On the Evolution of Density Dependent Dispersal in a Spatially Structured Population Model

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A simple metapopulation lattice model of two competing phenotypes is presented, where one phenotype reacts more sensitively to overcrowding by migrating to neighboring local habitats. The sensitivity is formulated by means of a threshold density of the subpopulations, above which dispersal is triggered off. If this threshold density is not very far from the local carrying capacity, an increased mobility provides benefits on the metapopulation level. At a surprisingly small difference between migrational triggering thresholds, the phenotype of larger mobility (or lower threshold) squeezes out the less mobile one from the whole system in a wide parameter range. Evolutionary considerations give an optimal threshold level for our model metapopulation.

1. Introduction

It has been recognized long ago that dispersal might be a significant regulatory factor which promotes the coexistence of species in a complex ecosystem. Any study of migratory processes necessarily involves the consideration of spatial scales, which may lead directly to the concept of metapopulations (e.g., Gilpin & Hanski, 1991; Hanski et al., 1995). Coexistence of different species is also accompanied in most cases by competition for resources and/or by predator-prey relationships (e.g., Law & Watkinson, 1989). Recently, the problem of interaction between local competition and dispersal has received much attention in spatially structured models (Hamilton & May, 1977; Comins et al., 1980, 1992; Czárán & Bartha, 1992; Solé et al., 1992; Hanski & Zhang, 1993; Hassel et al., 1994; Bascompte & Solé, 1995; Doebeli, 1995; Olivieri et al., 1995). Most of the models characterize the dispersal ability by means of a global parameter, the dispersal rate, which is usually defined as a prescribed fraction of the subpopulations leaving the habitats in each generation. A key question in many studies is the existence of an evolutionarily stable dispersal strategy (ESDS), which maximizes site or patch occupancy, and it is stable against any rare mutation altering the dispersal rate (e.g., Hamilton & May, 1977; Comins et al., 1980; Maynard-Smith, 1982; Crespi & Taylor, 1990; Hanski & Zhang, 1993; Doebeli, 1995; Olivieri et al., 1995). On one hand, the parameterization of dispersal with a single rate coefficient is a reasonable concept and fits many observations (Krebs, 1994). On the other hand, it is easy to recognize that a fixed dispersal rate does not always represent an optimum, especially in a patchy environment. A genetically coded constant dispersal rate has definite drawbacks at low population densities far below the local carrying capacity, where the optimal strategy would be to avoid the risks of migration. Also at densities which are too high, where the demand is a fast decrease of the local population, an increased dispersal activity leads to a higher efficiency in the release of population

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over-runs than a fixed migration rate. Consequently, the unconditional dispersal strategies (constant rate) are ruled out by conditional (e.g., density dependent) dispersal strategies in many biologically relevant cases. In the case of density dependent migrational behavior, the subject of evolution is not the dispersal rate itself, but some related properties.

Recently, we have introduced a metapopulation lattice model to discuss the regulatory effects of a density dependent dispersal mechanism (Csilling et al., 1994; Jánosi & Scheuring, 1995; Scheuring & Jánosi, 1996). As Ruxton and others pointed out (Ruxton, 1995a, b, c; Paradis, 1995; Hastings & Higgins, 1995), our model has two main ingredients differing from similar studies (Comins et al., 1992; Paradis, 1995; Hastings & Higgins, 1994). First, migration of a subpopulation fraction to neighboring habitats occurs only if the local population size exceeds a threshold value. This threshold rule can be considered as one of the simplest adaptive migrational mechanisms, the sole associated parameter is the threshold value itself. Although this model assumption is probably too simple to compare with real situations, there are some experimental indications for intrinsic mechanisms against overcrowding (Lidicker, 1975; Ostfeld et al., 1993; Nakajima & Kurihara, 1994; Korona, 1995). Second, migration is supposed to be much faster than reproduction, moreover dispersal events continue until all subpopulations decrease below the threshold. Note that this mechanism is neither “stepping-stone” nor “common-pool” dispersal. While in the former case dispersers reach only neighboring patches in one reproductivity cycle, in a common-pool or “island” model all individuals are equally likely to reach all patches. In our model, migrating population fragments can reach distant patches with a series of elementary dispersal steps, if and only if the sites connecting the source and the destination are densely populated. In other words, long-range correlations can build up via long-range migrations, but these correlations are not strong enough e.g., for the case of complete synchronization (Csilling et al., 1994; Jánosi & Scheuring, 1995; Scheuring & Jánosi, 1996).

