

Forecasting range shifts of a dioecious plant species under climate change

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

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

²Institute
of Biology, Martin Luther University Halle-Wittenberg, Halle, Germany; and
German Centre for Integrative Biodiversity Research (iDiv), Leipzig, Germany

Running header: Forecasting range shifts

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

Submitted to: *Ecology letters* (Letter)

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

Conflict of interest statement: None.

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

Abstract:

Main Text:

Figures: 6

Tables: 0

References: 106

^{*}Corresponding author: jmoutouama@gmail.com

Abstract

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

Introduction

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

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

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

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

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

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

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

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

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

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

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

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

Materials and methods

Study species and climate context

Texas bluegrass (*Poa arachnifera*) is a dioecious perennial, summer-dormant cool-season (C3) grass that occurs in the south-central U.S. (Texas, Oklahoma, and southern Kansas) (Figure 1) (Hitchcock, 1971)^{6,7} **Latitudinal limits of the Texas bluegrass distribution span 7.74 °C to 16.94**

⁵Please improve the legend for these figures.

⁶I have updated the map

⁷I think the GBIF records greatly underestimate the distribution, especially in Oklahoma. Compare this to the county records map in the Am Nat paper. I am not sure how that happens—I assumed that GBIF would be pulling all those county records.

°C of temperature during the dormant season and 24.38 °C to 28.80 °C during the dormant season. Longitudinal limits span 244.9 mm to 901.5 mm of precipitation during the growing season and 156.3 mm to 373.3 mm.⁸

Texas bluegrass grows between October and May, flowers in spring, and goes dormant during the hot summer months of June to September (Kindiger, 2004). Following this life history, we divide the calendar year into growing (October 1 - May 31) and dormant (June 1 - September 30) seasons. Biological sex is genetically based and the birth (seed) sex ratio is 1:1 (Renganayaki et al., 2005). Females and males are morphologically indistinguishable except for their inflorescences. Like all grasses, this species is wind pollinated (Hitchcock, 1971) and most male-female pollen transfer occurs within 10-15m (Compagnoni et al., 2017). Surveys of 22 natural populations throughout the species' distribution indicated that operational sex ratio (the female fraction of inflorescences) ranged from 0.007 to 0.986 with a mean of 0.404 (Miller and Compagnoni, 2022b).

Common garden experiment

Experimental design

We conducted a range-wide common garden experiment to quantify sex-specific demographic responses to climate variation. Details of the experimental design are provided in Miller and Compagnoni (2022b); we provide a brief overview here. The experiment was installed at 14 sites throughout and, in some cases, beyond the natural range of Texas bluegrass that sampled a broad range of temperature and precipitation (Figure 1).⁹ At each site, we established 14 blocks. For each block we planted three female and three male individuals that were clonally propagated from females and males from eight natural source populations (Figure 1); because sex is genetically-based, clones never deviated from their expected sex. The experiment was established in November 2013 with a total of # female and # male plants¹⁰, and was censused in May of 2014, 2015, and 2016. At each census, we collected data on survival, size (number of tillers), and number of panicles (reproductive inflorescences). For the analyses that follow, we focus on the 2014-15 and 2015-16 transitions years, since the start of the experiment did not include the full 2013-14 transition year.

⁸ Rather than just describe climate, this would be a good place to say more about climate change. For example, summer temperatures have increased by XX-XX degrees C since 1900, and climate models predict another XX-XX degrees of warming by 2100. Compare summer warming to winter warming, and compare temperature change to precipitation change. All of this sets the stage for why this is an important system to forecast climate change responses.

⁹ A few comments about figure 1 (I cannot comment in the legend). Please update the gray diamonds as GBIF occurrences, not natural population surveys. Please add "mm" and "°C" to the titles. It would also be good to spell out "growing" and "dormant" seasons.

¹⁰ Add numbers.

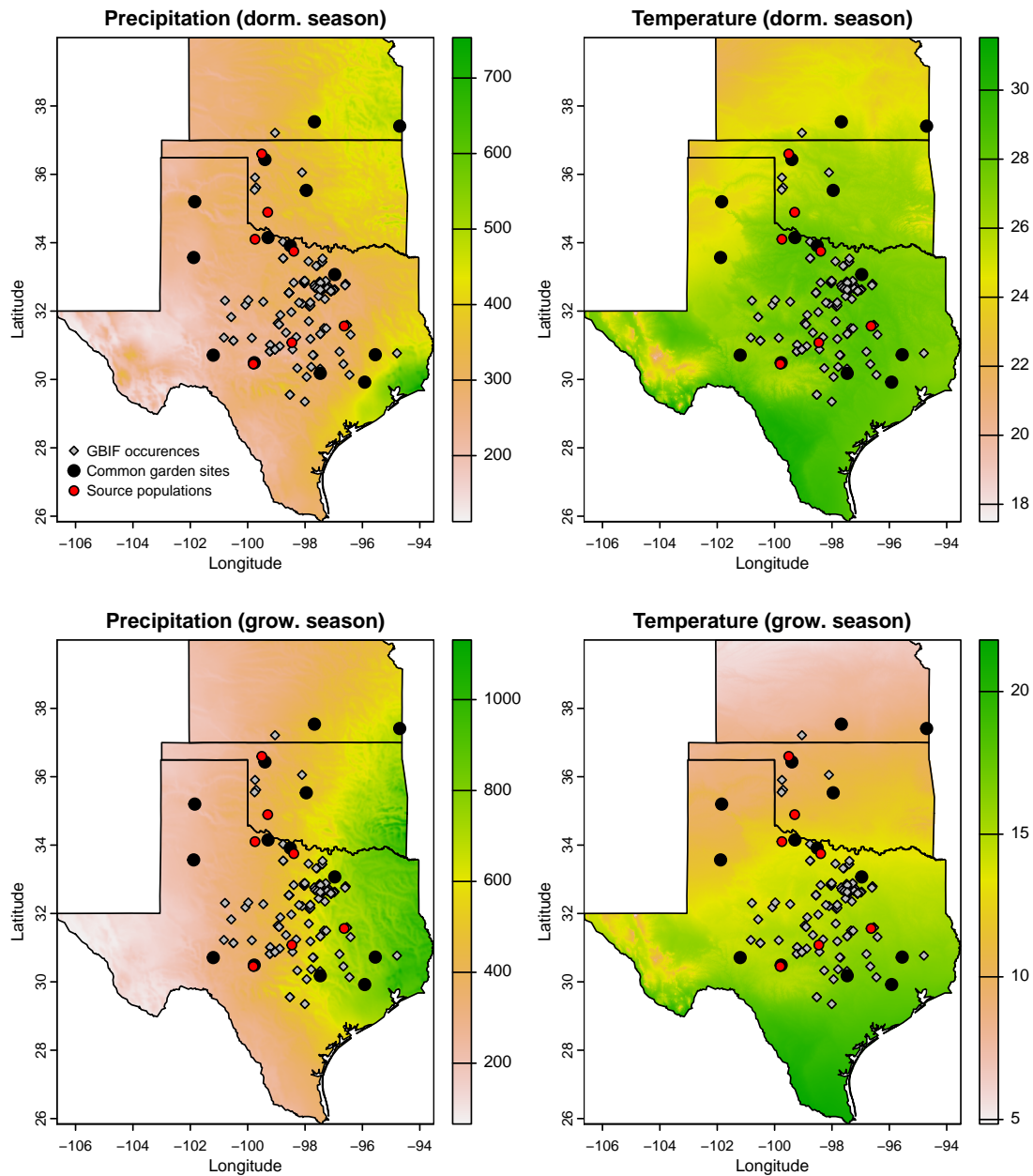


Figure 1: Maps of 30-year (1990-2019) climate normals and study sites used for demographic monitoring of *Poa arachnifera* in Texas, Kansas and Oklahoma in the United States. Precipitation is in mm and temperature is in °C. We surveyed 22 natural populations (grey diamond). The common garden sites were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

Climatic data collection

We gathered downscaled monthly temperature and precipitation for each site from Chelsea to describe observed climate conditions during our study period (Karger et al., 2017). These

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

Projection data for the three 30-year periods included warmer or colder conditions than observed in our experiment, so extending our inferences to these conditions required some extrapolation, as we describe below. However, across all sites, both study years were 2-3°C warmer than their corresponding 1990–2019 temperature normals (Fig. S-8). Additionally, the 2014–15 growing season was substantially wetter and cooler across the study region than 2015–16 (Fig. S-7). Thus, the geographic and inter-annual replication of the common garden experiment provided good coverage of most past, present, and future conditions throughout the study region (Fig. S-3, Fig. S-4, Fig. S-5, Fig. S-6).

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

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

rate models were fit with the same linear predictors for the expected value (μ)(Eq.1):

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

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

A different link function ($f(\mu)$) was applied depending on the the vital rate distributions. 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 conditional on flowering) was modeled as zero-truncated negative binomial. We used generic, weakly informative priors to fit coefficients for survival, growth, flowering models ($\beta \sim N(0, 1.5)$) and random effect variances ($\sigma \sim Gamma(\gamma(0.1, 0.1))$). **We fit fertility model with regularizing priors for coefficients ($\mu = 0, \sigma = 0.15$).**¹¹

Sex ratio responses to climatic variation across common garden sites

¹² We also used the experimental data to investigate how climatic variation across the range influenced sex ratio and operational sex ratio of the common garden populations. To understand the impact of climate change on sex ratio, we used two methods. First, we developed eight Bayesian linear models using data collected during three years. Each model had OSR or SR as response variable and a climate variable as predictor (Eq.2).

