Community extinction patterns in coloured environments

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Understanding community responses to environmental variation is a fundamental aspect of ecological research, with direct ecological, conservation and economic implications. Here, we examined the role of the magnitude, correlation and autocorrelation structures of environmental variation on species' extinction risk (ER), and the probability of actual extinction events in model competitive communities. Both ER and probability increased with increasing positive autocorrelation when species responded independently to the environment, yet both decreased with a strong correlation between species-specific responses. These results are framed in terms of the synchrony between—and magnitude of variation within—species population sizes and are explained in terms of differences in noise amplification under different conditions. The simulation results are robust to changes in the strength of interspecific density dependence, and whether noise affects density-independent or density-dependent population processes. Similar patterns arose under different ranges of noise severity when these different model assumptions were examined. We compared our results with those from an analytically derived solution, which failed to capture many features of the simulation results.

Keywords: competition; environmental variation; extinction risk; population synchrony; noise colour; disturbance severity

1. INTRODUCTION

An important goal of population biology is to understand what processes lead to extinctions. Population extinction may arise either due to intrinsic or extrinsic factors or through their interaction. Intrinsic factors include, for example, low or negative intrinsic growth rates and demographic stochasticity (Pimm *et al.* 1988). Observations and experimental evidence suggest that, in real world conditions, population extinction may result from extrinsic factors such as habitat fragmentation (Gonzalez & Chaneton 2002), stochastic environmental variation (Benton *et al.* 2002; Pike *et al.* 2004), climate change (McCarty 2001) and overexploitation (Fryxell *et al.* 2005). In addition, invasive species may also be an important cause of population extinction (Clavero & García-Berthou 2005). In model populations, the route to extinction differs between different forms of dynamical behaviour in population renewal (Ripa & Heino 1999; Ripa & Lundberg 2000). In general, populations that have undercompensating dynamics approach extinction from low densities and extinctions are due to sufficiently long runs of bad conditions (Ripa & Heino 1999). By contrast, populations that have overcompensating dynamics tend to extinction from high densities, due to, for example, catastrophic events in the environment (Ripa & Heino 1999). These differences can be important when evaluating the risk of extinction, as the extinction mechanism may differ under the above different circumstances (Greenman & Benton 2005).

Here, we consider the influence of stochastic forcing on population extinctions in communities of competing species. Important components of the environmental variation that affects species' dynamics are its magnitude and temporal (and/or spatial) autocorrelation, often referred to as the colour of the noise time series. The influence of these factors on single-species populations has been well documented (Ripa & Lundberg 1996; Petchey *et al.* 1997; Heino 1998; Cuddington & Yodzis 1999; Ripa & Heino 1999; Heino *et al.* 2000; Wichmann *et al.* 2003, 2005; Schwager *et al.* 2006).

While understanding the detailed responses of single-species systems to external perturbation is an important first step, species rarely occur alone in nature—i.e. in the absence of interspecific interactions. One important implication is that interactions between species can influence population responses to environmental fluctuation (e.g. Ives 1995). For a multi-species community, an additional complication is that the response of individual species to environmental variation may vary within the community. That is, the response of different species to the same environmental signal may be correlated or uncorrelated. The responses of communities to different environmental correlation and autocorrelation structures have only recently started to be explored (Ives *et al.* 1999; Ripa & Ives 2003; Greenman & Benton 2005; Ruokolainen *et al.* 2007), and the behaviour of complex systems under environmental forcing is not yet completely understood.

In addition to external factors, the fate of a population is also affected by intrinsic properties. For example, population growth rate may interact with environmental autocorrelation in influencing extinction events. It has been observed, both in single- (Petchey *et al.* 1997;

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Schwager *et al.* 2006) and multi-species community models (Ruokolainen *et al.* 2007), that while undercompensatory population growth increases extinction probability (EP) in association with increasing environmental autocorrelation, overcompensatory growth results in an opposite trend. In addition, the magnitude of change in extinction patterns is due to the similarity (correlation) in species' responses to environmental variation. This suggests that the extinction mechanisms in single-species systems are not exactly the same as those in multi-species systems. We examined this by modelling multi-species competitive communities under the influence of environmental variation of different strengths, correlation and autocorrelation structures. We compared the results from models that considered extinction risk (ER), defined as the proportion of time species' densities spent below a critical threshold density, with models that considered explicit extinction events in populations affected by demographic stochasticity.

