

Two-sex demography, sexual niche differentiation,  
and the formation of range limits over an  
environmental gradient

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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 the  
6 sexes in their limits of environmental suitability. We studied the mechanisms of  
7 range boundary formation in the perennial dioecious grass *Poa arachnifera*, test-  
8 ing the alternative hypotheses that range limits reflect the niche limits of females  
9 only, as assumed by classic ecological theory, versus the combined contributions of  
10 females and males, including their inter-dependence via male-limitation of female  
11 fertility. Common garden experiments across the longitudinal aridity gradient of  
12 the southern Great Plains, US revealed female-biased flowering and panicle pro-  
13 duction approaching eastern range limits, consistent with surveys of operational  
14 sex ratio variation in natural populations. A process-based demographic model  
15 predicted longitudinal limits of population viability ( $\lambda \geq 1$ ) that matched the  
16 observed eastern and western range limits, and further showed that declines in  $\lambda$   
17 approaching range limits were driven almost entirely by declines in female vital  
18 rates. Thus, despite the potential for mate limitation particularly at eastern mar-  
19 gins, the geographic distribution was effectively female-dominant, reflecting the  
20 environmental niche of females with little contribution from males. The dominant  
21 role of females was attributable to female fertility being quite robust to sex ratio  
22 variation (which declined only at extreme under-representation of males) and to  
23 relatively low sensitivity of  $\lambda$  to reproductive transitions in the life cycle. This sug-

<sup>24</sup> gests that female-dominant limitation of geographic distribution may be common  
<sup>25</sup> to long-lived species with polygamous mating systems.

<sup>26</sup> **Keywords**

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

## <sup>29</sup> Introduction

<sup>30</sup> Understanding the processes that generate species' distributional limits is a foun-  
<sup>31</sup> dational objective of ecology. The niche concept is central to theory for range limits  
<sup>32</sup> (Hutchinson, 1958) and available evidence suggests that geographic distributions  
<sup>33</sup> may commonly be interpreted as ecological niches "writ large" (Lee-Yaw *et al.*,  
<sup>34</sup> 2016; Hargreaves *et al.*, 2013). Species distribution modeling has long capital-  
<sup>35</sup> ized on this idea to infer niche characteristics from statistical associations between  
<sup>36</sup> occurrence and environmental variables. In contrast, there is growing interest in  
<sup>37</sup> process-based models of range limits, where individual-level demographic responses  
<sup>38</sup> to environmental variation inform predictions about the ecological niche and envi-  
<sup>39</sup> ronmental limits of population viability (i.e., at least replacement-level population  
<sup>40</sup> growth,  $\lambda \geq 1$ ) (Merow *et al.*, 2014, 2017; Diez *et al.*, 2014). The mechanistic  
<sup>41</sup> understanding offered by process-based models of range limits provides a poten-  
<sup>42</sup> tially powerful vehicle for predicting range shifts in response to current and future  
<sup>43</sup> environmental change (Evans *et al.*, 2016; Ehrlén & Morris, 2015).

<sup>44</sup> The widespread idea that range limits reflect niche limits intersects awkwardly  
<sup>45</sup> with another pervasive concept in ecology: intra-specific niche heterogeneity. This  
<sup>46</sup> refers to the fact that individuals within a population or species may differ in  
<sup>47</sup> their interactions with the biotic and/or abiotic environment (Bolnick *et al.*, 2002;  
<sup>48</sup> Araújo *et al.*, 2011; Holt, 2009). Intra-specific niche differences may be based on  
<sup>49</sup> demographic state variables such as life stage, size class or other, unmeasured  
<sup>50</sup> aspects of individual identity. If range limits are a geographic manifestation of  
<sup>51</sup> niche limits, but a single population or species may be comprised of many niches,  
<sup>52</sup> then whose niche is it that determines the geographic distribution and how would

<sup>53</sup> we know?

<sup>54</sup> 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  
<sup>55</sup> majority of which are dioecious) and plants (ca. 6% of angiosperms are dioecious:  
<sup>56</sup> Renner & Ricklefs 1995). The prevalence of sexual niche differentiation was rec-  
<sup>57</sup> ognized by Darwin (1871), who described “different habits of life, not related...to  
<sup>58</sup> the reproductive functions” of females and males. There are now numerous ex-  
<sup>59</sup> amples of sex differences in trophic position (Pekár *et al.*, 2011; Law & Mehta,  
<sup>60</sup> 2018), habitat use (Bowyer, 2004; Phillips *et al.*, 2004), and responses to climate  
<sup>61</sup> (Petry *et al.*, 2016; Rozas *et al.*, 2009; Gianuca *et al.*, 2019), differences that may  
<sup>62</sup> or may not be accompanied by sexual dimorphism. It has been hypothesized that  
<sup>63</sup> sex-specific niches may evolve by natural selection when it reduces competitive or  
<sup>64</sup> other antagonistic interactions between the sexes (Bierzychudek & Eckhart, 1988;  
<sup>65</sup> Bolnick & Doebeli, 2003) or as a byproduct of naturally or sexually selected size  
<sup>66</sup> dimorphism (Shine, 1989; Temeles *et al.*, 2010).

<sup>68</sup> Sexual niche differentiation can translate to sex-specific advantages in different  
<sup>69</sup> environments, causing skew in the operational sex ratio (OSR: relative abundance  
<sup>70</sup> of females and males available for mating) even if the primary (birth) sex ratio is  
<sup>71</sup> unbiased (Veran & Beissinger, 2009; Shelton, 2010; Eberhart-Phillips *et al.*, 2017).  
<sup>72</sup> Indeed, environmental clines in OSR have been widely documented in plants and  
<sup>73</sup> animals at fine spatial scales (Eppley, 2001; Bertiller *et al.*, 2002; Groen *et al.*,  
<sup>74</sup> 2010) as well as broader climatic clines across alititudtes or latitudes (Petry *et al.*,  
<sup>75</sup> 2016; Ketterson & Nolan Jr, 1976; Caruso & Case, 2007). At range margins,  
<sup>76</sup> where environments are extreme relative to the range core, demographic differences  
<sup>77</sup> between the sexes, and hence skew in the OSR, may be greatest. In dioecious

<sup>78</sup> plants, for example, populations at the upper altitudes and latitudes and in the  
<sup>79</sup> more xeric margins of species' ranges tend to be male-biased (Field *et al.*, 2013).

