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Metapopulation dynamics with quasi-local competition

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Abstract

Stepping-stone models for the ecological dynamics of metapopulations are often used to address general questions about the effects of spatial structure on the nature and complexity of population fluctuations. Such models describe an ensemble of local and spatially isolated habitat patches that are connected through dispersal. Reproduction and hence the dynamics in a given local population depend on the density of that local population, and a fraction of every local population disperses to neighboring patches. In such models, interesting dynamic phenomena, e.g. the persistence of locally unstable predator–prey interactions, are only observed if the local dynamics in an isolated patch exhibit non-equilibrium behavior. Therefore, the scope of these models is limited. Here we extend these models by making the biologically plausible assumption that reproductive success in a given local habitat not only depends on the density of the local population living in that habitat, but also on the densities of neighboring local populations. This would occur if competition for resources occurs between neighboring populations, e.g. due to foraging in neighboring habitats. With this assumption of quasi-local competition the dynamics of the model change completely. The main difference is that even if the dynamics of the local populations have a stable equilibrium in isolation, the spatially uniform equilibrium in which all local populations are at their carrying capacity becomes unstable if the strength of quasi-local competition reaches a critical level, which can be calculated analytically. In this case the metapopulation reaches a new stable state, which is, however, not spatially uniform anymore and instead results in an irregular spatial pattern of local population abundance. For large metapopulations, a huge number of different, spatially non-uniform equilibrium states coexist as attractors of the metapopulation dynamics, so that the final state of the system depends critically on the initial conditions. The existence of a large number of attractors has important consequences when environmental noise is introduced into the model. Then the metapopulation performs a random walk in the space of all attractors. This leads to large and complicated population fluctuations whose power spectrum obeys a red-shifted power law. Our theory reiterates the potential importance of spatial structure for ecological processes and proposes new mechanisms for the emergence of non-uniform spatial patterns of abundance and for the persistence of complicated temporal population fluctuations.

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1. Introduction

The past decade has seen an upsurge of interest in the role of spatial structure on ecological and evolutionary processes (e.g. Gilpin and Hanski, 1997; Bascompte and Sole, 1998; Dieckmann et al., 2000). Models for spatially structured populations have a long tradition in population genetics and in ecology (e.g. Wright, 1943; Levene,

1953; Kimura and Weiss, 1964), but such models tend to quickly become analytically intractable, and advances in computational power have greatly facilitated the numerical investigation of spatial models in recent years. In ecological theory, the principal interest in spatial structure concerns its effects on the nature of population fluctuations and on geographical patterns of population abundance. For example, starting with Levins' classic metapopulation model (Levins, 1970), the study of the effects of spatial structure on processes of extinction has been a recurrent theme, and it has for instance been shown that spatial pattern formation in the form of

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spiral waves of population abundance can prevent extinction in intrinsically unstable predator–prey systems (Hassell et al., 1991, 1994; Comins et al., 1992).

One of the main questions in this context is whether population dynamics tend to become simpler, and hence population fluctuations decrease, when ecological interactions are localized and migration induces mixing between local populations. A common model used to investigate this question is an ecological version of Kimura's stepping stone model (Kimura, 1953), in which one envisages a metapopulation consisting of a number of local populations occupying local habitat patches that are arranged on a spatial grid and that are coupled by migration between habitats. In each habitat patch the dynamics of the local populations is given by difference equations that describe population growth or decline resulting from the local ecological interactions. After the local dynamics have taken place in each generation, migration to neighboring patches occurs, typically in the form of passive dispersal, in which a constant fraction of the local population is distributed evenly among the surrounding habitat patches. Such spatially and temporally discrete dynamical systems have been studied extensively in the physics literature (e.g. Kaneko, 1998), and have also attracted considerable attention in theoretical ecology (e.g. Hastings, 1993; Gyllenberg et al., 1993; Lloyd, 1995; Doebeli, 1995; Ruxton, 1996; Scheuring and Janosi, 1996; Holt and McPeck, 1996; Earn et al., 2000). One common message emerging from this large body of work is that spatial structure typically tends to simplify population dynamics by inducing coherent spatial patterns in the metapopulation. For example, even if the local populations would exhibit chaotic dynamics in isolation, the coupling between them induced by dispersal can lead to spatially and temporally regular patterns of abundance (Kaneko, 1998). In particular, in a metapopulation consisting of two chaotic local populations, coupling through dispersal can induce a spatially inhomogeneous but temporally stable equilibrium for the metapopulation dynamics (Doebeli, 1995). Further simplifying effects can be observed if dispersal occurs over larger distances than just to neighboring habitat patches (Doebeli and Ruxton, 1998), or if dispersal is conditional and depends on the local population size in a habitat (Ruxton, 1996; Scheuring and Janosi, 1996; Doebeli and Ruxton, 1998).

However, to observe these effects in single-species models one always needs to assume very complicated local dynamics and hence strong density dependence. In fact, if one assumes that the local populations exhibit stable equilibrium dynamics in isolation, and that all habitat patches are identical (i.e. that the demographic parameters are the same in each patch) then one can show that passive dispersal cannot induce any change in the dynamics: there is always a spatially homogeneous

and temporally constant equilibrium for the metapopulation in which each local population is at the equilibrium size it would have in isolation (Rohani et al., 1996). Therefore, these types of models for spatial structure only yield interesting results if some form of dynamical instability resulting from the local ecological interactions in each patch is assumed.

In situations in which two or more species are present it is possible, in continuous time systems, to have stable spatially inhomogeneous configuration even with stable local dynamics via the Turing mechanism (Turing, 1952). For continuous-time predator–prey systems such diffusion driven instability seems to occur only under rather restrictive conditions (Levin and Segel, 1976; Mimura and Murray, 1978). Spatially structured interspecific competition models, either in discrete time (Karlin and McGregor, 1972) or in continuous time (Levin, 1974, 1979), can also result in stable spatially inhomogeneous population distributions. It is also possible to obtain stable inhomogeneous spatial distributions in discrete-time predator–prey systems in which the local dynamics has a spiral instability (Hassell et al., 1991, 1994; Comins et al., 1992; White et al., 1996), in age-structured single-species models in which different age classes have different dispersal parameters (Hastings, 1992), and in invasion models which incorporate an Allee effect (Keitt et al., 2001). These models are fundamentally different from the type of model introduced in this paper in that in the former, all non-dispersive ecological interactions are confined to take place within each habitat patch, with dispersal being the only coupling between the patches.

The novelty of the approach taken here is that we consider the coupling between neighboring habitat patches to include other ecological interactions in addition to simple dispersal. In this approach we also assume that each local population is described by a difference equation, but we assume that the coupling occurs primarily through ecological interactions, such as competition, rather than through dispersal. Thus, we assume that the reproductive dynamics of a local population in a given patch depends not only on the population density in that patch, but also to a certain extent on the population densities in the neighboring patches. This is a reasonable assumption for situations in which reproduction and hence population dynamics takes place in a habitat patch whose resources are also used, e.g. through foraging, by individuals that live and reproduce in neighboring patches. Then the depletion of resources in a given habitat patch occurs not only due to the individuals living and reproducing in that patch, but also due to individuals living in a certain neighborhood of that patch. In other words, competition for resources is not strictly local, but *quasi-local*: the strength of competition impinging on reproduction of an individual in a given patch depends not only on the density of the

population inhabiting that patch, but also on the population densities of neighboring patches. Such an assumption is commonly used for individual-based models for spatially structured populations (e.g. Neuhauser and Pacala, 1999; Sasaki, 1997). In those models it is assumed that the strength of the ecological interactions impinging on an individual is a function of the number of neighboring individuals as well as of their spatial distance, with more distant individuals having a smaller impact. However, to our knowledge this form of coupling has never been used for spatially discrete metapopulations consisting of a number of local habitat patches.

In contrast to the case where the coupling is due to dispersal alone, coupling through quasi-local competition can lead to very interesting dynamical phenomena even if the local population dynamics exhibit a stable equilibrium in isolation, as we will show below. If the dynamics of a local population in isolation exhibit a stable equilibrium, then it is still true that the dynamics of the whole metapopulation will always converge to a temporally constant equilibrium state. However, despite the fact that all habitat patches are ecologically identical, this equilibrium state is typically spatially inhomogeneous, with some habitat patches having high population densities and others having low densities. Thus, coupling through quasi-local ecological interactions can lead to spatial pattern formation even if the habitat quality is spatially homogenous throughout the metapopulation and if the local population dynamics exhibit a stable equilibrium. This ecological mechanism for pattern formation seems to have been overlooked in the past.

In fact, spatial pattern formation due to quasi-local interactions may be relevant for many spatially structured ecological systems in nature, for which the assumptions of local population dynamics but quasi-local competition dynamics are plausibly satisfied. For example, many territorial birds, such as Dunnocks, occupy spatial regions within which they carry out most of their foraging, but different territories often overlap (Davies, 1992), suggesting the possibility of quasi-local competition between populations in neighboring territories. Also, in social insects such as ants the colonies occupy territories and regularly engage in competitive activities with neighboring colonies, e.g. robbing of food (Wilson, 1971; Holldobler and Wilson, 1990). Finally, quasi-local competition for water appears to be important for many plant populations, simply because the effect of a plant taking up water locally is to remove water from the surrounding regions. Thus quasi-local competition can result from resource diffusion. Interestingly, spatial pattern formation in plant populations is found in many semi-arid regions (White, 1970; Belsky, 1986; Klausmeier, 1999), in which quasi-local competition for resources would appear to be particularly

strong. These patterns are in qualitative agreement with the results obtained below from our models. Therefore, the basic mechanisms of spatial pattern formation due to quasi-local interactions introduced in this paper may well be relevant for explaining spatial patterns in ecological systems.

Our models not only exhibit spatially inhomogeneous equilibria, but for a given set of model parameters the equilibrium spatial pattern is not unique and depends critically on the initial conditions. In fact, even for metapopulations consisting of a moderate number of local populations the number of different attractors, i.e. different spatially inhomogeneous equilibrium states, can be very large. The existence of a multitude of attractors has important consequences for the population dynamics when a small amount of noise is introduced in the system. With many attractors each one of them tends to have a small basin of attraction, i.e. the set of all initial conditions from which the given attractor is reached is typically small. In the presence of environmental noise, the metapopulation therefore continually jumps between the basins of attraction of different attractors and thus performs a random walk in the set of all attractors. This random walk results in persistent population fluctuations of the local population densities as well as of the density of the whole metapopulation. Since the fluctuations are the result of a random walk, their power spectrum is red-shifted and obeys a power law, in which long-term fluctuations have a much larger amplitude than short-term fluctuations. Such red-shifted power spectra are well-known from empirical analyses of population time series (Diamond and May, 1977; Pimm and Redfearn, 1988; Arino and Pimm, 1995). Our results indicate a potential new explanation for red-shifted ecological time series that require neither strong density-dependence inducing dynamic instabilities nor a red shift in the demographic noise. Instead, a repeated sequence of convergence towards different equilibrium attractors and noise-induced dislocation from these equilibria can produce red-shifted time series for population abundances. Thus, despite its inherent simplicity due to non-overcompensating density dependence, our model exhibits very rich dynamical behavior.

2. Model and results

2.1. Spatially one-dimensional metapopulations: chains of local habitat patches

For ease of presentation we first consider the case where the metapopulation extends along one spatial dimension and therefore consists of a chain of m local populations N_i , $i = 1, \dots, m$. Such a one-dimensional case could arise, for example, if the habitats lie along a

coastline or along the shore of a lake or pond. In each habitat patch the dynamics of the local populations is assumed to be described by a difference equation of the form

$$N'_i(t) = N_i(t) \cdot f(N_{i-1}(t), N_i(t), N_{i+1}(t)), \quad (1)$$

where $N_j(t)$ is the local population size in patch j at the start of year t , and where $N'_i(t)$ is the local population size in patch i after reproduction, but before dispersal. Thus we assume that the per capita number of descendants, f , in a patch is a function of the density of the local population in that patch as well as of the densities of the local populations in the two neighboring patches, e.g. due to foraging or interference of individuals from the neighboring patches.

