

# Forecasting range shifts of dioecious plants under climate change

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**Global climate change has triggered an urgent need for predicting the reorganization of Earth's biodiversity. For dioecious species (those with separate sexes), it is unclear how commonly unique climate sensitivities of females and males could influence projections for species-level responses to climate change. 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. We contrasted predictions of a standard female-dominant model with those of a two-sex model that accounts for feedbacks between sex ratio and vital rates. Both model versions predict that future climate change will induce a poleward shift of niche suitability beyond current northern limits. However, the magnitude of the poleward shift was underestimated by the female-dominant model because females have broader temperature tolerance than males but become mate-limited under female-biased sex ratios, which are forecasted to become more common under future climate. Our result illustrate how explicitly accounting for both sexes could enhance population viability forecasts and conservation planning for dioecious species in response to climate change.**

global warming | matrix projection model | population dynamics | sex ratio

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 (1). Species' range limits, when not driven by dispersal limitation, should generally reflect the limits of the ecological niche (2). Niches and geographic ranges are often limited by climatic factors including temperature and precipitation (3). Therefore, changes in these climatic factors could impact population viability, with implications for range expansion or contraction based on which regions of a species' range become more or less suitable (4, 5). Forecasting range shifts for dioecious species (most animals and ca. 7% of plant species (6)) is complicated by the potential for sexual niche differentiation, i.e. distinct responses of females and males to shared climate drivers (7, 8). 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 (9). 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 (10). Across dioecious plants, studies suggest that future climate change toward hotter and drier conditions may favor male-biased sex ratios (7, 11). 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 (7, 12).

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 13–15). Traditional “female-dominant” 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 differences between females and males and how these differences may influence population dynamics (16, 17). 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 (9, 18). 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 (10, 19).

In this study, we combined 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 their implications for past, present, and future range dynamics. Our work focused on

## Significance Statement

Females and males of dioecious species may differ in their sensitivity to climate change, yet most forecasts of population viability and range shifts overlook the complexity of sex structure. Here, we used demographic data collected from a common garden experiment, climate change forecasts, and mathematical models to demonstrate that accounting for only one sex could underestimate the impact of climate change on dioecious species, particularly in regions of their range that are biased toward one sex. This work highlights how incorporating demographic complexity can improve biodiversity forecasts in a changing world.

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, T.E.X.M. and A.C. contributed to revisions.

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the dioecious plant species 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 season across longitude (Fig. S1). Along that environmental gradient, we installed a common garden on 14 sites to collect demographic data and conducted a sex ratio manipulation experiment to measure the influence of the OSR on sex-specific demographic rates. The south-central U.S. has experienced rapid climate warming since 1900 and warming is projected to continue through the end of the century (Fig. 1, Fig. S2). 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 (20). 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. S2). 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 ( $Pr(\lambda > 1)$ ) in relation to geographic variation in the 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 (survival, growth, and flowering) to variation in temperature and precipitation across the species' range?
2. How do sex-specific vital rates combine to determine the influence of climate on operational sex ratio and population viability ( $Pr(\lambda > 1)$ )?
3. What are the likely historical and projected dynamics of the Texas bluegrass geographic niche and how does accounting for sex structure modify these predictions?

## Results

**Sex specific demographic responses and sex ratio variation across climatic conditions.** Bayesian mixed effect models, describing how each vital rate varies as a function of sex, size, and climate covariates (precipitation and temperature of growing and dormant seasons), revealed the demographic response of Texas bluegrass to climate drivers across common garden sites and years, and identified demographic differences between the sexes. Regression coefficients related to sex and/or sex: size interactions were significantly non-zero (95% credible intervals excluding zero) for most vital rates (Fig. S3), suggesting sexual divergence in demography. Females generally had an advantage over males, especially in survival and flowering (Fig. 2). Furthermore, there were significant interactions between sex and one or more climate variables (Fig. S3), indicating sexual niche divergence in response to shared climate drivers. Fig. S4 and S5 visualize the magnitude of sexual divergence in demography across niche space, revealing that female advantages in survival and flowering were greatest at both high and low growing season temperature extremes.

Across 14 common garden sites, operational sex ratio (proportion of panicles that are female) of the experimental populations was female-biased on average ( $\approx 60\%$  female), reflecting the overall greater rates of female vs. male flowering. OSR was most female-biased (up to 80% female) at extreme values of temperature, especially growing season temperature (Fig. S6, Fig. S7), consistent with the female reproductive advantage at temperature extremes seen in the vital rate data. In contrast, there was very little variation in sex ratio (proportion of plants that are female) in the years following common garden establishment (all sites were planted with equal numbers of females and males) and no detectable influence of climate covariates (Fig. S8), indicating that skew in the OSR comes from sex-biased reproductive rates more so than sex-biased survival.

**Climate drivers of population viability across niche space.** We integrated the vital rate responses in a climate-explicit matrix projection model (MPM) framework. Female-dominant and two-sex versions of the MPM both allow for sex-specific response to climate, but only the two-sex model accounts for the feedback between operational sex ratio and seed fertilization (pollen limitation under female-biased sex ratios). Figure 3 shows the estimated probability of population viability ( $\lambda \geq 1$ ) across seasonal climate niche space; these probabilities account for uncertainty in the vital rate parameters as well as process error related to spatial heterogeneity and genotypic variation. For both female-dominant and two-sex models, fitness variation across niche space indicated intermediate temperature optima and declines in fitness at high and low temperature extremes, with weaker effects of precipitation (compare vertical and horizontal contours in Fig. 3). These visual trends are supported by Life Table Response Experiment (LTRE) decomposition indicating that variation in fitness across climatic conditions is most strongly driven by responses to growing and dormant season temperature, with weaker interactive effects of precipitation that modulate the effects of temperature (Fig. S9). LTRE analysis also showed that declines in population viability at high and low temperatures were driven most strongly by reductions in vegetative growth and panicle production, with stronger contributions from females than males (Fig. S10). Points in Fig. 3 show that climate change forecasted for the common garden locations would move many of them toward lower-suitability regions of niche space associated with high growing and dormant season temperatures (see also Fig. S11).

