Lecture 10: Logistic growth 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 process of logistic growth

We have implemented the stochastic logistic growth process in a C program and confirmed that the stochastic dynamics exhibits a feature that is similar to the deterministic logistic growth. The process is that for N individuals (N is now non-negative integer), 1) a new individual is born with probability $birth(N)\Delta t$, 2) the individual dies and is removed from the population with probability $death(N)\Delta t$, and 3) the individual neither gives birth nor dies with probability $1 - birth(N)\Delta t - death(N)\Delta t$. The birth and death rate, $birth(N)$ and $death(N)$, are given as some functions of the population size N. In this lecture we explore the stochastic dynamics from analytic viewpoint.

2 Master equation

We assume that the time interval Δt is so small that the change of the population size n during the interval is at most ± 1, i.e., transition to a state n is possible either from $n-1$ or $n+1$ ($n \geq 1$). Then the probability that the population size is n at time $t + \Delta t$, $P_n(t + \Delta t)$, is given as

$$\begin{aligned} P_n(t+\Delta t) =& P_n(t)\left\{1 - birth(n)n\Delta t - death(n)n\Delta t\right\} \\ &+ P_{n-1}(t)birth(n-1)(n-1)\Delta t + P_{n+1}(t)death(n+1)(n+1)\Delta t \end{aligned} \tag{1}$$

As in the birth and death process, transition from $n = 0$ to $n = 1$ is now impossible. This means that empty (extinct) population cannot produce offspring anymore. The boundary $n = 0$ is an absorbing boundary that separates positive and negative region of n. By assuming that $P_n(t)$ for negative n is always zero, equation (1) is valid for all integers of n.

Arranging equation (1) and letting $\Delta t \to 0$, we obtain

$$\begin{aligned} \frac{dP_n(t)}{dt} =& birth(n-1)(n-1)P_{n-1}(t) + death(n+1)(n+1)P_{n+1}(t) \\ &- \left\{birth(n) + death(n)\right\} nP_n(t) \end{aligned} \tag{2}$$

Equation (2) is the master equation of the stochastic logistic growth. Once the functional forms of $birth(n)$ and $death(n)$ are given, $P_n(t)$ can be solved with a certain initial condition, e.g., $P_0(0) = 1, P_n(0) = 0$ for $n \geq 1$, but it is in general not easy. In the next section we explore some properties of the process using moment dynamics.

Hereafter we assume a general case that the per-capita birth rate is a linearly decreasing function of N and the per-capita death rate is a linearly increasing function of N

$$\begin{aligned} birth(N) &= b_1 - b_2 N \\ death(N) &= d_1 + d_2 N \end{aligned}$$

where b_1, b_2, d_1, d_2 are positive. If $b_2 = 0$ and $d_2 = 0$ this is the birth-death process we learned in previous lectures.

In deterministic world the birth and death rate assumed above gives the ODE

$$\begin{aligned} \frac{dN}{dt} &= \{b_1 - d_1 - (b_2 + d_2)N\} N \\ &= (b_1 - d_1)\left(1 - \frac{N}{\frac{b_1 - d_1}{b_2 + d_2}}\right) N \end{aligned}$$

This is a logistic growth with the intrinsic rate of increase $r = b_1 - d_1$ and the carrying capacity $K = (b_1 - d_1)/(b_2 + d_2)$.

3 Moment dynamics

From the master equation we now try to derive moment dynamics, especially of the first and the second moment. The master equation is now

$$\begin{aligned} \frac{dP_n(t)}{dt} =& \{b_1 - b_2(n-1)\}(n-1)P_{n-1}(t) \\ &+ \{d_1 + d_2(n+1)\}(n+1)P_{n+1}(t) \\ &- \{b_1 - b_2 n + d_1 + d_2 n)\} n P_n(t) \end{aligned} \tag{3}$$

We multiply equation (3) with n and taking summation for n we have

$$\begin{aligned} \frac{d}{dt}\langle n \rangle =& \sum_0^\infty \{b_1 - b_2(n-1)\} n(n-1)P_{n-1}(t) \\ &+ \sum_0^\infty \{d_1 + d_2(n+1)\} n(n+1)P_{n+1}(t) \\ &- \sum_0^\infty \{b_1 - b_2 n + d_1 + d_2 n)\} n^2 P_n(t) \\ =& (b_1 - d_1)\langle n \rangle - (b_2 + d_2)\langle n^2 \rangle \end{aligned} \tag{4}$$

Note that the second moment $\langle n^2 \rangle$ appears in the ODE of the first moment.