In this paper we will always assume that all the local habitat patches are ecologically identical, so that the demographic parameters influencing the density-dependent reproductive output are the same in all patches. Moreover, we assume that the per capita reproductive output f is of Beverton–Holt type (Yodzis, 1989):

$$f(N_{i-1}(t), N_i(t), N_{i+1}(t)) = \frac{\lambda}{1 + a[N_i(t) + \alpha\{N_{i-1}(t) + N_{i+1}(t)\}]}. \quad (2)$$

Thus, compared to individuals living in patch i , individuals from the two neighboring patches have a relative competitive impact α on reproduction in patch i . If we define

$$\tilde{N}_i(t) = N_i(t) + \alpha(N_{i-1}(t) + N_{i+1}(t)), \quad (3)$$

then $\tilde{N}_i(t)$ is the effective density that impinges on reproduction in patch i , and the per capita reproductive output in patch i can be written as

$$f(N_{i-1}(t), N_i(t), N_{i+1}(t)) = f(\tilde{N}_i(t)) = \frac{\lambda}{1 + a\tilde{N}_i(t)}. \quad (4)$$

The parameter λ in Eq. (4) describes the maximal per capita reproductive output attained under ideal conditions, i.e. in the absence of competition, and the parameter a is a measure of the impact of individuals in patch i on reproduction in patch i . As mentioned above, we assume that these parameters are the same in all patches, hence all local habitats are ecologically identical, and any difference between patches resulting from a non-uniform distribution of local population abundances must be due to internal dynamical properties of the model.

To complete the description of the metapopulation dynamics, we assume that in each year reproduction is followed by passive dispersal of a constant fraction of the local populations, which is distributed evenly between the two neighboring patches. Therefore, the population density in patch i at the start of year $t + 1$ is

given by

$$N_i(t + 1) = (1 - d)N'_i(t) + \frac{d}{2}N'_{i-1}(t) + \frac{d}{2}N'_{i+1}(t). \quad (5)$$

Here the population sizes $N'_j(t)$ after reproduction in year t , but before dispersal, are given by Eqs. (1) and (2), and d is the fraction of dispersers, which we assume to be the same in each patch.

We note that the Beverton–Holt equation (4) is one of the standard difference equations used to describe the dynamics of discrete-time ecological systems (Skellam, 1951; Leslie, 1957; Utida, 1967) and is a special case of other well-known difference equations employed in ecology (Hassell, 1974; Hassell et al., 1976; Maynard Smith and Slatkin, 1973). The Beverton–Holt equation is particularly well-suited to our purpose in this paper since, provided λ is greater than 1, a local population in isolation whose dynamics is described by Eq. (4) will always converge monotonically towards a globally stable equilibrium K defined by $f(K) = 1$, i.e. towards the carrying capacity $K = \frac{\lambda-1}{a}$. In fact, it is easy to see that for any $N(0) > 0$, the general solution of the (local) Beverton–Holt difference equation is given by

$$N(t) = \frac{\lambda^t}{\frac{a(\lambda^t-1)}{\lambda-1} + \frac{1}{N(0)}}, \quad (6)$$

which shows that $N(t) \rightarrow 0$ as $t \rightarrow \infty$ for $\lambda < 1$, and $N(t) \rightarrow \frac{\lambda-1}{a}$ as $t \rightarrow \infty$ for $\lambda > 1$. Consequently, we can be assured that any dynamic complexity exhibited by the metapopulation dynamics (5) results from the effects of spatial structure and not from intrinsically complex local dynamics.

Now that we have formally defined the model that we will study it may be helpful to explain how the quasi-local competitive interactions can be interpreted in terms of foraging. Note that this interpretation of the parameter α is of course not the only possible one and is meant as an illustrative example of quasi-local ecological interactions. Recall that the parameter α measures the competitive impact of individuals from the neighboring patches on reproduction in a given patch, relative to the impact of individuals living in that patch. To illustrate how this parameter can be related to quasi-local foraging outside the natal patch, let p be the fraction of time an individual born in a given patch i spends, on average, foraging in neighboring patches before it returns to the natal patch i to reproduce. Alternatively, p could be interpreted as the fraction of resources that individuals born and reproducing in a given patch acquire from outside that patch. Given p , the amount of resource depletion in patch i that is due to individuals born in patch i is determined by the scaled population size $(1 - p)N_i(t)$. As mentioned we assume that individuals always reproduce in their natal patch. If we further assume that reproduction in patch i is described by a Beverton–Holt equation, and if we

neglect for a moment foraging in patch i by individuals born in neighboring patches, then the equation for reproduction in patch i would have the form

$$N'_i(t) = \frac{\lambda N_i(t)}{1 + a'(1-p)N_i(t)}, \tag{7}$$

where a' is a parameter that scales resource depletion due to the effective natal population $(1-p)N_i(t)$. Note that this equation incorporates a benefit to foraging in neighboring patches because due to foraging outside the natal patch the effective natal population that is depleting resources is smaller than the total population size in patch i , i.e. because $(1-p)N_i(t) < N_i(t)$. Of course, we now have to incorporate the depletion of resources in patch i that is due to foraging by individuals from neighboring patches. Clearly, given p , which is assumed to be the same for all patches, the effective population size of individuals from the neighboring patch $i-1$ that forage in patch i is $pN_{i-1}(t)/2$, and similarly for the neighboring patch $i+1$. Therefore, when foraging by individuals from neighboring patches is included, the equation for reproduction in patch i becomes

$$N'_i(t) = \frac{\lambda N_i(t)}{1 + a'[(1-p)N_i(t) + \frac{p}{2}\{N_{i-1}(t) + N_{i+1}(t)\}]}. \tag{8}$$

If we now set $a = a'(1-p)$, this equation takes the form of Eq. (2), i.e.

$$N'_i(t) = \frac{\lambda N_i(t)}{1 + a[N_i(t) + \alpha(N_{i-1}(t) + N_{i+1}(t))]}, \tag{9}$$

with

$$\alpha = \frac{p}{2(1-p)}. \tag{10}$$

Note that with this interpretation of the model, in which quasi-local competitive interactions measured by α are due to quasi-local foraging described by p , $\alpha > \frac{1}{2}$ if and only if $p > \frac{1}{2}$. Thus, the combined relative impact of individuals from the two neighboring patches exceeds 1 if the fraction of resources acquired outside the natal patch is bigger than 50%. Note also that α is a non-linear function of p , so that, e.g. $\alpha = 2$ for $p = 0.8$. Since foraging outside the natal patch reduces resource depletion in the natal patch and is thus advantageous from the point of view of the individuals living and reproducing in that patch, it would therefore appear to be justified to consider a large range of α -values as biologically realistic. This should be kept in mind during the subsequent analysis.

Before describing the stability and dynamics in the general case it is instructive to consider the simple case of two patches with no dispersal. If we denote the population densities in the two patches by $N(t)$ and $M(t)$, respectively, then system (1) and (2) takes

the form

$$\begin{aligned} N(t+1) &= \frac{\lambda N(t)}{1 + a[N(t) + \alpha M(t)]}, \\ M(t+1) &= \frac{\lambda M(t)}{1 + a[M(t) + \alpha N(t)]}. \end{aligned} \tag{11}$$

If the parameter α is interpreted in terms of foraging as above, so that quasi-local competition is due to individuals in both patches acquiring a fraction p of their resources in the other patch, then similar arguments as above show that in this case $\alpha = p/(1-p)$. In particular, we have $\alpha > 1$ if $p > \frac{1}{2}$, i.e. in each habitat the relative competitive impact of individuals from the other habitat is larger than 1 if the fraction of time spent foraging outside the natal patch is larger than $\frac{1}{2}$. Note that system (10) is formally equivalent to a discrete-time version of the standard Lotka–Volterra equations for competition between two species. Therefore, the standard analysis of the Lotka–Volterra system directly applies. Accordingly, the dynamical system (10) has four equilibria, with the trivial equilibrium $N = M = 0$ only being stable if $\lambda < 1$, a case we will not consider further. In addition, there are two asymmetric equilibria $(\tilde{N}, 0)$ and $(0, \tilde{M})$, where $\tilde{N} = \tilde{M} = (\lambda - 1)/a$, and a symmetric equilibrium (N^*, M^*) , where $N^* = M^* = (\lambda - 1)/[a(1 + \alpha)]$. It is well known that this symmetric equilibrium is stable, and the two asymmetric equilibria are unstable, if and only if $\alpha < 1$ (i.e. if and only if $p < \frac{1}{2}$). For $\alpha > 1$, i.e. for $p > \frac{1}{2}$, the symmetric equilibrium is destabilized, and the two asymmetric equilibria both become locally stable. Thus, if $\alpha < 1$ any initial configuration will converge to the stable symmetric equilibrium (N^*, M^*) . For $\alpha > 1$, however, symmetry breaking occurs and any initial configuration will converge either to $(\tilde{N}, 0)$ or to $(0, \tilde{M})$. In particular, for $\alpha > 1$ there are two attractors, with the corresponding basins of attraction being separated by the diagonal $N = M$. These features, the existence of a unique stable equilibrium for α below a certain critical value with destabilization of this equilibrium and the appearance of multiple attractors for larger α values, which appear here in prototype form, are also present in the general case in both one and two spatial dimensions. The most significant difference between the two-patch case and the general case is that, after symmetry breaking has occurred, in the former there are only two attractors while in the latter there are typically a very large number of attractors (which increases rapidly with the number of patches).

We now turn to the analysis of the dynamical properties of the model in the general case. Eqs. (1) and (5) fully describe the dynamics of a metapopulation with quasi-local interactions and dispersal, except for the fact that we have not yet specified how to deal with the marginal populations N_1 and N_m in the

one-dimensional chain of local populations. The model that is most easily tractable analytically is obtained by assuming that the two marginal populations are actually neighbors, i.e. one assumes periodic boundary conditions, so that the chain of habitat patches is actually a ring. In case of a one-dimensional habitat distribution it is biologically perfectly plausible to consider periodic boundary conditions, for example habitat patches lying around the shore of a lake or pond might have this property, as well as absorbing or reflecting boundary conditions which might be plausible in other situations, such as for habitat patches lying along a coastline. In view of the analytic tractability of periodic boundary condition, and their biological plausibility in certain one-dimensional situations, we will focus on this case in this section. In the next section, when we discuss two-dimensional habitat distributions for which periodic boundary conditions are clearly less biologically plausible, we will still consider periodic boundary conditions for reasons of analytical tractability, but we will also present numerical results for absorbing boundary conditions. In general the dynamical behavior of the models with different boundary conditions is qualitatively very similar and the same ecologically relevant features are present in all cases.

With periodic boundary conditions when N_1 and N_m occupy neighboring patches, the index $i - 1$ in Eqs. (1)–(5) has to be substituted by m whenever the index $i = 1$ on the left-hand side of these equations. Similarly, the index $i + 1$ must be substituted by the index 1 in Eqs. (1)–(5) whenever $i = m$ on the left-hand side of these equations. With periodic boundaries the conditions in all patches are exactly the same, because there are no marginal patches that have to be treated separately. As a consequence, the metapopulation always has a unique spatially uniform equilibrium of local population abundances, which can be found by noting that if N^* is the size of each local population at such a uniform equilibrium, then the effective density in each patch is given by

$$\tilde{N}^* = N^* + 2\alpha N^*. \tag{12}$$

Since dispersal is passive a homogenous equilibrium must be characterized by the fact that the per capita reproductive output in each patch is 1, hence \tilde{N}^* can be found by solving the equation $f(\tilde{N}^*) = 1$. Therefore, $\tilde{N}^* = (1 + 2\alpha)N^* = \frac{\lambda - 1}{a}$, and hence

$$N^* = \frac{\lambda - 1}{a(1 + 2\alpha)}. \tag{13}$$

Substituting $N^* = \frac{\lambda - 1}{a(1 + 2\alpha)}$ into Eqs. (1)–(5) shows that the metapopulation state in which each local population has size N^* is indeed an equilibrium. The uniqueness of this homogenous equilibrium follows from the fact that the equations which define the equilibrium are linear.

It is well known that for metapopulations consisting of a number of identical single-species difference equations that are coupled only by passive dispersal, but not by any quasi-local ecological interactions, the stability of the unique spatially homogenous equilibrium is identical to the stability of the equilibrium of the local difference equation. More precisely, the spatially uniform metapopulation equilibrium state in which each local population is at the equilibrium of the local difference equation is stable if and only if this equilibrium is stable for the difference equation when considered in isolation, i.e. if and only if the difference equation taken in isolation does not exhibit periodic or chaotic fluctuations (Rohani et al., 1996).

