

Forecasting range shifts of a dioecious plant species under climate change

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1 Abstract

2 Rising temperatures and extreme drought events associated with global climate change have
3 triggered an urgent need for predicting species response to climate change. Currently, the vast
4 majority of theory and models in population biology, including those used to forecast biodiver-
5 sity responses to climate change ignore the complication of sex structure. To address this issue,
6 we developed two contrasting climate-driven population matrix models (one that does not ac-
7 count for sex structure and another one that does account for sex structure) using demographic
8 data of dioecious species (Texas bluegrass), past and future climate (different carbon gas emis-
9 sion scenarios) to forecast and backcast the effect of climate change on range shifts. Both models
10 predict a sex specific demographic response to climate change. Female individuals have a
11 demographic advantage (higher vital rate) over males. Climate change assuming moderate car-
12 bon emission has no negative impact on population viability. However, high carbon emission
13 will likely alter population viability in dioecious species and will induce a North-West shift
14 in suitable conditions. Overall, our work suggest that tracking only the female could lead to
15 an underestimation of the impact of climate change on dioecious species. This study provides
16 a framework for predicting the impact of climate on species using population demography.

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 many plants) might be particularly vulnerable to the
²² influence of climate change because they often display skewed sex ratios that are generated or
²³ reinforced by sexual niche differentiation (distinct responses of females and males to shared cli-
²⁴ mate drivers) (Tognetti, 2012). Accounting for such a niche differentiation within a population
²⁵ is a long-standing challenge in accurately predicting which sex will successfully track environ-
²⁶ mental change and how this will impact population viability and range shifts (Gissi et al., 2023;
²⁷ Jones et al., 1999). The vast majority of theory and models in population biology, including
²⁸ those used to forecast biodiversity responses to climate change, ignore the complication of sex
²⁹ structure (Ellis et al., 2017; Pottier et al., 2021). As a result, accurate forecasts of colonization-
³⁰ extinction dynamics for dioecious species under future climate scenarios are limited.

³¹ Species's range limits, when not driven by dispersal limitation, should generally reflect
³² the limits of the ecological niche (Lee-Yaw et al., 2016). For most species, niches and geographic
³³ ranges are often limited by climatic factors including temperature and precipitation (Sexton
³⁴ et al., 2009). Therefore, any substantial changes in the magnitude of these climatic factors in a
³⁵ given location across the range could impact population viability, with implications for range
³⁶ shifts based on which regions become more or less suitable (Davis and Shaw, 2001; Pease
³⁷ et al., 1989). Forecasting range shifts for dioecious species is complicated by the potential for
³⁸ each sex to respond differently to climate variation (Morrison et al., 2016; Pottier et al., 2021).
³⁹ Populations in which males are rare under current climatic conditions could experience low
⁴⁰ reproductive success due to sperm or pollen limitation that may lead to population decline in
⁴¹ response to climate change that disproportionately favors females (Eberhart-Phillips et al., 2017).
⁴² In contrast, climate change could expand male habitat suitability (e.g. upslope movement),
⁴³ which might increases seed set for pollen-limited females and favor range expansion (Petry
⁴⁴ et al., 2016). Although the response of species to climate warming is an urgent and active area
⁴⁵ of research, few studies have disentangled the interaction between sex and climate drivers
⁴⁶ to understand their combined effects on population dynamics and range shifts.

⁴⁷ Our ability to track the impact of climate change on the population dynamics of
⁴⁸ dioecious plants and the implication of such impact on range shift depends on our ability
⁴⁹ to build mechanistic models that take into account the spatial and temporal context in which
⁵⁰ sex specific response to climate change affects population viability (Czachura and Miller, 2020;
⁵¹ Davis and Shaw, 2001; Evans et al., 2016). Structured models that are built from long-term

52 demographic data collected from common garden experiments have emerged as powerful
53 technic to study the impact of climate change on species range shift (Merow et al., 2017;
54 Schwinnning et al., 2022). These structured models are increasingly utilized for several reasons.
55 First, structured models enable the manipulation of treatments that can isolate spatial and
56 temporal correlations between environmental factors, thus overcoming a main disadvantage
57 with many types of correlative studies (Leicht-Young et al., 2007). Second, structured models
58 link individual-level demographic trait to population demography allowing the investigation
59 of the demographic mechanisms behind vital rates (e.g. survival, fertility, growth and seed
60 germination) response environmental variation (Dahlgren et al., 2016; Louthan et al., 2022).
61 Third, these structured models can be used to identify which aspect of climate is more
62 important for population dynamics. For example, Life Table Response Experiment (LTRE)
63 build from structured models is an approach that has become widely used to understand
64 how a given treatment (eg. temperature or precipitation) could affect population dynamics
65 (Caswell, 1989; Iler et al., 2019; Morrison and Hik, 2007; O'Connell et al., 2024).

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

- 77 1. What are the sex-specific vital rate responses to variation in temperature and precipitation
78 across the species' range ?
- 79 2. How sex-specific vital rates combine to determine the influence of climate variation on
80 population growth rate (λ) ?
- 81 3. What are the historical and projected changes in climate across the species range ?
- 82 4. What are the back-casted and fore-casted dynamics of this species' geographic niche
83 ($\lambda \geq 1$) and how does accounting for sex structure modify these predictions ?

⁸⁴ **Materials and methods**

⁸⁵ **Study species**

⁸⁶ Texas bluegrass (*Poa arachnifera*) is a dioecious perennial, summer-dormant cool-season (C3)
⁸⁷ grass that occurs in the south-central U.S. (Texas, Oklahoma, and southern Kansas) (Hitchcock,
⁸⁸ 1971). Average temperatures along the distribution of the species tend to decrease northward
⁸⁹ as a result of the influence of latitude: lower latitudes receive more heat from the sun over
⁹⁰ the course of a year. Similarly the average precipitation decrease eastward as a result of
⁹¹ the influence of longitude: lower longitudes receive less precipitation over the year. Texas
⁹² bluegrass grows between October and May (growing season), with onset of dormancy often
⁹³ from June to September (dormant season) (Kindiger, 2004). Flowering occurs in May and
⁹⁴ the species is wind pollinated (Hitchcock, 1971).

⁹⁵ **Common garden experiment**

⁹⁶ We set up a common garden experiment throughout and beyond the range of Texas bluegrass
⁹⁷ to enable study of sex-specific demographic responses to climate and the implications for range
⁹⁸ shifts. The novelty of this study lies in the fact that we use a precise climate variable to build
⁹⁹ a mechanistic model to forecast the response of species to climate change. Details of the exper-
¹⁰⁰ imental design are provided in Miller and Compagnoni (2022b); we provide a brief overview
¹⁰¹ here. The common experiment was installed at 14 sites across a climatic gradient (Fig.1. At
¹⁰² each site, we established 14 blocks. For each block we planted three female and three male indi-
¹⁰³ viduals that were clonally propagated from eight natural source populations of Texas bluegrass.
¹⁰⁴ The experiment was established in November 2013 and was census annually through 2016, pro-
¹⁰⁵ viding both spatial and inter-annual variation in climate. Each May (2014-2016), we collected
¹⁰⁶ individual demographic data including survival (alive or dead), growth (number of tillers),
¹⁰⁷ flowering status (reproductive or vegetative), and fertility (number of panicles, conditional on
¹⁰⁸ flowering). For the analyses that follow, we focus on the 2014-15 and 2015-16 transitions years.

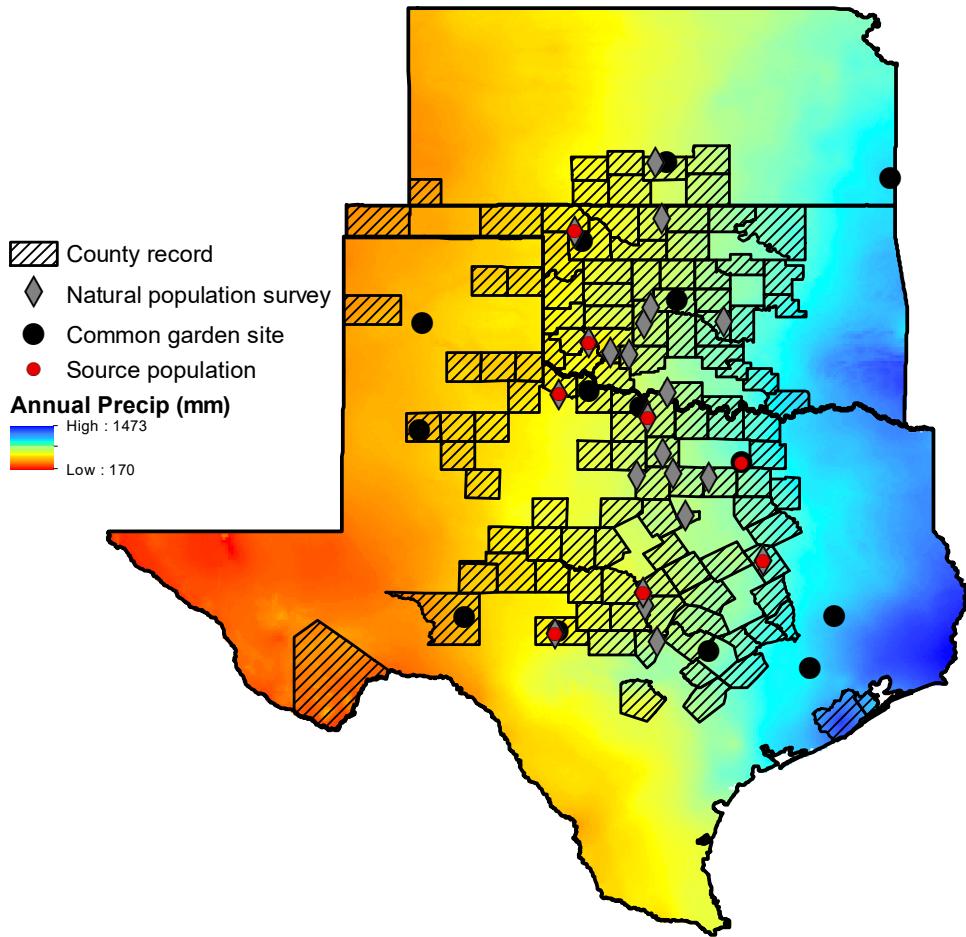


Figure 1: XXX

109 Climatic data collection

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

¹I am not sure if these are actually the right dates.

¹¹⁸ Across years and sites, the experiment included substantial variation in growing and dormant
¹¹⁹ season temperature and precipitation (Supporting Information S-1, S-2).

