

# On the relation between temporal variability and persistence time in animal populations

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## Summary

1. The relationship between temporal variability, spectral redness and population persistence for a large number of long-term time series was investigated. Although both intuition and theory suggest that more variability in population abundance would mean greater probability of extinction, previous empirical support for this view has not been conclusive. Possible reasons are the shortage of long-term data and the difficulties of adequately characterizing temporal variability, two issues that are explicitly addressed in this paper.

2. We examined the relationship between population variability and quasi-extinction time (measured as the time required to observe a 90% decline of population abundance) for a large set of data comprising 554 populations for 123 species that were censused for more than 30 years. Two aspects of temporal variability were considered in relation with the quasi-extinction time: a baseline value (coefficient of variation over a fixed, 30-year, time scale), and a measure of the rate of increase of the population variability over time (spectral exponent).

3. The results show that the quasi-extinction time was shorter for populations having higher temporal variability and redder dynamics. The relation between persistence time and population variability was compared for different taxa, trophic levels, habitat type (aquatic and terrestrial) and body sizes and compared with theoretical expectations.

*Key-words:* autocorrelation, conservation, extinction, noise, spectral colour.

*Journal of Animal Ecology* (2003) **72**, 899–908

## Introduction

Is the probability of extinction greater for populations having higher temporal variability? Intuitively, for a given average abundance, one expects the risk of extinction to increase with temporal variability (Leigh 1981; Pimm, Jones & Diamond 1988; Pimm 1991; Lande 1993; Vucetich *et al.* 2000). Indeed, some studies use temporal variability as a direct proxy for population vulnerability (Fagan *et al.* 2001). A direct relation between extinction risk and population variability stems from the basic stochastic, density-independent model  $N_{t+1} = R_t * N_t$  where  $R_t$  is the stochastic linear population growth rate. The probability of extinction increases (and the time to extinction becomes smaller) as the average growth rate becomes smaller and the variance of the population growth rate becomes larger (Turelli 1978;

Ginzburg *et al.* 1982; Dennis, Munholland & Scott 1991). For numerous models, both continuous and discrete time (Lande 1993; Foley 1994; Halley & Iwasa 1999; Hakoyama & Iwasa 2000), it can be demonstrated that extinction risk increases with variability. Recently, Alvarez (2001) has shown that extinction risk increases with the level of stochasticity for a comprehensive class of density-dependent models, provided that the dynamics can be expressed as a stochastic diffusion. However, population variability measures calculated from time series data (Std log  $N$ , CV  $N$ ) are not the same as, and need not have a simple relation to, the parameters of stochastic population models incorporating environmental variability.

Long-term data from natural populations do not endorse the 'more variation, faster extinction' view so well. Pimm *et al.* (1988) attempted the first empirical corroboration of this view using data from birds from islands surrounding Britain. They found the expected relationship of 'more variation faster extinction' only after controlling for mean population size, body size and migratory status (see also Tracy & George 1992,

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Haila & Hanski 1993 and Diamond & Pimm 1993 for reanalysis and discussion of Pimm *et al.*'s data). Schoener & Spiller (1992) and Lima, Marquet & Jaksic (1996) came to the opposite conclusion to Pimm *et al.* (1988): population variability was positively related to the time to extinction (and hence negatively related to the probability of extinction) for orb-weaving in the Bahamas and for North American small mammals, respectively. Summarizing the evidence for a direct relation between population variability and extinction risk, Vucetich *et al.* (2000: 1707) remarked that 'of six published data sets used to test the predicted relationship between population variability and extinction risk, ... only one appears to offer unequivocal support'. Pimm (1993) conjectured that if highly variable populations are especially prone to extinction, then they might go extinct so quickly that population variability would be underestimated thus hindering the detection of the expected positive relation between population variability and extinction risk. Following Pimm's (1993) suggestion, Vucetich *et al.* (2000) advised restricting the analysis only to data sets showing low extinction risk to improve the chance of detecting the expected relationship. An analysis consisting of a large number of time series may be able to avoid this, as a relationship between persistence time and population variability would be easier to detect. This would bring two benefits. First, there would be no need to distinguish *a priori* which data sets were of 'low extinction risk'. Second, one would be able to avoid restricting the analysis to certain data sets, something that might be unduly restrictive and wasteful of long-term data and also a potential source of unquantified bias.

In this paper we argue that the reasons for the disparity between the expected relation and what has been found in data thus far, lies not only on the shortage of long-term population data, but also on the shortcomings of our theoretical expectations. The abundance of natural populations inevitably changes over time owing to environmental vagaries and to fluctuations in the strength of the links connecting species in food webs. The relative importance of environmental variability on population dynamics (Andrewartha & Birch 1954), as opposed to density dependence, has been the subject of a long and acrimonious debate among ecologists (Turchin 1999). Current ecological thinking about temporal variability includes a spectrum of stochastic models. At one pole of this spectrum is 'white noise', where year-to-year values of the variable are independent and variability entirely stationary: constrained within a well-defined 'basin of attraction' (e.g. Royama 1992; Turchin 1999). At the other end of the spectrum of stochastic models is the random walk or density-independent drift, for which the expected variance grows at a rate proportional to the length of the series (Ariño & Pimm 1995; Halley & Kunin 1999). The analysis of long-term data has shown that the temporal variability of animal populations increases with the length of the survey (Pimm & Redfearn 1988; Pimm 1991; Murdoch 1994;

