

Synchronous dynamics and rates of extinction in spatially structured populations

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SUMMARY

We explore extinction rates using a spatially arranged set of subpopulations obeying Ricker dynamics. The population system is subjected to dispersal of individuals among the subpopulations as well as to local and global disturbances. We observe a tight positive correlation between global extinction rate and the level of synchrony in dynamics among the subpopulations. Global disturbances and to a lesser extent, migration, are capable of synchronizing the temporal dynamics of the subpopulations over a rather wide span of the population growth rate r . Local noise decreases synchrony, as does increasing distance among the subpopulations. Synchrony also levels off with increasing r : in the chaotic region, subpopulations almost invariably behave asynchronously. We conclude that it is asynchrony that reduces the probability of global extinctions, not chaos as such: chaos is a special case only. The relationship between global extinction rate, synchronous dynamics and population growth rate is robust to changes in dispersal rates and ranges.

1. INTRODUCTION

Fluctuations in the numbers of individuals over time and space are typical for all animal populations. The understanding of the processes behind these fluctuations is one of the major goals of contemporary population ecology (e.g. Royama 1992). Despite the fact that the Hudson Bay Company's records of fur returns demonstrate large-scale spatial synchrony of lynx population dynamics in Canada (Elton & Nicholson 1942), theoreticians have largely ignored the possibility of synchrony in population dynamics. Nonetheless, since Elton's days synchronous fluctuations have been documented in many other populations of different animal taxa, such as snowshoe hare (Keith 1963), microtine rodents and vole-eating predators in Fennoscandia (Henttonen *et al.* 1987; Ims & Steen 1990), Finnish grouse populations (Lindén 1989; Ranta *et al.* 1995a), small game in Finland (Lindén 1988) and a variety of vertebrate taxa in Finland, including fish, mammals and birds (Ranta *et al.* 1995b), butterfly, moth and aphid populations in the British Isles (Pollard 1991; Thomas 1991; Hanski & Woiwod 1993; Sutcliffe *et al.* 1996) and a few carabid beetle species in the Netherlands (Baars 1979; den Boer 1981). The presumable generality of spatial synchrony calls for an analysis of its effect on extinction risks of local and global populations.

Chaotic population dynamics are usually characterized by low minimum population sizes, which are expected to increase the probability of extinction (Berryman & Millstein 1989). However, Allen *et al.* (1993) showed that chaotic population dynamics may actually reduce the risk of extinction in a spatially

structured population. They hypothesized that this 'protective' effect of chaos is based on its desynchronizing effect. Unfortunately, they do not give any measures of spatial synchrony to validate their hypothesis.

In this endeavour we take the model by Allen *et al.* (1993) as a starting point in assessing the significance of spatial synchrony to the risk of extinction. The system we deal with is a spatially arranged set of subpopulations. Extinction rates of the subpopulations will be scored, together with the rates of global extinction, under varying conditions of subpopulation growth rates and local and global disturbances. We extend the model to acknowledge a more explicit spatial structure by making dispersal of individuals depend on the distances among the subpopulations. We show that it is asynchrony that reduces the probability of global extinctions, not chaos as such: chaos is a special case only among other desynchronizing factors including local noise and spatial arrangements.

2. METHODS

We use a spatially structured population dynamics model, in which the dynamics of the local populations obey the Ricker equation (Allen *et al.* 1993):

$$x_i(t+1) = x_i^m(t)e^{r(1-x_i^m(t))} + u_{i,t} + z_t, \quad (1)$$

where $x_i(t)$ and $x_i^m(t)$ are the numbers of individuals in patch i at time t before and after migration, respectively, r is population growth rate, $u_{i,t}$ is local noise, and z_t is global noise, which we refer to as the Moran effect (Moran 1953; Royama 1992). Following Allen *et al.* (1993), z_t were normally distributed random variables with mean 0 and standard deviation 1 with probability $p = 0.05$, and equal to

