

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

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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).

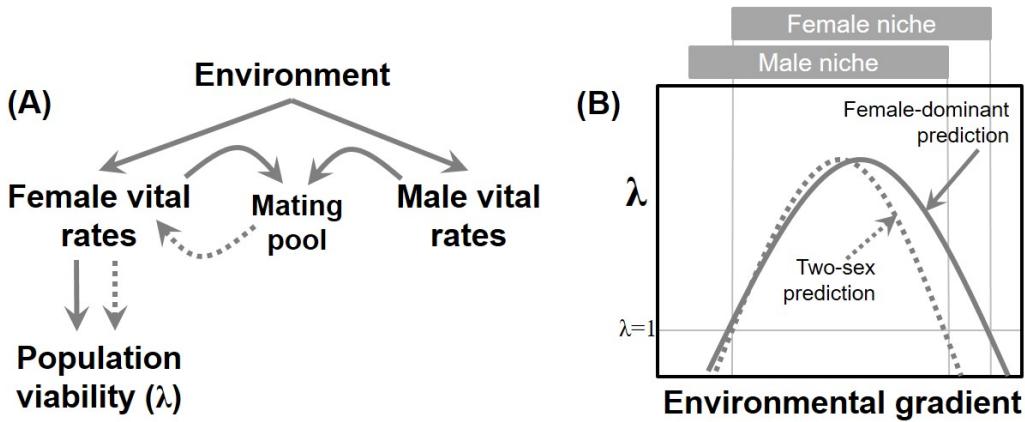


Figure 1: Hypotheses for how environmental variation can affect population viability and range limits in dieocious species. Under the female-dominant hypothesis, environmental drivers affect population growth (λ) through effects on females, alone (A). In geographic / environmental space, this translates 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>

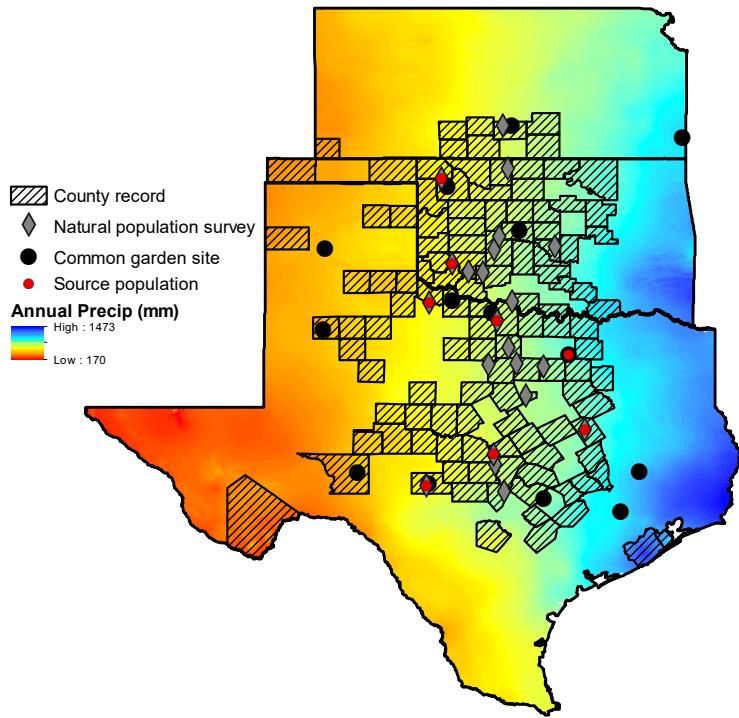


Figure 2: Geographic and environmental distribution of *P. arachnifera* in Texas, Oklahoma, and Kansas. Hatched shapes show counties with herbarium records of occurrence. Color shows geographic variation in annual precipitation (mm) based on 30-year normals from WorldClim (Fick and Hijmans, 2017). Grey 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 of
124 inflorescences in each patch. **We targeted our visits late in the flowering season to limit**
125 **the influence of possible sex differences in phenology (inflorescences can be sexed after**
126 **flowering is finished but not before it starts).** To quantify the mating environment, we
127 focus our analyses on the sex ratio of inflorescences rather than patches, since a single
128 patch makes different contributions to the mating pool depending on whether it has few
129 or many inflorescences.

130 *Statistical analysis of natural population surveys*

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

141

Common garden experiment

142 Source material and experimental design

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

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

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

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

167 *Statistical analysis of common garden experiment*

168 We analyzed the demographic vital rates with generalized linear mixed models in a
169 hierarchical Bayesian framework. All the vital rates shared a common linear predictor for
170 the expected value that included fixed effects of size, sex, linear and quadratic terms for
171 longitude, and all 2- and 3-way interactions. We included quadratic effects of longitude
172 to account for the possibility of non-monotonic responses, following the hypothesis that
173 fitness may peak in the center of the range. The linear predictor also included random
174 effects of site, block, and source population of the transplant. We pooled all three years
175 of observations for analysis so our results are implicitly averaged over years. In Table B1,
176 we used WAIC-based model selection ('loo' package: Vehtari et al. (2017)) to show that
177 vital rate models using precipitation and longitude as environmental covariates were
178 statistically indistinguishable, which suggests that longitude is an adequate proxy for
179 aridity.

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

187 predictive checks indicated that these models described the data well (Fig. B1).

188 In follow-up analyses, we tested the addition of a climate mismatch variable that
189 quantified the deviation between mean annual precipitation of each source population
190 and common garden location. This analysis allowed us to evaluate whether local adap-
191 tation to climate may have contributed to variation in demographic performance across
192 common garden sites. This was motivated by the observation that most source pop-
193 ulations came from the interior of the geographic range and were brought to edge and
194 beyond-edge locations that were much drier or wetter than their historical climate regime
195 (Fig. 2). The local adaptation hypothesis predicts that demographic performance de-
196 clines with increasing climatic deviation between common garden and source population
197 locations. To test this hypothesis we added the absolute value of mean annual precipita-
198 tion mismatch (using 30-year normals) as a covariate to the vital rate models described
199 above.

200 *Sex ratio experiment*

201 At one site near the center of the range (Lake Lewisville Environmental Learning Area,
202 Texas), we established a separate experiment to quantify how sex ratio variation affects
203 female reproductive success. Details of this experiment, which was conducted in 2014–
204 2015, are described in Compagnoni et al. 2017. Briefly, we established 124 experimental
205 populations in $0.4m \times 0.4m$ plots that varied in population density (1–48 plants/plot)
206 and sex ratio (0–100%female), with 2–4 replicates for each of 34 density-sex ratio com-
207 binations. We used plants from a single source population located ca. 200 km from the
208 experimental site. The experiment was established ca. 1 km from a natural population at
209 this site and plots were situated with a minimum of 15 m spacing, a buffer that was in-

210 tended to limit pollen movement between plots (pilot data indicated that \geq 90% of wind
211 pollination occurred within 13m). We measured female reproductive success in different
212 density and sex ratio environments by collecting panicles from a subset of females in
213 each plot at the end of the reproductive season. In the lab, we counted the total number
214 of seeds on each panicle.

