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

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Abstract

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

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.

Keywords

Introduction

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

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

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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 numerous examples of sex differences in trophic position (Pekár *et al.*, 2011; Law & Mehta, 2018), habitat use (Bowyer, 2004; Phillips *et al.*, 2004), 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 (Bierzychudek & Eckhart, 1988; Bolnick & Doebeli, 2003) or as a byproduct of naturally or sexually selected size dimorphism (Shine, 1989; Temeles *et al.*, 2010). In an ecological context, 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) as well as broader climatic clines across alititutdes or latitudes (Petry *et al.*, 2016; Ketterson & Nolan Jr, 1976; Caruso & Case, 2007). At range margins, where environments are extreme relative to the range core, demographic differences between the sexes,

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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.*, 2013).

Returning to the question of whose niche determines range limits given potential for sexual niche differentiation, classic ecological theory assumes 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, of course, wrong but it may often be a convenient approximation 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 & Inouye, 2011) or in life histories where population viability is weakly sensitive to female fertility (Franco & Silvertown, 2004).
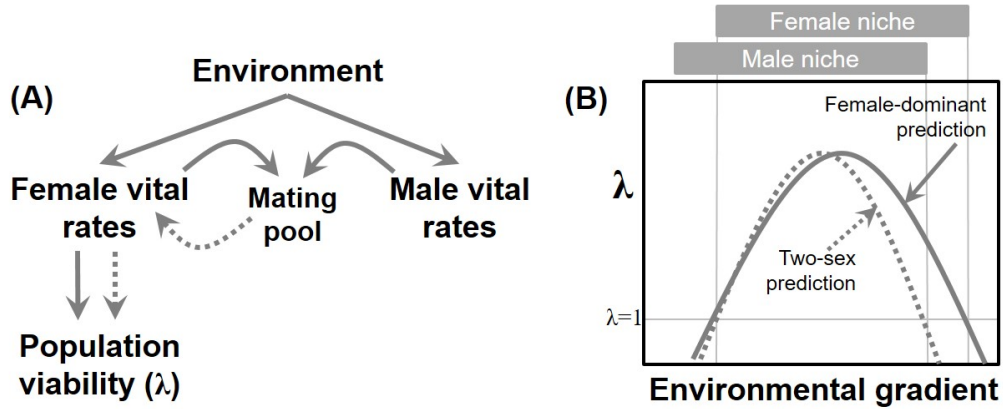
Figure 1: Hypotheses for how environmental variation can affect population viability and range limits in dioecious species. Under the female-dominant hypothesis, environmental drivers affect population growth (λ) through effects on females, alone (A). In geographic / environmental space, this translates to range boundaries that arise at the limits of the female environmental niche, irrespective of where they fall with respect to the male niche (B). Under the two-sex hypothesis, environmental drivers can affect λ through sex-specific responses, which may skew the sex ratio of the mating pool and feed back to affect female fertility via mate availability (A). In this case, expectations for range limits may differ from the female-dominant prediction, since mate limitation in environments that favor females over males may reduce population viability. These are alternative hypotheses in the strict sense, but as the role of males becomes weaker the two-sex prediction converges on the female-dominant prediction.

