

# 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.

<sup>1</sup>

## **Abstract**

<sup>2</sup> Sex-specific response to rising temperature and drought raises the questions of whether  
<sup>3</sup> global change could lead to a drastic change in the sex ratio and whether that change in  
<sup>4</sup> the sex ratio could drive population extinction or population range shift. We developed  
<sup>5</sup> a forecasting model using hierarchical Bayesian matrix models for Texas bluegrass (*Poa*  
<sup>6</sup> *arachnifera*) to project its potential range shifts in response to climate change.

<sup>7</sup>

## **Keywords**

## Introduction

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

23 Females and males respond differently to climate change, especially in species where  
24 the two sexes have different energetic requirements or habitat preferences (Gissi et al.,  
25 2023a,b; Hultine et al., 2016). This sex-specific response to climate change may help  
26 one sex to succeed in extreme climatic conditions rather than the other sex (Zhao et al.,  
27 2012; Bürl et al., 2022). Experimentation manipulation revealed that when exposed to  
28 increasing temperatures, for example, in two populations of Atlantic marine copepods  
29 (*Acartia tonsa*), males showed significantly lower survival than females (Sasaki et al.,  
30 2019). In some species, such as the Australian flying fox or *Populus cathayana*, females  
31 showed lower survival than males in response to extreme temperature (Welbergen et al.,

32 2008; Zhao et al., 2012). Thus in the context of climate, populations in which males are  
33 rare could experience low reproductive success due to sperm or pollen limitation that  
34 may lead to population decline (Eberhart-Phillips et al., 2017).

35 The geographic range of most species is limited by climatic factors, including tem-  
36 perature, precipitation. Any shift in the magnitude of these factors in a given location  
37 will impact the population viability, with potential implication on range shift (Davis and  
38 Shaw, 2001; Pease et al., 1989). This is particularly true for dioecious species. For in-  
39 stance, a reduction in water availability due to climate change means that male valarians  
40 (*Valeriana edulis*) are likely to move upslope, which reduces pollen limitation and in-  
41 creases seedset and favor range expansion (Petry et al., 2016). Although the response to  
42 warming is generally understood, it is difficult to disentangle the interaction between sex  
43 and climate drivers to understand their relative contribution and effects on population  
44 dynamics and the consequence of such population dynamics on range dynamic.

45 Our ability to track the impact of climate change on the population dynamics of  
46 dioecious plants and the implication of such impact on range shift depends on our ability  
47 to build mechanistic models that take into account the spatial and temporal context in  
48 which sex specific response to climate change affects population viability (Davis and  
49 Shaw, 2001; Evans et al., 2016; Czachura and Miller, 2020). At their range edge where  
50 climatic conditions are expected to be less favorable, if dioecious species populations are  
51 non-viable in response to climate change, global warming will induce range contraction  
52 in dioecious species. In reverse, if populations at the edge are viable habitats in response  
53 to global warming, dioecious species populations could shift their range and relocate to  
54 more favorable and thereby favored range expansion.

55 In this study, we used a matrix projection model to understand the demographic  
56 response of dioecious species to climate change and its implications for future range dy-

namics. Our study system is a dioecious plant species (*Poa arachnifera*) distributed along environmental gradients in the south-central US corresponding to variation in temperature across latitude and precipitation across longitude (MAP). A previous study showed that, despite the differentiation of the climatic niche between sexes, the female niche mattered the most in driving the environmental limits of population viability (Miller and Compagnoni, 2022). Thus, under current climate conditions, we hypothesized that high temperature and lower precipitation during the growing season have negative effects on population growth rate through a reduction in female growth, survival, and fecundity rate. However, that reduction in population growth rate will not go below a viable population (population growth rate less than one) even at range edge. Future climate will exacerbate the effect of temperature and precipitation on female vital rates and drive population to extinction, particularly at range edge.<sup>1</sup>

## Materials and methods

2

### Study system

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

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<sup>1</sup>These 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.

<sup>2</sup>General 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.

77        We studied 14 sites along the distribution of these species in the United States in 2014  
78        and 2015.<sup>3</sup>

79            *Demographic and climatic data collection*

80        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)  
81        to build our demographic models. The details of the data collection has been provided  
82        in Miller and Compagnoni (2022).<sup>4</sup>

83        We want to understand how current and future climate affect the *dynamic*<sup>5</sup> of *Poa arachnifera*. Therefore, we considered the climatic data from the time we collected demographic data (2015 and 2016 censuses)<sup>6</sup> as the current condition for the species<sup>7</sup>. Additionally, months were aligned to match demographic transition years rather than calendar years.<sup>8</sup> Monthly temperature and precipitation data were downloaded for each site from Chelsea (Karger et al., 2017). We define June to September as the dormant season of the year and the rest of the year as the growing season. We used seasonal data because they allowed us to quantify the response of species to change in seasonal change in climate.<sup>9</sup> We evaluated future climate projections from two scenarios<sup>10</sup>: SSP 370, an intermediate-to-pessimistic scenario assuming a radiative forcing to amount to  $7.0 \text{ Wm}^{-2}$  by 2100, and SSP 585, a pessimistic emission scenario which project a radiative forcing to

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

<sup>4</sup>You need to say a little more here.