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

229 *Statistical analysis of sex ratio experiment*

230 Our previous study examined how interactions between density and frequency (sex ra-
231 tio) dependence contributed to female reproductive success (Compagnoni et al., 2017).
232 Here we focus solely on sex ratio variation, averaging over variation in density. Our goal

233 was to estimate a ‘mating function’ that defines how availability of male panicles affects
234 the viability of seeds on female panicles. We modeled the seed viability data with a
235 binomial distribution where the probability of viability (v) was given by:

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

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

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

249 *Demographic model of range limits*

250 The statistical models for the common garden and sex ratio experiments provided the
251 backbone of the full demographic model, a matrix projection model (MPM) structured

252 by size (tiller number) and sex. Following the statistical modeling, the MPM accommodates
 253 longitude as a predictor variable, allowing us to identify the longitudinal limits of
 254 population viability ($\lambda \geq 1$) and investigate the underlying drivers of population decline
 255 at range limits.

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

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

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

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

266 where p^F and c^F are flowering probability and panicle production for females of size x , d
 267 is the number of seeds (fertilized or unfertilized) per female panicle, v is the probability
 268 that a seed is fertilized, m is the probability that a fertilized seed germinates, and ρ is
 269 the primary sex ratio (proportion of recruits that are female). Seed fertilization depends
 270 on the OSR of panicles (following Eq. 1) which was derived from the $U \times 1$ vectors of

²⁷¹ population structure \mathbf{F}_t and \mathbf{M}_t :

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

²⁷² Finally, the dynamics of the size-structured component of the population are given
²⁷³ by:

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

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

²⁷⁴ For both females and males, the first term represents seedlings that survived their first
²⁷⁵ year and enter the size distribution of established plants. Because our common garden
²⁷⁶ experiment relied on greenhouse-raised transplants we had little information on these
²⁷⁷ early life cycle transitions, **and filling these gaps was important for generating realistic**
²⁷⁸ **predictions from the demographic model.** We used the seedling survival probability (σ)
²⁷⁹ from our demographic studies of the hermaphroditic, perennial congener *Poa autumnalis* in east Texas (T.E.X. Miller and J.A. Rudgers, *unpublished data*) as a stand-in for
²⁸⁰ *P. arachnifera*, and we assume this probability was constant across sexes and longitudes
²⁸¹ (posterior mean $\sigma = 0.09$). We also assume that surviving seedlings reach size y with
²⁸² probability $g(y, x = 1)$, the expected future size of 1-tiller plants from the transplant ex-
²⁸³ periment. The second term represents survival and size transition of established plants
²⁸⁴ from the previous year, where s and g give the probabilities of surviving at size x and
²⁸⁵ from the previous year, where s and g give the probabilities of surviving at size x and

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

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

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

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

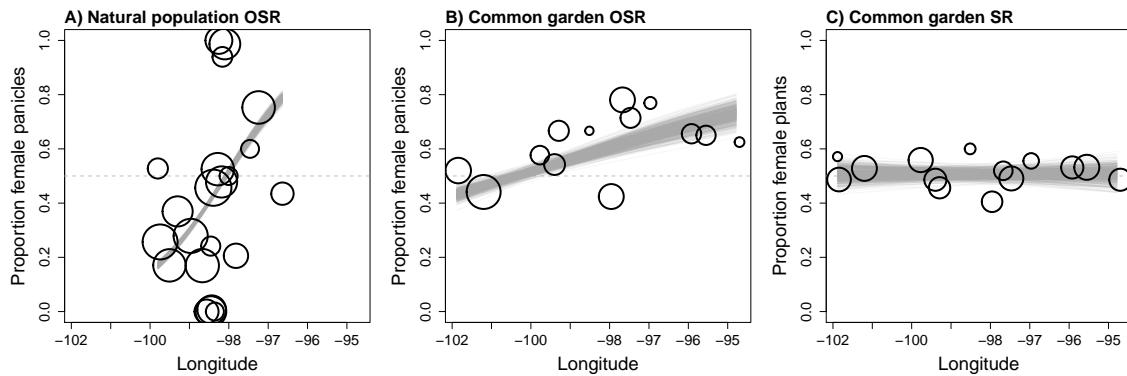


Figure 3: Sex ratio variation of *P. arachnifera* across its longitudinal distribution. **A**, Operational sex ratio (fraction of panicles that were female) in 22 natural populations; **B**, Operational sex ratio and **C**, sex ratio (fraction of plants that were female) in 14 common gardens. Within 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.**

Results

303

304 *Sex ratio variation in natural populations*

305 We found wide variation in operational sex ratio (proportion of total panicles that were
 306 female) across 22 natural populations of *P. arachnifera*, including female-only and male-
 307 only populations (Fig. 3A). There was a longitudinal trend to sex ratio variation, with
 308 male-biased panicle production in the **xeric** western parts of the range and female-biased
 309 panicle production in the **mesic** east.

