

Kalle Parvinen

Evolutionary branching of dispersal strategies in structured metapopulations

Received: 6 March 2001 / Revised version: 12 February 2002 /

Published online: 17 July 2002 – © Springer-Verlag 2002

Abstract. Dispersal polymorphism and evolutionary branching of dispersal strategies has been found in several metapopulation models. The mechanism behind those findings has been temporal variation caused by cyclic or chaotic local dynamics, or temporally and spatially varying carrying capacities. We present a new mechanism: spatial heterogeneity in the sense of different patch types with sufficient proportions, and temporal variation caused by catastrophes. The model where this occurs is a generalization of the model by Gyllenberg and Metz (2001). Their model is a size-structured metapopulation model with infinitely many identical patches. We present a generalized version of their metapopulation model allowing for different types of patches. In structured population models, defining and computing fitness in polymorphic situations is, in general, difficult. We present an efficient method, which can be applied also to other structured population or metapopulation models.

1. Introduction

Dispersal is a key feature in metapopulations and the evolution of dispersal has recently received a lot of attention (Doebeli 1995; Holt and McPeck 1996; Doebeli and Ruxton 1997; Gandon 1999; Gandon and Michalakis 1999; Johst *et al.* 1999; Parvinen 1999; Gyllenberg *et al.* 2002; Parvinen *et al.* in press; Ronce *et al.* 2000; Gyllenberg and Metz 2001; Heino and Hanski 2001; Metz and Gyllenberg 2001; Clobert *et al.* 2001; Parvinen 2001).

Adaptive dynamics (Metz *et al.* 1992, 1996; Geritz *et al.* 1997, 1998) gives the appropriate general framework to analyze the evolutionary phenotype dynamics of a population or a metapopulation. It is assumed that a resident population has reached its population dynamical attractor. Then an initially rare mutant with a slightly different strategy appears. If the mutant is able to grow in population size, it can invade and possibly replace the old resident and become the new resident itself. These mutation-invasion events result in the change of the strategy of the individuals constituting the population.

If no mutant can invade the resident, then the strategy of the resident is unbeatable, and it is called an evolutionarily stable strategy (Maynard Smith 1976). A

K. Parvinen: Department of Mathematics, FIN-20014 University of Turku, Finland.
e-mail: kalle.parvinen@utu.fi

Mathematics Subject Classification (1991): 92D15, 37N25

Keywords or phrases: Evolutionary branching – Evolution of dispersal – Adaptive dynamics – Migration – Structured metapopulation

strategy k^* is convergence stable or an evolutionary attractor if the repeated invasion of nearby mutant strategies into resident strategies will lead to the convergence of resident strategies towards k^* (Christiansen 1991). If an evolutionary attractor is also evolutionarily stable, it is called a continuously stable strategy (Eshel 1983) and it is a feasible final outcome of an evolutionary process. If an evolutionary attractor is not unbeatable, evolution will not stop there, but evolutionary branching occurs. The population will then divide into two groups, and the strategies of these groups will evolve further away from each other.

In this paper we present a new mechanism for dispersal polymorphism in structured metapopulations through evolutionary branching. Branching can occur if there is enough spatial heterogeneity in the sense of different patch types in sufficient quantities, and temporal variation caused by catastrophes. Previously found mechanisms are temporal variation caused by cyclic or chaotic local dynamics in deterministic models with finitely many patches (Holt and McPeck 1996; Doebeli and Ruxton 1997; Johst *et al.* 1999; Parvinen 1999; Kisdi 2002), and temporally and spatially varying carrying capacities (McPeck and Holt 1992; Mathias *et al.* 2001).

The classical Levins metapopulation (Levins 1969, 1970) neglects local dynamics and assumes that all habitat patches are identical. Structured metapopulation models that take into account local dynamics, are more challenging to study. Metz and Gyllenberg (2001) and Gyllenberg and Metz (2001) presented a size-structured metapopulation model with local growth and catastrophes. That model was studied also by Parvinen *et al.* (in press) and Gyllenberg *et al.* (2002). See also Gyllenberg and Parvinen (2001).

The model in Gyllenberg and Metz (2001), however, assumes that habitat patches are identical and differ only in population size. The population dynamics in the context of models where patches have different quality has been studied, for example, by Gyllenberg and Hanski (1997) and Hanski and Gyllenberg (1993). Here we present a generalization of the model by Gyllenberg and Metz (2001). This generalized model incorporates several different types of patches. These patches have different growth conditions and catastrophe rates.

