

Two-sex demography, sexual niche differentiation, and the geographic range limits of Texas bluegrass (*Poa* *arachnifera*)

Tom E.X. Miller^{1,*} and Aldo Compagnoni^{2,3}

The authors wish to be identified to the reviewers.

1. Program in Ecology and Evolutionary Biology, Department of BioSciences, Rice University, Houston, TX 77005; 2. Institute of Biology, Martin Luther University Halle-Wittenberg, Halle, Germany; 3. German Centre for Integrative Biodiversity Research (iDiv), Leipzig, Germany; * Corresponding author; e-mail: tom.miller@rice.edu

Manuscript elements: Figures 1–6, online appendices A–C. Figure 2 and Figure 6 are to print in color.

Keywords: demography; dioecy; intra-specific niche heterogeneity; matrix projection model; sex ratio; range limits.

Manuscript type: Article.

Prepared using the suggested L^AT_EX template for *Am. Nat.*

Abstract

1 Understanding the mechanisms that generate biogeographic range limits is a long-standing
2 goal of ecology. It is widely hypothesized that distributional limits reflect the envi-
3 ronmental niche, but this hypothesis is complicated by widespread potential for intra-
4 specific niche heterogeneity. In dioecious species, sexual niche differentiation may cause
5 divergence between the sexes in their limits of environmental suitability. We studied
6 range boundary formation in Texas bluegrass (*Poa arachnifera*), a perennial dioecious
7 plant, testing the alternative hypotheses that range limits reflect the niche limits of fe-
8 males only versus the combined contributions of females and males, including their
9 inter-dependence via mating. Common garden experiments across a longitudinal aridity
10 gradient revealed female-biased flowering approaching eastern range limits, suggesting
11 that mate limitation may constrain the species' distribution. However, a demographic
12 model showed that declines in λ approaching range limits were driven almost entirely
13 by female vital rates. The dominant role of females was attributable to seed viability
14 being robust to sex ratio variation and to low sensitivity of λ to reproductive transitions.
15 We suggest that female-dominant range limits may be common to long-lived species
16 with polygamous mating systems, and that female responses to environmental drivers
17 may often be sufficient for predicting range shifts in response to environmental change.

Keywords

18
19 demography; dioecy; intra-specific niche heterogeneity; matrix projection model; sex
20 ratio; range limits

21

Introduction

22 Understanding the processes that generate species' distributional limits is a foundational
23 objective of ecology. The niche concept is central to theory for range limits (Hutchinson,
24 1958) and available evidence suggests that geographic distributions may often be inter-
25 preted as ecological niches "writ large" (Hargreaves et al., 2013; Lee-Yaw et al., 2016).
26 Species distribution modeling has long capitalized on this idea to infer niche charac-
27 teristics from statistical associations between occurrence and environmental variables.
28 In contrast, there is growing interest in process-based models of range limits, where
29 individual-level demographic responses to environmental variation inform predictions
30 about the ecological niche and environmental limits of population viability (i.e., at least
31 replacement-level population growth, $\lambda \geq 1$) (Diez et al., 2014; Merow et al., 2017, 2014).
32 The mechanistic understanding offered by process-based models of range limits pro-
33 vides a potentially powerful vehicle for predicting range shifts in response to current
34 and future environmental change (Ehrlén and Morris, 2015; Evans et al., 2016).

35 The widespread idea that range limits reflect niche limits intersects awkwardly with
36 another pervasive concept in ecology: intra-specific niche heterogeneity. This refers to
37 the fact that individuals within a population or species may differ in their interactions
38 with the biotic and/or abiotic environment (Araújo et al., 2011; Bolnick et al., 2002; Holt,
39 2009). Intra-specific niche differences may correspond to demographic state variables
40 such as life stage, size class or other, unmeasured aspects of individual identity. If range
41 limits are a geographic manifestation of niche limits, but a single population or species
42 may be comprised of many niches, then whose niche is it that determines the geographic
43 distribution and how would we know?

44 Sexual niche differentiation is a common form of intra-specific niche heterogeneity
45 (Bolnick et al., 2002) and has been widely documented in animals (the vast majority
46 of which are dioecious) and plants (ca. 6% of angiosperms are dioecious: Renner and
47 Ricklefs 1995). The prevalence of sexual niche differentiation was recognized by Darwin
48 (1871), who described “different habits of life, not related...to the reproductive functions”
49 of females and males. There are now many examples of sex differences in trophic posi-
50 tion (Law and Mehta, 2018; Pekár et al., 2011), habitat use (Bowyer, 2004; De Lisle et al.,
51 2018; Phillips et al., 2004), and responses to climate (Gianuca et al., 2019; Petry et al.,
52 2016; Rozas et al., 2009), differences that may or may not be accompanied by sexual
53 dimorphism. It has been hypothesized that sexual niche differentiation may evolve by
54 natural selection when it reduces competitive or other antagonistic interactions between
55 the sexes (Bolnick and Doebeli, 2003; De Lisle and Rowe, 2015), as a byproduct of nat-
56 urally or sexually selected size dimorphism (Shine, 1989; Temeles et al., 2010), or when
57 females and males pay different costs of reproduction (Bierzychudek and Eckhart, 1988).

58 Sexual niche differentiation can translate to sex-specific **demographic** advantages in
59 different environments, causing skew in the operational sex ratio (OSR: relative abun-
60 dance of females and males available for mating) even if the primary (birth) sex ratio is
61 unbiased (Eberhart-Phillips et al., 2017; Shelton, 2010; Veran and Beissinger, 2009). In-
62 deed, environmental clines in OSR have been widely documented in plants and animals
63 at fine spatial scales (Bertiller et al., 2002; Bisang et al., 2020; Eppley, 2001; Groen et al.,
64 2010; Hultine et al., 2018) as well as broader climatic clines across alititudtes or latitudes
65 (Caruso and Case, 2007; Dudaniec et al., 2021; Ketterson and Nolan Jr, 1976; Petry et al.,
66 2016). At range margins, where environments **may be** extreme relative to the range core,
67 demographic differences between the sexes, and hence skew in the OSR, may be greatest.

68 In dioecious plants, for example, populations at upper altitudes and latitudes and in the
69 more xeric margins of species' ranges tend to be male-biased, **possibly due to the greater**
70 **resource demands of female flower and seed production** (Field et al., 2013b).

71 Returning to the question of whose niche determines range limits given the potential
72 for sexual niche differentiation, classic ecological theory assumes the answer. "Female
73 dominance" is a pervasive, often implicit feature of population-dynamic models whereby
74 male availability is assumed to have no influence on female fertility (Caswell and Weeks,
75 1986; Miller and Inouye, 2011; Rankin and Kokko, 2007). This assumption is wrong,
76 of course, but it may be *adequate* when the sex ratio is balanced or exhibits little varia-
77 tion. The female-dominant perspective predicts that female responses to environmental
78 variation should govern range limits (Fig. 1). However, females may be mate-limited
79 in environments in which they are favored, which could reduce population viability in
80 marginal environments **that are more suitable for females than males**. This creates an
81 additional, "two-sex" pathway by which environmental drivers may set distributional
82 limits, via perturbations to the mating pool that arise from sex-specific responses to the
83 environment (Fig. 1).

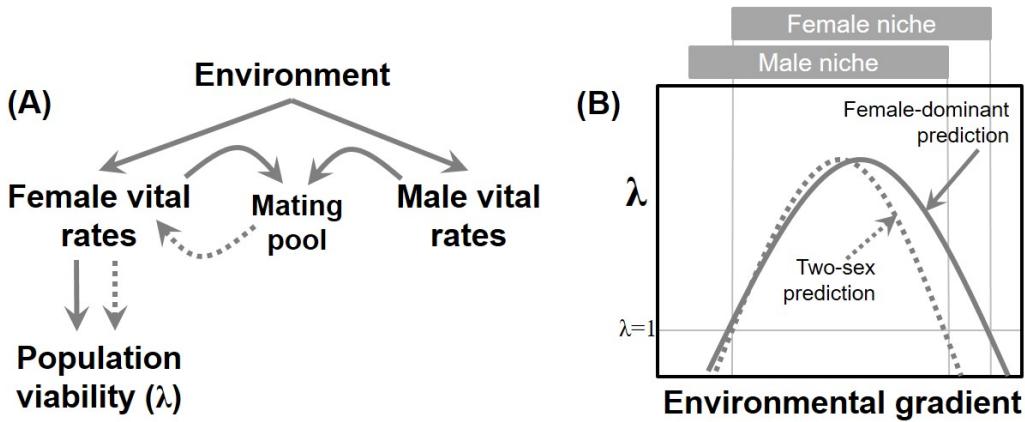


Figure 1: Hypotheses for how environmental variation can affect population viability and range limits in dieocious species. Under the female-dominant hypothesis, environmental drivers affect population growth (λ) through effects on females, alone (A). In geographic / environmental space, this translates to range boundaries that arise at the limits of the female environmental niche, irrespective of where they fall with respect to the male niche (B). Under the two-sex hypothesis, environmental drivers can affect λ through sex-specific responses, which may skew the sex ratio of the mating pool and feed back to affect female fertility via mate availability (A). In this case, expectations for range limits may differ from the female-dominant prediction, since mate limitation in environments that favor females over males may reduce population viability (B). These are alternative hypotheses in the strict sense, but as the role of males becomes weaker the two-sex prediction converges on the female-dominant prediction.

84 Here we ask whether female demographic responses to environmental variation,
 85 alone, are sufficient to understand the ecological origins of range limits, or whether
 86 males and female-male interactions must additionally be considered. As an experimen-
 87 tal model, we worked with a dieocious plant species (Texas bluegrass [*Poa arachnifera*])
 88 narrowly distributed across the sharp longitudinal aridity gradient of the southern Great
 89 Plains, US (Fig. 2). We hypothesized that sexual niche differentiation with respect to lon-
 90 gitudinal variation in aridity may lead to skewed sex ratios approaching range limits,
 91 and that mate limitation at environmental extremes could cause range boundaries to

92 deviate from female-dominant expectations.

93 This study was conducted in four parts. First, we conducted surveys to ask whether
94 natural populations of Texas bluegrass exhibit longitudinal clines in operational sex ra-
95 tio across the aridity gradient. Second, we conducted a common garden experiment at
96 14 sites throughout the southern Great Plains to quantify sex-specific demography in
97 variable abiotic environments. Third, we conducted a local sex ratio manipulation ex-
98 periment to quantify how viable seed production by females responds to variation in
99 OSR. Finally, we connected sex-specific demography with inter-sexual mating dynam-
100 ics in a two-sex modeling framework to derive demographically-driven predictions for
101 geographic limits of population viability ($\lambda \geq 1$). We analyzed the demographic model
102 to decompose the decline in λ approaching range limits into contributions from female-
103 dominant and two-sex pathways (Fig. 1).

104 **Materials and methods**

105 *Study system and natural population surveys*

106 *Poa arachnifera* (Texas bluegrass) is a perennial, cool-season grass endemic to the southern
107 Great Plains. This species occurs almost exclusively in central Texas, Oklahoma, and
108 southern Kansas (Fig. 2) though there are occasional records of adventive populations in
109 other U.S. states¹. Seasonal rainfall in this region has two annual peaks, in spring and fall,
110 which coincide with the growing-season of this C3 species. Like all grasses, *P. arachnifera*
111 is wind-pollinated. Individuals can be sexed only when flowering, in early spring, based
112 on the presence of stigmas (females) or anthers (males) in the inflorescence. Following

¹<http://bonap.net/Napa/TaxonMaps/Genus/County/Poa>

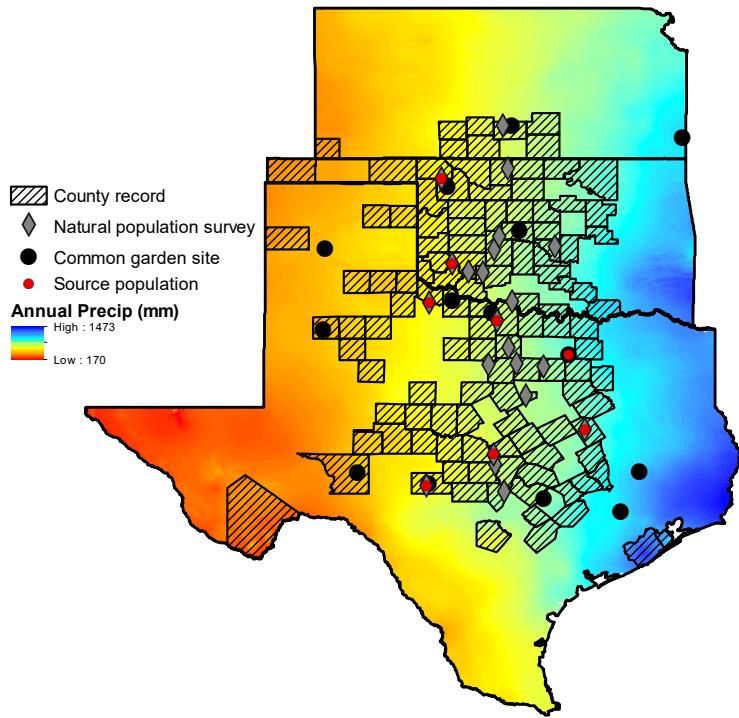


Figure 2: Geographic and environmental distribution of *P. arachnifera* in Texas, Oklahoma, and Kansas. Hatched shapes show counties with herbarium records of occurrence. Color shows geographic variation in annual precipitation (mm) based on 30-year normals from WorldClim (Fick and Hijmans, 2017). Grey diamonds show natural population census locations, black points show sites for the common garden transplant experiment, and red points show locations of the source populations planted in each common garden site.

inflorescence and seed production, plants go dormant for the hot summer months and vegetative growth resumes in fall. Individuals grow via rhizomes to form patches that may be as large as $50m^2$ in area. Sex in *P. arachnifera* is genetically based (Renganayaki et al., 2005, 2001) and the primary sex ratio is 1:1 (J. Goldman, USDA-ARS, *unpubl. data*). The rhizomatous growth habit allowed us to clonally propagate large numbers of known-sex individuals for experiments, as we describe below.