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

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

¹¹I think you need to explain a little more about why fertility was handled differently and what you mean by regularizing.

¹²This section will need to be updated with the new model.

Model-fitting procedures

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

Two-sex and female-dominant matrix projection models

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

Let $F_{x,t}$ and $M_{x,t}$ be the number of female and male plants of size x in year t , where $x \in [1, \dots, U]$. The minimum possible size is one tiller and U is the 95th percentile of observed maximum size (# tillers)¹³. Let F_t^R and M_t^R be new female and male recruits in year t , which we treat as distinct from the rest of the size distribution because we assume they do not reproduce in their first year, consistent with our observations. For a pre-breeding census, the expected numbers of recruits in year $t+1$ is given by:

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

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

where p^F and c^F are flowering probability and panicle production for females of size x , d is the number of seeds per female panicle, v is the probability that a seed is fertilized, m is the probability that a fertilized seed germinates, and ρ is the primary sex ratio (proportion of recruits that are female), which we assume to be 0.5¹⁴.

In the two-sex model, seed fertilization is a function of population structure, allowing for feedback between vital rates and operational sex ratio (OSR). In the context of the model, OSR

¹³Give this number.

¹⁴I believe we can cite this - check the Am Nat paper.

is defined as the fraction of panicles that are female and is derived from the $U \times 1$ vectors \mathbf{F}_t and \mathbf{M}_t :

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

The summations tally the total number of female and male panicles over the size distribution, giving the fraction of total panicles that are female. We focus on the female fraction of panicles and not female fraction of reproductive individuals because panicle number can vary widely depending on size; we assume that few males with many panicles vs. many males with few panicles are interchangeable pollination environments. Eq. 5 has the properties that seed fertilization is maximized at v_0 as OSR approaches 100% male, goes to zero as OSR approaches 100% female, and parameter α controls how female seed viability declines as male panicles become rare. We estimated these parameters using data from a sex ratio manipulation experiment, conducted in the center of the range, in which seed fertilization was measured in plots of varying OSR; this experiment is described elsewhere (Compagnoni et al., 2017) and is summarized in [Supplementary Method S.2](#)¹⁵. This experiment also provided estimates for seed number per panicle (d) and germination rate (m). Lacking data on climate-dependence, we assume that seed fertilization, seed number, and germination rate do not vary with climate.

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

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

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

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

¹⁵I think the supplement should also include a data figure showing the fit of the model to the experimental data.

growing from sizes x to y , respectively, and superscripts indicate that these functions may be unique to females (F) and males (M).

The model described above yields a $2(U+1) \times 2(U+1)$ transition matrix. We estimated the population growth rate λ of the female dominant model as the leading eigenvalue of the transition matrix. Since the two-sex MPM is nonlinear (matrix elements affect and are affected by population structure) we estimated λ and stable sex ratio (female fraction of all individuals) and operational sex ratio (female fraction of panicles) by numerical simulation. Since all parameters were estimated using MCMC sampling, we were able to propagate the uncertainty in our estimates of the vital rate parameters to uncertainty in λ . Furthermore, by sampling over distributions associated with site, block, and source population variance terms, we are able to incorporate process error into the total uncertainty in λ , in addition to the uncertainty that arises from imperfect knowledge of the parameter values. For example, sampling over site and block variances accounts for regional and local spatial heterogeneity that is not explained by climate, and sampling over source population variance accounts for genetically-based demographic differences across the species' range.¹⁶

Life Table Response Experiments

We conducted two types of Life Table Response Experiments (LTRE) to isolate contributions of climate variables and sex-specific vital rates to variation in λ . First, to identify which aspect of climate is most important for population viability, we used an LTRE based on a nonparametric model for the dependence of λ on parameters associated with seasonal temperature and precipitation (Ellner et al., 2016). To do so, we used the RandomForest package to fit a regression model with four climatic variables (temperature of growing season, precipitation of growing season, temperature of the dormant season and precipitation of the dormant season) as predictors and λ ¹⁷ as response (Liaw et al., 2002). The regression model allowed the estimation of the relative importance of each predictor. The importance is measured by asking: how wrongly is λ predicted if we replaced the focal predictor (e.g., temperature of growing season) by a random value of the other predictors.¹⁸

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

¹⁶*I just want to confirm that this is actually what you did.*

¹⁷*Is this lambda from the female-dominant or two-sex model? Does it matter?*

¹⁸*I do not understand this.*

(Caswell, 1989, 2000). This LTRE decomposes the sensitivity of λ to climate according to:

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

where, θ_i^F and θ_i^M represent sex-specific parameters (the regression coefficients of the vital rate functions). Because LTRE contributions are additive, we summed across vital rates to compare the total contributions of female and male parameters.¹⁹²⁰

Population viability across the climatic niche and geographic range

To understand how climate shapes the niche and geographic range of Texas bluegrass, we estimated the probability of self-sustaining populations, which is $\Pr(\lambda \geq 1)$ conditional to temperature and precipitation of the dormant and growing seasons. $\Pr(\lambda > 1)$ was calculated for the two-sex model and the female dominant MPMs using the proportion of the 300 posterior samples that lead to a $\lambda \geq 1$ (Diez et al., 2014). Population viability in climate niche space was then represented as a contour plot with values of $\Pr(\lambda > 1)$ at given temperature and precipitation for the growing season, holding dormant season climate constant, and vice versa. We also visualized how our common garden sites have moved and are expected to move through climate space through time due to climate change.

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

To compare the probability of self-sustaining populations between the female dominant and the two-sex model, we used a zero-inflated beta model in brms (Bürkner, 2017).²¹

¹⁹ θ_i^F and θ_i^M include the interaction and second order effect. I think we are good with this formula

²⁰I do not agree. It is true that you can compute this, but only by “turning off” the interaction by holding the interacting variable constant. I still think this needs to be better addressed in both LTRE analyses.

²¹This just floats here without much context. Not sure we need it, but I am flagging for now and will come back to this after reading the results.

Results

Sex specific demographic response to climatic gradient

We found strong demographic responses to climate drivers across our Texas bluegrass common garden sites and evidence for demographic differences between the sexes.²²

²²*I am skipping the rest of this section for now because I think the figure needs to be re-worked and that will change the rest of this paragraph. I also think this section should include the common garden sex ratio results, since they are connected to the vital rate responses.*

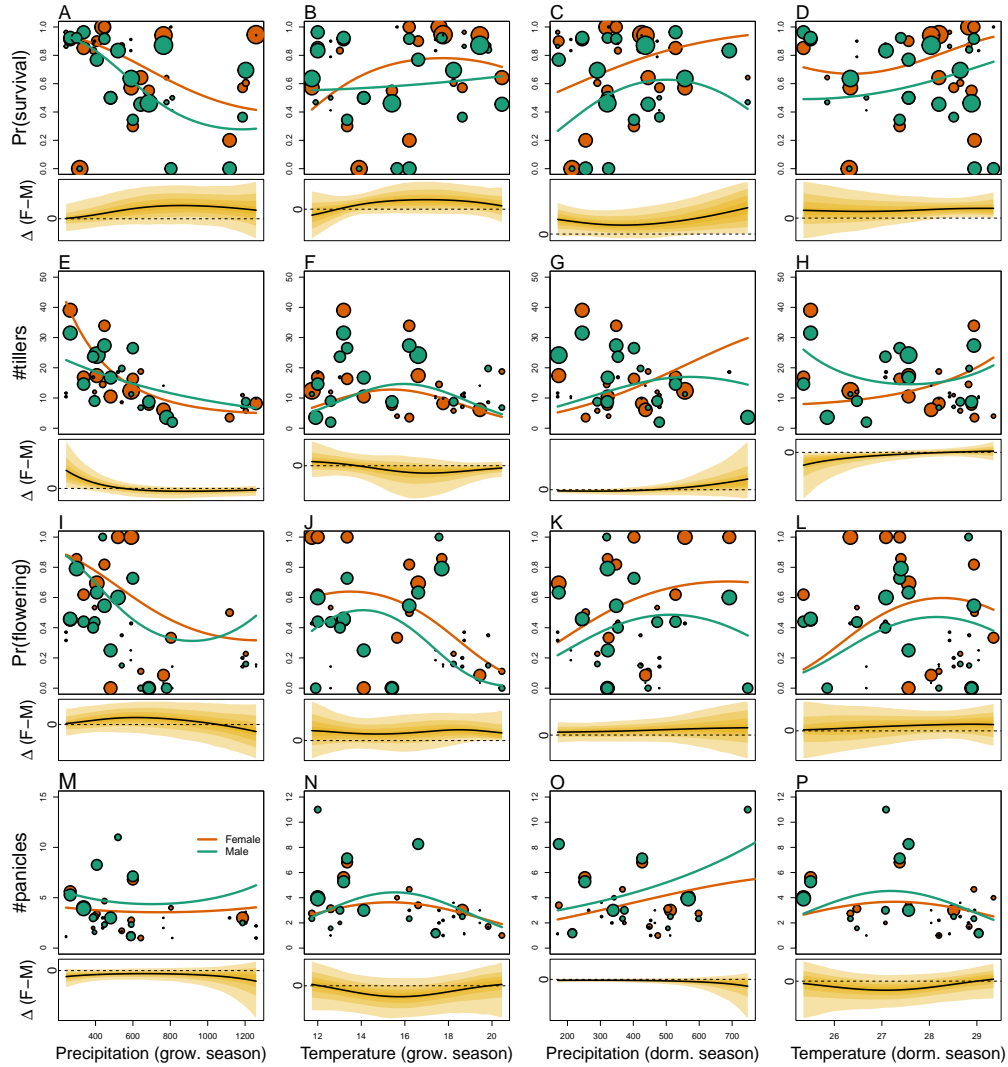


Figure 2: Sex specific demographic response to climate across species range. (A, B, C, D) Probability of survival as a function of precipitation and temperature of the growing and dormant season. (E, F, G, H) Change in number of tillers as a function of precipitation and temperature of the growing and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

