

Effect of the Seed Bank on Evolutionary Rescue in Small Populations: Univariate and Multivariate Demogenetic Dynamics

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ABSTRACT: Under global change, the impact of seed banks on evolutionary rescue is uncertain. They buffer plant populations from demographic and genetic stochasticity but extend generation time and can become a reservoir of maladapted alleles. We built analytical and individual-based models to predict the effect of seed banks on the persistence of small annual plant populations facing an abrupt or sustained directional change in uni- or multivariate trait optima. Demogenetic dynamics predict that under most scenarios seed banks increase the lag yet enhance persistence to 200–250 years by absorbing demographic losses. Simulations indicate that the seed bank has a minimal impact on the genetic skew, although we suggest that this result could depend on the fitness component under selection. Our multivariate model reveals that by enlarging and reshaping the **G** matrix, seed banks can diminish the impact of mutational correlation and even accelerate adaptation under antagonistic pleiotropy relative to populations without a bank. We illustrate how the magnitude of optimum fluctuations, type and degree of optimum change, selection strength, and vital rates are weights that tip the scales determining persistence. Finally, our work highlights that migration from the past is not maladaptive when optimum fluctuations are large enough to create stepping stones to the new optimum.

Keywords: evolutionary rescue, genetic correlation, **G** matrix, environmental change, fluctuating selection, seed bank.

Introduction

Rapid changes in global climate and land use are altering selection regimes for a wide range of organisms across habitats worldwide (Siepielski et al. 2017; Otto 2018). Particularly in the face of increasing habitat fragmentation, dispersing to more favorable habitats is not an option, making

extinction more likely unless adaptation can keep pace with environmental change (Jump and Peñuelas 2005). While plasticity could mitigate some effects on population growth, evolutionary rescue via genetic adaptation is required for recovery and long-term persistence under strong shifts in the optimal phenotype (Bürger and Lynch 1995; Gomulkiewicz and Holt 1995; Jump and Peñuelas 2005; Hoffmann and Willi 2008; Hoffmann and Sgrò 2011). Indeed, the prevailing paradigm in conservation emphasizes the maintenance of genetic diversity as paramount for facilitating adaptation to environmental change (reviewed in Jump and Peñuelas 2005). However, the concept of evolutionary rescue highlights that the rate of change also depends on demographic factors (Bürger and Lynch 1995; Gomulkiewicz and Houle 2009; Hoffmann and Sgrò 2011), making explicit consideration of demogenetic feedbacks essential to predicting persistence in a changing environment (Bürger and Lynch 1995; Gomulkiewicz and Holt 1995; Gomulkiewicz and Houle 2009; Bell 2013, 2017; Gonzalez et al. 2013; Carlson et al. 2014; Anciaux et al. 2018; Schmid et al. 2022).

One critical life history stage that also strongly influences population dynamics and genetic diversity is the persistent dormant stage (Nunney 2002; Vitalis et al. 2004; Evans and Dennehy 2005; Honnay et al. 2008). This stage creates a “seed bank” or “germ bank” and is found in a wide diversity of organisms, including plants, algae, crustaceans, rotifers, and insects throughout terrestrial and aquatic environments (Evans and Dennehy 2005). In plants, seed banks appear across angiosperm families in desert, arctic, tropical, and wetland habitats, with seeds lasting from only a couple of years to decades in the soil (Baskin and Baskin 1998; Fenner and Thompson 2005). Seed dormancy is considered a type of bet-hedging strategy that sacrifices high immediate

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germination rates and thus arithmetic mean fitness in unpredictable environments in favor of greater geometric mean fitness and longer-term persistence (Ellner 1985; Kalisz and McPeck 1993; Evans et al. 2007; Gremer and Venable 2014). From a demographic standpoint, the germination of seeds from the bank can restore population size even after a strong decline in the aboveground population following extreme events (e.g., Kalisz and McPeck 1993). Moreover, the seed bank can serve as a reservoir of genetic diversity, protecting against loss of alleles from stochastic events and increasing effective population size (McCue and Holtsford 1998; Nunney 2002; Lundemo et al. 2009; Mandák et al. 2012). In a fluctuating environment, the seed bank becomes an archive or “memory” of alleles selected under different conditions, thereby increasing the probability that a part of the germinating seeds is well adapted to the current conditions (Ellner and Hairston 1994; Evans et al. 2007). In short, seed banks are demographic and genetic buffers that reduce extinction risk associated with stochasticity in highly fluctuating environments.

It is less clear, however, how seed banks influence adaptation and population persistence (i.e., evolutionary rescue) under directional environmental change (as opposed to fluctuations around a constant mean). Since genetic variation fundamentally enables a population to adapt (e.g., Lande 1979; Falconer 1996), the greater genetic diversity expected in seed banks could facilitate adaptation, at least in the short term. In scenarios where a sudden and significant environmental alteration leads to a rapid shift in the optimal phenotype (a “step” change), such as industrial catastrophes, habitat devastation, or invasion by novel antagonists (Boulding and Hay 2001), this advantage should be particularly important because the higher degree of standing genetic diversity can serve to minimize the initial lag of the mean phenotype behind the new optimum. This, in turn, reduces initial population decline, facilitating the evolution of the mean phenotype toward the new optimum and the associated rebound in population size before extinction can occur (Gomulkiewicz and Holt 1995). A distinct challenge emerges when a population is confronted with a prolonged directional shift in the environment, often referred to as a “moving optimum,” as seen in situations like rising temperatures. Under such circumstances, the lag progressively escalates over time until reaching a dynamic equilibrium where the evolution of the mean phenotype is expected to keep pace with the rate of change in the optimum, resulting in a constant lag (e.g., Lynch et al. 1991). The further the population lags behind the moving optimum, the larger the population decline and the greater the extinction risk. Because the initial lag in the first generations after the shift begins is relatively small, the short-term advantage of

greater standing genetic variation with a seed bank may be reduced. Here, evolution of genetic variance is expected to be key for populations to continually adapt and stay in step with the moving optimum (Lynch et al. 1991; Lynch and Lande 1993; Bürger and Lynch 1995; Lande and Shannon 1996; Jones et al. 2004; Kopp and Matuszewski 2014), promoting evolutionary rescue (Gomulkiewicz and Holt 1995).

In the long term, however, the seed bank should slow down adaptation to a directional environmental change because the genetic diversity in the bank is composed of alleles selected under past conditions. Therefore, most alleles in the bank might be maladapted to the new optimum. This negative impact of the storage effect on adaptation after environmental change has been demonstrated empirically in one study of egg banks in copepods (Hairston and De Stasio 1988). Continued “migration from the past” should also affect the shape of the distribution of genotypic values, especially in the case of a moving optimum, causing a trailing tail in the distribution and dragging the mean phenotype behind the mode (i.e., a negative skew) in the same way gene flow in space can skew the distribution toward immigrants (Yeaman and Guillaume 2009). Depending on the size of seed banks and length of time seeds can survive, memories can be long and the skew extremely negative. For example, recent theoretical work considering extremely large populations with a germ bank have linked slower adaptation under a gradually moving optimum to the degree of negative skew in the trait distribution (Yamamichi et al. 2019). Consequently, the response to selection could significantly deviate from that expected based on estimates of additive genetic variance and selection strength alone (Turelli and Barton 1990; Bürger 1999; Yeaman and Guillaume 2009; Jones et al. 2012).

Predicting the effect of seed banks on evolutionary rescue may be further complicated by the genetic architecture of the traits under selection. Most quantitative genetic studies of evolutionary rescue have focused on a single trait, but selection under a new optimum is likely to target a combination of traits (Blows and Hoffmann 2005; Hoffmann and Sgrò 2011) that are often genetically correlated. For example, Etterson and Shaw (2001) demonstrated how genetic correlations involving leaf number, leaf thickness, and reproductive stage in the annual plant *Chamaecrista fasciculata* could be either antagonistic or reinforcing under a scenario of climate change. Genetic covariation among traits, represented by the *G* matrix, is thus another fundamental aspect of the genetic architecture that governs the response to selection (Lande 1979; Lande and Arnold 1983; Kirkpatrick and Lofsvold 1992; Jones et al. 2003, 2004; Blows and Hoffmann 2005; Hellmann and Pineda-Krch 2007; Gomulkiewicz and Houle 2009; Hoffmann and Sgrò 2011; Duputié et al. 2012; Chevin

2013; Kopp and Matuszewski 2014). Genetic correlation can be caused by correlation among allelic effects at pleiotropic loci and is partly controlled by mutational correlation. For populations without a seed bank, quantitative genetic models show that mutational correlation can facilitate adaptation when the genetic line of least resistance of the $\mathbf{G}$ matrix (representing the direction with the maximum amount of genetic variance; Schluter 1996) is aligned with the direction of selection but thwart adaptation when the genetic line of least resistance is orthogonal to the direction of selection (Arnold et al. 2008; Duputié et al. 2012; Chevin 2013). A seed bank could expand the $\mathbf{G}$ matrix (and, hence, increase overall genetic variation) but also create a greater jumble of genetic memories from independent fluctuations in selection pressures acting on two or more genetically correlated traits. Hence, the extent to which the seed bank will exaggerate or alter the impacts of mutational correlations under a directional shift in the environment is an open question.

Here we use a quantitative genetics framework to explore how a seed bank impacts short- and medium-term persistence in annual plant populations facing either abrupt or gradual environmental change. Unlike previous studies (Templeton and Levin 1979; Yamamichi et al. 2019; Schmid et al. 2022), we center our attention on populations characterized by small carrying capacities, such as those experiencing the double threat of habitat fragmentation and global change (Leimu et al. 2010). In such populations, which experience strong genetic and demographic stochasticity, the “tug-of-war” between potentially opposing effects of seed banks (larger genetic variance vs. maladapted alleles from the past and longer generation time; demographic buffer vs. lower total number of germinating seeds) should be most intense. We use the complementarity and flexibility of analytical models, based on the deterministic framework defined by Barfield et al. (2011), and individual-based models to tease apart the forces that tip the delicate balance of weights determining persistence in small populations: initial genetic variance and its evolution, migration from the past, generation time, demography, and genetic and demographic stochasticity. We first explore the univariate case, estimating extinction probabilities of populations with and without a seed bank and explicitly following their demogenetic dynamics, which can provide further insight into the extent to which currently persisting populations are merely accumulating an “extinction debt” (reviewed in Kuussaari et al. 2009). We subsequently investigate how the relative persistence advantage or disadvantage of a seed bank depends on the extent of environmental change, amplitude of environmental fluctuations, population size, selection intensity, key vital rates (germination, maximum time in the seed bank, and survival in the seed bank), and carrying capacity. Finally, we

extend our analysis to the multivariate case by investigating how the effect of seed banks on evolutionary rescue is influenced by mutational correlations across a range of magnitudes of environmental changes, building on the mechanisms identified in the univariate model.

