

Extinction Risk and the $1/f$ Family of Noise Models

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In order to predict extinction risk in the presence of reddened, or correlated, environmental variability, fluctuating parameters may be represented by the family of $1/f$ noises, a series of stochastic models with different levels of variation acting on different timescales. We compare the process of parameter estimation for three $1/f$ models (white, pink and brown noise) with each other, and with autoregressive noise models (which are not $1/f$ noises), using data from a model time-series (length, T) of population. We then calculate the expected increase in variance and the expected extinction risk for each model, and we use these to explore the implication of assuming an incorrect noise model. When parameterising these models, it is necessary to do so in terms of the *measured* ("sample") parameters rather than fundamental ("population") parameters. This is because these models are non-stationary: their parameters need not stabilize on measurement over long periods of time and are uniquely defined only over a specified "window" of timescales defined by a measurement process. We find that extinction forecasts can differ greatly between models, depending on the length, T , and the coefficient of variability, CV, of the time series used to parameterise the models, and on the length of time into the future which is to be projected. For the simplest possible models, ones with population itself the $1/f$ noise process, it is possible to predict the extinction risk based on CV of the observed time series. Our predictions, based on explicit formulae and on simulations, indicate that (a) for very short projection times relative to T , brown and pink noise models are usually optimistic relative to equivalent white noise model; (b) for projection timescales equal to and substantially greater than T , an equivalent brown or pink noise model usually predicts a greater extinction risk, unless CV is very large; and (c) except for very small values of CV, for timescales very much greater than T , the brown and pink models present a more optimistic picture than the white noise model. In most cases, a pink noise is intermediate between white and brown models. Thus, while reddening of environmental noise may increase the long-term extinction probability for stationary processes, this is not generally true for non-stationary processes, such as pink or brown noises. © 1999 Academic Press

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1. INTRODUCTION

Considerable effort has been devoted to the development of models of extinction in the past two decades. This has included a number of studies directed toward population viability analysis (Soulé, 1987) and toward metapopulations (Hanski, 1991) or patchy habitats (Halley and Lawton, 1997) and investigations in a broader context (Lawton and May, 1995). Most models of extinction are stochastic with extinction occurring by chance, even in populations with positive mean growth rates. Various types of stochastic models have been proposed and investigated. If we are to divide these into categories, there are two primary ways in which stochasticity may be structured. First of all, there are many ways of structuring the probability distribution of variation (e.g., normal, lognormal, and Poisson). The implications of different probability distributions for extinction modelling are explored by Halley and Iwasa (1997; see also Lande, 1993; Ludwig, 1996). The other important aspect of variation is the temporal correlation structure of the variation, the relative influence of processes acting on different timescales. This second issue is the subject of this paper.

A population will be affected by processes acting on very different timescales, ranging from daily temperature variation to climatic events occurring on geological timescales. The resulting temporal population variation can be expressed as a power spectrum across frequencies. By analogy with light spectra, such power spectra are often described in terms of their characteristic “colours.” “White noise,” for instance, like white light, consists of an even mixture of variation over all frequencies. By contrast, Brownian or “brown” noise (so called for its strongly reddened spectrum as well as its links to Brownian motion) is a mixture with a much greater share of low-frequency (long-period) components. Both white and brown noise models belong to a family of “ $1/f$ noise” (or “ $1/f^\gamma$ noise”), for which spectral density $S(f)$ for each frequency f is proportional to $1/f^\gamma$ with the exponent γ being zero in white noise and 2 in brown. Between these two extremes lies a wide range of possible noise colours with more or less reddened frequency spectra, including most notably “pink” noise, which is exactly intermediate ($\gamma = 1$) between them. These different frequency spectra are modelled in very different ways, and have very different properties.

White noise is extremely easy to simulate. It can be generated by adding a random variable (usually with a normal distribution with mean zero) to the mean value of the parameter in question (e.g., population size) at every time interval of a simulation. Thus despite the fact that

white noise contains many low-frequency (long-period) components, white noise models have no memory of past events. In a white noise model of daily temperature, for instance, an unusually hot day is as likely to be followed by an unusually cold day as by another hot one. White noise is also entirely “stationary,” in that a white noise population model can be thought of as a constant baseline value, plus a noise component whose variance remains constant. White noise models are ubiquitous in the literature and have been applied with success to explain a wide variety of processes, especially in the physical sciences.

Brown noise models, first developed to describe the Brownian motion of particles, are constructed rather differently. The parameter in question is calculated at each time step by taking the previous value and adding a random variable (with zero mean) to it. The parameter’s value takes a random walk, wandering up or down with equal probability. In contrast to the white noise model (which has no memory), brown noise processes are dominated by their recent history. This dominance by recent events is so complete that only the most recent past need be considered (the “Markov property”). Such processes are not stationary: populations far from their initial values have no inbuilt tendency to return to it. However, the parameter’s value typically spends a relatively long period of time in any given neighbourhood in which it starts. This accounts for the predominance of long-period components in the noise power spectrum.

Clearly, both white and brown noise models have properties which limit their applicability to many real-world problems, including the modelling of extinction. An intermediate model of variation structure is required to plausibly reflect processes with both historical memories and stationary tendencies.

An intermediate member of the $1/f$ family of models is “pink noise,” which lies precisely halfway between white and brown, with an exponent $\gamma = 1$. If spectral density is expressed on a per octave scale (Halley, 1996), a pink noise spectrum contains equal influences from all time-scale intervals across the spectrum (just as white noise does if frequencies are plotted on a linear scale). This means that events (e.g., environmental fluctuations) occurring on timescales of between 1 and 10 years contribute as much to the overall variance of the quantity in question as do events happening on timescales between a decade and a century, or between a century and a millennium (Keshner, 1982). Pink noise shares properties of both white and brown noise; it is sometimes considered to be quasi-stationary in its behaviour as its variance grows only slowly, at a rate approximately proportional

to the logarithm of time (Keshner, 1982). There is a large body of evidence showing that many processes, ranging from DNA base sequences to economic time series, display $1/f^\gamma$ variation spectra with values of γ between 0 and 2, and thus might be approximated using pink noise spectra (Wornell, 1993; Halley, 1996). The $1/f^\gamma$ family of noise models can be considered fractional Brownian motions (with the exception of $\gamma = 1$) and fractal processes (West and Deering, 1994) with the exponent γ associated with a fractal dimension. Some other recent papers involving this kind of noise applied in the biological and medical fields are those by Renshaw (1994) and Hausdorff and Peng (1996).

The most commonly used method of generating reddened noise involves combining a white noise model with diminishing influences from successive past parameter values through an autoregressive (AR) model. This technique is the basis of most models of environmental variation (Foley, 1994; Caswell and Cohen, 1995; Ripa and Lundberg, 1996; Petchey *et al.*, 1997). Pure AR models describe a fairly constrained subset of reddened noise models, being restricted to processes with exponentially decreasing time correlation beyond a characteristic temporal scale. Also, they are all stationary. Combinations of AR models can be used to synthesize a wider variety of noise types, within a specified time frame, including all members of the $1/f^\gamma$ (for $0 \leq \gamma < 2$) noise family (Keshner, 1982; Corsini and Saletti, 1987).

Most extinction models have relied almost exclusively upon white noise models of population variability. In recent years there has been a growth of interest in extinction models with correlated environmental noise. Foley (1994), Caswell and Cohen (1995), Ripa and Lundberg (1996), and Petchey *et al.* (1997) have used AR methods to simulate extinction with an intermediate structure of temporal variation. Surprisingly few models of extinction have used brown noise, despite the wealth of evidence for environmental processes with brown spectra (Steele, 1985; Ariño and Pimm, 1995). The apparently contradictory behaviour of Brownian models in having assured extinction yet infinite “persistence time” (see Middleton *et al.*, 1995, for a discussion of this) have probably limited their appeal to biologists; indeed, where they have been used (Leigh, 1981; Goodman, 1987; Middleton *et al.*, 1995) population caps have generally been imposed. No attempt has been made to model extinction probability using a pink noise spectrum, nor any other intermediate member of the $1/f^\gamma$ family, although a connection with extinctions on an evolutionary timescale has been the subject of recent controversy (Solé *et al.*, 1997; Hewzullah *et al.*, 1997; Kirchner and Weil, 1998). In this paper, we will attempt to fill some of the gaps.

