

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 because of at least two reasons: firstly, the population size counted as the number of individuals present (rather than as population density) changes in discrete steps, and secondly, because of demographic stochasticity, i.e., chance fluctuations 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 fluctuations are averaged out by the statistical Law of the Large Numbers, but 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

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

Suppose that given a population size n , birth and death are independent Poisson processes with respective rates B_n and D_n and with $B_n = D_n = 0$ for $n \leq 0$. The probability of having i births and j deaths in a time interval of length Δt in a population of size n then is

$$(2) \quad \frac{(B_n \Delta t)^i e^{-B_n \Delta t}}{i!} \cdot \frac{(D_n \Delta t)^j e^{-D_n \Delta t}}{j!}$$

i.e., the product of two Poisson distributions. (One might wonder how the population size can stay fixed 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 (2) we find that for small Δt

$$(3) \quad \begin{cases} \text{Prob}\{\text{one birth \& no deaths}\} & = B_n \Delta t + O(\Delta t)^2 \\ \text{Prob}\{\text{no births \& one death}\} & = D_n \Delta t + O(\Delta t)^2 \\ \text{Prob}\{\text{no births \& no deaths}\} & = 1 - B_n \Delta t - D_n \Delta t + O(\Delta t)^2 \\ \text{Prob}\{\text{anything else}\} & = O(\Delta t)^2 \end{cases}$$

From this it follows that

$$(4) \quad P_n(t + \Delta t) = (B_{n-1} \Delta t) P_{n-1}(t) + (D_{n+1} \Delta t) P_{n+1}(t) + (1 - B_n \Delta t - D_n \Delta t) P_n(t) + O(\Delta t)^2$$

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

$$(5) \quad \frac{P_n(t + \Delta t) - P_n(t)}{\Delta t} = B_{n-1} P_{n-1}(t) + D_{n+1} P_{n+1}(t) - (B_n + D_n) P_n(t) + O(\Delta t)$$

which, as we let $\Delta t \rightarrow 0$, becomes the ordinary differential equation

$$(6) \quad \frac{dP_n}{dt} = B_{n-1} P_{n-1} + D_{n+1} P_{n+1} - (B_n + D_n) P_n$$

where $B_n = D_n = 0$ for $n \leq 0$. One readily checks that

$$(7) \quad \sum_{n=0}^{\infty} \frac{dP_n}{dt} = 0 \quad \forall t \geq 0$$

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

$$(8) \quad \sum_{n=0}^{\infty} P_n = 1 \quad \forall t \geq 0$$

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 (6) 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 . Then, with $D_n > 0$ for $n \geq 1$,

$$\begin{aligned}
 \frac{d}{dt}P_0 &= D_1P_1 \implies P_1 = 0 \\
 \implies \frac{d}{dt}P_1 &= D_2P_2 \implies P_2 = 0 \\
 \implies \frac{d}{dt}P_2 &= D_3P_3 \implies P_3 = 0 \\
 &\implies \text{etc.}
 \end{aligned}
 \tag{9}$$

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. The linear birth-death process. In the linear birth-death process the birth and death rates are linear in n , i.e.,

$$B_n = \beta n \quad \& \quad D_n = \delta n \tag{10}$$

where $\beta, \delta > 0$ are the *per capita* birth and death rates. Let μ_i denote the i^{th} moment of the population size distribution, i.e.,

$$\mu_i(t) = \sum_{n=0}^{\infty} n^i P_n(t) \tag{11}$$

For the first moment it follows from equation (6) that

$$\frac{d\mu_1(t)}{dt} = (\beta - \delta)\mu_1(t) \tag{12}$$

and so

$$\mu_1(t) = \mu_1(0)e^{t(\beta - \delta)} \tag{13}$$

Likewise, for the second moment we get

$$\frac{d\mu_2(t)}{dt} = 2(\beta - \delta)\mu_2(t) + (\beta + \delta)\mu_1(t) \tag{14}$$

and so

$$\mu_2(t) = \mu_2(0)e^{2t(\beta - \delta)} + \mu_1(0)e^{t(\beta - \delta)} \left(e^{t(\beta - \delta)} - 1 \right) \frac{\beta + \delta}{\beta - \delta} \tag{15}$$

For the population variance $\sigma^2(t) = \mu_2(t) - \mu_1(t)^2$ we thus have

$$\sigma^2(t) = \sigma^2(0)e^{2t(\beta - \delta)} + \mu_1(0)e^{t(\beta - \delta)} \left(e^{t(\beta - \delta)} - 1 \right) \frac{\beta + \delta}{\beta - \delta} \tag{16}$$

whenever $\beta \neq \delta$. The case $\beta = \delta$ is left as an exercise.