Methods

Quantitative Genetic Model

We describe the model with two correlated traits, denoted a and b , in a diploid organism (see “Life Cycle” below); the case of a single trait is easily deduced as a simplified version of the former. Genetic components of the two traits are determined by 50 pleiotropic, freely recombining, additive loci. Each allele has an effect value for each trait, and the trait’s genotypic value is the sum of the trait’s allelic effects over all loci.

The individual vector of genotypic values at stage i is $\mathbf{g}_i = (g_{i,a} \ g_{i,b})^T$, where T indicates the transpose of the vector. This vector is assumed to be distributed as a bivariate Gaussian with mean $\bar{\mathbf{g}}_i$ and covariance

$$\mathbf{G}_i = \begin{pmatrix} G_{i,aa} & G_{i,ab} \\ G_{i,ba} & G_{i,bb} \end{pmatrix}.$$

Environmental effects at stage i , $\mathbf{e}_i$, are independent of $\mathbf{g}_i$ and are bivariate Gaussian with mean $\bar{\mathbf{e}}_i = \mathbf{0}$ and covariance

$$\mathbf{E}_i = \begin{pmatrix} E_{i,aa} = 1 & 0 \\ 0 & E_{i,bb} = 1 \end{pmatrix}.$$

We assume that the vector of phenotypes at stage i , $\mathbf{z}_i$, is the sum of the genotypic values and environmental effects at stage i such that, in the newborns, $\mathbf{z}_i$ is also Gaussian with mean $\bar{\mathbf{z}}_i = \bar{\mathbf{g}}_i$ and covariance $\mathbf{P}_i = \mathbf{G}_i + \mathbf{E}_i$.

As $\mathbf{g}_i$ is bivariate Gaussian, the $\mathbf{G}$ matrix can be represented by an ellipse. The major axis of this ellipse is in the direction of maximum variance, which is the direction of the eigenvector associated with the dominant eigenvalue of the $\mathbf{G}$ matrix and defines the line of least resistance (Schluter 1996; Arnold et al. 2008).

Life Cycle

We modeled the life cycle of an annual plant (fig. 1). Plants are self-compatible hermaphrodites without inbreeding depression. In a single year, plants germinate, develop into rosettes (juveniles), and mature into adults that reproduce. We describe this as the “aboveground” stage of the life cycle and model the transition from rosette to rosette across years. The number of rosettes is denoted N_t . We considered that rosettes are subjected to viability selection prior to adulthood. Rosette survival depends on the value of either a single quantitative trait or

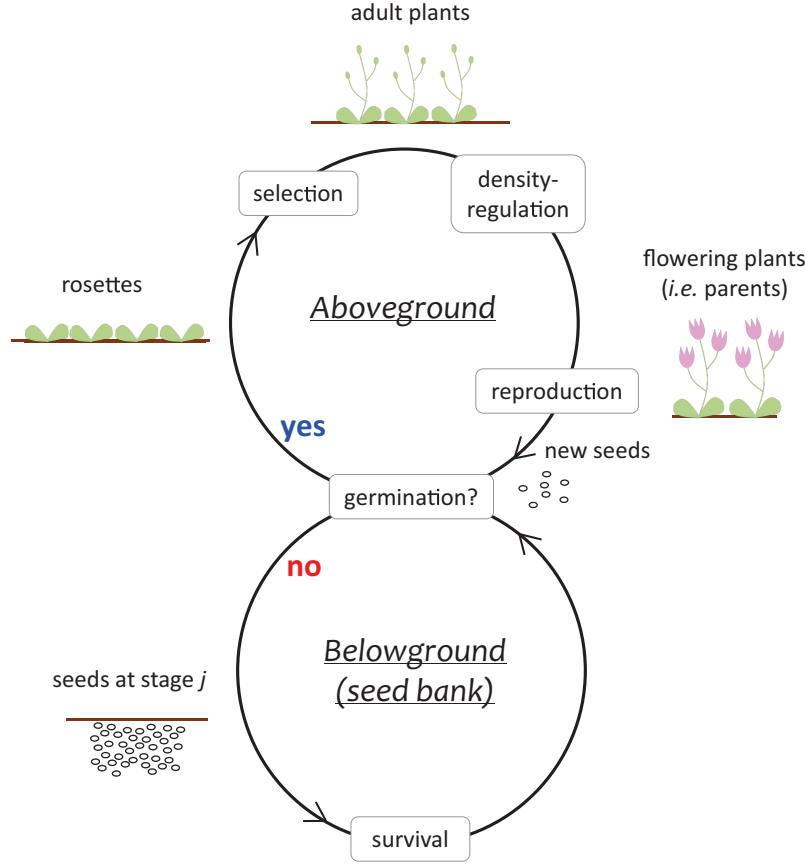


Figure 1: Life cycle of an annual plant with a persistent seed bank. Juveniles (rosettes) are subject to viability selection, then transition to adult plants. Adult plants undergo density regulation and reproduce. Newly produced seeds either germinate and develop into rosettes or enter the seed bank at the next time step. Seeds in the bank must survive, then at the next time step they either germinate and develop into rosettes or remain in the bank for a maximum of k years. Note that if $k = 0$, the life cycle corresponds to an annual plant without a seed bank.

two correlated traits, which we refer to as the “univariate case” and the “multivariate case,” respectively. Viability selection was implemented according to a Gaussian selection function, which implies stabilizing selection around some optimal phenotypic value(s). Hence, the probability of survival of a rosette with phenotype $\mathbf{z}_1$, $w(\mathbf{z}_1)$, was given by

$$w(\mathbf{z}_1) = \exp\left(-\frac{1}{2}(\mathbf{z}_1 - \boldsymbol{\theta})^T \mathbf{W}^{-1}(\mathbf{z}_1 - \boldsymbol{\theta})\right), \quad (1)$$

where the -1 superscript indicates matrix inversion and $\boldsymbol{\theta}$ is the vector of the optimum phenotypes. Diagonal terms ω_{aa} and ω_{bb} in the positive definite matrix $\mathbf{W}$ give the width of the fitness function for each individual trait, which is inversely proportional to the strength of stabilizing selection on this trait. Off-diagonal terms in $\mathbf{W}$ were set to zero, corresponding to absence of selectional correlation. We set ω_{aa} and ω_{bb} to 10 (see table 1 for parameter values), such that the absolute value for the standardized quadratic selection gradient (i.e., $\text{cov}(w(\mathbf{z}_1), \mathbf{z}_1) \mathbf{P}^{-1}$) falls

in the range of values found in natural populations (Kingsolver et al. 2001). After selection, the number of adults (i.e., rosettes that have successfully passed viability selection but have not yet flowered) drops to N_A . Adults undergo density regulation by random mortality before flowering such that the adult population N_A cannot exceed the carrying capacity, $N_{\max}$, but it can decrease in size and even eventually become extinct if less than $N_{\max}$ plants survived selection.

Adults flower and produce f seeds that either germinate with probability γ or enter a dormant state (i.e., seed bank) with probability $(1 - \gamma)$; table 1). Seeds already in the bank from previous years similarly either germinate with probability γ or remain in the bank with probability $(1 - \gamma)$. Each year, seeds in the bank (newly entered and remaining) pay a cost $(1 - s_b)$, where s_b is the annual rate of survival in the seed bank. Thus, from one year to the next the probability of entering or staying in the bank is $(1 - \gamma)s_b$. For simplicity, germination and survival probabilities are independent of phenotype (genotype) and time spent in

Table 1: Values and description for each parameter

Category, parameter	Reference values	Other values used	Description
Input parameters:			
f	20		Fecundity
m	.02		Allelic mutation probability
r_m	0	-.5, .5	Mutational correlation
γ	.1 and 1	.3, .5, .7, .9	Germination rate
s_b	.8	.4	Survival rate of seeds in the bank
k	0 or 5	10	Maximum number of years in the seed bank
$\mathbf{W}$	$\begin{pmatrix} 10 & 0 \\ 0 & 10 \end{pmatrix}$	$\begin{pmatrix} 15 & 0 \\ 0 & 15 \end{pmatrix}$	Matrix defining the width of the fitness surface
σ_θ^2	7.5	0, 2.5, 5, 10	Amplitude of random fluctuations in the optima (same value for both optima)
δ_θ	8 and $6/\sqrt{2}$	2, 4, 6, 8, 10, 12	Step change in the optima (divided by $\sqrt{2}$ for multivariate model)
r_θ	.08 and $.06/\sqrt{2}$	.02, .04, .08, .1, .12	Rate of change in the optima (divided by $\sqrt{2}$ for multivariate model)
$N_{\max}$	100	500	Carrying capacity
Internal parameters:			
ρ_A			Persistence probability in analytical model
ρ_S			Persistence probability in simulations
$p_j(\mathbf{g}, \mathbf{z})$			Joint distribution of phenotypic and genotypic values at stage j
$\mathbf{g}_i = (g_{i,a} \quad g_{i,b})^T$			Vector of genotypic values of traits a and b
$\mathbf{z}_i = \mathbf{g}_i$			Vector of phenotypic values of traits a and b
$\mathbf{e}_i$			Vector of individual random environmental effects of traits a and b
$\mathbf{P}_j$			Phenotypic variance-covariance matrix at stage j
$\mathbf{G}_j$			Additive genetic variance-covariance matrix at stage j
$\mathbf{E}_j$			Variance-covariance matrix of random effect at stage j
$\mathbf{M}$			Mutational variance-covariance matrix
$w(\mathbf{z}_i)$			Fitness of a rosette with phenotype $\mathbf{z}_i$
$\boldsymbol{\theta} = (\theta_a \quad \theta_b)^T$			Vector of optimum phenotypes of traits a and b
$\bar{w}_j$			Mean fitness of stage j
N_A			Number of flowering plants (after selection and density regulation)
N_j			Number of individuals in stage j (a prime symbol denotes the value in the next year)

Note: Input parameters correspond to the parameters varying among scenarios, while internal parameters correspond to parameters evolving within a replicate.

the seed bank. Seeds can remain in the bank for multiple years; the maximum number of years after which a seed can germinate is set to k ; we used $k = 5$ as the default (table 1). Only rosettes and seeds in the bank remain at the beginning of each new year. Populations with a bank are both stage (bank vs. rosettes) and age (years in bank) structured. However, for simplicity we refer to rosettes and different ages of seeds in the bank as “stages.” Thus, populations without a seed bank have one stage (rosettes, N_1), and populations with a seed bank have $k + 1$ stages. The number of seeds per stage j in the seed bank is N_j with j from 2 to $k + 1$.

