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# The long-term temporal variability and spectral colour of animal populations

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## ABSTRACT

We analysed the temporal variability and the spectral colour of 544 natural populations of 123 species that have been censused for more than 30 years. We compared the tendency for variability to increase with time (equivalent to spectral reddening) using three basic measures: an exponent of increasing variance, the 30 year temporal variability and the spectral exponent. For each, we considered the main ecological correlates: taxon, trophic level, latitude, and habitat type and body size. Our results confirm previous findings that population variability increases over time, and those ecological populations have reddened spectra. This effect is universally prevalent, being similar for populations of different taxa, having different body sizes, belonging to different trophic levels, living at different latitudes and exhibiting different types of population dynamics. Generally, the amount of reddening appears to be greater than that expected from environmental forcing alone. Also, there is no evidence that ecological variability tends towards a finite limit, although the increase of variability does decelerate. Our results suggest that widely used measures of population variability, such as the coefficient of variation or standard deviation of the logarithm of abundance, should be supplemented by measures of either spectral reddening or the rate of increase of the population variance.

*Keywords*: autocorrelation, conservation, extinction, fractal, noise, spectral colour, temporal variability.

## INTRODUCTION

Understanding the patterns of fluctuations in the abundance of natural populations is one of the central problems in ecology. These patterns also have important applied and theoretical consequences. In particular, the amount of variability of natural populations is crucial to the assessment of extinction risk. Only after quantifying the magnitude of populations' natural variability can we ascertain the likely effect of human actions on them.

Although population variability is a very intuitive concept, obtaining an adequate and robust measure of temporal variability has proven rather complex. Such a measure should

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have certain properties to allow comparison of species with very different life histories, such as insects, mammals and plankton. First, the measure should be unit-free and independent of mean abundance, since we are generally interested in the *proportional* variability of the dynamics (Gaston and MacArdle, 1994). Secondly, it should account for the different lengths of data sets when comparing populations. Two measures have been favoured in most studies: the coefficient of variation of population abundance and the standard deviation of the log-transformed population abundance (MacArdle *et al.*, 1990; Pimm, 1991; Gaston and MacArdle, 1994). Although both measures satisfy the first criterion, reflecting variability on a relative scale, they do not satisfy the second criterion. This is because variability tends to increase with the length of the survey (Pimm and Redfearn, 1988; Murdoch, 1994; Cyr, 1997) and there is no simple way to standardize the estimates of temporal variability by the length of the data.

The so-called 'more time–more variation' effect (Lawton, 1988) was first discussed explicitly by Pimm and Redfearn (1988), who found that that the standard deviation of the log-transformed population abundance increased with census length for 75 populations of farmland or woodland birds and 26 other populations of mammals, birds and insects. Subsequently, Ariño and Pimm (1995) confirmed this trend in their analysis of 115 populations representing 58 species of birds, mammals, insect, fish, algae and plants. Other studies (Murdoch and Walde, 1989; Murdoch, 1994; Cyr, 1997) have confirmed the general observation that 'more time means more variation'. This effect has inspired considerable discussion as to its possible origin (MacArdle, 1989; Pimm 1991; Halley, 1996), theoretical exploration (Cohen, 1995; Ripa and Lundburg, 1996; White *et al.*, 1996; Cuddington and Yodzis, 1999; Halley and Kunin, 1999) and some experimental work (Petchey, 2000).

The 'more time–more variation' effect has two basic forms (Mandelbrot, 1999). First, it can be associated with a 'reddened' spectrum of population abundance. A reddened spectrum is one in which the low-frequency events (those happening on long time-scales) explain more of the total variability of population data than high-frequency ones (Halley, 1996). Such processes are always 'statistically persistent' or positively autocorrelated, because past values of population abundance tend to be followed (i.e. persist over time) by similar values. Secondly, an alternative form for this 'more time–more variation' effect is when consecutive values of population abundance are uncorrelated, but their probability distribution follows a 'heavy-tailed' probability form generating sequences of values whose variance typically increase with the length of the data due to rare extreme events (Mandelbrot, 1963). Such extreme non-Gaussian ('Lévy-stable') behaviour is believed to be the cause of the 'more time–more variation' effect in economic time-series and various other complex processes (Adler *et al.*, 1997). We have discussed this possibility in a companion paper (Halley and Inchausti, in press) and found that the likelihood of 'heavy-tailed' behaviour is almost negligible for ecological populations. Also in an earlier paper (Inchausti and Halley, 2001), we found a strong correlation between an increase in variance and spectral redness. Thus, it is probable that spectral reddening is the dominant cause of the 'more time–more variation' effect in ecological time-series.

Here, we investigate the nature of the 'more time–more variation' effect, which we believe deserves closer examination, using a wide range of ecological time-series. The aim of the paper is to examine several important questions related to this pattern. First, what is the magnitude of the 'more time–more variation' effect? Secondly, is the spectral reddening of ecological time-series just a reflection of environmental variability or is it something generated ecologically? Thirdly, is ecological variability 'stationary' – does it tend towards a finite limit as in auto-regressive models or should we expect it to increase indefinitely as series length increases as with multi-scale $1/f$-noise (Halley and Kunin, 1999)? Fourthly, do we see important differences in this effect between different taxa, body sizes and latitudes? Finally, what are the implications for ecological theory, practice and future research of what we now know?

