Seed banks in *Clarkia xantiana*

Gregor-Fausto Siegmund and Monica Geber

Last updated: February 3, 2020

Introduction

Seed banks have important consequences for population persistence by acting as a buffer against environmental change and population stochasticity (**??**), increasing effective population size (**??**), and genetic diversity (**?**). The presence of a seed bank can also affect the outcome of evolution (**??**). Theory thus suggests that seed banks have ecological and evolutionary consequences (**?**).

A previous study 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.

Population vital rates are known to vary across *C. 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.]

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 for in populations which experience higher levels of interannual variation in

fitness. To investigate this empirical relationship, I will estimate the correlation between interannual variation in fitness 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 fitness.

Table 1 outlines key references that develop theory and expectations for what drives the evolution of delayed germination. The table also includes some papers that have tested the theory empirically. The main set of papers I've included are ones that look at variation in germination among Sonoran Desert annuals (papers by Venable, Gremer). Finally, the table briefly lists predictions made by different models. I think examining the following relationships would be good starting points. The correlation between variance in fitness (seeds/seedling) and germination fraction should be negative – this is true under the density-independent and -dependent model. The correlation between seed survivorship and germination fraction should be negative under both a density-independent and -dependent model but the limit as survivorship approaches 1 differs. Finally, the correlation between mean seed yield and germination fraction will be positive if fitness is density-independent but is not necessarily positive if fitness is density-dependent.

Table 1: Table 1: Models for germination delays: references and predictions

	Density-independent fitness	Density-dependent fitness	Predictive germination	Structured model
Key theory references	??	??	?	?
Key empirical tests	?	?	?	...
Mean of seed yield	increase in $\bar{Y}$ increases G^*	increase in $\bar{K}$ can increase or decrease $\hat{G}$	...	...
CV of seed yield	increasing ρ_Y decreases G^*	increasing ρ_K or ρ_C decreases $\hat{G}$	...	...
Seed survivorship	increasing s decreases G^*; limit near $s = 1$ is p	increasing s decreases $\hat{G}$; limit near $s = 1$ is 0	...	...

Methods

Background on study system

46 Monica Geber and collaborators have collected 12+ years of annual estimates for demo-
47 graphic data on a species of annual plant: survival of seedlings to fruiting adults, fruits per
48 adult plant, and seeds per fruit. As part of the long-term work on *Clarkia xantiana*, there 3
49 sources of data on the transition between seeds in fruits and seedlings: 1 observational data
50 set and 2 experimental data sets. Here, I present analyses of 1 observational data set and 1
51 experimental data set.

52   Starting in 2007, there are (1) estimates of fruits/plant and seeds/fruit that provide an
53 estimate of seed input into a plot and (2) estimates of germinants the following year. For
54 most plots, the number of seeds entering a plot in year t-1 is much greater than the number
55 of seedlings emerging in a plot in year t. However, this is not uniformly true, and there is
56 also experimental data suggesting these seeds may survive in the seed bank for at least 10
57 years at some locations.

58   There are two experiments conducted at non-overlapping points in time we use to estimate
59 transitions in the seed bank. From 2006-2010, Geber and collaborators buried seeds in bags
60 and periodically dug them up to count seedlings and intact, viable seeds. This data estimates
61 transitions leading to germination or survival of seeds that are 1, 2, and 3 years old. Starting
62 in 2013, Geber and collaborators placed seeds in pots and counted seedlings. This data
63 estimates transitions of seeds in the soil seed bank but cannot separate germination and
64 survival in the same way as the first experiment.

4

Parameter estimates for belowground transitions

Here, we analyze data from an experiment that involved burying seeds in seed bags (2005-2009). We seek to estimate (1) seed survival for different periods of the year or as a monthly rate, (2) germination of 0-, 1- and 2-year old seeds, and (3) viability of intact seeds unearthed in October.

Figure 1 illustrates the transitions in the first year the seed bags are buried. 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 transitions and are labeled with corresponding vital rates. In the models, I have adopted $s_1 = \phi$, $g_1 = \gamma$, $s_2 = \rho$, and $v_1 = \upsilon$.

In the seed bag experiment, the parameter s_1 is the proportion of seeds from the start of the experiment that remain intact in January. In January, the remaining seeds are in one possible state: intact (this includes viable and non-viable seeds). We assume that there is no decay during germination (seed loss happens over extended periods of time, not instantaneously in January) so that the number of seeds before germination is equal to the number of seeds and seedlings after germination. At this point, the seeds have transitioned into one of four possible states. Intact and viable seeds may have (1) germinated or (2) not germinated and thus remain dormant. Because non-viable seeds could not have germinated (forbidden state 3), all other intact seeds would have been non-viable (4).

