

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

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## Abstract

1 Understading the mechanisms that generate biogeographic patterns of distribution and  
2 abundance is a long-standing goal of ecology. It is widely hypothesized that distri-  
3 butional limits reflect the environmental niche, but this hypothesis is complicated by  
4 widespread potential for intra-specific niche heterogeneity. In dioecious species, for ex-  
5 ample, sexual niche differentiation may cause divergence between the sexes in their limits  
6 of environmental suitability. We studied the mechanisms of range boundary formation  
7 in Texas bluegrass (*Poa arachnifera*), a perennial dioecious plant, testing the alternative  
8 hypotheses that range limits reflect the niche limits of females only, as assumed by clas-  
9 sic ecological theory, versus the combined contributions of females and males, including  
10 their inter-dependence via male-limitation of female fertility. Common garden experi-  
11 ments across the longitudinal aridity gradient of the southern Great Plains, US revealed  
12 female-biased flowering and panicle production approaching eastern range limits, con-  
13 sistent with surveys of operational sex ratio variation in natural populations. A process-  
14 based demographic model predicted longitudinal limits of population viability ( $\lambda \geq 1$ )  
15 that matched the observed eastern and western range limits, and further showed that  
16 declines in  $\lambda$  approaching range limits were driven almost entirely by declines in fe-  
17 male vital rates. Thus, despite the potential for mate limitation, particularly at eastern  
18 margins, the geographic distribution was effectively female-dominant, reflecting the en-  
19 vironmental niche of females with little contribution from males. The dominant role  
20 of females was attributable to female fertility being quite robust to sex ratio variation  
21 (which declined only at extreme under-representation of males) and to relatively low  
22 sensitivity of  $\lambda$  to reproductive transitions in the life cycle. This suggests that female-

<sup>23</sup> dominant limitation of geographic distribution may be common to long-lived species  
<sup>24</sup> with polygamous mating systems, and that female responses to environmental drivers  
<sup>25</sup> may often be sufficient for predicting range shifts in response to environmental change.

<sup>26</sup>

## Keywords

<sup>27</sup> demography; dioecy; intra-specific niche heterogeneity; matrix projection model; sex  
<sup>28</sup> ratio; range limits

## Introduction

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

43 The widespread idea that range limits reflect niche limits intersects awkwardly with  
44 another pervasive concept in ecology: intra-specific niche heterogeneity. This refers to  
45 the fact that individuals within a population or species may differ in their interactions  
46 with the biotic and/or abiotic environment (Araújo et al., 2011; Bolnick et al., 2002; Holt,  
47 2009). Intra-specific niche differences may correspond to demographic state variables  
48 such as life stage, size class or other, unmeasured aspects of individual identity. If range  
49 limits are a geographic manifestation of niche limits, but a single population or species  
50 may be comprised of many niches, then whose niche is it that determines the geographic  
51 distribution and how would we know?

52 Sexual niche differentiation is a common form of intra-specific niche heterogeneity  
53 (Bolnick et al., 2002) and has been widely documented in animals (the vast majority  
54 of which are dioecious) and plants (ca. 6% of angiosperms are dioecious: Renner and  
55 Ricklefs 1995). The prevalence of sexual niche differentiation was recognized by Darwin  
56 (1871), who described “different habits of life, not related...to the reproductive functions”  
57 of females and males. There are now many examples of sex differences in trophic posi-  
58 tion (Law and Mehta, 2018; Pekár et al., 2011), habitat use (Bowyer, 2004; De Lisle et al.,  
59 Phillips et al., 2004), and responses to climate (Gianuca et al., 2019; Petry et al.,  
60 2016; Rozas et al., 2009), differences that may or may not be accompanied by sexual  
61 dimorphism. It has been hypothesized that sex-specific niches may evolve by natural se-  
62 lection when it reduces competitive or other antagonistic interactions between the sexes  
63 (Bolnick and Doebeli, 2003; De Lisle and Rowe, 2015), as a byproduct of naturally or  
64 sexually selected size dimorphism (Shine, 1989; Temeles et al., 2010), or when females  
65 and males pay different costs of reproduction (Bierzychudek and Eckhart, 1988).

66 Sexual niche differentiation can translate to sex-specific advantages in different envi-  
67 ronments, causing skew in the operational sex ratio (OSR: relative abundance of females  
68 and males available for mating) even if the primary (birth) sex ratio is unbiased (Eberhart-  
69 Phillips et al., 2017; Shelton, 2010a; Veran and Beissinger, 2009). Indeed, environmental  
70 clines in OSR have been widely documented in plants and animals at fine spatial scales  
71 (Bertiller et al., 2002; Bisang et al., 2020; Eppley, 2001; Groen et al., 2010; Hultine et al.,  
72 2018) as well as broader climatic clines across alititudtes or latitudes (Caruso and Case,  
73 2007; Dudaniec et al., 2021; Ketterson and Nolan Jr, 1976; Petry et al., 2016). At range  
74 margins, where environments are extreme relative to the range core, demographic dif-  
75 ferences between the sexes, and hence skew in the OSR, may be greatest. In dioecious

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

78 Returning to the question of whose niche determines range limits given the potential  
79 for sexual niche differentiation, classic ecological theory assumes the answer. "Female  
80 dominance" is a pervasive, often implicit feature of population-dynamic models whereby  
81 male availability is assumed to have no influence on female fertility (Caswell and Weeks,  
82 1986; Miller and Inouye, 2011; Rankin and Kokko, 2007). This assumption is wrong,  
83 of course, but it may be *adequate* when the sex ratio is balanced or does not vary. The  
84 female-dominant perspective predicts that female responses to environmental variation  
85 should govern range limits (Fig. 1). However, females may be male-limited in environ-  
86 ments in which they are favored, which could reduce population viability in marginal  
87 environments. This creates an additional, "two-sex" pathway by which environmental  
88 drivers may set distributional limits, via perturbations to the mating pool that arise from  
89 sex-specific responses to the environment (Fig. 1). While sexual niche divergence sets  
90 the stage for two-sex dynamics to play an important role in marginal environments, this  
91 influence may be dampened in mating systems where single males can fertilize many fe-  
92 males (Miller et al., 2011) or in life histories where population viability is weakly sensitive  
93 to female fertility (Franco and Silvertown, 2004).

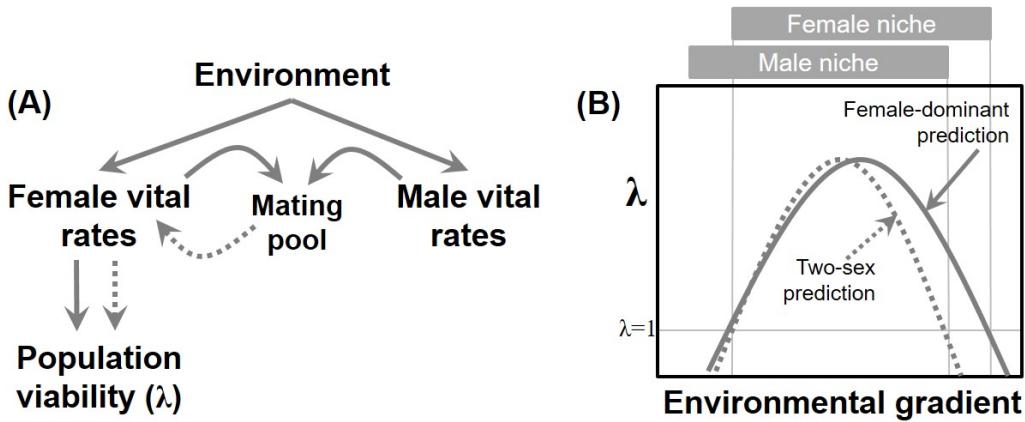


Figure 1: Hypotheses for how environmental variation can affect population viability and range limits in dieocious species. Under the female-dominant hypothesis, environmental drivers affect population growth ( $\lambda$ ) through effects on females, alone (A). In geographic / environmental space, this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

94 Here we ask whether female demographic responses to environmental variation,  
 95 alone, are sufficient to understand the ecological origins of range limits, or whether  
 96 males and female-male interactions must additionally be considered. As an experimen-  
 97 tal model, we worked with a dieocious plant species (the grass *Poa arachnifera*) narrowly  
 98 distributed across the sharp longitudinal aridity gradient of the southern Great Plains,  
 99 US (Fig. 2). The environmental isoline governing aridity in this region is expected to  
 100 shift eastward under climate change (Karl et al., 2009), so understanding how it sets dis-  
 101 tributional limits may aid in forecasting future range shifts. We hypothesized that sexual  
 102 niche differentiation with respect to longitudinal variation in aridity may lead to skewed

103 sex ratios approaching range limits, and that mate limitation at environmental extremes  
104 could cause range boundaries to deviate from female-dominant expectations.

