1 Diffusions: An Informal Overview

In this lecture, we consider a different scaling limit of the Wright-Fisher model—this time going forward in time. This limit involves diffusion processes. Because of the technical difficulties arising in the theory of diffusions, we only give a rather informal discussion of this topic.

Informal Definition. Formally:

A real-valued, continuous-time stochastic process \( \{X(t) : t \in \mathbb{R}_+\} \) which satisfies the strong Markov property and possesses (almost surely) continuous sample paths is called a (one-dimensional) diffusion.

Instead of explaining what this means, we give a canonical example which should be familiar:

EX 23.1 (Brownian motion) A real-valued stochastic processes \( \{B_t : t \in \mathbb{R}_+\} \) is a Brownian motion if it has the following properties:

1. \( B_0(\omega) = 0, \forall \omega. \)
2. The map \( t \mapsto B_t(\omega) \) is a continuous function of \( t \) for all \( \omega. \)
3. For every \( t, h \geq 0, B_{t+h} - B_t \) is independent of \( \{B_u : 0 \leq u \leq t\} \) and has a Gaussian distribution with mean 0 and variance \( h. \)

Brownian motion arises naturally as the properly re-scaled limit of random walks. For our purposes, it will be enough to consider diffusions defined on a closed interval \( I = [l, r] \). Moreover, we only consider diffusions that satisfy the following properties:
Notes 23: Wright-Fisher diffusion

- For every $\varepsilon > 0$,
  \[
  \lim_{h \downarrow 0} \frac{1}{h} \mathbb{P}\left[|X(t + h) - x| > \varepsilon \mid X(t) = x\right] = 0, \tag{1}
  \]
  for all $x \in I$. (All diffusions satisfy this version of “continuity,” unlike jump chains for instance.)

- Let $\Delta_h X(t) = X(t + h) - X(t)$. For all $l < x < r$ and $t \in \mathbb{R}_+$,
  \[
  \lim_{h \downarrow 0} \frac{1}{h} \mathbb{E}\left[\Delta_h X(t) \mid X(t) = x\right] = \mu(x), \tag{2}
  \]
  and
  \[
  \lim_{h \downarrow 0} \frac{1}{h} \mathbb{E}\left[(\Delta_h X(t))^2 \mid X(t) = x\right] = \sigma^2(x), \tag{3}
  \]
  where $\mu$, the infinitesimal drift (not to be confused with genetic drift), and $\sigma^2$, the infinitesimal variance, are continuous functions of $x$. In particular, the process is time-homogeneous. Moreover for $r = 3, 4, \ldots$
  \[
  \lim_{h \downarrow 0} \frac{1}{h} \mathbb{E}\left[|\Delta_h X(t)|^r \mid X(t) = x\right] = 0. \tag{4}
  \]

- The process is regular, that is, for all $x, y$ in the interior of $I$
  \[
  \mathbb{P}[T(y) < \infty \mid X(0) = x] > 0, \tag{5}
  \]
  where $T(y)$ is the hitting time of $y$, that is, the first time $y$ is reached.

We illustrate the moment conditions in the case of Brownian motion.

**EX 23.2 (Brownian motion: Infinitesimal moments)** By the Gaussian increments, we have immediately
  \[
  \mathbb{E}\left[\Delta_h X(t) \mid X(t) = x\right] = 0,
  \]
  \[
  \mathbb{E}\left[(\Delta_h X(t))^2 \mid X(t) = x\right] = h,
  \]
  and
  \[
  \mathbb{E}\left[(\Delta_h X(t))^4 \mid X(t) = x\right] = 3h^2.
  \]

More generally, for Brownian motion with drift $\mu$ and variance $\sigma^2$, that is, $\mu t + \sigma B_t$, the first limit above is $\mu$ and the second, $\sigma^2$. 

Convergence to diffusions. Let \( \{X_N^n\}_{n \geq 0} \) be a sequence of Markov chains over \( I \). Let \( \Delta X_N^n = X_N^{n+1} - X_N^n \). Assume the following conditions are satisfied:

\[
\mathbb{E}[\Delta X_N^n | X_N^n] = h_N \mu(X_N^n) + \varepsilon^N_{1,n}, \tag{6}
\]

\[
\mathbb{E}[(\Delta X_N^n)^2 | X_N^n] = h_N \sigma^2(X_N^n) + \varepsilon^N_{2,n}, \tag{7}
\]

and

\[
\mathbb{E}[(\Delta X_N^n)^4 | X_N^n] = \varepsilon^N_{4,n}, \tag{8}
\]

where \( h_N \downarrow 0 \) and for all \( t > 0 \) and \( i = 1, 2, 4 \)

\[
\sum_{n < \lceil t/h_N \rceil} \mathbb{E} |\varepsilon^N_{i,n}| \to 0, \tag{9}
\]

where \( \lfloor z \rfloor \) is the integer part of \( z \). Then, under further technical conditions (\( \mu \) and \( \sigma^2 \) must correspond to a well-defined diffusion; see e.g. [Dur96, (2.2) or (3.3) in Chapter 5]), the finite-dimensional distributions of the process

\[
X^N(t) = X^N_{\lfloor t/h_N \rfloor}
\]

converge to the finite-dimensional ditributions of a diffusion \( \{X(t)\}_{t \in \mathbb{R}_+} \) with infinitesimal drift \( \mu \) and variance \( \sigma^2 \).

