

# Evolution of complex dynamics in spatially structured populations

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Dynamics of populations depend on demographic parameters which may change during evolution. In simple ecological models given by one-dimensional difference equations, the evolution of demographic parameters generally leads to equilibrium population dynamics. Here we show that this is not true in spatially structured ecological models. Using a multi-patch metapopulation model, we study the evolutionary dynamics of phenotypes that differ both in their response to local crowding, i.e. in their competitive behaviour within a habitat, and in their rate of dispersal between habitats. Our simulation results show that evolution can favour phenotypes that have the intrinsic potential for very complex dynamics provided that the environment is spatially structured and temporally variable. These phenotypes owe their evolutionary persistence to their large dispersal rates. They typically coexist with phenotypes that have low dispersal rates and that exhibit equilibrium dynamics when alone. This coexistence is brought about through the phenomenon of evolutionary branching, during which an initially uniform population splits into the two phenotypic classes.

**Keywords:** density dependence; dispersal; competition; evolutionary branching; chaos; metapopulation

## 1. INTRODUCTION

Even though many ecological models exhibit complex dynamics for certain parameter regions (e.g. May & Oster 1976; Hastings & Powell 1991; Hastings *et al.* 1993; McCann & Yodzis 1994; Ruxton 1996; Higgins *et al.* 1997), it is an open question whether the demographic traits representing these parameters in natural populations actually evolve towards these regions.

The findings of positive Lyapunov exponents in several empirical data sets are an indication that ecological systems may show complex dynamic behaviour (Turchin & Taylor 1990; Ellner & Turchin 1995). Locating real populations in the parameter space of models, Dennis *et al.* (1995) found population dynamics within the cyclic range (see also Witteman *et al.* 1990). Chaotic dynamics of natural populations were found for example in predator–prey systems (Hanski *et al.* 1993), epidemics in measles (Sugihara & May 1990; Rand & Wilson 1991), or in insect populations (Costantino *et al.* 1997).

Evolutionary models studying individual selection on demographic parameters showed both the propensity to avoid chaotic dynamics (Stokes *et al.* 1988; Doebeli & Koella 1995; Ebenman *et al.* 1996) and to exhibit chaotic dynamics under special conditions (Gatto 1993; Ferriere & Gatto 1993; Ferriere & Fox 1995). Ferriere & Gatto (1993) argued that age structure makes the evolution of chaos more likely to occur. However, such structured models may also lead to the evolution of more stable

population dynamics (Ebenman *et al.* 1996). A common argument against the evolution to chaotic dynamics is that a population will then frequently approach low densities and will therefore be more susceptible to extinction (Thomas *et al.* 1980; Berryman & Millstein 1989). However, it is rather easy to give examples of chaotic dynamics that are bounded well away from zero population densities (e.g. Hastings & Powell 1991). In addition, if the population is divided into subpopulations connected by dispersal, Allen *et al.* (1993) showed that although chaotic dynamics may increase extinction risk on the local level it may reduce extinction risk on the global level. Of course, this does not necessarily imply that individual selection leads to complex dynamics. In fact, it was shown by Doebeli & Koella (1995) that the evolution of demographic parameters in simple difference equation models typically leads to parameter values that induce equilibrium dynamics. Here we extend these studies to the analysis of spatially structured population models. One demographic parameter, the evolution of which has been studied extensively in such models, is the dispersal rate (e.g. Johnson & Gaines 1990; McPeck & Holt 1992; Holt & McPeck 1996; Johst & Brandl 1997a; Doebeli & Ruxton 1997). Besides dispersal the sensitivity to local crowding is another way to respond to the detrimental effects of high densities. Therefore, in our model, dispersal is also allowed to evolve, but in addition we include a further evolving trait: the sensitivity of an individual to the local density which characterizes the density dependence of its reproductive rate and hence influences the complexity of the local ecological dynamics. Density

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dependence is a consequence of the intraspecific competition for limiting resources: the reproductive rate of an individual in isolation is greater than that of an individual in a crowded habitat. Density dependence also has population dynamic consequences: compensating density dependence leads to equilibrium dynamics, while overcompensating density dependence may induce complex population dynamics.