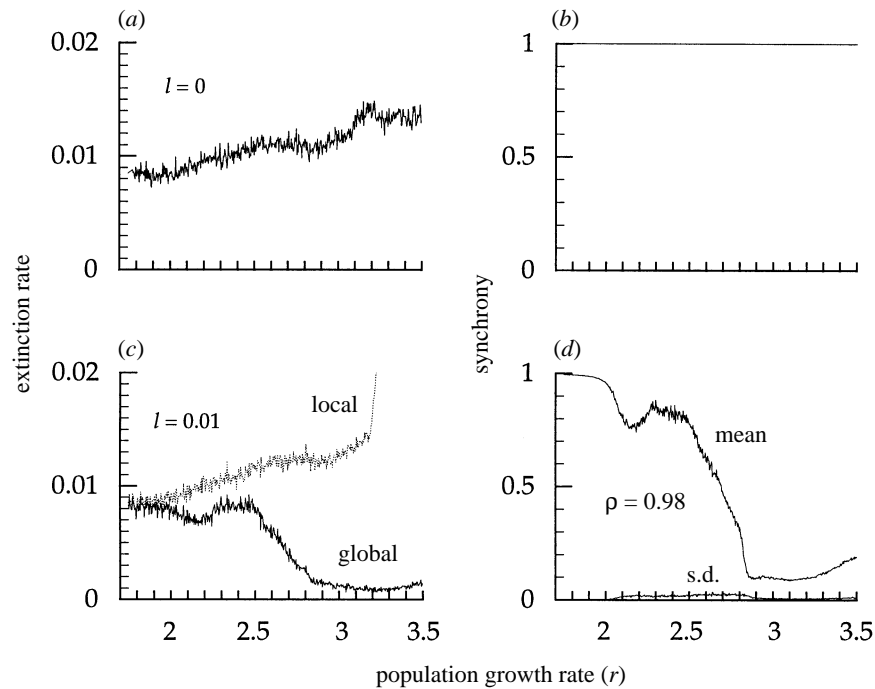


Figure 1. (a, c) Global (lower lines) and local (upper lines) extinction rates as functions of population growth rate (r) in a spatially structured population with distance-independent migration. (b, d) The corresponding measures of synchrony in population dynamics (cross-correlation) among the subpopulations. Both the mean and standard deviation of the synchrony measures are indicated. The correlation coefficients (ρ) between level of synchrony and the global extinction rate are inserted. There is no local noise in the upper panels, while $l = 0.1$ in the lower panels. Other parameter values: $c = 0$, $m = 0.01$.

zero with probability $1 - \beta$. Local noise, $u_{i,t}$, was drawn from uniform distribution on $[-l, l]$, henceforth $U(-l, l)$. The dynamics of the Ricker model depend on the parameter r : for $r < 2$, dynamics are stable, for $2 \leq r \leq 2.69$ cyclic (with periods 2, 4, 8, ...) and thereafter chaotic (May & Oster 1976).

In linking the subpopulations we applied a spatially explicit migration model (Ranta *et al.* 1995b), in which $x_i^m(t)$ are given by

$$x_i^m(t) = (1 - m)x_i(t) + \sum_{j, j \neq i} mx_j(t) \frac{e^{-cd_{ij}}}{\sum_{k, k \neq j} e^{-cd_{jk}}}, \quad (2)$$

where i, j and k are patch indices, m is a constant, patch-independent fraction of migrating individuals, d_{ij} is the distance between patches, and c is a parameter in which low values correspond to long migration distances. Migration occurs only between patches, and consequently, no boundary problems arise. Setting $c = 1$ yields a model in which a patch will receive the majority of immigrants only from the two or three nearest patches. When $c = 0.2$, distance-dependence is weak. If the distance-dependence in migration is ignored altogether ($c = 0$), our model reduces to that used by Allen *et al.* (1993).

A new patch system of ten subpopulations randomly assigned in a 10×10 coordinate space was used for every simulation, and the Euclidean distances between subpopulations were calculated. In the beginning of a simulation, and after a global extinction, the subpopulations were initiated with $0.025 + U(-l, l)$, as in Allen *et al.* (1993). Local extinction was scored when $x_i(k) \leq 0$. Global extinction was scored, in turn, when all ten subpopulations became extinct at one time. The simulations were run for a total of 50000 generations for each of 501 different values of r in $[1.75, 3.5]$. Cross-correlations with lag zero (e.g. Chatfield 1989) were

used as a measure of synchrony in dynamics among the subpopulations. We take the average of all pairwise cross-correlations calculated from the entire simulation as a measure of synchrony among the subpopulations.