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

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forecasting range future 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 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 exhibit clines in operational sex ratio across longitudinal environmental variation. 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 sex ratio. 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 grass endemic to the southern Great Plains. This species occurs almost exclusively in central Texas, Oklahoma, and Kansas (Fig. 2) though there are occasional records of adventive populations in
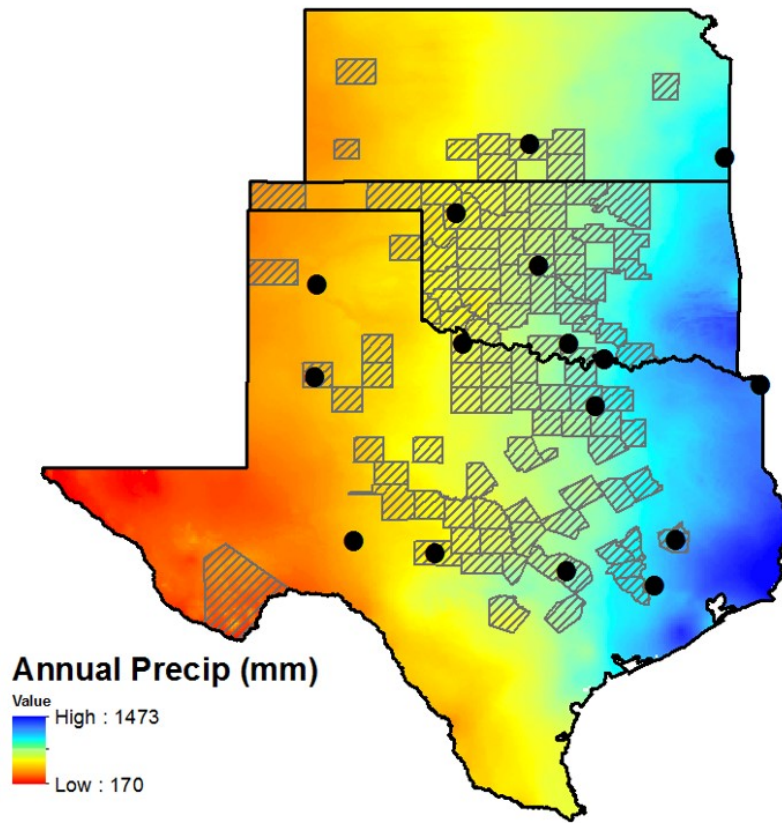
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Figure 2: Geographic and environmental distribution of *P. arachnifera* in Texas, Oklahoma, and Kansas. Hatched shapes show counties with herbarium records of occurrence. Color shows geographic variation in annual precipitation (mm) based on 30-year normals from WorldClim (Fick & Hijmans, 2017). Points show sites for the common garden transplant experiment.

other 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

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[1]http://bonap.net/Napa/TaxonMaps/Genus/County/Poa

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, *personal communication*). The rhizomatous growth habit allowed us to clonally propagate 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 operational sex ratio 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 on each. 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 operational sex ratio 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* (MAP). Experimental sites spanned latitudinal and longitudinal variation, though we focus here on longitude. During the three years of this experiment, total precipitation at each site closely tracked longitude (Fig. A1), as expected based on longer-term climate trends (map). Source material for this experiment came from 8 sites, which were of subset of the sites that were visited for the natural population survey (Table). For a subset of the natural populations we visited, we collected tillers from flowering individuals of each sex (mean: 11.6 individuals per site, range: 2–18) (Table A1). These were brought back to the Rice University greenhouse, where they were clonally propagated in ProMix potting soil and supplemental Osmocote fertilizer at 78–80°F under natural 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 micro-environment. 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.

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To promote establishment, we cleared vegetation immediately surrounding trans-plants 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 do 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 tiller and panicle counts as zero-truncated negative binomial using the log link. 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).

Sex ratio experiment

At one site near the center of the range (Lake Lewisville Environmental Learning Area in North-central 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 with tetrazolium assays of 25 seeds per panicle. We also conducted germination trials in the greenhouse (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 (p_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, that seed viability is maximized at v_0 as OSR approaches zero and goes to zero as OSR approaches 1. Parameter α controls how viability declines with increasing female bias.

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

Demographic model of range limits

The statistical models for the common garden and sex ratio experiments provided the backbone of the full demograhpic 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 (assumed to be the same for females and males). 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).

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

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

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

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

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

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

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functions may be unique to females (F) and males (M). All parameter estimates are reported in Table A1[2].

Because the two-sex MPM is nonlinear (vital rates affect and are affected by population structure) we estimated the asynmptotic 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.
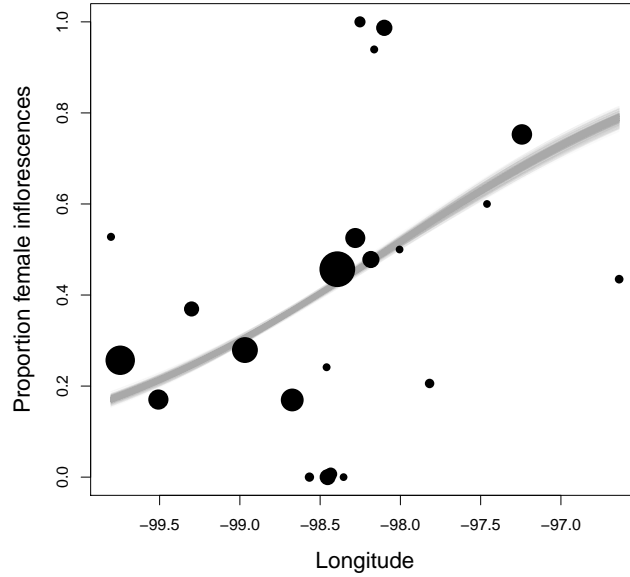
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Figure 3: Variation in operational sex ratio (proportion of panicles that were female) across 22 natural populations of *P. arachnifera*. Point size is proportional to population size (total panicles; min: 45, max: 2148). Lines show the fitted binomial regression for 500 samples from the posterior distribution of regression coefficients.

