

THE INCREASING IMPORTANCE OF $1/f$ -NOISES AS MODELS OF ECOLOGICAL VARIABILITY

JOHN M. HALLEY

Dept. of Ecology, School of Biology, Aristotle University, U.P. Box 119, 54006 Thessaloniki, Greece
jmax@bio.auth.gr

PABLO INCHAUSTI

ECOBIO UMR 6553 Université de Rennes 1 Av. Général Leclerc Rennes 35042 France
pablo.inchausti@univ-rennes1.fr

Received 11 September 2003

Revised 29 January 2004

Accepted 1 February 2004

The features of $1/f$ -noise processes offer important new insights into the field of population biology, greatly helping our quest for understanding and for prediction of ecological processes. $1/f$ -noises account quite satisfactorily for the observed nature of ecological fluctuations. This article reviews the application of $1/f$ -noise processes to ecology. After a discussion of the basic problems of population ecology that makes such an innovation necessary, we review the features of $1/f$ -noises concentrating especially on those aspects that make these processes attractive as a solution. We also present a discussion of the analysis of real ecological data, which confirms that there are good empirical as well as good theoretical reasons to establish a leading role for pink $1/f$ noise. We then discuss the consequences of such a model for our understanding of ecology. The article finishes with a number of observations about some aspects of ecological data and applications that are likely to drive research in a different direction from that associated with engineering and the physical sciences.

Keywords: $1/f$ noise; ecology; fractals; stochastic processes.

1. Introduction

The number of ecological publications about $1/f$ -noise is doubling every 7 years, faster than the rate of increase of $1/f$ -noises articles in general (doubling time ~ 10 years).^a However, in ecology, there is a tendency for ideas to generate excitement and flourish for a while and, when they fail to deliver their original promise, they are consigned to oblivion with the same enthusiasm that they were initially embraced. It is possible that the current interest in $1/f$ -noise will suffer the fate of such ideas, once-fashionable in

^a From the authors' library and from the database maintained by Wentian Li about $1/f$ -noise at the website <http://www.nslj-genetics.org/wli/1fnoise/>

ecology, as information-theoretic approaches to community ecology [1] and the use of local stability analysis of food webs as a measure of the relationship between the complexity and stability of ecosystems [2]. Nevertheless, there are some good reasons to believe that the current interest is not a “fad” but a part of a genuine paradigm-shift towards a different kind of model and a different way of using models. For the specific area of population ecology, these may be written briefly as follows:

- Classical population models (even chaotic ones) fail to deliver the kind of complex population dynamics that we observe in nature. By contrast $1/f$ -noises account for the type of complex ecological variability in a highly satisfactory way.
- Various theoretical arguments support the $1/f$ hypothesis.
- Observed population fluctuations are consistent with the $1/f$ hypothesis.
- The growth in the importance of $1/f$ -noise is part of the global “complexity revolution”, which is happening in all sciences, and which involves fractals, power-laws, long-range dependence.

Using population dynamics as the prototype, we will begin by explaining classical ecological models and their afflictions in Sec. 2. Section 3 reviews the properties of $1/f$ -noise, concentrating on those properties that make it relevant to ecology. Section 4 expands on the various theoretical arguments in favour of $1/f$ -noise, particularly the scale-invariant pink noise. Section 5 discusses the empirical evidence for the hypothesis: data collected so far are consistent with the $1/f$ -noise hypothesis but do not confirm it beyond doubt or above competing hypotheses. Assuming a $1/f$ -noise model, what are the effects of $1/f$ -noise on the predictions of models in ecology? This is discussed in Sec. 6. Finally, Sec. 7 discusses the unique flavour of the ecological uptake of scale-invariance ideas, and how this is likely to affect the course of research on $1/f$ -noise.

In this review we will focus on ecology, especially population ecology, but will occasionally widen the perspective to an “evolutionary” perspective, since evolution can be viewed to some extent as ecology on a large time scale.

2. Population Ecology and its Discontents

Single species population models are the fundamental building block of population dynamics theory and thus provide the basic platform in which various sources of stochastic variation have been incorporated in ecology. The classical theory of regulated population growth is due to Verhulst [3] and Pearl [4] who modified the exponential model of Robert Malthus to incorporate the concept of *density-dependence* yielding:

$$\frac{dN}{dt} = rN \left[1 - \frac{N}{K} \right], \quad K \geq 0, \quad (1)$$

where $N(t)$ represents *population size* or *population density*, r is basic *per-capita growth rate* (births minus deaths per unit time) and K is the *carrying capacity* or maximum population size that the environment can sustain. This *Logistic* equation can also be viewed as the result of a Taylor-series expansion around $N=0$ of a more general relation between population abundance and the per capita growth rate $N^{-1}dN/dt=R(N)$ [5,6]. This equation describes an exponential growth at low population density, followed by equilibration at high population density (Fig. 1). The logistic equation has a various discrete time versions (suitable for annually-reproducing species), such as the Ricker equation:

$$N_{t+1} = N_t \exp\left[r - \frac{rN_t}{K}\right] \quad (2)$$

that was instrumental in the discovery of limit cycles and chaos in models of population dynamics [7]. Chaos, which appears in (2) when $r \geq 2.8$, has been a useful concept in population dynamics, but does not account for all of the complexity seen in real populations. Demonstrating the occurrence of chaotic behaviour in the dynamics of natural populations has proven to be a rather elusive and technically challenging problem (e.g. [8,9]).

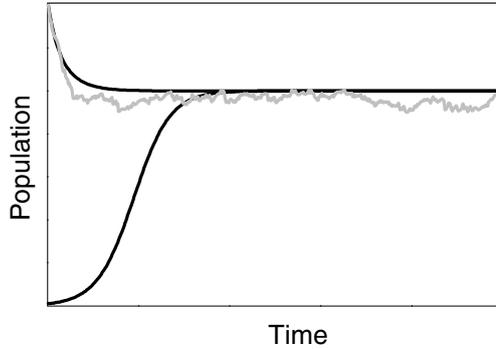


Fig. 1. Population dynamics according to the logistic, with and without stochastic influence on parameters. The carrying capacity is $K = 100$. Two deterministic trajectories are shown: one starting at $N = 1$ and another at $N = 140$. Also shown is a stochastic trajectory starting at $N = 140$. Note: the carrying capacity is slightly lower in the stochastic case, which is caused by a second-order perturbation correction.

Other important population-dynamics systems included delay difference equations $N_{t+1}/N_t = F(N_t, N_{t-\tau})$ [6,10] and delayed differential equations $N^1 dN/dt = R[N, N(t-\tau)]$ [2,11]. Two-species models, involving predator-prey or host-parasite interactions, using both discrete and continuous-time formulations, have a long and prestigious pedigree in ecology [12,13], but these multispecific models are almost always strictly deterministic and hence will not be discussed further.

2.1. Stochastic population models

Equations (1) and (2) are rather idealized pictures and have been criticised on various grounds, the most important of which is that rarely, if ever, do they match what has been observed in the field. In reality, all the parameters of these equations are likely to be perturbed by various “random” (as far as we are concerned) influences. Thus, there is thus good reason to explore a stochastic version of the logistic equation that can be done by adding “nuisance terms” to its parameters as:

$$\frac{dN}{dt} = (r + \alpha)N \left[1 - \frac{N}{K + \beta}\right] + \varepsilon. \quad (3)$$

One can think of $\alpha(t)$, $\beta(t)$ and $\varepsilon(t)$ as simple Gaussian noise terms (with mean zero and variances σ_α , σ_β and σ_ε respectively): the effects of a variable environment on the evolution of the population, driving it outside its ‘normal’ deterministic trajectory. This equa-

tion can be solved by perturbation analysis [14], by assuming that $N(t)=N_o+n(t)$ and that n , α , β and ϵ are small relative to the values of the parameters they perturb. Expanding the Taylor series and just retaining the linear terms yields:

$$\frac{dn}{dt} = r(n - \beta)[1 + \alpha/r - (n - \beta)/K + \dots] + \epsilon \approx -r(n - \beta) + \epsilon \quad (4)$$

In this case, the process n , is Markovian so the auto-correlation function of n is [15] :

$$R_n(\tau) = \frac{\pi[r^2\sigma_\beta^2 + \sigma_\epsilon^2]}{r^3} \text{Exp}[-r\tau]. \quad (5)$$

Thus we would expect to see fluctuations on a characteristic time-scale $1/r$, “regulated” within a basin of attraction surrounding the mean $N_o=K$, having a characteristic size $\sqrt{R_n(0)}$. The finite time taken for reproduction and death of individuals, assumed to be balanced, is implicit in the time constant, $\tau_\Lambda = 1/r$. The solution of the logistic equation (Fig. 1) is an embodiment of the archetypal notion of the “balance of Nature” that underlies classical thinking about ecological dynamics [16]. There is a substantial theoretical literature in ecology dealing with the stochastic versions of Logistic (and Gompertz) differential equations leading to either lognormal or gamma distributions of population abundance (e.g. [17,18]). This theoretical research dating back to the late 1960s (e.g. [2,19]) was instrumental in promoting the use of stochastic models of population dynamics for predicting extinction risks of natural populations and species. Under the name of Population Viability Analysis (PVA), stochastic models based on the logistic-type equations or age-structured matrices have become a standard approach in conservation biology for estimating the probability of extinction/decline of natural populations (reviews in [20,21]).

2.2. Stochastic models require an adequate representation of ecological variability

Ecological variability refers to all environmental processes that codetermine the observed dynamics. It includes not just physical processes such as temperature and rainfall, but also the fluctuations of other populations with which the population interacts. Here some of the problems arising in stochastic modelling of ecological processes are discussed with regard to the formulation of suitable stochastic models of ecological variability.

