

**[Working title]: Intraspecific variation in range-wide seed bank dynamics is not  
consistent with density-independent bet hedging alone**

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# 1 Introduction

Organisms across the tree of life exhibit life history strategies to persist in environments with different levels of variability, uncertainty, and predictability. In annual plants, temporal variation in fitness can favor the evolution of delayed germination and seed dormancy that establish soil seed banks. Seed banks can buffer plant populations against environmental change and stochasticity (Eager et al. (2014); Paniw et al. (2017)), increase effective population size (Nunney (2002); Waples (2006)), and maintain genetic diversity (McCue and Holtsford (1998)). Theory thus suggests that seed banks have key ecological and evolutionary consequences (Evans and Dennehy (2005)).

Evolutionary ecologists have classically theorized seed banks as a bet-hedging strategy that maximizes geometric mean fitness (reviewed in Philippi and Seger (1989); Simons (2011)). Because the geometric mean is multiplicative, optimal bet-hedging strategies reduce variance in geometric mean fitness even if they decrease the arithmetic mean fitness (Cohen (1966)). Density-independent models have been expanded to density-dependent cases with competition, in which case seed banks are an evolutionary stable strategy (Ellner (1985*a,b*)). However, seed strategies are shaped by environments that vary in both their levels of uncertainty and predictability. Predictive germination is expected if seeds are able to detect and respond to cues that reliably predict fitness upon germination (Cohen (1967)). Ultimately, it is likely that life history strategies are the product of a combination of these factors (Simons (2011)), an idea supported by research carried out with a guild of Sonoran Desert annuals (Gremer et al. (2016); Gremer and Venable (2014); Venable (2007)).

A variety of approaches have also been used to examine support for bet hedging and predictive germination hypotheses within species. Studies have correlated genetic variation or morphological traits with putative bet hedging strategies (e.g. Clauss and Venable (2000); Hacker (1984); Hacker and Ratcliff (1989); Philippi (1993*b*)), identified clines in seed behav-

ior (e.g. [Fernández-Pascual et al. \(2013\)](#); [Gremer et al. \(2020\)](#)), and correlated life history patterns with environmental variation (e.g. [Philippi \(1993a\)](#)). Experimental studies have also decomposed the multifactorial contributions to germination and dormancy, establishing that these seed behaviors are complex traits jointly influenced by genetics, maternal effects, and the environment. Despite this wealth of research on patterns of intraspecific variation, tests of bet hedging theory in plants in the field have been conducted by examining (co)-variation in germination, seed survival, and reproductive success in a group of species at a single site in the Sonoran Desert (e.g. [Gremer et al. \(2016\)](#); [Gremer and Venable \(2014\)](#); [Venable \(2007\)](#)). Here, we examine intraspecific variation in life-history patterns of a winter annual plant with a seed bank, and use a combination of field experiments, surveys, and modeling to test whether the observed variation is consistent with bet hedging theory.

Populations of the winter annual *Clarkia xantiana* ssp. *xantiana* are distributed across a complex landscape in the southern Sierra Nevada Mountains (Fig. 1). Although earlier work suggested the species lacked a soil seed bank ([Lewis \(1962\)](#)), multiple lines of evidence now support the presence and relevance of a seed bank in populations of *C. xantiana* ssp. *xantiana*. In field experiments burying seeds in bags ([Eckhart et al. \(2011\)](#)) and pots ([Geber, unpublished data](#)), seeds can germinate at least up to 3 years after burial. Fifteen years of surveys suggest that the seed bank may allow some populations to persist exclusively as seeds for as long as 4 consecutive years (Fig. 1D). Seeds lack morphological adaptations for dispersal ([Knies et al. \(2004\)](#)) and spatial distribution patterns in populations are consistent with dispersal limitation ([Kramer et al. \(2011\)](#)). We thus expect limited seed dispersal among populations over the relatively short temporal scales reported in this study.

Intraspecific variation in fitness and demography in *C. xantiana* prompted us to consider whether bet hedging might explain life-history patterns in the species. A study of *C. xantiana* population dynamics identified an increase in the germination rate of first-year seeds from west to east ([Eckhart et al. \(2011\)](#)). Variability in rainfall during the growing season shows

the opposite pattern, from wetter and less variable in the west to drier and more variable in the east (Eckhart et al. (2011); Fig. 1B&C for pattern from 2005-2020). Demographic observations Eckhart et al. (2011) and transplant experiments also demonstrate that fitness can exhibit dramatic interannual variation (e.g. 30-fold between a wet and dry year in Geber and Eckhart (2005)). Because environmental variability is an imperfect proxy for fitness, we sought to understand intraspecific variation in *C. xantiana* seed vital rates in the context of temporal variation in fitness. We thus sought to test whether bet hedging theory helps explains observed patterns of life history variation.

Here, we test whether life history patterns in *Clarkia xantiana* ssp. *xantiana* are consistent with predictions made by bet hedging models. We combine seed burial experiments and 15 years of observations on aboveground vital rates from 20 populations to address the following questions: (1) Is there a negative correlation between germination and seed survival (Fig. 1E)? (2) Is there a negative correlation between germination and variance in per-capita reproductive success (Fig. 1F)? (3) Is per-capita reproductive success positively correlated with growing season precipitation? (4) Does germination predicted by density-independent bet hedging models match observed germination? Because we find that life history patterns are not consistent with predictions, we examined two additional pieces of evidence to explore support for complementary hypotheses: (4) Is there a correlation between variation in the environment and per-capita reproductive success? (5) What is the relative contribution of different fitness components to total variance in per-capita reproductive success?

## 2 Methods

### 2.1 *Clarkia* life history

*Clarkia xantiana* ssp. *xantiana* is a winter annual that germinates with late fall and winter rains. In our study region, the Kern Valley in the southern Sierra Nevada Mountains, germination historically happens between October and late February or early March. Seedlings grow throughout the winter and spring, and surviving plants flower in late spring and early summer, April into early July. Pollinated fruits set seed in the early summer, June to July. Seeds of *C. xantiana* are produced in early summer, with fruits that dry out and gradually split open. Most seeds appear to be shed from fruits within 3-4 months after production, but can remain on the plant for up to a year. Seeds are small ( $< 1$  mm in width) and have no structures to aid in aerial dispersal.

We represent the *C. xantiana* life history in terms of transitions from October of year  $t$  to October of year  $t + 1$ . Transitions are the product of seed survival and germination, and aboveground seedling survival to fruiting, fruit production, and seeds per fruit. For this study, we assume that the new and old seeds differ in their survival rates, but do not include additional age structure and assume germination of new and old seeds is the same. We also assume that all plants experience the same vital rates upon germination. We describe population growth rate by the following equation:

$$\lambda = g_1 Y(t) s_0 s_1 + (1 - g_1) s_2 s_3. \quad (1)$$

Germination is given by  $g_1$ . Seed survival from seed production to the first October is  $s_0$ , and survival from October to February is  $s_1$  and  $s_3$  for age 0, and 1 seeds, respectively. Survival from February to October is given as  $s_2$ . Per-capita reproductive success in year

$t$ ,  $Y(t)$  is the product of seedling survival to fruiting ( $\sigma$ ), fruits per plant ( $F$ ), or seeds per fruit ( $\phi$ ).

## 2.2 Creating the dataset

We used field experiments and surveys to assemble observations of below- and above-ground demography for 20 populations of *Clarkia xantiana* (Table 1). Specifically, we used experiments to estimate transitions in the seed bank and surveys to estimate per-capita reproductive success. These demographic data have been used to test hypotheses about the geography of demography (Eckhart et al. (2011)) and species distributions (Pironon et al. (2018)). Here, we use them to obtain population-level estimates of germination and seed survival, and yearly estimates of per-capita reproductive success.

