

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

Tom E.X. Miller<sup>1,\*</sup> and Aldo Compagnoni<sup>2,3</sup>

The authors wish to be identified to the reviewers.

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

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

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

*Manuscript type:* Article.

Prepared using the suggested L<sup>A</sup>T<sub>E</sub>X template for *Am. Nat.*

## Abstract

1 Understanding the mechanisms that generate biogeographic range limits is a long-standing  
2 goal of ecology. It is widely hypothesized that distributional limits reflect the envi-  
3 ronmental niche, but this hypothesis is complicated by widespread potential for intra-  
4 specific niche heterogeneity. In dioecious species, sexual niche differentiation may cause  
5 divergence between the sexes in their limits of environmental suitability. We studied  
6 range boundary formation in Texas bluegrass (*Poa arachnifera*), a perennial dioecious  
7 plant, testing the alternative hypotheses that range limits reflect the niche limits of fe-  
8 males only versus the combined contributions of females and males, including their  
9 inter-dependence via mating. Common garden experiments across a longitudinal aridity  
10 gradient revealed female-biased flowering approaching eastern range limits, suggesting  
11 that mate limitation may constrain the species' distribution. However, a demographic  
12 model showed that declines in  $\lambda$  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  $\lambda$  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 alititudtes 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 **may be** 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).

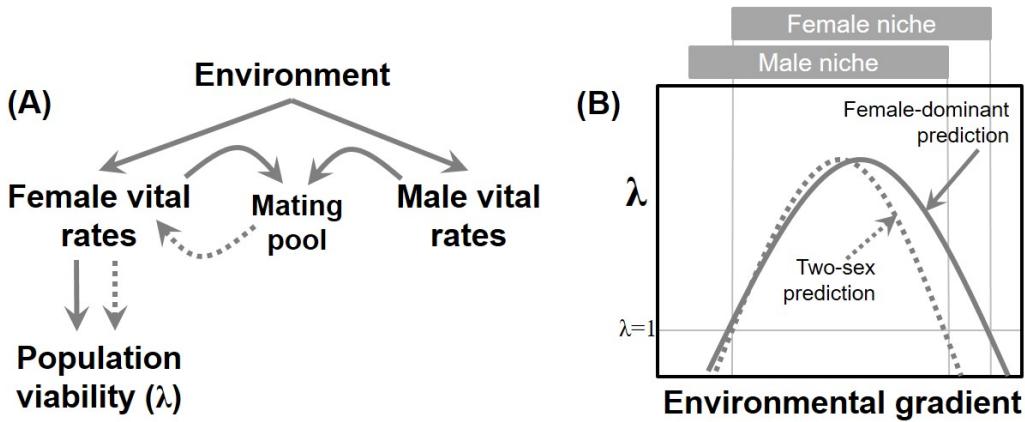


Figure 1: Hypotheses for how environmental variation can affect population viability and range limits in dieocious species. Under the female-dominant hypothesis, environmental drivers affect population growth ( $\lambda$ ) through effects on females, alone (A). In geographic / environmental space, this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

---

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

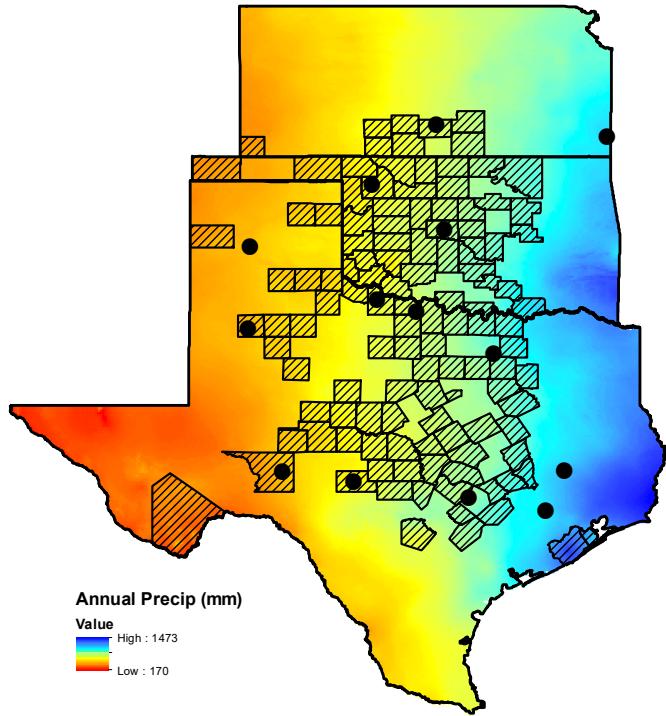


Figure 2: Geographic and environmental distribution of *P. arachnifera* in Texas, Oklahoma, and Kansas. Hatched shapes show counties with herbarium records of occurrence. Color shows geographic variation in annual precipitation (mm) based on 30-year normals from WorldClim (Fick and Hijmans, 2017). Points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

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

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

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

<sup>157</sup> We visited each site during May of 2015, 2016, and 2017. For each individual in each  
<sup>158</sup> year, we recorded data for four demographic vital rates: survival status (alive or dead),  
<sup>159</sup> size (number of tillers and patch area), flowering status (reproductive or vegetative), the  
<sup>160</sup> 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 our results are implicitly averaged over years.

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

178 In follow-up analyses, we tested the addition of a climate mismatch variable that  
179 quantified the deviation between mean annual precipitation of each source population  
180 and common garden location. This analysis allowed us to evaluate whether local adap-  
181 tation to climate may have contributed to variation in demographic performance across  
182 common garden sites. This was motivated by the observation that most source pop-  
183 ulations came from the interior of the geographic range (MAP) and were brought to  
184 edge and beyond-edge locations that were much drier or wetter than their historical cli-

185 mate regime. The local adaptation hypothesis predicts that demographic performance  
186 declines with increasing climatic deviation between common garden and source popu-  
187 lation locations. We added the absolute value of mean annual precipitation mismatch  
188 (using 30-year normals) as a covariate to the vital rate models described above.

189

### *Sex ratio experiment*

190 At one site near the center of the range (Lake Lewisville Environmental Learning Area,  
191 Texas), we established a separate experiment to quantify how sex ratio variation affects  
192 female reproductive success. Details of this experiment, which was conducted in 2014–  
193 2015, are described in Compagnoni et al. 2017. Briefly, we established 124 experimental  
194 populations in  $0.4m \times 0.4m$  plots that varied in population density (1–48 plants/plot) and  
195 sex ratio (0–100%female), with 2–4 replicates for each of 34 density-sex ratio combina-  
196 tions. The experiment was established ca. 1 km from a natural population at this site and  
197 plots were situated with a minimum of 15 m spacing, a buffer that was intended to limit  
198 pollen movement between plots (pilot data indicated that  $\geq 90\%$  of wind pollination oc-  
199 curred within 13m). We measured female reproductive success in different density and  
200 sex ratio environments by collecting panicles from a subset of females in each plot at the  
201 end of the reproductive season. In the lab, we counted the total number of seeds on each  
202 panicle.

203 In Texas bluegrass, unfertilized seeds shatter from the panicle along with fertilized  
204 seeds, so seed counts reflect female reproductive effort (seeds initiated) and not mating  
205 success (seeds fertilized). We therefore assessed seed fertilization in two ways. First,  
206 we conducted greenhouse-based germination trials using 25 seeds per panicle from 112  
207 panicles belonging to 84 census females spanning the range of sex ratio variation. We

208 also conducted tetrazolium-based seed viability assays to estimate seed fertilization in-  
209 dependently of germination, since some fertilized seeds may fail to germinate during  
210 our trials. Tetrazolium trials used 17–57 seeds per panicle (mode: 30) from 65 panicles  
211 belonging to 63 females, a subset of those used for the germination trials. To perform  
212 these assays, we first let seed batches imbibe on a moistened paper towel for 12 h. We  
213 then bisected the seeds in half and soaked them in a pH buffer solution containing 0.1%  
214 of tetrazolium for 12 h. The pH buffer solution contained 0.57% of sodium phosphate  
215 and 0.36% of potassium phosphate. A seed was scored as viable if the embryo stained  
216 pink.

217 *Statistical analysis of sex ratio experiment*

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

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

224 where  $OSR$  is the operational sex ratio (fraction of panicles that were female) in our  
225 experimental populations. This function has the properties, supported by our previous  
226 work (Compagnoni et al., 2017), that seed viability is maximized at  $v_0$  as  $OSR$  approaches  
227 zero (strongly male-biased) and goes to zero as  $OSR$  approaches 1 (strongly female-

228 biased). Parameter  $\alpha$  controls how viability declines with increasing female bias.

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

237 *Demographic model of range limits*

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

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

251 order polynomial, following the statistical models. We assume that the parameters of sex  
 252 ratio-dependent mating (Eq. 1) do not vary with longitude.