The main result of our earlier single-species analysis is that the threshold triggered fast migration stabilizes the dynamics at the metapopulation level very effectively, even if the local time evolution is strongly chaotic at each site. Decreasing threshold increases the coupling between the local “habitats”, and the global dynamics changes from a noisy fixpoint behavior to a strongly correlated periodic one without collective chaos (Csilling et al., 1994; Jánosi & Scheuring, 1995; Scheuring & Jánosi, 1996). However, the migrational threshold in the single-species model is a free parameter, and there is no way to predict which threshold value can be considered as optimal and can be expected to be naturally selected in a real ecosystem.

In this work we extend our earlier analysis of the metapopulation dynamics by introducing exploitative competition between two phenotypes or species. According to the approach of Odum (1959), two species are said to be in competition if populations of each adversely affect the growth of the other in the struggle for common resources. On a model level this means that competing species should have a common controlling factor, which is the total population in the simplest case (exploitive competition). It is widely debated whether this sort of competition might be a major force in natural selection or not. Indeed, it is not clear which of the many phenotypic characteristics that contribute to the competitive ability could undergo evolutionary change through competition (Law & Watkinson, 1989). In our model investigation, we focus on a particular phenotypic characteristic, which is supposed to contribute to the competitive ability on the metapopulation level, namely on the sensitivity to overcrowding.

Several model investigations indicate that spatially patchy environments can markedly influence the dynamics of a dispersed metapopulation, even in the case of a single species (e.g. Ives & May, 1985; Comins et al., 1992; Solé et al., 1992; Hastings & Higgins, 1994). First, migration of a subpopulation fraction to neighboring habitats occurs only if the local population size exceeds a threshold value. This threshold rule can be considered as one of the simplest adaptive migrational mechanisms, the sole associated parameter is the threshold value itself. Although this model assumption is probably too simple to compare with real situations, there are some experimental indications for intrinsic mechanisms against overcrowding (Lidicker, 1975; Ostfeld et al., 1993; Nakajima & Kurihara, 1994; Korona, 1995). Second, migration is supposed to be much faster than reproduction, moreover dispersal events continue until all subpopulations decrease below the threshold. Note that this mechanism is neither “stepping-stone” nor “common-pool” dispersal. While in the former case dispersers reach only neighboring patches in one reproductivity cycle, in a common-pool or “island” model all individuals are equally likely to reach all patches. In our model, migrating population fragments can reach distant patches with a series of elementary dispersal steps, if and only if the sites connecting the source and the destination are densely populated. In other words, long-range correlations can build up via long-range migrations, but these correlations are not strong enough e.g., for the case of complete synchronization (Csilling et al., 1994; Jánosi & Scheuring, 1995; Scheuring & Jánosi, 1996). In our model system the spatial interaction also changes the global behavior drastically. While a mobile phenotype living in a single open habitat together with a less mobile competitor is doomed to extinction, we found that in a spatially patchy system the mobile phenotype is generally the superior one. This is a consequence of the immigration into relatively underpopulated local habitats, which can have a drastic effect on the overall dynamics (McCallum, 1992; Stone, 1993; Ruxton, 1994; Rohani & Miramontes, 1995). Furthermore, we found that a mobile phenotype can coexist with a less mobile one at parameter ranges where the extinction of the former would occur necessarily according to Volterra’s competitive exclusion principle. We argue that there is an evolutionary pressure to select a particular migrational sensitivity, which can be considered as an ESDS in the framework of our model.
2. Model for Two Competing Phenotypes