3. RESULTS

(a) The basic model

To begin with, we first reproduce some of the findings by Allen *et al.* (1993). These results then serve as a reference point for illustrating the divergence of our more elaborated approach from their results. This is justified by the fact that Allen *et al.* (1993) did not provide any measure for synchrony in the dynamics among the subpopulations. Besides cross-correlation, our crucial measures are the local and global extinction rates in the global population. In these simulations we set the migration parameter $c = 0$ in equation (2).

Our simulations faithfully repeat the general finding by Allen *et al.* (1993) that, in the presence of local noise, the local and global extinction rates diverge with increasing growth rate (figure 1). Furthermore, global extinction rates decrease with sufficiently high population growth rates (figure 1c). In the absence of local noise, however, all the subpopulations fluctuate in perfect synchrony over the entire range of population growth rates used (figure 1b). In this case the local and global extinction rates are identical (figure 1a). On the other hand, the local noise may allow a drastic decrease in the level of synchrony when $r > 2.6$ (figure 1d). The decrease in the level of synchrony is associated with an equally drastic decrease in the rate of global extinctions.

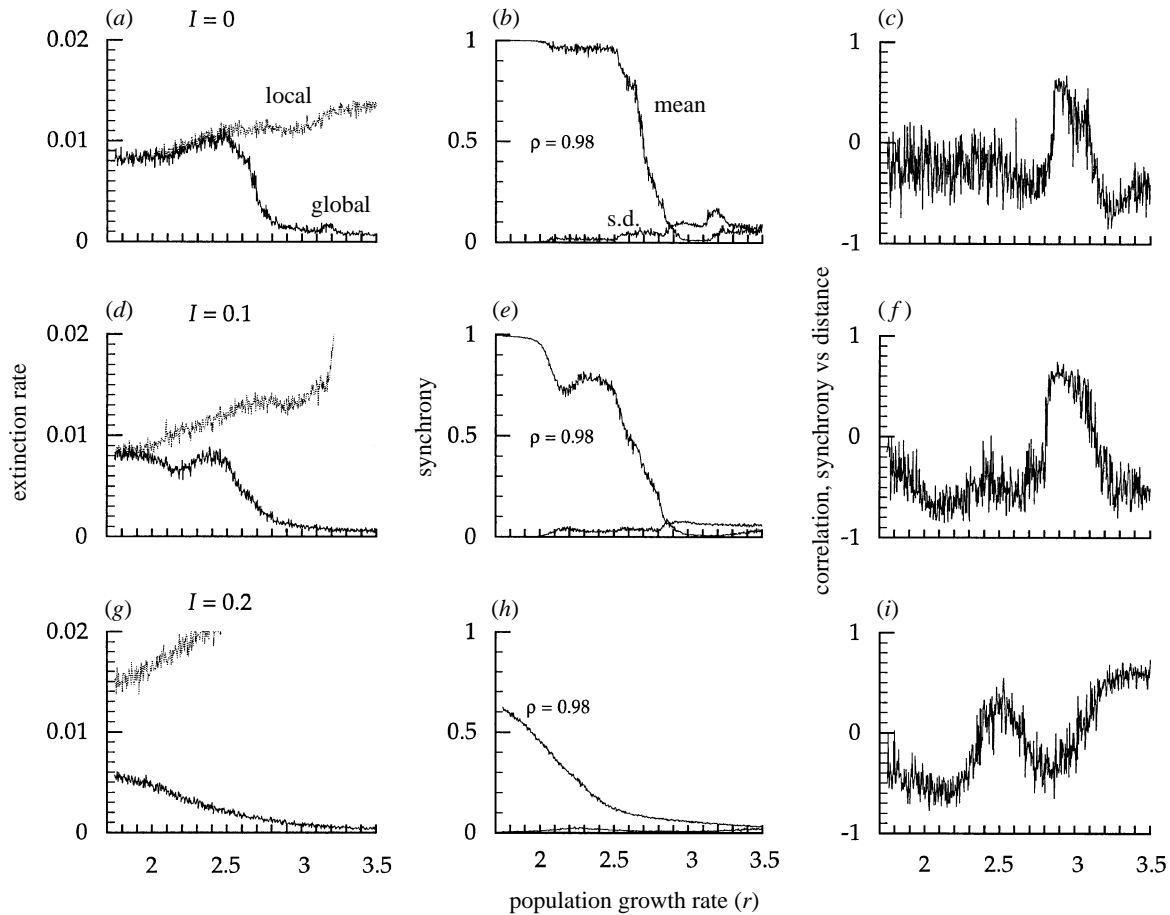


Figure 2. The analyses of figure 1 repeated with a spatially explicit model ($c = 1$). The results are similar for $l = 0.01$, but strikingly different for the model without local noise. We also applied a very high level of local noise ($l = 0.2$). (a, d, g) Global and local extinction rates. (b, e, h) The synchrony measure (cross-correlation). (c, f, i) Correlation between the level of synchrony in population dynamics and distance among the subpopulations. Negative values indicate synchrony decreasing with distance. Note that for a certain range of r synchrony increases with distance.

Our simulations show (figure 1c, d) that the correlation between global extinction rate and the level of synchrony among the subpopulations is high ($\rho = 0.98$). We also scored such high correlations between the synchrony measure and global extinction probabilities with other local noise levels used by Allen *et al.* (1993): $l = 1 \times 10^{-6}$ $\rho = 0.95$ and $l = 0.001$ $\rho = 0.97$. Thus, the lower the degree of synchrony is, the lower is also the probability of global extinction.