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

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

<sup>7</sup>Unclear what this means.

<sup>8</sup>Needs to be explained.

<sup>9</sup>This sentence contains no information.

<sup>10</sup>I 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.

amount to  $8.5 \text{ Wm}^{-2}$  by 2100 (O'Neill et al., 2017; Brun et al., 2022). The precipitation of growing season and dormant season were not explained by the Temperature of growing season and dormant season (Appendix S1: Figure S1).<sup>11</sup>

### 98                   Sex ratio experiment

We<sup>12</sup> also conducted a sex-ratio experiment to measure the effect of male panicle availability on seed viability on females panicles. Details of the experiment are provided in Compagnoni et al. (2017) and Miller and Compagnoni (2022).<sup>13</sup>

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

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

where  $OSR$  is the operational sex ratio<sup>14</sup> (proportion of panicles that were female) in the experimental populations. The properties of the above function is supported by our previous work (Compagnoni et al., 2017). Here, 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  $\alpha$  controls how viability declines with increasing female bias.

We used a binomial distribution to model the germination data from greenhouse trials. Given that 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.

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<sup>11</sup>Explain why this is significant and why you looked for this.

<sup>12</sup>I would describe the demographic data before the sex ratio experiment.

<sup>13</sup>Again, you need more info here.

<sup>14</sup>This concept should be described in the Introduction.

114

## *Vital rate responses to climate*

115 We used individual level measurements of survival, growth (number of tillers), flow-  
116 ering, number of panicles to independently develop Bayesian mixed effect models de-  
117 scribing how each vital rate varies as a function of sex, size, precipitation of growing and  
118 dormant season and temperature of of growing and dormant season. We fit two versions  
119 of the vital rate models, with either linear or second-degree polynomial functions for the  
120 influence of climate, and used model selection to quantify their empirical support. We  
121 included a second-degree polynomial because we expected that climate variables would  
122 affect vital rates through a hump-shaped relationship.

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

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<sup>15</sup>*You have not described these.*

<sup>16</sup>*show these*

<sup>137</sup> et al., 2017).

<sup>138</sup> To understand the effect of climate on vital rates, we used the 95 % credible interval  
<sup>139</sup> of the final model for each vital rate. When the 95 % credible interval of the coefficient  
<sup>140</sup> of a given climatic variable did not include zero, we concluded that there is a strong  
<sup>141</sup> effect of that variable on the vital rate. In contrast, when we have a credible interval of  
<sup>142</sup> a climatic variable that includes zero, we used the empirical cumulative distribution to  
<sup>143</sup> find the probability that the coefficient of that climatic variable is greater than zero.<sup>17</sup>

<sup>144</sup> *Population growth rate responses to climate*

<sup>145</sup> To understand the effect of climate on population growth rate, we used the vital rate es-  
<sup>146</sup> timated earlier to build a matrix projection model (MPM) structured by size (number of  
<sup>147</sup> tillers) and sex with "Climate"<sup>18</sup> as covariate. For a given climatic variable<sup>19</sup>, let  $F_{x,t}$  and  
<sup>148</sup>  $M_{x,t}$  be the number of female and male plants of size  $x$  in year  $t$ , where  $x \in \{1, 2, \dots, U\}$   
<sup>149</sup> and  $U$  is the maximum number of tillers a plant can reach (here 99th percentile of ob-  
<sup>150</sup> served maximum size). Let  $F_t^R$  and  $M_t^R$  be the new recruits, which we assume do not  
<sup>151</sup> reproduce in their first year. We assume that the parameters of sex ratio-dependent mat-  
<sup>152</sup> ing (Eq. 1) do not vary with climate. For a pre-breeding census, the expected numbers  
<sup>153</sup> of recruits in year  $t + 1$  is given by:

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

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

---

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

<sup>18</sup>why quotes?

