Chapitre 3

More on diffusion approximation of fixed–size population models

3.1 Introduction

Here we shall start with an alternative to the Wright–Fisher model, namely the continuous–time Moran model. We shall then present the look–down construction due to Donnelly and Kurtz [7] (see also [8]), and show that this particular version of the Moran model converges a. s., as the population size N tends to infinity, towards the Wright–Fisher diffusion.

3.2 The Moran model

Consider a population of fixed size N, which evolves in continuous time according to the following rule. For each ordered pair (i, j) with $1 \le i \ne j \le N$, at rate $1/2N$ individual i gives birth to an individual who replaces individual j, independently of the other ordered pairs. This can be graphically represented as follows. For each ordered pair (i, j) we draw arrows from i to j at rate $1/2N$. If we denote by $\mathcal{P}$ the set of ordered pairs of elements of the set $\{1, \dots, N\}$, μ the counting measure on $\mathcal{P}$, and λ the Lebesgue measure on $\mathbb{R}_+$, the arrows constitute a Poisson process on $\mathcal{P} \times \mathbb{R}_+$ with intensity measure $(2N)^{-1}\mu \times \lambda$.

Suppose now that as in the preceding chapter the population includes two types of individuals, type a and type A. Each offspring is of the same

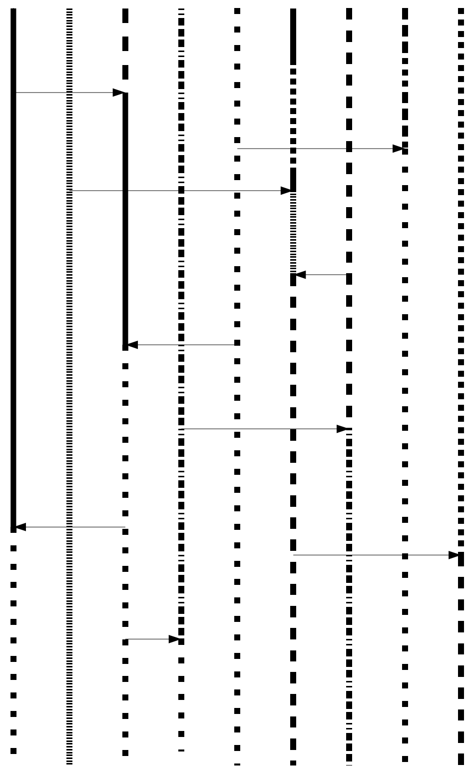

Fig. 3.1 – The Moran model

type as his parent, we do not consider mutations so far. Denote

$$Y_t^N = \text{ number of type } A \text{ individuals at time } t.$$

Provided we specify the initial number of type A indviduals, the above model completely specifies the law of $\{Y_t^N,\ t \geq 0\}$. We now introduce the *proportion* of type A individuals in rescaled time, namey

$$X_t^N = N^{-1} Y_{Nt}^N, \quad t \geq 0.$$

Note that in this new time scale, the above Poisson process has the intensity measure $\mu \times \lambda$. We have, similarly as in Theorem 2.1.1,

Theorem 3.2.1. *Suppose that $X_0^N \Rightarrow X_0$, as $N \to \infty$. Then $X^N \Rightarrow X$ in $D(\mathbb{R}_+; [0,1])$, where $\{X_t,\ t \geq 0\}$ solves the SDE*

$$dX_t = \sqrt{X_t(1 - X_t)} dB_t,\ t \geq 0.$$

PROOF: As for Theorem 2.1.1, the proof goes through two steps.
PROOF OF TIGHTNESS One needs to show that $\mathbb{E}[|X_t^N - X_s^N|^2] \leq c(t-s)^2$.
IDENTIFICATION OF THE LIMIT Note that the process $\{Z_t^N := Y_{Nt}^N,\ t \geq 0\}$ is a jump Markov process with values in the finite set $\{0, 1, 2, \dots, N\}$, which, when in state k, jumps to

1. $k - 1$ at rate $k(N-k)/2$,
2. $k + 1$ at rate $k(N-k)/2$.