Climate change alters population viability

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

a female dominant model and a two-sex model²³. For both models, population growth rate decreased toward high precipitation of growing season (Figure 3A). In contrast population growth rate increased with an increase in precipitation of the dormant season (Figure 3C). Furthermore, population growth rate was maximized between 14 and 17 °C and decreased below zero beyond 18 °C during the growing season (Figure 3B). Similarly population fitness was maximized between 27 and 31 °C and decreased below zero just beyond 20 °C during the dormant season (Figure 3D).²⁴

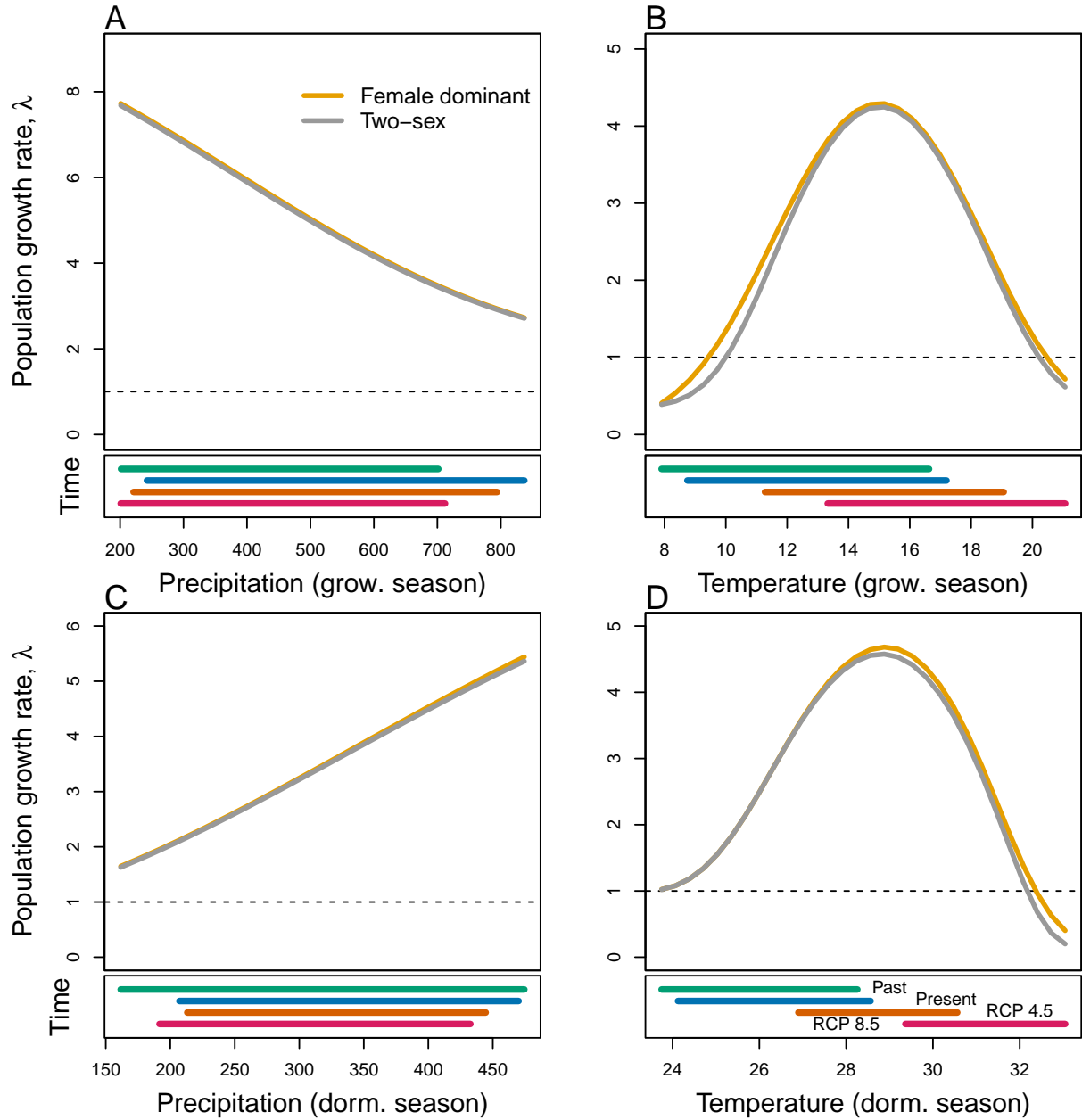
We have also detected a strong association between predicted lambda and different ranges of climate (past, present and future). Under past climate conditions, population growth rate decreased below one for temperature of the growing season. Populations will still be viable under moderate gas emission (RCP4.5). However high gas emission (RCP8.5) will alter population viability (Figure 3B, D).²⁵

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

²³I have now provided the methods for this contrast.

²⁴I think we should keep this figure. The 2-D niche plots are the better representation of these results, because there are temp*precip interactions that we cannot see here but you can see in the 2-D niche plot. However a model with the 4 predictors together will also give a better approximation of lambda than the 2D. I added the conditional part in the description of the results. I see the 2D as a way of showing the difference in niche. That said if you really want to remove this I am down you have more experience than me.

²⁵I changed how I write the first sentence to remove the "effect of climate on". Again I don't mind removing the Figure.



Climatic change induces niche and range shifts

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

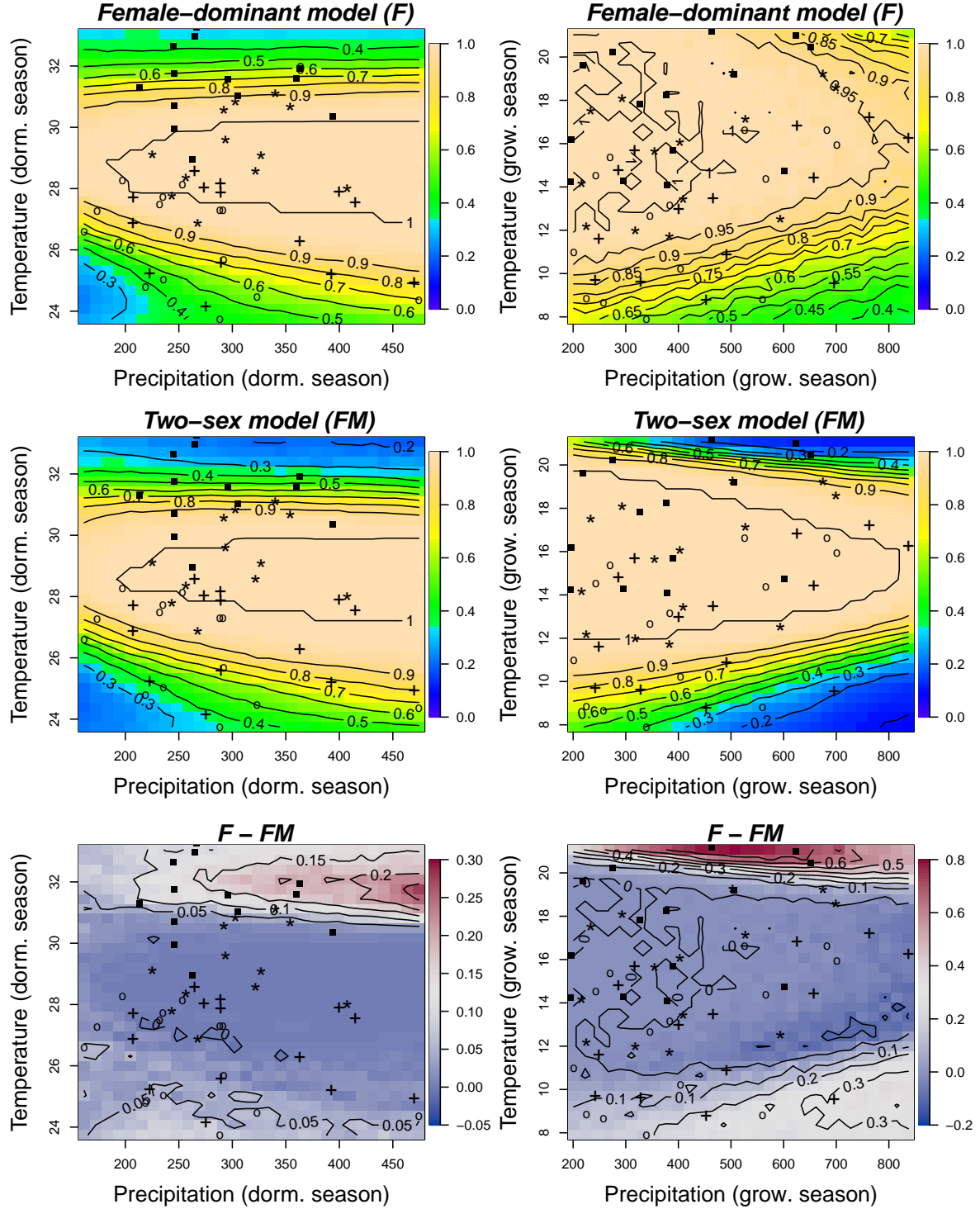


Figure 4: A two-dimensional representation of the predicted niche shift over time (past, present and future climate conditions). Contours on the first four panels show predicted probabilities of self-sustaining populations, $\Pr(\lambda > 1)$ conditional on precipitation and temperature of the dormant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

