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

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Abstract

Understading the mechanisms that generate biogeographic patterns of distribution and abundance is a long-standing goal of ecology. It is widely hypothesized that distributional limits reflect the environmental niche, but this hypothesis is complicated by widespread potential for intra-specific niche heterogeneity. In dioecious species, for example, sexual niche differentiation may cause divergence between the sexes in their limits of environmental suitability. We studied the mechanisms of range boundary formation in Texas bluegrass (*Poa arachnifera*), a perennial dioecious plant, testing the alternative hypotheses that range limits reflect the niche limits of females only, as assumed by classic ecological theory, versus the combined contributions of females and males, including their inter-dependence via male-limitation of female fertility. Common garden experiments across the longitudinal aridity gradient of the southern Great Plains, US revealed female-biased flowering and panicle production approaching eastern range limits, consistent with surveys of operational sex ratio variation in natural populations. A process-based demographic model predicted longitudinal limits of population viability ($\lambda \geq 1$) that matched the observed eastern and western range limits, and further showed that declines in λ approaching range limits were driven almost entirely by declines in female vital rates. Thus, despite the potential for mate limitation, particularly at eastern margins, the geographic distribution was effectively female-dominant, reflecting the environmental niche of females with little contribution from males. The dominant role of females was attributable to female fertility being quite robust to sex ratio variation (which declined only at extreme under-representation of males) and to relatively low sensitivity of λ to reproductive transitions in the life cycle. This suggests that female-dominant limitation of geographic distribution may be common to long-lived species with polygamous mating systems, and that female responses to environmental drivers may often be sufficient for predicting range shifts in response to environmental change.

Keywords

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

Introduction

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

The widespread idea that range limits reflect niche limits intersects awkwardly with another pervasive concept in ecology: intra-specific niche heterogeneity. This refers to the fact that individuals within a population or species may differ in their interactions with the biotic and/or abiotic environment (Bolnick *et al.*, 2002; Araújo *et al.*, 2011; 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?

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

Sexual niche differentiation can translate to sex-specific advantages in different environments, causing skew in the operational sex ratio (OSR: relative abundance of females and males available for mating) even if the primary (birth) sex ratio is unbiased (Veran & Beissinger, 2009; Shelton, 2010; Eberhart-Phillips *et al.*, 2017). Indeed, environmental clines in OSR have been widely documented in plants and animals at fine spatial scales (Eppley, 2001; Bertiller *et al.*, 2002; Groen *et al.*, 2010; Hultine *et al.*, 2018; Bisang *et al.*, 2020) as well as broader climatic clines across alititutdes or latitudes (Petry *et al.*, 2016; Ketterson & Nolan Jr, 1976; Caruso & Case, 2007; Dudaniec *et al.*, 2021). At range margins, where environments are extreme relative to the range core, demographic differences between the sexes, and hence skew in the OSR, may be greatest. In dioecious plants, for example, populations at the upper altitudes and latitudes and in the more xeric margins of species' ranges tend to be male-biased (Field *et al.*, 2013b).

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

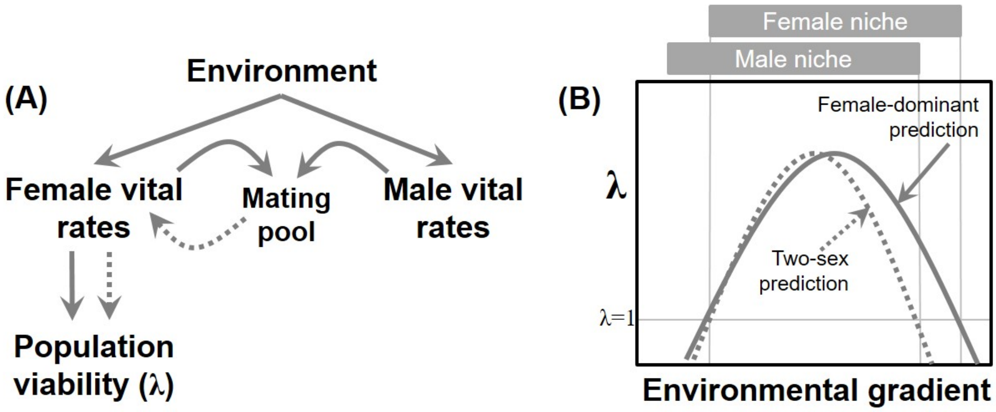

Figure 1: Hypotheses for how environmental variation can affect population viability and range limits in dieocious species. Under the female-dominant hypothesis, environmental drivers affect population growth (λ) through effects on females, alone (A). In geographic / environmental space, this translates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

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

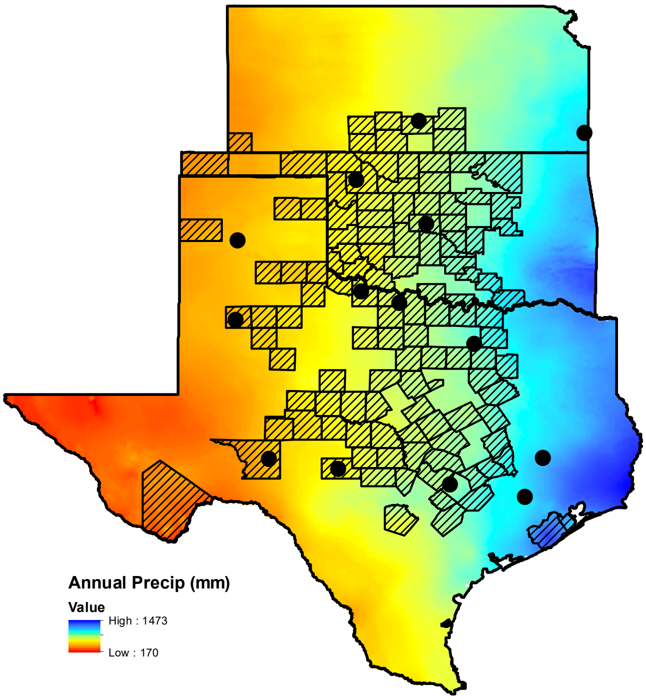

Figure 2: Geographic and environmental distribution of *P. arachnifera* in Texas, Oklahoma, and Kansas. Hatched shapes show counties with herbarium records of occurrence. Color shows geographic variation in annual precipitation (mm) based on 30-year normals from WorldClim (Fick & Hijmans, 2017). Points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

populations in other states[1]. 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

