

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

Tom E.X. Miller* and Aldo Compagnoni

Program in Ecology and Evolutionary Biology, Department of
BioSciences, Rice University, Houston, TX USA

*Corresponding author: tom.miller@rice.edu (1-713-348-4218)

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

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

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

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

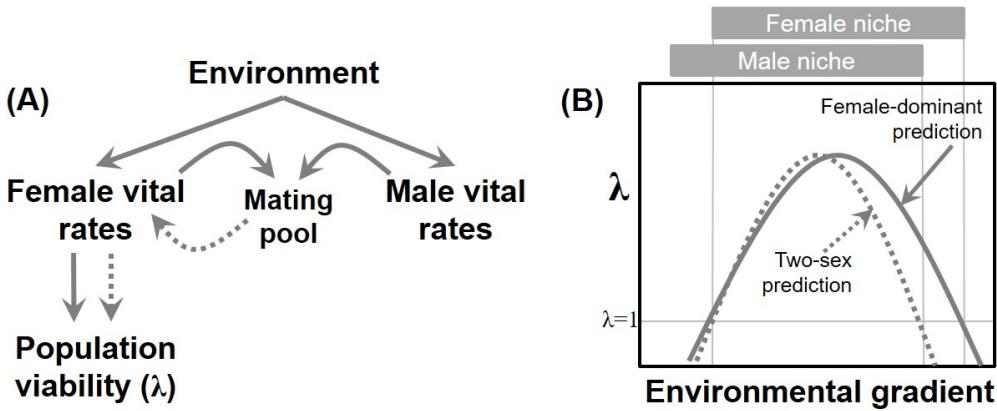


Figure 1: Hypotheses for how environmental variation can affect population viability and range limits in dieocious species. Under the female-dominant hypothesis, environmental drivers affect population growth (λ) through effects on females, alone (A). In geographic / environmental space, this translates 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 whether female demographic responses to environmental variation,
 102 alone, are sufficient to understand the ecological origins of range limits, or whether
 103 males and female-male interactions must additionally be considered. As an experi-
 104 mental model, we worked with a dieocious plant species (the grass *Poa arachnifera*)
 105 narrowly distributed across the sharp longitudinal aridity gradient of the southern
 106 Great Plains, US (Fig. 2). The environmental isocline governing aridity in this
 107 region is expected to shift eastward under climate change (Karl *et al.*, 2009), so
 108 understanding how it sets distributional limits may aid in forecasting future range

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

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

Materials and methods

Study system and natural population surveys

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

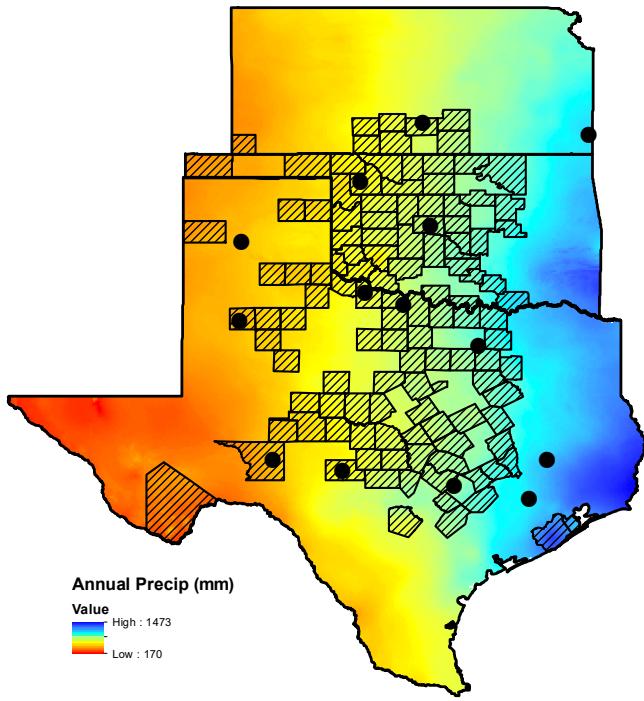


Figure 2: Geographic and environmental distribution of *P. arachnifera* in Texas, Oklahoma, and Kansas. Hatched shapes show counties with herbarium records of occurrence. Color shows geographic variation in annual precipitation (mm) based on 30-year normals from WorldClim (Fick & Hijmans, 2017). Points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

populations in other 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 popu-
140 lations exhibited geographic clines in OSR corresponding to the longitudinal aridity
141 gradient. We visited 14 populations in spring 2012 and 8 in spring 2013 (Table
142 A1). At each location, we searched for *P. arachnifera* along roads, trails, or creek
143 drainages and recorded the number of female and male patches that we encoun-
144 tered and the number of inflorescences in each patch. To quantify the mating
145 environment, we focus our analyses on the sex ratio of inflorescences rather than
146 patches, since a single patch makes different contributions to the mating pool
147 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 OSR var-
151 ied systematically with respect to longitude. Here and in the experiments that
152 follow we use longitude as a proxy variable that captures all east-west environ-
153 mental variation, notably precipitation (Fig. 2) but also factors that co-vary
154 with precipitation such as productivity. This statistical model and all those
155 that follow were fit in a Bayesian statistical framework using Stan (Carpenter
156 *et al.*, 2017) and rstan (Team *et al.*, 2018) with vague priors on all parame-
157 ters. In all cases, model fit was assessed with posterior predictive checks (Conn
158 *et al.*, 2018). All code for statistical and demographic modeling is available at
159 <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 (2014–2017), total precipitation at each site
¹⁶⁶ closely tracked longitude (Fig. A1), as expected based on longer-term climate
¹⁶⁷ trends (Fig. 2). Source material for the experiment came from 8 sites, which were
¹⁶⁸ a subset of the sites that were visited for the natural population survey (Table
¹⁶⁹ A1). At these sites, we collected vegetative tillers from flowering individuals of
¹⁷⁰ each sex (mean: 11.6 individuals per site, range: 2–18). These were brought back
¹⁷¹ to the Rice University greenhouse, where they were clonally propagated in ProMix
¹⁷² potting soil and supplemented with Osmocote slow-release fertilizer at 78–80°F
¹⁷³ under natural humidity and 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 spondes, 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 did 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 mod-
200 els applied the logit link function. We modeled panicle counts as zero-truncated
201 negative binomial using the log link. For growth, we modeled tiller number with
202 a zero-truncated Poisson-Inverse Gaussian (PIG) distribution. For flowering and
203 panicle production in year t , the size covariate was the natural logarithm of tiller
204 number in year t . For survival and size in year t , the size covariate was the natural
205 logarithm of tiller number in year $t - 1$ (for 2015 data, size in year $t - 1$ was
206 transplant size at the time of planting). Posterior predictive checks indicated that
207 these models described the data well (Fig. B1).

208 **Sex ratio experiment**

209 At one site near the center of the range (Lake Lewisville Environmental Learning
210 Area, Texas), we established a separate experiment to quantify how sex ratio
211 variation affects female reproductive success. Details of this experiment, which
212 was conducted in 2014–2015, are described in Compagnoni *et al.* 2017. Briefly, we
213 established 124 experimental populations in $0.4m \times 0.4m$ plots that varied in popu-
214 lation density (1–48 plants/plot) and sex ratio (0–100%female), with 2–4 replicates
215 each of 34 density-sex ratio combinations. The experiment was established ca. 1
216 km from a natural population at this site and plots were situated with a minimum
217 of 15 m spacing, a buffer that was intended to limit pollen movement between
218 plots (pilot data indicated that $\geq 90\%$ of wind pollination occurred within 13m).
219 We measured female reproductive success in different density and sex ratio envi-
220 ronments by collecting panicles from a subset of females in each plot at the end
221 of the reproductive season. In the lab, we counted the total number of seeds on
222 each panicle and assessed seed viability in the greenhouse with germination trials
223 of 25 seeds per panicle. We also conducted tetrazolium-based seed viability assays
224 (17–57 seeds per panicle, mode: 30).

225 **Statistical analysis of sex ratio experiment**

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

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

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

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

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

247 Demographic model of range limits

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

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

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

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

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

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

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

²⁷⁰ Seed fertilization depends on the OSR of panicles (following Eq. 1) which was
²⁷¹ derived from the $U \times 1$ vectors of population structure \mathbf{F}_t and \mathbf{M}_t :

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

²⁷² Finally, the dynamics of the size-structured component of the population are
²⁷³ given by:

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

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

²⁷⁴ For both females and males, the first term represents seedlings that survived their
²⁷⁵ first year and enter the size distribution of established plants. Because our common
²⁷⁶ garden experiment relied on greenhouse-raised transplants, we had little informa-
²⁷⁷ tion on these early life cycle transitions. We used the seedling survival probability
²⁷⁸ (σ) from our demographic studies of the perennial congener *Poa autumnalis* in
²⁷⁹ east Texas (T.E.X. Miller and J.A. Rudgers, *unpublished data*) as a stand-in for *P.*
²⁸⁰ *arachnifera*, and we assume this probability was constant across sexes and longi-
²⁸¹ tudes ($\sigma = 0.09$). We also assume that surviving seedlings reach size y with prob-
²⁸² ability $g(y, x = 1)$, the expected future size of 1-tiller plants from the transplant
²⁸³ experiment. The second term represents survival and size transition of established
²⁸⁴ plants from the previous year, where s and g give the probabilities of surviving at
²⁸⁵ size x and growing from sizes x to y , respectively, and superscripts indicate that

286 these functions may be unique to females (F) and males (M).

