

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

<sup>24</sup> cycle. This suggests that female-dominant limitation of geographic distribution  
<sup>25</sup> may be common to long-lived species with polygamous mating systems, and that  
<sup>26</sup> female responses to environmental drivers may often be sufficient for predicting  
<sup>27</sup> range shifts in response to environmental change.

<sup>28</sup> **Keywords**

<sup>29</sup> demography; dioecy; intra-specific niche heterogeneity; matrix projection model;  
<sup>30</sup> sex ratio; range limits

## <sup>31</sup> Introduction

<sup>32</sup> Understanding the processes that generate species' distributional limits is a foun-  
<sup>33</sup> dational objective of ecology. The niche concept is central to theory for range limits  
<sup>34</sup> (Hutchinson, 1958) and available evidence suggests that geographic distributions  
<sup>35</sup> may commonly be interpreted as ecological niches "writ large" (Lee-Yaw *et al.*,  
<sup>36</sup> 2016; Hargreaves *et al.*, 2013). Species distribution modeling has long capital-  
<sup>37</sup> ized on this idea to infer niche characteristics from statistical associations between  
<sup>38</sup> occurrence and environmental variables. In contrast, there is growing interest in  
<sup>39</sup> process-based models of range limits, where individual-level demographic responses  
<sup>40</sup> to environmental variation inform predictions about the ecological niche and envi-  
<sup>41</sup> ronmental limits of population viability (i.e., at least replacement-level population  
<sup>42</sup> growth,  $\lambda \geq 1$ ) (Merow *et al.*, 2014, 2017; Diez *et al.*, 2014). The mechanistic  
<sup>43</sup> understanding offered by process-based models of range limits provides a poten-  
<sup>44</sup> tially powerful vehicle for predicting range shifts in response to current and future  
<sup>45</sup> environmental change (Evans *et al.*, 2016; Ehrlén & Morris, 2015).

<sup>46</sup> The widespread idea that range limits reflect niche limits intersects awkwardly  
<sup>47</sup> with another pervasive concept in ecology: intra-specific niche heterogeneity. This  
<sup>48</sup> refers to the fact that individuals within a population or species may differ in  
<sup>49</sup> their interactions with the biotic and/or abiotic environment (Bolnick *et al.*, 2002;  
<sup>50</sup> Araújo *et al.*, 2011; Holt, 2009). Intra-specific niche differences may correspond  
<sup>51</sup> to demographic state variables such as life stage, size class or other, unmeasured  
<sup>52</sup> aspects of individual identity. If range limits are a geographic manifestation of  
<sup>53</sup> niche limits, but a single population or species may be comprised of many niches,  
<sup>54</sup> then whose niche is it that determines the geographic distribution and how would

55 we know?

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

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

80 and hence skew in the OSR, may be greatest. In dioecious plants, for example,  
81 populations at the upper altitudes and latitudes and in the more xeric margins of  
82 species' ranges tend to be male-biased (Field *et al.*, 2013).

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

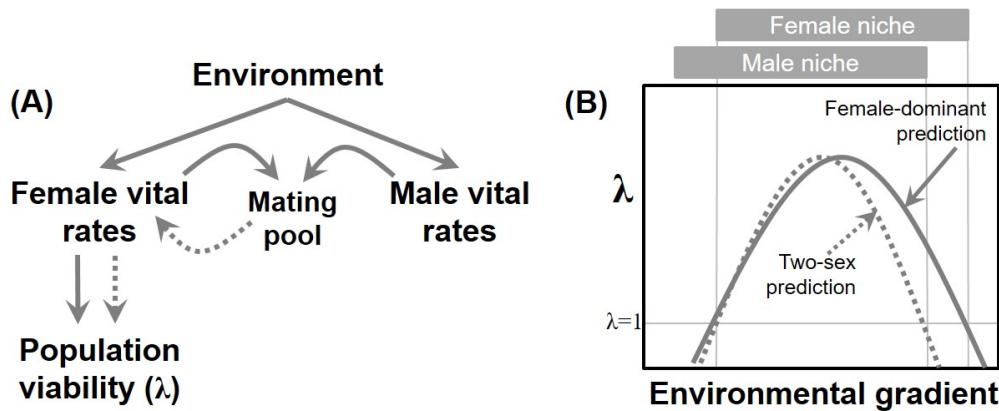


Figure 1: Hypotheses for how environmental variation can affect population viability and range limits in dieocious species. Under the female-dominant hypothesis, environmental drivers affect population growth ( $\lambda$ ) through effects on females, alone (A). In geographic / environmental space, this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

100 Here we ask whether female demographic responses to environmental variation,  
 101 alone, are sufficient to understand the ecological origins of range limits, or whether  
 102 males and female-male interactions must additionally be considered. As an experi-  
 103 mental model, we worked with a dieocious plant species (the grass *Poa arachnifera*)  
 104 narrowly distributed across the sharp longitudinal aridity gradient of the southern  
 105 Great Plains, US (Fig. 2). The environmental isocline governing aridity in this  
 106 region is expected to shift eastward under climate change (Karl *et al.*, 2009), so  
 107 understanding how it sets distributional limits may aid in forecasting future range

shifts. We hypothesized that sexual niche differentiation with respect to longitudinal variation in aridity may lead to skewed sex ratios approaching range limits, and that mate limitation at environmental extremes could cause range boundaries to deviate from female-dominant expectations.

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

## Materials and methods

### Study system and natural population surveys

*Poa arachnifera* is a perennial, cool-season (C3) grass endemic to the southern Great Plains. This species occurs almost exclusively in central Texas, Oklahoma, and southern Kansas (Fig. 2) though there are occasional records of adventive

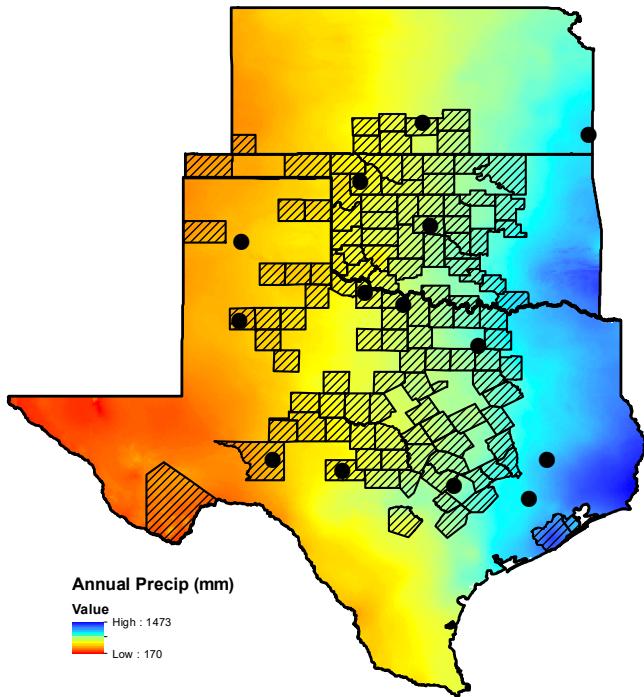


Figure 2: Geographic and environmental distribution of *P. arachnifera* in Texas, Oklahoma, and Kansas. Hatched shapes show counties with herbarium records of occurrence. Color shows geographic variation in annual precipitation (mm) based on 30-year normals from WorldClim (Fick & Hijmans, 2017). Points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

populations in other states<sup>1</sup>. Like all grasses, *P. arachnifera* is wind-pollinated. Individuals can be sexed only when flowering, in early spring, based on the presence of stigmas (females) or anthers (males) in the inflorescence. Following inflorescence and seed production, plants go dormant for the hot summer months and vegetative growth resumes in fall. Individuals grow via rhizomes to form “patches” that may be as large as  $50m^2$  in area. Sex in *P. arachnifera* is genetically based (Renganayaki *et al.*, 2001, 2005) and the primary sex ratio is 1:1 (J. Goldman, USDA-ARS, *unpubl. data*). The rhizomatous growth habit allowed us to clonally propagate

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

137 large numbers of known-sex individuals for experiments, as we describe below.

138 We surveyed *P. arachnifera* across its range to establish whether natural popu-  
139 lations exhibited geographic clines in OSR corresponding to the longitudinal aridity  
140 gradient. We visited 14 populations in spring 2012 and 8 in spring 2013 (Table  
141 A1). At each location, we searched for *P. arachnifera* along roads, trails, or creek  
142 drainages and recorded the number of female and male patches that we encoun-  
143 tered and the number of inflorescences in each patch. To quantify the mating  
144 environment, we focus our analyses on the sex ratio of inflorescences rather than  
145 patches, since a single patch makes different contributions to the mating pool  
146 depending on whether it has few or many inflorescences.

#### 147 Statistical analysis of natural population surveys

148 We fit a binomial generalized linear model (glm), where females were “successes”  
149 and total inflorescences was the number of “trials”, to test whether the OSR var-  
150 ied systematically with respect to longitude. Here and in the experiments that  
151 follow we use longitude as a proxy variable that captures all east-west environ-  
152 mental variation, notably precipitation (Fig. 2) but also factors that co-vary  
153 with precipitation such as productivity. This statistical model and all those  
154 that follow were fit in a Bayesian statistical framework using Stan (Carpenter  
155 *et al.*, 2017) and rstan (Team *et al.*, 2018) with vague priors on all parame-  
156 ters. In all cases, model fit was assessed with posterior predictive checks (Conn  
157 *et al.*, 2018). All code for statistical and demographic modeling is available at  
158 <https://github.com/texmiller/POAR-range-limits>.