Communities responded to forcing by different coloured environmental noise in different ways. This result was affected by the degree of equivalency in species-specific responses to forcing. We also found quantitative differences in ER and the number of actual extinction events. Both population synchrony and the magnitude of population fluctuations were affected by the colour and the strength of environmental variation, as well as by the correlation between species' responses to the environment. The results can be understood in terms of differences in the amplification of environmental noise under different conditions. We show that the patterns of species' ER and probability are robust to changes in the assumptions about the way noise affects population renewal (density-independent or -dependent population processes). Contrary to previous findings, we note that the same patterns also arise when populations display undercompensating growth. However, results under different assumptions are quantitatively sensitive to changes in noise severity. We also compared these results with those from an algebraically derived solution (Greenman & Benton 2005), which was not able to capture all features of the simulation results. This was most probably due to a failure of the linearization techniques employed in the analytical derivation to capture population variation under strong environmental forcing. This work generalizes the results from previous reports (Ripa & Ives 2003; Ruokolainen *et al.* 2007) and extends our knowledge of the behaviour of multi-species competitive communities in variable environments.

The work presented here examines extinction probabilities using model communities, as they are difficult or even impossible to measure in real ecosystems. This allows us to develop an understanding of how species with low population sizes embedded in communities respond to external forcing. Current rates of habitat loss and species harvesting make understanding these processes particularly relevant to current management purposes and conservation planning.

2. MATERIAL AND METHODS

(a) Population model

The population renewal of each species in an S species community was modelled using the Ricker function,

incorporating Lotka–Volterra-type species interactions,

$$N_{i,t+1} = N_{i,t} \exp \left[r_i \left(1 - \frac{\sum_{j=1}^S \alpha_{ij} N_{j,t}}{K_i (1 + \varepsilon_{i,t})} \right) \right], \quad (2.1)$$

where N_i is the population density; r_i is the intrinsic growth rate; K_i is the carrying capacity of species i ; and $\varepsilon_{i,t}$ is a species-specific environmental noise term. The *per capita* effect of species j on the growth rate of species i is α_{ij} , whose values determine the off-diagonal elements in the interaction matrix $\mathbf{A}$ (the diagonal elements α_{ii} are intraspecific interaction terms, here equal to 1).

In our simulations, community size was set at $S=3$, but the results from larger communities are qualitatively similar to those reported here. Owing to the absence of indirect interactions, smaller communities with one or two species can have a quite different dynamical behaviour from larger multi-species communities. However, as species are usually surrounded by many other species in natural conditions, we feel that there is a great interest in understanding the behaviour of more complex assemblages.

For simplicity, the intrinsic growth rate of all species was set at $r_i = r = 1.8$. This value of r yields equilibrium dynamics with damped oscillations following a single perturbation from equilibrium (in the absence of interspecific interactions). Choosing an r -value that results in undercompensating growth in the absence of interspecific competition ($r < 1$) did not have a qualitative effect on the results, which suggests that our results might be rather general in the stable region of population dynamics. However, choosing $r < 1$ requires higher levels of noise severity to produce patterns similar to those when $r > 1$. Species' carrying capacities were set at $K_i = K = 100$, in order to examine the behaviour of relatively small populations under environmental forcing.

Interspecific interaction strengths were set equal for all species pairs, $\alpha_{ij} = \alpha = 0.5$ (diffuse competition), yielding equilibrium densities of $N_i^* = N^* = 50$ (increasing α amplifies the reported patterns, whereas decreasing it quantitatively reduced the results, but there were no qualitative differences). The analysis of locally stable communities where $\alpha_{ij} (i \neq j)$ was drawn from a uniform distribution with limits $[0, 1]$, where all species had a minimum equilibrium density $N_i^* \geq 50$, also yielded qualitatively similar results. Preliminary results also suggest that generating communities through a sequential assembly algorithm does not have a qualitative influence on the results. It has been shown elsewhere (using a similar model structure) that, with symmetric (diffuse) competition, the value of α does not affect community stability (Lehman & Tilman 2000). We selected $\alpha_{ij} = 0.5$ in order to simplify the analysis and a comparison between the different model frameworks is presented here. Since the value of α affects species population densities at equilibrium (see §2c), it will influence the actual value of the extinction threshold (i) that is here set to $0.01 \times K_i = 1$. This is a natural reference point to the second scenario (ii), where population densities are expressed as integer values.

