STOCHASTIC POPULATION MODELS (SPRING 2011)

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2. Fluctuating parameters

2.1. **The general idea.** Consider the scalar population equation

$$\frac{dx}{dt} = f(x, \theta) \tag{1}$$

where θ is a scalar parameter. How would x respond to fluctuations in θ? We study the response to small fluctuations near a stable equilibrium. Suppose

$$\begin{aligned} f(\bar{x}, \bar{\theta}) &= 0 \\ \partial_x f(\bar{x}, \bar{\theta}) &< 0 \end{aligned} \tag{2}$$

i.e., that $x = \bar{x}$ is a stable equilibrium for given constant $\theta = \bar{\theta}$.

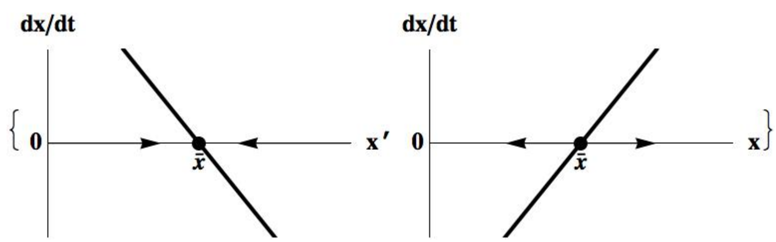

Figure 1. Stability and instability of $\bar{x}$ depending on the slope of $f(x, \bar{\theta})$.

If $\bar{x}$ is stable, then small fluctuations in θ around $\bar{\theta}$ will cause only small fluctuations in x around $\bar{x}$. We write

$$\begin{aligned} x(t) &= \bar{x} + \xi(t) \\ \theta(t) &= \bar{\theta} + \eta(t) \end{aligned} \tag{3}$$

where $\xi(t)$ and $\eta(t)$ are the deviations of, respectively, x from $\bar{x}$ and θ from $\bar{\theta}$. If $|\xi(t)|$ and $|\eta(t)|$ are uniformly small (i.e., for all $t \geq 0$), then we can replace the population equation by the linear approximation

$$\frac{d\xi}{dt} = \partial_x f(\bar{x}, \bar{\theta})\xi + \partial_\theta f(\bar{x}, \bar{\theta})\eta \tag{4}$$

The solution of this is

$$\xi(t) = \xi(t_0)e^{(t-t_0)\partial_x f(\bar{x},\bar{\theta})} + \partial_\theta f(\bar{x},\bar{\theta}) \int_{t_0}^{t} \eta(\tau)e^{(t-\tau)\partial_x f(\bar{x},\bar{\theta})} d\tau \tag{5}$$

Since $\partial_x f(\bar{x},\bar{\theta}) < 0$, the first term converges to zero as $t \to \infty$ (or $t_0 \to -\infty$) and therefore is called the transient part of the solution. We are interested in the rest, i.e., the persistent solution,

$$\xi(t) = \partial_\theta f(\bar{x},\bar{\theta}) \int_{-\infty}^{t} \eta(\tau)e^{(t-\tau)\partial_x f(\bar{x},\bar{\theta})} d\tau \tag{6}$$

Notice that the above defines a linear map $\Lambda : \eta \longmapsto \xi$ that converts fluctuations in the "input" θ into fluctuations in the "output" x.

In particular, we have

$$e^{i\omega t} \overset{\Lambda}{\longmapsto} \frac{\partial_\theta f(\bar{x},\bar{\theta})e^{i\omega t}}{i\omega - \partial_x f(\bar{x},\bar{\theta})} \tag{7}$$

i.e., $\eta(t) = e^{i\omega t}$ is an eigenfuction of Λ with corresponding eigenvalue

$$T(\omega) = \frac{\partial_\theta f(\bar{x},\bar{\theta})}{i\omega - \partial_x f(\bar{x},\bar{\theta})} \tag{8}$$

called the transfer function. The theory of Fourier series tells us that every (sufficiently smooth) periodic function can be written as a linear combination of countably many functions of the form $e^{i\omega t}$ for different values of ω. As a simple example, consider

$$\sin(\omega t) = \frac{e^{i\omega t} - e^{-i\omega t}}{2i} \tag{9}$$

Exploiting the linearity of Λ and the fact that $e^{i\omega t}$ and $e^{-i\omega t}$ are eigenfunctions with respective eigenvalues $T(\omega)$ and $T(-\omega)$, we have

$$\sin(\omega t) \overset{\Lambda}{\longmapsto} \frac{T(\omega)e^{i\omega t} - T(-\omega)e^{-i\omega t}}{2i} \tag{10}$$

which can be written more conveniently as

$$\sin(\omega t) \overset{\Lambda}{\longmapsto} |T(\omega)| \sin\big(\omega t + \arg T(\omega)\big) \tag{11}$$

where $|T(\omega)|$ is the modulus of the transfer function and $\arg T(\omega)$ its argument.