Defining and computing fitness in polymorphic situations, that is, when there are several phenotypes having different dispersal behaviour, is definitely not trivial. We present a method for studying resident dynamics and to compute the fitness of a mutant in an environment set by the resident populations. The idea of this method can be applied to other structured population or metapopulation models.

In Section 2 we introduce our metapopulation model. In Section 3 we show that evolutionary branching of dispersal strategies can occur in our model if there is enough spatial heterogeneity, that is, enough variability in the patch types, and temporal variability caused by catastrophes. The existence of different patch types is not necessarily enough to observe branching. The environment that an individual experiences has to have enough variability.

2. Model presentation

We study a metapopulation with an infinite number of patches of different quality. It is a generalization of a model presented by Gyllenberg and Metz (2001) and Metz

and Gyllenberg (2001). The number of different types of patches is denoted by M and the fraction of type j is p_j , where $\sum_{j=1}^M p_j = 1$.

In a patch of type j , local population growth due to birth and death events is described by a per capita growth function $g_j(x)$, where x is the local population size. Individuals emigrate to a dispersal pool at a per capita rate $k(x)$ and immigrate at a per capita rate α . Dispersal is often costly in the sense that a migrating individual may die before reaching a new patch. This is incorporated in this model by having the individuals in the dispersal pool experience death at per capita rate ν . The probability to survive dispersal is thus $\pi = \alpha/(\alpha + \nu)$. The density of dispersers (per patch) is D and the gross immigration rate is therefore $I := \alpha D$. Immigrants choose their patch at random, independently of the patch type and the local population size. Therefore the probability that a randomly selected individual will arrive in a patch of type j is p_j . In patches of type j and population size x , catastrophes occur at rate $\mu_j(x)$. A catastrophe wipes out the local population in the patch, but the patch remains habitable and it can be re-colonized by immigrants from the dispersal pool immediately after the catastrophe.

The state of the metapopulation is the collection of population size distributions n_j , where $j = 1, \dots, M$. As n_j are probability distributions, the quantity $\int_{[x_1, x_2]} n_j(dx)$ is the probability that the local population size in a patch of type j is between x_1 and x_2 . Furthermore, $\int_{[0, \infty)} n_j(dx) = 1$ for all $j = 1, \dots, M$. Instead of using a partial differential equation formulation for the dynamics of n_j we use the so-called cumulative formulation (Diekmann *et al.* 1998, 2001). The main reason for this is that it follows from Diekmann *et al.* (2001) that the model in the cumulative formulation is well-posed. Diekmann *et al.* (2000) gave examples of innocent looking hyperbolic systems very similar to the case here, that lack unique solutions. Another reason for this is that, as will be seen later, the equilibrium population size distributions n_j have a one-dimensional support also in a polymorphic population. The distribution is thus concentrated on a curve. For such a distribution, the partial derivatives $\frac{\partial}{\partial x_i} n_j$ do not exist, and therefore the situation cannot be described with partial differential equations. For a more detailed description of the cumulative formulation see the appendix.

The population in the dispersal pool decreases from immigration and death, which occur at per capita rates α and ν , respectively. The population increase from emigration is added over all patch types and local population sizes.

$$\frac{d}{dt}D(t) = -(\alpha + \nu)D(t) + \sum_{j=1}^M p_j \int_0^\infty k(x) x n_j(t, dx). \quad (1)$$

The dynamics of the immigration rate $I = \alpha D$ is then given by

$$\frac{d}{dt}I(t) = -(\alpha + \nu)I(t) + \sum_{j=1}^M p_j \alpha \int_0^\infty k(x) x n_j(t, dx). \quad (2)$$

If $M = 1$ this model is identical to the model presented in Gyllenberg and Metz (2001) and Metz and Gyllenberg (2001).

2.1. Polymorphic resident

In this paper the words monomorphic and polymorphic correspond to the number of different resident phenotypes present. A polymorphic resident consists thus of two or more phenotypes.

