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Spatial self-organization and persistence of transients in a metapopulation model

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SUMMARY

We extend the analysis of a previously published type of model representing a linear set of habitat fragments each of which supports populations which reproduce in (synchronized) discrete generations. The populations are linked by a dispersal phase which occurs after each reproductive bout. Previously, this model has been shown to produce transient behaviour lasting thousands of generations and characterized by sudden changes in behaviour. We confirm the existence of these effects and characterize the conditions under which they are likely to occur. We also demonstrate that the model predicts organized spatial heterogeneity across the system. This means that the dynamics of the ensemble can be a poor predictor of the behaviour of individual populations, and further, that different populations within the same linked system can experience quantitatively very different dynamics. We also demonstrate that the model predicts that the peripheral populations should be subject to greater temporal variation than the interior. We discuss the appropriateness of the model to a variety of natural systems and the implications of its predictions.

1. INTRODUCTION

The existence of spatial heterogeneity in many ecological systems has inspired much investigation of the properties of population models representing many different types of spatial structure (see Kareiva 1990 and de Roos & Sabelis 1995 for an overview). One particularly well studied model is that of a metapopulation: a group of distinct populations which are linked by migration of individuals between them (for a review, see Gilpin & Hanski 1991). The most common mathematical representation of a metapopulation is as a collection of one-step difference equations with added transport terms. These models are often termed coupled map lattices (Kaneko 1989).

There is good empirical and theoretical evidence that spatial structure can have profound effects on population processes (e.g. promoting species coexistence (Tilman 1994), and preventing extinction (Huffaker 1958; Holt & Hassell 1993)). Several theoretical papers have argued that coupling between populations can have a simplifying effect on population dynamics (Gonzalez-Andujar & Perry 1993; Hastings 1993; McCallum 1994; Stone 1994; Doebeli 1995; Lloyd 1995; Janosi & Scheuring 1995). In contrast, however, Hastings & Higgins (1994) demonstrate that a system of linked Ricker maps can display very long and unpredictable transient behaviour.

If the behaviour of the Hastings & Higgins model mirrors that of natural populations then this suggests that the traditional emphasis on the final solution of model ecological systems is misplaced, as the transient

leading to the final solution will be of much greater biological relevance. Coupled map lattices are also studied in physics and very long 'supertransients' have been reported (Lai 1995; Lai & Winslow 1995). Hence one aim of our study is to investigate whether Hastings & Higgins observations can be extended to a related but more general model. If this proves so, we will probe the conditions which need to be satisfied for supertransients to be produced. Further, Hastings & Higgins only reported on the behaviour of the total ensemble population size. It is well established, however, that the dynamics of metapopulations can be very different from that of their constituent local populations (Gilpin & Hanski 1991). Hence we will investigate how long transients are characterized both at an ensemble and at a local population level.

2. THE MODEL

We envisage a metapopulation consisting of many localized populations existing in discrete habitat fragments. These fragments are distributed along a one-dimensional ecosystem, such as a sea coast, a lake shore or the edge of a forest. We label the local populations $0, \dots, R$. Each population reproduces in synchronized discrete generations, each reproductive bout being separated by a period where individuals can migrate between populations. We define each generation to start with a reproductive bout followed by migration. At the start of a given generation t , the population size in the i th habitat fragment is denoted

$N_t[i]$. To model density-dependent reproduction, we use the difference equation due to Maynard Smith & Slatkin (1973). The density of individuals after reproduction (but before dispersal) in each patch is given by

$$M_t[i] = N_t[i]f(N_t[i]) = \frac{\lambda N_t[i]}{1 + (aN_t[i])^b}. \quad (1)$$

The parameter λ is the intrinsic growth rate, a is the inverse of the carrying capacity of the environment and b describes the intensity of competition (for a fuller description of the biology behind this formulation see Hassell 1975).

