

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

68 plants, for example, populations at upper altitudes and latitudes and in the more xeric
69 margins of species' ranges tend to be male-biased (Field et al., 2013b).

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

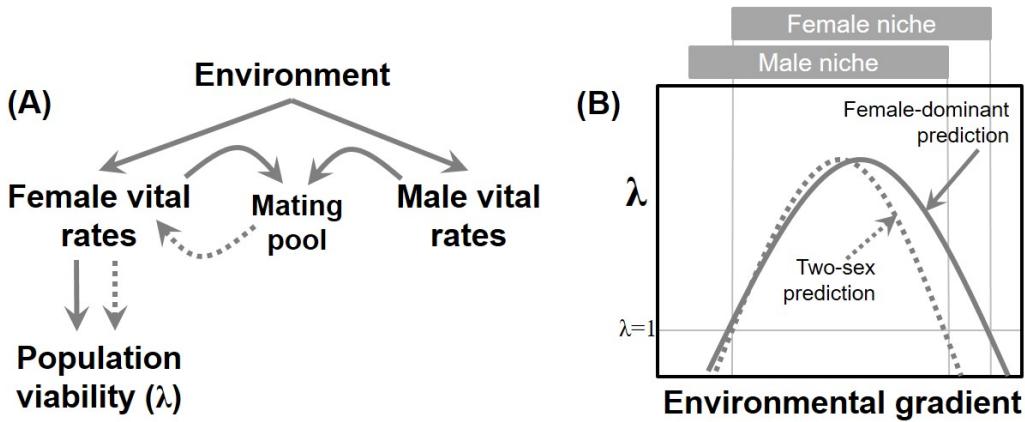


Figure 1: Hypotheses for how environmental variation can affect population viability and range limits in dieocious species. Under the female-dominant hypothesis, environmental drivers affect population growth (λ) through effects on females, alone (A). In geographic / environmental space, this translates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

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

90 deviate from female-dominant expectations.

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

102 **Materials and methods**

103 *Study system and natural population surveys*

104 *Poa arachnifera* (Texas bluegrass) is a perennial, cool-season (C3) grass endemic to the
105 southern Great Plains. This species occurs almost exclusively in central Texas, Okla-
106 homa, and southern Kansas (Fig. 2) though there are occasional records of adventive
107 populations in other U.S. states¹. Like all grasses, *P. arachnifera* is wind-pollinated. In-
108 dividuals can be sexed only when flowering, in early spring, based on the presence of
109 stigmas (females) or anthers (males) in the inflorescence. Following inflorescence and
110 seed production, plants go dormant for the hot summer months and vegetative growth

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

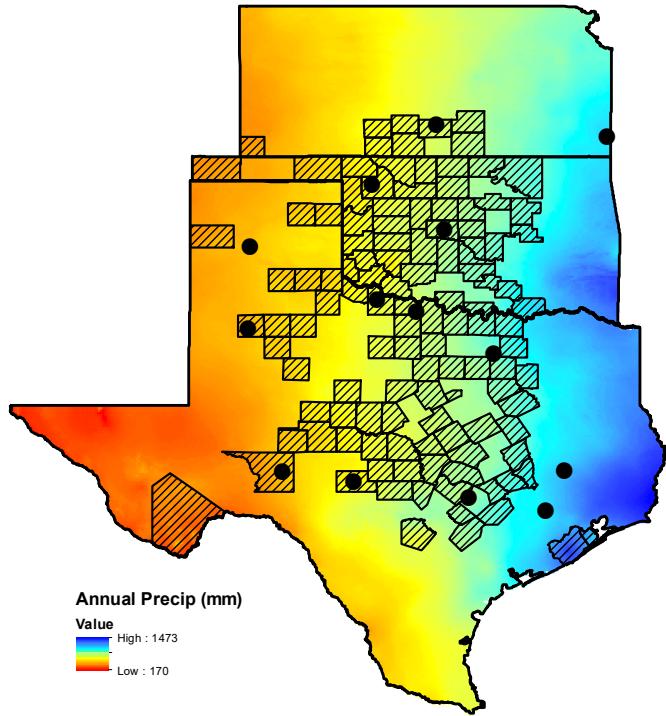


Figure 2: Geographic and environmental distribution of *P. arachnifera* in Texas, Oklahoma, and Kansas. Hatched shapes show counties with herbarium records of occurrence. Color shows geographic variation in annual precipitation (mm) based on 30-year normals from WorldClim (Fick and Hijmans, 2017). Points show sites for the common garden transplant experiment.

111 resumes in fall. Individuals grow via rhizomes to form patches that may be as large as
 112 $50m^2$ in area. Sex in *P. arachnifera* is genetically based (Renganayaki et al., 2005, 2001)
 113 and the primary sex ratio is 1:1 (J. Goldman, USDA-ARS, *unpubl. data*). The rhizomatous
 114 growth habit allowed us to clonally propagate large numbers of known-sex individuals
 115 for experiments, as we describe below.

116 We surveyed *P. arachnifera* across its range to establish whether natural populations
 117 exhibited geographic clines in OSR corresponding to the longitudinal aridity gradient.

118 We visited 14 populations in spring 2012 and 8 in spring 2013 (Table A1). At each loca-
119 tion, we searched for *P. arachnifera* along roads, trails, or creek drainages and recorded
120 the number of female and male patches that we encountered and the number of inflores-
121 cences in each patch. To quantify the mating environment, we focus our analyses on the
122 sex ratio of inflorescences rather than patches, since a single patch makes different con-
123 tributions to the mating pool depending on whether it has few or many inflorescences.

124 *Statistical analysis of natural population surveys*

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

135 *Common garden experiment*

136 *Source material and experimental design*

137 We established a common garden experiment at 14 sites throughout and beyond the
138 geographic distribution of *P. arachnifera* (Fig. 2, Table A2). Experimental sites spanned

¹³⁹ latitudinal and longitudinal variation, though we focus here on longitude. During the
¹⁴⁰ three years of this experiment (2014–2017), total precipitation at each site closely tracked
¹⁴¹ longitude (Fig. A1), as expected based on longer-term climate trends (Fig. 2). Source
¹⁴² material for the experiment came from 8 sites, which were a subset of the sites that
¹⁴³ were visited for the natural population survey (Table A1). At these sites, we collected
¹⁴⁴ vegetative tillers from flowering individuals of each sex (mean: 11.6 individuals per
¹⁴⁵ site, range: 2–18). These were brought back to the Rice University greenhouse, where
¹⁴⁶ they were clonally propagated in ProMix potting soil and supplemented with Osmocote
¹⁴⁷ slow-release fertilizer at 78–80°F under natural humidity and light.

¹⁴⁸ Common gardens were set up in Fall (October–December) 2014. At each site, we es-
¹⁴⁹ tablished 14 experimental blocks, which corresponded to a tree or woodland edge, pro-
¹⁵⁰ viding partial shade that mimics this species' natural micro-environment. We planted
¹⁵¹ 3 females and 3 males in each block, for a total of 42 individuals per sex per site and
¹⁵² 1176 total plants across sites, with all source collections represented at all sites. Indi-
¹⁵³ viduals were spaced within blocks to allow space for rhizomatous growth that could be
¹⁵⁴ clearly attributed to individual transplants. To promote establishment, we cleared vege-
¹⁵⁵ tation immediately surrounding transplants and provided ca. 1 L of water at the time of
¹⁵⁶ transplanting but provided no subsequent watering, fertilization, or competitor removal.

