rates.³⁵

240 Unlike precipitation, temperature of the growing season has a positive effect of the probability
241 of survival, a negative effect of the probability of flowering, and the number of tillers, but no
242 significant effect on the number of panicles. Further, there was a female survival and flowering
243 advantage across both climatic seasons³⁶ (Figures. 3A-3D, 3I-3L). On the contrary, there was a

³⁰I think you did this separately for past, present, and future, and for multiple futures? Needs to be explained.

³¹If you actually intend this as model validation then it needs to be presented more thoroughly and analyzed more rigorously.

³²I am not sure you need this – it was still done in R.

³³A few comments here: 1-This undermines the entire premise of the paper! If that's the result, it is what it is, but it suggests that the current Introduction does not serve the Results very well. 2-Your figure masks a lot of variation and interactions, and I think these are worth looking into more deeply. 3-This result is inconsistent with what we found in the Am Nat paper, and that concerns me, and will concern reviewers. 4-The niche plot indicates differences between two-sex and female dominant, which could only happen if there were sex-specific responses in the vital rates.

³⁴I am not sure this is true. The scales are very different.

³⁵I think these trends are conditional on temperature - see other comments.

³⁶I am not sure what you mean by "climatic seasons". More precise language will help.

244 male panicle advantage across all climatic variables (Figure3M-3P).³⁷ Counter-intuitively, there
245 was no significant sex growth advantage in all season climatic variables (Figures. 3E-3H).^{38 39}

³⁷*The points and lines look very similar*

³⁸*I cannot follow what this sentence is saying or why it is counter-intuitive.*

³⁹*I found this paragraph difficult to read, and obviously there are a lot of results to explain. I suggest you put some thought into how to organize these results in a way that communicates what you think are the most important points and makes it easier to digest. I think you also need to be careful about providing statistical support for your assertions.*

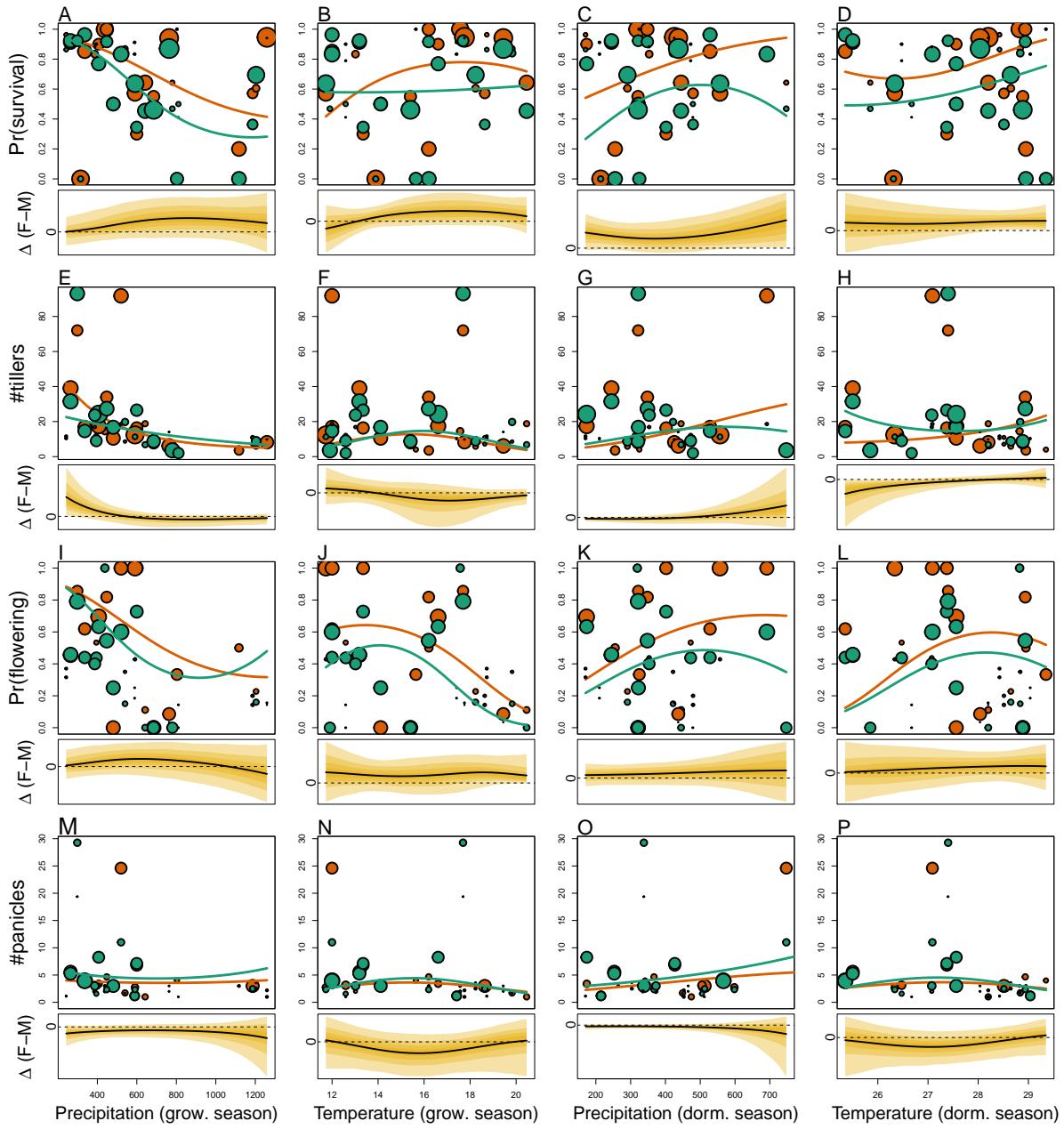


Figure 2: Sex specific demographic response to climate across species range. (A, B) Probability of survival during the growing season; (C, D) Probability of survival during the dormant season (E, F) Change in number of tillers during the growing season; (F, G) Change in number of tillers during the dormant season (I, J), Probability of flowering during the growing season; (K, L) Probability of flowering during the dormant season (M, N), Change in number of panicles produced given flowering during the growing season; (O, P) Change in number of panicles produced given flowering during the 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. Statistical results are shown in Fig. S-5.

246 **Climate change alters population viability**

247 We estimated population growth rate response to seasonal climate gradients using two
248 models: a female dominant model and a two-sex model⁴⁰. Consistent with the effect of
249 climate on the individual vital rate, we found a strong effect of seasonal climate on population
250 fitness (Fig.3).⁴¹ For both models, population growth rate decreased toward high precipitation
251 of growing season (Fig.3 A, C). In contrast population growth rate increased with an increase
252 in precipitation of the dormant season. Furthermore, population growth rate was maximized
253 between 14 and 17 °C and decreased below zero beyond 18 °C during the growing season
254 (Fig.3 B). Similarly population fitness was maximized between 27 and 31 °C and decreasesd
255 below zero just beyond 20 °C during the dormant season (Fig.3 D).⁴²

256 We have also detected a strong effect of the past and future climate on population growth
257 rate. However, the magnitude of the effect of future climate on population growth rate was
258 different between emissions scenarios. Under past climate conditions, population growth
259 rate decreased below one for temperature of the growing season. A moderate emission gas
260 scenario (RCP4.5) has a no effect on the population growth rate while a high emission scenario
261 (RCP8.5) has a strong negative effect on population growth rate (Fig.3 B, D).^{43 44}

⁴⁰You do not provide any methods for this contrast.

⁴¹Here and in the preceding figure, I think we need to be more transparent about at what climate values we are purely extrapolating. If I recall correctly, the "present" ranges shown in the lambda figure are not the actual range you fit the models over.

⁴²I would like to discuss possibly not using this figure. I actually think the 2-D niche plots are the better representation of these results, because there are temp*precip interactions that you cannot see here but you can see in the 2-D niche plot. For example, the result that lambda increases with lower temperature is kind of weird, but you can see in the 2-D plot that this is only true at low temperature, and it reverses at high temperature. There are probably important interactions that we should try to visualize in the vital rates.

⁴³I understand what you are describing here, but I would not say that this shows "effects of climate change on population growth". Rather it shows what we predict lambda would be in different ranges of climate. That is a subtle distinction but I think it is important because "effects of climate change" depend on where in the range you are. All this might be moot if we don't use figure, although I love the way you show changes in climate from past to future, so we should find a way to keep that.

⁴⁴I cannot write comments in the figure captions, so this comment applies to "Lower panels below each data panel".THis is not an adequate explanation of what is shown here. These are the ranges (min-max) of monthly climate values for the entire set of experimental sites over specific years, which need to be identified here.

