

Noise colour, synchrony and extinctions in spatially structured populations

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I analyse the importance and influence of noise with positive autocorrelation ('red noise') to extinction risk in spatially structured populations using a set of simple population dynamical simulation models. Noise colour has a major influence on both local and global extinction risk, level of synchrony in population dynamics, and spatial patterns of the synchrony. Generally, the stronger the autocorrelation in the noise is, the higher is the global extinction risk – even though local extinction risk may decrease. Populations with high intrinsic growth rate are more prone to global extinction than populations with low growth rate. The influence of autocorrelated noise on population synchrony depends strongly on the way in which environmental noise is introduced into the model.

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One of the most important goals for contemporary population ecology is to gain an understanding into the influence of different environmental factors (along with factors intrinsic to populations) on the risk of population extinction. It is now generally recognized that it is important to take population structure, e.g., age-, stage-, or spatial structure, into account in analyses of extinction risk (Pimm 1991, Kokko and Ebenhard 1996, Hanski and Gilpin 1997). However, only recently it has been acknowledged that environmental variation may also have a structure – in time.

In most analyses the description of environmental variation is effectively 'white noise': the magnitude of stochastic environmental influence is independent from year to year. This is very puzzling since positive autocorrelation often characterizes temporal variation observed in nature (Steele 1985, Pimm 1991, Halley 1996, Lawton 1997). Recently, in their seminal paper, Ripa and Lundberg (1996) attacked the problem and were able to show that autocorrelated noise, as compared to white noise, may severely bias estimates of extinction risk derived from simple population dynamical models.

In particular, they showed that increasing positive autocorrelation in the environmental noise results in decreasing risk of extinction. However, this result is not generally true: whether autocorrelated noise increases the extinction risk or not depends very much on model details (M. Heino, V. Kaitala and J. Ripa unpubl.). In particular, the way noise is incorporated into a model, and the time scales in which the extinctions are scored and that the variance of noise is independent of its colour, are important.

Positive autocorrelation in noise results in a dominance of low frequencies in the spectral decomposition of the time series (Halley 1996, Ripa and Lundberg 1996). Similarly, low frequencies are dominating in red visible light. Therefore, the terms 'red noise' and 'red-shifted noise' have been coined for noise with positive autocorrelation. In a similar manner, noise with negative autocorrelation is called 'blue' (or blue-shifted), because of the dominance of high frequencies. Blue-shift is an unlikely property of natural noise, and the analysis I present here is restricted to noise with non-negative autocorrelation (white or red noise). I use the

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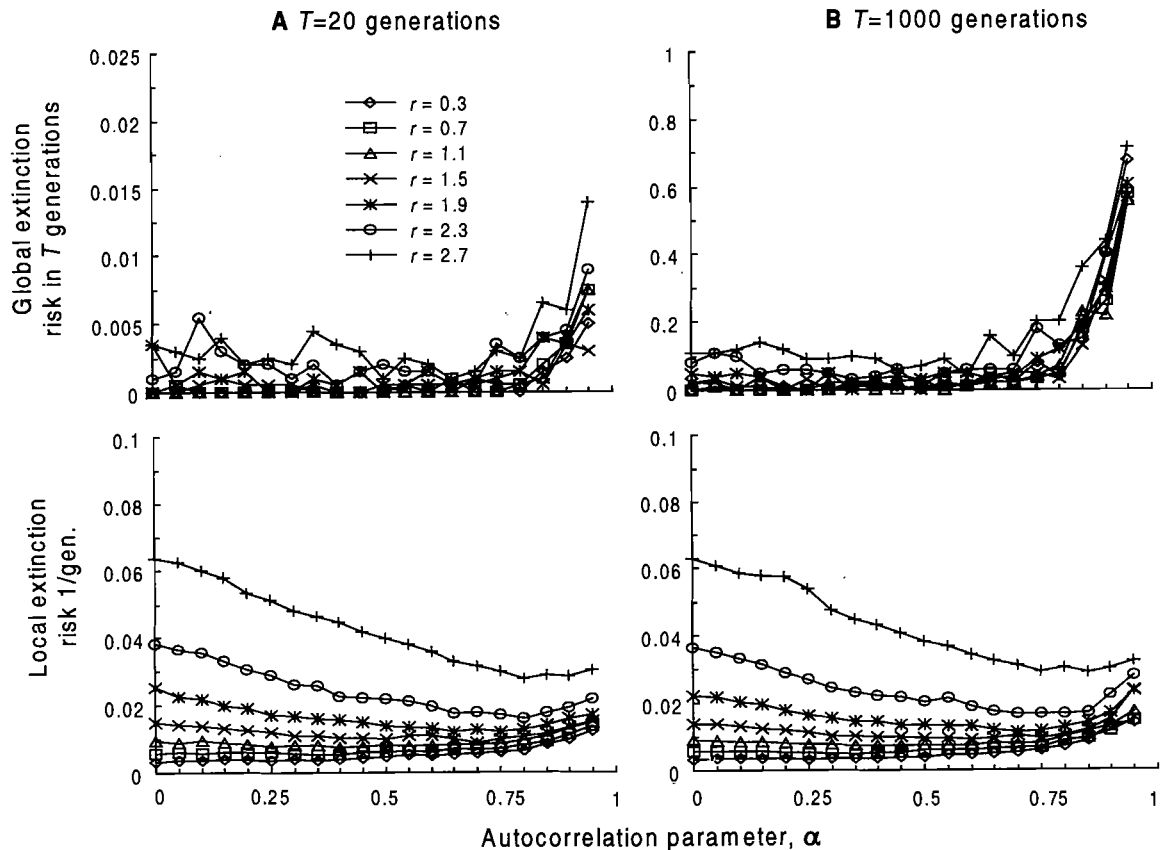


