Spatially autocorrelated disturbances and patterns in population synchrony

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Spatially synchronous population dynamics have been documented in many taxa. The prevailing view is that the most plausible candidates to explain this pattern are extrinsic disturbances (the Moran effect) and dispersal. In most cases disentangling these factors is difficult. Theoretical studies have shown that dispersal between subpopulations is more likely to produce a negative relationship between population synchrony and distance between the patches than perturbations. As analyses of empirical data frequently show this negative relationship between the level of synchrony and distance between populations, this has emphasized the importance of dispersal as a synchronizing agent. However, several weather patterns show spatial autocorrelation, which could potentially produce patterns in population synchrony similar to those caused by dispersal. By using spatially extended versions of several population dynamic models, we show that this is indeed the case. Our results show that, especially when both factors (spatially autocorrelated perturbations and distance-dependent dispersal) act together, there may exist groups of local populations in synchrony together but fluctuating asynchronously with some other groups of local populations. We also show, by analysing 56 long-term population data sets, that patterns of population synchrony similar to those found in our simulations are found in natural populations as well. This finding highlights the subtlety in the interactions of dispersal and noise in organizing spatial patterns in population fluctuations.

Keywords: Moran effect; population dynamics; spatial autocorrelation; dispersal; synchrony

1. INTRODUCTION

Why do spatially distinct populations fluctuate in synchrony? Moran, an Australian statistician, proposed a hypothesis to account for synchronous dynamics between two (or more) populations following a common structure of density dependence (Moran 1953). He suggested that stochastic density-independent but correlated processes may cause local populations to fluctuate synchronously. This idea, which has become known as the Moran theorem or the Moran effect (Royama 1992), was largely ignored by contemporary ecologists. Leslie (1959) was a notable exception, showing that an external random factor can also bring isolated, age-structured populations into phase.

The Moran effect was recently rejuvenated when research in population ecology shifted focus from isolated populations to populations linked by dispersing individuals (Bascompte & Solé 1995, 1997; Hanski & Gilpin 1997; Tilman & Kareiva 1997). This shift towards spatially extended dynamics has substantiated Moran's ideas theoretically as well as empirically; spatial synchrony due to external perturbations is commonly achieved with many dynamic models (Ranta *et al.* 1995a; Heino *et al.* 1997; Haydon & Steen 1997; Lambin *et al.*

1998) and it is a common phenomenon in natural animal populations (Pollard 1991; Royama 1992; Hanski & Woiwod 1993; Ranta *et al.* 1995b; Lindström *et al.* 1996; Steen *et al.* 1996; Sutcliffe *et al.* 1996; Liebhold *et al.* 1996; Myers 1998; Bjørnstad *et al.* 1999) as well as in infectious diseases (Grenfell & Harwood 1997; Earn *et al.* 1998).

The Moran effect (Moran 1953; Royama 1992) is currently interpreted as a global disturbance influencing population renewal. Even though the synchronizing effect of extrinsic perturbations is known (see above), it does not explain another commonly observed pattern in population synchrony: a negative correlation between synchrony and distance (Hanski & Woiwod 1993; Ranta *et al.* 1995a,b; Lindström *et al.* 1996; Koenig 1999). Dispersal of individuals between population subunits has been put forward to explain this feature (Ranta *et al.* 1995a,b, 1997a,b; Heino *et al.* 1996; Kaitala & Ranta 1998; Lambin *et al.* 1998).

However, as density-independent factors are often climatic (Royama 1992), a global perturbation is not necessarily always a correct interpretation. This is because many climatic factors are spatially autocorrelated and therefore do not always act with the same strength everywhere (Nordo & Hjortnes 1967; Goodridge 1991; Heino 1994; Hurrell 1995; Kripalani & Kulkarni 1997). Here we show, by using a set of spatial population models, that a spatially autocorrelated disturbance can

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actually have an effect on the correlation between synchrony and distance similar to the effect of dispersal between local populations. The findings of this modelling are compared with results from an analysis of 56 spatial data sets.

2. SPATIALLY AUTOCORRELATED MORAN EFFECT AND DISPERSAL-COUPLED POPULATIONS

We define a spatially autocorrelated Moran effect as a stochastic disturbance occurring at a random location and affecting nearby populations more severely than populations far away from the place of the impact. Both the area covered and the impact strength against distance are allowed to vary.