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

¹³⁰ Sex ratio experiment

¹³¹ We conducted a sex-ratio experiment on a site close (1 km) to a natural population of the
¹³² focal species at the center of the range to estimate the effect of sex-ratio variation on female
¹³³ reproductive success. Details of the experiment are provided in Compagnoni et al. (2017) and
¹³⁴ Miller and Compagnoni (2022b). In short, we established 124 experimental populations on
¹³⁵ plots measuring $0.4 \times 0.4\text{m}$ and separated by at least 15m from each other at that site. We chose
¹³⁶ 15m because our pilot data show that more than 90% of wind pollination occurred within 13m.
¹³⁷ We varied population density (1-48 plants/plot) and sex ratio (0%-100% female) across the ex-
¹³⁸ perimental populations, and we replicated 34 combinations of density-sex ratios. We collected
¹³⁹ the number of panicles from a subset of females in each plot and collected the number of
¹⁴⁰ seeds in each panicle. Since the number of panicles (proxy of reproduction effort) does not nec-
¹⁴¹ essarily reflect reproduction success in *Poar arachnifera*, we accessed reproduction success (seed
¹⁴² fertilized) using greenhouse-based germination and trazolium-based seed viability assays.

¹⁴³ We used the sex-ratio to estimate the probability of viability and the germination rate.
¹⁴⁴ Seed viability was modeled with a binomial distribution where the probability of viability
¹⁴⁵ (v) was given by:

$$\sup{146} v = v_0 * (1 - OSR^\alpha) \quad (1)$$

¹⁴⁷ where OSR is the operational sex ratio (proportion of panicles that were female) in the
¹⁴⁸ experimental populations. The properties of the above function is supported by our previous
¹⁴⁹ work (Compagnoni et al., 2017). Here, seed viability is maximized at v_0 as OSR approaches

150 zero (strongly male-biased) and goes to zero as *OSR* approaches 1 (strongly female-biased).
151 Parameter α controls how viability declines with increasing female bias.

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

155 Sex specific demographic responses to climate

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

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

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

170 where β_0 is the grand mean intercept, β_1 is the size dependent slopes. *size* was on a natural log-
171 arithm scale. $\beta_2 \dots \beta_{13}$ represent the climate dependent slopes. $\beta_{14} \dots \beta_{23}$ represent the sex-climate
172 interaction slopes. *pptgrow* is the precipitation of the growing season (standardized to mean
173 zero and unit variance), *tempgrow* is the temperature of the growing season (standardized to
174 mean zero and unit variance), *pptdorm* is the precipitation of the dormant season (standardized
175 to mean zero and unit variance), *tempdorm* is the temperature of the dormant season (standard-
176 ized to mean zero and unit variance). The model also includes normally distributed random ef-

fects for block-to-block variation ($\phi \sim N(0, \sigma_{block})$) and source-to-source variation that is related to the provenance of the seeds used to establish the common garden ($\rho \sim N(0, \sigma_{source})$), site to site variation ($v \sim N(0, \sigma_{site})$). We fit survival, growth, flowering models with generic weakly informative priors for coefficients ($\mu = 0, \sigma = 1.5$) and variances ($\gamma[0.1, 0.1]$). **We fit fertility model with regularizing priors for coefficients ($\mu = 0, \sigma = 0.15$)**. We ran three chains for 1000 samples for warmup and 4000 for interactions, with a thinning rate of 3. We accessed the quality of the models using trace plots and predictive check graphs (Piironen and Vehtari, 2017) (Supporting Information S-4). To understand the effect of climate on vital rates, we got the 95 % credible interval of the posterior distribution. Then we assumed that there is 95 % probability that the true (unknown) estimates would lie within that interval, given the evidence provided by the observed data for each vital rate. All models were fit in Stan (Stan Development Team, 2023).

188 Influence of climate variation on population growth rate

To understand the effect of climate on population growth rate, we used the vital rate estimated earlier to build a matrix projection model (MPM) structured by size (number of tillers), sex and climate (dormant and growing) as covariate. Let $F_{x,z,t}$ and $M_{x,z,t}$ be the number of female and male plants of size x in year t present at a location that has z as climate, where $x \in \{1, 2, \dots, U\}$ and U is the maximum number of tillers a plant can reach (here 95th percentile of observed maximum size). Let F_t^R and M_t^R be the new recruits, which we assume do not reproduce in their first year. We assume that the parameters of sex ratio-dependent mating (Eq. 1) do not vary with climate. For a pre-breeding census, the expected numbers of recruits in year $t+1$ is given by:

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

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

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

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

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

207

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

208

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

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

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

223 Identifying the mechanisms of population growth rate sensitivity to climate

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

229

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

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

232 To identify the mechanism by which climate affects population growth rate for each sex,
233 we decomposed the effect of each climate variable (here Climate) on population growth rate (λ)
234 into contribution arising from the effect on each stage-specific vital rate (Caswell, 2000). At this

235 end we used a life table response experiment (LTRE) with a regression designs. The LTRE ap-
236 proximates the change in λ with climate as the product of the sensitivity of λ to the parameters
237 times the sensitivity of the parameters to climate, summed over all parameters (Caswell, 1989):

$$238 \quad \frac{\partial \lambda}{\partial Climate} \approx \sum_i \frac{\partial \lambda}{\partial \theta_i^F} \frac{\partial \theta_i^F}{\partial Climate} + \frac{\partial \lambda}{\partial \theta_i^M} \frac{\partial \theta_i^M}{\partial Climate} \quad (9)$$

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

243 Impact of climate change on niche and range shifts

244 A species' ecological niche can be defined as the range of resources and conditions (physical
245 and environmental) allowing the species to maintain a viable population ($\lambda \geq 1$). To
246 understand the impact of climate change on species niche shifts, we estimated the probability
247 of population viability being greater than 1, $\Pr(\lambda > 1)$ conditional to two environmental
248 axes (Diez et al., 2014). Because the study species is a cool season grass species, we used
249 two environmental axes: (1) temperature and precipitation of the dormant season and (2)
250 temperature and precipitation of the growing season. $\Pr(\lambda > 1)$ was calculated using the
251 proportion of the Markov chain Monte Carlo iterations (here, 300) that lead to a $\lambda > 1$.
252 Population viability-environment relationship was mapped onto geographic layers of three
253 state (Texas, Oklahoma and Kansas) to delineate past, current and future potential distribution
254 of the species. To do so, we estimated $\Pr(\lambda > 1)$ as a function of all climate covariates for
255 each pixel (1km*1km) across the species range using the posterior distribution. Because of
256 amount of the computation involve in the Markov chain Monte Carlo iterations, use only
257 100 posterior samples to estimate $\Pr(\lambda > 1)$ across the Texas, Oklahoma and Kansas.

258 All calculations were processed in parallel using open-source software on the Rice
259 Super computer (NOTS) and the German Centre for Integrative Biodiversity Research (iDiv)
260 High-Performance Computing (HPC) Cluster. [This was achieved by splitting the global point](#)
[occurrence records sent to single computational node.](#)

262 **Results**

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

264 Most vital rates were strongly climate dependent, but the magnitude of their response
265 differed between sexes suggesting a sex-specific demographic response to climate. Survival
266 and flowering were strongly more dependent on climate than growth (number of tillers) and
267 reproduction (number of panicles) (Fig.2; Supporting Information S-5). In addition, we found
268 opposite patterns in the direction of the effect on seasonal climate on the probability of survival
269 and flowering. The growing season (precipitation) has a negative effect on the probability of
270 survival, number of tillers, and the probability of flowering, whereas the dormant season has
271 a positive effect on these vital rates. Unlike precipitation, temperature had different effects on
272 different vital rates. Temperature of the growing season has a positive effect of the probability
273 of survival, a negative effect of the probability of flowering, and the number of tillers, but no
274 significant effect on the number of panicles. Further, there was a female survival and flowering
275 advantage across both climatic seasons (Figures. 3A-3D, 3I-3L). On the contrary, there was
276 a male panicle advantage across all climatic variables (Figure3M-3P). Counter-intuitively, there
277 was no significant sex growth advantage in all season climatic variables (Figures. 3E-3H).
278 Plant size x sex interaction was significant for all vitals rates (Supporting Information S-5). For
279 survival, flowering and reproduction the interaction between temperature and precipitation
280 of the growing season and dormant season was not significant (Supporting Information S-5).
281 However, for growth the interaction between temperature and precipitation of the growing
282 season and dormant season was significantly higher than zero (Supporting Information S-5).

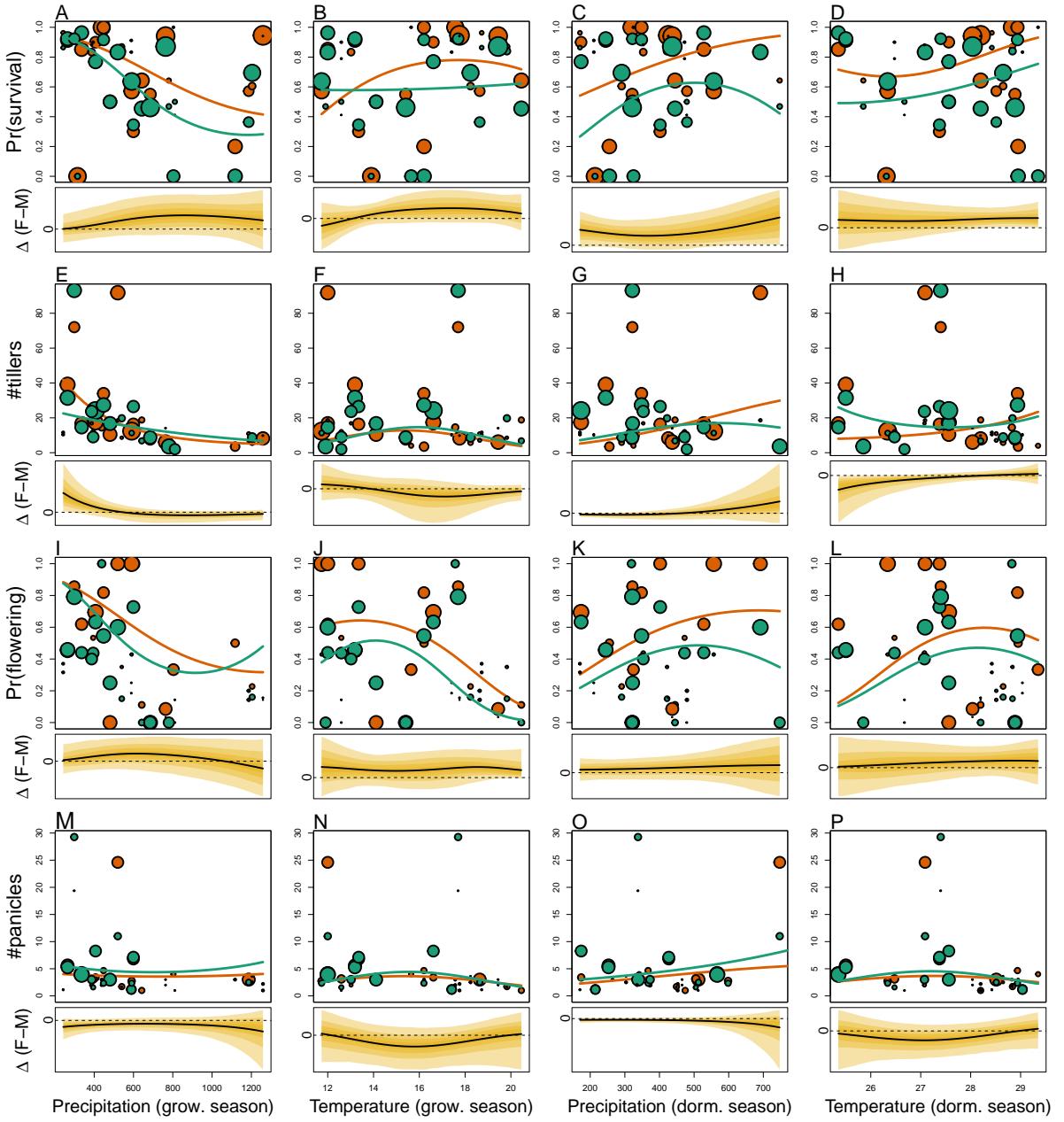


Figure 2: Sex specific demographic response to climate across species range: A–D, inter-annual probability of survival; E–H, inter-annual growth (change in number of tillers); I–L, probability of flowering; M–P, number of panicles produced given flowering. Points show means by site for females (orange) and males (green). Point size is proportional to the sample size of the mean. Lines show fitted statistical models for females (orange) and males (green) based on posterior mean parameter values. Lower panels below each data panel show the posterior distribution of the difference between females and males as a function of climate (positive and negative values indicate female and male advantage, respectively); dashed horizontal line shows zero difference.

