



Stabilization through spatial pattern formation in metapopulations with long-range dispersal

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Many studies of metapopulation models assume that spatially extended populations occupy a network of identical habitat patches, each coupled to its nearest neighbouring patches by density-independent dispersal. Much previous work has focused on the temporal stability of spatially homogeneous equilibrium states of the metapopulation, and one of the main predictions of such models is that the stability of equilibrium states in the local patches in the absence of migration determines the stability of spatially homogeneous equilibrium states of the whole metapopulation when migration is added. Here, we present classes of examples in which deviations from the usual assumptions lead to different predictions. In particular, heterogeneity in local habitat quality in combination with long-range dispersal can induce a stable equilibrium for the metapopulation dynamics, even when within-patch processes would produce very complex behaviour in each patch in the absence of migration. Thus, when spatially homogeneous equilibria become unstable, the system can often shift to a different, spatially inhomogeneous steady state. This new global equilibrium is characterized by a standing spatial wave of population abundances. Such standing spatial waves can also be observed in metapopulations consisting of identical habitat patches, i.e. without heterogeneity in patch quality, provided that dispersal is density dependent. Spatial pattern formation after destabilization of spatially homogeneous equilibrium states is well known in reaction–diffusion systems and has been observed in various ecological models. However, these models typically require the presence of at least two species, e.g. a predator and a prey. Our results imply that stabilization through spatial pattern formation can also occur in single-species models. However, the opposite effect of destabilization can also occur: if dispersal is short range, and if there is heterogeneity in patch quality, then the metapopulation dynamics can be chaotic despite the patches having stable equilibrium dynamics when isolated. We conclude that more general metapopulation models than those commonly studied are necessary to fully understand how spatial structure can affect spatial and temporal variation in population abundance.

Keywords: metapopulation dynamics; chaos; stability; spatial wave; migration; source–sink equilibria

1. INTRODUCTION

Coupled map lattices (CMLs) are often used as tractable representations of metapopulations, i.e. populations consisting of a network of local populations that are coupled by dispersal. One distinct class of CMLs has proved particularly popular. Key identifying features of this class of CMLs are that the metapopulation is made up of a number of ecologically identical habitats, and that density-independent dispersal occurs from each habitat to its nearest neighbours. A considerable theory about the dynamics of such models has recently developed (reviewed in Bascompte & Solé (1995)). The main questions in this theory concern the stability of metapopulations, and spatial pattern formation, i.e. the emergence of spatial patterns of population abundance that are due to the interactions between the local populations and cannot be explained solely by ecological differences between the habitats of the metapopulation.

An important study of these models was made by Rohani *et al.* (1996). For one-species CML models of the

type described above, their analysis makes the following prediction about stability. In a CML metapopulation model with density-independent dispersal and ecologically identical habitats, there is a global equilibrium in which every local population has the same density as it would have at the equilibrium of the local dynamics in an isolated habitat patch. Rohani *et al.* (1996) proved that this global equilibrium is stable for the metapopulation dynamics if and only if the local equilibrium in an isolated patch is stable for the local dynamics. This result is quite general and is independent of the exact form of the equations for the local population dynamics, and of the form of the dispersal function (T. Killingback, personal communication).

The predictions above are so clear and easy to interpret that they are of considerable ecological utility. However, by concentrating the analysis on the stability of spatially homogeneous equilibria, in which all local populations have the same size, the problem of the formation of spatially heterogeneous patterns is left aside. Because pattern formation is one of the most striking phenomena

in CML models, which may also have important ecological consequences, one must also look for spatially heterogeneous equilibrium states of the metapopulations, and investigate their stability. In addition, it is very important to know how robust previous results are to deviations in the underlying assumptions about the ecological equality of all local habitats and about nearest neighbour dispersal, as both sets of assumptions are likely to be violated in natural metapopulations. The purpose of the present paper is to investigate these questions.

We will first recall an example of spatial pattern formation in a simple two-patch system. Subsequently, we show that ecological heterogeneity in the habitats of large metapopulations can lead to temporally stationary spatial patterns even if the local dynamics of isolated populations are very complicated. Lastly, we show that density-dependent dispersal in a metapopulation consisting of ecologically identical habitats can also induce stationary spatial patterns despite highly complex local dynamics.