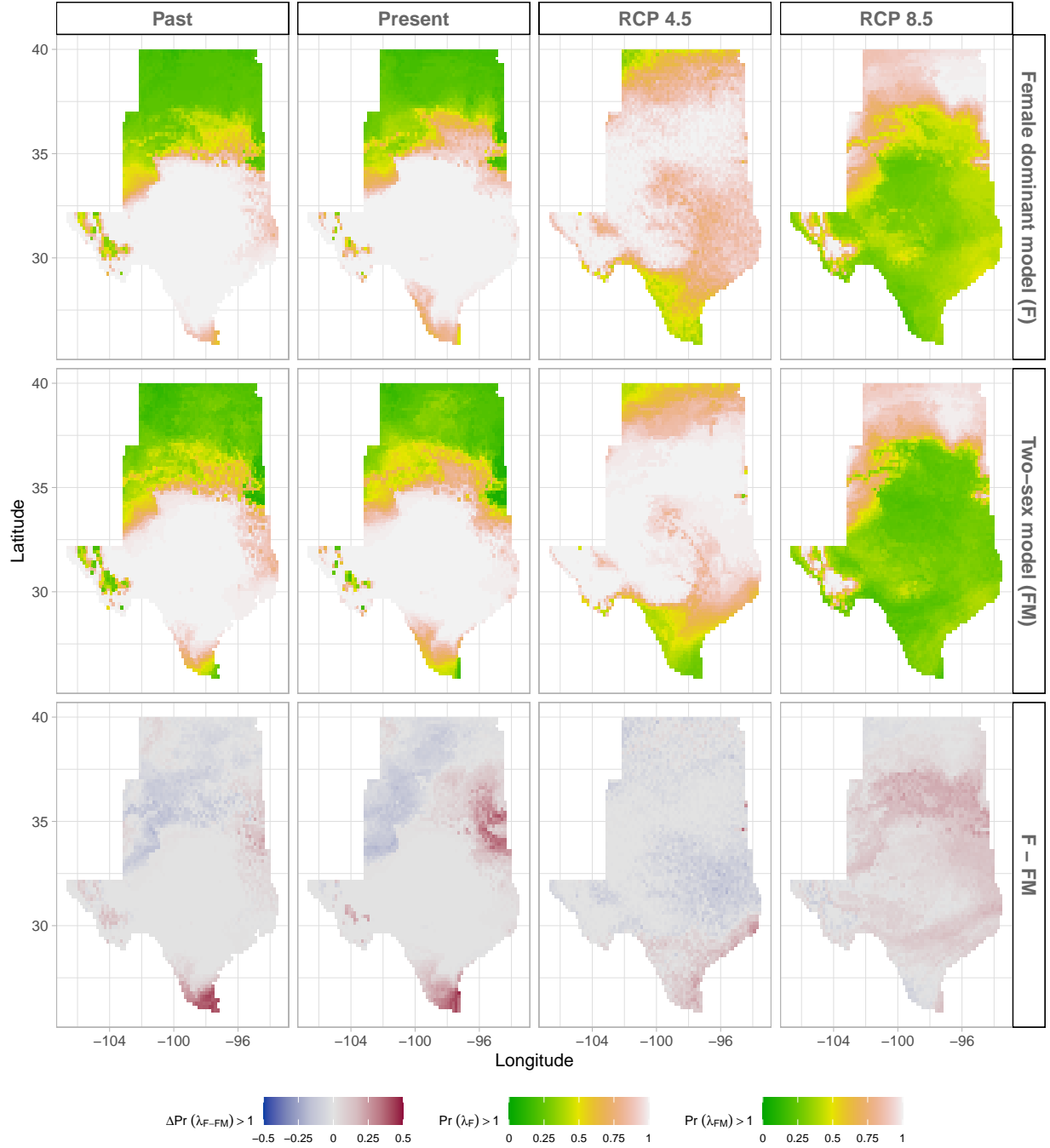


Figure 5: Climate change favors range shift towards north edge. (A) Past, (B) Current, (C and D) Future predicted range shift based on the predicted probabilities of self-sustaining populations, $\Pr(\lambda > 1)$, using the two-sex model that incorporates sex-specific demographic responses to climate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

Female bias in sex-ratio in response to climate change

²⁶ Operational-Sex Ratio (proportion of females panicles) increased significantly with an increase of precipitation and temperature of the growing season and precipitation and temperature of dormant season (Figure ??, Figure ??). Similarly, the proportion of female plants increased with an increase of temperature of growing season and temperature of dormant season (Figure ?? B, D, Figure ??). However, the proportion of female plants did not vary significantly with precipitation of dormant and growing season (Figure ?? A, C). Future climate drive to extreme female-biased in *Poa arachnifera* populations (Figure 6, Figure ??).

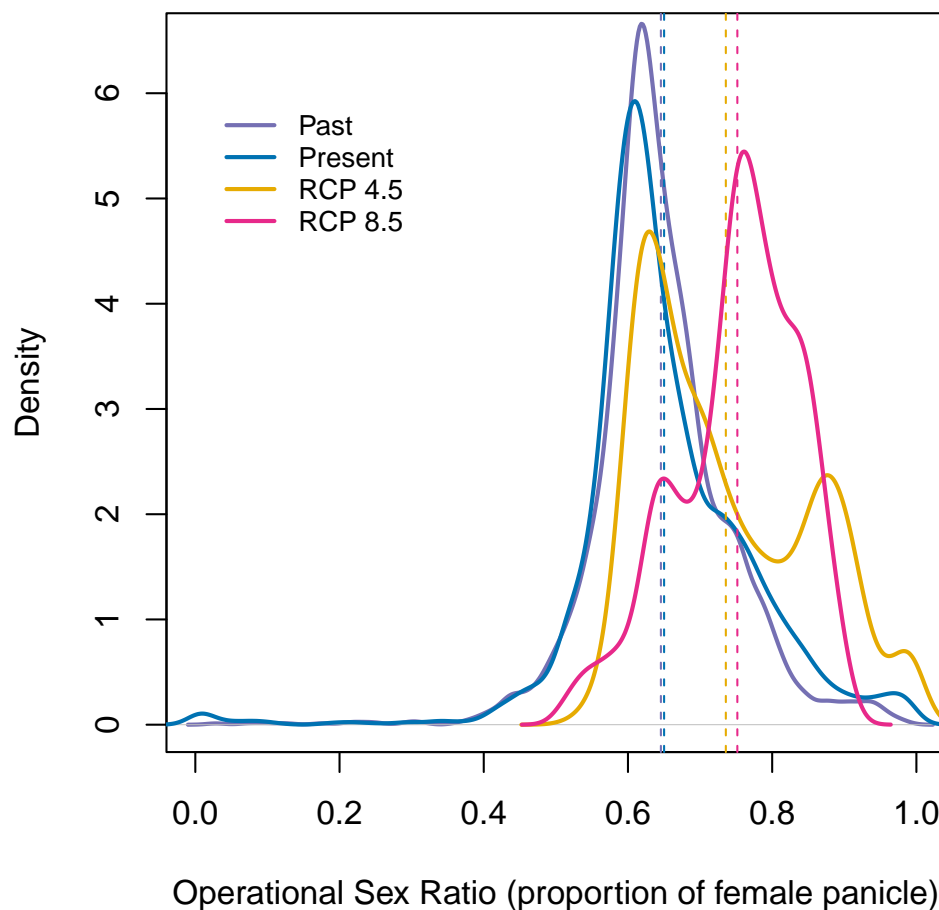


Figure 6: Change in Operational Sex Ratio (proportion of female panicle) over time (past, present, future). Future projections were based on the CMCC-CM model. The mean sex ratio for each time period is shown as vertical dashed line.

²⁶I moved this section because it only makes sense with respect to the geographic projections, because the histograms are showing distributions across the study region. Are these locations conditional on lambda greater than 1 or Pr lambda greater than some value?

