

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

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Abstract

1 Understanding the mechanisms that generate biogeographic range limits is a long-standing
2 goal of ecology. It is widely hypothesized that distributional limits reflect the envi-
3 ronmental niche, but this hypothesis is complicated by widespread potential for intra-
4 specific niche heterogeneity. In dioecious species, sexual niche differentiation may cause
5 divergence between the sexes in their limits of environmental suitability. We studied
6 range boundary formation in Texas bluegrass (*Poa arachnifera*), a perennial dioecious
7 plant, testing the alternative hypotheses that range limits reflect the niche limits of fe-
8 males only versus the combined contributions of females and males, including their
9 inter-dependence via mating. Common garden experiments across a longitudinal aridity
10 gradient revealed female-biased flowering approaching eastern range limits, suggesting
11 that mate limitation may constrain the species' distribution. However, a demographic
12 model showed that declines in λ approaching range limits were driven almost entirely
13 by female vital rates. The dominant role of females was attributable to seed viability
14 being robust to sex ratio variation and to low sensitivity of λ to reproductive transitions.
15 We suggest that female-dominant range limits may be common to long-lived species
16 with polygamous mating systems, and that female responses to environmental drivers
17 may often be sufficient for predicting range shifts in response to environmental change.

Keywords

18
19 demography; dioecy; intra-specific niche heterogeneity; matrix projection model; sex
20 ratio; range limits

Introduction

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

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

44 Sexual niche differentiation is a common form of intra-specific niche heterogeneity
45 (Bolnick et al., 2002) and has been widely documented in animals (the vast majority
46 of which are dioecious) and plants (ca. 6% of angiosperms are dioecious: Renner and
47 Ricklefs 1995). The prevalence of sexual niche differentiation was recognized by Darwin
48 (1871), who described “different habits of life, not related...to the reproductive functions”
49 of females and males. There are now many examples of sex differences in trophic posi-
50 tion (Law and Mehta, 2018; Pekár et al., 2011), habitat use (Bowyer, 2004; De Lisle et al.,
51 2018; Phillips et al., 2004), and responses to climate (Gianuca et al., 2019; Petry et al.,
52 2016; Rozas et al., 2009), differences that may or may not be accompanied by sexual
53 dimorphism. It has been hypothesized that sexual niche differentiation may evolve by
54 natural selection when it reduces competitive or other antagonistic interactions between
55 the sexes (Bolnick and Doebeli, 2003; De Lisle and Rowe, 2015), as a byproduct of nat-
56 urally or sexually selected size dimorphism (Shine, 1989; Temeles et al., 2010), or when
57 females and males pay different costs of reproduction (Bierzychudek and Eckhart, 1988).

58 Sexual niche differentiation can translate to sex-specific demographic advantages in
59 different environments, causing skew in the operational sex ratio (OSR: relative abun-
60 dance of females and males available for mating) even if the primary (birth) sex ratio is
61 unbiased (Eberhart-Phillips et al., 2017; Shelton, 2010; Veran and Beissinger, 2009). In-
62 deed, environmental clines in OSR have been widely documented in plants and animals
63 at fine spatial scales (Bertiller et al., 2002; Bisang et al., 2020; Eppley, 2001; Groen et al.,
64 2010; Hultine et al., 2018) as well as broader climatic clines across altitudes or latitudes
65 (Caruso and Case, 2007; Dudaniec et al., 2021; Ketterson and Nolan Jr, 1976; Petry et al.,
66 2016). At range margins, where environments may be extreme relative to the range core,
67 demographic differences between the sexes, and hence skew in the OSR, may be greatest.

68 In dioecious plants, for example, populations at upper altitudes and latitudes and in the
69 more xeric margins of species' ranges tend to be male-biased, possibly due to the greater
70 resource demands of female flower and seed production (Field et al., 2013b).