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

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

Statistical analysis of natural population surveys

We fit a binomial generalized linear model (glm), where females were "successes" and total inflorescences was the number of "trials", to test whether the OSR varied systematically with respect to longitude. Here and in the experiments that follow we use longitude as a proxy variable that captures all east-west environmental variation, notably precipitation (Fig. 2) but also factors that co-vary with precipitation such as productivity. This statistical model and all those that follow were fit in a Bayesian statistical framework using Stan (Carpenter *et al.*, 2017) and rstan (Team *et al.*, 2018) with vague priors on all parameters. In all cases, model fit was assessed with posterior predictive checks (Conn *et al.*, 2018). All code for statistical and demographic modeling is available at `https://github.com/texmiller/POAR-range-limits`.

Common garden experiment

Source material and experimental design

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

Common gardens were set up in Fall (October–December) 2014. At each site, we established 14 experimental blocks, which typically corresponded to a tree or woodland edge, providing partial shade that mimics this species' natural microenvironment. We planted 3 females and 3 males in each block, for a total of 42 individuals per sex per site and 1176 total plants across sites, with all source collections represented at all sites. Individuals 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), 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 we did not explicitly model temporal variation but our results are implicitly averaged over years.

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

Sex ratio experiment

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

Statistical analysis of sex ratio experiment

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

$$v = v_0 * (1 - OSR^{\alpha}) \tag{1}$$

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

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

Demographic model of range limits

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

MPM accommodates longitude as a predictor variable, allowing us to identify the 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 $x \in \{1, 2, ..., U\}$ 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:

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

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

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

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

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

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

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

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

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

$$\frac{\partial \lambda}{\partial Longitude} \approx \sum_i \frac{\partial \lambda}{\partial \theta_i^F} \frac{\partial \theta_i^F}{\partial Longitude} + \frac{\partial \lambda}{\partial \theta_i^M} \frac{\partial \theta_i^M}{\partial Longitude} \tag{7}$$

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 fertility from the composition of the mating pool.

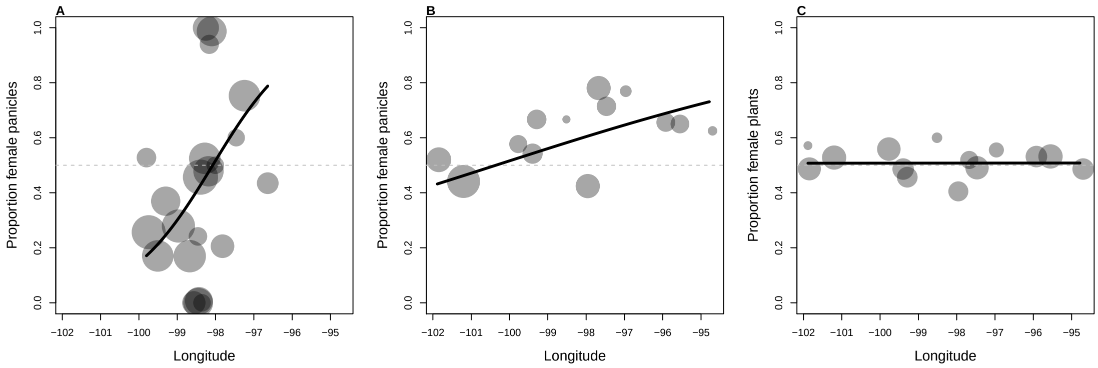

Figure 3: Sex ratio variation of *P. arachnifera* across its longitudinal distribution. **A**, Operational sex ratio (fraction of panicles that were female) in 22 natural populations; **B**, Operational sex ratio and **C**, sex ratio (fraction of plants that were female) in 14 common gardens. Within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