(b) Models with distance-dependent dispersal

We next introduce an explicit spatial structure into the model by setting the migration parameter $c > 0$. We first examine a case where the average migration ranges are short, $c = 1$. We observe the divergence of local and global extinction rates even in the absence of local noise ($l = 0$, figure 2a). The discrepancy between these results and the results from previous simulations (figure 1a) are due to differences between patches in net migration rates. This initial randomness introduced by explicit spatial arrangement is then amplified by chaos. Similar desynchronization and divergence of local and global extinction rates is achieved if we allow differences in local carrying capacities or growth rates, instead of distance-dependent migration (not illustrated).

In the presence of local noise, the extinction rates are qualitatively similar whether spatial structure is included (figure 2d) or not (figure 1c). Again, the global extinction rate is closely correlated with the synchrony among the local population dynamics.

We also analysed an example with a notably higher level of local noise, $l = 0.2$ (figure 2g–i). As expected, local extinctions became increasingly common. However, the rate of global extinctions is clearly decreased, as compared to the simulations with lower levels of local noise. This decrease seems to be attributable to a decrease in the synchrony measure.

If no dispersal occurs between the subpopulations (that is $m = 0$), the level of synchrony among the populations hardly changes as compared to figure 1. This indicates a negligible effect of dispersal on the overall level of spatial synchrony in the current model: the spatial synchrony appears to be almost entirely caused by the Moran effect, i.e. the regional disturbance. Higher migration rate ($m = 0.1$, $c = 1$) results in a slight increase in synchrony and population extinction rates (figure 3a, b). When dispersal is weakly distance-dependent (average dispersal ranges long, $m = 0.1$, $c = 0.2$; figure 3d, e), the overall level of synchrony in population dynamics among the subpopulations increases clearly. Population extinction rates increase correspondingly.