We consider the case of two phenotypes competing for common resources. One simple growth rule for involving this competition in a local patch is the following:

\[
N_i(y + 1) = \lambda_i N_i(y)[1 + N_i(y) + N_j(y)]^{-\beta_i} \quad (1a)
\]

\[
N_j(y + 1) = \lambda_j N_j(y)[1 + N_i(y) + N_j(y)]^{-\beta_j} \quad (1b)
\]

where \(N_i\) represents the populational density of the \(i\)th phenotype (\(i = 1,2\)) given by a census at a year \(y\), \(\lambda_i\) is the intrinsic growth rate and \(\beta_i\) is the density dependent damping parameter. [In general, a scaling parameter associated with the local carrying capacity is also used in eqn (1). Since this parameter does not affect the dynamics, we do not represent it in our formulæ.] Similar discrete difference equations are widely used to model population dynamics (e.g., Cohen, 1995). This particular map has the benefit of comparing e.g. in the logistic equation, it has a positive solution on the whole domain of positive real numbers. If the parameters are equal, i.e. \(\lambda_1 = \lambda_2\) and \(\beta_1 = \beta_2\), the sum of the two populations obeys a single discrete equation with the common parameters. In this case the time evolution of the subpopulations \(N_1\) and \(N_2\) is simple in the sense that they evolve coherently, and their overall ratio depends exclusively on the initial values \(N_i(y = 0)\) and \(N_j(y = 0)\). [Note that the ratio depends on, but is not fixed by, the initial ratio \(N_i(y = 0)/N_j(y = 0)\), because during the approach to the attractor this ratio can change. On the other hand, the ratio remains constant forever on the attractor itself.] In general, if the parameters are different (\(\lambda_i \neq \lambda_2\) or/and \(\beta_i \neq \beta_2\), one of the phenotypes becomes extinct after a while. This behavior is known in the literature as “Volterra’s competitive exclusion principle” (e.g., Rescigno & Richardson, 1973), i.e. the species of lower food utilization is doomed to extinction. This means in the particular case of eqn (1) that the phenotype of smaller growth rate \(\lambda\) or larger damping exponent \(\beta\) becomes extinct when the other parameters are equal. Since the effects of changing the two parameters are opposite, there exists a proper set of non-equal parameters supporting coexistence; the analysis of this question is beyond the scope of the present work.

Let us extend eqn (1) by considering competing metapopulations of spatially dispersed, interactive local populations. The local habitats are represented as nodes on an \(L \times L\) square lattice, and the local dynamics obeys eqn (1) at each node. The metapopulations of the phenotypes are associated with the appropriate spatial (lattice) averages \(\langle N_i \rangle\) and \(\langle N_j \rangle\). Let us suppose then that the phenotype \(N_1\) is more sensitive to overcrowding than the other phenotype \(N_2\). This characteristic is associated with two appropriate threshold parameters \(k_1 < k_2\). For the sake of simplicity we assume that these values are uniform on the whole lattice. If the two thresholds are equal, we get back the single species—or single phenotype—metapopulation model already described in detail (Csilling et al., 1994; Scheuring & Jánosi, 1996). In a preliminary version of this work (Jánosi & Scheuring, 1996) we studied the dynamics of the other limiting case, where one of the phenotypes was practically immobile (\(k_2 = \infty\)). In this not very realistic situation, the dispersal rule is very simple because only one phenotype, the mobile one, migrates. In the model of two dispersing phenotypes of two different triggering thresholds, the elementary dispersal step is a little more complicated.

We should distinguish two different cases depending on the density of the total population \(N_{tot} = N_1 + N_2\) in a given patch. If the density lies between the thresholds, \(k_1 < N_{tot} < k_2\), a fragment of the more mobile phenotype \(N_1\) disperses to the neighboring habitats, until the density of the total population drops to a subcritical level \(N_{sc} < k_1\) (this relationship mimics a hysteresis in the dispersal step).

