Seed banks in *Clarkia xantiana*

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Introduction

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)). Dormancy can affect the outcome of evolution (Heinrich et al. (2018); Ritland (1983)). Theory thus suggests that seed banks have ecological and evolutionary consequences (Evans and Dennehy (2005)).

What drives the evolution of delayed germination? The theory developed by Cohen (1966) 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 (Appendix Figure X). 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* (Eckhart et al. (2011)). 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) Cohen (1966, 1968); Ellner (1985*a*,*b*). 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 ques-

tions about the geography of demography (Eckhart et al. (2011)) and species distributions (Pironon et al. (2018)).

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. [Eckhart et al. (2011): 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 $X^t h$ 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 $X^t h$ 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 $X^t h$ 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 $X^t h$ 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 0.5 m^2 plots at 20 populations from 2006–present (Eckhart et al. (2011)). Each population was visited in February and June to count the number of seedlings and fruiting plants, respectively. Seedlings and plants in each plot are counted by a single person at each visit.

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 in 0.5m^2 plots at 20 populations (Eckhart et al. (2011)). For each of 15-20 plants, we counted the number of undamaged fruits. We then took the damaged fruits 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.

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

- y_{ijk}^{TFE} = 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 (Eckhart et al. (2011)). 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 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 to obtain year- and population-specific estimates for aboveground vital rates. We use these transition probabilities to analyze correlations between germination probability and variance in per-capita reproductive success, correlation between germination probability and seed survival, and to compare the optimal germination fraction from a density-independent model to the observed germination fraction.

Parameter estimates for belowground transitions

To estimate population-specific estimates for belowground vital rates, we use data from seed burial experiments in the field and seed viability trials in the lab. We combine these data to infer seed survival across different parts of the year and germination. I estimate probabilities of success using the data, and compose these estimates to obtain transition probabilities for the life history of *Clarkia xantiana*. I provide details of this approach in the **Appendix on Conditional Probability**. Briefly, I estimate probabilities of success

$(\theta_1, \theta_2, \theta_3, \theta_4, \theta_5, \nu_1, \nu_2)$ using data from seed burial experiments and viability trials. I use these probabilities of success to compose transition probabilities (s_1, s_2, s_3, g_1).

Figure 2 illustrates the relationship between the data and the estimated probability of success. 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 estimated probabilities and are labeled with corresponding parameters.

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). We estimate the probability of a seedling emerging, conditional on being intact as θ_2. I assume that there is no decay during germination (i.e., seed loss is instantaneous in January). The number of intact seeds before germination is equal to the number of seeds and seedlings after germination. At this point, the seeds transition into one of four possible states. Intact and viable seeds may have (1) germinated or (2) not germinated and remain 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 of year $t + 1$. I need to 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 total seeds in January pre-germination is viable ($\nu_1^{1/3}$) and some of those viable seeds germinate.

The seed burial experiments and viability trials thus 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. We 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 each of the transition probabilities as follows:

$$\begin{aligned} s_1 &= \theta_1 \times (\theta_2 + (1-\theta_2) \times \nu_1^{1/3}) \\ g_1 &= \frac{\theta_2}{1 - (1-\nu_1^{1/3}) \times (1-\theta_2)} \\ s_2 &= \theta_3 \times \nu_1^{2/3} \\ s_3 &= \frac{\theta_4 \times (\theta_5 + (1-\theta_5) \times \nu_2^{1/3})}{s_1 \times (1-g_1) \times s_2} \end{aligned} \tag{1}$$

Parameter estimates for aboveground transitions

To estimate 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.

Models

Across all datasets, we have data from multiple years and populations. The goal is to estimate

Model for seed burial experiment data

The models below represent the joint likelihood for data from the seed bag experiments. All of 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:

$$\begin{aligned}
[\boldsymbol{\mu}, \boldsymbol{\sigma}, \boldsymbol{\alpha}, \boldsymbol{\theta} | \boldsymbol{n}, \boldsymbol{y_{\text{total}}},] \propto & \prod_{k=1}^{K} \prod_{j=1}^{J} \prod_{i=1}^{I} \text{binomial}(y_{ijk}^{\text{tot}} | n_{ijk}, \text{logit}^{-1}(\alpha_{ijk})) \\
& \times \text{normal}(\alpha_{ijk} | \mu_{jk}, \sigma_{jk}) \\
& \times \text{normal}(\mu_{jk} | \mu_{0,k}, \sigma_{0,k}) \\
& \times \text{uniform}(\sigma_{jk} | 0, 100) \\
& \times \text{normal}(\mu_{0,k} | 0, 100) \text{uniform}(\sigma_{0,k} | 0, 100).
\end{aligned} \tag{2}$$