We argue that the way that individuals locally respond to limiting resources may be linked to their dispersal behaviour. Consequently, we change the perspective of the discussion about the evolution of complex dynamics from the local to the global scale: can individual selection favour phenotypes with complex dynamics when the population is spatially structured and both the competitive behaviour within the habitat and the dispersal rate between the habitats are evolving traits?

## 2. THE MODEL

### (a) *The metapopulation model*

We envisage a metapopulation consisting of a number of habitats that are arranged on a square  $n \times n$  lattice. Time is discrete, and in each generation, reproduction in each habitat is followed by dispersal between habitats. The local reproductive dynamics of a phenotype  $p$  in habitat  $h$  are described by the difference equation

$$M_p^h(t) = f_p(N^h(t)) \times N_p^h(t). \quad (1)$$

Here  $N_p^h(t)$  and  $M_p^h(t)$  are the densities of phenotype  $p$  in habitat  $h$  before and after reproduction in generation  $t$ , and  $N^h(t) = \sum_p N_p^h(t)$  is the total density in habitat  $h$ , i.e. the sum of the densities of all phenotypes present in this habitat, at the beginning of generation  $t$ . This implies that the reproductive output within the habitat is influenced by the total density, but not how the various phenotypes in the habitat contribute to this total density. The fitness function  $f_p(N^h(t))$  in equation (1) gives the density dependent per capita reproductive output of phenotype  $p$  in habitat  $h$  and has the form

$$f_p(N^h(t)) = \frac{R}{1 + (R-1) \left( \frac{N^h(t)}{K^h(t)} \right)^{b_p}}. \quad (2)$$

Equation (2) implies that the demographic parameter  $b$  may vary between phenotypes, and that the carrying capacity in habitat  $h$  at time  $t$ ,  $K^h(t)$ , may vary between habitats and over time. The fitness function, equation (2), was originally introduced by Maynard Smith & Slatkin (1973) and proposed by Bellows (1981) to describe a wide range of field data. The parameter  $R$  is the intrinsic growth rate, i.e. the reproductive rate at low density, which we assume to be the same for all phenotypes. All phenotypes compete for the same resource within a habitat. The parameter  $b_p$  determines the strength of density dependence that a phenotype  $p$  experiences (e.g. Getz 1996; Pulliam 1986). Figure 1 shows how different values of  $b$  result in qualitatively different shapes of the fitness function given by equation (2). Phenotypes with small  $b_p$  start to experience density effects on their reproductive success already at low densities, but they do not suffer severely from high densities beyond the carrying capacity. In contrast, for phenotypes with large

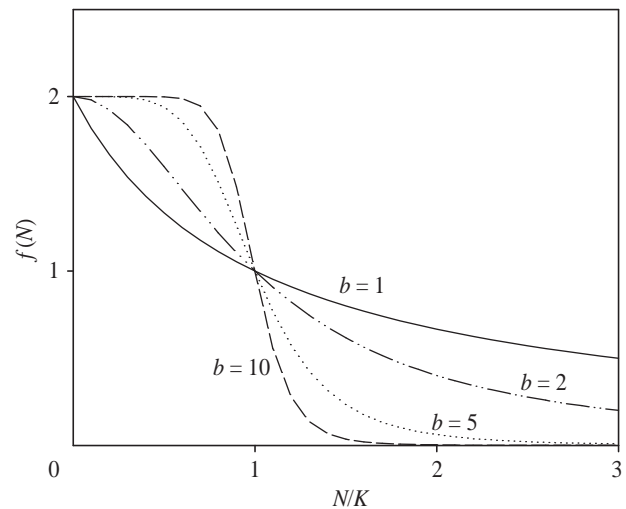


Figure 1. Reproductive rate  $f(N)$  corresponding to equation (2). The different curves show  $f(N)$  for different values of  $b$  at given  $R=2$ .

$b_p$  the effects of population density are quite small until the carrying capacity is reached, beyond which the effects are severe and lead to overcompensation.

In each generation, local reproductive dynamics are followed by dispersal between nearest-neighbour habitats. Dispersal of phenotype  $p$  is characterized by the dispersal rate  $m_p$ . Thus, the number of emigrants of a particular phenotype  $p$  in habitat  $h$  and in generation  $t$  is given by  $m_p \times M_p^h(t)$ . For the results presented in this paper we assumed that these emigrants are uniformly distributed over the four nearest-neighbour habitats in the metapopulation. However, qualitatively similar results are obtained if we use global dispersal, in which emigrants from each patch are distributed uniformly over the whole metapopulation. We further assume that dispersers experience no mortality during dispersal. For the results presented below we used periodic boundary conditions for the square lattice of habitats representing the metapopulation, but again similar results are obtained with absorbing boundary conditions.