The subcritical level can depend on the threshold, the simplest choice is a proportionality \(N_{sc} = rk_1\) with \(r < 1\). If the density of the less mobile phenotype itself exceeds the subcritical level, \(N_1 > N_{sc}\), then all of the individuals belonging to \(N_1\) have to leave the local habitat. In formulæ this reads:

if \(k_1 < N_{tot} < k_2\), then

\[
N_{tot} \rightarrow \max\{N_{sc}, N_2\} \quad (2a)
\]

\[
N_{tot}^{nn} \rightarrow N_{tot}^{nn} + \begin{cases} \Delta N_{tot} - N_{tot}^{nn} & \text{if } N_{tot}^{nn} > N_2; \\ \Delta N_1/4, & \text{otherwise}. \end{cases} \quad (2b)
\]

The superscript \(nn\) denotes nearest neighboring sites and \(\Delta\) is a “dissipation” factor representing a loss during dispersal.

If the total density exceeds the larger threshold, \(N_{tot} > k_2\), dispersal is triggered off in both phenotypes. Many different scenarios are conceivable to describe this simultaneous migration. The simplest is probably to assume that the composition of the dispersing fractions is the same as of the initial local population, from which we can construct the following rule (rule 4):

if \(N_{tot} > k_2\), then
\[ N_{tot} \rightarrow N_a(N_1, N_2) \quad (3a) \]

\[ N_1^{nn} \rightarrow N_1^{nn} + \begin{cases} \Delta p(N_{tot} - N_a) \over 4, & \text{if } N_1 > p(N_{tot} - N_a); \\ \Delta N_1 \over 4, & \text{otherwise}; \end{cases} \quad (3b) \]

\[ N_2^{nn} \rightarrow N_2^{nn} + \begin{cases} \Delta (1-p)(N_{tot} - N_a) \over 4, & \text{if } N_2 > (1-p)(N_{tot} - N_a); \\ \Delta N_2 \over 4, & \text{otherwise}. \end{cases} \quad (3c) \]

We note again that many other migrational rules are possible according to different assumptions on the simultaneous migration. However, we found that the collective dynamics at the metapopulation level is remarkably insensitive to this detail, apart from very low threshold values (see below).

Since the immigrated population fragments increase the density at the neighboring sites, further dispersal events may be triggered off, leading to a chain of local migrations on a set of connected sites (migrational “avalanche”).

Now the global dynamics is the following. We start from a random initial configuration and all sites are simultaneously updated according to eqn (1) (reproductive step). When on one or more sites the local density \( N_{tot} \) exceeds the thresholds \( k_1 \) or \( k_2 \), the time evolution stops, and relaxation proceeds according to eqn (2) if \( k_1 < N_{tot} < k_2 \), or eqns (3) or (4) if \( N_{tot} > k_2 \), until every site becomes subcritical (migrational step). Then a new reproductive step begins. In this way we introduced a time-scale separation, i.e., the dispersal is supposed to be much faster than reproduction. This time-scale separation might be adequate to characterize species of high mobility and low reproduction rate (e.g. birds, mammals, or flying insects). We stress here that this time-scale separation has an important consequence in the interpretation of the underlying lattice. Since the migration itself is very fast, the lattice structure of the local habitats or patches represents connectivity, i.e. a topological relationship rather than a topographical one. With this remark we would like to argue that two-dimensional coupled map lattice models—like ours—may have some relevance in metapopulation studies, in spite of the fact that e.g. a checker-board-like topographical arrangement of patches in Nature is really rare (Paradis, 1996).

Our lattice has open boundaries, that is migrating population fragments leave the system freely at the borders. This is comfortable to ensure the existence of a global subcritical state. In the case of a periodic or reflecting boundary condition, the system can be
locked into a state of endless migration, if there is no loss of population during the dispersal ($\Delta = 1.0$). Note, however, that the dynamics is “dissipative” in the reproduction phase even at $\Delta = 1.0$, i.e. drops of local populations occur everywhere in the lattice, not only at the borders.