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

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

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

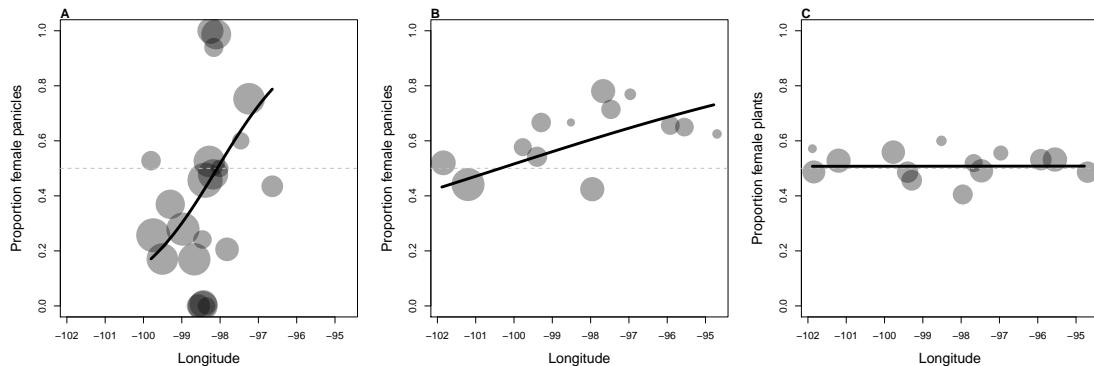


Figure 3: Sex ratio variation of *P. arachnifera* across its longitudinal distribution. **A**, Operational sex ratio (fraction of panicles that were female) in 22 natural populations; **B**, Operational sex ratio and **C**, sex ratio (fraction of plants that were female) in 14 common gardens. Within 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.

302 Results

303 Sex ratio variation in natural populations

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

309 Geographic variation in sex-specific demography

310 In year one, there was near-total mortality of transplants at three sites in the
 311 common garden experiment due to various catastrophes (a flood, a drought, a
 312 pack of voles); otherwise, there was high (95%) establishment. There was strong

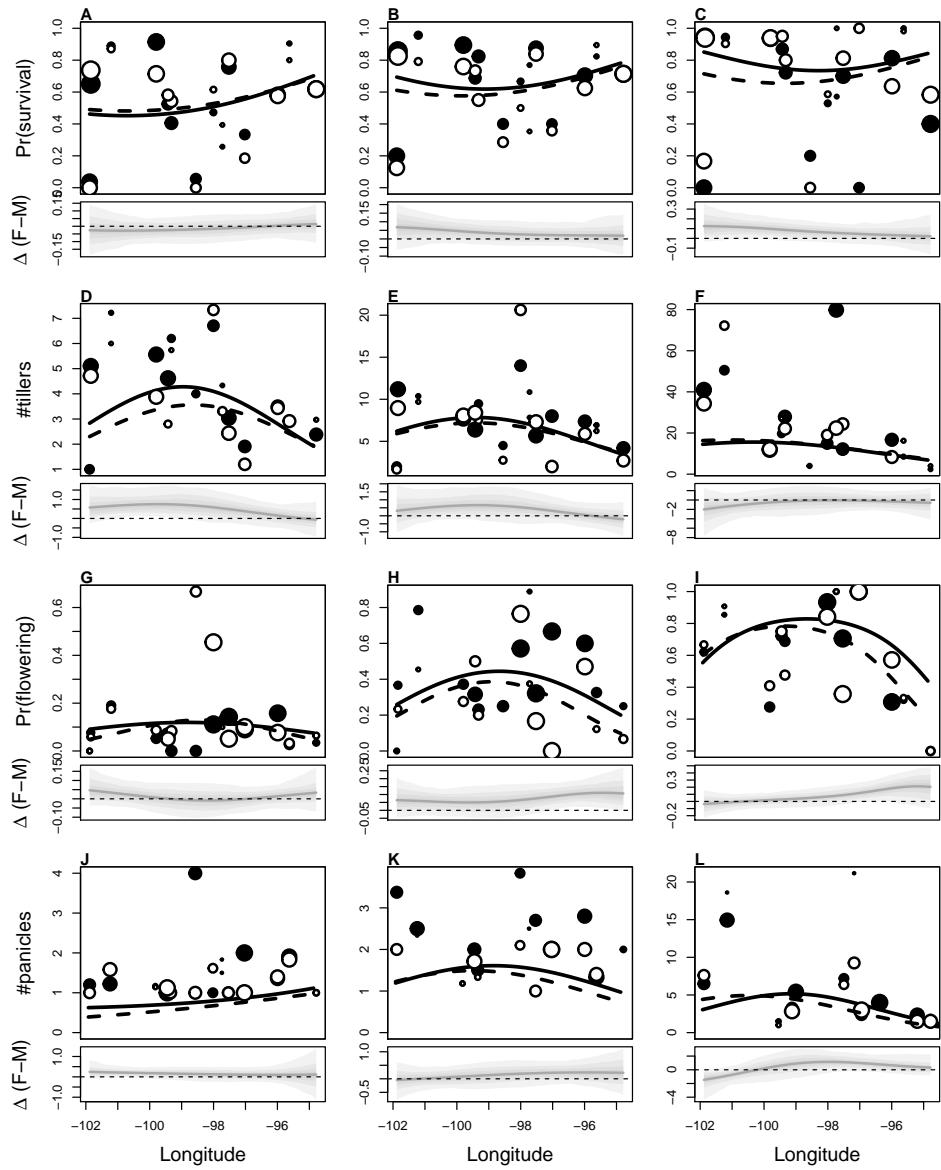


Figure 4: Sex-, size-, and longitude-related variation in: A–C, inter-annual probability of survival; D–F, inter-annual growth (change in number of tillers); G–I, probability of flowering; J–L, number of panicles produced given flowering. Points show means by site for females (filled) and males (open) 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 longitudinal variation in demography, including sex-specific demographic responses
314 that varied across vital rates and interactions between size, sex, and longitude.
315 Where sex-specific demographic responses occurred, they were almost always in
316 favor of females. In Fig. 4, we show binned means of raw data and fitted vital
317 rate models for four vital rates (rows) and three size classes (columns); size was
318 discretized for visualization only. This figure also shows the posterior distributions
319 for the difference between the sexes across longitudes.

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

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

³³⁸ mating pool of natural populations was due to the reproductive niche of females
³³⁹ extending farther east than that of males, and not to sex differences in mortality.

³⁴⁰ **Sex-ratio dependent seed fertilization**

³⁴¹ Seed fertilitzation by females declined with increasing female bias in the sex ratio
³⁴² manipulation experiment. Fertilization success was greatest for females that were
³⁴³ rare in male-biased populations, where 75-80% of initiated seeds were viable (Fig.
³⁴⁴ 5). Fertilization was robust to sex ratio variation until ca. 75% of the panicles
³⁴⁵ in a population were female, at which point fertilization strongly declined due to
³⁴⁶ pollen limitation. The fitted model specifies that seed fertilization goes to zero as
³⁴⁷ female bias goes to 100% (Eq. 1), and this assumption was generally consistent
³⁴⁸ with the experimental results, where the majority (63%) of females from female-
³⁴⁹ only populations produced zero viable seeds. The occasional production of viable
³⁵⁰ seeds in female-only populations (Fig. 5) likely reflects rare pollen contamination
³⁵¹ between experimental plots.

³⁵² **Two-sex model of range limits**

³⁵³ The processed-based demographic model connected sex-specific vital rate responses
³⁵⁴ to longitudinal variation (Fig. 4) with sex ratio-dependent mating (Fig. 5) to
³⁵⁵ predict the contributions of females and males to range limitation. The model
³⁵⁶ predicted maximum fitness in the center of the range and loss of population viabil-
³⁵⁷ ity at longitudes that corresponded well with observed range limits. Specifically,
³⁵⁸ the western-most and eastern-most county records of *P. arachnifera* fell within the
³⁵⁹ uncertainty distribution of the model's predictions (represented by the shading in

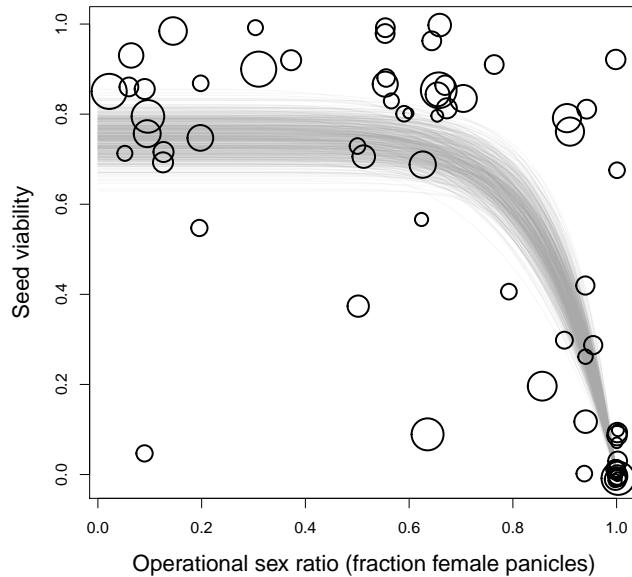


Figure 5: Seed fertilization success in relation to operational sex ratio (fraction of panicles that are female) in experimental populations. Circles show data from tetrazolium assays of seed viability; circle size is proportional to the number of seeds tested (min: 14, max: 57). Lines show model predictions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

Fig. 6A), bolstering our confidence that the model effectively captured the demographic drivers of range limitation in this species. Also, the asymptotic population structure predicted by the model showed female bias in the operational (panicle) sex ratio toward the eastern range margins, consistent with observations from the common garden and natural populations (Fig. B4A). Female bias in the OSR was predicted to cause declines in seed viability toward eastern range margins (Fig. B4B). 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 the sex ratio manipulation experiment (Fig. 5). Furthermore,

369 population viability at the eastern range margin was weakly sensitive to seed via-
370 bility relative to other vital rates (B4C). These observations underscore the next
371 set of results.