I represent two transitions between pre-germination seeds in January and post-germination seeds and seedlings in January. The first is for seeds that are viable and germinate; these become seedlings. The second is for seeds that do not germinate; these remain seeds and include both viable and non-viable seeds (the sum of $(1 - g_1)v_1^{\frac{1}{3}}$ and $(1 - g_1)(1 - v_1^{\frac{1}{3}})$. For the purposes of parameter estimation, we only represent the number of seedlings—viability is estimated separately.
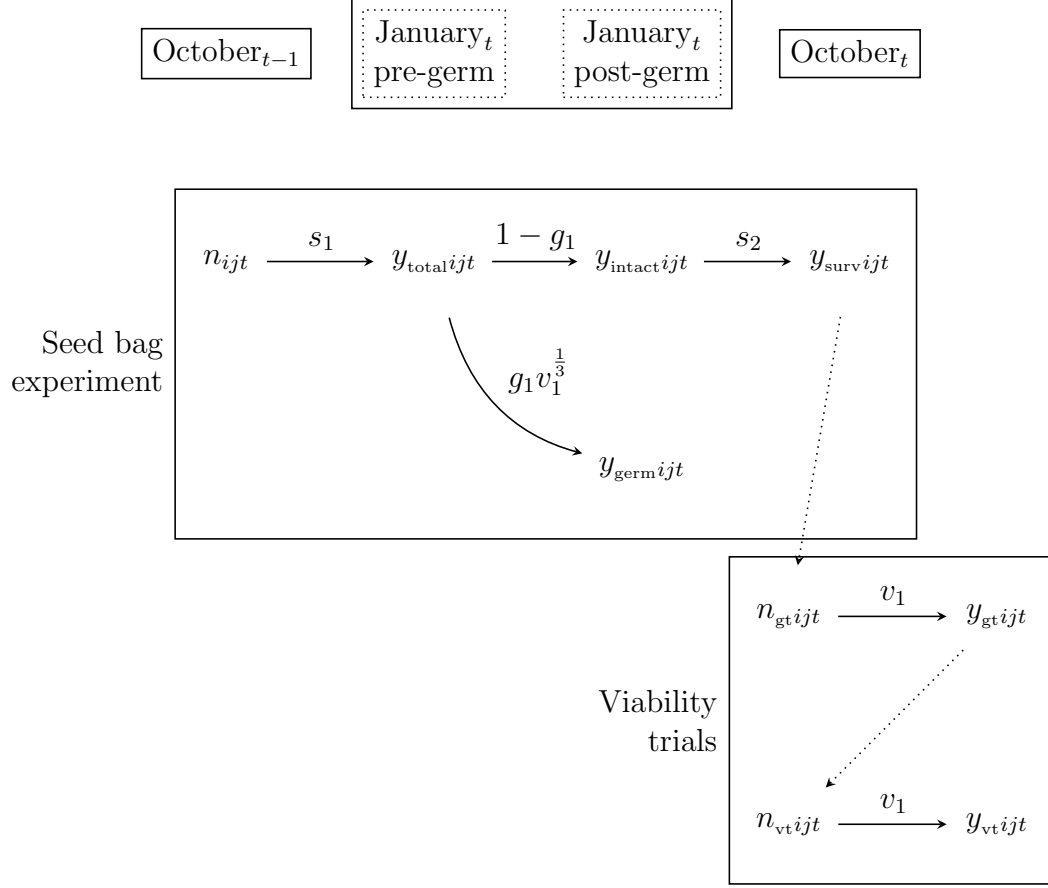
Figure 1: Diagram of data from the seed bag experiments and viability trials.

⁸⁹   We want to incorporate the loss of viability into our model. We assume that the rate

⁹⁰ of loss of viability is constant, and that germination removes some number of seeds from

⁹¹ the pool of viable seeds but does not change the rate of decay. Some fraction of the total

⁹² seeds in January pre-germination is viable $(v_1^{\frac{1}{3}})$ and some of those viable seeds germinate.

⁹³ We include viability in our estimates of germination rate so as to not overestimate the true

⁹⁴ germination rate. The number of seeds that remain intact are those that do not germinate

⁹⁵ $(1-g_1)$, which includes both viable $(v_1^{\frac{1}{3}})$ and non-viable $(1-v_1^{\frac{1}{3}})$ seeds. Seeds that germinate

⁹⁶ must be viable.