¹⁵⁷ We visited each site during May of 2015, 2016, and 2017. For each individual in each
¹⁵⁸ year, we recorded data for four demographic vital rates: survival status (alive or dead),
¹⁵⁹ size (number of tillers and patch area), flowering status (reproductive or vegetative), the
¹⁶⁰ number of panicles produced by flowering plants.

161 *Statistical analysis of common garden experiment*

162 We analyzed the demographic vital rates with generalized linear mixed models in a
163 hierarchical Bayesian framework. All the vital rates shared a common linear predictor for
164 the expected value that included fixed effects of size, sex, linear and quadratic terms for
165 longitude, and all 2- and 3-way interactions. We included quadratic effects of longitude
166 to account for the possibility of non-monotonic responses, following the hypothesis that
167 fitness may peak in the center of the range. The linear predictor also included random
168 effects of site, block, and source population of the transplant. We pooled all three years
169 of observations for analysis so we did not explicitly model temporal variation but our
170 results are implicitly averaged over years.

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

179 *Sex ratio experiment*

180 At one site near the center of the range (Lake Lewisville Environmental Learning Area,
181 Texas), we established a separate experiment to quantify how sex ratio variation affects
182 female reproductive success. Details of this experiment, which was conducted in 2014–

183 2015, are described in Compagnoni et al. 2017. Briefly, we established 124 experimental
184 populations in $0.4m \times 0.4m$ plots that varied in population density (1–48 plants/plot) and
185 sex ratio (0–100% female), with 2–4 replicates for each of 34 density-sex ratio combina-
186 tions. The experiment was established ca. 1 km from a natural population at this site and
187 plots were situated with a minimum of 15 m spacing, a buffer that was intended to limit
188 pollen movement between plots (pilot data indicated that $\geq 90\%$ of wind pollination oc-
189 curred within 13m). We measured female reproductive success in different density and
190 sex ratio environments by collecting panicles from a subset of females in each plot at the
191 end of the reproductive season. In the lab, we counted the total number of seeds on each
192 panicle.

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

207 *Statistical analysis of sex ratio experiment*

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

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

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

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

Demographic model of range limits

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

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

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

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

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

where p^F and c^F are flowering probability and panicle production for females of size x , d

245 is the number of seeds (fertilized or unfertilized) per female panicle, v is the probability
 246 that a seed is fertilized, m is the probability that a fertilized seed germinates, and ρ is
 247 the primary sex ratio (proportion of recruits that are female). Seed fertilization depends
 248 on the OSR of panicles (following Eq. 1) which was derived from the $U \times 1$ vectors of
 249 population structure \mathbf{F}_t and \mathbf{M}_t :

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

250 Finally, the dynamics of the size-structured component of the population are given
 251 by:

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

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

252 For both females and males, the first term represents seedlings that survived their first
 253 year and enter the size distribution of established plants. Because our common gar-
 254 den experiment relied on greenhouse-raised transplants, we had little information on
 255 these early life cycle transitions. We used the seedling survival probability (σ) from our
 256 demographic studies of the hermaphroditic, perennial congener *Poa autumnalis* in east
 257 Texas (T.E.X. Miller and J.A. Rudgers, *unpublished data*) as a stand-in for *P. arachnifera*,
 258 and we assume this probability was constant across sexes and longitudes (posterior
 259 mean $\sigma = 0.09$). We also assume that surviving seedlings reach size y with probabil-

260 ity $g(y, x = 1)$, the expected future size of 1-tiller plants from the transplant experiment.
 261 The second term represents survival and size transition of established plants from the
 262 previous year, where s and g give the probabilities of surviving at size x and growing
 263 from sizes x to y , respectively, and superscripts indicate that these functions may be
 264 unique to females (F) and males (M).

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

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

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

Results

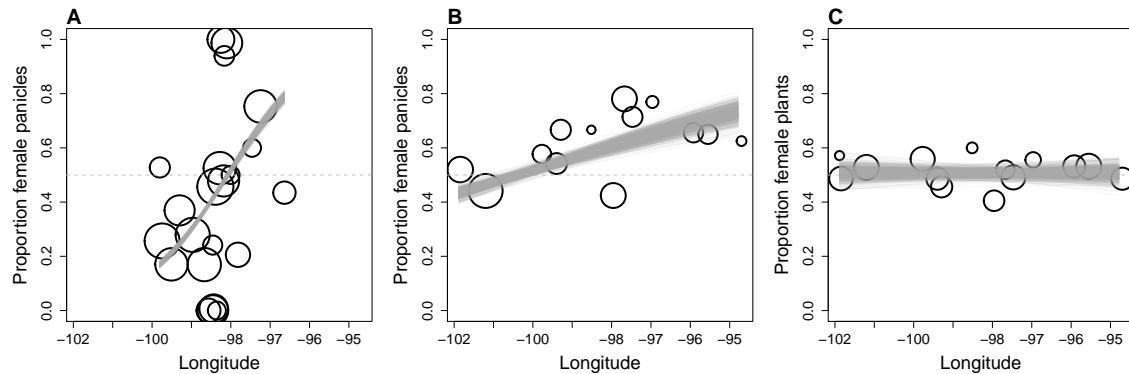


Figure 3: Sex ratio variation of *P. arachnifera* across its longitudinal distribution. **A**, Operational sex ratio (fraction of panicles that were female) in 22 natural populations; **B**, Operational sex ratio and **C**, sex ratio (fraction of plants that were female) in 14 common gardens. Within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

