Seed banks in *Clarkia xantiana*

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To Do list

1. Write paragraph about history of studies of bet hedging via seed bank, with emphasis on how this study addresses this question at an intraspecific level. Lower level of variation in intraspecific germination fraction. [INTRODUCTION]
2. Write models for belowground vital rates
3. Revise description for density-independent model for germination probability
4. Write and implement model checking process

Introduction

Seed banks can buffer plant populations against environmental change and stochasticity (**??**), increase effective population size (**??**), and maintain genetic diversity (**?**). Dormancy can affect the outcome of evolution (**??**). Theory thus suggests that seed banks have ecological and evolutionary consequences (**?**).

What drives the evolution of delayed germination? The theory developed by **?** frames the problem in the following terms. What is the optimal germination fraction for a given level of interannual variation in fitness and seed survivorship? These models make it clear that the germination fraction that maximizes long-term population growth rate is a function of the distribution of fitness (characterized by the variation in fitness), the fitness values, and the rate of seed survivorship. For a given mean fitness, increasing the variance in fitness decreases the optimal germination fraction (see: Supplementary Material: Theoretical background for hypotheses). Increasing seed survivorship decreases the optimal germination fraction, and the degree to which it does so depends on the probability of a 'good year'. Specifically, as the probability of a high-fitness year decreases, the optimal germination fraction decreases.

Population vital rates are known to vary across *Clarkia xantiana*'s geographic range. Population growth rates determine species abundance and distribution, and are ultimately what limit persistence beyond range edges. Geographic patterns to vital rates have so far been studied to help understand the demography of geography. Seed banks are a strategy that annual plants may use to buffer against environmental variation and may be part of population persistence. I will begin by characterizing geographic variation in belowground vital rates. [What is the geographic pattern to variation in germination or seed survival?] [I think this question could be expanded to make clear predictions and/or address another aspect such as variation in time.]

A previous study with *Clarkia xantiana* suggests that the soil seed bank is important for population dynamics in *Clarkia xantiana* (**?**). A separate set of seed burial experiments suggests that seeds of *C. xantiana* can remain viable in the soil for at least 10 years (Moeller personal communication). In the study of *C. xantiana* population dynamics that showed a decline of long-term stochastic population growth rate from west to east across the range, Eckhart et al. 2011 inferred a decrease in survival through winter (s1) and an increase in germination rate (g1) of first-year seeds from west to east.

Bet hedging should evolve to maximize the long-term geometric population growth rate (as compared to the arithmetic population growth rate) **????**. Seed banks are more likely to be selected in populations which experience higher levels of interannual variation in per-capita reproductive success. To investigate this empirical relationship, I will estimate the correlation between interannual variation in per-capita reproductive success and the proportion of seeds that germinate in the winter immediately following seed production. I predict that germination is negatively correlated with interannual variation in per-capita reproductive success.

Methods

Background on study system

Starting in 2006, Monica Geber and collaborators have collected 12+ years of annual estimates for demographic data on the winter annual plant *Clarkia xantiana*. The data include annual estimates for survival of seedlings to fruiting adults, fruits per adult plant, and seeds per fruit. In addition the data on above-ground vital rates, experiments have been used to infer germination and seed survival in the seed bank. The data has been used to study questions about the geography of demography (**?**) and species distributions (**?**).

Data

Seed bag burial experiments

To assess germination and seed survival throughout the year in *C. xantiana*, we use data collected from a series of seed burial experiments. In June-July 2005, we collected seeds at each of the 20 populations included in this study. In October 2005, we buried 30 5×5-cm nylon mesh bags at each population. Each nylon mesh bag contained 100 seeds collected at that population. In January 2006, we removed 10 of these bags and counted the number of germinated seedlings and the number of ungerminated, intact seeds in each bag. We then returned the ungerminated, intact seeds to the resealed bag and returned the bag to the field. In October 2006, we removed these bags and counted the number of ungerminated, intact seeds. We collected the following data:

- n_{ijt} = observed count of seeds in the seed bags at the start of the experiment in October in the i^{th} bag, from the j^{th} population, in the t^{th} year, assumed to be measured perfectly
- y_{ijt}^{intact} = observed count of ungerminated, intact seeds in the seed bags in January in the i^{th} bag, from the j^{th} population, in the t^{th} year, assumed to be measured perfectly
- y_{ijt}^{germ} = observed count of germinated seedlings in the seed bags in January in the i^{th} bag, from the j^{th} population, in the t^{th} year, assumed to be measured perfectly
- y_{ijt}^{total}= observed count of ungerminated, intact seeds plus germinated seedlings in the seed bags in January in the i^{th} bag, from the j^{th} population, in the t^{th} year, assumed to be measured perfectly
- y_{ijt}^{surv} = observed count of ungerminated, intact seeds in the seed bags in October in the i^{th} bag, from the j^{th} population, in the t^{th} year, assumed to be measured perfectly

We started these seed burial experiments in three subsequent years (2005, 2006, 2007) to obtain multiple estimates for seed survival and germination.

Viability trials

To assess what proportion of intact seeds are viable, we use data collected from viability assays conducted on seeds when they are unearthed in October. Only some proportion of the seeds that are unearthed intact in the seed burial experiments are likely to be viable–put another way, seeds that are intact may not be viable.Because seeds unearthed in January are reburied, we do not have direct estimates of viability in January.

Each year that we conducted seed burial experiments, we also conducted seed viability trials. After bags were removed from the field in October, we returned the bags to the lab. In the lab, we conducted germination trials and viability assays on subsets of the seeds from each bag to estimate the viability of the ungerminated, intact seeds. First, we placed up to 15 seeds from each bag on to moist filter paper in a disposable cup and observed germination over 10 days; we counted and removed germinants every 2 days.

After 10 days, all remaining ungerminated seeds (up to a total of 10 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. [**?**: not all ungerminated seeds were tested; most were] 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.

We collected the following data:

- n_{ijt}^{germ} = observed count of seeds at the start of the X^th germination trial for the i^{th} bag, from the j^{th} population, in the t^{th} year, assumed to be measured perfectly

- y_{ijt}^{germ} = observed count of germinated seedlings in the X^th germination trial for the i^{th}

bag, from the j^{th} population, in the t^{th} year, assumed to be measured perfectly

- n_{ijt}^{viab} = observed count of seeds at the start of the X^th viability trial for the i^{th} bag, from the j^{th} population, in the t^{th} year, assumed to be measured perfectly

- y_{ijt}^{viab} = observed count of viable seedlings in the X^th viability trial for the i^{th} bag, from the j^{th} population, in the t^{th} year, assumed to be measured perfectly

Seedling survival to fruiting

To assess the survival of germinants to fruiting plants for *C. xantiana*, we use data of counts of seedlings and fruiting plants in 30 0.5 m^2 plots at 20 populations from 2006–present (**?**). Each population was visited in February and June to count the number of seedlings and fruiting plants, respectively. Seedlings and fruiting plants in each plot are counted by a single person at each visit.

For now, we assume that the data on seedlings is measured perfectly (i.e. we did not under- or over-count seedlings). However, there are at least two possible sources of error: (1) measurement error that arises because we failed to count seedlings that were present and (2) error that arises because seedlings germinated after we visited the population. Germination phenology varies from year to year and by geography. In particular, populations at higher elevations may have delayed phenology. We may want to develop a model that relates our estimate of seedlings to the true number of seedlings in a plot because we sometimes observe more fruiting plants than seedlings. For now, I ignored data that involved undercounting by filtering out those rows in the dataset. I had trouble developing a model for undercounting.

We assume that the data on fruiting plants is measured perfectly (i.e. we did not under- or over- count) because plants stand out from the background vegetation in June. Our model estimates the proportion of seedlings that survive to become fruiting plants. Define:

- n_{ijk} = observed counts of seedlings in the i^{th} plot, from the j^{th} population, from the k^{th} year

- y_{ijk} = observed counts of fruiting plants in the i^{th} plot, from the j^{th} population, from the k^{th} year, assumed to be measured perfectly

Fruits per plant

To assess the number of fruits per plant for *C. xantiana*, we use data on counts of the number of fruits per plant at 20 populations (**?**). At each population, we made two sets of counts. First, we counted the number of fruits per plant on all plants in the 0.5m^2 permanent plots. Second, we counted the number of fruits per plant on plants that we sampled haphazardly across the site using throws of a 0.5m^2 grid.

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 these counts to estimate the number fruits produced per plant.

From 2013–present, we counted the number of undamaged and damaged fruits on a plant plant. We used these counts to estimate the number of fruits produced per plant.