While spatial structure is given by the square lattice of local habitats, we additionally introduce spatial environmental heterogeneity by assuming that the carrying capacities  $K^h(t)$  in equation (2) differ between habitats. Finally, we assume that these carrying capacities also vary with time, representing temporal environmental fluctuations. Thus, for the results reported below we first assigned to each habitat a uniformly randomly chosen carrying capacity  $C^h$  in the interval (500, 1500), and then we chose  $K^h(t)$  in each habitat  $h$  and in each generation  $t$  from a uniform distribution in the range  $C^h \pm \Delta \times C^h$ , where the parameter  $\Delta$  determines the amount of temporal variability present in the system.

### (b) *Evolutionary dynamics*

We are interested in the joint evolution of the demographic parameters  $b$  and  $m$ . As described above, the parameter  $b$  can be taken as a measure of the sensitivity of an individual to the density within the habitat, and hence of its local competitive behaviour. A measure for

the dynamic complexity as a function of  $b$  and  $R$  is given by the slope  $c$  of the function  $N \times f(N)$  at the equilibrium  $N^* = K$  (Doebeli & Koella 1995):

$$c = 1 - b \times \frac{R-1}{R}. \quad (3)$$

If  $|c| < 1$  the equilibrium is stable, if  $|c| > 1$  the system exhibits the period-doubling route to chaos (May & Oster 1976). The carrying capacity itself does not appear in equation (3), hence the carrying capacities have no influence on whether the dynamics in a habitat have a stable equilibrium or not. Note that even within large  $|c|$  there is the possibility of windows of cyclic dynamics within the chaotic range. For a given  $R$ , a small value for  $b$  leads to small values of  $|c|$ , while large  $b$ -values lead to large values of  $|c|$ . We monitor the evolution of the competitive behaviour described by  $b$  by monitoring the parameter  $c$ . We denote phenotypes with  $|c| < 1$  as equilibrium phenotypes, and phenotypes with  $|c| > 1$  as complex phenotypes, depending on the dynamics they would have when isolated in a single habitat patch. The evolution of dispersal is simply monitored by the parameter  $m$ , which describes the probability that an individual leaves a habitat in a given generation.

To simulate evolutionary dynamics, we start out with a given phenotype  $p = (b_p, m_p)$  and run the ecological dynamics through time. In each generation a mutant appears in the metapopulation with a certain probability, the mutation rate (equal to 0.005 per generation in our simulations). If a mutation occurs, we first select one of the phenotypes already present in the metapopulation with probabilities equal to their frequencies in the population. Once an existing phenotype is selected, we choose the mutant phenotype from a bivariate Gaussian distribution with means  $b_p$  and  $m_p$  of the selected phenotype  $p$  and variances equal to a certain proportion of the means (5% in our simulations). We then initialize this new mutant with a small density on a randomly chosen patch (Doebeli & Ruxton 1997). In order to prevent the number of phenotypes from growing indefinitely, we sporadically purge the metapopulation by removing all phenotypes with densities lying below a certain threshold ( $10^{-8}$  in our simulations). By monitoring the phenotypes with frequencies lying above, say, 5%, at any given time we can then follow the evolutionary dynamics.

### 3. RESULTS

Evolutionary dynamics have been studied numerically for a wide range of cases. We found that under certain environmental conditions the evolution of complex phenotypes is possible. Figure 2 shows a typical case for evolutionary dynamics in a spatially heterogeneous and temporally varying environment. Starting with a small dispersal rate  $m$  and small dynamic complexity  $|c|$  there is first a period of gradual evolution to larger  $m$  whereas dynamic complexity  $|c|$  splits rather early into two phenotypic clusters: one retaining a low complexity ( $|c| \approx 0.8$ ) and one with further increasing complexity. Around 20 000 time-steps the complexity of this latter phenotypic cluster exceeds the cyclic range (a rough