Results

Sex ratio variation in natural populations

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

Geographic variation in sex-specific demography

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

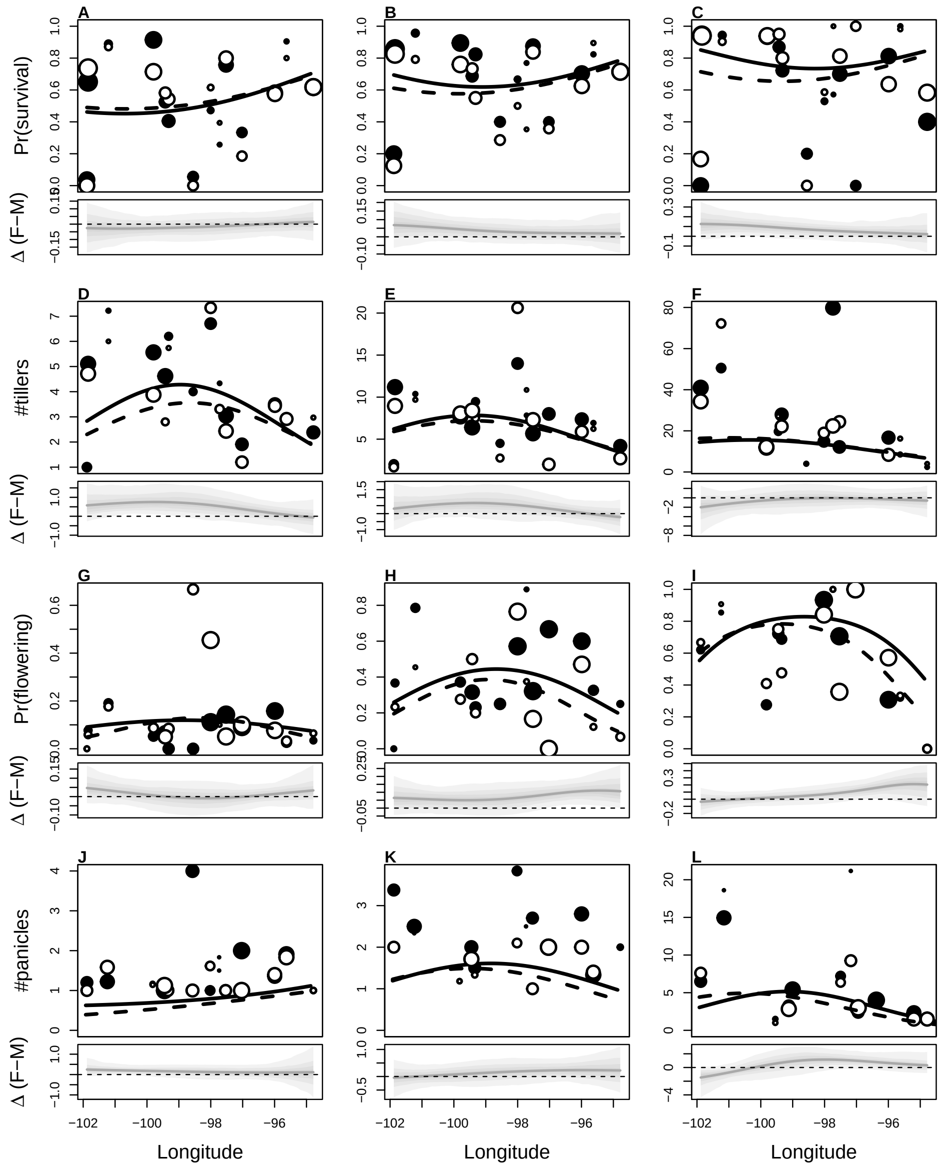

Figure 4: Sex-, size-, and longitude-related variation in: A–C, inter-annual probability of survival; D–F, inter-annual growth (change in number of tillers); G–I, probability of flowering; J–L, number of panicles produced given flowering. Points show means by site for females (filled) and males (open)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

longitudinal variation in demography, including sex-specific demographic responses that varied across vital rates and interactions between size, sex, and longitude. Where sex-specific demographic responses occurred, they were almost always in favor of females. In Fig. 4, we show binned means of raw data and fitted vital rate models for four vital rates (rows) and three size classes (columns); size was discretized for visualization only. This figure also shows the posterior distributions for the difference between the sexes across longitudes.

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

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

Sex-ratio dependent seed fertilization

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

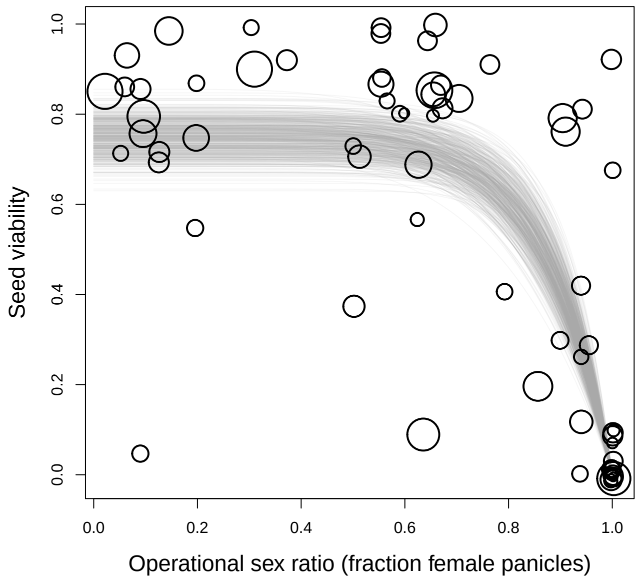

Figure 5: Seed fertilization success in relation to operational sex ratio (fraction of panicles that are female) in experimental populations. Circles show data from tetrazolium assays of seed viability; circle size is proprtional to the number of seeds tested (min: 14, max: 57). Lines show model predictions (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, population viability at the eastern range margin was weakly sensitive to seed viability relative to other vital rates (B4C). These observations underscore the next set of results.

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

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

Skew in the OSR predicted by the demographic model was less extreme than was observed in natural and experimental populations (B4A). This occurred because sex 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 natu-

