La vie en rose: extinction risk under environmental red noise

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Abstract

These notes are based on a chalk-talk I gave to Alan Hastings Lab Group, November 15, 2007. The original talk covered only sections 1-3, I have expanded the discussion for a more thorough treatement of Brownian motion. Details not included in the talk are provided in the appendices here.

1 Current Context

Ecologists have long been aware that much environmental noise is temporally correlated.

2 Roughgarden's Result

Ricker Model

$$N_{t+1} = N_t \exp\left(r\left(1 - \frac{N_t}{K_t}\right)\right) \tag{1}$$

$$\approx N_t\left(1 + r\left(1 - \frac{N_t}{K_t}\right)\right) \tag{2}$$

Recall $r \in (0,1)$, N_t approaches equilibrium monotonically, $r \in (1,2)$ approaches in damped oscillations, and $r > 2$ results in chaos. We'll assume $r \in (0,2)$. Take the transformation: $n_t = N_t - \bar{K}$ and $k_t = K_t - \bar{K}$. Substituting in and rearranging we have:

$$\left[1 - r\left(\frac{\bar{K}}{\bar{K} + k_t}\right)\right] n_t + r\left(\frac{\bar{K}}{\bar{K} + k_t}\right) k_t + r\left(\frac{k_t - n_t}{\bar{K} + k_t}\right) n_t \tag{3}$$

Near equilibrium, $1 - N_t/K_t \ll 1$, the first two fractions are approximately unity, while the last is approximately zero, and the behavior of the model can be approximated by the linear equation:

$$(1 - r)n_t + rk_t \tag{4}$$

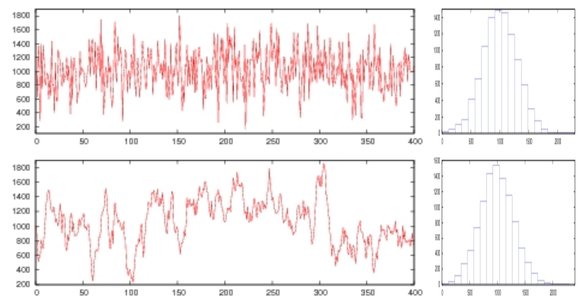

Figure 1: Top figure shows a white noise process, while bottom figure shows the same distribution under a red noise (first-order autoregressive) process. Histograms of the data (right) give the same underlying normal distribution. Correlation in the red noise process is strong ($\rho = 0.9$), and provides a more intuitive representation of environmental noise than the white-noise process at top.

taking $n_0 = 0$ (that is, $N_0 = \bar{K}$), we can iterate the expression and see:

$$n_1 = rk_0 \tag{5}$$

$$n_2 = (1-r)rk_0 + rk_1 \tag{6}$$

$$n_3 = (1-r)^2 rk_0 + (1-r)rk_1 + rk_2 \tag{7}$$

$$n_t = \sum_{i=1}^{t} r(1-r)^{i-1} k_{t-i} \tag{8}$$

Using this expression we can find various quantites of interest. For instance, the second moment $\langle n_t n_t \rangle \equiv \sigma_n^2$:

$$\langle n_t n_t \rangle = \langle \sum_{i=1}^{t} \sum_{j=1}^{t} r^2 (1-r)^{i-1} (1-r)^{j-1} k_{t-i} k_{t-j} \rangle \tag{9}$$

$$= \sum_{i=1}^{t} \sum_{j=1}^{t} r^2 (1-r)^{i-1} (1-r)^{j-1} \langle k_{t-i} k_{t-j} \rangle \tag{10}$$

