Weak seed banks influence the signature and detectability of selective sweeps

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Abstract

Seed banking (or dormancy) is a widespread bet-hedging strategy, generating a form of population overlap, which decreases the magnitude of genetic drift. The methodological complexity of integrating this trait means it is ignored when developing tools to detect selective sweeps. But, as dormancy lengthens the ancestral recombination graph, increasing times to fixation, it can radically change the genomic signals of selection. To detect genes under positive selection in seed banking species it is important to 1) determine whether the efficacy of selection is affected, and 2) predict the patterns of nucleotide diversity at and around positively selected alleles. We present the first tree sequence-based simulation program integrating a weak seed bank to examine the dynamics and genomic footprints of beneficial alleles in a finite population. We find that seed banking generally decreases the probability of fixation and magnifies (respectively decreases) the efficacy of selection for alleles under strong (respectively weak) selection. As seed banking increases the effective recombination rate, footprints of sweeps appear more narrow around the selected sites and are detectable for longer periods of time. The developed simulation tool can be used to predict the footprints of selection and draw statistical inference of past evolutionary events in plants, invertebrates, or fungi with seed banks.

1 Introduction

Seed banking is an ecological bet-hedging strategy, by which seeds or eggs lay in a dormant state of reduced metabolism until conditions are more favourable to hatch or germinate and complete the life-cycle. This life-history trait acts therefore as a buffer in uncertain environments (Cohen 1966; Templeton and Levin 1979) and has evolved several times independently in prokaryotes, plants, and invertebrates (Evans and Dennehy 2005; Willis *et al.* 2014; Tellier 2019; Lennon *et al.* 2021). Because several generations of seeds are simultaneously maintained, seed banks act as a temporal storage of genetic information (Evans and Dennehy 2005), decreasing the effect of genetic drift and lengthening the time to fixation of neutral and selected alleles (Templeton and Levin 1979; Hairston Jr and De Stasio Jr 1988). Seed banks play therefore an important role as the maintenance of genetic diversity is central to the adaptive potential of a species. In bacteria (Shoemaker and Lennon 2018; Lennon *et al.* 2021), invertebrates (Evans and Dennehy 2005) or plants (Willis *et al.* 2014; Tellier 2019), dormancy determines the neutral and selective diversity of populations/species by affecting the effective population size and buffering population size changes (Nunney and Ritland 2002), mutation rate (Levin 1990; Whittle 2006; Dann *et al.* 2017), spatial structure (Vitalis *et al.* 2004), rates of population extinction/recolonization (J. H. Brown and Kodric-Brown 1977; Manna *et al.* 2017) and the efficacy of positive (Hairston Jr and De Stasio Jr 1988; Koopmann *et al.* 2017; Heinrich *et al.* 2018; Shoemaker and Lennon 2018) and balancing selection(Tellier and J. K. M. Brown 2009; Verin and Tellier 2018).

Seed banking, or dormancy, introduces a time delay between the changes in the active population (above-ground for plants) and changes in the dormant compartment (seeds for plants) which considerably increases the time to reach the common ancestor of a sample or population (Kaj *et al.* 2001; Blath, González Casanova, *et al.* 2015; Blath, Casanova, *et al.* 2016; Blath, Buzzoni, Koskela, *et al.* 2020). We note that two models of seed banks are proposed, namely the weak and strong dormancy models. These make different assumptions regarding the scale of the importance of dormancy relative to the evolutionary history of the species. On the one hand, the strong version is conceptualized after a modified two-island model with coalescent events occurring only in the active compartment as opposed to the dormant compartment (seed bank) with migration (dormancy and resuscitation) between the two (Blath, González Casanova, *et al.* 2015; Blath, Casanova, *et al.* 2016; Blath, Buzzoni, González Casanova, *et al.* 2019; Shoemaker and Lennon 2018). Strong seed bank applies more specifically to organisms, such as bacteria or viruses, which exhibit very quick multiplication cycles and can stay dormant for times on the order of the population size (thousands to millions of generations, Blath, González Casanova, *et al.* 2015; Blath, Buzzoni, Koskela, *et al.* 2020; Lennon *et al.* 2021). On the other hand, the weak seed bank model assumes that dormancy occurs only over a few (tens to hundred) generations compared to the population size making it applicable to plant, fungi or invertebrate (*e.g. Daphnia sp.*) species (Kaj *et al.* 2001; Tellier, Laurent, *et al.* 2011; Živković and Tellier 2012; T. Sellinger *et al.* 2019). We focus here on the weak seed bank model as we provide novel insights into the population genomic analysis of plant, fungi and invertebrate species which undergo sexual reproduction. We come back in the discussion on the applicability of

our results by highlighting the differences and similarities between the strong and weak seed bank models.

The weak seed bank model can be formulated forward-in-time as an extension of the classic Wright-Fisher model for a population of size N haploid individuals. The constraint of choosing the parents of offspring at generation t only from the previous generation $(t-1)$ is lifted, and replaced with the option of choosing parents from previous generations $(t-2, t-3, ...$ up to a predetermined boundary $t-m)$(Nunney and Ritland 2002). The equivalent backward-in-time model extends the classic Kingman coalescent and assumes an urn model in which lineages are thrown back-in-time into a sliding window of size m generations, representing the populations of size N from the past (Kaj *et al.* 2001). Coalescent events occur when two lineages choose randomly the same parent in the past. The germination probability of a seed of age i is b_i, which is equivalent to the probability for one offspring to choose a parent i generations ago. The weak dormancy model is shown to converge to a standard Kingman coalescent with a scaled coalescent rate of $1/\beta^2$, in which $\beta = \frac{\sum_{i=1}^{m} b_i}{\sum_{i=1}^{m} ib_i}$ is the inverse of the mean time seeds spend in the seed bank, and m is the maximum time seeds can be dormant (Kaj *et al.* 2001). The germination function was previously simplified by assuming that the distribution of germination rate follows a geometric function with rate b, so that $b = \beta$ when m is large enough (Tellier, Laurent, *et al.* 2011; Živković and Tellier 2012; T. Sellinger *et al.* 2019, see methods). A geometric germination function is also assumed in the forward-in-time diffusion model analysed in Koopmann *et al.* 2017; Heinrich *et al.* 2018; Blath, Buzzoni, Koskela, *et al.* 2020.