<sup>159</sup> **Common garden experiment**

<sup>160</sup> **Source material and experimental design**

<sup>161</sup> We established a common garden experiment at 14 sites throughout and beyond  
<sup>162</sup> the geographic distribution of *P. arachnifera* (Fig. 2). Experimental sites spanned  
<sup>163</sup> latitudinal and longitudinal variation, though we focus here on longitude. During  
<sup>164</sup> the three years of this experiment (2014–2017), total precipitation at each site  
<sup>165</sup> closely tracked longitude (Fig. A1), as expected based on longer-term climate  
<sup>166</sup> trends (Fig. 2). Source material for the experiment came from 8 sites, which were  
<sup>167</sup> a subset of the sites that were visited for the natural population survey (Table  
<sup>168</sup> A1). At these sites, we collected vegetative tillers from flowering individuals of  
<sup>169</sup> each sex (mean: 11.6 individuals per site, range: 2–18). These were brought back  
<sup>170</sup> to the Rice University greenhouse, where they were clonally propagated in ProMix  
<sup>171</sup> potting soil and supplemented with Osmocote slow-release fertilizer at 78–80°F  
<sup>172</sup> under natural humidity and light.

<sup>173</sup> Common gardens were set up in Fall (October–December) 2014. At each site,  
<sup>174</sup> we established 14 experimental blocks, which typically corresponded to a tree or  
<sup>175</sup> woodland edge, providing partial shade that mimics this species' natural micro-  
<sup>176</sup> environment. We planted 3 females and 3 males in each block, for a total of 42  
<sup>177</sup> individuals per sex per site and 1176 total plants across sites, with all source collec-  
<sup>178</sup> tions represented at all sites. Individuals were spaced within blocks to allow space  
<sup>179</sup> for rhizomatous growth that could be clearly attributed to individual transplants.  
<sup>180</sup> To promote establishment, we cleared vegetation immediately surrounding trans-  
<sup>181</sup> plants and provided ca. 1 L of water at the time of transplanting but provided no  
<sup>182</sup> subsequent watering, fertilization, or competitor removal.

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

187 **Statistical analysis of common garden experiment**

188 We analyzed the demographic vital rates with generalized linear mixed models in  
189 a hierarchical Bayesian framework. All the vital rates shared a common linear  
190 predictor for the expected value that included fixed effects of size, sex, linear and  
191 quadratic terms for longitude, and all 2- and 3-way interactions. We included  
192 quadratic effects of longitude to account for the possibility of non-monotonic re-  
193 spondes, following the hypothesis that fitness may peak in the center of the range.  
194 The linear predictor also included random effects of site, block, and source popula-  
195 tion of the transplant. We pooled all three years of observations for analysis so we  
196 did not explicitly model temporal variation but our results are implicitly averaged  
197 over years.

198 The survival and flowering data were Bernoulli distributed, and these mod-  
199 els applied the logit link function. We modeled panicle counts as zero-truncated  
200 negative binomial using the log link. For growth, we modeled tiller number with  
201 a zero-truncated Poisson-Inverse Gaussian (PIG) distribution. For flowering and  
202 panicle production in year  $t$ , the size covariate was the natural logarithm of tiller  
203 number in year  $t$ . For survival and size in year  $t$ , the size covariate was the natural  
204 logarithm of tiller number in year  $t - 1$  (for 2015 data, size in year  $t - 1$  was  
205 transplant size at the time of planting). Posterior predictive checks indicated that  
206 these models described the data well (Fig. C1).

207 **Sex ratio experiment**

208 At one site near the center of the range (Lake Lewisville Environmental Learning  
209 Area, Texas), we established a separate experiment to quantify how sex ratio  
210 variation affects female reproductive success. Details of this experiment, which  
211 was conducted in 2014–2015, are described in Compagnoni *et al.* 2017. Briefly, we  
212 established 124 experimental populations in  $0.4m \times 0.4m$  plots that varied in popu-  
213 lation density (1–48 plants/plot) and sex ratio (0–100%female), with 2–4 replicates  
214 each of 34 density-sex ratio combinations. The experiment was established ca. 1  
215 km from a natural population at this site and plots were situated with a minimum  
216 of 15 m spacing, a buffer that was intended to limit pollen movement between  
217 plots (pilot data indicated that  $\geq 90\%$  of wind pollination occurred within 13m).  
218 We measured female reproductive success in different density and sex ratio envi-  
219 ronments by collecting panicles from a subset of females in each plot at the end  
220 of the reproductive season. In the lab, we counted the total number of seeds on  
221 each panicle and assessed seed viability in the greenhouse with germination trials  
222 of 25 seeds per panicle. We also conducted tetrazolium-based seed viability assays  
223 (17–57 seeds per panicle, mode: 30).

224 **Statistical analysis of sex ratio experiment**

225 Our previous study examined how interactions between density and frequency (sex  
226 ratio) dependence contributed to female reproductive success (Compagnoni *et al.*,  
227 2017). Here we focus solely on sex ratio variation, averaging over variation in  
228 density. Our goal was to estimate a ‘mating function’ that defines how availability  
229 of male panicles affects the viability of seeds on female panicles. We modeled the

230 seed viability data with a binomial distribution where the probability of viability  
231 ( $v$ ) was given by:

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

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

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

## 246 Demographic model of range limits

247 The statistical models for the common garden and sex ratio experiments provided  
248 the backbone of the full demographic model, a matrix projection model (MPM)  
249 structured by size (tiller number) and sex. Following the statistical modeling, the

250 MPM accommodates longitude as a predictor variable, allowing us to identify the  
 251 longitudinal limits of population viability ( $\lambda \geq 1$ ) and investigate the underlying  
 252 drivers of population decline at range limits.

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

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

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

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

265 where  $p^F$  and  $c^F$  are flowering probability and panicle production for females of  
 266 size  $x$ ,  $d$  is the number of seeds (fertilized or unfertilized) per female panicle,  $v$  is  
 267 the probability that a seed is fertilized,  $m$  is the probability that a fertilized seed  
 268 germinates, and  $\rho$  is the primary sex ratio (proportion of recruits that are female).

<sup>269</sup> Seed fertilization depends on the OSR of panicles (following Eq. 1) which was  
<sup>270</sup> derived from the  $U \times 1$  vectors of population structure  $\mathbf{F}_t$  and  $\mathbf{M}_t$ :

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

<sup>271</sup> Finally, the dynamics of the size-structured component of the population are  
<sup>272</sup> given by:

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

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

<sup>273</sup> For both females and males, the first term represents seedlings that survived their  
<sup>274</sup> first year and enter the size distribution of established plants. Because our common  
<sup>275</sup> garden experiment relied on greenhouse-raised transplants, we had little informa-  
<sup>276</sup> tion on these early life cycle transitions. We used the seedling survival probability  
<sup>277</sup> ( $\sigma$ ) from our demographic studies of the perennial congener *Poa autumnalis* in  
<sup>278</sup> east Texas (T.E.X. Miller and J.A. Rudgers, *unpublished data*) as a stand-in for *P.*  
<sup>279</sup> *arachnifera*, and we assume this probability was constant across sexes and longi-  
<sup>280</sup> tudes ( $\sigma = 0.09$ ). We also assume that surviving seedlings reach size  $y$  with prob-  
<sup>281</sup> ability  $g(y, x = 1)$ , the expected future size of 1-tiller plants from the transplant  
<sup>282</sup> experiment. The second term represents survival and size transition of established  
<sup>283</sup> plants from the previous year, where  $s$  and  $g$  give the probabilities of surviving at  
<sup>284</sup> size  $x$  and growing from sizes  $x$  to  $y$ , respectively, and superscripts indicate that

285 these functions may be unique to females ( $F$ ) and males ( $M$ ). All parameter es-  
 286 timates were derived from the statistical modeling described above, except where  
 287 noted, and are reported in Table A1<sup>2</sup>.

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

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

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

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<sup>2</sup>This table does not exist yet.

## 303 Results

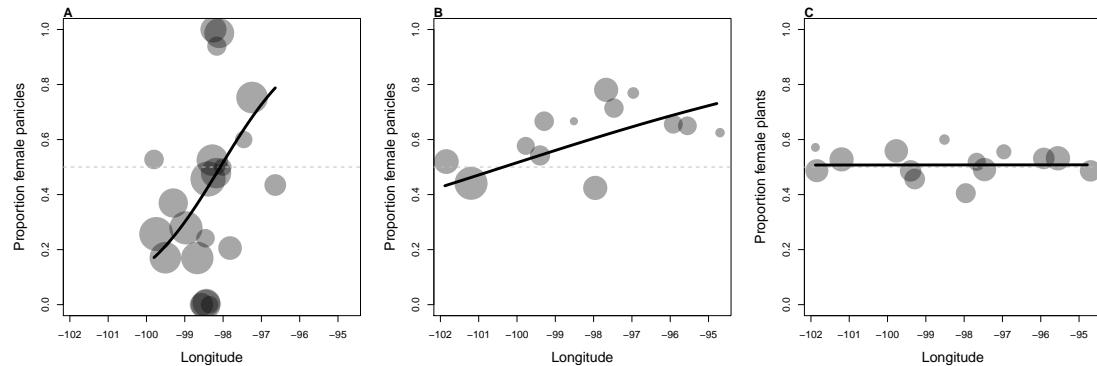


Figure 3: Sex ratio variation of *P. arachnifera* across its longitudinal distribution. **A**, Operational sex ratio (fraction of panicles that were female) in 22 natural populations; **B**, Operational sex ratio and **C**, sex ratio (fraction of plants that were female) in 14 common gardens. Within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