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

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

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

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

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

260 Finally, the dynamics of the size-structured component of the population are given  
 261 by:

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

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

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

275 Because the two-sex MPM is nonlinear (vital rates affect and are affected by popu-  
 276 lation structure) we estimated the asymptotic geometric growth rate ( $\lambda$ ) by numerical  
 277 simulation, and repeated this across a range of longitudes. We used a regression-style  
 278 Life Table Response Experiment (Caswell, 2001) to decompose the change in  $\lambda$  towards  
 279 range limits into contributions from female and male vital rates (the female-dominant  
 280 hypothesis predicts that declines in  $\lambda$  at range limits are driven solely by females). The

281 LTRE approximates the change in  $\lambda$  with longitude as the product of the sensitivity of  $\lambda$   
282 to the parameters times the sensitivity of the parameters to longitude, summed over all  
283 parameters:

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

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

## 290 Results

### 291 *Sex ratio variation in natural populations*

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

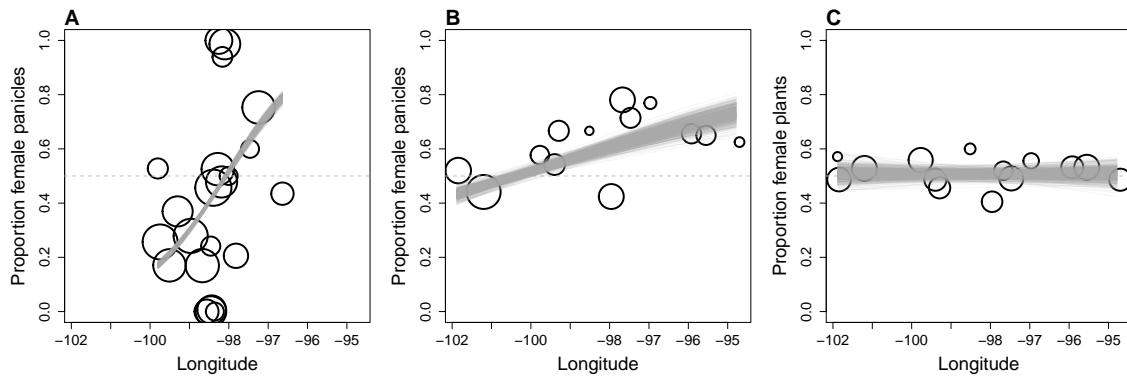


Figure 3: Sex ratio variation of *P. arachnifera* across its longitudinal distribution. **A**, Operational sex ratio (fraction of panicles that were female) in 22 natural populations; **B**, Operational sex ratio and **C**, sex ratio (fraction of plants that were female) in 14 common gardens. Within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

297

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

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

307 Annual survival probability was predicted to peak at western and eastern range

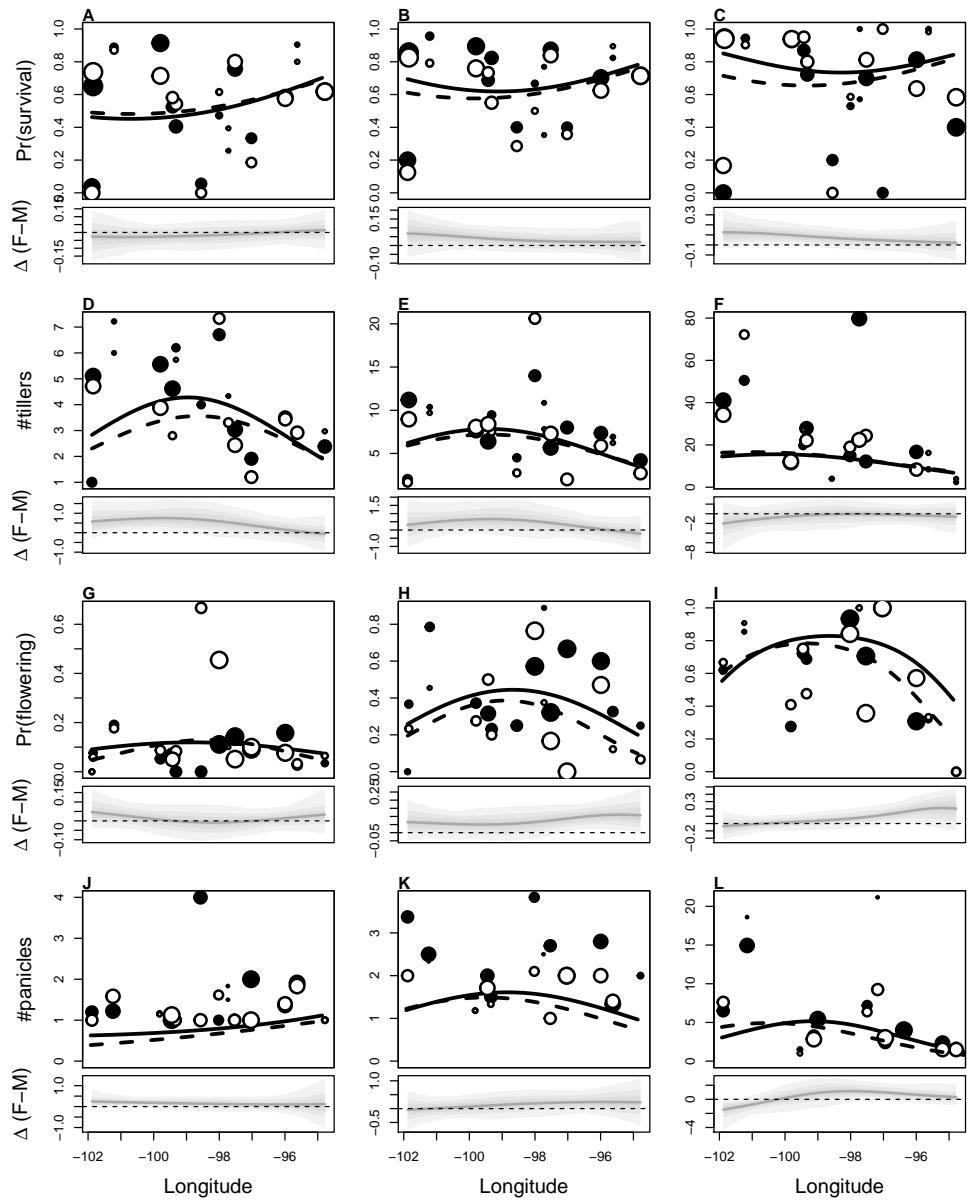


Figure 4: Sex-, size-, and longitude-related variation in: A–C, inter-annual probability of survival; D–F, inter-annual growth (change in number of tillers); G–I, probability of flowering; J–L, number of panicles produced given flowering. Points show means by site for females (filled) and males (open)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

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

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

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

331

### *Sex-ratio dependent seed fertilization*

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

342

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

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

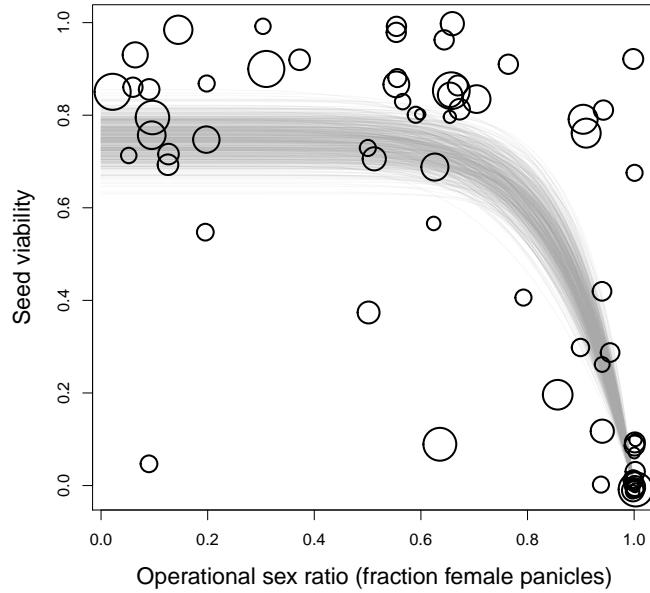


Figure 5: Seed fertilization success in relation to operational sex ratio (fraction of panicles that are female) in experimental populations. Circles show data from tetrazolium assays of seed viability; circle size is proportional to the number of seeds tested (min: 14, max: 57). Lines show model predictions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

353 sistent with observations from the common garden and natural populations (Fig. B5A).  
 354 Female bias in the OSR was predicted to cause declines in seed viability toward eastern  
 355 range margins (Fig. B5B). However, this effect was weak in magnitude because predicted  
 356 OSR bias was not extreme enough to cause strong declines in viability, given the re-  
 357 lationship derived from the sex ratio manipulation experiment (Fig. 5). Furthermore,  
 358 population viability at the eastern range margin was weakly sensitive to seed viability  
 359 relative to other vital rates (B5C). These observations underscore the next set of results.  
 360 LTRE decomposition revealed that declines in  $\lambda$  approaching range limits were driven

361 almost exclusively by females (Fig. 6B) with near-zero contributions from males (Fig.  
362 6C). Thus, range limitation was an effectively female-dominant process, despite system-  
363 atic geographic variation in sex ratio. Correspondingly, predictions of the two-sex model  
364 were nearly indistinguishable from a corresponding female-dominant model with all else  
365 equal, with only very modest differences in predictions of the two models emerging in  
366 the eastern part of the range (Fig. B4).

