¹ [Working title]: **Intraspecific variation in range-wide seed bank dynamics is not**

² **consistent with density-independent bet hedging alone**

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Writing list

⁵ 1. Update Figure 1 to focus on components of life cycle discussed in this MS.

⁶ 2. Revise Figure 2 to talk about seeds being **intact** rather than **persistent**

⁷ 3. Revise description of seed bag experiment to include timing of experiment, temporal

⁸ focus, and spatial design

⁹ 4. Revise Figure 5 and 6 to change scale of geometric SD RS axis, change label size in

¹⁰ observed vs. predicted plot, change axes in observed vs. predicted plot, move plots of

¹¹ germination probability elsewhere in MS

¹² 5. Read Cohen & Ellner to identify the role of complete reproductive failure in the original

¹³ models for the evolution of bet hedging

¹⁴ 6. Write about strong and weaker test of the hypothesis (partial pooling, no partial pool-

¹⁵ ing)

¹⁶ 7. Write paragraph about history of studies of bet hedging via seed bank, with emphasis

¹⁷ on how this study addresses this question at an intraspecific level. Lower level of

18   variation in intraspecific germination fraction. (link)

19   8. Write and implement model checking process

1   Introduction

General introduction to seed banks - why do they matter? Seed banks are a strategy that annual plants may use to buffer against environmental variation and may be part of population persistence. 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)).

Theory - why do seed banks evolve? 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. 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. 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*)).[1]

Intraspecific variation; history of empirical studies Several studies have examined intraspecific variation in seed dormancy Clauss and Venable (2000); Hacker (1984); Hacker

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[1] In paragraph on theory, discuss density-independent models Cohen (1966, 1968), density-dependent models Ellner (1985*a*,*b*), predictive germination Cohen (1967), and unstructured versus structured models Easterling and Ellner (2000) (Tuljaparkur 1993, Valleriani and Tielborger 2006).

and Ratcliff (1989); Philippi (1993). The main set of papers I've included are ones that look at variation in germination among Sonoran Desert annuals (Gremer et al. (2016); Gremer and Venable (2014); Venable (2007)). The table 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.

Include altitudinal cline in the paragraph above

Genetic basis of seed banking; traits associated with seed banks; clines in seed banks/genetic variation. Cline associated with summer temperature Wagmann 2012

Altitudinal clines: more dormancy in seeds produced with lower annual temperature and precipitation Fernandez-Pascual 2012; low elevation pops have high germination fractions but high elevation pops require stratification to attain high germination fractions Gremer 2020. Studies of intraspecific variation in germination and dormancy behavior have identified correlations between these traits and climate at populations of origins. Other studies have used crosses to identify the genetic bases of germination and dormancy. Environmental variation is an indirect proxy for what theory predicts should drive the evolution of germination delays; variation in per-capita reproductive success. Seed dormancy and germination in the field is shaped by local adaptation and parental environment, which are functions of natural selection and transgenerational plasticity, respectively.

Experimental studies have elegantly decomposed multifactorial contributions to dormancy and germination. Consequences of a particular trait only become apparent in the context of geometric mean fitness over the long term.

See also the comments in Lewis 1953 on lifespan of seeds, absence of dormancy, and cued germination. Lewis 1963 Presidential address at SSE on catastrophic selection is also relevant. Discusses extinction and possible absence of a seed bank in populations of Clarkia species. Specifically mentions a population in the upper Kern Valley that had both whites and pinks; the pinks went extinct during a drought year while the whites maintained their population size. This work was followed up by others on different species in Clarkia genus. I think its important to consider the possibility that C. xantiana being studied in 1963 was a xantiana/parviflora ssp. which may have different dynamics than the outcrossing xantiana/xantiana. Furthermore: the upper parts of the range have the highest rates of germination which may also trade off with low survival. It would be interesting to put that observation in the range-wide context!

Knies et al. 2004 studied 2 C. xantiana populations; seeds of outcrosser are heavier than selfers. Identify heavier seeds (.1 mg heavier at SC than WH population). Seeds from both populations were bullet-shaped but differ in shape of exotesta cells; WH cells are gourd shaped, SC shapes are even width and spherical. Seed size/number trade-off: smaller size for dispersal; greater mass increases germination probability. Smaller seed size also facilitates seed integration into soil seed bank. Small seed size is also correlated with a persistent seed bank (Thompson et al. 1993). Larger seeds may germinate under more conditions and perhaps have smaller seed bank.

Moeller et al. 2011 population genetic study.

Eckhart and Geber 1999 identify more populations than those of Lewis, populations that they have since monitored intensively.

Price et al. 1985 followed a population for 2 years, did an elimination experiment. determined a dormant seed bank. Snow 1960 reports eliminating plants and not observing plants the following year.

Geber and Eckhart 2005 observed a 30-fold difference in lifetime fitness [calculated as

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number of germinants times survival, flower number, fruit set and seed set] between two transplant years (one wet, one dry). Fitness was very low in the dry year of the study (0.02-0.03 seeds per seed planted). They observed a 2-4 fold difference between years in germination, seedling survival, and flower number. They did not observe a difference in fruit or seed set. Western populations showed evidence of regional adaptation: survival and flower number. Germination declined from the western to eastern transplant sites [in contrast to what we observe here?] Germination is consistently higher in subspecies xantiana than parviflora. From west to east, rainfall declines and becomes more variable. Low survivorship is the product of end-of-season drought, small mammal herbivory (Geber and Eckhart 2005, Benning et al. 2019), competition by higher vegetation cover of grasses (survivorship increases with plant size), fungal rust infection. Plants from western populations are larger. Note that the transplant experiments took place on igneous soils, and later work by Vince has shown that soil type is important.

Eckhart et al. 2010 IJPS: geographic patterns in precipitation, decline from west to east, mirrored geographic pattern in midday water potential (reduced performance). Metasedimentary soils were more resistant and finer. Soil characteristic curves indicated that metasedimentary soils can hold more water but that it becomes unavailable to plants at higher water contents. Higher water potential on steeper, eroding slopes; this soil was softer and coarser. Decline in soil water potential (more negative) decreases plant size and fruit number. However, soil water potential is unrelated to seedling survival in the study years. Metasedimentary rocks may compound effect of decline in precipitation. Metasedimentary rocks may hold more water but it may be more available to plants in igneous soils.

