The effects of large- and small-scale random events on the synchrony of metapopulation dynamics: a theoretical analysis

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SUMMARY

We present an analysis of the conditions under which migration and global random factors may determine large-scale synchrony in the dynamics of spatially structured populations. We derive an analytic approximation which describes how the desynchronizing influence of local environmental stochasticity combines with the synchronizing influences of larger-scale environmental stochastic variation and migration to determine population cross-correlation coefficients. Despite the simplifications made by this analysis, computer simulations show that the behaviour of more complicated models is well described by our approximation over considerable regions of parameter space. We conclude that population synchrony is largely determined by the coefficients of variation (*CVs*) of the local- and larger-scale stochastic processes, and that migration alone is only likely to maintain population synchrony when the *CV* of the local stochastic process is very small.

1. INTRODUCTION

A growing number of studies document the existence of large-scale regional synchrony in the population dynamics of various species. These include the cycles of hare and lynx populations throughout Canada as deduced from fur return figures from The Hudson Bay Company (Smith 1983), voles and lemmings in Norway (Christiansen 1983; Steen *et al.* 1990), tetraonids (Ranta *et al.* 1995a) and red squirrels (Ranta *et al.* 1997) in Finland, and moths and aphids in England (Hanski & Woiwod 1993). Three hypotheses exist to explain this synchrony: (i) spatially distant populations are exposed to similar environmental influences which apply on a large spatial scale and affect their growth rates in the same way (termed the Moran effect (Moran 1953)); (ii) density-independent or -dependent migration can act to smooth out variation in the growth rates of populations that are connected directly or indirectly by migration (we neglect here the possibility that populations may be destabilized by high dispersal (see, for example, Neubert *et al.* 1995)); and (iii) nomadic predators can seek out areas containing high densities of prey, increasing local mortality rates and consequently smoothing out heterogeneity in population density (Ydenberg 1987). Levels of synchrony observed between field populations presumably arise as a balance of these three influences, together with the desynchronizing influence of more localized stochastic variation.

Assessing the preponderance and relative strengths of the synchronizing effects of migra-

tion and/or a Moran effect and the desynchronizing effect of local noise is a challenging problem, both empirically and theoretically. Synchrony arising between populations as a result of a Moran effect should be independent of the distance separating the populations. Ranta *et al.* (1995b) suggested that the degree of synchrony arising between populations as a result of a migration effect should decline as populations are increasingly disconnected and used computer simulation studies to show that the additional synchronizing influence of a Moran effect, over and above that of a dispersal effect, could be so slight as to be very hard to detect in field data. Although this observation was shown to hold for a variety of density-dependent models, the simulations were only carried out over a limited range of potential parameter space. The matter has been further investigated by Ranta *et al.* (1997) who used computer simulations to examine how metapopulation synchrony changed as a function of the intensity and inherent variance of an intermittent Moran effect. They found the most synchronous behaviour at intermediate values of application frequency and mean intensity, while the variance in the strength of the effect when applied had little effect on synchrony.

It is our intention here to derive a very simple statistical prediction of how random local and global variation in population growth rates combine with migration effects to determine the spatial cross-correlation coefficients between population growth rates in a greatly simplified model of a metapopulation (here defined simply as a population of pop-

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ulations). Computer simulation studies are used to verify that this simple model captures the behaviour of more complex models over a large region of parameter space surprisingly well. We suggest that the reason such a simple approach may work so well is that limited levels of stochastic noise are required to disrupt the complex spatial and temporal feedback loops that are responsible for the often much more complicated results reported with the use of purely deterministic models.

2. THE MODEL

Consider a discrete time model of a metapopulation comprised of n populations at n sites. Let the population dynamics at time t at site x be governed by three processes: (i) a random local component, $R_{Lx}(t)$, independently and identically distributed at each site and drawn from a stationary distribution with mean u_L and variance σ_L^2 ; (ii) a random global component, $R_G(t)$, drawn from a stationary distribution with mean u_G and variance σ_G^2 , and chosen independently at each time interval but common to all sites; and (iii) a per capita population growth rate determined by the general function $f[N_x(t)]$, which may include a density-dependent component.