Real populations rarely reproduce the behavior observed in Fig. 1. A selection of these from the GPDD^b is shown in Fig. 2. The dynamic events in time series of actual populations span stable behavior (both mono-tonic and oscillatory), cycles, quasi-cycles, and chaos (e.g. [22]). While the initial growth of populations from low abundance often follows the Malthusian pattern, the subsequent stabilization by density-dependence remains much more elusive in real data [23–25]). Although the existence of the stabilization term N/K in Eq. (2) in principle ought to be simple to establish, ecologists typically find a very wide scatter of population abundances in the short time and noisy series available, leading to a long and acrimonious debate about the statistical testing of density dependent regulation (reviews in [10,25]). It is difficult, if not impossible, to distinguish between different types of density dependence in actual population time-series. Faced

^b Global Population Dynamics Database, created by the Centre for Population Biology Imperial College (UK), and accessible at <http://cpbnts1.bio.ic.ac.uk/gpdd/>.

with the limited descriptive power of basic models, some have adopted the strategy of “let the data decide”. The most extreme in stance of this approach is that of Peters (e.g. [26]) who went as far as to deny entirely the relevance of mechanistic models for ecology and instead championed a wholly phenomenological approach. A more popular approach is that of Turchin (e.g. [10]) who progressively increases the complexity of the deterministic skeleton of ecological models until it fits the observed data. However, these “data-driven” approaches often amount essentially to curve-fitting exercises, shedding little or no light upon the mechanistic basis of the interactions between species, resources and their physical environment. A second issue is that invariably this fitting process implicitly assumes that the stochastic component of the model is white noise and that all the “interesting and ecologically relevant” aspects of the data ought to be embodied in the deterministic skeleton of the model. However, an adequate representation of ecological variability is first needed before such an assumption can be considered.

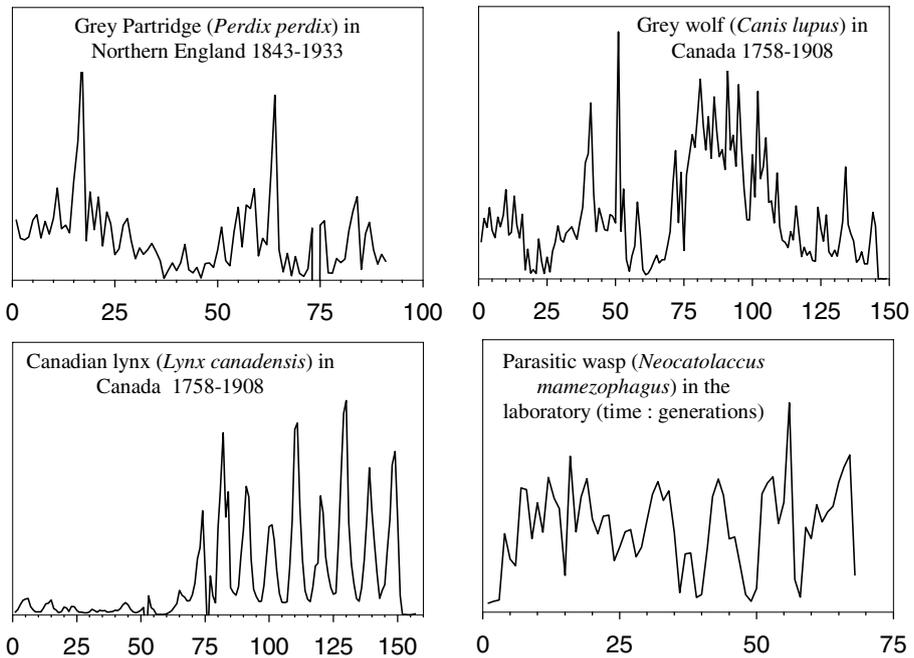


Fig. 2. Four ecological population time-series from the GPDD. Apart from being longer than average, these series are fairly typical, and show a variety of forms of behaviour. Note the absence of a clear basin of attraction as seen in Fig. 1 and the presence of detail on all timescales within the observation window.

Any ‘full’ population-dynamic model would have to take into account the potentially very large number of deterministic interactions among species depicted in a food web including competitive, parasitic and mutualistic interactions (Fig. 3), each element of which would also be perturbed by abiotic stochastic effects. This is clearly out of the question in most real cases. For any given parameter, careful study (typically taking years for most species) can usually reveal the basic structure of the environmental contribution, but this is slow and expensive. For example, only in a few cases do we have simultaneous census data of interacting species, or measurements of relevant environ-

mental factors together with population densities. Faced with describing the complexity of ecosystems, ecologists have traditionally described ecological dynamics (e.g. Eq. (3)) by a deterministic skeleton being acted upon by a stochastic environment. The deterministic skeleton is a small number of (usually nonlinear) interactions amongst a few species or populations selected on the basis of prior knowledge. The environment, which acts upon one or more of the parameters of the deterministic part, stands for all those meteorological, ecological, and other influences that cannot be comprehensively included in the explicit framework of the model. By replacing detailed interactions by noise sources of appropriate spectrum, probability distribution and autocorrelation, we may arrive at a suitably graceful specification of the model of ecological dynamics.

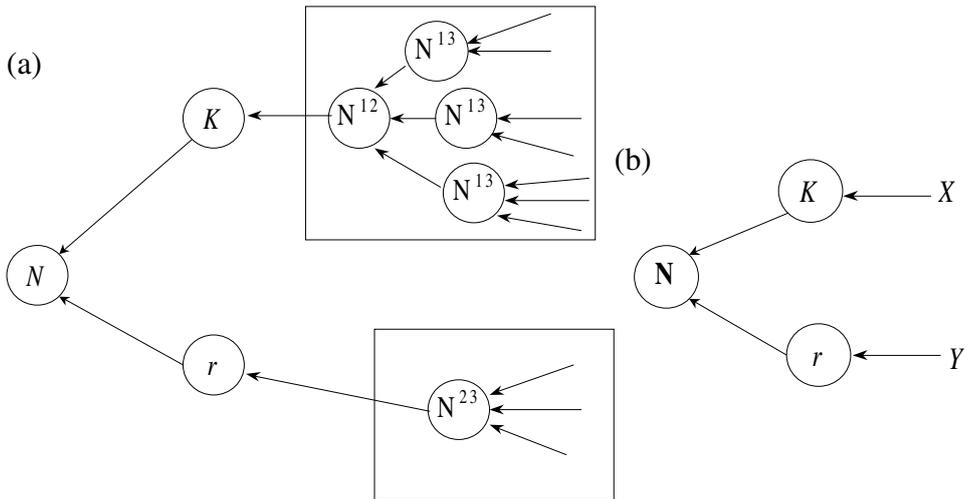


Fig. 3. Environmental variability in ecological models is intrinsically complex since the temporal fluctuation of each parameter of the discrete logistic equation can be viewed as a cascade of biotic and abiotic interactions in a food web (a) that can be represented in the model by a few appropriately-distributed interactions denoting random effects (b).

Such a model would then constitute a parsimonious and acceptable compromise between our need to model the parameters plausibly and the limitations of our ability to measure them precisely. Because ecological systems are highly coupled to their environment, this environment term is very important, and if the environmental noise sources are chosen wrongly, then this will cause problems in ecological prediction. Our approach is to generalize or modify this part of the model by choosing the appropriate stochastic process that is likely to reflect the nature of the true ecological environment. Thus, with reference to Eq. (3), this means carefully choosing stochastic processes α , β and ϵ . Most stochastic models of population dynamics has traditionally assumed white noise sources for these variables, not only because of the convenience of analysing such models using the formidable toolbox of stochastic differential equations, but also because by offering no advantage to any specific frequency, white noise seems a “natural null model” of environmental variability. Also, until recently, the task of describing a fluctuating environment in ecological models (with any serious intent to predict) was considered too difficult to touch. However, some features of $1/f$ -noise processes offer important new

approach for understanding and describing the complexity of the ecological environment.

3. The Properties of 1/f-Noise

1/f noise, or $1/f^\nu$ -noise, is an evolutionary random process [27] in the sense that the parameters characterizing the stochastic process (mean, variance, covariances) slowly drift over time. The terminology associated with the 1/f-noise in different fields varies considerably. In this review we will use the following terminology: “1/f-noise” refers to $1/f^\nu$ -noise for which $0 \leq \nu \leq 2$; “near-pink 1/f-noise” refers to cases where $0.5 \leq \nu \leq 1.5$ and “pink noise” refers to the specific case where $\nu = 1$. All $1/f^\nu$ -noises are defined by the shape of their power spectrum $S(\omega)$:

$$S_1(\omega) \propto \frac{1}{\omega^\nu}. \quad (6)$$

Here $\omega = 2\pi f$, is the angular frequency. A vast array of diverse natural processes is found to obey this relationship. Typically the spectral exponent, ν , lies in the range 0 to 2. Many reviews have been written discussing this phenomenon from various standpoints [27–29]. A fairly comprehensive bibliography, covering a wide variety of aspects of 1/f-noises, can also be found at the website maintained by Wentian Li.^c

The spectrum (6) does not constitute a valid spectrum in the sense of stationary random processes because it is non-integrable either as $\omega \rightarrow 0$ (for $\nu \geq 1$) or as $\omega \rightarrow \infty$ (for $\nu \leq 1$). The non-integrability in the cases $\nu \geq 1$ is associated with infinite power in low frequency events; this is called the infrared catastrophe. Conversely for $\nu \leq 1$, which contains infinite power at high frequencies, it is called the ultraviolet catastrophe. Pink noise ($\nu = 1$) is non-integrable at both ends of the spectrum. The upper and lower frequencies of observation are limited by the length of the time series and the resolution of the measurement, respectively. As a result, all 1/f-noises have a number of subtleties associated with the interpretation of their spectrum. For electronic applications, at least, the general form of these spectra has been found to prevail over a very large range of frequencies [27,30].

1/f-noises share with ecological time series a number of important properties: features on many scales (fractality), variance growth and long-term memory.

3.1. Scaling and fractality of the 1/f-process

1/f-noises are often considered as statistical fractal processes [31,32], a property that is most plainly expressed through the scaling relationship for the spectrum: for any constant a ,

$$S_1(\omega) = |a|^\nu S_1(a\omega). \quad (7)$$

In words, the meaning of this is that the spectrum can be considered to be a power-law superposition of disturbances on different scales of time.

1/f-noises have close links with fractional Brownian motion (fBm,[15,33]), which is also a model with potential ecological applications. A fBm process $X(t)$ obeys a scaling defined through its probability density function $f(x,t)$:

^c See note a.

$$f(a^H x, at) = a^H f(x, t) . \quad (8)$$

The parameter H is called the Holder exponent [34] and also the ‘‘Hurst exponent’’ of the fBm. This follows the work of H.E. Hurst [35] on the quantification of variance-growth as a risk factor when considering the long-term behaviour of reservoirs. In fact, the more precise definition of the Hurst exponent is different ([36], p. 149; [37]), but usually the two definitions yield the same results. For ordinary Brownian motion $H = 1/2$. The spectrum of fBm is approximately $1/f^\nu$ [38], with $\nu = 2H+1$, so fBm is often used as a model of $1/f$ -noise, for $\nu > 1$. fBm is only valid for the range $0 < H < 1$ and so cannot be used for $1/f$ -noises with $\nu \leq 1$ [33]. However, if fBm is first differentiated the result is fractional Gaussian noise (fGn). This is $1/f$ -noise with spectral exponent $\nu = 2H-1$ and so can be used for the range $1 > \nu > -1$ [33]. A discrete version of fBm (called ‘‘fractional differencing’’) was developed by Hosking [39].