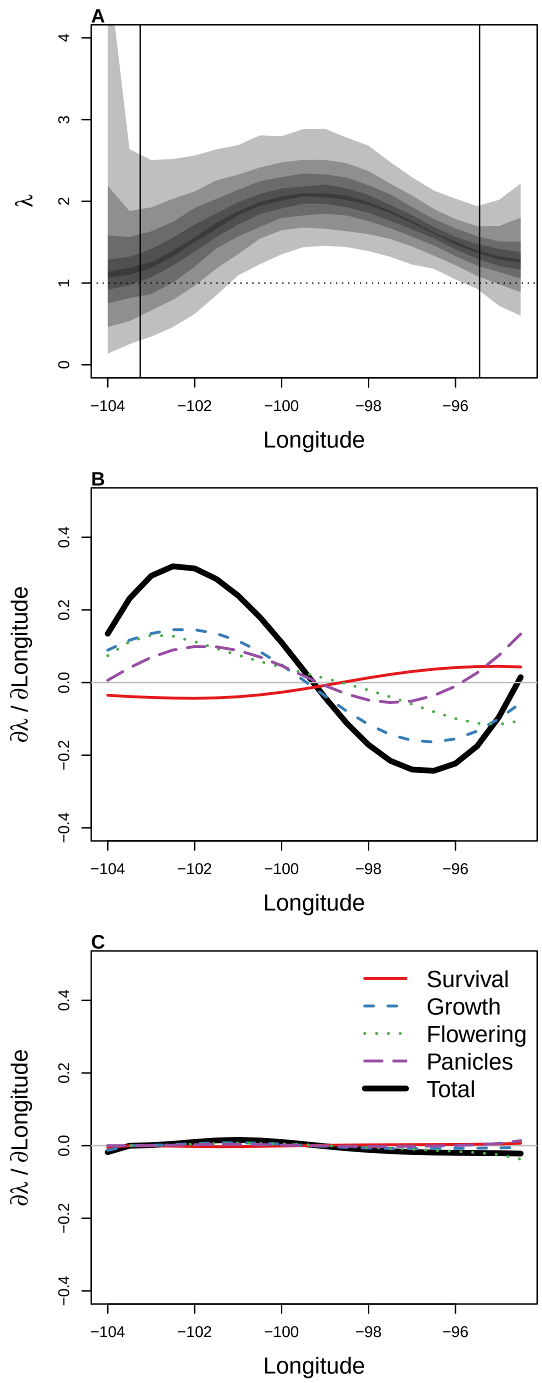

Figure 6: Population growth (λ) as a function of longitude, predicted by the two-sex MPM that incorporates sex-specific demographic responses to longitude with sex ratio-dependent seed fertilization. A, posterior distribution of λ, where shaded regions show the 25, 50, 75, and 95% percentiles of parameter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

ral 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 reproductive failure at range edges of dioecious species. In Texas bluegrass, we found evidence for sexual niche differentiation that manifested over 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 *et al.*, 2003) or range expansion (Miller & Inouye, 2013), other examples suggest limited demographic consequences of sex ratio variation (Mysterud *et al.*, 2002; Ewen *et al.*, 2011; Gownaris *et al.*, 2020). Ultimately, sensitivity of female reproductive success to sex ratio should depend strongly on mating system, with female dominance at the "extremely polygamous" end of a continuum (Miller *et al.*, 2011). The sensitivity of population viability to female reproductive success, in turn, is likely predicted by life history strategy: in long-lived, iteroparous species, population growth rates are often weakly sensitive to reproduction relative to growth and survival (Franco & Silvertown, 2004). We therefore hypothesize that range limits are more likely to be dominated by the female environmental niche in longer-lived species with more polygamous mating systems, while males are more likely to play an important role in shorter-lived, monogamous species that may be particularly sensitive to missed mating opportunities. As studies of sex ratio variation and sex-specific demography across species' ranges accumulate in the literature (Dudaniec *et al.*, 2021; Petry *et al.*, 2016; Lynch *et al.*, 2014, e.g.,), this hypothesis may be tractably pursued with comparative analyses.

While life history and mating system may determine the demographic consequences of skewed sex ratios, the sensitivity of sex ratio to environmental factors is another critical ingredient of how environmental variation can affect the population dynamics of dioecious species. Our study adds to a small but growing body of work quantifying the demographic mechanisms giving rise to skewed operational sex ratios along environmental gradients (Bialic-Murphy *et al.*, 2020)**OTHERS?**, highlighting that OSR bias need not reflect differential mortality between the sexes (Ueno *et al.*, 2007; Morrison *et al.*, 2016). However, as a field, we lack a strong predictive 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 no clear sex differences or sex ratio variation with respect to latitude.

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

Third, our results highlight some important considerations in how environment-dependent demographic models are best parameterized to derive insights into the drivers of range limits. Our approach relied heavily on common garden populations, which allowed us to plant and track known-sex individuals in contrasting environmental conditions that encompass and exceed the natural geographic distribution. The ability to robustly sample edge and beyond-edge environments is a powerful advantage of the common garden transplant approach (Hargreaves *et al.*, 2013). However, this also limited the size variation that we were able to model, and the size distributions of common garden populations skewed consistently smaller 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 details must be accounted for and which others can be safely ignored. Our results show that complex, non-linear dynamics involving females, males, and frequency-dependent reproduction can be reasonably approximated as a simple, linear process (female-dominant population growth). We suggest that this is good news. The next challenge is to figure out how often and under what conditions ecologists can get away with it.

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Author contributions

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

Data accessibility

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

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Appendix A: Site locations and climate