2. MODEL AND RESULTS

We will consider models of only a single species without age structure. We assume that the system is made up of a number of distinct regions, commonly called patches. Each of these patches supports a population of a given species with non-overlapping generations. The sizes of these populations at the beginning of generation t are denoted by $N_i(t)$, where i refers to the i th patch. Each generation consists of two distinct stages: a reproductive stage and a dispersal stage. The density-dependent, per capita reproduction in patch i is assumed to be given by a function $f_i[N_i(t)]$. Thus, after reproduction, the population size in patch i is

$$N_i'(t) = N_i(t) f_i[N_i(t)]. \quad (1)$$

After reproduction, dispersal occurs. Let $p(i,j)$ be the fraction of the population in patch j that disperses to patch i . (In particular, $p(i,i)$ is the fraction of the population in patch i that stays there.) Then, at the start of the next generation the population size in patch i is

$$N_i(t+1) = \sum_j p(i,j) N_j'(t), \quad (2)$$

where the sum runs over all patches in the metapopulation. Many different fitness functions f_i have been used in previous studies (see Bellows (1981) and Cohen (1995) for partial lists). Here we use the fitness function of Maynard Smith & Slatkin (1973), which is mathematically more general and flexible than most other forms:

$$f_i[N_i(t)] = \frac{\lambda_i}{1 + [a_i N_i(t)]^{b_i}}. \quad (3)$$

By labelling the parameters λ , a and b with a subscript we have assumed that these parameters may differ between patches. The parameter λ is the intrinsic growth rate in the absence of competition, a scales the carrying capacity, and b defines the form and strength of competition occurring in a patch. The unique positive equilibrium N_i^* of the local dynamics defined by $f_i(N_i^*) = 1$ is the carrying capacity in patch i and is given by $N_i^* = [(\lambda_i - 1)^{1/b_i}] / a_i$. It is well known that the stability of

this equilibrium is determined by the quantity $c_i = 1 - [b_i(\lambda_i - 1) / \lambda_i]$. The equilibrium N_i^* is stable if and only if $|c_i| < 1$. For convenience, we will use the parameters λ_i , N_i^* and c_i to describe the ecological characteristics of patch i . The results of Rohani *et al.* (1996) hold for metapopulations in which these parameters are the same in all patches. In contrast, in the present text we will also consider cases in which the local carrying capacities N_i^* differ between patches.

What remains to fully specify the metapopulation model is the dispersal function $p(i,j)$. Depending on whether dispersal is long or short range, and density dependent or independent, this function can take various forms, which we will specify in each of the cases we discuss below.

(a) *An illustrative example in two-patch systems*

In the simplest spatial systems with only two patches $\{1,2\}$ and density-independent dispersal given by a probability μ of dispersing from each patch, the dispersal function is given by $p(1,2) = p(2,1) = \mu$ and $p(1,1) = p(2,2) = 1 - \mu$, which yields the following recursion for the dynamics of the metapopulation:

$$\begin{aligned} N_1(t+1) &= (1-\mu)N_1(t)f_1[N_1(t)] + \mu N_2(t)f_2[N_2(t)] \\ N_2(t+1) &= (1-\mu)N_2(t)f_2[N_2(t)] + \mu N_1(t)f_1[N_1(t)]. \end{aligned} \quad (4)$$

In this simple system, spatial pattern formation leading to a steady state for the metapopulation dynamics can occur even when the two patches are ecologically identical. If $N_1^* = N_2^*$, $\lambda_1 = \lambda_2$ and $c_1 = c_2$ (i.e. $a_1 = a_2$, $\lambda_1 = \lambda_2$ and $b_1 = b_2$ in equation (3)), then the joint state (N_1^*, N_2^*) is a global equilibrium of the metapopulation described by model (4). Rohani *et al.*'s (1996) results imply that this global equilibrium is stable if and only if the local equilibria N_i^* are stable in the isolated patches, i.e. if and only if $|c_1| = |c_2| < 1$. Thus, supposing complicated local dynamics (i.e. $|c_1| = |c_2| \gg 1$), a careless reading of Rohani *et al.* (1996) might lead one to predict that for all dispersal rates μ , the population dynamics of patches in the linked system would also be highly complex. This impression would be false, because their analysis only considers the stability of the homogeneous equilibrium where each population is the same size as it would be in the absence of migration. However, other equilibria are possible, and their theory makes no predictions about them.

