

The colour of noise in short ecological time series data

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The statistical properties of ecological time series data and general trends therein have historically been of great interest to ecologists. In recent years, there has been a focus on establishing the relative importance of ‘memory’ in these data. The classic study by Pimm & Redfearn (1988 *Nature*, **334**, 613–614) has been extremely important in establishing within the ecological community the idea that population time series are generally ‘red-shifted’ (dominated by long-term trends). This conclusion was reached by exploring the relationship between observed variability and census length in ecological data and comparing them with those for artificially generated data. Here, we highlight some subtle problems with this approach and suggest possible alternative methods of analysis, especially when the time series of interest are short.

Keywords: population dynamics; time-series data; power spectra; pink noise; white noise.

1. Introduction

Ecologists have long been interested in the statistical properties of time series data and what these may reveal about underlying ecological mechanisms (Elton, 1927; Ito, 1978; Royama, 1992; Gaston & McArdle, 1994; Inchausti & Halley, 2001; Akcakaya *et al.*, 2003). One of the key findings of recent years, which has become broadly accepted within the ecological community, is that populations tend to exhibit ‘reddened’ spectra, namely that fluctuations in density combine a mixture of high frequency (short-term) variability with a dominant long-term ‘memory’ or trend. More intuitively, reddened dynamics imply that successive points in a time series of population densities are more correlated than would be expected purely by chance. Successive entries in a time series may also be uncorrelated, in which case they are referred to as ‘white’ noise. In the rare case of negative correlation between these terms, the data are said to be ‘blue’ (Schroeder, 1991).

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The ecological importance of these distinctions has been established by theoretical studies that have shown how the statistical properties of time series (notably the colour) can have profound effects on expected extinction likelihoods (e.g. Ripa & Lunberg, 1996; Halley & Kunin, 1999). The colour of time series has also been useful in generating debate concerning whether commonly used ecological models are good descriptors of the systems they attempt to portray given their general inability to produce reddened dynamics (Cohen, 1995; Sugihara, 1995; White *et al.*, 1996; Kaitala & Ranta, 1996; Miramontes & Rohani, 1998; Balmforth *et al.*, 1999). More importantly, if population time series really are ubiquitously reddened, then we may need to evaluate the usefulness of the 'equilibrium-based' deterministic approaches that have dominated theoretical ecology for much of the last century.

Arguably, the most influential ecological study in this area has been the classic work of Pimm & Redfearn (1988), who detected redness in 100 population time series. Although there have been other studies of ecological time series in which red-shifted dynamics have been reported (e.g. Sumi *et al.*, 1997; Miramontes & Rohani, 1998; Petchey, 2000; Inchausti & Halley, 2001), because of the range of taxa and number of datasets analysed, the Pimm & Redfearn (1988) paper remains the most influential and frequently cited study in this field.

The exploration of the colour of a time series in the physical sciences usually involves the Fourier analysis of the data (Handel & Chung, 1993; Pilgrim & Kaplan, 1998). Essentially, it can yield a relationship (called a power spectrum) between a range of frequencies and their relative importance (or power) in a given time series. This approach works most effectively for relatively long data, consisting of around 1000 or more points (Pilgrim & Kaplan, 1998). Pimm and Redfearn argued, however, that 'population data are rarely long enough for sensible spectral analyses', hence they relied on a surrogate method of detecting long-term trends. In their analysis, Pimm and Redfearn instead calculated the observed population variability (measured as the standard deviation of logarithmic abundance or SDL; McArdle *et al.*, 1990) as a function of census length. For artificially generated reddened noise, variability was shown to increase dramatically with the length of the census period, while for white noise there was no systematic trend (Fig. 1(a)). Pimm and Redfearn repeated their analysis for the time series of 100 populations, encompassing insects, mammals and birds and observed patterns consistent with a red noise process (but see McArdle, 1989).