Seed banking influences therefore neutral and selective processes via its influence on the rate of genetic drift. In a nutshell, seed bank delays the time to fixation of a neutral allele and increase the effective population size by a factor $1/b^2$. The effective population size under weak seed bank is defined as $N_e = \frac{N_{cs}}{b^2}$ where N_{cs} is the census size of the above-ground population (Nunney and Ritland 2002; Tellier, Laurent, *et al.* 2011; Živković and Tellier 2012). Mutation under an infinite site model can occur in seeds with probability μ_s and μ_a in the active population (above-ground for plants), so that we can define θ the population mutation rate under the weak seed bank model: $\theta = \frac{4N_{cs}(b\mu_a+(1-b)\mu_s)}{b^2}$ (Tellier, Laurent, *et al.* 2011). If mutations occur in seeds at the same rate as above-ground (in pollen and ovules), we define $\mu_s = \mu_a = \mu$ yielding $\theta = \frac{4N_{cs}\mu)}{b^2}$, while if seeds do not mutate, $\mu_s = 0$ and $\mu_a = \mu$, yielding $\theta = \frac{4N_{cs}\mu}{b}$. Empirical evidence (Levin 1990; Whittle 2006; Dann *et al.* 2017) and molecular biology experiments showing that even under reduced metabolism DNA integrity has to be protected (Waterworth *et al.* 2016), suggest that mutations occur in seeds (at the same rate as above-ground for simplicity) as assumed in most weak seed bank models. Furthermore, recombination and the rate of crossing-over is also affected by seed banking. Only one lineage is, however, affected by recombination in the backward-in-time model so that the population recombination rate is $\rho = 4N_erb = \frac{4N_{cs}r}{b}$. Indeed, the recombination rate r needs to be multiplied by the probability of germination b as only active individuals can recombine (Živković and Tellier 2018; T. Sellinger *et al.* 2019). Importantly, the balance of population mutation rate and recombination rate defines the amount of nucleotide diversity in the genome as well as the amount of linkage disequilibrium, a property which we used to develop an Sequential Markovian Coalescent

(SMC) approach to jointly estimate past demographic history and the germination rate (T. Sellinger *et al.* 2019; T. P. P. Sellinger *et al.* 2021).

While there is now a thorough understanding of how neutral diversity is affected by seed banking, the dynamics of alleles under selection have not been fully explored. Koopmann *et al.* 2017 developed a diffusion model of infinite (deterministic) seed bank model with positive selection and show surprisingly that the time to fixation is not multiplied by $1/b^2$ (as for neutral alleles) but at a smaller rate. The interpretation is as follows: while the time to fixation of an advantageous allele is lengthened compared to a model without dormancy, the efficacy of selection should be increased compared to a neutral allele (the effect of genetic drift). Namely, the Site Frequency Spectrum (SFS) of independently selected alleles shows an increased deviation from neutrality with a decreasing value of b. This result is confirmed in Heinrich *et al.* 2018 in which the deterministic seed bank assumption is relaxed, generating two additional insights: 1) a finite small seed bank decreases the efficacy of selection, and 2) selection on fecundity (production of offspring/seeds) yields different selection efficiency from the selection on viability (seed viability) as observable in the Site-Frequency Spectrum (SFS) of independent alleles under selection. Furthermore, based on the effect of seed bank θ and ρ and on selection, verbal predictions on the genomic signatures of selection have been put forth (Živković and Tellier 2018).

These theoretical and conceptual studies, while paving the way for studying selection under seed banks, did not consider the following argument. If the time to fixation of an advantageous alleles increases due to the seed bank, it can be expected that 1) drift has more time to drive this allele to extinction, and 2) the signatures of selective sweeps can be erased by new mutations appearing in the vicinity of the selected alleles. These effects would counter-act the predictions from 1) Koopmann *et al.* 2017 that selection is more efficient under a stronger seed bank compared to genetic drift, and 2) from Živković and Tellier 2018 that selective sweeps are more easily observable under stronger seed bank. It is the aim of the present study to resolve this paradox. We therefore develop and make available the first simulation method for the weak seed bank model which allows generating full genome data under neutrality and selection. We first present a simulation model in which we follow the frequencies of an adaptive allele in a population with seed banking, and examine the ensuing selective sweeps to predict times to, probabilities and detection of allele fixation. Therefore, this study aimed to provide insights into the characteristics of selective sweeps, including the time and probability of fixation as well as suggestions for their detection in species exhibiting seed banks.

2 Methods

Forward-in-time individual-based simulations are implemented in C++. Genealogies are stored and manipulated with the tree sequence toolkit (tskit, Kelleher *et al.* 2018), which allows for a general approach to handling arbitrary evolutionary models and an efficient workflow through well-documented functions.

2.1 Model

The model represents a single, panmictic population of N hermaphroditic diploid adults. Population size is fixed to $2N$ and generations are discrete. In the absence of dormancy and selection, the population follows a classic Wright-Fisher model. In this case, at the beginning of each generation, new individuals are produced by sampling parents from the previous generation. Parents are sampled with probability $\frac{1}{N}$ (multinomial sampling):

$$X_{parent} \sim Mult(N, \tfrac{1}{N})$$

Once sampled, each parent contributes a (recombined) gamete to generate the new individual. Dormancy adds a layer of complexity, by introducing seeds that can germinate after being dormant for many generations. This relaxes the implicit Wright-Fisher assumption, as parents are no longer only sampled from the previous generation, but also from seeds produced up to m generations ago. The probability of being sampled from generation k_i depends on the probability of germination, which is a function of the age of the dormant seed. Parents are sampled using a probability vector Y_i^{norm} written as:

$$\begin{aligned} &\Pr(Y_i = k_i) = (1-b)^{k_i - 1} b \\ &\text{from which we obtain:} \\ &Y_i^{norm} = \frac{Y_i}{\sum_{j=1}^{m} Y_j} \end{aligned} \tag{1}$$

From the expression above, the probability of being sampled follows a geometric distribution parameterized with germination rate b and then normalized. The generation G of each parent is randomly sampled using a multinomial sampling with the probability vector Y_i^{norm}.

$$G_{parent1} \sim Mult(m, Y_i^{norm}) \tag{2}$$

Once the age of each of the parents has been determined, a random individual from each of the sampled age groups is picked, and a gamete is generated which contributes to creating an offspring. Gametes are produced by recombination using the two initial genome copies carried by the sampled parent. The number of recombination events is sampled from a Poisson distribution with parameter r. At the end of this process, new mutations can be introduced. Unless stated otherwise, mutations are neutral and the number of new mutations is sampled analogously from a Poisson distribution with rate parameter μ. We assume here that mutations are also introduced at every generation in dormant individuals at the same rate (see justification in T. Sellinger *et al.* 2019). Recombination breakpoints and mutations are distributed uniformly across the genome.

To model selection signatures within a neutral genomic background, we consider non-neutral bi-allelic loci, placed at predefined and fixed genomic positions, with beneficial mutations arising after the burn-in period. The locus under selection has a dominance h and selection coefficient s, respectively. The expressions for the fitness of heterozygote and homozygote individuals are thus

$1 + hs$ and $1 + s$, respectively. Fitness affects the probability that an individual germinates and becomes a reproducing adult. In the case of dormancy, the choice of the germinating generation when sampling the parents is unaffected by their fitness values, but the sampling of individuals within a given generation is determined by the fitness. A selection coefficient of 0 would lead to multinomial Wright-Fisher sampling, which can be used to track neutral mutations over time. This two-step process of first choosing the generation and afterwards the individual is presented in Figure 2.1. In other words, selection acts on fecundity as the fitness of an allele determines the number of offspring produced and not the survival of the seed (viability selection).