## METHODS

### Sources of data

As explained elsewhere (Inchausti and Halley, 2001), we searched the Global Population Dynamics Database (GPDD, http://cpbnts1.bio.ic.ac.uk/gpdd/) for all the annual time-series of population abundance that were longer than 30 years, arriving at a set of time-series comprising 544 populations of 123 species. This length of time-series was chosen as the reasonable minimum duration that could allow a reliable estimation of temporal variability and degree of autocorrelation in the dynamics of natural populations.

Besides population counts, the GPDD contains auxiliary variables such as the geographic coordinates, trophic level (herbivores, carnivores and secondary carnivores), type of habitat (aquatic, terrestrial) and body size. These variables were used as explanatory factors to compare the estimates of redness for different taxa, latitudes, trophic levels, body sizes and types of habitat. The choice of these explanatory variables was motivated by previous studies of population variability (Gaston and Lawton, 1988; MacArdle *et al.*, 1990; Pimm, 1991; Ariño and Pimm, 1995). For example, large-bodied species should have smaller population variability than small-bodied ones because the latter reproduce more slowly and live longer than the former (Pimm, 1991). The increase of inter-seasonal differences with latitudes could generate a positive association between population variability and latitude. Simple models (e.g. Pimm and Lawton, 1977; Pimm, 1991) and some empirical observations (e.g. Schoener and Spiller, 1992; Jenkins *et al.*, 1992) suggest that temporal variability increases along the trophic chain. According to Steele's (1985) ideas, since marine environmental variation is redder than terrestrial variation, marine taxa should have redder spectra.

For some species and locations, some of the complementary variables were not available: trophic level membership was not always available; body size was unavailable for non-vertebrate taxa; latitude was not available when the geographic location was not specified precisely. Thus, the number of series used in some analyses differed, depending on whether we had information for the explanatory variables.

### Temporal variability

We characterized the temporal variability of each population by the coefficient of variation of population abundance calculated over the first 30 years of each time-series. Besides describing the proportional temporal variability, the coefficient of variation has the additional advantage of being unit-less, thus allowing a comparison of data sets of populations and species that were censused using different methods. By using a common time horizon to estimate population variability, one can separate the background value of temporal variability from its increase as a function of its spectral colour, which would permit a comparison of the temporal variability of populations that were censused for different lengths of time.

## Spectral colour of population dynamics

We used the spectral exponent (Feder, 1988; Schroeder, 1991; Allegrini *et al.*, 1995) to measure the spectral colour of ecological time-series, which is related to the rate of increase of temporal variability with the length of the time-series (Inchausti and Halley, 2001). The spectral exponents (Fig. 1) were estimated as minus the regression slope of the spectral power versus frequency (on a doubly logarithmic scale) obtained from the spectral analysis of each linearly detrended, log-transformed data set. The spectral analysis of a time-series is equivalent to decomposing its total variation in terms of amounts explained by the harmonic frequencies defined in $[1/n, 1/2]$, where $n$ is the length of the time-series. In a white noise process, each frequency interval explains the same amount of total variation (i.e. it has the same spectral power) and thus the spectral exponent is equal to zero. This contrasts with a reddened process, in which low frequencies explain more of the variation in population data (i.e. would have higher spectral power) than higher frequencies, thus leading to a negative spectral exponent.

## Variance growth exponent

We used the variance growth exponent, $\gamma$, to assess the rate of increase of the variance of log-transformed time-series as a function of the length of the time-series. Some of the series contain zero counts, which raises problems when taking logarithms. These are often met by using transformation $\log(1 + N_t)$ instead of $\log N_t$ to avoid infinities at zero. In addition to problems discussed by MacArdle *et al.* (1990), this approach was unsuitable for us because of the variety of units in which the populations were expressed. Therefore, we treated the zeroes as blanks and excluded them from analyses involving logarithms. For each time-series, we first calculated the average variance $\bar{V}_k$ for all windows of size $k$ ($3 \le k \le n$; there are $n - k + 1$ possible windows of size $k$ in a time-series of length $n$ years) as a function of $k$ (Allegrini *et al.*, 1995; Fig. 1). The variance growth exponent was estimated as the regression slope in a doubly logarithmic scale of the average variance $V_k$ as a function of $k$ (Feder, 1988). Since $\gamma$ is estimated as a slope calculated in a doubly logarithmic scale, one is effectively estimating the exponent in the $\bar{V}_k\,(t - t_0) \approx (t - t_0)^{\gamma}$ for the time-series beginning at $t_0$. Although the estimation of $\bar{V}_k$ involved a set of partially overlapping windows (Fig. 1), no claim is made on the statistical significance of the regression slope calculated using these non-independent data points. Values of $\gamma = 0$ would correspond to a strictly stationary time-series of infinite length. For finite stationary time-series, $\gamma$ will be different from zero, but it will converge to zero for longer time-series (Halley and Kunin, 1999). A value of $\gamma = 1$ corresponds to a random walk, a process equivalent to the stochastic, density-independent population growth for which the variance of population abundance increases linearly with the length of the time-series (Feder, 1988). Values of $\gamma$ between zero and one indicate that variance increased with the length of the time-series but at a decelerating rate. Pink $1/f$-noise processes, whose variance increases approximately as the logarithm of their length, are often considered as the boundary between stationary and non-stationary processes, at least for the family of $1/f$-noises (Halley, 1996). Thus, for our purposes, we considered a time-series to be stationary whenever its rate of increase of variance was strictly slower than logarithmic.