105 This study was conducted in four parts. First, we conducted surveys to ask whether  
106 natural populations of Texas bluegrass exhibit longitudinal clines in operational sex ra-  
107 tio across the aridity gradient. Second, we conducted a common garden experiment at  
108 14 sites throughout the southern Great Plains to quantify sex-specific demography in  
109 variable abiotic environments. Third, we conducted a local sex ratio manipulation ex-  
110 periment to quantify how viable seed production by females responds to variation in  
111 OSR. Finally, we connected sex-specific demography with inter-sexual mating dynam-  
112 ics in a two-sex modeling framework to derive demographically-driven predictions for  
113 geographic limits of population viability ( $\lambda \geq 1$ ). We analyzed the demographic model  
114 to decompose the decline in  $\lambda$  approaching range limits into contributions from female-  
115 dominant and two-sex pathways (Fig. 1).

116 **Materials and methods**

117 *Study system and natural population surveys*

118 *Poa arachnifera* is a perennial, cool-season (C3) grass endemic to the southern Great Plains.  
119 This species occurs almost exclusively in central Texas, Oklahoma, and southern Kansas  
120 (Fig. 2) though there are occasional records of adventive populations in other states<sup>1</sup>.  
121 Like all grasses, *P. arachnifera* is wind-pollinated. Individuals can be sexed only when  
122 flowering, in early spring, based on the presence of stigmas (females) or anthers (males)  
123 in the inflorescence. Following inflorescence and seed production, plants go dormant

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

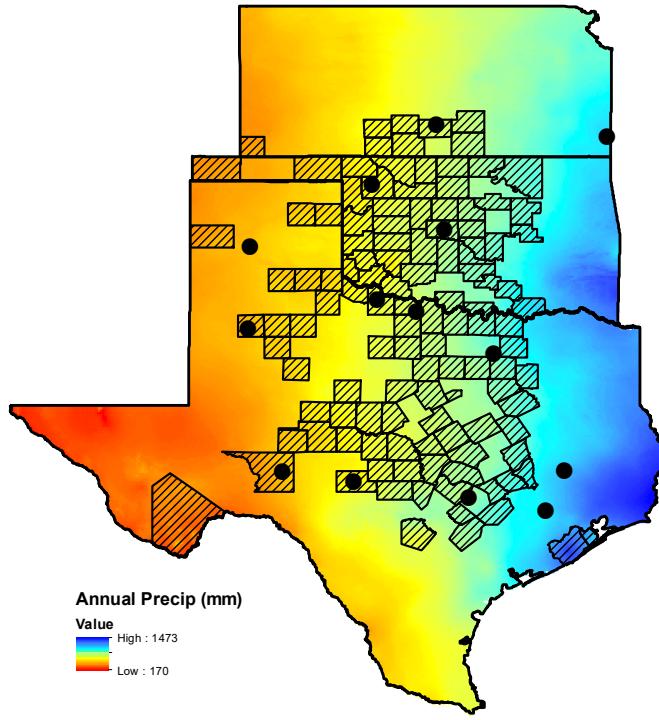


Figure 2: Geographic and environmental distribution of *P. arachnifera* in Texas, Oklahoma, and Kansas. Hatched shapes show counties with herbarium records of occurrence. Color shows geographic variation in annual precipitation (mm) based on 30-year normals from WorldClim (Fick and Hijmans, 2017). Points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

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

<sup>131</sup> exhibited geographic clines in OSR corresponding to the longitudinal aridity gradient.  
<sup>132</sup> We visited 14 populations in spring 2012 and 8 in spring 2013 (Table A1). At each location,  
<sup>133</sup> we searched for *P. arachnifera* along roads, trails, or creek drainages and recorded  
<sup>134</sup> the number of female and male patches that we encountered and the number of inflores-  
<sup>135</sup> cences in each patch. To quantify the mating environment, we focus our analyses on the  
<sup>136</sup> sex ratio of inflorescences rather than patches, since a single patch makes different con-  
<sup>137</sup> tributions to the mating pool depending on whether it has few or many inflorescences.

<sup>138</sup> *Statistical analysis of natural population surveys*

<sup>139</sup> We fit a binomial generalized linear model (glm), where females were “successes” and  
<sup>140</sup> total inflorescences was the number of “trials”, to test whether the OSR varied systemati-  
<sup>141</sup> cally with respect to longitude. Here and in the experiments that follow we use longitude  
<sup>142</sup> as a proxy variable that captures all east-west environmental variation, notably precipi-  
<sup>143</sup> tation (Fig. 2) but also factors that co-vary with precipitation such as productivity. This  
<sup>144</sup> statistical model and all those that follow were fit in a Bayesian statistical framework  
<sup>145</sup> using Stan (Carpenter et al., 2017) and rstan (Team et al., 2018) with vague priors on  
<sup>146</sup> all parameters. In all cases, model fit was assessed with posterior predictive checks  
<sup>147</sup> (Gelman et al., 1996). All code for statistical and demographic modeling is available at  
<sup>148</sup> <https://github.com/texmiller/POAR-range-limits>.

149

## Common garden experiment

### 150 Source material and experimental design

151 We established a common garden experiment at 14 sites throughout and beyond the geo-  
152 graphic distribution of *P. arachnifera* (Fig. 2). Experimental sites spanned latitudinal and  
153 longitudinal variation, though we focus here on longitude. During the three years of this  
154 experiment (2014–2017), total precipitation at each site closely tracked longitude (Fig.  
155 A1), as expected based on longer-term climate trends (Fig. 2). Source material for the  
156 experiment came from 8 sites, which were a subset of the sites that were visited for the  
157 natural population survey (Table A1). At these sites, we collected vegetative tillers from  
158 flowering individuals of each sex (mean: 11.6 individuals per site, range: 2–18). These  
159 were brought back to the Rice University greenhouse, where they were clonally propa-  
160 gated in ProMix potting soil and supplemented with Osmocote slow-release fertilizer at  
161 78–80°F under natural humidity and light.

162 Common gardens were set up in Fall (October–December) 2014. At each site, we  
163 established 14 experimental blocks, which typically corresponded to a tree or woodland  
164 edge, providing partial shade that mimics this species' natural micro-environment. We  
165 planted 3 females and 3 males in each block, for a total of 42 individuals per sex per  
166 site and 1176 total plants across sites, with all source collections represented at all sites.  
167 Individuals were spaced within blocks to allow space for rhizomatous growth that could  
168 be clearly attributed to individual transplants. To promote establishment, we cleared  
169 vegetation immediately surrounding transplants and provided ca. 1 L of water at the  
170 time of transplanting but provided no subsequent watering, fertilization, or competitor  
171 removal.

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

176 *Statistical analysis of common garden experiment*

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

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

194

## *Sex ratio experiment*

195 At one site near the center of the range (Lake Lewisville Environmental Learning Area,  
196 Texas), we established a separate experiment to quantify how sex ratio variation affects  
197 female reproductive success. Details of this experiment, which was conducted in 2014–  
198 2015, are described in Compagnoni et al. 2017. Briefly, we established 124 experimental  
199 populations in  $0.4m \times 0.4m$  plots that varied in population density (1–48 plants/plot) and  
200 sex ratio (0–100%female), with 2–4 replicates for each of 34 density-sex ratio combina-  
201 tions. The experiment was established ca. 1 km from a natural population at this site and  
202 plots were situated with a minimum of 15 m spacing, a buffer that was intended to limit  
203 pollen movement between plots (pilot data indicated that  $\geq 90\%$  of wind pollination oc-  
204 curred within 13m). We measured female reproductive success in different density and  
205 sex ratio environments by collecting panicles from a subset of females in each plot at the  
206 end of the reproductive season. In the lab, we counted the total number of seeds on each  
207 panicle and assessed seed viability in the greenhouse with germination trials of 25 seeds  
208 per panicle. We also conducted tetrazolium-based seed viability assays (17–57 seeds per  
209 panicle, mode: 30).

210 *Statistical analysis of sex ratio experiment*

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

216 binomial distribution where the probability of viability ( $v$ ) was given by:

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

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

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

230 *Demographic model of range limits*

231 The statistical models for the common garden and sex ratio experiments provided the  
232 backbone of the full demographic model, a matrix projection model (MPM) structured  
233 by size (tiller number) and sex. Following the statistical modeling, the MPM accommo-  
234 dates longitude as a predictor variable, allowing us to identify the longitudinal limits of

<sup>235</sup> population viability ( $\lambda \geq 1$ ) and investigate the underlying drivers of population decline  
<sup>236</sup> at range limits.