Ariño & Pimm 1995; Cyr 1997; Inchausti & Halley 2001, 2002), though the rate is less than proportional to length. Thus real abundance data lie between the two poles. This 'more time, more variation effect' has been linked to a reddened spectrum in which small amplitude, short-term fluctuations variation are superimposed on ever larger, long-period variations. Longer time series expose to observation more of these larger-amplitude long-term fluctuations (Ariño & Pimm 1995; Halley 1996). The alternative origin of the 'more time, more variation' effect, uncorrelated population abundance with a 'heavy-tailed' probability form (Mandelbrot 1999), was found to be highly unlikely for ecological populations (Halley & Inchausti 2002). Our recent survey of long-term ecological data series (Inchausti & Halley 2001, 2002) shows that a large majority of long-term ecological series exhibit spectral reddening with an overall average spectral exponent value of  $\nu = 1.02$  (SE = 0.03,  $n = 544$ ), close to the value associated with  $1/f$  or pink noise (Halley 1996). The observed deceleration of the increase of this variability (Murdoch 1994; Cyr 1997) with the length of the time series need not imply convergence to a finite value.  $1/f$  noise, for example, is a process whose variance continues to grow slowly but indefinitely (logarithmically) with the length of the series observed (Keshner 1982). An immediate consequence of this fact is that population variability cannot be characterized by a single fixed quantity. Rather, traditional measures of population variability such as the coefficient of variation or the standard deviation of population abundance need be supplemented by a measure of spectral reddening that describes how population variability increases with time (Inchausti & Halley 2002).

Since it is very hard to collect data on populations that have gone (or will shortly go) extinct, an analysis of the relation between persistence time and temporal variability needs to use data from the extant populations. This is most easily accomplished by using 'quasi-extinction' time as a proxy for true extinction time (Ludwig 1999; Vucetich *et al.* 2000). In this paper, we examine the relation between population variability and quasi-extinction time in long-term population data, taking into consideration the spectral attributes of population variability. This analysis is carried out using the GPDD, one of the largest databases of population time series available to date. The findings are related to theoretical predictions about reddened population dynamics. The relation between persistence time and population variability was compared for different taxa, trophic levels, habitat type (aquatic and terrestrial) and body size.

## Methods

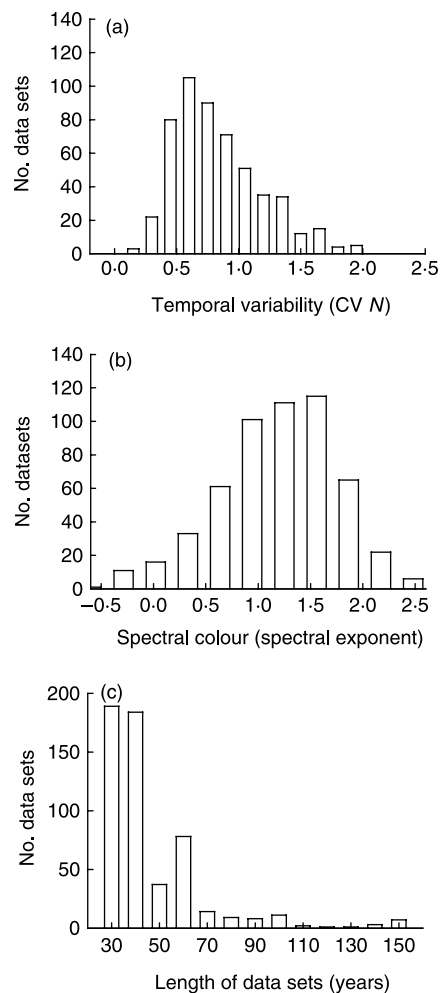
### SOURCES OF DATA

The Global Population Dynamics Database (GPDD; see Inchausti & Halley 2001) comprises over 4500 data

sets longer than 10 years (or generations) for more than 1800 species of animals and plants. Created by the Centre for Population Biology Imperial College (UK), and accessible at <http://cpbnts1.bio.ic.ac.uk/gpdd/>, the GPDD is one of the largest databases of its kind. Besides population counts, the GPDD contains auxiliary data such as the location and geographical coordinates where each population was counted, trophic level and body size (for birds and mammals). From the GPDD we extracted 544 data sets of 123 species that were annually censused or counted for more than 30 years (a complete list of taxa analysed in this paper is available upon request). The median length of the data sets was 46.5 years, while the longest contained series 157 observations (Fig. 1).