3. Robustness of the Model

Before starting the analysis of the main questions, we would like to single out which are the relevant parameters from the following list: lattice size $L$; dynamical parameters of the local reproduction $\lambda_1, \lambda_2$ and $\beta_1, \beta_2$; threshold values $k_1$ and $k_2$; subcritical densities $N_{sc1}$ and $N_{sc2}$ (or alternatively the proportionality factors $r_1$ and $r_2$ using $N_{sc1} = r_1k_1$, $N_{sc2} = r_2k_2$); migrational loss factor $\Delta$; and the rule for the elementary dispersal steps $A$ and $B$. We ran the simulations from random initial configurations, however we usually prescribed an initial ratio $N_i(y = 0)/N_i(y = 0)$ at each lattice site.

Obviously, the dynamical parameters have a key role to determine the local time evolution. Since we believe that migrational interactions represent a significant regulatory factor in metapopulations, we usually fix the values in an instable dynamical range, where the underlying time evolution is chaotic. Moreover, we will focus on the role of sensitivity to overcrowding associated with the dispersal trigger levels $k_1$ and $k_2$, which shows up more transparently in case there are not differences in the local competitive abilities. Therefore, we first fixed the dynamical parameters as $\lambda_1 = \lambda_2 = 100.0$, $\beta_1 = \beta_2 = 8.8$. Results for different choices are also discussed below.

We did not observe significant finite-size effects whenever the lattice size $L$ was larger than four. Considering statistical averages, the larger the lattice the smaller the amplitude of fluctuations [see also, Scheuring & Jánosi (1996)]. A practical limit for $L$ comes from the steeply increasing computational time, therefore we used lattices in the ranges $L = 8 \ldots 36$.

As an example, we show in Fig. 1 the effect of migrational loss. This and most of the following “bifurcation diagrams” were obtained for a lattice of $L = 16$, starting from random initial configurations at each of the 200 $k_1$ values. After discarding the first 1000 generations, the lattice averages of the next 1500 reproductory cycles were plotted at each $k_1$. Without going into detail here, one can clearly observe that the effect of a strong migrational loss ($\Delta = 0.8$ means a loss of 20% at each elementary step of a dispersal avalanche) is not very dramatic. At low thresholds, the maximum and minimum values of the global oscillations are slightly smeared out. The most apparent difference appears in a narrow window around $k_1 \approx 3.6$: the amplitude of metapopulation fluctuations increases anomalously without migrational loss [Fig. 1(a)]. This resonance-like broadening is not present at finite losses [Fig. 1(b)]. Another consequence of a finite loss parameter is that the migrational avalanches are strongly damped compared to a “conservative” spreading. An assumption of zero loss is certainly too artificial, especially in a patchy metapopulation model, therefore we usually took $\Delta = 0.8$ in the simulations to be discussed below. However, we stress again the $\Delta$ is not a significant parameter whenever its value is not extremely small.

Note that the initial ratios $N_i(0)/N_i(0)$ are different in Fig. 1(a) and Fig. 1(b). This has absolutely no effect when the migrational interaction is switched on ($k_1 < 4.4$ for the given parameters).
In Fig. 2 we show the effect of the two different elementary migrational steps, rule $A$ [eqns (3)] and rule $B$ [eqns (4)]. Here the changes are more pronounced than in Fig. 1, but located at relatively low threshold values $k_1 < 2.4$. If the composition of the migrating fragments is determined by the ratio of the initial local populations (rule $A$), the suppression of the more mobile phenotype is stronger at these small thresholds. Apparently, rule $B$ has a benefit for $N_1$ at the metapopulation level if the density is low in most patches, because this rule implies that almost all individuals start to disperse and search for a relatively underpopulated patch, while for rule $A$ some small fragments of $N_1$ are “forced” to stay at the given node. Note that at higher values ($k_1 > 2.5$) there is no observable dependence on the local dispersal rule.

Finally we note that the effect of different subcritical levels is negligible. We tested the range $0.7 < r < 1.0$ for both of $N_{si} = rk_1$ and $N_{s2} = rk_2$, but we did not observe any visible changes in the bifurcation diagrams. Obviously, extreme values result in drastic changes in the dynamics, but we intend to analyse our model in a reasonable parameter range where it shows the above mentioned remarkable robustness.

