

Multi-colony Wright-Fisher with seed-bank

Frank den Hollander¹, Giulia Pederzani¹

Abstract

We consider a multi-colony version of the Wright-Fisher model with seed-bank that was recently introduced by Blath et al. Individuals live in colonies and change type via resampling and mutation. Each colony contains a seed-bank that acts as a genetic reservoir. Individuals can enter the seed-bank and become dormant or can exit the seed-bank and become active. In each colony at each generation a fixed fraction of individuals swap state, drawn randomly from the active and the dormant population. While dormant, individuals suspend their resampling. While active, individuals resample from their own colony, but also from different colonies according to a random walk transition kernel representing migration. Both active and dormant individuals mutate.

We derive a formula for the probability that two individuals drawn randomly from two given colonies are identical by descent, i.e., share a common ancestor. This formula, which is formulated in Fourier language, is valid when the colonies form a discrete torus. We consider the special case of a symmetric slow seed-bank, for which in each colony half of the individuals are in the seed-bank and at each generation the fraction of individuals that swap state is small. This leads to a simpler formula, from which we are able to deduce how the probability to be identical by descent depends on the distance between the two colonies and various relevant parameters. Through an analysis of random walk Green functions, we are able to derive explicit scaling expressions when mutation is slower than migration. We also compute the spatial second moment of the probability to be identical by descent for all parameters when the torus becomes large. For the special case of a symmetric slow seed-bank, we again obtain explicit scaling expressions.

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Wright-Fisher, seed-bank, multi-colony, resampling, mutation, genealogy.

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¹Mathematical Institute, Leiden University, P.O. Box 9512, 2300 RA Leiden, The Netherlands.

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1. Introduction

1.1. Background

The Wright-Fisher model with seed-bank aims at modelling the genetic evolution of populations in which individuals are allowed to achieve a dormant state and maintain it for many generations. Dormancy is understood as a reversible rest period, characterised by low metabolic activity and interruption of phenotypic development (see Lennon and Jones [10]). This type of behaviour is observed in many taxa, including plants, bacteria and other micro-organisms, as a response to unfavourable environmental conditions. Dormant individuals can be resuscitated under more favourable conditions, after a varying and possibly large number of generations, and reprise reproduction. This strategy has been shown to have important implications for population persistence, maintenance of genetic variability and even stability of ecosystem processes, acting as a buffer against such evolutionary forces as genetic drift, selection and environmental variability. The importance of this evolutionary trait has led to attempts at modelling seed-banks from a mathematical perspective.

The mathematical modelling of seed-bank effects has been somewhat challenging. In fact, since individuals can remain dormant for arbitrarily many generations, it is problematic to retain the Markov property. The most successful models to date are extensions of the Wright-Fisher model, the classical model for genetic evolution of a population viewed from a probabilistic perspective. However, so far these extensions have been able to capture only weak seed-bank effects, resulting in a delayed Wright-Fisher model, or they have led to extreme behaviours that seem artificial.

The most relevant model was proposed by Kaj, Krone and Lascoux [9], who allowed individuals in a population of fixed size to select a parent from a random number B of generations in the past, where B is an \mathbb{N} -valued random variable assumed to be independent and identically distributed for each individual. The authors show that if B is bounded, then after the usual rescaling of time by the population size the model converges to a delayed Kingman coalescent, where the rates are multiplied by $1/\mathbb{E}[B]^2$. More generally, it was proven by Blath, González Casanova, Kurt and Spanò [3] that a sufficient condition for convergence to the Kingman coalescent is $\mathbb{E}[B] < \infty$. The sampling from past generations only leads to a delay in the coalescence process and leaves the coalescent structure unchanged. Therefore it is not capturing the role of seed-banks in maintaining genetic variability. One therefore speaks of *weak* seed-bank effects.

A further extension of the model, which allows for *strong* seed-bank effects, was proposed in [3]. In particular, the authors study the case in which the age-distribution χ of B is heavy-tailed, namely,

$$\chi(B \geq n) = L(n) n^{-\alpha}, \quad n \in \mathbb{N}, \quad 0 < \alpha < \infty, \quad (1.1)$$

where L is slowly varying as $n \rightarrow \infty$. It is proved that for $\alpha > \frac{1}{2}$ the most recent common ancestor (MRCA) of two randomly sampled individuals exists with probability 1, but the expected time to the MRCA is infinite as soon as $\alpha < 1$, while for $0 < \alpha < \frac{1}{2}$ with positive probability a MRCA does not even exist at all.

Such extreme behaviour may seem artificial, and for this reason González Casanova et al. in [6] and Blath et al. in [2] have studied the case in which B scales with the total population size N . In

particular, the age-distribution χ of B is given by

$$\chi = (1 - \epsilon) \delta_1 + \epsilon \delta_{N^\beta}, \quad 0 < \beta < \infty, \quad \epsilon \in (0, 1). \quad (1.2)$$

For $\beta < \frac{1}{3}$, this model again shows convergence to the Kingman coalescent, but requires a rescaling of time by the non-classical factor $N^{1+2\beta}$. In other words, this choice of χ considerably increases the expected time to the MRCA. Still, it leaves the coalescent structure unchanged, and results in other parameter regimes remain somewhat elusive.

In summary, the mathematical results to date have been effective in modelling weak seed-bank effects, but for strong seed-bank effects they have so far been unsatisfying in suggesting new limiting coalescent structures. Blath et al. [4] propose a new model in which individuals can enter and exit a seed-bank at each generation. While in the seed-bank, individuals *suspend* their resampling and preserve their type. The main advantage of this model is that it retains the Markov property, while the long-term behaviour is in line with our intuition and does not require artificial scaling assumptions. It also offers a natural interpretation for the scaling limit of both the forward and the backward process, and the limiting genealogy is given by a new coalescent structure.

1.2. Outline

The goal in the present paper is to study a *multi-colony* version of the model in [4], where individuals can *migrate* between different colonies, each carrying a seed-bank, and are also subject to *mutation*. The main quantity we are after is the probability that two individuals drawn randomly from two given colonies are *identical by descent*, i.e., share a common ancestor.

The remaining sections are organised as follows. In Section 2 we define the single-colony Wright-Fisher model with seed-bank. In Section 3 we present the multi-colony version of this model and derive a formula for the probability that two individuals drawn randomly from two given colonies are identical by descent. This formula (stated in Theorem 3.4 below) comes in Fourier language and is valid when the colonies form a discrete torus. In Section 4 we consider the special case of a symmetric slow seed-bank, for which in each colony half of the individuals are in the seed-bank and at each generation the fraction of individuals that swap state is small. This leads to a simpler formula (stated in Theorems 4.1 and 4.3 below), from which we are able to deduce how the probability to be identical by descent depends on the distance between the two colonies and various relevant parameters. Through an analysis of random walk Green functions, we are able to derive explicit scaling expressions when mutation is slower than migration (stated in Theorems 4.4–4.7 below). In Section 5 we compute the spatial second moment of the probability to be identical by descent for all parameters when the torus becomes large (stated in Theorem 5.3 below). For the special case of a symmetric slow seed-bank, we again obtain explicit scaling expressions (stated in Theorem 5.4 below).

2. The Wright-Fisher model with seed-bank

In Section 2.1 we recall the standard Wright-Fisher model, the simplest model for population genetics, where the only evolutionary force at play is *resampling*. In Section 2.2 we recall the extension of this model studied in [4], namely, with a *seed-bank*. In Section 3 we will introduce a multi-colony version of the extended model, which will be our main object of study. In what follows, we write $\mathbb{N} = \{1, 2, \dots\}$ and $\mathbb{N}_0 = \mathbb{N} \cup \{0\}$.

2.1. Wright-Fisher model

Consider a population of N haploid individuals, with N fixed. For each genetic locus, an individual carries one copy of the gene at that locus that is assumed to be one of two types, denoted by a and A . The model is discrete in time. At each time unit, every individual from the new generation chooses an individual from the previous population uniformly at random and adopts its type. This choice is independent of time and of the choices of the other individuals. This type of resampling mechanism is called parallel updating (all individuals choose an ancestor at the same time and independently of each other). Let

$$X_n = \text{number of individuals of type } a \text{ at time } n. \quad (2.1)$$

The sequence $X = (X_n)_{n \in \mathbb{N}_0}$ is the discrete-time Markov chain with state space

$$\Omega = \{0, 1, 2, \dots, N\} \quad (2.2)$$

and transition kernel

$$p_{ij} = \binom{N}{j} \left(\frac{i}{N}\right)^j \left(\frac{N-i}{N}\right)^{N-j}, \quad i, j \in \Omega. \quad (2.3)$$

The latter follows from the fact that, if at time n there are i individuals of type a , then there will be j individuals at time $n+1$ if and only if precisely j individuals choose an ancestor of type a and $N-j$ individuals choose an ancestor of type A . The initial condition can be any state $X_0 \in \Omega$.

The states 0 and N are traps: $p_{00} = p_{NN} = 1$. Consequently, one of the two genetic types eventually becomes extinct: genetic variability is lost through chance.

2.2. Wright-Fisher model with seed-bank

The model introduced in [4] consists of a haploid population of fixed size N that reproduces in discrete generations. Each individual carries a genetic type from a generic type space E . In what follows we will focus on the bi-allelic case, $E = \{a, A\}$. Alongside the active population, there is a seed-bank of fixed size M containing the dormant individuals.

Given $M, N \in \mathbb{N}$, take $\epsilon \in [0, 1]$ such that $\epsilon N \leq M$ and set $\delta = \epsilon N / M$. For convenience we assume that $\epsilon N = \delta M \in \mathbb{N}$. The dynamics of the model is as follows (see Fig. 1):

- The N active individuals produce $(1-\epsilon)N$ active individuals in the next generation, where every new individual randomly chooses a parent from the previous generation and adopts its type.
- The remaining $\epsilon N (= \delta M)$ individuals from the active population produce individuals that become dormant, i.e., seeds in the next generation.
- From the seed-bank, $\delta M (= \epsilon N)$ individuals become active and leave the seed-bank. Therefore in the next generation the active population again consists of $(1-\epsilon)N + \epsilon N = N$ individuals, where the first term comes from the previously active population and the second term from the previously dormant population.
- The remaining $(1-\delta)M$ seeds remain inactive and stay in the seed-bank. Therefore in the next generation the population in the seed-bank again consists of $(1-\delta)M + \delta M = M$ individuals, where the first term comes from the previously dormant population and the second term from the previously active population.

Definition 2.1. Let M, N, ϵ, δ and E be as above. Given an initial genetic type configuration (ξ_0, η_0) with $\xi_0 \in E^N, \eta_0 \in E^M$, denote by

$$\xi_k = (\xi_k(i))_{i \in [N]}, \quad \eta_k = (\eta_k(j))_{j \in [M]}, \quad k \in \mathbb{N}_0, \quad (2.4)$$

the random genetic type configuration of, respectively, the active individuals and the dormant individuals in generation k . The discrete-time Markov chain $(\xi_k, \eta_k)_{k \in \mathbb{N}_0}$ with state space $E^N \times E^M$ is called the type configuration process of the Wright-Fisher model with geometric seed-bank component.

Note that the time a dormant individual stays in the seed-bank before becoming active is a random variable with a geometric distribution with parameter δ , and that the times for different dormant individual are i.i.d. Similarly, the probability that an active individual becomes dormant is ϵ .

We want to understand the behaviour of the frequency of a alleles in both the active population and the seed-bank. We therefore define

$$X_k^N = \frac{1}{N} \sum_{i \in [N]} \mathbb{1}_{\{\xi_k(i)=a\}}, \quad Y_k^M = \frac{1}{M} \sum_{j \in [M]} \mathbb{1}_{\{\eta_k(j)=a\}}, \quad (2.5)$$

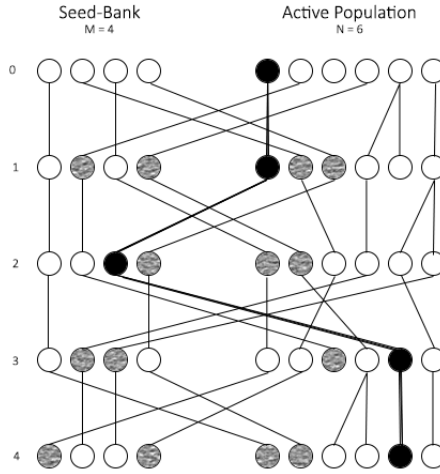


Figure 1: Evolution over 4 generations of a population with $N + M = 10$ individuals, of which $N = 6$ are active and $M = 4$ are inactive (in the seed-bank). The lines indicate the genealogy of the population. The bold line shows a single line of ancestry.

which represent the fraction of individuals having type a in generation k in, respectively, the active population and the dormant population. Together they form a discrete-time Markov chain taking values in $I^N \times I^M$, with

$$I^N = \left\{0, \frac{1}{N}, \frac{2}{N}, \dots, 1\right\} \subset [0, 1], \quad I^M = \left\{0, \frac{1}{M}, \frac{2}{M}, \dots, 1\right\} \subset [0, 1]. \quad (2.6)$$

Abbreviate

$$\mathbb{P}_{x,y}(\cdot) = \mathbb{P}(\cdot \mid X_0^N = x, Y_0^M = y), \quad (x, y) \in I^N \times I^M. \quad (2.7)$$

The transition probabilities of this Markov chain can be characterised through the following proposition.