### 304 Sex ratio variation in natural populations

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

### 310 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

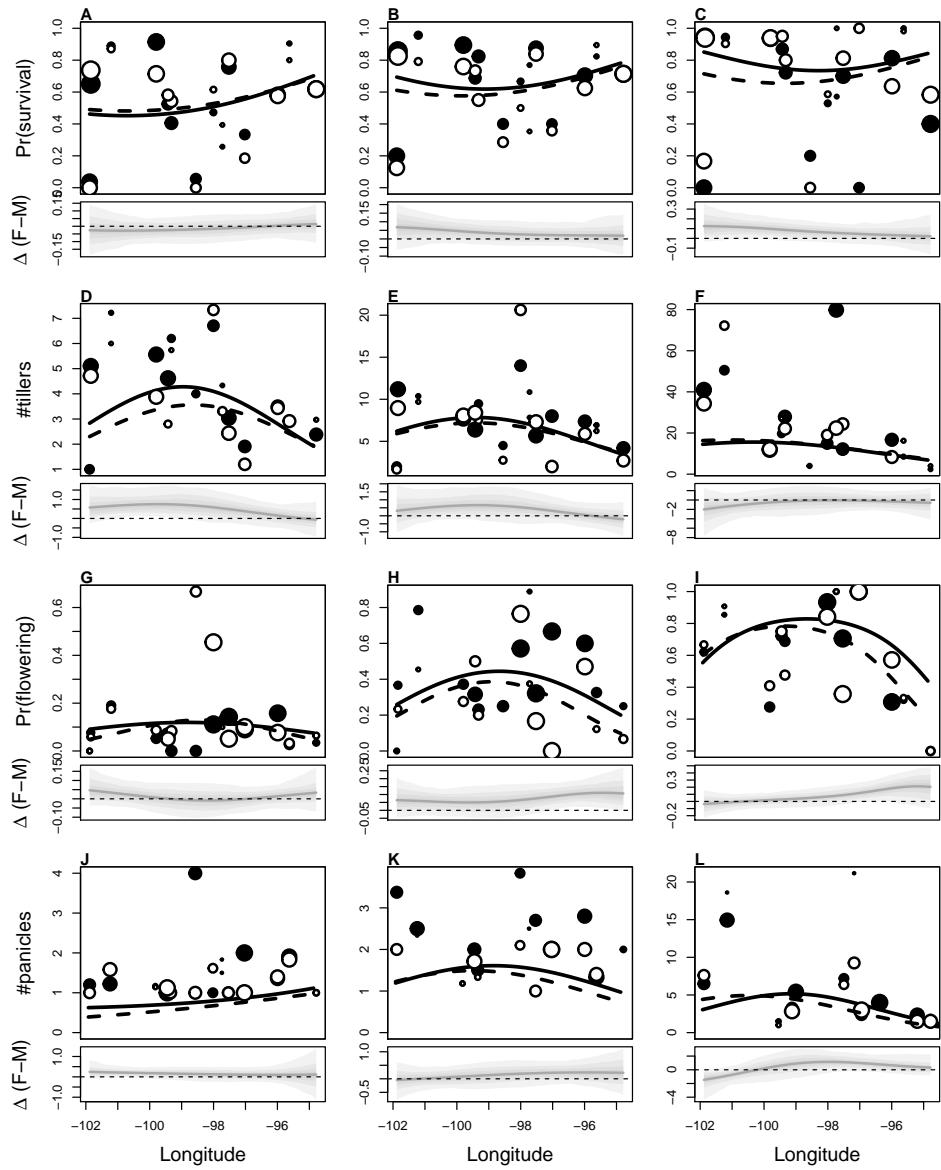


Figure 4: Sex-, size-, and longitude-related variation in: A–C, inter-annual probability of survival; D–F, inter-annual growth (change in number of tillers); G–I, probability of flowering; J–L, number of panicles produced given flowering. Points show means by site for females (filled) and males (open)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

313 pack of voles); otherwise, there was high (95%) establishment. There was strong  
314 longitudinal variation in demography, including sex-specific demographic responses  
315 that varied across vital rates and interactions between size, sex, and longitude.  
316 Where sex-specific demographic responses occurred, they were almost always in  
317 favor of females. In Fig. 4, we show binned means of raw data and fitted vital  
318 rate models for four vital rates (rows) and three size classes (columns); size was  
319 discretized for visualization only. This figure also shows the posterior distributions  
320 for the difference between the sexes across longitudes.

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

332 Sex differences in flowering and panicle production generated a longitudinal  
333 trend in the operational sex ratio of our common garden populations consistent  
334 with (but quantitatively weaker than) the trend in natural populations: the frac-  
335 tion of total panicles that were female in our common gardens increased from west  
336 to east (Fig. 3B) even as the fraction of surviving plants that were female did not  
337 show a longitudinal trend (Fig. 3C). Thus, in recapitulating the natural OSR pat-

338 tern, the common garden experiment revealed that the longitudinal trend in the  
339 mating pool of natural populations was due to the reproductive niche of females  
340 extending farther east than that of males, and not to sex differences in mortality.

### 341 **Sex-ratio dependent seed fertilization**

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

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

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

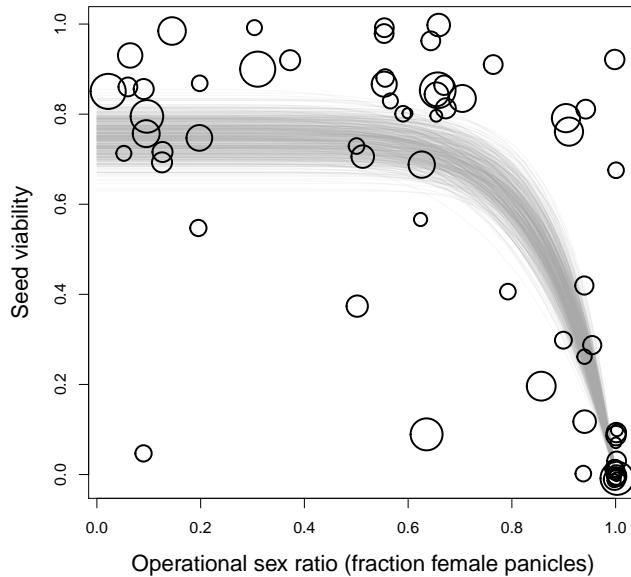


Figure 5: Seed fertilization success in relation to operational sex ratio (fraction of panicles that are female) in experimental populations. Circles show data from tetrazolium assays of seed viability; circle size is proportional to the number of seeds tested (min: 14, max: 57). Lines show model predictions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

uncertainty distribution of the model's predictions (represented by the shading in Fig. 6A), bolstering our confidence that the model effectively captured the demographic drivers of range limitation in this species. Also, the asymptotic population structure predicted by the model showed female bias in the operational (panicle) sex ratio toward the eastern range margins, consistent with observations from the common garden and natural populations (Fig. C3A). Female bias in the OSR was predicted to cause declines in seed viability toward eastern range margins (Fig. C3B). However, this effect was weak in magnitude because predicted OSR bias was not extreme enough to cause strong declines in viability, given the relation-

ship derived from the sex ratio manipulation experiment (Fig. 5). Furthermore, population viability at the eastern range margin was weakly sensitive to seed viability relative to other vital rates (C3C). These observations underscore the next set of results.

LTRE decomposition revealed that declines in  $\lambda$  approaching range limits were driven almost exclusively by females (Fig. 6B) with near-zero contributions from males (Fig. 6C). Thus, range limitation was an effectively female-dominant process, despite systematic geographic variation in sex ratio. Correspondingly, predictions of the two-sex model were nearly indistinguishable from a corresponding female-dominant model with all else equal, with only very modest differences in predictions of the two models emerging in the eastern part of the range (Fig. C2).

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

Skew in the OSR predicted by the demographic model was less extreme than was observed in natural and experimental populations (C3A). This occurred because sex differences in demography, especially flowering, were most pronounced at the largest sizes, and the MPM predicted that these sizes were very rare at stable population structure. The stable size distribution predicted by the MPM corresponded well to the common garden data (from which the MPM was built)

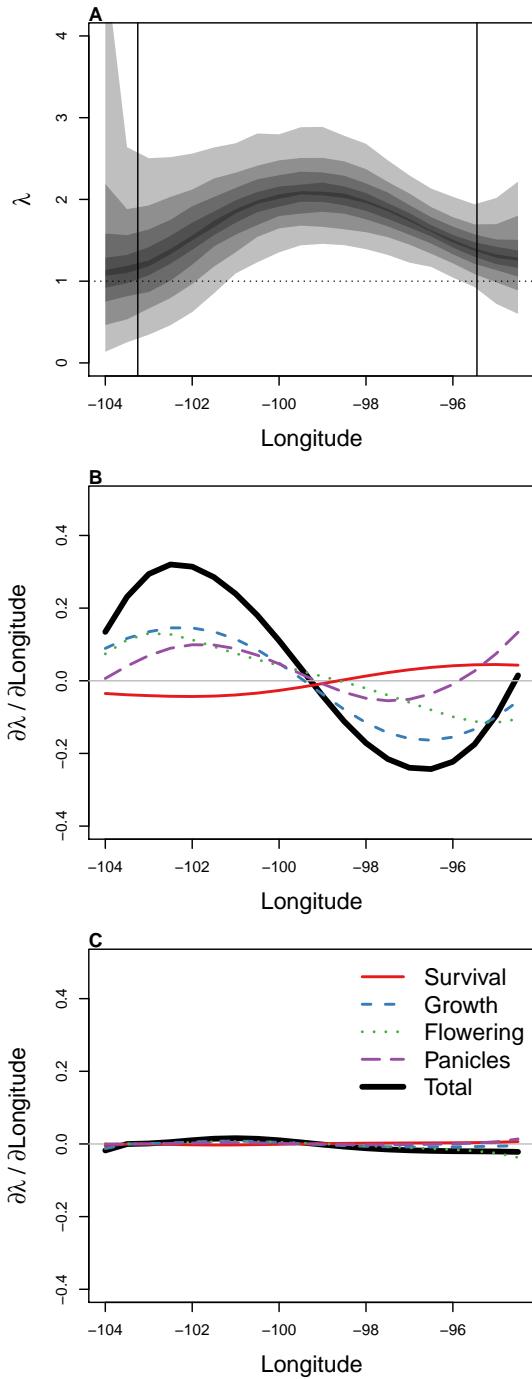


Figure 6: Population growth ( $\lambda$ ) as a function of longitude, predicted by the two-sex MPM that incorporates sex-specific demographic responses to longitude with sex ratio-dependent seed fertilization. A, posterior distribution of  $\lambda$ , where shaded regions show the 25, 50, 75, and 95%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

394 but was much smaller, on average, than the size distribution we observed in natu-  
395 ral populations (Fig. D2), presumably because transplants did not grow like “real”  
396 plants or did not have time in our three-year experiment to reach those sizes. In  
397 Appendix D, we explore whether higher growth rates, leading to a more realistic  
398 size distribution, would lead to a more important role for males. In numerical  
399 experiments with growth parameters, we found that larger size distributions led to  
400 stronger female bias and thus stronger reductions in seed viability at eastern range  
401 margins (Fig. D3). While these changes increased the contributions of males to  
402 range limitation, female contributions were still more than twice as important as  
403 males, and there was very little difference between predictions of the two-sex and  
404 female-dominant models even under this elevated growth scenario (Fig. D4). This  
405 leads us to conclude that, while our common garden-parameterized may quan-  
406 titatively underestimate OSR bias and its demographic consequences in natural  
407 population, our qualitative conclusion that range boundary formation is effectively  
408 female-dominant in this system is robust to any biases imposed by the size distri-  
409 butions of common garden populations.

