STOCHASTIC POPULATION MODELS (SPRING 2015)

STEFAN GERITZ
DEPARTMENT OF MATHEMATICS AND STATISTICS
UNIVERSITY OF HELSINKI

11-S. Multi-type processes (supplement)

11.5. **Example.** Consider the SIS model defined by the following individual level Poisson processes where S denotes a susceptible individual and I an infected individual:

$$\begin{array}{rcll} \mathrm{S} & \xrightarrow{\lambda} & \mathrm{S}+\mathrm{S} & \text{(birth)} \\ \mathrm{S} & \xrightarrow{\nu} & \dagger & \text{(background death)} \\ \mathrm{I} & \xrightarrow{\nu} & \dagger & \text{(background death)} \\ \mathrm{I} & \xrightarrow{\alpha} & \dagger & \text{(disease-induced death)} \\ \mathrm{S}+\mathrm{I} & \xrightarrow{\beta} & \mathrm{I}+\mathrm{I} & \text{(transmission)} \\ \mathrm{I} & \xrightarrow{\gamma} & \mathrm{S} & \text{(recovery)} \end{array}$$

Writing s and i for the population densities of, respectively, susceptible and infected individuals, the transmission process also can be represented by

$$\begin{array}{rcll} \mathrm{S} & \xrightarrow{\beta i} & \mathrm{I} & \text{(transmission)} \\ \mathrm{I} & \xrightarrow{\beta s} & \mathrm{I} & \text{(transmission)} \end{array}$$

This representation is more convenient for setting up the table of changes in the numbers S and I (italics!) of individuals at the population level:

event	ΔS	ΔI	rate
birth	$+1$	0	λS
background death S	-1	0	νS
background death I	0	-1	νI
disease-induced death I	0	-1	αI
transmission	-1	$+1$	$\beta i S$
recovery	$+1$	-1	γI

With Ω denoting system size and $\varepsilon = \Omega^{-1}$ the change in population density corresponding to adding or removing a single individual, the above table can be re-written in terms of changes in population densities:

event	Δs	Δi	rate
birth	$+\varepsilon$	0	$\varepsilon^{-1}\lambda s$
background death S	$-\varepsilon$	0	$\varepsilon^{-1}\nu s$
background death I	0	$-\varepsilon$	$\varepsilon^{-1}\nu i$
disease-induced death I	0	$-\varepsilon$	$\varepsilon^{-1}\alpha i$
transmission	$-\varepsilon$	$+\varepsilon$	$\varepsilon^{-1}\beta is$
recovery	$+\varepsilon$	$-\varepsilon$	$\varepsilon^{-1}\gamma i$

From the table we calculate the expected rate of change and the expected rate of change squared:

$$\begin{aligned}
\mu_{\mathrm{S}}(s,i) &:= \mathcal{E}\left\{\tfrac{\Delta s}{\mathrm{d}t}\right\} &&= +(\lambda-\nu)s - \beta si + \gamma i \\
\mu_{\mathrm{I}}(s,i) &:= \mathcal{E}\left\{\tfrac{\Delta i}{\mathrm{d}t}\right\} &&= -(\nu+\alpha)i + \beta si - \gamma i \\
\varepsilon\,\sigma_{\mathrm{SS}}(s,i) &:= \mathcal{E}\left\{\tfrac{\Delta s \Delta s}{\mathrm{d}t}\right\} &&= +\varepsilon\big((\lambda-\nu)s + \beta si + \gamma i\big) \\
\varepsilon\,\sigma_{\mathrm{SI}}(s,i) &:= \mathcal{E}\left\{\tfrac{\Delta s \Delta i}{\mathrm{d}t}\right\} &&= -\varepsilon\big(\beta si + \gamma i\big) \\
\varepsilon\,\sigma_{\mathrm{IS}}(s,i) &:= \mathcal{E}\left\{\tfrac{\Delta i \Delta s}{\mathrm{d}t}\right\} &&= -\varepsilon\big(\beta si + \gamma i\big) \\
\varepsilon\,\sigma_{\mathrm{II}}(s,i) &:= \mathcal{E}\left\{\tfrac{\Delta i \Delta i}{\mathrm{d}t}\right\} &&= +\varepsilon\big((\nu+\alpha)i + \beta si + \gamma i\big)
\end{aligned}$$