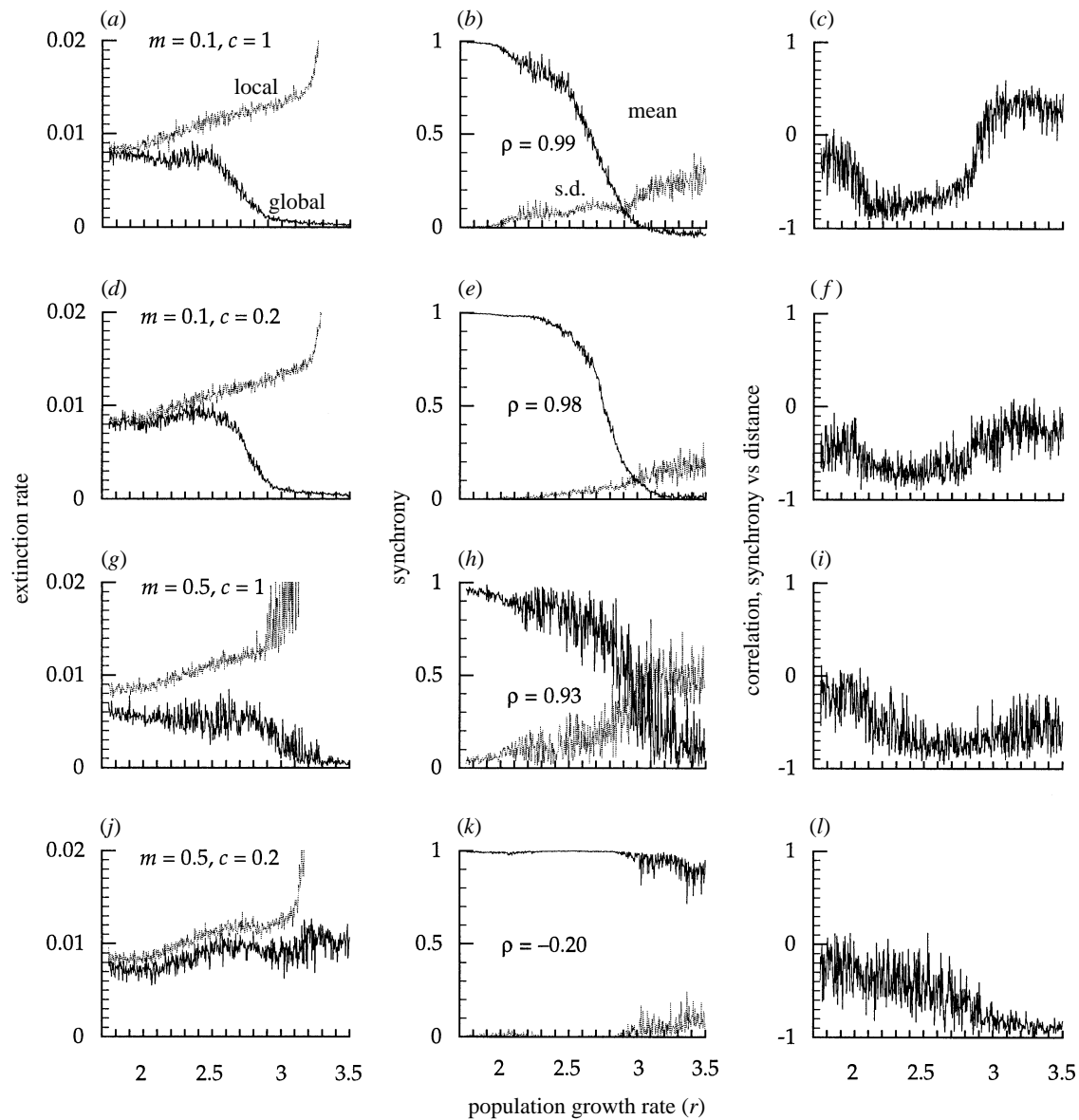


Figure 3. The effects of more intense migration ($m = 0.1$ or $m = 0.5$) and/or less distance-dependent migration ($c = 0.2$) on extinction rates and spatial synchrony. (a, d, g, j) Global and local extinction rates. (b, e, h, k) The synchrony measure (cross-correlation). The correlation coefficients (ρ) between level of synchrony and the global extinction rate are inserted. (c, f, i, l) Correlation between the level of synchrony and distance among the subpopulations. The results obtained in figure 2 appear to be robust (cf. the first and second row panels with figure 2). However, with high migration rate and long migration distances, the population is in close synchrony (k) and the risk of extinction is high for all r (j). Correspondingly, population extinction rate and spatial synchrony are not correlated. Spatial patterns of synchrony are diverse, as is indicated by the high standard deviation of the synchrony measure and the highly variable correlation between distance and synchrony. Local noise: $l = 0.01$.