We assume that there are N coexisting phenotypes, which differ only in dispersal tendency, with dispersal rates $k_i(x)$, $i = 1, \dots, N$. In general, the state of a polymorphic metapopulation is a collection of N -dimensional measures $n_j(dx_1, dx_2, \dots, dx_N, t)$, $j = 1, \dots, M$ (See Figure 1a) together with the immigration rates $I_i(t)$. At an equilibrium the immigration rates and the measures are constant.

Now consider the case of constant immigration rates I_i . Our strategy is to derive conditions for these immigration rates I_i to be equilibrium immigration rates. The conditions will be that for each phenotype i , the basic reproduction ratio must be equal to 1.

Consider the lifetime of a local population in a patch of type j : We define the patch ‘‘age’’ τ as the time elapsed since the last catastrophe. A local population is born when an empty patch is colonized, therefore $x_i(0) = 0$. As the immigration rates are constant, all local populations in patches of type j grow according to

$$\begin{cases} \frac{d}{d\tau}x_i(\tau) = g_j \left(\sum_{i=1}^N x_i(\tau) \right) x_i(\tau) - k_i \left(\sum_{i=1}^N x_i(\tau) \right) x_i(\tau) + I_i \\ x_i(0) = 0 \end{cases} \quad (3)$$

All extant local populations of age τ in patches of type j thus have the population sizes $(x_1(\tau), \dots, x_N(\tau))$. Therefore each measure n_j has one-dimensional support in the sense that it is concentrated on the curve $(x_1(\tau), \dots, x_N(\tau)) \in \mathbb{R}^N$, $\tau \geq 0$. (See Figure 1b)

2.2. Basic reproduction ratio for the resident

At an equilibrium the immigration rates are constant, the population size distributions are constant, and each local population must exactly replace itself. The basic reproduction ratio R_i^{res} measures population growth between dispersal events, and is the expected number of new dispersers (of phenotype i) produced by a disperser (of phenotype i). In a more abstract way, it can be defined as the spectral radius of the next generation operator. The equilibrium condition can be formulated as $R_i^{\text{res}} = 1$. Note that we do not obtain the equilibrium immigration rates explicitly.

Gyllenberg and Metz (2001) defined the basic reproduction ratio in the monomorphic case in their model with one patch type. (In a monomorphic situation one R suffices.) Next we define the basic reproduction ratios R_i^{res} in a polymorphic case, i.e. when there are several resident phenotypes present, with one patch type. After that we expand the definition to the case with several patch types. We also present an efficient method for computing the basic reproduction ratios.

2.2.1. One patch type ($M = 1$)

First we study the case with one patch type ($M = 1$). All extant populations of age τ have population size $x_1(\tau), x_2(\tau), \dots, x_N(\tau)$ given by (3). We denote

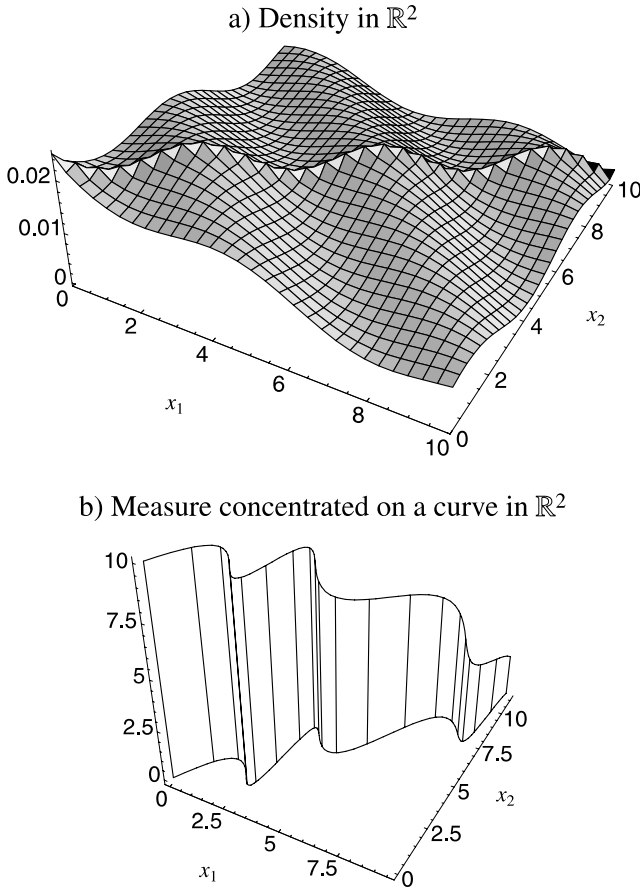


Fig. 1. a) An example of a 2-dimensional measure, which has a density. b) An example of a 2-dimensional measure with a 1-dimensional support in the sense that it is concentrated on a curve.

