LUND UNIVERSITY

Extinction risk under coloured environmental noise

Heino, M; Ripa, Jörgen; Kaitala, V

Link to publication

Extinction risk under coloured environmental noise

Mikko Heino, Jörgen Ripa and Veijo Kaitala

Positively autocorrelated red environmental noise is characterized by a strong dependence of expected sample variance on sample length. This dependence has to be taken into account when assessing extinction risk under red and white uncorrelated environmental noise. To facilitate a comparison between red and white noise, their expected variances can be scaled to be equal, but only at a chosen time scale. We show with a simple one-dimensional population dynamics model that the different but equally reasonable choices of the time scale yield qualitatively different results on the dependence of extinction risk on the colour of environmental noise: extinction risk might increase as well as decrease when the temporal correlation of noise increases.

M. Heino (mikko.heino@helsinki.fi), Div. of Population Biology, Univ. of Helsinki, Box 17, FIN-00014 Helsinki, Finland. – J. Ripa, Dept of Theoretical Ecology, Lund Univ., Ecology Building, SE-223 62 Lund, Sweden. – V. Kaitala, Dept of Biological and Environmental Sciences, Univ. of Jyväskylä, Box 35, FIN-40351 Jyväskylä, Finland.

How do temporal correlations in environmental variability influence risk of population extinction? This is an important question in conservation biology, which calls both for analysis of empirical data sets, and for theoretical studies on model populations (Lawton 1997, Kaitala et al. 1997). Empirical data show that many biotic and abiotic time series are positively autocorrelated, i.e. they are red-shifted (Pimm and Redfearn 1988, Schroeder 1991, Ariño and Pimm 1995). In effect, positive autocorrelation means that a bad year is likely to be followed by another bad year. A commonly expressed intuitive argument is that temporally correlated environments lead to higher risk of population extinction than white noise environments, where long runs of bad years are unlikely (Lawton 1997).

Surprisingly, theoretical studies have yielded no general results on the influence of temporal correlations on extinction risk. Only few papers give strong support to the intuitive argument that red-shifted environments pose a higher risk of extinction than white noise environments (Foley 1994, Johst and Wissel 1997, Petchey et al. 1997), whereas others show opposite (Roughgarden 1975, Ripa and Lundberg 1996) or indecisive results (Mode and Jacobson 1987a, b, Petchey et al. 1997, Heino 1998, Cuddington and Yodzis 1999). In this paper we show that seemingly subtle differences in modelling of noise help to explain differences in the results.

The theoretical approach boils down to comparing behaviour of a model of population dynamics under the alternative assumptions of red and white environmental noise, the latter being de facto null model of noise in ecology. Intuitively, the comparison should be made between white and red noise which are somehow as similar as possible, except for "colour". But what is a proper criterion for similarity? Variability obviously counts when dealing with questions related to extinction risk. Thus, variances of red and white environmental noise should be similar. However, there is a major conceptual problem: no unambiguous criterion for similarity exists. Expected variance of environmental noise changes with length of a time interval, and the strength of this response depends strongly on colour. In statistical terms, the expected sample variance depends on the length of the sample, and on the correlation structure of the time series.

In this paper we first analyze the dependence of variance on sample length in a first-order autoregressive process, and present some methods on how to tackle with this complication. We then show how different scaling procedures influence predictions on extinction risk in a simple population dynamics model.

Sample variance in autoregressive processes

The behaviour of the expected sample variance can be demonstrated with the simplest possible model for coloured noise, the first-order autoregressive process (AR(1)) – practically the standard model for correlated noise (but see Cuddington and Yodzis 1999). The magnitude of environmental noise at time t depends only on its previous value, and some random influence:

$$x_t = \begin{cases} 0 & \text{for } t = 0 \\ \alpha x_{t-1} + \beta \epsilon_{t-1} & \text{otherwise,} \end{cases} \quad (1)$$

where $\beta > 0$ is a constant parameter scaling the variance of time series, and α ($|\alpha| < 1$) is a constant autocorrelation parameter, and ϵ_t are normally distributed uncorrelated random variates with zero mean and unity variance. Autocorrelation parameter α determines the colour of the resulting time series: for $\alpha > 0$, the time series $\{x_t\}$ is positively correlated (red-shifted), while $\alpha < 0$ results to negative correlation (blue-shift). Nega-

tively autocorrelated noise is unlikely to be important in nature, but is included in this section for the sake of completedness. If there is no autocorrelation ($\alpha = 0$), the time series is white noise.