In general, while $1/f$ -noises have some fractal properties, their behaviour is more diverse, and their description less restrictive, than the families of fBm’s and fGn’s. For example, $1/f$ -noises need not have Gaussian increments [40]; nor need they have a random phase spectrum [41]; and they are not restricted in their spectral exponents [33].

3.2. Growing variance and non-stationarity

Variance is a measure of the spread of values in a process and may be defined as $V = E\{n(t)^2\} - E\{n(t)\}^2$ where $E\{ \}$ denotes expected value. $1/f$ -noises are characterized by growing variance [27]. For an observation time Δt , the observed variance of a sample of the process series depends on Δt as follows:

$$V(\Delta t) \propto 1 - \Delta t^{\nu-1}, \quad \forall \nu < 1 \quad (a)$$

$$V(\Delta t) \propto \ln(\Delta t), \quad \nu = 1 \quad (b) \quad (9)$$

$$V(\Delta t) \propto \Delta t^{\nu-1}, \quad \forall \nu > 1. \quad (c)$$

Only for $\nu < 1$ does this growth reach a limit. In this paper, we define as non-stationary those members whose variance does not converge to any finite value as $\Delta t \rightarrow \infty$ (i.e. $\nu \geq 1$). Of course, for near-pink noises, the fact that they are ultimately stationary will be of little comfort to the ecologist, since most realistic ecological observation periods are short and this means that convergence to asymptotic behaviour is slow [38]. The above result (9c), for non-stationary $1/f$ -noises, also prevails for fBm, for which (using (9c) and the fact that $\nu = 2H+1$) the variance is proportional to Δt^{2H} . Note that for the case of stationary $1/f$ -noises ($\nu < 1$), a long-term average exists, while for non-stationary members ($\nu \geq 1$) it is not possible to define a long-term average.

3.3. The autocorrelation and memory of $1/f$ -processes

A key feature of $1/f$ -noises is their long memory. Whereas auto-regressive processes of the type described by Eq. (5) are characterized by exponentially-decaying memory, $1/f$ -

noises have an altogether longer memory, and their autocorrelation function, $R(\tau) = E\{n(t+\tau)n(t)\}$, typically has power law dependence on the lag τ :

$$R(\tau) \propto \frac{1}{|\tau|^{1-\nu}}, \quad \nu < 1 \tag{10}$$

[15,27,38]. For the non-stationary members ($\nu \geq 1$) of the family, problems of definition arise in the definition of autocorrelation functions [15], because there the autocorrelation also depends on the time of observation, t , and not just on τ [15,27]. The memory of 1/f-noises has been discussed in detail by Keshner [27], who shows that memory is greatest, with the past playing the most important role, for pink noise ($\nu = 1$).

Figure 4 gives a summary of the leading definitions and characteristics of 1/f-noises.

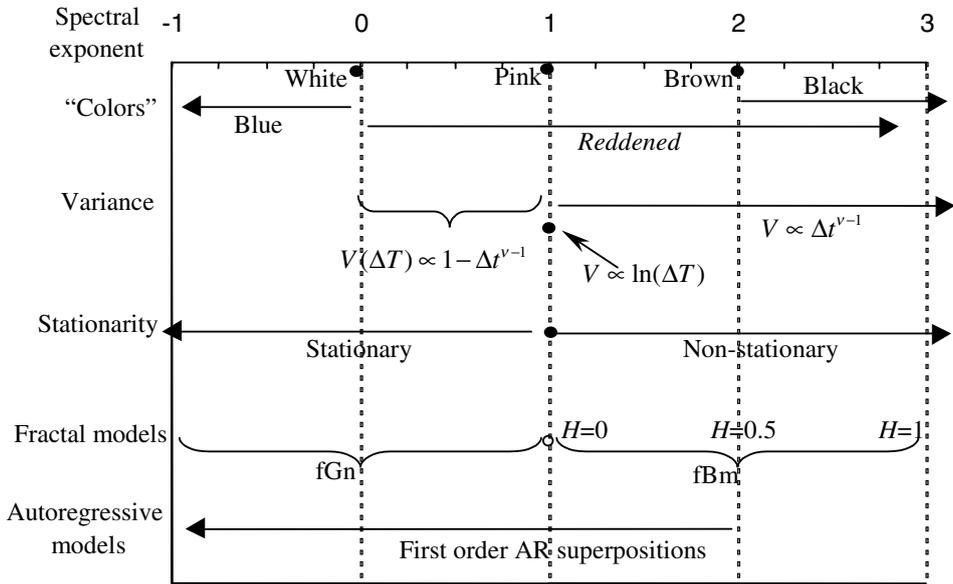


Fig 4. Summary of different kinds of $1/f^\nu$ -noises in terms of their conventional "color" (not always a very well defined concept), variance growth, stationarity and the scope of some of the models used to generate the process, in terms of their spectral exponent ν over the range of exponents from -1 to $+3$.

4. The Canonical Role of Pink Noise: Democracy, Equality, Complexity

This section lists some important reasons why the properties of pink noise, or near-pink noise, make it attractive as a null-model of ecological variability.

4.1. Bias-free representation of time and frequency scales

Given the inherent complexity of ecological variability, when trying to describe the ecological factors impacting the phenomena of interest, from a statistical perspective it makes sense to seek a stochastic process that contains the minimum hidden bias towards

any one range of time-scales or frequencies. One approach is to use $1/f$ -noise for the stochastic variation of model parameters, since $1/f$ -noise contains no preferred scale. But is there a way to decide which $1/f$ -noise is best, which value of ν is least biased? The following account argues that pink noise ($\nu = 1$) as the least biased.

$1/f$ -noise by definition, has a spectral density given by Eq. (6). Hence, demanding that the fluctuations of the natural environment constitute an equal partition of frequencies sets $\nu = 0$: i.e. white noise. However, the usual power spectrum, $S(\omega)$, is only one of four ways of representing the power spectrum of a stochastic process. Alternative representations can be obtained by expressing the power spectrum in a different way. Recall that the power spectrum of a stochastic process is just its representation in terms of a probability density of sinewaves of different angular frequency ω . Note that each sine-wave can also be understood in terms of its cycle time, of $T = 1/\omega$, rather than of its frequency. Thus, the cycle-time spectrum of a sinewave can be found by simple transformation of its probability density, using the fact that $\omega = 1/T$ and $d\omega = dT/T^2$ so that we have a spectrum of cycle-times, given by the equation:

$$S_2(T) \propto S_1(\omega) \frac{d\omega}{dT} = \frac{1}{T^{2-\nu}}. \tag{11}$$

Thus, the demand for an equal partition of cycle-times (a flat S_2 spectrum) leads to $\nu=2$ which corresponds to Brown noise. Similarly, we can define a third spectrum by taking frequency on a logarithmic (or per-decade) scale, ϕ , where $\omega = \exp(\phi)$ which, in turn, leads to:

$$S_3(\phi) \propto \exp[(1-\nu)\phi] \tag{12}$$

and finally there is a spectrum of cycle-time on a per-decade scale where $T = \exp(\theta)$:

$$S_4(\theta) \propto \exp[(\nu - 1)\theta]. \tag{13}$$

Thus the demand that we have an equal partition between different frequency scales or time scales on per-decade scales leads to $\nu = 1$, which is pink or $1/f$ -noise. The spectra (6), (11)–(13) are shown in Fig. 5. White noise is often considered as a null model of temporal variation of environmental and ecological variables. Because all frequencies in white noise have equal power per unit frequency, it is thought to be an unbiased representation of stochastic variation (Fig. 5(a)). However, this is entirely a matter of

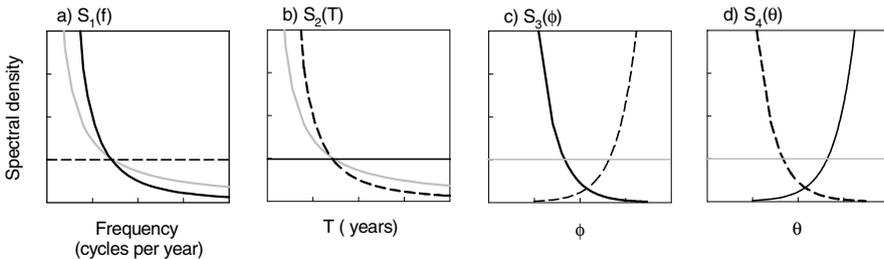


Fig. 5. The Power Spectral Density (PSD) of white noise ($\nu = 0$: dashed), pink noise ($\nu = 1$: grey) and brown noise or random walk ($\nu = 2$: black) drawn (a) on per-cycle scale, (b) per-cycle-period scale and on the respective per-decade scales (c) and (d).

perspective and bias lies in the eye of the beholder. If we consider the other types of power spectra, other members will appear more “democratic”. For the spectrum of cycle-periods, $S_2(T)$, it is “brown noise” ($\nu = 2$) that is impartial (Fig. 5(b)). If one now expresses things in terms of logarithmic scales, and draw both sets of “spectra” on per-decade scales, $S_3(\phi)$ and $S_4(\theta)$, we find that the contribution from all scales is the same only for pink noise, which retains this privilege for both time and frequency domains. This remarkable feature (Figs. 5(c), (d)), shows that it is pink noise, and not white noise (nor brown noise) which should be considered as the null model of environmental variability. Clearly, pink-noise is the most assumption-free *a priori* stochastic process to deploy in the absence of more detailed information to the contrary [29]. A similar point has been made by Szendro *et al.* [42] regarding similarity of the power-spectrum and the autocorrelation function.

4.2. Multiscaled randomness

The power spectra, Eqs. (7), (11)–(13), are interpretations of 1/f-noise that involve the decomposition of 1/f-noise into sinewaves. However, several other decompositions of 1/f-noise into simpler processes are possible. For example, 1/f-noise may be seen as a superposition of various forms of clustered pulse trains [43,44] or as a sequence of pulses having a $t^{-1/2}$ rolloff [45]. A decomposition particularly suitable for ecology is multiscaled randomness, where 1/f-noise is seen as a superposition is a first-order autoregressive (AR-1) processes [46,47], acting on different timescales. AR-1 processes fit easily within an ecological framework (via Eq. (5) for example) and have been widely used in ecology (e.g. [48–53]).