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

Table A1: Sites of natural population surveys corresponding to Figure

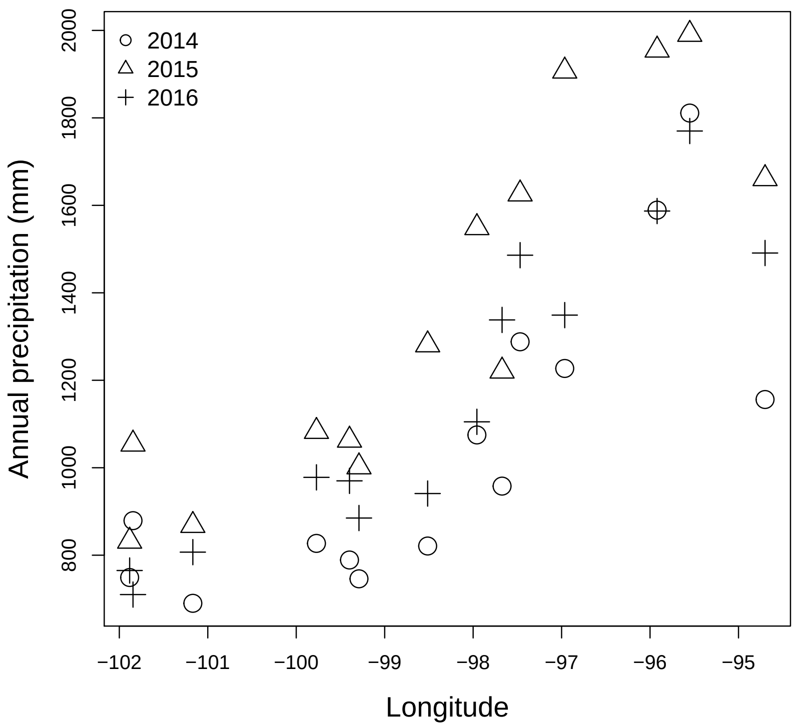

Figure A1: Total annual precipitation at common garden sites during the study years tracked long-term trends of increasing aridity from east to west.

Appendix B: Additional results

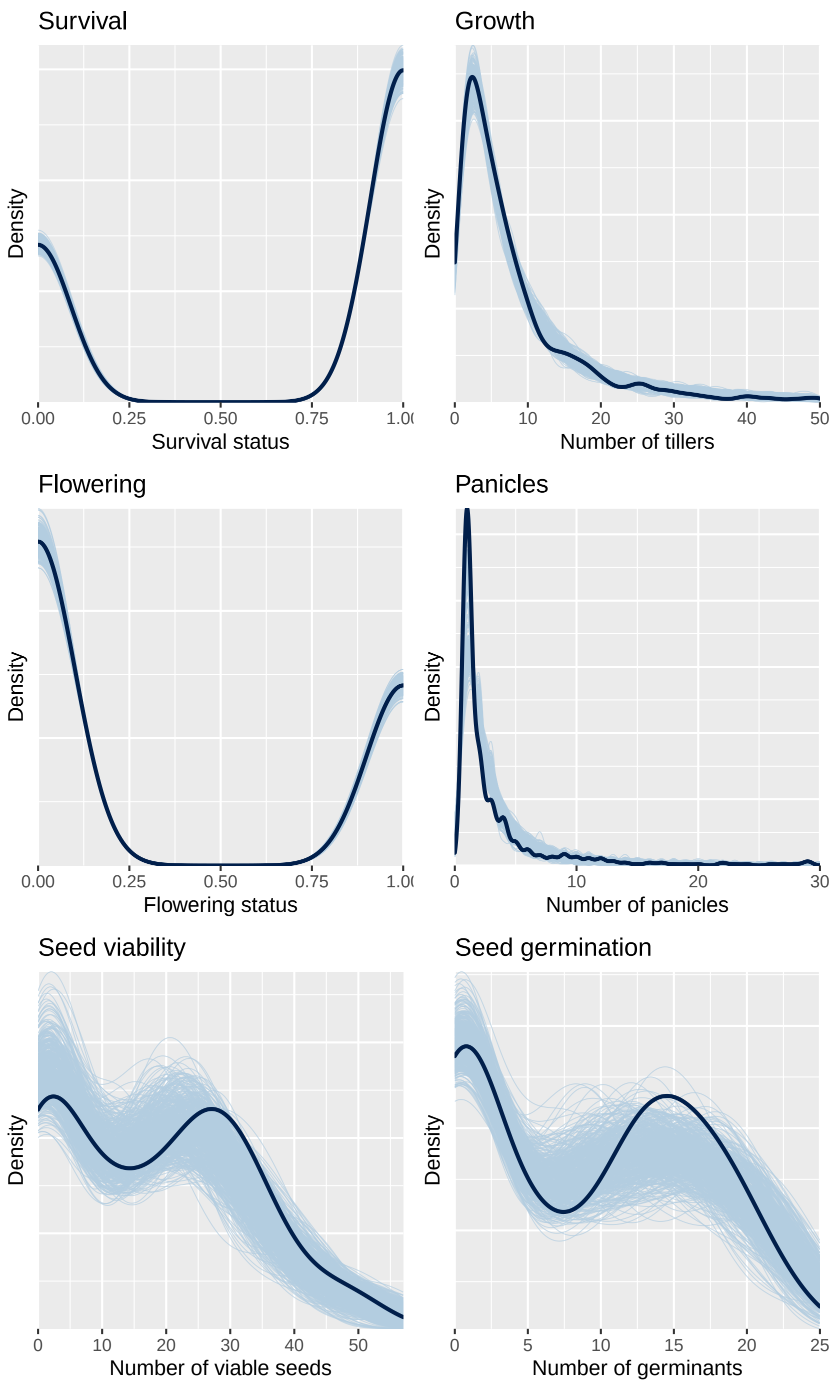

Figure B1: Posterior predictive checks of statistical models for demographic vital rates. Lines show density distributions of real data (thick, dark blue) compared to simulated data sets (thin, light blue) generated from the fitted models based on 500 draws of the posterior distribution of parameter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

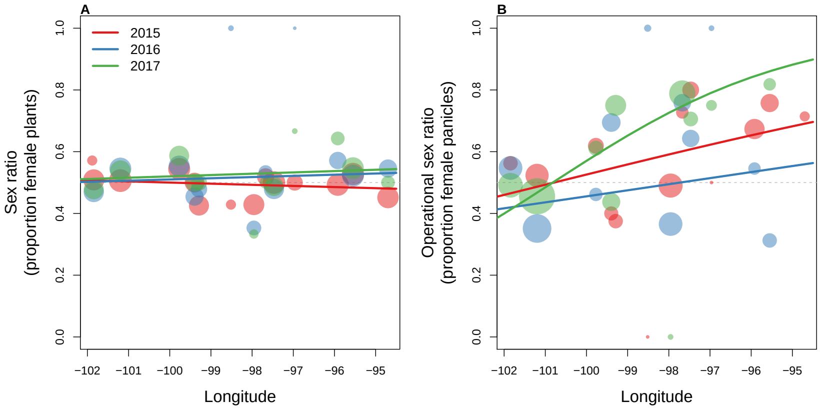

Figure B2: Year-specific sex ratios of plants (A) and panicles (B) in common garden populations spanning the longitudinal aridity gradient. Points sizes are proportional to sample sizes and lines show fitted binomial GLMs.