To estimate transitions in the seed bank, we used observations from a seed bag burial experiment conducted in all populations from 2005-2008 (Figure 2). In June-July of these years, one of us (MAG) collected mature fruits at all study populations. In each population, seeds were pooled and distributed across 5×5-cm nylon mesh bags (100 seeds/bag). In October, MAG placed 30 bags at each population; one bag was staked into the ground near each permanent survey plot and covered with soil. In all populations, ten bags each were unearthed twice (in January and October) during their first, second, or third year; bags that were dug up in a given year were only used in that year and were removed at the end of the year (Figure 2A). The experiment was repeated in 3 consecutive years (3 rounds). In round 1 (started in October 2005 with 30 bags/population), bags were dug up in year 1, 2, and 3. In round 2 (started in October 2006 with 20 bags/population), bags were dug up in year 1 and 2. In round 3 (started in October 2007 with 10 bags/population), bags were dug up in year 1. We thus have 3 sets of observations associated with 1 year old seeds, 2 sets of observations associated with 2 year old seeds, and 1 set of observations associated with 3

year old seeds. We use data from the experiment to estimate germination and seed survival (see Joint model for seed vital rates) but note that we test predictions of bet-hedging theory using only a subset of transitions relevant to our analysis (see Computing vital rates).

During each experimental round, we counted the number of intact seeds ( $y_{ijkm}$ ) for up to 3 years. We counted the number of seeds in bag  $i$ , in population  $j$ , and in year  $k$  at times indexed by  $m$ , corresponding to the times at which bags were unearthed. These counts represent the number of seeds that remain intact in the soil seed bank. We also counted the number of seedlings ( $y_{g,ijk}$ ) when we unearthed the seed bags in January. We illustrate the relationship between the experimental design and data in (Figure 2B), in which we show the hypothetical, average seed counts in seed bags from the first experimental round at one population. Seeds are lost from bags through physical destruction (continuous decline in seed counts along solid lines) and germination (discrete decline in seed counts along dotted lines).

We conducted viability experiments in each year we conducted seed burial experiments. At the end of each experimental year, bags were brought to the lab and intact seeds were tested in a two-stage viability trial (Figure 2C). In the lab, we conducted germination trials and viability assays on subsets of the seeds from each bag to estimate the viability of the intact seeds. First, we placed up to 15 seeds from each bag on to moist filter paper in a disposable cup and observed the number of germinants over 10 days; we counted and removed germinants every 2 days. For each bag, we summed the number of seeds tested and germinating to obtain the number of trials ( $n_{ijk}^{\text{test}_g}$ ) and successes ( $y_{ijk}^{\text{germ}}$ ) summarizing the germination trials.

After 10 days, up to 10 remaining ungerminated seeds were sliced in half and individually placed into the wells of 96-well plates filled with a solution of tetrazolium chloride, which stains viable tissue red. We covered the plates with foil. Each 96-well plate contained seed from at least one bag per population of a given seed-age class. Two or three tests of up to

15 seeds each were conducted for each bag. We checked and counted for viable seeds every 2 days for 10 days. For each bag, we summed the number of seeds tested and stained to obtain the number of trials ( $n_{ijk}^{\text{test}_v}$ ) and successes ( $y_{ijk}^{\text{viab}}$ ) summarizing the viability trials.

To estimate the survival of seedlings to fruiting plants, we counted seedlings and fruiting plants in 30  $0.5 \text{ m}^2$  permanent plots from 2006–2020 (Eckhart et al. (2011)). Seedlings ( $n_{ijk}$ ) and fruiting plants ( $y_{ijk}$ ) were counted in February and June, respectively, in plot  $i$ , in population  $j$ , and in year  $k$ . Plants in each plot are counted by a single person at each visit.

To estimate seed production by plants that survive to reproduction, we combined estimates of fruits per plant and seeds per fruit (Eckhart et al. (2011)). To determine the number of fruits per plant, we made two sets of counts at each population. First, from 2007–2020, we counted the number of fruits per plant on all plants in the  $0.5\text{m}^2$  permanent plots. Second, from 2006–2020, we counted the number of fruits per plant on additional plants that we sampled haphazardly across the site using throws of a  $0.5\text{m}^2$  grid. We chose to combine counts from plants in permanent and haphazardly distributed plots, because the latter often sampled a broader distribution of plant sizes and combining them allowed us to better estimate fruit number per plant in years with relatively few plants in permanent plots.

From 2006–2012, we counted the number of undamaged fruits on a plant. We then took the damaged fruits on a plant and visually stacked them end to end to estimate how many additional undamaged fruits that was equivalent to (e.g. two half fruits corresponded to one undamaged fruit). We used this as our count ( $y_{ijk}^{TFE}$ ) of total fruit equivalents on plant  $i$ , in population  $j$ , and in year  $k$ . From 2013–2020, we counted and separately recorded the number of undamaged ( $y_{ijk}^{UF}$ ) and damaged ( $y_{ijk}^{DF}$ ) fruits on a plant plant.

From 2006–2020, we collected one undamaged fruit from each of 20–30 plants that were haphazardly chosen in each population. For each population in each year, we attempted



to obtain 20-30 counts of seeds produced per undamaged fruit. The plants were outside permanent plots to avoid affecting seed input. In the lab, we counted the number of seeds in the fruit ( $y_{ijk}^{US}$ ), corresponding to fruit  $i$ , in population  $j$ , and in year  $k$ . From 2013–2020, we additionally collected a damaged fruit from the same plant whenever available. We counted the number of seeds in the fruit ( $y_{ijk}^{DS}$ ), corresponding to fruit  $i$ , in population  $j$ , and in year  $k$ .

Table 1: Summary of data sets used to estimate demographic parameters.

Parameter data	Description	Data set	Time span
SEED VITAL RATES	—	—	—
Seed survival and germination	Seed bag burial	$\mathbf{Y}_1$	2006-2009
Seed viability	Viability trials	$\mathbf{Y}_2$	2006-2009
SEEDLING SURVIVAL	—	—	—
Seedling survival to fruiting	Field surveys	$\mathbf{Y}_4$	2006-2020
FRUITS PER PLANT	—	—	—
Total fruit equivalents per plant	Field surveys	$\mathbf{Y}_5$	2006-2012
Undamaged and damaged fruits per plant	Field surveys	$\mathbf{Y}_6$	2013-2020
Total fruit equivalents per plant	Extra plots	$\mathbf{Y}_7$	2006-2012
Undamaged and damaged fruits per plant	Extra plots	$\mathbf{Y}_8$	2013-2020
SEEDS PER FRUIT	—	—	—
Seeds per undamaged fruit	Lab counts	$\mathbf{Y}_9$	2006-2020
Seeds per damaged fruit	Lab counts	$\mathbf{Y}_{10}$	2013-2020

## 2.3 Model

We use observational and experimental data from 20 populations to estimate transition probabilities across the life cycle. We fit multilevel models to obtain population-specific estimates for belowground vital rates, and year- and population-specific estimates for aboveground vital rates. Because we were interested in describing the life histories of individual populations, we built separate models for each population. The details of each model depend on the dataset and are fully described in [Appendix: Joint Posteriors](#), but our general approach applies a common model structure to partially pool observations in each population.

We first explicitly describe our formulation in terms linear mixed models before defining the joint posterior (Evans et al. (2010); Ogle and Barber (2020)). We assume that the latent

mean of observations in year  $j$  at a population  $k$ ,  $\theta_{jk}$ , is drawn from a normal distribution with mean  $\theta_{0,k}$  and variance  $\sigma_j^2$ .

$$\theta_{jk} = \theta_{0,k} + \epsilon_{(jk)}. \quad (2)$$

Our model includes a population-level intercept  $\theta_{0,k}$  and random effects  $\epsilon_{(jk)}$ . The random effects can be written as  $\epsilon_{(jk)} \sim N(0, \varsigma^2)$ . For the moment, we focus on describing the hierarchical structure of the model but note that we use link functions for transformation to parameters that are appropriate for specific likelihoods (e.g. binomial for seed bag experiments; Poisson for counts of seed per fruit). We note that such a linear mixed effects model with random intercepts for years is one method commonly used to model interannual variation in demographic rates (e.g. [Metcalf et al. \(2015\)](#)). Using hierarchical centering, the same model is rewritten as

$$\theta_{jk} = \alpha_{(jk)}. \quad (3)$$

The mean  $\theta_{jk}$ , is now drawn from a normal distribution with mean  $\alpha_{(jk)}$  and variance  $\sigma_j^2$ . We place a prior on  $\alpha_{(jk)}$  such that  $\alpha_{(jk)} \sim N(\theta_{0,k}, \varsigma^2)$ . The expressions are related by  $\alpha_{(jk)} = \theta_{0,k} + \epsilon_{(jk)}$ . We thus draw year-level means from the population-level means.