283 **Climate change alter population viability**

284 We estimated the predicted response of population growth rate (population fitness) to
285 seasonal climate gradients using a model assuming a female dominant model and another
286 model using the two sexes. Consistent with the effect of climate on the individual vital
287 rate, we found a strong effect of seasonal climate on population fitness (Fig.3). For both
288 models (female dominant and two sexes), population fitness decreased with an increase of
289 precipitation of growing season. In contrast population fitness increased with precipitation
290 of the dormant season. Furthermore, population fitness was maximized between 23 and 17
291 °C and decreases to zero just beyond 32 °C during the growing season. Similarly population
292 fitness was maximized between 13 and 17 °C and decreases to zero just beyond 20 °C during
293 the growing season. We have also detected a strong effect of the past and future climate
294 on population growth rate. However, for future climate, the magnitude of that effect was
295 different between gas-scenario emissions. A moderate emission gas scenario (RCP4.5) has a
296 no effect on the population growth rate while a high emission scenario (RCP8.5) has a strong
297 negative effect on the population growth rate. High-emission scenario (RCP8.5) will lead
298 to an alteration of population viability. Under past climate conditions, population growth
299 rate decreased below one for temperature of the growing season and the dormant season.

300 Population viability was most sensitive to change in temperature of the growing season
301 and temperature of the dormant season. LTRE decomposition reveals that, for each sex, the
302 reduction of lambda for high value of temperature of the growing season (Northern range)
303 was driven by a reduction of survival rate, growth rate, flowering and a reduction in number
304 of panicles. However, the reduction of for higher value of temperature of the dormant season
305 was driven by only the female.

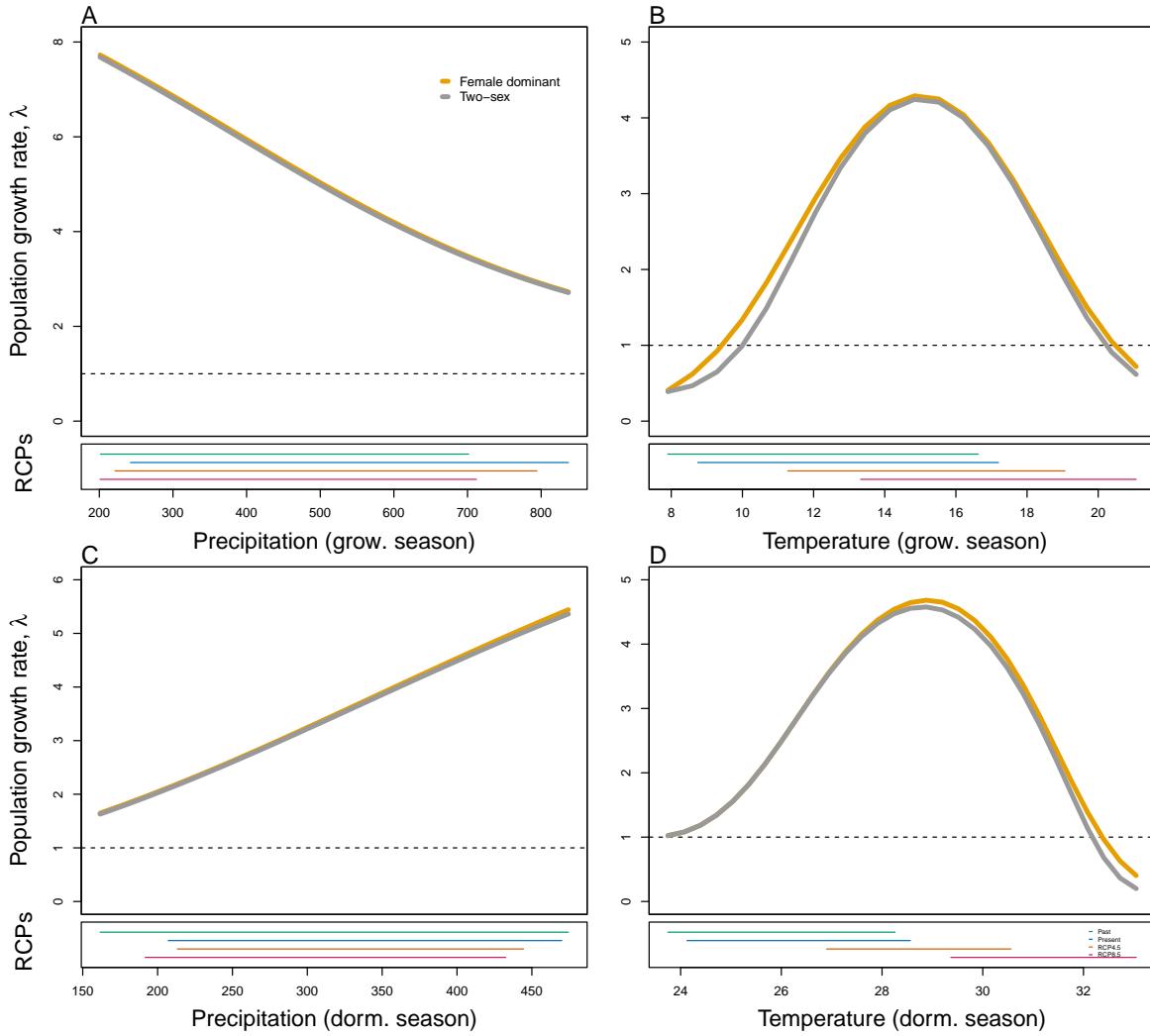


Figure 3: Population growth rate (λ) as a function of climate (past climate, present and predicted future climates). For future climate, we show a Representation Concentration Pathways 4.5 and 8.5. Values of (λ) are derived from the mean climate variables across 4 GCMs. The solid bold curve shows prediction by the two-sex matrix projection model that incorporates sex- specific demographic responses to climate with sex ratio dependent seed fertilization. The bold dashed curve represents the prediction by the female dominant matrix projection model. The dashed horizontal line indicates the limit of population viability ($\lambda = 1$)

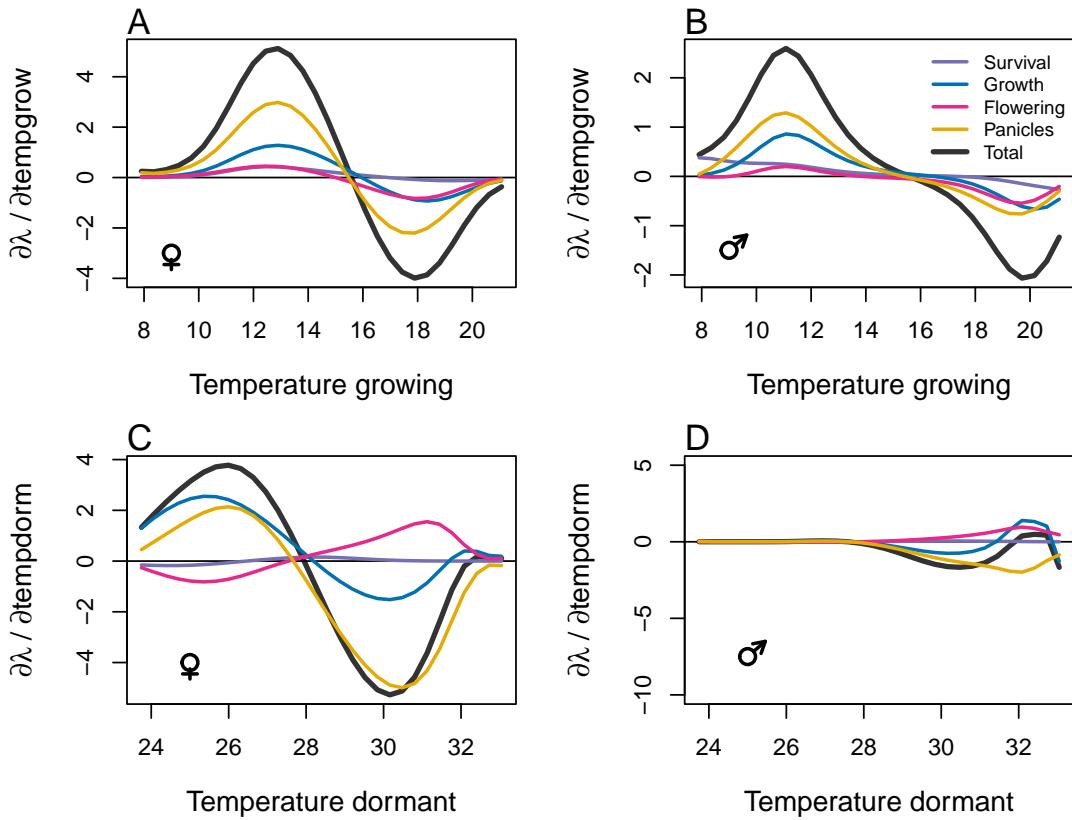


Figure 4: XXX

306 Climatic change induce range shifts

307 Across species niche population persistence was maximized at higher temperature during the
 308 dormant season (27 to 31) and intermediate temperature during the growing season (11 to
 309 20). Our demographically based range predictions broadly captured the known distribution
 310 of the species (Fig. 1). More specifically, the predicted population viable ($\lambda > 1$) matches
 311 the presence and absence of the species. Furthermore, viable populations of *P. arichnifera*
 312 were only predicted at the center of the range for current climatic conditions (Fig1). Future
 313 and past projections of climate change showed a north-west range shift compared to current
 314 distributions. Although *P. arichnifera* was predicted to have suitable habitat in the center of the
 315 range under the current climate, future warming is predicted to reduce much of the suitable
 316 habitat in the southern part (Figure).

