

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 λ
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 λ to reproductive transitions in the life cycle. This sug-

gests that female-dominant limitation of geographic distribution may be common
to long-lived species with polygamous mating systems.

Keywords

demography; dioecy; intra-specific niche heterogeneity; matrix projection model;
sex ratio; range limits

29 Introduction

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

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

53 we know?

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

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

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

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

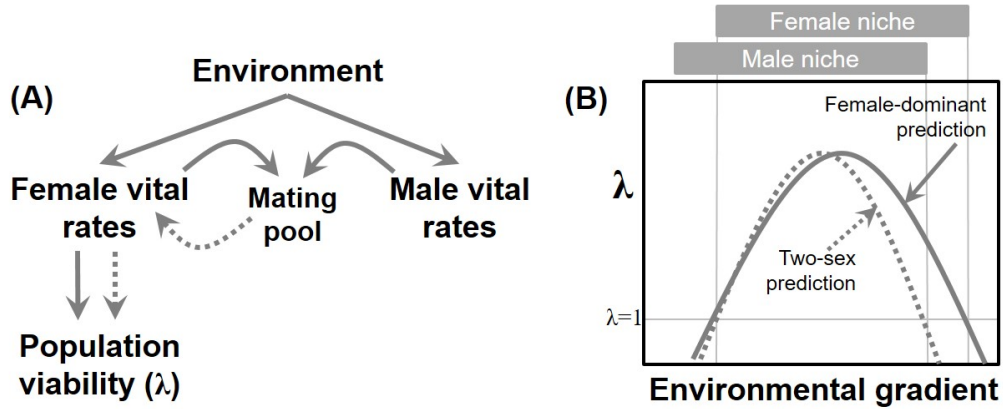


Figure 1: Hypotheses for how environmental variation can affect population viability and range limits in dioecious species. Under the female-dominant hypothesis, environmental drivers affect population growth (λ) through effects on females, alone (A). In geographic / environmental space, this translates to range boundaries that arise at the limits of the female environmental niche, irrespective of where they fall with respect to the male niche (B). Under the two-sex hypothesis, environmental drivers can affect λ through sex-specific responses, which may skew the sex ratio of the mating pool and feed back to affect female fertility via mate availability (A). In this case, expectations for range limits may differ from the female-dominant prediction, since mate limitation in environments that favor females over males may reduce population viability. 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 dioecious 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 λ 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

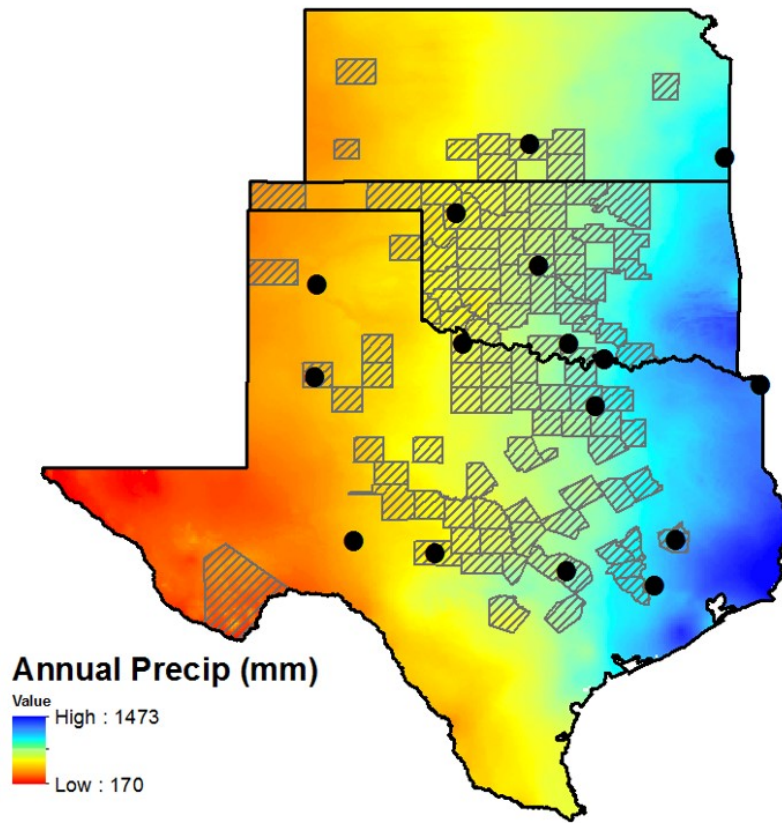


Figure 2: Geographic and environmental distribution of *P. arachnifera* in Texas, Oklahoma, and Kansas. Hatched shapes show counties with herbarium records of occurrence. Color shows geographic variation in annual precipitation (mm) based on 30-year normals from WorldClim (Fick & Hijmans, 2017). Points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

