

Using matrix projection model to predict climate-induced range expansion/contraction for a dioecious range-limited species

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Manuscript/Forescasting.Rnw. All data are provided at <https://github.com/jmoutouama/>
POAR-Forecasting/tree/main/data.

1

Abstract

2

Keywords

2

Introduction

Rising temperatures and extreme drought events associated with global climate change are leading to increased concern about how species will become redistributed across the globe under future climate conditions (Bertrand et al., 2011; Gamelon et al., 2017). Dioecious species might be particularly vulnerable to the influence of climate change because they often display skewed sex ratios that are generated or reinforced by sexual niche differentiation (distinct responses of females and males to shared climate drivers) (Tognetti, 2012). Accounting for such a niche differentiation between male and female within a population is a long-standing challenge in accurately predicting which sex will successfully track environmental change and how this will impact population dynamics (Jones et al., 1999; Gissi et al., 2023a). The vast majority of theory and models in population biology, including those used to forecast biodiversity responses to climate change, ignore the complication of sex structure (Pottier et al., 2021; Ellis et al., 2017). As a result, accurate forecasts of colonization-extinction dynamics for dioecious species under future climate scenarios are limited.

There is a vast literature from animal, plant and insect documenting the effect of climate change on sex ratio in dioecious species (Gissi et al., 2023a,b). Experiment manipulation revealed that photosynthetic responses to elevated CO₂ and elevated temperature are sex-specific in ways that could help males to succeed in extreme climatic conditions rather than females (Zhao et al., 2012; Bürli et al., 2022). Additionally, the lower cost of reproduction of males may allow them to invest their energy in other functions that produce higher growth rates, higher clonality, or even higher survival rates compared to females (Cipollini and Whigham, 1994; Bruijning et al., 2017). As a result, more often there is a sex ratio skewness in a significant number of populations (Hultine et al.,

27 2016). Climate change could magnify skewed sex ratios and potentially affect population
28 viability and, therefore, species distribution across their geographical ranges (Davis and
29 Shaw, 2001; Pease et al., 1989). However, the demographic consequence of skewness of
30 the sex ratio in response to global warming and how the change in the sex ratio under
31 global warming will lead to range shift is unclear because most studies on dioecious
32 species infer range shift from one vital rate (e.g., survival or reproduction), ignoring life
33 history trade-off (Gianuca et al., 2019; Petry et al., 2016).

34 Our ability to track the impact of climate change on the population dynamics of
35 dioecious plants and the implication of such impact on range shift depends on our abil-
36 ity to build mechanistic models that take into account the spatial and temporal context
37 in which sex ratio biased affect survival, reproduction, growth and population viabil-
38 ity (Davis and Shaw, 2001; Evans et al., 2016; Czachura and Miller, 2020). Sex ratio
39 bias could affect population viability by reducing the survival rate of limiting sex or by
40 reducing the probability of female flowering (Eberhart-Phillips et al., 2017; Miller and
41 Compagnoni, 2022). Thus, at their range edge where climatic conditions are expected to
42 be less favorable, if dioecious species populations are non-viable in response to climate
43 change, global warming will induce range contraction in dioecious species. In reverse,
44 if populations at the edge are viable habitats in response to global warming, dioecious
45 species populations could shift their range and relocate to more favorable and thereby
46 favored range expansion.

47 In this study, we used a matrix projection model to understand the demographic
48 response of dioecious species to climate change and its implications for future range dy-
49 namics. Our study system is a dioecious plant species (*Poa arachnifera*) distributed along
50 environmental gradients in the south-central US corresponding to variation in tempera-
51 ture across latitude and precipitation across longitude (MAP). A previous study showed

52 that, despite the differentiation of the climatic niche between sexes, the female niche
53 mattered the most in driving the environmental limits of population viability (Miller
54 and Compagnoni, 2022). Thus, under current climate conditions, we hypothesized that
55 high temperature and lower precipitation during the growing season have negative ef-
56 fects on population growth rate through a reduction in female growth, survival, and
57 fecundity rate. However, that reduction in population growth rate will not go below
58 a viable population (population growth rate less than one) even at range edge. Future
59 climate will exacerbate the effect of temperature and precipitation on female vital rates
60 and drive population to extinction, particularly at range edge.¹