Assume that the populations may be linked by density-independent migration, whereby a fixed fraction, p_{xy} , of the y th population migrates (subsequent to growth) to the x th population at each time interval. We assume that these n populations/sites are positioned in some regular manner on a torus, so that, while there may be variation in the degree to which population x is connected to the other $n - 1$ populations, all populations are connected in an equivalent way. That is, $p_{xy} = p_{yx}$ and the total fraction of any population that migrates out at each time interval is

$$\dot{p} = \dot{p}_x = \sum_{\substack{y=1 \\ y \neq x}}^n p_{yx}.$$

So $\dot{p}$ represents the total fraction of each population that migrates at each time interval. The fraction migrating, $\dot{p}$, is identical for all populations.

Define also the quantities

$$\ddot{p} = \ddot{p}_x = \sum_{\substack{y=1 \\ y \neq x}}^n p_{yx}^2 \quad \text{and} \quad \vec{p}_{xy} = \sum_{\substack{i=1 \\ i \neq x \\ i \neq y}}^n p_{xi} p_{yi},$$

where $\vec{p}_{xy}$ is a measure of the extent to which populations x and y share common neighbouring populations; it is likely to be larger if x and y are close to each other.

The dynamics of this metapopulation given these assumptions may be represented as

$$N_x(t+1) = N_x(t)f[N_x(t)]R_G(t)R_{Lx}(t)(1-\dot{p}) + \sum_{\substack{y=1 \\ y \neq x}}^n p_{xy}N_y(t)f[N_y(t)]R_G(t)R_{Ly}(t). \quad (1)$$

We are interested in deriving an estimate of the cross-correlation coefficients between pairs of populations. Strictly speaking this is a difficult nonlinear high-dimensional analysis and could only be approached by numerical simulation. However, analytical progress can be made with the following crude simplifications. First, assume that the populations are statistically stationary over the period of study. Second, assume that it is possible to divide both sides of equation (1) by $N_x(t)$ and that the average value of $N_y(t)/N_x(t) \sim 1$, so that the equation for the per capita growth rate $\lambda_x(t)$ is given by

$$\lambda_x(t) = f[N_x(t)]R_G(t)R_{Lx}(t)(1-\dot{p}_x) + \sum_{\substack{y=1 \\ y \neq x}}^n p_{xy}f[N_y(t)]R_G(t)R_{Ly}(t). \quad (2)$$

Third, assume that the combined variance of the local and global stochasticity is sufficiently large, relative to the intensity of the density dependence, that $\lambda_x(t)$ is only weakly correlated with $f[N_x(t)]$, and that $f[N_y(t)]/f[N_x(t)]$ is again, on average, unity. By dividing both sides of equation (2) by $f[N_x(t)]$, we define a quantity $Z_x(t)$ whose behaviour remains a good statistical guide to the relative changes of the population at site x :

$$Z_x(t) = R_G(t)R_{Lx}(t)(1-\dot{p}_x) + \sum_{\substack{y=1 \\ y \neq x}}^n p_{xy}R_G(t)R_{Ly}(t). \quad (3)$$

This treatment renders the population changes at each site to be random variables, that share a covariance with each other induced by the global stochastic process and a migration term. Note that because $Z_x(t)$ is determined only by the value of variables at time t , there is no temporal feedback of any kind in this model. Note particularly that because only current migration may influence population synchrony, these simplifications specifically eliminate the synchronizing influence of migration that may arise over multiple time units. The model contains no history and no multigenerational ‘memory’.

Using the approximations $E[R_{Lx}^2] \approx u_L^2 + \sigma_L^2$ and $E[R_G^2] \approx u_G^2 + \sigma_G^2$, the covariance of Z_x and Z_y can be shown to be well approximated by

$$\text{Cov}(Z_x, Z_y) \approx \sigma_G^2 u_L^2 + (u_G^2 + \sigma_G^2)\sigma_L^2[\vec{p}_{xy} + 2(1-\dot{p})p_{xy}] \quad (4)$$

and the variance of Z_x by

$$\text{Var}(Z_x) \approx \sigma_G^2 u_L^2 + (u_G^2 + \sigma_G^2)\sigma_L^2[\ddot{p} + (1-\dot{p})^2]. \quad (5)$$

