

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

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1 Abstract

2 Sex-specific response to rising temperature and drought raises the questions of whether
3 global change could lead to a drastic change in the sex ratio and whether that change in
4 the sex ratio could drive population extinction or population range shift.

5 We developed a forecasting model using hierarchical Bayesian matrix models for
6 Texas bluegrass (*Poa arachnifera*) to project its potential range shifts in response to cli-
7 mate change.

8 Keywords

Introduction

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

24 Females and males respond differently to climate change, especially in species where
25 the two sexes have different energetic requirements or habitat preferences (Gissi et al.,
26 2023a,b; Hultine et al., 2016). This sex-specific response to climate change may help one
27 sex to succeed in extreme climatic conditions rather than the other sex (Zhao et al., 2012;
28 Bürl et al., 2022). Experimentation manipulation revealed that when exposed to increas-
29 ing temperatures, for example, in two populations of Atlantic marine copepods (*Acartia*
30 *tonsa*), males showed significantly lower survival than females (Sasaki et al., 2019). High
31 male mortality drives low reproductive success due to sperm limitation that may lead to
32 population decline. Furthermore, the lower cost of reproduction of males could allow

33 them to invest their energy in other functions that produce higher growth rates, higher
34 clonality, or even higher survival rates compared to females (Cipollini and Whigham,
35 1994; Bruijning et al., 2017). In some species, such as the Australian flying fox, females
36 showed lower survival than males in response to extreme temperature (Welbergen et al.,
37 2008).

38 The geographic range of most dioecious species is limited by climatic factors, includ-
39 ing temperature, precipitation. Any shift in the magnitude of these factors in a given
40 location will impact the populating viability, with potential implication on range shift
41 (Davis and Shaw, 2001; Pease et al., 1989). For instance, a reduction in water availabil-
42 ity due to climate change means that male valarians (*Valeriana edulis*) are likely to move
43 upslope, which reduces pollen limitation and increases seedset (Petry et al., 2016). Al-
44 though the response to warming is generally understood, it is difficult to disentangle the
45 interaction between sex and climate drivers to understand their relative contribution and
46 effects on population dynamics and the consequence of such population dynamics on
47 range dynamic.

48 Our ability to track the impact of climate change on the population dynamics of dioe-
49 cious plants and the implication of such impact on range shift depends on our ability
50 to build mechanistic models that take into account the spatial and temporal context in
51 which sex specific response to climate change affects population viability (Davis and
52 Shaw, 2001; Evans et al., 2016; Czachura and Miller, 2020). Sex ratio bias could affect
53 population viability by reducing the survival rate of limiting sex or by reducing the
54 probability of female flowering (Eberhart-Phillips et al., 2017; Miller and Compagnoni,
55 2022). At their range edge where climatic conditions are expected to be less favorable,
56 if dioecious species populations are non-viable in response to climate change, global
57 warming will induce range contraction in dioecious species. In reverse, if populations

58 at the edge are viable habitats in response to global warming, dioecious species populations could shift their range and relocate to more favorable and thereby favored range expansion.

61 In this study, we used a matrix projection model to understand the demographic response of dioecious species to climate change and its implications for future range dynamics. 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.¹

75 Materials and methods

76 2

¹*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.*

²*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

Study system

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

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

85

Demographic and climatic data collection

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

90 We want to understand how current and future climate affect the dynamic⁵ of *Poa*
91 *arachnifera*. Therefore, we considered the climatic data from the time we collected de-
92 mographic data (2015 and 2016 censuses)⁶ as the current condition for the species⁷.
93 Additionally, months were aligned to match demographic transition years rather than
94 calendar years.⁸ Monthly temperature and precipitation data were downloaded for each
95 site from Chelsea (Karger et al., 2017). We define June to September as the dormant

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

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.

96 season of the year and the rest of the year as the growing season. We used seasonal data
97 because they allowed us to quantify the response of species to change in seasonal change
98 in climate.⁹ We evaluated future climate projections from two scenarios¹⁰: SSP 370, an
99 intermediate-to-pessimistic scenario assuming a radiative forcing to amount to 7.0 Wm^{-2}
100 by 2100, and SSP 585, a pessimistic emission scenario which project a radiative forcing to
101 amount to 8.5 Wm^{-2} by 2100 (O'Neill et al., 2017; Brun et al., 2022). The precipitation of
102 growing season and dormant season were not explained by the Temperature of growing
103 season and dormant season (Appendix S1: Figure S1).¹¹

104 *Sex ratio experiment*

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

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

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

111 where OSR is the operational sex ratio¹⁴ (proportion of panicles that were female) in
112 the experimental populations. The properties of the above function is supported by our

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.

