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**REPORT**

# Dispersal and transient dynamics in metapopulations

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## Abstract

Recent studies of spatially explicit metapopulation models have shown the existence of complex transient behaviour (supertransients and mesotransients) characterized by spontaneous changes in the system's dynamics after thousands or hundreds of generations, respectively. Their detection in simple ecological models has been taken as evidence that transient dynamics may be common in nature. In this study, we explore the generality of these phenomena in a simple one-dimensional spatially explicit metapopulation model. We investigate how frequently supertransient behaviour emerges in relation to the shape and type of the dispersal kernel used (normal and Laplace), system size, boundary conditions and how sensitive they are to initial conditions. Our results show that supertransients are rare, are heavily affected by initial conditions and occur for a small set of dispersal parameter values, which vary according to kernel type, system size, and boundary conditions. Similarly, mesotransients emerge over a very narrow range of dispersal parameter values and are rare under all circumstances. Thus, transient dynamics are not likely to be either common or widespread in simple models of ecological systems.

## Keywords

Transient dynamics, dispersal kernel, spatial model, coupled map lattice, metapopulations.

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## INTRODUCTION

The study of spatial population dynamics and persistence has received renewed attention in the past few years (Maurer 1994; Tilman & Kareiva 1997; Bascompte & Solé 1998a,b; Turchin 1998; Keymer *et al.* 2000), and has been the source of many new insights to ecological phenomena (Paradis *et al.* 2000; Williams & Liebhold 2000). One of the most popular forms of spatial population models considers metapopulations, or ensembles of local populations coupled by dispersal. These simple models, known as coupled map lattices (CML) (Kaneko 1989, 1998) predict a range of spatiotemporal patterns, some of which have been found in nature (Maron & Harrison 1997; Ranta *et al.* 1997; Lambin *et al.* 1998; Solé & Bascompte 1998; Blasius *et al.* 1999), and have been extensively used in the study of complex systems (Kaneko & Tsuda 2000). Theoretical studies of CMLs have suggested that the population dynamics we observe in nature may well correspond to a transient dynamical behaviour, which shows spontaneous changes from apparent chaotic dynamics to cyclic behaviour and vice versa occurring at time scales longer than a typical ecological time series (Hastings & Higgins 1994). Recently, Saravia *et al.* (2000) noted that CML may show sudden changes in behaviour at shorter temporal scales, similar to that of ecological studies, and have suggested that these mesoscale changes in dynamics (termed 'mesotransients' by the authors) may be of greater relevance than longer transient behaviour. These claims contrast with the traditional emphasis on the analysis of long-term solutions (asymptotic states) in the study of ecological models (Hastings & Higgins 1994; Hastings 1998; Earn & Rohani 1999). If transient behaviour is common in nature, then ecological systems might often be in a transient state, and changes in their dynamics might be compounded by intrinsic dynamical effects and also by changes in the environment wherein they are embedded.

The first step towards determining whether we can expect such complex transient behaviour to be common in nature is the assessment of their generality in model ecological systems. It is known that supertransient dynamics are likely to appear when coupled local populations are in a chaotic regime (Kaneko 1989; Hastings & Higgins 1994; Ruxton & Doebeli 1996) and that average transient length increases with system size and the degree of global coupling between populations (Kaneko 1990, 1998; Hastings 1998). In ecological models, however, coupling has only been modelled assuming a normal (gaussian) dispersal kernel and for a restricted set of dispersal intensities and spatial ranges (Hastings & Higgins 1994; Ruxton & Doebeli 1996; but see Saravia *et al.* 2000). However, many organisms, such as plants or aquatic invertebrates and vertebrates, might be better represented by a fat-tailed, leptokurtic kernel such as Laplace dispersal kernel (Neubert *et al.* 1995; Clark *et al.* 1999; Fraser *et al.* 2001), where settlement is probabilistic (i.e. there is a failure rate or hazard function).

In this paper, we explore the generality of both supertransient and mesotransient dynamics in terms of dispersal (kernel type and coupling), system size, boundary conditions and sensitivity to initial conditions. We do this by analysing a model system for which both complex transient behaviours has been reported. Our results show that supertransient dynamics are a rare phenomenon emerging for a restricted set of dispersal parameter values, which nonetheless vary between kernels, and is affected by system size, boundary conditions and depends heavily on initial conditions. Mesotransients on the other hand are seen to occur for a smaller range of dispersal parameter values. We discuss the implications of these results both for theoretical and empirical population dynamics.