While the female-dominant and two-sex models were generally in agreement about high confidence in intermediate temperature optima, they differed around the edges of niche space (Fig. 3C, D, S11). The female-dominant model over-predicted population viability, especially with respect to growing season temperature. For example, the female-dominant model predicted that, for most levels of precipitation, warm growing season (winter) temperatures of  $\sim 20^\circ\text{C}$  had high suitability ( $Pr(\lambda \geq 1) > 0.9$ ), while the two-sex model indicated that these conditions were most likely unsuitable ( $Pr(\lambda \geq 1) < 0.5$ ). Similarly, at low winter temperatures that the two-sex model identifies with high certainty as unsuitable ( $Pr(\lambda \geq 1) < 0.1$ ), the female-dominant model is more optimistic ( $Pr(\lambda \geq 1) > 0.4$ ). Across growing season climate space, the female-dominant model over-estimates population viability by 9.2%, on average (Fig. 3 E, F, Fig. S11, Fig.

177 S12)). The difference between female-dominant and two-sex  
178 models was qualitatively similar but weaker in magnitude for  
179 niche dimensions of the dormant season (Fig. 3C, Fig. S11).  
180 Female-dominant and two-sex models diverged most strongly  
181 in regions of niche space that favored strongly female-biased  
182 operational sex ratios, suggesting mate limitation as the bio-  
183 logical mechanism underlying model differences. The two-sex  
184 model accounts for feedbacks between OSR and female fertility  
185 that were estimated through a separate sex ratio manipulation  
186 experiment, showing reduced seed viability at OSR exceeding  
187  $\sim 75\%$  female panicles (Fig. S13). Lacking this feedback, the  
188 female-dominant model over-predicts population viability in  
189 regions of niche space where male flowering is not sufficient to  
190 maximize seed set.

191 **Climatic change induces shifts in geographic niche and pop-**  
192 **ulation OSR.** We next projected the climatic niche onto geo-  
193 graphic space (Texas, Oklahoma and Kansas) to examine how  
194 suitable niche conditions for Texas bluegrass are shifting due  
195 to climate change (Fig. 4). For both female-dominant and  
196 two-sex models, the predicted geographic niche generally cor-  
197 responds well to independent observations of Texas bluegrass  
198 occurrence from the Global Biodiversity Information Facility  
199 (GBIF) (Fig. 4). The predicted geographic niche is more ex-  
200 pensive than the GBIF occurrences, particularly at southern,  
201 western, and eastern edges, suggesting some degree of range  
202 disequilibrium (e.g., due to dispersal limitation), geographic  
203 bias in occurrence records, and/or model mis-specification.  
204 Under past (1901-1930) and present (1990-2019) conditions,  
205 the two-sex and female-dominant models predict widespread  
206 suitability with high confidence ( $Pr(\lambda \geq 1) \approx 1$ ) across much  
207 of Texas and Oklahoma. Comparing past to present conditions,  
208 the geographic niche for both models has shifted slightly pole-  
209 ward, with reductions in viability at the southern margins and  
210 expansions of viability at northern margins. The northward  
211 shift of suitable niche conditions is even more pronounced in  
212 projections to end-of-century (2071-2100) conditions, with the  
213 most dramatic changes in the most pessimistic (RCP8.5) sce-  
214 nario (Fig. 4). In fact, under the pessimistic scenario, Texas  
215 bluegrass will have very little remaining climate suitability  
216 in the state of Texas by the end of the 21st century. The  
217 predicted poleward niche shift is consistent across different  
218 global circulation models (Fig. S14, Fig. S15, Fig. S16).

219 Female-dominant and two-sex models are in broad agree-  
220 ment about northward migration of the climatic niche, but  
221 the geographic projections reveal hotspots of disagreement  
222 where the female-dominant model over-predicts climate suit-  
223 ability and under-predicts the likelihood of range shifts (Fig.  
224 4). These hotspots are generally regions of predicted strong  
225 female bias in the operational sex ratio (Fig. S17 to Fig.  
226 S20). The strongest contrast between the two models is in  
227 the pessimistic climate change scenario (RCP8.5), where the  
228 female-dominant model over-predicts population viability by  
229 as much as 20% across much of the region (Fig. S21) and thus  
230 under-estimates the magnitude of a potential range shift. In  
231 this scenario, a broad swath of the current distribution that is  
232 forecasted to be unsuitable ( $Pr(\lambda \geq 1) \approx 0$ ) by the two-sex  
233 model is identified as marginally suitable ( $Pr(\lambda \geq 1) \approx 0.5$ )  
234 by the female-dominant model. That difference arises because  
235 the two-sex model recognizes that strongly female-biased sex  
236 ratios cannot support viable populations. The OSR of Texas  
237 bluegrass across its range is projected to be ca. 75% female

panicles, on average, by end of century under RCP8.5, an  
increase from ca. 60% female under projections for past and  
current conditions (Fig. S22). The more optimistic climate  
change scenario (RCP4.5) predicts an intermediate shift in  
OSR, with hotspots of change at northern and southern range  
edges becoming strongly female-biased but most of the range  
remaining near current levels of 60% female (Fig. S17 to Fig.  
S20).

## Discussion

246 Dioecious species make up a large fraction of Earth's biodi-  
247 versity – most animals and many plants – yet we have little  
248 knowledge about how sex-specific demography and responses  
249 to climate drivers may affect population viability and range  
250 shifts of dioecious species under climate change. We used de-  
251 mographic data collected from common garden and sex ratio  
252 manipulation experiments, hierarchical Bayesian statistical  
253 modeling, and sex-structured demographic modeling to fore-  
254 cast, for the first time, the likely impact of climate change  
255 on range dynamics of a dioecious species. We found that  
256 demographic rates of Texas bluegrass and their sensitivities  
257 to climate drivers show significant sex bias, with females out-  
258 performing males, on average, and high and low temperature  
259 extremes negatively affecting flowering rates of males more so  
260 than females, leading to female skew in the operational sex ra-  
261 tio. Future climate change will likely not only shift this species'  
262 geographic niche northward, but it will also further skew op-  
263 erational sex ratios toward stronger female bias: for Texas  
264 bluegrass, the future is female, and it is in Kansas. Our two-sex  
265 modeling framework accounts for reductions in female fertility  
266 with increasing female bias, and therefore predicts a narrower  
267 climatic niche than the corresponding female-dominant model  
268 that ignores the feedback between population structure and  
269 vital rates. Failure to account for population sex structure  
270 can therefore lead to overestimation of suitable niche space  
271 and underestimation of range shifts under global change.