⁹⁷   Here, we use viability in our germination estimates. For the full life cycle, this would

⁹⁸ model the rates of intact seeds and only incorporate viability in the germination transition.

Viability trials

99 In October (year $t+1$), we first removed the bags and counted the number of ungerminated,
100 intact seeds. In the lab, we conducted germination trials and viability assays on subsets
101 of the seeds from each bag to estimate the viability of the ungerminated, intact seeds. We
102 collected the following data:

- 103 $n_{\mathrm{germ}ijt}$ = observed count of seeds at the start of the germination trial for the ith bag,
  104 from the jth site, in the tth year, assumed to be measured perfectly

- 105 $y_{\mathrm{germ}ijt}$ = observed count of germinated seedlings in the ith bag, from the jth site, in
  106 the tth year, assumed to be measured perfectly

- 107 $n_{\mathrm{viab}ijt}$ = observed count of seeds at the start of the viability trial for the ith bag, from
  108 the jth site, in the tth year, assumed to be measured perfectly

- 109 $y_{\mathrm{viab}ijt}$ = observed count of viable seedlings in the ith bag, from the jth site, in the tth
  110 year, assumed to be measured perfectly

Seed bag experiments

111 In October (year t), we buried 10 5 × 5-cm nylon mesh bags at each site, each containing 100
112 seeds collected at the site in June-July. In January (year $t + 1$), we removed these 10 bags
113 and counted the number of germinated seedlings and the number of ungerminated, intact
114 seeds in each bag. We then returned the ungerminated, intact seeds to the resealed bag and
115 returned the bag to the field. In October (year $t + 1$), we removed these bags and counted
116 the number of ungerminated, intact seeds. We collected the following data:

- 117 n_{ijt} = observed count of seeds in the seed bags at the start of the experiment in October
  118 in the ith bag, from the jth site, in the tth year, assumed to be measured perfectly

119 • $y_{\text{intact}ijt}$ = observed count of ungerminated, intact seeds in the seed bags in January in

120 the ith bag, from the jth site, in the tth year, assumed to be measured perfectly

121 • $y_{\text{germ}ijt}$ = observed count of germinated seedlings in the seed bags in January in the ith

122 bag, from the jth site, in the tth year, assumed to be measured perfectly

123 • $y_{\text{total}ijt}$= observed count of ungerminated, intact seeds plus germinated seedlings in the

124 seed bags in January in the ith bag, from the jth site, in the tth year, assumed to be

125 measured perfectly

126 • $y_{\text{surv}ijt}$ = observed count of ungerminated, intact seeds in the seed bags in October in

127 the ith bag, from the jth site, in the tth year, assumed to be measured perfectly

128 We fit the following model for bag i at site j in year k:

$$
\begin{aligned}
[\boldsymbol{\phi}, \boldsymbol{\gamma}, \boldsymbol{\rho}, \boldsymbol{\alpha} | \boldsymbol{n}, &\boldsymbol{n}_{\text{viab}}, \boldsymbol{y}_{\text{total}}, \boldsymbol{y}_{\text{germ}}, \boldsymbol{y}_{\text{surv}}, \boldsymbol{y}_{\text{viab}}] \propto \\
&\prod_{j=1}^{J}\prod_{i=1}^{I} \text{binomial}(y_{ij}^{\text{tot}}|n_{ij}, f_1(\alpha_{0,j}^{s1}, \beta_j^{s1})) \\
&\times \text{binomial}(y_{ij}^{\text{germ}}|y_{ij}^{\text{tot}}, f_2(\gamma_j, \alpha_{ijk})) \\
&\times \text{binomial}(y_{ij}^{\text{surv}}|y_{ij}^{\text{tot}} - y_{ij}^{\text{germ}}, f_3(\alpha_{0,j}^{s2}, \beta_j^{s2})) \\
&\times \text{binomial}(y_{ij}^{\text{viab}}|n_{ij}^{\text{viab}}, \text{logit}^{-1}(\alpha_{ijk})) \\
&\times \text{normal}(\alpha_{0,j}^{s1}|0, 10)\text{normal}(\alpha_{0,j}^{g1}|0, 10)\text{normal}(\alpha_{0,j}^{s2}|0, 10) \\
&\times \text{normal}(\beta_j^{s1}|0, \sigma_j^{s1})\text{normal}(\beta_j^{g1}|0, \sigma_j^{g1})\text{normal}(\beta_j^{s2}|0, \sigma_j^{s2}) \\
&\times \text{uniform}(\sigma_j^{s1}|0, 100)\text{uniform}(\sigma_j^{g1}|0, 100)\text{uniform}(\sigma_j^{s2}|0, 100) \\
&\times \text{normal}(\alpha_{ijk}|\mu_{jk}, \sigma_{jk}) \\
&\times \text{normal}(\mu_{jk}|0, 100)\text{uniform}(\sigma_{jk}|0, 100).
\end{aligned}
\tag{1}
$$

