STOCHASTIC POPULATION MODELS (SPRING 2011)

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8. Introduction to birth-death processes

8.1. **The Basic model.** Small populations cannot reasonably be modeled with a differential equation for the population size because of demographic stochasticity, i.e., chancefluctuations in the number of births and deaths within a given interval of time. While in a very large population (not necessarily large in population density, but large in number of individuals) such uctuations are averaged out by the statistical Law of the Large Numbers this does not happen when the population is small, and hence a different modeling approach is needed.

Let $N(t)$ denote the number of individuals at time $t \geq 0$. Then $\{N(t)\}_{t\geq 0}$ is a stochastic process on the non-negative integers. Let further

$$P_n(t) := \text{Prob}\big\{N(t) = n\big\} \tag{1}$$

Suppose that given a population size n, birth and death are independent Poisson processes with rates B_n and D_n, respectively with

$$B_n = D_n = 0 \quad \forall n \leq 0 \tag{2}$$

The probability of having i births and j deaths in a time interval of length Δt in a population of size n then is

$$\frac{(B_n\Delta t)^i e^{-B_n\Delta t}}{i!}\,\frac{(D_n\Delta t)^j e^{-D_n\Delta t}}{j!} \tag{3}$$

i.e., the product of two Poisson distributions. (One might wonder how the population size can stay xed if births and deaths are going on. The solution to this paradox is to imagine that there is an experimenter who removes every newborn and replaces every dead individual. In this way the population size stays constant in spite of births and deaths.)

From equation (3) we find that for small Δt

$$\begin{cases} \text{Prob}\{\text{one birth \& no deaths}\} & = & B_n\Delta t + \text{O}(\Delta t)^2 \\ \text{Prob}\{\text{no births \& one death}\} & = & D_n\Delta t + \text{O}(\Delta t)^2 \\ \text{Prob}\{\text{no births \& no deaths}\} & = & 1 - B_n\Delta t - D_n\Delta t + \text{O}(\Delta t)^2 \\ \text{Prob}\{\text{anything else}\} & = & \text{O}(\Delta t)^2 \end{cases} \tag{4}$$

From this it follows that

$$\begin{aligned} &P_n(t+\Delta t) = \\ &\quad \big(B_{n-1}\Delta t\big)P_{n-1}(t) + \big(D_{n+1}\Delta t\big)P_{n+1}(t) + \big(1 - B_n\Delta t - D_n\Delta t\big)P_n(t) + \mathrm{O}(\Delta t)^2 \end{aligned} \tag{5}$$

Subtracting $P_n(t)$ from both sides and dividing by Δt, we have

$$\frac{P_n(t+\Delta t) - P_n(t)}{\Delta t} = B_{n-1}P_{n-1}(t) + D_{n+1}P_{n+1}(t) - (B_n + D_n)P_n(t) + \mathrm{O}(\Delta t) \tag{6}$$

which, as we let $\Delta t \to \infty$ becomes the ordinary differential equation

$$\frac{dP_n}{dt} = B_{n-1}P_{n-1} + D_{n+1}P_{n+1} - (B_n + D_n)P_n \tag{7}$$

One readily checks that

$$\sum_{n=0}^{\infty} \frac{dP_n}{dt} = 0 \quad \forall t \geq 0 \tag{8}$$

so that the sum of all P_n stays constant. What this constant is depends on the initial condiion, but since we are dealing with a probability distribution over the non-negative integers, we choose

$$\sum_{n=0}^{\infty} P_n = 1 \quad \forall t \geq 0 \tag{9}$$

The above birth-death process is called a *single-type nonlinear birth-death process*: single-type because there is only one type of individuals (we do not distinguish between, e.g., juveniles and adults), and nonlinear because the B_n and the D_n may depend on n in a nonlinear way. The latter is somewhat confusing, because equation (7) is, technically speaking, a system of *linear* differential equations (i.e., linear in the P_n) with constant (i.e., time-independent) coefficients B_n and D_n.