$\bar{x}(\tau) = \sum_{i=1}^N x_i(\tau)$. The probability \mathcal{F} that a catastrophe has not occurred before time t , and thus the population is still extant, has to satisfy the differential equation

$$\frac{d}{dt} \mathcal{F}_{I_1, \dots, I_N}(t) = -\mu(\bar{x}_{I_1, \dots, I_N}(t)) \mathcal{F}_{I_1, \dots, I_N}(t). \quad (4)$$

The probability that a population is extant at age τ is thus

$$\mathcal{F}_{I_1, \dots, I_N}(\tau) = \exp \left[- \int_0^\tau \mu(\bar{x}(s)) ds \right]. \quad (5)$$

The amount of emigrants of phenotype i during a short time-interval $d\tau$ equals $k_i(\bar{x}(\tau))x_i(\tau)$. An emigrant will survive dispersal with probability π . The expected number of surviving emigrants for a local population during its entire life is therefore

$$\pi E_i(I_1, \dots, I_N) = \pi \int_0^\infty k(\bar{x}(\tau)) x_i(\tau) \mathcal{F}_{I_1, \dots, I_N}(\tau) d\tau, \quad (6)$$

The expected number of immigrants arriving into a patch during its entire life is $I_i L(I_1, \dots, I_N)$, where

$$L(I_1, \dots, I_N) = \int_0^\infty \tau \mu(\bar{x}(\tau)) \mathcal{F}_{I_1, \dots, I_N}(\tau) d\tau = \int_0^\infty \mathcal{F}_{I_1, \dots, I_N}(\tau) d\tau \quad (7)$$

is the expected life-time of a local population. The second equality follows from integration by parts.

The basic reproduction ratio for the phenotype i is the expected number of surviving emigrants divided by the expected number of immigrants. It is thus obtained by

$$R_i^{\text{res}} = \frac{\pi E_i(I_1, \dots, I_N)}{I_i L(I_1, \dots, I_N)} = \frac{\pi}{I_i L(I_1, \dots, I_N)} \int_0^\infty k(\bar{x}(\tau)) x_i(\tau) \mathcal{F}_{I_1, \dots, I_N}(\tau) d\tau, \quad (8)$$

where τ is the age of a local population and $x_i(\tau)$ is the population size of the phenotype i in a local population of age τ determined by (3).

An alternative interpretation of R_i^{res} starts by noting that at an equilibrium, the patch age distribution has density

$$m(\tau) = \frac{\mathcal{F}_{I_1, \dots, I_N}(\tau)}{L(I_1, \dots, I_N)}. \quad (9)$$

The rate at which all patches send surviving emigrants of phenotype i is then $\pi \int_{\tau=0}^\infty k(\bar{x}(\tau)) x_i(\tau) m(\tau) d\tau$. The basic reproduction ratio is then this amount divided by I_i , which results in (8).

The basic reproduction ratio can be computed numerically using the following system of differential equations:

$$\begin{cases} x'_i = g\left(\sum_{i=1}^N x_i\right) x_i - k_i\left(\sum_{i=1}^N x_i\right) x_i + I_i & x_i(0) = 0 \\ \mathcal{F}' = -\mu\left(\sum_{i=1}^N x_i\right) \mathcal{F} & \mathcal{F}(0) = 1 \\ L' = \mathcal{F} & L(0) = 0 \\ E'_i = k_i\left(\sum_{i=1}^N x_i\right) x_i \mathcal{F} & E_i(0) = 0 \end{cases} \quad (10)$$

$x_i(\tau)$ is the population size of phenotype i as given by (3), $\mathcal{F}(\tau) = \mathcal{F}_{I_1, \dots, I_N}(\tau)$ as in (5), $E_i(\infty) = E_i(I_1, \dots, I_N)$ as in (6) and $L(\infty) = L(I_1, \dots, I_N)$ from (7) is the expected lifetime of a local population. The basic reproduction ratio for a phenotype i is

$$R_i^{\text{res}} = \pi \frac{E_i(\infty)}{L(\infty) I_i}. \quad (11)$$

As Metz and Gyllenberg (2001) stated, it takes a long integration to arrive at $\tau = \infty$. In practice we can replace the tail of the integration by an analytical approximation.