Change in the Optima

In the period before the change in the environment, which we refer to as the “initialization period,” the optima for

each year are drawn from a zero-mean bivariate Gaussian distribution with variance-covariance matrix

$$\begin{pmatrix} \sigma_\theta^2 & 0 \\ 0 & \sigma_\theta^2 \end{pmatrix}$$

(table 1) so that the optima fluctuate randomly around a constant mean and fluctuations are not autocorrelated (e.g., random fluctuations in temperature among years). We consider two changing environments defined by the nature of the change in the mean optima: (i) a step change where the mean optima change immediately in the first year after the initialization period and remain constant thereafter at δ_θ (same magnitude for both traits; table 1) and (ii) a gradual change where the mean optima move at a constant rate, r_θ (same rate for both traits; table 1). To generate similar Euclidian distances in the optimum

shift between the univariate and multivariate models, we divided the magnitude of the optimum change used in the univariate model by $\sqrt{2}$ for the multivariate model (Jones et al. 2004).

Analytical Model

We used the deterministic model derived in Barfield et al. (2011), which can be derived for any life cycle with stage structure, to compare persistence probability ρ (the number of extant populations over the number of replicated populations), evolution, and demography of populations with and without a seed bank (hereafter called “bank” and “no-bank” populations, respectively). We ran the analytical models for 200 years after the environmental change (extended to 250 years for the dynamics in figs. 2 and 3 after a gradual change).

For every stage i , this model tracks changes in the population size and the joint distribution of phenotypic and genotypic values $(\mathbf{g}_i \ \mathbf{z}_i)^T$ with evolving mean $(\bar{\mathbf{g}}_i \ \bar{\mathbf{z}}_i)^T$ and constant variance-covariance matrix

$$\begin{pmatrix} \mathbf{G}_i & \mathbf{G}_i \\ \mathbf{G}_i & \mathbf{P}_i \end{pmatrix}.$$

Let $p_i(\mathbf{g}, \mathbf{z})$ be the probability density function of this joint distribution. The average contribution across generations from stage j to i for an annual plant with a seed bank and random mating as well as derivations of the model equations are given in the supplemental PDF. Selection acts only on survival of rosettes to adult plants, and the mean fitness of the rosettes is written as

$$\begin{aligned} \bar{w}_i &= \int w(\mathbf{z}_i) p_i(\mathbf{g}, \mathbf{z}) d\mathbf{g} d\mathbf{z} \\ &= |(\mathbf{W} + \mathbf{P}_i)^{-1} \mathbf{W}|^{1/2} \\ &\quad \times \exp\left(-\frac{1}{2}(\bar{\mathbf{z}}_i - \boldsymbol{\theta})^T (\mathbf{W} + \mathbf{P}_i)^{-1} (\bar{\mathbf{z}}_i - \boldsymbol{\theta})\right), \end{aligned} \quad (2)$$

where $|(\mathbf{W} + \mathbf{P}_i)^{-1} \mathbf{W}|$ denotes the determinant of the matrix $(\mathbf{W} + \mathbf{P}_i)^{-1} \mathbf{W}$.

Population Size. Without a seed bank ($\gamma = 1$), the number of rosettes in the next generation (indicated by a prime symbol; fig. 1) is

$$N'_1 = fN_A, \quad (3)$$

where $N_A = \min(N_{\max}, \bar{w}_1 N_1)$ is the population size of the parents.

For a population with a seed bank, the number of rosettes results from the direct contribution of parents and germinating seeds from the seed bank:

$$N'_1 = f\gamma N_A + \gamma \sum_{j=2}^{k+1} N_j. \quad (4)$$

The number of seeds in the seed bank evolves according to $N'_2 = f s_b(1 - \gamma)N_A$ for stage 2 and $N'_j = s_b(1 - \gamma)N_{j-1}$ for any other stage j .

The number of rosettes in bank populations (eq. [4]) may be smaller than that in no-bank populations (eq. [3]) because newly produced seeds germinate with probability $\gamma < 1$ and not all seeds with delayed germination survive. Nevertheless, bank populations might be less prone to extinction because of the contribution of seeds germinating from the seed bank each year. An extreme scenario is when the adult population is decimated in a catastrophic year but restored the next year by seeds germinating from the bank. Population size in the model being a continuous variable, we defined no-bank populations as extinct when $N_A < 1$; for bank populations, extinction occurs when $N_A < 1$ and $N_j < 1$ for all j stages in the bank.

Mean Genotypic and Phenotypic Values. In the absence of a seed bank ($\gamma = 1$), the mean genotypic value in the next year (see, e.g., Lande 1976) is

$$\bar{\mathbf{g}}'_i = \bar{\mathbf{g}}_i + \mathbf{G}_i \boldsymbol{\beta}_i, \quad (5)$$

where $\boldsymbol{\beta}_i = (\boldsymbol{\theta} - \bar{\mathbf{z}}_i)(\mathbf{W} + \mathbf{P}_i)^{-1}$ is the selection gradient vector.

In the presence of a seed bank, the mean genotypic value of the rosettes (fig. 1) is a weighted average of the direct contribution of the genotypic values from the parents and the contribution of genotypic values from the seed bank:

$$\bar{\mathbf{g}}'_i = \frac{1}{N'_1} \left(f\gamma N_A \bar{\mathbf{g}}_A + \sum_{j=2}^{k+1} N_j \gamma \bar{\mathbf{g}}_j \right), \quad (6)$$

where $\bar{\mathbf{g}}_A = \bar{\mathbf{g}}_1 + \mathbf{G}_1 \boldsymbol{\beta}_1$ is the mean genotypic value of the parents after selection. Note that density regulation applied to adults consists of random mortality, such that the expectation for the mean genotypic value of the parents does not change.

In the seed bank, the mean genotypic value is $\bar{\mathbf{g}}'_2 = \bar{\mathbf{g}}_A$ for stage 2 and $\bar{\mathbf{g}}'_j = \bar{\mathbf{g}}_{j-1}$ for any other stage j .

As parents pass on genotypes—not phenotypes—to offspring and there is no selection in the seed bank, the mean phenotypic value of each stage is equal to its mean genotypic value (eqq. [5], [6]) in both no-bank and bank populations.

The initial mean phenotypic and genotypic values for each stage are zero (corresponding to the initial mean optima), and all stages within a population have the same genetic and phenotypic variance-covariance matrices. Genetic and phenotypic variance-covariance matrices were defined according to values measured at equilibrium for

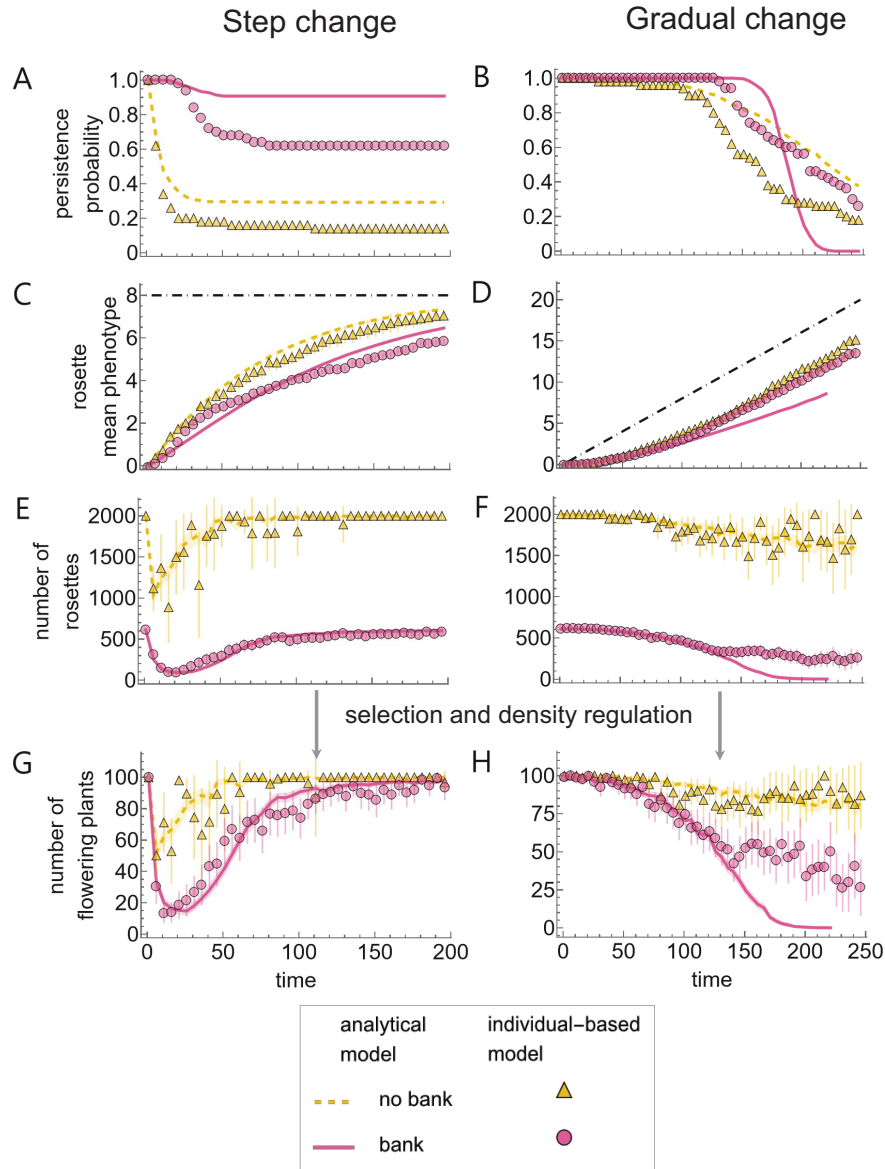


Figure 2: Demogenetic dynamics of bank and no-bank populations under a step ($\delta_\theta = 8$; left column) or gradual ($r_\theta = 0.08$; right column) change in the optimum in univariate models. A, B, Persistence probability. C, D, Population (weighted) mean phenotype of rosettes. The black dotted-dashed line indicates the mean optimum. E, F, Rosette number. G, H, Number of flowering (reproducing) plants. Means (95% confidence interval) of replicates are presented as lines (shaded areas) for the analytical model and symbols (vertical bars) for simulations. Symbols are shown every 5 years for readability. C–H present data for extant populations at each time step. See the main text for details, including default parameters.

the rosettes at the end of the initialization period in individual-based simulations (see next section). Population size for each stage was similarly based on equilibrium values at the end of the initialization period.