Fig. 1. Extinction risk and synchrony when environmental variation influences carrying capacity. The autocorrelation parameter α determines the colour of environmental noise: for $\alpha = 0$ the noise is white, and for $\alpha > 0$ red-shifted. In A the duration of the simulation ($T = 20$) is the same as the time window W in which the variance of environmental noise is independent of its colour. In B the extinctions were scored over an extended period (1000 generations). Different curves are for different (mean) intrinsic growth rates (r). The deterministic dynamics are chaotic for $r = 2.7$, cyclic for $r = 2.3$ and stable for other values used. The results are based on 2000 (A) or 100 (B) replicate runs. Parameter values: $\sigma_g = \sigma_r = 0.25$, $P = 0.1$, $m = 0.1$ and $c = 1$.

terms positive autocorrelation and red-shift interchangeably.

Many populations have some spatial structure, such that semi-independent local populations are linked by migration, thus forming a 'global' population or metapopulation (Hanski and Gilpin 1997, Ranta et al. 1997). Migrating individuals can recolonize habitat patches where a local population has gone extinct. Thus, the extinction risk of the global population is usually much lower than in any of the local populations, at least if the dynamics of local populations are not too synchronous (Harrison and Quinn 1989, Foley 1997, Heino et al. 1997, Palmqvist and Lundberg 1998). However, previous analyses on extinction risk in spatially structured populations have not considered the complication arising from the autocorrelation structure of environmental noise. The aim of this paper is to bring these two threads of theory together in an analysis of the extinction risk in spatial structured populations subjected to red-shifted environmental noise.

Methods

I use a spatially structured population dynamics model adapted from Ranta et al. (1995). Each local population (patch) obeys the Ricker type population dynamics, and they are connected by migration. Migration and reproduction/density dependence are assumed to be temporally separated: migration occurs between time t and $t + \epsilon$, followed by density-dependent reproduction between time $t + \epsilon$ and $t + 1$. The population dynamics can then be represented by the difference equation

$$N_{t+1}^i = N_{t+\epsilon}^i \exp(r_t^i (1 - N_{t+\epsilon}^i / K_t^i)), \quad (1)$$

where i is the patch index, N_t^i is size (density) of subpopulation i at time t , r is the intrinsic rate of increase, and K is the carrying capacity. Either r or K is assumed to be influenced by environmental variation.