372 LTRE decomposition revealed that declines in λ approaching range limits were
373 driven almost exclusively by females (Fig. 6B) with near-zero contributions from
374 males (Fig. 6C). Thus, range limitation was an effectively female-dominant pro-
375 cess, despite systematic geographic variation in sex ratio. Correspondingly, pre-
376 dictions of the two-sex model were nearly indistinguishable from a corresponding
377 female-dominant model with all else equal, with only very modest differences in
378 predictions of the two models emerging in the eastern part of the range (Fig. B3).

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

387 Skew in the OSR predicted by the demographic model was less extreme than
388 was observed in natural and experimental populations (B4A). This occurred be-
389 cause sex differences in demography, especially flowering, were most pronounced
390 at the largest sizes, and the MPM predicted that these sizes were very rare at
391 stable population structure. The stable size distribution predicted by the MPM
392 corresponded well to the common garden data (from which the MPM was built)
393 but was much smaller, on average, than the size distribution we observed in natu-

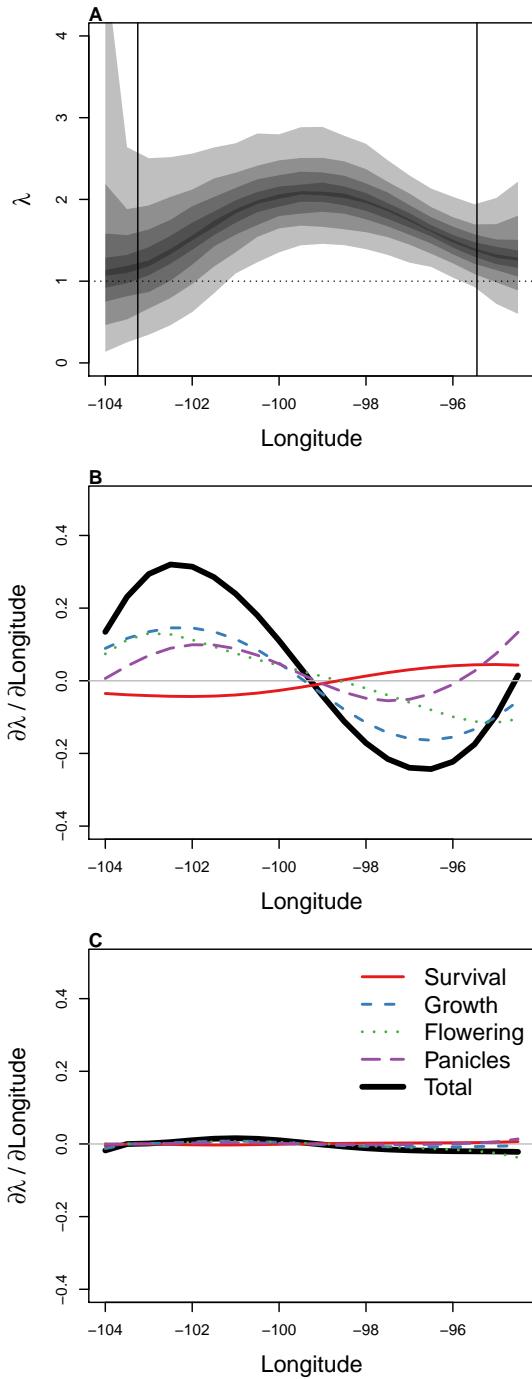


Figure 6: Population growth (λ) as a function of longitude, predicted by the two-sex MPM that incorporates sex-specific demographic responses to longitude with sex ratio-dependent seed fertilization. A, posterior distribution of λ , where shaded regions show the 25, 50, 75, and 95% percentiles of parameter 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 ral populations (Fig. C2), presumably because transplants did not grow like “real”
395 plants and/or did not have time in our three-year experiment to reach those sizes.
396 In Appendix C, we explore whether higher growth rates, leading to a more realistic
397 size distribution, would lead to a more important role for males. In numerical
398 experiments with growth parameters, we found that larger size distributions led to
399 stronger female bias and thus stronger reductions in seed viability at eastern range
400 margins (Fig. C3). While these changes increased the contributions of males to
401 range limitation, female contributions were still more than twice as important as
402 males, and there was very little difference between predictions of the two-sex and
403 female-dominant models even under this elevated growth scenario (Fig. C4). This
404 leads us to conclude that, while our common garden-parameterized model may
405 quantitatively underestimate OSR bias and its demographic consequences relative
406 to natural populations, our qualitative conclusion that range boundary formation
407 is effectively female-dominant in this system is robust to any biases imposed by
408 the growth trajectories and size distributions of common garden populations.

409 Discussion

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

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

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

⁴⁴² *et al.*, 2003) or range expansion (Miller & Inouye, 2013), other examples suggest
⁴⁴³ limited demographic consequences of sex ratio variation (Mysterud *et al.*, 2002;
⁴⁴⁴ Ewen *et al.*, 2011; Gownaris *et al.*, 2020). Ultimately, sensitivity of female repro-
⁴⁴⁵ ductive success to sex ratio should depend strongly on mating system, with female
⁴⁴⁶ dominance at the “extremely polygamous” end of a continuum (Miller *et al.*, 2011).
⁴⁴⁷ The sensitivity of population viability to female reproductive success, in turn, is
⁴⁴⁸ likely predicted by life history strategy: in long-lived, iteroparous species, popula-
⁴⁴⁹ tion growth rates are often weakly sensitive to reproduction relative to growth and
⁴⁵⁰ survival (Franco & Silvertown, 2004). We therefore hypothesize that range limits
⁴⁵¹ are more likely to be dominated by the female environmental niche in longer-lived
⁴⁵² species with more polygamous mating systems, while males are more likely to play
⁴⁵³ an important role in shorter-lived, monogamous species that may be particularly
⁴⁵⁴ sensitive to missed mating opportunities. As studies of sex ratio variation and sex-
⁴⁵⁵ specific demography across species’ ranges accumulate in the literature (Dudaniec
⁴⁵⁶ *et al.*, 2021; Petry *et al.*, 2016; Lynch *et al.*, 2014, e.g.,), this hypothesis may be
⁴⁵⁷ tractably pursued with comparative analyses.

⁴⁵⁸ While life history and mating system may determine the demographic conse-
⁴⁵⁹ quences of skewed sex ratios, the sensitivity of sex ratio to environmental factors
⁴⁶⁰ is another critical ingredient of how environmental variation can affect the popula-
⁴⁶¹ tion dynamics of dioecious species. Our study adds to a small but growing body of
⁴⁶² work quantifying the demographic mechanisms giving rise to skewed operational
⁴⁶³ sex ratios along environmental gradients (Bialic-Murphy *et al.*, 2020)**OTHERS?**,
⁴⁶⁴ highlighting that OSR bias need not reflect differential mortality between the sexes
⁴⁶⁵ (Ueno *et al.*, 2007; Morrison *et al.*, 2016). However, as a field, we lack a strong pre-
⁴⁶⁶ dictive framework for how often and in which direction environmental drivers are

likely to skew the operational sex ratio – and this gap is particularly important in the context of global change. We have focused on the limits of population viability with respect to geographic environmental variation but analogous processes will likely govern how populations respond to temporal environmental change, including direct effects on female demography and indirect effects via perturbations to the mating pool (Fig. 1). There is a need to better understand and predict which species and types of species are susceptible to climate change-induced shifts in OSR. Geographic variation in OSR may be an instructive proxy for how dioecious species will respond to climate change (Petry *et al.*, 2016), which adds value to studies of the causes and consequences of spatial variation in sex ratio, particularly at geographic scales that encompass “past” and “future” conditions.

Previous studies of dioecious plants have shown that male bias is more common than female bias and is particularly pronounced in harsh abiotic environments, likely reflecting the greater resource requirements needed to pay the female cost of reproduction (Field *et al.*, 2013a,b; Bierzychudek & Eckhart, 1988). Our surveys of natural populations are consistent with the broader pattern of male-biased OSR at xeric range edges. However, our common garden populations did not exhibit male bias in the xeric west – averaged across years or in any single year (Fig. B2) – nor did we find any strong demographic evidence for a western male advantage (in fact, there was a western female advantage in growth and survival for some sizes). If male advantage / female disadvantage under harsh abiotic conditions is driven by the greater resource requirements of females then it is possible that clonal propagation and/or legacies of greenhouse rearing masked the ‘true’ sex differences at xeric-edge common garden sites. Instead, the stronger pattern of sex ratio bias was the female reproductive advantage at the mesic, eastern range

edge. We hypothesize that the mesic edge is limited by competition and that the female reproductive advantage reflects competitive superiority of females, which has been suggested in previous studies of Texas bluegrass (Compagnoni *et al.*, 2017) and shown in other dioecious plants (Eppley, 2006), particularly under mesic conditions (Chen *et al.*, 2014). Theory suggests that biotic interactions such as competition are likely to limit species' ranges at the benign (e.g., mesic) end of abiotic gradients (Louthan *et al.*, 2015) though this has not been explored, to our knowledge, in the context of sex-structured dynamics. Future studies in our system or others could test whether females and males differ in their responses to biotic stressors at xeric and mesic range edges to reveal how biotic factors shape range limits via sex-specific demography.

