Principles of seed banks: complexity emerging from dormancy

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ABSTRACT

Across the tree of life, populations have evolved the capacity to contend with suboptimal conditions by engaging in dormancy, whereby individuals enter a reversible state of reduced metabolic activity. The resulting seed banks are complex, storing information and imparting memory that gives rise to multi-scale structures spanning collections of cells to entire ecosystems. We outline the fundamental attributes and emergent phenomena associated with dormancy and seed banks with the goal of developing a unifying framework that can address problems in the life sciences, ranging from global change to cancer biology.

INTRODUCTION

Seed banks are reservoirs of metabolically inactive individuals. The genetic, phenotypic, and functional diversity contained in seed banks influences the behavior of biological systems in important and wide-ranging ways. Perhaps the most conspicuous and well-studied examples are the seed banks generated by plants (Fig. 1B). Thousands of years ago, major transformations in culture and society arose when humans began to harness the diversity and longevity of seeds[1]. Much later, Darwin's curiosity was piqued by seed banks when more than 500 types of plants germinated from only three tablespoons of mud collected from the margins of an English pond. This led him to ponder the ways in which animals might promote the movement of dormant propagules, and how this in turn might affect the geographic distribution of species[2]. Since then, high-tech seed-banking vaults have been constructed around the world to help preserve biodiversity and food security, ensuring the long-term persistence of rare plant cultivars that may be at risk of extinction, owing to rising temperatures, disease outbreaks, and other natural disasters[3].

Yet, seed banks are not restricted to the world of plants. They are prevalent among invertebrates, mammals, and microorganisms, too. The principles of seed banks can even be used to understand stem cell dynamics[4], tumor persistence[5], and the distribution of neural activity in brains[6]. Despite being found across seemingly disparate systems and scales, seed banks are governed by a shared set of dormancy-related processes that determine how individuals transition between metabolic states[7] (Fig. 2). Dormancy has independently evolved numerous times throughout Earth's history and has even been considered in origins-of-life models[8,9]. In today's inventory of biodiversity, dormancy is integrated into diverse modes of reproduction across domains of life (Fig. 1). This leads to variations on a common theme in biology that involves two fundamental criteria. First, by entering dormancy, individuals avoid conditions that are suboptimal for survival and reproduction. Second, cohorts of long-lived individuals resuscitate from the seed bank at different times. This ability to delay reproduction, despite developmental preparedness, is a form of bet hedging that spreads risk out over time in order to maximize fitness in variable environments[10].

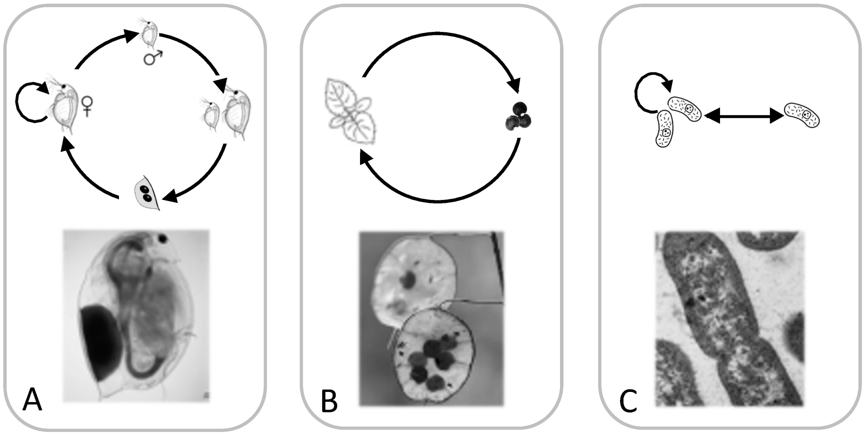


Fig. 1. Seed banks develop among diverse taxa with different life-histories and reproductive modes. **A**. *Daphnia* are planktonic crustaceans with parthenogenic reproduction, where females generate offspring without fertilization. Often, when stressed, males are produced that fertilize females, leading to the production of ephippia, which are dormant resting stages that can persist for extended periods of time in aquatic sediments. **B**. Annual plants produce seeds at the end of a growing season, which are deposited into the soil. As a well-recognized example of bet hedging, some fraction of these seeds delay germination despite optimal conditions. **C**. Among many groups of microorganisms, individuals can enter and exit from a dormant state independently of reproduction and without the need of generating physical resting structures.

Because seed banks are an important biological buffer, considerable effort has been devoted towards characterizing the mechanisms that control dormancy. Sometimes transitions between metabolic states occur stochastically, but in many instances they involve finely tuned regulation of signals, hormones, and even neural circuits[11] (Box 1). Such detail is critical for an in-depth understanding of how dormancy operates within a particular organism or population. A complementary perspective can be gained by viewing seed banks through the lens of systems theory and mathematical modeling, which emphasize common features and nonlinear interactions in large systems that lead to the emergence of complex behaviors. In addition to providing generalizable and predictive insight, this approach can foster cross-disciplinary efforts by alleviating confusion stemming from the lexicon that is commonly associated with dormancy and seed banking[12].

More than half a century ago, theoreticians took the initial steps to formalize a seed bank theory. Inspired by the natural history of plants, macroscale phenomena were modeled with the help of ordinary differential equations[13]. While laying a foundation for researchers to come, these efforts were not designed to capture all of the multiscale features and complexities of seed banks found in diverse systems. Since then, novel mathematical and computational approaches have been developed, which take into account individuality, stochastic processes, history, and scale, while allowing for emergent features and scaling limits[14-16]. These quantitative perspectives present an opportunity for unification and universality, while creating a foundation that will facilitate applications in a range of practical topics spanning the life sciences.

FUNDAMENTALS OF SEED BANK THEORY

In this section, we identify the core attributes and processes that are essential for establishing a general framework for seed banks and their dynamics. We emphasize that seed banks have multiscale properties. For example, metabolic transitions occur on times scales spanning seconds to millennia, and operate across levels of biological organization, ranging from genes within individuals to energy flow within food webs. While some seed bank properties are tractable to empirical measurement, others can be more challenging to describe, which creates opportunities for investigations that leverage theory and modeling.

Seed bank attributes: The primary object of a seed bank is the pool of dormant individuals. A critical attribute of this pool is its size, which is simply the sum of all viable but inactive individuals or biomass (Fig. 2). In some cases, seed banks are large, making up nearly all of the individuals in a system. For example, 90% or more of all the bacteria and fungi living in soil can be dormant[7]. In marine sediments alone, there are an estimated 10^{29} endospores, suggesting that microbial seed banks are significant at the global scale[17]. In many plant systems, dormant individuals attain densities that exceed the abundance of actively growing individuals by orders of magnitude[18].

In addition to their absolute and relative sizes, seed banks have other important attributes. Dormant individuals belong to different classes, which might represent genotypes in a population or species in a community (Fig. 2). There are many ways in which the diversity of these classes can be quantified[19]. For example, the α-diversity of the seed bank can be represented as the number of different classes (i.e., richness) or the equitability in abundance of the different classes (i.e., evenness), while the β-diversity of the seed bank emphasizes the compositional dissimilarity between classes in the active and inactive pools. For example, in an alpine grassland there was only 20% overlap in the species found in the aboveground plant community compared to the belowground seed bank[20].