<sup>80</sup> Returning to the question of whose niche determines range limits given po-  
<sup>81</sup> tential for sexual niche differentiation, classic ecological theory assumes answer.  
<sup>82</sup> "Female dominance" is a pervasive, often implicit feature of population-dynamic  
<sup>83</sup> models whereby male availability is assumed to have no influence on female fer-  
<sup>84</sup> tility (Miller & Inouye, 2011; Rankin & Kokko, 2007; Caswell & Weeks, 1986).  
<sup>85</sup> This assumption is, of course, wrong but it may often be a convenient approx-  
<sup>86</sup> imation when the sex ratio is balanced or does not vary. The female-dominant  
<sup>87</sup> perspective predicts that female responses to environmental variation should gov-  
<sup>88</sup> ern range limits (Fig. 1). However, females may be male-limited in environments  
<sup>89</sup> in which they are favored, which could reduce population viability in marginal  
<sup>90</sup> environments. This creates an additional, "two-sex" pathway by which environ-  
<sup>91</sup> mental drivers may set distributional limits, via perturbations to the mating pool  
<sup>92</sup> that arise from sex-specific responses to the environment (Fig. 1). While sexual  
<sup>93</sup> niche divergence sets the stage for two-sex dynamics to play an important role in  
<sup>94</sup> marginal environments, this influence may be dampened in mating systems where  
<sup>95</sup> single males can fertilize many females (Miller *et al.*, 2011) or in life histories where  
<sup>96</sup> population viability is weakly sensitive to female fertility (Franco & Silvertown,  
<sup>97</sup> 2004).

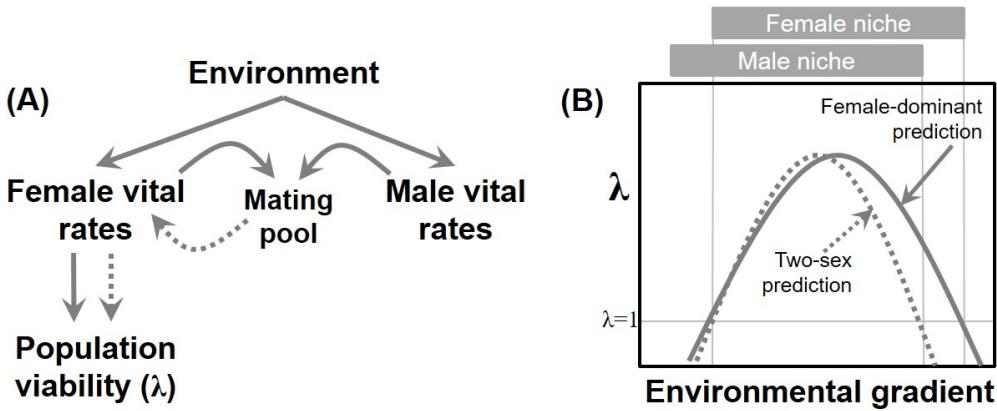


Figure 1: Hypotheses for how environmental variation can affect population viability and range limits in dieocious species. Under the female-dominant hypothesis, environmental drivers affect population growth ( $\lambda$ ) through effects on females, alone (A). In geographic / environmental space, this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

98 Here we ask, for the first time, whether female demographic responses to en-  
 99 vironmental variation, alone, are sufficient to understand the ecological origins of  
 100 range limits, or whether the additional role of males determines range boundary  
 101 formation. As an experimental model, we worked with a dieocious plant species  
 102 (the grass *Poa arachnifera*) narrowly distributed across the sharp longitudinal arid-  
 103 ity gradient in the southern Great Plains, US (Fig. 2). The environmental isocline  
 104 governing aridity in this region is expected to shift eastward under climate change  
 105 (Karl *et al.*, 2009), so understanding how it sets distributional limits may aid in

106 forecasting range future shifts. We hypothesized that sexual niche differentiation  
107 with respect to longitudinal variation in aridity may lead to skewed sex ratios ap-  
108 proaching range limits, and that mate limitation could cause range boundaries to  
109 deviate from female-dominant expectations.

110 This study was conducted in four parts. First, we conducted surveys to ask  
111 whether natural populations exhibit clines in operational sex ratio across longi-  
112 tudinal environmental variation. Second, we conducted a common garden exper-  
113 iment at 14 sites throughout the southern Great Plains to quantify sex-specific  
114 demography in variable abiotic environments. Third, we conducted a local sex  
115 ratio manipulation experiment to quantify how viable seed production by females  
116 responds to variation in sex ratio. Finally, we connected sex-specific demogra-  
117 phy with inter-sexual mating dynamics in a two-sex modeling framework to derive  
118 demographically-driven predictions for geographic limits of population viability  
119  $\lambda \geq 1$ . We analyzed the demographic model to decompose the decline in  $\lambda$  ap-  
120 proaching range limits into contributions from female-dominant and two-sex path-  
121 ways (Fig. 1).

## 122 Materials and methods

### 123 Study system and natural population surveys

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

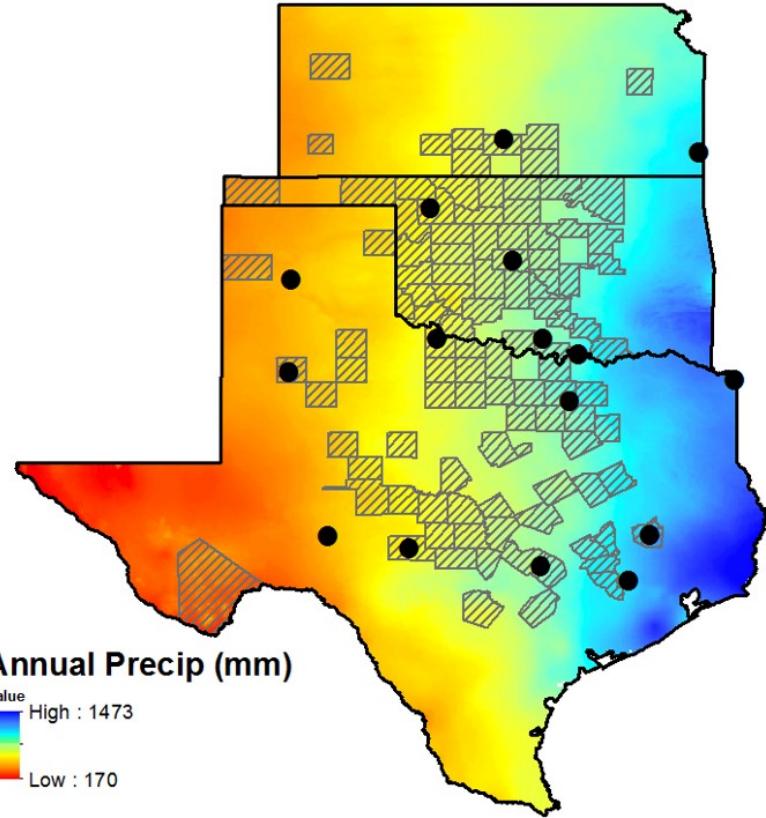


Figure 2: Geographic and environmental distribution of *P. arachnifera* in Texas, Oklahoma, and Kansas. Hatched shapes show counties with herbarium records of occurrence. Color shows geographic variation in annual precipitation (mm) based on 30-year normals from WorldClim (Fick & Hijmans, 2017). Points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

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

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

132 large as  $50m^2$  in area. Sex in *P. arachnifera* is genetically based (Renganayaki  
133 *et al.*, 2001, 2005) and the primary sex ratio is 1:1 (J. Goldman, USDA-ARS,  
134 *personal communication*). The rhizomatous growth habit allowed us to clonally  
135 propagate large numbers of known-sex individuals for experiments, as we describe  
136 below.