It is possible in spatially structured populations that, despite a high degree of synchrony in general, some of the subpopulations fluctuate in an opposite phase compared with the others. Calculating an average measure of synchrony in such a situation would result in a highly misleading figure. To address this problem more cautiously, we calculated a central tendency for synchrony. Central tendency is defined as the proportion of cross-correlation coefficients clustered closely with the average synchrony. That is, the cross-correlation coefficients are pooled into 0.1 bins from -1 to 1 . The mean of the resulting frequency distribution is then calculated and the bin it lies in is located. Finally a count is made of the number of correlation coefficients in the same bin as the mean plus the number in one bin on either side of the bin containing the mean. If the majority of populations fluctuate in step this proportion is high, but when mutually out-of-phase population groups exist (bimodal distribution of cross-correlations) the proportion of correlations with the mean is low.

To analyse to what extent an autocorrelated Moran effect is capable of synchronizing the dynamics of populations we proceeded as follows. We located 25 populations randomly on a 20×20 grid. The dynamics of the populations are coupled by dispersal and spatially structured external disturbance. Assuming a constant fraction m ($0 \leq m \leq 1$) of the population dispersing annually, the spatially linked dynamics becomes

$$X_i(k+1) = (1-m)F[X_i(k), X_i(k-1), \mu(q_i)] + \sum_{s, s \neq i} M_{si}(k), \quad (1)$$

where $X_i(k)$ is the population size in patch i at time k , $\mu(q_i)$ is the Moran effect and $M_{si}(k)$ is the number of immigrants arriving in patch i from patch s as a consequence of dispersal. The Moran effect is characterized by its annual probability of occurrence, $p(k)$, its intensity, $\mu(q_i)$, for the focal subpopulation, and the distance q_i of each subpopulation i from the place of the impact. Thus, we write

$$\mu(q_i) = \begin{cases} 1 - \exp(-c_{\text{MORAN}} q_i) & \text{if } p(k) < \hat{p} \\ 1 & \text{otherwise,} \end{cases} \quad (2)$$

where $\hat{p}$, $0 \leq \hat{p} \leq 1$, is a constant. If $\mu(q_i) < 0.2$ we set $\mu(q_i) = 0.2$ (that is, at a maximum 80% of a subpopulation located precisely at the site of impact of the effect is wiped off, or if the Moran effect is global, 80%

of all populations are eliminated). The parameter c_{MORAN} takes care of the spatial extent of the Moran effect ($c_{\text{MORAN}} = 0$ is equivalent to global disturbance; the spatial coverage of the Moran effect goes down with increasing values of c_{MORAN}). Here we report results with $\hat{p} = 0.2$, i.e. the Moran effect taking place on average at five-year intervals (the value of $p(k)$ is drawn from uniform random numbers in the interval from 0 to 1). Experimentation shows, however, that the major conclusions based on our simulations as reported here are rather robust on the selection of $\hat{p}$ (we have simulated equations (1) and (3) with $\hat{p}$ ranging from 0.04 to 1).

The populations were allowed to renew after two different model categories: the Moran–Ricker dynamics and autoregressive dynamics. This is to ensure that the results emerging are not solely due to a single type of long-term population dynamics. The number of offspring alive after reproduction in equation (1) is given as

$$F = X_i(k) \mu(q_i) f[X_i(k), X_i(k-1)], \quad (3)$$

where the arguments of F have been omitted. Function f defines the delayed density-dependent per capita reproductive rate. For the Moran–Ricker dynamics we write (Turchin 1990)

$$f[X_i(k), X_i(k-1)] = \exp[r(1 - a_1 X_i(k) - a_2 X_i(k-1))], \quad (4)$$

where r is the maximum per capita rate of increase and a_1 and a_2 are parameters determining density dependence. The parameters were selected such that they yield damped ($r=0.4$, $a_1=0.05$, $a_2=-0.1$), cyclic ($r=0.53$, $a_1=0.05$, $a_2=-0.1$) and chaotic ($r=3.5$, $a_1=a_2=-0.05$) dynamics. The autoregressive renewal, in turn, is given as

$$X_i(k+1) = \phi_1 X_i(k) + \phi_2 X_i(k-1) + \delta + \varepsilon(k), \quad (5)$$

where ϕ_1 and ϕ_2 are the first- and second-order autoregressive parameters, δ is a constant and ε is normally distributed (with mean 0 and variance 1) noise to take care of demographic stochasticity. The parameter values for the first-order autoregressive model, AR1, are $\phi_1 = 0.9$, $\phi_2 = 0$, $\delta = 3$, and for the second-order autoregressive model, AR2, are $\phi_1 = 0.9$, $\phi_2 = -0.5$, $\delta = 10$.