In fact, it was shown by Doebeli (1995) that even with highly complex local dynamics, for a range of high dispersal rates μ in system (4), a stable equilibrium state emerges in which the local population sizes differ: at the start of each generation, one local population has a very high density (the sink) and the other has a very low density (the source). After reproduction, this spatial pattern is reversed (reproduction is low in the high-density patch, whereas reproduction is high in the low-density patch), and the high dispersal rates leading to migration from the source to the sink then exactly restore the original situation at the start of the next generation. See Doebeli (1995) for more details and for the stability analysis of these source-sink equilibria. These equilibria may coexist with more complicated attractors, for which the local dynamics in each isolated patch are appropriate

representations (Gyllenberg *et al.* 1993). However, the important point here is that the coupling through dispersal can lead to spatial pattern formation, i.e. to a spatially heterogeneous configuration that is stationary despite the isolated local dynamics being highly chaotic. In particular, destabilization of the homogeneous equilibrium will not necessarily lead to temporal variability in local dynamics. This may happen, but heterogeneous stationary states are also possible. These emergent structures can also occur in circumstances where the underlying system is ecologically heterogeneous, as we will show now.

(b) Spatial pattern formation in larger systems

We now turn to metapopulations consisting of many patches that differ in their carrying capacities. We assume that the patches are distributed on a two-dimensional lattice on which each lattice point represents a habitat patch. In this situation, the most common dispersal assumption is that migrants from each patch are split equally between the nearest neighbouring patches. This may be a fair representation of some species where dispersal is very short range, although there are other species where the dispersers from a given donor patch reach a larger number of receiver patches. Therefore, we assume that migrants disperse according to a Gaussian distribution in all directions. If patch i has coordinates (i_1, i_2) on the square lattice and patch j has coordinates (j_1, j_2) , then the dispersal function is

$$p(i, j) = \frac{1}{2\pi\sigma^2} \exp\left[-\frac{(i_1 - j_1)^2 + (i_2 - j_2)^2}{2\sigma^2}\right]. \quad (5)$$

Here, σ is the standard deviation of the migration distribution: the larger σ is, the further individuals disperse. It is implicitly assumed that individuals have no preferred direction for dispersal on the lattice, and that the probability of migration decreases with Euclidean distance between donor and receiver patches. For our simulations, we scaled distances so that the distance across the lattice in one dimension is unity. In large lattices, for central patches i the sum $\sum_j p(j, i)$ over all patches j in the lattice should equal 1, because there is no explicit mortality due to dispersal in our model. However, if the number of patches is small, or if σ is small, this sum may deviate from 1, in which case we used a normalization procedure to make sure that the total number of individuals remains the same during the dispersal phase. With periodic boundary conditions, this implies that the total population size before and after dispersal is the same, i.e. that there is no loss of individuals due to dispersal. However, if the boundaries of the metapopulation lattice are absorbing, individuals can migrate out of the metapopulation, in which case they are lost by assumption. Such models have been studied by Hastings & Higgins (1994), by Ruxton & Doebeli (1996) and by Doebeli & Ruxton (1997) for cases with only one spatial dimension.

For the fitness function in each patch we still use equation (3), but now we assume that the carrying capacities differ among patches. For the results presented in figure 1, we assumed that the carrying capacity in each patch was drawn from a uniform random distribution in

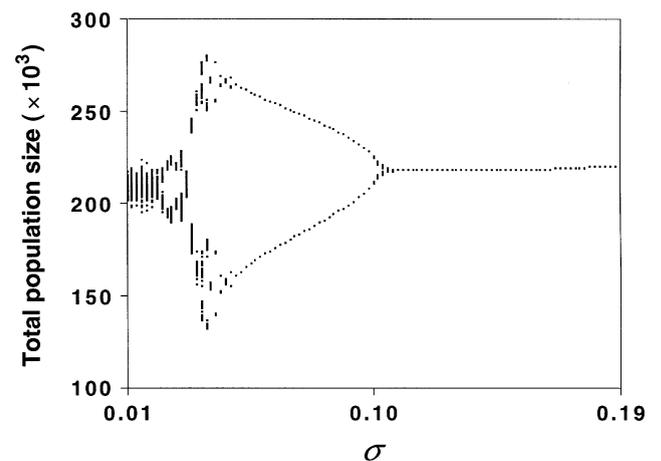


Figure 1. Effect of dispersal distance on the dynamics of metapopulations with heterogeneous habitats. Shown is a bifurcation diagram for the total population size with σ (equation (5)) as the bifurcation parameter. For short dispersal distances (low σ), the dynamics of the metapopulation are chaotic, with the total population size fluctuating in a broad band. For larger dispersal distances (higher σ), the dynamics change qualitatively, until for large enough σ the metapopulation has a stable equilibrium. Local dynamics in each patch are chaotic ($c = -2$), with a low intrinsic growth rate ($\lambda = 2$). These parameters are the same in all patches, whereas the carrying capacities vary uniformly and randomly in the interval [500, 1500]. Boundaries are periodic on a 15×15 lattice.

the interval [500, 1500]. The complexity c and the intrinsic growth rate λ were the same in all patches.