where

$$\mathrm{f}_1(\alpha_{0,j}^{s1}, \beta_{jk}^{s1}) = \phi_{jk} = \mathrm{logit}^{-1}(\alpha_{0,j}^{s1} + \beta_{jk}^{s1})$$

$$\mathrm{f}_2(\alpha_{0,j}^{g1}, \beta_{jk}^{g1}, \alpha_{ijk}) = \gamma_{jk} \times v_{ijk}^{\frac{1}{3}} = \mathrm{logit}^{-1}(\alpha_{0,j}^{s1} + \beta_{jk}^{s1}) \times (\mathrm{logit}^{-1}(\alpha_{ijk}))^{\frac{1}{3}} \qquad (2)$$

$$\mathrm{f}_3(\alpha_{0,j}^{s2}, \beta_{jk}^{s2}) = \rho_{jk} = \mathrm{logit}^{-1}(\alpha_{0,j}^{s1} + \beta_{jk}^{s1})$$

We fit this model with JAGS in R.

Seedling survival to fruiting

The data consist of counts of seedlings and fruiting plants in 0.5 m^2 plots at 20 sites from 2006–present. Each site 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.

For now, we assume that the data on seedlings is measured perfectly (i.e. no under- or over-counts of 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 site. Germination phenology varies may vary from year to year but also by geography; higher elevation sites 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.

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_{ijt} = observed counts of seedlings in the ith plot, from the jth site, from the kth year

- y_{ijt} = observed counts of fruiting plants in the ith plot, from the jth site, from the kth year, assumed to be measured perfectly

We estimated survival across all sites taking into account both temporal and between-site variability with the following model. In this model, $\alpha_{0,j}^S$ is the logit mean survival probability at site j, β_{jk}^S are independent identically distributed random variables drawn from normal distributions with mean 0 and site-specific temporal variance parameters σ_j^S. Writing the site-specific logit survival as a fixed effect means that each site parameter estimate is estimated separately with no shared variance term. The site-specific temporal variance parameter is written as a random effect, which means that each site 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 sites in different years:

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

where

$$
\text{f}(\alpha_{0,j}^S, \beta_k^S)) = \text{logit}^{-1}(\alpha_{0,j}^S + \beta_{jk}^S)
\tag{4}
$$

Fruits per plant

From 2006–2012, "we recorded...the number of fruits per plant for up to 15-20 plants per 0.5 m^{2}" (**?**). For each plant, 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 (1) the number of fruits produced per plant and (2) the proportion of fruits that are damaged per plant. Define:

- y_{ijk}^{TFE} = observed counts of total fruit equivalents per plant on the ith plant, from the jth site, from the kth year, assumed to be measured perfectly

- n_{ijk} = observed counts of total fruits per plant (sum of $\boldsymbol{y_{ijk}}$) on the ith plant, from the jth site, from the kth year, assumed to be measured perfectly

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 (**?**). We estimated fruits per plant across all sites taking into account both temporal and between-site 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:

11

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

178 where

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

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

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

Seeds per fruit

181 From 2006–2012, "we collected one fruit from each of 20-30 haphazardly selected plants
182 distributed across each population (but outside plots, to avoid influencing seed input within
183 them) to estimate the mean number of seeds produced per fruit" (Eckhart et al. 2011). We
184 collected fruits that were undamaged in the field, and fruits were broken open to count seeds.
185 For each population in each year, we attempted to obtain 20-30 counts of seeds produced
186 per undamaged fruit.

