

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

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Abstract

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

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

²⁸ **Keywords**

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

³¹ Introduction

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

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

55 we know?

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

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

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

83 Returning to the question of whose niche determines range limits given poten-
84 tial for sexual niche differentiation, classic ecological theory assumes the answer.
85 "Female dominance" is a pervasive, often implicit feature of population-dynamic
86 models whereby male availability is assumed to have no influence on female fer-
87 tility (Miller & Inouye, 2011; Rankin & Kokko, 2007; Caswell & Weeks, 1986).
88 This assumption is, of course, wrong but it may often be a convenient approx-
89 imation when the sex ratio is balanced or does not vary. The female-dominant
90 perspective predicts that female responses to environmental variation should gov-
91 ern range limits (Fig. 1). However, females may be male-limited in environments
92 in which they are favored, which could reduce population viability in marginal
93 environments. This creates an additional, "two-sex" pathway by which environ-
94 mental drivers may set distributional limits, via perturbations to the mating pool
95 that arise from sex-specific responses to the environment (Fig. 1). While sexual
96 niche divergence sets the stage for two-sex dynamics to play an important role in
97 marginal environments, this influence may be dampened in mating systems where
98 single males can fertilize many females (Miller *et al.*, 2011) or in life histories where
99 population viability is weakly sensitive to female fertility (Franco & Silvertown,
100 2004).

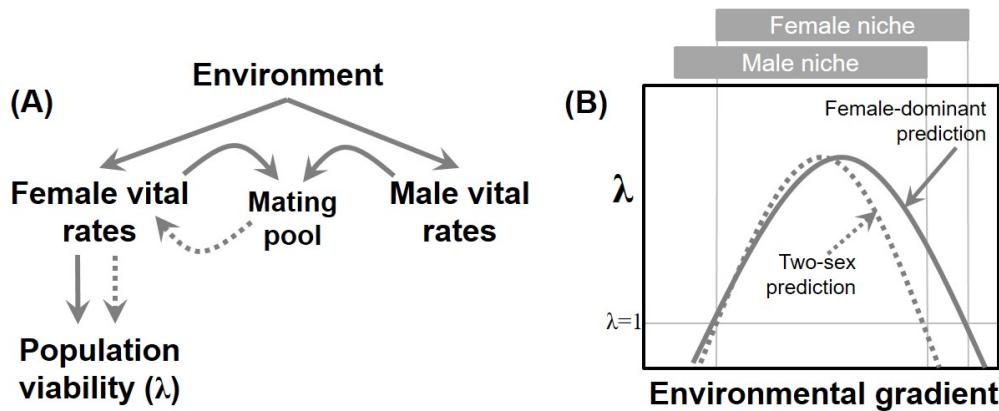


Figure 1: Hypotheses for how environmental variation can affect population viability and range limits in dieocious species. Under the female-dominant hypothesis, environmental drivers affect population growth (λ) through effects on females, alone (A). In geographic / environmental space, this translates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

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

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

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

125 Materials and methods

126 Study system and natural population surveys

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

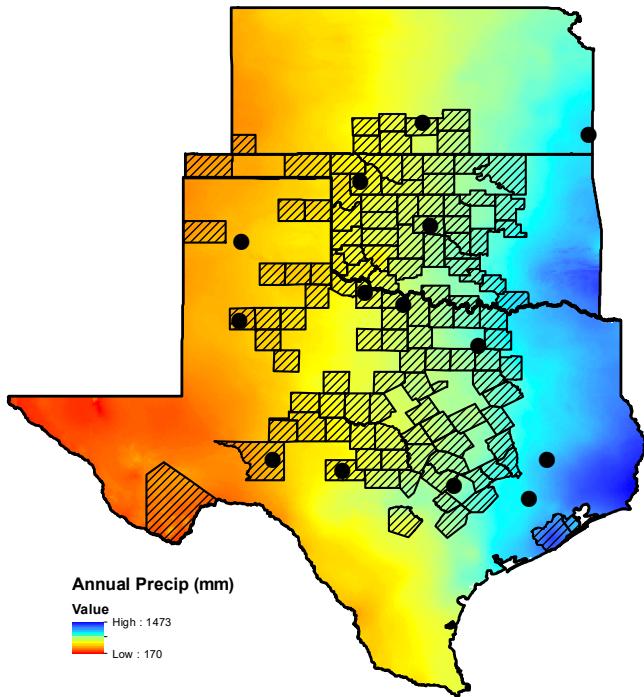


Figure 2: Geographic and environmental distribution of *P. arachnifera* in Texas, Oklahoma, and Kansas. Hatched shapes show counties with herbarium records of occurrence. Color shows geographic variation in annual precipitation (mm) based on 30-year normals from WorldClim (Fick & Hijmans, 2017). Points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

other states¹. Like all grasses, *P. arachnifera* is wind-pollinated. Individuals can be sexed only when flowering, in early spring, based on the presence of stigmas (females) or anthers (males) in the inflorescence. Following inflorescence and seed production, plants go dormant for the hot summer months and vegetative growth resumes in fall. Individuals grow via rhizomes to form “patches” that may be as large as $50m^2$ in area. Sex in *P. arachnifera* is genetically based (Renganayaki *et al.*, 2001, 2005) and the primary sex ratio is 1:1 (J. Goldman, USDA-ARS, *unpubl. data*). The rhizomatous growth habit allowed us to clonally propagate

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

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

139 We surveyed *P. arachnifera* across its range to establish whether natural pop-
140ulations 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 patch. To
145 quantify the mating environment, we focus our analyses on the sex ratio of inflo-
146 rescences rather than patches, since a single patch makes different contributions
147 to 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-
151tional 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-
154tors 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* (Fig. 2). 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 (Fig. 2).
¹⁶⁷ Source material for this experiment came from 8 sites, which were a subset of the
¹⁶⁸ sites that were visited for the natural population survey (Table A1). At these sites,
¹⁶⁹ we collected tillers from flowering individuals of each sex (mean: 11.6 individuals
¹⁷⁰ per site, range: 2–18). These were brought back to the Rice University greenhouse,
¹⁷¹ where they were clonally propagated in ProMix potting soil and supplemental
¹⁷² Osmocote fertilizer at 78–80°F under natural humidity and light.

