Evolution of Specialization on Resource Utilization in Structured Metapopulations
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Abstract

We study the evolution of resource utilization in a structured discrete time metapopulation model with an infinite number of patches, prone to local catastrophes that wipe out the entire local population but leave the patch itself habitable. We assume that there are two distinct resources in each patch and the strategy of an individual is the degree of specialization on the usage of these resources. We study the course of evolution using the adaptive dynamics approach. We show that slow local growth and high catastrophe probability favor generalism whereas fast local growth and low catastrophe probability favor specialization. The relation between the evolutionary dynamics of the model and the emigration probability is, however, more complicated. High emigration probability always favors generalism but there exists also parameter combinations such that also low values of emigration probability are more favorable to generalism than intermediate values. Such a non-monotonous relation between emigration probability and evolutionary dynamics has not been observed before. Evolutionary branching (i.e., appearance of two phenotypically distinct lineages) is possible in the model. The parameter domain where it is possible becomes larger when catastrophe probability is increased. For different parameter values and initial states the following endpoints of evolution are possible: monomorphic metapopulation specializing on one of the two resources, monomorphic generalist metapopulation or dimorphic metapopulation consisting of the two specialists. In the model also a trimorphism of the generalist and the two specialists is possible but not reachable in an initially monomorphic population if mutation steps are small and occur only infrequently. Our modeling approach offers a natural way to include more than two patch types into the models. This has not been usually possible in the previous metapopulation models focusing on the evolution of specialization.

Keywords: Adaptive dynamics, Specialization, Resource utilization, Metapopulation, Trade-Off


1 Introduction

The evolution of habitat specialization and resource utilization has received a lot of interest during the past decades (Amadon, 1943; Berenbaum, 1996; Day, 2000; Futuyma and Moreno, 1988; Irschick et al., 2005; Lawlor and Maynard Smith, 1976; MacArthur and Pianka, 1966; Pyke, 1984; Schreiber and Tobiason, 2003; Schoener, 1971; Van Tienderen, 1991; Wilson and Yoshimura, 1994). The basic question is always which circumstances favor the evolution of generalists and which favor the evolution of specialists. Here we study this question in a structured metapopulation setting in order to relate the evolution of generalists and specialists to emigration rate, local population growth rate and local catastrophe rate.

The simplest metapopulation models are those of the Levins type (Levins, 1969), where all the ecological interactions occur at the level of the local populations that are prone to catastrophes. However, natural selection occurs at the level of individuals and thus the Levins (1969) model or related models (Gyllenberg and Hanski, 1997; Hanski, 1994) are not suitable for the purpose of evolutionary analysis. Instead we need to model the local dynamics in the patches explicitly. Thus we must join the deterministic local dynamics and the possibility of occasional local catastrophes. We analyze the evolution of specialization on resource utilization in our model using the adaptive dynamics approach (Dieckmann and Law, 1996; Geritz et al., 1997, 1998; Metz et al., 1992, 1996) and the cumulative model formulation technique introduced by Diekmann et al. (1998, 2001, 2003) and adapted to metapopulations by Gyllenberg et al. (1997). When applying adaptive dynamics to structured metapopulations we adopt the approach introduced by Gyllenberg and Metz (2001). This modeling approach requires us to assume that the number of individuals in each patch is large so that we can neglect other stochastic effects than local catastrophes. High local population densities also allow us to assume that rare mutants do not affect the resident population dynamics when doing the invasion analysis of the adaptive dynamics. Also note that adaptive dynamics is based on the assumption of clonal reproduction.

Our model is a generalized and modified version of the model introduced by Gyllenberg and Metz (2001). Their model is in continuous time, but can be quite simply transformed into a discrete time model. Also the analysis of the model remains simple as long as the parameter values are chosen such that the dynamical attractor of the metapopulation is a fixed point or a periodic orbit. In this article we only consider parameter ranges corresponding to steady state metapopulations and thus we need not take into account the possibility of chaotic dynamics. A corresponding discrete time model has been analyzed by Parvinen (2006) focusing on the evolution of migration.

We assume that there are two alternative resources available in each patch and the strategy of an individual is the degree of specialization on these resources. The resources are identical in all of their energetic contents etc, but the utilization of
these resources requires some special features such that the better an individual can utilize one resource the worse it will be in utilizing the other resource. As a biological example of such a situation we can mention the birds that need differently formed beak to prey on worms from different sources even if the worm species is the same.

We assume that the availabilities of the two resources in each patch remain constant independently of the population dynamics in the patches. In most biological scenarios this is an unrealistic simplification and our work can thus only serve as a starting point for further research with explicit resource dynamics. Although unrealistic itself, our model is the first step in adding some more biological realism into the models of specialization on patch usage (Brown, 1990; Brown and Pavlovic, 1992; Egas et al., 2004; Kisdi, 2002; Parvinen and Egas, 2004). It is characteristic to these models that they assume that there are only two patches or two different patch types available in the environment. Then it is simple to assume that there exists some trade-off between the abilities to survive and reproduce in these two patches or patch types and the strategy of an individual defines the degree of specialization on these abilities. In our model the availabilities of the two resources define a "patch type" in the sense of the patch usage models since they together with the local population size define how "good" this patch is to a certain individual. If we in addition assume in our model that there are only two different patch types we can interpret the strategy of an individual as the degree of specialization between the abilities to survive and reproduce in these two patch types. To sum up, our modeling approach is a generalization of the approach used in the models of specialization on patch usage. Our modeling approach offers a natural way to include more than two patch types into the models. This is not usually possible in the patch usage models. Our model also offers an explanation to the differences between patches. This explanation, however, is not mechanistic and thus there is still an obvious need for more research work to include mechanistic modeling of resource dynamics into our modeling approach. In other words, this to some extent unrealistic case with constant resource availabilities is an extension of the models of patch usage and thus of interest as an intermediate step towards the metapopulation models of specialization on resource use that include also explicit resource dynamics.

We analyze the evolutionary dynamics in this setting in order to define the possible endpoints of evolution and to find the conditions promoting evolution towards different endpoints. We focus especially on the effects of varying emigration probability and the local growth rate. We also study the effects caused by different trade-off structures, environmental configurations and catastrophe probabilities. We show that evolutionary branching is possible in the model and study the evolutionary dynamics of the dimorphic population.


\section{A model in discrete time}

\subsection{Components of the model}

We consider an environment that consists of an infinite number of local habitat patches. Each of these patches can support a local population. During one time step a single patch encounters a catastrophe with probability $c$. These catastrophes occur independently in different patches. When a catastrophe takes place, it wipes out the entire local population. After a catastrophe a new local population is founded by dispersers from a disperser pool.

We model explicitly the local population dynamics in each patch. We assume the following order of events for local populations: Potential catastrophe – local growth – emigration – immigration. We assume that the individuals in the local populations and in the disperser pool are all identical to each other in their dynamically relevant behavior independently of their age, size etc. This means that we do not have to pay attention to the possibility of overlapping generations, but we can simply calculate the new size of a local population as a function of the previous local population size and the disperser pool size.

We model migration using a disperser pool. That is, every emigrant enters the pool of dispersers. At each time unit, a certain fraction of the migrants in the disperser pool immigrates into each patch, a certain fraction of migrants dies and the rest remain in the disperser pool. In most biological cases it is, however, realistic to assume that the dispersers either immigrate or die but are not able to stay in the disperser pool.

We assume that patches are structured according to three quantities: one dynamic (the local population size) and two fixed parameters. These fixed parameters represent the availabilities of two alternative resources $U$ and $V$. We start by studying the case in which the environment is symmetric in the sense that the distributions of the resources in different patch types are mirror images of each other. This assumption ensures that there is also certain amount of symmetry in evolutionary dynamics, such as that the unbiased generalist strategy is singular. In our prospective research we shall generalize the model by allowing different asymmetries in the environment and by including explicit resource dynamics into our model.

We assume that the exploitation strategy $s$ takes values between 0 and 1. Strategy $s = 0$ corresponds to full specialization on resource $V$ and $s = 1$ to full specialization on resource $U$. The strategy $s = 0.5$ corresponds to an unbiased generalist.