The significance of the transfer now becomes clear: (1) $|T(\omega)|$ is the ω-dependent gain, i.e., the factor by which fluctuations in the input θ of the specific frequency ω are amplified in the output x, and (2) $\arg T(\omega)$ is the phase-shift between the output and the input for fluctuations of the specific frequency ω.

2.2. **The population as a filter.** If the input θ combines different frequencies, then some of these frequencies are suppressed in the output x while others are amplified, and the phase-shift in the response is different for different frequencies as well. The population thus acts as a filter on the input signal.

For small fluctuations in the input, the filter characteristics of the population are given by the modulus and the argument of the transfer function. From equation (8) we have

$$|T(\omega)| = \frac{|\partial_\theta f(\bar{x},\bar{\theta})|}{\sqrt{\omega^2 + \partial_x f(\bar{x},\bar{\theta})^2}} \tag{12}$$

which is a decreasing function of $|\omega|$, i.e., high frequencies are suppressed, and so the population acts as a low-pass filter. The bandwidth of the filter is characterized by the so-called "cutoff frequency"

$$\omega_c = |\partial_x f(\bar{x},\bar{\theta})| \tag{13}$$

The meaning of the cutoff frequency is clear if we plot $|T(\omega)|$ against $|\omega|$ on a double logarithmic scale.

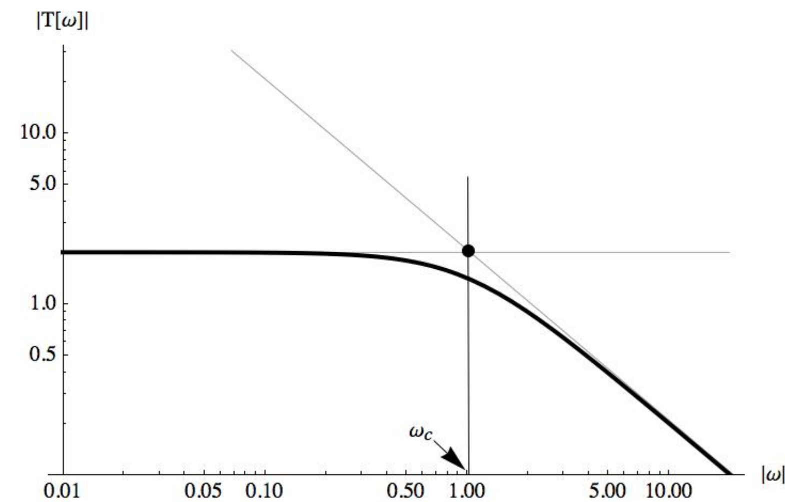

FIGURE 2. The gain as a function of signal frequency.

From equation (8) we also have

$$\arg T(\omega) = \arctan\left(\frac{\omega}{\partial_x f(\bar{x},\bar{\theta})}\right) \tag{14}$$

For low frequencies $|\omega|$ the phase-shift is small, obviously because the population has enough time to react to the changing input. Large phase-shifts of maximally $\pm\pi/2$ occur at high frequencies.

2.3. **The logistic equation.** We apply the above to the logistic equation

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right) \tag{15}$$

with

$$\begin{aligned} r &= b - d \\ K &= 2(b-d)/c \end{aligned} \tag{16}$$

(see section 1.8 of these lecture notes), and suppose that the birth rate and death rate fluctuate around their average values $\bar{b}$ and $\bar{d}$. How does this affect the population?