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

#### 146 Statistical analysis of natural population surveys

147 We fit a binomial generalized linear model (glm), where females were “successes”  
148 and total inflorescences was the number of “trials”, to test whether the opera-  
149 tional sex ratio varied systematically with respect to longitude. Here and in the  
150 experiments that follow we use longitude as a proxy variable that captures all  
151 east-west environmental variation, notably precipitation (Fig. 2) but also fac-  
152 tors that co-vary with precipitation such as productivity. This statistical model  
153 and all those that follow were fit in a Bayesian statistical framework using Stan  
154 (Carpenter *et al.*, 2017) and rstan (Team *et al.*, 2018) with vague priors on all  
155 parameters. In all cases, model fit was assessed with posterior predictive checks

<sup>156</sup> (Conn *et al.*, 2018). All code for statistical and demographic modeling is available  
<sup>157</sup> at <https://github.com/texmiller/POAR-range-limits>.

## <sup>158</sup> Common garden experiment

### <sup>159</sup> Source material and experimental design

<sup>160</sup> We established a common garden experiment at 14 sites throughout and beyond  
<sup>161</sup> the geographic distribution of *P. arachnifera* (Fig. 2). Experimental sites spanned  
<sup>162</sup> latitudinal and longitudinal variation, though we focus here on longitude. During  
<sup>163</sup> the three years of this experiment, total precipitation at each site closely tracked  
<sup>164</sup> longitude (Fig. A1), as expected based on longer-term climate trends (Fig. 2).  
<sup>165</sup> Source material for this experiment came from 8 sites, which were of subset of the  
<sup>166</sup> sites that were visited for the natural population survey (Table A1). At these sites,  
<sup>167</sup> we collected tillers from flowering individuals of each sex (mean: 11.6 individuals  
<sup>168</sup> per site, range: 2–18). These were brought back to the Rice University greenhouse,  
<sup>169</sup> where they were clonally propagated in ProMix potting soil and supplemental  
<sup>170</sup> Osmocote fertilizer at 78–80°F under natural humidity and light.

<sup>171</sup> Common gardens were set up in Fall (October–December) 2014. At each site,  
<sup>172</sup> we established 14 experimental blocks, which typically corresponded to a tree or  
<sup>173</sup> woodland edge, providing partial shade that mimics this species' natural micro-  
<sup>174</sup> environment. We planted 3 females and 3 males in each block, for a total of 42  
<sup>175</sup> individuals per sex per site and 1176 total plants across sites, with all source collec-  
<sup>176</sup> tions represented at all sites. Individuals were spaced within blocks to allow space  
<sup>177</sup> for rhizomatous growth that could be clearly attributed to individual transplants.  
<sup>178</sup> To promote establishment, we cleared vegetation immediately surrounding trans-

179 plants and provided ca. 1 L of water at the time of transplanting but provided no  
180 subsequent watering, fertilization, or competitor removal.

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

### 185 Statistical analysis of common garden experiment

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

196 The survival and flowering data were Bernoulli distributed, and these models  
197 applied the logit link function. We modeled panicle counts as zero-truncated nega-  
198 tive binomial using the log link. For growth, we modeled tiller number in year  $t + 1$   
199 with a zero-truncated Poisson-Inverse Gaussian (PIG) distribution. For flowering  
200 and panicle production in year  $t$ , the size covariate was the natural logarithm of  
201 tiller number in year  $t$ . For survival and size in year  $t$ , the size covariate was the  
202 natural logarithm of tiller number in year  $t - 1$  (for 2015 data, size in year  $t - 1$

203 was transplant size at the time of planting). Posterior predictive checks indicated  
204 that these models described the data well (Fig. B1).

205 **Sex ratio experiment**

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

222 **Statistical analysis of sex ratio experiment**

223 Our previous study examined how interactions between density and frequency (sex  
224 ratio) dependence contributed to female reproductive success (Compagnoni *et al.*,

225 2017). Here we focus solely on sex ratio variation, averaging over variation in  
226 density. Our goal was to estimate a ‘mating function’ that defines how availability  
227 of male panicles affects the viability of seeds on female panicles. We modeled the  
228 seed viability data with a binomial distribution where the probability of viability  
229 ( $v$ ) was given by:

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

230 where  $OSR$  is the operational sex ratio (fraction of panicles that were female) in  
231 our experimental populations. This function has the properties, supported by our  
232 previous work, that seed viability is maximized at  $v_0$  as  $OSR$  approaches zero and  
233 goes to zero as  $OSR$  approaches 1. Parameter  $\alpha$  controls how viability declines  
234 with increasing female bias.

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

<sup>243</sup> **Demographic model of range limits**

<sup>244</sup> The statistical models for the common garden and sex ratio experiments provided  
<sup>245</sup> the backbone of the full demographic model, a matrix projection model (MPM)  
<sup>246</sup> structured by size (tiller number) and sex. Following the statistical modeling, the  
<sup>247</sup> MPM accommodates longitude as a predictor variable, allowing us to identify the  
<sup>248</sup> longitudinal limits of population viability ( $\lambda \geq 1$ ) and investigate the underlying  
<sup>249</sup> drivers of population decline at range limits.

<sup>250</sup> For a given longitude, let  $F_{x,t}$  and  $M_{x,t}$  be the number of female and male  
<sup>251</sup> plants of size  $x$  in year  $t$ , where  $x \in \{1, 2, \dots, U\}$  and  $U$  is the maximum number  
<sup>252</sup> of tillers a plant can attain (assumed to be the same for females and males). We  
<sup>253</sup> also include additional state variables for new recruits,  $F_t^R$  and  $M_t^R$ , which we  
<sup>254</sup> assume do not reproduce in their first year. For ease of presentation, we do not  
<sup>255</sup> symbolically show longitude effects in the vital rate functions for growth, survival,  
<sup>256</sup> flowering, and panicle production but these all included longitude effects on the  
<sup>257</sup> intercept and slope (with respect to size) as a second-order polynomial, following  
<sup>258</sup> the statistical models. We assume that the parameters of sex ratio-dependent  
<sup>259</sup> mating (Eq. 1) do not vary with longitude.

<sup>260</sup> For a pre-breeding census, the expected numbers of recruits in year  $t + 1$  is  
<sup>261</sup> given by:

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

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

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

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

268 Finally, the dynamics of the size-structured component of the population are  
 269 given by:

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

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

270 For both females and males, the first term represents seedlings that survived their  
 271 first year and enter the size distribution of established plants. Because our common  
 272 garden experiment relied on greenhouse-raised transplants, we had little informa-  
 273 tion on these early life cycle transitions. We used the seedling survival probability  
 274 ( $\sigma$ ) from our demographic studies of the perennial congener *Poa autumnalis* in  
 275 east Texas (T.E.X. Miller and J.A. Rudgers, *unpublished data*) as a stand-in for *P.*  
 276 *arachnifera*, and we assume this probability was constant across sexes and longi-  
 277 tudes ( $\sigma = 0.09$ ). We also assume that surviving seedlings reach size  $y$  with prob-

278 ability  $g(y, x = 1)$ , the expected future size of 1-tiller plants from the transplant  
 279 experiment. The second term represents survival and size transition of established  
 280 plants from the previous year, where  $s$  and  $g$  give the probabilities of surviving at  
 281 size  $x$  and growing from sizes  $x$  to  $y$ , respectively, and superscripts indicate that  
 282 these functions may be unique to females ( $F$ ) and males ( $M$ ). All parameter es-  
 283 timates were derived from the statistical modeling described above, except where  
 284 noted, and are reported in Table A1<sup>2</sup>.