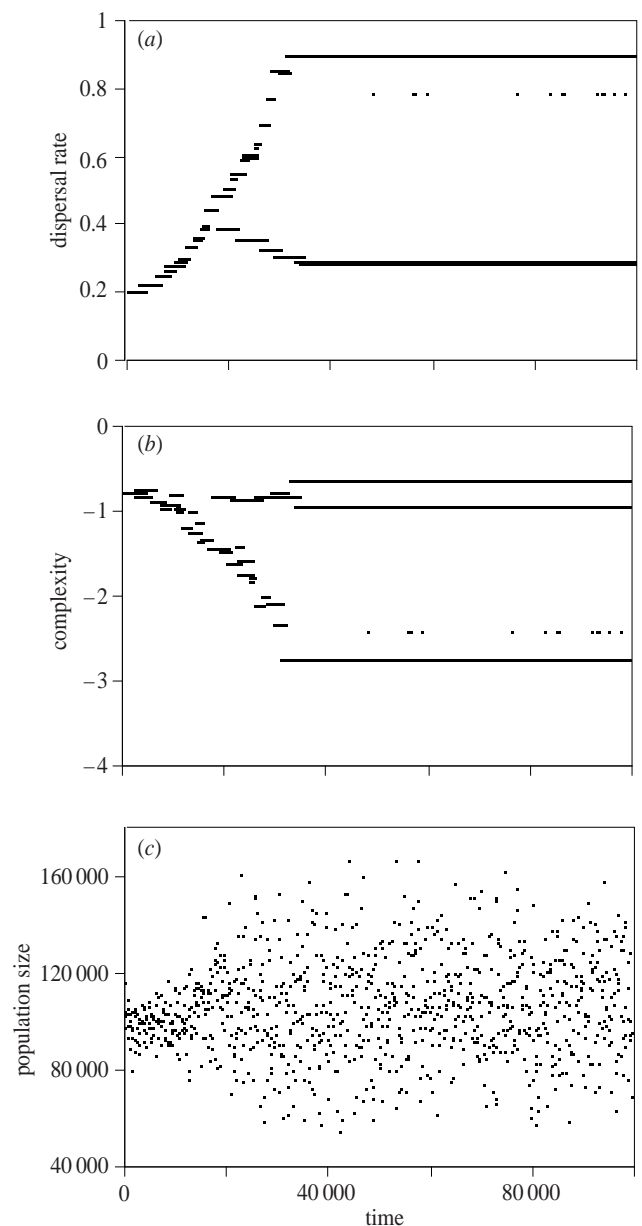


Figure 2. (a) Evolution of the dispersal rate  $m$ , and (b) the dynamic complexity  $c$  in a spatially structured and temporally varying environment (grid size  $10 \times 10$ ,  $R = 10$ ,  $\Delta = 0.5$ , see § 2a), starting with  $m = 0.2$  and  $c = -0.8$ . All phenotypes  $p$  with a frequency  $> 5\%$  within the population are shown. Evolutionary branching leads to the coexistence of highly dispersing complex phenotypes and phenotypes with low dispersal rates and equilibrium dynamics. (c) Dynamics of the total population size of the metapopulation. A qualitative change occurs when complex phenotypes evolve.

estimate for the transition from the cyclic to the chaotic region is around  $|c| \approx 2$ ) and reaches the chaotic region of the basic model given by equation (2). This transition causes a branching in the dispersal rate: the phenotypic cluster with the low  $|c|$ -value decreases its dispersal rate again to a final value ( $m \approx 0.3$ ,  $|c| \approx 0.8$ ) whereas the one with the higher  $|c|$ -value increases further both its dispersal rate and its complexity to reach high values ( $m \approx 0.9$ ,  $|c| \approx 2.8$ ). The split into phenotypic clusters of an initially uniform population shown in figure 2 are typical cases of

evolutionary branching as described by the theory of adaptive dynamics (Metz *et al.* 1996; Geritz *et al.* 1997). It implies that very complex phenotypes can evolve, but only when they are linked to high dispersal. They coexist with equilibrium phenotypes, which in turn are linked to low dispersal. Note that we did not assume any constraining relationships between the dispersal rate  $m$  and the competition parameter  $b$ , and that the association between  $m$  and  $b$  emerges dynamically from the evolutionary process in our model.