71 Returning to the question of whose niche determines range limits given the potential
72 for sexual niche differentiation, classic ecological theory assumes the answer. "Female
73 dominance" is a pervasive, often implicit feature of population-dynamic models whereby
74 male availability is assumed to have no influence on female fertility (Caswell and Weeks,
75 1986; Miller and Inouye, 2011; Rankin and Kokko, 2007). This assumption is wrong,
76 of course, but it may be *adequate* when the sex ratio is balanced or exhibits little varia-
77 tion. The female-dominant perspective predicts that female responses to environmental
78 variation should govern range limits (Fig. 1). However, females may be mate-limited
79 in environments in which they are favored, which could reduce population viability in
80 marginal environments that are more suitable for females than males. This creates an
81 additional, "two-sex" pathway by which environmental drivers may set distributional
82 limits, via perturbations to the mating pool that arise from sex-specific responses to the
83 environment (Fig. 1).

84 Here we ask whether female demographic responses to environmental variation,
85 alone, are sufficient to understand the ecological origins of range limits, or whether
86 males and female-male interactions must additionally be considered. As an experimen-
87 tal model, we worked with a dioecious plant species (Texas bluegrass [*Poa arachnifera*])
88 narrowly distributed across the sharp longitudinal aridity gradient of the southern Great
89 Plains, US (Fig. 2). We hypothesized that sexual niche differentiation with respect to lon-
90 gitudinal variation in aridity may lead to skewed sex ratios approaching range limits,
91 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 (Texas bluegrass) is a perennial, cool-season 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 populations in other U.S. states¹. Seasonal rainfall in this region has two annual peaks, in spring and fall, which coincide with the growing-season of this C3 species. 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

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

113 inflorescence and seed production, plants go dormant for the hot summer months and
114 vegetative growth resumes in fall. Individuals grow via rhizomes to form patches that
115 may be as large as $50m^2$ in area. Sex in *P. arachnifera* is genetically based (Renganayaki
116 et al., 2005, 2001) and the primary sex ratio is 1:1 (J. Goldman, USDA-ARS, *unpubl.*
117 *data*). The rhizomatous growth habit allowed us to clonally propagate large numbers of
118 known-sex individuals for experiments, as we describe below.

119 We surveyed *P. arachnifera* across its range to establish whether natural populations
120 exhibited geographic clines in OSR corresponding to the longitudinal aridity gradient.
121 We visited 14 populations in spring 2012 and 8 in spring 2013 (Table A1, Fig. 2). At
122 each location, we searched for *P. arachnifera* along roads, trails, or creek drainages and
123 recorded the number of female and male patches that we encountered and the number of
124 inflorescences in each patch. We targeted our visits late in the flowering season to limit
125 the influence of possible sex differences in phenology (inflorescences can be sexed after
126 flowering is finished but not before it starts). To quantify the mating environment, we
127 focus our analyses on the sex ratio of inflorescences rather than patches, since a single
128 patch makes different contributions to the mating pool depending on whether it has few
129 or many inflorescences.

130 *Statistical analysis of natural population surveys*

131 We fit a binomial generalized linear model (glm), where “successes” were female in-
132 florescences and “trials” were total inflorescences, to test whether the OSR varied sys-
133 tematically with respect to longitude. Here and in the experiments that follow we use
134 longitude as a proxy variable that captures all east-west environmental variation, notably
135 precipitation (Fig. 2) but also factors that co-vary with precipitation such as productivity.

136 This statistical model and all those that follow were fit in a Bayesian statistical framework
137 using Stan (Carpenter et al., 2017) and R package ‘rstan’ (Stan Development Team, 2020)
138 with vague priors on all parameters. In all cases, model fit was assessed with posterior
139 predictive checks (Gelman et al., 1996).

140 *Common garden experiment*

141 *Source material and experimental design*

142 We established a common garden experiment at 14 sites throughout and beyond the
143 geographic distribution of *P. arachnifera* (Fig. 2, Table A2). Experimental sites spanned
144 latitudinal and longitudinal variation, though we focus here on longitude. During the
145 three years of this experiment (2014–2017), total precipitation at each site closely tracked
146 longitude (Fig. A1), as expected based on longer-term climate trends (Fig. 2). Source
147 material for the experiment came from 8 sites, most of which were a subset of the sites
148 that were visited for the natural population survey (Table A1, Fig. 2). At these sites, we
149 collected vegetative tillers from flowering individuals of each sex (mean: 11.6 individuals
150 per site, range: 2–18). These were brought back to the Rice University greenhouse, where
151 they were clonally propagated in ProMix potting soil and supplemented with Osmocote
152 slow-release fertilizer at 78–80°F under natural humidity and light.