Migration is distance-dependent with the functional form

$$N_{t+\epsilon}^i = (1-m)N_t^i + m \sum_{j,j \neq i} Z N_t^j \frac{\exp(-cd_{ij})}{\sum_{k,k \neq j} \exp(-cd_{jk})}, \quad (2)$$

where m is the fraction of individuals leaving a patch, c is a parameter determining the distance dependence of migration (low values correspond to long migration distances/weak distance dependence), and d_{ij} is the distance between patches. Z is a random variable which takes value 1 with probability P and value 0 with probability $1-P$. Thus, P is the probability that migration from patch j to i is successful – otherwise all migrants die.

The environmental variation is modelled as a stationary first-order autoregressive process (AR₁, cf. Ripa and Lundberg 1996)

$$\phi_t = \begin{cases} 0 & \text{for } t = 0, \\ \alpha\phi_{t-1} + \beta(\alpha, W)\epsilon_t & \text{otherwise,} \end{cases} \quad (3)$$

where α ($|\alpha| < 1$) is an autocorrelation parameter determining the colour of the time series: for $\alpha > 0$, the time series is red-shifted, while $\alpha < 0$ results in a blue-shift.

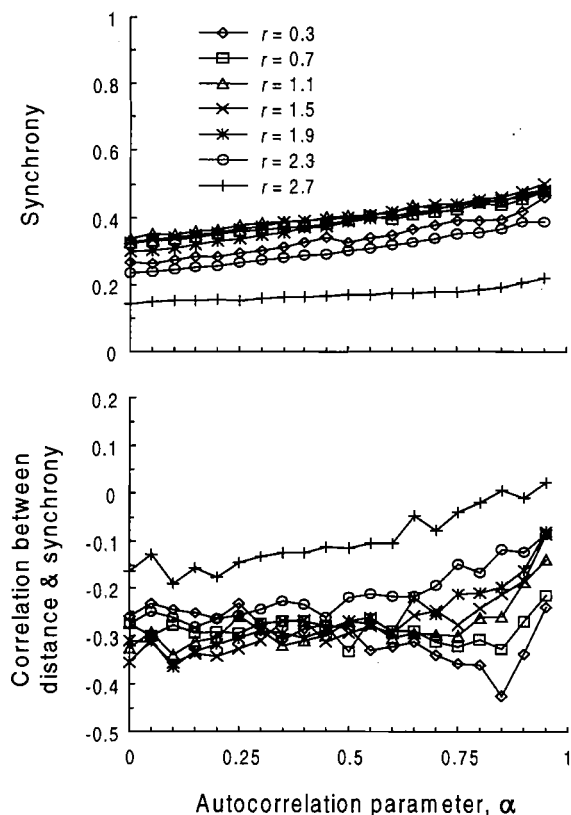


Fig. 2. Synchrony in population dynamics as a function of 17 autocorrelation parameter α . The level of synchrony is measured as the average pair-wise cross-correlation (time lag zero). Negative correlation between distance and synchrony indicates that the level of synchrony decays with increasing distance between subpopulations. Other details as in Fig. 1.

Random variables ϵ_t were normally distributed with zero mean and unity variance. The parameter $\beta(\alpha, W)$ was determined numerically such that the (expected) variance for time series of length $W=20$ is constant at unity for all α . For time series shorter than W , the expected variance is <1 , for longer time series >1 . The problem of strong dependence of variance on sample length for red-shifted noise, and the rationale for different scalings of variance are discussed in Heino et al. (M. Heino, V. Kaitala and J. Ripa unpubl.).

In all simulations, ten local populations with mean carrying capacity one were used. The patches had random locations in a 10×10 coordinate space; the coordinates were used to calculate Euclidean distances between the patches.

Local extinction was scored if N_{t+1}^i was below 0.01. Global extinction was scored if all ten local populations were extinct. Global extinction risk is the proportion of replicate simulations ending in global extinction in either 20 or 1000 generations. In each simulation, a new random patch set was used.

Results

In a first set of simulations, environmental variation influences carrying capacity:

$$K_t^i = K_0 + \sigma_g \phi_t^g + \sigma_i \phi_t^i, \quad (4)$$

where superscript g stands for global noise (that is, noise identical for all local populations) and i for local noise (unique to each local population). Here both local and global noise are assumed to have same colour (α) and standard deviation $\sigma^g = \sigma^i$. The simulations were initiated with population size one and carrying capacity K_1^i in each patch.

