Population dynamics with seed-bank
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Master Thesis

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CHAPTER 1

Introduction

Population models with seed-bank have, in addition to an active population, a dormant population that resides in the seed-bank. Dormancy refers to a reversible state of low metabolic activity, which may last for any amount of time (see Lennon and Jones [**11**]). This type of behaviour is observed in a wide range of taxa, both in macro-organisms and in micro-organisms. It occurs as a response to unfavourable environmental conditions, allowing dormant individuals to become active again under more favourable conditions. It is not a cost-free strategy, as for instance organisms must invest resources in the transitioning into and out of the dormant state. Despite these costs, such a strategy has been shown to positively influence maintenance of genetic variability and stability of ecosystems. It is this importance that led to attempts at modelling seed-banks from a mathematical perspective.

The Wright-Fisher model with seed-bank to date has been studied in several ways, one of which involves a coalescent process. Kaj, Krone and Lascoux [**10**] considered an extension of the classical Wright-Fisher model, in which each individual in a population of fixed size N selects its parent from the population as it existed a random number of generations B in the past. The number of generations between an offspring and its parents is the time the offspring spends in the seed-bank. The authors show that if B is bounded, then after the usual scaling of time by N, the model converges to a delayed Kingman coalescent where the rates are multiplied by $1/\mathbb{E}(B)^2$. As the structure of the coalescent is unchanged, this is referred to as a *weak* seed-bank effect.

Blath, González-Casanova, Kurt and Spanò [**3**] showed that a sufficient condition for convergence to the Kingman coalescent in this model is $\mathbb{E}(B) < \infty$, with B independent of N. A further extension in [**3**] allows for *strong* seed-bank effects. Under the assumption that the seed-bank age distribution μ of B is 'heavy-tailed', i.e., $\mu(B \geq k) = L(k)k^{-\alpha}$, $k \in \mathbb{N}$, where L is slowly varying as $k \to \infty$, the authors show that for $\alpha > \frac{1}{2}$ the most recent common ancestor (MRCA) of two randomly sampled individuals exists with probability 1. However, the expected time to the MRCA is infinite for $\alpha < 1$. Moreover, for $0 < \alpha < \frac{1}{2}$ with positive probability a common ancestor does not exist at all. As this behaviour is very different from the Kingman coalescent, one can indeed speak of strong seed-bank effects.

As such extreme behaviour may seem artificial, González-Casanova et al. [**7**] and Blath, Eldon et al. [**2**] considered the case in which B scales with the population size N, and assumed the seed-bank age distribution μ to be $\mu = (1-\varepsilon)\delta_1 + \varepsilon\delta_{N^\beta}$ with $\beta > 0$ and $\varepsilon \in (0,1)$. This means that, in each new generation, a fraction $(1-\varepsilon)$ of the total population obtains its genetic type from the previous generation, while the remaining fraction ε obtains its type from generation N^β in the past. The authors show that after rescaling time by the nonclassical factor $N^{1+2\beta}$, the model converges to the Kingman coalescent. Apparently, this choice of μ significantly increases the time to the MRCA. However, it leaves the coalescent structure unchanged and therefore one speaks again of weak seed-bank effects.

Blath, González-Casanova, Kurt and Wilke-Berenguer [4] considered a model that does not require artificial scaling assumptions and gives rise to a new coalescent structure. Individuals can enter and exit the seed-bank at each generation, and dormant individuals suspend their resampling and preserve their type. The authors showed, in particular, that the seed-bank coalescent does not come down from infinity and the expected time to the MRCA of an n sample is of asymptotic order $\log\log n$ as $n \to \infty$. Den Hollander and Pederzani [9] considered a multi-colony version of the model in [4], where individuals can migrate between colonies, each containing a seed-bank, and are subject to mutation. The quantity of interest is the probability that two individuals drawn randomly from two colonies are identical by descent, i.e., share a common ancestor without mutation affecting their ancestral lines. The authors, in particular, derived a formula for this probability as a function of the two colonies on a discrete torus, stated in Fourier language, and were able to derive explicit scaling expressions when mutation is slower than migration.

Finally, Blath, Buzzoni, González-Casanova and Wilke-Berenguer [1] investigated several scaling limits of the seed-bank diffusion, the limiting object that is obtained by letting the population size go to infinity and rescaling time appropriately, and commented on the relation with the two-island Wright-Fisher diffusion. In particular, they showed that under a certain rescaling of time the seed-bank diffusion converges to a new coalescent-related ancestral process, called the *ancient ancestral lines process*. Let c denote the rate of exchange between the active and the dormant population. By assuming that c goes to zero while time is speeded up by a factor $1/c$, the authors showed that in the limiting diffusion that arises in the scaling limit, migration still happens at rate 1 while coalescence occurs almost instantaneously. This ensures that at any positive time there is at most one active line.

The goal of this master thesis is to study a population model with seed-bank to which selection is added. In Chapter 2 we determine diffusion limits of several models. We consider the Moran model with seed-bank and extend it to include selection in resampling, selection in exchange, and migration. We also consider the Wright-Fisher model with seed-bank and selection in resampling and show that it gives rise to the same diffusion limit as in the Moran model.

In Chapter 3 we consider a multi-colony Moran model on a discrete torus, with migration and mutation. Note that while there is no seed-bank in this model, it does develop a benchmark to which we can later refer. We obtain a recursion relation for the probability of being identical by descent as a function of the distance between the two colonies the two individuals are drawn from. After that, we turn to Fourier analysis, which allows us to obtain a closed form expression for the Fourier transform of this probability. We show that, under certain circumstances, it is possible to apply Fourier inversion and express the probability of being identical by descent in terms of the Green function of a simple random walk.

In Chapter 4 we extend the previous model, by adding a seed-bank. In particular, we consider the model in [**9**] with selection added, namely, the rate at which individuals migrate between colonies depends on their type. We again obtain a recursion relation for the probability of being identical by descent as a function of the distance between the two colonies the two individuals are drawn from, and are able to obtain a closed form expression for its Fourier transform. To get a more tangible expression, we consider weak exchange between the active and the dormant population and weak mutation, for which we obtain an expansion of the Fourier transform. Under certain circumstances, it is again possible to apply Fourier inversion and obtain an expansion for the probability of being identical by descent in terms of the Green function of a simple random walk. Finally, we offer two examples for which a closed form expression of the Green function exists: the infinite torus and the finite torus, both in dimension $d = 1$.

CHAPTER 2

Diffusion limits of several models from population dynamics

In this chapter we introduce five models from population dynamics and determine to which diffusion they converge after space-time rescaling. In Section 2.1, we consider the Moran model with seed-bank. We extend this model to include selection in resampling, selection in resampling and exchange, and migration in Sections 2.2 through 2.4. In Section 2.5, we consider the Wright-Fisher model with seed-bank and selection in resampling, and show that it gives rise to the same diffusion as in the corresponding Moran model, up to a factor two in time speed.

2.1. Moran model with seed-bank

In this section we introduce the Moran model with seed-bank, by adapting to continuous time the Wright-Fisher model with geometric seed-bank component introduced in [4]. We show that after space-time rescaling the Moran model with seed-bank converges to the same diffusion limit, up to a factor two in time speed.

We define the model as follows. Consider a haploid population where each individual carries a genetic type from state space $E = \{A, a\}$. The total population is divided into an active population of size N and a seed-bank of size M containing the dormant population.

Given $N, M \in \mathbb{N}$, let $\varepsilon \in [0,1]$ be such that $\varepsilon N \leq M$ and set $\delta = \varepsilon N/M$. Assume for convenience that $\varepsilon N = \delta M$ is a natural number. The dynamics of the model are as follows:

- An active individual at rate 1 either:
  (1) with probability $(1-\varepsilon)$ produces another active indivual which uniformly at random chooses a parent among the previous active population and adopt its type;
  (2) or with probability ε produces an individual that becomes dormant in the seed-bank.
- A dormant individual at rate 1 either:
  (1) with probability $(1-\delta)$ remains dormant in the seed-bank;
  (2) or with probability δ leaves the seed-bank and becomes active.

Let X_t^N and Y_t^M denote the number of individuals of type A at time t, in the active and the dormant population, respectively. Here, we add upper indices to exhibit the underlying dependence on N and M. Then $(X_t^N, Y_t^M)_{t\geq 0}$ is the continuous-time Markov process on state space

$$\{0,1,\ldots,N\} \times \{0,1,\ldots,M\} \tag{2.1.1}$$

with transitions

$$(i,j) \to \begin{cases} (i-1,j+1) & \text{at rate } i\varepsilon \\ (i+1,j-1) & \text{at rate } j\delta \\ (i-1,j) & \text{at rate } i(1-\varepsilon)\left(\frac{N-i}{N}\right) \\ (i+1,j) & \text{at rate } (N-i)(1-\varepsilon)\frac{i}{N}. \end{cases} \tag{2.1.2}$$

We thus either have an exchange between the active and the dormant population, or a death or birth of an active individual. Note that in the latter case the birth and death rates are identical. For notational convenience, write

$$c_i^{\mathrm{act}} = i\varepsilon, \quad c_j^{\mathrm{dorm}} = j\delta, \quad d_i^{\mathrm{act}} = b_i^{\mathrm{act}} = i\left(1 - \frac{i}{N}\right)(1-\varepsilon). \tag{2.1.3}$$

As we are interested in the limiting diffusion process, we consider the space-time rescaling

$$\left(\overline{X}_t^N, \overline{Y}_t^M\right) = \left(\frac{1}{N} X_{\lceil Nt \rceil}^N, \frac{1}{M} Y_{\lceil Nt \rceil}^M\right), \quad t \geq 0, \tag{2.1.4}$$

which represents the fraction of individuals of type A at time t on time scale N, in the active and the dormant population, respectively. Define

$$B = \left\{ f \in C^3([0,1]^2) \mid \text{all partial third order derivatives of } f \text{ are bounded} \right\}. \tag{2.1.5}$$

Then $(\overline{X}_t^N, \overline{Y}_t^M)_{t \geq 0}$ is the continuous-time Markov process on state space

$$I_N \times I_M = \left\{0, \frac{1}{N}, \frac{2}{N}, \ldots, 1\right\} \times \left\{0, \frac{1}{M}, \frac{2}{M}, \ldots, 1\right\} \tag{2.1.6}$$

with infinitesimal generator L_N acting on $f \in B$ given by

$$\begin{aligned} (L_N f)\left(\frac{i}{N}, \frac{j}{M}\right) = N \Bigg(& c_i^{\mathrm{act}} \left[f\left(\frac{i-1}{N}, \frac{j+1}{M}\right) - f\left(\frac{i}{N}, \frac{j}{M}\right) \right] \\ & + c_j^{\mathrm{dorm}} \left[f\left(\frac{i+1}{N}, \frac{j-1}{M}\right) - f\left(\frac{i}{N}, \frac{j}{M}\right) \right] \\ & + d_i^{\mathrm{act}} \left[f\left(\frac{i-1}{N}, \frac{j}{M}\right) - f\left(\frac{i}{N}, \frac{j}{M}\right) \right] \\ & + b_i^{\mathrm{act}} \left[f\left(\frac{i+1}{N}, \frac{j}{M}\right) - f\left(\frac{i}{N}, \frac{j}{M}\right) \right] \Bigg). \end{aligned} \tag{2.1.7}$$

Henceforth, we write $x_N = i/N$ and $y_M = j/M$.

As in [4], we obtain an interesting limiting structure after the parameters of the model are scaled with the population size N. Assume that there exist $c, K \in (0,\infty)$ such that

$$\varepsilon = \varepsilon(N) = \frac{c}{N}, \quad M = M(N) = \frac{N}{K}. \tag{2.1.8}$$

Note that

$$\delta = \delta(N) = \frac{\varepsilon N}{M} = \frac{cK}{N}. \tag{2.1.9}$$

The parameter c is the average number of active individuals in each generation that becomes dormant, or equivalently, the average number of dormant individuals that become active. The parameter K represents the relative size of the seed-bank with respect to the size of the active population.

PROPOSITION 2.1.1. *Assume that* (2.1.8) *holds. For all* $f \in B$ *and* $(x_N, y_M) \in I_N \times I_M$,

$$\lim_{N\to\infty} (L_N f)(x_N, y_M) = (Lf)(x, y) \quad \text{if} \quad \lim_{N\to\infty} (x_N, y_M) = (x, y) \in [0,1]^2, \tag{2.1.10}$$

where L *is given by*

$$(Lf)(x,y) = c(y-x)\frac{\partial f}{\partial x}(x,y) + cK(x-y)\frac{\partial f}{\partial y}(x,y) + x(1-x)\frac{\partial^2 f}{\partial x^2}(x,y). \tag{2.1.11}$$

PROOF. We use Taylor expansion up to second order around (x_N, y_M) of the functions given in (2.1.7), obtaining

$$\begin{aligned} f\left(\frac{i\mp 1}{N}, \frac{j\pm 1}{M}\right) &= f\left(x_N, y_M\right) \mp \frac{1}{N} f_x\left(x_N, y_M\right) \pm \frac{1}{M} f_y\left(x_N, y_M\right) \\ &\quad + \frac{1}{2N^2} f_{xx}\left(x_N, y_M\right) - \frac{1}{NM} f_{xy}\left(x_N, y_M\right) + \frac{1}{2M^2} f_{yy}\left(x_N, y_M\right) \\ &\quad + \sum_{\substack{\alpha,\beta\in\mathbb{N}_0 \\ \alpha+\beta=3}} R^N_{\alpha,\beta}\left(\frac{i\mp 1}{N}, \frac{j\pm 1}{M}\right)\left(\frac{\mp 1}{N}\right)^\alpha \left(\frac{\pm 1}{M}\right)^\beta \end{aligned} \tag{2.1.12}$$

and

$$\begin{aligned} f\left(\frac{i\mp 1}{N}, \frac{j}{M}\right) &= f(x_N, y_M) \mp \frac{1}{N} f_x(x_N, y_M) + \frac{1}{2N^2} f_{xx}(x_N, y_M) \\ &\quad + \sum_{\substack{\alpha,\beta\in\mathbb{N}_0 \\ \alpha+\beta=3}} R^N_{\alpha,\beta}\left(\frac{i\mp 1}{N}, \frac{j}{M}\right)\left(\frac{\mp 1}{N}\right)^\alpha (0)^\beta, \end{aligned} \tag{2.1.13}$$

where we use the notation

$$f_{x^a y^b} = \frac{\partial^{a+b} f}{\partial x^a \partial x^b}, \quad a, b \in \{0,1,2,3\}. \tag{2.1.14}$$

We call the summations in (2.1.12) and (2.1.13) the remainder term.

For $x, y \in [0,1]^2$ and $\alpha, \beta \in \mathbb{N}_0$ such that $\alpha + \beta = 3$, we have

$$R^N_{\alpha,\beta}(x,y) = \frac{\alpha+\beta}{\alpha!\beta!}\int_0^1 (1-t)^{\alpha+\beta-1}\frac{\partial^3 f}{\partial x^\alpha y^\beta}(x_N - t(x_N - x), y_M - t(y_M - y))\, dt. \tag{2.1.15}$$

Because $f \in B$, we have that all third order derivatives of f are bounded. Since we have a finite integral, we can thus bound $R^N_{\alpha,\beta}(x,y)$ uniformly for all $x, y \in [0,1]^2$. It is then clear that the remainder term in each of the expansions is of order $O(1/N^3)$. Next, note that we can express the rates in terms of x_N, y_M and c, namely,

$$c_i^{\text{act}} = i\varepsilon = \varepsilon N \frac{i}{N} = c x_N,$$

$$c_j^{\text{dorm}} = j\delta = \delta M \frac{j}{M} = c y_M,$$

$$d_i^{\text{act}} = b_i^{\text{act}} = i\left(1 - \frac{i}{N}\right)(1-\varepsilon) = N\frac{i}{N}\left(1 - \frac{i}{N}\right)(1-\varepsilon) = N x_N (1 - x_N)\left(1 - \frac{c}{N}\right).$$

We thus see that all rates are at most of order $O(N)$, and hence we can bound the total error term in our Taylor approximation by $O(1/N^2)$.

These results can be substituted into the generator given in (2.1.7), so that we can write down the generator in terms of the partial derivatives of f. It follows that

$$\begin{aligned}(L_N f)(x_N, y_M) = {} & f_x(x_N, y_M) c(y_M - x_N) + \frac{N}{M} f_y(x_N, y_M) c(x_N - y_M) \\ & + \frac{1}{2N} f_{xx}(x_N, y_M)\left[c(x_N + y_M) + 2N x_N(1 - x_N)\left(1 - \frac{c}{N}\right)\right] \\ & + \frac{1}{M} f_{xy}(x_N, y_M) c(-x_N - y_M) + \frac{N}{2M^2} f_{yy}(x_N, y_M) c(x_N + y_M) \\ & + O\left(\frac{1}{N}\right).\end{aligned} \tag{2.1.16}$$

Since $M = N/K$, it follows that

$$\begin{aligned}(L_N f)(x_N, y_M) = {} & f_x(x_N, y_M) c(y_M - x_N) + K f_y(x_N, y_M) c(x_N - y_M) \\ & + \frac{1}{2N} f_{xx}(x_N, y_M)\left[c(x_N + y_M) + 2N x_N(1 - x_N)\left(1 - \frac{c}{N}\right)\right] \\ & + \frac{K}{N} f_{xy}(x_N, y_M) c(-x_N - y_M) + \frac{K^2}{2N} f_{yy}(x_N, y_M) c(x_N + y_M) \\ & + O\left(\frac{1}{N}\right).\end{aligned} \tag{2.1.17}$$

Taking the limit $N \to \infty$, we now easily get

$$\lim_{N\to\infty} (L_N f)(x_N, y_M) = c(y - x) f_x(x, y) + cK(x - y) f_y(x, y) + x(1 - x) f_{xx}(x, y) \tag{2.1.18}$$

and the right-hand side is exactly $(Lf)(x, y)$. □

The state space $I_N \times I_M$ of the frequency chain can be embedded into the unit square $[0, 1]^2$, so by standard arguments we obtain tightness and convergence on path-space (cf. [6], Chapter 4, Theorem 8.2). We recognize the limit of the process as a pair of SDEs, uniquely defined by the limiting generator.

Corollary 2.1.2. *Under the conditions of Proposition 2.1.1, if* $\lim_{N\to\infty} \overline{X}_0^N = x$ *a.s. and* $\lim_{N\to\infty} \overline{Y}_0^M = y$ *a.s., then*

$$w - \lim_{N\to\infty} \left(\overline{X}_t^N, \overline{Y}_t^M\right)_{t\geq 0} = (X_t, Y_t)_{t\geq 0}. \tag{2.1.19}$$

The process $(X_t, Y_t)_{t\geq 0}$ *is the two-dimensional diffusion on* $[0,1]^2$ *solving*

$$\begin{aligned} dX_t &= c(Y_t - X_t)\, dt + \sqrt{2X_t(1-X_t)}\, dW_t, \\ dY_t &= cK(X_t - Y_t)\, dt, \end{aligned} \tag{2.1.20}$$

with initial conditions $X_0 = x$, $Y_0 = y$ *and where* $(W_t)_{t\geq 0}$ *is standard Brownian motion.*

Note that $w - \lim$ stands for weak limit, namely, convergence in distribution on path space. To formally prove Corollary 2.1.2, we must show that L is indeed the generator of a Markov process and use the fact that convergence of the generator on a dense class of test functions implies convergence of the Markov process (cf. [6], Chapter 8, Proposition 2.4).

Comparing Corollary 2.1.2 with Corollary 2.5 in [4], we see that after space-time rescaling we obtain the same diffusion limit for the Moran model with seed-bank. The sole difference is that the Moran model with seed-bank runs at twice the speed of the Wright-Fisher model with seed-bank.

2.2. Moran model with seed-bank and selection in resampling

We next consider an extension of the model introduced in Section 2.1 by adding selection in the resampling mechanism.

Let $s \in [0,1]$. Consider the same dynamics, only now assume that individuals of type A in the active population resample at rate $1-s$ rather than at rate 1. Define X_t^N and Y_t^M as before. Then $(X_t^N, Y_t^M)_{t\geq 0}$ is the Markov process on state space $\{0,\dots,N\} \times \{0,\dots,M\}$ with transitions

$$(i,j) \to \begin{cases} (i-1, j+1) & \text{at rate } i\varepsilon \\ (i+1, j-1) & \text{at rate } j\delta \\ (i-1, j) & \text{at rate } i\left(1-\frac{i}{N}\right)(1-\varepsilon)(1-s) \\ (i+1, j) & \text{at rate } i\left(1-\frac{i}{N}\right)(1-\varepsilon). \end{cases} \tag{2.2.1}$$

Note that if $s \neq 0$, then $b_i^{\text{act}} \neq d_i^{\text{act}}$ for all i.

We again consider the rescaled process $(\overline{X}_t^N, \overline{Y}_t^M)_{t\geq 0}$ on state space $I_N \times I_M$ and with infinitesimal generator L_N given by (2.1.7), with rates as specified above. In addition to (2.1.8), we also assume *weak selection*, i.e., the selection parameter scales with N. Namely, we assume that there exists a $\sigma \in (0,\infty)$ such that

$$s = \frac{\sigma}{N}. \tag{2.2.2}$$

We look at the effect that adding weak selection has on the model.

PROPOSITION 2.2.1. *Assume that (2.1.8) and (2.2.2) hold. For all $f \in B$ and $(x_N, y_M) \in I_N \times I_M$,*

$$\lim_{N\to\infty} (L_N f)(x_N, y_M) = (Lf)(x,y) \quad \text{if} \quad \lim_{N\to\infty} (x_N, y_M) = (x,y) \in [0,1]^2, \tag{2.2.3}$$

where L is given by

$$(Lf)(x,y) = c(y-x)\frac{\partial f}{\partial x}(x,y) + \sigma x(1-x)\frac{\partial f}{\partial x}(x,y) + cK(x-y)\frac{\partial f}{\partial y}(x,y) + x(1-x)\frac{\partial^2 f}{\partial x^2}(x,y). \tag{2.2.4}$$

PROOF. The proof is done in the same way as the proof of Proposition 2.1.1. Namely, we use Taylor expansion to derive an expression for $(L_N f)(x_N, y_M)$ expressed solely in terms of x_N, y_M and the parameters.

Note that we only change the rate d_i^{act}. Since this rate corresponds to a transition in the x-value of f, we only see a change occurring in the terms for the derivatives of f in the x-direction. As to the remainder term, the expressions for $R^N_{\alpha,\beta}(x,y)$ are still valid for this model and so again the remainder term in each Taylor expansion is of order $O(1/N^3)$. We do change the rate d_i^{act}, but since this rate is still of order $O(N)$, this has no significant effect on the error term. It follows that

$$\begin{aligned}
&(L_N f)(x_N, y_M) \\
&= f_x(x_N, y_M)\left[c(y_M - x_N) + \frac{\sigma}{N} N x_N(1-x_N)\left(1-\frac{c}{N}\right)\right] + K f_y(x_N, y_M) c(x_N - y_M) \\
&\quad + \frac{1}{2N} f_{xx}(x_N, y_M)\left[c(x_N + y_M) + \left(2 - \frac{\sigma}{N}\right) N x_N(1-x_N)\left(1-\frac{c}{N}\right)\right] \\
&\quad + \frac{K}{N} f_{xy}(x_N, y_M) c(-x_N - y_M) + \frac{K^2}{2N} f_{yy}(x_N, y_M) c(x_N + y_M) \\
&\quad + O\left(\frac{1}{N}\right).
\end{aligned} \tag{2.2.5}$$

If we take the limit $N \to \infty$, then it is clear that we get $(Lf)(x,y)$. ☐

The limiting generator again uniquely defines a Markov process, defined by the following system of SDEs.

COROLLARY 2.2.2. *Under the conditions of Proposition 2.2.1, if $\lim_{N\to\infty} \overline{X}_0^N = x$ a.s. and $\lim_{N\to\infty} \overline{Y}_0^M y$ a.s., then*

$$w - \lim_{N\to\infty} \left(\overline{X}_t^N, \overline{Y}_t^M\right)_{t\geq 0} = (X_t, Y_t)_{t\geq 0}. \tag{2.2.6}$$

The process $(X_t, Y_t)_{t\geq 0}$ is the two-dimensional diffusion on $[0,1]^2$ solving

$$\begin{aligned}
dX_t &= c(Y_t - X_t)\,dt + \sigma X_t(1-X_t)\,dt + \sqrt{2X_t(1-X_t)}\,dW_t, \\
dY_t &= cK(X_t - Y_t)\,dt
\end{aligned} \tag{2.2.7}$$

with initial conditions $X_0 = x$, $Y_0 = y$ and where $(W_t)_{t\geq 0}$ is standard Brownian motion.

Contrary to Corollary 2.1.2, the differential equation for X_t now contains both a deterministic and a random part due to the resampling mechanism. In the presence of selection, there is a drift term pushing the system to 'all A' in the active population.

2.3. Moran model with seed-bank and selection in resampling and exchange

We extend the model of Section 2.2 by also adding selection in the mechanism that deals with the exchange between active and dormant individuals.

Let $r \in [0,1]$. Consider the same dynamics, but additionally assume that individuals of type A in the dormant population become active at rate $1-r$ rather than at rate 1. Then $(X_t^N, Y_t^M)_{t\geq 0}$ is the continuous-time Markov process on state space $\{0,\dots,N\}\times\{0,\dots,M\}$ with transitions

$$(i,j) \to \begin{cases} (i-1,j+1) & \text{at rate } i\varepsilon \\ (i+1,j-1) & \text{at rate } j\delta(1-r) \\ (i-1,j) & \text{at rate } i\left(1-\frac{i}{N}\right)(1-\varepsilon)(1-s) \\ (i+1,j) & \text{at rate } i\left(1-\frac{i}{N}\right)(1-\varepsilon). \end{cases} \tag{2.3.1}$$

We again consider the rescaled process, and determine the effect that adding selection in exchange has on the limiting structure. Contrary to the two previous models, we now do not consider weak selection since this would have little effect in the limit $N\to\infty$.