(b) Environmental forcing

Environmental variation was introduced into the system as a multiplicative process, through dynamic variation of the carrying capacity of all community members. Environmental stochasticity ($\varepsilon_{i,t}$) was generated with an autoregressive process that is potentially intercorrelated between different

species (Ripa & Lundberg 1996), which is given by

$$\begin{aligned}\varepsilon_{i,t+1} &= \kappa \varepsilon_{i,t} + \sqrt{1-\kappa^2} \frac{(\varphi_t + \beta \omega_{i,t})}{\sqrt{1+\beta^2}}, \\ \beta &= \sqrt{\frac{1-|\rho|}{|\rho|}},\end{aligned}\quad (2.2)$$

where ρ is the correlation coefficient between all pairs of environmental time series and κ is the autocorrelation coefficient. The terms φ_t and $\omega_{i,t}$ are standard normal random components, where the former is common for all species and the latter independent between species. Parameter β is a scaling factor ensuring that noise variance remains independent of ρ . This method scales the noise time series to its asymptotical variance (σ_i^2) independently of noise autocorrelation (Heino *et al.* 2000). After creating the noise time series, they were standardized. The ε_i were then scaled such that 99% of the values fitted within a specified range $[-w, w]$. Any remaining values exceeding this range were truncated to these limits. This did not have a significant effect on the realized variance of noise time series.

We varied the strength of the environmental noise by increasing the amplitude range of the noise time series w from ± 0.05 to ± 0.95 in increments of 0.05, which means that fluctuations in species' K_i range between $K_i \pm (K_i \times 0.05)$ and $K_i \pm (K_i \times 0.95)$. This is equivalent to increasing noise variance from approximately 0.0005 to 0.15 (asymptotical noise variances were estimated from 1000 replicate time series of 10 000 time steps). We have examined the generated noise time series and are confident that their standard deviation (over the simulation time-span of 200 steps) is not significantly affected by changing their desired autocorrelation and/or correlation structure. Thus, the results presented here are not an artefact of the algorithm used to generate the environmental noise time series.

The equivalency of species' response to the environmental variation was examined by varying the correlation between all pairs of species-specific environmental time series. This was done by assuming that the species-specific noise components $\varepsilon_{i,t}$ have a variance-covariance matrix, whose off-diagonal elements $\rho\sigma^2$ determine the covariance between the environments of different species (Ripa & Ives 2003). The results are presented here using values of $\rho=0$ or 0.9 (the covariance of standardized variables is equal to the correlation between them).

As environmental forcing affects population carrying capacity $[K_i(1+\varepsilon_{i,t})]$, the attractor that populations are approaching will change over time (attractor $= \mathbf{A}^{-1}\mathbf{K}$; elements of which can be negative even if $\mathbf{K}$ is positive). This temporally fluctuating attractor (species' target densities) can appear anywhere above, on or below the extinction threshold ($N=1$). Despite this stochasticity in species' target densities, populations may still fluctuate around the deterministic equilibrium point due to the stationary distribution of the autoregressive noise. However, when species display overcompensating growth, the location of the attractor in relation to the previous population size has an important influence on the direction of temporal population fluctuations.

Simulations were run over 200 time steps. This period allowed us to capture the essential behaviour of the community and minimized computing time. Furthermore, it represents a reasonable time-scale to operate over in terms of the management of real populations.

(c) Extinction scenarios

In the first scenario (i), we examined the ER to community members, without explicit extinctions occurring. Each species was assigned an extinction threshold equal to 1% of their respective equilibrium densities in the absence of competitors (K_i). The model was run for $T=200$ time steps and the amount of time any community member spent under the extinction threshold (ER) was recorded ($N_i^E = 0.01 \times K_i = 1$),

$$\text{ER} = \frac{\sum_{t=1}^T \sum_{i=1}^S N_{i,t} < N_i^E}{ST}. \quad (2.3)$$

Species equilibrium densities in the presence of competitors were found from the equation $\mathbf{N}^* = \mathbf{A}^{-1}\mathbf{K}$, where $\mathbf{A}^{-1}$ is the inverse of the interaction matrix $\mathbf{A}$ (Levins 1969; May 1974); in this case, all $N_i^* = 50$. As the noise term appears within the exponent in equation (2.1), population densities were always positive if initiated at a value $N_{i,1} > 0$.

In the second scenario (ii), we set $N_{i,t+1} = \text{Poisson}(N'_{i,t+1})$, i.e. the population density of each species was selected at random from a Poisson distribution with $N'_{i,t+1}$ as the expectation. As the Poisson process generates integer values, explicit extinction events ($N_{i,t+1}=0$) could occur in this scenario. This method can be thought of as introducing demographic stochasticity in small populations (e.g. Petchey *et al.* 1997; Ranta *et al.* 2006; Ruokolainen *et al.* 2007). Communities were simulated maximally 200 time steps and simulation was terminated at the first extinction. EP was then calculated as a percentage of the 10 000 simulation runs that led to the extinction of at least one species.