The Fokker-Plack equation for semi-large systems then becomes

$$\begin{aligned}
\partial_t p &= -\partial_s(\mu_{\mathrm{S}}\, p) - \partial_i(\mu_{\mathrm{I}}\, p) \\
&+ \tfrac{\varepsilon}{2}\Big(\partial_{ss}(\sigma_{\mathrm{SS}}\, p) + \partial_{si}(\sigma_{\mathrm{SI}}\, p) + \partial_{is}(\sigma_{\mathrm{IS}}\, p) + \partial_{ii}(\sigma_{\mathrm{II}}\, p)\Big)
\end{aligned} \tag{1}$$

with the corresponding stochastic differential equation

$$\mathrm{d}\begin{pmatrix} s \\ i \end{pmatrix} = \begin{pmatrix} \mu_{\mathrm{S}} \\ \mu_{\mathrm{I}} \end{pmatrix} \mathrm{d}t + \sqrt{\varepsilon}\begin{pmatrix} \sigma_{\mathrm{SS}} & \sigma_{\mathrm{SI}} \\ \sigma_{\mathrm{IS}} & \sigma_{\mathrm{II}} \end{pmatrix}^{\frac{1}{2}} \mathrm{d}\begin{pmatrix} W_{\mathrm{S}} \\ W_{\mathrm{I}} \end{pmatrix} \tag{2}$$

where W_{S} and W_{I} are two independent Wiener processes. Large systems can be approximated by letting $\Omega \to \infty$ and correspondingly $\varepsilon \to 0$, which gives the system of ordinary differential equations

$$\mathrm{d}\begin{pmatrix} s \\ i \end{pmatrix} = \begin{pmatrix} \mu_{\mathrm{S}} \\ \mu_{\mathrm{I}} \end{pmatrix} \mathrm{d}t \tag{3}$$

In more traditionally notation this is

$$\begin{cases} \frac{\mathrm{d}s}{\mathrm{d}t} = (\lambda-\nu)s - \beta si + \gamma i \\ \\ \frac{\mathrm{d}s}{\mathrm{d}t} = -(\nu+\alpha)i + \beta si - \gamma i \end{cases} \tag{4}$$

which has a unique and stable positive equilibrium id and only if $\lambda > \nu$. The dynamics of the deterministic system are summarised in the following figure.

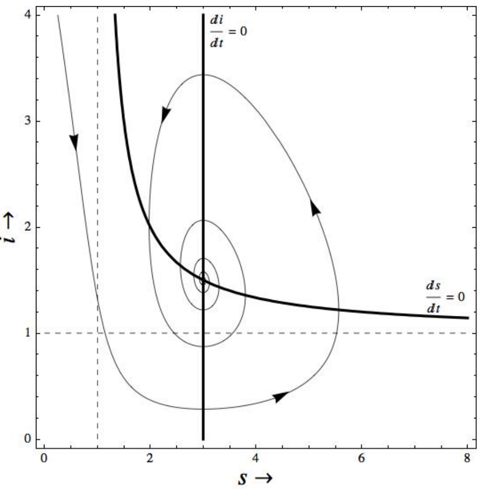

FIGURE 1. Dynamics of the deterministic SIS dynamics for $\lambda > \nu$: thick black lines represent the zero-clines; dashed lines are horizontal and vertical asymptotes of the zero-cline for s; this solid line is an example orbit.

We want to study the stochastic dynamics of the SDE (2) for small ε when the quasi-stationary distribution is concentrated around the deterministic equilibrium. That's why we first looked at the deterministic limit, i.e., to make sure that there is a positive and stable equilibrium at all.

