

Ecology, evolution and $1/f$ -noise

John M. Halley

Among ecologists, there has been a growing recognition of the importance of long-term correlations in environmental time series. The family of $1/f$ -noises – fluctuations defined in terms of the different timescales present – is a useful approach to this problem. White noise and the random walk, the two currently favoured descriptions of environmental fluctuations, lie at extreme ends of this family of processes. Recent analyses of data, results of models, and examination of basic $1/f$ -noise properties, suggest that pink $1/f$ -noise, which lies midway between white noise and the random walk, might be the best null model of environmental variation. If true, this would have important consequences for the interpretation of ecological time series and for ecological and evolutionary modelling.

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Typically, when we read a time series, we see a pattern or signal corrupted by noise. Noise is the part of the series that is 'unwanted' according to the model used to interpret it. In ecological and evolutionary studies, the magnitude of the noise relative to the signal is always very large, so it seems natural to search for models that describe the behaviour of the system statistically.

To be successful, such models require a good understanding of the statistics of the background noise processes. In spite of this obvious need, there have been few attempts to parameterize these stochastic models in ecology. The builders of stochastic models pray that ecological statistics (e.g. birth rate) will 'settle down' to a norm as we accumulate more data. The unfortunate experience of many ecologists is the reverse: the more data we include, the more variable the statistics become. Furthermore, in comparisons of model predictions and real data, stochastic models often perform as poorly as deterministic ones.

This has led to a tendency among theorists to ignore the actual structure of environmental noise in favour of the comfort of pure theory ('If environmental noise has *that* property then *this* follows...'). Environmental noise is regarded as something of a mathematical and statistical hydra: as soon as we cut off one head of the monster (by including an extra parameter in our model) several more spring up in its place (the new parameter itself is subject to its own noisy perturbations). In ecology and evolution, it is not so easy to separate what is 'signal' from what is 'noise'.

In fact, the prospects are not as gloomy as we have previously thought. There are good reasons to believe that the structure of environmental fluctuation is well described by a phenomenon called

' $1/f$ -noise'. Although this has many technical aspects, its basic essence and its implications are easily understood.

What is $1/f$ -noise?

Ecologists expect both rare and common events to be important. The diversity of a desert ecosystem, for example, will be influenced by numerous small changes each day. Some rare events, such as desert storms, will have longer-lasting influence. $1/f$ -noise is a way of describing these kinds of events. It has been described as 'an evolutionary random process'¹, and is charac-

terized by strong correlations on a multitude of scales. (This discussion is confined to temporal fluctuations, but $1/f$ -noise can also characterize spatial correlations.)

Most stochastic models assume that noise has no temporal correlation: that the values of a random signal at two instants in time are completely independent of each other. This kind of noise, called 'white noise' (see Fig. 1), is an excellent model of most noise found in physics and electronics. In the environmental sciences, however, the prevalent assumption – that noise is white noise – is more difficult to sustain. Environmental fluctuations arise from various factors, correlated on different timescales. Such noise is often assumed to be white because it leads to mathematically tractable models, and because there is doubt about what should replace it. Introducing correlation structure into a noise process almost always makes life more complicated for the theorist. Where this has been done, it is usually some kind of autoregressive process, in which the correlation between two events declines exponentially with their separation in time. The assumption is that the correlation with past events dies away rapidly above a certain characteristic scale.

$1/f$ -noise is associated with an altogether slower decline in correlation. In contrast to autoregressive processes, the correlation of fluctuations falls off as a power law. For example, the correlation between two events might be proportional