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.

113 previous work (Compagnoni et al., 2017). Here, seed viability is maximized at v_0 as OSR
114 approaches zero (strongly male-biased) and goes to zero as OSR approaches 1 (strongly
115 female-biased). Parameter α controls how viability declines with increasing female bias.

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

120 *Vital rate responses to climate*

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

129 We centered and standardized all predictors to facilitate model convergence. We
130 included site, **source, and block**¹⁵ as random effect. All the vital rate models used the
131 same **linear and quadratic predictor**¹⁶ for the expected value (μ). However, we applied
132 a different link function ($f(\mu)$) depending on the distribution the vital rate (Appendix
133 S1: Section S1). We modeled survival and flowering data with a Bernoulli distribution.
134 We modeled the growth (tiller number) with a zero-truncated Poisson inverse Gaussian
135 distribution. Fertility (panicle count) was model as zero-truncated negative binomial. We

¹⁵You have not described these.

¹⁶show these

136 fit all models in Stan (Stan Development Team, 2023), with weakly informative priors for
137 coefficients ($\mu = 0, \sigma = 100$) and variances ($\gamma[0.001, 0.001]$). We ran three chains for 1000
138 samples for warmup and 40000 for interactions, with a thinning rate of 3. We accessed
139 the quality of the models using trace plots and predictive check graphs (Piironen and
140 Vehtari, 2017) (Appendix S1: Figure S1). Then, we used approximate Bayesian leave-
141 one-out cross-validation (LOOIC) to select the best model describing the effect of climate
142 variable on vital rate. The final model was the model with the lowest LOOIC (Vehtari
143 et al., 2017).

144 To understand the effect of climate on vital rates, we used the 95 % credible interval
145 of the final model for each vital rate. When the 95 % credible interval of the coefficient
146 of a given climatic variable did not include zero, we concluded that there is a strong
147 effect of that variable on the vital rate. In contrast, when we have a credible interval of
148 a climatic variable that includes zero, we used the empirical cumulative distribution to
149 find the probability that the coefficient of that climatic variable is greater than zero.¹⁷

150 *Population growth rate responses to climate*

151 To understand the effect of climate on population growth rate, we used the vital rate es-
152 timated earlier to build a matrix projection model (MPM) structured by size (number of
153 tillers) and sex with "Climate"¹⁸ as covariate. For a given climatic variable¹⁹, let $F_{x,t}$ and
154 $M_{x,t}$ be the number of female and male plants of size x in year t , where $x \in \{1, 2, \dots, U\}$
155 and U is the maximum number of tillers a plant can reach (here 99th percentile of ob-
156 served maximum size). Let F_t^R and M_t^R be the new recruits, which we assume do not

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 $F_{x,c,t}$

157 reproduce in their first year. We assume that the parameters of sex ratio-dependent mat-
 158 ing (Eq. 1) do not vary with climate. For a pre-breeding census, the expected numbers
 159 of recruits in year $t + 1$ is given by:

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

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

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

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

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

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

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

167 In the two formula above, the first term represents seedlings that survived their first
 168 year and enter the size distribution of established plants. Instead of using *P. arachnifera*
 169 survival probability, we used the seedling survival probability (σ) from demographic
 170 studies of the hermaphroditic congener *Poa autumnalis* in east Texas (T.E.X. Miller and

¹⁷¹ J.A. Rudgers, *unpublished data*), and we assume this probability was constant across sexes
¹⁷² and climatic variables. We did this because we had little information on the early life
¹⁷³ cycle transitions of **greenhouse-raised transplants**²⁰. We also assume that $g(y, x = 1)$ is
¹⁷⁴ the probability that a surviving seedlings reach size y , the expected future size of 1-tiller
¹⁷⁵ plants from the transplant experiment. The second term represents survival and size
¹⁷⁶ transition of established plants from the previous year, where s and g give the probabili-
¹⁷⁷ ties of surviving at size x and growing from sizes x to y , respectively, and superscripts
¹⁷⁸ indicate that these functions may be unique to females (F) and males (M).