<sup>19</sup>I 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  $F_{x,c,t}$

154 where  $p^F$  and  $c^F$  are flowering probability and panicle production for females of size  $x$ ,  
 155  $d$  is the number of seeds per female panicle,  $v$  is the probability that a seed is fertilized,  
 156  $m$  is the probability that a fertilized seed germinates, and  $\rho$  is the primary sex ratio  
 157 (proportion of recruits that are female). Seed fertilization depends on the OSR of panicles  
 158 (following Eq. 1) which was derived from the  $U \times 1$  vectors of population structure  $\mathbf{F}_t$   
 159 and  $\mathbf{M}_t$ :

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

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

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

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

161 In the two formula above, the first term represents seedlings that survived their first  
 162 year and enter the size distribution of established plants. Instead of using *P. arachnifera*  
 163 survival probability, we used the seedling survival probability ( $\sigma$ ) from demographic  
 164 studies of the hermaphroditic congener *Poa autumnalis* in east Texas (T.E.X. Miller and  
 165 J.A. Rudgers, *unpublished data*), and we assume this probability was constant across sexes  
 166 and climatic variables. We did this because we had little information on the early life  
 167 cycle transitions of *greenhouse-raised transplants*<sup>20</sup>. We also assume that  $g(y, x=1)$  is  
 168 the probability that a surviving seedlings reach size  $y$ , the expected future size of 1-tiller  
 169 plants from the transplant experiment. The second term represents survival and size  
 170 transition of established plants from the previous year, where  $s$  and  $g$  give the probabili-  
 171 ties of surviving at size  $x$  and growing from sizes  $x$  to  $y$ , respectively, and superscripts

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<sup>20</sup>You have not described these.

172 indicate that these functions may be unique to females ( $F$ ) and males ( $M$ ).

173 Because the two-sex MPM is nonlinear (vital rates affect and are affected by popu-  
174 lation structure) we estimated the asymptotic geometric growth rate ( $\lambda$ ) by numerical  
175 simulation, and repeated this across a range of climate.

176 *Identifying the mechanisms of population growth rate sensitivity to  
177 climate*

178 <sup>21</sup> To identify the mechanism by which climate affects population growth rate, we de-  
179 composed the effect of each climate variable (here Climate) on population growth rate ( $\lambda$ )  
180 into contribution arising from the effect on each stage-specific vital rate (Caswell, 2000).  
181 At this end we used a life table response experiment (LTRE) with a regression designs.  
182 The LTRE approximates the change in  $\lambda$  with climate as the product of the sensitivity of  
183  $\lambda$  to the parameters times the sensitivity of the parameters to climate, summed over all  
184 parameters (Caswell, 1989):

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

185 where,  $\theta_i^F$  and  $\theta_i^M$  represent sex-specific parameters: the regression coefficients for the  
186 intercepts and slopes of size-dependent vital rate functions. Because LTRE contributions  
187 are additive, we summed across vital rates to compare the total contributions of female  
188 and male parameters.

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<sup>21</sup>I don't think the LTRE analysis is adequately motivated by the Intro.

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

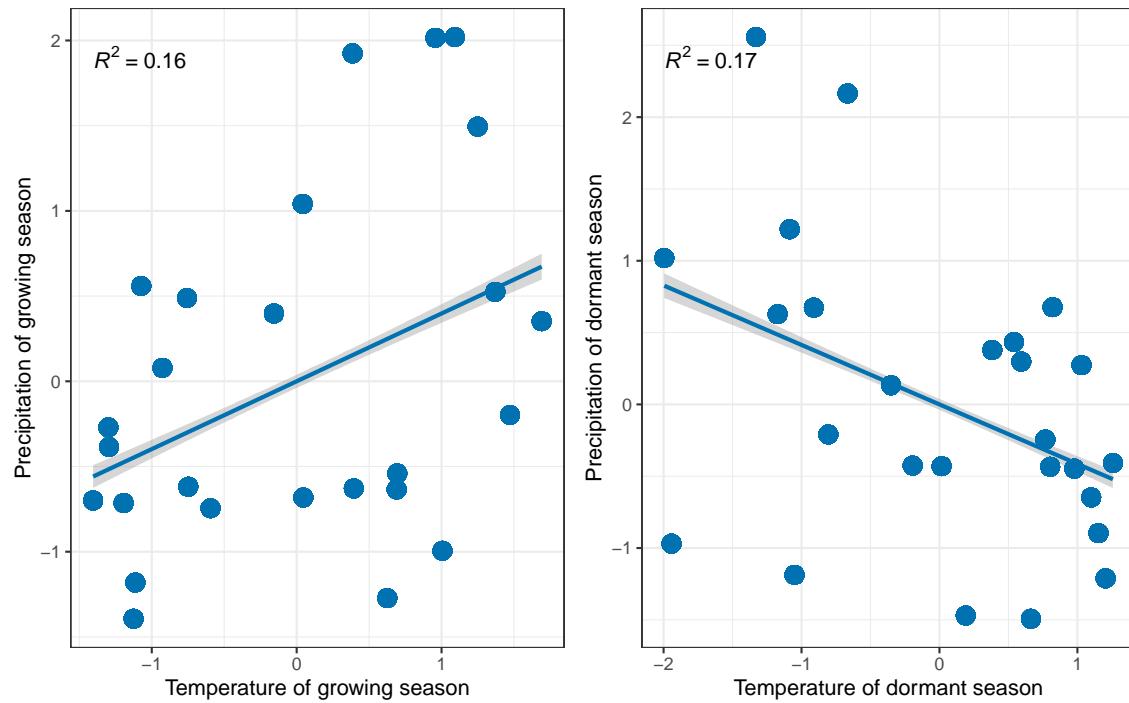
190        To understand the implication of our study on **niche breath**<sup>22</sup>, we projected the popula-  
191        tion growth current and future prediction on two axes of climatic conditions (tempera-  
192        ture and precipitation) of each seasonal season (dormant and growing season). Similarly,  
193        to understand the implication of our study on range contraction on expansion, we extrap-  
194        olate population growth current and future prediction across the range to map species  
195        distributions.