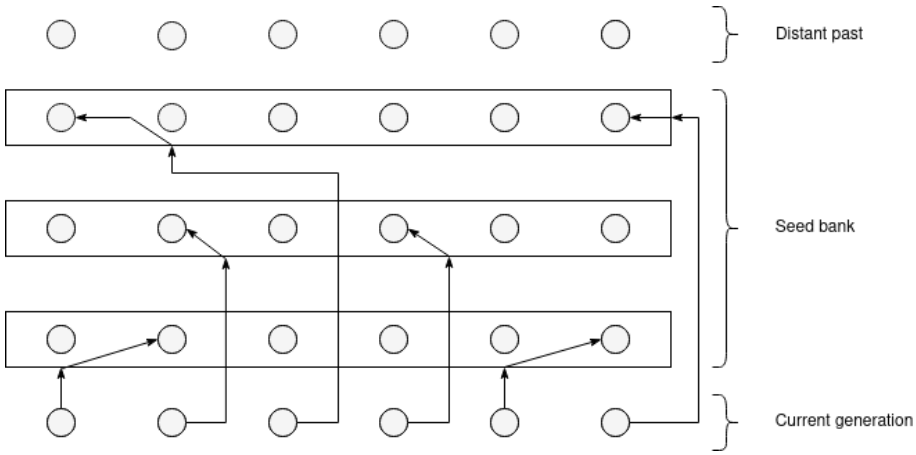


Figure 1: Schematic representation of the weak dormancy seed bank model by a forward-in-time two step process (Kaj *et al.* 2001). The arrows originating from the current generation represent the geometric sampling process of the parent or seed generation, while the second arrow constitute the sampling of the individual within the given generation based on the respective fitness value.

From a technical perspective, individuals are stored in the tskit-provided table data structures. The tables used in this simulation are as follows: 1) a node table representing a set of genomes, 2) an edge-table defining parent-offspring relationships between node pairs over a genomic interval, 3) a site table to store the ancestral states of positions in the genome, and 4) a mutation table defining state changes at particular sites. The simulation code works with these tables through tskit functions, e.g. the addition of information to a table after sampling a particular individual or through the removal of parents who do not have offspring in the current generation in a recurrent simplification process. However, a noticeable difference to the classic use of the tskit function is in our case that individuals which have not produced offspring in the past, but are still within the dormancy upper-bound defined range of m generations, need to be kept as well during the simplification process. Indeed, forward-in-time, a parent can give offspring many generations later (maximum m) through germinating seeds. Selective mutations are tracked externally in order to avoid the time-consuming step of generating a genotype matrix from tskit tables at every generation to determine fitness values per individual.

2.2 Simulations

Simulations start with a burn-in phase of 100,000 generations, to make sure full coalescence has occurred and a most-recent common ancestor is present. We consider that after this initial phase, the population is at an equilibrium state in terms of neutral diversity, including within the seed bank. After this phase, selectively advantageous mutations are introduced one at a time at the predefined site. To study sweep signatures as well as the time it takes for sweep signatures to recover, simulations are run for several generations after fixation of the beneficial allele (up to 4,000 generations after fixation).

Except when indicated otherwise, the population size is generally set to $N = 500$ individuals or $2N = 1,000$ chromosomes. We specifically change population size when testing whether sweep signatures can be explained by simple size scaling, and use values of N of 1,000, 2,000, 4,000 and 8,000 individuals with a germination rate of $b = 1$. Our seed bank setup is in that case a population of $N = 500$ individuals with a germination rate $b = 0.35$. The genome map length is set to 10,000. The neutral mutation rate μ is set at $5e - 5$ per locus and to check whether the strength of a sweep behaves in accordance to expectation *i.e.* lower recombination rates result in wider sweeps, recombination rates of $r = 5e - 5$, $1e - 5$ and $1e - 4$ are tested. These rates were multiplied by the map length to get the respective random Poisson sampling rate. Simulations are run for the germination rate b ranging from 0.25 up to 1 (with $b = 1$ meaning no dormancy). The upper-bound number of generations m which is the maximum time that seeds can remain dormant (*i.e.* seeds older than m are removed from the population) is set at 100 generations. Beneficial mutations have a selective coefficient s_i from 0.01 to 10 and dominance h takes values $0, 0.5$ and 1.1.

2.3 Statistics and sweep detection

We calculate first several statistics relative to the forward-in-time change of advantageous allele frequency in the population such as time to fixation and the probability of fixation using 1,000 simulations per parameter configuration. Each simulation run consist of the recurrent introduction over time of an allele (mutant in frequency 1/2N) which is either lost or fixed. When an allele is lost a new allele is introduced at the same position, and this procedure is repeated until one allele reaches fixation at which time the simulation run stops. An allele is considered to be fixed if it stays a frequency 2N for 50 consecutive generations. We store for each simulation run 1) the time it takes for the last introduced allele to reach fixation (time between allele introduction until fixation), and 2) the number of alleles which were introduced until one has reached fixation (yielding the probability of fixation of an allele per simulation run). The resulting times to fixation and fixation probabilities are calculated as the averages over the 1,000 simulation runs.

We also compute statistics on the underlying coalescent tree and ancestral recombination graph (ARG) such as time to the most recent common ancestor, linkage disequilibrium (r^2, Hill and Robertson 1968), as well as Tajima's π (Nei and Li 1979) over windows of size 50 (or 200 windows for a map length of 10,000). This allows us to analyse the effects of seed-dormancy on the amount

of linkage disequilibrium and nucleotide diversity along the genome, as well as the footprint of a selective sweep on these quantities. *Tskit* functions are used for diversity and linkage disequilibrium calculations. Nucleotide diversity (π) is normalized by the map interval length and calculated based on the polymorphic sites and not the branch length. Sweeps are detected using the Omega statistic as implemented and applied with OmegaPlus (Alachiotis, Stamatakis, *et al.* 2012). A difficult issue in detecting selective sweeps is choosing the correct window size to perform the computations. If the window is too large, the sweep can be missed, if the window is too narrow, the number of false-positives can be inflated. It is documented that the optimal window size depends on the recombination rate and thus the observed amount of linkage disequilibrium (Alachiotis, Stamatakis, *et al.* 2012; Alachiotis and Pavlidis 2016). We thus use two different setups with different window sizes: –minwin 100 –maxwin 1000 and –minwin 50 –maxwin 100. The larger window size is based on the model without dormancy ($b = 1$), and the narrower window size is based on the model with dormancy ($b < 1$), –grid 1000 –length 100000 parameters are set equally for both cases. The statistic is computed for a sample size of 500 over 400 simulations for each recovery scenario.

2.4 Code description and availability

Source code of the simulator and demonstration of the analysis can be found at `https://github.com/kevinkorfmann/sleepy` and `https://github.com/kevinkorfmann/sleepy-analysis`. On a Intel(R) Core(TM) i7-9750H CPU @ 2.60GHz processor, CPU/Wall times for a single time to the most recent common ancestor simulation of $N = 500$ individuals (no burn-in period) took 19.5 ms/44.7s and 21 ms/2 min 6s for b=1.0 and b=0.5, respectively. Including burn-in periods of 100 000 generations with a succeeding selection phase (selection coefficient $s = 1$) modified the run-times to 26.5 ms/3min 59s and 19.4 ms/4min 44s for b=1.0 and b=0.5.

```python
import tskit
from utils import sleepy

sleepy(N=500, b=1.0, m=100, output_directory="./b1/")
ts_no_selection = tskit.load("./b1/run_0.trees")

sleepy(N=500, b=1.0, m=100, s=1, output_directory="./b1_s1/")
ts_selection = tskit.load("./b1_s1/run_0.trees")
```

Listing 1: Python code example for a simulation with and without selection. Tree sequence results are stored in a specified output directory and are loaded via *tskit* function for further processing or analysis of e.g. linkage disequilibrium or nucleotide diversity along the genome.