The generality of Pimm and Redfearn's findings has been widely accepted by the ecology community. Here, we report significant and unexpected qualitative errors in the diagnostic capabilities of Pimm and Redfearn's methods. In particular, we show that their approach may give rise to both type I and type II errors when dealing with a single short time series. This would suggest that perhaps a detailed re-analysis of their data may be appropriate, and we propose two robust methods that may be more reliably used to achieve this.

2. Methods

To investigate the robustness of different methods of colour detection we applied each statistical technique to artificially generated pink and white noise data, using two different methods in each case. Note that pink noise is a special class of red noise where the

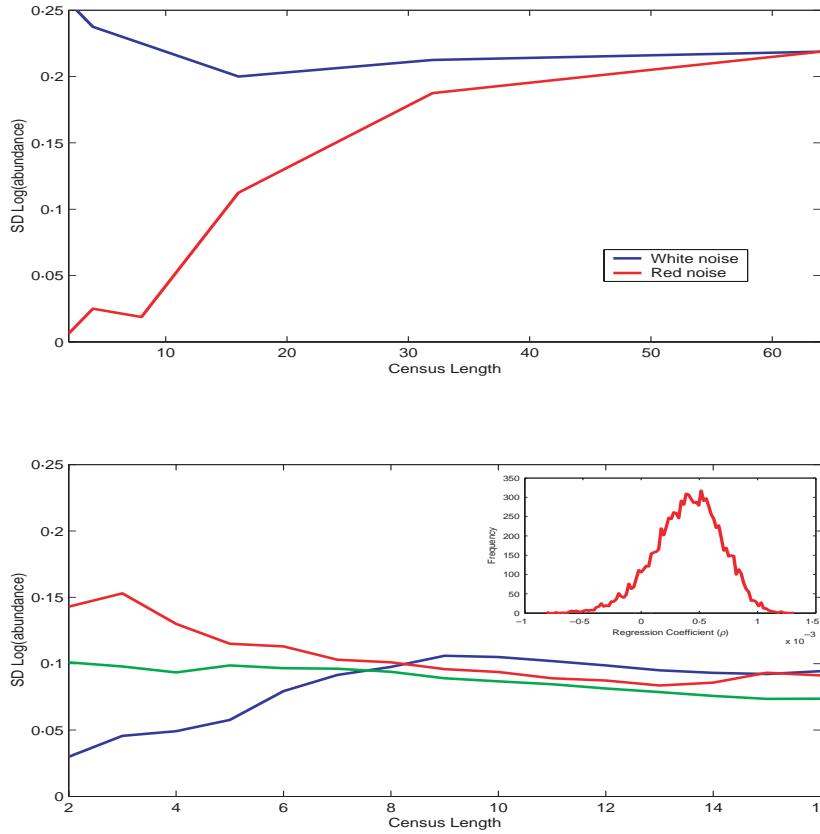


FIG. 1. (a) Pimm and Redfearn’s Fig. 1(d), showing changes in population variability as a function of the length of census period for a white (blue line) and a red (red line) noise process. (b) Our analysis of three realizations of an artificially generated (RPD) pink noise process ($\beta = 0.69$), showing qualitatively different patterns. In one case, there is a pronounced increase in SDL with census length, while in another there is no trend; the third case shows a clear decline. The inset shows the slope of the linear regression of SDL on census length for 10 000 replicate pink time series. While in general there is an initial increase in SDL with census length, in more than 20% there is no change and in 10% there is a significant initial decline.

$\log(\text{power})$ (power is the squared magnitude of the Fourier spectrum) scales linearly with $\log(1/\text{frequency})$ (Schroeder, 1991; Pilgrim & Kaplan, 1998). We stress that our results are only determined by the colour of the generating process and not by the method of generation.