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

374 Skew in the OSR predicted by the demographic model was less extreme than was  
375 observed in natural and experimental populations (B5A). This occurred because sex dif-  
376 ferences in demography, especially flowering, were most pronounced at the largest sizes,  
377 and the MPM predicted that these sizes were very rare at stable population structure.  
378 The stable size distribution predicted by the MPM corresponded well to the common  
379 garden data (from which the MPM was built) but was much smaller, on average, than  
380 the size distribution we observed in natural populations (Fig. C2), presumably because  
381 transplants did not grow like “real” plants and/or did not have time in our three-year  
382 experiment to reach those sizes. In Appendix C, we explore whether higher growth  
383 rates, leading to a more realistic size distribution, would lead to a more important role  
384 for males. In numerical experiments with growth parameters, we found that larger size

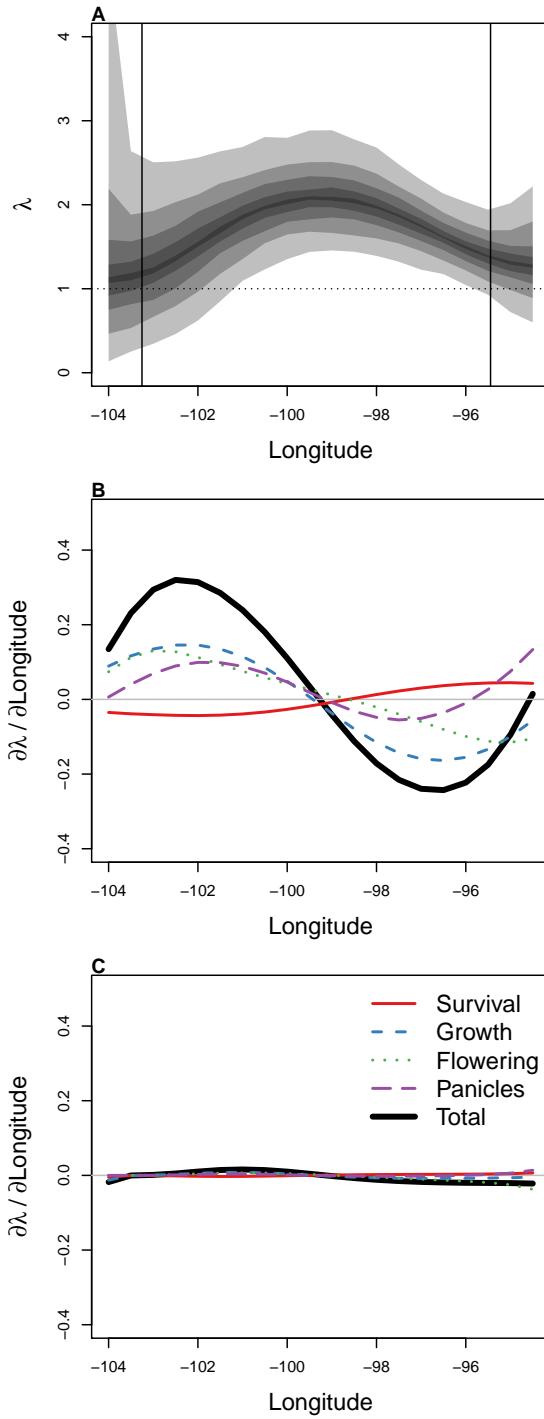


Figure 6: Population growth ( $\lambda$ ) as a function of longitude, predicted by the two-sex MPM that incorporates sex-specific demographic responses to longitude with sex ratio-dependent seed fertilization. A, posterior distribution of  $\lambda$ , where shaded regions show the 25, 50, 75, and 95%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

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

## 395 Discussion

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

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

417 The limited role of males in our experimental system can be explained by two factors.  
418 First, seed fertilization was robust to variation in OSR and was not predicted to strongly  
419 decline within the range of OSR bias that we observed and modeled, suggesting that few  
420 males are required to pollinate all or most females. Second, population growth ( $\lambda$ ) was  
421 weakly sensitive to seed viability, which further buffered the demographic consequences  
422 of sex ratio bias. We speculate that our qualitative conclusions should apply to other  
423 species or systems that satisfy either, but especially both, of these conditions. While  
424 there are striking examples of female-biased sex ratios causing declines in population  
425 growth (Milner-Gulland et al., 2003) or range expansion (Miller and Inouye, 2013), other  
426 examples suggest limited demographic consequences of sex ratio variation (Ewen et al.,  
427 2011; Gownaris et al., 2020; Mysterud et al., 2002). Ultimately, sensitivity of female repro-  
428 ductive success to sex ratio should depend strongly on the mating system, with female  
429 dominance at the “extremely polygamous” end of a continuum (Miller et al., 2011). The  
430 sensitivity of population viability to female reproductive success, in turn, is likely pre-  
431 dicted by life history strategy: in long-lived, iteroparous species, population growth rates

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

440 While life history and mating system may determine the demographic consequences  
441 of skewed sex ratios, the sensitivity of sex ratio to environmental drivers is another crit-  
442 ical ingredient of how environmental variation can affect the population dynamics of  
443 dioecious species. Our study adds to a growing body of work quantifying the demo-  
444 graphic mechanisms giving rise to skewed operational sex ratios using two-sex models  
445 (Eberhart-Phillips et al., 2017; Shelton, 2010; Veran and Beissinger, 2009) and parsing the  
446 contributions of environmental drivers (Bialic-Murphy et al., 2020). However, as a field,  
447 we lack a strong predictive framework for how often and in which direction environ-  
448 mental drivers are likely to skew the operational sex ratio – and this gap is particularly  
449 important in the context of global change. We have focused on the limits of population  
450 viability with respect to geographic environmental variation but analogous processes  
451 will likely govern how populations respond to temporal environmental change (e.g., cli-  
452 mate change), including direct effects on female demography and indirect effects via  
453 perturbations to the mating pool (Fig. 1). There is a need to better understand and pre-  
454 dict which species and types of species are susceptible to climate change-induced shifts  
455 in OSR. Geographic variation in OSR may be an instructive proxy for how dioecious

<sup>456</sup> species will respond to climate change (Petry et al., 2016). The link between OSR and  
<sup>457</sup> responses to climate adds value to studies of the causes and consequences of spatial vari-  
<sup>458</sup> ation in sex ratio, particularly at geographic scales that encompass “past” and “future”  
<sup>459</sup> conditions.

<sup>460</sup> Previous studies of dioecious plants have shown that male bias is more common than  
<sup>461</sup> female bias and is particularly pronounced in harsh abiotic environments, likely reflect-  
<sup>462</sup> ing the greater resource requirements needed to pay the female cost of reproduction  
<sup>463</sup> (Bierzychudek and Eckhart, 1988; Field et al., 2013a,b). Our surveys of natural popula-  
<sup>464</sup> tions are consistent with the broader pattern of male-biased OSR at xeric range edges.  
<sup>465</sup> However, our common garden populations did not exhibit male bias in the xeric west  
<sup>466</sup> – averaged across years or in any single year (Fig. B3) – nor did we find any strong  
<sup>467</sup> demographic evidence for a western male advantage (in fact, there was a western female  
<sup>468</sup> advantage in growth and survival for some sizes). If male advantage / female disad-  
<sup>469</sup> vantage under harsh abiotic conditions is driven by the greater resource requirements of  
<sup>470</sup> females then it is possible that clonal propagation and/or legacies of greenhouse rearing  
<sup>471</sup> masked the ‘true’ sex difference at xeric-edge common garden sites, **or that reproductive**  
<sup>472</sup> **costs accumulate over longer time scales than considered here**. Instead, the stronger pat-  
<sup>473</sup> tern of sex ratio bias was the female reproductive advantage at the mesic, eastern range  
<sup>474</sup> edge. We hypothesize that the mesic edge is limited by competition and that the female  
<sup>475</sup> reproductive advantage reflects competitive superiority of females, which has been sug-  
<sup>476</sup> gested in previous studies of Texas bluegrass (Compagnoni et al., 2017) and shown in  
<sup>477</sup> other dioecious plants (Eppley, 2006), particularly under mesic conditions (Chen et al.,  
<sup>478</sup> 2014). Theory suggests that biotic interactions such as competition are likely to limit  
<sup>479</sup> species’ ranges at the benign (e.g., mesic) end of abiotic gradients (Louthan et al., 2015)

480 though this has not been explored, to our knowledge, in the context of sex-structured  
481 dynamics. Future studies in our system or others could test whether females and males  
482 differ in their responses to biotic stressors at xeric and mesic range edges to reveal how  
483 biotic factors shape range limits via sex-specific demography.