4. Global Dynamics

In Fig. 3 we plotted the bifurcation diagrams for both phenotypes at different triggering thresholds. At each of the $200 k_1$ values in the range $0.0 < k_1 < 5.0$, the lattice of size $L = 16$ was initialized by random densities. After discarding the first 1000 generations, the next 1500 values were plotted. Lattice averages were measured at each generation after finishing all dispersal rearrangements. If $k_1 > 4.4$, there is no dispersal in the system, because the threshold is larger than the available maximum density prescribed by the parameters of eqn (1).

Surprisingly, a very low difference in the triggering thresholds results in the extinction of the less mobile phenotype [Fig. 3(b)], in a wide range $2.5 < k_1 < 4.3$. Another remarkable fact is the stability of the dynamics of the remaining phenotype, i.e. essentially there is no dependence on $k_1$ in this range. At lower thresholds however, the tables are turned. Especially at low $\delta k = k_1 - k_1$ differences the more mobile phenotype becomes extinct in the window $0 < k_1 < 1.5$. The larger $\delta k$, the narrower this window. If $N_1$ has low migrational activity ($\delta k > 2.0$), a coexistence is established again up to very low $k_1$ thresholds. The collective dynamics also changes markedly, global oscillations become characteristics. Note however, that at such low thresholds the overall dispersal activity becomes very intensive, at each generation large parts of the populations are rearranged, therefore this parameter range probably has no natural analogy at all [see also Scheuring & Jánosi (1996)]

We plotted in Fig. 4 the time averages of the metapopulations as a function of $\delta k = k_2 - k_1$ at two characteristic $k_1$ values. While extinction of the more mobile phenotype occurs in a limited range $0.09 < \delta k < 0.30$ at approximately $k_1 = 2$ [Fig. 4(a)], a complete outsqueezing of the less mobile one is surprisingly effective at $k_1 = 2.8$ (a threshold difference of $\delta k > 0.05$ is enough for the total suppression of the less mobile phenotype).

We can summarize these result with a schematic “phase diagram” plotted in Fig. 5. Depending on the relationship between the thresholds $k_1$ and $k_2$, either one of the phenotypes squeezes the other out completely, or a coexistence is established. The diagram is symmetric with respect to the $k_1 = k_2$ line for obvious reasons. We stress here that the diagram
shows the asymptotic situation with fixed $k_1$ and $k_2$ values. Evolutionary considerations give an optimal threshold (ESDS) denoted by the heavy circle, a detailed explanation of which is given in the next section. Particular threshold values are not indicated on the axes, because the location of the regions and the optimal threshold depend on the dynamical parameters $\lambda$, and $\beta$, of the growth law eqn (1). We will return to this point too.

In the case of Figs 3 and 4, the dynamical parameters of the basic eqn (1) were fixed in a strong chaotic domain. The question naturally arises
whether our results are connected with the chaotic
time evolution of the local populations or not.

In a preliminary version of this work (Jánosi &
Scheuring, 1996), we have analysed in detail the
mechanisms of extinction. We found that the
character of the underlying dynamics does not play an
important role: at \( \lambda_1 = \lambda_2 = 100.0, \beta_1 = \beta_2 = 4.2 \) [see
eqn (1)], where the local dynamics is also chaotic (in
a period-8 window), the migrational suppression does
not work, even the more mobile phenotype becomes
extinct at almost every \( k_1 \) values [see Fig. 6(a, b)].
Whereas we found a period-3 dynamical range at
around \( \lambda_1 = \lambda_2 = 100.0 \) and \( \beta_1 = \beta_2 = 6.7 \), where the
suppression of the less mobile phenotype is so
effective as in the chaotic case \( \lambda_1 = \lambda_2 = 100.0, \beta_1 = \beta_2 = 8.8 \) discussed above (Jánosi & Scheuring,
1996). Further systematic analysis gave the result that
the key factor is not the character of the dynamics,
but the minimal value of local population densities
reached sometimes spontaneously by iterating
eqn (1).