Sex ratio variation in natural populations

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

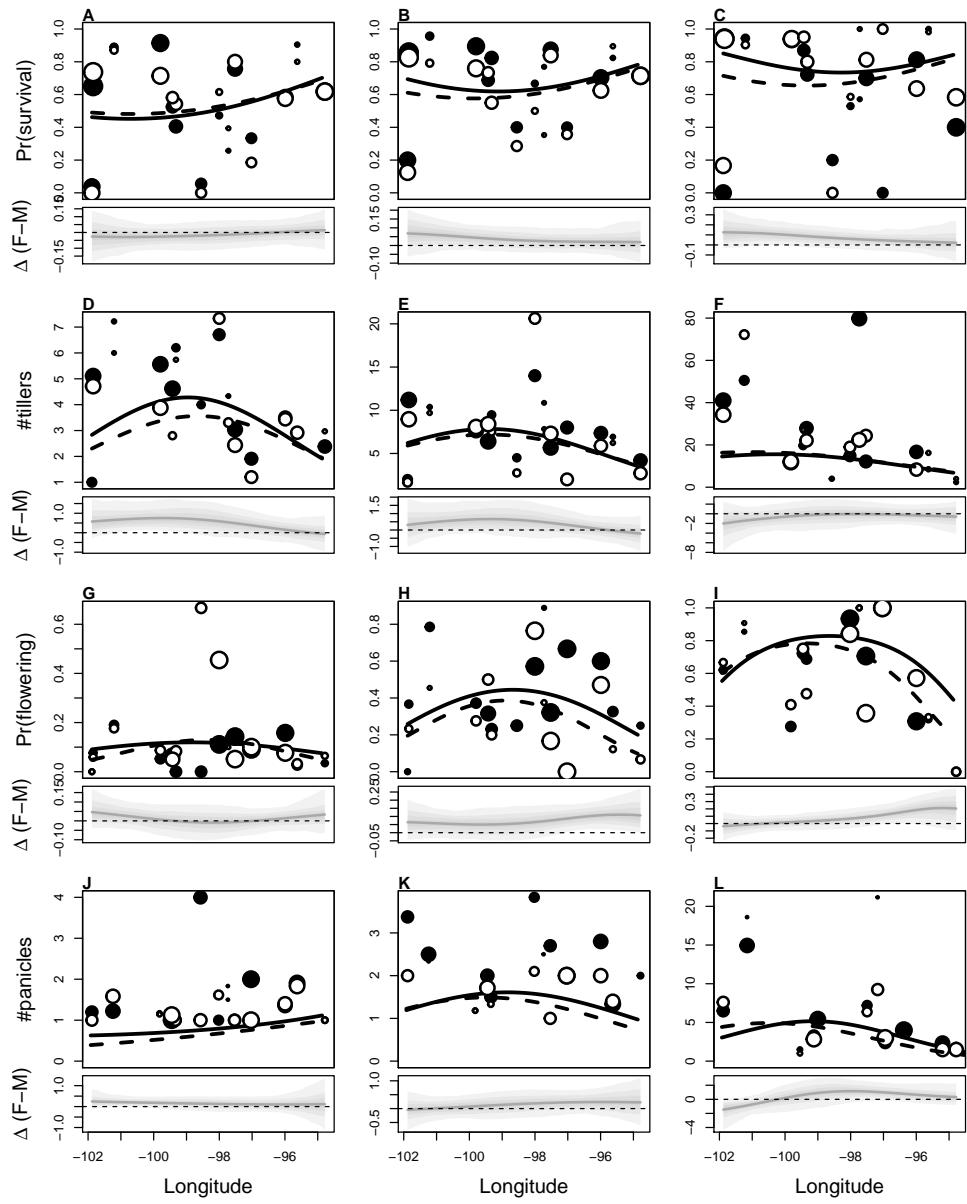


Figure 4: Sex-, size-, and longitude-related variation in: A–C, inter-annual probability of survival; D–F, inter-annual growth (change in number of tillers); G–I, probability of flowering; J–L, number of panicles produced given flowering. Points show means by site for females (filled) and males (open)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

287

Geographic variation in sex-specific demography

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

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

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

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

316 *Sex-ratio dependent seed fertilization*

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

327 *Two-sex model of range limits*

328 The processed-based demographic model connected sex-specific vital rate responses to
329 longitudinal variation (Fig. 4) with sex ratio-dependent mating (Fig. 5) to predict the
330 contributions of females and males to range limitation. The model predicted maxi-
331 mum fitness in the center of the range and loss of population viability at longitudes

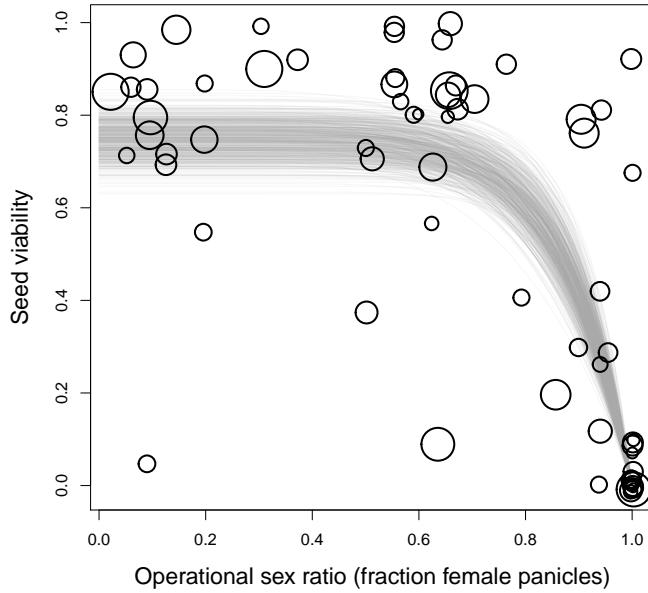


Figure 5: Seed fertilization success in relation to operational sex ratio (fraction of panicles that are female) in experimental populations. Circles show data from tetrazolium assays of seed viability; circle size is proportional to the number of seeds tested (min: 14, max: 57). Lines show model predictions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

that corresponded well with observed range limits. Specifically, the western-most and 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. B4A). Female bias in the OSR was predicted to cause declines in seed viability toward eastern

range margins (Fig. B4B). 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 (B4C). 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. B3).

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 eastern and western limits (Fig. 6B).

Skew in the OSR predicted by the demographic model was less extreme than was observed in natural and experimental populations (B4A). This occurred because sex differences in demography, especially flowering, were most pronounced at the largest sizes, and the MPM predicted that these sizes were very rare at stable population structure. The stable size distribution predicted by the MPM corresponded well to the common

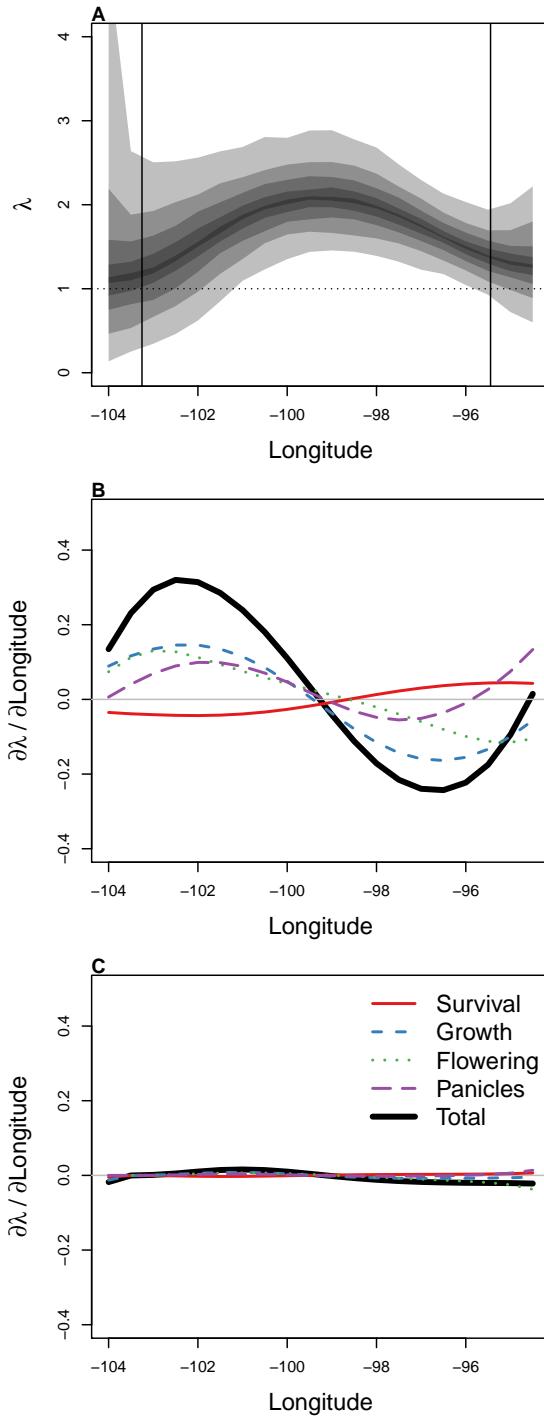


Figure 6: Population growth (λ) as a function of longitude, predicted by the two-sex MPM that incorporates sex-specific demographic responses to longitude with sex ratio-dependent seed fertilization. A, posterior distribution of λ , where shaded regions show the 25, 50, 75, and 95% percentiles of parameter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