61 Materials and methods

62 2

63 Study system

64 Texas bluegrass (*Poa arachnifera*) is a perennial, summer-dormant cool-season (C3) grass.
65 The species occurs in Texas, Oklahoma, and southern Kansas, USA (Hitchcock, 1971).
66 Texas bluegrass grows during cool months between October and May, with onset of
67 dormancy often from June to September (Kindiger, 2004). Flowering occurs in May and
68 the species is pollinated by wind (Hitchcock, 1971).

69 We studied 14 sites along the distribution of these species in the United States in 2014
70 and 2015.³

¹These hypotheses / predictions are hard to follow. I think it would be helpful to identify 2-3 main questions that this study aims to address and describe these here at the end of the Intro. We could brainstorm these together.

²General comment: the methods section needs better organization and clearer structure. It also needs better motivation, the **why** behind these methods. Strengthening and focusing the end of the Introduction will help.

³You need to make clear that this was a common garden experiment. Describe the experiment in sufficient detail.

71

Demographic and climatic data collection

72 In each site we collected individual demographic data including survival, growth (number of tillers), flowers and fertility (number of panicle) for two censuses (2015 and 2016)
73 to build our demographic models. The details of the data collection has been provided
74 in Miller and Compagnoni (2022).⁴
75

76 We want to understand how current and future climate affect the dynamic⁵ of *Poa*
77 *arachnifera*. Therefore, we considered the climatic data from the time we collected de-
78 mographic data (2015 and 2016 censuses)⁶ as the current condition for the species⁷.
79 Additionally, months were aligned to match demographic transition years rather than
80 calendar years.⁸ Monthly temperature and precipitation data were downloaded for each
81 site from Chelsea (Karger et al., 2017). We define June to September as the dormant
82 season of the year and the rest of the year as the growing season. We used seasonal data
83 because they allowed us to quantify the response of species to change in seasonal change
84 in climate.⁹ We evaluated future climate projections from two scenarios¹⁰: SSP 370, an
85 intermediate-to-pessimistic scenario assuming a radiative forcing to amount to 7.0 Wm^{-2}
86 by 2100, and SSP 585, a pessimistic emission scenario which project a radiative forcing to
87 amount to 8.5 Wm^{-2} by 2100 (O'Neill et al., 2017; Brun et al., 2022). The precipitation of
88 growing season and dormant season were not explained by the Temperature of growing
89 season and dormant season (Appendix S1: Figure S1).¹¹

⁴You need to say a little more here.

⁵This is vague. This carefully about the target of your analysis and the best way to describe it.

⁶The timeline of the experiment and the censuses need to be clarified. Above you say 2014-15 and here you say 2015-16.

⁷Unclear what this means.

⁸Needs to be explained.

⁹This sentence contains no information.

¹⁰I suggest that you first introduce the model and its parameterization with current climate data, and then describe the climate projections in a later section of the methods.

¹¹Explain why this is significant and why you looked for this.

90

Sex ratio experiment

91 We¹² also conducted a sex-ratio experiment to measure the effect of male panicle avail-
 92 ability on seed viability on females panicles. Details of the experiment are provided in
 93 Compagnoni et al. (2017) and Miller and Compagnoni (2022).¹³

94 We used the sex-ratio to estimate the probability of viability and the germination
 95 rate. Seed viability was modeled with a binomial distribution where the probability of
 96 viability (v) was given by:

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

97 where OSR is the operational sex ratio¹⁴ (proportion of panicles that were female) in
 98 the experimental populations. The properties of the above function is supported by our
 99 previous work (Compagnoni et al., 2017). Here, seed viability is maximized at v_0 as OSR
 100 approaches zero (strongly male-biased) and goes to zero as OSR approaches 1 (strongly
 101 female-biased). Parameter α controls how viability declines with increasing female bias.

102 We used a binomial distribution to model the germination data from greenhouse
 103 trials. Given that germination was conditional on seed viability, the probability of success
 104 was given by the product $v * g$, where v is a function of OSR (Eq. 1) and g is assumed to
 105 be constant.