Discussion

²⁷ Dioecious species make up a large fraction of Earth's biodiversity – most animals and many plants – yet we have little knowledge about how sex-specific demography and responses to climate drivers may affect population viability and range shifts of dioecious species under climate change.²⁸

We used three years of demographic data collected common garden experiments across climatic gradient to forecast for the first time the impact of climate change on dioecious species. Our future projections require extrapolation to warmer or colder conditions than observed in our experiment and subsequently should be interpreted with caution (Chen et al., 2024). Despite all these limitations, the qualitative implications of the response of our study species to increase temperature (dormant and growing season) seems consistent across all GCMs (Figure ??, Figure ??, Figure ??). Three 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 suggests a sex specific demographic response to climate change that lead to higher proportion of female as climate increase. Second, climate change favors a northern range shifts in suitable habitats. Third, the female dominant model (model that does not account for sex structure) overestimates species niche and range shifts.

There was a female demographic advantage leading to a female biased in response to climate change in *Poa arachnifera* populations. The extreme female-bias in response to climate change contrast with previous studies suggesting that an increase in male frequency in response in climate change (Hultine et al., 2016; Petry et al., 2016). Two mechanisms 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 and 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; Bürli et al., 2022; Cipollini and Whigham, 1994; Field et al., 2013).

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

²⁷This is my new proposition regarding the discussion

²⁸Love this opening sentence.

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

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

Conclusion

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

Acknowledgements

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

References

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

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

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

- 476 Iler, A. M., Compagnoni, A., Inouye, D. W., Williams, J. L., CaraDonna, P. J., Anderson, A., and
477 Miller, T. E. (2019). Reproductive losses due to climate change-induced earlier flowering are
478 not the primary threat to plant population viability in a perennial herb. *Journal of Ecology*,
479 107(4):1931–1943.
- 480 Jones, M. H., Macdonald, S. E., and Henry, G. H. (1999). Sex-and habitat-specific responses
481 of a high arctic willow, *salix arctica*, to experimental climate change. *Oikos*, pages 129–138.
- 482 Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann,
483 N. E., Linder, H. P., and Kessler, M. (2017). Climatologies at high resolution for the earth's
484 land surface areas. *Scientific data*, 4(1):1–20.
- 485 Kindiger, B. (2004). Interspecific hybrids of *poa arachnifera* × *poa secunda*. *Journal of New*
486 *Seeds*, 6(1):1–26.
- 487 Knight, T. M., Steets, J. A., Vamosi, J. C., Mazer, S. J., Burd, M., Campbell, D. R., Dudash,
488 M. R., Johnston, M. O., Mitchell, R. J., and Ashman, T.-L. (2005). Pollen limitation of plant
489 reproduction: pattern and process. *Annu. Rev. Ecol. Evol. Syst.*, 36:467–497.
- 490 Konapala, G., Mishra, A. K., Wada, Y., and Mann, M. E. (2020). Climate change will affect
491 global water availability through compounding changes in seasonal precipitation and
492 evaporation. *Nature communications*, 11(1):3044.
- 493 Kremer, A., Ronce, O., Robledo-Arnuncio, J. J., Guillaume, F., Bohrer, G., Nathan, R., Bridle,
494 J. R., Gomulkiewicz, R., Klein, E. K., Ritland, K., et al. (2012). Long-distance gene flow and
495 adaptation of forest trees to rapid climate change. *Ecology letters*, 15(4):378–392.
- 496 Lee-Yaw, J. A., Kharouba, H. M., Bontrager, M., Mahony, C., Csergő, A. M., Noreen, A. M.,
497 Li, Q., Schuster, R., and Angert, A. L. (2016). A synthesis of transplant experiments and
498 ecological niche models suggests that range limits are often niche limits. *Ecology letters*,
499 19(6):710–722.
- 500 Liaw, A., Wiener, M., et al. (2002). Classification and regression by randomforest. *R news*,
501 2(3):18–22.
- 502 Louthan, A. M., Keighron, M., Kiekebusch, E., Cayton, H., Terando, A., and Morris, W. F.
503 (2022). Climate change weakens the impact of disturbance interval on the growth rate of
504 natural populations of venus flytrap. *Ecological Monographs*, 92(4):e1528.

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

- Pulliam, H. R. (2000). On the relationship between niche and distribution. *Ecology letters*, 3(4):349–361.
- R Core Team (2023). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Reed, P. B., Peterson, M. L., Pfeifer-Meister, L. E., Morris, W. F., Doak, D. F., Roy, B. A., Johnson, B. R., Bailes, G. T., Nelson, A. A., and Bridgham, S. D. (2021). Climate manipulations differentially affect plant population dynamics within versus beyond northern range limits. *Journal of Ecology*, 109(2):664–675.
- Renganayaki, K., Jessup, R., Burson, B., Hussey, M., and Read, J. (2005). Identification of male-specific aflp markers in dioecious texas bluegrass. *Crop science*, 45(6):2529–2539.
- Sanderson, B. M., Knutti, R., and Caldwell, P. (2015). A representative democracy to reduce interdependency in a multimodel ensemble. *Journal of Climate*, 28(13):5171–5194.
- Schultz, E. L., Hülsmann, L., Pillet, M. D., Hartig, F., Breshears, D. D., Record, S., Shaw, J. D., DeRose, R. J., Zuidema, P. A., and Evans, M. E. (2022). Climate-driven, but dynamic and complex? a reconciliation of competing hypotheses for species' distributions. *Ecology letters*, 25(1):38–51.
- Schwalm, C. R., Glendon, S., and Duffy, P. B. (2020). Rcp8. 5 tracks cumulative co2 emissions. *Proceedings of the National Academy of Sciences*, 117(33):19656–19657.
- Schwinning, S., Lortie, C. J., Esque, T. C., and DeFalco, L. A. (2022). What common-garden experiments tell us about climate responses in plants.
- Sexton, J. P., McIntyre, P. J., Angert, A. L., and Rice, K. J. (2009). Evolution and ecology of species range limits. *Annu. Rev. Ecol. Evol. Syst.*, 40:415–436.
- Shelton, A. O. (2010). The ecological and evolutionary drivers of female-biased sex ratios: two-sex models of perennial seagrasses. *The American Naturalist*, 175(3):302–315.
- Sherry, R. A., Zhou, X., Gu, S., Arnone III, J. A., Schimel, D. S., Verburg, P. S., Wallace, L. L., and Luo, Y. (2007). Divergence of reproductive phenology under climate warming. *Proceedings of the National Academy of Sciences*, 104(1):198–202.
- Sletvold, N. and Ågren, J. (2015). Climate-dependent costs of reproduction: Survival and fecundity costs decline with length of the growing season and summer temperature. *Ecology Letters*, 18(4):357–364.