The true variance of time series $\{x_t\}$ (the variance of time series of infinite length) is $\beta^2/(1 - \alpha^2)$ (thick line in Fig. 1a; for a derivation, see e.g. Chatfield 1996, pp. 35–36). The expected variance of a sample of length T, assuming that $t \gg 0$ such that the initial condition has no effect, is (see the Appendix for the derivation):

$$E(s^2) = \frac{\beta^2}{(1 - \alpha^2)(T - 1)} \left(T - \frac{(1 + \alpha)^2}{1 - \alpha^2} + \frac{2\alpha(1 - \alpha^T)}{T(1 - \alpha)^2} \right). \quad (2)$$

This result has earlier been given in slightly different form by McArdle (1989). If noise is positively autocorrelated, its variance is lower the shorter the sample, as illustrated in Fig. 1a. The opposite is true for negatively autocorrelated noise. For white noise, the expected sample variance does not depend on sample length.

Because of the strong increase in variance with increasing autocorrelation parameter α in model (1), it is expected that the extinction risk increases with increasing autocorrelation of environmental noise. This intuitive reasoning has been confirmed by Mode and Jacobson (1987a, b) and Johst and Wissel (1997). However, this result is not straightforward to interpret: the effect of change in colour will be masked by the effect of increased variance. An elegant solution to this prob-
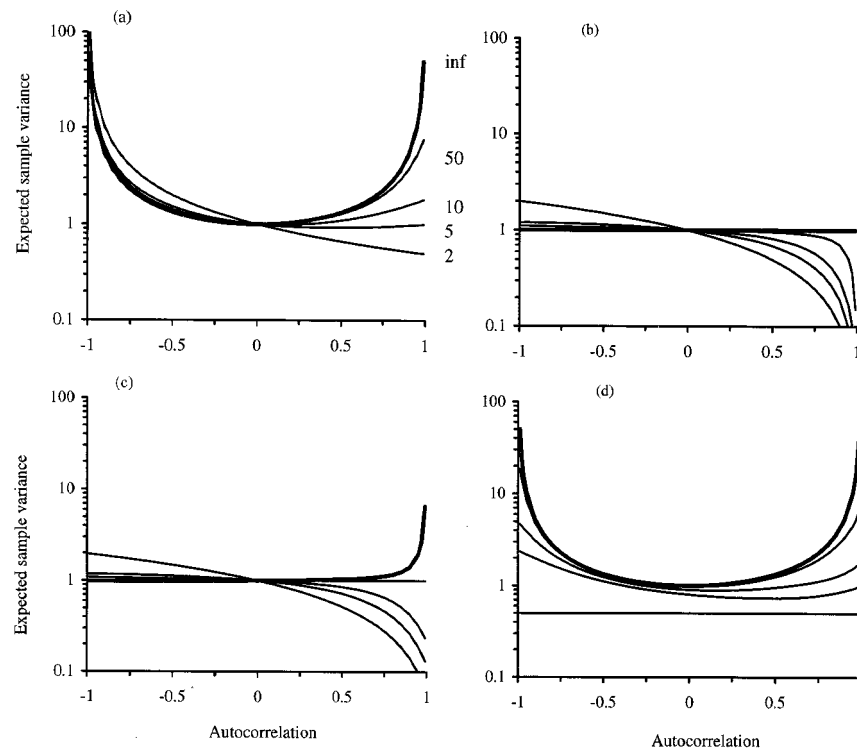
Fig. 1. Dependence of expected sample variance (thin lines for samples of different lengths: T = 2, 5, 10 and 50) and asymptotic variance (thick lines; sample length "infinity") on autocorrelation in the first-order autoregressive process (eq. 1). In (a), parameter β is constant at unity for all values of the autocorrelation parameter α. In (b) and (c), β depends on α such that the asymptotic variance and expected variance in samples of 50, respectively, are constant. Now the expected variance in short samples is greatly reduced if autocorrelation parameter α is large. In (d), if the process (eq. 1) is started from its mean value (zero), then the variance of the first T values is smaller than in random samples of the same length (a).