As time goes on, $x_i(\tau)$ converge to x_i^* defined as a solution of the equation obtained by putting $\frac{dx_i(\tau)}{d\tau} = 0$ in (3). When $x_i(\tau)$ is sufficiently close to x_i^* at time T , we can stop integrating and write

$$\begin{aligned} E_i(\infty) &= E_i(T) + k_i(\bar{x}(T))x_i(T) \frac{\mathcal{F}(T)}{\mu(\bar{x}(T))} \\ L(\infty) &= L(T) + \frac{\mathcal{F}(T)}{\mu(\bar{x}(T))}, \end{aligned} \quad (12)$$

where $\bar{x}(T) = \sum_{i=1}^N x_i(T)$.

At an equilibrium (I_1, \dots, I_N) the basic reproduction ratios should satisfy $R_i^{\text{res}} = 1$. In general it is not possible to find an equilibrium I_i explicitly, but it is possible to find a numerical solution.

2.2.2. Several patch types ($M > 1$)

In the previous section all patches were assumed to be identical with respect to population growth and catastrophes. Next we study the general case with M different patch types with frequencies p_j as described in Section 2.

We assume that dispersers choose the patch into which they immigrate patch at random, independently of the patch type and the local population size. Therefore the expected number of dispersers produced by a typical disperser is the weighted sum of dispersers from different patch types:

$$R_i^{\text{res}} = \sum_{j=1}^M p_j R_{ij}^{\text{res}} \quad (13)$$

where R_{ij}^{res} is obtained from (8) where in each R_{ij} the growth function $g_j(x)$ and the catastrophe intensity function $\mu_j(x)$ must be used. This follows directly from the assumptions. A resident disperser has probability p_j to enter into a patch of type j . It will there produce dispersers as if these patches were the only ones, because local populations do not affect each other directly, only via dispersal.

2.3. Fitness of the mutant

Now we assume that the present phenotypes have lived in the metapopulation long enough that the system has reached an equilibrium. We want to answer the question whether an initially rare mutant with dispersal strategy k_{mut} can grow in population size. Metz *et al.* (1996) defined fitness as the long-term exponential growth rate r of a mutant phenotype in an environment set by the resident. The mutant cannot invade if $r < 0$. If $r > 0$ the mutant may invade, but will not necessarily do so (demographic stochasticity may prevent it). The basic reproduction ratio R can be used instead of r , because the quantities r and $\ln R$ are sign equivalent: $r > 0$ if and only if $R > 1$.

To compute the fitness we should measure the disperser production of a mutant arriving in a typical patch, that is, a patch randomly sampled from the equilibrium distribution of patches with respect to resident population size and composition. (cf. Gyllenberg and Metz 2001). Again we shall use patch age as the bookkeeping variable, i.e. exploit the fact that the support of this distribution is a curve.

2.3.1. One patch type ($M = 1$)

Consider a very small mutant population arriving in a patch, where the patch age is t_{res} . The mutant population does not affect the dynamics of the resident. The mutant population will therefore grow with a per capita growth rate $g(\bar{x}(t))$, and mutants will emigrate with a per capita rate $k_{\text{mut}}(\bar{x}(t))$, where \bar{x} is the total resident population size. The expected per capita number of mutant emigrants is therefore

$$\begin{aligned} E^{\text{mut}}(t_{\text{res}}, I_1^*, \dots, I_N^*) \\ = \int_{t_{\text{res}}}^{\infty} k_{\text{mut}}(\bar{x}(t)) \exp \left[\int_{t_{\text{res}}}^t g(\bar{x}(\tau)) - k_{\text{mut}}(\bar{x}(\tau)) - \mu(\bar{x}(\tau)) d\tau \right] dt, \end{aligned} \quad (14)$$

where $\bar{x}(t) = \sum_{i=1}^N x_i(t)$, and $x_i(t)$ is determined by (3). Fitness is now the expected number of dispersers produced by a mutant arriving in a typical patch.

