Lecture 11: Logistic growth models #3

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13 July 2009

1 Equilibrium probability distribution

In the last lecture we have explored the stochastic logistic growth model. The master equation was given as

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

where the per-capita birth and death rates depend on the population size N as

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

The state $n = 0$ is absorbing state and we have assumed that $P_n(t)$ is zero for negative n.

Now we look for the probability distribution $P_n(t)$ in depth. If there exists an equilibrium probability distribution $P_n = P_n(t \to \infty)$, the time derivatives of $P_n(t)$ in the master equation must be zero. Then we see

$$0 = (d_1 + d_2)P_1 \tag{2}$$

$$0 = 2(d_1 + 2d_2)P_2 - (b_1 - b_2 + d_1 + d_2)P_1 \tag{3}$$

$$\begin{aligned} 0 =& \{b_1 + b_2(n-1)\}(n-1)P_{n-1} + \{d_1 + d_2(n+1)\}(n+1)P_{n+1} \\ & - (b_1 - b_2 n + d_1 + d_2 n)nP_n \quad \text{for } n \geq 2 \end{aligned} \tag{4}$$

From equation (2) we have

$$P_1 = 0$$

and substituting this to equation (3) yields

$$P_2 = 0$$

Repeating this shows a general rule

$$P_n = 0$$

for $n \geq 1$.

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

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

Then we see that $P_0 = 1, P_n = 0$ $(n \geq 1)$ is an equilibrium distribution which means that the population eventually goes extinct with probability 1 (extinction is inevitable!).

Intuitively we are convinced that the population size cannot explode indefinitely in this logistic growth model. But it might be counter-intuitive that the population ultimately goes extinct. This discrepancy could be reasoned as follows. The state $n = 0$ is absorbing wall and once trapped in this state the population size remains zero forever. Because the transition to $n = 0$ from any positive population size is always possible (with non-zero probability although it could be extreme low), the population size is gradually absorbed to $n = 0$ and eventually all populations are trapped there. The time to extinction can be extremely long once the population size becomes large enough fluctuating around the equilibrium n_e large enough. In this case we might observe **quasi-stationary** probability distribution of P_n which can be readily demonstrated by simulation.

2 Time to extinction

In the stochastic logistic growth, extinction is inevitable as shown in the previous section. Although ultimate extinction is certain, we are curious to know how long it will take for a population to be extinct. Let $\tau_E(N_0)$ be the mean time to extinction of a population whose initial size is N_0.

As the transition from N_0 is to one of the following three cases, 1) no change, 2) change to $N_0 + 1$, 3) change to $N_0 - 1$, we can derive a difference equation for the mean time to extinction $\tau_E(N_0)$ as

$$\tau_E(N_0) = \frac{1}{B(N_0) + D(N_0)} + \frac{B(N_0)}{B(N_0) + D(N_0)}\tau_E(N_0 + 1) + \frac{D(N_0)}{B(N_0) + D(N_0)}\tau_E(N_0 - 1) \quad (5)$$

The fist term on the r.h.s is the mean time spent before the first change occurs (it is the inverse of the rate of exponential distribution), the second term is that representing the mean time to extinction when the first change is to $N_0 + 1$ and the third term is that the mean time to extinction when the first change is to $N_0 - 1$.

To solve this difference equation we need $\tau_E(0)$ and $\tau_E(1)$. The fomer is naturally $\tau_E(0) = 0$ but the latter $\tau_E(1)$ might be given arbitrary. This equation is readily solved after some algebra (see Appendix) and it turns out

$$\tau_E(N_0 + 1) - \tau_E(N_0) = \frac{\prod_{i=1}^{N_0} D(i)}{\prod_{i=1}^{N_0} B(i)} \left\{ \tau_E(1) - \sum_{i=1}^{N_0} q_i \right\} = F(N_0) \quad (6)$$

where

$$q_i = \frac{B(1)B(2)\cdots B(i-1)}{D(1)D(2)\cdots D(i)} = \frac{\prod_{j=1}^{i-1} B(j)}{\prod_{j=1}^{i} D(j)} \quad \text{for} \quad i \geq 2$$

$$q_1 = \frac{1}{D(1)}$$

By summing up both the sides of equation (6) we reach

$$\tau_E(N_0) = \tau_E(1) + \sum_{k=1}^{N_0-1} F(k) \tag{7}$$

Still $\tau_E(1)$ remains to be determined to obtain the mean time to extinction starting from a population of N_0. But from equation (6) we might expect that $\tau_E(N_0+1) - \tau_E(N_0) \to 0$ as we let $N_0 \to \infty$ for the following reason. For extremely large N_0 it is most likely that death rate $D(N_0)$ overwhelms birth date $B(N_0)$ so that we can ignore transition via the state $N_0 + 1$, thus $\tau_E(N_0 + 1) \approx \tau_E(N_0)$ for large N_0. Then we have