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 (1985a,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 relation-

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ship, 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. [What is the relationship between interannual variation in fitness and dormancy? This is a question about whether fitness variation and dormancy are positively correlated as expected ? this is what selects for bet hedging.]

Seed dormancy and persistence in the soil seed bank may be a bet-hedging strategy that is favored by environmental uncertainty. If this is the case in *C. xantiana*, I think we might expect increased seed survival and decreased germination at the eastern range edge (precipitation is more variable at eastern populations in winter and spring). This seems to be opposite of what was observed in the previous study ? though I could also be misinterpreting this. This is could be one reason to revisit this question with a new analysis.

Why using the Clarkia system? We expect to see differences among populations in either seed survivorship or variance in fitness. 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. [need to be clear about this] also know that the environment changes across the range; that will affect the mean fitness

I expect bet hedging stages to be sensitive to variation in an environmental cue. For something to be an adaptive strategy, it should respond to variation in the environment to capitalize on good years such as ones with high precipitation. To investigate the sensitivity of vital rates to the environment, I estimate the slope of the relationship between environmental cues and vital rates at individual sites using a random coefficients model that estimates covariation between intercepts and slopes. I predict that I will estimate variation both in the intercept and slope for populations, and that variation in the modeled cue [to be

determined] will be positively related to the estimated slope. [What is the relationship between dormancy and environmental cues? This is a question about whether we can make any inferences about the mechanism responsible for bet hedging in this system.]

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

The fitness consequences of germination delays only become evident when placed in context of reproductive success variation.

Studies with *Clarkia xantiana* ssp. *xantiana* have also observed strong variation in fitness in time (Geber and Eckhart (2005)), and for range-wide variation in population growth rate (Eckhart et al. (2011)). Transplant experiments demosntrate local adaptation of fitness components; these studies have compared the relative fitness of populations. Continued surveys have provided insight into the demographic patterns and their relation to environmental variables. In light of this work, we sought to reexamine life history patterns in populations of Clarkia in order to understand; fitness consequences of seed banks are expected to affect geometric mean fitness rather than arithmetic mean so multiple years are required to understand them.

Eckhart et al. 2004 conducted a transplant experiment in two years in which seed set

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varied ten-fold. There are additional studies that did elimination experiments (with other species of Clarkia) and suggested limited role/role for seed bank because plants did or did not come up with following year.

An earlier study focused on range-wide variation in demography identified a gradient in rainfall variability during the growing season, from wetter and less variable in the west to drier and more variable in the east (Eckhart et al. (2011); Fig. 1B&C for pattern from 2005-2020).

Variation and coverage in (D) also led to testing what shaped seed banks and life history patterns. We focus on bet hedging as this is a classic case of dealing with environmental variability.

Population vital rates exhibit intraspecific variation across *Clarkia xantiana*'s geographic range, including age-specific germination and seed survival (Eckhart et al. (2011)). In a study of *C. xantiana* population dynamics that identified 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 (s_1) and an increase in germination rate (g_1) of first-year seeds from west to east. Demographic observations Eckhart et al. (2011) and transplant experiments demonstrate that fitness can exhibit dramatic interannual variation (e.g. 30-fold between a wet and dry year in Geber and Eckhart (2005)).

Seed dormancy and persistence in the soil seed bank may be a bet-hedging strategy that is favored by environmental uncertainty. If this is the case in *C. xantiana*, we might expect increased seed survival and decreased germination probabilities in populations with more variability in per-capita reproductive success. However, broad geographic patterns in rainfall variability and life history are not consistent with this cursory explanation since variation in rainfall increases from west to east, and germination probability also increases Eckhart et al. (2011). We thus sought to understand intraspecific variation in *C. xantiana* seed vital rates in the context of broader life history patterns.

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, we estimate the correlation between germination and seed survival, and between germination variance in per-capita reproductive success. We also examined whether observed levels of germination are consistent with germination levels predicted by a density-independent model of bet hedging.

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

2 Methods

2.1 Clarkia life history

Clarkia xantiana is a winter annual that germinates with late fall and winter rains. In our study region, the Kern Valley in the southern Sierra Nevada Mountains, historically happens

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between October and late February or early March. Seedlings grow throughout the winter and spring, and surviving plants flower in late spring and early summer, April into early July. Pollinated fruits set seed in the early summer, June to July. Seeds of *C. xantiana* are produced in early summer, with fruits that dry out and gradually split open. Most seeds appear to be shed from fruits within 3-4 months after production, but can remain on the plant for up to a year. Seeds are small (< 1 mm in width) and have no structures to aid in aerial dispersal.

We represent the *Clarkia xantiana* as a life cycle graph (Figure **??**A) that describes transitions from October of year t to October of year $t+1$ in terms of underlying vital rates. The census period occurs when the entire population is seeds, and corresponds to the time at which seed bags are placed into the field (see below). Seeds are grouped into three stages: age 0 seeds, which were produced in the current year; age 1 seeds, which were produced in the previous year; age 2+ seeds, which were produced two or more years ago. Persistence of seeds in the seed bank is represented by transitions from younger to older seeds. Production of new seeds is captured by transition to the age 0 seed state.

Transitions in the life cycle graph are the product of age-specific seed survival and germination, and aboveground seedling survival to fruiting, fruit production, and seeds per fruit. Seed-related rates are represented separately for age 0, 1, and 2+ seeds. Germination for each age class is given as g_1, g_2, and g_3, respectively. Seed survival from seed production to the first October is given as s_0, and survival from October to February is given as s_1, s_3, and s_5 for age 0, 1, and 2+ seeds, respectively. Survival from February to October is given as s_2, s_4, and s_6 for age 0, 1, and 2+ seeds, respectively. We assume that vital rates remain unchanged after age 2. We also we assume that all plants experience the same vital rates upon germination seed age at germination does not affect seedling survival to fruiting (σ), fruits per plant (F), or seeds per fruit (ϕ).

The life cycle graph (Figure **??**A) corresponds to the annual projection matrix

$$
\boldsymbol{A} = \begin{bmatrix} s_1 g_1 \sigma F \phi s_0 & s_3 g_2 \sigma F \phi s_0 & s_5 g_3 \sigma F \phi s_0 \\ s_1(1-g_1)s_2 & 0 & 0 \\ 0 & s_3(1-g_2)s_4 & s_5(1-g_3)s_6 \end{bmatrix} \tag{1}
$$

that summarizes transitions between stages.