In the past little attention has been paid to non-stationary noise models because, as well as being less mathematically tractable, the interpretation of non-finite power noise spectra can be problematic. At very low frequencies, one is dealing with changes so gradual that they cannot be observed over realistic experimental timescales. In addition the choice of stationary noise models is based on the view that in many cases the longer timescale events can be considered as being dealt with by other, explicit dynamic processes. Current evidence suggests that ecological time series are not stationary (Steele, 1985; Pimm and Redfearn, 1988; Pimm, 1994). If the timescale of prediction is comparable to the timescale over which the model parameters were measured, this is unlikely to make much difference. However, in most viability projections, the assumption of comparable timescales will not hold. When one is interested in predicting into the distant future, processes too gradual or too infrequent to have been picked up in field studies will contribute to the population dynamics. In such a situation, the non-stationarity of the process plays an important role. For example, the parameters might be perturbed by a self-organised critical process (Bak and Chen, 1991) or be subject to multiscaled randomness (Halley, 1996; Hausdorff and Peng, 1996). The slowly varying components of these processes, because they are not observed in the initial measurements, cannot be modelled by systematic factors; however, their magnitude can be inferred, because both of these processes generate $1/f$ noise. Any such means of guessing the likely frequency or distribution of long-term events will vastly improve the value of population viability predictions.

This paper has three major goals. We will begin by exploring the process by which future population variability is projected from past time series data. Such projections differ depending on the assumed spectrum of temporal variation. We then derive the implications of such differences for extinction in mathematically explicit models of white and brown processes, and compare with the results of simulations of white, brown, and pink models. Finally, with reference to the findings of these simulations, we will examine the implications of assuming different models. To what extent are current extinction forecasts influenced by the rather arbitrary choice of noise spectrum models?

A major feature of this paper is that our models are directly driven by the statistics, in the sense that the model parameters are given in terms of the *measured* “sample” parameters rather than fundamental “population” parameters. This may seem like an unusual and unnecessary complication, since most population models proceed along the latter lines. In models yielding finite

power it is not necessary. However, it is necessary in our case because we are dealing with non-stationary models whose parameters do not stabilize on measurement over long periods of time. The total variability in such models is uniquely defined only over a specified “window” of timescales. This window is defined by the measurement process. Because of this complication, we will restrict this paper to analyses of variation in a population time series per se. The effects of given types of coloured noise spectra acting on parameters within a population model (e.g., fecundity or carrying-capacity variation) and the effects of density dependence and/or population caps will not be considered here. Although these are important to understanding population dynamics and extinction, our initial aim (the aim of this paper) is to explore the subtle and sometimes unexpected way that stochastic non-stationarity (alone) interacts with extinction probability. We will also limit our attention here to equally spaced discrete samples of the continuous-time domain.

2. MODELS OF COLOURED NOISE

Each noise can be represented by a stochastic process, X , whose properties will be different for each model.

White Noise. A white noise process is the simplest stochastic process, where each value of X has a normal distribution of standard deviation σ_w about a mean μ . Thus,

$$X_t \sim N(\mu, \sigma_w^2). \quad (1)$$

Simulating such a process therefore consists simply of generating a sequence of independent normal random variables with specified mean and variance.

Brown Noise. If we adopt a brown noise model, each value of X_t is a realization of the Brownian process, where it is the increments of X_t that are independent random variables:

$$X_{t+1} = X_t + W_t, \quad W_t \sim N(0, \sigma_b^2). \quad (2)$$

In discrete time, brown noise is simulated simply by adding an independent normal random variable, centred at zero and of constant variance, to the previous value.

Autoregressive Noise. This type of noise is characterised by a correlation, ρ_a , on a characteristic timescale

of τ_a defined by $\rho = \exp(-1/\tau_a)$. This is expressed mathematically by

$$\begin{aligned} X_{t+1} &= \mu + A_{t+1} \\ A_{t+1} &= \rho A_t + \sqrt{1-\rho^2} W_t, \quad W_t \sim N(0, \sigma_a^2). \end{aligned} \quad (3)$$

The expectation for this process X_t is μ and its standard deviation is σ_a .

Pink Noise. Simulation models for pink noise are more complicated than those for white, brown, or AR noise. Pink noise can arise through a number of diverse mechanisms (Weissman, 1988; Halley, 1996). The spirit of the pink $1/f$ process is to throw a coin once and to pick up $+1$ for each head or -1 for each tail, producing a time series of -1 's and $+1$'s. To this first series is added a second series of ± 1 which changes half as often, the result of a coin which is thrown every second round. A third coin thrown every fourth round adds a further ± 1 , and so on. In this way we would obtain a time series whose variance increased with time in an approximately logarithmic fashion, and which would have an approximately pink $1/f$ spectrum.

In a similar fashion, a series of AR models can be combined to simulate a pink noise process. Several models of pink noise, suitable for computational purposes, have been proposed (Keshner, 1982; Corsini and Saletti, 1987; Wornell, 1993). In this paper we will follow Keshner's approach (see also Schroeder, 1991, p. 125), which consists of approximating the spectrum by a series of AR models, one for each scale. This may be considered the sum of a series of autoregressive stochastic processes, each with a correlation on a characteristic scale. The value of X_t in continuous time will be a summation (note that we must include negative as well as positive powers):

$$\begin{aligned} X &= A^{(0)} \text{ (1-year timescale)} \\ &+ A^{(1)} \text{ (10-year timescale)} \\ &+ A^{(-1)} \text{ (1/10-year timescale)} \\ &+ A^{(2)} \text{ (100-year timescale)} \\ &+ A^{(-2)} \text{ (1/100-year timescale)} + \dots \end{aligned} \quad (4)$$

Note that in the above equation, the time subscripts have been dropped for clarity. More formally, we write for a series of discrete samples of a continuous-time process

$$X_t = \sum_{k=-\infty}^{+\infty} A_t^{(k)}. \quad (5)$$

Each of the component AR processes, $A^{(k)}$, has its own timescale τ_k , which is related to the correlation ρ_k by

$$\rho_k = \exp\left[-\frac{1}{\tau_k}\right]. \quad (6)$$

For pink noise, the timescales are separated from one another by a constant ratio, r

$$\frac{\tau_{k+1}}{\tau_k} = r. \quad (7)$$

Ideally, $r \rightarrow 0$, whereas in (4) above $r = 10$. For most purposes, however, we only require r to be sufficiently small. Each of the component processes contributes σ_A^2 to the overall variance of the process, and because there are an infinite number of them, the potential reservoir of variability is infinite. Most change on very large time-scales, or very small ones, so only a finite number (K) of them need be used in simulations. K will be determined by the length of the time series we wish to generate. The largest timescale should be significantly longer than T . Without loss of generality, we may assign the lowest timescale, the shortest timescale in the real system which we wish to model, a subscript of $k = 1$. This (associated with ρ_1) is the smallest timescale which is likely to affect the observations for the T samples in the time series. (Note: This is *not* the interval between samples, but the time it takes to measure the parameter of interest. For population this is the census time.) Perturbations occurring at higher frequencies will not be observed. Thus,

$$X_t \approx \mu + \sum_{k=1}^K A_t^{(k)}. \quad (8)$$

Note how in (8) X_t can be interpreted as a combination of K autoregressive processes plus a residue of other low-frequency ones too slow to be seen over the time-scales of interest which appears as a “mean,” μ .