Figure 2c shows the concomitant change in the population dynamics that is brought about by the evolution of complex phenotypes shown in figure 2a and 2b. In the region of equilibrium population dynamics (up to 20 000 time-steps), fluctuations in the total population size (summed over all habitats) are exclusively caused by temporal fluctuations of the carrying capacities. The emergence of complex phenotypes after around 20 000 time-steps amplifies these fluctuations, although on this global scale these fluctuations are bounded well away from zero.

Our extensive numerical simulations suggest that the results shown in figure 2 are typical for the evolutionary dynamics in our system over a wide range of parameter values (including the amplitude of temporal fluctuations of the carrying capacities, the spatial variation of the carrying capacities, the parameters of the mutation process, the initial conditions, and the boundary conditions). Furthermore, the results do not depend on the special form of the fitness function (similar results can be obtained for example with the Hassell equation, see Bellows (1981)). However, there are two important prerequisites for the evolution of highly complex phenotypes: on the one hand, the spatial arrays must be large enough, i.e. the metapopulation must be sufficiently structured, and on the other hand the habitats must be temporally variable. This is illustrated in figure 3, in which we show for a range of intrinsic growth rates  $R$  the phenotypes that are present in the population after evolutionary dynamics over 80 000 generations, by which time the evolutionary equilibrium has typically been reached. In figure 3a, we used a large metapopulation consisting of 100 habitats on a  $10 \times 10$  lattice and a large amount of temporal variability in these habitats. Clearly, for a large range of growth rates  $R$  the final outcome of evolution is the coexistence of a complex with an equilibrium phenotype, as shown before in figure 2. Once again, in all these cases the complex phenotypes have large dispersal rates, while the equilibrium phenotypes have low dispersal rates. Figure 3b shows the same system but without temporal variability in habitat quality, and figure 3c is the same as figure 3a but on a much smaller lattice. In both cases evolutionary branching and coexistence of distinct phenotypic classes still occurs for a wide range of  $R$ -values, but the  $|c|$ -values of the coexisting phenotypic clusters now all lie in the region of stable equilibrium or cyclic dynamics. These results are again typical for our system: with increasing spatial structure and with increasing temporal variability we consistently found an increasing tendency for complex phenotypes to appear in the metapopulation. Thus, besides a link to high dispersal rates, sufficient spatial structure and temporal

variability of the environment are necessary conditions for the evolution of highly complex phenotypes.

#### 4. DISCUSSION

We studied evolution in a spatially structured environment by assuming two independently evolving phenotypic traits: the dispersal rate  $m$ , i.e. the probability to migrate to other habitats, and the sensitivity to local crowding (that is, the local competitive behaviour) characterized by the parameter  $b$ , which determines the dynamic complexity of the local dynamics in each habitat. Up to now the evolution of complex dynamics has been considered only on a local scale (that is, without the possibility to disperse to other habitats). With our model, however, we turn from the local to a global scale. In contrast to the previous results of spatially unstructured models (Doebeli & Koella 1995; Ebenman *et al.* 1996), we found that phenotypes exhibiting very complex population dynamics easily evolve provided that the number of coupled habitats is sufficiently large and provided that there is temporal variability in habitat quality. This indicates that spatial structure and temporal variability promote the evolution of complex phenotypes. Interestingly, these phenotypes only persist when they have a high dispersal rate: complex phenotypes with low dispersal rates never evolved in our system.

In order to interpret these results, we need to remember that the realized fitness values  $f(N(t))$  of rare mutants depend on the dynamics  $N(t)$  of the resident phenotypes and on the temporal variability of the abiotic environment. Therefore these fitness values vary over time (see equation (2)). If the geometric mean of the realized fitness values is larger than one, invasion of a rare mutant phenotype is possible (e.g. Metz *et al.* 1992; Doebeli & Koella 1995). For a dispersing mutant phenotype, the realized fitness at time  $t$  is the arithmetic average over all habitats  $f(N(t)) = \sum_h p_h f(N^h(t))$  ( $p_h$  denotes the fraction of the corresponding total population that ends up in habitat  $h$ ; Metz *et al.* 1983).

Therefore, temporal variability of the environment favours dispersing phenotypes: due to the arithmetic mixing of  $f(N^h(t))$ , bad local conditions at time  $t$  can be compensated (provided that there is a spatially uncorrelated variance in fitness; Holt & McPeck 1996). In contrast, spatial heterogeneity of the environment favours non-dispersing individuals: since better habitats harbour more individuals, individuals would on average disperse to unfavourable environments (e.g. Johnson & Gaines 1990; Olivieri *et al.* 1995; exceptions from these general rules appear with conditional dispersal strategies; see McPeck & Holt 1992; Johst & Brandl 1997a,b). In a spatially heterogeneous and temporally varying environment these two influences interact, and the degree of spatial heterogeneity compared to that of temporal variability influences the evolution of dispersal rates.