Proposition 2.3.1. *Assume that (2.1.8) and (2.2.2) hold. For all $f \in B$ and $(x_N, y_M) \in I_N \times I_M$,*

$$\lim_{N\to\infty} (L_N f)(x_N,y_M) = (Lf)(x,y) \quad \text{if} \quad \lim_{N\to\infty}(x_N,y_M) = (x,y) \in [0,1]^2, \tag{2.3.2}$$

where L is given by

$$\begin{aligned}(Lf)(x,y) = c(y-x)\frac{\partial f}{\partial x}(x,y) + \sigma x(1-x)\frac{\partial f}{\partial x}(x,y) - cry\frac{\partial f}{\partial x}(x,y) \\ + cK(x-y)\frac{\partial f}{\partial y}(x,y) + cKry\frac{\partial f}{\partial y}(x,y) + x(1-x)\frac{\partial^2 f}{\partial x^2}(x,y).\end{aligned} \tag{2.3.3}$$

Proof. As the new selection parameter changes the rate c_j^{dorm}, which corresponds to transitions in the x- and y-value of f, we will see changes in all partial derivates of f. Using the same methods as before, we get

$$
\begin{aligned}
&(L_N f)(x_N, y_M) \\
&\quad = f_x(x_N, y_M)\left[c(y_M - x_N) - c r y_M + \frac{\sigma}{N} N x_N (1 - x_N)\left(1 - \frac{c}{N}\right)\right] \\
&\quad + K f_y(x_N, y_M)\left[c(x_N - y_M) + c r y_M\right] \\
&\quad + \frac{1}{2N} f_{xx}(x_N, y_M)\left[c(x_N + y_M) - c r y_M + \left(2 - \frac{\sigma}{N}\right) N x_N (1 - x_N)\left(1 - \frac{c}{N}\right)\right] \\
&\quad + \frac{K}{N} f_{xy}(x_N, y_M)\left[c(-x_N - y_M) + c r y_M\right] + \frac{K^2}{2N} f_{yy}(x_N, y_M)\left[c(x_N + y_M) - c r y_M\right] \\
&\quad + O\left(\frac{1}{N^2}\right).
\end{aligned}
\tag{2.3.4}
$$

Taking the limit $N \to \infty$, we obtain $(Lf)(x, y)$. □

We recognize the following set of SDEs from the limiting generator.

COROLLARY 2.3.2. *Under the conditions of Proposition 2.3.1, if* $\lim_{N\to\infty} \overline{X}_0^N = x$ *a.s. and* $\lim_{N\to\infty} \overline{Y}_0^M = y$ *a.s., then*

$$
w - \lim_{N\to\infty} \left(\overline{X}_t^N, \overline{Y}_t^M\right)_{t\geq 0} = (X_t, Y_t)_{t\geq 0}. \tag{2.3.5}
$$

The process $(X_t, Y_t)_{t\geq 0}$ *is the two-dimensional diffusion on* $[0,1]^2$ *solving*

$$
\begin{aligned}
dX_t &= c(Y_t - X_t)\, dt + \sigma X_t(1 - X_t)\, dt - c r Y_t\, dt + \sqrt{2X_t(1 - X_t)}\, dW_t, \\
dY_t &= cK(X_t - Y_t)\, dt + cK r Y_t\, dt,
\end{aligned}
\tag{2.3.6}
$$

with initial conditions $X_0 = x$, $Y_0 = y$ *and where* $(W_t)_{t\geq 0}$ *is standard Brownian motion.*

2.4. Moran model with seed-bank and migration

In this section we consider a spatial version of the models introduced so far, by considering multiple colonies and migration between colonies. We do not allow individuals to actually migrate, but rather their genetic types, namely, individuals will be allowed to choose an ancestor from another colony. We adapt only the simplest model introduced in Section 2.1.

Consider an arbitrary undirected graph $G = (V, E)$, where V denotes the set of vertices and E the set of edges. Without loss of generality, we may assume that G is connected. Each vertex of the graph contains a colony, which consists of an active population of size N and a seed-bank of size M. For $u, v \in V$, let $p(u, v)$ be a transition kernel on V that determines the migration. Consider ε and δ as before.

The dynamics of the model are as follows:

- An active individual in colony $u \in V$ at rate 1 either:
  (1) with probability $(1-\varepsilon)p(u, v)$ produces another active individual which first chooses a colony $v \in V$ and then an ancestor in this colony uniformly at random;

(2) or with probability ε produces an individual that becomes dormant in the seed-bank.

- A dormant individual in colony $u \in V$ at rate 1 either:
  (1) with probability $(1-\delta)$ remains dormant in the seed-bank;
  (2) or with probability δ leaves the seed-bank and becomes active.

Note that in the resampling mechanism we allow the chosen colony v to be equal to u itself. Furthermore, migration only occurs in the active population and hence the dynamics for the seed-bank individuals do not change.

For each $u \in V$, let $X_t^{(u),N}$ and $Y_t^{(u),M}$ be the number of individuals of type A at time t in colony u, in the active and the dormant population, respectively. Then $(X_t^{(u),N}, Y_t^{(u),M})_{t\geq 0}$ is the continuous-time Markov process on state space $\{0,\dots,N\}\times\{0,\dots,M\}$, with transitions:

$$(i,j) \to \begin{cases} (i-1,j+1) & \text{at rate } i\varepsilon \\ (i+1,j-1) & \text{at rate } j\delta \\ (i-1,j) & \text{at rate } i(1-\varepsilon)\sum_{v\in V}\left[p(u,v)\left(\frac{N-X_t^{(v),N}}{N}\right)\right] \\ (i+1,j) & \text{at rate } (N-i)\,(1-\varepsilon)\sum_{v\in V}\left[p(u,v)\frac{X_t^{(v),N}}{N}\right]. \end{cases} \tag{2.4.1}$$

We consider the transition kernel

$$p(u,v) = (1-\nu)\delta_{u,v} + \nu q(u,v), \quad u,v \in V, \tag{2.4.2}$$

where $\nu \in [0,1]$ is the migration parameter, $\delta_{u,v} = \mathbb{1}\{u=v\}$ and $q(u,v)$ is a prescribed transition kernel. Here we may assume that $q(u,u) = 0$ for all $u \in V$. Thus, with probability $1-\nu$ an active individual chooses its own colony u, while with probability ν it chooses a different colony v according to $q(u,v)$.

To obtain a limiting distribution, we now also assume *weak migration*, i.e., we assume that there exists a $w \in (0,\infty)$ such that

$$\nu = \frac{w}{N}. \tag{2.4.3}$$

We again consider the rescaled process and determine the limiting generator, as in the previous sections. Since we consider multiple colonies, we obtain a rescaled process and a generator for each $u \in V$. This will eventually lead to a system of coupled SDEs.

For $u \in V$, write $x_N^{(u)}$ and $y_M^{(u)}$ for the fractions of individuals of type A in colony u, in the active and the dormant population, respectively. We obtain a generator for each $u \in V$, given by (2.1.7).

PROPOSITION 2.4.1. *Assume that* (2.1.8) *and* (2.4.3) *hold. For all* $f \in B$ *and* $(x_N^{(u)}, y_M^{(v)}) \in I_N \times I_M$,

$$\lim_{N\to\infty} \left(L_N^{(u)}\right)\left(x_N^{(u)}, y_M^{(u)}\right) = \left(L^{(u)} f\right)\left(x^{(u)}, y^{(u)}\right), \quad u \in V \tag{2.4.4}$$

if

$$\lim_{N\to\infty} \left(x_N^{(u)}, y_M^{(u)}\right) = \left(x^{(u)}, y^{(u)}\right) \in [0,1]^2, \quad u \in V. \tag{2.4.5}$$

The limiting generator $L^{(u)}$ *is given by*

$$\begin{aligned}
&\left(L^{(u)} f\right)\left(x^{(u)}, y^{(u)}\right) \\
&= \left[c\left(y^{(u)} - x^{(u)}\right) - x^{(u)} + \sum_{v\in V}\left((1-w)\delta_{u,v} + wq(u,v)\right)x^{(v)}\right]\frac{\partial f}{\partial x}\left(x^{(u)}, y^{(y)}\right) \\
&\quad + cK\left(x^{(u)} - y^{(u)}\right)\frac{\partial f}{\partial y}\left(x^{(u)}, y^{(u)}\right) + x^{(u)}\left(1 - x^{(u)}\right)\frac{\partial^2 f}{\partial x^2}\left(x^{(u)}, y^{(u)}\right).
\end{aligned} \tag{2.4.6}$$

PROOF. If we compare the multi-colony model with the Moran model introduced in Section 2.1, we note the following:

(i) We do not change the rates c_i^{act} and c_j^{dorm}, so any term in the generator consisting only of these rates has the same limit as in the single-colony model. The only difference is that we obtain this limit for each colony $u \in V$.

(ii) The remainder term in the Taylor expansions is again of order $O(1/N^3)$, and the rates are again at most of order $O(N)$. It follows that the total error term in the approximation is of order $O(1/N^2)$. As we multiply the generator with a factor N, this becomes order $O(1/N)$ and converges to zero in the limit $N \to \infty$.

We thus only have changes in the rates d_i^{act} and b_i^{act}, which leads to a change in the derivatives of f in the x-value. It follows that

$$
\begin{aligned}
&\left(L_N^{(u)} f\right)\left(x_N^{(u)}, y_M^{(u)}\right) = \\
&\quad f_x\left(x_N^{(u)}, y_M^{(u)}\right)\left[c\left(y_M - x_N\right) + \left(1 - \frac{c}{N}\right)\left(-x_N^{(u)} + \sum_{v\in V}((1-w)\delta_{u,v} + wq(u,v))x_N^{(v)}\right)\right] \\
&\quad + K f_y\left(x_N^{(u)}, y_M^{(u)}\right) c\left(x_N^{(u)} - y_M^{(u)}\right) \\
&\quad + \frac{1}{2N} f_{xx}\left(x_N^{(u)}, y_M^{(u)}\right)\left[c\left(x_N^{(u)} + y_M^{(u)}\right) + 2N x_N^{(u)}\left(1 - x_N^{(u)}\right)\left(1 - \frac{c}{N}\right)\left(1 - \frac{w}{N}\right)\right. \\
&\quad \left. + \left(1 - \frac{c}{N}\right)\left(x_N^{(u)} \sum_{v\neq u} wq(u,v)\left(1 - x_N^{(v)}\right) + \left(1 - x_N^{(u)}\right)\sum_{v\neq u} wq(u,v) x_N^{(v)}\right)\right] \\
&\quad + \frac{K}{N} f_{xy}\left(x_N^{(u)}, y_M^{(u)}\right) c\left(-x_N^{(u)} - y_M^{(u)}\right) + \frac{K^2}{2N} f_{yy}\left(x_N^{(u)}, y_M^{(u)}\right) c\left(x_N^{(u)} + y_M^{(u)}\right) \\
&\quad + O\left(\frac{1}{N}\right).
\end{aligned} \tag{2.4.7}
$$

If $N \to \infty$, then we obtain the limit $\left(L^{(u)} f\right)\left(x^{(u)}, y^{(u)}\right)$. □

As we now have a limiting generator for each colony u, that may depend on the state in the other colonies v, we obtain a system of coupled SDEs.

Corollary 2.4.2. *Under the conditions of Proposition 2.4.1, if, for each $u \in V$, $\lim_{N\to\infty} \overline{X}_0^{(u)} = x^{(u)}$ a.s. and $\lim_{N\to\infty} \overline{Y}_0^{(u)} = y^{(u)}$ a.s., then*

$$
w - \lim_{N\to\infty} \left(\overline{X}_t^{(u)}, \overline{Y}_t^{(u)}\right)_{t\geq 0} = \left(X_t^{(u)}, Y_t^{(u)}\right)_{t\geq 0}. \tag{2.4.8}
$$

The process $(X_t^{(u)}, Y_t^{(u)})_{t\geq 0}$ is the two-dimensional diffusion on $[0,1]^2$ solving

$$
\begin{aligned}
dX_t^{(u)} &= c\left(Y_t^{(u)} - X_t^{(u)}\right)\, dt - X_t^{(u)}\, dt \\
&\quad + \sum_{v\in V}\left((1-w)\delta_{u,v} + wq(u,v)\right) X_t^{(v)}\, dt + \sqrt{2X_t^{(u)}\left(1 - X_t^{(u)}\right)}\, dW_t, \\
dY_t^{(u)} &= cK\left(X_t^{(u)} - Y_t^{(u)}\right)\, dt,
\end{aligned} \tag{2.4.9}
$$

with initial conditions $X_0^{(u)} = x^{(u)}$, $Y_0^{(u)} = y^{(u)}$ and where $(W_t)_{t\geq 0}$ is standard Brownian motion.

One natural choice for the transition kernel $q(u,v)$ is to let the migration from colony to colony happen with equal probability between neighbours. This corresponds to

$$q(u,v) = \begin{cases} \frac{1}{d(u)} & \text{if } (u,v) \in E, \\ 0 & \text{otherwise,} \end{cases} \tag{2.4.10}$$

where $d(u)$ denotes the degree of vertex u in G. As a consequence, the system of coupled SDEs given in Corollary 2.4.2 simplifies to

$$\begin{aligned} dX_t^{(u)} &= c\left(Y_t^{(u)} - X_t^{(u)}\right)\, dt - X_t^{(u)}\, dt \\ &\quad + \sum_{(u,v)\in E} \left((1-w)\delta_{u,v} + \frac{w}{d(u)}\right) X_t^{(v)}\, dt + \sqrt{2X_t^{(u)}\left(1 - X_t^{(u)}\right)}\, dW_t, \\ dY_t^{(u)} &= cK\left(X_t^{(u)} - Y_t^{(u)}\right)\, dt. \end{aligned} \tag{2.4.11}$$

2.5. Wright-Fisher model with seed-bank and selection in resampling

Adding selection in resampling to the model is relatively straightforward in continuous time, as seen in Section 2.2. However, it is also possible to do this in a discrete-time setting. In this section we adapt the Wright-Fisher model with seed-bank from [4] by adding selection, and we show that we obtain the same diffusion limit as in Corollary 2.2.2, up to a factor two time speed.

We again consider a haploid population where each individual carries a genetic type from $E = \{A, a\}$. The population consists of an active population of size N, and a seed-bank of size M. Given $N, M \in \mathbb{N}$, let $\varepsilon \in [0,1]$ be such that $\varepsilon N \le M$ and set $\delta = \varepsilon N/M$. Let $s \in [0,1]$. The dynamics of the model are as follows:

- The N active individuals produce $(1-\varepsilon)N$ active individuals in the next generation. Each new individual chooses a parent from the previous generation according to p_i and adopt its type. Here, p_i is the probability that an individual in the next generation chooses a parent of type A from the current generation, given that there are i individuals of type A in the current generation, i.e.,

$$p_i = \frac{(1+s)i}{(1+s)i + N - i}. \tag{2.5.1}$$

- The remaining $\varepsilon N = \delta M$ individuals from the active population become dormant in the seed-bank.
- From the seed-bank, $\delta M = \varepsilon N$ individuals become active and leave the seed-bank.
- The remaining $(1-\delta)M$ individuals remain inactive in the seed-bank.

Thus, in the next generation, the active population again consists of $(1-\varepsilon)N + \varepsilon N = N$ individuals. Similarly, the dormant population again consists of $\delta M + (1-\delta)M = M$ individuals.

Let X_n^N and Y_n^M denote the fraction of individuals of type A in generation n, in the active and the dormant population, respectively. Then $(X_n^N, Y_n^M)_{n\in\mathbb{N}_0}$ is the discrete-time Markov chain with state space $I_N \times I_M$. Abbreviate

$$\mathbb{P}_{x,y}(\cdot) = \mathbb{P}(\,\cdot \mid X_0^N = x, Y_0^M = y), \quad (x,y) \in I_N \times I_M. \tag{2.5.2}$$

If $x \in I_N$ and $x = i/N$ for some $i \in \{0, \dots, N\}$ then (2.5.1) becomes

$$p_i = \frac{(1+s)i/N}{(1+s)i/N + 1 - i/N} = \frac{(1+s)x}{(1+s)x + 1 - x} = \frac{(1+s)x}{1+sx}. \tag{2.5.3}$$

From now on we will denote this probability by p_x. Note that X_{n+1}^N is binomially distributed with parameters N and p_x, given that $X_n^N = x$. Denote by $Z \sim \mathcal{D}$ that the random variable Z is distributed according to distribution $\mathcal{D}$. We have the following transition probabilities.

PROPOSITION 2.5.1. *Let $c = \varepsilon N = \delta M$. For $(x,y), (\bar{x}, \bar{y}) \in I_N \times I_M$,*

$$\mathbb{P}_{x,y}(X_1^N = \bar{x}, Y_1^M = \bar{y}) = \sum_{i=0}^{c} \mathbb{P}_{x,y}(Z = i)\mathbb{P}_{x,y}(U = \bar{x}N - i)\mathbb{P}_{x,y}(V = (\bar{y} - y)M + i), \tag{2.5.4}$$

where Z, U, V are independent under $\mathbb{P}_{x,y}$ and $Z \sim \mathrm{Hyp}_{M,c,yM}, U \sim \mathrm{Bin}_{N-c,p_x}$ and $V \sim \mathrm{Bin}_{c,x}$. Here, $\mathrm{Hyp}_{M,c,ym}$ denotes the hypergeometric distribution with parameters M, c and yM, and Bin_{N-c,p_x} denotes the binomial distribution with parameters $N - c$ and p_x.

PROOF. The interpretation of the random variables introduced above is as follows:

- Z is the number of active individuals in generation 1 that originate from a dormant individual (or seed) of type A in generation 0. The total size of the seed-bank is equal to M, and the number of seeds in generation 0 of type A is equal to yM. There are $\delta M = c$ seeds that become active, so this indeed corresponds to a hypergeometric distribution with parameters M, c and yM.
- U is the number of active individuals in generation 1 that are offspring of active individuals of type A in generation 0. There is a total of $(1-\varepsilon)N = N - c$ individuals that are offspring of active individuals in generation 0. As each of these individuals chooses a parent of type A with probability p_x, it follows that U has a binomial distribution with parameters $N - c$ and p_x.
- V is the number of dormant individuals in generation 1 that originate from active individuals of type A in generation 0. There are $\varepsilon N = c$ active individuals that become dormant, and with probability x each of these individuals is of type A. It thus follows that V is binomially distributed with parameters c and x.

By construction, we have that

$$X_1^N = \frac{U+Z}{N}, \quad Y_1^M = y + \frac{V-Z}{M}. \tag{2.5.5}$$

As the random variables Z, U and V are all independent under $\mathbb{P}_{x,y}$, the claim follows. □

We now consider the same space-time rescaling of the process and the same scaling of the parameters as before, and show that the process converges to the diffusion limit from Corollary

2.2.2, up to a factor two time speed. The generator of the process acting on $f \in B$ is now given by

$$(L_N f)(x_N, y_M) = N\mathbb{E}_{x_N,y_M}\left[f\left(X_1^N, Y_1^N\right) - f(x_N, y_M)\right], \quad (x_N, y_M) \in I_N \times I_M. \tag{2.5.6}$$

PROPOSITION 2.5.2. *Assume that* (2.1.8) *and* (2.2.2) *hold. For all* $f \in B$ *and* $(x_N, y_M) \in I_N \times I_M$,

$$\lim_{N\to\infty} (L_N f)(x_N, y_M) = (Lf)(x, y) \quad \text{if} \quad \lim_{N\to\infty} (x_N, y_M) = (x, y) \in [0, 1]^2, \tag{2.5.7}$$

where L *is given by*

$$(Lf)(x, y) = c(y - x)\frac{\partial f}{\partial x}(x, y) + \sigma x(1 - x)\frac{\partial f}{\partial x}(x, y) + cK(x - y)\frac{\partial f}{\partial y}(x, y) + \frac{1}{2}x(1 - x)\frac{\partial^2 f}{\partial x^2}(x, y). \tag{2.5.8}$$

PROOF. We use Taylor expansion of $f(X_1^N, Y_1^N)$ around (x_N, y_M) up to second order, and substitute this into (2.5.6). This yields

$$\begin{aligned}
(L_N f)(x_N, y_M) = N\Bigg[& f_x(x_N, y_M)\mathbb{E}_{x_N,y_M}[X_1^N - x_N] + f_y(x_N, y_M)\mathbb{E}_{x_N,y_M}[Y_1^M - y_M] \\
& + \frac{1}{2}f_{xx}(x_N, y_M)\mathbb{E}_{x_N,y_M}[(X_1^N - x_N)^2] \\
& + f_{xy}(x_N, y_M)\mathbb{E}_{x_N,y_M}[(X_1^N - x_N)(Y_1^M - y_M)] \\
& + \frac{1}{2}f_{yy}(x_N, y_M)\mathbb{E}_{x_N,y_M}[(Y_1^M - y_M)^2] \\
& + \mathbb{E}_{x_N,y_M}\Bigg[\sum_{\substack{\alpha,\beta\in\mathbb{N}_0\\ \alpha+\beta=3}} R^N_{\alpha,\beta}(X_1^N, Y_1^M)(X_1^N - x_N)^\alpha (Y_1^M - y_M)^\beta\Bigg]\Bigg].
\end{aligned} \tag{2.5.9}$$

For $x, y \in [0, 1]^2$ and $\alpha, \beta \in \mathbb{N}_0$ such that $\alpha + \beta = 3$, we have

$$R^N_{\alpha,\beta}(x, y) = \frac{\alpha + \beta}{\alpha!\beta!}\int_0^1 (1 - t)^{\alpha+\beta-1}\frac{\partial^3 f}{\partial x^\alpha y^\beta}(x_N - t(x_N - x), y_M - t(y_M - y))\, dt. \tag{2.5.10}$$

We next calculate and bound all the moments. Before doing so, we first state some basic facts that will be used in the calculations. By Proposition 2.5.1, we have that

$$X_1^N = \frac{1}{N}(U + Z), \quad Y_1^M = \frac{1}{M}(y_M M + V - Z), \tag{2.5.11}$$

where $Z \sim \mathrm{Hyp}_{M,c,y_M M}$, $U \sim \mathrm{Bin}_{N-c,p_{x_N}}$ and $V \sim \mathrm{Bin}_{c,x_N}$. It immediately follows that

$$\mathbb{E}_{x_N,y_M}[Z] = cy_M, \quad \mathbb{E}_{x_N,y_M}[V] = cx_N, \tag{2.5.12}$$

and

$$\mathbb{E}_{x_N,y_M}[U] = (N - c)p_{x_N}, \ \mathrm{Var}_{x_N,y_M}[U] = (N - c)p_{x_N}(1 - p_{x_N}), \ \mathrm{Skew}_{x_N,y_M}[U] = \frac{1 - 2p_{x_N}}{\sqrt{\mathrm{Var}[U]}}. \tag{2.5.13}$$

Here, the skewness of a random variable X is defined as

$$\text{Skew}[X] = \frac{\mathbb{E}[(X - \mathbb{E}[X])^3]}{\text{Var}[X]^{\frac{3}{2}}}. \tag{2.5.14}$$

As $s = \sigma/N$ and $N \to \infty$, we can use Taylor expansion of $1/(1+sx)$ around $s = 0$. For $x \in I_N$, we have

$$p_x = \frac{(1+s)x}{1+sx} = (1+s)x(1 - sx + O(s^2)) = x - sx^2 + sx + O(s^2). \tag{2.5.15}$$

Finally, we have that $0 \le V \le c$ and $0 \le Z \le c$. It follows that $|Z - cx_N| \le c$ and $|V - Z| \le c$, and hence for every $\alpha \in \mathbb{N}_0$,

$$\left|\mathbb{E}_{x_N,y_M}[(Z - cx_N)^\alpha]\right| \le c^\alpha, \quad \left|\mathbb{E}_{x_N,y_M}[(V - Z)^\alpha]\right| \le c^\alpha. \tag{2.5.16}$$

For every $\alpha, \beta \in \mathbb{N}_0$ we therefore have

$$\left|\mathbb{E}_{x_N,y_M}[(Z - cx_N)^\alpha (V - Z)^\beta]\right| \le c^{\alpha+\beta}. \tag{2.5.17}$$

We are now ready to calculate the terms in the generator. We will do this per partial derivative of f. For the first moments, we have

$$\begin{aligned} N\mathbb{E}_{x_N,y_M}[X_1^N - x_N] &= \mathbb{E}_{x_N,y_M}[U + Z] - Nx_N \\ &= (N - c)(x_N - sx_N^2 + sx_N + O(s^2)) + cy_M - Nx_N \\ &= c(y_M - x_N) + \sigma x_N(1 - x_N) + O\left(\frac{1}{N}\right), \end{aligned} \tag{2.5.18}$$

where we use (2.5.11), (2.5.12), (2.5.13), (2.5.15) and (2.2.2) consecutively, and

$$N\mathbb{E}_{x_N,y_M}[Y_1^M - y_M] = \frac{N}{M}\mathbb{E}_{x_N,y_M}[V - Z] = cK(x_N - y_M), \tag{2.5.19}$$

where we use (2.5.11), (2.5.12) and (2.1.8).

To calculate the second moments, note that from (2.5.15) we also have

$$\mathbb{E}_{x_N,y_M}[U] = (N - c)p_{x_N} = (N - c)x + O(1). \tag{2.5.20}$$

From this, and the fact that $X_1^N - x_N = \frac{1}{N}(U - (N - c)x_N) + \frac{1}{N}(Z - cx_N)$, it follows that

$$\begin{aligned} \frac{N}{2}\mathbb{E}_{x_N,y_M}[(X_1^N - x_N)^2] &= \frac{1}{2N}\mathbb{E}_{x_N,y_M}[(U - (N - c)x_N)^2] \\ &\quad + \frac{1}{N}\mathbb{E}_{x_N,y_M}[(U - (N - c)x_N)(Z - cx_N)] \\ &\quad + \frac{1}{2N}\mathbb{E}_{x_N,y_M}[(Z - cx_N)^2] \\ &= \frac{1}{2N}\text{Var}_{x_N,y_M}[U] + O\left(\frac{1}{N}\right) + \frac{1}{2N}\mathbb{E}_{x_N,y_M}[(Z - cx_N)^2] \\ &= \frac{1}{2N}\text{Var}_{x_N,y_M}[U] + O\left(\frac{1}{N}\right), \end{aligned} \tag{2.5.21}$$

where we use (2.5.12) in the second to last equality and (2.5.17) in the last equality. Using (2.5.13) and (2.5.15), we conclude that

$$\frac{N}{2}\mathbb{E}_{x_N,y_M}[(X_1^N - x_N)^2] = \frac{1}{2N}\mathrm{Var}_{x_N,y_M}[U] + O\left(\frac{1}{N}\right) = \frac{1}{2}x(1-x) + O\left(\frac{1}{N}\right). \tag{2.5.22}$$

As these are the only terms we expect to see in our limiting generator, it remains to show that the other moments converge to zero as $N \to \infty$. First,

$$\begin{aligned} &N\mathbb{E}_{x_N,y_M}[(X_1^N - x_N)(Y_1^M - y_M)] \\ &= \frac{1}{M}\mathbb{E}_{x_N,y_M}[(U-(N-c)x_N)]\mathbb{E}_{x_N,y_M}[V-Z] + \frac{1}{M}\mathbb{E}_{x_N,y_M}[(Z-cx_N)(V-Z)] \\ &= \frac{K}{N}\mathbb{E}_{x_N,y_M}[(U-(N-c)x_N)]\mathbb{E}_{x_N,y_M}[V-Z] + \frac{K}{N}\mathbb{E}_{x_N,y_M}[(Z-cx_N)(V-Z)], \end{aligned} \tag{2.5.23}$$

where we use (2.5.11) and the fact that $X_1^N - x_N = 1/N(U-(N-c)x_N) + 1/N(Z-cx_N)$. Using (2.5.17) and (2.5.20), we easily find that

$$N\mathbb{E}_{x_N,y_M}[(X_1^N - x_N)(Y_1^M - y_M)] = O\left(\frac{1}{N}\right) \tag{2.5.24}$$

Next,

$$\frac{N}{2}\mathbb{E}_{x_N,y_M}[(Y_1^M - y_M)^2] = \frac{K^2}{2N}\mathbb{E}_{x_N,y_M}[(V-Z)^2] = O\left(\frac{1}{N}\right), \tag{2.5.25}$$

where we use (2.5.11), (2.5.17) and (2.1.8).