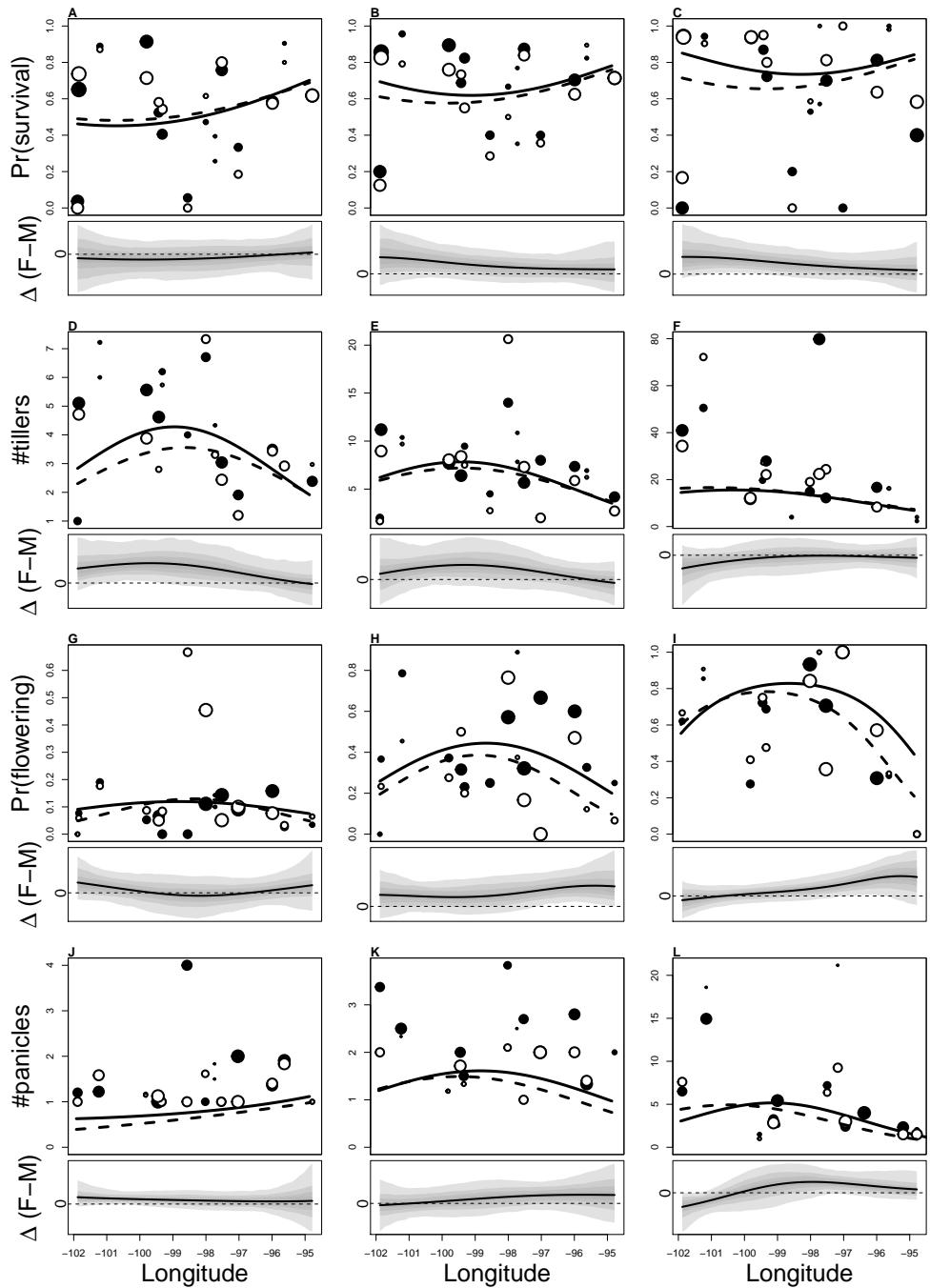


Figure 4: Sex-, size-, and longitude-related variation in: A–C, inter-annual probability of survival; D–F, inter-annual growth (change in number of tillers); G–I, probability of flowering; J–L, number of panicles produced given flowering. Points show means by site for females (filled) and males (open) and small (left column), medium (middle column), and large (right column) size classes (discritized, 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.

310

Geographic variation in sex-specific demography

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

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

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

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

339 For survival, flowering, and panicle production we did not find strong evidence for
340 local adaptation based on the posterior distributions of the climate mismatch coefficient
341 (Fig. B2A,C,D). However, climate mismatch negatively affected growth such that plants
342 from populations whose mean annual precipitation strongly differed from that of the
343 common garden location exhibited reduced growth (Fig. B2B).

344 *Sex-ratio dependent seed fertilization*

345 Seed **fertilization** declined with increasing female bias in the sex ratio manipulation ex-
346 periment. Fertilization success was greatest for females that were rare in male-biased
347 populations, where 75-80% of initiated seeds were viable (Fig. 5). Fertilization was ro-
348 bust to sex ratio variation until ca. 75% of the panicles in a population were female,
349 at which point fertilization strongly declined due to pollen limitation. The fitted model
350 specifies that seed fertilization goes to zero as female bias goes to 100% (Eq. 1), and this
351 assumption was generally consistent with the experimental results, where the majority
352 (63%) of females from female-only populations produced zero viable seeds. The occa-
353 sional production of viable seeds in female-only populations (Fig. 5) likely reflects rare
354 pollen contamination between experimental plots.

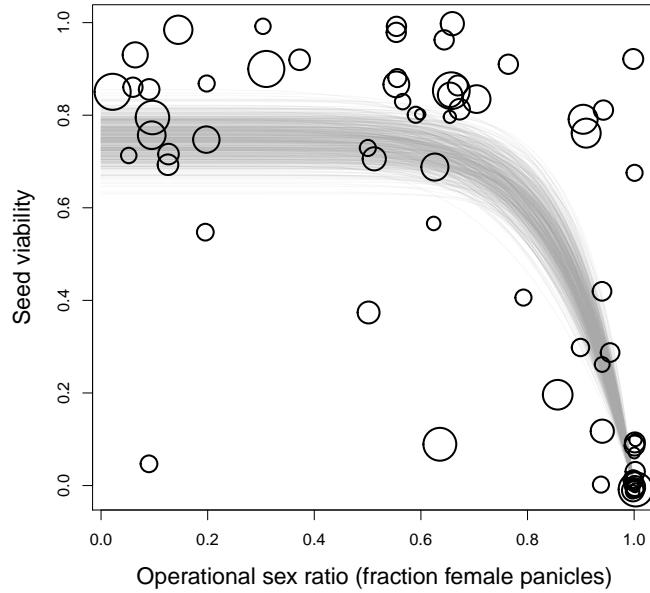


Figure 5: Seed fertilization success in relation to operational sex ratio (fraction of panicles that are female) in experimental populations. Circles show data from tetrazolium assays of seed viability; circle size is proportional to the number of seeds tested (min: 14, max: 57). Lines show model predictions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

355

Two-sex model of range limits

356 The process-based demographic model connected sex-specific vital rate responses to
 357 longitudinal variation (Fig. 4) with sex ratio-dependent mating (Fig. 5) to predict the
 358 contributions of females and males to range limitation. == The model predicted max-
 359 imum fitness in the center of the range and loss of population viability at longitudes
 360 that corresponded well with observed range limits. Specifically, the western-most and
 361 eastern-most county records of *P. arachnifera* fell within the uncertainty distribution of

