

The importance of transients' dynamics in spatially extended populations

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Recent theoretical works on the dynamics of metapopulations have highlighted the existence of very long transients (supertransients) with abrupt changes in behaviour which occur following perturbation of the system away from its attractor. If this phenomenon is common in natural systems, populations that do not oscillate can begin to fluctuate wildly without any change in the environmental conditions. However, the frequency of occurrence of supertransients is currently poorly understood even in model systems. Here we explore their occurrence in metapopulation models which relax the important assumption of global synchrony of events implicit in all the coupled map lattice models for which supertransients have so far been demonstrated. We find supertransients in all the models but always only for a very restricted range of parameter combinations. However, we also report for the first time another type of longer-lived transient (mesotransients) that occurs on shorter time-scales than supertransients and is found for a much wider set of conditions. We argue that these medium-term changes in the dynamics of populations can be of more ecological relevance than the long-term changes of supertransients.

Keywords: supertransients; synchrony; asynchrony; spatial models

1. INTRODUCTION

The realization that the spatial dimension may be the key to understanding many ecological phenomena has opened up a new world of problems and questions for biologists. One of the most popular modelling frameworks is the coupled map lattice (CML). In such systems, each individual site changes in response to local factors, generally following a discrete equation. All sites change at the same time, then migration occurs between patches (again in synchrony).

The range of possible dynamic behaviours of CMLs is considerable, ranging from simple cycles to spiral waves and crystal lattice structures (Hassell *et al.* 1991; Kaneko 1998). One of the most striking and potentially biologically relevant features of these models is the production of very long transients with changes in the qualitative dynamics (Crutchfield & Kaneko 1988; Hastings & Higgins 1994; Ruxton & Doebeli 1996). Theoretical ecology has traditionally placed great emphasis on the dynamics of the final attractor of a system. However, the observation of these supertransients suggests that, in some cases, the transient behaviour will have far greater ecological relevance than an attractor, which is only reached after 10 000 generations of unchanging conditions. The transient time before approaching an attractor usually scales exponentially or faster with the number of sites considered (Kaneko 1995). Another important feature of these supertransients is that they can show one type of behaviour for hundreds or even thousands of generations before abruptly changing to another behaviour, even in the absence of some external trigger. If this is a good model for real systems, then it means that, when we see a sudden great change in the behaviour of a system (e.g.

local extinction), this may have been the result of an intrinsically generated dynamic effect rather than a response to a change in the environment.

Given the potentially extreme ecological significance of such phenomena, it is imperative that we look for them beyond the confines of the limited range of models in which they have so far been demonstrated. In a first step towards this, we explore here their occurrence in a suite of models which relax one of the key assumptions implicit in the models where it has been demonstrated so far, that of global synchrony of events.

2. MODEL DESCRIPTION

We used a model similar to the one studied by Hastings & Higgins (1994). In this model, space is represented as a one-dimensional array of discrete habitat fragments, such as bays along a coastline or orchards along a narrow valley. For simplicity, these habitat fragments are assumed to be identical and equally spaced. Each habitat fragment supports a local population of a given species, with local populations being linked to a subset of other populations via dispersal between habitat fragments that are spatially close. The local populations have discrete generations with separate dispersal and reproductive phases. We assume that the dispersers are juveniles or larvae and only adults reproduce. This model can be used to represent the dynamics of scale insects (Greathead 1997), annual plants with no persistent seed pool (Silvertown & Lovett Doust 1993) or some marine species with pelagic larvae (Hastings & Higgins 1994).

It is usual to assume in this kind of model that individuals in all the populations reproduce and then disperse in a synchronized way (Hassell *et al.* 1995). This assumption of synchrony across the spatial extent of the system may be valid for certain species of algae and corals

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(Kenyon 1995; Clifton 1997) where there are strong global and seasonal triggers to which individuals respond. In natural populations, environmental conditions can be different for each habitat patch and these can modify the timing of reproduction and dispersal. The timing can also be modified by localized disturbances or stochastic demographic events.

We sought to make these models more general by exploring the consequences of relaxing the assumption of perfect synchrony across the spatial domain of the meta-population. However, we kept the less-stringent assumption of synchrony of individuals within a local population. We did this by dividing each generation into a discrete number of time-periods, allowing a fraction of the populations to disperse and/or reproduce in each period.

We assumed that each generation was subdivided into P periods of time. In each period a proportion pD_k of the populations experience migration from them and a proportion pR_k experience reproduction with $k = 1, \dots, P$. Each population can reproduce and disperse only once during a generation and, if both events occur in the same period for any population, the reproduction event is always evaluated first. As a simple example, if we define $P = 2$ and $pD_1 = 0$, $pD_2 = 1$, $pR_1 = 1$ and $pR_2 = 0$, we recover the globally synchronized behaviour where all the populations first reproduce and then disperse.