An increase in the fraction of migrating individuals from $m = 0.1$ to $m = 0.5$ results in a still lowered global extinction rate ($c = 1$; figure 3g, h), while the degree of synchrony increases for high values of r , as compared to figure 3a, b. The degree of synchrony is highly variable with small changes of r , indicating increased sensitivity to the spatial configuration of the subpopulations in the simulations. In all other simulations shown in this paper the spatial structure seems to make little difference in the degree of synchrony. If migration rate is very high and distance-dependence is weak ($m = 0.5, c = 0.2$), the subpopulations are in close synchrony irrespective of population growth rate (figure 3j, k). Correspondingly, the population extinction rate remains high for all values of r . Overall, the relationship

between global extinction rate, spatial synchrony and population growth rate is rather robust to changes in dispersal rates and distances.

(c) Significance of spatial arrangement of patches

In the majority of the examples studied here, local and global extinction rates and the overall degree of synchrony are affected only a little by the specific spatial arrangement of the patches. On the other hand, the relation between synchrony and distance may vary considerably between different spatial arrangements, exemplified by high variability in the correlation between synchrony and distance (figure 2c, f, i and figure 3c, f, i, l, see below).

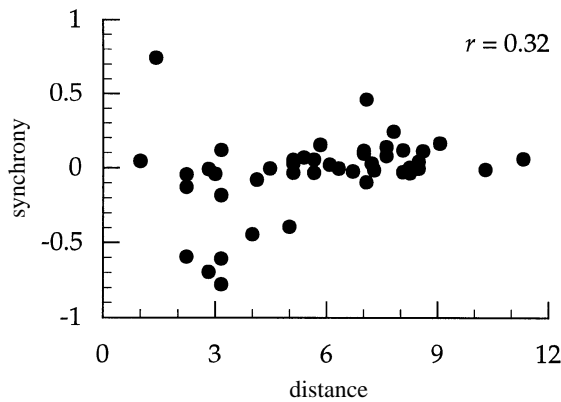


Figure 4. An example of a rare positive correlation (coefficient inserted) between distance and the measure of synchronous dynamics among the subpopulations. Patches close by tend to be in opposite phases. Average cross-correlation is -0.028 (s.d. 0.269). Parameter values: $r = 3.22$, $c = 1$, $m = 0.1$, $l = 0.001$.

Our migration model is not invariant to changes in scale: decreasing the distances between the patches is equivalent to decreasing the degree of distance-dependence, which can be modelled by lowering the value of parameter c controlling distance-dependence. We have shown that lowering c tends to increase the interpatch synchrony and the rate of global extinctions (figure 3).

(d) Spatial patterns of synchrony

We calculated the average correlation between distance and synchrony in dynamics between pairs of subpopulations (figure 2*c, f, i* and figure 3*c, f, i, k*). Most correlations are negative, indicating that the level of synchrony among the subpopulations decreases with distance. In a few cases, however, relatively high positive correlations between distance and synchrony may be observed. A characteristic example of such a situation is illustrated in figure 4. In all the cases studied closely, positive correlations result from a few pairs of patches that tend to be in opposite phases, while the rest of the cross-correlations are slightly positive and show no obvious relation to distance. The possibility that spatial synchrony may first decay and then increase with distance has been indicated by Ranta *et al.* (1997) in empirical population data on the snowshoe hare.

With large population growth rates and a high migration rate ($m \geq 0.1$), the standard deviation in the measure of population synchrony becomes very high (figure 3*b, e, h*). At the same time, the overall level of synchrony is close to zero. A closer study of such examples usually reveals the existence of two groups of patches oscillating in phase within the group, and out of phase between the groups. These two groups are relatively permanent: the asynchrony between the two groups is soon re-established after the synchronizing effect of global disturbance. The rest of the patches may oscillate in synchrony with either of the groups, but associations are more fragile. These groupings are very difficult to deduce *a priori* from spatial locations of

patches: the dynamics of nearby patches need not be correlated. Within one spatial arrangement, the grouping also depends on population growth rate, migration rate and distance-dependence of migration.