Figure 1 shows the dynamics of the total metapopulation size as a function of the dispersal distance given by σ for a case in which the local dynamics in an isolated patch are chaotic ($c = -2$). For low dispersal distances, the local populations are basically uncoupled and fluctuate chaotically and asynchronously. The dynamics of the total population appears as an average of all the local dynamics. The global dynamics change qualitatively as dispersal distances get larger, until eventually, when dispersal distances are large enough, a stable equilibrium for the global dynamics appears. In this equilibrium state, the local populations in each patch are also at an equilibrium, but the equilibrium size differs between patches. Thus, the system is characterized by a temporally stationary spatial wave. Examples of such spatial waves are shown in figure 2.

Figure 2a shows the standing spatial wave occurring for the demographic parameters used in figure 1 and for a dispersal distance given by $\sigma = 0.12$. Shown are the local population sizes on a 30×30 lattice at the start of every generation in the equilibrium state. In every generation, reproduction will first change the spatial configuration, but dispersal then restores the original pattern. The remaining panels in figure 2 show the influence of changing various parameters in the model on the shape of the standing spatial wave at equilibrium. Figure 2b,c illustrates that the wave flattens with lower intrinsic growth rates (but the same complexity of the local dynamics, figure 2b) and larger dispersal distances (figure 2c). For figure 2d, a different randomization for the local carrying capacities in each patch was used (recall that local