Lastly, we have to bound the remainder term in the Taylor expansion. Since $f \in B$, all third order derivatives of f are bounded, and hence we can bound $R^N_{\alpha,\beta}$ uniformly. It thus remains to be shown that the mixed moments $N\mathbb{E}_{x_N,y_M}[(X_1^N - x)^\alpha(Y_1^M - y)^\beta]$ are bounded, for all $\alpha, \beta \in \mathbb{N}_0$ such that $\alpha + \beta = 3$. Let $\alpha, \beta \in \mathbb{N}_0$ be such that $\alpha + \beta = 3$. Then

$$\begin{aligned} &N\mathbb{E}_{x_N,y_M}[(X_1 - x_N)^\alpha(Y_1^M - y_M)^\beta] \\ &= \frac{N}{N^\alpha M^\beta}\sum_{i=0}^{\alpha}\binom{\alpha}{i}\mathbb{E}_{x_N,y_M}[(U-(N-c)x_N)^i]\mathbb{E}_{x_N,y_M}[(Z-cx_N)^{\alpha-i}(V-Z)^\beta]. \end{aligned} \tag{2.5.26}$$

Note that, for all α, β and i, the mixed moments of $Z - cx_N$ and $V - Z$ are of order $O(1)$, due to (2.5.17). We thus have to check the moments of $(U-(N-c)x_N)^\alpha$ for $\alpha \in \{0,1,2,3\}$.

If $\alpha = 0$, then it is trivially of order $O(1)$. For $\alpha = 1$, it is also of order $O(1)$, due to (2.5.20). If $\alpha = 2$, then using the previous calculations we have

$$\mathbb{E}_{x_N,y_M}[(U-(N-c)x_N)^2] = \mathrm{Var}_{x_N,y_M}[U] + O(1) = O(N). \tag{2.5.27}$$

If $\alpha = 3$, then using (2.5.13) we find

$$\begin{aligned} \mathbb{E}_{x_N,y_M}[(U-(N-c)x_N)^3] &= \mathrm{Skew}_{x_N,y_M}[U](\mathrm{Var}_{x_N,y_M}[U])^{\frac{3}{2}} + O(1) \\ &= (1-2p_{x_N})\mathrm{Var}_{x_N,y_M}[U] + O(1) \\ &= O(N). \end{aligned} \tag{2.5.28}$$

We thus see that the leading term in the mixed moments is of order $O(N)$. It follows that

$$N\mathbb{E}_{x_N,y_M}[(X_1-x_N)^\alpha(Y_1^M-y_M)^\beta]=\frac{N}{N^\alpha M^\beta}O(N)=O\left(\frac{1}{N}\right), \tag{2.5.29}$$

where we use the above bounds and the scaling of M in (2.1.8).

Combining all the previous computations, we get

$$\begin{aligned}&\lim_{N\to\infty}(L_Nf)(x_N,y_M)\\&\quad=c(y-x)f_x(x,y)+\sigma x(1-x)f_x(x,y)+cK(x-y)f_y(x,y)+\frac{1}{2}x(1-x)f_{xx}(x,y).\end{aligned} \tag{2.5.30}$$

□

Thus, we see that, up to a factor two in time speed, we indeed obtain the same limiting generator as in Proposition 2.2.1.

Corollary 2.5.3. *Under the conditions of Proposition 2.5.2, if* $\lim_{N\to\infty}\overline{X}_0^N=x$ *a.s. and* $\lim_{N\to\infty}\overline{Y}_0^M=y$ *a.s., then*

$$w-\lim_{N\to\infty}\left(\overline{X}_t^N,\overline{Y}_t^M\right)_{t\geq 0}=(X_t,Y_t)_{t\geq 0}. \tag{2.5.31}$$

The process $(X_t,Y_t)_{t\geq0}$ *is the two-dimensional diffusion on* $[0,1]^2$ *solving*

$$\begin{aligned}dX_t&=c(Y_t-X_t)\,dt+\sigma X_t(1-X_t)\,dt+\sqrt{X_t(1-X_t)}\,dW_t,\\dY_t&=cK(X_t-Y_t)\,dt,\end{aligned} \tag{2.5.32}$$

with initial conditions $X_0=x$, $Y_0=y$ *and where* $(W_t)_{t\geq0}$ *is standard Brownian motion.*

A similar extension may be done for the models introduced in Section 2.3 and Section 2.4, by adding selection in resampling and exchange and by adding migration to the Wright-Fisher model with seed-bank.

CHAPTER 3

Multi-colony Moran model with migration and mutation

In this chapter, we consider a model with simpler dynamics, namely, without seed-bank, to develop a benchmark to which we can refer in Chapter 4. We consider a multi-colony Moran model on a discrete torus with sequential dynamics consisting of resampling, mutation and migration. If an individual does not mutate, then it may resample from another colony, which we refer to as migration. We are interested in calculating the probability $\Psi(x, y)$ at equilibrium that two individuals from colonies x and y are *identical by descent*, i.e., they share a common ancestor without encountering a mutation in their ancestral line.

In Section 3.1 we define the model. In Section 3.2 we define $\Psi(x, y)$ and relate it to $F_t(x, y)$, $t \geq 0$, the probability density per unit of time that the two individuals from colonies x and y share their most recent common ancestor at time t. We then derive a recursion relation for $F_t(x, y)$ in Section 3.3. This implies a relation for $\Psi(x, y)$, which allows us to compute its Fourier transform $\hat{\Psi}(\theta)$ in Section 3.4. In Section 3.5 we show that, for a special choice for the migration, we can apply Fourier inversion on $\hat{\Psi}(\theta)$ to obtain a closed form expression for $\Psi(x, 0)$. It follows that $\Psi(x, 0)$ can be expressed in terms of the Green function of a simple random walk.

3.1. Definition of the model

For $L \in \mathbb{N}$, consider the discrete torus $\mathbb{T} = \mathbb{Z}^d \cap [0, L]^d$ in any dimension $d \in \mathbb{N}$, with periodic boundary conditions. Each site contains a colony of N individuals. Define the base-types $\{A, a\}$. A mutation changes the type of an individual into a new type. In absence of mutation, an individual may migrate and resample.

Formally, let $\mu, \nu \in \mathbb{R}_{>0}$ be the rate of the mutation and migration, respectively. Let $p(x, y)$ be a translation-invariant transition kernel on $\mathbb{T}$. The dynamics of the model are as follows. An individual in colony x mutates to a new type at rate μ and migrates at rate ν. In the event of migration, it chooses a colony y with probability $p(x, y)$, from which it chooses an ancestor uniformly at random.

3.2. Probability of being identical by descent

Fix $x, y \in \mathbb{T}$. Define $\Psi(x, y)$ to be the probability at equilibirum that two individuals from colonies x and y are identical by descent, i.e., they share a common ancestor without encountering a mutation in their ancestral lines. If $x = y$, then we assume that the two individuals drawn are distinct.

Consider the model in which we only allow migration at rate ν, and let $F_t(x,y)$ be the probability density per unit of time that two individuals drawn from colonies x and y share their most recent common ancestor at time t. In the model with mutation, an individual undergoes mutation at rate $\mu \in \mathbb{R}_{>0}$. The probability that the two individuals do not encounter a mutation up until time t is therefore equal to $e^{-2\mu t}$. We thus obtain the following relation between $\Psi(x,y)$ and $F_t(x,y)$, $t \geq 0$:

$$\Psi(x,y) = \int_0^\infty e^{-2\mu t} F_t(x,y)\ dt. \tag{3.2.1}$$

Note that, as the rates of the model only depend on the distance between x and y, the same is true for $F_t(x,y)$ and $\Psi(x,y)$, i.e., $F_t(x,y) = F_t(x-y,0)$ and $\Psi(x,y) = \Psi(x-y,0)$.

3.3. Recursion relation

We can derive a recursion relation for $F_t(x,y)$ by reasoning as follows. We integrate over the time interval $[0,t]$ and consider the event in which only one of the individuals undergoes a change in this time interval. Say that this happens at a time s, and that the individual in colony x changes to colony z (possibly $x = z$). If coalescence of the two ancestral lines does not happen at time s, then it is clear that we should subsequently consider $F_{t-s}(z,y)$. Note that it is sufficient to consider the event in which only one of the individuals changes. Indeed, if both do not change, then nothing happens, while the event of them both changing at the same time has probability zero.

Before we start, we state some basic facts that we use throughout the calculations. Write $Z \sim \mathcal{D}$ when the random variable Z has distribution $\mathcal{D}$. Let $X_1, \ldots, X_n$ be independently exponentially distributed with parameters $\lambda_1, \ldots, \lambda_n$, respectively, i.e., $X_i \sim \text{Exp}(\lambda_i)$. Denote the distribution function and the density function of X_i by G_i and g_i, respectively. We have that

$$\mathbb{P}(X_i > x) = 1 - G_i(x) = e^{-\lambda_i x}, \quad g_i(x) = \lambda_i e^{-\lambda_i x}, \quad x \in \mathbb{R}_{>0}. \tag{3.3.1}$$

Using this, we obtain the following recursion relation.

Proposition 3.3.1. *For $x, y \in \mathbb{T}$ and $t \geq 0$,*

$$\begin{aligned} F_t(x,y) = \sum_{z\in\mathbb{T}} p(x,z) \Bigg[\int_0^t \nu e^{-2\nu s} \left(\mathbb{1}\{z \neq y\} F_{t-s}(z,y) + \mathbb{1}\{z = y\} \frac{N-1}{N} F_{t-s}(y,y) \right) ds \\ + \mathbb{1}\{z = y\} \frac{1}{N} \nu e^{-2\nu t} \Bigg] \\ + \sum_{z\in\mathbb{T}} p(y,z) \Bigg[\int_0^t \nu e^{-2\nu s} \left(\mathbb{1}\{z \neq x\} F_{t-s}(x,z) + \mathbb{1}\{z = x\} \frac{N-1}{N} F_{t-s}(x,x) \right) ds \\ + \mathbb{1}\{z = x\} \frac{1}{N} \nu e^{-2\nu t} \Bigg]. \end{aligned} \tag{3.3.2}$$

PROOF. Note that we have the same sum twice, with the roles of x and y reversed. It thus suffices to explain the first sum. The only change occuring for individuals is through migration, but we must keep track of whether or not coalescence occurs. The three terms in the sum can be explained as follows:

- In the first term, the probability of one individual not changing before time s is $e^{-\nu s}$, while the probability density of the other individual changing at time s is $\nu e^{-\nu s}$. The product of the two equals the probability in the integral. If the x-individual migrates to a colony $z \neq y$, then no coalescence occurs, and we continue from colonies z and y.
- In the second term, we have the same probability. If the x-individual migrates to colony $z = y$, then with probability $(N-1)/N$ it does not coalesce with the y-individual, and we continue with both (distinct) individuals from colony y.
- In the third term, we account for coalescence occurring. If the x-individual migrates to colony y, then with probability $1/N$ it does coalesce with the y-individual. Recall, however, that we are interested in the existence of the *most recent* common ancestor at time t. If coalescence occurs at time $s \in [0, t)$, then the most recent common ancestor cannot occur at time t. We thus only get a positive contribution when the coalescence happens exactly at time t, which gives the same probability as in the second term, except at time t.

□

Using (3.2.1), we see that Proposition 3.3.1 in turn implies a recursive relation for $\Psi(x, y)$.

PROPOSITION 3.3.2. *For $x, y \in \mathbb{T}$,*

$$\Psi(x,y) = \frac{\nu}{\mu+\nu}\left[\frac{1}{N}p(x,y) - \frac{1}{N}p(x,y)\Psi(0,0) + \sum_{z\in\mathbb{T}}\frac{1}{2}p(x,z)\Psi(z,y) + \frac{1}{2}p(y,z)\Psi(x,z)\right]. \quad (3.3.3)$$

Note that there is some inductive reasoning behind this equation. Namely, $\frac{\nu}{\mu+\nu}$ is the probability that migration occurs before mutation. In the first term, we consider the situation in which we coalesce. In the second term, we have to account for the situation in which we migrate to the same colony but do not coalesce. In the final two terms, we consider the situation in which we migrate to a different colony.

PROOF. Recall that $F_t(x, y)$ consists of twice the same sum, with the roles of x and y reversed. It thus suffices to consider the first sum. First, we simplify:

$$\sum_{z\in\mathbb{T}} \mathbb{1}\{z \neq y\}F_{t-s}(z,y) + \mathbb{1}\{z = y\}\frac{N-1}{N}F_{t-s}(y,y) = \sum_{z\in\mathbb{T}} F_{t-s}(z,y) - \mathbb{1}\{z=y\}\frac{1}{N}F_{t-s}(y,y). \quad (3.3.4)$$

To obtain an expression for $\Psi(x,y)$, we use (3.2.1). As the integral is a linear operator, it suffices to apply this relation to the following three quantities:

$$\sum_{z\in\mathbb{T}} p(x,z) \int_0^t \nu e^{-2\nu s} F_{t-s}(z,y)\ ds, \tag{3.3.5}$$

$$-\sum_{z\in\mathbb{T}} p(x,z) \int_0^t \nu e^{-2\nu s} \mathbb{1}\{z=y\} \frac{1}{N} F_{t-s}(y,y)\ ds, \tag{3.3.6}$$

$$\sum_{z\in\mathbb{T}} p(x,z) \mathbb{1}\{z=y\} \frac{1}{N} \nu e^{-2\nu t}. \tag{3.3.7}$$

For (3.3.5) we have

$$\begin{aligned} &\int_0^\infty e^{-2\mu t} \sum_{z\in\mathbb{T}} p(x,z) \left[\int_0^t \nu e^{-2\nu s} F_{t-s}(z,y)\ ds \right] dt \\ &= \sum_{z\in\mathbb{T}} p(x,z) \int_0^\infty \nu e^{-2(\mu+\nu)s} \left[\int_s^\infty e^{-2\mu(t-s)} F_{t-s}(z,y)\ dt \right] ds \\ &= \frac{\nu}{2(\mu+\nu)} \sum_{z\in\mathbb{T}} p(x,z)\Psi(z,y). \end{aligned} \tag{3.3.8}$$

For (3.3.6) we have

$$\begin{aligned} &\int_0^\infty e^{-2\mu t} \sum_{z\in\mathbb{T}} p(x,z) \left[\int_0^t \nu e^{-2\nu s} \mathbb{1}\{z=y\} \frac{1}{N} F_{t-s}(y,y)\ ds \right] dt \\ &= \frac{1}{N} p(x,y) \int_0^\infty \nu e^{-2(\mu+\nu)s} \left[\int_s^\infty e^{-2\mu(t-s)} F_{t-s}(y,y)\ dt \right] ds \\ &= \frac{1}{N} \frac{\nu}{2(\mu+\nu)} p(x,y)\Psi(0,0), \end{aligned} \tag{3.3.9}$$

where in the last equality we use that $\Psi(y,y) = \Psi(0,0)$ by translation invariance. Similarly, for (3.3.7) we have

$$\frac{1}{N} \frac{\nu}{2(\mu+\nu)} p(x,y). \tag{3.3.10}$$

The second sum in (3.3.2) produces the same terms, only with the roles of x and y reversed. The equivalents of (3.3.8), (3.3.9) and (3.3.10) for the y-individual are hence given by

$$\frac{\nu}{2(\mu+\nu)} \sum_{z\in\mathbb{T}} p(y,z)\Psi(x,z), \quad \frac{1}{N} \frac{\nu}{2(\mu+\nu)} p(y,x)\Psi(0,0), \quad \frac{1}{N} \frac{\nu}{2(\mu+\nu)} p(y,x). \tag{3.3.11}$$

Note that by symmetry, $p(x,y) = p(y,x)$. Adding all terms, we get the desired result. □

As it is not obvious how to determine a closed-form expression for $\Psi(x,y)$ from Proposition 3.3.2, we consider its Fourier transform.

3.4. Fourier analysis

For any dimension $d \in \mathbb{N}$, let $\hat{\mathbb{T}} = \{0, \frac{1}{L}, \dots, \frac{L-1}{L}\}^d$. For $f\colon \mathbb{T} \times \mathbb{T} \to \mathbb{R}$, define the Fourier transform $\hat{f}$ by

$$\hat{f}(\theta, \eta) = \sum_{x,y \in \mathbb{T}} e^{2\pi i(\theta \cdot x + \eta \cdot y)} f(x, y), \quad \theta, \eta \in \hat{\mathbb{T}}, \tag{3.4.1}$$

(cf. [8], Chapter 2, Table 2.1). Here, $\theta \cdot x$ denotes the inner product of θ and x. Conversely, the function f can be retrieved from $\hat{f}$ by using the Fourier inversion formula, defined by

$$f(x, y) = \frac{1}{|\hat{\mathbb{T}}|^2} \sum_{\theta,\eta \in \hat{\mathbb{T}}} e^{-2\pi i(\theta \cdot x + \eta \cdot y)} \hat{f}(\theta, \eta), \quad x, y \in \mathbb{T}, \tag{3.4.2}$$

(cf. [8], Chapter 3, Equations 3.13 and 3.14).

As mentioned before, the rates of the model only depend on the distance between x and y and hence the same holds for $\Psi(x, y)$. It follows that $\hat{\Psi}(\theta, \eta)$ also only depends on one parameter, so it suffices to consider $\hat{\Psi}(\theta) := \hat{\Psi}(\theta, -\theta)$. We thus write:

$$\hat{\Psi}(\theta) = \sum_{x,y \in \mathbb{T}} e^{2\pi i(\theta \cdot (x-y))} \Psi(x - y, 0), \quad \theta \in \hat{\mathbb{T}}. \tag{3.4.3}$$

Using Proposition 3.3.2, we now find an expression for $\hat{\Psi}(\theta)$. Write $\Psi(0) = \Psi(0, 0)$.

PROPOSITION 3.4.1. *For $\theta \in \hat{\mathbb{T}}$,*

$$\hat{\Psi}(\theta) = \frac{\nu}{\mu + \nu} \hat{p}(\theta) \hat{\Psi}(\theta) - \frac{\nu}{\mu + \nu} \frac{1}{N} \hat{p}(\theta) \Psi(0) + \frac{\nu}{\mu + \nu} \frac{1}{N} \hat{p}(\theta). \tag{3.4.4}$$

PROOF. As the Fourier transform is linear, it suffices to apply the Fourier transform to each of the four terms in (3.3.3) separately. For the first term, we have

$$\begin{aligned} &\sum_{x,y \in \mathbb{T}} e^{2\pi i(\theta \cdot (x-y))} \left[\frac{\nu}{\mu + \nu} \sum_{z \in \mathbb{T}} \frac{1}{2} p(x - z, 0) \Psi(z - y, 0) \right] \\ &= \frac{1}{2} \frac{\nu}{\mu + \nu} \sum_{x,y \in \mathbb{T}} \sum_{z \in \mathbb{T}} e^{2\pi i(\theta \cdot (x-z))} p(x - z, 0) e^{2\pi i(\theta \cdot (z-y))} \Psi(z - y, 0) \\ &= \frac{1}{2} \frac{\nu}{\mu + \nu} \hat{p}(\theta) \hat{\Psi}(\theta). \end{aligned} \tag{3.4.5}$$

In the second term, the roles of x and y are reversed. By symmetry, we have that $p(y - z, 0) = p(z - y, 0)$, so for the second term we also have

$$\frac{1}{2} \frac{\nu}{\mu + \nu} \hat{p}(\theta) \hat{\Psi}(\theta). \tag{3.4.6}$$

For the third term, note that $\Psi(0)$ is a constant, and so

$$\sum_{x,y \in \mathbb{T}} e^{2\pi i(\theta \cdot (x-y))} \left[- \frac{\nu}{\mu + \nu} \frac{1}{N} p(x - y, 0) \Psi(0) \right] = - \frac{\nu}{\mu + \nu} \frac{1}{N} \hat{p}(\theta) \Psi(0). \tag{3.4.7}$$

Similarly, for the last term we have

$$\frac{\nu}{\mu+\nu}\frac{1}{N}\hat{p}(\theta). \tag{3.4.8}$$

Adding all terms, we get the desired result. □

From Proposition 3.4.1, we obtain a closed-form expression for $\hat{\Psi}(\theta)$.

THEOREM 3.4.2. *For $\theta \in \hat{\mathbb{T}}$,*

$$\hat{\Psi}(\theta) = \frac{1-\Psi(0)}{N}\frac{\nu\hat{p}(\theta)}{\mu+\nu-\nu\hat{p}(\theta)} \tag{3.4.9}$$

with

$$\Psi(0) = \frac{\frac{1}{N}\frac{1}{|\hat{\mathbb{T}}|^2}\sum_{\theta\in\hat{\mathbb{T}}}\frac{\nu\hat{p}(\theta)}{\mu+\nu-\nu\hat{p}(\theta)}}{1+\frac{1}{N}\frac{1}{|\hat{\mathbb{T}}|^2}\sum_{\theta\in\hat{\mathbb{T}}}\frac{\nu\hat{p}(\theta)}{\mu+\nu-\nu\hat{p}(\theta)}}. \tag{3.4.10}$$

PROOF. From (3.4.4), it follows that

$$\left[1-\frac{\nu}{\mu+\nu}\hat{p}(\theta)\right]\hat{\Psi}(\theta) = \frac{\nu}{\mu+\nu}\frac{1}{N}\hat{p}(\theta)(1-\Psi(0)) \tag{3.4.11}$$

and hence

$$\hat{\Psi}(\theta) = \frac{1-\Psi(0)}{N}\frac{1}{\frac{\mu+\nu-\nu\hat{p}(\theta)}{\mu+\nu}}\frac{\nu}{\mu+\nu}\hat{p}(\theta) = \frac{1-\Psi(0)}{N}\frac{\nu\hat{p}(\theta)}{\mu+\nu-\nu\hat{p}(\theta)}. \tag{3.4.12}$$

To determine $\Psi(0)$, note that by the Fourier inversion formula (3.4.2) we have

$$\Psi(0) = \frac{1}{|\hat{\mathbb{T}}|^2}\sum_{\theta\in\hat{\mathbb{T}}}\hat{\Psi}(\theta). \tag{3.4.13}$$

Substitution of (3.4.12) into (3.4.13) yields

$$\Psi(0) = \frac{1}{|\hat{\mathbb{T}}|^2}\frac{1-\Psi(0)}{N}\sum_{\theta\in\hat{\mathbb{T}}}\frac{\nu\hat{p}(\theta)}{\mu+\nu-\nu\hat{p}(\theta)}. \tag{3.4.14}$$

Solving this expression for $\Psi(0)$ we get (3.4.10). □

With the help of the Fourier inversion formula, it is in principle possible to find an expression for $\Psi(x,0)$ by inverting (3.4.9). In reality, however, this is not always easy as the degree of difficulty depends on the model chosen. In the next section, we invert (3.4.9) for a special choice of $p(x,y)$ and show that it can be written in terms of the Green function of a simple random walk.

3.5. Fourier inversion

In this section, we consider a special choice of $p(x, y)$ for which we are able to invert the expression found for $\hat{\Psi}(\theta)$ in Theorem 3.4.2, and express it in terms of the Green function of a simple random walk. Define the function $\hat{\beta} : \hat{\mathbb{T}} \to \mathbb{R}$ by

$$\hat{\beta}(\theta) = \frac{\nu \hat{p}(\theta)}{\mu + \nu - \nu \hat{p}(\theta)}, \tag{3.5.1}$$

and let β be its Fourier inverse function.

THEOREM 3.5.1 (Simplification of Theorem 3.4.2). *For $\theta \in \hat{\mathbb{T}}$,*

$$\hat{\Psi}(\theta) = \frac{1 - \Psi(0)}{N} \hat{\beta}(\theta) \tag{3.5.2}$$

with

$$\Psi(0) = \frac{\frac{1}{N}\beta(0)}{1 + \frac{1}{N}\beta(0)}. \tag{3.5.3}$$

It is clear that to invert (3.5.2) and to determine (3.5.3), we only have to determine the inverse function β.

Let $\lambda \in [0, 1]$. For the random walk transition kernel p we consider

$$p(x, y) = (1 - \lambda)\delta_{x,y} + \lambda q(x, y), \quad x, y \in \mathbb{T}, \tag{3.5.4}$$

where $\delta_{x,y} = \mathbb{1}\{x = y\}$ and with q the transition kernel of a simple random walk. Let $||\cdot||$ denote the lattice norm, then

$$q(x, y) = \begin{cases} \frac{1}{2d}, & ||x - y|| = 1, \\ 0, & \text{otherwise.} \end{cases} \tag{3.5.5}$$

Note that p is indeed translation invariant, so we may consider $p(x) := p(x, 0)$. It follows that

$$\hat{p}(\theta) = (1 - \lambda) + \lambda \hat{q}(\theta). \tag{3.5.6}$$

For $x \in \mathbb{T}$ and $l \in \mathbb{N}_0$, let $q_l(x)$ be the probability that a simple random walk starting from the origin is at site x at time l. The Green function of a simple random walk at site x is

$$G_x(z) = \sum_{l \in \mathbb{N}_0} q_l(x) z^l, \quad |z| < 1. \tag{3.5.7}$$

PROPOSITION 3.5.2. *Let p as in (3.5.4). For $x \in \mathbb{T}$,*

$$\beta(x) = \frac{1}{1 - b} G_x\left(\frac{a}{1 - b}\right) - \delta_{x,0}, \tag{3.5.8}$$

with $a = \frac{\nu}{\mu+\nu}\lambda$ and $b = \frac{\nu}{\mu+\nu}(1 - \lambda)$.