$$\begin{aligned} R^{\text{mut}}(I_1^*, \dots, I_N^*) &= \pi \int_0^{\infty} E^{\text{mut}}(t_{\text{res}}, I_1^*, \dots, I_N^*) n^*(t_{\text{res}}) dt_{\text{res}} \\ &= \frac{\pi}{L(I_1^*, \dots, I_N^*)} \int_0^{\infty} E^{\text{mut}}(t_{\text{res}}, I_1^*, \dots, I_N^*) \mathcal{F}_{I_1^*, \dots, I_N^*}(t_{\text{res}}) dt_{\text{res}}, \end{aligned} \quad (15)$$

since $n^*(t_{\text{res}}) = \mathcal{F}_{I_1^*, \dots, I_N^*}(t_{\text{res}}) / L(I_1^*, \dots, I_N^*)$ is the equilibrium patch-age distribution.

Now the integrals in (14) and (15) do not have the same integration boundaries and a direct transformation to a system of differential equations is not possible. Using certain auxiliary quantities, we can do the transformation, and the resulting system of differential equations is

$$\left\{ \begin{array}{ll} x_i' = g \left(\sum_{i=1}^N x_i \right) x_i - k_i \left(\sum_{i=1}^N x_i \right) x_i + I_i & x_i(0) = 0 \\ \mathcal{F}' = -\mu \left(\sum_{i=1}^N x_i \right) \mathcal{F} & \mathcal{F}(0) = 1 \\ L' = \mathcal{F} & L(0) = 0 \\ U' = \left[g \left(\sum_{i=1}^N x_i \right) - k_{\text{mut}} \left(\sum_{i=1}^N x_i \right) - \mu \left(\sum_{i=1}^N x_i \right) \right] U & U(0) = 1 \\ E_2' = k_{\text{mut}} \left(\sum_{i=1}^N x_i \right) U & E_2(0) = 0 \\ V' = \left[k_{\text{mut}} \left(\sum_{i=1}^N x_i \right) - g \left(\sum_{i=1}^N x_i \right) \right] V & V(0) = 1 \\ W' = V & W(0) = 0 \\ Q' = E_2 V & Q(0) = 0 \end{array} \right. \quad (16)$$

Reason behind this is as follows. The quantities $U(t)$ and $E_2(t)$ defined by (16) can be written in integral form

$$U(t) = \exp \left[\int_0^t g(\bar{x}(\tau)) - k_{\text{mut}}(\bar{x}(\tau)) - \mu(\bar{x}(\tau)) d\tau \right] \quad (17)$$

and

$$E_2(t) = \int_0^t k_{\text{mut}}(\bar{x}(\sigma)) U(\sigma) d\sigma, \quad (18)$$

thus $E^{\text{mut}}(t, I_1^*, \dots, I_N^*) = (E_2(\infty) - E_2(t))/U(t)$. The integral in (15) equals

$$\begin{aligned} \int_0^\infty E^{\text{mut}}(t_{\text{res}}, I_1^*, \dots, I_N^*) \mathcal{F}_{I_1^*, \dots, I_N^*}(t_{\text{res}}) dt_{\text{res}} &= \int_0^\infty \frac{E_2(\infty) - E_2(t)}{U(t)} \mathcal{F}(t) dt \\ &= E_2(\infty) \int_0^\infty V(t) dt - \int_0^\infty E_2(t) V(t) dt = E_2(\infty) W(\infty) - Q(\infty), \end{aligned} \quad (19)$$

because $\mathcal{F}(t)/U(t) = V(t)$. The fitness R^{mut} of the mutant is formally

$$R^{\text{mut}} = \pi \frac{E_2(\infty) W(\infty) - Q(\infty)}{L(\infty)}, \quad (20)$$

but this expression creates numerical problems ($W(\infty) = \infty$ and $Q(\infty) = \infty$). To avoid these problems, we can use the same scheme as in the monomorphic case (See also Metz and Gyllenberg 2001). As time goes on, $x_i(\tau)$ converge to x_i^* defined as a solution of the equation obtained by putting $\frac{dx_i(\tau)}{d\tau} = 0$ in (3). When $x_i(\tau)$ is sufficiently close to x_i^* at time T , we can stop integrating and replace the tails of the integrations by analytical approximations. Denote $k_{\text{mut}} = k_{\text{mut}}(\bar{x}(T))$, $g = g(\bar{x}(T))$, and $\mu = \mu(\bar{x}(T))$. For $t \geq T$ we have, to good approximation,

