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LETTER

Viability in a pink environment: why "white noise" models can be dangerous

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Abstract

Analysis of long time series suggests that environmental fluctuations may be accurately represented by $1/f$ noise (pink noise), where temporal correlation is found at several scales, and the range of fluctuations increases over time. Previous studies on the effects of coloured noise on population dynamics used first or second order autoregressive noise. I examined the importance of coloured noise for extinction risk using true $1/f$ noise. I also considered the problem of estimating extinction risk with a limited sample of environmental variation. Pink noise environments increased extinction risk in random walk models where environmental variation affected the growth rate. However, pink noise environments decreased extinction risk in the Ricker model where environmental variation modified the carrying capacity. Underestimation of environmental variance almost always yielded underestimation of extinction risk. For either population viability analysis or management, we should carefully consider the long-term behaviour of the environment as well as how we include environmental noise in population models.

Keywords

$1/f$ noise, environmental variation, extinction risk, population dynamics, population viability analysis, red noise

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INTRODUCTION

Ecologists have long recognized that environmental variation has important effects on population dynamics (Andrewartha & Birch 1954). Although discussion about the relative roles of density dependence and density independence still continues (Murdoch 1994; Turchin 1995), it is clear that deterministically growing populations can be driven to extinction by environmental stochasticity. This "environmental noise" is usually incorporated into models used to estimate extinction risk or to assess management decisions (Groom & Pascual 1998). Typically, environmental variability is modelled by sampling from some probability density function, or by bootstrapping observed population parameters. As a consequence, the values in two consecutive time steps are independent and environmental variance is fixed over time (white noise). However, analyses of long time series suggest that fluctuations in population size and environmental factors are positively autocorrelated, resulting in "reddened" spectra (Mandelbrot & Wallis 1969; Steele 1985; Lawton 1988; Pimm & Redfearn 1988; Ariño & Pimm 1995; Miramontes & Rohani 1998).

Recent investigations have shown that a red environment can either increase or decrease extinction risk depending on model structure (Mode & Jacobson 1987; Ripa & Lundberg 1996; Johst & Wissel 1997; Petchey *et al.* 1997; Heino 1998). All of these authors made their environmental fluctuations reddish using a first order or second order autoregressive process (AR1, AR2), in which correlation decreases exponentially with time, and the variance quickly converges to a fixed value. However, long time series usually show a slower decline in autocorrelation, which is better represented by $1/f$ noise (pink noise), where the power (magnitude) of fluctuations is inversely proportional to their frequency f (Press 1978; Keshner 1982; Halley 1996). In contrast with AR1 and AR2, $1/f$ noise has temporal correlation at a multitude of scales, and the longer we observe a process the larger the range of fluctuations becomes. I examine two problems related to coloured environments: (i) how does environmental colour affect extinction risk?, and (ii) how does underestimation of environmental variance due to small sample size affect calculations of extinction risk in pink noise environments?

METHODS

The same environmental factor can be effectively white noise, pink noise, or static environment for populations with different time scales of variation (Nisbet & Gurney 1982). I consider yearly fluctuations in the environment affecting a truly annual population, which ignores smaller scale variations. I simulated population dynamics for 200 "years" in environments of different colours (white noise, pink noise, and AR1), and calculated extinction probabilities based on 1000 replicates. To explore the problem of assessing extinction risk with a limited sample of environmental variability, I compared extinction time under pink noise environments with those obtained with white noise where environmental variance was calculated from samples of 10, 50, and 100 years of the coloured noise.

Environments

To generate a $1/f$ noise time series of $x = 50{,}000$ time steps, I added cosine waves with frequencies (f) from 1 to $x/2$, and phases (δ_f) randomly and uniformly distributed between one and x (Hastings & Sugihara 1993). For every frequency, its amplitude (c_f) was drawn from a normal distribution with zero mean and variance equal to $1/f$ (note that $1/f^0$ yields white noise). The value for the time series p at time t is

$$p_t = \sum_{f=1}^{x/2} c_f \cos\left(2\frac{\pi}{x} ft - \delta_f\right) \qquad (1\ \ )$$

where $2\pi/x$ is included so that the time series has a complete cycle of length x. For every population simulation I randomly choose a 200-year segment of $1/f$ noise and re-scaled it to zero mean and unit variance. To make my results comparable to previous work, I ran population models using AR1

$$\varnothing_{t+1} = \alpha\varnothing_t + \varepsilon_{t+1} \qquad (2)$$

where α is an autocorrelation parameter ($|\alpha| < 1$) and ε is normally distributed white noise with zero mean and unit variance (N(0,1)). Positive values of α produce time series shifted to the red. I set a very strong positive autocorrelation ($\alpha = 0.999$), and re-scaled the time series to zero mean and unit variance. For white noise environments, I sampled from a normal distribution.