In the same way we multiply equation (3) with n^2 and taking summation for n we have

$$\begin{aligned} \frac{d}{dt}\langle n^2 \rangle =& \sum_0^\infty \{b_1 - b_2(n-1)\}\, n^2(n-1)P_{n-1}(t) \\ &+ \sum_0^\infty \{d_1 + d_2(n+1)\}\, n^2(n+1)P_{n+1}(t) \\ &- \sum_0^\infty \{b_1 - b_2 n + d_1 + d_2 n)\}\, n^3 P_n(t) \\ =&(b_1 + d_1)\langle n \rangle + (2b_1 - b_2 - 2d_1 + d_2)\langle n^2 \rangle - 2(b_2 + d_2)\langle n^3 \rangle \end{aligned} \tag{5}$$

Note again that the third moment $\langle n^3 \rangle$ appears in the ODE of the second moment.

We have derive the first and second moment dynamics as follows.

$$\frac{d}{dt}\langle n \rangle = (b_1 - d_1)\langle n \rangle - (b_2 + d_2)\langle n^2 \rangle \tag{6}$$

$$\frac{d}{dt}\langle n^2 \rangle = (b_1 + d_1)\langle n \rangle + (2b_1 - b_2 - 2d_1 + d_2)\langle n^2 \rangle - 2(b_2 + d_2)\langle n^3 \rangle \tag{7}$$

These two equations are not closed with respect to $\langle n \rangle$ and $\langle n^2 \rangle$ and they cannot be solved without the knowledge of $\langle n^3 \rangle$. But we will find that the ODE for the third moment contains the fourth moment, the ODE for the fourth moment contains the fifth, $\cdots$ and we cannot derive a set of ODE in a closed form. This is a general property when $birth(N)$ and $death(N)$ are function of N, i.e., transition probability becomes non-linear. Then how can we solve the dynamics? One way to resolve this problem is to derive an approximation with an assumption that higher-order moment be given as some function of lower-oder moment. But we will not step into such details further here.

Remember that $Var[n] = \langle n^2 \rangle - \langle n \rangle^2$, then equation (6) can be arranged as

$$\begin{aligned} \frac{d}{dt}\langle n \rangle &= (b_1 - d_1)\langle n \rangle - (b_2 + d_2)\langle n^2 \rangle \\ &= (b_1 - d_1)\langle n \rangle - (b_2 + d_2)\langle n \rangle^2 - (b_2 + d_2)Var[n] \\ &= (b_1 - d_1)\left(1 - \frac{\langle n \rangle}{\frac{b_1 - d_2}{b_2 + d_2}}\right)\langle n \rangle - (b_2 + d_2)Var[n] \end{aligned} \tag{8}$$

We find in equation (8) that the dynamics of the first moment $\langle n \rangle$, or the expected value of population size n (ensemble average of n), obeys a dynamics that is no longer logistic growth because of the additional term in the right hand side ($Var[n] \geq 0$). Although we have not yet determined $Var[n]$ this is a remarkable result we have never observed in the previous models of immigration-emigration and birth-death where the first moment dynamics obeys the same deterministic dynamics.

In the previous models, we obtained the dynamics of the first moment that is exactly the same as the corresponding deterministic dynamics. But in the stochastic logistic growth where $birth(N)$

and $death(N)$ depend on N, we no longer have such coincidence. This is typical to cases when transition probabilities $n \to n+1, n, n-1$ are non-linear with respect to n. Transition probabilities in immigration-emigration and birth-death models are linear so that the deterministic dynamics and the first moment dynamics exactly match with each other (Table).

	Prob$[n \to n+1]$	Prob$[n \to n-1]$	Prob$[\ n \to n]$
Immigration-emigration	$\alpha\Delta t$	$\beta\Delta t$	$1-\alpha\Delta t-\beta\Delta t$
Birth-death	$\beta n\Delta t$	$\delta n\Delta t$	$1-\beta n\Delta t-\delta n\Delta t$
Logistic	$(b_1-b_2n)n\Delta t$	$(d_1+d_2n)n\Delta t$	$1-(b_1-b_2n)n\Delta t-(d_1+d_2n)n\Delta t$

In the simulation of the logistic process we found that the ensemble average of the population size $E[n]$ and the variance of population size $Var[n]$ are eventually stabilized at certain levels (this is actually a quasi-stationary state, not a true stationary state as we will see in the next lecture). If the ensemble average and variance of population size converge to constant, n_e, and σ_e^2, respectively, they should satisfy equation (8) with the time derivative be zero

$$0 = (b_1-d_1)\left(1-\frac{n_e}{\frac{b_1-d_2}{b_2+d_2}}\right)n_e-(b_2+d_2)\sigma_e^2$$

This is a quadratic equation of n_e and we can solve n_e as follows if the variance is small enough

$$n_e = \frac{b_1-d_1}{b_2+d_2}-\frac{b_2+d_2}{b_1-d_1}\sigma_e^2 \tag{9}$$

where we used an approximation $\sqrt{1+x} \approx 1+x/2$ when $x \ll 1$.