Beyond the novel elements of sex-structured demography and mate limitation, our work informs and advances the broader literature on the processes generating species' range limits. First, the Texas bluegrass case study demonstrates that a process-based model capturing environment-dependent demography can accurately predict geographic range limits: the predicted limits of $\lambda \geq 1$ corresponded well to observed longitudinal limits from historical records, particularly given the uncertainty characterized by our hierarchical Bayesian statistical approach. We parameterized the model with respect to longitude, which tightly covaries with aridity in the southern Great Plains. Extensions of this model that transition from implicit to explicit consideration of aridity will allow us to forecast range responses of Texas bluegrass to future climate change and ask whether climate change will reduce or amplify OSR bias and mate limitation at range edges. It would be interesting to additionally consider this species' latitudinal limits, which correspond to a temperature gradient, though our exploratory analyses revealed

517 no clear sex differences or sex ratio variation with respect to latitude.

518 Second, our results also provide novel evidence for contrasting demographic
519 responses to environmental drivers throughout a species' range – or “demographic
520 compensation” (Villellas *et al.*, 2015; Doak & Morris, 2010). Elevated performance
521 in some life history processes can compensate for declines in other processes and
522 thus buffer range-edge populations against harsh environmental conditions. In
523 Texas bluegrass, most vital rates declined toward eastern and western range lim-
524 its but survival showed the opposite pattern. Increased survival at longitudinal
525 extremes partially offset declines in other vital rate but this positive response was
526 weaker than the negative responses in other vital rates. Ultimately, increased sur-
527 vival was not sufficient to prevent declines in population viability from the range
528 center to eastern and western limits, which were dominated by declining female
529 growth and flowering. A recent study found a similar pattern, where compensation
530 between vital rates could not prevent a decrease of population growth rate towards
531 the southern range edge of *Erythranthe cardinalis* (Sheth & Angert, 2018).

532 Third, our results highlight some important considerations in how environment-
533 dependent demographic models are best parameterized to derive insights into the
534 drivers of range limits. Our approach relied heavily on common garden popula-
535 tions, which allowed us to plant and track known-sex individuals in contrasting
536 environmental conditions that encompass and exceed the natural geographic dis-
537 tribution. The ability to robustly sample edge and beyond-edge environments is a
538 powerful advantage of the common garden transplant approach (Hargreaves *et al.*,
539 2013). However, this also limited the size variation that we were able to model, and
540 the size distributions of common garden populations skewed consistently smaller
541 than natural populations. In Appendix C, we show that our conclusions are likely

robust to this feature of the common gardens. However, our ability to quantify the consequences of size representation is itself limited by size representation: we can simulate a population in which the largest common garden sizes are more common than they actually were, but simulating a population with sizes much larger than what we observed requires extrapolation of our statistical models to unobserved states, and we are skeptical about what insights such an exercise could provide (in Appendix C, we extrapolated demographic performance to sizes 50% greater than observed **CHECK**). This issue is not unique to our study but will be encountered by any transplant study intended to yield inferences about range limits of species with significant size structure. If we could re-do our experiment knowing what we know now, we would combine data from natural and transplanted populations to more realistically model size-dependent demography. Other investigators inspired by similar questions about the demographic drivers of range limits should consider such a hybrid approach.

Conclusion. We have documented geographic variation in operational sex ratio; elucidated how sexual niche differentiation and sex-specific demography generate this pattern; quantified how female fertility responds to availability of males; and demonstrated that, in the end, sex ratio variation is a rather inconsequential component of declines in population viability at range limits. In Texas bluegrass and, we speculate, other dioecious plants and animals with similar life history and reproductive traits, the geographic distribution is essentially the *female's* environmental niche ‘writ large’ (Hargreaves *et al.*, 2013).

Understanding and predicting geographic distributions and their responses to environmental change demands careful consideration of which biological de-

566 tails must be accounted for and which others can be safely ignored. Our results
567 show that complex, non-linear dynamics involving females, males, and frequency-
568 dependent reproduction can be reasonably approximated as a simple, linear process
569 (female-dominant population growth). We suggest that this is good news. The
570 next challenge is to figure out how often and under what conditions ecologists can
571 get away with it.

572 Acknowledgements

573 We gratefully acknowledge the many individuals who facilitated our field work,
574 especially Dariusz Malinowski, Jason Goldman, Tom Arsuffi, Alan Byboth, John
575 Walker, Kenneth Steigman, Steven Gibson, Wesley Newman, Kerry Griffis, Liz
576 Martin, Melanie Hartman, Brian Northup, Leland Russell, Dexter R Mardis, and
577 Dixie Smith. This work was made possible by a network of biological field sta-
578 tions that hosted our geographically distributed experiment. We acknowledge Sam
579 Houston State University, Texas A&M University, University of Texas, Texas Tech
580 University, Pittsburgh State University, and Wichita State University for invest-
581 ing in field stations and making these facilities available to us. We thank Marion
582 Donald, Kory Kolis, Nakian Kim, and Alex Espana for valuable assistance in the
583 field, lab, and greenhouse. Our work was supported by NSF Division of Environ-
584 mental Biology awards 1543651 and 1754468 and by the Rice University Faculty
585 Initiatives Fund.

586 **Author contributions**

587 A.C. and T.E.X.M. designed the study, carried out the study, and conducted the
588 statistical analyses. T.E.X.M drafted the manuscript and both authors finalized
589 the submission.

590 **Data accessibility**

591 A data package will be formally published in parallel with this manuscript. For
592 now, reviewers may access our raw data at [https://github.com/texmiller/](https://github.com/texmiller/POAR-range-limits)
593 `POAR-range-limits`.

594 **References**

595 Araújo MS, Bolnick DI, Layman CA (2011) The ecological causes of individual
596 specialisation. *Ecology letters*, **14**, 948–958.

597 Bertiller MB, Sain CL, Bisigato AJ, Coronato FR, Aries JO, Graff P (2002) Spatial
598 sex segregation in the dioecious grass *poa ligularis* in northern patagonia: the
599 role of environmental patchiness. *Biodiversity & Conservation*, **11**, 69–84.

600 Bialic-Murphy L, Heckel CD, McElderry RM, Kalisz S (2020) Deer indirectly alter
601 the reproductive strategy and operational sex ratio of an unpalatable forest
602 perennial. *The American Naturalist*, **195**, 56–69.

603 Bierzychudek P, Eckhart V (1988) Spatial segregation of the sexes of dioecious
604 plants. *The American Naturalist*, **132**, 34–43.

- 605 Bisang I, Ehrlén J, Hedenäs L (2020) Sex expression and genotypic sex ratio vary
606 with region and environment in the wetland moss *drepanocladus lycopodioides*.
607 *Botanical journal of the Linnean Society*, **192**, 421–434.
- 608 Bolnick DI, Doebeli M (2003) Sexual dimorphism and adaptive speciation: two
609 sides of the same ecological coin. *Evolution*, **57**, 2433–2449.
- 610 Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister
611 ML (2002) The ecology of individuals: incidence and implications of individual
612 specialization. *The American Naturalist*, **161**, 1–28.
- 613 Bowyer RT (2004) Sexual segregation in ruminants: definitions, hypotheses, and
614 implications for conservation and management. *Journal of Mammalogy*, **85**,
615 1039–1052.
- 616 Carpenter B, Gelman A, Hoffman MD, *et al.* (2017) Stan: A probabilistic pro-
617 gramming language. *Journal of statistical software*, **76**.
- 618 Caruso C, Case A (2007) Sex ratio variation in gynodioecious *lobelia siphilitica*:
619 effects of population size and geographic location. *Journal of Evolutionary Bi-
620 ology*, **20**, 1396–1405.
- 621 Caswell H (2001) *Matrix Population Models*. Sinauer Associates, Inc., Sunderland,
622 MA, 2 edn.
- 623 Caswell H, Weeks DE (1986) Two-sex models: chaos, extinction, and other dy-
624 namic consequences of sex. *The American Naturalist*, **128**, 707–735.
- 625 Chen J, Duan B, Wang M, Korpelainen H, Li C (2014) Intra-and inter-sexual