¹⁷⁹ Because the two-sex MPM is nonlinear (vital rates affect and are affected by popu-
¹⁸⁰ lation structure) we estimated the asymptotic geometric growth rate (λ) by numerical
¹⁸¹ simulation, and repeated this across a range of climate.

¹⁸² *Identifying the mechanisms of population growth rate sensitivity to*
¹⁸³ *climate*

¹⁸⁴ ²¹ To identify the mechanism by which climate affects population growth rate, we de-
¹⁸⁵ composed the effect of each climate variable (here Climate) on population growth rate (λ)
¹⁸⁶ into contribution arising from the effect on each stage-specific vital rate (Caswell, 2000).
¹⁸⁷ At this end we used a life table response experiment (LTRE) with a regression designs.
¹⁸⁸ The LTRE approximates the change in λ with climate as the product of the sensitivity of
¹⁸⁹ λ to the parameters times the sensitivity of the parameters to climate, summed over all
¹⁹⁰ parameters (Caswell, 1989):

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

²⁰You have not described these.

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

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

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

196 To understand the implication of our study on **niche breath**²², we projected the popula-
197 tion growth current and future prediction on two axes of climatic conditions (tempera-
198 ture and precipitation) of each seasonal season (dormant and growing season). Similarly,
199 to understand the implication of our study on range contraction on expansion, we extrap-
200 olate population growth current and future prediction across the range to map species
201 distributions.