## MATERIALS AND METHODS

Following Hastings (1998), we modelled a small set of $M$ discrete local populations, of a semelparous species, distributed along a linearly structured environment, such as may be found along a stretch of coastline. In each of these populations, reproduction occurs synchronously in a density-dependent fashion. At the start of a given generation $t$, population size in the $i$th population is denoted $N_{[t,i]}$. The reproductive events generate a larval stage, $L$, which disperses among the local populations. Abundance of larvae in each population $L_{[t,i]}$, after reproduction and before they disperse, is given by (see Maynard-Smith & Slatkin 1973; Ruxton & Doebeli 1996),

$$L_{[t,i]} = N_{[t,i]}f(N_{[t,i]}) = \frac{\lambda N_{[t,i]}}{1 + aN^{b}_{[t,i]}} \tag{1}$$

The parameter $\lambda$ is the growth rate, $a$ is the inverse of the environmental carrying capacity and $b$ describes the intensity of density dependence (for further discussion of this model see Hassell 1975; Bellows 1981; Doebeli 1995). All larvae are produced synchronously and settlement is simultaneous throughout the metapopulation. Larvae are redistributed in a density-independent fashion according either to Laplace or normal kernel, which reflect different dispersal strategies of larvae. In comparison with the normal kernel, larvae under Laplace kernel have at the same time a higher probability of remaining at the source and of dispersing over a longer range (Fig. 1). For the normal dispersal kernel (Neubert *et al.* 1995), the proportion of the larvae on patch $i$ that move to patch $j$ is:

$$P_{[i,j]} = \frac{1}{2\sqrt{\pi\sigma}}e^{\frac{1}{4\sigma}(i-j)^2} \tag{2}$$

In the case of Laplace dispersal kernel (Neubert *et al.* 1995), the proportion of the larvae on patch $i$ which moves to patch $j$ is:

$$P_{[i,j]} = \frac{1}{2\sigma}e^{\frac{1}{\sigma}|(i-j)|} \tag{3}$$

For both dispersal kernels the shape of the dispersal curve, which is controlled by the parameter $\sigma$, gives the intensity and extent of dispersal: the smaller the parameter, the larger the proportion of individuals that will remain in the parental habitat and more local populations will remain unconnected (Fig. 1). High values of $\sigma$ will result in greater spatial spread of the individuals with lower intensity.

The model assumes non-overlapping generations, and so all adult individuals die at the end of the reproductive period. Local population size at the next generation is the result of the recruitment of all the larvae dispersed from all

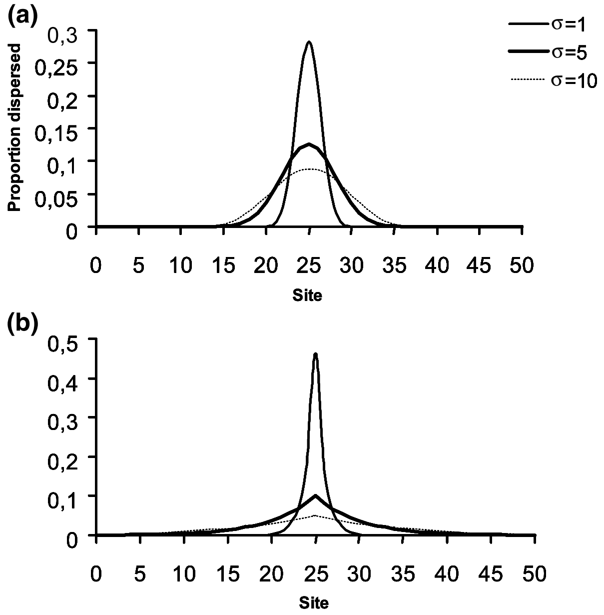

**Figure 1** Dispersal kernels used in this study. Note the leptokurtic shape of the Laplace distribution. The figure shows the proportion of propagules dispersed to different distances from a central focal population (site 25) for $\sigma = 1$, $\sigma = 5$ and $\sigma = 10$ (a) normal dispersal kernel and (b) Laplace dispersal kernel. Note that for a small system size ($M = 10$) large values of dispersal result in loss of propagules from the system under dissipative boundary conditions while periodic boundaries result in essentially a more platikurtic redistribution kernel.