We assume that dispersal is density independent. The proportion of the population on patch i which moves to patch j is given by a Gaussian distribution:

$$p(i,j) = \sqrt{\frac{D}{\pi}} \exp(-D(i-j)^2). \quad (2)$$

This proportion is maximized when $i = j$, this being the fraction of each population which remains on the patch of their birth. Generally, the further two patches are apart, the smaller the proportion of migrants which transfer between them. The size of the proportions is controlled by the parameter D : the smaller D is, the greater the spatial spread of migrants. D is assumed always to be positive and is bounded above such that the sum of $p(i,j)$ over all possible values of j is always less than unity.

The size of each local population at the start of the next generation is given as the number of its own offspring which remain from the last generation, plus all the migrants from other patches,

$$N_{t+1}[i] = \sum_{j=0}^N M_t[j] \times p(i,j). \quad (3)$$

We assume dissipative boundary conditions. A fraction of migrants from each patch will disperse beyond the edges of the system, and are considered lost.

3. POPULATION DYNAMICS

Hastings & Higgins (1994) investigated the behaviour of a model very similar to that used in this investigation except for their use of the Ricker function to describe within-patch dynamics. Bellows (1981) & Doebeli (1995) argue that the function used in our study has properties which make it more generally applicable than the simpler Ricker function. Hastings & Higgins (1994) reported that their model displayed long transients featuring very sudden changes in the form of the dynamics. This behaviour was also observed in our study (see figure 1*a*). In this example, we can see that for the first 3000 generations coupling seems to have little effect, with the ensemble varying chaotically over a wide range. Then there is a sudden shift in behaviour, the population still appears aperiodic but the fluctuations are contained within a much narrower band of values. After another 1500 generations, the system switches back to the broad-band fluctuations. At around 7000 generations there is another switch to a completely different type of behaviour. Now the ensemble population appears to perform something

close to a two-point cycle for periods, interspersed with periods of wild chaotic fluctuations. This behaviour is strongly reminiscent of intermittent chaos, akin to that shown by Doebeli (1993, 1994) and Vandermeer (1993). After showing this behaviour for over 1000 generations, the system switches back to broad-band chaos.

We found, however, that the conditions required for the observation of such behaviour were quite strict. First, the density dependence in the reproduction function must be sufficiently strong that the populations would behave chaotically in the absence of migration. Second, the parameter D (which controls dispersal) must be tuned to a value within a narrow range of possible values. If it is too high, then migration is too weak to influence the dynamics and the ensemble behaves like a collection of uncoupled populations; if it is too low, the coupling is sufficiently strong to bring the populations under control after a very short transient (as illustrated in figure 1*b*). We also note that long transients are often associated with parameter values which lead to multiple attractors. In this case, the initial values chosen at the start of the simulation can affect the final dynamic attractor which is selected, and hence the transient phase leading to that attractor.

In figure 1*b*, the transient lasts less than 300 generations and leads to a two-point cycle with a very small amplitude. Hastings & Higgins (1994) only reported the dynamics of the ensemble, not of the individual populations. Figure 2*a* shows the final behaviour of all the individual populations of the ensemble used in figure 1*b*. It can be seen that the final attractor is characterized by strong spatial structuring. At any instant, the local population sizes are arranged to form a wave structure across the length of the spatial domain. Each local population undergoes a two-point cycle, and in this respect the behaviour of the ensemble is a good guide to the behaviour of the individual populations, although this is not always true (see later and figure 2*b*). Moreover, the behaviour of the ensemble is a very poor indicator of the amplitude of fluctuations experienced by the local populations. As can be seen in figure 2*a*, some local populations exhibit very high amplitude oscillations with their populations changes over orders of magnitude between successive generations, whereas some others exhibit such small oscillations that they are effectively at a steady state.