$$\tau_E(1) = \sum_{i=1}^{\infty} q_i \tag{8}$$

As an example, let us assume $B(N) = (b_1 - b_2N)N = b_1N$ and $D(N) = (d_1 + d_2N)N = d_2N^2$ ($b_2 = d_1 = 0$). In this case

$$q_i = \frac{1}{b_1}\left(\frac{b_1}{d_2}\right)^i \frac{1}{i!i}$$

and

$$\tau_E(1) = \sum_{i=1}^{\infty} q_i \approx \frac{1}{b_1}\frac{d_2}{b_1}\exp\left[\frac{b_1}{d_2}\right] \tag{9}$$

Remember that the carrying capacity K in the corresponding deterministic growth was

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

When $b_2 = d_1 = 0$, $K = b_1/d_2$ and the mean time to extinction when starting from $N_0 = 1$ is

$$\tau_E(1) \propto \frac{1}{K}\exp[K]$$

This shows that as the carrying capacity K increases the mean time to extinction can be extremely long.

3 Appendix

We introduce a variable $x(N_0) = \tau_E(N_0) - \tau_E(N_0 - 1)$ and equation (5) is arranged

$$x(N_0 + 1) = \frac{D(N_0)}{B(N_0)}x(N_0) - \frac{1}{B(N_0)}$$

where $x(1) = \tau_E(1)$. Deriving $x(2)$ and $x(3)$ will guide you to the solution candidate equation (6) and by induction it can be shown as the solution.

4 Problem

1. Observe in simulation the quasi-stationary distribution P_n as follows. Write the population size $n(t)$ into a file at $t = 500, 1000, 1500, \cdots, 5000$ and repeat this for many times, e.g., 1000.

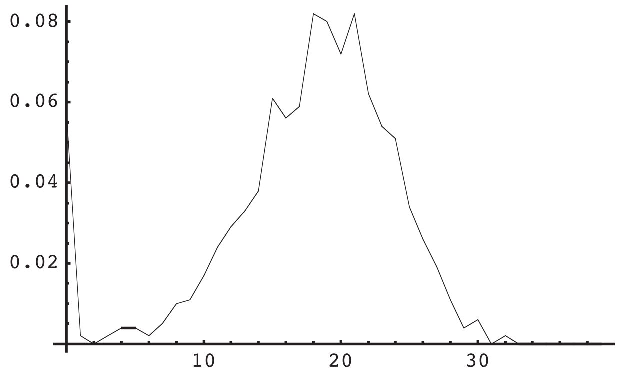
Trial 1:	$n(500)$	$n(1000)$	$n(1500)$	$\cdots$	$n(5000)$
Trial 2:	$n(500)$	$n(1000)$	$n(1500)$	$\cdots$	$n(5000)$
Trial 3:	$n(500)$	$n(1000)$	$n(1500)$	$\cdots$	$n(5000)$
$\vdots$					

   Using *Mathematica* observe the quasi-stationary equilibrium of probability distribution P_n and see that some unfortunate populations can go extinct as time passes. We would have to choose parameters so that the carrying capacity is not large enough if we are to see populations eventually go extinct (within your patience).

2. Using appropriate parameter values of b_1 and d_2 ($b_2 = d_1 = 0$), calculate by simulation the time to extinction starting from initial population size $N_0 = 1$ for many trials. Output the time into a file when the population size reaches zero. Each output should be separated with a white space. Read these data in Mathematica and compare the results with the analytical results of equation (9).

Stochastic logistic process: Quasi-stationary distribution

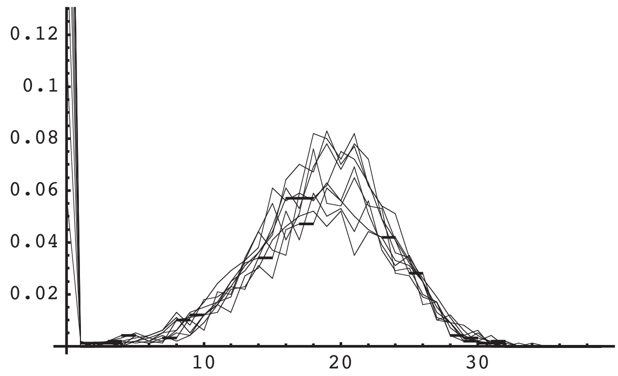
```
In[2]:= << Statistics`DataManipulation`

In[3]:= << Graphics`Graphics3D`

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/Logistic growth model/logistic_models/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/Logistic growth model/logistic_models/build

In[62]:= data = ReadList["data-QS", Number, RecordLists ? True];
         len = Length[data]
         max = Max[data]
         lenT = Length[Transpose[data]]

Out[63]= 1000

Out[64]= 34

Out[65]= 10

In[66]:= points = Table[i, {i, 0, max + 5}];

In[67]:= tmp = ColumnTake[data, {2}] // Flatten;
         category = CategoryCounts[tmp, points] / len;
         seq = Transpose[{points, category}];
         ListPlot[seq, PlotJoined ? True]
```




```
Out[70]= - Graphics -
```