We seek to estimate the number of fruits produced per plant. Define:

- y^{TFE}_{ijk} = observed counts of total fruit equivalents per plant on the i^{th} plant, from the j^{th} population, from the k^{th} year, assumed to be measured perfectly

- n_{ijk} = observed counts of total fruits per plant (sum of $\boldsymbol{y_{ijk}}$) on the i^{th} plant, from the j^{th} population, from the k^{th} year, assumed to be measured perfectly

Seeds per fruit

To assess the number of seeds per fruit for *C. xantiana*, we use data on counts of the seeds per fruit of fruits that were haphazardly collected in 20 populations (?). In the field, we collected fruits that were undamaged. In the lab, we broke open the fruits to count the number of seeds per fruit. For each population in each year, we attempted to obtain 20-30 counts of seeds produced per undamaged fruit.

From 2006–2012, we collected one undamaged fruit from each of 20-30 plants that were haphazardly collected across each population.

From 2013–present, we collected one undamaged and one damaged fruit from each of 20-30 haphazardly selected plants distributed across each population. The plants were outside permanent plots to avoid affecting seed input. We used these fruits to estimate the mean number of seeds produced by undamaged and damaged fruits. In the lab, we broke open the fruits to count the number of seeds per fruit. For each population in each year, we attempted to obtain 20-30 counts of seeds produced per undamaged fruit and 20-30 counts of seeds produced per damaged fruit.

We seek to estimate the number of seeds per undamaged fruit. Define:

- y_{ijk}^{und} = observed counts of seeds in the i^{th} undamaged fruit, from the j^{th} population, from the k^{th} year, assumed to be measured perfectly
- λ_{jk} = true, unobserved mean number of seeds per undamaged fruit from the j^{th} population, from the k^{th} year

Model framework

We use observational and experimental data from 20 populations of *Clarkia xantiana* to estimate transition probabilities across the life cycle. We obtain population-specific estimates for belowground vital rates, and obtain year- and population-specific estimates for aboveground vital rates. We use these parameter estimates to analyze correlations between germination probability and variance in per-capita reproductive success, correlation between germination probability and seed survival, and to compare the observed germination fraction to the optimal germination fraction from a density-independent model.

Parameter estimates for belowground transitions

To estimate population-specific estimates for belowground vital rates, I use data from seed burial experiments in the field and seed viability trials in the lab. I combine these data to infer germination and seed survival. Briefly, I estimate probabilities of success using data from seed burial experiments and viability trials $(\theta_1, \theta_2, \theta_3, \theta_4, \theta_5, \theta_g, \theta_v)$. I use these probabilities to compose transition probabilities that correspond to the life history of *Clarkia xantiana*(s_1, s_2, s_3, g_1). I describe this approach in detail in the **Appendix on Conditional Probability**. Figure 2 illustrates the relationship between the data and the estimated probability of success.

The probability that seeds from the start of the experiment remain intact in January is represented as θ_1. In January, all seeds are intact (this includes viable and non-viable seeds). I estimate the probability of a seedling emerging, conditional on being intact as θ_2. I assume that there is no decay or loss of viability during germination. The number of intact seeds before germination is equal to the sum of the number of seeds and seedlings after germination. At this point, seeds transition into one of four possible states. Intact and viable seeds may have (1) germinated or (2) not germinated and remained dormant. All (3) other intact seeds are non-viable because (4) seeds that were not viable could not have germinated. Finally, we represent the probability of a seed being intact in October, conditional on being intact in January as θ_3.

We use the viability trials to estimate the probability of viability (ν_1) for a seed that is intact in October one year after the seed bags were buried. The viability trials are a two-stage process: seeds are subject to germination trials before a fraction of the remaining, ungerminated seeds are tested for viability. The probability that a seed germinates in the germination trial is θ_g and the probability that it is viable, conditional on not germinating in the germination trial, is θ_v. I estimate the overall probability of viability, ν, as $\theta_g + \theta_v(1 - \theta_g)$. This weights the estimates relative to the probability of germination (eg. if no seeds germinate the estimate of viability will mostly come from the viability test).

I make some assumptions in order to incorporate the loss of viability into the model. I assume that viability is lost at a constant rate, and that germination removes some number of seeds from the pool of viable seeds but does not change the rate of decay. Some fraction of the intact seeds in January are viable before germination ($\nu_1^{1/3}$), and some of those viable seeds germinate.