We developed two ways of choosing which populations will reproduce or disperse in a particular period.

- (i) Random asynchrony. At the beginning of each generation the timing of both reproduction and dispersal is chosen randomly for each site from the same probability distributions, subject to the constraint that reproduction must occur before dispersal at each site.
- (ii) Fixed asynchrony. The timing of each population's two events within a generation are obtained as in the case above at the start of the simulation but are then fixed for every generation. These two times can be the same on every site, but need not be. However, the relative ordering of events between sites will be fixed over time.

The fixed scheme allows us to maintain the deterministic nature of the original model but relaxes the assumption of spatial synchrony. In this way, we can tease apart the effects of adding spatial asynchrony and spatio-temporal variation to the standard model.

The size of the i th local population at the start of a given generation t is denoted as $N_t[i]$ where i goes from 1 to S , the total number of habitats. To model density-dependent reproduction, we use the Maynard Smith & Slatkin (1973) difference equation. The production of immature individuals or larvae (L) in each patch is given by

$$L_{t+1}[i] = N_t[i]f(N_t[i]) = \frac{\lambda N_t[i]}{1 + (a(N_t[i] + L_t))^b}. \tag{1}$$

The parameter λ is the intrinsic per-capita growth rate in the absence of competition effects, a is the inverse of the carrying capacity of the environment and b describes the intensity and form of competition (see Bellows (1981) and Doebeli (1995) for further discussion).

L_t is the larvae dispersed from sites where the reproduction and dispersal events have already occurred. These migrants act to strengthen the apparent competition experienced by the breeding residents with whom they compete for resources; however, they are immature and, thus, are not added to the breeding population. Hence, the term on the numerator remains the local population size at the start of the generation and the denominator is the sum of both stages. The competition of adults and immature stages is common in scales (Gullan 1997). We take this case for our model because it is one of the simplest ways in which asynchrony of events affects the dynamics of a population.

Following previous works (e.g. Hastings & Higgins 1994; Ruxton & Doebeli 1996), we assumed that dispersal is density independent and that the proportion of the population on patch i which moves to patch j is given by a Gaussian distribution:

$$p(i,j) = \sqrt{\frac{d}{n}}e^{-d(1-j)^2}. \tag{2}$$

The value of $p(i,j)$ when $i = j$ determines the fraction of each population that remains on patch i . When the distance between two patches increases, the proportion of the population that migrates between them decreases exponentially. The rate of this exponential decrease is controlled by the parameter d : the smaller d is the greater the spatial spread of migrants. Therefore, the adult population in the next generation is given by

$$N_{t+1}[i] = \sum_{j=1}^S p(i,j)L_t[j]. \tag{3}$$

We further assumed dissipative boundary conditions so that the fraction of migrants that disperses beyond the edges of the system is lost.

Long transients have been observed in systems with periodical boundary conditions too (Kaneko 1990), but these are equivalent to an infinite habitat which might not seem a very realistic assumption in a highly fragmented world.

In this paper, we will explore the consequences of breaking the assumption of complete spatial synchrony for local and ensemble population dynamics and how these consequences can be related to the strength of asynchrony.

3. RESULTS

We observed previously reported dynamics (Hastings & Higgins 1994; Ruxton & Doebeli 1996) of very long transients with sudden changes in the form of the dynamics separating periods of thousands of generations within which the dynamics appear unchanging (figure 1a). This behaviour is strongly dependent on the initial conditions and is structurally unstable as slight modifications in the parameters produce different kinds of dynamics (Ruxton & Doebeli 1996). For the particular example of figure 1a, small perturbations to the initial conditions generally produce a short initial transient followed by relatively simpler cyclic dynamics, although sometimes a long transient of complex dynamics is