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

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

294 Here,  $\theta_i^F$  and  $\theta_i^M$  represent sex-specific parameters: the regression coefficients for  
 295 the intercepts and slopes of size-dependent vital rate functions. Because LTRE  
 296 contributions are additive, we summed across vital rates to compare the total con-  
 297 tributions of female and male parameters. Finally, we compared the two-sex MPM

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

298 to the corresponding female-dominant model (Fig. 1B) by setting  $v(\mathbf{F}_t, \mathbf{M}_t) = v_0$ ,  
299 which decouples female fertility from the composition of the mating pool.

300 **Results**

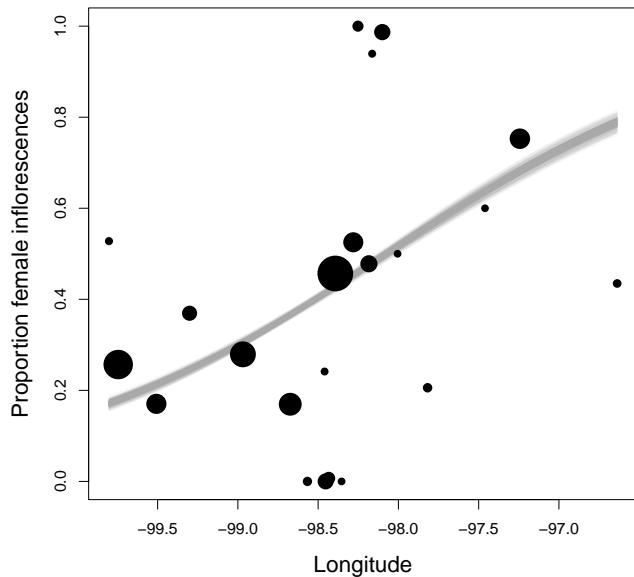


Figure 3: Variation in operational sex ratio (proportion of panicles that were female) across 22 natural populations of *P. arachnifera*. Point size is proportional to population size (total panicles; min: 45, max: 2148). Lines show the fitted binomial regression for 500 samples from the posterior distribution of regression coefficients.

301 **Sex ratio variation in natural populations**

302 We found wide variation in operational sex ratio (proportion of total panicles that  
303 were female) across 22 natural populations of *P. arachnifera*, including female-

304 only and male-only populations (Fig. 3). There was a longitudinal trend to sex  
305 ratio variation, with male-biased panicle production in the western parts of the  
306 range and female-biased panicle production in the east. Not surprisingly, small  
307 populations deviated most strongly from the mean trend (Fig. 3).

### 308 Geographic variation in sex-specific demography

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

319 Annual survival probability was predicted to peak at western and eastern range  
320 edges and was lowest at intermediate longitudes (Fig. 4A-C). There was a modest  
321 female survival advantage but only at the western range edge for large sizes. Other  
322 vital rates showed the opposite longitudinal pattern for most sizes, with peaks in  
323 the center of the range and declines at eastern and western edges. There was a  
324 female growth advantage for small sizes at western longitudes (Fig. 4D-F). The  
325 strongest sex difference was in the probability of flowering: females had a flowering  
326 advantage, especially for large sizes and at eastern longitudes (Fig. 4G-I). Finally,

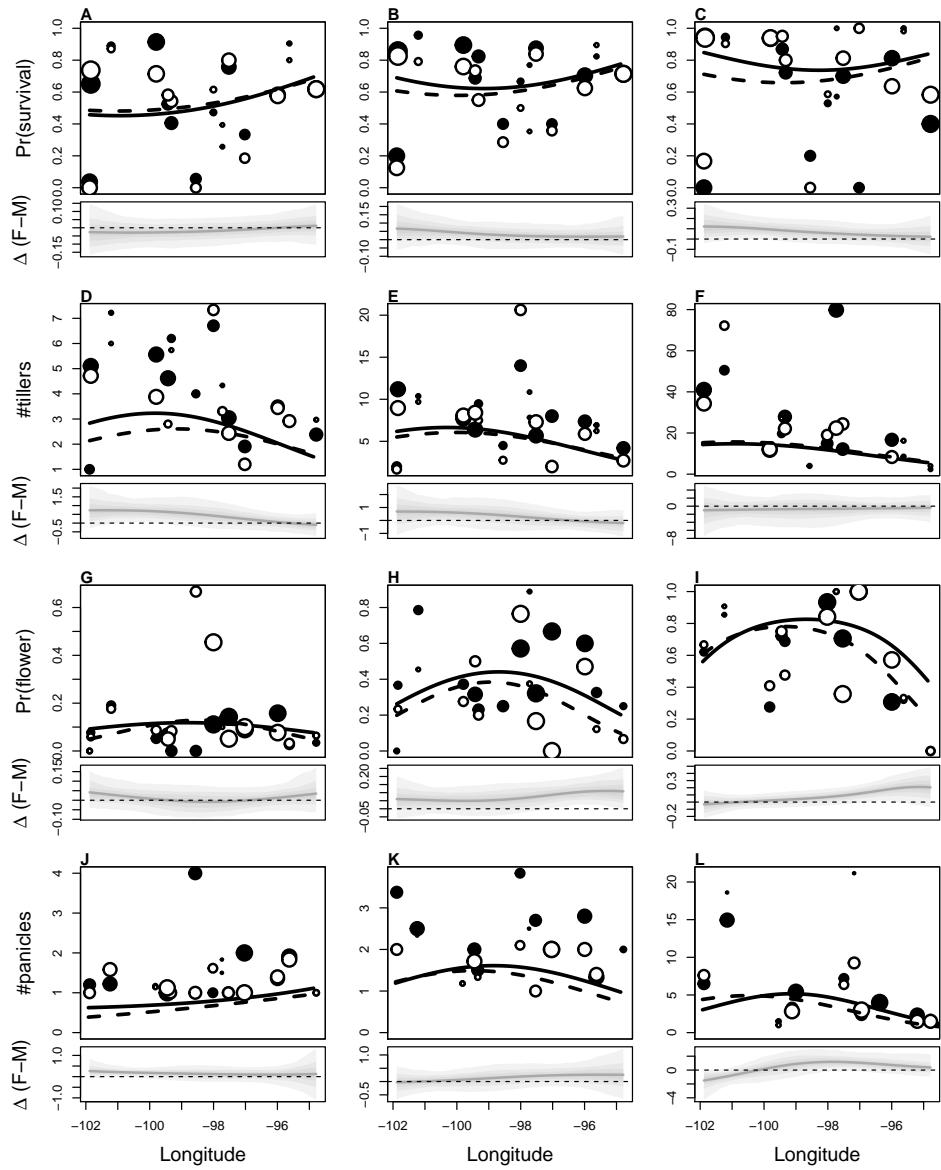


Figure 4: Sex-, size-, and longitude-related variation in: A–C, inter-annual probability of survival; D–F, inter-annual growth (change in number of tillers); G–I, probability of flowering; J–L, number of panicles produced given flowering. Points show means by site for females (filled) and males (open)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

327 panicle production by flowering plants was similar between the sexes for most sizes,  
328 though for the largest sizes there were advantages for males in the west and females  
329 in the east (Fig. 4J-L).