2.2   Creating the dataset

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

To estimate transitions in the seed bank, we used observations from a seed bag burial experiment conducted in all populations from 2006-2009 (Figure 2). The experiment has been previously described in Eckhart et al. (2011) and we reanalyze the data here. Geber and collaborators buried seeds in bags and unearthed 1, 2, or 3 years after being buried to count seedlings and intact, viable seeds. The experiment was repeated in 3 consecutive years and ended in 2009. We thus have 3 sets of observations associated with 1 year old seeds, 2 sets of observations associated with 2 year old seeds, and 1 set of observations associated with 3 year old seeds. We use data from the experiment to estimate age-specific germination and seed survival (see Joint model for seed vital rates) but note that we test predictions of bet-hedging theory that are based on an unstructured seed bank and use only the relevant

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²⁶² subset of transitions in our analysis (see Computing vital rates).

²⁶³ To estimate per-capita reproductive success, we combine censuses of seedlings and fruiting

²⁶⁴ plants, surveys of fruits per plant, and lab counts of seeds per fruit. To assess the survival of

²⁶⁵ seedlings to fruiting plants, we counted seedlings and fruiting plants in 30 0.5 m² permanent

²⁶⁶ plots from 2006–2020 (Eckhart et al. (2011)). To assess seed production by plants that

²⁶⁷ survive to reproduction, we counted fruits per plant on individual plants in permanent plots,

²⁶⁸ and on additional haphazardly chosen plants throughout the population. We then attempted

²⁶⁹ to obtain 20-30 fruits per population, which we used to count seeds per fruit (Eckhart et al.

²⁷⁰ (2011)).

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

Parameter data	Description	Data set	Time span
SEED VITAL RATES	—	—	—
Seed survival and germination	Seed bag burial	$\mathbf{Y}_1$	2006-2009
Seed viability	Viability trials	$\mathbf{Y}_2$	2006-2009
SEEDLING SURVIVAL	—	—	—
Seedling survival to fruiting	Field surveys	$\mathbf{Y}_4$	2006-2019
FRUITS PER PLANT	—	—	—
Total fruit equivalents per plant	Field surveys	$\mathbf{Y}_5$	2006-2012
Undamaged and damaged fruits per plant	Field surveys	$\mathbf{Y}_6$	2013-2019
Total fruit equivalents per plant	Extra plots	$\mathbf{Y}_7$	2006-2012
Undamaged and damaged fruits per plant	Extra plots	$\mathbf{Y}_8$	2013-2019
SEEDS PER FRUIT	—	—	—
Seeds per undamaged fruit	Lab counts	$\mathbf{Y}_9$	2006-2019
Seeds per damaged fruit	Lab counts	$\mathbf{Y}_{10}$	2013-2019

2.3 Model

²⁷³ We use observational and experimental data from 20 populations of *Clarkia xantiana* to

²⁷⁴ estimate transition probabilities across the life cycle. We fit multilevel models to obtain

²⁷⁵ population-specific estimates for belowground vital rates, and year- and population-specific

²⁷⁶ estimates for aboveground vital rates. Because we were interested in describing the life

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histories of individual populations, we built separate models for each population. Our general approach applies a common model structure to partially pool observations from each population.

We first explicitly describe our formulation in terms linear mixed models before defining the joint posterior (Evans et al. (2010); Ogle and Barber (2020)). We assume that the latent mean of observations in year j at a population k, θ_{jk}, is drawn from a normal distribution with mean $\theta_{0,k}$ and variance σ_j^2.

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

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

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

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

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

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

The distribution of the observations y_{ij} is conditional on the year-specific parameters θ_j and σ_j^2. In turn, the year-specific parameter θ_j is conditional on the population-specific parameters θ_0 and ς^2. We placed priors on all parameters found only on the right hand side of conditional statements $(\theta_0, \sigma_j^2, \varsigma^2)$. In practice, we implemented this model by specifying the population- and year-levels of the model with normal distributions; for example, $[\theta_j | \theta_0, \varsigma^2]$ is $\theta_j \sim N(\theta_0, \varsigma^2)$. The model thus describes a structure in which years are nested within populations.

2.4 Model statements, implementation, and fitting

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

We prepared data for analysis using the tidyverse and tidybayes packages (CITE) in R VERSION; CITE. We wrote, fit all models, and estimated posterior distributions using JAGS VERSION with rjags (Plummer 2016). We randomly generated initial conditions for all parameters with a prior by drawing from the corresponding probability distribution in R before passing the initial values to rjags. We ran three chains for XX,000 iterations. The first XX,000 samples were discarded as burn-in and we sampled the following XX,000 iterations. We did not thin the chains (Elderd and Miller (2015)).

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

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

2.5 Computing vital rates

2.5.1 Belowground vital rates

338 We used the age-specific germination probabilities, survival function, and viability estimates

339 to account for viability in estimates for the probability of germination and survival. We first

340 discretized the survival function to times at which we observed germination and counted

341 seeds (January and October). Estimates of survival over these intervals are the probability

342 that a seed remains intact, but does not account for loss of viability. Next, we used viability

343 estimates from October to calculate viability for January by interpolation (Figure 2D). We

344 tested the viability of seeds in October, and were thus able to estimate the proportion of

345 viable seeds (Figure 2B; filled points). We inferred the viability of intact seeds in January

346 by assuming that seeds lost viability at a constant rate (exponential decay). Further, we

347 interpolated between estimates by assuming that viability changed at a constant rate between

348 years, and that all seeds were viable at the start of the experiment (Figure 2B; open points).

349 We combined the discretized survival function and viability estimates to construct a

350 survival function for the probability that a seed remains intact and viable (Table 2, col-

351 umn X). Specifically, we multiplied the posteriors of the discretized survival and viability

352 estimates. Because we combined estimates, some portions of the posterior for seed survival

353 probability was than 1, especially for later seed ages. We restricted the posterior to be less

354 than 1 by truncating the distribution and resampling to redistribute the probability mass.

355 We take this step to retain parameter uncertainty about survival probability in cases where

356 combining the estimates implies a high probability of survival. The survival function for

357 viable seeds (ϕ) is composed of estimates of persistence over time (θ.), estimates of viability

358 (ν.), and estimates of germination conditional on persistence (γ.).

