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Extinction risk, coloured noise and the scaling of variance

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Abstract

The impact of temporally correlated fluctuating environments (coloured noise) on the extinction risk of populations has become a main focus in theoretical population ecology. In this study we particularly focus on the extinction risk in strongly correlated environments. Here, we found that, in contrast to moderate auto-correlation, the extinction risk was highly dependent on the process of noise generation, in particular on the method of variance scaling. Such scaling is commonly applied to avoid variance-driven biases when comparing the extinction risk under white and coloured noise. We show that for strong auto-correlation often-used scaling techniques lead to a high variability in the variances of the resulting time series and thus to deviations in the subsequent extinction risk. Therefore, we present an alternative scaling method that always delivers the target variance, even in the case of strong auto-correlation. In contrast to earlier techniques, our very intuitive method is not bound to auto-regressive processes but can be applied to all types of coloured noises. We strongly recommend our method to generate time series when the target of interest is the effect of noise colour on extinction risk not obscured by any variance effects.

Keywords: Environmental noise; Noise colour; Auto-correlation; Population dynamics; Extinction risk; Variance scaling

1. Introduction

Research into theoretical population ecology has focused on factors impacting populations' performance and hence their extinction risk. On the one hand, these factors include all the parameters characteristic to the system (e.g. birth rate, mortality, intra-specific competition, carrying capacity) yielding the population's growth rate and competition mode. On the other hand, these factors are subject to variations in time—often-called noise—occurring as demographic noise (intrinsic to the population) and environmental noise (extrinsic to the population). While demographic noise is regarded as temporally uncorrelated (white noise), environmental noise is known to be often auto-correlated to various degrees (Steele, 1985; Pimm and Redfearn, 1988; Lande, 1993; Halley, 1996).

There are at least four descriptive attributes of time series of environmental noise affecting corresponding population dynamics: (1) the mean, (2) variance, (3) the frequency distribution of values and (4) noise colour, i.e. temporal auto-correlation. The effects of the first two attributes, the mean and variance, have been studied extensively during the past (e.g. Goel and Richter-Dyn, 1974; Roughgarden, 1975; Tuljapurkar, 1989; Lande, 1993; Foley, 1994; Wissel et al., 1994). The third attribute, frequency distribution, remains insufficiently studied and has not been primarily addressed by any publications. Recent research has focused on the fourth

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attribute, i.e. the colour of environmental noise, and complex relationships have been found between noise colour, underlying population dynamics and extinction risk by several authors (Roughgarden, 1975; Ripa and Lundberg, 1996; Johst and Wissel, 1997; Petchey et al., 1997; Kaitala et al., 1997a, b; Heino, 1998; Halley and Kunin, 1999; Cuddington and Yodzis, 1999; Ripa and Heino, 1999; Ripa and Lundberg, 2000). All these studies emphasized the importance of considering the colour of environmental noise in studies of population dynamics and extinction risk.

In this paper we investigate the effects of temporally correlated fluctuating environments on population dynamics. While auto-correlation has been found to cause severe effects on the dynamics and extinction risk of populations (e.g. Ripa and Lundberg, 1996), the noise generating process is particularly important when studying the effects of strong auto-correlation (Heino et al., 2000). Cuddington and Yodzis (1999) investigated the effects on population dynamics where underlying environmental noise is best described as $1/f^b$ noises. However, results of these authors may not apply when the underlying environmental noise can be better described by auto-regressive processes. Such auto-regressive processes have been frequently used to study population dynamics and extinctions risk in fluctuating environments (Ripa and Lundberg, 1996; Johst and Wissel, 1997; Petchey et al., 1997, 2000; Kaitala et al., 1997a, b; Heino, 1998; Ripa and Heino, 1999; Ripa and Lundberg, 2000; Wichmann et al., 2003a, b).

Therefore, we study the impact of auto-regressive environmental noise on population dynamics and the resulting extinction risk. We compare various procedures to generate coloured noise putting emphasis on highly auto-correlated environments. Here, we evidence the impact of the noise generating process on the estimated extinction risk and the according biological implications. In particular, we reveal that, depending on the method of scaling the variance, differences in the subsequent extinction risk arise. We then propose an alternative method of generating coloured noise with specific target variance. This method is very simple to handle when assessing extinction risk. It is particularly appropriate for the generation of strongly correlated noise of any type.

2. Extinction risk in auto-correlated environments

2.1. Background

Populations are always under the influence of noisy environments. Such environmental noise has important effects on population dynamics as it has long been recognised by ecologists. In particular, it is common knowledge that deterministically growing populations can be driven to extinction by environmental noise. In general, the actual risk of population extinction is increasing with the strength of environmental noise. This has been studied by numerous authors (Goel and Richter-Dyn, 1974; Roughgarden, 1975; May and Oster, 1976; Mode and Jacobsen, 1987; Tuljapurkar, 1989; Lande, 1993; Morales, 1999).

Usually, in these studies non-correlated noise has been used. However, in practice environmental noise is auto-correlated, i.e. coloured (Steele, 1985; Lawton, 1988; Pimm and Redfearn, 1988; Halley, 1996). Hence, the danger of using white noise instead of red noise for projections of extinction risk has been highlighted (e.g. Morales, 1999). Consequently, the issue of calculating the extinction risk in auto-correlated environments has been targeted by numerous earlier studies. However, while some of these studies suggest decreased extinction risk in coloured environments (e.g. Ripa and Lundberg, 1996; Heino et al., 2000) other studies found increased extinction risk (e.g. Mode and Jacobsen, 1987; Foley, 1994; Johst and Wissel, 1997; Wichmann et al., 2003b). Cuddington and Yodzis (1999), as well as Morales (1999) suggest that these contradicting results might be driven by different structures of the noise generation process.

Therefore, in this section we compare the extinction risk in auto-correlated environments for various types of the generating auto-regressive process (AR_1). In a later section the technical differences and biological appropriateness among these types of generation are discussed in more detail and we finally recommend a practical alternative.