272 While a two-sex modeling approach clearly adds biological  
273 realism, it was also additional work (in the form of experi-  
274 ments, data, equations, code, and computation). Was it worth  
275 the trouble? Generally, we suggest the answer should depend  
276 on the aims of the investigator. Predictions of the two-sex  
277 and female-dominant models were in strong agreement about  
278 climate niche optima, and LTRE decomposition suggested that  
279 female vital rates determine population responses to climate  
280 variation much more so than male vital rates. If we wanted  
281 to know whether a poleward range shift is likely for Texas  
282 bluegrass, the simpler female-dominant approach could have  
283 given us the correct answer. But more focused questions, es-  
284 pecially around the edges of niche space where sex ratio skew  
285 is more likely to impair population viability, may require an  
286 explicit accounting for feedbacks associated with sex structure.  
287 If we aimed to identify specific regions that are more or less  
288 inclined toward contraction or expansion, or sites that might  
289 be suitable for assisted migration, we would reach qualitatively  
290 different conclusions with female-dominant and two-sex mod-  
291 els. For example, the female-dominant model is over-confident  
292 that large swaths of Oklahoma will remain marginally suit-  
293 able for Texas bluegrass under the business-as-usual emissions  
294 scenario, while the two-sex model is more pessimistic, because  
295 this region will become too female-biased to support viable  
296 populations. More generally, we hypothesize that accounting



for sex structure should be most important under conditions that are already near the limits of population viability, where effects of mate limitation could be more consequential. This suggests a particularly important role of sex-structured modeling for threatened and endangered species, as conservation biologists have already recognized (21, 22).

Our results suggest that climate change, and specifically climate warming, will drive a classic pattern of poleward expansion: contraction at the southern trailing edge due to temperatures exceeding tolerable limits and expansion at the northern leading edge due to release from low temperature limitation. Our statistical models captured temperature-dependence in a phenomenological way, and the physiological mechanisms underlying these responses remain to be explored. Increasing temperature could increase evaporative demand, affect plant phenology (23, 24), and germination rate (25). The potential for temperature to influence these different processes changes seasonally (26). For example, studies suggested that grass species can have delayed phenology in response to global warming, particularly if temperatures rise above their physiological tolerances (27). Regardless of the mechanism, it is clear that climate warming will generate leading and trailing edges. Whether and at what pace the realized species' distribution tracks geographic changes in suitable niche space is a different, open question. Expansion of the leading edge could lag behind availability of suitable habitat due to dispersal limitation (28), and legacies of long-lived individuals can promote persistence of trailing edge populations even as environmental conditions deteriorate (29). Environmentally-explicit demographic models are emerging as powerful tools to understand and predict the limits of population viability under global change (30, 31), but incorporating non-equilibrium dynamics that emerge from dispersal limitation and historical legacies is an important new direction for this field.

Our finding that climate change in the south-central US will likely lead to female-biased operational sex ratios contrasts with previous studies of dioecious plants. While a baseline female demographic advantage has been observed in several dioecious species (32, 33), studies focused on sex-specific sensitivity to climate drivers often predict an increase in male frequency in response to climate stress (7, 10). We speculate that differences in the costs of reproduction related to pollination mode may help explain which sex is favored under climate stress. For most dioecious plant species, the cost of reproduction is often higher for females than males due to the requirement to develop seeds and fruits (34). However, several studies reported a higher cost of reproduction for males in wind pollinated species, such as Texas bluegrass, due to the larger amounts of pollen they produce (11, 35). Additional comparative studies across species that differ in life history traits are needed to draw inferences regarding which types of species are likely to become female- or male-biased in response to global change stressors.

Our forecasts for responses to climate change in Texas bluegrass should be interpreted in light of several features of our study design. First, the design of our common garden experiment and statistical modeling (which treats source population as a random effect) means that our geographic projections correspond to an "average" genotype from across the range of Texas bluegrass. Local adaptation to climate could make southern and northern edge populations more

resilient to high and low temperature stress, respectively, than the range-wide average (36). The role of local adaptation in mitigating population response to climate is an important next step in forecasting species' responses to global change. Second, as is true for many ecological systems, future climate is likely to include conditions that have no present-day analog (37), a major challenge for ecological forecasting. The years and locations of our experiment provided us with unusually good coverage of likely past, present, and future conditions expected throughout the study region, but we still had to extrapolate the statistical models to predict responses to colder winter temperatures (that were more common in the past) and hotter summer temperatures (that are expected in the future) than we directly observed (Fig. 1). By employing a probabilistic measure of niche and geographic suitability ( $Pr(\lambda) \geq 1$ ), our projections account for the uncertainty associated with these extrapolated climate responses, but there would be value in combining the spatiotemporal sampling of a common garden design with experimental manipulations that push systems toward historical and/or future conditions. Third, while we incorporated uncertainty associated with parameter estimation and process error, there is additional uncertainty in future climate conditions. Future forecasts for Texas bluegrass were generally consistent across different global circulation models (Fig. S14, Fig. S15, Fig. S16), but combining uncertainty in future conditions alongside uncertainty in biological responses to those conditions is an important frontier in ecological forecasting (38).

## Conclusion

We investigated how demographic differences between the sexes and contrasting sensitivity to climate can drive skewness in operational sex ratio and possible range shifts in the context of climate change. Our results suggest that tracking only females could lead to an underestimation of the effect of climate change on population dynamics, because it misses the feedback between population structure and female fertility. But in broad strokes, a female-dominant perspective tells much of the story, and that will likely be true for dioecious plants and animals with mating systems in which few males can fertilize many females. Our work provides a mechanistic framework for predicting the impact of global change on population dynamics and range shifts using probabilistic measures that can incorporate the many types of uncertainty that arise when reconstructing the past or forecasting the future.

## 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) (39). Texas bluegrass grows between October and May, flowers in spring, and goes dormant during the hot summer months of June to September (40). Following this life history, we divided the calendar year into growing (October 1 - May 31) and dormant (June 1 - September 30) seasons in the analyses below. Biological sex is genetically based and the birth (seed) sex ratio is 1:1 (41). Like all grasses, this species is wind-pollinated (39) and most male-female pollen transfer occurs within 15m (42). 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 (20).