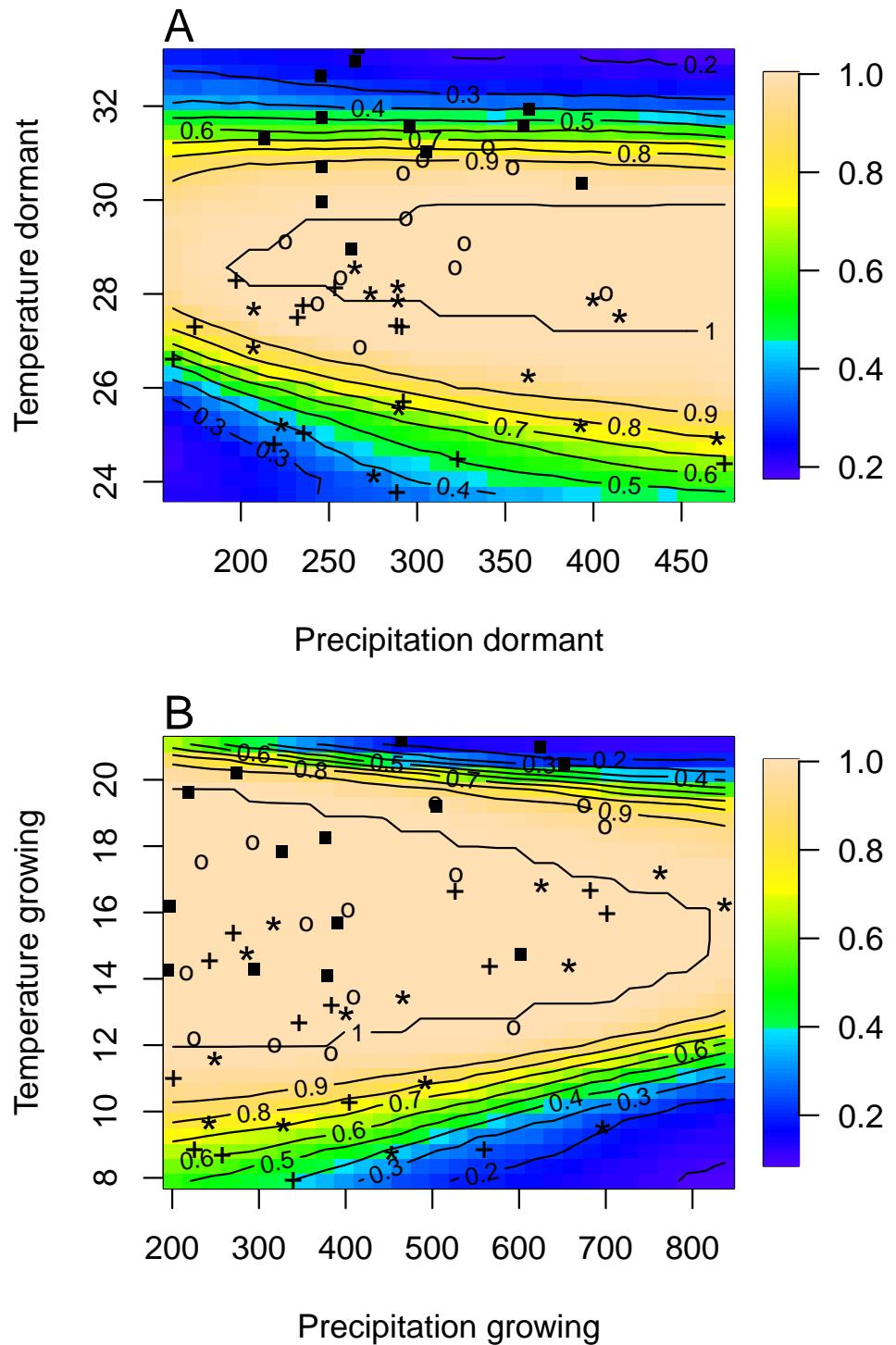


Figure 5: Predicted niche shift for past, present and future climate conditions based on $\text{Pr} (\lambda \geq 1)$. Niche of dormant season (A), Niche of growing season (B). Contours show predicted probabilities of self-sustaining populations $\text{Pr} (\lambda \geq 1)$ conditional on precipitation and temperature of the dormant and growing season."+" Past, "*" Current,"o" RCP 45,"." RCP 85

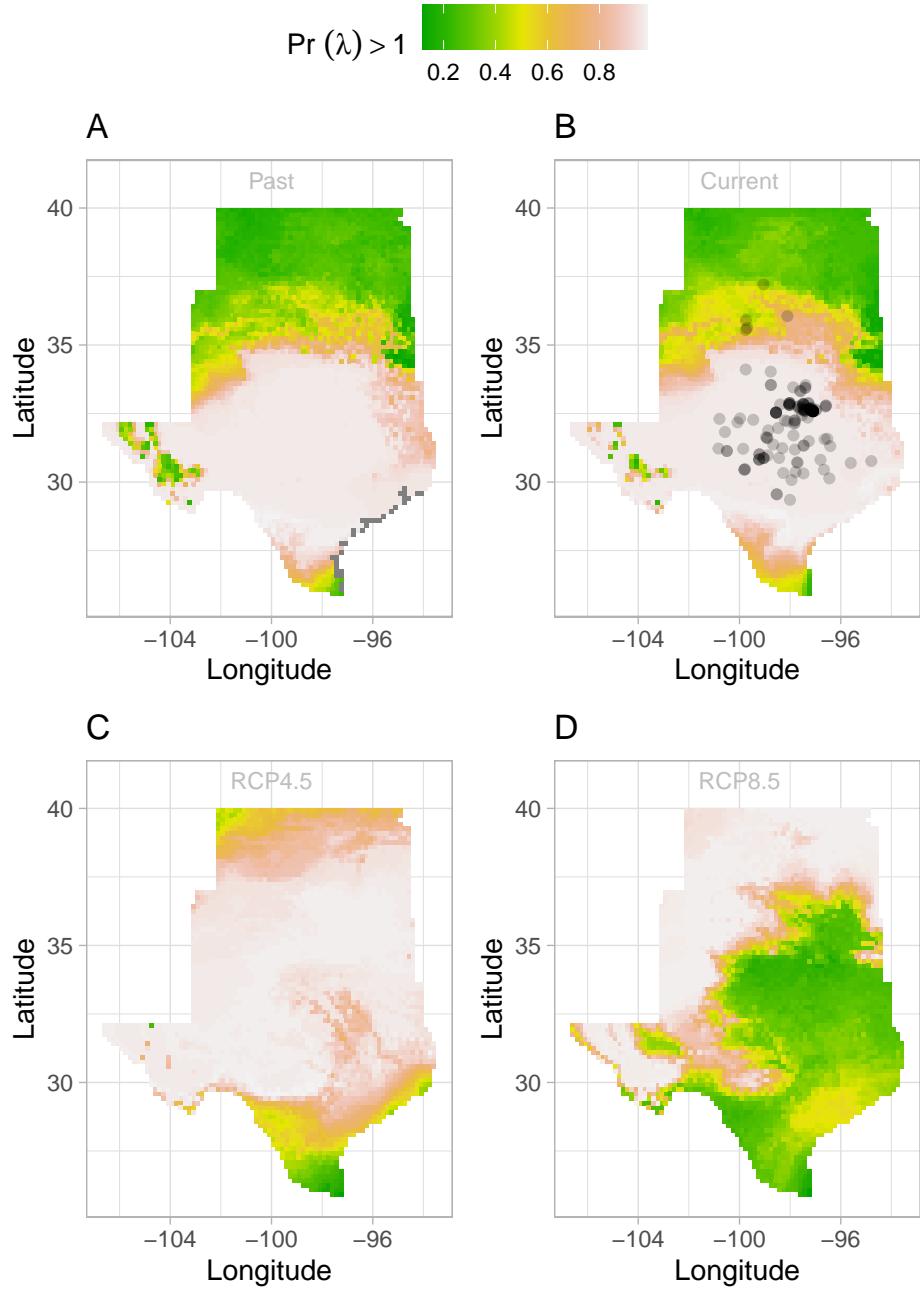


Figure 6: Past (A), Current (B), Future (2070–20100) (C and D) predicted range shift based on population growth rate using the two sex model. Future projections were based on MIROC. The black circles on panel B indicate all known presence points collected from GBIF from 1990 to 2019, which corresponds to the current condition in our prediction. The occurrences of GBIFs are distributed in with higher population fitness habitat ($\lambda > 1$), confirming that our study approach can reasonably predict range shifts.

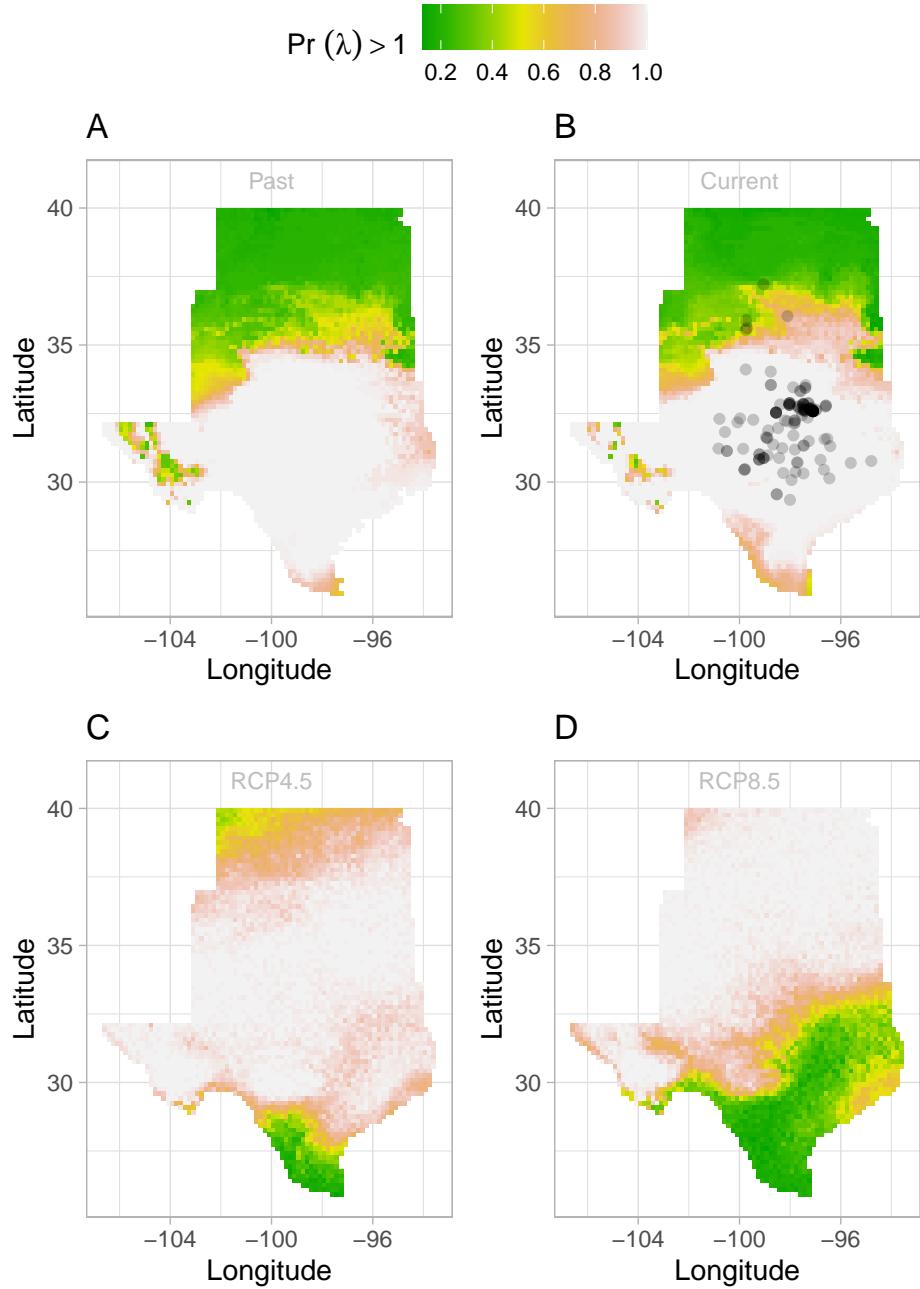


Figure 7: Past (A), Current (B), Future (2070–20100) (C and D) predicted range shift based on population growth rate using the female dominant model. Future projections were based on the average population growth rate in four GCMs. The black circles on panel B indicate all known presence points collected from GBIF from 1990 to 2019, which corresponds to the current condition in our prediction. The occurrences of GBIFs are distributed in with higher population fitness habitat ($\lambda > 1$), confirming that our study approach can reasonably predict range shifts.