For a single population (ie. suppressing subscript  $k$ ), we write the the posterior proportional to the joint distribution as

$$[\theta_j, \theta_0, \sigma_j^2, \varsigma^2 | y_{ij}] \propto [y_{ij} | \theta_j, \sigma_j^2] [\theta_j | \theta_0, \varsigma^2] [\theta_0] [\sigma_j^2] [\varsigma^2]. \quad (4)$$

The distribution of the observations  $y_{ij}$  is conditional on the year-specific parameters  $\theta_j$  and  $\sigma_j^2$ . In turn, the year-specific parameter  $\theta_j$  is conditional on the population-specific parameters  $\theta_0$  and  $\varsigma^2$ . We placed priors on all parameters found only on the right hand side of conditional statements  $(\theta_0, \sigma_j^2, \varsigma^2)$ . In practice, we implemented this model by specifying the population- and year-levels of the model with normal distributions; for example,  $[\theta_j | \theta_0, \varsigma^2]$  is  $\theta_j \sim N(\theta_0, \varsigma^2)$ . The model thus describes a structure in which years are nested within populations.

## 2.4 Model statements, implementation, and fitting

We include the expression for the posterior proportional to the joint distribution, and corresponding directed acyclic graphs, in [Appendix: Joint Posterior](#). Priors for all parameters are defined in [Table: Priors](#). We applied the following principles to specify priors: (1) we used weakly informative priors that avoided placing probability mass on biologically implausible values ([Gelman Lemoine \(2019\)](#); [Wesner and Pomeranz \(2020\)](#)), (2) we placed positive, unbounded priors on variance components ([REF](#)), (3) we conducted prior predictive checks to assess the scale of priors after parameter transformation ([Gabry et al. \(2019\)](#); [Hobbs and Hooten \(2015\)](#); [Wesner and Pomeranz \(2020\)](#)), and (4) we simulated prior predictive distributions to confirm that the joint likelihood generated data within the observed range ([Conn et al. \(2018\)](#); [Gabry et al. \(2019\)](#); [Hobbs and Hooten \(2015\)](#)). We provide additional detail regarding our choice of priors in [Appendix: Priors](#).

We prepared data for analysis using the tidyverse and tidybayes packages ([CITE](#)) in R ([VERSION; CITE](#)). We wrote, fit all models, and estimated posterior distributions using JAGS 4.3.0 with rjags ([Plummer 2016](#)). We randomly generated initial conditions for all parameters with a prior by drawing from the corresponding probability distribution in R before passing the initial values to rjags. We ran three chains for 45,000 iterations. The first

10,000 iterations were for adaptation, the next 15,000 iterations were discarded as burn-in, and we sampled the following 15,000 iterations. To improve computational efficiency, we thinned the chains by keeping every 10th iteration.

We assessed convergence of the MCMC samples with visual inspection of trace plots, by calculating the Brooks-Gelman-Rubin diagnostic (R-hat), and by calculating the Heidelberg-Welch diagnostic (Elder and Miller (2015)). The Gelman-Rubin diagnostic is used to assess convergence between chains and the Heidelberg-Welch for stationarity within chains. We show trace plots for all chains, histograms of R-hat, and the percentage of chains that passed the HW in the appendix.

To evaluate the fit of our models to the data, we performed model checks that are described in full in [Appendix: Model Checking](#). We used the posterior distribution to simulate replicate datasets based on the parameters of our model. We compared samples from the simulated datasets to the real, observed datasets using both graphical, visual checks and by calculating Bayesian  $p$ -values for test statistics calculated for the observed and simulated data. In the following section, we describe how we used the models we fit to obtain the parameters that describe the *Clarkia* life history. While we do not perform model checks for these derived quantities (e.g. winter seed survival accounting for the combined effect of seed decay and loss of viability) because we combine the output of multiple models, the model checks are still essential to determine whether our inferences are reasonable.

## 2.5 Computing vital rates

### 2.5.1 Belowground vital rates

We used the germination probabilities, survival function, and viability estimates to account for viability in estimates for the probability of germination and survival. We first discretized the survival function to times at which we observed germination and counted seeds (January

and October). Estimates of survival over these intervals are the probability that a seed remains intact, but does not account for loss of viability. Next, we used viability estimates from October to calculate viability for January by interpolation (Figure 2D). We tested the viability of seeds in October, and were thus able to estimate the proportion of viable seeds (Figure 2B; filled points). We inferred the viability of intact seeds in January by assuming that seeds lost viability at a constant rate (exponential decay). Further, we interpolated between estimates by assuming that viability changed at a constant rate between years, and that all seeds were viable at the start of the experiment (Figure 2B; open points).

We combined the discretized survival function and viability estimates to construct a survival function for the probability that a seed remains intact and viable (Table 2). Specifically, we multiplied the posteriors of the discretized survival and viability estimates. Because we combined estimates, some portions of the posterior for seed survival probability was than 1, especially for later seed ages. We restricted the posterior to be less than 1 by truncating the distribution and resampling to redistribute the probability mass. We take this step to retain parameter uncertainty about survival probability in cases where combining the estimates implies a high probability of survival. The survival function for viable seeds ( $\phi$ ) is composed of estimates of seeds remaining intact over time ( $\theta$ ), estimates of viability ( $\nu$ ), and estimates of germination conditional on being intact ( $\gamma$ ).

We used the discretized survival function and germination probability to obtain the estimates of germination and seed survival required to test predictions from bet-hedging theory. Table 2 defines the seed-related rates in equation 1 in terms of the survival function and germination probabilities. Figure 2E-F illustrate the relationship among the various probabilities of germination and seed survival. Estimates from the seed bag experiment correspond to the probability of germination or survival conditional on being intact (e.g.  $\gamma_1$ ). Multiplying these estimates by the probability of being intact up to a certain time gives the unconditional probability (e.g.  $\theta_1 \times \gamma_1$ ). Finally, the probability conditional on being

intact and viable is estimated by incorporating loss of viability into the survival function  
(e.g.  $\gamma_1/\phi_1$ ), and defines the parameters in the structured population model.

Table 2: Seed persistence and viability in the soil seed bank

	Intact	Intact & viable
Time ( $x_i$ )	$S(x_i)$	$S(x_i)$
Oct <sub>0</sub>	$\theta_0$	$\phi_0 = \theta_0$
Jan <sub>1,total</sub>	$\theta_1$	$\phi_1 = \theta_1(\gamma_1 + (1 - \gamma_1)\nu_1^{1/3})$
Jan <sub>1,intact</sub>	$\theta_2$	$\phi_2 = \theta_2\nu_1^{1/3}$
Oct <sub>1</sub>	$\theta_3$	$\phi_3 = \theta_3\nu_1$
Jan <sub>2,total</sub>	$\theta_4$	$\phi_4 = \theta_4(\gamma_2 + (1 - \gamma_2)\nu_1(\nu_2/\nu_1)^{1/3})$
Description	Parameter	Probability
July-October	$s_0$	
October-January	$s_1$	$\phi_1$
1-year old germination	$g_1$	$\gamma_1/\phi_1$
January-October	$s_2$	$\phi_3/\phi_2$
October-January	$s_3$	$\phi_4/\phi_3$