106

Vital rate responses to climate

107 We used individual level measurements of survival, growth (number of tillers), flow-
 108 ering, number of panicles to independently develop Bayesian mixed effect models de-

¹²I would describe the demographic data before the sex ratio experiment.

¹³Again, you need more info here.

¹⁴This concept should be described in the Introduction.

scribing how each vital rate varies as a function of sex, size, precipitation of growing and dormant season and temperature of of growing and dormant season. We fit two versions of the vital rate models, with either linear or second-degree polynomial functions for the influence of climate, and used model selection to quantify their empirical support. We included a second-degree polynomial because we expected that climate variables would affect vital rates through a hump-shaped relationship.

We centered and standardized all predictors to facilitate model convergence. We included site, **source, and block**¹⁵ as random effect. All the vital rate models used the same **linear and quadratic predictor**¹⁶ for the expected value (μ). However, we applied a different link function ($f(\mu)$) depending on the distribution the vital rate (Appendix S1: Section S1). We modeled survival and flowering data with a Bernoulli distribution. We modeled the growth (tiller number) with a zero-truncated Poisson inverse Gaussian distribution. Fertility (panicle count) was model as zero-truncated negative binomial. We fit all models in Stan (Stan Development Team, 2023), with weakly informative priors for coefficients ($\mu = 0, \sigma = 100$) and variances ($\gamma[0.001, 0.001]$). We ran three chains for 1000 samples for warmup and 40000 for interactions, with a thinning rate of 3. We accessed the quality of the models using trace plots and predictive check graphs (Piironen and Vehtari, 2017) (Appendix S1: Figure S1). Then, we used approximate Bayesian leave-one-out cross-validation (LOOIC) to select the best model describing the effect of climate variable on vital rate. The final model was the model with the lowest LOOIC (Vehtari et al., 2017).

To understand the effect of climate on vital rates, we used the 95 % credible interval of the final model for each vital rate. When the 95 % credible interval of the coefficient of a given climatic variable did not include zero, we concluded that there is a strong

¹⁵You have not described these.

¹⁶show these

133 effect of that variable on the vital rate. In contrast, when we have a credible interval of
 134 a climatic variable that includes zero, we used the empirical cumulative distribution to
 135 find the probability that the coefficient of that climatic variable is greater than zero.¹⁷

136 *Population growth rate responses to climate*

137 To understand the effect of climate on population growth rate, we used the vital rate es-
 138 timated earlier to build a matrix projection model (MPM) structured by size (number of
 139 tillers) and sex with "Climate"¹⁸ as covariate. For a given climatic variable¹⁹, let $F_{x,t}$ and
 140 $M_{x,t}$ be the number of female and male plants of size x in year t , where $x \in \{1, 2, \dots, U\}$
 141 and U is the maximum number of tillers a plant can reach (here 99th percentile of ob-
 142 served maximum size). Let F_t^R and M_t^R be the new recruits, which we assume do not
 143 reproduce in their first year. We assume that the parameters of sex ratio-dependent mat-
 144 ing (Eq. 1) do not vary with climate. For a pre-breeding census, the expected numbers
 145 of recruits in year $t + 1$ is given by:

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

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

146 where p^F and c^F are flowering probability and panicle production for females of size x ,
 147 d is the number of seeds per female panicle, v is the probability that a seed is fertilized,
 148 m is the probability that a fertilized seed germinates, and ρ is the primary sex ratio

¹⁷I would prefer to not interpret the coefficient posteriors in this way, because it is effectively frequentist hypothesis-testing.

¹⁸why quotes?