Proposition 2.2. *Let $c = \epsilon N = \delta M \in \mathbb{N}$. For $(x, y), (\bar{x}, \bar{y}) \in I^N \times I^M$,*

$$\begin{aligned} & \mathbb{P}_{x,y}(X_1^N = \bar{x}, Y_1^M = \bar{y}) \\ &= \sum_{i=0}^c \mathbb{P}_{x,y}(Z = i) \mathbb{P}_{x,y}(U = \bar{x}N - i) \mathbb{P}_{x,y}(V = \bar{y}M + i), \end{aligned} \quad (2.8)$$

where Z, U, V are independent under $\mathbb{P}_{x,y}$, with $Z \cong \text{Hyp}_{M,c,yM}$ (hypergeometric distribution), $U \cong \text{Bin}_{N-c,x}$ and $V \cong \text{Bin}_{c,x}$ (binomial distributions).

Proof. The random variables have a simple interpretation:

- Z is the number of individuals of type a that become active in the next generation or, equivalently, the number of individuals at generation 1 that are offspring of an individual of type a at generation 0.
- U is the number of individuals that are offspring of individuals of type a in the previous generation (and therefore are themselves of type a).
- V is the number of individuals that are offspring of individuals of type a in the previous generation.

With this interpretation the distributions of Z, U and V are immediate from Definition 2.1. By construction, $X_1^N = \frac{U+Z}{N}$ and $Y_1^M = y + \frac{V-Z}{M}$, and so the claim follows. \square

3. A multi-colony extension

In this section we analyse a spatial version of the model introduced in Section 2. Namely, we add *migration*, i.e., we allow individuals to adopt the type of individuals in colonies different from their own (in the literature this is called the stepping stone model). In Section 3.1 we define the model without mutation, in Section 3.2 we add mutation. In Section 3.3 we turn to our key object of interest, the probability that two individuals drawn randomly from two given colonies are identical by descent. We derive a formula for this probability involving convolutions of matrices. In Section 3.4 we simplify this formula by turning to Fourier analysis, which leads to our first main theorem: Theorem 3.4.

3.1. Migration

Consider the *discrete torus* \mathbb{T} in any dimension $d \in \mathbb{N}$. This may be identified with the lattice $\mathbb{Z}^d \cap [0, L]^d$, $L \in \mathbb{N}$, with periodic boundaries. At each lattice site there is a colony, which consists of an active population of size N and a seed-bank of size M . At each generation, every individual chooses a colony according to a random walk transition kernel $p(x, y)$, $x, y \in \mathbb{T}$, and chooses from that colony an individual that was active in that colony in the previous generation. We assume that $p(x, y)$, $x, y \in \mathbb{T}$, depends only on the distance between the two colonies x and y , not on their position. This makes our system translation invariant. An example for a transition kernel that satisfies this assumption is

$$p(x, y) = (1 - \nu)\delta_{x,y} + \nu q(x, y), \quad x, y \in \mathbb{T}, \quad (3.1)$$

with $\delta_{x,y} = \mathbb{1}_{\{x=y\}}$ and $q(x, y)$, $x, y \in \mathbb{T}$, a random walk transition kernel that controls the migration. The parameter $\nu \in (0, 1]$ is the migration probability. An example is the uniform nearest-neighbour model

$$q(0, z) = \begin{cases} \frac{1}{2d}, & \text{if } \|z\| = 1, \\ 0, & \text{otherwise,} \end{cases} \quad (3.2)$$

where $\|\cdot\|$ is the lattice norm. This corresponds to a simple random walk on \mathbb{T} .

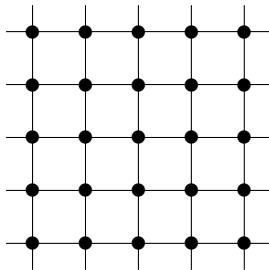


Figure 2: A 5×5 torus, with edges connecting neighbouring vertices. The boundary is periodic: opposite ends horizontally and vertically are connected. Simple random walk corresponds to transitions north, east, south and west, each with probability $\frac{1}{4}$.

We are interested, for the system *in equilibrium*, to compute the probability $\psi((x, a), (y, b))$ that two individuals drawn uniformly at random from two colonies $x, y \in \mathbb{T}$ in states $a, b \in \{0, 1\}$ are *identical by descent*, i.e., their lineages coalesce. The states $a, b \in \{0, 1\}$ indicate whether the individual is drawn from the dormant population (state 0) or the active population (state 1), e.g. $(x, 0)$ means that an individual is drawn from the seed-bank in colony $x \in \mathbb{T}$. If $x = y$, then we require the two individuals to be distinct. We want to find an expression for the 4-vector

$$\Psi_{x,y} = \begin{pmatrix} \psi((x, 0), (y, 0)) \\ \psi((x, 0), (y, 1)) \\ \psi((x, 1), (y, 0)) \\ \psi((x, 1), (y, 1)) \end{pmatrix}, \quad x, y \in \mathbb{T}. \quad (3.3)$$

Note that, since $p(x, y)$ depends on $x - y$ only, the same is true for $\Psi_{x, y}$. Naturally, since \mathbb{T} and N are finite we have

$$\Psi_{x, y} = \begin{pmatrix} 1 \\ 1 \\ 1 \\ 1 \end{pmatrix}, \quad x, y \in \mathbb{T}. \quad (3.4)$$

Indeed, no matter what colonies the individuals are drawn from, their lineages move in and out of the seed-bank and migrate to other colonies in \mathbb{T} . Eventually, going infinitely far back in time, the lineages coalesce. The problem becomes more interesting when we modify the dynamics to include *mutation*.

3.2. Migration and mutation

Assume that at each generation, every individual with probability $\mu \in (0, 1)$ mutates to a *new type* and with probability $1 - \mu$ does not mutate and proceeds to become either active, respectively, dormant (with probability δ , respectively, ϵ). In addition, if an individual is active and remains active, then it chooses an individual from any colony $y \in \mathbb{T}$ (with probability $(1 - \epsilon)p(x, y)$) and adopts its type. More precisely, a dormant individual in the seed-bank may

- mutate to a new type, with probability μ ,
- maintain its type and remain in the seed-bank, with probability $(1 - \mu)(1 - \delta)$,
- maintain its type and become active, with probability $(1 - \mu)\delta$.

Similarly, an active individual may

- mutate to a new type, with probability μ ,
- remain active and choose a random ancestor from colony $y \in \mathbb{T}$ (possibly $y = x$), with probability $(1 - \mu)(1 - \epsilon)p(x, y)$,
- maintain its type and become dormant, with probability $(1 - \mu)\epsilon$.

Since a lineage is interrupted when a mutation occurs, we define two individuals to be *identical by descent* if their lineages coalesce *before* a mutation affects either lineage. Our goal is to compute the 4-vector $\Psi_{x, y}$ in (3.3) in the presence of mutation, again for the system *in equilibrium*. This will be achieved in several steps, resulting in Theorem 3.4 below. Note that individuals may change their type multiple times. What matters for $\Psi_{x, y}$ is that the lineages of the two individuals drawn at x and y meet without encountering a mutation.

3.3. Computation of the probability to be identical by descent

We begin by deriving a recursive relation for the family $\{\Psi_{x, y}\}_{x, y \in \mathbb{T}}$.

Proposition 3.1. *For $x, y \in \mathbb{T}$,*

$$\Psi_{x, y} = \Phi_{x, y} + A_{x, y}\Psi_{0, 0} + \sum_{w, z \in \mathbb{T}} B_{w-x, z-y}\Psi_{w, z}, \quad (3.5)$$

where

$$\Phi_{x, y} = (1 - \mu)^2(1 - \epsilon)^2 \begin{pmatrix} 0 \\ 0 \\ 0 \\ p^2(x, y)\frac{1}{N} \end{pmatrix}, \quad (3.6)$$

$$A_{x, y} = -(1 - \mu)^2(1 - \epsilon)^2 \begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & p^2(x, y)\frac{1}{N} \end{pmatrix}, \quad (3.7)$$

$$B_{w-x, z-y} = C\delta_{x, w}\delta_{y, z} + D_{w-x, z-y}, \quad (3.8)$$

with

$$C = (1 - \mu)^2 \times \begin{pmatrix} (1 - \delta)^2 & (1 - \delta)\epsilon & (1 - \delta)\epsilon & \epsilon^2 \\ \delta(1 - \delta) & 0 & \delta\epsilon & 0 \\ \delta(1 - \delta) & \delta\epsilon & 0 & 0 \\ \delta^2 & 0 & 0 & 0 \end{pmatrix}, \quad (3.9)$$

$$D_{w-x, z-y} = (1 - \mu)^2(1 - \epsilon) \times \begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & (1 - \delta)p(y, z)\delta_{x, w} & 0 & \epsilon p(y, z)\delta_{x, w} \\ 0 & 0 & (1 - \delta)p(x, w)\delta_{y, z} & \epsilon p(x, w)\delta_{y, z} \\ 0 & \delta p(y, z)\delta_{x, w} & \delta p(x, w)\delta_{y, z} & (1 - \epsilon)p(x, w)p(y, z) \end{pmatrix}. \quad (3.10)$$

Proof. We begin by writing down a recursion relation for

$$\Psi_{x, y}^{(n)} = \begin{pmatrix} \psi_n((x, 0), (y, 0)) \\ \psi_n((x, 0), (y, 1)) \\ \psi_n((x, 1), (y, 0)) \\ \psi_n((x, 1), (y, 1)) \end{pmatrix}, \quad x, y \in \mathbb{T}, \quad (3.11)$$

the probability at time n that two individuals randomly drawn from colonies x, y are identical by descent. This reads as follows:

$$\begin{aligned} \psi_{n+1}((x, 0), (y, 0)) &= (1 - \mu)^2 \left[(1 - \delta)^2 \psi_n((x, 0), (y, 0)) + \epsilon^2 \psi_n((x, 1), (y, 1)) \right. \\ &\quad \left. + \epsilon(1 - \delta) [\psi_n((x, 1), (y, 0)) + \psi_n((x, 0), (y, 1))] \right], \\ \psi_{n+1}((x, 1), (y, 0)) &= (1 - \mu)^2 \left[\delta(1 - \delta) \psi_n((x, 0), (y, 0)) + \delta\epsilon \psi_n((x, 0), (y, 1)) \right. \\ &\quad \left. + \sum_{w \in \mathbb{T}} (1 - \epsilon)(1 - \delta)p(x, w) \psi_n((w, 1), (y, 0)) + \epsilon(1 - \epsilon)p(x, w) \psi_n((w, 1), (y, 1)) \right], \\ \psi_{n+1}((x, 0), (y, 1)) &= (1 - \mu)^2 \left[\delta(1 - \delta) \psi_n((x, 0), (y, 0)) + \delta\epsilon \psi_n((x, 1), (y, 0)) \right. \\ &\quad \left. + \sum_{z \in \mathbb{T}} (1 - \epsilon)(1 - \delta)p(y, z) \psi_n((x, 0), (z, 1)) + \epsilon(1 - \epsilon)p(y, z) \psi_n((x, 1), (z, 1)) \right], \\ \psi_{n+1}((x, 1), (y, 1)) &= (1 - \mu)^2 \left[\delta^2 \psi_n((x, 0), (y, 0)) \right. \\ &\quad + \sum_{z \in \mathbb{T}} \delta(1 - \epsilon)p(y, z) \psi_n((x, 0), (z, 1)) \\ &\quad + \sum_{w \in \mathbb{T}} \delta(1 - \epsilon)p(x, w) \psi_n((w, 1), (y, 0)) \\ &\quad + \sum_{\substack{w, z \in \mathbb{T} \\ w \neq z}} (1 - \epsilon)^2 p(x, w)p(y, z) \psi_n((w, 1), (z, 1)) \\ &\quad \left. + \sum_{z \in \mathbb{T}} (1 - \epsilon)^2 p(x, z)p(y, z) \left[\frac{1}{N} + \left(1 - \frac{1}{N}\right) \psi_n((z, 1), (z, 1)) \right] \right]. \quad (3.12) \end{aligned}$$

The reasoning behind the above expressions comes from considering the possible choices of the two individuals. In the first expression, for example, the drawn individuals are both in the seed-bank and there are three scenarios:

- they were both in the seed bank in the previous generation (with probability $1 - \delta$ each, independently of each other),
- they are both offspring of active individuals (with probability ϵ each),
- one was in the seed-bank in the previous generation and did not become active (with probability $1 - \delta$), and the other is offspring of an active individual (with probability ϵ).