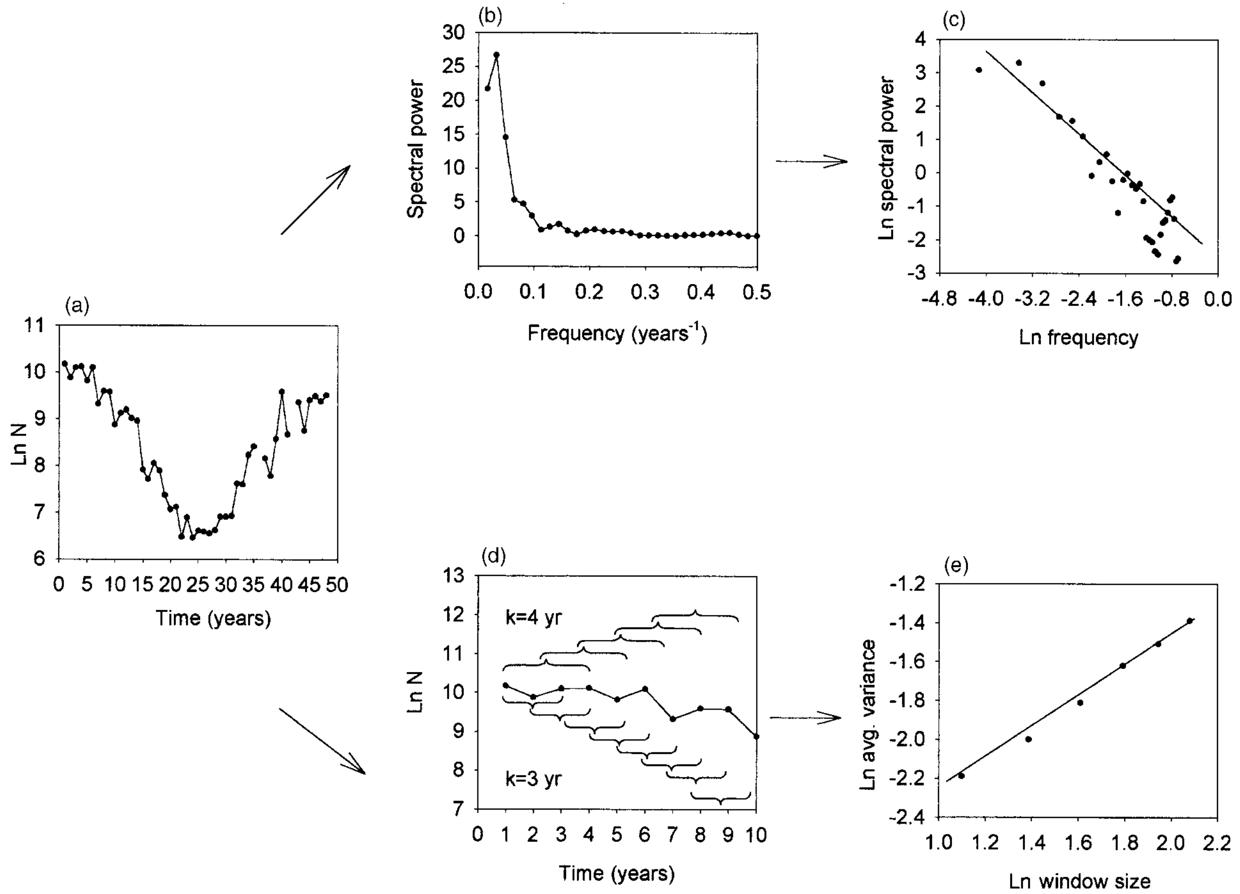

**Fig. 1.** Calculation of the variance growth and the spectral exponents of a time-series. (a) Population abundance (log-transformed) over time. (b) Spectral analysis of the log-transformed time-series, expressed as spectral density (in units of variance $\times f^{-1}$) against frequency (in units of years$^{-1}$). (c) The spectral exponent calculated as the regression slope of log-spectral density against log-frequency. (d) The first 10 points of the time-series shown in panel (a) with windows of size $k = 3$ and $k = 4$ observations over which the average variance, $V_k$, is calculated, for various starting points. (e) The variance exponent calculated as the regression slope of the $\log \overline{V}_k$ (the average is over all possible starting points) as a function of $\log k$.

### Ecological correlates of temporal variability and of spectral exponents

The sets of estimates of temporal variability and spectral exponents were compared among main taxa, latitude, body weights, trophic level and type of habitat using two sets of analysis of variance. We log-transformed the estimates whenever necessary to satisfy the normality assumption of the analysis of variance. We arranged the data sets into the following taxonomic groups: Mammalia, Insecta, Aves, Osteichtyes, Crustacea and Mollusca. We considered two sets (one for the temporal variability, the other for the spectral exponents) of five separate analyses motivated on the ecological considerations outlined above. The first analysis evaluated latitudinal and taxonomic effects; the second included habitat and trophic effects; the third contrasted vertebrates and invertebrates; and the fourth included taxonomic and functional effects [trophic level, (log-transformed) body mass]. The length of each time-series was used as a covariate in all analyses to prevent spurious significant results being generated because of the unequal number or lengths of the data sets for peculiar combinations of some of the explanatory factors.