330 Sex differences in flowering and panicle production generated a longitudinal  
331 trend in the operational sex ratio of our common garden populations that mirrored  
332 the trend in natural populations: the fraction of total panicles that were female in  
333 our common gardens increased from west to east (Fig. B3A) even as the fraction  
334 of surviving plants that were female did not show a longitudinal trend (Fig. B3B).  
335 Thus, the common garden experiment suggested that the longitudinal trend in the  
336 mating pool of natural populations (Fig. 3) was due to the reproductive niche of  
337 females extending farther east than that of males, and not to sex differences in  
338 mortality.

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

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

350 between experimental plots.

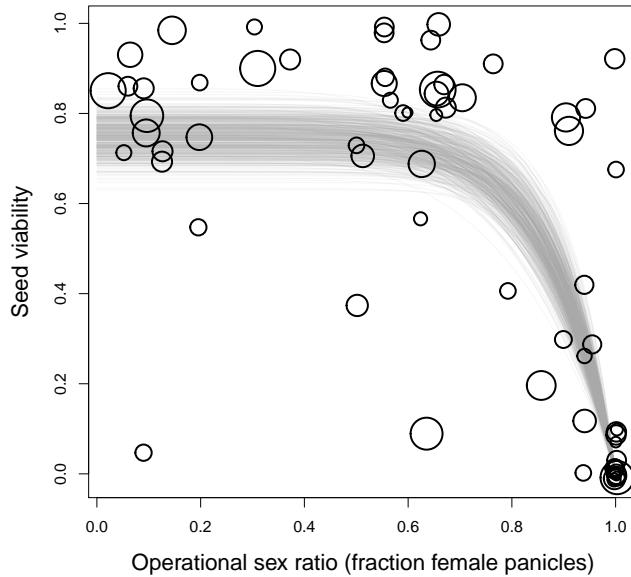


Figure 5: Seed fertilization success in relation to operational sex ratio (fraction of panicles that are female) in experimental populations. Circles show data from tetrazolium assays of seed viability; circle size is proportional to the number of seeds tested (min: 14, max: 57). Lines show fitted model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

### 351 Two-sex model of range limits

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

358 the uncertainty distribution of the model's predictions (represented by the shad-  
359 ing in Fig. 6A), bolstering our confidence that the model effectively captured the  
360 population dynamics of the focal species.

361 Decomposition methods revealed that declines in  $\lambda$  approaching range lim-  
362 its were driven almost exclusively by females (Fig. 6B) with near-zero contri-  
363 butions from males (Fig. 6C). Thus, range limitation was an effectively female-  
364 dominant process, despite female bias in the mating pool at eastern range margins.  
365 Correspondingly, the two-sex model was nearly indistinguishable from a female-  
366 dominant model with all else equal except that female seed fertilization did not  
367 depend on males (Fig B2). Decomposition analysis further revealed that multiple  
368 female vital rates contributed to range limits, some in opposing directions. Be-  
369 cause female survival increased toward range limits (Fig 4A-C), this vital rate had  
370 a contribution to  $\frac{\partial \lambda}{\partial Longitude}$  that was opposite in sign to the other vital rates (Fig.  
371 6B). However, increased survival at range edges was not sufficient to offset declines  
372 in other vital rates. The overall decline in  $\lambda$  was driven most strongly by the de-  
373 cline in female flowering probability at the western limit and by a combination of  
374 reduced female flowering and growth at the eastern limit (Fig. 6B).

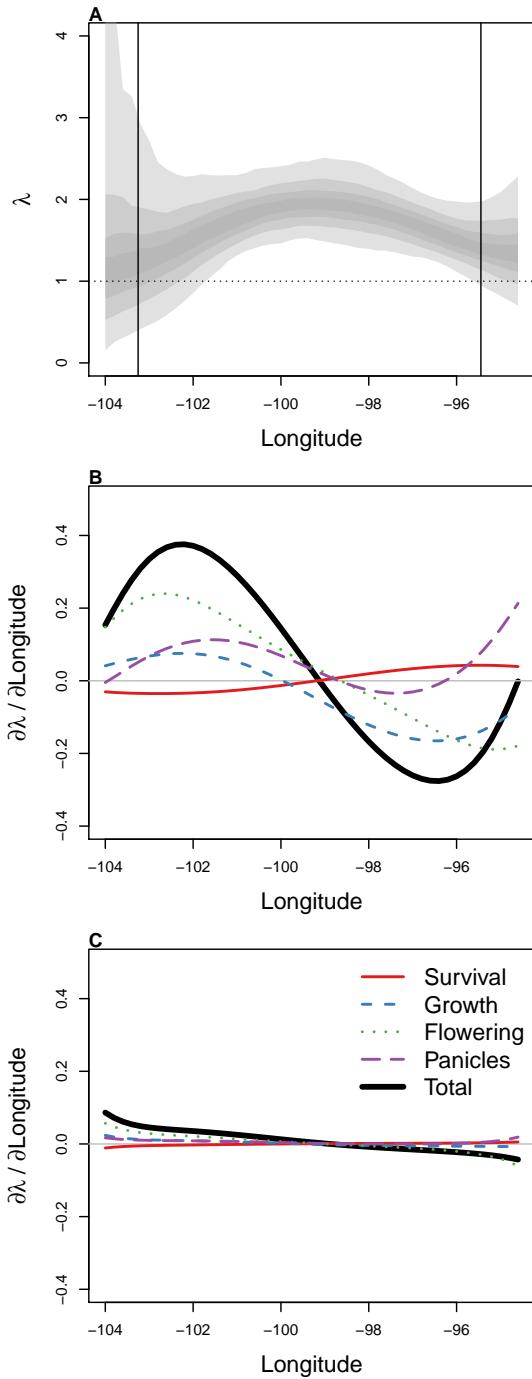


Figure 6: Population growth ( $\lambda$ ) as a function of longitude, predicted by the two-sex MPM that incorporates sex-specific demographic responses to longitude with sex ratio-dependent seed fertilization. A, posterior distribution of  $\lambda$ , where shaded regions show the 25, 50, 75, and 95%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