For simplicity we assume that there are only finitely many different patch types. In other words, there are only finitely many different possible combinations of resource availabilities.
We use the following notations and definitions:

- \( n \) The number of different patch types.
- \( i \in \{1, \ldots, n\} \) An index denoting the different patch types.
- \( p_i \) The fraction of type \( i \) patches. Naturally \( \sum_i p_i = 1 \).
- \( u_i, v_i \) The availabilities of resources \( U \) and \( V \), respectively, in a patch of type \( i \).
- \( q_i(s) = q(s, u_i, v_i) \) The patch quality of a type \( i \) patch for a strategy \( s \) individual.
- \( x_s(t) \) The size of the strategy \( s \) subpopulation in a single patch at time \( t \).
- \( X(t) = \sum_s x_s(t) \) The total local population size in a single patch at time \( t \).
- \( \eta_i(t, s) \) The population size distribution of the strategy \( s \) subpopulations in the patches of type \( i \) at time \( t \), i.e. \( \int_{x_1}^{x_2} \eta_i(t, s)(dx) \) defines the fraction of type \( i \) patches where the size of the strategy \( s \) subpopulation is between \( x_1 \) and \( x_2 \) at time \( t \). Naturally \( \int_0^\infty \eta_i(t, s)(dx) = 1 \).
- \( f_i(s, X) = F(q_i(s), X) \) The fecundity function.
- \( f_i(s, X)x_s \) Number of strategy \( s \) individuals in the patch immediately after reproduction but before migration and catastrophes given that before reproduction there were \( X \) individuals in the patch of which \( x_s \) practicing strategy \( s \).
- \( c \) Catastrophe probability of the local patches. Catastrophes occur randomly and independently in each patch. A catastrophe wipes out the whole local population, but the patch remains habitable.
- \( e_i(s, X) = e(q_i(s), X) \) The emigration probability from a type \( i \) patch with total local population size \( X \).
- \( D_s(t) \) Size per patch of the disperser pool of strategy \( s \) dispersers at time \( t \).
- \( k \) The survival probability of dispersers over one time unit.
- \( a_i(s) = a(q_i(s)) \) The immigration probability of a strategy \( s \) disperser into a patch of type \( i \).

In this article we focus on the simplified case with uniform migration. In other words, we assume that the functions \( a_i \) and \( e_i \) have constant values

\[
e_i \equiv e, \quad a_i \equiv a \quad \text{for all } i. \tag{1}
\]

In our future research we shall relax this assumption and focus on the different consequences of different forms of habitat selection.

With these notations we can define the local dynamics in a single type \( i \) patch.
as

\[ x_s(t + 1) = (1 - e) f_i(s, X(t)) x_s(t) + aD_s(t) \]

\[ X(t) = \sum_s x_s(t). \]

The actual dynamics of the disperser pool is rather complicated to calculate. Luckily there is shortcut to find the equilibrium value of the disperser pool size. We first introduce the actual dynamics and then explain the shortcut.

For a monomorphic population with only strategy \( s \) present, the dynamics of the disperser pool is given by

\[ D_s(t + 1) = k(1 - a) D_s(t) \]

\[ + k \sum_i p_i \int_0^\infty e f_i(s, x_s(t + 1)) x_s(t + 1) \eta_i(t + 1, s)(dx). \]  

(2)

In the case of polymorphic populations the corresponding calculation includes multiple integration over the size distributions of all the subpopulations.

In the general case the measure \( \eta_i(t, s) \) is difficult to determine. However, as long as we are interested only in the steady states of the metapopulation we do not have to consider this problem since we can neglect the disperser pool dynamics. This is because we can assume that in a steady state the size of the disperser pool has a constant value. Since in a steady state each clan must exactly replace itself we can solve the actual size of the disperser pool from a fixed point equation without using equation (2) or the concept of measure at all. The details of this calculation are described in the Appendix A.

We assume that strategy \( s \in [0, 1] \) measures the ability of an individual to use resource \( U \). To create a rational model of specialization, we must then naturally assume that the ability of an individual to use resource \( V \) is a decreasing function of \( s \). We set this ability simply to \( 1 - s \). Together with the availabilities of the resources in a certain patch these values define the patch quality experienced by a strategy \( s \) individual. We assume that the patch quality function \( q \) can be defined as \( q_i(s) = s^\alpha u_i + (1 - s)^\alpha v_i \), where parameter \( \alpha \) determines the form of the trade-off between the ability to use one or the other resource. In case \( \alpha > 1 \) there is an additional cost to being a generalist and in case \( \alpha < 1 \) an additional benefit. In this article we consider mostly the case \( \alpha = 1 \). In this case

\[ q_i(s) = su_i + (1 - s)v_i. \]

The fecundity function is given by the Ricker model with patch quality corresponding to the carrying capacity of the patch:

\[ f_i(s, X) = C(t) \exp \left( \ln(r) \left( 1 - \frac{X}{q_i(s)} \right) \right) = C(t) r \exp \left( -\frac{\ln r X}{q_i(s)} \right), \]  

(3)
where \( X \) is the local population size in the considered patch and coefficient \( C(t) \) is a random variable drawn from Bernoulli-distribution with parameter \( 1 - c \), where \( c \) is the catastrophe probability. In other words

\[
C(t) = \begin{cases} 
1, & \text{if there is no local catastrophe.} \\
0, & \text{if a local catastrophe occurs.}
\end{cases}
\]

This means that each patch encounters a local catastrophe with probability \( c \) on each time unit independently of the fate of the other patches or the catastrophe history of the patch.

The assumption (1) of uniform migration enables us to calculate the overall probability of surviving dispersal as

\[
\pi = \sum_{t=0}^{\infty} a(1-a)k^t = \frac{a}{1-(1-a)k},
\]

It can easily be seen that metapopulation dynamical equilibria and invasion fitness depend on parameters \( k \) and \( a \) only through the quantity \( \pi \); see (Parvinen, 2006) for details. For this reason, if the dispersal survival probability \( \pi \) is kept constant, all results presented in this article are independent of the details of the dispersal process.

To summarize, we have the following essential parameters in our model:

- \( e \) Emigration probability from a patch to the disperser pool.
- \( r \) Speed of the local growth in the patches.
- \( c \) Catastrophe probability in a patch.
- \( \pi \) The probability that a migrant survives dispersal.

### 2.2 Adaptive dynamics in the model

We now study the evolution of specialization in the model described above. Our agenda is as follows:

1. Study the dynamics of a metapopulation with only one strategy present and determine the attractors of the metapopulation.

2. Let one mutant enter the resident metapopulation at the metapopulation dynamical equilibrium. Mutants differ from residents only in their reproductive behavior according to equation (3). In a patch this mutant starts a new mutant clan.

3. Calculate how many new mutant clans an average mutant clan with strategy \( s_{\text{mutant}} \) is expected to initiate in the environment \( E_{\text{resident}} \) set by the resident. Let this quantity be

\[
R_0(s_{\text{mutant}}, E_{\text{resident}}).
\]
This quantity is analogous to the basic reproduction ratio familiar from the theory of infectious diseases. If \( R_0(s_{\text{mutant}}, E_{\text{resident}}) > 1 \), the mutant will be capable to invade the metapopulation. If \( R_0(s_{\text{mutant}}, E_{\text{resident}}) < 1 \), the mutation will sooner or later vanish from the metapopulation. This invasion criterion is equivalent with the one given by Metz et al. (1992), namely that the long-term exponential growth rate \( r(s_{\text{mutant}}, E_{\text{resident}}) \) is greater than 0.

We are interested in the invasion problem, i.e. whether the new mutant will be able to invade the resident metapopulation. In this initial phase the size of the local mutant population will remain small. We thus can assume that the effect of the mutant to the total local population size is negligible. This means that the equations defining the dynamics of the new mutant metapopulation are linear and fully determined by the dynamics of the resident metapopulation.

Despite the simplifying assumption (1) of uniform migration, numerical methods are needed in the practical calculation of the invasion fitness. See the Appendix A for details.

As we mentioned in the introduction, a metapopulation model largely corresponding to our model has been derived by Parvinen (2006). There the main focus is on the evolution of migration. The difference between the modeling approaches of Parvinen (2006) and ours is that our approach allows unified treatment of the resident and mutant reproduction in a sense that we use the same fitness function to find the resident equilibria and to calculate the fitness of a mutant whereas Parvinen (2006) analyzes the resident dynamics and the mutant dynamics separately.

3 Results

3.1 Parameter values

Once spatial factors are included into a model, dispersal becomes a central feature. Hence emigration probability is naturally a parameter of interest also in this model. Also the catastrophe probability \( c \) and local growth parameter \( r \) are potentially important parameters in metapopulation models. During the evolutionary analysis of the model we found that small variations in the probability \( \pi \) to survive dispersal did not significantly affect the adaptive dynamics of specialization. Altogether, we analyze the evolutionary consequences of varying \( e \) and \( r \) within appropriate limits. This analysis is done for two different values of catastrophe probability \( c \). This approach reveals all the significant evolutionary properties that we were able to detect from the model, at least for the case of a stable fixed point.

We start by presenting the results from the analysis of the case with a symmetric environment. That is, the availability distribution of the resource \( U \) is the mirror image of that of the resource \( V \). In this case there must naturally be a certain amount of symmetry in the invasion dynamics also. The results below have
been achieved using an environment with an equal amount of four different patch types. The resource availabilities \((u, v)\) in the patch types are \((1, 4), (2, 3), (3, 2)\) and \((4, 1)\). We assume a linear trade-off \((\alpha = 1)\) in the specialization between the two resources. If the probability \(k\) to survive in the disperser pool over one time unit is positive then the dispersers may spend several time units in the disperser pool without a possibility for reproduction. This is unrealistic in most biological scenarios. Thus we set \(k = 0\). This immediately implies that \(\pi = a\) (the probability to survive migration). This value is set to \(a = 0.82\).