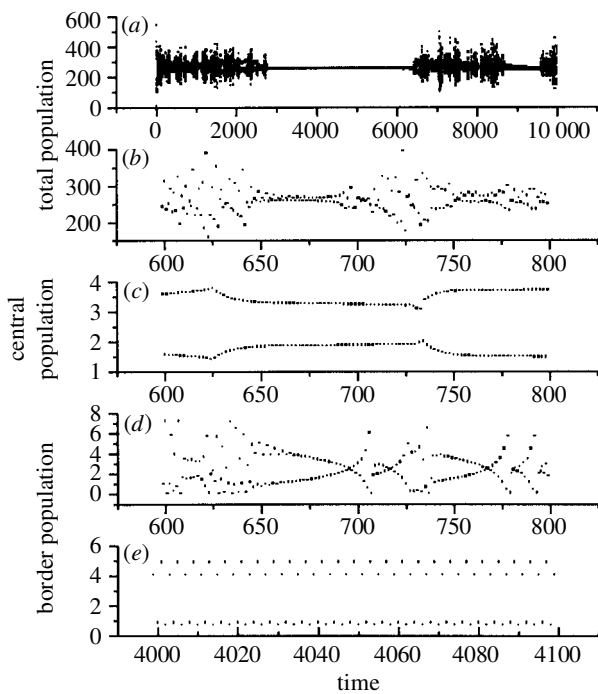


Figure 1. Simulation of a system with 100 patches of suitable habitat. Each patch is initialized with a population value drawn from a uniform distribution between 0 and $1/a$. The parameters used were $a = 1$, $b = 3.9$, $\lambda = 15$, $d = 0.045$, $pD = \{0, 1\}$ and $pR = \{1, 0\}$ and the unit of time is a generation of the population. (a) The sum of the populations in the system; in this time-scale long transients with sudden changes in behaviour are observed. (b) The same as (a) but on a shorter time-scale; note the existence of zones with different behaviours. (c) An individual population near the centre of the system. (d) An individual population close to the edge of the system. (e) The same as (d) but in the region of simple dynamics.

observed but without the sudden changes in the form of the dynamics.

Let us now look at the behaviour of the total population on a time-scale more similar to that of the long-term ecological time-series available (Royama 1992), i.e. under 200 generations. Although the long time-scale of figure 1a might suggest periods of thousands of generations with no change in dynamics, this is not so: a pattern resembling that of the full-length time-series, i.e. with abrupt changes in behaviour ('mesotransients') can be observed within these sections when we look on a finer temporal scale (figure 1b). These mesotransients are perhaps more relevant ecologically than supertransients because we can observe qualitative changes in the dynamics on a time-scale amenable to ecological experimentation or sampling. As we will show later, these mesotransients also seem to be a more common phenomenon in our models than the supertransients described previously by others and shown here in figure 1a.

In the zone of complex dynamics (e.g. for the first 2800 generations of figure 1a), the behaviours of the individual populations present remarkable differences to both each other and to that shown by the total population (figure 1b). The populations close to the borders of the array of suitable habitat (figure 1d) have a more complex dynamics than the central ones which show almost cyclic

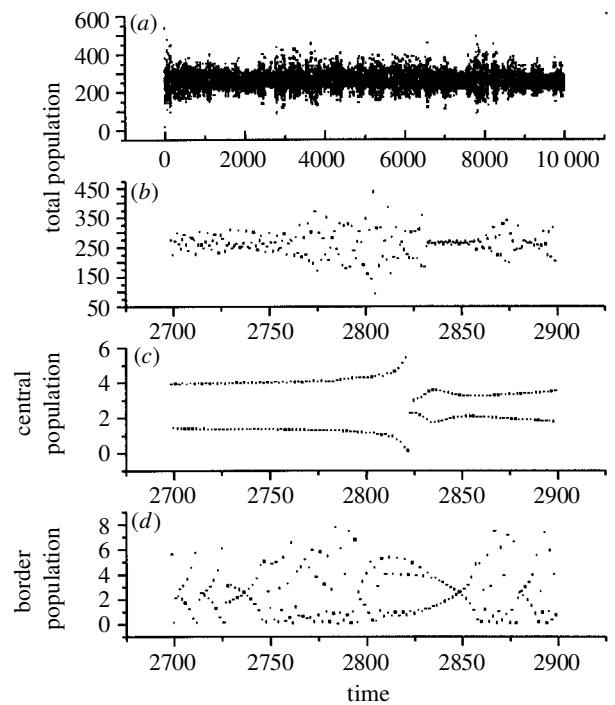


Figure 2. A simulation using the same parameters as in figure 1 but, instead of using a synchronic updating, we used the fixed asynchrony scheme with parameters $pD = \{0.0, 0.1, 0.9\}$ and $pR = \{0.9, 0.1, 0.0\}$.

dynamics of period 2 most of the time (figure 1c). In contrast, in the zone of simpler global dynamics (e.g. between generations 3000 and 6000 of figure 1a) both the border and central populations show similar cyclic dynamics (figure 1e). Again, this observation has important practical implications for population monitoring since it suggests that population fluctuations at a source spatial scale can be a very poor indication of even qualitative feature fluctuations within a smaller subsample.

