

## S5B.2. Linear Birth-Death Processes

Setting

$$b_n = \beta n \text{ and } d_n = \gamma n$$

turns the master equation (5.100) into

$$\frac{\partial P(n, t)}{\partial t} = \beta(n-1)P(n-1, t) + \gamma(n+1)P(n+1, t) - (\beta n + \gamma n)P(n, t) \quad (5.104)$$

which describes a linear process since the coefficients of  $P$  are all linear in  $n$ .

Note that since the bacteria number  $n \geq 0$ , the flow of  $P$  must never enter the region  $n < 0$ . We can prove that (5.104) satisfies this requirement. To begin,

$$\begin{aligned} \frac{\partial P(0, t)}{\partial t} &= -\beta P(-1, t) + \gamma P(1, t) \\ \frac{\partial P(-1, t)}{\partial t} &= -2\beta P(-2, t) + (\beta + \gamma)P(-1, t) \\ &\vdots \\ \frac{\partial P(-n, t)}{\partial t} &= -\beta(n+1)P(-(n+1), t) - \gamma(n-1)P(-(n-1), t) + (\beta n + \gamma n)P(-n, t) \end{aligned}$$

Thus,  $\frac{\partial P(n, t)}{\partial t}$  for  $n < 0$  depend only on  $P(m, t)$  with  $m < 0$ . If we start with

$$P(m, t) = 0 \quad \forall m < 0 \quad (a)$$

then

$$\frac{\partial P(m, t)}{\partial t} = 0 \quad \forall m < 0$$

and (a) holds forever. In which case, we need only concern with

$$\begin{aligned} \frac{\partial P(0, t)}{\partial t} &= \gamma P(1, t) \\ \frac{\partial P(1, t)}{\partial t} &= 2\gamma P(2, t) - (\beta + \gamma)P(1, t) \\ &\vdots \end{aligned}$$

Since the probability current never flows into the  $n < 0$  region, (5.104) is said to have a **natural boundary** at  $n = 0$ .

Linear master equations for discrete stochastic variables are often easily solved by means of a **generating function** defined as

$$\begin{aligned} F(z, t) &\equiv \sum_{n=-\infty}^{\infty} z^n P(n, t) \\ &= \sum_{n=0}^{\infty} z^n P(n, t) \end{aligned} \quad (5.105)$$

The inclusion of  $n < 0$  terms in the sum does not contribute to its value because of (a). However, it frees us from the necessity to adjust the lower bound of  $n$  in subsequent calculations [ see, e.g., derivation of (5.108) ].

$F(z, t)$  is called a generating function since it generates various moments of  $n(t)$  by differentiation at the limit  $z \rightarrow 1$ . For example,

$$\begin{aligned}
\lim_{z \rightarrow 1} \frac{\partial F(z, t)}{\partial z} &= \lim_{z \rightarrow 1} \sum_{n=-\infty}^{\infty} n z^{n-1} P(n, t) \\
&= \sum_{n=-\infty}^{\infty} n P(n, t) \\
&= \langle n(t) \rangle
\end{aligned} \tag{5.106}$$

$$\begin{aligned}
\lim_{z \rightarrow 1} \frac{\partial^2 F(z, t)}{\partial z^2} &= \lim_{z \rightarrow 1} \sum_{n=-\infty}^{\infty} n(n-1) z^{n-2} P(n, t) \\
&= \sum_{n=0}^{\infty} n^2 P(n, t) - \sum_{n=0}^{\infty} n P(n, t) \\
&= \langle n^2(t) \rangle - \langle n(t) \rangle
\end{aligned} \tag{5.107}$$