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

¹⁸³ We visited each site during May of 2015, 2016, and 2017. For each individual in

184 each year, we recorded data for four demographic vital rates: survival status (alive
185 or dead), size (number of tillers), flowering status (reproductive or vegetative), the
186 number of panicles produced by flowering plants.

187 **Statistical analysis of common garden experiment**

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

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

207 **Sex ratio experiment**

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

224 **Statistical analysis of sex ratio experiment**

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

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

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

232 where OSR is the operational sex ratio (fraction of panicles that were female) in
233 our experimental populations. The OSR therefore quantifies the availability of
234 males to each female individual in a population. This function has the properties,
235 supported by our previous work, that seed viability is maximized at v_0 as OSR
236 approaches zero and goes to zero as OSR approaches 1. Parameter α controls how
237 viability declines with increasing female bias.

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

246 Demographic model of range limits

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

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

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

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

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

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

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

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

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

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

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

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

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

285 these functions may be unique to females (F) and males (M). All parameter es-
 286 timates were derived from the statistical modeling described above, except where
 287 noted, and are reported in Table A1².

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

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

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

²This table does not exist yet.

303 Results

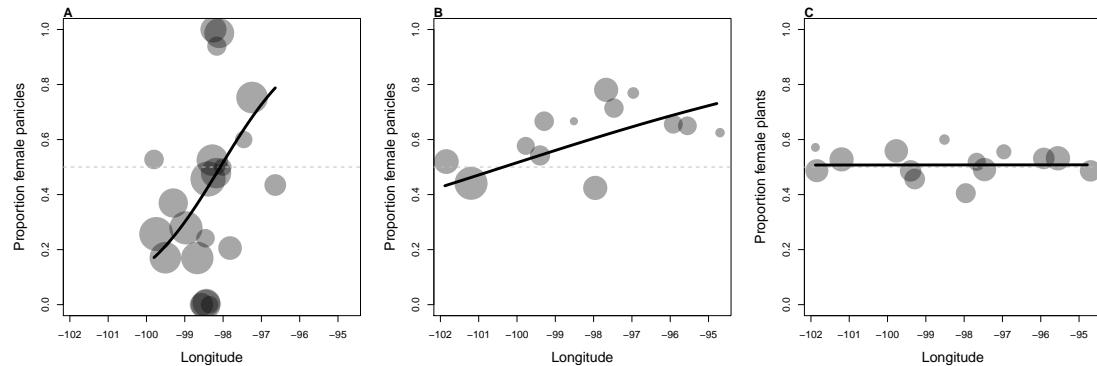


Figure 3: Sex ratio variation of *P. arachnifera* across its longitudinal distribution. **A**, Operational sex ratio (fraction of panicles that were female) in 22 natural populations; **B**, Operational sex ratio and **C**, sex ratio (fraction of plants that were female) in 14 common gardens. Within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

304 Sex ratio variation in natural populations

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

310 Geographic variation in sex-specific demography

In year one, there was near-total mortality of transplants in the common garden experiment at three sites due to various catastrophes (a flood, a drought, a pack of