## 410 Discussion

411 Understanding the causes of decline in population viability at range edges is the  
412 foundation for predicting how species’ ranges will respond to global change drivers.  
413 Sexual niche differentiation has the potential to generate skew in the mating pool  
414 across environmental gradients and may therefore contribute to reproductive fail-  
415 ure at range edges of dioecious species. In Texas bluegrass, we found evidence for  
416 sexual niche differentiation that manifested over a large-scale geographic gradi-

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

The limited role of males in our experimental system can be explained by two factors. First, seed fertilization was robust to variation in OSR and was not predicted to strongly decline within the range of OSR bias that we observed and modeled, suggesting that few males are required to pollinate all or most females. Second, population growth ( $\lambda$ ) was weakly sensitive to seed viability, which further buffered the demographic consequences of sex ratio bias. We speculate that our results should apply to other species or systems that satisfy either, but especially both, of these conditions. While there are striking examples of skewed

442 sex ratios causing declines in population growth (Milner-Gulland *et al.*, 2003) or  
443 expansion (Miller & Inouye, 2013), other examples suggest limited demographic  
444 consequences of sex ratio variation (Mysterud *et al.*, 2002; Ewen *et al.*, 2011; Gow-  
445 naris *et al.*, 2020). Ultimately, sensitivity of female reproductive success to sex  
446 ratio should depend strongly on mating system, with female dominance at the “ex-  
447 tremely polygamous” end of the continuum (Miller *et al.*, 2011). The sensitivity of  
448 population viability to female reproductive success, in turn, is likely predicted by  
449 life history strategy: in long-lived, iteroparous species population growth rates are  
450 often weakly sensitive to reproduction (Franco & Silvertown, 2004). We therefore  
451 hypothesize that range limits are more likely to be dominated by the female envi-  
452 ronmental niche in longer-lived species with more polygamous mating systems. As  
453 studies of sex ratio variation and sex-specific demography across species’ ranges  
454 accumulate in the literature (Dudaniec *et al.*, 2021; Petry *et al.*, 2016; Lynch *et al.*,  
455 2014), this hypothesis could be pursued with comparative analyses.

456 Our results suggest that in long-lived species with polygamous mating systems,  
457 range limits should reflect the niche limits of females. Polygyny implies mate  
458 limitation only at highly skewed sex ratios, and the population of long-lived species  
459 do not strongly depend on reproduction. Our polygynous model organism showed  
460 that mate limitation occurred became substantial only in populations comprised of  
461 70% females. Moreover, in long-lived species population growth rates will depend  
462 only weakly to reproduction (Franco & Silvertown, 2004). However, our results do  
463 not rule out the possibility that range limits are determined by both sexes in short-  
464 lived, polygynous species. Because short-lived species are sensitive to reproduction,  
465 mate limitation will have substantial effects on their long-term population growth  
466 rate. Mate limitation would therefore affect range limit formation when the OSR

of a short-lived species changed dramatically across environmental gradients. The literature provides several examples of short-lived species with environmentally controlled OSR (Freeman *et al.*, 1976; Freeman & Vitale, 1985; Purrington, 1993; Eppley, 2001). However, we have still no way to predict species whose OSR changes predictable across environmental gradients. We do have species-specific studies that explain the mechanisms that determine skewed OSR, such as sex differences in mortality (Meagher, 1981). However, there is no theory to predict dioecious species with environmentally controlled OSR.

However, the premises for males to contribute in range limit formation, albeit rare, are likely to occur in nature. First, female-skewed sex ratios are common both plants (Barrett *et al.*, 2010) and animals (Caswell, 2001). Second, there are several examples of plants responding in contrasting ways to environmental gradients according to sex (Bierzychudek & Eckhart, 1988). These patterns can be driven by several mechanisms, such as physiology (Dawson & Geber, 1999), differences in competitive ability (Eppley, 2006), or demographic rates (Delph, 1999). Third, mate limitation is common in both animals (Gascoigne *et al.*, 2009) and plants (Ashman *et al.*, 2004). Accordingly, in plants, pollen limitation is considered the reason why dioecious plant species tend to have a substantially smaller range than selfing species (Grossenbacher *et al.*, 2015).

Our results reinforce the commonality of demographic compensation in nature. Demographic compensation occurs when the vital rates of a species have opposing trends across an environmental gradient (Villellas *et al.*, 2015). Our results show that in *P. arachnifera*, survival tended to compensate the negative response of the remaining vital rates at latitudinal extremes. However, this compensation was not sufficient to prevent a decrease in population growth rates at the extremes

492 of the longitudinal range of the species. A recent study found a similar pattern,  
493 where compensation between vital rates could not prevent a decrease of population  
494 growth rate towards the southern range edge of *Erythranthe cardinalis* (Sheth &  
495 Angert, 2018).

496 Despite demographic compensation, our evidence is consistent with the abundant  
497 center hypothesis of range formation. This hypothesis posits that the fitness  
498 and abundance of species will gradually decrease towards range edges (Brown  
499 *et al.*, 1995). This is what our population model predicts, with maximum popu-  
500 lation growth rates at the center of the longitudinal gradient. However, to date  
501 the literature found mixed or contradictory evidence for this hypothesis. These  
502 previous tests relied on vital rates rather than population growth rates, providing  
503 contrasting results (Sexton *et al.*, 2009; Abeli *et al.*, 2014). As we show here, con-  
504 trasting results among vital rates are expected, because demographic compensation  
505 is adaptive (Villellas *et al.*, 2015). Accordingly, studies that calculate population  
506 growth rates along an environmental gradient tend to support the abundant cen-  
507 ter hypothesis. We know of four such studies in the existing literature, three of  
508 which showed a decrease in population growth rates towards at least one end of  
509 the environmental gradients (Eckhart *et al.*, 2011; Sheth & Angert, 2018; Baer &  
510 Maron, 2019). The fourth study showed population growth rate along environmen-  
511 tal gradients was unpredictable (Oldfather & Ackerly, 2019). However, this last  
512 study emphasized the importance of microclimate, which can vary dramatically  
513 in alpine environments (Scherrer & Koerner, 2010). Hence, our results suggest  
514 that the abundant center hypothesis might hold in the studies that use population  
515 growth rate as response variable.

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<sup>522</sup> **Author contributions**

<sup>523</sup> A.C. and T.E.X.M. designed the study. A.C., and T.E.X.M. carried out the study.  
<sup>524</sup> T.E.X.M. and A.C. conducted the statistical analyses and drafted the manuscript.  
<sup>525</sup> A.C. and T.E.X.M. finalized the manuscript.

<sup>526</sup> **Data accessibility**

<sup>527</sup> **References**

- <sup>528</sup> Abeli T, Gentili R, Mondoni A, Orsenigo S, Rossi G (2014) Effects of marginality  
<sup>529</sup> on plant population performance. *Journal of Biogeography*, **41**, 239–249.
- <sup>530</sup> Araújo MS, Bolnick DI, Layman CA (2011) The ecological causes of individual  
<sup>531</sup> specialisation. *Ecology letters*, **14**, 948–958.
- <sup>532</sup> Ashman TL, Knight TM, Steets JA, *et al.* (2004) Pollen limitation of plant re-  
<sup>533</sup> production: ecological and evolutionary causes and consequences. *Ecology*, **85**,  
<sup>534</sup> 2408–2421.

- 535 Baer KC, Maron JL (2019) Declining demographic performance and dispersal lim-  
536 itation influence the geographic distribution of the perennial forb *astragalus*  
537 *utahensis* (fabaceae). *Journal of Ecology*, **107**, 1250–1262.
- 538 Barrett SC, Yakimowski SB, Field DL, Pickup M (2010) Ecological genetics of sex  
539 ratios in plant populations. *Philosophical Transactions of the Royal Society B:*  
540 *Biological Sciences*, **365**, 2549–2557.
- 541 Bertiller MB, Sain CL, Bisigato AJ, Coronato FR, Aries JO, Graff P (2002) Spatial  
542 sex segregation in the dioecious grass *poa ligularis* in northern patagonia: the  
543 role of environmental patchiness. *Biodiversity & Conservation*, **11**, 69–84.
- 544 Bierzychudek P, Eckhart V (1988) Spatial segregation of the sexes of dioecious  
545 plants. *The American Naturalist*, **132**, 34–43.
- 546 Bisang I, Ehrlén J, Hedenäs L (2020) Sex expression and genotypic sex ratio vary  
547 with region and environment in the wetland moss *drepanocladus lycopodioides*.  
548 *Botanical journal of the Linnean Society*, **192**, 421–434.
- 549 Bolnick DI, Doebeli M (2003) Sexual dimorphism and adaptive speciation: two  
550 sides of the same ecological coin. *Evolution*, **57**, 2433–2449.
- 551 Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister  
552 ML (2002) The ecology of individuals: incidence and implications of individual  
553 specialization. *The American Naturalist*, **161**, 1–28.
- 554 Bowyer RT (2004) Sexual segregation in ruminants: definitions, hypotheses, and  
555 implications for conservation and management. *Journal of Mammalogy*, **85**,  
556 1039–1052.