Proof. First, note that as $\mu, \nu > 0$,

$$0 < \frac{a}{1-b} = \frac{\nu\lambda}{\mu + \nu\lambda} < 1. \tag{3.5.9}$$

Next, we have that

$$\begin{aligned}\beta(x) &= \frac{1}{|\hat{\mathbb{T}}|^2} \sum_{\theta\in\hat{\mathbb{T}}} e^{-2\pi i(\theta\cdot x)} \hat{\beta}(\theta) \\ &= \frac{1}{|\hat{\mathbb{T}}|^2} \sum_{\theta\in\hat{\mathbb{T}}} e^{-2\pi i(\theta\cdot x)} \frac{\frac{\nu}{\mu+\nu}\hat{p}(\theta)}{1-\frac{\nu}{\mu+\nu}\hat{p}(\theta)} \\ &= -\delta_{x,0} + \frac{1}{|\hat{\mathbb{T}}|^2} \sum_{\theta\in\hat{\mathbb{T}}} e^{-2\pi i(\theta\cdot x)} \frac{1}{1-\frac{\nu}{\mu+\nu}\hat{p}(\theta)},\end{aligned} \tag{3.5.10}$$

where we use that the Fourier inverse of the constant function 1 is the delta function $\delta_{x,0}$. It follows that

$$\begin{aligned}\frac{1}{|\hat{\mathbb{T}}|^2} \sum_{\theta\in\hat{\mathbb{T}}} e^{-2\pi i(\theta\cdot x)} \frac{1}{1-\frac{\nu}{\mu+\nu}\hat{p}(\theta)} &= \frac{1}{|\hat{\mathbb{T}}|^2} \sum_{\theta\in\hat{\mathbb{T}}} e^{-2\pi i(\theta\cdot x)} \sum_{k\in\mathbb{N}_0} \left(\frac{\nu}{\mu+\nu}\hat{p}(\theta)\right)^k \\ &= \sum_{k\in\mathbb{N}_0} \left(\frac{\nu}{\mu+\nu}\right)^k \frac{1}{|\hat{\mathbb{T}}|^2} \sum_{\theta\in\hat{\mathbb{T}}} e^{-2\pi i(\theta\cdot x)} \hat{p}(\theta)^k \\ &= \sum_{k\in\mathbb{N}_0} \left(\frac{\nu}{\mu+\nu}\right)^k \sum_{l=0}^{k} \binom{k}{l} (1-\lambda)^{k-l}\lambda^l \frac{1}{|\hat{\mathbb{T}}|^2} \sum_{\theta\in\hat{\mathbb{T}}} e^{-2\pi i(\theta\cdot x)} \hat{q}(\theta)^l \\ &= \sum_{k\in\mathbb{N}_0} \left(\frac{\nu}{\mu+\nu}\right)^k \sum_{l=0}^{k} \binom{k}{l} (1-\lambda)^{k-l}\lambda^l q_l(x) \\ &= \sum_{l\in\mathbb{N}_0} q_l(x) a^l \sum_{k=l}^{\infty} \binom{k}{l} b^{k-l} \\ &= \sum_{l\in\mathbb{N}_0} q_l(x) a^l (1-b)^{-l-1} \\ &= \frac{1}{1-b} G_x\left(\frac{a}{1-b}\right).\end{aligned} \tag{3.5.11}$$

We conclude the proof by combining the two equations. ☐

It now only remains to invert the expression in Theorem 3.5.1, to obtain the expression for $\Psi(x) := \Psi(x, 0)$.

THEOREM 3.5.3. *For p as in (3.5.4) and for $x \in \mathbb{T}$,*

$$\Psi(x) = \frac{1 - \Psi(0)}{N}\beta(x) \tag{3.5.12}$$

with

$$\Psi(0) = \frac{\frac{1}{N}\beta(0)}{1 + \frac{1}{N}\beta(0)}. \tag{3.5.13}$$

We now have an expression for the probability of being identical by descent expressed in terms of the Green function of a simple random walk. In Chapter 4 we present two examples for the Green function.

CHAPTER 4

Multi-colony Moran model with seed-bank, selection, migration and mutation

In this chapter, we consider a multi-colony Moran model on a discrete torus with sequential dynamics. The dynamics consist of exchange between the active and the dormant population, resampling, mutation and migration. We consider two types of mutation: a harmless mutation and a deleterious mutation. Migration between colonies is dependent on the type of the individual. Consequently, we consider four reservoirs in each colony: A-active, a-active, A-dormant and a-dormant. We are interested in calculating the probability $\Psi(x, y)$ at equilibrium that two individuals from colonies x and y share a common ancestor without encountering a *deleterious* mutation in their ancestral lines.

In Section 4.1 we define the model. In Section 4.2 we define $\Psi(x, y)$ and relate it to $F_t(x, y)$, $t \geq 0$, the probability density per unit of time that the two individuals from colonies x and y share their most recent common ancestor at time t. In Section 4.3 we derive a recursion relation for $F_t(x, y)$, which implies a relation for $\Psi(x, y)$. Using the latter, we compute its Fourier transform $\hat{\Psi}(\theta)$ in Section 4.4, from which we are able to gain more insight into its properties as a function of x,y and the underlying parameters. In Section 4.5 we consider a special case of the parameters, namely, weak exchange and weak harmless mutation, for which we obtain a more explicit expression for $\hat{\Psi}(\theta)$. We invert this expression in Section 4.6 and show that $\Psi(x)$ can be written in terms of the Green function of a simple random walk. We conclude by offering two examples for which a closed form expression of the Green function exists: the infinite torus and the finite torus, both in dimension $d = 1$.

4.1. Definition of the model

For $L \in \mathbb{N}$, consider the discrete torus $\mathbb{T} = \mathbb{Z}^d \cap [0, L]^d$ in any dimension $d \in \mathbb{N}$, with periodic boundary conditions. Each site contains a colony, consisting of an active population of size N and a dormant population of size M that resides in the seed-bank. Define $\{A, a\}$ to be the base-types. Harmless mutations can only affect active individuals, and cause an active individual to change base-types. Deleterious mutations can affect both active and dormant individuals, and change the type of an individual to an entirely new type. Only active individuals can migrate and resample. We consider selection in migration, i.e., the migration rate is dependent on the type of the individual.

Formally, let $\mu, \chi \in \mathbb{R}_{>0}$ be the rate of the deleterious and the harmless mutation, respectively. Let $\rho \in \mathbb{R}_{>0}$ be the rate of the exchange between the active and the dormant population. For $x, y \in \mathbb{T}$, let $k_A(x,y), k_a(x,y) \in \mathbb{R}_{>0}$ be the rates of the migration from colony x to colony y, for individuals of type A and type a, respectively. We assume that the migration rates only depend on the distance between the colonies x and y and not on their position, which makes our system translation-invariant.

We consider the following dynamics (in colony x):

- An active individual of type A or of type a:
  (1) mutates to a new type at rate μ;
  (2) becomes dormant at rate ρ;
  (3) mutates into type a or type A, respectively, at rate χ;
  (4) migrates to colony y and chooses an ancestor uniformly at random at rate $k_A(x,y)$ or rate $k_a(x,y)$, respectively.
- A dormant individual of type A or of type a:
  (1) mutates to a new type at rate μ;
  (2) becomes active at rate ρ.

Note that the only difference in the dynamics for active individuals of type A and a is the migration rate, and that dormant individuals obey the same dynamics, regardless of their type. We give an overview of the rates for the active and the dormant individuals in Table 4.1.1. We also illustrate the dynamics of the model in Figure 4.1.1, by displaying all different incoming and outgoing rates for individuals in a colony.

Rate	**Explanation**	**Active**	**Dormant**
ρ	exchange between active and dormant	✓	✓
μ	deleterious mutation	✓	✓
χ	harmless mutation	✓	✗
$k_A(x,y), k_a(x,y)$	migration from colony x to colony y	✓	✗

TABLE 4.1.1. Overview of the rates for the active and the dormant individuals in colony x.

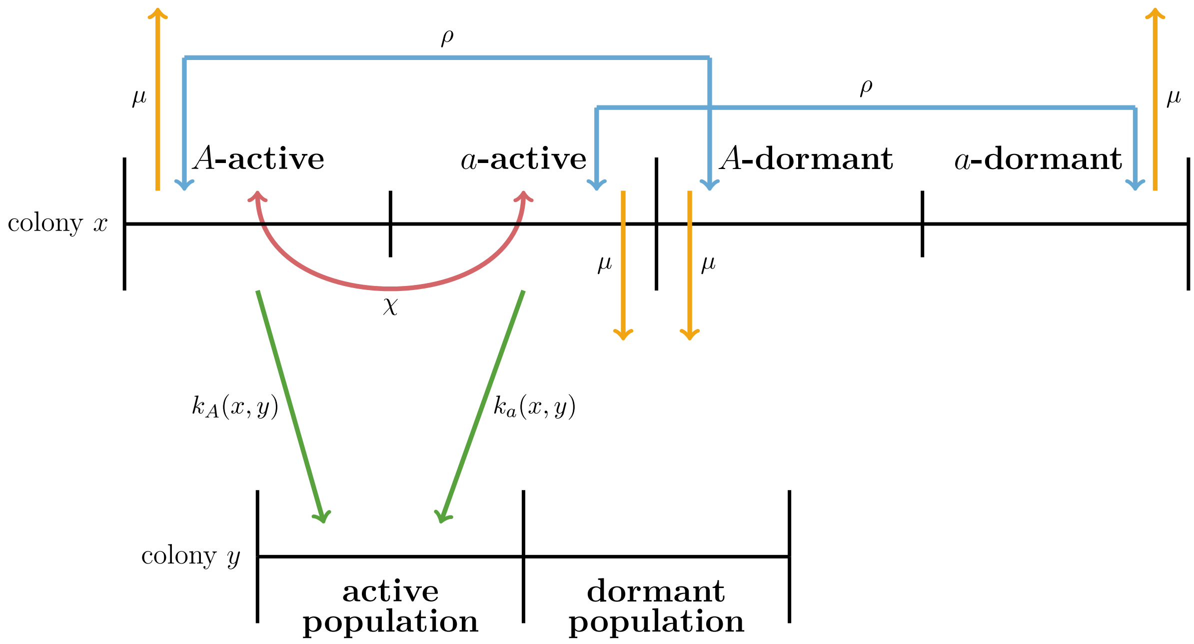

FIGURE 4.1.1. Illustration of the dynamics of the model. The dynamics that occur within colonies are illustrated in colony x, while the dynamics that occur between colonies are illustrated between colony x and colony y.

4.2. Probability of being identical by descent

Fix $x, y \in \mathbb{T}$. Contrary to the model in Chapter 3, the migration rate depends on the type of the individual. We are hence interested in $\psi((x,i),(y,j))$, the probability at equilibrium that two individuals drawn uniformly at random from colonies x and y in states $i, j \in \{0,1\}^2$ share a common ancestor without encountering a deleterious mutation in their ancestral lines. The states i and j denote the four reservoirs specified, where we use the allocation given in Table 4.2.1. If $x = y$, then we assume that the two individuals drawn are distinct.

Reservoir	A-active	a-active	A-dormant	a-dormant
State	00	01	10	11

TABLE 4.2.1. Allocation of the states $i, j \in \{0,1\}^2$ to the four reservoirs.

We want to find an expression for the 16-vector

$$\Psi(x,y) = \Big(\psi((x,i),(y,j))\Big)_{i,j\in\{0,1\}^2}, \quad x, y \in \mathbb{T}, \tag{4.2.1}$$

which is ordered as a list of increasing binary numbers, i.e., the first element of the vector represents the state $(i,j) = (00,00)$, the second element represents the state $(i,j) = (00,01)$ and so on, ending with the 16th element representing the state $(i,j) = (11,11)$.

Consider the model from Section 4.1 without the deleterious mutation and define $f_t((x,i),(y,j))$ to be the probability density per unit of time that two individuals drawn uniformly at random from colonies x and y in states $i,j \in \{0,1\}^2$ share their most recent common ancestor at time t. Consider the 16-vector

$$F_t(x,y) = \Big(f_t((x,i),(y,j))\Big)_{i,j\in\{0,1\}^2}, \quad x,y \in \mathbb{T},\ t \geq 0, \tag{4.2.2}$$

with the same binary ordering as in $\Psi(x,y)$. We obtain the same relation between $\Psi(x,y)$ and $F_t(x,y)$ as in Chapter 3, namely

$$\Psi(x,y) = \int_0^\infty e^{-2\mu t} F_t(x,y)\, dt. \tag{4.2.3}$$

Note that as the rates of the model only depend on the distance between x and y, the same is true for $F_t(x,y)$ and $\Psi(x,y)$, i.e., $F_t(x,y) = F_t(x-y,0)$ and $\Psi(x,y) = \Psi(x-y,0)$.

Finally, throughout this chapter, we will assume the migration rates to be

$$k_A(x,y) = \nu_A p(x,y), \quad k_a = \nu_a p(x,y), \quad x,y \in \mathbb{T}, \tag{4.2.4}$$

with $\nu_A, \nu_a \in \mathbb{R}_{>0}$ given rates and p a given translation-invariant transition kernel on $\mathbb{T}$.

4.3. Recursion relation

In this section, we obtain an expression for $\Psi(x,y)$ in terms of $\Psi(w,z)$, $w,z \in \mathbb{T}$. We first derive a recursion relation for each of the terms $f_t((x,i),(y,j))$, $i,j \in \{0,1\}^2$. This in turn implies a relation for $\psi((x,i),(y,j))$. From these relations, we define matrices with which we can write the expression for $\Psi(x,y)$.

We derive a recursion relation for $F_t(x,y)$, by applying the approach of Section 3.3 to each of the 16 terms $f_t((x,i),(y,j))$, $i,j \in \{0,1\}^2$. Recall that the general approach is as follows. We integrate over the time interval $[0,t]$ and consider the event in which only one of the individuals undergoes a change in this time interval. Say that this happens at a time s, and that the individual with state i in colony x changes to state k in colony z (possibly $x = z$ or $i = k$). If coalescence of the two ancestral lines does not happen at time s, then it is clear that we should subsequently consider $f_{t-s}((z,k),(y,j))$. Note that it is sufficient to consider the event in which only one of the individuals changes. Indeed, if both do not change, then nothing happens, while the event of them both changing at the same time has probability zero.

Before we start, we state some basic facts that we use throughout the calculations. Let $X_1,\dots,X_n$ be independently exponentially distributed with parameters $\lambda_1,\dots,\lambda_n$, respectively, i.e., $X_i \sim \mathrm{Exp}(\lambda_i)$. Denote the distribution function and the density function of X_i by G_i and g_i, respectively. In addition to (3.3.1), we make use of a well-known fact about the minimum of independent random variables with an exponential distribution, namely,

$$\min\{X_1, \dots, X_n\} \sim \text{Exp}\left(\sum_{i=1}^n \lambda_i\right), \quad \mathbb{P}\Big(X_i = \min\{X_1, \dots, X_n\}\Big) = \frac{\lambda_i}{\sum_{i=1}^n \lambda_i}, \; i = 1, \dots, n. \tag{4.3.1}$$

We are now ready to derive the recursion equations. We will not do so in the order of the vector $F_t(x,y)$, but rather in four groups of states that have similar equations. We consider the four groups specified in Table 4.3.1, where we also provide an overview of where the results can be found.

Group	**Combinations of states**	**States**	**Results**
First	Dormant states	$(10, 10), (10, 11)$, $(11, 10), (11, 11)$.	Proposition 4.3.1.
Second	Active and dormant states	$(00, 10), (00, 11)$, $(01, 10), (01, 11)$, $(10, 00), (10, 01)$, $(11, 00), (11, 01)$.	Proposition 4.3.2 - 4.3.4.
Third	Active states with different types	$(00, 01), (01, 00)$.	Proposition 4.3.5.
Fourth	Active states with identical types	$(00, 00), (01, 01)$.	Proposition 4.3.6 - 4.3.7.

TABLE 4.3.1. Specification of the four groups considered for the recursion equations.

PROPOSITION 4.3.1 (First group). *For $x, y \in \mathbb{T}$,*

$$f_t((x, 10), (y, 10)) = \int_0^t \rho e^{-2\rho s}\Big(f_{t-s}((x, 00), (y, 10)) + f_{t-s}((x, 10), (y, 00))\Big)\, ds, \tag{4.3.2}$$

$$f_t((x, 10), (y, 11)) = \int_0^t \rho e^{-2\rho s}\Big(f_{t-s}((x, 00), (y, 11)) + f_{t-s}((x, 10), (y, 01))\Big)\, ds, \tag{4.3.3}$$

$$f_t((x, 11), (y, 10)) = \int_0^t \rho e^{-2\rho s}\Big(f_{t-s}((x, 01), (y, 10)) + f_{t-s}((x, 11), (y, 00))\Big)\, ds, \tag{4.3.4}$$

$$f_t((x, 11), (y, 11)) = \int_0^t \rho e^{-2\rho s}\Big(f_{t-s}((x, 01), (y, 11)) + f_{t-s}((x, 11), (y, 01))\Big)\, ds. \tag{4.3.5}$$

PROOF. It suffices to give the proof for (4.3.2), as the other relations can be proven similarly. The reasoning is as follows. A dormant individual can only change states by becoming active, with rate ρ. The probability of one individual not changing state before time s is $e^{-\rho s}$, while the probability density of the other individual changing state at time s is $\rho e^{-\rho s}$. The product of the two equals the probability in the integral. We multiply this probability with the corresponding f_{t-s}. In the first term, the x-individual changes state from $i = 10$ to $i = 00$, i.e., from A-dormant to A-active. The y-individual does not change. In the second term, we observe the same behaviour but with the roles of x and y reversed. □

For the second group, note that the equations for the first four and the last four combinations, as given in Table 4.3.1, will be identical with the roles of x and y reversed. As the equations for $i = 00$ and $i = 01$ are also similar, we first state and prove the equations for $i = 00$.

PROPOSITION 4.3.2 (Second group, $i = 00$). *For* $x, y \in \mathbb{T}$,

$$\begin{aligned} &f_t((x,00),(y,10)) \\ &= \int_0^t \left[\frac{\rho}{\rho+\chi+\nu_A} \rho e^{-2\rho s} f_{t-s}((x,10),(y,10)) + \frac{\chi}{\rho+\chi+\nu_A} \chi e^{-(\rho+\chi)s} f_{t-s}((x,01),(y,10)) \right] ds \\ &\quad + \sum_{z\in\mathbb{T}} p(x,z) \int_0^t \frac{\nu_A}{\rho+\chi+\nu_A} \nu_A e^{-(\rho+\nu_A)s} f_{t-s}((z,00),(y,10))\ ds \\ &\quad + \int_0^t \rho e^{-(2\rho+\chi+\nu_A)s} f_{t-s}((x,00),(y,00))\ ds, \end{aligned} \tag{4.3.6}$$

$$\begin{aligned} &f_t((x,00),(y,11)) \\ &= \int_0^t \left[\frac{\rho}{\rho+\chi+\nu_A} \rho e^{-2\rho s} f_{t-s}((x,10),(y,11)) + \frac{\chi}{\rho+\chi+\nu_A} \chi e^{-(\rho+\chi)s} f_{t-s}((x,01),(y,11)) \right] ds \\ &\quad + \sum_{z\in\mathbb{T}} p(x,z) \int_0^t \frac{\nu_A}{\rho+\chi+\nu_A} \nu_A e^{-(\rho+\nu_A)s} f_{t-s}((z,00),(y,11))\ ds \\ &\quad + \int_0^t \rho e^{-(2\rho+\chi+\nu_A)s} f_{t-s}((x,00),(y,01))\ ds. \end{aligned} \tag{4.3.7}$$

PROOF. We only give the proof for (4.3.6), as (4.3.7) can be derived in a similar way. The y-individual can only change state by becoming active. However, the x-individual has three possibilities to change state. Namely, it can become dormant with rate ρ, mutate to type a with rate χ, or migrate with rate ν_A. Consider the first integral. Due to (3.3.1) and (4.3.1), the x-individual becomes dormant with probability $\rho/(\rho+\chi+\nu_A)$ with corresponding probability density $\rho e^{-\rho s}$. The probability for the y-individual to remain in the same state is $e^{-\rho s}$. We multiply these terms and multiply them with the corresponding f_{t-s}. The same reasoning applies to the second term in the first integral, and to the second integral, where we must also sum over the possible states $z \in \mathbb{T}$.

In the last integral, we consider the event in which the y-individual changes state at time s and the x-individual does not change state before time s. The former has probability density $\rho e^{-\rho s}$, while the latter has probability $e^{-(\rho+\chi+\nu_A)s}$ by (4.3.1), as this corresponds to the minimum of exponential random variables with rate ρ, χ and ν_A being larger than s. □

It is clear that we obtain similar equations for $i = 01$, with ν_A replaced by ν_a and with the states updated correspondingly. Hence, we state these without proof.

Proposition 4.3.3 (Second group, $i = 01$). *For* $x, y \in \mathbb{T}$,

$$\begin{aligned}
&f_t((x,01),(y,10)) \\
&= \int_0^t \left[\frac{\rho}{\rho+\chi+\nu_a} \rho e^{-2\rho s} f_{t-s}((x,11),(y,10)) + \frac{\chi}{\rho+\chi+\nu_a} \chi e^{-(\rho+\chi)s} f_{t-s}((x,00),(y,10)) \right] ds \\
&\quad + \sum_{z\in\mathbb{T}} p(x,z) \int_0^t \frac{\nu_a}{\rho+\chi+\nu_a} \nu_a e^{-(\rho+\nu_a)s} f_{t-s}((z,01),(y,10))\ ds \\
&\quad + \int_0^t \rho e^{-(2\rho+\chi+\nu_a)s} f_{t-s}((x,01),(y,00))\ ds,
\end{aligned} \tag{4.3.8}$$

$$\begin{aligned}
&f_t((x,01),(y,11)) \\
&= \int_0^t \left[\frac{\rho}{\rho+\chi+\nu_a} \rho e^{-2\rho s} f_{t-s}((x,11),(y,11)) + \frac{\chi}{\rho+\chi+\nu_a} \chi e^{-(\rho+\chi)s} f_{t-s}((x,00),(y,11)) \right] ds \\
&\quad + \sum_{z\in\mathbb{T}} p(x,z) \int_0^t \frac{\nu_a}{\rho+\chi+\nu_a} \nu_a e^{-(\rho+\nu_a)s} f_{t-s}((z,01),(y,11))\ ds \\
&\quad + \int_0^t \rho e^{-(2\rho+\chi+\nu_a)s} f_{t-s}((x,01),(y,01))\ ds.
\end{aligned} \tag{4.3.9}$$

Finally, we obtain identical equations for $j = 00$ and $j = 01$ as in Propositions 4.3.2 and 4.3.3, respectively, with only the roles of x and y reversed.

Proposition 4.3.4 (Second group, $j = 00$ and $j = 01$). *For* $x, y \in \mathbb{T}$,

$$\begin{aligned}
&f_t((x,10),(y,00)) \\
&= \int_0^t \left[\frac{\rho}{\rho+\chi+\nu_A} \rho e^{-2\rho s} f_{t-s}((x,10),(y,10)) + \frac{\chi}{\rho+\chi+\nu_A} \chi e^{-(\rho+\chi)s} f_{t-s}((x,10),(y,01)) \right] ds \\
&\quad + \sum_{z\in\mathbb{T}} p(y,z) \int_0^t \frac{\nu_A}{\rho+\chi+\nu_A} \nu_A e^{-(\rho+\nu_A)s} f_{t-s}((x,10),(z,00))\ ds \\
&\quad + \int_0^t \rho e^{-(2\rho+\chi+\nu_A)s} f_{t-s}((x,00),(y,00))\ ds,
\end{aligned} \tag{4.3.10}$$

$$\begin{aligned}
&f_t((x,10),(y,01)) \\
&= \int_0^t \left[\frac{\rho}{\rho+\chi+\nu_a} \rho e^{-2\rho s} f_{t-s}((x,10),(y,11)) + \frac{\chi}{\rho+\chi+\nu_a} \chi e^{-(\rho+\chi)s} f_{t-s}((x,10),(y,00)) \right] ds \\
&\quad + \sum_{z\in\mathbb{T}} p(y,z) \int_0^t \frac{\nu_a}{\rho+\chi+\nu_a} \nu_a e^{-(\rho+\nu_a)s} f_{t-s}((x,10),(z,01))\ ds \\
&\quad + \int_0^t \rho e^{-(2\rho+\chi+\nu_a)s} f_{t-s}((x,00),(y,01))\ ds,
\end{aligned} \tag{4.3.11}$$

$$
\begin{aligned}
&f_t((x,11),(y,00))\\
&=\int_0^t\left[\frac{\rho}{\rho+\chi+\nu_A}\rho e^{-2\rho s}f_{t-s}((x,11),(y,10))+\frac{\chi}{\rho+\chi+\nu_A}\chi e^{-(\rho+\chi)s}f_{t-s}((x,11),(y,01))\right]ds\\
&\quad+\sum_{z\in\mathbb{T}}p(y,z)\int_0^t\frac{\nu_A}{\rho+\chi+\nu_A}\nu_A e^{-(\rho+\nu_A)s}f_{t-s}((x,11),(z,00))\,ds\\
&\quad+\int_0^t\rho e^{-(2\rho+\chi+\nu_A)s}f_{t-s}((x,01),(y,00))\,ds,
\end{aligned}
\tag{4.3.12}
$$

$$
\begin{aligned}
&f_t((x,11),(y,01))\\
&=\int_0^t\left[\frac{\rho}{\rho+\chi+\nu_a}\rho e^{-2\rho s}f_{t-s}((x,11),(y,11))+\frac{\chi}{\rho+\chi+\nu_a}\chi e^{-(\rho+\chi)s}f_{t-s}((x,11),(y,00))\right]ds\\
&\quad+\sum_{z\in\mathbb{T}}p(y,z)\int_0^t\frac{\nu_a}{\rho+\chi+\nu_a}\nu_a e^{-(\rho+\nu_a)s}f_{t-s}((x,11),(z,01))\,ds\\
&\quad+\int_0^t\rho e^{-(2\rho+\chi+\nu_a)s}f_{t-s}((x,01),(y,01))\,ds.
\end{aligned}
\tag{4.3.13}
$$

For the third group, we consider the combinations of active individuals with different types. Each of the individuals now has three options for changing state, so we get a total of six terms within the recursion relation. The separate terms can be derived by using reasoning similar to that for the second group and hence we state the equations without proof.