#### TEMPORAL VARIABILITY AND THE SPECTRAL COLOUR OF POPULATION DYNAMICS

The baseline temporal variability was characterized by the coefficient of variation of the abundance calculated



**Fig. 1.** Frequency distributions of (a) temporal variability (coefficient of variation calculated over 30 years), (b) spectral redness (spectral exponent, indicating the rate of increase of temporal variability) and (c) the length of the time series for the ensemble of the 544 long-term data sets analysed in this paper.

over the first 30 years of each time series. Besides describing the proportional temporal variability, the coefficient of variation of population abundance has the additional advantage of being dimensionless, thus allowing the comparison of the temporal variability of populations and species that were censused using different methodologies. By using a common time horizon to estimate population variability, one can separate the background value of temporal variability from the increase associated with its spectral colour, thereby allowing the comparison of the temporal variability of populations censused for different lengths of time (Inchausti & Halley 2002).

The spectral exponent is a measure that can be used to characterize the level of the reddening of ecological time series (Miramontes & Rohani 1998; Inchausti & Halley 2001, 2002). These exponents were estimated as (minus) the regression slope of the spectral power vs. the frequency (on a doubly logarithmic scale) obtained after carrying out a spectral analysis for each time series. When finding spectra, we first log-transformed the data as in Inchausti & Halley (2002). A spectral analysis of a time series is essentially a decomposition of its total variation in terms of the percentage explained by the harmonic frequencies defined in  $[1/n, 1/2]$  where  $n$  is the time series length (Diggle 1990). We can relate these spectral exponents to the rate of increase of temporal variability: the larger the spectral exponent, the faster the increase of population variability with the length of the time series (Inchausti & Halley 2001, 2002).

#### POPULATION PERSISTENCE: ESTIMATION AND ANALYSES

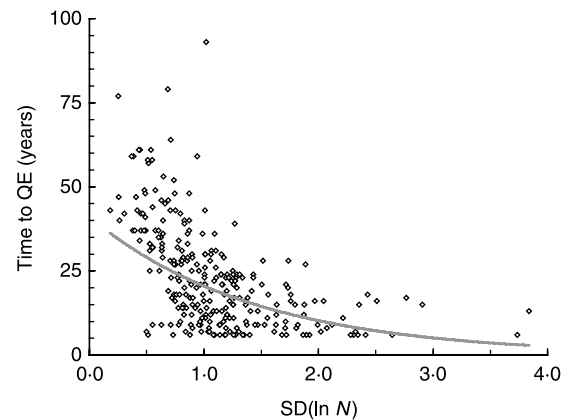
Assessing the degree of threat faced by a population involves estimating the probability that a population experiences a partial or total loss (i.e. the risk of quasi-extinction) over a given time horizon. We characterized population persistence for each of the 544 time series as the Time to Quasi-Extinction (TQE), estimated as the number of years for population abundance to exhibit a 90% decline of its initial abundance. Viewing population extinction as an extreme case of a population decline (quasi-extinction) allows us to focus on three different aspects of a population decline: its probability (or quasi-extinction risk; Ginzburg *et al.* 1982), the time to quasi-extinction (number of years to observe the decline) and the magnitude of the decline (Akçakaya 1991). We chose to focus on the time to observe a 90% decline from the initial abundance, based on the ease of estimating a biologically relevant component of population decline that has direct conservation implications. Focusing on the TQE, as a measure of the degree of threat, has three main advantages. Firstly, studying quasi-extinction time allows comparison of extremely heterogeneous population data. The abundance data comprising the GPDD are expressed on different scales, have been obtained in a large variety of ways, and cover different geographical ranges. It would be very difficult to express such

abundances on an absolute or even a common scale, but through TQE (a measure of *relative* population decline) comparison is possible and meaningful. Secondly, since quasi-extinction is a more frequent occurrence than true extinction, it is possible to make use of a greater body of existing data. Thirdly, assessing the time to quasi-extinction may be more useful in the context of conservation (Burgman, Ferson & Akcakaya 1993; Beissinger & McCullough 2002; Reed *et al.* 2002) because by highlighting the occurrence of a large decline rather than an actual extinction, it can motivate precautionary measures.

Of course there are two provisos. First, precisely because TQE is defined as a proportion of abundance, it means that effects depending on absolute numbers are ignored. For example, demographic stochasticity, which can play an important role in extinction, plays no role in the estimation of quasi-extinction. Second, initial values can cause problems. What if the population is at an extreme value when recording is started? A consequent TQE event (or the absence thereof) might be more a reflection on the initial value than on the true risk. We considered this possible problem in a test analysis, in which we analysed the same data but discounted all 90% declines that occurred within the first 5 years of the census. Since the results of this analysis did not differ significantly from those obtained without this constraint, we chose to carry out the analysis, and discuss the results, for the entire data rather than to introduce arbitrary choices of the length of the initial censoring.

Population persistence was related to the temporal variability and the spectral colour of the population dynamics using Cox proportional hazards (Kleinbaum 1993; see Muenchow 1986 and Fox 2001 for some ecological applications). This is a non-parametric regression method that analyses the effect of independent variables on the hazard or 'conditional failure rate' which indicates the potential that population abundance will suffer a 90% decline during a small time interval given that it has not declined before (Kleinbaum 1993). The term 'proportional' in the name of the method reflects that the effect of the independent variables at each time step acts multiplicatively on an unknown, common baseline hazard rate that is assumed to be identical for all individuals (see Kleinbaum 1993 for details). We favoured the Cox proportional hazards regression over traditional least-squares regression approaches (Fig. 2) because Cox proportional hazards correctly accounts for censored observations (i.e. those populations that did not show a 90% decline from the initial abundance during the length of the census) without any loss of information (Kleinbaum 1993; Fox 2001).

