Lecture 9: Birth-death models #3

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1 Analysis of the stochastic process using generating function

The master equation for the stochastic birth-death process was given as follows.

$$\frac{dP_n(t)}{dt} = \beta(n-1)P_{n-1}(t) + \delta(n+1)P_{n+1}(t) - (\beta+\delta)nP_n(t) \tag{1}$$

where the range of n is all integers and the probability for negative n is assumed to be zero ($P_n(t) = 0$ for $n < 0$ for non-negative initial population size $n(0) > 0$).

We have derived the first and the second moment dynamics and seen that the simulations result in good match with the analytic equations of the first and second moments. Now we try to solve the probability $P_n(t)$ explicitly using probability generating function as we did for immigration-emigration process.

2 Solving the pgf

Remember that probability generating function for a probability distribution $P_n(t)$ is defined as

$$G(t, z) = \sum_n P_n(t)z^n \tag{2}$$

Differentiating equation (2) with respect to t yields

$$\frac{\partial}{\partial t}G(t, z) = \sum_n \frac{\partial}{\partial t}P_n(t)z^n$$

Using the master equation (1) we have

$$\frac{\partial}{\partial t}G(t, z) = \beta\sum_n (n-1)P_{n-1}(t)z^n + \delta\sum_n (n+1)P_{n+1}(t)z^n - (\beta+\delta)\sum_n nP_n(t)z^n$$

$$= \beta\sum_n nP_n(t)z^{n+1} + \delta\sum_n nP_n(t)z^{n-1} - (\beta+\delta)\sum_n nP_n(t)z^n$$

Here we re-indexed the summation.

We now remember

$$\frac{\partial}{\partial z}G(t,z) = \sum_n nP_n(t)z^{n-1}$$

and we finally have a partial differential equation of $G(t,z)$.

$$\frac{\partial}{\partial t}G(t,z) = \left\{\beta z^2 - (\beta+\delta)z + \delta\right\}\frac{\partial}{\partial z}G(t,z) \tag{3}$$

This should be solved using initial and boundary condition. If we start the stochastic process with $N(0)$ individual at time $t = 0$, the initial condition is $P_n(0) = 0$ for $n \neq N(0)$ and $P_{N(0)}(0) = 1$, i.e.,

$$G(0,z) = \sum_n P_n(0)z^n = z^{N(0)} \tag{4}$$

The boundary condition determines $G(t,0)$ and $G(t,1)$ and it is expressed as

$$G(t,0) = P_0 \tag{5}$$

$$G(t,1) = \sum_n P_n(t) = 1 \tag{6}$$

where P_0 is undetermined at this moment.

Solving $P_n(t)$ is now reduced to solving the partial differential equation of $G(t,z)$ (3) with condition (4), (5) and (6). This partial differential equation is called **Lagrange** type and it can be solved explicitly with messy calculus as follows. See Appendix for how to solve Lagrangian type PDE.

We re-arrange the partial differential equation (3) as

$$\frac{\partial}{\partial t}G(t,z) - (z-1)(\beta z - \delta)\frac{\partial}{\partial z}G(t,z) = 0 \tag{7}$$

First we think of the auxiliary equation of (7).

$$\frac{dt}{1} = -\frac{dz}{(z-1)(\beta z - \delta)} = \frac{dG}{0}$$

We can integrate the first equation by expanding (when $\beta \neq \delta$)

$$-dt = \frac{dz}{(z-1)(\beta z - \delta)} = \frac{1}{(\beta - \delta)}\left(\frac{1}{z-1} - \frac{\beta}{\beta z - \delta}\right)dz$$

to yield

$$-t = \frac{1}{\beta - \delta}\left(\log|z-1| - \log|\beta z - \delta|\right) + c_1$$

From the second equation we see $dG = 0$ and have

$$G = c_2$$

Then the general solution of (7) is given as

$$G(t, z) = F\left((\beta - \delta)t + \log|z - 1| - \log|\beta z - \delta|\right)$$