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 converge. 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. In this model, $\alpha_{0,j}^{S}$ is the logit mean survival

probability at population j, β^S_{jk} are independent identically distributed random variables drawn from normal distributions with mean 0 and population-specific temporal variance parameters σ^S_j. Writing the population-specific logit survival as a fixed effect means that each population parameter estimate is estimated separately with no shared variance term. The population-specific temporal variance parameter is written as a random effect, which means that each population has has year components that are drawn from a distribution with a shared variance term. I estimated the probability of surviving to fruiting using data from plots at populations in different years:

$$\begin{aligned}[\boldsymbol{\alpha_0^S}, \boldsymbol{\beta^S}, \sigma^S | \boldsymbol{n}, \boldsymbol{y}] \propto & \prod_{i=1}^{I}\prod_{j=1}^{J}\prod_{k=1}^{K} \text{binomial}(y_{ijk}|n_{ijt}, \text{f}(\alpha^S_{0,j}, \beta^S_{jk})) \\ & \times \text{normal}(\beta^S_{jk}|0, \sigma^S_j) \\ & \times \text{normal}(\alpha^S_{0,j}|0, 10)\text{uniform}(\sigma^S_j|0, 100)\end{aligned} \tag{3}$$

where

$$\text{f}(\alpha^S_{0,j}, \beta^S_k)) = \text{logit}^{-1}(\alpha^S_{0,j} + \beta^S_{jk}) \tag{4}$$

Fruits per plant

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 1.99. The fit is close to quadratic which means a negative binomial is likely to be an appropriate distribution (Lindn and Mntyniemi (2011)). 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:

$$
\begin{aligned}
[\boldsymbol{\alpha_0^F}, \boldsymbol{\beta^F}, \sigma^F | \boldsymbol{n}, \boldsymbol{y}] \propto & \prod_{i=1}^{I} \prod_{j=1}^{J} \prod_{k=1}^{K} \text{negative binomial}(y_{ijk}^{\text{TFE}} | \text{f}_1(\alpha_{0,j}^F, \beta_{jk}^F), \kappa^F)) \\
& \times \text{normal}(\alpha_{0,j}^F | 0, 10) \\
& \times \text{normal}(\beta_{jk}^F | 0, \sigma_j^F) \\
& \times \text{normal}(\sigma_j^F | 0, 100)
\end{aligned} \tag{5}
$$

where

$$
\text{f}_1(\alpha_{0,j}^F, \beta_{jk}^F)) = \lambda_{jk}^F = \exp(\alpha_{0,j}^F + \beta_{jk}^F) \tag{6}
$$

$$
\text{negative binomial}(y_{ijk}^{\text{TFE}} | \frac{\kappa^F}{\kappa^F + \lambda_{jk}^F}, \kappa^F) \tag{7}
$$

where the negative binomial is parameterized with probability parameter p and dispersion parameter r [negative binomial(p, r)]. In this case $p = \frac{\kappa}{\kappa+\mu}$.

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 (Lindn and Mntyniemi (2011)). 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:

$$
\begin{aligned}
[\boldsymbol{\alpha_0^P}, \boldsymbol{\beta^P}, \sigma^P | \boldsymbol{n}, \boldsymbol{y}] \propto & \prod_{i=1}^{I} \prod_{j=1}^{J} \prod_{k=1}^{K} \text{negative binomial}(y_{ijk}^{\text{und}} | \text{f}_1(\alpha_{0,j}^P, \beta_{jk}^P), \kappa^P)) \\
& \times \text{normal}(\alpha_{0,j}^P | 0, 10) \\
& \times \text{normal}(\beta_{jk}^P | 0, \sigma_j^P) \\
& \times \text{normal}(\sigma_j^P | 0, 100)
\end{aligned} \tag{8}
$$