- 557 Brown JH, Mehlman DW, Stevens GC (1995) Spatial variation in abundance.
- 558     *Ecology*, **76**, 2028–2043.
- 559 Carpenter B, Gelman A, Hoffman MD, *et al.* (2017) Stan: A probabilistic pro-
- 560     gramming language. *Journal of statistical software*, **76**.
- 561 Caruso C, Case A (2007) Sex ratio variation in gynodioecious lobelia siphilitica:
- 562     effects of population size and geographic location. *Journal of Evolutionary Bi-*
- 563     *iology*, **20**, 1396–1405.
- 564 Caswell H (2001) *Matrix Population Models*. Sinauer Associates, Inc., Sunderland,
- 565     MA, 2 edn.
- 566 Caswell H, Weeks DE (1986) Two-sex models: chaos, extinction, and other dy-
- 567     namic consequences of sex. *The American Naturalist*, **128**, 707–735.
- 568 Compagnoni A, Steigman K, Miller TE (2017) Can't live with them, can't live
- 569     without them? balancing mating and competition in two-sex populations. *Pro-*
- 570     , **284**, 20171999.
- 571 Conn PB, Johnson DS, Williams PJ, Melin SR, Hooten MB (2018) A guide to
- 572     bayesian model checking for ecologists. *Ecological Monographs*, **88**, 526–542.
- 573 Darwin C (1871) *The descent of man*. BoD–Books on Demand.
- 574 Dawson TE, Geber MA (1999) Sexual dimorphism in physiology and morphology.
- 575     In: *Gender and sexual dimorphism in flowering plants*, pp. 175–215. Springer.
- 576 De Lisle SP, Paiva S, Rowe L (2018) Habitat partitioning during character dis-
- 577     placement between the sexes. *Biology letters*, **14**, 20180124.

- 578 De Lisle SP, Rowe L (2015) Ecological character displacement between the sexes.
- 579       *The American Naturalist*, **186**, 693–707.
- 580 Delph LF (1999) Sexual dimorphism in life history. In: *Gender and sexual dimor-*
- 581       *phism in flowering plants*, pp. 149–173. Springer.
- 582 Diez JM, Giladi I, Warren R, Pulliam HR (2014) Probabilistic and spatially vari-
- 583       able niches inferred from demography. *Journal of ecology*, **102**, 544–554.
- 584 Dudaniec RY, Carey AR, Svensson EI, Hansson B, Yong CJ, Lancaster LT (2021)
- 585       Latitudinal clines in sexual selection, sexual size dimorphism, and sex-specific
- 586       genetic dispersal during a poleward range expansion. *Journal of Animal Ecology*.
- 587 Eberhart-Phillips LJ, Küpper C, Miller TE, *et al.* (2017) Sex-specific early sur-
- 588       vival drives adult sex ratio bias in snowy plovers and impacts mating system
- 589       and population growth. *Proceedings of the National Academy of Sciences*, **114**,
- 590       E5474–E5481.
- 591 Eckhart V, Geber M, Morris W, Fabio E, Tiffin P, Moeller D (2011) The geography
- 592       of demography: long-term demographic studies and species distribution models
- 593       reveal a species border limited by adaptation. *The American Naturalist*, **178**,
- 594       S26–S43.
- 595 Ehrlén J, Morris WF (2015) Predicting changes in the distribution and abundance
- 596       of species under environmental change. *Ecology Letters*, **18**, 303–314.
- 597 Eppley S (2001) Gender-specific selection during early life history stages in the
- 598       dioecious grass *distichlis spicata*. *Ecology*, **82**, 2022–2031.

- 599 Eppley SM (2006) Females make tough neighbors: sex-specific competitive effects  
600 in seedlings of a dioecious grass. *Oecologia*, **146**, 549–554.
- 601 Evans ME, Merow C, Record S, McMahon SM, Enquist BJ (2016) Towards  
602 process-based range modeling of many species. *Trends in Ecology & Evolution*,  
603 **31**, 860–871.
- 604 Ewen JG, Thorogood R, Armstrong DP (2011) Demographic consequences of adult  
605 sex ratio in a reintroduced hihi population. *Journal of Animal Ecology*, **80**, 448–  
606 455.
- 607 Fick SE, Hijmans RJ (2017) Worldclim 2: new 1-km spatial resolution climate  
608 surfaces for global land areas. *International journal of climatology*, **37**, 4302–  
609 4315.
- 610 Field DL, Pickup M, Barrett SC (2013) Ecological context and metapopulation  
611 dynamics affect sex-ratio variation among dioecious plant populations. *Annals  
612 of botany*, **111**, 917–923.
- 613 Franco M, Silvertown J (2004) A comparative demography of plants based upon  
614 elasticities of vital rates. *Ecology*, **85**, 531–538.
- 615 Freeman DC, Klikoff LG, Harper KT (1976) Differential resource utilization by  
616 the sexes of dioecious plants. *Science*, **193**, 597–599.
- 617 Freeman DC, Vitale JJ (1985) The influence of environment on the sex ratio and  
618 fitness of spinach. *Botanical Gazette*, **146**, 137–142.
- 619 Gascoigne J, Berec L, Gregory S, Courchamp F (2009) Dangerously few liaisons:  
620 a review of mate-finding allee effects. *Population Ecology*, **51**, 355–372.

- 621 Gianuca D, Votier SC, Pardo D, *et al.* (2019) Sex-specific effects of fisheries and  
622 climate on the demography of sexually dimorphic seabirds. *Journal of Animal*  
623 *Ecology*.
- 624 Gownaris NJ, García Borboroglu P, Boersma PD (2020) Sex ratio is variable and  
625 increasingly male biased at two colonies of magellanic penguins. *Ecology*, **101**,  
626 e02939.
- 627 Groen KE, Stieha CR, Crowley PH, McLetchie DN (2010) Sex-specific plant re-  
628 spondes to light intensity and canopy openness: implications for spatial segre-  
629 gation of the sexes. *Oecologia*, **162**, 561–570.
- 630 Grossenbacher D, Briscoe Runquist R, Goldberg EE, Brandvain Y (2015) Geo-  
631 graphic range size is predicted by plant mating system. *Ecology letters*, **18**,  
632 706–713.
- 633 Hargreaves AL, Samis KE, Eckert CG (2013) Are species' range limits simply niche  
634 limits writ large? a review of transplant experiments beyond the range. *The*  
635 *American Naturalist*, **183**, 157–173.
- 636 Holt RD (2009) Bringing the hutchinsonian niche into the 21st century: ecological  
637 and evolutionary perspectives. *Proceedings of the National Academy of Sciences*,  
638 **106**, 19659–19665.
- 639 Hultine KR, Bush SE, Ward JK, Dawson TE (2018) Does sexual dimorphism  
640 predispose dioecious riparian trees to sex ratio imbalances under climate change?  
641 *Oecologia*, **187**, 921–931.

- 642 Hutchinson GE (1958) Concluding remarks. In: *Cold Spring Harbour Symposium*  
643      *on Quantitative Biology*, vol. 22, pp. 415—427.
- 644 Karl TR, Melillo JM, Peterson TC, Hassol SJ (2009) *Global climate change impacts*  
645      *in the United States*. Cambridge University Press.
- 646 Ketterson ED, Nolan Jr V (1976) Geographic variation and its climatic correlates  
647      in the sex ratio of eastern-wintering dark-eyed juncos (*junco hyemalis hyemalis*).  
648      *Ecology*, **57**, 679–693.
- 649 Law CJ, Mehta RS (2018) Carnivory maintains cranial dimorphism between males  
650      and females: evidence for niche divergence in extant musteloidea. *Evolution*, **72**,  
651      1950–1961.
- 652 Lee-Yaw JA, Kharouba HM, Bontrager M, *et al.* (2016) A synthesis of transplant  
653      experiments and ecological niche models suggests that range limits are often  
654      niche limits. *Ecology letters*, **19**, 710–722.
- 655 Lynch HJ, Rhainds M, Calabrese JM, Cantrell S, Cosner C, Fagan WF (2014)  
656      How climate extremes-not means-define a species' geographic range boundary  
657      via a demographic tipping point. *Ecological Monographs*, **84**, 131–149.
- 658 Meagher TR (1981) Population biology of chameleurium luteum, a dioecious lily. ii.  
659      mechanisms governing sex ratios. *Evolution*, pp. 557–567.
- 660 Merow C, Bois ST, Allen JM, Xie Y, Silander JA (2017) Climate change both  
661      facilitates and inhibits invasive plant ranges in new england. *Proceedings of the*  
662      *National Academy of Sciences*, **114**, E3276–E3284.