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

498 Second, our results also provide novel evidence for contrasting demographic re-  
499 sponses to environmental drivers throughout a species' range – or “demographic com-  
500 pensation” (Doak and Morris, 2010; Villegas et al., 2015). Elevated performance in some  
501 life history processes can compensate for declines in other processes and thus buffer  
502 range-edge populations against harsh environmental conditions. In Texas bluegrass,  
503 most vital rates declined toward eastern and western range limits but survival showed

504 the opposite pattern. Increased survival at longitudinal extremes partially offset declines  
505 in other vital rates but this positive response was weaker than the negative responses.  
506 Ultimately, increased survival was not sufficient to prevent declines in population vi-  
507 ability from the range center to eastern and western limits, which were dominated by  
508 declining female growth and flowering. However, we also found evidence that growth  
509 patterns exhibited local adaptation: individuals planted into locations that were climati-  
510 cally similar to locations of their source population exhibited greater growth, on average,  
511 irrespective of sex. It is therefore possible that our demographic model (which does not  
512 explicitly account for local adaptation) over-estimates the decline in fitness approaching  
513 range edges, since local adaptation in a high-sensitivity vital rate may dampen the effects  
514 of environmental forcing. There is growing awareness that local adaptation can modify  
515 expectations for species' distributions under global change (Peterson et al., 2019). Mech-  
516 anistic models of range limits that incorporate potential for local adaptation would be a  
517 valuable next step.

518 Third, our results highlight some important considerations in how environment-  
519 dependent demographic models are best parameterized to derive insights into the drivers  
520 of range limits. Our approach relied heavily on common garden populations, which  
521 allowed us to plant and track known-sex individuals in contrasting environmental con-  
522 ditions that encompass and exceed the natural geographic distribution. The ability to  
523 robustly sample edge and beyond-edge environments is a powerful advantage of the  
524 common garden transplant approach (Hargreaves et al., 2013). However, this also lim-  
525 ited the size variation that we were able to include and model, and the size distributions  
526 of common garden populations skewed consistently smaller than natural populations.  
527 In Appendix C, we show that our conclusions are likely robust to this feature of the

528 common gardens. However, our ability to quantify the consequences of size representa-  
529 tion is itself limited by size representation: we can simulate a population in which the  
530 largest common garden sizes are more common than they actually were, but simulating  
531 a population with sizes much larger than observed requires extrapolation of our statisti-  
532 cal models, and we are skeptical about what insights such an exercise could provide (in  
533 Appendix C, we extrapolated demographic performance to sizes 50% greater than the  
534 observed maximum). This issue is not unique to our study but will be encountered by  
535 any transplant study intended to yield inferences about range limits of species with sig-  
536 nificant size structure, such as trees. If we could re-do our experiment knowing what we  
537 know now, we would combine data from natural and transplanted populations to model  
538 size-dependent demography over a more realistic size distribution. Other investigators  
539 inspired by similar questions about the demographic drivers of range limits should con-  
540 sider such a hybrid approach.

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

549 Understanding and predicting geographic distributions and their responses to en-  
550 vironmental change demands careful consideration of which biological details must be

551 accounted for and which others can be safely ignored. Our results show that complex,  
552 non-linear dynamics involving females, males, and frequency-dependent reproduction  
553 can be reasonably approximated as a simple, linear process (female-dominant popula-  
554 tion growth). We suggest that this is good news. The next challenge is to figure out how  
555 often and under what conditions ecologists can get away with it.

556

## Acknowledgements

557 We gratefully acknowledge the many individuals who facilitated our field work, es-  
558 pecially Dariusz Malinowski, Jason Goldman, Tom Arsuffi, Alan Byboth, John Walker,  
559 Kenneth Steigman, Steven Gibson, Wesley Newman, Kerry Griffis, Liz Martin, Melanie  
560 Hartman, Brian Northup, Leland Russell, Dexter R Mardis, and Dixie Smith. This work  
561 was made possible by a network of biological field stations that hosted our geograph-  
562 ically distributed experiment. We acknowledge Sam Houston State University, Texas  
563 A&M University, University of Texas, Texas Tech University, Pittsburgh State University,  
564 and Wichita State University for investing in field stations and making these facilities  
565 available to us. We thank Marion Donald, Kory Kolis, Nakian Kim, and Alex Espana  
566 for valuable assistance in the field, lab, and greenhouse. Our work was supported by  
567 NSF Division of Environmental Biology awards 1543651 and 1754468 and by the Rice  
568 University Faculty Initiatives Fund.

569

## Author contributions

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

572

## Data accessibility

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

575

## Literature Cited

576 Araújo, M. S., Bolnick, D. I., and Layman, C. A. (2011). The ecological causes of individ-  
577 ual specialisation. *Ecology letters*, 14(9):948–958.

578 Bertiller, M. B., Sain, C. L., Bisigato, A. J., Coronato, F. R., Aries, J. O., and Graff, P. (2002).  
579 Spatial sex segregation in the dioecious grass *poa ligularis* in northern patagonia: the  
580 role of environmental patchiness. *Biodiversity & Conservation*, 11(1):69–84.

581 Bialic-Murphy, L., Heckel, C. D., McElderry, R. M., and Kalisz, S. (2020). Deer indi-  
582 rectly alter the reproductive strategy and operational sex ratio of an unpalatable forest  
583 perennial. *The American Naturalist*, 195(1):56–69.

584 Bierzychudek, P. and Eckhart, V. (1988). Spatial segregation of the sexes of dioecious  
585 plants. *The American Naturalist*, 132(1):34–43.

586 Bisang, I., Ehrlén, J., and Hedenäs, L. (2020). Sex expression and genotypic sex ratio  
587 vary with region and environment in the wetland moss *drepanocladus lycopodioides*.  
588 *Botanical journal of the Linnean Society*, 192(2):421–434.

589 Bolnick, D. I. and Doebeli, M. (2003). Sexual dimorphism and adaptive speciation: two  
590 sides of the same ecological coin. *Evolution*, 57(11):2433–2449.

- 591 Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D.,  
592 and Forister, M. L. (2002). The ecology of individuals: incidence and implications of  
593 individual specialization. *The American Naturalist*, 161(1):1–28.
- 594 Bowyer, R. T. (2004). Sexual segregation in ruminants: definitions, hypotheses, and  
595 implications for conservation and management. *Journal of Mammalogy*, 85(6):1039–1052.
- 596 Carpenter, B., Gelman, A., Hoffman, M. D., Lee, D., Goodrich, B., Betancourt, M.,  
597 Brubaker, M., Guo, J., Li, P., and Riddell, A. (2017). Stan: A probabilistic program-  
598 ming language. *Journal of statistical software*, 76(1).
- 599 Caruso, C. and Case, A. (2007). Sex ratio variation in gynodioecious lobelia siphilit-  
600 ica: effects of population size and geographic location. *Journal of Evolutionary Biology*,  
601 20(4):1396–1405.
- 602 Caswell, H. (2001). *Matrix Population Models*. Sinauer Associates, Inc., Sunderland, MA,  
603 2 edition.
- 604 Caswell, H. and Weeks, D. E. (1986). Two-sex models: chaos, extinction, and other  
605 dynamic consequences of sex. *The American Naturalist*, 128(5):707–735.
- 606 Chen, J., Duan, B., Wang, M., Korpelainen, H., and Li, C. (2014). Intra-and inter-sexual  
607 competition of populus cathayana under different watering regimes. *Functional Ecol-*  
608 *ogy*, 28(1):124–136.
- 609 Compagnoni, A., Steigman, K., and Miller, T. E. (2017). Can't live with them, can't live  
610 without them? balancing mating and competition in two-sex populations. *Proceedings*  
611 *of the Royal Society B: Biological Sciences*, 284(1865):20171999.

- 612 Darwin, C. (1871). *The descent of man*. BoD–Books on Demand.
- 613 De Lisle, S. P., Paiva, S., and Rowe, L. (2018). Habitat partitioning during character  
614 displacement between the sexes. *Biology letters*, 14(6):20180124.
- 615 De Lisle, S. P. and Rowe, L. (2015). Ecological character displacement between the sexes.  
616 *The American Naturalist*, 186(6):693–707.
- 617 Diez, J. M., Giladi, I., Warren, R., and Pulliam, H. R. (2014). Probabilistic and spatially  
618 variable niches inferred from demography. *Journal of ecology*, 102(2):544–554.
- 619 Doak, D. F. and Morris, W. F. (2010). Demographic compensation and tipping points in  
620 climate-induced range shifts. *Nature*, 467(7318):959–962.
- 621 Dudaniec, R. Y., Carey, A. R., Svensson, E. I., Hansson, B., Yong, C. J., and Lancaster, L. T.  
622 (2021). Latitudinal clines in sexual selection, sexual size dimorphism, and sex-specific  
623 genetic dispersal during a poleward range expansion. *Journal of Animal Ecology*.
- 624 Eberhart-Phillips, L. J., Küpper, C., Miller, T. E., Cruz-López, M., Maher, K. H., Dos Reme-  
625 dios, N., Stoffel, M. A., Hoffman, J. I., Krüger, O., and Székely, T. (2017). Sex-specific  
626 early survival drives adult sex ratio bias in snowy plovers and impacts mating system  
627 and population growth. *Proceedings of the National Academy of Sciences*, 114(27):E5474–  
628 E5481.
- 629 Ehrlén, J. and Morris, W. F. (2015). Predicting changes in the distribution and abundance  
630 of species under environmental change. *Ecology Letters*, 18(3):303–314.
- 631 Eppley, S. (2001). Gender-specific selection during early life history stages in the dioe-  
632 cious grass *distichlis spicata*. *Ecology*, 82(7):2022–2031.

