STOCHASTIC POPULATION MODELS (SPRING 2011)

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9. Fokker-Planck approximation for semi-large systems

9.1. **System size.** Consider the birth-death process with birth and death rates B_n and D_n and probability distribution P_n satisfying

$$\frac{dP_n}{dt} = B_{n-1}P_{n-1} + D_{n+1}P_{n+1} - (B_n + D_n)P_n \quad \forall n \geq 0 \tag{1}$$

We introduce the notion of *system size* as the total area or volume in which the population lives. Given system size Ω and population size n, the population density is n/Ω. The objective is to re-write system (1) in terms of population density and see what is the effect of increasing the system size. To this end we make the following change of variables:

$$\varepsilon = \Omega^{-1} \tag{2}$$
$$x = \varepsilon n \tag{3}$$
$$\varepsilon p(t,x) = P_n(t) \tag{4}$$
$$b(x)/x = B_n/n \tag{5}$$
$$d(x)/x = D_n/n \tag{6}$$

(Note, that $b(x)/x$ and $d(x)/x$ are the *per capita* birth and death rates as functions of population density rather than population number. These are more natural objects than the B_n and the D_n in the sense that if we derive a population model using the law of mass-action, then we directly get expressions for $b(x)/x$ and $d(x)/x$. As a second step, these can be translated into the B_n and the D_n as $B_n = b(\varepsilon n)/\varepsilon$ and $D_n = d(\varepsilon n)/\varepsilon$. Also note that system size has no effect on the linear birth-death process.)

Re-writing system (1) in terms of the new variables we get

$$\varepsilon\frac{\partial p(t,x)}{\partial t} = b(x-\varepsilon)p(t,x-\varepsilon) + d(x+\varepsilon)p(t,x+\varepsilon) - \big(b(x)+d(x)\big)p(t,x) \tag{7}$$

Taylor-expansion for small ε gives

$$\frac{\partial p}{\partial t} = -\frac{\partial (b-d)p}{\partial x} + \frac{1}{2}\varepsilon\frac{\partial^2 (b+d)p}{\partial x^2} + \mathrm{O}(\varepsilon^2) \tag{8}$$

Letting $\varepsilon \to 0$ this converges point-wise for each fixed x to

$$\frac{\partial p}{\partial t} = -\frac{\partial (b-d)p}{\partial x} \tag{9}$$

which is known as the *transport equation* corresponding to the deterministic population model

$$\frac{dx}{dt} = b(x) - d(x) \tag{10}$$

In other words, if we increase the system size (i.e., the area or volume in which the population lives) while keeping the population density constant, we lose the demographic stochasticity and eventually are left with a pure deterministic population model.

9.2. **Semi-large systems.** Instead of taking the limit $\varepsilon \to 0$ in equation (8) we can simply take any small $\varepsilon > 0$ and ignore the $\mathrm{O}(\varepsilon^2)$ terms. This gives us the *Fokker-Planck* approximation of the birth-death process for *semi-large systems* (i.e., systems that are large but still have a finite area or volume):

$$\partial_t p = -\partial_x(\mu p) + \frac{\varepsilon}{2}\,\partial_x^2(\sigma^2 p) \tag{11}$$

where

$$\mu(x) := b(x) - d(x) \tag{12}$$

$$\sigma^2(x) := b(x) + d(x) \tag{13}$$

To understand the meaning of the $\mu(x)$ and the $\sigma^2(x)$, recall from section 8.1 that the probability of a single birth event during Δt time is $B_n \Delta t + \mathrm{O}(\Delta t)^2$. In terms of the new variables this is $\varepsilon^{-1} b(x)\Delta t + \mathrm{O}(\Delta t)^2$ and gives a change in population density from x at time t to $x + \varepsilon$ at time $t + \Delta t$. Likewise, the probability of a single death event during Δt time is $D_n \Delta t + \mathrm{O}(\Delta t)^2$. In terms of the new variables this is $\varepsilon^{-1} d(x)\Delta t + \mathrm{O}(\Delta t)^2$ and gives a change in population density from x at time t to $x - \varepsilon$ at time $t + \Delta t$. So, the average change in x per Δt time is