where

$$
\text{f}_1(\alpha_{0,j}^P, \beta_{jk}^P)) = \lambda_{jk}^P = \exp(\alpha_{0,j}^P + \beta_{jk}^P) \tag{9}
$$

$$
\text{negative binomial}(y_{ijk}^{\text{und}} | \frac{\kappa^P}{\kappa^P + \lambda_{jk}^P}, \kappa^F P) \tag{10}
$$

where the negative binomial is parameterized with probability parameter p and dispersion parameter r [negative binomial(p, r)]. In this case $p = \frac{\kappa}{\kappa+\mu}$.

Analysis

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)). Per-capita reproductive success F_{jk} at population j in year k was

calculated at the per year and per population level as follows:

$$F_{jk} = \phi_{jk} \times \lambda^F_{jk} \times \lambda^P_{jk} \tag{11}$$

where

$$\begin{aligned} \phi_{jk} &= \text{logit}^{-1}(\alpha^S_{0,j} + \beta^S_{jk}) \\ \lambda^F_{jk} &= \exp(\alpha^F_{0,j} + \beta^F_{jk}) \\ \lambda^P_{jk} &= \exp(\alpha^P_{0,j} + \beta^P_{jk}) \end{aligned} \tag{12}$$

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. Results of this analysis are shown in Figure **??**. 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.

Correlation between germination probability and seed survival

Increased seed survivorship is predicted to decrease the optimal germination probability Cohen (1966); Ellner (1985*a*). I assessed whether the observed germination probability was negatively correlated with seed survival (Gremer and Venable (2014)). I calculated seed survival as $s_2 s_3$ as 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 correlation estimates. Results of this analysis are shown in Figure **??**. 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.

Density-independent model for germination probability

We used 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 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:

$$\lambda_j = s_1 g_1 Y(t) s_0 + s_1(1 - g_1) s_2 \tag{13}$$

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 (11)). Variation is incorporated into the model by varying per-capita reproductive success, $Y(t)$, between years.

I numerically calculated the optimal germination probability for the observed level of variation in reproductive success and seed survival in each population. For each population, I randomly selected 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 used 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 maximized geometric mean of the population growth rate. I repeated 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 (Cohen (1966)). 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

Figures

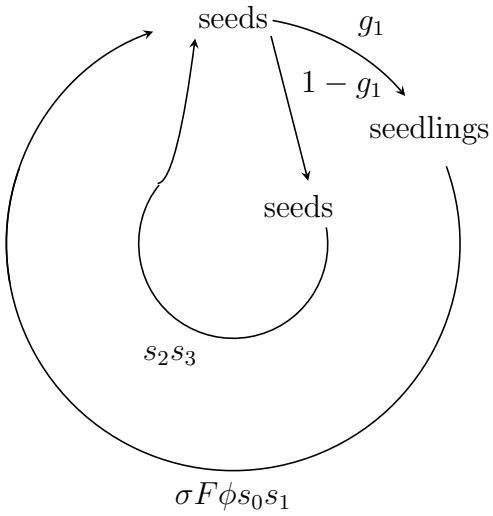

Figure 1: Life cycle diagram for *Clarkia xantiana*.