11.6. **General case.** First consider the more general multi-type SDE

$$\mathrm{d}X = \mu(X)\,\mathrm{d}t + \sqrt{\varepsilon\sigma^2(X)}\,\mathrm{d}W \tag{5}$$

where X, μ and W are vector-valued and where σ^2 is a matrix. Let $\overline{x}$ be a positive and hyperbolically stable equilibrium of the corresponding deterministic system obtained by taking $\varepsilon \to 0$, i.e., $\mu(\overline{x}) = 0$ (equilibrium condition) and the Jacobi matrix $\mu'(\overline{x})$ of partial derivatives evaluated at the equilibrium has only eigenvalues with a strictly negative real part (stability condition). A matrix all eigenvalues of which have negative real parts also is called hyperbolically stable.

Linearisation of (5) about the deterministic equilibrium $\overline{x}$ gives the multi-type Ornstein-Uhlenbeck process

$$\mathrm{d}(X - \overline{x}) = \mu'(\overline{x})(X - \overline{x})\,\mathrm{d}t + \sqrt{\varepsilon\sigma^2(\overline{x})}\,\mathrm{d}W \tag{6}$$

To simplify notation, we write this as

$$\mathrm{d}u = A\,u\,\mathrm{d}t + B\,\mathrm{d}W \tag{7}$$

where u and W are vectors, A a hyperbolically stable square matrix, and B a symmetric and positive semi-definite matrix (i.e., $x^{\mathrm{T}}Bx \geq 0$ for any vector $x \neq 0$). We already have analysed the multi-type OU process in section 11.3, but here we present a more direct and computationally friendly method.

The solution of (7) with initial condition $u(0) = u_0$ is

$$u(t) = e^{At}u_0 + e^{At}\int_0^t e^{-A\tau}B\,\mathrm{d}W(\tau) \tag{8}$$

as can be verified by differentiation. Since A is hyperbolically stable, the first term on the right hand side is transient and converges exponentially to zero. The second term converges to the normal distribution with mean zero and covariance matrix Σ, i.e.,

$$\lim_{t\to\infty} u(t) \sim \mathcal{N}(0,\Sigma) \tag{9}$$

where by definition

$$\Sigma = \mathcal{E}\{u\,u^{\mathrm{T}}\}. \tag{10}$$

Covariance: To calculate the covariance matrix Σ we use Ito's multiplication table for independent Wiener increments $\mathrm{d}W_i$ and $\mathrm{d}W_j$:

	$\mathrm{d}t$	$\mathrm{d}W_i$	$\mathrm{d}W_j$
$\mathrm{d}t$	0	0	0
$\mathrm{d}W_i$	0	$\mathrm{d}t$	0
$\mathrm{d}W_j$	0	0	$\mathrm{d}t$

From this we get

$$\begin{aligned}\mathrm{d}(u\,u^{\mathrm{T}}) &= \mathrm{d}u\,u^{\mathrm{T}} + u\,\mathrm{d}u^{\mathrm{T}} + \mathrm{d}u\,\mathrm{d}u^{\mathrm{T}}\\ &= \big(A\,u\,u^{\mathrm{T}} + u\,u^{\mathrm{T}}A^{\mathrm{T}} + B^2\big)\,\mathrm{d}t + B\,\mathrm{d}W\,u^{\mathrm{T}} + u\,\mathrm{d}W^{\mathrm{T}}B\end{aligned} \tag{11}$$

Taking expectations on both sides gives

$$\mathrm{d}\Sigma = \big(A\,\Sigma + \Sigma\,A^{\mathrm{T}} + B^2\big)\,\mathrm{d}t \tag{12}$$

which at the stationary distribution becomes

$$0 = A\,\Sigma + \Sigma\,A^{\mathrm{T}} + B^2 \tag{13}$$

Note that this is only a linear equation in the entries of Σ which is easily solved.

Cross-covariance: To calculate the cross-covariance matrix

$$C(\tau) = \mathcal{E}\{u(t+\tau)\,u(t)^{\mathrm{T}}\} \tag{14}$$

consider the process $\{u(t+\tau)\}_{\tau\geq 0}$ for given fixed $t \geq 0$, which satisfies the same SDE as $\{u(t)\}_{t\geq 0}$, i.e.,

$$\mathrm{d}u(t+\tau) = A\,u(t+\tau)\,\mathrm{d}\tau + B\,\mathrm{d}W(t+\tau) \tag{15}$$