In our metapopulation model, the coupling between local populations occurs both through passive dispersal and through quasi-local competition. However, the case in which coupling is by dispersal only is of course obtained by setting the interaction parameter $\alpha = 0$ in Eq. (2). In this case, the local population size at the spatially uniform equilibrium is $N^* = \frac{\lambda - 1}{a}$, i.e. equal to the carrying capacity K of the local habitat patches. Thus, since K is always a stable equilibrium for the Beverton–Holt difference equation, the spatially uniform metapopulation equilibrium is stable if $\alpha = 0$, independent of the dispersal rate d . We will now show that increasing the strength of the quasi-local interactions by increasing the parameter α can destabilize the spatially uniform equilibrium

For the stability analysis we write the dynamics of the metapopulation in vector form as

$$\begin{aligned} N_1(t + 1) &= g_1(N_1(t), \dots, N_m(t)) \\ &\vdots \\ N_i(t + 1) &= g_i(N_1(t), \dots, N_m(t)) \\ &\vdots \\ N_m(t + 1) &= g_m(N_1(t), \dots, N_m(t)), \end{aligned} \tag{14}$$

where the functions g_i are obtained by combining Eqs. (1), (2) and (5) as

$$\begin{aligned} &g_i(N_1(t), \dots, N_m(t)) \\ &= (1 - d) \frac{\lambda N_i(t)}{1 + a[N_i(t) + \alpha(N_{i-1}(t) + N_{i+1}(t))]} \\ &\quad + \frac{d}{2} \frac{\lambda N_{i-1}(t)}{1 + a[N_{i-1}(t) + \alpha(N_{i-2}(t) + N_i(t))]} \\ &\quad + \frac{d}{2} \frac{\lambda N_{i+1}(t)}{1 + a[N_{i+1}(t) + \alpha(N_i(t) + N_{i+2}(t))]} \end{aligned} \tag{15}$$

In these equations the various indices have to be adjusted to take the periodic boundary conditions into account. Expression (13) makes it clear that due to the quasi-local interactions and dispersal the dynamics of each local population N_i actually depends on its two

nearest neighbors on either side, i.e. on $N_{i-2}, N_{i-1}, N_{i+1}$, and N_{i+2} (as well as on N_i itself).

To determine the stability of the uniform equilibrium given by $(N_1, \dots, N_m) = (N^*, \dots, N^*)$ with $N^* = \frac{\lambda-1}{a(1+2\alpha)}$, we have to consider the Jacobian matrix J whose ij -th entry is the derivative of the function g_i with respect to N_j evaluated at the equilibrium:

$$J = \left(\frac{\partial g_i}{\partial N_j}(N^*, \dots, N^*) \right)_{i,j=1, \dots, m} \tag{16}$$

Taking into account that the local population size is $N^* = \frac{\lambda-1}{a(1+2\alpha)}$ at the uniform equilibrium, one calculates that

$$\begin{aligned} u &= \left. \frac{\partial g_i}{\partial N_i} \right|_* \\ &= (1-d) \left(1 - \frac{\lambda-1}{\lambda} \frac{1}{1+2\alpha} \right) - d \frac{\lambda-1}{\lambda} \frac{\alpha}{1+2\alpha}, \\ v &= \left. \frac{\partial g_i}{\partial N_{i-1}} \right|_* = \left. \frac{\partial g_i}{\partial N_{i+1}} \right|_* \\ &= \frac{d}{2} \left(1 - \frac{\lambda-1}{\lambda} \frac{1}{1+2\alpha} \right) - (1-d) \frac{\lambda-1}{\lambda} \frac{\alpha}{1+2\alpha}, \\ w &= \left. \frac{\partial g_i}{\partial N_{i-2}} \right|_* = \left. \frac{\partial g_i}{\partial N_{i+2}} \right|_* = -\frac{d}{2} \frac{\lambda-1}{\lambda} \frac{\alpha}{1+2\alpha} \end{aligned} \tag{17}$$

(where the notation $|_*$ means evaluated at the equilibrium N^*). We already know that $\frac{\partial g_i}{\partial N_j} = 0$ if $j \neq i-2, i-1, i, i+1, i+2$, and therefore the Jacobian matrix at the uniform equilibrium has the form

$$J = \begin{pmatrix} u & v & w & 0 & \dots & 0 & w & v \\ v & u & v & w & 0 & \dots & 0 & w \\ w & v & u & v & w & 0 & \dots & 0 \\ & & & \ddots & & & & \\ 0 & \dots & 0 & w & v & u & v & w & 0 & \dots & 0 \\ & & & \ddots & & & & & & & \\ 0 & \dots & \dots & 0 & w & v & u & v & w \\ w & 0 & \dots & \dots & 0 & w & v & u & v \\ v & w & 0 & \dots & \dots & 0 & w & v & u \end{pmatrix} \tag{18}$$

This is a circulant matrix, i.e. a matrix in which all rows are identical, except for a cyclic shift by one element that is applied to each row of the matrix to obtain the row below. The circulant property is simply a reflection of the periodic boundary conditions that we assumed for the metapopulation.

To determine the stability of the uniform equilibrium we have to calculate the dominant eigenvalue of the matrix J , i.e. the eigenvalue with largest absolute value. The equilibrium is stable if and only if the dominant eigenvalue has absolute value < 1 . It is well known (Davis, 1979) how to calculate all the eigenvalues of circulant matrices. Suppose first that $d = 0$, i.e. that

there is no dispersal, and that the number of patches m in the metapopulation, and hence the size of the matrix J , is even. If $d = 0$, then $w = 0$ in Eq. (15), so that each row of J has three adjacent entries. Because m is even, the dominant eigenvalue of J is then given by the sum over the absolute values of the three entries in a row (Davis, 1979). For $d = 0$ we have $u > 0$ and $v < 0$ in Eq. (15), because $\lambda > 1$ and $\alpha > 0$ by assumption. Therefore, the dominant eigenvalue ζ of J is given by

$$\begin{aligned} \zeta &= u - 2v \\ &= \left(1 - \frac{\lambda-1}{\lambda} \frac{1}{1+2\alpha} \right) + 2 \frac{\lambda-1}{\lambda} \frac{\alpha}{1+2\alpha} \\ &= \frac{4\lambda\alpha - 2\alpha + 1}{2\lambda\alpha + \lambda}. \end{aligned} \tag{19}$$

Therefore, ζ will be larger than 1 if $4\lambda\alpha - 2\alpha + 1 > 2\lambda\alpha + \lambda$, i.e. if $1 - 2\alpha > \lambda(1 - 2\alpha)$. This occurs as soon as $\alpha > \frac{1}{2}$.

In other words, if there is no dispersal, quasi-local competition destabilizes the spatially uniform equilibrium if the competitive impact on reproduction in a given patch from an individual from a neighboring patch exceeds one half of the impact of an individual from the given patch itself. This result holds for an even number m of patches, but one can show that it is also true for odd m as long as m is not very small. Moreover, qualitatively similar results hold if dispersal rates are non-zero. In fact, dispersal has a stabilizing effect, so that the strength of quasi-local competition needed to destabilize the uniform equilibrium is larger than $\frac{1}{2}$ if dispersal rates are non-zero. Nevertheless, with non-zero dispersal the equilibrium still becomes unstable if α is large enough. More precisely, it can be shown by a detailed analysis of the Jacobian matrix J that the critical α -value $\alpha^*(d)$ needed for destabilization of the spatially uniform equilibrium in a chain of habitat patches with dispersal rate d is given by

$$\alpha^*(d) = \frac{\lambda - 1 + 2d}{2d(1 - 3\lambda) + 2(\lambda - 1)}, \tag{21}$$

where λ is the basic growth rate in the Beverton–Holt model (4). This expression holds as long as dispersal rates are not too large. In Fig. 1 the critical α -values are plotted as a function of dispersal rates d .

Thus we have obtained our first main result: in a metapopulation consisting of a chain of identical habitat patches each of which is coupled to its two nearest neighbors by quasi-local competition and dispersal, the spatially uniform equilibrium state becomes unstable if quasi-local competition is strong enough. Similar results also hold when different boundary conditions are used, although the systems then tend to become analytically intractable. For example, in a metapopulation with

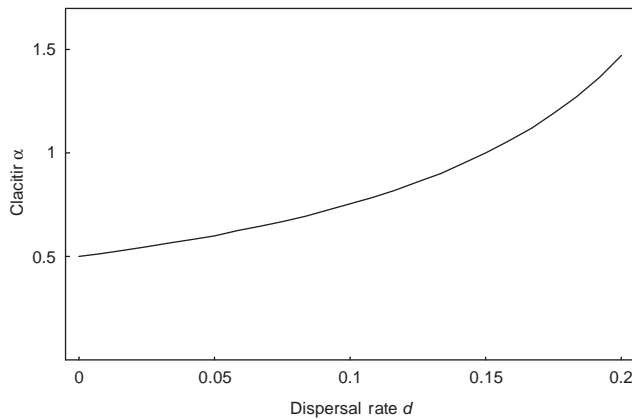


Fig. 1. Strength of quasi-local competition destabilizing the spatially uniform steady state in a chain of local habitats as a function of dispersal rates. The critical α -value above which the uniform equilibrium becomes unstable is given by Eq. (15) and shown here for $\lambda = \exp(2.3)$ as a function of the dispersal rate d .

absorbing boundary conditions there is always an equilibrium state that corresponds to the uniform equilibrium for periodic boundary conditions. However, due to the absorbing boundaries this equilibrium is not spatially uniform anymore. Nevertheless, it is still true that while dispersal alone does not destabilize this equilibrium, the equilibrium becomes unstable if quasi-local competition is strong enough.

What we have seen so far is that quasi-local competition can break the symmetry in an intrinsically homogenous metapopulation by destabilizing the spatially uniform equilibrium. The question we now address is: what are the ecological consequences of this broken symmetry, i.e. what is the dynamics of the metapopulation when the uniform equilibrium is unstable?

To study the dynamics of spatially non-uniform patterns of population abundance we have used extensive numerical simulation, which revealed two main results. First, the metapopulation always converges to an equilibrium state and never exhibits periodic or chaotic dynamics. Thus, the intrinsic stability provided by the local Beverton–Holt difference equation always ensures convergence to a necessarily spatially non-uniform stable equilibrium if the uniform equilibrium is unstable. The second result, however, is that for large metapopulations there are a large number of different spatially non-uniform equilibrium states which are locally stable for the metapopulation dynamics. The different stable equilibria tend to have small basins of attraction so that the final equilibrium pattern of local abundances that is attained by the metapopulation depends critically on the initial distribution of local population sizes in the various habitat patches. Fig. 2 shows examples of different equilibrium configurations to which the metapopulation converges

depending on the initial conditions. One source for the plethora of different stable equilibrium states is that if an equilibrium is spatially non-uniform one obtains a new equilibrium by shifting the given one along the chain of local populations. For example, if there is no dispersal, and if the number of local populations m is even, then one obvious non-uniform equilibrium configuration of local abundances is to have local population sizes of 0 and K , the local carrying capacity, alternate across the metapopulation. This can obviously be done in two different ways (depending on whether the even numbered local populations are at 0 or at K), and hence this spatially non-uniform equilibrium corresponds to two different equilibrium states of the metapopulation. Note that the difference between the two equilibria is biologically not trivial since they induce very different population sizes in a given habitat patch.

Most non-uniform equilibrium configurations are much less symmetrical than the one alternating between 0 and K just described, and therefore most non-uniform equilibria give rise to many other equilibria by shifting them across the metapopulation. This is particularly true in large metapopulations consisting of many patches. In fact, the number of different stable equilibria can be very large. This is illustrated in Fig. 3, where we have plotted the cumulative number of different equilibrium states attained as a function of the number of trials in which the metapopulation dynamics was started using different initial conditions. Fig. 3 illustrates that the number of different equilibrium attractors can become very large if the metapopulation consists of many patches. In the next section we will see that this result is also true for metapopulations that extend over two spatial directions and consist of a two-dimensional grid of local populations. In the subsequent section we then discuss the significance of the existence of a multitude of attractors for the ecological dynamics in metapopulations that are subject to environmental noise.