Dormant individuals possess other important characteristics that affect seed bank dynamics. For example, those individuals may have unique evolutionary histories, demographic properties, or functional traits that affect growth rates, sensitivity to grazing, drug resistance, light tolerance, etc. When combined with pool sizes and transition probabilities, these characteristics can influence seed bank turnover and other emergent phenomena.

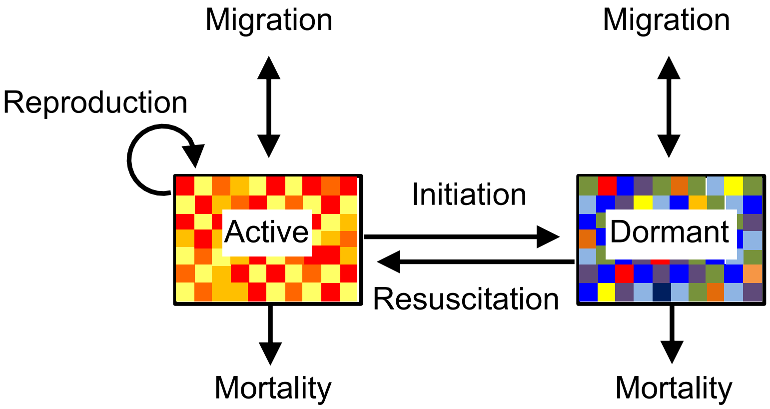


Fig. 2. Primary attributes (boxes) and transitions (arrows) in a generalized seed bank model. In this example, the sizes of the active and dormant pools are made up of an equal number of individuals (N = 70). In the active pool, individuals can be gained through reproduction and lost through mortality. In the dormant pool, there is no reproduction and mortality of dormant individuals is assumed to be much lower than for the active individuals. In addition, pool sizes are influenced by stochastic or deterministic transitions between metabolic states (i.e., initiation and resuscitation), which determine the size and rate at which pools undergo turnover. In terms of α-diversity, the richness of classes (colored squares) in the dormant pool (S_d = 9) is greater than the richness in the active pool (S_a = 4). In terms of β-diversity, the active and inactive pools are 82 % dissimilar based on the abundance-weighted Bray-Curtis metric: $\sum_{k=1}^{S}[x_{ak} - x_{dk}]/\sum_{k=1}^{S}(x_{ak} + x_{dk})$, where x_{ak} and x_{dk} correspond to the abundance of class k in the active (a) and dormant (d) pools, respectively, and S is the number of classes contained in the pools. Seed bank attributes can also be influenced by migration, especially when dormancy facilitates the dispersal and colonization of individuals in a regional landscape.

<u>Seed bank transitions:</u> Ultimately, seed bank attributes are governed by the transitions of individuals between metabolic states. Therefore, it is crucial to understand the mechanisms that control how individuals move into and out of dormancy. In some populations, a fraction of the

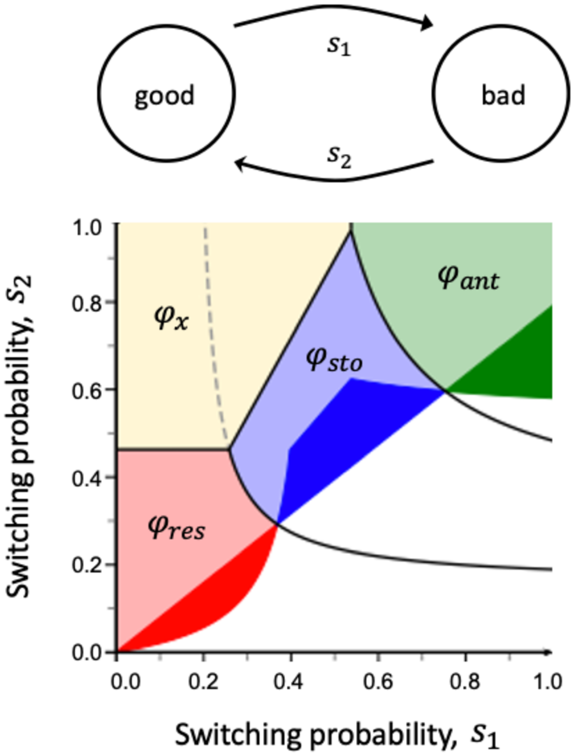
individuals will randomly transition between metabolic states. This type of phenotypic plasticity has been well documented among various types of bacteria and tends to be favored in unpredictable environments[21] (Box 1). For example, the scout hypothesis considers stochastic resuscitation from dormancy in a large population where individuals randomly wake up and sample their environment[22]. If conditions are bad, then the individual may die or go back to sleep. If conditions are good, then the individual can communicate and coordinate resuscitation with other individuals in the population.

While nature is often uncertain, there are features of an organism's environment that change relatively slowly or in a fairly predictable manner (e.g., photoperiod, temperature, rainfall). As a result, many organisms have evolved responsive mechanisms that regulate dormancy in a more deterministic fashion. While this requires an investment in cellular machinery, such organisms are better equipped to make decisions based on internal and external cues that will improve fitness outcomes, and can even give rise to anticipatory behaviors (Box 1).

In many instances, it is justifiable to model seed banks by using a simplified two-compartment model with one-step stochastic or deterministic transitions (Fig. 2). However, it is important to acknowledge that dormancy can be more complicated. For example, in some plant systems seeds pass through a series of metabolic states 'en route' to germination, which means that a given individual from a population can be in a shallow or deep state of dormancy[18]. Similarly, for some bacteria, there are critical developmental stages of spore formation where an individual becomes irreversibly committed to the decision to enter dormancy, irrespective of environmental conditions[23]. Still, in other systems, individuals may fall into dormancy without generating a distinct resting stage [7]. These organisms may be positioned along a continuum of metabolic activity that reflects quantitative variation in physiological characteristics such as resource quota[24], ribosome number[25], or the degree of DNA methylation[26].

Box 1. Optimal dormancy strategies in fluctuating environments

Over the past two decades, various mathematical formulations have been developed to investigate the optimal strategy for living in a fluctuating environment [21,27-29]. In the context of seed banks, organisms employ spontaneous, responsive, or anticipatory strategies to transition between active and dormant states. To illustrate, consider an idealized population reproducing in discrete generations according to a two-type branching process. One of these types corresponds to the active state of an individual and the other type corresponds to the dormant state of an individual. Further, assume that the process evolves in a randomly fluctuating environment with a good condition that is favorable for reproduction and a bad condition that is unfavorable for reproduction. The per generation switching probabilities between environments are denoted by s_1 (good → bad) and s_2 (bad → good). Different dormancy strategies can then be easily incorporated into the model. First, we can consider stochastic transitions, where individuals move between metabolic states irrespective of the environmental condition (good vs. bad). Second, we can consider responsive transitions where individuals enter a dormant state when conditions are bad and resuscitate into the active state when conditions are good. Last, we can consider anticipatory (or prescient) transitions where individuals enter a dormant state during good conditions in preparation of impending bad conditions. The optimality of these switching strategies can be explicitly evaluated in relation to environmental conditions and underlying parameters[29]. As shown in the figure below, responsive transitioning has positive fitness and is optimal among all strategies when the environment slowly changes (red-colored regions). Stochastic transitioning is optimal and has positive fitness when there are moderate fluctuations in environmental conditions (blue-colored regions). Anticipatory transitioning is most adaptive in environments where there are rapid changes between good and bad conditions that occur on the time scale of a generation (green-colored regions). Dormancy is not favorable when environmental conditions are good most of the time (yellow-colored region).