- 633 Eppley, S. M. (2006). Females make tough neighbors: sex-specific competitive effects in  
634 seedlings of a dioecious grass. *Oecologia*, 146(4):549–554.
- 635 Evans, M. E., Merow, C., Record, S., McMahon, S. M., and Enquist, B. J. (2016). To-  
636 wards process-based range modeling of many species. *Trends in Ecology & Evolution*,  
637 31(11):860–871.
- 638 Ewen, J. G., Thorogood, R., and Armstrong, D. P. (2011). Demographic consequences of  
639 adult sex ratio in a reintroduced hihi population. *Journal of Animal Ecology*, 80(2):448–  
640 455.
- 641 Fick, S. E. and Hijmans, R. J. (2017). Worldclim 2: new 1-km spatial resolution climate  
642 surfaces for global land areas. *International journal of climatology*, 37(12):4302–4315.
- 643 Field, D. L., Pickup, M., and Barrett, S. C. (2013a). Comparative analyses of sex-ratio vari-  
644 ation in dioecious flowering plants. *Evolution: International Journal of Organic Evolution*,  
645 67(3):661–672.
- 646 Field, D. L., Pickup, M., and Barrett, S. C. (2013b). Ecological context and metapopula-  
647 tion dynamics affect sex-ratio variation among dioecious plant populations. *Annals of*  
648 *botany*, 111(5):917–923.
- 649 Franco, M. and Silvertown, J. (2004). A comparative demography of plants based upon  
650 elasticities of vital rates. *Ecology*, 85(2):531–538.
- 651 Gelman, A., Meng, X.-L., and Stern, H. (1996). Posterior predictive assessment of model  
652 fitness via realized discrepancies. *Statistica sinica*, pages 733–760.
- 653 Gianuca, D., Votier, S. C., Pardo, D., Wood, A. G., Sherley, R. B., Ireland, L., Choquet,

- 654 R., Pradel, R., Townley, S., Forcada, J., et al. (2019). Sex-specific effects of fisheries and  
655 climate on the demography of sexually dimorphic seabirds. *Journal of Animal Ecology*.
- 656 Gownaris, N. J., García Borboroglu, P., and Boersma, P. D. (2020). Sex ratio is vari-  
657 able and increasingly male biased at two colonies of magellanic penguins. *Ecology*,  
658 101(3):e02939.
- 659 Groen, K. E., Stieha, C. R., Crowley, P. H., and McLetchie, D. N. (2010). Sex-specific plant  
660 responses to light intensity and canopy openness: implications for spatial segregation  
661 of the sexes. *Oecologia*, 162(3):561–570.
- 662 Hargreaves, A. L., Samis, K. E., and Eckert, C. G. (2013). Are species' range limits simply  
663 niche limits writ large? a review of transplant experiments beyond the range. *The  
664 American Naturalist*, 183(2):157–173.
- 665 Holt, R. D. (2009). Bringing the hutchinsonian niche into the 21st century: ecological and  
666 evolutionary perspectives. *Proceedings of the National Academy of Sciences*, 106(Supple-  
667 ment 2):19659–19665.
- 668 Hultine, K. R., Bush, S. E., Ward, J. K., and Dawson, T. E. (2018). Does sexual dimorphism  
669 predispose dioecious riparian trees to sex ratio imbalances under climate change? *Oe-  
670 cologia*, 187(4):921–931.
- 671 Hutchinson, G. E. (1958). Concluding remarks. In *Cold Spring Harbour Symposium on  
672 Quantitative Biology*, volume 22, pages 415—427.
- 673 Ketterson, E. D. and Nolan Jr, V. (1976). Geographic variation and its climatic correlates in  
674 the sex ratio of eastern-wintering dark-eyed juncos (*junco hyemalis hyemalis*). *Ecology*,  
675 57(4):679–693.

- 676 Law, C. J. and Mehta, R. S. (2018). Carnivory maintains cranial dimorphism between  
677 males and females: evidence for niche divergence in extant musteloidea. *Evolution*,  
678 72(9):1950–1961.
- 679 Lee-Yaw, J. A., Kharouba, H. M., Bontrager, M., Mahony, C., Csergő, A. M., Noreen,  
680 A. M., Li, Q., Schuster, R., and Angert, A. L. (2016). A synthesis of transplant exper-  
681 iments and ecological niche models suggests that range limits are often niche limits.  
682 *Ecology letters*, 19(6):710–722.
- 683 Louthan, A. M., Doak, D. F., and Angert, A. L. (2015). Where and when do species  
684 interactions set range limits? *Trends in Ecology & Evolution*, 30(12):780–792.
- 685 Lynch, H. J., Rhainds, M., Calabrese, J. M., Cantrell, S., Cosner, C., and Fagan, W. F.  
686 (2014). How climate extremes-not means-define a species' geographic range boundary  
687 via a demographic tipping point. *Ecological Monographs*, 84(1):131–149.
- 688 Merow, C., Bois, S. T., Allen, J. M., Xie, Y., and Silander, J. A. (2017). Climate change both  
689 facilitates and inhibits invasive plant ranges in new england. *Proceedings of the National  
690 Academy of Sciences*, 114(16):E3276–E3284.
- 691 Merow, C., Latimer, A. M., Wilson, A. M., McMahon, S. M., Rebelo, A. G., and Silander Jr,  
692 J. A. (2014). On using integral projection models to generate demographically driven  
693 predictions of species' distributions: development and validation using sparse data.  
694 *Ecography*, 37(12):1167–1183.
- 695 Miller, T. E. and Inouye, B. D. (2011). Confronting two-sex demographic models with  
696 data. *Ecology*, 92(11):2141–2151.

- 697 Miller, T. E. and Inouye, B. D. (2013). Sex and stochasticity affect range expansion of  
698 experimental invasions. *Ecology Letters*, 16(3):354–361.
- 699 Miller, T. E., Shaw, A. K., Inouye, B. D., and Neubert, M. G. (2011). Sex-biased dispersal  
700 and the speed of two-sex invasions. *The American Naturalist*, 177(5):549–561.
- 701 Milner-Gulland, E., Bukreeva, O., Coulson, T., Lushchekina, A., Kholodova, M., Bekenov,  
702 A., and Grachev, I. A. (2003). Reproductive collapse in saiga antelope harems. *Nature*,  
703 422(6928):135–135.
- 704 Mysterud, A., Coulson, T., and Stenseth, N. C. (2002). The role of males in the dynamics  
705 of ungulate populations. *Journal of Animal Ecology*, 71(6):907–915.
- 706 Pekár, S., Martišová, M., and Bilde, T. (2011). Intersexual trophic niche partitioning in an  
707 ant-eating spider (araneae: Zodariidae). *PloS one*, 6(1):e14603.
- 708 Peterson, M. L., Doak, D. F., and Morris, W. F. (2019). Incorporating local adaptation  
709 into forecasts of speciesâ??t distribution and abundance under climate change. *Global  
710 Change Biology*, 25(3).
- 711 Petry, W. K., Soule, J. D., Iler, A. M., Chicas-Mosier, A., Inouye, D. W., Miller, T. E.,  
712 and Mooney, K. A. (2016). Sex-specific responses to climate change in plants alter  
713 population sex ratio and performance. *Science*, 353(6294):69–71.
- 714 Phillips, R., Silk, J., Phalan, B., Catry, P., and Croxall, J. (2004). Seasonal sexual segre-  
715 gation in two thalassarche albatross species: competitive exclusion, reproductive role  
716 specialization or foraging niche divergence? *Proceedings of the Royal Society of London.  
717 Series B: Biological Sciences*, 271(1545):1283–1291.

- 718 Rankin, D. J. and Kokko, H. (2007). Do males matter? the role of males in population  
719 dynamics. *Oikos*, 116(2):335–348.
- 720 Renganayaki, K., Jessup, R., Burson, B., Hussey, M., and Read, J. (2005). Identification of  
721 male-specific afp markers in dioecious texas bluegrass. *Crop science*, 45(6):2529–2539.
- 722 Renganayaki, K., Read, J., and Fritz, A. (2001). Genetic diversity among texas bluegrass  
723 genotypes (poa arachnifera torr.) revealed by afp and rapd markers. *Theoretical and*  
724 *Applied Genetics*, 102(6-7):1037–1045.
- 725 Renner, S. S. and Ricklefs, R. E. (1995). Dioecy and its correlates in the flowering plants.  
726 *American journal of botany*, 82(5):596–606.
- 727 Rozas, V., DeSoto, L., and Olano, J. M. (2009). Sex-specific, age-dependent sensitivity of  
728 tree-ring growth to climate in the dioecious tree juniperus thurifera. *New Phytologist*,  
729 182(3):687–697.
- 730 Shelton, A. O. (2010). The origin of female-biased sex ratios in intertidal seagrasses  
731 (phyllospadix spp.). *Ecology*, 91(5):1380–1390.
- 732 Shine, R. (1989). Ecological causes for the evolution of sexual dimorphism: a review of  
733 the evidence. *The Quarterly Review of Biology*, 64(4):419–461.
- 734 Stan Development Team (2020). RStan: the R interface to Stan. R package version 2.21.2.
- 735 Temeles, E. J., Miller, J. S., and Rifkin, J. L. (2010). Evolution of sexual dimorphism  
736 in bill size and shape of hermit hummingbirds (phaethornithinae): a role for eco-  
737 logical causation. *Philosophical Transactions of the Royal Society B: Biological Sciences*,  
738 365(1543):1053–1063.