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

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

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

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

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

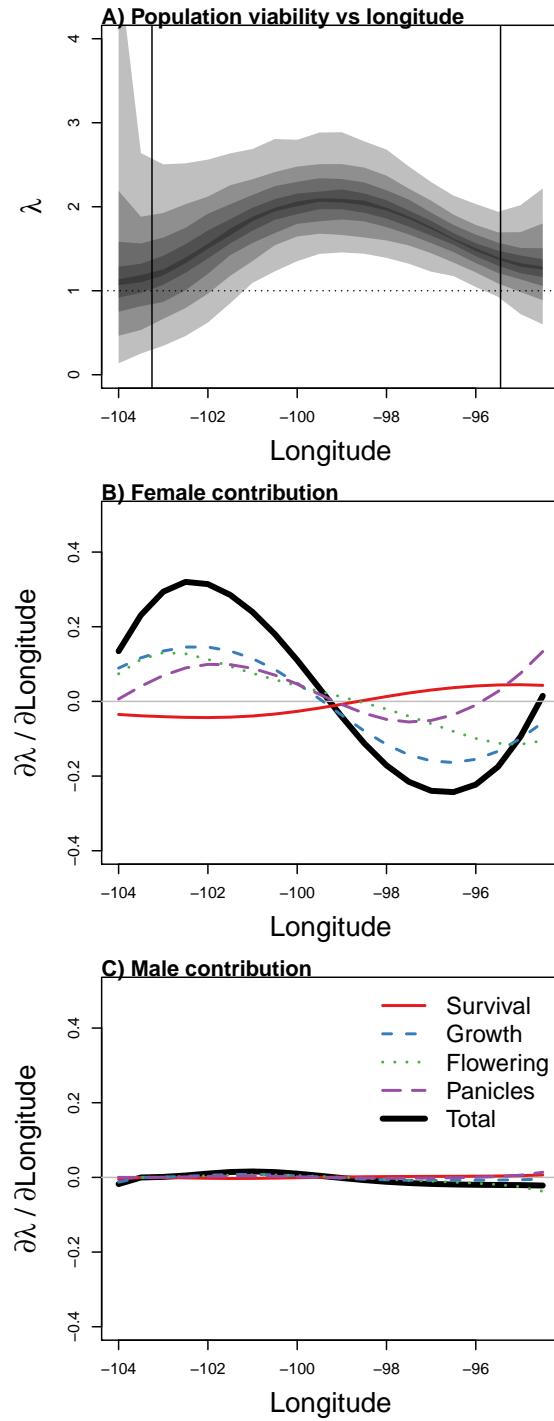


Figure 6: Population growth (λ) as a function of longitude, predicted by the two-sex MPM that incorporates sex-specific demographic responses to longitude with sex ratio-dependent seed fertilization. A, posterior distribution of λ , where shaded regions show the 25, 50, 75, and 95% percentiles of parameter 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

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

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

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

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

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

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

479 west – averaged across years (Fig. 3B) or in any single year (Fig. B3) – nor did we find
480 any strong demographic evidence for a western male advantage (in fact, there was a
481 western female advantage in growth and survival for some sizes). If male advantage /
482 female disadvantage under harsh abiotic conditions (**suggested by the natural popula-**
483 **tion trend: Fig. 3A**) is driven by the greater resource requirements of females then it is
484 possible that clonal propagation and/or legacies of greenhouse rearing masked the ‘true’
485 sex difference at xeric-edge common garden sites, **or that reproductive costs accumulate**
486 **over longer time scales than considered here**. Instead, the stronger pattern of sex ratio
487 bias was the female reproductive advantage at the mesic, eastern range edge. We hy-
488 pothesize that the mesic edge is limited by competition and that the female reproductive
489 advantage reflects competitive superiority of females, which has been suggested in pre-
490 vious studies of Texas bluegrass (Compagnoni et al., 2017) and shown in other dioecious
491 plants (Eppley, 2006), particularly under mesic conditions (Chen et al., 2014). Theory
492 suggests that biotic interactions such as competition are likely to limit species’ ranges at
493 the benign (e.g., mesic) end of abiotic gradients (Louthan et al., 2015) though this has
494 not been explored, to our knowledge, in the context of sex-structured dynamics. Future
495 studies in our system or others could test whether females and males differ in their re-
496 sponds to biotic stressors at xeric and mesic range edges to reveal how biotic factors
497 shape range limits via sex-specific demography.

498 Beyond the novel elements of sex-structured demography and mate limitation, our
499 work informs and advances the broader literature on the processes generating species’
500 range limits in at least three ways. First, the Texas bluegrass case study demonstrates
501 that a process-based model capturing environment-dependent demography can accu-
502 rately predict geographic range limits: the predicted limits of $\lambda \geq 1$ corresponded well

503 to observed longitudinal limits from collection records, particularly given the uncer-
504 tainty characterized by our hierarchical Bayesian statistical approach. We parameterized
505 the model with respect to longitude, which tightly covaries with aridity in the southern
506 Great Plains. Extensions of this model that transition from implicit to explicit consid-
507 eration of aridity will allow us to forecast range responses of Texas bluegrass to future
508 climate change and ask whether climate change will reduce or amplify OSR bias and
509 mate limitation at longitudinal range edges. It would be interesting to additionally con-
510 sider this species' latitudinal limits, though our exploratory analyses revealed no clear
511 sex differences or sex ratio variation with respect to latitude.

512 Second, our results also provide novel evidence for contrasting demographic re-
513 sponses to environmental drivers throughout a species' range – or “demographic com-
514 pensation” (Doak and Morris, 2010; Villegas et al., 2015). Elevated performance in some
515 life history processes can compensate for declines in other processes and thus buffer
516 range-edge populations against harsh environmental conditions. In Texas bluegrass,
517 most vital rates declined toward eastern and western range limits but survival showed
518 the opposite pattern. Increased survival at longitudinal extremes partially offset declines
519 in other vital rates but this positive response was weaker than the negative responses.
520 Ultimately, increased survival was not sufficient to prevent declines in population vi-
521 ability from the range center to eastern and western limits, which were dominated by
522 declining female growth and flowering. However, we also found evidence that growth
523 patterns exhibited local adaptation: individuals planted into locations that were climati-
524 cally similar to locations of their source population exhibited greater growth, on average,
525 irrespective of sex. It is therefore possible that our demographic model (which does not
526 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 of environmental forcing. There is growing awareness that local adaptation can modify expectations for species' distributions under global change (Peterson et al., 2019). Mechanistic models of range limits that incorporate potential for local adaptation would be a valuable next step.

Third, our results highlight some important considerations in how environment-dependent demographic models are best parameterized to derive insights into the drivers of range limits. Our approach relied heavily on common garden populations, which allowed us to plant and track known-sex individuals in contrasting environmental conditions that encompass and exceed the natural geographic distribution. The ability to robustly sample edge and beyond-edge environments is a powerful advantage of the common garden transplant approach (Hargreaves et al., 2013). However, this also limited the size variation that we were able to include and model, and the size distributions of common garden populations skewed consistently smaller than natural populations. In Appendix C, we show that our conclusions are likely robust to this feature of the common gardens. However, our ability to quantify the consequences of size representation is itself limited by size representation: we can simulate a population in which the largest common garden sizes are more common than they actually were, but simulating a population with sizes much larger than observed requires extrapolation of our statistical models, and we are skeptical about what insights such an exercise could provide (in Appendix C, we extrapolated demographic performance to sizes 50% greater than the observed maximum). This issue is not unique to our study but will be encountered by any transplant study intended to yield inferences about range limits of species with significant size structure, such as trees. If we could re-do our experiment knowing what we

551 know now, we would combine data from natural and transplanted populations to model
552 size-dependent demography over a more realistic size distribution. Other investigators
553 inspired by similar questions about the demographic drivers of range limits should con-
554 sider such a hybrid approach.