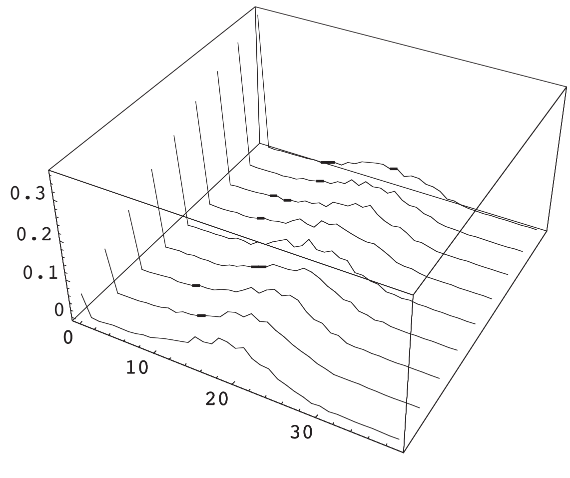
```
In[71]:= glist = {};
         Do[
          tmp = ColumnTake[data, {i}] // Flatten;
          category = CategoryCounts[tmp, points] / len;
          seq = Transpose[{points, category}];
          g = ListPlot[seq, PlotJoined → True, DisplayFunction → Identity];
          AppendTo[glist, g], {i, 2, lenT}
         ]
```

```
In[73]:= Show[glist, DisplayFunction → $DisplayFunction]
```




```
Out[73]= - Graphics -
```

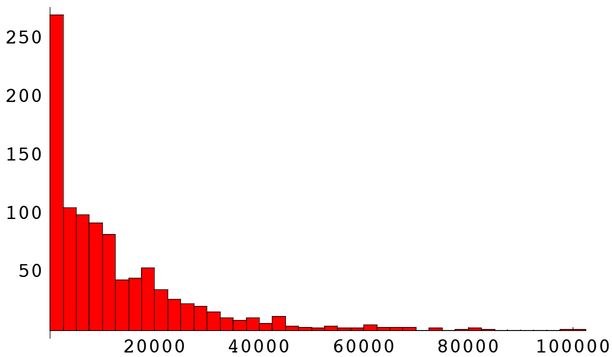
```
In[74]:= Show[StackGraphics[glist], BoxRatios → {2, 2, 1}, PlotRange → All]
```




```
Out[74]= - Graphics3D -
```

Stochastic logistic process: Time to extinction

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

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

In[3]:= << Statistics`DataManipulation`

In[4]:= SetDirectory["/Users/takasu/home/情報科学科の仕事/講義/平成１８年度/H18
          大学院講義/Logistic growth model/logistic_models/build/Development/"]

Out[4]= /Users/takasu/home/[illegible]          /議 /[illegible]        /H18
         [illegible]      /Logistic growth model/logistic_models/build/Development

In[5]:= data = ReadList["data-time_extinction", Real];
        Length[data]
        Min[data]
        Max[data]

Out[6]= 1000

Out[7]= 0.0498

Out[8]= 100000.

In[9]:= Mean[data]

Out[9]= 12701.3

In[10]:= Histogram[data]
```




```
Out[10]= - Graphics -

In[11]:= para = {b1 → 0.2, b2 → 0, d1 → 0, d2 → 0.02}

Out[11]= {b1 → 0.2, b2 → 0, d1 → 0, d2 → 0.02}

In[12]:= carryingCapacity = (b1 - b2) / (d1 + d2)
```

Out[12]= $\frac{b1 - b2}{d1 + d2}$


```
In[13]:= timeToExtinction = d2 / b1 / b1 Exp[b1 / d2]
```

Out[13]= $\frac{d2\, e^{b1/d2}}{b1^2}$

```
In[14]:= carryingCapacity /. para

Out[14]= 10.

In[15]:= timeToExtinction /. para

Out[15]= 11013.2

In[16]:= {carryingCapacity, timeToExtinction} /. {b1 → 0.2, b2 → 0, d1 → 0, d2 → 0.01}

Out[16]= {20., 1.21291 × 10^8}

In[17]:= {carryingCapacity, timeToExtinction} /. {b1 → 0.2, b2 → 0, d1 → 0, d2 → 0.002}

Out[17]= {100., 1.34406 × 10^42}
```