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External disturbances and population dynamics

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Using a set of 10 randomly allocated populations in a coordinate space we subjected them to population renewal after the Ricker model and the Turchin model. Parameter values were selected so that the Ricker model yielded oscillations with Period 2 and the Turchin model with Period 10. The subpopulations were subjected to global disturbance (the Moran effect) with varying probability of occurrence and intensity. The populations were initially set out of phase, and the population renewal and the Moran effect was let to act for 1 500 generations, the final 1 000 were used to score the level of synchrony in dynamics among the 10 subpopulations. From these data we also estimated the parameter values of the Ricker and Turchin models. The Moran effect is capable of synchronising dynamics of the subpopulations regardless of the population renewal model. However, frequent enough disturbances do not yield synchronous dynamics. Also, the Moran effect, when frequent enough, or when strong enough, has a feature to alter the characteristics of the population dynamics.

1. Introduction

Moran (1953) was far ahead of his time when proposing that stochastic density-independent but correlated processes may cause local populations with a common structure of density dependence to fluctuate in synchrony. Surprisingly enough, the Moran's theorem, also known as the Moran effect (Royama 1992), has been explicitly considered by a few authors only (Royama 1984, 1992, Myers 1988, Pollard & Rothery 1994, Ranta *et al.* 1995ab). Nonetheless, the Moran effect has not only proven to be capable of synchronizing dynamics of a set of populations (Moran 1953, Royama 1992, Ranta *et al.* 1995ab) but also to yield rich variety of population dynamic patterns (Kaitala *et al.* 1996ab). In this note we shall address the dual face of the Moran effect, viz., to cause synchrony in population fluctuations and to affect the dynamics of populations. In particular, we show that besides the synchronizing capability, the Moran effect, when deleterious and frequent enough, or when strong enough, may crucially modify or remove typical patterns of population dynamics. This result has been totally neglected in the interpretations and the development of the Moran's theorem. We also study the particular problem of the identification of population dynamics under external Moran-type disturbances. We show that the identification of the underlying intrinsic population dynamics may largely depend on the specific type of the external Moran effect.

2. The Moran effect

Consider a population under density-dependent regulation with $x(k)$ denoting the population size at time k. Dynamics of such a population, when subjected to the Moran effect $\mu(k)$, is given as (Ranta et al. 1996):

$$x_i(k+1) = x_i(k)\mu_i(k)\exp\left(r + a_1 x_i(k) + a_2 x_i(k-1)\right), \quad (1)$$

where r is an intrinsic rate of increase, a_1 and a_2 are constant parameters. The Moran effect is characterized by two elements, viz., its annual probability p of occurrence ($0 < p \leq 1$) and its intensity μ. Thus, we write:

$$\mu_i(k) = \begin{cases} \hat{\mu} \text{ if } p(k) < \bar{p},\ 0 \leq \bar{p} \leq 1, \\ \quad 1 \text{ otherwise,} \end{cases} \quad (2)$$

where $\hat{\mu}$ is ~Uniform ($\mu_{\min}$, $\mu_{\max}$) and $p(k)$ is ~Uniform (0, 1). The lower the $\mu_i(k)$, the stronger the impact the Moran effect is causing the population in the year k.

As in Ranta *et al.* (1996), we consider two modifications of the model (1): in the Ricker model (Ricker 1954) $a_2 = 0$, whereas in the Turchin model (Turchin 1990) $a_1 \neq 0$ and $a_2 \neq 0$. For brevity of presentation we use here the following parameter values: Ricker: $r = 2.1$ and $a_1 = -1$; Turchin: $r = 0.5$, $a_1 = 0.05$ and $a_1 = -0.1$. With these choices, when undisturbed, the Ricker model produces oscillations with Period 2, and the Turchin model produces oscillations with Period length 10. Suffice it to say that we experimented with a rather large number of differing parameter combinations but the outcome of the analyses remained qualitatively unchanged (except for the r values yielding chaotic Ricker dynamics).

In our simulations the Moran effect was split into its components, probability of occurrence (drawn from an uniform distribution) and intensity. For the Ricker model the Moran effect occurred either every year ($\bar{p} = 1$), on average at two-year ($\bar{p} = 0.5$) intervals, three-year intervals ($\bar{p} = 0.33$) and finally averaging at four-year intervals ($\bar{p} = 0.25$). For the Turchin model the corresponding probabilities were $\bar{p} = 0.5$ (2-yr. interval, on average), $\bar{p} = 0.2$ (5-yr.), $\bar{p} = 0.1$ (10-yr.), and $\bar{p} = 0.05$ (20-yr.).