8.2. **Stationary distribution.** To find an equilibrium (or *stationary distribution*) of the model (if any), we set $\frac{d}{dt}P_n = 0$ for all n. Assuming that $D_n > 0$ for $n \geq 1$, this gives

$$\begin{aligned} & \tfrac{d}{dt}P_0 = D_1P_1 \implies P_1 = 0 \\ \implies & \tfrac{d}{dt}P_1 = D_2P_2 \implies P_2 = 0 \\ \implies & \tfrac{d}{dt}P_2 = D_3P_3 \implies P_3 = 0 \\ \implies & \text{etc.} \end{aligned} \tag{10}$$

So, at equilibrium, $P_n = 0$ for all $n \geq 1$, and since the P_n must sum up to one, it follows that $P_0 = 1$. In other words, there is only one equilibrium, and that is the degenerate distribution where all probability mass is concentrated at zero corresponding to the extinct population.

8.3. **Extinction probability for the linear birth-death process.** In the linear birth-death process, the birth rate and death rate are linear in n, i.e.,

$$B_n = \beta n \quad \& \quad D_n = \delta n \tag{11}$$

for given $\beta, \delta > 0$. Let $E_n := \lim_{t\to\infty} P_0(t)$ denote the probability of eventual extinction if $N(0) = n$. Then

$$\begin{cases} E_0 = 1 \\ E_n = \frac{\beta}{\beta+\delta} E_{n+1} + \frac{\delta}{\beta+\delta} E_{n-1} \quad (n \geq 1) \end{cases} \tag{12}$$

where $\beta/(\beta+\delta)$ and $\delta/(\beta+\delta)$ are, respectively, the probability that the first event is a birth event or death event. Define $\Delta E_n := E_n - E_{n-1}$. Then we have

$$\Delta E_{n+1} = \frac{\delta}{\beta} \Delta E_n \tag{13}$$

and so

$$\Delta E_n = \Delta E_1 \left(\frac{\delta}{\beta}\right)^{n-1} \tag{14}$$

and

$$\begin{aligned} E_n &= E_0 + \textstyle\sum_{i=1}^n \Delta E_i \\ &= 1 - (1 - E_1) \textstyle\sum_{i=1}^n \left(\frac{\delta}{\beta}\right)^{n-1} \end{aligned} \tag{15}$$

We distinguish two cases:

Case $0 < \beta \leq \delta$*:*

If $0 < \beta \leq \delta$, then the series $\sum_{i=1}^n \left(\frac{\delta}{\beta}\right)^{n-1}$ diverges as $n \to \infty$, and

$$E_1 \neq 1 \quad \& \quad \lim_{n\to\infty} E_n = \pm\infty \tag{16}$$

or

$$E_1 = 1 \quad \& \quad \lim_{n\to\infty} E_n = 1 \tag{17}$$

Since the E_n are probabilities, only the second option is possible, and so $E_1 = 1$. But that implies via equation (15) that $E_n = 1$ for all n. In other words, if the birth rate does not exceed the death rate, then eventual extinction is certain for all initial population sizes.

Case $0 < \delta < \beta$*:*

If $0 < \delta < \beta$, then the series $\sum_{i=1}^n \left(\frac{\delta}{\beta}\right)^{n-1}$ converges as $n \to \infty$, and

$$\lim_{n\to\infty} E_n = 1 - \frac{1 - E_1}{1 - \delta/\beta} \tag{18}$$

The only reasonable assumption is that $\lim_{n\to\infty} E_n = 0$, which implies that $E_1 = \frac{\delta}{\beta}$ and hence, via equation (15),

$$E_n = \left(\frac{\delta}{\beta}\right)^n \quad \forall n \geq 0 \tag{19}$$

In other words, extinction is possible also if the birth rate exceeds the death rate, but extinction is not certain and in fact decreases with the initial population size.

8.4. **Conditional probability distribution for the nonlinear birth-death process.** Consider the conditional probability distribution given that the population is not extinct:

$$P_n^c(t) := \frac{P_n(t)}{1 - P_0(t)} \tag{20}$$

Differentiation with respect to time and using system (7) gives

$$\frac{dP_n^c}{dt} = B_{n-1}P_{n-1}^c + D_{n+1}P_{n+1}^c - (B_n + D_n)P_n^c + D_1P_1^cP_n^c \quad (n \geq 1) \tag{21}$$

This is a non-linear system in the P_n^c, and there is no *a priori* reason why this equation should not have a (non-degenerate) equilibrium even if equation (7) has not.