When it is not explicitly mentioned, catastrophe probability has relatively small value, \(c = 0.05\), but for comparison we also present the essential parts of our results for a higher catastrophe probability, \(c = 0.25\). The emigration probability \(e\) is varied between 0 and 1. The values of the local growth parameter \(r\) affect crucially the structure of the attractors of the population dynamics of the metapopulation. The values of \(r\) are always chosen such that the population dynamical attractor of the metapopulation is a fixed point. See the next chapter for details.

### 3.2 Population dynamics of the monomorphic population

We start by studying the ecological dynamics of a monomorphic population. Because the methods we use in the numerical analysis are based on the assumption that the dynamical attractor of the metapopulation is a fixed point, we have to find a parameter range where this is the case.

In the traditional Ricker model the population is not viable when \(r\) is small. When \(r\) is increased the population comes viable and it has a stable fixed point equilibrium. As \(r\) is further increased the attractor undergoes a series of period doubling bifurcations and finally becomes chaotic. In our model a corresponding phenomenon can be observed as \(r\) is increased, but the values of \(r\) where the bifurcations occur are different.

For very low emigration probabilities the disperser pool size behaves as the population size in an ordinary Ricker model. Increasing migration first stabilizes the dynamics, but then starts to synchronize the dynamics in different patches and complicates again the structure of the attractors. This phenomenon has to some extent been studied before; see for example Gyllenberg et al. (1993) and references therein.

Altogether, we are able find a rather large domain of parameter values where the dynamical attractor of the metapopulation is a fixed point. In this article we focus on this parameter domain.

For the catastrophe probability \(c = 0.05\) we mainly let the local growth parameter \(r\) vary between 1.5 and 8.5 but present also some pairwise invadability plots for the case \(r = 9.5\). For the higher catastrophe probability \(c = 0.25\) local growth is varied only between 3.5 and 8.5 since for the small values of the local growth the metapopulation is no longer viable.
3.3 Evolutionary dynamics in a monomorphic resident population

For a monomorphic resident population (i.e., with only one strategy present) there is a convenient graphical method to illustrate which mutant strategies can invade and which cannot, namely, the pairwise invadability plot, or PIP (Metz et al., 1996; Geritz et al., 1997, 1998). In figure 1 we have collected several PIP:s for different values of $r$ and $e$. We have chosen the selection of PIP:s in figure 1 to illustrate the different types of evolutionary phenomena and bifurcations present in the model. A more extensive presentation of the evolutionary dynamics is given in the form of evolutionary bifurcation diagrams in figure 2.

The horizontal axis of each PIP corresponds to the set of all possible resident strategies and the vertical axis to the set of all possible mutant strategies. A white point in the PIP indicates that the corresponding mutant strategy can invade a population of the corresponding resident strategy. A black point indicates that the mutant cannot invade. The curve separating white and black regions in the PIP is the fitness contour curve given by the trait combinations where $R_0(s_{\text{mut}}, E_{\text{res}}) = 1$.

Assuming that only mutants slightly different from the resident can occur, we can confine the analysis of each PIP to a narrow strip along the main diagonal where the mutant and resident strategies are identical. For example, consider the PIP in the lower right corner of figure 1 with $r = 3.5$ and $e = 1$. From the black-and-white pattern it can be seen that a resident population of an arbitrary strategy $s < 0.5$ can be invaded by mutants with a slightly larger strategy but not by mutants with a slightly smaller strategy. The opposite is true for a resident population of any strategy $s > 0.5$. In this sense $s = 0.5$, the generalist, is evolutionarily attracting. Moreover, from the black-and-white pattern it can also be seen that a resident population with strategy $s = 0.5$ cannot be invaded by any nearby mutant and therefore is evolutionarily stable (ESS).

Strategy $s = 0.5$ is an example of a so-called evolutionarily singular strategy. Singular strategies are such points where the selection gradient is equal to zero

$$\left.\frac{\partial}{\partial s_{\text{mutant}}} R_0(s_{\text{mutant}}, E_{\text{resident}})\right|_{s_{\text{mutant}}=s_{\text{resident}}} = 0.$$ 

In the pairwise invadability plots, singular strategies lie at those points where fitness contour curves (boundaries between the black and white regions) cross the diagonal $s_{\text{mutant}} = s_{\text{resident}}$. A classification of all possible generic types of singular strategies and their interpretation is given by Geritz et al. (1997, 1998) and Metz et al. (1996). Thus, the singular strategy $s = 0.5$ in the PIP in the lower right corner of figure 1 is evolutionarily attracting as well as uninvadable (ESS) and represents an evolutionary endpoint. The singular strategy $s = 0.5$ in the PIP in the upper right corner has opposite properties. It is evolutionarily repelling and moreover can be invaded by every mutant. The strategy $s = 0.5$ is singular for
all values of $e$, $r$ and $c$, because the environment is symmetric. In what follows we refer to this strategy as the generalist singular strategy and to other singular strategies as non-generalist singular strategies.

Note that there is variation in the terminology used by different authors. Term ESS (evolutionarily stable strategy) (Maynard Smith, 1974, 1982; Maynard Smith and Price, 1973) is nowadays well established. Evolutionarily attracting strategies are also called convergence stable strategies (Christiansen, 1991). Eshel and coworkers (Eshel, 1983; Eshel and Motro, 1981; Eshel et al., 1997) called a convergence stable ESS a continuously stable strategy (CSS).

The singular strategy $s = 0.5$ in the PIP for $r = 3.5$ and $e = 0.7$ is evolutionarily attracting but invadable. A singular strategy of this type is called a branching point: close to the branching point the population becomes dimorphic such that with each successive invasion the two resident strategies become more and more distinct from one another (Geritz et al., 1997, 1998; Metz et al., 1996).

The PIP for $r = 7.5$ and $e = 0.95$ has three singular strategies. The generalist $s = 0.5$ is attracting but invadable, i.e., it is a branching point. The other two (non-generalist) singular strategies that are located symmetrically with respect to the generalist strategy are repelling. Given that the strategy of the initial population is sufficiently close to 0.5 branching will occur, otherwise the population will evolve to either $s = 0$ or $s = 1$, i.e. the population will specialize on a single resource.

When the emigration probability $e$ has small values the evolutionary possibilities are more limited. The PIP:s in this case are characterized by the fact that two strategies are almost always mutually invadable, i.e. there exists only a narrow black area around the diagonal in the PIP:s. Thus the metapopulation is liable to become dimorphic. However, if the largest possible mutation size is small enough compared to the width of the black area in the PIP, the metapopulation may still remain monomorphic. For low values of catastrophe probability this is always the case when mutational step size is small enough: evolution will end up to a fully specialized metapopulation with all individuals practicing strategy $s = 0$ or $s = 1$ depending on the initial strategy of the metapopulation. For higher catastrophe probabilities evolution to generalist strategy is possible also for low emigration probabilities. In this case the generalist strategy is a branching point. See the evolutionary bifurcation diagrams in figure 2 for details.

The collection of pairwise invadability plots in figure 1 only offers information of different evolutionary possibilities there exist for specific parameter values. More complete information of the evolutionary scenarios for different values of parameters $e$ and $r$ is collected to bifurcation diagrams in figure 2.

In area A evolution takes the monomorphic population towards a specialist strategy. The evolutionary endpoint is a monomorphic population playing either strategy $s = 0$ or strategy $s = 1$, depending on the initial state.

In areas B through E the generalist strategy in an evolutionarily attracting strategy. In areas B and E this attraction is global and in areas C and D there exist two evolutionarily repelling non-generalist singular strategies. These non-generalist
Figure 1: Pairwise invadability plots for different values of $r$ and $e$. Catastrophe probability $c = 0.05$ and the other parameter values are as described in chapter 3.1. The resident population dynamics is always stable within the parameter range presented here. White=invasion possible, Black=Invasion not possible.

singular strategies split the strategy space $[0,1]$ into three parts and the evolutionary dynamics of a monomorphic population will direct towards strategy 0, 0.5 or 1, depending on the initial state of the metapopulation.

Whenever evolution takes the population to the specialist strategy ($s = 0$ or $s = 1$), this strategy is also an endpoint of evolution. This is because the specialist strategies are usually not singular strategies but border values of the strategy space and thus their attractivity corresponds to uninvadability. Evolutionary branching may occur only in areas B and C where the generalist strategy is evolutionarily attracting but not uninvadable. In areas D and E the generalist strategy is an evolutionary endpoint.

Below we have listed the properties of different areas in figure 2:

- A: Generalist strategy repelling; evolution to monomorphic specialist population $s = 0$ or $s = 1$, depending on the initial value of $s$. 

\begin{align*}
\begin{array}{cccccc}
\text{r} & e = 0.7 & e = 0.9 & e = 0.95 & e = 0.99 & e = 1 \\
9.5 & + & + & & & \\
7.5 & & & & & \\
6.5 & & & & & \\
5.5 & & & & & \\
3.5 & & & & & \\
\end{array}
\end{align*}
Figure 2: Evolutionary bifurcation diagrams of the monomorphic population with respect to the local growth parameter $r$ and emigration probability $e$. In panel a $c = 0.05$ and in panel b $c = 0.25$. The other parameter values are as described in chapter 3.1. (Thin solid curve $\Leftrightarrow$ generalist attractivity, thick solid curve $\Leftrightarrow$ generalist ESS, dashed curve $\Leftrightarrow$ specialist attracting ESS.)