### Testing the hypotheses of the causes of the redness in population data

A direct test of the environmental forcing hypothesis would be to compare the spectral exponents of environmental variables with those of population abundance for the same location. We do not have access to the long-term meteorological data for the same locations and years for which we have long-term population data. Instead, we used the longest data set of a directly measured environmental variable, the daily record of temperature in Central England (1772–1997, comprising 82,546 observations; data courtesy of the British Atmospheric Data Centre), to calculate the spectral exponents at several time-scales. The daily temperature data were used to calculate the maximum and minimum temperature for all weeks, months, seasons and years and to estimate the spectral exponents for the time-series of the maxima and minima temperatures obtained at these different temporal scales. These spectral exponents were used to identify the time-scales at which the temperature fluctuations can be considered to have a reddened spectral signal.

## RESULTS

The frequency distribution of values of the variance growth exponent, $\gamma$, shows that most series yield a variance exponent between zero and one (Fig. 2). The rate of increase of the variance of log $N$ with the length of the data series was positive for 96.9% (=527/544) of the series. The median value of $\gamma$ was 0.358 (range = −0.128 to 1.643), indicating that the temporal variability of time-series typically increased at a decelerating rate over time. Figure 3 shows the histogram obtained if the series are first randomized before calculating growth exponents. The median value of $\gamma$ in this case is 0.0035, a drop of two orders of magnitude. This establishes fairly solidly that the growth of variance is indeed due to autocorrelation (Inchausti and Halley, 2001).

The variance increases faster than logarithmically in over half the series, which attests to their non-stationary character. For example, the variance of 59% of the 256 series longer than 48 years increased faster between years 12 and 48 than between years 3 and 12.

Estimates of the coefficient of variation of the ensemble of time-series had an asymmetric distribution ranging between 0.073 and 4.212, with a median of 0.720 (Fig. 3), which

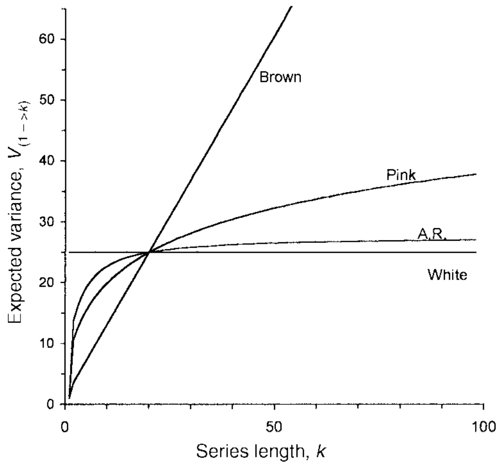

**Fig. 2.** Increase in the variance of population abundance with the length of time-series for white, stationary reddened (auto-regressive, A.R.), pink or $1/f$, and brown (random walk) noise (after Halley and Kunin, 1999).

prompted us to log-transform them in subsequent analyses of variance. There were no differences in the temporal variability among taxa, trophic levels or habitat type with respect to latitude (Fig. 3, Table 1). Although the average variability of invertebrates was significantly higher than that of invertebrate populations (Tables 1), this should be interpreted with caution, as the temporal variability of these two groups showed opposite latitudinal trends (Table 2). The relationship between body mass and temporal variability changed along the trophic chain (Table 1): whereas temporal variability decreased for larger herbivores, it increased for larger carnivores (Table 2). Population variability increased overall with body size (partial slope = 0.046, standard error = 0.013, $P < 0.001$) and decreased with latitude (partial slope = −0.0054, standard error = 0.003, $P < 0.001$). It must be pointed out that body size was independent of latitude (Pearson correlation = 0.057, $n = 408$, $P = 0.126$) in the data sets analysed.

The estimates of the spectral exponents for the ensemble of populations showed a tendency to be clustered in the range 0 to 2 (Fig. 2) with a median value of 1.02, close to the value for pink noise. Relative to the variance increase exponents, the histogram of spectral exponents is quite symmetric. The spectral exponents did not differ significantly among taxa, trophic levels or between vertebrates and invertebrates with respect to latitude (Table 1, Fig. 3). We found significant differences among populations of different trophic levels depending on habitat type (aquatic, terrestrial) (Tables 1 and 2; Fig. 3), but this should be interpreted with caution, since only aquatic secondary carnivores, for which we have very few data sets, differed from the other taxa. More importantly, we found that overall populations of larger bodied species had redder dynamics (slope for body size = – 0.047, standard error = 0.013, $P < 0.001$; slope for latitude = 0.0029, standard error = 0.003, $P = 0.260$), but that the relationship between the spectral exponent and body size changed across the trophic chain (Table 2).

The analysis of the long-term record of daily temperature in Central England showed that the variability of this environmental variable could be considered uncorrelated at time-

