

# Two-sex demography, sexual niche differentiation, and range limits

Tom E.X. Miller\* and Aldo Compagnoni

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

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

## Abstract

### <sub>1</sub> Keywords

## 2 Introduction

3 Understanding the processes that generate species' distributional limits is a foun-  
4 dational objective of ecology. The niche concept is central to theory for range limits  
5 (Hutchinson, 1958), and available evidence suggests that geographic distributions  
6 may commonly be interpreted as ecological niches “writ large” (Lee-Yaw *et al.*,  
7 2016; Hargreaves *et al.*, 2013). Species distribution modeling (or “environmen-  
8 tal niche modeling”) has long capitalized on this idea to infer niche characteristics  
9 from statistical associations between occurrence across environmental variables. In  
10 contrast, there is growing interest in process-based models of range limits, where  
11 individual-level demographic responses to environmental variation inform predic-  
12 tions about the ecological niche and environmental limits of population viability  
13 (i.e., at least replacement-level population growth,  $\lambda \geq 1$ ) (Merow *et al.*, 2014,  
14 2017; Diez *et al.*, 2014). The mechanistic understanding offered by process-based  
15 models of range limits provides a potentially powerful vehicle for predicting range  
16 shifts in response to current and future environmental change (Evans *et al.*, 2016;  
17 Ehrlén & Morris, 2015).

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

26 of many niches, then whose niche is it that determines the geographic distribution  
27 and how would we know?

28 Sexual niche differentiation is a common form of intra-specific niche hetero-  
29 geneity (Bolnick *et al.*, 2002) and has been widely documented in animals (the  
30 vast majority of which are dioecious) and plants (ca. 6% of angiosperms are dioe-  
31 cious: Renner & Ricklefs 1995). The prevalence of sexual niche differentiation  
32 was recognized by Darwin (2019), who described “different habits of life, not re-  
33 lated...to the reproductive functions” of females and males. There are numerous  
34 examples of sex differences in trophic position (Pekár *et al.*, 2011), habitat use  
35 (Bowyer, 2004; Phillips *et al.*, 2004), and responses to climate, differences that  
36 may or may not be accompanied by sexual dimorphism. It has been hypothesized  
37 that sex-specific niches may evolve by natural selection when it reduces compet-  
38 itive or other antagonistic interactions between the sexes (cite). In an ecological  
39 context,

40 P3: Sexual niche differentiation in dioecious species is a widespread form of  
41 intra-specific niche heterogeneity. Sex-specific responses to environmental drivers  
42 can generate geographic clines in operational sex ratio and strongly biased sex  
43 ratios especially at range limits. While this pattern is well documented in a variety  
44 of taxa, the role of sex ratio bias in limiting species’ ranges is poorly understood.

45 P4: Most ecological theory assumes female dominance. In this case, there is a  
46 straightforward answer to the question above – the female niche is the relevant set  
47 of constraints for understanding range limits. However, while female dominance is  
48 often a reasonable and useful assumption, it may break down under extreme sex  
49 ratio bias, where mates may be limiting. If so, this creates an additional, two-sex  
50 pathway by which males could limit the position of species ranges.

51 P5: In this study we used a dioecious grass species as a focal species to quan-  
52 tify the relative importance of female-dominant and two-sex mechanisms of range  
53 limitation.

## 54 Materials and methods

### 55 Study system and natural population surveys

56 *Poa arachnifera* is a perennial, cool-season grass endemic to the southern Great  
57 Plains. This species occurs almost exclusively in central Texas, Oklahoma, and  
58 Kansas (Fig. 1) though there are occasional records of adventive populations in  
59 other state<sup>1</sup>. Like all grasses, *P. arachnifera* is wind-pollinated. Individuals can  
60 be sexed only when flowering, in early spring, based on the presence of stigmas  
61 (females) or anthers (males) in the inflorescence. Following inflorescence and seed  
62 production, plants go dormant for the hot summer months and vegetative growth  
63 resumes in fall. Individuals grow via rhizomes to form patches that may be as large  
64 as 50m<sup>2</sup> in area. Sex in *P. arachnifera* is genetically based (Renganayaki *et al.*,  
65 2001, 2005) and the primary sex ratio is 1:1 (J. Goldman, USDA-ARS, *personal*  
66 *communication*). The rhizomatous growth habit allowed us to clonally propagate  
67 large numbers of known-sex individuals for experiments, as we describe below.

