A general approach to environmental red noise

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October 27, 2010

Abstract

The impact of environmental red noise is explored through the multivariate linear noise approximation. This allows a continuous time treatment that explicitly includes demographic noise and can describe non-equilibrium dynamics.

1 Theory

Consider a population $\phi(t)$ whose dynamics are described by

$$\dot{\phi}(t) = \alpha_{1,0}(\phi(t), \psi(t)) \tag{1}$$

where $\psi(t)$ represents the contribution of environmental variation on the population. The equilibrium variance in the population size is given by[1]

$$\langle \xi^2 \rangle_s = \frac{\alpha_{2,0} + \nu}{-2\partial_\phi \alpha_{1,0}} \tag{2}$$

Where ν describes the contribution of the environmental noise,

$$\nu = 2\frac{\left(\partial_\psi \alpha_{1,0}\right)^2 \sigma_\eta^2}{-\partial_\phi \alpha_{1,0} + 1/\tau_c} \tag{3}$$

Where we assume that the environmental variable ψ has mean zero, variance σ_η^2 and correlation time τ_c. Hence $\tau_c = 0$ represents a white noise process, while $\tau_c = \infty$ corresponds to perfect correlation. This equation is rather powerful, but requires some interpretation. First, we note that the contribution is proportional to the variance in the environmental variable, σ_η^2, as we might expect. Next, we see that the impact of the noise color depends on how the environmental correlation time compares to the correlation time of the population dynamics, $1/\partial_\phi \alpha_{1,0}$. If the correlation times of the environmental and population dynamics processes are significantly different, the smaller correlation time dominates. Hence if the correlation time of the environment is much longer than that of the population, its particular degree of correlation doesn't matter.

[1] See appendix B, equation (12).

The contribution is also proportional to the term $(\partial_\psi \alpha_{1,0})^2$ which describes how the population dynamics vary with changing environmental conditions.

It may seem strange that in the white noise limit $\tau_c \to 0$ that environmental noise makes no contribution. This is a consequence of the continuous-time formulation, or, more precisely, a consequence of the physical process driving the environmental noise. Simply, one can imagine that with no correlation time, the white noise fluctuations are simply being averaged out. A more meaningful explanation arises from a discussion of what gives rise to environmental red noise.

In the red-noise limit $\tau_c \to \infty$ we can write the variation as a sum of demographic noise and environmental contribution:

$$\langle \xi \rangle_s = \left(\frac{\partial_\psi \alpha_{1,0}}{\partial_\phi \alpha_{1,0}} \right)^2 \sigma_\eta^2 + \frac{\alpha_{2,0}}{2|\partial_\phi \alpha_{1,0}|} \tag{4}$$

2 Examples

Several examples will help to illustrate the usefulness of (3) in understanding the impact of environmental red noise.

2.1 logistic growth

Consider the logistic growth equation:

$$\alpha_{1,0} = r\phi \left(1 - \frac{\phi}{K(\psi)}\right) \tag{5}$$

The correlation time for the population dynamics is independent of how the environmental variation enters. At equilibrium $\phi_s = K$ we have:

$$\begin{aligned} \frac{\partial \alpha_{1,0}}{\partial \phi} &= r - \frac{2r\phi_s}{K} \\ &= -r \end{aligned}$$

We might imagine that r depends on environmental variation rather than K; but (3) tells us we can safely ignore this at equilibrium, as then

$$\frac{\partial \alpha_{1,0}}{\partial \psi} = \frac{\partial r(\psi)}{\partial \psi} \phi \left(1 - \frac{\phi}{K}\right)$$

which is necessarily zero at equilibrium $\phi = K$. Meanwhile, if K depends on the environmental variation, it enters as

$$\begin{aligned} \frac{\partial \alpha_{1,0}}{\partial \psi} &= \frac{r\phi_s^2}{K(\psi)^2} \frac{\partial K(\psi)}{\partial \psi} \\ &= r \frac{\partial K(\psi)}{\partial \psi} \end{aligned}$$

Hence (3) becomes:

$$\nu = 2\frac{\left(r\frac{\partial K(\psi)}{\partial \psi}\right)^2 \sigma_\eta^2}{r + 1/\tau_c}$$

Since this term is negligible in the white-noise limit as discussed earlier, consider for the moment the red-noise limit in which $r \gg 1/\tau_c$, and hence we can ignore the contribution of τ_c.

To evaluate the equilibrium population variance, equation (2), we need to know $\alpha_{2,0}$, which describes the strength of demographic fluctuations, and is given by the sum of birth and death rates. Until now we have not had to specify how the deterministic equation, $\alpha_{1,0}$, is partitioned into birth and death terms. Several choices are possible. For instance, the simplest choice is to consider density dependent death (the purely quadratic term) and density independent growth. Then at equilibrium for the logistic model we have

$$\alpha_{2,0}(\phi = K) = r\phi + \frac{r\phi^2}{K} = 2rK$$

The equilibrium population variance from (2) is then

$$\langle \xi^2 \rangle_s = K + \left(\frac{\partial K(\psi)}{\partial \psi}\right)^2 \sigma_\eta^2$$

Which is to say that the variance in the population is the sum of demographic variance and the variance in $K(\psi)$.