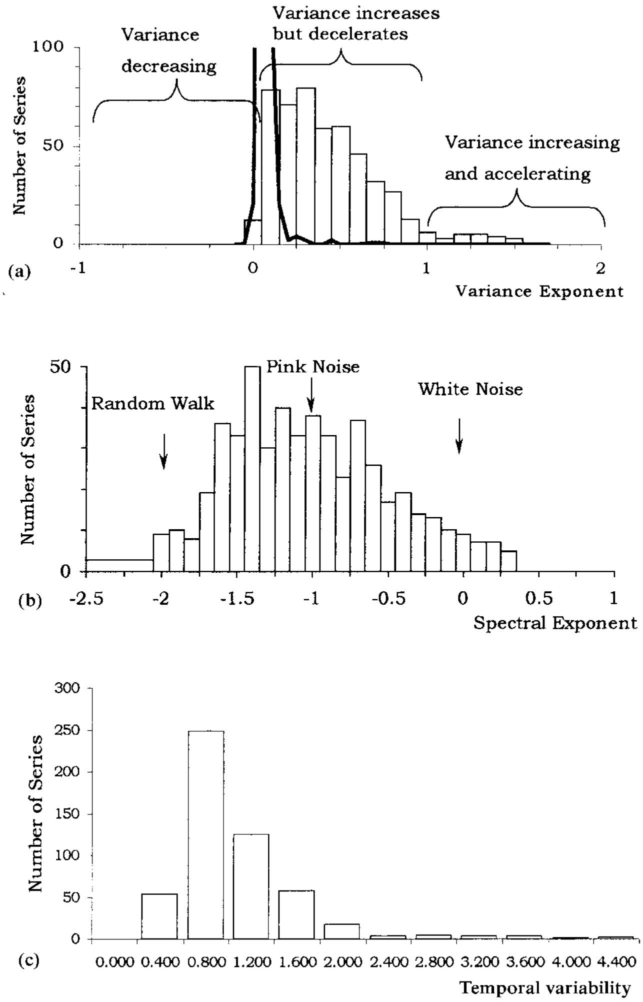

**Fig. 3.** Frequency distributions of the variance growth (a) and spectral (b) exponents and (c) the temporal variability (coefficient of variation of population abundance over 30 years) for the 544 ecological time-series. The values of each exponent corresponding to white, pink and red noise are indicated in (b). The heavy truncated curve in (a) is the expected distribution the exponents would have in the absence of correlation. It was obtained by randomizing the 544 series before finding the exponent, to eliminate time correlations, and shows a virtual collapse of variance growth.

scales longer than a season (Fig. 5). In other words, only for scales shorter than 3 months can variation in temperature be considered different from a white noise process.

## DISCUSSION

Our results confirm and extend the findings of previous studies (Pimm and Redfearn, 1988; Murdoch and Walde, 1989; Murdoch, 1994; Ariño and Pimm, 1995; Cyr, 1997) that population variability increases with the length of a time-series. Using a direct estimate of the rate

**Table 1.** Results of analyses of variance comparing the temporal variability and the spectral colour of long-term time-series of populations of different taxa, trophic levels, habitat type (aquatic, terrestrial), body size (only for mammals and birds), type of taxa (vertebrates, invertebrates) and habitats at different latitudes

| | Temporal variability | | | | Spectral exponent | | | |
|---|---|---|---|---|---|---|---|---|
| Source of variation | d.f. | MS | *F* | *P*-value | d.f. | MS | *F* | *P*-value |
| Taxa | 4 | 0.496 | 1.912 | 0.107 | 5 | 0.609 | 1.897 | 0.110 |
| Latitude | 1 | 0.640 | 2.468 | 0.117 | 1 | 0.010 | 0.030 | 0.862 |
| Taxa × latitude | 4 | 0.261 | 1.005 | 0.404 | 5 | 0.388 | 1.207 | 0.307 |
| Error | 527 | 0.259 | | | 527 | 0.321 | | |
| Trophic level | 2 | 0.669 | 2.254 | 0.199 | 2 | 0.722 | 2.169 | 0.115 |
| Latitude | 1 | 0.490 | 1.653 | 0.106 | 1 | 0.005 | 0.014 | 0.908 |
| Trophic level × latitude | 2 | 0.890 | 3.000 | 0.051 | 2 | 0.652 | 1.958 | 0.142 |
| Error | 532 | 0.297 | | | 532 | 0.333 | | |
| Trophic level | 2 | 0.566 | 2.622 | 0.074 | 2 | 0.270 | 1.113 | 0.330 |
| Body size | 1 | 0.084 | 0.387 | 0.534 | 1 | 0.847 | 3.498 | 0.062 |
| Trophic level × body size | 2 | 4.376 | 20.281 | *<0.001* | 2 | 0.788 | 3.252 | *0.040* |
| Error | 402 | 0.216 | | | 402 | | | |
| Trophic level | 2 | 0.390 | 1.338 | 0.263 | 2 | 0.425 | 1.292 | 0.276 |
| Habitat type | 1 | 1.679 | 5.76 | 0.017 | 1 | 0.007 | 0.207 | 0.649 |
| Trophic level × habitat | 2 | 0.734 | 2.518 | 0.082 | 2 | 1.094 | 3.326 | 0.037 |
| Error | 538 | 0.291 | | | 538 | 0.329 | | |
| Habitat | 1 | 0.353 | 1.202 | 0.273 | 1 | 0.090 | 0.271 | 0.603 |
| Latitude | 1 | 0.271 | 0.924 | 0.337 | 1 | 0.902 | 2.719 | 0.100 |
| Habitat type × latitude | 1 | 0.059 | 0.202 | 0.654 | 1 | 0.268 | 0.807 | 0.370 |
| Error | 534 | 0.294 | | | 534 | 0.332 | | |
| Taxa type | 1 | 1.703 | 9.153 | 0.015 | 1 | 0.076 | 0.226 | 0.635 |
| Latitude | 1 | 1.506 | 5.228 | 0.023 | 1 | 0.086 | 0.026 | 0.873 |
| Taxa type × latitude | 1 | 2.637 | 5.911 | *0.003* | 1 | 0.073 | 0.219 | 0.640 |
| Error | 534 | 0.288 | | | 534 | 0.334 | | |

*Note*: Italic *P*-values highlight the heterogeneity of slopes for different trophic levels and types of taxa that are examined in Table 2.