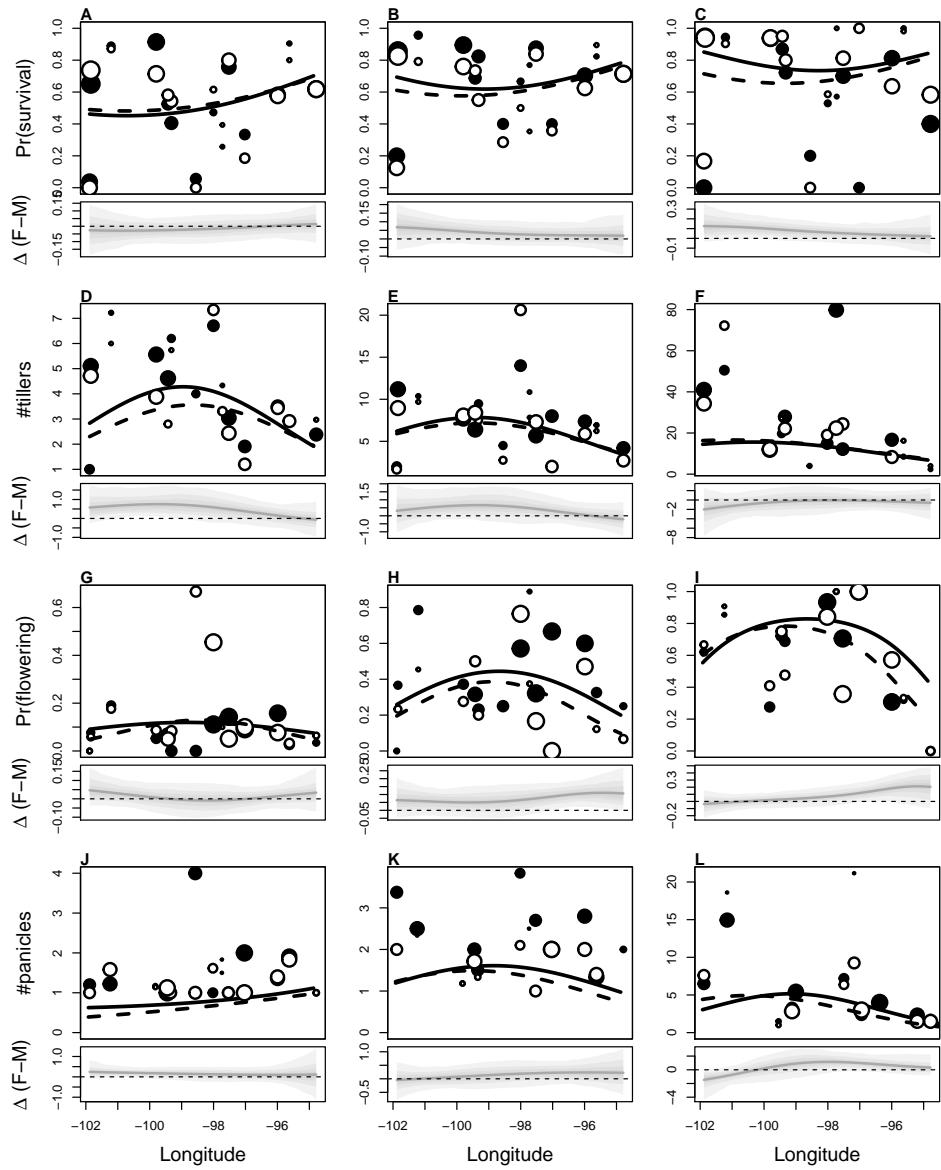


Figure 4: Sex-, size-, and longitude-related variation in: A–C, inter-annual probability of survival; D–F, inter-annual growth (change in number of tillers); G–I, probability of flowering; J–L, number of panicles produced given flowering. Points show means by site for females (filled) and males (open) and small (left column), medium (middle column), and large (right column) size classes (discretized, for visualization only). Point size is proportional to the sample size of the mean. Lines show fitted statistical models for females (solid) and males (dashed) based on posterior mean parameter values. Lower panels below each data panel show the posterior distribution of the difference between females and males as a function of longitude (positive and negative values indicate female and male advantage, respectively); dashed horizontal line shows zero difference.

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

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

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

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

341 **Sex-ratio dependent seed fertilization**

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

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

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

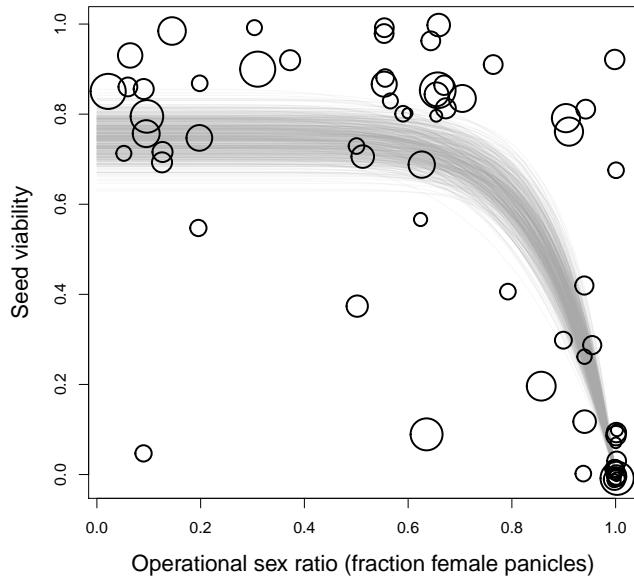


Figure 5: Seed fertilization success in relation to operational sex ratio (fraction of panicles that are female) in experimental populations. Circles show data from tetrazolium assays of seed viability; circle size is proportional to the number of seeds tested (min: 14, max: 57). Lines show model predictions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

uncertainty distribution of the model's predictions (represented by the shading in Fig. 6A), bolstering our confidence that the model effectively captured geographic patterns in the population viability of this species. Also, the asymptotic population structure predicted by the model showed skew in the operational (panicle) sex ratio with increasing female bias toward the eastern range margins, consistent with observations in the field (Fig. C3A). Female bias in the OSR was predicted to cause declines in seed viability toward eastern range margins (Fig. C3B). However, this effect was weak in magnitude because predicted OSR bias was not extreme enough to cause strong declines in viability, given the relationship derived from

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

372 LTRE decomposition methods revealed that declines in λ approaching range
373 limits were driven almost exclusively by females (Fig. 6B) with near-zero contribu-
374 tions from males (Fig. 6C). Thus, range limitation was an effectively female-
375 dominant process, despite systematic geographic variation in sex ratio. Corre-
376 spondingly, predictions of the two-sex model were nearly indistinguishable from
377 a corresponding female-dominant model with all else equal except that female
378 seed fertilization did not depend on males, with only very modest differences in
379 predictions of the two models emerging in the eastern part of the range (Fig. C2).

380 Decomposition analysis further revealed that multiple female vital rates con-
381 tributed to range limits, some in opposing directions. Because female survival
382 increased toward range limits (Fig 4A-C), this vital rate had a contribution to
383 $\frac{\partial \lambda}{\partial Longitude}$ that was opposite in sign to the other vital rates (Fig. 6B). However,
384 increased survival at range edges was not sufficient to offset declines in other vi-
385 tal rates. The overall decline in λ was driven most strongly by a combination of
386 reduced flowering and growth in females at both the eastern and western limits
387 (Fig. 6B).