We surveyed *P. arachnifera* across its range to establish whether natural populations

120 exhibited geographic clines in OSR corresponding to the longitudinal aridity gradient.
121 We visited 14 populations in spring 2012 and 8 in spring 2013 (Table A1, Fig. 2). At
122 each location, we searched for *P. arachnifera* along roads, trails, or creek drainages and
123 recorded the number of female and male patches that we encountered and the number
124 of inflorescences in each patch. To quantify the mating environment, we focus our anal-
125 yses on the sex ratio of inflorescences rather than patches, since a single patch makes
126 different contributions to the mating pool depending on whether it has few or many
127 inflorescences.

128 *Statistical analysis of natural population surveys*

129 We fit a binomial generalized linear model (glm), where “successes” were female in-
130 florescences and “trials” were total inflorescences, to test whether the OSR varied sys-
131 tematically with respect to longitude. Here and in the experiments that follow we use
132 longitude as a proxy variable that captures all east-west environmental variation, notably
133 precipitation (Fig. 2) but also factors that co-vary with precipitation such as productivity.
134 In Appendix XX, we used WAIC-based model selection to show that models using pre-
135 cipitation and longitude as environmental covariates were statistically indistinguishable,
136 which suggests that longitude is an adequate proxy for aridity. This statistical model
137 and all those that follow were fit in a Bayesian statistical framework using Stan (Carpen-
138 ter et al., 2017) and R package ‘rstan’ (Stan Development Team, 2020) with vague priors
139 on all parameters. In all cases, model fit was assessed with posterior predictive checks
140 (Gelman et al., 1996). All code for statistical and demographic modeling is available at
141 <https://github.com/texmiller/POAR-range-limits>.

142

Common garden experiment

143 Source material and experimental design

144 We established a common garden experiment at 14 sites throughout and beyond the
145 geographic distribution of *P. arachnifera* (Fig. 2, Table A2). Experimental sites spanned
146 latitudinal and longitudinal variation, though we focus here on longitude. During the
147 three years of this experiment (2014–2017), total precipitation at each site closely tracked
148 longitude (Fig. A1), as expected based on longer-term climate trends (Fig. 2). Source
149 material for the experiment came from 8 sites, most of which were a subset of the sites
150 that were visited for the natural population survey (Table A1, Fig. 2). At these sites, we
151 collected vegetative tillers from flowering individuals of each sex (mean: 11.6 individuals
152 per site, range: 2–18). These were brought back to the Rice University greenhouse, where
153 they were clonally propagated in ProMix potting soil and supplemented with Osmocote
154 slow-release fertilizer at 78–80°F under natural humidity and light.

155 Common gardens were set up in Fall (October–December) 2014. At each site, we es-
156 tablished 14 experimental blocks, which corresponded to a tree or woodland edge, pro-
157 viding partial shade that mimics this species' natural micro-environment. We planted
158 3 females and 3 males in each block, for a total of 42 individuals per sex per site and
159 1176 total plants across sites, with all source collections represented at all sites. Indi-
160 viduals were spaced within blocks to allow space for rhizomatous growth that could be
161 clearly attributed to individual transplants. To promote establishment, we cleared vege-
162 tation immediately surrounding transplants and provided ca. 1 L of water at the time of
163 transplanting but provided no subsequent watering, fertilization, or competitor removal.

164 We visited each site during May of 2015, 2016, and 2017. For each individual in each

165 year, we recorded data for four demographic vital rates: survival status (alive or dead),
166 size (number of tillers and patch area), flowering status (reproductive or vegetative), the
167 number of panicles produced by flowering plants.

168 *Statistical analysis of common garden experiment*

169 We analyzed the demographic vital rates with generalized linear mixed models in a
170 hierarchical Bayesian framework. All the vital rates shared a common linear predictor for
171 the expected value that included fixed effects of size, sex, linear and quadratic terms for
172 longitude, and all 2- and 3-way interactions. We included quadratic effects of longitude
173 to account for the possibility of non-monotonic responses, following the hypothesis that
174 fitness may peak in the center of the range. The linear predictor also included random
175 effects of site, block, and source population of the transplant. We pooled all three years
176 of observations for analysis so our results are implicitly averaged over years.

177 The survival and flowering data were Bernoulli distributed, and these models applied
178 the logit link function. We modeled panicle counts as zero-truncated negative binomial
179 using the log link. For growth, we modeled tiller number with a zero-truncated Poisson-
180 Inverse Gaussian (PIG) distribution. For flowering and panicle production in year t , the
181 size covariate was the natural logarithm of tiller number in year t . For survival and
182 size in year t , the size covariate was the natural logarithm of tiller number in year $t - 1$
183 (for 2015 data, size in year $t - 1$ was transplant size at the time of planting). Posterior
184 predictive checks indicated that these models described the data well (Fig. B1).

185 In follow-up analyses, we tested the addition of a climate mismatch variable that
186 quantified the deviation between mean annual precipitation of each source population
187 and common garden location. This analysis allowed us to evaluate whether local adap-

tation to climate may have contributed to variation in demographic performance across common garden sites. This was motivated by the observation that most source populations came from the interior of the geographic range (MAP) and were brought to edge and beyond-edge locations that were much drier or wetter than their historical climate regime. The local adaptation hypothesis predicts that demographic performance declines with increasing climatic deviation between common garden and source population locations. We added the absolute value of mean annual precipitation mismatch (using 30-year normals) as a covariate to the vital rate models described above.

Sex ratio experiment

At one site near the center of the range (Lake Lewisville Environmental Learning Area, Texas), we established a separate experiment to quantify how sex ratio variation affects female reproductive success. Details of this experiment, which was conducted in 2014–2015, are described in Compagnoni et al. 2017. Briefly, we established 124 experimental populations in $0.4m \times 0.4m$ plots that varied in population density (1–48 plants/plot) and sex ratio (0–100%female), with 2–4 replicates for each of 34 density-sex ratio combinations. The experiment was established ca. 1 km from a natural population at this site and plots were situated with a minimum of 15 m spacing, a buffer that was intended to limit pollen movement between plots (pilot data indicated that $\geq 90\%$ of wind pollination occurred within 13m). We measured female reproductive success in different density and sex ratio environments by collecting panicles from a subset of females in each plot at the end of the reproductive season. In the lab, we counted the total number of seeds on each panicle.

210 In Texas bluegrass, unfertilized seeds shatter from the panicle along with fertilized
211 seeds, so seed counts reflect female reproductive effort (seeds initiated) and not mating
212 success (seeds fertilized). We therefore assessed seed fertilization in two ways. First,
213 we conducted greenhouse-based germination trials using 25 seeds per panicle from 112
214 panicles belonging to 84 census females spanning the range of sex ratio variation. We
215 also conducted tetrazolium-based seed viability assays to estimate seed fertilization in-
216 dependently of germination, since some fertilized seeds may fail to germinate during
217 our trials. Tetrazolium trials used 17–57 seeds per panicle (mode: 30) from 65 panicles
218 belonging to 63 females, a subset of those used for the germination trials. To perform
219 these assays, we first let seed batches imbibe on a moistened paper towel for 12 h. We
220 then bisected the seeds in half and soaked them in a pH buffer solution containing 0.1%
221 of tetrazolium for 12 h. The pH buffer solution contained 0.57% of sodium phosphate
222 and 0.36% of potassium phosphate. A seed was scored as viable if the embryo stained
223 pink.

224 *Statistical analysis of sex ratio experiment*

225 Our previous study examined how interactions between density and frequency (sex ra-
226 tio) dependence contributed to female reproductive success (Compagnoni et al., 2017).
227 Here we focus solely on sex ratio variation, averaging over variation in density. Our goal
228 was to estimate a ‘mating function’ that defines how availability of male panicles affects
229 the viability of seeds on female panicles. We modeled the seed viability data with a
230 binomial distribution where the probability of viability (v) was given by:

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

231 where OSR is the operational sex ratio (fraction of panicles that were female) in our
232 experimental populations. This function has the properties, supported by our previous
233 work (Compagnoni et al., 2017), that seed viability is maximized at v_0 as OSR approaches
234 zero (strongly male-biased) and goes to zero as OSR approaches 1 (strongly female-
235 biased). Parameter α controls how viability declines with increasing female bias.

236 We modeled germination data from greenhouse trials similarly, where counts of ger-
237 minants were modeled as binomial successes. Since germination was conditional on seed
238 viability, the probability of success was given by the product $v * g$, where v is a function
239 of OSR (Eq. 1) and g is assumed to be constant. The germination trials alone do not
240 provide enough information to independently estimate v and g but the combination of
241 viability and germination data allowed us to do so. For both viability and germination,
242 we found that accounting for overdispersion with a beta-binomial response distribution
243 improved model fit.

244 *Demographic model of range limits*

245 The statistical models for the common garden and sex ratio experiments provided the
246 backbone of the full demographic model, a matrix projection model (MPM) structured
247 by size (tiller number) and sex. Following the statistical modeling, the MPM accommo-
248 dates longitude as a predictor variable, allowing us to identify the longitudinal limits of
249 population viability ($\lambda \geq 1$) and investigate the underlying drivers of population decline

250 at range limits.

251 For a given longitude, let $F_{x,t}$ and $M_{x,t}$ be the number of female and male plants of
252 size x in year t , where $x \in \{1, 2, \dots, U\}$ and U is the maximum number of tillers a plant can
253 attain (set to the 99th percentile of observed maximum size). We also include additional
254 state variables for new recruits, F_t^R and M_t^R , which we assume do not reproduce in their
255 first year. For ease of presentation, we do not symbolically show longitude effects in the
256 vital rate functions for growth, survival, flowering, and panicle production but these all
257 included longitude effects on the intercept and slope (with respect to size) as a second-
258 order polynomial, following the statistical models. We assume that the parameters of sex
259 ratio-dependent mating (Eq. 1) do not vary with longitude.

260 For a pre-breeding census, the expected numbers of recruits in year $t + 1$ is given by:

$$F_{t+1}^R = \sum_{x=1}^U [p^F(x) \cdot c^F(x) \cdot d \cdot v(\mathbf{F}_t, \mathbf{M}_t) \cdot m \cdot \rho] F_{x,t} \quad (2)$$

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

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

$$v(\mathbf{F}_t, \mathbf{M}_t) = v_0 * \left[1 - \left(\frac{\sum_{x=1}^U p^F(x)c^F(x)F_{x,t}}{\sum_{x=1}^U p^F(x)c^F(x)F_{x,t} + p^M(x)c^M(x)M_{x,t}} \right)^\alpha \right] \quad (4)$$

267 Finally, the dynamics of the size-structured component of the population are given
 268 by:

$$F_{y,t+1} = [\sigma \cdot g^F(y, x = 1)] F_t^R + \sum_{x=1}^U [s^F(x) \cdot g^F(y, x)] F_{x,t} \quad (5)$$

$$M_{y,t+1} = [\sigma \cdot g^M(y, x = 1)] M_t^R + \sum_{x=1}^U [s^M(x) \cdot g^M(y, x)] M_{x,t} \quad (6)$$

269 For both females and males, the first term represents seedlings that survived their first
 270 year and enter the size distribution of established plants. Because our common gar-
 271 den experiment relied on greenhouse-raised transplants, we had little information on
 272 these early life cycle transitions. We used the seedling survival probability (σ) from our
 273 demographic studies of the hermaphroditic, perennial congener *Poa autumnalis* in east
 274 Texas (T.E.X. Miller and J.A. Rudgers, *unpublished data*) as a stand-in for *P. arachnifera*,
 275 and we assume this probability was constant across sexes and longitudes (posterior
 276 mean $\sigma = 0.09$). We also assume that surviving seedlings reach size y with probabil-
 277 ity $g(y, x = 1)$, the expected future size of 1-tiller plants from the transplant experiment.
 278 The second term represents survival and size transition of established plants from the
 279 previous year, where s and g give the probabilities of surviving at size x and growing
 280 from sizes x to y , respectively, and superscripts indicate that these functions may be
 281 unique to females (F) and males (M).

