STOCHASTIC POPULATION MODELS
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7. Population models with stochastic parameters

7.1. **Motivating example.** Consider the population model

$$\frac{dX}{dt} = f(X, \theta) \tag{1}$$

where θ is a ergodic stochastic process with mean $\bar{\theta}$. Let $\bar{X}$ be a positive equilibrium for constant $\theta = \bar{\theta}$, i.e.,

$$f(\bar{X}, \bar{\theta}) = 0 \tag{2}$$

Local linearization around the point $(\bar{X}, \bar{\theta})$ gives

$$\frac{du}{dt} = au + b\eta \tag{3}$$

where $a = \partial_X f(\bar{X}, \bar{\theta})$ and $b = \partial_\theta f(\bar{X}, \bar{\theta})$ and $u = X - \bar{X}$ and $\eta = \theta - \bar{\theta}$. For deterministic stability of $\bar{X}$ we assume that $a < 0$.

(Note that, because of non-linearities, $\bar{X}$ is typically *not* the mean of the stationary process generated by equation (1). However, $\bar{X}$ *is* the mean of $X(t)$ in the stationary process generated by the linear equation (3). Indeed, if $\{u(t)\}$ is stationary, then $0 = \frac{\mathrm{d}}{\mathrm{d}t}\mathcal{E}\{u\} = \mathcal{E}\{\frac{\mathrm{d}}{\mathrm{d}t}u\} = \mathcal{E}\{au + b\eta\} = a\mathcal{E}\{u\}$ because $\mathcal{E}\{\eta\} = \mathcal{E}\{\theta\} - \bar{\theta} = 0$. Hence, $0 = \mathcal{E}\{u\} = \mathcal{E}\{X\} - \bar{X}$ and so $\mathcal{E}\{X\} = \bar{X}$.)

Calculating the auto-covariances from the linear equation (3) we get

$$-C_u''(\tau) + a^2 C_u(\tau) = b^2 C_\eta(\tau) \tag{4}$$

Taking Fourier transforms gives

$$\omega^2 S_u(\omega) + a^2 S_u(\omega) = b^2 S_\eta(\omega) \tag{5}$$

from which we get

$$\begin{cases} S_u(\omega) = |T(\omega)|^2 S_\eta(\omega) \\ T(\omega) = \frac{b}{i\omega - a} \end{cases} \tag{6}$$

where $T(\omega)$ is our old friend the transfer function from Section 2.1 equation (8). This raises the question whether it is always so that the spectral density of the output of a linear system is equal to the spectral density of the input signal times the modulus of the transfer function squared. i.e., $S_u(\omega) = |T(\omega)|^2 S_\eta(\omega)$ irrespective of the particulars of the model?

7.2. **Ergodic processes.** A stationary process $\{X(t)\}$ is *ergodic* if time-averages equal ensemble averages, i.e., if

$$\mathcal{E}\{f(X(t))\} = \lim_{T\to\infty} \frac{1}{2T} \int_{-T}^{T} f(x(t'))dt' \tag{7}$$

for every integrable function f and almost every single sample path (i.e., realization) $\{x(t)\}$ of the process $\{X(t)\}$.

If a stationary process is ergodic, then a single realization of the process over infinite time contains all information about the distribution of the process at any particular fixed time. For convenience we denote the time-average by $\langle\cdot\rangle$, and hence a stationary stochastic process $\{X(t)\}$ is ergodic if

$$\mathcal{E}\big\{f\big(X(t)\big)\big\} = \big\langle f(x(t))\big\rangle \tag{8}$$

for almost every integrable function f and every realization $x(t)$.

In particular, if $\{X(t)\}$ is ergodic, then for the mean we have

$$\overline{X} = \big\langle x(t)\big\rangle \tag{9}$$

and for the auto-covariance

$$C(\tau) = \big\langle (x(t+\tau) - \overline{X})(x(t) - \overline{X})\big\rangle \tag{10}$$

A sufficient condition for a stationary process $\{X(t)\}$ to be ergodic is (**a**) that its auto covariance $C_X(t) \to 0$ as $t \to \infty$ and (**b**) that the process is irreducible, i.e., for every starting point x_0 and every non-empty open set A there is $t > 0$ such that $\mathrm{Prob}\{X(t) \in A \,|\, X(0) = x_0\} > 0$.

7.3. **The Wiener-Khinchin theorem.** Suppose $\{X(t)\}$ is ergodic with auto-covariance $C(\tau)$ and spectral density $S(\omega)$, and define the random variable

$$S_T(\omega) := \frac{1}{2T}\left|\int_{-T}^{T} \big(X(t) - \overline{X}\big)e^{-i\omega t}dt\right|^2 \tag{11}$$

Then

$$S(\omega) = \lim_{T\to\infty} \mathcal{E}\big\{S_T(\omega)\big\} \tag{12}$$

whenever $|\tau|C(\tau)$ is integrable.

(The Wiener-Khinchin theorem provides us with an interpretation of the spectral density: the spectral density gives the relative contributions of different angular frequencies in the sample path $x(t)$.)