2.2. Methods to calculate the extinction risk

For all calculations of extinction risk, we use a well-known model of population dynamics, the Maynard Smith-Slatkin model (Maynard Smith and Slatkin, 1973; May and Oster, 1976; Bellows, 1981):

$$N_{t+1} = N_t \frac{R}{1 + (R-1)\left(N_t/K_t\right)^b}, \tag{1}$$

where N describes the population size at time steps t and $t+1$, respectively; R the growth rate, K_t the carrying capacity at time step t and b is a competition parameter controlling the dynamic behaviour of the model (compare Petchey et al., 1997). We chose this model since it was found to be particularly flexible, broadly applicable and well capable to describe a wide range of data (Bellows, 1981).

We studied the extinction risk for short time scales of 50 time steps and longer time scales of 1000 time steps. For our simulations we chose a parameter set of $K_{\text{mean}} = 100, R = 4.5$ and $b = 1.0$. Demographic noise was included by letting N_{t+1} be an integer number Z_t

drawn from a Poisson distribution with the deterministic expectation for N_{t+1} as its mean, i.e. $N_{t+1} = Z_t(N_{t+1})$ (Petchey et al., 1997). Environmental noise was generated according to the temporally correlated fluctuating quantity, Φ_t, with

$$\Phi_{t+1} = \alpha\Phi_t + \beta\varepsilon_{t+1}, \tag{2}$$

where, ε_t is a random number drawn from a normal distribution with unit variance and zero mean, β the scaling parameter that sets the overall variance of the time series and the initial value is arbitrarily set to zero, $\Phi_0 = 0$. Note, that auto-correlation coefficient $\alpha > 0$ corresponds to positive temporal correlations ("red noise"). We varied α in steps of 0.05 between 0.00 and 0.95 but we also studied $\alpha = 0.99$. Standard deviation σ was also varied ($\sigma = 25; 30; 35; 40; 45$) using the factor β in Eq. (2). The variance, σ^2, was then rescaled according to different approaches resulting in various guises of the AR_1 process.

According to the length of population time series we used two different commonly applied approaches of variance rescaling. When generating long time series for 1000 population time steps (Fig. 1a) we followed Ripa and Lundberg (1996) (compare Eq. (4) below) but for short time series of 50 time steps we rescaled variances according to Heino et al. (2000) (compare Eq. (5) below). For both, short and long time series, we also used an alternative approach of variance correction, which will be presented in detail in the technical section of this paper (Eq. (6) below).

The resulting time series of environmental noise had an additive effect on the mean carrying capacity K, i.e. $K_t = K_{\text{mean}} + \Phi_t$. In the case of $K_t < 0$ we set $K_t = 0$ in order to avoid artificially negative values for carrying capacity. The rules of this model are very close to those

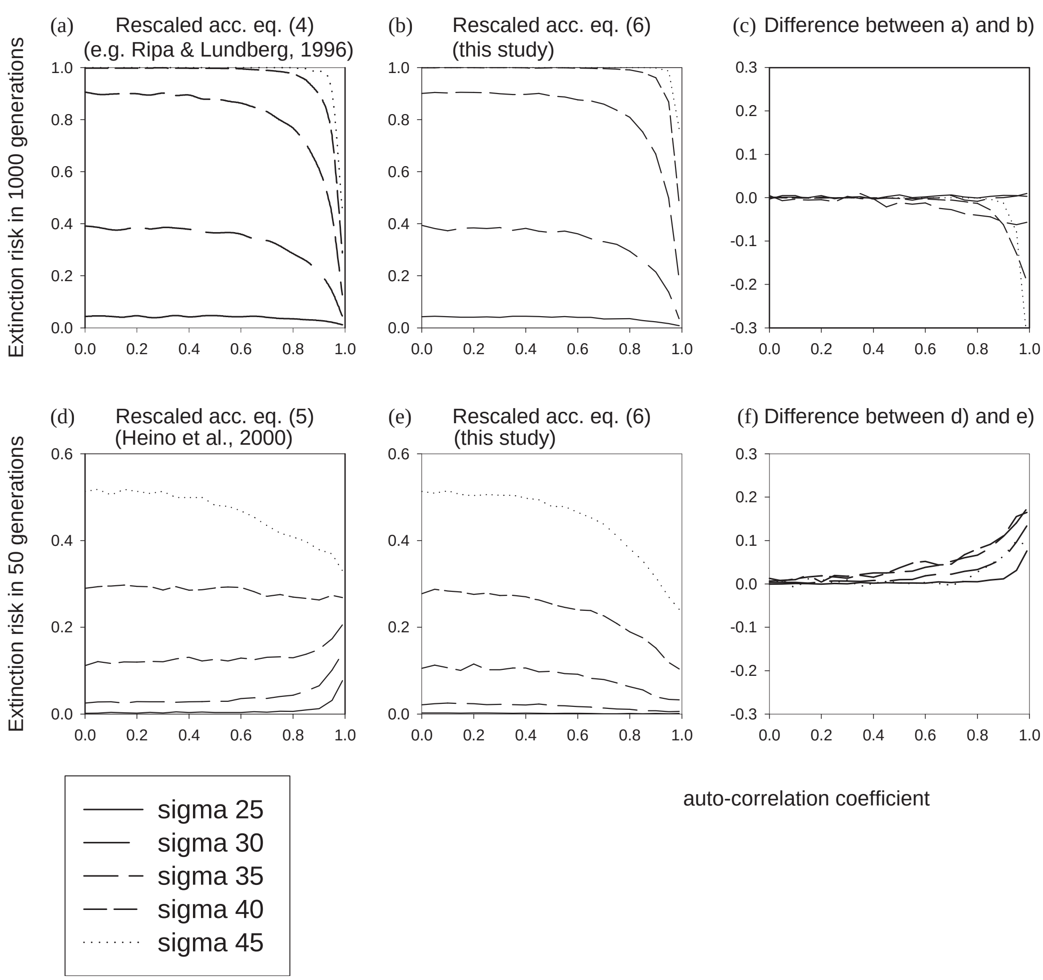


Fig. 1. Extinction risk is plotted versus auto-correlation coefficient α (bottom axis) when coloured noise, Φ_t, has been created by various techniques. Extinction risks were assessed on two different time scales: after 1000 time steps (a–c) and after 50 time steps (d–f). The results are compared for different methods of rescaling the variance in dyed time series: the commonly used methods (a, d) and the method to be introduced in this study (b, e). Additionally, the absolute differences between the resulting extinction risks of the compared approaches (a–b and d–e, respectively) are shown (c, f). Various line styles represent varying standard deviation from $\sigma = 25$ (solid line) to $\sigma = 45$ (dotted line).

of earlier investigations which used the Ricker equation instead of the Maynard Smith–Slatkin model (Ripa and Lundberg, 1996; Petchey et al., 1997; Cuddington and Yodzis, 1999; Heino et al., 2000).