$\sum_{n=-\infty}^{\infty} z^n \times (5.104)$  will give us a differential equation for  $F(z, t)$ . Using

$$\begin{aligned}
\sum_{n=-\infty}^{\infty} z^n (n-1) P(n-1, t) &= z^2 \frac{\partial}{\partial z} \sum_{n=-\infty}^{\infty} z^{n-1} P(n-1, t) \\
&= z^2 \frac{\partial}{\partial z} \sum_{n=-\infty}^{\infty} z^n P(n, t) \\
&= z^2 \frac{\partial F(z, t)}{\partial z}
\end{aligned}$$

$$\begin{aligned}
\sum_{n=-\infty}^{\infty} z^n (n+1) P(n+1, t) &= \frac{\partial}{\partial z} \sum_{n=-\infty}^{\infty} z^{n+1} P(n+1, t) \\
&= \frac{\partial}{\partial z} \sum_{n=-\infty}^{\infty} z^n P(n, t) \\
&= \frac{\partial F(z, t)}{\partial z}
\end{aligned}$$

$$\sum_{n=-\infty}^{\infty} n z^n P(n, t) = z \frac{\partial}{\partial z} \sum_{n=-\infty}^{\infty} z^n P(n, t) = z \frac{\partial F(z, t)}{\partial z}$$

(5.104) becomes

$$\begin{aligned}
\frac{\partial F}{\partial t} &= \beta z^2 \frac{\partial F}{\partial z} + \gamma \frac{\partial F}{\partial z} - (\beta + \gamma) z \frac{\partial F}{\partial z} \\
&= (z-1)(\beta z - \gamma) \frac{\partial F}{\partial z}
\end{aligned} \tag{5.108}$$

which can be solved by the **method of characteristics** [ see §(Method of Characteristics) ].

Setting

$$g(z) = -(z-1)(\beta z - \gamma) \quad h(z) = 0$$

we have [ see §Code ]

$$\begin{aligned}
\int \frac{dz}{g(z)} &= - \int \frac{dz}{(z-1)(\beta z - \gamma)} = - \frac{1}{\beta - \gamma} \ln \frac{z-1}{\beta z - \gamma} = \ln \left( \frac{z-1}{\beta z - \gamma} \right)^{-\frac{1}{\beta - \gamma}} \\
\exp \left( \int \frac{dz}{g(z)} - t \right) &= \left( \frac{z-1}{\beta z - \gamma} \right)^{-\frac{1}{\beta - \gamma}} e^{-t} = \left( \frac{z-1}{\beta z - \gamma} e^{(\beta - \gamma)t} \right)^{-\frac{1}{\beta - \gamma}}
\end{aligned}$$

(4) of §(Method of Characteristics) becomes

$$F(z, t) = F\left(\frac{z-1}{\beta z - \gamma} e^{(\beta-\gamma)t}\right) \quad (5.109)$$

The exact form of  $F(z, t)$  can be determined by initial conditions.

Consider the case where we start with  $m$  bacteria at  $t = 0$ . Then

$$P(n, 0) = \delta_{nm} \quad \rightarrow \quad F(z, 0) = z^m \quad [ (5.105) \text{ used. } ]$$

Combing with (5.109) gives

$$F(z, 0) = F\left(\frac{z-1}{\beta z - \gamma}\right) = z^m \quad (5.110)$$

The functional form of  $F$  is obtained by setting

$$u = \frac{z-1}{\beta z - \gamma} \quad \rightarrow \quad z = \frac{\gamma u - 1}{\beta u - 1}$$

so that (5.10) becomes

$$F(z, 0) = F(u) = z^m = \left(\frac{\gamma u - 1}{\beta u - 1}\right)^m \quad (5.111)$$

(5.109) then gives

$$\begin{aligned} F(z, t) &= F\left(u e^{(\beta-\gamma)t}\right) \\ &= \left(\frac{\gamma \frac{z-1}{\beta z - \gamma} e^{(\beta-\gamma)t} - 1}{\beta \frac{z-1}{\beta z - \gamma} e^{(\beta-\gamma)t} - 1}\right)^m \quad [ (5.111) \text{ used. } ] \\ &= \left(\frac{\gamma(z-1) e^{(\beta-\gamma)t} - \beta z + \gamma}{\beta(z-1) e^{(\beta-\gamma)t} - \beta z + \gamma}\right)^m \end{aligned} \quad (5.112)$$

