

POPULATION DYNAMICS

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1. THE BIRTH-DEATH PROCESS

Let $N(t) \in \mathbb{N}_0$ denote the population size, i.e., the *number* of individuals present at time $t \in \mathbb{R}_+$. Given $N(t) = n$, assume that birth and death are independent Poisson processes with rates B_n and D_n respectively. This means that in a population of fixed size n the probability of having i birth events and j death events during a time period of length Δt is

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

for $i, j = 0, 1, 2, \dots$ (N.B. births and deaths would change the population size, and so to keep it fixed in this thought experiment, every newborn is immediately removed and every dead individual is immediately replaced.) From the above it follows that during a time period of length Δt

$$\begin{aligned} \text{Prob}\{1 \text{ births \& } 0 \text{ deaths}\} &= B_n \Delta t + O(\Delta t)^2 \\ \text{Prob}\{0 \text{ births \& } 1 \text{ deaths}\} &= D_n \Delta t + O(\Delta t)^2 \\ \text{Prob}\{0 \text{ births \& } 0 \text{ deaths}\} &= 1 - (B_n + D_n) \Delta t + O(\Delta t)^2 \\ \text{Prob}\{\text{anything else}\} &= O(\Delta t)^2 \end{aligned}$$

as $\Delta t \downarrow 0$. Hence,

$$\begin{aligned} \text{Prob}\{N(t + \Delta t) = N(t) + 1\} &= B_n \Delta t + O(\Delta t)^2 \\ \text{Prob}\{N(t + \Delta t) = N(t) - 1\} &= D_n \Delta t + O(\Delta t)^2 \\ \text{Prob}\{N(t + \Delta t) = N(t)\} &= 1 - (B_n + D_n) \Delta t + O(\Delta t)^2 \end{aligned}$$

while larger jumps in population size are $O(\Delta t)^2$. Let

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

denote the probability that the population at time t has size $n \geq 0$. Then, from the above,

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

or equivalently,

$$\begin{aligned} \frac{P_n(t + \Delta t) - P_n(t)}{\Delta t} &= B_{n-1} P_{n-1}(t) + D_{n+1} P_{n+1}(t) \\ &- (B_n + D_n) P_n(t) + O(\Delta t). \end{aligned}$$

Letting $\Delta t \downarrow 0$ we get

$$(1) \quad \dot{P}_n = B_{n-1}P_{n-1} + D_{n+1}P_{n+1} - (B_n + D_n)P_n$$

for $n \geq 0$. For biological consistency we assume that B_{-1} , B_0 and D_0 are all zero. (Why?)

The system (1) of differential equations describes the evolution of the probability distribution of the population size. One readily checks that

$$\frac{d}{dt} \sum_{n=0}^{\infty} P_n(t) = 0$$

and so the simplex $\sum_{n=0}^{\infty} P_n(t) = 1$ is invariant indeed. (Exercise!)

2. POPULATION EXTINCTION

Setting $\dot{P}_n = 0$ in (1) and solving for the P_n , we find that $P_0 = 1$ and $P_n = 0$ for all $n \geq 1$. In other words, the extinct population is the only equilibrium. In fact, if $D_n > 0$ for all $n \geq 1$ and $D_n > B_n$ for large values of n , then eventual extinction of the population is certain no matter what is the initial condition.

To be able to say something about the expected time till extinction, we introduce the *conditional probability distribution* for non-extinct populations

$$P_n^c(t) := \text{Prob}\{N(t) = n \mid N(t) \geq 1\}$$

to denote the probability that at time t the population size is $n \geq 1$ conditioned on the event that the population is not extinct, i.e., that $N(t) \geq 1$. Since

$$P_n^c(t) = \frac{P_n(t)}{1 - P_0(t)},$$

it readily follows from (1) that

$$(2) \quad \dot{P}_n^c = B_{n-1}P_{n-1}^c + D_{n+1}P_{n+1}^c - (B_n + D_n)P_n^c + D_1P_1^cP_n^c$$

for $n \geq 1$. (Exercise.) In fact, there is no reason why the system (2) would not have an equilibrium. So, let us suppose it has and denote this equilibrium by \hat{P}_n^c ($n \geq 1$).