2.3. Results on extinction risk

With our calculations of extinction risk we were able to reproduce the results of earlier studies when using conventional scaling methods (Ripa and Lundberg, 1996 and Heino et al., 2000; for example, compare Fig. 1a and d, with Fig. 4c and 3b in Heino et al., 2000, respectively). This agreement underlines that the deviations in extinction risk highlighted in Figs. 1c and f are due to different rescaling techniques but not to the usage of deviating models of population dynamics.

Fig. 1 shows the calculated extinction risks for commonly applied rescaling methods (Figs. 1a and d) and an alternative method presented here (Figs. 1b and e) on two different time scales based on 10,000 repeated simulation runs. In particular, Fig. 1c and f evidence that both methods produce consistent results for small and intermediate auto-correlation but different results for high auto-correlation.

Note that these results in principle maintain when assuming $T = 1000$ to be a "short" time series and replacing the approach by Ripa and Lundberg (1996) by the more cumbersome approach of Heino et al. (2000). It remains, however, indistinct why extinction risk on different time scales is driven in different directions (Fig. 1c, f). We conclude that, concerning the resulting extinction risks, (1) the choice of the rescaling method does not matter for moderate auto-correlation but (2) this choice obviously becomes very important for strongly auto-correlated environmental noise (Fig. 1c, f).

Therefore, in the following main part of this paper we review alternative methods of variance rescaling. In particular, we point out limitations of commonly applied methods and we evidence the variability in auto-correlated time series. We then introduce a practical alternative.

3. The issue of generating coloured noise

Usually, when investigating the effects of noise colour on extinction risk, one is faced with the problem to generate random time series with given colour. Therefore, an original time series of white noise is dyed, i.e. the temporal correlation of environmental fluctuations is modified in order to study the resulting effects on population dynamics. For this purpose a AR_1 process (Eq. (2)) is often used to generate the temporally correlated fluctuating quantity, Φ_t (alternatively cf. Cuddington and Yodzis, 1999). Note, that in Eq. (2) a possible bias by initialising $\Phi_0 = 0$ is customary removed by omitting an initial transient of Φ. The time series of an environmental parameter, for example, the carrying capacity K, then is calculated as $K_t = K_0 + \Phi_t$ with K_0 being the desired average.

When modifying the colour of time series according to Eq. (2), however, a problem arises: As the standard deviation of the AR_1-process (Eq. (2)) is given by

$$\sigma = \frac{\beta}{\sqrt{1-\alpha^2}} \tag{3}$$

modifications in the degree of auto-correlation, α, always entail a change in variance σ^2 of Φ (Roughgarden, 1975; Chatfield, 1984; Ripa and Lundberg, 1996). Since $|\alpha| < 1$ Eq. (3) implies that this variance is always larger than the variance of the underlying white noise, $\sigma^2 > \beta^2$. Thus, one faces the problem that "the effects of change in colour will be masked by the effects of [changing] variance" (Heino et al., 2000, p. 178). Hence, various techniques have been developed to rescale the time series depending on the auto-correlation parameter α such that the red noise of different α and white noise can be compared on the basis of the same variance (Chatfield, 1984; Heino et al., 2000).

However, as we show these scaling techniques are very intricate and can lead to ambiguous results, in particular for strong auto-correlation (Fig. 1). In our study we explore new approaches for tackling these problems in order to avoid variance-induced biases when calculating the extinction risk of populations in coloured environments. This includes a novel alternative to the current practice of generating dyed time series.

4. Scaling to expected variance

4.1. Scaling to expected asymptotic variance

As pointed out in the introduction problems arise by the generation of coloured time series since the variance of the time series resulting from the AR_1-process depends on the auto-correlation parameter α (Eq. (3)). Those problems can be circumvented by rescaling Φ_t and choosing an appropriate value of the free parameter β in Eq. (2). Many authors (Roughgarden, 1975; Foley, 1994; Ripa and Lundberg, 1996; Petchey et al., 1997; Cuddington and Yodzis, 1999 and others) used a factor that scales the coloured noise to the desired *asymptotic* variance σ^2_∞ depending on the auto-correlation coefficient α

$$\beta \equiv \beta(\alpha) = \sigma_\infty \sqrt{1-\alpha^2}. \tag{4}$$

Note that Eq. (4) corrects the variance as it is *expected* to result from the AR_1 process (Eq. (2)).

4.2. Scaling to expected variance over a certain time scale T

When studying Eq. (4), Heino et al. (2000) pointed out that the expected variance, σ_T^2, of short coloured time series of finite length T may deviate from the asymptotic variance, σ_∞^2, i.e. from the expected variance of an infinitely long time series. These findings confirm with our simulation results in Figs. 2 and 3. Fig. 2a shows that this deviation decreases with increasing T (compare also dash/double dot lines in Fig. 3). This problem that the expected value of the variance increases with the length of the time series is a feature common to all coloured time series (Pimm and Redfearn, 1988; Lawton, 1988).

Heino et al. (2000) discussed this problem intensively, and suggested that the length of the time series be taken into account when rescaling the variance. These authors call for scaling to the expected variance of the time horizon T over which the extinction risk is to be assessed. Starting an AR_1 process from its mean value, they suggest *to vary the scaling factor* β depending on time series length T:

$$\beta \equiv \beta(\alpha, T) = \sigma_T \sqrt{\frac{(1-\alpha^2)(T-1)}{T - \frac{2+2\alpha+\alpha^2-\alpha^{2T}}{1-\alpha^2} + \frac{(1-\alpha^T)(1+2\alpha-\alpha^T)}{T(1-\alpha)^2}}}, \quad (5)$$

where σ_T^2 is now the target variance of a time series of length T. Note that Eq. (5) approaches Eq. (4) in the limit of large T.