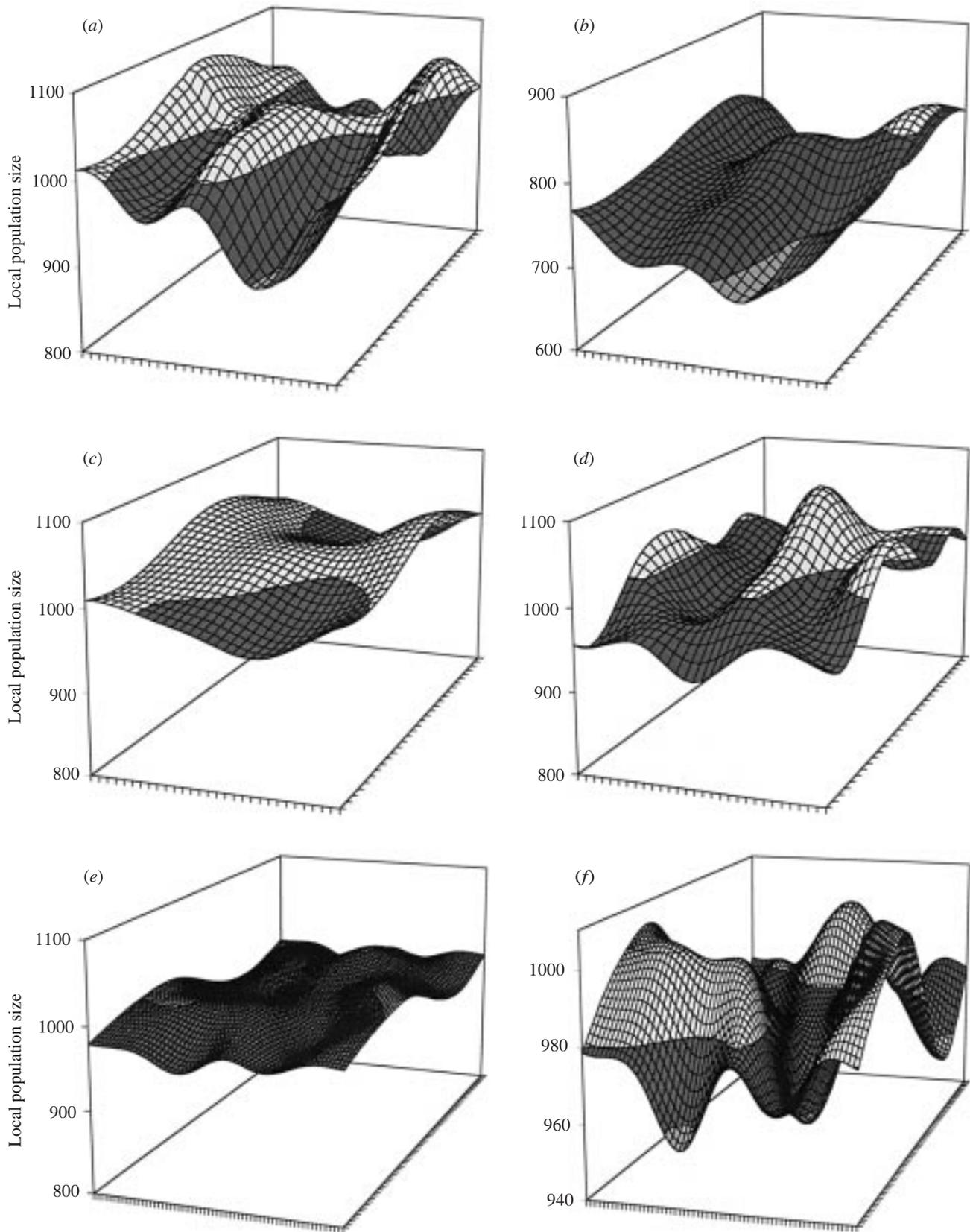


Figure 2. Standing spatial waves for various parameter combinations. In (a), the demographic parameters in each patch are the same as in figure 1, i.e. $\lambda = 2$ and $c = -2$, while the local carrying capacities are drawn uniformly and randomly from the interval [500, 1500] on a 30×30 lattice. The dispersal distance is given by $\sigma = 0.12$. (b) As (a), except that $\lambda = 1.2$. (c) As (a) except that $\sigma = 0.2$. (d) The same as (a) but with a different random configuration of the local carrying capacities. (e) The same as (a) but on a 60×60 lattice, with the first 30×30 patches having the same carrying capacities as in (a). (f) The same as (e) but with a finer scale to reveal the intricacies of the standing wave.

carrying capacities are drawn randomly uniformly from the interval [500,1500]). This panel shows that the shape of the equilibrium wave depends on the configuration of the local carrying capacities. Figure 2*e,f* shows the effect of enlarging the lattice size. Here, a 60×60 lattice was used on which the first 30×30 local patches (i.e. those with coordinates (i,j) with $1 \leq i,j \leq 30$) had the same local carrying capacities as those in figure 2*a-c*. Figure 2*e,f* shows that although the variation in local population size at equilibrium decreases on larger lattices (figure 2*e*), larger lattices allow for more intricate patterns in the standing spatial wave (figure 2*f*; note the different scale).

Interestingly, the complexity c of the local dynamics seems to have little influence on the shape of the standing wave as long as $|c|$ is small enough for standing waves to occur. That is, for a given intrinsic growth rate and dispersal distance, very similar spatial waves emerge over the range of local complexities that allow a spatially inhomogeneous global equilibrium. In addition, note that because the carrying capacities vary uniformly and randomly between patches, there is little correlation between the carrying capacity in a patch and the final equilibrium size in this patch as determined by the spatial wave. Rather, the heterogeneity in carrying capacities together with large dispersal distances leads to spatial pattern formation which induces local and global stable equilibrium dynamics. In some sense, this is the multi-patch equivalent of the source-sink equilibrium described earlier for two-patch systems.

Standing spatial waves can be observed for a large range of demographic parameters and dispersal distances. Even in the presence of demographic stochasticity, the formation of wave-like quasi-steady states can be observed. This is illustrated in figure 3*a*, which is the same as figure 1 but with stochastic effects added. To include stochasticity we assumed that the local density-dependent fitness values in equation (1) are not the deterministic quantities $f_i[N_i(t)]$, but instead are chosen in each patch independently from a normal distribution with mean the deterministic fitness value and variance 10% of the mean. (Thus we assumed no spatial correlation in stochasticity.) The figure shows that long-range dispersal can induce quasi-equilibrium states even in the presence of noise. Note that the dynamics for small dispersal distances on the left of figure 3*a* are qualitatively different from the dynamics for large dispersal distances. Whereas the latter are the product of stochastic fluctuations around a global equilibrium, the former are a stochastic version of the deterministic chaos that results from averaging over the asynchronous chaotic dynamics in each patch (cf. figure 1).

One requirement for the emergence of standing spatial waves seems to be that intrinsic growth rates are not very large. Figure 3*b* shows a bifurcation diagram for a fixed dispersal distance and for varying intrinsic growth rates λ , again under the assumption that the local dynamics in an isolated patch are chaotic ($c = -2.5$ in all patches for all values of λ). This figure illustrates that large growth rates prevent the stationary spatial pattern formation in our model.