Using the same parameters and the same initial conditions, we simulated the system with fixed asynchrony, assuming a simple scheme for seasonality of the reproduction and dispersal events. We divided the total time-step into three seasons: in the first, 90% of the populations have a reproductive event and in the last, 90% of the dispersal events occur. In the middle season there exists an overlapping of the 10% of dispersal and the 10% of reproduction events. In this way, a small fraction of the populations will experience dispersal before others experience reproduction. This is the only difference from our previous simulations, which yielded figure 1. However, this small perturbation has a profound effect on the dynamics of the model.

The dramatic changes over a very long time-scale are lost (compare figure 2a with figure 1a), although those observed on a medium time-scale are retained (figure 1b). The patterns of the individual populations in figure 2c,d are also similar to those in figure 1c,d. The extended regions of simple periodic behaviour in figure 1a were produced when the central and border populations both produced a simple population dynamic pattern (figure 1c,e). The fixed asynchrony prevents the formation of the periodic pattern in the border populations destroying the periodic behaviour in the total population.

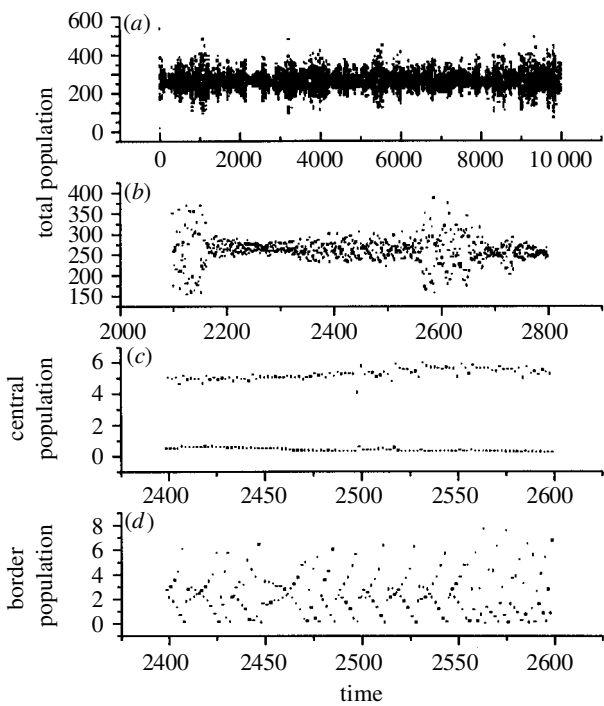


Figure 3. A simulation using the same parameters as in figure 1 but, instead of using a synchronic updating, we used the random asynchrony scheme with parameters $pD = \{0.0, 0.1, 0.9\}$ and $pR = \{0.9, 0.1, 0.0\}$.

Next, we simulated the system using the random asynchrony method (figure 3). The behaviour of the total population (figure 3a) over very long time-periods was similar to that obtained using fixed asynchrony, there being no extended regions of simple periodic dynamics. However, the total population viewed on a shorter time-scale still showed behaviour similar to the fixed asynchrony simulation (figure 3b). However, the key difference compared to the synchronic and fixed asynchronic models was that there was no region of simple periodic dynamics. There was only variation in the amplitude of the oscillations and a larger interval between zones of augmented amplitude. The individual populations maintained the pattern observed for both synchronic and fixed asynchronic simulations (figure 3c,d), i.e. the central and border populations had quantitatively different behaviours which could change over medium time-scales. Notice also that considerable change in the dynamics of some populations (e.g. figure 3d) may not be mirrored by any significant change in other populations at the same time (figure 3c).

In order to investigate the effects of asynchrony further, we performed extensive simulations choosing the parameters at random in an ecological meaningful range. For the three methods of evaluation we ran approximately 5000 simulations detecting the number of long-term transients and 5000 simulations detecting the number of medium-scale transients, always choosing the initial conditions at random (table 1).