Latitudinal limits of the Texas bluegrass distribution span 7.74 °C to 16.94 °C of temperature during the growing 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 during the dormant season. This region has experienced *ca.* 0.5 °C of climate warming since 1900, with faster warming during the cool-season months (0.0055°C/yr) than the hot summers (0.0046°C/yr) (Fig. S2). Future warming is projected to accelerate to 0.03 – 0.06°C/yr by the end of the century depending on the season and forecast model. On the other hand, precipitation has increased over the past century for much of the region but is forecasted to decline back to early-20th century levels (Fig. S2).

### 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 (20); 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, providing coverage of a broad range of latitude and longitude (Figure 1A). 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 seven natural source populations (Figure 1A); because sex is genetically-based, clones never deviated from their expected sex. The experiment was established in November 2013 with a total of 588 female and 588 male plants, 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 transition years, since the start of the experiment did not include the full 2013-14 transition year.

**Climatic data collection.** We gathered downscaled monthly temperature and precipitation for each site from Chelsea (43) to describe observed climate conditions during our study period. 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). We evaluated future climate projections from two scenarios of representative concentration pathways (RCPs): RCP4.5, and RCP8.5, using four general circulation models (GCMs) (SI Appendix, section A).

**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 (yes/no), 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, seasonal climate covariates and the interaction between sex and climate covariates (SI Appendix, section B).

### Sex ratio responses to climatic variation across common garden sites.

The experimental data were used to investigate how climatic variation across the range influenced sex ratio and operational sex ratio of the common garden populations. To do so, we developed two Bayesian linear models using data collected during three years. Each model had OSR or SR as response variable and a climate variable (temperature and precipitation of the growing season and dormant season) as predictor (SI Appendix, section C).

**Model-fitting procedures.** All models were fit using Stan (44) in R 4.3.1 (45). We centered and standardized all climatic predictors to mean zero and unit variance, 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 (46) (Fig. S23).

**Two-sex and female-dominant matrix projection models.** We used the climate-dependent vital rate regressions estimated above, combined with seed number, seed viability and seed germination 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  $x$  is a natural number with  $x \in [1, \dots, U]$ . The minimum possible size is one tiller and  $U$  is the 95th percentile of observed maximum size (35 tillers). 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:

$$F_{t+1}^R = \sum_1^U [p^F(x) \cdot c^F(x) \cdot d \cdot v(F_t, M_t) \cdot m \cdot \rho] F_{x,t} \quad (1)$$

$$M_{t+1}^R = \sum_1^U [p^F(x) \cdot c^F(x) \cdot d \cdot v(F_t, M_t) \cdot m \cdot (1 - \rho)] F_{x,t} \quad (2)$$

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  $\rho$  is the primary sex ratio (proportion of recruits that are female), which we assume to be 0.5 (20).

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

OSR is defined as the fraction of panicles that are female and is derived from the  $U \times 1$  vectors  $F_t$  and  $M_t$ :

$$v(F_t, M_t) = v_0 * [1 - \Phi(x)] \quad [3]$$

$$\text{where } \Phi(x) = \left( \frac{\sum_1^U p^F(x, z) c^F(x, z) F_{x, t}}{\sum_1^U p^F(x, z) c^F(x, z) F_{x, t} + p^M(x, z) c^M(x, z) M_{x, t}} \right)^\alpha$$

The summations tally the numbers 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. 3 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  $\alpha$  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 (42) and is summarized in (SI Appendix, section D). This experiment also provided parameters for seed number per panicle ( $d$ ) and germination rate ( $m$ ) estimated from a bayesian model to propagate the uncertainty in our estimates. 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:

$$F_{y, t+1} = [\sigma \cdot g^F(y, x = 1)] F_t^R + \sum_L^U [s^F(x) \cdot g^F(y, x)] F_{x, t} \quad [4]$$

$$M_{y, t+1} = [\sigma \cdot g^M(y, x = 1)] M_t^R + \sum_L^U [s^M(x) \cdot g^M(y, x)] M_{x, t} \quad [5]$$

The first terms indicate recruits that survived their first year and enter the size distribution of established plants. We estimated the seedling survival probability  $\sigma$  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  $\sigma$  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 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  $\lambda$  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  $\lambda$  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  $\lambda$ . 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  $\lambda$ , 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.

**Life Table Response Experiments.** 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  $\lambda$  on parameters associated with seasonal temperature and precipitation (47). 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  $\lambda$  calculated from the two sex model as response (48).

Second, to understand how climate drivers influence  $\lambda$  via sex-specific demography, we decomposed the effect of each climate variable on population growth rate ( $\lambda$ ) into contributions arising from the effect on each female and male vital rate using a "regression design" LTRE (49). This LTRE decomposes the sensitivity of  $\lambda$  to climate according to:

$$\frac{\partial \lambda}{\partial \text{climate}} \approx \sum_i \frac{\partial \lambda}{\partial \theta_i^F} \frac{\partial \theta_i^F}{\partial \text{climate}} + \frac{\partial \lambda}{\partial \theta_i^M} \frac{\partial \theta_i^M}{\partial \text{climate}} \quad [6]$$

where,  $\theta_i^F$  and  $\theta_i^M$  represent sex-specific parameters (the regression coefficients of the vital rate functions).

**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 ( $\Pr(\lambda > 1)$ ) conditional to temperature and precipitation of the dormant and growing seasons.  $\Pr(\lambda > 1)$  was calculated for the two-sex and female dominant MPMs using the proportion of the 300 posterior samples that lead to a  $\lambda \geq 1$  (50). Population viability in climate niche space was then represented as a contour plot with values of  $\Pr(\lambda \geq 1)$  at given temperature and precipitation for the growing season, holding dormant season climate constant, and vice versa.

$\Pr(\lambda > 1)$  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). Then, we added the species occurrences extracted from GBIF to the present time period map to explore how well our model predicts the presence of the species across its range.