Suppose that $\beta < \delta$. Then $\mu_1(t) \rightarrow 0$ and $\sigma^2(t) \rightarrow 0$ as $t \rightarrow \infty$. This is consistent with our finding in the previous section that there does not exist a positive equilibrium distribution, and we expect the population do die out. Next, suppose that $\beta > \delta$. Then $\mu_1(t) \rightarrow \infty$ and $\sigma^2(t) \rightarrow \infty$ as $t \rightarrow \infty$. On first sight, this may seem to contradict

our finding in the previous section, however, as we shall see in the next section, what happens is that with a given non-zero probability the population escapes to infinity, i.e., grows without bounds.

8.4. 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.,

$$(17) \quad B_n = \beta n \quad \& \quad D_n = \delta n$$

for given $\beta, \delta > 0$. Let $E_n := \lim_{t \rightarrow \infty} P_0(t)$ denote the *probability of eventual extinction* for a population of initial size $n \geq 0$. Then

$$(18) \quad \begin{cases} E_0 = 1 \\ E_n = \frac{\beta}{\beta + \delta} E_{n+1} + \frac{\delta}{\beta + \delta} E_{n-1} \quad (n \geq 1) \end{cases}$$

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

$$(19) \quad \Delta E_{n+1} = \frac{\delta}{\beta} \Delta E_n$$

and so

$$(20) \quad \Delta E_n = \Delta E_1 \left(\frac{\delta}{\beta} \right)^{n-1}$$

and

$$(21) \quad \begin{aligned} E_n &= E_0 + \sum_{i=1}^n \Delta E_i \\ &= 1 - (1 - E_1) \sum_{i=1}^n \left(\frac{\delta}{\beta} \right)^{i-1} \end{aligned}$$

The sub-critical case:

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

$$(22) \quad E_1 \neq 1 \quad \& \quad \lim_{n \rightarrow \infty} E_n = \pm \infty$$

or

$$(23) \quad E_1 = 1 \quad \& \quad \lim_{n \rightarrow \infty} E_n = 1$$

Since the E_n are probabilities, only the second option is possible, and so $E_1 = 1$. But that implies via equation (21) 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.

The super-critical case:

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

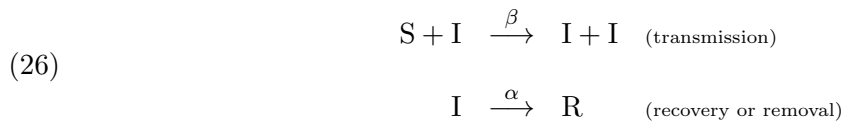
$$(24) \quad \lim_{n \rightarrow \infty} E_n = 1 - \frac{1 - E_1}{1 - \delta/\beta}$$

The only reasonable assumption is that $\lim_{n \rightarrow \infty} E_n = 0$, which implies that $E_1 = \frac{\delta}{\beta}$ and hence, via equation (21),

$$(25) \quad E_n = \left(\frac{\delta}{\beta}\right)^n \quad \forall n \geq 0$$

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

8.5. Example. Consider the SIR model, which involves the following individual-level processes:



where “S” denotes an uninfected but susceptible individual, “I” an infected individual, and “R” an individual that has recovered from the infection and has become immune. Assuming mass-action (see Section 1.5), the corresponding differential equations for the population densities are

$$(27) \quad \begin{cases} \frac{d}{dt}S = -\beta SI & \text{(susceptible)} \\ \frac{d}{dt}I = +\beta SI - \alpha I & \text{(infected)} \end{cases}$$

The recovered individuals (R) do not have an active role, and so their differential equation is left out. The dynamics of the model is given by the following figure.

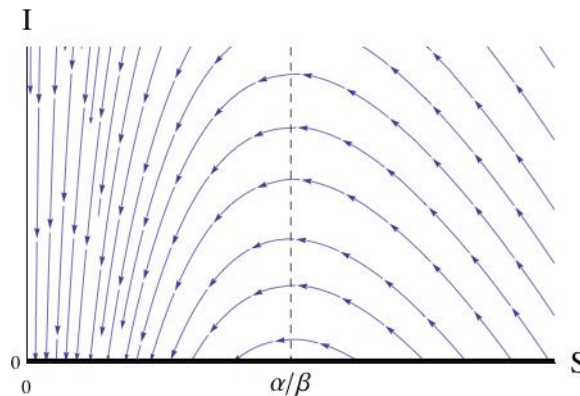


FIGURE 1. Phase-plane analysis of the SIR model.