Upper panel: Switching dynamics in a randomly fluctuating environment. When the values of s_1 and s_2 are small, the environment is relatively stable. When the values of s_1 and s_2 are large, the environment rapidly fluctuates between good vs. bad environmental conditions, changing almost every generation. **Lower panel:** optimality regions where fitness corresponds to different transition strategies[29]. Specifically, φ_{sto}, φ_{res}, and φ_{ant} depict the fitness of the stochastic, responsive, and anticipatory (or prescient) strategies, respectively, while φ_x reflects the fitness of a population that does not engage in dormancy. Within a color family, the dark-colored regions indicate that the optimal strategy is the only one with positive fitness. In the light-colored regions, there is at least one other strategy with positive, but strictly lower than optimal, fitness. In the white regions where environmental conditions are stably bad (e.g., small s_1 and large s_2), all strategies, including the optimal one, have negative fitness. Precise model definitions and parameters can be found elsewhere[29].

Physical features of seed banks: The physical manifestation of seed banks has important implications for understanding dormancy dynamics and emergent phenomena. Compared to metabolically active adults, dormant individuals take on different sizes, densities, and motilities. These morphological differences can facilitate transport propagules to new environments. This is especially true when dormant individuals act as agents of dispersal for future generations, as in plants and zooplankton (Fig. 1A, B). As a result, dormant individuals can accumulate in locations that are geographically separated from metabolically active individuals.

In some systems, however, active and dormant individuals have similar morphological features and occupy the same habitat. For example, in the surface waters of lakes and oceans, phytoplankton are at the mercy of currents, which can lead to the homogenization of individuals within water masses, irrespective of their metabolic status[30]. In such environments, if active and dormant individuals cannot be distinguished, cryptic patterns may arise that are not predicted by theory[15,31].

Finally, there are examples where seed banks contribute to the development of biophysical structures. For example, dormant individuals are integrated into the organization of multicellular biofilms and tumors. The mixture of active and dormant cells create structures that alter fluid dynamics, oxygen availability, and the generation of heat, which in turn can influence toxin production, communication networks, and even the lateral transfer of DNA[32,33]. In this way, variation in the metabolic activity of neighboring individuals and spatial arrangements of seed banks can generate feedbacks that influence system behavior.

SEED BANKS AND EMERGENT PHENOMENA

Once established, seed banks can lead to the emergence of interesting patterns and dynamics that may be at odds with classical theory. This is because seed banks contain structure, which imparts memory on the system. Through the process of delayed resuscitation, individuals from the past can emerge in the future and influence system behavior, including equilibria and stability, but also multiscale organization and feedback. In this section, we outline some of the fundamental processes that are modified by seed banks and how dormancy influences major evolutionary and ecological patterns. We highlight some of the mathematical theory underlying emergent seed bank phenomenon in boxes that accompany the main text.

Evolution with a seed bank: Seed banks modify the fundamental forces of evolution acting upon a population. The ultimate source of genetic variation is mutation, which changes DNA composition owing to copying errors resulting in point mutations, frameshifts, and duplication events. Most mutations entering a population are associated with genome replication, which occurs in metabolically active individuals. While dormant individuals can still accumulate damage from external or internal stressors (e.g., starvation, oxygen radicals, UV), the number of mutations entering a population per unit time should go down for organisms in a metabolically inactive state.

Once generated, the fate of a mutation is affected by the seed bank. Under neutral conditions, genetic drift can lead to the fixation of alleles through random sampling, which is especially important in small populations. Seed banks tend to increase the effective population size, which results in longer times for alleles to reach fixation[34]. Such effects can be seen in the site frequency spectrum, which is a relationship describing how segregating alleles are distributed among loci in a population. The shape of the site frequency spectrum is often interpreted with respect to demographic processes, such as bottlenecking, population expansion, and immigration, which can influence the frequency of rare vs. common mutations in a population. However, the site frequency spectrum (SFS) is also affected by the seed bank[35]. Based on coalescent approaches (Box 2), the SFS is found to be much more uneven in populations with a seed bank owing to the retention of rare mutations[35]. However, the degree to which the SFS is skewed depends on the average amount of time that individuals spend in a dormant state (see Box 2). Such findings not only have important implications for quantifying genetic diversity, but also for properly interpreting the processes that give rise to these estimates.

Seed banks also alter the strength of natural selection, which has important consequences for other evolutionary patterns. Individuals with mildly deleterious alleles may persist because they are not seen by natural selection while residing in the seed bank. When those individuals resuscitate, perhaps under different environmental conditions, they contribute to the standing genetic diversity of a population[16,34]. For example, the maintenance of a color polymorphism in an annual plant population can be explained by a diffusion approximation model that accounts for fluctuating selection with a seed bank[36]. When considering population genetic processes at larger spatial scales, seed banks may provide an anchoring effect that buffers populations against gene flow in the landscape[37].

Ultimately, seed banks can influence macroscale evolutionary phenomena. In addition to reducing the probability of extinction, the ability of individuals to persist in a non-replicating state for prolonged periods of time may alter rates of lineage diversification. For example, bacteria that are capable of forming endospores diverge much more slowly than close lineages that have lost this trait[38]. In contrast, plants that engage in physiological dormancy diversify much more rapidly than taxa that do not rely on dormancy[39]. Seed banks can also affect phylogenetic reconstruction and evolutionary inference in other important ways. For example, coalescent models predict that dormancy can distort genealogical patterns and obstruct our ability to accurately predict the time to the most recent common ancestor, which depends on the size and turnover of the seed bank (Box 2).

Box 2. Coalescent theory for seed banks

Coalescents are stochastic processes that are widely used to model genealogies on evolutionary time scales. They are indispensable for understanding the interplay of classical genetic drift with other evolutionary forces, including mutation, selection, recombination[40]. Below we describe some novel variations on the coalescent theory that allow for evolutionary inference with regard to seed bank processes:

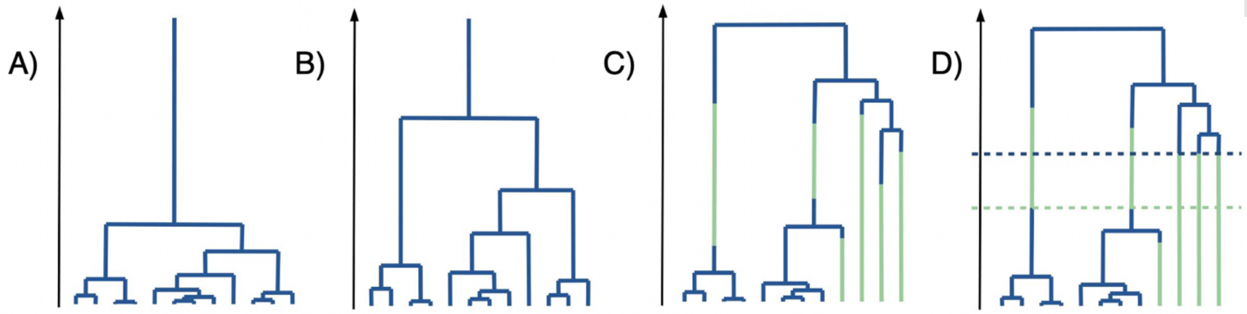
1. The Kingman coalescent: Introduced nearly 40 years ago, “the coalescent” has played an important role in advancing population genetic theory and application[41]. For describing the genealogy of a population under genetic drift, it is the standard null-model for neutral evolution, since the coalescent arises as the universal scaling limit of the ancestral process in the Wright-Fisher and Moran models, among others. Looking back in time, the coalescent approach makes pairwise mergers with ancestors at an exponential rate of 1 (panel A) on the evolutionary time scale. Based on assumptions of a haploid Wright-Fisher model with a finite effective population size N, it generates a random genealogical tree, where time t in the coalescent corresponds to Nt generations in the finite population. This tree can be used to infer the expected time until the most

recent common ancestor, which with a sample of size n, is always bounded by 2 corresponding to $2N$ generations in the underlying Wright-Fisher model. If mutations happen with probability μ per generation, then they will be visible on the coalescent with rate $\theta = 2N\mu$, providing the expected number of segregating sites in two lineages from the sample n. This allows for a simple calculation of the mutation rate from DNA samples using metrics like the Watterson estimator. Since its inception, the coalescent has been used and modified by evolutionary biologists and mathematicians to explore a range of topics and processes. As we will see later, features of the coalescent (e.g., θ) also play an important role in ecological models used to predict patterns of biodiversity, including the species abundance distribution (Box 4).

2. The stretched coalescent: When individuals enter dormancy for a relatively short period of time, this gives rise to what is called a weak seed bank. Because it increases the effective population size, the resulting genealogy becomes "stretched"[42,43], such that pairwise mergers of ancestors occur less frequently. Specifically, if an individual spends on average β generations in the seed bank, then the time to coalescence for two lineages is increased by a factor of β^2. The upper bound for the expected time to the most recent common ancestor therefore increases to $2\beta^2$, which again translates to $2\beta^2 N$ generations. Likewise, estimates of the mutation rate θ will be affected by a factor of β^2. However, other population genetic quantities, like the normalized site frequency spectrum and the topology of the genealogy, remain unchanged (panel B).

3. The seed bank coalescent: When the time spent in a dormant state is longer, on the order of the effective population size, a strong seed bank emerges. This necessitates a distinction between active and dormant ancestral lineages in the genealogy. Only lineages of active individuals may

coalesce, while mergers between dormant lineages are prohibited. As a result, the overall time to the most recent common ancestor increases further. Unlike in the stretched coalescent, where time to the most recent common ancestor was extended by a constant, the time to most recent common ancestor in the strong seed bank regime is unbounded in the sample size. The mechanisms underlying metabolic transitions can further modify coalescent statistics in non-trivial ways[14,44]. For example, when lineages transition between states independently of other events, the seed bank coalescent emerges (panel C). On the other hand, responsive or anticipatory transitions (see Box 1) may cause lineages to enter and exit dormant states simultaneously, leading to a more generalized on/off coalescent pattern (panel D).



Genealogies with different seed bank attributes. **Panel A:** typical genealogy based on the Kingman coalescent without a seed bank. **Panel B:** genealogy from the stretched coalescent which arises when there is a weak seed bank effect. This leads to an increased amount of time for pairs of lineages to merge. **Panel C:** genealogy under a strong seed bank where lineages stochastically transition between active and dormant states, which leads to the seed bank coalescent. **Panel D:** genealogy under a strong seed bank where lineages undergo simultaneous transitioning, which captures behaviors where individuals respond to environmental cues, resulting in a more general on/off coalescent. Blue lines depict active lineages and green lines represent dormant lineages. Horizontal dotted lines in panel D reflect times of simultaneous transitioning.

<u>Population dynamics with a seed bank:</u> Seed banks have important implications for the dynamics and long-term stability of populations made up of individuals belonging to the same species. The combined use of models and empirical data have demonstrated that population dynamics are better

predicted when dormancy is included, even if those stages and transitions are sometimes difficult to quantify in nature[45]. Recent studies have begun to leverage the power of models, like the coalescent (Box 2), along with whole-genome data to infer the importance of dormancy on the demographic history of populations[46]. Such approaches have led to the prevailing view that seed-bank effects should be most pronounced in fluctuating environments, where the fitness of a population is affected by the mean and variance of births and deaths. Dormancy reduces the probability of individuals succumbing to unfavorable conditions, while distributing reproductive output over longer periods of time. As a consequence, important demographic features of a population, including its size and age-structure, are influenced by seed bank dynamics[45,47].

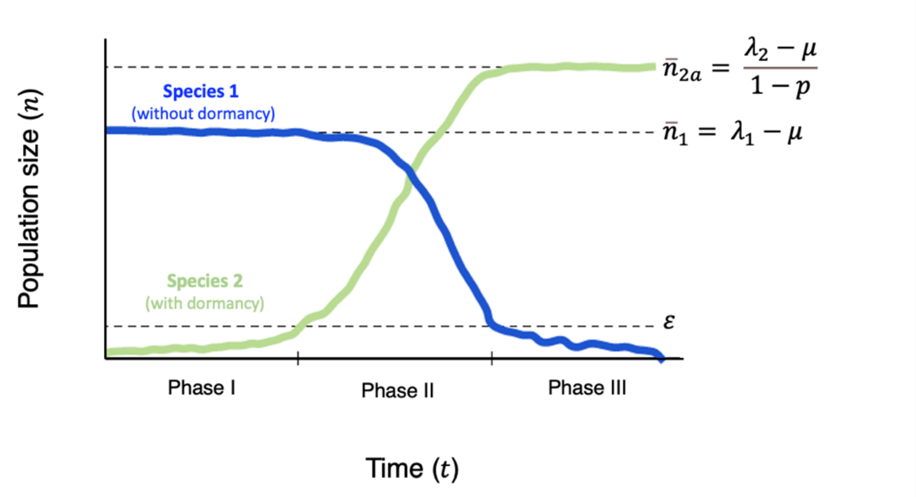
The population-level consequences of seed banks are particularly sensitive to the amount of time that an individual is capable of spending in a dormant state. While dormancy can help an individual conserve energy, there are still other basal metabolic demands that must be met, including costs associated with cellular homeostasis and the repair of macromolecular damage, which can contribute to diminished fitness associated with aging[48]. Other factors affecting seed-bank residence time include the compounded risk of consumption by predators, infection by pathogens, and physical burial[18]. Because of these constraints, some seed banks turnover more rapidly than others. For example, less than 10% of seeds belonging to an annual plant species in the Sonoran Desert persisted beyond five years[47]. However, radiometric dating has revealed that diapausing zooplankton can hatch from lake sediments after more than 100 years[49]. Astonishingly, viable microorganisms can be recovered from ancient materials that are 100 million years old[50].

