Lecture 8: Birth-death models #2

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1 Analysis of the stochastic process of birth and death

In the last lecture we have implemented a stochastic birth and death process in a C program. The process is that for N individuals (N is now non-negative integer), 1) a new individual is born with probability $\beta\Delta t$, 2) the individual dies and is removed from the population with probability $\delta\Delta t$, and 3) the individual nether gives birth nor dies with probability $1-\beta\Delta t-\delta\Delta t$ where Δt is a short time interval. These three events 1), 2), 3), occur mutually exclusively.

The population size N as non-negative integer is no longer determined uniquely, but is associated with a certain probability distribution that evolves with time t. As we did in the immigration-emigration model we want to look for the probability distribution, i.e., the probability that the population size is n at time t, $P_n(t)$ where $n \geq 0$.

To do this we derive master equation for the probability distribution $P_n(t)$. As we have seen in the simulation, the state $n = 0$ is an absorbing state, i.e., once trapped in this state the system remains unchanged because transition from $n = 0$ to $n = 1$ is impossible (offspring cannot be reproduced from empty). So $n = 0$ is the boundary that separates $n > 0$ and $n < 0$, the former makes biological sense but the latter not.

2 Master equation

Let us now assume that the time interval Δt is small enough that the change of the population size within the time interval, $N(t + \Delta t) - N(t)$, is at most ± 1, i.e., transition to a state n is possible either from $n-1$ or $n+1$ ($n \geq 1$). In the simulation we assumed that each individual can experience one of the three possible cases listed above. Thus, for n individuals, the probability that there are n individuals again after Δt is given as

$$\text{Prob}[N(t+\Delta t)=n|N(t)=n]=\sum_{i=0}^{[n/2]}\frac{(n-2i)!i!i!}{n!}(1-\beta\Delta t-\delta\Delta t)^{n-2i}(\beta\Delta t)^i(\delta\Delta t)^i$$

where [x] is the maximum integer that does not exceed x. As $\Delta t \to 0$ this transition probability that population size does not change during Δt is $1-\beta n\Delta t-\delta n\Delta t$ by ignoring higher orders of Δt.

In the same way we see that if Δt is small enough, the transition probability that population size changes from $n-1$ to n can be given as $\beta(n-1)\Delta t$ and that from $n+1$ to n as $\delta(n+1)\Delta t$.

Then the probability that the population size is n at time $t+\Delta t$, $P_n(t+\Delta t)$, is given as

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

Note that transition from $n=0$ to $n=1$ is now impossible. This means that empty (extinct) population cannot produce offspring anymore.

Equation (1) is valid for $n\geq 1$. For $n=0$, we have

$$P_0(t+\Delta t)=P_0(t)+P_1(t)\delta\Delta t \tag{2}$$

Arranging equation (1) and (2) by letting $\Delta t\to 0$, we obtain

$$\frac{dP_n(t)}{dt}=\beta(n-1)P_{n-1}(t)+\delta(n+1)P_{n+1}(t)-(\beta+\delta)nP_n(t) \quad \text{for } n\geq 1 \tag{3}$$

$$\frac{dP_0(t)}{dt}=\delta P_1(t) \tag{4}$$

The set of equation (3) and (4) is the master equation of the birth-death process. $P_n(t)$ can be solved with certain initial condition, e.g., when initial population size is 1, $P_0(0)=1, P_n(0)=0$ for $n\geq 1$. The population size n starting from a positive initial number cannot pass through the boundary $n=0$ and it cannot be negative. So we can assume that $P_n(t)$ for negative n is always zero. Now equation (4) is naturally derived from equation (3) by setting $n=0$.

3 Equilibrium probability distribution

Before solving the master equation, we look for stationary probability distribution. If there exists an equilibrium probability distribution $P_n=P_n(t\to\infty)$, the time derivative of $P_n(t)$ must be zero.

From the master equation we see

$$0=\delta P_1=0 \tag{5}$$

$$0=\beta(n-1)P_{n-1}+\delta(n+1)P_{n+1}-(\beta+\delta)nP_n \quad \text{for } n\geq 1 \tag{6}$$

From equation (5) we have

$$P_1=0$$

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

$$P_2 = 0$$

Repeating this shows a general rule

$$P_n = 0$$

for $n \geq 1$.