Simulations rely on regular simplification intervals for efficiency of the genealogy recording, yet the weak dormancy model requires keeping up to m generations in memory even for past individuals (seeds) which do not have offspring in the current generation after a simplification procedure. To make sure that this assumption is realized in the code, up to m generations are technically defined

as leaf nodes, thus hiding them from the regular memory clean-up process. Further, the presence or absence of an allele with an associated selection coefficient needs to be retrievable even under the influence of recombination for all individuals up to m generations in order to determine the fitness value of the individuals. Therefore, recombination and selective alleles are tracked additionally outside of the *tskit* table data structure to avoid building the tree sequence from the tables at each generation. This would have been necessary to determine which individuals have a selective allele or not. Both of these model requirements, namely maintaining individuals which do not have offspring in the current generation (but potentially could have due to stochastic resuscitation of a seed) as well as the knowledge about the precise state of that given individual in the past, are reasons to choose our own implementation over the otherwise advisable option SLiM (Haller and Messer 2019).

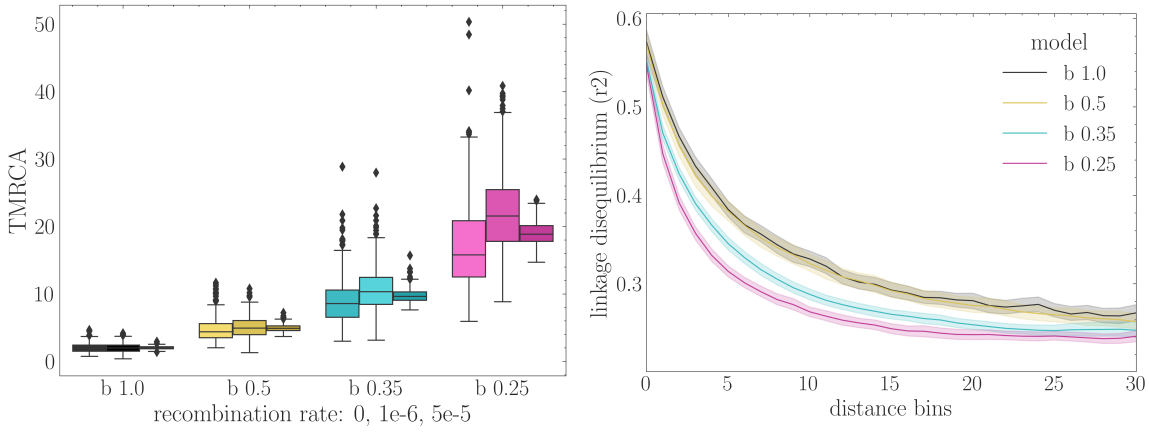
3 Results

3.1 Neutral coalescence

We first verify that our simulator accurately produces the expected coalescent tree in a population with a seed bank with germination parameter b and population size $2N$. To do so, we first compute the time to the most recent common ancestor (TMRCA) of a coalescent tree for a sample size $n = 500$. We find that, as expected, the coalescent trees are scaled by a factor of $\frac{1}{b^2}$ independently of the chosen recombination rate (Figure 2a). The variance of the TMRCA decreases with increasing recombination rate due to lower linkage disequilibrium among adjacent loci as expected under the classic Kingman coalescent with recombination (Hudson 1983). Moreover, we also find that decreasing the value of b, *i.e.* the longer seeds remain dormant, decreases linkage disequilibrium (Figure 2b). This is a direct consequence of the scaling of the recombination rate by $\frac{1}{b}$, because any plant above-ground can undergo recombination (and can be picked as a parent with a probability b backward in time). Therefore, we observe here two simultaneous effects of seed banks on the ARG: 1) the length of the coalescent tree and the time between coalescent events is increased by a factor $\frac{1}{b^2}$ meaning an increase in nucleotide diversity (under a given mutation parameter μ), and 2) a given lineage has a probability br to undergo an event of recombination backward in time. In other words, even if the recombination rate is slowed down by a factor b because only above-ground plants may recombine, as the coalescent tree is lengthened by a factor $\frac{1}{b^2}$ there are on average $\frac{1}{b}$ recombination events per coalescent tree. This property of the ARG was used in T. Sellinger *et al.* 2019 to estimate the germination parameter using the Sequential Markovian Coalescent approximation along the genome.

3.2 Allele fixation under positive selection

We examine the trajectory of allele frequency of neutral and beneficial mutations, by computing the probabilities and times to fixation over a large number of simulations. As expected for the case without dormancy ($b = 1$), the probability of fixation of a beneficial allele increases with the strength of selection (Figure 3a). The discrepancy between the mathematically expected time to fixation in this case (Figure 3a - gray line) is likely an artifact of choosing the population size to be



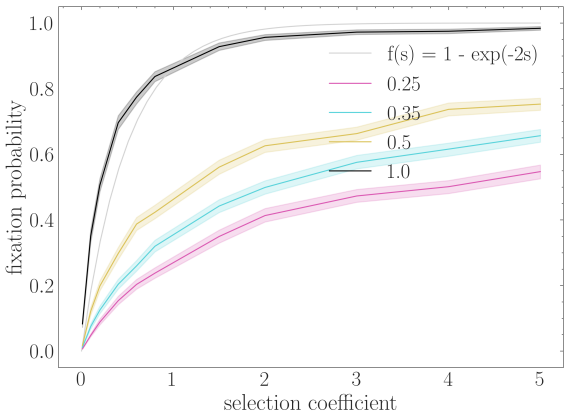
(a) (b)

Figure 2: (a) Time to the most recent common ancestor (TMRCA) as a function of the germination rate b and scaled by the $b = 1$ estimates taking diploidy into account. For each germination rate, three recombination rates per site are presented ($r = 0$, $r = 1e-6$ and $r = 5e-5$ from left to right). (b) Monotonous decrease of linkage disequilibrium as a function of distance between pairs of SNPs, calculated using 50 equally spaced bins. Distance bin 10 represents two SNPs which are 10 distance bins apart.

500 diploid individuals, in which genetic drift plays an important role. However, larger population sizes increase the simulation run time considerably, especially when taking the scaling factor of $\frac{1}{b^2}$ of the germination rate into account. Thus, we avoid increasing the population size due to technical time and memory constraints of such forward simulation and point out that our conclusions are not affected by this discrepancy. With dormancy, we also observe a positive correlation between selection coefficients and the probability of fixation, while we also observe much lower probabilities of fixation (than in the absence of dormancy). Furthermore, as selection increases, so does the difference in fixation probability between simulations with $b = 1$ and $b < 1$. However, the difference of fixation probability between the case $b = 1$ and $b < 1$ is larger for weak selection than for strong selection coefficients (Figure 3a). Indeed, we note that for the strongest selection coefficients, the fixation probability under seed bank is a fraction of that under $b = 1$, and that factor is higher than b (for example, at $s = 5$, the probability of fixation for $b = 1$ is approx. 1, and it is 0.55 for $b = 0.25$). For smaller selection coefficient, this factor decreases (for example, at $s = 1.5$, the probability of fixation of fixation for $b = 1$ is approx. 0.9, and it is 0.35 for $b = 0.25$).