The demographic effects of seed banks are also influenced by resuscitation dynamics (Fig. 2). The awakening of certain genotypes from the past into contemporary environments can have important eco-evolutionary consequences for a population. Using novel genome barcoding approaches in combination with Bayesian methods, researchers have characterized the variance of reproductive output associated with the resuscitation of dormant bacteria. Such approaches revealed that stochastic resuscitation from a heavy-tailed distribution of variants resulted in a few individuals effectively winning a demographic sweepstake[51]. Not only can these long-range jumps diminish genetic diversity, but they can also alter the underlying coalescent structure of a population [52,53]. Although genotypes from the past are not always well adapted to conditions of the future, resuscitation tends to benefit populations in many scenarios. In addition to minimizing competition among kin at similar developmental stages, recruitment of dormant propagules from the seed bank can buffer populations from various environmental stressors[49] and reflect coevolutionary Red-Queen dynamics between hosts and their parasites[54].

Box 3. Emergence of dormancy under competitive pressure

Dormancy is an evolutionarily stable strategy in fluctuating environments (Box 1). Under such conditions, seed banks provide a buffer, which can offset the opportunity and investment costs associated with dormancy. Indeed, dormancy is often investigated in the context of fluctuations that are caused by external factors like rainfall patterns, seasonal photoperiods, and resource supply schedules. However, recent mathematical models predict that dormancy can also emerge when fluctuations are internally generated[55,56]. Specifically, if intraspecific and interspecific competition is strong enough, individuals can escape mortality associated with overcrowding by transitioning into a dormant state, conferring a benefit that offsets the reproductive investment in dormancy.

As an example, let us consider a stochastic individual-based model with two species. Species 1 is at equilibrium and reproduces at rate $\lambda_1 > 0$, which means that each individual divides after an exponential time independently of others. Individuals of the newly arriving Species 2 have a reduced rate of reproduction ($\lambda_2 < \lambda_1$) that reflects the cost of them being able to engage in dormancy. Further, we assume that active individuals belonging to both species have a death rate μ that is less than λ_2. Then, competition is proportional to the sum of all active individuals (n_a) belonging to Species 1 (n_1) and Species 2 (n_{2a}). This results in individuals from Species 1 being removed from the system due to competition at rate n_a. Because they can escape with probability p into the dormant state, individuals from Species 2 are less sensitive to competition. Specifically, those individuals are removed from the community due to competition at rate $(1-p)n_a$ and transition into competition-induced dormancy at rate pn_a. Last, dormant individuals from Species 2 can resuscitate at rate 1. The invasion and subsequent fixation of dormancy-capable Species 2 is possible if and only if $\lambda_1 - \mu < (\lambda_2 - \mu)/(1-p)$[55]. While $\lambda_1 - \mu$ is always larger than $\lambda_2 - \mu$, due to the reproductive trade-off, this is balanced by the pre-factor $1/(1-p)$, which is always larger than one. In fact, for any choice of $\lambda_1$and λ_2, it is possible to find an escape probability p such that the dormant type has a chance to invade and lead to the competitive exclusion of Species 1. Thus, dormancy reduces the effects of competition, which compensates for lower reproductive rates, which together has important implications for biodiversity and coexistence theory.



Invasion dynamics and fixation of a dormancy trait in a non-fluctuating environment despite reproductive trade off. In Phase I, individuals belonging to Species 1 are close to their equilibrium abundance ($\bar{n}_1 = \lambda_1 - \mu$), when an individual from Species 2 invades, which is capable of engaging in dormancy. Since its reproductive rate is larger than its overall death rate (including natural mortality and competition-induced mortality), the abundance of Species 2 increases, reaching a small but notable size where it begins to contribute to overcrowding, and from where any initial stochastic fluctuations are minimal (ε). In Phase II, competition becomes more intense due to overcrowding, which results in the decreased abundance of Species 1. However, since individuals belonging to Species 2 can temporarily escape into dormancy, they are less sensitive to competition. This allows Species 2 to continue growing towards its equilibrium population size $\bar{n}_{2a} = (\lambda_2 - \mu)/(1-p)$, which is larger than $\bar{n}_1$ since they can tolerate higher levels of competition. In Phase III, Species 2 is close to its equilibrium. Meanwhile, since $\bar{n}_{2a} > \bar{n}_1$, Species 1 is driven to critically low abundances (ε) where stochasticity again becomes visible, leading to ultimate extinction. More detail can be found elsewhere [55].

Species interactions with a seed bank: Seed banks modify species interactions with consequences for community stability and the maintenance of biodiversity. Many of the leading theories developed to understand ecological dynamics focus on the sign and strength of species interactions. For example, competition can often result in one species driving another species locally extinct owing to its ability to draw down resources or grow more rapidly under certain conditions. However, this outcome can be modified through a mechanism known as the storage effect[57]. Specifically, competitors can coexist if three criteria are met: there are species-specific responses to environmental conditions, there is covariance between environmental conditions and competition, and there is buffered of population growth under unfavorable conditions. The last criterion can be satisfied by the long-lived individuals that make up a seed bank. Evidence from diverse ecosystems has documented the importance of the storage effect as a stabilizing mechanism allowing for species coexistence[58-60].

Dormancy can also buffer species interactions when it provides a refuge from predators[61,62], while some theory suggests that antagonistic interactions between hosts and parasites can lead to the emergence of seed banks[63]. Experimental evidence from microbial systems tends to support these notions. For example, just the physical contact between a virus and its archaeal host can initiate a transition into dormancy[64]. Meanwhile, some species of algae fall into dormancy when they detect the chemical cues that are released by predators in their environment[65], a mechanism that could promote anticipatory transitioning behavior (Box 1).

Less is known about how seed banks modify mutualisms, which arise when there is a beneficial exchange of resources or services among species. Often thought to be easily disrupted, mutualistic dynamics depend on the degree to which individuals cooperate vs. cheat. Theory suggests that dormancy may stabilize mutualistic interactions, but this effect is sensitive to the time scale that organisms transition between metabolic states[66]. When taken together, a more comprehensive view of species interactions suggests that there may be overlooked mechanisms that offset the costs of delayed reproduction, which might help explain the prevalence of dormancy and seed banks in nature.