4.3. Limitations

To summarize, for the correction of variance two solutions have been proposed: either to rescale to the asymptotic variance (e.g. Eq. (4) e.g. Ripa and Lundberg, 1996) or to rescale to the expected variance at a certain time scale T (e.g. Eq. (5), Heino et al., 2000).

The first alternative has the advantage to keep calculations simple, as well as leaving the rescaling independent from time series length, T (Table 2). However, Eq. (4) bears problems for short time series. In particular, Heino et al. (2000) call for scaling to the expected asymptotic variance only if long-term properties of noise are likely to be important for extinction risk. Moreover, the first alternative is restricted to those types of noise with finite variance. In contrast, $1/f^b$ noise (where the variance increases with time according to a power law) does not have finite variance when time approaches infinity (Halley, 1996). Therefore scaling to the asymptotic variance is not applicable for such noise types.

These problems can be overcome by the second approach of rescaling the variance for a certain length of

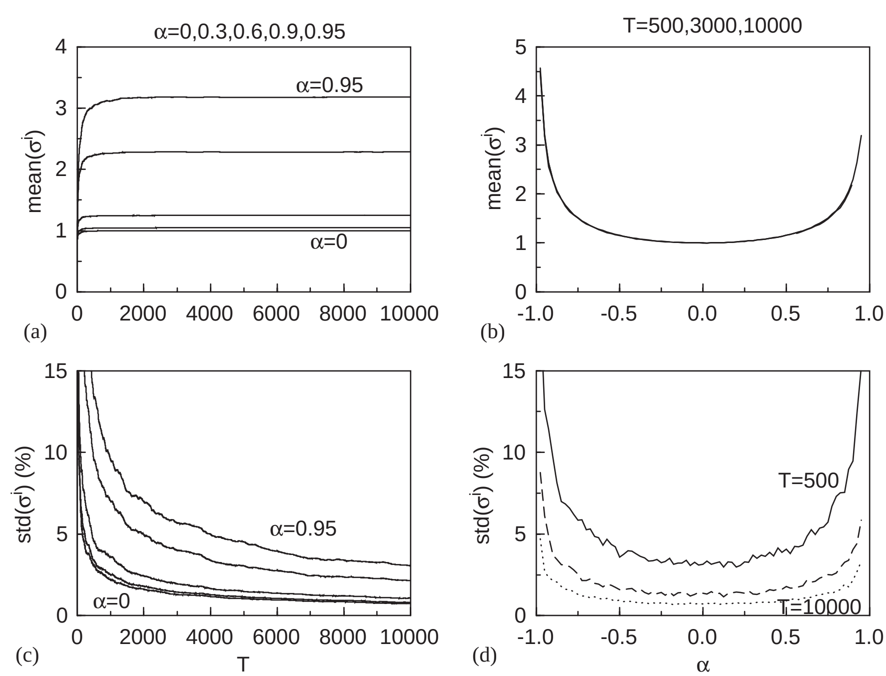


Fig. 2. Variability of the standard deviation $\sigma^i(T, \alpha)$ in an ensemble of 200 coloured time series generated by the AR_1 process (Eq. (2)). Plotted are the ensemble average of the standard deviation, mean(σ^i) (top), and the standard deviation of σ^i in percentage of the ensemble mean, std(σ^i) (bottom), in dependence on the time series length T (left) and auto-correlation parameter α (right). No additional scaling has been performed. Note, that there is a high variability in variances for large auto-correlation parameters (d) which maintains when applying Eq. (4) or Eq. (5) but is eliminated by Eq. (6).

a time series. Thus, Eq. (5) can also be used for short sample length. Furthermore, the second alternative points yet in another direction as, in principle, it allows for variance correction even when the asymptotic variance does not exist (e.g. $1/f^b$ noise).

However, we want to stress that also Eq. (5) is not unproblematic because the final time of the simulated population dynamics has to be fixed, i.e. $\beta \equiv \beta(T)$. This is only partly a problem when investigating the extinction risk $P_0(T)$ at a certain time T. Though, when focusing on the Mean Time to Extinction (Grimm and Wissel, 2004) the extinction risk for different time horizons T has to be calculated (Wissel et al., 1994; Johst and Wissel, 1997; Wichmann et al., 2003a, b). Then, the question remains to which T the variance should be scaled. Also Eq. (4) is not satisfactory solving this problem as, here, the underlying assumption is that time series length equals infinity ($T = \infty$).

Moreover, we claim at least two more problems of both approaches that in principle cannot be solved by either Eq. (4) or Eq. (5). First, both scaling methods are specifically attached to the AR_1-process and in this sense, they are not valid in a general case. For any other process of noise generation it becomes necessary to replace Eq. (4) and (5) by a cumbersome derivation of expected variances. (For example Eq. (5) has to be replaced by a different formula if initial transients of time series are omitted; see Heino et al., 2000.) Second, Eqs. (4) and (5) both rescale to the *expected* variance but do not consider variability in the actual variance. The latter point is explained in more detail in the following paragraph.

Table 2 provides an overview on the different rescaling methods and their benefits.

4.4. Variability of variance

In this section we highlight the difference between the expected variance of a noisy process and the actual variance of a given time series. *Actual variance* we understand as the variance of a time series which results from an individual simulation run with a given realisation of random numbers. This has to be distinguished carefully from the *expected variance* which is defined as the average variance in a large number of repeated simulation runs. In our simulations we found that for strong auto-correlation there can be considerable deviations between the *actual* and the *expected* variance.