153 Common gardens were set up in Fall (October–December) 2014. At each site, we es-
154 tablished 14 experimental blocks, which corresponded to a tree or woodland edge, pro-
155 viding partial shade that mimics this species’ natural micro-environment. We planted
156 3 females and 3 males in each block, for a total of 42 individuals per sex per site and
157 1176 total plants across sites, with all source collections represented at all sites. Indi-

viduals were spaced within blocks to allow space for rhizomatous growth that could be clearly attributed to individual transplants. To promote establishment, we cleared vegetation immediately surrounding transplants and provided ca. 1 L of water at the time of transplanting but provided no subsequent watering, fertilization, or competitor removal.

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

Statistical analysis of common garden experiment

We analyzed the demographic vital rates with generalized linear mixed models in a hierarchical Bayesian framework. All the vital rates shared a common linear predictor for the expected value that included fixed effects of size, sex, linear and quadratic terms for longitude, and all 2- and 3-way interactions. We included quadratic effects of longitude to account for the possibility of non-monotonic responses, following the hypothesis that fitness may peak in the center of the range. The linear predictor also included random effects of site, block, and source population of the transplant. We pooled all three years of observations for analysis so our results are implicitly averaged over years. In Table B1, we used WAIC-based model selection ('loo' package: Vehtari et al. (2017)) to show that vital rate models using precipitation and longitude as environmental covariates were statistically indistinguishable, which suggests that longitude is an adequate proxy for aridity.

The survival and flowering data were Bernoulli distributed, and these models applied the logit link function. We modeled panicle counts as zero-truncated negative binomial

181 using the log link. For growth, we modeled tiller number with a zero-truncated Poisson-
182 Inverse Gaussian (PIG) distribution. For flowering and panicle production in year t , the
183 size covariate was the natural logarithm of tiller number in year t . For survival and
184 size in year t , the size covariate was the natural logarithm of tiller number in year $t - 1$
185 (for 2015 data, size in year $t - 1$ was transplant size at the time of planting). Posterior
186 predictive checks indicated that these models described the data well (Fig. B1).

187 In follow-up analyses, we tested the addition of a climate mismatch variable that
188 quantified the deviation between mean annual precipitation of each source population
189 and common garden location. This analysis allowed us to evaluate whether local adap-
190 tation to climate may have contributed to variation in demographic performance across
191 common garden sites. This was motivated by the observation that most source pop-
192 ulations came from the interior of the geographic range and were brought to edge and
193 beyond-edge locations that were much drier or wetter than their historical climate regime
194 (Fig. 2). The local adaptation hypothesis predicts that demographic performance de-
195 clines with increasing climatic deviation between common garden and source population
196 locations. To test this hypothesis we added the absolute value of mean annual precipita-
197 tion mismatch (using 30-year normals) as a covariate to the vital rate models described
198 above.

199 *Sex ratio experiment*

200 At one site near the center of the range (Lake Lewisville Environmental Learning Area,
201 Texas), we established a separate experiment to quantify how sex ratio variation affects
202 female reproductive success. Details of this experiment, which was conducted in 2014–
203 2015, are described in Compagnoni et al. 2017. Briefly, we established 124 experimental

204 populations in $0.4m \times 0.4m$ plots that varied in population density (1–48 plants/plot)
205 and sex ratio (0–100%female), with 2–4 replicates for each of 34 density-sex ratio com-
206 binations. We used plants from a single source population located ca. 200 km from the
207 experimental site. The experiment was established ca. 1 km from a natural population at
208 this site and plots were situated with a minimum of 15 m spacing, a buffer that was in-
209 tended to limit pollen movement between plots (pilot data indicated that $\geq 90\%$ of wind
210 pollination occurred within 13m). We measured female reproductive success in different
211 density and sex ratio environments by collecting panicles from a subset of females in
212 each plot at the end of the reproductive season. In the lab, we counted the total number
213 of seeds on each panicle.