- 626 competition of *populus cathayana* under different watering regimes. *Functional*
627 *Ecology*, **28**, 124–136.
- 628 Compagnoni A, Steigman K, Miller TE (2017) Can't live with them, can't live
629 without them? balancing mating and competition in two-sex populations. *Pro-*
630 *ceedings of the Royal Society B: Biological Sciences*, **284**, 20171999.
- 631 Conn PB, Johnson DS, Williams PJ, Melin SR, Hooten MB (2018) A guide to
632 bayesian model checking for ecologists. *Ecological Monographs*, **88**, 526–542.
- 633 Darwin C (1871) *The descent of man*. BoD–Books on Demand.
- 634 De Lisle SP, Paiva S, Rowe L (2018) Habitat partitioning during character dis-
635 placement between the sexes. *Biology letters*, **14**, 20180124.
- 636 De Lisle SP, Rowe L (2015) Ecological character displacement between the sexes.
637 *The American Naturalist*, **186**, 693–707.
- 638 Diez JM, Giladi I, Warren R, Pulliam HR (2014) Probabilistic and spatially vari-
639 able niches inferred from demography. *Journal of ecology*, **102**, 544–554.
- 640 Doak DF, Morris WF (2010) Demographic compensation and tipping points in
641 climate-induced range shifts. *Nature*, **467**, 959–962.
- 642 Dudaniec RY, Carey AR, Svensson EI, Hansson B, Yong CJ, Lancaster LT (2021)
643 Latitudinal clines in sexual selection, sexual size dimorphism, and sex-specific
644 genetic dispersal during a poleward range expansion. *Journal of Animal Ecology*.
- 645 Eberhart-Phillips LJ, Küpper C, Miller TE, *et al.* (2017) Sex-specific early sur-
646 vival drives adult sex ratio bias in snowy plovers and impacts mating system

- 647 and population growth. *Proceedings of the National Academy of Sciences*, **114**,
648 E5474–E5481.
- 649 Ehrlén J, Morris WF (2015) Predicting changes in the distribution and abundance
650 of species under environmental change. *Ecology Letters*, **18**, 303–314.
- 651 Eppley S (2001) Gender-specific selection during early life history stages in the
652 dioecious grass *distichlis spicata*. *Ecology*, **82**, 2022–2031.
- 653 Eppley SM (2006) Females make tough neighbors: sex-specific competitive effects
654 in seedlings of a dioecious grass. *Oecologia*, **146**, 549–554.
- 655 Evans ME, Merow C, Record S, McMahon SM, Enquist BJ (2016) Towards
656 process-based range modeling of many species. *Trends in Ecology & Evolution*,
657 **31**, 860–871.
- 658 Ewen JG, Thorogood R, Armstrong DP (2011) Demographic consequences of adult
659 sex ratio in a reintroduced hihi population. *Journal of Animal Ecology*, **80**, 448–
660 455.
- 661 Fick SE, Hijmans RJ (2017) Worldclim 2: new 1-km spatial resolution climate
662 surfaces for global land areas. *International journal of climatology*, **37**, 4302–
663 4315.
- 664 Field DL, Pickup M, Barrett SC (2013a) Comparative analyses of sex-ratio varia-
665 tion in dioecious flowering plants. *Evolution: International Journal of Organic*
666 *Evolution*, **67**, 661–672.
- 667 Field DL, Pickup M, Barrett SC (2013b) Ecological context and metapopulation

- 668 dynamics affect sex-ratio variation among dioecious plant populations. *Annals*
669 *of botany*, **111**, 917–923.
- 670 Franco M, Silvertown J (2004) A comparative demography of plants based upon
671 elasticities of vital rates. *Ecology*, **85**, 531–538.
- 672 Gianuca D, Votier SC, Pardo D, *et al.* (2019) Sex-specific effects of fisheries and
673 climate on the demography of sexually dimorphic seabirds. *Journal of Animal*
674 *Ecology*.
- 675 Gownaris NJ, García Borboroglu P, Boersma PD (2020) Sex ratio is variable and
676 increasingly male biased at two colonies of magellanic penguins. *Ecology*, **101**,
677 e02939.
- 678 Groen KE, Stieha CR, Crowley PH, McLetchie DN (2010) Sex-specific plant re-
679 spondes to light intensity and canopy openness: implications for spatial segre-
680 gation of the sexes. *Oecologia*, **162**, 561–570.
- 681 Hargreaves AL, Samis KE, Eckert CG (2013) Are species' range limits simply niche
682 limits writ large? a review of transplant experiments beyond the range. *The*
683 *American Naturalist*, **183**, 157–173.
- 684 Holt RD (2009) Bringing the hutchinsonian niche into the 21st century: ecological
685 and evolutionary perspectives. *Proceedings of the National Academy of Sciences*,
686 **106**, 19659–19665.
- 687 Hultine KR, Bush SE, Ward JK, Dawson TE (2018) Does sexual dimorphism
688 predispose dioecious riparian trees to sex ratio imbalances under climate change?
689 *Oecologia*, **187**, 921–931.

- 690 Hutchinson GE (1958) Concluding remarks. In: *Cold Spring Harbour Symposium*
691 *on Quantitative Biology*, vol. 22, pp. 415—427.
- 692 Karl TR, Melillo JM, Peterson TC, Hassol SJ (2009) *Global climate change impacts*
693 *in the United States*. Cambridge University Press.
- 694 Ketterson ED, Nolan Jr V (1976) Geographic variation and its climatic correlates
695 in the sex ratio of eastern-wintering dark-eyed juncos (*junco hyemalis hyemalis*).
696 *Ecology*, **57**, 679–693.
- 697 Law CJ, Mehta RS (2018) Carnivory maintains cranial dimorphism between males
698 and females: evidence for niche divergence in extant musteloidea. *Evolution*, **72**,
699 1950–1961.
- 700 Lee-Yaw JA, Kharouba HM, Bontrager M, *et al.* (2016) A synthesis of transplant
701 experiments and ecological niche models suggests that range limits are often
702 niche limits. *Ecology letters*, **19**, 710–722.
- 703 Louthan AM, Doak DF, Angert AL (2015) Where and when do species interactions
704 set range limits? *Trends in Ecology & Evolution*, **30**, 780–792.
- 705 Lynch HJ, Rhainds M, Calabrese JM, Cantrell S, Cosner C, Fagan WF (2014)
706 How climate extremes-not means-define a species' geographic range boundary
707 via a demographic tipping point. *Ecological Monographs*, **84**, 131–149.
- 708 Merow C, Bois ST, Allen JM, Xie Y, Silander JA (2017) Climate change both
709 facilitates and inhibits invasive plant ranges in new england. *Proceedings of the*
710 *National Academy of Sciences*, **114**, E3276–E3284.

- 711 Merow C, Latimer AM, Wilson AM, McMahon SM, Rebelo AG, Silander Jr JA
712 (2014) On using integral projection models to generate demographically driven
713 predictions of species' distributions: development and validation using sparse
714 data. *Ecography*, **37**, 1167–1183.
- 715 Miller TE, Inouye BD (2011) Confronting two-sex demographic models with data.
716 *Ecology*, **92**, 2141–2151.
- 717 Miller TE, Inouye BD (2013) Sex and stochasticity affect range expansion of ex-
718 perimental invasions. *Ecology Letters*, **16**, 354–361.
- 719 Miller TE, Shaw AK, Inouye BD, Neubert MG (2011) Sex-biased dispersal and
720 the speed of two-sex invasions. *The American Naturalist*, **177**, 549–561.
- 721 Milner-Gulland E, Bukreeva O, Coulson T, Lushchekina A, Kholodova M, Bekenov
722 A, Grachev IA (2003) Reproductive collapse in saiga antelope harems. *Nature*,
723 **422**, 135–135.
- 724 Morrison CA, Robinson RA, Clark JA, Gill JA (2016) Causes and consequences
725 of spatial variation in sex ratios in a declining bird species. *Journal of Animal*
726 *Ecology*, **85**, 1298–1306.
- 727 Mysterud A, Coulson T, Stenseth NC (2002) The role of males in the dynamics of
728 ungulate populations. *Journal of Animal Ecology*, **71**, 907–915.
- 729 Pekár S, Martišová M, Bilde T (2011) Intersexual trophic niche partitioning in an
730 ant-eating spider (araneae: Zodariidae). *PloS one*, **6**, e14603.
- 731 Petry WK, Soule JD, Iler AM, Chicas-Mosier A, Inouye DW, Miller TE, Mooney

- 732 KA (2016) Sex-specific responses to climate change in plants alter population
733 sex ratio and performance. *Science*, **353**, 69–71.
- 734 Phillips R, Silk J, Phalan B, Catry P, Croxall J (2004) Seasonal sexual segregation
735 in two thalassarche albatross species: competitive exclusion, reproductive role
736 specialization or foraging niche divergence? *Proceedings of the Royal Society of*
737 *London. Series B: Biological Sciences*, **271**, 1283–1291.
- 738 Rankin DJ, Kokko H (2007) Do males matter? the role of males in population
739 dynamics. *Oikos*, **116**, 335–348.
- 740 Renganayaki K, Jessup R, Burson B, Hussey M, Read J (2005) Identification of
741 male-specific afip markers in dioecious texas bluegrass. *Crop science*, **45**, 2529–
742 2539.
- 743 Renganayaki K, Read J, Fritz A (2001) Genetic diversity among texas bluegrass
744 genotypes (poa arachnifera torr.) revealed by afip and rapd markers. *Theoretical*
745 *and Applied Genetics*, **102**, 1037–1045.
- 746 Renner SS, Ricklefs RE (1995) Dioecy and its correlates in the flowering plants.
747 *American journal of botany*, **82**, 596–606.
- 748 Rozas V, DeSoto L, Olano JM (2009) Sex-specific, age-dependent sensitivity of
749 tree-ring growth to climate in the dioecious tree juniperus thurifera. *New Phy-*
750 *tologist*, **182**, 687–697.
- 751 Shelton AO (2010) The ecological and evolutionary drivers of female-biased sex
752 ratios: two-sex models of perennial seagrasses. *The American Naturalist*, **175**,
753 302–315.