Fig. 1 shows the dependence of extinction risk on the colour of environmental noise. In Fig. 1A the extinction risk is scored over 20 generations, while in 1B the period is extended to 1000 generations. The dependence of extinction risk on noise colour is very similar for both time scales: global extinction risk is almost independent of noise colour for $\alpha < 0.75$, and then increases as the noise gets more red-shifted. The local extinction risk behaves in a similar manner for low intrinsic growth rates. For $r \geq 1.5$, the local extinction risk first decreases as α increases, and then slightly increases. Both local and global extinction risk increase along with increasing r .

The level of synchrony in population dynamics (measured as the average pair-wise cross-correlation with time lag zero) increases with increasing autocorrelation parameter α (Fig. 2). The level of synchrony decreases with increasing intrinsic growth rate. A marked decrease in synchrony occurs when intrinsic growth rate

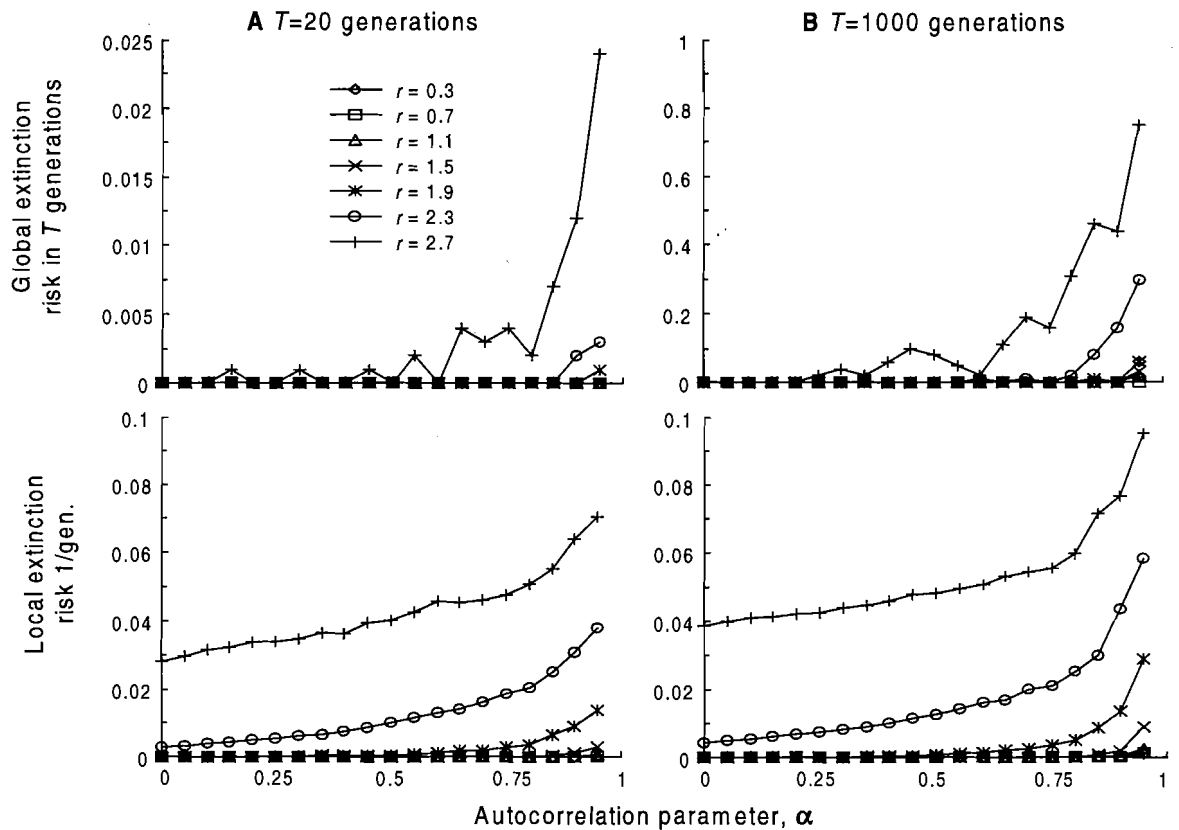


Fig. 3. Extinction risk and synchrony when environmental variation influences intrinsic growth rate. The results are based on 1000 (A) or 100 (B) replicate runs. See Fig. 1 for other details.

increases from $r=2.3$ to $r=2.7$. For the latter value, deterministic dynamics are chaotic. The level of synchrony between any two patches usually decreases with increasing distance between them (Fig. 2). There is a tendency for this decay in synchrony to become weaker as environmental autocorrelation increases.