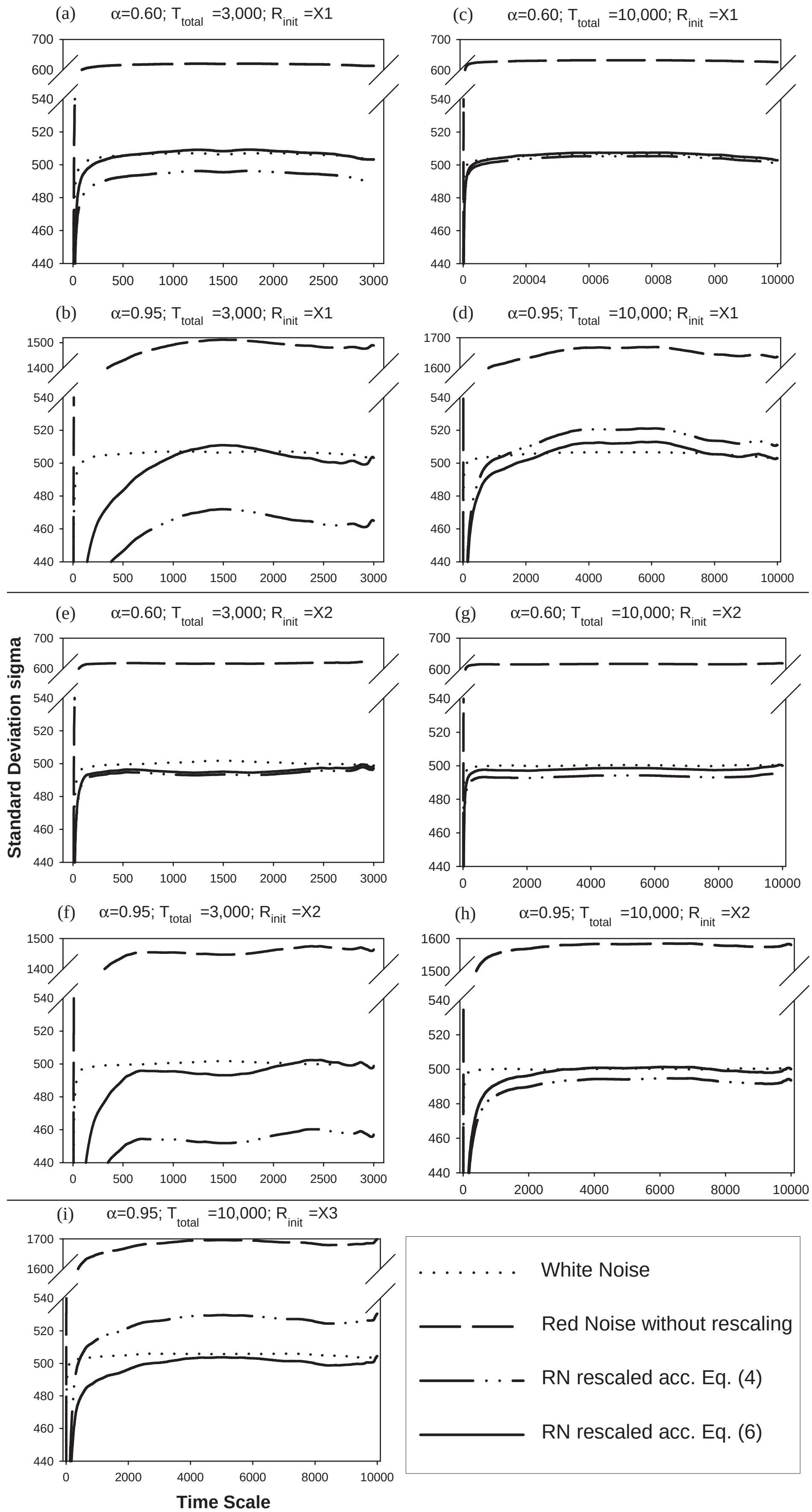
This is demonstrated, for example, in Fig. 3 which reveals that the variances (standard deviations) of single time series produced by Eq. (4) can be either reduced (Figs. 3a, b, f, h) *or* elevated (Figs. 3d, i) depending on the underlying random number series. Similar results appear in the alternative scaling scheme for small but fixed sample lengths (Eq. (5)) as evidenced in Fig. 4. In summary, for large α the actual variance of single time series scatters largely around the expected variance.

To explore this case more systematically in Fig. 2 we generated an entire set of time series, Φ^i, by repeated simulations of the un-scaled AR_1 process (Eq. (2)). For each time series, *i*, a different realisation of random numbers was used and we calculated the actual standard deviation $\sigma^i(T, \alpha)$. The ensemble average $\langle \sigma^i \rangle$ then gives an estimate for the *expected* variance (Figs. 2a and b). In contrast, the standard deviation of the variances in the ensemble of time series, std(σ^i), is a measure for the variability of the actual variance (Figs. 2c and d).

In agreement with earlier studies we found that the expected variance $\langle \sigma^i \rangle$ increases with the absolute value of the auto-correlation parameter α (Figs. 2a and b). However, our simulations reveal a surprising variability of the actual variances in the ensemble of time series over the whole parameter range. This variability decreases with increasing sample length, T (Fig. 2c) but increases dramatically with the absolute value of α (Fig. 2d).

If the auto-correlation is small we can rapidly reduce this variability by increasing the length of the time series (Fig. 2c: $\alpha = 0$). This confirms with the common wisdom that from single short time series it is hard or even impossible to draw conclusions on general features. In contrast, for sufficiently long time series variability essentially plays no role and individual simulation runs give a valid representation for the whole ensemble. To measure this effect quantitatively in our simulation runs we determine the *critical sample length*, T_{min}, beyond

Fig. 3. Standard deviation σ (left axis) of time series created by various techniques versus the length of time series fragments (bottom axis). We took a time series of constant length ($T_{total} = 3000$, left, and 10,000, right). In order to calculate σ we average over *all samples of fragments* of smaller lengths T. The number of realisations yielding $\langle \sigma \rangle$ for a given T is $T_{total} - T + 1$. Accordingly, on right plots σ is averaged over a larger number of samples when compared to the same time scale value on left plots. The underlying assumption is to use time series fragments drawn randomly from a long time series to perform repeats in the simulation of extinction risk (by contrast see Fig. 4). The standard deviations σ of coloured noise are shown without scaling (dashed line), scaling according to Eq. (4) (dash/double-dot line) and scaling according to Eq. (6) (solid line). The standard deviation of white noise is given as a reference (dotted line). Plots are shown for two different random number initialisations ($R_{init} = X_1$: a–d and $R_{init} = X_2$: e–h) and for two different time series lengths ($T_{total} = 3000$: a, b, e, f and $T_{total} = 10,000$: c, d, g, h). The auto-correlation parameters are $\alpha = 0.60$ (a, c, e, g) and $\alpha = 0.95$ (b, d, f, h). Additionally, a third random number initialisation ($R_{init} = X_3$: i) is shown for $\alpha = 0.95$ and 10,000 time steps that produces variances larger than white noise variance.