- B: Generalist strategy globally evolutionarily attracting branching point.
- C: Non-generalist evolutionarily repelling singular strategies exist; generalist strategy locally evolutionarily attracting branching point and specialist strategies locally evolutionarily attracting ESS’s.
- D: Non-generalist evolutionarily repelling singular strategies exist; generalist strategy and specialist strategies locally evolutionarily attracting ESS’s.
- E: Generalist strategy globally evolutionarily attracting ESS.

The curves bordering the different values have the following interpretations:

- Thin solid curve separates the areas where the generalist strategy $s = 0.5$ is evolutionarily attracting or not.
- Thick solid curve separates the areas where the generalist strategy is invadable (ESS) or not.
- Thin dashed curve separates the areas where the specialist strategies are or are not evolutionarily attracting and invadable.

The generalist strategy becomes attracting via a pitchfork bifurcation when crossing from A to C. At the same time two non-generalist singular strategies
appear symmetrically (due to the symmetry of the model) on either side of the generalist. When \( e \) is further increased these singular strategies move further and further away from the generalist and finally leave the strategy space \([0, 1]\) (transition from C to B or from D to E). The lower the value of \( r \) the faster the non-generalist singular strategies leave the strategy space. For very slow local growth increasing emigration seems to take one directly from area A to area B. In this case the non-generalist singular strategies leave the strategy space very rapidly, in practice immediately.

**Conclusions from the case \( c = 0.05 \)**

We first study the case \( c = 0.05 \) (figure 2a) in more detail and in the next section compare these conclusions to those drawn from the case \( c = 0.25 \) (figure 2b).

Reducing emigration probability turns the generalist strategy into a repellor. For low migration probabilities evolution ends up to a monomorphic specialist population (area A). Also, the smaller is the emigration probability, the smaller is the difference between two types required for mutual invadability. This phenomenon has a natural interpretation: when there is only very little migration, the local populations live in a virtual isolation. Thus when there are no migrants from the disperser pool, the better competitor will always take over the patch. Hence in the symmetric environment both competing types will always have patches that they can take over. Thus they will be able to coexist if the emigration probability is small enough.

While emigration probability is increased such that the transition from area A to area C occur, one crosses a threshold value where two new singular strategies appear next to the singular generalist strategy. Due to the symmetry of the environment, these singular strategies are placed symmetrically on either side of the generalist. These non-generalist singular strategies are repelling and the generalist becomes attracting, but the extreme specialist strategies still preserve their attractivity (areas C and D). When the emigration probability is further increased, these non-generalist singular strategies move further and further away from the generalist. While these singular strategies remain in the interval \([0, 1]\) of possible strategy values, the extreme specialists (\( s = 0 \) and \( s = 1 \)) remain evolutionarily attracting even though the basin of attraction of the generalist strategy expands.

When the local growth parameter \( r \) has values small enough, the non-generalist singular strategies finally leave the interval \([0, 1]\) when emigration probability is increased. Then the generalist strategy turns into a globally attracting singular strategy (areas B and E). Slow local growth favors generalism. The faster the local growth, the higher is the emigration probability required for the generalist strategy to be attracting. For high values of the local growth parameter \( r \) the processes described above do not occur for emigration probabilities in the interval \([0, 1]\) and hence the generalist strategy remains repelling for all emigration probabilities.

Evolutionary branching is possible, and occurs usually for intermediate pa-
rameter values (areas B and C). When there is no branching, we already know that the evolution will end up to one of the strategies (0, 0.5, 1) and the next question to study is naturally: What will happen to a dimorphic population after branching? We shall address this question in chapter 3.4.

Comparison to the case $c = 0.25$

The results described in preceding section were achieved using catastrophe probability $c = 0.05$. The bifurcation diagram in figure 2b corresponds to the bifurcation diagram in figure 2a, but now the catastrophe probability is 0.25. Only a smaller parameter domain has now been studied because maintaining the viability of the metapopulation now requires faster local growth since catastrophes are more frequent.

Figures 2a and 2b mainly differ from each other in the domain where both emigration probability $e$ and local growth parameter $r$ have low values. In this domain the generalist strategy is evolutionarily repelling when $c = 0.05$ (panel a) but when $c = 0.25$ (panel b) it is a branching point. This means that evolutionary branching may occur in a considerably larger parameter domain when catastrophe probability is higher. In other words, in our model increased stochasticity promotes generalism in a monomorphic resident population. The benefit obtained by the generalist strategy is sufficient such that the evolution of a monomorphic population will lead to generalist strategy but as soon as the population becomes dimorphic the generalist strategy will become outcompeted and evolutionary branching occurs.

In figure 2a the relationship between parameter values and the evolutionary dynamics is always monotonous. In figure 2b increasing emigration probability from zero first debilitates the evolutionary capabilities of the generalist but increasing emigration probability further again improves these capabilities. This non-monotonicity in the relation between emigration probability and the evolutionary dynamics is not just a peculiarity of certain parameter combinations but rather generally present in the model. The relations between the values of the other parameters and the evolutionary dynamics are, however, monotonous as far as we have observed.

The effects of the structure of the environment

In figure 3 we again have a pair of evolutionary bifurcation diagrams. These diagrams correspond to those in figure 2, but now we have same catastrophe rate $c = 0.05$ in both of the panels. Instead we have changed the structure of the environment. In figure 3a the environment consists of equal amount of only two patch types with resource availabilities (1,4) and (4,1) whereas in figure 3b the environment consists of patches with resource availabilities (2,3) and (3,2). In other words, compared figure 2a we first let the environment to consist only of those
Figure 3: Evolutionary bifurcation diagrams where the environment consists only of two patch types. In panel a the difference between the resource availabilities in patches is rather large (1 vs 4) and in panel b small (2 vs 3). Catastrophe probability $c = 0.05$ and the other parameters as described in chapter 3.1. (Thin solid curve ⇔ generalist attractivity, thick solid curve ⇔ generalist ESS, dashed curve ⇔ specialist attracting ESS.)

patches where the differences between the resource availabilities are large (figure 3a) and secondly of those patches where the differences between the resource availabilities are small (figure 3b).

Figure 3a is virtually similar to figure 2a. Also figure 3b shares many qualitative features with figure 2a, but now the area where the non-generalist singular strategies exist is virtually absent. Altogether one may observe that in the combined environment the evolutionary dynamics are almost completely defined by the dynamics in more distinct patches.

The role of the trade-off structure

In our model the parameter $\alpha$ defines the strength of the trade-off through the equation $q_i(s) = s^\alpha u_i + (1 - s)^\alpha v_i$ defining the quality of a type $i$ patch to a strategy $s$ individual. In figure 4 we have again a pair of bifurcation diagrams that correspond to that in figure 2a. In figure 4 catastrophe probability $c = 0.05$ and the environment consist of the four patch types as in figure 2a but now different values are given to the trade-off parameter $\alpha$. In panel a we have $\alpha = 0.95$ and in panel b $\alpha = 1.05$. The interpretation of different areas is similar to those in figure 2a but now in panel a a qualitatively new feature enters in area H. In area H both the generalist strategy and the two specialist strategies are evolutionarily repelling and there exists two evolutionarily attracting non-generalist singular strategies. These
non-generalist singular strategies are, however, branching points. After branching evolution takes the dimorphic population to the combination of the two extreme specialists. Thus, no new evolutionary endpoints are found in area H even if the roads to these endpoints are different. We are not aware of any articles where such evolutionary behavior would have been observed in population models without spatial structure. In metapopulation context this evolutionary scenario has been observed by Parvinen and Egas (2004).

In case $\alpha < 1$ there is an additional benefit to the generalist. By comparing figures 2a and 4a one may note that this benefit only slightly enlarges the area where the generalist strategy is an evolutionary endpoint (area E). The main difference between two diagrams is that in case $\alpha = 0.95$ the parameter range where evolutionary branching occurs is much larger than in the case $\alpha = 1$. Branching takes place such that the evolution of the monomorphic population first converges either to the generalist strategy (area B) or to one of the two non-generalist branching points (area H), where branching occurs.

Since $\alpha \neq 1$ in figure 4 the exact locations of the dashed curves depend slightly on the definition of possible sizes of mutational steps. The reason for this is explained in Appendix B. In figure 4 the mutational step size is 0.01.
3.4 Evolutionary dynamics in a dimorphic resident population

In this chapter we study the question what will happen to a dimorphic population after evolutionary branching. For this purpose we have collected two series of pictures in figure 5 that are very much related to pairwise invadability plots. These pictures describe the expected course of evolution in a dimorphic population. The axis in these pictures correspond to the strategies of the two resident populations. The black areas in the pictures indicate that the two corresponding resident strategies are not mutually invadable. The arrows in the white areas indicate the feasible courses of evolution in a dimorphic population in these areas. These pictures are symmetric across the diagonal $s_1 = s_2$, because the labelling of the strategies present is arbitrary.