- 754 Sheth SN, Angert AL (2018) Demographic compensation does not rescue popula-
755 tions at a trailing range edge. *Proceedings of the National Academy of Sciences*,
756 **115**, 2413–2418.
- 757 Shine R (1989) Ecological causes for the evolution of sexual dimorphism: a review
758 of the evidence. *The Quarterly Review of Biology*, **64**, 419–461.
- 759 Team SD, *et al.* (2018) Rstan: the r interface to stan. r package version 2.17. 3.
- 760 Temeles EJ, Miller JS, Rifkin JL (2010) Evolution of sexual dimorphism in bill size
761 and shape of hermit hummingbirds (phaethornithinae): a role for ecological cau-
762 sation. *Philosophical Transactions of the Royal Society B: Biological Sciences*,
763 **365**, 1053–1063.
- 764 Ueno N, Suyama Y, Seiwa K (2007) What makes the sex ratio female-biased in
765 the dioecious tree salix sachalinensis? *Journal of Ecology*, **95**, 951–959.
- 766 Veran S, Beissinger SR (2009) Demographic origins of skewed operational and
767 adult sex ratios: perturbation analyses of two-sex models. *Ecology Letters*, **12**,
768 129–143.
- 769 Villegas J, Doak DF, García MB, Morris WF (2015) Demographic compensation
770 among populations: what is it, how does it arise and what are its implications?
771 *Ecology letters*, **18**, 1139–1152.
- 772 Wood S (2017) *Generalized Additive Models: An Introduction with R*. Chapman
773 and Hall/CRC, 2 edn.

⁷⁷⁴ **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

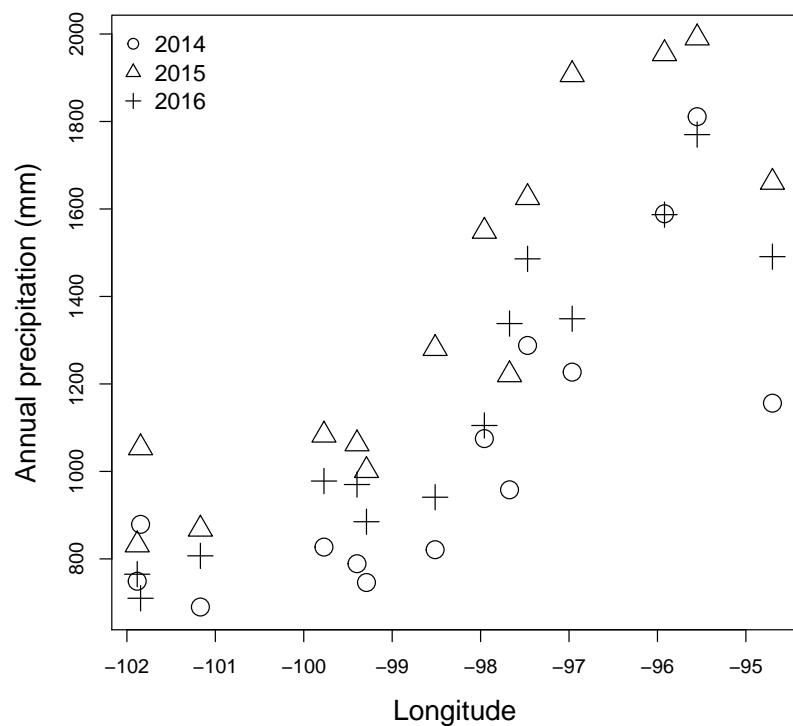


Figure A1: Total annual precipitation at common garden sites during the study years tracked long-term trends of increasing aridity from east to west.

775 **Appendix B: Additional results**

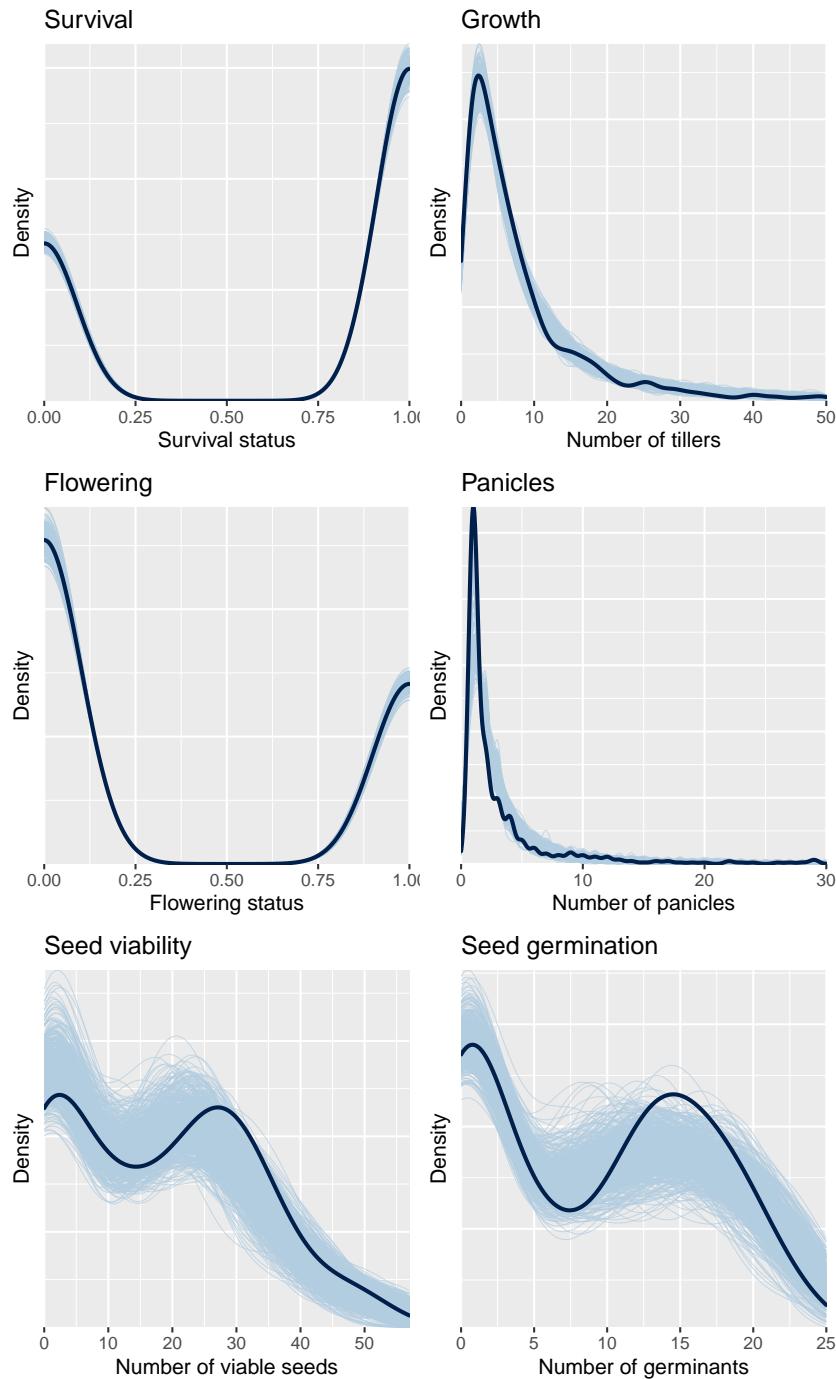


Figure B1: Posterior predictive checks of statistical models for demographic vital rates. Lines show density distributions of real data (thick, dark blue) compared to simulated data sets (thin, light blue) generated from the fitted models based on 500 draws of the posterior distribution of parameter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

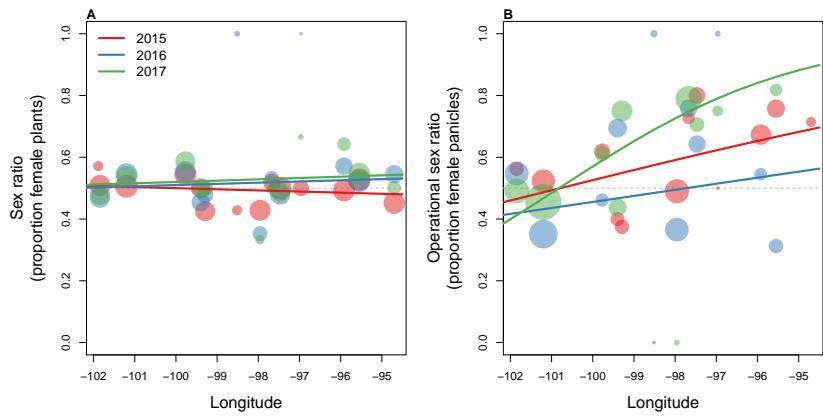


Figure B2: Year-specific sex ratios of plants (A) and panicles (B) in common garden populations spanning the longitudinal aridity gradient. Points sizes are proportional to sample sizes and lines show fitted binomial GLMs.