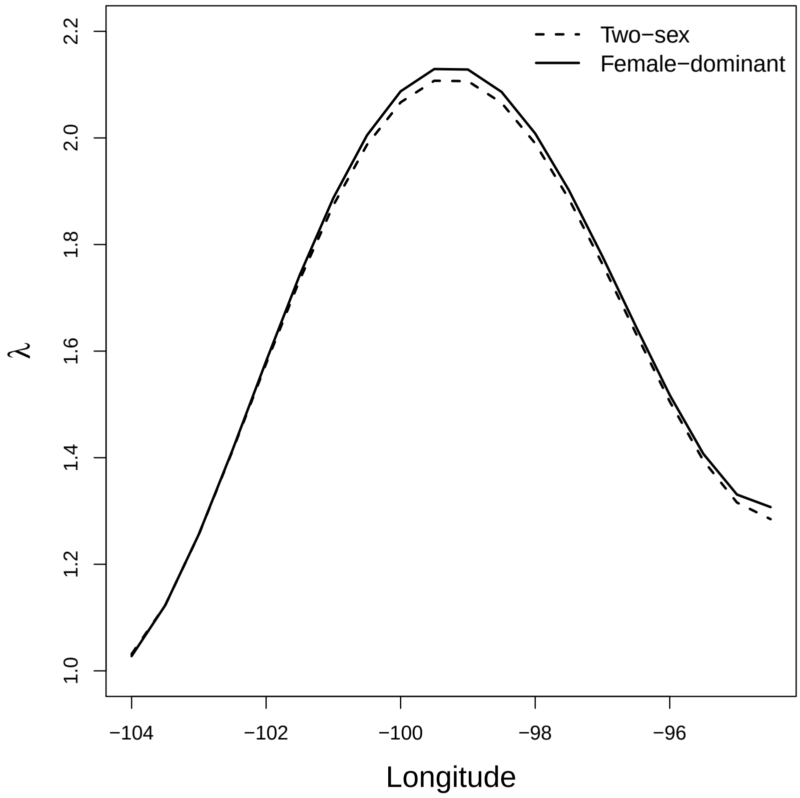

Figure B3: Comparison of longitudinal variation in λ between the two-sex demographic model (dashed line) that includes dependence of female seed production on population structure and the corresponding female-dominant model (solid line) with constant female fertility and all else equal. Models were evaluated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