Fig. 2. Examples of time series (with their marginal distributions) of different colour and scaling of variance. (a) White noise ($\alpha = 0$) with $\beta = 12$. (b)–(d) Red noise with $\alpha = 0.95$. In (b), $\beta = 12$ as in (a) (white noise). In panels (c)–(d) the parameter β is chosen such that the expected variance for the first 50 values (c) or asymptotic variance (d) of the whole time series is the same as for white noise process in (a). All the time series are based on the same random numbers. Sample variances of the particular time series are inserted.
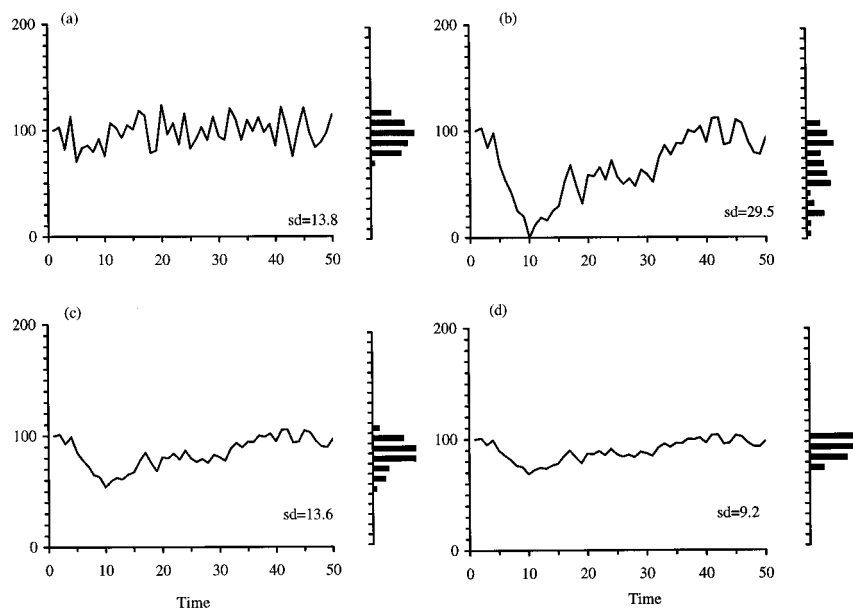
lem is to scale the time series such that its true variance is independent of the α by letting the parameter β be a function of α:

$$\beta \equiv \beta(\alpha) = \sigma_\infty \sqrt{1 - \alpha^2}, \tag{3}$$

where σ_∞^2 is the desired asymptotic variance of noise. This scaling has been used by many authors, e.g. Roughgarden (1975), Foley (1994), Ripa and Lundberg (1996) and Petchey et al. (1997). However, rescaling the noise has also its shortcoming: the expected variance in short samples is greatly reduced if autocorrelation parameter α is large, say > 0.5 (see Fig. 1b). In an extreme case, when α approaches one, short time series show hardly any variability. At short time scales, red noise with the same asymptotic variance as white noise is "milder" than white noise. Not surprisingly, under such scaling of noise, extinction risk may strongly decrease when noise gets more strongly autocorrelated (see below).

The two extremes, no scaling at all ($\beta = $ constant) and scaling to uniform variance at infinity (eq. 3), are not the only options: expected sample variance can be independent of autocorrelation parameter α at some finite time scale. One natural choice for the time scale of equal variances is the length of period over which extinction risk is evaluated: in this case, a comparison between red and white noise is made between time series with equal variability over the whole period, but with different temporal structure, i.e. colour. It is even possible (but very unlikely) that white and red time series have the same data points, but in different order. Figure 1c exemplifies a scaling to equal variability at the time scale of 50 time steps.

A final snag is that starting an autoregressive process (1) from its mean value ($x_0 = 0$) results in decreased variability in the beginning of the time series. The expected variance of the first T values becomes (see the Appendix)

$$E(s^2 | x_0 = 0) = \frac{\beta^2}{(1 - \alpha^2)(T - 1)}$$
$$\times \left(T - \frac{2 + 2\alpha + \alpha^2 - \alpha^{2T}}{1 - \alpha^2} + \frac{(1 - \alpha^T)(1 + 2\alpha - \alpha^T)}{T(1 - \alpha)^2} \right). \tag{4}$$

Figure 1d shows the dependence of the expected variance of first n values on the autocorrelation. There is a marked decrease in the variance of the very first values, especially for noise with negative correlation. This has to be taken into account if extinctions are scored over some short time period.

Scaling noise – an example

To cast the issue of scaling to a practical context, we have simulated some hypothetical time series of carrying capacities with a model $K_t = 100 + x_t$, where x_t is given by eq. (1). The first time series (Fig. 2a) is white noise with $\beta = 12$, yielding expected asymptotic variance equal to 12^2. In Fig. 2b, there is a strongly correlated ($\alpha = 0.95$) time series with the same β. The carrying capacity has now an asymptotic variance of $\sim 38.4^2$, and is seen to fluctuate wildly to very low values. In this exaggerated example, it would be expected that the red-shifted environment is more dangerous to some model population than the white

environment. However, it is difficult to tell apart the effects of high variability and colour, i.e. low carrying capacity per se, and low carrying capacity several time steps. A more informative procedure would be to compare white noise with the red time series in Fig. 2c with $\beta \sim 5.64$, such that both time series have the same expected variance (11.9^2) for the first 50 time steps. The last panel (Fig. 2d) represents time series scaled (with $\beta \sim 3.75$) to have the asymptotic variance as white noise in Fig. 2a, and has, in consequence, fairly tame short term fluctuations.