We seek to estimate (1) the number of seeds per undamaged fruit. Define:

- y_{ijk}^{und} = observed counts of seeds per undamaged fruit in the ith fruit, from the jth site, from the kth year, assumed to be measured perfectly

- λ_{jk} = true, unobserved mean number of seeds per undamaged fruit from the jth site, from the kth year

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 sites taking into account both temporal and between-site variability with the following model. I first worked only with data from undamaged fruits from the years (2006-2012). I estimated seeds per fruit as:

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

where

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

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

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

Correlation between germination probability and per-capita reproductive success

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

$$F_{jk} = \phi_{jk} \times \lambda_{jk}^F \times \lambda_{jk}^P \tag{11}$$

where

$$
\begin{aligned}
\phi_{jk} &= \mathrm{logit}^{-1}(\alpha_{0,j}^S + \beta_{jk}^S) \\
\lambda_{jk}^F &= \exp(\alpha_{0,j}^F + \beta_{jk}^F) \\
\lambda_{jk}^P &= \exp(\alpha_{0,j}^P + \beta_{jk}^P)
\end{aligned}
\tag{12}
$$

To calculate the temporal variation in fitness 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 obtained a posterior distribution for the

14

geometric SD of per capita reproductive success; I used this and the posterior distribution of germination probability from model XX to calculate the correlation between germination and fitness variance. 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.

Correlation between germination probability and seed survival

I assessed whether the observed germination probability was negatively correlated with seed survival (?). 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. 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 (?). Briefly, we parameterize a model of population growth rate and calculate the optimal germination strategy for different combinations of seed survival and reproductive success. We can use the following equation to summarize *Clarkia xantiana*'s life cycle and calculate population growth rate:

$$\lambda_j = g_1 Y(t) s_0 s_1 + (1 - g_1) s_2 s_3 \tag{13}$$

The parameters in this equation were fit in models corresponding to equations (1, 3, 5, 8). Seed survival rates (s_0, s_1, s_2, s_3) 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. Variation is incorporated into the model by having $Y(t)$ vary 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. 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 was calculated 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.

A model in which per-capita reproductive success is density-independent predicts 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.
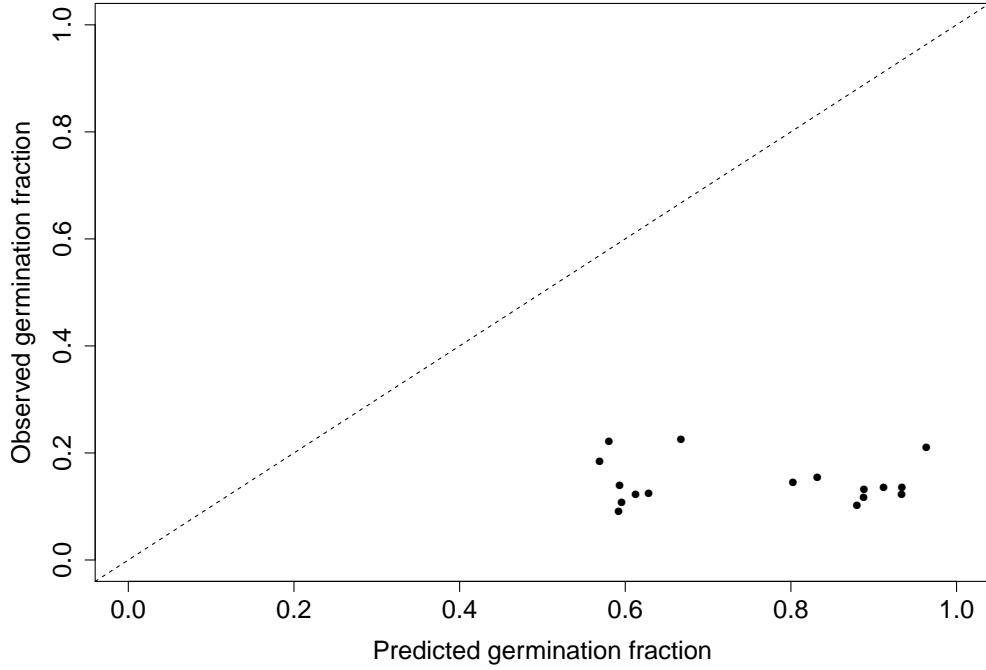
Results