Proposition 4.3.5 (Third group). *For $x,y\in\mathbb{T}$,*

$$
\begin{aligned}
f_t((x,00),(y,01))&=\int_0^t\frac{\rho}{\rho+\chi+\nu_A}\rho e^{-(2\rho+\chi+\nu_a)s}f_{t-s}((x,10),(y,01))\,ds\\
&\quad+\int_0^t\frac{\chi}{\rho+\chi+\nu_A}\chi e^{-(\rho+2\chi+\nu_a)s}f_{t-s}((x,01),(y,01))\,ds\\
&\quad+\sum_{z\in\mathbb{T}}p(x,z)\int_0^t\frac{\nu_A}{\rho+\chi+\nu_A}\nu_A e^{-(\rho+\chi+\nu_A+\nu_a)s}f_{t-s}((z,00),(y,01))\,ds\\
&\quad+\int_0^t\frac{\rho}{\rho+\chi+\nu_a}\rho e^{-(2\rho+\chi+\nu_A)s}f_{t-s}((x,00),(y,11))\,ds\\
&\quad+\int_0^t\frac{\chi}{\rho+\chi+\nu_a}\chi e^{-(\rho+2\chi+\nu_A)s}f_{t-s}((x,00),(y,00))\,ds\\
&\quad+\sum_{z\in\mathbb{T}}p(y,z)\int_0^t\frac{\nu_a}{\rho+\chi+\nu_a}\nu_a e^{-(\rho+\chi+\nu_A+\nu_a)s}f_{t-s}((x,00),(z,01))\,ds,
\end{aligned}
\tag{4.3.14}
$$

$$
\begin{aligned}
f_t((x,01),(y,00)) = &\int_0^t \frac{\rho}{\rho+\chi+\nu_a}\rho e^{-(2\rho+\chi+\nu_A)s} f_{t-s}((x,11),(y,00))\ ds \\
&+ \int_0^t \frac{\chi}{\rho+\chi+\nu_a}\chi e^{-(\rho+2\chi+\nu_A)s} f_{t-s}((x,00),(y,00))\ ds \\
&+ \sum_{z\in\mathbb{T}} p(x,z) \int_0^t \frac{\nu_a}{\rho+\chi+\nu_a}\nu_a e^{-(\rho+\chi+\nu_A+\nu_a)s} f_{t-s}((z,01),(y,00))\ ds \\
&+ \int_0^t \frac{\rho}{\rho+\chi+\nu_A}\rho e^{-(2\rho+\chi+\nu_a)s} f_{t-s}((x,01),(y,10))\ ds \\
&+ \int_0^t \frac{\chi}{\rho+\chi+\nu_A}\chi e^{-(\rho+2\chi+\nu_a)s} f_{t-s}((x,01),(y,01))\ ds \\
&+ \sum_{z\in\mathbb{T}} p(y,z) \int_0^t \frac{\nu_A}{\rho+\chi+\nu_A}\nu_A e^{-(\rho+\chi+\nu_A+\nu_a)s} f_{t-s}((x,01),(z,00))\ ds.
\end{aligned} \tag{4.3.15}
$$

For the fourth group, we consider the combinations of active individuals with identical types. The main difference with the other groups is that we now have an opportunity of coalescence occurring. We first state and prove the result for $(i,j) = (00,00)$.

Proposition 4.3.6 (Fourth group, $(i,j) = (00,00)$). *For $x, y \in \mathbb{T}$,*

$$
\begin{aligned}
&f_t((x,00),(y,00)) \\
&= \int_0^t \frac{\rho}{\rho+\chi+\nu_A}\rho e^{-(2\rho+\chi+\nu_A)s} f_{t-s}((x,10),(y,00))\ ds \\
&+ \int_0^t \frac{\chi}{\rho+\chi+\nu_A}\chi e^{-(\rho+2\chi+\nu_A)s} f_{t-s}((x,01),(y,00))\ ds \\
&+ \sum_{z\in\mathbb{T}} p(x,z) \Bigg[\int_0^t \frac{\nu_A}{\rho+\chi+\nu_A}\nu_A e^{-(\rho+\chi+2\nu_A)s} \Bigg(\mathbb{1}\{z\neq y\} f_{t-s}((z,00),(y,00)) \\
&+ \mathbb{1}\{z=y\} \frac{N-1}{N} f_{t-s}((y,00),(y,00)) \Bigg)\ ds + \mathbb{1}\{z=y\} \frac{1}{N} \frac{\nu_A}{\rho+\chi+\nu_A}\nu_A e^{-(\rho+\chi+2\nu_A)t} \Bigg] \\
&+ \int_0^t \frac{\rho}{\rho+\chi+\nu_A}\rho e^{-(2\rho+\chi+\nu_A)s} f_{t-s}((x,00),(y,10))\ ds \\
&+ \int_0^t \frac{\chi}{\rho+\chi+\nu_A}\chi e^{-(\rho+2\chi+\nu_A)s} f_{t-s}((x,00),(y,01))\ ds \\
&+ \sum_{z\in\mathbb{T}} p(y,z) \Bigg[\int_0^t \frac{\nu_A}{\rho+\chi+\nu_A}\nu_A e^{-(\rho+\chi+2\nu_A)s} \Bigg(\mathbb{1}\{z\neq x\} f_{t-s}((x,00),(z,00)) \\
&+ \mathbb{1}\{z=x\} \frac{N-1}{N} f_{t-s}((x,00),(x,00)) \Bigg)\ ds + \mathbb{1}\{z=x\} \frac{1}{N} \frac{\nu_A}{\rho+\chi+\nu_A}\nu_A e^{-(\rho+\chi+2\nu_A)t} \Bigg].
\end{aligned} \tag{4.3.16}
$$

PROOF. We only explain the first three integrals, in which the x-individual changes state. In the last three integrals, the y-individual changes state which yields similar results. The only difference compared to the third group is in the part concerning the migration. Indeed, we must now keep track of whether or not coalescence occurs and what the effect is of coalescence:

- If the x-individual migrates to a colony $z \neq y$, then coalescence never occurs, so we continue from colonies z and y.
- If the x-individual migrates to colony y, then with probability $(N-1)/N$ it does not coalesce with the y-individual and we continue with both (distinct) individuals from colony y. These two cases account for the third integral.
- If the x-individual migrates to colony y, then with probability $1/N$ it does coalesce with the y-individual. As we are still interested in the *most recent* common ancestor at time t, we only get a positive contribution when the coalescence happens exactly at time t. This accounts for the extra term.

□

It is clear that for $(i,j) = (01,01)$, we obtain a similar equation with ν_A replaced by ν_a and with the states updated correspondingly.

PROPOSITION 4.3.7 (Fourth group, $(i,j) = (01,01)$). *For $x, y \in \mathbb{T}$,*

$$\begin{aligned}
&f_t((x,01),(y,01)) \\
&= \int_0^t \frac{\rho}{\rho+\chi+\nu_a} \rho e^{-(2\rho+\chi+\nu_a)s} f_{t-s}((x,11),(y,01))\, ds \\
&+ \int_0^t \frac{\chi}{\rho+\chi+\nu_a} \chi e^{-(\rho+2\chi+\nu_a)s} f_{t-s}((x,00),(y,01))\, ds \\
&+ \sum_{z\in\mathbb{T}} p(x,z) \Bigg[\int_0^t \frac{\nu_a}{\rho+\chi+\nu_a} \nu_a e^{-(\rho+\chi+2\nu_a)s} \Bigg(\mathbb{1}\{z \neq y\} f_{t-s}((z,01),(y,01)) \\
&+ \mathbb{1}\{z = y\} \frac{N-1}{N} f_{t-s}((y,01),(y,01)) \Bigg)\, ds + \mathbb{1}\{z=y\} \frac{1}{N} \frac{\nu_a}{\rho+\chi+\nu_a} \nu_a e^{-(\rho+\chi+2\nu_a)t} \Bigg] \\
&+ \int_0^t \frac{\rho}{\rho+\chi+\nu_a} \rho e^{-(2\rho+\chi+\nu_a)s} f_{t-s}((x,01),(y,11))\, ds \\
&+ \int_0^t \frac{\chi}{\rho+\chi+\nu_a} \chi e^{-(\rho+2\chi+\nu_a)s} f_{t-s}((x,01),(y,00))\, ds \\
&+ \sum_{z\in\mathbb{T}} p(y,z) \Bigg[\int_0^t \frac{\nu_a}{\rho+\chi+\nu_a} \nu_a e^{-(\rho+\chi+2\nu_a)s} \Bigg(\mathbb{1}\{z \neq x\} f_{t-s}((x,01),(z,01)) \\
&+ \mathbb{1}\{z = x\} \frac{N-1}{N} f_{t-s}((x,01),(x,01)) \Bigg)\, ds + \mathbb{1}\{z=x\} \frac{1}{N} \frac{\nu_a}{\rho+\chi+\nu_a} \nu_a e^{-(\rho+\chi+2\nu_a)t} \Bigg].
\end{aligned} \tag{4.3.17}$$

Using (4.2.3), we see that the previous propositions in turn imply relations for $\psi((x,i),(y,j))$, $i,j \in \{0,1\}^2$. We again determine these relations according to the four groups specified in Table 4.3.1. Combining these relations, we then find a recursive relation for $\Psi(x,y)$ itself. An overview of the results according to the groups can be found in Table 4.3.2.

Group	**Results**
First	Proposition 4.3.8.
Second	Proposition 4.3.9.
Third	Proposition 4.3.10.
Fourth	Proposition 4.3.11 - 4.3.12.

TABLE 4.3.2. Overview of the results for relations for $\psi((x,i),(y,j))$ per group.

PROPOSITION 4.3.8 (First group). *For $x, y \in \mathbb{T}$,*

$$\psi((x,10),(y,10)) = \frac{\rho}{2(\mu+\rho)}\Big(\psi((x,00),(y,10)) + \psi((x,10),(y,00))\Big), \tag{4.3.18}$$

$$\psi((x,10),(y,11)) = \frac{\rho}{2(\mu+\rho)}\Big(\psi((x,00),(y,11)) + \psi((x,10),(y,01))\Big), \tag{4.3.19}$$

$$\psi((x,11),(y,10)) = \frac{\rho}{2(\mu+\rho)}\Big(\psi((x,01),(y,10)) + \psi((x,11),(y,00))\Big), \tag{4.3.20}$$

$$\psi((x,11),(y,11)) = \frac{\rho}{2(\mu+\rho)}\Big(\psi((x,01),(y,11)) + \psi((x,11),(y,01))\Big). \tag{4.3.21}$$

PROOF. It suffices to prove (4.3.18); the other equations follow similarly. We apply the relation in (4.2.3) to (4.3.2). As the integral is a linear operator, we can consider the two terms separately. Since they are similar, we only consider the first term. We have that

$$\begin{aligned}
&\int_0^\infty e^{-2\mu t}\left[\int_0^t \rho e^{-2\rho s} f_{t-s}((x,00),(y,10))\, ds\right] dt \\
&= \int_0^\infty \rho e^{-2(\mu+\rho)s}\left[\int_s^\infty e^{-2\mu(t-s)} f_{t-s}((x,00),(y,10))\, dt\right] ds \\
&= \frac{\rho}{2(\mu+\rho)}\psi((x,00),(y,10)).
\end{aligned} \tag{4.3.22}$$

□

For the second group, note that the only difference is that we now have a term in which we sum over $z \in \mathbb{T}$. However, this does not change anything about the evaluation of the two integrals, so results for the second group can be found in exactly the same way as for the first group. We thus state the results for the second group without proving them.

PROPOSITION 4.3.9 (Second group). *For $x, y \in \mathbb{T}$,*

$$\begin{aligned}
&\psi((x,00),(y,10)) \\
&= \frac{\rho}{\rho+\chi+\nu_A}\frac{\rho}{2(\mu+\rho)}\psi((x,10),(y,10)) + \frac{\chi}{\rho+\chi+\nu_A}\frac{\chi}{2\mu+\rho+\chi}\psi((x,01),(y,10)) \\
&\quad + \frac{\nu_A}{\rho+\chi+\nu_A}\frac{\nu_A}{2\mu+\rho+\nu_A}\sum_{z\in\mathbb{T}} p(x,z)\psi((z,00),(y,10)) + \frac{\rho}{2\mu+2\rho+\chi+\nu_A}\psi((x,00),(y,00)),
\end{aligned} \tag{4.3.23}$$

$$\begin{aligned}
&\psi((x,00),(y,11)) \\
&= \frac{\rho}{\rho+\chi+\nu_A}\frac{\rho}{2(\mu+\rho)}\psi((x,10),(y,11)) + \frac{\chi}{\rho+\chi+\nu_A}\frac{\chi}{2\mu+\rho+\chi}\psi((x,01),(y,11)) \\
&\quad + \frac{\nu_A}{\rho+\chi+\nu_A}\frac{\nu_A}{2\mu+\rho+\nu_A}\sum_{z\in\mathbb{T}} p(x,z)\psi((z,00),(y,11)) + \frac{\rho}{2\mu+2\rho+\chi+\nu_A}\psi((x,00),(y,01)),
\end{aligned} \tag{4.3.24}$$

$$\begin{aligned}
&\psi((x,01),(y,10)) \\
&= \frac{\rho}{\rho+\chi+\nu_a}\frac{\rho}{2(\mu+\rho)}\psi((x,11),(y,10)) + \frac{\chi}{\rho+\chi+\nu_a}\frac{\chi}{2\mu+\rho+\chi}\psi((x,00),(y,10)) \\
&\quad + \frac{\nu_a}{\rho+\chi+\nu_a}\frac{\nu_a}{2\mu+\rho+\nu_a}\sum_{z\in\mathbb{T}} p(x,z)\psi((z,01),(y,10)) + \frac{\rho}{2\mu+2\rho+\chi+\nu_a}\psi((x,01),(y,00)),
\end{aligned} \tag{4.3.25}$$

$$\begin{aligned}
&\psi((x,01),(y,11)) \\
&= \frac{\rho}{\rho+\chi+\nu_a}\frac{\rho}{2(\mu+\rho)}\psi((x,11),(y,11)) + \frac{\chi}{\rho+\chi+\nu_a}\frac{\chi}{2\mu+\rho+\chi}\psi((x,00),(y,11)) \\
&\quad + \frac{\nu_a}{\rho+\chi+\nu_a}\frac{\nu_a}{2\mu+\rho+\nu_a}\sum_{z\in\mathbb{T}} p(x,z)\psi((z,01),(y,11)) + \frac{\rho}{2\mu+2\rho+\chi+\nu_a}\psi((x,01),(y,01)),
\end{aligned} \tag{4.3.26}$$

$$\begin{aligned}
&\psi((x,10),(y,00)) \\
&= \frac{\rho}{\rho+\chi+\nu_A}\frac{\rho}{2(\mu+\rho)}\psi((x,10),(y,10)) + \frac{\chi}{\rho+\chi+\nu_A}\frac{\chi}{2\mu+\rho+\chi}\psi((x,10),(y,01)) \\
&\quad + \frac{\nu_A}{\rho+\chi+\nu_A}\frac{\nu_A}{2\mu+\rho+\nu_A}\sum_{z\in\mathbb{T}} p(y,z)\psi((x,10),(z,00)) + \frac{\rho}{2\mu+2\rho+\chi+\nu_A}\psi((x,00),(y,00)),
\end{aligned} \tag{4.3.27}$$

$$\begin{aligned}
&\psi((x,11),(y,00)) \\
&= \frac{\rho}{\rho+\chi+\nu_A}\frac{\rho}{2(\mu+\rho)}\psi((x,11),(y,10)) + \frac{\chi}{\rho+\chi+\nu_A}\frac{\chi}{2\mu+\rho+\chi}\psi((x,11),(y,01)) \\
&\quad + \frac{\nu_A}{\rho+\chi+\nu_A}\frac{\nu_A}{2\mu+\rho+\nu_A}\sum_{z\in\mathbb{T}} p(y,z)\psi((x,11),(z,00)) + \frac{\rho}{2\mu+2\rho+\chi+\nu_A}\psi((x,01),(y,00)),
\end{aligned} \tag{4.3.28}$$

$$
\begin{aligned}
&\psi((x,10),(y,01)) \\
&= \frac{\rho}{\rho+\chi+\nu_a}\frac{\rho}{2(\mu+\rho)}\psi((x,10),(y,11)) + \frac{\chi}{\rho+\chi+\nu_a}\frac{\chi}{2\mu+\rho+\chi}\psi((x,10),(y,00)) \\
&\quad + \frac{\nu_a}{\rho+\chi+\nu_a}\frac{\nu_a}{2\mu+\rho+\nu_a}\sum_{z\in\mathbb{T}} p(y,z)\psi((x,10),(z,01)) + \frac{\rho}{2\mu+2\rho+\chi+\nu_a}\psi((x,00),(y,01)),
\end{aligned} \tag{4.3.29}
$$

$$
\begin{aligned}
&\psi((x,11),(y,01)) \\
&= \frac{\rho}{\rho+\chi+\nu_a}\frac{\rho}{2(\mu+\rho)}\psi((x,11),(y,11)) + \frac{\chi}{\rho+\chi+\nu_a}\frac{\chi}{2\mu+\rho+\chi}\psi((x,11),(y,00)) \\
&\quad + \frac{\nu_a}{\rho+\chi+\nu_a}\frac{\nu_a}{2\mu+\rho+\nu_a}\sum_{z\in\mathbb{T}} p(y,z)\psi((x,11),(z,01)) + \frac{\rho}{2\mu+2\rho+\chi+\nu_a}\psi((x,01),(y,01)).
\end{aligned} \tag{4.3.30}
$$

For the third group, note that we again obtain similar results to those of the first and the second group, only with more terms, as each individual now has three possibilities to change state.

Proposition 4.3.10 (Third group). *For $x,y\in\mathbb{T}$,*

$$
\begin{aligned}
\psi((x,00),(y,01)) = &\frac{\rho}{\rho+\chi+\nu_A}\frac{\rho}{2\mu+2\rho+\chi+\nu_a}\psi((x,10),(y,01)) \\
&+ \frac{\chi}{\rho+\chi+\nu_A}\frac{\chi}{2\mu+\rho+2\chi+\nu_a}\psi((x,01),(y,01)) \\
&+ \frac{\nu_A}{\rho+\chi+\nu_A}\frac{\nu_A}{2\mu+\rho+\chi+\nu_A+\nu_a}\sum_{z\in\mathbb{T}} p(x,z)\psi((z,00),(y,01)) \\
&+ \frac{\rho}{\rho+\chi+\nu_a}\frac{\rho}{2\mu+2\rho+\chi+\nu_A}\psi((x,00),(y,11)) \\
&+ \frac{\chi}{\rho+\chi+\nu_a}\frac{\chi}{2\mu+\rho+2\chi+\nu_A}\psi((x,00),(y,00)) \\
&+ \frac{\nu_a}{\rho+\chi+\nu_a}\frac{\nu_a}{2\mu+\rho+\chi+\nu_A+\nu_a}\sum_{z\in\mathbb{T}} p(y,z)\psi((x,00),(z,01)),
\end{aligned} \tag{4.3.31}
$$

$$
\begin{aligned}
\psi((x,01),(y,00)) = &\frac{\rho}{\rho+\chi+\nu_a}\frac{\rho}{2\mu+2\rho+\chi+\nu_A}\psi((x,11),(y,00)) \\
&+ \frac{\chi}{\rho+\chi+\nu_a}\frac{\chi}{2\mu+\rho+2\chi+\nu_A}\psi((x,00),(y,00)) \\
&+ \frac{\nu_a}{\rho+\chi+\nu_a}\frac{\nu_a}{2\mu+\rho+\chi+\nu_A+\nu_a}\sum_{z\in\mathbb{T}} p(x,z)\psi((z,01),(y,00)) \\
&+ \frac{\rho}{\rho+\chi+\nu_A}\frac{\rho}{2\mu+2\rho+\chi+\nu_a}\psi((x,01),(y,10)) \\
&+ \frac{\chi}{\rho+\chi+\nu_A}\frac{\chi}{2\mu+\rho+2\chi+\nu_a}\psi((x,01),(y,01)) \\
&+ \frac{\nu_A}{\rho+\chi+\nu_A}\frac{\nu_A}{2\mu+\rho+\chi+\nu_A+\nu_a}\sum_{z\in\mathbb{T}} p(y,z)\psi((x,01),(z,00)).
\end{aligned} \tag{4.3.32}
$$

For the fourth group, we will see a difference compared to the other groups. Namely, in these equations we encounter coalescence, which will also be represented in the relation obtained for $\psi((x,i),(y,j))$. We first state and prove the result for $(i,j) = (00,00)$.

PROPOSITION 4.3.11 (Fourth group, $(i,j) = (00,00)$). *For $x, y \in \mathbb{T}$,*

$$\begin{aligned}
\psi((x,00),(y,00)) = {} & \frac{\rho}{\rho+\chi+\nu_A}\frac{\rho}{2\mu+2\rho+\chi+\nu_A}\psi((x,10),(y,00)) \\
& + \frac{\chi}{\rho+\chi+\nu_A}\frac{\chi}{2\mu+\rho+2\chi+\nu_A}\psi((x,01),(y,00)) \\
& + \frac{\nu_A}{\rho+\chi+\nu_A}\frac{\nu_A}{2\mu+\rho+\chi+2\nu_A}\sum_{z\in\mathbb{T}} p(x,z)\psi((z,00),(y,00)) \\
& - \frac{\nu_A}{\rho+\chi+\nu_A}\frac{\nu_A}{2\mu+\rho+\chi+2\nu_A}\frac{1}{N}p(x,y)\psi((y,00),(y,00)) \\
& + \frac{\nu_A}{\rho+\chi+\nu_A}\frac{\nu_A}{2\mu+\rho+\chi+2\nu_A}\frac{1}{N}p(x,y) \\
& + \frac{\rho}{\rho+\chi+\nu_A}\frac{\rho}{2\mu+2\rho+\chi+\nu_A}\psi((x,00),(y,10)) \\
& + \frac{\chi}{\rho+\chi+\nu_A}\frac{\chi}{2\mu+\rho+2\chi+\nu_A}\psi((x,00),(y,01)) \\
& + \frac{\nu_A}{\rho+\chi+\nu_A}\frac{\nu_A}{2\mu+\rho+\chi+2\nu_A}\sum_{z\in\mathbb{T}} p(y,z)\psi((x,00),(z,00)) \\
& - \frac{\nu_A}{\rho+\chi+\nu_A}\frac{\nu_A}{2\mu+\rho+\chi+2\nu_A}\frac{1}{N}p(y,x)\psi((x,00),(x,00)) \\
& + \frac{\nu_A}{\rho+\chi+\nu_A}\frac{\nu_A}{2\mu+\rho+\chi+2\nu_A}\frac{1}{N}p(y,x).
\end{aligned} \tag{4.3.33}$$

PROOF. We only focus on the terms in (4.3.16) that concern the x-individual. Note that for the first two terms, we obtain similar results to those of the first three groups. For the third term, as in the proof of Proposition 3.3.2, first rewrite

$$\begin{aligned}
& \sum_{z\in\mathbb{T}} \mathbb{1}\{z \neq y\} f_{t-s}((z,00),(y,00)) + \mathbb{1}\{z = y\}\frac{N-1}{N} f_{t-s}((y,00),(y,00)) \\
& \quad = \sum_{z\in\mathbb{T}} f_{t-s}((z,00),(y,00)) - \mathbb{1}\{z = y\}\frac{1}{N} f_{t-s}((y,00),(y,00)).
\end{aligned} \tag{4.3.34}$$

It follows that we only have to apply the relation between $\Psi(x,y)$ and $F_t(x,y)$ to the three seperate terms

$$\sum_{z\in\mathbb{T}} p(x,z)\int_0^t \frac{\nu_A}{\rho+\chi+\nu_A}\nu_A e^{-(\rho+\chi+2\nu_A)s} f_{t-s}((z,00),(y,00))\, ds, \tag{4.3.35}$$

$$-\frac{1}{N}p(x,y)\int_0^t \frac{\nu_A}{\rho+\chi+\nu_A}\nu_A e^{-(\rho+\chi+2\nu_A)s} f_{t-s}((y,00),(y,00))\, ds, \tag{4.3.36}$$

$$\frac{1}{N}p(x,y)\frac{\nu_A}{\rho+\chi+\nu_A}\nu_A e^{-(\rho+\chi+2\nu_A)t}. \tag{4.3.37}$$

As these are again similar to the terms in the other groups, the desired result follows. □

It is clear that we obtain a similar result for $(i,j) = (01,01)$. Note that by symmetry, we have $p(x,y) = p(y,x)$, so the final term for the x-individual and for the y-individual are identical.