![Figure 5: Expected directions of evolution in a dimorphic population for different values of $e$ when $r = 7.5$ (upper row) and when $r = 4.3$ (lower row). The other parameter values are as described in chapter 3.1 (Black = No mutual invadability).](image)

From figure 5 one may note that for smaller values of the emigration probability $e$ the generalist strategy is evolutionary repelling (case $e = 0.9$ on the upper row ($r = 7.5$) or an evolutionarily attracting branching point (case $e = 0.95$ on the upper row ($r = 7.5$) and case $e = 0.8$ on the lower row ($r = 4.3$)). In the other cases no branching occurs and the generalist strategy is an ESS. When the generalist strategy turns from a branching point into an ESS, two repelling dimorphic singular strategies appear symmetrically on either side of the generalist, but the
combination of the two extreme specialists (strategies 0 and 1) still maintains its attractivity (cases $e = 0.97$, and $e = 0.995$ on the upper row ($r = 7.5$) and cases $e = 0.82$ and $e = 0.84$ on the lower row ($r = 4.3$)). For some parameter values the combination of the two extreme specialists may finally lose its attractivity (case $e = 0.88$, $r = 4.3$).

Since the combination of the two extreme specialist strategies is a corner point of the strategy space and not a dimorphic singularity, its evolutionary attractivity corresponds to its uninvadability. Thus it is an evolutionary endpoint whenever it is reached by evolution.

One may note that the isoclines of the direction of dimorphic evolution connect to the borders of the area of mutual invadability as described by Geritz et al. (1999).

Our detailed numerical analysis of the evolutionary dynamics of a dimorphic population suggest that whenever branching occurs evolution ends up to the combination of the two extreme specialists. The combination of the two specialists is an endpoint of the dimorphic evolution also whenever one specialist strategy alone is an endpoint of the evolution of a monomorphic population. Thus, whenever evolutionary branching occurs, the small mutational steps will take the dimorphic evolution to the combination of the two extreme specialists. This is illustrated in figure 6, where we have plotted the outcome of an evolutionary simulation where $r = 3.5$, $e = 0.7$ and $c = 0.05$ (see a corresponding pairwise invadability plot from figure 1). This simulation is not an individual based simulation but it is based on the repeated iterations of the metapopulation dynamics and infrequent insertions of new mutants with strategy close to one of the strategies of the residents. Naturally we have a large number of patches instead of an infinite number of patches. We start the simulation with a monomorphic population playing strategy $s = 0.3$. On the horizontal axis is the evolutionary time and on the vertical axis we have marked all the strategies present just before the introduction of the next mutant.

4 Discussion

4.1 Results revisited

In short, our results state that in the model under consideration evolution starting from a monomorphic population may have the following four different endpoints for different parameter values:

1–2 Evolution may favor specialism. In this case it depends on the initial state on which resource the population specializes.

3 Evolution of a monomorphic population may also lead to generalism. In this case the parameter values define whether it is an evolutionary endpoint or a branching point.
Whenever branching occurs the population will end up to a combination of the two extreme specialists.

For intermediate parameter values non-generalist singular strategies may exist. In our model these strategies are typically evolutionarily repelling but there are also specific parameter combinations for which these non-generalist singular strategies are evolutionarily attracting. These strategies, however, are in our model never evolutionarily uninvadable. Thus, even in the cases where they are attracting, branching occurs and evolution ends up to the combination of the two extreme specialists.

The possibility of four different endpoints of evolution has been observed also in previous studies on evolution of specialization (Meszéna et al., 1997; Parvinen and Egas, 2004).

It was also shown that slow local growth favors generalism (figure 2). In other words, it enlarges both the parameter domain where the generalist strategy is evolutionarily attracting and the parameter domain where the generalist strategy is an ESS. This has the following natural explanation. Whenever the local population size in a patch is very small (after a catastrophe), all strategies produce approximately same local growth independently of the strategies. The competition between the individuals with different strategies does not take effect before the density dependence starts to affect the growth of the population. Consider first a patch where resource $U$ is abundant and resource $V$ scarce and compare a generalist with a specialist on resource $V$. When the total population size increases, the first ones to suffer from overcrowding are the maladapted specialists. The size of the specialist subpopulation starts to diminish as soon as the total population size
exceeds the patch quality witnessed by the specialists. Let this threshold value be \( q_1 \). Given that no catastrophe takes place in the patch, the generalist can finally outcompete the maladapted specialist from the patch. Due to the symmetry of the environment there is an equal amount of patches described above and patches where the resource availabilities are reversed. In the latter patches the specialist can outcompete the generalist. In these patches the size of the generalist subpopulation starts to diminish as soon as the total population size exceeds the patch quality witnessed by the generalist. Let this threshold value be \( q_2 \). One may easily deduce that \( q_1 < q_2 \). Take now a random patch and assume that there are no catastrophes for a sufficiently long time such that density dependence has time to affect. With probability 0.5 the patch is such that the generalist may outcompete the (maladapted) specialist. Also with the same probability the patch is such that the (well-adapted) specialist may outcompete the generalist. But, since \( q_1 < q_2 \) the generalist can outcompete the badly specialized specialist faster than the specialist can outcompete the generalist. The slower is the local growth, the bigger is the difference in these outcompeting times since the longer it takes for the total population size to increase from \( q_1 \) to \( q_2 \).

Also, the more often local catastrophes occur, the more often occur also the competitions described above. Thus the same phenomenon explains also the observation that high catastrophe probability favors generalism (compare 2a and 2b). Furthermore, increased stochasticity in the model (i.e. higher catastrophe probability) enlarges the parameter domain where evolutionary branching occurs. One biological explanation to this phenomenon is that as long as the resident population is monomorphic, the more generalized strategy can always outcompete the more specialized strategy because of the mechanism described above. But as soon as the resident population becomes dimorphic, there are no longer patches where the generalist would be the superior competitor and thus the generalist population becomes outcompeted by the two more specialized populations. However, this explanation obviously requires more detailed analysis.

Also the non-monotonous relation between the evolutionary dynamics and the emigration probability also calls for further research. This phenomenon has no immediate biological explanation and it has not been observed before.

In fact, we also found parameter values for which the two extreme specialists and the generalist can coexist (not illustrated in this article). This coexistence was observed only when \( \alpha < 1 \) and was essentially due to the this additional benefit for the generalist, since when \( \alpha < 1 \) we were able to create environments that simultaneously contain patches where the generalist is a superior competitor, patches where the specialist on resource \( U \) is a superior competitor and patches where the specialist on resource \( V \) is a superior competitor. Even though there was the possibility of coexistence, we were not able to find any evolutionary scenarios where small and infrequent mutational steps could lead to such a situation. This observation suggests that the models, for example (Wilson and Yoshimura, 1994), where this kind of coexistence is suggested to occur, would require also
evolutionary analysis.

The traditional interpretation of the principle of competitive exclusion (Armstrong and McGehee, 1980; Hardin, 1960) states that at steady state there cannot be more species (strategies) than there are resources. At first sight the above mentioned coexistence of three strategies therefore seems to violate this principle. However, as pointed out by Diekmann et al. (2003) (see also Gyllenberg and Meszéna (2005) and Meszéna et al. (2006)) the principle of competitive exclusion should be formulated as follows:”The maximum number of species (strategies) that can robustly coexist at steady state is less than or equal to the dimension of the interaction variable.” Roughly speaking, the interaction variable contains the information about the nonlinear feedback and thus the model becomes linear if its value is assumed to be known. Whether the components of the interaction variable can be interpreted as resources or not, is irrelevant. In our model the interaction variable contains the vector of the sizes of the dispersal pools of the different strategies present. Thus the dimension of the interaction variable is always larger than the number of competing strategies (or coexisting species). Therefore the introduction of one new strategy increases the dimension of the interaction variable by one. Hence there is no conflict between our result and the principle of competitive exclusion.

4.2 Comparison with previous studies

There are essentially two different approaches to include different resource availabilities into models of resource competition and specialization on resource utilization. The simpler approach assumes only a finite number of distinct resources (MacArthur and Levins, 1964; Matsuda and Namba, 1989; Levins, 1979; Li and Smith, 2003; Schreiber and Tobiason, 2003; Ma and Levin, 2006). In many biological scenarios it is more realistic to assume that there exists a continuum of resources, or in other words, a single resource having a continuously varying character that is distributed on the real line, often according to the Gaussian distribution (Day, 2000, 2001; Dieckmann and Doebeli, 1999; Doebeli and Dieckmann, 2004; Egas et al., 2005; Kisdi, 2002; Kisdi and Geritz, 1999a; Wilson and Richards, 2000). This approach links directly to the more traditional study of ecological character displacement and the study of niche widths (Ackermann and Doebeli, 2004; Abrams, 1986; Brown and Wilson, 1956; Doebeli, 1996; Mizera and Meszéna, 2003; Roughgarden, 1972; Slatkin, 1980) and to the theories of optimal foraging (MacArthur and Pianka, 1966; Pyke, 1984; Stephens and Krebs, 1986). In addition to the biological realism it also enables one to add many other biologically interesting features like metabolic aspects and foraging behavior to the model (Egas et al., 2005; Wilson and Richards, 2000).