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

Supporting Information

S.1 Supporting Figures

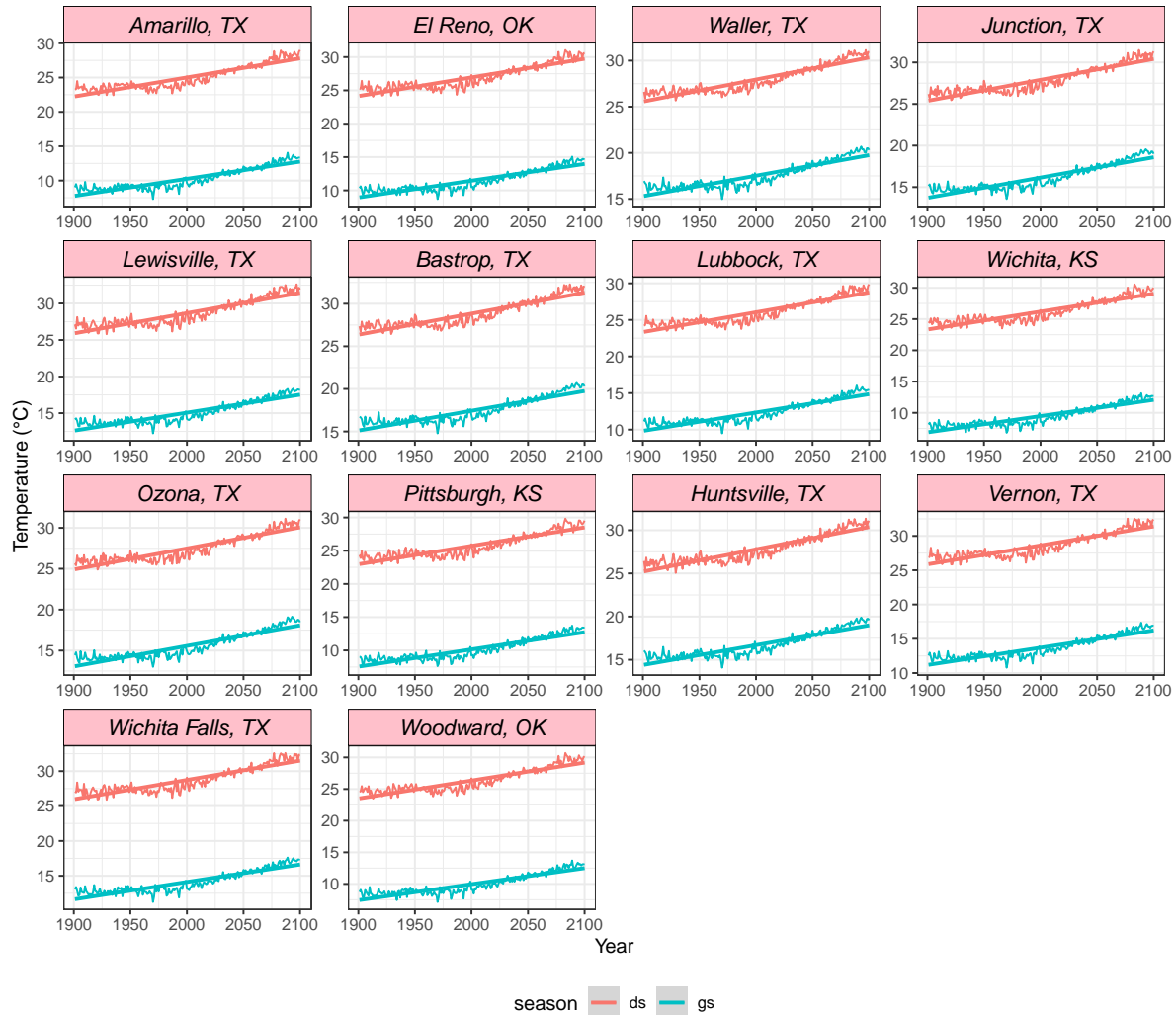


Figure S-1: Temperature variation across the study sites from 1990 to 2100, ds: Dormant season, dg: Growing season.



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

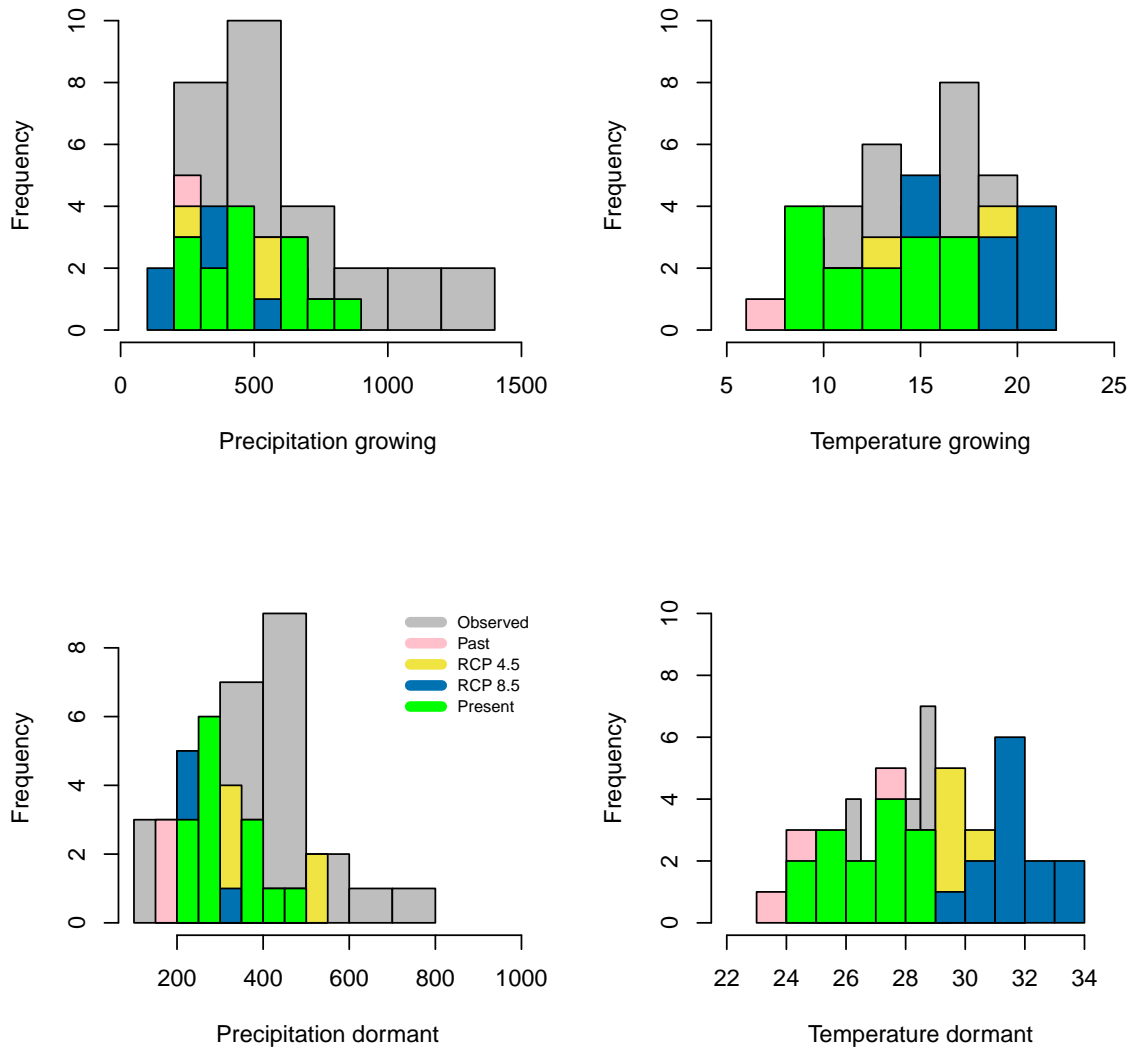


Figure S-3: Past, Observed, present and future (MIROC Model) climate data across the study area.

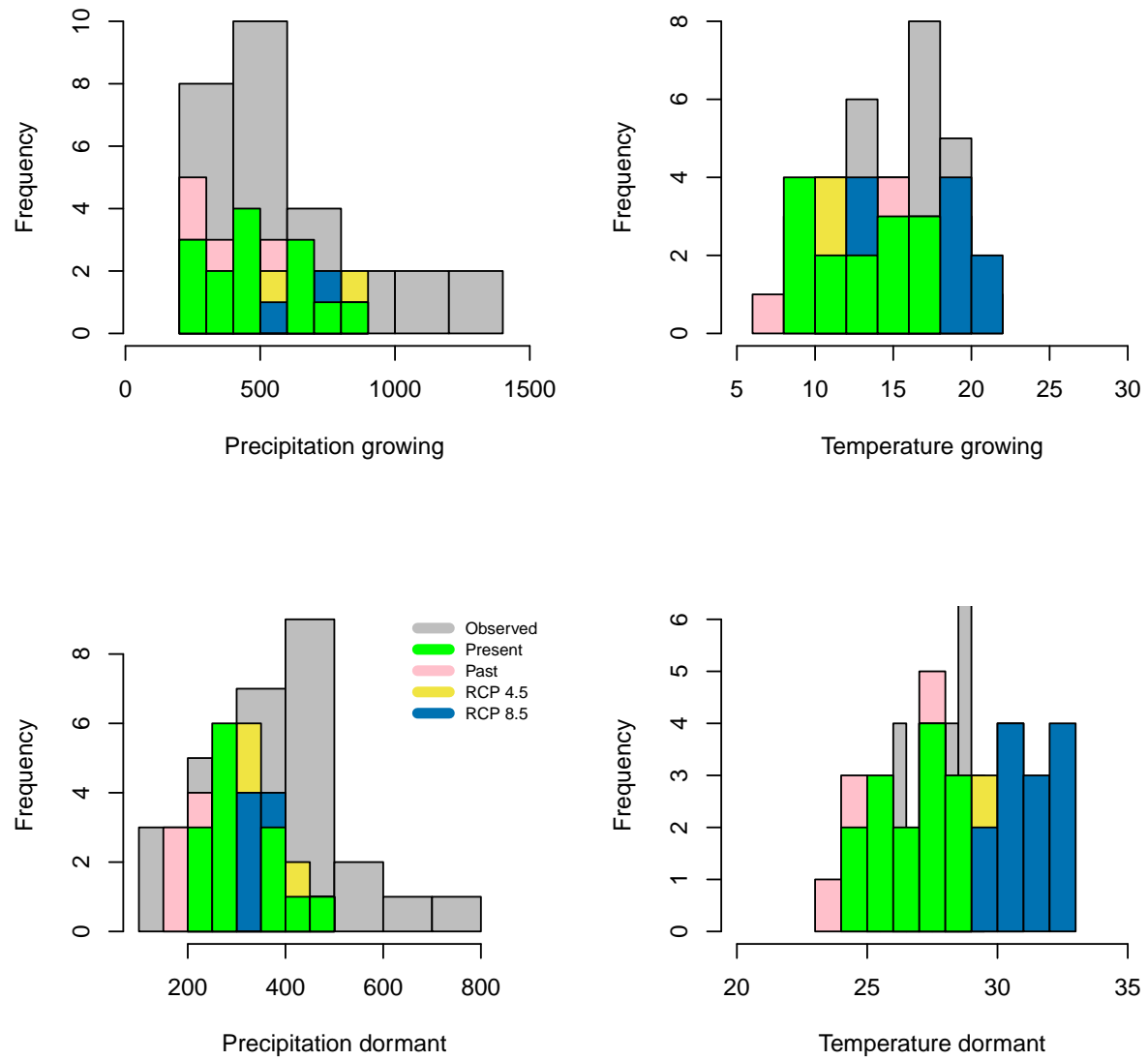


Figure S-4: Past, Observed, present and future (ACCESS Model) climate data across the study area.