PROPOSITION 4.3.12 (Fourth group, $(i,j) = (01,01)$). *For* $x, y \in \mathbb{T}$,

$$\begin{aligned}
\psi((x,01),(y,01)) = {} & \frac{\rho}{\rho+\chi+\nu_a}\frac{\rho}{2\mu+2\rho+\chi+\nu_a}\psi((x,11),(y,01)) \\
& + \frac{\chi}{\rho+\chi+\nu_a}\frac{\chi}{2\mu+\rho+2\chi+\nu_a}\psi((x,00),(y,01)) \\
& + \frac{\nu_a}{\rho+\chi+\nu_a}\frac{\nu_a}{2\mu+\rho+\chi+2\nu_a}\sum_{z\in\mathbb{T}} p(x,z)\psi((z,01),(y,01)) \\
& - \frac{\nu_a}{\rho+\chi+\nu_a}\frac{\nu_a}{2\mu+\rho+\chi+2\nu_a}\frac{1}{N}p(x,y)\psi((y,01),(y,01)) \\
& + 2\frac{\nu_a}{\rho+\chi+\nu_a}\frac{\nu_a}{2\mu+\rho+\chi+2\nu_a}\frac{1}{N}p(x,y) \\
& + \frac{\rho}{\rho+\chi+\nu_a}\frac{\rho}{2\mu+2\rho+\chi+\nu_a}\psi((x,01),(y,11)) \\
& + \frac{\chi}{\rho+\chi+\nu_a}\frac{\chi}{2\mu+\rho+2\chi+\nu_a}\psi((x,01),(y,00)) \\
& + \frac{\nu_a}{\rho+\chi+\nu_a}\frac{\nu_a}{2\mu+\rho+\chi+2\nu_a}\sum_{z\in\mathbb{T}} p(y,z)\psi((x,01),(z,01)) \\
& - \frac{\nu_a}{\rho+\chi+\nu_a}\frac{\nu_a}{2\mu+\rho+\chi+2\nu_a}\frac{1}{N}p(y,x)\psi((x,01),(x,01)).
\end{aligned} \tag{4.3.38}$$

To formulate the expression for $\Psi(x,y)$, we first introduce some notation. For $\alpha \in \{A, a\}$, define

$$\begin{aligned}
f(\alpha) &= \rho+\chi+\nu_\alpha, & g_1(\alpha) &= 2\mu+\rho+\chi+2\nu_\alpha, \\
h_1 &= 2\mu+\rho+\chi+\nu_A+\nu_a, & g_2(\alpha) &= 2\mu+2\rho+\chi+\nu_\alpha, \\
h_2 &= 2\mu+\rho+\chi, & g_3(\alpha) &= 2\mu+\rho+2\chi+\nu_\alpha, \\
h_3 &= 2\mu+2\rho, & g_4(\alpha) &= 2\mu+\rho+\nu_\alpha.
\end{aligned} \tag{4.3.39}$$

Next, for $\alpha, \beta \in \{A, a\}$ define

$$\begin{aligned}
P_1(\alpha) &= \tfrac{\nu_\alpha^2}{f(\alpha)g_4(\alpha)}, & Q_1(\alpha,\beta) &= \tfrac{\rho^2}{f(\alpha)g_2(\beta)}, & Q_4 &= \tfrac{\rho}{h_3}, \\
P_2(\alpha) &= \tfrac{\nu_\alpha^2}{f(\alpha)h_1}, & Q_2(\alpha) &= \tfrac{\rho}{g_2(\alpha)}, & R_1(\alpha,\beta) &= \tfrac{\chi^2}{f(\alpha)g_3(\beta)}, \\
P_3(\alpha) &= \tfrac{\nu_\alpha^2}{f(\alpha)g_1(\alpha)}, & Q_3(\alpha) &= \tfrac{\rho^2}{f(\alpha)h_3}, & R_2(\alpha) &= \tfrac{\chi^2}{f(\alpha)h_2}.
\end{aligned} \tag{4.3.40}$$

Let $\Phi_{x,y}$ be the vector of length 16 and let $A_{x,y}$ be the 16×16-matrix with elements given by

$$[\Phi_{x,y}]_k = \frac{1}{N}p(x,y)\begin{cases} 2P_3(A), & k=1, \\ 2P_3(a), & k=6, \\ 0, & \text{otherwise}, \end{cases} \tag{4.3.41}$$

$$[A_{x,y}]_{k,l} = -\frac{1}{N}p(x,y)\begin{cases} 2P_3(A), & (k,l)=(1,1), \\ 2P_3(a), & (k,l)=(6,6), \\ 0, & \text{otherwise.} \end{cases} \tag{4.3.42}$$

Define the 16×16-matrices C_ρ, C_χ, D and E by

$$C_\rho = \begin{pmatrix}
0 & 0 & Q_1(A,A) & 0 & 0 & 0 & 0 & 0 & Q_1(A,A) & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & Q_1(a,A) & 0 & 0 & 0 & 0 & 0 & Q_1(A,a) & 0 & 0 & 0 & 0 & 0 & 0 \\
Q_2(A) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & Q_3(A) & 0 & 0 & 0 & 0 & 0 \\
0 & Q_2(A) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & Q_3(A) & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & Q_1(A,a) & 0 & 0 & 0 & 0 & 0 & Q_1(a,A) & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & Q_1(a,a) & 0 & 0 & 0 & 0 & 0 & Q_1(a,a) & 0 & 0 \\
0 & 0 & 0 & 0 & Q_2(a) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & Q_3(a) & 0 \\
0 & 0 & 0 & 0 & 0 & Q_2(a) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & Q_3(a) \\
Q_2(A) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & Q_3(A) & 0 & 0 & 0 & 0 & 0 \\
0 & Q_2(a) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & Q_3(a) & 0 & 0 & 0 & 0 \\
0 & 0 & Q_4 & 0 & 0 & 0 & 0 & 0 & Q_4 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & Q_4 & 0 & 0 & 0 & 0 & 0 & Q_4 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & Q_2(A) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & Q_3(A) & 0 \\
0 & 0 & 0 & 0 & 0 & Q_2(a) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & Q_3(a) \\
0 & 0 & 0 & 0 & 0 & 0 & Q_4 & 0 & 0 & 0 & 0 & 0 & Q_4 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & Q_4 & 0 & 0 & 0 & 0 & 0 & Q_4 & 0 & 0
\end{pmatrix}, \tag{4.3.43}$$

$$C_\chi = \begin{pmatrix}
0 & R_1(A,A) & 0 & 0 & R_1(A,A) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
R_1(a,A) & 0 & 0 & 0 & 0 & R_1(A,a) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & R_2(A) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & R_2(A) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
R_1(a,A) & 0 & 0 & 0 & 0 & R_1(A,a) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & R_1(a,a) & 0 & 0 & R_1(a,a) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & R_2(a) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & R_2(a) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & R_2(A) & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & R_2(a) & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & R_2(A) & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & R_2(a) & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0
\end{pmatrix}, \tag{4.3.44}$$

$$D = \begin{pmatrix}
P_3(A) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & P_2(a) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & P_2(A) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & P_3(a) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & P_1(A) & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & P_1(a) & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & P_1(A) & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & P_1(a) & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0
\end{pmatrix}, \tag{4.3.45}$$

$$E = \begin{pmatrix}
P_3(A) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & P_2(A) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & P_1(A) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & P_1(A) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & P_2(a) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & P_3(a) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & P_1(a) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & P_1(a) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0
\end{pmatrix}. \tag{4.3.46}$$

It is clear that we obtain the vector and the matrices by combining all equations from Propositions 4.3.8 through 4.3.12. Using these definitions, we thus obtain an expression for $\Psi(x,y)$.

COROLLARY 4.3.13. *Let* $\delta_{x,y} = \mathbb{1}\{x=y\}$. *For* $x,y \in \mathbb{T}$,

$$\Psi(x,y) = \Phi_{x,y} + A_{x,y}\Psi(0,0) + \sum_{w,z\in\mathbb{T}} B_{w,z}\Psi(w,z) \tag{4.3.47}$$

where

$$B_{w,z} = \delta_{w,x}\delta_{z,y}C + \delta_{w,x}p(y,z)D + \delta_{z,y}p(x,w)E \tag{4.3.48}$$

with

$$C = C_\rho + C_\chi. \tag{4.3.49}$$

As it is not obvious how to obtain a closed-form expression for $\Psi(x,y)$ from Corollary 4.3.13, we consider its Fourier transform.

4.4. Fourier analysis

Consider the Fourier transform and the Fourier inversion formula given by (3.4.1) and (3.4.2), respectively. Recall that the dynamics of the model are translation-invariant, so we may consider

$$\hat{\Psi}(\theta) := \hat{\Psi}(\theta,-\theta) = \sum_{x,y\in\mathbb{T}} e^{2\pi i\theta\cdot(x-y)}\Psi(x-y,0). \tag{4.4.1}$$

Write $\Psi(0) = \Psi(0,0)$. Using Corollary 4.3.13, we find a relation for $\hat{\Psi}(\theta)$.

PROPOSITION 4.4.1. *For* $\theta \in \hat{\mathbb{T}}$,

$$\hat{\Psi}(\theta) = \hat{p}(\theta)\Phi + \hat{p}(\theta)A\Psi(0) + [C + \hat{p}(\theta)(D+E)]\hat{\Psi}(\theta), \tag{4.4.2}$$

where

$$C = C_\rho + C_\chi \tag{4.4.3}$$

with Φ *the vector of length 16 and* A *the* 16×16*-times matrix with elements given by*

$$[\Phi]_k = \frac{1}{N}\begin{cases} 2P_3(A), & k=1,\\ 2P_3(a), & k=6,\\ 0, & \text{otherwise},\end{cases} \tag{4.4.4}$$

$$[A]_{k,l} = -\frac{1}{N}\begin{cases} 2P_3(A), & (k,l)=(1,1),\\ 2P_3(a), & (k,l)=(6,6),\\ 0, & \text{otherwise}.\end{cases} \tag{4.4.5}$$

PROOF. First, note that the Fourier transform is a linear operator, so that we may determine the Fourier transform of each of the terms in the sum separately. Second, note that $\Psi(0)$ and the matrices C, D and E are all constant, so that they will not be affected. Finally, note that the vector $\Phi_{x,y}$ and the matrix $A_{x,y}$ are not constant, but we may take the Fourier transform per element of the vector and the matrix, respectively.

Consider the first term of (4.3.47). For any non-zero element of $\Phi_{x,y}$, we have that

$$\sum_{x,y\in\mathbb{T}} e^{2\pi i(\theta\cdot(x-y))}\frac{1}{N}p(x-y,0)2P_3(\alpha) = \frac{1}{N}\hat{p}(\theta)2P_3(\alpha). \tag{4.4.6}$$

Define Φ to be given by (4.4.4). Then it is clear that $\hat{\Phi}_{x,y} = \hat{p}(\theta)\Phi$. For the second term, note that the elements of $A_{x,y}$ are similar to those of $\Phi_{x,y}$. It follows immediately that $\hat{A}_{x,y} = \hat{p}(\theta)A$, where A is defined by (4.4.5).

For the third term, we have that

$$\sum_{x,y\in\mathbb{T}} e^{2\pi i(\theta\cdot(x-y))}\left[\sum_{w,z\in\mathbb{T}}\delta_{w,x}\delta_{z,y}C\Psi(w-z,0)\right] = \sum_{x,y\in\mathbb{T}} e^{2\pi i(\theta\cdot(x-y))}C\Psi(x-y,0) = C\hat{\Psi}(\theta). \tag{4.4.7}$$

For the fourth term, we have that

$$\begin{aligned}&\sum_{x,y\in\mathbb{T}} e^{2\pi i(\theta\cdot(x-y))}\left[\sum_{w,z\in\mathbb{T}}\delta_{w,x}p(y-z,0)D\Psi(w-z,0)\right]\\ &= \sum_{x,y\in\mathbb{T}}\sum_{z\in\mathbb{T}} e^{2\pi i(\theta\cdot(z-y))}p(y-z,0)e^{2\pi i(\theta\cdot(x-z))}D\Psi(x-z,0)\\ &= \hat{p}(\theta)D\hat{\Psi}(\theta),\end{aligned} \tag{4.4.8}$$

where we use that, by symmetry, $p(y-z,0) = p(z-y,0)$. Similarly, for the fifth term we obtain

$$\hat{p}(\theta)E\hat{\Psi}(\theta). \tag{4.4.9}$$

Adding all terms, we get the desired result. □

From Proposition 4.4.1, we obtain a closed-form expression for $\hat{\Psi}(\theta)$.

THEOREM 4.4.2. *Let I_{16} be the 16×16-identity matrix. For $\theta\in\hat{\mathbb{T}}$,*

$$\hat{\Psi}(\theta) = \hat{p}(\theta)\hat{X}(\theta)(\Phi + A\Psi(0)), \tag{4.4.10}$$

where

$$\Psi(0) = \left[I_{16} - \frac{1}{|\hat{\mathbb{T}}|^2}\sum_{\theta\in\hat{\mathbb{T}}}\hat{p}(\theta)\hat{X}(\theta)A\right]^{-1}\frac{1}{|\hat{\mathbb{T}}|^2}\sum_{\theta\in\hat{\mathbb{T}}}\hat{p}(\theta)\hat{X}(\theta)\Phi \tag{4.4.11}$$

with

$$\hat{X}(\theta) = [I_{16} - C - \hat{p}(\theta)(D+E)]^{-1}. \tag{4.4.12}$$

PROOF. From (4.4.2), it follows that

$$[I_{16} - C - \hat{p}(\theta)(D+E)]\hat{\Psi}(\theta) = \hat{p}(\theta)(\Phi + A\Psi(0)). \tag{4.4.13}$$

Write

$$\hat{X}(\theta) = [I_{16} - C - \hat{p}(\theta)(D+E)]^{-1}. \tag{4.4.14}$$

Then (4.4.10) follows. It remains to determine the value of $\Psi(0)$. For this we use the Fourier inversion formula (3.4.2), which yields

$$\Psi(0) = \frac{1}{|\hat{\mathbb{T}}|^2} \sum_{\theta \in \hat{\mathbb{T}}} \hat{\Psi}(\theta). \tag{4.4.15}$$

Substitute the expression for $\hat{\Psi}(\theta)$ to get

$$\Psi(0) = \frac{1}{|\hat{\mathbb{T}}|^2} \sum_{\theta \in \hat{\mathbb{T}}} \hat{p}(\theta)\hat{X}(\theta)(\Phi + A\Psi(0)). \tag{4.4.16}$$

Solving for $\Psi(0)$, we obtain

$$\Psi(0) = \left[I_{16} - \frac{1}{|\hat{\mathbb{T}}|^2} \sum_{\theta \in \hat{\mathbb{T}}} \hat{p}(\theta)\hat{X}(\theta)A \right]^{-1} \frac{1}{|\hat{\mathbb{T}}|^2} \sum_{\theta \in \hat{\mathbb{T}}} \hat{p}(\theta)\hat{X}(\theta)\Phi. \tag{4.4.17}$$

□

We found a closed-form expression for $\hat{\Psi}(\theta)$. However, to obtain an explicit expression, we have to invert several matrices. As these are all 16×16-matrices, determining the inverse is computationally complex. In the next section we consider a special regime of the parameters for which it is possible to derive a more tangible expression for $\hat{\Psi}(\theta)$.

4.5. Special choice of parameters

In this section, we consider a special regime of the parameters for which we can determine an explicit expression for $\hat{\Psi}(\theta)$. First, we consider $(\rho, \chi) = (0, 0)$, i.e., no exchange between the active and the dormant population and no harmless mutation. We show that Proposition 4.4.1 simplifies to a result similar to Proposition 3.4.1. Next, we expand $\hat{\Psi}(\theta)$ around $(\rho, \chi) = (0, 0)$ to analyze the effect of the seed-bank and of harmless mutation.

We denote all quantities in the case that $(\rho, \chi) = (0, 0)$ with subscript 0. We obtain the equivalent of Proposition 4.4.1 for $\hat{\Psi}_0(\theta)$.

Proposition 4.5.1 (No seed-bank and no harmless mutation). *Let $\rho = \chi = 0$. For $\theta \in \hat{\mathbb{T}}$,*

$$[\hat{\Psi}_0(\theta)]_k = \begin{cases} \frac{\nu_A}{\mu+\nu_A}\frac{1}{N}\hat{p}(\theta) - \frac{\nu_A}{\mu+\nu_A}\frac{1}{N}\hat{p}(\theta)[\Psi_0(0)]_k + \frac{\nu_A}{\mu+\nu_A}\hat{p}(\theta)[\hat{\Psi}_0(\theta)]_k, & k = 1, \\ \frac{\nu_a}{\mu+\nu_a}\frac{1}{N}\hat{p}(\theta) - \frac{\nu_a}{\mu+\nu_a}\frac{1}{N}\hat{p}(\theta)[\Psi_0(0)]_k + \frac{\nu_a}{\mu+\nu_a}\hat{p}(\theta)[\hat{\Psi}_0(\theta)]_k, & k = 6, \\ 0, & \textit{otherwise.} \end{cases} \tag{4.5.1}$$

Proof. By multiplying the matrices and vectors involved, we first find that $[\hat{\Psi}_0(\theta)]_k = 0$ for all $k \notin \{1, 6\}$. Indeed, this is what we would expect. The only opportunity for coalescence is when an active x-individual migrates and chooses the same ancestor as the y-individual (or vice versa). The x-individual then chooses an ancestor with a type identical to itself, the y-individual has an identical type as well. As $\rho = 0$ corresponds to no exchange between the active and the dormant population, it follows that the corresponding probability is zero for any combination of states involving a dormant individual. As $\chi = 0$ corresponds to no mutation between the types A and a, the corresponding probability is also zero for any combination of states with an individual of type A and an individual of type a.

Hence the only non-zero probability occurs for active individuals of identical types, i.e., the states $(i,j) = (00,00)$ and $(i,j) = (01,01)$. These correspond to $k = 1$ and $k = 6$, respectively. So we indeed should have that $[\hat{\Psi}_0(\theta)]_k = 0$ for all $k \notin \{1,6\}$.

Let $C(\rho,\chi)$ be the 16×16-matrix given by (4.3.49) and put $C_0 = C(0,0)$. Let $D(\rho,\chi)$ be the 16×16-matrix given by (4.3.45) and put $D_0 = D(0,0)$. Let $E(\rho,\chi)$ be the 16×16-matrix given by (4.3.46) and put $E_0 = E(0,0)$. For $k \in \{1,6\}$, the k-th element is given by

$$[\hat{\Psi}_0(\theta)]_k = \hat{p}(\theta)[\Phi_0]_k + \hat{p}(\theta)\sum_{r=1}^{16}[A_0]_{kr}[\Psi_0(0)]_r + \sum_{r=1}^{16}[C_0 + \hat{p}(\theta)(D_0+E_0)]_{kr}[\hat{\Psi}_0(\theta)]_r. \tag{4.5.2}$$

We determine all elements. First,

$$[\Phi_0]_k = \frac{1}{N}\begin{cases} \frac{\nu_A}{\mu+\nu_A}, & k=1,\\ \frac{\nu_a}{\mu+\nu_a}, & k=6,\\ 0, & \text{otherwise}, \end{cases} \tag{4.5.3}$$

and

$$[A_0]_{kr} = -\frac{1}{N}\begin{cases} \frac{\nu_A}{\mu+\nu_A}, & (k,r)=(1,1),\\ \frac{\nu_a}{\mu+\nu_a}, & (k,r)=(6,6),\\ 0, & \text{otherwise}. \end{cases} \tag{4.5.4}$$

Next, $[C_0]_{kr} = 0$ for all k and r. As D_0 and E_0 are diagonal matrices, we have that $[D_0+E_0]_{kr} \neq 0$ if and only if $r = k$, and hence

$$\sum_{r=1}^{16}[C_0 + \hat{p}(\theta)(D_0+E_0)]_{kr}[\hat{\Psi}_0(\theta)]_r = \hat{p}(\theta)[D_0+E_0]_{kk}[\hat{\Psi}_0(\theta)]_k = \hat{p}(\theta)[\hat{\Psi}_0(\theta)]_k \begin{cases} \frac{\nu_A}{\mu+\nu_A}, & k=1,\\ \frac{\nu_a}{\mu+\nu_a}, & k=6. \end{cases} \tag{4.5.5}$$

Combining these terms we get the desired result. □

Observe that we obtain a decoupled system, where the A-active and the a-active individuals behave as independent systems with mutation rate μ and migration rate ν equal to ν_A and ν_a, respectively. As we considered this model in Chapter 3, it is no surprise that we find the same relation for $\hat{\Psi}(\theta)$ as in Proposition 3.4.1.

We next determine an expression for $\hat{\Psi}(\theta)$ when ρ and χ are small and compare it to the expression found for $(\rho,\chi) = (0,0)$. Let $0 < \rho, \chi \ll 1$ be such that

$$\rho\chi \ll \rho, \quad \rho\chi \ll \chi. \tag{4.5.6}$$

We use Taylor expansion up to first order around $(\rho,\chi)=(0,0)$ of the functions given in (4.3.40), obtaining for $\alpha\in\{A,a\}$,

$$\begin{aligned}
P_1(\alpha) &= \frac{\nu_\alpha}{2\mu+\nu_\alpha} - \rho\frac{2(\mu+\nu_\alpha)}{(2\mu+\nu_\alpha)^2} - \chi + o(\rho\chi),\\
P_2(\alpha) &= \frac{\nu_\alpha}{2\mu+\nu_A+\nu_a} - (\rho+\chi)\frac{2\mu+\nu_A+\nu_a+\nu_\alpha}{(2\mu+\nu_A+\nu_a)^2} + o(\rho\chi),\\
P_3(\alpha) &= \frac{\nu_\alpha}{2(\mu+\nu_\alpha)} - (\rho+\chi)\frac{2\mu+3\nu_\alpha}{(2\mu+2\nu_\alpha)^2} + o(\rho\chi).
\end{aligned} \tag{4.5.7}$$

Furthermore, for $\alpha,\beta\in\{A,a\}$,

$$\begin{aligned}
&Q_1(\alpha,\beta)=o(\rho\chi), && Q_2(\alpha,\beta)=\rho\tfrac{1}{2\mu+\nu_\alpha}+o(\rho\chi),\\
&Q_3(\alpha)=o(\rho\chi), && Q_4=\rho\tfrac{1}{2\mu}+o(\rho\chi),
\end{aligned} \tag{4.5.8}$$

and

$$R_1(\alpha,\beta)=o(\rho\chi), \quad R_2(\alpha)=o(\rho\chi). \tag{4.5.9}$$

Using these expansions, we can split the vector Φ and the matrices A,C,D and E into independent terms, terms depending on ρ and on χ, and terms of higher order. Define Φ_1 to be the vector of length 16 and A_1 to be the 16×16-times matrix with elements given by

$$[\Phi_1]_k = \frac{1}{N}\begin{cases} 2\frac{2\mu+3\nu_A}{(2\mu+2\nu_A)^2}, & k=1,\\ 2\frac{2\mu+3\nu_a}{(2\mu+2\nu_a)^2}, & k=6,\\ 0, & \text{otherwise},\end{cases} \tag{4.5.10}$$

$$[A_1]_{k,l} = -\frac{1}{N}\begin{cases} 2\frac{2\mu+3\nu_A}{(2\mu+2\nu_A)^2}, & (k,l)=(1,1),\\ 2\frac{2\mu+3\nu_a}{(2\mu+2\nu_a)^2}, & (k,l)=(6,6),\\ 0, & \text{otherwise}.\end{cases} \tag{4.5.11}$$

Consider Φ_0 and A_0 given by (4.5.3) and (4.5.4), respectively. It follows that

$$\Phi = \Phi_0 + (\rho+\chi)\Phi_1 + o(\rho\chi), \tag{4.5.12}$$

$$A = A_0 + (\rho+\chi)A_1 + o(\rho\chi). \tag{4.5.13}$$

Define C_1 to be the 16×16-matrix with elements given by

$$[C_1]_{kl} = \begin{cases} \frac{1}{2\mu+\nu_A}, & (k,l)\in\{(3,1),(4,2),(9,1),(13,5)\},\\ \frac{1}{2\mu+\nu_a}, & (k,l)\in\{(7,5),(8,6),(10,2),(14,6)\},\\ \frac{1}{2\mu}, & (k,l)\in\{(11,3),(11,9),(12,4),(12,10),(15,7),(15,13),(16,8),(16,14)\},\\ 0, & \text{otherwise}.\end{cases} \tag{4.5.14}$$

It follows that

$$C = \rho C_1 + o(\rho\chi). \tag{4.5.15}$$

Before we determine the remaining expansions, we introduce extra notation. For $\alpha \in \{A, a\}$, define

$$P_1^*(\alpha) = -\tfrac{2(\mu+\nu_\alpha)}{(2\mu+\nu_\alpha)^2}, \quad P_2^*(\alpha) = -\tfrac{2\mu+\nu_A+\nu_a+\nu_\alpha}{(2\mu+\nu_A+\nu_a)^2}, \quad P_3^*(\alpha) = -\tfrac{2\mu+3\nu_\alpha}{(2\mu+2\nu_\alpha)^2}. \tag{4.5.16}$$

Let D_0 and E_0 be defined as in the proof of Proposition 4.5.1. It follows that

$$D = D_0 + \rho D_1 + \chi D_2 + o(\rho\chi), \tag{4.5.17}$$

$$E = E_0 + \rho E_1 + \chi E_2 + o(\rho\chi), \tag{4.5.18}$$

where D_1, D_2, E_1 and E_2 are the 16×16-matrices given by

$$D_1 = \begin{pmatrix}
P_3^*(A) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & P_2^*(a) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & P_2^*(A) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & P_3^*(a) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & P_1^*(A) & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & P_1^*(a) & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & P_1^*(A) & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & P_1^*(a) & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0
\end{pmatrix}, \tag{4.5.19}$$

$$D_2 = \begin{pmatrix}
P_3^*(A) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & P_2^*(a) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & P_2^*(A) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & P_3^*(a) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & -1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & -1 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & -1 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & -1 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0
\end{pmatrix}, \tag{4.5.20}$$

$$E_1 = \begin{pmatrix}
P_3^*(A) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & P_2^*(A) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & P_1^*(A) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & P_1^*(A) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & P_2^*(a) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & P_3^*(a) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & P_1^*(a) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & P_1^*(a) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0
\end{pmatrix}, \tag{4.5.21}$$

$$E_2 = \begin{pmatrix}
P_3^*(A) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & P_2^*(A) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & -1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & -1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & P_2^*(a) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & P_3^*(a) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & -1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & -1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0
\end{pmatrix}. \tag{4.5.22}$$

Using these expansions, we can also expand $\hat{X}(\theta)$ and $\Psi(0)$ around $(\rho, \chi) = (0, 0)$ to find an expansion for $\hat{\Psi}(\theta)$. We first state and prove a useful fact that we will need throughout the calculations.