364 garden data (from which the MPM was built) but was much smaller, on average, than
365 the size distribution we observed in natural populations (Fig. C2), presumably because
366 transplants did not grow like “real” plants and/or did not have time in our three-year
367 experiment to reach those sizes. In Appendix C, we explore whether higher growth
368 rates, leading to a more realistic size distribution, would lead to a more important role
369 for males. In numerical experiments with growth parameters, we found that larger size
370 distributions led to stronger female bias and thus stronger reductions in seed viability
371 at eastern range margins (Fig. C3). While these changes increased the contributions of
372 males to range limitation, female contributions were still more than twice as important as
373 males, and there was very little difference between predictions of the two-sex and female-
374 dominant models even under this elevated growth scenario (Fig. C4). This leads us to
375 conclude that, while our common garden-parameterized model may quantitatively un-
376 derestimate OSR bias and its demographic consequences relative to natural populations,
377 our qualitative conclusion that range boundary formation is effectively female-dominant
378 in this system is robust to any biases imposed by the growth trajectories and size distri-
379 butions of common garden populations.

380 Discussion

381 Understanding the causes of decline in population viability at range edges is a classic
382 ecological problem and the foundation for predicting how species’ ranges will respond
383 to global change drivers. Sexual niche differentiation has the potential to generate skew
384 in the mating pool across environmental gradients and may therefore contribute to re-
385 productive failure at range edges of dioecious species. In Texas bluegrass, we found
386 evidence for sexual niche differentiation that manifested over a large-scale geographic

gradient: the female reproductive niche (environment-dependent flowering and panicle production) extended farther east than that of males, generating female-biased operational sex ratios toward the eastern, mesic range margins, a pattern detected in natural populations and recapitulated in our common garden populations. Furthermore, seed viability declined with increasing skew in the OSR, indicating that mate (pollen) limitation can limit the reproductive output of female-biased mating pools. It would appear that all the pieces are in place for an important role of two-sex dynamics in contributing to distributional limits of Texas bluegrass, particularly at the eastern range edge. Yet, insights derived from the field-parameterized population model indicate the opposite: range limitation in this species is an effectively female-dominant process, with negligible contributions from males. Thus, in this system and likely others, female dominance is an adequate framework for understanding range dynamics: despite evidence for sexual niche differentiation, only the female niche mattered for determining the environmental limits of population viability. This does not mean that sex is unimportant, but rather that lack of sex is never so severe that it limits population viability.

The limited role of males in our experimental system can be explained by two factors. First, seed fertilization was robust to variation in OSR and was not predicted to strongly decline within the range of OSR bias that we observed and modeled, suggesting that few males are required to pollinate all or most females. Second, population growth (λ) was weakly sensitive to seed viability, which further buffered the demographic consequences of sex ratio bias. We speculate that our qualitative conclusions should apply to other species or systems that satisfy either, but especially both, of these conditions. While there are striking examples of female-biased sex ratios causing declines in population growth (Milner-Gulland et al., 2003) or range expansion (Miller and Inouye, 2013), other

examples suggest limited demographic consequences of sex ratio variation (Ewen et al., 2011; Gownaris et al., 2020; Mysterud et al., 2002). Ultimately, sensitivity of female reproductive success to sex ratio should depend strongly on the mating system, with female dominance at the “extremely polygamous” end of a continuum (Miller et al., 2011). The sensitivity of population viability to female reproductive success, in turn, is likely predicted by life history strategy: in long-lived, iteroparous species, population growth rates are often weakly sensitive to reproduction relative to growth and survival (Franco and Silvertown, 2004). We therefore hypothesize that range limits are more likely to be dominated by the female environmental niche in longer-lived species with more polygamous mating systems, while males are more likely to play an important role in shorter-lived, monogamous species that may be particularly sensitive to missed mating opportunities. As studies of sex ratio variation and sex-specific demography across species’ ranges accumulate in the literature (e.g., Dudaniec et al., 2021; Lynch et al., 2014; Petry et al., 2016), this hypothesis may be tractably pursued with comparative analyses.

While life history and mating system may determine the demographic consequences of skewed sex ratios, the sensitivity of sex ratio to environmental drivers is another critical ingredient of how environmental variation can affect the population dynamics of dioecious species. Our study adds to a growing body of work quantifying the demographic mechanisms giving rise to skewed operational sex ratios using two-sex models (Eberhart-Phillips et al., 2017; Shelton, 2010; Veran and Beissinger, 2009) and parsing the contributions of environmental drivers (Bialic-Murphy et al., 2020). However, as a field, we lack a strong predictive framework for how often and in which direction environmental drivers are likely to skew the operational sex ratio – and this gap is particularly important in the context of global change. We have focused on the limits of population

435 viability with respect to geographic environmental variation but analogous processes
436 will likely govern how populations respond to temporal environmental change (e.g., cli-
437 mate change), including direct effects on female demography and indirect effects via
438 perturbations to the mating pool (Fig. 1). There is a need to better understand and pre-
439 dict which species and types of species are susceptible to climate change-induced shifts
440 in OSR. Geographic variation in OSR may be an instructive proxy for how dioecious
441 species will respond to climate change (Petry et al., 2016). The link between OSR and
442 responses to climate adds value to studies of the causes and consequences of spatial vari-
443 ation in sex ratio, particularly at geographic scales that encompass “past” and “future”
444 conditions.

445 Previous studies of dioecious plants have shown that male bias is more common than
446 female bias and is particularly pronounced in harsh abiotic environments, likely reflect-
447 ing the greater resource requirements needed to pay the female cost of reproduction
448 (Bierzychudek and Eckhart, 1988; Field et al., 2013a,b). Our surveys of natural popula-
449 tions are consistent with the broader pattern of male-biased OSR at xeric range edges.
450 However, our common garden populations did not exhibit male bias in the xeric west
451 – averaged across years or in any single year (Fig. B2) – nor did we find any strong
452 demographic evidence for a western male advantage (in fact, there was a western female
453 advantage in growth and survival for some sizes). If male advantage / female disad-
454 vantage under harsh abiotic conditions is driven by the greater resource requirements of
455 females then it is possible that clonal propagation and/or legacies of greenhouse rearing
456 masked the ‘true’ sex difference at xeric-edge common garden sites, **or that reproductive**
457 **costs accumulate over longer time scales than considered here.** Instead, the stronger pat-
458 tern of sex ratio bias was the female reproductive advantage at the mesic, eastern range

⁴⁵⁹ edge. We hypothesize that the mesic edge is limited by competition and that the female
⁴⁶⁰ reproductive advantage reflects competitive superiority of females, which has been sug-
⁴⁶¹ gested in previous studies of Texas bluegrass (Compagnoni et al., 2017) and shown in
⁴⁶² other dioecious plants (Eppley, 2006), particularly under mesic conditions (Chen et al.,
⁴⁶³ 2014). Theory suggests that biotic interactions such as competition are likely to limit
⁴⁶⁴ species' ranges at the benign (e.g., mesic) end of abiotic gradients (Louthan et al., 2015)
⁴⁶⁵ though this has not been explored, to our knowledge, in the context of sex-structured
⁴⁶⁶ dynamics. Future studies in our system or others could test whether females and males
⁴⁶⁷ differ in their responses to biotic stressors at xeric and mesic range edges to reveal how
⁴⁶⁸ biotic factors shape range limits via sex-specific demography.