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

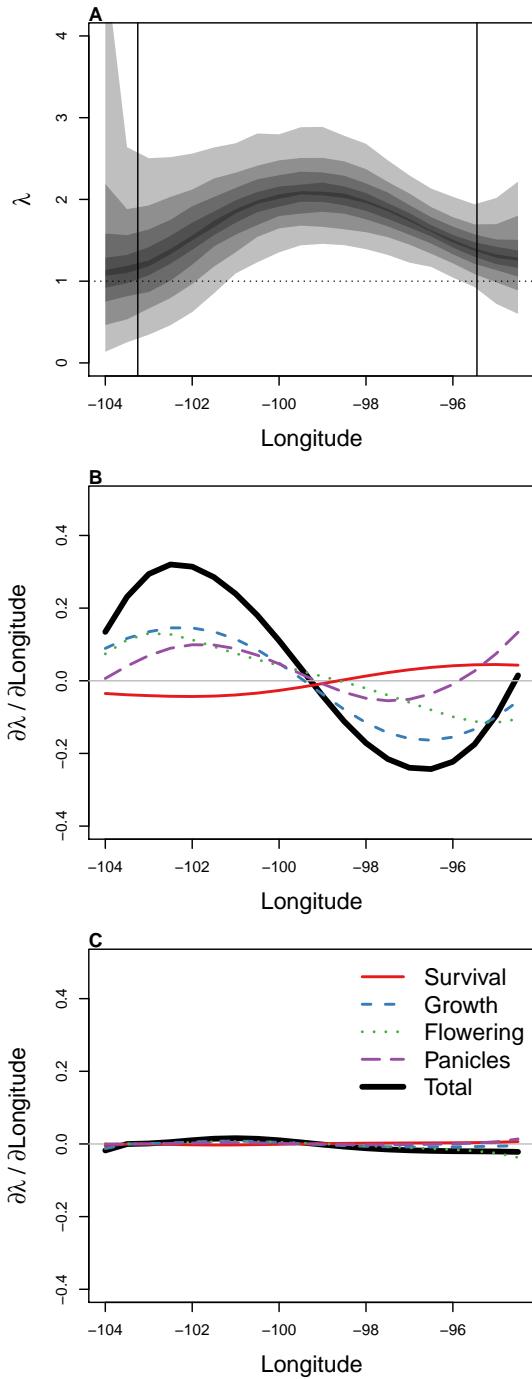


Figure 6: Population growth (λ) as a function of longitude, predicted by the two-sex MPM that incorporates sex-specific demographic responses to longitude with sex ratio-dependent seed fertilization. A, posterior distribution of λ , where shaded regions show the 25, 50, 75, and 95% percentiles of parameter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

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

410 Discussion

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

the female reproductive niche extended farther east than that of males, generating female-biased operational sex ratios toward the eastern, mesic range margins, a pattern detected in natural populations and recapitulated in our common garden experiment. Furthermore, seed viability declined with increasing skew in the OSR, indicating that mate (pollen) limitation can limit female reproductive output in female-biased mating pools. It would appear that all the pieces are in place for an important role of two-sex dynamics in generating distributional limits, particularly at the eastern edges of Texas bluegrass. Yet, the insights derived from a field-parameterized population model indicate the opposite: range limitation in this species was an effectively female-dominant process, with negligible contributions from males. Thus, female dominance is not a “straw man” null hypothesis; in this system and likely others, males did not meaningfully contribute to population dynamics. Of course, *some* males are required for successful regeneration but within this species’ range of sex ratio variation, and given the demographic sensitivities to sex ratio, explicitly accounting for inter-sexual interactions did not meaningfully improve understanding of range limitation. In the remainder of this section, we discuss these results and their broader significance in greater depth.

Our results suggest that in long-lived species with polygamous mating systems, range limits should reflect the niche limits of females. Polygyny implies mate limitation only at highly skewed sex ratios, and the population of long-lived species do not strongly depend on reproduction. Our polygynous model organism showed that mate limitation occurred became substantial only in populations comprised of 70% females. Moreover, in long-lived species population growth rates will depend only weakly to reproduction (Franco & Silvertown, 2004). However, our results do not rule out the possibility that range limits are determined by both sexes in short-

442 lived, polygynous species. Because short-lived species are sensitive to reproduction,
443 mate limitation will have substantial effects on their long-term population growth
444 rate. Mate limitation would therefore affect range limit formation when the OSR
445 of a short-lived species changed dramatically across environmental gradients. The
446 literature provides several examples of short-lived species with environmentally
447 controlled OSR (Freeman *et al.*, 1976; Freeman & Vitale, 1985; Purrington, 1993;
448 Eppley, 2001). However, we have still no way to predict species whose OSR changes
449 predictable across environmental gradients. We do have species-specific studies
450 that explain the mechanisms that determine skewed OSR, such as sex differences
451 in mortality (Meagher, 1981). However, there is no theory to predict dioecious
452 species with environmentally controlled OSR.

453 However, the premises for males to contribute in range limit formation, albeit
454 rare, are likely to occur in nature. First, female-skewed sex ratios are common
455 both plants (Barrett *et al.*, 2010) and animals (Caswell, 2001). Second, there
456 are several examples of plants responding in contrasting ways to environmental
457 gradients according to sex (Bierzychudek & Eckhart, 1988). These patterns can
458 be driven by several mechanisms, such as physiology (Dawson & Geber, 1999),
459 differences in competitive ability (Eppley, 2006), or demographic rates (Delph,
460 1999). Third, mate limitation is common in both animals (Gascoigne *et al.*, 2009)
461 and plants (Ashman *et al.*, 2004). Accordingly, in plants, pollen limitation is
462 considered the reason why dioecious plant species tend to have a substantially
463 smaller range than selfing species (Grossenbacher *et al.*, 2015).

464 Our results reinforce the commonality of demographic compensation in nature.
465 Demographic compensation occurs when the vital rates of a species have opposing
466 trends across an environmental gradient (Villellas *et al.*, 2015). Our results show

467 that in *P. arachnifera*, survival tended to compensate the negative response of the
468 remaining vital rates at latitudinal extremes. However, this compensation was
469 not sufficient to prevent a decrease in population growth rates at the extremes
470 of the longitudinal range of the species. A recent study found a similar pattern,
471 where compensation between vital rates could not prevent a decrease of population
472 growth rate towards the southern range edge of *Erythranthe cardinalis* (Sheth &
473 Angert, 2018).

474 Despite demographic compensation, our evidence is consistent with the abun-
475 dant center hypothesis of range formation. This hypothesis posits that the fitness
476 and abundance of species will gradually decrease towards range edges (Brown
477 *et al.*, 1995). This is what our population model predicts, with maximum popu-
478 lation growth rates at the center of the longitudinal gradient. However, to date
479 the literature found mixed or contradictory evidence for this hypothesis. These
480 previous tests relied on vital rates rather than population growth rates, providing
481 contrasting results (Sexton *et al.*, 2009; Abeli *et al.*, 2014). As we show here, con-
482 trasting results among vital rates are expected, because demographic compensation
483 is adaptive (Villellas *et al.*, 2015). Accordingly, studies that calculate population
484 growth rates along an environmental gradient tend to support the abundant cen-
485 ter hypothesis. We know of four such studies in the existing literature, three of
486 which showed a decrease in population growth rates towards at least one end of
487 the environmental gradients (Eckhart *et al.*, 2011; Sheth & Angert, 2018; Baer &
488 Maron, 2019). The fourth study showed population growth rate along environmen-
489 tal gradients was unpredictable (Oldfather & Ackerly, 2019). However, this last
490 study emphasized the importance of microclimate, which can vary dramatically
491 in alpine environments (Scherrer & Koerner, 2010). Hence, our results suggest

⁴⁹² that the abundant center hypothesis might hold in the studies that use population
⁴⁹³ growth rate as response variable.