Investigating the population dynamics at a local level can also be instructive when the ensemble is undergoing transient behaviour, as illustrated in figure 2*b*. This shows the state of all of the populations at three instants, each separated by two generations, for the system used to create figure 1*a*. These measurements were taken at generations $t = 3000, 3002$ and 3004 , when the ensemble was displaying narrow band aperiodic oscillations. Perhaps rather surprisingly, most populations within the system do not show the wild oscillations shown by the ensemble but are very close to a simple two cycle. Only at one extreme, i.e. for $i < 10$, do the populations exhibit less orderly behaviour. Extensive numerical investigations suggest that ordered behaviour of most of the system with wild oscillations only in the peripheral populations is

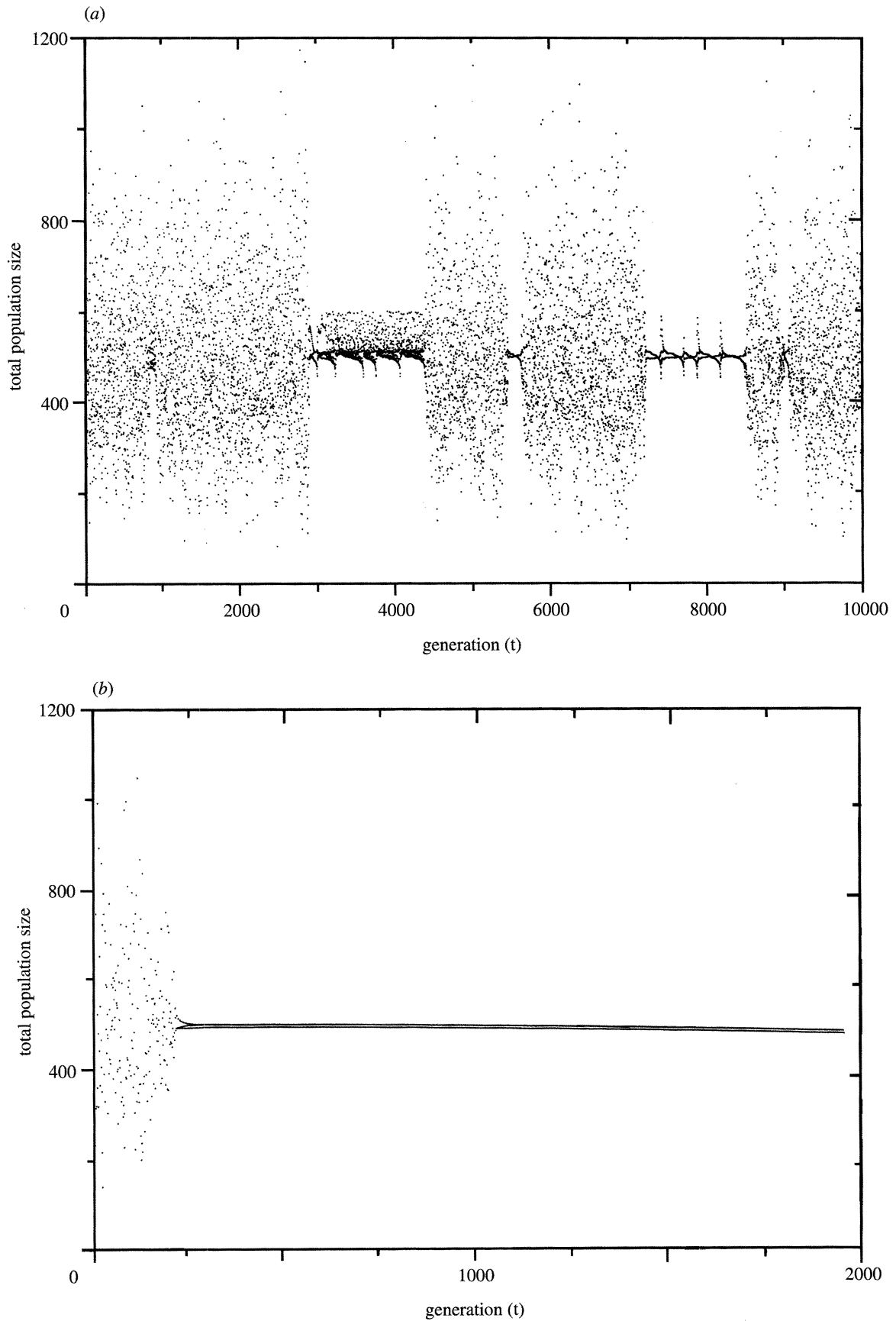


Figure 1. The sum of the populations in a system of 100 patches described by equations (1)–(3). Each patch is initialized with a population value drawn independently from $[0, 1/a]$. The dispersal parameter D is (a) 0.0769 or (b) 0.06. The first case produces complex and long-lived transient behaviour; the second produces a short transient leading to a simple two point cycle of small amplitude. The parameter values $a = 1$, $b = 4.8$, $\lambda = 7$ are used in both (a) and (b).