Proof:

Writing the square in (11) as a double integral, we have

$$
\begin{aligned}
S_T(\omega) &= \tfrac{1}{2T}\int_{-T}^{T}\big(X(t_1)-\overline{X}\big)e^{-i\omega t_1}dt_1\int_{-T}^{T}\big(X(t_2)-\overline{X}\big)e^{+i\omega t_2}dt_2 \\
&= \tfrac{1}{2T}\int_{-T}^{T}\int_{-T}^{T}\big(X(t_1)-\overline{X}\big)\big(X(t_2)-\overline{X}\big)e^{-i\omega(t_1-t_2)}dt_1dt_2
\end{aligned} \tag{13}
$$

Taking expectations gives

$$
\mathcal{E}\big\{S_T(\omega)\big\} = \frac{1}{2T}\int_{-T}^{T}\int_{-T}^{T}C(t_1-t_2)e^{-i\omega(t_1-t_2)}dt_1dt_2 \tag{14}
$$

A simple exercise in calculus shows that for any integrable function f we have

$$
\int_{-T}^{T}\int_{-T}^{T}f(t_1-t_2)dt_1dt_2 = \int_{-2T}^{2T}(2T-|\tau|)f(\tau)d\tau \tag{15}
$$

and so, with $f(t)=C(t)e^{-i\omega t}$, we get

$$
\begin{aligned}
\mathcal{E}\big\{S_T(\omega)\big\} &= \tfrac{1}{2T}\int_{-2T}^{2T}(2T-|\tau|)C(\tau)e^{-i\omega\tau}d\tau \\
&= \int_{-2T}^{2T}C(\tau)e^{-i\omega\tau}d\tau - \tfrac{1}{2T}\int_{-2T}^{2T}|\tau|C(\tau)e^{-i\omega\tau}d\tau
\end{aligned} \tag{16}
$$

If $|\tau|C(\tau)$ is integrable, then the last term vanishes as $T\to\infty$. The first term, however, converges to the Fourier transform of the auto-covariance, i.e., to the spectral density $S(\omega)$. This completes the proof.

7.4. **A general property of population models with ergodic parameters.** Let $T(\omega)$ be the transfer function of an arbitrary (linearized) population model, i.e.,

$$
\tilde{u}(\omega) = T(\omega)\tilde{\eta}(\omega) \tag{17}
$$

where $u = x-\bar{x}$ and $\eta = \theta-\bar{\theta}$ are small deviations of, respectively, the population density from the deterministic equilibrium and a randomly fluctuating parameter from its time-average. Then

$$
S_X(\omega) = \big|T(\omega)\big|^2 S_\theta(\omega) \tag{18}
$$

Proof:

From the Wiener-Khinchin theorem we have

$$\begin{aligned} S_X(\omega) &= \lim_{T\to\infty} \tfrac{1}{2T}\mathcal{E}\left\{\left|\int_{-T}^{T} u(t)e^{-i\omega t}dt\right|^2\right\} \\ &= \lim_{T\to\infty} \tfrac{1}{2T}\mathcal{E}\left\{|\tilde{u}(\omega)+\mathrm{o}(1)|^2\right\} \\ &= \lim_{T\to\infty} \tfrac{1}{2T}\mathcal{E}\left\{|T(\omega)\tilde{\eta}(\omega)+\mathrm{o}(1)|^2\right\} \\ &= \left|T(\omega)\right|^2 \lim_{T\to\infty} \tfrac{1}{2T}\mathcal{E}\left\{|\tilde{\eta}(\omega)+\mathrm{o}(1)|^2\right\} \\ &= \left|T(\omega)\right|^2 \lim_{T\to\infty} \tfrac{1}{2T}\mathcal{E}\left\{\left|\int_{-T}^{T} \eta(t)e^{-i\omega t}dt+\mathrm{o}(1)\right|^2\right\} \\ &= \left|T(\omega)\right|^2 S_\theta(\omega) \end{aligned} \tag{19}$$

7.5. **Example.** Consider the model of section 4.5 with a fluctuating birth rate, i.e.,

$$\frac{dX(t)}{dt} = e^{-\alpha\tau}\beta_\tau(t)X_\tau(t) - \delta X(t) - \frac{1}{2}\gamma X(t)^2 \tag{20}$$

In section 4.7 we calculated the transfer function as

$$T(\omega) = \frac{\bar{X}e^{-\alpha\tau-i\omega\tau}}{i\omega+\delta+\gamma\bar{X}-\bar{\beta}e^{-\alpha\tau-i\omega\tau}} \tag{21}$$

where $\bar{\beta}$ is the average birth rate and

$$\bar{X} = 2\big(e^{-\alpha\tau}\bar{\beta}-\delta\big)/\gamma \tag{22}$$

is the deterministic equilibrium of the population density if the birth rate were a constant $\bar{\beta}$. We have seen in section 3.3 that the deterministic equilibrium is stable whenever it exists. Suppose the birth rate $\beta(t)$ is given by the stochastic process

$$\beta(t) = \beta_0 e^{\zeta(t)} \tag{23}$$

where $\{\zeta(t)\}$ is the stationary Ornstein-Uhlenbeck generated by the linear SDE