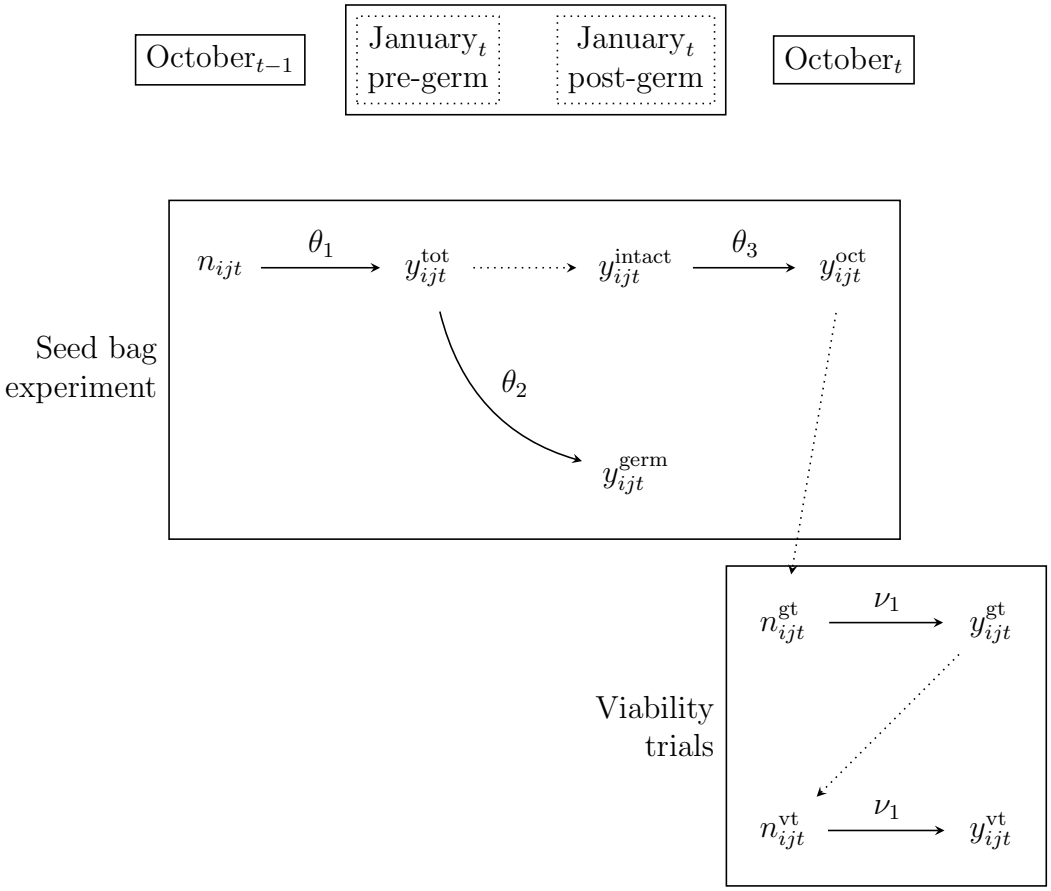

Figure 2: Diagram of data from the seed bag experiments and viability trials.

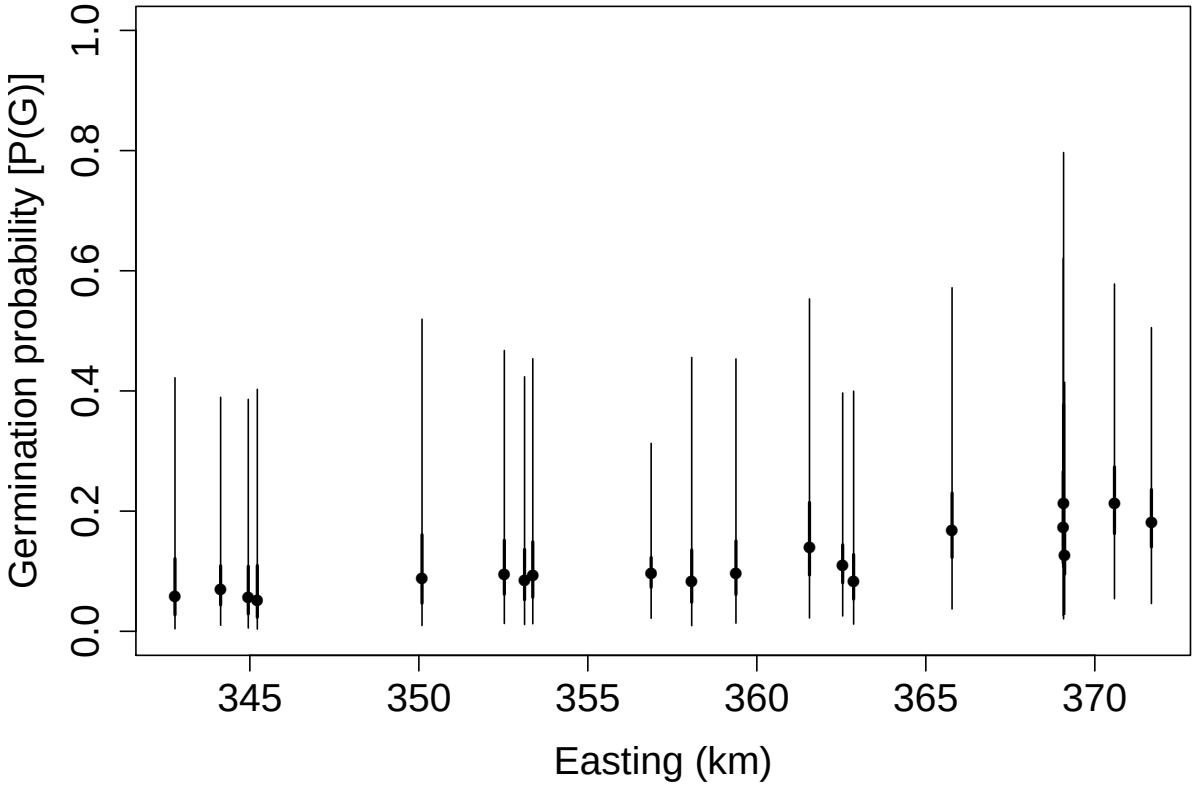
Germination probability [P(G)]
0.0
0.2
0.4
0.6
0.8
1.0
345
350
355
360
365
370
Easting (km)