### 2.5.2 Per-capita reproductive success

We calculate per-capita reproductive success as the number of seeds produced per seedling,  
on average (as in Gremer and Venable (2014); Venable (2007)), and is thus the product of the  
probability of seedling survival to fruiting, fruits per plant, and seeds per fruit. In terms of  
parameters from our statistical models (Appendix: Joint Posteriors), per-capita reproductive  
success  $Y_j(k)$  at population  $j$  in year  $k$  is calculated as

$$Y_j(k) = \phi_{jk} \times \lambda_{\text{TFE},jk} \times \lambda_{\text{US},jk}, \quad (5)$$

where

$$\phi_{jk} = \text{logit}^{-1}(\mu_{S,jk})$$

$$\lambda_{\text{TFE},jk} = \exp(\mu_{\text{TFE},jk}) \quad (6)$$

$$\lambda_{\text{US},jk} = \exp(\mu_{\text{US},jk}).$$

280 We used a consistent method to estimate seedling survival to fruiting throughout the  
 281 experiment, and use the population- and year-level estimates ( $\mu_{S,jk}$ ) in our calculation. Be-  
 282 cause we estimated fruit production in 2 different ways during the study, we chose to use  
 283 total fruit equivalents (TFE) per plant as our common estimate of fruit production. From  
 284 2006–2012, we used  $\mu_{\text{TFE},jk}$ ) as estimated in the statistical model. From 2013–2020, we used  
 285 the ratio of seeds per damaged to undamaged fruit to calculate a proportion of damaged  
 286 fruits to add to undamaged fruit counts, as in

$$\text{TFE} = \text{undamaged fruits} + \frac{\text{seeds per damaged fruit}}{\text{seeds per undamaged fruit}} \times \text{damaged fruits.} \quad (7)$$

287 We used posterior distributions for population- and year-level parameters (e.g.  $\mu_{\text{US},jk}$ )  
 288 for these calculations and obtained estimates of  $\mu_{\text{TFE},jk}$ ) for 2013–2020. Finally, we used  
 289 estimates of seeds per undamaged fruit ( $\mu_{\text{US},jk}$ ) as our estimate of seeds per fruit.

290 Our multilevel models for aboveground vital rates pooled data more strongly in years with  
 291 relatively little data. A benefit of this approach is that it implicitly corrects for variation  
 292 in sample size. While this is beneficial for distinguishing between spurious estimates and  
 293 true temporal variation, it may also underestimate variation in reproductive success. At  
 294 the extreme, estimates in years without any data are pooled to the population-level means.  
 295 Years with zero seedling survivorship would have estimates for fruits per plant that are pooled  
 296 towards the population-mean (because there were no fruiting plants on which to count fruits).

Our estimates of per-capita reproductive success are thus likely to be conservative.

Because estimates of fruits per plant are based on surveys of the whole population, we are relatively confident that per-capita reproductive success is 0 in years in which we observed no fruits per plant and obtained no counts of seeds per fruit (orange Xs in Figure 1D). We thus considered a second, less conservative estimate in which we assumed those years to have per-capita reproductive success of 0. We did this after parameter estimation, before estimating the correlation between germination and per-capita reproductive success. Finally, we also considered modeling components of per-capita reproductive success without partial pooling, but as this did not change our conclusions (to include in the appendix?) we only report the results of the models based on partial pooling in the main text.

## 2.6 Climate data

A weather station network was established as part of the long-term study of *C. xantiana* demography (described in Eckhart et al. (2011)). The network consists of 21 data loggers (Onset Computer Corporation) that recorded temperature and precipitation starting in October 2005; between 8 and 18 weather stations were actively recording throughout the study. Data from the network was used to spatially interpolate precipitation accumulation on a 1 hectare grid throughout the study area and estimate seasonal, cumulative precipitation at the study populations. Additionally, seasonal temperatures in each year were estimated using linear models with elevation, potential estimated solar radiation, and linear azimuth as covariates; year was a categorical covariate. Coefficients of the linear model were subsequently used to project temperature across the landscape. Mean temperature and cumulative precipitation for November-January (winter) and February-June (spring) are summarized in Figure S#.



## 2.7 Analysis

### 2.7.1 Correlation between germination probability and seed survival

Increased seed survivorship is predicted to decrease the optimal germination probability (Cohen (1966); Ellner (1985a)). I tested whether the observed germination probability was negatively correlated with seed survival (Gremer and Venable (2014)). I calculated the probability that seeds which do not germinate in January remain in the seed bank until the following January ( $s_2s_3$ ). I obtained the posterior distribution for the correlation between germination and seed survival by calculating the correlation of  $g_1$  and  $s_2s_3$  at each iteration of the MCMC output (Hobbs and Hooten (2015), p 194-5). Results of this analysis are shown in Figure 3. Bet hedging models predict that germination probability should be negatively correlated with seed survival; 95% credible intervals that do not overlap zero provide support for this prediction. The bottom panel shows the posterior distribution of correlation between the probability of germination and seed survival.

### 2.7.2 Correlation between germination probability and variance in per-capita reproductive success

Increased variance in per-capita reproductive success is predicted to decrease the optimal germination probability (Cohen (1966); Ellner (1985a)). I assessed whether the observed germination probability was negatively correlated with variance in per-capita reproductive success (Venable (2007)).

To calculate the temporal variation in per-capita reproductive success for each population, I sampled the posterior distribution of reproductive success for each year and calculated the geometric standard deviation of per capita reproductive success. The geometric SD of per capita reproductive success was calculated as  $\exp(\text{SD}(\log(\text{per capita reproductive success} + 0.5)))$  (as in Venable (2007)). I obtained the sample correlation of germination

and geometric SD of per capita reproductive success at each iteration of the MCMC output (Hobbs and Hooten (2015), p 194-5). Bet hedging models predict that germination probability should be negatively correlated with temporal variance in fitness; 95% credible intervals that do not overlap zero provide support for this prediction. Results of this analysis are shown in Figures 4.

### 2.7.3 Density-independent model for germination probability

We use estimates of seed survival and reproductive success to investigate the adaptive value of delayed germination (Gremer and Venable (2014)). We parameterize a model of population growth rate (equation 1) and calculate the optimal germination strategy for different combinations of seed survival and reproductive success. Seed survival rates ( $s_0, s_1, s_2, s_3$ ) are population-level estimates. Per capita reproductive success ( $Y(t)$ ) is calculated as the product of seedling survival to fruiting, fruits per plant, and seeds per fruit (equation (5)). Temporal variation is incorporated into the model by varying the per-capita reproductive success,  $Y(t)$ , between years.

For each population, I numerically calculate the optimal germination probability for the observed variation in reproductive success and seed survival. In each case, I use the posterior mode of the parameter estimates in the equation for density-independent growth (equation (1)). I resampled the posterior modes of per-capita reproductive success ( $Y(t)$ ) to obtain a sequence of 1000 years. I used this same sequence of  $Y(t)$  and the seed survival probabilities to calculate long-term stochastic population growth rates ( $\lambda_s$ ) at each germination probability along an evenly spaced grid of possible germination probabilities ( $G$ ) between 0 and 1. The optimal germination probability is estimated as the value of  $G$  that maximizes the geometric mean of the population growth rate. I repeat the simulations 50 times for each population, resampling the sequence of per-capita reproductive success,  $Y(t)$ , each time. I then calculated the mean of the optimal germination fractions.

Models in which per-capita reproductive success is density-independent predict that germination probability should respond to variance in fitness (Cohen (1966)). To evaluate the density-independent model, I compared modeled germination probabilities to predicted germination optima. I plot this comparison in Figure 4 and 5. The dotted line indicates a 1:1 relationship between observations and predictions. Values below the line indicate that the model predicts higher germination probabilities than observed; values above the line would indicate that the model predicts lower germination probabilities than observed.

#### 2.7.4 Relationship of reproductive success and growing season precipitation

When we did not observe a negative correlation between germination and the geometric standard deviation of per-capita reproductive success (see Results), we examined one of our assumptions about the relationship between precipitation and fitness. Specifically, we examined the sensitivity of reproductive success to growing season precipitation. We conducted a linear regression of the log of per-capita reproductive success on the log of growing season precipitation (Venable (2007)). For this exploratory analysis, we used the posterior mode as our point estimate per-capita reproductive success (as in the density-independent simulation). We applied a Bonferroni correction and assessed significance of our regressions at a confidence level of  $p = 0.05/20 = 0.0025$ .