The results presented in figures 1, 2 and 3*a,b* were obtained with periodic boundary conditions. However, similar results hold for absorbing boundary conditions. In

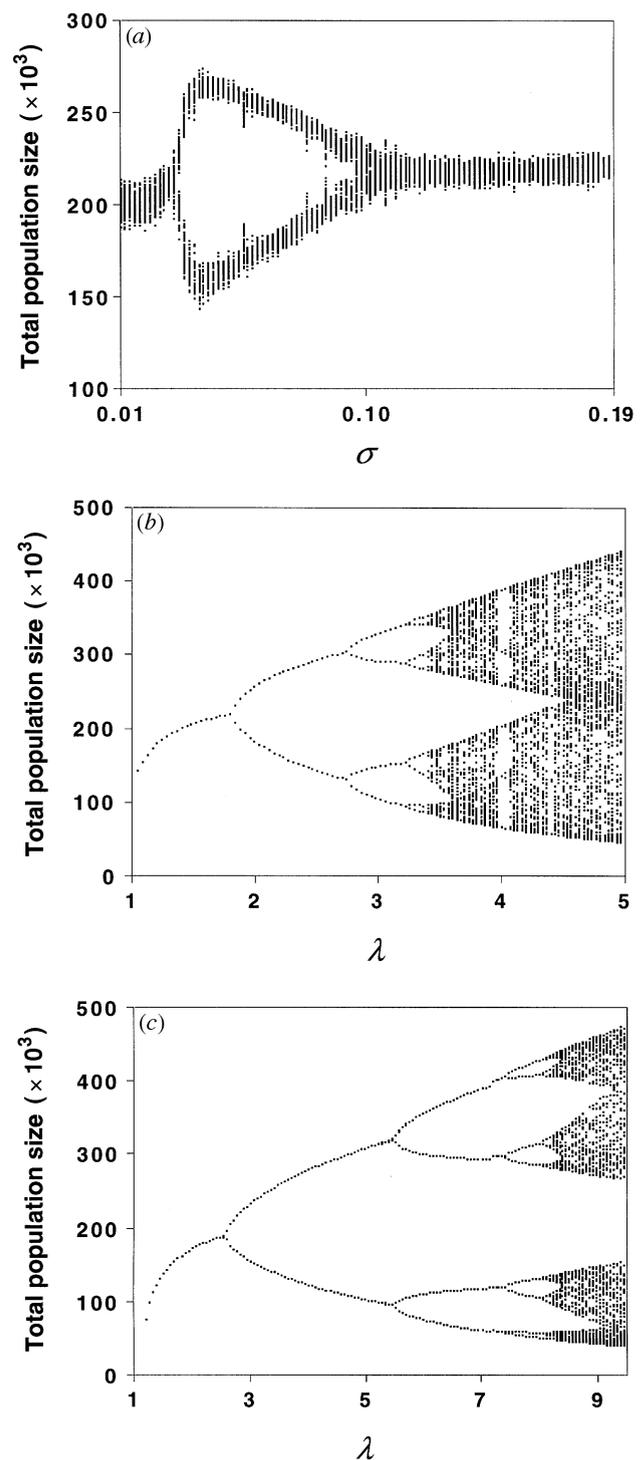


Figure 3. Effects of stochasticity and of changing the intrinsic growth rate on metapopulation dynamics. (a) The same as figure 1 with demographic stochasticity added (see text). Despite noise, a quasi-steady state emerges for large dispersal distances (see text). (b) A bifurcation diagram with the growth rate λ as the bifurcation parameter for a fixed dispersal distance ($\sigma = 0.18$). All patches have complicated local dynamics ($c = -2.5$) and the same intrinsic growth rate, whereas carrying capacities vary uniformly and randomly in the interval [500,1500]. Boundaries are periodic on a 15×15 lattice. For low values of λ , long-range dispersal induces stable equilibrium dynamics. (c) The same as (b) but with absorbing boundary conditions. The range of λ values for which global stable equilibria are possible despite chaotic local dynamics is much greater than with periodic boundaries.

fact, if boundaries are absorbing, then the marginal patches effectively have a lower intrinsic growth rate, because individuals are lost from such patches owing to migration out of the metapopulation. This enhances the stabilizing effects of dispersal, and standing spatial waves are more likely to occur in this case. This is illustrated in figure 3c. More generally, and in common with other recent studies (Ruxton *et al.* 1997a,b), the addition of mortality during dispersal has a stabilizing influence in our model, making the appearance of standing spatial waves more likely. This happens because introducing mortality for dispersers is formally equivalent to lowering the intrinsic growth rate, and hence to decreasing the dynamic complexity in the local patches.