Since$t \geq 0$ is fixed, right-multiplication by $u(t)^{\mathrm{T}}$ gives

$$\mathrm{d}u(t+\tau)u(t)^{\mathrm{T}} = A\,u(t+\tau)u(t)^{\mathrm{T}}\,\mathrm{d}\tau + B\,\mathrm{d}W(t+\tau)u(t)^{\mathrm{T}} \tag{16}$$

Taking expectations on both side then gives

$$\mathrm{d}C(\tau) = A\,C(\tau)\,\mathrm{d}\tau \tag{17}$$

from which we get

$$C(\tau) = e^{A\,\tau} C(0) \tag{18}$$

where $C(0) = \Sigma$ from equation (13). We now return to the example.

11.7. **Example.** The following figure gives a stochastic orbit of the original non-linearised SDE (2) of section 11.5 superimposed on the deterministic structures presented in Figure 1.

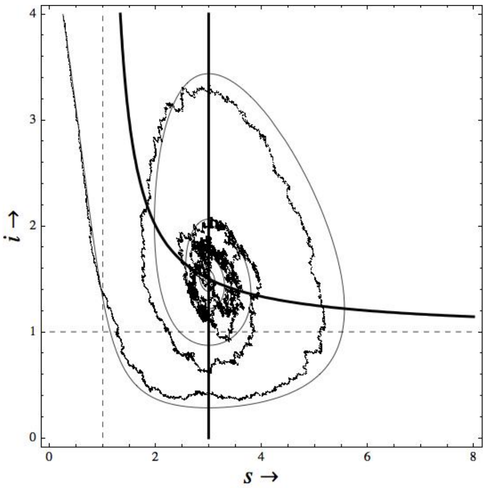

FIGURE 2. Stochastic orbit.

We use the results of section 11.6 to describe the asymptotic stochastic dynamics. Close to the deterministic equilibrium, the dynamics of the non-linear system (2) are approximated by the stationary Ornstein-Uhlenbeck process in (6). In particular, the approximating quasi-stationary distribution is

$$\begin{pmatrix} s \\ i \end{pmatrix} \sim \mathcal{N}\left(\begin{pmatrix} \bar{s} \\ \bar{i} \end{pmatrix}, \Sigma \right) \tag{19}$$

where

$$\begin{pmatrix} \bar{s} \\ \bar{i} \end{pmatrix} = \begin{pmatrix} \frac{\alpha+\gamma+\nu}{\beta} \\ \\ \frac{(\lambda-\nu)(\alpha+\gamma+\nu)}{\beta(\alpha+\nu)} \end{pmatrix} \tag{20}$$

is the deterministic equilibrium for $\lambda > \nu$. The covariance matrix Σ is calculated from (13) with

$$A = \begin{pmatrix} -\frac{\gamma(\lambda-\nu)}{\alpha+\nu} & -\alpha-\nu \\ \\ \frac{(\lambda-\nu)(\alpha+\gamma+\nu)}{\alpha+\nu} & 0 \end{pmatrix} \tag{21}$$

and

$$B^2 = \varepsilon \begin{pmatrix} \frac{2(\alpha+\gamma+\nu)(\alpha\lambda+\gamma(\lambda-\nu)+\lambda\nu)}{\beta(\alpha+\nu)} & -\frac{(\lambda-\nu)\left(\alpha^2+3\alpha\gamma+2\gamma^2+2\alpha\nu+3\gamma\nu+\nu^2\right)}{\beta(\alpha+\nu)} \\ -\frac{(\lambda-\nu)\left(\alpha^2+3\alpha\gamma+2\gamma^2+2\alpha\nu+3\gamma\nu+\nu^2\right)}{\beta(\alpha+\nu)} & \frac{2(\lambda-\nu)(\alpha+\gamma+\nu)^2}{\beta(\alpha+\nu)} \end{pmatrix} \tag{22}$$

which gives

$$\Sigma = \varepsilon \begin{pmatrix} \frac{(\alpha+\gamma+\nu)\left(\alpha^2+\gamma(\lambda-\nu)+\nu(\lambda+\nu)+\alpha(\lambda+2\nu)\right)}{\beta\gamma(\lambda-\nu)} & -\frac{\alpha+\gamma+\nu}{\beta} \\ -\frac{\alpha+\gamma+\nu}{\beta} & \frac{(\alpha+\gamma+\nu)^2(\alpha+\lambda+\nu)}{\beta\gamma(\alpha+\nu)} \end{pmatrix} \tag{23}$$

Stationary distribution: The following figure compares stochastic orbits of the non-linear SDE (2) with the stationary distribution of the approximating Ornstein-Uhlenbeck process. The latter is represented by the 50%, 95% and 99% quantiles of the approximating normal distribution.

