Effects on population persistence: the interaction between environmental noise colour, intraspecific competition and space

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SUMMARY

It is accepted that accurate estimation of risk of population extinction, or persistence time, requires prediction of the effect of fluctuations in the environment on population dynamics. Generally, the greater the magnitude, or variance, of environmental stochasticity, the greater the risk of population extinction. Another characteristic of environmental stochasticity, its colour, has been found to affect population persistence. This is important because real environmental variables, such as temperature, are reddened or positively temporally autocorrelated. However, recent work has disagreed about the effect of reddening environmental stochasticity. Ripa & Lundberg (1996) found increasing temporal autocorrelation (reddening) *decreased* the risk of extinction, whereas a simple and powerful intuitive argument (Lawton 1988) predicts *increased* risk of extinction with reddening. This study resolves the apparent contradiction, in two ways, first, by altering the dynamic behaviour of the population models. Overcompensatory dynamics result in persistence times increasing with increased temporal autocorrelation; undercompensatory dynamics result in persistence times decreasing with increased temporal autocorrelation. Secondly, in a spatially subdivided population, with a reasonable degree of spatial heterogeneity in patch quality, increasing temporal autocorrelation in the environment results in decreasing persistence time for both types of competition. Thus, the inclusion of coloured noise into ecological models can have subtle interactions with population dynamics.

1. INTRODUCTION

Physical environments are rarely static, and the variability in important environmental parameters such as temperature and rainfall, have widely recognized impacts on natural populations of plants and animals. It is generally acknowledged that an important characteristic of environmental variability, or noise, is its temporal variance (Leigh 1981; Goodman 1987; Wissel & Stöcker 1991; Lande 1993). Recently, the potential importance of another characteristic of environmental noise has been recognized: the variance spectra, or colour, of the noise (Goodman 1987; Halley 1996). White noise (or noise with a white variance spectrum) contains no temporal autocorrelation and is essentially a series of independent random numbers. For example, if a series of daily temperatures were white, tomorrow's temperature would be independent of today's temperature. Red noise, however, contains positive temporal autocorrelation: tomorrow's temperature is likely to be similar to today's. The colour of environmental noise is potentially important because (i) the variance spectra of real environmental variables are reddened

(Mandelbrot & Wallis 1969; Monin *et al.* 1977; Steele 1985; Williamson 1987; Halley 1996); (ii) the variance spectra of natural population sizes through time are reddened (Pimm & Redfearn 1988; Ariño & Pimm 1995; Sugihara 1995); and (iii) recent theoretical investigations suggest that population dynamics are sensitive to noise colour (Roughgarden 1975; Foley 1994; Caswell & Cohen 1995). A seemingly strong intuitive argument for how noise colour might affect population dynamics is that reddened noise contains runs of bad conditions, and whereas a population may survive one setback, a series of poor conditions will lead to a higher risk of extinction (Lawton 1988; see also Halley 1996). Thus, deciding whether environmental fluctuations are correlated or not is essential when attempting to estimate a population's probability of extinction.

This paper investigates the problem of how environmental autocorrelation affects time to extinction and, specifically, why in some cases it increases estimated persistence time, while in others it decreases estimated persistence time (Ripa & Lundberg 1996; Foley 1994). In an interesting recent paper, Ripa & Lundberg (1996) (hereafter referred to as R & L) showed that

increasing temporal autocorrelation in the noise process (reddening the noise) caused a *decrease* in extinction risk. This is in direct contradiction to Lawton's (1988) intuitive argument, which predicts reddened noise to *increase* (relative to white) the risk of population extinction. Both overestimation of time to extinction, and underestimation are potentially very dangerous; while species become extinct at unprecedented rates (Lawton & May 1995), and more become endangered, accurate predictions about extinctions are paramount. The apparent contradiction in the effects of environmental autocorrelation on extinction probabilities raises serious doubts about the accuracy of predictions of population persistence: not even the expected direction of the effect of reddened spectra appears to be consistent, let alone the magnitude. R & L suggest that model choice may severely influence estimates of extinction times. This paper extends that of R & L by including different forms of intraspecific competition, thereby changing the dynamic behaviour of the model and identifying the difference between R & L's study and the intuitive argument. The significance of spatial subdivision of populations on the risk of extinction under different types of noise is also investigated, further demonstrating that the inclusion of coloured noise into extinction models can have subtle interactions with population dynamics.