127 other states¹. Like all grasses, *P. arachnifera* is wind-pollinated. Individuals can
 128 be sexed only when flowering, in early spring, based on the presence of stigmas
 129 (females) or anthers (males) in the inflorescence. Following inflorescence and seed
 130 production, plants go dormant for the hot summer months and vegetative growth
 131 resumes in fall. Individuals grow via rhizomes to form “patches” that may be as

¹<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-
138 ulations 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

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

158 **Common garden experiment**

159 **Source material and experimental design**

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

171 Common gardens were set up in Fall (October–December) 2014. At each site,
172 we established 14 experimental blocks, which typically corresponded to a tree or
173 woodland edge, providing partial shade that mimics this species’ natural micro-
174 environment. We planted 3 females and 3 males in each block, for a total of 42
175 individuals per sex per site and 1176 total plants across sites, with all source collec-
176 tions represented at all sites. Individuals were spaced within blocks to allow space
177 for rhizomatous growth that could be clearly attributed to individual transplants.
178 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 sponses, 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 tiller and panicle counts as zero-
198 truncated negative binomial using the log link. For flowering and panicle produc-
199 tion in year t , the size covariate was the natural logarithm of tiller number in year
200 t . For survival and size in year t , the size covariate was the natural logarithm of
201 tiller number in year $t - 1$ (for 2015 data, size in year $t - 1$ was transplant size at
202 the time of planting).

Sex ratio experiment

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

Statistical analysis of sex ratio experiment

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

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

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

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

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

Demographic model of range limits

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

246 longitudinal limits of population viability ($\lambda \geq 1$) and investigate the underlying
 247 drivers of population decline at range limits.

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

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

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

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

260 where p^F and c^F are flowering probability and panicle production for females of
 261 size x , d is the number of seeds (fertilized or unfertilized) per female panicle, v is
 262 the probability that a seed is fertilized, m is the probability that a fertilized seed
 263 germinates, and ρ is the primary sex ratio (proportion of recruits that are female).
 264 Seed fertilization depends on the OSR of panicles (following Eq. 1) which was

265 derived from the $U \times 1$ vectors of population structure \mathbf{F}_t and \mathbf{M}_t :

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

266 Finally, the dynamics of the size-structured component of the population are
267 given by:

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

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

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

281 timates were derived from the statistical modeling described above, except where
 282 noted, and are reported in Table A1².

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

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

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

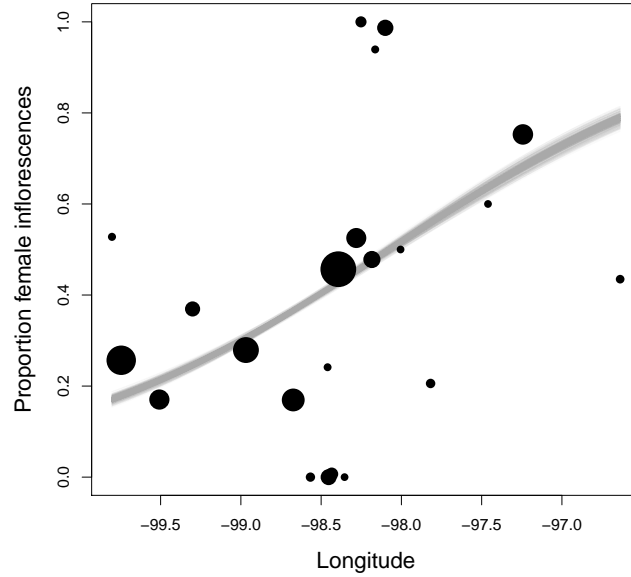


Figure 3: Variation in operational sex ratio (proportion of panicles that were female) across 22 natural populations of *P. arachnifera*. Point size is proportional to population size (total panicles; min: 45, max: 2148). Lines show the fitted binomial regression for 500 samples from the posterior distribution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

Results

Sex ratio variation in natural populations

We found wide variation in operational sex ratio (proportion of total panicles that were female) across 22 natural populations of *P. arachnifera*, including female-only and male-only populations (Fig. 3). 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. Not surprisingly, small

²This table does not exist yet.