By (5.105),  $P(n, t)$  is just the coefficient of  $z^n$  in a Taylor expansion of  $F(z, t)$ , i.e.,

$$P(n, t) = \frac{1}{n!} \left. \frac{\partial^n F}{\partial z^n} \right|_{z=0}$$

On the other hand, (5.106) gives the 1st moment as [see §Code ]

$$\langle n(t) \rangle = \left. \frac{\partial F}{\partial z} \right|_{z=1} = m e^{(\beta-\gamma)t} \quad (5.113)$$

The population thus grows exponentially if  $\beta > \gamma$  or dies out if  $\beta < \gamma$ .

The variance is [see §Code ],

$$\begin{aligned} \langle n^2(t) \rangle - \langle n(t) \rangle^2 &= \left[ \frac{\partial^2 F}{\partial z^2} + \frac{\partial F}{\partial z} - \left(\frac{\partial F}{\partial z}\right)^2 \right]_{z=1} \\ &= \frac{m(\beta + \gamma) e^{t(\beta-\gamma)} (-1 + e^{t(\beta-\gamma)})}{\beta - \gamma} \end{aligned} \quad (5.114)$$

## Code

$$A = \int \frac{1}{(z-1)(\beta z - \gamma)} dz$$

$$\frac{\text{Log}[-1+z] - \text{Log}[z\beta - \gamma]}{\beta - \gamma}$$

$$\text{Solve}\left[u == \frac{z-1}{\beta z - \gamma}, z\right]$$

$$\left\{\left\{z \rightarrow \frac{-1+u\gamma}{-1+u\beta}\right\}\right\}$$

$$F[z_, t_] := \left(\frac{\gamma(z-1)e^{(\beta-\gamma)t} - \beta z + \gamma}{\beta(z-1)e^{(\beta-\gamma)t} - \beta z + \gamma}\right)^m$$

$\partial_z F[z, t] /. z \rightarrow 1 // \text{Simplify}$

$$e^{t(\beta-\gamma)} m$$

$(\partial_{z,z} F[z, t] + \partial_z F[z, t] - (\partial_z F[z, t])^2) /. z \rightarrow 1 // \text{Simplify}$

$$\frac{e^{t(\beta-\gamma)}(-1 + e^{t(\beta-\gamma)})^m(\beta + \gamma)}{\beta - \gamma}$$

## Method of Characteristics

Consider the 1st order linear differential equation for  $F(z, t)$ ,

$$\frac{\partial F}{\partial t} + g(z) \frac{\partial F}{\partial z} + h(z) F = 0 \quad (1)$$

Let

$$F(z, t) = \exp\left(-\int dz \frac{h(z)}{g(z)}\right) \Phi(z, t) \quad (2)$$

$$\rightarrow \frac{\partial F}{\partial t} = \exp\left(-\int dz \frac{h(z)}{g(z)}\right) \frac{\partial \Phi}{\partial t}$$

$$\frac{\partial F}{\partial z} = \exp\left(-\int dz \frac{h(z)}{g(z)}\right) \left(-\frac{h(z)}{g(z)} \Phi + \frac{\partial \Phi}{\partial z}\right)$$

(1) thus becomes

$$\frac{\partial \Phi}{\partial t} + g(z) \frac{\partial \Phi}{\partial z} = 0 \quad (3)$$

The **characteristics** of (3) are curves in the  $t$ - $z$  plane along which  $\Phi = \text{const}$ , i.e., they are the contour lines of  $\Phi$ . Therefore, they satisfy

$$d\Phi = \frac{\partial \Phi}{\partial t} dt + \frac{\partial \Phi}{\partial z} dz = 0$$

Comparing with (3), we have

$$dt - \frac{dz}{g(z)} = 0$$

$$\rightarrow t - \int \frac{dz}{g(z)} = C \quad C = \text{const} \quad (a)$$

Consider now any function

$$f = f(\xi) \text{ where } \xi = t - \int \frac{dz}{g(z)}$$

$$\rightarrow \frac{\partial f}{\partial t} = \frac{\partial \xi}{\partial t} \frac{df}{d\xi} = \frac{df}{d\xi}$$

$$\frac{\partial f}{\partial z} = \frac{\partial \xi}{\partial z} \frac{df}{d\xi} = -\frac{1}{g(z)} \frac{df}{d\xi}$$

$$\therefore \frac{\partial f}{\partial t} + g(z) \frac{\partial f}{\partial z} = 0$$

i.e.,  $f(\xi)$  is a solution to (3).