¹⁹I am not sure why this is conditional on a climate variable. I think you are suggesting that this model applies to a specific level of climate values. However, I think you should instead modify the notation of the model so that it is explicitly climate-dependent, eg $F_{x,c,t}$

¹⁴⁹ (proportion of recruits that are female). Seed fertilization depends on the OSR of panicles
¹⁵⁰ (following Eq. 1) which was derived from the $U \times 1$ vectors of population structure \mathbf{F}_t
¹⁵¹ and \mathbf{M}_t :

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

¹⁵² Thus, the dynamics of the size-structured component of the population are given by:

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

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

¹⁵³ In the two formula above, the first term represents seedlings that survived their first
¹⁵⁴ year and enter the size distribution of established plants. Instead of using *P. arachnifera*
¹⁵⁵ survival probability, we used the seedling survival probability (σ) from demographic
¹⁵⁶ studies of the hermaphroditic congener *Poa autumnalis* in east Texas (T.E.X. Miller and
¹⁵⁷ J.A. Rudgers, *unpublished data*), and we assume this probability was constant across sexes
¹⁵⁸ and climatic variables. We did this because we had little information on the early life
¹⁵⁹ cycle transitions of **greenhouse-raised transplants**²⁰. We also assume that $g(y, x = 1)$ is
¹⁶⁰ the probability that a surviving seedlings reach size y , the expected future size of 1-tiller
¹⁶¹ plants from the transplant experiment. The second term represents survival and size
¹⁶² transition of established plants from the previous year, where s and g give the probabili-
¹⁶³ ties of surviving at size x and growing from sizes x to y , respectively, and superscripts
¹⁶⁴ indicate that these functions may be unique to females (F) and males (M).

¹⁶⁵ Because the two-sex MPM is nonlinear (vital rates affect and are affected by popu-
¹⁶⁶ lation structure) we estimated the asymptotic geometric growth rate (λ) by numerical

²⁰You have not described these.

¹⁶⁷ simulation, and repeated this across a range of climate.

¹⁶⁸ *Identifying the mechanisms of population growth rate sensitivity to*
¹⁶⁹ *climate*

¹⁷⁰ ²¹ To identify the mechanism by which climate affects population growth rate, we de-
¹⁷¹ composed the effect of each climate variable (here Climate) on population growth rate (λ)
¹⁷² into contribution arising from the effect on each stage-specific vital rate (Caswell, 2000).
¹⁷³ At this end we used a life table response experiment (LTRE) with a regression designs.
¹⁷⁴ The LTRE approximates the change in λ with climate as the product of the sensitivity of
¹⁷⁵ λ to the parameters times the sensitivity of the parameters to climate, summed over all
¹⁷⁶ parameters (Caswell, 1989):

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

¹⁷⁷ where, θ_i^F and θ_i^M represent sex-specific parameters: the regression coefficients for the
¹⁷⁸ intercepts and slopes of size-dependent vital rate functions. Because LTRE contributions
¹⁷⁹ are additive, we summed across vital rates to compare the total contributions of female
¹⁸⁰ and male parameters.

¹⁸¹ *Implication on niche breath and range expansion/contraction*

¹⁸² To understand the implication of our study on **niche breath**²², we projected the popula-
¹⁸³ tion growth current and future prediction on two axes of climatic conditions (tempera-
¹⁸⁴ ture and precipitation) of each seasonal season (dormant and growing season). Similarly,

²¹I don't think the LTRE analysis is adequately motivated by the Intro.

²²You have not defined this, or described how it relates to geographic ranges.

185 to understand the implication of our study on range contraction on expansion, we extrapolate
186 population growth current and future prediction across the range to map species
187 distributions.