2.2. Spatially two-dimensional metapopulations: grids of local habitat patches

Here we extend the result of the previous section to metapopulations in which the local populations occupy a two-dimensional lattice of habitat patches. We assume, as before, that quasi-local competition and dispersal occur between neighboring patches, and we thus have to specify what constitutes a neighborhood of a given local population. Typical choices for neighborhoods consist of taking either the four or the eight patches that are closest to a given site on the lattice. In addition, we again have to specify boundary conditions, which can for example be periodic or absorbing. However, our extensive numerical simulations showed

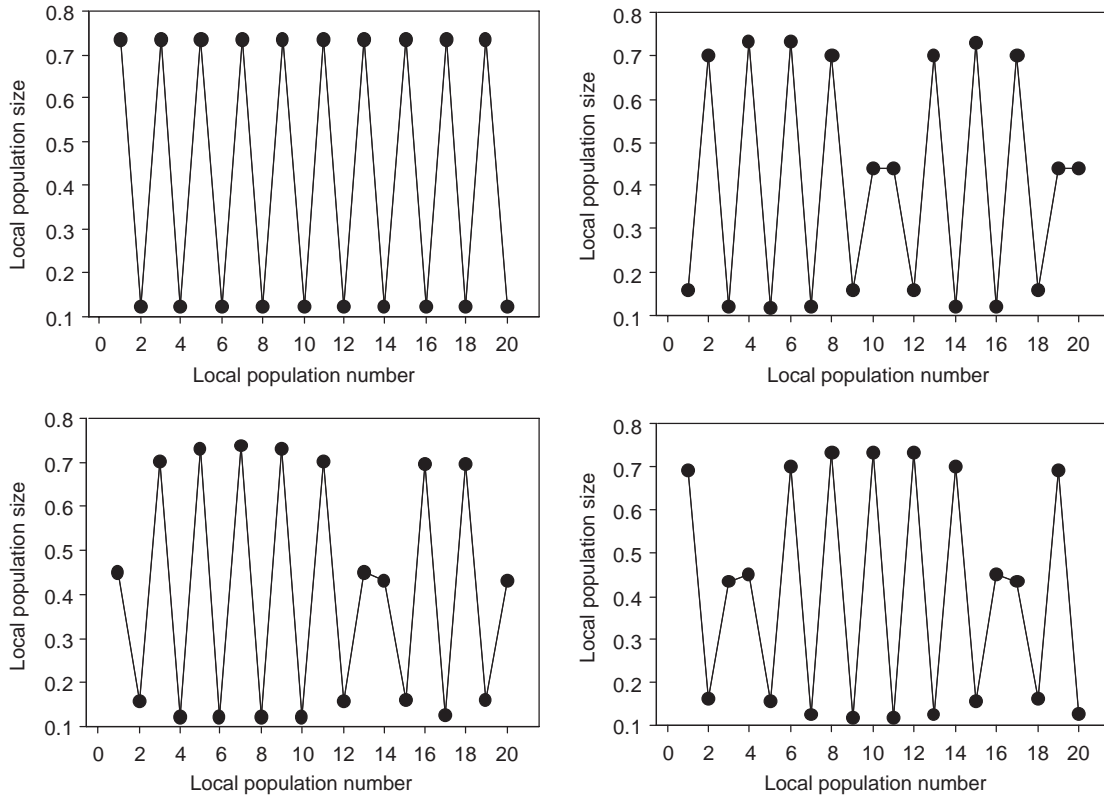


Fig. 2. Different spatially non-uniform equilibrium attractors for a chain of 20 local habitats in which the strength of quasi-local competition is strong enough to destabilize the spatially uniform equilibrium. The top left panel shows the alternating steady state described in the text. The remaining panels show attractors with a less regular pattern of local population abundance. The two lower panels show attractors that are obtained from each other by a permutation of the local habitats. Note that despite this permutational symmetry the steady state of a given local population may be very different in the two attractors. Parameter values are $\lambda = \exp(2.3)$, $\alpha = 0.9$, and $d = 0.05$.

that all these choices have little qualitative effect on the results reported below.

We again assume that all habitat patches are ecologically identical, and that the local ecological dynamics in each patch are described by a Beverton–Holt equation f . Thus, if $N_{ij}(t)$ is the population size in the patch with coordinates (i, j) on the metapopulation lattice ($i, j = 1, \dots, n$, where n^2 is the size of the square lattice), then we have

$$\begin{aligned}
 N'_{ij}(t) &= N_{ij}(t) \cdot f(\tilde{N}_{ij}(t)) \\
 &= N_{ij}(t) \frac{\lambda}{1 + a\tilde{N}_{ij}(t)},
 \end{aligned}
 \tag{22}$$

where $N'_{ij}(t)$ is the population size in patch (i, j) after reproduction, but before dispersal in year t , f is the per capita reproductive output, and $\tilde{N}_{ij}(t)$ is the effective population density impinging on reproduction in patch (i, j) in year t . In analogy to the one-dimensional metapopulation of the previous section we assume that the effective population size is a function of the population sizes in patch (i, j) itself and of the population sizes in neighboring patches. For example, if the four nearest neighbors constitute the neighborhood

of a local population, then

$$\begin{aligned}
 \tilde{N}_{ij}(t) &= N_{ij}(t) + \alpha(N_{i-1j}(t) + N_{i+1j}(t) + N_{ij-1}(t) \\
 &\quad + N_{ij+1}(t)).
 \end{aligned}
 \tag{23}$$

Following the same arguments as in the case of a one-dimensional chain of habitats, it is easy to see that if the quasi-local ecological interactions occur because individuals in a given patch forage a fraction p of the time in neighboring patches, then the parameter α is given by

$$\alpha = \frac{p}{k(1-p)},
 \tag{24}$$

where k is the number of neighboring patches involved. Since foraging outside a given patch is advantageous for the individuals reproducing in that patch, it follows again that a large range of α -values is biologically feasible.

In addition to quasi-local interactions we again assume that passive dispersal from and to nearest neighbors completes the dynamics in a given year. For example, with four nearest neighbors we have

$$\begin{aligned}
 N_{ij}(t+1) &= (1-d)N'_{ij}(t) + \frac{d}{4}(N'_{i-1j}(t) + N'_{i+1j}(t) \\
 &\quad + N'_{ij-1}(t) + N'_{ij+1}(t)).
 \end{aligned}
 \tag{25}$$

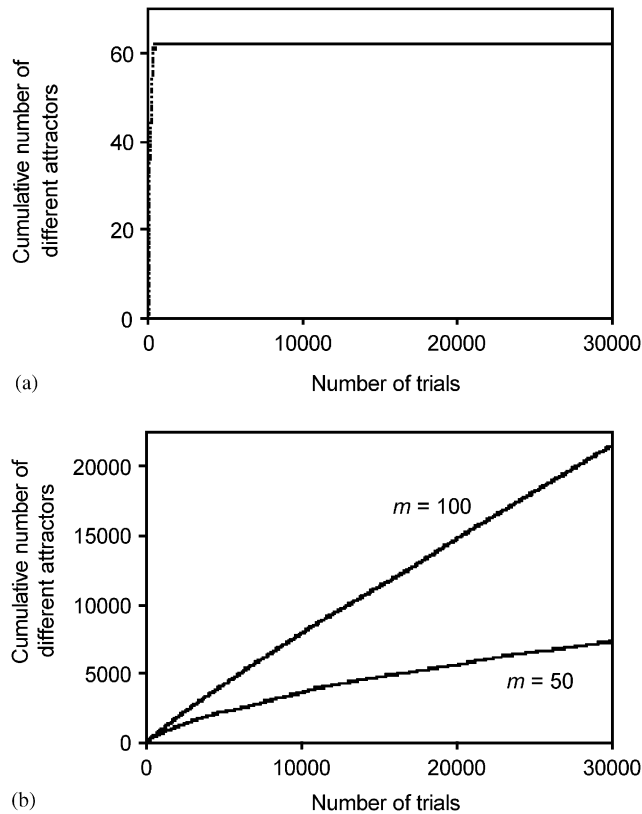


Fig. 3. Cumulative number of different spatially non-uniform attractors in chains of local populations of different length. In each case, the metapopulation dynamics were run 30,000 times, each time from different, randomly chosen starting conditions, until an equilibrium state was reached. The program then counted the number of different equilibria attained during the course of the 30,000 trials. (a) With $m = 20$ local habitats, the cumulative number of different attractors saturates at 62. (b) With $m = 50$ and 100 local habitats, the cumulative number does not saturate and instead increases steadily. The increase is steeper with more habitats. This indicates that the number of different attractors would further increase with larger numbers of trials, suggesting the presence of a huge total number of different attractors. Parameter values used were $\lambda = \exp(2.3)$, $\alpha = 0.7$ and $d = 0.07$.

Eqs. (22) and (24) have to be appropriately adjusted for marginal patches and if different neighborhoods are used. With periodic boundary conditions there is again a spatially uniform equilibrium state in which all local populations have size N^* , which can be obtained by solving the equation $f(\tilde{N}_{ij}) = 1$. For example, with neighborhoods consisting of the four nearest neighbors we have $\tilde{N}_{ij} = N^* + 4\alpha N^*$ at the equilibrium, hence solving $\frac{\lambda}{1 + a\tilde{N}_{ij}(t)} = 1$ yields

$$N^* = \frac{\lambda - 1}{a(1 + 4\alpha)}. \tag{26}$$

If there is no quasi-local competition, i.e. if $\alpha = 0$, then $N^* = K$, the carrying capacity of the Beverton–Holt equation, and the local populations are only coupled by dispersal. In this case it is again true that the stability of

the spatially uniform equilibrium is exactly the same as the stability of the equilibrium K for the dynamics of an isolated local population (Jansen and Lloyd, 2000). In particular, in the case considered here the uniform equilibrium is always stable, because K is a stable equilibrium for the Beverton–Holt dynamics. However, quasi-local competition can again destabilize this equilibrium.

This can be seen by noting that one can approximate the spatially two-dimensional metapopulation by a spatially one-dimensional description if one numbers the patches consecutively by going through the rows of the lattice one after the other. In a square lattice with n patches in each of n rows, the patch at position (i, j) is then assigned the number $in + j$. In this way one obtains a spatially one-dimensional metapopulation consisting of a chain of habitat patches as used in the previous section, except that now the coupling between different patches in this chain does not only occur between nearest neighbors, but also between distant patches. For example, if in a square lattice, N_{ij} receives competition from N_{i-1j} , N_{i+1j} , N_{ij-1} and N_{ij+1} , then the local population N_{in+j} in the corresponding one-dimensional chain of habitats receives competition from its two immediate neighbors N_{in+j-1} and N_{in+j+1} , as well as from $N_{(i-1)n+j}$ and from $N_{(i+1)n+j}$, i.e. from populations that are n steps away on either side in the chain. Therefore, the analysis of the two-dimensional lattice case reduces to an analysis of a one-dimensional chain of habitats with a more general form of couplings than considered in the previous section. Similar remarks apply for other choices of neighborhoods on the square lattice.

It must be noted that this one-dimensional description is not a completely faithful representation of the two-dimensional metapopulation. For example, in a square lattice of size $m = n^2$ with periodic boundary conditions and local neighborhoods consisting of four neighboring patches, every patch with index $(1, j)$ or (n, j) has two neighbors on the same row as the patch itself, but to obtain the one-dimensional description one of these neighbors is replaced by a corresponding patch on an adjacent row. However, for our results this discrepancy only has visible effects for metapopulations with a very small number of patches. We also note that it is straightforward to show that the Jacobian of the two-dimensional model is exactly given by a block circulant matrix. We have chosen to use the approximate representation given above rather than the exact block circulant description as the former allows us to reduce the calculation to the one-dimensional case considered earlier. Furthermore, the technique of reducing the stability analysis of a two-dimensional system to a one-dimensional one seems to be of some intrinsic interest.