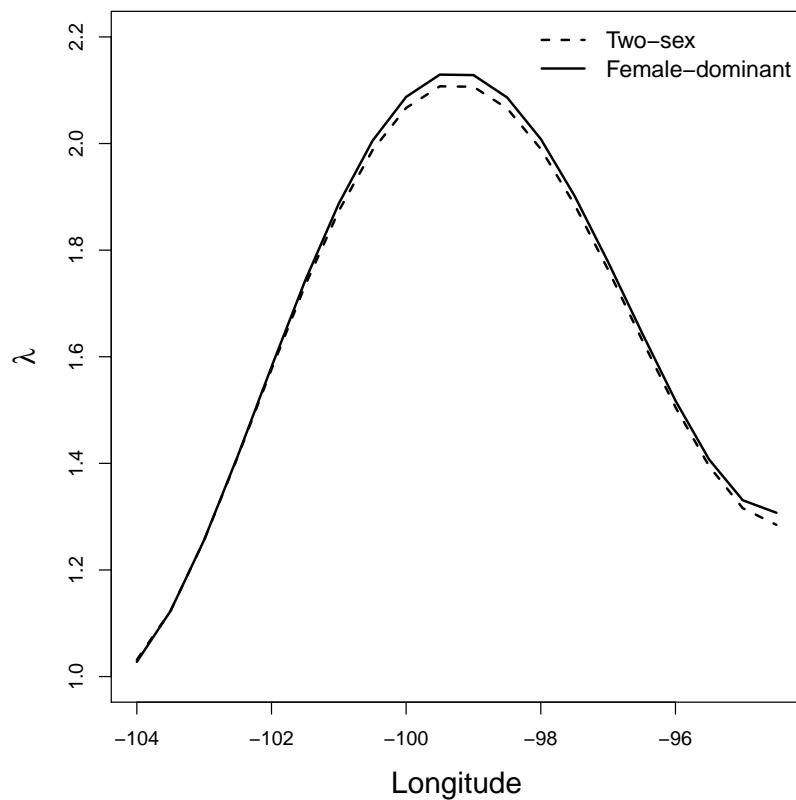


Figure B3: Comparison of longitudinal variation in λ between the two-sex demographic model (dashed line) that includes dependence of female seed production on population structure and the corresponding female-dominant model (solid line) with constant female fertility and all else equal. Models were evaluated at posterior mean parameter estimates

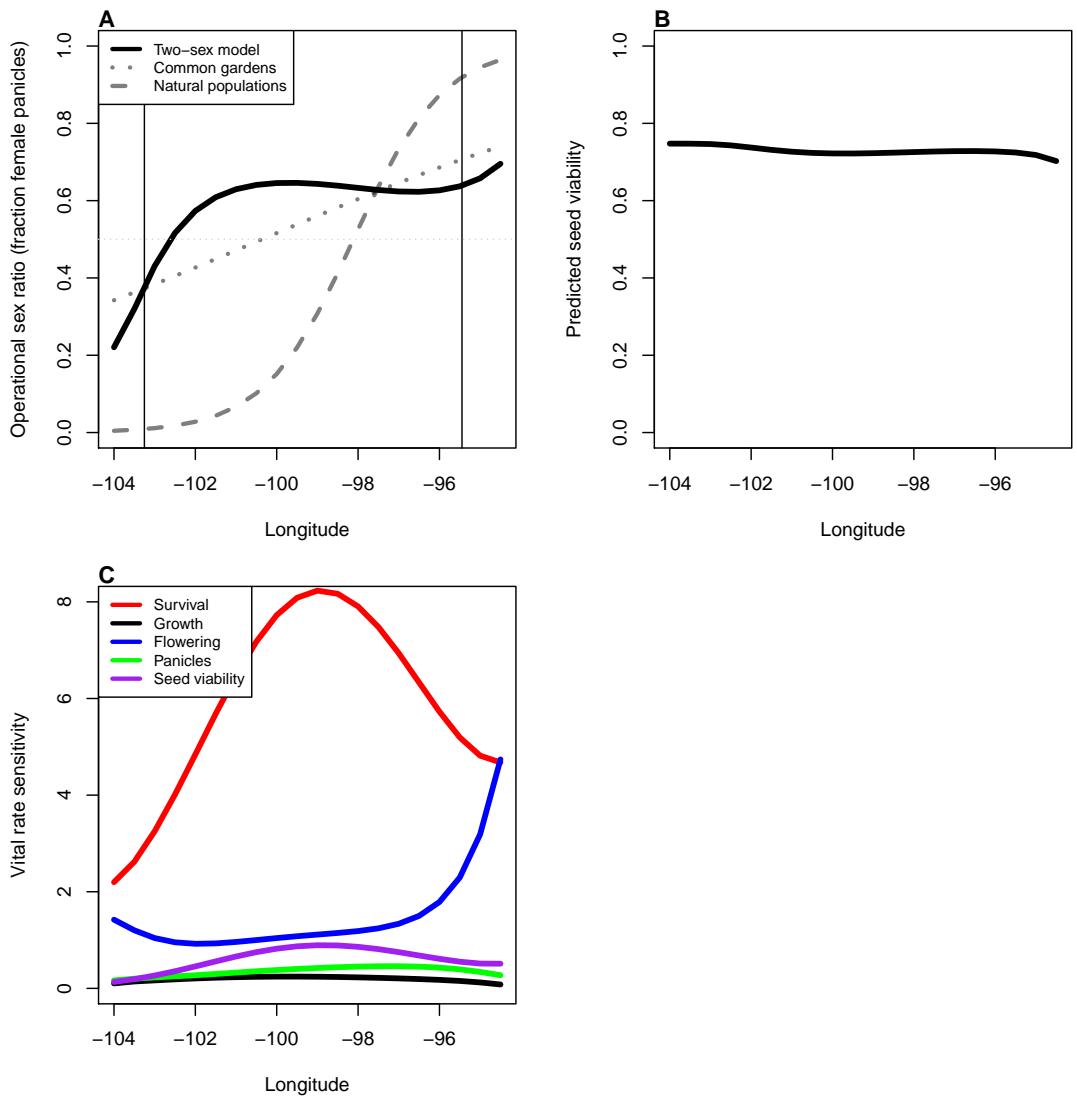


Figure B4: **A**, Longitudinal variation in operational sex ratio (fraction of panicles that are female) predicted by the two-sex MPM (solid line) compared to the sex ratio clines fitted to data from common gardens (dotted line) or natural populations (dashed line). Vertical lines show the longitudes 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.

776 **Appendix C: Size distribution comparisons and sim-**

777 **ulation experiments**

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

781 **Observed and predicted size distributions**

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

785 **Common garden populations** Common garden data collection included tiller
786 counts and the maximum length and width of each patch, which we converted to
787 area (m^2) assuming an oval shape. We used these data to estimate the relationship
788 between patch area and tiller count (Fig. C1) using a generalized additive model
789 (Wood, 2017) and applied this fitted relationship to area measurements from nat-
790 ural populations. This allowed us to compare the size distributions of natural
791 and common garden populations (pooled across the range) in the same size unit
792 ($\log(\text{tillers})$).

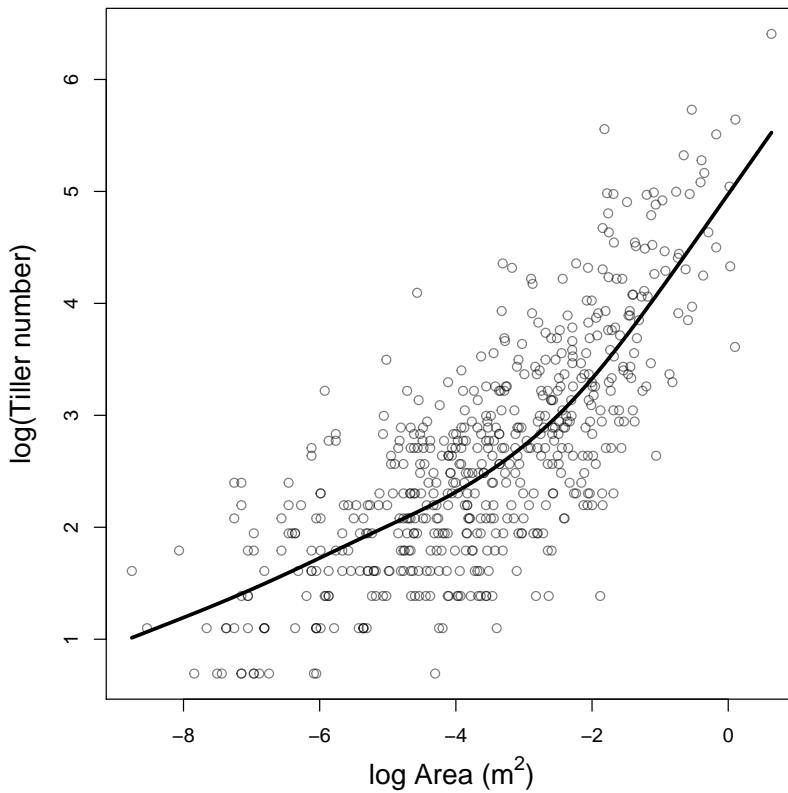


Figure C1: Relationship between area (m^3) and tiller count from plants in the common garden experiment. The fitted gam model (line) was used to convert area measurements from natural populations to tiller counts.

793 **Two-sex MPM** The two-sex MPM predicts asymptotic population structure,
 794 including stable size distribution (SSD) and sex ratio. For comparison with em-
 795 pirical data, we calculated the SSD (pooling both sexes) predicted in the center of
 796 the range (the conclusions that we draw from this analysis hold up if we consider
 797 SSD from different parts of the range). Because the MPM is structured by tiller
 798 number, we converted the SSD to $\log(\text{tillers})$ by simulating an arbitrarily large
 799 (10000) population at SSD, taking the natural logarithm of tiller number, and
 800 then estimating the empirical distribution of this variable.