Concerning the evolution of dispersal our results agree with those of models concentrating exclusively on the evolution of dispersal (Hastings 1983; Levin *et al.* 1984; Holt 1985; Johnson & Gaines 1990; McPeck & Holt 1992; Johst & Brandl 1997a; Doebeli & Ruxton 1997): in a temporally constant environment there is selection for low dispersal (figure 3b), whereas in a temporally varying environment

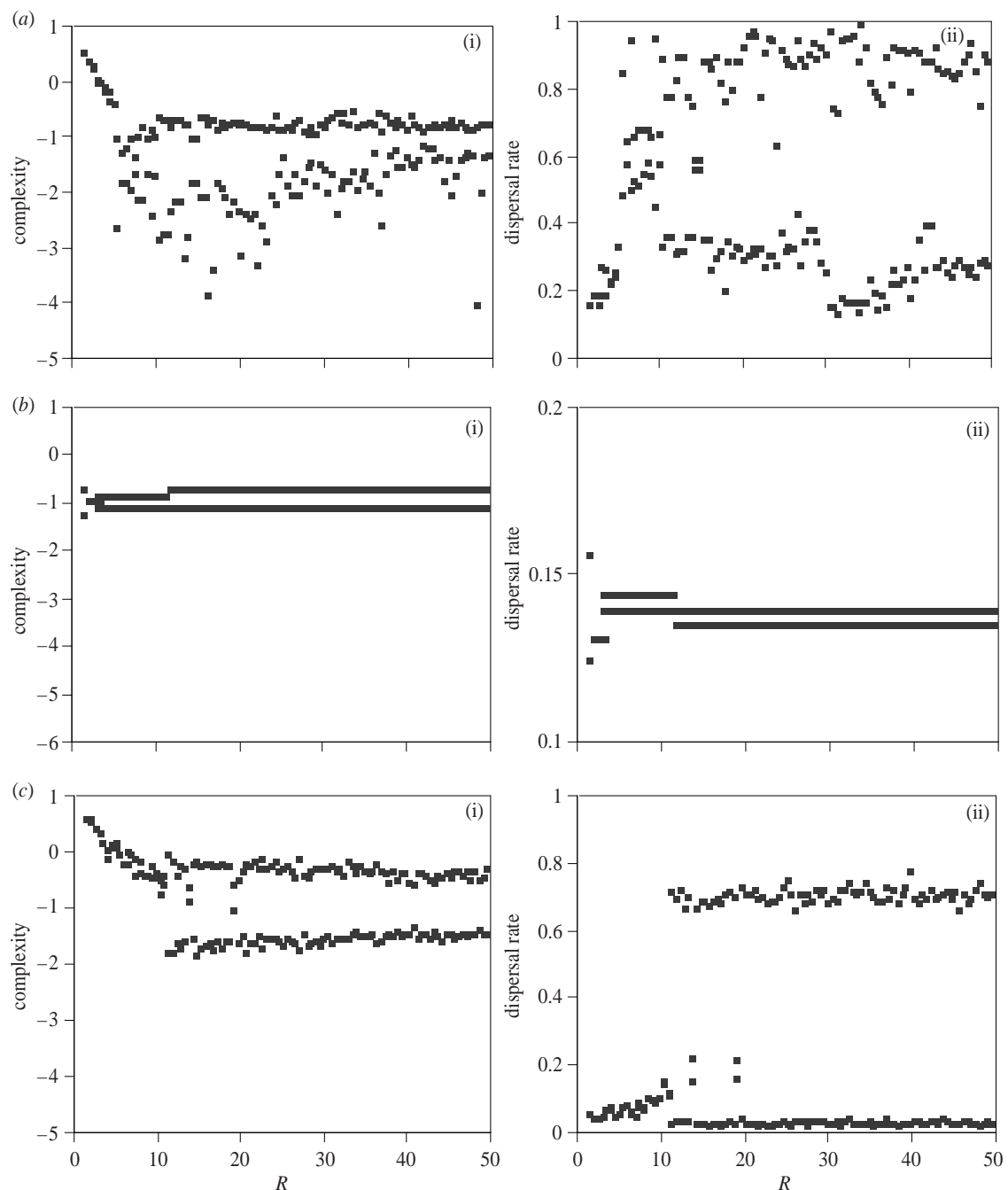


Figure 3. Evolutionary outcome of the dispersal rate  $m$  (right column) and the dynamic complexity  $c$  (left column) as a function of  $R$ , starting with  $m=0.2$  and  $c=-0.8$ . Typically, for a given  $R$ -value two phenotypic clusters coexist after 80 000 time-steps. In these clusters only the phenotype with the highest respectively the lowest values of the complexity among those with frequency  $> 10\%$  in the total population are shown. For all values of  $R$  the same initial conditions and the same random configuration of the means of the carrying capacities in each habitat were used. (a) (i), (ii) Temporally varying environment (grid size  $10 \times 10$ ,  $\Delta = 0.5$ , see § 2a). Note that the evolutionary outcome may differ considerably for  $R$ -values that differ only slightly. This indicates that when evolutionary branching leads to the evolution of complex phenotypes, then the exact evolutionary end-state may depend on the initial conditions and on the mutational process. This is in contrast to figure 3*b* and 3*c*, where equilibrium phenotypes or phenotypes with low complexity may evolve, but not highly complex phenotypes. (b) (i), (ii) Temporally constant environment (grid size  $10 \times 10$ ,  $\Delta = 0$ ). (c) (i), (ii) Temporally varying environment with a low number of habitats (grid size  $2 \times 2$ ,  $\Delta = 0.5$ ).

there can also be selection for high dispersal rates (figure 3*a,c*). Doebeli & Ruxton (1997) have shown that if temporal variability is caused by complex population dynamics (i.e. fluctuations of the biotic environment), then high and low dispersers often coexist, and their coexistence is brought about by the phenomenon of evolutionary

branching. That is, starting from phenotypically uniform populations, dispersal rates evolve gradually at first, but then the population splits into a high and a low dispersal branch. Here, we have extended these results by showing that if in addition there is an external, abiotic component in the environment which fluctuates over time (given by