To characterize the equilibrium, first write

$$\mathbf{P}^c := \begin{pmatrix} P_1^c \\ P_2^c \\ P_3^c \\ \vdots \end{pmatrix} \tag{22}$$

and

$$\mathbf{A} := \begin{pmatrix} -B_1 - D_1 & D_2 & 0 & \dots \\ B_1 & -B_2 - D_2 & D_3 & \dots \\ 0 & B_2 & -B_3 - D_3 & \dots \\ 0 & 0 & B_3 & \dots \\ \dots & \dots & \dots & \dots \end{pmatrix} \tag{23}$$

and so system (21) becomes

$$\frac{d}{dt}\mathbf{P}^c = \big(\mathbf{A} + D_1P_1^c\mathbf{I}\big)\mathbf{P}^c \tag{24}$$

where $\mathbf{I}$ is the identity matrix. The equilibrium equation then is

$$0 = \big(\mathbf{A} + D_1P_1^c\mathbf{I}\big)\mathbf{P}^c \tag{25}$$

i.e, the equilibrium (or *quasi-stationary distribution*) is a normalized eigenvector of the matrix $\mathbf{A}$ with corresponding eigenvalue $D_1 P_1^c$.

If $\text{Prob}\{N(t) \leq N_0\} = 1$ for all t and given N_0, then $\mathbf{A}$ can be truncated by deleting all rows and columns corresponding to population sizes $n > N_0$ (which cannot be reached anyway) and so becomes finite-dimensional. If this truncated matrix $\mathbf{A}$ is moreover *irreducible*, then the theorem of Perron-Frobenius (see Appendix) tells us that the quasi-stationary distribution $\mathbf{P}^c$ is the positive eigenvector corresponding to the single eigenvalue with the greatest real part (the so-called *dominant eigenvalue of* $\mathbf{A}$. Moreover, the quasi-stationary distribution is stable. For the case where $\mathbf{A}$ cannot be truncated, similar results hold (search for "Yaglom limits").

8.5. **Extinction in the nonlinear birth-death process.** Suppose $(P_1^c, P_2^c, \dots)$ is a quasi-stationary distribution, and suppose we use this distribution as the initial distribution in system (7) for the unconditional distribution. That is, we take $P_0(0) = 0$ and $P_n(0) = P_n^c$ for all $n \geq 1$. Under these assumptions we can calculate the probability of extinction and the expected time till extinction for the nonlinear birth-death process.

Concerning the probability of eventual extinction, from equation (7) we have

$$\frac{dP_0(t)}{dt} = D_1 P_1(t) \tag{26}$$

Since, by assumption, we start at the quasi-stationary distribution, we have

$$P_1^c = P_1^c(t) := \frac{P_1(t)}{1 - P_0(t)} \quad \forall t \tag{27}$$

from which we find

$$P_1(t) = P_1^c\big(1 - P_0(t)\big) \quad \forall t \tag{28}$$

Substitution of this into equation (26) gives

$$\frac{dP_0(t)}{dt} = D_1 P_1^c\big(1 - P_0(t)\big) \tag{29}$$

which can be solved explicitly:

$$P_0(t) = 1 - e^{-t\, D_1 P_1^c} \tag{30}$$

where we used that, by assumption, $P_0(0) = 0$. So, for the probability of eventual extinction we find

$$\lim_{t\to\infty} P_0(t) = 1 \tag{31}$$

In other words, extinction is certain.

Concerning the time till extinction, note that $P_0(t)$ is the probability that the population is extinct at time t, which is the same as the probability that the population went extinct at some time less than or equal to t. So, if $p(t)$ denotes the probability density of the exact time of extinction, then

$$p(t) = \frac{dP_0(t)}{dt} \tag{32}$$

Since $P_0(t)$ we have already calculated above, we find

$$p(t) = D_1 P_1^c e^{-t/,D_1 P_1^c} \tag{33}$$

which is the probability density of the exponential distribution with expected value

$$\mathcal{E}\{t\} = \left(D_1 P_1^c\right)^{-1} \tag{34}$$

So, if we start at the quasi-stationary distribution $P_n(0) = P_n^c$ for $n \geq 1$, then eventually extinction is certain, and the time till extinction is exponentially distributed, and the expected time till extinction is equal to $(D_1 P_1^c)^{-1}$.