of variance increase, we found that temporal variability increases with census length for 527 of the 544 ecological time-series. We also confirmed the observations of others (e.g. Murdoch, 1994; Ariño and Pimm, 1995; Cyr, 1997) that the increase of variability tends to decelerate (Fig. 3). However, such deceleration need not imply that the variance stops increasing (stationarity), since the rate of increase may slow down without converging to any limit (Fig. 2). While in the autoregressive model the variance reaches an upper limit, in the pink 1/*f*-noise model the variance continues to increase without limit. Judging stationarity based on short time-series is difficult in practice (e.g. Beran, 1994). However, in

**Table 2.** Latitudinal and body size variation of the temporal variability and of the spectral exponents of different trophic levels and types of taxa corresponding to the italic *P*-values in Table 1

| **Body mass** | Temporal variability | | | Spectral exponent | | |
|---|---|---|---|---|---|---|
| Trophic level | Slope | Standard error | *P*-value | Slope | Standard error | *P*-value |
| Herbivores | −0.131 | 0.033, $n = 96$ | <0.001 | 0.014 | 0.027, $n = 96$ | 0.596 |
| Carnivores | 0.098 | 0.014, $n = 398$ | <0.001 | −0.078 | 0.016, $n = 398$ | <0.001 |
| Secondary carnivores | −0.023 | 0.043, $n = 41$ | 0.602 | −0.058 | 0.060, $n = 41$ | 0.335 |
| **Latitude** | Temporal variability | | | | | |
| Type of taxa | Slope | Standard error | *P*-value | | | |
| Vertebrates | −0.005 | 0.002, $n = 498$ | 0.044 | | | |
| Invertebrates | 0.035 | 0.020, $n = 38$ | 0.087 | | | |

*Note*: The upper part of the table shows how the regression slopes of temporal variability (three leftmost columns) and spectral exponents (three rightmost columns) on body size change for populations at different trophic levels. The lower part of the table shows the differences in the regression slopes of temporal variability on latitude for vertebrates and invertebrates.

nearly 60% of the longer series, variance increased faster than logarithmically (the rate for the non-stationary 1/*f*-noise model) and this is certainly evidence against stationarity.

Stationarity and density-dependent regulation are closely associated, since the latter (especially that based on logistic-type models) implies the existence of a ‘basin of attraction’ wherein population abundance is constrained to lie (e.g. Royama, 1992; Turchin, 1999). Thus, in a sense, density-dependent processes would operate as a ‘filter’ or as a ‘muffler’ dampening or constraining the effects of the environmental vagaries on population dynamics. Ecological thinking about temporal variability has included a range of stochastic models. At one end of the spectrum is ‘white noise’, where year-to-year values are independent and constrained within well-defined bounds so that a time-series would have the same expected variance irrespective of its length (variance increase exponent $\gamma$, in Fig. 3, equal to zero). This corresponds loosely to the extreme case of tight density-dependent regulation. At the other end of this spectrum is the random walk, for which the expected variance grows at a rate proportional to the length of the series (Halley and Kunin, 1999), corresponding to density-independent drift (variance increase exponent $\gamma = 1$; Fig. 3). The variance increase exponent of the set of ecological time-series lies somewhere between these extremes ($\bar{\gamma} = 0.4$).

The results of the spectral analysis broadly agree with those of the variance growth exponent. That the ‘more time–more variation’ effect is due to spectral reddening, which we confirmed using randomization here, was argued for previously (Inchausti and Halley, 2001) based on an association between the two exponents. The overall average spectral exponent observed ($\bar{\nu} = 1.02$) lies intermediate between white noise ($\nu = 0$) and the random walk ($\nu = 2.0$) and is close to that of 1/*f*-noise, thus highlighting the potential relevance of pink noise processes in ecology (Halley, 1996). Although most series have spectral exponents in the range $0 \leq \nu \leq 2$, a few have spectral exponents greater than zero that can be