Figure 3: ...

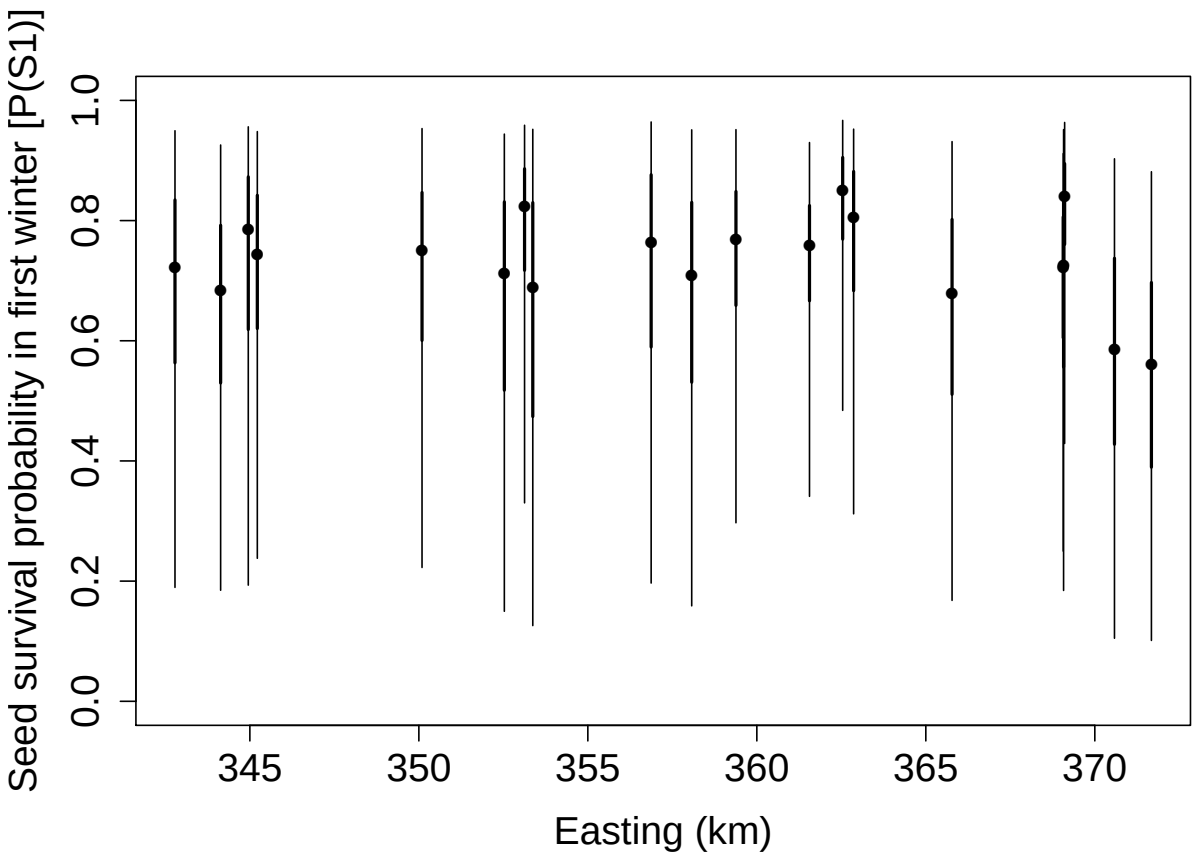
Seed survival probability in first winter [P(S1)]
0.0
0.2
0.4
0.6
0.8
1.0
345
350
355
360
365
370
Easting (km)

Figure 4: ...