This method can be used to generate other $1/f^\gamma$ noises with various spectral exponents in the range $0 < \gamma < 2$. In each case the relationship in Eq. (7) will have a different form.

3. PARAMETERISING DIFFERENT NOISE MODELS

To predict future extinction risk, we must predict the degree to which its numbers are likely to vary. However, we must do more than simply choose a model of

variability; we must also parameterise that model. The parameters will generally be taken from analyses of past population behaviour, and the interpretation of that history will itself depend on the model we impose. The potential variance is infinite for all of the $1/f^\gamma$ family of noises, and for those non-stationary members ($\gamma \geq 1$) it diverges as the series gets longer: consequently, it is only possible to define the variance within a given context. For this we will assume that our time series consists of a series of T equally spaced (without loss of generality, we can assume yearly) observations. Each observation is a sample of a background continuous-time coloured noise process. The observations $\{x_1, x_2, x_3, \dots, x_T\}$ are of the logarithm of a population. The mean and standard deviation of this finite time series are M_T and S_T , respectively. Throughout this paper we will describe a set of stochastic processes as equivalent on a timescale T if they all would be expected to produce, over the interval T , a series with the same mean (M_T) and standard deviation (S_T) as the observed time series.

Our first question is, what is the expected level of variability in the population over a subsequent time interval of Δt years? First, for simplicity, we will assume that population variability is lognormal, a reasonable assumption for a number of biological reasons (Middleton *et al.*, 1995). The remaining question is the spectral structure of the population variation, the implications of which is the focus of this paper. We will limit ourselves to a comparison white, brown, pink, and AR noise; we do not consider blue noise in this paper. We can then predict the level of variability up to an arbitrary moment in the future, provided that we choose the right model. The problem of discerning the spectral (or fractal) properties of a model on the basis of a given time series has been addressed by many authors in a number of different contexts (e.g., Geweke and Porter-Hudak, 1983; Wornell and Oppenheim, 1992; Cutler, 1993,1994). Figure 1 shows three sample time series of length 40 (simulated), one of each of the colours white, brown, and pink. At a glance, it is not at all easy to distinguish even white and brown processes, and harder to distinguish the pink process from either. This problem, which is more acute with shorter time series, persists even with sophisticated spectral analysis methods. In this paper we merely discuss inference of the parameters of the stochastic processes in white, brown, and pink models, on the basis of the observed statistics M_T and S_T .

White Noise. If we assume that the observations come from a white noise process, the measured mean and

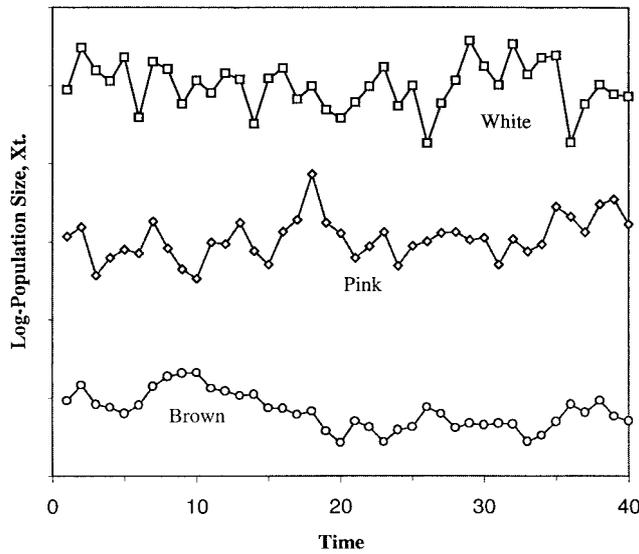


FIG. 1. Three sample time series of brown noise (\circ), pink noise (\diamond), and white noise (\square), each containing 40 yearly observations. Each of the three generating processes were equivalent on a 40-year timescale with $CV = 0.26$.

variance of our series are respectively unbiased estimators of the expectation ($\mu = E[M_T]$) and variance ($\sigma_w^2 = E[S_T^2]$) of the process so we can parameterise it as

$$\begin{aligned} \mu &\approx M_T \\ \sigma_w^2 &\approx S_T^2. \end{aligned} \quad (9)$$

Brown Noise. In a brown noise model, the parameters of the process can be found from the recorded observations on the basis of the results (17) and (29) in the Appendix:

$$\begin{aligned} X_1 &\approx M_T \\ \sigma_b^2 &\approx \frac{6S_T^2}{T+1}. \end{aligned} \quad (10)$$

Notice how the standard deviation, S_T , of the series of observations grows with T , the length of the time series. A better estimate of X_1 can be found by obtaining the initial value of the population and projecting from there, but this may not be available.

Pink Noise. If the background variation process is pink noise, the sample variance also grows with the length of the time series but now in an approximately logarithmic fashion. Here, the expressions are more complicated (see Appendix for derivations) but reflect the superposition of AR processes discussed in the earlier section, and the

mean and variance can be parameterised in the following way, using respectively (21) and (33):

$$\begin{aligned} M_T &\approx \mu + \frac{1}{T} \sum_{k=1}^K \frac{1 - \rho_k^T}{1 - \rho_k} E[A_1^{(k)}] \\ \sigma_p^2 &\approx \frac{S_T^2}{\sum_{k=1}^K \left[\frac{T+1}{T-1} - \frac{2[T(1-\rho_k) - \rho_k(1-\rho_k^T)]}{T(T-1)(1-\rho_k)^2} \right]}. \end{aligned} \quad (11)$$

The parameterisation of the mean is more problematic. Note how its value depends on the coefficients $A^{(k)}$, which are the initial values of the component processes. This cumulative dependence of the mean (though not of the variance) on long-term components illustrates the evolutionary character of pink noise (Keshner, 1982). This is fundamentally different from brown noise, which “remembers” only one piece of information (its value in the previous time step), and from white noise, which has no memory.

AR Noise. The parameterisation of AR noise is the same as that for pink noise but with $K = 1$.

4. GROWTH OF VARIANCE IN $1/f$ NOISE MODELS

The projected trends in variance, for the three models based on the parameterisations (6)–(8), are shown in Fig. 2. In a white noise world, the variance of a time series remains constant indefinitely, and so the measured variance in a past time series can be projected forward into the future without change. In pink and brown models, however, population variance increases progressively over time, with low variation (relative to the white noise model) in the short term, and relatively high variation in the long term. The operational definition of “short” and “long” terms in the previous sentence will depend on the length of the time series used to measure variance in the first place. If, for example, a 20-year time series were used to estimate a population’s variance, then all three models would concur on the degree of population variance 20 years into the future. They would disagree, however, about variance projections on significantly shorter (e.g., 5 year) and longer (e.g., 100 year) timescales. Thus, if a white noise model was fit to a time series that was actually brown or pink, it would overestimate future short-term variation in the population, but would underestimate population variation in the more distant future. Fitting a brown noise