The seed burial experiments and viability trials provide information about the fate of seeds in the seed bank. We define s_1 as the probability of a seed being intact and viable from October in year t to January in year $t+1$. We define g_1 as the probability of germination for a seed that is intact and viable. We define s_2 as the probability of survival from January to October in year t for a seed that was intact and viable in January. Mathematically, we write each of the transition probabilities as follows:

$$
\begin{aligned}
s_1 &= \theta_1 \times (\theta_2 + (1 - \theta_2) \times \nu_1^{1/3}) \\
g_1 &= \frac{\theta_2}{1 - (1 - \nu_1^{1/3}) \times (1 - \theta_2)} \\
s_2 &= \theta_3 \times \nu_1^{2/3}
\end{aligned} \tag{1}
$$

To estimate the survival of two-year old seeds from October to January ($s3$) requires some additional assumptions. First, we used a different set of bags for these estimates than for the estimates of first-year rates (s_1, s_2, g_1). We use the second set of bags to estimate the probability of viability (ν_2) as described above, combining θ_g and θ_v. We calculate the viability in the second January as the product of viability at the end of the first year (ν_1) and the fraction of first year viability remaining in January ($(\nu_2 \div \nu_1)^{1/3}$). For cases where $\nu_2 \geq \nu_1$, we assumed that all seeds in the bag were viable in October $t+1$ and calculated the fraction of first year viability remaining in January as $(\nu_2)^{1/3}$.

When I estimate the probability of seedling survival from the second October to second January ($s3$), I incorporate the expected proportion of seeds that are expected to be intact at the end of the first year ($\theta_1(1-\theta_2)\theta_3$). I define s_3 as the probability of survival from October in year t to January in year $t+1$ for a seed that was intact and viable in October. Mathematically, we write the transition probability as follows:

$$s_3 = \theta_4 \times (\theta_5 + (1-\theta_5) \times \nu_2^{1/3}) \tag{2}$$

Parameter estimates for aboveground transitions

To obtain year- and population-specific estimates for aboveground vital rates, we use data from annual observational surveys of 20 *Clarkia xantiana* populations. We use data from surveys of plots to estimate seedling survival to fruiting (ϕ). We also estimate fruits per plant (parameter) and seeds per fruit (parameter). We combine these data to obtain annual estimates of per-capita reproductive reproductive success.

From 2006–2012, we counted total fruit equivalents in the field, and estimated the number of seeds in undamaged fruits in the lab. Starting in 2013, we began to count undamaged and damaged fruits in the field, and estimate the number of seeds in both undamaged and damaged fruits in the lab. To compare these components of fitness across all years of the study, we converted the number of undamaged and damaged fruits to total fruit equivalents with the following relationship:

$$\text{TFE} = \text{undamaged fruits} + \frac{\text{seeds per damaged fruit}}{\text{seeds per undamaged fruit}} \times \text{damaged fruits} \tag{3}$$

We use the number of seeds per undamaged fruit to calculate per-seed fitness.

Models

Across all datasets, we have data from multiple years and populations. The goal is to get model-based estimates of vital rates. We use the models to separate variability in parameters between temporal variability and variability due to sampling (e.g. Gould and Nichols 1998). This is particularly important for our estimates of per capita reproductive success because we calculate annual estimates to get a sense of the interannual variation. Failing to account for sampling variation can upwardly bias estimates of temporal variation.

Sample sizes for parameters vary both within years across populations, as well as across populations. Accounting for sampling variability is important for making conclusions about differences among populations.

Model for seed burial experiment data

The models below represent the joint likelihood for data from the seed bag experiments. All data from seed bags and viability trials is in the form of binomial trials: we have counts of seeds at the start and end of an experimental window of time. All models for the parameters $\theta_1, \theta_2, \theta_3, \theta_4, \theta_5$ have the same structure for seeds in bag i in year j in population k. If the number of seeds starting the trial (trials) is n_{ijk} and the number of seeds at the end of the trial (successes) is y_{ijk}, we write a model that has a population-level mean and year-level means drawn from the population-level distribution. The probability of success for each bag is drawn from this year- and population-level distribution:

I compared convergence diagnostics (R-hat, effective sample size) for centered and non-centered parameterizations of the model. Here, I use the centered parameterization because this led to improved convergence. In each model, we obtain the population-level posterior distribution probability of success (the θs) by marginalizing across years and taking the inverse logit.