Only the difference of the birth rate and the death rate enters the equations. We therefore can write $\theta = b - d$ as a single fluctuating parameter and define

$$f(x, \theta) = \theta x \left(1 - \frac{cx}{2\theta}\right) \tag{17}$$

If θ is fixed at $\bar{\theta}$, then there is a stable equilibrium

$$\bar{x} = 2\bar{\theta}/c \tag{18}$$

Substitution of this into expression (8) for the transfer function gives

$$T(\omega) = \frac{2\bar{\theta}/c}{i\omega + \bar{\theta}} \tag{19}$$

and hence the gain is given by

$$|T(\omega)| = \frac{2\bar{\theta}/c}{\sqrt{\omega^2 + \bar{\theta}^2}} \tag{20}$$

the phase-shift by

$$\arg T(\omega) = -\arctan\left(\frac{\omega}{\bar{\theta}}\right) \tag{21}$$

and the cutoff frequency by

$$\omega_c = \bar{\theta} \tag{22}$$

We know already from the previous subsection that all populations described by a single ODE act as a low-pass filter. What we now see in addition is that in the present model the bandwidth as characterized by the cutoff frequency is independent of the contest rate c but increases linearly with the difference of the average birth and death rates $\bar{b} - \bar{d}$. The phase-shift, too, is independent of c but decreases in absolute value with $\bar{b} - \bar{d}$.

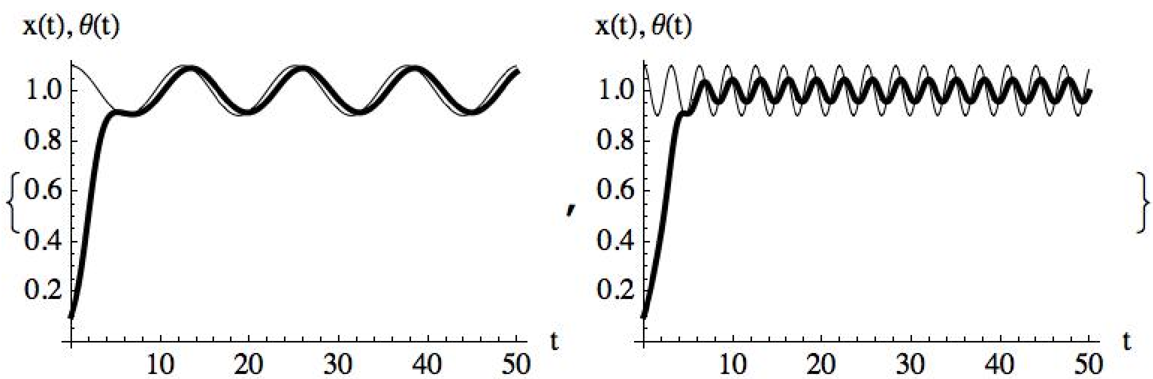

FIGURE 3. Gain and phase-shift in the response (bold lines) to inputs (thin lines) with different frequencies but the same amplitude.

Since a low-pass filter suppresses high frequencies, the response x to a mixed input θ containing many frequencies tend to look smoother than the input itself. This is illustrated by the next figure where the input is te linear combination of a hundred different sinusoids with random frequencies and phase-shifts.

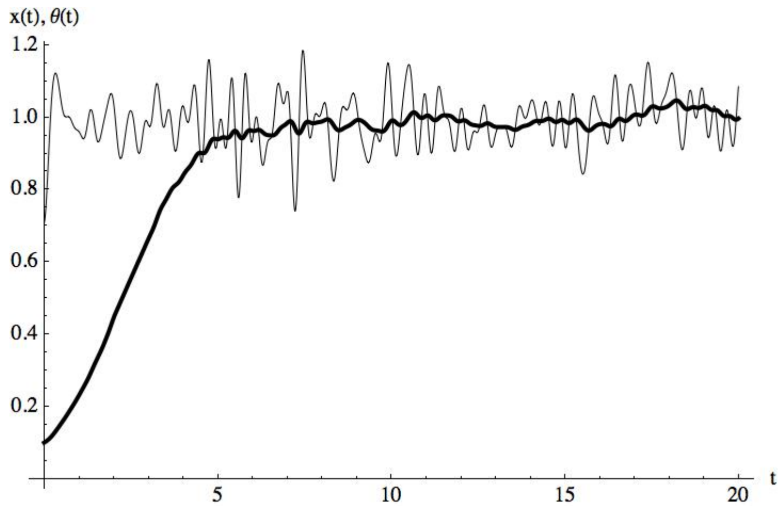

FIGURE 4. Smoothing effect of a low-pass filter.