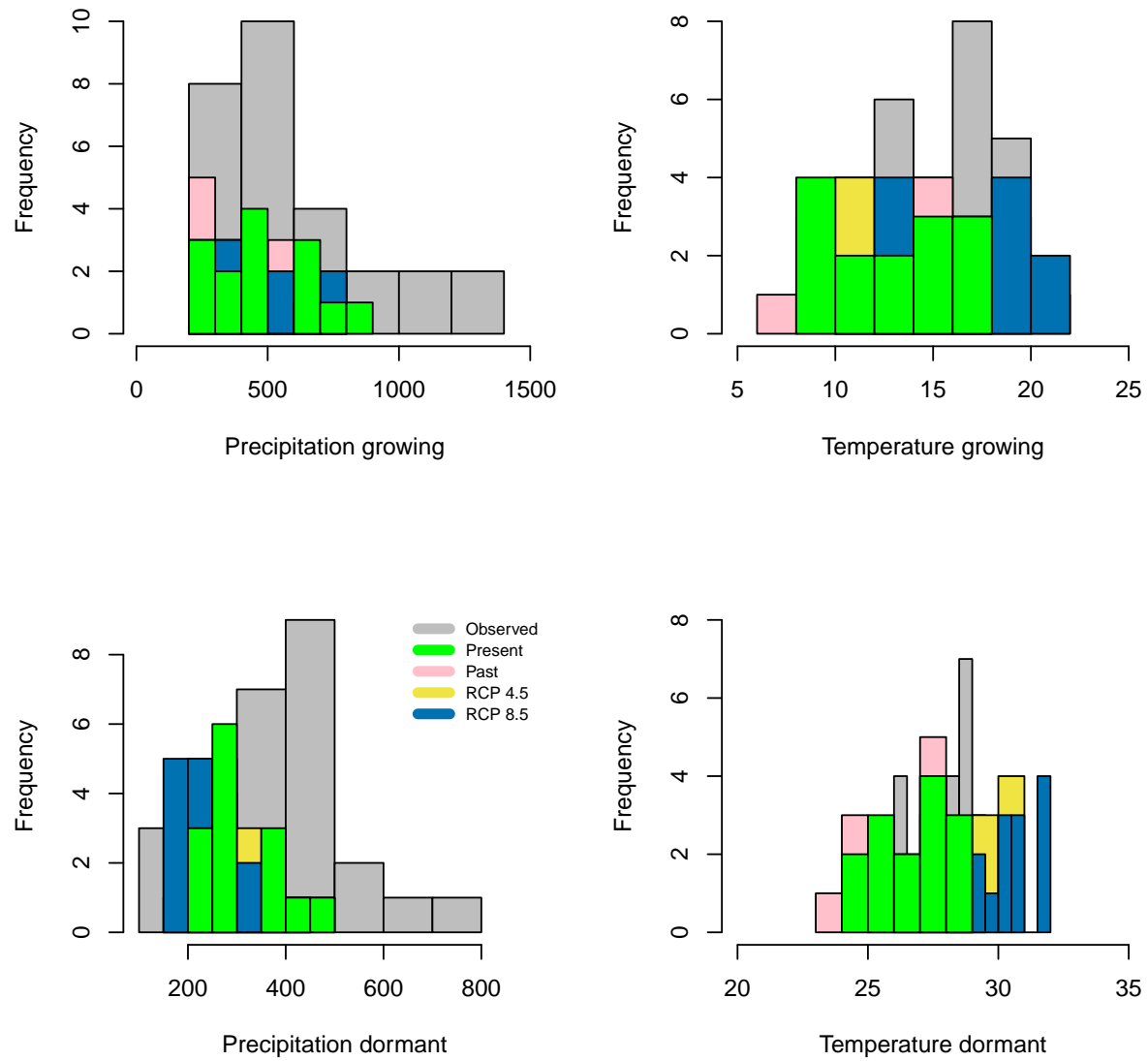


Figure S-5: Past, Observed, present and future (CESM1 Model) climate data across the study area.

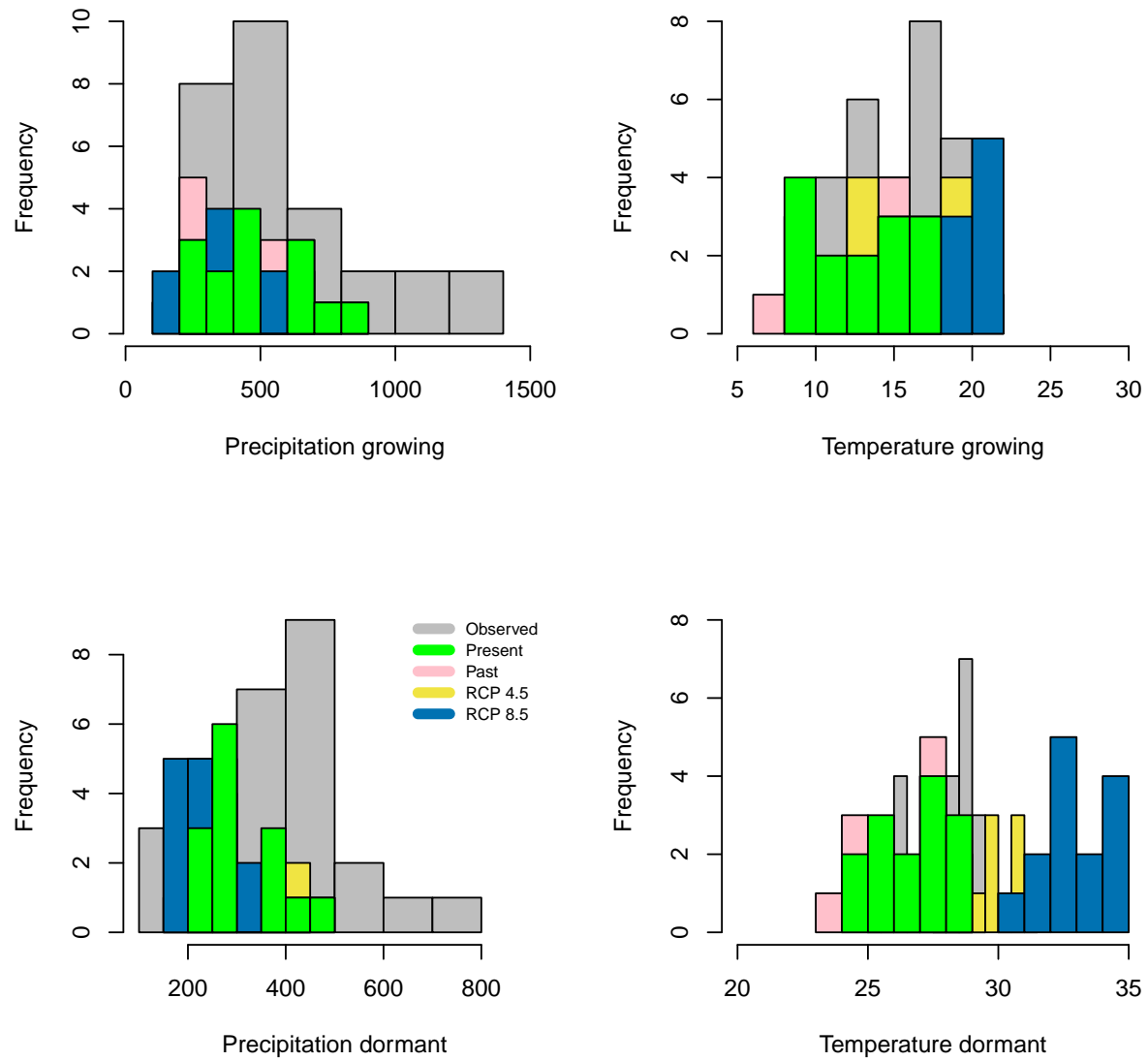


Figure S-6: Past, Observed, present and future (CMCC Model) climate data across the study area.