Model for viability trial data

[need to add explanation for this]

Seedling survival to fruiting

We estimated survival across all populations taking into account both temporal and between-population variability with the following model. We write a model that has a population-level mean and year-level means drawn from the population-level distribution. The probability of success (seedling survival to fruiting) for each plot is drawn from this year- and population-level distribution. The model thus has a similar structure as the model for data on seed survival.

Fruits per plant

Visual inspection of the data on total fruit equivalents (2006–2012) per plant suggests these counts are overdispersed. To assess what probability distribution to use when fitting this model, I fit a power model with an intercept to the mean and variance using the **nls** function in R, which returned an exponent of 1.85. The fit is close to quadratic which means a negative binomial is likely to be an appropriate distribution (**?**).

We estimated fruits per plant across all populations taking into account both temporal and between-population variability with the following model. I first worked only with data on total fruit equivalents on a plant (2006-2012). I estimated total fruit equivalents per plant as:

Visual inspection of the data on undamaged fruits per plant (2013–2018) per plant suggests these counts are overdispersed. To assess what probability distribution to use when fitting this model, I fit a power model with an intercept to the mean and variance using the **nls** function in R, which returned an exponent of 1.97. The fit is close to quadratic which means a negative binomial is likely to be an appropriate distribution (**?**).

Here I calculate fruits per plant across all plant populations taking into account both temporal and between-population variability. I think what I need to do is estimate the mean seeds per undamaged fruit (as below) and the seeds per damaged fruit (same model as below), take the ratio of the means and use that to get an annual estimate of the ratio by which to correct damaged fruits.

I use the ratio and multiply it by the number of damaged fruits and add it to the number of damaged fruits to get a number of total fruit equivalents. I can round that value so that it's a count similar to that for the other dataset.

THEN I can fit a model that calculates a per year fruits per plant (for total fruit equivalents) for all years.

$$\text{TFE} = \text{undamaged fruits} + \frac{\text{seeds per damaged fruit}}{\text{seeds per undamaged fruit}} \times \text{damaged fruits} \tag{4}$$

Alternatively, I calculate fitness in two different ways for the different sets of years. From 2006–2012 I calculate the mean number of fruits per plant for total fruit equivalents and then for 2013–2018 I calculate the number of undamaged and damaged fruits and then multiply each by

Seeds per fruit

To assess what probability distribution to use when fitting this model, I fit a power model with an intercept to the mean and variance using the `nls` function in R, which returned an exponent of 1.38. The fit is greater than linear but less than quadratic which means that neither a Poisson nor negative binomial are likely to be entirely appropriate distributions for the data (?). I might try the parameterization in that reference but for now I am using the negative binomial because the data are overdispersed. We estimated seeds per fruit across all populations taking into account both temporal and between-population variability with the following model. Here, I used data from undamaged fruits from the years 2006-2012. I estimated seeds per fruit as:

Model checking

Convergence

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Posterior predictive checks

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Analysis

Correlation between germination probability and seed survival

Increased seed survivorship is predicted to decrease the optimal germination probability **??**. I assessed whether the observed germination probability was negatively correlated with seed survival (?). I calculated seed survival, $s_2 s_3$; the product of these vital rates is the probability that seeds which do not germinate in January remain in the seed bank until the following

January. I used the posteriors of g_1 and $s_2 s_3$ to calculate the correlation between germination and seed survival. Using this approach, I obtained a distribution of estimates of correlation. Results of this analysis are shown in Figure 4. 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 observed germination probability and the probability of seed survival; the median correlation is negative (-0.07) and the 95% credible interval overlaps 0.

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 (**??**). I assessed whether the observed germination probability was negatively correlated with variance in per-capita reproductive success (**?**). Per-capita reproductive success F_{jk} at population j in year k was calculated at the per year and per population level as follows:

$$F_{jk} = \phi_{jk} \times \lambda^F_{jk} \times \lambda^P_{jk} \tag{5}$$

where

$$\begin{aligned} \phi_{jk} &= \text{logit}^{-1}(\alpha^S_{0,j} + \beta^S_{jk}) \\ \lambda^F_{jk} &= \exp(\alpha^F_{0,j} + \beta^F_{jk}) \\ \lambda^P_{jk} &= \exp(\alpha^P_{0,j} + \beta^P_{jk}) \end{aligned} \tag{6}$$

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 SD of per capita reproductive success. For each population, I calculated the correlation between germination and variance in per-capita reproductive success with the posterior distribution for the geometric SD of per capita reproductive success and the posterior distribution of germination probability from model XX. Using this approach, I obtained a distribution of correlation estimates. 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 Figure **??**.