The special scale-symmetry of pink or 1/f noise can also be expressed through the following equivalent argument, proposed as a generic cause of microscopic pink noise by Van der Ziel [54]. Consider a stochastic process made up of a large number of sub-processes. Each subprocess, of correlation time τ_A , has an exponential decay of correlation, like Eq. (5), leading to a power spectral density:

$$S_A(\omega) = \frac{\tau_A \sigma^2}{1 + \tau_A^2 \omega^2}, \tag{14}$$

that has white noise behaviour at low frequencies and brown-noise behaviour at high frequencies. If these sub-processes are mutually independent and the distribution of correlation times is $\rho(\tau_A) \propto 1/\tau_A$, then the overall spectral density is:

$$S(\omega) = \int_0^\infty \frac{\tau_A \rho(\tau_A)}{1 + \tau_A^2 \omega^2} d\tau_A = \int_0^\infty \frac{d\tau_A}{1 + \tau_A^2 \omega^2} = \frac{\pi}{2\omega}. \tag{15}$$

The requirement that $\rho(\tau) \propto 1/\tau_A$ over a large range of relaxation times may seem artificial but is seen to be natural if we express the above calculations with the per-decade frequency spectrum, as we did earlier. Making the substitutions $\omega = \exp(\phi)$ and $\tau_A = \exp(\epsilon)$, we can derive $S_3(\phi)$:

$$S_3(\phi) = \frac{1}{2} \int_{-\infty}^\infty \operatorname{sech}[\phi + \epsilon] d\epsilon. \tag{16}$$

In the microscopic situations, the characteristic time taken for an electron to cross an energy barrier of height E is given by Arrhenius' law $\tau_A \propto \exp[E/kT]$ [31]. Thus, ε can be interpreted as an energy ($\varepsilon = E/kT$) and the pink spectrum can be seen as continuous superposition of elementary components, each associated with a single scale, translated from one another by different barrier-energies. The requirement that $\rho(\tau) \propto 1/\tau_A$ is equivalent to the demand for a uniform distribution of barrier energies [28]. The spirit of this argument is also attractive for ecologists [29] and for biology in general [55] because the principle of multi-scaled randomness interprets the overall spectrum as the sum of many elementary components each acting on its own time scale. Schlesinger [56] had argued that a $\rho(\tau) \propto 1/\tau_A$ distribution follows from a lognormal distribution of τ_A which in turn follows naturally from multiplicative Gaussian processes through the central limit theorem. Since the lognormal distribution has a $\rho(\tau) \propto 1/\tau_A$ distribution over a range of values, then this might explain the $1/f$ spectrum in complex systems. This corresponds to a Gaussian distribution of ε , with a standard deviation much larger than the width of the sech-kernel, in Eq. (16) above. On the other hand, Hausdorff & Peng [46] criticised this idea, arguing that a uniform distribution of $\log(\tau_A)$ was an artificial construct compared with a uniform distribution of τ_A . Nevertheless, in addition to the arguments of the previous subsection, it can be argued that the logarithm is so prevalent in nature that a uniform distribution in the logarithm of cycle-times is no more arbitrary than a uniform distribution of cycle-times itself.

4.3. *Mother nature must have maximum complexity*

Among ecologists, time and again it is found that Nature is more complex than anticipated. A model of environmental noise describing stochastic variation of parameters, therefore, should anticipate maximum complexity. However, there has yet to be an unambiguous definition of complexity. Information might seem to be a natural choice, since the sequence with highest information content might also be considered the most complex. In such terms white noise should have maximum complexity. While sequences with autocorrelation can be always be compressed to yield fewer bits of information, white noise cannot because every value is independent. So in these terms white noise contains the maximum information per value [57]. However, intuitively it seems obvious that white noise cannot have maximum complexity, since it is such an easy process to simulate: a simple pseudo-random number generator can simulate white noise. Brown noise can also be generated simply, by integrating white noise. Only two parameters are required in each case.

A number of approaches demonstrate that pink noise is the most complex $1/f$ -noise process. When measuring complexity, the obvious approach is via entropy and information theory. This approach has been followed by a number of authors. A straightforward attack shows that the Shannon information is always maximised for white noise, which contains the maximum information per bit. Zhang [57,58] defined a fractal-motivated measure of complexity to be the entropy/information per time scale. Agu & Yamada [59] considered other measures of information less tied to fractality. In all of the measures that were introduced by these authors, pink noise emerged as the most complex.

Another way of characterizing complexity is to ask how many state variables are needed to characterize the process. Keshner [27] demonstrated that pink noise requires more state variables than any other $1/f$ -noise, using a $1/f$ -noise generator consisting of a cascade of sections, each containing a linear amplifier and a filter. This ensemble acts as

a filter whose power spectrum is a series of steps, the number of which corresponds to the number of sections. By altering the frequency spacing of the sections, it is possible to adjust the aggregate slope of the spectrum in the range 0 to +2, and by increasing the number of sections one improves the approximation of a 1/f spectrum. How many sections are needed to produce acceptable approximations of the 1/f-noises? Keshner found that in order to keep the errors in spectral density down below 5%, about one section per decade was needed for 1/f-noise with slightly fewer for 1/f^{0.5} and 1/f^{1.5} noises. The total number of sections decreased almost to one for white and Brown noise. This is equivalent to the method implied in Fig. 6. For multiscaled random AR-1 processes, each sub-process contributes a sech-function to the overall per-decade spectrum. For each pair of orders added a distance ±Δφ away, it is possible to prove (Halley, unpublished) that the ripple reduction contributed at φ is proportional to cosh[(ν-1)Δφ] which is minimum at ν = 1. Thus the number of processes needed to simulate pink noise is higher at ν = 1 than at any other value.

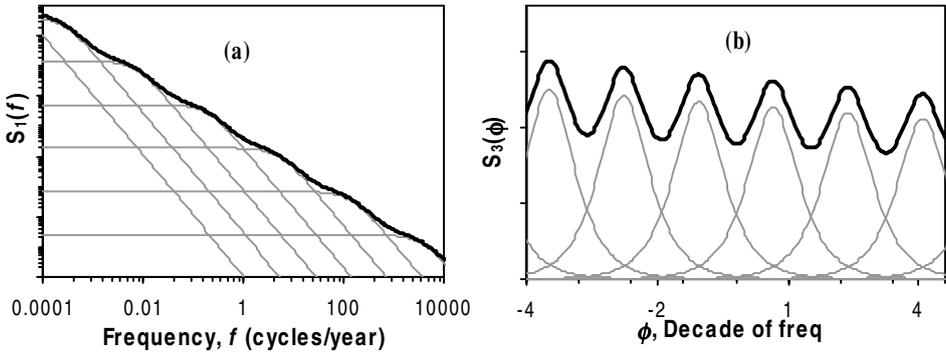


Fig. 6. Pink noise can be considered to be the superposition of many sub-processes acting on different time-scales, in such a way that the power from each timescale is the same. This interpretation of the PSD of pink noise is shown for (a) $S_1(f)$ on per-cycle frequency scale and (b) $S_3(\phi)$ per-decade frequency scale.

5. Observational Evidence of 1/f-Noise

Pimm and Redfearn [60] were the first to mention 1/f-noise in the ecological literature when they noted that the temporal variability of animal population abundance did not seem to converge to a well-defined value with longer studies, but continued to increase with the length of the survey. Pimm and colleagues [37,60] argued that this phenomenon was caused by temporal autocorrelation. Inheriting the terminology of the earth sciences, particularly the work of Steele [61,62], such correlation is referred to as *reddening*^d. Although there was not yet a systematic appreciation of the difference between short-range (exponential) and long-range (power-law) correlations, Pimm and his colleagues did suggest that the variance might increase without limit [37,60]. Although, these papers had a cool reception at first in the ecology research community, they have since become very influential. Since then, further work [63,64] has established that variance increases

^d Although the term has been used rather loosely, *reddened* variation is that for which the PSD (by analogy with light) has greater power at low frequencies than at higher frequencies. Usually, it means that PSD decreases with increasing frequency: i.e. $dS/d\omega \leq 0$.

with the length of census. A later article, by one of us [29], recognising the unlimited increase of variance as an attribute of non-stationary processes, hypothesised that ecological time series might fluctuate in a non-stationary way with a $1/f$ spectrum of variability. This latter article also has also been influential, although at the time there had been little done in the way of systematic study to test this assertion. Since then a considerable number of papers have appeared, connected with the concept $1/f$ -noise in ecology.

There have been a number of specific reports of observations of $1/f$ -noise in ecological research. Gillman & Dodd [65] reported Hurst exponents, in the temporal and spatial variability of orchid numbers in experimental plots, consistent with $1/f$ -noise. Miramontes & Rohani's analyses of long-term time series of insects kept under constant laboratory conditions [66] also showed a $1/f$ -type of spectra. Storch *et al.* [67] have measured the spatial distribution of bird abundance in sampling sites along a Czech forest transect and found the spectra of the first ordination axis to broadly conform to the shape of $1/f$ -noises. Kitabayashi *et al.* [68] observed that shell-changing behaviour of hermit crabs was related to $1/f$ -noise.

Important components of environmental stochasticity are the population fluctuations of other organisms in an organism's "environment" (predators, competitors, prey, etc). Thus an important question is whether natural populations fluctuate as $1/f$ -noise, as do other natural complex processes? If they do, then this provides strong evidence that an organism's environment fluctuates with a pink spectrum. To answer this question it is necessary to analyse time series of real ecological populations. The problem with undertaking such analyses is that due to the expense and difficulty of collecting real data from real populations of organisms in the wild, few reliable time-series exist lasting longer than a century. (This situation is unlikely to change in the near future!) In earlier work, we addressed this problem by using a very large database of time series [69,70]. This analysis was carried out using the *logarithm* of population abundance, $x_k = \log N_k$. This is necessary because distributions of abundance itself are highly skewed. Although the exact distribution of x_k can vary, being Normal only in about 50% of tested series [70], the skewness is usually low, so that techniques such as Fourier analysis do not run into problems. This analysis, like those preceding it, found that temporal variability increases with the length of the survey.

Figure 7(a) illustrates the distribution of values of the variance growth exponent, γ ($=2H$, twice the Hurst exponent), which is found by linear regression of the logarithm of variance, V , against logarithm of subsequence length, Δt . From Eq. (9c) we thus have:

$$\log[V(\Delta t)] = \gamma \log(\Delta t) + c . \quad (17)$$

In order to obtain $V[\Delta t]$, one averages the variance of all contiguous subsequences of duration Δt (e.g. $\{ x_k \dots x_{k+\Delta t} \}$) in the series [70].