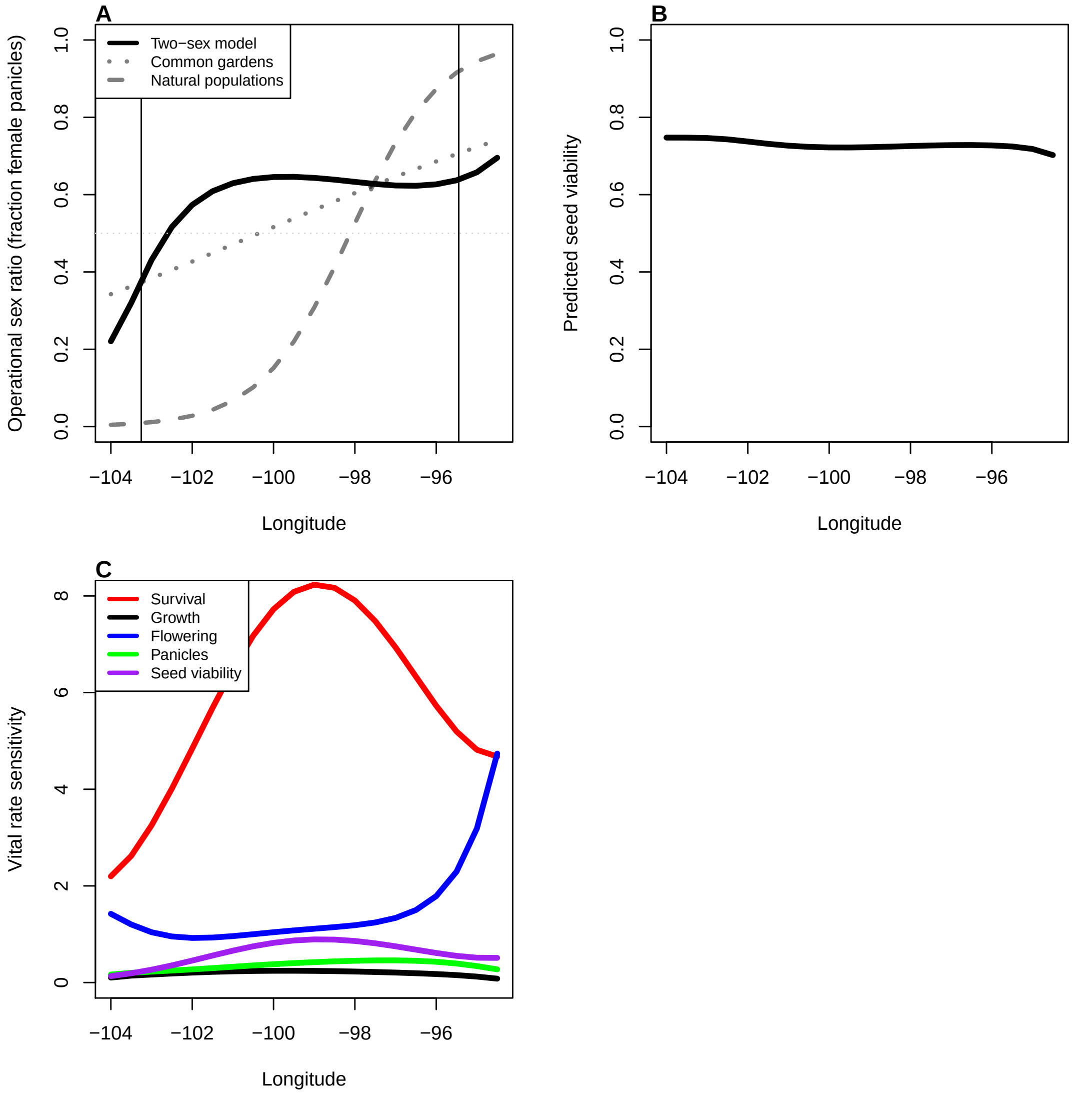

Figure B4: **A**, Longitudinal variation in operational sex ratio (fraction of panicles that are female) predicted by the two-sex MPM (solid line) compared to the sex ratio clines fitted to data from common gardens (dotted line) or natural populations (dashed line). Vertical lines show the longitudes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

Appendix C: Size distribution comparisons and simulation experiments

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

Observed and predicted size distributions

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

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

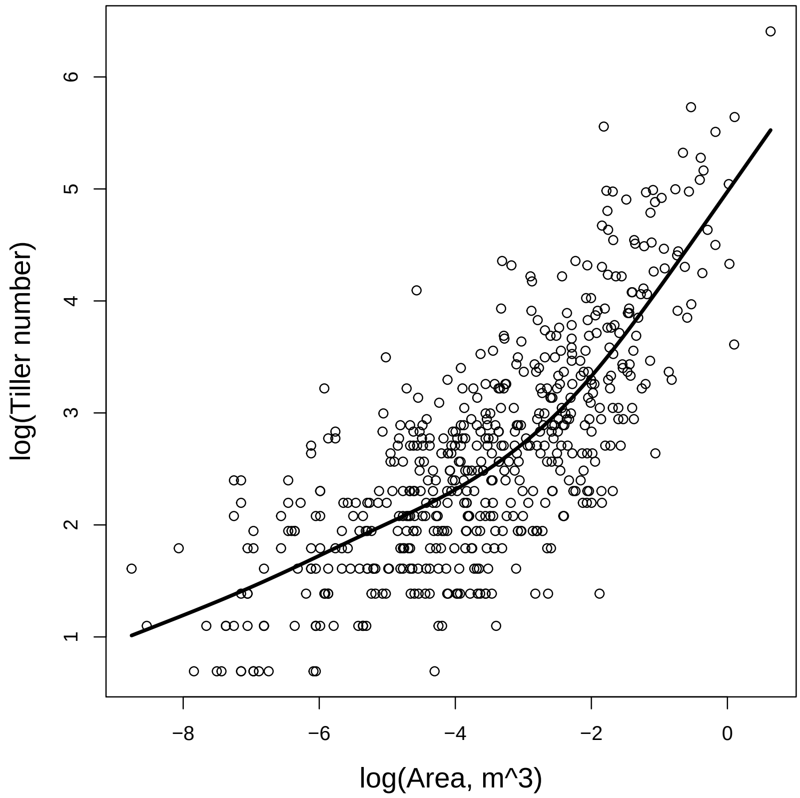

Figure C1: Relationship between area (m^3) and tiller count from plants in the common garden experiment. The fitted gam model (line) was used to convert area measurements from natural populations to tiller counts.

Two-sex MPM The two-sex MPM predicts asymptotic population structure, including stable size distribution (SSD) and sex ratio. For comparison with empirical data, we calculated the SSD (pooling both sexes) predicted in the center of the range (the conclusions that we draw from this analysis hold up if we consider SSD from different parts of the range). Because the MPM is structured by tiller number, we converted the SSD to log(tillers) by simulating an arbirarily large (10000) population at SSD, taking the natural logarithm of tiller number, and then estimating the empirical distribution of this variable.

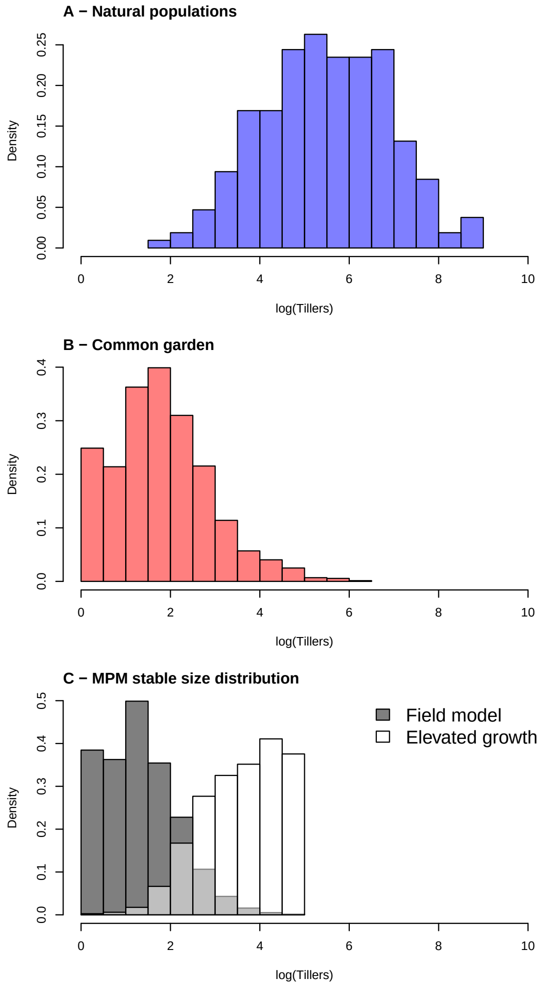

Figure C2: Size distribution of Texas bluegrass from natural populations (**A**), common garden populations (**B**), and predicted by the two-sex MPM (**C**). In **C**, the two size distributions come from the base model parameterized following methods described in the main manuscript (gray) and a numerical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