We went on to examine how species- and community-level population patterns were related to ERs, through the analysis of population synchrony between species, under environmental variation with different characteristic structures. When the system is not too close to the period-doubling boundary ($r=2$), covariance between interacting populations can be approximated as follows (Greenman & Benton 2005):

$$\text{Vec}(\mathbf{C}) = \left. \begin{aligned} &(\mathbf{I} - \kappa^2 \mathbf{B} \otimes \mathbf{B})(\mathbf{I} - \kappa \mathbf{I} \otimes \mathbf{B})^{-1} \mathbf{g} \\ &(\mathbf{I} - \kappa \mathbf{B} \otimes \mathbf{I})^{-1} (\mathbf{I} - \mathbf{B} \otimes \mathbf{B})^{-1} \text{Vec}(\mathbf{S}) \end{aligned} \right\}, \quad (2.4)$$

where $\text{Vec}(\mathbf{C})$ is the vectorized variance-covariance matrix; $\mathbf{I}$ is an identity matrix; κ is the autocorrelation coefficient of the environmental noise; $\mathbf{B}$ is the Jacobian matrix—summarizing linearized effects of community members upon each other (see appendix A)—and $\text{Vec}(\mathbf{S})$ is a vectorized variance-covariance matrix for the environmental noise (diagonal elements equal to noise variances σ_i^2 and off-diagonal elements equal to $\rho\sigma_i^2$). The $\otimes$ symbol indicates the Kronecker tensor product (producing all possible combinations between the elements in two matrices). The predictions from equation (2.4) were scaled to give the expected coefficient of variation ($\text{CV} = \sqrt{C_{ii}}/N_i^*$) and compared against the stochastic simulations in the first scenario (i.e. ER), which were also scaled to find the CV in the fluctuations of population density [$\text{s.d.}(N_{i,T})/\bar{N}_{i,T}$], where s.d. represents the standard deviation and $\bar{N}$ is the mean population density, for each species i , taken across the whole time series, $T=1-200$. The final stochastic CV was then averaged across all species. Mean cross-correlation (lag 0) between species was also recorded from simulations. Owing to the different persistence times of the full three-species community, under different disturbance regimes, these

Figure 1. The effect of environmental autocorrelation (κ) and the severity of environmental forcing (w) on (a,b) mean ER (measured as the amount of time a species spends with its density below a critical threshold) and (c,d) the probability of actual extinction events in simulated communities (EP). Species-specific noise terms are either (a,c) uncorrelated ($\rho=0$) or (b,d) positively correlated ($\rho=0.9$). Other parameter values are as follows: $K=100$, $r=1.8$, $S=3$, $\alpha_{ij}=0.5$. Results are based on 1000 simulated communities for each parameter combination in (a,b) and on 10 000 communities in (c,d).

analyses were not carried out for the second scenario (ii), as the noise time series was scaled to have the same variance independently of noise colour (equation (2.2)) at the desired time-scale (200 time steps). As a result, the analysis of population variability at a shorter time-scale could have been burdened by potentially increasing variance with increasing noise reddening (Lawton 1988), leading to unreliable results.

In both the scenarios, we analysed the model with the species-specific noise terms $\varepsilon_{i,t}$ being either uncorrelated or positively correlated. Across simulations, autocorrelation in the environmental variation (κ) was varied between -0.75 and 0.75 . In nature, environmental variation is most likely to be pink in colour (Vasseur & Yodzis 2004), but some climatic indices are known to have negative autocorrelation over specific time-scales (e.g. Burgers 1999). All parameter combinations were replicated 1000 times, unless stated otherwise. For each replicate, a new environmental time series was generated.