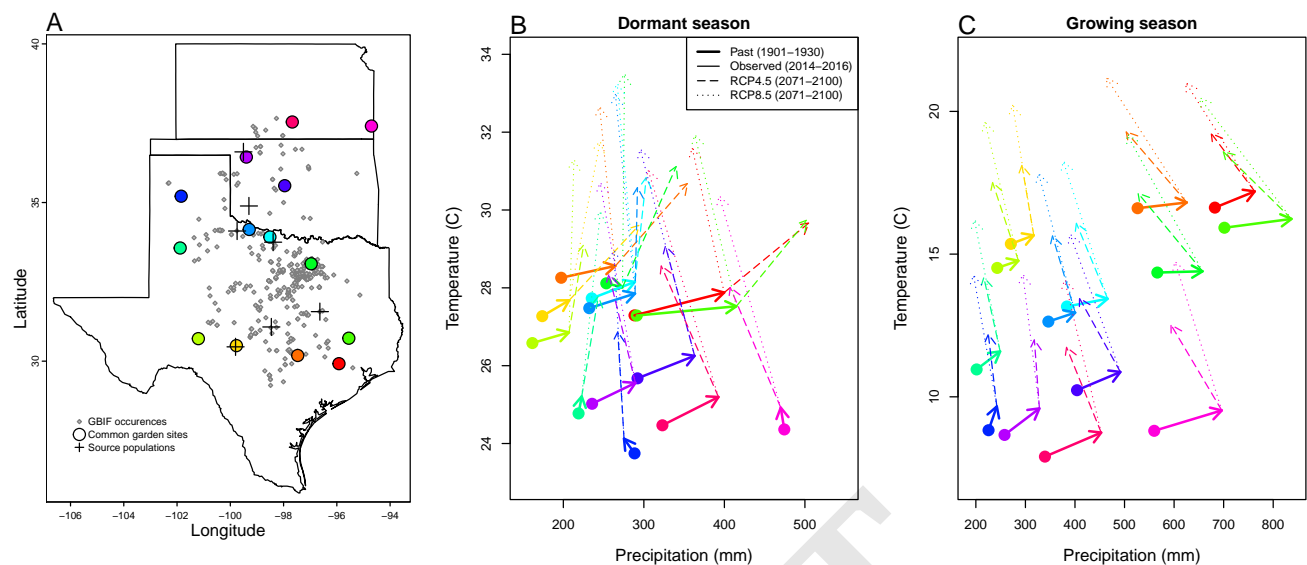
## 637 Data, Materials, and Software Availability

638 All data used in this paper are publicly available and cited  
639 appropriately (51). Should the paper be accepted, all computer  
640 scripts supporting the results will be archived in a Zenodo  
641 package, with the DOI included at the end of the article.  
642 During peer review, our code (Stan and R) is available at  
643 <https://github.com/jmoutouama/POAR-Forecasting>.