#### 2.7.5 Partitioning contributions to the total geometric standard deviation of reproductive success

We also conducted an exploratory analysis to understand how each fitness component contributed to the total variance in reproductive success. By identifying how components contribute to the total variance, we expect to guide additional hypotheses about the observed life history patterns. The log of the geometric variance of a quantity is the arithmetic variance of the log (Kirkwood 1979, deCarvalho 2016). By the properties of logarithms this is

the arithmetic variance of the sum of the logs. We can then expand the expression to:

$$\text{geometric var(per capita RS)} = e^{\text{Var}(\ln \sigma)} e^{\text{Var}(\ln F)} e^{\text{Var}(\ln \phi)} (e^{\text{Cov}(\ln \sigma, \ln F)})^2 (e^{\text{Cov}(\ln \sigma, \ln \phi)})^2 (e^{\text{Cov}(\ln F, \ln \phi)})^2 \quad (8)$$

We use the median of annual estimates for seedling survival to fruiting, fruits per plant, seeds per fruit, and reproductive success. Interpretation of the variance decomposition is different than for an arithmetic variance. First, the variance has a minimum value of 1; this corresponds to an arithmetic variance of 0. Second, covariances have a minimum of 0; Values of 1 for the covariance indicate a lack of covariation; values less than 1 indicate negative covariation; values greater than one indicate positive covariation. Here, we focus on presenting the variances.

## Results

### Correlation between germination probability and seed survival

We did not observe a correlation between population-level germination and seed survival in the seed bank (Fig. 3A). The 95% credible interval for the posterior distribution of the correlation between probabilities of germination and seed survival overlaps 0 (Fig. 3B).

### Correlation between germination probability and variance in per-capita reproductive success

We examined the correlation between germination and variance in per-capita reproductive success (Figure 4 and 5). The bottom left panel shows the posterior distribution of correlation between modeled germination probability and geometric SD in per-capita reproductive

success. Setting years without any observed plants to have a fitness of zero increases the range of the geometric standard deviation in reproductive success (compare panels A in Figure 4 and 5). However, for both calculations of per capita reproductive success, the median correlation is slightly positive and the 95% credible interval overlaps 0.

### **Optimal germination probability predicted by a density-independent model**

Optimal germination probabilities were less than 1 in all populations when we assumed that years without plants had zero fitness, but not when we used the partially pooled estimates of per-capita reproductive success (Figure 4 and 5). In both cases, predictions from the density-independent model overestimated the probability of germination (points fall below the 1:1 line).

### **Environment and life history**

The lack of correlation between germination and variance in reproductive success suggests that populations may not share the same relationship to environmental variability. We found that populations vary in how sensitive per capita reproductive success is to growing season precipitation. While growing season precipitation alone does not explain variation in reproductive success at any population, the slope of the relationship varied from 0-3.3 indicating that sensitivity to rainfall varies among populations.

### **Variance decomposition**

The geometric variance in seedling survival to fruiting tends to make the greatest contribution to total variance. Fruits per plant and seeds per fruit have, on average, much smaller variances. Populations also vary in how the variance is distributed among components of reproductive success. Variance in seedling survival to fruiting dominates the other components at roughly half the sites, while the other half of sites have a more even distribution

(e.g. compare SM and CP3). High variance in seedling survival to fruiting is likely the result of some populations experiencing very low survivorship in some years.

## Discussion

Note: the discussion is an outline at this point. I've thought about some of the points that I would like to make here but have not written it out completely.

**Summarize results.** (1) We use field experiments, 15 years of observation on reproductive success, and models to examine life history patterns. (2) We test multiple predictions of density-independent models of bet hedging and do not find support for these predictions. Neither correlations within seed rates, or among germination and variance in reproductive success are in line with predictions.

**Place study in context of other tests of bet hedging** (1) Tests of bet hedging theory that use estimates of fitness rather than proxies remain relatively uncommon ([Simons \(2011\)](#)). Good intraspecific examples but lack interspecific cases. (2) Intraspecific studies take various experimental approaches but it may be important to understand the fitness consequences in the field in order to understand relative importance of bet hedging.

**Revisit how bet hedging, predictive germination, environmentally determined germination interact** (1) Seed banks are not only shaped by bet hedging but by interaction of factors. (2) Variation in sensitivity of reproductive success to precipitation across the range supports that populations are responding to different selective pressures across distribution. (3) Emphasize value of taking an approach that focuses on geometric mean fitness in order to understand relative contribution.

**Explanation of result of much higher germination than predicted under bet hedging.** Possible explanations: (1) Environmental pattern and timing of rainfall/temperature might mean that eastern populations experience higher soil moisture. (2) Correlation between

plant size and dormancy/germination in first year. Seeds produced on larger plants are smaller and may thus exhibit higher dormancy. Plant fruit number generally declines from west to east, which may lead to plants with lower germination in the west vs. the east, all else being equal. (3) Density-dependence; density-dependent models of bet hedging predict lower germination fractions than density-independent models. In this case the problem is no longer one of optimization but of finding an ESS strategy.

**Assumption of unstructured seed bank.** (1) Describe assumptions of bet hedging models and how this means that the seed bank in models is unstructured. (2) Discuss studies that have looked at structured seed bank (Philippi (1993b)). (3) What are the prospects/challenges for including structure in seed bank? E.g. More limited data.

**Revisit theory to discuss role of complete reproductive failure vs. low fitness years more generally, discuss sampling** Cohen (1966) emphasizes the role of particularly bad years. This is highlighted by the inequality in equation (12), which states that for the optimal germination strategy to be bet hedging, it is sufficient that the harmonic mean is less than the survival probability of seeds that do not germinate. Minimum fitness thus has a strong impact on harmonic mean of fitness. This means that sampling variation is important to consider because it might be important if estimates of zero fitness are the result of sampling vs. true zeros. Also emphasizes the importance of long time scales of sampling; fifteen years is already long but may not be enough to capture the lows in all populations.