2.1 Pink noise

The first method, the results of which we call the relaxation process data (RPD), uses the following recursive relationship to generate a time series:

$$X_{t+1} = \beta X_t + (1 - \beta)\epsilon_t, \quad (1)$$

where ϵ_t is normally distributed with mean 0 and variance 1. The key parameter is β , which defines the strength of autocorrelation and hence the colour of the data. Note that this method does not produce perfect $1/f$ noise since correlations between two points decay exponentially (rather than as a power law) and typically the scaling breaks down at very low frequencies; for our purposes, however, these are an acceptable approximation to $1/f$ data (Miramontes & Rohani, 2002). For all RPD, the first term of the series was assigned a uniformly distributed random value ($X_0 \sim U[0, 1]$) and in order to run off transients we discarded the first 100 values.

The second method of generating a coloured noise time series of length N relies on summing up $N/2$ sine waves, with phases randomly and uniformly distributed between 0 and 2π (Cohen *et al.*, 1998). More precisely, we use

$$X_t = \sum_{i=1}^{N/2} \sin\left(\frac{2\pi t}{i} + \phi_i\right) \times S(f), \quad (2)$$

where $\phi_i \sim U[0, 2\pi]$ defines the phase shift. The term $S(f)$ determines the amplitude of the component sine waves as a function of the frequency, f , which is defined as the number of cycles per N points. To generate pink noise, we set $S(f) = \sqrt{1/f}$ (hence $S(f) = \sqrt{\frac{i}{N}}$ in (2)) and refer to the data generated using this method as sinusoidal pink noise (or SPN).

2.2 White noise

Two different white noise data were used in this study: (i) normal and (ii) uniformly distributed. They were obtained both by using the built-in random number generators in Matlab, and by employing the `ran2` and `gasdev` routines from Numerical Recipes (Press *et al.*, 1988). No significant differences between these different random number generators were observed.

Note that when applying the Pimm and Redfearn method to our various data sets, we used their ‘nested’ algorithm, in which SDL is successively calculated for the first i points, where $i = 2, 3, \dots, n$. The use of their ‘non-nested’ algorithm gives rise to very similar results.

3. Results

As stated earlier, Pimm and Redfearn showed that variability increased for data with a reddened spectrum (Fig. 1(a)). Our numerical explorations have shown, however, that this need not always be the case. For different realizations of the same artificially generated pink noise process (whether RPD or SPN), it is possible to observe no change, an initial decline in variability with length of census period, or the expected increase (Fig. 1(b)). To document how often we may observe these contrasting patterns, we generated 10 000 replicate pink noise time series data using (1) and (2). For each time series, we first carried out a linear regression of SDL versus census length—the frequency distribution of regression slopes for RPD is presented in Fig. 1(b) (inset). Next, we explored the frequency histograms of variability as a function of census length. The distribution of the slope of the linear regressions provides an indicator of the frequency with which SDL shows a