188 All the analysis were performed in R 4.3.1 (R Core Team, 2023)

189

Appendix S1

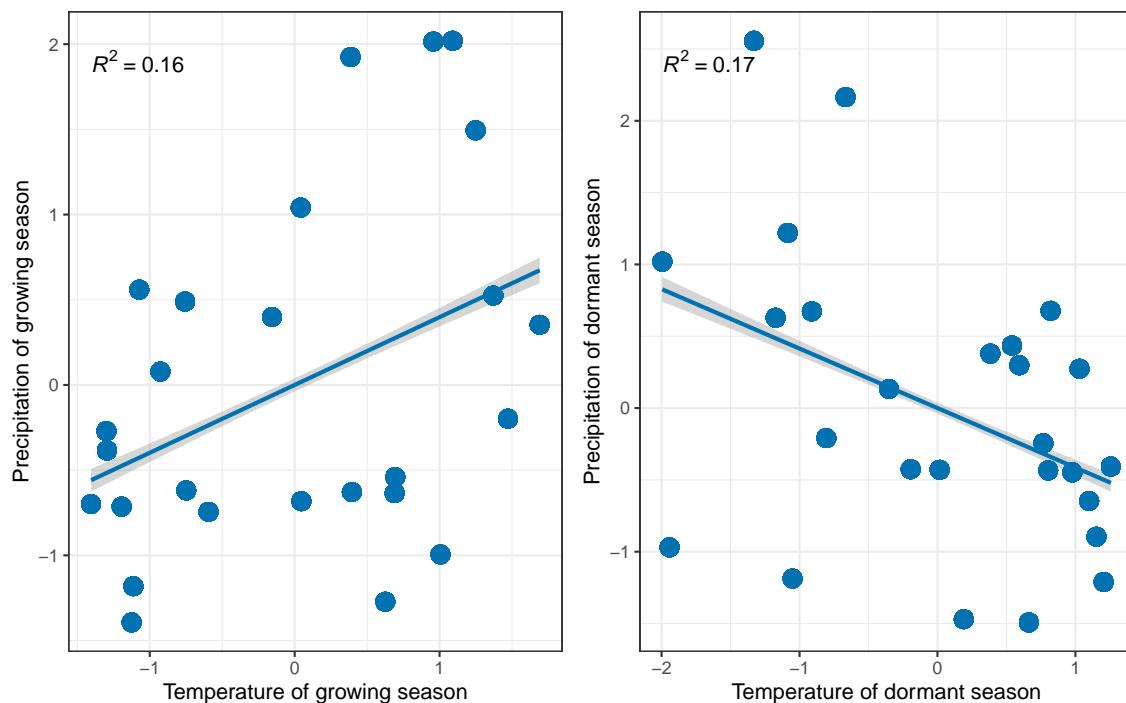


Figure S1: Relation between precipitation and temperature for each season (growing and dormant). R^2 indicates the value of proportion of explained variance between the temperature and precipitation

