Stochastic models: Birth and death process I

We have already discussed population modelling using ordinary differential equations, including exponential and logistic growth models. These models are deterministic because they assume that each organism reproduces at a constant, predictable rate. However, in reality, population growth is stochastic, i.e., random. Given a population of cells that grow by division, one cannot say that a particular cell will divide within a specific time interval; one can only say that there is a certain probability that it will. The stochastic birth-and-death processes considered here are examples of continuous-time and discrete-space stochastic models.

Pure birth process: We first consider the pure birth process in a population. The birth rate in each state is only dependent on the current state. Let $X(t)$ be the number of births up to and including time t, given that there are initially n_0 births. We are interested in

$$p_n(t) = \text{prob}[X(t) = n \big| X(0) = n_0], \qquad n = n_0, n_0 + 1, \cdots$$

The following are the assumptions underlying the pure birth process:

i. Given $X(t) = n$, the probability of a new birth occurring in $(t, t+h]$ is $\lambda_n\, h + o(h)$, where λ_n is a function of n only.

ii. The probability that more than one birth will occur in the time interval $(t, t + h]$ is $o(h)$

Hence, the probability of no birth in $(t, t + h]$ is $1 - \lambda_n h - o(h)$.
First, consider the case of $n > n_0$:

$$\begin{aligned} p_n(t+h) &= p_n(t) \times \text{prob}\{\text{no birth in } (t, t+h]\} + p_{n-1}(t) \times \text{prob}\{\text{one birth in } (t, t+h]\} + \\ &+ \sum_{i \geq 2}^{n-n_0} p_{n-i}(t) \times \text{prob}\{\ i \text{ birth in } (t, t+h]\} \\ &= p_n(t)[1 - \lambda_n h - o(h)] + p_{n-1}(t)[\lambda_{n-1} h + o(h)] + o(h) \end{aligned}$$

Note that the sum in the last term contributes $o(h)$ only when $n \geq n_0 + 2$. Rearranging and dividing both sides by h, we get

$$\frac{p_n(t+h) - p_n(t)}{h} = -\lambda_n p_n(t) + \lambda_{n-1} p_{n-1}(t) + \frac{o(h)}{h}$$

Taking $h \to 0$, we find

$$\frac{dp_n(t)}{dt} = -\lambda_n p_n(t) + \lambda_{n-1} p_{n-1}(t)$$

Next, suppose there are n_0 births up to and including time t, given that there are initially n_0 births. Now $p_{n_0 - i}(t) = 0$ for $i \geq 1$, since the number of births can't go below n_0. Consequently,

$$\begin{aligned} p_{n_0}(t+h) &= p_{n_0}(t) \times \text{prob}\{\text{no birth in } (t, t+h]\} \\ &= p_{n_0}(t)[1 - \lambda_{n_0} h - o(h)] \\ \implies \frac{dp_{n_0}(t)}{dt} &= -\lambda_{n_0} p_{n_0}(t) \end{aligned}$$

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Hence, the governing equations become

$$\begin{aligned}\frac{dp_{n_0}(t)}{dt} &= -\lambda_{n_0} p_{n_0}(t), \quad p_{n_0}(0) = 1 \\ \frac{dp_n(t)}{dt} &= -\lambda_n p_n(t) + \lambda_{n-1} p_{n-1}(t), \quad p_n(0) = 0, \quad n > n_0.\end{aligned}$$

The initial conditions imply that if there are n_0 births at $t = 0$, then the probability of $X(t) = n_0$ at time $t = 0$ will be 1. Similarly, the probability of the event $X(t) = n$ at time $t = 0$ will be 0 for $n > n_0$.