LEMMA 4.5.2. *Let M_0, M_1 and M_2 be $n \times n$-matrices such that M_0 is invertible. Then*

$$[M_0 - \rho M_1 - \chi M_2]^{-1} = M_0^{-1} + (\rho M_0^{-1} M_1 + \chi M_0^{-1} M_2) M_0^{-1} + o(\rho\chi). \tag{4.5.23}$$

PROOF. Let I_n be the $n \times n$-identity matrix. It is easy to verify that

$$[I_n - \rho M_1 - \chi M_2]^{-1} = I_n + \rho M_1 + \chi M_2 + o(\rho\chi). \tag{4.5.24}$$

It follows that

$$\begin{aligned}
[M_0 - \rho M_1 - \chi M_2]^{-1} &= [M_0(I_n - \rho M_0^{-1} M_1 - \chi M_0^{-1} M_2)]^{-1} \\
&= [I_n - \rho M_0^{-1} M_1 - \chi M_0^{-1} M_2]^{-1} M_0^{-1} \\
&= (I_n + \rho M_0^{-1} M_1 + \chi M_0^{-1} M_2) M_0^{-1} + o(\rho\chi).
\end{aligned} \tag{4.5.25}$$

□

We state and prove an expansion for $\hat{X}(\theta)$.

PROPOSITION 4.5.3. *Let $\hat{X}(\theta)$ be given by (4.4.12). Define*

$$\begin{aligned}
M_0(\theta) &= I_{16} - \hat{p}(\theta)(D_0 + E_0), \\
M_1(\theta) &= C_1 + \hat{p}(\theta)(D_1 + E_1), \\
M_2(\theta) &= \hat{p}(\theta)(D_2 + E_2).
\end{aligned} \tag{4.5.26}$$

Then

$$\hat{X}(\theta) = \hat{X}_0(\theta) + \rho \hat{X}_1(\theta) + \chi \hat{X}_2(\theta) + o(\rho\chi), \tag{4.5.27}$$

where

$$\begin{aligned}
\hat{X}_0(\theta) &= M_0^{-1}(\theta), \\
\hat{X}_1(\theta) &= M_0^{-1}(\theta) M_1(\theta) M_0^{-1}(\theta), \\
\hat{X}_2(\theta) &= M_0^{-1}(\theta) M_2(\theta) M_0^{-1}(\theta).
\end{aligned} \tag{4.5.28}$$

Note that $\hat{X}_0(\theta)$ is indeed the expression we obtain when we substitute $(\rho, \chi) = (0, 0)$ in (4.4.12).

PROOF. Since D_0 and E_0 are non-zero diagonal matrices, $M_0(\theta)$ is invertible. We have that

$$\begin{aligned}\hat{X}(\theta) &= [I_{16} - \rho C_1 - \hat{p}(\theta)(D_0 + \rho D_1 + \chi D_2 + E_0 + \rho E_1 + \chi E_2)]^{-1} + o(\rho\chi) \\ &= [M_0(\theta) - \rho M_1(\theta) - \chi M_2(\theta)]^{-1} + o(\rho\chi) \\ &= M_0^{-1}(\theta) + (\rho M_0^{-1}(\theta) M_1(\theta) + \chi M_0^{-1}(\theta) M_2(\theta)) M_0^{-1}(\theta) + o(\rho\chi),\end{aligned} \tag{4.5.29}$$

where we apply Lemma 4.5.2 in the last equality. □

Next, we obtain an expansion for $\Psi(0)$. First, observe that, due to (4.4.11), $\Psi(0)$ consists of two terms multiplied by each other. Second, the expansion for the second term is clear, as we already have an expansion for $\hat{X}(\theta)$ and Φ. It remains to determine an expansion for the first term. Abbreviate

$$Y = \left[I_{16} - \frac{1}{|\hat{\mathbb{T}}|^2} \sum_{\theta \in \hat{\mathbb{T}}} \hat{p}(\theta) \hat{X}(\theta) A\right]^{-1}. \tag{4.5.30}$$

PROPOSITION 4.5.4. *Define*

$$\begin{aligned}N_0 &= I_{16} - \frac{1}{|\hat{\mathbb{T}}|^2} \sum_{\theta \in \hat{\mathbb{T}}} \hat{p}(\theta) \hat{X}_0(\theta) A_0, \\ N_1 &= \frac{1}{|\hat{\mathbb{T}}|^2} \sum_{\theta \in \hat{\mathbb{T}}} \hat{X}_0(\theta) A_1 + \hat{X}_1(\theta) A_0, \\ N_2 &= \frac{1}{|\hat{\mathbb{T}}|^2} \sum_{\theta \in \hat{\mathbb{T}}} \hat{X}_0(\theta) A_1 + \hat{X}_2(\theta) A_0.\end{aligned} \tag{4.5.31}$$

Then

$$Y = Y_0 + \rho Y_1 + \chi Y_2 + o(\rho\chi), \tag{4.5.32}$$

where

$$Y_0 = N_0^{-1}, \quad Y_1 = N_0^{-1} N_1 N_0^{-1}, \quad Y_2 = N_0^{-1} N_2 N_0^{-1}. \tag{4.5.33}$$

Note that Y_0 is indeed the expression we obtain when we substitute $(\rho, \chi) = (0, 0)$ in (4.5.30).

PROOF. Since $\hat{X}_0(\theta)$ and A_0 are non-zero diagonal matrices, N_0 is invertible. We have that

$$\begin{aligned}Y &= \left[I_{16} - \frac{1}{|\hat{\mathbb{T}}|^2} \sum_{\theta \in \hat{\mathbb{T}}} \hat{p}(\theta) \Big(\hat{X}_0(\theta) + \rho \hat{X}_1(\theta) + \chi \hat{X}_2(\theta)\Big) \Big(A_0 + (\rho + \chi) A_1\Big)\right]^{-1} + o(\rho\chi) \\ &= \left[I_{16} - \frac{1}{|\hat{\mathbb{T}}|^2} \sum_{\theta \in \hat{\mathbb{T}}} \hat{p}(\theta) \Big[\hat{X}_0(\theta) A_0 + \rho \Big(\hat{X}_0(\theta) A_1 + \hat{X}_1(\theta) A_0\Big) + \chi \Big(\hat{X}_0(\theta) A_1 + \hat{X}_2(\theta) A_0\Big)\Big]\right]^{-1} \\ &\quad + o(\rho\chi) \\ &= [N_0 - \rho N_1 - \chi N_1]^{-1} + o(\rho\chi) \\ &= N_0^{-1} + (\rho N_0^{-1} N_1 + \chi N_0^{-1} N_2) N_0^{-1} + o(\rho\chi),\end{aligned} \tag{4.5.34}$$

where we again use Lemma 4.5.2 in the final equality. □

Using Proposition 4.5.4, we obtain the expansion for $\Psi(0)$.

PROPOSITION 4.5.5. *Let* $\Psi(0)$ *be given by* (4.4.11). *Then*

$$\Psi(0) = \Psi_0 + \rho\Psi_1 + \chi\Psi_2 + o(\rho\chi), \tag{4.5.35}$$

where

$$\begin{aligned} \Psi_0 &= Y_0 \frac{1}{|\hat{\mathbb{T}}|^2} \sum_{\theta\in\hat{\mathbb{T}}} \hat{p}(\theta)\hat{X}_0(\theta)\Phi_0, \\ \Psi_1 &= Y_0 \frac{1}{|\hat{\mathbb{T}}|^2} \sum_{\theta\in\hat{\mathbb{T}}} \hat{p}(\theta)\Big(\hat{X}_0(\theta)\Phi_1 + \hat{X}_1(\theta)\Phi_0\Big) + Y_1 \frac{1}{|\hat{\mathbb{T}}|^2} \sum_{\theta\in\hat{\mathbb{T}}} \hat{p}(\theta)\hat{X}_0(\theta)\Phi_0, \\ \Psi_2 &= Y_0 \frac{1}{|\hat{\mathbb{T}}|^2} \sum_{\theta\in\hat{\mathbb{T}}} \hat{p}(\theta)\Big(\hat{X}_0(\theta)\Phi_1 + \hat{X}_2(\theta)\Phi_0\Big) + Y_2 \frac{1}{|\hat{\mathbb{T}}|^2} \sum_{\theta\in\hat{\mathbb{T}}} \hat{p}(\theta)\hat{X}_0(\theta)\Phi_0. \end{aligned} \tag{4.5.36}$$

Note that Ψ_0 is indeed the expression we obtain when we substitute $(\rho, \chi) = (0, 0)$ in (4.4.11).

PROOF. Using the previous expansions, we have that

$$\begin{aligned} \Psi(0) &= Y \left(\frac{1}{|\hat{\mathbb{T}}|^2} \sum_{\theta\in\hat{\mathbb{T}}} \hat{p}(\theta)\hat{X}(\theta)\Phi \right) \\ &= (Y_0 + \rho Y_1 + \chi Y_2) \left(\frac{1}{|\hat{\mathbb{T}}|^2} \sum_{\theta\in\hat{\mathbb{T}}} \hat{p}(\theta)\Big(\hat{X}_0(\theta) + \rho\hat{X}_1(\theta) + \chi\hat{X}_2(\theta)\Big)\Big(\Phi_0 + (\rho+\chi)\Phi_1\Big) \right) \\ &\quad + o(\rho\chi) \\ &= Y_0 \frac{1}{|\hat{\mathbb{T}}|^2} \sum_{\theta\in\hat{\mathbb{T}}} \hat{p}(\theta)\hat{X}_0(\theta)\Phi_0 \\ &\quad + \rho \left(Y_0 \frac{1}{|\hat{\mathbb{T}}|^2} \sum_{\theta\in\hat{\mathbb{T}}} \hat{p}(\theta)\Big(\hat{X}_0(\theta)\Phi_1 + \hat{X}_1(\theta)\Phi_0\Big) + Y_1 \frac{1}{|\hat{\mathbb{T}}|^2} \sum_{\theta\in\hat{\mathbb{T}}} \hat{p}(\theta)\hat{X}_0(\theta)\Phi_0 \right) \\ &\quad + \chi \left(Y_0 \frac{1}{|\hat{\mathbb{T}}|^2} \sum_{\theta\in\hat{\mathbb{T}}} \hat{p}(\theta)\Big(\hat{X}_0(\theta)\Phi_1 + \hat{X}_2(\theta)\Phi_0\Big) + Y_2 \frac{1}{|\hat{\mathbb{T}}|^2} \sum_{\theta\in\hat{\mathbb{T}}} \hat{p}(\theta)\hat{X}_0(\theta)\Phi_0 \right) + o(\rho\chi). \end{aligned} \tag{4.5.37}$$

□

We now have all the terms that are necessary to derive an expansion for $\hat{\Psi}(\theta)$ around $(\rho, \chi) = (0, 0)$, which we state in the following theorem.

THEOREM 4.5.6. *For* $\theta \in \hat{\mathbb{T}}$,

$$\hat{\Psi}(\theta) = \hat{\Psi}_0(\theta) + \rho\hat{\Psi}_1(\theta) + \chi\hat{\Psi}_2(\theta) + o(\rho\chi), \tag{4.5.38}$$

where

$$\begin{aligned} \hat{\Psi}_0(\theta) &= \hat{p}(\theta)\hat{X}_0(\theta)\Big(\Phi_0 + A_0\Psi_0\Big), \\ \hat{\Psi}_1(\theta) &= \hat{p}(\theta)\Big(\hat{X}_0(\theta)\Big(\Phi_1 + A_0\Psi_1 + A_1\Psi_0\Big) + \hat{X}_1(\theta)\Big(\Phi_0 + A_0\Psi_0\Big)\Big), \\ \hat{\Psi}_2(\theta) &= \hat{p}(\theta)\Big(\hat{X}_0(\theta)\Big(\Phi_1 + A_0\Psi_2 + A_1\Psi_0\Big) + \hat{X}_2(\theta)\Big(\Phi_0 + A_0\Psi_0\Big)\Big). \end{aligned} \tag{4.5.39}$$

Note that $\hat{\Psi}_0(\theta)$ is indeed the expression we obtain when we substitute $(\rho, \chi) = (0, 0)$ in (4.4.10). By considering $\hat{\Psi}(\theta) - \hat{\Psi}_0(\theta)$, it is clear that we obtain the influence of the seed-bank and of the harmless mutation. The influence of the former is reflected in $\hat{\Psi}_1(\theta)$, while the influence of the latter is reflected in $\hat{\Psi}_2(\theta)$.

PROOF. We have that

$$\begin{aligned} \hat{\Psi}(\theta) &= \hat{p}(\theta)\hat{X}(\theta)(\Phi + A\Psi(0)) \\ &= \hat{p}(\theta)\Big[\hat{X}_0(\theta) + \rho\hat{X}_1(\theta) + \chi\hat{X}_2(\theta)\Big]\Big[\Phi_0 + \rho\Phi_1 + \chi\Phi_2 \\ &\qquad + \Big(A_0 + (\rho+\chi)A_1\Big)\Big(\Psi_0 + \rho\Psi_1 + \chi\Psi_2\Big)\Big] + o(\rho\chi) \\ &= \hat{p}(\theta)\hat{X}_0(\theta)\Big(\Phi_0 + A_0\Psi_0\Big) \\ &\quad + \rho\,\hat{p}(\theta)\Big(\hat{X}_0(\theta)\Big(\Phi_1 + A_0\Psi_1 + A_1\Psi_0\Big) + \hat{X}_1(\theta)\Big(\Phi_0 + A_0\Psi_0\Big)\Big) \\ &\quad + \chi\,\hat{p}(\theta)\Big(\hat{X}_0(\theta)\Big(\Phi_2 + A_0\Psi_2 + A_1\Psi_0\Big) + \hat{X}_2(\theta)\Big(\Phi_0 + A_0\Psi_0\Big)\Big) + o(\rho\chi). \end{aligned} \tag{4.5.40}$$

□

By inverting the expansion found for $\hat{\Psi}(\theta)$, we obtain an expansion of $\Psi(x) := \Psi(x, 0)$ around $(\rho, \chi) = (0, 0)$. However, as in Section 3.4 in Chapter 3, the degree of difficulty depends on the model chosen. In the next section, for a special choice of $p(x, y)$, we invert (4.5.38) and show that it can be written in terms of the Green function of a simple random walk.

4.6. Fourier inversion

In this section, we consider a special choice of $p(x, y)$ for which we are able to invert the expression found for $\hat{\Psi}(\theta)$ in Theorem 4.5.6. The inverse can be expressed in terms of the Green function of a simple random walk. We first simplify the expression found. For $i \in \{0, 1, 2\}$, consider $\hat{X}_i(\theta)$ as defined in Proposition 4.5.3. Define

$$\hat{\mathcal{X}}_i(\theta) = \hat{p}(\theta)\hat{X}_i(\theta), \tag{4.6.1}$$

with X_i and $\mathcal{X}_i$ their respective Fourier inverses. Next, recall that the Fourier inverse is defined by (3.4.2). Then, for any $\hat{f} : \mathbb{T} \to \mathbb{R}$ with Fourier inverse f, we have

$$f(0) = \frac{1}{|\hat{\mathbb{T}}|^2} \sum_{\theta \in \hat{\mathbb{T}}} \hat{f}(\theta). \tag{4.6.2}$$

It is now possible to simplify the expressions given in Propositions 4.5.4 and 4.5.5, and in Theorem 4.5.6. Note that this simplification is not dependent on p and indeed is true for any choice of p. Recall that Φ_i is given by (4.5.12) and A_i is given by (4.5.13).

PROPOSITION 4.6.1 (Simplification of Proposition 4.5.4). *Define*

$$N_0 = I_{16} - \mathcal{X}_0(0)A_0, \quad N_1 = X_0(0)A_1 + X_1(0)A_0, \quad N_2 = X_0(0)A_1 + X_2(0)A_0. \tag{4.6.3}$$

Then

$$Y = Y_0 + \rho Y_1 + \chi Y_2 + o(\rho\chi), \tag{4.6.4}$$

where

$$Y_0 = N_0^{-1}, \quad Y_1 = N_0^{-1} N_1 N_0^{-1}, \quad Y_2 = N_0^{-1} N_2 N_0^{-1}. \tag{4.6.5}$$

PROPOSITION 4.6.2 (Simplification of Proposition 4.5.5). *Let* $\Psi(0)$ *be given by* (4.4.11). *Then*

$$\Psi(0) = \Psi_0 + \rho\Psi_1 + \chi\Psi_2 + o(\rho\chi), \tag{4.6.6}$$

where

$$\begin{aligned} \Psi_0 &= Y_0\mathcal{X}_0(0)\Phi_0 \\ \Psi_1 &= Y_0(\mathcal{X}_0(0)\Phi_1 + \mathcal{X}_1(0)\Phi_0) + Y_1\mathcal{X}_0(0)\Phi_0 \\ \Psi_2 &= Y_0(\mathcal{X}_0(0)\Phi_1 + \mathcal{X}_2(0)\Phi_0) + Y_2\mathcal{X}_0(0)\Phi_0. \end{aligned} \tag{4.6.7}$$

THEOREM 4.6.3 (Simplification of Theorem 4.5.6). *For* $\theta \in \hat{\mathbb{T}}$,

$$\hat{\Psi}(\theta) = \hat{\Psi}_0(\theta) + \rho\hat{\Psi}_1(\theta) + \chi\hat{\Psi}_2(\theta) + o(\rho\chi), \tag{4.6.8}$$

where

$$\begin{aligned} \hat{\Psi}_0(\theta) &= \hat{\mathcal{X}}_0(\theta)(\Phi_0 + A_0\Psi_0), \\ \hat{\Psi}_1(\theta) &= \hat{\mathcal{X}}_0(\theta)(\Phi_1 + A_0\Psi_1 + A_1\Psi_0) + \hat{\mathcal{X}}_1(\theta)(\Phi_0 + A_0\Psi_0), \\ \hat{\Psi}_2(\theta) &= \hat{\mathcal{X}}_0(\theta)(\Phi_1 + A_0\Psi_2 + A_1\Psi_0) + \hat{\mathcal{X}}_2(\theta)(\Phi_0 + A_0\Psi_0). \end{aligned} \tag{4.6.9}$$

It is clear that to invert (4.6.8) and to determine all constants involved, we only have to determine the Fourier inverse functions X_i and $\mathcal{X}_i$, $i \in \{0, 1, 2\}$. We introduce several functions and constants, which we use to determine expressions for the functions $\hat{X}_i$ and $\hat{\mathcal{X}}_i$ and their respective inverses.

First, consider two basic functions. For $\theta \in \hat{\mathbb{T}}$ and $c \in \mathbb{R}$, let

$$\hat{\alpha}_c(\theta) = \frac{1}{1 - c\hat{p}(\theta)}, \quad \hat{\beta}_c(\theta) = \frac{c\hat{p}(\theta)}{1 - c\hat{p}(\theta)}, \tag{4.6.10}$$

with α_c and β_c their respective Fourier inverses. From this, we construct three more functions.

For $\theta \in \hat{\mathbb{T}}$ and $c, d \in \mathbb{R}$, let

$$\hat{\gamma}_{c,d}(\theta) = \frac{1}{(1 - c\hat{p}(\theta))(1 - d\hat{p}(\theta))}, \quad \hat{\varepsilon}_c(\theta) = \left(\frac{c\hat{p}(\theta)}{1 - c\hat{p}(\theta)}\right)^2, \quad \hat{\zeta}_{c,d}(\theta) = \frac{c\hat{p}(\theta)}{(1 - c\hat{p}(\theta))(1 - d\hat{p}(\theta))}, \tag{4.6.11}$$

with Fourier inverses $\gamma_{c,d}$, ε_c and $\zeta_{c,d}$, respectively. Finally, for $\alpha \in \{A, a\}$, define

$$\begin{aligned} c_1(\alpha) &= \frac{\nu_\alpha}{2\mu + \nu_\alpha}, & c_2 &= \frac{\nu_A + \nu_a}{2\mu + \nu_A + \nu_a}, & c_3(\alpha) &= \frac{\nu_\alpha}{\mu + \nu_\alpha}, & c_4(\alpha) &= -\frac{2(\mu + \nu_\alpha)}{(2\mu + \nu_\alpha)^2}, \\ c_5 &= -\frac{2\mu + 3\nu_A + 3\nu_a}{(2\mu + \nu_A + \nu_a)^2}, & c_6(\alpha) &= -\frac{2\mu + 3\nu_\alpha}{2(\mu + \nu_\alpha)^2}, & c_7(\alpha) &= \frac{1}{2\mu + \nu_\alpha} & c_8 &= \frac{1}{2\mu}. \end{aligned} \tag{4.6.12}$$

It is now possible to express $\hat{X}_i$ and $\hat{\mathcal{X}}_i$ solely in terms of these functions and constants.

Proposition 4.6.4. *Let $\hat{X}_0(\theta)$ be given by Proposition 4.5.3. For $\theta \in \hat{\mathbb{T}}$, $\hat{X}_0(\theta)$ and $\hat{\mathcal{X}}_0(\theta)$ are the diagonal matrices with elements given by*

$$[\hat{X}_0(\theta)]_{kk} = \begin{cases} \hat{\alpha}_{c_3(A)}(\theta), & k = 1, \\ \hat{\alpha}_{c_2}(\theta), & k \in \{2, 5\}, \\ \hat{\alpha}_{c_1(A)}(\theta), & k \in \{3, 4, 9, 13\}, \\ \hat{\alpha}_{c_3(a)}(\theta), & k = 6, \\ \hat{\alpha}_{c_1(a)}(\theta), & k \in \{7, 8, 10, 14\}, \\ 1, & k \in \{11, 12, 15, 16\}, \end{cases} \tag{4.6.13}$$

$$[\hat{\mathcal{X}}_0(\theta)]_{kk} = \begin{cases} \frac{1}{c_3(A)}\hat{\beta}_{c_3(A)}(\theta), & k = 1, \\ \frac{1}{c_2}\hat{\beta}_{c_2}(\theta), & k \in \{2, 5\}, \\ \frac{1}{c_1(A)}\hat{\beta}_{c_1(A)}(\theta), & k \in \{3, 4, 9, 13\}, \\ \frac{1}{c_3(a)}\hat{\beta}_{c_3(a)}(\theta), & k = 6, \\ \frac{1}{c_1(a)}\hat{\beta}_{c_1(a)}(\theta), & k \in \{7, 8, 10, 14\}, \\ \hat{p}(\theta), & k \in \{11, 12, 15, 16\}. \end{cases} \tag{4.6.14}$$

Proof. As defined in Proposition 4.5.3, we have that

$$\hat{X}_0(\theta) = M_0^{-1}(\theta) = [I_{16} - \hat{p}(\theta)(D_0 + E_0)]^{-1}. \tag{4.6.15}$$

Since D_0 and E_0 are diagonal matrices, it follows that $\hat{X}_0(\theta)$ is again a diagonal matrix with elements given by

$$[\hat{X}_0(\theta)]_{kk} = \frac{1}{[I_{16} - \hat{p}(\theta)(D_0 + E_0)]_{kk}}, \quad k \in \{1, \ldots, 16\}. \tag{4.6.16}$$

Using the definitions of D_0 and E_0, and the notation introduced, (4.6.13) follows. By definition,

$$[\hat{\mathcal{X}}_0(\theta)]_{kk} = [\hat{p}(\theta)\hat{X}_0(\theta)]_{kk}, \quad k \in \{1, \ldots, 16\}. \tag{4.6.17}$$

Observe that for all $c \neq 0$,

$$\hat{p}(\theta)\hat{\alpha}_c(\theta) = \frac{1}{c}\hat{\beta}_c(\theta) \tag{4.6.18}$$

and hence (4.6.14) follows. □

PROPOSITION 4.6.5. *Let $\hat{X}_1(\theta)$ be given by Proposition 4.5.3. For $\theta \in \hat{\mathbb{T}}$, $\hat{X}_1(\theta)$ and $\hat{\mathcal{X}}_1(\theta)$ are the matrices with elements given by*

$$[\hat{X}_1(\theta)]_{kl} = \begin{cases} \frac{c_6(A)}{c_3(A)}\hat{\zeta}_{c_3(A),c_3(A)}(\theta), & (k,l) = (1,1), \\ \frac{c_5}{c_2}\hat{\zeta}_{c_2,c_2}(\theta), & (k,l) \in \{(2,2),(5,5)\}, \\ c_7(A)\hat{\gamma}_{c_1(A),c_3(A)}(\theta), & (k,l) \in \{(3,1),(9,1)\}, \\ \frac{c_4(A)}{c_1(A)}\hat{\zeta}_{c_1(A),c_1(A)}(\theta), & (k,l) \in \{(3,3),(4,4),(9,9),(13,13)\}, \\ c_7(A)\hat{\gamma}_{c_1(A),c_2}(\theta), & (k,l) \in \{(4,2),(13,5)\}, \\ \frac{c_6(a)}{c_3(a)}\hat{\zeta}_{c_3(a),c_3(a)}(\theta), & (k,l) = (6,6), \\ c_7(a)\hat{\gamma}_{c_1(a),c_2}(\theta), & (k,l) \in \{(7,5),(10,2)\}, \\ \frac{c_4(a)}{c_1(a)}\hat{\zeta}_{c_1(a),c_1(a)}(\theta), & (k,l) \in \{(7,7),(8,8),(10,10),(14,14)\}, \\ c_7(a)\hat{\gamma}_{c_1(a),c_3(a)}(\theta), & (k,l) \in \{(8,6),(14,6)\}, \\ c_8\hat{\alpha}_{c_1(A)}(\theta), & (k,l) \in \{(11,9),(12,4),(15,13)\}, \\ c_8\hat{\alpha}_{c_1(a)}(\theta), & (k,l) \in \{(15,7),(16,8),(16,14)\}, \\ 0, & \textit{otherwise}, \end{cases} \tag{4.6.19}$$

$$[\hat{\mathcal{X}}_1(\theta)]_{kl} = \begin{cases} \frac{c_6(A)}{c_3(A)^2}\hat{\varepsilon}_{c_3(A)}(\theta), & (k,l) = (1,1), \\ \frac{c_5}{c_2^2}\hat{\varepsilon}_{c_2}(\theta), & (k,l) \in \{(2,2),(5,5)\}, \\ \frac{c_7(A)}{c_1(A)}\hat{\zeta}_{c_1(A),c_3(A)}(\theta), & (k,l) \in \{(3,1),(9,1)\}, \\ \frac{c_4(A)}{c_1(A)^2}\hat{\varepsilon}_{c_1(A)}(\theta), & (k,l) \in \{(3,3),(4,4),(9,9),(13,13)\}, \\ \frac{c_7(A)}{c_1(A)}\hat{\zeta}_{c_1(A),c_2}(\theta), & (k,l) \in \{(4,2),(13,5)\}, \\ \frac{c_6(a)}{c_3(a)^2}\hat{\varepsilon}_{c_3(a)}(\theta), & (k,l) = (6,6), \\ \frac{c_7(a)}{c_1(a)}\hat{\zeta}_{c_1(a),c_2}(\theta), & (k,l) \in \{(7,5),(10,2)\}, \\ \frac{c_4(a)}{c_1(a)^2}\hat{\varepsilon}_{c_1(a)}(\theta), & (k,l) \in \{(7,7),(8,8),(10,10),(14,14)\}, \\ \frac{c_7(a)}{c_1(a)}\hat{\zeta}_{c_1(a),c_3(a)}(\theta), & (k,l) \in \{(8,6),(14,6)\}, \\ \frac{c_8}{c_1(A)}\hat{\beta}_{c_1(A)}(\theta), & (k,l) \in \{(11,9),(12,4),(15,13)\}, \\ \frac{c_8}{c_1(a)}\hat{\beta}_{c_1(a)}(\theta), & (k,l) \in \{(15,7),(16,8),(16,14)\}, \\ 0, & \textit{otherwise}. \end{cases} \tag{4.6.20}$$