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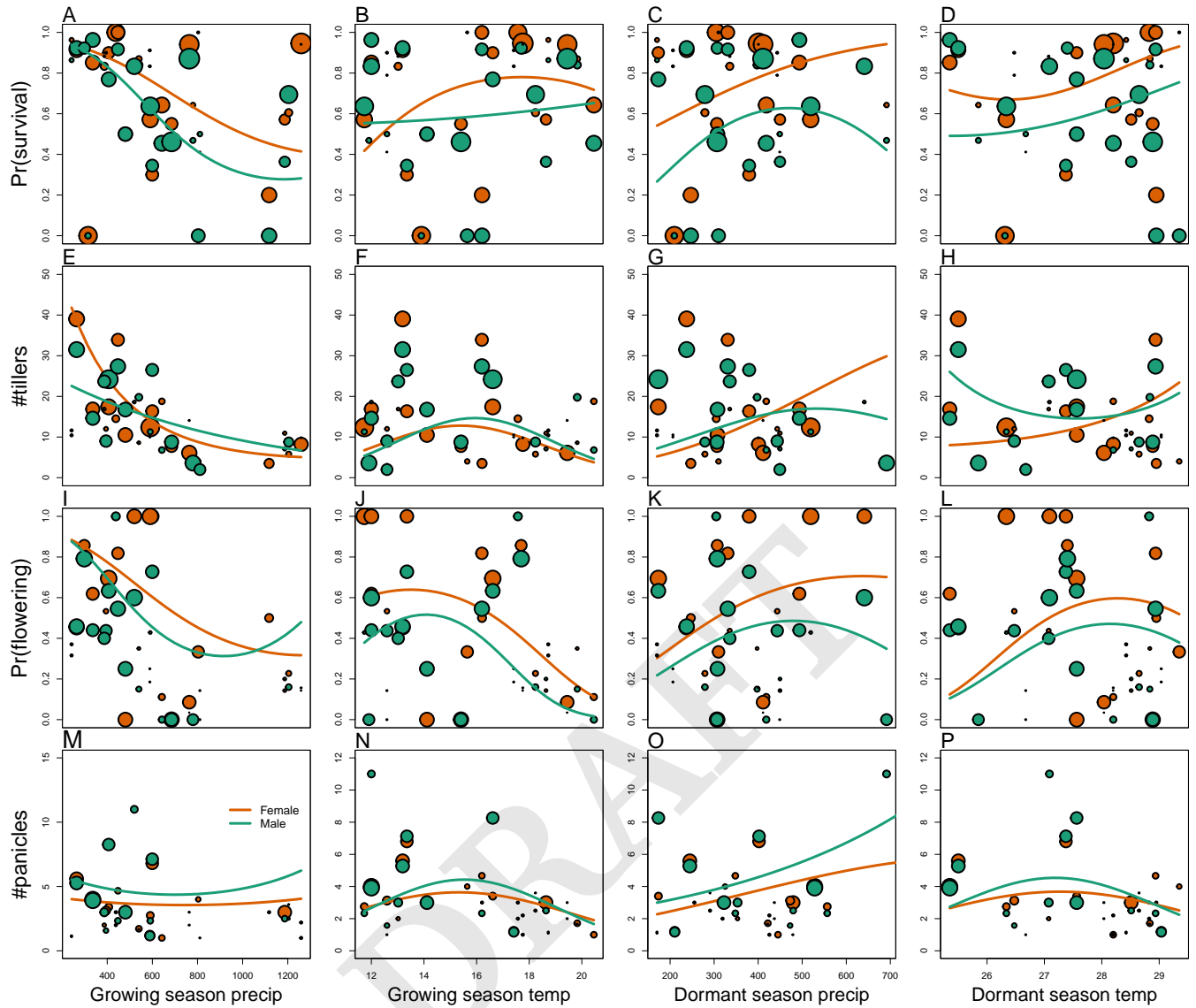
- 652 1. Bertrand R, et al. (2011) Changes in plant community composition lag behind climate warming  
653 in lowland forests. *Nature* 479(7374):517–520.
- 654 2. Lee-Yaw JA, et al. (2016) A synthesis of transplant experiments and ecological niche models  
655 suggests that range limits are often niche limits. *Ecology letters* 19(6):710–722.
- 656 3. Sexton JP, McIntyre PJ, Angert AL, Rice KJ (2009) Evolution and ecology of species range  
657 limits. *Annu. Rev. Ecol. Syst.* 40:415–436.
- 658 4. Davis MB, Shaw RG (2001) Range shifts and adaptive responses to quaternary climate  
659 change. *Science* 292(5517):673–679.
- 660 5. Pease CM, Lande R, Bull J (1989) A model of population growth, dispersal and evolution in a  
661 changing environment. *Ecology* 70(6):1657–1664.
- 662 6. Heilbut JC (2000) Lower species richness in dioecious clades. *The American Naturalist*  
663 156(3):221–241.
- 664 7. Hultine KR, et al. (2016) Climate change perils for dioecious plant species. *Nature Plants*  
665 2(8):1–8.
- 666 8. Morrison CA, Robinson RA, Clark JA, Gill JA (2016) Causes and consequences of spatial  
667 variation in sex ratios in a declining bird species. *Journal of Animal Ecology* 85(5):1298–1306.
- 668 9. Eberhart-Phillips LJ, et al. (2017) Sex-specific early survival drives adult sex ratio bias in  
669 snowy plovers and impacts mating system and population growth. *Proceedings of the National*  
670 *Academy of Sciences* 114(27):E5474–E5481.
- 671 10. Petry WK, et al. (2016) Sex-specific responses to climate change in plants alter population  
672 sex ratio and performance. *Science* 353(6294):69–71.
- 673 11. Field DL, Pickup M, Barrett SC (2013) Comparative analyses of sex-ratio variation in dioecious  
674 flowering plants. *Evolution* 67(3):661–672.
- 675 12. Gissi E, et al. (2023) Exploring climate-induced sex-based differences in aquatic and terrestrial  
676 ecosystems to mitigate biodiversity loss. *nature communications* 14(1):4787.
- 677 13. Pottier P, Burke S, Drobniak SM, Lagisz M, Nakagawa S (2021) Sexual (in) equality? a meta-  
678 analysis of sex differences in thermal acclimation capacity across ectotherms. *Functional*  
679 *Ecology* 35(12):2663–2678.
- 680 14. Ellis RP, et al. (2017) Does sex really matter? explaining intraspecific variation in ocean  
681 acidification responses. *Biology letters* 13(2):20160761.
- 682 15. Gissi E, Bowyer RT, Bleich VC (2024) Sex-based differences affect conservation. *Science*  
683 384(6702):1309–1310.
- 684 16. Gerber LR, White ER (2014) Two-sex matrix models in assessing population viability: when  
685 do male dynamics matter? *Journal of Applied Ecology* 51(1):270–278.
- 686 17. Miller TE, Shaw AK, Inouye BD, Neubert MG (2011) Sex-biased dispersal and the speed of  
687 two-sex invasions. *The American Naturalist* 177(5):549–561.
- 688 18. Shelton AO (2010) The ecological and evolutionary drivers of female-biased sex ratios: two-sex  
689 models of perennial seagrasses. *The American Naturalist* 175(3):302–315.
- 690 19. Lynch HJ, et al. (2014) How climate extremes—not means—define a species' geographic  
691 range boundary via a demographic tipping point. *Ecological Monographs* 84(1):131–149.
- 692 20. Miller TE, Compagnoni A (2022) Two-sex demography, sexual niche differentiation, and  
693 the geographic range limits of texas bluegrass (poa arachnifera). *The American Naturalist*  
694 200(1):17–31.
- 695 21. Milner-Gulland E (1994) A population model for the management of the saiga antelope. *Journal*  
696 *of Applied Ecology* pp. 25–39.
- 697 22. Jenouvrier S, et al. (2012) Effects of climate change on an emperor penguin population:  
698 analysis of coupled demographic and climate models. *Global Change Biology* 18(9):2756–  
699 2770.
- 700 23. McLean N, Lawson CR, Leech DI, van de Pol M (2016) Predicting when climate-driven  
701 phenotypic change affects population dynamics. *Ecology Letters* 19(6):595–608.
- 702 24. Iler AM, et al. (2019) Reproductive losses due to climate change-induced earlier flowering  
703 are not the primary threat to plant population viability in a perennial herb. *Journal of Ecology*  
704 107(4):1931–1943.
- 705 25. Reed PB, et al. (2021) Climate manipulations differentially affect plant population dynamics  
706 within versus beyond northern range limits. *Journal of Ecology* 109(2):664–675.
- 707 26. Konapala G, Mishra AK, Wada Y, Mann ME (2020) Climate change will affect global water  
708 availability through compounding changes in seasonal precipitation and evaporation. *Nature*  
709 *communications* 11(1):3044.
- 710 27. Cleland EE, Chiariello NR, Loarie SR, Mooney HA, Field CB (2006) Diverse responses of  
711 phenology to global changes in a grassland ecosystem. *Proceedings of the National Academy*  
712 *of Sciences* 103(37):13740–13744.
- 713 28. Pagel J, et al. (2020) Mismatches between demographic niches and geographic distributions