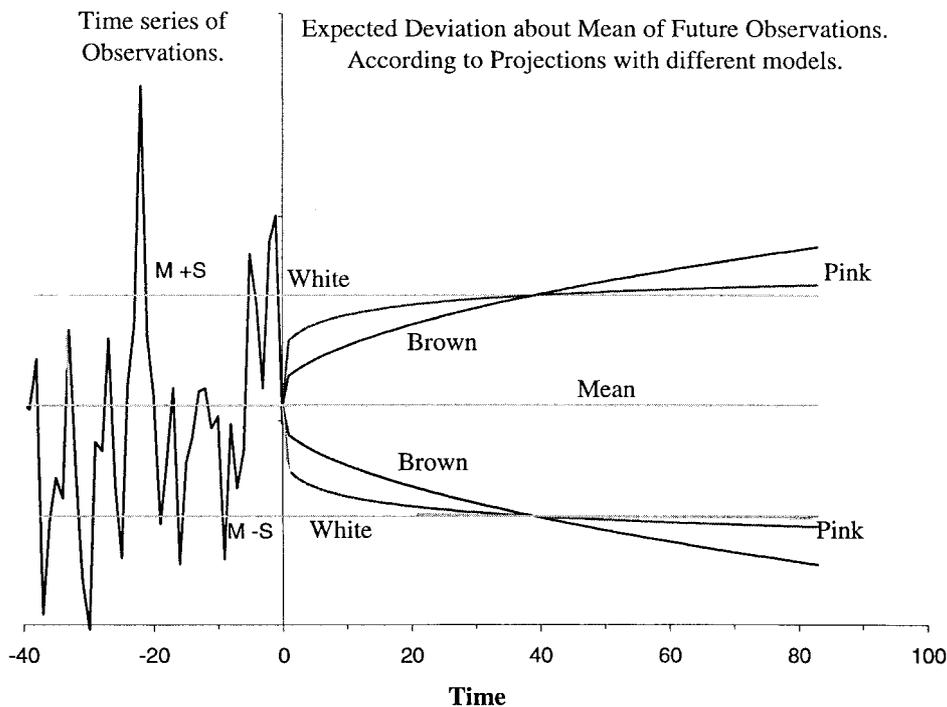


FIG. 2. Diagram showing a sample time series with $T=40$ observations, one observation per year up to year 40. This is followed (on the right for time) by a chart of the expected mean and standard deviations ($E[M_{\Delta t}] \pm \sqrt{E[S_{\Delta t}^2]}$) projected (ignoring extinctions) in three equivalent models (white, brown, and pink), using Eqs. (9)–(11). Each model is equivalent on a 40-year timescale. Variance is constant for white noise, so the projected envelope is constant. For brown noise the envelope grows as the square root of Δt , and for pink noise it grows approximately logarithmically. Note that all the envelopes are equal when we are projecting for $\Delta t = T = 40$ years.

(random walk) model to a time series that was in fact white or pink would produce the opposite set of biases, underestimating short-term variance but overestimating population variation in the long term. Autoregressive reddening produces patterns similar to those of pink or brown noise, but only up to a certain timescale. Unlike brown and pink processes, autoregressive processes are stationary: their variance increases with the length of a time series but converge to a finite value. If the real population variation is simple autoregressive noise, the equations are the same as for pink noise above, except that there is only one term in the summation in Eq. (5) corresponding to the characteristic correlation time τ_a of the AR process. If $T < \tau_a$, yet we adopt a white noise model, the situation will be the same as for brown noise: we would overestimate variance in the short term ($t < T$) but underestimate it in the long term ($t > T$).

5. FORMULAS FOR EXTINCTION PROBABILITY

We now proceed to the task of projecting extinction risk. Several researchers have speculated on the effects of

changing variance on extinction probability (Pimm and Redfearn, 1988; Lawton, 1988; Halley, 1996) and some work has been done to verify if this is indeed the case (Ripa and Lundburg, 1996; Petchey *et al.*, 1997) for population models driven by reddened noise. In fact, we show here that, even for simple absorption problems without the complications of population dynamics, the picture contains some subtle effects. Increased variance does not necessarily increase the risk of extinction in the long run.

The Appendix presents derivations of the following formulae for the probability of extinction within Δt years for a population whose fluctuations have the spectrum of white noise:

$$E_{\Delta t}^{(w)} = 1 - \left[1 - \frac{1}{2} \operatorname{erfc} \left(\frac{\mu}{\sigma_w \sqrt{2}} \right) \right]^{\Delta t}. \quad (12)$$

The error function $\operatorname{erfc}(x)$ is simply a measure of the cumulative distribution of the normal distribution (Spiegel, 1968). For the corresponding brown noise model, there is no explicit exact formula for discrete time,

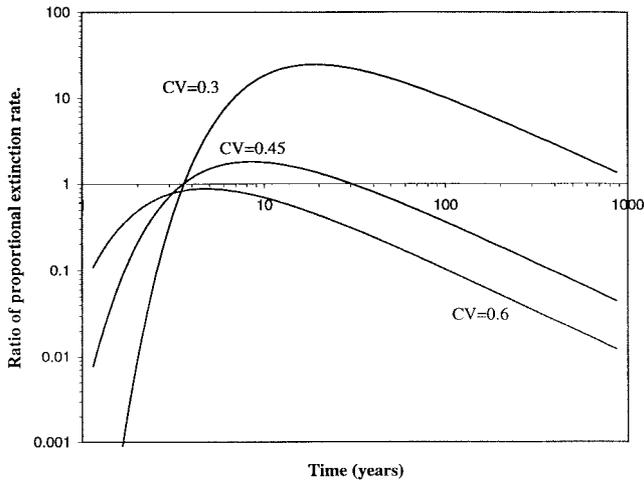


FIG. 3. Proportional rate of extinction of three brown noise models relative to the equivalent white noise models, drawn on logarithmic scales. The models were based on three series ($T=25$) having $CV = 0.3, 0.45,$ and $0.6,$ respectively.

but an approximate formula (based on the continuous-time version) is good for large values of Δt ($\Delta t \gg X_1/\sigma_b$):

$$E_{\Delta t}^{(b)} = \operatorname{erfc} \left(\frac{X_1}{\sigma_b \sqrt{2 \Delta t}} \right). \quad (13)$$

To use these formulas one employs the inference scheme of Eq. (9) and Eq. (10). As mentioned earlier, one can only meaningfully compare the two models in the context of an observed time series of specified length. Unfortunately, we know of no equivalent formulae for calculating the probability of extinction for pink noise models, nor for AR models.

Estimates of extinction risk are very sensitive to the choice of noise model. By fitting an inappropriate model (e.g., by assuming white noise in a world governed by Brownian dynamics), one may produce estimates of extinction rates which differ by several orders of magnitude from the actual values. The precise nature of the biases involved depend critically on two factors: the variability of the time series used to parameterise the model, and the length of time into the future that one wishes to predict.

White noise extinction models have a constant risk of extinction per unit time; by their very nature they assume that the odds of randomly drawing the losing card are the same at each time interval. Consequently, the probability of a population surviving for some period Δt is simply one minus the probability of extinction per unit time raised to the power Δt , and the extinction risk to surviving populations per unit time is fixed. Consequently, we can express the relative vulnerability of populations

governed by white and brown noise processes by dividing brown noise extinctions by this fixed value.

Figure 3 shows the proportional extinction rate (probability of extinction given that the population has so far survived) for brown noise, relative to that of white noise for various values of the sample series' coefficient of variation, which we have defined as follows:

$$CV = \frac{S_T}{M_T}. \quad (14)$$

Figure 3 is based on Eqs. (12) and (13). Equation (12) is parameterised from a time series with parameters M_T and S_T for white noise using Eq. (9), while Eq. (13) is parameterised from the same time series using Eq. (10) for brown noise. While this graph is only approximate (since Eq. (13) is not exact for discrete time), it is a good approximation at large Δt .

Where very variable time series (e.g., $CV > 0.6$) are considered, white noise models always predict higher extinction probabilities than do brown noise models. Here, the curve always lies below 1, indicating that the Brownian extinction rate is always lower than that for populations exhibiting white noise for large CV . The result is much lower cumulative survivorship in populations governed by white noise than in comparably variable brown populations. The reason for the lower extinction rate with a brown noise model is that even if the variance is greater, the population may drift upward, without any restoring force, to very large ("safe") values. Assuming a brown model in a population for which white noise is the appropriate model would thus produce unrealistically optimistic estimates of survival probabilities. The opposite error would produce an extremely pessimistic forecast. These biases remain whatever the timescale, but the degree of bias can shift, with differences in cumulative extinction probability growing progressively larger as time passes.