## Figures



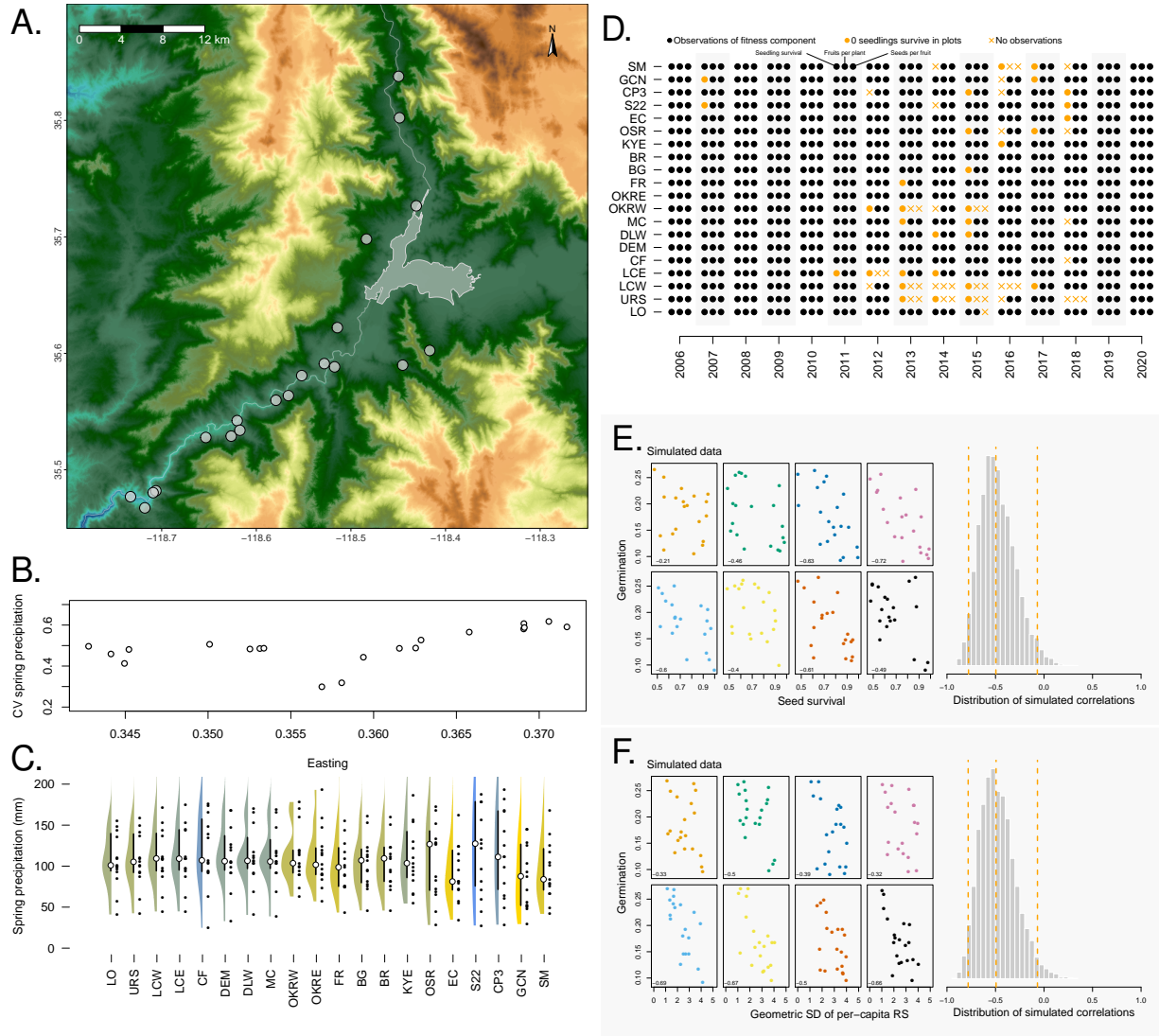


Figure 1: (A) Elevation map of populations. (B) Coefficient of variation of 15 years of spring (February–June) precipitation plotted against easting. (C) Summary of 15 years of spring precipitation for study populations; study populations are arranged by position on easting. Density plots summarize the distribution of estimates, which are also represented by a point and line showing the median and interquartile range. Fifteen years of estimates are plotted to the left of the summaries. (D) Graphical summary of fifteen years of aboveground observations at study populations. Orange circles indicate that no seedlings survived in permanent plots; orange Xs indicate that no seedlings or plants were observed in surveys. (E) Simulations for a negative correlation between germination and seed survival. A copula was used to simulate a negative correlation among 20 populations using the range of values reported in [Eckhart et al. \(2011\)](#). Plots show 8 replicate simulations; the histogram summarizes 100,000 replicates and shows the range of data consistent with a negative correlation of -0.5. (F) Simulations for a negative correlation between germination and variance in reproductive success. The range of values for geometric SD of reproductive success was determined by the average reproductive success of populations in [Eckhart et al. \(2011\)](#) and probability of a year with zero fitness (panel D). Plots show 8 replicate simulations; the histogram summarizes 100,000 replicates and shows the range of data consistent with a negative correlation of -0.5.

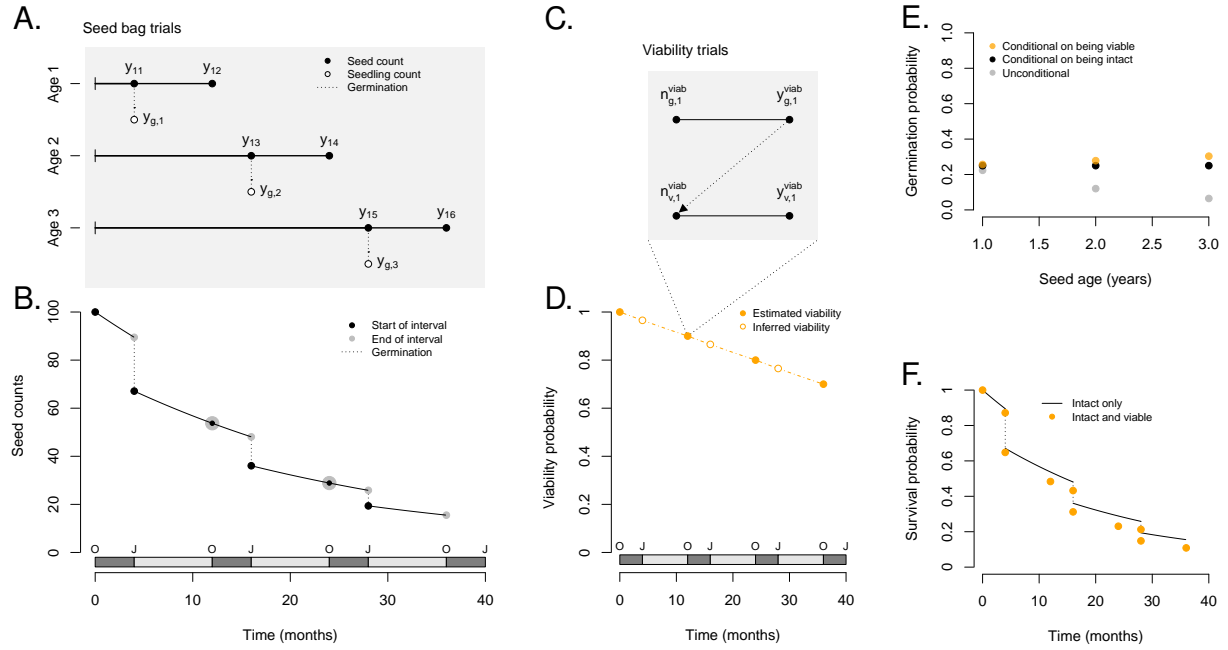


Figure 2: Summary of the seed bag burial experiments and viability trials. (A) A graphical representation of the seed bag trials. Seeds were buried at the start of each experiment (100 seeds in month 0). Seed bags were unearthed and intact seeds ( $y_{\cdot}$ ) and seedlings ( $y_{g,\cdot}$ ) counted. (B) A hypothetical survival function associated with seeds remaining intact in the soil seed bank. (C) A graphical representation of the viability trials. Seeds were tested in two rounds; germination trials were performed and then some or all of the ungerminated seeds were tested for viability. (D) Hypothetical data from a series of viability trials and the interpolated, inferred viabilities at times when viability was unobserved. (E) Germination probability is summarized in three ways. (F) The survival function for seeds remaining intact in the soil seed bank (black line) and the estimated discrete survival probabilities for intact and viable of seeds (orange points).

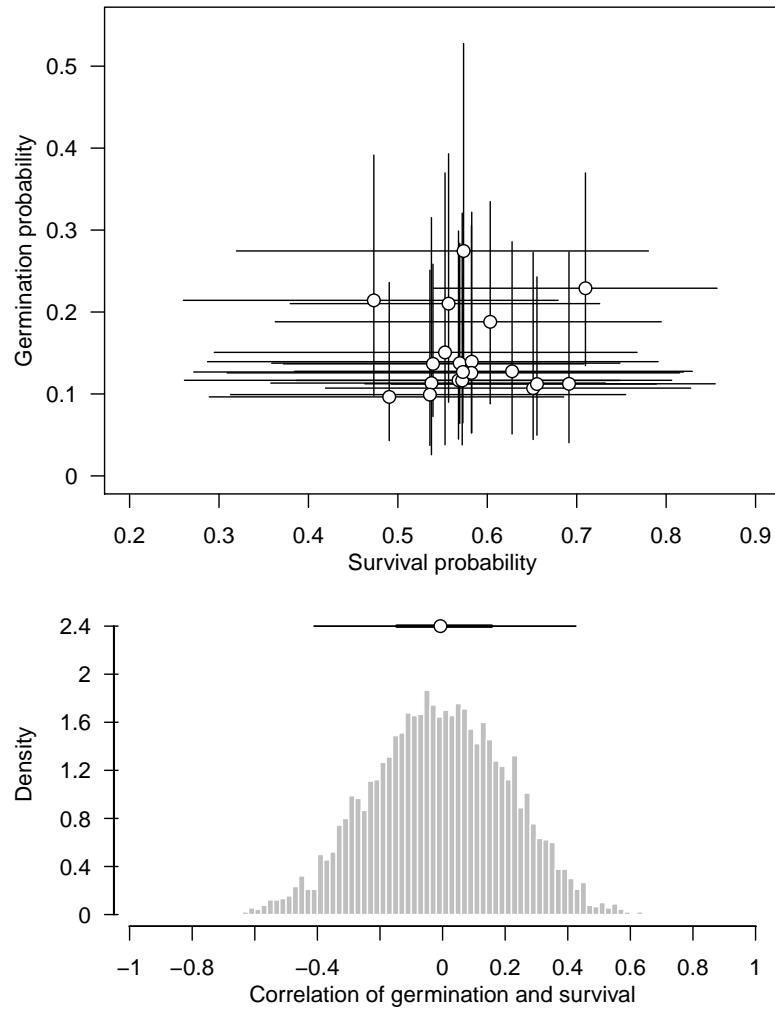


Figure 3: (A) The observed germination probability plotted against probability of seed survival. (B) The posterior distribution of correlation between observed germination probability and the probability of seed survival.