- 739 Veran, S. and Beissinger, S. R. (2009). Demographic origins of skewed operational and  
740 adult sex ratios: perturbation analyses of two-sex models. *Ecology Letters*, 12(2):129–  
741 143.
- 742 Villegas, J., Doak, D. F., García, M. B., and Morris, W. F. (2015). Demographic compen-  
743 sation among populations: what is it, how does it arise and what are its implications?  
744 *Ecology letters*, 18(11):1139–1152.
- 745 Wood, S. (2017). *Generalized Additive Models: An Introduction with R*. Chapman and  
746 Hall/CRC, 2 edition.

## Appendix A: Site locations and climate

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

Table A1: Sites of natural population surveys

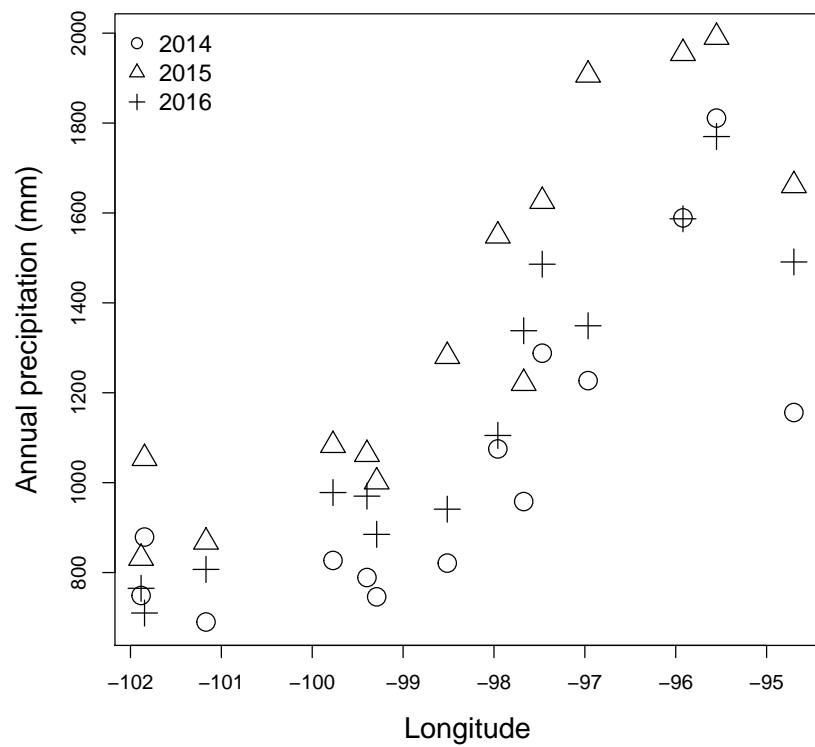


Figure A1: Total annual precipitation at common garden sites during the study years tracked long-term trends of increasing aridity from east to west.

## Appendix B: Additional results

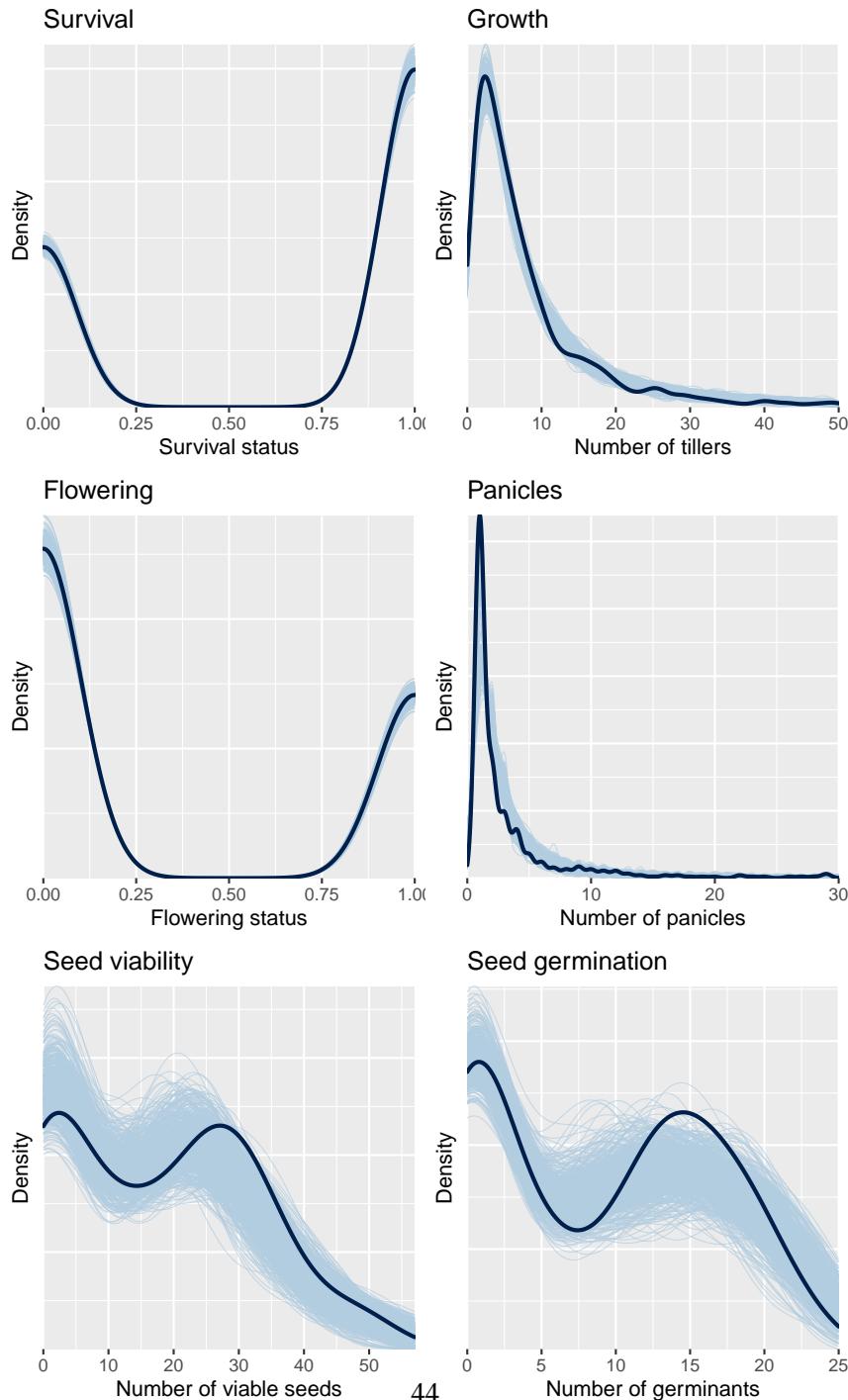
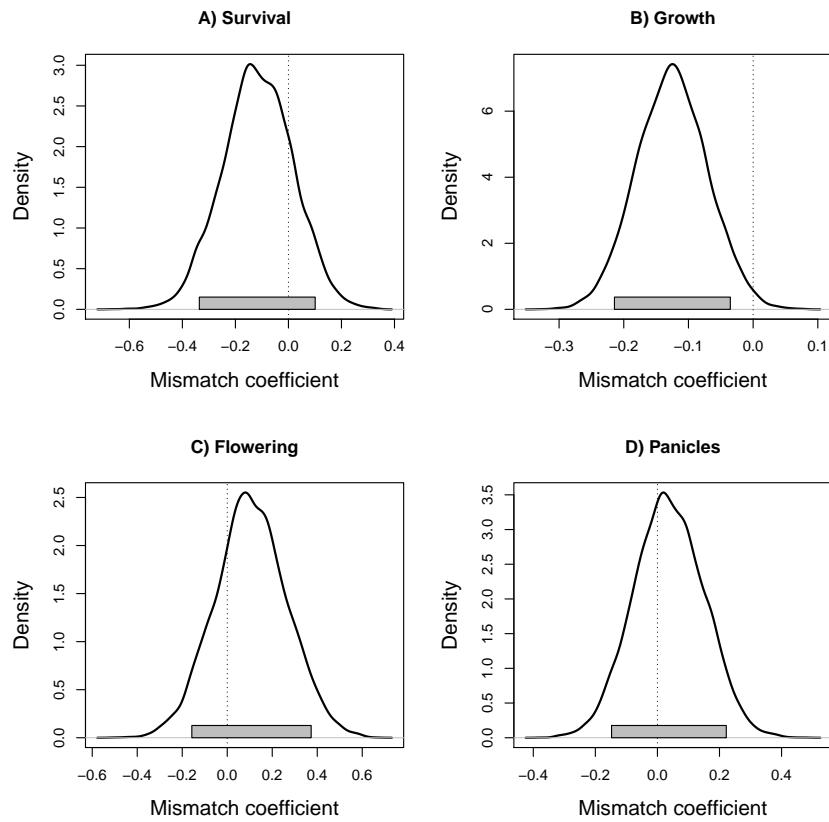