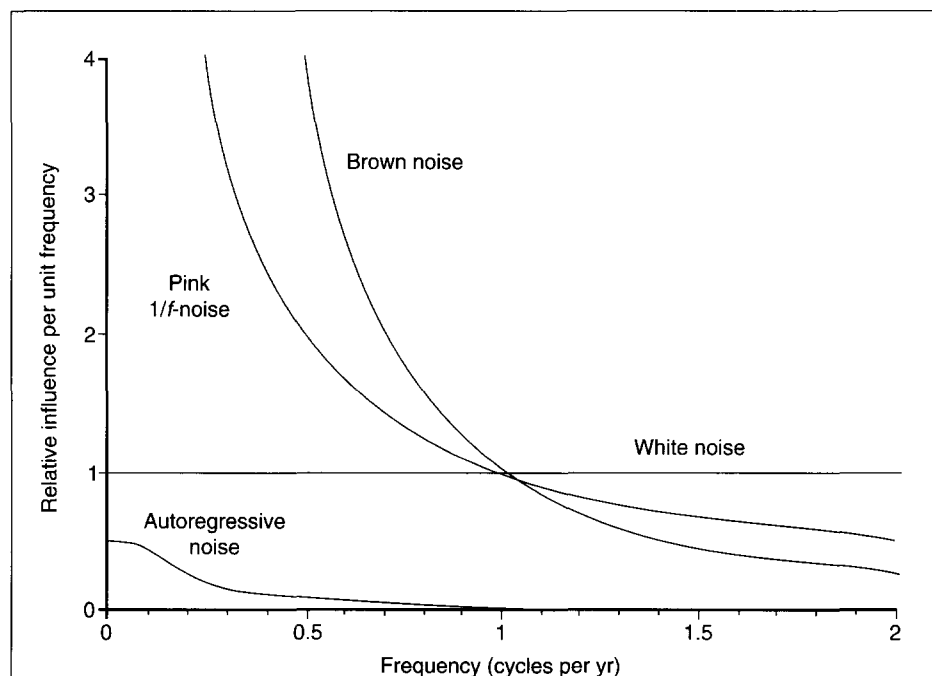


Fig. 1. Spectral density of various kinds of noise. White noise is so called because of its analogy with white light, which contains equal amounts of all frequencies. Reddened spectra are similarly understood in optical terms, since optical spectra that have a surplus of lower frequency light appear redder. A brown process is one where the random variable is allowed to drift. If a particle undergoes brownian motion, for example, its position, $x(t)$, is a brown noise process, while its velocity, $dx(t)/dt$, is a white noise process. Thus, a brown process is 'non-stationary'.

Box 1. Types of spectra

Spectral density, $S(f)$: this is a decomposition of the noise signal into its various component frequencies per unit frequency. By analogy with light, white noise is noise whose spectral density is flat, containing equal amounts of all frequencies (see Fig. 1). If the spectral density at low frequencies is greater than that at high frequencies, the overall effect of low frequency (rare) events has a greater influence than that of high frequency (common) events per unit frequency. Noise that contains an excess of low-frequency components is said to have a 'reddened' noise spectrum, similarly understood in optical terms, since optical spectra that have a surplus of lower frequency light appear redder. A brown spectrum (from brownian motion) is the spectrum generated by a signal doing a random walk. As its name suggests, pink noise lies midway between white noise and brown noise on a scale of redness.

Spectral density on a log scale: often when showing the scaling properties of power spectra, it is common to plot the graph on a log scale. This spectrum simply has the value of $S_x[\log(f)]$.

Spectral Density per Octave (SDO): is derived from the spectral density, $S(f)$, by transformation, using the formula:

$$F(\phi) = \frac{df}{d\phi} \cdot S(f)$$

where $\phi = \log_2(f)$. This is the power spectrum of frequencies pre-arranged on a logarithmic scale (Fig. 3). The difference from spectral density on a log scale (above) is that SDO is density per logarithm of frequency as distinct from density per unit frequency plotted against $\log(f)$.

Phase spectrum: contains the information about the relative timing of the spectral components. A detailed discussion of this aspect of $1/f$ -noise is beyond the scope of this paper.

to τ , τ^2 or some other power of time separating them. In fact, these processes behave in an essentially fractal way, having statistical self-similarity on all scales². $1/f$ -noise was so named because of the shape of its spectral density¹ (see Box 1).

The extended family of $1/f$ -noise is characterized by power-law spectra of the form: $S(f) \propto 1/f^\gamma$, where $0 \leq \gamma \leq 2$. The family takes its name from that member for which $\gamma=1$, which is often called 'pink noise'³ (see Box 1 for an explanation of 'coloured' noises). Other members of the family include white noise (for which, $\gamma=0$) and the random walk, also called 'brown noise' (after brownian motion, $\gamma=2$). Noises with $\gamma > 2$ are called 'black noises'³. In this paper ' $1/f$ -noise' refers to any member of the family for which $\gamma > 0$.