3. RESULTS

(a) Extinction risk and extinction probability

We first examined how different environmental autocorrelation structures, in combination with the severity of environmental forcing (noise severity), affected ER—defined as the proportion of time the density of each species spent below the threshold density, $N_i^E=1$ —or the probability of explicit extinction events occurring in a three-species competitive community (figure 1). We also considered the degree of equivalency in species' responses to a common environment (correlation between species-specific noise terms). In general, with uncorrelated

environmental forcing ($\rho=0$), mean ER in the community (the amount of time any species' density spent below the extinction threshold, N_i^E) increased with both increasing noise severity (w) and increasing noise autocorrelation (κ ; figure 1a). ER was reduced with a high correlation in species-specific noise ($\rho=0.9$) under all conditions (figure 1b). Contrary to the previous case (figure 1a), ER tended to decrease with increasing reddening in the environmental noise. The decrease in ER observed under high w and low κ is associated with the decreased correlation between population fluctuations (see below, §3b). In the first scenario (i), demographic stochasticity was not incorporated into the population dynamics, and consequently a non-zero ER was only related to a relatively high noise severity.

In the second scenario (ii), we examined the effects of varying noise autocorrelation and severity on EP by recording explicit extinction events in the presence of demographic stochasticity. With uncorrelated species-specific noise terms, EP increased with increasing positive autocorrelation under low to intermediate noise severity (figure 1c). Relatively high noise severity ($w \geq 0.75$) led to certain extinction of at least one species, irrespective of noise autocorrelation. Correlated environmental forcing always resulted in a reduction in extinction probabilities with increasing noise autocorrelation (figure 1d).

(b) Population variability and synchrony

To understand why the above results arose, we examined the characteristics of species-level population processes. When species were affected by independent disturbances

Figure 2. Population variability in simple three-species competitive communities under environmental forcing with different correlation and autocorrelation structures, predicted by (a,b) analytical linear analysis (equation (2.4)) or (c,d) stochastic simulation (equation (2.1)) methods. Variability is presented as the CV in all cases, which is identical for each species in (a,b) and taken as the mean across all species in (c,d). The autocorrelation (κ) and severity of environmental forcing (w) were varied in communities that experienced (a,c) independent ($\rho=0$) or (b,d) correlated ($\rho=0.9$) environmental variation. Results in (c,d) are based on simulations without explicit extinction events. Communities were simulated as described in figure 1.

($\mathbf{S}$ had zeros on the off-diagonal, $\rho=0$), equation (2.4) predicted increasing population variability (s.d.) when noise autocorrelation increases in absolute value $|\kappa|$, with blue noise generally associated with a higher variability than red noise (with the same $|\kappa|$; figure 2a). Our stochastic simulations revealed a similar relationship between κ and noise severity (w); increasing w led to an increase in population variability and red noise generally led to a higher variance than blue noise in uncorrelated environments (figure 2c). When populations had similar responses to the environment ($\mathbf{S}$ had non-zero off-diagonal, $\rho=0.9$), equation (2.4) predicted a decrease in population variance associated with increasing κ (figure 2b). This pattern was qualitatively repeated in our stochastic simulations (figure 2d).

The linear analysis predicted that population correlation should decrease with increasing noise reddening (figure 3a); this decrease should be stronger when populations face independent disturbances ($\rho=0$) than when species-specific disturbances are highly correlated ($\rho=0.9$; figure 3b). If the correlation in noise terms is equal to 1, populations fluctuate in perfect synchrony, irrespective of the sign of κ . In more detail, $\rho=0$ led to high synchrony under blue noise and asynchrony under red noise, whereas $\rho=0.9$ resulted in differing levels of synchrony under both blue and red noise. These aspects of equation (2.4) were in agreement with the stochastic simulations with very weak noise (figure 3c,d). However, while the linear analysis did not indicate any influence on population synchrony with increasing variance in

the environmental noise (figure 3b), our stochastic simulations revealed a strong relationship between synchrony and noise severity (figure 3d), to the extent that at the highest levels of noise variance examined here, changes in the autocorrelation structure had little effect on population synchrony. The inability of equation (2.4) to predict any effect of increasing w can be understood through a closer examination of its algebraic terms and that of the matrix of between-species correlation coefficients ($\mathbf{R}$), given as

$$\mathbf{R} = \frac{\mathbf{C}}{\sqrt{\text{diag}(\mathbf{C})\text{diag}(\mathbf{C})^T}}, \quad (3.1)$$

where $\text{diag}(\mathbf{C})$ is a column vector of the main diagonal of the variance-covariance matrix of population densities (equation (2.4)). The term for the variance of the noise (σ^2) appears only once as a simple multiplicative factor of the main-diagonal and off-diagonal elements of $\mathbf{C}$. Therefore, while the between-species covariance varies with w , this is not seen in the correlation matrix, as it is cancelled in equation (3.1).