To conclude, we return to the homogeneous case where all patches are ecologically identical. However, we now assume that dispersal is density dependent by assuming that the dispersal distance is a linear function of the local population density in a patch:

$$\sigma_i(t) = \sigma_0 + \sigma_1 N_i'(t), \quad (6)$$

where $\sigma_i(t)$ determines the dispersal distance from patch i at time t , $N_i'(t)$ is the local population size after reproduction in generation t , and σ_0 and σ_1 are constants. Figure 4 shows the dynamics of a large metapopulation with absorbing boundaries as a function of the strength of density dependence of the dispersal distance. This figure shows that if the density dependence of dispersal is strong enough, migration can induce stable equilibrium dynamics in ecologically homogenous metapopulations despite the local dynamics in an isolated patch being highly chaotic. As in the heterogeneous case with density-independent dispersal (figure 1), this equilibrium is characterized by a standing spatial wave. This stability-inducing spatial pattern formation can be observed for a wide range of parameters, including high intrinsic growth rates λ .

3. CONCLUSIONS

We have given examples of dispersal-induced stability in two classes of metapopulation models. In the first type of model, the local habitat patches constituting the metapopulation differ ecologically because they are assumed to have different carrying capacities. In the second class of models, the patches are ecologically identical, but dispersal is density dependent. In both cases, the stable equilibrium for the metapopulation dynamics is characterized by a temporally stationary spatial wave. That is, the local population in each patch is also at an equilibrium, but the equilibrium size differs between patches in a wave-like manner. This happens even though the local population dynamics in an isolated patch are chaotic. In particular, the local dynamics are a very poor predictor for the dynamics in a patch when it is linked to the other patches in the metapopulation by long-range dispersal. The same holds for the local carrying capacities. In the ecologically heterogeneous metapopulations, the carrying capacities in each patch were chosen randomly from a uniform distribution, which is very different from the distribution of the local equilibrium sizes given by the standing spatial wave (figure 2). The equilibrium sizes

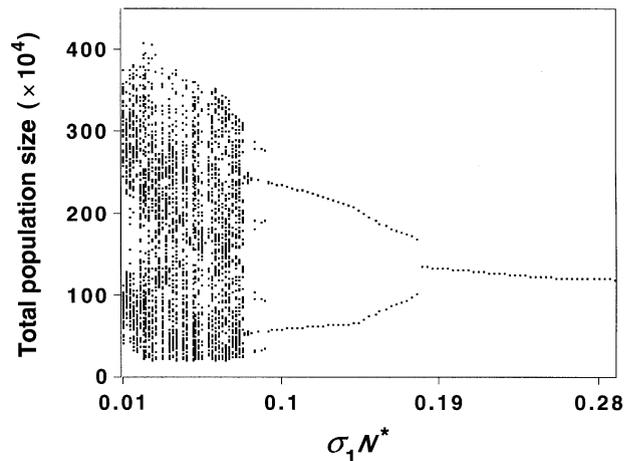


Figure 4. Metapopulation dynamics as a function of density dependence of dispersal distances. All patches had the same intrinsic growth rate ($\lambda = 10$), the same complexity ($c = -3$) and the same carrying capacity ($N^* = 1000$). The parameter σ_0 in equation (6) was set to 0.005, and we used the parameter σ_1 in equation (6), multiplied by the local carrying capacity N^* , as bifurcation parameter. Thus the parameter shown on the x -axis of the diagram determines the dispersal distance from a patch in which the local population is at the carrying capacity. If dispersal at carrying capacity is sufficiently long range, stable equilibrium dynamics for the whole metapopulation result. Absorbing boundaries on a 40×40 lattice were used.

given by the spatial wave are also very different from the uniform carrying capacities that were assumed in the ecologically homogeneous models with density-dependent dispersal. Thus, the spatial patterns are emergent phenomena in systems of coupled local populations, which cannot be extrapolated from the dynamical and ecological properties of isolated local populations.

The qualitative conclusions concerning the emergence of standing spatial waves are not sensitive to our choice of a Gaussian dispersal kernel, equation (5). For example, Neubert *et al.* (1995) argue that the leptokurtic Laplace (or double exponential) distribution provides a better representation of dispersal than a Gaussian, being more peaked and having fatter tails. Numerical simulations indicate that substitution of this formulation (equation (11) in Neubert *et al.* (1995)) for the dispersal kernel in our models does not substantially change the models' general behaviour.