359 We used the discretized survival function and age-specific germination probability to

360 obtain the estimates of germination and seed survival required to test predictions from bet-

hedging theory. Table **??** defines the age-specific germination probabilities and survival probabilities for the structured model in Eckhart et al. (2011) in terms of the survival function and age-specific germination probabilities. Figure 2E-F illustrate the relationship among the various probabilities of germination and seed survival. Estimates from the seed bag experiment correspond to the probability of germination or survival conditional on persistence (e.g. γ_1). Multiplying these estimates by the probability of persistence up to a certain time gives the unconditional probability (e.g. $\theta_1 \times \gamma_1$). Finally, the probability conditional on persistence and viability is estimated by incorporating loss of viability into the survival function (e.g. γ_1/ϕ_1), and defines the parameters in the structured population model.

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

Time (x_i)	Persistence $S(x_i)$	Persistence & viability $S(x_i)$
Oct_0	θ_0	$\phi_0 = \theta_0$
$\text{Jan}_{1,\text{total}}$	θ_1	$\phi_1 = \theta_1(\gamma_1 + (1-\gamma_1)\nu_1^{1/3})$
$\text{Jan}_{1,\text{intact}}$	θ_2	$\phi_2 = \theta_2\nu_1^{1/3}$
Oct_1	θ_3	$\phi_3 = \theta_3\nu_1$
$\text{Jan}_{2,\text{total}}$	θ_4	$\phi_4 = \theta_4(\gamma_2 + (1-\gamma_2)\nu_1(\nu_2/\nu_1)^{1/3})$
Description	Parameter	Probability
July-October	s_0	
October-January	s_1	ϕ_1
1-year old germination	g_1	γ_1/ϕ_1
January-October	s_2	ϕ_3/ϕ_2
October-January	s_3	ϕ_4/ϕ_3

2.5.2 Per-capita reproductive success

In order to make our analysis comparable to previous empirical studies of bet hedging, we calculated per-capita reproductive success as the product of the probability of seedling survival to fruiting, fruits per plant, and seeds per fruit. We thus calculate per-capita reproductive success as the number of seeds produced per seedling, on average (e.g. Gremer

$_{375}$ and Venable (2014); Venable (2007)).

$_{376}$ We used a consistent method to estimate seedling survival to fruiting throughout the

$_{377}$ experiment, and use the population- and year-level means ($\mu_{\text{S},jk}$) in our calculation. Because

$_{378}$ we estimated fruit production in 2 different ways during the study, we chose to use total fruit

$_{379}$ equivalents (TFE) per plant as our common estimate of fruit production. From 2006–2012,

$_{380}$ we used $\mu_{\text{TFE},jk}$) as estimated in the statistical model. From 2013–2020, we used the ratio

$_{381}$ of seeds per damaged to undamaged fruit to calculate a proportion of damaged fruits to add

$_{382}$ to undamaged fruit counts, as in

$$\text{TFE} = \text{undamaged fruits} + \frac{\text{seeds per damaged fruit}}{\text{seeds per undamaged fruit}} \times \text{damaged fruits.} \qquad (5)$$

$_{383}$ We used posterior distributions for population- and year-level parameters (e.g. $\mu_{\text{US},jk}$)

$_{384}$ for these calculations and obtained estimates of $\mu_{\text{TFE},jk}$) for 2013–2020. Finally, we used

$_{385}$ estimates of seeds per undamaged fruit ($\mu_{\text{US},jk}$) as our estimate of seeds per fruit.

$_{386}$ In terms of parameters from our statistical models, per-capita reproductive success F_{jk}

$_{387}$ at population j in year k is calculated as

$$F_{jk} = \phi_{jk} \times \lambda_{\text{TFE},jk} \times \lambda_{\text{US},jk}, \qquad (6)$$

$_{388}$ where

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

$$\lambda_{\text{TFE},jk} = \exp(\mu_{\text{TFE},jk}) \tag{7}$$

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

Our multilevel models for aboveground vital rates pooled data more strongly in years with relatively little data. A benefit of this approach is that it implicitly corrects for variation in sample size. While this is beneficial for distinguishing between spurious estimates and true temporal variation, it may also underestimate variation in reproductive success. At the extreme, estimates in years without any data are pooled to the population-level means. Years with zero seedling survivorship would have estimates for fruits per plant that are pooled towards the population-mean (because there were no fruiting plants on which to count fruits). Because estimates of fruits per plant are based on surveys of the whole population, we are confident that per-capita reproductive success was 0 in years in which we observed no fruits per plant and obtained no counts of seeds per fruit (years with no observations for fruits per plant and seeds per fruit in Figure **??**). We also considered a second, less conservative estimate of reproductive success in which we assumed that per-capita reproductive success was 0 in years with no seedlings germinated or survived in our permanent plots. This is equivalent to basing our calculations of per-capita reproductive success on a model with no pooling, as the posterior mode of seedling survivorship to fruiting should be very small (0) in years without any seedlings surviving.

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Analysis

Correlation between germination probability and seed survival

Increased seed survivorship is predicted to decrease the optimal germination probability Cohen (1966); Ellner (1985a). I assessed whether the observed germination probability was negatively correlated with seed survival (Gremer and Venable (2014)). I calculated the probability that seeds which do not germinate in January remain in the seed bank until the following January ($s_2 s_3$). I obtained the posterior distribution for the correlation between germination and seed survival by calculating the correlation of g_1 and $s_2 s_3$ at each iteration of the MCMC output (Hobbs and Hooten (2015), p 194-5). Results of this analysis are shown in Figure 3. Bet hedging models predict that germination probability should be negatively correlated with seed survival; 95% credible intervals that do not overlap zero provide support for this prediction. The bottom panel shows the posterior distribution of correlation between the probability of germination and seed survival.

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

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

To calculate the temporal variation in per-capita reproductive success for each population, I sampled the posterior distribution of reproductive success for each year and calculated the geometric SD of per capita reproductive success. I obtained the sample correlation of germination and geometric SD of per capita reproductive success at each iteration of the MCMC output (Hobbs and Hooten (2015), p 194-5). Bet hedging models predict that

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germination probability should be negatively correlated with temporal variance in fitness; 95% credible intervals that do not overlap zero provide support for this prediction. The geometric SD of per capita reproductive success was calculated as exp(SD (log (per capita reproductive success+0.5))) (Venable (2007)). Results of this analysis are shown in Figures 4 and 5.