The cross-correlation coefficient between quantities Z_x and Z_y is given by

$$r_{xy} = \frac{\text{Cov}(Z_x, Z_y)}{\sqrt{\text{Var}(Z_x)\text{Var}(Z_y)}}$$

and may be expressed in terms of the coefficients of variations of the local ($CV_L = \sigma_L/u_L$) and global

Figure 1. (a) Population cross-correlation coefficients between immediately adjacent populations predicted by equation (6). Dispersal was assumed to follow a declining exponential function with distance such that $p_{xy} = \exp[-2.46 \text{ dist}(x - y)]$. Thus $\dot{p} = 0.5$, $\ddot{p} = 0.031$, $\bar{p} = 0.003$, $p_{xy} = 0.085$ and 50% of any population at each time interval migrates. (b)–(d) The results of numerical simulation of equation (1), using the density-dependent function in equation (9), K set equal to 1 and $c = 0.01$ (figure 1b), 0.1 (figure 1c), 1.0 (figure 1d). The means of the local and global noise processes were set equal to 2.0, and random variables drawn from Weibull distributions. Simulations were carried out on a 15×15 square lattice ($n = 225$), with absorbing boundary conditions, and the distance between cells sharing edges equal to 1. (Note that this treatment of the boundaries creates an ‘edge’ over which individuals will migrate and disappear from the simulation, and thus the assumption of spatial equivalence made in the analytic derivation is violated—the effect of this violation on the results is inconsequential). Simulations were run for 100 time units to eliminate transients and then correlation coefficients calculated over the next 50 time units, randomly selecting four pairs of adjacent populations lying within the 68 most central populations at each time period, and the average correlation coefficient calculated. This process was repeated 20 times for each of 81 combinations of local and global noise.

($CV_G = \sigma_G/u_G$) processes:

$$r_{xy} = \frac{(\bar{p}_{xy} + 2(1 - \dot{p})p_{xy})CV_L^2[1 + CV_G^2] + CV_G^2}{(\ddot{p} + (1 - \dot{p})^2)CV_L^2[1 + CV_G^2] + CV_G^2}. \quad (6)$$

In the absence of local noise ($CV_L = 0$), $r_{xy} = 1$. In the absence of a Moran effect ($CV_G = 0$),

$$r_{xy} = \frac{(\bar{p}_{xy} + 2(1 - \dot{p})p_{xy})}{(\ddot{p} + (1 - \dot{p})^2)}. \quad (7)$$

Note that dispersal synchronizes growth rates between populations x and y in three different ways: (i)

the direct, mutually smoothing effect of dispersal between the two populations, as enumerated by the parameter p_{xy} ; (ii) the effect of migration from shared neighbouring populations, as enumerated by the parameter $\bar{p}_{xy}$; and (iii) a weak effect that synchronizes totally disconnected populations, merely by virtue of the fact that any dispersal will tend to smooth out the heterogeneity in the growth rates of the individual populations across the entire metapopulation (note that in the case of large n , $\ddot{p} \approx n \text{Var}(p_{xy})$, $\text{Var}(p_{xy})$ will decrease as the total number of migrants from a population disperse to greater num-

Figure 2. (a) Population cross-correlation coefficients predicted by equation (6) with dispersal eliminated. (b)–(d) Simulation runs of the full model (equation (1)), same parameter configurations as in figure 1, but dispersal eliminated, thus $p_{xy} = \dot{p} = \ddot{p} = \vec{p}_{xy} = 0$.

bers of other populations, hence the intensity of this ‘smoothing’ effect will decrease as the populations become evermore spatially structured.)

If all dispersal between all populations is set to zero ($p_{xy} = \dot{p} = \ddot{p} = \vec{p}_{xy} = 0$),

$$r_{xy} = \frac{CV_G^2}{CV_L^2[1 + CV_G^2] + CV_G^2}. \quad (8)$$

We suggest here, that despite the rather crude assumptions made by this analysis, equation (6) remains an adequate guide to the synchrony between populations encountered within a large region of its parameter space. Note that synchrony is related only to the coefficients of variation on the local and global processes. Synchrony increases with CV_G (note, therefore, that it is *inversely* proportional to the mean intensity of a Moran effect), and decreases with CV_L . These expressions allow rapid assessment of the expected degree of synchrony between populations that are connected in different ways and subject to different combinations of local and global perturbation.