Individual-Based Model

We created an individual-based model that considers the evolution of the **G** matrix (shaped by mutation, recom-

ination, genetic drift, and selection) and demographic stochasticity (i.e., probability distribution of mortality in the seed bank and survival to flowering). In contrast to the analytical model, wherein the distributions of genotypic and phenotypic values must be Gaussian, simulations allow deviations. The individual-based model uses the same quantitative genetics framework as the analytical model. Allelic mutation occurs with probability m . If an allele mutates, its effect on each trait is modified

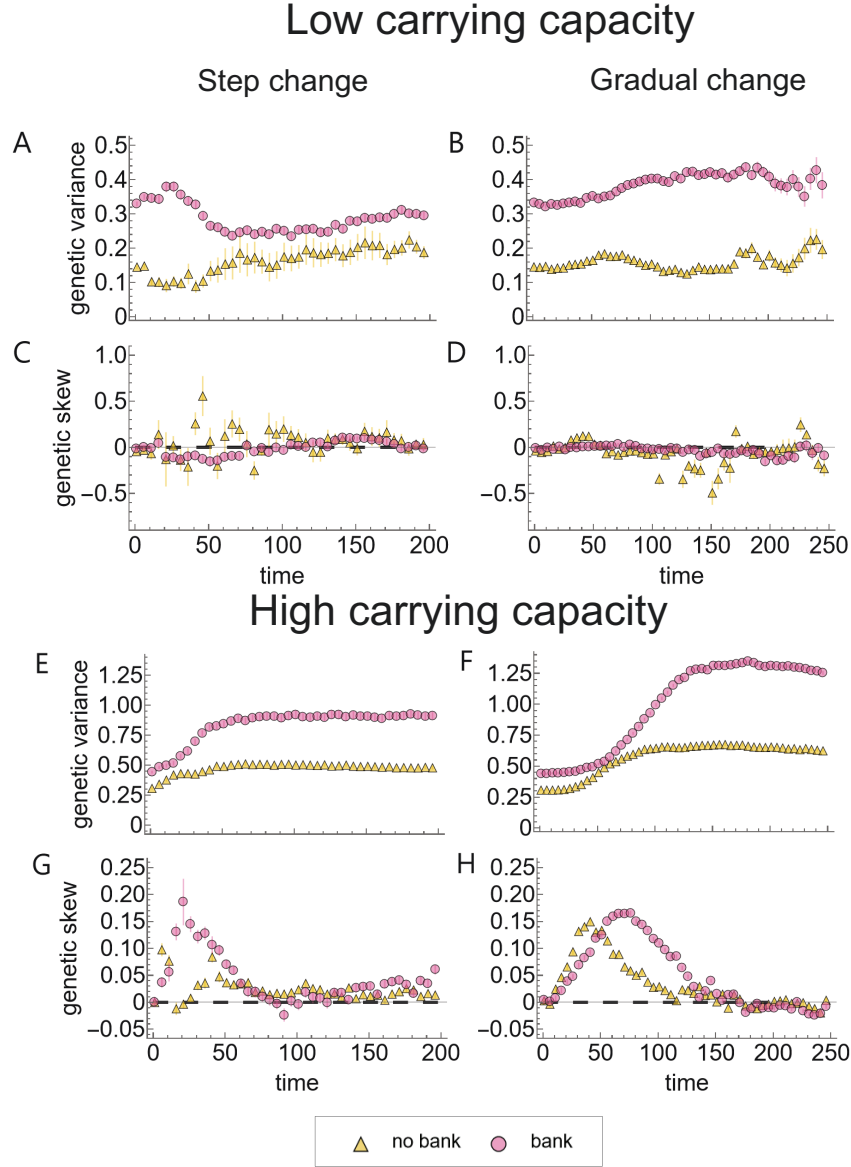


Figure 3: Dynamics for the variance and skew of the genotypic distribution of rosettes in bank and no-bank populations under a step ($\delta_{\theta} = 8$; left column) or gradual ($r_{\theta} = 0.08$; right column) change in the optimum in univariate simulations considering small ($N_{\max} = 100$; A–D) and larger ($N_{\max} = 500$; E–H) carrying capacities. Note the difference in y-axis scales between carrying capacities. Symbols (vertical bars) correspond to weighted means (95% confidence interval) of replicate simulations, shown every 5 years for readability. We began with 50 replicates; data for extant populations are presented at subsequent time steps. See the main text for details, including default parameters.

by adding a new effect value to the previous one. Following a continuum-of-alleles mutation model (Kimura and Crow 1964), the new effects are drawn from a bivariate normal distribution with mean $(0 \ 0)^T$ and variance-covariance matrix

$$\mathbf{M} = \begin{pmatrix} M_{aa} = 0.05 & r_m \sqrt{M_{aa} M_{bb}} \\ r_m \sqrt{M_{aa} M_{bb}} & M_{bb} = 0.05 \end{pmatrix},$$

where r_m is the mutational correlation (table 1). Negative mutational correlations are orthogonal, while positive correlations are parallel to the direction of environmental change (and thus directional selection). Therefore, we consider negative mutational correlations as antagonistic and positive correlations as reinforcing.

For each year, we tracked the number of rosettes and flowering plants, the genotypic distribution of rosettes,

and persistence probability ρ . For each combination of environmental change (sudden vs. gradual) and population type (bank vs. no-bank), we ran 50 replicate simulations of the initialization period. At the beginning of the initialization period, the number of flowering plants was set to $N_{\max}$. The starting number of seeds per stage in bank populations was calculated assuming a stable age distribution based on the Leslie matrix as defined in Caswell (2001) or Vitalis et al. (2004). Initial allelic effects were set to zero at all 50 loci. We simulated the initialization period for 5,000 years. We assumed that populations reached quasi equilibrium after this time because (i) the mean slope (absolute value) of the relationship between genetic variance and time over the past 1,000 years was less than 3×10^{-5} and (ii) the standard deviation in slope among replicates was less than 2×10^{-4} . For each simulated population, we recorded individual allelic and environmental effects in the last year of the initialization period for each stage. The step or gradual change in the mean optima occurs the next year. For computational efficiency, we used the same set of 50 allelic and environmental effects from the last year of the initialization period for each stage to start simulations of both types of optimum change. As in the analytical model, we simulated populations under these new environmental conditions for 200–250 years.

Model Comparisons

Based on preliminary explorations, we selected parameter values for the size or rate of environmental change that best allow us to understand the demogenetic consequences of a seed bank. We begin by considering analytical models and simulations with $\delta_\theta = 8$ and $r_\theta = 0.08$. For the multivariate model, most no-bank populations become extinct within 200 years with $\delta_\theta = 8/\sqrt{2}$ and $r_\theta = 0.08/\sqrt{2}$; thus, we used $\delta_\theta = 6/\sqrt{2}$ and $r_\theta = 0.06/\sqrt{2}$.

We take advantage of the power and complementarity of our analytical and individual-based models to answer our first question about the impact of seed banks on persistence and demogenetic dynamics in changing environments in the univariate case. To help disentangle the non-mutually-exclusive effects of genetic variance at the end of the initialization period (hereafter, “standing genetic variance”), demography, storage of alleles from the past, and their effective migration, we compare demogenetic dynamics of no-bank or bank populations with an artificial type of population that has a seed bank but no memory from the initialization period. In this way, the seed bank resembles a tabula rasa (“blank slate”), only beginning to record memories of selective events in the year before the change in the optimum occurs. These tabula rasa bank (hereafter, “tr-bank”) populations have the same standing genetic variance as no-bank populations but the same de-

mography (initial population size and vital rates) as true seed bank populations once the environmental change occurs. Comparisons between the tr-bank and normal seed bank populations therefore point toward the impacts of standing genetic variance at the onset of environmental change on adaptation and persistence. In contrast, comparison of tr-bank to no-bank populations eliminates differences in standing genetic variation and historical memory but retains differences in demography and stored memory in the changing environment. We note that in these and all subsequent comparisons generation time differs between bank and no-bank populations. However, we cannot explicitly control for generation time because the stable age distribution is not reached during transient dynamics following environmental change (Caswell 2001). We use the notation ρ_A and ρ_S to differentiate persistence probabilities predicted by the analytical and simulation models, respectively. Finally, to begin probing the impact of migration from the past on evolution, we calculate the skew of the genotypic distributions of all populations each year. We measured skew for cases where $N_{\max} = 100$ and 500.

We vary key parameters to evaluate their effects on the benefit (or cost) of the seed bank for persistence in the univariate case, changing one parameter while keeping all others (k , $N_{\max}$, $\mathbf{W}$, s_b , γ , δ_θ or r_θ and σ_θ^2) the same as in the reference case (table 1). We determined ρ_S for bank and no-bank populations across a range of amplitudes of random environmental fluctuations, germination rates, and degree of change in the optimum in the new environment. As life history traits and strength of selection are likely to affect ρ_S , we also explored an alternative value for each of the following: maximal age and survival probability in the seed bank, carrying capacity, and the width of the selection function. For each case, we present the benefit (or cost) of the seed bank as the difference between the persistence probabilities of bank- and no-bank populations, Δ_p . Positive (negative) Δ_p values indicate that the bank provides a persistence advantage (disadvantage).

We next focus on the multivariate case. We examine the effect of mutational correlations on Δ_p and the size ($G_{11} + G_{22}$) and eccentricity (inversely proportional to ϵ , the smaller eigenvalue divided by the larger) of the $\mathbf{G}$ matrix of bank and no-bank populations. Larger values of $\mathbf{G}$ matrix size correspond to greater genetic diversity; lower versus greater eccentricity values correspond to a rounder (circle-shaped) versus “cigar”-shaped ellipse, respectively. We note that the utility of the tr-bank in the univariate case was to disentangle the relative impact of demography and genetics on population responses. Since we do not believe it will offer additional insight for the multivariate case, we focus on our central question: the effect of seed banks when selection acts on correlated traits. We further examine how the benefit of seed banks varies with

the amount of change in the optima (δ_θ and r_θ) in the new environment.

To account for variability in outcomes when modeling stochastic fluctuations of the optima, we ran 500 replicates of the analytical model and 50 replicates of the individual-based simulations for each unique scenario. Comparisons are based on means and 95% confidence intervals across replicate populations. For each year t , we calculate the average number of rosettes and flowering plants based only on populations extant in year t (i.e., populations extinct by that point are excluded). We calculated weighted averages for the mean phenotype and the variance and skew of the genotypic distribution of the rosettes across replicate populations per year t , using only populations extant in year t weighted by their rosette population size in this same year. We note that results do not change qualitatively if we look only at values for populations that survive until 200 years.