In a second set of simulations, environmental variation influences intrinsic growth rate:

$$r_t^i = r_0(1 + \sigma\phi_t^g + \sigma\phi_t^l). \quad (5)$$

The simulations were initiated with population size one and intrinsic growth rate r_0^i in each patch.

When the noise influences intrinsic rate of increase, both local and global extinction risk increase with increasing autocorrelation of noise, i.e. red-shift (Fig. 3). For low intrinsic growth rate, however, the risk is negligible and below the detection limit of the simulations. The risk of extinction increases when r increases.

There is a slight tendency for the level of synchrony in population dynamics to decrease with increasing autocorrelation of noise; for some values of intrinsic growth rate there is hardly any change (Fig. 4). Again, the level of synchrony decreases with increasing intrinsic growth rate. The dependence of synchrony on distance is very weak. Note that there is a tendency of

correlation to decrease with increasing autocorrelation – an opposite pattern to the one observed when noise affects the carrying capacity.

Both above models yielded the result that the extinction risk increases with increasing intrinsic growth rate, despite a decreasing level of synchrony in population dynamics. This observation seems to contradict some earlier studies, in which asynchronous dynamics tended to protect populations from global extinction (Allen et al. 1993, Heino et al. 1997, Palmqvist and Lundberg 1998). A possibility is that in the present simulations the protective effect of asynchronous dynamics is overshadowed by other factors, e.g., the wilder oscillations in population size associated with chaotic dynamics. To resolve whether this might be the case, I repeated the simulations with relative importance of local noise changed.

The total variance of environmental noise is the sum of the variances of local and global noise: $\sigma_t^2 = \sigma_g^2 + \sigma_l^2$. In the following simulations, σ_g and σ_l are chosen such that $\sigma_l^2 = 0.8\sigma_t^2$ (local noise dominating) or $\sigma_l^2 = 0.2\sigma_t^2$ (global noise dominating; see also Palmqvist and Lundberg (1998) who use a similar procedure). The total environmental variance is constant at $\sigma_t^2 = 0.125$, as in the previous simulations.

Global extinction risk is negligible if local noise dominates the environmental variation influencing carrying capacity (Fig. 5). However, if global noise dominates, the global extinction risk is much higher, despite a similar local extinction risk in both cases. The difference seems to be attributable to a difference in the level of synchrony: if local noise dominates the environmental variation, the local dynamics are largely asynchronous. The level of synchrony is much higher when global noise dominates. Note also that the distance dependence of synchrony is much lower when local noise dominates environmental fluctuations.

Largely similar results are obtained if noise influences intrinsic growth rate (Fig. 6). If global noise dominates the environmental variation, a high risk of extinction co-occurs with a high level of synchrony. The opposite is true if local noise dominates: low level of synchrony is associated with low global extinction risk, while the local extinction risk hardly changes. The distance dependence of synchrony is generally weak.