⁴⁶⁹ Beyond the novel elements of sex-structured demography and mate limitation, our
⁴⁷⁰ work informs and advances the broader literature on the processes generating species'
⁴⁷¹ range limits in at least three ways. First, the Texas bluegrass case study demonstrates
⁴⁷² that a process-based model capturing environment-dependent demography can accu-
⁴⁷³ rately predict geographic range limits: the predicted limits of $\lambda \geq 1$ corresponded well
⁴⁷⁴ to observed longitudinal limits from collection records, particularly given the uncer-
⁴⁷⁵ tainty characterized by our hierarchical Bayesian statistical approach. We parameterized
⁴⁷⁶ the model with respect to longitude, which tightly covaries with aridity in the southern
⁴⁷⁷ Great Plains. Extensions of this model that transition from implicit to explicit consid-
⁴⁷⁸ eration of aridity will allow us to forecast range responses of Texas bluegrass to future
⁴⁷⁹ climate change and ask whether climate change will reduce or amplify OSR bias and
⁴⁸⁰ mate limitation at longitudinal range edges. It would be interesting to additionally con-
⁴⁸¹sider this species' latitudinal limits, though our exploratory analyses revealed no clear
⁴⁸² sex differences or sex ratio variation with respect to latitude.

483 Second, our results also provide novel evidence for contrasting demographic re-
484 sponses to environmental drivers throughout a species' range – or “demographic com-
485 pensation” (Doak and Morris, 2010; Villellas et al., 2015). Elevated performance in some
486 life history processes can compensate for declines in other processes and thus buffer
487 range-edge populations against harsh environmental conditions. In Texas bluegrass,
488 most vital rates declined toward eastern and western range limits but survival showed
489 the opposite pattern. Increased survival at longitudinal extremes partially offset declines
490 in other vital rates but this positive response was weaker than the negative responses.
491 Ultimately, increased survival was not sufficient to prevent declines in population vi-
492 ability from the range center to eastern and western limits, which were dominated by
493 declining female growth and flowering. A recent study found a similar pattern, where
494 compensation between vital rates could not prevent a decrease of population growth rate
495 towards the southern range edge of *Erythranthe cardinalis* (Sheth and Angert, 2018).

496 Third, our results highlight some important considerations in how environment-
497 dependent demographic models are best parameterized to derive insights into the drivers
498 of range limits. Our approach relied heavily on common garden populations, which
499 allowed us to plant and track known-sex individuals in contrasting environmental con-
500 ditions that encompass and exceed the natural geographic distribution. The ability to
501 robustly sample edge and beyond-edge environments is a powerful advantage of the
502 common garden transplant approach (Hargreaves et al., 2013). However, this also lim-
503 ited the size variation that we were able to include and model, and the size distributions
504 of common garden populations skewed consistently smaller than natural populations.
505 In Appendix C, we show that our conclusions are likely robust to this feature of the
506 common gardens. However, our ability to quantify the consequences of size representa-

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

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

Understanding and predicting geographic distributions and their responses to environmental change demands careful consideration of which biological details must be accounted for and which others can be safely ignored. Our results show that complex,

530 non-linear dynamics involving females, males, and frequency-dependent reproduction
531 can be reasonably approximated as a simple, linear process (female-dominant popula-
532 tion growth). We suggest that this is good news. The next challenge is to figure out how
533 often and under what conditions ecologists can get away with it.

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547 Author contributions

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

550

Data accessibility

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

553

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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

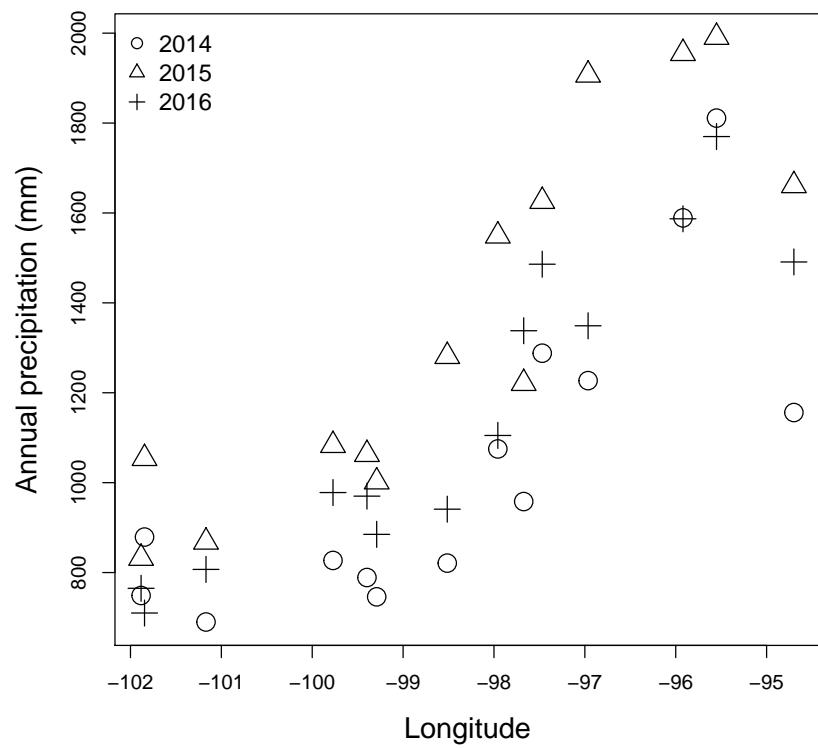


Figure A1: Total annual precipitation at common garden sites during the study years tracked long-term trends of increasing aridity from east to west.