If we consider moderate levels of population variability (e.g., $CV = 0.45$), a more complex set of biases appears. As Fig. 3 shows, at moderate levels of variability the relative extinction rate curve crosses the unity line in two places. In such circumstances, the nature of extinction forecast biases will depend critically on how far into the future we are looking. Short-term forecasts (that is, $\Delta t < T$) of instantaneous extinction rates will be biased in the manner described above: white noise models will be pessimistic about population persistence and brown noise models will be optimistic. This comes about because white noise models can bounce to extinction instantaneously, whereas a Brownian random walk takes some time to travel the distance to zero. Moving to

longer timescales ($\Delta t \sim T$), the biases are reversed: extinction becomes more likely in a population governed by Brownian dynamics than in one exhibiting white noise variation. This occurs because many Brownian populations, having no stationary tendency to draw them back toward their initial value, will have had sufficient time to wander into the abyss. Using a white noise model in a reddened world here results in significantly underestimating the risk of extinction. At still longer timescales ($\Delta t > T$), the tables are turned back again, and the original set of biases (with white pessimistic) is restored. The reason for the bias is different, however. After such a long time period, a large proportion of the Brownian populations that have survived will be those that have achieved very large (and thus relatively invulnerable) population sizes, while white noise populations continue to face a constant per generation risk. Cumulative survivorship also shows two crossovers in extinction biases.

The relative performance of white and brown noise extinction models is different yet again when we turn to lower levels of variation. The smallest value of CV in Fig. 3 is $CV = 0.3$, for which the curve re-crosses unity at about 1000 years, but for still smaller values of CV the ratio of extinction rates rises so steeply that it does not re-cross unity within a biologically reasonable time. Thus, for all practical purposes, there are now only two relevant time periods: a short term (where the white noise model is pessimistic relative to the brown model) and a long term (where the situation is reversed). These are precisely analogous to the short- and moderate-term regions of the previous (moderate CV) case, but the degree of differentiation in extinction rates is much more extreme. In the short term, extinction rates calculated from white noise models can be many orders of magnitude higher than those generated in brown models, but this difference is of no practical significance, as extinction rates in either model are exceedingly low. Beyond the crossover point, however, very real differences appear. Extinction rates under brown noise are here many orders of magnitude higher than corresponding white noise estimates, resulting in profound differences in cumulative extinctions. In such circumstances, applying a white noise extinction model to a population governed by brown or pink noise could result in extremely optimistic viability forecasts.

6. SIMULATIONS COMPARING EXTINCTION

So far, we have considered only white and brown noise models of extinction, due to the fact that explicit

formulae (or approximations) for such probabilities are easily derived. Given the potential importance of pink noise processes, however, it is desirable to calculate extinction risks in this case as well. Owing to the absence (to our knowledge) of closed formulae for the time-dependent absorption probabilities for pink and AR models, we compared extinction probability using simulation models. Simulation models were also necessary for short-term predictions with brown noise since Eq. (13) is only accurate for long-term predictions. A description of how these simulations were carried out is in the final section of the Appendix.

Figure 4 shows results of simulations for the proportional extinction rates for the three equivalent models (all parameterised from the same time series) relative to the equivalent white noise process. It is obvious from this picture that projections of extinction rates are not affected in a simple way by reddening. Each of the curves (except the theoretical curve for Brownian extinction rates based on Eq. (13)) represents the results of a Monte Carlo simulation of one million runs for each noise model. As before, the parameterisation was simply on the basis of a time series with $S_T/M_T = CV = 0.45$ for $T = 25$. The correlation time for the AR process, τ_a , is 30 years.

The brown noise model (\square) behaved as it did in Fig. 3, except that the rise in relative proportional extinction rate is not as pronounced as predicted by Eq. (10).

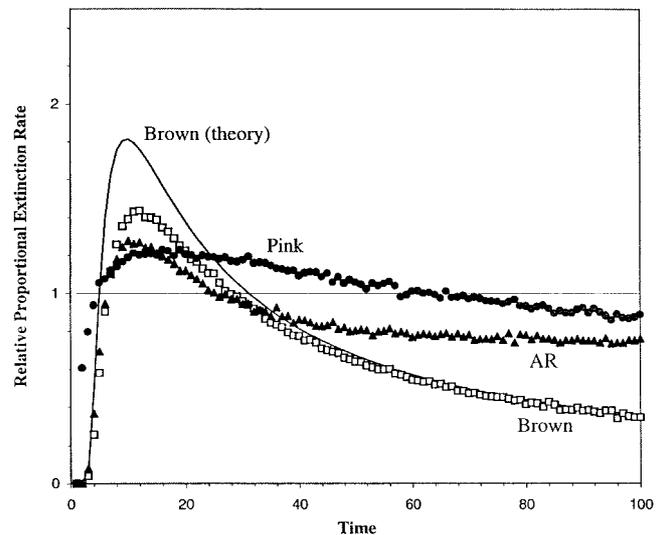


FIG. 4. Proportional rates of extinction for three noise models equivalent on a 25-year timescale having a coefficient of variation for $\log X_t$ of $CV = 0.45$. Brown noise model (\square); pink noise model (\bullet); AR model with $\tau_a = 30$ (\blacktriangle). All rates are relative to the equivalent white noise model, as in Fig. 3.

The pink noise model (●) differs, as we might expect, less from the white noise model than does the brown noise model, beginning with a projected extinction rate closer to that of the white noise model. The long-term extinction rate of the pink noise model is also closer to that of the white noise model than to that of the brown noise model. Thus, as we might expect, the pink noise model is an intermediate case between brown and white noises. However, this is not so at all values. For example, at $t = 35$, the extinction rate is higher for pink noise than it is for the equivalent white noise model, whereas the brown model has a lower extinction rate than the white model at this value. The reason for this behaviour may lie in the conditioning. As was mentioned earlier, while the mean value of brown noise is X_1 and that of white noise is μ , the mean value of a pink noise population series is dependent on an infinite number of initial conditions, see Eq. (21). In our simulations we must assign initial values to each of the component AR processes. In theory, we therefore have an entire spectrum of possible behaviours. In the simulations we performed here we assumed that each of the initial values was zero, but that the overall offset (which can be seen as arising from AR processes on much longer timescales than explicitly included in the simulations) is X_1 . This results in a non-uniqueness of equivalent pink noise processes. Another factor which leads to a non-uniqueness of equivalent pink noise processes is that different proportions of long-term and short-term components could both produce the same M_T and S_T . This results in the fact that there is no unique pink noise parameterisation for the set of observations $\{x_1, x_2, x_3, \dots, x_T\}$ (in the same way that there is for a white, brown, or AR model) based only on M_T and S_T . In our simulations we assumed that there was a minimum timescale of $1/100$ of a year. A full discussion of this topic is beyond the scope of this paper. However, as we shall see, these problems cause less confusion in long-term extinction projections than in short-term ones. The AR model (Δ) initially differs from white noise in much the same way as brown noise does, but as soon as the length of the projected time series is comparable to τ_a , the rate of extinction becomes constant though not at the same value for the white noise model. In general this value may lie above or below the white noise model depending on τ_a and the other parameters.