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⁵⁰⁰ Author contributions

⁵⁰¹ A.C. and T.E.X.M. designed the study. A.C., and T.E.X.M. carried out the study.
⁵⁰² T.E.X.M. and A.C. conducted the statistical analyses and drafted the manuscript.
⁵⁰³ A.C. and T.E.X.M. finalized the manuscript.

⁵⁰⁴ Data accessibility

⁵⁰⁵ References

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688 **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

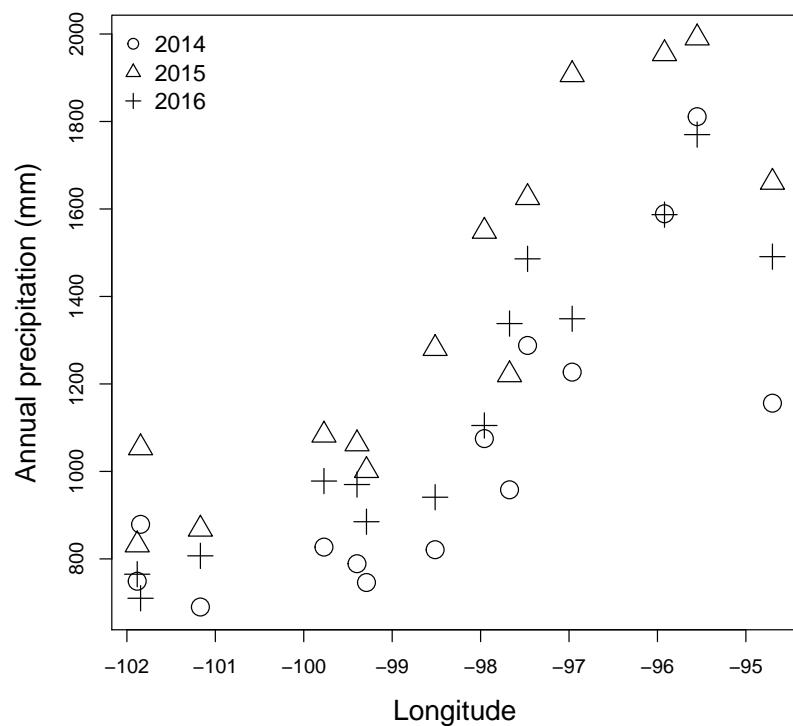


Figure A1: Total annual precipitation at common garden sites during the study years tracked long-term trends of increasing aridity from east to west.

⁶⁸⁹ Appendix B: Parameter estimates of two-sex MPM

690 Appendix C: Additional results

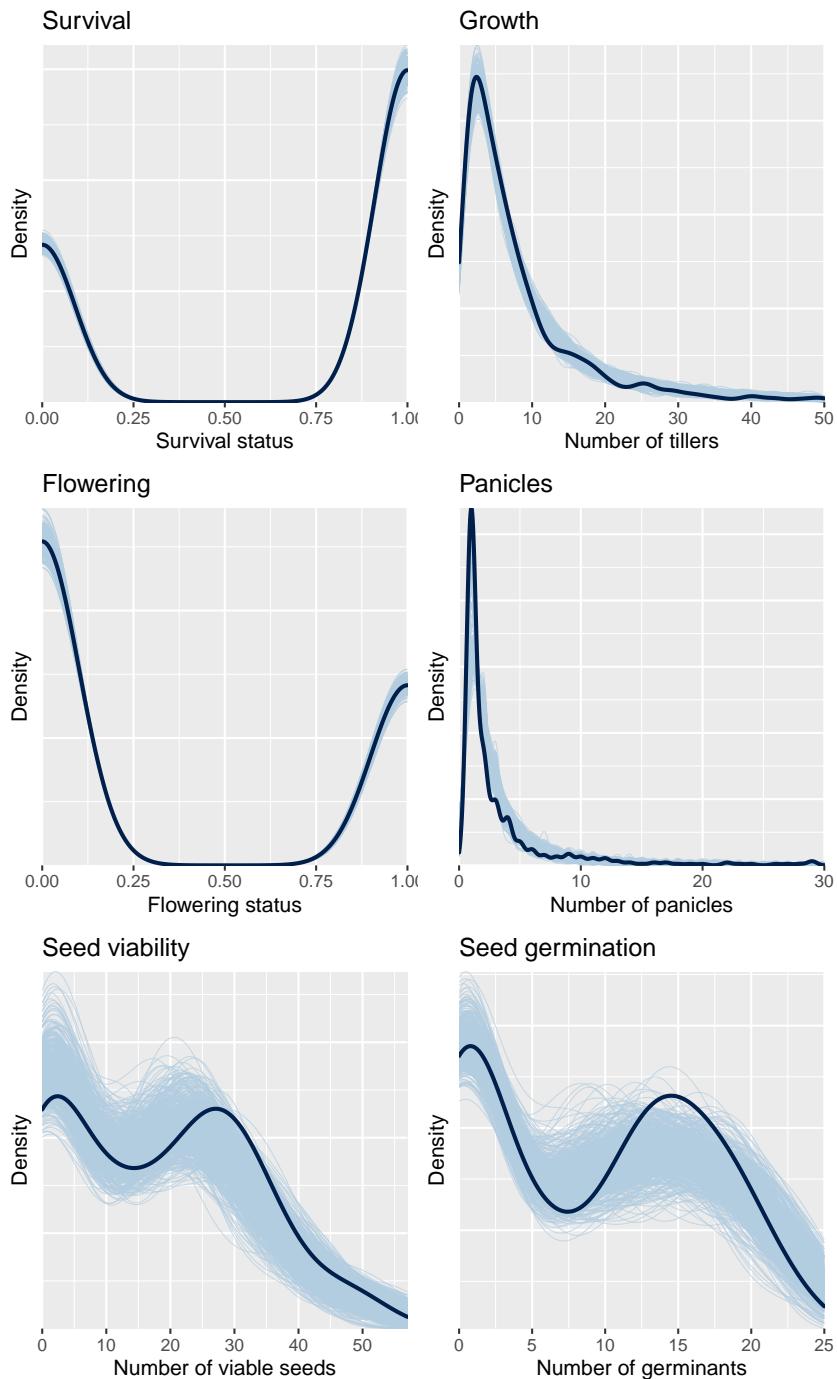


Figure C1: Posterior predictive checks of statistical models for demographic vital rates. Lines show density distributions of real data (thick, dark blue) compared to simulated data sets (thin, light blue) generated from the fitted models based on 500 draws of the posterior distribution of parameter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