For the stability analysis the reduction to a one-dimensional chain of patches implies that the Jacobian matrix J at the spatially uniform equilibrium in which

all local populations have size N^* has the same form as (17), except that now not only entries adjacent to the diagonal entries are non-zero, but also entries that are some distances away, reflecting the fact that in the reduced descriptions interactions occur between distant local populations. For example, when considering interactions with the four nearest neighbors on a square lattice with $d = 0$, so that there is no dispersal, and with periodic boundaries, every local population interacts, through quasi-local competition, with four other patches in the reduced one-dimensional description: two of these are its adjacent neighbors, and two are n steps away on either side in the chain. (Note that if dispersal is non-zero, then interactions occurs with more local populations, some of which are even further away from the focal patch in the chain.) Therefore, the derivative of the function g_i describing the population dynamics of a patch through

$$N_i(t + 1) = g_i(N_1(t), \dots, N_m(t)), \tag{27}$$

(where $m = n^2$ is the size of the lattice, and hence the length of the corresponding one-dimensional chain) is non-zero only with respect to $N_{i-n}, N_{i-1}, N_i, N_{i+1}$, and N_{i+n} , and at the uniform equilibrium N^* we have

$$u = \left. \frac{\partial g_i}{\partial N_i} \right|_* = 1 - \frac{\lambda - 1}{\lambda} \frac{1}{1 + 4\alpha},$$

$$v = \left. \frac{\partial g_i}{\partial N_{i-n}} \right|_* = \left. \frac{\partial g_i}{\partial N_{i-1}} \right|_* = \left. \frac{\partial g_i}{\partial N_{i+1}} \right|_* = \left. \frac{\partial g_i}{\partial N_{i+n}} \right|_*$$

$$= - \frac{\lambda - 1}{\lambda} \frac{\alpha}{1 + 4\alpha}. \tag{28}$$

Therefore, the Jacobian matrix J at the uniform equilibrium has the form

$$J = \begin{pmatrix} 0 & \dots & 0 & v & \underbrace{0 \dots 0}_{n-1} & v & u & v & \underbrace{0 \dots 0}_{n-1} & v & 0 & \dots & 0 \end{pmatrix}. \tag{29}$$

With periodic boundaries J is again a circulant matrix, so that all the rows have the same form as the one indicated in (28), except for a cyclic shift depending on the position of the focal patch. In particular, all rows have the same non-zero entries. If $m = n^2$ is even, it follows as in the previous section that the dominant eigenvalue of J is simply the sum of all the absolute values of the entries in a given row of J . Since $u > 0$ and $v < 0$ because $\lambda > 1$ and $\alpha > 0$, the dominant eigenvalue ζ of J is then

$$\zeta = u - 4v,$$

$$= \frac{8\lambda\alpha - 4\alpha + 1}{4\lambda\alpha + \lambda}. \tag{30}$$

It easily follows that $\zeta > 1$ if

$$\alpha > \frac{1}{4}. \tag{31}$$

Thus, in the absence of dispersal the uniform equilibrium becomes unstable when the relative competitive impact of individuals from neighboring patches on the lattice exceed $\frac{1}{4}$ that from individuals living in the same patch. More generally, for small non-zero dispersal rates d a detailed analysis of the Jacobian matrix J yields the following formula for the critical α -value $\alpha^*(d)$ needed for destabilization of the spatially uniform equilibrium in a square metapopulation with periodic boundary conditions

$$\alpha^*(d) = \frac{\lambda - 1 + 2d}{2d[1 - \lambda(k + 1)] + k(\lambda - 1)}. \tag{32}$$

Here k is the number of neighbors in the local neighborhood, i.e. $k = 4$ or $k = 8$. Note that for $k = 2$ Eq. (31) reduces to the corresponding Eq. (20) for chains of habitat patches. It follows from Eq. (31) that dispersal has a stabilizing effect, but that quasi-local competition can destabilize the spatially uniform equilibrium also for non-zero dispersal rates, and that the more interacting neighboring populations there are, the more likely it is that the symmetry of the uniform equilibrium will be broken. This is illustrated in Fig. 4. Similar results can be obtained for other types of boundary conditions, although in such cases the corresponding equilibrium that is destabilized by quasi-local competition is not strictly spatially uniform anymore, because the marginal patches are intrinsically different from all the other patches in the metapopulation.

The instability of the uniform equilibrium again raises the question about the ensuing dynamics. The results for two-dimensional lattice metapopulations are qualitatively similar to those of spatially one-dimensional metapopulations described in the previous section: the lattice metapopulations always converge to a spatially

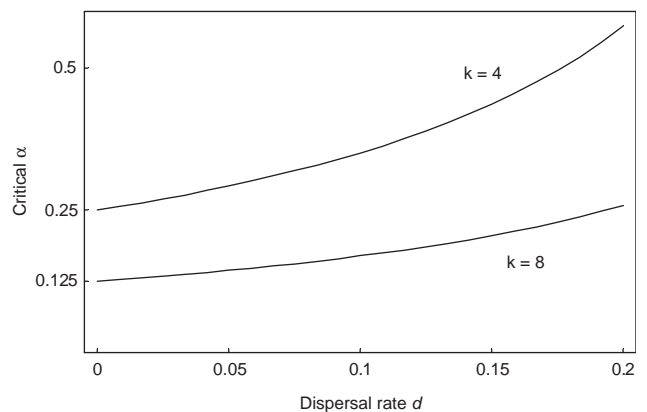


Fig. 4. Strength of quasi-local competition destabilizing the spatially uniform steady state in a square lattice of local habitats as a function of dispersal rates. The critical α -value above which the uniform equilibrium becomes unstable is given by Eq. (25) and shown here for $\lambda = \exp(2.3)$ as a function of the dispersal rate d for two different neighborhood sizes, $k = 4$ and 8 .

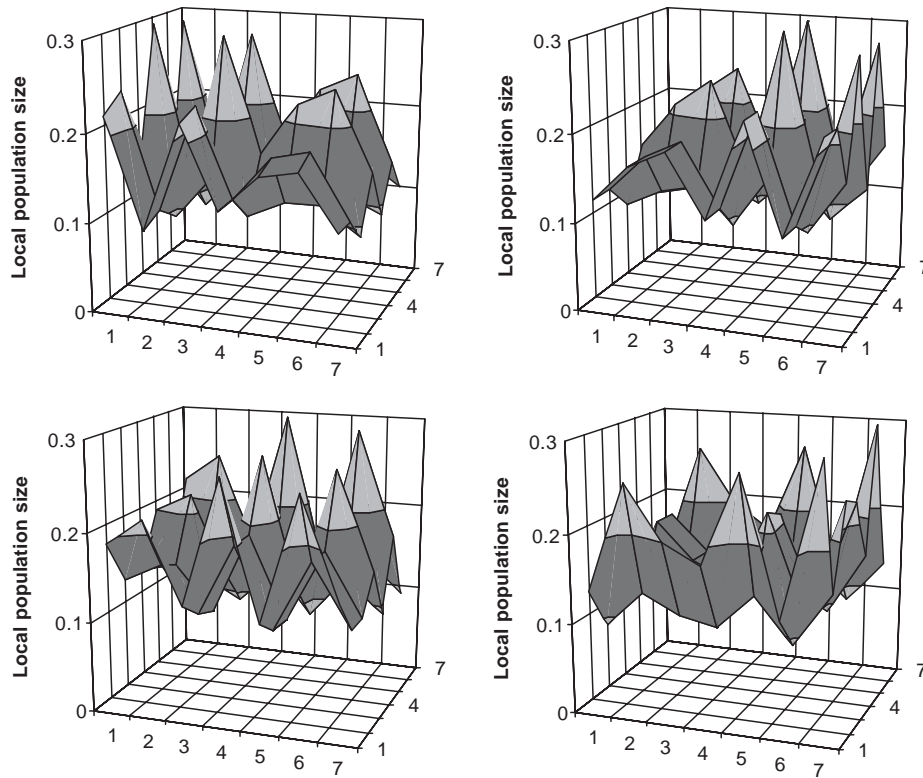


Fig. 5. Different spatially non-uniform equilibrium attractors for a square lattice of 7×7 local habitats in which the strength of quasi-local competition is strong enough to destabilize the spatially uniform equilibrium. All attractors have irregular patterns of local population abundance. The two top panels show attractors that are obtained from each other by a permutation of the local habitats. Note that despite this permutational symmetry the steady state of a given local population may be very different in the two attractors. Parameter values were $\lambda = \exp(2.3)$, $\alpha = 0.7$ and $d = 0.05$.

non-uniform equilibrium and never exhibit non-equilibrium dynamics. However, there is typically a large number of different equilibrium states to which the metapopulation may converge depending on initial conditions. Examples of possible configurations of local population abundances at non-uniform equilibria are shown in Fig. 5.

In Fig. 6 we have plotted the numbers of different ecological attractors reached in 10,000 trials started from different initial conditions as a function of the strength of quasi-local competition α . This is shown for different boundary conditions in the metapopulation and for different dispersal rates. The results indicate that there can be huge numbers of different attractors. For example, with zero dispersal and $\alpha = 0.6$, which corresponds to spending approximately 55% of the time foraging in neighboring patches, we get more than 5000 different attractors out of 10,000 trials, which suggests that the total number of different attractors (which could be obtained only from a much larger number of trials) is indeed exceedingly large. In Fig. 6 we also illustrate the fact that the occurrence of large numbers of different attractors is not an artefact of periodic boundary conditions in the metapopulation.

Due to the decreased symmetry in the system the number of attractors tends to be lower in metapopulations with absorbing boundaries than in metapopulations with periodic boundaries. However, with absorbing boundaries the number of attractors also becomes very large even for moderate values of α as the system size increases. Fig. 6 also shows that dispersal tends to have a stabilizing effect in the sense that for higher dispersal rates the number of attractors increases more slowly with α .

We have presented above detailed results for the Beverton–Holt model with quasi-local competition, and it may be appropriate here to describe briefly the results we obtained for other models with quasi-local competition. We have studied discrete-time models with quasi-local competition in which the reproductive output f is of Ricker (1954) or Bellows (1981) type, rather than of Beverton–Holt type. For parameter values which yield stable local dynamics the results we obtain are exactly analogous to those obtained using the Beverton–Holt models, namely: (i) for any values of α and d the system converges to a stable equilibrium; (ii) for $d = 0$ and $\alpha < \frac{1}{2}$, in one dimension, or $\alpha < \frac{1}{4}$ in two dimensions with four neighbors, or $\alpha < \frac{1}{8}$ in two dimensions with eight

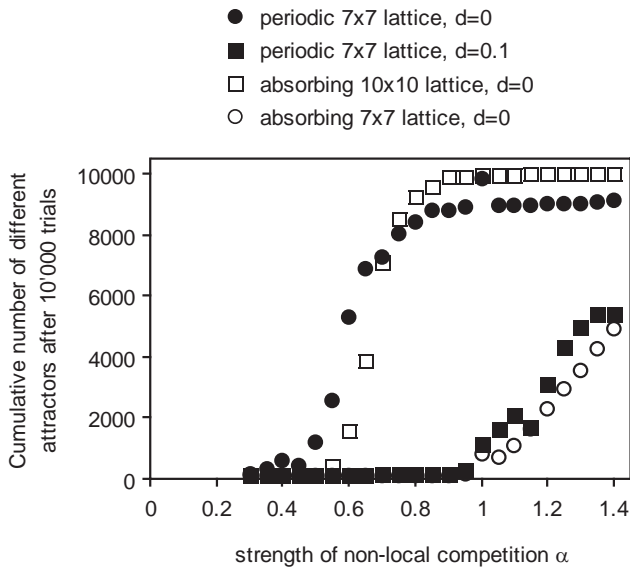


Fig. 6. Cumulative numbers of different spatially non-uniform attractors as a function of the strength of quasi-local competition α . For equidistant values of α (increments of 0.05) the metapopulation dynamics were run 10,000 times, each time from different, randomly chosen starting conditions, until an equilibrium state was reached. For each value of α the simulation counted the number of different equilibria attained during the 10,000 trials. This was done for lattices with different boundary conditions and for different dispersal rates. With absorbing boundaries the number of attractors is generally smaller than with periodic boundary conditions (cf. filled triangles and circles). However, even with absorbing boundaries the number of attractors becomes very large as the lattice size is increased (open squares). In general, the number of attractors decreases as dispersal rates increase (cf. filled circles and squares), but even for relatively high dispersal rates the number of attractors becomes very large for high intensities of quasi-local competition. The parameter $\lambda = \exp(2.3)$ in all simulations.

neighbors, the system converges to a unique homogeneous stable equilibrium; (iii) if α is sufficiently large to break the homogeneous equilibrium then there exist, in general, a large number of stable inhomogeneous equilibria. Thus the features we have described above for the Beverton–Holt model with quasi-local competition seem to be quite general features of any single-species difference equation with quasi-local competition.