As expected, in the simulations white and brown models behave very much as they did in the explicit analyses above. Our examination of population variability, above, suggested that a pink noise model of extinctions should produce results intermediate between the two more extreme models. This prediction was borne out in our simulations. Thus the relation between

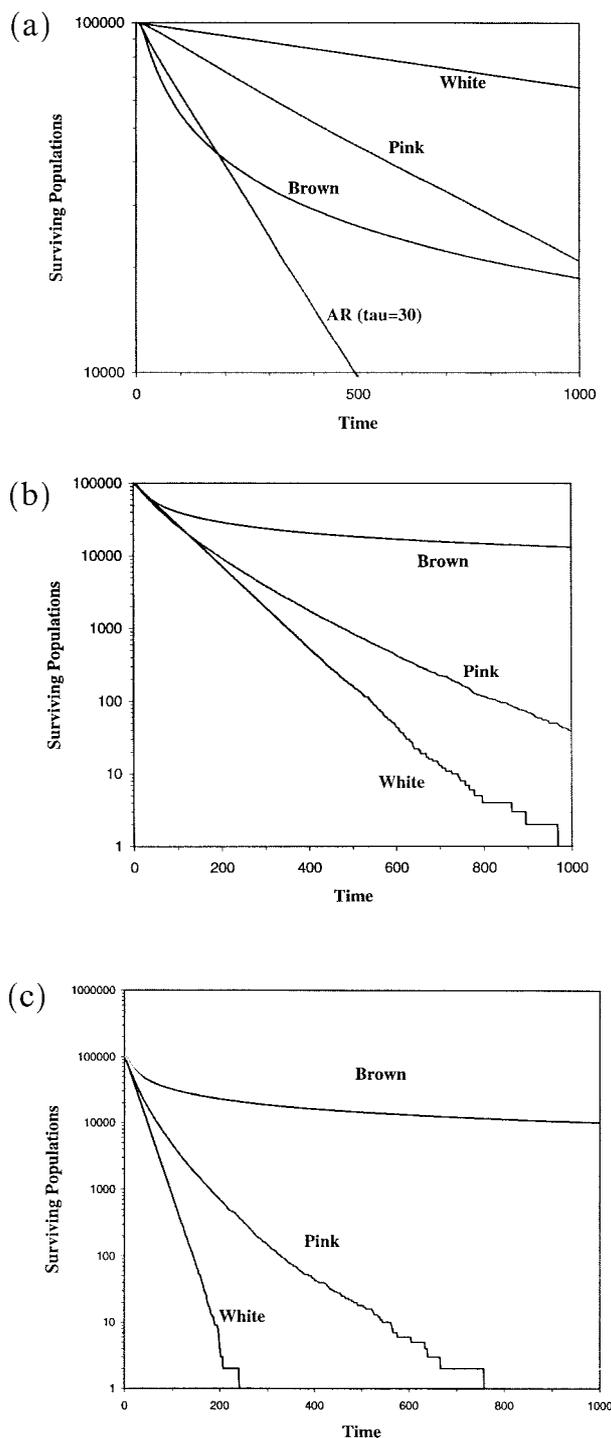


FIG. 5. Long-term projections for survival. (a) Vertical axis shows total surviving populations out of 100,000 Monte Carlo simulations for three equivalent noise models based on the same series of 25 observations ($T = 25$) of populations where the coefficient of variation for the series of T observations is $CV = 0.3$. In this diagram an AR model with $\tau_a = 30$ is also shown. (b) As for (a), but with $CV = 0.45$. (c) As for (a), but with $CV = 0.6$.

increasing variance and extinction in the short-term picture is not at all simple, and is strongly dependent on the conditioning of initial conditions. This conditioning is less important in long-term predictions as exhibited in Fig. 5.

Figures 5a–5c show the projections for survivorship on a timescale of up to 1000 years (40 times as long as T itself). On each of these we have the projections for the models equivalent over a 25-year timescale for $CV = 0.3, 0.45, \text{ and } 0.6$, respectively. It is clear that as we increase Δt , the projection timescale, the detailed complex behaviour and dependence on conditioning seen for short-term predictions begin to vanish. Figures 5b and 5c exhibit a clear trend: with moderate or high population variability, long-term survival is greatest for the brown noise model and least for white noise model, with pink noise intermediate. With low CV this is less obvious but the outcome is expected to be the same in the long term. In the Appendix, we show that irrespective of the values of T and CV , there always exists a projection time Δt^* for which the probability of survival in a brown model is greater than that of the equivalent white noise model. Therefore, in a sufficiently long-term projection, the white noise model always overestimates extinction probability.

We have also included results from the equivalent AR model (with $\tau_a = 30$ years) in Fig. 5a. This behaves like white noise in the long term, having a constant asymptotic rate of extinction, but this is higher than that of any of the equivalent 1/f family members. In general, the asymptotic extinction rate of an AR process, equivalent on a timescale of T at a coefficient of variability CV , may or may not be greater than the corresponding white noise process. Whether or not it is depends on T , CV , and τ_a .

7. DISCUSSION AND CONCLUSIONS

The analyses and simulations reported above demonstrate that projections of extinction risk, based on the parameterisation from a time series, can differ by orders of magnitude for different noise colours. Predictions based on inappropriate noise models may thus be highly misleading.

We have used three members of the 1/f noises (white, pink, and brown) as models of environmental variation which might lead to extinction. We considered only the simplest possible model, one in which the population itself is a stochastic process with a 1/f noise spectrum. By parameterising the models in terms of an observed time

series of length T , it is possible to predict the extinction risk based on the coefficient of variation, CV , of the series. Our predictions, using explicit formulae and on simulations, indicate that brown and pink noise models may present either an optimistic or a pessimistic picture relative to a white noise model. These models tend to be optimistic, predicting lower extinction rates, on timescales either much less than or much greater than T . On intermediate timescales they tend to present a more pessimistic prediction. Usually, a pink noise model makes predictions intermediate between white and brown noise models.

Thus, although the effect of reddening within the 1/f noise family is to increase the variance observed for longer time series, this does not necessarily mean a concomitant rise in extinction risk for long-term projections. This is somewhat contrary to the reasonable intuitive expectations (see Lawton, 1988; Halley, 1996) that reddening increases extinction risk, as well as seeming to contradict the findings of other models (Caswell and Cohen, 1995; Petchey *et al.*, 1997). However, we stress that the mechanism of reddening in our 1/f noise models (increasing the spectral exponent γ) also leads to non-stationarity (for $\gamma \geq 1$), so that now there exists the possibility of a population wandering upward toward relatively invulnerable population size, an effect which may offset the increased risk through higher variability. This does not contradict the finding that for stationary processes the effect of reddening is to increase the risk of extinction.

In our results an important role is played by the time series length, T . The resulting apparent sensitivity to parameter estimates arises from the fact that we are comparing the predictions of stationary models (white or autoregressive noise) with non-stationary ones (brown or pink noise). Non-stationary noises can only be uniquely defined via a specific set of measurements over a specified timescale. Because of this, the effects of such noises cannot meaningfully be compared in the context of their fundamental parameters, but only through of a set of observations, in this case a time series of known mean and variance and a duration T .

Many aspects of the behaviour of 1/f noises are still poorly understood and research is clearly at an early stage. Spatial extension seems to be an important aspect in the origins of low-frequency environmental noise (Renshaw, 1994; Pimm, 1994), and this spatial aspect needs further study. In this paper we considered the simplest kind of population modelling approach: where the population varies as 1/f noise. A systematic investigation of the effect of 1/f noises entering biological systems

through demographic parameters such as growth rate and carrying capacity is an extension which must be carried out. Many aspects of $1/f$ noises themselves are still poorly understood. For example, mathematical formulations of the stationary members of the family are usually very different from those of the non-stationary members, with pink noise often fitting into both, either, or neither camps. Little attention has been given to the relationship between pink noise in continuous and discrete time, and to the phase spectrum of $1/f$ noise (J. H. Steele, personal communication).