Results

Sex ratio variation in natural populations

We found wide variation in operational sex ratio (proportion of total panicles that were female) across 22 natural populations of *P. arachnifera*, including female-only and male-only populations (Fig. 3). There was a longitudinal trend to sex ratio variation, with male-biased panicle production in the western parts of the range and female-biased panicle production in the east. Not suriprisingly, small

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[2]This table does not exist yet.

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

Geographic variation in sex-specific demography

In year one, there was near-total mortality of transplants in the common garden experiment at three sites due to various catastrophes (a flood, a drought, a pack of voles); otherwise, we had good establishment in the common gardens. There was strong 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), 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 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).
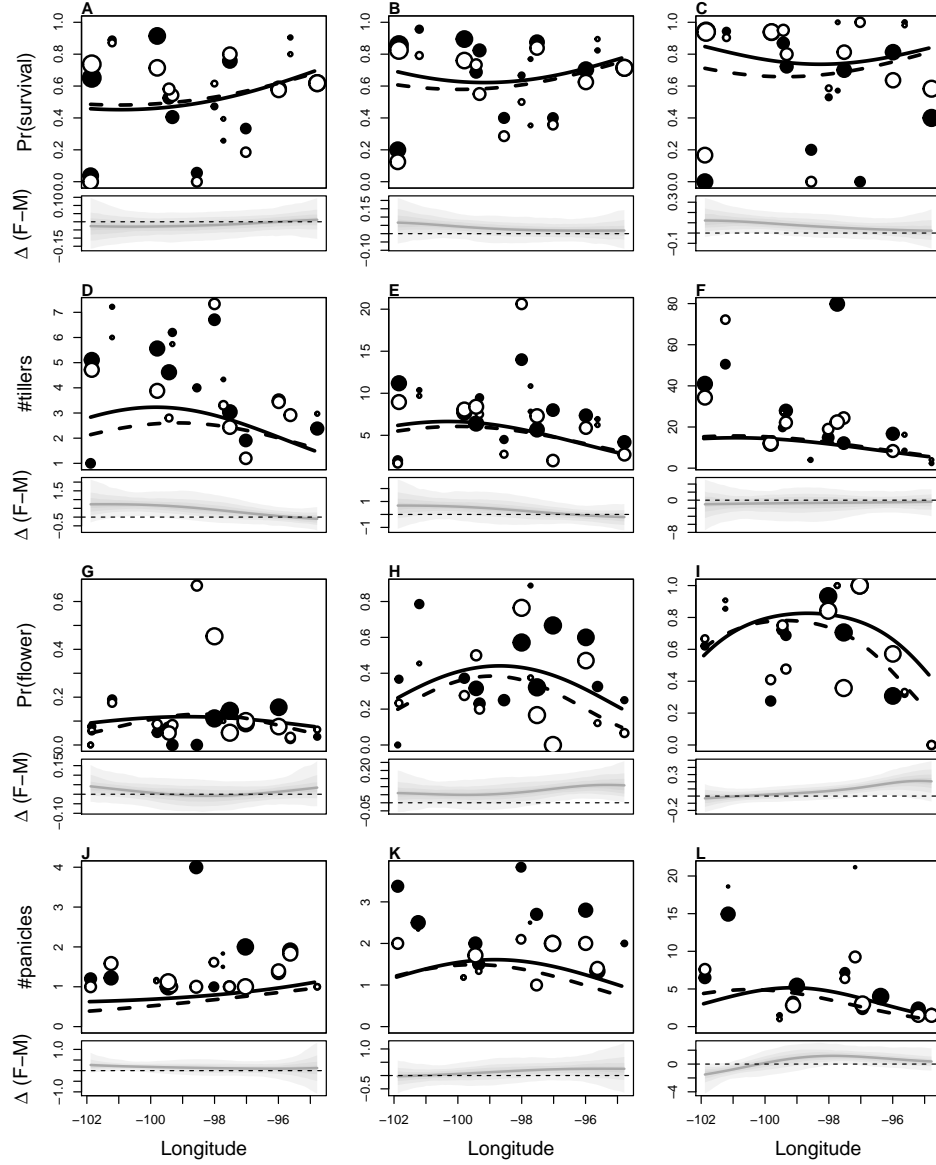
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Figure 4: Sex-, size-, and longitude-related variation in: A–C, inter-annual probability of survival; D–F, inter-annual growth (change in number of tillers); G–I, probability of flowering; J–L, number of panicles produced given flowering. Points show means by site for females (filled) and males (open) and small (left column), medium (middle column), and large (right column) size classes (discretized, for visualization only). Point size is proportional to the sample size of the mean. Lines show fitted statistical models for females (solid) and males (dashed) based on posterior mean parameter values. Lower panels below each data panel show the posterior distribution of the difference between females and males as a function of longitude (positive and negative values indicate female and advantage, respectively); dashed horizontal line shows zero difference.