Figure B1: Posterior predictive checks of statistical models for demographic vital rates. Lines show density distributions of real data (thick, dark blue) compared to simulated data sets (thin, light blue) generated from the fitted models based on 500 draws of the posterior distribution of parameter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



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

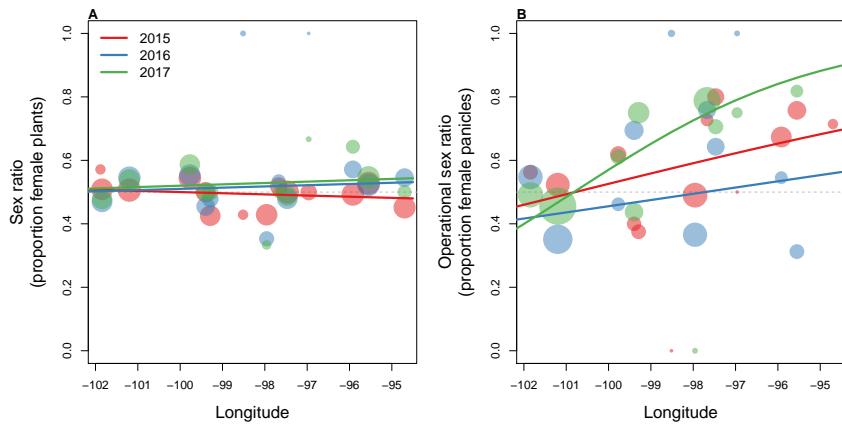


Figure B3: Year-specific sex ratios of plants (A) and panicles (B) in common garden populations spanning the longitudinal aridity gradient. Points sizes are proportional to sample sizes and lines show fitted binomial GLMs.

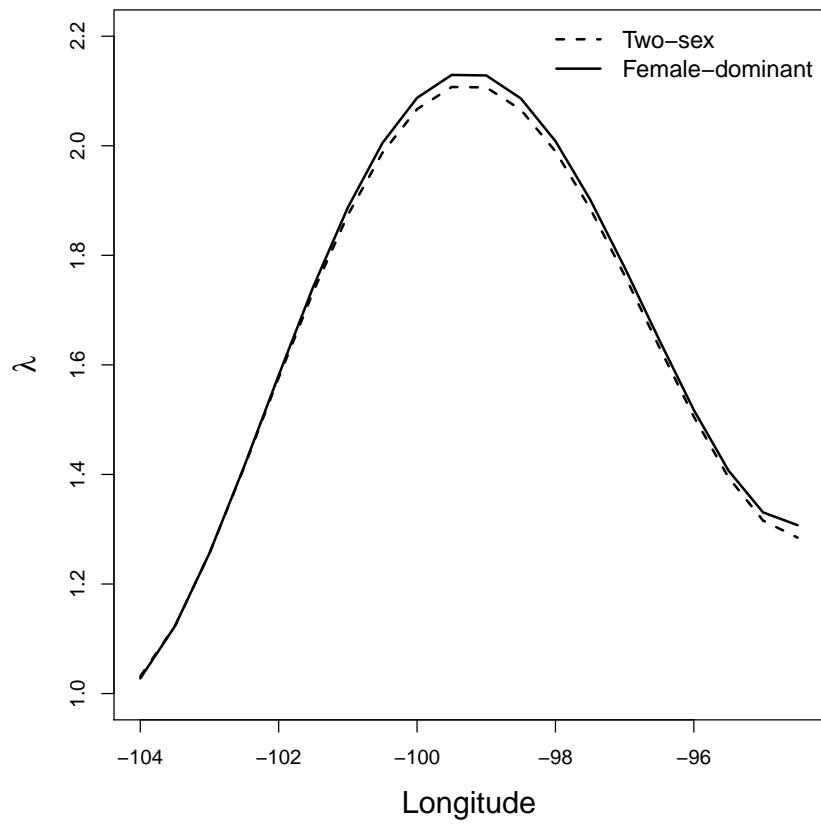


Figure B4: Comparison of longitudinal variation in  $\lambda$  between the two-sex demographic model (dashed line) that includes dependence of female seed production on population structure and the corresponding female-dominant model (solid line) with constant female fertility and all else equal. Models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

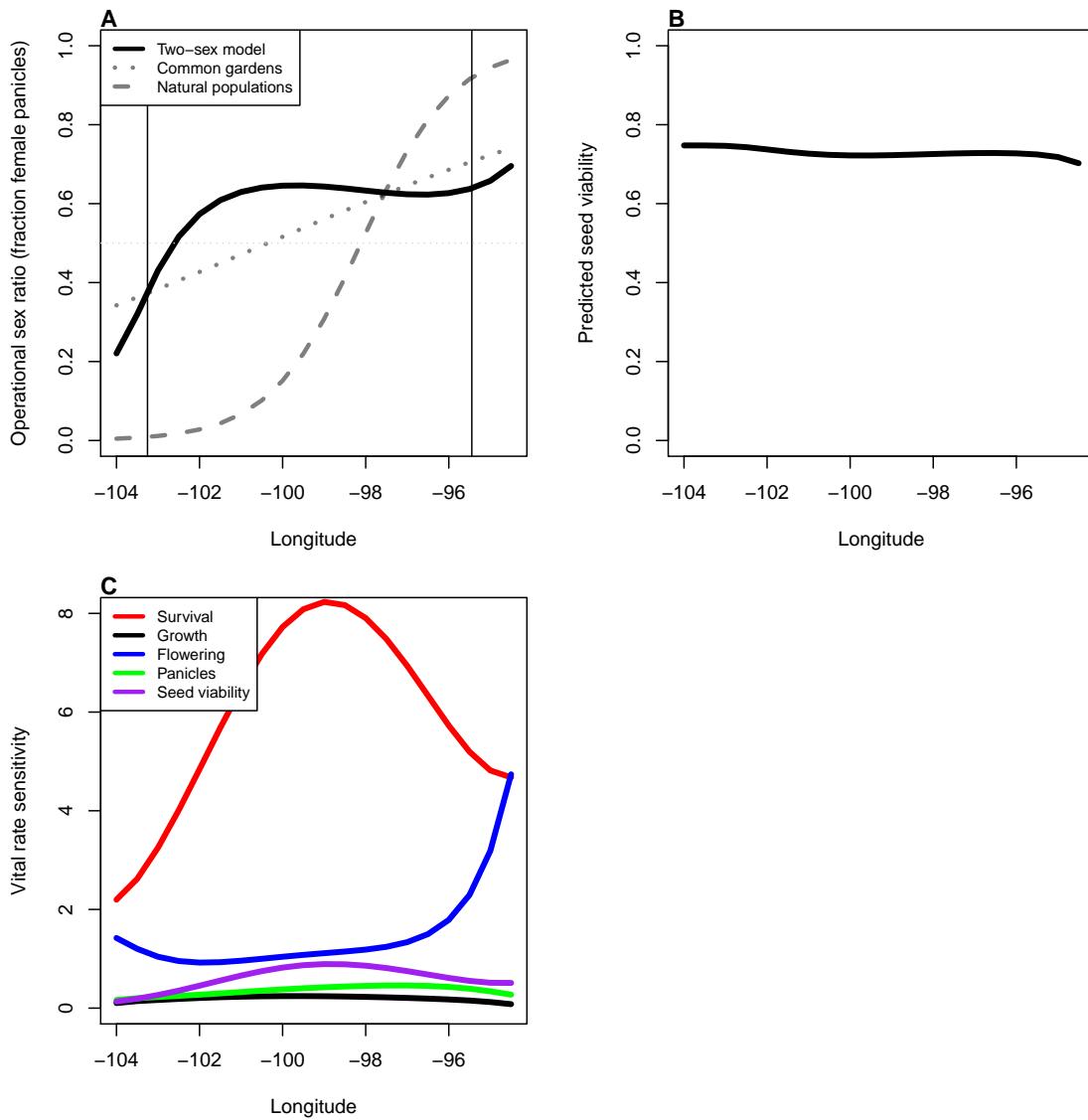


Figure B5: **A**, Longitudinal variation in operational sex ratio (fraction of panicles that are female) predicted by the two-sex MPM (solid line) compared to the sex ratio clines fitted to data from common gardens (dotted line) or natural populations (dashed line). Vertical lines show the longitudes of the westernmost and easternmost counties with occurrence records of *P. arachnifera*. **B**, Longitudinal variation in seed viability predicted by the two-sex MPM according to Eq. 1 and the OSR variation shown in **A**. **C**, Sensitivities of  $\lambda$  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.

## Appendix C: Size distribution comparisons and simulation experiments

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

## 754 Observed and predicted size distributions

<sup>755</sup> *Natural populations.* During natural population surveys (2012–2013) we recorded the  
<sup>756</sup> area ( $m^2$ ) of Texas bluegrass patches using a Trimble GeoExplorer hand-held GPS re-  
<sup>757</sup> ceiever with sub-meter accuracy.

