



Fisher–Wright model with deterministic seed bank and selection



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ABSTRACT

Seed banks are common characteristics to many plant species, which allow storage of genetic diversity in the soil as dormant seeds for various periods of time. We investigate an above-ground population following a Fisher–Wright model with selection coupled with a deterministic seed bank assuming the length of the seed bank is kept constant and the number of seeds is large. To assess the combined impact of seed banks and selection on genetic diversity, we derive a general diffusion model. The applied techniques outline a path of approximating a stochastic delay differential equation by an appropriately rescaled stochastic differential equation. We compute the equilibrium solution of the site-frequency spectrum and derive the times to fixation of an allele with and without selection. Finally, it is demonstrated that seed banks enhance the effect of selection onto the site-frequency spectrum while slowing down the time until the mutation–selection equilibrium is reached.

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1. Introduction

Dormancy of reproductive structures, that is seeds or eggs, is described as a bet-hedging strategy (Evans and Dennehy, 2005; Cohen, 1966) in plants (Honny et al., 2008; Evans et al., 2007; Tielbörger et al., 2012), invertebrates, e.g., *Daphnia* (Decaestecker et al., 2007), and microorganisms (Lennon and Jones, 2011) to buffer against environmental variability. Bet-hedging is widely defined as an evolutionary stable strategy in which adults release their offspring into several different environments, here specifically with dormancy at different generations in time, to maximize the chance of survival and reproductive success, thus magnifying the evolutionary effect of good years and dampening the effect of bad years (Evans and Dennehy, 2005; Cohen, 1966). Dormancy and quiescence sometimes have surprising and counterintuitive consequences, similar to diffusion in activator–inhibitor models (Hadeler, 2013). In the following study, we focus more specifically on the evolution of dormancy in plant species (Honny et al., 2008; Evans et al., 2007; Tielbörger et al., 2012) but the theoretical models also apply to microorganisms and invertebrate species (Decaestecker et al., 2007; Lennon and Jones, 2011).

Seed banking is a specific life-history characteristic of most plant species, which produce seeds remaining in the soil for short to long periods of time (up to several generations), and it has large but yet underappreciated consequences (Evans and Dennehy, 2005) for the evolution and conservation of many plant species.

First, polymorphism and genetic diversity are increased in a plant population with seed banks compared to the situation without banks. This is mostly due to storage of genetic diversity in the soil (Kaj et al., 2001; Nunney, 2002). Seed banks also damp off the variation in population sizes over time (Nunney, 2002). Under unfavorable conditions at generation t , the small offspring production is compensated at the next generation $t + 1$ by individuals from the bank germinating at a given rate. Under the assumption of large seed banks, the observed population sizes between consecutive generations (t and $t + 1$) may then be uncoupled.

Second, seed banks may counteract habitat fragmentation by buffering against the extinction of small and isolated populations, a phenomenon known as the “temporal rescue effect” (Brown and Kodric-Brown, 1977). Populations which suffer dramatically from events of decrease in population size can be rescued by seeds from the bank. Improving our understanding of the evolutionary conditions for the existence of long-term dormancy and its genetic underpinnings is thus important for the conservation of endangered plant species in habitats under destruction by human activities.

Third, germ banks influence the rate of natural selection in populations. On the one hand, seed banks promote the occurrence

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of balancing selection for example for color morphs in *Linanthus parryae* (Turelli et al., 2001) or in host–parasite coevolution (Tellier and Brown, 2009). On the other hand, the storage effect is expected to decrease the efficiency of positive selection in populations, thus natural selection, positive or negative, would be slowed down by the presence of long-term seed banks. Empirical evidence for this phenomenon has been shown (Hairston and Destasio, 1988), but no quantitative model exists so far. In general terms, understanding how seed banks evolve, affect the speed of adaptive response to environmental changes, and determine the rate of population extinction in many plant species is of importance for conservation genetics under the current period of anthropologically driven climate change.

Two classes of theoretical models have been developed for studying the influence of seed banks on genetic variability. First, Kaj et al. (2001) have proposed a backward in time coalescent seed bank model which includes the probability of a seed to germinate after a number of years in the soil and a maximum amount of time that seeds can spend in the bank. Seed banks have the property to enhance the size of the coalescent tree of a sample of chromosomes from the above ground population by a quadratic factor of the average time that seeds spend in the bank. This leads to a rescaling of the Kingman coalescent (Kingman, 1982) because two lineages can only coalesce in the above-ground population in a given ancestral plant. The consequence of longer seed banks with smaller values of the germination rate is thus to increase the effective size of populations and genetic diversity (Kaj et al., 2001) and to reduce the differentiation among populations connected by migration (Vitalis et al., 2004; Blath et al., 2013). This rescaling effect on the coalescence of lineages in a population has also important consequences for the statistical inference of past demographic events (Živković and Tellier, 2012). In practice this means that the spatial structure of populations and seed bank effects on demography and selection are difficult to disentangle (Böndel et al., 2015). Nevertheless, Tellier et al. (2011a) could use this rescaled seed bank coalescent model (Kaj et al., 2001) and Approximate Bayesian Computation to infer the germination rate in two wild tomato species *Solanum chilense* and *S. peruvianum* from polymorphism data (Tellier et al., 2011b).