Random walk models

The effects of environmental fluctuations on population dynamics have been studied using random walk models and their diffusion approximations (e.g. Turelli 1977; Dennis *et al.* 1991; Lande 1993; Foley 1994)). The general model is a continuous time Brownian motion with drift. I used the discrete time version

$$n_{t+1} = n_t + r_d + \sqrt{\nu_r}\varepsilon_{t+1} \qquad (3\ \ )$$

where r_d is the population growth rate. The variance (ν_r) is calculated from $1/f$ noise and depends on the sample size, and ε_{t+1} is the value at time t_{+1} of a N(0,1). In the coloured noise versions of this model, and those considered below, the terms $\nu_r\varepsilon_{t+1}$ are replaced by p_{t+1}, or AR1 t_{+1} for $1/f$ and AR1 noise, respectively.

When density dependence occurs only near the carrying capacity, the appropriate diffusion approximation has a reflecting boundary at $k = \log_e K$, and an absorbing boundary at $n = 0$ (Lande 1993). I used a discrete time version

$$n_t = \min\ \left\{n_t + r_d\sqrt{\nu_r}\varepsilon_{t+1}\ , k\right\} \qquad (4\ \ )$$

Ricker model

A more complex density dependence can be modelled by letting the carrying capacity of the Ricker equation be a function of environmental variation.

$$N_{t+1} = N_t \exp\ \left[r\left[1 - \left(\frac{N_t}{K_{t+1}}\right)^b\right]\right] \qquad (5\ \ )$$

where N_t is the population size at time t, r is maximum growth rate for very low densities, and K is carrying capacity. The value of the carrying capacity at time t_{+1} (K_{t+1}) is equal to the mean carrying capacity (K_0) plus $\beta\varepsilon_{t+1}$, where β is a parameter determining the magnitude of environmental variation and ε_{t+1} is a N(0,1), replaced by p_{t+1}, or $\mathrm{AR1}_{t+1}$ in the coloured versions. The parameter b controls the dynamics from overcompensation when $b = 1$ to under-compensation when b is close to 0.1, with compensation somewhere in between.

RESULTS

Environmental variance known

For random walk models (with and without ceiling), autocorrelation resulted in higher extinction risk (Fig. 1). In a pink noise environment the extinction risk is less sensitive to population parameters. The differences in population extinction risk between white noise, AR1, and pink noise depended on the parameter combinations. Bigger population growth and smaller overall environmental variance resulted in a general increase in population survival, but also in greater difference between noise types. The Ricker model showed trends opposite to those of the random walk models; populations under white noise had higher extinction risk than those under AR1, or