68 We surveyed *P. arachnifera* across its range to establish whether natural pop-  
69 ulations exhibited geographic clines in sex ratio corresponding to the longitudinal  
70 aridity gradient. We visited 14 populations in spring 2012 and 8 in spring 2013.  
71 Survey locations are shown in **map** and coordinates are provided in Table A1. At

---

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

72 each location, we searched for *P. arachnifera* along roads, trails, or creek drainages  
73 and recorded the number of female and male inflorescences that we encountered.

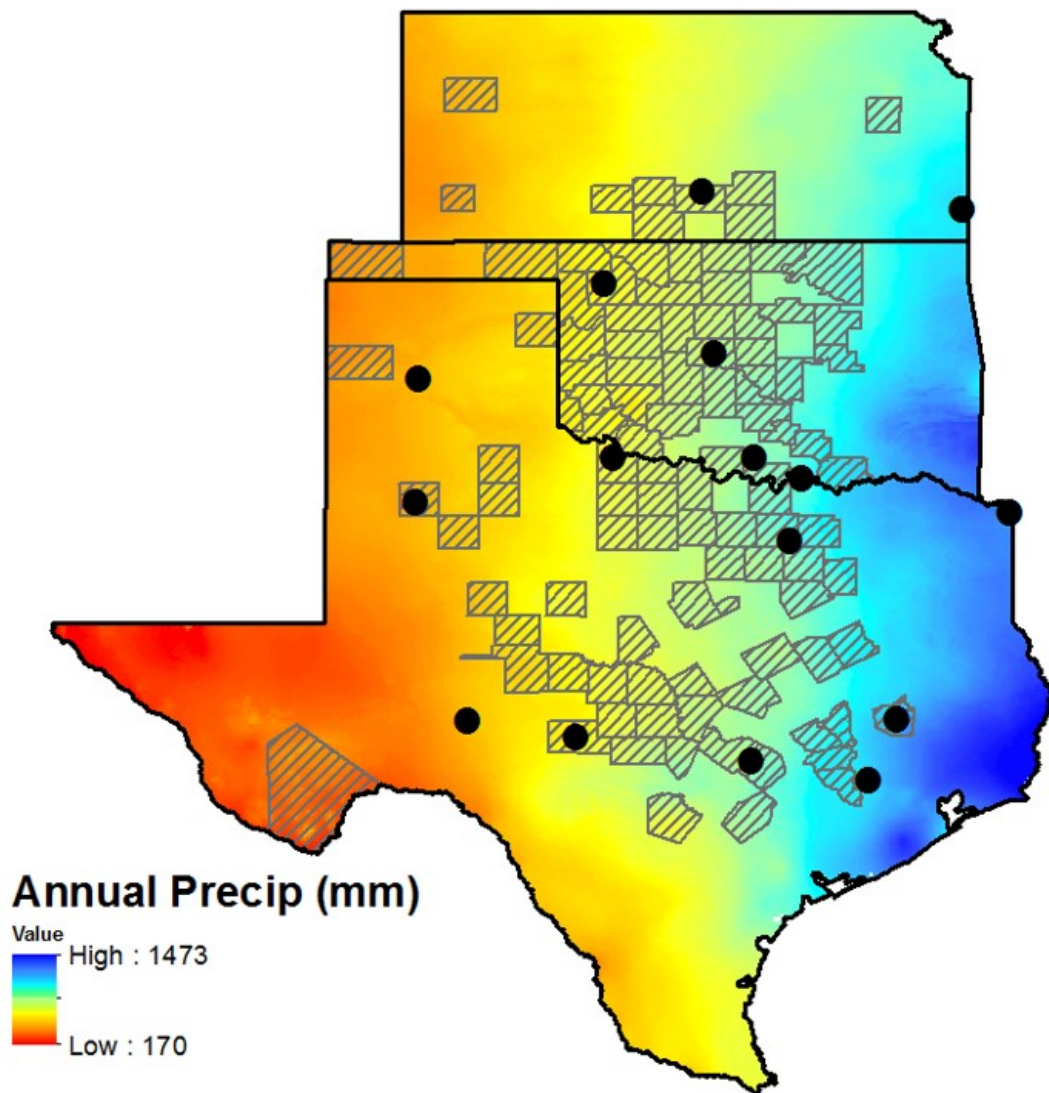


Figure 1: Caption.

#### 74 Statistical analysis of natural population surveys

75 We fit a binomial generalized linear model (glm), where females were “successes”  
 76 and total inflorescences was the number of “trials”, to test whether the operational

sex ratio (OSR) varied systematically with respect to longitude. Here and in the experiment that follows we use longitude as a proxy variable that captures all east-west environmental variation, notably precipitation (map figure) 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).

## 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). At each of these site visits in 2013 and 2014, we collected 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 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



100 woodland edge, providing partial shade that mimics this species' natural micro-  
101 environment. We planted 3 females and 3 males in each block, for a total of 42  
102 individuals per sex per site and 1176 total plants across sites, with all source collec-  
103 tions represented at all sites. Individuals were spaced within blocks to allow space  
104 for rhizomatous growth that could be clearly attributed to individual transplants.  
105 To promote establishment, we cleared vegetation immediately surrounding trans-  