the temporally varying carrying capacities of the habitats), and if demographic parameters influencing the competitive behaviour within the habitat and thus the local dynamic complexity  $|c|$  are allowed to evolve as well, then the evolutionary branching in dispersal rate  $m$  is accompanied by a branching in  $|c|$ . These branchings can occur at different times, but the final outcome is typically the coexistence of high  $m$ –high  $|c|$  phenotypes with low  $m$ –low  $|c|$  phenotypes (figure 2). It is interesting to note that Holt *et al.* (1999) have found another example of the evolution of complex dynamics in a model with spatial structure. In their host–parasitoid model, some hosts are protected from parasitoids in a refuge habitat, which leads to a stabilization of the system. However, if variation in habitat use is permitted, hosts will be selected to use the refuge less, and as a consequence the dynamics become more complex.

The advantage of complex phenotypes consists in a large reproductive rate  $f(N)$  even at large population sizes up to the carrying capacity  $K$ , the disadvantage in small  $f(N)$  already at population sizes slightly larger than  $K$  (figure 1). This steep decrease of  $f(N)$  around  $K$  implies that in the course of time an invading complex phenotype has exclusively extreme (very high or very low) values of  $f(N)$ , which reduces its geometric average over the realized fitness values. It can be shown numerically that this implies a selective disadvantage for these phenotypes in the local, spatially unstructured setting (Doebeli & Koella 1995). With dispersal, however, the extreme local values of  $f(N)$  can be mitigated by the arithmetic averaging over the habitats. If this mechanism is effective enough i.e. if the dispersal rate is high enough and if there are enough local habitats, then dispersing complex phenotypes become competitive and are able to invade and coexist with non-dispersing equilibrium phenotypes (figure 2). In particular, this argument implies that evolution of complex phenotypes is even more likely if dispersal and thus averaging is global as confirmed in our simulations.