Results

Univariate Model

Step Change: Analytical Predictions. The analytical model predicts a sharp decline in persistence probability ρ_A for no-bank populations immediately following the step change (fig. 2A). This decline stabilizes around $\rho_A = 0.3$ approximately 40 years after the shift, indicating that most extinctions happen early (fig. 2A). In seed bank populations, however, ρ_A drops only to about 0.93 across the 200 years. Consequently, bank populations are predicted to persist more than three times as often as no-bank populations. This advantage seems at odds with the slower rate of evolution in persisting bank populations and a lag twice that of persisting no-bank populations 200 years after the shift, on average (fig. 2C). We can see an impact of slower evolution on population mean fitness in bank populations as declining numbers of rosettes and flowering plants in the first years after the optimum shift (fig. 2E, 2G). As a result of slower evolution and the initial decline in the population sizes, recovery to $N_{\max}$ is slower. Still, the impact on persistence of bank populations is delayed because of the demographic buffering effect of the seed bank (see plateau of persistence probability for bank populations during the first 15 years in fig. 2A). The same delay in the decline of ρ_A is predicted for tr-bank populations, which have the same demographic parameters as bank populations (fig. S1A; figs. S1–S9 are available online). Furthermore, tr-bank populations are almost twice as likely to persist than no-bank populations, even though they adapt more slowly because of their increased generation time (and without the benefit of an increased initial genetic variance enjoyed by regular bank populations). This highlights the

importance of the demographic buffer provided by the seed bank (see also fig. S2, which shows frequent extinctions in a sample of no-bank populations despite their lag being smaller than that of bank populations). In addition to the demographic buffer, the greater genetic variance associated with the memory of the seed bank contributes to the high ρ_A of bank populations; if bank populations had the same genetic variance as no-bank populations, ρ_A would drop to ~ 0.5 versus > 0.9 (compare bank to tr-bank in fig. S1A). Put together, the demographic “backup” provided by the seed bank initially compensates for the fitness cost of the lag. This attenuates population decline after a step change, which, together with their initial genetic advantage, helps compensate for the negative impacts of longer generation time and/or migration of maladapted alleles from the past on evolution toward the optimum, facilitating evolutionary rescue.

Step Change: Predictions from Simulations. Results of the individual-based simulations qualitatively match analytical predictions: bank populations are more likely to persist than no-bank populations (fig. 2A). Quantitatively, persistence probabilities in the simulations are considerably lower than those in the analytical model ($\rho_s < \rho_A$), partly owing to the negative impacts of genetic and demographic stochasticity that are integral to simulations. Beyond demographic stochasticity, lower persistence in simulations may arise because population sizes are treated as whole numbers versus continuous in the analytical model (persistence is easier to achieve when fractions of individuals count, even though we do not allow population sizes less than 1). By 200 years, ρ_s for no-bank and bank populations is one-half and one-third of ρ_A , respectively. Still, we see a large difference between bank and no-bank populations; ρ_s of bank populations is 4.4 times that of no-bank populations 200 years after the step change. Simulated population size and mean phenotype dynamics of extant populations closely align with predictions from the analytical model (fig. 2C, 2E, 2G).

The simulations emphasize the important role of standing genetic variance and its evolution on the persistence advantage provided by the seed bank. Over the first 20 years, the genetic variance in bank populations increases by up to 15% relative to the initial genetic variance (fig. 3A), leading to a slightly faster initial adaptation and population size recovery than predicted by the analytical model (fig. 2C, 2E, 2G). The amplification of genetic variance is more evident and pronounced in populations with larger carrying capacities (fig. 3E). Tr-bank populations ultimately also enjoy an increase in genetic variance (not shown), but it cannot compensate for low standing genetic variation at the start, such that they are almost as (un)likely to persist as no-bank populations (fig. S1A). These populations appear

to undergo mutational meltdown: lower genetic variance results in a larger initial lag compared with bank populations, so population size decreases and remains depressed for longer, reducing the number of new mutations entering the population and rendering populations more vulnerable to random loss of genetic variance and demographic stochasticity (see fig. S3 for a sample of replicated runs). This process might also occur in bank and no-bank populations but to a lesser extent, as the former's greater initial genetic variance and the latter's shorter generation time allow faster adaptation compared with tr-bank populations.

We expected that migration of alleles from the past in simulated bank populations would induce a negative skew (i.e., long trailing left tail) in the distribution of genotypic values. However, in our baseline model with $N_{\max} = 100$, the skew fluctuates around zero (fig. 3C), which would also explain the close match between the analytical and individual-based models (fig. 2C, 2E, 2G). Variation in the direction and degree of skewness around zero may be partially caused by very small population sizes, making the estimates of the moments of the distribution less accurate. We see clearer patterns from simulations of larger populations ($N_{\max} = 500$), wherein persistence probability is $\rho_s = 1$ and $\rho_A = 0.8$ for bank and no-bank populations, respectively. In larger populations, the skew is generally lower and trends positive (i.e., long leading right tail) during the first ~25–50 years after the step change before gradually returning to zero (fig. 3G). This result corresponds to the typical expectation for skew under directional selection in the absence of migration (spatial or temporal): after a step change, the frequency of initially rare, high-quality (in terms of survival) alleles increases, but the mass of the distribution of genotypic values still lags farther behind the optimum, inducing both a positive skew (fig. 3G) and an increase in the genetic variance (fig. 3E; see also “Discussion”). Indeed, the peak of the positive skew in bank populations occurs when the increase in genetic variation is fastest. Subsequently, the genetic variance stabilizes, and the skew diminishes toward zero. Note that despite having greater genetic variance with limited skew, bank populations still evolve more slowly than no-bank populations because of their longer generation time.

Gradual Change: Analytical Predictions. Under a moving optimum, the analytical model predicts that populations avoid extinction over the first 100 years with or without a seed bank. After that, ρ_A progressively declines for no-bank populations. Bank populations continue to avoid extinction ($\rho_A = 1$) until they reach a tipping point at the ~150-year mark, when ρ_A suddenly plunges and reaches zero by 238 years (fig. 2B). Thus, the persistence advantage for bank populations is short-lived. In fact, they are incurring an extinction debt from accruing lag (fig. 2D). Evi-

dence of their fate is discernible from the continuous decline in population sizes of rosettes and flowering plants (fig. 2F, 2H). With environmental change increasing each generation, the lag grows in bank populations. Fewer rosettes survive to flower, fewer and fewer seeds enter the bank, and the demographic buffer of the seed bank erodes (fig. S4). Greater genetic variation likely enables bank populations to stave off extinction for longer than no-bank populations. This inference is supported by the comparison to tr-bank populations. Our models predict that ρ_A would plunge to zero earlier if seed bank populations did not benefit from higher initial genetic variance (see tr-bank dynamics in fig. S1B). Without this advantage, the burdens of longer generation time and migration of alleles from the past on adaptation are too great to facilitate evolutionary rescue; no-bank populations, free from those constraints, are thus expected to evolve faster and survive longer (compare no-bank to tr-bank in fig. S1B).

Gradual Change: Predictions from Simulations. Individual-based models similarly predict that all population types are headed to extinction, but the rate at which they do so changes compared with analytical predictions. The initial rate of persistence decline in simulations is sharper for no-bank populations, and by the 250-year mark, ρ_s is nearly half of ρ_A (fig. 2B). We attribute these differences primarily to the negative impacts of genetic and demographic stochasticity, as in the step change scenario. In contrast, bank (and tr-bank) populations experience an earlier but smoother decline in persistence (figs. 2B, S1B). As a result, $\rho_s > \rho_A$ over the last 50 years examined, with ~30% of bank populations projected to persist up to 250 years. This result can be linked to the evolution of greater genetic variance in bank populations in simulations (fig. 3B), an effect that is amplified when $N_{\max} = 500$ (fig. 3F). The increased genetic variation balances the cost of the longer generation time on adaptation such that the lag decreases faster than predicted by the analytical model and approaches the observed lag of no-bank populations (fig. 2D). The smaller lag translates into a smoother decline in population sizes compared with analytical predictions (fig. 2F, 2H). The results are even more dramatic for tr-bank populations; genetic variance is predicted to increase up to 168% over 250 years (result not shown), reflecting their capacity to build up genetic memory in the seed bank at the start of the optimum shift. The increase in genetic variance offsets the effects of genetic and demographic stochasticity, as ρ_s is mostly higher than ρ_A (fig. S1). Still, the advantage arises too late, leaving tr-bank populations less likely to persist compared with bank and no-bank populations (fig. S1), consistent with findings from the analytical model. Ultimately, ρ_s values for all populations begin to converge and the advantage of the bank declines. At 250 years, bank

populations are 1.4 times more likely to persist than no-bank populations.

Because the optimum is continuously moving in this scenario, we expected to see a stronger negative skew in the genotypic distribution of bank populations compared with the step change scenario. However, as in the case of the step change, results did not match the expected effect of migration of past alleles on the shape of the genotypic distribution in our small populations (fig. 3D). Again, results with a larger carrying capacity are more illustrative (fig. 3H). Simulations reveal a transitive positive skew in both population types, consistent with an increase in the frequency of genotypes leading to high fitness in response to directional selection (fig. 3H). The positive skew and increase in genetic diversity arise in parallel (fig. 3F). Interestingly, the peak skew is reached first by no-bank populations, followed by bank populations (fig. 3H). We suspect that this delay is the consequence of maladaptive alleles migrating from the bank, increasing the weight of the left tail (i.e., the opposite direction of the optimum shift; see “Discussion”).

Extended Parameter Range. In this section, we investigate the robustness of our previous results by varying additional parameters. We first focus on the amplitude of random fluctuations of the optimum (σ_θ^2). Even during the initialization period (where the mean optimum stays constant), these fluctuations may induce population extinctions in no-bank populations, provided they are large enough ($7.5 < \sigma_\theta^2 < 10$; fig. S5A). Bank populations, in contrast, never become extinct, highlighting the known role of the seed bank as a bet-hedging strategy in unpredictable environments with an otherwise stable mean.

When the mean optimum shifts, simulations show that the seed bank is a liability when σ_θ^2 is small but transitions to be an asset as σ_θ^2 increases (fig. 4A). Consequently, the benefit of the seed bank, Δ_p , increases with σ_θ^2 (fig. 4A). The underlying dynamics, however, depend on the type of environmental change. Increasing σ_θ^2 with a step change has opposing effects on the persistence of bank and no-bank populations; ρ_s declines for no-bank populations but increases for bank populations (fig. S5B). Under a gradual change, ρ_s declines with σ_θ^2 for both population types, but less rapidly with a seed bank (fig. S5C). The increase in Δ_p with σ_θ^2 can be explained by considering that the range of alleles stored in a seed bank scales with the amplitude of optimum fluctuations. Indeed, genetic variance at equilibrium (slightly) increased with the amplitude of optimum fluctuations for bank populations during the simulated initialization period (data not shown). Most alleles in the seed bank may prove maladaptive following an environmental change. But the bank may also harbor rare alleles that turn out to be adaptive because they were favored under condi-

tions once considered extreme deviations from the mean optimum and now, after the environmental change, closely resemble the new optimum. This is particularly clear in the step change scenario, where large fluctuations increase ρ_s of bank populations. Although large fluctuations make persistence more difficult for both population types under a moving optimum, the stepping-stone effect of these rare alleles can facilitate adaptation in bank populations. In contrast, no-bank populations can only lean on limited genetic diversity from the previous year and are always negatively affected by fluctuations.