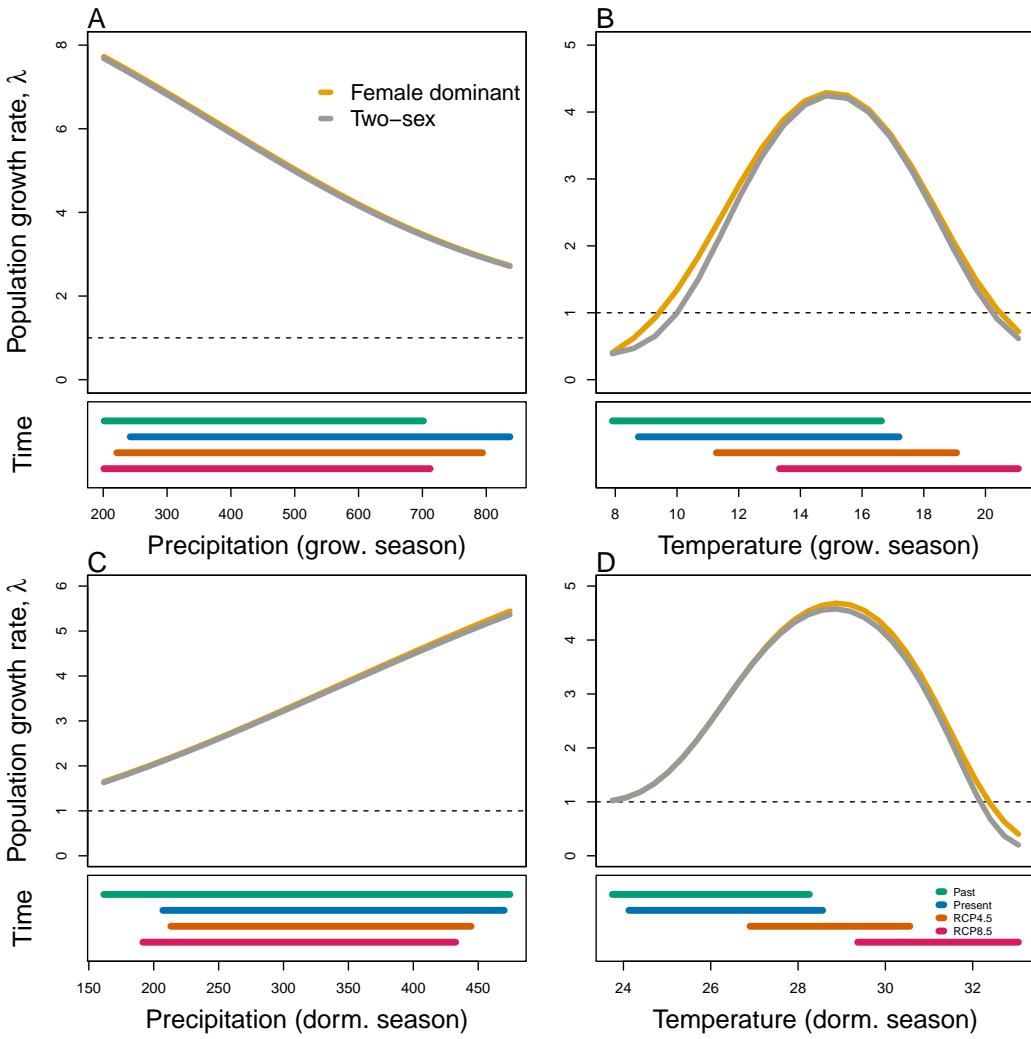


Figure 3: Population growth rate (λ) as a function of seasonal climate. (A) Precipitation of the growing season, (B) Temperature of the growing season, (C) Precipitation of the dormant season, (D) Temperature of the dormant season. The grey curve shows prediction by the two-sex matrix projection model 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 climate values at different time periods (past climate, present and future climates). For future climate, we show a Representative 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).

262 Temperature as a driver of population growth rate decline

263 Population growth rate was most sensitive to change in temperature of the growing season
 264 and temperature of the dormant season (Supporting Information S-6). LTRE decomposition
 265 revealed that, for each sex, the reduction of λ for high value of temperature of the growing
 266 season was driven by a reduction of survival rate, growth rate, and a reduction in number

267 of panicles (Fig.4 A, B). However, the reduction of population growth rate for higher value
 268 of temperature of the dormant season was driven by only female individuals(Fig.4 C, D).
 269 ⁴⁵ The increase of the probability of flowering was sufficient to prevent population growth
 270 rate from declining for high tmeprature of the dormant season (Fig.4 C). ⁴⁶

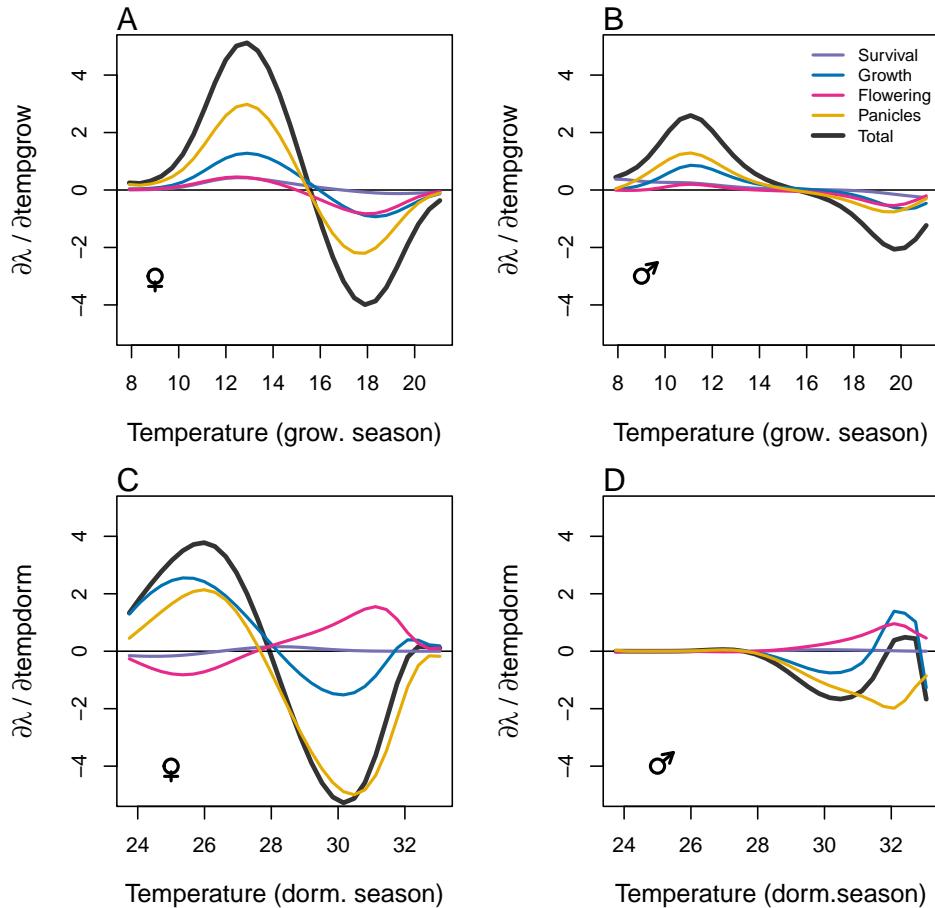


Figure 4: Life table response experiment decomposition of the sensitivity of λ to seasonal climate into additive vital rate contributions of males and females based on posterior mean parameter estimates. (A) Temperature of growing season (contribution of female), (B) Temperature of growing season (contribution of male), (C) Temperature of dormant season (contribution of female) and (D) Temperature of dormant season (contribution of male).

271 Climatic change induce niche and range shifts

⁴⁵This is not how I interpret the figure.

⁴⁶I don't think readers will understand how to process these results, or what they mean with respect to the motivating questions. I think this can be presented in a more reader-friendly way that connects more clearly to the conceptual aims of the study.

272 47 Our results suggested niche sifts for both models (female dominant and two-sex) during the
273 dormant and growing season (Fig. 5). 48 However, the female dominant model overestimated
274 the magnitude of niche shifts (Fig. 5 D). 49 Further, our demographically based range
275 predictions broadly captured the known distribution of the species. More specifically, the
276 predicted probabilities of self-sustaining ($\lambda > 1$) matches the presence and absence of the
277 species (Fig. 6 B, Fig. 6 F). 50 Furthermore, viable populations of *P. arichnifera* were only
278 predicted at the center of the range for current climatic conditions (Fig. 6 B). Although *P.*
279 *arichnifera* was predicted to have suitable habitats in the center of the range under current
280 climate, global warming (regardless of the future scenario of carbon emission used) is
281 predicted to reduce much of these suitable habitats (Fig. 6 C, D). Most of the current suitable
282 habitats will move toward the Northern range edge.

47 General comment on this section: these are the most important results of the paper but they are described only briefly
and without much statistical support. That is true for much of the Results section. I think this could be strengthened.
I also think for both the niche and the map figures we need a more visually intuitive way to contrast the two-sex and
female-dominant models.

48 I do not understand this statement.

49 This needs to be quantified more rigorously and statistically better supported. This also is inconsistent with the result
that there were no sex-specific climate responses, because that is the only way the predictions could differ.

50 Again, these results need to be reported in a more quantitatively rigorous way. I also do not agree that the model captures
the known distribution. I think it drastically over-predicts known occurrence, and that warrants some attention.

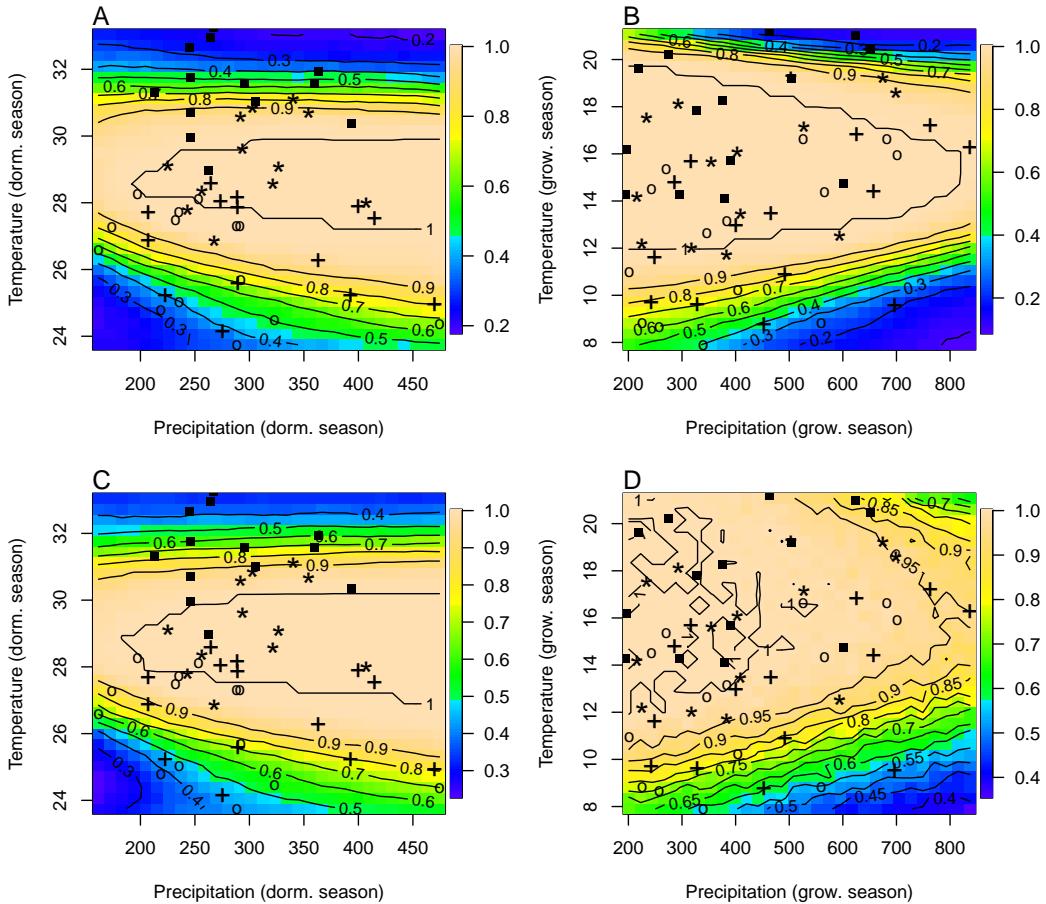


Figure 5: A two-dimensional representation of the predicted niche shift over time (past, present and future climate conditions). Contours show predicted probabilities of self-sustaining populations, $\text{Pr}(\lambda > 1)$ conditional on precipitation and temperature of the dormant and growing season. (A) Niche of dormant season for the two sex model, (B) Niche of growing season for the two sex model, (C) Niche of dormant season for female dominant model, (D) Niche of growing season for female dominant model. "○": Past, "+" Current, "*" RCP 4.5, "■": RCP 8.5.