282 Because the two-sex MPM is nonlinear (vital rates affect and are affected by popu-
 283 lation structure) we estimated the asymptotic geometric growth rate (λ) by numerical
 284 simulation, and repeated this across a range of longitudes. We used a regression-style
 285 Life Table Response Experiment (Caswell, 2001) to decompose the change in λ towards
 286 range limits into contributions from female and male vital rates (the female-dominant
 287 hypothesis predicts that declines in λ at range limits are driven solely by females). The
 288 LTRE approximates the change in λ with longitude as the product of the sensitivity of λ
 289 to the parameters times the sensitivity of the parameters to longitude, summed over all
 290 parameters:

$$\frac{\partial \lambda}{\partial \text{Longitude}} \approx \sum_i \frac{\partial \lambda}{\partial \theta_i^F} \frac{\partial \theta_i^F}{\partial \text{Longitude}} + \frac{\partial \lambda}{\partial \theta_i^M} \frac{\partial \theta_i^M}{\partial \text{Longitude}} \quad (7)$$

291 Here, θ_i^F and θ_i^M represent sex-specific parameters: the regression coefficients for the
 292 intercepts and slopes of size-dependent vital rate functions. Because LTRE contributions
 293 are additive, we summed across vital rates to compare the total contributions of female
 294 and male parameters. Finally, we compared the two-sex MPM to the corresponding
 295 female-dominant model (Fig. 1B) by setting $v(\mathbf{F}_t, \mathbf{M}_t) = v_0$, which decouples female
 296 fertility from the composition of the mating pool.

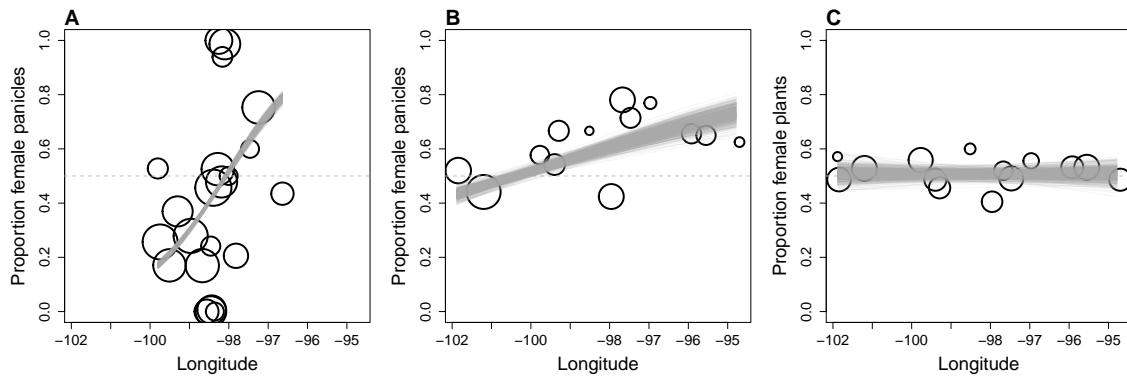


Figure 3: Sex ratio variation of *P. arachnifera* across its longitudinal distribution. **A**, Operational sex ratio (fraction of panicles that were female) in 22 natural populations; **B**, Operational sex ratio and **C**, sex ratio (fraction of plants that were female) in 14 common gardens. Within panels, point size is proportional to sample size (total number of panicles in **A,B** and total plants in **C**) as follows: **A**, min: 45, max: 2148; **B**, min: 1, max: 1021; **C**, min: 2, max: 79. In **B,C**, data are pooled across years. **Gray lines show 500 samples from the posterior distribution of fitted binomial GLMs.**

297

Results

298

Sex ratio variation in natural populations

299 We found wide variation in operational sex ratio (proportion of total panicles that were
 300 female) across 22 natural populations of *P. arachnifera*, including female-only and male-
 301 only populations (Fig. 3A). There was a longitudinal trend to sex ratio variation, with
 302 male-biased panicle production in the western parts of the range and female-biased pan-
 303 icle production in the east.

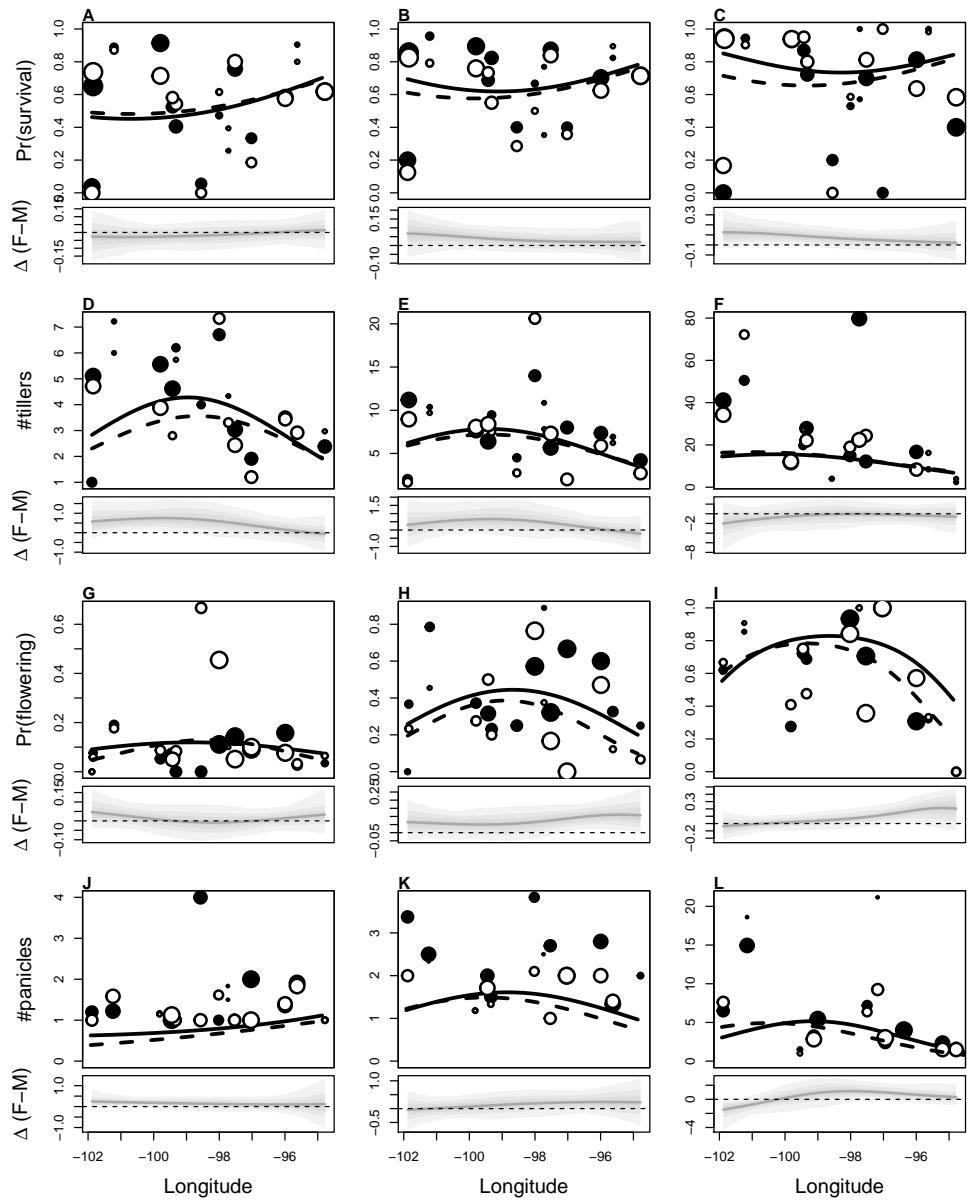


Figure 4: Sex-, size-, and longitude-related variation in: A–C, inter-annual probability of survival; D–F, inter-annual growth (change in number of tillers); G–I, probability of flowering; J–L, number of panicles produced given flowering. Points show means by site for females (filled) and males (open) and small (left column), medium (middle column), and large (right column) size classes (discretized, for visualization only). Point size is proportional to the sample size of the mean. Lines show fitted statistical models for females (solid) and males (dashed) 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 longitude (positive and negative values indicate female and male advantage, respectively). Shaded contours show the 25, 50, 75, and 95 percentiles of the posterior distribution. Dashed horizontal line shows zero difference.

304

Geographic variation in sex-specific demography

305 In year one, there was near-total mortality of transplants at three sites in the common
306 garden experiment due to various catastrophes (a flood, a drought, a pack of voles);
307 otherwise, there was high (95%) establishment. There was strong longitudinal variation
308 in demography, including sex-specific demographic responses that varied across vital
309 rates and interactions between size, sex, and longitude. Where sex-specific demographic
310 responses occurred, they were almost always in favor of females. In Fig. 4, we show
311 binned means of raw data and fitted vital rate models for four vital rates (rows) and
312 three size classes (columns); size was discretized for visualization only. This figure also
313 shows the posterior distributions for the difference between the sexes across longitudes.

314 Annual survival probability was predicted to peak at western and eastern range
315 edges and was lowest at intermediate longitudes (Fig. 4A-C). There was a modest fe-
316 male survival advantage but only at the western range edge for large sizes. Other vital
317 rates showed the opposite (and more expected) longitudinal pattern for most sizes, with
318 peaks in the center of the range and declines at eastern and western edges. There was a
319 female growth advantage for small sizes at western longitudes (Fig. 4D-F). The strongest
320 sex difference was in the probability of flowering: females had a flowering advantage,
321 especially for large sizes and at eastern longitudes (Fig. 4G-I). Finally, panicle production
322 by flowering plants was similar between the sexes for most sizes, though for the largest
323 sizes there were advantages for males in the west and females in the east (Fig. 4J-L).

324 Sex differences in flowering and panicle production generated a longitudinal trend in
325 the operational sex ratio of our common garden populations consistent with (but weaker
326 than) the trend in natural populations: the fraction of total panicles that were female

327 in our common gardens increased from west to east (Fig. 3B) even as the fraction of
328 surviving plants that were female did not show a longitudinal trend (Fig. 3C). Thus, in
329 recapitulating the natural OSR pattern, the common garden experiment revealed that the
330 longitudinal trend in the mating pool of natural populations was due to the reproductive
331 niche of females extending farther east than that of males, and not to sex differences in
332 mortality.

333 For survival, flowering, and panicle production we did not find strong evidence for
334 local adaptation based on the posterior distributions of the climate mismatch coefficient
335 (Fig. ??A,C,D). However, climate mismatch negatively affected growth such that plants
336 from populations whose mean annual precipitation strongly differed from that of the
337 common garden location exhibited reduced growth (Fig. ??B).

338 *Sex-ratio dependent seed fertilization*

339 Seed fertilization by females declined with increasing female bias in the sex ratio ma-
340 nipulation experiment. Fertilization success was greatest for females that were rare in
341 male-biased populations, where 75-80% of initiated seeds were viable (Fig. 5). Fertiliza-
342 tion was robust to sex ratio variation until ca. 75% of the panicles in a population were
343 female, at which point fertilization strongly declined due to pollen limitation. The fitted
344 model specifies that seed fertilization goes to zero as female bias goes to 100% (Eq. 1),
345 and this assumption was generally consistent with the experimental results, where the
346 majority (63%) of females from female-only populations produced zero viable seeds. The
347 occasional production of viable seeds in female-only populations (Fig. 5) likely reflects
348 rare pollen contamination between experimental plots.

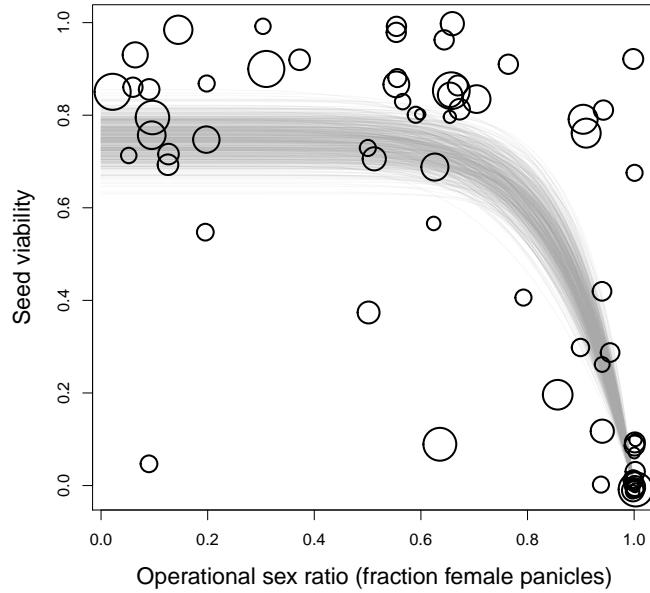


Figure 5: Seed fertilization success in relation to operational sex ratio (fraction of panicles that are female) in experimental populations. Circles show data from tetrazolium assays of seed viability; circle size is proportional to the number of seeds tested (min: 14, max: 57). Lines show model predictions (Eq. 1) for 500 samples from the posterior distribution of parameter estimates.

349

Two-sex model of range limits

350 The process-based demographic model connected sex-specific vital rate responses to
 351 longitudinal variation (Fig. 4) with sex ratio-dependent mating (Fig. 5) to predict the
 352 contributions of females and males to range limitation. The model predicted maxi-
 353 mum fitness in the center of the range and loss of population viability at longitudes
 354 that corresponded well with observed range limits. Specifically, the western-most and
 355 eastern-most county records of *P. arachnifera* fell within the uncertainty distribution of

356 the model's predictions (represented by the shading in Fig. 6A), bolstering our confi-
357 dence that the model effectively captured the demographic drivers of range limitation in
358 this species. Also, the asymptotic population structure predicted by the model showed
359 female bias in the operational (panicle) sex ratio toward the eastern range margins, con-
360 sistent with observations from the common garden and natural populations (Fig. B5A).
361 Female bias in the OSR was predicted to cause declines in seed viability toward eastern
362 range margins (Fig. B5B). However, this effect was weak in magnitude because predicted
363 OSR bias was not extreme enough to cause strong declines in viability, given the re-
364 lationship derived from the sex ratio manipulation experiment (Fig. 5). Furthermore,
365 population viability at the eastern range margin was weakly sensitive to seed viability
366 relative to other vital rates (B5C). These observations underscore the next set of results.