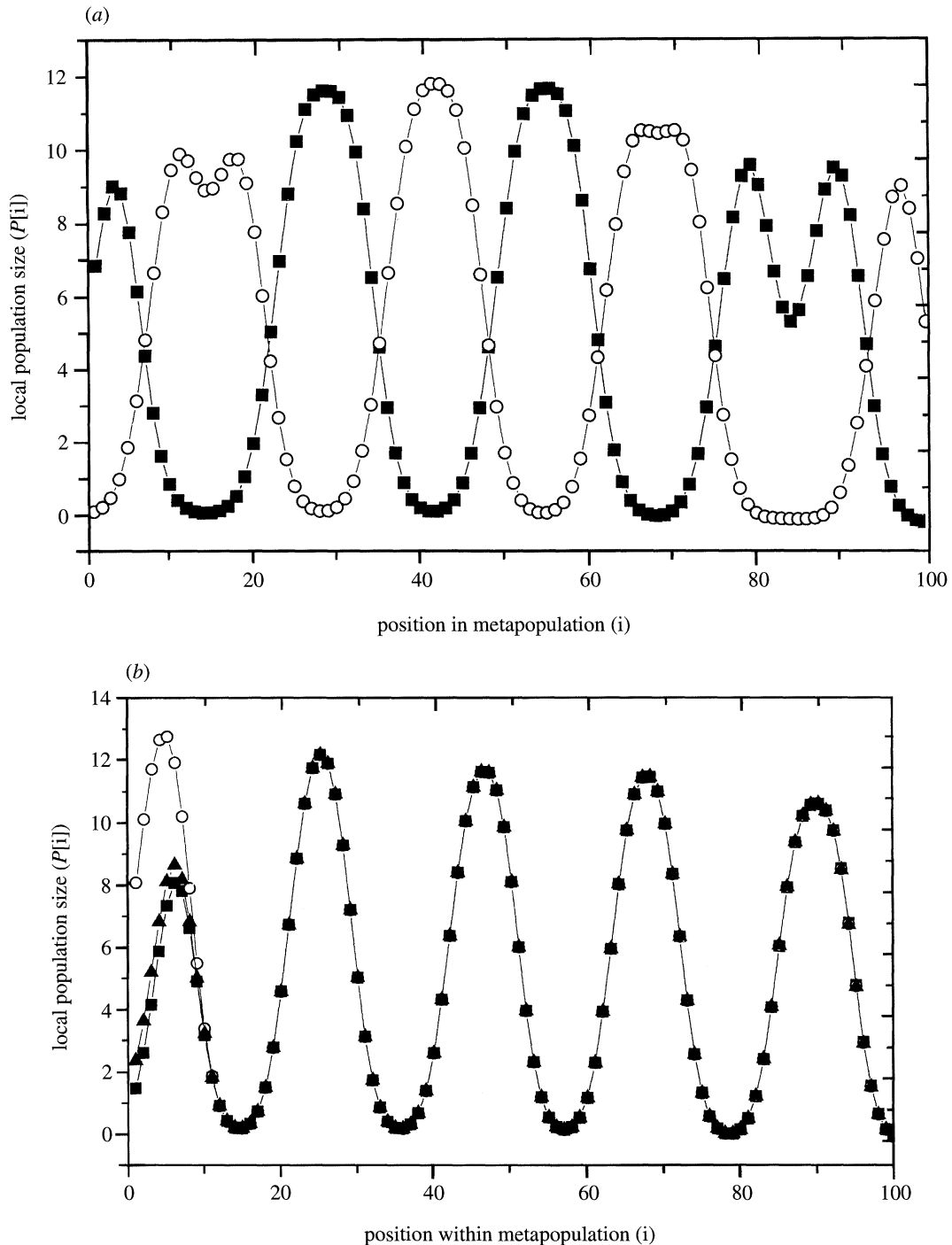


Figure 2. (a) The sizes of each individual population at generations $500 < t < 600$ for the simulation used to construct figure 1b, filled squares represent even numbered generations, open circles represent odd ones. Each population undergoes a two cycle. However there is a strong self-organized spatial wave structure across the system, which leads to strong and systematic variation in the size of the oscillation experienced by each population. (b) The sizes of each individual population at generations $t = 3000$ (squares), 3002 (circles) and 3004 (triangles) for the simulation used to construct figure 1a. Again a self-organized spatial wave structure is observed. Most populations approximate a two cycle, however those for which $i < 10$, show wild aperiodic fluctuations. Such 'loose ends' are characteristic of the narrow band chaos shown for $3000 < t < 4000$ in figure 1a.

characteristic of the narrow band aperiodic behaviour of the type illustrated in figure 1a. Again, this shows that observation of the behaviour of the sum of the populations can be a poor indicator of the behaviour of individual populations. Observation of figure 1a around $t = 3000$ and figure 1b around $t = 500$, would lead us to expect that the dynamics of local populations

would be quite different in both cases. However figure 2 demonstrates that, for most of the populations, there is little qualitative difference in behaviour between the two cases. It also emphasizes that there can be radical differences in behaviour between different populations within the same system, as a result of self-organized spatial wave structures.

4. DISCUSSION

Hastings & Higgins (1994) found that their model of coupled Ricker maps displayed long lived and complex transients featuring sudden shifts in behaviour. We have observed similar behaviour in a more general model. This result has important implications for the use of models in ecology. Until now, the focus of model analysis has been on the long term equilibrium behaviour of models. However, if transient behaviour (in the absence of external influences) can last many thousands of generations, as has been shown here, then this transient behaviour may be of much more practical relevance than the final attractor. Further it is