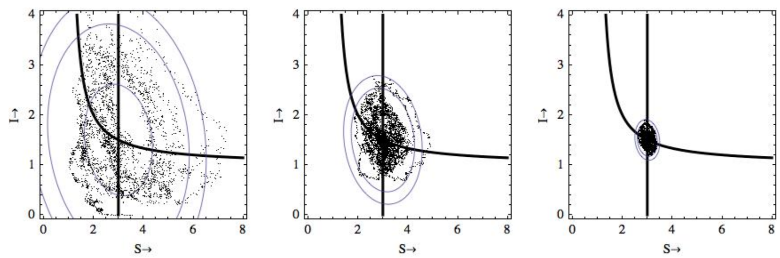

FIGURE 3. Comparison of stochastic orbits of the non-linear SDE with the stationary distribution of the approximating OU process for different system sizes. From left to right: $\Omega = 20,\ 100,\ 1000$.

These quantiles are the contour lines of the probability density function that enclose 50%, 95% and 99% of the total probability mass, respectively. Formulated differently, for an geodic process, an orbit will spend 50%, 95% and 99% of all time within the corresponding quantile. It can be seen that as the system size increases, the fit becomes better in the sense that fewer data points fall outside the 95% and 99% quantiles of the approximating normal distribution.

Cross-covariance: While the deterministic system converges to the equilibrium, the stochastic orbits of the non-linear system (2) exhibit persistent quasi-periodic behaviour as illustrated in the next figure. The quasi-periodicity is due to complex eigenvalues of Jacobi matrix A.

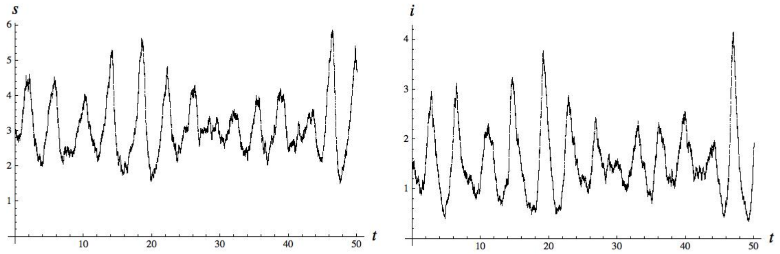

FIGURE 4. Quasi-periodic orbits of the non-linear SDE for susceptibles (left) and infected (right).

The periodicity is also reflected in the cross-covariance function $C(\tau)$ of the approximating Ornstein-Uhlenbeck process (6). The cross-covariance calculated in (18) exhibits damped oscillations as shown in the next figure. The length of a full period is $2\pi/\omega$, where ω is the absolute value of the imaginary part of the two eigenvalues.

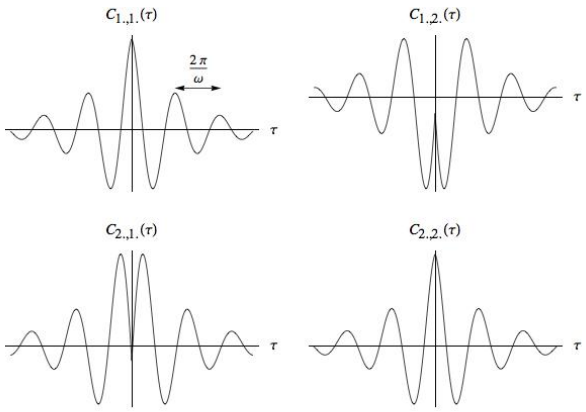

FIGURE 5. Cross-covariance of the approximating stationary Ornstein-Uhlenbeck process .