The main drawback of the models with continuous resource distribution is that it is difficult to include spatial aspects into them. Day (2001) analyzed a patch model with continuously varying resource availability, but all patches were
assumed to be identical and also no local catastrophes had been taken into account. In fact, the spatial model there was built mainly for a single purpose, to show that spatial structure of the resources may prevent speciation when genetic issues are taken into account. One way to include spatial aspects into these models is to resort to individual based models (Kawata, 1996; Doebeli and Dieckmann, 2000, 2004). Kawata (1996) studied whether selection is in the case of two competing species more likely to lead to character displacement or to competitive exclusion. He concluded that both scenarios were possible, but competitive exclusion was much more likely to occur in the parameter range under consideration. Doebeli and Dieckmann (2000, 2004) claimed, opposite to Day (2001), that evolutionary branching is a common and robust phenomenon that is often even an appropriate tool for predicting speciation in sexual populations.

On can add spatial heterogeneity to individual based models simply by letting the location of each individual to define the resource availabilities for this individual. However, the results from such models should, whenever possible, be backed up by corresponding conclusions drawn, for example, from metapopulation theory. Thereby, a more simplified model is required in order to be able to build tractable metapopulation models for specialization on resource utilization. We have chosen the most simple way: to study the specialization on the utilization of two alternative resources. This simplification enables us to study the evolution of specialization on resource use in a structured metapopulation model with local catastrophes.

The approach using two different resources has also been used in the setting of ordinary population models (Abrams, 1986, 1999; Ma and Levin, 2006; Lawlor and Maynard Smith, 1976; Schreiber and Tobiason, 2003). Schreiber and Tobiason (2003) studied a model where individual’s strategy set the portions of search effort allocated to the search of different resources. In this approach the trade-off between resources becomes automatically linear. They studied four resource types: antagonistic, complementary, essential and perfectly substitutable. Although their approach is very different from ours, there is a kind of correspondence between our model and their case of perfectly substitutable resources. For this case they conjectured that the evolution of a monomorphic population should lead towards generalist strategy, which is evolutionarily stable. Our results show that this conclusion cannot be generalized to other models. Abrams (1999) built his evolutionary analysis on the assumption that the rate of evolution is proportional to the corresponding rate of change in the individual fitness (Lande, 1976; Taylor and Day, 1997), but his interest was mainly in the interplay between the dynamics of the resources and the evolution of the consumer. In (Abrams, 1986) a model with two competitors and two resources was analyzed. There the main interest was in the ecological character displacement and niche shift and thus also the modelling approach was different. The conclusions Abrams drew concerning the possible outcomes of evolution are in accordance with ours. The other conclusions can not be compared due to the different modelling approach. Lawlor
and Maynard Smith (1976) studied the evolutionary dynamics of the consumers in a model with two consumers and two resources. They concluded that evolution was liable to reduce the competition between the consumer species. This is in accordance with our results concerning the evolutionary dynamics of a dimorphic population, namely that evolution takes the dimorphic population to the combination of the two extreme specialists.

Ma and Levin (2006) use the adaptive dynamics approach to study the evolution of resource adaption in a spatially unstructured continuous time model with two distinct resources ($R_1$ and $R_2$). They study the system

\[
\frac{dR_1}{dt} = r_1 R_1 \left[ 1 - R_1 - \sum_i \beta_1(s_i)C_i \right]
\]

\[
\frac{dR_2}{dt} = r_2 R_2 \left[ 1 - R_2 - \sum_i \beta_2(s_i)C_i \right]
\]

\[
\frac{dC_i}{dt} = C_i \left[ -1 + \gamma_1 \beta_1(s_i)R_1 + \gamma_2 \beta_2(s_i)R_2 \right],
\]

where $s_i$ denotes the strategy of the consumer $C_i$. From this simple system they derive analytic results that relate the evolutionary dynamics to the signs of $\beta''_1(s)$ and $\beta''_2(s)$. They assume that these signs are always the same. The case with $\beta''_1 < 0$ corresponds in our model to the case $\alpha < 0$ (additional benefit of generalism) and the case with $\beta''_1 > 0$ to the case with $\alpha > 0$ (additional cost of generalism). Ma and Levin (2006) show that if $\int_0^1 \beta''_i(s)ds \gg 0$ specialist strategies are evolutionary endpoints. They also show that non-specialist singular strategy $s^*$ (which in their model does not have to be the unbiased generalist) is locally evolutionarily attracting if $\beta''_i(s^*) \ll 1$ and that if $\beta''_i(s^*) > 0$, then $s^*$ is a branching point and else an ESS. Altogether, Ma and Levin (2006) find the same four different evolutionary endpoints present also in our model. Also the sign of $\beta''_i$ affects the evolutionary dynamics in the same way as the sign of $\alpha$ in our model.

Whenever there are only two patch types and the availabilities of the resources are constant in each patch, there is no difference between our modeling approach and the modeling approach of the models of habitat specialization (Brown, 1990; Brown and Pavlovic, 1992; Egas et al., 2004; Kisdi, 2002; Parvinen and Egas, 2004; Van Dooren, 1999; Van Tienderen, 1991). This connection is explained in the Introduction. A continuous time metapopulation model with local catastrophes for the evolution of specialization on patch usage with an infinite number of patches but only two different patch types was studied by Parvinen and Egas (2004). Their results are in accordance with ours, although they did not observe the surprising character of our model that increased catastrophe probability may promote evolutionary branching. Brown (1990) analyzed the course of evolution in a metapopulation using the approach of evolutionary game theory. Although his approach is very different from ours, the possible endpoints of evolution are equivalent to ours whenever the environment is not uneven.
Many mathematical problems can be solved if one assumes that there are only two – or finite number of – local patches. In fact, when there are no local catastrophes, there is no need to distinguish the models with exactly two patches from the models with an arbitrary number of patches but only two patch types. Evolution of specialization on patch use or resource utilization in this type of models has been studied by several authors (Abrams, 1999; Brown and Pavlovic, 1992; Day, 2000; Egas et al., 2004; Kisdi, 2002; Kisdi and Geritz, 1999a; Levins, 1962; Meszéna et al., 1997; Van Dooren, 1999; Wilson and Yoshimura, 1994). Of these especially Meszéna et al. (1997) is noteworthy in this context because there the manners of representation are very similar to ours and in their model the same four possible endpoints of evolution are possible that were also found in our model. Meszéna et al. (1997) found that if the two patches in their model were strongly connected by migration, the generalist strategy was an evolutionarily attracting ESS. When migration was weakened the generalist strategy first became a branching point and finally lost its evolutionary attractivity. This result is in complete accordance with our results. However, since they used only two patches they were not able to study the phenomena related to local catastrophes.

In his now classical studies Levins (1962, 1963) introduced the concept of fitness sets. In our model case $0 \leq \alpha < 1$ corresponds to the case with convex fitness set and case $\alpha > 1$ to the case with concave fitness set. Levins predicted, based on the analysis of model with frequency independent selection that in the case of concave fitness sets evolution should end up to monomorphic specialist population and in the case of convex fitness sets to generalist population. In our results all the four possible endpoints are present both in the case $\alpha = 0.95$ and in the case $\alpha = 1.05$. Later Levins’ fitness set approach has been extended to include also frequency dependent selection (Rueffler et al., 2004, 2006). This extended approach also predicts the possibility of branching in the evolution of specialization (Rueffler et al., 2006).

Brown and Pavlovic (1992) considered the effects of migration to the combination of evolutionarily stable strategies when population dynamics was given either by the logistic equation or by explicit resource–consumer equations and the environmental variability was either fine- or coarse-grained. The case with coarse-grained environment resembles our modelling approach and also the conclusion in this case is similar to ours, namely that for low values of migration there exists two evolutionarily stable specialist strategies but for high values only one evolutionarily stable generalist strategy. The possible coexistence of three ESS’s (two specialists and the generalist) observed in our model was not observed by Brown and Pavlovic (1992).

Wilson and Yoshimura (1994) presented an overview on published works on specialization but besides that merely demonstrated that for a certain two patch model and for certain parameter values two specialists and a generalist can coexist. This result, as noted before, would require detailed evolutionary analysis. In fact in some recent articles (Abrams, 2006a,b; Egas et al., 2004) this analysis is
performed for different extended versions of the model of Wilson and Yoshimura. Egas et al. (2004) found that the coexistence of the specialists and the generalist was attainable even by small mutational steps, but this required very high foraging accuracy and strong temporal variability in resource availabilities. Abrams (2006a,b) extended the model by adding explicit resource dynamics to it and showed that in the extended model evolution towards the trimorphic coexistence of the two specialists and the generalist was a rather common scenario.

