

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

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Abstract

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

24 relatively low sensitivity of λ to reproductive transitions in the life cycle. This sug-
25 gests that female-dominant limitation of geographic distribution may be common
26 to long-lived species with polygamous mating systems.

27 **Keywords**

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

Introduction

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

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

54 of many niches, then whose niche is it that determines the geographic distribution
55 and how would we know?

56 Sexual niche differentiation is a common form of intra-specific niche heterogene-
57 ity (Bolnick *et al.*, 2002) and has been widely documented in animals (the vast
58 majority of which are dioecious) and plants (ca. 6% of angiosperms are dioecious:
59 Renner & Ricklefs 1995). The prevalence of sexual niche differentiation was recog-
60 nized by Darwin (1871), who described “different habits of life, not related...to the
61 reproductive functions” of females and males. There are now numerous examples
62 of sex differences in trophic position (Pekár *et al.*, 2011; Law & Mehta, 2018), habi-
63 tat use (Bowyer, 2004; Phillips *et al.*, 2004), and responses to climate (Petry *et al.*,
64 2016; Rozas *et al.*, 2009; Gianuca *et al.*, 2019), differences that may or may not
65 be accompanied by sexual dimorphism. It has been hypothesized that sex-specific
66 niches may evolve by natural selection when it reduces competitive or other antag-
67 onistic interactions between the sexes (Bierzychudek & Eckhart, 1988; Bolnick &
68 Doebeli, 2003) or as a byproduct of naturally or sexually selected size dimorphism
69 (Shine, 1989; Temeles *et al.*, 2010). In an ecological context, sexual niche differen-
70 tiation can translate to sex-specific advantages in different environments, causing
71 skew in the operational sex ratio (OSR: relative abundance of females and males
72 available for mating) even if the primary (birth) sex ratio is unbiased (Veran &
73 Beissinger, 2009; Shelton, 2010; Eberhart-Phillips *et al.*, 2017). Indeed, environ-
74 mental clines in OSR have been widely documented in plants and animals at fine
75 spatial scales (Eppley, 2001; Bertiller *et al.*, 2002; Groen *et al.*, 2010) as well as
76 broader climatic clines across altitudes or latitudes (Petry *et al.*, 2016; Ketterson
77 & Nolan Jr, 1976; Caruso & Case, 2007). At range margins, where environments
78 are extreme relative to the range core, demographic differences between the sexes,

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

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

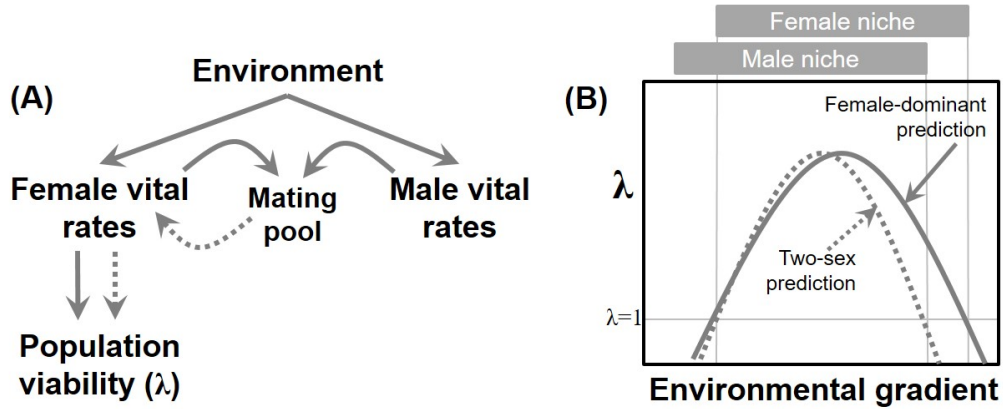


Figure 1: Hypotheses for how environmental variation can affect population viability and range limits in dioecious species. Under the female-dominant hypothesis, environmental drivers affect population growth (λ) through effects on females, alone (A). In geographic / environmental space, this translates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