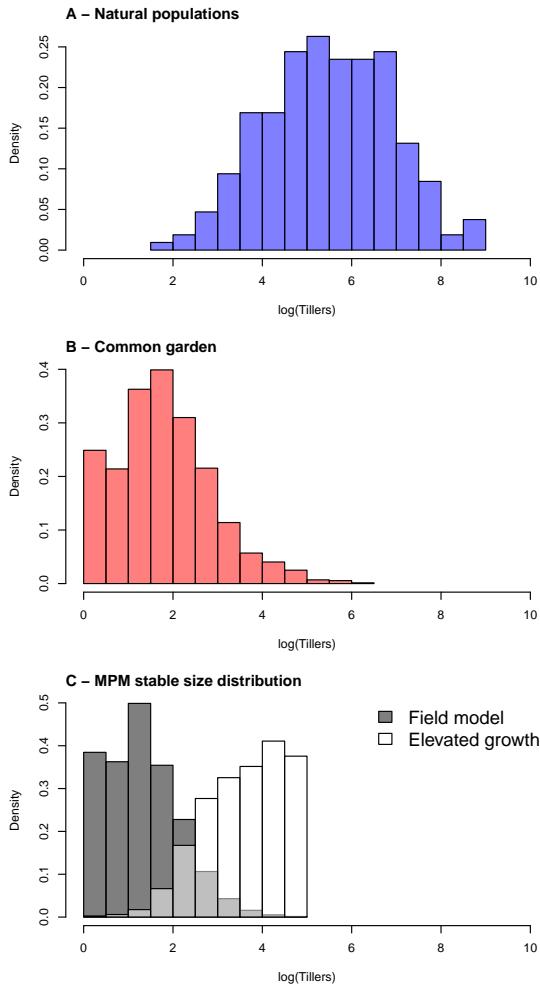


Figure C2: Size distribution of Texas bluegrass from natural populations (A), common garden populations (B), and predicted by the two-sex MPM (C). In C, the two size distributions come from the base model parameterized following methods described in the main manuscript (gray) and a numerical experiment where growth parameters were numerically increased to generate a size distribution more consistent with natural populations (white).

801 **Results** Plants from natural populations were larger, on average, than plants
 802 in our common garden experiment (Fig. C2A,B). Common garden plants were
 803 generally larger each year but the largest sizes in the final year of the common

garden corresponded to smaller sizes observed in natural populations (although natural population surveys were subject to detection bias: small plants were likely under-sampled relative to their occurrence). The predicted SSD from the two-sex MPM was consistent with the common garden size distribution (Fig. C2C), as expected since the model was built with common garden data. These results suggest that common garden plants did not have the same growth trajectories of naturally occurring plants and / or were not given sufficient time to reach the sizes observed in natural populations.

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

The preceding results indicate that the common garden populations, and thus the two-sex MPM built from common garden data, under-estimate the size distribution of Texas bluegrass, relative to what we find in natural populations. Sex differences in demography, and especially flowering, were most pronounced for the largest sizes (Fig. 4), but these sizes were predicted to be very rare in a stable population (Fig. C2C). The under-estimation of large sizes may explain why longitudinal clines in OSR predicted by the MPM and seen in the common garden were weaker than the OSR cline observed in natural populations (Fig. B4). It is therefore possible that our main finding – that males contribute little-to-nothing toward range limitation – reflects a limitation of the model, since real populations tended to be more female-biased (and potentially more mate-limited) in the eastern range margins than the model predicted. To explore this possibility, we conducted a numerical experiment that allowed modeled plants to reach larger sizes by increasing the

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

831 As expected, this led to stronger sex ratio clines and stronger reductions in
832 seed viability at eastern range margins (Fig. C3). These changes increased the
833 contributions of males to eastern range limitation in the elevated-growth numerical
834 experiment. However, the contribution of males to range limitation was still weak
835 relative to that of females (the maximum male contribution was less than half of
836 the female maximum) and differences between the two-sex and female-dominant
837 MPMs were still very minor (Fig. C4). Collectively, these results suggest that the
838 small size distribution of the common garden experiment led to a weaker role of
839 males than would be expected in populations with a more realistic size distribution,
840 but that even with a larger size distribution, declines in female performance still
841 dominate range boundary formation.

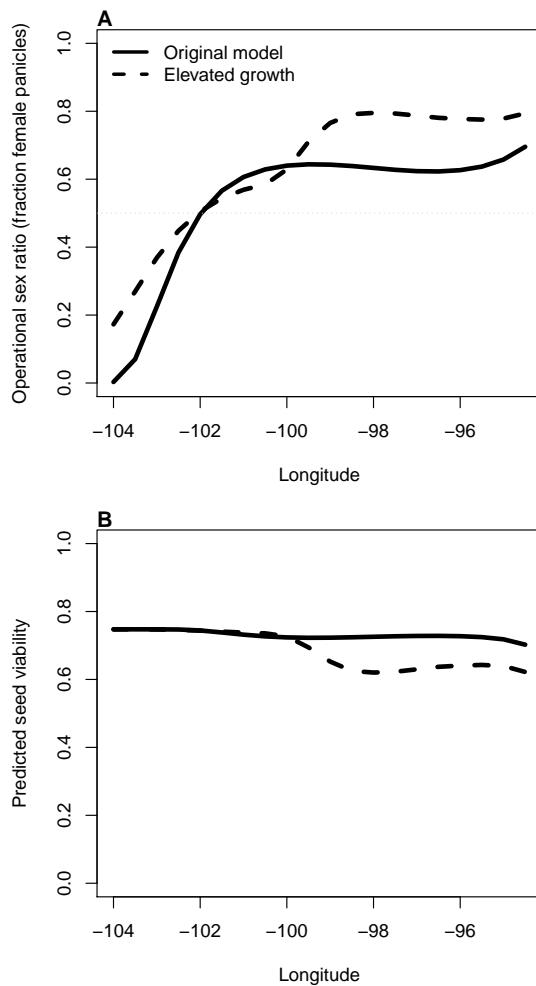


Figure C3: Two-sex model predictions for **A** operational sex ratio (fraction of panicles that are female) and **B** seed viability at stable population structure in relation to longitude. Solid line shows predictions of the base model using field-estimated parameter values and dashed line shows the same model with elevated growth of both sexes and across all longitudes (intercept of growth function increased by a factor of 2.75).

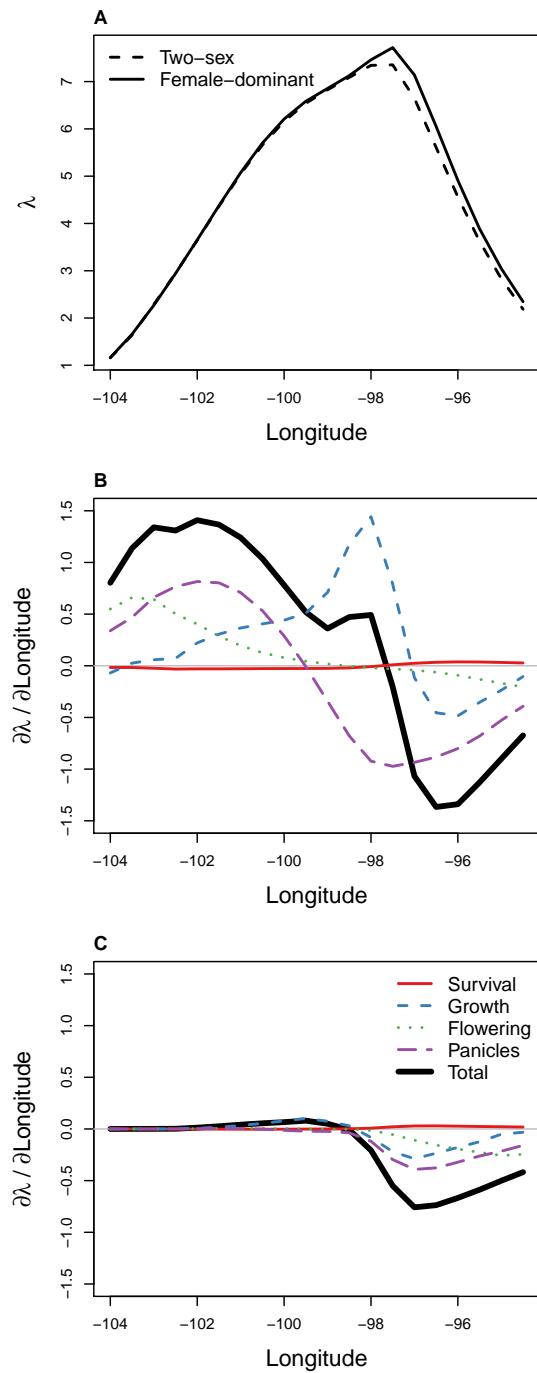


Figure C4: Results for the elevated growth model, in which the intercept of growth function was increased by a factor of 2.75. **A**, contrast of two-sex and female-dominant models, as in Fig. B3; **B,C**, Life Table Response Experiments decomposing the change in λ with respect to longitude into contributions from female **B** and male **C** vital rates (layout as in Fig. 6).