We analysed the relations between population persistence and temporal variability and spectral colour of the population dynamics at various levels besides that of the ensemble of the 544 data sets using SPSS 9.0 (SPSS 1998). These analyses were carried out for the entire data set as well as for individual taxa (Mammalia, Aves, Osteichthyes, Insecta), trophic levels (herbivores,

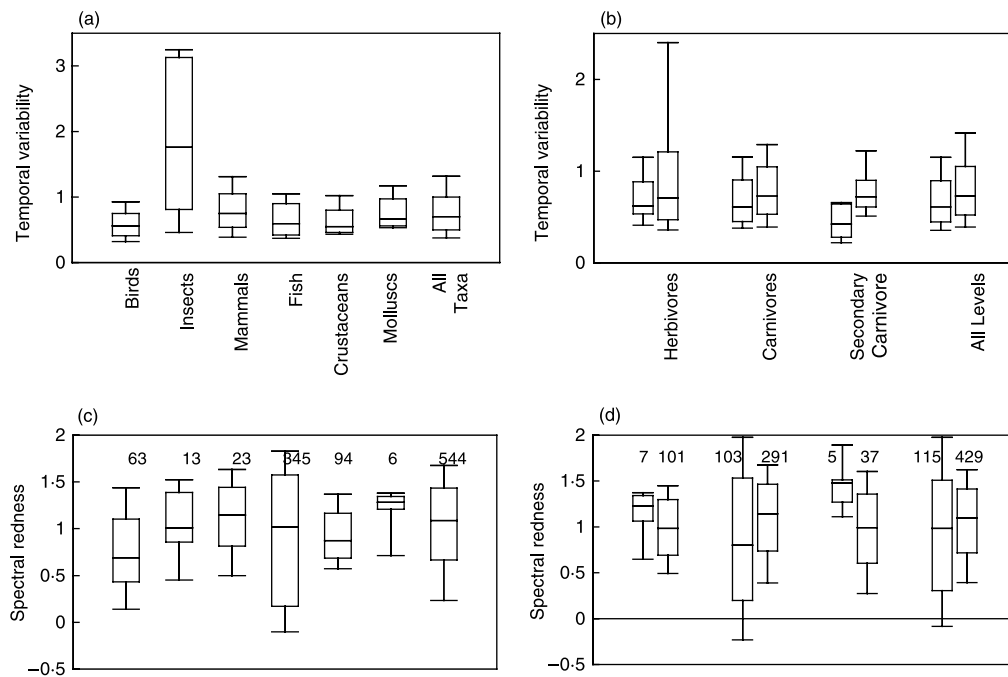


**Fig. 2.** The time to quasi-extinction (TQE; defined as a 90% decline from the initial population abundance) plotted as a function of variability (standard deviation of  $\log N$ ) for the 273 populations that suffered TQE. The exponential curve was obtained by finding the least squares regression of  $\log(TQE)$  against  $SD(\log N)$ . While the pattern suggests that more variability means earlier extinction, this alone does not suffice to prove the hypothesis since the interpretation does not properly account for censored observations (series which did not suffer TQE) because the series which make up the database have different lengths.

carnivores, secondary carnivores), and type of habitat (terrestrial or aquatic). The main outcomes of the Cox proportional hazards analyses are the partial slopes indicating the effects of the covariates (population variability and spectral colour in our case) and the estimated survival curves (or, equivalently, the hazard ratios) that denote the differences between groups (for instance, aquatic vs. terrestrial). It is important to point out that a positive partial slope indicates that a covariate increases the hazard rate (also called 'conditional failure rate' or 'force of mortality'; Kleinbaum 1993; which we will here refer to as the *quasi-extinction rate*), thereby decreasing the failure time (or time to quasi-extinction in our case). The partial slopes relating the temporal variability and the spectral colour of population dynamics with the hazard rate were compared among groups by verifying the overlap of the 95% confidence intervals of the partial slopes of each covariate that were estimated in separate analyses for each taxa, trophic level and habitat. The statistical significance of all Cox proportional hazards analyses was determined by the log-likelihood test and that of partial slopes using Wald statistics (Kleinbaum 1993).

## Results

The estimates of temporal variability of the ensemble of time series had an asymmetric distribution ranging between 0.073 and 4.212 with a median of 0.720 whereas those of spectral exponents had reasonably symmetric distribution clustered in the range 0–2 with a average value of 1.02 close to the value for pink noise (Fig. 1). Our previous analyses (Inchausti & Halley 2001, 2002) showed that the temporal variability of animal



**Fig. 3.** Box plots (showing 10th, 25th, median, 75th and 90th percentiles) of the temporal variability (measured as the coefficient of variation of population abundance over 30 years) and the spectral exponent (indicating the rate of increase of population variability) for main taxa (plots a and c) trophic level and habitat type (aquatic and terrestrial). The number of data sets for each group is indicated in the two bottom panels. For each trophic level, the left-hand side boxes correspond to aquatic populations, and the right-hand side boxes to terrestrial populations.

populations did not significantly differ among taxa, trophic levels or habitat type (Fig. 3). By contrast, there were significant differences among populations of different trophic levels depending on the habitat type (aquatic, terrestrial) (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 (Inchausti & Halley 2002).