<sup>375</sup> **Discussion**

<sup>376</sup> **Acknowledgements**

<sup>377</sup> **Author contributions**

<sup>378</sup> **Data accessibility**

<sup>379</sup> **References**

- <sup>380</sup> Araújo MS, Bolnick DI, Layman CA (2011) The ecological causes of individual  
<sup>381</sup> specialisation. *Ecology letters*, **14**, 948–958.
- <sup>382</sup> Bertiller MB, Sain CL, Bisigato AJ, Coronato FR, Aries JO, Graff P (2002) Spatial  
<sup>383</sup> sex segregation in the dioecious grass *poa ligularis* in northern patagonia: the  
<sup>384</sup> role of environmental patchiness. *Biodiversity & Conservation*, **11**, 69–84.
- <sup>385</sup> Bierzychudek P, Eckhart V (1988) Spatial segregation of the sexes of dioecious  
<sup>386</sup> plants. *The American Naturalist*, **132**, 34–43.
- <sup>387</sup> Bolnick DI, Doebeli M (2003) Sexual dimorphism and adaptive speciation: two  
<sup>388</sup> sides of the same ecological coin. *Evolution*, **57**, 2433–2449.
- <sup>389</sup> Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister  
<sup>390</sup> ML (2002) The ecology of individuals: incidence and implications of individual  
<sup>391</sup> specialization. *The American Naturalist*, **161**, 1–28.
- <sup>392</sup> Bowyer RT (2004) Sexual segregation in ruminants: definitions, hypotheses, and

- 393      implications for conservation and management. *Journal of Mammalogy*, **85**,  
394      1039–1052.
- 395      Carpenter B, Gelman A, Hoffman MD, *et al.* (2017) Stan: A probabilistic pro-  
396      gramming language. *Journal of statistical software*, **76**.
- 397      Caruso C, Case A (2007) Sex ratio variation in gynodioecious lobelia siphilitica:  
398      effects of population size and geographic location. *Journal of Evolutionary Bi-  
399      ology*, **20**, 1396–1405.
- 400      Caswell H (2001) *Matrix Population Models*. Sinauer Associates, Inc., Sunderland,  
401      MA, 2 edn.
- 402      Caswell H, Weeks DE (1986) Two-sex models: chaos, extinction, and other dy-  
403      namic consequences of sex. *The American Naturalist*, **128**, 707–735.
- 404      Compagnoni A, Steigman K, Miller TE (2017) Can't live with them, can't live  
405      without them? balancing mating and competition in two-sex populations. *Pro-  
406      ceedings of the Royal Society B: Biological Sciences*, **284**, 20171999.
- 407      Conn PB, Johnson DS, Williams PJ, Melin SR, Hooten MB (2018) A guide to  
408      bayesian model checking for ecologists. *Ecological Monographs*, **88**, 526–542.
- 409      Darwin C (1871) *The descent of man*. BoD–Books on Demand.
- 410      Diez JM, Giladi I, Warren R, Pulliam HR (2014) Probabilistic and spatially vari-  
411      able niches inferred from demography. *Journal of ecology*, **102**, 544–554.
- 412      Eberhart-Phillips LJ, Küpper C, Miller TE, *et al.* (2017) Sex-specific early sur-  
413      vival drives adult sex ratio bias in snowy plovers and impacts mating system

- <sup>414</sup> and population growth. *Proceedings of the National Academy of Sciences*, **114**,  
<sup>415</sup> E5474–E5481.
- <sup>416</sup> Ehrlén J, Morris WF (2015) Predicting changes in the distribution and abundance  
<sup>417</sup> of species under environmental change. *Ecology Letters*, **18**, 303–314.
- <sup>418</sup> Eppley S (2001) Gender-specific selection during early life history stages in the  
<sup>419</sup> dioecious grass *distichlis spicata*. *Ecology*, **82**, 2022–2031.
- <sup>420</sup> Evans ME, Merow C, Record S, McMahon SM, Enquist BJ (2016) Towards  
<sup>421</sup> process-based range modeling of many species. *Trends in Ecology & Evolution*,  
<sup>422</sup> **31**, 860–871.
- <sup>423</sup> Fick SE, Hijmans RJ (2017) Worldclim 2: new 1-km spatial resolution climate  
<sup>424</sup> surfaces for global land areas. *International journal of climatology*, **37**, 4302–  
<sup>425</sup> 4315.
- <sup>426</sup> Field DL, Pickup M, Barrett SC (2013) Ecological context and metapopulation  
<sup>427</sup> dynamics affect sex-ratio variation among dioecious plant populations. *Annals  
of botany*, **111**, 917–923.
- <sup>429</sup> Franco M, Silvertown J (2004) A comparative demography of plants based upon  
<sup>430</sup> elasticities of vital rates. *Ecology*, **85**, 531–538.
- <sup>431</sup> Gianuca D, Votier SC, Pardo D, *et al.* (2019) Sex-specific effects of fisheries and  
<sup>432</sup> climate on the demography of sexually dimorphic seabirds. *Journal of Animal  
Ecology*.
- <sup>434</sup> Groen KE, Stieha CR, Crowley PH, McLetchie DN (2010) Sex-specific plant re-

- 435      sponses to light intensity and canopy openness: implications for spatial segre-  
436      gation of the sexes. *Oecologia*, **162**, 561–570.
- 437      Hargreaves AL, Samis KE, Eckert CG (2013) Are species' range limits simply niche  
438      limits writ large? a review of transplant experiments beyond the range. *The  
439      American Naturalist*, **183**, 157–173.
- 440      Holt RD (2009) Bringing the hutchinsonian niche into the 21st century: ecological  
441      and evolutionary perspectives. *Proceedings of the National Academy of Sciences*,  
442      **106**, 19659–19665.
- 443      Hutchinson GE (1958) Concluding remarks. In: *Cold Spring Harbour Symposium  
444      on Quantitative Biology*, vol. 22, pp. 415—427.
- 445      Karl TR, Melillo JM, Peterson TC, Hassol SJ (2009) *Global climate change impacts  
446      in the United States*. Cambridge University Press.
- 447      Ketterson ED, Nolan Jr V (1976) Geographic variation and its climatic correlates  
448      in the sex ratio of eastern-wintering dark-eyed juncos (*junco hyemalis hyemalis*).  
449      *Ecology*, **57**, 679–693.
- 450      Law CJ, Mehta RS (2018) Carnivory maintains cranial dimorphism between males  
451      and females: evidence for niche divergence in extant musteloidea. *Evolution*, **72**,  
452      1950–1961.
- 453      Lee-Yaw JA, Kharouba HM, Bontrager M, *et al.* (2016) A synthesis of transplant  
454      experiments and ecological niche models suggests that range limits are often  
455      niche limits. *Ecology letters*, **19**, 710–722.