Appendix B: Additional results

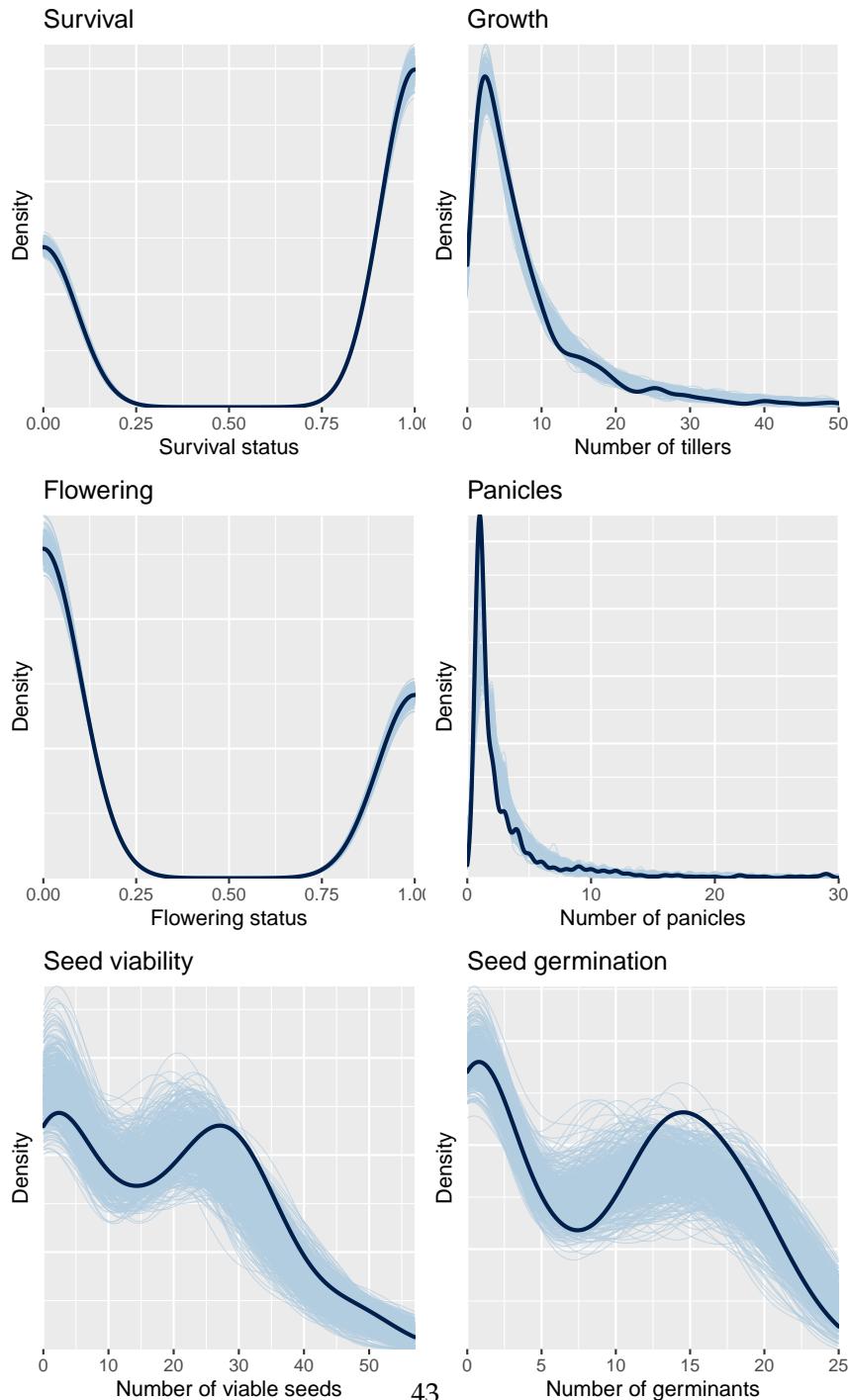


Figure B1: Posterior predictive checks of statistical models for demographic vital rates. Lines show density distributions of real data (thick, dark blue) compared to simulated data sets (thin, light blue) generated from the fitted models based on 500 draws of the posterior distribution of parameter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

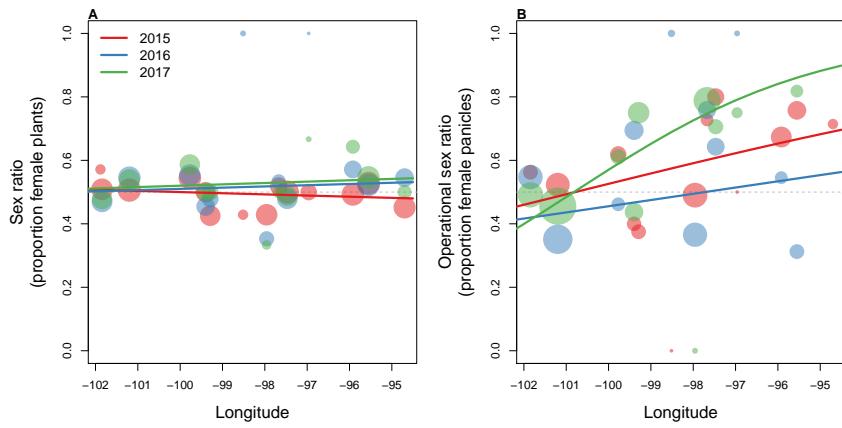


Figure B2: Year-specific sex ratios of plants (A) and panicles (B) in common garden populations spanning the longitudinal aridity gradient. Points sizes are proportional to sample sizes and lines show fitted binomial GLMs.

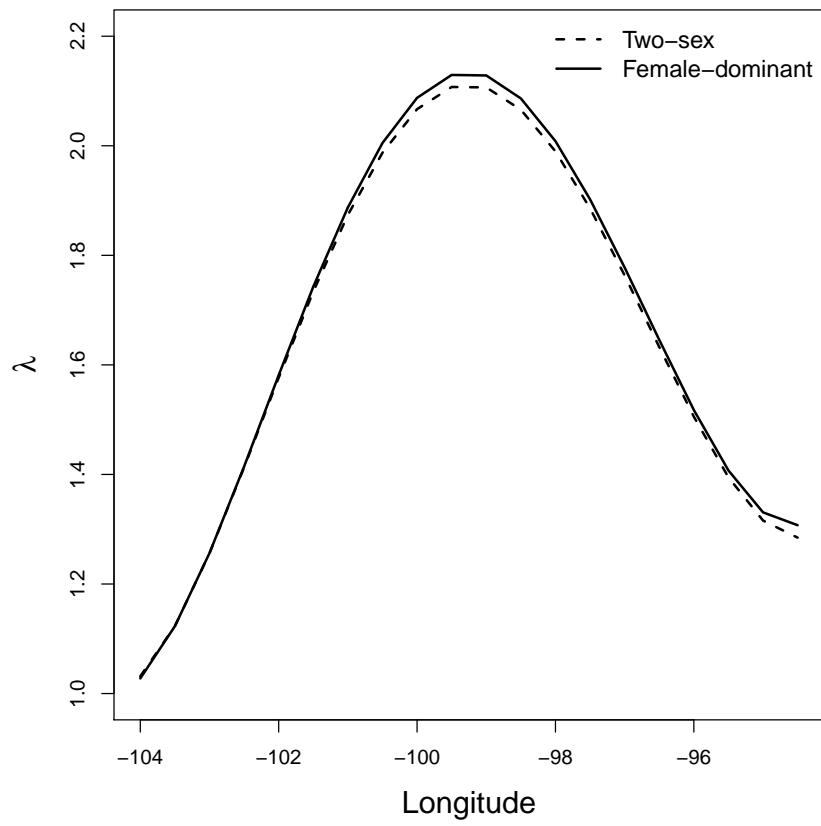


Figure B3: Comparison of longitudinal variation in λ between the two-sex demographic model (dashed line) that includes dependence of female seed production on population structure and the corresponding female-dominant model (solid line) with constant female fertility and all else equal. Models were evaluated at posterior mean parameter estimates