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

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

Appendix S1

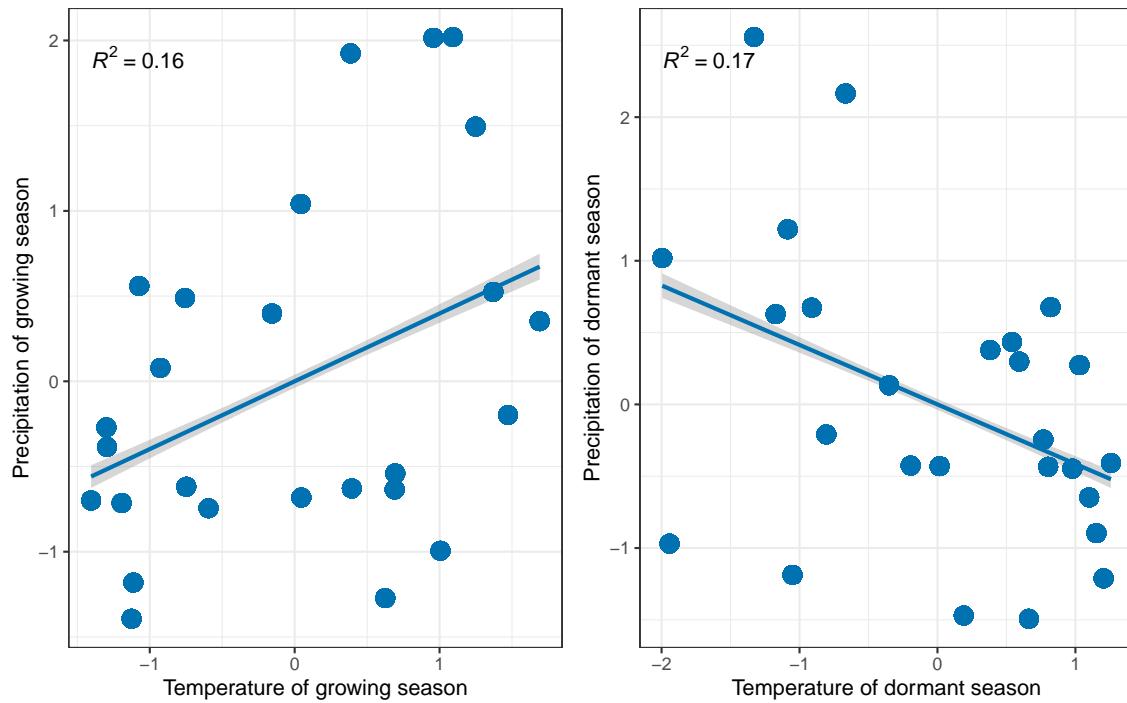
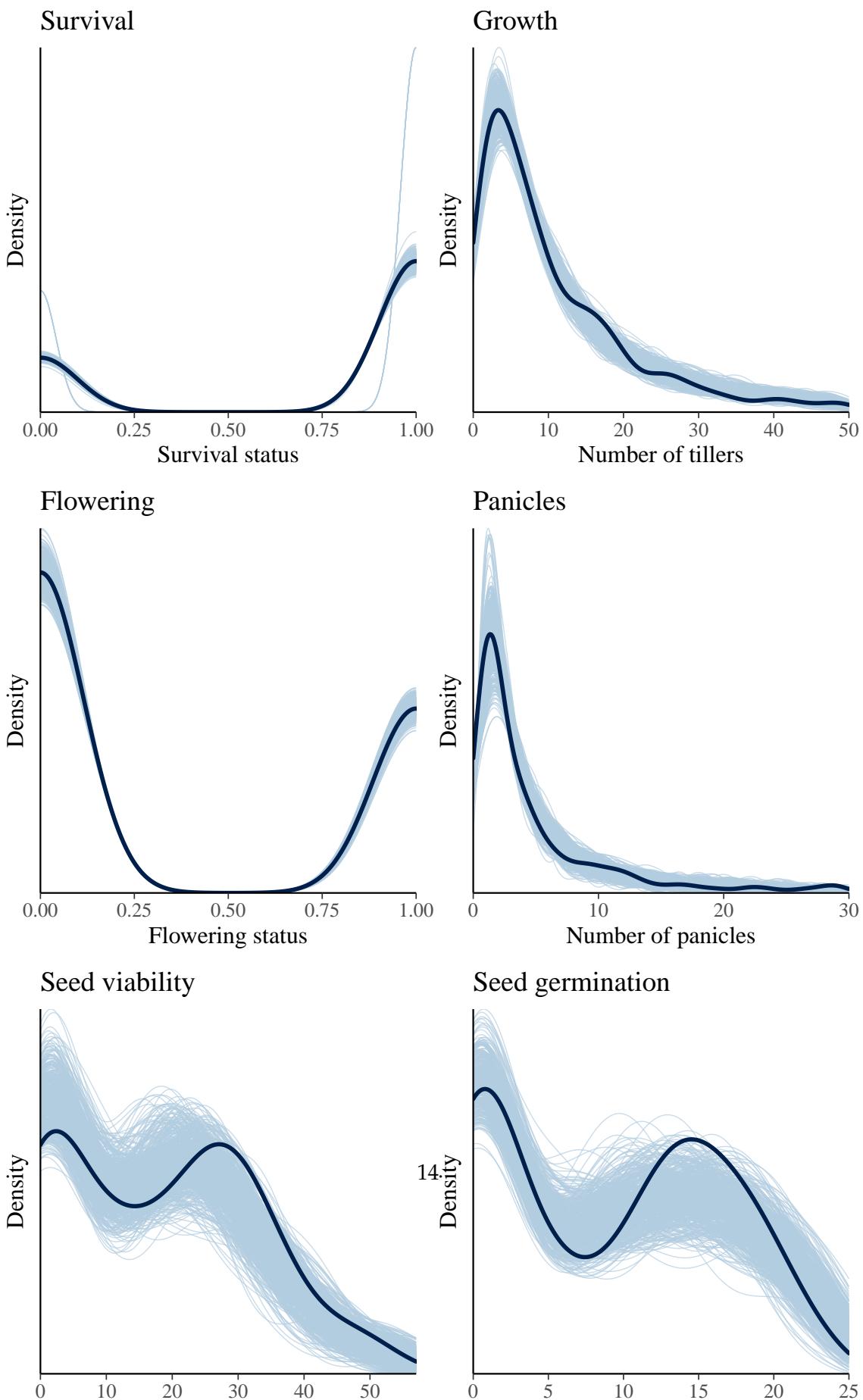


Figure S1: Relation between precipitation and temperature for each season (growing and dormant). R^2 indicates the value of proportion of explained variance between the temperature and precipitation



Section S1

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

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

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

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

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

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

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

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

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

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