16

Figure 2: Observed germination probability plotted against the optimal germination proba-bility predicted by a density-independent model. For each population, the observed germi-nation 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.
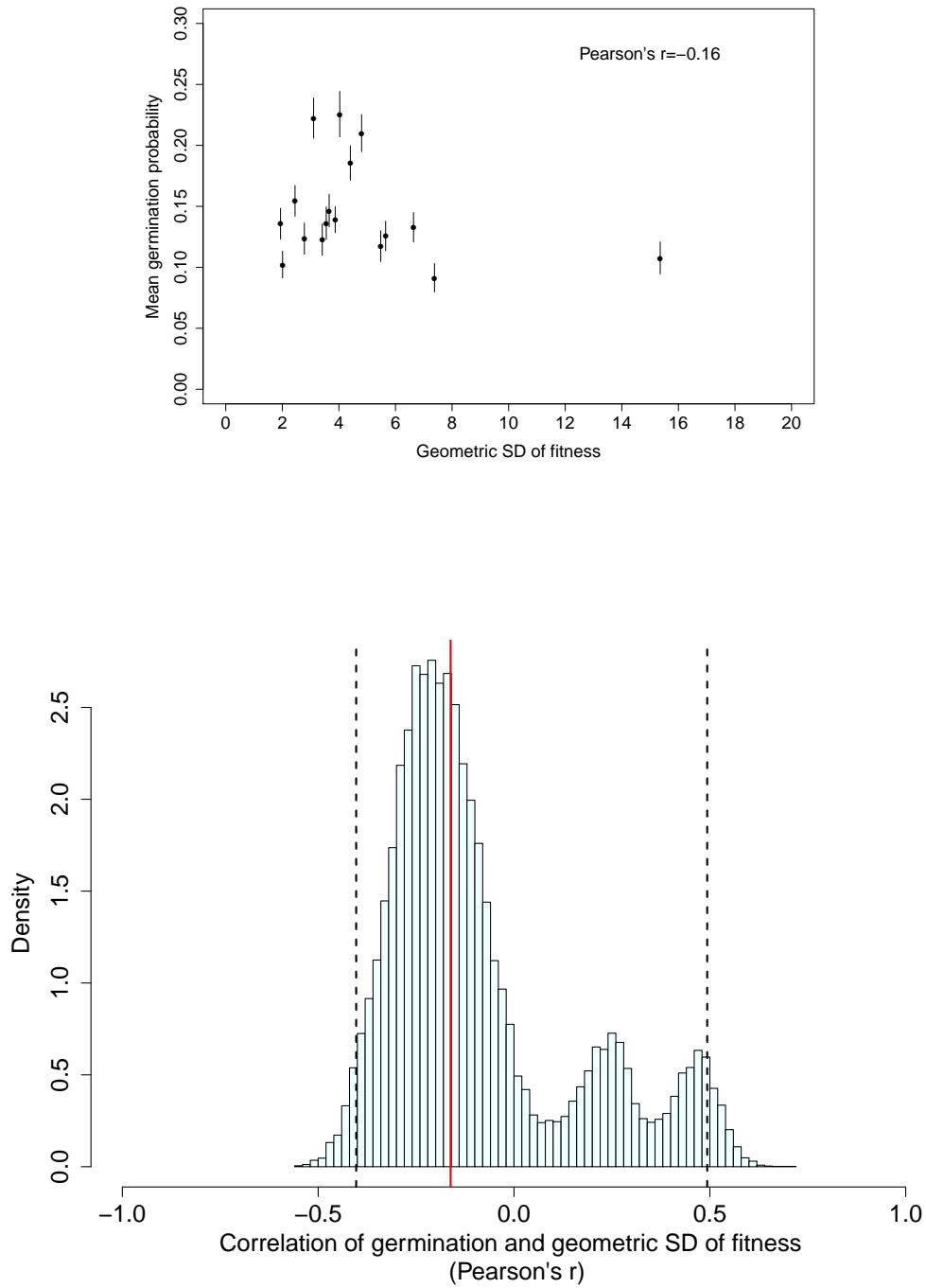
Figure 3: The top panel shows the observed germination probability plotted against the temporal variation in per capita reproductive success. The bottom panel shows the posterior distribution of correlation between observed germination probability and geometric SD of per capita reproductive success; the median correlation is negative (-0.16) but the 95% credible interval overlaps 0.
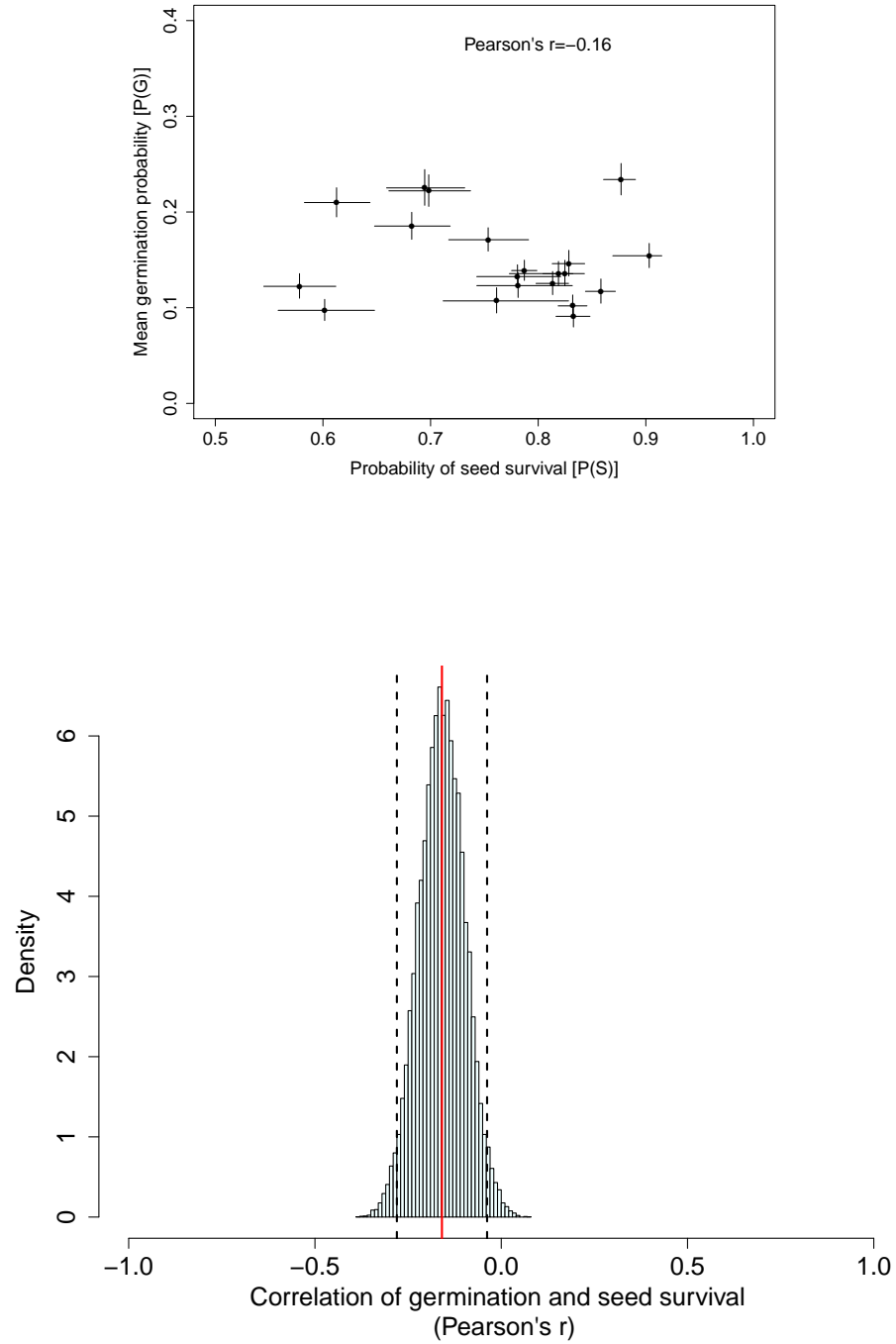
18