subpopulations. The number of individuals in each population in the next generation is given by the sum of the larvae dispersed over the entire ensemble to that particular population.

$$N_{[t+1,i]} = \sum_{j=0}^{M} L_{[t,j]} p_{[j,i]} \tag{4}$$

On the other hand, total population abundance for the metapopulation at generation $t$ is given by the sum of individuals present in the metapopulation after dispersal and prior to reproduction. Previous studies (Hastings & Higgins 1994; Ruxton & Doebeli 1996) have assumed dissipative boundary conditions (but see Hastings 1998). This means that a fraction of the larvae disperse beyond the edges of the ensemble and do not influence the dynamics of the system. It may be argued that this loss of individuals may lower the local growth rate, thus lowering the likelihood of observing transient dynamics. To assess the importance of larval loss we compared, for each dispersal kernel, the effect of dissipative vs. periodic boundary conditions. To allow easier comparison of the results we set the parameters $a = 1$, $b = 4.8$ and $\lambda = 7$, as used by Ruxton & Doebeli (1996). Under these parameter values, isolated local populations show chaotic dynamics. Initial local population abundances (i.e. initial conditions) were drawn independently from a random uniform distribution between 0 and 4. In each simulation, the model was iterated for 10 000 generations, and the dynamics examined for the occurrence of transient dynamics (Hastings & Higgins 1994). This procedure was performed for both dispersal kernels using two ranges of the dispersal parameter ($\sigma$), from 0.01 to 5 and from 5.01 to 10.00 (with increments of 0.01 with each range) and for two different system sizes $M = 10$ and $M = 50$. To assess the effect of each factor in isolation and the interaction among factors (i.e. kernel, boundary, $\sigma$, and lattice size) on the emergence of transient behaviour, we used a full factorial experimental design (Quinn & Keough 2002) considering the two levels of $\sigma$ ($\sigma \leq 5$ and $\sigma > 5$). All factorial combinations of factors resulted in 16 different scenarios. Twenty replicates were run for each of them.

To evaluate the effect of initial conditions of local abundance on the observed results, we also carried out 50 simulations with different initial conditions for a subset of parameter values ($\sigma$), uniformly spread between 0.01 and 10. We report the proportion of the 50 replicates for each value of s, which exhibited transient behaviour under normal and Laplace kernels and for both boundary conditions.

Following Hastings & Higgins (1994) and Saravia *et al.* (2000), transient dynamics were identified by noting the existence of abrupt and spontaneous changes between different dynamic regimes with time scales of hundreds of iterations (mesotransients) and with a time scale greater than one thousand iterations (supertransients). Detection of these changes was carried out by calculating the ratio of variances (RV) between two adjacent halves of a sliding window of size W (Saravia *et al.* 2000). Both RV and W were determined empirically to allow detection of supertransients ($RV = 10$, $W = 1000$) and mesotransients ($RV = 20$, $W = 100$). For a given simulation, transient length was defined by the time interval at which the maximum value of RV was observed. The changes in metapopulation dynamics were corroborated by the inspection of the temporal dynamics and return maps (Hasting & Higgins 1994; Saravia *et al.* 2000).

## RESULTS

In agreement with previous studies, we observed supertransient dynamics in this simple metapopulation model (Fig. 2a). These changes occurred once or several times in