<sup>237</sup> For a given longitude, let  $F_{x,t}$  and  $M_{x,t}$  be the number of female and male plants of  
<sup>238</sup> size  $x$  in year  $t$ , where  $x \in \{1, 2, \dots, U\}$  and  $U$  is the maximum number of tillers a plant can  
<sup>239</sup> attain (set to the 99th percentile of observed maximum size). We also include additional  
<sup>240</sup> state variables for new recruits,  $F_t^R$  and  $M_t^R$ , which we assume do not reproduce in their  
<sup>241</sup> first year. For ease of presentation, we do not symbolically show longitude effects in the  
<sup>242</sup> vital rate functions for growth, survival, flowering, and panicle production but these all  
<sup>243</sup> included longitude effects on the intercept and slope (with respect to size) as a second-  
<sup>244</sup> order polynomial, following the statistical models. We assume that the parameters of sex  
<sup>245</sup> ratio-dependent mating (Eq. 1) do not vary with longitude.

<sup>246</sup> For a pre-breeding census, the expected numbers of recruits in year  $t + 1$  is given by:

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

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

<sup>247</sup> where  $p^F$  and  $c^F$  are flowering probability and panicle production for females of size  $x$ ,  $d$   
<sup>248</sup> is the number of seeds (fertilized or unfertilized) per female panicle,  $v$  is the probability  
<sup>249</sup> that a seed is fertilized,  $m$  is the probability that a fertilized seed germinates, and  $\rho$  is  
<sup>250</sup> the primary sex ratio (proportion of recruits that are female). Seed fertilization depends  
<sup>251</sup> on the OSR of panicles (following Eq. 1) which was derived from the  $U \times 1$  vectors of  
<sup>252</sup> population structure  $\mathbf{F}_t$  and  $\mathbf{M}_t$ :

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

253 Finally, the dynamics of the size-structured component of the population are given  
 254 by:

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

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

255 For both females and males, the first term represents seedlings that survived their first  
 256 year and enter the size distribution of established plants. Because our common garden  
 257 experiment relied on greenhouse-raised transplants, we had little information on these  
 258 early life cycle transitions. We used the seedling survival probability ( $\sigma$ ) from our de-  
 259 mographic studies of the perennial congener *Poa autumnalis* in east Texas (T.E.X. Miller  
 260 and J.A. Rudgers, *unpublished data*) as a stand-in for *P. arachnifera*, and we assume this  
 261 probability was constant across sexes and longitudes ( $\sigma = 0.09$ ). We also assume that  
 262 surviving seedlings reach size  $y$  with probability  $g(y, x = 1)$ , the expected future size of  
 263 1-tiller plants from the transplant experiment. The second term represents survival and  
 264 size transition of established plants from the previous year, where  $s$  and  $g$  give the proba-  
 265 bilities of surviving at size  $x$  and growing from sizes  $x$  to  $y$ , respectively, and superscripts  
 266 indicate that these functions may be unique to females ( $F$ ) and males ( $M$ ).

267 Because the two-sex MPM is nonlinear (vital rates affect and are affected by popu-

lation structure) we estimated the asymptotic geometric growth rate ( $\lambda$ ) by numerical simulation, and repeated this across a range of longitudes. We used a regression-style Life Table Response Experiment (Caswell, 2001) to decompose the change in  $\lambda$  towards range limits into contributions from female and male vital rates (the female-dominant hypothesis predicts that declines in  $\lambda$  at range limits are driven solely by females). The LTRE approximates the change in  $\lambda$  with longitude as the product of the sensitivity of  $\lambda$  to the parameters times the sensitivity of the parameters to longitude, summed over all parameters:

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

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

## Results

### *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-

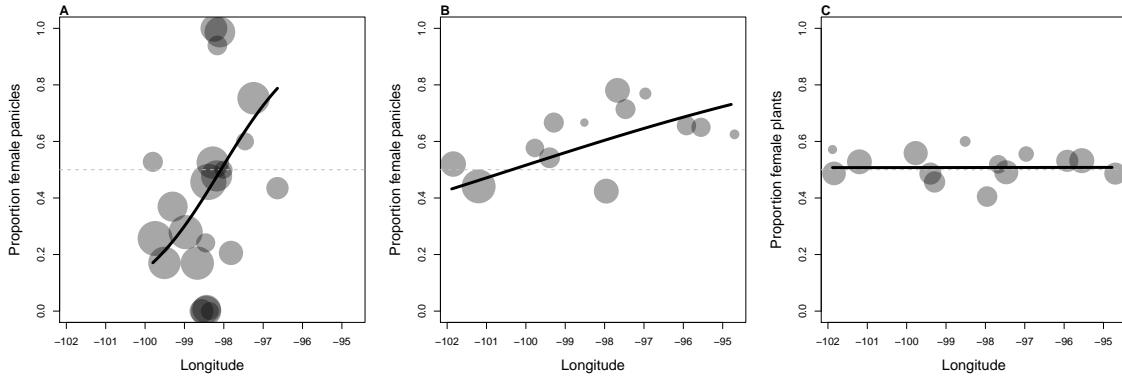


Figure 3: Sex ratio variation of *P. arachnifera* across its longitudinal distribution. **A**, Operational sex ratio (fraction of panicles that were female) in 22 natural populations; **B**, Operational sex ratio and **C**, sex ratio (fraction of plants that were female) in 14 common gardens. Within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

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.

### *Geographic variation in sex-specific demography*

In year one, there was near-total mortality of transplants at three sites in the common garden experiment due to various catastrophes (a flood, a drought, a pack of voles); otherwise, there was high (95%) establishment. There was strong longitudinal variation in demography, including sex-specific demographic responses that varied across vital rates and interactions between size, sex, and longitude. Where sex-specific demographic responses occurred, they were almost always in favor of females. In Fig. 4, we show binned means of raw data and fitted vital rate models for four vital rates (rows) and

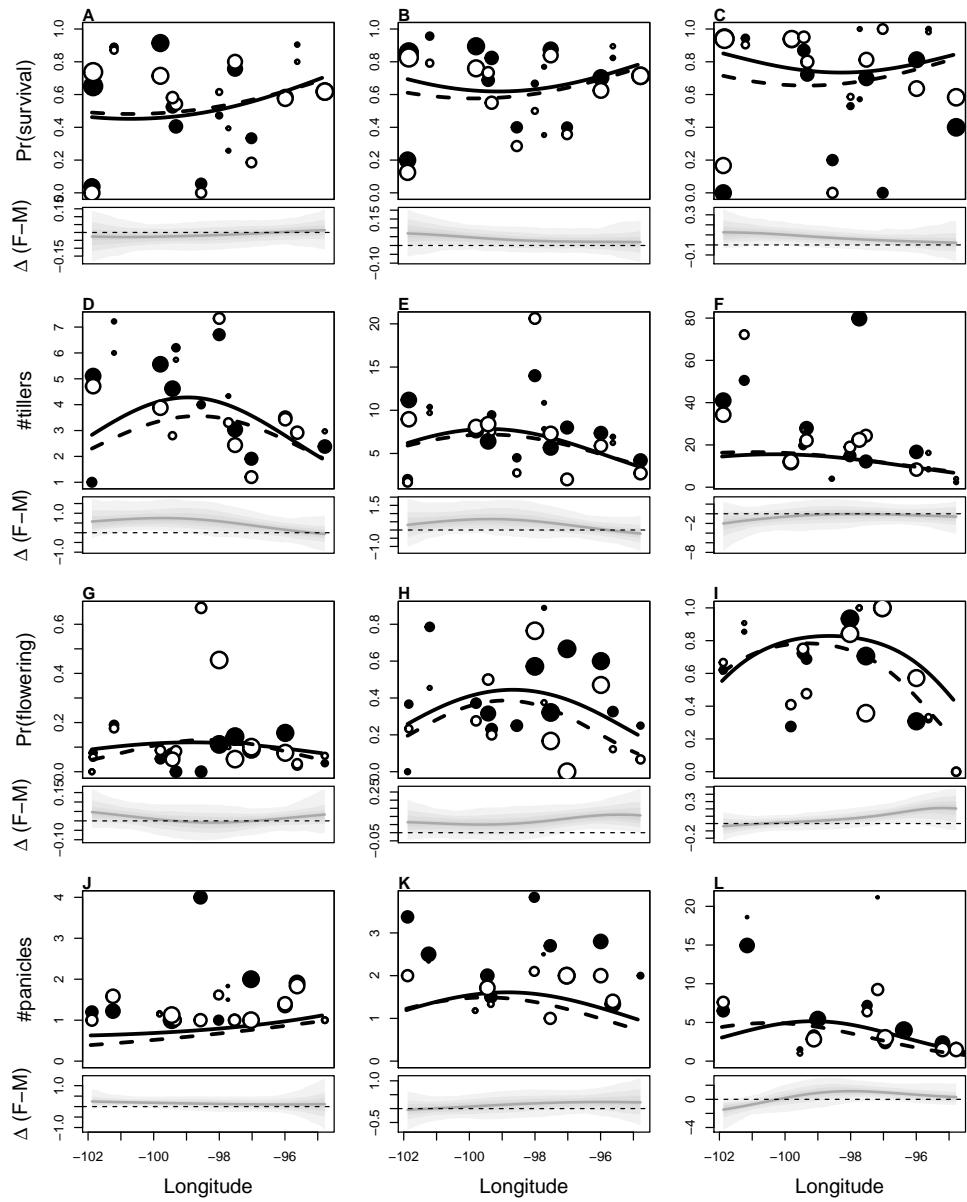


Figure 4: Sex-, size-, and longitude-related variation in: A–C, inter-annual probability of survival; D–F, inter-annual growth (change in number of tillers); G–I, probability of flowering; J–L, number of panicles produced given flowering. Points show means by site for females (filled) and males (open)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

<sup>297</sup> three size classes (columns); size was discretized for visualization only. This figure also  
<sup>298</sup> shows the posterior distributions for the difference between the sexes across longitudes.