Note that if individuals are in the seed-bank, then the individuals they are offspring of cannot be from a different colony, which is why the transition kernels do not always appear in the recursive relations. When they appear, they are always multiplied by $1 - \epsilon$, since the transition kernels are probabilities *conditional* on the event that the individuals were not in the seed-bank in the previous generation. In the last term of $\psi_{n+1}((x, 1), (y, 1))$ we are looking at the event in which the ancestors of the two individuals are in the same colony: either they are the same individual (with probability $1/N$ and the iteration ends) or they are two distinct individuals (with probability $1 - \frac{1}{N}$). In this equation we add and subtract the term $(1 - \mu)^2(1 - \epsilon)^2 p(x, w)p(y, z)\psi_n((w, 1), (z, 1))$ for $w = z$ (the expression in the fourth line) to obtain

$$\begin{aligned}
\psi_{n+1}((x, 1), (y, 1)) &= (1 - \mu)^2 \left[\delta^2 \psi_n((x, 0), (y, 0)) \right. \\
&+ \sum_{z \in \mathbb{T}} \delta(1 - \epsilon) p(y, z) \psi_n((x, 0), (z, 1)) \\
&+ \sum_{w \in \mathbb{T}} \delta(1 - \epsilon) p(x, w) \psi_n((w, 1), (y, 0)) \\
&+ \sum_{w, z \in \mathbb{T}} (1 - \epsilon)^2 p(x, w) p(y, z) \psi_n((w, 1), (z, 1)) \\
&\left. + \sum_{z \in \mathbb{T}} (1 - \epsilon)^2 p(x, z) p(y, z) \left[\frac{1}{N} - \frac{1}{N} \psi_n((z, 1), (z, 1)) \right] \right]. \tag{3.13}
\end{aligned}$$

By ergodicity, we have

$$\lim_{n \rightarrow \infty} \Psi_{x,y}^{(n)} = \Psi_{x,y} \quad \forall x, y \in \mathbb{T}. \tag{3.14}$$

Therefore, in equilibrium, we may drop the time indices from the above expressions and obtain

$$\begin{aligned}
& \begin{pmatrix} \psi((x, 0), (y, 0)) \\ \psi((x, 0), (y, 1)) \\ \psi((x, 1), (y, 0)) \\ \psi((x, 1), (y, 1)) \end{pmatrix} \\
&= (1 - \mu)^2 \begin{pmatrix} (1 - \delta)^2 & (1 - \delta)\epsilon & (1 - \delta)\epsilon & \epsilon^2 \\ \delta(1 - \delta) & 0 & \delta\epsilon & 0 \\ \delta(1 - \delta) & \delta\epsilon & 0 & 0 \\ \delta^2 & 0 & 0 & 0 \end{pmatrix} \begin{pmatrix} \psi((x, 0), (y, 0)) \\ \psi((x, 0), (y, 1)) \\ \psi((x, 1), (y, 0)) \\ \psi((x, 1), (y, 1)) \end{pmatrix} \\
&+ \sum_{w, z \in \mathbb{T}} (1 - \mu)^2 (1 - \epsilon) \times \\
&\quad \begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & (1 - \delta)p(y, z)\delta_{x, w} & 0 & \epsilon p(y, z)\delta_{x, w} \\ 0 & 0 & (1 - \delta)p(x, w)\delta_{y, z} & \epsilon p(x, w)\delta_{y, z} \\ 0 & \delta p(y, z)\delta_{x, w} & \delta p(x, w)\delta_{y, z} & (1 - \epsilon)p(x, w)p(y, z) \end{pmatrix} \begin{pmatrix} \psi((w, 0), (z, 0)) \\ \psi((w, 0), (z, 1)) \\ \psi((w, 1), (z, 0)) \\ \psi((w, 1), (z, 1)) \end{pmatrix} \quad (3.15) \\
&- \sum_{z \in \mathbb{T}} (1 - \mu)^2 (1 - \epsilon)^2 \times \\
&\quad \begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & p(x, z)p(y, z)\frac{1}{N} \end{pmatrix} \begin{pmatrix} \psi((z, 0), (z, 0)) \\ \psi((z, 0), (z, 1)) \\ \psi((z, 1), (z, 0)) \\ \psi((z, 1), (z, 1)) \end{pmatrix} \\
&+ \sum_{z \in \mathbb{T}} (1 - \mu)^2 (1 - \epsilon)^2 \begin{pmatrix} 0 \\ 0 \\ 0 \\ p(x, z)p(y, z)\frac{1}{N} \end{pmatrix}.
\end{aligned}$$

After using that $\sum_{z \in \mathbb{T}} p(x, z)p(y, z) = \sum_{z \in \mathbb{T}} p(x, z)p(z, y) = p^2(x, y)$, and $\Psi_{z, z} = \Psi_{0, 0}$ by translation invariance, we obtain the expression in (3.5). \square

Now that we have a recursive relation for $\Psi_{x, y}$ as expressed in Proposition 3.1, we proceed to solve this relation to find a closed form expression for $\Psi_{x, y}$. To do so, we iterate (3.5) and, after noting that the last summand tends to 0 as the number of iterations tends to infinity (since $0 < \mu < 1$), we obtain the following expression.

Proposition 3.2. *For all $x, y \in \mathbb{T}$,*

$$\Psi_{x, y} = \frac{1 - \Psi_{0, 0}^{(4)}}{N} \sum_{n \in \mathbb{N}_0} (B * \Gamma)_{x, y}^{(n)}, \quad (3.16)$$

where $\Psi_{0, 0}^{(4)}$ is the 4-th entry of the 4-vector $\Psi_{0, 0}$ and (with $\mathbb{1}$ the (4×4) -identity matrix)

$$(B * \Gamma)_{x, y}^{(n)} = \sum_{w, z \in \mathbb{T}} B_{w-x, z-y}^{(n)} \Gamma_{w, z}, \quad (3.17)$$

$$B_{w-x, z-y}^{(n)} = \sum_{w', z' \in \mathbb{T}} B_{w'-x, z'-y}^{(n-1)} B_{w-w', z-z'}, \quad (3.18)$$

$$B_{w-x, z-y}^{(0)} = \mathbb{1} \delta_{x, w} \delta_{y, z}, \quad (3.19)$$

$$\Gamma_{w, z} = (1 - \mu)^2 (1 - \epsilon)^2 \begin{pmatrix} 0 \\ 0 \\ 0 \\ p^2(w, z) \end{pmatrix}. \quad (3.20)$$

Proof. The claim follows by repeatedly substituting $\Psi_{w,z}$ into (3.5). Indeed,

$$\begin{aligned}
\Psi_{x,y} &= \Phi_{x,y} + A_{x,y}\Psi_{0,0} + \sum_{w,z \in \mathbb{T}} B_{w-x,z-y}\Psi_{w,z} \\
&= \Phi_{x,y} + D_{x,y}\Psi_{0,0} + \sum_{w,z \in \mathbb{T}} B_{w-x,z-y} \left(\Phi_{w,z} + A_{w,z}\Psi_{0,0} + \sum_{w',z' \in \mathbb{T}} B_{w'-z,z'-z}\Psi_{w',z'} \right) \\
&= \left(\mathbf{1}\delta_{xw}\delta_{yz} + \sum_{w,z \in \mathbb{T}} B_{w-x,z-y} \right) \Phi_{w,z} + \left(\mathbf{1}\delta_{xw}\delta_{yz} + \sum_{w,z \in \mathbb{T}} B_{w-x,z-y} \right) A_{w,z}\Psi_{0,0} \\
&\quad + \sum_{w,z \in \mathbb{T}} \sum_{w',z' \in \mathbb{T}} B_{w-x,z-y} B_{w'-z,z'-z} \Psi_{w',z'} \\
&= \sum_{k=0}^1 \sum_{w,z \in \mathbb{T}} B_{w-x,z-y}^{(k)} (\Phi_{w,z} + A_{w,z}\Psi_{0,0}) \\
&\quad + \sum_{w'',z'' \in \mathbb{T}} B_{w''-x,z''-y}^{(2)} \Psi_{w'',z''}, \tag{3.21}
\end{aligned}$$

where $B_{w-x,z-y}^{(0)}$ is defined by (3.19) and $B_{w-x,z-y}^{(n)}$ is defined recursively as in (3.18). After n substitutions we obtain

$$\Psi_{x,y} = \sum_{k=0}^n \sum_{w,z \in \mathbb{T}} B_{w-x,z-y}^{(k)} (\Phi_{w,z} + A_{w,z}\Psi_{0,0}) + \sum_{w'',z'' \in \mathbb{T}} B_{w''-x,z''-y}^{(n+1)} \Psi_{w'',z''}. \tag{3.22}$$

Letting $n \rightarrow \infty$ and noting that $\lim_{n \rightarrow \infty} B_{w-x,z-y}^{(n)} = 0$ (each term is finite and is multiplied by $(1-\mu)^{2n}$ with $0 < \mu < 1$), we see that the summand in the second line of the last equality tends to 0. We therefore obtain

$$\Psi_{x,y} = \sum_{k \in \mathbb{N}_0} \sum_{w,z \in \mathbb{T}} B_{w-x,z-y}^{(k)} (\Phi_{w,z} + A_{w,z}\Psi_{0,0}). \tag{3.23}$$

We can rewrite

$$\Phi_{w,z} + A_{w,z}\Psi_{0,0} = (1-\mu)^2(1-\epsilon)^2 \begin{pmatrix} 0 \\ 0 \\ 0 \\ \frac{1-\Psi_{0,0}^{(4)}}{N} p^2(w,z) \end{pmatrix} = \frac{1-\Psi_{0,0}^{(4)}}{N} \Gamma_{w,z} \tag{3.24}$$

with $\Gamma_{w,z}$ given by (3.20), and the claim follows. \square

Taking $x = y = 0$ in (3.23), we get

$$\Psi_{0,0} = \left(\mathbf{1} - \sum_{n \in \mathbb{N}_0} (B * A)_{0,0}^{(n)} \right)^{-1} \left(\sum_{n \in \mathbb{N}_0} (B * \Phi)_{0,0}^{(n)} \right). \tag{3.25}$$

This can be substituted into (3.16) to obtain an explicit expression for $\Psi_{x,y}$. Since this expression contains convolutions, we turn to Fourier analysis to gain more insight into the properties of $\Psi_{x,y}$.

3.4. Fourier analysis

Let $\hat{\mathbb{T}} = \{0, \frac{1}{L}, \dots, \frac{L-1}{L}\}^d$. Define for $f: \mathbb{T} \times \mathbb{T} \mapsto \mathbb{R}$, $x, y \in \mathbb{T}$ and $\theta, \eta \in \hat{\mathbb{T}}$,

$$\hat{f}(\theta, \eta) = \sum_{x, y \in \mathbb{T}} f_{x, y} e^{2\pi i(x \cdot \theta + y \cdot \eta)}, \quad (3.26)$$

$$f_{x, y} = \frac{1}{|\hat{\mathbb{T}}|^2} \sum_{\theta, \eta \in \hat{\mathbb{T}}} \hat{f}(\theta, \eta) e^{-2\pi i(x \cdot \theta + y \cdot \eta)}. \quad (3.27)$$

Proposition 3.3. For $\theta, \eta \in \hat{\mathbb{T}}$,

$$\hat{\Psi}(\theta, \eta) = \frac{1 - \Psi_{0,0}^{(4)}}{N} (\mathbf{1} - \hat{B}(\theta, \eta))^{-1} \hat{\Gamma}(\theta, \eta). \quad (3.28)$$

Proof. By the linearity of the Fourier transform and the convolution theorem, we get from (3.16) that

$$\hat{\Psi}(\theta, \eta) = \frac{1 - \Psi_{0,0}^{(4)}}{N} \sum_{n \in \mathbb{N}_0} \hat{B}^{(n)}(\theta, \eta) \hat{\Gamma}(\theta, \eta). \quad (3.29)$$

Since $B_{x-w, y-z}^{(n)}$ is defined by the recursion in (3.18), we have

$$\hat{B}^{(n)}(\theta, \eta) = \hat{B}^{(n-1)}(\theta, \eta) \hat{B}(\theta, \eta) = (\hat{B}(\theta, \eta))^n, \quad (3.30)$$

and therefore

$$\sum_{n \in \mathbb{N}_0} \hat{B}^{(n)}(\theta, \eta) \hat{\Gamma}(\theta, \eta) = \sum_{n \in \mathbb{N}_0} (\hat{B}(\theta, \eta))^n \hat{\Gamma}(\theta, \eta) = (\mathbf{1} - \hat{B}(\theta, \eta))^{-1} \hat{\Gamma}(\theta, \eta). \quad (3.31)$$

The claim follows after substitution of (3.31) into (3.29). \square

Our next objective is to compute the right-hand side of (3.28). We obtain

$$\hat{B}(\theta, \eta) = \sum_{u, v \in \mathbb{T}} B_{u, v} e^{2\pi i(\theta \cdot u + \eta \cdot v)} = \sum_{u, v \in \mathbb{T}} (C \delta_{u,0} \delta_{v,0} + D_{u, v}) e^{2\pi i(\theta \cdot u + \eta \cdot v)} = C + \hat{D}(\theta, \eta), \quad (3.32)$$

where C is given in (3.9) and

$$\hat{D}(\theta, \eta) = (1 - \mu)^2 (1 - \epsilon) \begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & (1 - \delta) \hat{p}(\eta) & 0 & \epsilon \hat{p}(\eta) \\ 0 & 0 & (1 - \delta) \hat{p}(\theta) & \epsilon \hat{p}(\theta) \\ 0 & \delta \hat{p}(\eta) & \delta \hat{p}(\theta) & (1 - \epsilon) \hat{p}(\theta) \hat{p}(\eta) \end{pmatrix}, \quad (3.33)$$

with

$$\hat{p}(\theta) = \sum_{z \in \mathbb{T}} p(0, z) e^{2\pi i \theta \cdot z}. \quad (3.34)$$

