Journal of Animal Ecology 1995,
64, 662–664

FORUM

Appropriate formulations for dispersal in spatially structured models: comments on Bascompte & Solé

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Introduction

In a recent paper, Bascompte & Solé (1994) have explored the dynamics of a metapopulation version of a familiar model for density-dependent population growth (Hassell 1975; Hassell *et al.* 1976); namely,

$$N_{t+1} = \lambda N_t(1+aN_t)^{-\beta}. \qquad \text{eqn 1}$$

Here N is the population density in successive generations, t and $t+1$, λ is the finite rate of increase of the population, and a and β are constants defining the density-dependent survival. The stability properties of this model hinge solely on λ and β, as shown in Fig. 1a. Bascompte & Solé (henceforth referred to as 'B&S') applied this model to a grid or array of local populations which they linked with dispersal to four nearest neighbours, with the aim of exploring how such spatial structure affects the population dynamics. Using the Coupled Map Lattice formalism (Kaneko 1993), they express their model as:

$$N_{t+1}(i,j) = \lambda N_t(i,j)[1+\alpha N_t(i,j)]^{-\beta} + D\nabla^2 N_t(\mathbf{r}) \qquad \text{eqn 2}$$

where D is the diffusion rate and

$$\nabla^2 N_t(\mathbf{r}) = N_t(i-1,j)+N_t(i+1,j)+N_t(i,j-1) + N_t(i,j+1)-4N_t(i,j). \qquad \text{eqn 3}$$

This diffusion term defines the individuals that disperse to the four adjacent cells, and those that immigrate from these cells.

Bascompte & Solé's results are surprising: as dispersal rate is increased, the dynamics become increasingly *unstable*, and thus increasingly diverge from those of the non-spatial, homogeneous model (eqn 1). Figure 1b, reproduced from B&S and based on numerical simulations, illustrates this. More generally, we have obtained an analytic criterion for the constant equilibrium solution to become unstable. For periodic boundary conditions on an $n \times n$ lattice, this stability criterion is (Rohani, May & Hassell, unpublished)

$$\theta \equiv \beta(1-\lambda^{-1/\beta}) < 2(1-\gamma D). \qquad \text{eqn 4}$$

We have defined θ for notational convenience. The constant $\gamma \rightarrow 4$ for $n \gg 1$, being slightly smaller for small values of n (so that, for fixed D, the stability criterion is slightly easier to satisfy for small arrays).

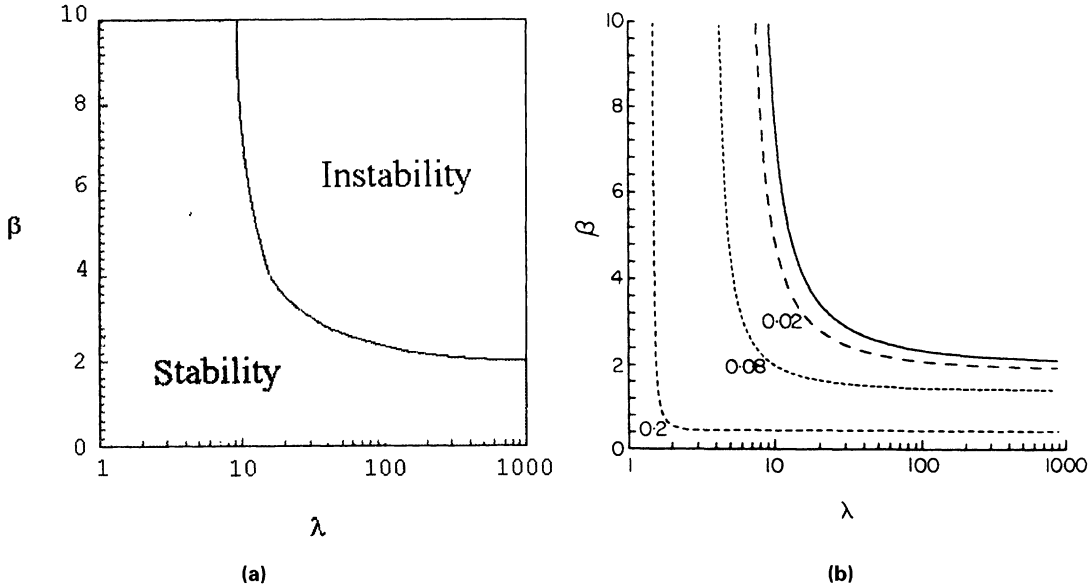

Fig. 1. (a) Regions of stable and unstable population dynamics obtained from equation 1. The unstable region includes both limit cycles and chaotic behaviour (after Hassell 1975). (b) The comparable figure showing the effects on the stable region in (a) of different levels of diffusion (D) in Bascompte & Solé's model. Notice that larger values of diffusion decrease the size of the stable region (from Bascompte & Solé 1994).