In each generation, a proportion of individuals from each population disperses to neighbouring populations, and consequently each population receives immigrants arriving from other populations. The term $M_{si}(k)$ in equation (1) refers to the number of immigrants arriving in the subpopulation i from the population s as a consequence of dispersal, and is given as

$$M_{si}(k) = \frac{m F \exp(-c_{\text{DISP}} d_{si})}{\sum_{j, j \neq s} \exp(-c_{\text{DISP}} d_{sj})}, \quad (6)$$

where m is the dispersing proportion of the population, d_{si} is the distance from s to i and c_{DISP} is a constant parameter describing how far the dispersing individuals move. Note that density-dependent population renewal in equation (1) takes place before dispersal. The range of values used for both c_{MORAN} and c_{DISP} was from 0 to 1, from global towards increasingly local effects.

Figure 1. The influence of autocorrelated Moran effect, c_{MORAN} , and spatially limited dispersal, c_{DISP} , on the level of synchrony among 25 populations initiated in random phase and randomly located into a 20×20 coordinate space. Note that small values of c_{MORAN} and c_{DISP} mean that distance has no effect on the disturbance or dispersal of individuals among the populations, whereas increasing values mean that the Moran effect becomes more localized and distance will limit dispersal. For this reason the axes are reversed. Three measures are used to characterize the temporal dynamics of the populations: (a) average level of synchronous dynamics (measured as the mean of all 300 cross-correlations in pairs between the 25 populations), (b) central tendency of the cross-correlations, and (c) distance dependence in synchrony (correlation between the level of synchrony and distance among the populations compared). The darker the shading, the higher the intensity of the measured coefficient: for the correlation between synchrony and distance the range is from 0 to -1 (from light to dark shading), for the average level of synchrony from 0 to 1, and for the central tendency from 0 to 100%. Note that in the graphs of central tendency light shading often indicates bimodal distribution of the cross-correlation coefficients. The data are summarized for five differing population-renewal model classes: damped, cyclic and chaotic Moran–Ricker dynamics, and for the first- (AR1) and second- (AR2) order autoregressive models.

At the beginning of each simulation 25 local populations were randomly placed in a 20×20 grid and initiated in random phase. They were then allowed to renew after equations (1) and (4) or (5) for 1000 time-steps and the next 1500 steps were used for our analyses. To characterize the behaviour of the population dynamics we scored the average level of synchrony in dynamics among the populations, the central tendency of the level of synchrony, and the correlation between the level of synchrony and distance among the populations compared. We report averages of 100 replicated simulations for each parameter-value combination of c_{MORAN} and c_{DISP} . The central tendency was calculated as for the population data (i.e. how large a proportion of the observed correlations coincided with the 0.1 class bin of the mean plus one bin on either side of the mean). High values of this measure indicate that most populations are fluctuating coherently; low values suggest that the overall synchrony among the populations has a wide range or is bimodal. Bimodal distribution is achieved when there are two (or more) sets of populations fluctuating internally in step, but out of phase when compared across the population sets.

The dispersal process is set to be negatively distance dependent: equation (6). We disturbed the populations with the Moran effect, which was set to be spatially auto-correlated: equation (2). This was achieved by randomly selecting the coordinates of the hit, and letting the impact decay exponentially with increasing distance. In the simulations we allowed the extent of the spatially auto-correlated Moran effect to vary from a local to a global effect. The dispersal of individuals was either highly dependent on the distances among the populations or distance independent.

3. SIMULATION RESULTS AND COMPARISON WITH DATA

First, both dispersal and the autocorrelated Moran effect alone are capable of synchronizing population dynamics, but their effect is strengthened if both processes act together (figure 1). High levels of synchrony are achievable with all of the five different population-renewal processes analysed, however, such that there exist notable differences among the renewal models (figure 1). Second, negative distance dependence in the synchrony was observed with all models and with most combinations of c_{MORAN} and c_{DISP} . The highest values were mostly associated with the autocorrelated Moran effect covering quite large areas (c_{MORAN} from 0 to 0.3) and the dispersing individuals moving widely across the coordinate space (c_{DISP} from 0 to 0.7). Quite often, however, the frequency distribution of synchrony measures among population pairs was either flat or even bimodal, indicating low values of central tendency (figure 1). This indicates that a spatially autocorrelated Moran effect together with dispersal-linked populations often organizes population groups within which fluctuations occur in step but out of phase compared with other population groups. We also experimented with parameter values differing from those reported above. However, the major conclusions drawn from these values are rather robust to parameter changes.