What has this to do with the expected time till extinction? Since $B_0 = 0$, the probability that the population goes extinct at or before time t is equal to $P_0(t)$. In other words, $P_0(t)$ is the (cumulative) distribution function of the time of extinction, and so its derivative $\dot{P}_0(t)$ is the probability density of extinction times. From (1) and the definition of $P_n^c(t)$ we have

$$\dot{P}_0(t) = D_1P_1(t) = D_1P_1^c(t)(1 - P_0(t)).$$

Given the initial condition $P_0(0) = 0$ and $P_n(0) = \hat{P}_n^c$ for all $n \geq 1$, we have that $P_1^c(t) = \hat{P}_1^c$ for all t . Solving the above equation we get

$$(3) \quad P_0(t) = 1 - e^{-tD_1\hat{P}_1^c},$$

which is the (cumulative) distribution function of the exponential distribution. In other words, a population starting with the conditional distribution \hat{P}_n^c ($n \geq 1$) has an exponentially distributed extinction time with expectation $(D_1\hat{P}_1^c)^{-1}$ and variance $(D_1\hat{P}_1^c)^{-2}$.

What about the extinction time for a population with arbitrary initial condition? How good (3) is an approximation then depends on how fast the conditional distribution P_n^c converges to its equilibrium. We shall not go into this now.

3. DIFFUSION APPROXIMATION

We now investigate under what conditions we can provide a Fokker-Planck approximation of the system (1). To this end, define the *probability flux* as

$$(4) \quad J_N(t) := B_N P_N(t) - D_{N+1} P_{N+1}(t).$$

Then, from (1),

$$(5) \quad \frac{d}{dt} \sum_{n=0}^N P_n(t) = -J_N(t).$$

Let $\Delta x > 0$ be a dimensionless scaling parameter, and let $p \in C^2(\mathbb{R}_+^2)$ be such that

$$\Delta x p(x, t) = P_N(t),$$

whenever $x = N\Delta x$. Suppose further that there exists $\mu, \sigma \in C^2(\mathbb{R}_+)$ with

$$(6) \quad \begin{aligned} \Delta x (B_N - D_N) &\rightarrow \mu(x) \\ \Delta x^2 (B_N + D_N) &\rightarrow \sigma^2(x) \end{aligned}$$

as $\Delta x \rightarrow 0$ and $N \rightarrow \infty$ such that $x = N\Delta x > 0$ remains constant. From (4) and (6) we have

$$\begin{aligned} J_N &= \frac{\Delta x (B_N - D_N) p(x, t) + \Delta x (B_{N+1} - D_{N+1}) p(x + \Delta x, t)}{2} \\ &\quad - \frac{\Delta x^2 (B_{N+1} + D_{N+1}) p(x + \Delta x, t) + \Delta x^2 (B_N + D_N) p(x, t)}{2\Delta x} \\ &\rightarrow \mu(x) p(x, t) - \partial_x (\sigma^2(x) p(x, t)) \end{aligned}$$

and

$$\frac{d}{dt} \sum_{n=0}^N P_n(t) \rightarrow \frac{d}{dt} \int_0^x p(\xi, t) d\xi$$

as $\Delta x \rightarrow 0$, and hence from (5)

$$\frac{d}{dt} \int_0^x p(\xi, t) d\xi = -\mu(x)p(x, t) + \frac{1}{2} \partial_x (\sigma^2(x)p(x, t)).$$

Differentiation with respect to x gives the Fokker-Planck equation

$$(7) \quad \partial_t p = -\partial_x (\mu(x)p(x, t)) + \frac{1}{2} \partial_x^2 (\sigma^2(x)p(x, t))$$

with corresponding Ito stochastic differential equation

$$(8) \quad dx = \mu(x)dt + \sigma(x)d\omega$$

where $\sigma(x) := \sqrt{\sigma^2(x)}$. These limits hold at least point-wise, i.e., for fixed x .

3.1. Example. The model in this example is called the "SIS-model" or "Levin's metapopulation model", depending on the interpretation of the parameters. In either case

$$(9) \quad B_N = \beta N(N_{\max} - N) \quad \& \quad D_N = \delta N$$

for $0 \leq N \leq N_{\max}$. (As the SIS-model, N is the number of infected individuals and $N_{\max} - N$ the number of susceptible individuals, and B_N is the rate of new infections, while D_N is the rate at which infected individuals recover and become susceptible again. The total population of infected plus susceptibles is a constant N_{\max} . As Levin's metapopulation model, N is the number of occupied patches, $N_{\max} - N$ the number of unoccupied patches, N_{\max} the total number of patches occupied or not, and B_N is the colonization rate of unoccupied patches, while D_N is the extinction rate of local populations.)