(2) thus becomes

$$F(z, t) = \exp\left(-\int dz \frac{h(z)}{g(z)}\right) \Phi\left(t - \int \frac{dz}{g(z)}\right)$$

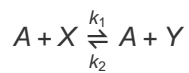
Since  $\Phi$  is any function, we can also write

$$F(z, t) = \exp\left(-\int dz \frac{h(z)}{g(z)}\right) \Phi\left[\exp\left(\int \frac{dz}{g(z)} - t\right)\right] \quad (4)$$

which ensures  $\Phi$  behaves nicely as  $t \rightarrow \infty$ .

## Chemical Reaction

Consider the reaction



where  $k_1$  ( $k_2$ ) is the probability per unit time that a reaction takes place if an  $X$  ( $Y$ ) molecule collides with an  $A$  molecule.

In the forward reaction, an  $X$  molecule collides with an  $A$  molecule and turns into an  $Y$  molecule, while the  $A$  molecule merely scatters off. The changes in the numbers of molecules are therefore

$$\Delta n_A = 0 \quad \Delta n_X = -1 \quad \Delta n_Y = +1 \quad \text{for forward reaction}$$

In the backward reaction, the roles of  $X$  and  $Y$  are reversed so that

$$\Delta n_A = 0 \quad \Delta n_X = +1 \quad \Delta n_Y = -1 \quad \text{for backward reaction}$$

Since for all reactions,

$$\Delta n_X + \Delta n_Y = 0 \rightarrow n_X + n_Y = N = \text{const}$$

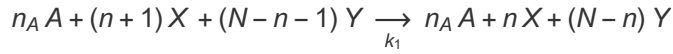
there is only 1 independent stochastic variable, which we choose to be  $n_X$ .

As all reactions involve only  $\Delta n_X = \pm 1$ , the reaction is a birth-death process.

Let  $P(n, t)$  be the probability at time  $t$  that  $n_X = n$ , and hence  $n_Y = N - n$ .

Consider first reactions that have  $n_X = n$  as the final state.

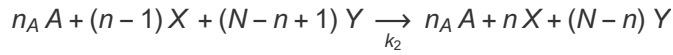
The relevant forward reactions satisfy



The corresponding transition rate  $w_1$  is proportional to the number of collisions between  $A$  &  $X$  molecules, and hence to the initial value of the product  $n_A n_X$ . Therefore,

$$w_1 = n_A k_1 (n+1)$$

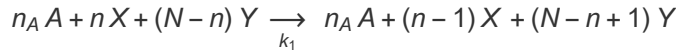
Similarly, the relevant backward reactions satisfy



with transition rate

$$w_2 = n_A k_2 (N-n+1)$$

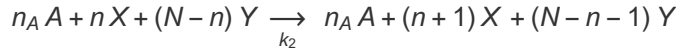
Next, for reactions that have  $n_X = n$  as the initial state, the forward reactions satisfy



with transition rate

$$w_1' = n_A k_1 n$$

while the backward reactions satisfy



with transition rate

$$w_2' = n_A k_2 (N-n)$$

The master equation is therefore

$$\begin{aligned} \frac{\partial P(n, t)}{\partial t} &= P(n+1, t) w_1 + P(n-1, t) w_2 - P(n, t) (w_1' + w_2') \\ &= P(n+1, t) n_A k_1 (n+1) + P(n-1, t) n_A k_2 (N-n+1) \\ &\quad - P(n, t) n_A (k_1 n + k_2 (N-n)) \end{aligned} \tag{5.115}$$