very unlikely that a system of populations would experience a unchanging environment over this timescale. Environmental fluctuations may extend the length of the transient still further (Rand & Wilson 1991), although more research into the effect on noise on spatial dynamic systems is required. The observation that the transient can show periods of hundreds of generations featuring generally similar behaviour followed by a sudden change in behaviour is also of practical importance. When a natural population suddenly undergoes a population explosion or crash, we naturally look for some external force which triggered this change. Our work, and that of Hastings & Higgins, suggest that there may not always be an external trigger, such dramatic changes in behaviour may be an intrinsic feature of the population dynamics.

Given the great import of these long and complex transients, it is vital that we evaluate how likely they are to occur in natural populations. Hastings & Higgins report that in their system of linked Ricker maps, 'if the density-dependence is strong enough, then the time required to reach the final dynamics is usually very long and there are typically very sudden changes in the form of the dynamics.' In our model, we also find that a necessary condition for long transients is strong over-compensation in recruitment, so strong that the populations would behave chaotically if isolated. Even in this case, we can only obtain long transients for a restricted range of the dispersal parameter D . If D is too low, then coupling between populations is sufficiently strong that the chaos is reduced to a simple cycle after only a short transient. If D is too large, then coupling is too weak and the system simply behaves chaotically, as if the populations were uncoupled. Further studies must investigate if less general but more realistic models can also be made to show this long, complex transients. One obvious generalization of our model would be to relax the restriction that the reproduction function is the same for each population in the system. In physics, Brayman *et al.* (1995) have demonstrated that removing this homogeneity in a system of linked oscillators considerably reduced their propensity to exhibit chaos, although the resulting dynamics were still very complicated.