214 In Texas bluegrass, unfertilized seeds shatter from the panicle along with fertilized
215 seeds, so seed counts reflect female reproductive effort (seeds initiated) and not mating
216 success (seeds fertilized). We therefore assessed seed fertilization in two ways. First,
217 we conducted greenhouse-based germination trials using 25 seeds per panicle from 112
218 panicles belonging to 84 census females spanning the range of sex ratio variation. We
219 also conducted tetrazolium-based seed viability assays to estimate seed fertilization in-
220 dependently of germination, since some fertilized seeds may fail to germinate during
221 our trials. Tetrazolium trials used 17–57 seeds per panicle (mode: 30) from 65 panicles
222 belonging to 63 females, a subset of those used for the germination trials. To perform
223 these assays, we first let seed batches imbibe on a moistened paper towel for 12 h. We
224 then bisected the seeds in half and soaked them in a pH buffer solution containing 0.1%
225 of tetrazolium for 12 h. The pH buffer solution contained 0.57% of sodium phosphate
226 and 0.36% of potassium phosphate. A seed was scored as viable if the embryo stained
227 pink.

228 *Statistical analysis of sex ratio experiment*

229 Our previous study examined how interactions between density and frequency (sex ra-
230 tio) dependence contributed to female reproductive success (Compagnoni et al., 2017).
231 Here we focus solely on sex ratio variation, averaging over variation in density. Our goal
232 was to estimate a ‘mating function’ that defines how availability of male panicles affects
233 the viability of seeds on female panicles. We modeled the seed viability data with a
234 binomial distribution where the probability of viability (v) was given by:

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

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

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

Demographic model of range limits

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

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

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

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

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

where p^F and c^F are flowering probability and panicle production for females of size x , d

266 is the number of seeds (fertilized or unfertilized) per female panicle, v is the probability
 267 that a seed is fertilized, m is the probability that a fertilized seed germinates, and ρ is
 268 the primary sex ratio (proportion of recruits that are female). Seed fertilization depends
 269 on the OSR of panicles (following Eq. 1) which was derived from the $U \times 1$ vectors of
 270 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 given
 272 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 first
 274 year and enter the size distribution of established plants. Because our common garden
 275 experiment relied on greenhouse-raised transplants we had little information on these
 276 early life cycle transitions, and filling these gaps was important for generating realistic
 277 predictions from the demographic model. We used the seedling survival probability (σ)
 278 from our demographic studies of the hermaphroditic, perennial congener *Poa autumn-*
 279 *nalis* in east Texas (T.E.X. Miller and J.A. Rudgers, *unpublished data*) as a stand-in for
 280 *P. arachnifera*, and we assume this probability was constant across sexes and longitudes

(posterior mean $\sigma = 0.09$). We also assume that surviving seedlings reach size y with probability $g(y, x = 1)$, the expected future size of 1-tiller plants from the transplant experiment. The second term represents survival and size transition of established plants from the previous year, where s and g give the probabilities of surviving at size x and growing from sizes x to y , respectively, and superscripts indicate that these functions may be unique to females (F) and males (M).

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

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

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

301 fertility from the composition of the mating pool.

302 **Results**

303 *Sex ratio variation in natural populations*

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

309 *Geographic variation in sex-specific demography*

310 In year one, there was near-total mortality of transplants at three sites in the common
311 garden experiment due to various catastrophes (a flood, a drought, a pack of voles);
312 otherwise, there was high (95%) establishment. There was strong longitudinal variation
313 in demography, including sex-specific demographic responses that varied across vital
314 rates and interactions between size, sex, and longitude. Where sex-specific demographic
315 responses occurred, they were almost always in favor of females. In Fig. 4, we show
316 binned means of raw data and fitted vital rate models for four vital rates (rows) and
317 three size classes (columns); size was discretized for visualization only. This figure also
318 shows the posterior distributions for the difference between the sexes across longitudes.

319 Annual survival probability was predicted to peak at western and eastern range
320 edges and was lowest at intermediate longitudes (Fig. 4A-C). There was a modest fe-
321 male survival advantage but only at the western range edge for large sizes. Other vital

322 rates showed the opposite (and more expected) longitudinal pattern for most sizes, with
323 peaks in the center of the range and declines at eastern and western edges. There was a
324 female growth advantage for small sizes at western longitudes (Fig. 4D-F). The strongest
325 sex difference was in the probability of flowering: females had a flowering advantage,
326 especially for large sizes and at eastern longitudes (Fig. 4G-I). Finally, panicle production
327 by flowering plants was similar between the sexes for most sizes, though for the largest
328 sizes there were advantages for males in the west and females in the east (Fig. 4J-L).