367 LTRE decomposition revealed that declines in λ approaching range limits were driven
368 almost exclusively by females (Fig. 6B) with near-zero contributions from males (Fig.
369 6C). Thus, range limitation was an effectively female-dominant process, despite system-
370 atic geographic variation in sex ratio. Correspondingly, predictions of the two-sex model
371 were nearly indistinguishable from a corresponding female-dominant model with all else
372 equal, with only very modest differences in predictions of the two models emerging in
373 the eastern part of the range (Fig. B4).

374 Decomposition analysis further revealed that multiple female vital rates contributed
375 to range limits, some in opposing directions. Because female survival increased toward
376 range limits (Fig 4A-C), this vital rate had a contribution to $\frac{\partial \lambda}{\partial Longitude}$ that was opposite
377 in sign to the other vital rates (Fig. 6B). However, increased survival at range edges was
378 not sufficient to offset declines in other vital rates. The overall decline in λ was driven
379 most strongly by a combination of reduced flowering and growth in females at both the

380 eastern and western limits (Fig. 6B).

381 Skew in the OSR predicted by the demographic model was less extreme than was
382 observed in natural and experimental populations (B5A). This occurred because sex dif-
383 ferences in demography, especially flowering, were most pronounced at the largest sizes,
384 and the MPM predicted that these sizes were very rare at stable population structure.
385 The stable size distribution predicted by the MPM corresponded well to the common
386 garden data (from which the MPM was built) but was much smaller, on average, than
387 the size distribution we observed in natural populations (Fig. C2), presumably because
388 transplants did not grow like “real” plants and/or did not have time in our three-year
389 experiment to reach those sizes. In Appendix C, we explore whether higher growth
390 rates, leading to a more realistic size distribution, would lead to a more important role
391 for males. In numerical experiments with growth parameters, we found that larger size
392 distributions led to stronger female bias and thus stronger reductions in seed viability
393 at eastern range margins (Fig. C3). While these changes increased the contributions of
394 males to range limitation, female contributions were still more than twice as important as
395 males, and there was very little difference between predictions of the two-sex and female-
396 dominant models even under this elevated growth scenario (Fig. C4). This leads us to
397 conclude that, while our common garden-parameterized model may quantitatively un-
398 derestimate OSR bias and its demographic consequences relative to natural populations,
399 our qualitative conclusion that range boundary formation is effectively female-dominant
400 in this system is robust to any biases imposed by the growth trajectories and size distri-
401 butions of common garden populations.

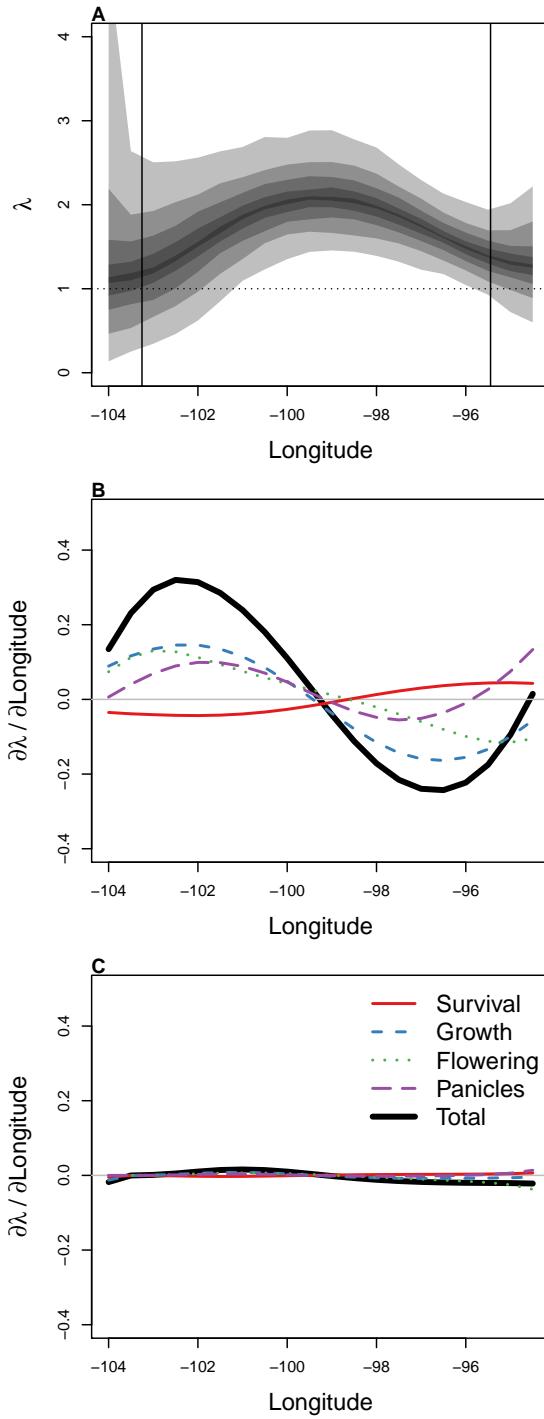


Figure 6: Population growth (λ) as a function of longitude, predicted by the two-sex MPM that incorporates sex-specific demographic responses to longitude with sex ratio-dependent seed fertilization. A, posterior distribution of λ , where shaded regions show the 25, 50, 75, and 95% percentiles of parameter uncertainty. Dashed horizontal line indicates the limit of population viability ($\lambda = 1$) and vertical lines show the longitudes of Brewster and Brazoria Counties, TX, the western- and eastern-most occurrence records of *P. arachnifera*. B–C, LTRE decomposition of the sensitivity of λ to longitude into additive vital rate contributions of females (B) and males (C) based on posterior mean parameter estimates.

Discussion

403 Understanding the causes of decline in population viability at range edges is a classic
404 ecological problem and the foundation for predicting how species' ranges will respond
405 to global change drivers. Sexual niche differentiation has the potential to generate skew
406 in the mating pool across environmental gradients and may therefore contribute to re-
407 productive failure at range edges of dioecious species. In Texas bluegrass, we found
408 evidence for sexual niche differentiation that manifested over a large-scale geographic
409 gradient: the female reproductive niche (environment-dependent flowering and panicle
410 production) extended farther east than that of males, generating female-biased opera-
411 tional sex ratios toward the eastern, mesic range margins, a pattern detected in natural
412 populations and recapitulated in our common garden populations. Furthermore, seed
413 viability declined with increasing skew in the OSR, indicating that mate (pollen) limita-
414 tion can limit the reproductive output of female-biased mating pools. It would appear
415 that all the pieces are in place for an important role of two-sex dynamics in contributing
416 to distributional limits of Texas bluegrass, particularly at the eastern range edge. Yet,
417 insights derived from the field-parameterized population model indicate the opposite:
418 range limitation in this species is an effectively female-dominant process, with negligible
419 contributions from males. Thus, in this system and likely others, female dominance is
420 an adequate framework for understanding range dynamics: despite evidence for sexual
421 niche differentiation, only the female niche mattered for determining the environmental
422 limits of population viability. This does not mean that sex is unimportant, but rather that
423 lack of sex is never so severe that it limits population viability.

424 The limited role of males in our experimental system can be explained by two factors.

425 First, seed fertilization was robust to variation in OSR and was not predicted to strongly
426 decline within the range of OSR bias that we observed and modeled, suggesting that few
427 males are required to pollinate all or most females. Second, population growth (λ) was
428 weakly sensitive to seed viability, which further buffered the demographic consequences
429 of sex ratio bias. We speculate that our qualitative conclusions should apply to other
430 species or systems that satisfy either, but especially both, of these conditions. While
431 there are striking examples of female-biased sex ratios causing declines in population
432 growth (Milner-Gulland et al., 2003) or range expansion (Miller and Inouye, 2013), other
433 examples suggest limited demographic consequences of sex ratio variation (Ewen et al.,
434 2011; Gownaris et al., 2020; Mysterud et al., 2002). Ultimately, sensitivity of female repro-
435 ductive success to sex ratio should depend strongly on the mating system, with female
436 dominance at the “extremely polygamous” end of a continuum (Miller et al., 2011). The
437 sensitivity of population viability to female reproductive success, in turn, is likely pre-
438 dicted by life history strategy: in long-lived, iteroparous species, population growth rates
439 are often weakly sensitive to reproduction relative to growth and survival (Franco and
440 Silvertown, 2004). We therefore hypothesize that range limits are more likely to be dom-
441 inated by the female environmental niche in longer-lived species with more polygamous
442 mating systems, while males are more likely to play an important role in shorter-lived,
443 monogamous species that may be particularly sensitive to missed mating opportunities.
444 As studies of sex ratio variation and sex-specific demography across species’ ranges ac-
445 cumulate in the literature (e.g., Dudaniec et al., 2021; Lynch et al., 2014; Petry et al., 2016),
446 this hypothesis may be tractably pursued with comparative analyses.

447 While life history and mating system may determine the demographic consequences
448 of skewed sex ratios, the sensitivity of sex ratio to environmental drivers is another crit-

449 ical ingredient of how environmental variation can affect the population dynamics of
450 dioecious species. Our study adds to a growing body of work quantifying the demo-
451 graphic mechanisms giving rise to skewed operational sex ratios using two-sex models
452 (Eberhart-Phillips et al., 2017; Shelton, 2010; Veran and Beissinger, 2009) and parsing the
453 contributions of environmental drivers (Balic-Murphy et al., 2020). However, as a field,
454 we lack a strong predictive framework for how often and in which direction environ-
455 mental drivers are likely to skew the operational sex ratio – and this gap is particularly
456 important in the context of global change. We have focused on the limits of population
457 viability with respect to geographic environmental variation but analogous processes
458 will likely govern how populations respond to temporal environmental change (e.g., cli-
459 mate change), including direct effects on female demography and indirect effects via
460 perturbations to the mating pool (Fig. 1). There is a need to better understand and pre-
461 dict which species and types of species are susceptible to climate change-induced shifts
462 in OSR. Geographic variation in OSR may be an instructive proxy for how dioecious
463 species will respond to climate change (Petry et al., 2016). The link between OSR and
464 responses to climate adds value to studies of the causes and consequences of spatial vari-
465 ation in sex ratio, particularly at geographic scales that encompass “past” and “future”
466 conditions.

467 Previous studies of dioecious plants have shown that male bias is more common than
468 female bias and is particularly pronounced in harsh abiotic environments, likely reflect-
469 ing the greater resource requirements needed to pay the female cost of reproduction
470 (Bierzychudek and Eckhart, 1988; Field et al., 2013a,b). Our surveys of natural popula-
471 tions are consistent with the broader pattern of male-biased OSR at xeric range edges.
472 However, our common garden populations did not exhibit male bias in the xeric west

⁴⁷³ – averaged across years or in any single year (Fig. B3) – nor did we find any strong
⁴⁷⁴ demographic evidence for a western male advantage (in fact, there was a western female
⁴⁷⁵ advantage in growth and survival for some sizes). If male advantage / female disad-
⁴⁷⁶ vantage under harsh abiotic conditions is driven by the greater resource requirements of
⁴⁷⁷ females then it is possible that clonal propagation and/or legacies of greenhouse rearing
⁴⁷⁸ masked the ‘true’ sex difference at xeric-edge common garden sites, **or that reproductive**
⁴⁷⁹ **costs accumulate over longer time scales than considered here.** Instead, the stronger pat-
⁴⁸⁰ tern of sex ratio bias was the female reproductive advantage at the mesic, eastern range
⁴⁸¹ edge. We hypothesize that the mesic edge is limited by competition and that the female
⁴⁸² reproductive advantage reflects competitive superiority of females, which has been sug-
⁴⁸³ gested in previous studies of Texas bluegrass (Compagnoni et al., 2017) and shown in
⁴⁸⁴ other dioecious plants (Eppley, 2006), particularly under mesic conditions (Chen et al.,
⁴⁸⁵ 2014). Theory suggests that biotic interactions such as competition are likely to limit
⁴⁸⁶ species’ ranges at the benign (e.g., mesic) end of abiotic gradients (Louthan et al., 2015)
⁴⁸⁷ though this has not been explored, to our knowledge, in the context of sex-structured
⁴⁸⁸ dynamics. Future studies in our system or others could test whether females and males
⁴⁸⁹ differ in their responses to biotic stressors at xeric and mesic range edges to reveal how
⁴⁹⁰ biotic factors shape range limits via sex-specific demography.

⁴⁹¹ Beyond the novel elements of sex-structured demography and mate limitation, our
⁴⁹² work informs and advances the broader literature on the processes generating species’
⁴⁹³ range limits in at least three ways. First, the Texas bluegrass case study demonstrates
⁴⁹⁴ that a process-based model capturing environment-dependent demography can accu-
⁴⁹⁵ rately predict geographic range limits: the predicted limits of $\lambda \geq 1$ corresponded well
⁴⁹⁶ to observed longitudinal limits from collection records, particularly given the uncer-

tainty characterized by our hierarchical Bayesian statistical approach. We parameterized the model with respect to longitude, which tightly covaries with aridity in the southern Great Plains. Extensions of this model that transition from implicit to explicit consideration of aridity will allow us to forecast range responses of Texas bluegrass to future climate change and ask whether climate change will reduce or amplify OSR bias and mate limitation at longitudinal range edges. It would be interesting to additionally consider this species' latitudinal limits, though our exploratory analyses revealed no clear sex differences or sex ratio variation with respect to latitude.