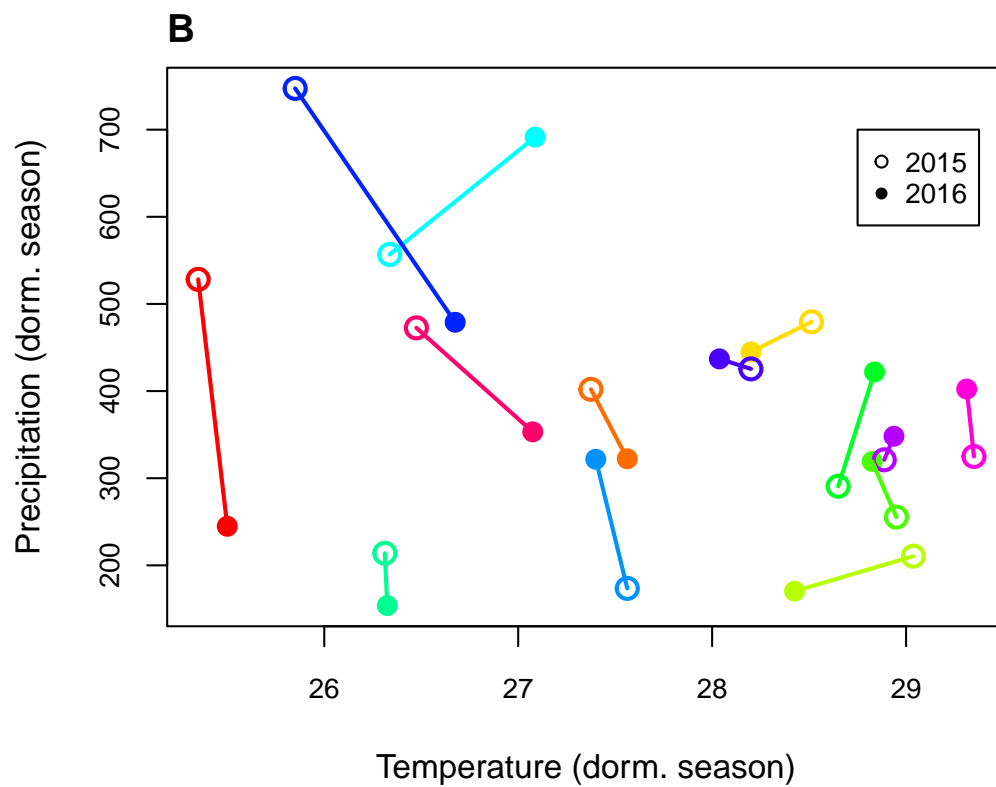
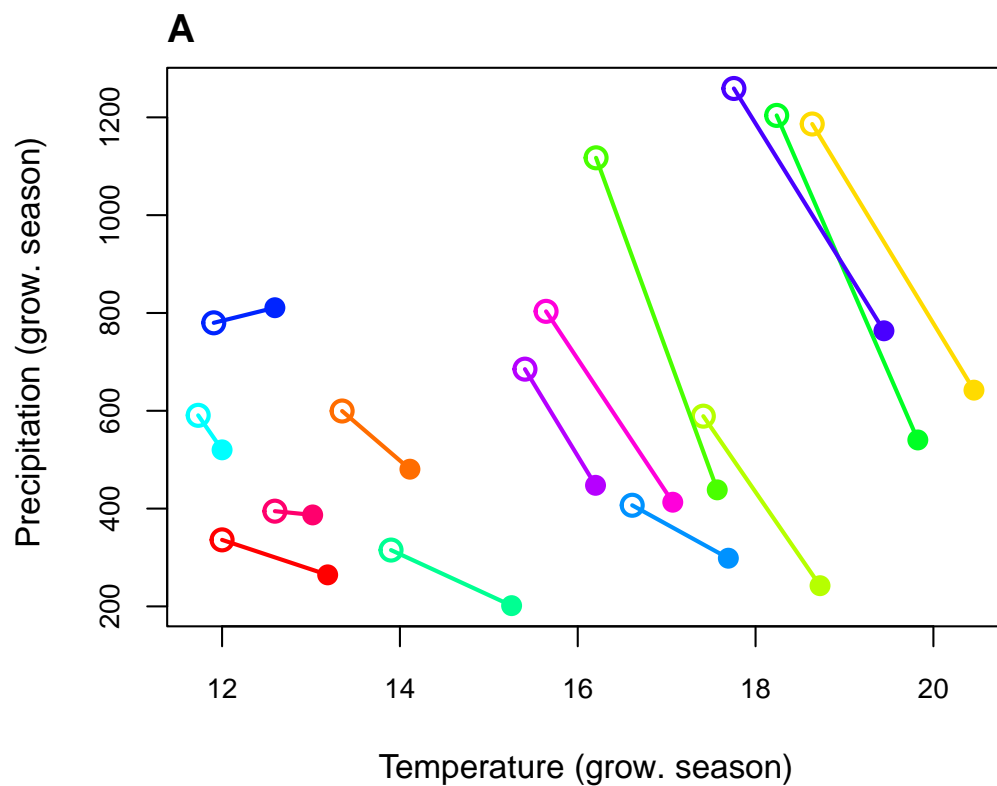


Figure S-7: Seasonal climate variation (temperature in °C and precipitation in *mm*) across the common garden sites during the 2014–15 and 2015–16 census periods. Each color represents a site and lines connect the same site between years.

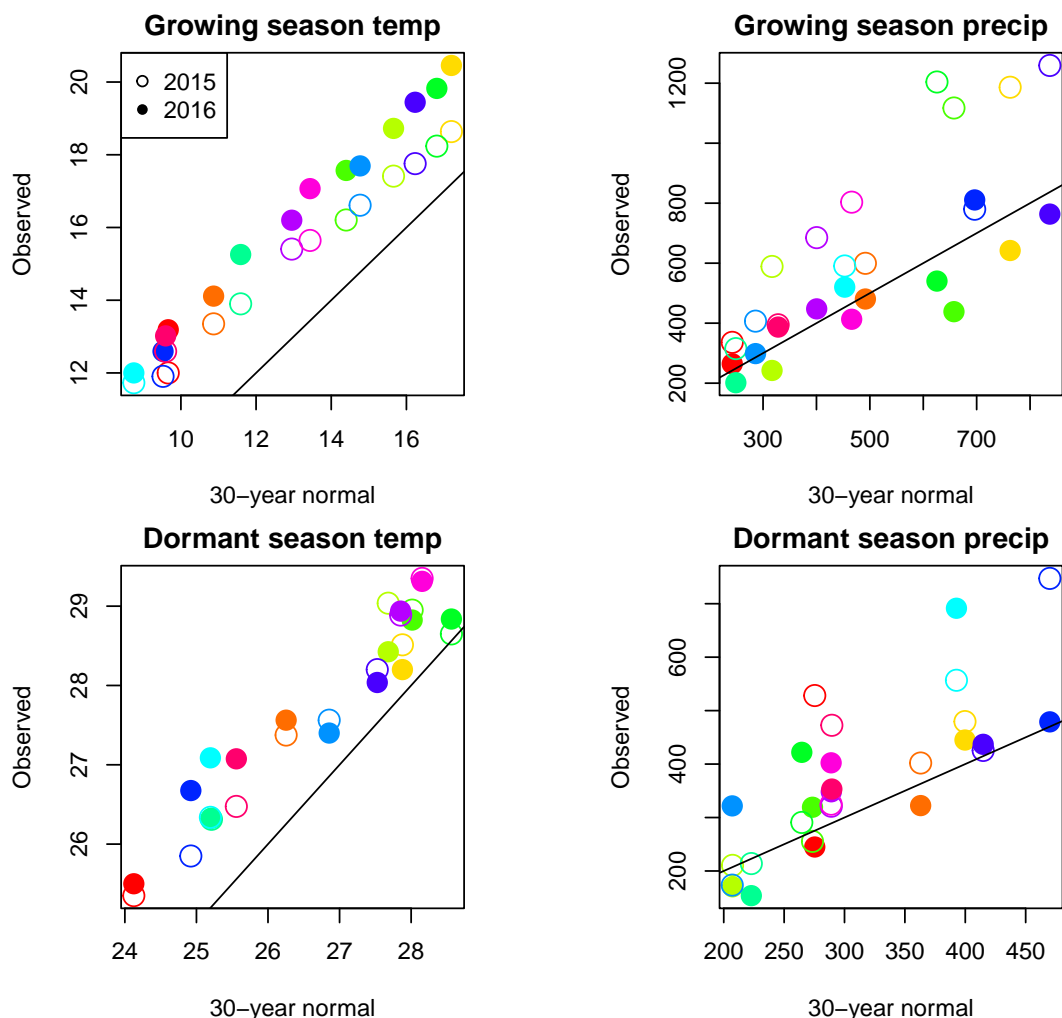


Figure S-8: Comparison of 30-year (1990-2019) climate normals and observed weather conditions at common garden sites during the 2014–15 and 2015–16 census periods. Temperature is in °C and precipitation is in *mm*. Colors represent sites and lines show the $y=x$ relationship.

S.2 Supporting Methods

Sex ratio experiment

To estimate the probability of seed viability, the germination rate and the effect of sex-ratio variation on female reproductive success, we conducted a sex-ratio experiment at one site near the center of the range to estimate the effect of sex-ratio variation on female reproductive success. The details of the experiment are provided in Compagnoni et al. (2017) and Miller and Compagnoni (2022b). Here we provide a summary of the experiment. We established 124 experimental populations in plots measuring 0.4 x 0.4m and separated by at least 15m from each other. We varied population density (1-48 plants/plot) and sex ratio (0%-100%

female) across the experimental populations, and we replicated 34 combinations of density and sex ratio. We collected panicles from a subset of females in each plot and recorded the number of seeds in each panicle. We assessed reproductive success (seeds fertilized) using greenhouse-based germination and trazolium-based seed viability assays. Seed viability was modeled with a binomial distribution where the probability of viability (v) was given by:

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

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