2. IMPORTANCE OF COMPETITION

(a) Model formulation

R & L used the discrete-time Ricker growth model to investigate the effect of the colour of environmental noise on the probability of extinction of a single-species population. Density dependence in the Ricker model results in overcompensatory dynamic behaviour. In order to investigate the effects of a range of dynamic behaviour, the model used by R & L was generalized to

$$N_{t+1} = N_t \exp(r(1 - [N_t/K_t]^b)), \quad (1)$$

where the parameter b controls the dynamic behaviour, from overcompensatory dynamics when $b = 1.0$ (the case of R & L) with a continuous change to undercompensatory dynamics when $b \approx 1$ (with perfect compensation lying somewhere in-between) (figure 1). The form of mortality for equation (1) is unusual because mortalities are not equal at low densities for different values of b (figure 1a). Whereas in the model of Hassell (1975), given by

$$N_{t+1} = \lambda N_t / (1 + N_t/K_t)^\gamma, \quad (2)$$

mortalities are equal at low densities (figure 1b). In equation (2), K_t is the reciprocal of the a usually used in the Hassell model. We concentrate on equation (1) to allow comparison with R & L, but also present results using Hassell's model (in both cases the qualitative results are the same). Demographic stochasticity was included in both models by taking population size as an integer. The population size in the next generation was then a random number taken from a Poisson distribution with the deterministic expectation of the

Figure 1. Mortality as K values ($\log(N_t/N_{t+1})$) against log population size for (a) equation (1) and (b) equation (2) showing the effect of altering (a) b and (b) γ on the type of intraspecific competition. A high value of b or γ results in overcompensatory dynamics (or scramble competition); a low value of b or γ results in undercompensatory dynamics (more similar to contest competition).

population size as its mean. Hence, equation (1) becomes

$$N_{t+1} = \mathcal{Z}(N_t \exp(r(1 - [N_t/K_t]^b))), \quad (3)$$

where $\mathcal{Z} \sim \text{Poisson}(N_t \exp(r(1 - [N_t/K_t]^b)))$. The distribution of the sum of N_t independent Poisson distributions each with the same mean ($\exp(r(1 - [N_t/K_t]^b))$), is the same as a Poisson distribution with mean ($N_t \exp(r(1 - [N_t/K_t]^b))$). Therefore, equation (3) can be interpreted as representing N_t individuals each having a random (Poisson-distributed) number of offspring with mean $\exp(r(1 - [N_t/K_t]^b))$, so that competition between individuals decreases with per capita fecundity. By formulating the model in a stochastic framework, extinctions occur in a biologically plausible manner, rather than by setting a minimum population size.

Environmental noise entered the model in exactly the same manner as in the model studied by R & L. Noise had an additive effect on the mean carrying capacity K_0 ; $K_{t+1} = K_0 + \phi_{t+1}$. Autocorrelation in the noise process, ϕ_t , was determined by a first order autoregressive process described by

$$\phi_{t+1} = \alpha \phi_t + \beta \epsilon_{t+1}, \quad (4)$$

where the parameter α controls the degree of autocorrelation, ϵ_t is a normally distributed random deviate with zero mean and unit variance, and β

determines the magnitude of the environmental fluctuations. When $\beta = C(1 - \alpha^2)^{1/2}$, the variance in K_t is constant for any value of α . C is therefore used to alter the magnitude of environmental fluctuations, and is set here at 70. (R & L used a C value of 20, but this results in very long persistence times when the parameter b is low, hence C is set at 70 instead. The exact value of C used does not influence the qualitative results presented later.) As in R & L, our objective is simply to study the effects of the degree of autocorrelation in the noise process, not to study the full range of possible noise signals. When $\alpha = 0$, the noise is white; for $0 < \alpha < 1$, the noise is positively autocorrelated, i.e. reddened. If $-1 < \alpha < 0$, the noise is negatively correlated (blue noise); however, blue noise is not generally considered to be a relevant model of environmental variation and is not included here.

Although threshold effects (such as the probability of extinction within 1000 model generations) are a perfectly reasonable measure for comparing different effects, where exactly the threshold is drawn can be arbitrary. Instead, therefore, we used the mean persistence time, $t(e)$, over 1000 independent simulations. The maximum length of one simulation $t_{\max}$ was set very large (200 000 generations); if extinction did not occur by $t_{\max}$, $t(e)$ was set to $t_{\max}$.