The quasi-extinction rate associated with a 90% decline increased with population variability and spectral redness for the ensemble of the 544 data sets (Table 1). In other words, the persistence time of animal populations decreased both with temporal variability and with reddening of their dynamics. The comparison of partial slopes of the temporal variability of population dynamics showed only that the slopes of mammalian populations were significantly smaller than that of avian populations, and that the slopes for aquatic populations were significantly larger than those of terrestrial populations. Thus, for the same value of population variability, the quasi-extinction (hazard) rate of avian and aquatic populations was larger (and the persistence time shorter) than those of mammalian and terrestrial populations, respectively (Table 1; Fig. 4). Body mass had a significant interaction with spectral redness in determining the quasi-extinction rate of a population (Table 2). Dividing the ensemble of avian and mammalian populations into small- (less than 1.0 kg and thus likely to have a generation time shorter than a year) and large-bodied taxa (more than 1.0 kg) showed that the magnitude of the partial slope of spectral redness changed

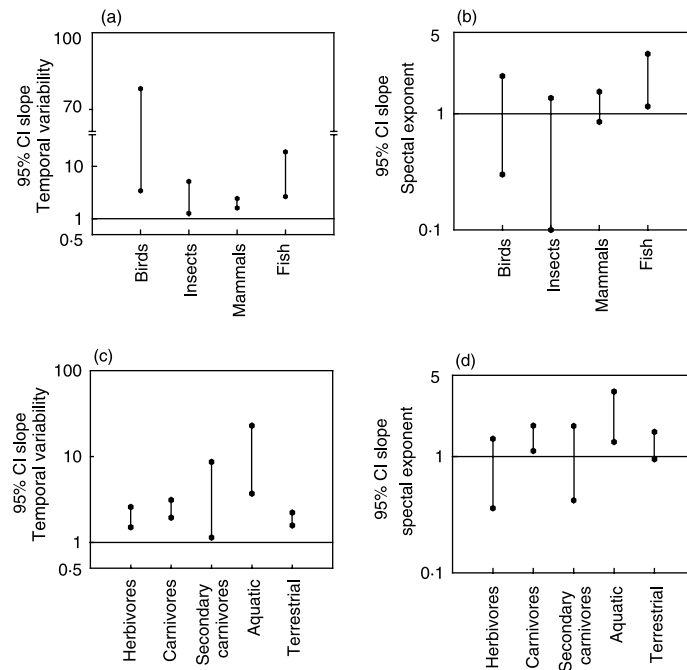
depending on the body size (Table 2). Population variability was significantly and positively related with the quasi-extinction rate regardless of body size and hence persistence time decreased with population variability and spectral redness, though at different rates for small- and large-bodied taxa (Table 2). Figure 5 shows the different survival curves estimated separately for the main taxa, trophic level and habitat type, and body mass type (small- and large-bodied taxa). 'Survival' in this context refers to the probability that a population will suffer a 90% decrease relative to initial abundance *later than* a given year, i.e. the higher the curve, the longer the persistence time of a population. These curves provide a graphical illustration of the decrease of the persistence time of aquatic–terrestrial populations (Fig. 5c) and according to body size (Fig. 5d) due to spectral reddening.

## Discussion

Our results reproduce the behaviour expected both by intuition and by a large number of models: increasing variability also increases extinction rate. We find that the expected relationship between population persistence and temporal variability is borne out by long-term population data without recourse to trimming or preselection of data (cf. Pimm 1993; Vucetich *et al.* 2000). Our results also illustrate the difficulties encountered by previous attempts to secure this result with field data. Given that our study uses a significantly larger sample of long-term data sets, these results confirm previous

**Table 1.** Results of the Cox proportional hazards analyses for the main taxa, trophic level and habitat type. Censored data sets are those populations whose abundance did not show a 90% decline from their initial abundances before the end of the census period. Positive slopes indicate that the hazard rate of quasi-extinction increases (and the expected time to quasi-extinction declines) as population variability increases faster or as population dynamics becomes redder (i.e. as the spectral exponent attains larger values)