8.6. **Example.** Consider the nonlinear birth-death process in a system with a total number K individual living sites. Then the population size is at most K when all sites are occupied. The matrix $\mathbf{A}$ in section 8.4 thus is finite-dimensional. Suppose further that the colonization of empty sites follows the law of mass-action, while the *per capita* death rate is a constant. This gives

$$B_n = \beta n(K-n) \quad \& \quad D_n = \delta n \tag{35}$$

for some positive constants α and β. In the following figure, the quasi-stationary distribution $(P_1^c, \dots, P_K^c)$ was calculated as the normalized eigenvector corresponding to the dominant eigenvalue of the matrix $\mathbf{A}$ and the expected time till extinction was calculated as $(\delta P_1^c)^{-1}$.

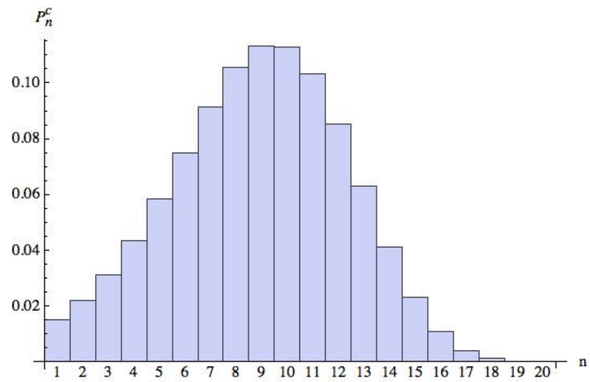

FIGURE 1. The quasi-stationary distribution for $\beta = 0.1$ and $\delta = 1$ per unit of time and $K = 20$The corresponding expected time till extinction is 66 time units.

8.7. **Another example.** Consider the nonlinear birth-death process in a system with

$$B_n = \frac{\beta n^2}{(\gamma+n)^2} \quad \& \quad D_n = \delta n \tag{36}$$

This system has an *Allee threshold*, which means that the process is subcritical for small population sizes (i.e., $B_n < D_n$) and supercritical for intermediate population sizes (i.e., $B_n > D_n$). A mechanistic underpinning of the model is given in a later section. The matrix $\mathbf{A}$ is essentially infinite-dimensional. However, since for large population sizes the process is subcritical again, for numerical purposesthe matrix can be truncated at some level beyond which the population is unlikely to grow. In the following figure, the quasi-stationary distribution $(P_1^c, P_2^c, \dots)$ was calculated as the normalized eigenvector corresponding to the dominant eigenvalue of the (truncated) matrix $\mathbf{A}$ and the expected time till extinction was calculated as $(\delta P_1^c)^{-1}$.

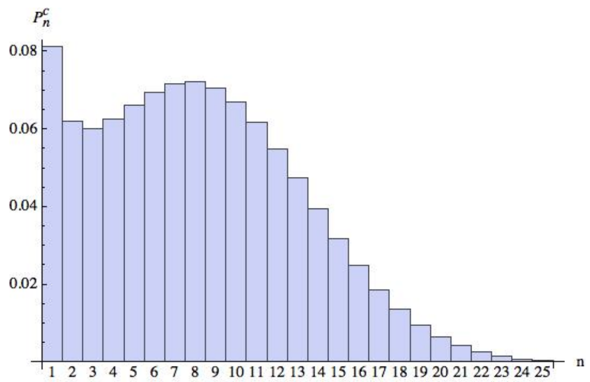

FIGURE 2. The quasi-stationary distribution for $\beta = 22$ and $\gamma = 5$ and $\delta = 1$. The Allee threshold is between $n = 2$ and $n = 3$. Also for $n \geq 10$ the process becomes subcritical. The matrix $\mathbf{A}$ was truncated at $n = 25$. The expected time till extinction is 10 time units.