F can be any function of $(\beta - \delta)t + \log|z - 1| - \log|\beta z - \delta|$. This can be re-arranged as

$$G(t, z) = H(w)$$

where H can be any function of

$$w = e^{(\beta - \delta)t} \frac{z - 1}{\beta z - \delta} \tag{8}$$

We look for H that satisfies the initial and boundary condition $G(0, z) = z^{N(0)}$ and $G(t, 1) = 1$. When $t = 0$

$$w = \frac{z - 1}{\beta z - \delta}$$

and this leads to

$$z = \frac{\delta w - 1}{\beta w - 1}$$

Substituting this into the initial condition (4)

$$G(0, z) = H(w|_{t=0}) = z^{N(0)}$$

yields

$$G(0, z) = H(w|_{t=0}) = \left(\frac{\delta\, w|_{t=0} - 1}{\beta\, w|_{t=0} - 1}\right)^{N(0)} \tag{9}$$

Now we have determined the functional form of H.

In equation (8) $w = 0$ for $t \geq 0$ when $z = 1$. Therefore $G(t, z) = H(w)$ satisfies the boundary condition (6), $G(t, 1) = H(0) = 1$ for $t \geq 0$. With the uniqueness of solution of PDE, we have solved the solution $G(t, z)$ and it is

$$
\begin{aligned}
G(t, z) &= H(w) \\
&= \left(\frac{\delta w - 1}{\beta w - 1}\right)^{N(0)} \\
&= \left\{ \frac{\delta e^{(\beta - \delta)t} \frac{z-1}{\beta z - \delta} - 1}{\beta e^{(\beta - \delta)t} \frac{z-1}{\beta z - \delta} - 1} \right\}^{N(0)} \\
&= \left\{ \frac{(z - 1)\delta e^{(\beta - \delta)t} - \beta z + \delta}{(z - 1)\beta e^{(\beta - \delta)t} - \beta z + \delta} \right\}^{N(0)}
\end{aligned}
\tag{10}
$$

The probability of population size n at time t, $P_n(t)$, is obtained by Taylor expanding $G(t, z)$ around $z = 0$. We also should have the same moment dynamics from $G(t, z)$ as we derived directly from the master equation. Derivation is left to readers as an exercise.

3

3   Probability of extinction

From the definition of probability generating function $G(t, z)$, the probability of extinction (population size $n = 0$) at time t, $P_0(t)$, is given by $G(t, 0)$. In the birth-death process it is

$$P_0(t) = G(t, 0) = \left(\frac{-\delta e^{(\beta - \delta)t} + \delta}{-\beta e^{(\beta - \delta)t} + \delta} \right)^{N(0)}$$

If $\beta > \delta$

$$P_0(t \to \infty) = \left(\frac{\delta}{\beta} \right)^{N(0)} < 1 \tag{11}$$

Otherwise $(\beta < \delta)$

$$P_0(t \to \infty) = 1 \tag{12}$$

It is natural that the population eventually goes extinct always (with probability 1) if the birth rate is less than the death rate ($\beta < \delta$). Contrary, however, it is counter-intuitive to us that even if the birth rate is larger than the death rate ($\beta > \delta$) the population can go extinct with non-zero probability $(\delta/\beta)^{N(0)}$. This behavior is very different from the corresponding deterministic dynamics where extinction never occurs when $\beta > \delta$. In stochastic process the probability of extinction is always positive because unlucky events can occur consecutively and population can be trapped at $n = 0$. Population is never free from extinction in the stochastic world.

From (11) we see that the probability of extinction becomes prominent when 1) initial population size $N(0)$ is small, or 2) birth rate is larger than but close to death rate. This effect is called **demographic stochasticity** which is caused by individuals' stochastic breeding and death. From a conservation view point, a small-sized population faces a great risk of extinction simply because the number of individuals is small. Such a population can easily go extinct due to the demographic stochasticity (if birth and death of individuals are stochastic event, which is in most cases true in the wild).