305 populations deviated most strongly from the mean trend (Fig. 3).

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

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

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

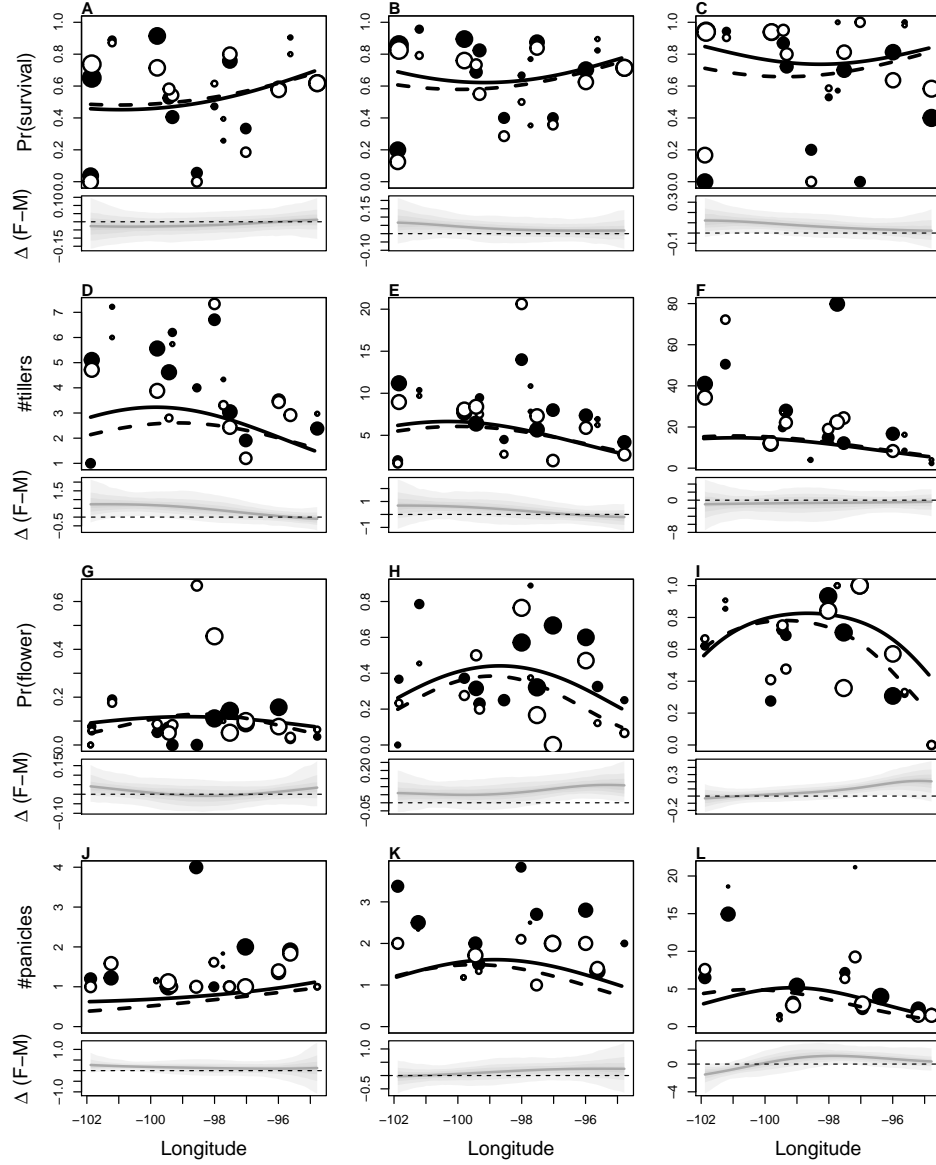


Figure 4: Sex-, size-, and longitude-related variation in: A–C, inter-annual probability of survival; D–F, inter-annual growth (change in number of tillers); G–I, probability of flowering; J–L, number of panicles produced given flowering. Points show means by site for females (filled) and males (open)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

328 Sex differences in flowering and panicle production generated a longitudinal
329 trend in the operational sex ratio of our common garden populations that mirrored
330 the trend in natural populations: the fraction of total panicles that were female in
331 our common gardens increased from west to east (Fig. B2A) even as the fraction
332 of surviving plants that were female did not show a longitudinal trend (Fig. B2B).
333 Thus, the common garden experiment suggested that the longitudinal trend in the
334 mating pool of natural populations (Fig. 3) was due to the reproductive niche of
335 females extending farther east than that of males, and not to sex differences in
336 mortality.