- 663 Merow C, Latimer AM, Wilson AM, McMahon SM, Rebelo AG, Silander Jr JA  
664 (2014) On using integral projection models to generate demographically driven  
665 predictions of species' distributions: development and validation using sparse  
666 data. *Ecography*, **37**, 1167–1183.
- 667 Miller TE, Inouye BD (2011) Confronting two-sex demographic models with data.  
668 *Ecology*, **92**, 2141–2151.
- 669 Miller TE, Inouye BD (2013) Sex and stochasticity affect range expansion of ex-  
670 perimental invasions. *Ecology Letters*, **16**, 354–361.
- 671 Miller TE, Shaw AK, Inouye BD, Neubert MG (2011) Sex-biased dispersal and  
672 the speed of two-sex invasions. *The American Naturalist*, **177**, 549–561.
- 673 Milner-Gulland E, Bukreeva O, Coulson T, Lushchekina A, Kholodova M, Bekenov  
674 A, Grachev IA (2003) Reproductive collapse in saiga antelope harems. *Nature*,  
675 **422**, 135–135.
- 676 Mysterud A, Coulson T, Stenseth NC (2002) The role of males in the dynamics of  
677 ungulate populations. *Journal of Animal Ecology*, **71**, 907–915.
- 678 Oldfather MF, Ackerly DD (2019) Microclimate and demography interact to shape  
679 stable population dynamics across the range of an alpine plant. *New Phytologist*,  
680 **222**, 193–205.
- 681 Pekár S, Martišová M, Bilde T (2011) Intersexual trophic niche partitioning in an  
682 ant-eating spider (araneae: Zodariidae). *PloS one*, **6**, e14603.
- 683 Petry WK, Soule JD, Iler AM, Chicas-Mosier A, Inouye DW, Miller TE, Mooney

- 684 KA (2016) Sex-specific responses to climate change in plants alter population  
685 sex ratio and performance. *Science*, **353**, 69–71.
- 686 Phillips R, Silk J, Phalan B, Catry P, Croxall J (2004) Seasonal sexual segregation  
687 in two thalassarche albatross species: competitive exclusion, reproductive role  
688 specialization or foraging niche divergence? *Proceedings of the Royal Society of  
689 London. Series B: Biological Sciences*, **271**, 1283–1291.
- 690 Purrington CB (1993) Parental effects on progeny sex ratio, emergence, and flow-  
691 ering in silene latifolia (caryophyllaceae). *Journal of Ecology*, pp. 807–811.
- 692 Rankin DJ, Kokko H (2007) Do males matter? the role of males in population  
693 dynamics. *Oikos*, **116**, 335–348.
- 694 Renganayaki K, Jessup R, Burson B, Hussey M, Read J (2005) Identification of  
695 male-specific aflp markers in dioecious texas bluegrass. *Crop science*, **45**, 2529–  
696 2539.
- 697 Renganayaki K, Read J, Fritz A (2001) Genetic diversity among texas bluegrass  
698 genotypes (poa arachnifera torr.) revealed by aflp and rapd markers. *Theoretical  
699 and Applied Genetics*, **102**, 1037–1045.
- 700 Renner SS, Ricklefs RE (1995) Dioecy and its correlates in the flowering plants.  
701 *American journal of botany*, **82**, 596–606.
- 702 Rozas V, DeSoto L, Olano JM (2009) Sex-specific, age-dependent sensitivity of  
703 tree-ring growth to climate in the dioecious tree juniperus thurifera. *New Phy-  
704 tologist*, **182**, 687–697.

- 705 Scherrer D, Koerner C (2010) Infra-red thermometry of alpine landscapes challenges climatic warming projections. *Global Change Biology*, **16**, 2602–2613.
- 707 Sexton JP, McIntyre PJ, Angert AL, Rice KJ (2009) Evolution and ecology of species range limits. *Annual review of ecology, evolution, and systematics*, **40**.
- 709 Shelton AO (2010) The ecological and evolutionary drivers of female-biased sex ratios: two-sex models of perennial seagrasses. *The American Naturalist*, **175**, 710 302–315.
- 712 Sheth SN, Angert AL (2018) Demographic compensation does not rescue populations at a trailing range edge. *Proceedings of the National Academy of Sciences*, 713 **115**, 2413–2418.
- 715 Shine R (1989) Ecological causes for the evolution of sexual dimorphism: a review 716 of the evidence. *The Quarterly Review of Biology*, **64**, 419–461.
- 717 Team SD, *et al.* (2018) Rstan: the r interface to stan. r package version 2.17. 3.
- 718 Temeles EJ, Miller JS, Rifkin JL (2010) Evolution of sexual dimorphism in bill size 719 and shape of hermit hummingbirds (phaethornithinae): a role for ecological cau- 720 sation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 721 **365**, 1053–1063.
- 722 Veran S, Beissinger SR (2009) Demographic origins of skewed operational and 723 adult sex ratios: perturbation analyses of two-sex models. *Ecology Letters*, **12**, 724 129–143.
- 725 Villegas J, Doak DF, García MB, Morris WF (2015) Demographic compensation

726 among populations: what is it, how does it arise and what are its implications?  
727 *Ecology letters*, **18**, 1139–1152.

728 Wood S (2017) *Generalized Additive Models: An Introduction with R*. Chapman  
729 and Hall/CRC, 2 edn.

<sup>730</sup> **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

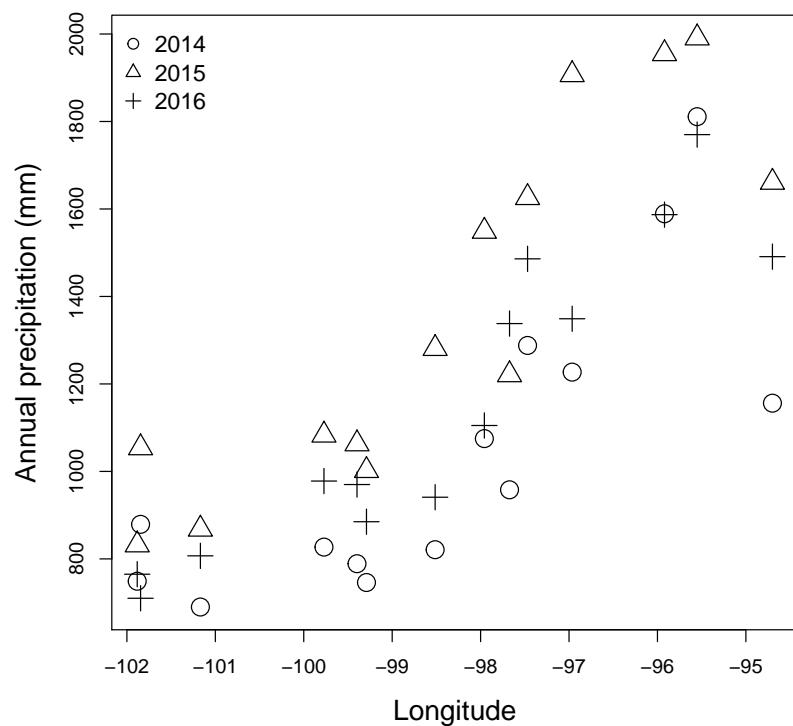


Figure A1: Total annual precipitation at common garden sites during the study years tracked long-term trends of increasing aridity from east to west.

<sup>731</sup> Appendix B: Parameter estimates of two-sex MPM

<sub>732</sub> Appendix C: Additional results

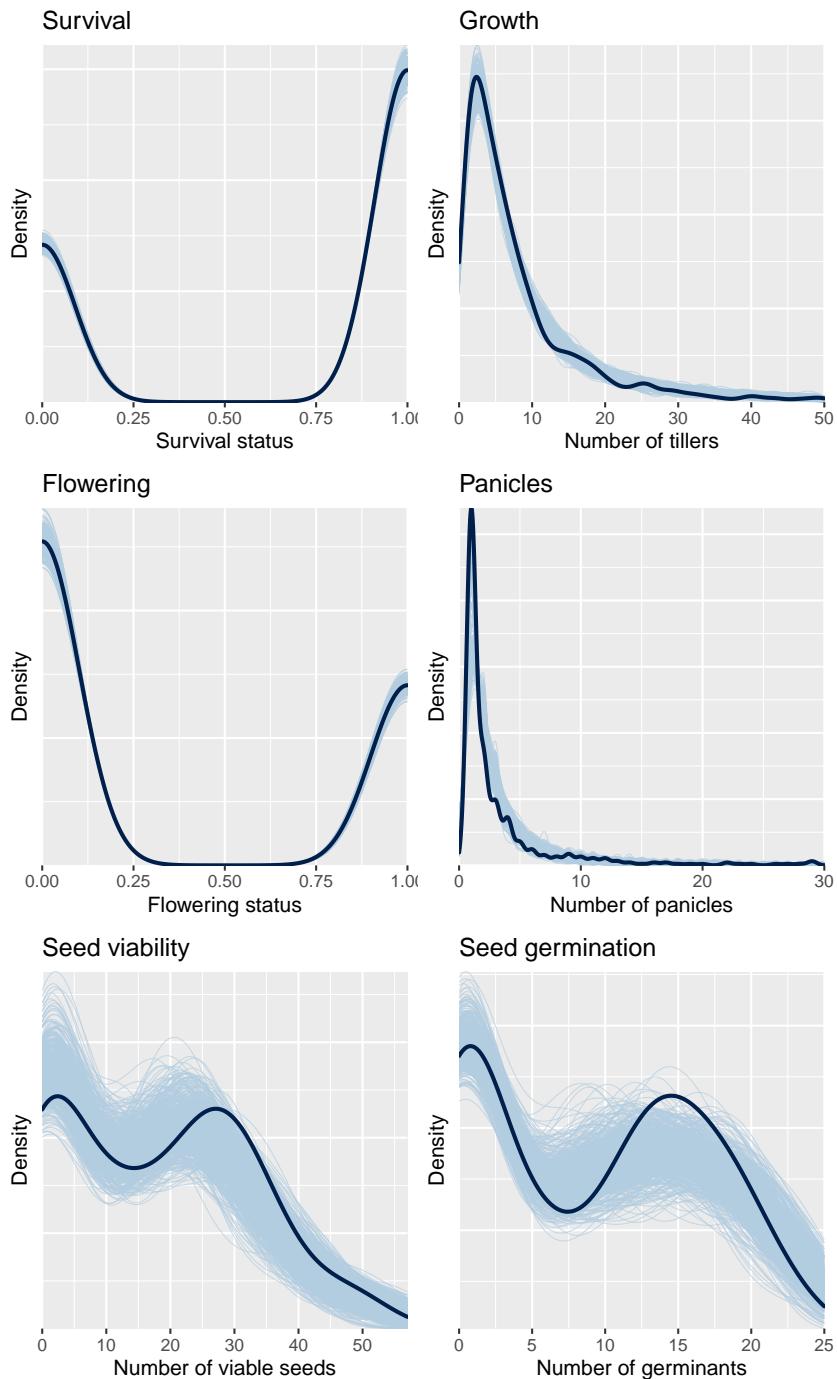


Figure C1: Posterior predictive checks of statistical models for demographic vital rates. Lines show density distributions of real data (thick, dark blue) compared to simulated data sets (thin, light blue) generated from the fitted models based on 500 draws of the posterior distribution of parameter estimates. Correspondence of the real and simulated data suggests that the fitted models describe the data well.

