in their fluctuations about the trend. These are examples of a process in which the first requirement in persistence is violated, whereas the second requirement is satisfied: they have an unchecked trend, but their fluctuations are regulated about the trend.

Now, we can think of a third situation in which a_1 and a_2 change so that a_1^*, a_2^*, and X^* change with time, whereas R_m and a_0 do not; that is, the environmental changes affect the dynamics of the population nonlinearly. [For causal mechanisms, see section 1.7.3.] Under the above assumptions:

$$X^*(t) = -(\log R_m + a_0)/[a_1(t) + a_2(t)] \tag{2.46a}$$

$$a_1^*(t) = a_1(t)R_m \tag{2.46b}$$

$$a_2^*(t) = a_2(t)R_m. \tag{2.46c}$$

Although not illustrated, we see that a generated series would have a nonlinear trend by (2.46a), and the pattern of fluctuation about the trend would also change by (2.46b and c). Again, a generated series would be doubly nonstationary. A combination of all three situations is, of course, possible.

2.5 THE MORAN EFFECT OF DENSITY-INDEPENDENT FACTORS: INTER-REGIONAL SYNCHRONY OF POPULATION FLUCTUATIONS

To conclude the present chapter, I shall discuss an important effect of density-independent factors that Moran (1953b) suggested.

The famous Hudson's Bay Co. statistics of fur trade since the last century indicate that Canada lynx (*Lynx canadensis*) populations have not only exhibited remarkably regular 10-year cycles, but also, and more intriguingly, have been very well synchronized across all regions of Canada (Chapter 5). Spruce budworm (*Choristoneura fumiferana*) populations, too, tend to fluctuate in unison, although on a much more restricted regional scale (Chapter 9). Probably, if we paid close attention, such synchronous fluctuations among local populations, e.g. a more or less simultaneous occurrence of insect outbreaks over a wide area, would be found to be common rather than unusual in many species from diverse taxa.

Many ecologists and naturalists have sought meteorological factors as a cause of such synchrony. There seems to be one tacit assumption in their minds, i.e. that the cause of population cycles, or that of the occurrence of outbreaks, is also the cause of their synchrony. The proposition is, in other words, that there is one common extrinsic factor that governs the cyclic fluctuations in the populations and, hence, the synchrony among them. Many suggestions in the literature explaining the synchrony of the lynx cycles, for instance, typically include such factors as sunspot cycles, ozone cycles, ultraviolet-ray cycles, forest fire cycles, or even lunar cycles (Chapter 5).

However, there is no convincing evidence which, in principle, supports these suggestions.

If, on the other hand, we abandon the single-causation hypothesis, an entirely new possibility appears. As early as 1953, Moran suggested an important theorem which I restate as below:

> If two regional populations have the same intrinsic (density-dependent) structure, they will be correlated under the influences of density-independent factors (such as climatic factors), if the factors are correlated between the regions.

In particular, Moran pointed out that if the density-dependent structure is linear (as in model (2.6)) the correlation between the regional populations will be equal to that between the local density-independent conditions. This, however, would not hold exactly if the density-dependent structure is nonlinear.

In order to demonstrate Moran's theorem graphically, I compare three series of log population densities $\{X_t\}$ in Fig. 2.22. The series $\{X_t\}$ in graph a is a copy of series IV(7) from Fig. 2.17. Recall that I generated this series using the nonlinear model (2.39b) in which $a_1^* = 0.5$ and $a_2^* = -0.9$, and in which the perturbation effect u_t is an independent, normally distributed random number with mean $= 0$ and variance $= 0.04$ (Fig. 2.14a).

I now generate another series of independent random numbers, $\{v_t\}$, identically distributed as, but uncorrelated with, the series $\{u_t\}$. Then, I generate another series $\{X_t\}$ in graph c using the same model (2.39b) with the identical a_1^* and a_2^* values as in series a, but using the perturbation series $\{v_t\}$ in place of $\{u_t\}$.

I generate one more series $\{X_t\}$ in graph b, using, again, the same a_1^* and a_2^* values in model (2.39b), but using yet another perturbation series $\{w_t\}$. I generate the series $\{w_t\}$ as a blend of 0.8 part $\{u_t\}$ and 0.6 part $\{v_t\}$:

$$w_t = 0.8u_t + 0.6v_t. \tag{2.47}$$

The mixed variable w also has exactly the same distribution as its components, u_t and v_t. The mean of w_t is zero because both u_t and v_t have mean zero. The variance of w_t is also 0.04 because it is the weighted sum of the variances of u_t and v_t, i.e.

$$\begin{aligned}\mathrm{Var}(w_t) &= 0.8^2\mathrm{Var}(u_t) + 0.6^2\mathrm{Var}(v_t)\\ &= (0.64 + 0.36) \times 0.04 = 0.04.\end{aligned}$$

Further, w_t is normally distributed because the sum of constant multiples of independent, normally distributed random numbers is again normally distributed.