106 plants and provided ca. 1 L of water at the time of transplanting but provided no  
107 subsequent watering, fertilization, or competitor removal.

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

## 112 **Statistical analysis of common garden experiment**

113 We analyzed the demographic vital rates with generalized linear mixed models in  
114 a hierarchical Bayesian framework. All the vital rates shared a common linear  
115 predictor for the expected value that included fixed effects of size, sex, linear and  
116 quadratic terms for longitude, and all 2- and 3-way interactions. We included  
117 quadratic effects of longitude to account for the possibility of non-monotonic re-  
118 sponses, following the hypothesis that fitness may peak in the center of the range.  
119 The linear predictor also included random effects of site, block, and source pop-  
120 ulation of the transplant; the corresponding variance terms were used in the de-  
121 mographic model (below) to capture process error in demography. We pooled all  
122 three years of observations for analysis so we do not explicitly model temporal  
123 variation but our results are implicitly averaged over years.

124 The survival and flowering data were Bernoulli distributed, and these models  
125 applied the logit link function. We modeled tiller and panicle counts as zero-  
126 truncated negative binomial using the log link. For flowering and panicle pro-  
127 duction in year  $t$ , the size covariate was the natural logarithm of tiller number  
128 in year  $t$ . For survival and size in year  $t$ , the size covariate was the natural  
129 logarithm of tiller number in year  $t - 1$  (for 2015 data, size in year  $t - 1$  was  
130 transplant size at the time of planting). Code for these analyses is available at  
131 <https://github.com/texmiller/POAR-range-limits>.