Density-independent model for germination probability

We use estimates of seed survival and reproductive success to investigate the adaptive value of delayed germination (Gremer and Venable (2014)). We parameterize a model of population growth rate and calculate the optimal germination strategy for different combinations of seed survival and reproductive success. We describe *C. xantiana*'s life cycle and calculate population growth rate with the equation:

$$\lambda = g_1 Y(t) s_0 s_1 + (1 - g_1) s_2 s_3 \tag{8}$$

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

For each population, I numerically calculate the optimal germination probability for the observed variation in reproductive success and seed survival. In each case, I use the posterior mode of the parameter estimates in the equation for density-independent growth (equation (8)). I resampled the posterior modes of per-capita reproductive success $(Y(t))$ to obtain a sequence of 1000 years. I used this same sequence of $Y(t)$ and the seed survival probabilities to calculate long-term stochastic population growth rates (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 the geometric mean of the population growth rate. I repeat the simulations 50 times for each population, resampling the sequence of per-capita reproductive success, $Y(t)$, each time. I then calculated the mean of the optimal germination fractions.

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

Results

Correlation between germination probability and seed survival

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

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

I examined the correlation between germination and variance in per-capita reproductive success (Figure 4 and 5). The bottom left panel shows the posterior distribution of correlation between modeled germination probability and geometric SD in per-capita reproductive success. Setting years without any observed plants to have a fitness of zero increases the range of the geometric standard deviation in reproductive success (compare panels A in Figure 4 and

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5). However, for both calculations of per capita reproductive success, the median correlation is slightly positive and the 95% credible interval overlaps 0.

Optimal germination probability predicted by a density-independent model

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

Discussion

Results summary paragraph.

Comparison to other summaries.

Explanation of result with much higher germination than predicted under bet hedging. One possible factor is a correlation between plant size and dormancy/germination in first year. Seeds produced on larger plants are smaller and may thus exhibit higher dormancy. Plant fruit number generally declines from west to east, which may lead to plants with lower germination in the west vs. the east, all else being equal.

Another related factor might be density-dependent bet hedging. It also predicts lower than expected dormancy. But the problem is no longer optimization but an ESS strategy.

Dormancy, dispersal, seed size (see Venable and Brown 1988 in Philippi and Seger 1989)

Research has illuminated the influence of abiotic and biotic factors on population distribution and performance: topography (**?**), climate (Eckhart et al. (2011)), pollinator availability (**?**), and herbivory (**?**).

Revisit theory to see particular role of complete reproductive failure versus low fitness

years more generally. Cohen (1966) emphasizes the role of particularly bad years. This is highlighted by the inequality in equation (12), which states that for the optimal germination strategy to be bet hedging, it is sufficient that the harmonic mean is less than the survival probability of seeds that do not germinate. The minimum fitness has a strong impact on the harmonic mean of fitness (see definition of harmonic mean on Wikipedia), and a single year of very low fitness would tend to make the harmonic mean small. In particular, the harmonic mean is 0 when any of its values is 0. The probability of complete reproductive failure is thus particularly important. Years with no seedling survival in the plots or no germination are those in which fitness would be zero; there are only 4/20 populations in which this does not happen. We fit two types of models to the aboveground data; one with partial pooling and one with no pooling. The first was an attempt to correct for sampling variation; the latter an attempt to estimate per-capita reproductive success as-is, providing a more extreme estimate of interannual variation but one that reflects the combined effect of sampling variation and true variation.

Simons 2011 adaptive tracking: optimal trait values change continually and follow from natural selection; depends on standing genetic variation and mutational variance; not clear how rate interacts with fluctuating selection; effectiveness of adaptive tracking may be reduced under environmental variance but needs exploration phenotypic plasticity: range of phenotypes expressed over range of environments (phenotypic norm of reaction); evolution of adaptive plasticity depends on the phenotype-fitness association being predictable; plasticity is expected to be adaptive if cues are appropriate; effectiveness of plasticity under environmental variation depends on temporal stability of the mechanism underlying the relationship between phenotype and fitness; evolution of plasticity interacts with evolution of adaptation bet hedging: adaptation to unpredictability or change itself rather than adaptation to specific or predictable environmental changes; bet hedging is expected to evolve under conditions of unpredictable environmental variance & where adaptive tracking and evolution

of plasticity are constrained; bet hedging traits maximize fitness across generations but do not maximize fitness within a generation, bet-hedging can appear detrimental on short time scales; **conservative bet hedging** is a character that is safe; diversification bet hedging spreads risk among an array of phenotypes

Adaptive tracking vs. bet hedging: Annual plants with multi-generational trend of lengthening then contracting seasons would show delayed than contracting seasons. Unpredictable variance in season length (on the other hand) is expect to result in early reproduction that minimizes the risk of reproductive failure (bet hedging strategy). Phenotypic plasticity vs. bet hedging: Plastic norms of reaction result in expression of an optimal phenotype over a range of environments; bet hedging expresses a single phenotype (may be fixed level of diversification) that is neither optimal nor a failure across all environments. Adaptive plasticity would be an environment-appropriate adjustment to flowering time and evolution would depend on reliability of season length cue. Predictable and unpredictable environmental variance influence fitness: in these cases, expect a blend of plasticity and bet hedging. Eg. may expect diversification bet hedging around norms of reaction. Plasticity in seed germination may evolve in response to available cues, but the cues are imperfect representations of environment-fitness relationships, leading to evolution of both adaptive plasticity and diversification. Even more... If fitness consequences of norms of reaction vary over time, the norms may themselves be subject to geometric mean principle; norms of reaction may thus be bet hedging characters that differ in shape from those that maximize fitness in short term; eg. from salmon where norm of reaction influencing freshwater vs. sea water in salmon is advantageous only over long term

Key is to look at geometric mean fitness first. Prevalence of bet hedging depends on whether selection for geometric mean fitness differs from arithmetic mean

Types of evidence

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1. Candidate bet hedging trait (CBH) may point to environmental variation

2. Observe unpredictable environmental factor OR genetic variation in CBH

3. Relate environmental variation to CBH among populations, genetic basis to CBH, CBH occurs at level of genotype (environment AND genotype)

4. Evidence linking environmental variance to fluctuating selection (fitness consequences) acting on the CBH

5. (direct test of adaptive significance of CBH) Compare fitness of CBH trait to a a non-bet-hedging alternative and show higher fitness (eg. diapause favored over not)

6. (direct test of adaptive significance of CBH) Degree of bet hedging is tested for optimality against an observed extent of fluctuating selection (ideal test of bet hedging)

In 15 years of data on 20 populations across the species range, we observed high seedling mortality and/or low germination in at least one year in all but four populations. Although most populations had at least some flowering plants in most years, there were also four populations in which no flowering plants were observed in the entire population. None of these populations, however, went extinct during the period of the study. Seeds can remain viable in the field and laboratory for at least 5 years, contrary to previous suggestions that seeds are unlikely to persist past a few years (Lewis 1962).