Varying the germination rate considerably altered the benefit of the bank based on simulations with $\sigma_\theta^2 = 7.5$. We find that intermediate germination rates γ maximize ρ_s for a given change in the optimum ($\delta_\theta = 8$ or $r_\theta = 0.08$; fig. 4B). The advantage for bank populations ($\Delta_p > 0$) is consistently greater under a step change compared with a moving optimum, but the effect of the germination rate is the same.

We show the influence of additional parameters across a gradient of optimum size changes (holding $\sigma_\theta^2 = 7.5$) in figure 4C and 4D. For our reference case, we find that Δ_p is maximal under intermediate-sized optimum changes and overall larger under step change versus gradual change scenarios. Increasing the maximal age in the seed bank to $k = 10$ can substantially amplify Δ_p under intermediate-sized optimum changes (fig. 4C, 4D), even though its impact on the lag is small (data not shown). This suggests that the increase in Δ_p is a result of the larger demographic cushion provided by longer storage in the bank. In contrast, lowering survival of seeds in the bank (s_b from 0.8 to 0.4) turns it into a liability ($\Delta_p < 0$) over a range of optimum changes (pink circles vs. green inverted triangles in fig. 4C, 4D), with the greatest detriment seen under a gradual change. Weakening stabilizing selection can diminish, erase, or invert Δ_p depending on the type and magnitude of change (pink circles vs. blue squares in fig. 4C, 4D). Decreased selection strength increases the lag, but it also reduces the impact of the lag on the population mean fitness (i.e., reduces the lag load). Consequently, demographic stochasticity is reduced and, along with it, the advantage of the seed bank as a safety net. Combined with the weights of longer generation time and migration of maladaptive alleles from the past, bank populations may be more likely to become extinct within 200 years compared with no-bank populations, especially under a moving optimum, where Δ_p is negative under a wider range of optimum change (fig. 4D). Finally, increasing $N_{\max}$ has an impact comparable to reduced selection after a step change (fig. 4C). Under a moving optimum, increasing $N_{\max}$ erases any advantage of the bank so that $\Delta_p = 0$ across the range of r_θ (fig. 4D). Similar to the effect of reduced selection, a larger carrying capacity disproportionately helps no-bank

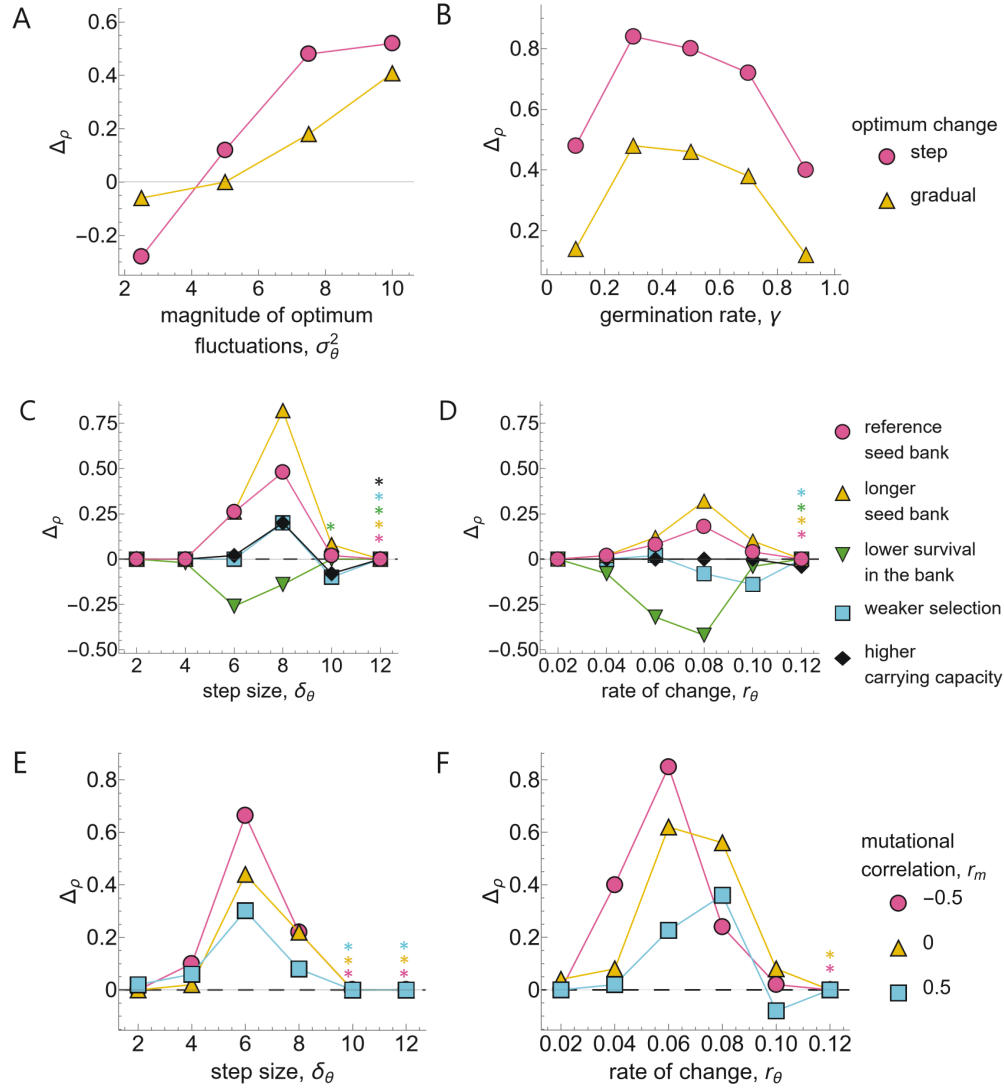


Figure 4: Differences in persistence probability (Δ_p) between bank and no-bank populations after 200 years across a range of parameters in univariate (A–D) and multivariate (E, F) simulations. A, B, Magnitude of optimum fluctuations (A) and germination rate (B) for a step (circles) or gradual (triangles) change in the optimum. C, D, Comparison of the reference case ($k = 5$; pink circles) to cases with a longer-lived seed bank ($k = 10$; yellow triangle), lower seed survival in the bank ($s_b = 0.4$; green inverted triangles), weaker selection ($\omega_{aa} = 15$; blue squares), and higher carrying capacity ($N_{\max} = 500$; black diamonds) across optimum step sizes or rates of change. E, F, Effects of mutational correlation on Δ_p across optimum step sizes or rates of change. Lines connect symbols for readability. Positive (negative) Δ_p values indicate greater (lower) persistence of bank populations. Asterisks indicate conditions where all populations become extinct (color according to the inset legends). See the main text for parameter details.

populations by reducing demographic stochasticity and boosting their ρ_s compared with smaller populations.

Multivariate Model

The multivariate analytical model incorporating mutational correlations produces demogenetic dynamics that are consistent with the univariate model. Ultimately, seed banks increase ρ_A . Given this and the fact that the individual-

based model more realistically incorporates the effects of stochasticity, as well as evolution of the $\mathbf{G}$ matrix, we focus on the simulation results. Persistence, population size, and evolutionary dynamics for the multivariate cases are explored in figures S6 and S7.

Simulations predict that the seed bank increases the size of the $\mathbf{G}$ matrix and lowers its eccentricity (i.e., makes it rounder; measured as an increase in the parameter ϵ) under both types of environmental change (figs. 5, S8). In

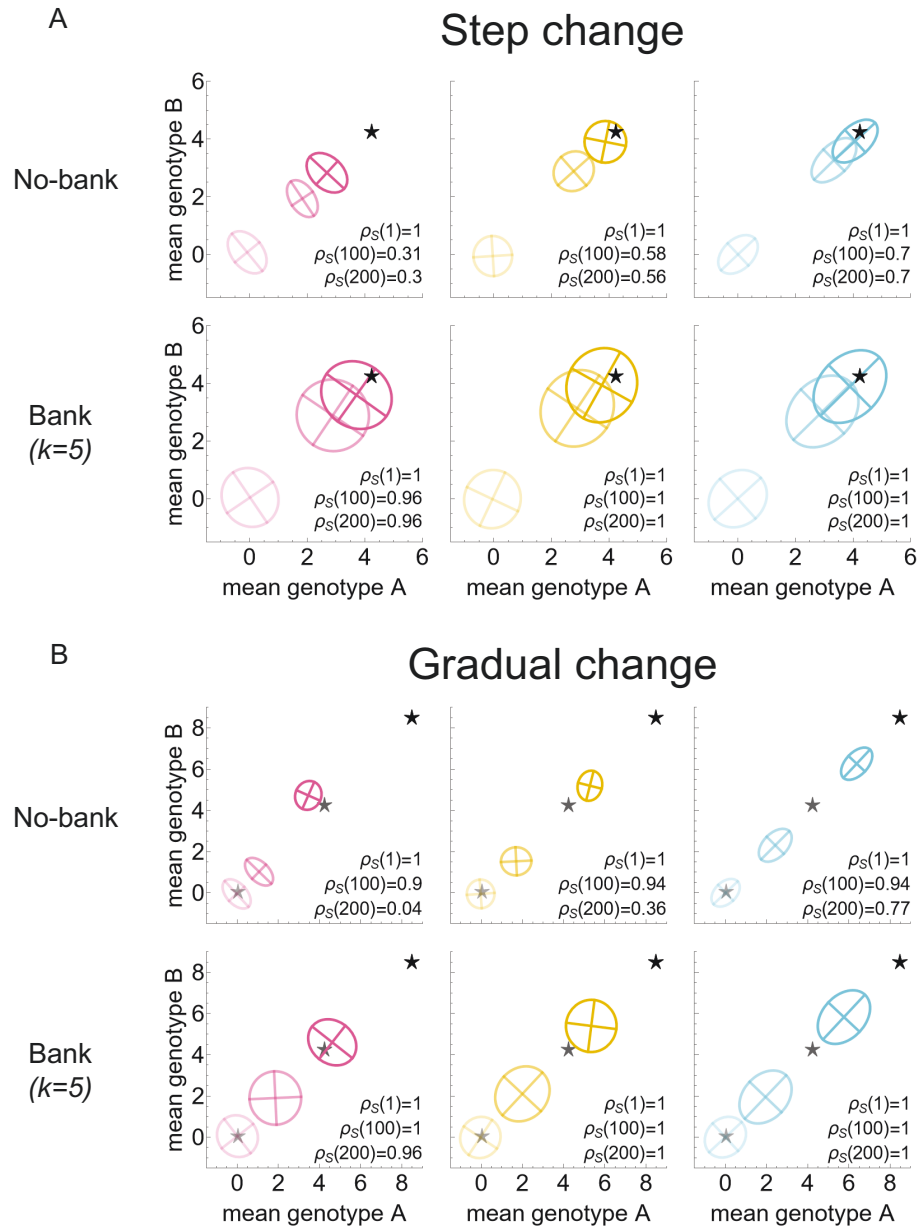


Figure 5: Changes in the $\mathbf{G}$ matrix of rosettes in no-bank and bank populations considering negative (pink; *left column*), null (yellow; *middle column*), and positive (blue; *right column*) mutational correlations under a step (A) and gradual (B) optimum change in multivariate simulations. Optimal phenotypes (stars) and average $\mathbf{G}$ matrices (ellipses) across extant replicates are shown for 1, 100, and 200 years after the environmental change begins (increasing opacity gradient). The lines of most and least resistance are shown in ellipses and are in the direction of the eigenvectors of the $\mathbf{G}$ matrix; their length in each direction is equal to 1.96 times the square root of the corresponding eigenvalue. Note the difference in axis scales and thus the scale of $\mathbf{G}$ matrices between A and B. Insets give persistence probabilities ($\rho_s(t)$) for each scenario. See the main text for parameter details.

general, these effects make seed bank populations less sensitive to mutational correlation. Regardless of the presence or sign of mutational correlation, $\rho_s \geq 0.96$ for bank populations 200 years after a step or gradual change in the environment, at least for the parameter values explored here (figs. 5,

S6, S7). Populations without a bank, however, are highly sensitive to mutational correlation, with ρ_s at the 200-year mark ranging between 0.3 and 0.7 under a step change and between 0.04 and 0.77 under a gradual change. Consequently, Δ_p depends on the interaction between the effects of

population type, mutational correlation, and type of environmental change (figs. 4E, 4F, S6, S7).