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

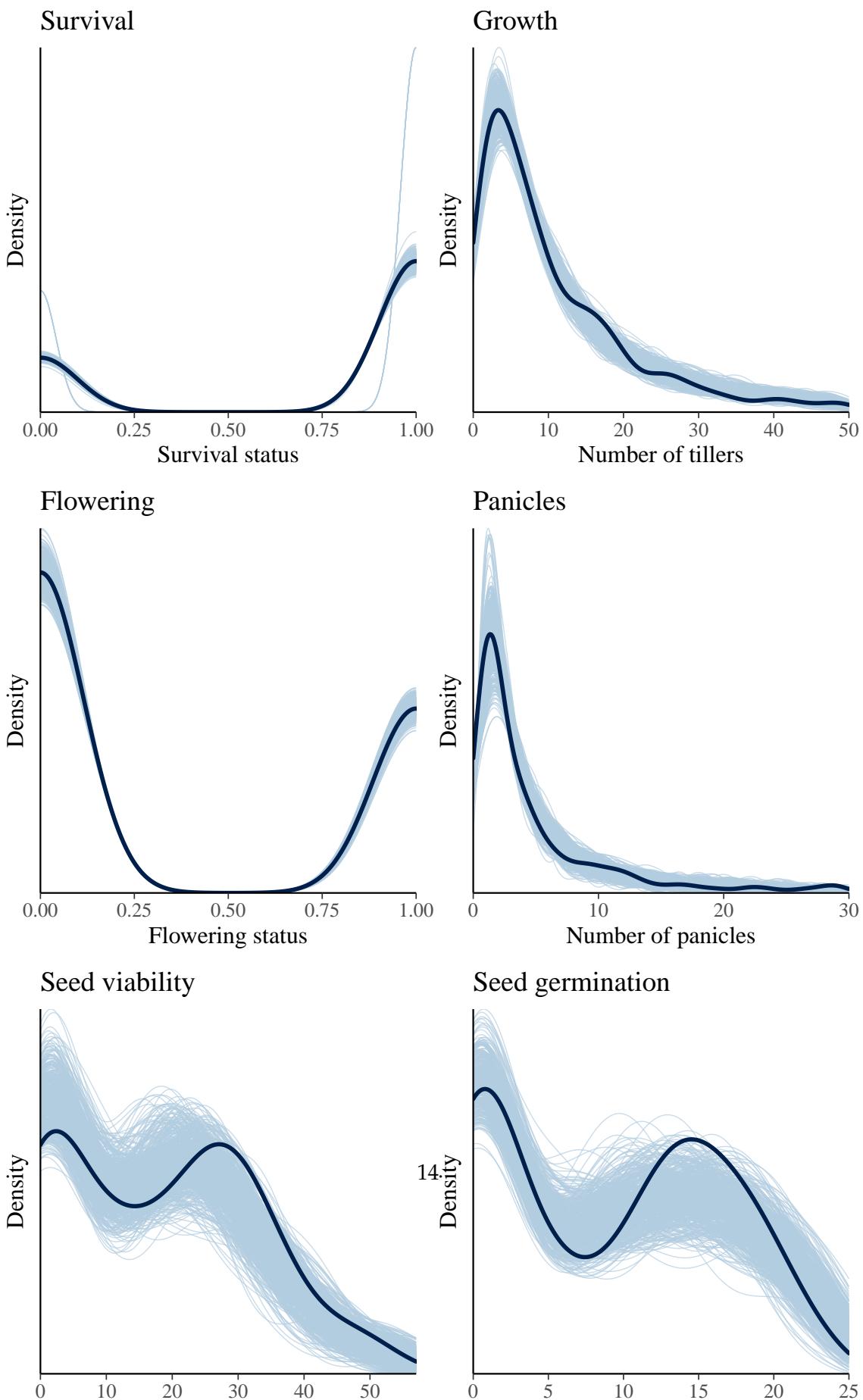
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<sup>22</sup>*You have not defined this, or described how it relates to geographic ranges.*

## 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



## Section S1

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

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

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

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

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

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

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

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

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

201

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