We have also considered continuous-time single-species ecological models with quasi-local competition. The simplest example of such a model, which describes a metapopulation in one dimension, is the following system of Lotka–Volterra type. If we let $X_i(t)$ denote the population size in patch i as a function of time t , then the dynamics of the corresponding metapopulation is given by the following system of ordinary differential equations:

$$\frac{dX_i}{dt} = rX_i[1 - a(\alpha X_{i-1} + X_i + \alpha X_{i+1})]. \quad (33)$$

This equation has obvious analogs in two dimensions with four and eight neighbors. Here we have neglected

dispersal, however, this can easily be included by adding a suitable dispersal term. The stability analysis of this system (without dispersal) can be carried out in complete analogy with that given above for the discrete-time model. We find (in one dimension with periodic boundaries) that for $\alpha < \frac{1}{2}$ there is a unique spatially homogeneous stable equilibrium. For $\alpha > \frac{1}{2}$ this homogenous equilibrium becomes unstable and the system always converges to an inhomogeneous stable equilibrium. Numerical integration of the system (32) shows that for $\alpha > \frac{1}{2}$ there are, in general, for both periodic and absorbing boundary conditions, many distinct inhomogeneous stable equilibria. The obvious analogs of these results hold in two dimensions. That is, we find that points (i)–(iii) above hold for this continuous time system with quasi-local competition. This does not come as a surprise, since the discrete-time Beverton–Holt equation that we used for most of our analysis is homologous, i.e. dynamically equivalent, to the continuous time logistic equation on which system (32) is based (Yodzis, 1989). Hence, it appears that these features are very general properties of single-species population models, in both discrete and continuous time, with quasi-local competition.

The central theme of this paper has been that quasi-local competition can lead to the destabilization of the homogenous equilibrium and the appearance of a multitude of inhomogeneous stable equilibria. This phenomenon can have important consequences for the population dynamics of the system in the presence of noise. When there are many different attractors the basins of attraction of each one of them is likely to be small. In this case, environmental stochasticity can easily perturb the metapopulation from one basin of attraction to another. As a consequence, the dynamics of the metapopulation will continually shift between convergence to different equilibrium attractors and hence exhibit persistent fluctuations. Therefore, small amounts of environmental stochasticity can have profound effects on the dynamics of metapopulations with quasi-local competition. In the next section we explore in more detail the nature of the population fluctuations that environmental noise induces.

2.3. Random walks in attractor space

We introduce environmental stochasticity into the local population dynamics given by Eq. (4) and by Eq. (21) for the spatially one and two-dimensional metapopulations, respectively, by assuming that the deterministic per capita reproductive output described by these equations is multiplied by a random variable with mean 1. Thus, in a two-dimensional lattice metapopulation the per capita reproductive output in

a local population N_{ij} in year t is

$$f(\tilde{N}_{ij}(t)) = \frac{\lambda}{1 + a\tilde{N}_{ij}(t)} \exp(x_{ij}(t)), \quad (34)$$

where $\tilde{N}_{ij}(t)$ is, as before, the effective density impinging on reproduction in year t in the patch considered, and where $x_{ij}(t)$ is a random number that is drawn from a Gaussian distribution with mean 0 and variance σ independently for each patch in each year. This form of incorporating noise into the model ensures that biologically meaningless, negative noise terms do not occur as multipliers of the per capita reproductive output. However, for small values of the parameter σ , as we will use below, the noise multipliers are still approximately normally distributed with mean 1 and variance σ .

If the deterministic Eq. (21) is replaced by its stochastic version (33) in lattice metapopulations in which there is no quasi-local competition (i.e. in which $\alpha = 0$, so that the only coupling between local populations occurs through dispersal) then the uniform equilibrium that is the only attractor in the corresponding deterministic models is constantly perturbed by the environmental stochastic fluctuations. As a consequence the local population sizes as well as the total metapopulation undergo persistent fluctuations, but these fluctuations simply reflect repeated returns to the unique uniform equilibrium after each perturbation. As a consequence, the size of the population fluctuations is comparable to the size of the environmental perturbations. In particular, local fluctuations are small when the environmental perturbations are small, and the fluctuations at the scale of the whole metapopulation are even smaller because fluctuations on the local scale tend to average out on the global scale.

A very different picture emerges in metapopulations in which local populations are coupled through quasi-local competition, and in which the strength of the quasi-local competition α is large enough to destabilize the uniform metapopulation equilibrium. In this case there are typically very many different, spatially non-uniform equilibrium attractors for the metapopulation dynamics, as we have shown in the previous sections. It is helpful to view each attractor as a point in m -space, where the dimension m is the number of habitat patches in the metapopulation. For example, a uniform equilibrium would then correspond to a point on the diagonal in m -space. Each attractor has associated with it its basin of attraction, and m -space is divided into mutually disjoint basins of attraction. Since there are typically many attractors, there are also very many basins of attraction, and each one of them is typically small.

It is now easy to imagine what happens when the system is constantly perturbed by small amounts of environmental noise, as described by Eq. (33). While the metapopulation is converging to one of the many attractors an environmental perturbation can easily

throw the system off its path and into the basin of attraction of a different attractor, to which it starts to converge. Since the new attractor may correspond to a very different distribution of local population sizes, the corresponding change in population size can be large, both on the local and on the global scale. Repeated operation of this process can therefore lead to substantial and persistent fluctuations in both local and total population size. These fluctuations are thus due to an interaction between environmental stochasticity and the deterministic dynamical properties of the metapopulation. In the form of a multitude of different equilibrium attractors the deterministic metapopulation dynamics provides the raw material which allows environmental noise to induce a random walk in which the system constantly jumps from one attractor to another. In other words, due to environmental noise, the system performs a random walk in the space of all attractors.

This random walk in attractor space is reflected in the dynamics of the local populations comprising the metapopulation, as is shown in Fig. 7a and b. The local population sizes undergo large fluctuations with a distinct ‘random walk’ pattern. Recall that in the purely deterministic case the equilibrium to which the metapopulations converge depends sensitively on the initial configuration of local population abundances. In stochastic metapopulations, this dependence on initial conditions results in a dependence of the fluctuating population trajectories on the initial conditions. Thus, the random walk dynamics of local populations can depend critically on the initial distribution of local population sizes. To illustrate this, panels a and b in Fig. 7 show the dynamics of a particular local population in a metapopulation undergoing a random walk in attractor space. The series of randomly generated environmental perturbations is exactly the same in the two cases, and the only difference between the panels is that the metapopulation dynamics was started from different initial conditions. Clearly, for extended periods of time the local population trajectories may follow very different paths for different initial conditions. This phenomenon is reminiscent of the sensitive dependence on initial conditions of chaotic systems, but occurs here not due to chaos in the underlying deterministic system, but due to the existence of many different attractors.

Fluctuations in the total population size of the metapopulation of which the local population shown in Fig. 7a is a part are shown in Fig. 7c. Here the random walk properties are less apparent, because local fluctuations tend to average out on the scale of the total metapopulation. Nevertheless, the time series still has some attributes of a random walk (see below), in contrast to the time series of population fluctuations in metapopulations in which there is no quasi-local competition ($\alpha = 0$), and in which environmental noise

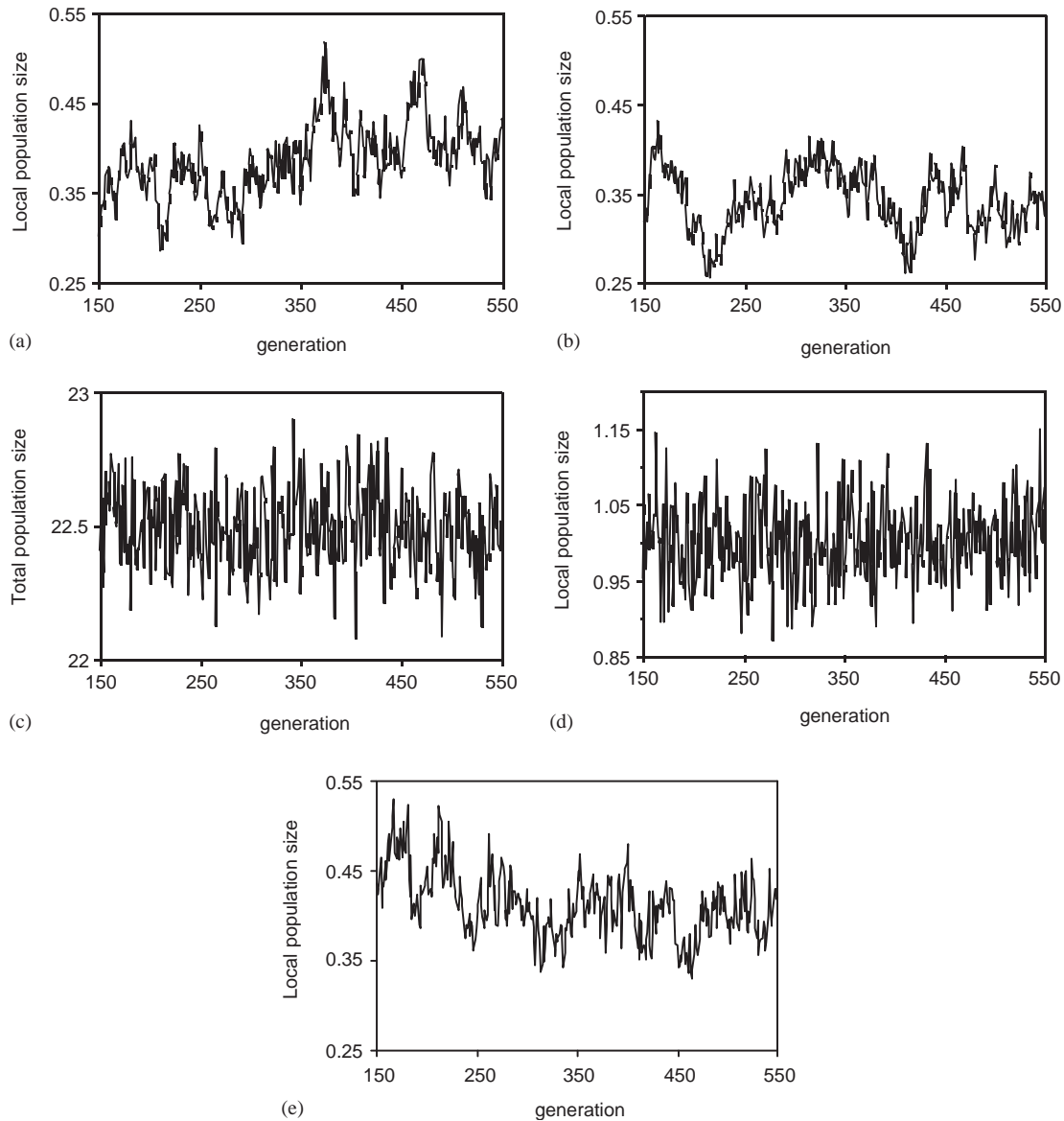


Fig. 7. Time series for local and total population sizes in stochastic metapopulations. (a) Time series of a local population that is part of a 10×10 square lattice metapopulation with periodic boundaries that performs a random walk in attractor space due to environmental perturbations. The local population undergoes large fluctuations with a distinct pattern reflecting the random walk in attractor space. (b) Same as (a) except that a different initial configuration of local population abundance was used to simulate the dynamics, for which exactly the same random environmental perturbations were used as in (a). This shows the sensitive dependence of the trajectories on the initial conditions in the stochastic systems. (c) The corresponding time series of the total population size of the metapopulation. (d) Time series of a local population in a metapopulation in which there is no quasi-local competition ($\alpha = 0$). In this case the local populations fluctuate around the steady state corresponding to the spatially uniform metapopulation equilibrium, and the local fluctuations have the same magnitude and frequencies as the environmental perturbations. (e) Same as (a) but with absorbing rather than periodic boundary conditions for the metapopulation. This shows that random walk fluctuations in local population size are not an artefact of periodic boundary conditions. Parameter values were $\lambda = \exp(2.3)$, $\alpha = 0.5$ and $d = 0.05$, except for (d) in which $\alpha = 0$. For the environmental noise, a normal distribution with variance $\sigma = 0.05$ was used in Eq. (25).

therefore only induces perturbations around the spatially uniform attractor. Fig. 7d shows the fluctuations of a local population in a stochastic metapopulation without quasi-local competition. The local fluctuations simply track the environmental noise around the spatially uniform steady state, and the qualitative difference to the dynamics shown in Fig. 7a and b is apparent. Finally, Fig. 7e illustrates that random walks

of local population densities are not artefacts of periodic boundary conditions in the metapopulation. In Fig. 7e everything was exactly the same as in Fig. 7a, except that absorbing rather than periodic boundary conditions were used. Again, the local populations undergo large fluctuations in a distinct random walk pattern.