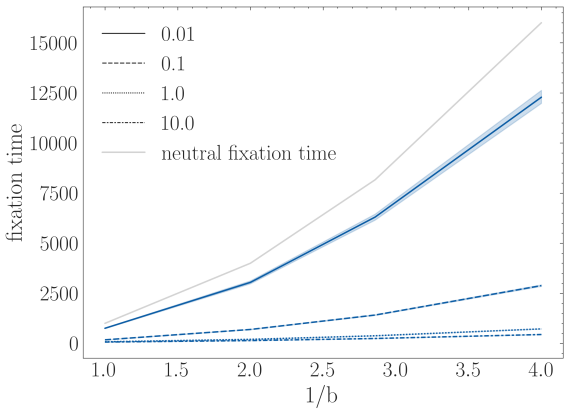
As expected from the neutral case, the time to fixation with dormancy becomes longer with smaller values of b (Figure 3b). When selection is weak (*i.e.* selection coefficient 0.01) the time to fixation is close to the expectation for neutral mutations (Figure 3c). Increasing the strength of selection tends to reduce the differences in times to fixation between the different germination rates. For strong selection, it becomes apparent that the times to fixation are not scaled by a simple factor of $\frac{1}{b^2}$, which is the scaling for neutral mutations under dormancy.

The latter observation that the time to fixation of strongly beneficial alleles, as well as for strongly deleterious alleles, does not scale with $\frac{1}{b^2}$ but rather almost as a linear function of b was already

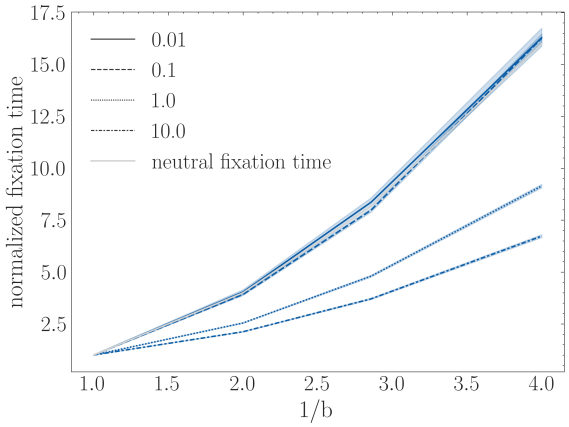


(a)

Figure 3: (a) Expected and simulated estimates of the probability of fixation: for germination rate of $b = 1$ for different selection coefficients, and simulated estimates of seed dormancy fixation probabilities with germination rate between $b = 0.25$ to $b = 1.0$. (b) Time to fixation for different selection coefficients. Y-axis is the unnormalized time in generations, and X-axis is the germination rate written as $\frac{1}{b}$. (c) Time to fixation for different selection coefficients s normalized by the expected time to fixation with $b = 1$. Y-axis is the time in generations and X-axis is the germination rate written as $\frac{1}{b}$.



(b)



(c)

computed (Formula 19, Koopmann *et al.* 2017). However, the probability of fixation of beneficial alleles had not been addressed. Taken together, the results in Figure 3a, 3b and 3c demonstrate that the selection is slowed down by dormancy (Hairston Jr and De Stasio Jr 1988; Shoemaker and Lennon 2018) and leads to many more mutations to occur and get lost. This is due to an increased time window for the loss of a mutation due to beneficial alleles remaining at very low frequencies for a longer period of time, and thus being more subjected to loss by genetic drift (Figure 3a). However, when the beneficial allele reaches fixation, the time to fixation does not scale by the inverse of the square of the germination rate as for neutral alleles (as was expected in Shoemaker and Lennon 2018). This effect becomes non-linearly more pronounced with stronger selection coefficients and stronger the seed bank (Figure 3c), yielding the counter-intuitive result that dormancy enhances the efficiency of selection compared to genetic drift (Koopmann *et al.* 2017).

3.3 Footprints of selective sweep

Following on the time and probability of fixation results, we now make use of our new simulation tool to investigate the genomic diversity and signatures of selective sweeps at and near the locus

under positive selection by simulating long portions of the genome (Figure 4). In accordance with the results from Figures 2 and the effects of the seed bank in maintaining genetic diversity, smaller germination rates lead to higher neutral genetic diversity due to the lengthening of the coalescent trees (e.g. Figure 4a measured as Tajima's π). Moreover, stronger dormancy generates also narrower selective sweeps around sites under positive selection which have reached fixation, in other words, there is a narrower genomic region of hitch-hiking effect around the site under selection (Smith and Haigh 1974). This is due to the re-scaling of the recombination rate as a consequence of dormancy (e.g. Figure 4a and 4c). We note that the depth of the sweeps increases in absolute diversity term (Figure 4a) but not in relative diversity (Figure 4c) with lower germination rates, due to 1) the higher diversity under dormancy, and 2) the increased efficacy of selection compared to drift at the site under selection. However, we observe that nucleotide diversity close to the site under selection is not zero (Figure 4a) because of the longer times to fixation of a positive mutation and longer time for drift and new mutation to occur at neutral alleles close to the selected site. The results in Figure 4 reflect the manifold effect of dormancy on neutral and selected diversity as well as recombination rate (Figures 2 and 3c). Furthermore, as recombination and selection are scaled by different functions of the germination rate, the results in Figure 4 cannot be produced by scaling only the effective population size in the absence of dormancy. We present different simulations with population sizes in the absence of dormancy and show that these do not produce the footprint of selective sweep under dormancy ($b = 0.35$, Figure 4d). Additionally, seed bank diversity appears to increase visibility of the sweep when a strong dominance coefficient ($d = 1.1$ with $b = 0.35$, Appendix Figure 2) is associated with the selective allele due to the increased efficacy of selection under dormancy. We finally point out that while the signatures of sweeps appear sharp in Figure 4, it is because these are averaged footprints over 100 repetitions. Each individual simulation produces variance in nucleotide diversity and of the sweep signature which conditions the detectability of the sweep against the genomic background.

3.4 Detectability of selective sweeps

As a result of the previous results, we hypothesize that, compared to the absence of seed banking, the detectability of selective sweeps in a species with seed bank is affected 1) in the genome space, that is the ability to detect the site under selection, and 2) in time, that is the ability to detect a sweep after the fixation of the beneficial allele. First, as the footprints of selective sweeps are sharper and narrower in the genome under a stronger seed bank, we expect that the detection of these sweeps likely requires adapting the different parameters of sweep detection tools, namely the window size to compute sweep statistics. Second, in a population without dormancy, the time for which the detection of a selective sweep signature is possible is approximately 0.1N generations (Kim and Stephan 2002). We hypothesize that as the rate of mutation and genetic drift is scaled by $1/b^2$, the time it takes a sweep to recover after it has reached the state of fixation is slowed down. The time window for which a sweep could still be detected would then be potentially longer than 0.1N generations.