Some of the phenomena with which approximately $1/f$ -spectra ($0 < \gamma \leq 2$) have been associated include:

- electronic device noises^{4,5}
- geophysical time series^{6,7}
- economic time series⁸
- traffic flow⁹
- music¹⁰
- protein dynamics¹¹
- DNA-base sequences¹²
- ecological time series^{7,13}

That such a wide variety of phenomena seems to obey this simple scaling pattern is remarkable. Although some of these findings are better established than others, the sheer ubiquity of the phenomenon suggests that it deserves serious consideration.

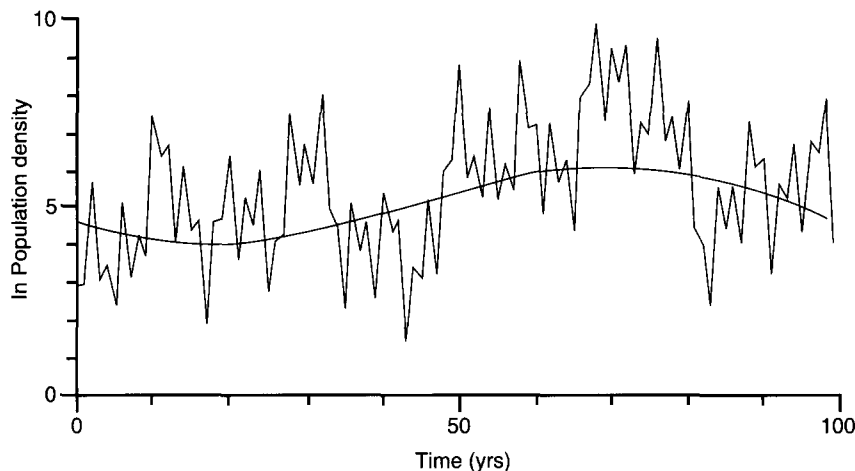
$1/f$ -noise in ecological time series

The habit of ecological time series – to get 'messier' as more data (from wider timescales) are included – becomes more understandable if the environmental fluctuations are seen as having a 'reddened spectrum'. (Spectral representations of ecological time series have already been used by Schaffer¹⁴ and others.) Variance, instead of settling down to a nice gaussian statistic, increases with the length of the series^{13,15}. Slow variations have much greater 'strength' than rapid ones (Fig. 1; see also Box 2), but these are only 'revealed' in longer time series. $1/f$ -noise has a reddened spectrum. What distinguishes pink noise (and any $1/f$ -noise for which $\gamma \geq 1$) from other noises with reddened spectra is that variance continues increasing, no matter how long the time series.

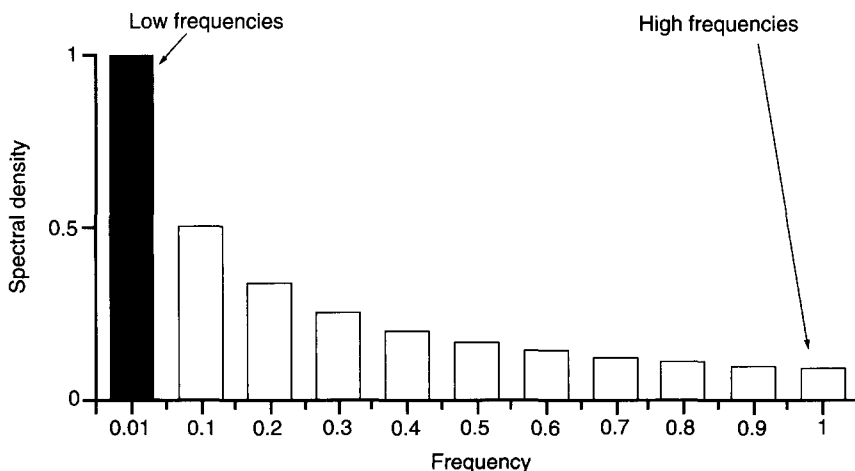
Ecological time series will tend to exhibit $1/f$ -noise (at least on longer timescales) if the underlying abiotic perturbations are $1/f$ -noise¹⁶. Mandelbrot and Wallis⁶ demonstrated long-term $1/f$ -type scaling for a number of abiotic factors. Steele⁷ also showed that abiotic perturbations influencing marine systems were