Each of the red time series, or more properly, each process that were used to create them in Fig. 2 could be used to assess influence of red-shift to extinction risk, with fairly good justification. Short pieces of the unscaled time series (Fig. 2b) seem to have much the same variability as the white one. This is no coincidence because in unscaled noise the expected variance is roughly constant in samples of length five (see Fig. 1a)! Thus, in a sense, unscaled red noise from model (1) is similar to white noise at a very short time scale. The time series scaled to have the same variance at an intermediate time scale has a very similar 'spread' of the carrying capacities (compare the marginal distributions). Finally, red noise in Fig. 2d is similar to white noise when it comes to the very long term properties of the time series. The bottom line is that the variabilities of time series of different colours can be similar only at some time scale, while at all other time scales they are bound to differ. Any choice of the time scale is always somewhat arbitrary. Nevertheless, this choice will greatly influence the predictions on extinction risk, as is shown in the examples below.

Colour of noise and extinction risk

Population dynamics model

We used the generalized, individual-based version of the Moran-Ricker model used by Petchey et al. (1997), where demographic stochasticity is accounted for by drawing the population size in next generation from the Poisson distribution with its deterministic value as the mean:

$$N_{t+1} = \text{Poisson}(N_t \exp(r(1 - (N_t/K_t)^b))), \qquad (5)$$

where r is intrinsic growth rate and parameter b determines the nature of density dependence (overcompensatory for $b = 1$ and undercompensatory for $b = 0.1$). Ripa and Lundberg (1996) also used eq. (5) as the basic model, but with $b = 1$ and without demographic stochasticity. Equation (5) can produce complex dynamics, although we use here parameter values which would in the deterministic formulation result in equilibrium dynamics. As in Ripa and Lundberg (1996) and

Petchey et al. (1997), environmental noise is assumed to influence carrying capacity, such that $K_t = K + x_t$. We did not assume any lower limit for K_t. However, $K_t \leq 0$ was taken to imply an extinction.

We took the proportion of replicate runs that ended in extinction as an estimate of extinction probability; 10^4 replicates were used. Simulations were initiated with $N_0 = K_0 = 100$ and run for 50 or 1000 time steps.

Simulation results

We now focus only on noise with non-negative correlation. The qualitative predictions of the influence of noise colour on extinction risk in the Moran-Ricker model are sensitive to the assumptions on scaling (Fig. 3). If the dynamics are overcompensating, scaling the noise such that its asymptotic variance is independent of its colour causes the extinction risk to steadily decrease with increasing autocorrelation (red-shift) (Fig. 3c). If there is no scaling at all (Fig. 3a), extinction risk increases strongly with increasing autocorrelation, except for low correlations ($\alpha \lesssim 0.25$). In the intermediate case (Fig. 3b), where the scaling is such that the expected variance is independent of colour, extinction risk first decreases with increasing autocorrelation, followed by a small increase for strong correlations.

For undercompensating dynamics, lower extinction risk under red than white noise is observed only if the time scale of uniform variance is in infinity (Fig. 3d–f). If correlation is low, there is hardly any change in extinction risk, however. In all the cases, extinction risk is lower for undercompensating than for overcompensating dynamics. Studying the population size and carrying capacity helps to gain understanding on the results. If density dependence is overcompensating, extinctions occur mostly as population crashes where population size prior to the extinction is high above the carrying capacity, resulting in virtually zero recruitment to the next generation (Fig. 3g). However, if noise is strongly correlated, an increasing fraction of extinctions are caused by environment becoming uninhabitable, i.e. $K_t \leq 0$ (dotted lines in Fig. 3a–f). In case of undercompensating dynamics, this is practically always the cause of extinction (Fig. 3h). The population size prior to the extinction tends still to be much higher than the carrying capacity, but this happens because undercompensating population is tracking the environment slowly. Extinction because of demographic stochasticity is unlikely simply because population size do not stay low long enough – usually an extinction because uninhabitable environment occurs first. Thus, for populations with undercompensating dynamics, the extinction risk is really a characteristic of the environment, not population dynamics.