What happens if we introduce the infection in an initially infection-free population? It all depends on the population density S_0 of the infection-free state. All points on the horizontal axis in the above figure are equilibria, but only points left of α/β are stable, while points right of α/β are unstable. In other words, the infection can spread (i.e., becomes an epidemic) if $S_0 > \alpha/\beta$. Moreover, it can be seen from the figure that the

size of the epidemic (i.e., the proportion of individuals that eventually have got the infection) increases with S_0 . If $S_0 \leq \alpha/\beta$, however, the infection cannot spread and dies out without doing much harm.

This is what the deterministic SIR model tells us. But the picture is incomplete. In particular, the model does not capture the possibility that even if $S_0 > \alpha/\beta$, the infection may nevertheless die out due to random demographic fluctuations during the initial phase when there are still only a few infected individuals around. To calculate the probability of an epidemic, we model the initial phase of a potential epidemic as a stochastic birth-death process.

To this end, let $i \in \{0, 1, 2, \dots\}$ denote the *number* of infected individuals. While i is small compared to the total size of the population, changes in i will have a negligible effect on the *population density* S_0 of uninfected individuals, which therefore will be assumed constant. The rate at which new individuals enter the I-state (i.e., the “birth” rate of infected individuals) then is $\beta S_0 i$, and the rate at which individuals leave the I-state (i.e., the “death” rate of infected individuals) is αi . For the initial phase of a potential epidemic we thus have a *linear* birth-death process with birth and death rates

$$(28) \quad B_i = \beta S_0 i \quad \& \quad D_i = \alpha i$$

The probability of an epidemic given the initial number of i_0 infected individuals is equal to one minus the probability of extinction. The probability of extinction was calculated in the previous section for the sub-critical case and for the super-critical case. From this we find

$$(29) \quad \text{Prob}\{\text{epidemic}\} = \begin{cases} 0 & \text{if } S_0 \leq \frac{\alpha}{\beta} \\ 1 - \left(\frac{\alpha}{\beta S_0}\right)^{i_0} & \text{if } S_0 > \frac{\alpha}{\beta} \end{cases}$$

We can express these probabilities also in terms of the *basic reproductive number* (R_0), which is defined as the expected number of secondary cases (of the infection) produced by each primary case. The R_0 plays an important role in epidemiology and has been measured for many diseases. We can calculate the R_0 for the SIR model as follows: the expected time an individual is ill is α^{-1} ; while ill, the rate of infecting others is βS_0 ; the expected number of secondary cases infected by our focal individual therefore is $\beta S_0 / \alpha$. In terms of the R_0 we thus have

$$(30) \quad \text{Prob}\{\text{epidemic}\} = \begin{cases} 0 & \text{if } R_0 \leq 1 \\ 1 - R_0^{-i_0} & \text{if } R_0 > 1 \end{cases}$$

For example, Wikipedia gives for measles an estimate $12 \leq R_0 \leq 18$ (depending on population density, social contact rates etc.). This corresponds to a probability of 92–94% that a single infected individual causes an epidemic of measles. For SARS and for HIV/AIDS, Wikipedia gives an estimate $2 \leq R_0 \leq 5$, corresponding to a probability of 50–80% of an outbreak caused by just a single primary case.

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

$$(31) \quad P_n^c(t) := \frac{P_n(t)}{1 - P_0(t)}$$

Differentiation with respect to time and using system (6) gives

$$(32) \quad \frac{dP_n^c}{dt} = B_{n-1}P_{n-1}^c + D_{n+1}P_{n+1}^c - (B_n + D_n)P_n^c + D_1P_1^cP_n^c \quad (n \geq 1)$$

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 (6) has not.

To characterize the equilibrium, first write

$$(33) \quad \mathbf{P}^c := \begin{pmatrix} P_1^c \\ P_2^c \\ P_3^c \\ \vdots \end{pmatrix}$$

and

$$(34) \quad \mathbf{A} := \begin{pmatrix} -B_1 - D_1 & D_2 & 0 & \dots \\ B_1 & -B_2 - D_2 & D_3 & \dots \\ 0 & B_2 & -B_3 - D_3 & \dots \\ 0 & 0 & B_3 & \dots \\ \dots & \dots & \dots & \dots \end{pmatrix}$$

and so system (32) becomes

$$(35) \quad \frac{d}{dt}\mathbf{P}^c = (\mathbf{A} + D_1P_1^c\mathbf{I})\mathbf{P}^c$$

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

$$(36) \quad 0 = (\mathbf{A} + D_1P_1^c\mathbf{I})\mathbf{P}^c$$

i.e., the equilibrium (or *quasi-stationary distribution*) is a normalized eigenvector of the matrix \mathbf{A} with corresponding eigenvalue $D_1P_1^c$.

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" in, e.g., Wikipedia).