Computing $(\mathbf{1} - \hat{B}(\theta, \eta))^{-1}$, we find

$$(\mathbf{1} - \hat{B}(\theta, \eta))^{-1} = \frac{1}{r_0(\theta, \eta)} \begin{pmatrix} r_{1,1}(\theta, \eta) & r_{1,2}(\theta, \eta) & r_{1,3}(\theta, \eta) & r_{1,4}(\theta, \eta) \\ r_{2,1}(\theta, \eta) & r_{2,2}(\theta, \eta) & r_{2,3}(\theta, \eta) & r_{2,4}(\theta, \eta) \\ r_{3,1}(\theta, \eta) & r_{3,2}(\theta, \eta) & r_{3,3}(\theta, \eta) & r_{3,4}(\theta, \eta) \\ r_{4,1}(\theta, \eta) & r_{4,2}(\theta, \eta) & r_{4,3}(\theta, \eta) & r_{4,4}(\theta, \eta) \end{pmatrix}, \quad (3.35)$$

where the 17 functions in the above expression are polynomials of degree ≤ 4 in $\hat{p}(\theta)$ and $\hat{p}(\eta)$ whose coefficients depend on the parameters δ, ϵ . Since $(\mathbf{1} - \hat{B}(\theta, \eta))^{-1}$ pre-multiplies $\hat{\Gamma}(\theta, \eta)$, whose first three

entries are 0, we only need the entries in the fourth column. These are given by the following, where we abbreviate $m = (1 - \mu)^2$:

$$\begin{aligned}
r_0(\theta, \eta) &= (1 - m^2 \delta^2 \epsilon^2) \left(1 - m \left(1 - \delta(2 - 2\epsilon - \delta(1 - m\epsilon^2)) \right) \right) \\
&\quad - m^2 (1 - \epsilon)^2 \hat{p}(\eta)^2 (\delta\epsilon - (1 - \delta)(1 - \epsilon)\hat{p}(\theta)) \\
&\quad \times \left(1 - m(1 - \delta(2 - \delta - \epsilon)) - m(1 - m(1 - \delta)^2)(1 - \delta)(1 - \epsilon)\hat{p}(\theta) \right) \\
&\quad - m(1 - \epsilon)(1 - \delta) \left(1 - m \left(1 - \delta(2 - \epsilon + \delta(1 - m\epsilon^2(1 - m\delta\epsilon))) \right) \right) (\hat{p}(\eta) + \hat{p}(\theta)) \\
&\quad + m^2 \delta\epsilon(1 - \epsilon)^2 (1 - m(1 - \delta(2 - \delta - \epsilon))) \hat{p}(\theta)^2 \\
&\quad - m(1 - \epsilon)^2 \hat{p}(\eta) \hat{p}(\theta) \left((1 - m(1 - \delta)^2)^2 - 2m\delta\epsilon + m^2 \delta^2 \epsilon^2 \right. \\
&\quad \left. - m(1 - \delta)(1 - \epsilon)(1 - m(1 - \delta)^2(1 + m\delta\epsilon)) \hat{p}(\theta) \right)
\end{aligned} \tag{3.36}$$

and

$$\begin{aligned}
r_{1,4}(\theta, \eta) &= m\epsilon^2 \left((1 - m\delta\epsilon)^2 - m^2(1 - \delta)^2(1 - \epsilon)^2 \hat{p}(\theta) \hat{p}(\eta) \right), \\
r_{2,4}(\theta, \eta) &= m\epsilon \left(m\delta\epsilon(1 - \delta)(1 - m\delta\epsilon) + (1 - \epsilon)\hat{p}(\eta) \left(1 - m(1 - \delta(2 - \delta - \epsilon)) \right. \right. \\
&\quad \left. \left. - m(1 - m(1 - \delta)^2)(1 - \delta)(1 - \epsilon)\hat{p}(\theta) \right) \right), \\
r_{3,4}(\theta, \eta) &= m\epsilon \left(m\delta\epsilon(1 - \delta)(1 - m\delta\epsilon) + (1 - \epsilon)\hat{p}(\theta) \left(1 - m(1 - \delta(2 - \delta - \epsilon)) \right. \right. \\
&\quad \left. \left. - m(1 - m(1 - \delta)^2)(1 - \delta)(1 - \epsilon)\hat{p}(\eta) \right) \right), \\
r_{4,4}(\theta, \eta) &= -m^2 \delta\epsilon(1 - \delta)^2 (1 - m\delta\epsilon - (1 - \delta)(1 - \epsilon)\hat{p}(\eta)) \\
&\quad + \left(1 - m(1 - \delta(2 - \delta - \epsilon)) - m(1 - m(1 - \delta)^2)(1 - \delta)(1 - \epsilon)\hat{p}(\eta) \right) \\
&\quad \times \left(1 - m\delta\epsilon - m(1 - \delta)(1 - \epsilon)\hat{p}(\theta) \right).
\end{aligned} \tag{3.37}$$

Looking at $\hat{\Gamma}(\theta, \eta)$, we have

$$\begin{aligned}
\hat{\Gamma}(\theta, \eta) &= (1 - \mu)^2 \sum_{w, z \in \mathbb{T}} \Gamma_{w, z} e^{2\pi i(\theta \cdot w + \eta \cdot z)} \\
&= (1 - \mu)^2 \sum_{w, z \in \mathbb{T}} \begin{pmatrix} 0 \\ 0 \\ 0 \\ (1 - \epsilon)^2 \frac{1}{N} p^2(w, z) \end{pmatrix} e^{2\pi i(\theta \cdot w + \eta \cdot z)} \\
&= \frac{1}{N} (1 - \mu)^2 (1 - \epsilon)^2 \begin{pmatrix} 0 \\ 0 \\ 0 \\ \hat{p}(\theta) \hat{p}(\eta) \end{pmatrix} \delta_{\theta, -\eta}.
\end{aligned} \tag{3.38}$$

Therefore we get

$$(\mathbf{1} - \hat{B}(\theta, \eta))^{-1} \hat{\Gamma}(\theta, \eta) = \frac{(1 - \mu)^2 (1 - \epsilon)^2}{N} \frac{1}{r_0(\theta, \eta)} \begin{pmatrix} r_{1,4}(\theta, \eta) \\ r_{2,4}(\theta, \eta) \\ r_{3,4}(\theta, \eta) \\ r_{4,4}(\theta, \eta) \end{pmatrix} \hat{p}(\theta) \hat{p}(\eta) \delta_{\theta, -\eta}, \tag{3.39}$$

Note that, because of the multiplicative factor $\delta_{\theta, -\eta}$, $\hat{\Psi}(\theta, \eta)$ in (3.28) actually depends on θ only. This is in agreement with the fact that $\Psi_{x, y}$ actually depends on $x - y$ only. Henceforth we write

$\hat{\Psi}(\theta, -\theta) = \hat{\Psi}(\theta)$, and similarly for the other symbols.

At this point, all the terms in (3.28) are known objects, except for $\Psi_{0,0}$. In order to compute $\Psi_{0,0}$, we take the Fourier transform of (3.23) to obtain

$$\hat{\Psi}(\theta) = (\mathbf{1} - \hat{B}(\theta))^{-1}(\hat{\Phi}(\theta) + \hat{A}(\theta)\Psi_{0,0}). \quad (3.40)$$

We then use the Fourier inversion formula (3.27), which gives

$$\frac{1}{|\hat{\mathbb{T}}|} \sum_{\theta \in \hat{\mathbb{T}}} \hat{\Psi}(\theta) = \Psi_{0,0}. \quad (3.41)$$

Substitution of (3.40) therefore yields

$$\Psi_{0,0} = \left(\mathbf{1} - \frac{1}{|\hat{\mathbb{T}}|} \sum_{\theta \in \hat{\mathbb{T}}} (\mathbf{1} - \hat{B}(\theta))^{-1} \hat{A}(\theta) \right)^{-1} \left(\frac{1}{|\hat{\mathbb{T}}|} \sum_{\theta \in \hat{\mathbb{T}}} (\mathbf{1} - \hat{B}(\theta))^{-1} \hat{\Phi}(\theta) \right). \quad (3.42)$$

With (3.39) and (3.42) we have obtained an explicit expression for $\hat{\Psi}(\theta)$ in (3.28), which we summarise in a theorem. Abbreviate

$$K = \frac{(1 - \mu)^2(1 - \epsilon)^2}{N}, \quad (3.43)$$

let

$$s_{i,4}(\theta) = K \hat{p}(\theta)^2 \frac{r_{i,4}(\theta)}{r_0(\theta)}, \quad i = 1, 2, 3, 4, \quad (3.44)$$

where $r_0(\theta)$ and $r_{i,4}(\theta) = r_{i,4}(\theta)$, $i = 1, 2, 3, 4$, are defined in (3.36) and (3.37), and let

$$s_{i,4} = \frac{1}{|\hat{\mathbb{T}}|} \sum_{\theta \in \hat{\mathbb{T}}} s_{i,4}(\theta), \quad i = 1, 2, 3, 4. \quad (3.45)$$

.

Theorem 3.4. For every $\theta \in \hat{\mathbb{T}}$,

$$\hat{\Psi}(\theta) = \sum_{x \in \mathbb{T}} \Psi_{0,x} e^{2\pi i(x \cdot \theta)} = \frac{1 - \Psi_{0,0}^{(4)}}{N} \begin{pmatrix} s_{1,4}(\theta) \\ s_{2,4}(\theta) \\ s_{3,4}(\theta) \\ s_{4,4}(\theta) \end{pmatrix} \quad (3.46)$$

with

$$\Psi_{0,0}^{(4)} = \frac{s_{4,4}}{1 - s_{4,4}}. \quad (3.47)$$

Proof. The vector $\hat{\Phi}(\theta)$ and the matrix $\hat{A}(\theta)$ are simple, namely, (3.6) and (3.7) give

$$\hat{\Phi}(\theta) = K \hat{p}(\theta)^2 \begin{pmatrix} 0 \\ 0 \\ 0 \\ 1 \end{pmatrix}, \quad \hat{A}(\theta) = -K \hat{p}(\theta)^2 \begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 \end{pmatrix}. \quad (3.48)$$

Hence (3.35) gives (3.46) with

$$\Psi_{0,0} = \left(\mathbf{1} - \begin{pmatrix} 0 & 0 & 0 & s_{1,4} \\ 0 & 0 & 0 & s_{2,4} \\ 0 & 0 & 0 & s_{3,4} \\ 0 & 0 & 0 & s_{4,4} \end{pmatrix} \right)^{-1} \begin{pmatrix} s_{1,4} \\ s_{2,4} \\ s_{3,4} \\ s_{4,4} \end{pmatrix} = \left(\mathbf{1} + \frac{1}{1 - s_{4,4}} \begin{pmatrix} 0 & 0 & 0 & s_{1,4} \\ 0 & 0 & 0 & s_{2,4} \\ 0 & 0 & 0 & s_{3,4} \\ 0 & 0 & 0 & s_{4,4} \end{pmatrix} \right) \begin{pmatrix} s_{1,4} \\ s_{2,4} \\ s_{3,4} \\ s_{4,4} \end{pmatrix}. \quad (3.49)$$

The latter in turn yields (3.47). \square

The formula in (3.46) is difficult to analyse. The θ -dependence sits in the quotients of $r_{i,4}(\theta)$, $i = 1, 2, 3, 4$, and $r_0(\theta)$. These are second-degree and fourth-degree polynomials in $\hat{p}(\theta)$, respectively, with coefficients that depend on the parameters δ , ϵ and μ . In order to find $\Psi_{0,x}$ we need to Fourier invert the 4-vector in the right-hand side of (3.46).

Remark 3.5. The result in Theorem 3.4 is *general*. Our colonies form a discrete torus \mathbb{T} , but we could arrange them on any regular lattice, since only translation invariance and periodicity are needed. The formulas are also valid for a generic random walk transition kernel $p(x, y)$, $x, y \in \mathbb{T}$, beyond the special case considered in (3.1)–(3.2). Moreover, if we would have had $K \in \mathbb{N}$ seed-banks instead of one, then we would have to work with $(K+1)^2 \times (K+1)^2$ matrices rather than 4×4 matrices, but the structure would be the same.

4. Special choice of parameters

In Section 4.1 we look at the special case $M = N$, for which $\delta = \epsilon \frac{M}{N} = \epsilon$, and that $0 < \delta \ll 1$. We refer to this case as the *symmetric slow seed-bank* (see Fig. 3). This choice will allow us to simplify the polynomials $r_{i,4}(\theta)$, $i = 1, 2, 3, 4$, and $r_0(\theta)$ appearing in (3.44), and deduce from Theorem 3.4 a more manageable formula for $\Psi_{0,x}$, $x \in \mathbb{T}$, stated in Theorems 4.1 and 4.3, in terms of the Green function associated with the random walk q in (3.1). In Section 4.2 we recall what is known for this Green function, both on the infinite torus and the finite torus. In Section 4.3 we use this information to obtain explicit scaling expressions when $0 < \mu/\nu \ll 1$ (= slower mutation than migration). In Sections 4.4–4.5 we use these expressions to discuss various regimes for $\Psi_{0,x}$, $x \in \mathbb{T}$, as a function of N , L and μ/ν , stated in Theorems 4.4–4.7.

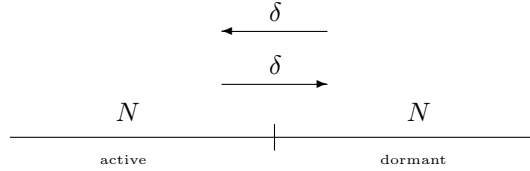


Figure 3: Symmetric slow seed-bank: equal size N for the active and the dormant population, with equal and small crossover rate $0 < \delta \ll 1$ in both directions.