Box 2. An ecological example of $1/f$ -noise

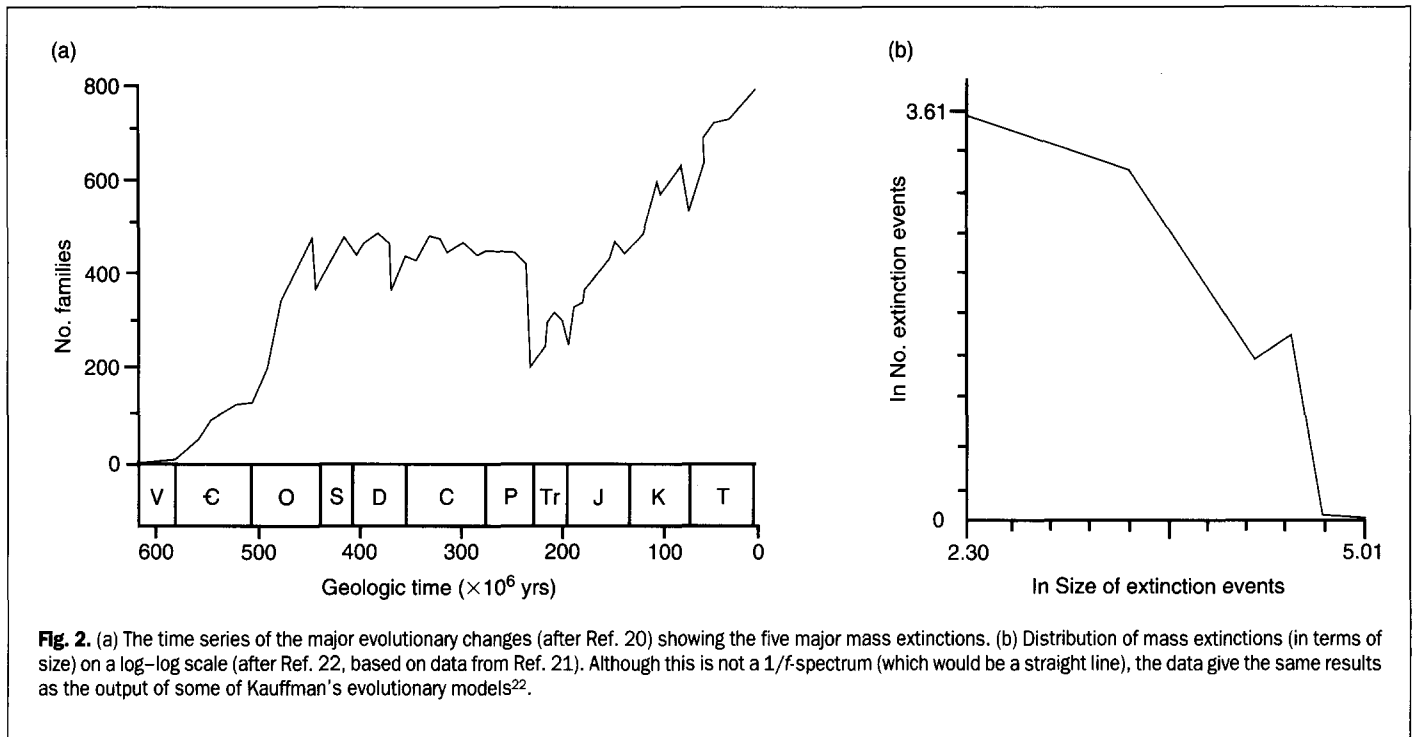
An imaginary ecological time series, having a pink $1/f$ -spectrum, is drawn below along with its longest component sinewave, its **fundamental harmonic**.



The spectral density of the above series may be decomposed into constituent sinewaves of different frequencies. Note the density (shown below) at the fundamental harmonic (black bar) is highest.



Often we see 'trends' in the noise, like the trend upwards in this example, which may be interpreted as longer timescale components of the $1/f$ -noise process.



reddened, lying close to brown noise, $\gamma \approx 2$. Terrestrial fluctuations had more in common with white noise for timescales of <50 years, but were reddened for longer timescales.