Figure 2. Summary of the results of an analysis of spatial long-term data on 56 species. The following statistics are reported. (a) Frequency distribution of correlation coefficients characterizing how the level of synchrony (measured with cross-correlation) levels off with distance among the populations compared. (b) The relationship of the average level of synchronous dynamics (marginal distribution is given in panel c) is related to (a). (d) Central tendency of the synchrony measures (marginal distribution is given in panel e) plotted against distance dependency of synchrony (i.e. the correlation between the level of synchrony among populations and how it levels off with increasing distance). Pearson correlation coefficients are inserted ($p < 0.05$) and the major taxa are identified with differing symbols. The data originate from the following sources: insects (forest pests: Schwerdtfeger 1941; noctuid and geometrid moths: M. Nieminen and E. Ranta, unpublished data), fish (whitefish: Ranta *et al.* 1995a; Norwegian salmon: A. Langeland and E. Ranta, unpublished data; Pacific salmon: E. Ranta and V. Kaitala, unpublished data), Dungeness crab (Higgins *et al.* 1997), birds (Lindén 1988; Lindström *et al.* 1996; Ranta *et al.* 1995a), terrestrial vertebrates (Keith 1963; Lindén 1988; Royama 1992).

The two novel findings, (1) bimodality in the central tendency, and (2) a negative correlation between the central tendency and distance among the populations compared (figure 1), prompted us to ask whether these patterns exist in real data as well. To answer this question we compiled all spatially replicated long-term time-series to which we have access (see legend to figure 2). These data comprise 56 sets of spatially replicated time-series on the dynamics of insects, fish, birds and terrestrial vertebrates. Before analysis the time-series were detrended and

standardized to zero mean and unit variance. Based on the analysis of these data we conclude that populations of a given species fluctuate in synchrony (figure 2*c,e*) and there exists distance dependence in the degree of synchrony. The level goes down with increasing distance among the populations compared (figure 2*a*). The finding that there is negative correlation between the average synchrony and its distance dependency (figure 2*b*) matches the model predictions.

Our analysis indicates that when the synchrony in fluctuations is strong its distance dependency is also strong, that is, the level of synchronous fluctuations decreases tightly when distance among the populations compared increases. Further, when the distance dependency is low the central tendency in the synchrony level is less concentrated around the mean. When the central tendency is low its frequency distribution is often also bimodal, one mode with high positive correlations and the other one with high negative correlations. This indicates that there are two sets of populations internally roughly in synchrony but out of synchrony when members of the two groups are compared. This warns against trusting to the mean of all synchrony coefficients as an exhaustive description of the prevailing level of matching fluctuations in the population system (see, e.g. Hanski & Woiwod 1993).

In summary, the characteristics of synchronous dynamics of populations are (i) the overall level of synchrony, (ii) the central tendency, (iii) the (usually negative) distance dependency of synchrony, and (iv) the interrelations between these variables.

4. DISCUSSION

To sum up, spatially autocorrelated disturbances and dispersal among subpopulations are both capable of producing synchronous population fluctuations by acting either separately or in concert. This theoretical finding matches the observations from a wide array of empirical data sets (figure 2) (Hanski & Woiwod 1993; Ranta *et al.* 1995*b*, 1997*a,b,c*; Lindström *et al.* 1996; Koenig 1999).

Recent studies on population synchrony have stressed the importance of the scale of disturbances in spatial population dynamics (Steen *et al.* 1996; Haydon & Steen 1997; Paradis *et al.* 1999). Our findings here add to this discussion; the spatial scale of environmental disturbances is clearly of importance in population synchrony. In some cases, weather patterns can be autocorrelated over large areas (Nordo & Hjortnes 1967; Goodridge 1991; Heino 1994; Hurrell 1995; Kripalani & Kulkarni 1997). Spatial autocorrelation in environmental variables can also be rather small scaled, covering only distances of some tens or hundreds of metres (Xu *et al.* 1997; Arnfield 1998). However, studying environmental factors at small spatial scales necessarily introduces some small-scale variation, which would be 'averaged out' in a larger-scale study. Therefore, the scale of a given population system dictates the relevant scale of environmental autocorrelation. To conclude, our results show that disentangling the contribution of dispersal and extrinsic perturbations is even more difficult than previously thought. Even a pattern where synchrony levels off with increasing distance between populations cannot be readily inter-

preted as being caused by dispersal (Ranta *et al.* 1995*a*); it could be caused by spatially autocorrelated noise as well, or by both factors acting together.

We suggest considering a global Moran effect as a special case of external perturbations, which are often likely to be of different strength at different parts of the spatial population system. Thus, the problem appears even more subtle and challenging than it did originally. This is even more so, because there are probably very few opportunities to exclude either extrinsic perturbations or dispersal in natural systems. In the case of Soay sheep in the St Kilda archipelago, synchrony of sheep populations inhabiting different islands could be solely attributed to a Moran effect as the sheep do not disperse between islands (Grenfell *et al.* 1998). Excluding perturbations from the study is probably likely to succeed only in laboratory conditions. However, when this was done in a laboratory predator-prey system in ciliates, no consistent relationship between dispersal rate and spatial synchrony was found (Holyoak & Lawler 1996).

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