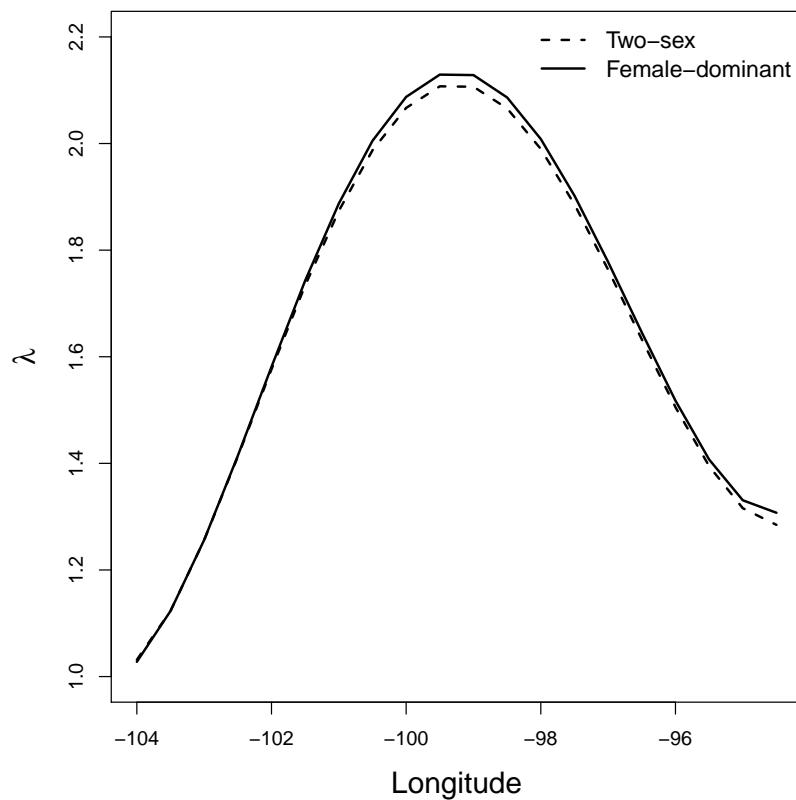


Figure C2: Comparison of longitudinal variation in λ between the two-sex demographic model (dashed line) that includes dependence of female seed production on population structure and the corresponding female-dominant model (solid line) with constant female fertility and all else equal. Models were evaluated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