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Sex differences in flowering and panicle production generated a longitudinal trend in the operational sex ratio of our common garden populations that mirrored the trend in natural populations (Fig. 3): the fraction of total panicles that were female in our common gardens increased from west to east (Fig. B2A) even as the fraction of surviving plants that were female did not show a longitudinal trend (Fig. B2B). Thus, the common garden experiment suggested 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 experimental populations. 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.
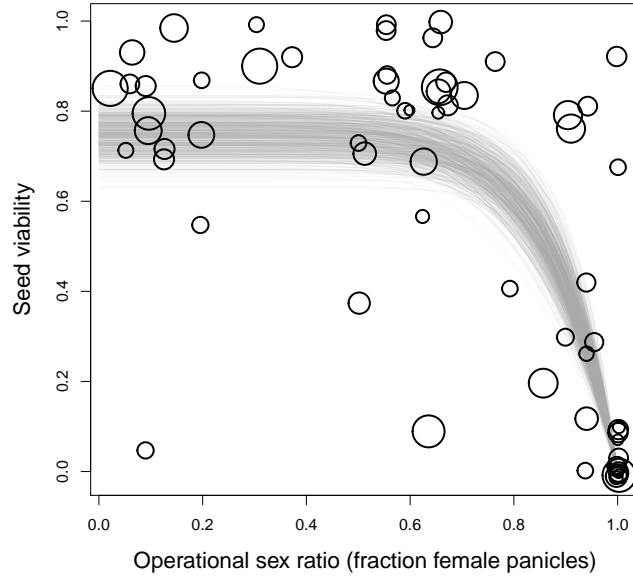
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Figure 5: Seed fertilization success in relation to operational sex ratio (fraction of panicles that are female) in experimental populations. Circles show data from tetrazolium assays of seed viability; circle size is proprtional to the number of seeds tested (min: 14, max: 57). Lines show fitted model (Eq. 1) for 500 samples from the posterior distribution of parameter estimates.

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 declines in 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 captures

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the population dynamics of the focal species.