3. Results

3.1. Synchrony

To examine the synchronizing capability of the Moran effect we chose 10 independent subpopulations obeying eq (1). Initially, the populations were set in random phase. Both the Ricker and Turchin populations were subjected to correlated perturbations with the model-specific probabilities (above) using values of μ ranging from 0.05 to 1. Simulations were run for 1 500 time steps, and the final 1 000 were used in the calculations. Synchrony in fluctuations among all the populations was assessed by calculating cross correlations with time lag 0. For the present purpose, averages of the cross correlation coefficients were then calculated for all values of p and μ. It turns out that the Moran effect is potent enough to cause populations to fluctuate in synchrony, over a rather wide range of μ with all the p-values applied (Fig. 1). The conclusion is valid both for the Ricker and Turchin dynamics. Deviations from the common pattern of strong synchrony are achievable only with values of μ close to 1.0 (weak scaling effect).

3.2. Population dynamics

The impact of the Moran effect on the population dynamics was assessed by scaling the population with values of μ from 0.25 to 1 with step 0.05. A focal population was selected and its dynamics was simulated after Equation 1 for 1 500 time steps of which the last 1 000 observations, denoted by X_R and X_T, Ricker and Turchin outcomes, respectively, were taken for a closer evaluation. To the $\{X_R\}$ we fitted the Ricker (r, a_1) and to the $\{X_T\}$ the Turchin (r, a_1, a_2) models using the Levenberg-Marquard algorithm for minimizing the sum of squared errors (Levenberg 1994). Also, we scored the mean and variance of the $\{X_R\}$ and $\{X_T\}$ and calculated autocorrelation functions (ACF, with lag ranging from 0 to 5 yrs. for the Ricker model

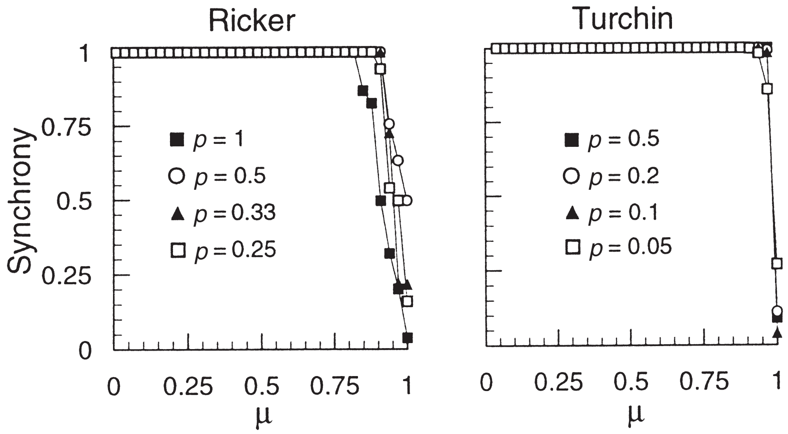

Fig. 1. Synchrony of the Moran effect perturbed population dynamics (average cross correlation among 10 populations) obeying the Ricker and Turchin versions of Equation 1. The dynamics of the populations were subjected to four different probabilities of the Moran effect (Ricker: $p(k) = 1$, $p(k) = 0.5$, $p(k) = 0.33$, $p(k) = 0.25$; Turchin: $p(k) = 0.5$, $p(k) = 0.2$, $p(k) = 0.1$, $p(k) = 0.05$) with intensities μ varying from 0.1 to 1. Note that for the Ricker model populations went extinct with $p(k) = 1$, and with $p(k) = 0.5$ when $\mu < 0.15$, likewise, extinctions were scored with the Turchin model with $p(k) = 0.5$ when $\mu < 0.4$, and with $p(k) = 0.2$ when $\mu < 0.2$.