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

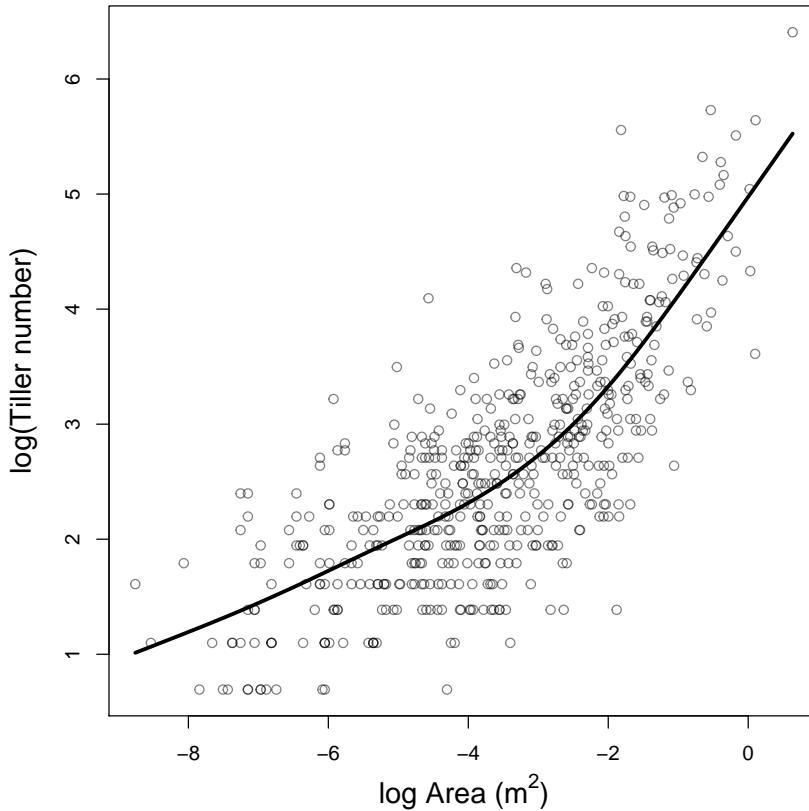


Figure C1: Relationship between area ( $m^2$ ) and tiller count from plants in the common garden experiment. The fitted gam model (line) was used to convert area measurements from natural populations to tiller counts.

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

<sup>771</sup> logarithm of tiller number, and then estimating the empirical distribution of this variable.

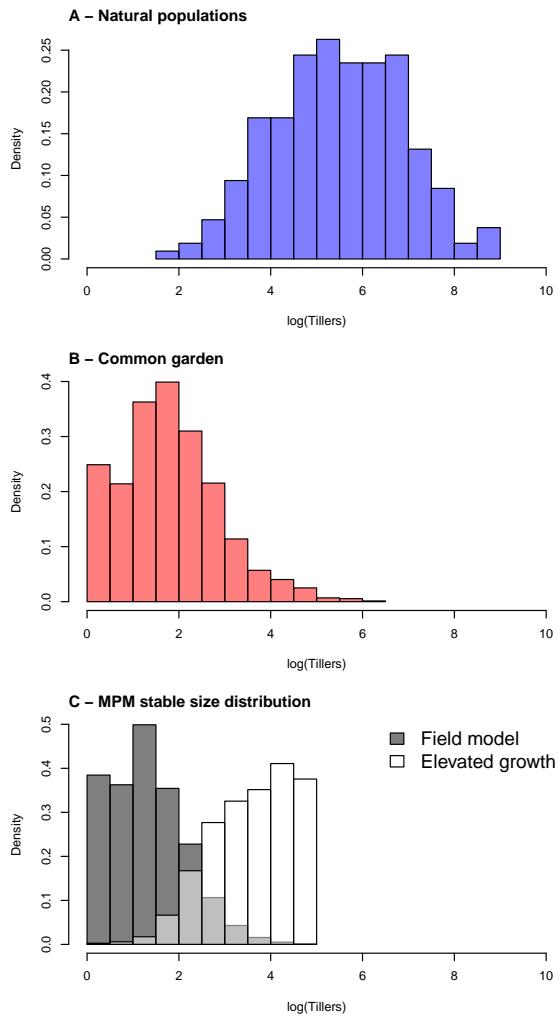


Figure C2: Size distribution of Texas bluegrass from natural populations (A), common garden populations (B), and predicted by the two-sex MPM (C). In C, the two size distributions come from the base model parameterized following methods described in the main manuscript (“field model”, in gray) and a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

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

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

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

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

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

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

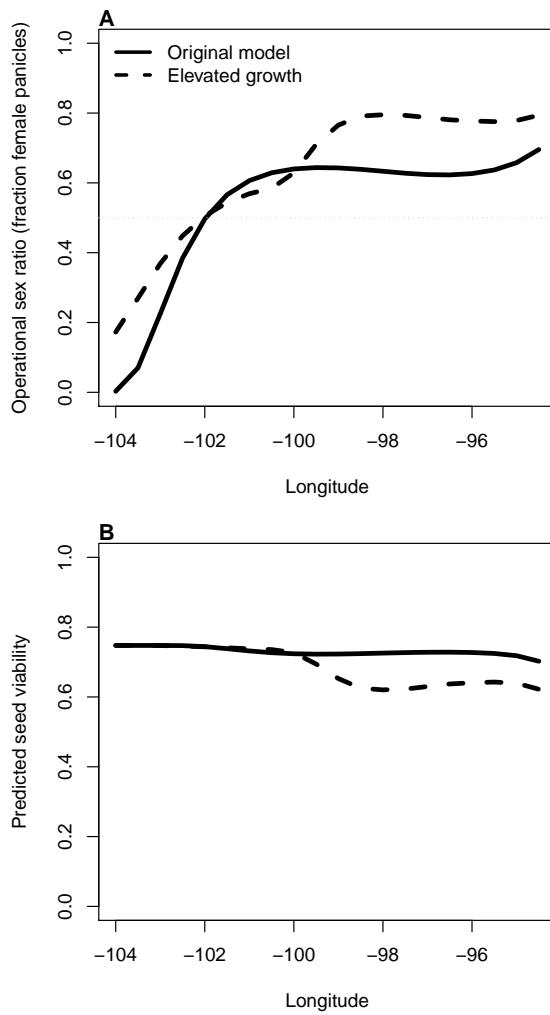


Figure C3: Two-sex model predictions for **A** operational sex ratio (fraction of panicles that are female) and **B** seed viability at stable population structure in relation to longitude. Solid line shows predictions of the base model using field-estimated parameter values and dashed line shows the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

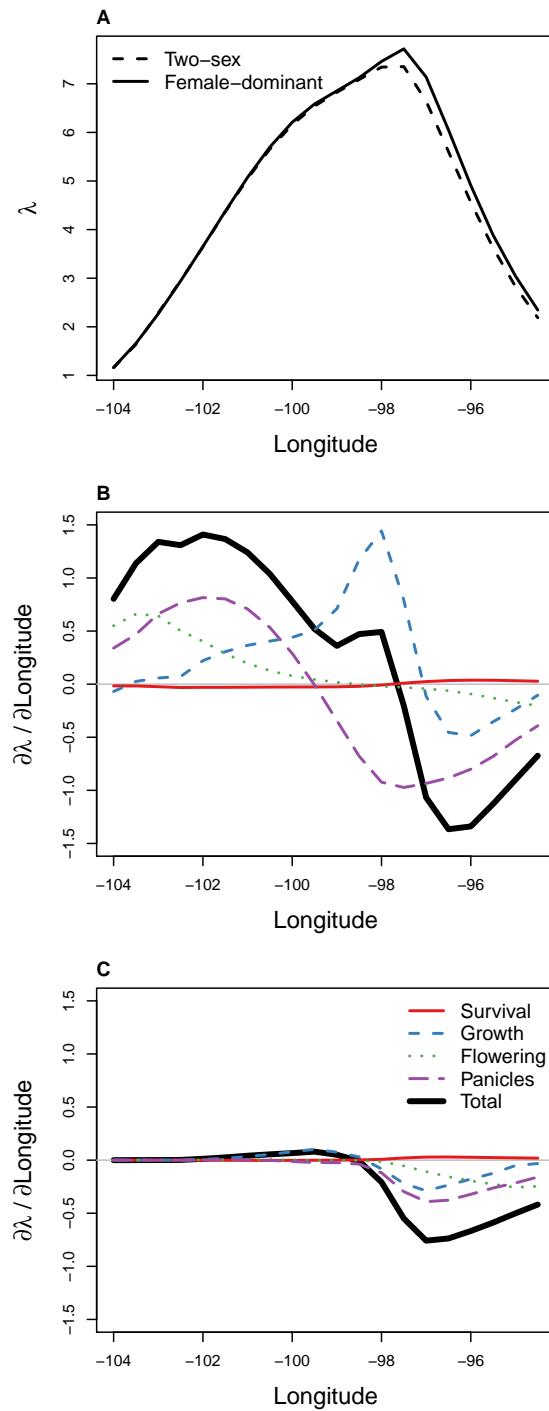


Figure C4: Results for the elevated growth model, in which the intercept of growth function was increased by a factor of 2.75. **A**, contrast of two-sex and female-dominant models, as in Fig. B4; **B,C**, Life Table Response Experiments decomposing the change in  $\lambda$  with respect to longitude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