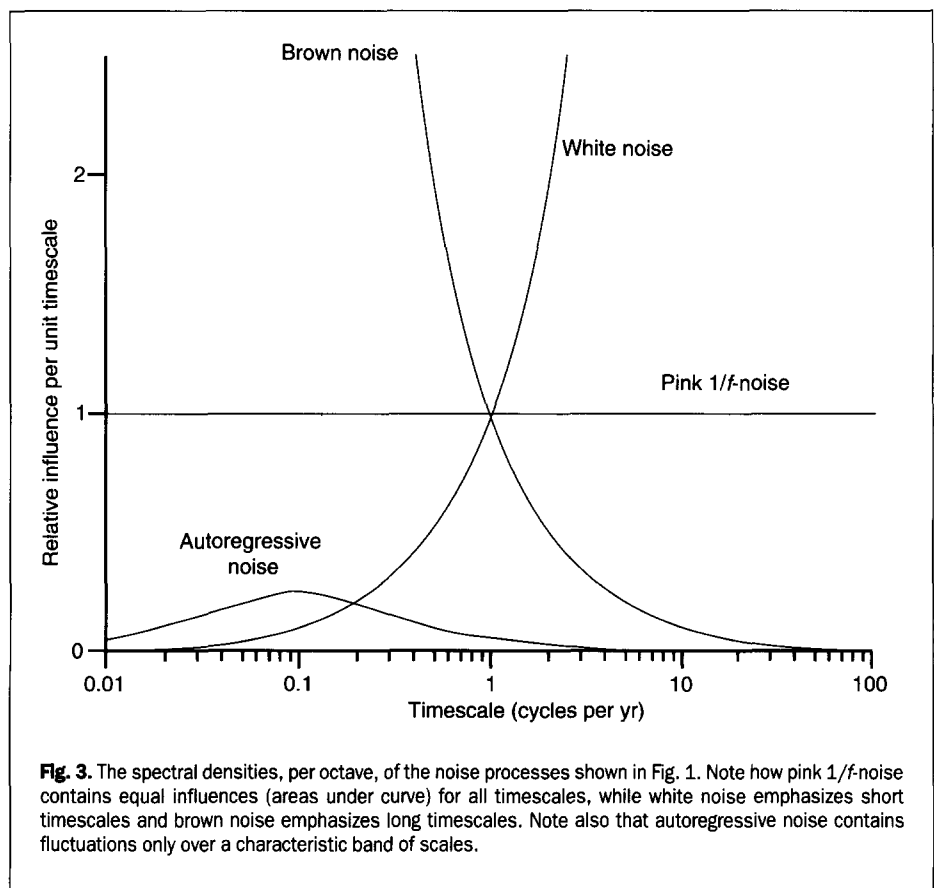
Abiotic perturbations, of course, are only part of the picture. Biotic perturbations will also influence population dynamics. Using population time series directly, Pimm and Redfean¹³ argued that the population dynamics of birds, mammals and insects reflected an underlying reddened spectrum of environmental variation. They showed that the standard deviation of the logarithm of density increased with census length in the time series for 42 species of farmland birds, 32 species of woodland birds, 22 miscellaneous birds and mammals and four insect species. Some objections were raised to Pimm and Redfean's conclusions, on statistical grounds¹⁷ and on the grounds of alternative explanations based on intergenerational correlation¹⁸ (with white-noise forcing). On balance, these criticisms seem unlikely to undermine the conclusions of Pimm and Redfean, whose data covered a wide variety of organisms in different locations with different generation times. More recently, Arino and Pimm¹⁶ have calculated Hurst exponents (another measure of reddening) for the time series of 58 different species. Their results span the range from white noise to black noise but they observe that the mean Hurst exponent lies 'about halfway between Brownian and white noise' suggesting the central importance of pink noise. Arino and Pimm's results also reflect the stronger reddening in marine than in

terrestrial ecosystems as suggested by Steele⁷.

Even so, it may not be possible to measure variation of ecological parameters over a sufficient time to detect environmental $1/f$ -noises with certainty. However, there are other reasons (see below) why we might expect environmental noise to be closer to pink noise than to white noise.