The discrepancy between the linear analysis and the simulation results in the case where $\rho=0$ was not due to the failure of the linear approximation at the relatively high r -value used here ($r=1.8$; Greenman & Benton 2005). The evaluation of equation (2.4) at a lower r -value (e.g. $r=1.5$) shifted only the parameter region producing the observed pattern in population variability, such that an increase in population variability with increasing noise autocorrelation was observed at higher values of κ . The

Figure 3. Population synchrony in simple three-species competitive communities under environmental forcing with different correlation and autocorrelation structures, predicted by (a,b) analytical linear analysis (equation (2.4)) or (c,d) stochastic simulation (equation (2.1)) methods. Synchrony is predicted by the (a,b) linear analysis and (c,d) stochastic simulation methods, taken as Pearson's correlation coefficients in all the cases. Results in (c,d) are based on simulations without explicit extinction events. In (a,b), all species pairs have an identical predicted level of synchrony, whereas, in (c,d), results are given as the mean synchrony across all unique species pairs ($i \neq j$). Environmental noise is either (a,c) independent ($\rho = 0$) or positively correlated (b,d) between species. Communities were simulated as described in figure 1.

examination of eqn (12) in Greenman & Benton (2005), which was derived for communities close to the bifurcation boundary, confirms this. This function was also incapable of replicating the simulation results under large w values. Our results therefore extend those of Greenman & Benton (2005) by illustrating the actual influence of increasing strengths of environmental variation on population variability and synchrony.

4. DISCUSSION

The behaviour of interacting populations in variable conditions depends on the interplay between the intrinsic and extrinsic factors: different intrinsic growth rates interact with different environmental autocorrelation structures, impacting upon population variability and ER (Kaitala *et al.* 1997; Petchey *et al.* 1997; Ripa & Heino 1999; Heino *et al.* 2000; Heino & Sabadell 2003; Schwager *et al.* 2006). One interesting feature is that with overcompensatory population dynamics, increasing noise autocorrelation can lead to a decrease in EP (Petchey *et al.* 1997; Schwager *et al.* 2006; Ruokolainen *et al.* 2007). We have shown here that this result arises due to the way environmental noise is amplified in the community dynamics, under different regimes of environmental forcing. We also note that the results reported here are not only restricted to overcompensatory dynamics, but also apply to undercompensating population growth (results not shown), contrary to previous results (Petchey *et al.* 1997; Ruokolainen *et al.* 2007). An interesting

finding was that there were considerable discrepancies between the results from a linear approximation technique (Greenman & Benton 2005) and stochastic simulations of our model, especially when considering between-population synchrony under anything other than weak environmental variation. This raises at least some doubt over the applicability of linear approximation of noisy nonlinear systems (see also Bjørnstad *et al.* 2004; Reuman *et al.* 2006), and knowledge of how species respond to environmental fluctuations in natural ecosystems (e.g. Inchausti & Halley 2001, 2002) will help us to decide when certain model assumptions are valid.

The numerical evaluation of the analytical solutions reveals an inability to capture some of the broad patterns or the magnitude of variability in the simulated time series (figure 2; electronic supplementary material). This rises in part from the loss of information on realized densities, when the Jacobian matrix is used in equation (2.4). As $K_i = K$ for all i , the K term is lost from the Jacobian and information about species' realized densities is missing from the function used to derive the population variance. Scaling K to unity has a number of important effects on the difference between the analytical and simulation results. As well as changing the dominant eigenvalue of the system, scaling K results in a massive reduction in the variance of the simulated time series (of the order of 10^5), but does not change the qualitative pattern at all. There is no change in the predicted variance from equation (2.4). However, when equation (2.4) is scaled to give the CV $\sqrt{C_{ii}/N_i^2}$, scaling K to 1 increases the predicted CV by a

factor of 100. This effect is not seen in the simulated time series. Therefore, while scaling K at least brings the analytical and simulation CV results within an order of magnitude, it does not change the qualitative results. When $K=1$, simulated CV is overestimated by equation (2.4) in highly variable (high w), blue environments whether they are correlated or not (bottom right of figure 2a–d). This contrasts with the case when $K=100$, where the CV derived analytically always underestimates the CV found from simulations. Scaling K had no effect on between-species correlations.

In theoretical models and laboratory microcosms, population ER generally increases with increasing temporal autocorrelation (Halley 1996; Petchey *et al.* 1997; Pike *et al.* 2004; Schwager *et al.* 2006). However, populations with different dynamical behaviour (over- or undercompensating) tend to react differently to increased temporal autocorrelation (Roughgarden 1975; Ripa & Lundberg 1996; Petchey *et al.* 1997; Ripa & Heino 1999; Schwager *et al.* 2006). In general, ER increases with increasing noise reddening in undercompensating populations, whereas the opposite is true for overcompensating populations (Petchey *et al.* 1997; Ripa & Heino 1999; Schwager *et al.* 2006).