Alternate birth-death partitioning is possible. For instance, the Levins model has the same quadratic form, but provides a different partitioning which has a natural interpretation in the model as it is originally framed:

$$\alpha_{1,0}(\phi) = c\phi(1-\phi) - e\phi \tag{6}$$

By equation (4) the population variance is

$$\begin{aligned}\langle \xi^2 \rangle_s &= \frac{(\partial_\psi \alpha_{1,0})^2 \sigma_\eta^2}{c\left(1 - \frac{e}{c}\right)} + \frac{e}{c} \\ &= \frac{1}{c}\left(1 - \frac{e}{c}\right)\sigma_\eta^2 + \frac{e}{c}\end{aligned}$$

Consequently c can tune up or down the contribution of the environmental noise while keeping the equilibrium $1 - \frac{e}{c}$ the same.

A Comparison to the first-order autoregressive process

Red noise is often represented in discrete time by the first-order autoregressive process:

$$\psi_{t+1} = \rho\psi_t + \sqrt{1-\rho^2}\sigma Z_t \tag{7}$$

where Z_t is a standard (variance unity) normal random variable. We can compare this to the continuous time process given by the Langevin equation

$$\dot{\psi} = -\gamma\psi + \sqrt{2\gamma K_b T}\; Z(t) \tag{8}$$

Which has mean 0 and variance $K_b T$. To make the analogy to (7), we discretize (8) as

$$\begin{aligned} \frac{\psi_{t+1} - \psi_t}{\Delta t} &= -\gamma\psi_t + \sqrt{2\gamma K_b T}\; Z_t \\ \psi_{t+1} &= (1 - \Delta t\gamma)\,\psi_t + \Delta t\sqrt{2\gamma K_b T}\; Z_t \end{aligned}$$

The variance of this discrete equation is given by:

$$\begin{aligned} \langle\psi^2\rangle &= \frac{2\Delta t^2 K_b T\gamma}{1 - (1-\gamma\Delta t)^2} \\ &= \frac{2K_b T\Delta t}{2 - \gamma\Delta t} \end{aligned} \tag{9}$$

We can compare the continuous time Langevin equation (8) with the one-step Markov process with $s_+(\psi)$ and $s_-(\psi)$ step operators given by

$$s_+(\psi) = \gamma\psi \tag{10}$$

$$s_-(\psi) = \gamma\frac{\psi^2}{K_b T} \tag{11}$$

B Derivation from the linear noise approximation

The multivariate linear noise approximation for a partially coupled system is given by:

$$\frac{\mathrm{d}\langle\xi^2\rangle}{\mathrm{d}t} = 2\frac{\partial\alpha_{1,0}}{\partial\phi}\langle\xi^2\rangle + 2\frac{\partial\alpha_{1,0}}{\partial\psi}\langle\xi\eta\rangle + \alpha_{2,0} \tag{12}$$

$$\frac{\mathrm{d}\langle\xi\eta\rangle}{\mathrm{d}t} = \left(\frac{\partial\alpha_{1,0}}{\partial\phi} + \frac{\partial\beta_{1,0}}{\partial\psi}\right)\langle\xi\eta\rangle + \frac{\partial\alpha_{1,0}}{\partial\psi}\langle\eta^2\rangle \tag{13}$$

$$\frac{\mathrm{d}\langle\xi^2\rangle}{\mathrm{d}t} = 2\frac{\partial\beta_{1,0}}{\partial\psi}\langle\eta^2\rangle + \beta_{2,0} \tag{14}$$

We assume that the environmental variable is at equilibrium, $\langle\psi\rangle = \psi_s$ and $\langle\eta^2\rangle = \sigma_\eta^2$. The covariance term will be at equilibrium if either the population ϕ is near its equilibrium ϕ_s or if $\partial_\psi\beta_{1,0}$ dominates $\partial_\phi\alpha_{1,0}$ (that is, the environmental dynamics have a much shorter correlation time than the population dynamics). Taking both (13) and (14) to equilibrium, we can rewrite (12) as

$$\langle\xi^2\rangle_s = 2\frac{\partial\alpha_{1,0}}{\partial\phi}\langle\xi^2\rangle + 2\frac{\left(\partial_\psi\alpha_{1,0}\right)^2\sigma_\eta^2}{-\partial_\phi\alpha_{1,0} - \partial_\psi\beta_{1,0}} + \alpha_{2,0} \tag{15}$$