A second class of models assumes a strong seed bank effect, whereby the time seeds can spend in the bank is very long, that is longer than the population coalescent time. This latest model generates a seed bank coalescent (Blath et al., 2016), which may not come down from infinity and for which the expected site-frequency spectrum (SFS) may differ significantly from that of the Kingman coalescent (Blath et al., 2015). In effect, the model of Kaj et al. (2001) represents a special case, also called a weak seed bank, where the time for lineages to coalesce is finite because the maximum time that seeds can spend in the bank is bounded.

In the following we mainly have the weak seed bank model in mind where the time in the seed bank is bounded to a small finite number assumed to be realistic for most plant species (Honnay et al., 2008; Evans et al., 2007; Tielbörger et al., 2012; Tellier et al., 2011b). Even if we allow for unbounded times a seed may be stored within the soil, we assume that the germination probability decreases rapidly with age such that e.g. the expected time a seed rests in the soil is finite. We develop a forward in time diffusion for seed banks following a Fisher–Wright model with random genetic drift and selection acting on one of two genotypes. The time rescaling induced by the seed bank is shown to be equivalent for the Fisher–Wright and the Moran model. We provide the first theoretical estimates of the effect of seed bank on natural selection by deriving the expected SFS of alleles observed in a sample of chromosomes and the time to fixation of an allele.

The main difficulty in the present paper is the non-Markovian character of seedbank models (with the exception of a geometric

survival distribution for seeds, in which case the model can be reduced to a Markovian model, see below). The way to deal with this non-Markovian character is based on a separation of time scales. The genetic composition of the population only changes on a slow, so-called evolutionary time scale (thousands of generations), while being fairly stable on a fast, ecological time scale (tens of generations). We assume seeds to have a life span corresponding to this ecological time scale, and thus the seedbank tends to a quasi-stationary state. The non-Markovian character of the model is visible at the ecological time scale, while it vanishes on the evolutionary time-scale due to the quasi-steady-state assumption. In other words we ensure the separation of time scales by assuming that most seeds die after a few generations. We demonstrate thereafter that seed banks affect selection and genetic drift differently.

2. Model description

We consider a finite plant-population of size N . The plants appear in two genotypes A and a . We assume non-overlapping generations. Let X_n denote the number of type- A plants in generation n (that is, the number of living type- a plants in this generation is $N - X_n$). Plants produce seeds. The number of seeds is assumed to be large, such that noise in the seed bank does not play a role (therefore we call the seed bank “deterministic”). As a consequence, the state of the seedbank is deterministic conditioned on the history of the above-ground population. The amount of seeds produced by type- A plants in generation n is $\beta_A X_n$, that of type- a plants $\beta_a(N - X_n)$. The seeds are stored e.g. in the soil; some germinate in the next generation, some only in later generations, and some never.

To obtain the next generation of living plants X_n , we need to know which seeds are likely to germinate. Let $b_A(i)$ be the fraction of type- A seeds of age i able to germinate, and $b_a(i)$ that of type- a seeds. Hence, the total amount of type- A seeds that are able to germinate is given by

$$\sum_{i=1}^{\infty} b_A(i) \beta_A X_{n-i},$$

and accordingly, the total amount of all seeds that may germinate in the next generation is

$$\sum_{i=1}^{\infty} b_A(i) \beta_A X_{n-i} + \sum_{i=1}^{\infty} b_a(i) \beta_a (N - X_{n-i}).$$

The probability that a plant in generation n is of phenotype A is given by the fraction of type- A seeds that may germinate among all germinable seeds. The frequency process of the di-allelic Fisher–Wright model with deterministic seed bank reads

$$X_n \sim \text{Bin}(N, q_n(X_{\bullet})), \quad (1)$$

$$q_n(X_{\bullet}) = \frac{\sum_{i=1}^{\infty} b_A(i) \beta_A X_{n-i}}{\sum_{i=1}^{\infty} b_A(i) \beta_A X_{n-i} + \sum_{i=1}^{\infty} b_a(i) \beta_a (N - X_{n-i})}.$$

Next we introduce (weak) selection. The fertility of type- a plants is given by

$$\beta_a = (1 - s_1) \beta_A,$$

such that $s_1 = 0$ corresponds to the neutral case. Furthermore, the fraction of surviving seeds is affected. We relate $b_a(i)$ to $b_A(i)$ by

$$b_a(i) = (1 - s_2) b_A(i).$$

Of course, s_2 has to be small enough to ensure that $b_a(i) \in [0, 1]$. There are other ways to incorporate a fitness difference in the surviving probabilities of seeds, but we feel that this is the most

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