<sup>299</sup> Annual survival probability was predicted to peak at western and eastern range  
<sup>300</sup> edges and was lowest at intermediate longitudes (Fig. 4A-C). There was a modest fe-  
<sup>301</sup> male survival advantage but only at the western range edge for large sizes. Other vital  
<sup>302</sup> rates showed the opposite (and more expected) longitudinal pattern for most sizes, with  
<sup>303</sup> peaks in the center of the range and declines at eastern and western edges. There was a  
<sup>304</sup> female growth advantage for small sizes at western longitudes (Fig. 4D-F). The strongest  
<sup>305</sup> sex difference was in the probability of flowering: females had a flowering advantage,  
<sup>306</sup> especially for large sizes and at eastern longitudes (Fig. 4G-I). Finally, panicle production  
<sup>307</sup> by flowering plants was similar between the sexes for most sizes, though for the largest  
<sup>308</sup> sizes there were advantages for males in the west and females in the east (Fig. 4J-L).

<sup>309</sup> Sex differences in flowering and panicle production generated a longitudinal trend  
<sup>310</sup> in the operational sex ratio of our common garden populations consistent with (but  
<sup>311</sup> quantitatively weaker than) the trend in natural populations: the fraction of total panicles  
<sup>312</sup> that were female in our common gardens increased from west to east (Fig. 3B) even as  
<sup>313</sup> the fraction of surviving plants that were female did not show a longitudinal trend (Fig.  
<sup>314</sup> 3C). Thus, in recapitulating the natural OSR pattern, the common garden experiment  
<sup>315</sup> revealed that the longitudinal trend in the mating pool of natural populations was due  
<sup>316</sup> to the reproductive niche of females extending farther east than that of males, and not to  
<sup>317</sup> sex differences in mortality.

318

### *Sex-ratio dependent seed fertilization*

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

329

### *Two-sex model of range limits*

330 The process-based demographic model connected sex-specific vital rate responses to  
331 longitudinal variation (Fig. 4) with sex ratio-dependent mating (Fig. 5) to predict the  
332 contributions of females and males to range limitation. The model predicted maxi-  
333 mum fitness in the center of the range and loss of population viability at longitudes  
334 that corresponded well with observed range limits. Specifically, the western-most and  
335 eastern-most county records of *P. arachnifera* fell within the uncertainty distribution of  
336 the model's predictions (represented by the shading in Fig. 6A), bolstering our confi-  
337 dence that the model effectively captured the demographic drivers of range limitation in  
338 this species. Also, the asymptotic population structure predicted by the model showed  
339 female bias in the operational (panicle) sex ratio toward the eastern range margins, con-

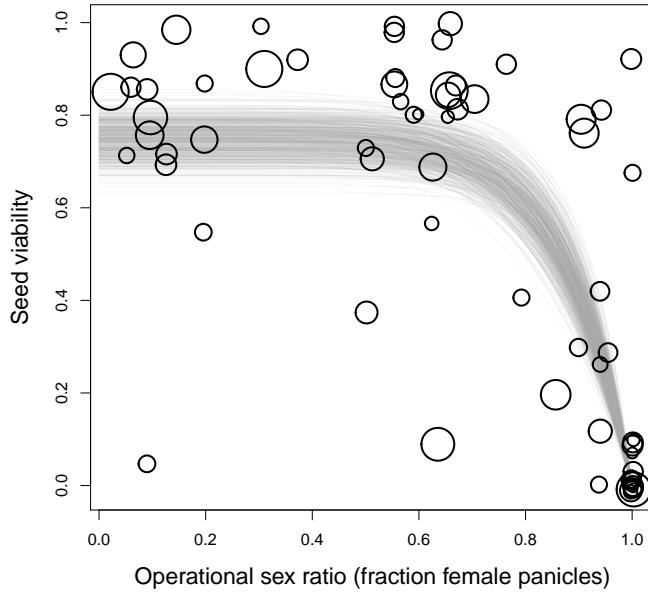


Figure 5: Seed fertilization success in relation to operational sex ratio (fraction of panicles that are female) in experimental populations. Circles show data from tetrazolium assays of seed viability; circle size is proportional to the number of seeds tested (min: 14, max: 57). Lines show model predictions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

340 sistent with observations from the common garden and natural populations (Fig. B4A).  
 341 Female bias in the OSR was predicted to cause declines in seed viability toward eastern  
 342 range margins (Fig. B4B). However, this effect was weak in magnitude because predicted  
 343 OSR bias was not extreme enough to cause strong declines in viability, given the re-  
 344 lationship derived from the sex ratio manipulation experiment (Fig. 5). Furthermore,  
 345 population viability at the eastern range margin was weakly sensitive to seed viability  
 346 relative to other vital rates (B4C). These observations underscore the next set of results.  
 347 LTRE decomposition revealed that declines in  $\lambda$  approaching range limits were driven

348 almost exclusively by females (Fig. 6B) with near-zero contributions from males (Fig.  
349 6C). Thus, range limitation was an effectively female-dominant process, despite system-  
350 atic geographic variation in sex ratio. Correspondingly, predictions of the two-sex model  
351 were nearly indistinguishable from a corresponding female-dominant model with all else  
352 equal, with only very modest differences in predictions of the two models emerging in  
353 the eastern part of the range (Fig. B3).

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

361 Skew in the OSR predicted by the demographic model was less extreme than was  
362 observed in natural and experimental populations (B4A). This occurred because sex dif-  
363 ferences in demography, especially flowering, were most pronounced at the largest sizes,  
364 and the MPM predicted that these sizes were very rare at stable population structure.  
365 The stable size distribution predicted by the MPM corresponded well to the common  
366 garden data (from which the MPM was built) but was much smaller, on average, than  
367 the size distribution we observed in natural populations (Fig. C2), presumably because  
368 transplants did not grow like “real” plants and/or did not have time in our three-year  
369 experiment to reach those sizes. In Appendix C, we explore whether higher growth  
370 rates, leading to a more realistic size distribution, would lead to a more important role  
371 for males. In numerical experiments with growth parameters, we found that larger size

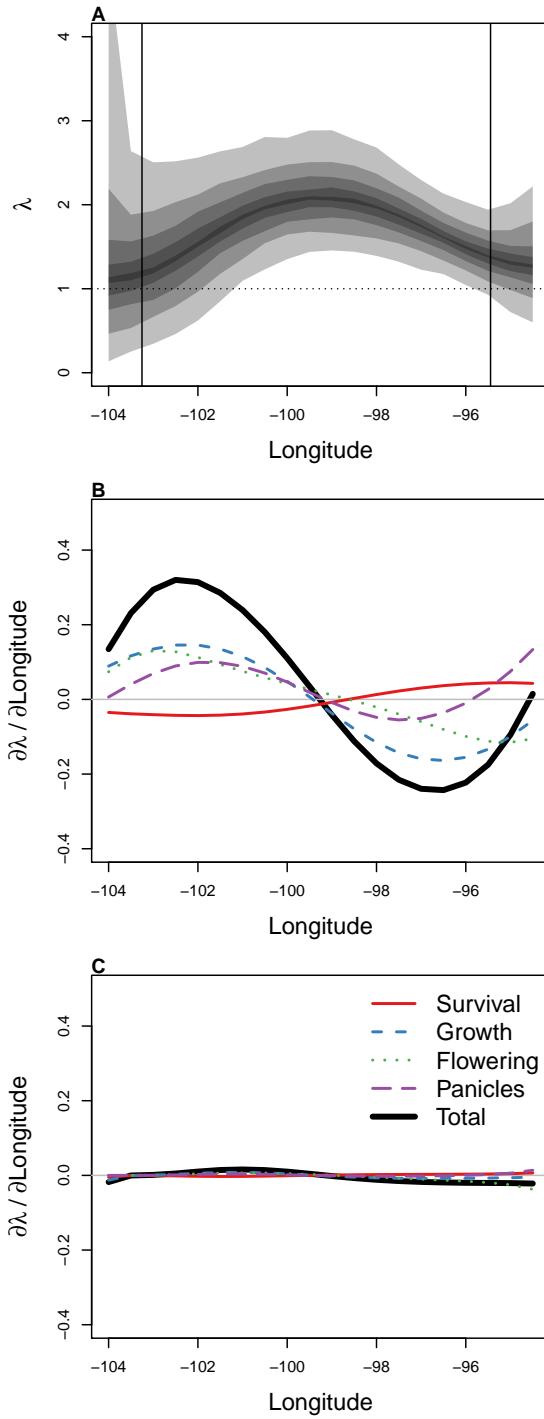


Figure 6: Population growth ( $\lambda$ ) as a function of longitude, predicted by the two-sex MPM that incorporates sex-specific demographic responses to longitude with sex ratio-dependent seed fertilization. A, posterior distribution of  $\lambda$ , where shaded regions show the 25, 50, 75, and 95% 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  $\lambda$  to longitude into additive vital rate contributions of females (B) and males (C) based on posterior mean parameter estimates.