In the meantime, a knowledge of the biases inherent in currently used white and brown models should allow them to be used with appropriate caution. Although current methods of projecting extinction risk usually ignore temporal variance and spectral reddening, there is evidence of greater interest in these issues (Pimm, 1994; Bengtsson *et al.*, 1997). If conservationists are to allow for such effects, how should an appropriate extinction model be chosen? Probably, the best option would be to examine the colour spectrum exhibited by past variation, and to use this to guide the choice of an appropriate model for projecting into the future. Unfortunately, sufficiently long time series are seldom available for populations of conservation concern. In the absence of specific information about the spectral structure of past population variability, one should choose a model which is as unbiased as possible. Because the $1/f$ family of models has no specific timescale, we believe that changing the spectral exponent γ , as a mechanism of reddening, is preferable to introducing reddening through a single AR process, since such a process implies a bias toward a preferred timescale. In an earlier publication (Halley, 1996) one of us argued that among the $1/f$ noises the most appropriate choice of spectral exponent was $\gamma = 1$, corresponding to pink noise. This is because of its intermediate predictions—it is unlikely to be as misleading in its predictions as either of the more extreme models could be. White and brown noise models make rather unrealistic assumptions about the dynamics of populations over time: in white noise models, populations vary instantaneously and without memory; in brown noise models they wander rootlessly and without bounds. Most real populations exhibit both continuity and quasi-stationary tendencies, features that suggest that they sit somewhere in the middle of the range of $1/f$ spectral models. Moreover, analysis of ecological time series produces a median Hurst exponent closer to that of pink than to that of either brown or white (Ariño and Pimm, 1995; Halley, 1996). Perhaps the best simple strategy at present is to use the various extinction models in parallel, and to rely on whichever is most conservative in a given

context. The results outlined above should be useful in indicating which that is likely to be.

APPENDIX

A. Sample Mean of a Series of T Observations

For a stochastic process $\{X_t; t \in \mathbb{N}\}$, the sample mean for T observations of this process is

$$M_T = \frac{1}{T} \sum_{t=1}^T X_t. \quad (15)$$

Brown Noise. We use Eq. (2) (in text) recursively:

$$X_t = X_{t-1} + W_{t-1} = X_1 + \sum_{j=1}^{t-1} W_j. \quad (16)$$

Substitute this into Eq. (15) and take the expectation of both sides (noting that $E[W_t] = 0$) to get

$$E[M_T] = \frac{1}{T} \sum_{t=1}^T E[X_t] = E[X_1]. \quad (17)$$

Thus we can use M_T as an estimator for X_1 , hence Eq. (10) follows.

Autoregressive Noise. Suppose that X_t is an AR process of Eq. (3) with correlation coefficient ρ driven by a white noise process of expectation zero.

$$\begin{aligned} A_t &= \rho A_{t-1} + \sqrt{1-\rho^2} W_{t-1} \\ &= \rho^{t-1} A_1 + \sqrt{1-\rho^2} \sum_{j=1}^{t-1} \rho^j W_j. \end{aligned} \quad (18)$$

If we now substitute Eq. (18) into Eq. (15) with (3), we get

$$E[M_T] = \mu + \frac{1}{T} \frac{1-\rho^T}{1-\rho} E[A_1]. \quad (19)$$

Pink Noise. Pink noise in this paper is modelled by a superposition of AR processes Eq. (5), each behaving as Eq. (18) and related by (7). For the “band-limited” pink noise which we generate in the simulations for

this paper, we can replace the upper limit by K and the lower limit by $k = 1$:

$$X_t = \sum_{k=-\infty}^{\infty} A_t^{(k)} \quad (20)$$

$$\approx \mu + \sum_{k=1}^K A_t^{(k)}.$$

Note that in the second equation above, the mean, μ , is interpreted as a cumulative effect arising from all the low-frequency components which appear stationary over the timescales of interest. By analogy with the AR model we may proceed:

$$E[M_T] = \frac{1}{T} \sum_{t=1}^T \sum_{k=-\infty}^{\infty} E[A_t^{(k)}] \quad (21)$$

$$\approx \mu + \frac{1}{T} \sum_{k=1}^K \frac{1-\rho_k^T}{1-\rho_k} E[A_1^{(k)}].$$

B. The Sample Variance of a Series of T Observations

For a stochastic process $\{X_t; t \in \mathbb{N}\}$, the sample variance for T observations of this process is

$$S_T^2 = \frac{1}{T-1} \sum_{j=1}^T (X_j - M_T)^2. \quad (22)$$

Brown Noise. Given a set of sequential random variables $\{X_1, X_2, X_3, \dots, X_T\}$, we assume that its noise model is brown (discrete in time) such that $E[X_t] = x_1$ and $E[(X_t - X_{t-1})^2] = \sigma_b^2$. We take the expectation of both sides of Eq. (22):

$$E[S_T^2] = E \left[\frac{1}{T-1} \sum_{j=1}^T \left(X_j - \frac{1}{T} \sum_{i=1}^T X_i \right)^2 \right]$$

$$= \frac{1}{T^2(T-1)}$$

$$\times \sum_{i=1}^T \sum_{j=1}^T \sum_{k=1}^T E[(X_j - X_i)(X_j - X_k)]. \quad (23)$$

We now introduce new terminology: $\Delta X_{ji} = X_j - X_i$ so that the expression becomes

$$V_T^{(b)} = E[S_T^2] = \frac{1}{T^2(T-1)} \sum_{i,j,k} E[\Delta X_{ji} \Delta X_{jk}]. \quad (24)$$

This involves summing the expression $E[\Delta X_{ji} \Delta X_{jk}]$ over an ijk lattice. Each pair ΔX_{ji} and ΔX_{jk} can be considered two time segments consisting of overlapping and non-overlapping parts.

If $k = i$ we have two completely overlapping segments with an overlap of $j - i$. The expectation of their product can be calculated from the well-known formula pertaining to Brownian processes:

$$E[\Delta X_{ji}^2] = |j - i| \sigma_b^2. \quad (25)$$

Conversely, for entirely non-overlapping segments, for example, when $i > j$ and $k < j$, the variables ΔX_{ji} and ΔX_{jk} are independent, so

$$E[\Delta X_{ji} \Delta X_{jk}] = 0. \quad (26)$$

In general, the contributions to Eq. (24) above can be found by dividing each pair of segments into overlapping and non-overlapping parts and applying the above formulae Eqs. (25) and (26).

Consider a single slice of the three-dimensional lattice, associated with a specific value of j . There will be T such slices in the lattice. We can associate i with columns and k with rows in this slice. Each cell contains $E[\Delta X_{ji} \Delta X_{jk}]$. The values of this quantity will define ‘‘contours’’ of constant overlap. For example, the number of cells with an overlap of one (i.e., $E[\Delta X_{ji} \Delta X_{jk}] = \sigma_b^2$) will be $[2(j-1) - 1]$ in number. Similarly there are $[2(T-j) - 1]$ cells having an overlap of negative one. Similarly there will be $[2(j-2) - 1]$ cells with an overlap of two, and so on. A table is shown below of $E(\Delta X_{ji} \Delta X_{jk})/\sigma_b^2$ for $T = 6$ with $j = 4$ (blank cells denote zero).