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

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

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

124 Materials and methods

125 Study system and natural population surveys

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

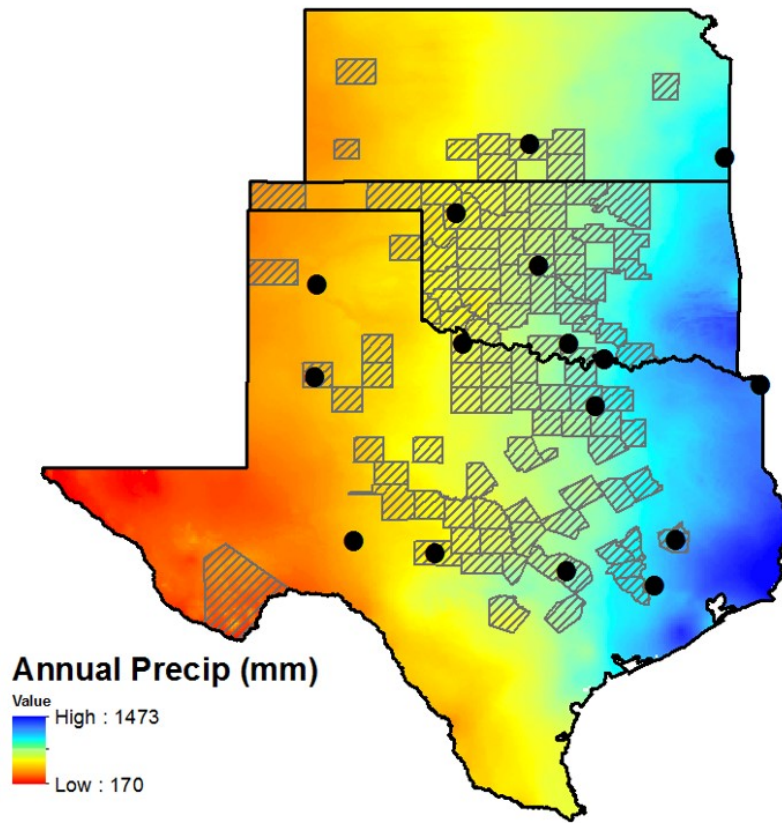


Figure 2: Geographic and environmental distribution of *P. arachnifera* in Texas, Oklahoma, and Kansas. Hatched shapes show counties with herbarium records of occurrence. Color shows geographic variation in annual precipitation (mm) based on 30-year normals from WorldClim (Fick & Hijmans, 2017). Points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

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

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

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

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

148 **Statistical analysis of natural population surveys**

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

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

160 Common garden experiment

161 Source material and experimental design

162 We established a common garden experiment at 14 sites throughout and beyond
163 the geographic distribution of *P. arachnifera* (MAP). Experimental sites spanned
164 latitudinal and longitudinal variation, though we focus here on longitude. During
165 the three years of this experiment, total precipitation at each site closely tracked
166 longitude (Fig. A1), as expected based on longer-term climate trends (map).
167 Source material for this experiment came from 8 sites, which were of subset of the
168 sites that were visited for the natural population survey (Table). For a subset of
169 the natural populations we visited, we collected tillers from flowering individuals
170 of each sex (mean: 11.6 individuals per site, range: 2–18) (Table A1). These
171 were brought back to the Rice University greenhouse, where they were clonally
172 propagated in ProMix potting soil and supplemental Osmocote fertilizer at 78–
173 80°F under natural light.

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

181 To promote establishment, we cleared vegetation immediately surrounding trans-
182 plants and provided ca. 1 L of water at the time of transplanting but provided no
183 subsequent watering, fertilization, or competitor removal.