(b) Results of model simulation

For model (3), when $b = 1$ (overcompensatory dynamics), our results concurred with the study of R & L: increasing autocorrelation in the noise process increased mean persistence time from about eight generations at $\alpha = 0$ to about 100 generations at $\alpha = 0.95$ (in both cases all 1000 simulations went extinct by $t_{\max}$) (figure 2a). However, when $b = 0.1$ (undercompensation), mean persistence time decreased from 150 000 generations (572 extinctions by $t_{\max}$) when $\alpha = 0$ to about 700 generations (1000 extinctions by $t_{\max}$) when $\alpha = 0.95$. The effect of increasing autocorrelation in the noise process was, therefore, reversed by decreasing b , and the effect was continuous from $b = 1.0$ to $b = 0.1$. Hassell's model returns qualitatively similar results: overcompensatory dynamics result in an increase in persistence time with increased autocorrelation and a decrease in persistence time with undercompensatory dynamics (figure 2b). In Hassell's model, only γ effects whether the model is overcompensatory ($\gamma > 1$), undercompensatory ($\gamma < 1$) or has perfect compensation ($\gamma = 1$). The value of λ has no effect on this (although it can change the stability of the equilibrium). Therefore, the change in the two types of pattern seen in figure 2b occurs at $\gamma = 1$. In equation (1), the change from overcompensation to undercompensation is a complex function of both r and b , with an increase in either leading to more overcompensatory dynamics. However, the change in the types of pattern seen in figure 2a occurs, as in Hassell's model, at the point where the dynamics change from over- to undercompensation. It should be stressed that we are interested in making comparisons of how persistence time changes with α ; rather than comparing persistence times for different values of b (as, for example,

Figure 2. Mean persistence time (of 1000 simulations) as a function of temporal autocorrelation in the environment, α , and the dynamic behaviour of the model, controlled with b , for the non-spatial model ((a) equation (1), and (b) equation (2)). The carrying capacity K_t is given by the stochastic process $K_{t+1} = K_0 + \phi_{t+1}$; $\phi_{t+1} = \alpha\phi_t + \beta\epsilon_{t+1}$, where ϵ_t is a normally distributed deviate with mean zero and unit variance. The amplitude of the noise, β , is given by $\beta = 70(1 - \alpha^2)^{1/2}$, hence the variance (K_t) = 70^2 for all α . Other parameters are $r = \lambda = 1.5$, $K_0 = 100$ and $t_{\max} = 200\,000$.

changing b in Hassell's model changes the equilibrium population size).

By examining the distribution of population sizes just before extinction ($N_{t(e-1)}$), R & L identified the mechanism causing extinction as overcompensatory crashes (all population sizes prior to extinction were greater than K). Figure 3a shows distributions of $N_{t(e-1)}$ for the four combinations of α and b representing the four extremes of the simulations. The distribution of $N_{t(e-1)}$ when $\alpha = 0$ and $b = 1$ was spread widely, but the high population density prior to extinction suggests that demographic stochasticity was not the mechanism responsible for extinction. When $\alpha = 0.95$ and $b = 0.1$, all values of $N_{t(e-1)}$ were less than 10. This strongly suggests that demographic stochasticity was the mechanism responsible for extinction; an overcompensatory crash would be very unlikely from such a low density. Due to the fluctuating carrying capacity, however, distributions of $N_{t(e-1)}$ give limited information when attempting to determine the extinction mechanism.

To elucidate the mechanisms causing extinctions, therefore, the distributions of $\log_{10}(N_{t(e-1)}/K_{t(e-1)})$

were plotted for each case (figure 3b). $\text{Log}_{10}(\mathcal{N}_{t(e-1)}/K_{t(e-1)}) > 0$, was used to determine whether population size should have increased or decreased from $t(e-1)$ to $t(e)$, and then to infer the mechanism responsible for extinction. If $\text{Log}_{10}(\mathcal{N}_{t(e-1)}/K_{t(e-1)}) > 0$, population size should have decreased from $t(e-1)$ to $t(e)$ and if, in addition, population density was high, an overcompensatory crash alone is inferred to have caused extinction. Conversely, if $\text{Log}_{10}(\mathcal{N}_{t(e-1)}/K_{t(e-1)}) < 0$, population size should have increased from $t(e-1)$ to $t(e)$ and if, in addition, population density was small, demographic stochasticity alone is inferred to have caused extinction. Simulations with $b=1$ resulted in distributions with $\text{Log}_{10}(\mathcal{N}_{t(e-1)}/K_{t(e-1)})$ being generally greater than zero (see figure 3b) and population densities were generally high before extinction (see figure 3a). Thus, overcompensatory crashes were inferred as the extinction mechanism. Distributions from simulations with $b=0.1$ were generally less than zero, indicating that population growth was expected, when actually the population density decreased to zero (see figure 3b). In addition, population sizes were generally small (see figure 3a), so that demographic stochasticity was therefore the mechanism responsible for extinction.