Results Plants from natural populations were larger, on average, than plants in our common garden experiment (Fig. C2A,B). Common garden plants were 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 empirically-estimated intercept of the growth vital rate function by a factor of 2.75 (values larger than this caused numerical instabilities). This adjustment caused all plants to increase in size more strongly regardless of initial size, sex, or geographic location.

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

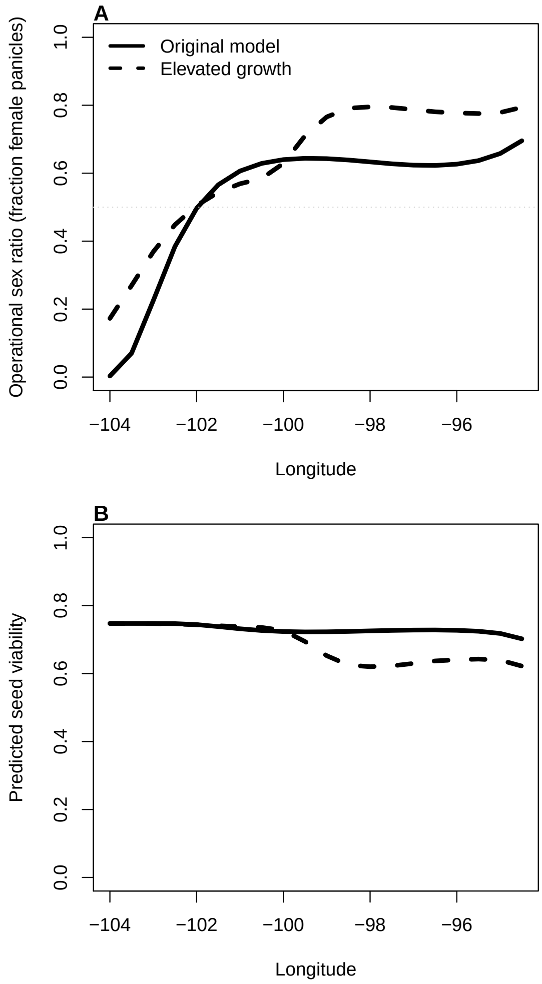

Figure C3: Two-sex model predictions for **A** operational sex ratio (fraction of panicles that are female) and **B** seed viability at stable population structure in relation to longitude. Solid line shows predictions of the base model using field-estmated parameter values and dashed line shows the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

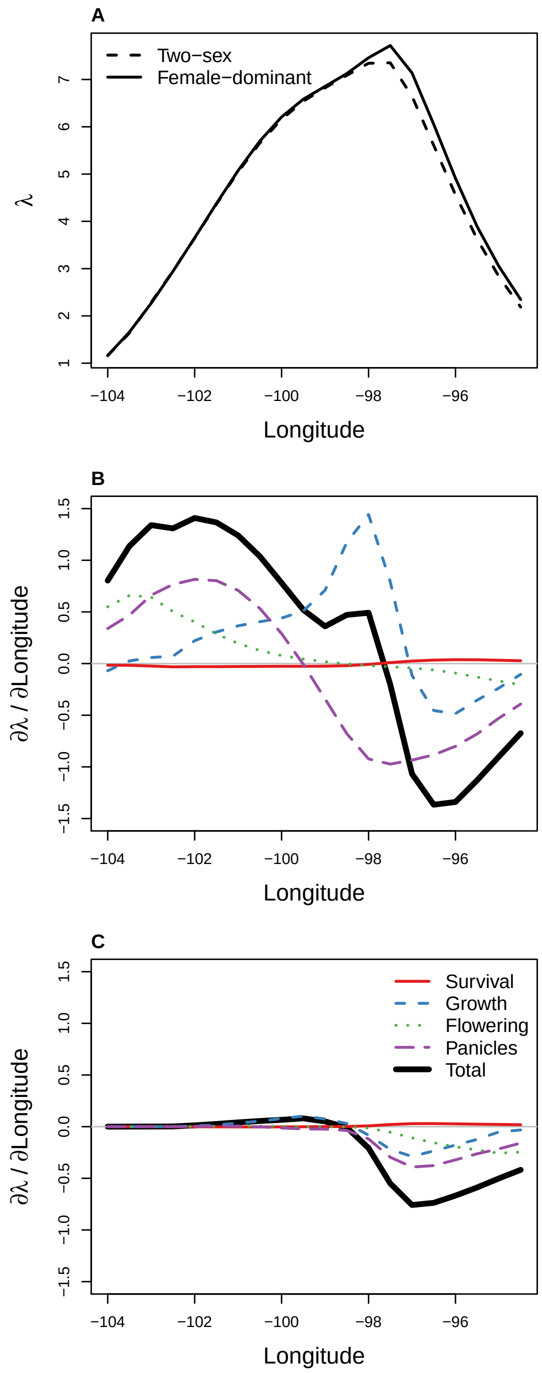

Figure C4: Results for the elevated growth model, in which the intercept of growth function was increased by a factor of 2.75. **A**, contrast of two-sex and female-dominant models, as in Fig. B3; **B,C**, Life Table Response Experiments decomposing the change in λ with respect to longitude into contributions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