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

338 For survival, flowering, and panicle production we did not find strong evidence for
339 local adaptation based on the posterior distributions of the climate mismatch coefficient
340 (Fig. B2A,C,D). However, climate mismatch negatively affected growth such that plants
341 from populations whose mean annual precipitation strongly differed from that of the
342 common garden location exhibited reduced growth (Fig. B2B).

Sex-ratio dependent seed fertilization

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

Two-sex model of range limits

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

365 vations from the common garden and natural populations (Fig. B5A). Female bias in the
366 OSR was predicted to cause declines in seed viability toward eastern range margins (Fig.
367 B5B). However, this effect was weak in magnitude because predicted OSR bias was not
368 extreme enough to cause strong declines in viability, given the relationship derived from
369 the sex ratio manipulation experiment (Fig. 5). Furthermore, population viability at the
370 eastern range margin was weakly sensitive to seed viability relative to other vital rates
371 (Fig. B5C). These observations underscore the next set of results.

372 LTRE decomposition revealed that declines in λ approaching range limits were driven
373 almost exclusively by females (Fig. 6B) with near-zero contributions from males (Fig.
374 6C). Thus, range limitation was an effectively female-dominant process, despite system-
375 atic geographic variation in sex ratio. Correspondingly, predictions of the two-sex model
376 were nearly indistinguishable from a corresponding female-dominant model with all else
377 equal, with only very modest differences in predictions of the two models emerging in
378 the eastern part of the range (Fig. B4).

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

386 Skew in the OSR predicted by the demographic model was less extreme than was
387 observed in natural and experimental populations (Fig. B5A). This occurred because sex
388 differences in demography, especially flowering, were most pronounced at the largest

sizes, and the MPM predicted that these sizes were very rare at stable population structure. The stable size distribution predicted by the MPM corresponded well to the common garden data (from which the MPM was built) but was much smaller, on average, than the size distribution we observed in natural populations (Fig. C2), presumably because transplants did not grow like “real” plants and/or did not have time in our three-year experiment to reach those sizes. In Appendix C, we explore whether higher growth rates, leading to a more realistic size distribution, would lead to a more important role for males. In numerical experiments with growth parameters, we found that larger size distributions led to stronger female bias and thus stronger reductions in seed viability at eastern range margins (Fig. C3). While these changes increased the contributions of males to range limitation, female contributions were still more than twice as important as males, and there was very little difference between predictions of the two-sex and female-dominant models even under this elevated growth scenario (Fig. C4). This leads us to conclude that, while our common garden-parameterized model may quantitatively underestimate OSR bias and its demographic consequences relative to natural populations, our qualitative conclusion that range boundary formation is effectively female-dominant in this system is robust to any biases imposed by the growth trajectories and size distributions of common garden populations.

Discussion

Understanding the causes of decline in population viability at range edges is a classic ecological problem and the foundation for predicting how species’ ranges will respond to global change drivers. Sexual niche differentiation has the potential to generate skew in the mating pool across environmental gradients and may therefore contribute to re-

412 productive failure at range edges of dioecious species. In Texas bluegrass, we found
413 evidence for sexual niche differentiation that manifested over a large-scale geographic
414 gradient: the female reproductive niche (environment-dependent flowering and panicle
415 production) extended farther east than that of males, generating female-biased opera-
416 tional sex ratios toward the eastern, mesic range margins, a pattern detected in natural
417 populations and recapitulated in our common garden populations. Furthermore, seed
418 viability declined with increasing skew in the OSR, indicating that mate (pollen) limita-
419 tion can limit the reproductive output of female-biased mating pools. It would appear
420 that all the pieces are in place for an important role of two-sex dynamics in contributing
421 to distributional limits of Texas bluegrass, particularly at the eastern range edge. Yet,
422 insights derived from the field-parameterized population model indicate the opposite:
423 range limitation in this species is an effectively female-dominant process, with negligible
424 contributions from males. Thus, in this system and likely others, female dominance is
425 an adequate framework for understanding range dynamics: despite evidence for sexual
426 niche differentiation, only the female niche mattered for determining the environmental
427 limits of population viability. This does not mean that sex is unimportant, but rather that
428 lack of sex is never so severe that it limits population viability.