- are strongest in poorly dispersed and highly persistent plant species. *Proceedings of the*  
714 *National Academy of Sciences* 117(7):3663–3669.
- 715 29. Margaret EK E, et al. (2023) The trailing edge is everywhere: tree rings reveal the transient  
716 risk of extinction hidden inside climate envelope forecasts, (Los Alamos National Laboratory  
717 (LANL), Los Alamos, NM (United States)), Technical report.
- 718 30. Schultz EL, et al. (2022) Climate-driven, but dynamic and complex? a reconciliation of  
719 competing hypotheses for species' distributions. *Ecology letters* 25(1):38–51.
- 720 31. Merow C, Bois ST, Allen JM, Xie Y, Silander Jr JA (2017) Climate change both facilitates  
721 and inhibits invasive plant ranges in new england. *Proceedings of the National Academy of*  
722 *Sciences* 114(16):E3276–E3284.
- 723 32. Bawa KS (1980) Evolution of dioecy in flowering plants. *Annual review of ecology and*  
724 *systematics* 11:15–39.
- 725 33. Sasaki M, Hedberg S, Richardson K, Dam HG (2019) Complex interactions between local  
726 adaptation, phenotypic plasticity and sex affect vulnerability to warming in a widespread marine  
727 copepod. *Royal Society open science* 6(3):182115.
- 728 34. Cipollini ML, Whigham DF (1994) Sexual dimorphism and cost of reproduction in the dioecious  
729 shrub lindera benzoin (lauraceae). *American Journal of Botany* 81(1):65–75.
- 730 35. Bürlil S, Pannell JR, Tonnabel J (2022) Environmental variation in sex ratios and sexual  
731 dimorphism in three wind-pollinated dioecious plant species. *Oikos* 2022(6):e08651.
- 732 36. Angert AL, Bontrager MG, Ågren J (2020) What do we really know about adaptation at range  
733 edges? *Annual Review of Ecology, Evolution, and Systematics* 51(1):341–361.
- 734 37. Intergovernmental Panel On Climate Change (Ipcc) (2023) *Climate Change 2022 – Impacts,*  
735 *Adaptation and Vulnerability: Working Group II Contribution to the Sixth Assessment Report*  
736 *of the Intergovernmental Panel on Climate Change.* (Cambridge University Press), 1 edition.
- 737 38. Dietze MC, et al. (2018) Iterative near-term ecological forecasting: Needs, opportunities, and  
738 challenges. *Proceedings of the National Academy of Sciences* 115(7):1424–1432.
- 739 39. Hitchcock AS (1971) *Manual of the grasses of the United States.* (Courier Corporation) Vol. 2.
- 740 40. Kindiger B (2004) Interspecific hybrids of poa arachnifera × poa secunda. *Journal of New*  
741 *Seeds* 6(1):1–26.
- 742 41. Renganayaki K, Jessup R, Burson B, Hussey M, Read J (2005) Identification of male-specific  
743 aflp markers in dioecious texas bluegrass. *Crop science* 45(6):2529–2539.
- 744 42. Compagnoni A, Steigman J, Miller TE (2017) Can't live with them, can't live without them?  
745 balancing mating and competition in two-sex populations. *Proceedings of the Royal Society B:*  
746 *Biological Sciences* 284(1865):20171999.
- 747 43. Karger DN, et al. (2017) Climatologies at high resolution for the earth's land surface areas.  
748 *Scientific data* 4(1):1–20.
- 749 44. Stan Development Team (2023) RStan: the R interface to Stan. R package version 2.21.8.
- 750 45. R Core Team (2023) *R: A Language and Environment for Statistical Computing* (R Foundation  
751 for Statistical Computing, Vienna, Austria).
- 752 46. Piironen J, Vehtari A (2017) Comparison of bayesian predictive methods for model selection.  
753 *Statistics and Computing* 27:711–735.
- 754 47. Ellner SP, Childs DZ, Rees M, , et al. (2016) Data-driven modelling of structured populations.  
755 *A practical guide to the Integral Projection Model.* Cham: Springer.
- 756 48. Liaw A, Wiener M, , et al. (2002) Classification and regression by randomforest. *R news*  
757 2(3):18–22.
- 758 49. Caswell H (1989) Analysis of life table response experiments i. decomposition of effects on  
759 population growth rate. *Ecological Modelling* 46(3-4):221–237.
- 760 50. Diez JM, Giladi I, Warren R, Pulliam HR (2014) Probabilistic and spatially variable niches  
761 inferred from demography. *Journal of ecology* 102(2):544–554.
- 762 51. Miller T, Compagnoni A (2022) Data from: Two-sex demography, sexual niche differentiation,  
763 and the geographic range limits of texas bluegrass (*Poa arachnifera*). *American Naturalist,*  
764 *Dryad Digital Repository.* <https://doi.org/10.5061/dryad.kkwh70s5x>.
- 765