4.1. Symmetric slow seed-bank

Let

$$\hat{\alpha}(\theta) = \frac{m\hat{p}(\theta)^2}{1 - m\hat{p}(\theta)^2}, \quad \hat{\beta}(\theta) = \frac{m^2\hat{p}(\theta)^3}{(1 - m\hat{p}(\theta))(1 - m\hat{p}(\theta)^2)}, \quad \hat{\gamma}(\theta) = \frac{m\hat{p}(\theta)^2}{(1 - m\hat{p}(\theta)^2)^2}, \quad (4.1)$$

and

$$\alpha(x) = \frac{1}{|\hat{\mathbb{T}}|} \sum_{\theta \in \hat{\mathbb{T}}} \hat{\alpha}(\theta) e^{-2\pi i(\theta \cdot x)}, \quad \beta(x) = \frac{1}{|\hat{\mathbb{T}}|} \sum_{\theta \in \hat{\mathbb{T}}} \hat{\beta}(\theta) e^{-2\pi i(\theta \cdot x)}, \quad \gamma(x) = \frac{1}{|\hat{\mathbb{T}}|} \sum_{\theta \in \hat{\mathbb{T}}} \hat{\gamma}(\theta) e^{-2\pi i(\theta \cdot x)}. \quad (4.2)$$

Theorem 4.1. For every $x \in \mathbb{T}$, $M = N$, $\epsilon = \delta$, $\mu \in [0, 1)$ and $\nu \in [0, 1]$, as $\delta \downarrow 0$,

$$\Psi_{0,x} = c_N \left[\begin{pmatrix} 0 \\ 0 \\ 0 \\ \alpha(x) \end{pmatrix} + \delta \begin{pmatrix} 0 \\ \beta(x) \\ \beta(x) \\ 2c_N\alpha(x)\gamma(0) - 2\gamma(x) \end{pmatrix} \right] + O(\delta^2), \quad (4.3)$$

where

$$c_N = \frac{1}{N + \alpha(0)}. \quad (4.4)$$

In particular,

$$\frac{1 - \Psi_{0,0}^{(4)}}{N} = c_N \left[1 + \delta \frac{2\alpha(0)\gamma(0)}{N} + O(\delta^2) \right]. \quad (4.5)$$

Proof. Taylor expand in δ the expressions in (3.46) and (3.47), and take the inverse Fourier transform. \square

Remark 4.2. The first vector in the right-hand side (4.3) must have all entries in $[0, 1]$ because $\Psi_{0,x}$ is a probability. However, the second vector may in principle take values in \mathbb{R} because the seed-bank has a tendency to increase *and* decrease $\Psi_{0,x}$. Indeed, while in the seed-bank, individuals are dormant and continue to mutate, yet at the same time are more easily traced by other individuals. Thus, there are two competing effects, exemplified by the different signs in the fourth entry of the second vector.

We next compute $\alpha(x)$, $\beta(x)$, $\gamma(x)$ for the uniform nearest-neighbour model in (3.2). For $x \in \mathbb{T}$ and $l \in \mathbb{N}_0$, let $q_l(x)$ be the probability that simple random walk starting from the origin is at site x at time l . The Green function of simple random walk at site x is

$$G_x(z) = \sum_{l \in \mathbb{N}_0} q_l(x) z^l, \quad |z| \leq 1. \quad (4.6)$$

Theorem 4.3. For q as in (3.2),

$$\begin{aligned} \alpha(x) &= \frac{1}{2(1-b)} G_x\left(\frac{a}{1-b}\right) + \frac{1}{2(1+b)} G_x\left(-\frac{a}{1+b}\right) - \delta_{0,x}, \\ \beta(x) &= \frac{1-\mu}{2\mu} \frac{1}{1-b} G_x\left(\frac{a}{1-b}\right) - \frac{1-\mu}{2(2-\mu)} \frac{1}{1+b} G_x\left(-\frac{a}{1+b}\right) \\ &\quad - \frac{1}{1-(1-\mu)^2} \frac{1}{1-(1-\mu)b} G_x\left(\frac{(1-\mu)a}{1-(1-\mu)b}\right) + \delta_{0,x}, \\ \gamma(x) &= \frac{b}{4(1-b)^2} G_x\left(\frac{a}{1-b}\right) + \frac{a}{4(1-b)^3} G'_x\left(\frac{a}{1-b}\right) \\ &\quad - \frac{b}{4(1+b)^2} G_x\left(-\frac{a}{1+b}\right) - \frac{a}{4(1+b)^3} G'_x\left(-\frac{a}{1+b}\right) \end{aligned} \quad (4.7)$$

with $a = (1-\mu)\nu$, $b = (1-\mu)(1-\nu)$ and G'_x the derivative of G_x .

Proof. From (3.1) we have $\hat{p}(\theta) = (1 - \nu) + \nu\hat{q}(\theta)$. Substituting this into the first sum in (4.2), we get

$$\begin{aligned}
\delta_{0,x} + \alpha(x) &= \sum_{k \in \mathbb{N}_0} m^k \frac{1}{|\hat{\mathbb{T}}|} \sum_{\theta \in \hat{\mathbb{T}}} \hat{p}(\theta)^{2k} e^{-2\pi i(\theta \cdot x)} \\
&= \sum_{k \in \mathbb{N}_0} m^k \sum_{l=0}^{2k} \binom{2k}{l} (1 - \nu)^{2k-l} \nu^l \frac{1}{|\hat{\mathbb{T}}|} \sum_{\theta \in \hat{\mathbb{T}}} \hat{q}(\theta)^l e^{-2\pi i(\theta \cdot x)} \\
&= \sum_{k \in \mathbb{N}_0} m^k \sum_{l=0}^{2k} \binom{2k}{l} (1 - \nu)^{2k-l} \nu^l q_l(x) \\
&= \sum_{l \in \mathbb{N}_0} q_l(x) a^l \sum_{k=\lceil l/2 \rceil}^{\infty} \binom{2k}{l} b^{2k-l} \\
&= \sum_{l \in \mathbb{N}_0} q_l(x) a^l \sum_{k'=l}^{\infty} \binom{k'}{l} b^{k'-l} \frac{1}{2} [(+1)^{k'} + (-1)^{k'}] \\
&= \sum_{l \in \mathbb{N}_0} q_l(x) a^l \frac{1}{2} [(+1)^l (1-b)^{-l-1} + (-1)^l (1+b)^{-l-1}] \\
&= \frac{1}{2(1-b)} G_x \left(\frac{a}{1-b} \right) + \frac{1}{2(1+b)} G_x \left(-\frac{a}{1+b} \right),
\end{aligned} \tag{4.8}$$

which gives the formula for $\alpha(x)$. Next, define

$$\hat{\delta}(\theta) = \frac{m\hat{p}(\theta)}{1 - m\hat{p}(\theta)} \tag{4.9}$$

and write the second term in (4.1) as $\hat{\beta}(\theta) = \hat{\alpha}(\theta)\hat{\delta}(\theta)$. Then the second sum in (4.2) becomes

$$\beta(x) = \sum_{y \in \mathbb{T}} \alpha(x-y)\delta(y). \tag{4.10}$$

A computation similar to (4.8) yields

$$\begin{aligned}
\delta_{0,x} + \delta(x) &= \sum_{k \in \mathbb{N}_0} m^k \frac{1}{|\hat{\mathbb{T}}|} \sum_{\theta \in \hat{\mathbb{T}}} \hat{p}(\theta)^k e^{-2\pi i(\theta \cdot x)} \\
&= \sum_{k \in \mathbb{N}_0} m^k \sum_{l=0}^k \binom{k}{l} (1 - \nu)^{k-l} \nu^l \frac{1}{|\hat{\mathbb{T}}|} \sum_{\theta \in \hat{\mathbb{T}}} \hat{q}(\theta)^l e^{-2\pi i(\theta \cdot x)} \\
&= \sum_{k \in \mathbb{N}_0} m^k \sum_{l=0}^k \binom{k}{l} (1 - \nu)^{k-l} \nu^l q_l(x) \\
&= \sum_{l \in \mathbb{N}_0} q_l(x) a^l \sum_{k=l}^{\infty} \binom{k}{l} b^{k-l} \\
&= \sum_{l \in \mathbb{N}_0} q_l(x) a^l (1-b')^{-l-1} \\
&= \frac{1}{1-b'} G_x \left(\frac{a'}{1-b'} \right)
\end{aligned} \tag{4.11}$$

with $a' = (1 - \mu)^2 \nu = (1 - \mu)a$ and $b' = (1 - \mu)^2 (1 - \nu) = (1 - \mu)b$. Moreover, for any $|z|, |z'| \leq 1$ with

$z \neq z'$ we have the identities

$$\begin{aligned}
\sum_{x \in \mathbb{T}} G_x(z) &= \sum_{l \in \mathbb{N}_0} \sum_{x \in \mathbb{T}} z^l q_l(x) = \sum_{l \in \mathbb{N}_0} z^l = (1-z)^{-1}, \\
\sum_{y \in \mathbb{T}} G_{x-y}(z) G_y(z') &= \sum_{l, l' \in \mathbb{N}_0} z^l z'^{l'} \sum_{y \in \mathbb{T}} q_l(x-y) q_{l'}(y) = \sum_{l, l' \in \mathbb{N}_0} z^l z'^{l'} q_{l+l'}(x) \\
&= \sum_{k \in \mathbb{N}_0} q_k(x) \sum_{\substack{l, l' \in \mathbb{N}_0 \\ l+l'=k}} z^l z'^{l'} = \sum_{k \in \mathbb{N}_0} q_k(x) z^k \frac{1 - (\frac{z'}{z})^{k+1}}{1 - (\frac{z'}{z})} = \frac{1}{z-z'} [z G_x(z) - z' G_x(z')].
\end{aligned} \tag{4.12}$$

Inserting (4.8) and (4.11) into (4.10) and using (4.12), we get the formula for $\beta(x)$ after a short computation. Finally, note from (4.1) that $\hat{\gamma}(\theta) = m \frac{\partial \hat{\alpha}(\theta)}{\partial m}$, $\theta \in \hat{\mathbb{T}}$. After substitution into the third sum in (4.2) this gives $\gamma(x) = m \frac{\partial \alpha(x)}{\partial m} = \frac{1}{2} (1-\mu) \frac{\partial \alpha(x)}{\partial (1-\mu)}$, $x \in \mathbb{T}$. Inserting the formula for $\alpha(x)$, we get the formula for $\gamma(x)$ after a short computation. \square

By combining Theorems 4.1 and 4.3, we obtain a formula for $\Psi_{0,x}$ (up to leading order in δ for $\delta \downarrow 0$) in terms of the Green function of simple random walk. The latter has been studied extensively in the literature. We recall the relevant formulas.

4.2. Green functions

The following properties are collected from Montroll [11], [12], Montroll and Weiss [13], Spitzer [14, Sections I.1, III.15], den Hollander and Kasteleyn [7], Hughes [8, Section 3.3, Appendix A.1], Abramowitz and Stegun [1, Items 9.6.12, 9.6.13, 9.7.2].

• *Infinite torus.* For $L = \infty$, we have $\mathbb{T} = \mathbb{Z}^d$. For $d = 1$, the Green function is known in closed form:

$$G_x(z) = y(z)^{|x|} (1-z^2)^{-1/2}, \quad x \in \mathbb{Z}, \quad 0 < |z| < 1, \tag{4.13}$$

where $y(z) = [1 - (1-z^2)^{1/2}]/z$. For $d \geq 2$ no closed form expression is available, but there are asymptotic formulas for $z \uparrow 1$. For $d = 2$,

$$G_x(z) = \frac{1}{\pi} \left[\log \left(\frac{1}{1-z} \right) - C(x) + \bar{C}(x)(1-z) \log \left(\frac{1}{1-z} \right) + O(1-z) \right], \quad x \in \mathbb{Z}^2, \tag{4.14}$$

where

$$C(0) = 0, \quad \bar{C}(0) = -\frac{1}{2}, \tag{4.15}$$

and

$$\begin{aligned}
C(x) &= \log \|x\|^2 + (2\gamma + \log 8) + O\left(\frac{1}{\|x\|^2}\right), \quad \bar{C}(x) = \|x\|^2 + O(1), \\
\|x\| \rightarrow \infty, \quad \|x\| &= \sqrt{x_1^2 + x_2^2},
\end{aligned} \tag{4.16}$$

with $\gamma = 0.57721 \dots$ Euler's constant. In particular, $C(k, k) = 4 \sum_{l=1}^{|k|} \frac{1}{2l-1}$, $k \in \mathbb{Z}$. For $d = 3$,

$$G_x(z) = C(x) - \bar{C}(x)(1-z)^{1/2} + O(1-z), \quad x \in \mathbb{Z}^3, \tag{4.17}$$

where

$$C(0) = 1.51638 \dots, \quad \bar{C}(0) = \frac{3\sqrt{3}}{\pi\sqrt{2}}, \quad \frac{C(x)}{C(0)} = \frac{\bar{C}(x)}{\bar{C}(0)}, \quad x \in \mathbb{Z}^3, \tag{4.18}$$

and

$$C(x) = \frac{3}{2\pi\|x\|} \left[1 + \frac{1}{8\|x\|^2} \left(-3 + 5 \frac{x_1^4 + x_2^4 + x_3^4}{\|x\|^4} \right) + O\left(\frac{1}{\|x\|^4}\right) \right], \quad \|x\| \rightarrow \infty. \tag{4.19}$$

For $d \geq 4$ the second term in the right-hand side of (4.17) is of higher order. For $d = 1, 2$ the Green functions show diffusive scaling:

$$\begin{aligned} d = 1: \lim_{z \uparrow 1} \sqrt{2(1-z)} G_{y/\sqrt{1-z}}(z) &= e^{-\sqrt{2}|y|}, \quad y \in \mathbb{R}, \\ d = 2: \lim_{z \uparrow 1} G_{y/\sqrt{1-z}}(z) &= \frac{2}{\pi} K_0(2\|y\|), \quad y \in \mathbb{R}^2 \setminus \{0\}, \end{aligned} \quad (4.20)$$

where K_0 is the modified Bessel function (of the third kind) of order 0. The latter satisfies $K_0(u) = [\log(2/u) - \gamma](1 + \frac{1}{4}u^2 + O(u^4)) + \frac{1}{4}u^2 + O(u^4)$, $u \downarrow 0$, and $K_0(u) = e^{-u} \sqrt{\pi/2u} [1 - \frac{8}{u} + O(u^{-2})]$, $u \rightarrow \infty$. The diffusive scaling also holds for the derivative of the Green functions.