From (2.47), w_t is, as expected, 80% correlated with u_t and 60% with v_t, although the realized correlations in the simulation are 78.2% and 49.6%,

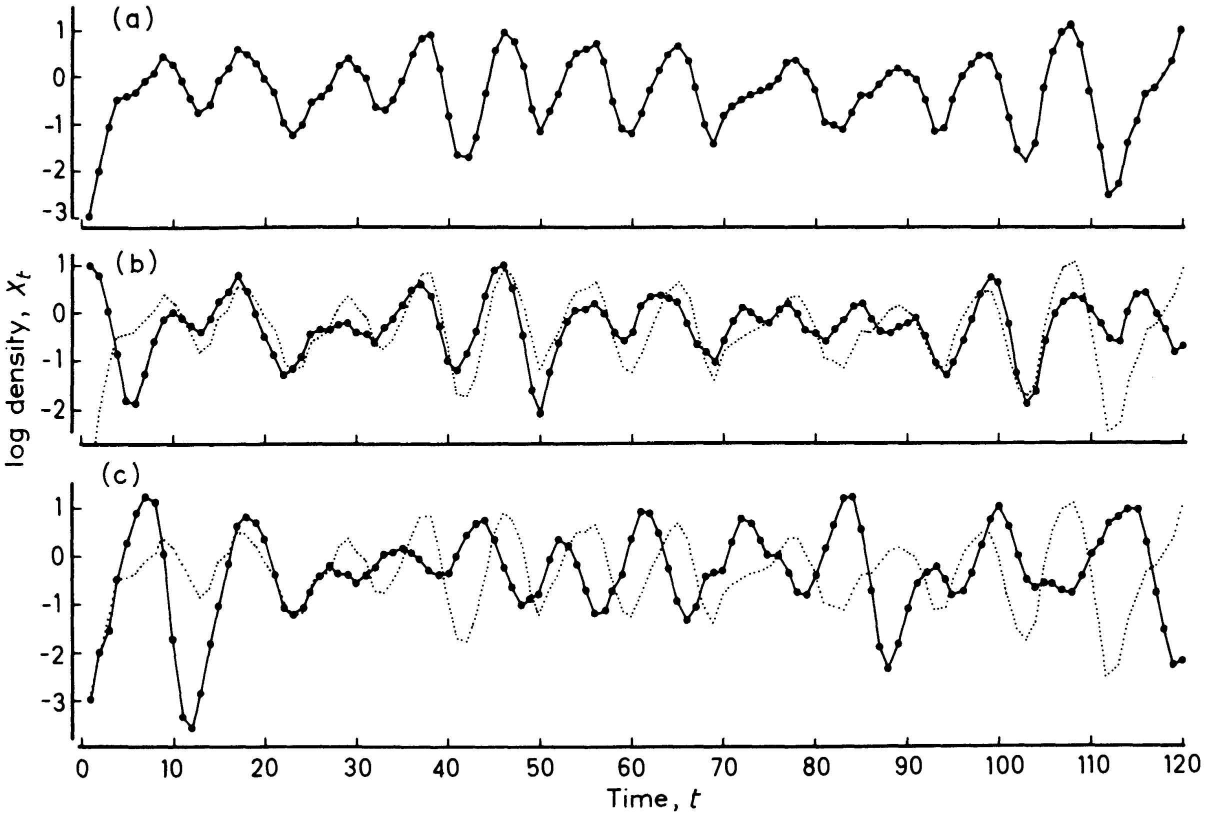

Figure 2.22 A demonstration of the Moran effect by simulation, showing a good synchrony between series a and b but little synchrony between a and c (a is reproduced in dots to compare with b and c), and a moderately good synchrony between b and c.

respectively. As a result, we see a good synchrony in cyclic pattern between series a and b; to a lesser extent between b and c; and little or no synchrony between a and c (synchrony, if any, is coincidental).

The significance of the Moran theorem is that the cause of synchrony can be completely independent of the cause of the cyclic population fluctuation. Thus, we have considerable flexibility in looking around for a possible cause of the cycles and, independently, for one of their synchrony.