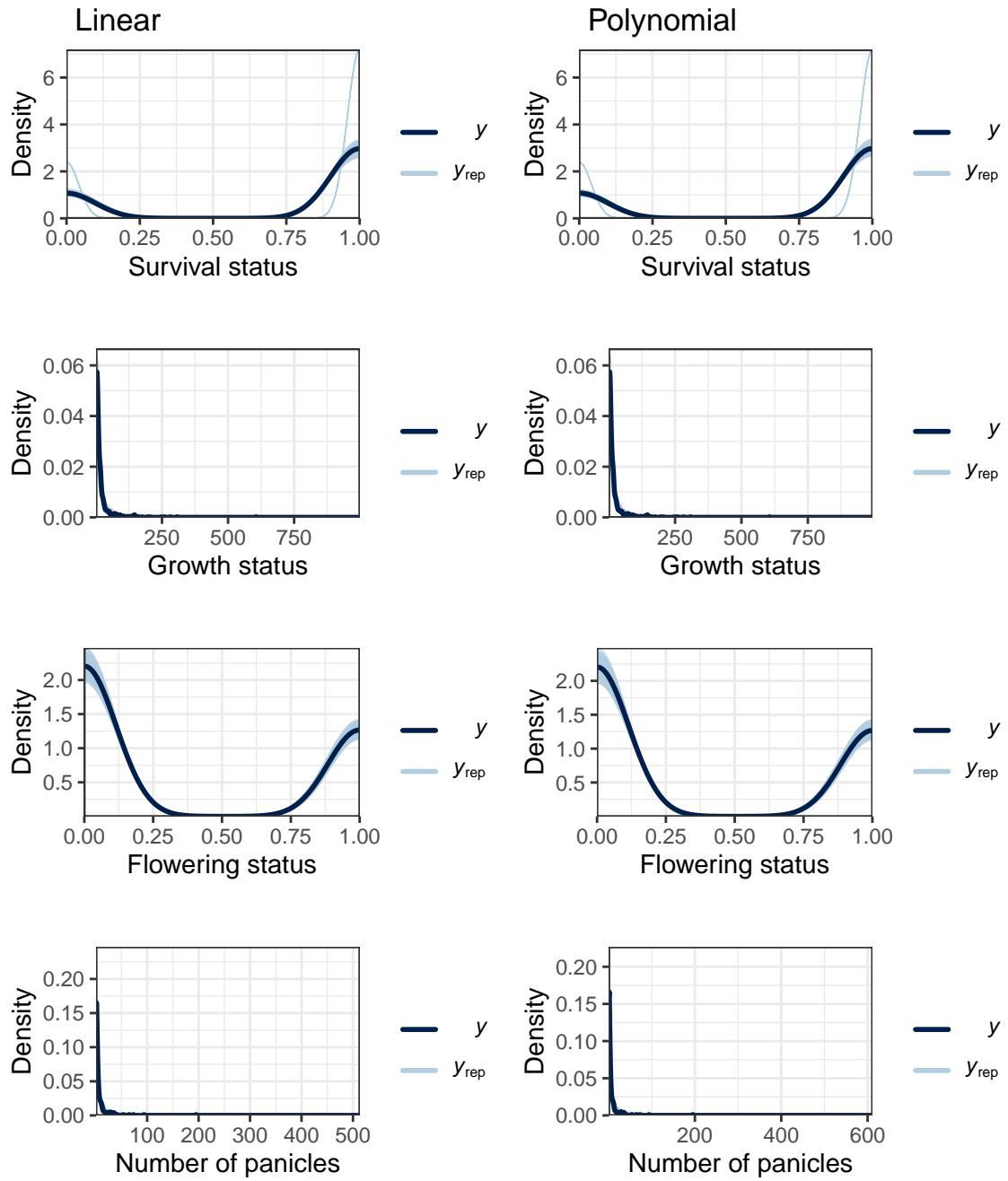


Figure S2: Consistency between real data and simulated values suggests that the fitted model accurately describes the data. Graph shows density curves for the observed data (light blue) along with the simulated values (dark blue). The first column shows the linear models and the second column shows the 2 degree polynomial models.

Section S1

$$S \sim Bernoulli(\hat{S}) \quad (1a)$$

$$F \sim Bernoulli(\hat{F}) \quad (1b)$$

$$G \sim Zero-truncated Poisson inverse Gaussian(\hat{G}) \quad (1c)$$

$$Fer \sim Zero-truncated negative binomial(\hat{Fer}) \quad (1d)$$

$$\hat{S} = \frac{\exp(f(\mu))}{1 + \exp(f(\mu))} \quad (2a)$$

$$\hat{F} = \frac{\exp(f(\mu))}{1 + \exp(f(\mu))} \quad (2b)$$

$$\hat{G} = \exp(f(\mu)) \quad (2c)$$

$$\hat{Fer} = \exp(f(\mu)) \quad (2d)$$

$$\begin{aligned}
f(\mu) = & \beta_0 + \beta_1 size + \beta_2 sex + \beta_3 pptgrow + \beta_4 pptdorm + \beta_5 tempgrow \\
& + \beta_6 tempdorm + \beta_7 pptgrow * sex + \beta_8 pptdorm * sex + \beta_9 tempgrow * sex \\
& + \beta_{10} tempdorm * sex + \beta_{11} size * sex + \beta_{12} pptgrow * tempgrow \\
& + \beta_{13} pptdorm * tempdorm + \beta_{14} pptgrow * tempgrow * sex \\
& + \beta_{15} pptdorm * tempdorm * sex + \beta_{16} pptgrow^2 + \beta_{17} pptdorm^2 \\
& + \beta_{18} tempgrow^2 + \beta_{19} tempdorm^2 + \beta_{20} pptgrow^2 * sex \\
& + \beta_{21} pptdorm^2 * sex + \beta_{22} tempgrow^2 * sex \\
& + \beta_{23} tempdorm^2 * sex + \phi + \rho + \nu
\end{aligned} \tag{3}$$