$$d\zeta + a\zeta dt = bdW \tag{24}$$

for $a, b > 0$ (see section 6.2). The average birth rate $\bar{\beta}$ then can be approximated as

$$\bar{\beta} \approx \beta_0\Big(1+\frac{b^2}{4a}\Big) \tag{25}$$

and the spectral density as

$$S_\beta \approx \frac{\beta_0^2 b^2}{\omega^2+a^2} \tag{26}$$

provided $b^2/2a$ (i.e., the variance of ζ) is not too large (see section 6.7). Applying equation (18) in the previous section, we thus have

$$\begin{aligned} S_X(\omega) &= \left|T(\omega)\right|^2 S_\beta(\omega) \\ &\approx \left|T(\omega)\right|^2 \tfrac{\beta_0^2 b^2}{\omega^2+a^2} \end{aligned} \tag{27}$$

which is plotted in the figure below.

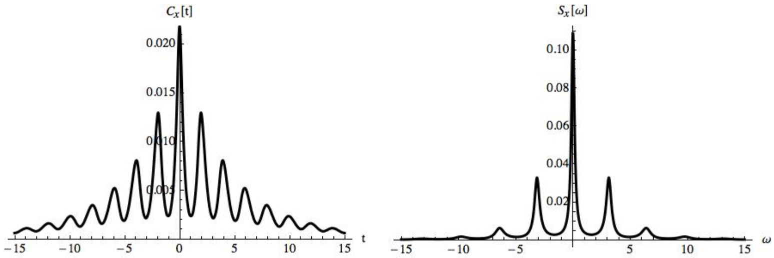

FIGURE 1. The auto-covariance and spectral density of the population process $\{X(t)\}$ for $\alpha = 1$, $\bar{\beta} = 20$, $\gamma = 1$, $\delta = 2$, $\tau = 1.8$, $a = 10$ and $b = 0.5$. The auto-covariance was calculated numerically as the inverse-Fourier transform of the spectral density.

Notice that the spectral density shows a strong resonance peak at $\omega = \pm 3$. This is solely due to the transfer function, because there are no dominant peaks in the spectrum of the Ornstein-Uhlenbeck process for any $\omega \neq 0$.

The following figure gives a sample path of the population process $\{X(t)\}$ obtained by numerical integration of the differential equation (20).

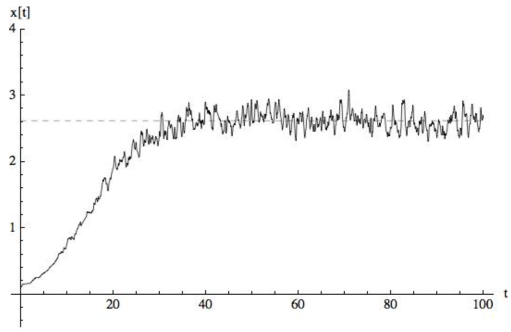

FIGURE 2. Sample path of $\{X(t)\}$ for for the same parameter values as in the previous figure. The dashed line indicates the value of $\bar{X}$.

The presence of a periodic component with frequency $\omega = \pm 3$ in the sample path may not be very obvious. Still, it is there. We can exploit the ergodicity of the population process to calculate the auto-covariance and spectral density also directly from the "data", i.e., from the sample path: Given the sample path $\{x(t)\}$ for $t \in (t_1, t_2)$, the average $\bar{X}$ can be calculated as the time-average

$$\bar{X} \approx \Big\langle x(t) \Big\rangle_{t\in(t_1,t_2)} \tag{28}$$

and the auto-covariance as the time-average

$$C_X(\tau) \approx \Big\langle (x(t+\tau) - \bar{X})(x(t) - \bar{X}) \Big\rangle_{t\in(t_1,t_2)} \tag{29}$$

and using the Wiener-Khinchin theorem, the spectral density as the time-average

$$S_X(\tau) \approx (t_2 - t_1)\Big|\Big\langle (x(t) - \bar{X})e^{-i\omega t} \Big\rangle_{t\in(t_1,t_2)}\Big|^2 \tag{30}$$

as illustrated in the following figure.

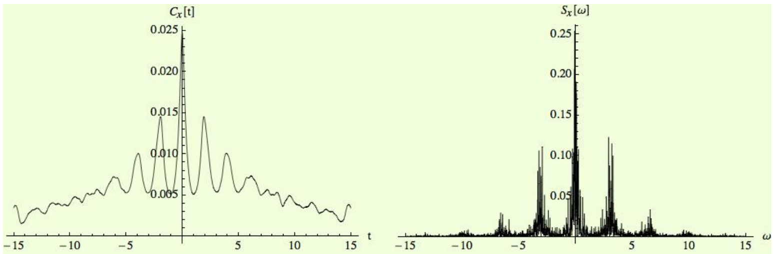

FIGURE 3. The auto-covariance and spectral density estimated from the sample path $\{x(t)\}$.

Note that while these approximations are calculated from a single sample path of the original *nonlinear* model, the results are very similar to the auto-covariance and spectral density calculated analytically from a linearization of the model assuming small amplitude fluctuations. The linearization thus gives fairly robust results.