Now remember that P_n is probability distribution and it must sum up to 1

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

From this we see that $P_0 = 1, P_n = 0$ $(n \geq 1)$ is an equilibrium distribution (population finally goes extinct). Or if $0 < P_0 < 1$ there is no equilibrium distribution because the probabilities never sum up to 1 (population explodes to infinity). In the stochastic birth-death process, population 1) always goes extinct or 2) it either goes extinct with a certain probability P or explodes to infinity with probability $1 - P$. We will later explore these behavior in details.

4 Moment dynamics

As we did in the immigration-emigration model, we can derive moment dynamics of the birth-death process from the master equation.

For the first moment dynamics we multiply equation (3) with n and take summation for $n = 0, 1, 2, \cdots \infty$.

$$\begin{aligned}
\frac{d\langle n\rangle}{dt} &= \sum_{n=0}^{\infty} \left\{ \beta n(n-1)P_{n-1}(t) + \delta n(n+1)P_{n+1}(t) - (\beta+\delta)n^2 P_n(t) \right\} \\
&= \beta \sum_{n=1}^{\infty} \left\{ (n-1)^2 P_{n-1}(t) + (n-1)P_{n-1}(t) \right\} + \\
&\quad \delta \sum_{n=0}^{\infty} \left\{ (n+1)^2 P_{n+1}(t) - (n+1)P_{n+1}(t) \right\} - (\beta+\delta) \sum_{n=0}^{\infty} n^2 P_n(t) \\
&= \beta \left\{ \langle n^2\rangle + \langle n\rangle \right\} + \delta \left\{ \langle n^2\rangle - \langle n\rangle \right\} - (\beta+\delta)\langle n^2\rangle \\
&= (\beta-\delta)\langle n\rangle
\end{aligned} \tag{7}$$

Here we used identity $\sum_{n=0} nP_n = \sum_{n=1} nP_n$. This result shows that the ensemble average $\langle n\rangle$ obeys the same exponential growth of the deterministic model.

$$\frac{d\langle n\rangle}{dt} = (\beta-\delta)\langle n\rangle$$

If the process starts with the same initial population size, $\langle n\rangle$ at $t = 0$ is equal to $N(0)$ because $P_n(0) = 1$ for $n = N(0)$ and $P_n(0) = 0$ for otherwise. The solution is

$$\langle n\rangle = N(0)\exp[(\beta-\delta)t] \tag{8}$$

This is exactly the same as the solution of the deterministic birth-death process.

In the same way we have the second moment dynamics after tedious calculus.

$$
\begin{aligned}
\frac{d\langle n^2\rangle}{dt} &= \sum_{n=0}^{\infty}\left\{\beta n^2(n-1)P_{n-1}(t)+\delta n^2(n+1)P_{n+1}(t)-(\beta+\delta)n^3P_n(t)\right\} \\
&= \cdots \text{It would be nice if you ever try to derive this result by yourself} \cdots \\
&= 2(\beta-\delta)\langle n^2\rangle+(\beta+\delta)\langle n\rangle
\end{aligned} \tag{9}
$$

Substituting equation (8) into equation (9) completes an ordinary differential equation for the second moment $\langle n^2\rangle$. If the process starts with the same initial population size $N(0)$, the ODE (9) can be solved with the initial condition $\langle n^2\rangle = N(0)^2$ at $t = 0$.

$$
\frac{d\langle n^2\rangle}{dt} = 2(\beta-\delta)\langle n^2\rangle+(\beta+\delta)\langle n\rangle
$$

See Appendix for how this type of ODE can be solved. The solution is a bit lengthly

$$
\langle n^2\rangle = N(0)\frac{\beta+\delta}{\beta-\delta}\exp[(\beta-\delta)t]\left(\exp[(\beta-\delta)t]-1\right)+N(0)^2\exp[2(\beta-\delta)t]
$$

but it turns out that the variance $Var[n] = \langle n^2\rangle - \langle n\rangle^2$ turns out to be a simple form as

$$
Var[n] = N(0)\frac{\beta+\delta}{\beta-\delta}\exp[(\beta-\delta)t]\left(\exp[(\beta-\delta)t]-1\right) \tag{10}
$$

We have solved the first and the second moment dynamics, both of which would be useful to understand the behavior of the stochastic birth and death process we have simulated. When $\beta > \delta$ the average population size exponentially increases $\langle n\rangle \propto \exp[(\beta-\delta)t]$. The variance also increases roughly exponentially as $Var[n] \sim \exp[2(\beta-\delta)t]$ for large t. This means that the square root of variance alias the degree of variation around the average increases in the same order of the average. This poses a serious problem to predict the behavior of this stochastic process as we will see in the exercise.