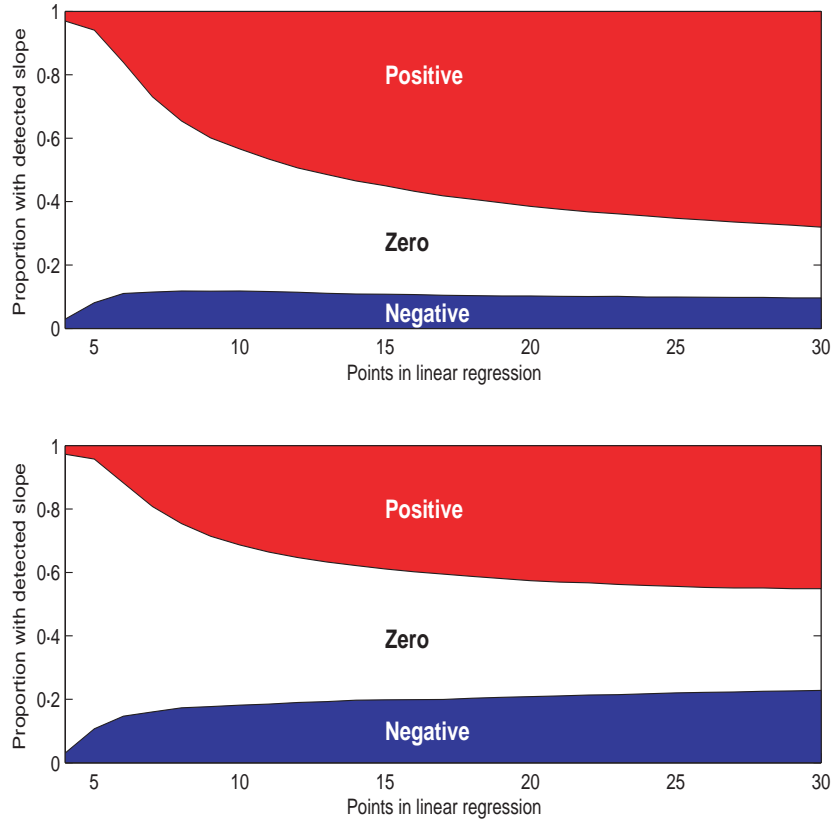


FIG. 2. (a) We plot the frequency with which 10 000 replicate RPD are detected as red, white or blue. This is achieved by carrying out a linear regression of SDL (calculated using Pimm and Redfeare's nested method) against census period length and determining whether the slope is statistically different from zero (at the 95% level). (b) The same procedure is repeated for white noise data, generated by a normal distribution, with mean 0 and variance 1. To ensure all series are positive, the value of 100 was arbitrarily added to the data, which were then detrended and had the mean subtracted.

systematic trend with census length. We found that in around 10% of cases there is a statistically significant initial decline (at the 95% level) in variability with census length, independent of the algorithm used to generate the data. More importantly, however, in more than 20% of cases, the slope is not significantly different from zero. This is shown in Fig. 2(a), where for 10 000 pink noise time series of various lengths, the probability of the generated data being significantly red, white or blue are calculated. Hence, using this method, it is clearly unwise to attempt to infer the colour of a time series based on a single (or a very few) replicate(s). Once the output from a very large number (10 000) of replicate time series are averaged, however, a pronounced and consistent increase in variability with length of census period can be detected (Fig. 3, navy blue and green lines).

Our analyses also suggest there are subtleties involved when the data are generated by a white noise process. Given data with uncorrelated successive terms, variability should,