The mechanism behind the contrasting differences in ER between populations with under- and overcompensating dynamics is due to the interference between the noise frequency and population frequency (Greenman & Benton 2005). That is, if population dynamics and environmental forcing coincide in their frequencies, noise variance is amplified in the population dynamics (Ripa & Ives 2003; Greenman & Benton 2005). By contrast, when the two have incoherent frequencies, noise variance is dampened in the populations. Therefore, in a single-species system, high (low)-frequency fluctuations in an overcompensating (undercompensating) population are dampened (amplified) by red (i.e. low-frequency) noise, and amplified (dampened) by blue (i.e. high-frequency) noise (Roughgarden 1975; Kaitala *et al.* 1997; Ripa & Heino 1999; Greenman & Benton 2005). When populations are engaged in competitive interactions in multi-species communities, the influence of environmental variation on population ER may not be as straightforward (Ripa & Ives 2003; Ruokolainen *et al.* 2007).

An additional complication is added by the fact that species may vary in their innate response to the environment. In a theoretical context, the species-specific noise terms that are applied to a system may be correlated with different degrees. In general, decreasing correlation between species-specific noise terms decreases between-species synchrony in a community (Ripa & Ives 2003). For example, in the present model of multi-species competition, populations fluctuate due to external (environmental) forcing that directly affected density-dependent population processes (e.g. Heino *et al.* 2000; Lehman & Tilman 2000; Ives & Hughes 2002). Population density in these types of models can be thought of population biomass without loss of generality; therefore, the sum of all community members' densities can represent the community biomass, which will affect individual species' dynamics directly through the competition terms in equation (2.1), indicating that the level of population synchrony will impact upon dynamics at the community level (Ives *et al.* 1999; Ripa & Ives 2003). In addition to

the degree of correlation between species-specific noise terms, population synchrony is also affected by noise colour, such that increased noise reddening decreases the correlation between populations (Ripa & Ives 2003; Greenman & Benton 2005).

What results is that positively (negatively) autocorrelated environmental variation reduces (increases) population synchrony and consequently the variability in community biomass fluctuations (Kaitala *et al.* 1997; Ripa & Heino 1999; Ripa & Ives 2003). Hence, positive noise autocorrelation has an opposite effect on the dynamics rather than on the environmental correlation (correlation between species-specific noise terms), whereas negative autocorrelation has a similar effect. Analysing randomly assembled model communities of five competitors, Ruokolainen *et al.* (2007) found that there was a decrease in EP associated with increased noise reddening with both zero and positive environmental correlation, when all community members had overcompensating renewal. However, Ruokolainen *et al.* (2007) measured EP independently for each species in the community and did not terminate their simulations upon the first extinction event. The result is that EP is elevated especially under blue noise due to 'mass' extinctions, where several or even all species go extinct nearly simultaneously, induced by high population synchrony (figure 3c,d), while any species remaining after an extinction in a red environment experienced less competition and their mean densities increased, moving away from the extinction boundary.

When single-species populations are coupled spatially, global extinction rate is related to subpopulation synchrony (Heino *et al.* 1997; Palmqvist & Lundberg 1998; Amritkar & Rangarajan 2006). Increasing synchrony between habitat patches increases global ER in a spatially structured population. In addition, there is an interaction between noise severity and between-patch synchrony, such that decreasing synchrony allows higher population fluctuations and vice versa (Palmqvist & Lundberg 1998). Here, we demonstrated that the above factors reported for single-species systems in space and time and for two-species models in time, act in tandem in affecting EP in multi-species communities. An important feature of our results is that while population synchrony is detrimental in a blue environment, decreasing population synchrony in a red environment leads to an increased ER. By contrast, when a community is partitioned over several patches, increasing noise autocorrelation increases species persistence (Gonzalez & Holt 2002; Long *et al.* 2007), which can again be accounted to decreased subpopulation synchrony.