Literature Cited

- 194 Bertrand, R., J. Lenoir, C. Piedallu, G. Riofrío-Dillon, P. De Ruffray, C. Vidal, J.-C. Pierrat,
195 and J.-C. Gégout. 2011. Changes in plant community composition lag behind climate
196 warming in lowland forests. *Nature* **479**:517–520.
- 197 Bruijning, M., M. D. Visser, H. C. Muller-Landau, S. J. Wright, L. S. Comita, S. P. Hubbell,
198 H. de Kroon, and E. Jongejans. 2017. Surviving in a cosexual world: A cost-benefit
199 analysis of dioecy in tropical trees. *The American Naturalist* **189**:297–314.
- 200 Brun, P., N. E. Zimmermann, C. Hari, L. Pellissier, and D. N. Karger. 2022. Global climate-
201 related predictors at kilometer resolution for the past and future. *Earth System Science
202 Data* **14**:5573–5603.
- 203 Bürli, S., J. R. Pannell, and J. Tonnabel. 2022. Environmental variation in sex ra-
204 tios and sexual dimorphism in three wind-pollinated dioecious plant species. *Oikos*
205 **2022**:e08651.
- 206 Caswell, H. 1989. Analysis of life table response experiments I. Decomposition of effects
207 on population growth rate. *Ecological Modelling* **46**:221–237.
- 208 Caswell, H. 2000. Matrix population models. Sinauer Sunderland, MA.
- 209 Cipollini, M. L., and D. F. Whigham. 1994. Sexual dimorphism and cost of reproduc-
210 tion in the dioecious shrub *Lindera benzoin* (Lauraceae). *American Journal of Botany*
211 **81**:65–75.
- 212 Compagnoni, A., K. Steigman, and T. E. Miller. 2017. Can't live with them, can't live
213 without them? Balancing mating and competition in two-sex populations. *Proceedings
214 of the Royal Society B: Biological Sciences* **284**:20171999.

- 215 Czachura, K., and T. E. Miller. 2020. Demographic back-casting reveals that subtle
216 dimensions of climate change have strong effects on population viability. *Journal of*
217 *Ecology* **108**:2557–2570.
- 218 Davis, M. B., and R. G. Shaw. 2001. Range shifts and adaptive responses to Quaternary
219 climate change. *Science* **292**:673–679.
- 220 Eberhart-Phillips, L. J., C. Küpper, T. E. Miller, M. Cruz-López, K. H. Maher,
221 N. Dos Remedios, M. A. Stoffel, J. I. Hoffman, O. Krüger, and T. Székely. 2017. Sex-
222 specific early survival drives adult sex ratio bias in snowy plovers and impacts mating
223 system and population growth. *Proceedings of the National Academy of Sciences*
224 **114**:E5474–E5481.
- 225 Ellis, R. P., W. Davison, A. M. Queirós, K. J. Kroeker, P. Calosi, S. Dupont, J. I. Spicer, R. W.
226 Wilson, S. Widdicombe, and M. A. Urbina. 2017. Does sex really matter? Explaining
227 intraspecies variation in ocean acidification responses. *Biology letters* **13**:20160761.
- 228 Evans, M. E., C. Merow, S. Record, S. M. McMahon, and B. J. Enquist. 2016. Towards
229 process-based range modeling of many species. *Trends in Ecology & Evolution* **31**:860–
230 871.
- 231 Gamelon, M., V. Grøtan, A. L. Nilsson, S. Engen, J. W. Hurrell, K. Jerstad, A. S. Phillips,
232 O. W. Røstad, T. Slagsvold, B. Walseng, et al. 2017. Interactions between demogra-
233 phy and environmental effects are important determinants of population dynamics.
234 *Science Advances* **3**:e1602298.
- 235 Gianuca, D., S. C. Votier, D. Pardo, A. G. Wood, R. B. Sherley, L. Ireland, R. Choquet,
236 R. Pradel, S. Townley, J. Forcada, et al. 2019. Sex-specific effects of fisheries and