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

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

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583 **Author contributions**

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

586 **Data accessibility**

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

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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

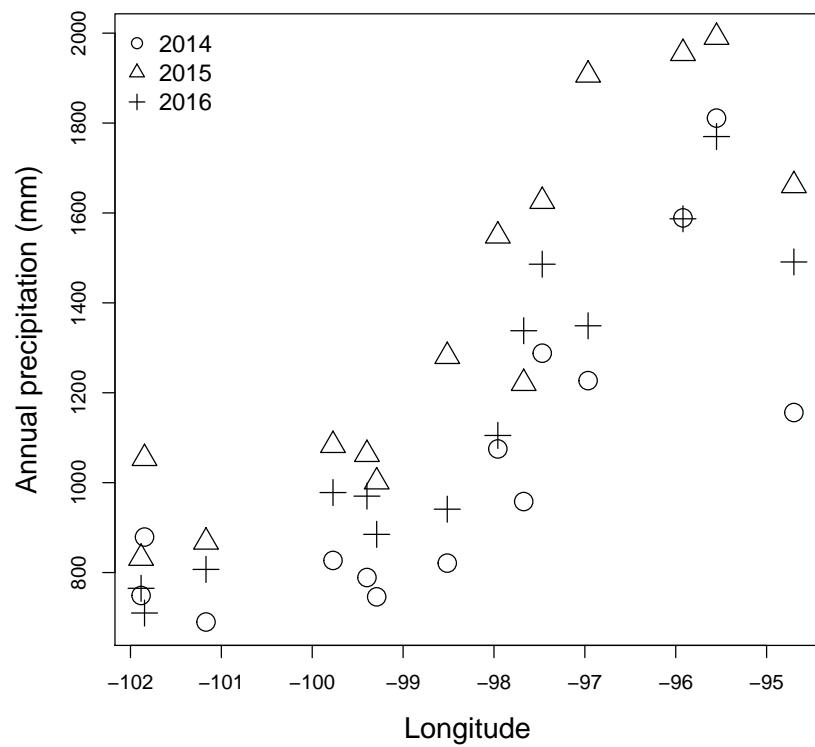


Figure A1: Total annual precipitation at common garden sites during the study years tracked long-term trends of increasing aridity from east to west.

Appendix B: Additional results

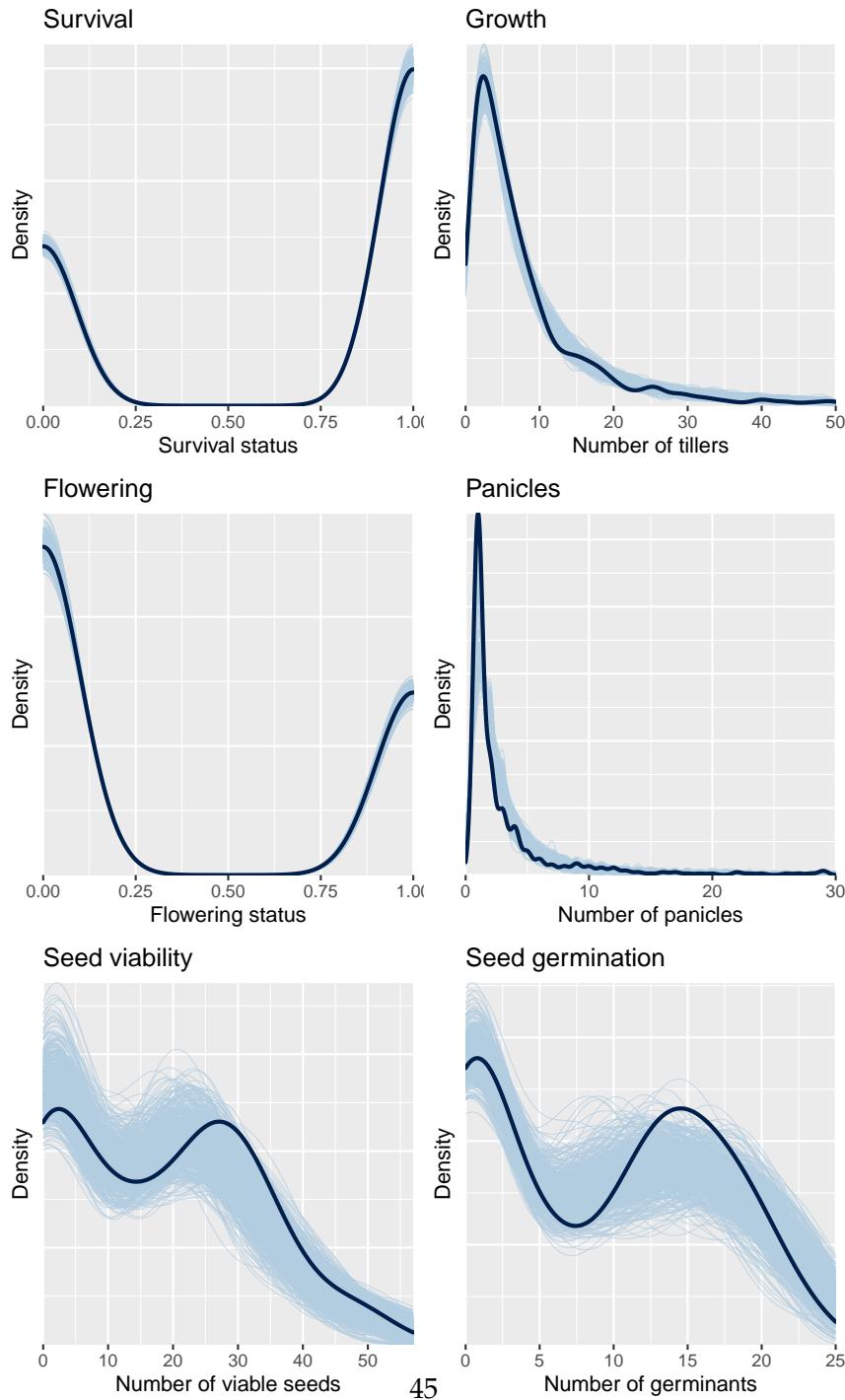


Figure B1: Posterior predictive checks of statistical models for demographic vital rates. Lines show density distributions of real data (thick, dark blue) compared to simulated data sets (thin, light blue) generated from the fitted models based on 500 draws of the posterior distribution of parameter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