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

188 **Statistical analysis of common garden experiment**

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

199 The survival and flowering data were Bernoulli distributed, and these models
200 applied the logit link function. We modeled tiller and panicle counts as zero-
201 truncated negative binomial using the log link. For flowering and panicle produc-
202 tion in year t , the size covariate was the natural logarithm of tiller number in year
203 t . For survival and size in year t , the size covariate was the natural logarithm of
204 tiller number in year $t - 1$ (for 2015 data, size in year $t - 1$ was transplant size at

205 the time of planting).

206 **Sex ratio experiment**

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

223 **Statistical analysis of sex ratio experiment**

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

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

260 For a pre-breeding census, the expected numbers of recruits in year $t + 1$ is
 261 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 ρ is the primary sex ratio (proportion of recruits that are female).

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

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

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

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

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

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

282 functions may be unique to females (F) and males (M). All parameter estimates
 283 are reported in Table A1².

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

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

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

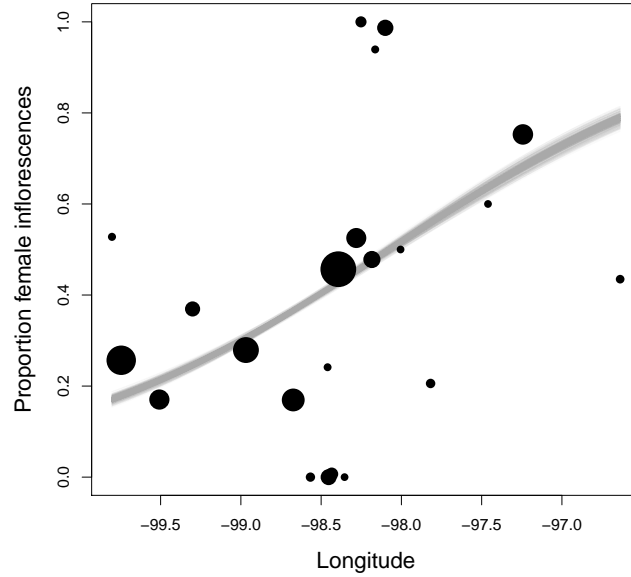


Figure 3: Variation in operational sex ratio (proportion of panicles that were female) across 22 natural populations of *P. arachnifera*. Point size is proportional to population size (total panicles; min: 45, max: 2148). Lines show the fitted binomial regression for 500 samples from the posterior distribution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