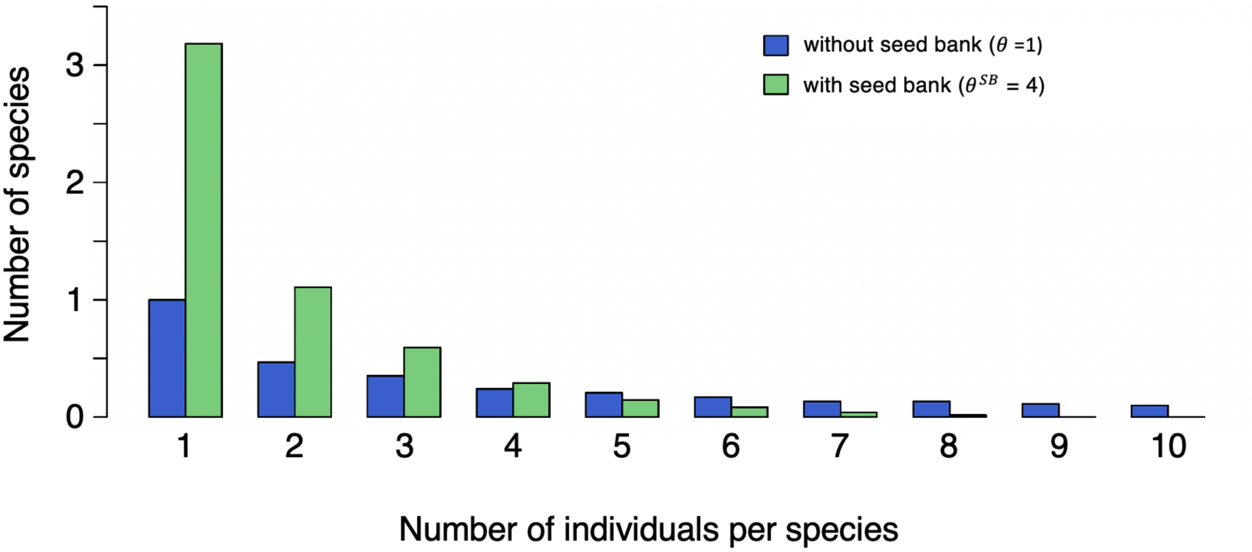
Box 4. Seed banks and biodiversity

One of the most fundamental and ubiquitous aspects of biodiversity is that there are very few common species and many rare species. This pattern, which is universally found among plants, invertebrates, mammals, and microorganisms, is described by the species abundance distribution (SAD). The SAD has attracted attention from ecologists for decades, and has led to debates about the most appropriate statistical model to explain the classical hollow-shaped curve[67]. During the same period, researchers have been tempted to attribute variation in the SAD to different underlying mechanisms, some of which invoke the partitioning of niches or the fact that disturbed communities tend to have highly uneven abundance distributions[67]. It has also been shown that a typical SAD can emerge under neutral expectations, when there are no differences among species[68]. Understanding what gives rise to this relationship is important because many other phenomena can be derived from the SAD, including the scaling law that describes how diversity changes with increasing habitat size (i.e., the species area relationship).

Because seed banks affect the population sizes and persistence of species over time, we explored how dormancy might influence the SAD using neutral theory[68]. In the absence of dispersal limitation, the law of a sample is given by Ewen's Sampling Formula (ESF)[69]. Besides the sample size (n), the single parameter in this formula is the speciation rate θ, which in an ecological context is known as the universal biodiversity constant. From the ESF, species richness of the sample (S_n) is sufficient for estimating θ, and its expected value is given by $E[S] = \sum_{k=1}^{n}[\theta/(\theta + k - 1)] \sim \theta \log n$.

A particularly valuable feature of the ESF is that it can be derived from coalescent theory, and that samples can easily be generated using the Kingman coalescent[70]. Note that, in this interpretation, the universal biodiversity constant (θ) agrees with the coalescent mutation rate (θ) as defined in Box 2. It is thus natural to consider the effect of seed banks on the SAD and the universal biodiversity constant through their underlying coalescent structure. Therefore, we employed the weak seed bank model[42], where the underlying coalescent is stretched by a factor β^2 when the expected number of generations that individuals spend in the seed bank is given by β. Thus, if a hypothetical species without a seed bank could be described by a biodiversity constant θ, then a similar species with a seed bank could be described in terms of the modified constant given by $\theta^{SB} = \theta\beta^2$. This translates into a new expression for the expected species richness in the presence of a weak seed bank given by $E[S^{SB}] \sim \theta^{SB} \log n$.

From this, we find that seed banks significantly alter the shape of the SAD, increasing both species richness (S) and the number of rare species in a way that can be explicitly computed from the ESF and the above formulas. Even when individuals only stay dormant on average for two generations, the expected richness with a seed bank ($E[S^{SB}] = \theta^{SB}$) increases by a factor of four. Such coalescent-based reasoning could help explain why separate models are needed to fit the SAD for different groups of organisms. For example, the log-series distribution implemented through the maximum entropy theory of ecology (METE) does an excellent job of describing the SAD for plants and animals[71], while the lognormal distribution is better for describing diversity among microbial taxa[72]. This discrepancy has been attributed to the fact that microbial samples typically contain many more individuals (N) than plant and animal communities, which can lead to uneven SADs with longer tails of rare species. An alternate explanation is that seed banks influence the SAD. If so, this effect that should be pronounced in microbial communities because seed banks are prevalent in these systems [7] and because active and dormant cells are challenging to differentiate. Although the ESF is not valid for predicting the effects of strong seed banks (Box 2), explicit recursive sampling formulas can be still derived[35] and should yield even more pronounced effects on the SAD.



Seed banks affect the species abundance distribution (SAD) derived from the neutral theory of biodiversity [68] coupled with coalescent approaches. With a weak seed bank ($\theta^{SB} = 4$), where individuals spend on average two generations in a dormant state, species richness is higher and there is more rarity, compared to communities without a seed bank ($\theta = 1$). The figure represents SADs with a sample size of $n = 20$ averaged over 1000 iterations.

Biogeography with a seed bank: Biogeography seeks to understand how contemporary processes and historical events determine the spatial distribution and abundance of species. Thus, a major focus of biogeography is dispersal, a strategy that evolves among species living in spatially variable landscapes. In contrast, dormancy tends to be overlooked in most biogeographical frameworks even though the two strategies are not independent. Despite having different risks and benefits, dormancy and dispersal are substitutable under some conditions. For example, modeling efforts have demonstrated that in environments where there is positive temporal correlation, dormancy can increase the optimal dispersal distance of a population[73]. Such observations have inspired investigations that have explored the joint evolution of dormancy and dispersal[74].

While there is evidence to support the commonly held assumption that there is a trade-off between dispersal and dormancy, this is not a universal pattern. For example, neutral and positive correlation between dispersal- and dormancy-related traits have been reported. Such relationships may arise when dormancy facilitates dispersal[75]. Not only do anatomical features of dormant life stages assist with the passive movement of individuals in a patchy landscape, they may also increase the odds of surviving harsh conditions during transit. Finally, upon arrival in a new environment, dormancy may provide an extended window of opportunity for conditions to arrive that will trigger resuscitation, which in turn, should increase the probability of successful colonization[75].