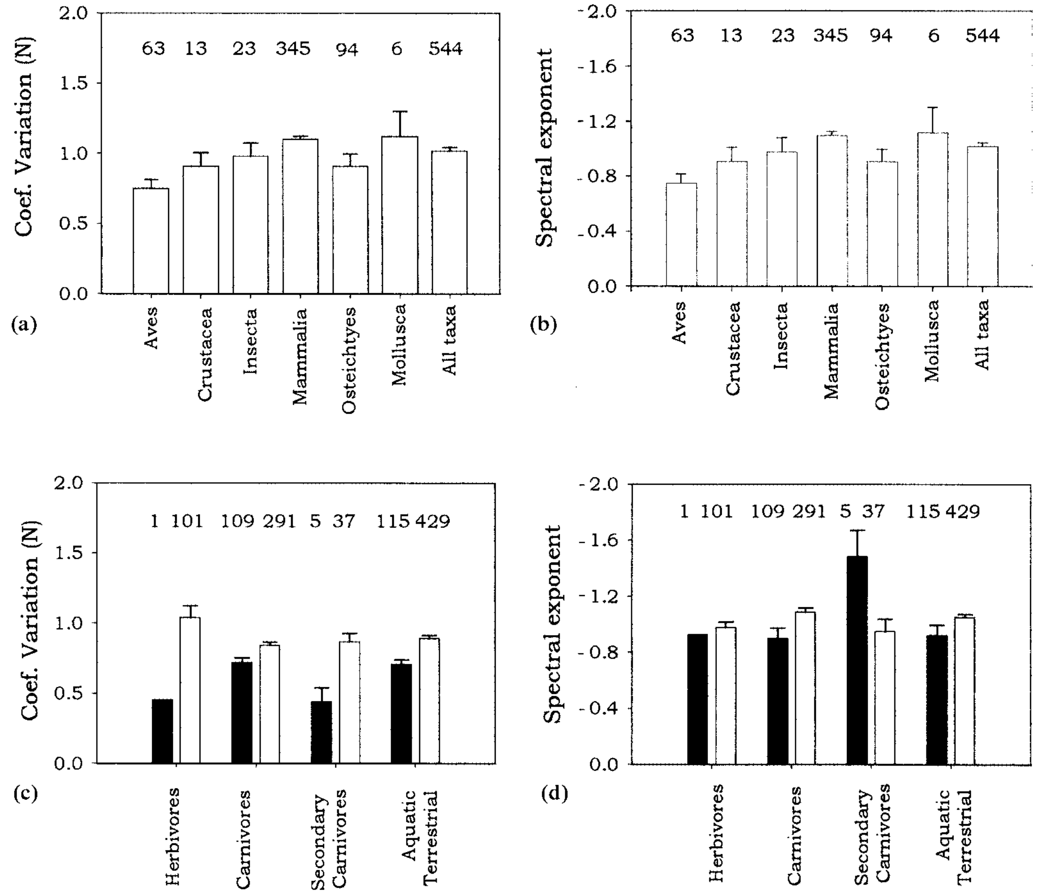

**Fig. 4.** Temporal variability (standard deviation of the log-transformed population abundance over 30 years) and of the spectral exponent of populations of different taxa (a and b) and of different trophic levels and type of habitat (c and d) (mean ± standard error). The number of populations in each category is indicated at the top of each panel.

associated with a negative correlation or 'blue noise' (Schroeder, 1991). Other series with an exponent larger than +2 might be interpreted as 'black noise' (Schroeder, 1991; Cuddington and Yodzis, 1999). Closely related to the question of stationarity is whether spectral reddening is of a complex multi-scale type such as 1/*f*-noise (non-stationary), occurring over a range of temporal scales, or whether it can be attributed to a simple auto-regressive process (stationary) reflecting, for example, age structure (MacArdle, 1989) and associated with a single dominant scale. The failure of population variance to converge to an upper value for longer series suggests that there are processes acting on a range of scales, some very slow, so that longer observation means the effects of these processes occurring at low frequency contribute to the variance of longer time-series. Although variance shows no clear sign of stabilizing and although one of us has argued in favour of the multi-scale (1/*f*-noise) interpretation of ecological variability (Halley, 1996), a definitive answer to this question will require more sophisticated statistical analysis, longer time-series or both.

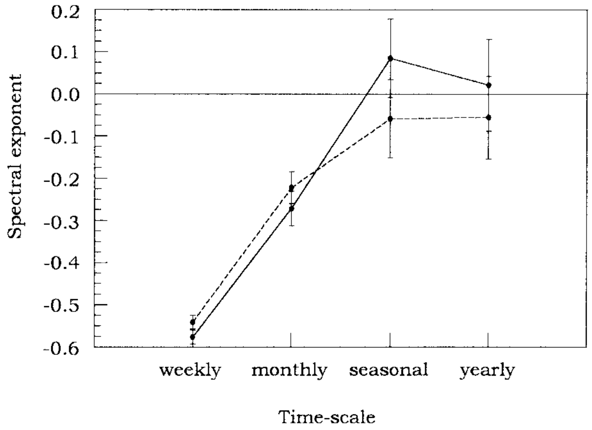

**Fig. 5.** Spectral exponents of the maximum (continuous line) and minimum temperature (dashed line) in Central England between 1772 and 1997 (data provided by the British Atmospheric Data Centre) at weekly, monthly, seasonal and yearly temporal scales. The error bars correspond to the 95% confidence intervals for the spectral exponent at each temporal scale.

## The causes of ecological reddening

Lawton (1988), Williamson (1987) and others have suggested that population data are reddened because of the influence of environmental variation of similar spectral colour ('reddened forcing hypothesis'). Everyday experience tells us that cold days are more likely than not to be followed by cold days. This positive, short-term autocorrelation is associated with a reddened spectrum, but such weather patterns only prevail over time-scales much shorter than those of interest (seasons to years) for examining the dynamics of ecological populations. Our analysis coincides with previous analyses in ecology (Swanson, 1998) and with a large body of evidence in the meteorological literature (for a review, see Lovejoy and Schertzer, 1986) showing that variation in temperature and precipitation on time-scales from days to years can be considered white noise. Other analyses (for a review, see Pelletier, 1997), however, have shown that the spectral exponents of rainfall and temperature at time-scales that are relevant for describing population dynamics can be reddened with values in the range of about 0.5. Either way, the spectra of population data seem to be considerably redder (with exponents of 0.8–1.2) than those of environmental variables. This suggests that environmental forcing, occurring at time-scales relevant for population dynamics, cannot explain the extent and magnitude of spectral reddening observed in ecological data. The evidence presented here and elsewhere suggests that, on scales of ecological interest, terrestrial populations at least 'redden themselves' rather than merely reflecting the spectral colour of the variation of the environment in which they live.