We solve these equations assuming that all λ_n are distinct. For $n = n_0$, we solve

$$\frac{dp_{n_0}(t)}{dt} = -\lambda_{n_0} p_{n_0}(t), \quad p_{n_0}(0) = 1 \implies p_{n_0}(t) = e^{-\lambda_{n_0} t}$$

For $n = n_0 + 1$, we have

$$\frac{dp_{n_0+1}(t)}{dt} = -\lambda_{n_0+1} p_{n_0+1}(t) + \lambda_{n_0} p_{n_0}(t), \quad p_{n_0+1}(0) = 0,$$

which becomes

$$\frac{dp_{n_0+1}(t)}{dt} + \lambda_{n_0+1} p_{n_0+1}(t) = \lambda_{n_0} e^{-\lambda_{n_0} t}, \quad p_{n_0+1}(0) = 0.$$

This is a linear ordinary differential equation, whose solution is

$$p_{n_0+1}(t) = \frac{\lambda_{n_0}}{\lambda_{n_0+1} - \lambda_{n_0}} \left(e^{-\lambda_{n_0} t} - e^{-\lambda_{n_0+1} t} \right),$$

which we write as

$$p_{n_0+1}(t) = (-1)^{n_0+1-n_0} \lambda_{n_0} \left(\frac{e^{-\lambda_{n_0} t}}{\lambda_{n_0} - \lambda_{n_0+1}} + \frac{e^{-\lambda_{n_0+1} t}}{\lambda_{n_0+1} - \lambda_{n_0}} \right),$$

It can be proved by induction that

$$P_n(t) = (-1)^{n-n_0} \lambda_{n_0} \lambda_{n_0+1} \cdots \lambda_{n-1} \sum_{i=n_0}^{n} \frac{e^{-\lambda_i t}}{\prod_{j=n_0, i \neq j}^{n} (\lambda_i - \lambda_j)}, \quad n = n_0,\, n_0 + 1, \cdots .$$

Linear birth process: In this case, $\lambda_n = \lambda\, n$. Using the solution derived above, we find

$$\begin{aligned}p_n(t) &= (-1)^{n-n_0} n_0 \cdot \lambda \cdot (n_0 + 1) \cdot \lambda \cdots (n-1) \cdot \lambda \sum_{i=n_0}^{n} \frac{e^{-\lambda \cdot i \cdot t}}{\prod_{j=n_0, i \neq j}^{n} (\lambda \cdot i - \lambda \cdot j)} \\ &= (-1)^{n-n_0} \lambda^{n-n_0} (n-1) \cdot (n-2) \cdots (n_0 + 1) \cdot n_0 \sum_{i=n_0}^{n} \frac{e^{-\lambda \cdot i \cdot t}}{\lambda^{n-n_0} \prod_{j=n_0, i \neq j}^{n} (i - j)}\end{aligned}$$

Now we make further simplification as shown below:

$$\begin{aligned}
p_n(t) &= (-1)^{n-n_0}(n-1)\cdot(n-2)\cdots(n_0+1)\cdot n_0 \cdot \frac{(n_0-1)!}{(n_0-1)!}\sum_{i=n_0}^{n}\frac{e^{-\lambda\cdot i\cdot t}}{\prod_{j=n_0, i\neq j}^{n}(i-j)} \\
&= (-1)^{n-n_0}\frac{(n-1)!}{(n_0-1)!}\frac{(n-n_0)!}{(n-n_0)!}\sum_{i=n_0}^{n}\frac{e^{-\lambda\cdot i\cdot t}}{(i-n_0)\cdot(i-n_0-1)\cdots(2)\cdot(1)\cdot(-1)\cdot(-2)\cdots(-(n-i))} \\
&= (-1)^{n-n_0}\binom{n-1}{n_0-1}(n-n_0)!\sum_{i=n_0}^{n}\frac{e^{-\lambda\cdot i\cdot t}}{(-1)^{n-i}(i-n_0)!(n-i)!} \\
&= \binom{n-1}{n_0-1}\sum_{i=n_0}^{n}(-1)^{i-n_0}e^{-\lambda\cdot i\cdot t}\binom{n-n_0}{i-n_0} \\
&= \binom{n-1}{n_0-1}e^{-n_0\lambda t}\sum_{i=n_0}^{n}(-1)^{i-n_0}(e^{-\lambda t})^{i-n_0}\binom{n-n_0}{i-n_0} \\
&= \binom{n-1}{n_0-1}e^{-n_0\lambda t}\sum_{i=n_0}^{n}\binom{n-n_0}{i-n_0}(-e^{-\lambda t})^{i-n_0} \\
&= \binom{n-1}{n_0-1}e^{-n_0\lambda t}\sum_{r=0}^{n-n_0}\binom{n-n_0}{r}(-e^{-\lambda t})^{r}, \qquad i-n_0=r
\end{aligned}$$