(For more general tightness and truncated moment conditions, see [Dur96, (7.1) or (8.2) in Chapter 8]. Moreover, the discrete-time process need not be Markov.)

2 Wright-Fisher diffusion

Consider a haploid population with \( N \) individuals and two alleles \( A \) and \( a \). Denote by \( i \) the number of \( A \)-types. Assume that a \( A \to a \) (respectively \( a \to A \)) mutation occurs immediately after birth with probability \( \alpha \) (respectively \( \beta \)). Further suppose that \( A \) is positively selected so that the relative survival abilities of \( A \) and \( a \) in contributing to the next generation are in the ratio \( 1+s \) to 1 where \( s > 0 \). (One way to think about this is to assume that all \( A \)-types survive to maturity, but only a fraction \( \frac{1}{1+s} \) of \( a \)-types survive.) We still assume that the next generation has \( N \) individuals following a binomial sampling scheme where the probability of being \( A \) is

\[
p_i = \frac{[i(1-\alpha) + (N-i)\beta]}{[i(1-\alpha) + (N-i)\beta] + \frac{1}{1+s}[i\alpha + (N-i)(1-\beta)]}. \tag{10}
\]
Assume $\alpha$, $\beta$ and $s$ scale with $N$ as

$$\alpha = \frac{\gamma_1}{N}, \quad \beta = \frac{\gamma_2}{N}, \quad s = \frac{\phi}{N}.$$ 

Let $Z^N_n$ be the number of $A$-types in generation $n$ (at birth). We are claiming that, in the limit $N \to \infty$, the process

$$\frac{Z^N_{[Nt]}}{N},$$

behaves like a diffusion. We apply the conditions above to $X^N_n = \frac{Z^N_n}{N}$.

**Mutation only.** Assume that $\gamma_1, \gamma_2 > 0$ and $s = 0$. We compute the limiting infinitesimal drift and variance. By (10),

\[
\mathbb{E} \left[ \Delta X^N_n \mid X^N_n = \frac{i}{N} \right] = p_i - \frac{i}{N}
\]

\[
= \frac{i(1 - \alpha) + (N - i)\beta}{N} - \frac{i}{N}
\]

\[
= -\alpha \frac{i}{N} + \beta \left(1 - \frac{i}{N}\right)
\]

\[
= \frac{1}{N} \left[ -\gamma_1 \frac{i}{N} + \gamma_2 \left(1 - \frac{i}{N}\right) \right],
\]

so that

$$\mu(x) = -\gamma_1 x + \gamma_2 (1 - x).$$

Similarly,

\[
\mathbb{E} \left[ (\Delta X^N_n)^2 \mid X^N_n = \frac{i}{N} \right] = \frac{i^2}{N^2} - 2 \frac{i}{N} p_i + \frac{Np_i(1 - p_i) + N^2 p^2_i}{N^2}
\]

\[
= \frac{1}{N} \left\{ p_i(1 - p_i) + \left(p_i - \frac{i}{N}\right)^2 \right\}
\]

\[
= \frac{1}{N} \left\{ i \frac{1 - i}{N} + O \left(\frac{1}{N}\right) \right\},
\]

so that

$$\sigma^2(x) = x(1 - x).$$

See [KT81] for a computation of the fourth moment.
Selection only. Assume $\phi > 0$ and $\alpha = \beta = 0$. As above

$$
\mathbb{E} \left[ \Delta X_n^N | X_n^N = \frac{i}{N} \right] = p_i - \frac{i}{N}
$$

$$
= \frac{(1 + s)i}{(1 + s)i + (N - i)} - \frac{i}{N}
$$

$$
= \frac{1}{N} \left\{ N \frac{(1 + s)i}{N + si} - i \right\}
$$

$$
= \frac{1}{N} \left\{ N \frac{i - i^2}{N + si} \right\}
$$

$$
= \frac{1}{N} \left\{ \phi \frac{i}{N} - \frac{i^2}{N^2} \right\}
$$

$$
= \frac{1}{N} \left\{ \phi \frac{i}{N} \left( 1 - \frac{i}{N} \right) + O \left( \frac{1}{N} \right) \right\}
$$

so that

$$
\mu(x) = \phi x (1 - x).
$$

The second moment calculation is essentially identical to the mutation only case.

Further reading

The material in this section was taken from Chapter 15 of [KT81].

References