The influence of different scaling procedures is similar in longer assessment periods (1000 generations): for

180

unscaled noise (Fig. 4a, d), extinction risk increases with increasing correlation of noise, whereas an opposite pattern is observed if asymptotic variance of noise is independent of its colour (Fig. 4c, f). Scaling at an intermediate scale (50 generations) yields a marked increase in extinction risk with increasing autocorrelation for undercompensatory dynamics (Fig. 4b), but indecisive results for overcompensatory dynamics (Fig. 4e). The time scale of 50 generations, however, is here very arbitrary. In longer samples, the difference between expected sample variance and asymptotic variance gets insignificant, except for very high autocorrelations. Accordingly, dependence of extinction risk on noise colour gets increasingly similar. However, for very high autocorrelations, an increase in extinction risk can always be observed. Changing the assessment period does not change observed population sizes and carrying capacities prior to extinctions.

Discussion

Assessing the influence of coloured noise on extinction risk is confounded by their complex temporal structure. In coloured noise, sample variance depends on sample length, which is not the case for white noise. By scaling the variance in a proper manner, it is possible to make fair comparisons between red and white noise environments, in a sense that their expected variabilities are the

same at some time scale. However, there is no single correct time scale to do this, which excludes the possibility of general results on extinction risk in coloured environments.

Our results clearly show that the choice of the scaling procedure matters – especially when the time scales of interest are fairly short, as is often the case in conservation biology. Below we give some considerations in favour of each of the three scaling schemes: no scaling, scaling to uniform variance in finite samples, and scaling to uniform true variance.

In the autoregressive process (eq. 1), no scaling results in red noise which corresponds roughly to a view of red noise many people probably have in their minds: rather wild fluctuations, where extreme values often occur in runs. Although this may offer a good baseline, strongly increased long-term variability may cause artefactual results. Thus, it is usually a good practice to scale the variance to be independent of sample length at some time scale. Threat of extinction is usually assessed over some predetermined, short time period (Mace and Lande 1991). This time scale is often a natural choice for scaling to uniform variance: time series of different colours will have, on average, similar data points, but in different orders, according to their autocorrelation. Another intermediate time scale may be obtained if data on environmental variability is available: the length of this time series. If very long-term properties of noise are likely to be important, then scaling to uniform

Fig. 3. Dependence of extinction risk in 50 generations (continuous line) on colour of environmental noise, and different ways of scaling variance of noise. (a)–(c) Overcompensatory dynamics (b = 1), (d)–(f) undercompensatory dynamics (b = 0.1). In the left hand side panels, there is no scaling: $\beta = 30$ in eq. (1) for all α. In the middle panels, β is scaled such that the expected variance of the first 50 generations is independent of colour. In the right hand side panels, β is scaled such that the asymptotic variance is independent of colour. The dashed line gives the risk of extinction caused by carrying capacity drifting to or below zero. Panels (g) and (h) give the mean population size and carrying capacity before extinction in simulations of panels (b) and (e), respectively. All results are based on 10^4 replicates. Parameter values: r = 1.5, b = 1 (a)–(c), (g) or b = 0.1 (d)–(f), (h).