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

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

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

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

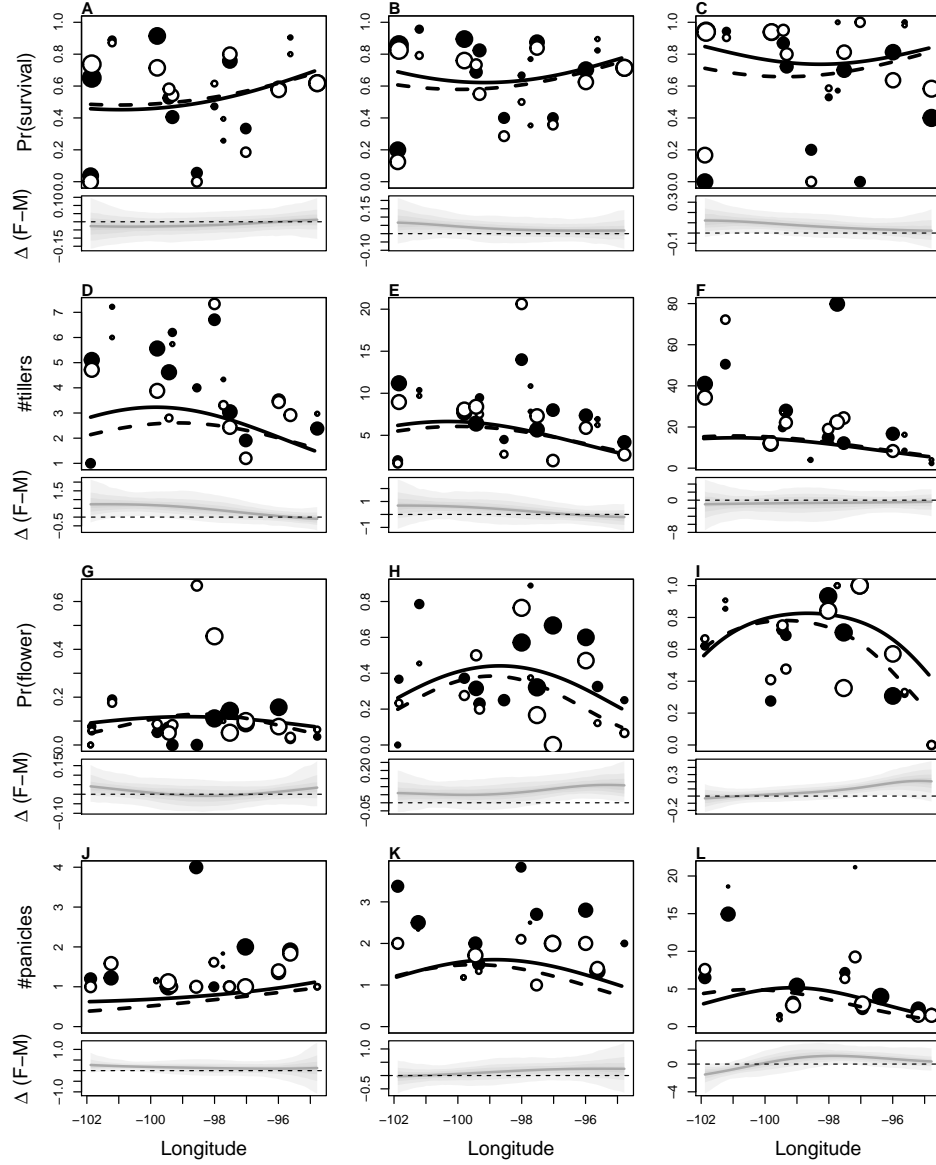


Figure 4: Sex-, size-, and longitude-related variation in: A–C, inter-annual probability of survival; D–F, inter-annual growth (change in number of tillers); G–I, probability of flowering; J–L, number of panicles produced given flowering. Points show means by site for females (filled) and males (open)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

329 rates generated a longitudinal trend in the operational sex ratio of our common
330 garden populations that mirrored the trend in natural populations, with over-
331 representation of female panicles increasing toward eastern range limits. Thus,
332 the common garden experiment indicated that the reproductive niche of females
333 extended farther east than that of males.

334 **Sex-ratio dependent seed fertilization**

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

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

347 The processed-based demographic model connected sex-specific vital rate responses
348 to longitudinal variation (Fig. 4) with sex ratio-dependent mating (Fig. 5) to
349 predict the contributions of females and males to range limitation. The model
350 predicted maximum fitness in the center of the range and declines in population

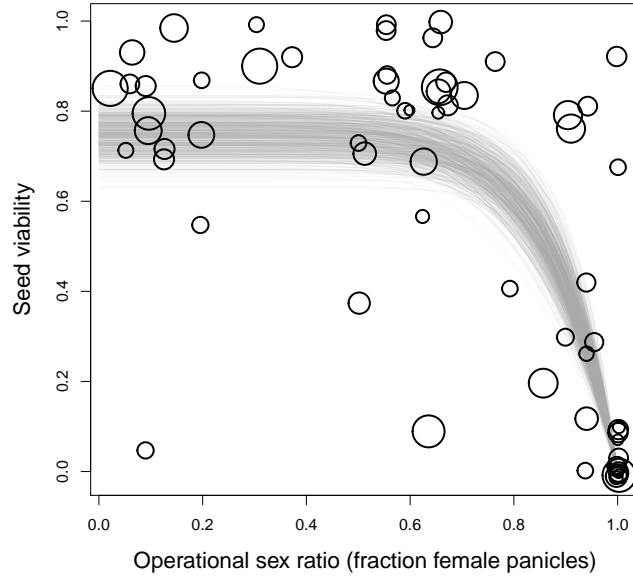


Figure 5: Seed fertilization success in relation to operational sex ratio (fraction of panicles that are female) in experimental populations. Circles show data from tetrazolium assays of seed viability; circle size is proportional to the number of seeds tested (min: 14, max: 57). Lines show fitted model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

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 captures the population dynamics of the focal species.