8.7. 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 (6) 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 (6) we have

$$(37) \quad \frac{dP_0(t)}{dt} = D_1 P_1(t)$$

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

$$(38) \quad P_1^c = \frac{P_1(t)}{1 - P_0(t)} \quad \forall t$$

from which we find

$$(39) \quad P_1(t) = P_1^c (1 - P_0(t)) \quad \forall t$$

Substitution of this into equation (37) gives

$$(40) \quad \frac{dP_0(t)}{dt} = D_1 P_1^c (1 - P_0(t))$$

which can be solved explicitly:

$$(41) \quad P_0(t) = 1 - e^{-t D_1 P_1^c}$$

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

$$(42) \quad \lim_{t \rightarrow \infty} P_0(t) = 1$$

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

$$(43) \quad p(t) = \frac{dP_0(t)}{dt}$$

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

$$(44) \quad p(t) = D_1 P_1^c e^{-t/D_1 P_1^c}$$

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

$$(45) \quad \mathcal{E}\{t\} = (D_1 P_1^c)^{-1}$$

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 $(D_1 P_1^c)^{-1}$.

8.8. Example. The quasi-stationary distribution of the *subcritical linear birth-death process* with $B_n = \beta n$ and $D_n = \delta n$ for $0 < \beta < \delta$ is

$$(46) \quad P_n^c = \left(\frac{\beta}{\delta}\right)^{n-1} - \left(\frac{\beta}{\delta}\right)^n$$

for $n = 1, 2, \dots$, as is readily verified by substitution into (32). The expected time till extinction starting from the quasi-stationary distribution thus is $(\delta - \beta)^{-1}$ with variance $(\delta - \beta)^{-2}$. The *super-critical* and the *critical* cases do not have a quasi-stationary distribution.

8.9. Another 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

$$(47) \quad B_n = \beta n(K - n) \quad \& \quad D_n = \delta n$$

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 $(\delta P_1^c)^{-1}$ time units (see last line of previous section). The expected life time of an individual is δ^{-1} time units, and so the expected time till population extinction expressed in units of expected individual life times becomes $1/P_1^c$.

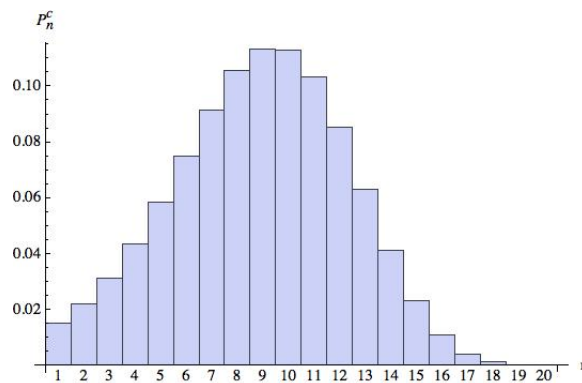


FIGURE 2. The quasi-stationary distribution for $\beta = 0.1$, $\delta = 1$ and $K = 20$. The corresponding expected time till extinction is 66 times the expected life time of an individual.

Note that we can interpret equation (47) as the SIS-model where K is the (constant) total population size, n the number of infected individuals and $K - n$ the number of susceptibles. Then β is the transmission rate and δ the recovery rate. The expected length that an individual stays ill then is δ^{-1} .

8.10. **Last example.** Consider the nonlinear birth-death process in a system with

$$(48) \quad B_n = \frac{\beta n^2}{(\gamma + n)^2} \quad \& \quad D_n = \delta n$$

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 purposes, the 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 $(\delta P_1^c)^{-1}$.

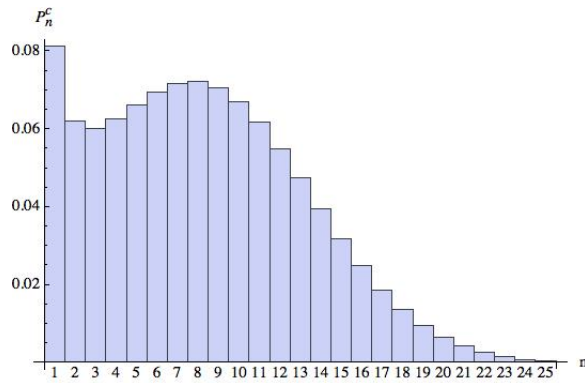


FIGURE 3. The quasi-stationary distribution for $\beta = 22$ and $\gamma = 5$ and $\delta = 1$. The Allee threshold is between $n = 2$ and $n = 3$. Also for $n \geq 10$ the process becomes subcritical. The matrix \mathbf{A} was truncated at $n = 25$. The expected time till extinction is 10 time units.