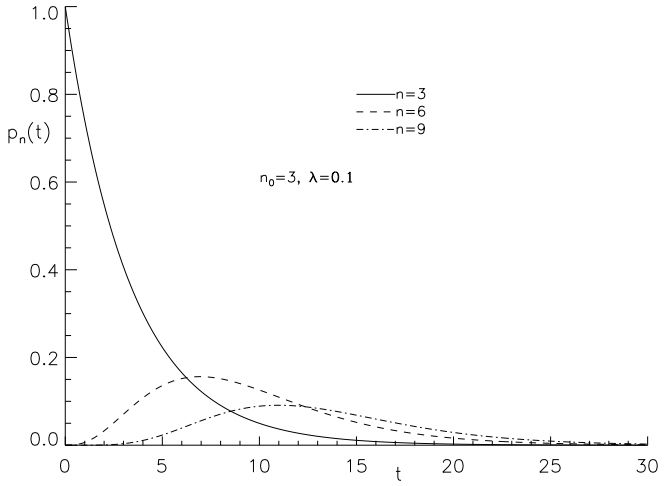
The term inside the summation is the binomial expansion of $(1-e^{-\lambda t})^{n-n_0}$, and thus

$$p_n(t)=\binom{n-1}{n_0-1}e^{-n_0\lambda t}(1-e^{-\lambda t})^{n-n_0}=\binom{n-1}{n_0-1}\left(e^{-\lambda t}\right)^{n_0}(1-e^{-\lambda t})^{n-n_0}, \qquad n=n_0,n_0+1,\cdots$$

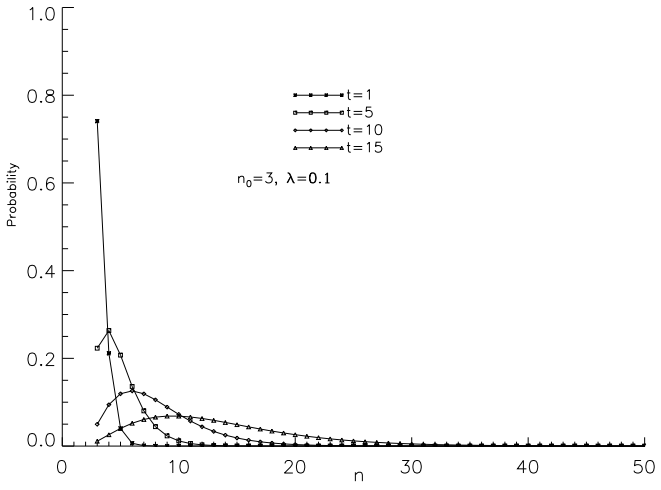
If we denote $p=e^{-\lambda t}$ and $q=1-p$, then the above is equivalent to

$$p_n(t)=\binom{n-1}{n_0-1}p^{n_0-1}q^{n-1-(n_0-1)}p, \qquad n=n_0,n_0+1,\cdots$$

This is nothing but the negative binomial distribution for having exactly n_0 successes in n trials. Note that we have n_0-1 successes in $n-1$ trials and a success in the n-th trial.



The figure above shows the evolution of probability $p_n(t)$ against time for three values of n. For $n=n_0=3$, the probability is unity at $t=0$ due to the initial conditions. At any instant of time, the sum of probabilities for all n must sum to unity.



In this figure, we plot the probability as a function of population size for different values of t. Although we have drawn continuous curves, the probability values are defined only for the integer values $n = 3, 4, 5, \cdots$. The sum of probabilities for all possible n, for a fixed t, sums to unity.