Second, our results also provide novel evidence for contrasting demographic responses to environmental drivers throughout a species' range – or “demographic compensation” (Doak and Morris, 2010; Villellas et al., 2015). Elevated performance in some life history processes can compensate for declines in other processes and thus buffer range-edge populations against harsh environmental conditions. In Texas bluegrass, most vital rates declined toward eastern and western range limits but survival showed the opposite pattern. Increased survival at longitudinal extremes partially offset declines in other vital rates but this positive response was weaker than the negative responses. Ultimately, increased survival was not sufficient to prevent declines in population viability from the range center to eastern and western limits, which were dominated by declining female growth and flowering. However, we also found evidence that growth patterns exhibited local adaptation: individuals planted into locations that were climatically similar to locations of their source population exhibited greater growth, on average, irrespective of sex. It is therefore possible that our demographic model (which does not explicitly account for local adaptation) over-estimates the decline in fitness approaching range edges, since local adaptation in a high-sensitivity vital rate may dampen the effects

521 of environmental forcing. There is growing awareness that local adaptation can modify
522 expectations for species' distributions under global change (Peterson et al., 2019). Mech-
523 anistic models of range limits that incorporate potential for local adaptation would be a
524 valuable next step.

525 Third, our results highlight some important considerations in how environment-
526 dependent demographic models are best parameterized to derive insights into the drivers
527 of range limits. Our approach relied heavily on common garden populations, which
528 allowed us to plant and track known-sex individuals in contrasting environmental con-
529 ditions that encompass and exceed the natural geographic distribution. The ability to
530 robustly sample edge and beyond-edge environments is a powerful advantage of the
531 common garden transplant approach (Hargreaves et al., 2013). However, this also lim-
532 ited the size variation that we were able to include and model, and the size distributions
533 of common garden populations skewed consistently smaller than natural populations.
534 In Appendix C, we show that our conclusions are likely robust to this feature of the
535 common gardens. However, our ability to quantify the consequences of size representa-
536 tion is itself limited by size representation: we can simulate a population in which the
537 largest common garden sizes are more common than they actually were, but simulating
538 a population with sizes much larger than observed requires extrapolation of our statisti-
539 cal models, and we are skeptical about what insights such an exercise could provide (in
540 Appendix C, we extrapolated demographic performance to sizes 50% greater than the
541 observed maximum). This issue is not unique to our study but will be encountered by
542 any transplant study intended to yield inferences about range limits of species with sig-
543 nificant size structure, such as trees. If we could re-do our experiment knowing what we
544 know now, we would combine data from natural and transplanted populations to model

545 size-dependent demography over a more realistic size distribution. Other investigators
546 inspired by similar questions about the demographic drivers of range limits should con-
547 sider such a hybrid approach.

548 *Conclusion.* We have documented geographic variation in operational sex ratio; eluci-
549 dated how sex-specific demographic responses to environmental drivers generate this
550 pattern; quantified how female fertility responds to availability of males; and demon-
551 strated that, in the end, sex ratio variation is a rather inconsequential component of
552 declines in population viability at range limits. In Texas bluegrass and, we speculate,
553 other dioecious plants and animals with similar life history and reproductive traits, the
554 geographic distribution is essentially the *female* environmental niche ‘writ large’ (Harg-
555 reaves et al., 2013).

556 Understanding and predicting geographic distributions and their responses to en-
557 vironmental change demands careful consideration of which biological details must be
558 accounted for and which others can be safely ignored. Our results show that complex,
559 non-linear dynamics involving females, males, and frequency-dependent reproduction
560 can be reasonably approximated as a simple, linear process (female-dominant popula-
561 tion growth). We suggest that this is good news. The next challenge is to figure out how
562 often and under what conditions ecologists can get away with it.

563 Acknowledgements

564 We gratefully acknowledge the many individuals who facilitated our field work, es-
565 pecially Dariusz Malinowski, Jason Goldman, Tom Arsuffi, Alan Byboth, John Walker,
566 Kenneth Steigman, Steven Gibson, Wesley Newman, Kerry Griffis, Liz Martin, Melanie

567 Hartman, Brian Northup, Leland Russell, Dexter R Mardis, and Dixie Smith. This work
568 was made possible by a network of biological field stations that hosted our geograph-
569 ically distributed experiment. We acknowledge Sam Houston State University, Texas
570 A&M University, University of Texas, Texas Tech University, Pittsburgh State University,
571 and Wichita State University for investing in field stations and making these facilities
572 available to us. We thank Marion Donald, Kory Kolis, Nakian Kim, and Alex Espana
573 for valuable assistance in the field, lab, and greenhouse. Our work was supported by
574 NSF Division of Environmental Biology awards 1543651 and 1754468 and by the Rice
575 University Faculty Initiatives Fund.

576 Author contributions

577 A.C. and T.E.X.M. designed the study, carried out the study, and conducted the statistical
578 analyses. T.E.X.M drafted the manuscript and both authors finalized the submission.

579 Data accessibility

580 A data package will be formally published in parallel with this manuscript. For now,
581 reviewers may access our data at <https://github.com/texmiller/POAR-range-limits>.

582 Literature Cited

- 583 Araújo, M. S., Bolnick, D. I., and Layman, C. A. (2011). The ecological causes of individ-
584 ual specialisation. *Ecology letters*, 14(9):948–958.
- 585 Bertiller, M. B., Sain, C. L., Bisigato, A. J., Coronato, F. R., Aries, J. O., and Graff, P. (2002).

- 586 Spatial sex segregation in the dioecious grass *poa ligularis* in northern patagonia: the
587 role of environmental patchiness. *Biodiversity & Conservation*, 11(1):69–84.
- 588 Bialic-Murphy, L., Heckel, C. D., McElderry, R. M., and Kalisz, S. (2020). Deer indi-
589 rectly alter the reproductive strategy and operational sex ratio of an unpalatable forest
590 perennial. *The American Naturalist*, 195(1):56–69.
- 591 Bierzychudek, P. and Eckhart, V. (1988). Spatial segregation of the sexes of dioecious
592 plants. *The American Naturalist*, 132(1):34–43.
- 593 Bisang, I., Ehrlén, J., and Hedenäs, L. (2020). Sex expression and genotypic sex ratio
594 vary with region and environment in the wetland moss *drepanocladus lycopodioides*.
595 *Botanical journal of the Linnean Society*, 192(2):421–434.
- 596 Bolnick, D. I. and Doebeli, M. (2003). Sexual dimorphism and adaptive speciation: two
597 sides of the same ecological coin. *Evolution*, 57(11):2433–2449.
- 598 Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D.,
599 and Forister, M. L. (2002). The ecology of individuals: incidence and implications of
600 individual specialization. *The American Naturalist*, 161(1):1–28.
- 601 Bowyer, R. T. (2004). Sexual segregation in ruminants: definitions, hypotheses, and
602 implications for conservation and management. *Journal of Mammalogy*, 85(6):1039–1052.
- 603 Carpenter, B., Gelman, A., Hoffman, M. D., Lee, D., Goodrich, B., Betancourt, M.,
604 Brubaker, M., Guo, J., Li, P., and Riddell, A. (2017). Stan: A probabilistic program-
605 ming language. *Journal of statistical software*, 76(1).
- 606 Caruso, C. and Case, A. (2007). Sex ratio variation in gynodioecious *lobelia siphilit-*

- 607 ica: effects of population size and geographic location. *Journal of Evolutionary Biology*,
608 20(4):1396–1405.
- 609 Caswell, H. (2001). *Matrix Population Models*. Sinauer Associates, Inc., Sunderland, MA,
610 2 edition.
- 611 Caswell, H. and Weeks, D. E. (1986). Two-sex models: chaos, extinction, and other
612 dynamic consequences of sex. *The American Naturalist*, 128(5):707–735.
- 613 Chen, J., Duan, B., Wang, M., Korpelainen, H., and Li, C. (2014). Intra-and inter-sexual
614 competition of *populus cathayana* under different watering regimes. *Functional Ecol-*
615 *ogy*, 28(1):124–136.
- 616 Compagnoni, A., Steigman, K., and Miller, T. E. (2017). Can't live with them, can't live
617 without them? balancing mating and competition in two-sex populations. *Proceedings*
618 *of the Royal Society B: Biological Sciences*, 284(1865):20171999.
- 619 Darwin, C. (1871). *The descent of man*. BoD–Books on Demand.
- 620 De Lisle, S. P., Paiva, S., and Rowe, L. (2018). Habitat partitioning during character
621 displacement between the sexes. *Biology letters*, 14(6):20180124.
- 622 De Lisle, S. P. and Rowe, L. (2015). Ecological character displacement between the sexes.
623 *The American Naturalist*, 186(6):693–707.
- 624 Diez, J. M., Giladi, I., Warren, R., and Pulliam, H. R. (2014). Probabilistic and spatially
625 variable niches inferred from demography. *Journal of ecology*, 102(2):544–554.
- 626 Doak, D. F. and Morris, W. F. (2010). Demographic compensation and tipping points in
627 climate-induced range shifts. *Nature*, 467(7318):959–962.

- 628 Dudaniec, R. Y., Carey, A. R., Svensson, E. I., Hansson, B., Yong, C. J., and Lancaster, L. T.
629 (2021). Latitudinal clines in sexual selection, sexual size dimorphism, and sex-specific
630 genetic dispersal during a poleward range expansion. *Journal of Animal Ecology*.
- 631 Eberhart-Phillips, L. J., Küpper, C., Miller, T. E., Cruz-López, M., Maher, K. H., Dos Reme-
632 dios, N., Stoffel, M. A., Hoffman, J. I., Krüger, O., and Székely, T. (2017). Sex-specific
633 early survival drives adult sex ratio bias in snowy plovers and impacts mating system
634 and population growth. *Proceedings of the National Academy of Sciences*, 114(27):E5474–
635 E5481.
- 636 Ehrlén, J. and Morris, W. F. (2015). Predicting changes in the distribution and abundance
637 of species under environmental change. *Ecology Letters*, 18(3):303–314.
- 638 Eppley, S. (2001). Gender-specific selection during early life history stages in the dioe-
639 cious grass *distichlis spicata*. *Ecology*, 82(7):2022–2031.
- 640 Eppley, S. M. (2006). Females make tough neighbors: sex-specific competitive effects in
641 seedlings of a dioecious grass. *Oecologia*, 146(4):549–554.
- 642 Evans, M. E., Merow, C., Record, S., McMahon, S. M., and Enquist, B. J. (2016). To-
643 wards process-based range modeling of many species. *Trends in Ecology & Evolution*,
644 31(11):860–871.
- 645 Ewen, J. G., Thorogood, R., and Armstrong, D. P. (2011). Demographic consequences of
646 adult sex ratio in a reintroduced hihi population. *Journal of Animal Ecology*, 80(2):448–
647 455.
- 648 Fick, S. E. and Hijmans, R. J. (2017). Worldclim 2: new 1-km spatial resolution climate
649 surfaces for global land areas. *International journal of climatology*, 37(12):4302–4315.

- 650 Field, D. L., Pickup, M., and Barrett, S. C. (2013a). Comparative analyses of sex-ratio vari-
651 ation in dioecious flowering plants. *Evolution: International Journal of Organic Evolution*,
652 67(3):661–672.
- 653 Field, D. L., Pickup, M., and Barrett, S. C. (2013b). Ecological context and metapopula-
654 tion dynamics affect sex-ratio variation among dioecious plant populations. *Annals of*
655 *botany*, 111(5):917–923.
- 656 Franco, M. and Silvertown, J. (2004). A comparative demography of plants based upon
657 elasticities of vital rates. *Ecology*, 85(2):531–538.
- 658 Gelman, A., Meng, X.-L., and Stern, H. (1996). Posterior predictive assessment of model
659 fitness via realized discrepancies. *Statistica sinica*, pages 733–760.
- 660 Gianuca, D., Votier, S. C., Pardo, D., Wood, A. G., Sherley, R. B., Ireland, L., Choquet,
661 R., Pradel, R., Townley, S., Forcada, J., et al. (2019). Sex-specific effects of fisheries and
662 climate on the demography of sexually dimorphic seabirds. *Journal of Animal Ecology*.
- 663 Gownaris, N. J., García Borboroglu, P., and Boersma, P. D. (2020). Sex ratio is vari-
664 able and increasingly male biased at two colonies of magellanic penguins. *Ecology*,
665 101(3):e02939.
- 666 Groen, K. E., Stieha, C. R., Crowley, P. H., and McLetchie, D. N. (2010). Sex-specific plant
667 responses to light intensity and canopy openness: implications for spatial segregation
668 of the sexes. *Oecologia*, 162(3):561–570.
- 669 Hargreaves, A. L., Samis, K. E., and Eckert, C. G. (2013). Are species' range limits simply
670 niche limits writ large? a review of transplant experiments beyond the range. *The*
671 *American Naturalist*, 183(2):157–173.