The quantity $\langle k_{t-i} k_{t-j} \rangle$ is simply the covariance of the k_t. Defining the covariance function $\gamma_x(h) = \langle x(t)x(t+h) \rangle$ we have $\langle k_{t-i} k_{t-j} \rangle = \gamma_k(i-j)$. If we know something about the process generating k_t we can compute $\gamma_k(i-j)$ and then compute the sum. For instance, if k_t is a white-noise process, then $\gamma_k(i-j)$ is zero except when $i = j$ (because successive k_t are independent), where $\gamma(0) = \sigma_k^2$ is simply the variance of k_t. We then only have to sum over $i = j$ since all other terms are multiplied by $\gamma(i-j) = 0$. As we are interested in the long-term behavior[1] which we take $t \to \infty$. Then using the fact that

$$\sum_{i=0}^{\infty} s^i = \frac{1}{1-s} \qquad |s| < 1 \tag{11}$$

these sums (10) converge (recall $r \in (0, 2)$), and we can compute:

$$\begin{aligned}
\sigma_n^2 &= \sum_{i=1}^{\infty} r^2 (1-r)^{i-1} (1-r)^{i-1} \sigma_k^2 &(12)\\
&= r^2 \sigma_k^2 \sum_{i=1}^{\infty} (1-r)^{i-1} (1-r)^{i-1} &(13)\\
&= r^2 \sigma_k^2 \sum_{i=0}^{\infty} s^i \qquad \text{where } s \equiv (1-r)^2 &(14)\\
&= r^2 \sigma_k^2 \frac{1}{1-s} &(15)\\
&= \sigma_k^2 \frac{r^2}{1-(1-r)^2} &(16)\\
&= \sigma_k^2 \frac{r^2}{1-1+2r-r^2} &(17)\\
&= \frac{r}{2-r} \sigma_k^2 &(18)
\end{aligned}$$

A common model for temporally correlated noise is a first-order autoregressive (AR1) process, which simply assumes that k_{t+1} depends on its value in the previous year with strength $\rho \in (-1, 1)$:

$$k_t \sim \rho k_{t-1} + Z_t \tag{19}$$

where the Z_t are independent, identically distributed random numbers with $\langle Z_t \rangle = 0$ and $\langle Z_t^2 \rangle = \sigma_k^2$. In this case we then have $\gamma(h) = \sigma_k^2 \rho^{|h|}$.

Now all terms in the sum (10) contribute. Taking $s \equiv (1-r)$ we have

$$\begin{aligned}
\sigma_n^2 &= r^2 \sigma_k^2 \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} s^{i+j} \rho^{|i-j|} &(20)\\
&= r^2 \sigma_k^2 \sum_{i=0}^{\infty} \sum_{h=-\infty}^{\infty} s^{2i+h} \rho^h &(21)\\
&= r^2 \sigma_k^2 \sum_{i=0}^{\infty} s^{2i} \sum_{h=-\infty}^{\infty} s^h \rho^{|h|} &(22)
\end{aligned}$$

[1] we could equally well treat this as finite sums to time T, but this would require that we know how long it has been since we began at $n_t = 0$. It is simpler to assume we started this process some point in the distant past.

Then summing over i and multiplying by $r^2\sigma_k^2$ gives us the same term we found before in (18), $\frac{r}{2-r}\sigma_k^2$. The sum over h can be rewritten, giving us

$$\sigma_k^2 \frac{r}{2-r}\left(1 + 2\sum_{h=1}^{\infty}(s\rho)^h\right) \tag{23}$$

where we get the 1 from the $h = 0$ case and the factor of 2 accounts for all the pairs of terms $\pm h$.[2] Then this sum is also of the form (11), but starting at 1 (so we have to subtract $s^0 = 1$ from the answer). Hence expression (23) becomes

$$\sigma_n^2 = \sigma_k^2 \frac{r}{2-r}\left(1 + 2\left(\frac{1}{1-(1-r)\rho} - 1\right)\right) \tag{24}$$

$$= \sigma_k^2 \frac{r}{2-r}\left(\frac{2}{1-(1-r)\rho} - 1\right) \tag{25}$$

$$= \sigma_k^2 \frac{r}{2-r}\frac{2-1+(1-r)\rho}{1-(1-r)\rho} \tag{26}$$

$$\boxed{\sigma_n^2 = \frac{r}{2-r}\frac{1+(1-r)\rho}{1-(1-r)\rho}\sigma_k^2} \tag{27}$$

This is a very useful expression. First, we observe that it reduces to equation (18) when $\rho = 0$, as it should. Next, we observe that this result explains the descrepancy investigated by [3].