Density-independent model for germination probability

We use estimates of seed survival and reproductive success to investigate the adaptive value of delayed germination (**?**). We parameterize a model of population growth rate and calculate the optimal germination strategy for different combinations of seed survival and reproductive success. We use the following equation to describe *Clarkia xantiana*'s life cycle and calculate population growth rate:

$$\lambda = g_1 Y(t) s_0 s_1 + (1 - g_1) s_2 s_3 \tag{7}$$

The parameters in this equation were fit in models corresponding to equations (**??**), (**??**), and (**??**). 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 (8)). Temporal variation is incorporated into the model by varying the per-capita reproductive success, $Y(t)$, between years.

I numerically calculate the optimal germination probability for the observed level of variation in reproductive success and seed survival in each population. For each population, I randomly select values 1000 from the posterior distribution for reproductive success. [note from SPE: The issue is that the posterior distribution samples parameter uncertainty. If the model includes temporal variability in certain ways, it may be sampling from the combined variance of parameter uncertainty and temporal variance. In any case, sampling the posterior does not get you a sample from the estimated distribution of temporal variability. To sample from the estimated temporal variability distribution, you estimate its parameters and sample from the fitted distribution. Between now and the committee meeting, think about how you could do that. Afterwards, to account for parameter uncertainty, you can repeat that with several different parameter sets sampled from the posterior.] I use this same sequence of $Y(t)$ and the observed seed survival probabilities to calculate long-term stochastic population growth rates (λ_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 geometric mean of the population growth rate. I repeat the simulations 50 times for each population, resampling from the posterior distribution for reproductive success each time. I 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 (**?**). To evaluate a density-independent model for germination probability, I compared observed germination probability to predicted germination optima. I plot this comparison in Figure **??**. 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.

Results

Correlation between germination probability and seed survival

I examined the correlation between germination probability and seed survival in the seed bank. Results of this analysis are shown in Figure 4. The bottom panel shows the posterior distribution of correlation between observed germination probability and the probability of seed survival; the median correlation is negative (-0.07) and the 95% credible interval overlaps 0. There is no correlation between germination and seed survival.

Correlation between germination probability and variance in reproductive success

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Optimal germination probability predicted by a density-independent model

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Figures

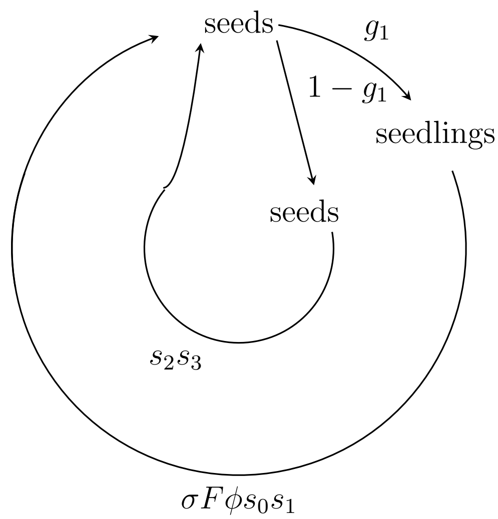

Figure 1: Life cycle diagram for *Clarkia xantiana*.