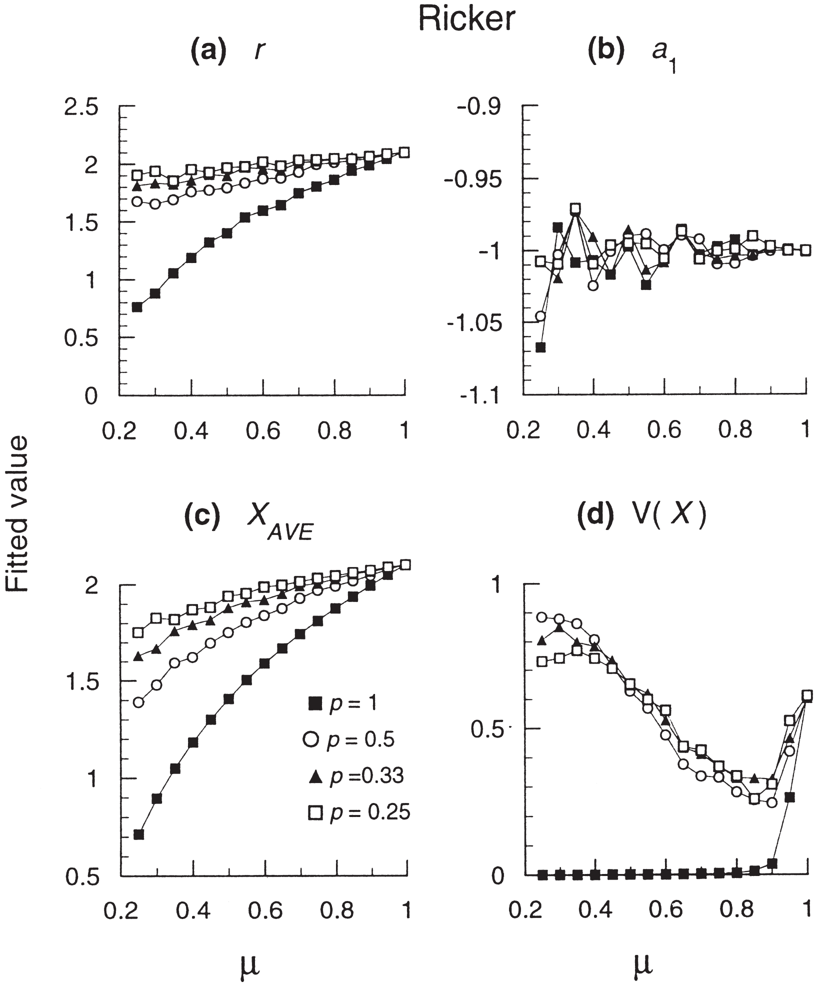

Fig. 2. Fitted parameter values (r and a_1) for the Ricker model simulated $\{X_R\}$ population data as a function of the intensity μ of the Moran effect with four different p-values. Also the mean X_{AVE} and the variance V(X) of the time series are shown.