In our default scenarios ($\delta_\theta = 6/\sqrt{2}$, $r_\theta = 0.06/\sqrt{2}$), the benefit of the bank, Δ_p , is greatest for a negative mutational correlation ($r_m = -0.5$) and lowest for a positive correlation ($r_m = 0.5$; figs. 4E, 4F, S6A, S7A). This pattern is qualitatively similar across most step sizes and rates of change we explored (fig. 4E, 4F). Bank populations are 3.2, 1.8, and 1.4 times more likely to persist than no-bank populations 200 years after a step change with negative, null, and positive mutational correlations, respectively (fig. 5; see also fig. 4E, 4F). At the 200-year mark under a moving optimum, ρ_s for bank populations is 2.7 and 1.3 times ρ_s for no-bank populations, considering null and positive correlations, respectively. The relative benefit surges to 24 times when the correlation is negative (fig. 5; see also fig. 4E, 4F).

To understand why, it is easiest to start from the scenario of zero correlation ($r_m = 0$). Without correlation, the **G** matrix of both population types is round (figs. 5, S8). In bank populations, the size of the **G** matrix increases substantially while eccentricity temporarily increases shortly after the environment changes, distributing more genetic variation in the direction of selection. So even with longer generation time they adapt as fast as no-bank populations (similar lag and decline over time; figs. S6B, S7B). Coupled with their demographic buffer, $\rho_s = 1$ for bank populations over 200 years in both environments. No-bank populations are more vulnerable to stochasticity, such that at 200 years $\rho_s = 0.56$ and 0.36 for step and gradual changes, respectively (fig. 5).

When there is a positive correlation (i.e., reinforcing pleiotropy), the overall size of the **G** matrix is still larger in bank populations at the start of the environmental change and increases rapidly after the start (fig. S8). In comparison to the case of no correlation, the main difference is that the eccentricity of the **G** matrix is much greater in no-bank populations (fig. S8). Although eccentricity increases slightly over time in bank populations, the **G** matrix is still rounder than in no-bank populations. This means that no-bank populations have relatively more of their genetic variation oriented in the direction of selection (i.e., along the path of least resistance) compared with (i) their **G** matrix in the absence of correlation and (ii) the **G** matrix of bank populations. As a result, the positive mutational correlation disproportionately improves adaptation and, consequently, persistence in no-bank populations compared with bank populations.

Finally, when the traits under selection are negatively correlated (i.e., antagonistic pleiotropy), our simulations predict that bank populations will adapt faster than no-bank populations, which, combined with the demographic buffer, inflates Δ_p (fig. 4). The accelerated adaptation in

bank populations is easily observable for the step change in figure 5; whereas the ellipse (representing the **G** matrix) for bank populations encircles the new optimum by 200 years, the ellipse for no-bank populations is still far away from the optimum. Even under a moving optimum where populations of both types lag behind the optimum after 200 years, bank populations are closer, and ρ_s for bank populations remains at 0.96 compared with only 0.04 in no-bank populations. Adaptation is strongly constrained in no-bank populations, as expected, because negative mutational correlation has shaped the **G** matrix in a way that the line of least resistance is orthogonal to the direction of selection by the start of the optimum shift. With a larger, rounder **G** matrix, bank populations face the new optima with disproportionately more genetic variation along the line of most resistance. The increase is enough to overcome the negative effects of longer generation time and migration of maladapted alleles from the past. The advantage of the bank becomes more pronounced over time as the disparity in lag between no-bank and bank populations widens progressively (figs. S6B, S7B).

Discussion

Our work builds on investigations of evolutionary rescue in structured populations by simultaneously integrating stochastic environmental fluctuations, low carrying capacity, and pleiotropy (mutational correlation) under two types of environmental change in complementary analytical and individual-based models. Incorporating mutational correlation may be particularly relevant in the context of global change considering observed pleiotropic links among traits associated with stress response and phenology (e.g., McKay et al. 2003; Des Marais and Juenger 2016). We find that in most cases seed banks slow the rate of adaptive evolution even as they increase genetic diversity of the persisting populations. This finding aligns with prior theoretical research focused on large populations (Templeton and Levin 1979; Yamamichi et al. 2019; Schmid et al. 2022). In addition, for small (e.g., fragmented) populations, we demonstrate that seed banks increase the probability of persistence over 200–250 years compared with populations without a seed bank, especially when year-to-year fluctuations in the environment are high. Interestingly, when optima of pleiotropic traits shift, the most significant persistence advantage over populations without a bank occurs in the case of antagonistic pleiotropy. While these outcomes seem at first counterintuitive, they illustrate how population persistence teeters on the balance of several forces. First, for bank populations, evolution of the lag depends on the relative benefits of greater genetic variation versus the burden of longer generation time coupled

with migration of (mostly) maladapted alleles from the past. Second, whether evolutionary rescue can occur in time depends, in addition to the speed of adaptation, on the balance between the demographic buffer provided by the seed bank and the cost of reduced overall germination rates. We demonstrate how the outcome can change with the type and degree of environmental change, amplitude of environmental fluctuations, carrying capacity, selection strength, vital rates, and pleiotropy.

Remembering the Good and the Bad: The Impact of Seed Banks on Adaptation to a Changing Environment

Prior models have shown that the demographic and genetic benefits of seed banks can facilitate persistence in stochastic environments (Cohen 1966; Ellner 1996). Those models pertain to scenarios without directional change in the environment. In this study, we demonstrate that the benefit of the bank on persistence under a step or gradual change in optima depends critically on the magnitude of stochastic environmental fluctuations relative to the degree of directional change. In an extreme case of seed bank populations initially adapted to an environment without fluctuations, a large directional shift in the optimum renders (nearly) all alleles stored in the seed bank maladaptive under the new conditions, and thus the memory can serve only as a burden for adaptation and persistence. As the amplitude of environmental fluctuations increases, migration from the past transitions from burden to benefit (fig. 4A). The transition arises because large fluctuations increase the range of conditions under which alleles in the seed bank have been selected, which in turn increases the probability that at least some genotypes emerging from the bank are well suited to the new environment. This effect plays a pivotal role in counterbalancing the handicap of longer generation time.

Still, the positive relationship between the benefit of a seed bank and the amplitude of optimum fluctuations depends on the type of environmental change (fig. 4A). The persistence of bank populations increases with the amplitude of optimum fluctuations under a step change but decreases if environmental change is gradual. Under a step change, the initial selection gradient is large, placing a premium on standing genetic variance and the storage of alleles that were favored under previously extreme conditions. These alleles can act as stepping stones, placing the population within reach of the new optimum. The larger the amplitude of the fluctuations in the past relative to the step change, the greater the likelihood of alleles in the bank that can survive under the new optimum, reducing population decline and promoting adaptation and persistence. Interestingly, Peniston et al. (2021) found that environmental stochasticity decreases the persistence of

iteroparous populations with clonal reproduction under a step change. While this seems a contradiction to our results, their populations gained only the ability for clonal reproduction and began experiencing environmental fluctuations after the step change occurred. Therefore, their populations were more akin to our hypothetical population with a seed bank that can begin storing alleles only after the environment starts changing. Those tabula rasa banks have the demographic safety net but no increased genetic variation and no memory of past events from before the environmental change.

Under a gradual change, seed bank populations still enjoy the boost from rare alleles favored in past environments that were serendipitously like the present, but they also continue to accrue maladapted alleles as the optima move further away. This tilts the balance toward a net decrease in persistence, but one that is less steep than would occur in the absence of the bank. Consistent with conclusions by Orive et al. (2017, 2019) that adaptation to a gradually changing environment requires evolution of the genetic variance, we found that the increase in genetic variance over time in simulated tabula rasa bank populations can offset the low initial standing genetic variance, permitting a drastically faster response to directional selection than predicted by the analytical model.

The Effect of the Seed Bank on the Genotypic Distribution When Selection Acts on Survival

At first consideration, it seemed intuitive that the migration of alleles from the past should affect the genotypic distribution of extant populations. Yamamichi et al. (2019) detected this accumulation of maladapted alleles as a negative skew (i.e., a long left tail shifting the mean below the mode) in the genotypic distribution of a very large population (10,000 individuals) with a germ bank under a moving optimum. Their model predicted that the lag of the population mean phenotype escalates as the negative skew becomes more pronounced. Yet in our simulations we did not see a negative skew and, if anything, the skew trended slightly positive, indicating a long tail in the direction of the optimum, with the mean leading the mode. The difference in model outcomes could, in part, be due to stronger selection or weaker drift in substantially large populations compared with the small ones we considered, and certainly several parameters are different between the models. However, we suspect that the divergent results between the two models might reflect how the impact of a seed bank on the genotypic distribution (and, subsequently, the lag and the probability of evolutionary rescue) may depend on mechanistic details related to the fitness component under selection (survival vs. fecundity) and density regulation.

Consider a population starting with a Gaussian distribution of phenotypes undergoing fecundity selection in a gradually changing environment. Each year, individuals can reproduce as many times as it takes to “fill” the population, and the fitness function determines the frequency with which an individual reproduces, akin to the model of Yamamichi et al. (2019). When the population lags far behind a new optimum, the phenotypic distribution of the population is situated in the convex part of the fitness landscape facing away from the optimum. As a result, the fitness function (i.e., the probability of reproducing based on phenotype) in the range of phenotypes present is exponential. Rare phenotypes on the leading edge of the distribution will thus have extremely high fitness, monopolizing reproduction and increasing the weight of the right-hand side of the distribution of offspring phenotypes (i.e., a negative skew). Over generations, the bank will resemble layers of negatively skewed genotypic distributions with progressively lower means (as the environment gradually shifts) and leave a trail of genotypes to the left (fig. S9A, S9C). We presume the skew can be quite exaggerated when populations are immune to extinction and there is no limit to the time spent in the bank.