Systems of difference equations linked by migration terms ('coupled map lattices' sensu Kaneko 1989) have become increasingly popular in the ecology literature: see, for example, Hassell *et al.* 1991, 1994; Allen *et al.* 1993; Ruxton 1994; Bascompte & Sole

1995; Rohani & Miramontes 1995. Given this intensive study of such systems, why have long, complex dynamics not been more widely reported? Most modelling studies assume either that all populations are equally well connected (migrants from any one patch divide equally among all the patches in the system) or they assume that migration is only possible between nearest neighbours (but, for an exception, see Neubert *et al.* 1995). We have been able to observe long and complex transients in our model with D values around unity, i.e. when long range dispersal is relatively uncommon and 98% of individuals either stay on their original patch or move to one of the two nearest-neighbours. However, if the model is modified so that all migrants which would have moved further than the nearest neighbours are instead forced to land on these patches, then we cannot obtain long transients. This highlights another requirement for obtaining long, complex transients: there must be some (albeit possibly very small) long-range migration. Another reason why many published studies will be less likely to show this behaviour is that many use periodic boundary conditions, which means that the ends of the habitat would be joined to form a continuous ring. In this case, even if long-range dispersal is allowed, the concept of peripheral habitat fragments has no meaning, and the 'loose ends' phenomenon illustrated in figure 2*b* could not be observed. Although we have followed Hastings & Higgins in studying a one-dimensional chain of habitat fragments, we expect that our qualitative conclusions will be preserved in higher-dimensional systems. Grassberger (1994) found very similar boundary effects to those reported here in a two-dimensional coupled map lattice.

One ubiquitous feature of our model which occurs in both the transient and final dynamic regions of simulations is the emergence of the strongly self-organized spatial wave structures illustrated in figure 2. Although they do not discuss this, simulations of the model presented by Hastings & Higgins (1994) also show this behaviour. Again this feature may have ramifications for our view of the natural world. If the populations of a certain species were measured in a number of habitat fragments and great variety in population size was found, it might be tempting to interpret this as mirroring an underlying variability in habitat 'suitability'. However, our results suggest that if the fragments are linked into a metapopulation through dispersal, this strong spatial variability may arise spontaneously and may have nothing to do with underlying variability in environment. Similarly our results suggest that the observation that some populations within the system fluctuate much more than others, may not necessarily indicate that some populations are subject to stronger environmental fluctuations than others, nor that they differ in intrinsic population-regulation properties. The self-organized pattern is a property of the system as a whole, hence another prediction from our model is that local alterations to the system could induce the self-organized pattern to re-adjust, thus potentially causing large changes in the behaviour of parts of the system which need not be strongly coupled to the modified

portion. The warning for human impact on natural ecosystems is obvious. Yet another ramification of the strong spatial structuring is the observation that the behaviour of the ensemble is a very poor predictor of the behaviour of individual local populations. Hence sampling exercises done at different scales may produce very different findings.

In view of the apparent generality of the conditions required to produce long and complex dynamic transients, and the serious ecological consequences of such behaviour, we believe that further research in this area is warranted. More complex models must be used to confirm our predictions as to the conditions required for the formation of long and complex transients, and to identify these conditions in terms of variables that can be measured in the field. We can then assess how common this behaviour is in the natural world. Another strand of worthwhile research would be to construct experimental systems of linked populations, to test some of our predictions (e.g. the existence of self-organization within the system and the loose ends' behaviour of peripheral populations). If long complex transients are commonplace in the natural world, then the ramifications for theoretical and applied ecology will be considerable.

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