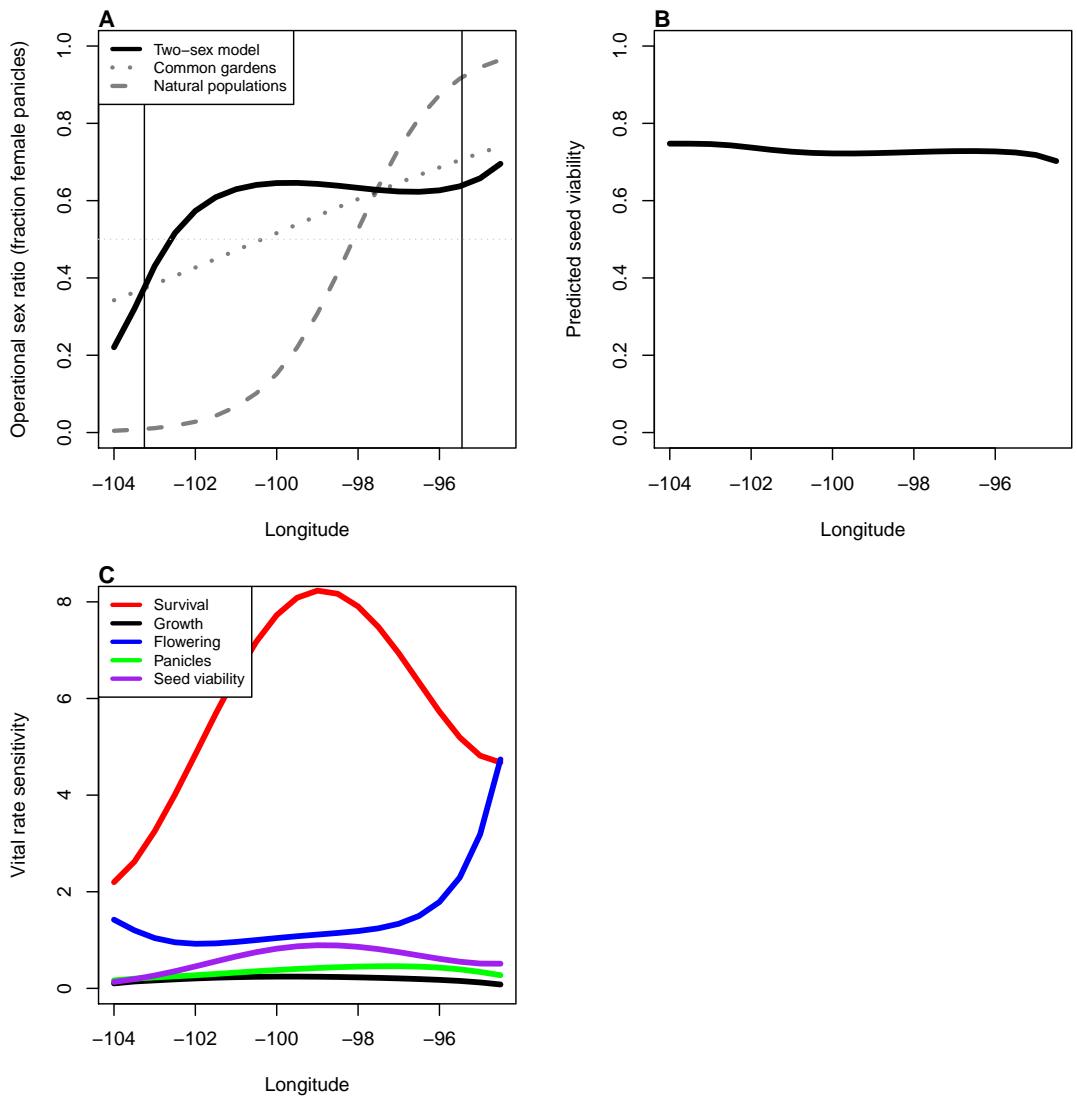


Figure C3: **A**, Longitudinal variation in operational sex ratio (fraction of panicles that are female) predicted by the two-sex MPM (solid line) compared to the sex ratio clines fitted to data from common gardens (dotted line) or natural populations (dashed line). Vertical lines show the longitudes of the westernmost and easternmost counties with occurrence records of *P. arachnifera*. **B**, Longitudinal variation in seed viability predicted by the two-sex MPM according to Eq. 1 and the OSR variation shown in **A**. **C**, Sensitivities of λ to vital rates in relation to longitude. Sensitivities were calculated numerically by perturbing vital rate functions (across all sizes) by 0.01, recalculating λ , and dividing the difference by 0.01. Vital rates were perturbed equally for both sexes though results in Fig 6B,C suggest that vital rate sensitivities were dominated by females.

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

692 **ulation experiments**

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

696 **Observed and predicted size distributions**

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

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

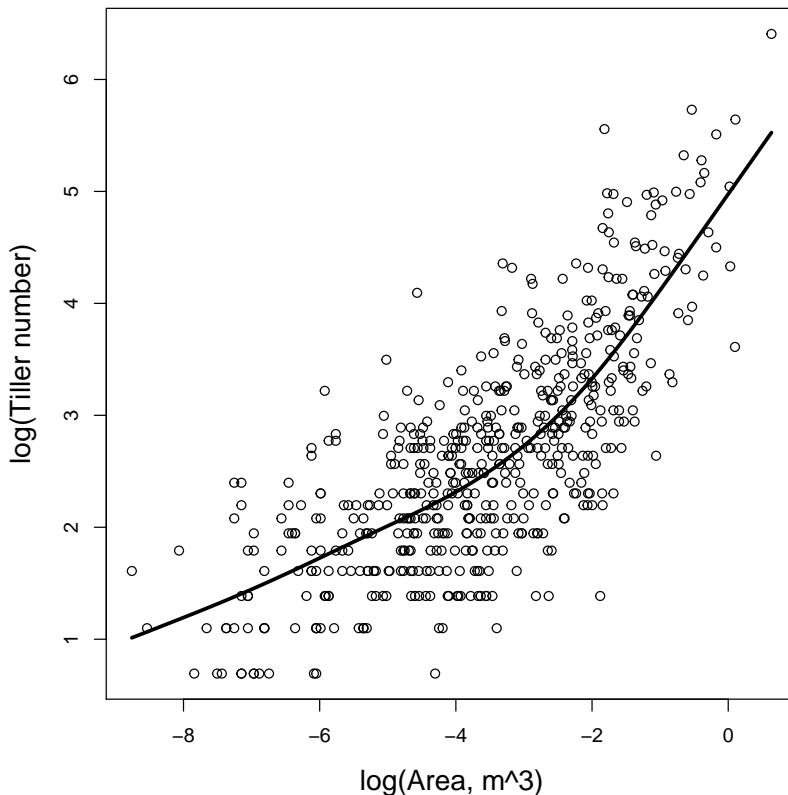


Figure D1: Relationship between area (m^3) and tiller count from plants in the common garden experiment. The fitted gam model (line) was used to convert area measurements from natural populations to tiller counts.

708 **Two-sex MPM** The two-sex MPM predicts asymptotic population structure,
 709 including stable size distribution (SSD) and sex ratio. For comparison with em-
 710 pirical data, we calculated the SSD (pooling both sexes) predicted in the center of
 711 the range (the conclusions that we draw from this analysis hold up if we consider
 712 SSD from different parts of the range). Because the MPM is structured by tiller
 713 number, we converted the SSD to $\log(\text{tillers})$ by simulating an arbitrarily large
 714 (10000) population at SSD, taking the natural logarithm of tiller number, and
 715 then estimating the empirical distribution of this variable.

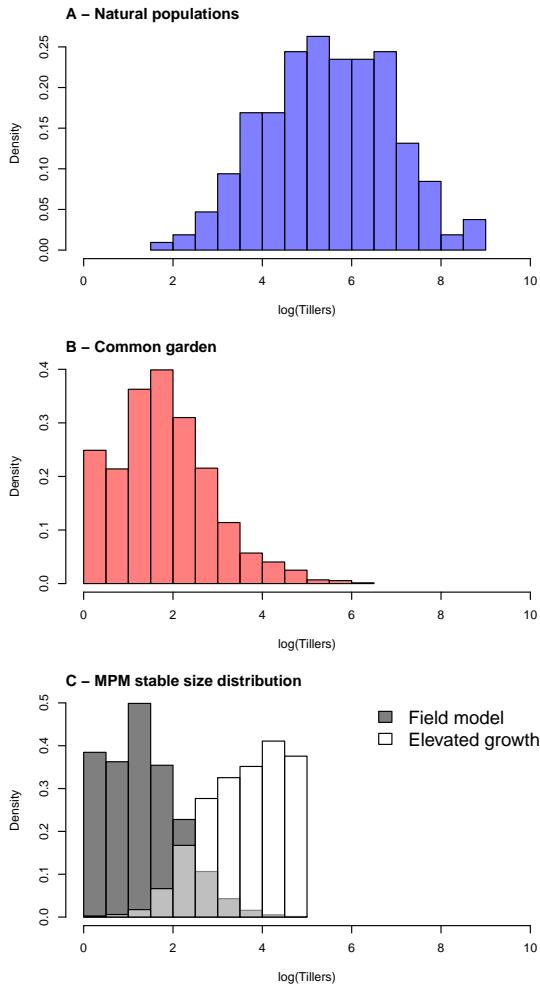


Figure D2: Size distribution of Texas bluegrass from natural populations (A), common garden populations (B), and predicted by the two-sex MPM (C). In C, the two size distributions come from the base model parameterized following methods described in the main manuscript (gray) and a numerical experiment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

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

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

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

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

⁷⁴² empirically-estimated intercept of the growth vital rate function by a factor of 2.75
⁷⁴³ (values larger than this caused numerical instabilities). This adjustment caused all
⁷⁴⁴ plants to increase in size more strongly regardless of initial size, sex, or geographic
⁷⁴⁵ location.