317 **Discussion**

318 Three general patterns emerged from our analysis. First, our Bayesian mixed effect model
319 predicts that seasonal climate (temperature and precipitation) affects sex-demographic
320 processes in distinctive and contrasting ways. While climate has a significant effect on the
321 probability of survival and growth, it has no effect on the number of panicles. Second, future
322 climate, by increasing seasonal temperature, will lead to decline in population viability and
323 favor range shifts. Third, using only one sex to forecast range shifts of dioecious under climate
324 change could lead to an underestimation of the impact of climate change on species.

325 Our results indicate a sex-specific demographic response to climate change. Females
326 have higher survival rate and fertility rate than males. This result is not unique to our study
327 system and has been observed in a range of abiotic pollen dispersal species across climatic
328 gradients (Sasaki et al., 2019; Welbergen et al., 2008; Zhao et al., 2012). Several hypotheses
329 could explain the observed demographic advantage of females over males for survival and
330 flowering and the opposite for growth and number of panicles. First, the trade-off between
331 fitness traits (survival, growth, fertility) due to resource limitation could explain such a result
332 (Cipollini and Whigham, 1994; Freeman et al., 1976). For most species, females often pay more
333 for reproduction than males due to the requirement to develop seeds and fruits. However,
334 several studies reported a higher cost of reproduction for males in wind pollinated species
335 due to the larger amounts of pollen they produce (Bruijning et al., 2017; Bürli et al., 2022;
336 Cipollini and Whigham, 1994; Field et al., 2013; Hultine et al., 2016).

337 Under current conditions, most populations across the range are viable. This result could
338 be explained by two hypotheses. First, demographic compensation whereby an increase of one
339 vital rate is coupled with a decrease of another vital rate could explain a viable population in
340 harsh conditions at the range edge (Doak and Morris, 2010; Villegas et al., 2015). In our system,
341 a decrease in fertility survival rate was counterbalanced by an increase in survival rate, pre-
342 venting the population growth rate from declining even at range edge for the growing season.
343 Second, local adaptation at the edge of the range explains the viable population throughout the
344 range (Miller and Compagnoni, 2022b). Our study was based on a common garden experiment;
345 therefore, individuals planted in climatic conditions that are similar to their source populations
346 climatic conditions suffer less from stressful environmental conditions. The question to ask is
347 whether the local population could help the population at the edge to buffer against climate.
348 Unfortunately, our model does not shed light on the role of local adaptation in species response
349 to climate change. Moreover, our future projections require extrapolation to warmer or colder
350 conditions than observed in our experiment and subsequently should be interpreted with cau-
351 tion. Despite this limitation, our model did well in predicting the suitable area for the species.

Projected future climate by inducing an increase in seasonal temperature will affect population viability. Temperature can impact plant populations through different mechanisms. Increasing temperature could increase evaporative demand, affect plant phenology and germination rate. The potential for temperature to influence these different processes changes seasonally (Körner, 2006). In the summer growing season, when the temperature is high, the effect on the water balance should be strong. In the dormant season, when evaporative demand is low, temperature should have a more important effect on phenology and germination. Because our study species was sensitive to temperatures in the growing season, the former mechanism deserve further attention.

The reduction in population viability across the range due to climate change will drive a shift to the north range in suitable habitat for the species.