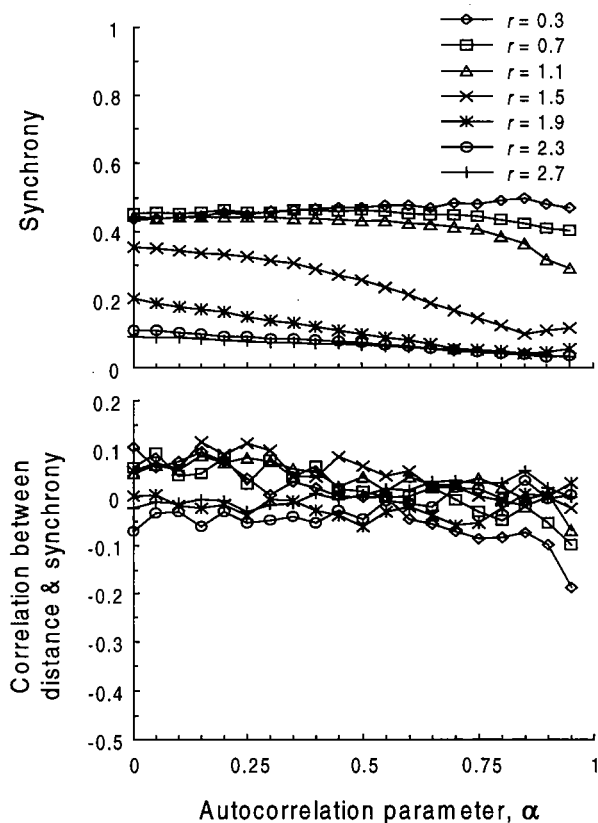


Fig. 4. Synchrony in population dynamics when environmental variation influences intrinsic growth rate. See Fig. 2 for other details.

Discussion

The results presented here unambiguously show the importance of considering temporal structure of environmental variation when extinction risk is assessed with the help of simple population dynamical models. This observation was first pointed out by Ripa and Lundberg (1996) in a context of models for single populations. Ripa and Lundberg (1996) found that increasing red-shift is associated with decreasing extinction risk. An opposite result is obtained here: red-shift in noise increases the extinction risk, at least if the red-shift is strong enough. This conclusion is in line with the result obtained, in a different context, that red-shifted noise tends to decrease local diversity (Caswell and Cohen 1995). The difference to the results by Ripa and Lundberg (1996) arises at least partially from different scaling of variance: Ripa and Lundberg (1996) scaled the variance to be asymptotically independent of colour ($W = \infty$). In this paper, variance of noise is scaled to be independent of colour at the short time scale ($W = 20$). The justification for such scaling is discussed elsewhere (M. Heino, V. Kaitala and J. Ripa unpubl.).

The autocorrelation of environmental noise (colour) affects also the synchrony in the population dynamics. However, the influence depends on the way environmental noise is included in the model. If noise influences carrying capacity, synchrony increases with increasing autocorrelation of noise. The opposite is usually true when noise influences intrinsic growth rate. Synchrony decaying markedly with distance, typical for large-scale spatial dynamics in the wild (Ranta et al. 1995, 1997), is observed only if noise influences the carrying capacity.

The influence of noise on population dynamics depends on the way noise is introduced into the model. If population size is close to carrying capacity, fluctuations in the intrinsic growth rate will have hardly any effect on the population growth ratio N_{t+1}/N_t . Therefore, populations which tend not to oscillate wildly (i.e., populations with low r) experience very little stochasticity, and hardly ever go extinct (see Figs 3 and 6). However, fluctuations in carrying capacity influence population growth ratio at all population sizes, and the effect is more pronounced the higher the population size is – only very small populations, well below the carrying capacity, remain virtually unaffected. Thus, these two ways of introducing noise represent rather different ecological scenarios on how populations might experience environmental stochasticity.

Some earlier analyses have indicated a generally tight correlation between the level of synchrony and global extinction risk (Heino et al. 1997, Palmqvist and Lundberg 1998). The relationship is more complex in the models analysed here. When intrinsic growth rate increases, the risk of global extinction increases. This