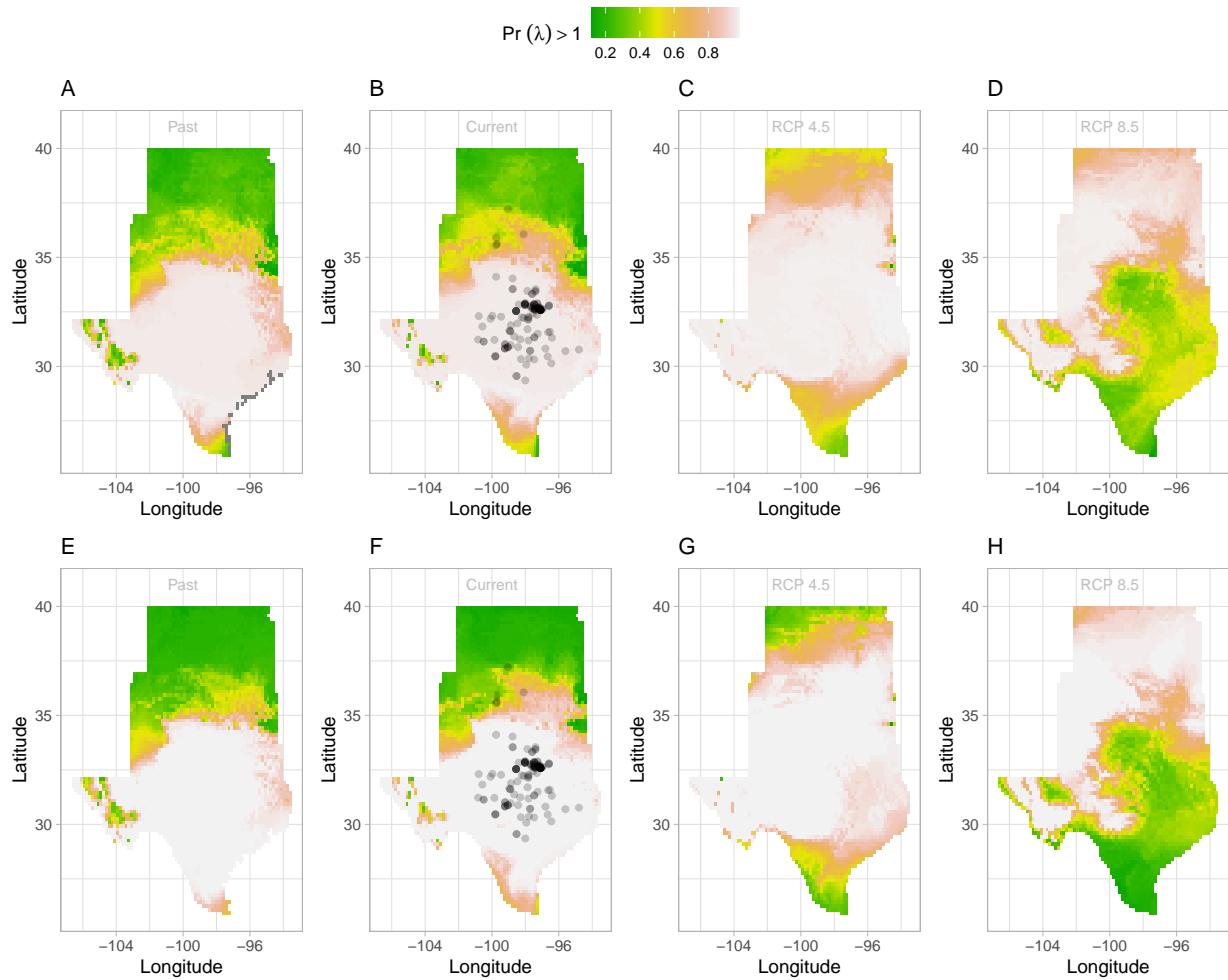


Figure 6: Climate change favors range shift toward the North edge of the current range. (A) Past, (B) Current, (C and D) Future predicted range shift based on the predicted probabilities of self-sustaining populations, $\text{Pr}(\lambda > 1)$, using the two-sex model that incorporates sex-specific demographic 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 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 $\text{Pr}(\lambda > 1)$, confirming that our study approach can reasonably predict range shifts.

283 Discussion

284 Dioecious species make up a large fraction of Earth's biodiversity – most animals and
 285 many plants – yet we have little knowledge about how **skewness in sex ratio**⁵¹ will affect
 286 population viability and range shifts of dioecious species under climate change. Three

⁵¹ You have not described anything about skewness in sex ratio, either from the model or in the data, and this is a glaring omission because as you correctly observe here, it is the way that sex structure matters for population viability

general patterns emerged from our analysis of range-wide common garden experiments and sex-structured, climate-explicit demographic models. First, our Bayesian mixed effect model predicts that seasonal climate (temperature and precipitation) affects sex-demographic processes in **distinctive and contrasting ways**⁵². While climate has a significant effect on the probability of survival and growth, it has no effect on the number of panicles. Second, future climate, by increasing **seasonal temperature**⁵³, **will reduce survival rate, growth rate and reproduction and thereby alter population viability.**⁵⁴ In addition, climate change favors range shifts. Third, **using only one sex to forecast range shifts of dioecious under climate change could lead to an overestimation of the impact of climate change on species.**⁵⁵

Our results indicate no sex-specific demographic response to climate change.⁵⁶ However, females have higher survival rate and fertility rate than males. **This result**⁵⁷ is not unique to our study system and has been observed in **a range of pollen dispersal species across climatic gradients**⁵⁸ (Sasaki et al., 2019; Welbergen et al., 2008; Zhao et al., 2012). Several hypotheses could explain the observed demographic advantage of females over males for survival and flowering and the opposite for growth and number of panicles. The trade-off between fitness traits (survival, growth fertility) due to resource limitation and the pollination mode of our study species (wind pollinated) could explain such a result (Cipollini and Whigham, 1994; Freeman et al., 1976). For most species, the cost of reproduction is often higher for females than males due to the requirement to develop seeds and fruits (Hultine et al., 2016). However, several studies reported a higher cost of reproduction for males in wind pollinated species due to the larger amounts of pollen they produce (Bruijning et al., 2017; Bürl et al., 2022; Cipollini and Whigham, 1994; Field et al., 2013). **In addition to life history trade-off, difference in non-climatic factors such as soil, or biotic interactions could explain decline in vital rate as an indirect effects of increase in temperature** (Alexander et al., 2015; Schultz et al., 2022).⁵⁹

Under current conditions, most populations across the range are viable.⁶⁰ This result could be explained by two hypotheses. First, demographic compensation whereby an increase of one vital rate is coupled with a decrease of another vital rate could explain viable populations in harsh conditions at the range edge (Doak and Morris, 2010; Nomoto and Alexander, 2021; Villegas et al., 2015). In our system, a decrease in fertility and survival rate was counterbalanced

⁵²I am not sure whether this is referring to distinct and contrasting climate variables or sex differences.

⁵³I don't know what you mean by "seasonal temperature" – be more specific

⁵⁴It will not do so everywhere – in some places these metrics will increase in others they will decrease, hence the range shifts.

⁵⁵This result needs a clearer biological mechanism.

⁵⁶Again, if this is true then there should be no difference between the female-dominant and two-sex models.

⁵⁷Which result are you referring to?

⁵⁸Not sure what this means.

⁵⁹This seems like a general comment about climate effects whereas I thought the paragraph was focused on sex differences.

⁶⁰I don't think this statement is well-supported. We don't have any data from natural populations.