Decomposition methods revealed that declines in λ approaching range limits were driven almost exclusively by females (Fig. 6B) with near-zero contributions from males (Fig. 6C). Thus, range limitation was an effectively female-dominant process, despite female bias in the mating pool at eastern range margins. Correspondingly, the two-sex model was nearly indistinguishable from a female-dominant model with all else equal except that female seed fertilization did not depend on males (Fig B1). Decomposition analysis further revealed that multiple female vital rates contributed to range limits, some in opposing directions. Because female survival increased toward range limits (Fig 4A-C), this vital rate had a contribution to $\frac{\partial \lambda}{\partial Longitude}$ that was opposite in sign to the other vital rates (Fig. 6B). However, increased survival at range edges was not sufficient to offset declines in other vital rates. The overall decline in λ was driven most strongly by the decline in female flowering probabilityat the western limit and by a combination of reduced female flowering and growth at the eastern limit.
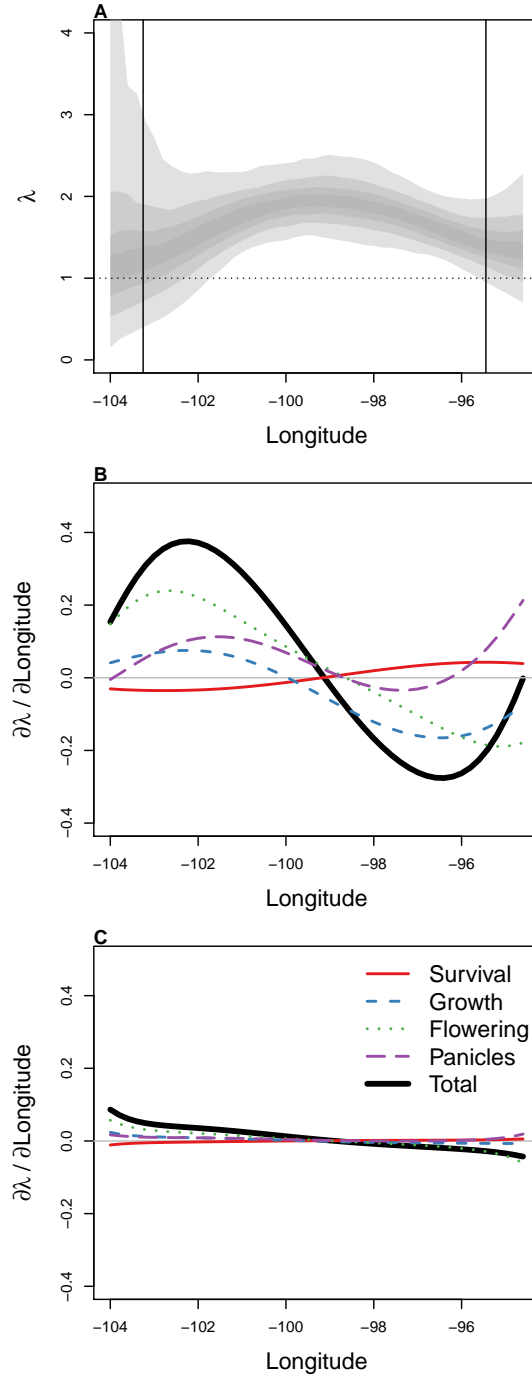
Figure 6: Population growth (λ) as a function of longitude, predicted by the two-sex MPM that incorporates sex-specific demographic responses to longitude with sex ratio-dependent seed fertilization. A, posterior distribution of λ reflecting parameter uncertainty, where shaded regions show the 25, 50, 75, and 95% percentiles of parameter uncertainty. Dashed horizontal line indicates the limit of population viability ($\lambda = 1$) and vertical lines show the longitudes of Brewster and Brazoria Counties, TX, the western- and eastern-most occurrence records of *P. arachnifera*. B–C, LTRE decomposition of the sensity of λ to longitude into additive vital rate contributions of females (B) and males (C) based on posterior mean parameter estimates.

Discussion

Acknowledgements

Author contributions

Data accessibility

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497   adult sex ratios: perturbation analyses of two-sex models. *Ecology Letters*, **12**,

498   129–143.

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

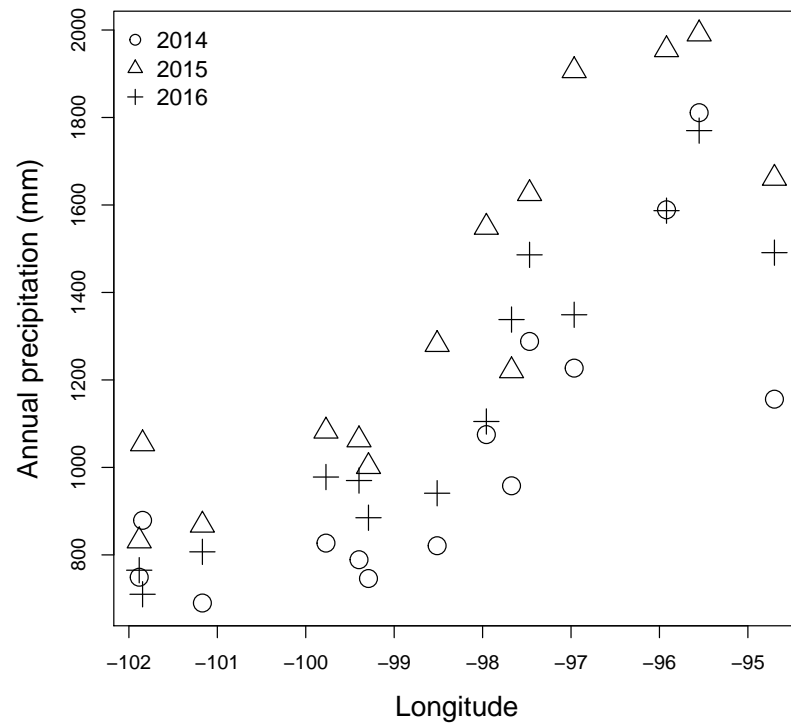Table A1: Sites of natural population surveys corresponding to Figure