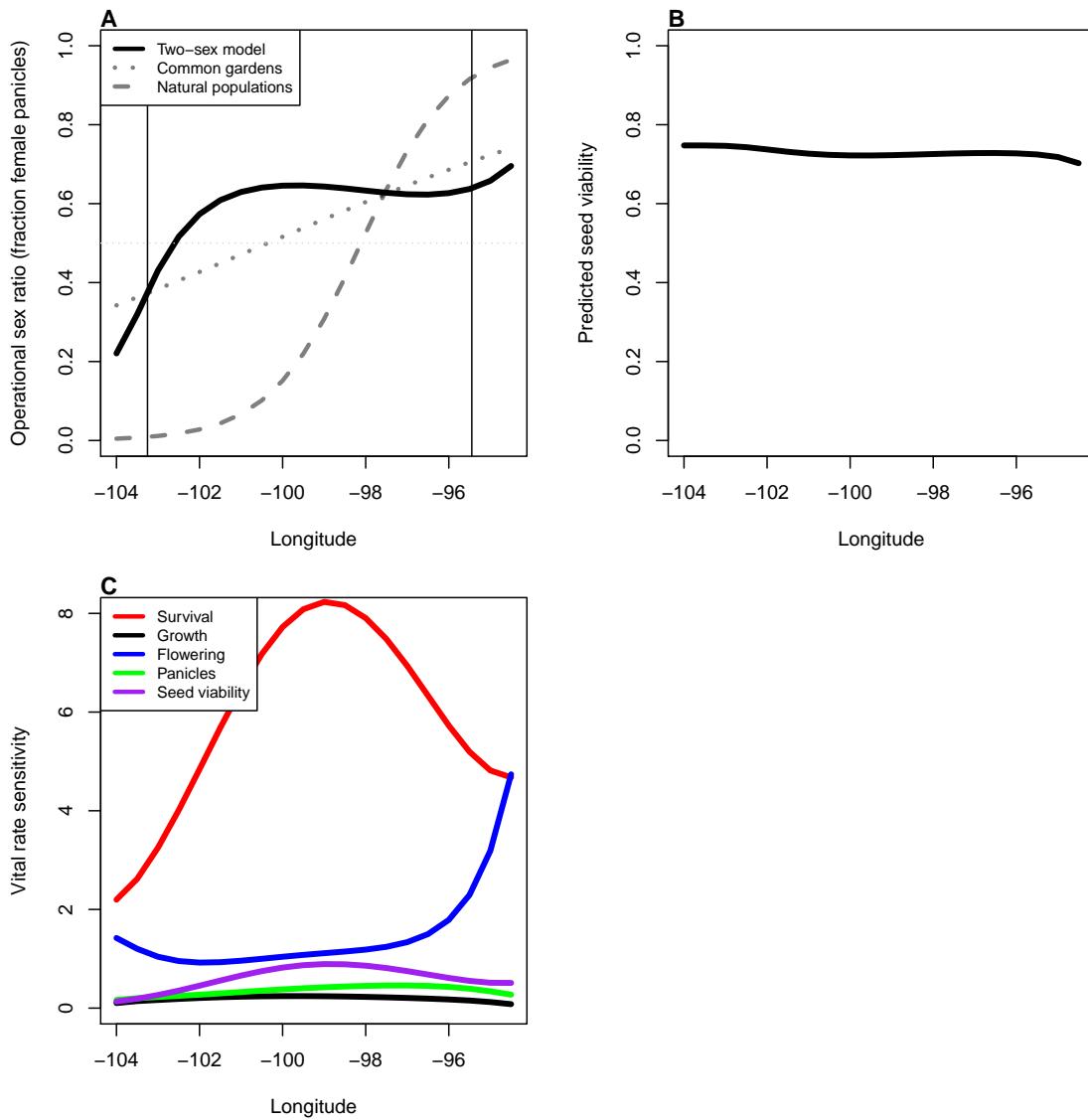


Figure B4: **A**, Longitudinal variation in operational sex ratio (fraction of panicles that are female) predicted by the two-sex MPM (solid line) compared to the sex ratio clines fitted to data from common gardens (dotted line) or natural populations (dashed line). Vertical lines show the longitudes 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.

727 **Appendix C: Size distribution comparisons and simulation
728 experiments**

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

732 *Observed and predicted size distributions*

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

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

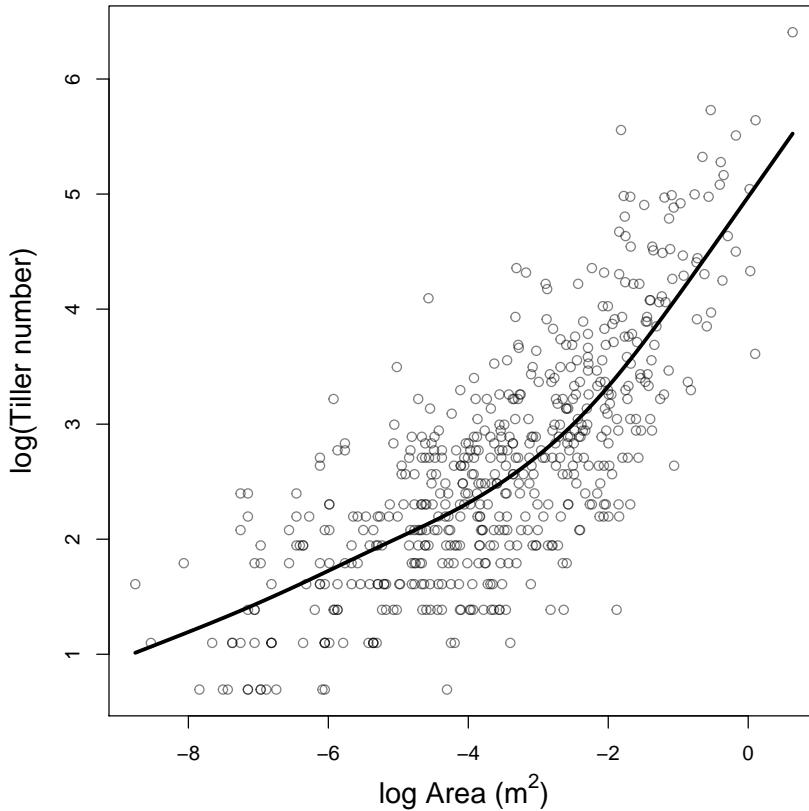


Figure C1: Relationship between area (m^2) and tiller count from plants in the common garden experiment. The fitted gam model (line) was used to convert area measurements from natural populations to tiller counts.

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

⁷⁴⁹ logarithm of tiller number, and then estimating the empirical distribution of this variable.