General introduction to seed banks/dormancy – Clarkia as a case where seed banks have been posited to be important – bet hedging theory and predictions – review of tests of bet hedging in plants – what we did

To empirically test this theory, "a density-independent model can be used to check quantitatively the optimality (or evolutionary stability) of a life history trait in a real population, because the density effects are manifested in the measured vital rates" and "to check if

a species germination fraction is optimal, one would estimate seed survivorship and the probability distribution of per capita seed yield. From these, the DI model predicts an "optimal" germination fraction, which can be compared with the actual germination fraction." Ellner (1985a).
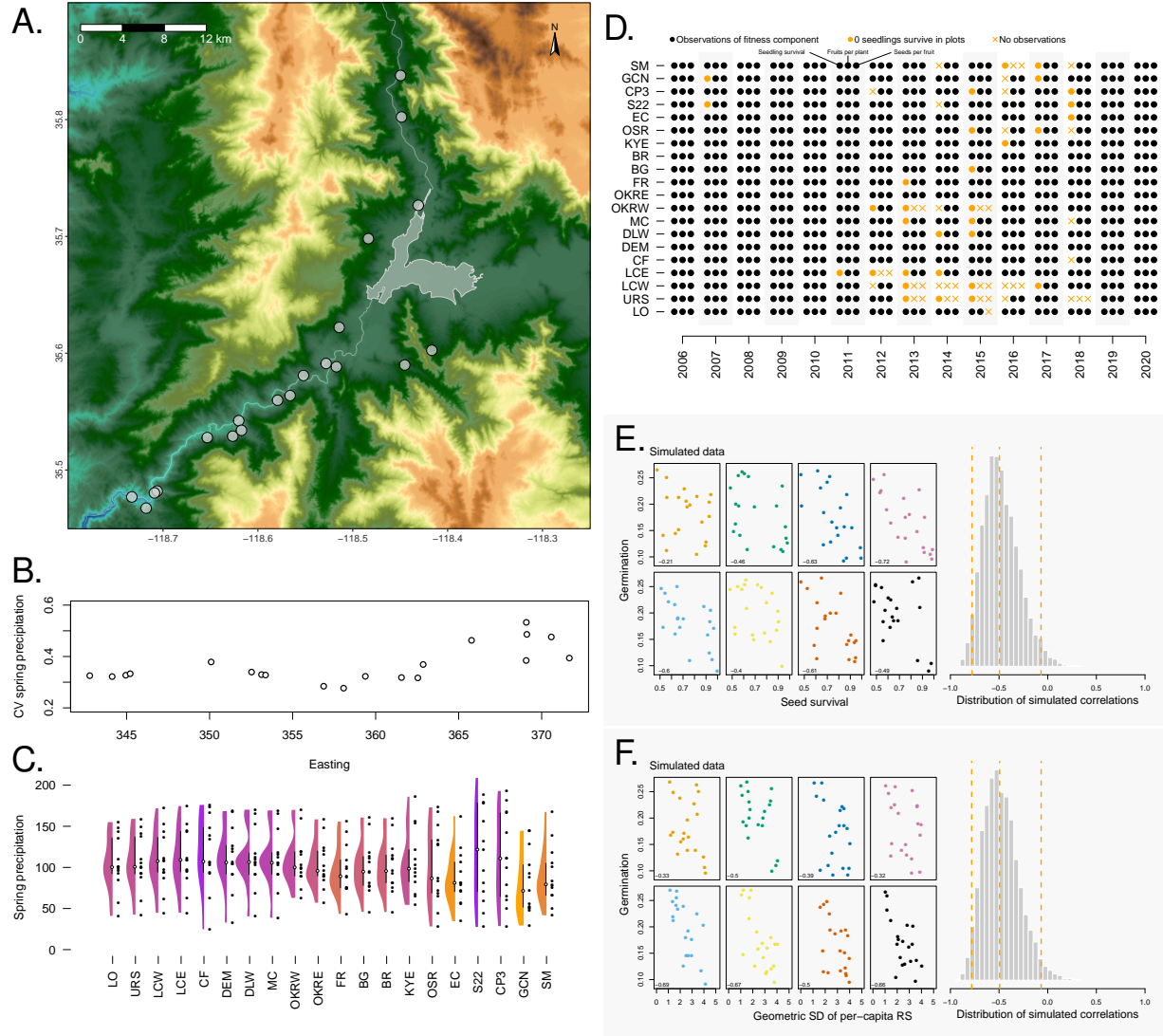
Figures