## 132 Sex ratio experiment

133 At one site near the center of the range (Lake Lewisville Environmental Learning  
134 Area: star in MAP), we established a separate experiment to quantify how sex ra-  
135 tio variation affects female reproductive success. Details of this experiment, which  
136 was conducted in 2014–2015, are described in Compagnoni et al. 2017. Briefly, we  
137 established 124 experimental populations in  $0.4m \times 0.4m$  plots that varied in popu-  
138 lation density (1–48 plants/plot) and sex ratio (0–100%female), with 2–4 replicates  
139 each of 34 density-sex ratio combinations. The experiment was established ca. 1  
140 km from a natural population at this site and plots were situated with a minimum  
141 of 15 m spacing, a buffer that was intended to limit pollen movement between  
142 plots (pilot data indicated that  $\geq 90\%$  of wind pollination occurred within 13m).  
143 We measured female reproductive success in different density and sex ratio envi-  
144 ronments by collecting panicles from a subset of females in each plot at the end of  
145 the reproductive season. In the lab, we counted the total number of seeds on each  
146 panicle and assessed seed viability with tetrazolium assays of 25 seeds per panicle.

147 We also conducted germination trials in the greenhouse (17–57 seeds per panicle,  
148 mode: 30).

## 149 **Statistical analysis of sex ratio experiment**

150 Our previous study examined how interactions between density and frequency (sex  
151 ratio) dependence contributed to female reproductive success (Compagnoni *et al.*,  
152 2017). Here we focus solely on sex ratio variation, averaging over variation in  
153 density. Our goal was to estimate a ‘mating function’ that defines how availability  
154 of male panicles affects the viability of seeds on female panicles. We modeled the  
155 seed viability data with a binomial distribution where the probability of viability  
156 ( $p_v$ ) was given by:

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

157 where  $OSR$  is the operational sex ratio (fraction of panicles that were female) in  
158 our experimental populations. This function has the properties, supported by our  
159 previous work, that seed viability is maximized at  $v_0$  as  $OSR$  approaches zero and  
160 goes to zero as  $OSR$  approaches 1. Parameter  $\alpha$  controls how viability declines  
161 with increasing female bias.

162 We modeled germination data from greenhouse trials similarly, where counts of  
163 germinants were modeled as binomial successes. Since germination was conditional  
164 on seed viability, the probability of success was given by the product  $v * g$ , where  
165  $v$  is a function of  $OSR$  (Eq. 1) and  $g$  is assumed to be constant. The germination  
166 trials alone do not provide enough information to independently estimate  $v$  and

167  $g$  but the combination of viability and germination data allowed us to do so. For  
 168 both viability and germination, we found that accounting for overdispersion with  
 169 a beta-binomial response distribution improved model fit.

## 170 Demographic model of range limits

171 The statistical models for the common garden and sex ratio experiments provided  
 172 the backbone of the full demographic model, a matrix projection model (MPM)  
 173 structured by size (tiller number) and sex. Following the statistical modeling, the  
 174 MPM accommodates longitude as a predictor variable, allowing us to identify the  
 175 longitudinal limits of population viability ( $\lambda \geq 1$ ) and investigate the underlying  
 176 drivers of population decline at range limits. For a given longitude, let  $F_{x,t}$  and  $M_{x,t}$   
 177 be the number of female and male plants of size  $x$  in year  $t$ , where  $x \in \{1, 2, \dots, U\}$   
 178 and  $U$  is the maximum number of tillers a plant can attain (assumed to be the  
 179 same for females and males). For a pre-breeding census, the coupled dynamics of  
 180 both sexes are given by:

$$F_{y,t+1} = \sum_{x=1}^U [s^F(x) \cdot g^F(y, x) + r^F(x, \mathbf{F}_t, \mathbf{M}_t) \cdot \rho \cdot e(y)] F_{x,t} \quad (2)$$

$$M_{y,t+1} = \sum_{x=1}^U [s^M(x) \cdot g^M(y, x)] M_{x,t} + [r^F(x, \mathbf{F}_t, \mathbf{M}_t) \cdot (1 - \rho) \cdot e(y)] F_{x,t} \quad (3)$$