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Supporting Information

501 S.1 XX

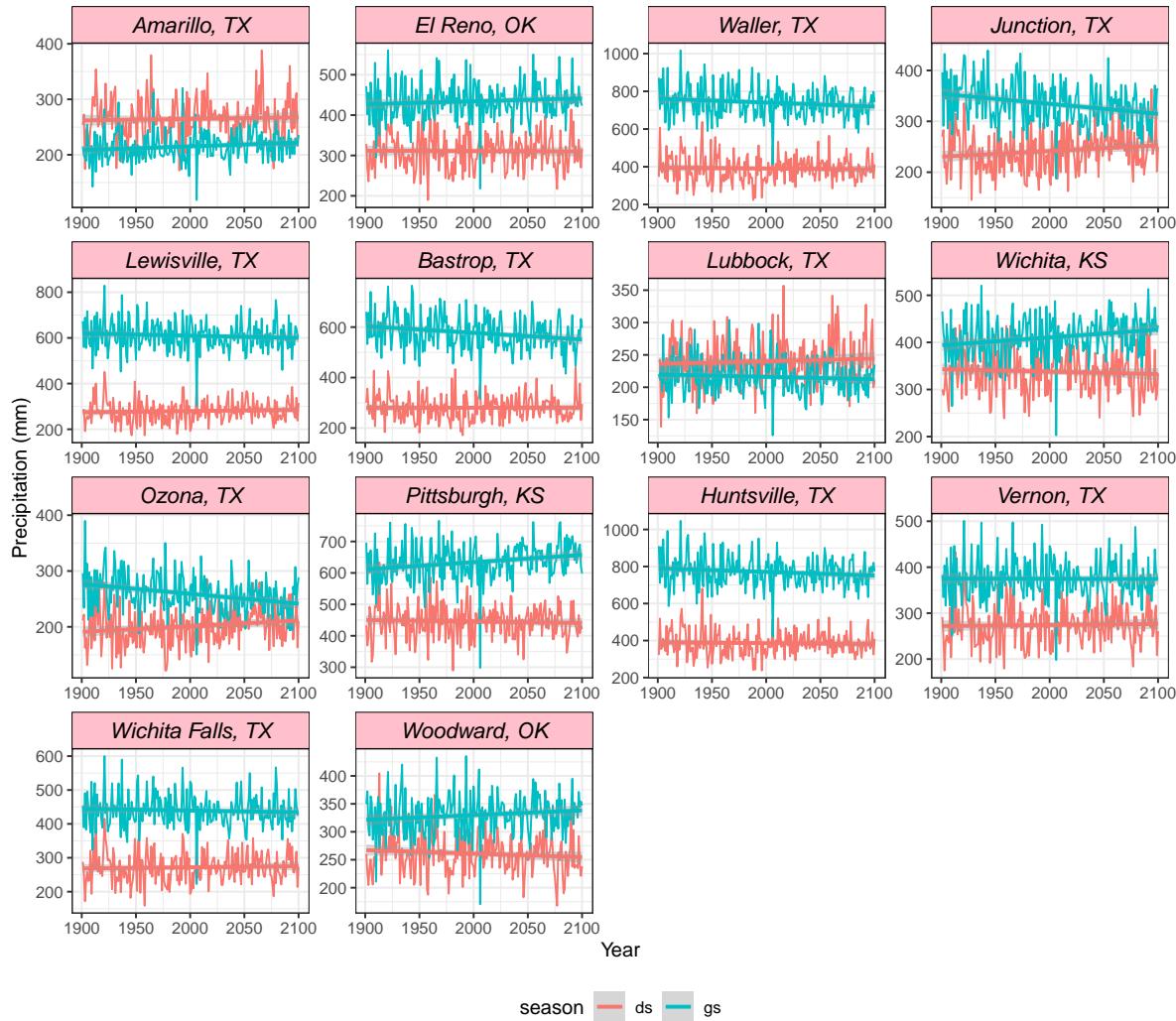


Figure S-1: Precipitation variation accross the study sites from 1990 to 2100

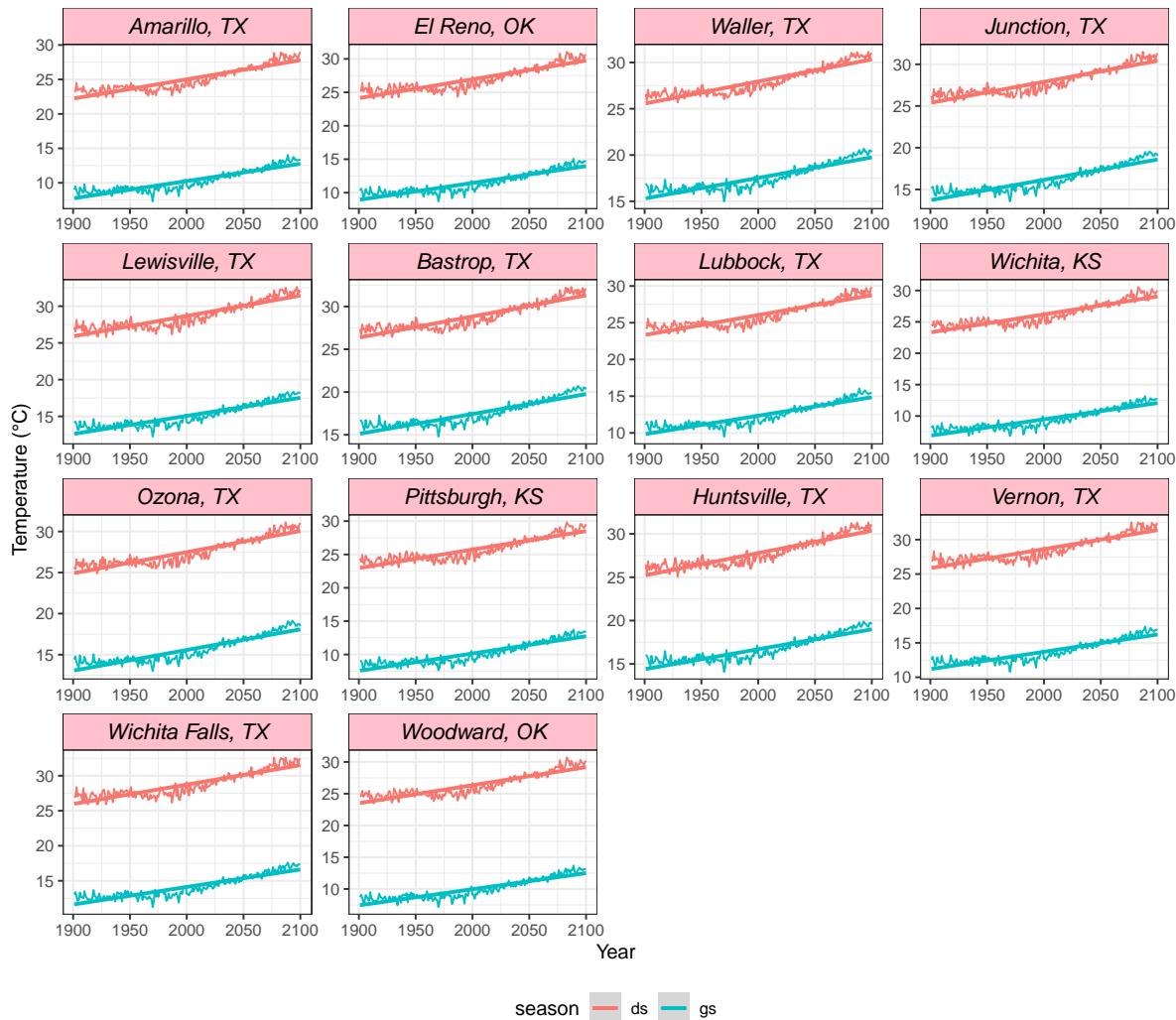


Figure S-2: Temperature variation accross the study sites from 1990 to 2100

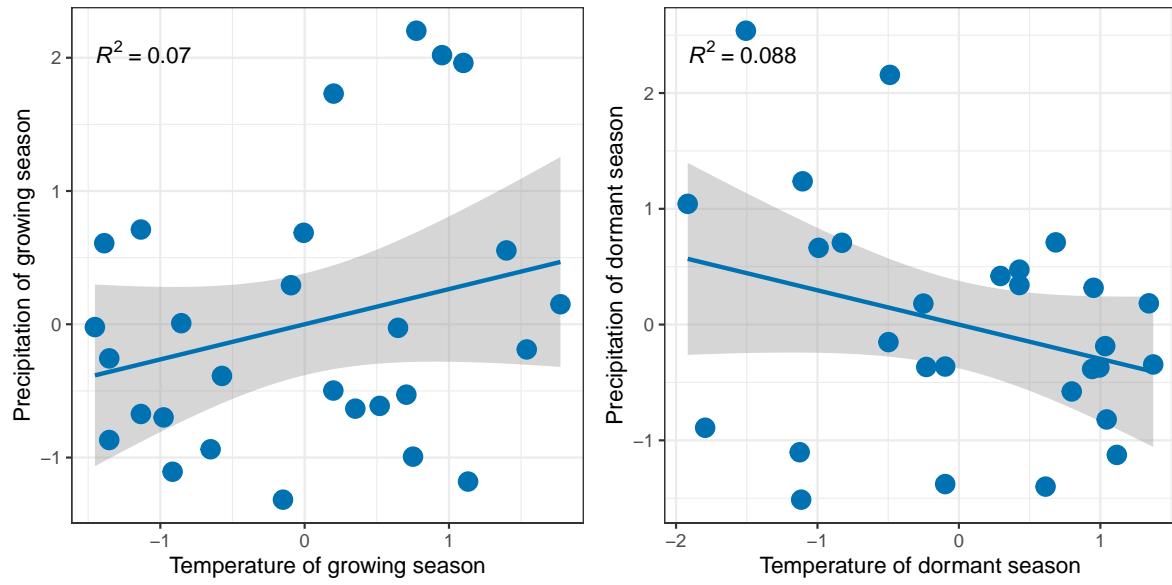


Figure S-3: Relation between precipitation and temperature for each season (growing and dormant). R^2 indicates the value of proportion of explained variance between the temperature and precipitation

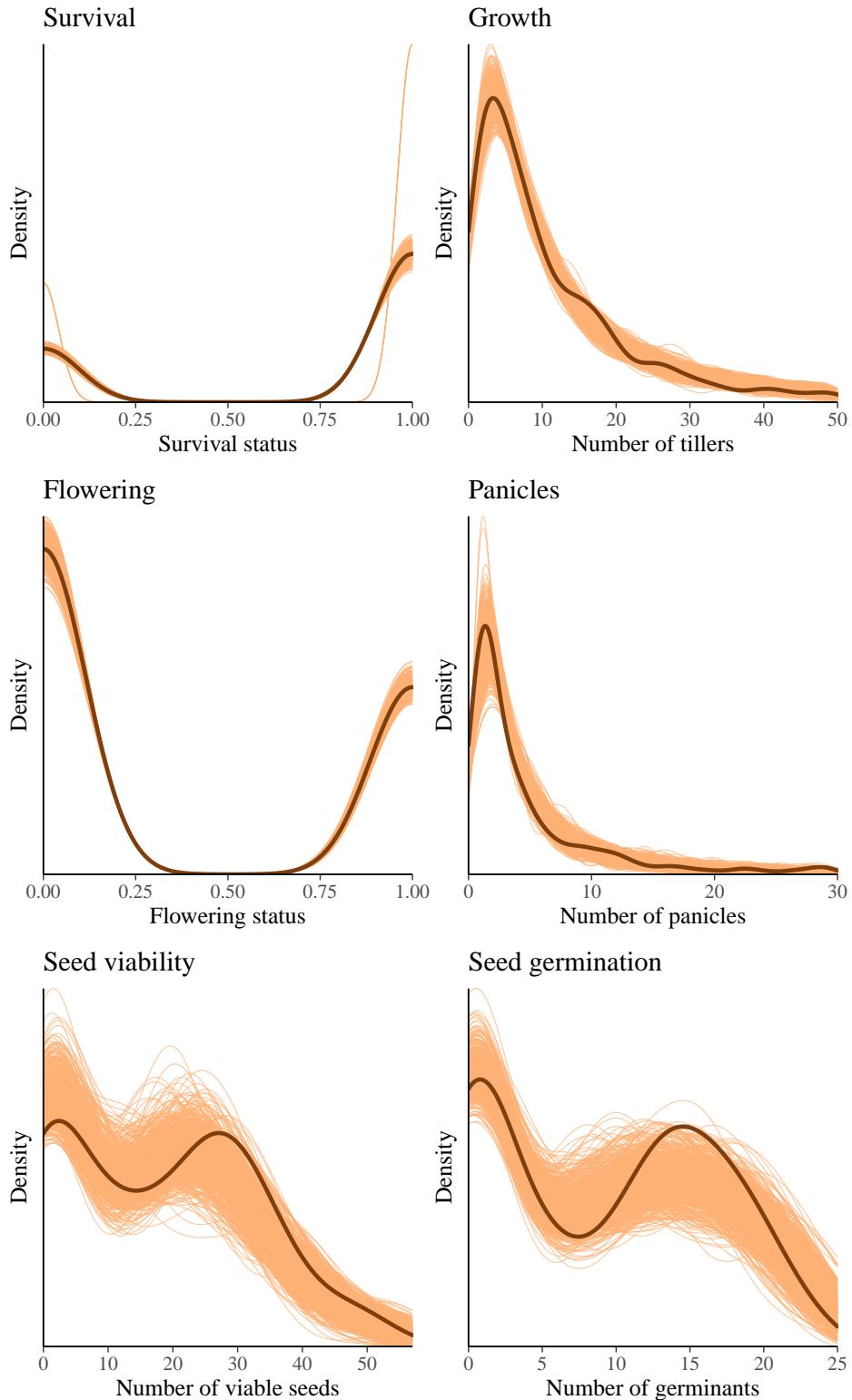


Figure S-4: Consistency between real data and simulated values suggests that the fitted model accurately describes the data. Graph shows density curves for the observed data (light blue) along with the simulated values (dark blue). The first column shows the linear models and the second column shows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

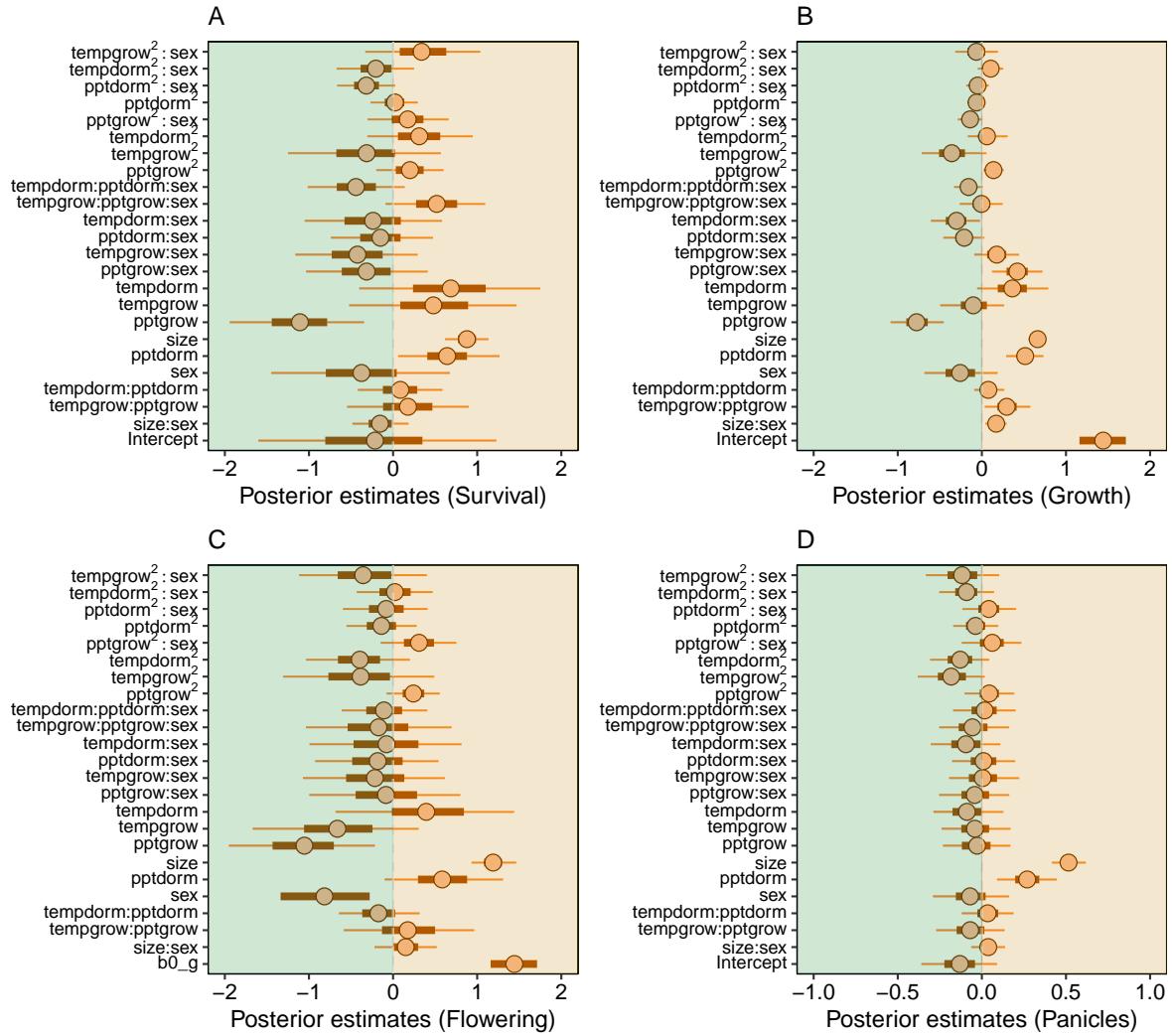


Figure S-5: Mean parameter values and 95% credible intervals for all vital rates.