Figure 1: (A) Map of populations; populations exist across a complex area (topography, edaphic, climate, etc). (B) Earlier study identified gradient in CV of precipitation (need to check colors on my plot (C)). (D) 15 years of demography support idea that seed bank is important, especially evidenced by total absence of plants in multiple populations across the range but recovery in contrast to earlier work. (E & F) Present 2 key predictions of bet hedging models on the scale appropriate for what is known about Clarkia life history
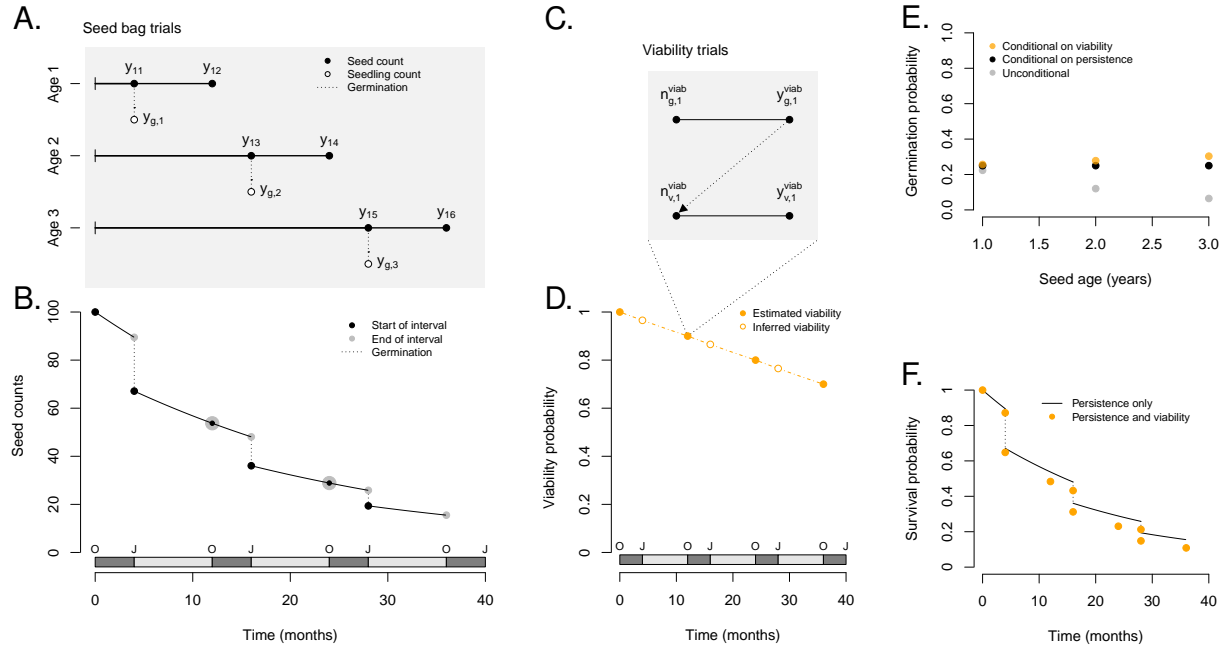
Figure 2: Summary of the seed bag burial experiments and viability trials. (A) A graphical representation of the seed bag trials. Seeds were buried at the start of each experiment (100 seeds in month 0). Seed bags were unearthed and intact seeds ($y_{..}$) and seedlings ($y_{g,.}$) counted. (B) A hypothetical survival function associated with persistence of seeds in the soil seed bank. (C) A graphical representation of the viability trials. Seeds were tested in two rounds; germination trials were performed and then some or all of the ungerminated seeds were tested for viability. (D) Hypothetical data from a series of viability trials and the interpolated, inferred viabilities at times when viability was unobserved. (E) Age-specific germination probably is summarized in three ways. (F) The survival function for persistence of seeds in the soil seed bank (black line) and the estimated discrete survival probabilities for persistence and viability of seeds (orange points).
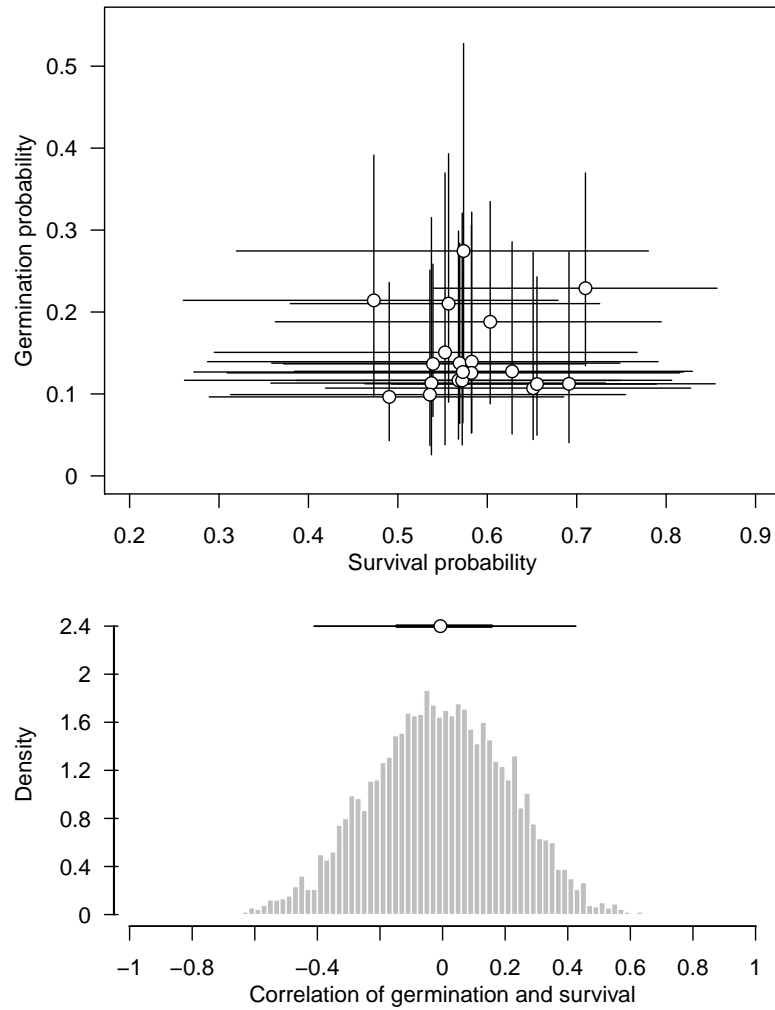
Figure 3: (A) The observed germination probability plotted against probability of seed survival. (B) The posterior distribution of correlation between observed germination probability and the probability of seed survival.
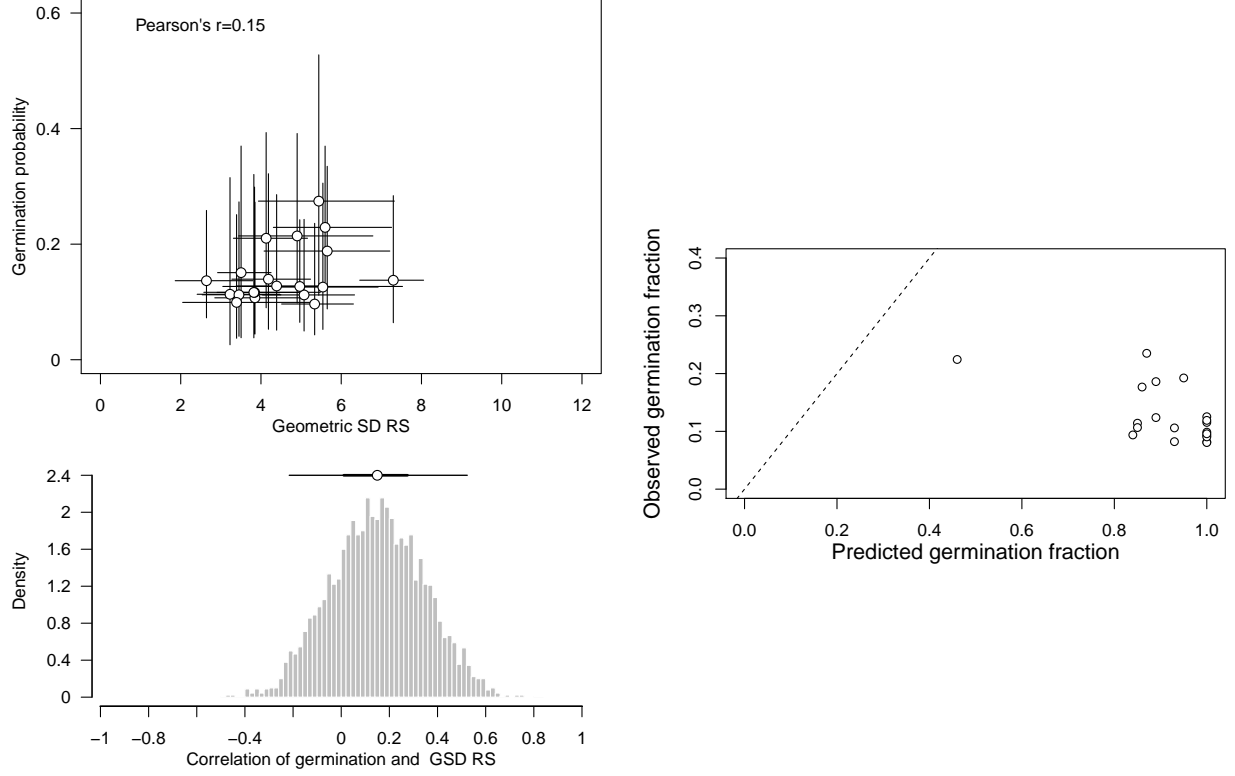
Figure 4: (A) The top left panel shows the observed germination probability plotted against the temporal variation in per capita reproductive success. (B) The bottom left panel shows the posterior distribution of correlation between observed germination probability and geometric SD of per capita reproductive success. (C) The top right panel shows observed germination probability