316 by an increase in flowering rate, preventing the population growth rate from declining even
317 at range edge⁶¹ during the dormant season⁶². Second, local adaptation at the edge of the
318 range could explain the viable populations throughout the range (Miller and Compagnoni,
319 2022b). Our study was based on a common garden experiment; therefore, individuals planted
320 in climatic conditions that are similar to their source populations climatic conditions were less
321 impacted by stressful environmental conditions.⁶³ An important question to ask is: what is the
322 role of local adaptation in buffering species response against climate change. Unfortunately,
323 our model does not shed light on that question. Adding another predictor to our complex
324 model would have lead to overfitting. Therefore, the role of local adaptation in mitigating
325 population response to climate should be the next step in forecasting species response to
326 climate.⁶⁴

327 Our LTRE analysis reveals that a small change in temperature of the growing and dor-
328 mant season could have a larger impact on population viability. Temperature can impact plant
329 populations through different mechanisms. Increasing temperature could increase evaporative
330 demand, affect plant phenology (Iler et al., 2019; McLean et al., 2016; Sherry et al., 2007), and
331 germination rate (Reed et al., 2021). The potential for temperature to influence these different
332 processes changes seasonally (Konapala et al., 2020). For example, studies suggested that
333 species that are active during the growing season such as cool grass species can have delayed
334 phenology in response to global warming, particularly if temperatures rise above their physio-
335 logical tolerances (Cleland et al., 2007; Williams et al., 2015). In addition, high temperature dur-
336 ing the growing season by affecting pollen viability, fertilization could affect seed formation and
337 germination (Hatfield and Prueger, 2015; Sletvold and Ågren, 2015). Temperature also affected
338 operational sex ratio (OSR) (Fig.S-12). That variation in OSR could affect population growth
339 rate by altering females' fitness (Haridas et al., 2014; Knight et al., 2005; Petry et al., 2016).⁶⁵

340 We found evidence of climatic niche shifts for the female dominant model and the
341 two-sex model. However the female dominant model overestimated species niche, suggesting
342 that using one sex to predict niche shifts could be misleading.⁶⁶ Despite that overestimation for
343 the female dominant model, both models agree on the fact that climatic conditions that are not
344 optimal under current conditions will be optimal for the species over the next years particularly

⁶¹Not sure I follow this - if lambda was not declining it would not be a range edge

⁶²Population growth rate is an annual measure, it does not refer to any season. I think what you mean here is that dormant season weather can affect population growth rate.

⁶³This statement lacks evidence.

⁶⁴I don't think this is a very effective use of the Discussion. If you want to address local adaptation maybe that can go in an appendix. I don't actually understand the point of this paragraph but maybe I am not understanding something.

⁶⁵These results need to be better developed because they underlie all the other results. And again, the only way you can get an effect on temperature on OSR is if there were sex-specific responses to climate, but you say there were none.

⁶⁶Again – what is the biological explanation for this result?

345 at the edge of species⁶⁷. Further, pollen dispersal may allow plants to resist climate change be-
346 cause pollen dispersal may provide the local genetic diversity necessary to adapt at the leading
347 edge of the population (Corlett and Westcott, 2013; Duputié et al., 2012; Kremer et al., 2012).
348 Since wind pollination is most effective at short distances, it is most often found in plant species
349 growing at high density such as our study species, it is less likely that dispersal limitation affect
350 niche shift in our study system.⁶⁸ However, others biotic factors such as species competition
351 might constrain the species to a narrower realized niche (Aguilée et al., 2016; Pulliam, 2000).

352 Our results suggest that climate change will drive range shifts and the magnitude and
353 rate of that range shift could be overestimated when tracking only one sex (Fig. S-9, Fig.
354 S-10, Fig. S-11). This overestimation of the impact of climate change using a female dominant
355 model could be due to several factors.⁶⁹ First, small change in seasonal temperature affects
356 population viability for both sexes⁷⁰. Second, operational sex ratio in *Poa arachnifera* become
357 female biased in areas with lower temperature of growing season such as Northern range edge
358 (Fig. S-12 B). Our results converge with previous studies that have found the same pattern⁷¹ for
359 other dioecious species (Varga and Soulsbury, 2020; Woldemelak et al., 2021). Our finding also
360 contrast with a previous study suggesting that an increase in male frequency induce range
361 shifts by reducing pollen limitation in conditions that were not suitable (Petry et al., 2016).

362 Three years represent a relatively decent time for demographic study for common garden
363 experiments across climatic gradient.⁷² Thus our models can only capture a certain range
364 of demographic and environmental variability (Fig. S-8). Moreover, our future projections
365 require extrapolation to warmer or colder conditions than observed in our experiment
366 and subsequently should be interpreted with caution (Chen et al., 2024).⁷³ Despite all
367 these limitations, the qualitative implications of a negative response of species to increase
368 temperature (dormant and growing season)⁷⁴ seems consistent across all GCMs. Most of the
369 suitable areas move toward the North of the current range in response to climate change.
370 Climate change will affect population growth rate primarily through the response of female
371 which is more sensitive to climate change (Miller and Compagnoni, 2022b).⁷⁵ Males also have
372 a significant contribution to population growth rate particularly for temperature.⁷⁶ Our work

⁶⁷ Which edge? I am not sure which specific results you are referring to here.

⁶⁸ I do not find this particularly relevant for interpreting the result that opens this paragraph.

⁶⁹ OK I was expecting this earlier.

⁷⁰ Population viability is a property of the entire population, so females and males cannot have their own population viability.

⁷¹ Unclear what pattern you are referring to

⁷² I am not sure whether this is intended to mean that three years is short or long – can you sharpen this?

⁷³ This is a good point, and it needs to be shown more clearly in methods and results.

⁷⁴ Again, it is not negative everywhere. Northern populations with benefit from warming, so these results need to be described with greater nuance.

⁷⁵ This paper says the opposite.

⁷⁶ I do not know what this is saying.

373 suggest that **current climate may not affect population viability**⁷⁷, but populations may be
374 impacted negatively over the next decades in response to a climate change. This is key because
375 most conservation actions are design from data on current responses to climate, rather than
376 future response to climate (Sletvold et al., 2013). Moreover, management strategies that focus
377 on both sexes would be effective and will enhance population growth rate in response to
378 global warming.

379 Conclusion

380 We have investigated the potential consequence of skewness in sex ratio on population
381 dynamics and range shift in the context of climate change. **We found that future climate will**
382 **affect population growth rate at the center of species range.**⁷⁸ This reduction in population
383 growth rate will induce a range shift to the northern edge of the species current range. Our
384 results also suggest that tracking only one sex could lead to an overestimation of the effect
385 of climate change on population dynamics. Our work provides a framework for predicting
386 the impact of global warming on species using population demography.

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400 grant CNS-1338099 and by Rice University's Center for Research Computing (CRC).

⁷⁷This statement does not make sense to me. Our data show that population viability is sensitive to climate under current (observed) conditions.

⁷⁸I do not follow what this is referring to.

⁷⁹Much of this looks like it is copied from the Am Nat paper.

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Supporting Information

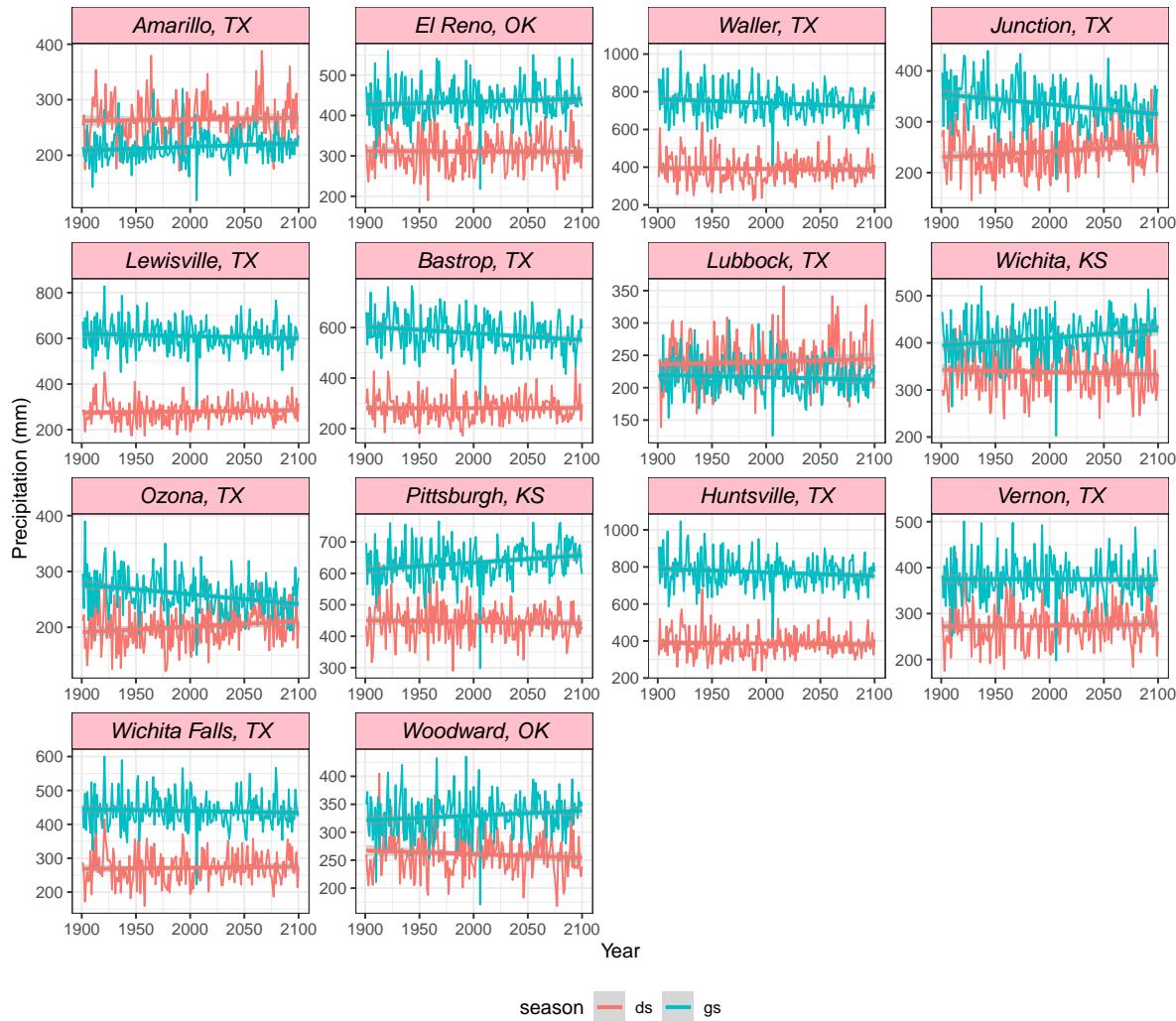


Figure S-1: Precipitation variation accross the study sites from 1990 to 2100. ds:Dormant season, dg:Growing season.