4   Problem

1. Using appropriate parameter values and initial population size, run the simulation many times and compare the probability of extinction with the analytical result (11). We run simulation many times, say 1000, and write the population size $n(500)$ into a file and count how many trials ended with population size $n = 0$.

2. Derive the first moment dynamics from the p.g.f. $G(t, z)$ we solved as equation (10). Is it the same as we derived from the master equation?

5 Appendix: Lagrangian partial differential equation

A partial differential equation for a function $u(x_1, x_2)$ is Lagrange type if it takes the form

$$P_1(x_1, x_2, u)\frac{\partial u}{\partial x_1} + P_2(x_1, x_2, u)\frac{\partial u}{\partial x_2} = R(x_1, x_2, u)$$

where P_1, P_2, R are functions of x_1, x_2, u.

We can solve this partial differential equation using auxiliary equation

$$\frac{dx_1}{P_1} = \frac{dx_2}{P_2} = \frac{du}{R}$$

If we can obtain two independent solutions of the auxiliary equation as

$$f_1(x_1, x_2, u) = c_1, f_2(x_1, x_2, u) = c_2$$

then the general solution of the Lagrange type PDE is given as

$$F(f_1(x_1, x_2, u), f_2(x_1, x_2, u)) = 0$$

where F is an arbitrary analytical function. Or in explicit form by solving this general solution for u,

$$u = G(x_1, x_2)$$

is the general solution.

5.1 Examples

Consider a PDE

$$\frac{\partial z}{\partial x} + \frac{\partial z}{\partial y} = 1$$

The auxiliary equation is

$$\frac{dx}{1} = \frac{dy}{1} = \frac{dz}{1}$$

From the first equation we have $dx = dy$ and we find $x - y = c_1$ is the solution. In the same way the solution of the second equation is $y - z = c_2$. Then the general solution of the PDE is

$$F(x - y, y - z) = 0$$

Or

$$y - z = G(x - y)$$

$(z = y - G(x - y))$ where F and G can be any function.

Consider another PDE

$$x^2\frac{\partial z}{\partial x} - xy\frac{\partial z}{\partial y} = -y^2$$

The auxiliary equation is

$$\frac{dx}{x^2} = -\frac{dy}{xy} = -\frac{dz}{y^2}$$

From the first equation we have

$$\frac{dx}{x} = \frac{dy}{-y}$$

By integrating we have the solution $xy = c_1$. From the second equation we have

$$\frac{dy}{x} = \frac{dz}{y}$$

Substituting $x = c_1/y$ yields

$$\frac{y^2}{c_1} dy = dz$$

and the solution is $z = y^3/(3c_1) + c_2 = y^2/(3x) + c_2$. The the general solution of the PDE is then

$$F(xy, z - \frac{y^2}{3x}) = 0$$

Or

$$z = \frac{y^2}{3x} + G(xy)$$

F and G can be any analytical function.

Stochastic birth-death process: Extinction probability

In[1]:= **<< Graphics`MultipleListPlot`**

In[2]:= **<< Statistics`DataManipulation`**

■ Simulation by C

In[3]:= **SetDirectory["/Users/takasu/home/情報科学科の仕事/講義/平成１７年度/H17 大学院講義/Birth-death model/birth-death/build/"]**

Out[3]= /Users/takasu/home/情報科学科の仕事/講義/
平成１７年度/H17 大学院講義/Birth-death model/birth-death/build

In[4]:= **data = ReadList["data-final", Real];
len = Length[data]**

Out[5]= 1000

In[17]:= **extnctCases = Count[data, 0.0]**

Out[17]= 137

In[19]:= **N[extnctCases / len]**

Out[19]= 0.137

In[22]:= **(delta / beta) ^ n0 /. {beta → 0.03, delta → 0.02, n0 → 5}**

Out[22]= 0.131687