In other words if Q^N denotes the infinitesimal generator of this process,

$$Q^N f(Z_t^N) = Z_t^N (N - Z_t^N) \left[\frac{f(Z_t^N + 1) + f(Z_t^N - 1)}{2} - f(Z_t^N) \right].$$

In other words,

$$\begin{aligned}\mathbb{E}\left[f(X_{t+\Delta t}^N) - f(X_t^N) | X_t^N = x\right] &= N^2 x(1-x) \left[\frac{f\left(x + \frac{1}{N}\right) + f\left(x - \frac{1}{N}\right)}{2} - f(x) \right] \Delta t + o(\Delta t) \\ &= \frac{x(1-x)}{2} f''(x) \Delta t + o(\Delta t),\end{aligned}$$

since from two applications of the order two Taylor expansion,

$$\frac{f\left(x + \frac{1}{N}\right) + f\left(x - \frac{1}{N}\right)}{2} - f(x) = \frac{1}{2N^2} f''(x) + o(N^{-2}).$$

□

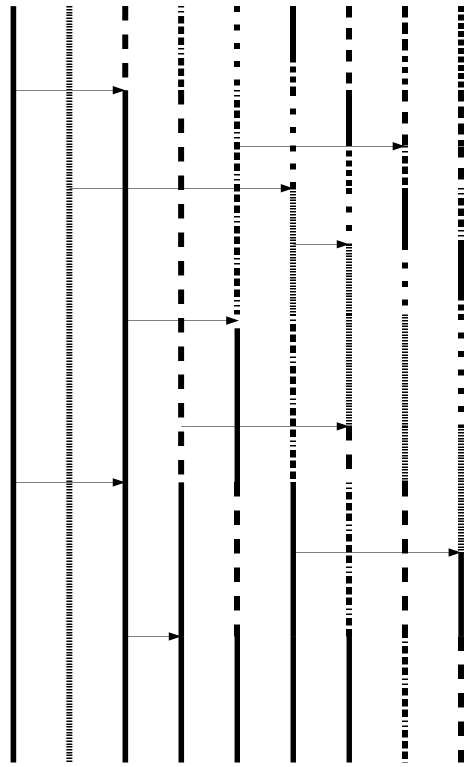

FIG. 3.2 – The look–down construction

3.3 The look–down construction

Let us again consider first the case where the size N of the population is finite and fixed. We redraw the Harris diagram of Moran's model, forbidding half of the arrows. We consider only arrows from left to right. Considering immediately the rescaled time, for each $1 \leq i < j \leq N$, we put arrows from i to j at rate 1 (twice the above $1/2$). At such an arrow, the individual at level i puts a child at level j. Individuals previously at levels $j, \dots, N-1$ are shifted one level up ; individual at site N dies.

Note that in this construction the level one individual is immortal, and the genealogy is not exchangeable.

However the partition at time t induced by the ancestors at time 0 is exchangeable, since going back each pair coalesces at rate 1.

Consider now the case where there are two types of individuals, type a, represented by black, and type A, represented by red. We want to choose the types of the N individuals at time 0 in an exchangeable way, with the constraint that the proportion of type red individuals is given. One possibility is to draw whithout replacement N balls from an urn where we have put k red balls and $N-k$ black balls. At each draw, each of the balls which remain in the urn has the same probability of being chosen.

It follows from the above considerations that at each time $t > 0$, the types of the N individuals are exchangeable.

3.4 A. s. convergence as $N \to \infty$

We now want to let $N \to \infty$. The look–down construction can be described directly with an infinite population. The description is the same as above, except that we start with an infinite number of lines, and that nobody is dying any more.