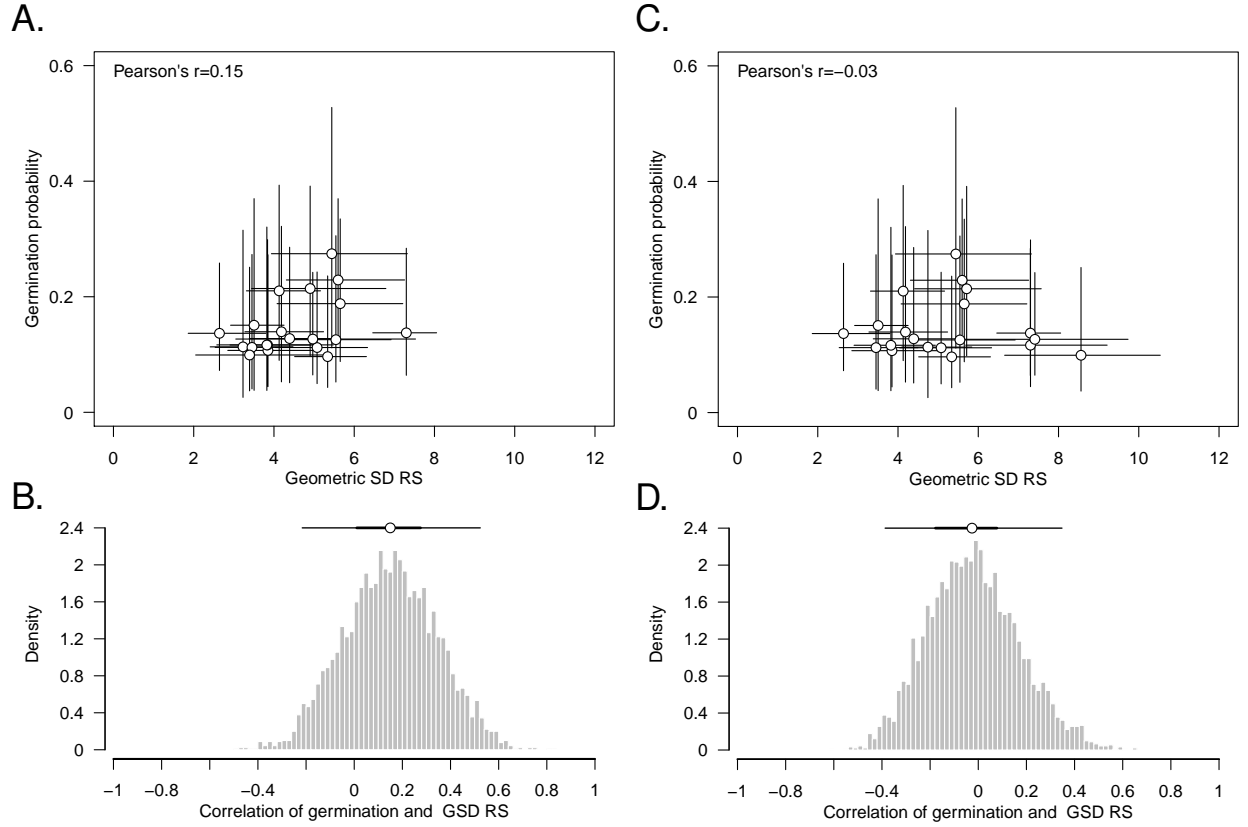


Figure 4: *Left column:* Correlation between germination and variance in reproductive success when reproductive success is calculated with partial pooling. (A) Observed germination probability plotted against the temporal variation in per capita reproductive success, expressed as geometric standard deviation of per capita reproductive success. (B) The posterior distribution of correlation between observed germination probability and geometric SD of per capita reproductive success. *Right column:* Correlation between germination and variance in reproductive success when reproductive success is calculated with partial pooling, but years without any observed plants are assumed to have reproductive success of zero. Panels (C) and (D) plot the same relationships as in (A) and (B), respectively.

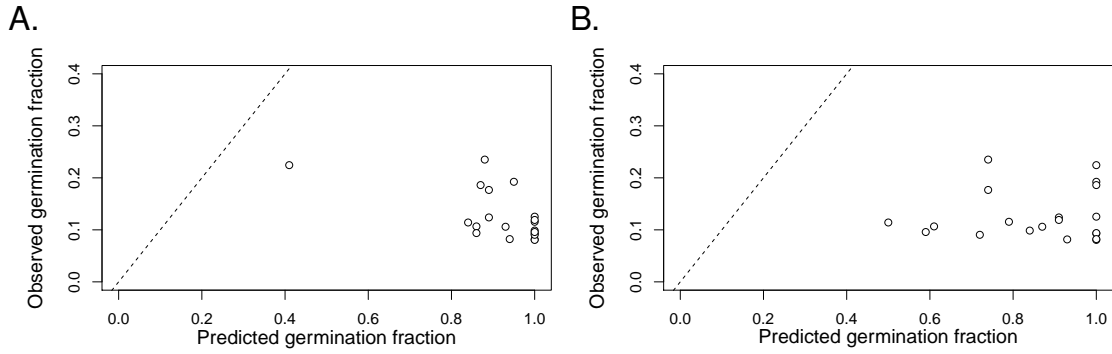


Figure 5: Comparison of observed and optimal germination probabilities from a density-independent model of bet hedging. (A) Observed vs. predicted probabilities for reproductive success estimated from models with partial pooling. (B) Observed vs. predicted probabilities for reproductive success estimated from models with partial pooling and fitness set to 0 in years without observations. For each population, the observed germination probability is the obtained from the model for seed bank vital rates. Each point is the population-specific median of the posterior of  $g_1$  for a model fit to data from seed bag experiments from 2006–2009. Data was pooled across years. The dotted line indicates a 1:1 relationship between observations and predictions. Values below the line indicate that the model predicts higher germination probabilities than observed; values above the line would indicate that the model predicts lower germination probabilities than observed.

