

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

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September 14, 2023

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Submitted to *Ecological Monographs*

Manuscript type: Article

Open Research statement: All of our data and code are available during peer review at <https://github.com/jmoutouama/POAR-Forecasting>. This manuscript and its contents can be reproduced from this file: <https://github.com/jmoutouama/POAR-Forecasting/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.

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

27 2008; Zhao et al., 2012). Therefore, in the context of climate, populations in which males
28 are rare could experience low reproductive success due to sperm or pollen limitation that
29 may lead to population decline (Eberhart-Phillips et al., 2017).

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

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

51 In this study, we used a mechanistic approach by combining common field experi-

52 ment and matrix projection modelling, to understand the demographic response of dioe-
53 cious species to climate change and its implications for future range dynamics. Our
54 study system is a dioecious plant species (*Poa arachnifera*) distributed along environmen-
55 tal gradients in the south-central US corresponding to variation in temperature across
56 latitude and precipitation across longitude (MAP). Here, we asked three questions: (1)
57 What is the sex-specific demographic response to rising temperature and precipitation
58 ? (2) How that sex-specific demographic response affects populations dynamics under
59 current and future climatic conditions ? (3) What are the implications of population
60 dynamics on range dynamics ?

61 **Materials and methods**

62 *Study species*

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

68 *Common garden experiment*

69 We set up a common garden experiment to manipulate climatic factors such as tem-
70 perature and precipitation to detect mechanisms underlying sex-specific demographic
71 response to climate and the implication of such a response on range limitation (Merow
72 et al., 2017; Schwinnig et al., 2022). At this end, we collected vegetative tillers from flow-
73 ering individuals of each sex in eight natural (sources) populations of the focal species.

74 We then propagated these tillers in ProMix plotting soil and supplemented them with
75 Osmocote slow-release fertilizer at 75°F to 85°F under natural climatic conditions at the
76 Rice University Greenhouse. The common experiment was installed on 14 sites across
77 a precipitation gradient (FigX). At each site, we established 14 blocks. Each block was
78 selected so that they resemble the natural environment of the species. For each block we
79 planted three females and three males individuals. We spared the individuals, provided
80 1 L of water, and removed surrounding vegetation to avoid competition and promote
81 establishment.

82 *Demographic and climatic data collection*

83 In each site we collected individual demographic data including survival, growth (num-
84 ber of tillers), flowers and fertility (number of panicle) for two censuses (2015 and 2016)
85 to build our demographic models. **The details of the data collection has been provided**
86 **in Miller and Compagnoni (2022).**¹

87 We want to understand how current and future climate affect the **dynamic**² of *Poa*
88 *arachnifera*. Therefore, we considered the climatic data from the time we collected de-
89 mographic data (**2015 and 2016 censuses**)³ as **the current condition for the species**⁴.
90 Additionally, months were aligned to match demographic transition years rather than
91 **calendar years**.⁵ Monthly temperature and precipitation data were downloaded for each
92 site from Chelsea (Karger et al., 2017). We define June to September as the dormant
93 season of the year and the rest of the year as the growing season. **We used seasonal**
94 **data because they allowed us to quantify the response of species to change in seasonal**

¹*You need to say a little more here.*

²*This is vague. This carefully about the target of your analysis and the best way to describe it.*

³*The timeline of the experiment and the censuses need to be clarified. Above you say 2014-15 and here you say 2015-16.*

⁴*Unclear what this means.*

⁵*Needs to be explained.*

95 change in climate.⁶ We evaluated future climate projections from two scenarios⁷: SSP
96 370, an intermediate-to-pessimistic scenario assuming a radiative forcing to amount to
97 7.0 Wm^{-2} by 2100, and SSP 585, a pessimistic emission scenario which project a radiative
98 forcing to amount to 8.5 Wm^{-2} by 2100 (O'Neill et al., 2017; Brun et al., 2022). The pre-
99 cipitation of growing season and dormant season were not explained by the Temperature
100 of growing season and dormant season (Appendix S1: Figure S1).⁸

101 *Sex ratio experiment*

102 We⁹ also conducted a sex-ratio experiment to measure the effect of male panicle avail-
103 ability on seed viability on females panicles. Details of the experiment are provided in
104 Compagnoni et al. (2017) and Miller and Compagnoni (2022).¹⁰

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

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

108 where OSR is the operational sex ratio¹¹ (proportion of panicles that were female) in
109 the experimental populations. The properties of the above function is supported by our
110 previous work (Compagnoni et al., 2017). Here, seed viability is maximized at v_0 as OSR
111 approaches zero (strongly male-biased) and goes to zero as OSR approaches 1 (strongly

⁶This sentence contains no information.