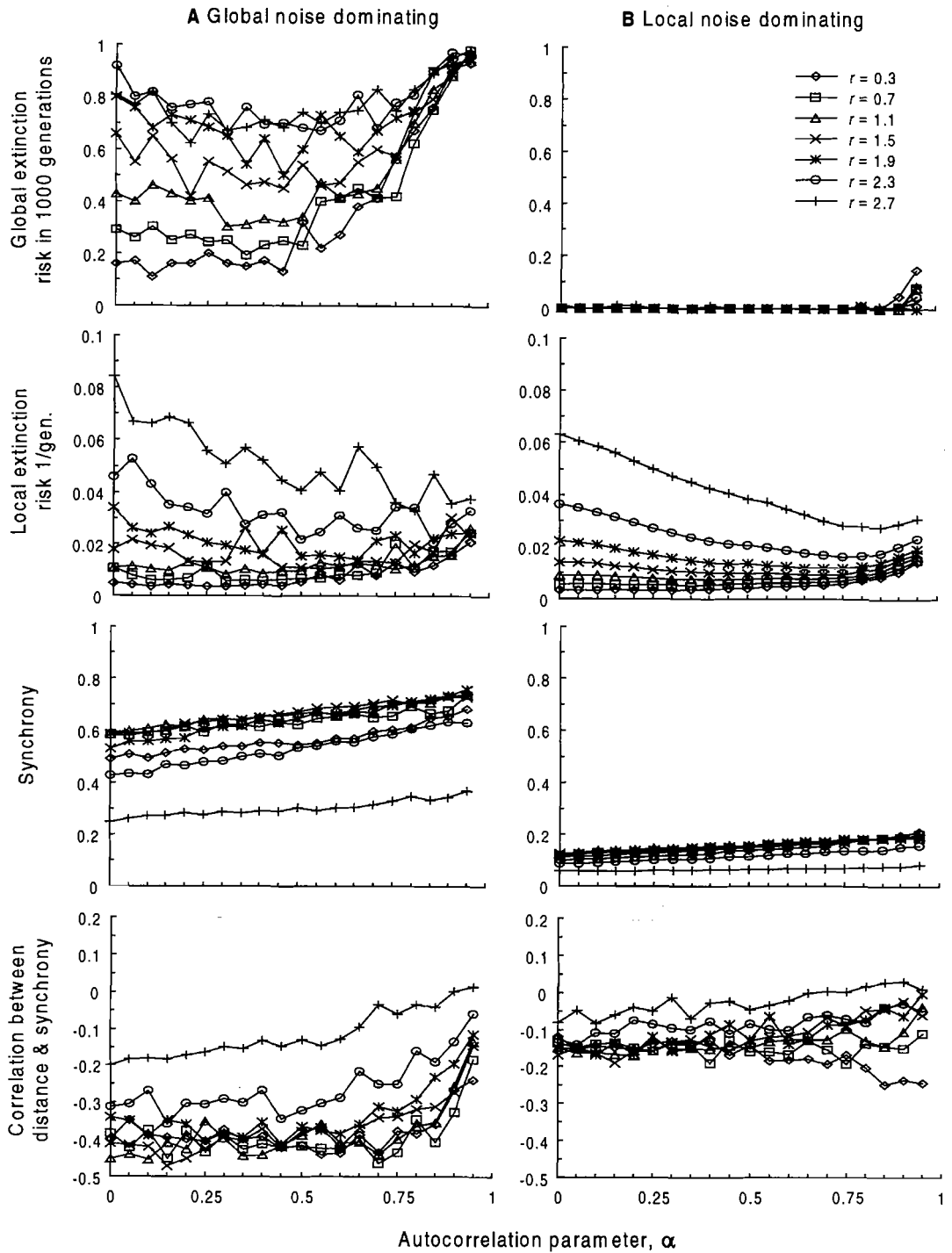


Fig. 5. Importance of relative strength of local vs global noise affecting carrying capacity. Global extinction risk and synchrony are very low when local noise dominates (B), as opposed to A in which global noise dominates. Local extinction risk is not greatly affected. This indicates high importance of desynchronization of local dynamics to global extinction risk. Global noise accounts for 30% of the total environmental variance $\sigma_g^2 + \sigma_l^2 = 0.125$ in A and only 20% in B. The total variance is the same as in Fig. 1 where global and local noise are equally important. The results are based on 100 replicate runs. Parameter values: $P = 0.1$, $m = 0.1$ and $c = 1$.