181  $s$  and  $g$  give the probabilities of surviving at size  $x$  and growing from sizes  $x$  to  
 182  $y$ , respectively, and superscripts indicate that these functions may be unique to  
 183 females ( $F$ ) and males ( $M$ ).  $r^F$  gives fertility of size- $x$  females (number of new  
 184 recruits per female per year) and is dependent on population structure (the  $U \times 1$

185 vectors  $\mathbf{F}_t$  and  $\mathbf{M}_t$ ). Parameter  $\rho$  is the primary sex ratio (proportion of recruits  
 186 that are female) and  $e(y)$  is the probability distribution of recruit size. We assume  
 187 that all recruits first appear in the population at 1 tiller in size regardless of sex,  
 188 so  $e(y = 1) = 1$  and  $e(y > 1) = 0$ . The female fertility function is further defined  
 189 as:

$$r^F(x, \mathbf{F}_t, \mathbf{M}_t) = p^F(x) \cdot c^F(x) \cdot d \cdot v(\mathbf{F}_t, \mathbf{M}_t) \cdot g \quad (4)$$

190 where  $p$  and  $c$  are flowering probability and panicle production for females of size  
 191  $x$ ,  $d$  is the number of seeds (fertilized or unfertilized) per female panicle,  $v$  is the  
 192 probability that a seed is fertilized, and  $g$  is the probability that a fertilized seed  
 193 germinates. Lastly, and following Eq. 1, seed fertilization depends on the OSR  
 194 according to:

$$v(\mathbf{F}_t, \mathbf{M}_t) = v_0 * \left[ 1 - \left( \frac{\sum_{x=1}^U p^F(x) c^F(x) F_{x,t}}{\sum_{x=1}^U p^F(x) c^F(x) F_{x,t} + p^M(x) c^M(x) M_{x,t}} \right)^\alpha \right] \quad (5)$$

