

### 5.2.3 Evolving composition of a population of fixed size

Let us examine the case of the dynamics of a fixed population of  $N$  individuals which can come in two variants (alleles)  $A_1$  and  $A_2$ . At a particular time, there can be  $n$  individuals of type 1, and  $(N - n)$  individuals of type 2. For  $N \gg 1$ , it is convenient to introduce the composition  $x = n/N$ , which in the continuum limit  $x$  is limited to the interval  $[0, 1]$ . We shall consider the following two processes contributing to the change of population over time:

#### Mutations:

In an infinitesimal time interval, the number  $n$  increases or decreases by 1, at rates given in Eq. (5.1.15) as  $R_{n,n+1} = \mu_2(n + 1)$  and  $R_{n,n-1} = \mu_1(N - n + 1)$ . This leads to

$$v_{\text{mutation}}(x) = \frac{\langle \Delta n \rangle}{N} = \frac{R_{n+1,n}(+1) + R_{n-1,n}(-1)}{N} = \frac{1}{N} [\mu_1(N - n) - \mu_2 n] = \mu_1(1 - x) - \mu_2 x, \quad (5.2.17)$$

while

$$D_{\text{mutation}}(x) = \frac{\langle \Delta n^2 \rangle}{2N^2} = \frac{R_{n+1,n} + R_{n-1,n}}{2N^2} = \frac{1}{2N^2} [\mu_1(N - n) + \mu_2 n] = \frac{\mu_1(1 - x) + \mu_2 x}{2N}. \quad (5.2.18)$$

#### Binary competition

Let us consider another form of population change, in which one individual is randomly chosen to die, and another chosen to reproduce (thus keeping the population fixed).<sup>5</sup> If the two individuals are from the same group there will be no change in composition, which if one individual is taken from group 1 and the other from group 2, the number  $n$  will change by  $\pm 1$ . The probability for latter is proportional to  $n(N - n)$ , accounting to the number of possible choices of individuals from the two groups. In principle, and the corresponding changes can be assigned rates

$$R_{n,n+1} = \alpha n(N - n), \quad \text{and} \quad R_{n,n-1} = \alpha' n(N - n). \quad (5.2.19)$$

In principle, the two rates  $\alpha$  and  $\alpha'$  can be different, providing a competitive edge that will allow one group to expand at the expense of the other. However, here we shall consider the symmetric case with  $\alpha = \alpha'$  which leads to

$$v_{\text{competition}}(x) = \frac{\langle \Delta n \rangle}{N} = \alpha \frac{n(N - n)(+1) + n(N - n)(-1)}{N} = 0, \quad (5.2.20)$$

and

$$D_{\text{competition}}(x) = \frac{\langle \Delta n^2 \rangle}{2N^2} = \alpha \frac{n(N - n) + n(N - n)}{2N^2} = \alpha x(1 - x). \quad (5.2.21)$$

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<sup>5</sup>In population dynamics, this is known as a *Moran process*.

Adding both contributions results in

$$v(x) = \mu_1(1 - x) - \mu_2x, \quad (5.2.22)$$

dominated by mutation, and

$$D(x) = \alpha x(1 - x) + \frac{\mu_1(1 - x) + \mu_2x}{2N} \approx \alpha x(1 - x). \quad (5.2.23)$$

The last approximation of ignoring the contribution from mutations to diffusion is justified as long  $N$  is large, while mutation and competition rates are comparable. It enables a closed form solution to the steady state, as

$$\begin{aligned} \log D(x)p^*(x) &= \int^x dx' \frac{v(x')}{D(x')} \\ &= \frac{1}{\alpha} \int^x dx' \left[ \frac{\mu_1}{x'} - \frac{\mu_2}{1 - x'} \right] \\ &= \frac{1}{\alpha} [\mu_1 \ln x + \mu_2 \ln(1 - x)] + \text{constant}, \end{aligned}$$

resulting in

$$p^*(x) \propto \frac{1}{x(1 - x)} \times x^{\mu_1/\alpha} \times (1 - x)^{\mu_2/\alpha}. \quad (5.2.24)$$

Setting for convenience  $\mu_1 = \mu_2 = \mu$ , the steady-state solution in Eq. (5.2.24) simplifies to

$$p^*(x) \propto [x(1 - x)]^{\mu/\alpha - 1}. \quad (5.2.25)$$

The shape of the solution is determined by the ration  $\mu/\alpha$ . If  $\mu > \alpha$ , then the distribution has a peak at  $x = 1/2$  and diminishes to the sides, while for  $\mu < \alpha$ ,  $p^*(x)$  has peaks at either extreme. This can be understood by considering the limit of no mutations ( $\mu = 0$ ): In this case fluctuations due to diffusion may randomly bring the population to a uniform state with  $n = 0$  or  $n = N$ . In the absence of mutation, there can then be no further change to the population. These two limiting states then act as sinks of probability and in the final state the discrete probabilities will be zero, expect for  $p_0^*$  and  $p_N^*$ . The absence of a proper continuum limit is then signaled by a  $p^*(x)$  in Eq. (5.2.24) that can not be normalized to unit.