4. DISCUSSION

Our major finding is that synchrony in population dynamics correlates strongly and positively with global extinction probability. Spatial synchrony may be caused by both the Moran effect (i.e. global noise) and by dispersal (Ranta *et al.* 1995*b*). It is largely a matter of scale which one is likely to be more important. Our results show that unless average migration ranges are long and the migration rate is very high, the synchronizing role of the Moran effect is dominating the overall level of synchrony. However, negative correlations between distance and synchrony indicate that migration is still important for synchrony of nearby patches. This result is in accordance with the results of Sutcliffe *et al.* (1996), who analysed synchrony in British butterfly data in different spatial scales. They showed that migration had a significant contribution to synchrony only on a local scale. On a regional scale, the effect of environmental stochasticity ('global perturbations') was dominant.

Our results roughly support those of Allen *et al.* (1993) that chaotic population dynamics may reduce the probability of global extinction. Moreover, we have shown that the protective effect of chaos results from its desynchronizing effect on population dynamics of the subpopulations. Only at a very local scale does the synchronizing effect of migration overcome the desynchronizing effect of chaos. Asynchronous dynamics might be one indication of chaos.

It is noteworthy that desynchronizing factors other than chaos also reduce global extinction rates. One such factor is local noise. Even though local noise increases local extinction rates, at the same time the global extinction rate is reduced. The existence of noise in natural populations is unquestionable. Contrary to that, the significance of chaos in population dynamics is controversial (Turchin & Taylor 1992; Godfray & Grenfell 1993).

The migration model (equation (2)) is deterministic, and subpopulations that become extinct are always recolonized in the next generation, as long as there is one non-extinct subpopulation. Consequently, global noise is the only cause of population extinctions in the current model. Therefore, increasing the number of patches in the model has barely any effect on global extinction risk. The probability of a negative global noise peak with magnitude exceeding the average population size is $p \approx 0.0079$. This probability is very close to the observed population extinction rate with low r , when local populations fluctuate in synchrony (figure 1). When subpopulations fluctuate asynchronously, the probability that all subpopulations are at low numbers during a negative global noise peak becomes very low.

Migration has a dual influence on the global extinction rate. Migration is essential for recolonization

of empty patches and may thus enhance the persistence time of a spatially structured population ('rescue effect'; Brown & Kodric-Brown 1977). On the other hand, migration may increase the synchrony between populations, which increases the global extinction risk. In our simulations, the latter effect dominated. This result is partially attributable to our deterministic migration model.

The role of synchrony in the persistence of populations has previously been acknowledged in spatially structured predator-prey and host-parasitoid models (Reeve 1988, 1990; Taylor 1988). The main focus of these studies was the influence of spatial subdivision to persistence properties of these interactions. One of the conclusions was that spatial subdivision enhances the persistence, as long as the dynamics are asynchronous. Not surprisingly, asynchronous dynamics is one of the basic assumptions underlying Levins's (1969) metapopulation model and its descendants. In these models synchrony in a strict sense is not even possible, as local populations have only two possible states. However, extinction and colonization probabilities may be correlated, a case treated by Harrison & Quinn (1989). They state, as our simulations tend to suggest, that in correlated environments, metapopulation persistence time may be greatly reduced.

The causes of spatial synchrony, global perturbations and dispersal, are ubiquitous even if their effects may be offset by other, desynchronizing factors. Our results clearly show the importance of synchrony to the risk of species extinction. Thus, analyses that fail to take spatial synchrony into account may lose one of the key determinants of the risk of species extinction in spatially structured populations.