To check our assumption on the critical role
of local density drops, we performed simulations by
introducing multiplicative noise into the dynamical
equation:

\[
N_1(y + 1) = \xi_1(y) \lambda N_1(y) [1 + N_1(y) + N_2(y)]^{-\beta}, \quad (5a)
\]
\[
N_2(y + 1) = \xi_2(y) \lambda N_2(y) [1 + N_1(y) + N_2(y)]^{-\beta}, \quad (5b)
\]
where \( \xi_i \) is a uniformly distributed random number in
the interval \((0, 1)\) generated in every reproduction
cycle for each lattice site separately. The multiplica-
tive noise sometimes reduces the level of local
populations drastically, however the overall stability
is conserved: negative density values are excluded,
which would not be guaranteed using additive noise.

The results of the simulations support that the
critical factor in the suppression process is the very
low local densities which occasionally appear. In the
presence of external noise, a stable coexistence is
established at \( \beta_1 = \beta_2 = 4.2 \) [compare Figures 6(a)
and (b) with Figs 6(c) and (d)]. Note however, that
even external noise cannot balance the drawbacks of
a mobility which is too high, if the underlying
dynamics is “super”-stable. This is illustrated in
Figs 6(e) and (f), the dynamics here is a stable
fixpoint.

We found in our numerical tests that a critical \( \beta \)
parameter value is approximately \( 5 \), at \( \lambda = 100 \)
(Jánosi & Scheuring, 1996). An increased mobility has
a benefit at \( \beta > 5 \), but has stronger negative
consequences at $\beta < 5$. We stress again that the type of the underlying dynamics does not play a role, the crucial factor is the minimal value of the local time evolution, which is approximately $10^{-2}$ at $\beta = 5$. We emphasize that this minimum is not meant to be a metapopulation value, but a local minimal density in a single habitat.

The possibility that dispersal can balance a weaker local competitive ability has long been recognized (e.g., Hassel et al., 1994). Our model also demonstrates this trade-off very clearly (see Fig. 7). A phenotype which has an intrinsic growth rate of only 50% compared with the competitor would be doomed to extinction in a couple of generations in an isolated habitat. In a patchy metapopulation however, stable coexistence is established with the help of the increased mobility. Mobility can even “over-balance” a lower local competing ability, a mobile phenotype of 80% growth rate squeezes out the less mobile phenotype from the whole system in a very short time (Fig. 7).

5. Evolutionary Considerations

In the last section we showed the typical behavior of our model system. The assumptions used are probably too simple to describe even semi-quantitatively an existing network of dispersely interacting

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**Fig. 6.** Bifurcation diagrams of the metapopulations $\langle N_1 \rangle$ and $\langle N_2 \rangle$ as a function of the lower threshold $k_1$, $k_2 = k_1 + 1.0$ in each case. The loss parameter is $\Delta = 0.8$, the intrinsic growth rates are $l_1 = l_2 = 100.0$ everywhere, migrational rule $A$. (a)-(b) $\bar{\beta}_1 = \bar{\beta}_2 = 4.2$, the local growth rule is given by eqn (1). (c)-(d) $\bar{\beta}_1 = \bar{\beta}_2 = 4.2$, the local growth rule is given by eqn (5) (multiplicative noise). (e)-(f) $\bar{\beta}_1 = \bar{\beta}_2 = 2.2$, the local growth rule is given by eqn (5).
populations of competing phenotypes, therefore we consider this model as a conceptual framework in the following discussion.

Firstly, let us think about a network of patches providing proper circumstances for a single species. We can assume that the local densities show large fluctuations, whatever their source (environmental instabilities, chaotic time evolution, interaction with other species, etc.). The density fluctuations are produced by a nonlinear growth law in our model, but this is not essential, because dispersal is connected to a triggering threshold density and not to the growth law. Our earlier results (Csilling et al., 1994; Jánosi & Scheuring, 1996) indicate that there might be an evolutionary pressure to start migrations in the single species model too, because dispersal has a very strong stabilizing effect at the metapopulation level. Nowadays, this is a widely accepted concept in ecology (e.g. Krebs, 1994). As for the triggering threshold, there is no way to deduce an evolutionary optimum for a single species in the model; this problem motivated the present extension.