(a) α=0.60; T total =3,000; R init =X1
(c) α=0.60; T total =10,000; R init =X1
(b) α=0.95; T total =3,000; R init =X1
(d) α=0.95; T total =10,000; R init =X1
(e) α=0.60; T total =3,000; R init =X2
(g) α=0.60; T total =10,000; R init =X2
(f) α=0.95; T total =3,000; R init =X2
(h) α=0.95; T total =10,000; R init =X2
(i) α=0.95; T total =10,000; R init =X3
Standard Deviation sigma
Time Scale
White Noise
Red Noise without rescaling
RN rescaled acc. Eq. (4)
RN rescaled acc. Eq. (6)

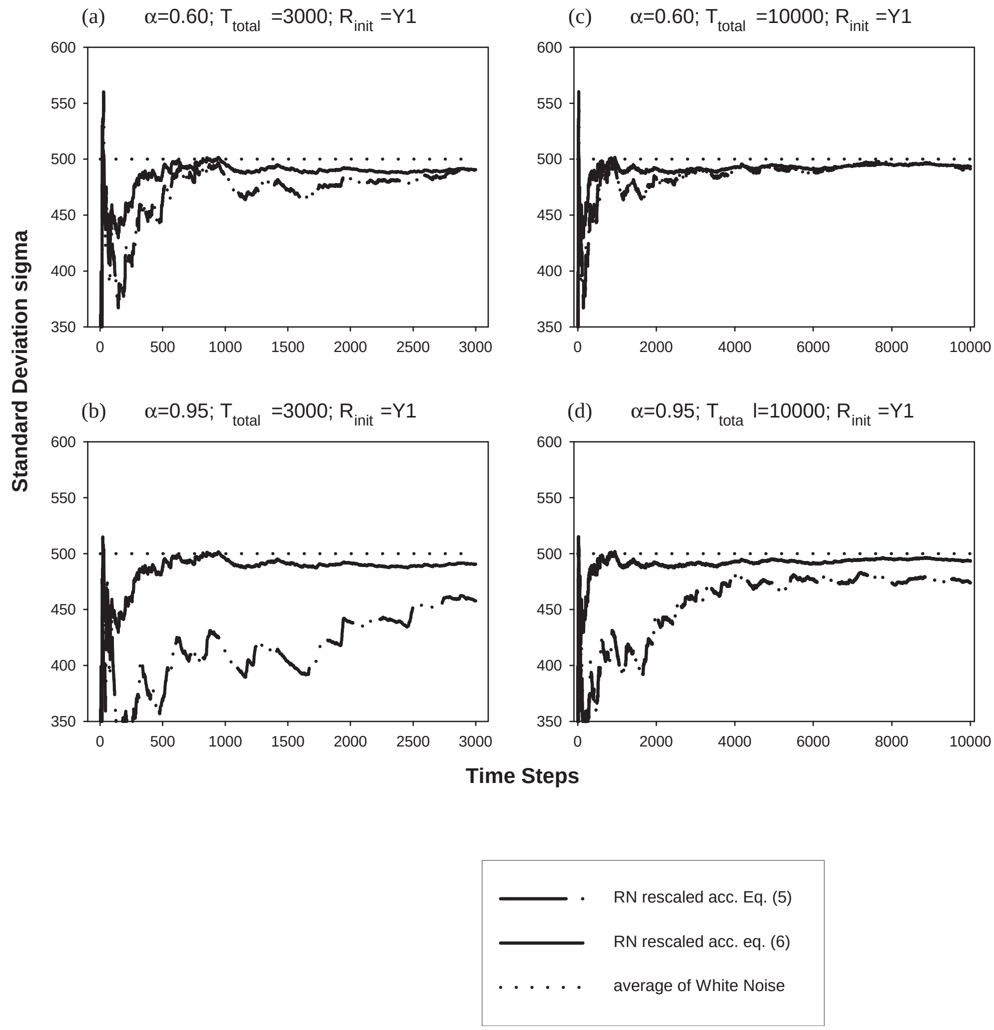


Fig. 4. Standard deviation σ (left axis) of time series created by various techniques versus the length of a particular time series (bottom axis). Note that in contrast to Fig. 3, σ is calculated from just *one particular time series fragment* (from time step 1 to time step bottom axis value) yielding the fluctuations in the plot, i.e. only one realisation, here. Therefore, left and right plots show identical data but the left plot gives a smaller scale on bottom axis. The standard deviations of coloured noise are shown for scaling according to Eq. (5) (dash/double dot line) and scaling according to Eq. (6) (solid line), the latter yielding exactly the same curve as desired (e.g. white noise (T)). Additionally, the asymptotic standard deviation of white noise is given as a further reference (dotted line). Like in Fig. 3, two different maximum lengths of the time series (3000: a, b and 10,000: c, d) and two degrees of auto-correlation ($\alpha = 0.60$: a, c, and $\alpha = 0.95$: b, d) are shown while random number initialisation remains constant ($R_{\text{init}} = Y_1$).

which the variability drops below the significance level and plays no longer a significant role (Table 1). For white noise we found a relatively short length of $T_{\min} = 200$ ($p = 0.05$).

This behaviour, i.e. $T_{\min}$, changes totally when the time series are coloured (Table 1). Most important, we observe that for strong auto-correlation the variability of variances is maintained even for much larger sample lengths (Fig. 2c: $\alpha = 0.95$). In particular, we find a critical sample length of $T_{\min} = 423$ if $\alpha = 0.6$ but much larger $T_{\min} = 3900$ for $\alpha = 0.95$. This reveals that, for example, with $\alpha = 0.95$, even a large sample of $T = 3000$ does not exceed corresponding $T_{\min}$ and that consequently the variability evidenced in Fig. 2c may cause significantly different variances among time series realisations ($p = 0.05$). Looking from yet another angle: when the auto-correlation parameter approaches limiting values ($\alpha \to 1; \alpha \to -1$) the variability of variances is dramatically elevated (Fig. 2d). To summarize, samples with a length of several thousand time steps that are representative for white noise must be seen as insufficient, i.e. too short, to be representative for strong auto-correlation.