⁷⁴⁶ As expected, this led to stronger sex ratio clines and stronger reductions in
⁷⁴⁷ seed viability at eastern range margins (Fig. D3). These changes increased the
⁷⁴⁸ contributions of males to eastern range limitation in the elevated-growth numerical
⁷⁴⁹ experiment. However, the contribution of males to range limitation was still weak
⁷⁵⁰ relative to that of females (the maximum male contribution was less than half of
⁷⁵¹ the female maximum) and differences between the two-sex and female-dominant
⁷⁵² MPMs were still very minor (Fig. D4). Collectively, these results suggest that the
⁷⁵³ small size distribution of the common garden experiment led to a weaker role of
⁷⁵⁴ males than would be expected in populations with a more realistic size distribution,
⁷⁵⁵ but that even with a larger size distribution, declines in female performance still
⁷⁵⁶ dominate range boundary formation.

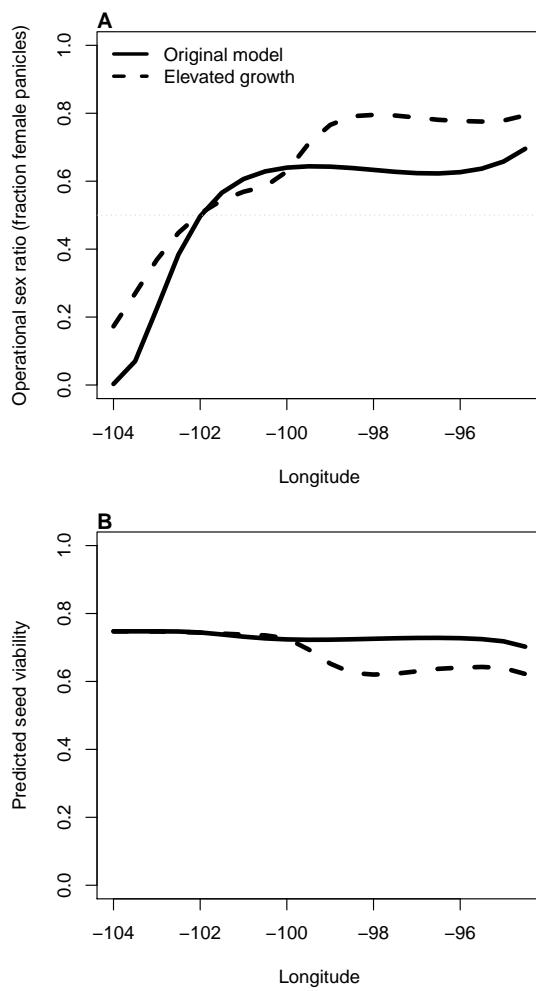


Figure D3: Two-sex model predictions for **A** operational sex ratio (fraction of panicles that are female) and **B** seed viability at stable population structure in relation to longitude. Solid line shows predictions of the base model using field-estimated parameter values and dashed line shows the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

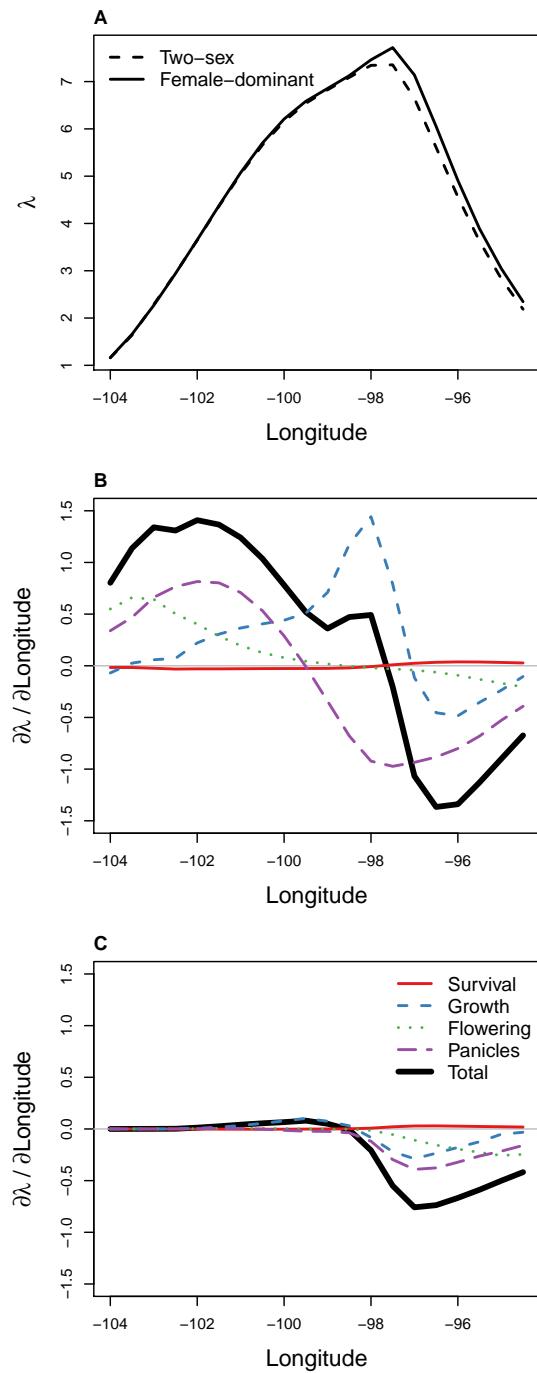


Figure D4: Results for the elevated growth model, in which the intercept of growth function was increased by a factor of 2.75. **A**, contrast of two-sex and female-dominant models, as in Fig. C2; **B,C**, Life Table Response Experiments decomposing the change in λ with respect to longitude into contributions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