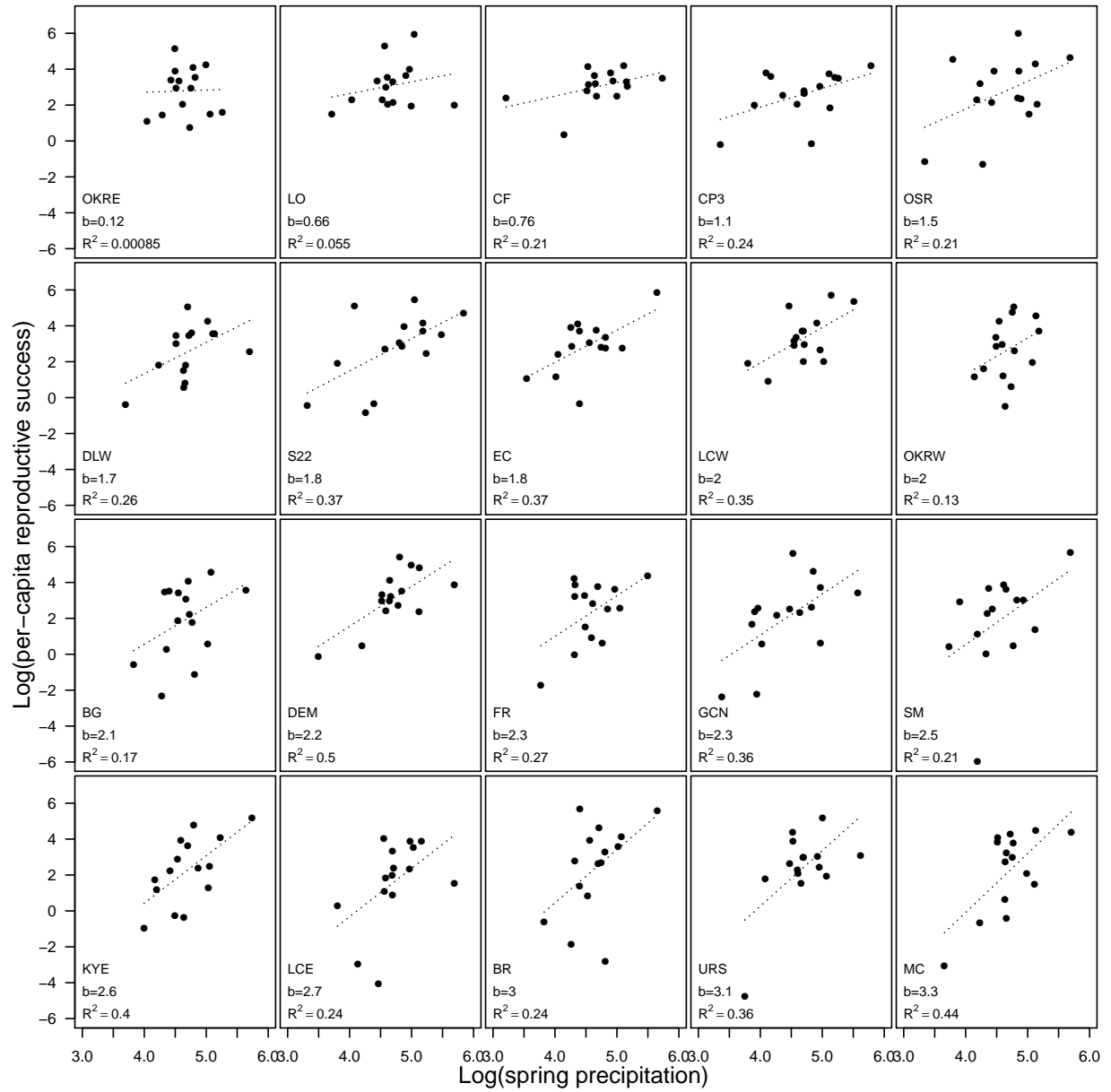


Figure 6: Log of per-capita reproductive success plotted against log of cumulative growing season (spring) precipitation. Plots are arrayed by the slope of a linear regression of per-capita reproductive success on precipitation.

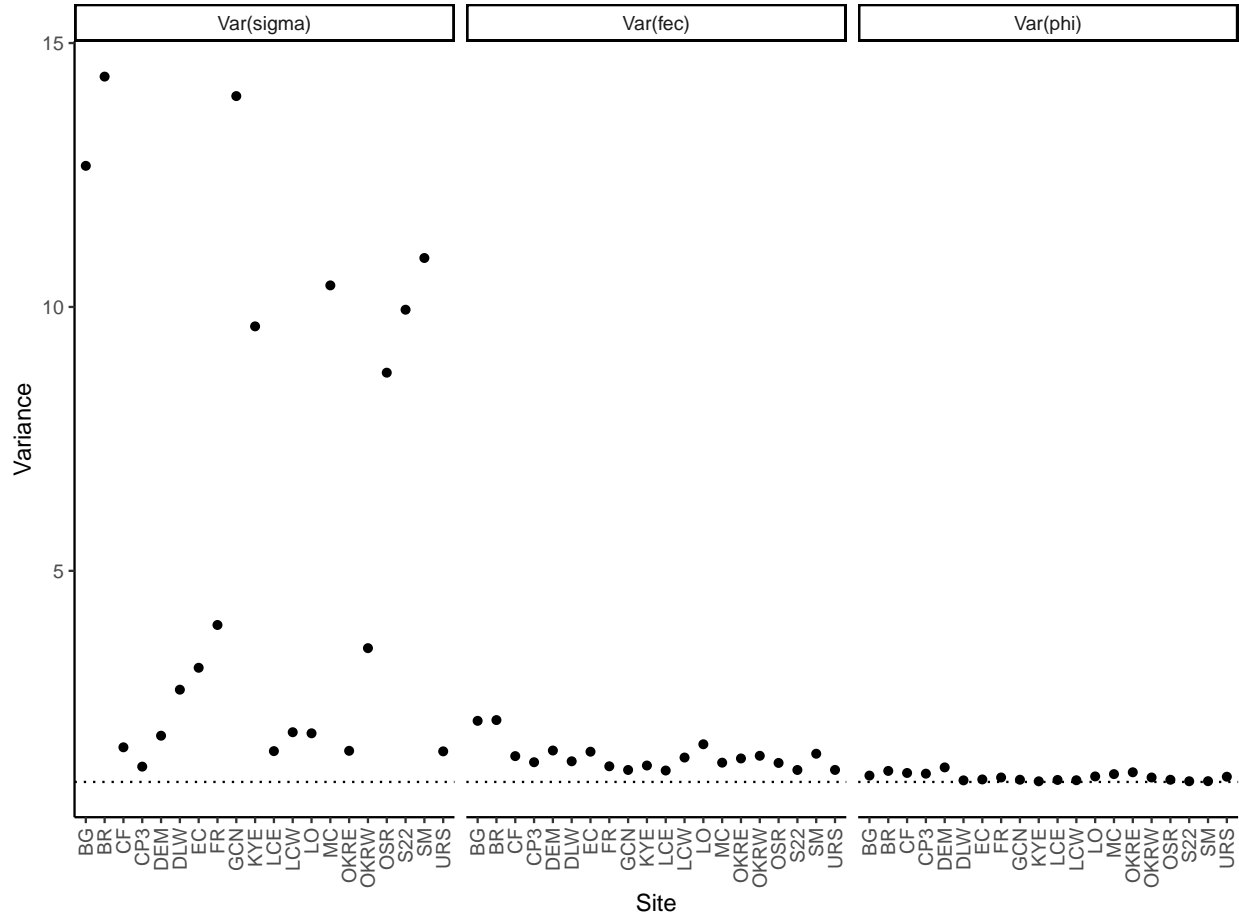


Figure 7: Variance decomposition for geometric standard deviation of per-capita reproductive success. Per-capita reproductive success and its components (seedling survivorship, fruits per plant, seeds per fruit) were summarized by their medians, and decomposed to assess the relative contribution of variance in each component to total geometric variance. The dotted line corresponds to  $\exp(0) = 1$ , the level at which the component makes no contribution to total geometric variance.

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# Supplementary material

## Data summary.

556 Summary tables for all datasets used in the manuscript. The document summarizes the types  
557 of data collected. The document provides a table summarizing each dataset (e.g. sample  
558 size per each site and year). Link to document: [https://github.com/gregor-fausto/  
559 clarkiaSeedBanks/blob/master/products/tables/data-summary.pdf](https://github.com/gregor-fausto/clarkiaSeedBanks/blob/master/products/tables/data-summary.pdf)

## Joint posterior.

560 Expression for the posterior proportional to the joint distribution, and corresponding directed  
561 acyclic graphs. Link to document: [https://github.com/gregor-fausto/clarkiaSeedBanks/  
562 blob/master/products/appendices/appendix-joint-posteriors/appendix-joint-posteriors.  
563 pdf](https://github.com/gregor-fausto/clarkiaSeedBanks/blob/master/products/appendices/appendix-joint-posteriors/appendix-joint-posteriors.pdf)

## Priors.

564 Explanation of priors. Link to document: [https://github.com/gregor-fausto/clarkiaSeedBanks/  
565 blob/master/products/appendices/appendix-priors/appendix-priors.pdf](https://github.com/gregor-fausto/clarkiaSeedBanks/blob/master/products/appendices/appendix-priors/appendix-priors.pdf)

## Model checks.

566 Model checks, including visual posterior predictive checks and assessments with Bayesian  $p$ -  
567 values for test statistics. Link to document: [https://github.com/gregor-fausto/clarkiaSeedBanks/  
568 blob/master/products/appendices/appendix-model-checks/appendix-x-model-checks.  
569 pdf](https://github.com/gregor-fausto/clarkiaSeedBanks/blob/master/products/appendices/appendix-model-checks/appendix-x-model-checks.pdf)