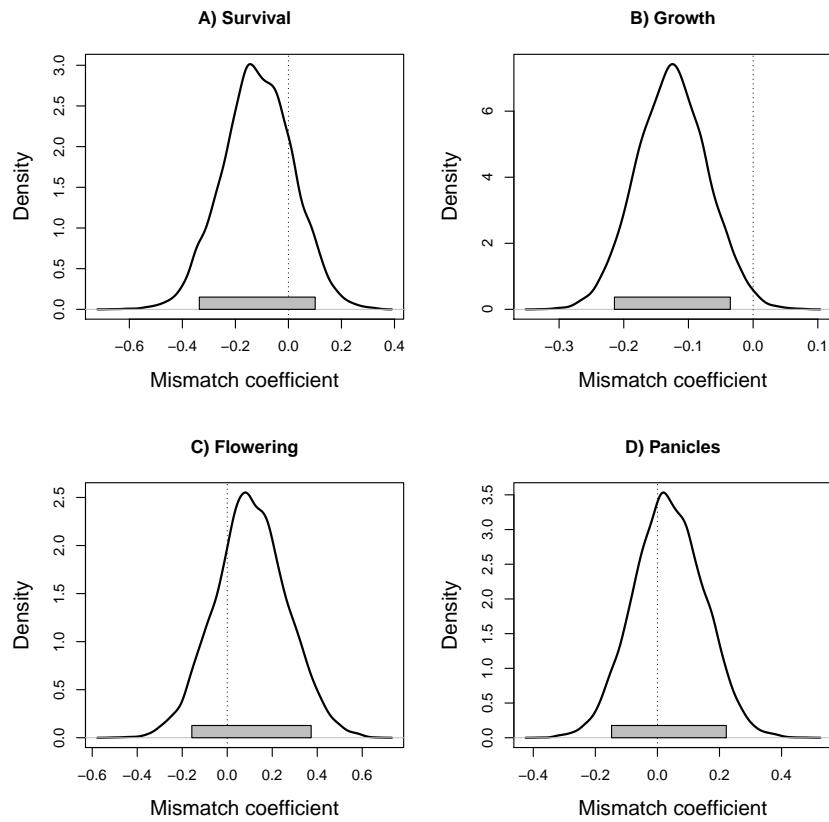


Figure B2: Posterior distributions of statistical coefficients for the influence of source-garden climate mismatch on survival (A), growth (B), flowering (C), and panicle production (D). Gray bars show the 95% credible interval of the coefficients. Climate mismatch was calculated as the absolute value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

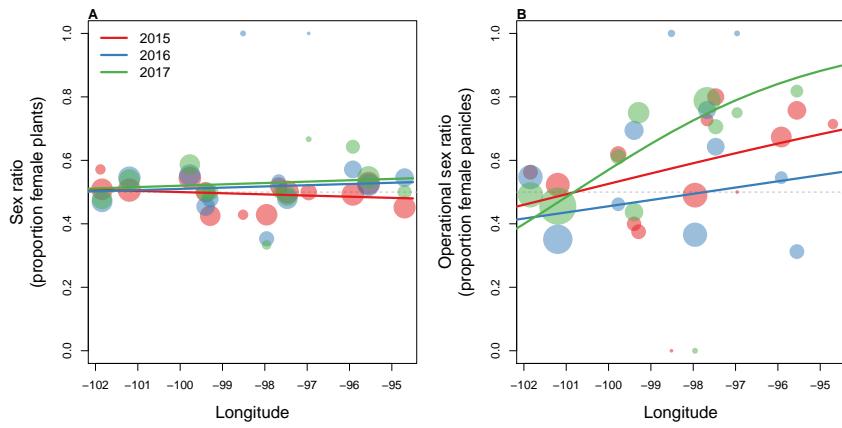


Figure B3: Year-specific sex ratios of plants (A) and panicles (B) in common garden populations spanning the longitudinal aridity gradient. Points sizes are proportional to sample sizes and lines show fitted binomial GLMs.

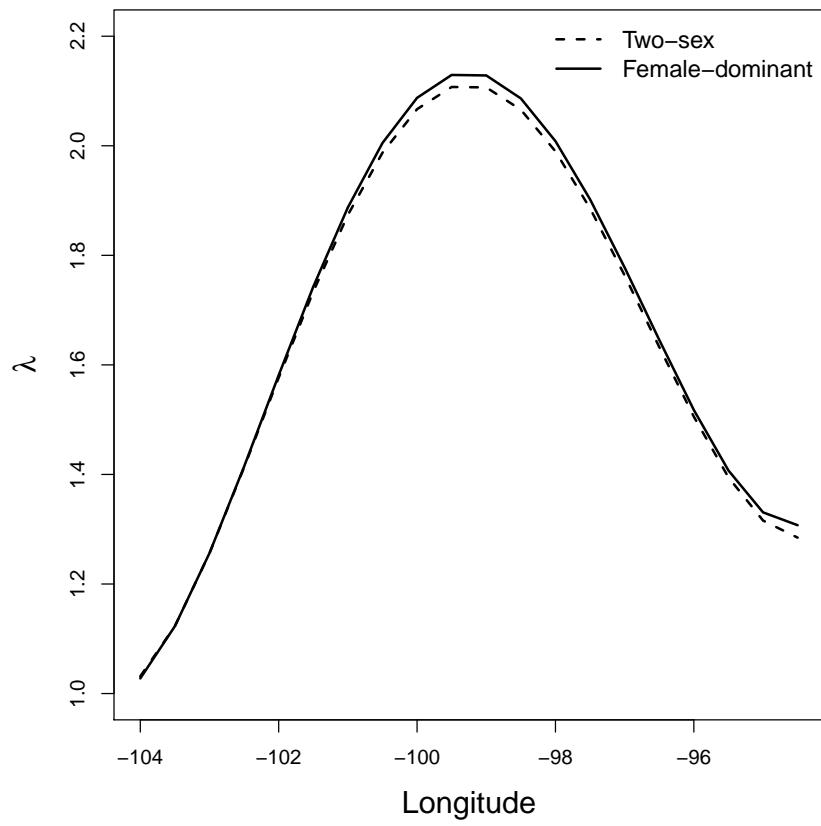


Figure B4: Comparison of longitudinal variation in λ between the two-sex demographic model (dashed line) that includes dependence of female seed production on population structure and the corresponding female-dominant model (solid line) with constant female fertility and all else equal. Models were evaluated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