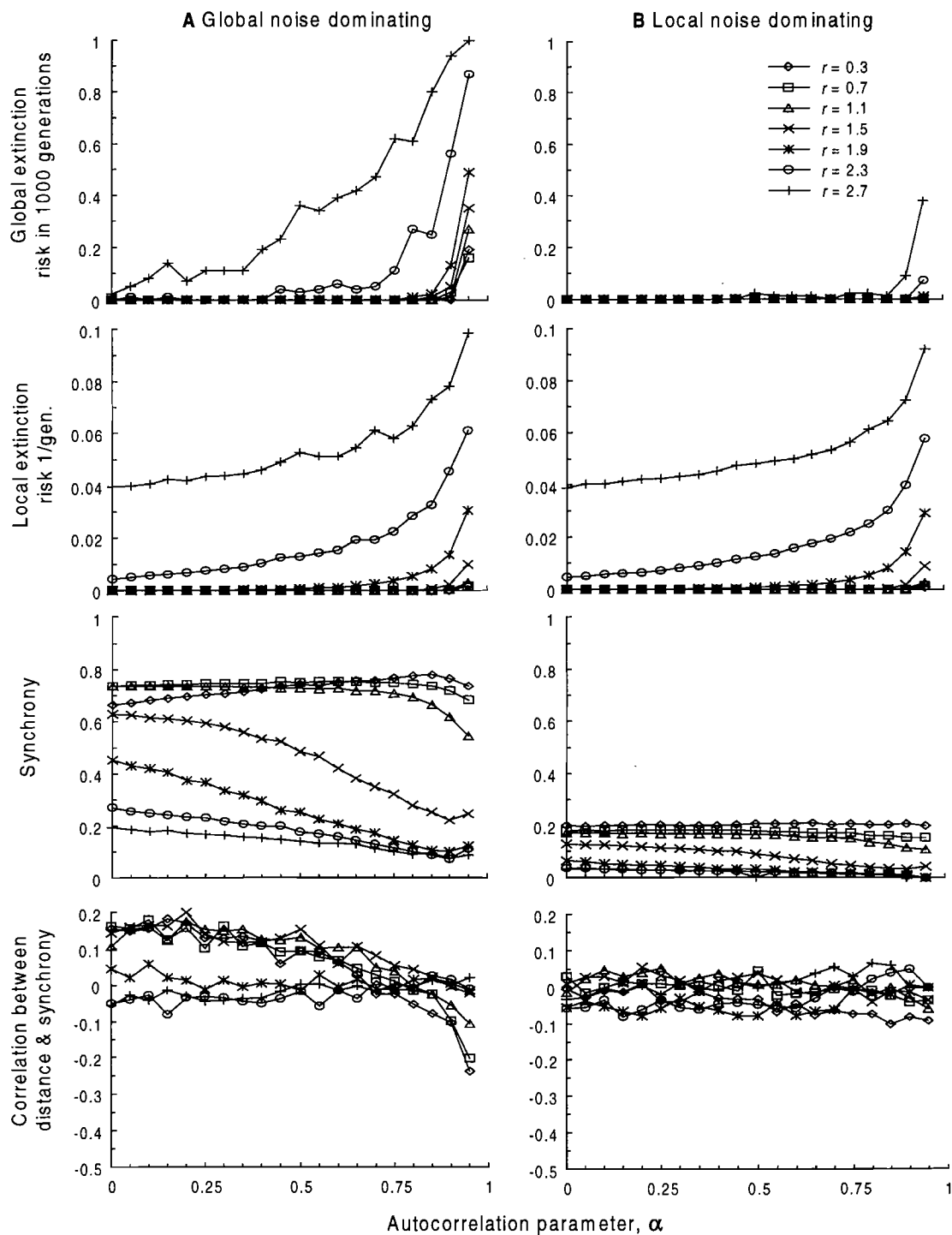


Fig. 6. As Fig. 5, but the environmental noise influences intrinsic growth rate. Compare also Figs 3B and 4 with equal importance of global and local noise.

occurs despite the decreasing level of synchrony. Moreover, when the autocorrelation in the noise is increased, the extinction risk increases, while the level of synchrony usually decreases. However, if synchrony decreases because the relative importance of local noise

increases, a marked decrease in global extinction risk is observed. Thus, the way in which a change in synchrony is achieved is important. Any change in level of synchrony is coupled with changes in other aspects of the dynamics. Even though a decrease in synchrony is

expected to have a decreasing influence on risk of extinction, this effect may be overshadowed by other factors influencing risk of extinction.

As a final word of warning, I want to stress the model dependence of the results of this paper. Depending on the way in which noise is introduced to the model, qualitatively different conclusions on the dependence of both extinction risk and patterns of population synchrony on noise colour may be drawn. This observation highlights the need to acknowledge the fact that conclusions drawn from some model might depend on seemingly subtle differences in model structure (e.g., Pascual et al. 1997). As the Ricker-type population dynamics models best represent the dynamics of univoltine arthropods, the generality of results obtained in this paper need to be checked with more complicated population dynamics models.

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