The patterns in persistence times described above were, for both models, with parameters that resulted in single point equilibria. The models can display non-equilibrium dynamics when density dependence is highly overcompensatory. However, the stability of the local equilibrium has no effect on the general pattern of increasing or decreasing persistence time with changes in the autocorrelation parameter (although it may have an effect on the absolute value of the persistence time). This is because fluctuations in K_t result in fluctuations in the population size far from the local equilibrium point. The effects of the type of competition (under- or overcompensation) are then the determining factor, rather than the dynamics in one local area of the phase space (around the equilibrium). To confirm this, we investigated the effects of noise colour on persistence times for parameter combinations that resulted in non-equilibrium dynamics. We found that persistence time increased with autocorrelation. This is consistent with the dynamic behaviour of the models being overcompensatory, the dominant cause of extinction being overcompensatory crashes and white noise therefore resulting in lower persistence times.

The conclusions about the mechanisms responsible for extinction in different simulations were reinforced when the strength of demographic stochasticity was increased (by increasing the variability around the mean population size). For example, a negative binomial distribution, with the variance greater than the mean, could be used in equation (3), instead of a Poisson distribution. Since demographic stochasticity does not cause extinction in the overcompensatory model, changing its strength should not change the mean persistence time. Accordingly, changing the strength of demographic stochasticity was found to decrease mean persistence time in the model with

Figure 3. Frequency distributions of (a) population size $\mathcal{N}_{t(e-1)}$, and (b) $\log_{10}(\mathcal{N}_{t(e-1)}/K_{t(e-1)})$ one time-step prior to extinction, $t(e-1)$, for equation (1). Four distributions are shown, for each combination of low (0) and high (0.95) α with undercompensatory ($b=0.1$) and overcompensatory ($b=1.0$) dynamics. All other model details are as in figure 2.

undercompensation, but to have no effect in the model with overcompensation.

The opposite effects of noise colour seen with different types of competition, and therefore dynamic behaviour, represent the intuitive argument of the introduction in this paper and the theoretical study of R & L. The intuitive argument assumes demographic stochasticity as the extinction mechanism. R & L studied the effects of noise colour in a model with overcompensatory dynamics, and thereby revealed a fascinating counter-intuitive result caused when overcompensatory crashes are the mechanism responsible for extinction.

3. THE IMPORTANCE OF SPACE

(a) Model formulation

Consider a spatially subdivided population. Changing habitat quality across a landscape leads to spatial variation in the chances of individual survival and reproduction, resulting in heterogeneity in the local number of individuals. This spatial variability, when coupled to temporal environmental variability, leads to an ever-changing spatial pattern in the chances of survival and reproduction for an individual, and consequently local variability in population size. Such circumstances, it has been suggested, result in a regional metapopulation structure in which persistence is attained via constant dispersal between transient local sub-populations (Gilpin & Hanski 1991).

The consequences of changing the temporal correlation in environmental noise for metapopulation persistence in a spatially heterogeneous environment were explored by employing a spatial extension of R & L's model. The metapopulation structure was modelled as 100 patches linked by dispersal. Local, within-patch dynamics were modelled using equation (1) with $b = 1.0$ (overcompensatory dynamics for all simulations) and were therefore identical to those used in R & L, except for the addition of demographic stochasticity.

After the local dynamics a dispersal phase follows, with the probability of any given individual dispersing being fixed and density independent. The dispersal process is global rather than local, so that the probability of a dispersing individual reaching any patch in the landscape is identical.

Metapopulation extinction occurs when $N_t = 0$ for all patches. Mean persistence time of the metapopulation over 100 simulations was used as the response variable. The maximum length of one simulation $t_{\max}$ was large (100 000 generations); if extinction did not occur by $t_{\max}$, $t(e)$ was set to $t_{\max}$.