Decomposition methods revealed that declines in λ 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 female bias in the mating pool at eastern range margins.

Correspondingly, the two-sex model was nearly indistinguishable from a female-dominant model with all else equal except that female seed fertilization did not depend on males (Fig B1). 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 λ was driven most strongly by the decline in female flowering probability at the western limit and by a combination of reduced female flowering and growth at the eastern limit.

Discussion

- Revisit conceptual importance of connecting niche heterogeneity with range limits.
- We found evidence for sexual niche differentiation.
 - Common garden data indicated that females had a reproductive advantage at eastern limits. This recapitulated what we saw in natural population surveys.

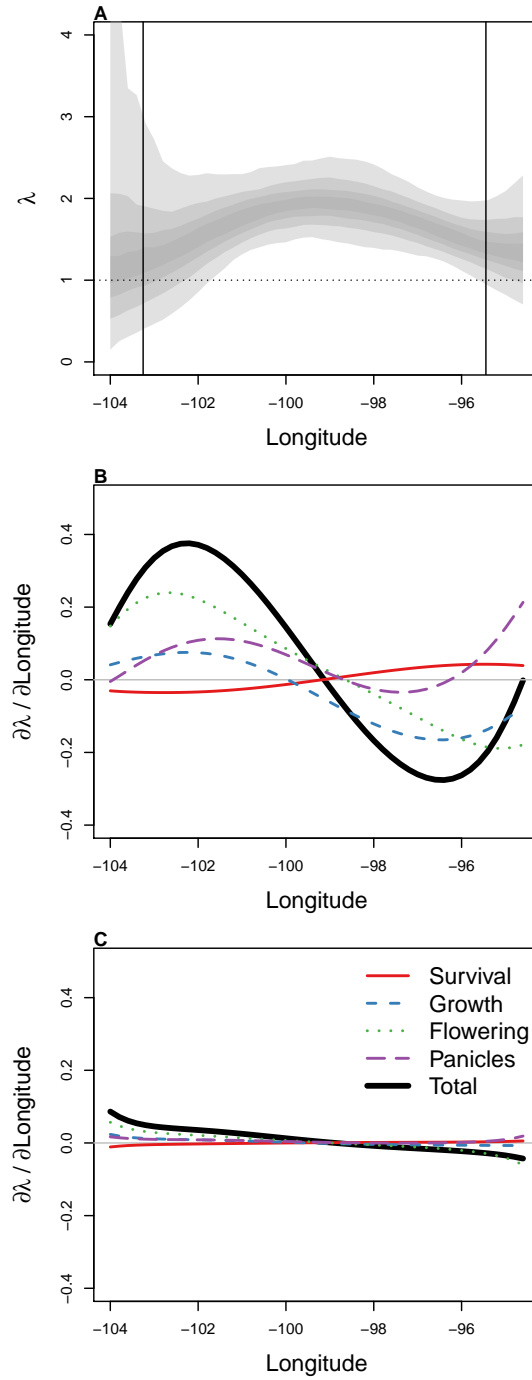


Figure 6: Population growth (λ) as a function of longitude, predicted by the two-sex MPM that incorporates sex-specific demographic responses to longitude with sex ratio-dependent seed fertilization. A, posterior distribution of λ reflecting parameter uncertainty, where shaded regions show the 25, 50, 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.