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 median correlation is negative (-0.16) and the 95% credible interval does not overlap 0.

References

D. Cohen. Optimizing reproduction in a randomly varying environment. *Journal of Theoretical Biology*, 12(1):119–129, Sept. 1966. ISSN 00225193. doi: 10.1016/0022-5193(66)90188-3. URL https://linkinghub.elsevier.com/retrieve/pii/0022519366901883.

D. Cohen. Optimizing Reproduction in a Randoruly Varying Environment when a Correlation May Exist between the Conditions at the Time a Choice has to be Made and the Subsequent Outcome. *Journal of Theoretical Biology*, 16:1–14, 1967.

D. Cohen. A General Model of Optimal Reproduction in a Randomly Varying Environment. *The Journal of Ecology*, 56(1):219, Mar. 1968. ISSN 00220477. doi: 10.2307/2258075. URL https://www.jstor.org/stable/2258075?origin=crossref.

E. A. Eager, R. Rebarber, and B. Tenhumberg. Modeling and Analysis of a Density-Dependent Stochastic Integral Projection Model for a Disturbance Specialist Plant and Its Seed Bank. *Bulletin of Mathematical Biology*, 76(7):1809–1834, 2014. ISSN 15229602. doi: 10.1007/s11538-014-9978-y.

M. R. Easterling and S. P. Ellner. Dormancy strategies in a random environment: Comparing structured and unstructured models. *Evolutionary Ecology Research*, 2:387–407, 2000.