337 **Sex-ratio dependent seed fertilization**

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

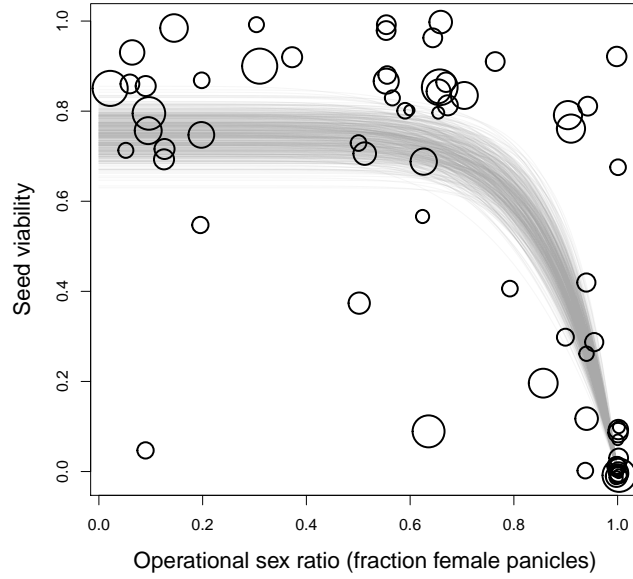


Figure 5: Seed fertilization success in relation to operational sex ratio (fraction of panicles that are female) in experimental populations. Circles show data from tetrazolium assays of seed viability; circle size is proportional to the number of seeds tested (min: 14, max: 57). Lines show fitted model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

Two-sex model of range limits

The processed-based demographic model connected sex-specific vital rate responses to longitudinal variation (Fig. 4) with sex ratio-dependent mating (Fig. 5) to predict the contributions of females and males to range limitation. The model predicted maximum fitness in the center of the range and loss of population viability at longitudes that corresponded well with observed range limits. Specifically, the western-most and eastern-most county records of *P. arachnifera* fell within the uncertainty distribution of the model's predictions (represented by the shading in Fig. 6A), bolstering our confidence that the model effectively captured the

358 population dynamics of the focal species.

359 Decomposition methods revealed that declines in λ approaching range lim-
360 its were driven almost exclusively by females (Fig. 6B) with near-zero contri-
361 butions from males (Fig. 6C). Thus, range limitation was an effectively female-
362 dominant process, despite female bias in the mating pool at eastern range margins.
363 Correspondingly, the two-sex model was nearly indistinguishable from a female-
364 dominant model with all else equal except that female seed fertilization did not
365 depend on males (Fig B1). Decomposition analysis further revealed that multiple
366 female vital rates contributed to range limits, some in opposing directions. Be-
367 cause female survival increased toward range limits (Fig 4A-C), this vital rate had
368 a contribution to $\frac{\partial \lambda}{\partial \text{Longitude}}$ that was opposite in sign to the other vital rates (Fig.
369 6B). However, increased survival at range edges was not sufficient to offset declines
370 in other vital rates. The overall decline in λ was driven most strongly by the de-
371 cline in female flowering probability at the western limit and by a combination of
372 reduced female flowering and growth at the eastern limit (Fig. 6B).