5 Problem

1. Carry out the simulation with appropriate parameter values, e.g., $\beta = 0.03$, $\delta = 0.02$, and check if the simulation is in good agreement with the analytical results in terms of the ensemble average and the variance (equation (8) and (10)). Does decreasing the interval Δt result in better fit?
2. Confirm that the population often goes extinct (population size is trapped in "zero") when the death rate δ is close to the birth rate β even when $\beta > \delta$.
3. The analysis has shown that the square root of the variance increases exponentially in the same order of the ensemble average. What does this mean in terms of the predictability of the stochastic dynamics?

6 Appendix

Solution of a linear differential equation

$$\frac{dx}{dt} = p(t)x + q(t)$$

is given as

$$x(t) = e^{\int p(t)dt}\left(C + \int e^{-\int p(t)dt} q(t)dt\right)$$

where C is integration constant which should be determined using initial condition $x(0)$.

How is this derived? If we multiply the original equation with $\exp[-\int p(t)dt]$, it can be arranged as

$$\frac{d}{dt}\left(e^{-\int p(t)dt} x\right) = e^{-\int p(t)dt} q(t)$$

We integrate this equation to have

$$e^{-\int p(t)dt} x(t) = \int e^{-\int p(t)dt} q(t)dt + C$$

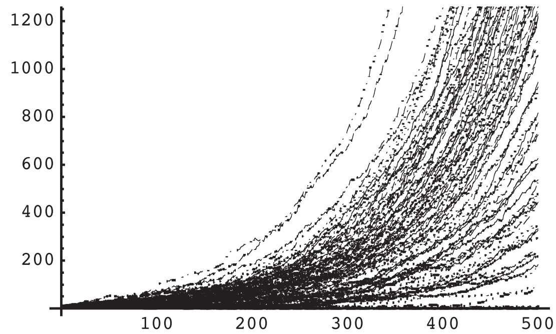
which results in the general solution given above.

In the birth-death process starting from a constant initial state $N(0)$, $p(t) = 2(\beta - \delta)$ and $q(t) = (\beta + \delta)\langle n \rangle = N(0)(\beta + \delta)e^{(\beta-\delta)t}$.

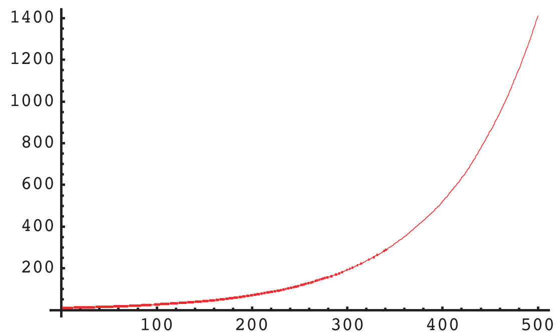
```
In[1]:= << Graphics`MultipleListPlot`

In[2]:= << Statistics`DescriptiveStatistics`
```

■ Simulation by C

```
In[4]:= 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[4]= /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[37]:= data = ReadList["data", Real, RecordLists->True];
         len = Length[data]

Out[38]= 100

In[39]:= gSimulation = MultipleListPlot[data, PlotJoined → True, SymbolShape → None]
```

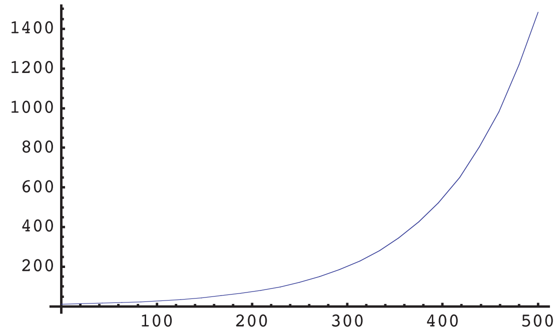



```
Out[39]= - Graphics -

In[40]:= dataT = Transpose[data];

In[41]:= averageDyna = Map[ Mean, dataT];

In[42]:= gAverage = ListPlot[ averageDyna, PlotJoined → True, PlotStyle → RGBColor[1, 0, 0]]
```