• *Finite torus..* For $L < \infty$, the analogue of (4.13) reads

$$G_x(z) = \frac{y(z)^x + y(z)^{L-x}}{1 - y(z)^L} (1 - z^2)^{-1/2}, \quad x \in \{0, 1, \dots, L-1\}, \quad 0 < |z| < 1, \quad (4.21)$$

while the analogue of (4.14) reads

$$G_x(z) = L^{-d}(1-z)^{-1} + C_L(x) - \bar{C}_L(x)(1-z) + O((1-z)^2), \quad x \in \mathbb{T}. \quad (4.22)$$

The latter expansion also holds for $d = 1$. Namely, inserting into (4.17) the expansion

$$y(z) = 1 - [2(1-z)]^{1/2} + \frac{1}{2}[2(1-z)] - \frac{3}{8}[2(1-z)]^{3/2} + O((1-z)^2), \quad (4.23)$$

we find, after a short computation,

$$\begin{aligned} C_L(x) &= C_L(0) - \frac{x(L-x)}{L}, \\ \bar{C}_L(x) &= \bar{C}_L(0) - \frac{x(L-x)}{6L} [x(L-x)(L^2-2) - (L^2-5)], \end{aligned} \quad (4.24)$$

with

$$C_L(0) = \frac{L^2-1}{6L}, \quad \bar{C}_L(0) = \frac{(L^2-1)(L^2-19)}{180L}. \quad (4.25)$$

For $d = 2$ it is known that $C_L(0) = \frac{2}{\pi} \log L + O(1)$, $\bar{C}_L(0) = cL^2 - \frac{1}{\pi} \log L + O(1)$, $L \rightarrow \infty$, with $c = 0.06187\dots$, while for $d = 3$ it is known that $\lim_{L \rightarrow \infty} C_L(0) = C(0)$ and $\bar{C}_L(0) = cL^4[1 + o(1)]$ for some $c \in (0, \infty)$. No formulas are available for $C_L(x)$, $\bar{C}_L(x)$, $x \neq 0$, for $d \geq 2$.

4.3. Slower mutation than migration

Return to Theorem 4.3. Let

$$\rho = \mu/\nu. \quad (4.26)$$

In terms of this ratio, we have $a = \nu(1 - \nu\rho)$ and $b = (1 - \nu)(1 - \nu\rho)$. We analyse what happens in the limit as $\rho \downarrow 0$. To do so, we abbreviate

$$u = \frac{a}{1-b}, \quad v = \frac{(1-\mu)a}{1-(1-\mu)b}. \quad (4.27)$$

Substitution of (4.27) into (4.7) gives, for $\rho \downarrow 0$ uniformly in ν and x ,

$$\begin{aligned} \alpha(x) &= \frac{1}{2\nu} \left[\frac{1}{1-\nu\rho} u G_x(u) \right] + O(1), \\ \beta(x) &= \frac{1}{2\nu^2} \frac{1}{\rho} \left[u G_x(u) - \frac{1}{(1-\nu\rho)^2(1-\frac{1}{2}\nu\rho)} v G_x(v) \right] + O(1), \\ \gamma(x) &= \frac{1}{4\nu^2} \left[\frac{1-\nu}{1+(1-\nu)\rho} u G_x(u) + \frac{1}{[1+(1-\nu)\rho]^2} u G'_x(u) \right] + O(1). \end{aligned} \quad (4.28)$$

Here, the error terms $O(1)$ are valid as long as ν remains bounded away from 1 (to make sure that the singularity of $G_x(z)$ at $z = -1$ does not contribute via the term with $z = -a/(1+b)$). For $\nu \downarrow 0$ these error terms can be refined to, respectively,

$$-\frac{3}{4}\delta_{0,x} + O(\nu), \quad -\frac{1}{16}\delta_{0,x} + O(\nu), \quad \frac{7}{8}\delta_{0,x} + O(\nu). \quad (4.29)$$

To investigate the leading order terms in (4.28), we expand

$$\begin{aligned} u &= 1 - \rho + (1 - \nu)\rho^2 - (1 - \nu)^2\rho^3 + O(\rho^4), \\ v &= 1 - 2\rho + (4 - 3\nu)\rho^2 - 4(1 - \nu)(2 - \nu)\rho^3 + O(\rho^4). \end{aligned} \quad (4.30)$$

In what follows we derive *expansions in ρ for fixed ν* and keep track of how the coefficients in these expansions depend on ν . The various expansions given below are *pushed to the lowest order in ρ for which the x -dependence becomes visible* via the functions $C(x), \bar{C}(x)$ and $C_L(x), \bar{C}_L(x)$ in the Green function formulas in Section 4.2. The result is a list of formulas for $\alpha(x), \beta(x), \gamma(x)$ that are technical, but we will see in Section 4.4 that the latter lead to *simple explicit scaling expressions* in various interesting limiting regimes.

• *Infinite torus..* For $d = 1$, (4.13) and (4.28)–(4.30) give, for $\rho \downarrow 0$ uniformly in ν and x ,

$$\begin{aligned} \alpha(x) &= \frac{1}{2\nu} \frac{1 + O(\rho)}{\sqrt{2\rho}} e^{(-\sqrt{2\rho} + O(\rho))|x|} + O(1), \\ \beta(x) &= \frac{1}{2\nu^2} \frac{1}{\rho} \left[\frac{1 + O(\rho)}{\sqrt{2\rho}} e^{(-\sqrt{2\rho} + O(\rho))|x|} - \frac{1 + O(\rho)}{\sqrt{4\rho}} e^{(-\sqrt{4\rho} + O(\rho))|x|} \right] + O(1), \\ \gamma(x) &= \frac{1}{4\nu^2} \left(\frac{1}{2\rho} + \frac{|x|}{\sqrt{2\rho}} \right) \frac{1 + O(\rho)}{\sqrt{2\rho}} e^{(-\sqrt{2\rho} + O(\rho))|x|} + O(1), \end{aligned} \quad (4.31)$$

where in the last line we use that $G'_x(z) = [\frac{z}{1-z} + |x|\frac{y'(z)}{y(z)}]G_x(z)$ with $\frac{y'(z)}{y(z)} = \frac{1}{z}G_0(z)$. The scaling in (4.31) gives us control over the dependence on x , uniformly in $|x| = O(1/\sqrt{\rho})$. Similarly, for $d = 2$, (4.14) and (4.28)–(4.30) give, for $\rho \downarrow 0$ uniformly in ν and x ,

$$\begin{aligned} \alpha(x) &= \frac{1}{2\pi\nu} \left[\log\left(\frac{1}{\rho}\right) - C(x) + [(1 - \nu) + \bar{C}(x)]\rho \log\left(\frac{1}{\rho}\right) + O(\rho) \right] + O(1), \\ \beta(x) &= \frac{1}{2\pi\nu^2} \left[\frac{\log 2}{\rho} - [(1 - \frac{5}{2}\nu) - \bar{C}(x)] \log\left(\frac{1}{\rho}\right) - (1 - \frac{5}{2}\nu)C(x) \right. \\ &\quad \left. - [(2 - \frac{5}{2}\nu) + 2\bar{C}(x)] \log 2 + O\left(\rho \log\left(\frac{1}{\rho}\right)\right) \right] + O(1), \\ \gamma(x) &= \frac{1}{4\pi\nu^2} \left[\frac{1}{\rho} + [(1 - \nu) - \bar{C}(x)] \log\left(\frac{1}{\rho}\right) - [(3 - 2\nu) + (1 - \nu)C(x) - \bar{C}(x)] \right. \\ &\quad \left. + O\left(\rho \log\left(\frac{1}{\rho}\right)\right) \right] + O(1). \end{aligned} \quad (4.32)$$

The scaling in (4.32) gives us control over the dependence on x , uniformly in $\|x\| = o(1/\sqrt{\rho})$ (recall (4.16)). In order to make sure that the error terms $O(1)$ are negligible compared to the terms containing $C(x)$ and $\bar{C}(x)$, we need to let $\nu \downarrow 0$ afterwards. For $d = 3$, (4.17) and (4.28)–(4.30) give, for $\rho \downarrow 0$

uniformly in ν and x ,

$$\begin{aligned}\alpha(x) &= \frac{1}{2\nu} \left[C(x) - \bar{C}(x)\sqrt{\rho} + O(\rho) \right] + O(1), \\ \beta(x) &= \frac{1}{2\nu^2} \left[\frac{(\sqrt{2}-1)\bar{C}(x)}{\sqrt{\rho}} + (1 - \frac{5}{2}\nu)C(x) + O(\sqrt{\rho}) \right] + O(1), \\ \gamma(x) &= \frac{1}{4\nu^2} \left[\frac{\bar{C}(x)}{2\sqrt{\rho}} + (1 - \nu)C(x) + O(\sqrt{\rho}) \right] + O(1).\end{aligned}\tag{4.33}$$

The scaling in (4.33) gives us control over the dependence on x uniformly in $\|x\| = O(1)$ (recall (4.19)), provided we let $\nu \downarrow 0$ afterwards.

• *Finite torus.* For $d \geq 1$, (4.21) and (4.28) combine to give, for $\rho \downarrow 0$ uniformly in ν and x ,

$$\begin{aligned}\alpha(x) &= \frac{1}{2\nu} \left[\frac{1}{L^d \rho} + C_L(x) - \frac{1-\nu}{L^d} + \left\{ \frac{\nu(1-\nu)}{L^d} - (1-\nu)C_L(x) - \bar{C}_L(x) \right\} \rho + O(\rho^2) \right] + O(1), \\ \beta(x) &= \frac{1}{2\nu^2} \left[\frac{1}{2L^d \rho^2} - \frac{5\nu}{4L^d \rho} + \left\{ \frac{\nu(20-17\nu)}{8L^d} + (1 - \frac{5}{2}\nu)C_L(x) + \bar{C}_L(x) \right\} + O(\rho) \right] + O(1), \\ \gamma(x) &= \frac{1}{4\nu^2} \left[\frac{1}{L^d \rho^2} + \frac{2-\nu}{L^d \rho} + \left\{ \frac{(2\nu-3)(\nu-1)}{L^d} + (1-\nu)C_L(x) + \bar{C}_L(x) \right\} + O(\rho) \right] + O(1).\end{aligned}\tag{4.34}$$

Again these formulas give us sharp control over the dependence on x , provided we let $\nu \downarrow 0$ afterwards.

In Sections 4.4–4.5 we use the above expansions to compute $\Psi_{0,x}$, $x \in \mathbb{T}$, in the limit as $\delta, \rho, \nu \downarrow 0$ (in that order). Again, we derive expansions in ρ whose coefficients depend on ν , and compute these coefficients up to order $O(\nu^2)$.

4.4. Regimes: no seed-bank

We first consider the case $\delta = 0$, i.e., there is no exchange between the active population and the seed-bank. Theorem 4.1 gives

$$\Psi_{0,x}^{(1)} = \Psi_{0,x}^{(2)} = \Psi_{0,x}^{(3)} = 0, \quad \Psi_{0,x}^{(4)} = \frac{\alpha(x)}{N + \alpha(0)}.\tag{4.35}$$

Indeed, if at least one of the two individuals is in the seed-bank, then there cannot be coalescence of their lineages, while if both individuals are active, then they remain active at all times and behave exactly like in the standard Wright-Fisher model. By inserting the expansions of $\alpha(x)$ found in (4.31)–(4.33) and (4.34), we obtain the following.

Theorem 4.4. *For $\delta = 0$, in the limit as $\rho, \nu \downarrow 0$ (in that order):*

(1) For $L = \infty$,

$$\begin{aligned}d = 1: \quad \Psi_{0,x}^{(4)} &= \frac{e^{(-\sqrt{2\rho} + O(\sqrt{\rho}))|x|} - [\frac{3}{2}\delta_{0,x}\nu + O(\nu^2)]\sqrt{2\rho} + O(\rho)}{1 + [(2N - \frac{3}{2})\nu + O(\nu^2)]\sqrt{2\rho} + O(\rho)} \\ &\text{uniformly in } |x| = O(1/\sqrt{\rho}), \\ d = 2: \quad \Psi_{0,x}^{(4)} &= \frac{[\log(1/\rho) - [C(x) + \frac{3}{2}\pi\delta_{0,x}\nu + O(\nu^2)]] + [-(1-\nu) + \bar{C}(x)]\rho \log(1/\rho) + O(\rho)}{\log(1/\rho) + [\pi(2N - \frac{3}{2})\nu + O(\nu^2)] + [-(1-\nu) + \bar{C}(0)]\rho \log(1/\rho) + O(\rho)} \\ &\text{uniformly in } \|x\| = o(1/\sqrt{\rho}), \\ d = 3: \quad \Psi_{0,x}^{(4)} &= \frac{[C(x) - \frac{3}{2}\delta_{0,x}\nu + O(\nu^2)] + O(\sqrt{\rho})}{[C(0) + (2N - \frac{3}{2})\nu + O(\nu^2)] + O(\sqrt{\rho})} \\ &\text{uniformly in } \|x\| = O(1).\end{aligned}\tag{4.36}$$

(2) For $L < \infty$,

$$d \geq 1: \quad \Psi_{0,x}^{(4)} = \frac{1 + [C_L(x) - \frac{3}{2}\delta_{0,x}\nu - \frac{1-\nu}{L^d} + O(\nu^2)]L^d\rho + O(\rho^2)}{1 + [C_L(0) + (2N - \frac{3}{2})\nu - \frac{1-\nu}{L^d} + O(\nu^2)]L^d\rho + O(\rho^2)} \quad (4.37)$$

uniformly in $x \in \mathbb{T}$.

The expansions in (4.36)–(4.37) are refinements of what is known from the literature (see e.g. Durrett [5, Chapter 5]). They simplify in various limiting regimes, corresponding to $N, L \rightarrow \infty$ in combination with $\rho, \nu \downarrow 0$.