⁷I 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.

⁸Explain why this is significant and why you looked for this.

⁹I would describe the demographic data before the sex ratio experiment.

¹⁰Again, you need more info here.

¹¹This concept should be described in the Introduction.

112 female-biased). Parameter α controls how viability declines with increasing female bias.

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

117 *Vital rate responses to climate*

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

126 We centered and standardized all predictors to facilitate model convergence. We
127 included site, **source, and block**¹² as random effect. All the vital rate models used the
128 same **linear and quadratic predictor**¹³ for the expected value (μ). However, we applied
129 a different link function ($f(\mu)$) depending on the distribution the vital rate (Appendix
130 S1: Section S1). We modeled survival and flowering data with a Bernoulli distribution.
131 We modeled the growth (tiller number) with a zero-truncated Poisson inverse Gaussian
132 distribution. Fertility (panicle count) was model as zero-truncated negative binomial. We
133 fit all models in Stan (Stan Development Team, 2023), with weakly informative priors for
134 coefficients ($\mu = 0, \sigma = 100$) and variances ($\gamma[0.001, 0.001]$). We ran three chains for 1000

¹²You have not described these.

¹³show these

135 samples for warmup and 40000 for interactions, with a thinning rate of 3. We accessed
136 the quality of the models using trace plots and predictive check graphs (Piironen and
137 Vehtari, 2017) (Appendix S1: Figure S1). Then, we used approximate Bayesian leave-
138 one-out cross-validation (LOOIC) to select the best model describing the effect of climate
139 variable on vital rate. The final model was the model with the lowest LOOIC (Vehtari
140 et al., 2017).

141 To understand the effect of climate on vital rates, we used the 95 % credible interval
142 of the final model for each vital rate. When the 95 % credible interval of the coefficient
143 of a given climatic variable did not include zero, we concluded that there is a strong
144 effect of that variable on the vital rate. In contrast, when we have a credible interval of
145 a climatic variable that includes zero, we used the empirical cumulative distribution to
146 find the probability that the coefficient of that climatic variable is greater than zero.¹⁴

147 *Population growth rate responses to climate*

148 To understand the effect of climate on population growth rate, we used the vital rate es-
149 timated earlier to build a matrix projection model (MPM) structured by size (number of
150 tillers) and sex with "Climate"¹⁵ as covariate. For a given climatic variable¹⁶, let $F_{x,t}$ and
151 $M_{x,t}$ be the number of female and male plants of size x in year t , where $x \in \{1, 2, \dots, U\}$
152 and U is the maximum number of tillers a plant can reach (here 99th percentile of ob-
153 served maximum size). Let F_t^R and M_t^R be the new recruits, which we assume do not
154 reproduce in their first year. We assume that the parameters of sex ratio-dependent mat-
155 ing (Eq. 1) do not vary with climate. For a pre-breeding census, the expected numbers

¹⁴I would prefer to not interpret the coefficient posteriors in this way, because it is effectively frequentist hypothesis-testing.

¹⁵why quotes?

¹⁶I 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 $F_{x,c,t}$

¹⁵⁶ of recruits in year $t + 1$ is given by:

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

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

¹⁵⁷ where p^F and c^F are flowering probability and panicle production for females of size x ,
¹⁵⁸ d is the number of seeds per female panicle, v is the probability that a seed is fertilized,
¹⁵⁹ m is the probability that a fertilized seed germinates, and ρ is the primary sex ratio
¹⁶⁰ (proportion of recruits that are female). Seed fertilization depends on the OSR of panicles
¹⁶¹ (following Eq. 1) which was derived from the $U \times 1$ vectors of population structure \mathbf{F}_t
¹⁶² and \mathbf{M}_t :

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

¹⁶³ Thus, the dynamics of the size-structured component of the population are given by:

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

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

¹⁶⁴ In the two formula above, the first term represents seedlings that survived their first
¹⁶⁵ year and enter the size distribution of established plants. Instead of using *P. arachnifera*
¹⁶⁶ survival probability, we used the seedling survival probability (σ) from demographic
¹⁶⁷ studies of the hermaphroditic congener *Poa autumnalis* in east Texas (T.E.X. Miller and
¹⁶⁸ J.A. Rudgers, *unpublished data*), and we assume this probability was constant across sexes
¹⁶⁹ and climatic variables. We did this because we had little information on the early life

170 cycle transitions of **greenhouse-raised transplants**¹⁷. We also assume that $g(y, x = 1)$ is
171 the probability that a surviving seedlings reach size y , the expected future size of 1-tiller
172 plants from the transplant experiment. The second term represents survival and size
173 transition of established plants from the previous year, where s and g give the probabili-
174 ties of surviving at size x and growing from sizes x to y , respectively, and superscripts
175 indicate that these functions may be unique to females (F) and males (M).