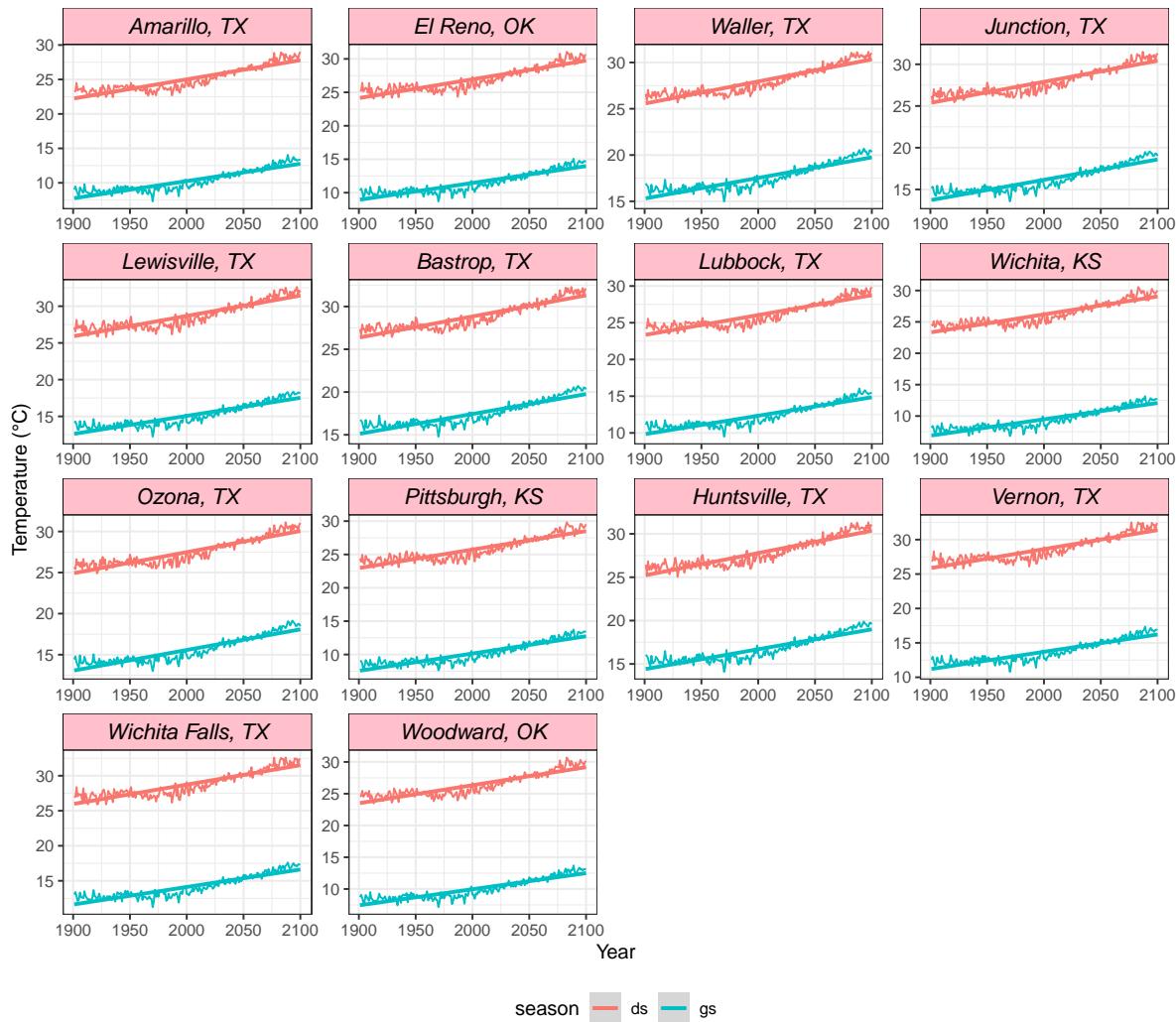


Figure S-2: Temperature variation accross the study sites from 1990 to 2100, ds: Dormant season, dg: Growing season.

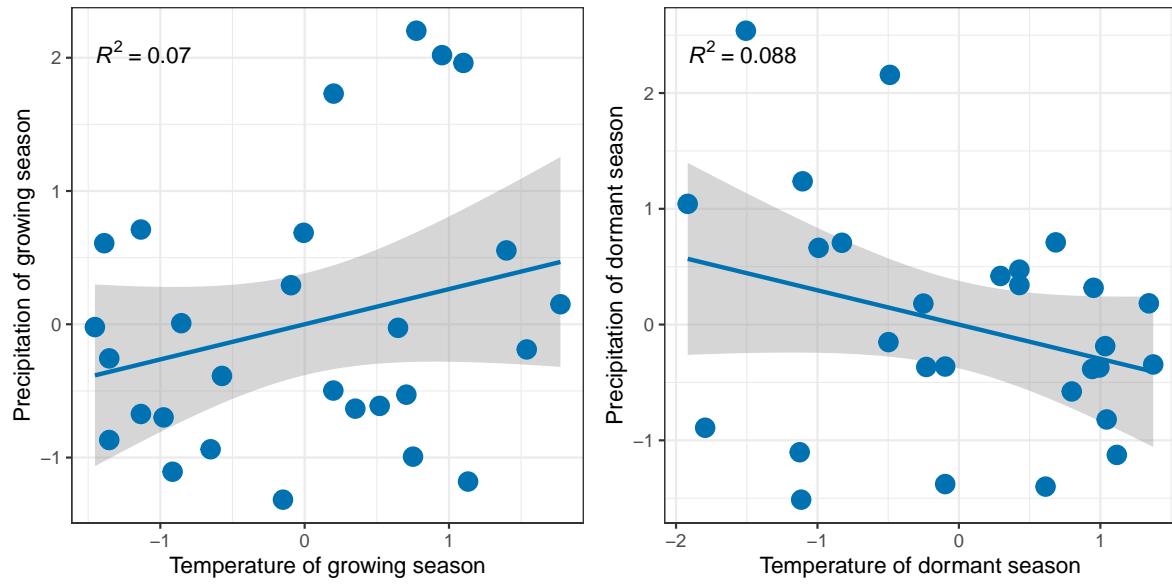


Figure S-3: Relation between precipitation and temperature for each season (growing and dormant). R^2 indicates the value of proportion of explained variance between the temperature and precipitation

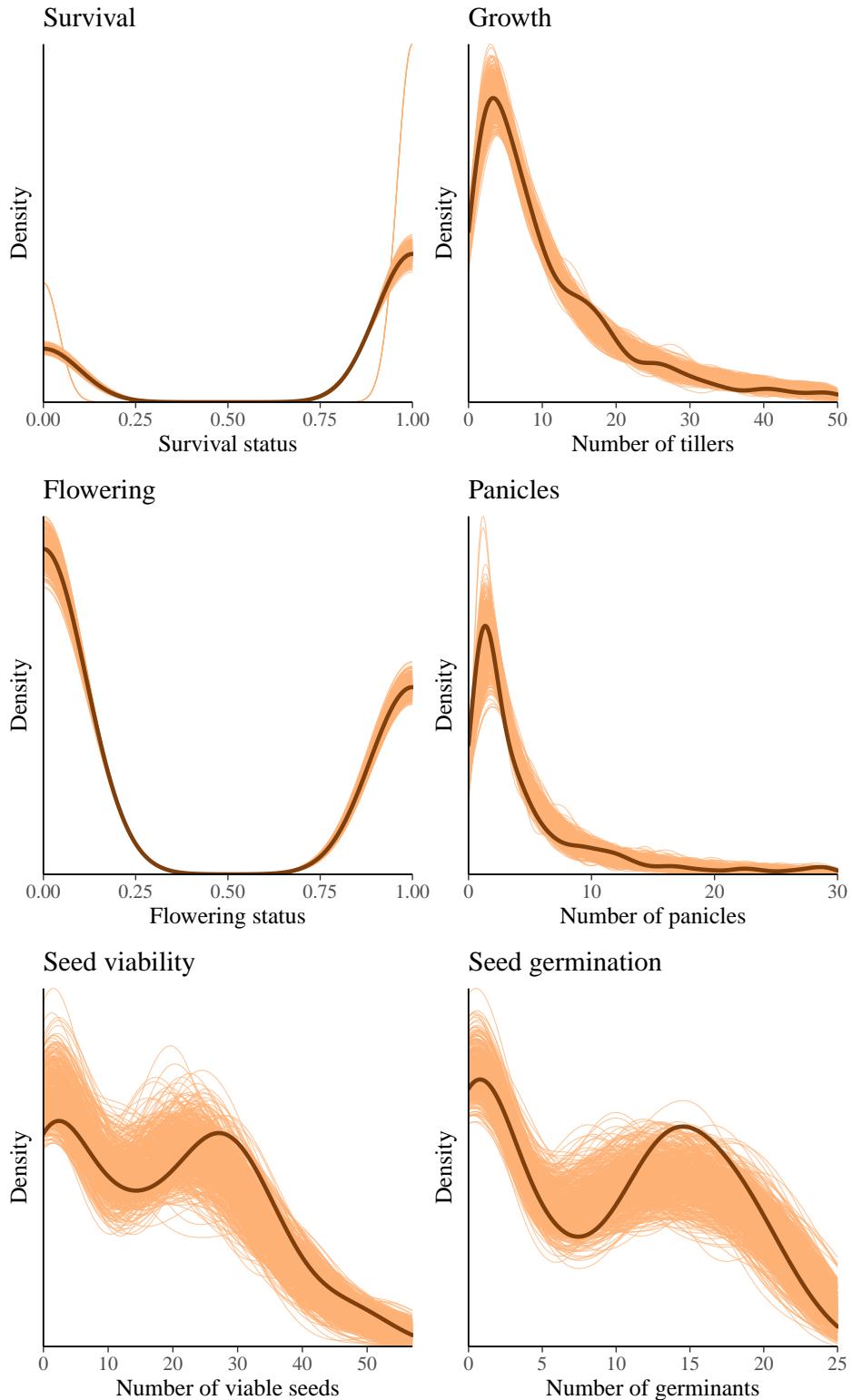


Figure S-4: Posterior predictive checks. Consistency between real data and simulated values suggests that the fitted model accurately describes the data. Graph shows density curves for the observed data (light blue) along with the simulated values (dark blue). The first column shows the linear models and the second column shows the 2 degree polynomial models.