Environmental variability is included in two ways: (i) temporal variability due to fluctuations in the mean carrying capacity across the landscape, K_t , determined in the same way as in the previous section (the value of α therefore determines the level of autocorrelation in the variability in K_t); and (ii) spatial heterogeneity in patch quality across the landscape, represented by different carrying capacities of the individual patches. At any time the carrying capacities of individual patches are normally distributed with mean K_t and standard deviation, σ . Therefore, σ is a parameter that controls the heterogeneity in patch quality across the landscape.

(b) Results of model simulation

When the model is run with a single patch, or when $\sigma = 0$, the results are qualitatively the same as those of the previous section and of those of R & L. However, when the population is subdivided between a number of patches (100 in this case), and σ is large enough, the results are reversed (figure 4). An interaction between the temporal autocorrelation in K_t and the level of spatial heterogeneity in patch carrying capacity (determined by σ) in determining mean metapopulation persistence time was found. With $\sigma \lesssim 20$, increasing α leads to increasing $t(e)$; but with $\sigma \gtrsim 20$, increasing α leads to decreased $t(e)$.

The effect of σ reveals the underlying mechanism behind this result. Starting with a low value of α (i.e. white noise), increasing σ increases the spatial heterogeneity in the carrying capacity of the environment. Above $\sigma = 20$, the carrying capacity of the patches at any given t now differs sufficiently such that when an unfavourable environmental event (for population growth) occurs, although some patches suffer local extinction through over compensatory crashes, others persist. Extinct patches are then rescued by dispersal from those that survived. It is the spatial heterogeneity of the landscape which desynchronizes population

Figure 4. Mean persistence time (100 simulations) as a function of temporal autocorrelation in the environment α and the degree of environmental heterogeneity, σ , among the 100 patches. K_t is the mean patch carrying capacity at time t and is given by the same stochastic process as in the non-spatial model. σ is the standard deviation of patch carrying capacities at any one time. $t_{\max} = 100\,000$, individuals' dispersal probability = 0.05.

dynamics (Heino *et al.* 1997), and then the rescue effect that promotes persistence. Increasing the level of temporal autocorrelation causes this mechanism to break down. The temporal smoothing of the environmental noise that results from an increase in autocorrelation now allows the populations to track their environment (figure 5) and synchronize through space, increasing extinction risk. Thus, during periods of poor environmental quality, because one bad event is more likely to be followed by another and more and more patches suffer sequential extinction, there is a decline in the number of rescuing patches. If the series of unfavourable events is long enough, the number of rescuing patches becomes too small to keep pace with the extinction of existing ones.

The results of the spatial model were found to be sensitive to the number of patches in the landscape, more patches increased persistence times. Landscape size did not alter the interaction of spatial heterogeneity (σ) with temporal autocorrelation, only the level of heterogeneity needed to cause reversal in the effect of environmental autocorrelation. The larger the landscape, the greater the probability that the dynamics in some patches are not in synchrony with all the other patches, and the lower the level of spatial heterogeneity therefore needed.

When the assumption of global dispersal was relaxed to local dispersal (dispersal only to eight nearest neighbours) persistence times were not affected significantly, and the reversal in the effect of autocorrelation still occurred when environmental heterogeneity was increased. In this case, assuming local dispersal has little effect since an individual's probability of dispersal is low (0.05), neither a decrease in the rescue effect nor a decrease in synchrony occurs as a result of assuming local dispersal (although at higher dispersal rates local dispersal can have an effect). The synchrony in population dynamics over the landscape, and therefore population extinction risk, is overwhelmingly

Figure 5. Time-series of metapopulation size and patch carrying capacity K_i for the spatial model with (a) no autocorrelation ($\alpha = 0$) in K_i , and (c) positive temporal autocorrelation ($\alpha = 0.95$) in K_i . Scatter plots of K_i against metapopulation size for (b) $\alpha = 0$ and (d) $\alpha = 0.95$ indicate how closely metapopulation size tracks K_i .

determined by landscape heterogeneity. However, when there are non-equilibrium population dynamics (e.g. chaos), changes in the persistence time effected by autocorrelation and environmental heterogeneity are complex. Asynchrony between patches (which promotes persistence) is now affected by the local dynamics, the landscape heterogeneity and the degree of dispersal between patches. In this case the outcome can be complex: for example, with local dispersal and chaotic dynamics, the relationship between autocorrelation and persistence can be humped with greatest persistence at intermediate autocorrelation. Lack of space here prevents exhaustive reporting of these results.