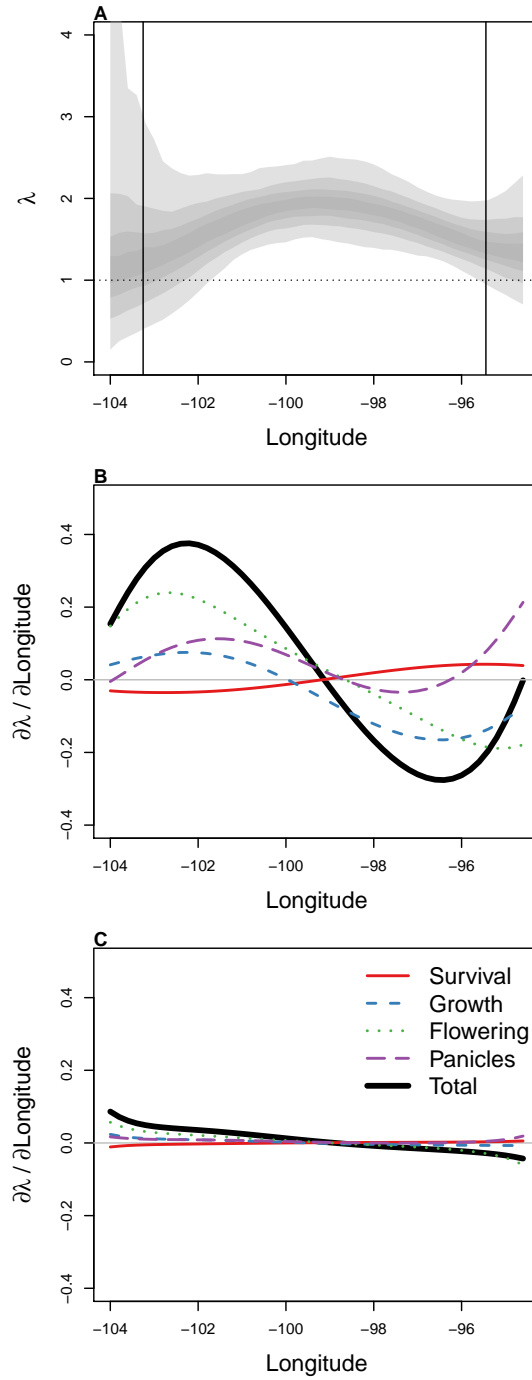


Figure 6: Population growth (λ) as a function of longitude, predicted by the two-sex MPM that incorporates sex-specific demographic responses to longitude with sex ratio-dependent seed fertilization. A, posterior distribution of λ , where shaded regions show the 25, 50, 75, and 95% percentiles of parameter uncertainty. Dashed horizontal line indicates the limit of population viability ($\lambda = 1$) and vertical lines show the longitudes of Brewster and Brazoria Counties, TX, the western- and eastern-most occurrence records of *P. arachnifera*. B–C, LTRE decomposition of the sensitivity of λ to longitude into additive vital rate contributions of females (B) and males (C) based on posterior mean parameter estimates.

373 Discussion

374 Acknowledgements

375 Author contributions

376 Data accessibility

377 References

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Appendix A: Site locations and climate

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

Table A1: Sites of natural population surveys corresponding to Figure

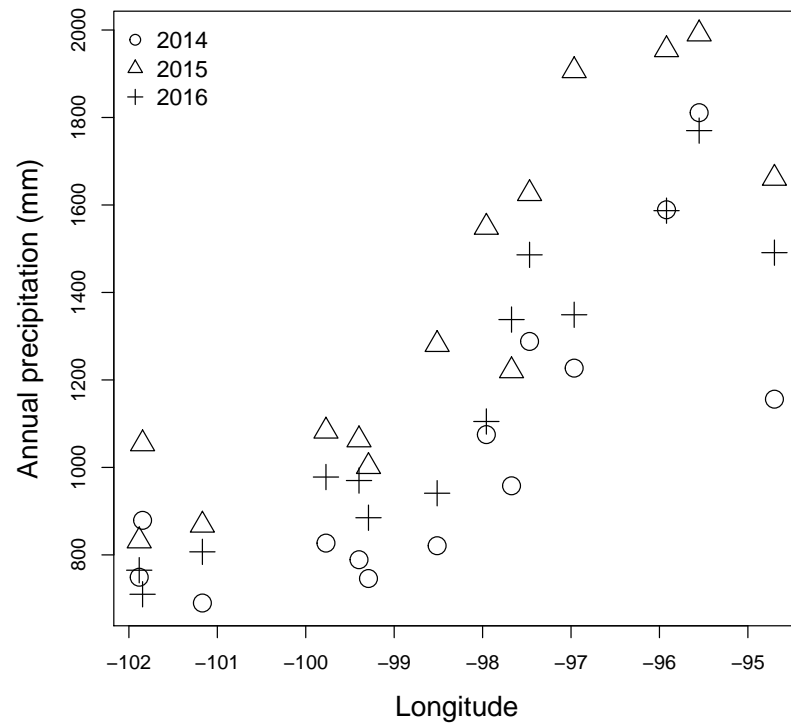


Figure A1: Total annual precipitation at common garden sites during the study years tracked long-term trends of increasing aridity from east to west.