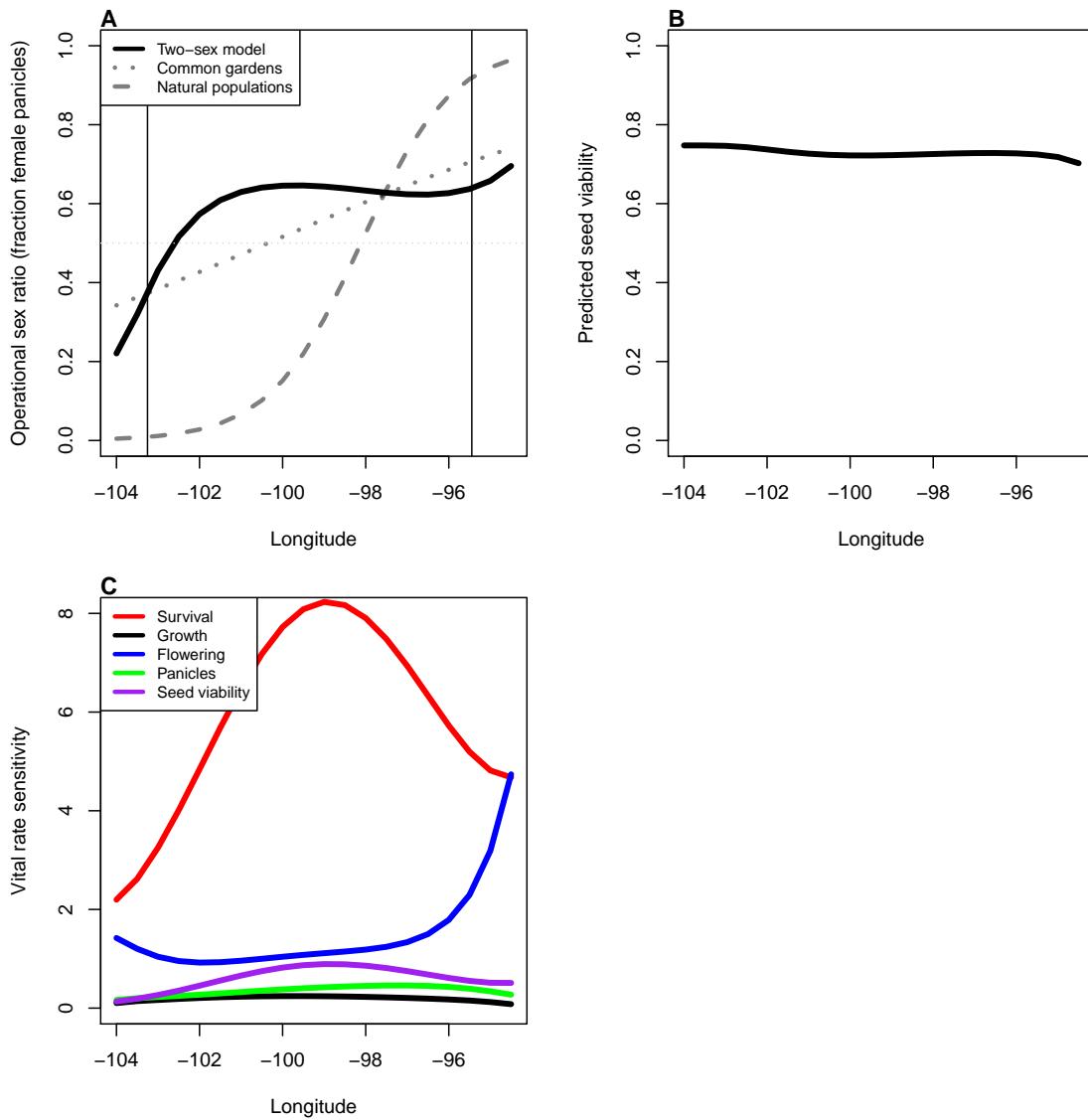


Figure B5: **A**, Longitudinal variation in operational sex ratio (fraction of panicles that are female) predicted by the two-sex MPM (solid line) compared to the sex ratio clines fitted to data from common gardens (dotted line) or natural populations (dashed line). Vertical lines show the longitudes 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.

765 **Appendix C: Size distribution comparisons and simulation
766 experiments**

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

770 *Observed and predicted size distributions*

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

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

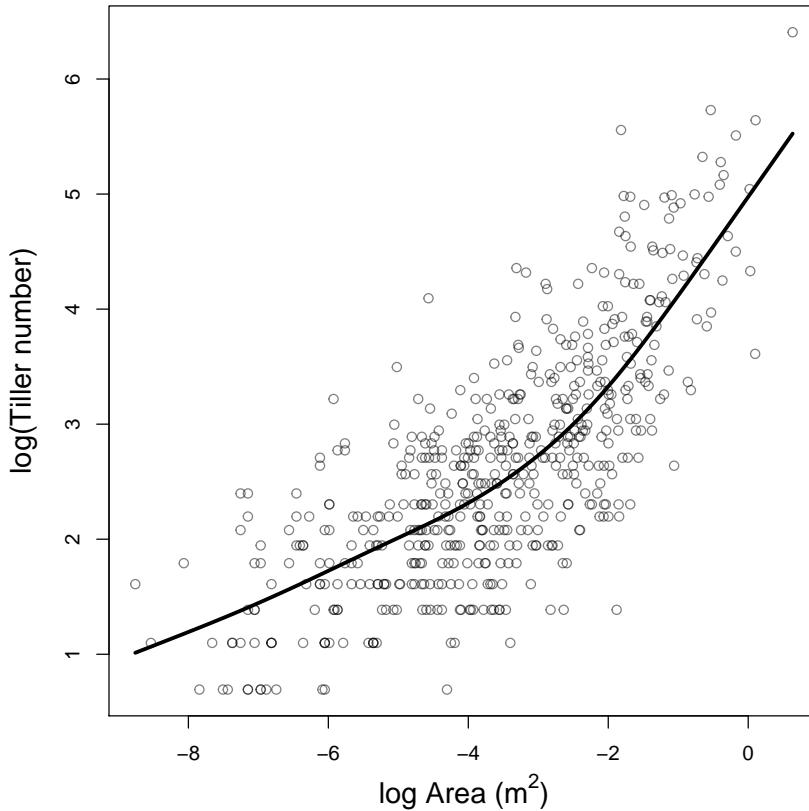


Figure C1: Relationship between area (m^2) and tiller count from plants in the common garden experiment. The fitted gam model (line) was used to convert area measurements from natural populations to tiller counts.

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

⁷⁸⁷ logarithm of tiller number, and then estimating the empirical distribution of this variable.