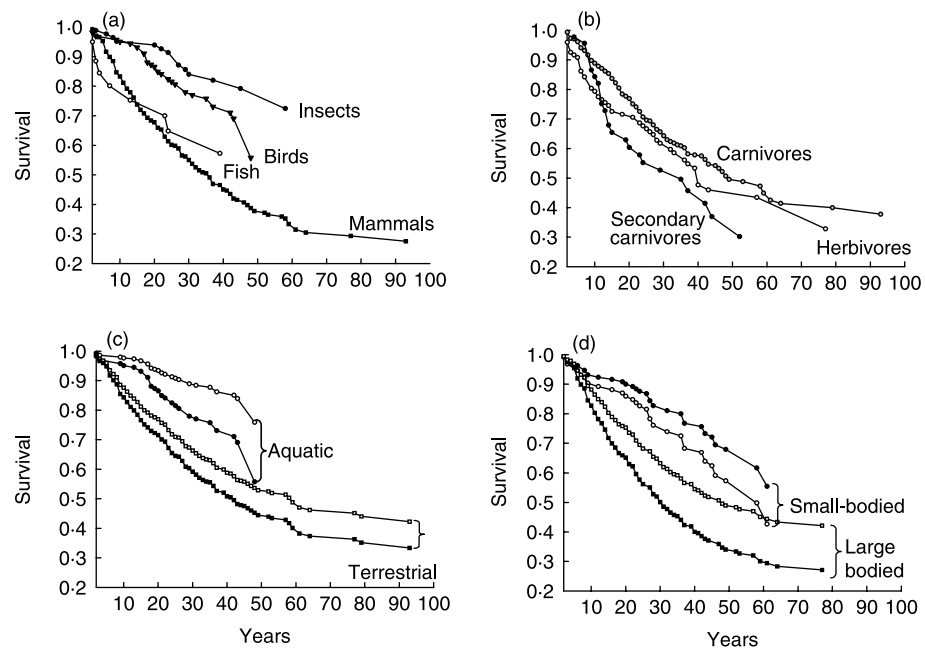
	Variable	Slope	SE	Probability	No. data sets (% censored)
<b>Taxa</b>					
Birds	Temporal variability	2.819	0.810	0.005	63 (74.6%)
	Spectral redness	-0.223	0.494	0.652	
Insects	Temporal variability	0.939	0.353	0.008	23 (56.6%)
	Spectral redness	-0.981	0.657	0.135	
Mammals	Temporal variability	0.683	0.106	<0.0001	345 (38.1%)
	Spectral redness	0.133	0.152	0.3792	
Fish	Temporal variability	1.956	0.498	<0.0001	94 (67.0%)
	Spectral redness	0.659	0.265	0.013	
All	Temporal variability	0.694	0.080	<0.0001	544 (48.9%)
	Spectral redness	0.274	0.111	0.001	
<b>Trophic level</b>					
Herbivores	Temporal variability	0.675	0.139	<0.0001	108 (49.1%)
	Spectral redness	-0.327	0.348	0.347	
Carnivores	Temporal variability	0.899	0.121	<0.0001	394 (50.0%)
	Spectral redness	0.366	0.125	0.004	
Secondary carnivores	Temporal variability	1.148	0.515	0.026	42 (38.1%)
	Spectral redness	-0.131	0.375	0.728	
<b>Habitat type</b>					
Aquatic	Temporal variability	2.217	0.464	<0.0001	115 (67.8%)
	Spectral redness	0.787	0.255	0.002	
Terrestrial	Temporal variability	0.624	0.089	<0.0001	429 (43.8%)
	Spectral redness	0.219	0.138	0.113	



**Fig. 4.** Upper and lower limits of the 95% confidence intervals for the partial slopes of temporal variability and spectral exponent on the time to quasi-extinction (defined as the 90% decline from the initial abundance) for the main taxa, trophic levels and habitat type. The partial slopes for each taxa, trophic level and habitat type were separately estimated. The logarithmic scale of the ordinate is due to the assumption of a log-linear relationship between the independent variables and the hazard function in the Cox proportional hazards model. The horizontal line at  $y = 1$  corresponds to a partial slope of zero in the Cox proportional hazards model. The overlap of the confidence intervals indicates that the slopes of two groups are not statistically different from each other.

**Table 2.** Results of the Cox proportional hazards regression for body mass, temporal variability and spectral redness. The initial regression equation including all single variables, first- and second-order effects was simplified using the forward stepwise approach. Based on the significant interactions between body mass and spectral redness, the populations were partitioned into small-bodied (smaller than 1.0 kg and likely to have a generation time shorter than 1 year) and large-bodied taxa. The interpretation of censored data and of the partial slopes is explained in the legend of Table 1

Variable	Slope	SE	Probability	No. data sets (% censored)
Temporal variability	2.563	0.409	<0.001	408 (43.1%)
Spectral redness	1.112	0.322	0.006	
Temporal variability * Spectral redness	-1.349	0.313	<0.001	
Spectral redness * Body mass	0.180	0.034	<0.001	
<b>Small-bodied taxa</b>				
Temporal variability	5.667	1.183	<0.001	118 (66.1%)
Spectral redness	2.399	0.811	0.003	
Temporal variability * Spectral redness	-3.985	1.038	<0.001	
<b>Large-bodied taxa</b>				
Temporal variability	2.010	0.544	0.002	290 (33.8%)
Spectral redness	1.181	0.445	0.032	
Temporal variability * Spectral redness	-0.943	0.412	0.022	