- 672 Holt, R. D. (2009). Bringing the hutchinsonian niche into the 21st century: ecological and
673 evolutionary perspectives. *Proceedings of the National Academy of Sciences*, 106(Supple-
674 ment 2):19659–19665.
- 675 Hultine, K. R., Bush, S. E., Ward, J. K., and Dawson, T. E. (2018). Does sexual dimorphism
676 predispose dioecious riparian trees to sex ratio imbalances under climate change? *Oe-
677 cologia*, 187(4):921–931.
- 678 Hutchinson, G. E. (1958). Concluding remarks. In *Cold Spring Harbour Symposium on
679 Quantitative Biology*, volume 22, pages 415—427.
- 680 Ketterson, E. D. and Nolan Jr, V. (1976). Geographic variation and its climatic correlates in
681 the sex ratio of eastern-wintering dark-eyed juncos (*junco hyemalis hyemalis*). *Ecology*,
682 57(4):679–693.
- 683 Law, C. J. and Mehta, R. S. (2018). Carnivory maintains cranial dimorphism between
684 males and females: evidence for niche divergence in extant musteloidea. *Evolution*,
685 72(9):1950–1961.
- 686 Lee-Yaw, J. A., Kharouba, H. M., Bontrager, M., Mahony, C., Csergő, A. M., Noreen,
687 A. M., Li, Q., Schuster, R., and Angert, A. L. (2016). A synthesis of transplant exper-
688 iments and ecological niche models suggests that range limits are often niche limits.
689 *Ecology letters*, 19(6):710–722.
- 690 Louthan, A. M., Doak, D. F., and Angert, A. L. (2015). Where and when do species
691 interactions set range limits? *Trends in Ecology & Evolution*, 30(12):780–792.
- 692 Lynch, H. J., Rhainds, M., Calabrese, J. M., Cantrell, S., Cosner, C., and Fagan, W. F.

- 693 (2014). How climate extremes-not means-define a species' geographic range boundary
694 via a demographic tipping point. *Ecological Monographs*, 84(1):131–149.
- 695 Merow, C., Bois, S. T., Allen, J. M., Xie, Y., and Silander, J. A. (2017). Climate change both
696 facilitates and inhibits invasive plant ranges in new england. *Proceedings of the National
697 Academy of Sciences*, 114(16):E3276–E3284.
- 698 Merow, C., Latimer, A. M., Wilson, A. M., McMahon, S. M., Rebelo, A. G., and Silander Jr,
699 J. A. (2014). On using integral projection models to generate demographically driven
700 predictions of species' distributions: development and validation using sparse data.
701 *Ecography*, 37(12):1167–1183.
- 702 Miller, T. E. and Inouye, B. D. (2011). Confronting two-sex demographic models with
703 data. *Ecology*, 92(11):2141–2151.
- 704 Miller, T. E. and Inouye, B. D. (2013). Sex and stochasticity affect range expansion of
705 experimental invasions. *Ecology Letters*, 16(3):354–361.
- 706 Miller, T. E., Shaw, A. K., Inouye, B. D., and Neubert, M. G. (2011). Sex-biased dispersal
707 and the speed of two-sex invasions. *The American Naturalist*, 177(5):549–561.
- 708 Milner-Gulland, E., Bukreeva, O., Coulson, T., Lushchekina, A., Kholodova, M., Bekenov,
709 A., and Grachev, I. A. (2003). Reproductive collapse in saiga antelope harems. *Nature*,
710 422(6928):135–135.
- 711 Mysterud, A., Coulson, T., and Stenseth, N. C. (2002). The role of males in the dynamics
712 of ungulate populations. *Journal of Animal Ecology*, 71(6):907–915.
- 713 Pekár, S., Martišová, M., and Bilde, T. (2011). Intersexual trophic niche partitioning in an
714 ant-eating spider (araneae: Zodariidae). *PloS one*, 6(1):e14603.

- 715 Peterson, M. L., Doak, D. F., and Morris, W. F. (2019). Incorporating local adaptation
716 into forecasts of speciesâ??t distribution and abundance under climate change. *Global*
717 *Change Biology*, 25(3).
- 718 Petry, W. K., Soule, J. D., Iler, A. M., Chicas-Mosier, A., Inouye, D. W., Miller, T. E.,
719 and Mooney, K. A. (2016). Sex-specific responses to climate change in plants alter
720 population sex ratio and performance. *Science*, 353(6294):69–71.
- 721 Phillips, R., Silk, J., Phalan, B., Catry, P., and Croxall, J. (2004). Seasonal sexual segre-
722 gation in two thalassarche albatross species: competitive exclusion, reproductive role
723 specialization or foraging niche divergence? *Proceedings of the Royal Society of London.*
724 *Series B: Biological Sciences*, 271(1545):1283–1291.
- 725 Rankin, D. J. and Kokko, H. (2007). Do males matter? the role of males in population
726 dynamics. *Oikos*, 116(2):335–348.
- 727 Renganayaki, K., Jessup, R., Burson, B., Hussey, M., and Read, J. (2005). Identification of
728 male-specific afip markers in dioecious texas bluegrass. *Crop science*, 45(6):2529–2539.
- 729 Renganayaki, K., Read, J., and Fritz, A. (2001). Genetic diversity among texas bluegrass
730 genotypes (poa arachnifera torr.) revealed by afip and rapd markers. *Theoretical and*
731 *Applied Genetics*, 102(6-7):1037–1045.
- 732 Renner, S. S. and Ricklefs, R. E. (1995). Dioecy and its correlates in the flowering plants.
733 *American journal of botany*, 82(5):596–606.
- 734 Rozas, V., DeSoto, L., and Olano, J. M. (2009). Sex-specific, age-dependent sensitivity of
735 tree-ring growth to climate in the dioecious tree juniperus thurifera. *New Phytologist*,
736 182(3):687–697.

- 737 Shelton, A. O. (2010). The origin of female-biased sex ratios in intertidal seagrasses
- 738 (*phyllospadix* spp.). *Ecology*, 91(5):1380–1390.
- 739 Shine, R. (1989). Ecological causes for the evolution of sexual dimorphism: a review of
- 740 the evidence. *The Quarterly Review of Biology*, 64(4):419–461.
- 741 Stan Development Team (2020). RStan: the R interface to Stan. R package version 2.21.2.
- 742 Temeles, E. J., Miller, J. S., and Rifkin, J. L. (2010). Evolution of sexual dimorphism
- 743 in bill size and shape of hermit hummingbirds (*phaethornithinae*): a role for eco-
- 744 logical causation. *Philosophical Transactions of the Royal Society B: Biological Sciences*,
- 745 365(1543):1053–1063.
- 746 Veran, S. and Beissinger, S. R. (2009). Demographic origins of skewed operational and
- 747 adult sex ratios: perturbation analyses of two-sex models. *Ecology Letters*, 12(2):129–
- 748 143.
- 749 Villegas, J., Doak, D. F., García, M. B., and Morris, W. F. (2015). Demographic compen-
- 750 sation among populations: what is it, how does it arise and what are its implications?
- 751 *Ecology letters*, 18(11):1139–1152.
- 752 Wood, S. (2017). *Generalized Additive Models: An Introduction with R*. Chapman and
- 753 Hall/CRC, 2 edition.

Appendix A: Site locations and climate

	Population	Latitude	Longitude	Year_visited	Experimental_source
1	Canyon_of_Eagles	30.88	-98.43	2012	no
2	ClearBay-Thunderbird	35.23	-97.24	2013	no
3	CooperWMA	36.60	-99.51	2012	yes
4	Copper Breaks	34.10	-99.75	2013	yes
5	Dinosaur_Valley	32.25	-97.82	2012	no
6	Fort_Worth_Nature_Center	32.83	-97.46	2012	no
7	Ft Cobb	35.18	-98.45	2013	no
8	Ft Richardson	33.20	-98.16	2013	no
9	Great Plains	34.74	-98.97	2013	no
10	Great_Salt_Plains	36.79	-98.18	2012	no
11	Horn_Hill_Cemetery	31.56	-96.64	2012	yes
12	Kingman_Fishing_Lake	37.65	-98.28	2012	no
13	Lake Arrowhead	33.75	-98.39	2013	yes
14	Mineral_Wells	32.89	-98.01	2012	no
15	Pedernales_Falls	30.33	-98.25	2012	no
16	Possum Kingdom	32.87	-98.57	2013	no
17	Quartz_Mountain	34.89	-99.30	2012	yes
18	Red Rock Canyon	35.44	-98.35	2013	no
19	Red_River	34.13	-98.10	2012	no
20	South_Llano	30.45	-99.80	2012	yes
21	Sulfur_Springs	31.08	-98.46	2012	yes
22	Wichita_Mountains	34.70	-98.67	2012	no

Table A1: Sites of natural population surveys

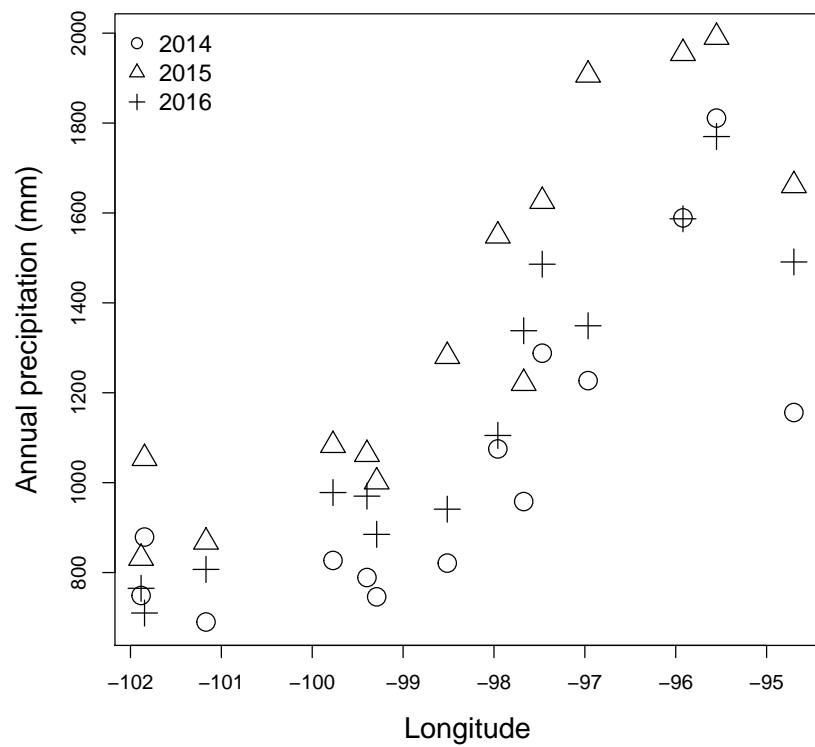


Figure A1: Total annual precipitation at common garden sites during the study years tracked long-term trends of increasing aridity from east to west.

Appendix B: Additional results

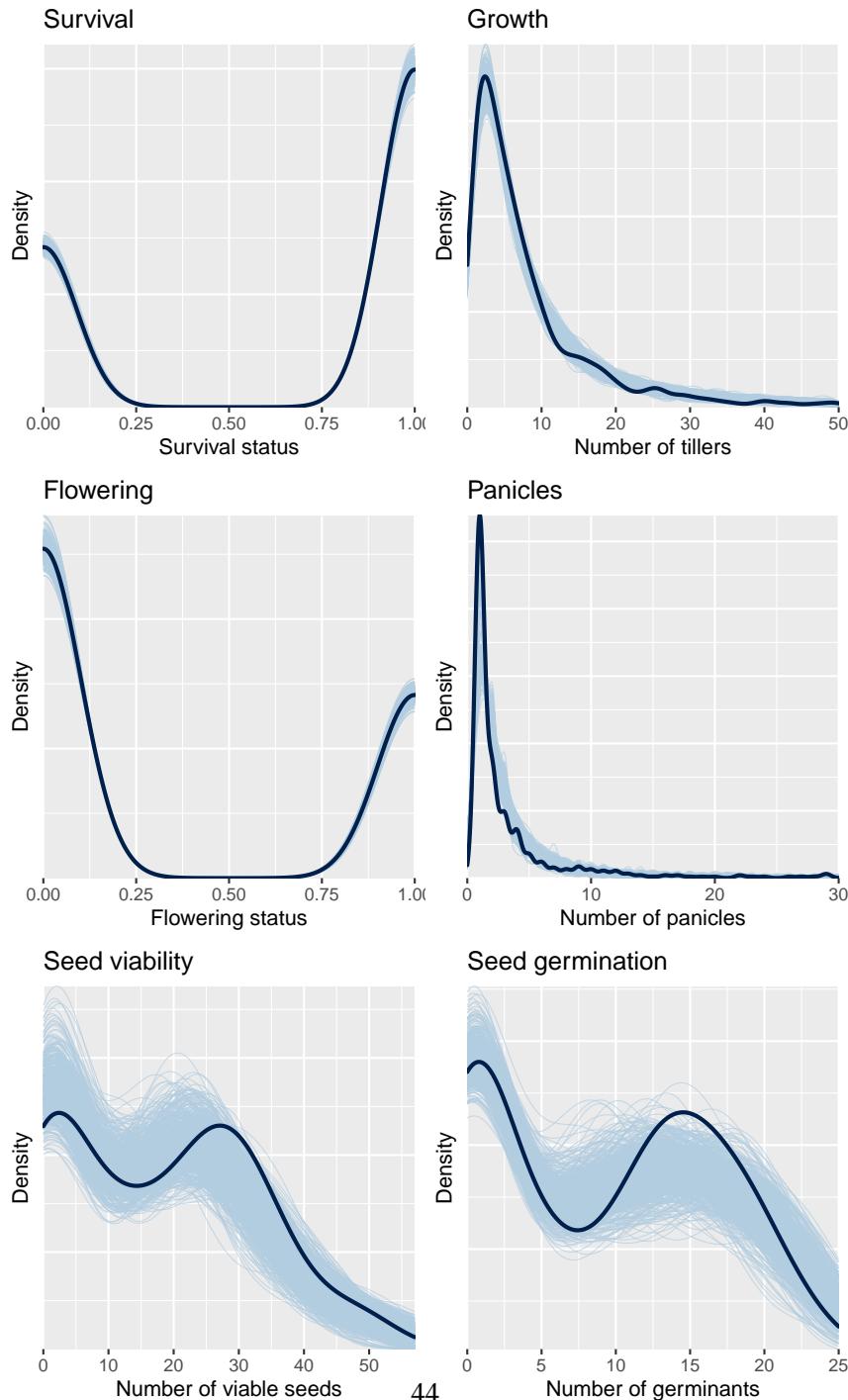


Figure B1: Posterior predictive checks of statistical models for demographic vital rates. Lines show density distributions of real data (thick, dark blue) compared to simulated data sets (thin, light blue) generated from the fitted models based on 500 draws of the posterior distribution of parameter estimates. Correspondence of the real and simulated data suggests that the fitted models describe the data well.