In this framework, the basic random walk is associated with $\gamma = 1$, while $\gamma = 0$ indicates white noise [70]. As evident in Fig. 7(a), the vast majority of observed series have a variance exponent between these two values. This analysis indicates that ecological stochasticity is a form of variation smoother and more persistent than white noise, but rougher and less persistent than a random walk. However, the distribution is very skewed: there is a large number just above $\gamma = 0$ but negligibly few just below it. This is due to the following: in deriving values for γ , the regression procedure assumes Eq. 9(c) to hold and thus is assuming that $\nu > 1$. If, however, $\nu \leq 1$, then the slope fitted will not correspond to ν at all.

In fact, according to Eq. (9), the limiting (as $T \rightarrow \infty$) value of γ should be zero. For finite stationary time-series, however, γ will be positive, decreasing to zero for longer observation times [47]. For this reason, although γ is indeed a measure of variance growth, it is not recommended for situations where $\nu \leq 1$, as it is highly sensitive to series length. Also in cases of mixed series it will have a highly skewed distribution, as observed in the “pile up” near $\gamma=0$ in Fig. 7(a).

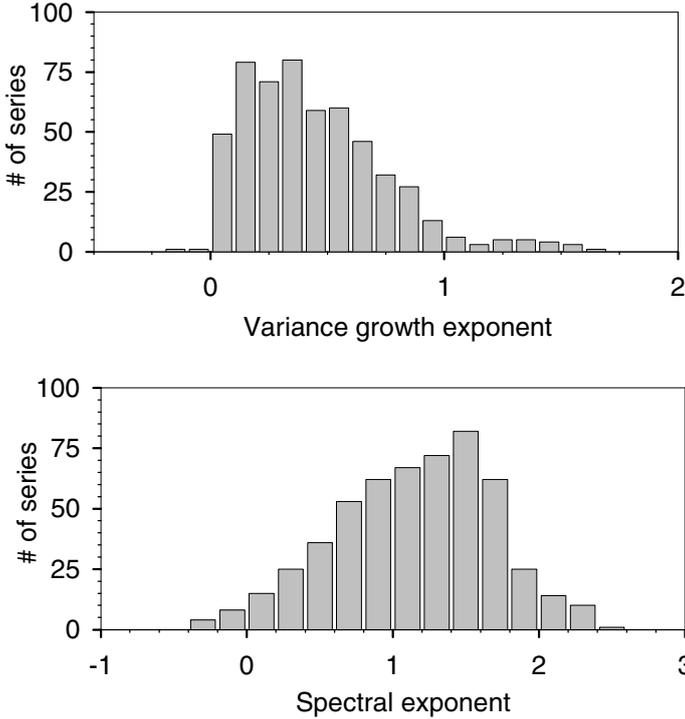


Fig. 7. (a) Histogram showing the distribution of the measured exponent of increase of the variance, γ and (b) of the measured spectral exponent, ν , for time series of ecological populations ($\log N$). Note $\gamma = 2H$ always, twice the Hurst exponent, and (fBm processes only) $\gamma = \nu - 1$.

The spectral exponent itself, ν , is shown in Fig. 7(b) for the ecological time series, can be interpreted as an indication of $1/f$ -noise processes. Although this histogram is also skewed, it is less so than Fig. 7(a), and this suggests that it is a better measure of variance growth for ecological time series than γ , at least for statistical purposes. We investigated [70] the power spectral density of x_k , using the discrete Fourier transform with a Hamming window function. Spectra broadly conform to the shape of $1/f$ -noises, with a strong decay at higher frequencies, although the shortness of the series lead to relatively high scatter. In contrast to variance increase exponents, spectral exponents, mostly in the range $\nu \in [0, 2]$, are spread relatively symmetrically about their mean value $\bar{\nu} = 1.022$, which is slightly red-shifted from pink noise (Fig. 7(b)).

Since according to the traditional perspective of the “Balance of Nature” discussed above, persistent ecological populations are often thought of as fluctuating about a “carrying capacity”, within a basin of attraction due to density dependent regulation (e.g. [10,25]), one might expect that (above some appropriate time-scale) variability would be bounded. Various studies [63,64,70] show that the growth of variance tends to slow down as the observation time grows (Fig. 8(a)). However, as Fig. 8(b) shows, the growth of variance in ecological series is well approximated by unbounded logarithmic growth, consistent with the behaviour of pink noise. Although the variance growth might stop entirely for much longer series, there is no evidence of this so far.

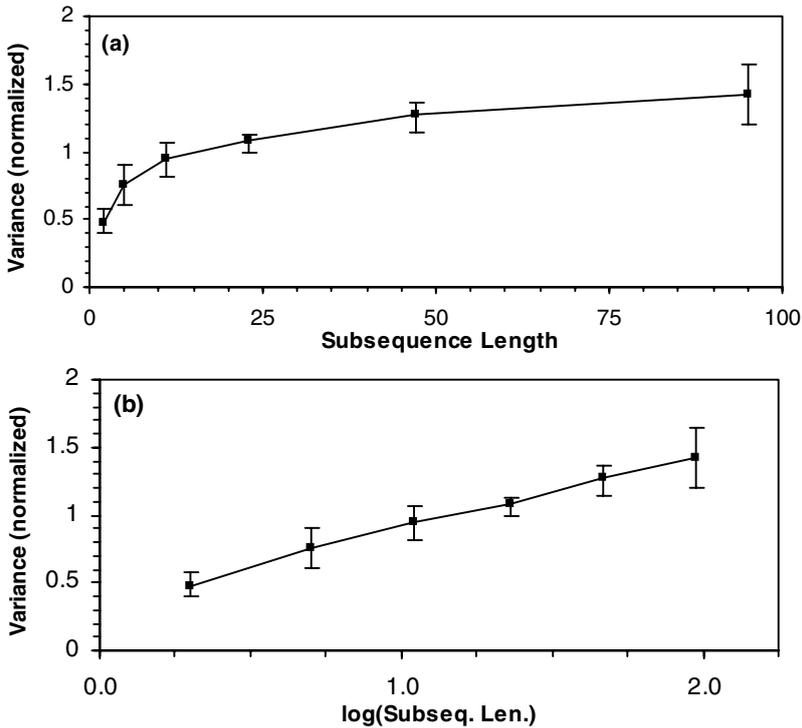


Fig. 8. The increase of variance of ecological time-series (like that for pink noise, Eq. 9(b)) is linear in log-time. Here is shown variance growth as a function of (a) observation time and (b) logarithm of observation time, for all series in the GPDD for which the duration is at least 96 years. For each of these 31 series, the variance was calculated for subsequence lengths 3, 6, 12, 24, 48 and 96 and then divided by the average of these values. The locus in the figure shows the locus of the median of these values for each ΔT ; the error bars denote the 25% and 75% levels.

There is currently no proposed ecological mechanism for $1/f$ -noise other than multi-scaled randomness [29]. Although there has been some interest in self-organised criticality as a universal driving mechanism in evolution [71] and in epidemiology [72], this process does not generate a near-pink $1/f$ -noise spectrum. Thus, while many aspects of $1/f$ -noise are attractive to ecologists, the hypothesis is not generally accepted in ecology. This is partly due to the perceived absence of a mechanism and to the belief that $1/f$ -noise is a very complex kind of variability. MacArdle [50] argued that the observations of Pimm & Redfearn [60] could be explained adequately by autocorrelation introduced

by age-structure (leading to an equation like (6)). This view is still very popular [53]. However, as pointed out by Pimm & Redfearn [60] and by Miramontes & Rohani [66], significant correlations are found in species, such as insects, that do not have significant age-structure. Conversely, Akçakaya *et al.* [73] showed that realistic stochastic demographic models having weak density regulation and measurement error can produce spectra indistinguishable from $1/f$ spectra for short time series. Given the shortness of most time-series, it remains difficult to distinguish a true $1/f$ -noise process from other kinds of reddening (Fig. 8). In sum, observations in ecology are consistent with the hypothesis that the environmental variability is best described by $1/f$ -noise, but this evidence is not indisputable, since various mechanisms (environmental variation, age-structure, measurement uncertainty) acting in concert can mimic $1/f$ behaviour in time series of population abundance.

Another argument against the $1/f$ -noise hypothesis concerns the fact that human behaviour also generates fluctuations well described by $1/f$ -noise [74]. Indeed, there is a large body of similar observations, dating back to the work of Zipf [75], which can be related to $1/f$ -noise [76]. Proceeding on this basis, Scheuring & Zeöld [77] found that human subjects tend to overestimate low frequency variations and underestimate high frequencies effectively biasing spectra towards the red. On this basis they argue that perhaps the reddening reported by Pimm and others is not really anything to do with ecological populations but the result of human error! However, as Scheuring & Zeöld did not specify the range of temporal scales to which their experimental subjects were exposed, it is hard to determine whether the range of time scales of human error matches that of reported ecological reddening. In addition it is questionable whether the behavioural process involved in their analysis corresponds to the cognitive process involved in the estimation of population abundance.

6. Ecological Consequences

As discussed earlier, while most stochastic models used in ecology still use white noise, real ecological variability may be closer to pink noise or near-pink $1/f$ -noise. There are good theoretical arguments for this, while the evidence from the field is consistent with it. Various studies have been undertaken to investigate what this will mean.

The most studied implication of $1/f$ -noise in ecology is its importance for extinction forecasts [47,73,78,79]. So far, the most important implication of $1/f$ -noise for extinction forecasts seems to be its non-stationary behaviour. Earlier models had studied the effects of simple autoregressive processes on extinction [48,49,51,52,80]. Although such autoregressive models have only a single time scale [29,47], they may appear non-stationarity over limited windows of time. For this reason, it has proved difficult to assess the effect of redness on extinction probability [81]. Intuitively it was argued that the effect of correlation should be adverse because bad years can come in runs and this would more than offset the counter-effect of runs of favourable years for population growth. However, the results of the numerous theoretical studies show no overall consensus on the importance that the autocorrelation of noise in population models would have on population persistence. This issue was examined by Heino *et al.* [82] who noted that the conflicting results of numerous studies (e.g. [52,79,80]) arose from the different scaling conventions used. Since the variance of coloured noise changes with time, there is in general no way of standardising different processes according to variance over all time scales. In general they can only be made equivalent on *one* specific time scale. This

makes comparison difficult, and hence the confusion on the effects of the colour of noise for the probability of extinction.