We also demonstrate that these predictions can be matched to simulations.

3 Extinction Probabilities – Beyond Moments

3.1 Fieberg and Ellner

This is the general density-independent approach, which will apply to small populations for any deterministically persisting, density dependent model and which can easily be extended to structured populations. See [1].

$$N_{t+1} = (1 + r_t)N_t \tag{28}$$

$$\log(N_{t+1}) = \log(1 + r_t) + \log(N_t) \tag{29}$$

$$x(t+1) = x(t) + L(t) \qquad \text{where } x(t) = \log(N_t) - \log(N_0) \tag{30}$$

$L(t)$ has mean μ_r equal to the minus the drift rate, (equal to the mean of $\log(1 + r_t)$), and variance σ^2. Note that r_t must be distributed such that $1 + r_t$ is always positive. This looks like Brownian motion with drift. *Under the requirement that $L(t)$ are independent random variables* the first passage times

[2] If you imagine the summation over all i and j as summing over a matrix of elements a_{ij}, then the unity is the contribution of the diagonal, and while the matrix is symmetric so all off-diagonal elements occur twice.

are well understood, and can be characterized as follows [6]. The probability that the population has gone extinct (at a time we define as τ) by time T is given by:

$$\mathbf{P}(\tau < T) = \Phi\left(\frac{-\mu_r T - N_0}{\sqrt{\sigma^2 T}}\right) + \exp\left(\frac{-2\mu_r N_0}{\sigma^2}\right)\Phi\left(-\frac{-\mu_r T + K}{\sqrt{\sigma^2 T}}\right) \tag{31}$$

Where $\Phi(z)$ is the cumulative standard normal distribution. In the case of zero average growth (zero drift, $\mu_r = 0$), this simplifies to:

$$P(\tau < T) = 2\Phi\left(\frac{-K}{\sqrt{\sigma^2 T}}\right) \tag{32}$$

If $\mu_r < 0$, then the population faces deterministic extinction. In this case we can then also calculate the distribution of extinction times, which is simply the probability density function (derivative) of the cumulative distribution (31). This is known as the inverse Gaussian distribution:

$$p(T) = \sqrt{\frac{\lambda}{2\pi T^3}}\exp\left(\frac{-\lambda(T-\mu)^2}{2\mu^2 T}\right) \tag{33}$$

where $\lambda = N_0^2/\sigma^2$ and $\mu = -a/\mu_r$. The mean time to extinction is μ, while λ is a shape parameter. Smaller λ (larger σ^2) result in a more left-skewed distribution, with most extinctions happening very early coupled with a long tail of low probability, long living populations. Note that this allows most populations to go extinct very early *despite the mean extinction time being unchanged*. These predictions can be confirmed by simulation.

[1] attempts to calculate an effective σ^2 under correlated (first order autoregressive) noise. In this way correlation increases the effective σ^2, with the increased extinction risk (but not increased average) consequences discussed above. My understanding is that this is done using similar techniques as before (11), (27),

$$\sum_i \sum_j \langle \mu_r(t-i)\mu_r(t-j)\rangle = \tag{34}$$

$$\sum_i \sum_j \rho^{i-j}\sigma^2 = \tag{35}$$

$$\frac{1+\rho}{1-\rho}\sigma^2 \tag{36}$$

It is unclear that such a technique is permissible, since it violates the independence assumption upon which the derivations of [6] rely.

$$\dot{n} = an - n^2 \tag{37}$$

$$\ddot{n} = a - 2n \tag{38}$$

References

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