## 195 Results

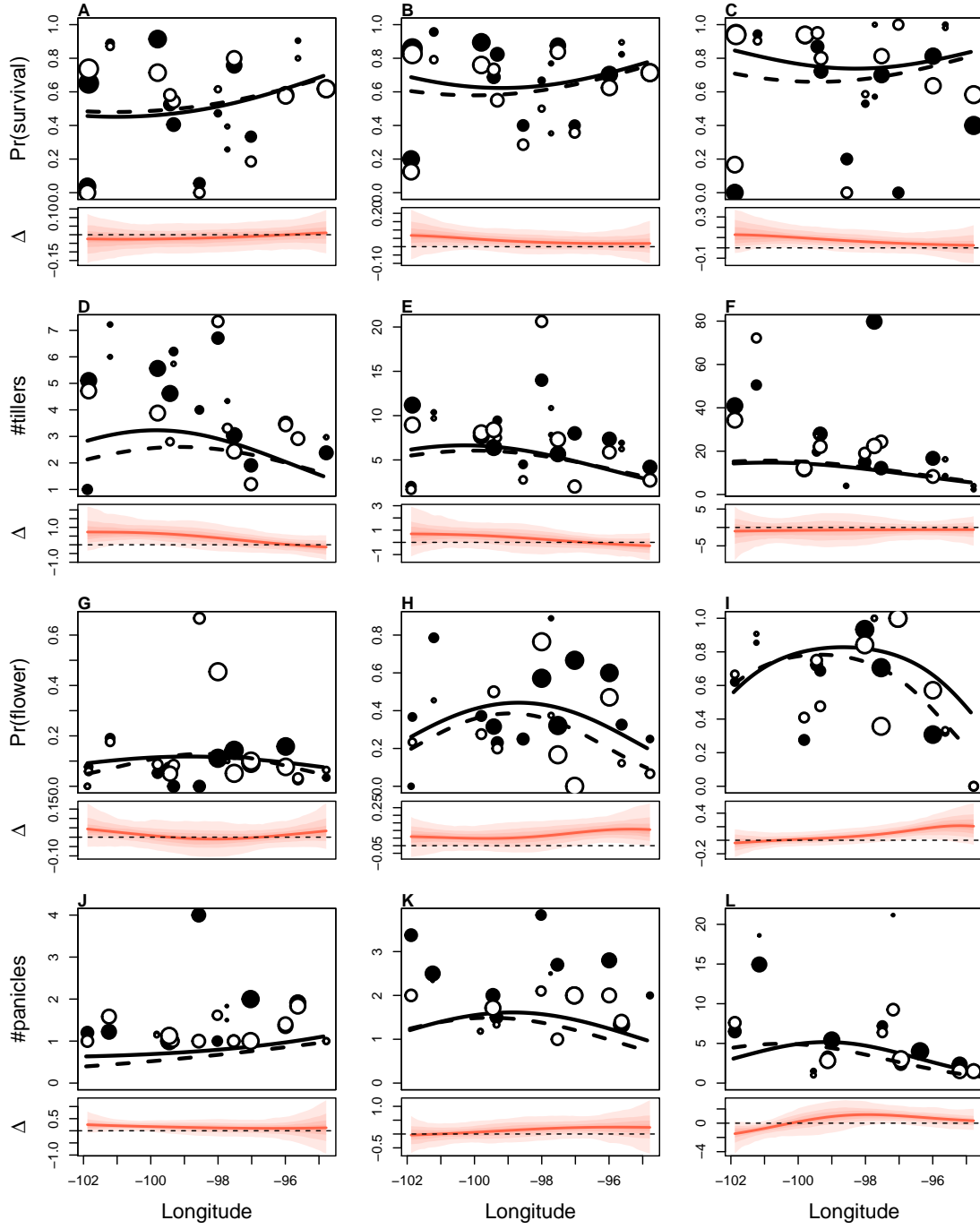


Figure 2: Caption.

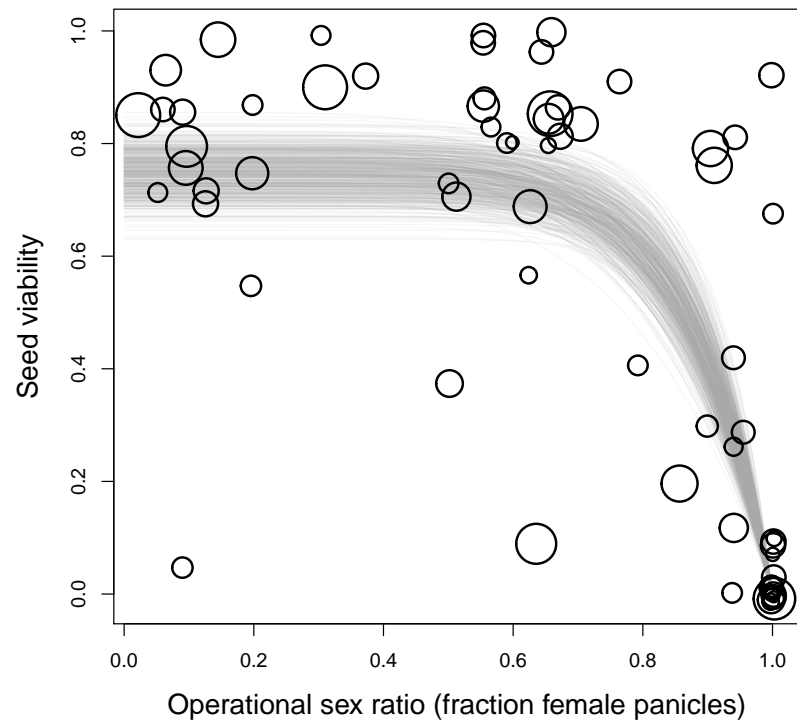


Figure 3: Caption.