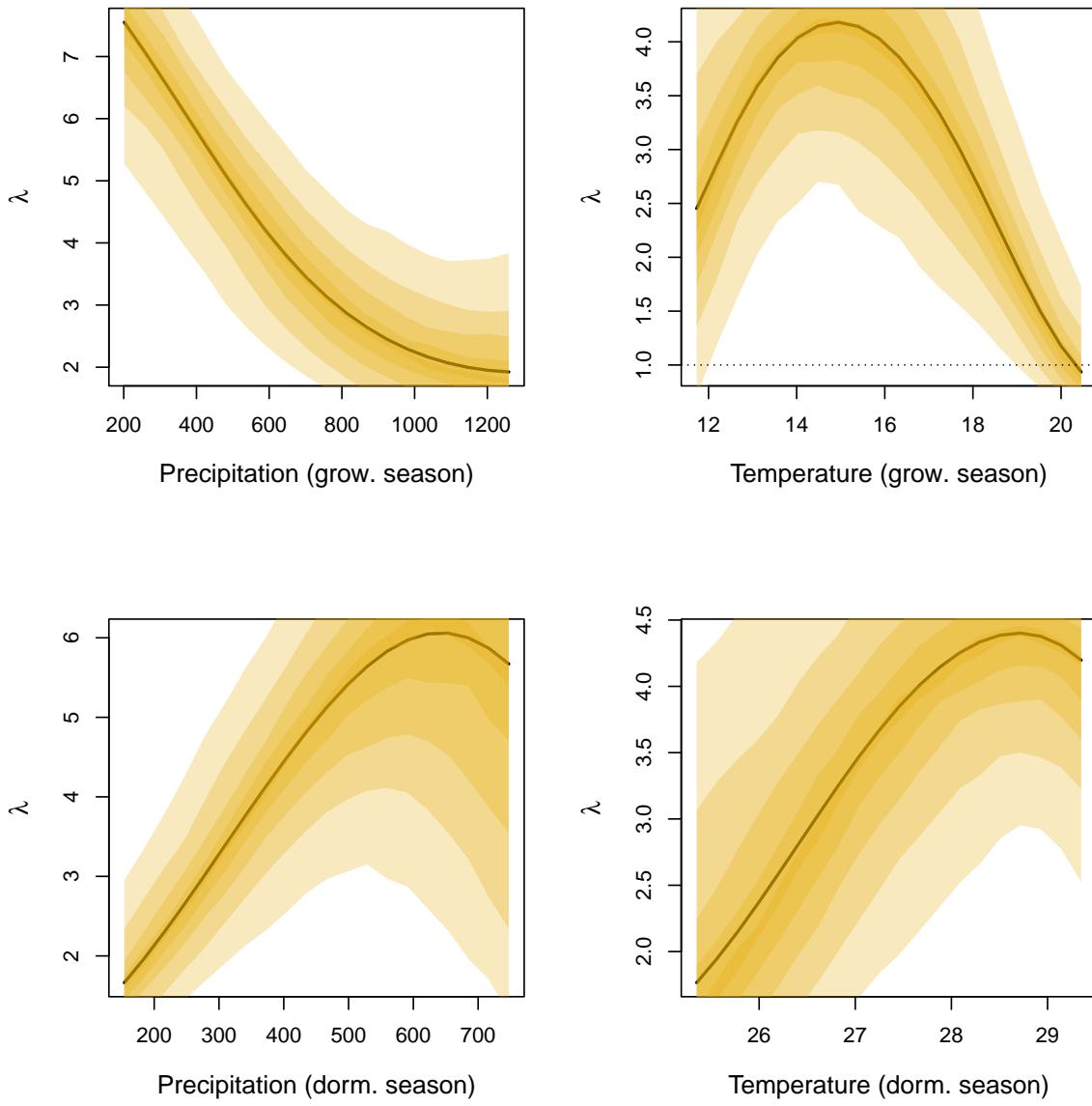


Figure S-6: Population growth rate (λ) as a function of seasonal climate (2016-2017), predicted by the two-sex matrix projection model that incorporates sex-specific demographic responses to climate with sex ratio-dependent seed fertilization. We show the mean posterior distribution of λ in solid lines, and the 5, 25, 50, 75, and 95% percentiles of parameter uncertainty in shaded gold color. The dashed horizontal line indicates the limit of population viability ($\lambda = 1$)

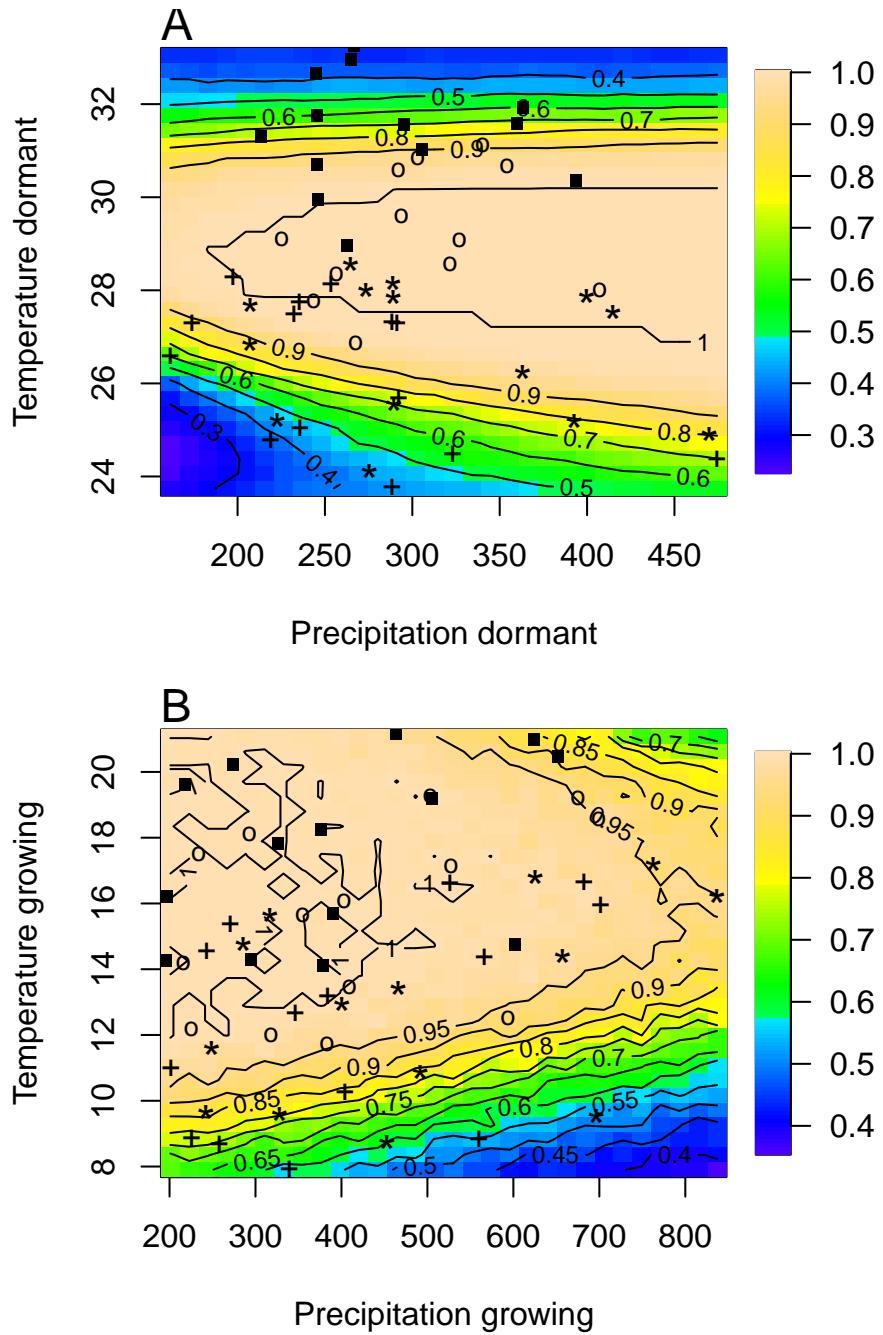


Figure S-7: Predicted niche shift for past, present and future climate conditions based on $\text{Pr} (\lambda \geq 1)$. Niche of dormant season (A), Niche of growing season (B). Contours show predicted probabilities of self-sustaining populations $\text{Pr} (\lambda \geq 1)$ conditional on precipitation and temperature of the dormant and growing season. "+" Past, "*" Current, "o" RCP 45, " ." RCP 85