In our models, global steady states are characterized by spatial pattern formation. Such phenomena are well known from reaction-diffusion systems (see Murray (1989) for an overview), and have been observed in a number of ecological models. For example, Neubert *et al.* (1995) observed destabilization of a spatially homogeneous equilibrium and formation of standing spatial waves in a spatially continuous, temporally discrete predator-prey model with prey overdispersal. Similar phenomena were observed by Rohani *et al.* (1996) in a discrete time, discrete space host-parasitoid model, and by Hastings *et al.* (1997) in a continuous time, continuous space predator-prey model. In such systems, spatial pattern formation occurs through Turing instabilities and hinges upon one of the species having much larger migration rates than the other. In particular, the mechanism

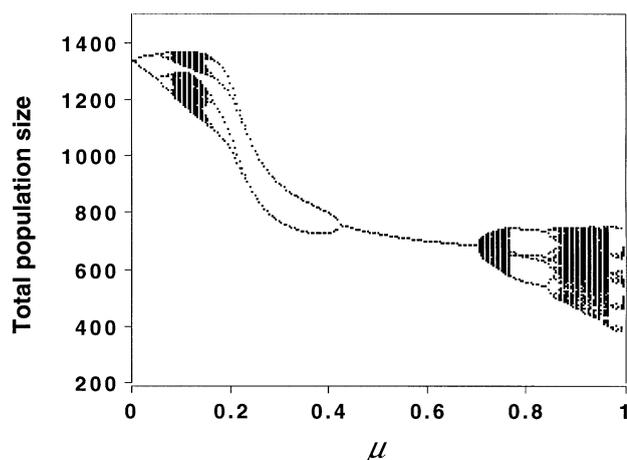


Figure 5. Dynamics of the two-patch system (4) as a function of the dispersal rate μ . Both local populations are stable when isolated ($c = -0.85$), and have the same intrinsic growth rate ($\lambda = 1.2$). The carrying capacity of patch 1 ($N_1^* = 1000$) was three times that of patch 2. The coupled system shows complicated non-equilibrium dynamics for a wide range of dispersal rates μ .

for spatial pattern formation operating in these models requires the presence of more than one species. In contrast, we present examples of standing spatial waves in single-species models. Thus, the mechanism inducing these spatial patterns is not the same as the mechanism inducing pattern formation in reaction–diffusion systems.

In fact, even though we have only presented examples in which emergent properties lead to global stabilization, the opposite can also happen. This can be seen by going back to the very simple metapopulation model with only two patches considered at the beginning of §2. If we assume that the two patches have a stable equilibrium when isolated, but that they differ in their carrying capacities, then the coupled system can have complicated dynamics for a wide range of dispersal rates. An example of this emergent destabilization is shown in figure 5, and similar phenomena can be observed in larger metapopulations with ecologically different patches provided that dispersal distances are short.

Thus, although dispersal is often a stabilizing factor, particularly if it occurs over large distances, it can also have a destabilizing effect, particularly if it occurs over short distances. Clearly, in any particular ecological situation, details about the amount of individuals dispersing and about how far they disperse must be known before the expected ecological consequences of dispersal can be assessed. One important ecological message of this paper is that different types of heterogeneity in the metapopulation can induce emergent spatial structures. For example, we have seen that heterogeneity in local carrying capacity as well as heterogeneity in dispersal itself, mediated by density dependence, can induce spatial pattern formation. In addition, the heterogeneity in carrying capacity can also be interpreted as heterogeneity in dispersal, because heterogeneity in carrying capacity is modelled by varying the scaling parameter a in equation (3), which is formally equivalent to assuming equal carrying capacities, but allowing the dispersal distance parameter σ in equation (5) to vary between patches. Consequently, spatial

heterogeneity in the Gaussian dispersal emanating from any one patch can also induce standing spatial waves. The ecological importance of such emergent spatial structures is that the characteristic scale of the spatial wave is a poor description of characteristic scale of the underlying spatial heterogeneity. In particular, if variation in local population size is induced by emergent pattern formation akin to that described here, one should be cautious about making inferences about scales of habitat differences on the basis of population measurements.

That migration between habitats in a metapopulation can have important effects on local and global population dynamics has of course been realized by many researchers (e.g. Kareiva 1994; Hanski & Gilpin 1997; Bascompte & Solé 1998). However, most of the theoretical literature concerns metapopulations consisting of ecologically identical patches with density-independent dispersal between nearest neighbours (but see Gyllenberg *et al.* (1993); Hastings & Higgins (1994); Scheuring & Jánosi (1996); and Ruxton (1996) for notable exceptions). Here we have considered effects of relaxing each of these assumptions, and we have given examples where ecological heterogeneity and density-dependent, long-range dispersal lead to stabilization owing to spatial pattern formation. We have never observed these phenomena in the corresponding homogeneous model with density-independent, long-range dispersal. Therefore, we believe that studying more general metapopulation models than commonly considered will lead to a greater understanding of how environmental and biotic conditions combine to affect temporal and spatial patterns of population dynamics.

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