Summing up, in our simple, spatially heterogeneous model, R & L's result is now seen to be a non-general case, in which populations exhibit overcompensatory dynamic behaviour, and where patches are relatively uniform in quality across the landscape ($\sigma < 20$). Where habitat quality varies from patch to patch ($\sigma > 20$), even with overcompensatory dynamics, the assertion that white noise leads to an optimistic extinction probability (Lawton 1988; Halley 1996) remains valid.

4. DISCUSSION

R & L showed that the probability of extinction in a single-species, single-patch model decreased as noise colour was reddened. As R & L suggested, this result is contingent on overcompensatory population dynamics. When dynamic behaviour is undercompensatory, reddening environmental noise increases the probability of extinction. It is the dynamic behaviour of the models that determines the effect of environmental noise colour. The dynamic behaviour of the models was controlled by changing the type of

competition (figure 1) from scramble competition, where high population densities result in high mortality, through pure contest competition, where a constant number of individuals survive competition, to undercompensatory competition. A new result has been found: the colour of environmental noise and the dynamic behaviour of the population interact. Furthermore, whether a population is spatially subdivided also has important influences on population persistence. Here it is shown that, when coupled with overcompensatory intraspecific competition, white noise results in a highly persistent metapopulation. Persistence of the same metapopulation, however, is significantly reduced as the environment is increasingly reddened, a process shown to be due to the sensitivity of population dynamics to noise colour. Harrison & Quinn (1989) showed a similar effect of decreased metapopulation persistence by reddening the temporal sequence of extinction probabilities. However, population dynamics were not explicitly modelled in this study, thereby precluding more detailed analysis of possible extinction-causing mechanisms.

An immediate question raised by our results is the relationship between environmental autocorrelation and persistence time that would we predict in real populations. We would argue that populations generally display undercompensatory dynamic behaviour and, therefore, that their persistence time will be overestimated (rather than underestimated as predicted by R & L) by the assumption of white noise. Although the evidence is limited for this assertion, Hassell *et al.* (1976), and Bellows (1981), estimated γ of Hassell's (1975) model for a limited number of (insect) taxa, and found values that were typically less than 1 (i.e. the predicted dynamic behaviour of the populations is undercompensatory).

Moreover, most natural populations are spatially subdivided, increasingly so due to habitat destruction. The results of the previous section suggest that, once again, use of white noise will overestimate population persistence times. The spatial model investigated above could also be extended to explore effects of spatial autocorrelation in patch quality: patches close to each other would be more similar than distant patches. This is obviously a more realistic assumption than assuming no spatial correlation, as in this study. The likely outcome is that since spatial autocorrelation will lead to less environmental heterogeneity, its effect should be the same as decreasing σ , it should lead to a greater risk of metapopulation extinction.

In summary, the demonstrated importance of intra-specific competition, in terms of how it alters dynamic behaviour, and space, strongly suggests that, for the majority of real populations, assuming white environmental noise in population models will bias estimates of risk of extinction and persistence time, and that the direction of this bias will be non-conservative.

These results need placing in context in the way in which environmental noise was simulated: an autoregressive process was used to produce reddened noise (as did R & L). Other processes can also produce reddened noise, such as $1/f$ processes (Halley 1996). An important difference between a first order autoregressive process and a $1/f$ process is that where a first order process converges with time to have a constant variance, the variance of a $1/f$ process increases continually with time, without limit. The likely importance of these two different ways of generating reddened environmental noise on the persistence of populations requires further investigation (Halley & Iwasa 1997; Halley & Kunin 1998). An experimental system designed to investigate the effects of $1/f$ noise on real populations has been designed (Cohen *et al.* 1998) and should provide insight into the sensitivity of real organisms to coloured noise.

With growing evidence that environmental variables really are reddened, the need to understand how this might affect population dynamics also grows. Theoretical studies have already shown environmental colour to influence populations (Rougharden 1975; Foley 1994) and communities (Caswell & Cohen 1995). Here the form of competition (under- or over-compensation) has been shown to have a large effect on the influence of environmental colour, as has the effect of spatial subdivision of a population on the influence of noise colour. These interactions between noise colour and competition, and noise colour and spatial subdivision, lead us to echo R & L's closing statement. If ecological theory is to give accurate, non-biased information on how best to direct conservation and restoration efforts, it must realize the importance of an accurate model of environmental variability, accurate with respect to mean, variance and colour.

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