Theorem 4.5. For $\delta = 0$, in the limit as $\rho, \nu \downarrow 0$ (in that order) and $N, L \rightarrow \infty$:

(1) For $L = \infty$ (recall (4.16) and (4.19)),

$$\begin{aligned} d = 1, N\nu\sqrt{2\rho} \rightarrow r: \quad & \Psi_{0,y/\sqrt{2\rho}}^{(4)} \rightarrow \frac{e^{-|y|}}{1+2r}, \quad r \in (0, \infty), y \in \mathbb{R}, \\ d = 2, \frac{N\nu}{\log(1/\rho)} \rightarrow r: \quad & (1 - 2\chi) \log(1/\rho) \left[\Psi_{0,y/\rho^\chi}^{(4)} - \frac{1-2\chi}{1+2\pi r} \right] \rightarrow \log\left(\frac{1}{\|y\|^2}\right), \\ & 0 < \chi < \frac{1}{2}, r \in (0, \infty), y \in \mathbb{R}^2 \setminus \{0\}, \\ d = 3, N\nu \rightarrow r: \quad & \Psi_{0,x}^{(4)} \rightarrow \frac{C(x)}{C(0)+2r}, \quad r \in (0, \infty), x \in \mathbb{Z}^3, \end{aligned} \quad (4.38)$$

and (recall (4.20))

$$d = 2, \frac{N\nu}{\log(1/\rho)} \rightarrow r: \quad \log(1/\rho) \Psi_{0,y/\sqrt{\rho}}^{(4)} \rightarrow \frac{2K_0(2\|y\|)}{1+2\pi r}, \quad r \in (0, \infty), y \in \mathbb{R}^2 \setminus \{0\}. \quad (4.39)$$

(2) For $L < \infty$ (recall (4.24)–(4.25)),

$$d = 1, N\nu/L \rightarrow r, L^2\rho \rightarrow s: \quad L^{1-\chi} \left[\Psi_{0,yL^\chi}^{(4)} - \frac{1 + \frac{1}{6}s}{1 + (\frac{1}{6} + 2r)s} \right] \rightarrow \frac{sy}{1 + (\frac{1}{6} + 2r)s}, \quad (4.40)$$

$0 < \chi < 1, r, s \in (0, \infty), y \in [0, \infty)$.

Theorem 4.5(1) shows the x -dependence of $\Psi_{0,x}^{(4)}$ for $L = \infty$, on scale $1/\sqrt{\rho}$ for $d = 1$ and on scales $1/\rho^\chi$, $0 < \chi \leq \frac{1}{2}$ for $d = 2$. The dependence is modulated by an r -dependent prefactor that is controlled by the colony size N . The case $r \gg 1$ corresponds to the situation where coalescence of the two lineages is slow because colonies are large and migration is fast. The case $r \ll 1$ corresponds to the opposite situation where the size of the colonies plays no role.

Theorem 4.5(2) does the same for $L < \infty$, on scales L^χ , $0 < \chi < 1$, for $d = 1$, modulated by an (r, s) -dependent prefactor controlled by the population size N and the torus size L . The case $s \gg 1$ corresponds to the situation where the boundary of the torus is not felt: it takes time L^2/ν to travel a distance L and time $1/\mu$ for a lineage to encounter a mutation. The case $s \ll 1$ corresponds to the situation where the system behaves like a homogeneously mixing population, i.e., a single colony with LN individuals (“panmictic behaviour”).

For $L < \infty$, no result is stated for $d \geq 2$ because no formulas are available for the coefficients $C_L(x)$, $\bar{C}_L(x)$, $x \neq 0$, of the Green functions.

4.5. Regimes: slow seed-bank

To monitor the first-order correction in δ , we define

$$\Phi_{0,x} = \lim_{\delta \downarrow 0} \frac{1}{\delta} [\Psi_{0,x} - \Psi_{0,x}^{\delta=0}]. \quad (4.41)$$

Theorem 4.1 gives

$$\Phi_{0,x}^{(1)} = 0, \quad \Phi_{0,x}^{(2)} = \Phi_{0,x}^{(3)} = \frac{\beta(x)}{N + \alpha(0)}, \quad \Phi_{0,x}^{(4)} = 2 \frac{[\alpha(x)\gamma(0) - \alpha(0)\gamma(x)] - N\gamma(x)}{[N + \alpha(0)]^2}. \quad (4.42)$$

By inserting the expansions of $\alpha(x)$ found in (4.31)–(4.33) and (4.34), we obtain the following.

Theorem 4.6. *In the limit as $\rho, \nu \downarrow 0$ (in that order):*

(1) For $L = \infty$,

$$\begin{aligned}
d = 1: \quad & \Phi_{0,x}^{(2)} = \Phi_{0,x}^{(3)} \\
& = \frac{1}{\nu\rho} \frac{[e^{(-\sqrt{2\rho}+O(\rho))|x|} - \frac{1}{\sqrt{2}}e^{(-\sqrt{4\rho}+O(\rho))|x|}] + O(\rho)}{1 + [(2N - \frac{3}{2})\nu + O(\nu^2)]\sqrt{2\rho} + O(\rho)}, \\
d = 2: \quad & \Phi_{0,x}^{(2)} = \Phi_{0,x}^{(3)} \\
& = \frac{1}{\nu\rho} \frac{\log 2 + [-(1 - \frac{5}{2}\nu) + \bar{C}(x)]\rho \log(1/\rho) + O(\rho)}{\log(1/\rho) + [\pi(2N - \frac{3}{2})\nu + O(\nu^2)] - [(1 - \nu) - \bar{C}(0)]\rho \log(1/\rho) + O(\rho)}, \\
d = 3: \quad & \Phi_{0,x}^{(2)} = \Phi_{0,x}^{(3)} \\
& = \frac{1}{\nu\sqrt{\rho}} \frac{(\sqrt{2} - 1)\bar{C}(x) + [(1 - \frac{5}{2}\nu)C(x) - \frac{1}{8}\nu^2\delta_{0,x}]\sqrt{\rho} + O(\rho)}{[C(0) + (2N - \frac{3}{2})\nu + O(\nu^2)] - \bar{C}(0)\sqrt{\rho} + O(\rho)},
\end{aligned} \tag{4.43}$$

and

$$\begin{aligned}
d = 1: \quad & \Phi_{0,x}^{(4)} \\
& = \frac{1 + O(\rho)}{\nu\sqrt{2\rho}} e^{(-\sqrt{2\rho}+O(\rho))|x|} \frac{[|x| + (2N - \frac{3}{2})\nu + O(\nu^2)] + [(2N - \frac{3}{2})\nu + O(\nu^2)]|x|\sqrt{2\rho} + O(\rho)}{[1 + [(2N - \frac{3}{2})\nu + O(\nu^2)]\sqrt{2\rho} + O(\rho)]^2}, \\
d = 2: \quad & \Phi_{0,x}^{(4)} \\
& = \frac{1}{\nu} \frac{[-C(x) - \pi(2N - \frac{3}{2})\nu](1/\rho) - [\bar{C}(0) - \bar{C}(x)]\log^2(1/\rho) + O(\log(1/\rho))}{[\log(1/\rho) + [-C(x) + \pi(2N - \frac{3}{2})\nu + O(\nu^2)] + O(\rho \log(1/\rho))]^2}, \\
d = 3: \quad & \Phi_{0,x}^{(4)} \\
& = \frac{1}{2\nu\sqrt{\rho}} \frac{[C(x)\bar{C}(0) - C(0)\bar{C}(x) - (2N - \frac{3}{2})\nu\bar{C}(x) + O(\nu^2)] + O(\sqrt{\rho})}{[(2N - \frac{3}{2})\nu + O(\nu^2)] + O(\sqrt{\rho})^2}.
\end{aligned} \tag{4.44}$$

(2) For $L < \infty$,

$$\begin{aligned}
d \geq 1: \quad & \Phi_{0,x}^{(2)} = \Phi_{0,x}^{(3)} = \frac{1}{2\nu\rho} \\
& \times \frac{1 - \frac{5}{2}\nu\rho + [2C_L(x) + 2\bar{C}_L(x) + O(\nu)]L^d\rho^2 + O(\rho^3)}{1 + [C_L(0) - \frac{1-\nu}{L^d} + (2N - \frac{3}{2})\nu + O(\nu^2)]L^d\rho - [C_L(0) + \bar{C}_L(0) + O(\nu)]L^d\rho^2 + O(\rho^3)}.
\end{aligned} \tag{4.45}$$

and

$$\begin{aligned}
d \geq 1: \quad & \Phi_{0,x}^{(4)} = \frac{L^d}{\nu} \frac{1}{[1 + [C_L(0) - \frac{1-\nu}{L^d} + (2N - \frac{3}{2})\nu + O(\nu^2)]L^d\rho + O(\rho^2)]^2} \\
& \times \left([C_L(x) - C_L(0) - (2N - \frac{3}{2})(1 - \delta_{0,x})\nu + O(\nu^2)] \right. \\
& \left. + [-2(\bar{C}_L(x) - \bar{C}_L(0)) + (C(x) - C_L(0) - (2N - \frac{3}{2})(1 - \delta_{0,x}))\nu + O(\nu^2)]\rho + O(\rho^2) \right).
\end{aligned} \tag{4.46}$$

Again, various limiting regimes are interesting, in analogy with (4.38)–(4.40).

Theorem 4.7. (1) For $L < \infty$,

$$\begin{aligned} d = 1, N\nu\sqrt{2\rho} \rightarrow r: & \quad \nu\rho\Phi_{0,y/\sqrt{2\rho}}^{(2)} \rightarrow \frac{e^{|y|} - \frac{1}{\sqrt{2}}e^{-\sqrt{2}|y|}}{1+2r}, \quad y \in \mathbb{R}, \\ d = 2, \frac{N\nu}{\log(1/\rho)} \rightarrow r: & \quad \nu\rho \log(1/\rho)\Phi_{0,y/\rho^\chi}^{(2)} \rightarrow \frac{\log 2}{1+2\pi r}, \quad 0 < \chi < \frac{1}{2}, \quad y \in \mathbb{R}^2, \\ d = 3, N\nu \rightarrow r: & \quad \nu\sqrt{\rho}\Phi_{0,x}^{(2)} \rightarrow \frac{(\sqrt{2}-1)\bar{C}(x)}{C(0)+2r}, \quad x \in \mathbb{Z}^3, \end{aligned} \quad (4.47)$$

and

$$d = 2, \frac{N\nu}{\log(1/\rho)} \rightarrow r: \quad \nu\rho \log(1/\rho)\Phi_{0,y/\sqrt{\rho}}^{(2)} \rightarrow \frac{2[K_0(2\|y\|) - K_0(2\sqrt{2}\|y\|)]}{1 + 2\pi r}, \quad y \in \mathbb{R}^2 \setminus \{0\}, \quad (4.48)$$

and

$$\begin{aligned} d = 1, N\nu\sqrt{2\rho} \rightarrow r: & \quad 2\nu\rho\Phi_{0,y/\sqrt{2\rho}}^{(4)} \rightarrow e^{-|y|} \frac{(1+2r)|y|+2r}{(1+2r)^2}, \quad y \in \mathbb{R}, \\ d = 2, \frac{N\nu}{\log(1/\rho)} \rightarrow r: & \quad \nu\rho \log(1/\rho)\Phi_{0,y/\rho^\chi}^{(4)} \rightarrow -\frac{2\chi+2\pi r}{(1-2\chi+2\pi r)^2}, \quad 0 < \chi < \frac{1}{2}, \quad y \in \mathbb{R}^2, \\ d = 3, N\nu \rightarrow r: & \quad 4\nu\sqrt{\rho}\Phi_{0,x}^{(4)} \rightarrow \frac{C(x)\bar{C}(0)-C(0)\bar{C}(x)-2rC(x)}{(C(0)+2r)^2}, \quad x \in \mathbb{Z}^3, \end{aligned} \quad (4.49)$$

and

$$d = 2, \frac{N\nu}{\log(1/\rho)} \rightarrow r: \quad \rho \log(1/\rho)\Phi_{0,y/\sqrt{\rho}}^{(4)} \rightarrow -\frac{2\|y\|K_0'(2\|y\|)}{(1+2\pi r)^2}, \quad y \in \mathbb{R}^2 \setminus \{0\}. \quad (4.50)$$

(2) For $L < \infty$,

$$d = 1, N\nu/L \rightarrow r, L^2\rho \rightarrow s: \quad 2\nu\rho\Phi_{0,yL^\chi}^{(2)} \rightarrow \frac{1}{1 + (\frac{1}{6} + 2r)s}, \quad 0 < \chi < 1, \quad y \in [0, \infty). \quad (4.51)$$

and

$$d = 1, N\nu/L \rightarrow r, L^2\rho \rightarrow s: \quad \nu\sqrt{\rho}\Phi_{0,yL^\chi}^{(4)} \rightarrow \frac{r\sqrt{s}}{\frac{1}{6} + 2r}, \quad 0 < \chi < 1, \quad y \in [0, \infty). \quad (4.52)$$

The same observations as made below Theorem 4.5 apply.

5. Spatial second moment

In Section 5.1 we identify the scaling of $\hat{\Psi}(\theta)$ for $\theta \rightarrow 0$. Since $\theta \in \hat{\mathbb{T}} = \{0, \frac{1}{L}, \dots, \frac{L-1}{L}\}^d$, we must require that $L \rightarrow \infty$, i.e., the torus becomes large. In Section 5.2 we use this scaling to compute the limiting second moment $\zeta = \lim_{L \rightarrow \infty} \sum_{x \in \mathbb{T}} |x|^2 \Psi_{0,x}$ in closed form for all choices of the parameters, stated in Theorem 5.3. In Section 5.3 we obtain explicit scaling expressions for the special case of the symmetric slow seed-back treated in Section 4. The value of ζ is important because it provides information about the *average time until the two lineages coalesce*. Namely, we have

$$\lim_{L \rightarrow \infty} \mathbb{E}(\tau) = \zeta/2\nu, \quad \tau = \text{time to coalescence}. \quad (5.1)$$

Indeed, on the infinite torus the second moment of simple random walk (with transition kernel (3.2)) after $n \in \mathbb{N}_0$ steps equals n . Since ν is the probability that a lineage migrates to a different colony (i.e., makes a move like simple random walk), it follows that the second moment of the distance between the two lineages after n steps equals $2\nu n$. Picking $n = \tau$ and taking the expectation, we get (5.1).