PROOF. As defined in Proposition 4.5.3, we have that

$$\hat{X}_1(\theta) = M_0^{-1}(\theta)M_1(\theta)M_0^{-1}(\theta). \tag{4.6.21}$$

Here, $M_0^{-1}(\theta) = \hat{X}_0(\theta)$ and hence is given in (4.6.13). Further, we have that

$$M_1(\theta) = C_1 + \hat{p}(\theta)(D_1 + E_1). \tag{4.6.22}$$

Using the definitions of C_1, D_1 and E_1, the notation introduced and by multiplying the three matrices, (4.6.19) follows. By definition,

$$[\hat{\mathcal{X}}_1(\theta)]_{kl} = [\hat{p}(\theta)\hat{X}_1(\theta)]_{kl}, \quad (k,l) \in \{1,\dots,16\} \times \{1,\dots,16\}. \tag{4.6.23}$$

Observe that in addition to (4.6.18), for all $c \neq 0$ and for all d,

$$\hat{p}(\theta)\hat{\zeta}_{c,c}(\theta) = \frac{1}{c}\hat{\varepsilon}_c(\theta), \quad \hat{p}(\theta)\hat{\gamma}_{c,d}(\theta) = \frac{1}{c}\hat{\zeta}_{c,d}(\theta), \tag{4.6.24}$$

and hence (4.6.20) follows. □

Proposition 4.6.6. *Let $\hat{X}_2(\theta)$ be given by Proposition 4.5.3. For $\theta \in \hat{\mathbb{T}}$, $\hat{X}_2(\theta)$ and $\hat{\mathcal{X}}_2(\theta)$ are the diagonal matrices with elements given by*

$$[\hat{X}_2(\theta)]_{kk} = \begin{cases} \frac{c_6(A)}{c_3(A)}\hat{\zeta}_{c_3(A),c_3(A)}(\theta), & k = 1, \\ \frac{c_5}{c_2}\hat{\zeta}_{c_2,c_2}(\theta), & k \in \{2,5\}, \\ \frac{-1}{c_1(A)}\hat{\zeta}_{c_1(A),c_1(A)}(\theta), & k \in \{3,4,9,13\}, \\ \frac{c_6(a)}{c_3(a)}\hat{\zeta}_{c_3(a),c_3(a)}(\theta), & k = 6, \\ \frac{-1}{c_1(a)}\hat{\zeta}_{c_1(a),c_1(a)}(\theta), & k \in \{7,8,10,14\}, \\ 0, & k \in \{11,12,15,16\}, \end{cases} \tag{4.6.25}$$

$$[\hat{\mathcal{X}}_2(\theta)]_{kk} = \begin{cases} \frac{c_6(A)}{c_3(A)^2}\hat{\varepsilon}_{c_3(A)}(\theta), & k = 1, \\ \frac{c_5}{c_2^2}\hat{\varepsilon}_{c_2}(\theta), & k \in \{2,5\}, \\ \frac{-1}{c_1(A)^2}\hat{\varepsilon}_{c_1(A)}(\theta), & k \in \{3,4,9,13\}, \\ \frac{c_6(a)}{c_3(a)^2}\hat{\varepsilon}_{c_3(a)}(\theta), & k = 6, \\ \frac{-1}{c_1(a)^2}\hat{\varepsilon}_{c_1(a)}(\theta), & k = \{7,8,10,14\}, \\ 0, & k \in \{11,12,15,16\}. \end{cases} \tag{4.6.26}$$

Proof. As defined in Proposition 4.5.3, we have that

$$\hat{X}_2(\theta) = M_0^{-1}(\theta)M_2(\theta)M_0^{-1}(\theta). \tag{4.6.27}$$

Here, $M_0^{-1}(\theta) = \hat{X}_0(\theta)$ and given by (4.6.13). We also have that

$$M_2(\theta) = \hat{p}(\theta)(D_2 + E_2). \tag{4.6.28}$$

Using the definitions of D_2 and E_2, the notation introduced and by multiplying the three matrices, (4.6.25) follows. By definition,

$$[\hat{\mathcal{X}}_2(\theta)]_{kk} = [\hat{p}(\theta)\hat{X}_2(\theta)]_{kk}, \quad k \in \{1,\dots,16\}. \tag{4.6.29}$$

Observe that (4.6.24) is true and hence (4.6.26) follows. □

Our objective is to find the inverse functions X_i and $\mathcal{X}_i$, $i \in \{0,1,2\}$. In Propositions 4.6.4 through 4.6.6, we expressed $\hat{X}_i$ and $\hat{\mathcal{X}}_i$ solely in terms of the functions $\hat{\alpha}_c$, $\hat{\beta}_c$, $\hat{\gamma}_{c,d}$, $\hat{\varepsilon}_c$ and $\hat{\zeta}_{c,d}$. As the Fourier inversion formula is applied to each element of a matrix seperately, it suffices to determine the inverse functions α_c, β_c, $\gamma_{c,d}$, ε_c and $\zeta_{c,d}$. As in Chapter 3, we consider a special choice of p, for which we are able to determine the inverses in terms of the Green function of a simple random walk. We briefly recall our choice for p.

Let $\lambda \in [0,1]$ and consider

$$p(x,y) = (1-\lambda)\delta_{x,y} + \lambda q(x,y), \quad x,y \in \mathbb{T} \tag{4.6.30}$$

where $\delta_{x,y} = \mathbb{1}\{x=y\}$ and with q the transition kernel of a simple random walk (see (3.5.5)). Note that p is indeed translation invariant, so we may consider $p(x) := p(x,0)$. It follows that

$$\hat{p}(\theta) = (1-\lambda) + \lambda\hat{q}(\theta). \tag{4.6.31}$$

For $x \in \mathbb{T}$ and $\ell \in \mathbb{N}_0$, let $q_l(x)$ be the probability that a simple random walk starting from the origin is at site x at time l. The Green function of a simple random walk at site x is

$$G_x(z) = \sum_{l\in\mathbb{N}_0} q_l(x) z^l, \quad |z|<1. \tag{4.6.32}$$

Note that while the functions $\hat{\alpha}_c$, $\hat{\beta}_c$, $\hat{\gamma}_{c,d}$, $\hat{\varepsilon}_c$ and $\hat{\zeta}_{c,d}$ are defined for all $c,d \in \mathbb{R}$, the Green function is only defined for z such that $|z|<1$. In determining the inverses, we only consider the appropriate values for c and d.

Proposition 4.6.7. *Let p as in (4.6.30). For $x \in \mathbb{T}$ and $0<c<1$,*

$$\begin{aligned} \alpha_c(x) &= \frac{1}{1-b_c} G_x\left(\frac{a_c}{1-b_c}\right), \\ \beta_c(x) &= \frac{1}{1-b_c} G_x\left(\frac{a_c}{1-b_c}\right) - \delta_{x,0}, \end{aligned} \tag{4.6.33}$$

with $a_c = c\lambda$ and $b_c = c(1-\lambda)$.

Proof. Note that if $0<c<1$, then

$$0 < \frac{a_c}{1-b_c} = \frac{c\lambda}{1-c+c\lambda} < 1. \tag{4.6.34}$$

To derive the claims, we refer to the proof of Proposition 3.5.2, where they are shown to be true for the fixed constant $c = \nu/(\mu+\nu)$. All steps used are valid for any constant c such that $0<c<1$, so this concludes the proof. □

Before we invert the remaining functions, we state the convolution theorem for Fourier inverse functions (cf. [5], Chapter 6, Section 6) and prove a property for convolutions of Green functions.

THEOREM 4.6.8 (Convolution Theorem). *Let $\hat{f}, \hat{g} : \hat{\mathbb{T}} \to \mathbb{R}$ and let $f, g : \mathbb{T} \to \mathbb{R}$ be their respective Fourier inverses. Let $\hat{h}(\theta) = \hat{f}(\theta)\hat{g}(\theta)$. Then the Fourier inverse of $\hat{h}$ is given by*

$$h(x) = \sum_{y\in\mathbb{T}} f(x-y)g(y) = \sum_{y\in\mathbb{T}} f(y)g(x-y). \tag{4.6.35}$$

LEMMA 4.6.9. *Let G'_x be the derivative of G_x. For $x \in \mathbb{T}$ and for any $|z_1|, |z_2| \leq 1$,*

$$\sum_{y\in\mathbb{T}} G_{x-y}(z_1)G_y(z_2) = \begin{cases} \dfrac{1}{z_1 - z_2}\left[z_1 G_x(z_1) - z_2 G_x(z_2)\right], & z_1 \neq z_2, \\ G_x(z_1) + z_1 G'_x(z_1), & z_1 = z_2. \end{cases} \tag{4.6.36}$$

PROOF. For any $|z_1|, |z_2| \leq 1$, we have that

$$\begin{aligned} \sum_{y\in\mathbb{T}} G_{x-y}(z_1)G_y(z_2) &= \sum_{l_1,l_2\in\mathbb{N}_0} z_1^{l_1} z_2^{l_2} \sum_{y\in\mathbb{T}} q_{l_1}(x-y)q_{l_2}(y) \\ &= \sum_{l_1,l_2\in\mathbb{N}_0} z_1^{l_1} z_2^{l_2} q_{l_1+l_2}(x) \\ &= \sum_{k\in\mathbb{N}_0} q_k(x) \sum_{\substack{l_1,l_2\in\mathbb{N}_0:\\ l_1+l_2=k}} z_1^{l_1} z_2^{l_2} \\ &= \sum_{k\in\mathbb{N}_0} q_k(x) \sum_{l_2=0}^{k} z_1^{k-l_2} z_2^{l_2}. \end{aligned} \tag{4.6.37}$$

If $z_1 \neq z_2$, then we continue on from (4.6.37) as

$$\begin{aligned} \sum_{k\in\mathbb{N}_0} q_k(x) z_1^k \sum_{l_2=0}^{k} \left(\frac{z_2}{z_1}\right)^{l_2} &= \sum_{k\in\mathbb{N}_0} q_k(x) z_1^k \frac{1-(z_2/z_1)^{k+1}}{1-z_2/z_1} \\ &= \frac{1}{z_1 - z_2}[z_1 G_x(z_1) - z_2 G_x(z_2)]. \end{aligned} \tag{4.6.38}$$

If $z_1 = z_2$, then we continue on from (4.6.37) as

$$\begin{aligned} \sum_{k\in\mathbb{N}_0} (k+1) q_k(x) z_1^k &= \frac{d}{dz_1}\left[\sum_{k\in\mathbb{N}_0} q_k(x) z_1^{k+1}\right] \\ &= \frac{d}{dz_1}\left[z_1 G_x(z_1)\right] \\ &= G_x(z_1) + z_1 G'_x(z_1), \end{aligned} \tag{4.6.39}$$

which concludes the proof. □

Using these convolutions, the remaining inverse functions can be determined.

Proposition 4.6.10. *Let p as in (4.6.30). For $x \in \mathbb{T}$ and $0 \leq c, d < 1$,*

$$\gamma_{c,d}(x) = \begin{cases} \frac{1}{a_c(1-b_d)-a_d(1-b_c)} \left[\frac{a_c}{1-b_c} G_x\left(\frac{a_c}{1-b_c}\right) - \frac{a_d}{1-b_d} G_x\left(\frac{a_d}{1-b_d}\right)\right], & c \neq d, \\ \frac{1}{(1-b_c)^2}\left[G_x\left(\frac{a_c}{1-b_c}\right) + \frac{a_c}{1-b_c} G'_x\left(\frac{a_c}{1-b_c}\right)\right], & c = d, \end{cases} \tag{4.6.40}$$

$$\varepsilon_c(x) = \frac{1}{(1-b_c)^2}\left[(1-2(1-b_c))G_x\left(\frac{a_c}{1-b_c}\right) + \frac{a_c}{1-b_c} G'_x\left(\frac{a_c}{1-b_c}\right)\right] + \delta_{x,0}, \tag{4.6.41}$$

$$\zeta_{c,d}(x) = \begin{cases} \frac{1}{a_c(1-b_d)-a_d(1-b_c)} \left[\frac{a_c}{1-b_c} G_x\left(\frac{a_c}{1-b_c}\right) - \frac{a_d}{1-b_d} G_x\left(\frac{a_d}{1-b_d}\right)\right] - \frac{1}{1-b_d} G_x\left(\frac{a_d}{1-b_d}\right), & c \neq d, \\ \frac{1}{(1-b_c)^2}\left[G_x\left(\frac{a_c}{1-b_c}\right) + \frac{a_c}{1-b_c} G'_x\left(\frac{a_c}{1-b_c}\right)\right] - \frac{1}{1-b_c} G_x\left(\frac{a_c}{1-b_c}\right), & c = d, \end{cases} \tag{4.6.42}$$

with $a_c = c\lambda$, $b_c = c(1-\lambda)$, $a_d = d\lambda$ and $b_d = d(1-\lambda)$.

Proof. We have that

$$\hat{\gamma}_{c,d}(x) = \hat{\alpha}_c(\theta)\hat{\alpha}_d(\theta). \tag{4.6.43}$$

By Theorem 4.6.8, it follows that

$$\gamma_{c,d}(x) = \sum_{y \in \mathbb{T}} \alpha_c(x-y)\alpha_d(y) = \frac{1}{(1-b_c)(1-b_d)} \sum_{y \in \mathbb{T}} G_{x-y}\left(\frac{a_c}{1-b_c}\right) G_y\left(\frac{a_d}{1-b_d}\right). \tag{4.6.44}$$

We then apply Lemma 4.6.9 to the convolution of Green functions. If $c \neq d$, then

$$\begin{aligned} \gamma_{c,d}(x) &= \frac{1}{(1-b_c)(1-b_d)} \frac{1}{\frac{a_c}{1-b_c} - \frac{a_d}{1-b_d}} \left[\frac{a_c}{1-b_c} G_x\left(\frac{a_c}{1-b_c}\right) - \frac{a_d}{1-b_d} G_x\left(\frac{a_d}{1-b_d}\right)\right] \\ &= \frac{1}{a_c(1-b_d)-a_d(1-b_c)} \left[\frac{a_c}{1-b_c} G_x\left(\frac{a_c}{1-b_c}\right) - \frac{a_d}{1-b_d} G_x\left(\frac{a_d}{1-b_d}\right)\right]. \end{aligned} \tag{4.6.45}$$

If $c = d$, then

$$\gamma_{c,c}(x) = \frac{1}{(1-b_c)^2}\left[G_x\left(\frac{a_c}{1-b_c}\right) + \frac{a_c}{1-b_c} G'_x\left(\frac{a_c}{1-b_c}\right)\right]. \tag{4.6.46}$$

To obtain the claims for ε_c and $\zeta_{c,d}$, note that

$$\hat{\varepsilon}_c(\theta) = (\hat{\beta}_c(\theta))^2, \qquad \hat{\zeta}_{c,d}(\theta) = \hat{\beta}_c(\theta)\hat{\alpha}_d(\theta), \tag{4.6.47}$$

and apply Theorem 4.6.8 and Lemma 4.6.9 consecutively. □

Using Propositions 4.6.4 through 4.6.6, we need to determine the inverse functions with constants $c_1(\alpha)$, c_2 and $c_3(\alpha)$. For the definition of all constants, see (4.6.12). As $\mu, \nu_\alpha > 0$, it is clear that

$$0 < c_1(\alpha), c_2, c_3(\alpha) < 1. \tag{4.6.48}$$

The inverse functions X_i and $\mathcal{X}_i$ now follow immediately.

Corollary 4.6.11. *For p as in (4.6.30) and $x \in \mathbb{T}$, $X_0(x)$ and $\mathcal{X}_0(x)$ are the 16×16 diagonal matrices with elements given by*

$$[X_0(x)]_{kk} = \begin{cases} \alpha_{c_3(A)}(x), & k = 1, \\ \alpha_{c_2}(x), & k \in \{2,5\}, \\ \alpha_{c_1(A)}(x), & k \in \{3,4,9,13\}, \\ \alpha_{c_3(a)}(x), & k = 6, \\ \alpha_{c_1(a)}(x), & k \in \{7,8,10,14\}, \\ \delta_{x,0}, & k \in \{11,12,15,16\}, \end{cases} \tag{4.6.49}$$

$$[\mathcal{X}_0(x)]_{kk} = \begin{cases} \frac{1}{c_3(A)}\beta_{c_3(A)}(x), & k = 1, \\ \frac{1}{c_2}\beta_{c_2}(x), & k \in \{2,5\}, \\ \frac{1}{c_1(A)}\beta_{c_1(A)}(x), & k \in \{3,4,9,13\}, \\ \frac{1}{c_3(a)}\beta_{c_3(a)}(x), & k = 6, \\ \frac{1}{c_1(a)}\beta_{c_1(a)}(x), & k \in \{7,8,10,14\}, \\ p(x), & k \in \{11,12,15,16\}. \end{cases} \tag{4.6.50}$$

Corollary 4.6.12. *For p as in (4.6.30) and $x \in \mathbb{T}$, $X_1(x)$ and $\mathcal{X}_1(x)$ are the 16×16 matrices with elements given by*

$$[X_1(x)]_{kl} = \begin{cases} \frac{c_6(A)}{c_3(A)}\zeta_{c_3(A),c_3(A)}(x), & (k,l) = (1,1), \\ \frac{c_5}{c_2}\zeta_{c_2,c_2}(x), & (k,l) \in \{(2,2),(5,5)\}, \\ c_7(A)\gamma_{c_1(A),c_3(A)}(x), & (k,l) \in \{(3,1),(9,1)\}, \\ \frac{c_4(A)}{c_1(A)}\zeta_{c_1(A),c_1(A)}(x), & (k,l) \in \{(3,3),(4,4),(9,9),(13,13)\}, \\ c_7(A)\gamma_{c_1(A),c_2}(x), & (k,l) \in \{(4,2),(13,5)\}, \\ \frac{c_6(a)}{c_3(a)}\zeta_{c_3(a),c_3(a)}(x), & (k,l) = (6,6), \\ c_7(a)\gamma_{c_1(a),c_2}(x), & (k,l) \in \{(7,5),(10,2)\}, \\ \frac{c_4(a)}{c_1(a)}\zeta_{c_1(a),c_1(a)}(x), & (k,l) \in \{(7,7),(8,8),(10,10),(14,14)\}, \\ c_7(a)\gamma_{c_1(a),c_3(a)}(x), & (k,l) \in \{(8,6),(14,6)\}, \\ c_8\alpha_{c_1(A)}(x), & (k,l) \in \{(11,9),(12,4),(15,13)\}, \\ c_8\alpha_{c_1(a)}(x), & (k,l) \in \{(15,7),(16,8),(16,14)\}, \\ 0, & \textit{otherwise}, \end{cases} \tag{4.6.51}$$

$$[\mathcal{X}_1(x)]_{kl} = \begin{cases} \frac{c_6(A)}{c_3(A)^2}\varepsilon_{c_3(A)}(x), & (k,l) = (1,1), \\ \frac{c_5}{c_2^2}\varepsilon_{c_2}(x), & (k,l) \in \{(2,2),(5,5)\}, \\ \frac{c_7(A)}{c_1(A)}\zeta_{c_1(A),c_3(A)}(x), & (k,l) \in \{(3,1),(9,1)\}, \\ \frac{c_4(A)}{c_1(A)^2}\varepsilon_{c_1(A)}(x), & (k,l) \in \{(3,3),(4,4),(9,9),(13,13)\}, \\ \frac{c_7(A)}{c_1(A)}\zeta_{c_1(A),c_2}(x), & (k,l) \in \{(4,2),(13,5)\}, \\ \frac{c_6(a)}{c_3(a)^2}\varepsilon_{c_3(a)}(x), & (k,l) = (6,6), \\ \frac{c_7(a)}{c_1(a)}\zeta_{c_1(a),c_2}(x), & (k,l) \in \{(7,5),(10,2)\}, \\ \frac{c_4(a)}{c_1(a)^2}\varepsilon_{c_1(a)}(x), & (k,l) \in \{(7,7),(8,8),(10,10),(14,14)\}, \\ \frac{c_7(a)}{c_1(a)}\zeta_{c_1(a),c_3(a)}(x), & (k,l) \in \{(8,6),(14,6)\}, \\ \frac{c_8}{c_1(A)}\beta_{c_1(A)}(x), & (k,l) \in \{(11,9),(12,4),(15,13)\}, \\ \frac{c_8}{c_1(a)}\beta_{c_1(a)}(x), & (k,l) \in \{(15,7),(16,8),(16,14)\}, \\ 0, & \textit{otherwise}. \end{cases} \tag{4.6.52}$$

Corollary 4.6.13. *For p as in (4.6.30) and $x \in \mathbb{T}$, $X_2(x)$ and $\mathcal{X}_2(x)$ are the 16×16 diagonal matrices with elements given by*

$$[X_2(x)]_{kk} = \begin{cases} \frac{c_6(A)}{c_3(A)}\zeta_{c_3(A),c_3(A)}(x), & k = 1, \\ \frac{c_5}{c_2}\zeta_{c_2,c_2}(x), & k \in \{2,5\}, \\ \frac{-1}{c_1(A)}\zeta_{c_1(A),c_1(A)}(x), & k \in \{3,4,9,13\}, \\ \frac{c_6(a)}{c_3(a)}\zeta_{c_3(a),c_3(a)}(x), & k = 6, \\ \frac{-1}{c_1(a)}\zeta_{c_1(a),c_1(a)}(x), & k \in \{7,8,10,14\}, \\ 0, & k \in \{11,12,15,16\}, \end{cases} \tag{4.6.53}$$

$$[\mathcal{X}_2(x)]_{kk} = \begin{cases} \frac{c_6(A)}{c_3(A)^2}\varepsilon_{c_3(A)}(x), & k = 1, \\ \frac{c_5}{c_2^2}\varepsilon_{c_2}(x), & k \in \{2,5\}, \\ \frac{-1}{c_1(A)^2}\varepsilon_{c_1(A)}(x), & k \in \{3,4,9,13\}, \\ \frac{c_6(a)}{c_3(a)^2}\varepsilon_{c_3(a)}(x), & k = 6, \\ \frac{-1}{c_1(a)^2}\varepsilon_{c_1(a)}(x), & k = \{7,8,10,14\}, \\ 0, & k \in \{11,12,15,16\}. \end{cases} \tag{4.6.54}$$

Since we have determined X_i and $\mathcal{X}_i$, all the constants in Propositions 4.6.1 and 4.6.2 are now known. It only remains to invert the expressions in Theorem 4.6.3.

THEOREM 4.6.14. *For p as in (4.6.30) and $x \in \mathbb{T}$,*

$$\Psi(x) = \Psi_0(x) + \rho\Psi_1(x) + \chi\Psi_2(x) + o(\rho\chi), \tag{4.6.55}$$

where

$$\begin{aligned} \Psi_0(x) &= \mathcal{X}_0(x)(\Phi_0 + A_0\Psi_0), \\ \Psi_1(x) &= \mathcal{X}_0(x)(\Phi_1 + A_1\Psi_1 + A_1\Psi_0) + \mathcal{X}_1(x)(\Phi_0 + A_0\Psi_0), \\ \Psi_2(x) &= \mathcal{X}_0(x)(\Phi_1 + A_0\Psi_2 + A_1\Psi_0) + \mathcal{X}_2(x)(\Phi_0 + A_0\Psi_0). \end{aligned} \tag{4.6.56}$$

Recall that the inverse functions X_i are used in the constants Ψ_i, as can be seen in Propositions 4.6.1 and 4.6.2. For our choice of p, we thus obtain an expansion of $\Psi(x)$ around $(\rho, \chi) = (0, 0)$ in terms of the Green function for a simple random walk. Note that for $(\rho, \chi) = (0, 0)$, we again obtain the expression for $\Psi(x)$ found in Theorem 3.5.3.

The Green function has been studied extensively, both for the infinite and the finite torus. For an overview of properties of the Green function, see den Hollander and Pederzani [9], Section 4.2. In dimensions $d \geq 2$, no closed form is available but some asymptotic formulas exist. In dimension $d = 1$, closed forms do exist. To conclude, we present the closed form for the Green function on the infinite and finite torus in dimension $d = 1$. This will give an impression of the form that the expansion of $\Psi(x)$ will take in dimension $d = 1$.

EXAMPLE 4.6.15 (Finite torus in $d = 1$). Pick $L < \infty$ and $\mathbb{T} = \{0, \dots, L-1\}$. Then the Green function has the closed form

$$G_x(z) = \frac{y(z)^x + y(z)^{L-x}}{1 - y(z)^L}(1 - z^2)^{-1/2}, \quad x \in \{0, \dots, L-1\}, \ 0 < |z| < 1, \tag{4.6.57}$$

where

$$y(z) = \frac{1 - (1 - z^2)^{1/2}}{z}. \tag{4.6.58}$$

With these formulas and Propositions 4.6.7 and 4.6.10, the functions α_c, β_c, $\gamma_{c,d}$, ε_c and $\zeta_{c,d}$ are explicitly computable. This in turn yields an explicit expression for the expansion of $\Psi(x)$ in (4.6.55).

EXAMPLE 4.6.16 (Infinite torus in $d = 1$). Pick $\mathbb{T} = \mathbb{Z}$. Then the Green function has the closed form

$$G_x(z) = y(z)^{|x|}(1 - z^2)^{-1/2}, \quad x \in \mathbb{Z}, \ 0 < |z| < 1, \tag{4.6.59}$$

where $y(z)$ is given by (4.6.58).

With these formulas, it is again possible to get an explicit expression for the expansion of $\Psi(x)$ in (4.6.55).

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