In general, if a dynamical system performs a random walk in its state space it tends to explore more and more

remote regions of this space as time progresses. As a consequence, the variation in the states attained by the system increases with the time window over which the states are sampled. Thus, in a system performing a random walk long-term fluctuations are larger than short-term fluctuations. As a consequence the power spectrum of a time series of the system's state tends to be red-shifted, i.e. it tends to have more power at low frequencies. In fact, the power spectrum of random walks typically obey power laws with negative exponents, so that the logarithm of the power is a linear function with negative slope of the logarithm of the frequency. For example, random walk models of Brownian motion yield a power law with exponent -2 (Hastings and Sugihara, 1993).

In the present case, in which environmental noise is superimposed on a deterministic framework consisting of many different basins of attraction, stochastic displacements and deterministic convergence to attractors in state space interact in a way that is dictated by the geometry of the basins of attraction, which may be very complicated. For example, the overall size of the basins of attraction can be different for different attractors, and any given

basin of attraction can have very irregular boundaries. Despite these complications one might expect that a random walk in the set of attractors leads to fluctuations whose power spectrum obeys a power law. Fig. 8a shows the power spectrum for the time series of the local population size whose dynamics are shown in Fig. 7a. Clearly, the power spectrum obeys a power law with distinctly negative exponent, showing a prominent red shift in the local fluctuations. This red shift is due to intermittent switches between convergence to different attractors, switches that are also apparent in the corresponding time series (Fig. 7a). Power spectra obeying power laws with negative exponents can be found for local populations in the stochastic metapopulation models whenever the underlying deterministic model has many different equilibrium attractors.

The corresponding power spectrum for the time series of the total population size of the metapopulation (time series shown in Fig. 7c) is shown in Fig. 8b. This spectrum also appears to follow a power law with negative exponent. However, the red shift is less apparent than in the local populations, and the

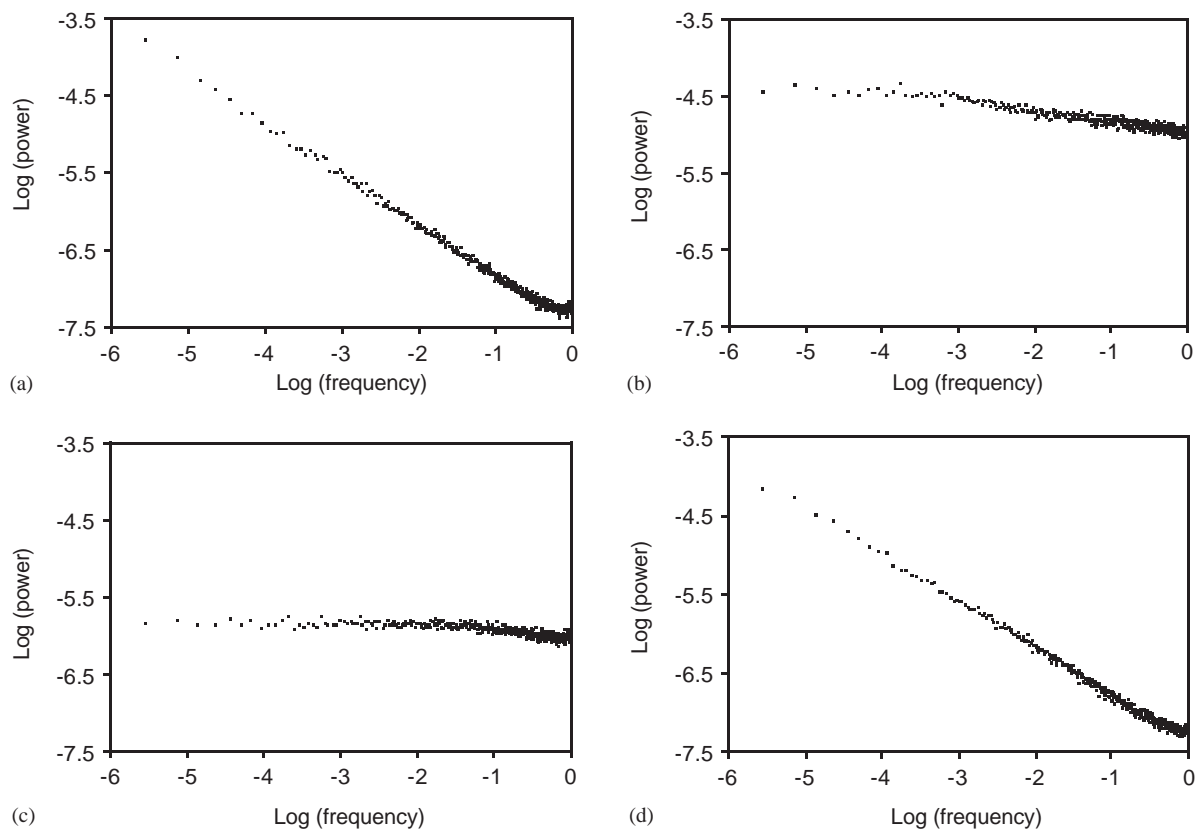


Fig. 8. Power spectra of the time series of local and total population sizes. (a) Power spectrum of the local population shown in Fig. 7a. The power spectrum is red-shifted and obeys a power law with negative exponent of approximately 0.62. (b) Power spectrum of the total population size of the metapopulation shown in Fig. 7c. The power spectrum is slightly red-shifted and obeys a power law with negative exponent of ca. 0.13. (c) Power spectrum of the local population shown in Fig. 7d. The power spectrum reflects the white spectrum of the environmental noise. (d) Power spectrum of the local population shown in Fig. 7e. The local fluctuations are again governed by a power law, with a negative exponent of ca. 0.58. For all panels power spectra were calculated as average of the spectra of 200 time series of length 1024 time steps obtained consecutively in a single run of the corresponding metapopulation dynamics.

corresponding exponent is closer to 0. Thus, despite its red shift the spectrum of the total population is similar to that of white noise, because the local fluctuations tend to average out on the global scale, so that the global fluctuations reflect the white power spectrum assumed for the environmental noise. The white fluctuations of the environmental noise are even better matched in stochastic metapopulations without quasi-local competition, in which environmental perturbations induce fluctuations around the spatially uniform equilibrium attractor. This can be seen in Fig. 8c, which shows the power spectrum of the time series of the local population shown in Fig. 7d. In this power spectrum very short frequencies still have slightly lower power than expected for white noise, which is likely due to the interaction between the white environmental noise and the non-linear Beverton–Holt dynamics of the local populations (for an interesting treatment of power spectra resulting from the interaction between environmental perturbations and non-linear deterministic dynamics see Kaitala et al., 1997). Finally, Fig. 8d shows the power spectrum of the time series of the local population shown in Fig. 7e, for which a metapopulation with absorbing rather than periodic boundaries was used. Again, the power spectrum obeys a power law with distinctly negative exponent, showing that the power law behavior is not an artefact of periodic boundary conditions, and that quasi-local competition can also lead to red-shifted population fluctuations in metapopulations with absorbing boundaries.

3. Discussion

In this paper we have presented a new way of modeling metapopulations consisting of a number of habitat patches occupied by local populations with discrete generations. Traditional models of such metapopulations assume that the ecological coupling between local populations occurs only through migration of individuals between local habitats. The novelty of our approach consists of assuming that coupling of local populations also occurs through quasi-local ecological interactions. For example, in the particular model considered here we assumed that competition for resources occurs not only between individuals with a given patch, but also to some extent between individuals reproducing in different (but neighboring) patches, an assumption that seems reasonable in many circumstances in which individuals leave their home territory in search of food.

Formally, single-species models with discrete time and space consist of a number of coupled difference equations and are examples of ‘coupled map lattices’. Coupled map lattices in which all the local difference equations are identical and in which the coupling occurs

through passive dispersal have been studied extensively (Kaneko, 1998). In this case, if the local difference equations exhibit stable equilibrium dynamics, then the total metapopulation also has a unique stable equilibrium, and nothing interesting happens unless the local dynamics are complicated when considered in isolation.

We have shown that the situation changes completely when the coupling between a number of identical difference equations occurs through quasi-local competition between individuals from neighboring habitat patches. In this case, the spatially uniform metapopulation equilibrium, in which all local populations have the same density, can become unstable even if the local difference equations exhibit a stable equilibrium in isolation.

Our results are threefold. First, destabilization of the spatially uniform metapopulation equilibrium occurs as soon as the quasi-local competition is strong enough. Second, if the uniform equilibrium is unstable, then the metapopulation always converges to a spatially non-uniform equilibrium distribution of population abundances, and the number of different non-uniform equilibrium attractors can be exceedingly large. Third, even small amounts of environmental noise can induce a random walk in the set of all attractors, thus leading to persistent population fluctuations with a red-shifted power spectrum. All these results are qualitatively independent of the spatial dimension of the metapopulation, the boundary conditions assumed, and the neighborhoods chosen for the quasi-local interactions.

It is not hard to find examples of spatially structured ecological systems for which the assumptions of local population dynamics but quasi-local competition dynamics are plausibly satisfied. Different systems illustrate the various ways in which the basic scenario of quasi-local competition may be realized in detail. Birds provide one class of examples of this type of ecological behavior. Dunnocks, for instance, occupy territorial regions within which they carry out most of their foraging. However, detailed study of dunnock territories has shown that different territories often overlap (Davies, 1992), suggesting the strong possibility of competition between populations in neighboring territories. Insects provide another possible class of examples. In social insects such as ants the colonies occupy territories and regularly engage in competitive activities with neighboring colonies, which often extends to robbing neighboring nests of food (Wilson, 1971; Holldobler and Wilson, 1990). Plants provide a particularly interesting class of systems in which quasi-local competition appears to be occurring. Since water is a diffusible resource it follows that the effect of a plant taking up water locally is to remove water from the surrounding regions. Thus the greater the rate of water uptake by a given plant, the lower the quantity of water available for neighboring plants. Therefore, in such

cases, even though the resource uptake is local, quasi-local competition results from the diffusion of the resource. The strength of quasi-local competition is determined by the rate of water uptake relative to the average amount of water per unit volume in the soil. Hence, quasi-local competition should be stronger in semi-arid regions. According to our model of metapopulation dynamics with quasi-local competition we would expect spatial pattern formation to occur under conditions of strong quasi-local competition. Interestingly, vegetation patterns consisting of stationary irregular mosaics are found in many semi-arid regions (White, 1970; Belsky, 1986; Klausmeier, 1999). These observed patterns are in good qualitative agreement with the results obtained from our model. It should be noted, however, that most natural populations do of course not exist in isolation and instead interact with populations of other species, e.g. through competition or predation. This is for example true for most of the plant populations in semi-arid regions mentioned above. Thus, the single-species models presented in this paper are but a first step in the study of the role of quasi-local interactions for the dynamics of spatially structured ecosystems. Nevertheless, we expect that the basic mechanism that quasi-local ecological interactions can induce spatial pattern formation will also be present in systems comprising interspecific interactions of various types. In this sense we expect our findings to be robust, an expectation that should be corroborated by future research.

Thus, our findings may shed new light on the main ecological question of what causes the spatial and temporal patterns of population abundance observed in the real world. Spatial pattern formation in population abundance is a classic theme in metapopulation theory, and apart from the rather trivial observation that spatial heterogeneity in productivity can induce a corresponding heterogeneity in population abundance, the main theoretical explanations for ecological pattern formation come from reaction diffusion models (e.g. Holmes et al., 1994). Stable spatially inhomogeneous population distributions have also been found in spatially structured models for interspecific competition, both in discrete time (Karlin and McGregor, 1972) and in continuous time (Levin, 1974, 1979). In all these models spatially inhomogeneous equilibrium distributions are more likely to occur when dispersal rates are low, which is in accordance with our results. However, these models are limited in the sense that spatial coupling only occurs through dispersal, and that they always require interactions between two or more species in order to produce non-uniform patterns of abundance. In one of the rare previous single-species models for spatial pattern formation Sasaki (1997) has shown in a model with continuous space that quasi-local competition within a single species can produce spatially non-

uniform equilibria if the average interaction radius is sufficiently different from the average dispersal distance. However, in contrast to the theory presented here his model does not yield a multitude of different attractors, and instead the population always converges to a given spatial wave of population abundance. In our models it is also true that quasi-local competition should be relatively strong while dispersal rates should be relatively small for the uniform equilibrium to become unstable. However, once this equilibrium is unstable there exist a multitude of potentially very irregular spatial patterns of abundance to which the metapopulation can converge (cf. Figs. 2 and 5). Therefore, even in the absence of any intrinsic differences between habitats quasi-local ecological interactions have the potential to induce complicated patterns of abundance, the details of which may vary significantly between different metapopulations not because of different ecological conditions, but because different metapopulations are likely to be on different trajectories and hence to converge to different equilibrium attractors. Thus, quasi-local ecological interactions may be very important in determining the spatial patterns of population abundance.