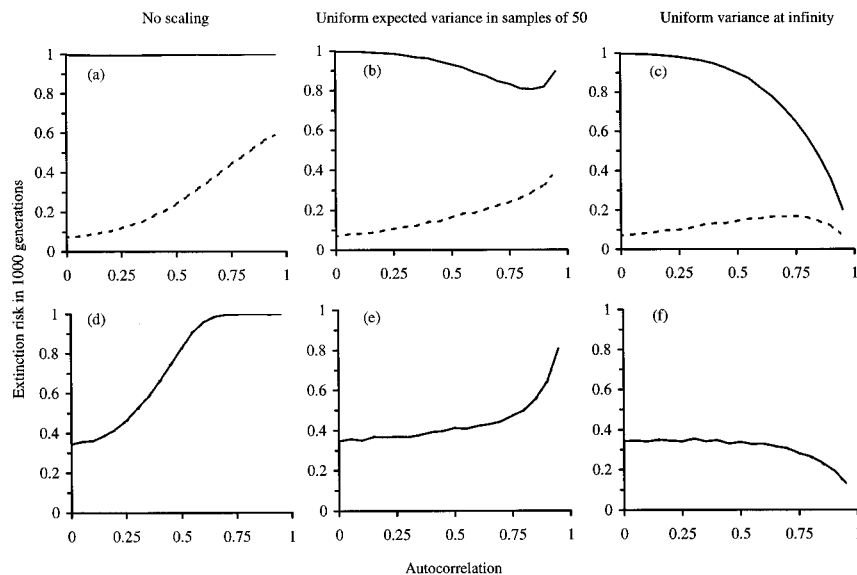No scaling   Uniform expected variance in samples of 50   Uniform variance at infinity
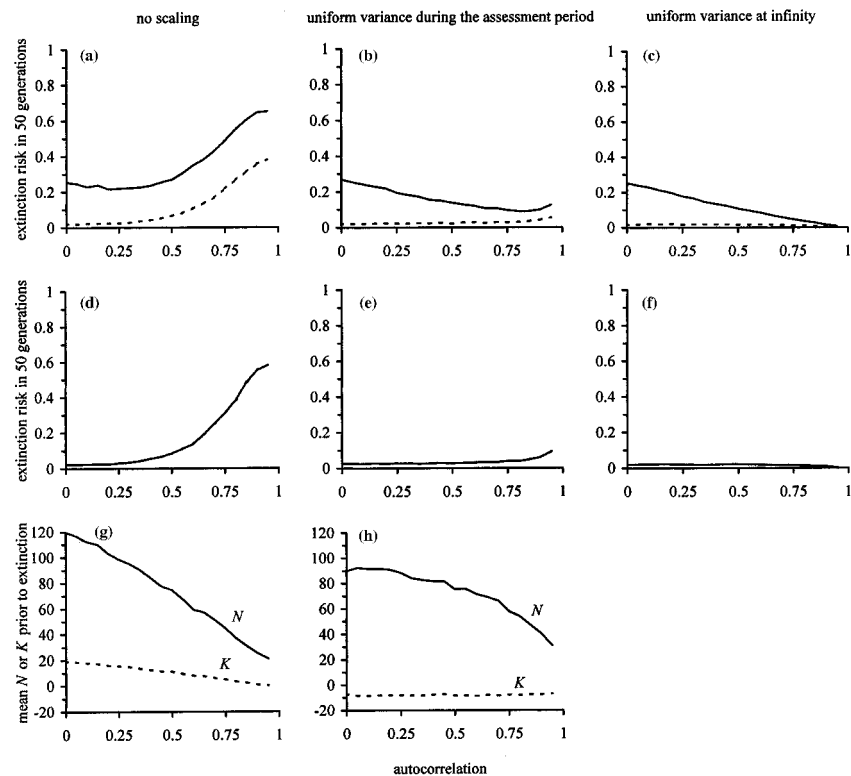
Fig. 4. Dependence of extinction risk in 1000 generations (continuous lines) on colour of environmental noise. (a)–(c) Overcompensatory dynamics (b = 1), (d)–(f) undercompensatory dynamics (b = 0.1). Other details as in Fig. 3.

variance at infinity can be used. Note, however, that not all models of environmental noise are stationary as the AR(1) process (1). Non-stationary processes do not have finite variance when time approaches infinity, and cannot be scaled to uniform true variance. Examples of non-stationary noise are brown noise (as eq. (1) but $\alpha = 1$) and pink 1/f noise, the latter suggested to be the null model of environmental noise (Halley 1996).

The results in this paper are based on the simplest model for coloured noise, the first-order autoregressive process. More complex models of noise are possible (Mode and Jacobson 1987a, b, Cuddington and Yodzis 1999), and they may be more realistic. However, the dependence of sample variance on sample length is a general property of coloured noise which needs to be taken into account in more complex models of noise as well.

Noise from the autoregressive model similar to eq. (1) with constant b has been used by Mode and Jacobson (1987a, b) and Johst and Wissel (1997); however, Johst and Wissel (1997) restricted the variability of demographic parameters to certain intervals. Johst and Wissel (1997) observed increased extinction risk in red-shifted environments, whereas Mode and Jacobson (1987a, b) got results to both directions. Scaling to constant variance at infinity has been used by Roughgarden (1975), Foley (1994), Ripa and Lundberg (1996) and Petchey et al. (1997). Roughgarden (1975) and Ripa and Lundberg (1996) observed clearly decreased extinction risk under red noise, as compared to white noise. Petchey et al. (1997) got the opposite results for a model with spatial structure or undercompensatory dynamics. Foley (1994) showed that a population with random growth rate with zero mean and no density dependence is at higher risk of extinction in red-shifted environments than in white environments. Thus, paying

attention to scaling practices can shed some light to the contrasting results.