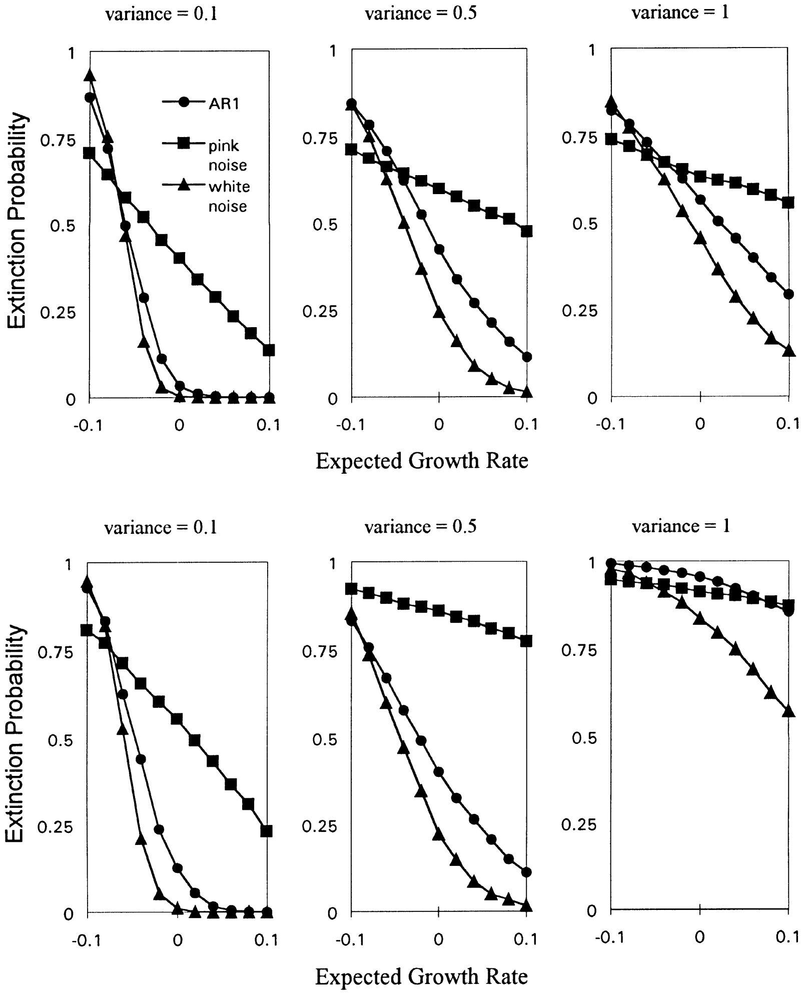

Figure 1 Extinction probabilities at a 100-year horizon under different types of environmental noise evaluated in random walk models with different expected population growth (r_d), and environmental variance. Upper graphs, unbounded populations; initial population size = 1000. Lower graphs, populations with a ceiling; initial population size = carrying capacity (K) = 1000.

pink noise (Fig. 2). As expected, extinction risk was higher when *b* was close to one, leading to overcompensation (Fig. 2).

Environmental variance estimated from samples of 1/*f* noise

Extinction risk was almost always underestimated when environmental variance was calculated from 10 year samples, and was usually underestimated with 50 year samples. This result was consistent for all population models studied here (Fig. 3). For the Ricker model, underestimation of extinction risk was more pronounced when density dependence was weak (Fig. 3).

DISCUSSION

Previous studies on the effects of "coloured" environments on extinction risk used first or second order autoregressive noise, and assumed perfect knowledge of noise characteristics (distribution, variance, and correlation structure). Here I used true 1/*f* noise, and also examined the problem of having a limited sample size when estimating environmental variance. As shown elsewhere using autoregressive noise (summarized in Kaitala *et al.* 1997a), or in a more general context (Pascual *et al.* 1997), my results suggest that noise effects on population extinction depend on model structure. Populations modelled as a random walk went extinct by becoming too small. In these models, environmental fluctuations affected the growth rate, and a reddish environment increased the chance of having several bad years in a row. In contrast, under the Ricker model, populations went extinct after a proportionally big reduction in carrying capacity, and positively correlated environments led to longer population persistence. The effects of AR1 and pink noise on extinction risk were qualitatively similar but pink noise had a stronger effect (Figs 1 and 2).

My results give quantitative support to the intuitive concern of several authors (Steele 1985; Ariño & Pimm 1995; Halley 1996; Lawton 1997) regarding the use of white noise as a model for environmental variation.

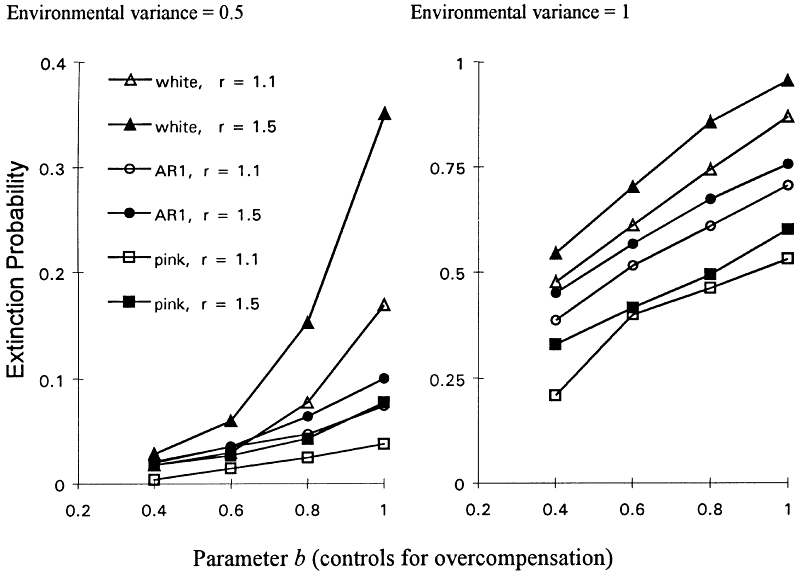

Figure 2 Extinction probabilities at 100 years horizon for the Ricker model under different types of environmental noise. Average carrying capacity (K_0) = initial population size = 100.