501 Appendix B: Additional results

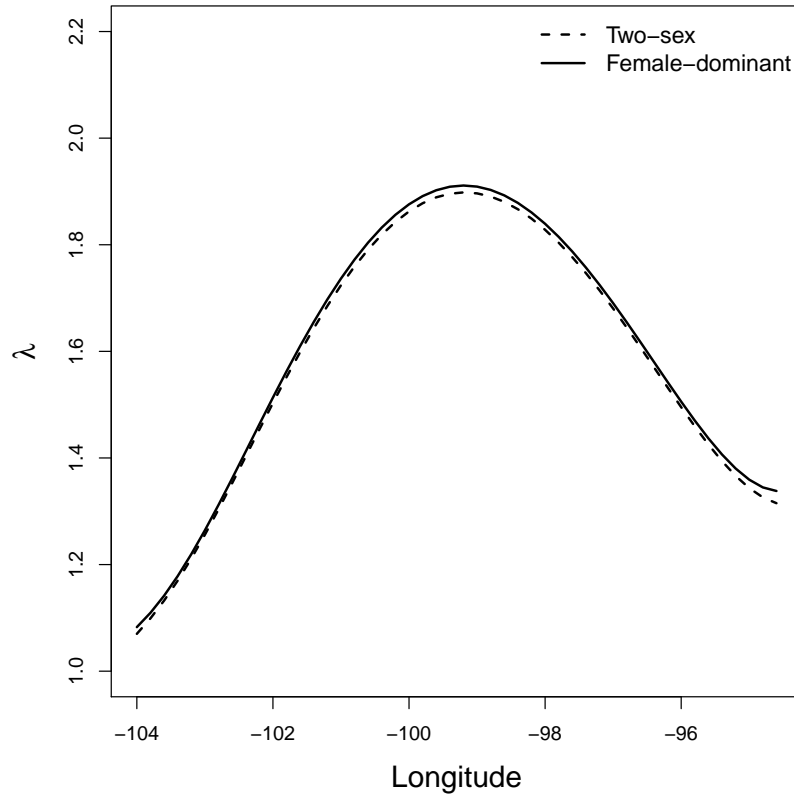


Figure B1: Comparison of longitudinal variation in λ between the two-sex demographic model (dashed line) that includes dependence of female seed production on population structure and the corresponding female-dominant model (solid line) with constant female fertility and all else equal. Models were evaluated at posterior mean parameter estimates

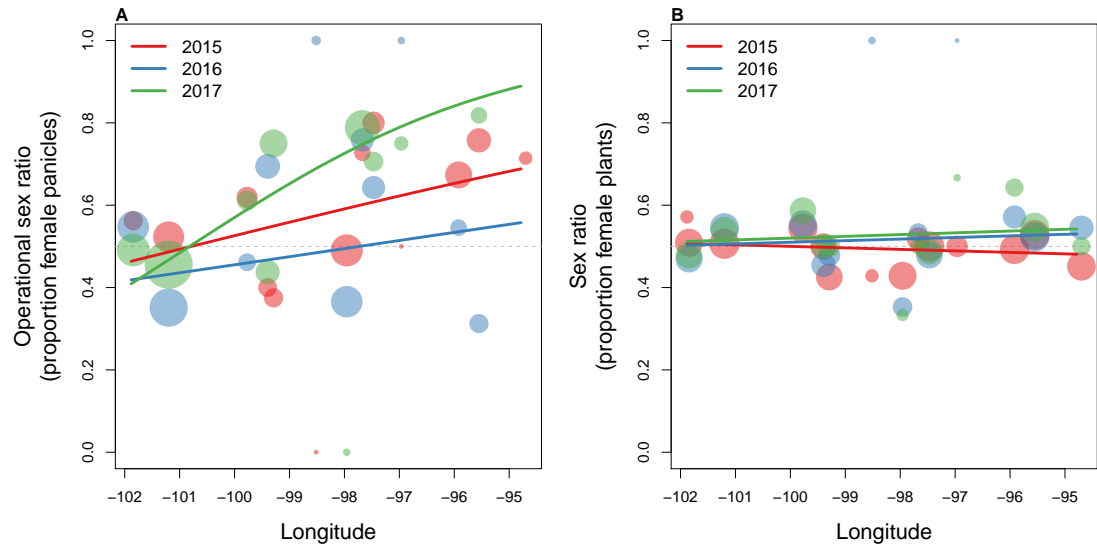


Figure B2: Longitudinal variation in: A, operational sex ratio (fraction of panicles that were female), and B, individual sex ratio (fraction of surviving plants that were female) across 14 common garden sites. Colors indicate year and point size is proportional to sample size of the fraction (total panicles in A [min: 1, max: 1021] and total plants in B [min: 2, max: 79]). Lines show fitted binomial GLMs.