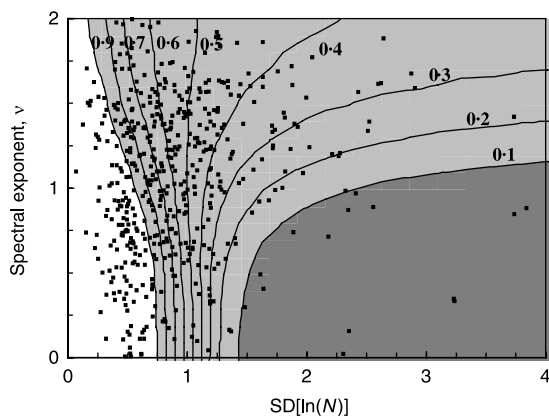


**Fig. 5.** Survival curves for each main taxa, trophic level and habitat type calculated at the means of temporal variability and spectral exponent calculated using Cox proportional hazards (see main text for details). 'Survival' at a specified year in this context denotes the probability that a population will suffer a 90% decrease relative to initial abundance *later than* that year. The length of each curve only reflects of the maximum length of the data sets of each group. The survival curves are evaluated at the average value of population variability and spectral exponent for each group unless stated otherwise. Symbols in (c): circles denote aquatic and squares terrestrial populations; curves evaluated at either the average spectral exponent (filled symbols) or spectral exponents equal to zero which corresponds to white noise (open symbols). Symbols in (d): circles and squares denote small- (less than 1 kg) and large-bodied (more than 1 kg) taxa; colours as in (c).

arguments (e.g. Schoener & Spiller 1992; Lima *et al.* 1996; reviews in Pimm 1991 and Vucetich *et al.* 2000) that the difficulties in demonstrating the expected negative relation between population persistence time and temporal variability stemmed from the absence of long-term data. The same generic result was found for all taxonomic groups, trophic levels and habitat types. Quasi-extinction time and temporal variability were

significantly and negatively related for all main taxa, trophic levels and habitat types: the larger the temporal variability, the shorter the time to quasi-extinction.

The observed quasi-extinction time is significantly affected by spectral redness, but not so much as it is by the temporal variability. In most cases when the spectral exponents were significantly related to quasi-extinction rate, the partial slope had a positive sign,



**Fig. 6.** Contour map of persistence as a function of overall variability and spectral redness based on the methods in Halley & Kunin (1999), assuming fluctuations are from the  $1/f$  noise family. This contour map was drawn by carrying out 10 000 simulations and estimating persistence at 53 years (the average length of the time series in our data set) over a range of values of overall variability (SD of  $\log(N_t)$ ) and redness (spectral exponent,  $v$ ). The levels of persistence probability (one minus quasi-extinction probability) are shown on the right of each contour. Superimposed on this map are the corresponding values found for each of the series in the data set analysed. Note that relatively few points lie in the region on the right of the graph, where increasing redness plays a strong and beneficial role.

revealing a generally detrimental effect of spectral reddening on population persistence, a feature that, to our knowledge, has never been shown with actual population dynamics data. From theoretical considerations, we expect the relationship between redness and persistence to be complex (Halley & Kunin 1999; Morales 1999) even before population dynamics are considered (Ripa & Lundberg 1996; Heino, Ripa & Kaitala 2000; Fagan *et al.* 2001). Spectral reddening causes populations to linger at low densities for longer periods of time, exposing them to extinction by demographic and other low-density effects. Also, because of the more time, more variation effect, the longer we wait, the higher the probability of a really big catastrophe. Hence, spectral redness may be considered detrimental to persistence. On the other hand, highly reddened variability might allow populations to escape from the 'danger zone' of low abundance faster than those that have smaller variability and/or whiter dynamics (Halley & Kunin 1999). Figure 6 shows how both of these features may be exhibited, depending on the variability and redness of the abundance fluctuations. The contour map in Fig. 6, shows expected persistence based on the methods described in Halley & Kunin (1999). According to this picture, we expect extinction probability to depend not only on temporal variability of population size in a given time frame but also upon spectral redness. The contour map shows that *for any given level of spectral redness*, increasing temporal variability increases the extinction risk. Also, for small variability, increasing redness is mostly detrimental while at large variability

increasing redness increases the chance of persistence. However, population persistence is significantly affected by spectral reddening only for deeply reddened fluctuations (spectral exponent  $\geq 1.5$ ). For data series showing low spectral redness (spectral exponent  $\leq 1.0$ ), temporal variability largely determines the probability of persistence. Figure 6 also shows the distribution of observed values of variability and redness. Although the expected persistence given by contours is very approximate, since the contours are based only on the *average* length of series and assume the  $1/f$  model of variability, this model does help us understand why the role of redness is not so important, and why it is mostly detrimental. For most of the series, the value of standard deviation (SD) [ $\log(N_t)$ ] lies between 0.25 and 1.25. In this range increasing redness is always detrimental, but relatively small. Thus the size and direction of the redness upon quasi-extinction are what we would expect from theoretical expectations. These results raise interesting questions. For example, in calculating both Table 1 and Fig. 6 the forecast has an average depth of 53 years, while variability (CV or SD  $\log(N_t)$ ) was calculated over 30 years. According to theory, if the average depth of the forecast greatly exceeds that of the length of the series used to calculate CV or SD  $\log(N_t)$ , then the relative importance of reddening should increase, because of the more time, more variation effect. These are the subjects of further and more detailed research.