In the deterministic logistic growth the population size converges to the carrying capacity

$$K = \frac{b_1-d_1}{b_2+d_2}$$

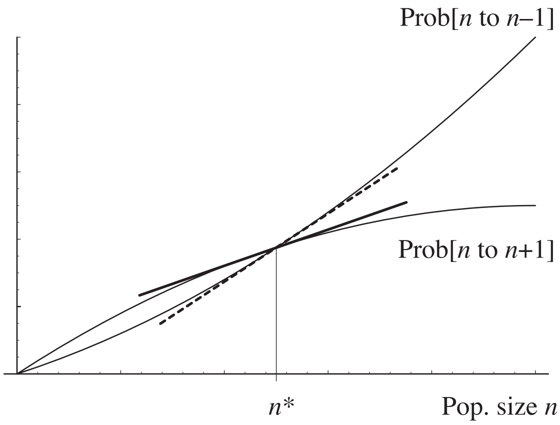
but equation (9) shows that the equilibrium ensemble average $E[n]$ in the stochastic logistic growth n_e is lowered by the amount proportional to the variance $Var[n]$ at equilibrium σ_e^2.

$$n_e = K-\frac{b_2+d_2}{b_1-d_1}\sigma_e^2 \tag{10}$$

We have not yet determined the dynamics of the variance $Var[n]$ because it contains the third moment and the dynamics of the third moment contains the fourth moment, and the fourth moment contains the fifth, $\cdots$. In the next section we see how much the variance will be.

4 Linear approximation

In the logistic process, the transition probability Prob$[n \to n+1]$ and Prob$[n \to n-1]$ is $(b_1-b_2n)n$ and$(d_1+d_2n)n$, respectively. The former is concave and the latter is convex and these are non-linear function of n. Due to the non-linearity we could not derive moment dynamics in a closed form. We now linearlize these functions around a state at which both the probabilities, $(b_1 - b_2 n)n$ and $(d_1 + d_2 n)n$, equal, i.e., at $n = n^* = (b_1 - d_1)/(b_2 + d_2) = K$. Note that K is the carrying capacity of the deterministic logistic model.



We focus on an approximated stochastic process where the transition probabilities, Prob$[n \to n+1]$ and Prob$[n \to n-1]$, are linear function of n. Let the slope of $(b_1 - b_2 n)n$ at $n = n^*$ be A and that of $(d_1 + d_2 n)n$ be B. Then the linearized (approximated) transient probabilities are given as

$$(b_1 - b_2 n)n \approx A(n - K) + C \tag{11}$$
$$(d_1 + d_2 n)n \approx B(n - K) + C \tag{12}$$

where

$$A = \frac{-b_1 b_2 + b_1 d_2 + 2b_2 d_1}{b_2 + d_2}$$
$$B = \frac{2b_1 d_2 + b_2 d_1 - d_1 d_2}{b_2 + d_2}$$
$$C = \frac{(b_1 - d_1)(b_2 d_1 + b_1 d_2)}{(b_2 + d_2)^2}$$

We expect that this linearization will work successfully if deviation from K is not large (variance, or standard derivation, is small relative to K).

Based on the linearized transient probabilities we construct master equation of the approximated linear system.

$$\begin{aligned}\frac{dP_t(t)}{dt} &= (A(n-1-K)+C)P_{n-1} + (B(n+1-K)+C)P_{n+1} \\ &\quad -(A(n-K)+C+B(n-K)+C)P_n\end{aligned} \tag{13}$$

From this master equation the first moment dynamics is derived as

$$\begin{aligned}\frac{d\langle n\rangle}{dt} &= (A-B)\langle n\rangle - (A-B)K \\ &= (b_1 - d_1)(K - \langle n\rangle)\end{aligned} \tag{14}$$

This is easily solved and we see $\langle n \rangle \to K$ if $b_1 > d_1$.

In the same way the second moment dynamics is obtained after some calculus.

$$\frac{d\langle n^2 \rangle}{dt} = 2(A-B)\langle n^2 \rangle + (A+B-2KA-2KB)\langle n \rangle - (A+B)K + 2C \tag{15}$$

Using the relationship $Var[n] = \langle n^2 \rangle - \langle n \rangle^2$, we derive the dynamics of the variance

$$\frac{d}{dt}Var[n] = 2(A-B)Var[n] + (A+B)\langle n \rangle - (A+B)K + 2C \tag{16}$$

ODE (16) can be readily solved, but if the variance converges to a constant σ_e^2, it must satisfy

$$\begin{aligned} 0 &= 2(A-B)\sigma_e^2 + (A+B)K - (A+B)K + 2C \\ &= 2(A-B)\sigma_e^2 + 2C \end{aligned}$$

because $\langle n \rangle \to K$ in this linear process.

The variance at quasi-equilibrium is then

$$\sigma_e^2 = \frac{C}{B-A} = \frac{b_1 d_2 + b_2 d_1}{(b_2+d_2)^2} \tag{17}$$

Remember that this is derived from the approximated linear process and is not exact evaluation of the variance. But we will see this gives good estimate of the variance of the logistic process.

5 Problem

1. Carry out simulation with appropriate parameter values of b_1, b_2, d_1, d_2 to see if the simulation is in good agreement with the analytical results in terms of the variance (equation 10 and 17).