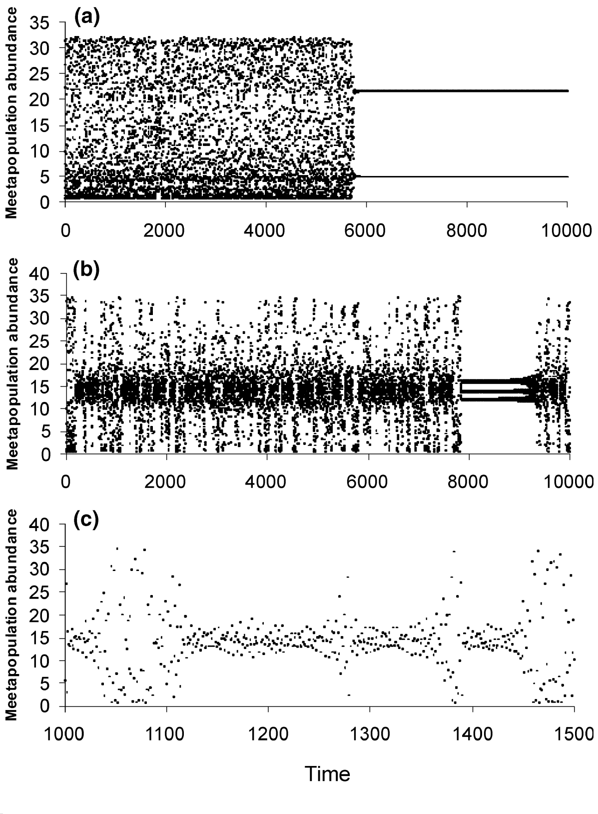

**Figure 2** Example of dynamics for the total metapopulation abundance observed for: (a) normal dispersal kernel with periodic boundaries and $\sigma = 9.01$. (b) Laplace dispersal kernel with dissipative boundaries and $\sigma = 8.44$. (c) A subset of the dynamics shown in (b). In all simulations only the dispersal parameter value and boundary conditions were changed and the following parameter values were used: $a = 1$, $b = 4.8$, $\lambda = 7$, $M = 50$.

the time series (Fig. 2b). Similarly, mesotransients were also observed (Fig. 2c). However, despite using local chaotic conditions of density dependence ($\lambda = 7$), we observed transients in a small proportion of the total number of the simulations. For simulations using $M = 50$ and a normal dispersal kernel, we found supertransients in 10.9 and 2.6% of the simulations across the range of $\sigma$-values used and for periodic and dissipative boundary conditions, respectively, while for Laplace kernel we observed 3.7 and 4.9% for periodic and dissipative boundary conditions. For a smaller system size ($M = 10$), the normal kernel showed supertransients in 3 and 13% of the simulations (periodic and dissipative boundary conditions, respectively) while Laplace kernel showed 0.8 and 13% (periodic and dissipative boundary conditions, respectively). In contrast, mesotransients occurred in <2.5% of the simulations carried out with $M = 50$ considering all different combinations of kernel type and boundary conditions. However, their frequency increased for $M = 10$ (4.8 and 13% under normal dispersal and 2 and 13.3% for Laplace kernel for periodic and dissipative boundary conditions, respectively).

For a large system size ($M = 50$), the occurrence of supertransients changes as a function of the dispersal parameter, boundary conditions, and dispersal kernel showing a bimodal pattern, for periodic boundary conditions under normal dispersal, that changes to unimodal and restricted to small $\sigma$, under dissipative boundary conditions (Fig. 3a). Interestingly, for Laplace dispersal, supertransients occur more frequently for large values of $\sigma$ under the dissipative boundary conditions (Fig. 3b). Furthermore, for both dispersal kernels we found that mesotransients were rare and restricted to a narrow, albeit different, range of $\sigma$-values (Fig. 3c, d). For the small size system ($M = 10$), transients are restricted to small values of $\sigma$, being more frequent under dissipative boundary conditions (Fig. 4a–d). The results of the fully factorial experiment show that all the analysed factors, either in isolation or in interaction, affect the emergence of transient dynamics. In the case of supertransients, kernel type and $\sigma$ have a significant effect ($F_{1,304} = 8.7$, $P = 0.003$ and $F_{1,304} = 19$, $P < 0.001$, respectively), while the interaction between boundary condition and lattice size is the most important in terms of the explained amount of variance ($F_{1,304} = 25.4$, $P < 0.001$). The only significant three way interaction was among boundary condition, lattice size and $\sigma$ ($F_{1,304} = 7.3$, $P = 0.007$). Similarly for mesotransients, kernel type, $\sigma$ and boundary condition have a significant effect ($F_{1,304} = 5.3$, $P = 0.02$; $F_{1,304} = 10.4$, $P = 0.001$ and $F_{1,304} = 14.6$, $P < 0.001$, respectively). The most important two-way interactions is between lattice size and $\sigma$, followed by the interaction between boundary condition and lattice size ($F_{1,304} = 33.5$, $P < 0.001$; $F_{1,304} = 16.9$, $P < 0.001$). Significant three-way interactions were found among boundary condition, lattice size and $\sigma$ followed by the interaction among kernel type, lattice size and $\sigma$ ($F_{1,304} = 37.4$, $P < 0.001$; $F_{1,304} = 10.2$, $P = 0.002$), with the former being the most important treatment effect in terms of amount of variance explained. For both supertransient and mesotransients, the four-way interaction was not significant.