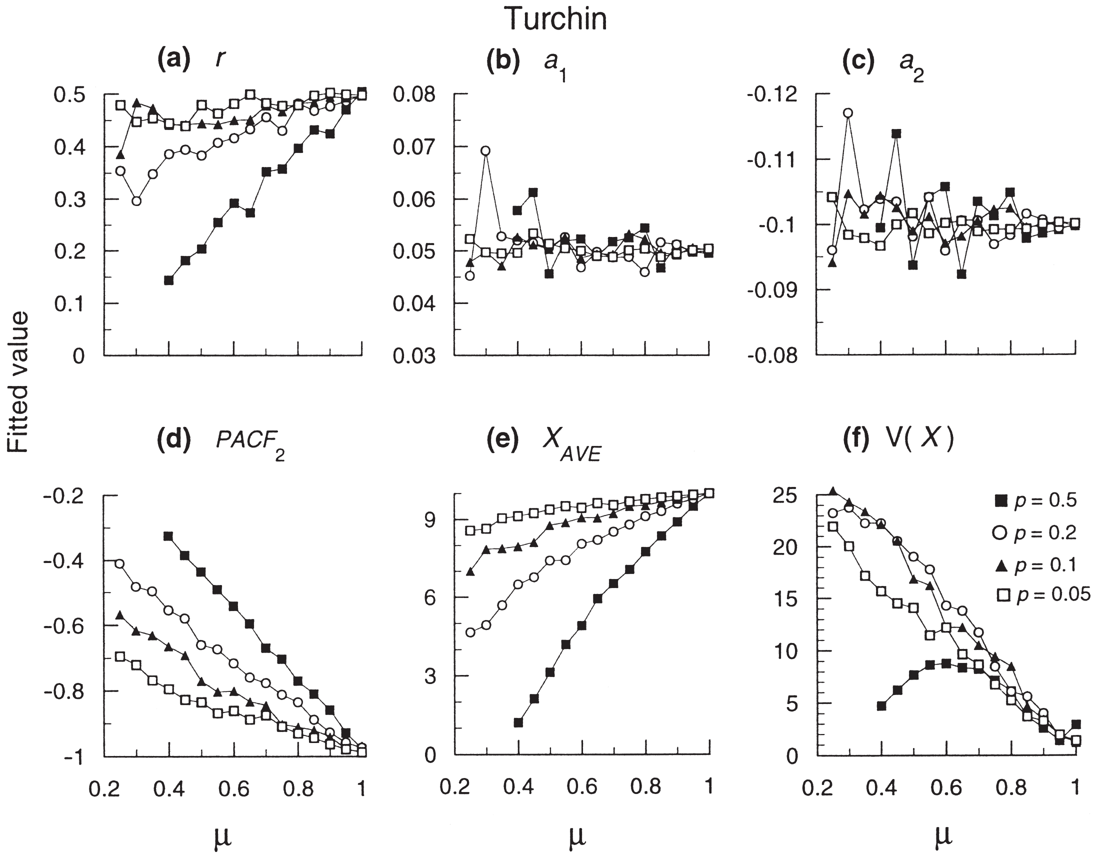

Fig. 3. Fitted parameter values (r, a_1 and a_2) for the Turchin model simulated X_T population data as a function of the intensity μ of the Moran effect with four different p-values. Also the mean X_{AVE} and the variance V(X) of the time series are shown together with the value of the partial autocorrelation coefficient (*PACF*) with lag 2.

and from 0 to 20 yrs. for the Turchin model). The ACF serves as an indication of the period length in X_R and X_T. For the $\{X_T\}$ we also calculated the partial autocorrelation, PACF, with lag 2, negative coefficients indicating delayed density dependence (e.g., Royama 1992).

The Moran effect perturbed time series rather faithfully returned the correct parameter values a_1 and a_2 as used originally in the simulation, the largest discrepancies being with small values of μ and large values of p (Figs. 2 and 3). The greatest disagreements between the simulation parameters and parameters calculated from the X_R and X_T were found with the intrinsic rate of increase, r, especially with the Moran effect having high probabilities of occurrence (Figs. 2 and 3). Also, mean and variance of the series were most faithfully reproduced with infrequently occurring and low intensity perturbations. In the $\{X_T\}$, values of the PACF$_2$ were throughout negative and below the Bartlett band (e.g., Box *et al.* 1994) of statistical significance at $\alpha = 0.05$ (Fig. 3d). Degeneration of the PACF$_2$-values increased with decreasing μ and increasing p. The most notable changes in the time series characteristics were observed in the ACF. Both with the p increasing and μ decreasing the time series X_R and X_T started to loose their characteristic periodicity (Figs. 4 and 5).

4. Conclusions

The Moran effect (Moran 1953, Royama 1992, Ranta *et al.* 1995a) is rather powerful in synchronizing dynamics of subpopulations over a rather broad range of intensity of the scaling effect and probability of occurrence. We have shown that the Moran effect may well produce deep qualita-