$$\frac{\mathcal{E}\{\Delta x\}}{\Delta t} = b(x) - d(x) + \mathrm{O}(\Delta t) \longrightarrow \mu(x) \tag{14}$$

as $\Delta t \to 0$. Likewise, the variance of the change in x per Δt time is

$$\frac{\mathcal{E}\{\Delta x^2\} - \mathcal{E}\{\Delta x\}^2}{\Delta t} = \varepsilon\big(b(x) + d(x)\big) + \mathrm{O}(\Delta t) \longrightarrow \varepsilon\sigma^2(x) \tag{15}$$

as $\Delta t \to 0$. So, $\mu(x)$ is the average change in x per unit of time, also called the (deterministic) *drift*, and $\varepsilon\sigma^2(x)$ is the variance of the change in x per unit of time. In particular, notice that the variance of the change in x per unit of time is proportional to ε.

The Fokker-Planck approximation (11) relates to the stochastic differential equation

$$dx = \mu(x)dt + \sqrt{\varepsilon\sigma^2(x)}\,dW \quad \text{(Ito)} \tag{16}$$

in the same way as the transport equation (9) relates to the deterministic equation (10). That is, both the Fokker-Planck equation and the transport equation describe how the

probability distribution of x at a given time changes with time, while both the deterministic equation (10) and the stochastic equation (16) describe a single orbit or sample path across time.

9.3. **Quasi-stationary distribution.** To study the quasi-stationary distribution in a semi-large system, we approximate the nonlinear SDE (16) by a linear SDE centered at the deterministic equilibrium, $\bar{x}$, which we get from the equation

$$\mu(\bar{x}) = 0 \tag{17}$$

To guarantee deterministic stability we assume that

$$\mu'(\bar{x}) < 0 \tag{18}$$

Linearization of the SDE (16) gives

$$d(x - \bar{x}) = \mu'(\bar{x})(x - \bar{x})dt + \sqrt{\varepsilon\sigma^2(\bar{x})}\, dW \tag{19}$$

which defines the Ornstein-Uhlenbeck process. So, the stationary distribution of x will be approximately Gaussian

$$x \sim \mathcal{N}\left(\bar{x}, \frac{\varepsilon\sigma^2(\bar{x})}{2|\mu'(\bar{x})|}\right) \tag{20}$$

with auto-covariance

$$C(\tau) = \frac{\varepsilon\sigma^2(\bar{x})}{2|\mu'(\bar{x})|}\, e^{-|\tau\mu'(\bar{x})|} \tag{21}$$

and spectral density

$$S(\omega) = \frac{\varepsilon\sigma^2(\bar{x})}{\omega^2 + \mu'(\bar{x})^2} \tag{22}$$

The approximation will improve towards smaller values of ε because the diffusion term in (19) becomes smaller and the population will stay closer to the deterministic equilibrium.

9.4. **Example.** Consider the SIS-model in which "S" denotes an uninfected (but "susceptible") individual and "I" an infected individual, and consider the following processes:

$$\begin{aligned} \mathrm{S} + \mathrm{I} &\xrightarrow{\beta} 2\,\mathrm{I} \quad \text{(transmission)} \\ \mathrm{I} &\xrightarrow{\delta} \mathrm{S} \quad \text{(recovery)} \end{aligned} \tag{23}$$

The first "reaction" represents the transmission of an infection from an infected person to an uninfected person through direct contact. The second "reaction" represents the recovery of an infected individual but without acquiring immunity. Applying the principle of mass-action (see section 1.5) this gives the following population equations:

$$\begin{cases} \frac{dx}{dt} &= +\beta xy - \delta x \\ \\ \frac{dy}{dt} &= -\beta xy + \delta x \end{cases} \tag{24}$$

where x and y denote the population densities of I and S, respectively. The total population density $x+y =: k$ stays constant, which is used to write $y = k - x$ in the equation for x, which leaves us with

$$\frac{dx}{dt} = \beta x(k-x) - \delta x \quad (0 \le x \le k) \tag{25}$$

The dynamics are straightforward: if $\beta k \le \delta$, we have that $x \to 0$ as $t \to 0$ (i.e., the infection dies out); if $\beta k > \delta$, we have that $x \to \bar{x}$ as $t \to 0$ where

$$\bar{x} := k - \frac{\delta}{\beta} \in (0, k) \tag{26}$$

(i.e., the infection spreads and reaches an equilibrium).