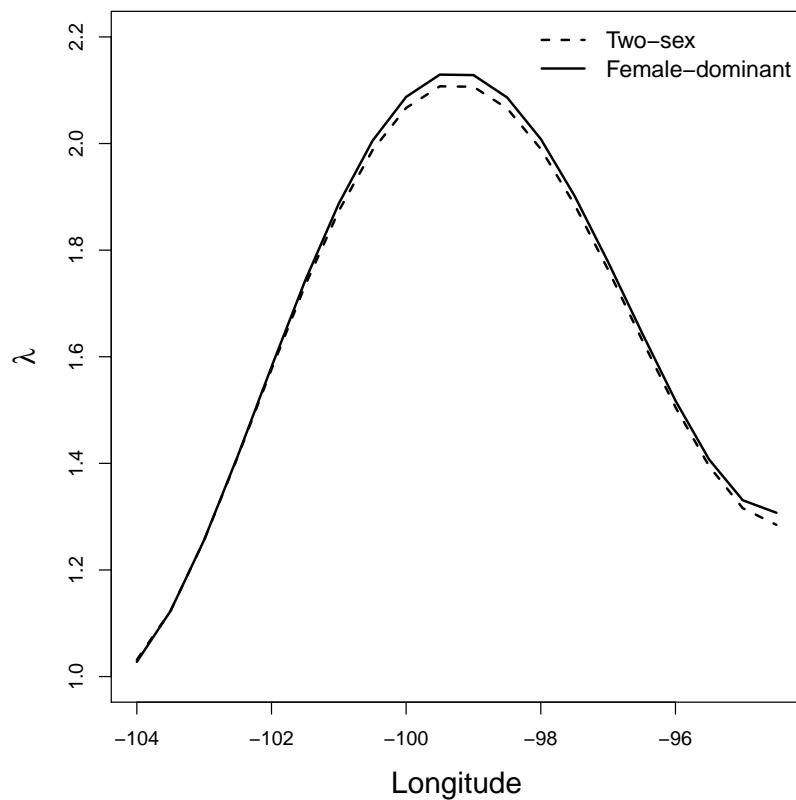


Figure C2: Comparison of longitudinal variation in  $\lambda$  between the two-sex demographic model (dashed line) that includes dependence of female seed production on population structure and the corresponding female-dominant model (solid line) with constant female fertility and all else equal. Models were evaluated at posterior mean parameter estimates

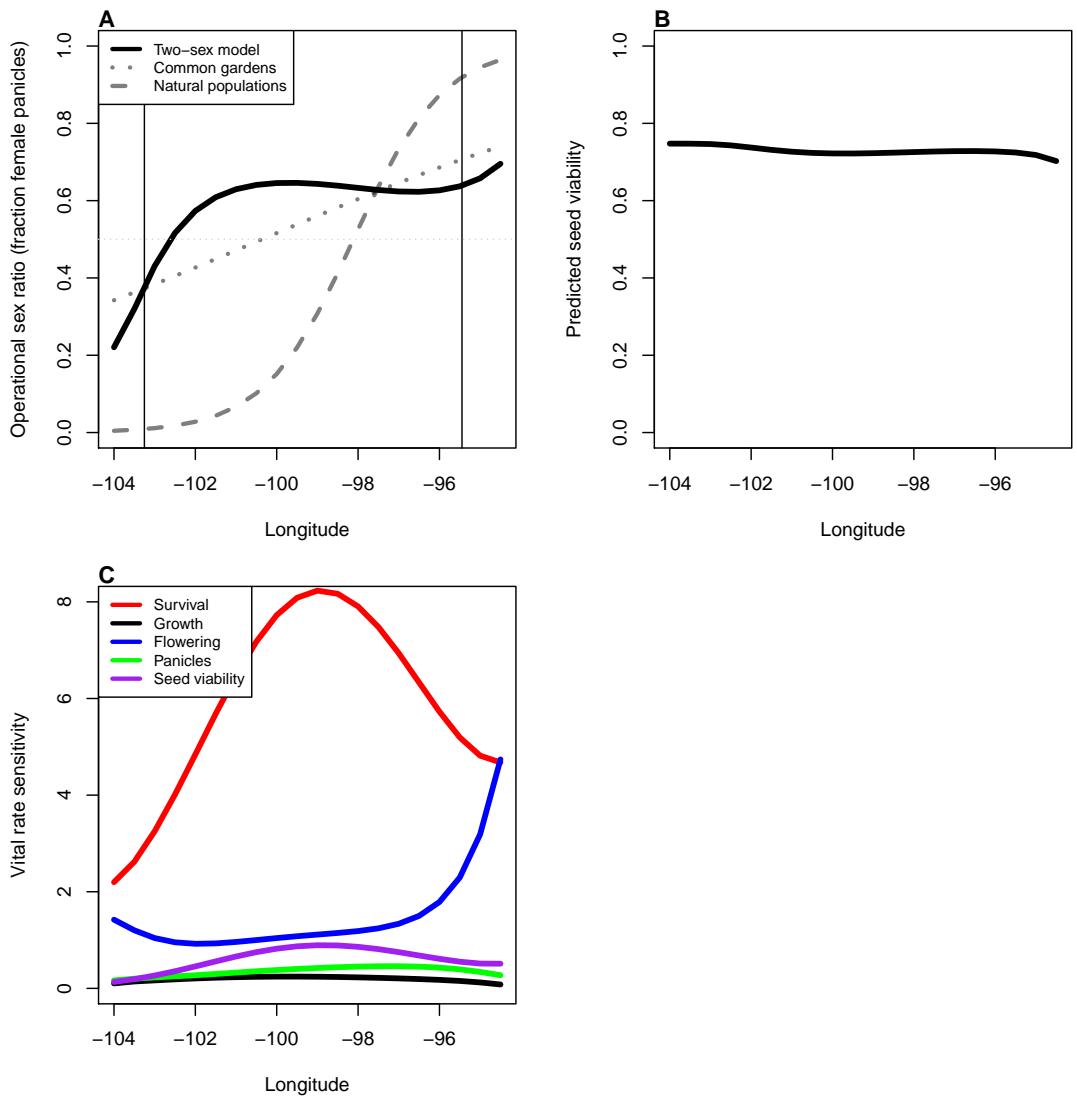


Figure C3: **A**, Longitudinal variation in operational sex ratio (fraction of panicles that are female) predicted by the two-sex MPM (solid line) compared to the sex ratio clines fitted to data from common gardens (dotted line) or natural populations (dashed line). Vertical lines show the longitudes 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.

733 **Appendix D: Size distribution comparisons and sim-**

734 **ulation experiments**

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

738 **Observed and predicted size distributions**

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

742 **Common garden populations** Common garden data collection included tiller  
743 counts and the maximum length and width of each patch, which we converted to  
744 area ( $m^2$ ) assuming an oval shape. We used these data to estimate the relationship  
745 between patch area and tiller count (Fig. D1) using a generalized additive model  
746 (Wood, 2017) and applied this fitted relationship to area measurements from nat-  
747 ural populations. This allowed us to compare the size distributions of natural  
748 and common garden populations (pooled across the range) in the same size unit  
749 ( $\log(\text{tillers})$ ).

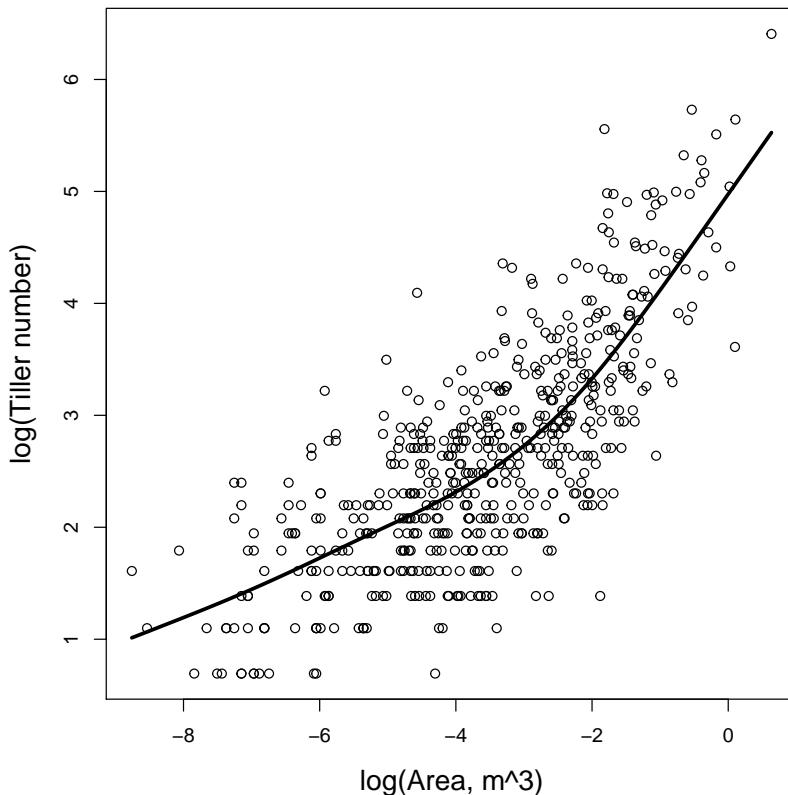


Figure D1: Relationship between area ( $m^3$ ) and tiller count from plants in the common garden experiment. The fitted gam model (line) was used to convert area measurements from natural populations to tiller counts.