Secondly, let us assume that a metapopulation of a single species occupies a patchy territory, and has a stable dynamics promoted by migrational interactions. The threshold which induces dispersal can be close to the local carrying capacity. What happens if a clone or another phenotype of different threshold appears? We have shown that in this case the competitor of the lower threshold becomes superior and squeezes out the less mobile phenotype totally (see Fig. 3). We found that a surprisingly small difference is enough to win. Note however, that the results above represent asymptotic behavior, i.e. a rather long transient is discarded in each case. Indeed, if we follow the time evolution of the metapopulations after the appearance of a more mobile competitor, we see that the temporal effectivity of suppression depends on the difference between the thresholds (see Fig. 7). If \( \delta k = k_2 - k_1 \) is small, the decay of the less mobile population is relatively slow, giving a chance to adapt to the new circumstances. It easily follows that the winning strategy involves a shift towards lower thresholds, i.e. more intensive dispersal: while the more mobile competitor should tend to increase \( \delta k \), the vital interest of the less mobile one is to decrease the difference and increase the migrational activity (Fig. 8).

It also seems plausible that a migrational trigger level which is too low has definite draw-backs by inducing unnecessary risky dispersal. This aspect is also clearly demonstrated by a drastic drop of metapopulation densities of the more mobile species if its threshold is below a critical value (Fig. 3). Now the identification of an optimum value \( k_{ESDS} \) is easy, and this optimum represents the evolutionary stable dispersal strategy (ESDS). For the parameters of Fig. 3, \( k_{ESDS} \approx 2.4 \) (this is roughly 55% of the local carrying capacity). Any clone or mutant of the same local competing ability but of different triggering threshold is regarded as inferior. We note that the threshold \( k_{ESDS} \approx 2.4 \) has also been identified as a critical value below which self-organized criticality appears with scaling migrational-avalanches (Scheuring & Jánosi, 1996). As for the dynamics, this is the threshold at which the noisy fixpoint behavior of many weakly interacting subsystems changes to a more correlated, self-organized state. Large migrational avalanches build up large-scale correlations in the system, and at lower threshold values a clear periodicity is established.

We emphasize again that a well-defined \( k_{ESDS} \) threshold exists only if the underlying dynamics is unstable “enough” [see Figs 6(e) and (f)]. This agrees
well with intuition: if the environment is stable, and an effective internal regulation keeps the density in equilibrium, there is absolutely no need to disperse. Such an ultimate underlying stability should be considered as a very strong idealization, probably a proper analogy is provided only by artificial laboratory populations.

We have checked the optimum migrational threshold $k^{ESDS}$ for several sets of values of the dynamical parameters (Fig. 9). The global behavior in the above cases was identical to that of Fig. 3, but the characteristic values were shifted.

Finally, we note that the optimal migrational trigger threshold $k^{ESDS}$ is a local (uniform) parameter in each subsystem, however the optimum is valid on a global metapopulation level. Tracing the dynamics at a particular site, local extinctions occur sometimes, especially if the population of one of the phenotypes is underrepresented.

In summary, we pointed out in the framework of our model that dispersal is clearly advantageous if the local population of a species or phenotype suffers from strong fluctuations. By introducing competition between phenotypes of different sensitivities to overcrowding, we found that a density dependent dispersal strategy represented by a migrational threshold has a unique optimal value. Considering only small deviations around the optimal threshold, we did not observe stable coexistence; in this respect the optimal threshold represents the evolutionary stable dispersal strategy. This sectional optimum also has a dynamical consequence, since the optimal threshold is associated with the appearance of long-range correlations in the metapopulation: the optimal migrational activity prevents the total population from chaos very effectively.

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