In Figure 5 we show the results obtained using OmegaPlus, a tool for detecting selective sweeps

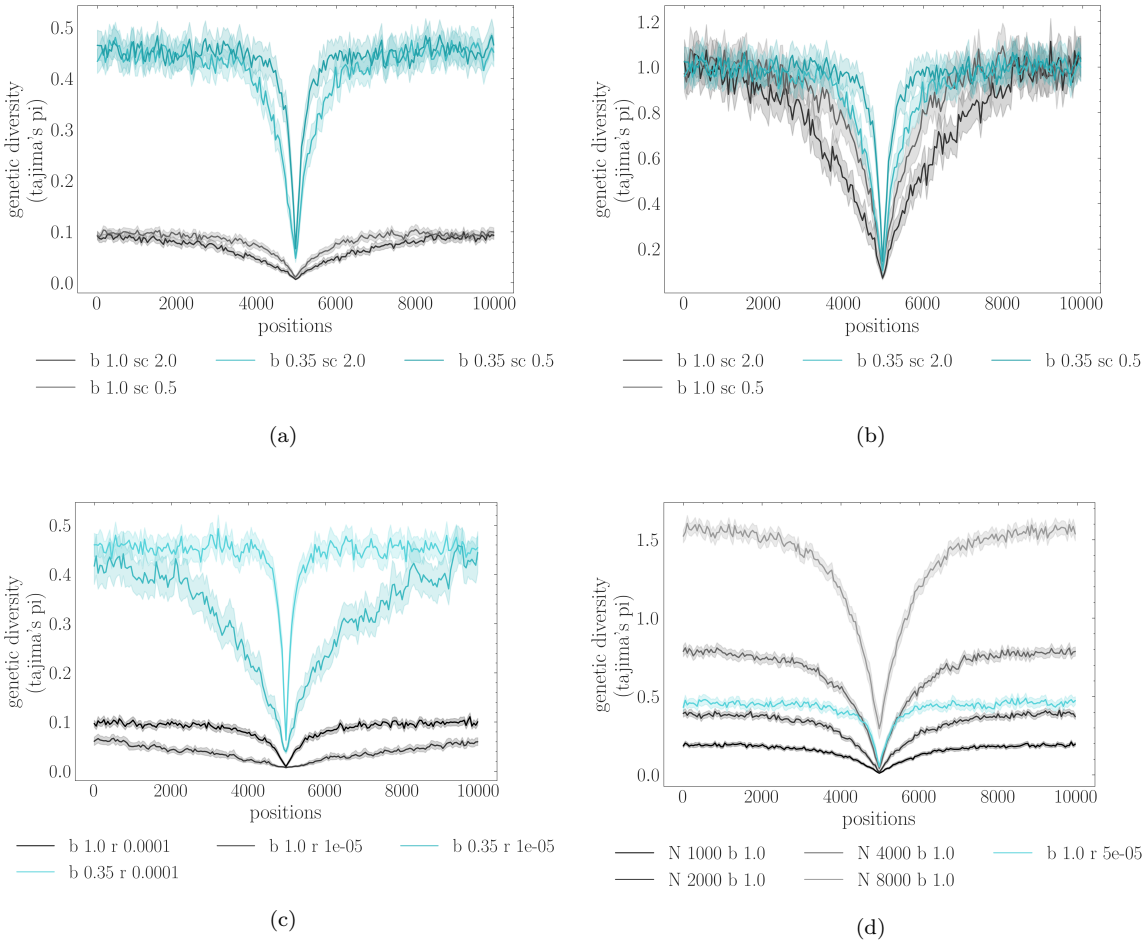


Figure 4: Nucleotide diversity (Tajima's π, Y-axis) over map length (X-axis) for sliding windows of size 50 mapping length and averaged over 100 repetitions. (A) Comparison between germination rate $b = 1$ and $b = 0.35$ for selection coefficients $s = 0.5$ and $s = 2.0$ with $h = 0.5$. (B) Normalized nucleotide diversity (π) computed as the diversity of the respected seed dormancy and selection coefficient combinations divided by the mean diversity of map length at position 0-1,000 and 9,000-10,000. (C) Effect of varying recombination rates with values $r = 10^{-4}$ and $r = 10^{-5}$ with and without dormancy. (D) Comparison of footprints of selective sweeps under different population sizes N=1,000; 2,000; 4,000 and 8,000 without dormancy with a selective sweep under germination rate of $b = 0.35$.

Alachiotis, Stamatakis, *et al.* 2012. As noted above, detection of a sweep is performed against the genomic background (nucleotide diversity, amount of LD) which varies for each individual simulation more than apparent in the above figures which are averages over several repetitions. This variation in nucleotide diversity and LD along a chromosome generates confounding effects and define the rates of false positives expected from the detection test. We find that when using the same large detection window "–minwin 100 –maxwin 1000" for $b = 1$ and $b = 0.35$ (Figures 5a and 5b), sweep detection almost completely fails for $b = 0.35$ (Figure 5b). Based on neutral simulations, we choose a threshold for detection of 2,000 for the case without seed bank (Figure 5a), in order to obtain a false positive rate of less than 0.1 and a detection power of approximately 85% of sweeps. Under this large window setting, we require a much smaller threshold (<500) when $b = 0.35$ only to obtain approximately 30% of sweeps detected. Without dormancy, the detectability of sweep is very low (approx. 25%) already 500 generations after the fixation event (Figure 5b, with a threshold of 2,000). However, when decreasing the window size to "–minwin 50 –maxwin 100" in Figure 5c and 5d, the detectability of sweeps is largely increased under seed banking (Figure 5d), while becoming worst in the absence of seed bank (Figure 5c). When setting a threshold of 300 in Figure 5d, about 85% of the sweeps can be detected at the time of fixation, and about 40-50% of sweeps as old as 500 up to 1,000 generations can be detected. We here note the much sharper decrease in the rate of detection of false positive sweeps (neutral simulation line in Figure 5) under seed bank compared to the absence of a seed bank. Lastly, the possibility to locate sweeps multiple generations after the fixation event emphasizes the slower recovery of nucleotide diversity post-fixation in combination with the already established narrowness of the signature in the presence of a seed bank ($b = 0.35$, Appendix Figure 1).