372 distributions led to stronger female bias and thus stronger reductions in seed viability  
373 at eastern range margins (Fig. C3). While these changes increased the contributions of  
374 males to range limitation, female contributions were still more than twice as important as  
375 males, and there was very little difference between predictions of the two-sex and female-  
376 dominant models even under this elevated growth scenario (Fig. C4). This leads us to  
377 conclude that, while our common garden-parameterized model may quantitatively un-  
378 derestimate OSR bias and its demographic consequences relative to natural populations,  
379 our qualitative conclusion that range boundary formation is effectively female-dominant  
380 in this system is robust to any biases imposed by the growth trajectories and size distri-  
381 butions of common garden populations.

## 382 Discussion

383 Understanding the causes of decline in population viability at range edges is a classic  
384 ecological problem and the foundation for predicting how species' ranges will respond  
385 to global change drivers. Sexual niche differentiation has the potential to generate skew  
386 in the mating pool across environmental gradients and may therefore contribute to re-  
387 productive failure at range edges of dioecious species. In Texas bluegrass, we found  
388 evidence for sexual niche differentiation that manifested over a large-scale geographic  
389 gradient: the female reproductive niche (environment-dependent flowering and panicle  
390 production) extended farther east than that of males, generating female-biased opera-  
391 tional sex ratios toward the eastern, mesic range margins, a pattern detected in natural  
392 populations and recapitulated in our common garden populations. Furthermore, seed  
393 viability declined with increasing skew in the OSR, indicating that mate (pollen) limita-  
394 tion can limit the reproductive output of female-biased mating pools. It would appear

395 that all the pieces are in place for an important role of two-sex dynamics in contributing  
396 to distributional limits of Texas bluegrass, particularly at the eastern range edge. Yet,  
397 insights derived from the field-parameterized population model indicate the opposite:  
398 range limitation in this species is an effectively female-dominant process, with negligible  
399 contributions from males. Thus, in this system and likely others, female dominance is  
400 an adequate framework for understanding range dynamics: despite evidence for sexual  
401 niche differentiation, only the female niche mattered for determining the environmental  
402 limits of population viability. This does not mean that sex is unimportant, but rather that  
403 lack of sex is never so severe that it limits population viability.

404 The limited role of males in our experimental system can be explained by two factors.  
405 First, seed fertilization was robust to variation in OSR and was not predicted to strongly  
406 decline within the range of OSR bias that we observed and modeled, suggesting that few  
407 males are required to pollinate all or most females. Second, population growth ( $\lambda$ ) was  
408 weakly sensitive to seed viability, which further buffered the demographic consequences  
409 of sex ratio bias. We speculate that our qualitative conclusions should apply to other  
410 species or systems that satisfy either, but especially both, of these conditions. While  
411 there are striking examples of female-biased sex ratios causing declines in population  
412 growth (Milner-Gulland et al., 2003) or range expansion (Miller and Inouye, 2013), other  
413 examples suggest limited demographic consequences of sex ratio variation (Ewen et al.,  
414 2011; Gownaris et al., 2020; Mysterud et al., 2002). Ultimately, sensitivity of female repro-  
415 ductive success to sex ratio should depend strongly on the mating system, with female  
416 dominance at the “extremely polygamous” end of a continuum (Miller et al., 2011). The  
417 sensitivity of population viability to female reproductive success, in turn, is likely pre-  
418 dicted by life history strategy: in long-lived, iteroparous species, population growth rates

419 are often weakly sensitive to reproduction relative to growth and survival (Franco and  
420 Silvertown, 2004). We therefore hypothesize that range limits are more likely to be dom-  
421 inated by the female environmental niche in longer-lived species with more polygamous  
422 mating systems, while males are more likely to play an important role in shorter-lived,  
423 monogamous species that may be particularly sensitive to missed mating opportunities.  
424 As studies of sex ratio variation and sex-specific demography across species' ranges ac-  
425 cumulate in the literature (e.g., Dudaniec et al., 2021; Lynch et al., 2014; Petry et al., 2016),  
426 this hypothesis may be tractably pursued with comparative analyses.

427 While life history and mating system may determine the demographic consequences  
428 of skewed sex ratios, the sensitivity of sex ratio to environmental factors is another crit-  
429 ical ingredient of how environmental variation can affect the population dynamics of  
430 dioecious species. Our study adds to a growing body of work quantifying the demo-  
431 graphic mechanisms giving rise to skewed operational sex ratios using two-sex models  
432 (Eberhart-Phillips et al., 2017; Shelton, 2010b; Veran and Beissinger, 2009) and parsing the  
433 contributions of environmental drivers (Bialic-Murphy et al., 2020). However, as a field,  
434 we lack a strong predictive framework for how often and in which direction environ-  
435 mental drivers are likely to skew the operational sex ratio – and this gap is particularly  
436 important in the context of global change. We have focused on the limits of population vi-  
437 ability with respect to geographic environmental variation but analogous processes will  
438 likely govern how populations respond to temporal environmental change, including  
439 direct effects on female demography and indirect effects via perturbations to the mating  
440 pool (Fig. 1). There is a need to better understand and predict which species and types  
441 of species are susceptible to climate change-induced shifts in OSR. Geographic variation  
442 in OSR may be an instructive proxy for how dioecious species will respond to climate

<sup>443</sup> change (Petry et al., 2016). The link between OSR and responses to climate adds value  
<sup>444</sup> to studies of the causes and consequences of spatial variation in sex ratio, particularly at  
<sup>445</sup> geographic scales that encompass “past” and “future” conditions.

<sup>446</sup> Previous studies of dioecious plants have shown that male bias is more common than  
<sup>447</sup> female bias and is particularly pronounced in harsh abiotic environments, likely reflect-  
<sup>448</sup> ing the greater resource requirements needed to pay the female cost of reproduction  
<sup>449</sup> (Bierzychudek and Eckhart, 1988; Field et al., 2013a,b). Our surveys of natural popula-  
<sup>450</sup> tions are consistent with the broader pattern of male-biased OSR at xeric range edges.  
<sup>451</sup> However, our common garden populations did not exhibit male bias in the xeric west –  
<sup>452</sup> averaged across years or in any single year (Fig. B2) – nor did we find any strong demo-  
<sup>453</sup> graphic evidence for a western male advantage (in fact, there was a western female ad-  
<sup>454</sup> vantage in growth and survival for some sizes). If male advantage / female disadvantage  
<sup>455</sup> under harsh abiotic conditions is driven by the greater resource requirements of females  
<sup>456</sup> then it is possible that clonal propagation and/or legacies of greenhouse rearing masked  
<sup>457</sup> the ‘true’ sex difference at xeric-edge common garden sites. Instead, the stronger pattern  
<sup>458</sup> of sex ratio bias was the female reproductive advantage at the mesic, eastern range edge.  
<sup>459</sup> We hypothesize that the mesic edge is limited by competition and that the female repro-  
<sup>460</sup> ductive advantage reflects competitive superiority of females, which has been suggested  
<sup>461</sup> in previous studies of Texas bluegrass (Compagnoni et al., 2017) and shown in other  
<sup>462</sup> dioecious plants (Eppley, 2006), particularly under mesic conditions (Chen et al., 2014).  
<sup>463</sup> Theory suggests that biotic interactions such as competition are likely to limit species’  
<sup>464</sup> ranges at the benign (e.g., mesic) end of abiotic gradients (Louthan et al., 2015) though  
<sup>465</sup> this has not been explored, to our knowledge, in the context of sex-structured dynamics.  
<sup>466</sup> Future studies in our system or others could test whether females and males differ in

467 their responses to biotic stressors at xeric and mesic range edges to reveal how biotic  
468 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-  
481 sider 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; Villegas 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.