To test the sensitivity of this approximation to our simplifying assumptions, we performed numerical simulations of equation (1) using the density-dependent function

$$f(N_i) = \exp[c\{K - N_i(t - 1)\}]. \quad (9)$$

Figure 1a shows the analytic expectation of the correlation coefficient (r_{xy}) between two immediately adjacent populations, with total dispersal from each population per time interval set at its most synchronizing (i.e. 50%). Figures 1b–d show the average value of r_{xy} between the densities of two populations immediately adjacent to each other in the middle of a 15×15 lattice for three simulation runs using the same levels of migration, but different levels of intensity of density dependence. Figure 2 is precisely analogous except that dispersal is now eliminated. The analytic and simulation models are in general agreement, suggesting the simplifying assumptions to be, for the most part, reasonable.

There is, however, an area of parameter space in which the simplifying assumptions are likely to be

violated and the analytic result rendered unreliable. When the effects of density dependence and migration are high relative to the local and global stochastic effects, the analytic approximation is likely to underestimate the degree of synchrony between populations. When density dependence is intense, $\lambda_x(t)$ is likely to be strongly correlated with $f[N_x(t)]$, and dividing both sides of equation (2) by $f[N_x(t)]$ is likely to result in a substantial reduction in the variance of $Z_x(t)$ and therefore to an underestimate of the correlation coefficient. When migration rates are high and the combined stochastic effects are weak, the synchronizing influence of migration is likely to accumulate above and beyond the single generation considered by the model, consequently leading to an underestimate of the observed synchrony. However, it seems that the underestimate is really only important when in the combined situation of intense density dependence and high migration rates. Such underestimates are visible on the left-hand side of figure 1*d*. This is confirmed by a more detailed exploration of this corner of parameter space (illustrated in figure 3*a,b*).

3. DISCUSSION

In the absence of dispersal, synchrony between populations is determined solely by the coefficients of variation of the local and global stochastic processes (equation (8)). We found that synchrony is proportional to the global variance and the local mean, and inversely proportional to the local variance and global mean. These relationships remain qualitatively the same when dispersal is added.

This result is likely to remain valid for any distribution of local and global noise for which the approximation $E(X^2) \sim u_X^2 + \sigma_X^2$ remains good. Simulation studies suggest that it is not unduly sensitive to the precise form of the per capita density-dependent growth rate function. The analysis is likely to work best when the populations are regulated by so-called density vague processes (Strong 1983), which only exert a significant influence on the population dynamics above and below certain threshold floors and ceilings. Because cross-correlation coefficients are determined only by changes in population sizes, these results could probably be extended to models with overlapping generations. Equation (6) could be viewed as a general rule of thumb for the quantitative behaviour of population synchrony.

Many different models can be written in the general form of equations (1) or (2). The same approximations can be used to study the case when local and global random processes act additively rather than multiplicatively, i.e.

$$N_x(t+1) = N_x(t)f[N_x(t)][R_G(t) + R_{Lx}(t)](1 - \dot{p}_x) + \sum_{\substack{y=1 \\ y \neq x}}^n p_{xy}N_y(t)f[N_y(t)][R_G(t) + R_{Ly}(t)], \quad (10)$$

Figure 3. The parameter combinations for which the analytic approximation will fail. (a) Migration is assumed to be at a synchronizing rate (as in figure 1, 50% of each population per generation), $CV_G = 0$, density dependence (c) varies as shown on graph (other parameters as in figure 1). (b) Density dependence set at most intense ($c = 1$), $CV_G = 0$ (other parameters as in figure 1), fraction of each population migrating per generation ($\bar{p}$) indicated on graph. Note that serious underestimates of the simulated average correlation coefficient only occurs when both migration and density dependence are strong.

in which case the analytic results depends only on the variances

$$r_{xy} = \frac{\sigma_L^2[\bar{p}_{xy} + 2(1 - \bar{p})p_{xy}] + \sigma_G^2}{\sigma_L^2[\bar{p} + (1 - \bar{p})^2] + \sigma_G^2}. \quad (11)$$