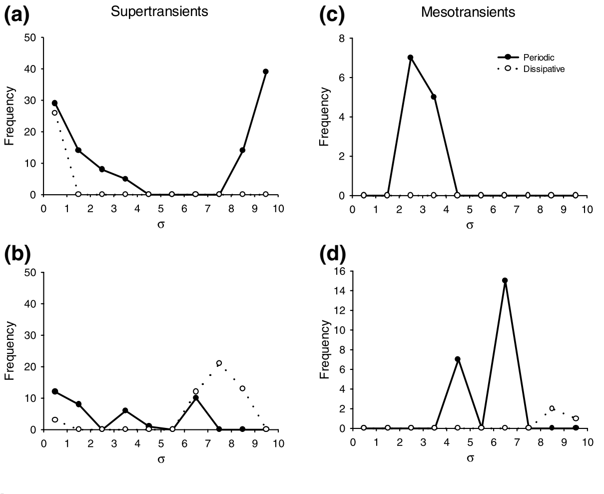

**Figure 3** Total number of supertransients and mesotransients observed per $\sigma$ unit interval for normal (a and c) and Laplace (b and d) dispersal kernels, respectively. Open and filled circles represent dissipative and periodic boundary conditions, respectively. Parameter values used were $a = 1$, $b = 4.8$, $\lambda = 7$, $M = 50$. Each point represents the frequency of transients in unit intervals of $\sigma$.

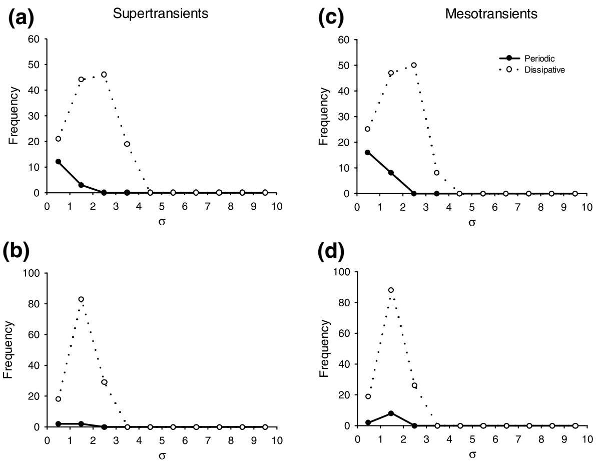

**Figure 4** Total number of supertransients and mesotransients observed per $\sigma$ unit interval for normal (a and c) and Laplace (b and d) dispersal kernels, respectively. Open and filled circles represent dissipative and periodic boundary conditions, respectively. Parameter values as in Fig. 3, but $M = 10$. Each point represents the frequency of transients in unit intervals of $\sigma$.

A system is highly dependent on initial conditions if for a specific set of parameter values, simulations originating with different initial numbers of individuals at different places lead the system to different types of dynamics. If this were the case, then we would find that for the same set of parameter values, some of the trajectories show transients while some do not, hence the results shown in Figs 3 and 4 might not accurately reflect the effect of parameter values upon the emergence of transient dynamics. As shown in Fig. 5, in most cases the proportion of simulations that showed either supertransients or mesotransients, for the same parameter values but for changing initial conditions, was highly variable and heavily affected by the value of $\sigma$. For a large system size ($M = 50$) and for both dispersal kernels, supertransients seemed to be more robust under periodic boundary conditions than under dissipative boundary conditions (Figs 5a,b) following a patterns similar to that shown in Fig. 3(a,b). However, in general the average proportion of simulations showing supertransients was low, ranging between 0.16 and 0.05 for the periodic boundary conditions under the normal and Laplace dispersal kernels, respectively. Under dissipative boundary conditions this range was between 0.02 and 0.01 for normal and Laplace kernels, respectively. Mesotransient dynamics, on the other hand, are more likely to be observed for intermediate values of $\sigma$ ranging between 2 and 6-under periodic boundary conditions, and for values of $\sigma$ ranging between 4 and 7 under dissipative boundary conditions and normal dispersal (Fig. 5c). On the other hand, for Laplace dispersal mesotransients were more common for large values of $\sigma$, particularly under dissipative boundary conditions (Fig. 5d). In general, the average proportion of simulations showing mesotransients was low (0.09) for the periodic boundary conditions under the normal and Laplace dispersal kernels. Under dissipative boundary conditions, the average proportion of simulations showing mesotransients ranged between 0.12 and 0.05 for Laplace and normal kernels, respectively. Although these results cannot be readily applied to assess the uncertainty of the results reported in Figs 3 and 4, because of the different values and intervals of $\sigma$ used in both analysis, they consistently show that for a given set of parameter values the emergence of transient behaviour is highly dependent on initial conditions. A similar result was observed for a smaller system size ($M = 10$, not shown).