The occurrence of long-term supertransients was very low compared with medium-term mesotransients, although both types of behaviour could be observed in all three models. The occurrence of supertransients from the random

Table 1. Proportions of randomly sampled simulations that demonstrated long and medium time-scale transients for 5000 simulations of each evaluation method

(The runs were performed choosing the parameters at random inside the following ranges: $\lambda = 1-20$, $b = 1-10$ and $d = 0.001-1$; a was fixed at 1 and the initial conditions were random. The detection of transients was aided by calculating the ratio of variances R_V in adjacent windows of size W . The values were determined empirically for long transients ($R_V = 50$ and $W = 500$) and for medium transients ($R_V = 20$ and $W = 50$).)

	long transients	medium transients
synchronic	0.0180	0.13
fixed asynchronic	0.0250	0.14
random asynchronic	0.0064	0.16

asynchronic model was unexpected. It is interesting to note that the range of parameters which produced supertransients from this model was very different from the range which produced them in the other models. While in the synchronic and fixed asynchronic methods the local dynamics were chaotic, for the random asynchronic method the local dynamics were outside the chaotic region (figure 4). In this last case, the dynamics of the total population moved slowly between two or more periodic attractors (figure 4a). If the total dynamics were to be observed on a medium time-scale, most of the time the system will be changing very slowly from one attractor to another (figure 4b). The central populations seemed to maintain a dynamics in one attractor (figure 4c), but the border population switched to different attractors much faster than the total population (figure 4d).

4. DISCUSSION

The importance of transient dynamics was stressed by Hastings & Higgins (1994). They showed the existence of long-lasting regions of very different qualitative dynamics with dramatic transitions between them. The existence of multiple attractors and, consequently, chaotic saddles is extremely common in spatially extended models. This is a necessary condition for the occurrence of long transients and the reason why long transients should be common. Moreover, the perturbation of the parameters with noise did not destroy the transients (Hastings 1998). These results suggest two key ecological points, that transient dynamics might have more ecological relevance than final attractors and that sudden changes in dynamics might be internally generated and might not reflect a change in the environment. It is of prime importance that we assess the likely applicability of these results to a wide range of systems. Here we took the same type of model used by earlier workers in order to demonstrate such supertransients and relaxed one of their assumptions, i.e. perfect global synchrony. We found that supertransients can be found in models that relax this assumption, but only for very restricted ranges of parameter values and initial conditions. Thus, we were forced to conclude that these very long time-scale patterns may be of limited ecological relevance because they only occur under very restrictive combinations of parameter values.

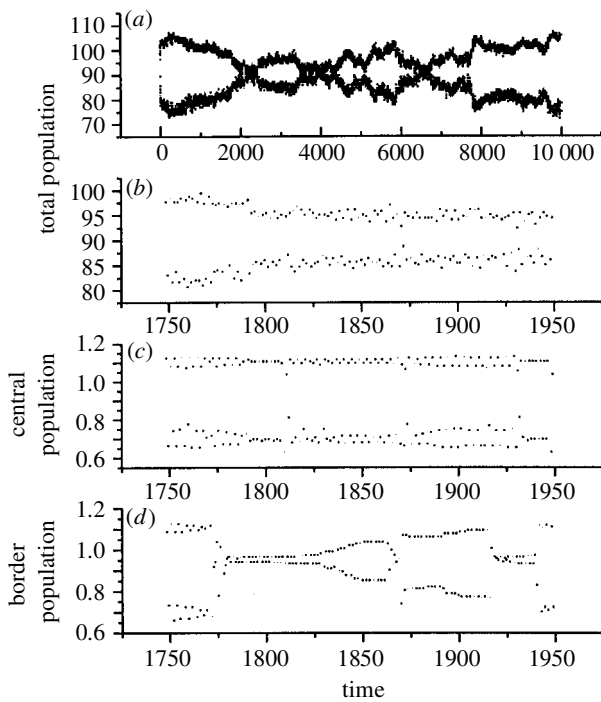


Figure 4. A simulation similar to that shown in figure 3 except for the following parameters: $b = 6$, $\lambda = 1.8$ and $d = 0.9$.

However, in addition to these very long time-scale changes which were observed by previous workers, our analysis showed that, within supertransients, there is also a change in dynamic behaviour over a much shorter time-scale, which has been previously unreported and which we called mesotransients. These might be argued to have even more ecological importance than the long-scale changes because they occur much more frequently in the models we studied and occur on a time-scale which makes them more amenable to measurement and manipulation (Hastings 1998).

Some of the patterns observed, such as the gradual change in the amplitude of the cycles (figures 1–4), have been detected in natural populations (Henttonen *et al.* 1987). This phenomenon has been attributed to a drift in the parameters of the models (Bascompte & Solé 1998) and has also been discovered in another spatial model with different assumptions (Ranta *et al.* 1997). This may suggest that the occurrence of these patterns does not depend on the details of the model, but only on the fact that populations are linked by dispersal in a spatially segregated habitat.

Another important aspect of these long and medium time-scale transient changes is that they are often accompanied by spatial heterogeneity. In particular, the dynamics of edge populations can be quite different from those in the centre. This has important implications for population monitoring; a sudden change in a local monitored population may not always be a good indicator of change in other parts of the system.

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