The essentials of this result are independent of the exact form of the density dependence in equations 1 and 2. Note that for $D \rightarrow 0$ we recover the standard stability result $\theta < 2$, for the homogeneous case. But as D increases, the system becomes less stable up to the point $D = 1/4$ where all individuals move.

B&S's results are counter-intuitive. One would expect increasing dispersal between the local populations to bring the spatially structured model closer to its non-spatial equivalent (by more effectively linking the separate local populations), as recently noted by Ruxton (1994), also in a comment on B&S's paper.

In this note, we show that B&S's counter-intuitive results arise solely from the biologically impossible way that the dispersal function (equation 3) is formulated within B&S's model. Couched as a discrete analogue of a reaction–diffusion equation, their model fails to segregate the processes of survival and dispersal. As a result, the same individuals may simultaneously fail to survive and yet disperse. At its most extreme, this leads to the production of negative local population densities. B&S were aware of this occurrence of negative populations, but thought it valid artificially to 'correct' the values to $N_t(i,j) = 0$. Avoiding this problem by using a biologically sensible model completely changes B&S's conclusions: spatial structure now has *no effect* on the stability boundaries shown in Fig. 1a. We illustrate this by segregating competition and dispersal (e.g. larvae compete for resources and adults disperse) and by defining a fraction μ of potential dispersers (adults) that move equally to the eight nearest neighbouring cells (Hassell, Comins & May 1991, 1994; Comins, Hassell & May 1992). This parameter relates directly to D in equation 2 ($\mu = 4D$).

Results

Our model retains competition from equation 1 for describing the survival of juveniles within cells, but now adopts a dispersal rule different from that in equations 2 and 3 such that within any cell a fraction μ of the emerging adults move equally to the eight nearest neighbouring cells, and hence a fraction $1-\mu$ remain behind. Reproduction is assumed to occur following dispersal, giving the model:

$$N_{A,t}(i,j) = N_{L,t}(i,j)[1+aN_{L,t}(i,j)]^{-\beta} \qquad \text{eqn 5a}$$

$$N_{L,t+1}(i,j) = \lambda[N_{A,t}(i,j)-\mu N_{A,t}(i,j)+\mu\bar{N}_{A,t}] \qquad \text{eqn 5b}$$

where N_A and N_L are, respectively, the density of adults and larvae within a cell, and $\bar{N}_{A,t}$ is the average number of adults over the eight neighbouring patches. Note that this model could have been formulated to have reproduction occurring prior to dispersal (e.g. dispersal of first instar insect larvae), but this has no effect in this case on the equilibrium stability properties.

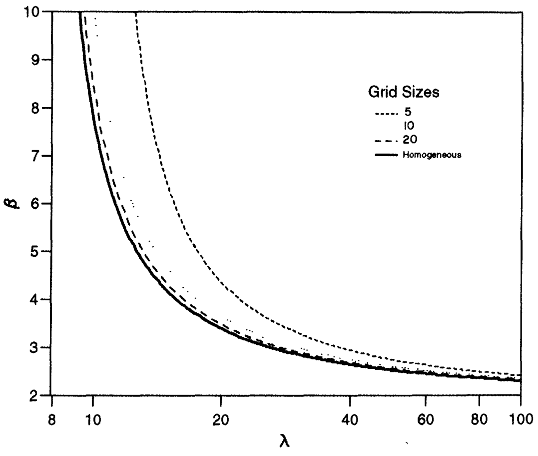

Fig. 2. The stability boundaries when the population is modelled as in equation 4. The thick line represents the stability boundary obtained with reflecting or periodic boundaries, regardless of the grid size or the dispersal rate. This boundary is identical to that obtained from the homogeneous model in equation 1 (Fig. 1a); in other words, space has no effect on stability. The dashed lines show the different stability boundaries obtained from equation 4 when simulated with absorbing boundaries and using grid sizes of 5 × 5, 10 × 10 and 20 × 20. In this case, stability is enhanced due to the density-dependent loss of individuals from the population, but this effect is only significant for relatively small grid sizes. (Grids of 50 × 50 are not distinguishable from the solid line.)

Figure 2 contrasts the stability properties of this model with that of B&S in Fig. 1b. For grids with periodic boundary conditions, the stability boundaries are identical with those for the homogeneous case, namely

$$\theta \equiv \beta(1-\lambda^{-1/\beta}) < 2. \qquad \text{eqn 6}$$

This result is true for all dispersal rates μ, and for all grid sizes. Furthermore, it does not depend on the number or location of cells to which propagules disperse, nor on the proportions migrating to different cells; all that is required for equation 6 is that these patterns of dispersal be the same for all cells. (For proofs and a more detailed discussion, see P. Rohani *et al.* (unpublished).) If the boundary conditions are absorptive, such that individuals are lost to the system from the cells around the edges of the lattice, then equation 6 still holds in the limit $n \gg 1$; in this case, however, the stability domain gets slightly larger from smaller arrays (because there is a density-dependent loss to the total population which becomes proportionately more significant as the grid size gets smaller). This is not to say that spatial structure has absolutely no effect on the dynamics: within the unstable region, self-organizing spatial patterns of abundance do occur, and an example is given in Fig. 3. There are also interesting differences between the dynamics at the local and global scales as shown in Fig. 4.