If the metapopulation consists of only a small number of coupled habitats the arithmetic averaging due to dispersal is less effective in dampening the extreme local values of  $f(N^h(t))$ . Therefore, the local disadvantages of highly complex phenotypes cannot be sufficiently mitigated by dispersal and only dispersing phenotypes with low complexities survive the evolutionary competition (figure 3c). Thus, even under conditions selecting for high dispersal, highly complex phenotypes cannot always evolve. (Note that on very small lattices local dispersal becomes global, but this is not the reason why highly complex phenotypes do not evolve on small lattices, see above.) Furthermore, very small reproductive rates  $R$  in equation (2) dampen the effects of temporal variability in the carrying capacities, thereby disfavours dispersing phenotypes even in a temporally varying environment. Therefore, under these conditions complex phenotypes are not expected to evolve. This is also the case when the spatial heterogeneity is large compared to the temporal variability: as explained above this disfavours dispersal and therefore disfavours the evolution of dispersing complex phenotypes.

An alternative explanation of the observed results which has been suggested by one of the reviewers is that

high dispersers experience, on average, less crowding than low dispersers because they are able to recolonize patches with low population densities (generated by the temporal variability of the carrying capacities) more efficiently than low dispersers. Therefore, the sensitivity to crowding at high densities is less important for high dispersers than for low dispersers.

In the figures shown we started our simulations with resident non-dispersing equilibrium phenotypes. However, we also tested a broad range of other initial conditions. If we start our simulations with resident non-dispersing complex phenotypes and assume temporally constant carrying capacities there is selection for higher dispersal rates provided that only the dispersal rate can evolve. This happens because these resident phenotypes generate a temporally varying biotic environment selecting for large dispersal rates similar to an abiotic environment with varying carrying capacities (Holt & McPeck 1996; Doebeli & Ruxton 1997). However, if both the dispersal rate and the local competitive behaviour are able to evolve, then two mechanisms influence the mean fitness of invading phenotypes. First, increasing dispersal lowers the variance in the realized fitness values due to arithmetic averaging over various local fitness values. Second, decreasing the complexity lowers the variance due to less extreme local fitness values. Our results suggest that in a temporally constant abiotic environment the second influence is more efficient. Here, equilibrium phenotypes are only inferior if the resident population already consists of highly dispersing complex phenotypes.

We have characterized equilibrium and complex phenotypes corresponding to their dynamics which they would show in isolation. However, the ecological dynamics of a spatially structured metapopulation do not only depend on demographic parameters in the local populations, but also on the interaction between the local populations brought about by dispersal. In fact, coupled map lattices like those used in the present study for describing spatially structured populations have attracted considerable attention. For example, it has been shown that dispersal can have a strong stabilizing effect and can induce simple metapopulation dynamics despite very complex local dynamics in isolated habitat patches (e.g. Hastings *et al.* 1993; Doebeli 1995; Doebeli & Ruxton 1998; Kaneko 1998). Thus, metapopulation dynamics might be simple despite the evolution to high values of the demographic parameter  $b$ , respectively  $|c|$ . In our model we have not observed these simplifying effects, and the evolution to high values of  $b$  was accompanied by very complicated metapopulation dynamics. However, our main focus is on the evolution of the sensitivity to local crowding, i.e. on the evolution of the complexity of the local population dynamics, and we have not attempted to further analyse and characterize the exact nature of the metapopulation dynamics that result from such evolution.

From the point of view of community ecology the coexistence of phenotypes using different strategies to compete for the same resource can be considered as different species coexisting without niche differences (McPeck & Holt 1992). In our simulations, non-dispersing equilibrium phenotypes are able to coexist with dispersing complex phenotypes. Thus, one species is locally adapted to high densities (small  $b$ ) and a bad

disperser, and the other one is a good disperser but locally inferior at high densities (large  $b$ ). Our results suggest that such a coexistence is especially probable in a temporally varying and spatially structured environment. The simultaneous evolution towards large dispersal rates  $m$  and large  $b$  suggests that scramble-type density dependence should be associated with high dispersal and contest-type density dependence with low dispersal.

Summarizing, we studied the simultaneous evolution of the dispersal rate and the sensitivity to local crowding in a spatially structured population. We show that dispersing phenotypes with the intrinsic potential for very complex dynamics can evolve under a range of conditions of the abiotic environment. Our results suggest that chaotic dynamics are more likely to be detected in natural populations existing in patchy and temporally varying environments. Thus, when searching for chaos, interpretation and reconciliation of the results may be more successful when one includes the attributes of the abiotic environment.

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