Traditionally, there are two main explanations for temporal patterns of population abundance. In the first scenario population fluctuations show a random pattern and are mainly due to stochastic perturbations from a deterministic equilibrium. In the second scenario, population fluctuations are due to overcompensating ecological interactions that lead to complex deterministic dynamics. Our results suggest a third alternative, in which complex population fluctuations arise due to an interaction between environmental noise and deterministic population dynamics. Interactions between stochastic and deterministic mechanisms in ecological systems have been studied before (e.g. Rand and Wilson, 1991; Petchey et al., 1997), however, the novel aspect of our scenario is that large population fluctuations occur even if the environmental noise is small and despite the fact that the deterministic dynamics always exhibit a stable equilibrium. Because the deterministic system has many different equilibrium attractors environmental noise induces a random walk between different basins of attraction and leads to red-shifted population time series, in which the variance in population size increases with the length of the time period over which population sizes are sampled.

Red-shifted population time series have attracted considerable attention, because even though red shifts seem to be common in time series of natural populations (Pimm and Redfearn, 1988; Arino and Pimm, 1995), it appears to be difficult to account for them in ecological models (Cohen, 1995, but see Blarer and Doebeli, 1996). For example, chaotic dynamics never yield a power law with negative exponent over the whole range of frequencies. In contrast, the power spectrum of time

series obtained from the interaction of stochastic and deterministic processes in our models can show distinct power law behavior with negative exponents (Fig. 8), thus suggesting a new mechanism for generating red-shifted power laws in ecological time series.

In sum, the theory presented here reiterates the potential importance of spatial structure for ecological processes and proposes new mechanisms for the emergence of non-uniform spatial patterns of abundance and for the persistence of complicated temporal population fluctuations. The concept of quasi-local ecological interactions lies at the basis of this theory, and it is easy to envisage a number of potentially interesting extensions of the theory in which the inclusion of quasi-local interactions could lead to new insights. Two extensions that appear to be particularly interesting consist of considering quasi-local interactions in ecological contexts other than competition, e.g. in metapopulation models for predator–prey interactions, and of considering quasi-local interactions in metapopulation models in which the local deterministic dynamics can be complicated even when habitat patches are considered in isolation. In such models it will be interesting to see how dispersal and quasi-local competition interact to determine the spatio-temporal dynamics of the system. These investigations will likely lead to further advances in understanding the role of spatial structure for ecological processes.

References

- Arino, A., Pimm, S.L., 1995. On the nature of population extremes. *Evol. Ecol.* 9, 429–443.
- Bascompte, J., Sole, R.V. (Eds.), 1998. *Modeling Spatiotemporal Dynamics in Ecology*. Springer, Berlin.
- Bellows, T.S., 1981. The descriptive properties of some models for density dependence. *J. Anim. Ecol.* 50, 139–156.
- Belsky, A.J., 1986. Population and community processes in a mosaic grassland in the Serengeti, Tanzania. *J. Ecol.* 74, 841–856.
- Blarer, A., Doebeli, M., 1996. In the red zone. *Nature* 380, 589–590.
- Cohen, J.E., 1995. Unexpected dominance of high frequencies in chaotic non-linear population models. *Nature* 378, 610–612.
- Comins, H.N., Hassell, M.P., May, R.M., 1992. The spatial dynamics of host-parasitoid systems. *J. Anim. Ecol.* 61, 735–748.
- Davies, N.B., 1992. *Dunnock Behaviour and Social Evolution*. Oxford University Press, Oxford.
- Davis, P.J., 1979. *Circulant Matrices*. Wiley, New York.
- Diamond, J.M., May, R.M., 1977. Species turnover rates on islands: dependence on census interval. *Science* 197, 266–270.
- Dieckmann, U., Law, R., Metz, J.A.J. (Eds.), 2000. *The Geometry of Ecological Interactions: Simplifying Spatial Complexity*. Cambridge University Press, Cambridge.
- Doebeli, M., 1995. Dispersal and dynamics. *Theor. Popul. Biol.* 47, 82–106.
- Doebeli, M., Ruxton, G.D., 1998. Stabilization through spatial pattern formation in metapopulations with long-range dispersal. *Proc. Roy. Soc. Lond. B* 265, 1325–1332.
- Earn, D.J.D., Levin, S.A., Rohani, P., 2000. Coherence and conservation. *Science* 290, 1360–1364.
- Gilpin, M.E., Hanski, I.A. (Eds.), 1997. *Metapopulation Biology: Ecology, Genetics, and Evolution*. Academic Press, New York.
- Gyllenberg, M., Soderbacka, G., Ericsson, S., 1993. Does migration stabilize local population dynamics? Analysis of a discrete metapopulation model. *Math. Biosci.* 118, 25–49.
- Hassell, M.P., 1974. Density dependence in single species populations. *J. Anim. Ecol.* 44, 283–296.
- Hassell, M.P., Lawton, J.H., May, R.M., 1976. Patterns of dynamical behaviour in single-species populations. *J. Anim. Ecol.* 45, 471–486.
- Hassell, M.P., Comins, N.H., May, R.M., 1991. Spatial structure and chaos in insect population dynamics. *Nature* 353, 255–258.
- Hassell, M.P., Comins, N.H., May, R.M., 1994. Species coexistence and self-organizing spatial dynamics. *Nature* 370, 290–292.
- Hastings, A., 1992. Age dependent dispersal is not a simple process: density dependence, stability, and chaos. *Theor. Popul. Biol.* 41, 388–400.
- Hastings, A., 1993. Complex interactions between dispersal and dynamics: lessons from coupled logistic equations. *Ecology* 74, 1362–1372.
- Hastings, H.M., Sugihara, G., 1993. *Fractals. A User's Guide for the Natural Sciences*. Oxford University Press, Oxford.
- Holldobler, B., Wilson, E.O., 1990. *The Ants*. Springer, Berlin.
- Holmes, E.E., Lewis, M.A., Banks, J.E., Veit, R.R., 1994. Partial differential equations in ecology: spatial interactions and population dynamics. *Ecology* 75, 19–29.
- Holt, R.D., McPeck, M.A., 1996. Chaotic population dynamics favors the evolution of dispersal. *Am. Nat.* 148, 709–718.
- Jansen, V.A.A., Lloyd, A.L., 2000. Local stability analysis of spatially homogeneous solutions of multi-patch systems. *J. Math. Biol.* 41, 232–252.
- Kaitala, V., Ylikarjula, J., Ranta, E., Lundberg, P., 1997. Population dynamics and the colour of environmental noise. *Proc. Roy. Soc. Lond. B* 264, 943–948.
- Kaneko, K., 1998. Diversity, stability, and metadynamics: remarks from coupled map studies. In: Bascompte, J., Sole, R.V. (Eds.) (Eds.), *Modeling Spatiotemporal Dynamics in Ecology*. Springer, Berlin, pp. 27–46.
- Karlin, S., McGregor, J., 1972. Polymorphisms for genetic and ecological systems with weak coupling. *Theor. Popul. Biol.* 3, 210–238.
- Keitt, T.H., Lewis, M.A., Holt, R.D., 2001. Allee effects, invasion pinning, and species' borders. *Am. Nat.* 157, 203–216.
- Kimura, M., 1953. 'Stepping-stone' model of population. *Ann. Rep. Nat. Inst. Genet. J.* 3, 62–63, reprinted. In: Kimura, M. (Ed.), *Population Genetics, Molecular Evolution, and the Neutral Theory*. University of Chicago Press, Chicago, 1994, p. 133.
- Kimura, M., Weiss, G.H., 1964. The stepping stone model of population structure and the decrease of genetic correlation with distance. *Genetics* 49, 561–576.
- Klausmeier, C.A., 1999. Regular and irregular patterns in semiarid vegetation. *Science* 284, 1826–1828.
- Leslie, P.H., 1957. An analysis of the data for some experiments carried out by Gause with populations of the protozoa *Paramecium aurelia* and *P. caudatum*. *Biometrika* 44, 314–327.
- Levene, H., 1953. Genetic equilibrium when more than one niche is available. *Am. Nat.* 87, 331–333.
- Levin, S.A., 1974. Dispersal and population interactions. *Am. Nat.* 108, 207–228.
- Levin, S.A., 1979. Non-uniform stable solutions to reaction-diffusion equations: applications to ecological pattern formation. In: Haken, H. (Ed.), *Pattern Formation by Dynamical Systems and Pattern Recognition*. Springer, Berlin, pp. 210–222.
- Levin, S.A., Segel, L., 1976. Hypothesis for the origins of plankton patchiness. *Nature* 259, 659.
- Levins, R., 1970. Extinction. In: Gerstenhaber, M. (Ed.), *Some Mathematical Questions in Biology*. American Mathematical Society, Providence, RI.

- Lloyd, A.L., 1995. The coupled logistic map—a simple model for the effects of spatial heterogeneity on population dynamics. *J. Theor. Biol.* 173, 217–230.
- Maynard Smith, J., Slatkin, M., 1973. The stability of predator–prey systems. *Ecology* 54, 384–391.
- Mimura, M., Murray, J.D., 1978. On a diffusive prey–predator model which exhibit patchiness. *J. Theor. Biol.* 75, 249–262.
- Neuhauser, C., Pacala, S.W., 1999. An explicitly spatial version of the Lotka–Volterra model with interspecific competition. *Ann. Appl. Probab.* 9, 1226–1259.
- Petchey, O.L., Gonzalez, A., Wilson, H.B., 1997. Effects on population persistence: the interaction between environmental noise colour, intraspecific competition and space. *Proc. Roy. Soc. Lond. B* 264, 1841–1847.
- Pimm, S.L., Redfearn, A., 1988. The variability of animal populations. *Nature* 334, 613–614.
- Rand, D.A., Wilson, H.B., 1991. Chaotic stochasticity—a ubiquitous source of unpredictability in epidemics. *Proc. Roy. Soc. Lond. B* 246, 179–184.
- Ricker, W.E., 1954. Stock and recruitment. *J. Fish. Res. Bd. Can.* 11, 559–623.
- Rohani, P., May, R.M., Hassell, M.P., 1996. Metapopulations and equilibrium stability: the effects of spatial structure. *J. Theor. Biol.* 181, 97–109.
- Ruxton, G.D., 1996. Density-dependent migration and stability in a system of linked populations. *Bull. Math. Biol.* 58, 643–660.
- Sasaki, A., 1997. Clumped distribution by neighborhood competition. *J. Theor. Biol.* 186, 415–430.
- Scheuring, I., Janosi, I.M., 1996. When two and two make four: a structured population without chaos. *J. Theor. Biol.* 178, 89–97.
- Skellam, J.G., 1951. Random dispersal in theoretical populations. *Biometrika* 38, 196–218.
- Turing, A.M., 1952. The chemical basis of morphogenesis. *Philos. Trans. Roy. Soc. Lond. B* 237, 37–72.
- Utida, S., 1967. Damped oscillations of population density at equilibrium. *Res. Popul. Ecol.* 9, 1–9.
- White, L.P., 1970. Brousse Tigree patterns in southern Niger. *J. Ecol.* 58, 549–553.
- White, A., Begon, M., Bowers, R.G., 1996. Host–pathogen systems in a spatially patchy environment. *Proc. Roy. Soc. Lond. B* 263, 325–332.
- Wilson, E.O., 1971. *The Insect Societies*. Harvard University Press, Cambridge, MA.
- Wright, S., 1943. Isolation by distance. *Genetics* 28, 114–138.
- Yodzis, P., 1989. *Introduction to Theoretical Ecology*. Harper and Row, Cambridge.