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

179 *Identifying the mechanisms of population growth rate sensitivity to
180 climate*

181 ¹⁸ To identify the mechanism by which climate affects population growth rate, we de-
182 composed the effect of each climate variable (here Climate) on population growth rate (λ)
183 into contribution arising from the effect on each stage-specific vital rate (Caswell, 2000).
184 At this end we used a life table response experiment (LTRE) with a regression designs.
185 The LTRE approximates the change in λ with climate as the product of the sensitivity of
186 λ to the parameters times the sensitivity of the parameters to climate, summed over all
187 parameters (Caswell, 1989):

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

188 where, θ_i^F and θ_i^M represent sex-specific parameters: the regression coefficients for the
189 intercepts and slopes of size-dependent vital rate functions. Because LTRE contributions

¹⁷You have not described these.

¹⁸I don't think the LTRE analysis is adequately motivated by the Intro.

190 are additive, we summed across vital rates to compare the total contributions of female
191 and male parameters.

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

193 To understand the implication of our study on **niche breath**¹⁹, we projected the popula-
194 tion growth current and future prediction on two axes of climatic conditions (tempera-
195 ture and precipitation) of each seasonal season (dormant and growing season). Similarly,
196 to understand the implication of our study on range contraction on expansion, we extrap-
197 olate population growth current and future prediction across the range to map species
198 distributions.

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

¹⁹You have not defined this, or described how it relates to geographic ranges.