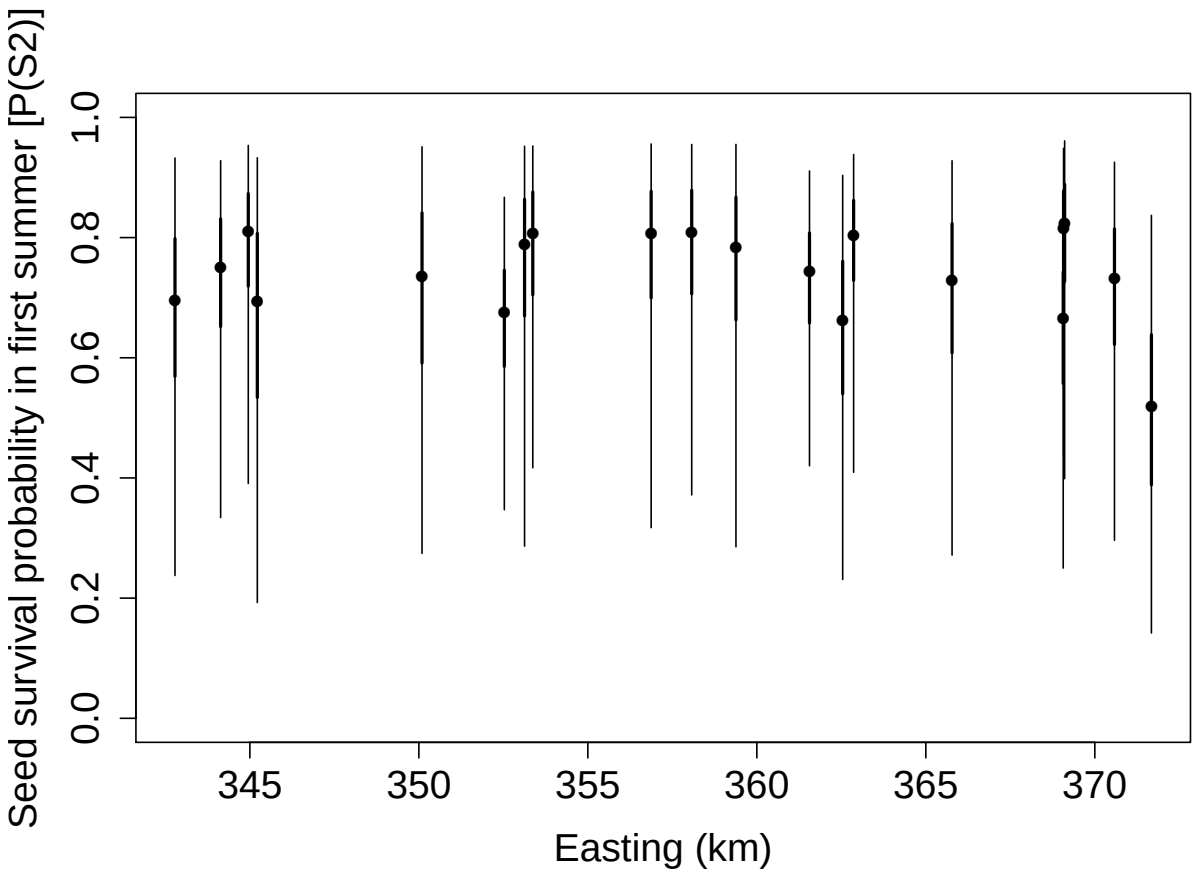
Seed survival probability in first summer [P(S2)]
0.0
0.2
0.4
0.6
0.8
1.0
345
350
355
360
365
370
Easting (km)

Figure 5: ...

References

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