Several mechanisms can produce reddened population dynamics. Stochastic, density-independent growth (random walk) results in the progressive accumulation of random, uncorrelated increments of population abundance over time that can generate reddened population dynamics. The 'growth trend hypothesis' (Ariño and Pimm, 1995; Pimm and

Redfearn, 1998) is effectively the same thing as the reddened forcing hypothesis. As mentioned earlier, the observed positive autocorrelation of populations may simply be due to overlapping generations (MacArdle, 1989). Spatially extended population dynamics may also exhibit reddened spectra (e.g. White *et al.*, 1996), since population variability would increase with time as larger-scale and longer-term spatial effects come into play. A good example of this type of process is self-organized criticality (e.g. Bak *et al.*, 1998). Although analysis of time-series can reveal the extent of reddening of ecological dynamics, the relative importance of these various routes to redness would in general require a more detailed investigation.

## Ecological correlates of increasing variance

Populations of all main taxa and trophic levels had very similar temporal variability and spectral exponents. Simple models (e.g. Pimm and Lawton, 1977; Pimm, 1991) and some empirical studies (e.g. Schoener and Spiller, 1992; Jenkins *et al.*, 1992) have suggested that temporal variability increases along the trophic chain, but this clearly was not borne out in our analyses. Terrestrial populations had higher temporal variability than aquatic ones; however, contrary to Steele's (1985) suggestion that marine populations would have a redder dynamics than terrestrial organisms, the spectral exponents of aquatic (mostly marine) organisms reflected *less* reddened behaviour than those of terrestrial ones.

Body mass is an easily measurable variable that summarizes many aspects of an organism's physiology and ecology (Peters, 1983; Calder, 1984). The wealth of allometric relationships among body mass and life-history traits suggests that some scaling relationship should exist between body mass and population variability. However, any such relationship is likely to be a very complex one because of the compounding of body size-related features having positive or negative effects on population variability (Pimm, 1991; Lawton, 1995). In our survey, we found that the overall population variability increased with body size, contradicting the hypothesis that long-lived species that also have long generation times should have low temporal variability because the same individuals are counted in consecutive censuses (Pimm, 1991; Gaston and MacArdle, 1994). Various arguments can be made for such relationships. The positive association between spectral reddening and body size is presumably due to the effect of age-structure dynamics in large-bodied species. Because large-bodied populations reproduce at generation times longer than 1 year, age-structured dynamics effectively buffers temporal variability at high frequencies (shorter than one generation), thus inducing an inertial effect that appears as spectral reddening. However, this buffering effect does not apply for time-scales significantly greater than the generation time, where populations may drift considerably. Indeed, it is the transition between these two regimes that causes the increase in variability and thus reddening. Thus, large-bodied organisms may not only have greater long-term temporal variability than small-bodied ones on a common time-scale, but also increased reddening in the transition between time-scales above and below generation time. It should be borne in mind that this discussion on the relationship between temporal variability, spectral reddening and body size is essentially based on single-species arguments. For instance, we found that both the magnitude and sign of the associations of temporal variability and spectral reddening with body size changed for different trophic levels (Table 1), something that should be interpreted with caution because the limited number of species and reduced range of body sizes of herbivores and secondary carnivores would hinder the reliability of allometric relationships for these trophic levels.

As expected, invertebrate populations were more variable in the short term than vertebrate populations, since the former are generally thought to be more prone to the effects of extreme environmental variation, and thus one would expect invertebrate populations to follow environmental variability more closely. Cyr (1997) found that the magnitude of the variability of planktonic populations was not altogether different from that of vertebrate taxa. It is possible, however, that the expected difference between vertebrates and invertebrates is being confounded by the effect of longevity and generation time on population variability through their effect on population resilience.

## Consequences of increasing population variability

The growth of variance with time has important consequences for ecological theory and practice; for example, the assessment of extinction risk in natural populations. Intuitively, we would expect a population whose numbers fluctuate more over time to have a greater risk of extinction. This has been found in stochastic population models (e.g. Lande, 1993; Foley, 1994) and has been corroborated for birds (Pimm *et al.*, 1988), spiders (Schoener and Spiller, 1992) and other taxa. Others, however, have generated alternative predictions. Halley and Kunin (1999), for example, calculated a longer persistence time for non-stationary $1/f$-noise processes than for a white noise process and several observations have suggested a *decreasing* extinction risk with variability. The resolution of this apparent conflict requires an appreciation of the dual nature of the 'more time–more variation' effect. A non-regulated population may benefit by being able to wander to an arbitrarily high (and thus relatively invulnerable) value. This cannot happen in a strongly regulated population whose abundance is constrained within a relatively narrow band of values by density-dependent interactions. Thus, increasing variance does not necessarily imply a greater probability of extinction.

We made extensive use of the GPDD, which, to our knowledge, is the largest compilation of population-dynamic data available to ecologists, which made it possible to extend the taxonomic, geographic and ecological coverage of other studies (e.g. MacArdle *et al.*, 1990; Ariño and Pimm, 1995; Cyr, 1997). As it is hard to envision that much more long-term population abundance data will become available in the near future, it is unlikely that the broad features of our findings will be much altered because of new data. However, our analysis has been very broad and there is considerable scope and need for improved analysis. More attention should be paid to the spatial distribution of the populations and to the methods used to collect the data. The continued improvement of our understanding of spectral reddening should help ecologists to develop improved summary measures of population variability.

The increase of population variability with time shows that population variability is not a simple attribute that can be fully characterized by a single metric. This further highlights the shortcomings (discussed by Pimm, 1991; Gaston and MacArdle, 1994) of widely used metrics, such as the coefficient of variation or the standard deviation of the log-transformed population abundance, when comparing the variability of populations censused using different methods and over different time-scales. Clearly, such metrics need to be supplemented by measures that take account of the increase of population variability.

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