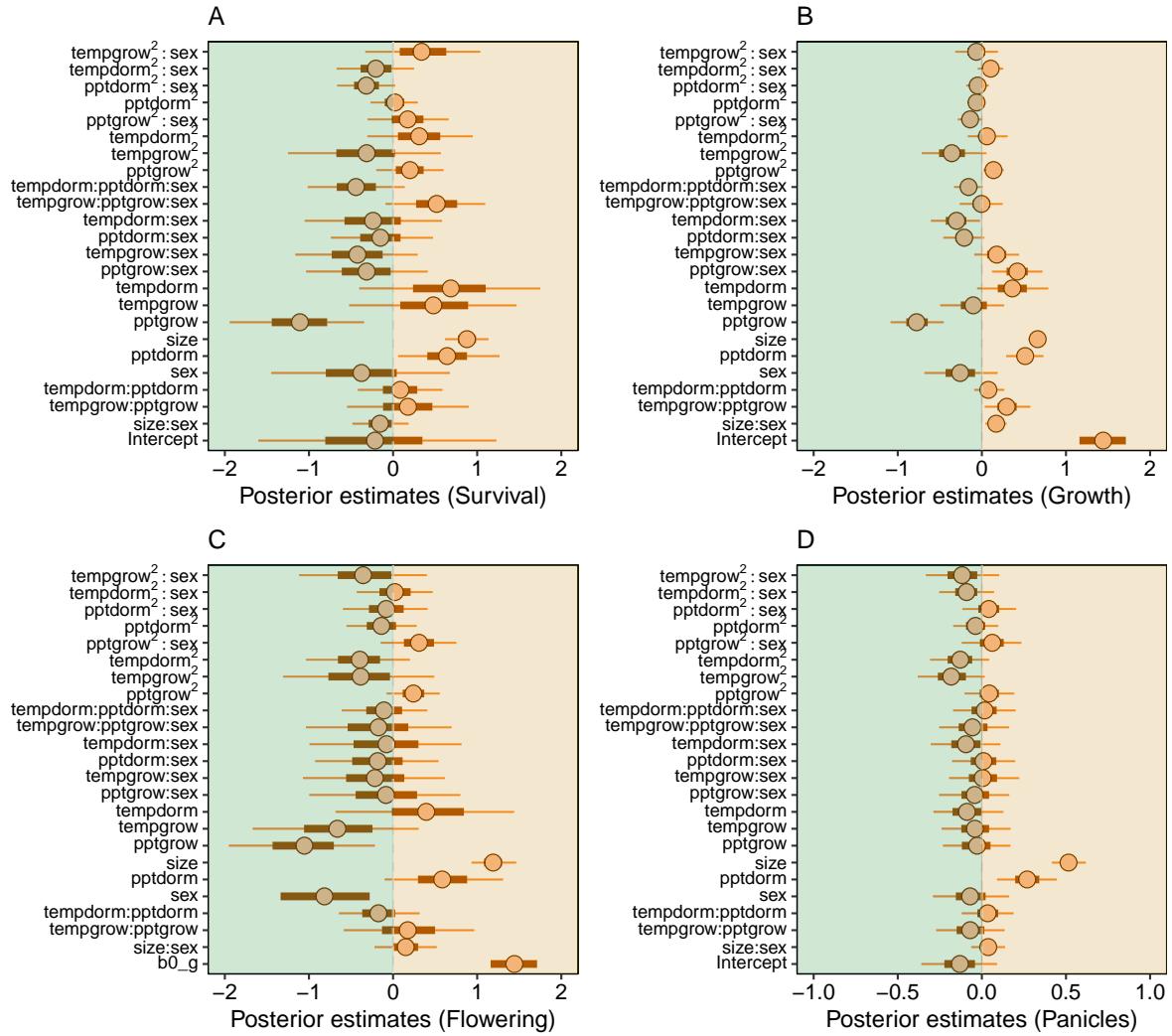


Figure S-5: Mean parameter values and 95% credible intervals for all vital rates. pptgrow is the precipitation of growing season, Tempgrow is the temperature of growing season, pptdorm is the temperature of dormant season, Tempdorm is the temperature of dormant season.

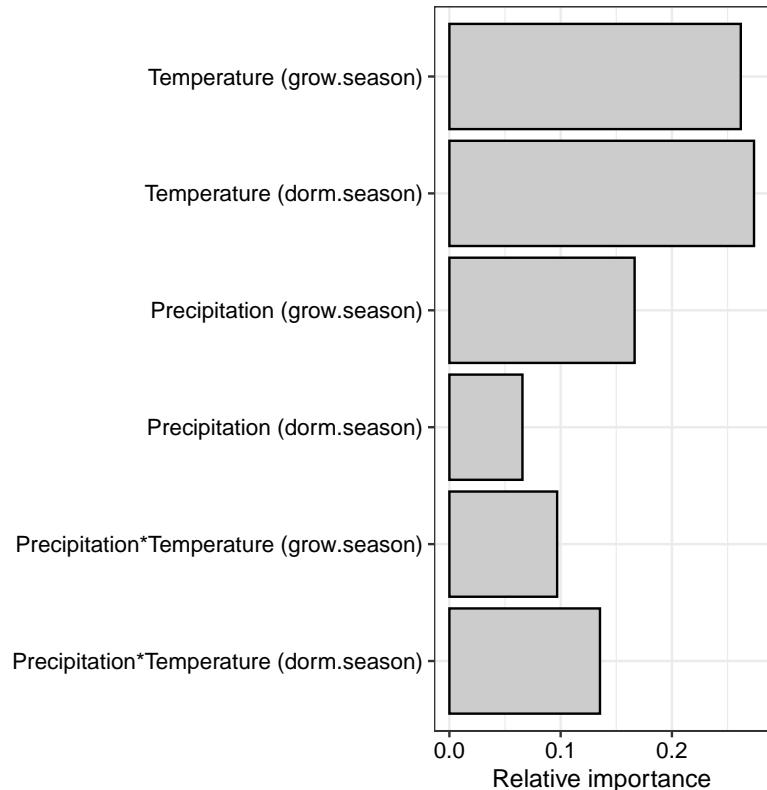


Figure S-6: Life Table Response Experiment: The bar represent the relative importance of each predictors

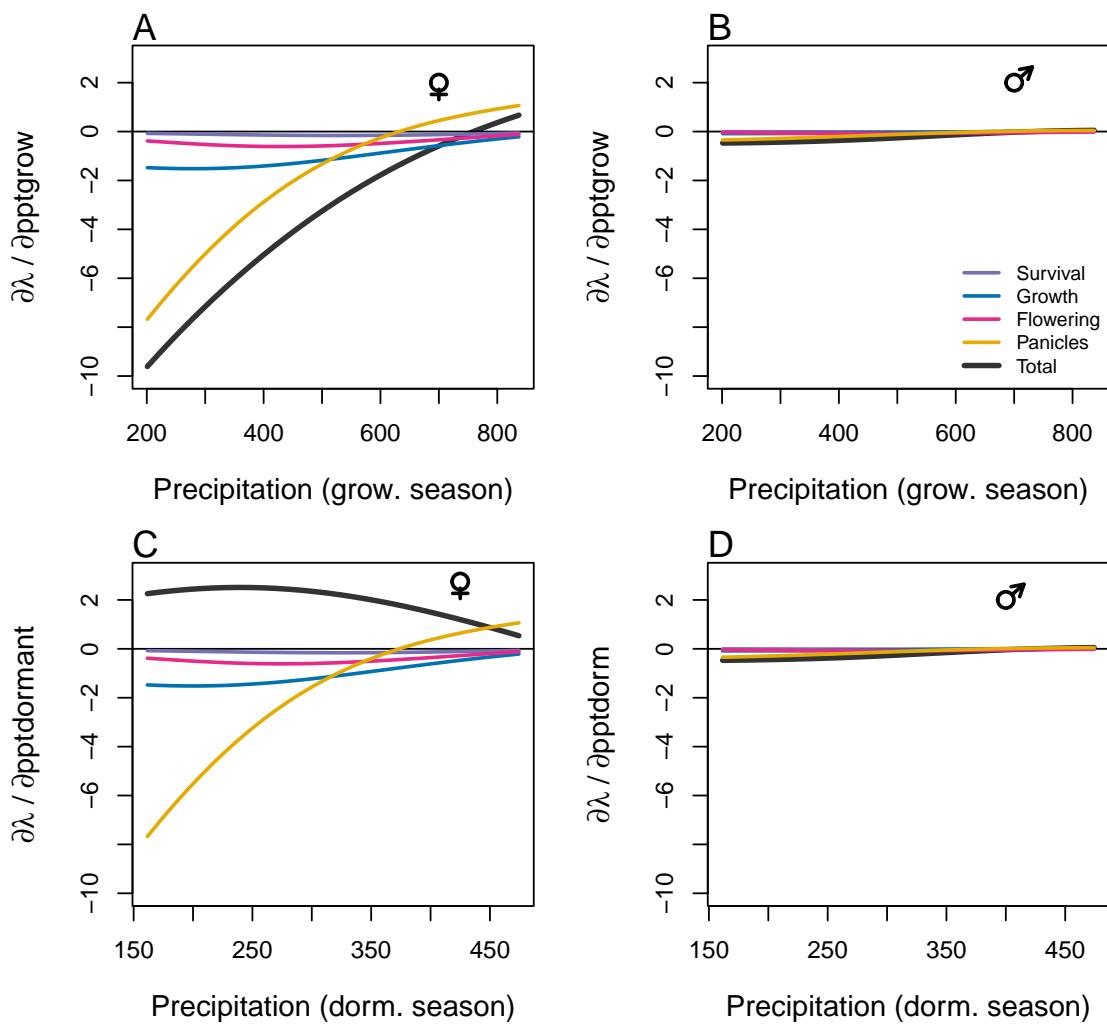


Figure S-7: Life table response experiment decomposition of the sensitivity of λ to seasonal climate into additive vital rate contributions of males and females based on posterior mean parameter estimates. (A) Precipitation of growing season (contribution of female), (B) Precipitation of growing season (contribution of male), (C) Precipitation of dormant season (contribution of female) and (D) Precipitation of dormant season (contribution of male).