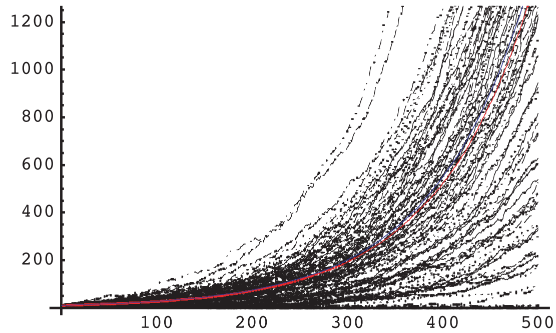



```
Out[42]= - Graphics -

In[43]:= Fit[ Log[averageDyna], {1, t}, t]

Out[43]= 2.26312 + 0.00998364 t
```

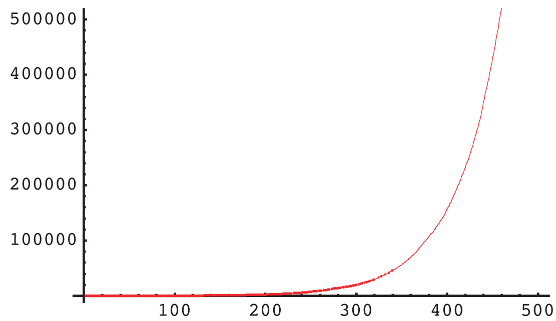
```
In[44]:= ensembleAverage = n0 Exp[(b - d) t] /. {n0 ? 10, b ? 0.03, d ? 0.02};
         gAverageAnalytic = Plot[ensembleAverage, {t, 0, 500}, PlotStyle ? RGBColor[0, 0, 1]]
```




```
Out[45]= - Graphics -

In[46]:= Show[gSimulation, gAverage, gAverageAnalytic]
```

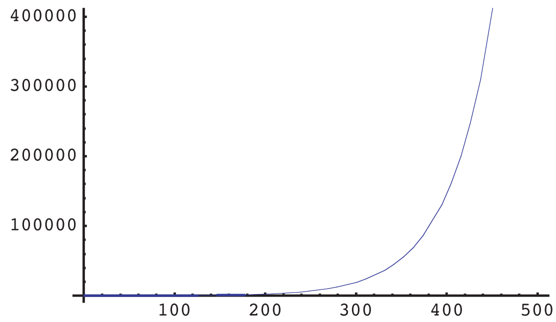



```
Out[46]= - Graphics -

In[47]:= varianceDyna = Map[VarianceMLE, dataT];

In[48]:= gVariance = ListPlot[varianceDyna, PlotJoined ? True, PlotStyle ? RGBColor[1, 0, 0]]
```



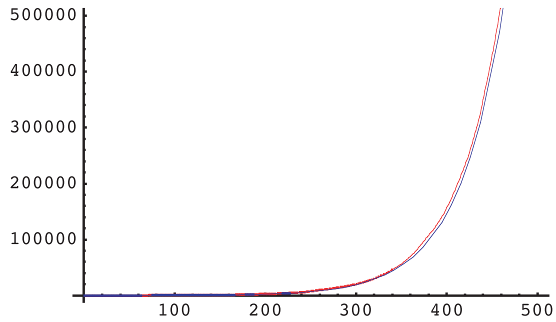

```
Out[48]= - Graphics -

In[49]:= Fit[Log[Take[varianceDyna, -200]], {1, t}, t]

Out[49]= 9.93148 + 0.0202347 t
```

In[50]:=
```
ensembleVariance =
  n0 (b + d) / (b - d) Exp[(b - d) t] (Exp[(b - d) t] - 1) /. {n0 ? 10, b ? 0.03, d ? 0.02};
gVarianceAnalytic = Plot[ensembleVariance, {t, 0, 500}, PlotStyle ? RGBColor[0, 0, 1]]
```



Out[51]= - Graphics -

In[52]:=
```
Show[gVariance, gVarianceAnalytic]
```



Out[52]= - Graphics -