A two patch model focusing on the evolution of specialization on resource utilization was analyzed by Day (2000). There he used a kind of a hybrid approach: he assumed that the single resource in the model has a continuously distributed characterizing variable, but he also assumed that there are two different patch types with different resource distributions. He assumed logistic local growth in the patches whereas we assume growth according to the Ricker model. Day (2000) compared the traditional models of character displacement to his two patch model of ecological character displacement and mainly focused on the question whether the models predict disruptive or convergent selection. He found out that spatial heterogeneity does not necessarily favor disruptive selection. He also found that the parameters describing emigration and local growth were evolutionarily crucial, as was the case in our model also. Day analyzed different combinations of resource availabilities. Of these the case where the resource distributions in the two patches are mirror images of each other corresponds to the environment we analyzed in this paper. Days results on the connection between the parameter values of emigration and local growth were astonishingly similar to our results. However, because he used only a finite number of patches he was not able analyze the effect of local catastrophes in his model.

Generally, in a model including only finite number of patches one cannot include one central feature of metapopulation models – the frequent but random local catastrophes. Only in (Kisdi, 2002) temporal fluctuations were taken into account by allowing “good” and “bad” years independently in each patch. Kisdi presented interesting results on the co-evolution of dispersal and specialization on patch usage. However, since she mainly focused on the evolution of dispersal and habitat specialization was only studied as a counterpart affecting the evolution of dispersal, there is no possibility to compare her results to ours.

Whenever evolution is studied, genetic issues should never be neglected, especially in a spatially heterogenous settings (Day, 2001; Fry, 1996; Kisdi and Geritz, 1999a; Van Tienderen, 1991; Van Dooren, 1999; Via, 2002; Weissing, 1996). The adaptive dynamics approach usually assumes clonal or haploid reproduction. Thus it is of interest to find out to what extent can one generalize the results of adaptive dynamics to diploid populations. Kisdi and Geritz (1999a) studied the course of evolution of a diploid population in a two patch model incorporating Levene’s soft selection approach. They concluded that in their model the evolutionary dynamics of haploid and diploid populations are similar as long as the resident population remains monomorphic but for the polymorphic resi-
dent populations the diploid case can produce much richer evolutionary patterns. Also Hammerstein (1996); Taylor and Day (1997) and Weissing (1996) considered the differences between the predictions made by models of genetic and phenotypic evolution and deduce that for some extent the phenotypic models can be used to approximate the genetic models. Doebeli and Dieckmann concentrated on the phenomenon of evolutionary branching (Doebeli and Dieckmann, 2000, 2004; Dieckmann and Doebeli, 1999) and claimed that the phenotypic modeling can be used to predict evolutionary branching whenever assortative mating can be assumed. Van Tienderen (1991) analyzed the evolution of specialization using genetic models in an environment consisting of two patch types. He concluded that under Levene's soft selection model evolution will always end up to a monomorphic population, but under hard selection also dimorphic or even trimorphic endpoints are possible.

To conclude, our results offer a new point of view to the field of the evolution of specialization on resource utilization. They are consistent with the previous studies on this field. In general, structured metapopulation models are a significant and useful tool when studying evolutionary dynamics. Thus it is important to study also the evolution of specialization on resource use in the context of structured metapopulations. This requires the use of the several simplifications that we have made, but still our results intensify the knowledge on this field significantly.

### 4.3 Topics for further research

We have already mentioned many questions that require further analysis. Until now we have only analyzed the most simple case with the symmetric environment and the results presented here can only serve as a starting point for further research.

The first and most important topic for further research is to add resource dynamics to the model. It is more than natural that increasing population density should directly decrease the share that an individual gets of each resource, of course depending on the strategies of competing individuals in the patch. In the present formulation it is more or less unclear how this reduction takes place. Thus one should rework the basic model to include competition for resources in the local dynamics or even explicit resource dynamics. The most natural way to include the resource dynamics is to follow the guidelines given by the mechanistic underpinning of discrete time population models without spatial structure (Geritz and Kisdi, 2004).

Already in the present setting it would be important to study the nonsymmetric environments. This should be done both altering the frequencies of the patch types and the patch types themselves.

It was shown that high emigration probability favors generalism, see figures 2a and 2b. This is quite natural since migrants were assumed to choose their target patches at random. In future it might be of interest to study the case in which
migrants are able to select their target patches according to their properties, and compare such a situation with the results from the optimal foraging theory and from the theory of habitat selection (Richards and De Roos, 2001; Rosenzweig, 1981).

Until now we have completely ignored genetic issues in our research. Although there are several studies (Doebeli and Dieckmann, 2000; Geritz and Kisdi, 2000; Kisdi and Geritz, 1999a,b; Weissing, 1996) indicating that the asexual adaptive dynamics approach can for some extent predict also the evolutionary outcomes in sexual populations, it would be important to consider also the effects of genetic structures in this model. Quantitative genetic models have been widely used in the study of ecological character displacement and speciation (Drossel and McKane (1999, 2000); Kawecki and Abrams (1999); Taper and Chase (1985), see also (Abrams, 2001) and (Taylor, 1996) for comparison between different modeling approaches). It would be interesting to try to fit our model to this approach and compare the results.

Appendix A

Invasion fitness of the mutant

Our methods of calculation are based on the assumption that the metapopulation always converges to a fixed point attractor in the sense that the size of the disperser pool stabilizes to some fixed value for each strategy present in the metapopulation. We have to take this assumption into account when defining the parameter values.

The catastrophe probability is assumed to have constant value. This, together with the discrete time dynamics immediately implies that the time elapsed since the latest local catastrophe in a single patch is geometrically distributed. The probability function of this distribution is \((1-c)^t\). Together with the assumption of the constant size of the disperser pool for each strategy this means that once we know the disperser pool sizes we immediately can also calculate the size distributions \(\eta_i(t, s)\) for all patch types \(i\) and strategies \(s\). From the assumption of the steady state metapopulation it immediately follows that \(\eta\) has to be independent of time \(t\). Due to the local catastrophes and discrete time dynamics of the model \(\eta\) is a discrete measure independently of the initial population size distribution and thus integration in the disperser pool size equation (2) simplifies into a summation.

Consider now a monomorphic resident population with strategy \(s_r\) and fix the disperser pool size to \(D\) in a metapopulation. Let \(\psi_i(t, s, D)\) be the local population size of a strategy \(s\) population in a type \(i\) patch \(t\) time units after the latest local catastrophe in this patch when the disperser pool has size \(D\). We can calculate \(\psi_i(t, s, D)\) recursively from

\[
\begin{align*}
\psi_i(0, s, D) &= a_i(s)D \\
\psi_i(t + 1, s, D) &= \left(1 - e_i(s, \psi_i(t, s, D))\right) f_i(s, \psi_i(t, s, D)) \psi_i(t, s, D) + a_i(s)D
\end{align*}
\]
Let now a disperser with strategy $s_m$ enter a type $i$ patch where the local dynamics is given by $\psi_i(t, s_r, D)$ when $t_0$ time units has elapsed since the latest local catastrophe. This disperser initiates a new local clan. By the basic assumptions of the adaptive dynamics approach the dynamics of this clan are determined by the population size of the local population in the patch. Thus the dynamics of the clan is linear and furthermore, since we are interested only in the disperser production per one incoming disperser, we can assume that the initial size of the clan is equal to one. Let now $y_i(t, t_0, s_m, s_r, D)$ be the size of a strategy $s_m$ clan initiated in a type $i$ patch $t_0$ time units after the latest local catastrophe in this patch. We can calculate $y_i$ from the formula

$$y_i(t, t_0, s_m, s_r, D) = \prod_{\tau=t_0}^{t} \left( 1 - e_i(s_m, \psi_i(\tau, s_r, D)) \right) f_i(s_m, \psi_i(\tau, s_r, D)).$$  (4)

This clan is expected to produce

$$\omega_i(t_0, s_m, s_r, D) = \Phi(s_m) \sum_{t=t_0}^{\infty} (1 - c)^{1+t-t_0} e_i(s_m, \psi_i(t, s_r, D)) y_i(t, t_0, s_m, s_r, D)$$

new successful migrants. Quantity

$$\Phi(s) = \frac{\sum p_i a_i(s)}{1 - k + k \sum p_i a_i(s)}$$

is the probability that a strategy $s$ disperser survives migration. The probability that a single disperser ends up to a type $i$ patch that has avoided the local catastrophes for $t_0$ time units is

$$\rho_i(t_0) = \frac{p_i a_i(s)}{\sum_i p_i a_i(s)} (1 - c)^{t_0} c.$$

Thus, given that strategy $s_r$ resident population has disperser pool size $D$, a strategy $s_m$ disperser is expected to produce

$$E(s_m, s_r, D) = \sum_i \rho_i(t_0) \omega_i(t_0, s_m, s_r, D)$$

new dispersers.