<sup>491</sup> Ultimately, increased survival was not sufficient to prevent declines in population vi-  
<sup>492</sup> ability from the range center to eastern and western limits, which were dominated by  
<sup>493</sup> declining female growth and flowering. A recent study found a similar pattern, where  
<sup>494</sup> compensation between vital rates could not prevent a decrease of population growth rate  
<sup>495</sup> towards the southern range edge of *Erythranthe cardinalis* (Sheth and Angert, 2018).

<sup>496</sup> Third, our results highlight some important considerations in how environment-  
<sup>497</sup> dependent demographic models are best parameterized to derive insights into the drivers  
<sup>498</sup> of range limits. Our approach relied heavily on common garden populations, which  
<sup>499</sup> allowed us to plant and track known-sex individuals in contrasting environmental con-  
<sup>500</sup> ditions that encompass and exceed the natural geographic distribution. The ability to  
<sup>501</sup> robustly sample edge and beyond-edge environments is a powerful advantage of the  
<sup>502</sup> common garden transplant approach (Hargreaves et al., 2013). However, this also lim-  
<sup>503</sup> ited the size variation that we were able to include and model, and the size distributions  
<sup>504</sup> of common garden populations skewed consistently smaller than natural populations.  
<sup>505</sup> In Appendix C, we show that our conclusions are likely robust to this feature of the  
<sup>506</sup> common gardens. However, our ability to quantify the consequences of size representa-  
<sup>507</sup> tion is itself limited by size representation: we can simulate a population in which the  
<sup>508</sup> largest common garden sizes are more common than they actually were, but simulating  
<sup>509</sup> a population with sizes much larger than observed requires extrapolation of our statisti-  
<sup>510</sup> cal models, and we are skeptical about what insights such an exercise could provide (in  
<sup>511</sup> Appendix C, we extrapolated demographic performance to sizes 50% greater than the  
<sup>512</sup> observed maximum). This issue is not unique to our study but will be encountered by  
<sup>513</sup> any transplant study intended to yield inferences about range limits of species with sig-  
<sup>514</sup> nificant size structure, such as trees. If we could re-do our experiment knowing what we

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

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

527 Understanding and predicting geographic distributions and their responses to en-  
528 vironmental change demands careful consideration of which biological details must be  
529 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, re-  
552 viewers may access our raw 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 corresponding to Figure

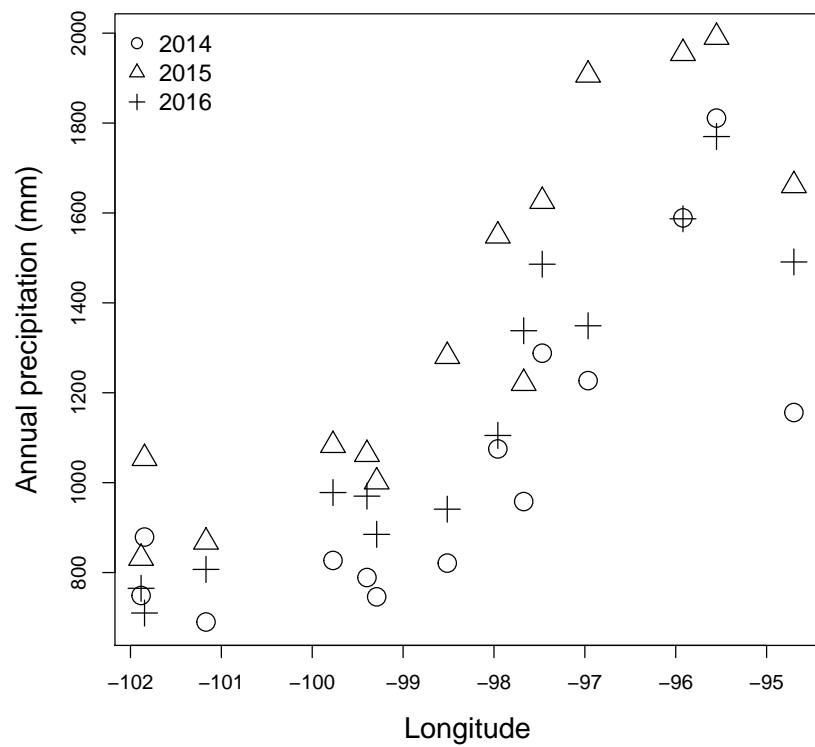


Figure A1: Total annual precipitation at common garden sites during the study years tracked long-term trends of increasing aridity from east to west.

## Appendix B: Additional results

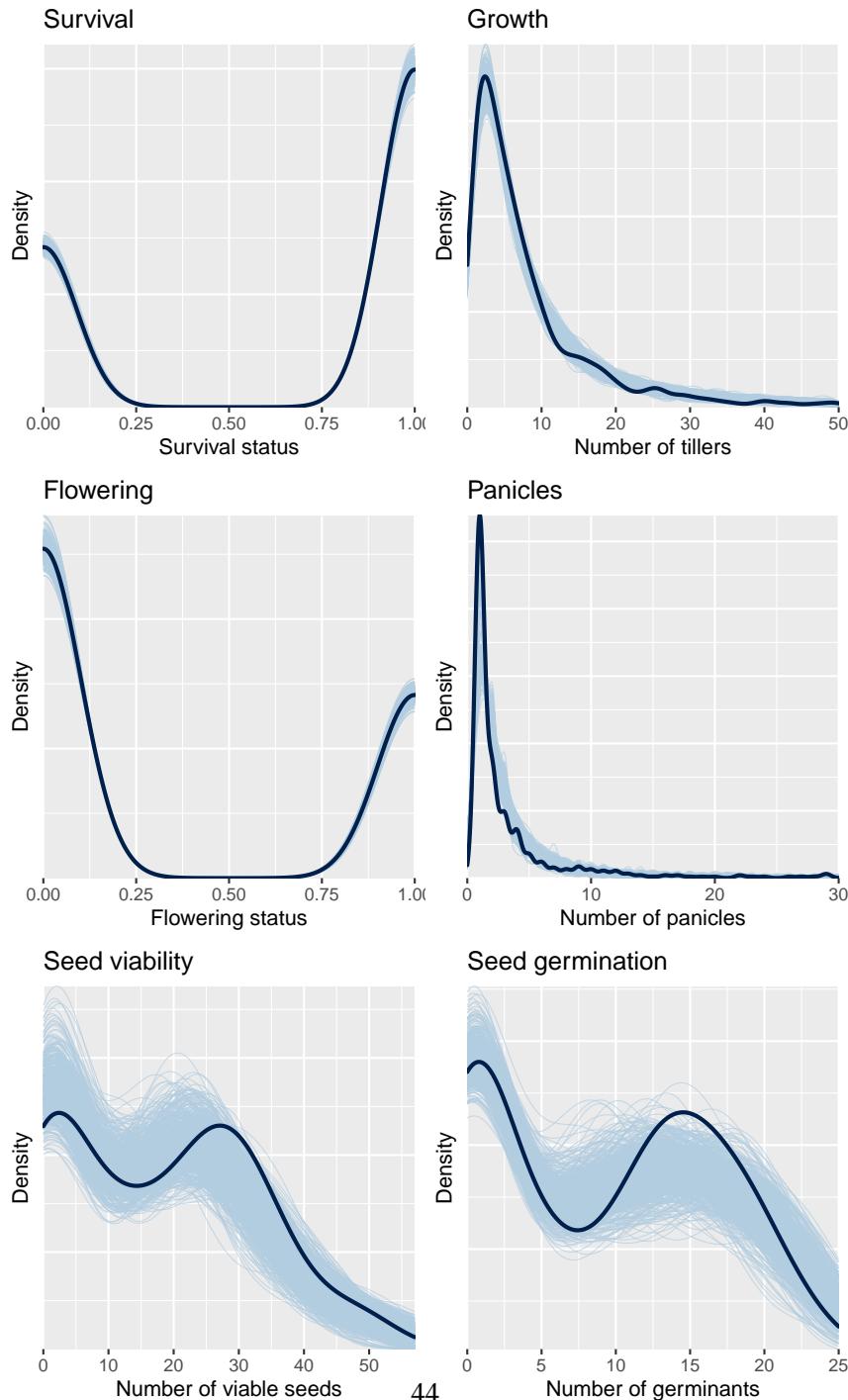


Figure B1: Posterior predictive checks of statistical models for demographic vital rates. Lines show density distributions of real data (thick, dark blue) compared to simulated data sets (thin, light blue) generated from the fitted models based on 500 draws of the posterior distribution of parameter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

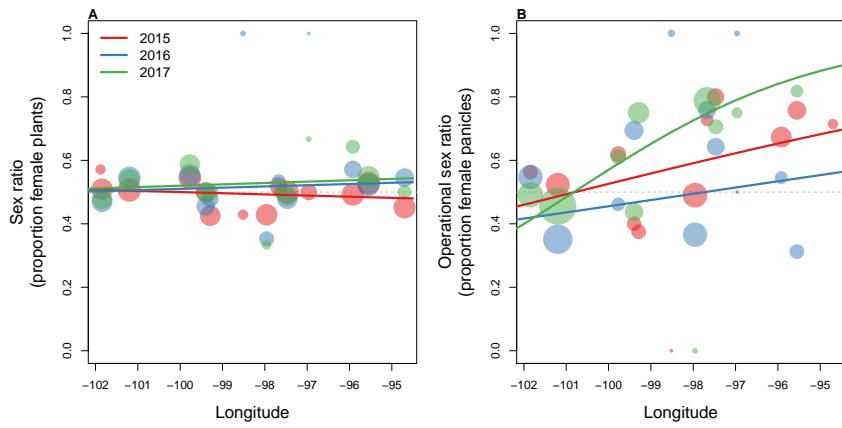


Figure B2: Year-specific sex ratios of plants (A) and panicles (B) in common garden populations spanning the longitudinal aridity gradient. Points sizes are proportional to sample sizes and lines show fitted binomial GLMs.