As a final point, we consider the difference between ER (relative time a population spends below a certain threshold) and the probability of actual extinctions (figure 1). ER was in general lower than the respective EP. ER may be virtually zero at low to intermediate noise severities (w), while EP may be considerable. This is because in the second scenario (ii), where we measure EP using Poisson-distributed population densities, extinctions may occasionally occur from much higher densities than the extinction threshold ($N^E=1$) in the first scenario (i). This point shows that whenever extinctions are considered, it should be made clear whether ER (preferable in natural populations) or actual EP is of interest, because these two measures do not necessarily

coincide (Schwager *et al.* 2006). It is also important to consider the specific way ER is measured, for example in terms of the time spent with a population density below some critical threshold density.

This work has demonstrated that qualitative and quantitative changes in external disturbances may have dramatic effects on community dynamics and potential extinction events. This can be important when assessing the effects of environmental changes for conservation purposes or when planning changes in species management strategies. Climate change has recently been shown to lead to differences in different features of the variation in a lake environment (O'Reilly *et al.* 2003). According to O'Reilly *et al.* (2003), increasing water temperature and decreasing wind velocity at Lake Tanganyika has decreased seasonal mixing of the water column and consequently reduced primary production. If environmental change involves a change in the autocorrelation structure (Wigley *et al.* 1998) and/or severity of fluctuations, species with different populations may find themselves at greater risk of extinction. Knowledge of how similar community members' responses are to environmental variation may help us to take appropriate actions to prevent species loss under different environmental scenarios.

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APPENDIX A

A.1 Population covariance

Calculation of equation (2.4) requires the community Jacobian, **B**. For the system considered in this paper, matrix **B** has $1 - r/(2\alpha + 1)$ on the diagonal and $-r\alpha/(2\alpha + 1)$ elsewhere,

$$\mathbf{B} = \begin{bmatrix} 1 - \frac{r}{2\alpha + 1} & -\frac{r\alpha}{2\alpha + 1} & -\frac{r\alpha}{2\alpha + 1} \\ -\frac{r\alpha}{2\alpha + 1} & 1 - \frac{r}{2\alpha + 1} & -\frac{r\alpha}{2\alpha + 1} \\ -\frac{r\alpha}{2\alpha + 1} & -\frac{r\alpha}{2\alpha + 1} & 1 - \frac{r}{2\alpha + 1} \end{bmatrix}. \quad (\text{A } 1)$$

In the present case where we consider diffuse competition ($\alpha_{ij} = \alpha_{ji} = \alpha$), the system (**B**) has the following three eigenvalues:

$$\left. \begin{aligned} \lambda_1 &= 1 - r \\ \lambda_{2,3} &= \frac{\alpha(2 + r) - r + 1}{2\alpha + 1} \end{aligned} \right\}. \quad (\text{A } 2)$$

The variance–covariance matrix for environmental noise is

$$\mathbf{S} = \begin{bmatrix} \sigma^2 & \rho\sigma^2 & \rho\sigma^2 \\ \rho\sigma^2 & \sigma^2 & \rho\sigma^2 \\ \rho\sigma^2 & \rho\sigma^2 & \sigma^2 \end{bmatrix}, \quad (\text{A } 3)$$

where σ^2 is the variance of the noise and ρ is the correlation between species-specific noise terms. Equation (2.4) combines the information in equations (A 1) and (A 3) to

produce a variance–covariance matrix for the interacting species (**C**, equation (2.4)). The exact algebraic solution of equation (2.4) is rather lengthy and is thus not presented here (but is available from the authors upon request). We note here that as noise variance (σ^2) appears only once as a simple multiplicative factor of each element of **C**, it is cancelled out when between-species correlations are calculated as

$$R_{ij} = \frac{C_{ij}}{\sqrt{C_{ii}C_{jj}}}. \quad (\text{A } 4)$$

Thus, equation (2.4) does not predict any changes in between-species synchrony with increasing noise severity (σ^2), contrary to what was observed in stochastic simulations.

A.2 Model sensitivity

The simulation results presented in this paper do not depend on the assumption of noise affecting density-dependent population processes, i.e. K . If noise is introduced additively into *per capita* growth rate rather than into carrying capacity, such that

$$N_{i,t+1} = N_{i,t} \exp \left[r \left(1 - \frac{1}{K_i} \sum_{j=1}^S \alpha_{ij} N_{j,t} \right) + \varepsilon_{i,t} \right], \quad (\text{A } 5)$$

the community dynamics remain somewhat unchanged from those considered in equation (2.1). Despite the similarity in community dynamics, a notable difference is that community variability is clearly lower when noise affects *per capita* growth rate than when it affects the carrying capacity (results not shown). This will have an impact on the absolute values of ER and probability, but not on their qualitative relationship with noise autocorrelation and severity.

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