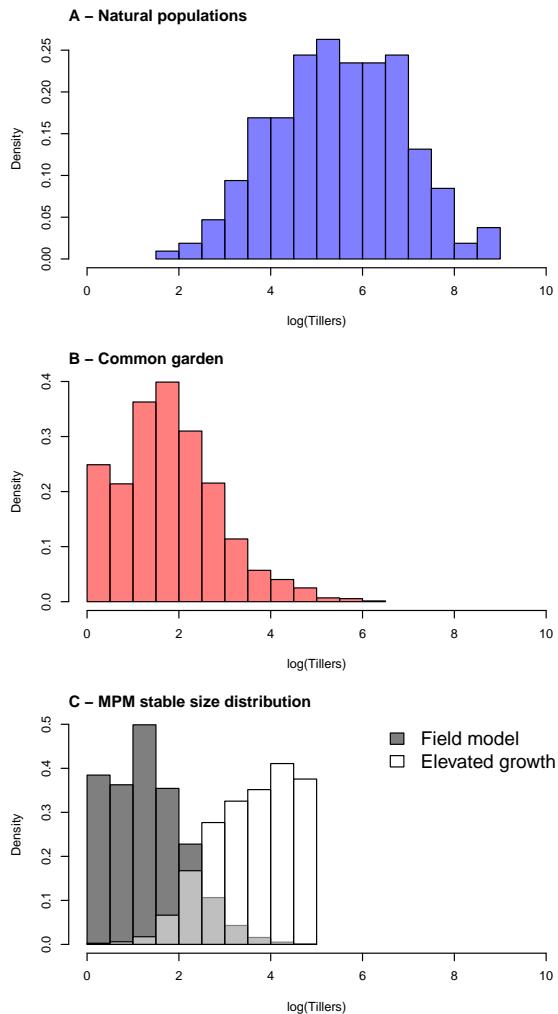


Figure C2: Size distribution of Texas bluegrass from natural populations (A), common garden populations (B), and predicted by the two-sex MPM (C). In C, the two size distributions come from the base model parameterized following methods described in the main manuscript (“field model”, in gray) and a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

788 *Results.* Plants from natural populations were larger, on average, than plants in our
 789 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

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

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

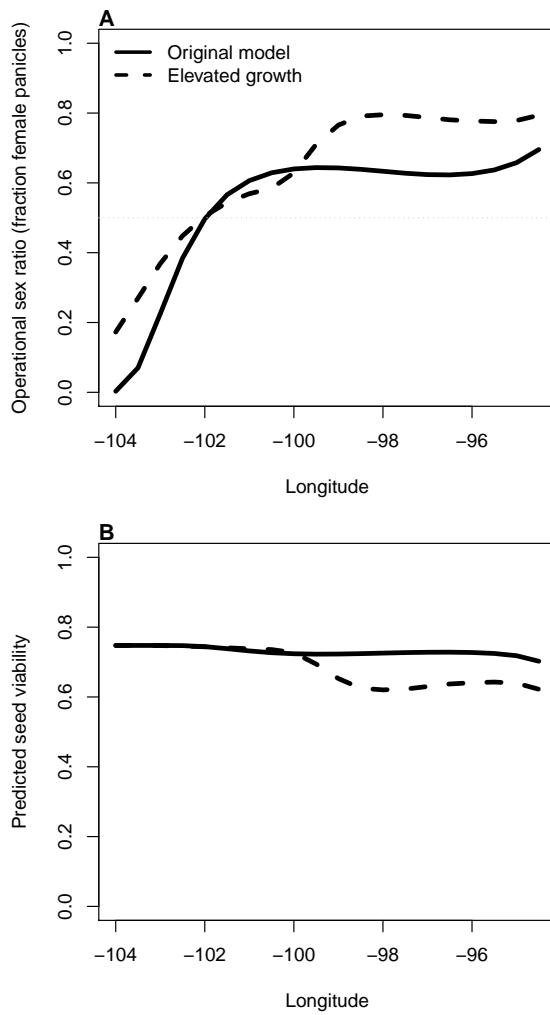


Figure C3: Two-sex model predictions for **A** operational sex ratio (fraction of panicles that are female) and **B** seed viability at stable population structure in relation to longitude. Solid line shows predictions of the base model using field-estimated parameter values and dashed line shows the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

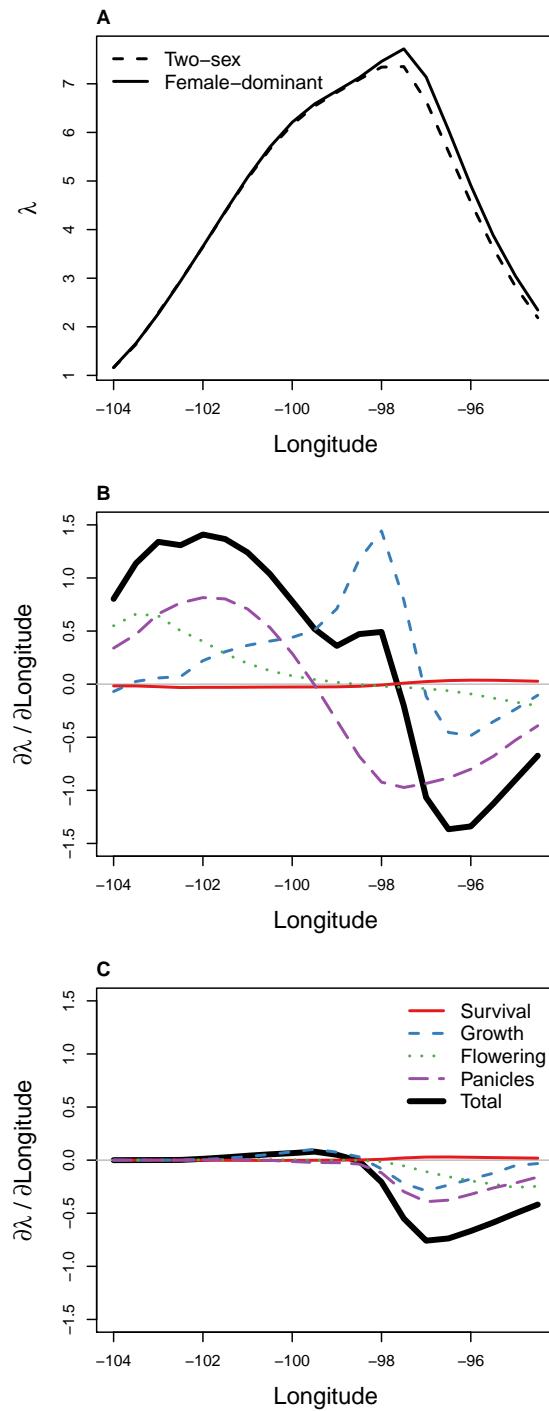


Figure C4: Results for the elevated growth model, in which the intercept of growth function was increased by a factor of 2.75. **A**, contrast of two-sex and female-dominant models, as in Fig. B4; **B,C**, Life Table Response Experiments decomposing the change in λ with respect to longitude into contributions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

Model	WAIC	ELPD	SE(ELPD)
1 Climate	13286.29	-6643.14	87.46
2 Longitude	13288.39	-6644.19	87.25

Table B1: Model selection results for candidate vital rate models with longitude or climate (mean annual precipitation) as environmental covariates. Table shows WAIC (Watanabe-Akaike Information Criterion), ELPD (expected log predictive density), and the standard error of ELPD. The fact that the SE of ELPD is much greater than the difference between models suggests that longitude and climate are effectively interchangeable as environmental covariates.