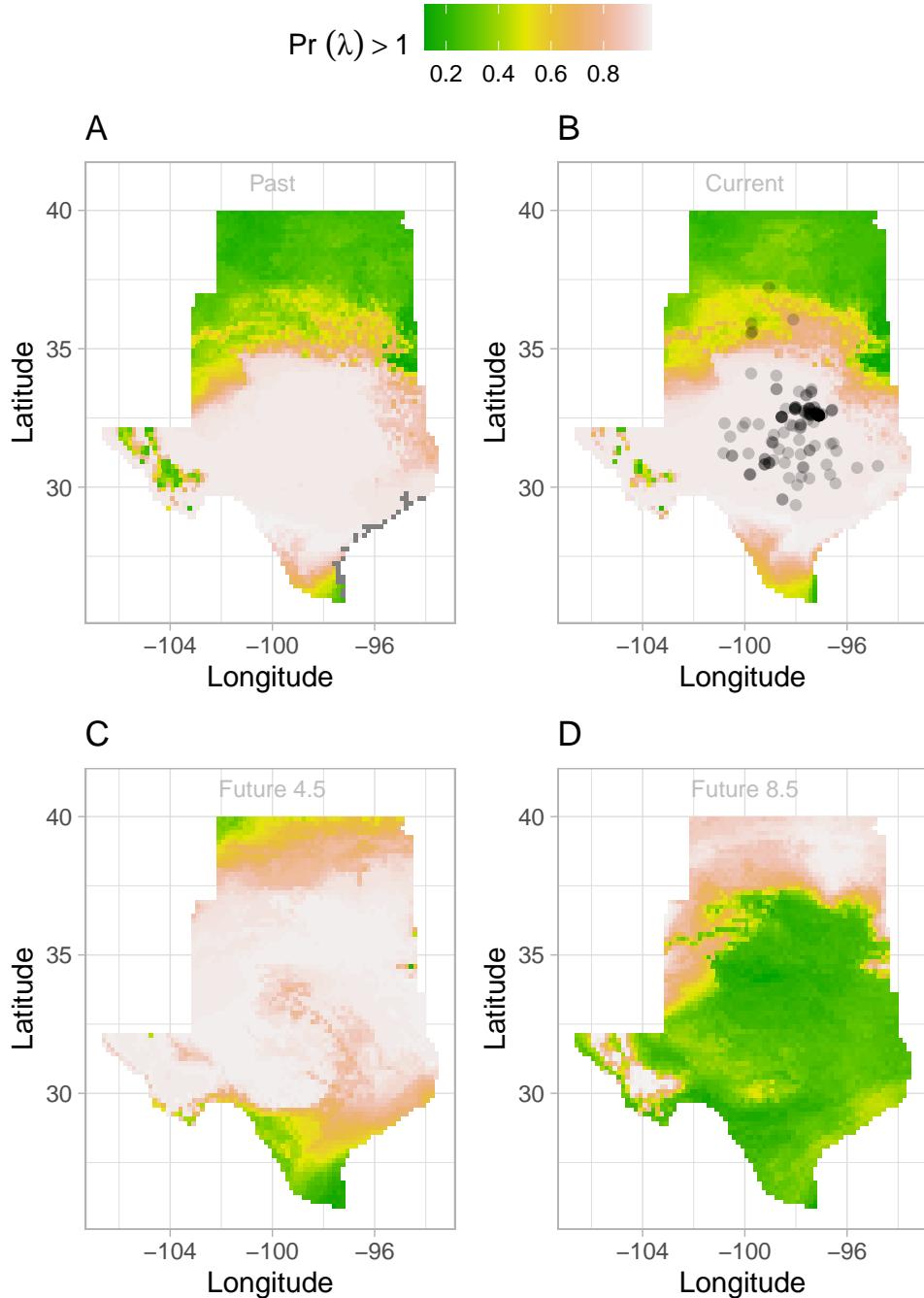


Figure S-8: Past (A), Current (B), Future CMCM (2070–20100) (C and D) predicted range shift based on population growth rate. Future projections were based on the average population growth rate in four GCMs. The black circles on panel B indicate all known presence points collected from GBIF from 1990 to 2019, which corresponds to the current condition in our prediction. The occurrences of GBIFs are distributed in with higher population fitness habitat ($\lambda > 1$), confirming that our study approach can reasonably predict range shifts.

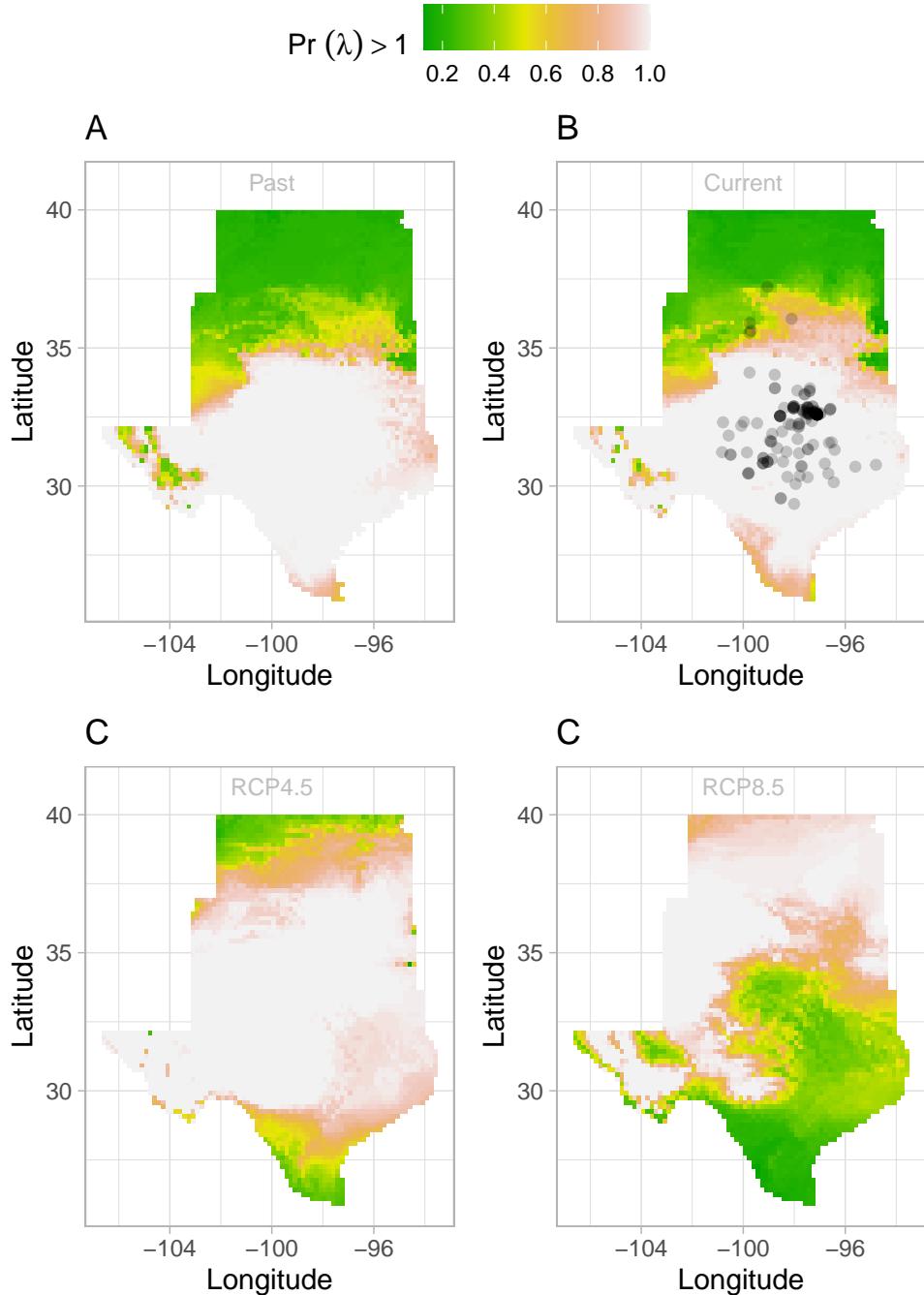


Figure S-9: Past (A), Current (B), Future ACCESS (2070–20100) (C and D) predicted range shift based on population growth rate suing the female dominat model. Future projections were based on the average population growth rate in four GCMs. The black circles on panel B indicate all known presence points collected from GBIF from 1990 to 2019, which corresponds to the current condition in our prediction. The occurrences of GBIFs are distributed inwith higher population fitness habitat ($\lambda > 1$) , confirming that our study approach can reasonably predict range shifts.

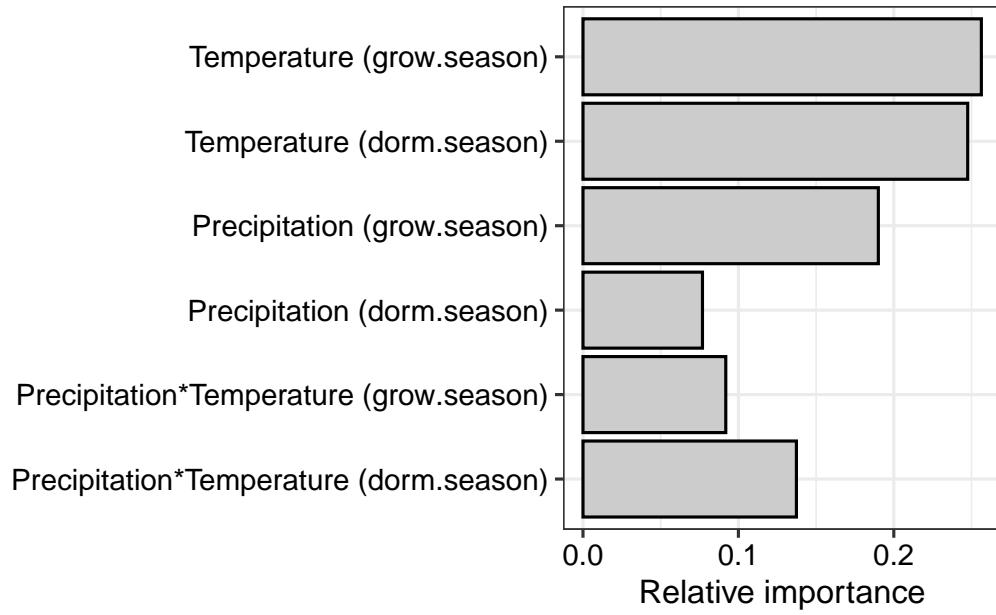


Figure S-10: XXX

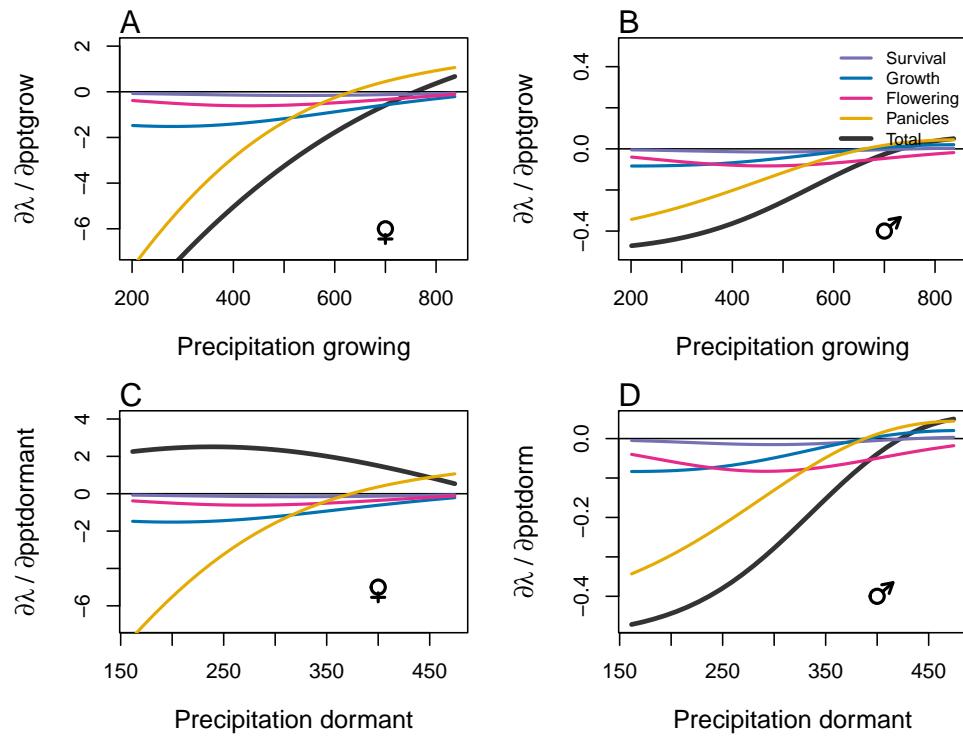


Figure S-11: XXX