In addition, for the $1/f$ family of noises, there is the added problem that the distribution of absorption (extinction) times changes drastically in form. For example, this is exponential in the case of white noise, but in the case of brown noise is an inverse Gaussian distribution, which has a power law tail [47]. This implies that although the median and quartiles of the distribution of absorption times are finite for all distributions, the mean time to extinction is finite for some members of the family and infinite for others. Figure 9 shows the proportional extinction rates for the three equivalent models: white noise, pink noise and brown noise [47]. Under white noise, survival declines linearly, indicating exponential decay. Under brown noise, initial fall is more complex, but persistence time will eventually always exceed that of white noise. Note that for the case of brown noise, there is no average time to extinction because the tail of the distribution of extinction times is too heavy [47]. An inverse Gaussian distribution for the expected time to extinction was also found by Dennis et al [83] for a basic exponential growth model driven by white noise. The pink-noise model, as we might expect, is intermediate between the two extremes.

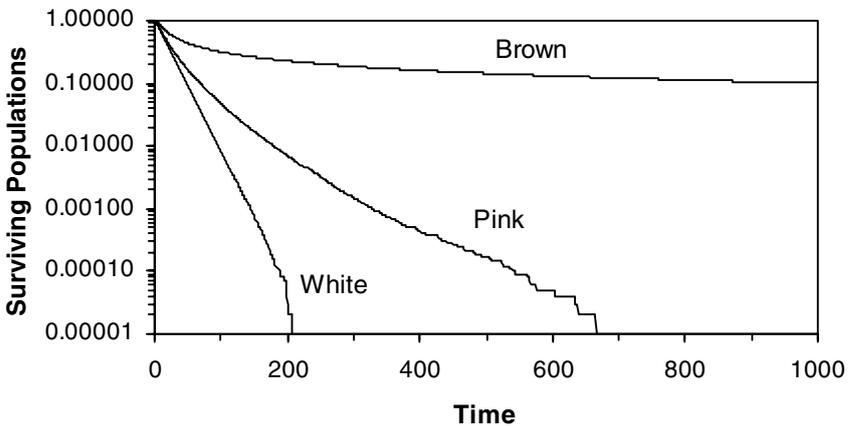


Fig. 9. The effect of noise color on extinction rate. Results of simulations for the proportional extinction rates for the three equivalent models: white noise, pink noise and brown noise. Each of the curves represents the results of a Monte-Carlo simulation of 10^5 runs for each noise model. The parameterisation was on the basis of a given mean and variance observed in 25-year time series.

Cuddington & Yodzis [79] carried out a fairly comprehensive set of simulations of extinction for population dynamic models driven by a wide range of $1/f$ -noises, all the way from white noise ($\nu = 0$) to black noise ($\nu = 3$). These authors concluded that persistence time increased with spectral redness, for $\nu > 1$ and that pink noise (which they call “red” noise) always had the highest coefficient of variation of extinction time. However, their statements are compromised because they do not include the distorting effect of heavy-tail behaviour on the moments of the distribution of extinction times, $f(T)$, which starts to become important when $\nu > 1$. Morales [78] compared pink noise to white noise in a Ricker-type model (see Eq. (2)). Morales, like Cuddington and Yodzis and others [52,80] found model structure for the deterministic skeleton played a significant role;

reddening of noise in growth rate r increased extinction probability but that reddening in the parameter K decreased it.

1/f-noise has also played a role in the various models of extinction on an evolutionary scale, reviewed by Newman & Palmer [71] and by Drossel [84]. Models of this variety typically have many species and usually involve some version of self-organised criticality. The purpose is to reproduce a variety of large-scale features of the fossil record, including mass extinctions and speciation events, using artificial-life type simulation. These features had previously been explained almost exclusively in terms of external events (climate change, meteors etc). Although none of these models reproduce precisely the behavior observed in the fossil record, they have put internal mechanisms (i.e. nonlinear ecosystem dynamics) firmly on the agenda as a possible explanation of mass extinction. Initially the power spectrum of mass extinction events was thought to be a 1/f-noise process [85], but later work has found against this: the power spectrum $S(\omega)$ seems to be flat at very long timescales (≥ 20 Myears) and fits well a $1/f^2$ spectrum at shorter timescales [71]. Of course, the environmental forcing of the ecosystem remains an issue and some authors have used 1/f-noise processes as external forcing processes such models. For example, De Blasio [86,87] found that if environmental variability was a 1/f-noise then so was the extinction rate, although the spectral exponent differed (it tended to be closer to one).

If estimates of extinction probability are to be useful in real conservation and management situations [20], the reliability of the prediction must be good. A number of authors had argued that parameter uncertainty would lead to confidence intervals for extinction probability so wide as to render extinction forecasts virtually worthless [88–90], see also [91–93]). This is due to the fact that the persistence forecast can have extreme sensitivity to certain parameters, particularly the population growth rate. However, Morales [78] found that under pink noise environmental variability, the sensitivity to parameter variability was modified considerably. More recent work has shown that a certain amount of non-stationarity in the temporal variability of population parameters may have a *stabilizing* effect on the forecasts so that the pathological sensitivity to certain parameters is washed out [94].

On ecological timescales, a better understanding of the temporal variation of population abundance itself is slowly emerging [70]. However, much less is known about the long-term (> 30 years) variability of the demographic parameters that might be used in models of extinction for most species. Since noise in single species population models is included by letting the values of demographic parameters change stochastically over time, a knowledge of this is essential. This also raises the question of how much population sizes (presumably through such parameters) track changes in environmental variables such as temperature. Others have used 1/f-noises in experimental microcosms [95,96] to investigate to what extent population variability tracked environmental variability, finding that while reddened environmental variability was not necessary to red- den population variability, the latter tracked the former more closely if environmental variability was strongly reddened.

Most of the work described in this section has been influenced by the initial observations by Pimm and others, that variance increases with time. This was the primary sources of the development of the 1/f-noise model. However, other related features of 1/f-noises, such as the occurrence of detail on all scales and the long memory of 1/f-noise, which have been explored less, are likely to have major impacts in the long run about how we view ecological variability in multispecies as well as single-species con-

texts. There has also been work aimed at looking at the occurrence and consequences of pink or near-pink $1/f$ -noises on ecological communities [97,98], but such work is at a relatively early stage. An interesting observation and application of this idea has been by Kitabayashi *et al* [68], where the $1/f$ -noise observed in the shell-changing behaviour of hermit crabs is related to concepts of hierarchy.

7. Outlook: Uniquely Ecological Flavours

This section briefly explores some of the issues that are likely to be important for $1/f$ -noise research specifically in ecology.

$1/f$ -noise has been reported in many different kinds of systems: electronic devices, physiology, network traffic, DNA sequences, meteorology, financial data, music and psychology to mention a few (see W. Li's website in Footnote 1). This has led to much work in trying to understand the origins of $1/f$ -noise especially in physics. Numerous models have been, and continue to be, developed. For example, it is fairly well established that $1/f$ -noise arises in a mechanistic way near the critical point of a phase transition. Indeed, this process was used by Tainaka and Itoh [98] in an ecological context. However, even in electronics, the primary contribution to the $1/f$ -noise effect continues to be debated; it is even less likely that in ecology, where complexity is greater and observability lower, any single universal mechanism will be found. In contrast with physics, the consequences of $1/f$ -noise and hence its statistical properties are likely to be more important in ecological research.

Given the undoubted ubiquity and importance of $1/f$ -noise, it is surprising that so much work still revolves about either observing the $1/f$ -noise in (yet more) novel situations, or chasing what seems to have become something of a "holy grail" in physics: a universal mechanism for $1/f$ -noise. Meanwhile, important statistical questions remain poorly understood. Apart from the general need for more statistical research into $1/f$ -noise, ecology has a number of issues peculiar to itself that are likely to propel research there in directions different to those of, say, electronic engineering.

A reasonable volume of high-quality statistical papers have been written about long-range correlations in noise (e.g.[38,100–102]). However, research has focussed on a small subset of issues such as estimation of spectral exponents or the presence-absence of long-memory. Furthermore, many of the current methods are geared towards long runs of data (typically longer than 1000 points) which do not exist in ecology. However, it is obvious that the range of spectral exponents compatible with even a short series is not infinite. Research is needed to explore the statistical behaviour of short data sets such as those existing in ecology.

The most important reality that will shape the direction of ecological research in $1/f$ -noise is that ecological data are expensive to collect. There are three immediate consequences:

- Time series are short. For example, there are only a few time series of population abundance longer than 150 years [69], and only a handful of these time series are divided into monthly or biannual intervals. In any case, for the time being, 150 years may be considered as an upper limit on the length of ecological time-series. This limits especially our knowledge of very low frequency components.
- The values in ecological time-series usually consist of time-averaged samples, which are the result of measurement or collecting periods that range from days to months. Dirac-delta sampling cannot be assumed, so issues of sampling bandwidth are very important. This limits our knowledge of the high-frequency com-

ponents. Up to now, this issue has received little attention, but in ecology it must be considered carefully. Since many ecological data originate from different sampling regimes, and hence have been subject to different spectral “filtering”, naïve comparison of their spectra is problematic.

- There is never full coverage in space.

These shortages of data collected mean that much greater attention must be given to statistical issues in ecology than in the physical sciences. One course of action is the development of more high-power statistical tests for long memory. Another possible approach is to turn to the fossil record in order to obtain longer time series and information about low-frequency behaviour. It may be possible to examine certain types of time-series by using the paleontological or the palynological records, for example, observing concentrations of fossils and pollen in different strata. Various problems need to be solved before we will be able to use these paleontological data in the context of detecting or parameterizing 1/f-noise. For instance, such time series are typically discontinuous with observations sampled at irregular intervals, which makes the detection of long-range dependencies difficult without recourse to interpolations that obviously entail further assumptions.

In many fields, such as in electronics, 1/f-noise only becomes a serious issue at very low frequencies, since at higher frequencies the spectrum is dominated by other sources, such as thermal noise. By contrast, in ecology it is likely to be important at all frequencies. Such ecological 1/f-noises, as shown in Fig. 7, tend to be near-pink noises. Spectral exponents range widely between 0 and 2, but predominantly congregate in the range 0.5 to 1.5, with a median near 1.0. This kind of pattern fits more snugly with some generation schemes than with others. For example, the multiscaled randomness model building up 1/f-noises through superpositions of first-order autoregressive processes can generate 1/f-noises with exponents in the range $0 \leq \nu \leq 2$, as can similar “Gauss–Markov” schemes [15] such as wavelets [33]. On the other hand the fBm framework, as mentioned above, can only generate spectral exponents in the range $1 < \nu < 3$ (although Kasdin [15] discusses a discrete-time modification with a wider range).