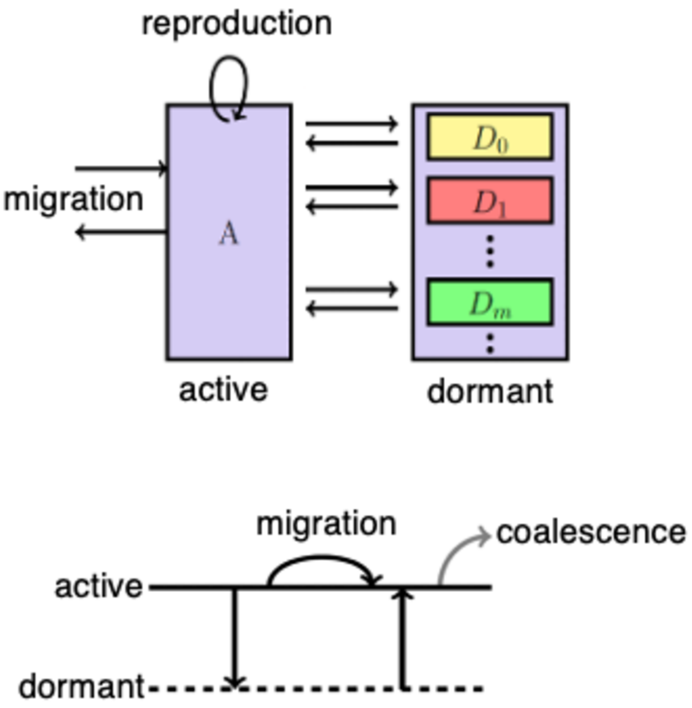
Growing evidence suggests that biogeographic patterns are influenced by seed bank dynamics. When explicitly incorporated into mathematical models, local and regional patterns of diversity are dependent on the degree to which dormancy and dispersal covary[75]. Empirical studies further support the view that dormancy is an important process that should be incorporated into biogeographical frameworks. For example, in a study of bacteria found in a network of forested ponds, molecular-based procedures were used to distinguish sequences that belonged to active and inactive individuals[31]. In combination with process-based models, researchers were able to evaluate the relative importance of dormancy and dispersal to a common biogeographic pattern known as the distance decay relationship (DDR). The DDR describes how the compositional similarity of samples made up of different species (Fig. 2) decreases with increasing geographic distance. Previous studies have shown that the slopes describing the DDR for microorganisms tend to be quite shallow compared to communities of plants and animals[76]. A reasonable explanation for this distinction is that microorganisms have more cosmopolitan distributions owing to their small size, which allows them to be more easily transported long distances. By explicitly accounting for variation in metabolic activity among microbial taxa, an alternate explanation is that spatial patterns of biodiversity can be affected by dormancy and seed bank dynamics[77].

Box 5. Spatial seed banks

In addition to affecting local population-genetic processes (Box 2), seed banks can affect patterns of diversity at larger spatial scales. Consider a metapopulation where each individual belongs to a colony (or patch) that has a fixed population size within a landscape of colonies. Active individuals can migrate between colonies and undergo clonal reproduction via resampling within a colony. Each of the colonies contains a structured seed bank. Upon entering the seed bank, dormant individuals forgo the opportunity to reproduce or migrate. Instead, those individuals are randomly assigned to a compartment (D_0, D_1,…,D_m), which specifies the amount of time it will spend in the seed bank prior to resuscitation. While preserving the Markov property of the evolution, this structuring of dormant individuals allows one to explore how the distribution of wake-up times affects genetic diversity in a spatially explicit manner. The system is then modeled via a set of coupled stochastic differential equations, describing the population in the large-colony-size limit.

The type of equilibrium the system is driven into depends on the interplay between dormancy and migration[78]. In the absence of a seed bank, colonies converge on a monotypic equilibrium, which is determined solely by migration. If p_t denotes the probability that at time t a lineage has returned to the colony it originated from, a monotypic equilibrium emerges if and only if the migration is recurrent: $\int_0^\infty p_t dt = \infty$. This means that, sooner or later, each lineage will return to its original colony. Looking back in time, if two or more lineages repeatedly meet in the same colony, then there is a considerable chance that they will have the same ancestor and thus coalesce (Box 1). As a result, their descendants will possess the same genotype in the contemporary population.

In the presence of a seed bank, the system is more likely to converge on a polytypic equilibrium. This is because dormancy creates a much more restrictive set of conditions for a monotypic equilibrium $\int_0^\infty t^{-(1-\gamma)/\gamma} p_t dt = \infty$. Here, γ controls the tail of the wake-up time from the seed bank in the sense that the probability for the resuscitation time to exceed t falls off like $t^{-\gamma}$ for large t. When $\gamma < 1$, it implies that that the wake-up time has infinite mean. For the integral to be infinite, migration not only needs to be recurrent, but lineages actually need to spend drastically more time at their original colony. Again, looking back in time, two lineages in a colony with a seed bank can coalesce, and thus share the same genotype in the present. But this will only occur if both lineages are active at the same time, which becomes increasingly unlikely with decreasing probabilities of resuscitation (i.e., small values of γ). Taken together, migration and seed bank structure have important implications for the genetic diversity of populations at the landscape scale.



Spatial model to understand diversity with a seed bank. **Top panel:** Individuals are subject to migration (dispersal) and resampling (reproduction). Individuals can also transition into and out of the seed bank via initiation and resuscitation. When individuals enter a dormant state (D), they are randomly assigned a color (m = 0; 1; …), which determines their wake-up time. When the dormant individuals ultimately resuscitate and enter the active state (A), they lose their color. **Bottom panel:** Ancestral lineages can migrate when they are in the active layer. When two ancestral lineages meet in the same colony (i.e., patch) they can coalesce (grey arrow), which indicates that they are derived from a common ancestor. Lineages can move in out of the dormant pool, but cannot migrate or coalesce in the dormant state.

FRONTIERS

After outlining the fundamental attributes and transitions that control seed banks, and describing how dormancy dynamics can give rise to emergent phenomena, we now switch gears to discuss opportunities, applications, and frontiers for seed bank theory. Some advances may be readily achieved using existing technology and resources, while others will require the development of new theories, modeling, and statistical approaches resulting from collaborations among mathematicians, physicists, computer scientists, and biologists.

Human health: To a large extent, theoretical and empirical efforts related to seed banks have focused on the evolution and ecology of environmental systems. However, the principles of seed banks are highly relevant to understanding the pathogenicity and spread of disease, which may be useful in identifying novel therapeutic treatments to improve host health.

Chronic infections — Many infectious diseases are caused by microorganisms that have the capacity to persist inside of hosts via dormancy[79]. These types of chronic infections are a serious and growing public health problem. Not only can dormant pathogens escape host immune defenses, they also contribute to the rise and spread and of antibiotic resistance[80]. Commonly used drugs typically target the transcriptional and translational machinery of actively growing cells. The efficacy of these drugs can be diminished if chronic infections are caused by microbes that form biofilms. Not only can these multicellular structures reduce the diffusion of drugs, but they can also serve as a seed bank of persister cells. Persister cells are generally thought to enter dormancy in a stochastic manner, but transitions may also reflect responses to external or internal stressors[81]. Because the persister phenomenon involves metabolic transitioning, it is amenable to mathematical modeling approaches (Box 1). In this way, seed bank theory has the potential to optimize treatment protocols, based on a better understanding of dormancy mechanisms and growth dynamics of persister cells, while reducing the threats associated with the evolution of antibiotic resistance.

Cancer — A non-communicable disease responsible for nearly 10 million deaths per year, cancer is often viewed as the uncontrolled growth of abnormal cells. However, patients can be in remission for decades while cancer remains in a dormant state[5]. Long-term cancer dynamics are complicated and highly dependent on cell type, the nature of underlying mutations, cell-cell signaling, and host immune responses. Emerging from these factors, are the phenotypic transitions that control key developmental stages of cancer[82]. While the awakening of dormant cancer cells can be stochastic, these transitions can also be triggered by environmental conditions (Box 1) found in micro-niches[5]. A key goal in managing disease progression is to prevent metastasis, which involves the spread of cancer cells from one location in the host (e.g., breast) to another (e.g., bone). The dispersal and metabolic activity of cancer cells are not necessarily independent of one another[5]. Therefore, seed bank theory may be valuable for understanding the persistence and dynamics in cancer patients. For example, stochastic individual-based models have been developed to help understand the role of phenotypic transitions, which can guide immunotherapies and strategies involving other drug treatments[83].