V. M. Eckhart, M. A. Geber, W. F. Morris, E. S. Fabio, P. Tiffin, and D. A. Moeller. The Geography of Demography: Long-Term Demographic Studies and Species Distribution Models Reveal a Species Border Limited by Adaptation. *The American Naturalist*, 178(S1):S26–S43, Oct. 2011. ISSN 0003-0147, 1537-5323. doi: 10.1086/661782. URL https://www.journals.uchicago.edu/doi/10.1086/661782.

S. Ellner. ESS germination strategies in randomly varying environments. II. Reciprocal Yield-Law models. *Theoretical Population Biology*, 28(1):80–116,

Aug. 1985a. ISSN 00405809. doi: 10.1016/0040-5809(85)90023-1. URL https://linkinghub.elsevier.com/retrieve/pii/0040580985900231.

S. Ellner. ESS germination strategies in randomly varying environments. I. Logistic-type models. *Theoretical Population Biology*, 28(1):50–79, Aug. 1985b. ISSN 00405809. doi: 10.1016/0040-5809(85)90022-X. URL https://linkinghub.elsevier.com/retrieve/pii/004058098590022X.

M. E. K. Evans and J. J. Dennehy. Germ Banking: BetHedging and Variable Release From Egg and Seed Dormancy. *The Quarterly Review of Biology*, 80(4):431–451, 2005. ISSN 0033-5770. doi: 10.1086/498282.

J. R. Gremer and D. L. Venable. Bet hedging in desert winter annual plants: optimal germination strategies in a variable environment. *Ecology Letters*, 17 (3):380–387, Mar. 2014. ISSN 1461023X. doi: 10.1111/ele.12241. URL http://doi.wiley.com/10.1111/ele.12241.

J. R. Gremer, S. Kimball, and D. L. Venable. Within-and among-year germination in Sonoran Desert winter annuals: bet hedging and predictive germination in a variable environment. *Ecology Letters*, 19(10):1209–1218, Oct. 2016. ISSN 1461023X. doi: 10.1111/ele.12655. URL http://doi.wiley.com/10.1111/ele.12655.

L. Heinrich, J. Mller, A. Tellier, and D. ivkovi. Effects of population- and seed bank size fluctuations on neutral evolution and efficacy of natural selection. *Theoretical Population Biology*, 123:45–69, 2018. ISSN 10960325. doi: 10.1016/j.tpb.2018.05.003. URL https://doi.org/10.1016/j.tpb.2018.05.003.

A. Lindn and S. Mntyniemi. Using the negative binomial distribution to model overdispersion in ecological count data. *Ecology*, 92(7):1414–1421, July 2011. ISSN 0012-9658. doi: 10.1890/10-1831.1. URL http://doi.wiley.com/10.1890/10-1831.1.

K. A. Mccue and T. P. Holtsford. Seed bank influences on genetic diversity in the rare annual Clarkia springvillensis (Onagraceae). *American Journal of Botany*, 85(1):30–36, 1998. ISSN 00029122. doi: 10.2307/2446551.

L. Nunney. The Effective Size of Annual Plant Populations: The Interaction of a Seed Bank with Fluctuating Population Size in Maintaining Genetic Variation. *The American Naturalist*, 160(2):195, 2002. ISSN 00030147. doi: 10.2307/3079137. URL `https://www.jstor.org/stable/10.2307/3079137`.

M. Paniw, P. F. Quintana-Ascencio, F. Ojeda, and R. Salguero-Gmez. Accounting for uncertainty in dormant life stages in stochastic demographic models. *Oikos*, 126(6):900–909, 2017. ISSN 16000706. doi: 10.1111/oik.03696.

K. Ritland. The joint evolution of seed dormancy and flowering time in annual plants living in variable environments. *Theoretical Population Biology*, 24(3):213–243, 1983. ISSN 10960325. doi: 10.1016/0040-5809(83)90026-6.

D. L. Venable. Bet hedging in a guild of desert annuals. *Ecology*, 88(5):1086–1090, May 2007. ISSN 0012-9658. doi: 10.1890/06-1495. URL `http://doi.wiley.com/10.1890/06-1495`.

R. S. Waples. Seed Banks, Salmon, and Sleeping Genes: Effective Population Size in Semelparous, Age-Structured Species with Fluctuating Abundance. *The American Naturalist*, 167(1):118, 2006. ISSN 00030147. doi: 10.2307/3491252. URL `https://www.jstor.org/stable/10.2307/3491252`.