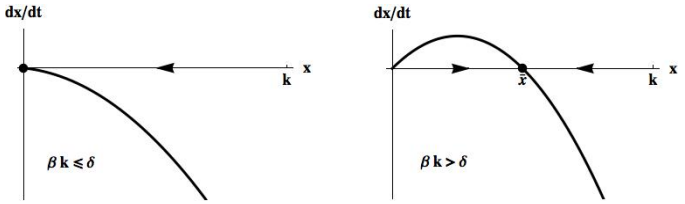

FIGURE 1. Dynamics in the SIS model.

From equation (25) we see immediately that

$$\begin{aligned} b(x) &:= \beta x(k-x) \\ d(x) &:= \delta x \end{aligned} \tag{27}$$

are the rates of recruitment and recovery (i.e., the "birth" and "death" rates) of infected individuals as functions of population density. Using the new variables in definition (2) we can translate these rates into the birth and death rate for a finite population:

$$\begin{aligned} B_n &= b(\varepsilon n)/\varepsilon &&= \beta n(k - \varepsilon n) \\ D_n &= d(\varepsilon n)/\varepsilon &&= \delta n \end{aligned} \tag{28}$$

where ε is the inverse of the system size. This allows us to calculate the quasi-stationary distribution and the expected extinction time in a finite populations as we did in sections 8.4 and 8.5.

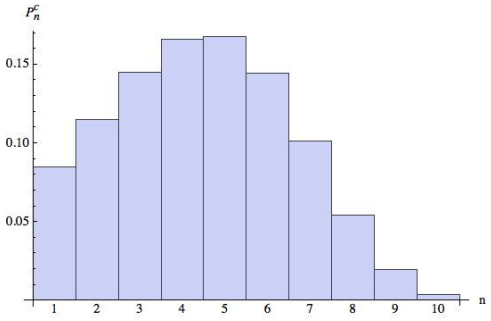

FIGURE 2. Quasi-stationary distribution P_n^c for $\beta = 2$, $\delta = 1$, $k = 1$ and $\varepsilon = 0.1$, and so the maximum population size is $k/\varepsilon = 10$.

We can calculate the expected time till extinction of the infection as a function of system size $\Omega := \varepsilon^{-1}$ by first calculating the stationary distribution P_n^c and next the expected extinction time $\tau_E := (D_1 P_1^c)^{-1}$ for several values of ε:

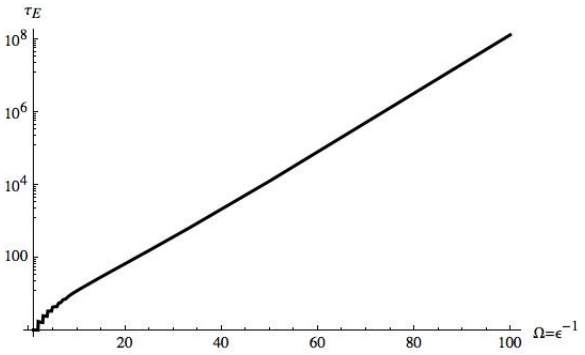

FIGURE 3. Extinction time τ_E as a function of system size Ω. (Note the logarithmic scale on the vertical axis.)

It can be seen that τ_E increases exponentially with system size Ω. For a system size $\Omega = 40$ the expected time till extinction is already as large as $\tau_E \approx 10^4$ times the typical length $1/\delta$ of an individual infection, and for $\Omega = 100$ this has become $\tau_E \approx 10^8$. If we think of an infection with a typical recovery time of 14 days, then the expected time till extinction (due to demographic stochasticity) in a populations of forty individuals, or a hundred individuals, is approximately 380 years or 3.8 million years, respectively. The point is that random extinction very rapidly becomes a negligible phenomena as the system size increases. Even fairly small systems can have very long extinction times.