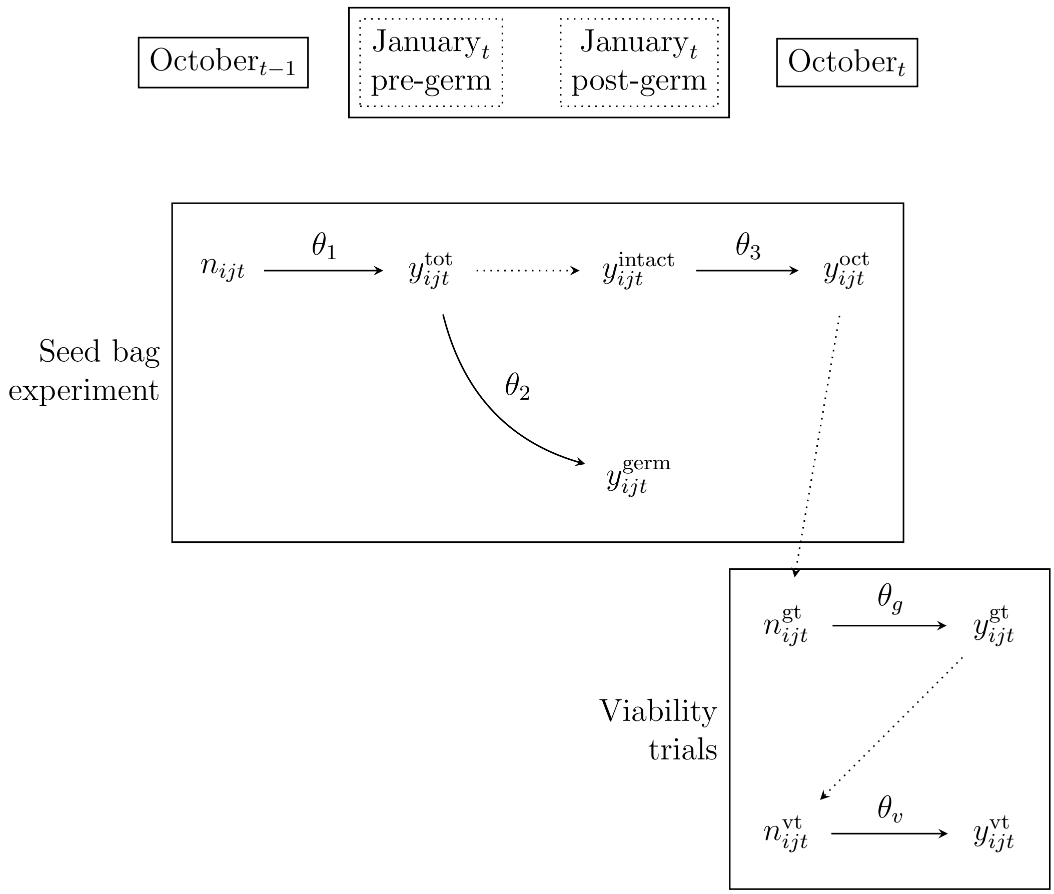

Figure 2: Diagram of data from the seed bag experiments and viability trials. There are two boxes: one for the seed bag experiment and one for the viability trials. In the seed bag experiment, I split January into two steps, one for just before germination and one for just after. Solid arrows represent probabilities estimated with a binomial experiment and are labeled with corresponding parameters. Dotted arrows represent cases where the seeds at the head of the arrow include some, possibly all, seeds at the tail of the arrow.