Ecological predictions are usually tied to a specific context. A pattern of known behaviour (say the population dynamics of a given species in some region) must be projected into the future on the basis of current behaviour and general principles. This, combined with the hypothesis of 1/f-noise fluctuation of ecological stochasticity, leads to the neglected issue of the initial-value spectrum of 1/f-noise (see [103] for a brief discussion). The general tendency to concentrate on finding and confirming spectral exponents rather than on initial conditions reflects a tacit assumption that we are still dealing with stationary processes, which are dominated by structural parameters, such as diffusion constants and spectral exponents. In a stationary world, as long as enough time is allowed, the process can be expected to settle down to behaviour entirely governed by these structural parameters; initial conditions are just ephemeral transients. This does not prevail for non-stationary processes. For near-pink noises, in particular, initial conditions affect the subsequent evolution of the process arbitrarily far into the future. While one may have a spectral exponent, the entire spectrum of initial conditions must be assigned, before simulations of future activity can be performed. Initial values cannot simply be assigned at random. The long and complicated memory of near-pink 1/f-noise means that all the known past must be sown into the model in order to have proper simulation of future behaviour and avoid discontinuous or contradictory behaviour. Some work of this

kind has been done for fractional-differencing models ([38], p164) which, as mentioned above, cover only half the range of spectral exponents.

It is well-known that in order to improve estimates of fractal or long-range processes, large increases in the numbers of data are required [104,105]. Analysis of spectral exponent falls into this category, so it is difficult to obtain highly accurate estimates of spectral exponent on the basis of anything but enormous sets of data. However, this is a two-edged sword. On the other hand, if only rough knowledge is needed, small numbers of data suffice nearly as well as “medium” datasets. Thus there is also an inherent robustness in fractal estimates. This argument was used by West & Deering [106] to claim that life chooses fractal forms because of their robustness in the face of errors. The opportunities raised by this possibility have yet to be explored in any detail.

8. Conclusions

The features of $1/f$ -noise processes offer important new insights into the field of population biology, greatly helping our quest for understanding and for prediction of ecological processes. This article reviewed the application of $1/f$ -noise processes to ecology. The most important properties of $1/f$ -noises in this context are its detail on all scales, its long memory and its non-stationarity. $1/f$ -noises account quite satisfactorily for the observed nature of ecological fluctuations, although it is not possible to rule out other contending hypotheses. If we interpret ecological variability as $1/f$ -noise, it changes substantially a number of ecological theories and results and leads to a major reinterpretation of some ecological observations. The statistics of $1/f$ -noises are still somewhat primitive in the light of what is needed in ecological research. Specifically ecological imperatives are likely to drive research in $1/f$ -noise along different directions from that associated with engineering and the physical sciences. Ecological work on $1/f$ -noise is likely to grow in the future for two reasons. Firstly, $1/f$ -noise is associated with complex systems of which ecosystems are a good example, which is one of the major frontiers of modern science. Irrespective of the fact that ecological data are expensive to collect, and that ecosystems are highly complex, there is a growing demand for some sort of forecasts, or for estimates of ecosystem health. The political interest in ecological issues has grown rapidly in the last few decades, as public perception of the importance of “ecosystem health” has spread. As we have argued in this article, traditional models of noise are in general inadequate to cover the complexity of environmental variation, and that ecological models incorporating $1/f$ -noise promise considerable improvements. This is highly desirable, even if they don't have a high level of attainable accuracy in absolute terms. Even limited mathematical predictions can be extremely useful.

References

- [1] R. Margalef, *Perspectives in Ecological Theory*, Chicago University Press, Chicago (1968).
- [2] R. M. May, *Stability and Complexity in Model Ecosystems*, Princeton University Press, Princeton (1973).
- [3] P. Verhulst, *Notices sur la loi que la population suit dans son accroissement, Correspondances Mathematiques et Physiques* **10** (1838) 113–121.
- [4] R. Pearl, *The Biology of Population Growth*, Alfred Knopf, New York (1925).
- [5] A. Lotka, *Elements of Physical Biology*, Wilkins, Baltimore (1925).
- [6] J. Royama, *Analytical Population Dynamics*, Chapman & Hall, New York (1992).
- [7] R. M. May, *Simple mathematical models with very complicated dynamics*, *Nature* **261** (1976) 459–467.

- [8] S. Ellner and P. Turchin, *Chaos in a noisy world: new methods and evidence from time-series methods*, *Am. Nat.* **145** (1995) 343–375.
- [9] J. Perry, R. Smith, I. Woiwod and D. Morse, *Chaos in real data: the analysis of non-linear dynamics from short ecological time series*, Kluwer Academic Publishers, Dordrecht (2000).
- [10] P. Turchin, *Complex Population Dynamics: A Theoretical/Empirical Synthesis*, Princeton University Press, Princeton, USA (2002).
- [11] G. E. Hutchinson, *Circular causal systems in ecology*, *Ann. N.Y. Acad. Sci.* **50** (1948) 221–246.
- [12] J. D. Murray, *Mathematical Biology*, Springer-Verlag, New York (1996).
- [13] T. Case, *An Illustrated Guide to Theoretical Ecology*, Oxford University Press, New York (2001).
- [14] E. Renshaw, *Modelling Biological Populations in Space and Time*, Cambridge University Press, Cambridge (1991).
- [15] N. J. Kasdin, *Discrete simulation of colored noise and stochastic-processes and 1/f(alpha) power-law noise generation*, *Proc. IEEE* **83** (1995) 802–827.
- [16] S. L. Pimm, *The Balance of Nature? Ecological Issues in the Conservation of Species and Communities*, Chicago University Press, Chicago (1991).
- [17] B. Dennis and G. P. Patil, *Applications in ecology*, in *Lognormal Distributions: Theory and Applications*, eds. E. L. Crow and K. Shimizu, Marcel Dekker, Inc., New York (1988) 303–330.
- [18] O. H. Diserud and S. Engen, *A general and dynamics species abundance model, embracing the lognormal and the gamma models*, *Am. Nat.* **155** (2000) 497–511.
- [19] R. Levins, *The effect of random variation of different types on population growth*, *Proc. Nat. Acad. Sci. USA* **62** (1969) 1061–1065.
- [20] W. Morris and D. Doak, *Quantitative Conservation Biology*, Sinauer Publ., Sunderland, Mass. (2002).
- [21] S. Beisinger and D. McCullough, *Population Viability Analysis*, University of Chicago Press, Chicago (2002).
- [22] A. Hastings, C. Hom, S. Ellner, P. Turchin and C. Godfrey, *Chaos in ecology: is mother nature a strange attractor?* *Annual Review of Ecology and Systematics* **24** (1993) 1–33.
- [23] B. Dennis and M. L. Taper, *Density-dependence in time-series observations of natural-populations - estimation and testing*, *Ecol. Monogr.* **64** (1994) 205–224.
- [24] T. Shenk, G. White and K. Burnham, *Sampling-variance effects on detecting density dependence from temporal trends in natural populations*, *Ecol. Monogr.* **68** (1998) 445–463.
- [25] P. Turchin, *Population regulation: a synthetic view*, *Oikos* **84** (1999) 153–159.
- [26] R.H. Peters, *A Critique for Ecology*, Cambridge University Press, Cambridge (1991).
- [27] M. S. Keshner, *1/f Noise*, *Proc. IEEE* **70** (1982) 212–218.
- [28] M. B. Weissman, *1/f noise and other slow, nonexponential kinetics in condensed matter*, *Rev. Mod. Phys.* **60** (1988) 537–571.
- [29] J. M. Halley, *Ecology, evolution and 1/f-noise*, *Trends Ecol. Evol.* **11** (1996) 33–37.
- [30] F. N. Hooge, *Discussion of recent experiment on 1/f noise*, *Physic A* **60** (1972) 130–144.
- [31] M. Schroeder, *Fractals, Chaos, Power Laws: Minutes from an Infinite Paradise*, W. H. Freeman (1991).
- [32] B. B. Mandelbrot, *Multifractals and 1/f noise*, Springer, New York (1999).
- [33] G. W. Wornell, *Wavelet-based representations for the 1/f family of fractal processes*, *Proc. IEEE* **81** (1993) 1428–1450.
- [34] K. Falconer, *Fractal Geometry: Mathematical Foundations and Applications*, John Wiley & Sons, Chichester (1990).
- [35] H. E. Hurst, *Long-term storage capacity of reservoirs*, *Trans. Am. Soc. Civ. Eng.* **116** (1951) 770–808.
- [36] J. Feder, *Fractals*, Plenum Press, New York (1988).