The approach may be extended to consider Ricker-like models (Ricker 1954) without dispersal, by taking logarithms of both sides, in which case a model of the form

$$\ln(\lambda_x(t)) = f[N_x(t)] + R_G(t) + R_{Lx}(t) \quad (12)$$

is obtained. Under our assumptions, $f[N_x(t)]$ may then be subtracted from each side and the equation for the correlation coefficient under these conditions is approximated by

$$r_{xy} = \frac{\sigma_G^2}{\sigma_L^2 + \sigma_G^2}. \quad (13)$$

It should, however, be remembered that the Pearson correlation coefficient of $\ln(N_x)$ and $\ln(N_y)$ is somewhat higher than that of the untransformed variables. The generality of our approach may be underlined by noting that this extension can be used to satisfactorily explain the numerical results of Ranta *et al.* (1997) when their probability of a global effect is 1. Ranta *et al.* (1997) used a conventional and modified Ricker model, but direct comparison with all their results is difficult since they have modelled the global effect by both the probability of its occurrence and its mean and variance when it does occur.

We consider that the broad-scale 'global' component of population growth rates is most parsimoniously viewed as originating from a single probability density distribution, with suitably extended tails, to incorporate effects of occurrences of extreme environmental conditions. We stress that the synchronizing influence of the Moran effect is not generated by the occurrence of extreme large-scale environmental conditions but by variation in these conditions. Distributions with very different shapes and tail structures may have similar coefficients of variation. The analysis proposed here predicts that distributions with different shapes but the same coefficient of variation should have the same synchronizing influences.

When CV_L falls below a certain threshold value, the synchronizing influence of migration accumulates over successive generations and our analytic approximation can seriously underestimate the observed levels of synchrony. The threshold level below which this underestimate occurs is proportional to both the intensity of density dependence and the extent of migration. Below this threshold, even very low levels of short range migration may result in almost total large-scale spatial synchrony. Above this threshold, even extreme levels of migration are, alone, unlikely to be able to generate large-scale synchrony. Our simulations suggest that even for quite strong density dependence (e.g. $c \sim 0.25$, $E[d[u_L u_G f(N)]/dN|_{N=K}] \sim -1$), and maximally synchronizing dispersal ($\hat{p} = 0.5$), the threshold over which the synchronizing influence of migration accumulation is overwhelmed by local variance may be as low as $CV_L \sim 0.005$. Recent analyses of genetic exchange within metapopulations have concluded that dispersal must be considerably weaker than $\hat{p} = 0.5$ (Jaarola & Tegelström 1996; Stacy *et al.* 1997), suggesting we must look to hypotheses other than migration to explain large-scale population synchrony.

The hypothesis that nomadic predators may act to synchronize the dynamics of discrete prey populations by concentrating predatory activity on localized areas of increased prey density has received explicit theoretical treatment (DeRoos *et al.* 1991; Ims & Steen 1990). We suggest that the effects of nomadic predation, acting either directly or indirectly through changes in the reproductive behaviour of the prey, might be implicitly included in our analysis by supposing that it acts to intensify the density-dependent dynamics of the prey populations.

Purely deterministic spatial population models have been shown to be potentially rich in structure, pattern and complexity (e.g. Comins *et al.* 1992; Sole *et al.* 1992; Hassell *et al.* 1994). Yet ecologists have struggled to convince themselves that this is the same type of complexity that is commonly encountered in natural populations. The complexities arise as a result of the myriad of feedback loops operating between different populations located over space and time. The relevance of all these complexities to real world population dynamics depends on the robustness of the feedback mechanisms to levels of disruptive stochastic variation that will inevitably be encountered in natural populations. Even the limited degree of variation induced by demographically stochastic formulations of deterministic models can be critical to model behaviour (e.g. Nisbet & Gurney 1982), and in many situations such variation is likely to be small relative to environmental stochasticity. Our analysis suggests that only limited degrees of stochastic variation may be required to disrupt the temporal and spatial feedback processes responsible for much of the dynamical complexity often attributed to spatial population processes, and that statistical properties of large-scale population patterns may have simpler explanations.

The authors thank B. Beisner, B. Mable, S. Otto, E. Ranta, J. Ruesink and an anonymous referee for helpful comments on the manuscript.

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Received 8 April 1997; accepted 30 April 1997