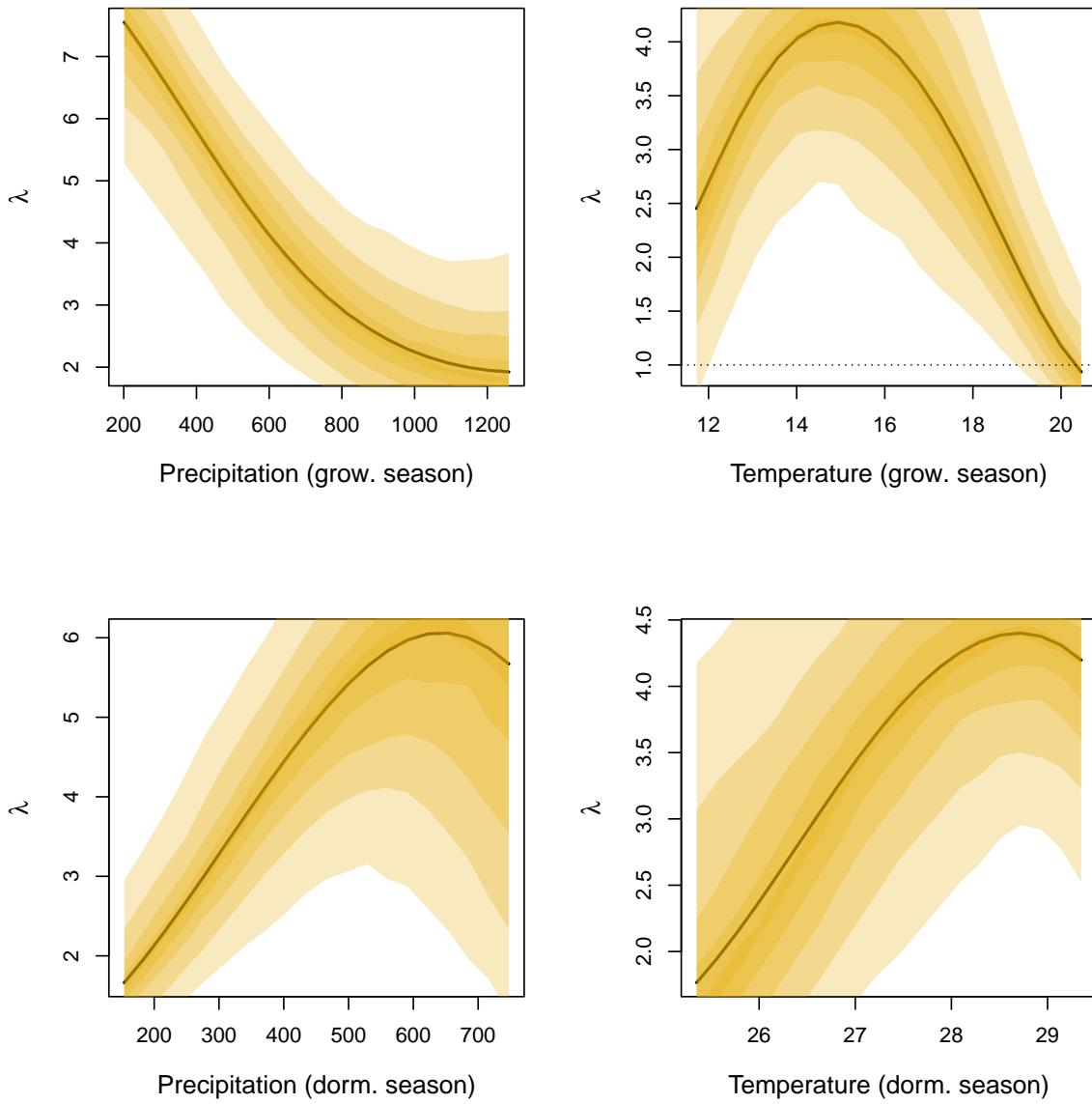


Figure S-8: Population growth rate (λ) as a function of seasonal climate (2015-2017), predicted by the two-sex matrix projection model that incorporates sex-specific demographic responses to climate with sex ratio-dependent seed fertilization. We show the mean posterior distribution of λ in solid lines, and the 5, 25, 50, 75, and 95% percentiles of parameter uncertainty in shaded gold color. The dashed horizontal line indicates the limit of population viability ($\lambda = 1$)

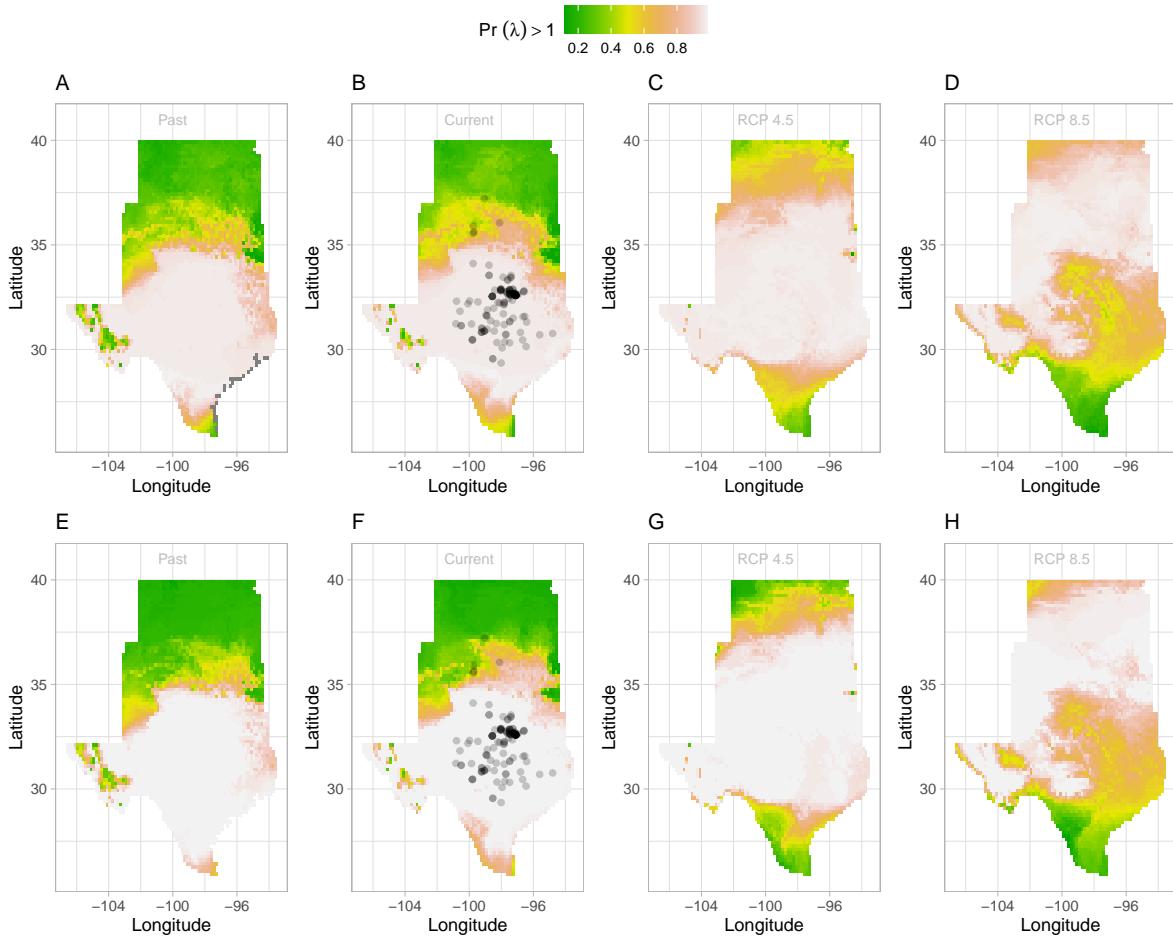


Figure S-9: Climate change favors range shift toward the North edge of the current range. (A) Past, (B) Current, (C and D) Future predicted range shift based on the predicted probabilities of self-sustaining populations, $\text{Pr}(\lambda > 1)$, using the two-sex model that incorporates sex-specific 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 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 $\text{Pr}(\lambda > 1)$, confirming that our study approach can reasonably predict range shifts.