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

436 there are striking examples of female-biased sex ratios causing declines in population
437 growth (Milner-Gulland et al., 2003) or range expansion (Miller and Inouye, 2013), other
438 examples suggest limited demographic consequences of sex ratio variation (Ewen et al.,
439 2011; Gownaris et al., 2020; Mysterud et al., 2002). Ultimately, sensitivity of female repro-
440 ductive success to sex ratio should depend strongly on the mating system, with female
441 dominance at the “extremely polygamous” end of a continuum (Miller et al., 2011). The
442 sensitivity of population viability to female reproductive success, in turn, is likely pre-
443 dicted by life history strategy: in long-lived, iteroparous species, population growth rates
444 are often weakly sensitive to reproduction relative to growth and survival (Franco and
445 Silvertown, 2004). We therefore hypothesize that range limits are more likely to be dom-
446 inated by the female environmental niche in longer-lived species with more polygamous
447 mating systems, while males are more likely to play an important role in shorter-lived,
448 monogamous species that may be particularly sensitive to missed mating opportunities.
449 As studies of sex ratio variation and sex-specific demography across species’ ranges ac-
450 cumulate in the literature (e.g., Dudaniec et al., 2021; Lynch et al., 2014; Petry et al., 2016),
451 this hypothesis may be tractably pursued with comparative analyses.

452 While life history and mating system may determine the demographic consequences
453 of skewed sex ratios, the sensitivity of sex ratio to environmental drivers is another crit-
454 ical ingredient of how environmental variation can affect the population dynamics of
455 dioecious species. Our study adds to a growing body of work quantifying the demo-
456 graphic mechanisms giving rise to skewed operational sex ratios using two-sex models
457 (Eberhart-Phillips et al., 2017; Shelton, 2010; Veran and Beissinger, 2009) and parsing the
458 contributions of environmental drivers (Bialic-Murphy et al., 2020). However, as a field,
459 we lack a strong predictive framework for how often and in which direction environ-

460 mental drivers are likely to skew the operational sex ratio – and this gap is particularly
461 important in the context of global change. We have focused on the limits of population
462 viability with respect to geographic environmental variation but analogous processes
463 will likely govern how populations respond to temporal environmental change (e.g., cli-
464 mate change), including direct effects on female demography and indirect effects via
465 perturbations to the mating pool (Fig. 1). There is a need to better understand and pre-
466 dict which species and types of species are susceptible to climate change-induced shifts
467 in OSR. Geographic variation in OSR may be an instructive proxy for how dioecious
468 species will respond to climate change (Petry et al., 2016). The link between OSR and
469 responses to climate adds value to studies of the causes and consequences of spatial vari-
470 ation in sex ratio, particularly at geographic scales that encompass “past” and “future”
471 conditions.

472 Previous studies of dioecious plants have shown that male bias is more common than
473 female bias and is particularly pronounced in harsh abiotic environments, likely reflect-
474 ing the greater resource requirements needed to pay the female cost of reproduction
475 (Bierzychudek and Eckhart, 1988; Field et al., 2013a,b). Our surveys of natural popula-
476 tions are consistent with the broader pattern of male-biased OSR at xeric range edges.
477 However, our common garden populations did not exhibit strong male bias in the xeric
478 west – averaged across years (Fig. 3B) or in any single year (Fig. B3) – nor did we find
479 any strong demographic evidence for a western male advantage (in fact, there was a
480 western female advantage in growth and survival for some sizes). If male advantage /
481 female disadvantage under harsh abiotic conditions (suggested by the natural popula-
482 tion trend: Fig. 3A) is driven by the greater resource requirements of females then it is
483 possible that clonal propagation and/or legacies of greenhouse rearing masked the ‘true’

sex difference at xeric-edge common garden sites, or that reproductive costs accumulate over longer time scales than considered here. 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 in at least three ways. 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 collection 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

508 mate limitation at longitudinal range edges. It would be interesting to additionally con-
509 sider this species' latitudinal limits, though our exploratory analyses revealed no clear
510 sex differences or sex ratio variation with respect to latitude.