## 196 Discussion

## 197 Acknowledgements

## 198 Author contributions

## 199 Data accessibility

## 200 References

- 201 Araújo MS, Bolnick DI, Layman CA (2011) The ecological causes of individual  
202 specialisation. *Ecology letters*, **14**, 948–958.
- 203 Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister  
204 ML (2002) The ecology of individuals: incidence and implications of individual  
205 specialization. *The American Naturalist*, **161**, 1–28.
- 206 Bowyer RT (2004) Sexual segregation in ruminants: definitions, hypotheses, and  
207 implications for conservation and management. *Journal of Mammalogy*, **85**,  
208 1039–1052.
- 209 Carpenter B, Gelman A, Hoffman MD, *et al.* (2017) Stan: A probabilistic pro-  
210 gramming language. *Journal of statistical software*, **76**.
- 211 Compagnoni A, Steigman K, Miller TE (2017) Can’t live with them, can’t live  
212 without them? balancing mating and competition in two-sex populations. *Pro-  
213 ceedings of the Royal Society B: Biological Sciences*, **284**, 20171999.



214 Conn PB, Johnson DS, Williams PJ, Melin SR, Hooten MB (2018) A guide to  
215 bayesian model checking for ecologists. *Ecological Monographs*, **88**, 526–542.

216 Darwin C (2019) *The descent of man*. BoD–Books on Demand.

217 Diez JM, Giladi I, Warren R, Pulliam HR (2014) Probabilistic and spatially vari-  
218 able niches inferred from demography. *Journal of ecology*, **102**, 544–554.

219 Ehrlén J, Morris WF (2015) Predicting changes in the distribution and abundance  
220 of species under environmental change. *Ecology Letters*, **18**, 303–314.

221 Evans ME, Merow C, Record S, McMahon SM, Enquist BJ (2016) Towards  
222 process-based range modeling of many species. *Trends in Ecology & Evolution*,  
223 **31**, 860–871.

224 Hargreaves AL, Samis KE, Eckert CG (2013) Are species’ range limits simply niche  
225 limits writ large? a review of transplant experiments beyond the range. *The*  
226 *American Naturalist*, **183**, 157–173.

227 Holt RD (2009) Bringing the hutchinsonian niche into the 21st century: ecological  
228 and evolutionary perspectives. *Proceedings of the National Academy of Sciences*,  
229 **106**, 19659–19665.

230 Hutchinson GE (1958) Concluding remarks. In: *Cold Spring Harbour Symposium*  
231 *on Quantitative Biology*, vol. 22, pp. 415–427.

232 Lee-Yaw JA, Kharouba HM, Bontrager M, *et al.* (2016) A synthesis of transplant  
233 experiments and ecological niche models suggests that range limits are often  
234 niche limits. *Ecology letters*, **19**, 710–722.

- 235 Merow C, Bois ST, Allen JM, Xie Y, Silander JA (2017) Climate change both  
236 facilitates and inhibits invasive plant ranges in new england. *Proceedings of the*  
237 *National Academy of Sciences*, **114**, E3276–E3284.
- 238 Merow C, Latimer AM, Wilson AM, McMahon SM, Rebelo AG, Silander Jr JA  
239 (2014) On using integral projection models to generate demographically driven  
240 predictions of species’ distributions: development and validation using sparse  
241 data. *Ecography*, **37**, 1167–1183.
- 242 Pekár S, Martišová M, Bilde T (2011) Intersexual trophic niche partitioning in an  
243 ant-eating spider (araneae: Zodariidae). *PloS one*, **6**, e14603.
- 244 Phillips R, Silk J, Phalan B, Catry P, Croxall J (2004) Seasonal sexual segregation  
245 in two thalassarche albatross species: competitive exclusion, reproductive role  
246 specialization or foraging niche divergence? *Proceedings of the Royal Society of*  
247 *London. Series B: Biological Sciences*, **271**, 1283–1291.
- 248 Renganayaki K, Jessup R, Burson B, Hussey M, Read J (2005) Identification of  
249 male-specific aflp markers in dioecious texas bluegrass. *Crop science*, **45**, 2529–  
250 2539.
- 251 Renganayaki K, Read J, Fritz A (2001) Genetic diversity among texas bluegrass  
252 genotypes (poa arachnifera torr.) revealed by aflp and rapd markers. *Theoretical*  
253 *and Applied Genetics*, **102**, 1037–1045.
- 254 Renner SS, Ricklefs RE (1995) Dioecy and its correlates in the flowering plants.  
255 *American journal of botany*, **82**, 596–606.
- 256 Team SD, *et al.* (2018) Rstan: the r interface to stan. r package version 2.17. 3.