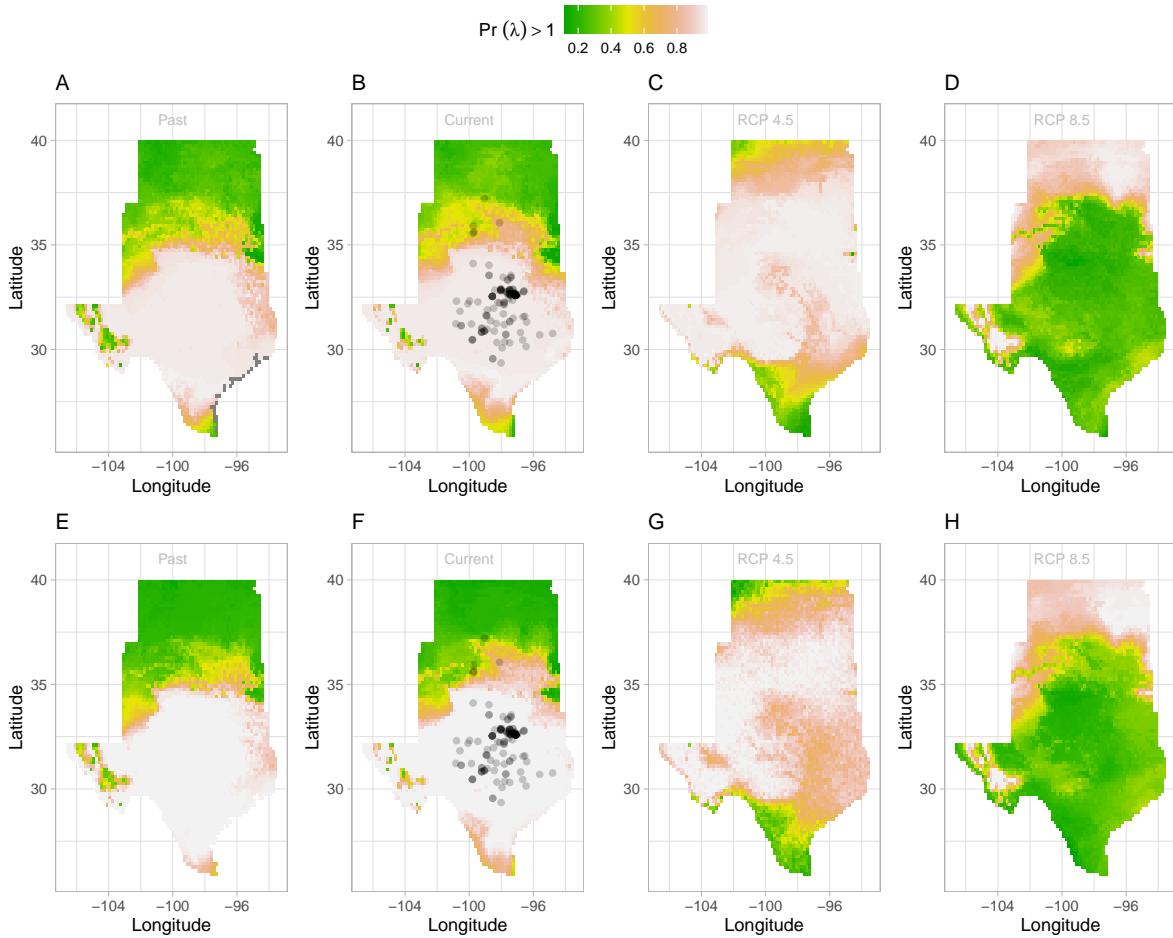


Figure S-10: Climate change favors range shift toward the North edge of the current range. (A) Past, (B) Current, (C and D) Future predicted range shift based on the predicted probabilities of self-sustaining populations, $\text{Pr}(\lambda > 1)$, using the two-sex model that incorporates sex-specific 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 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 $\text{Pr}(\lambda > 1)$, confirming that our study approach can reasonably predict range shifts.

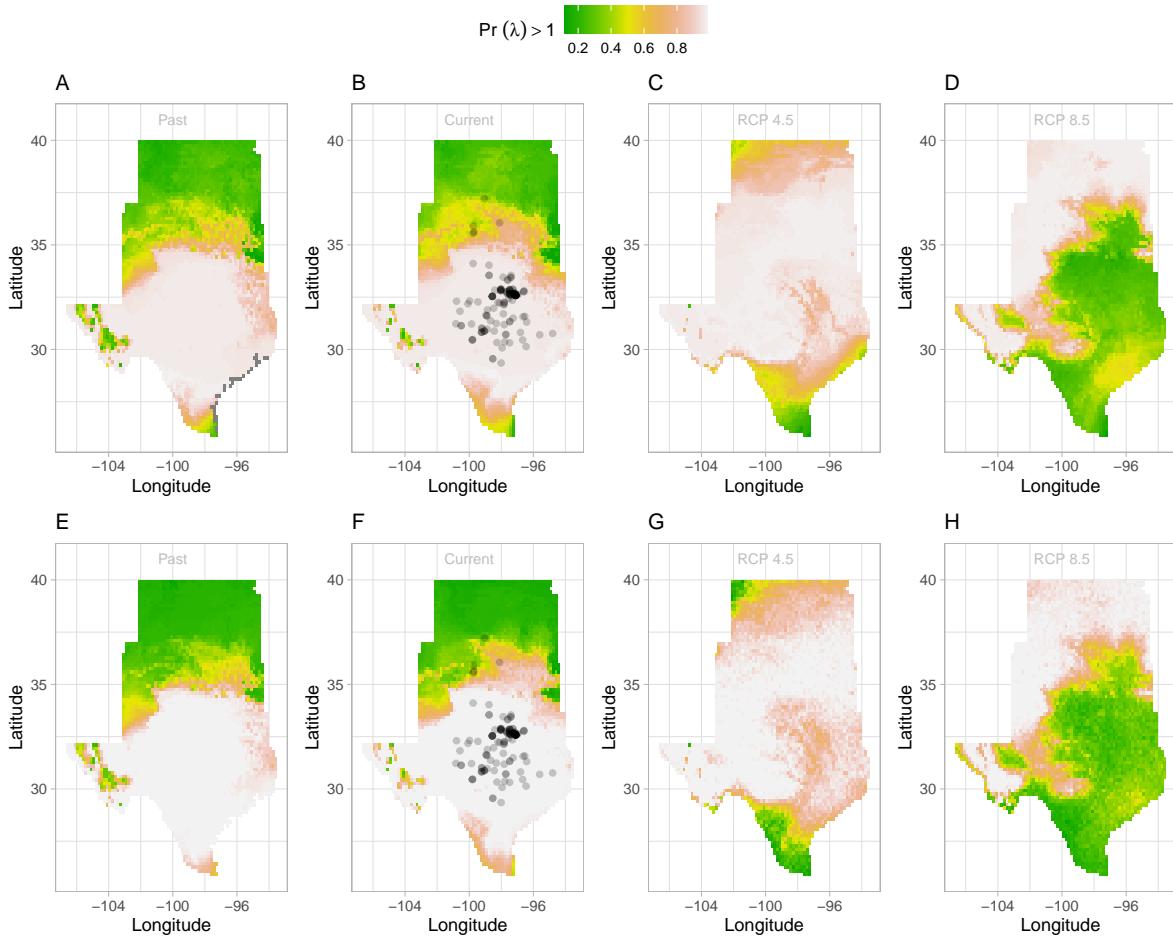


Figure S-11: Climate change favors range shift toward the North edge of the current range. (A) Past, (B) Current, (C and D) Future predicted range shift based on the predicted probabilities of self-sustaining populations, $\text{Pr}(\lambda > 1)$, using the two-sex model that incorporates sex-specific 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.

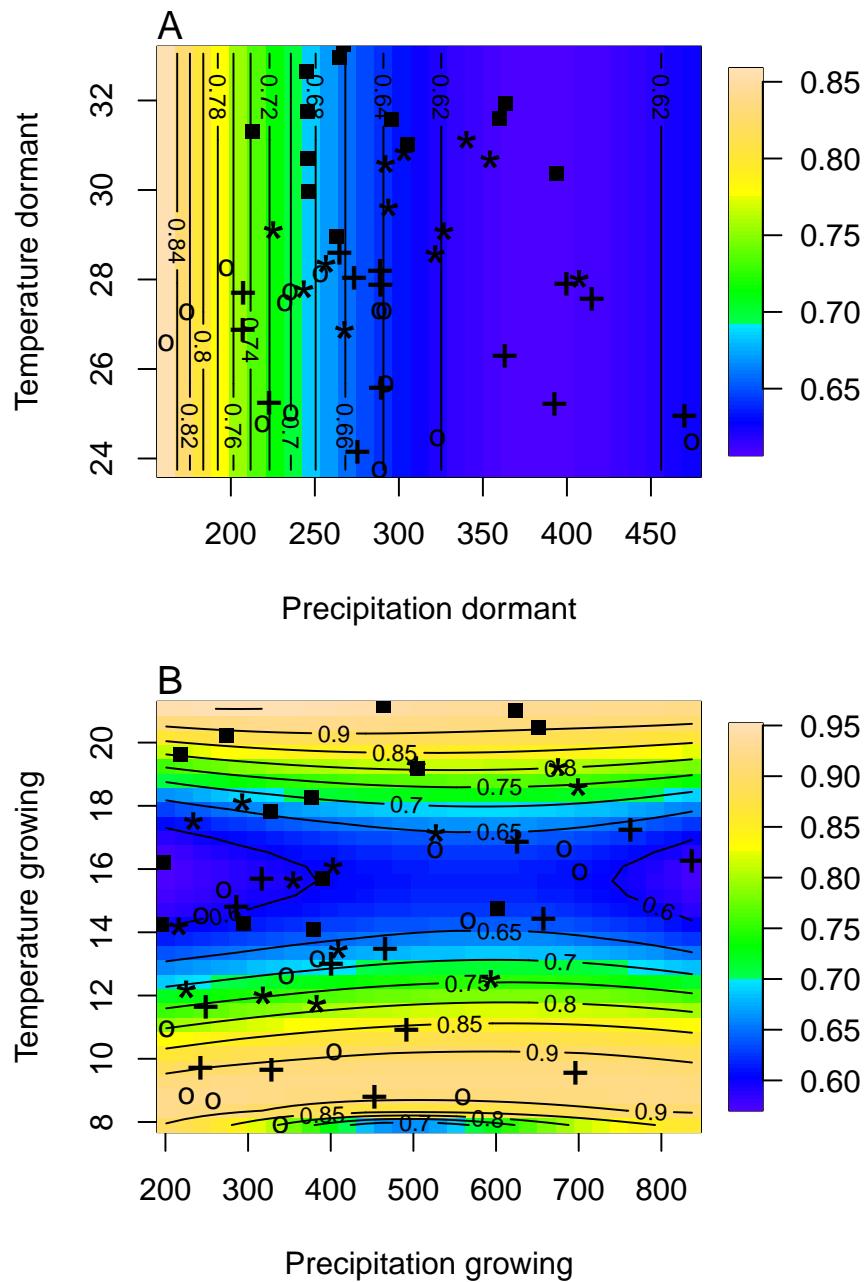


Figure S-12: A two-dimensional representation of the Operational Sex Ratio (OSR) over time (past, present and future climate conditions). OSR represents the proportion of females. Contours show predicted values of OSR conditional on precipitation and temperature of the dormant and growing season. Operational Sex Ratio during the dormant season for the two sex model (A), Operational Sex Ratio during the growing season for the two sex model (B). “○”: Past, “+”: Current, “*”: RCP 4.5, “■”: RCP 8.5.