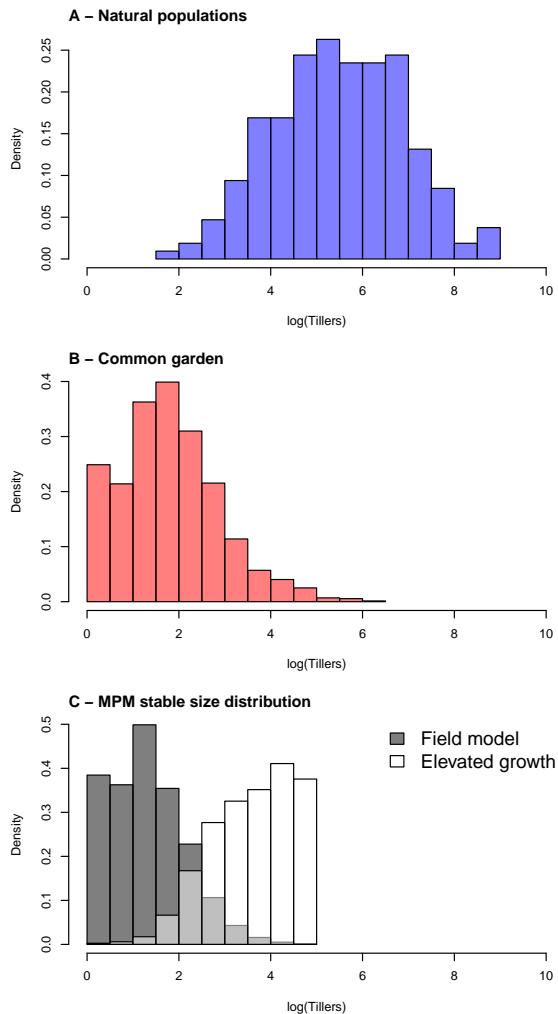


Figure C2: Size distribution of Texas bluegrass from natural populations (A), common garden populations (B), and predicted by the two-sex MPM (C). In C, the two size distributions come from the base model parameterized following methods described in the main manuscript (“field model”, in gray) and a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

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

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

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

762 The preceding results indicate that the common garden populations, and thus the two-
763 sex MPM built from common garden data, under-estimate the size distribution of Texas
764 bluegrass, relative to what we find in natural populations. Sex differences in demog-
765 raphy, and especially flowering, were most pronounced for the largest sizes (Fig. 4),
766 but these sizes were predicted to be very rare in a stable population (Fig. C2C). The
767 under-estimation of large sizes may explain why longitudinal clines in OSR predicted
768 by the MPM and seen in the common garden were weaker than the OSR cline observed
769 in natural populations (Fig. B4). It is therefore possible that our main finding – that
770 males contribute little-to-nothing toward range limitation – reflects a limitation of the
771 model, since real populations tended to be more female-biased (and potentially more
772 mate-limited) in the eastern range margins than the model predicted. To explore this
773 possibility, we conducted a numerical experiment that allowed modeled plants to reach
774 larger sizes by increasing the empirically-estimated intercept of the growth vital rate

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

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

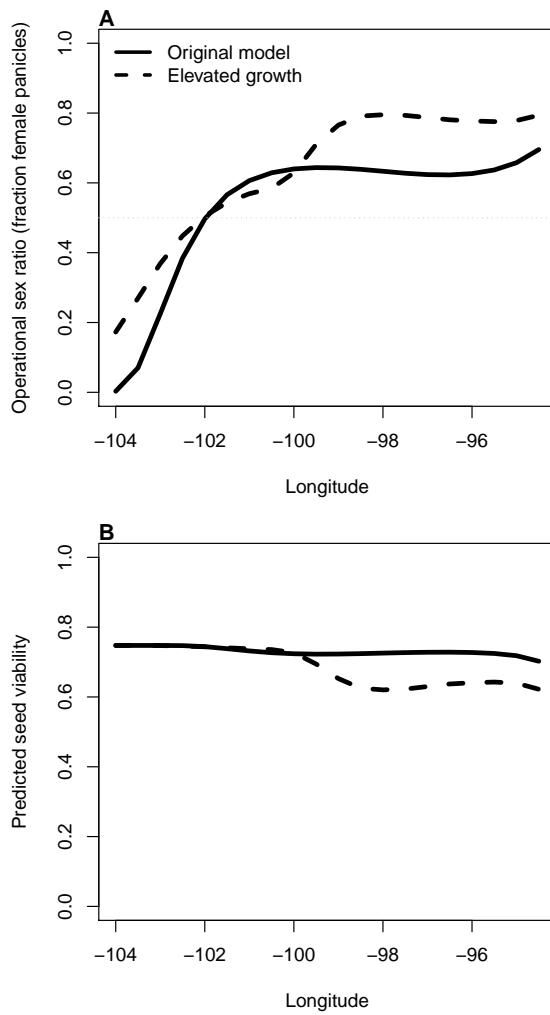


Figure C3: Two-sex model predictions for **A** operational sex ratio (fraction of panicles that are female) and **B** seed viability at stable population structure in relation to longitude. Solid line shows predictions of the base model using field-estimated parameter values and dashed line shows the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

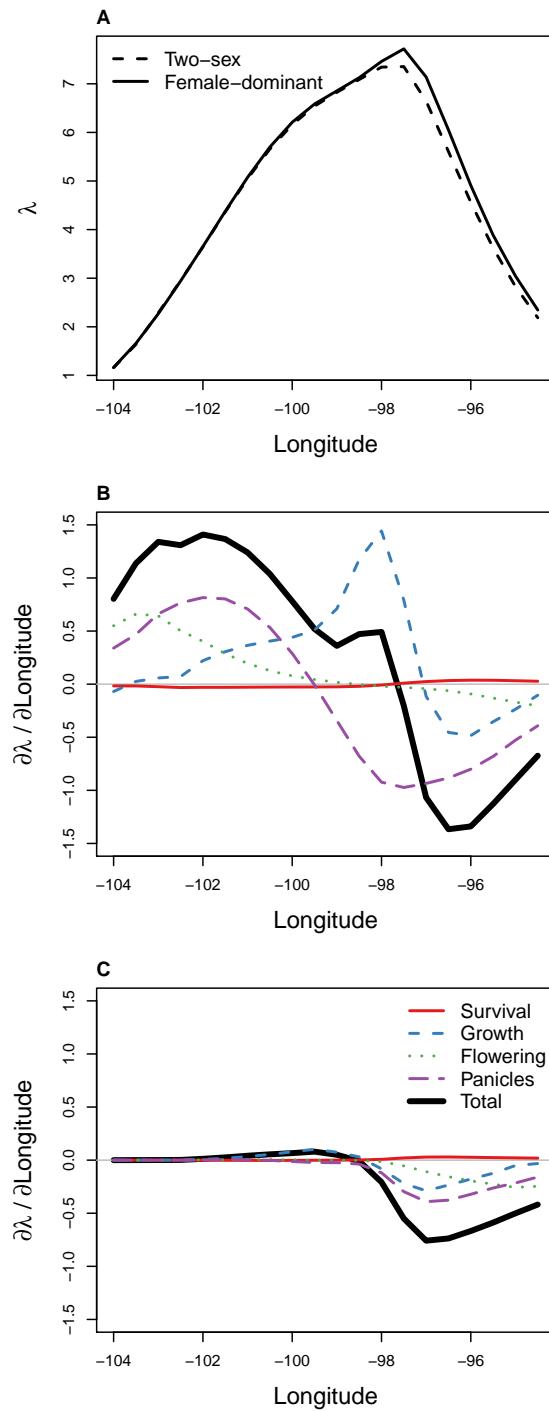


Figure C4: Results for the elevated growth model, in which the intercept of growth function was increased by a factor of 2.75. **A**, contrast of two-sex and female-dominant models, as in Fig. B3; **B,C**, Life Table Response Experiments decomposing the change in λ with respect to longitude into contributions 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