511 Second, our results also provide novel evidence for contrasting demographic re-
512 sponses to environmental drivers throughout a species' range – or “demographic com-
513 pensation” (Doak and Morris, 2010; Vilellas et al., 2015). Elevated performance in some
514 life history processes can compensate for declines in other processes and thus buffer
515 range-edge populations against harsh environmental conditions. In Texas bluegrass,
516 most vital rates declined toward eastern and western range limits but survival showed
517 the opposite pattern. Increased survival at longitudinal extremes partially offset declines
518 in other vital rates but this positive response was weaker than the negative responses.
519 Ultimately, increased survival was not sufficient to prevent declines in population vi-
520 ability from the range center to eastern and western limits, which were dominated by
521 declining female growth and flowering. However, we also found evidence that growth
522 patterns exhibited local adaptation: individuals planted into locations that were climati-
523 cally similar to locations of their source population exhibited greater growth, on average,
524 irrespective of sex. It is therefore possible that our demographic model (which does not
525 explicitly account for local adaptation) over-estimates the decline in fitness approaching
526 range edges, since local adaptation in a high-sensitivity vital rate may dampen the effects
527 of environmental forcing. There is growing awareness that local adaptation can modify
528 expectations for species' distributions under global change (Peterson et al., 2019). Mech-
529 anistic models of range limits that incorporate potential for local adaptation would be a
530 valuable next step.

531 Third, our results highlight some important considerations in how environment-

532 dependent demographic models are best parameterized to derive insights into the drivers
533 of range limits. Our approach relied heavily on common garden populations, which
534 allowed us to plant and track known-sex individuals in contrasting environmental con-
535 ditions that encompass and exceed the natural geographic distribution. The ability to
536 robustly sample edge and beyond-edge environments is a powerful advantage of the
537 common garden transplant approach (Hargreaves et al., 2013). However, this also lim-
538 ited the size variation that we were able to include and model, and the size distributions
539 of common garden populations skewed consistently smaller than natural populations.
540 In Appendix C, we show that our conclusions are likely robust to this feature of the
541 common gardens. However, our ability to quantify the consequences of size representa-
542 tion is itself limited by size representation: we can simulate a population in which the
543 largest common garden sizes are more common than they actually were, but simulating
544 a population with sizes much larger than observed requires extrapolation of our statisti-
545 cal models, and we are skeptical about what insights such an exercise could provide (in
546 Appendix C, we extrapolated demographic performance to sizes 50% greater than the
547 observed maximum). This issue is not unique to our study but will be encountered by
548 any transplant study intended to yield inferences about range limits of species with sig-
549 nificant size structure, such as trees. If we could re-do our experiment knowing what we
550 know now, we would combine data from natural and transplanted populations to model
551 size-dependent demography over a more realistic size distribution. Other investigators
552 inspired by similar questions about the demographic drivers of range limits should con-
553 sider such a hybrid approach.

554 *Conclusion.* We have documented geographic variation in operational sex ratio; eluci-
555 dated how sex-specific demographic responses to environmental drivers generate this
556 pattern; quantified how female fertility responds to availability of males; and demon-
557 strated that, in the end, sex ratio variation is a rather inconsequential component of
558 declines in population viability at range limits. In Texas bluegrass and, we speculate,
559 other dioecious plants and animals with similar life history and reproductive traits, the
560 geographic distribution is essentially the *female* environmental niche ‘writ large’ (Harg-
561 reaves et al., 2013).

562 Understanding and predicting geographic distributions and their responses to en-
563 vironmental change demands careful consideration of which biological details must be
564 accounted for and which others can be safely ignored. Our results show that complex,
565 non-linear dynamics involving females, males, and frequency-dependent reproduction
566 can be reasonably approximated as a simple, linear process (female-dominant popula-
567 tion growth). We suggest that this is good news. The next challenge is to figure out how
568 often and under what conditions ecologists can get away with it.

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583 **Author contributions**

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

586 **Data accessibility**

587 All data (Miller and Compagnoni, 2022b) and code (Miller and Compagnoni, 2022a) are
588 publicly available.

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

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 and Hijmans, 2017). Grey diamonds show natural population census locations, black points show sites for the common garden transplant experiment, and red points show locations of the source populations planted in each common garden site.

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. Gray lines show 500 samples from the posterior distribution of fitted binomial GLMs.

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). Shaded contours show the 25, 50, 75, and 95 percentiles of the posterior distribution. Dashed horizontal line shows zero difference.

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.

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.