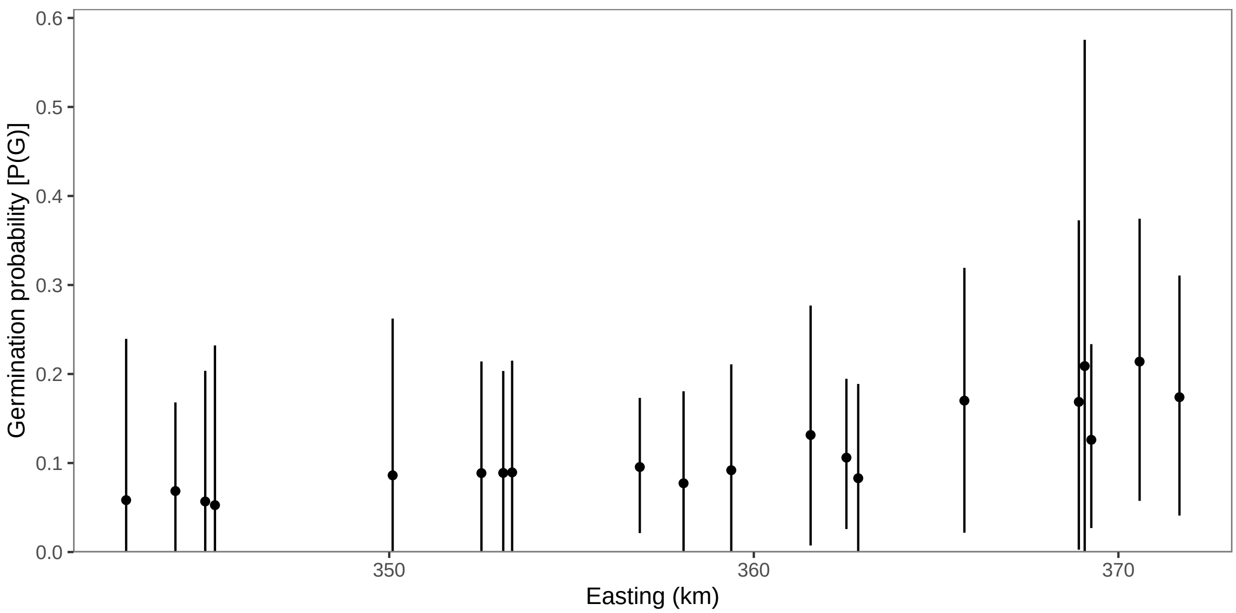

Figure 3: Germination probability plotted against easting (km). The plot shows the marginal posterior distribution for germination probability at each site. The points are the median of the posterior. The thinner line represents the 95% credible interval and the thicker line represents the 50% credible interval.

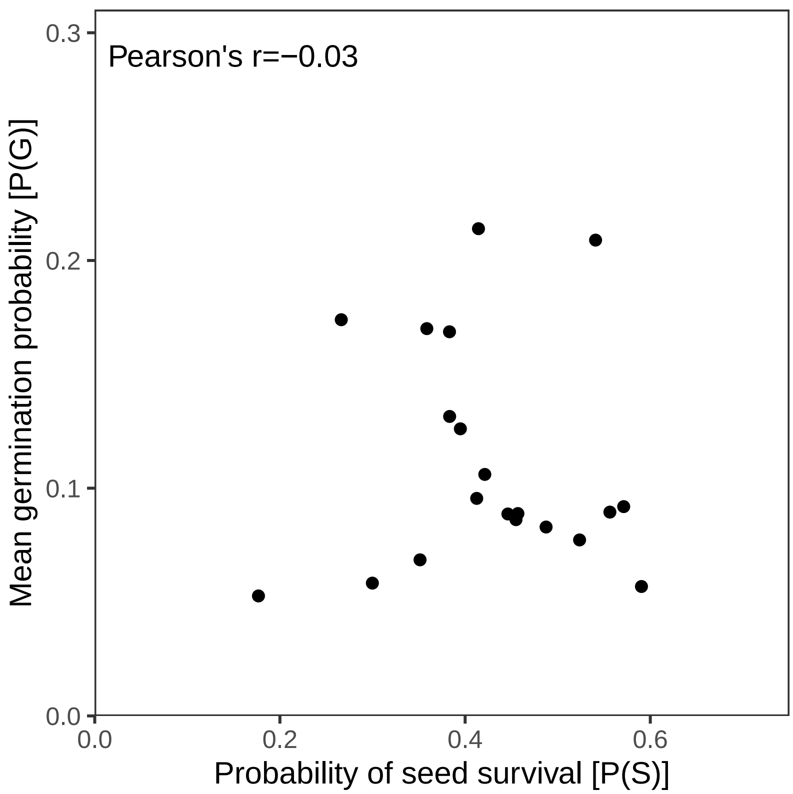

Figure 4: The top panel shows the observed germination probability plotted against probability of seed survival. The bottom panel shows the posterior distribution of correlation between observed germination probability and the probability of seed survival; the correlation is negative (-0.03).

Supplementary material

Theoretical background for hypotheses.

Explanation of key papers that develop theoretical results about seed banks. The document describes results from these papers that are relevant to understanding and interpreting the data in this manuscript. Link to document: `https://github.com/gregor-fausto/clarkiaSeedBanks/blob/master/products/appendices/appendix-cohen-results/appendix-x-cohen` `pdf`

Data summary.

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

Data processing workflow.

Description of workflow for processing the data used in the analysis. The document describes how comma-separated value (.csv) and Excel (.xls and .xlsx) files were read and processed in R. Link to document: `https://github.com/gregor-fausto/clarkiaSeedBanks/blob/master/library/dataProcessingWorkflow.md`

Method for estimating seed bank parameters using conditional probabilities.

The document explains how we compose conditional probabilities to calculate probabilities of survival and germination of seeds in the seed burial experiment. Link to document: `https://`

github.com/gregor-fausto/clarkiaSeedBanks/blob/master/products/appendices/appendix-condi appendix-x-conditional-probability.pdf