	ΔX_{41}	ΔX_{42}	ΔX_{43}	ΔX_{44}	ΔX_{45}	ΔX_{46}
ΔX_{41}	3	2	1	0		
ΔX_{42}	2	2	1	0		
ΔX_{43}	1	1	1	0		
ΔX_{44}	0	0	0	0	0	0
ΔX_{45}				0	1	1
ΔX_{46}				0	1	2

(27)

We can sum the contributions over the entire lattice ‘‘contour by contour.’’ It is relatively easy to see that there will be a total of $2(T-1)^2$ with an overlap of plus or minus one, $2(T-2)^2$ with an overlap of plus or minus two, and so forth, down to just two with an overlap of plus or minus $T-1$. We can now add up all of these

contributions as follows, calling s the degree of overlap, to get the following form equivalent to Eq. (24):

$$V_T^{(b)} = \frac{1}{T^2(T-1)} \sum_{s=1}^{T-1} [2(T-s)^2]_s \sigma_b^2. \quad (28)$$

We can expand the brackets to get summations involving s^2 and s^3 , for which there are known expressions (Spiegel, 1968), leading to

$$V_T^{(b)} = \left[\frac{T+1}{6} \right] \sigma_b^2. \quad (29)$$

Autoregressive Noise. The stochastic X_t process is defined by Eq. (18) with $E(W_t) = 0$ and $E(W_t^2) = \sigma_a^2$. Once again we start with the expectation of Eq. (22) in the following form (using Eq. (15) for M_T):

$$V_T^{(a)} = E[S_T^2] = \frac{1}{T-1} \sum_{j=1}^T E(X_j^2) - \frac{1}{T(T-1)} \sum_i \sum_j E[X_i X_j]. \quad (30)$$

The first term has the value $T\sigma_a^2/(T-1)$. For the second, we use the relation, appropriate for a first-order AR process,

$$E[A_i A_j] = \rho^{|i-j|} \sigma_a^2. \quad (31)$$

Thus if we consider the matrix of $E[A_i A_j]$ (with i the row and j the column) then the diagonal elements, of which there are T , have values $\rho\sigma_a^2$ while the first upper diagonal and lower diagonals each with $2(T-1)$ elements have values $\rho^2\sigma_a^2$. The second upper diagonal and lower diagonals each with $2(T-2)$ elements have values $\rho^3\sigma_a^2$ and so on, giving the following sum of contributions:

$$\begin{aligned} V_T^{(a)} &= \frac{T}{T-1} \sigma_a^2 - \frac{1}{T(T-1)} \\ &\quad \times [T + 2(T-1)\rho + 2(T-2)\rho^2 \\ &\quad + \dots + 2(2)\rho^{T-2} + 2(1)\rho^{T-1}] \sigma_a^2 \\ &= \left[\frac{T+1}{T-1} - 2 \frac{T(1-\rho) - \rho(1-\rho^T)}{T(T-1)(1-\rho^2)} \right] \sigma_a^2. \quad (32) \end{aligned}$$

The second line follows from the first above by means of the standard sum for an arithmetico-geometric series (Spiegel, 1968).

Pink Noise. The sample variance of a pink noise process is simply the sum of the contributions of the (independent) AR components, with correlation given by Eq. (6) and Eq. (7), each contributing variance σ_p^2 to the overall process. The variance of a series of T samples of this process is just the sum of all components according to Eq. (32) above:

$$V_T^{(p)} = \sum_{k=-\infty}^{\infty} \left[\frac{T+1}{T-1} - 2 \frac{T(1-\rho) - \rho(1-\rho^T)}{T(T-1)(1-\rho^2)} \right] \sigma_p^2. \quad (33)$$

For the ‘‘band-limited’’ pink noise which we generate in the simulations for this paper, only K of these components participate actively so that we can replace the upper limit of the summation above by K and the lower limit by $k = 1$.

C. Extinction Probability

Extinction under brown noise depends only upon the starting value X_1 , not on any carrying capacity. The process is non-stationary too; there is no limit to the amount of variance which can accumulate as the series grows longer. The absorption probability for this Brownian process is given for continuous time by Karlin and Taylor (1975, p. 355),

$$E_t^{(b)} = P[X_t = 0 \mid X_1 = x_1] = 2 \int_0^{\infty} p(u + x_1, t) du, \quad (34)$$

where

$$p(u, t) = \frac{1}{\sqrt{2\pi t}} \exp \left[-\frac{u^2}{2t} \right]. \quad (35)$$

If we just substitute the expression for $p(u, t)$ into the first equation, changing the variable of integration to $v = u + x_1$, noting that for normal time we replace the dimensionless t in the above by $\sigma_b^2 t$, then we get the following expression:

$$E_t^{(b)} = \operatorname{erfc} \left[\frac{x_1}{\sigma_b \sqrt{2t}} \right]. \quad (36)$$

The complementary error function used here is another form of the area under the normal curve (see Spiegel, 1968). When $t = \Delta t$, which is large, we have the approximation

$$E_{\Delta t}^{(b)} \approx 1 - \frac{2x_1}{\sigma_b \sqrt{2\pi\Delta t}}. \quad (37)$$

The survival probability is the second term on the rhs.

By contrast, for the white noise model, the extinction probability per year is constant; thus we have something of the form

$$E_{\Delta t}^{(w)} = 1 - \exp[-\alpha \Delta t]. \quad (38)$$

Thus while the probability of survival decreases exponentially for a white noise process, the probability of survival for a brown noise process decreases only as a power law. Therefore, it is always possible to find a value of time $\Delta t = \Delta t^*$ for which

$$E_{\Delta t^*}^{(w)} \geq E_{\Delta t^*}^{(b)}. \quad (39)$$

Thus in the long run the probability of extinction is always greater for such systems subject to white noise than to brown noise.

D. How Simulations Were Carried Out

The simulations were carried out using a program written in the C programming language and run on a PC. The graphs were drawn using Excel.

1. By assumption we chose $T = 30$ and $M_T = 100$ and $CV \in \{0.3, 0.45, 0.6\}$ as inputs to the program. S_T is thus constrained, through Eq. (14). Note, however, that as we assume a Gaussian distribution, the extinction formulas depend only on CV rather than on M_T itself. So the actual value of M_T does not affect the final result.

2. From Eq. (9) and Eq. (10) the program estimates μ_w , σ_w , X_1 , and σ_b .

3. For pink noise we assumed a range of timescales from 10^{-2} to 10^5 years to model the process by a superposition of 15 AR processes (two per frequency decade) on the basis that this gave a sufficiently smooth approximation to the $1/f$ spectrum in the frequency domain. The program was instructed to employ Eq. (8) with $K = 15$ with $\tau_1 = 10^{-2}$ and with a constant ratio of $\sqrt{10}$ between τ_k and τ_{k+1} in Eq. (7).

4. For pink noise the program calculated $\rho_k = \exp(-1/\tau_k)$ for each timescale.

5. Using Eq. (11) the program calculates σ_p .

6. Finding the initial values of the component processes was the most problematic aspect, as we had to run different models in an equivalent situation. Should the prediction part of the simulations be correlated with the measurement, or independent of it? We chose the former, and we chose to begin the prediction at $t = T + 1$ (the

year after the last measurement) with the following initial conditions:

$$X_{T+1} \sim N(0, S_T^2) \quad (40)$$

$$X_{T+1} \sim N(0, 2S_T^2) \quad (41)$$

$$X_{T+1} = A_{T+1}, \quad A_{T+1} \sim N(0, \sigma_a^2) \quad (42)$$

$$X_{T+1} = \sum_{k=1}^K A_{T+1}^{(k)}, \quad A_{T+1}^{(k)} \sim N(0, \sigma_p^2), \quad (43)$$

where Eqs. (40), (41), (42), and (43) were the starting values for the simulations for white, brown, AR, and pink noise models, respectively. The factor of 2 for the brown noise model is found by calculating

$$[X_{T+1} - M_T]^2 = TS_{T+1}^2 - (T-1)S_T^2 \quad (44)$$

and taking the expectation of both sides, using (29) and the assumption that $T \gg 1$. This leads to something of the form $(T/3)\sigma_b^2$ which is $2S_T^2$. This increase is due to the fact that the variance increases as T gets larger.

7. There were 100,000 simulations for each class of noise model, each run for 1000 iterations (each corresponding to 1 year). Each simulation was calculated independently according to the iteration formulas (1), (2), and (3) for white, brown, and AR noise, respectively, and according to (8) for pink noise with each component obeying Eq. (3).

8. Note that in Eqs. (40)–(43) the simulations X_t are centered on zero. Thus each simulation terminated (the model population became “extinct”) if and when $X_t \leq -\mu$.

9. For each model the number of surviving populations was recorded for each time t .

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