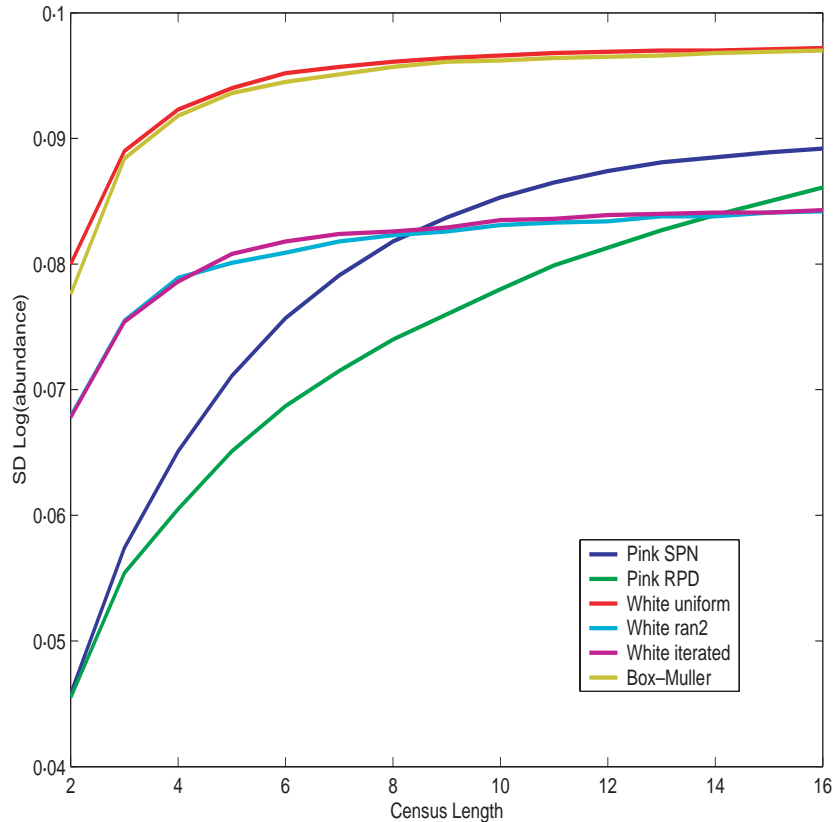


FIG. 3. Patterns of change in SDL with census length for a variety of white and pink noises for the means of 10 000 replicate time series (using Pimm and Redfearn's nested method). The figure clearly demonstrates that the qualitative behaviour observed is independent of the precise method used to generate the data. All white noise data show a dramatic initial increase in SDL but level out for reasonable census lengths of eight or more points (see main text). For uniformly distributed white noise, we used Matlab's in-built random number generator (red line) and the `ran2` routine (light blue line) from Numerical Recipes (Press *et al.*, 1988). We generated Gaussian white noise both according to the iterated method `gasdev` (purple line) outlined in Press *et al.* (1988, pp. 288–290) and the in-built generator in Matlab (gold line). To generate $1/f$ noise, again we used two different methods, as outlined in the main text. The results for SPN data are represented by the navy blue line and RPD are plotted in green. All data are treated as outlined in the legend of Fig. 2.

in theory, be independent of census period. We found, in contrast, that for both uniform and normally distributed random noise, there is (at the 95% level) a statistically significant initial increase in variability with census length (Figs 2(b) and 3). The explanation for these findings is straightforward. When the census length is short, the sample mean is not an accurate estimate of the underlying mean, resulting in underestimation of the sample variance (i.e. there is small sample bias). The implication of these results are clear: not all data that demonstrate an initial increase in variability with census length are necessarily reddened.

We explored this issue further by modifying Pimm and Redfearn's algorithm. Rather

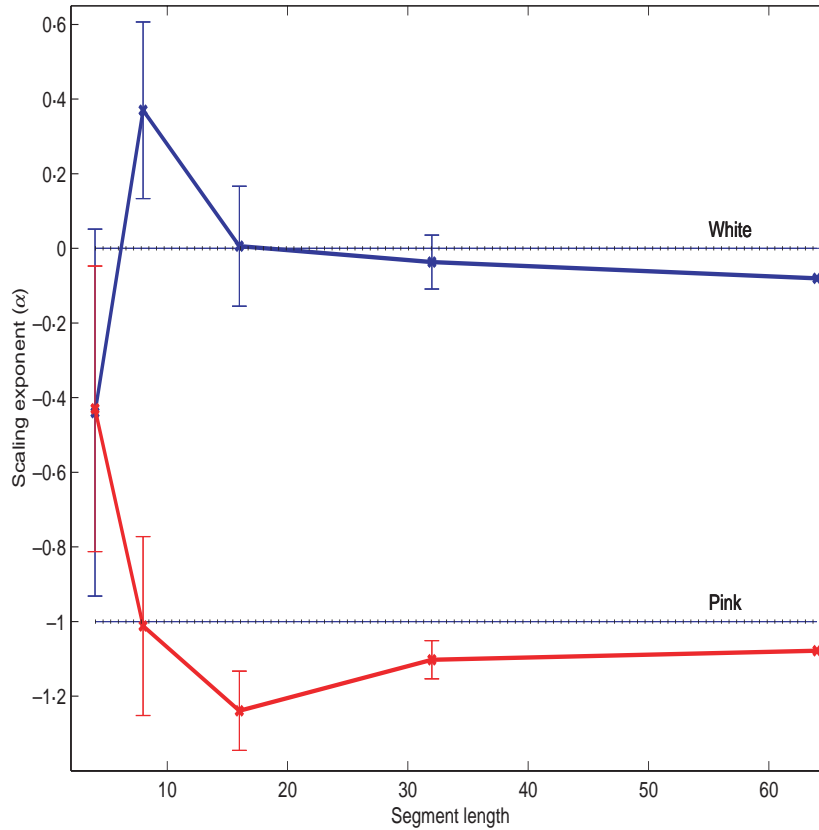


FIG. 4. Results of the segmentation method outlined by Miramontes & Rohani (2002) as applied to one white (uniformly distributed) and one pink (RPD) time series. Each time series consists of only 64 points. For each census length i , we have plotted the mean scaling exponent (α) estimated and the associated standard error.