## Appendix A: Site locations and climate

	Population	Latitude	Longitude
1	Canyon_of_Eagles	30.88	-98.43
2	ClearBay-Thunderbird	35.23	-97.24
3	CooperWMA	36.60	-99.51
4	Copper Breaks	34.10	-99.75
5	Dinosaur_Valley	32.25	-97.82
6	Fort_Worth_Nature_Center	32.83	-97.46
7	Ft Cobb	35.18	-98.45
8	Ft Richardson	33.20	-98.16
9	Great Plains	34.74	-98.97
10	Great_Salt_Plains	36.79	-98.18
11	Horn_Hill_Cemetery	31.56	-96.64
12	Kingman_Fishing_Lake	37.65	-98.28
13	Lake Arrowhead	33.75	-98.39
14	Mineral_Wells	32.89	-98.01
15	Pedernales_Falls	30.33	-98.25
16	Possum Kingdom	32.87	-98.57
17	Quartz_Mountain	34.89	-99.30
18	Red Rock Canyon	35.44	-98.35
19	Red_River	34.13	-98.10
20	South_Llano	30.45	-99.80
21	Sulfur_Springs	31.08	-98.46
22	Wichita_Mountains	34.70	-98.67

Table A1: Sites of natural population surveys corresponding to Figure

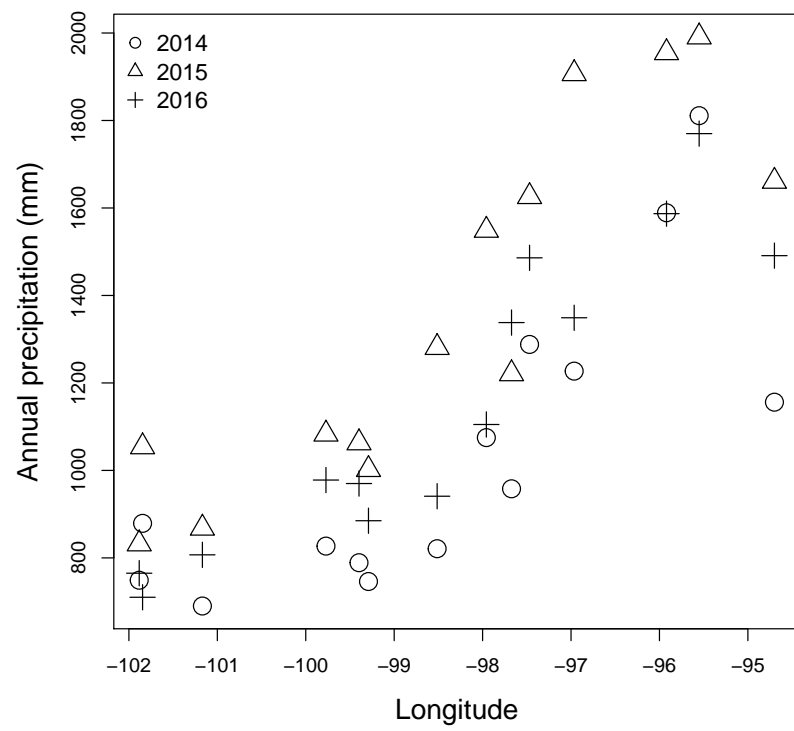


Figure A1: Caption.