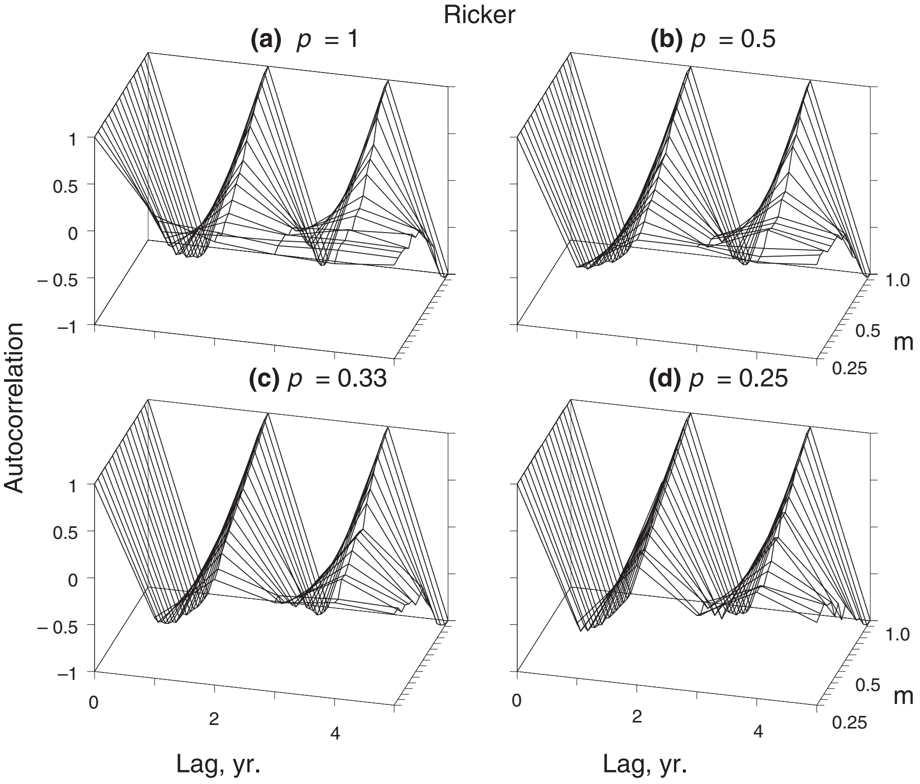

Fig. 4. Autocorrelation function surfaces (lag from 0 to 5 yrs.) for the Ricker model simulated data with varying intensity μ of the Moran effect with four probabilities of occurrence.

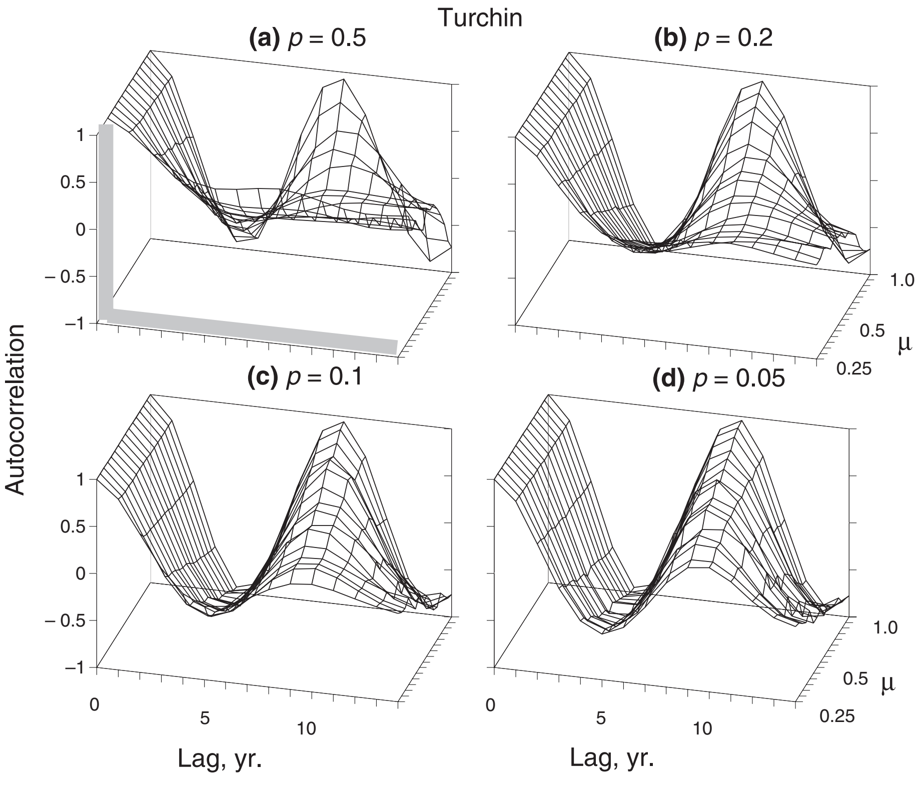

Fig. 5. Autocorrelation function surfaces (lag from 0 to 14 yrs.) for the Turchin model simulated data with varying intensity μ of the Moran effect with four probabilities of occurrence. Note that with $p(k) = 0.5$ the populations when extinct with $\mu < 0.4$ (shaded area).

tive differences in the results depending on the ecological interpretation of it, a result which emphasizes the fact that, besides neglecting the significance of correlated perturbations in the ecological literature (Royama 1992), advancing significance Moran's idea of correlated perturbances in affecting large-scale population dynamics has long been overlooked among the ecologists.

Specifically, we have shown in the present analysis that besides the synchronizing capability, the Moran effect, when frequent enough, or when strong enough, has a feature to alter the characteristics of the population dynamics. In fact, population dynamics yielded by a simple Ricker model with two-year periodicity and by a somewhat more complex Turchin model (with Period length 10) lose their cyclic components. Also, the model parameters, especially the intrinsic rate of increase *r*, starts to diverge from the value by which the simulated series was produced. Thus, the identification of the intrinsic population dynamics may depend on the type of the external Moran effect affecting the population.

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