Now consider, as in this article, a population with a similar initial phenotypic distribution lagging behind the optimum but wherein selection is on survival and per capita fecundity is constant (thus total offspring production is not constant). Even though the fitness function defining the probability of survival will also be exponential, individuals can survive only once (vs. being resampled to reproduce). Therefore, their abundance does not increase disproportionately, as in the case of repeated reproduction. The increase in relative frequency of rare genotypes on the leading edge of the distribution will pull the tail to the right but leave the mass of the distribution concentrated away from the optimum. This is consistent with the general expectation that directional selection causes a positive skew in the distribution of selected individuals and thus their offspring (Turelli and Barton 1994; Bürger 1999). Over years as the optimum shifts further to the right, individuals that emerge from the bank will show a positively skewed distribution with a lower mean compared with the distribution of directly germinating seeds. The weight of the distribution of germinating plants will continue to shift further to the left (fig. S9B, S9D). In this scenario, migration of maladapted alleles from the past would serve to delay and prolong the development of a positive skew in the genotypic distribution in seed bank populations relative to populations without a seed bank, although strong genetic drift in small populations can cause temporal fluctuations in the shape of the distribution (fig. 3). Ultimately, this illustrates how the impact of the bank on the skew, and thus predictions of evolutionary change, could depend on the fit-

ness component under selection. The bank exaggerates a negative skew caused by fecundity selection but mutes and delays the positive skew caused by viability selection, especially in the case of a moving optimum.

A Delicate Balance between Lag and Demography

Our results clearly demonstrate how the lag alone cannot predict population persistence; rather, it interacts with demography to determine the ultimate outcome. As Kopp and Matuszewski (2014) pointed out, this is true in evolutionary rescue because adaptation is a function of relative fitness, whereas persistence is one of absolute fitness. Our findings underscore how a substantial seed bank can enhance the resiliency of density-regulated populations with small carrying capacities in the face of environmental change, even when their lower germination rate diminishes the aboveground population compared with populations without a bank (fig. 2). In fact, our results illustrate that in extreme cases germination from the seed bank can restore a population decimated after a random and extreme change in the environment (figs. 2, S2, S4). This buffer is critical to buying time for evolutionary rescue to take place following a sudden shift in the environment. Under gradual change, it can extend the period over which the likelihood of persistence remains high. However, our results also highlight that a high likelihood of persistence can be deceptive. Rather than indicating evolutionary rescue, it can conceal extinction debt, wherein populations are too maladapted to persist in the long run, and their larger population size only postpones the inevitable (Tilman et al. 1994; Dullinger et al. 2012; Cotto et al. 2017; Schmid et al. 2022).

In exploring the effect of vital rates on evolutionary rescue, our study further demonstrates that the persistence advantage afforded by a seed bank can be particularly fragile in populations with small carrying capacities. We found sometimes drastic differences relative to the reference case and, for a given vital rate, across the range of step change sizes and rates of optimum movement examined (fig. 4). Germination rate and survival in the seed bank can strongly affect population growth rate and thus persistence. However, we show that germination rate also influences the rate of adaptation in seed bank populations in response to environmental change because it governs the rate of migration of alleles from the past (and associated generation time). Just as studies considering migration in space emphasize that intermediate migration rates are optimal for increasing adaptation in peripheral populations (Alleaume-Benharira et al. 2006), the fastest responses to selection may be predicted when there is intermediate generational overlap in large dormant populations (Yamamichi et al. 2019). We demonstrate that this effect translates to a clear peak in the persistence advantage of

seed bank populations at intermediate germination rates. Most notably, reduced seed survival in the bank completely changes the outcome compared with the reference case. When survival in the bank is low, the persistence probability of seed bank populations is predicted to be lower than that expected for populations without a seed bank. Together, these results also suggest that the demographic benefit depends on the size of the seed bank relative to the size of the aboveground population. While some species may have large, persistent seed banks like we modeled here, in other species the size of the seed bank may be similar to or even smaller than the aboveground population (e.g., Baskin and Baskin 1998; Lundemo et al. 2009).

Mutational Correlations Can Exaggerate the Advantage of the Seed Bank

Consideration of genetic architecture can improve persistence predictions (Barfield and Holt 2016), yet relatively few studies have considered genetic correlations in demographic models (but see Duputié et al. 2012). We considered whether mutational correlation (i.e., pleiotropy) might alter the impact of the seed bank on evolutionary rescue. Consistent with general expectations for populations without a seed bank, we show that antagonistic pleiotropy (represented by a negative correlation here) constrains evolution and decreases persistence (figs. 4, 5) because it causes genetic variation to be distributed away from the direction of imposed selection, effectively placing populations farther from the optimum than under the case of independent traits (Jones et al. 2003, 2004; Blows and Hoffmann 2005; Hoffmann and Sgrò 2011; Duputié et al. 2012). However, we also provide novel evidence that the relative influence of these correlations on persistence varies with population type. For the parameter range we examined, populations without a seed bank are highly sensitive to pleiotropy, seen as wide variation in persistence probability and lag with the sign of mutational correlation (figs. 4, 5, S6, S7). In contrast, persistence was almost insensitive to mutational correlations in bank populations. The result is a substantial difference in the advantage of the seed bank across scenarios of mutational correlation: greatest when traits under selection experience antagonistic pleiotropy and exaggerated in the case of a gradually moving optimum (figs. 4, S6, S7).

To further understand the disproportionate advantage of the seed bank in the presence of antagonistic pleiotropy, it is helpful to consider the impact of migration from the past on the $\mathbf{G}$ matrix. Guillaume and Whitlock (2007) described how migration from a mainland to an island can alter the $\mathbf{G}$ matrix by increasing its size, changing its orientation, and “stretching” it along the line of divergence between the optima of the mainland and the island. In the case of a seed bank, alleles selected under various past con-

ditions (i.e., a range of optima) migrate from the seed bank to the aboveground population, more akin to migration from multiple mainland sources to an island. As a result, the $\mathbf{G}$ matrix increases in size and is stretched not in a single direction but in various directions, such that eccentricity decreases and orientation bears less relevance (figs. 5, S8). The larger $\mathbf{G}$ matrix of seed bank populations increases genetic variation in the direction of the optimum compared with populations without a seed bank. However, by also reshaping the $\mathbf{G}$ matrix to be rounder—nearly as round as in the case of no correlation—disproportionately more of the total genetic variation is distributed in the direction of the optimum compared with populations without a seed bank, alleviating the constraint of the negative mutational correlation. In fact, negative pleiotropy is the only case examined in this study where simulations predict that seed bank populations will better track the optimum than populations without a seed bank (i.e., have a smaller lag; figs. 5, S6, S7). In contrast, with reinforcing pleiotropy, the distribution of genetic variance is already greatest in the direction of selection in both bank and no-bank populations. So although the $\mathbf{G}$ matrix of seed bank populations is still larger, the rounder shape translates to disproportionately more of the total genetic variation being distributed in the direction of selection. Consequently, although a reinforcing pleiotropy helps both population types approach the new optimum more quickly (figs. 5, S6, S7), the advantage of the seed bank is lower than under negative pleiotropy.

Extensions

Even as we found that evolutionary rescue dynamics are sensitive to changes in vital rates within a species, we also see how the main effects of a seed bank on persistence are qualitatively similar to other types of stage structure and/or complex life histories, including iteroparity (Orive et al. 2017; Schmid et al. 2022) and life cycles combining sexual and clonal reproduction (Orive et al. 2017). Seed banks, perenniality, and partial clonal reproduction all result in increased genetic variance and generation time (and thus total environmental change per generation) and preserve alleles from the past. Nevertheless, future models could probe potentially important biological differences to discern their relative impacts on lag and rescue. For example, clones and surviving adults represent storage of exact genotypes (somatic mutation aside), whereas a seed bank stores the progeny of selected types that are a product of recombination, which could alter the phenotypic (and genetic) variance and thus the lag (Barton 2010). In addition, for perennials with strong density dependence, there is the added consequence of adult survival from prior selection regimes reducing recruitment and, consequently,

the contribution of selected alleles to the next year (see also Schmid et al. 2022). Of course, many other extensions of the models are possible, and adding biological complexity could strongly impact the predicted pace of evolution and population persistence. For example, selection can operate on a particular trait at various points across the life cycle, sometimes with opposing effects that lead to complicated and counterintuitive outcomes for evolutionary rescue (Cotto et al. 2019). In addition, germination rate and survival in the seed bank—each of which dramatically altered the outcome in our study—covary with maximal age in the bank (Baskin and Baskin 1998; Cuello et al. 2019; Montaña-Arias et al. 2021). Finally, we assumed that the environment affected only juvenile (rosette) survival, but evidence indicates that environmental shifts such as climate change also affect seed viability, dormancy state, germination rate, and recruitment (Cochrane et al. 2015), and pleiotropic loci can link dormancy to adult traits (Chiang et al. 2009; Auge et al. 2019). Unexpected outcomes might also arise under correlated selection, given that it can also affect the lag by altering the eccentricity of the **G** matrix (Jones et al. 2004). From a conservation perspective, it would be interesting to further investigate how management actions favoring migration in space, such as increasing connectivity among fragmented populations via corridors, could interact with the effect of migration from the past on evolutionary rescue.

Conclusion

Understanding the impact of the seed bank on evolutionary rescue has implications for a broad diversity of organisms, considering that some form of germ banking can be found across all five kingdoms in aquatic and terrestrial environments. The extent to which at least some alleles in the seed bank are adapted to changing conditions will depend on the amplitude of random environmental fluctuations experienced by the population relative to the type and degree of environmental change and the longevity of seeds in the bank. Our analyses also suggest that observing natural populations with seed banks in the first years after an environmental change is not enough to predict their persistence, as they can already be destined to become extinct. Determining which population sizes are hiding an extinction debt will require knowledge of interaction among the environmental change, the genetic architecture of traits under selection, and life history traits.

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Statement of Authorship

R.B.S. and K.T. conceptualized the study. R.B.S. acquired funding. K.T. and C.G. wrote the simulation code. R.B.S. and K.T. drafted the initial version of the manuscript. C.G. joined the project and led the incorporation of analytical models and updated simulations into a revised version. C.G. derived the analytical models and performed all final model analyses and data visualization. R.B.S. and C.G. jointly revised subsequent drafts with input from K.T. All authors read and approved the final version.

Data and Code Availability

Code is publicly available on Zenodo (<https://doi.org/10.5281/zenodo.11151738>; Godineau et al. 2024).

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