- [37] A. Ariño and S. L. Pimm, *On the nature of population extremes*, *Evol. Ecol.* **9** (1995) 429–443.
- [38] J. Beran, *Long-term memory processes*, Chapman and Hall, New York (1994).
- [39] J. R. M. Hosking, *Fractional differencing*, *Biometrika* **68** (1981) 165–176.
- [40] J. Kertesz and L. B. Kiss, *The noise spectrum in the model of self-organized criticality*, *J. Phys. A-Math. Gen.* **23** (1990) L433–L440.
- [41] N. P. Greis and H. S. Greenside, *Implication of a power-law power-spectrum for self-affinity*, *Phys. Rev. A* **44** (1991) 2324–2334.
- [42] P. Szendro, G. Vincze and A. Szasz, *Pink-noise behaviour of biosystems*, *Eur. Biophys. J. Biophys.* **30** (2001) 227–231.
- [43] S. Thurner, S. B. Lowen, M. C. Feurstein, C. Heneghan, H. G. Feichtinger and M. C. Teich, *Analysis, synthesis, and estimation of fractal-rate stochastic point processes*, *Fractals* **5** (1997) 565–596.
- [44] F. Gruneis, *1/f noise, intermittency and clustering poisson process*, *Fluct. Noise Lett.* **1** (2001) R119–R130.
- [45] I. Nagy, Z. Gingl, L. B. Kiss and J. Vinko, *A method for testing first-order markovian property of noise phenomena including 1/f noise*, *Physica B* **216** (1995) 79–84.
- [46] J. M. Hausdorff and C. K. Peng, *Multiscaled randomness — a possible source of 1/f noise in biology*, *Phys. Rev. E* **54** (1996) 2154–2157.
- [47] J. M. Halley and W. E. Kunin, *Extinction risk and the 1/f family of noise models*, *Theor. Popul. Biol.* **56** (1999) 215–230.
- [48] J. Roughgarden, *A simple stochastic model for population dynamics in stochastic environments*. *Am. Nat.* **109** (1975) 713–726.
- [49] C. Mode and M. Jacobson, *On estimating critical population size for an endangered species in the presence of environmental stochasticity*, *Math. Biosci.* **85** (1987) 185–209.
- [50] B. McArdle, *Bird population densities*, *Nature* **338** (1989) 627–628.
- [51] P. Foley, *Predicting extinction times from environmental stochasticity and carrying capacity*, *Conserv. Biol.* **8** (1994) 124–137.
- [52] J. Ripa and P. Lundberg, *Noise color and the risk of population extinctions*, *Proc. R. Soc. Lond. Ser. B-Biol. Sci.* **263** (1996) 1751–1753.
- [53] R. Lande, S. Engen, B. Sæther, S. Filli, K. Matthysen and H. Weimerskirch, *Estimating density dependence from times series using demographic theory and life history data*, *Am. Nat.* **159** (2002) 321–337.
- [54] A. van der Ziel, *On the noise spectra of semi-conductor noise and of flicker effect*, *Physica* **16** (1950) 359–372.
- [55] T. Gisiger, *Scale invariance in biology: coincidence or footprint of a universal mechanism?*, *Biol. Rev.* **76** (2001) 161–209.
- [56] M. F. Shlesinger, *Fractal Time and 1/f noise in complex-systems*, *Ann. N.Y. Acad. Sci.* **504** (1987) 214–228.
- [57] Y. C. Zhang, *Complexity and 1/f Noise - a phase-space approach*, *J. Phys I* **1** (1991) 971–977.
- [58] H. C. Fogedby, *On the phase-space approach to complexity*, *J. Stat. Phys.* **69** (1992) 411–425.
- [59] M. Agu and M. Yamada, *Short-time information entropy as a complexity measure*, *Jpn. J. Appl. Phys.* **37** (1998) L1415–L1417.
- [60] S. L. Pimm and A. Redfearn, *The variability of population-densities*, *Nature* **334** (1988) 613–614.
- [61] J. H. Steele, *A comparison of terrestrial and marine ecological systems*, *Nature* **313** (1985) 355–358.
- [62] J. H. Steele and E. W. Henderson, *Coupling between physical and biological scales*, *Phil. Trans. R. Soc. Lond. B* **343** (1994) 5–9.
- [63] W. W. Murdoch and S. J. Walde, *Analysis of insect population dynamics*, in *Towards a more exact ecology*, eds. E. P. Grubb and J. Whittaker, Blackwell Scientific, Oxford (1989) 113–140.

- [64] H. Cyr, *Does inter-annual variability in population density increase with time?*, *Oikos* **79** (1997) 549–558.
- [65] M. P. Gillman and M. E. Dodd, *The variability of orchid population size*, *Bot. J. Linnean Soc.* **126** (1998) 65–74.
- [66] O. Miramontes and P. Rohani, *Intrinsically generated colored noise in laboratory insect populations*, *Proc. R. Soc. Lond. Ser. B-Biol. Sci.* **265** (1998) 785–792.
- [67] D. Storch, K. J. Gaston and J. Cepak, *Pink landscapes: 1/f spectra of spatial environmental variability and bird community composition*, *Proc. R. Soc. Lond. Ser. B-Biol. Sci.* **269** (2002) 1791–1796.
- [68] N. Kitabayashi, Y. Kusunoki and Y. P. Gunji, *Active behavior and 1/f noise in shell-changing behavior of the hermit crabs*, *Riv. Biol.-Biol. Forum* **95** (2002) 327–336.
- [69] P. Inchausti and J. Halley, *Investigating long-term ecological variability using the global population dynamics database*, *Science* **293** (2001) 655–657.
- [70] P. Inchausti and J. Halley, *The long-term temporal variability and spectral colour of animal populations*, *Evol. Ecol. Res.* **4** (2002) 1033–1048.
- [71] M. E. J. Newman and R. G. Palmer, *Models of extinction: a review*, *adap-org/9908002: Adaptation, noise, and self-organizing systems*, <http://arxiv.org/abs/adap-org/9908002> (1999) 1–49.
- [72] C. J. Rhodes and R. M. Anderson, *Power Laws governing epidemics in isolated populations*, *Nature* **381** (1996) 600–602.
- [73] H. R. Akçakaya, J. M. Halley and P. Inchausti, *Population-level mechanisms for reddened spectra in ecological time series*, *J. Anim. Ecol.* **72** (2003) 698–702.
- [74] D. L. Gilden, *Cognitive emissions of 1/f noise*, *Psychol. Rev.* **108** (2001) 33–56.
- [75] G. K. Zipf, *The Psychobiology of Language* Houghton Mifflin Co., Boston (1935).
- [76] J. S. Nicolis and I. Tsuda, *On the parallel between zipf's law and 1/f processes in chaotic systems possessing coexisting attractors*, *Prog. Theor. Phys.* **82** (1989) 254–274.
- [77] I. Scheuring and O. E. Zoeld, *Data estimation and the colour of time series*, *J. Theor. Biol.* **213** (2001) 427–434.
- [78] J. M. Morales, *Viability in a pink environment: why “white noise” models can be dangerous*, *Ecol. Lett.* **2** (1999) 228–232.
- [79] K. M. Cuddington and P. Yodzis, *Black noise and population persistence*, *Proc. R. Soc. Lond. Ser. B-Biol. Sci.* **266** (1999) 969–973.
- [80] O. L. Petchey, A. Gonzalez and H. B. Wilson, *Effects on population persistence: the interaction between environmental noise colour, intraspecific competition and space*, *Proc. R. Soc. Lond. Ser. B-Biol. Sci.* **264** (1997) 1841–1847.
- [81] P. Inchausti and J. Halley, *On the relation between temporal variability and persistence time in animal populations*, *J. Anim. Ecol.* **72** (2003) 899–908.
- [82] M. Heino, J. Ripa and V. Kaitala, *Extinction risk under coloured environmental noise*, *Ecography* **23** (2000) 177–184.
- [83] B. Dennis, P. L. Munholland and J. M. Scott, *Estimation of growth and extinction parameters for endangered species*, *Ecol. Monogr.* **61** (1991) 115–143.
- [84] B. Drossel, *Biological evolution and statistical physics*, *Adv. Phys.* **50** (2001) 209–295.
- [85] R. V. Sole, S. C. Manrubia, M. Benton and P. Bak, *Self-similarity of extinction statistics in the fossil record*, *Nature* **388** (1997) 764–767.
- [86] F. V. De Blasio, *Mirroring of environmental colored noise in species extinction statistics*, *Phys. Rev. E* **58** (1998) 6877–6879.
- [87] F. V. De Blasio, *Diversity and extinction in a lattice model of a population with fluctuating environment*, *Phys. Rev. E* **60** (1999) 5912–5917.
- [88] D. Ludwig, *Is it meaningful to estimate a probability of extinction*, *Ecology* **80** (1999) 298–310.
- [89] J. Fieberg and S. P. Ellner, *When is it meaningful to estimate an extinction probability?* *Ecology* **81** (2000) 2040–2047.
- [90] T. Coulson, G. M. Mace, E. Hudson and H. Possingham, *The use and abuse of population viability analysis*, *Trends Ecol. Evol.* **16** (2001) 219–221.

- [91] B. W. Brook, J. J. O'Grady, A. P. Chapman, M. A. Burgman, H. R. Akçakaya and R. Frankham, *Predictive accuracy of population viability analysis in conservation biology*, *Nature* **404** (2000) 385–387.
- [92] B. W. Brook, M. A. Burgman, H. R. Akçakaya, J. J. O'Grady and R. Frankham, *Critiques of PVA ask the wrong questions: throwing the heuristic baby out with the numerical bath water*, *Conserv. Biol.* **16** (2002) 262–263.
- [93] M. A. McCarthy, H. P. Possingham, J. R. Day and A. J. Tyre, *Testing the accuracy of population viability analysis*, *Conserv. Biol.* **15** (2001) 1030–1038.
- [94] J. M. Halley, *Parameter drift stabilizes long-range extinction forecasts*, *Ecol. Lett.* **6** (2003) 392–397.
- [95] O. L. Petchey, *Environmental colour affects the dynamics of single-species populations*, *Proc. R. Soc. Lond. Ser. B-Biol. Sci.* **267** (2000) 747–754.
- [96] A. E. Cohen, A. Gonzalez, J. H. Lawton, O. L. Petchey, D. Wildman and J. E. Cohen, *A novel experimental apparatus to study the impact of white noise and 1/f noise on animal populations*, *Proc. R. Soc. Lond. Ser. B-Biol. Sci.* **265** (1998) 11–15.
- [97] G. P. Harris, *Predictive models in spatially and temporally variable freshwater systems*, *Aust. J. Ecol.* **23** (1998) 80–94.
- [98] K. Tainaka and Y. Itoh, *Apparent self-organized criticality*, *Phys. Lett. A* **220** (1996) 58–62.
- [99] E. B. Muller and R. M. Nisbet, *Survival and production in variable resource environments*, *Bull. Math. Biol.* **62** (2000) 1163–1189.
- [100] C. W. J. Granger and R. Joyeux, *An introduction to long-range time series models and fractional differencing*, *J. Time Ser. Anal.* **1** (1980)
- [101] J. Geweke and S. Porter-Hudak, *The estimation and application of long memory time series models*, *J. Time Ser. Anal.* **4** (1983) 221–238.
- [102] B. Pilgram and D. T. Kaplan, *A Comparison of estimators for 1/f noise*, *Physica D* **114** (1998) 108–122.
- [103] J. M. Halley, *The initial-value spectrum of 1/f noise: notes on its importance and its estimation*, Proc. ICNF 2003: 17th International Conference on Noise and Fluctuations, Brno, Czech Republic (2003) 497–500.
- [104] J. B. Ramsey and H. J. Yuan, *The statistical properties of dimension calculations using small data sets*, *Nonlinearity* **3** (1990) 155–176.
- [105] A. S. Kallimanis, S. P. Sgardelis and J. M. Halley, *Accuracy of fractal dimension estimates for small samples of ecological distributions*, *Landscape Ecol.* **17** (2002) 281–297.
- [106] B. J. West and W. Deering, *Fractal physiology for physicists - Lévy statistics*, *Phys. Rep.* **246** (1994) 2–100.

Copyright of Fluctuation & Noise Letters is the property of World Scientific Publishing Company and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.