$1/f$ noise and extinctions

Mass extinction is an ubiquitous feature of the fossil record. The great mass extinction at the end of the Cretaceous period is usually explained by reference to 'external' isolated factors, such as meteorite impacts. However, some have argued for more internal causes for dinosaur extinctions. There is strong evidence, for



example, that all the major dinosaur groups were in decline before the end of the Cretaceous¹⁹. Perhaps the internal dynamics of evolution alone are sufficient to explain the recurrent phenomenon of mass extinction. Mass extinctions and punctuated equilibrium might emerge naturally, even in a world not subject to violent upheavals. The spectrum of mass extinctions should offer some clues as to their causes.

The mass extinction events, such as we can compile them²¹ (Fig. 2a), show a preference for larger scales (Fig. 2b) and implies a reddened spectrum. This is not necessarily because of the internal dynamics of evolution, since geophysical perturbations may also have reddened spectra. Kauffman²² and others²³ have created models of evolution yielding mass extinctions of various sizes that often follow a $1/f$ -spectrum. However, spectra based on the real thing do not have a general $1/f$ -form²², though more data will need to be gathered before this question can be answered conclusively.

Models of evolution leading to $1/f$ -noise

Although there is no firm evidence that evolutionary time series obey a $1/f$ -spectrum, the results of models of evolution are still worth considering, because of the fact that these models yield punctuated equilibrium and a reddened spectrum, in common with what the fossil record suggests.

One of the best known of these models is self-organized criticality (SOC)²⁴. $1/f$ -spectra are often regarded as the signature of SOC, despite a number of alternative explanations for such spectra^{5,25}. SOC is remarkable because of its 'holistic' character, and because it emerges in such a wide range of physical systems²⁶.

The classic model of SOC is Bak's sand pile^{25,26}. In this model, the sand pile is generated by the dropping of grains of sand onto the top of the pile. Eventually, an approximately conical pile of sand results. The angle of this pile will not rise significantly beyond some critical angle, because if it does the pile will be too steep and an avalanche will result. Neither will the angle fall significantly below this critical angle, because sand is constantly being added to the top of the pile. However, because of the friction of the sand pile, the critical angle will not be maintained in a smooth fashion. The pile will tend to 'maintain' itself close to this critical shape through a series of avalanches of various sizes. A spectral analysis of this series of avalanches yields a near-pink spectrum.

Artificial life models^{23,27,28} give some support to Bak's suggestion that SOC is the basis of punctuated equilibrium. In the evolutionary model, in place of a constant trickle of sand onto the top of the pile there

is a constant accumulation of mutations into the total genetic material of the ecosystem; in place of the friction of the sand pile is the resistance of the ecosystems to change; finally, major avalanches in the sand pile are like the sporadic and 'sudden' evolutionary realignments.

However, SOC is not the only means of punctuating evolutionary changes. Newman *et al.*²⁹ have shown that a 'standard Wrightian' model combining random drift and natural selection is sufficient. In a two-peak adaptive landscape, they observed rapid shifts between fitness peaks, punctuated by longer periods of relative stasis. Since pink noise can be interpreted as a random drift in a landscape with random-height barriers²⁵, the evolutionary jumps predicted by a 'standard Wrightian' model should also have a near-pink $1/f$ -spectrum, if we assume a random-height adaptive landscape.

Ecosystem changes could be modelled similarly. While research is still at an early stage and the models extremely simple, they provide further circumstantial evidence for the importance of $1/f$ -noise in ecology and evolution.

Fairness to all scales

It seems reasonable to suppose that environmental noise, being the accumulation of many different processes, ought to contain disturbances evenly distributed over different timescales. Thus, white noise is often assumed to be the 'natural' choice for environmental disturbance, since it seems democratically to assign equal weights to all different frequencies (Fig. 1). We might conclude that white noise contains different timescales in equal proportions. Such a conclusion would be false.

This can be seen by noting that the relative significance represented by all timescales greater than one year (decades, centuries, millenia, and so on) is simply found by adding up the area under the white-noise curve for frequencies between zero and one in Fig. 1, giving $1.0 \sigma_w^2$. Likewise, the relative significance of all timescales between six months and one year is the area under the curve between one and two cycles per year. This means that, if environmental perturbations are indeed white noise, the significance of all events on timescales longer than one year is no more than that of events on a scale of six to 12 months. Moreover, the significance of all events shorter than six months is infinite! White noise does not assign equal importance to all timescales.