Note that that possibility of just doing the same construction for $N = \infty$ is related to the fact that in any finite interval of time, if we restrict ourselves to the first N individuals, we have only to consider finitely many arrows. This would not be the case with the standard Moran model, which could not be described in the case $N = \infty$. Indeed in the Moran model with infinitely many individuals, there would be infinitely many arrows towards any individual i, in any time interval of positive length. We notice the great power of the look–down construction.

Consider now the case of two types of individuals. Suppose that the initial colours of all individual at time $t = 0$ are i. i. d., red with probability x, black with probability $1 - x$. Define

$$\eta_t(k) = \begin{cases} 1, & \text{if the } k\text{–th individual is red at time } t; \\ 0, & \text{if the } k\text{–th individual is black at time } t. \end{cases}$$

$\{\eta_0(k),\ k \geq 1\}$ are i. i. d. Bernoulli random variables, while at each $t > 0$, $\{\eta_t(k),\ k \geq 1\}$ is an exchangeable sequence of $\{0,1\}$–valued random variables. We have the following celebrated theorem due to de Finetti (see e. g. [4], [1]) which says that an exchangeable sequence of $\{0,1\}$–valued r. v. is a mixture of i. i. d. Bernoulli.

Theorem 3.4.1. *Let $\{\xi_k,\ k \geq 1\}$ be a sequence of exchangeable $\{0,1\}$–valued random variables. Then there exists a probability Q on the set $[0,1]$ equipped with its Borel σ–algebra such that for all $n \geq 1$, $(u_1, \ldots, u_n \in \{0,1\}^n$,*

$$\mathbb{P}(\xi_1 = u_1, \ldots, \xi_n = u_n) = \int_{[0,1]} x^{\sum_{i=1}^n u_i}(1-x)^{n-\sum_{i=1}^n u_i} Q(dx).$$

In other words, there exists a $[0,1]$–valued r. v. θ such that conditionally upon $\theta = p$, the ξ_k are i. i. d., Bernoulli with parameter p.

Consequently the following limit exists a. s.

$$X_t = \lim_{N\to\infty} \frac{1}{N}\sum_{i=1}^N \eta_i(t).$$

We now conclude that

Proposition 3.4.2. *The $[0,1]$–valued process $\{X_t,\ t \geq 0\}$ solves the Wright–Fisher SDE in the weak sense, i. e. there exists a standard Brownian motion $\{B_t,\ t \geq 0\}$ such that*

$$dX_t = \sqrt{X_t(1-X_t)}dB_t,\ t \geq 0.$$

PROOF: First $\{X_t,\ t \geq 0\}$ is a Markov process. Indeed, conditionally upon $X_s = x$, the $\eta_s(k)$ are i. i. d. Bernoulli with parameter x, hence for any $t > s$, X_t depends only upon the $\eta_s(k)$ and the arrows which are drawn between time s and time t, which are independent from $\{X_r,\ 0 \leq r \leq s\}$.

Now it remains to show is that the process $\{X_t,\ t \geq 0\}$ has the right transition probability, i. e. (see Proposition 6.5.1 below) that for all $n \geq 1$, $x \in [0,1]$,

$$\mathbb{E}_x[X_t^n] = \mathbb{E}_n[x^{D_t}].$$

For all $n \geq 1$,

$$Z_t^n = \mathbb{P}(\eta_t(1) = \cdots = \eta_t(n) = 1|Z_t),$$

consequently

$$\begin{aligned}
\mathbb{E}_x[Z_t^n] &= \mathbb{E}_x\left[\mathbb{P}(\eta_t(1) = \cdots = \eta_t(n) = 1|Z_t)\right] \\
&= \mathbb{P}(\eta_t(1) = \cdots = \eta_t(n) = 1) \\
&= \mathbb{P}(\text{the ancestors at time 0 of } 1, \ldots, n \text{ are red}) \\
&= \mathbb{E}_n\left[x^{D_t}\right],
\end{aligned}$$

where $\{D_t,\ t \geq 0\}$ is a death continuous–time process, which jumps from k to $k-1$ at rate $k(k-1)/2$. □