How important are demographic fluctuations in a population of a size where random extinction has already become negligible? To answer that question we use the Fokker-Plank approximation

$$\partial_t p = -\partial_x[(b-d)p] + \frac{1}{2}\partial_x^2[\varepsilon(b+d)p] \tag{29}$$

with the corresponding SDE

$$dx = (b-d)dt + \sqrt{\varepsilon(b+d)}dW \quad \text{(Ito)} \tag{30}$$

where $b(x) = \beta x(k-x)$ and $d(x) = \delta x$.

The figure below gives a sample path of the SDE starting at the population equilibrium $\bar{x}$ for $\Omega = 100$ but otherwise the same parameter values as in the previous figures. It can be seen that in spite of the negligibility of random extinction, the demographic noise is significant. Apparently, there is a range of system sizes where random extinction is negligible but where random fluctuations in population density are still significant.

To understand how it is possible that such a range of system sizes can exist, we note that the expected time till extinction increases exponentially with system size (see previous figure) while the standard deviation of the stationary distribution decreases slowly as the inverse of the square-root of the system size (see equation (20)).

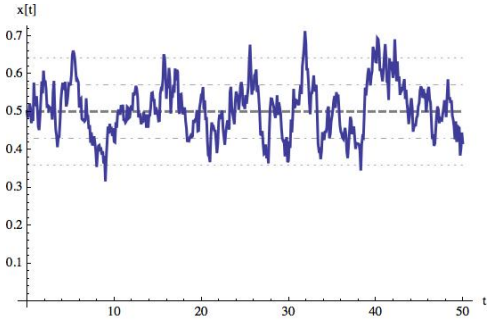

FIGURE 4. Sample path of the SDE for $\beta = 2$, $\delta = 1$, $k = 1$ and $\varepsilon = 0.01$ about the deterministic equilibrium $\bar{x}$ (thick dashed line).

The following figure gives the stationary probability distribution of the population density observed in a single sample path of the nonlinear SDE integrated over ten thousand time units (i.e. ten thousand times the average recovery time $1/\delta$), together with the theoretical prediction using the approximating distribution (20) obtained from the linear SDE (19). The somewhat smaller average of the observed distribution compared to that of the predicted distribution is due to the concavity of the drift $b(x) - d(x)$ (see Figure 1) and Jensen's inequality.

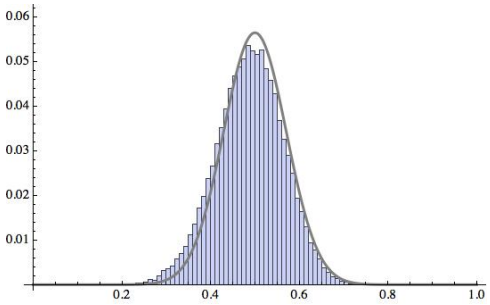

FIGURE 5. Stationary distribution observed in a single sample path (histogram) compared with the predicted appriximate distribution (20) (continuous distribution) for $\beta = 2$, $\delta = 1$, $k = 1$ and $\varepsilon = 0.01$.

Finally, we calculate the probability of invasion of the infection in an uninfected population if introduced at very low initial numbers. This was done by counting the number of successful invasions in a sample of one hundred sample paths for each initial number. The observed invasion probabilities coincide well with the probability of invasion

$$\text{Prob(invasion} \mid \text{initial number is } n) = 1 - \left(\frac{\delta}{\beta k}\right)^n \tag{31}$$

as predicted by the linear birth-death process (see equation (19) in section 8.3).

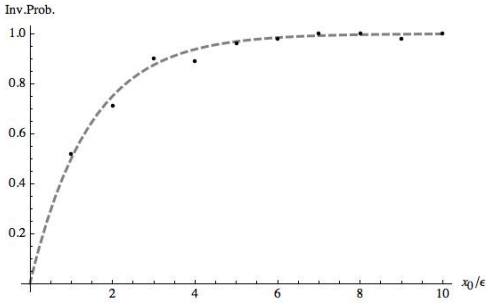

FIGURE 6. The probability of invasion as a function of initial number of infected individuals as observed in a sample of 100 sample paths of the nonlinear SDE (dots) and as predicted from the linear birth-death process (dashed) for $\beta = 2$, $\delta = 1$, $k = 1$ and $\varepsilon = 0.01$.