Rewriting the birth and death rates using $x = N\Delta x$ and $x_{\max} = N_{\max}\Delta x$ gives

$$B_N = \frac{\beta x(x_{\max} - x)}{\Delta x^2} \quad \& \quad D_N = \frac{\delta x}{\Delta x}.$$

If β , δ and x_{\max} are fixed, then $\Delta x(B_N - D_N) \rightarrow \infty$ as $\Delta x \rightarrow 0$. Obviously, we have to somehow scale β , δ and x_{\max} with Δx to keep $\mu(x)$ finite. To this end, expand β , δ and x_{\max} as (possibly truncated) Laurent series of powers of Δx :

$$\begin{aligned} \beta &= \beta_0 + \beta_1 \Delta x + \beta_2 \Delta x^2 + \dots \\ \delta &= \delta_0 \Delta x^{-1} + \delta_1 + \delta_2 \Delta x + \dots \\ x_{\max} &= x_0 \Delta x^{-1} + x_1 + x_2 \Delta x + \dots \end{aligned}$$

Then

$$\begin{aligned} \Delta x(B_N - D_N) &= xx_0\beta_0\Delta x^{-2} \\ &\quad - (x^2\beta_0 - xx_1\beta_0 - xx_0\beta_1 + x\delta_0)\Delta x^{-1} \\ &\quad - (x^2\beta_1 - xx_1\beta_1 + x\delta_1) + \dots, \\ (\Delta x)^2(B_N + D_N) &= xx_0\beta_0\Delta x^{-1} \\ &\quad - (x^2\beta_0 - xx_1\beta_0 - xx_0\beta_1 - x\delta_0) \\ &\quad - (x^2\beta_1 - xx_1\beta_1 - x\delta_1)\Delta x + \dots \end{aligned}$$

To keep limits finite as $\Delta x \downarrow 0$, necessarily $\beta_0 = 0$ and $x_0\beta_1 = \delta_0$. Consequently,

$$(10) \quad \begin{aligned} \beta &= \beta_1\Delta x + \mathcal{O}(\Delta x^2) \\ \delta &= x_0\beta_1\Delta x^{-1} + \delta_1 + \mathcal{O}(\Delta x) \\ x_{\max} &= x_0\Delta x^{-1} + x_1 + \mathcal{O}(\Delta x) \end{aligned}$$

and

$$\begin{aligned} \mu(x) &= \beta_1x(x_1 - x) - \delta_1x \\ \sigma^2(x) &= 2x_0\beta_1x. \end{aligned}$$

Conditions (10) ensure that (1) has a Fokker-Planck limit (7) (and corresponding SDE-limit (8)) with μ and σ^2 as given in the above equations.

3.2. Example. The model in this example is a simple mass-action model: new individuals are born at a constant *per capita* rate, and individuals die at a constant *per capita* rate or because of interaction with other individuals, leading to a quadratic term in the death rate:

$$(11) \quad B_N = \beta N \quad \& \quad D_N = \delta N + \gamma N^2.$$

Rewriting the birth and death rates using $x = N\Delta x$ and $x_{\max} = N_{\max}\Delta x$ gives

$$B_N = \frac{\beta x}{\Delta x} \quad \& \quad D_N = \frac{\delta x}{\Delta x} + \frac{\gamma x^2}{\Delta x^2}.$$

Expand β , δ and γ as a Laurent series of powers of Δx :

$$\begin{aligned} \beta &= \cdots + \beta_{-1}\Delta x^{-1} + \beta_0 + \beta_1\Delta x + \beta_2\Delta x^2 + \dots \\ \gamma &= \cdots + \gamma_{-1}\Delta x^{-1} + \gamma_0 + \gamma_1\Delta x + \gamma_2\Delta x^2 + \dots \\ \delta &= \cdots + \delta_{-1}\Delta x^{-1} + \delta_0 + \delta_1\Delta x + \delta_2\Delta x^2 + \dots \end{aligned}$$

Then, to keep $\Delta x(B_N - D_N)$ and $\Delta x^2(B_N + D_N)$ finite as $\Delta x \rightarrow 0$, necessarily

$$\beta_i = 0 \quad \forall i \leq -2 \quad \& \quad \gamma_i = 0 \quad \forall i \leq 0 \quad \& \quad \delta_i = \beta_i \quad \forall i \leq -1,$$

so that

$$\begin{aligned} \beta &= \beta_{-1}/\Delta x + \beta_0 + \mathcal{O}(\Delta x), \\ \gamma &= \gamma_1\Delta x + \mathcal{O}(\Delta x)^2, \\ \delta &= \delta_0 + \mathcal{O}(\Delta x). \end{aligned}$$

Under these conditions, and only under these conditions does there exist a Fokker-Plank limit of the birth-death process defined by (11). The corresponding drift term and diffusion coefficient are

$$\begin{aligned} \mu(x) &= \beta_0x - \delta_0x - \gamma_1x^2 \\ \sigma^2(x) &= 2\beta_{-1}x. \end{aligned}$$