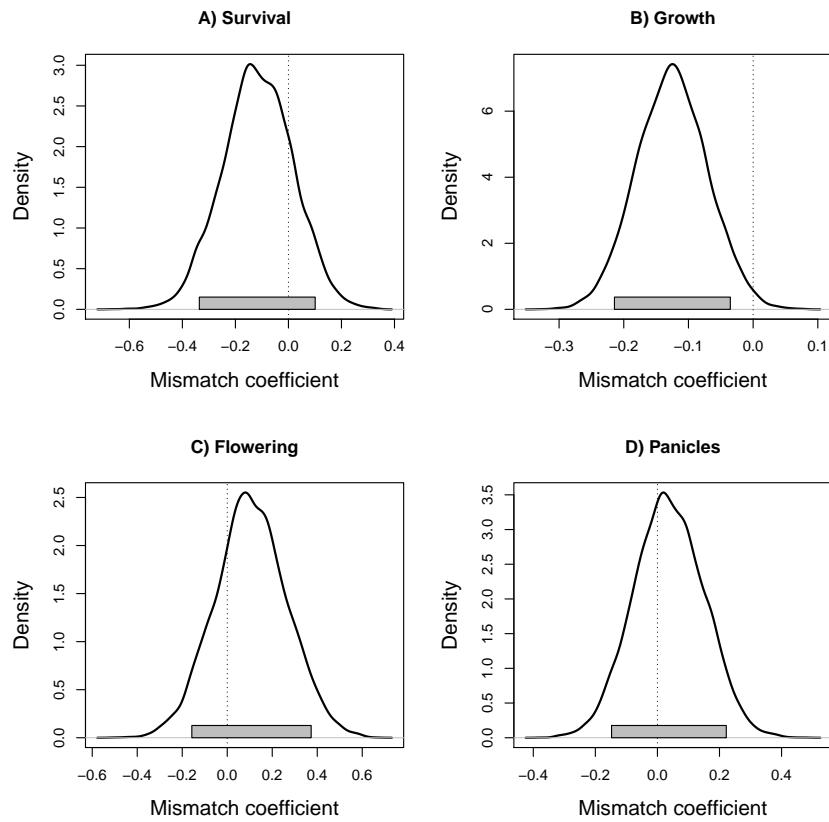


Figure B2: Posterior distributions of statistical coefficients for the influence of source-garden climate mismatch on survival (A), growth (B), flowering (C), and panicle production (D). Gray bars show the 95% credible interval of the coefficients. Climate mismatch was calculated as the absolute value of the difference in mean annual precipitation between source population and common garden location.

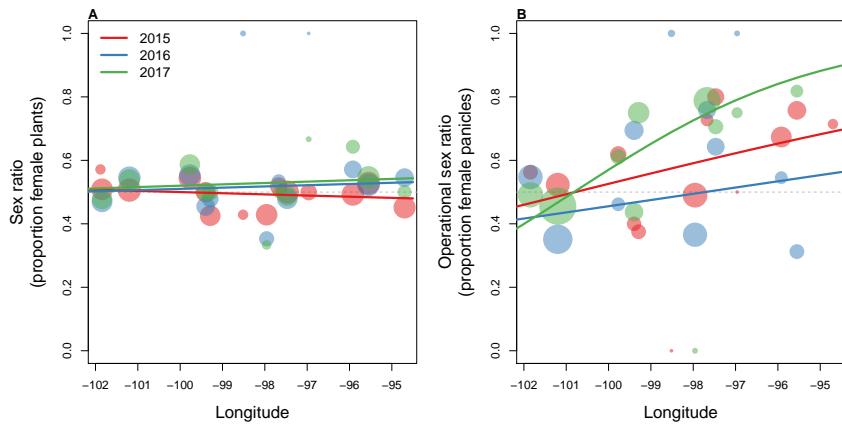


Figure B3: Year-specific sex ratios of plants (A) and panicles (B) in common garden populations spanning the longitudinal aridity gradient. Points sizes are proportional to sample sizes and lines show fitted binomial GLMs.

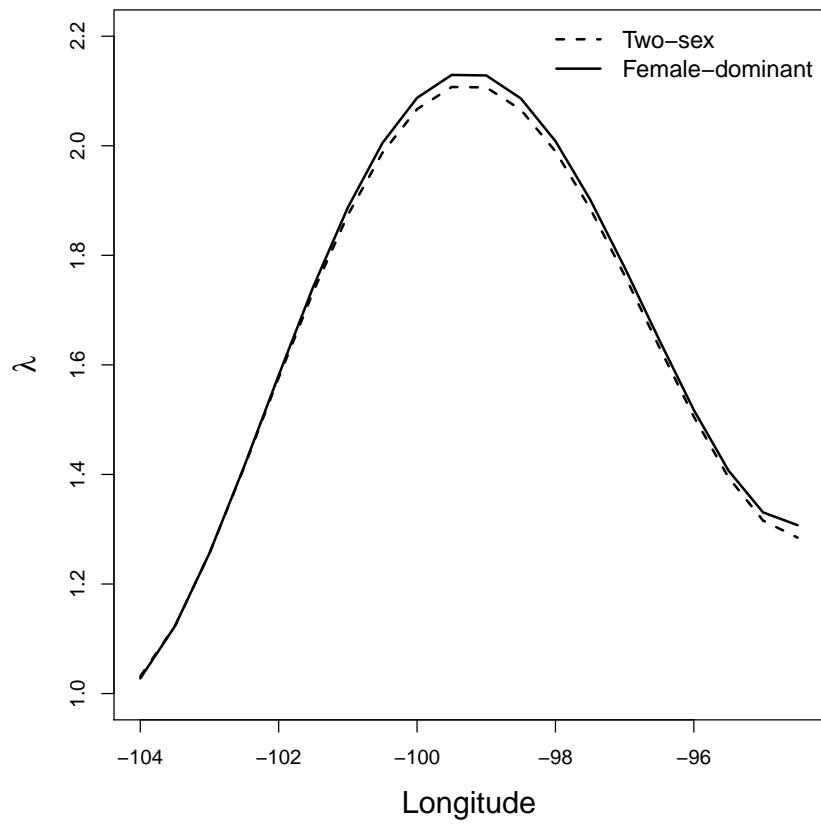


Figure B4: Comparison of longitudinal variation in λ between the two-sex demographic model (dashed line) that includes dependence of female seed production on population structure and the corresponding female-dominant model (solid line) with constant female fertility and all else equal. Models were evaluated at posterior mean parameter estimates

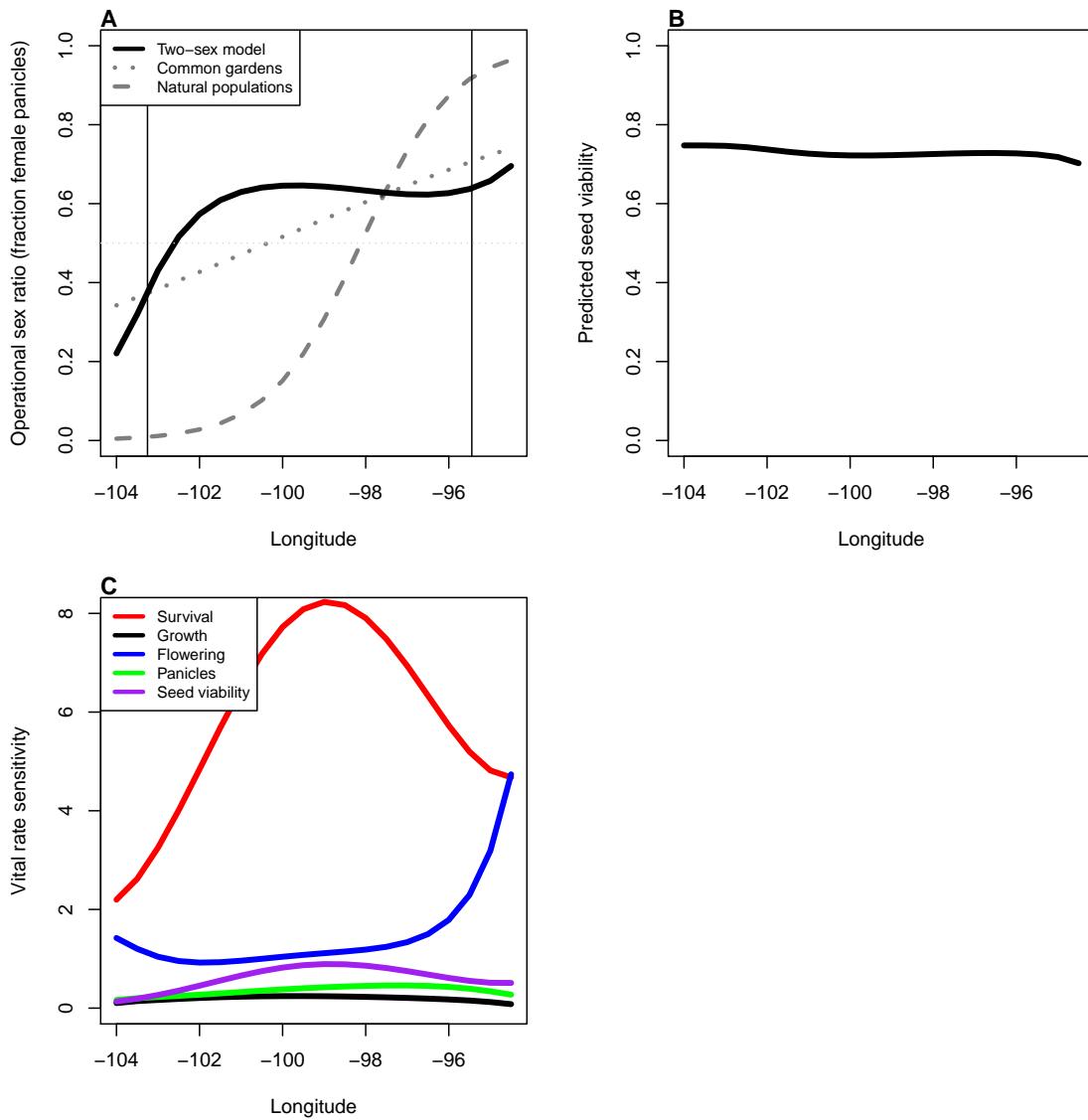


Figure B5: **A**, Longitudinal variation in operational sex ratio (fraction of panicles that are female) predicted by the two-sex MPM (solid line) compared to the sex ratio clines fitted to data from common gardens (dotted line) or natural populations (dashed line). Vertical lines show the longitudes of the westernmost and easternmost counties with occurrence records of *P. arachnifera*. **B**, Longitudinal variation in seed viability predicted by the two-sex MPM according to Eq. 1 and the OSR variation shown in **A**. **C**, Sensitivities of λ to vital rates in relation to longitude. Sensitivities were calculated numerically by perturbing vital rate functions (across all sizes) by 0.01, recalculating λ , and dividing the difference by 0.01. Vital rates were perturbed equally for both sexes though results in Fig 6B,C suggest that vital rate sensitivities were dominated by females.

756 **Appendix C: Size distribution comparisons and simulation
757 experiments**

758 In this section, we compare size distributions of natural and experimental populations,
759 and explore how the size distribution predicted by the two-sex MPM affects our conclu-
760 sions about the role of males in range boundary formation.

761 *Observed and predicted size distributions*

762 *Natural populations.* During natural population surveys (2012–2013) we recorded the
763 area (m^2) of Texas bluegrass patches using a Trimble GeoExplorer hand-held GPS re-
764 ceiever with sub-meter accuracy.

765 *Common garden populations.* Common garden data collection included tiller counts and
766 the maximum length and width of each patch, which we converted to area (m^2) assuming
767 an oval shape. We used these data to estimate the relationship between patch area and
768 tiller count (Fig. C1) using a generalized additive model (Wood, 2017) and applied this
769 fitted relationship to area measurements from natural populations. This allowed us to
770 compare the size distributions of natural and common garden populations (pooled across
771 the range) in the same size unit ($\log(\text{tillers})$).