In a steady state each disperser must in average produce exactly one new disperser. Thus we can solve the disperser pool size for a monomorphic strategy $s_r$ population from the fixed point equation

$$E(s_r, s_r, D) = 1.$$ 

Let $D^*(s_r)$ be the solution to this equation. Then

$$R_0(s_m, s_r) = E(s_m, s_r, D^*(s_r))$$
is the expected number of new dispersers produced by one average strategy \( s_m \) disperser in the environment set by strategy \( s_r \) resident metapopulation. This quantity can be used as invasion fitness to determine whether the mutant with strategy \( s_m \) is capable to invade the resident metapopulation with strategy \( s_r \). Invasion is possible if \( R_0(s_m, s_r) > 1 \).

Similar reasoning can be applied also when the resident population is polymorphic; the only difference is that solving the fixed point problem has to be done in several dimensions and thus becomes more complicated.

The calculations above involve infinite summations. These do not constitute a problem since the longer time elapses after a catastrophe, the closer the local population approaches its steady state and thus we are able to derive analytic approximations to the tails of the summations. In fact, the following handy shortcut has been presented by Parvinen (2006) to reduce the double summation into a single one.

**An efficient algorithm**

Let again \( \psi_i(t, s_r, D) \) describe the size of the local resident population in a type \( i \) patch \( t \) time units after the latest catastrophe when the resident metapopulation has strategy \( s_r \) and disperser pool size \( D \). After one time unit the newborn clan founded by a strategy \( s_m \) disperser is expected to have sent out

\[
\Theta_i(t_0, s_m, s_r, D) = (1 - c) f_i(s_m, \psi_i(t_0, s_r, D)) \]

new dispersers. Fraction \( \Phi(s_m) \) of these is expected to be successful in founding new clans. Simultaneously the clan is also expected to have produced

\[
\Lambda_i(t_0, s_m, s_r, D) = (1 - c) (1 - e_i(s_m, \psi_i(t_0, s_r, D))) f_i(s_m, \psi_i(t_0, s_r, D))
\]

individuals that remain in the same patch and are thus expected to produce

\[
\Lambda_i(t_0, s_m, s_r, D) \omega_i(t_0 + 1, s_m, s_r, D)
\]

successful dispersers more. This reasoning shows that \( \omega_i \) satisfies the recursive equation

\[
\omega_i(t_0, s_m, s_r, D) = \Phi(s_m) \Theta_i(t_0, s_m, s_r, D) + \Lambda_i(t_0, s_m, s_r, D) \omega_i(t_0 + 1, s_m, s_r, D).
\]  

(6)

On the other hand we also know that the resident population size in each patch approaches a fixed point as time elapses and no catastrophes occur. Let now time \( T \) be such that

\[
\psi_i(T, s_r, D) \approx \psi_i(T + t, s_r, D) \quad \forall t \in \{0, 1, 2, 3 \ldots \}.
\]
The actual value of $T$ naturally depends on $s_r$ and $D$ as well as on the criterion of the approximate equality. Now the size of a clan initiated at time $T$ is by definition (4) simply

$$y_i(t, T, s_m, s_r, D) = \left( (1 - e_i(s_m, \psi_i(T, s_r, D))) f_i(s_m, \psi_i(T, s_r, D)) \right)^t. \quad (7)$$

In what follows we shall for a while shorten the equations using the following abbreviations:

$$e^*_i = e_i(s_m, \psi_i(T, s_r, D))$$
$$f^*_i = f_i(s_m, \psi_i(T, s_r, D)).$$

Setting now formula (7) into the sum (5) defining the expected production of successful dispersers gives

$$\omega_i(T, s_m, s_r, D) = \Phi(s_m) \sum_{t=T}^\infty (1 - c)^{1+t-T} ce^*_i (1 - e^*_i)f^*_i t$$

and thus

$$\omega_i(T, s_m, s_r, D) = \begin{cases} 
\Phi(s_m) \frac{(1-c)(1-e^*_i)f^*_i}{1-(1-c)(1-e^*_i)f^*_i}, & \text{if } (1-c)(1-e^*_i)f^*_i < 1 \\
\infty, & \text{if } (1-c)(1-e^*_i)f^*_i \geq 1 \end{cases}. \quad (8)$$

One can easily deduce that $\omega_i(t, s_m, s_r, D) = \omega_i(T, s_m, s_r, D)$ for all $t \geq T$ and when $t < T$ one may calculate the value of $\omega_i(t, s_m, s_r, D)$ using recursion (6).

Probability that a disperser enters a local population of age $t$ is $(1-c)^t$ and the probability that the local population is older than $T$ time units is $(1-c)^T$. Altogether one can calculate the expected production of new disperser by an average disperser in a type $i$ patch using the following algorithm:

- Calculate $\omega_i(T, s_m, s_r, D)$ using the formula (8).
- Set
$$\hat{E}_i(T, s_m, s_r, D) = (1 - c)^T \omega_i(T, s_m, s_r, D).$$
- Use recursion (6) to calculate values
$$\omega_i(t, s_m, s_r, D) \text{ for } t \in \{T, T-1, T-2, \ldots, 3, 2, 1, 0\}$$

and simultaneously recursively define
$$\hat{E}_i(t, s_m, s_r, D) = \hat{E}_i(t+1, s_m, s_r, D) + c(1-c)^t \omega_i(t, s, s_r, D)$$

- Now $\hat{E}_i(0, s_m, s_r, D)$ is the expected number of dispersers produced by an average strategy $s_m$ disperser that enters patch of type $i$.  

Finally
\[
E(s_m, s_r, D) = \sum_i \frac{p_i a_i(s) \hat{E}_i(0, s_m, s_r, D)}{\sum p_i a_i(s)}
\]
is the expected number of new dispersers produced by an average strategy \(s_m\) dispersers in an environment set by a strategy \(s_r\) resident whose disperser pool size is \(D\).

From here one can proceed as before, first solve \(E_i(s_r, s_r, D) = 1\) to find \(D^*(s_r)\) and then calculate the expected number of successful dispersers produced by one newborn mutant clan as \(R_0(s_m, s_r) = E(s_m, s_r, D^*(s_r))\).

5 Appendix B

In chapter 3.3 we claim that the evolutionarily stability (and thus attractivity) of the specialist strategies depends on the definition of possible sizes of the mutational steps when \(\alpha \neq 1\). This definition affects thus the exact location of the dashed curves in figure 4 (separating the parameter areas where specialist strategies are ESS or not). This has the following reason. Consider a strategy \(s^*\) individual. A small increase in the strategy increases the gain achieved from utilizing resource \(U\). This increase is proportional to the availability of the resource \(U\) and to \(\left[ \frac{d\alpha}{ds} \right]_{s=s^*}\). Similarly a small increase in the strategy decreases the gain achieved from utilizing resource \(V\) and this decrease is proportional to \(\left[ \frac{\alpha(1-s)}{d} \right]_{s=s^*}\) and to the availability of the resource \(V\). Consider now the case \(s^* = 0\). Then \(\left[ \frac{\alpha(1-s)}{d} \right]_{s=0} = -\alpha\), but

\[
\lim_{s^* \to 0} \left[ \frac{d\alpha}{ds} \right]_{s=s^*} = \begin{cases} 
\infty, & \text{if } \alpha < 1 \\
1, & \text{if } \alpha = 1 \\
0, & \text{if } \alpha > 1.
\end{cases}
\]

Let now \(R_0(s_m, E_{s_r})\) define the fitness of a strategy \(s_m\) mutant in an environment \(E_{s_r}\) set by a strategy \(s_r\) resident. The above reasoning immediately indicates that

\[
\left[ \frac{dR_0(s_m, E_{s_r})}{ds_m} \right]_{s_m=s_r=0} > 0, \quad \text{if } \alpha < 1
\]

\[
\left[ \frac{dR_0(s_m, E_{s_r})}{ds_m} \right]_{s_m=s_r=0} < 0, \quad \text{if } \alpha > 1
\]

The similar reasoning holds also for the other specialist strategy \(s^* = 1\). Altogether, if infinitesimally small mutational steps were possible, the specialist strategies would be evolutionarily attracting whenever \(\alpha > 1\) and repelling whenever \(\alpha < 1\). However, in a rather large parameter domain singular strategies exists extremely close to the specialist strategies. This, together with the fact the adaptive dynamics approach assumes that there exists a positive lower limit, say \(\varepsilon\), of the sizes of possible mutations, allows more complicated evolutionary scenarios.
Namely, when the distance between such a singular strategy and a specialist strategy is less than $\varepsilon$ the evolutionary properties of the specialist strategy are set by the properties of this singular strategy. Thus the exact locations of the dashed curves in figure 4 are functions of $\varepsilon$. Note, that the phenomenon described above only affects the evolutionary properties of the specialists and that case $\alpha = 1$ is a limiting case, where this phenomenon does not affect the evolutionary dynamics.

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References