Conclusions

In this note, we show that the counter-intuitive results of B&S, whereby increasing dispersal between local

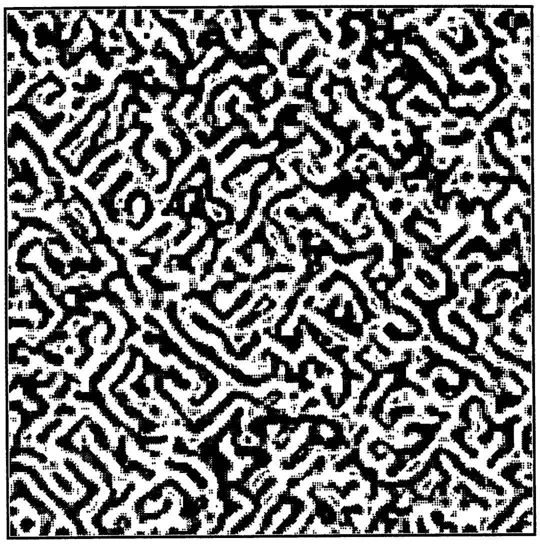

Fig. 3. The distribution of local population sizes in a grid of 200×200 cells given by equation 4. The self-organized structures observed are typical Turing patterns where regions of low (black dots) and high (white dots) density coexist over distances larger than the local patch scale. Parameter values: $a = 0.01, \mu = 0.9, \beta = 10$ and $\lambda = 100$. Picture obtained after 2000 time steps. Initial population size was set at 100 at one corner of the grid, and fixed boundary conditions were used.

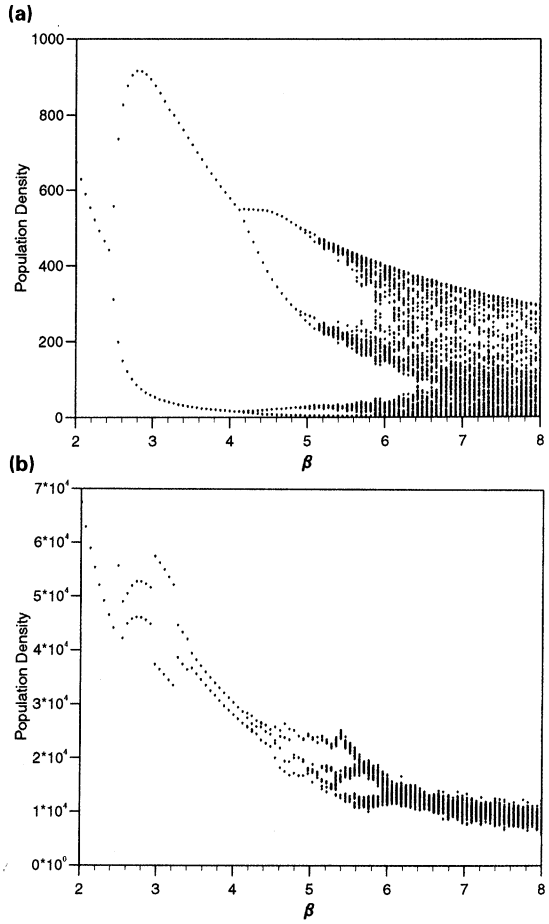

Fig. 4. Bifurcation diagrams for local (a) and global (b) populations (a single cell compared with the total population), showing different dynamics at the different scales. Lattice size $= 10 \times 10$ (fixed boundary conditions) and $a = 0.01$, $\mu = 0.006$ and $\lambda = 60$. The initial population was set at 100 in the central lattice cell and the first 3000 time steps were discarded.

populations decreases stability, disappear when dispersal and mortality no longer act on the same individuals. The results emphasize how important it is that assumptions about mortality and dispersal are properly ordered in the organisms' life cycle. An important feature of these results is the lack of any effect of spatial structure on the local stability properties in Figs 1a and 2. A subsequent paper demonstrates the generality of this conclusion for a broader range of species interactions.

Acknowledgements

The work was supported by a studentship from UNAM to O.M., a NERC studentship to P.R., a NERC grant to M.P.H., and the Royal Society (R.M.M.).

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Received 19 October 1994; revision received 16 December 1994