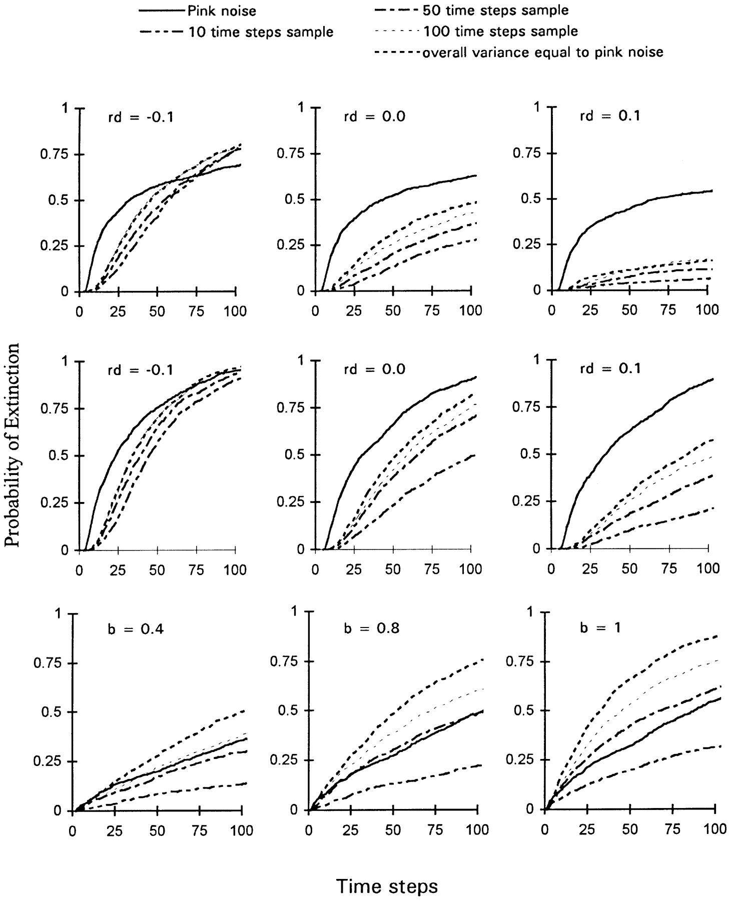

Figure 3 Cumulative extinction probabilities for random walk populations under pink noise. Overall environmental variance for pink noise is one. Dashed lines are white noise estimations where variance was calculated from pink noise samples. Upper graphs, random walk without ceiling. Initial population size = 1000. Middle graphs, random walk with ceiling at carrying capacity. Initial population size = carrying capacity (K) = 1000. Lower graphs, Ricker model where carrying capacity is pink noise. Average carrying capacity (K_0) = initial population size = 100, growth rate (r) = 1.1. Parameter b controls intensity of density dependence.

Although any real situation will be much more complicated than the case presented here, my results identify two potential sources of error when using white noise to model environmental variation. The first is related to the temporal structure in the environment (autocorrelation). The second is more subtle; white noise models assume that environmental factors vary within observed values. Ludwig (1999) has recently pointed out the difficulties in obtaining a good estimate of population growth, which in turn results in wide confidence intervals for extinction probabilities. Although in a pink noise environment extinction risk is less sensitive to population parameters (Fig. 2), an autocorrelated environment will make estimations of expected growth rate more difficult, resulting in more error.

For a particular species of interest we should ask which scales of environmental variation are relevant to their populations or metapopulations. One could then construct environmental fluctuations as I did here, but explicitly include those frequencies and amplitudes believed to be important. It is possible to simulate environments with annual variations, as well as less frequent events such as pest outbreaks, El Niño, or extreme environmental conditions. This approach would be analogous to including catastrophes in time series (see Mangel & Tier 1994). With $1/f$ noise, however, "normal" and "unusual" environmental values are part of the same process.

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BIOSKETCH

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