Appendix S1

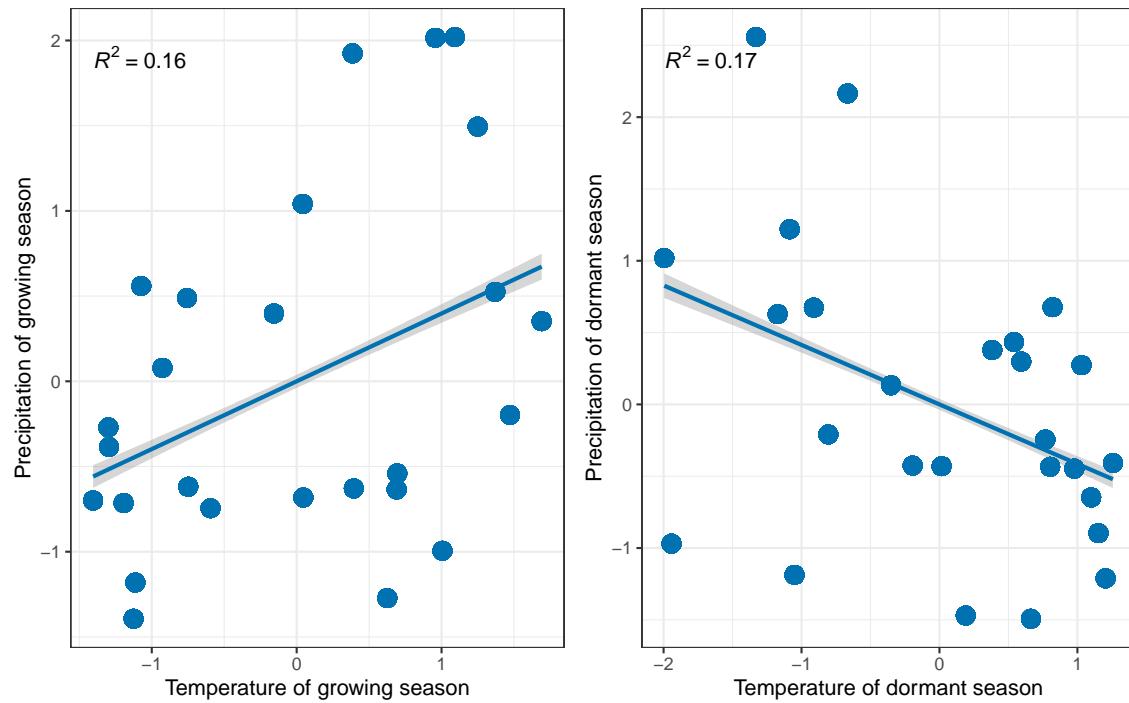
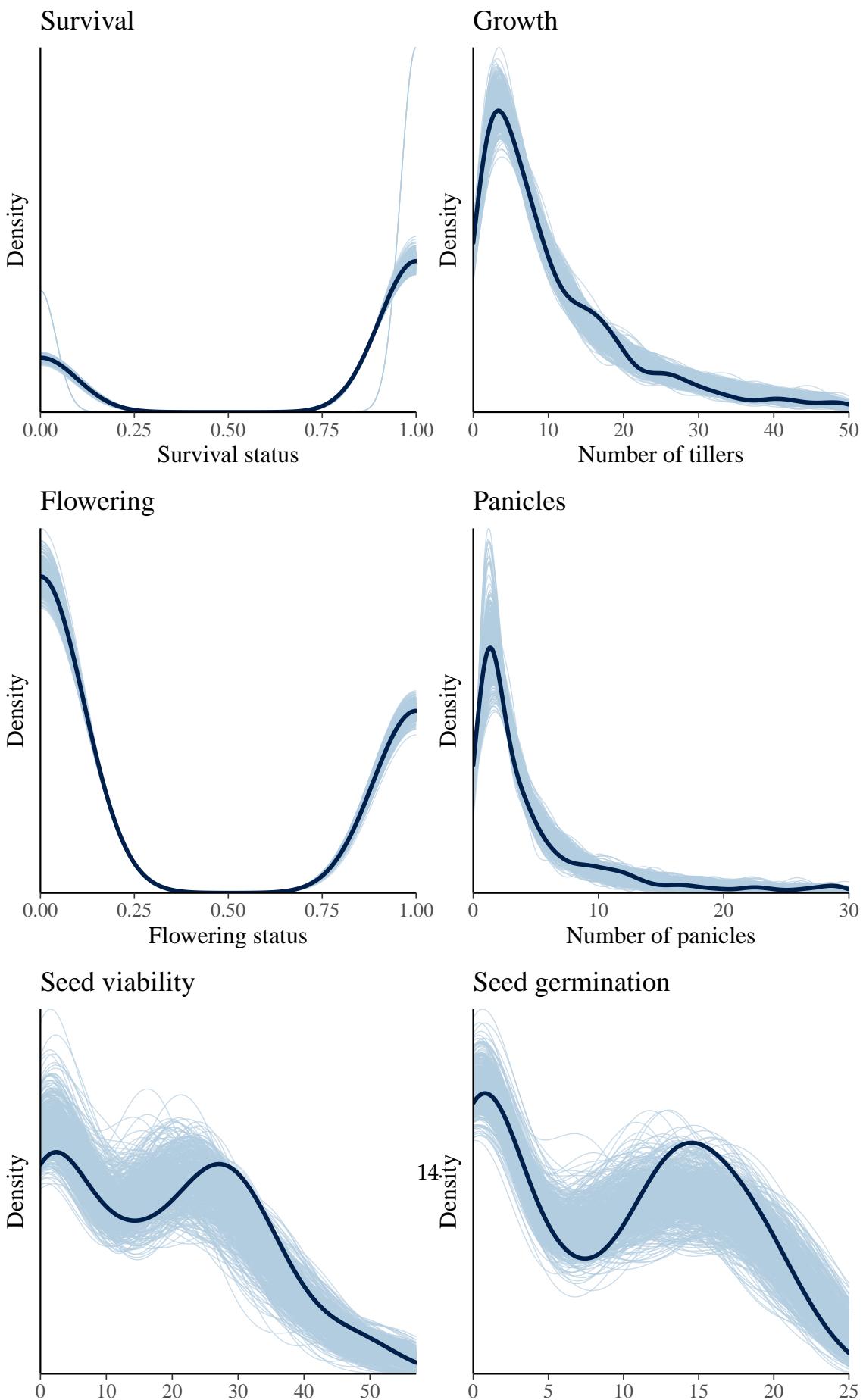


Figure S1: Relation between precipitation and temperature for each season (growing and dormant). R^2 indicates the value of proportion of explained variance between the temperature and precipitation



201

Section S1

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

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

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

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

202

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

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

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

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

203

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

204

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