- 456 Merow C, Bois ST, Allen JM, Xie Y, Silander JA (2017) Climate change both  
457 facilitates and inhibits invasive plant ranges in new england. *Proceedings of the*  
458 *National Academy of Sciences*, **114**, E3276–E3284.
- 459 Merow C, Latimer AM, Wilson AM, McMahon SM, Rebelo AG, Silander Jr JA  
460 (2014) On using integral projection models to generate demographically driven  
461 predictions of species' distributions: development and validation using sparse  
462 data. *Ecography*, **37**, 1167–1183.
- 463 Miller TE, Inouye BD (2011) Confronting two-sex demographic models with data.  
464 *Ecology*, **92**, 2141–2151.
- 465 Miller TE, Shaw AK, Inouye BD, Neubert MG (2011) Sex-biased dispersal and  
466 the speed of two-sex invasions. *The American Naturalist*, **177**, 549–561.
- 467 Pekár S, Martišová M, Bilde T (2011) Intersexual trophic niche partitioning in an  
468 ant-eating spider (araneae: Zodariidae). *PloS one*, **6**, e14603.
- 469 Petry WK, Soule JD, Iler AM, Chicas-Mosier A, Inouye DW, Miller TE, Mooney  
470 KA (2016) Sex-specific responses to climate change in plants alter population  
471 sex ratio and performance. *Science*, **353**, 69–71.
- 472 Phillips R, Silk J, Phalan B, Catry P, Croxall J (2004) Seasonal sexual segregation  
473 in two thalassarche albatross species: competitive exclusion, reproductive role  
474 specialization or foraging niche divergence? *Proceedings of the Royal Society of*  
475 *London. Series B: Biological Sciences*, **271**, 1283–1291.
- 476 Rankin DJ, Kokko H (2007) Do males matter? the role of males in population  
477 dynamics. *Oikos*, **116**, 335–348.

- 478 Renganayaki K, Jessup R, Burson B, Hussey M, Read J (2005) Identification of  
479 male-specific afp markers in dioecious texas bluegrass. *Crop science*, **45**, 2529–  
480 2539.
- 481 Renganayaki K, Read J, Fritz A (2001) Genetic diversity among texas bluegrass  
482 genotypes (*poa arachnifera* torr.) revealed by afp and rapd markers. *Theoretical*  
483 *and Applied Genetics*, **102**, 1037–1045.
- 484 Renner SS, Ricklefs RE (1995) Dioecy and its correlates in the flowering plants.  
485 *American journal of botany*, **82**, 596–606.
- 486 Rozas V, DeSoto L, Olano JM (2009) Sex-specific, age-dependent sensitivity of  
487 tree-ring growth to climate in the dioecious tree *juniperus thurifera*. *New Phy-*  
488 *tologist*, **182**, 687–697.
- 489 Shelton AO (2010) The ecological and evolutionary drivers of female-biased sex  
490 ratios: two-sex models of perennial seagrasses. *The American Naturalist*, **175**,  
491 302–315.
- 492 Shine R (1989) Ecological causes for the evolution of sexual dimorphism: a review  
493 of the evidence. *The Quarterly Review of Biology*, **64**, 419–461.
- 494 Team SD, *et al.* (2018) Rstan: the r interface to stan. r package version 2.17. 3.
- 495 Temeles EJ, Miller JS, Rifkin JL (2010) Evolution of sexual dimorphism in bill size  
496 and shape of hermit hummingbirds (*phaethornithinae*): a role for ecological cau-  
497 sation. *Philosophical Transactions of the Royal Society B: Biological Sciences*,  
498 **365**, 1053–1063.

<sup>499</sup> Veran S, Beissinger SR (2009) Demographic origins of skewed operational and  
<sup>500</sup> adult sex ratios: perturbation analyses of two-sex models. *Ecology Letters*, **12**,  
<sup>501</sup> 129–143.

<sup>502</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

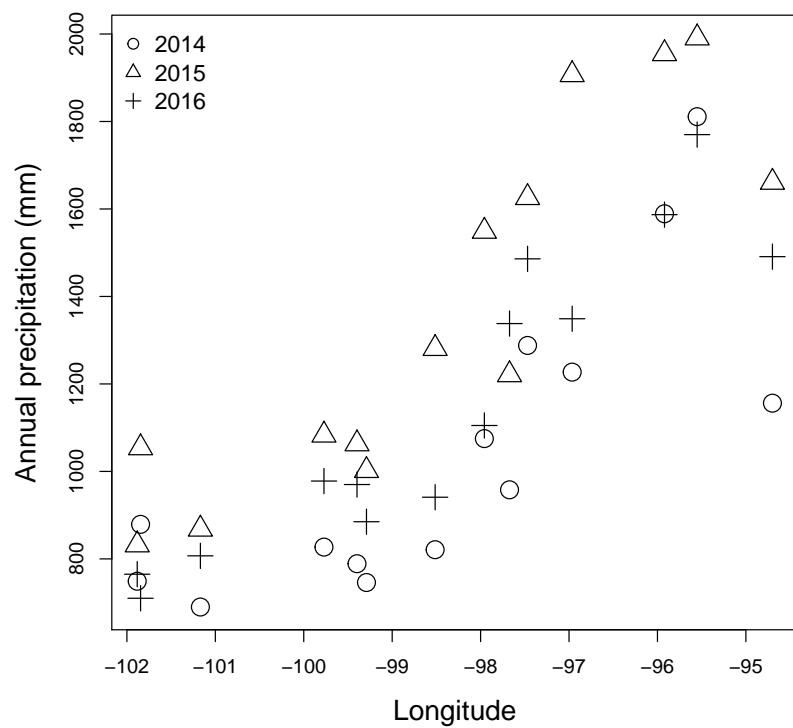


Figure A1: Total annual precipitation at common garden sites during the study years tracked long-term trends of increasing aridity from east to west.