Studies on extinction risk typically assess time scales which vary from several decades to several thousand, but sometimes can reach ten thousand time steps depending on the system, the species and objectives of the study (e.g. Shaffer, 1981). Correspondingly, the critical sample length $T_{\min}$ can easily reach or exceed time scales of population extinction as found in our simulations for stronger auto-correlation (Table 1). This suggests that the variability of variances can indeed play

Table 1
Critical sample length, $T_{\min}$, for various auto-correlation coefficients α and two significance levels, p

α	$T_{\min}$	
	$p = 0.05$	$p = 0.025$
0.00	200	795
0.10	206	814
0.20	220	865
0.30	242	954
0.40	276	1100
0.50	331	1334
0.60	423	1725
0.70	577	2320
0.80	900	3640
0.90	1890	7650
0.95	3900	15,600

The measure $T_{\min}$ gives the minimum sample lengths in an ensemble of time series generated by the AR_1 process (Eq. (2)) for which the standard variation of σ^i drops below the significance level p. For studies, which neglect the variability of variances, the length of a coloured time series with auto-correlation α must exceed $T_{\min}(\alpha)$ to avoid significant biases ($p = 0.05$ or $p = 0.025$). Note that $T_{\min}$ is dramatically elevated for strong auto-correlation when compared to white noise.

a role when estimating the risk of extinction for biological populations in an auto-correlated environment (compare Fig. 1).

We conclude that the variability of variances, as shown in Fig. 2b, c, must be taken into account when rescaling the variance of auto-correlated time series. Recall that the currently applied schemes (e.g. Eq. (4), and (5)) rescale the time series according to the *expected variance* while, at least for large α, the *actual variance* of a particular time series may considerably deviate from this value. As these deviations depend on the explicit random number realisation (Fig. 3) they, in principle, cannot be removed by scaling to the expected variance. As a result, even when using rescaling schemes Eq. (3) and (4), the extinction risk calculated for strong auto-correlation might be influenced by biases in the variance.

To overcome these problems we suggest to remove random deviations in variances by rescaling according to the *actual* variance. In the following we present an alternative method of rescaling the variances of coloured noise which tackles all major problems pointed out here: (1) dealing with short sample lengths, T, (2) overcoming restriction to the AR_1-process and, (3) taking the variability of the actual variance in repeated simulation runs into account.

5. Scaling to the actual variance

Below we present a simple but practical method in order to generate coloured time series of a given variance even for large auto-correlation parameters, α. In contrast to the current practice of coupling the AR_1 process (Eq. (2)) with rescaling β to the expected variance (Eq. (4) and (5)), we here suggest to scale to the actual variance. This means to run the AR_1 process in a first step without any rescaling and then, in a second, step to readapt the variance to the value of the original time series of white noise.

A very easy and intuitive way of determining the rescaling factor, c, yielding the target variance is to measure the ratio in variances of the auto-correlated but un-scaled time series and the original driving white noise

$$c \equiv c(\alpha, T) = \frac{\sigma_{T\_WN}}{\sigma_{T\_RN}}. \tag{6}$$

Here, σ_{T_WN} is the actual standard deviation of the original white noise time series with sample length T and σ_{T_RN} the actual standard deviation for un-scaled red noise. This yields the scaling factor c that might be regarded as equivalent to the term square root of $(1 - \alpha^2)$ in Eqs. (4) and (5). Here, however, the new scaling factor c is applied separately from the generating AR_1-process. Note, that for the unlikely case of $c > 1.0$ the variance would increase, while for the expected case of $c < 1.0$ the variance will decrease during the rescaling process.

When scaling to infinity the variability in variances disappears. Therefore, in the limit when T approaches ∞, σ_{T_WN} and σ_{T_RN} turn into their asymptotic variances, σ_{∞_WN} and σ_{∞_RN}, respectively. This immediately leads to

$$\lim_{T \to \infty} c = \sqrt{1 - \alpha^2} \tag{7}$$

which corresponds to the well known result from Eq. (4).

Post-AR_1-rescaling of environmental parameters can easily be done by multiplying the distance of each data point from the time series mean by the rescaling factor c and changing data values accordingly

$$\Phi_t^* = c(\Phi_t - \bar{\Phi}). \tag{8}$$

Here, Φ_t refers to the time series of the AR_1-process (Eq. (2)) before applying any variance correction, $\bar{\Phi}$ is the actual average of this time series. Finally, Φ_t^* gives the value for the new, rescaled time series.

We want to emphasize that in the rescaling process Eq. (6) the variability of the red noise time series is not totally removed. Only the additional variability, which is artificially caused during the dying scheme, is taken out. In contrast, the "natural" variability of the driving white noise, i.e. the variability which does not depend on the dying process, is maintained. As a result when scaling to "infinity", i.e. very long environmental time series, our method results in variances which are very close to that desired for white noise (Fig. 3). Here under moderate auto-correlation our method can reproduce the results of Eq. (4) (e.g. Figs. 3c and e). However, for large auto-correlation parameters α Eq. (6) leads to variances (standard deviations) much closer to the desired one (of white noise) than those produced by Eq. (4) (e.g. Figs. 3b, f and h).

6. Discussion

In this study we investigate the extinction risk of populations exposed to temporally correlated fluctuating environments (coloured noise). First, we compare the results for different types of the process generating environmental noise. We find the subsequent extinction risk to be biased by the method of variance scaling with most severe impacts occurring for strongly auto-correlated environments (Fig. 1). We then, secondly, discuss the limitations of commonly used scaling techniques and reveal several problems, in particular the high variability in variances of strongly auto-correlated time series (Fig. 2c, d). Consequentially, we present a new method (Eq. (6)) that overcomes these problems. Compared to commonly used methods our approach harbours various advantages as summarized in Table 2.