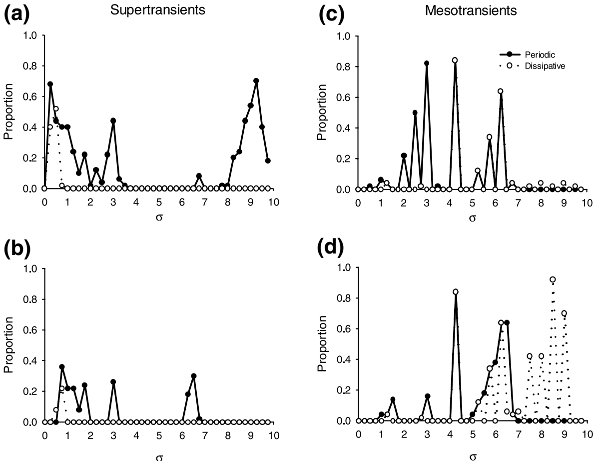

**Figure 5** Effect of initial conditions on the occurrence of supertransients and mesotransients as a function of $\sigma$. (a) and (b) show the proportion of 50 simulations with different initial conditions that show supertransients for normal and Laplace kernels, respectively. (c) and (d) show the proportion of simulations that show mesotransients dynamics for normal and Laplace kernels, respectively. Dissipative boundary conditions are represented by open symbols, while filled symbols represent periodic boundaries. Parameter value as in Figure 3.

In summary, our results show that both supertransients and mesotransients dynamics are rare; their emergence depends strongly on the kernel type, dispersal, boundary conditions and system size, and the interaction among these factors. Furthermore, we show that transient dynamics are strongly affected by initial conditions.

## DISCUSSION

It is known that long transients can occur in spatial ecological models with multiple attractors and hence chaotic saddles (Kaneko 1990; Hastings & Higgins 1994; Hastings 1998) even in the presence of noise (Hastings 1998). The existence of supertransients remained a mathematical eccentricity until Hastings and coworkers (Hastings & Higgins 1994; Hastings 1998, 2001) argued that transient dynamic behaviour is widespread in nature, suggesting that its emergence in spatial ecological models is likely to be the rule rather than the exception. Further, the fact that transient behaviour usually lasts for many generations implies that the transient state of the system could be potentially more important than its final attractor (Hastings & Higgins 1994). Thus, if transients are the rule rather than the exception for ecological systems, then traditional theoretical models based on asymptotic equilibrium behaviour might be of little relevance as tools for understanding.

In this paper, we showed that the emergence of supertransient dynamics is a rare event, which depends strongly on the type, extent and intensity of dispersal, as well as on the system size and boundary conditions. Ruxton & Doebeli (1996) first made the point that the shape of the dispersal kernel (as measured by $\sigma$) affected the emergence of supertransients in simple spatial models, but provided no systematic assessment of its effect, and restricted their analysis to a normal kernel. Similarly, Saravia *et al.*

(2000) point out that supertransients required a particular combination of $\lambda$, *b* and $\sigma$, to emerge but did not explicitly test for the effect of dispersal and also restricted their analysis to a normal dispersal kernel. Our analysis shows that, contrary to Ruxton & Doebeli's (1996) findings, supertransients can emerge for high values of the dispersal parameter $\sigma$, depending on the size of the system (Figs 3 and 4). However, these supertransients may be highly sensitive to initial conditions (Fig. 5), strengthening our conclusion that they are not the rule in simple ecological models.