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REFERENCES

- Allen, J. C., Schaffer, W. M. & Rosko, D. 1993 Chaos reduces species extinction by amplifying local population noise. *Nature, Lond.* **364**, 229–232.
- Baars, M. A. 1979 Patterns of movement of radioactive carabid beetles. *Oecologia* **44**, 125–140.
- Berryman, A. A. & Millstein, J. A. 1989 Are ecological systems chaotic—and if not, why not? *Trends Ecol. Evol.* **4**, 26–28.
- Brown, J. H. & Kodric-Brown, A. 1977 Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* **58**, 445–449.
- Chatfield, C. 1989 *The analysis of time series. An introduction*. London: Chapman & Hall.
- den Boer, P. J. 1981 On the survival of populations in a heterogeneous and variable environment. *Oecologia* **50**, 39–53.
- Elton, C. & Nicholson, M. 1942 The ten-year cycle in numbers of lynx in Canada. *J. Anim. Ecol.* **11**, 215–244.
- Godfray, H. C. J. & Grenfell, B. T. 1993 The continuing quest for chaos. *Trends Ecol. Evol.* **8**, 43–44.
- Hanski, I. & Woivod, I. P. 1993 Spatial synchrony in the dynamics of moth and aphid populations. *J. Anim. Ecol.* **62**, 656–668.
- Harrison, S. & Quinn, J. F. 1989 Correlated environments and the persistence of metapopulations. *Oikos* **56**, 293–298.
- Henttonen, H., Oksanen, T., Jortikka, A. & Haukiskalmi, V. 1987 How much do weasels shape microtine cycles in the northern Fennoscandian taiga? *Oikos* **50**, 353–365.
- Ims, R. A. & Steen, H. 1990 Geographical synchrony in microtine population cycles: a theoretical evaluation of the role of nomadic avian predators. *Oikos* **57**, 381–387.
- Keith, L. B. 1963 *Wildlife's ten-year cycle*. Madison: University of Wisconsin Press.
- Levins, R. 1969 Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. Entomol. Soc. Am.* **15**, 237–240.
- Lindén, H. 1988 Latitudinal gradients in predator-prey interactions, cyclicity and synchronism in voles and small game populations in Finland. *Oikos* **52**, 341–349.
- Lindén, H. 1989 Characteristics of tetraonid cycles in Finland. *Finnish Game Res.* **46**, 34–42.
- May, R. M. & Oster, G. F. 1976 Bifurcations and dynamic complexity in simple ecological models. *Am. Nat.* **110**, 573–599.
- Moran, P. A. P. 1953 The statistical analysis of the Canadian lynx cycle. II. Synchronization and meteorology. *Austr. J. Zool.* **1**, 291–298.
- Pollard, E. 1991 Synchrony of population fluctuations: the dominant influence of widespread factors on local butterfly populations. *Oikos* **60**, 7–10.
- Ranta, E., Lindström, J. & Lindén, H. 1995a Synchrony in tetraonid population dynamics. *J. Anim. Ecol.* **64**, 767–776.
- Ranta, E., Kaitala, V., Lindström, J. & Lindén, H. 1995b Synchrony in population dynamics. *Proc. R. Soc. Lond. B* **262**, 113–118.
- Ranta, E., Lindström, J., Kaitala, V., Kokko, H., Lindén, H. & E. Helle 1997 Solar activity and hare dynamics — a cross-continental comparison. *Am. Nat.* **149**, 765–775.
- Reeve, J. D. 1988 Environmental variability, migration, and persistence in host-parasitoid systems. *Am. Nat.* **132**, 810–836.
- Reeve, J. D. 1990 Stability, variability, and persistence in host-parasitoid systems. *Ecology* **71**, 422–426.
- Royama, T. 1992 *Analytical population dynamics*. London: Chapman & Hall.
- Sutcliffe, O. L., Thomas, C. D. & Moss, D. 1996 Spatial synchrony and asynchrony in butterfly population dynamics. *J. Anim. Ecol.* **65**, 85–95.
- Taylor, A. D. 1988 Large-scale spatial structure and population dynamics in arthropod predator-prey systems. *Ann. Zool. Fenn.* **25**, 63–74.
- Thomas, C. D. 1991 Spatial and temporal variability in a butterfly population. *Oecologia* **87**, 577–580.
- Turchin, P. & Taylor, A. D. 1992 Complex dynamics in ecological time series. *Ecology* **73**, 289–305.

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