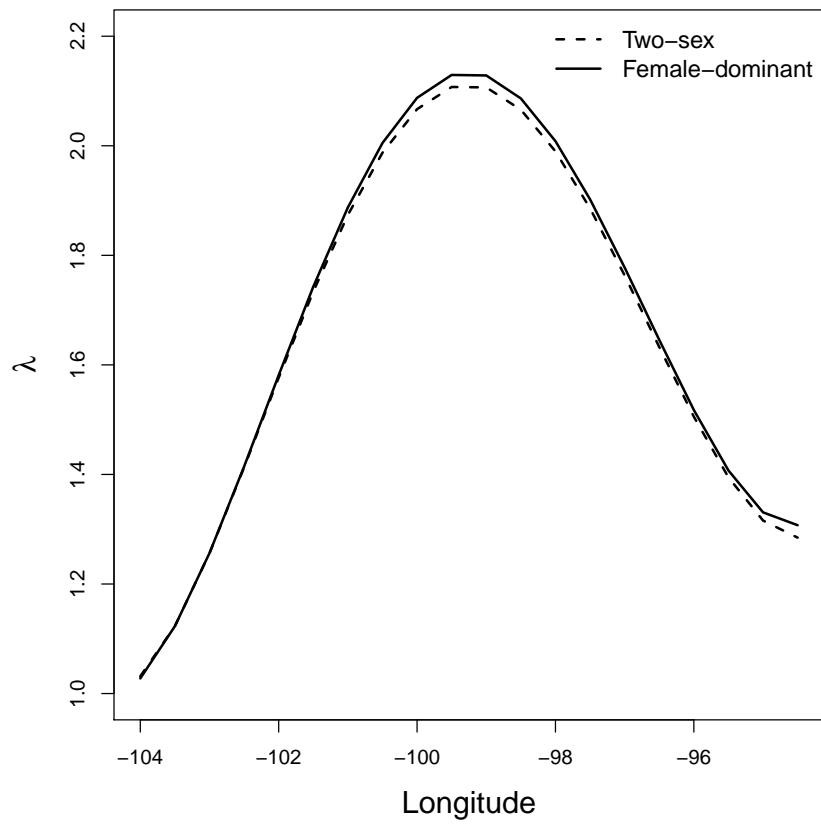


Figure B3: Comparison of longitudinal variation in  $\lambda$  between the two-sex demographic model (dashed line) that includes dependence of female seed production on population structure and the corresponding female-dominant model (solid line) with constant female fertility and all else equal. Models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

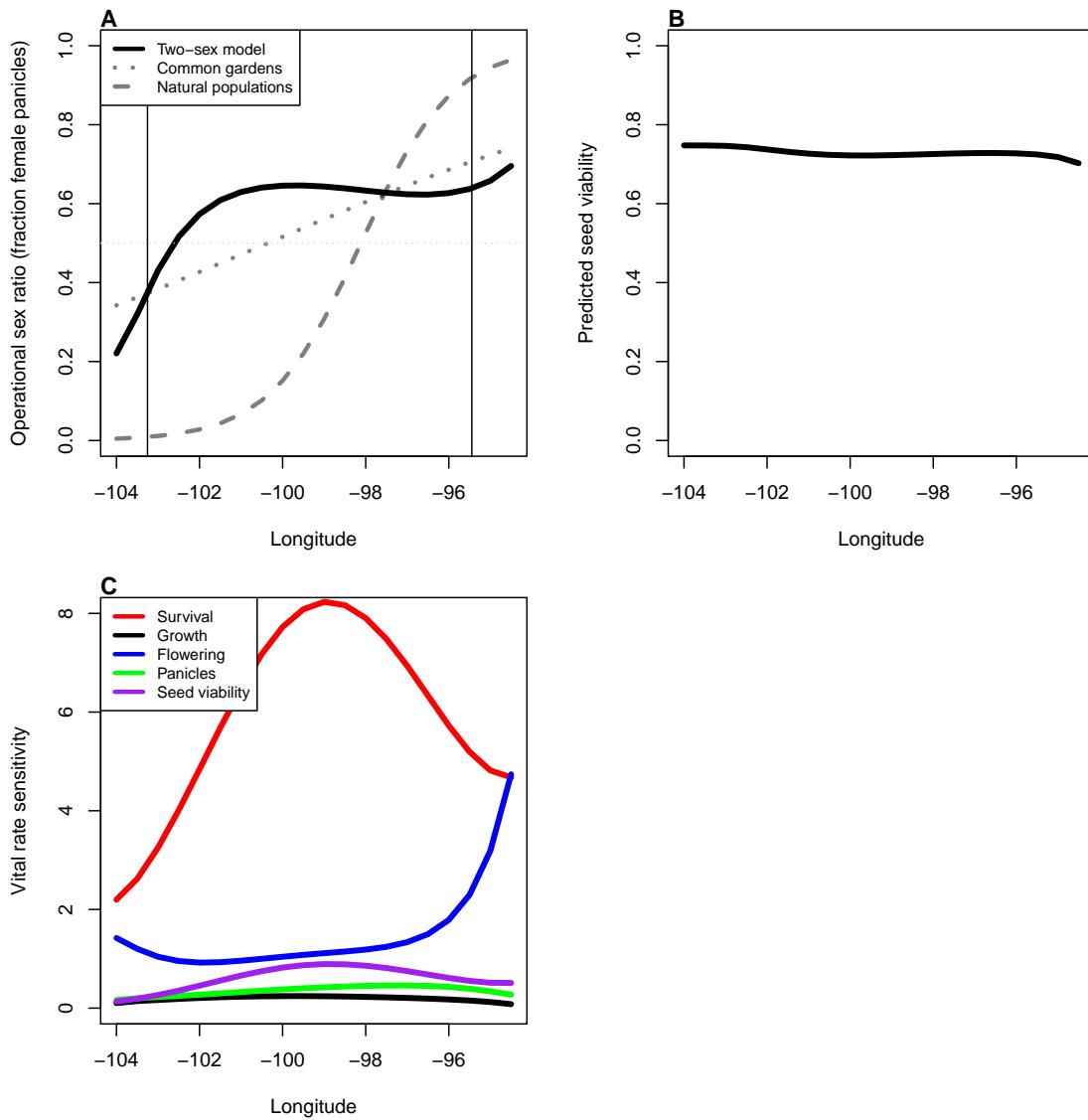


Figure B4: **A**, Longitudinal variation in operational sex ratio (fraction of panicles that are female) predicted by the two-sex MPM (solid line) compared to the sex ratio clines fitted to data from common gardens (dotted line) or natural populations (dashed line). Vertical lines show the longitudes 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  $\lambda$  to vital rates in relation to longitude. Sensitivities were calculated numerically by perturbing vital rate functions (across all sizes) by 0.01, recalculating  $\lambda$ , 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.