<sub>503</sub> Appendix B: Additional results

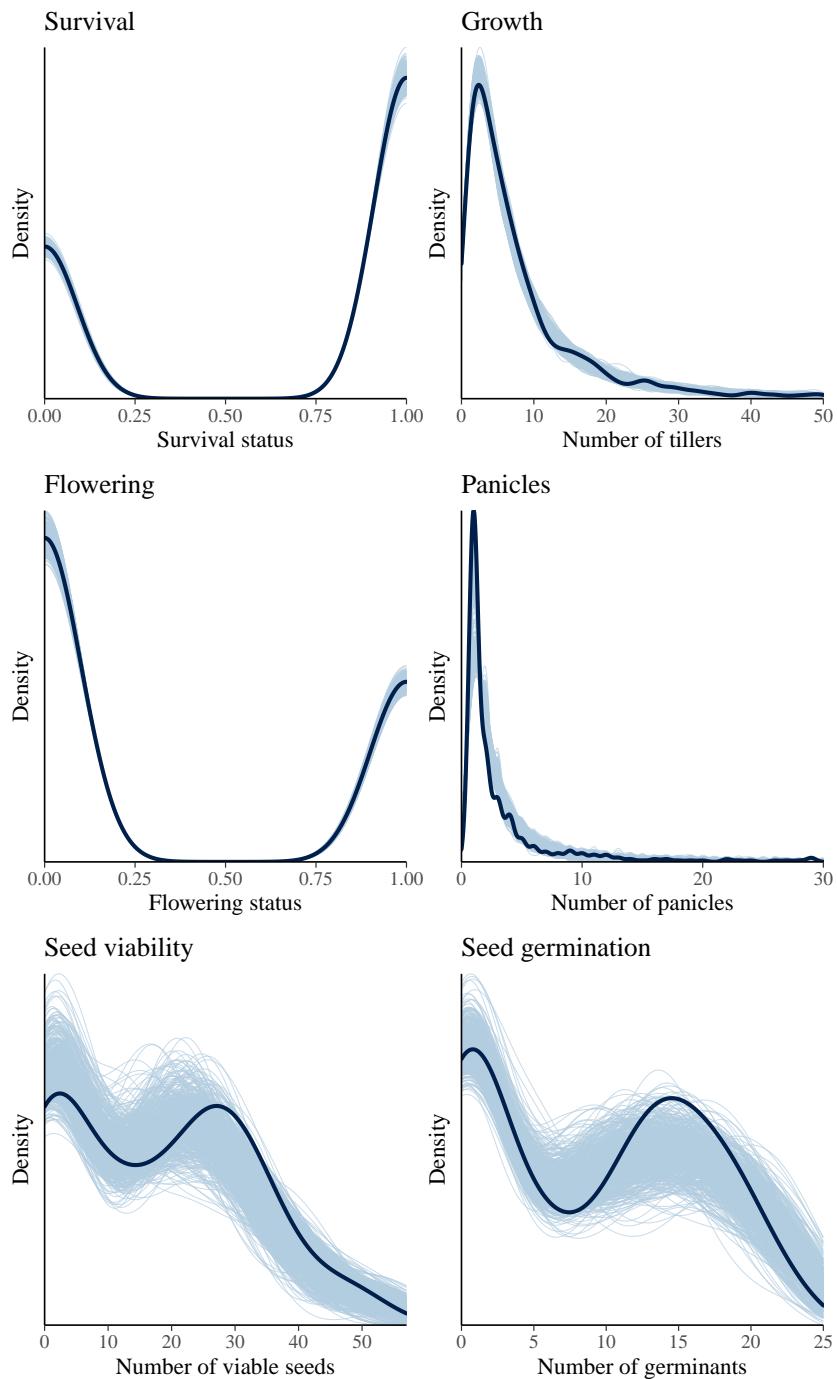


Figure B1: Posterior predictive checks of statistical models for demographic vital rates. Lines show density distributions of real data (thick, dark blue) compared to simulated data sets (thin, light blue) generated from the fitted models based on 500 draws of the posterior distribution of parameter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

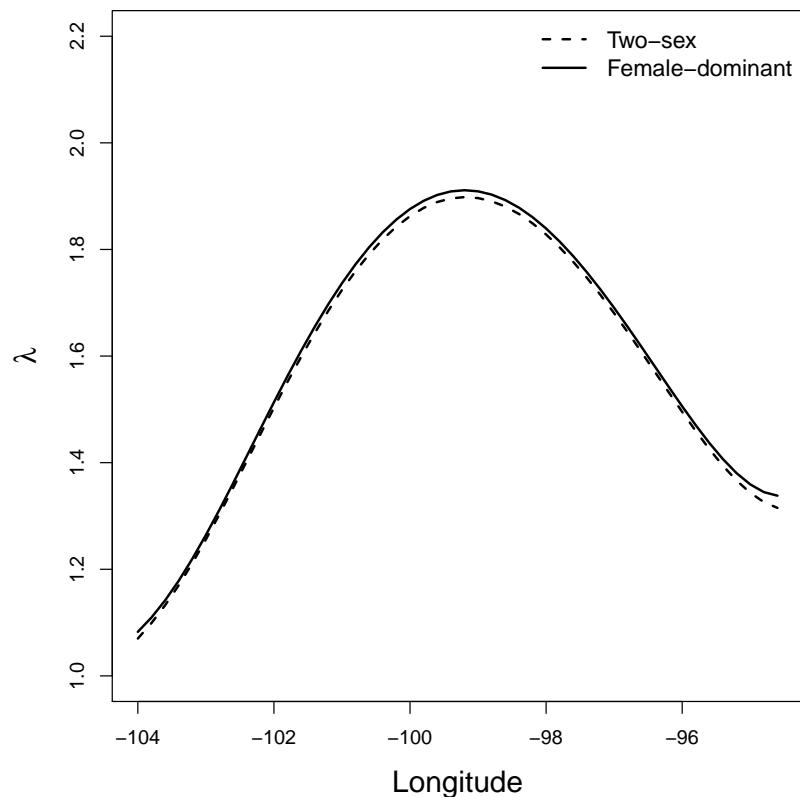


Figure B2: Comparison of longitudinal variation in  $\lambda$  between the two-sex demographic model (dashed line) that includes dependence of female seed production on population structure and the corresponding female-dominant model (solid line) with constant female fertility and all else equal. Models were evaluated at posterior mean parameter estimates

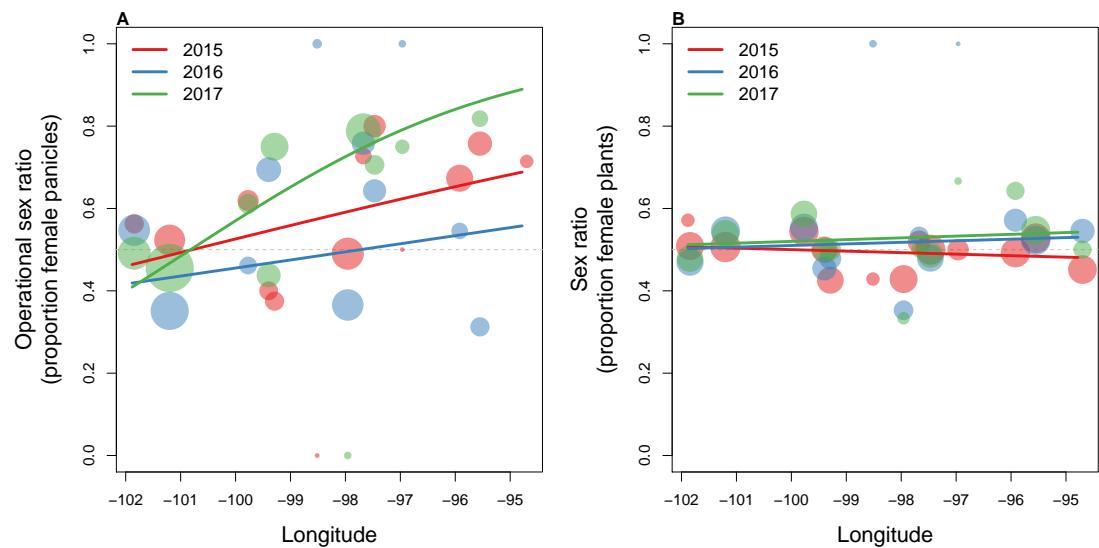


Figure B3: Longitudinal variation in: A, operational sex ratio (fraction of panicles that were female), and B, individual sex ratio (fraction of surviving plants that were female) across 14 common garden sites. Colors indicate year and point size is proportional to sample size of the fraction (total panicles in A [min: 1, max: 1021] and total plants in B [min: 2, max: 79]). Lines show fitted binomial GLMs.