750 **Two-sex MPM** The two-sex MPM predicts asymptotic population structure,  
 751 including stable size distribution (SSD) and sex ratio. For comparison with em-  
 752 pirical data, we calculated the SSD (pooling both sexes) predicted in the center of  
 753 the range (the conclusions that we draw from this analysis hold up if we consider  
 754 SSD from different parts of the range). Because the MPM is structured by tiller  
 755 number, we converted the SSD to  $\log(\text{tillers})$  by simulating an arbitrarily large  
 756 (10000) population at SSD, taking the natural logarithm of tiller number, and  
 757 then estimating the empirical distribution of this variable.

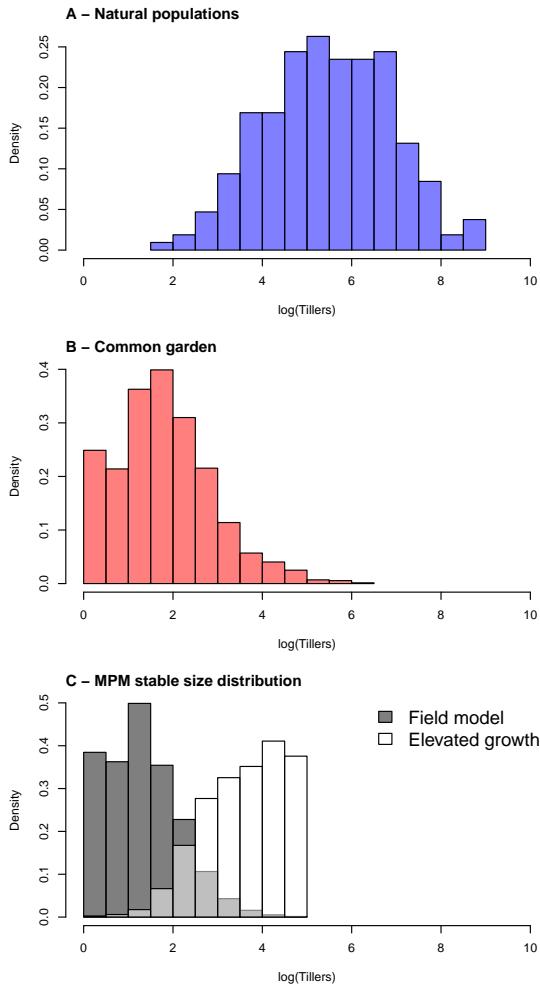


Figure D2: Size distribution of Texas bluegrass from natural populations (A), common garden populations (B), and predicted by the two-sex MPM (C). In C, the two size distributions come from the base model parameterized following methods described in the main manuscript (gray) and a numerical experiment where growth parameters were numerically increased to generate a size distribution more consistent with natural populations (white).

758 **Results** Plants from natural populations were larger, on average, than plants  
 759 in our common garden experiment (Fig. D2A,B). Common garden plants were  
 760 generally larger each year but the largest sizes in the final year of the common

761 garden corresponded to smaller sizes observed in natural populations (although  
762 natural population surveys were subject to detection bias: small plants were likely  
763 under-sampled relative to their occurrence). The predicted SSD from the two-  
764 sex MPM was consistent with the common garden size distribution (Fig. D2C),  
765 as expected since the model was built with common garden data. These results  
766 suggest that common garden plants did not have the same growth trajectories of  
767 naturally occurring plants and / or were not given sufficient time to reach the sizes  
768 observed in natural populations.

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

771 The preceding results indicate that the common garden populations, and thus the  
772 two-sex MPM built from common garden data, under-estimate the size distribution  
773 of Texas bluegrass, relative to what we find in natural populations. Sex differences  
774 in demography, and especially flowering, were most pronounced for the largest sizes  
775 (Fig. 4), but these sizes were predicted to be very rare in a stable population (Fig.  
776 D2C). The under-estimation of large sizes may explain why longitudinal clines in  
777 OSR predicted by the MPM and seen in the common garden were weaker than the  
778 OSR cline observed in natural populations (Fig. C3). It is therefore possible that  
779 our main finding – that males contribute little-to-nothing toward range limitation  
780 – reflects a limitation of the model, since real populations tended to be more  
781 female-biased (and potentially more mate-limited) in the eastern range margins  
782 than the model predicted. To explore this possibility, we conducted a numerical  
783 experiment that allowed modeled plants to reach larger sizes by increasing the

784 empirically-estimated intercept of the growth vital rate function by a factor of 2.75  
785 (values larger than this caused numerical instabilities). This adjustment caused all  
786 plants to increase in size more strongly regardless of initial size, sex, or geographic  
787 location.

788 As expected, this led to stronger sex ratio clines and stronger reductions in  
789 seed viability at eastern range margins (Fig. D3). These changes increased the  
790 contributions of males to eastern range limitation in the elevated-growth numerical  
791 experiment. However, the contribution of males to range limitation was still weak  
792 relative to that of females (the maximum male contribution was less than half of  
793 the female maximum) and differences between the two-sex and female-dominant  
794 MPMs were still very minor (Fig. D4). Collectively, these results suggest that the  
795 small size distribution of the common garden experiment led to a weaker role of  
796 males than would be expected in populations with a more realistic size distribution,  
797 but that even with a larger size distribution, declines in female performance still  
798 dominate range boundary formation.

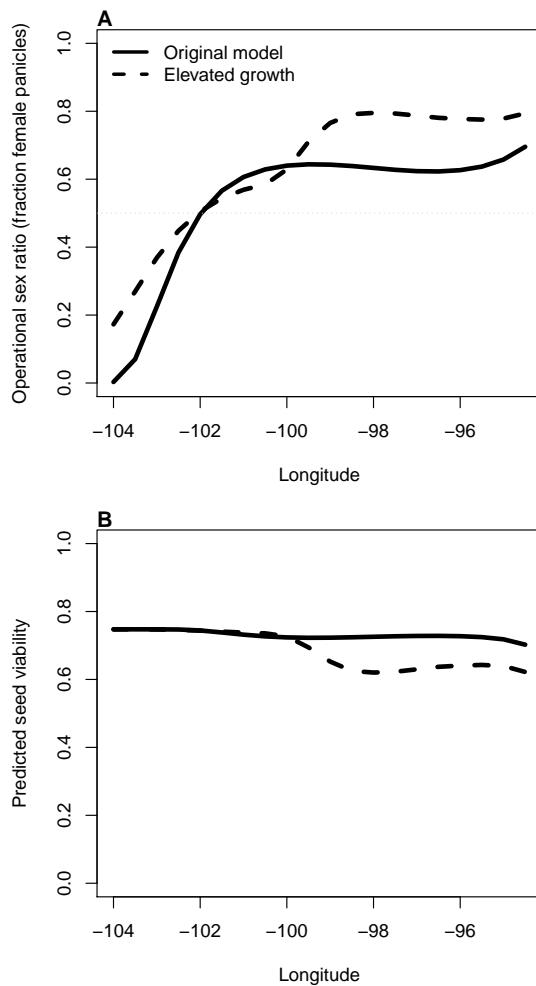


Figure D3: Two-sex model predictions for **A** operational sex ratio (fraction of panicles that are female) and **B** seed viability at stable population structure in relation to longitude. Solid line shows predictions of the base model using field-estimated parameter values and dashed line shows the same model with elevated growth of both sexes and across all longitudes (intercept of growth function increased by a factor of 2.75).

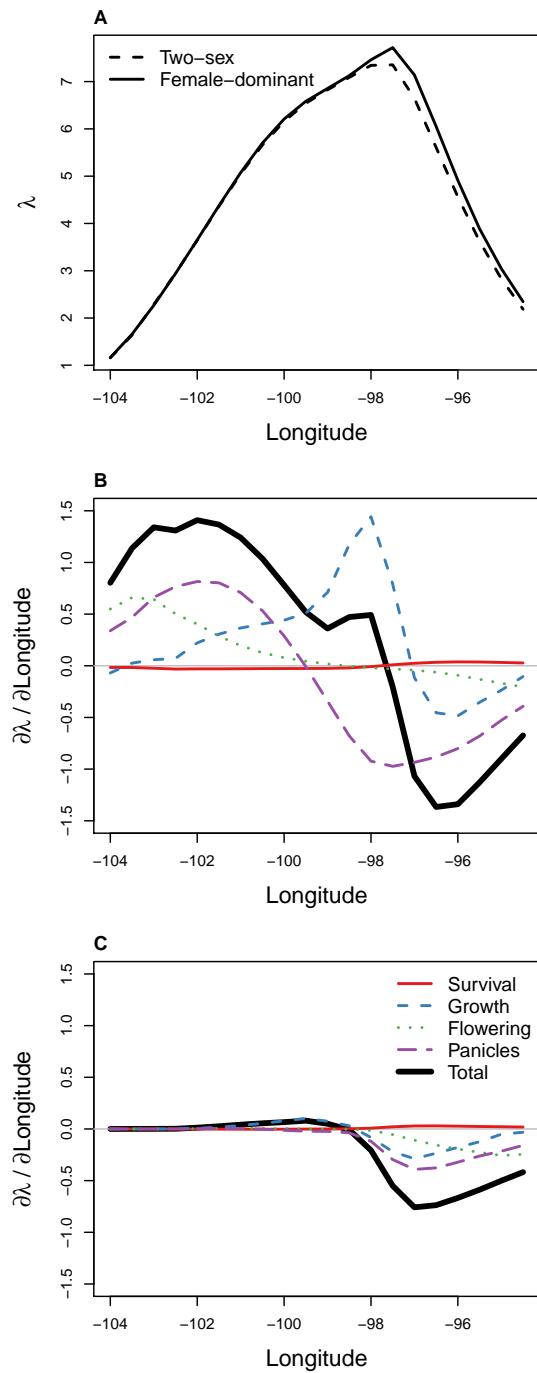


Figure D4: Results for the elevated growth model, in which the intercept of growth function was increased by a factor of 2.75. **A**, contrast of two-sex and female-dominant models, as in Fig. C2; **B,C**, Life Table Response Experiments decomposing the change in  $\lambda$  with respect to longitude into contributions from female **B** and male **C** vital rates (layout as in Fig. 6).