4 Discussion

We investigate the neutral and selective genome-wide characteristics of a weak seed bank model by means of a newly developed simulator. We first characterize the emergent behavior of an adaptive allele under a weak seed bank model, providing estimations of the times to and probabilities of fixation, considering different strengths of selection and recombination. In populations without seed banks, a neutral mutation is expected to fix after a period of $\frac{1}{2N_e}$ generations and $\approx \frac{1}{2N_e s}$ if the allele is under selection (Kimura 1962). Though both processes are re-scaled by the weak dormancy model (Koopmann *et al.* 2017), the time to fixation of a neutral mutation is lengthened by a factor b^2 (as $N_e = \frac{N}{b^2}$ in the case of a seed bank, with b the germination rate) but the scaling in the event of selection is not as simple to determine. Under strong selection the time to fixation is increased by a function approximately linear in b (Koopmann *et al.* 2017), while under weak selection, the factor is again $\frac{1}{b^2}$. Importantly, when computing the fixation probability for beneficial alleles, we also observe a non-linear effect of germination rate b depending on the selection coefficient. We conclude that the seed bank magnifies (respectively decreases) the efficacy of selection compared to genetic drift for strong (respectively small) selection coefficients. Combining this observation and the effect of seed banks on increasing the effective recombination rate, we find that the signatures of sweeps are easier to detect in the presence of seed banking as shown by the sharpness and depth of

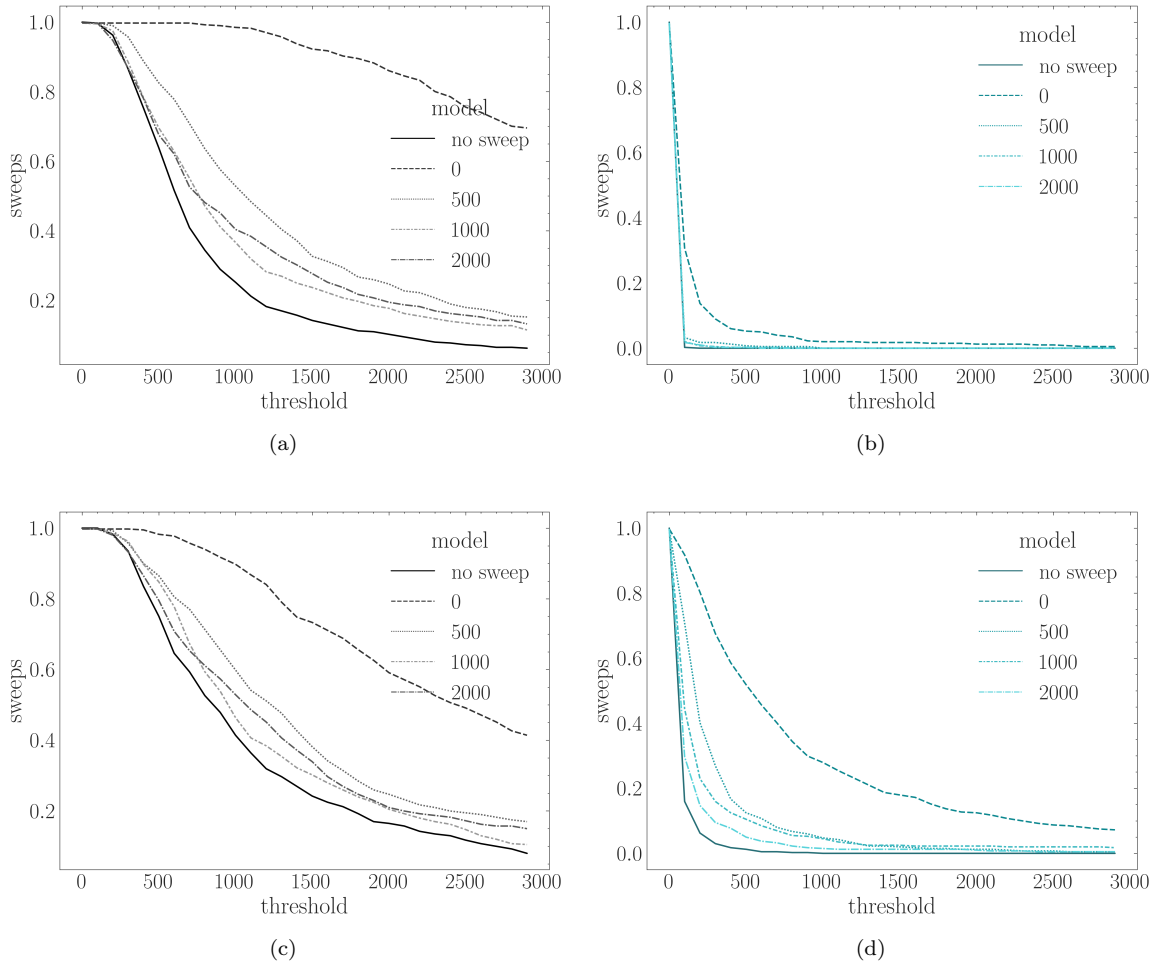


Figure 5: Selective sweep detectability depending on the threshold of OmegaPlus statistics. Results for two window sizes "–minwin 100 –maxwin 1000" (a,b) and "–minwin 50 –maxwin 100" (c,d) and without seed bank (a, c) and under germination rate of $b = 0.35$ (b, d), the lines indicate the time since fixation of the beneficial allele (time to fixation up 2,000 generations after fixation). The neutral simulation line represents the false positive rate of detection expected at a given threshold value of the statistics based on a sample size of 500 for 400 simulations. A selection coefficient of $s = 1.0$ and recombination rate $r = 5 \times 10^{-5}$ was set for all sweep simulations.

the nucleotide diversity pattern (the so-called valley of polymorphism due to genetic hitch-hiking, Smith and Haigh 1974; Kim and Stephan 2002) against the genomic background.

4.1 Dynamics of alleles under positive selection

Our results regarding the time to fixation of advantageous alleles are in line with previous works (Hairston Jr and De Stasio Jr 1988; Koopmann *et al.* 2017; Heinrich *et al.* 2018; Shoemaker and Lennon 2018) in showing that a weak seed bank delays the time to fixation. However, a novelty here is that we refine these results in showing that the time to fixation of a weakly ($s < 1$) and a strongly ($s >= 1$) positively selected allele differ under seed bank: the selection on weak alleles is delayed by a factor $\frac{1}{b^2}$ while the strong selection is delayed by a factor close to $\frac{1}{b}$ (see Figure 3b,3c). The analytical formula is found in Koopmann *et al.* 2017, though this model assumes an infinite deterministic seed bank. Moreover, we provide a second new result (Figure 3a): the probability of allele fixation as a function of the germination parameter and selection coefficient. Interestingly, the probability of allele fixation becomes lower with a longer seed bank, though there is a complex non-linear interaction between the germination rate and the selection coefficient. In other words, as a seed bank delays the action of selection under the weak seed bank model (due to the dormant compartment acting as a buffer slowing down allele frequency change), genetic drift has more time to act and advantageous alleles may be lost. This is especially true in the initial phase of selection when the advantageous allele is at a very low frequency in the (active) population, before reaching the phase of exponential allele frequency increase (which is almost deterministic, Kim and Stephan 2002). This delay in the initial selection phase is visible in Figure 4a in Shoemaker and Lennon 2018. Our results are valid for the weak seed bank model (likely realistic for plants and invertebrates, as studied in Figure 4a in Shoemaker and Lennon 2018, and Koopmann *et al.* 2017) and we find that there exists a unique phase of selection encompassing the time until all individuals (in the active and dormant population) have fixed the advantageous allele. Strong seed bank models behave differently with respect to time to fixation of alleles under selection (Shoemaker and Lennon 2018), showing two distinct phases: a first rapid phase of selection in the active population, followed by a second long delay until there is fixation in the dormant population. We are not aware of any results regarding the effect of strong seed banking on the probability of allele fixation. Our results suggest that the paradigm that (weak) seed banks enhance the effect of selection against drift (Koopmann *et al.* 2017; Shoemaker and Lennon 2018; Živković and Tellier 2018) is only valid for strong selection (high coefficients of selection) but not for weak selection. This implies that although seed banks promote genetic diversity, this does not necessarily equate with enhanced adaptive potential.