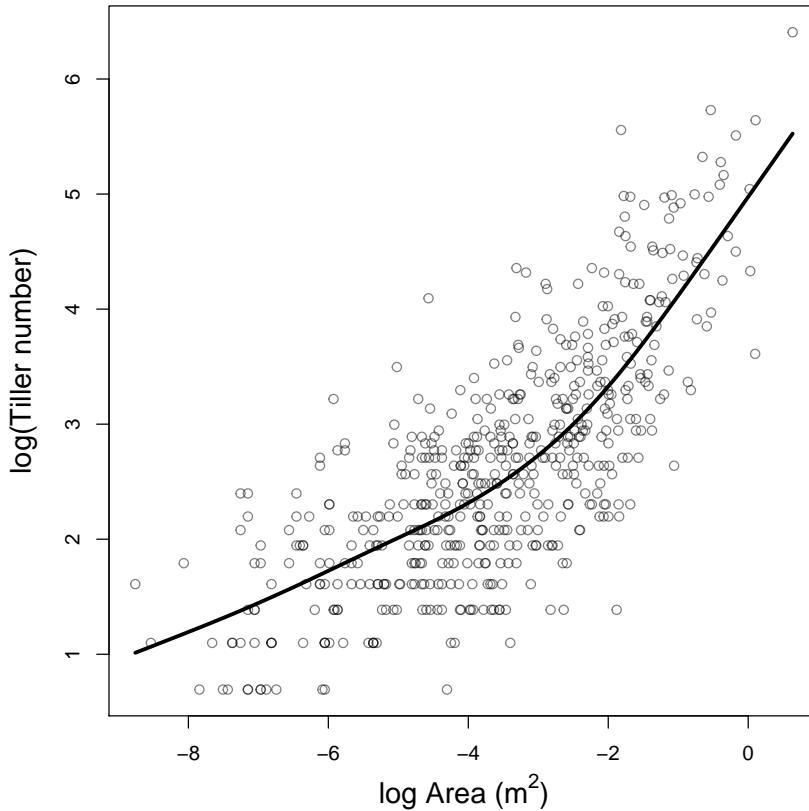


Figure C1: Relationship between area (m^2) and tiller count from plants in the common garden experiment. The fitted gam model (line) was used to convert area measurements from natural populations to tiller counts.

772 *Two-sex MPM.* The two-sex MPM predicts asymptotic population structure, including
 773 stable size distribution (SSD) and sex ratio. For comparison with empirical data, we
 774 calculated the SSD (pooling both sexes) predicted in the center of the range (the conclu-
 775 sions that we draw from this analysis hold up if we consider SSD from different parts
 776 of the range). Because the MPM is structured by tiller number, we converted the SSD to
 777 log(tillers) by simulating an arbitrarily large (10000) population at SSD, taking the natural

⁷⁷⁸ logarithm of tiller number, and then estimating the empirical distribution of this variable.

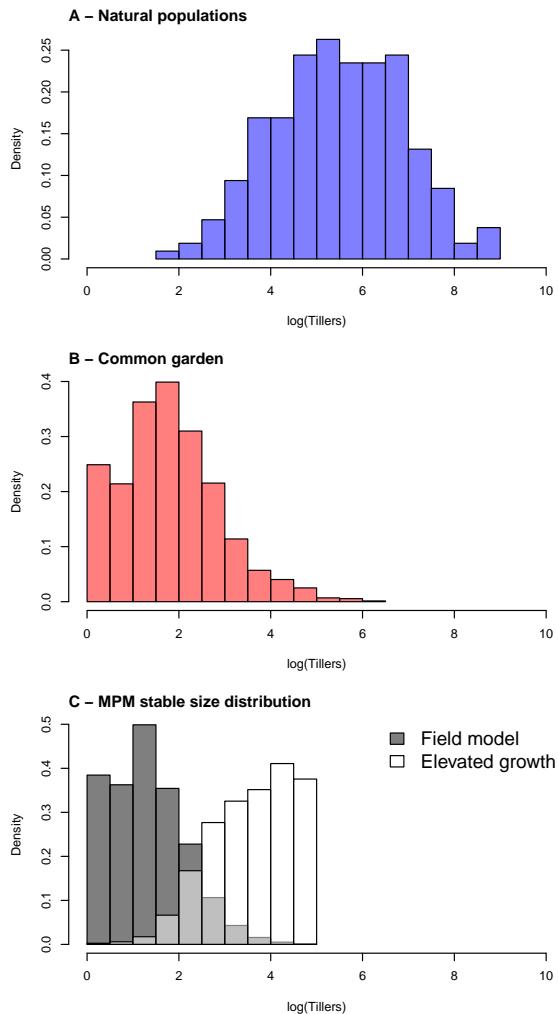


Figure C2: Size distribution of Texas bluegrass from natural populations (A), common garden populations (B), and predicted by the two-sex MPM (C). In C, the two size distributions come from the base model parameterized following methods described in the main manuscript (“field model”, in gray) and a numerical experiment where growth parameters were numerically increased to generate a size distribution more consistent with natural populations (“elevated growth model”, in white).

779 *Results.* Plants from natural populations were larger, on average, than plants in our
 780 common garden experiment (Fig. C2A,B). Common garden plants were generally larger

each year but the largest sizes in the final year of the common garden corresponded to smaller sizes observed in natural populations (although natural population surveys were subject to detection bias: small plants were likely under-sampled relative to their occurrence). The predicted SSD from the two-sex MPM was consistent with the common garden size distribution (Fig. C2C), as expected since the model was built with common garden data. These results suggest that common garden plants did not have the same growth trajectories of naturally occurring plants and / or were not given sufficient time to reach the sizes observed in natural populations.

*Numerical experiment to explore the consequences of under-estimating
the size distribution*

The preceding results indicate that the common garden populations, and thus the two-sex MPM built from common garden data, under-estimate the size distribution of Texas bluegrass, relative to what we find in natural populations. Sex differences in demography, and especially flowering, were most pronounced for the largest sizes (Fig. 4), but these sizes were predicted to be very rare in a stable population (Fig. C2C). The under-estimation of large sizes may explain why longitudinal clines in OSR predicted by the MPM and seen in the common garden were weaker than the OSR cline observed in natural populations (Fig. B5). It is therefore possible that our main finding – that males contribute little-to-nothing toward range limitation – reflects a limitation of the model, since real populations tended to be more female-biased (and potentially more mate-limited) in the eastern range margins than the model predicted. To explore this possibility, we conducted a numerical experiment that allowed modeled plants to reach larger sizes by increasing the empirically-estimated intercept of the growth vital rate

804 function by a factor of 2.75 (values larger than this caused numerical instabilities). This
805 adjustment caused all plants to increase in size more strongly regardless of initial size,
806 sex, or geographic location. We also increased the upper size limit to $U * 1.5$.

807 As expected, this led to stronger sex ratio clines and stronger reductions in seed vi-
808 ability at eastern range margins (Fig. C3). These changes increased the contributions of
809 males to eastern range limitation in the elevated-growth numerical experiment. How-
810 ever, the contribution of males to range limitation was still weak relative to that of females
811 (the maximum male contribution was less than half of the female maximum) and differ-
812 ences between the two-sex and female-dominant MPMs were stil very minor (Fig. C4).
813 Collectively, these results suggest that the small size distribution of the common garden
814 experiment led to a weaker role of males than would be expected in populations with a
815 more realistic size distribution, but that even with a larger size distribution, declines in
816 female performance still dominante range boundary formation.

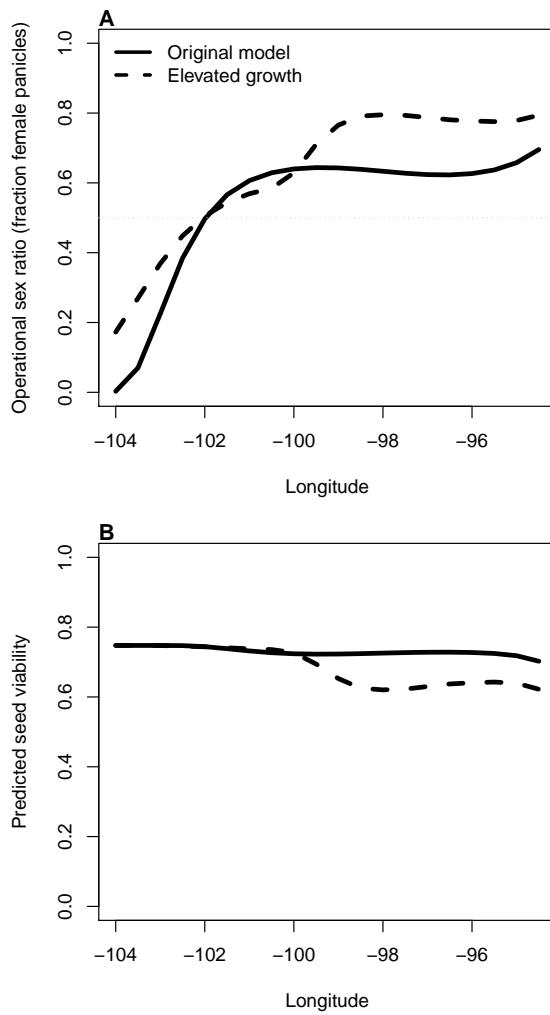


Figure C3: Two-sex model predictions for **A** operational sex ratio (fraction of panicles that are female) and **B** seed viability at stable population structure in relation to longitude. Solid line shows predictions of the base model using field-estimated parameter values and dashed line shows the same model with elevated growth of both sexes and across all longitudes (intercept of growth function increased by a factor of 2.75).

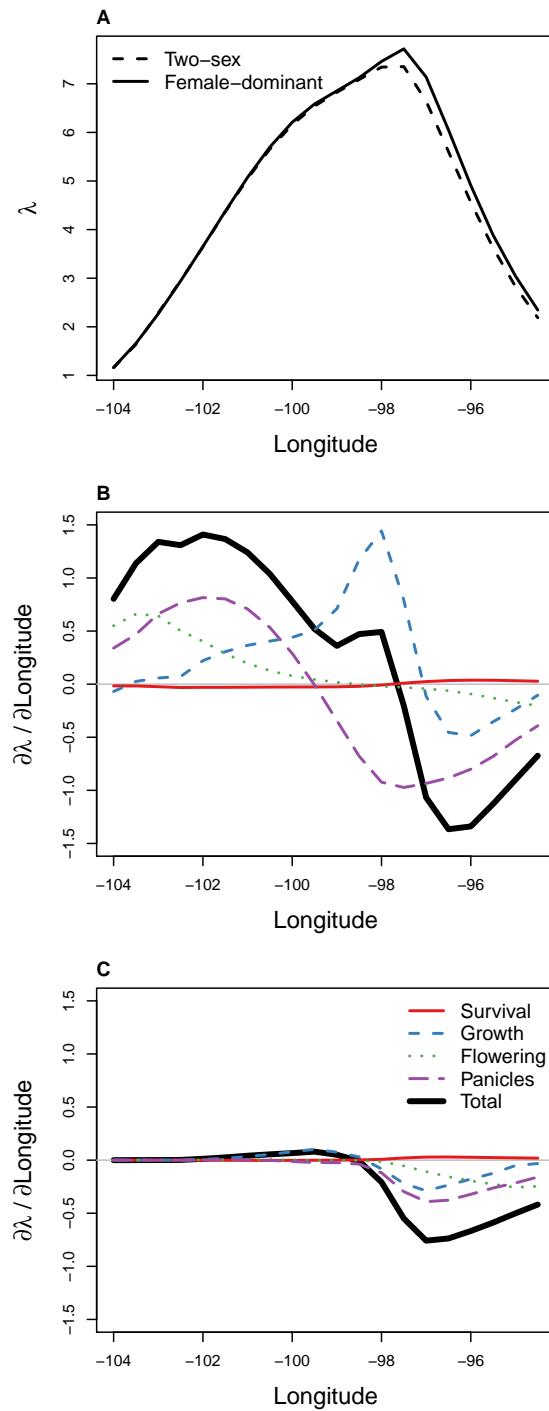


Figure C4: Results for the elevated growth model, in which the intercept of growth function was increased by a factor of 2.75. **A**, contrast of two-sex and female-dominant models, as in Fig. B4; **B,C**, Life Table Response Experiments decomposing the change in λ with respect to longitude into contributions from female **B** and male **C** vital rates (layout as in Fig. 6).

Site		City, State	Latitude	Longitude
1	Buffalo Lake National Wildlife Refuge	Amarillo, TX	35.20	-101.85
2	USDA-ARS Grazinglands Research Laboratory	El Reno, OK	35.53	-97.96
3	Katy Prairie Conservatory Indiangrass Preserve	Waller, TX	29.92	-95.92
4	Texas Tech University Llano River Research Station	Junction, TX	30.49	-99.77
5	Lake Lewisville Environmental Learning Area	Lewisville, TX	33.07	-96.96
6	University of Texas Stengl Lost Pines Biological Station	Bastrop, TX	30.18	-97.47
7	Texas Tech University	Lubbock, TX	33.57	-101.88
8	Wichita State University Ninnescah Field Station	Wichita, KS	37.54	-97.67
9	Texas A&M AgriLife Research and Extension Center	Ozona, TX	30.71	-101.20
10	Pittsburgh State University Field Station	Pittsburgh, KS	37.41	-94.70
11	Sam Houston State University Center for Biological Field Studies	Huntsville, TX	30.72	-95.55
12	Texas A&M AgriLife Research and Extension Center	Vernon, TX	34.15	-99.29
13	River Bend Nature Center	Wichita Falls, TX	33.91	-98.51
14	USDA-ARS Range and Pasture Research	Woodward, OK	36.43	-99.40

Table A2: Sites of common garden experiments