6.1. Applicability of rescaling to the actual variance

The main advantage of our method (Eq. (6)) compared to conventional methods (Eq. (4), (5)) is the ability to take the variability in variances into account. Hence, our approach enables us to properly rescale variances in strongly auto-correlated time series. Moreover, like the specifically designed Eq. (5) our new approach (Eq. (6)) is able to overcome the problems that go together with short sample lengths (Fig. 4; compare Heino et al., 2000). In contrast to conventional methods, Eq. (6) is not attached to a particular noise generating process but is applied *after* noise generation. Thus, our method can be applied to *any* noise type including AR_n-processes and $1/f^b$-noise. Moreover, it can even be applied to coloured time series where the underlying process of noise generation remains completely unknown.

An additional advantage of our method is that it reproduces white noise variance more reliably than the methods currently used (Eqs. (4) and (5)). It meets the initial aim by providing a way of generating coloured noise not only for slight and moderate, but also for strong auto-correlation with a given variance. Another advantage of this method is its straightforward practicality. It is very intuitive to measure a deviation in variance and to correct it accordingly, making our method very easy to grasp.

Our method of variance rescaling was applied to coloured noise generated by an AR_1-process. From a statistical point of view, however, post-AR_1 rescaling might bear a shortcoming because the rescaling process depends on the realisation of the random numbers. This implies that different noisy time series are essentially generated by an AR_1-process (Eq. (2)) using different values of β. Thus, one could argue that the stochastic process by which the red noise time series are generated is not constant. This is somewhat problematic because ad hoc it is not clear in which way different auto-correlated time series can be compared.

A closely related point of criticism would be that deviations of the actual from the expected variance are subject to stochasticity and thus they should not be removed. Here, the crucial question is whether the variability of variances must be seen as an artefact of the AR_1 process or if it is inherent to auto-correlation in nature. If the first case is valid this supports our method, the latter case would speak against its application in population biology. However, on the current state of knowledge and heading for the aim to investigate the effects of auto-correlation while keeping the variance constant we here recommend to rescale according to the actual rather than the expected variance.

Table 2
Overview of the three proposed methods of variance correction and the different problems to be solved by these methods

	Variance correction		Also applicable		Overcoming restriction to	
	Average variance, mean (σ^i)	Variability of variances, std (σ^i)	To short time series	If asymptotic variance does not exist	Fixed length of time series	A specific noisy process
Eq. (4), e.g. Ripa and Lundberg (1996)	X				X[a]	
Eq. (5), Heino et al. (2000)	X		X	X[b]		
Eq. (6), this study	X	X	X	X		X

A cross (X) indicates that this method solves the corresponding problem. Please note in particular that only our newly presented approach (Eq. (6)) corrects the variability of variances.

[a]However, it is assumed that $T = \infty$.

[b]In principle.

From yet another point of view one might argue that using the actual instead of the expected variance of the time series, as we do here, is subject of a particular assumption, i.e. the assumption of a more predictable future. Then, evidently, this assumption leads to different results than the assumptions underlying the existing methods for rescaled variances (Figs. 3 and 4), as well as for the subsequent extinction risk (Fig. 1). Thus, one might argue what the more reliable assumption is. We here claim that when systematically studying and modifying one parameter (e.g. auto-correlation) other conditions (e.g. variance) should be kept constant. Rescaling according to the actual variance, as we suggest, retains the variances of the original driving white noise time series and thus it explicitly gives respect to stochastic variability in variances as found in white noise (compare Fig. 4). Hence, our method of rescaling to the actual variances provides a simple and consistent way of tackling the problems discussed here.

If instead rescaling to the expected variances is used, then our results on the variability of variances point out that for large α individual simulation runs have no meaning. Therefore, an optimal strategy could be to support the conventional scaling with a very large number of simulation runs and then to study the statistical properties of the resulting distributions of noise variances and calculated extinction times. Such an approach is not necessary with our method.

We are aware that the problems claimed for the actual variance of time series also hold for further "attributes" of time series, such as the mean and levels of auto-correlation, which may randomly deviate from the expected value for short sample sizes. Accordingly to variances, in this study we preferred the actual to the expected mean value (Eq. (8)) while the object of modification, i.e. auto-correlation may be exactly measured in the resulting time series. However, one should also bear in mind that the characterisation of a time series using such descriptive attributes (e.g. mean, variance, auto-correlation) will always be imperfect. Even the sum of all known descriptive attributes can never completely describe a time series. Consequently, one may always find differences in the estimated extinction risk resulting from different time series with identical (but imperfect) descriptive attributes.

7. Conclusion

This manuscript contributes to the growing evidence that appropriate generation of coloured time series is not unproblematic and poses several problems in population ecology and the assessment of extinction risk. Heino et al. (2000) claimed differences in the impact of noise colour on extinction risk among various studies (e.g. higher extinction risk due to coloured noise: Mode and Jacobsen, 1987; Foley, 1994; Johst and Wissel, 1997; Roughgarden, 1975; Wichmann et al., 2003a, b; but lower extinction risk under coloured noise: Roughgarden, 1975; Ripa and Lundberg, 1996) and suggest that the reason can be found in different scaling practices of the variance of the coloured time series. Other authors stress the importance of density regulation on the results, i.e. whether there is undercompensatory or overcompensatory density dependence (Petchey et al., 1997; Cuddington and Yodzis, 1999; Petchey, 2000). It should also be borne in mind that the impact of coloured noise on extinction risk depends not only on the noise colour itself but also on its relation to the time scale of population growth (growth rate) of the species considered (Johst and Wissel, 1997). Furthermore, the results may significantly differ when $1/f^b$ noises are used instead of an AR_1 process to generate the dyed time series (Cuddington and Yodzis, 1999). Morales (1999) suggests that the noise effects on population extinction depend on model structure. The latter point is in particular accordance with the findings of this paper.

The suggestions for scaling the coloured time series made here can help to deal with the problems discussed above. In particular, we present a very simple and consistent procedure to generate time series with given colour and variance even for strong temporal auto-correlation. Compared to earlier studies, this method harbours two major advantages: (1) the variability in variances is reduced, and (2) this method is not restricted to the AR_1-process but can be applied independently of the type of noise generation. While the latter point favours the general applicability of this method the first point enables us to compare the extinction risk $P_0(T)$ of populations experiencing different colours of environmental noise on the basis of the same variance. Accordingly, we have shown that omitting variability in variances alters the calculated extinction risk particularly under strongly correlated noise. The method proposed here may help to increase our understanding of the impact of coloured environmental noise on extinction risk.

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