Petchey et al. (1997) reported that populations with undercompensating dynamics are more vulnerable to red noise than to white noise. Our results show that this is not a general result. The results of Petchey et al. (1997) are critically dependent on the assumption that carrying capacity cannot go below five individuals, that is $K_t = \max(K_0 + x_t, 5)$ (this assumption is accidentally missing from the paper of Petchey et al. (1997), Petchey pers. comm.). Under this assumption, population with undercompensating dynamics can go extinct only by demographic stochasticity. This is unlikely for the chosen minimum carrying capacity. Thus, very long persistence times are observed.

Does positive correlation in environmental noise increase extinction risk, as compared to temporally uncorrelated noise? We have shown in this paper that there is no simple answer – the answer depends crucially on the exact formulation of the question.

References

Ariño, A. and Pimm, S. L. 1995. On the nature of population extremes. – Evol. Ecol. 9: 429–443.
Chatfield, C. 1996. The analysis of time series, 5th ed. – Chapman and Hall.
Cuddington, K. M. and Yodzis, P. 1999. Black noise and population persistence. – Proc. R. Soc. Lond. B 266: 969–973.
Foley, P. 1994. Predicting extinction times from environmental stochasticity and carrying capacity. – Conserv. Biol. 8: 124–137.

Halley, J. M. 1996. Ecology, evolution and 1/f-noise. – Trends Ecol. Evol. 11: 33–37.

Heino, M. 1998. Noise colour, synchrony and extinctions in spatially structured populations. – Oikos 83: 368–375.

Johst, K. and Wissel, C. 1997. Extinction risk in a temporally correlated fluctuating environment. – Theor. Popul. Biol. 52: 91–100.

Kaitala, V. et al. 1997. Red, blue and green: dyeing population dynamics. – Ann. Zool. Fenn. 34: 217–228.

Lawton, J. H. 1997. The science and non-science of conservation biology. – Oikos 79: 3–5.

Mace, G. M. and Lande, R. 1991. Assessing extinction threats: toward a reevaluation of IUCN threatened species categories. – Conserv. Biol. 5: 148–157.

McArdle, B. H. 1989. Bird population densities. – Nature 338: 628.

Mode, C. J. and Jacobson, M. E. 1987a. On estimating critical population size for an endangered species in the presence of environmental stochasticity. – Math. Biosci. 85: 185–209.

Mode, C. J. and Jacobson, M. E. 1987b. A study of the impact of environmental stochasticity on extinction probabilities by Monte Carlo integration. – Math. Biosci. 83: 105–125.

Petchey, O. L., Gonzalez, A. and Wilson, H. B. 1997. Effects on population persistence: the interaction between environmental noise colour, intraspecific competition and space. – Proc. R. Soc. Lond. B 264: 1841–1847.

Pimm, S. L. and Redfearn, A. 1988. The variability of animal populations. – Nature 334: 613–614.

Ripa, J. and Lundberg, P. 1996. Noise colour and the risk of population extinctions. – Proc. R. Soc. Lond. B 263: 1751–1753.

Roughgarden, J. 1975. A simple model for population dynamics in stochastic environments. – Am. Nat. 109: 713–736.

Schroeder, M. 1991. Fractals, chaos, power laws: minutes from an infinite paradise. – W. H. Freeman.

Appendix 1: Derivation of equations (2) and (4)

Consider an AR(1) time series of length T:

$$x_t = \alpha x_{t-1} + \epsilon_t, \quad \epsilon_t \sim N(0, \beta^2), \quad t = 1, 2, \ldots, T-1, \tag{6}$$

and x_0 chosen from some distribution. Equation (6) can be used to express the sequence of x-values as linear functions of the initial value, x_0, and the random "inventions" ϵ_t:

$$x_t = \alpha x_{t-1} + \epsilon_t = \alpha(\alpha x_{t-2} + \epsilon_{t-1}) + \epsilon_t$$
$$= \ldots = \alpha^t x_0 + \sum_{k=0}^{t-1} \alpha^k \epsilon_{t-k}. \tag{7}$$

Equation (7) describes x_t as a sum of independent random deviates, which facilitates the further analysis. Now, the sample mean and sample variance of this time series are

$$m_x = \frac{1}{T} \sum_{t=0}^{T-1} x_t \tag{8}$$

and

$$s_x^2 = \frac{1}{T-1} \sum_{t=0}^{T-1} (x_t - m_x)^2 = \frac{1}{T-1} \sum_{t=0}^{T-1} x_t^2 - \frac{T}{T-1} m_x^2. \tag{9}$$