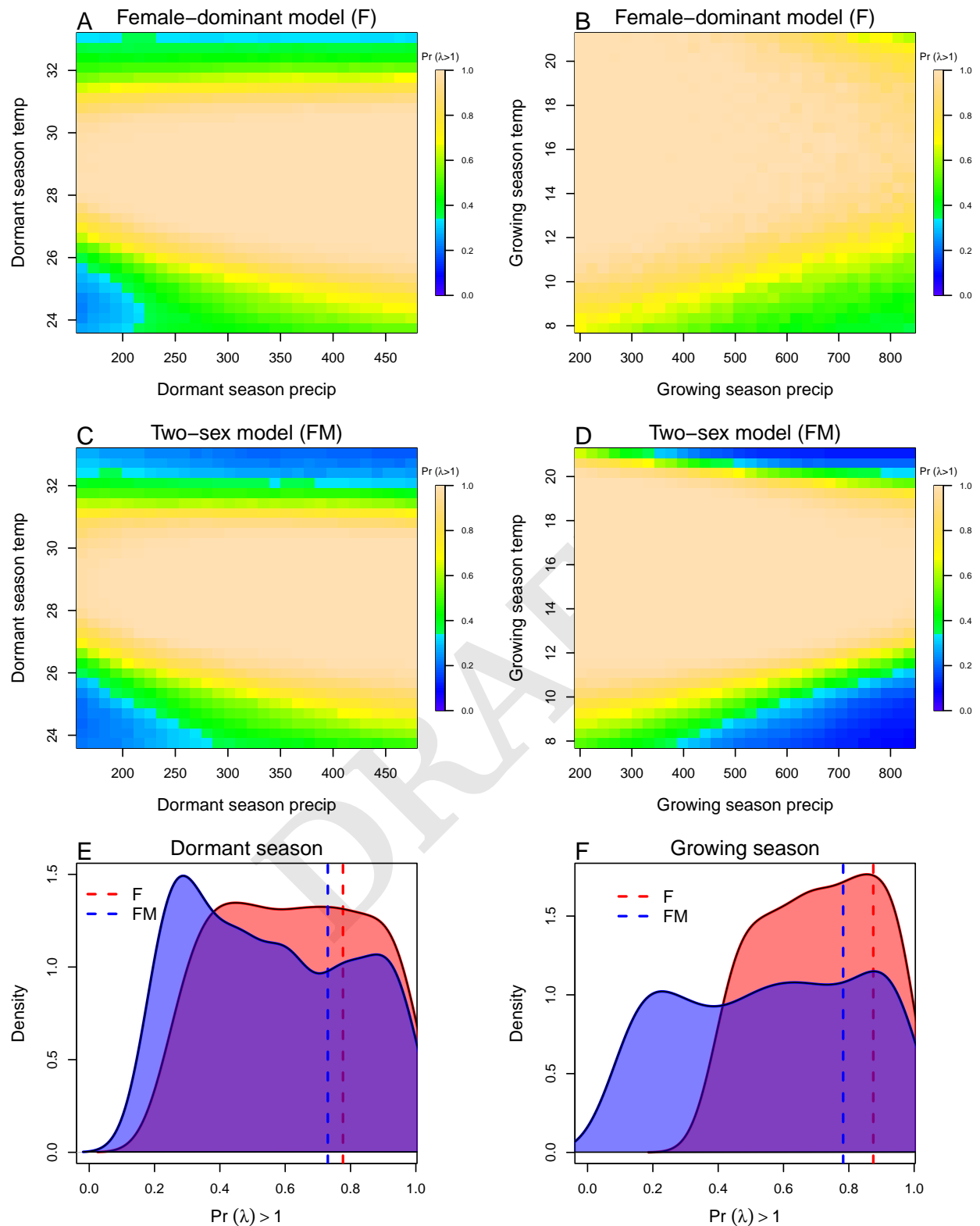


**Fig. 1.** (A), Common garden locations in Texas, Oklahoma, and Kansas (points) and (B, C) corresponding changes in growing and dormant season climate. Arrows in B,C connect past (1901–1930) and present (1990–2019) climate normals, and present and future (2071–2100) climate normals under RCP4.5 and RCP8.5 forecasts. Future forecasts are from MIROC5 but other climate models show similar patterns.

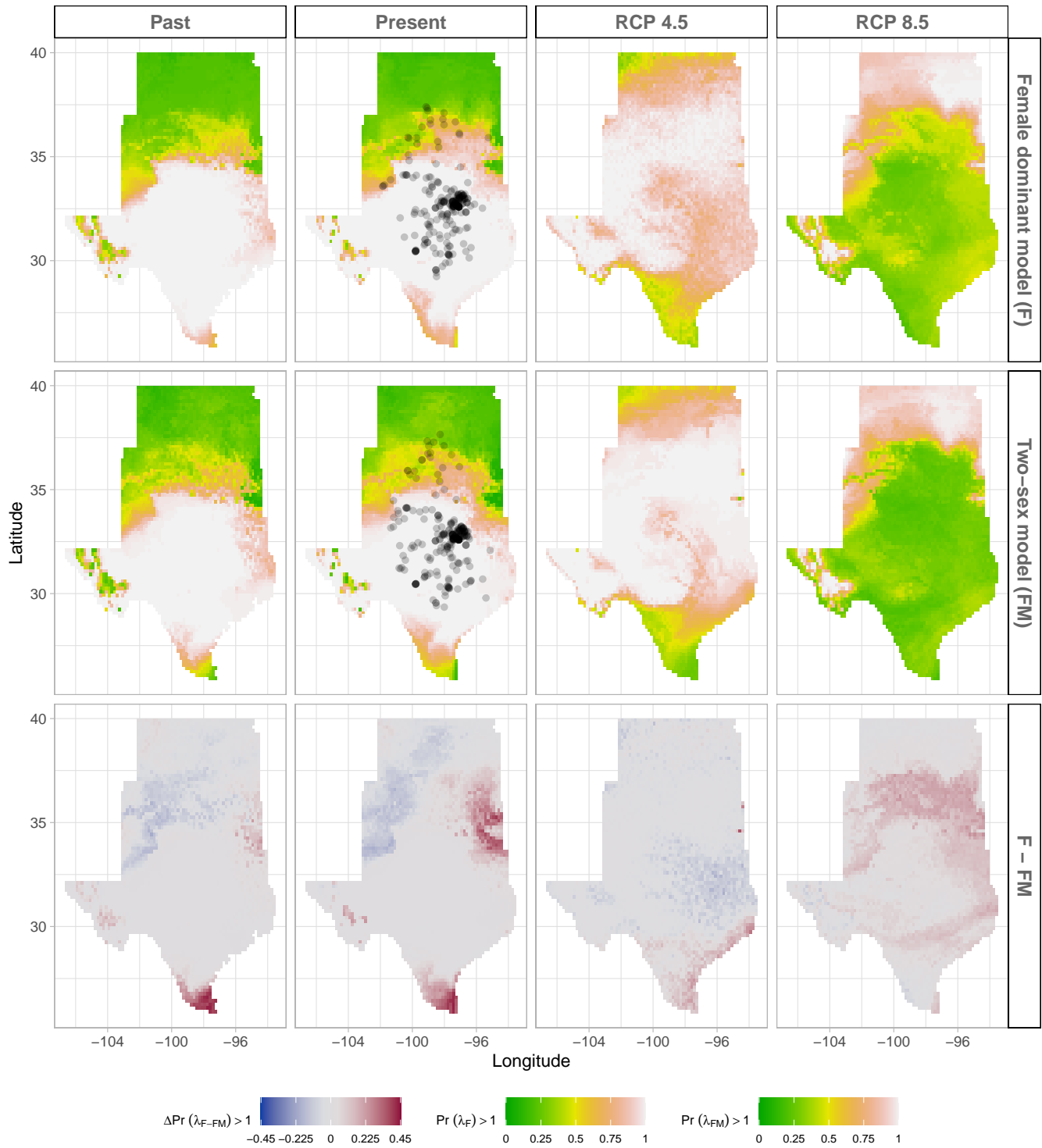




**Fig. 2.** Sex specific demographic response to climate across species range. (A, B, C, D) Probability of survival as a function of precipitation and temperature of the growing and dormant season. (E, F, G, H) Change in number of tillers as a function of precipitation and temperature of the growing 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. The fitted lines were estimated using only one climate covariate, while the other covariates and size were held constant.



**Fig. 3.** A two-dimensional representation of the predicted niche shift over time (past, present and future climate conditions). (A, B, C, D) show predicted probabilities of self-sustaining populations,  $\Pr(\lambda > 1)$  conditional on precipitation and temperature of the dormant and growing season. (E, F) show difference in niche estimation between the female dominant model and the two-sex model for each season. The pink color indicates the female dominant (F) while the violet represents the two-sex models (FM). The dash line represents the mean probability for each model.



**Fig. 4.** 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. 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.