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

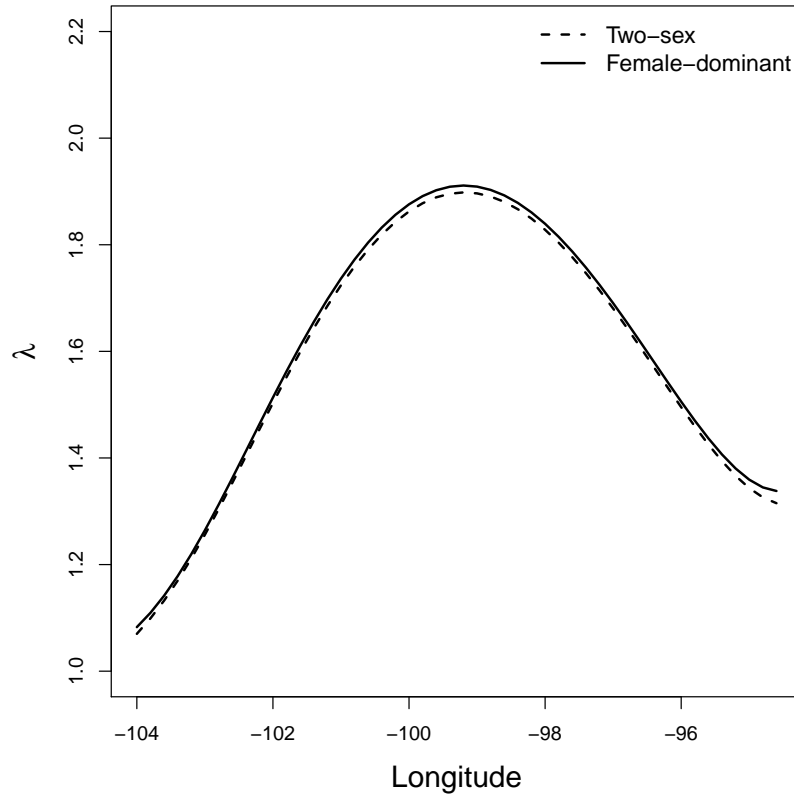# Appendix B: Additional results

Figure B1: 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
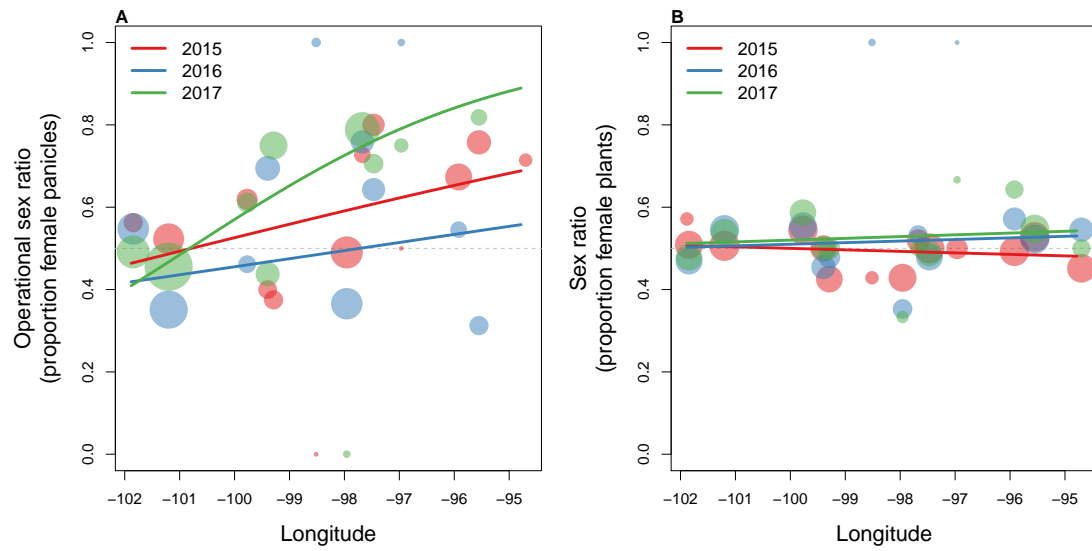
Figure B2: Longitudinal variation in: A, operational sex ratio (fraction of panicles that were female), and B, individual sex ratio (fraction of surviving plants that were female) across 14 common garden sites. Colors indicate year and point size is proportional to sample size of the fraction (total panicles in A [min: 1, max: 1021] and total plants in B [min: 2, max: 79]). Lines show fitted binomial GLMs.