4.2 Signals of selective sweeps

When selection is strong enough to overcome genetic drift, resulting in allele fixation, we can study its footprints in the genome. The precise signature of a positive selective sweep is dependent on a variety of factors, *i.e.* age of the observation after fixation, degree of linkage due to recombination, and its detectability depends on the specified window size to compute polymorphism statistics. However, in the case of sweeps under seed bank, two effects are at play and change the classic expectations

based on the hitch-hiking model without generation overlap. First, as the effective population size under seed bank increases with smaller values of b, an excess of new mutations is expected to occur after fixation around the site under selection compared to the absence of seed bank. As these new mutations are singleton SNPs, we suggest that the signature of selective sweeps observed in the site-frequency spectrum (U-shaped SFS) should be detectable under seed bank (Smith and Haigh 1974; Kim and Stephan 2002). This effect should be detectable by other sweep detection methods based on the SFS such as SweeD (CLR test, Pavlidis *et al.* 2013), a key point is that the genomic windows for CLR statistics have to be decreased due to the presence of seed bank, yet, they should contain enough SNPs.

Second, the signature of sweeps also depends on the distribution of linkage disequilibrium (LD) around the site under selection (Alachiotis, Stamatakis, *et al.* 2012; Bisschop *et al.* 2021), which is affected by the seed bank (Figure 4). Theoretically, it has been shown that patterns of LD both on either side and across the selected site generally provide good predictive power to detect the allele under selection. We use this property when using OmegaPlus, which relies on LD patterns across sites. Further past demography should be accounted to correct for false positives, due for example to bottlenecks (see review in Stephan 2019). We speculate that a high effective recombination rate around the site under selection, as a consequence of the seed bank, maybe an advantage when detecting sweeps. This allows the avoidance of confounding effects due to the SFS shape, which is sensitive to demographic history. We also highlight that the narrower shape of the selective sweep under stronger seed bank, and the smaller number of loci contained in the window, reduce the number of false positives.

As mentioned above, a crucial parameter to detect sweeps is the window length to compute the statistics that the various methods rely on. The optimal window size depends on the neutral background diversity around the site of interest, which is a consequence not only of the rate of recombination but also the scaled rate of neutral mutations. We choose a constant mutation rate over time, and make the assumption of mutations being introduced during the dormant phase (in the seeds) at a constant rate as well (see equations in introduction). This simplifying assumption is partially supported by empirical evidence (Levin 1990; Whittle 2006; Dann *et al.* 2017), and has so far been made in the wider field of inference models, notably in the ecological sequential Markovian coalescent method (eSMC, T. Sellinger *et al.* 2019). While assuming mutation in seeds favors the inference of footprints of selection by simply adding additional data, which subsequently increases the likelihood to observe recombination events, it remains unclear if this assumption is justified for all plant species and/or if mutations occur at a different rate depending on the age of seeds. More research on the rate of mutation and stability of DNA during dormant phases is needed in plant (*e.g.*Waterworth *et al.* 2016) and invertebrate species. Nevertheless, even if this mutation rate in seeds is relatively low, our results of a stronger signal of selection under seed banking than in populations without seed banking are still valid. In contrast to the weak seed bank model, it is possible to test for the existence of mutations during the dormant stage under a strong seed bank model as assumed in prokaryotes, because of the much longer dormant phase compared to the coalescent times (Blath, Buzzoni, Koskela, *et al.* 2020).

Finally, as for all sweep models, we show that selective events that are too far back in the past cannot

be detected under seed banks. Nonetheless, we show that when there is a seed bank, older sweeps can be detected with decent accuracy. The presence of a long persistent seed bank could therefore be convenient when studying older adaptation events in plants and invertebrates that have some form of dormancy. This prediction also agrees with the previous observation that the footprint of older demographic events is stored in the seed bank (predicted in Živković and Tellier 2012, observed theoretically in T. Sellinger *et al.* 2019, and empirical example in Daphnia Möst *et al.* 2015). Our results open avenues for further testing the correlation between past demographic events and selective events for species that present this life-history strategy. However, current methods estimating the age of selective sweeps (McSwan, Tournebize *et al.* 2019; Bisschop *et al.* 2021) would need to use an *ad hoc* simulator (*e.g.* such as the one we present here) to generate neutral and selected simulations under seed banking.

4.3 Strengths and limitations of the simulation method

The simulation program developed and used in this work, written in C++, is centered on the use of *tskit*. The toolkit allows for the efficient storage of genealogies through time, by removing lineages that have effectively gone extinct in the current population, thus simplifying the genealogy at regular intervals during the program run-time. Despite all our efforts to streamline the process, forward simulations are inherently limited, because each generation has to be produced sequentially. Thus, while being more flexible and intuitively easier to understand than their coalescent counterparts, forward simulations sacrifice computational efficiency in terms of memory and speed. While simulating hundreds or thousands of individuals is possible (also storing their genealogies in a reasonable amount of time), this limitation becomes exaggerated when adding genomic phenomena such as recombination, and even more so when considering ecological characteristics such as seed banking. The latter scales the process of finding the most recent common ancestor by an inverse factor of b^2. As this leads to an increase in run-time of the order of $O(n^2)$, we kept the population size at 500 (hermaphroditic) diploid individuals. Further, the output format of the simulations are tree sequences, which enables downstream processing and data analysis without the elaborate design of highly specific code. We believe that our code is the first to allow simulations of long stretches of DNA under the seed bank model including recombination and selection. In a previous study, we developed a modified version of the neutral coalescent simulator scrm (Staab *et al.* 2015) which includes a seed bank with recombination (T. Sellinger *et al.* 2019). Our current simulator can be used to study the effect and signatures of selection along the genome under dormancy for non-model species such as plants or invertebrates with reasonably small population sizes.

4.4 Towards more complete scenarios of selection

We here explore a scenario in which a single beneficial allele is introduced. The much longer times to fixation in the presence of seed banks suggest that such a scenario may be unlikely. Indeed, it is probable that several alleles under selection, potentially affecting the same biological processes, are maintained simultaneously in populations for longer periods of time. We can therefore surmise that under seed banking, polygenic selective processes and/or competing selective sweeps, often

associated with complex phenotypes and adaptation to changing environmental conditions in space and time, should be common.

From the point of view of genomic signatures of selection, the overall effectiveness of selection at a locus coupled with increased effective recombination with seed banking generate narrower selective sweeps, hence less genetic hitch-hiking throughout the genome. While we show that these effects can be advantageous to detect selective sweeps, we speculate that this might not be the case for balancing selection. If seed banks do promote balancing selection (Tellier and J. K. M. Brown 2009), the expected genomic footprints would be likely narrowly located around the site under selection, and the excess of nucleotide diversity would not be significantly different from the rest of the genome. The presence of seed banking would therefore obscure the signatures of balancing selection. Concomitantly, the Hill-Robertson-Effect and background selection are expected to be weaker under longer seed banks. These predictions could ultimately define the relationship between linkage disequilibrium, the efficacy of selection and observed nucleotide diversity in species with seed banks compared to species without it (Tellier 2019, Živković and Tellier 2018).

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