than plotting the SDL for the first $2, 3, \dots, n$ points, we estimated the SDL for all pairs, triplets, quadruplets etc. in the data. For example, if we have a time series of length 32, then at census length 2 we calculate the mean SDL of 31 pairs of consecutive numbers. Using this technique to analyse pink noise time series, we have *always* observed a statistically significant increase in SDL as census length increases, even for a single time series. Similarly, when data generated by a white noise process were analysed in this manner, a statistically significant trend in SDL with census length is never observed. Indeed, if we were to reproduce Figs 2(a) and (b) for this modified technique, we would observe purely red and purely white panels for pink and white noise, respectively. This approach is generally acknowledged as a more reliable indicator time series colour and has already been successfully applied to various data sets (Mandelbrot & Wallis, 1969; Cyr, 1997; Inchausti & Halley, 2001).

Elsewhere (Miramontes & Rohani, 2002), we have proposed an alternative frequency-based method for estimating the colour of short time series. This method is based on

splitting any given time series of length N into n smaller segments of length $N + 1 - n$. For each segment, the power spectrum is calculated and a linear regression is carried out on the $\log(\text{power})$ versus $\log(\text{frequency})$. This yields the scaling exponent α from the relationship $P(f) \approx f^\alpha$. Thus, for each segment length, we have n (non-independent) estimates of α , the average of which provides an accurate indication of the time series' inherent colour (for further details, we refer the reader to Miramontes & Rohani, 2002). An illustration of this technique is provided in Fig. 4, where the scaling exponent is estimated for white ($\alpha = 0$) and pink ($\alpha = -1$) time series data consisting of 64 points. The figure shows that when the segments are really short ($n = 4$), the method cannot reliably distinguish between pink and white noise. When the data are split into segments consisting of eight or more points, however, there is a significant difference between the estimated scaling exponents and the method correctly detects the underlying colour of the data. This approach is similar in spirit to that adopted by Inchausti & Halley (2001), with the key difference being the averaging of the exponent estimated from each segment.

4. Discussion

The accurate detection of the inherent colour of ecological datasets remains an interesting and topical issue. Recently, Inchausti & Halley (2001) have made an important contribution to this subject by analysing a large number of *long* population time series from the Global Population Dynamics Database. They concluded that more than 80% of these are red-shifted. The technique Inchausti & Halley (2001) employed is robust and their study clearly reinforces Pimm and Redfearn's findings. We believe, however, that important methodological issues remain over how one may explore temporal variability in relatively *short* time series. Unfortunately, the method Pimm and Redfearn applied to data may incorrectly detect 'redness' in time series generated using a white noise process, or attribute 'whiteness' to data from an autocorrelated process.

In this paper, we have suggested that one possible solution may be to investigate the relationship between SDL and all census segments of size i , for $i = 2, \dots, n$ (Cyr, 1997; Inchausti & Halley, 2001). This method, even for a very small number of replicates, gives much more consistent results and may be more reliable when attempting to detect the colour of a short time series, although greater care is needed when discussing the statistical significance of the averaged results. We have also proposed that Fourier analysis of such multiple segments may also be used to establish the inherent colour of time series. This approach has been shown to give very accurate results, even for very short time series (Miramontes & Rohani, 2002).

While we do not believe that the discrepancies and subtleties highlighted above cast doubt on the qualitative conclusions of Pimm & Redfearn—notably that many ecological processes are reddened—our results suggest that a careful re-examination of their data may be advisable. While there remain significant technical complications, the two approaches briefly outlined above may represent appealing alternatives.

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