We are interested in the expected sample variance:

$$E(s_x^2) = E\left(\frac{1}{T-1} \sum_{t=0}^{T-1} x_t^2 - \frac{T}{T-1} m_x^2 \right)$$
$$= \frac{1}{T-1} \sum_{t=0}^{T-1} E(x_t^2) - \frac{T}{T-1} E(m_x^2). \tag{10}$$

To calculate the first sum in (10) we need:

$$E(x_t^2) = E\left(\left(\alpha^t x_0 + \sum_{k=0}^{t-1} \alpha^k \epsilon_{t-k} \right)^2 \right)$$
$$= E\left(\alpha^{2t} x_0^2 + \sum_{k=0}^{t-1} \alpha^{2k} \epsilon_{t-k}^2 \right)$$
$$= \alpha^{2k} E(x_0^2) + \beta^2 \sum_{k=0}^{t-1} \alpha^{2k} = \alpha^{2k} E(x_0^2) + \beta^2 \frac{1 - \alpha^{2t}}{1 - \alpha^2}. \tag{11}$$

Using (11) we get

$$\sum_{t=0}^{T-1} E(x_t^2) = E(x_0^2) \sum_{t=0}^{T-1} \alpha^{2t} + \frac{\beta^2}{1-\alpha^2} \sum_{t=0}^{T-1} (1 - \alpha^{2t})$$
$$= E(x_0^2) \frac{1 - \alpha^{2T}}{1 - \alpha^2} + \frac{\beta^2}{1-\alpha^2} \left(T - \frac{1 - \alpha^{2T}}{1 - \alpha^2} \right). \tag{12}$$

The expected squared mean is calculated in a similar manner. First, evaluate the sum in (8) using (7):

$$\sum_{t=0}^{T-1} x_t = x_0 + \sum_{t=1}^{T-1} \left(\alpha^t x_0 + \sum_{k=0}^{t-1} \alpha^k \epsilon_{t-k} \right)$$
$$= x_0 \frac{1 - \alpha^t}{1 - \alpha} + \sum_{j=1}^{T-1} \epsilon_j \sum_{t=j}^{T-1} \alpha^{t-j}$$
$$= x_0 \frac{1 - \alpha^t}{1 - \alpha} + \sum_{j=1}^{T-1} \epsilon_j \frac{1 - \alpha^{T-j}}{1 - \alpha}. \tag{13}$$

Using (13) in (8) we get

$$E(m_x^2) = E\left(\left(\frac{1}{T} \sum_{t=0}^{T-1} x_t \right)^2 \right)$$
$$= \frac{1}{T^2} E\left(\left(x_0 \frac{1 - \alpha^t}{1 - \alpha} + \sum_{j=1}^{T-1} \epsilon_j \frac{1 - \alpha^{T-j}}{1 - \alpha} \right)^2 \right)$$

$$= \frac{1}{T^2} \left(E(x_0^2) \frac{(1-\alpha^t)^2}{(1-\alpha)^2} + \frac{\beta^2}{(1-\alpha)^2} \sum_{j=1}^{T-1} (1-\alpha^{T-j})^2 \right)$$

$$= \frac{1}{T^2} \left(E(x_0^2) \frac{(1-\alpha^t)^2}{(1-\alpha)^2} + \frac{\beta^2}{(1-\alpha)^2} \right.$$

$$\left. \times \left(T - 1 - 2 \frac{\alpha - \alpha^t}{1-\alpha} + \frac{\alpha^2 - \alpha^{2T}}{1-\alpha^2} \right) \right). \tag{14}$$

Finally, using (12) and (14) in (10) we get:

$$E(s^2) = \frac{E(x_0^2)}{T-1} \left(\frac{1-\alpha^{2T}}{1-\alpha^2} - \frac{(1-\alpha^T)^2}{T(1-\alpha)^2} \right) + \frac{\beta^2}{(1-\alpha^2)(T-1)}$$

$$\times \left(T - \frac{2 + 2\alpha + \alpha^2 - \alpha^{2T}}{1-\alpha^2} + \frac{(1-\alpha^T)(1+2\alpha-\alpha^T)}{T(1-\alpha)^2} \right). \tag{15}$$

We assume $x_0 = 0$, yielding eq. (4) for the expected variance of the first T values in the time series. For samples starting later, $E(x_0^2)$ in eq. (15) has to be replaced with $E(x_t^2)$, given by eq. (11). For t sufficiently large, the dependence on the initial conditions is lost and the eq. (11) simplifies to $E(x_t^2) = \beta^2/(1-\alpha^2)$. Substituting this expression to eq. (15) and simplifying yields eq. (2) in the main text.