We found that the relationship between spectral reddening and persistence time substantially changed with body size. In particular, we found that the persistence time of populations of small-bodied taxa is negatively related with spectral reddening, while the opposite trend was found for large-bodied species. Various arguments can be made for such relationships. The wealth of allometric relationships among body mass and life-history traits (Peters 1983; Calder 1984) suggests that some scaling relationship should also exist between body mass and population persistence. However, with so many body-size related effects on population variability (Pimm 1991; Lawton 1995) the relationship is likely to be a complex one. For example, the longevity and long generation times and low growth rate of large-bodied species (Peters 1983; Calder 1984) induce an inertial effect at the time scale of generations which induces spectral reddening in time series of population abundance. By contrast, this buffering effect and spectral reddening will be absent for small-bodied species, which have short generation times, reduced longevity and high per-capita growth rate. It would be interesting to isolate the amount of reddening that is due to this mechanism, that is the reddening due entirely to age-structure. This also is an important subject for further investigation.

An interesting feature of the results is a strong difference in the effect, depending on the habitat type. The relationship between quasi-extinction rate and both measures of variability is almost four times stronger for aquatic time series than it is for terrestrial populations. 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'). According to Steele's (1985) ideas, since marine environmental variation is redder than terrestrial variation, marine taxa should have redder spectra. More recent analyses (Pelletier 1997, 2001) have shown that the spectra of rainfall and temperature at time scales relevant for describing population dynamics (over both land and sea) are reddened with exponents of about 0.5. However, animal populations do not necessarily follow patterns of environmental forcing. For example, terrestrial populations have redder dynamics than aquatic ones (Fig. 3; Inchausti & Halley 2002), exactly the opposite of the pattern predicted by Steele (1985) and, with spectral exponents in the range 0.8 and 1.2 (Fig. 3), are considerably more reddened than Pelletier's models and analyses. However, none of these mechanisms can explain the existence of such a large differential sensitivity of persistence time to variability and its degree of reddening.

A possible reason for this may be that the GPDD is not a random sample of species. Moreover, the species in the GPDD are not pure ecological series. Many political, economic and historic factors affect both the presence of the species in the database and also the manner in which the data have been collected. Besides their intrinsic economic or aesthetic value, it is possible that ecologists have followed such populations for long time-spans precisely because they are not prone to local extinction. This is particularly true for time series associated with fisheries, which constitute a large portion of the aquatic data sets, and for which social and economic factors will play a major role. Thus, it is possible that some of the associations we have found may be prone to influence by factors other than ecological processes. A careful reanalysis of the GPDD, controlling for these factors, may throw more light on this issue.

This leads us to more general issues of the quality of the data in the GPDD more generally. Ideally, we would like all time series to be measured using standardized methods, scales, coverage and sampling effort. Since this is not possible, it is necessary to harmonize the various series using statistical tools to construct scale-free metrics and statistical tests. Moreover, obtaining estimates of average and standard deviation of the per capita population growth rate from time series data relies on the approximation that the former can be estimated as the finite difference between consecutive time series values that are monotonically related with population abundance. The Cox proportional hazard method, which we have used, is one such approach that avoids problems of scales and units, by confining itself to a relative drop of 90% as a quasi-extinction threshold. The criterion of quasi-extinction as used in this paper is not a perfect proxy for true extinction, since being a relative number, it ignores a number of important aspects of extinction, such as the role of demographic stochasti-

city, Allee effects and other things associated with low absolute numbers. For example, it is obvious that 10% of  $10^6$  is very much greater than 10% of  $10^3$ . Another limitation of the Cox proportional hazard analysis is that it does not yield a functional form that can be used to predict the persistence time, since the method is non-parametric and can only compute the hazard relative to unknown baseline value (Kleinbaum 1993). Thus, the Cox proportional hazard method should only be used to assess the effect of ecological covariates on population persistence in a comparative sense, and not in the assessment of the absolute degree of endangerment. It is important to point out that our analyses reflect relations between population persistence, temporal variability and spectral redness of the past trajectories of a variety of animal populations. It is important to point out that the 'more variability, faster extinction' view assumes that, other things being equal (which they are not), more variability should lead to faster and more likely extinction. Although trivial at first sight, there is no simple way of comparing the average or initial abundances for the ensemble of the data sets here analysed because of the many scales and methods used in the estimation of population abundance in different taxa and environments.

In conclusion, our analyses of the relationship between population persistence and temporal variability, one of the largest such surveys to date, strongly support both model predictions and intuition: increased variability means increased probability of extinction. This was true of all the taxonomic, trophic and habitat subgroups we examined. We have also shown, for the first time, that reddening affects the rate of quasi-extinction, and thus in all likelihood the rate of extinction itself. The size and direction of this effect are what we would expect from theoretical expectations. The study also raises interesting questions that can be illuminated by further and more specific analyses of the GPDD and other data sets.

### Acknowledgements

We thank the support of a TMR Marie Curie Fellowship from the European Commission to P.I. during the early stages of this research.

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Received 5 February 2003; revision received 23 April 2003