# Lecture 3: Immigration-emigration models #2

Fugo Takasu

Dept. Information and Computer Sciences

Nara Women's University

takasu@ics.nara-wu.ac.jp

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#### 1 Analysis of the stochastic immigration-emigratio process

In the last lecture we have implemented the stochastic immigration-emigration process. The process is that the population size N as integer 1) increases by one with probability  $\alpha \Delta t$ , 2) decreases by one with probability  $\beta \Delta t$ , and 3) remains unchanged with probability  $1 - \alpha \Delta t - \beta \Delta t$  where  $\Delta t$  is sufficiently small so that the three events 1), 2), 3), occur mutually exclusively.

As we observed in the simulation, the population size N at time t is no longer determined uniquely, but is associated with a certain probability distribution. To understand the stochastic process fully we need to know the probability distribution, i.e., the probability that the population size N is n at time t,  $P_n(t)$ . Because it is a probability distribution and population size is non-negative integer, it must satisfy

$$\sum_{n=0}^{\infty} P_n(t) = 1$$

for all time  $t \ge 0$ . Solving the probability distribution  $P_n(t)$  under the above three rules is our final goal. To do this, we derive **master equation** to solve  $P_n(t)$ .

# 2 Master equation

Master equation describes the dynamics of  $P_n(t)$  as a function of t. We have assumed that change of the population size during time interval  $\Delta t$  is at most  $\pm 1$ , i.e., transition to a state n is possible either from n-1 or n+1. Then the probability that the population size is n at time  $t+\Delta t$ ,  $P_n(t+\Delta t)$ , is given as

$$P_n(t + \Delta t) = P_n(t)(1 - \alpha \Delta t - \beta \Delta t) + P_{n-1}(t)\alpha \Delta t + P_{n+1}(t)\beta \Delta t \tag{1}$$

for  $n \ge 1$  because the three cases, 1) population size increment, 2) decrement, and 3) population size remains unchanged, are mutually exclusive. Here we assume that transition from n = 0 to

n=1 is possible but that transition from n=0 to n=-1 is not allowed (biologically non-sense). This means that empty (extinct) population can be always re-colonized by immigration but that population size cannot be negative.

For n=0, we have a different equation

$$P_0(t + \Delta t) = P_0(t)(1 - \alpha \Delta t) + P_1(t)\beta \Delta t \tag{2}$$

as population size cannot be incremented from negative value -1 ( $P_n(t) = 0$  for n < 0) and transition from n = 0 to n = -1 is not allowed in this process.

Arranging equation (1) and letting  $\Delta t \to 0$ , we obtain a set of ordinary differential equation ODE

$$\frac{dP_n(t)}{dt} = \alpha P_{n-1}(t) + \beta P_{n+1}(t) - (\alpha + \beta)P_n(t)$$
(3)

for  $n \geq 1$ .

In the same way from equation (2), we have

$$\frac{dP_0(t)}{dt} = \beta P_1(t) - \alpha P_0(t) \tag{4}$$

The set of equation (3) and (4) is called the master equation of  $P_n(t)$ .  $P_n(t)$  can be solved with certain initial condition, i.e.,  $P_0(0) = 1$ ,  $P_n(0) = 0$  for  $n \ge 1$  (the process starts from empty population).

### 3 Equilibrium probability distribution

Before looking for the solution of equation (3) and (4) with some initial condition, let us focus on the equilibrium probability distribution described (3) and (4). If there exists a steady state of the probability distribution  $P_n(t)$ , the time derivatives should be zero for all  $n \geq 0$ . We look for this asymptotic probability distribution  $P_n = P_n(t \to \infty)$  for  $n \geq 0$ . Such asymptotic distribution does not necessarily exist, especially when immigration rate is greater than emigration rate,  $\alpha > \beta$ , because the population size will explode to infinity as  $t \to \infty$ . But if  $\alpha < \beta$ , the population size will not explode as we observed in simulation (Figure 1), but will follow a certain probability distribution; in most trials population size remains fluctuated near zero but it can be as large. Hereafter in this section we assume  $\alpha < \beta$ .

At the steady-state, the master equations are reduced to

$$0 = \beta P_1 - \alpha P_0 \tag{5}$$

$$0 = \alpha P_{n-1} + \beta P_{n+1} - (\alpha + \beta) P_n \quad \text{for } n \ge 1$$

From equation (5) we have

$$P_1 = \frac{\alpha}{\beta} P_0$$

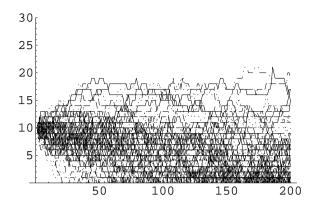


Figure 1: 100 realization of the stochastic process.  $\alpha = 0.15, \beta = 0.2, n(0) = 10$ 

and substituting this to equation (6) with n = 1 yields

$$P_2 = \left(\frac{\alpha}{\beta}\right)^2 P_0$$

Repeating this with simple induction we have a general rule

$$P_n = \left(\frac{\alpha}{\beta}\right)^n P_0$$

for  $n \geq 0$ .

Now remember that  $P_n$  is a probability distribution, so that it must sum up to 1, i.e,

$$\sum_{n=0}^{\infty} P_n = \sum_{n=0}^{\infty} \left(\frac{\alpha}{\beta}\right)^n P_0 = \frac{1}{1 - \alpha/\beta} P_0 = 1$$

Then  $P_0$  is determined as

$$P_0 = \frac{\beta - \alpha}{\beta}$$

As we have assumed this makes sense  $P_0 > 0$  only when  $\alpha < \beta$ .

We have derived the equilibrium probability distribution  $P_n$  as

$$P_n = \left(\frac{\alpha}{\beta}\right)^n \frac{\beta - \alpha}{\beta} \tag{7}$$

This is a geometric distribution. The next step is to confirm if our simulation agrees with this analytical derivation. Once the probability distribution is obtained in as explicit form it is easy to calculate the expected population size E[n] and the variance Var[n] where n is the population size at  $t \to \infty$ .

$$E[n] = \sum_{n=0}^{\infty} nP_n = \frac{\alpha}{\beta - \alpha}$$
 (8)

$$Var[n] = \sum_{n=0}^{\infty} (n - E[n])^2 P_n = \sum_{n=0}^{\infty} n^2 P_n - E[n]^2 = \frac{\alpha \beta}{(\beta - \alpha)^2}$$
(9)

#### 4 Problem:

- 1. Derive the mean and the variance of the population size at steady-state condition as obtained in (8) and (9) from (7).
- 2. Carry out the simulation with appropriate parameter values of  $\alpha$  and  $\beta$ , say  $\alpha = 0.15$  and  $\beta = 0.2$ , to see if the simulation is in agreement with the analytical derivation (7). In simulation, we start from an initial population size, say n(0) = 10, and we record the population size n(100) at t = 100 into a file (100 would be large enough but if the result is not satisfactory try larger t). We repeat this many times and obtain a series of the population size n(100) saved in the following format.

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Trial 1: n(100)
Trial 2: n(100)
Trial 3: n(100)
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Using Mathematica we check if these follows the geometric distribution (7).