Epidemiology — Because dormancy can affect spatial and temporal processes in complex ways, seed banks hold promise for understanding and predicting the spread of diseases in an epidemiological context. A first step in this direction would be to incorporate dormancy into classical SIR models, which track susceptible (S), infectious (I), and recovered (R) individuals based on simple transitions such as the infection rate (β), recovery rate (γ), and the rate at which recovered individuals become susceptible again (ζ). Although somewhat related forms of latency and carriers states have been explored[84], a systematic analysis of dormancy in an epidemiological context is undeveloped. When reflecting on the complexity of seed bank processes, a variety of modeling scenarios becomes possible. For example, SIR-like models could incorporate dormancy-related processes into host population, pathogen populations, or both. While such models could be used in public health, they may also be valuable for understanding disease dynamics in foodborne pathogens like *Listeria* that are infected by viruses. In such system, the CRISPR-based immunity encoded in the bacterial genome targets both the host and viral RNA, potentially conferring herd immunity to the bacterial population with implications for controlling epidemics[85].

Global change: Environmental change is occurring on a global scale at an unprecedented rate. Increasing temperatures, altered precipitation regimes, increased nutrient runoff, and habitat destruction pose major threats to the long-term persistence of species, while also altering the biogeochemical cycles with critical implications for the functioning of the biosphere. In addition to helping some species contend with current and future global change scenarios, seed banks may also be critical for forecasting ecosystem dynamics.

Conservation and restoration — Many natural and managed ecosystems benefit from seed banks. Reservoirs of dormant individuals can stabilize plant communities and contribute to patterns of succession following disturbance events[18]. However, seed banks are not a universal safeguard for maintaining species in the face of global change. For example, in the Arctic where environmental change is accelerating most rapidly, it is unclear whether seed banking strategies are robust for all plant populations[86]. Similarly, in arid regions of Australia, it was shown that some species in the seed bank will not be able to tolerate the temperature and moisture levels predicted in the coming decades[87]. While seed banks are often viewed as beneficial, they can also interfere with some conservation and restoration goals. For example, invasive species can create a positive feedback by enriching the local seed bank, which can then contribute to the spread of these nuisance taxa throughout the landscape[88]. Nevertheless, there are opportunities to use seed banks in combination with other conservation efforts to help protect at-risk species. In addition to collecting and storing germ plasm for the future, seed banks might be useful in the context of leveraging trait-based information to improve the efficacy of assisted migration efforts, which involve moving populations into new environments that will match their bioclimatic requirements in the future.

Ecosystem functioning — Seed banks may also have implications for the functioning and stability of entire ecosystems. Owing to their abundance and diversity, microorganisms play a particularly important role when it comes to regulating the flux of materials and energy in food webs. Yet, a non-trivial fraction of the microbial community is made up of metabolically inactive microorganisms[7], which raises questions about the links between seed banks and global change. Decades of nutrient enrichment altered the size and composition of microbial seed banks in a coastal estuarine ecosystem[89]. Such findings have inspired scientists to incorporate traits like dormancy into statistical and process-based models with the hope of better understanding the complex ways in which microbes influence Earth system processes. For example, in a global change experiment where drought and temperature were manipulated in a grassland ecosystem, soil respiration could be better explained when the fraction of dormant bacteria was taken into account[90]. When applied to Arctic ecosystems, models predict that substantially more carbon will be stored in soils owing to microbial dormancy, which has important implications for understanding microbial processes at regional and global scales[91].

Mathematics: The mathematical treatment of seed banks has been rapidly expanding over the past decade. Originally motivated by biological observations, the objects and properties of seed banks are now opening up important questions and approaches in various subfields of mathematics. Dormancy can fundamentally alter the behavior and resilience of a system by introducing memory, delays, and feedbacks, which should be visible across multiple modeling scales. In this section, we briefly outline a few of these growth areas.

Interacting particle systems — At the interface of probability theory and statistical physics, the field of interacting particle systems focuses on collective behaviors and phase transitions using graphical representation, coupling, duality, and coalescents[92]. The theory allows particles to exist in various states (e.g., present/absent, up/down), but also permits them to move through space. Thus, a natural extension would be to add dormancy to interacting particle systems. For example, a particle could fall asleep, remain idle for a period of time, and then resume spatial motion and interaction with other particles after waking up. Particles may also undergo metabolic transitions, which would make them behave differently than particles that consistently remain active. In such ways, dormancy should affect the collective behavior of particles and give rise to new types of phase transitions. Multi-type interacting particle systems represent a rich modelling class and typically have complicated duals, capable of incorporating a multitude of phenomena.

Complex networks — Many natural and engineered systems are organized into networks. Often large and complex, they represent connectedness and spatial relationships between different objects in social, technological, economic, and biological systems. As a result, network-based approaches have been used in a range of quantitative disciplines including graph theory, combinatorics, probability theory, and computer science. Researchers have begun to capture aspects of seed banks by investigating the importance of active and dormant connections in social networks[93,94]. Similarly, networks are being used to study the development and stability of mental disorders based on the notion that external events can cause dormant states to become activated and trigger other symptoms[95]. Despite advances in these areas, it remains unclear how the form and functionality of networks are influenced by the presence of dormancy and seed banks. It is possible that there are common motifs (e.g., autoregulation, feed-forward, and feed-back) involving seed banks that can be leveraged for robustness and adaptability in networks.

Adaptive dynamics — Adaptive dynamics is a mathematical framework that considers individuals that can move in space, carry multiple continuous traits, acquire mutations, and interact with each other in ways that depend on a continuum of possible fitness values [96]. Often applied to large systems with small mutation rates, adaptive dynamics exhibit rich scaling behaviors that are described by measure-valued diffusions[97]. Introducing memory with a seed bank should affect the dynamics of the trait substitution sequence, the polymorphic evolution sequence, and the canonical equation of adaptive dynamics. The increased diversity resulting from seed banks should also influences adaptive walks in fitness landscapes, especially those that change over time[98].

Stochastic partial differential equations — Seed banks can also be incorporated into classical stochastic partial differential equations. This could be achieved by allowing continuous two-way migration between the original system and a dormant state. Such systems may then admit a delay-representation, leading to a very explicit description of the memory introduced by a seed bank. Concrete effects of a seed bank have already been documented using the stochastic Fisher-KPP equation, where the addition of a dormant state significantly reduces the speed that beneficial alleles spread in the population[99]. Other seed bank mechanisms can be expected to manifest themselves in stochastic partial equations if they can be derived from microscopic systems that allow for dormant states. For example, one may speculate about the effects of dormancy on the KPZ-equation arising as a scaling limit from models for bacterial growth or the exclusion process.

CONCLUSION

We make the case that seed banks play a crucial role in determining the behavior observed in a variety of biological systems, spanning collections of cells to entire ecosystems. Seed banks come with different attributes and physical features, each of which can affect the transitions into and out of dormancy in complex ways, giving rise to a multitude of emergent phenomena. The mathematical description of seed banks is still in its infancy, but various new techniques are being developed and new challenges are being identified. We argue in favor of a systems theory perspective, in which different lines of research and different viewpoints are combined to facilitate further progress. Seed banks represent a paradigm that will keep us busy for decades to come.

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