5.1. Taylor expansion

Let

$$\partial\hat{\Psi}(\theta) = \hat{\Psi}(\theta) - \hat{\Psi}(0), \quad \partial\hat{B}(\theta) = \hat{B}(\theta) - \hat{B}(0), \quad \partial\hat{\Gamma}(\theta) = \hat{\Gamma}(\theta) - \hat{\Gamma}(0). \quad (5.2)$$

Abbreviate $U = (\mathbf{1} - \hat{B}(0))^{-1}$, and let $\Delta(\theta)$ be the first term in the Taylor expansion of $\partial\hat{B}(\theta)$:

$$\partial\hat{B}(\theta) = \Delta(\theta) + o(|\theta|^2). \quad (5.3)$$

Proposition 5.1. For $\theta \rightarrow 0$,

$$\partial\hat{\Psi}(\theta) = \frac{1 - \Psi_{0,0}^{(4)}}{N} \left[U \partial\hat{\Gamma}(\theta) + U \Delta(\theta) U \hat{\Gamma}(0) \right] + o(|\theta|^2). \quad (5.4)$$

Proof. Using (5.3), we get

$$\begin{aligned} (\mathbf{1} - \hat{B}(\theta))^{-1} &= \sum_{n \in \mathbb{N}_0} (\hat{B}(\theta))^n = \sum_{n \in \mathbb{N}_0} (\hat{B}(0) + \Delta(\theta) + o(|\theta|^2))^n \\ &= \sum_{n \in \mathbb{N}_0} (\hat{B}(0))^n + \sum_{n \in \mathbb{N}_0} \sum_{k=0}^{n-1} (\hat{B}(0))^{n-1-k} \Delta(\theta) (\hat{B}(0))^k + o(|\theta|^2) \\ &= (\mathbf{1} - \hat{B}(0))^{-1} + (\mathbf{1} - \hat{B}(0))^{-1} \Delta(\theta) (\mathbf{1} - \hat{B}(0))^{-1} + o(|\theta|^2). \end{aligned} \quad (5.5)$$

Substitution into (3.28) yields

$$\begin{aligned} \partial\hat{\Psi}(\theta) &= \frac{1 - \Psi_{0,0}^{(4)}}{N} \left((\mathbf{1} - \hat{B}(0))^{-1} \partial\hat{\Gamma}(\theta) + (\mathbf{1} - \hat{B}(0))^{-1} \Delta(\theta) (\mathbf{1} - \hat{B}(0))^{-1} \hat{\Gamma}(0) \right) + o(|\theta|^2). \end{aligned} \quad (5.6)$$

Using that $\hat{\Gamma}(\theta) \rightarrow \hat{\Gamma}(0)$ as $\theta \rightarrow 0$, we obtain (5.4). \square

To analyse (5.4), we first compute

$$U = (\mathbf{1} - \hat{B}(0))^{-1} = \frac{1}{u_0} \begin{pmatrix} u_{1,1} & u_{1,2} & u_{1,3} & u_{1,4} \\ u_{2,1} & u_{2,2} & u_{2,3} & u_{2,4} \\ u_{3,1} & u_{3,2} & u_{3,3} & u_{3,4} \\ u_{4,1} & u_{4,2} & u_{4,3} & u_{4,4} \end{pmatrix} = \frac{1}{u_0} \begin{pmatrix} t_1 & \epsilon s_1 & \epsilon s_1 & \epsilon^2 s_2 \\ \delta s_1 & t_2 & t_3 & \epsilon s_3 \\ \delta s_1 & t_3 & t_2 & \epsilon s_3 \\ \delta^2 s_2 & \delta s_3 & \delta s_3 & t_4 \end{pmatrix}, \quad (5.7)$$

where

$$\begin{aligned} u_0 &= (1 - m)(1 - m(1 - \delta - \epsilon) - 2m\delta\epsilon)(1 - m(1 - \delta - \epsilon))(1 - m(1 - \delta - \epsilon)^2), \\ s_1 &= m(1 - m(1 - \delta - \epsilon) - 2m\delta\epsilon)(1 - \delta - m(1 - \epsilon)(1 - \delta - \epsilon)), \\ s_2 &= m(1 - m(1 - \delta - \epsilon) - 2m\delta\epsilon)(1 + m(1 - \delta - \epsilon)), \\ s_3 &= m(1 - m(1 - \delta - \epsilon) - 2m\delta\epsilon)(1 - \epsilon - m(1 - \epsilon)(1 - \delta - \epsilon)), \\ t_1 &= (1 - m(1 - \delta - \epsilon) - 2m\delta\epsilon)(1 - m(1 - \epsilon)^2)(1 - m(1 - \delta - \epsilon)), \\ t_2 &= 1 - m \left[3(1 - \delta - \epsilon) + (\delta + \epsilon)^2 - m(1 - 6\delta + 4\delta^2 - \delta^3 + 1 - 6\epsilon + 4\epsilon^2 - \epsilon^3 \right. \\ &\quad \left. + 1 - \delta^3\epsilon + 5\delta^2\epsilon + 10\delta\epsilon - 5\delta\epsilon^2 + \delta\epsilon^3) - m^2(1 - \delta - \epsilon)(\delta\epsilon + (1 - \delta - \epsilon))^2 \right], \\ t_3 &= m^2\delta\epsilon \left[(1 - \epsilon)^2 + (1 - \delta)^2 - 2m(1 - \delta)(1 - \epsilon)(1 - \delta - \epsilon) \right], \\ t_4 &= (1 - m(1 - \delta - \epsilon) - 2m\delta\epsilon) \left[(1 - m(1 - \delta)^2)(1 - m(1 - \delta - \epsilon)) - 2m\delta\epsilon \right]. \end{aligned} \quad (5.8)$$

Note that there are several symmetries in the entries of the matrix in (5.7), which come from the symmetries in the model. Next, for the choice of p in (3.1) and (3.2), we have

$$\begin{aligned} \hat{p}(\theta) &= \sum_{z \in \mathbb{T}} p(0, z) e^{2\pi i(\theta \cdot z)} = \sum_{z \in \mathbb{T}} [(1 - \nu)\delta_{z,0} + \nu q(z)] e^{2\pi i(\theta \cdot z)} \\ &= (1 - \nu) + \nu \hat{q}(\theta) = 1 - \nu(1 - \hat{q}(\theta)) = 1 - \nu\pi^2|\theta|^2 + o(|\theta|^2), \end{aligned} \quad (5.9)$$

where we use that

$$\hat{q}(\theta) = 1 - \pi^2|\theta|^2 + o(|\theta|^2). \quad (5.10)$$

When we substitute (5.9) into (3.32), and use (3.9) and (3.33), we get

$$\Delta(\theta) = -\Delta_0\nu\pi^2|\theta|^2 + o(|\theta|^2) \quad (5.11)$$

with

$$\Delta_0 = m(1-\epsilon) \begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & 1-\delta & 0 & \epsilon \\ 0 & 0 & 1-\delta & \epsilon \\ 0 & \delta & \delta & 2(1-\epsilon) \end{pmatrix}. \quad (5.12)$$

Finally, recalling (3.20) we obtain $\hat{\Gamma}(0) = \Gamma_0$ with

$$\Gamma_0 = (1-\mu)^2(1-\epsilon)^2 \begin{pmatrix} 0 \\ 0 \\ 0 \\ 1 \end{pmatrix} \quad (5.13)$$

and

$$\partial\hat{\Gamma}(\theta) = -(1-\mu)^2(1-\epsilon)^2 \begin{pmatrix} 0 \\ 0 \\ 0 \\ 1-\hat{p}(\theta)^2 \end{pmatrix} = -2\Gamma_0\nu\pi^2|\theta|^2 + o(|\theta|^2). \quad (5.14)$$

Combining (5.4), (5.7), (5.11) and (5.4), (5.14), we arrive at the following proposition identifying the asymptotics of $\partial\hat{\Psi}(\theta)$.

Proposition 5.2. *For $\theta \rightarrow 0$,*

$$\partial\hat{\Psi}(\theta) = -\zeta\pi^2|\theta|^2 + o(|\theta|^2), \quad (5.15)$$

where ζ is the 4-vector

$$\zeta = \frac{1 - \Psi_{0,0}^{(4)}}{N} \nu U (2\mathbb{1} + \Delta_0 U) \Gamma_0 \quad (5.16)$$

with U, Δ_0 the (4×4) -matrices given by (5.7)–(5.8) and (5.12), Γ_0 the 4-vector given by (5.13), and $\Psi_{0,0}^{(4)}$ the number given by (3.47).

5.2. Fourier inversion

We next use Propositions 5.1 and 5.2 to compute $\sum_{x \in \mathbb{T}} |x|^2 \Psi_{0,x}$. Recalling the definition of the Fourier transform given in (3.26), we have for $\theta \rightarrow 0$,

$$\begin{aligned} \hat{\Psi}(\theta) &= \sum_{x \in \mathbb{T}} \Psi_{0,x} e^{2\pi i(x_1\theta_1 + x_2\theta_2)} \\ &= \sum_{x \in \mathbb{T}} \Psi_{0,x} \cos(2\pi(x_1\theta_1 + x_2\theta_2)) \\ &= \sum_{x \in \mathbb{T}} \Psi_{0,x} \left(1 - \frac{1}{2} 4\pi^2(x_1\theta_1 + x_2\theta_2)^2\right) + o(|\theta|^2) \\ &= \hat{\Psi}(0) - 2\pi^2 \sum_{x \in \mathbb{T}} \Psi_{0,x} (x_1^2\theta_1^2 + x_2^2\theta_2^2 + 2x_1x_2\theta_1\theta_2) + o(|\theta|^2), \end{aligned} \quad (5.17)$$

where $x = (x_1, x_2) \in \mathbb{T}$ and $\theta = (\theta_1, \theta_2) \in \hat{\mathbb{T}}$. Thus,

$$\partial\hat{\Psi}(\theta) = -2\pi^2 \sum_{x \in \mathbb{T}} \Psi_{0,x} (x_1^2\theta_1^2 + x_2^2\theta_2^2 + 2x_1x_2\theta_1\theta_2) + o(|\theta|^2). \quad (5.18)$$

Choosing $\theta_1 = \theta_2$, and combining (5.15) and (5.18), we find

$$\zeta = \sum_{x \in \mathbb{T}} (x_1^2 + x_2^2 + 2x_1x_2) \Psi_{0,x}. \quad (5.19)$$

We have $\sum_{x \in \mathbb{T}} x_1x_2\Psi_{0,x} = 0$ when L is odd and $\sum_{x \in \mathbb{T}} x_1x_2\Psi_{0,x} = |\mathbb{T}|\Psi_{0,z_L}$ when L is even, with z_L one of the corner points of \mathbb{T} . But $\Psi_{0,z_L} \leq (1-\mu)^{2L}$ and so this term is negligible in the limit as $L \rightarrow \infty$. We therefore arrive at the following result.

Theorem 5.3. *For all δ, ϵ, μ, N ,*

$$\lim_{L \rightarrow \infty} \sum_{x \in \mathbb{T}} |x|^2 \Psi_{0,x} = \zeta \quad (5.20)$$

with ζ given by (5.16).

Thus, we have found an explicit formula for the second moment in the limit of a large torus, valid for any choice of the parameters.

5.3. Symmetric slow seed-bank

We close by investigating how ζ behaves when we return to the special case of the symmetric slow seed-bank treated in Section 4. In that case we find (recall (5.7)–(5.8))

$$U = c \mathbb{1} + \delta mc^2 \begin{pmatrix} -2 & 1 & 1 & 0 \\ 1 & -2 & 0 & 1 \\ 1 & 0 & -2 & 1 \\ 0 & 1 & 1 & -2 \end{pmatrix} + O(\delta^2), \quad c = \frac{1}{1-m}, \quad m = (1-\mu)^2, \quad (5.21)$$

and (recall (5.12)–(5.13))

$$\Delta_0 = m \left\{ \begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 2 \end{pmatrix} + \delta \begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & -2 & 0 & 1 \\ 0 & 0 & -2 & 1 \\ 0 & 1 & 1 & -4 \end{pmatrix} + O(\delta^2) \right\}, \quad (5.22)$$

$$\Gamma_0 = m \left\{ \begin{pmatrix} 0 \\ 0 \\ 0 \\ 1 \end{pmatrix} + \delta \begin{pmatrix} 0 \\ 0 \\ 0 \\ -2 \end{pmatrix} + O(\delta^2) \right\}. \quad (5.23)$$

After substituting these expressions into (5.16) and using (4.5), we obtain the following.

Theorem 5.4. *For $\delta \downarrow 0$,*

$$\zeta = c_N \nu \left[1 + \delta \frac{2\alpha(0)\gamma(0)}{N} + O(\delta^2) \right] mc^2 \left\{ \begin{pmatrix} 0 \\ 0 \\ 0 \\ 2 \end{pmatrix} + \delta \begin{pmatrix} 0 \\ 3mc \\ 3mc \\ -4(2c-1) \end{pmatrix} + O(\delta^2) \right\}. \quad (5.24)$$

After inserting the expansions of $\alpha(0)$ and $\gamma(0)$ found in Section 4.3, we obtain expressions for ζ that are analogous to the expressions for $\Psi_{0,x}$ found in Sections 4.4–4.5. The details are left to the reader.

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