plotted against the optimal germination probability predicted by a density-independent model. For each population, the observed germination probability is the obtained from the model for seed bank vital rates. Each point is the population-specific median of the posterior of g_1 for a model fit to data from seed bag experiments from 2006–2009. Data was pooled across years. The dotted line indicates a 1:1 relationship between observations and predictions. Values below the line indicate that the model predicts higher germination probabilities than observed; values above the line would indicate that the model predicts lower germination probabilities than observed.
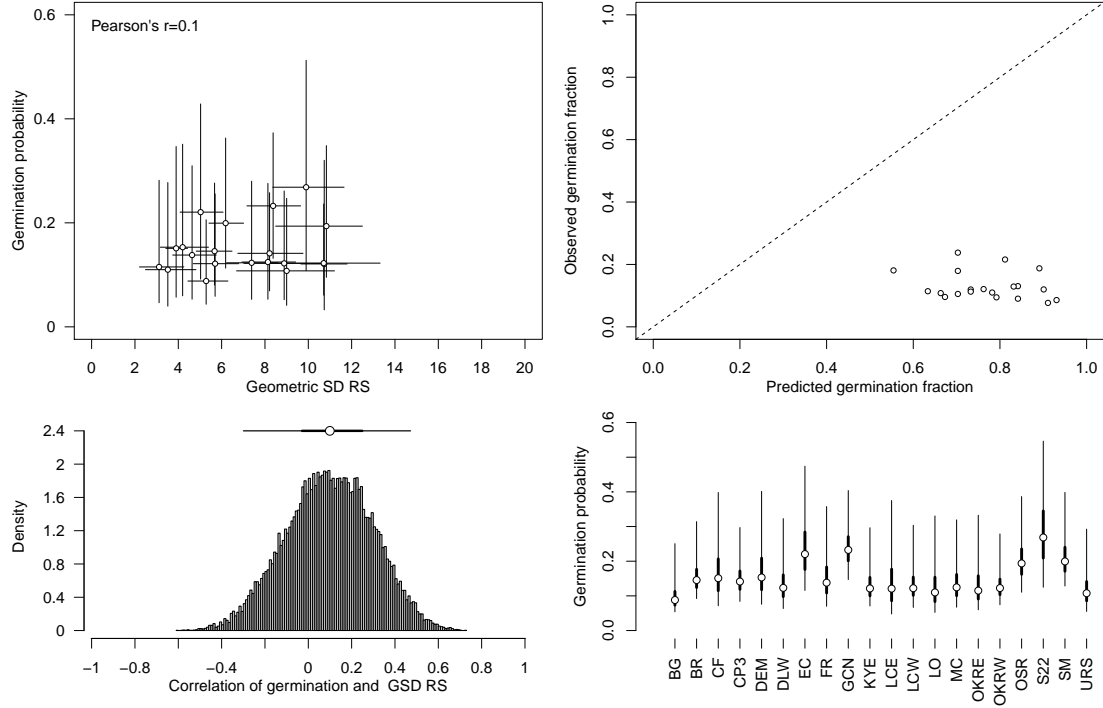
Figure 5: Results with low fitness years set to 0. (A) The top left panel shows the observed germination probability plotted against the temporal variation in per capita reproductive success. (B) The bottom left panel shows the posterior distribution of correlation between observed germination probability and geometric SD of per capita reproductive success. (C) The top right panel shows observed germination probability plotted against the optimal germination probability predicted by a density-independent model. For each population, the observed germination probability is the obtained from the model for seed bank vital rates. Each point is the population-specific median of the posterior of g_1 for a model fit to data from seed bag experiments from 2006–2009. Data was pooled across years. The dotted line indicates a 1:1 relationship between observations and predictions. Values below the line indicate that the model predicts higher germination probabilities than observed; values above the line would indicate that the model predicts lower germination probabilities than observed.

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Supplementary material

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

Joint posterior.

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

Priors.

Explanation of priors. Link to document: https://github.com/gregor-fausto/clarkiaSeedBanks/blob/master/products/appendices/appendix-priors/appendix-priors.pdf

Model checks.

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