Our results also point out the importance of boundary conditions and system size for the emergence of transient dynamics. It may be expected that loss of individuals through dissipative boundaries would result in a lowering of the local growth rates and hence in the likelihood of observing supertransients. For a small system size, however, supertransients were more common precisely under this scenario. Thus, loss of individuals through dispersal may still allow supertransients to emerge. However, system size, boundary conditions and initial conditions interact in complex ways such that for a large system size ($M = 50$) transient dynamics tend to be less affected by initial conditions under periodic boundaries, while the reverse is true when the system is smaller ($M = 10$, F. Labra, unpublished results). In a recent paper (Hastings 2001), it is reported that supertransients occur more frequently when the initial condition includes empty patches. The inclusion of empty sites in our simulations agree with this result. However, the observed increase in transients only occurs under dissipative conditions, and only for supertransients but not for mesotransients. To assess the relative importance of each of these factors is beyond the scope of the present paper and deserves further investigation. However, this complex dependency strengthens our point; the emergence of transient dynamic behaviour in simple ecological models is not a common phenomenon but occurs for a restricted set of conditions. Saravia *et al.* (2000), using the same model we used, reached a similar conclusion after relaxing the assumption of global synchrony in reproduction and dispersal. This implies that the set of conditions that lead to transient dynamics are likely to be even more restricted than we report here. Although for the sake of comparability we have followed previous authors in studying a one-dimensional chain of interacting populations (e.g. Hastings & Higgins 1994; Ruxton & Doebeli 1996; Saravia *et al.* 2000) it is likely that system dimensionality will also have an effect on the emergence of transient behaviour. However, further investigations on two-dimensional systems are necessary.

Most previous studies have not reported an exhaustive exploration of the parameters that may result in transient dynamics. We found that under both dispersal kernels, supertransient dynamics occur in very low frequency in spite of strong local nonlinearity. From this perspective, and considering that its emergence also depends, as in our case, on the initial conditions used in the simulations (see also Ruxton & Doebeli 1996) and the value of the parameters $\lambda$, *b* and $\sigma$, it can be argued that supertransients, contrary to Hastings & Higgins (1994) and Hastings (1998, 2001), might not be a common feature of spatial models, let alone real ecological systems and especially so, if chaotic dynamics are not common in nature (see Rai & Schaffer 2001; below). The range of dispersal we have explored here ranges from local coupling, when $\sigma$ is very low, to nearly global coupling when $\sigma$ is very high and periodic boundaries are imposed on the system. In agreement with Hastings (1998), who used a system of size $M = 10$, we found that supertransients were harder to find when dispersal conditions tended to be similar to global coupling (large $\sigma$-values). However, this is true only for a small system size ($M = 10$) (compare Figs 3 and 4) and not all small and intermediate values of $\sigma$ result in supertransients, and of those that do, several are sensitive to initial conditions.

It should be noted, however, that we observed supertransients much more frequently than Saravia *et al.* (2000) did. This discrepancy arises because their study encompasses parameter combinations that span regions of stable, cyclic and chaotic dynamics. However, supertransients arise only in the latter regime and for strong nonlinearity (Kaneko 1989, 1990; Kaneko & Tsuda 2000). Simulations carried out with a different set of parameters ($a = 0.5$, $b = 30$ and $\lambda = 2$), which produce chaotic dynamics, failed to produce either of the two complex behaviours under study when simulations were carried out for a large system size ($M = 50$). On the other hand, for a second parameter setting ($M = 50$, $a = 0.5$, $b = 15$ and $\lambda = 7$), the occurrence of supertransients increased under both kernels to 8.2 and 19.5% for normal dispersal (periodic and dissipative boundary conditions) while for Laplace kernel they occurred in 19.5 and 6.6% (periodic and dissipative boundary conditions, respectively). If supertransients occur only for fully developed spatiotemporal chaos, then the question should be how common are they in this regime. As we discussed above, they are not very common.

Mesotransients, on the other hand, were seen in low frequency, and emerged over a narrower range of dispersal parameter values, especially for the large system. For the two additional parameter settings we explored, mesotransients were completely absent in the first setting, while for the second parameter setting they were found in <1% of the simulations under all combinations of kernel types and boundary conditions. Mesotransients have been described by Saravia *et al.* (2000), as sudden changes in the behaviour of the total system over time scales of hundred of generations, which is similar to what has been reported as intermittent chaos (Doebeli 1994; Cavalieri & Koçak 1995; Gavrilets & Hastings 1995; Strogatz 1997) and spatiotemporal intermittency (Kaneko 1985, 1989). We are not aware of any formal attempt to ascertain if mesotransient dynamics are in fact intermittent chaos or spatiotemporal intermittency. If it turns out to be the same to either of them, then its prevalence and relevance in spatial ecological models might be determined more clearly.

In conclusion, we show that supertransient and mesotransient dynamics are not likely to be either common or widespread in ecological systems being heavily affected by dispersal intensity, boundary conditions, system size and initial conditions.

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