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378 Author contributions

379 Data accessibility

380 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

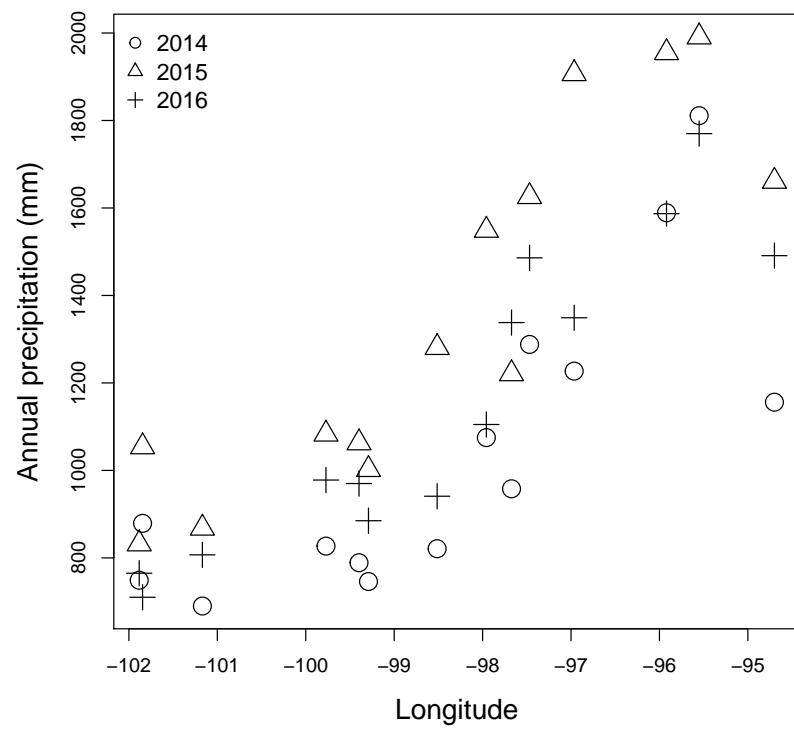


Figure A1: Caption.

502 **Appendix B: Additional results**

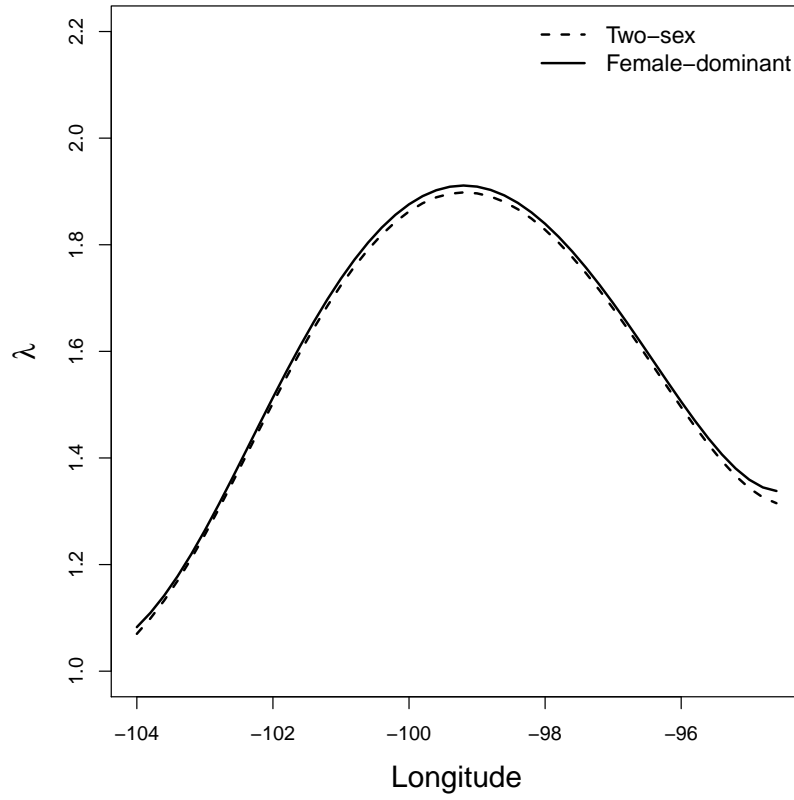


Figure B1: Caption.