- 237 climate on the demography of sexually dimorphic seabirds. *Journal of Animal Ecology*
238 88:1366–1378.
- 239 Gissi, E., L. Schiebinger, E. A. Hadly, L. B. Crowder, R. Santoleri, and F. Micheli. 2023a.
240 Exploring climate-induced sex-based differences in aquatic and terrestrial ecosystems
241 to mitigate biodiversity loss. *nature communications* 14:4787.
- 242 Gissi, E., L. Schiebinger, R. Santoleri, and F. Micheli. 2023b. Sex analysis in marine bio-
243 logical systems: insights and opportunities. *Frontiers in Ecology and the Environment*
244 .
- 245 Hitchcock, A. S. 1971. *Manual of the grasses of the United States*. Courier Corporation.
- 246 Hultine, K. R., K. C. Grady, T. E. Wood, S. M. Shuster, J. C. Stella, and T. G. Whitham.
247 2016. Climate change perils for dioecious plant species. *Nature Plants* 2:1–8.
- 248 Jones, M. H., S. E. Macdonald, and G. H. Henry. 1999. Sex-and habitat-specific responses
249 of a high arctic willow, *Salix arctica*, to experimental climate change. *Oikos* pages
250 129–138.
- 251 Karger, D. N., O. Conrad, J. Böhner, T. Kawohl, H. Kreft, R. W. Soria-Auza, N. E. Zim-
252 mermann, H. P. Linder, and M. Kessler. 2017. Climatologies at high resolution for the
253 earth's land surface areas. *Scientific data* 4:1–20.
- 254 Kindiger, B. 2004. Interspecific hybrids of *Poa arachnifera* × *Poa secunda*. *Journal of*
255 *New Seeds* 6:1–26.
- 256 Miller, T. E., and A. Compagnoni. 2022. Two-Sex Demography, Sexual Niche Differen-
257 tiation, and the Geographic Range Limits of Texas Bluegrass (*Poa arachnifera*). *The*
258 *American Naturalist* 200:17–31.

- 259 O'Neill, B. C., E. Kriegler, K. L. Ebi, E. Kemp-Benedict, K. Riahi, D. S. Rothman, B. J.
260 Van Ruijven, D. P. Van Vuuren, J. Birkmann, K. Kok, et al. 2017. The roads ahead:
261 Narratives for shared socioeconomic pathways describing world futures in the 21st
262 century. *Global environmental change* **42**:169–180.
- 263 Pease, C. M., R. Lande, and J. Bull. 1989. A model of population growth, dispersal and
264 evolution in a changing environment. *Ecology* **70**:1657–1664.
- 265 Petry, W. K., J. D. Soule, A. M. Iler, A. Chicas-Mosier, D. W. Inouye, T. E. Miller, and K. A.
266 Mooney. 2016. Sex-specific responses to climate change in plants alter population sex
267 ratio and performance. *Science* **353**:69–71.
- 268 Piironen, J., and A. Vehtari. 2017. Comparison of Bayesian predictive methods for model
269 selection. *Statistics and Computing* **27**:711–735.
- 270 Pottier, P., S. Burke, S. M. Drobniak, M. Lagisz, and S. Nakagawa. 2021. Sexual (in)
271 equality? A meta-analysis of sex differences in thermal acclimation capacity across
272 ectotherms. *Functional Ecology* **35**:2663–2678.
- 273 R Core Team, 2023. R: A Language and Environment for Statistical Computing. R
274 Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- 275
- 276 Stan Development Team, 2023. RStan: the R interface to Stan. URL <https://mc-stan.org/>.
- 277
- 278 Tognetti, R. 2012. Adaptation to climate change of dioecious plants: does gender balance
279 matter? *Tree Physiology* **32**:1321–1324. URL <https://doi.org/10.1093/treephys/tps105>.

- 281 Vehtari, A., A. Gelman, and J. Gabry. 2017. Practical Bayesian model evaluation using
282 leave-one-out cross-validation and WAIC. *Statistics and computing* **27**:1413–1432.
- 283 Zhao, H., Y. Li, X. Zhang, H. Korpelainen, and C. Li. 2012. Sex-related and stage-
284 dependent source-to-sink transition in *Populus cathayana* grown at elevated CO₂ and
285 elevated temperature. *Tree Physiology* **32**:1325–1338.