What kind of noise distribution partitions all the components 'fairly' between all scales? By looking at the Spectral Density per Octave, SDO (the relative influence of fluctuations associated with the various timescales in the signal; see Box 1),

we can see the scale dependence. This is given by $F(\phi) \propto 10^{(1-\gamma)\phi}$, where $\phi = \log_{10} f$. The SDO is shown in Fig. 3 for the various types of noise.

Now we can see clearly what is happening. White noise contains all frequencies but emphasizes shorter timescales. Brown noise conversely emphasizes longer timescales. Pink noise is special in that it contains disturbances equally on all timescales. Fluctuations happening from about every year to once a decade (area under $1/f$ -noise curve between 1 and 0.1) have, on average, as much influence on the present as events happening once a decade to once a century (area between 0.1 and 0.01), and so on, demonstrating the special connection that pink noise has to the idea of fractals⁶. Another way of saying this is that pink noise contains memory of past events on all timescales¹. Again this contrasts sharply with white noise, which is uncorrelated and has no memory, and with brown noise, which only 'remembers' its position in the previous timestep².

Despite the infinite information content of pink noise, efficient methods of generating it (and other $1/f$ -noises) are available, either by using wavelet transforms² or other novel methods³⁰. $1/f$ -noises may also be approximated over any range of frequencies using a combination of autoregressive noises of different timescales (J. Steele, pers. commun.; Ref. 3).

Pink noise is the natural result of a mixture of different phenomena acting impartially on different scales. Thus, although the data suggest a range of exponents¹⁶, it is pink noise, rather than white or brown noise, that we should regard as the null model for environmental fluctuations.

Why $1/f$ -noise is important

The $1/f$ -noise family offers a compelling description of the background environmental fluctuations in ecology and evolution, for several reasons.

There is strong evidence that background abiotic fluctuations have $1/f$ -noise spectra^{6,7}, though there may be significant differences between the terrestrial and marine environments⁷. Direct support for $1/f$ -noise^{13,16} in both ecological and evolutionary time series is more tentative. Until longer time series are available, it is only possible to say that the data are compatible with $1/f$ -noise.

In several important types of theoretical model²²⁻²⁹, pink $1/f$ -spectra arise naturally, or might reasonably be conjectured, as a consequence of the dynamics of the system. Although the status and applicability of some of these models to real systems remains controversial, their initial results deserve serious consideration.

If we suppose that the natural environment contains a mixture of disturbances

on all scales, then pink $1/f$ -noise seems the most natural 'null model'. This is because, in contrast to white or brown noise, pink noise shows no preference for short or long timescale disturbances^{1,2}. From seconds to millenia, all natural disturbances of various sizes can be seen as part of a seamless $1/f$ -noise process. In this picture we need not make any special distinction between normal environmental variation and ecological 'catastrophes': it is the same thing seen at different scales.

Another feature of general $1/f$ -noises is that only some of them are stationary. This too has implications for ecology. For example, white noise models of density-dependent regulation deliver a stationary, regulated picture: populations can fluctuate about carrying capacity but are nonetheless regulated by it. On the other hand, random walk (brown noise) models of population yield a model of a population with no regulation whatsoever. These extremes approximate the poles of the density-dependence/independence debate. Neither view has prevailed because of our experience of real ecosystems: they are neither completely fixed nor completely free. Pink noise, with its pseudo-stationary behaviour (stationary, but only over certain timescales¹), may offer some resolution in this respect.

Finally, if the suggestion is accepted, that environmental fluctuations are $1/f$ -noise, the interpretation of long time-series, and many current stochastic models in ecology and evolution, will need to be re-examined. For example, time-to-extinction estimates based on white noise will often turn out to be excessively optimistic^{13,31}.

Acknowledgements

I would like to thank the following for helpful comments on the manuscript: Vincent Jansen, Jin Yoshimura, Simon Fraser, Howard Wilson, Bob Holt, Pejman Rohani, Joel Cohen, Stuart Pimm, John Steele and John Lawton. This research was supported by an EEC-MAST grant.

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