732 **Appendix C: Size distribution comparisons and simulation  
733 experiments**

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

737 *Observed and predicted size distributions*

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

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

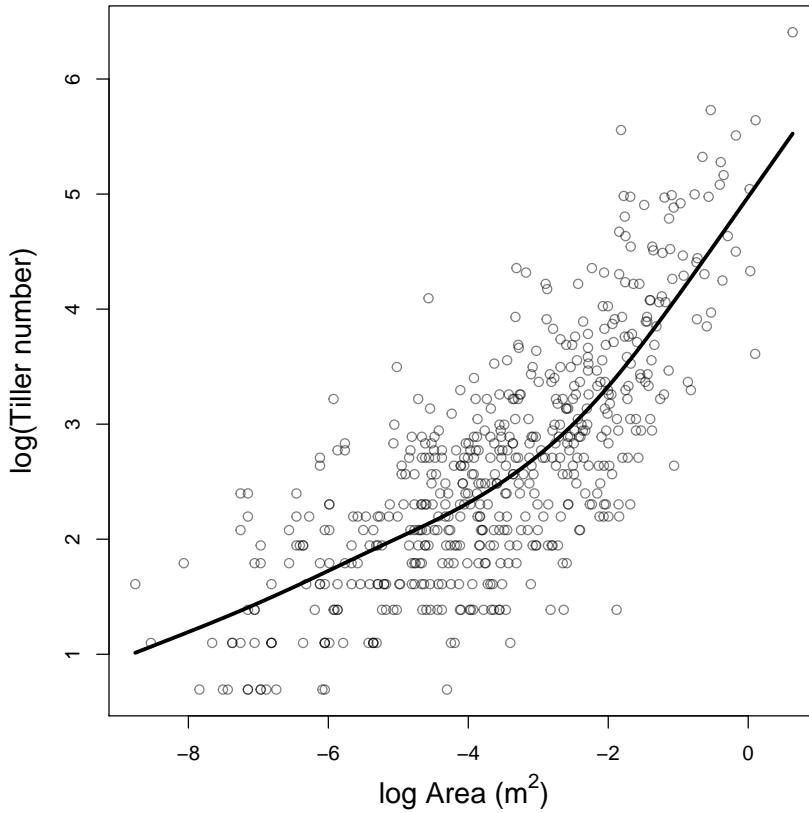


Figure C1: Relationship between area ( $m^2$ ) and tiller count from plants in the common garden experiment. The fitted gam model (line) was used to convert area measurements from natural populations to tiller counts.

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

<sup>754</sup> logarithm of tiller number, and then estimating the empirical distribution of this variable.

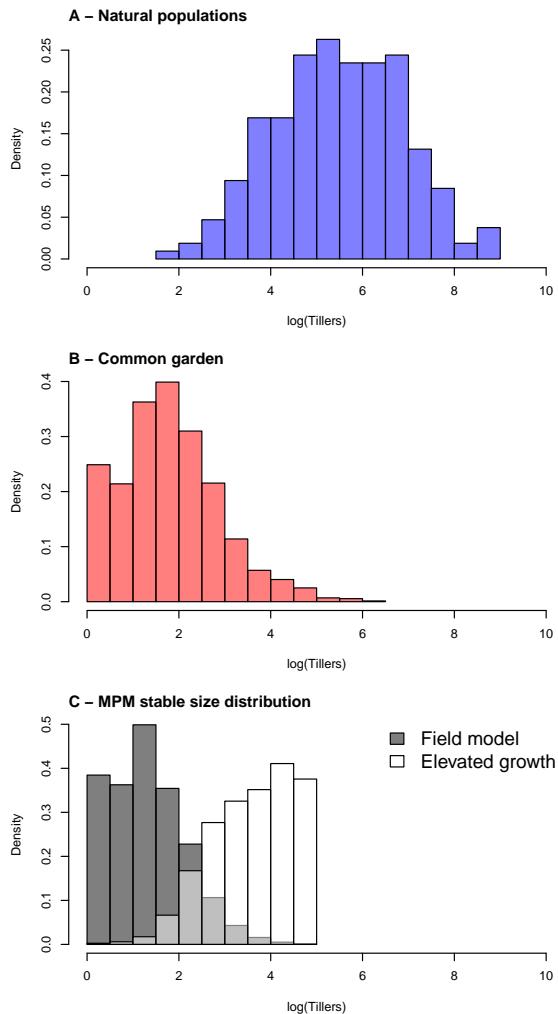


Figure C2: Size distribution of Texas bluegrass from natural populations (A), common garden populations (B), and predicted by the two-sex MPM (C). In C, the two size distributions come from the base model parameterized following methods described in the main manuscript (“field model”, in gray) and a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

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

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

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

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

780 function by a factor of 2.75 (values larger than this caused numerical instabilities). This  
781 adjustment caused all plants to increase in size more strongly regardless of initial size,  
782 sex, or geographic location.

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

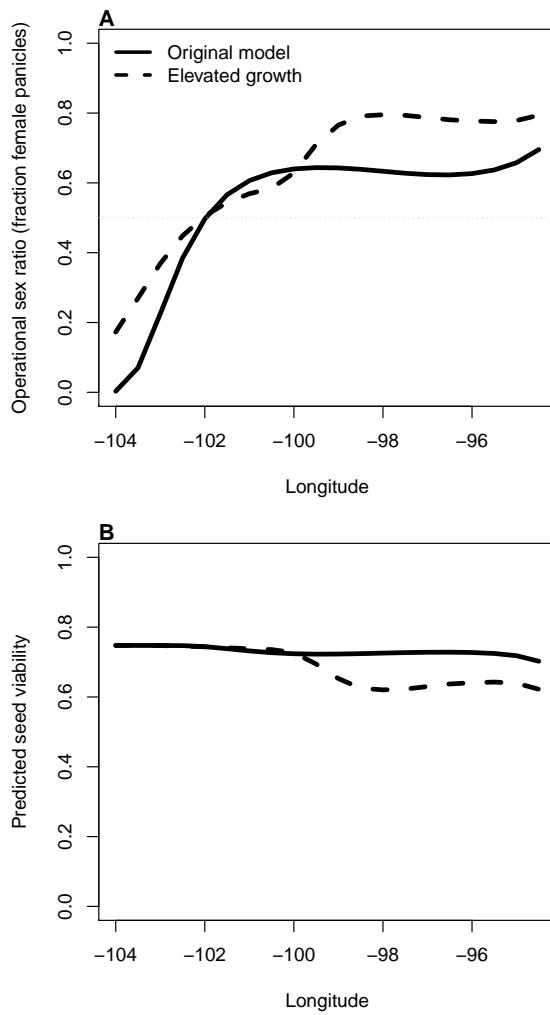


Figure C3: Two-sex model predictions for **A** operational sex ratio (fraction of panicles that are female) and **B** seed viability at stable population structure in relation to longitude. Solid line shows predictions of the base model using field-estimated parameter values and dashed line shows the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

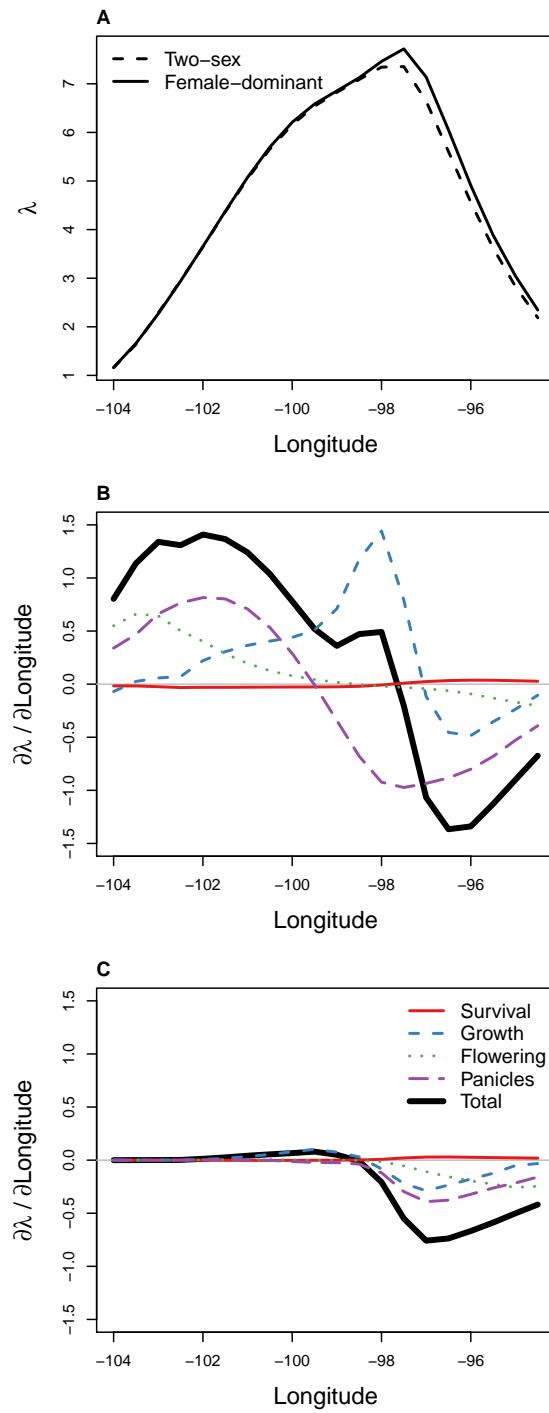


Figure C4: Results for the elevated growth model, in which the intercept of growth function was increased by a factor of 2.75. **A**, contrast of two-sex and female-dominant models, as in Fig. B3; **B,C**, Life Table Response Experiments decomposing the change in  $\lambda$  with respect to longitude into contributions from female **B** and male **C** vital rates (layout as in Fig. 6).