$$\begin{aligned} U(t) &= U(T) e^{(g - k_{\text{mut}} - \mu)(t - T)} \\ E_2(t) &= E_2(T) + \frac{k_{\text{mut}} U(T)}{(g - k_{\text{mut}} - \mu)} \left[e^{(g - k_{\text{mut}} - \mu)(t - T)} - 1 \right] \\ V(t) &= V(T) e^{(k_{\text{mut}} - g)(t - T)} \\ W(t) &= W(T) + \frac{V(T)}{k_{\text{mut}} - g} \left[e^{(k_{\text{mut}} - g)(t - T)} - 1 \right] \\ Q(t) &= Q(T) + \frac{E_2(\infty) V(T)}{k_{\text{mut}} - g} \left[e^{(k_{\text{mut}} - g)(t - T)} - 1 \right] \\ &\quad - k_{\text{mut}} \frac{U(T) V(T)}{(g - k_{\text{mut}} - \mu) \mu} \left[e^{-\mu(t - T)} - 1 \right] \end{aligned} \quad (21)$$

The limit of E_2 is therefore approximately given by

$$E_2(\infty) = E_2(T) - \frac{k_{\text{mut}} U(T)}{g - k_{\text{mut}} - \mu}. \quad (22)$$

Even though both W and Q tend to infinity, the difference $E_2(t)W(t) - Q(t)$ remains bounded and has, in the approximation that we use, the limit

$$E_2(\infty)W(\infty) - Q(\infty) = E_2(\infty)W(T) - Q(T) - k_{\text{mut}} \frac{U(T)V(T)}{(g - k_{\text{mut}} - \mu)\mu} \quad (23)$$

The expected life-time $L(\infty)$ of a local population is obtained, as in the resident case, from equation (12).

2.3.2. Several patch types ($M > 1$)

In the previous section we computed the fitness of a mutant in a metapopulation model where all patches are identical with respect to population growth and catastrophes. We now extend the fitness computation to cover the general case with M different patch types with frequencies p_j as described in Section 2. This is done in a way which is analogous to the way in which the computation of the basic reproduction ratio was extended in Section 2.2.2.

Since we assume that dispersers choose the patch into which they immigrate patch at random, independently of the patch type and the local population size, a dispersing mutant arrives in a patch of type j with probability p_j . The disperser production in that patch corresponds to the single-type case. The actual fitness is therefore the weighted sum of dispersers from different patch types:

$$R^{\text{mut}} = \sum_{j=1}^M p_j R_j^{\text{mut}} \quad (24)$$

with analogous growth and catastrophe function choices as in the resident case.

3. Results

3.1. The case without catastrophes

Gyllenberg *et al.* (2002) studied the model with one patch type ($M = 1$) and proved that if there are no catastrophes, the strategy not to disperse is evolutionarily stable, if $\pi < 1$. Their proof can be extended to the model with several patch types. As a consequence, if there are no catastrophes, evolutionary branching cannot occur.

3.2. Evolutionary branching

In this section we assume that the dispersal rate is independent of the local population size, i.e. $k_i(x) = k_i$. We study an example, where we have two kinds of patches with different growth functions $g_j(x) = a_j x(1 - x/K_j)$ (logistic) and catastrophe rates.

We study dispersal evolution by drawing pairwise invasibility plots (Figure 2). For each resident strategy k_{res} we find the non-zero stable monomorphic equilibrium (which is unique and also the unique attractor in the studied cases) using the condition that the basic reproduction ratio (13) must be equal to one, $R^{\text{res}} = 1$. Then we compute the fitness R^{mut} of the mutant with strategy k_{mut} from (24). Next we plot the areas consisting of points $(k_{\text{res}}, k_{\text{mut}})$ where $R^{\text{mut}} > 1$ in dark gray and those where $R^{\text{mut}} < 1$ in light gray. Evolutionarily singular strategies lie in those points, where the nontrivial isocline $R^{\text{mut}} = 1$ crosses the diagonal. For a detailed classification of pairwise invasibility plots in general see Geritz *et al.* (1998).

We now study the evolution of dispersal in dependence on the fraction p_1 , with $0 \leq p_1 \leq 1$, $p_2 = 1 - p_1$. When $p_1 = 0$ or $p_1 = 1$ we have only one type of patches present, and an evolutionarily singular dispersal strategy k^* exists, which

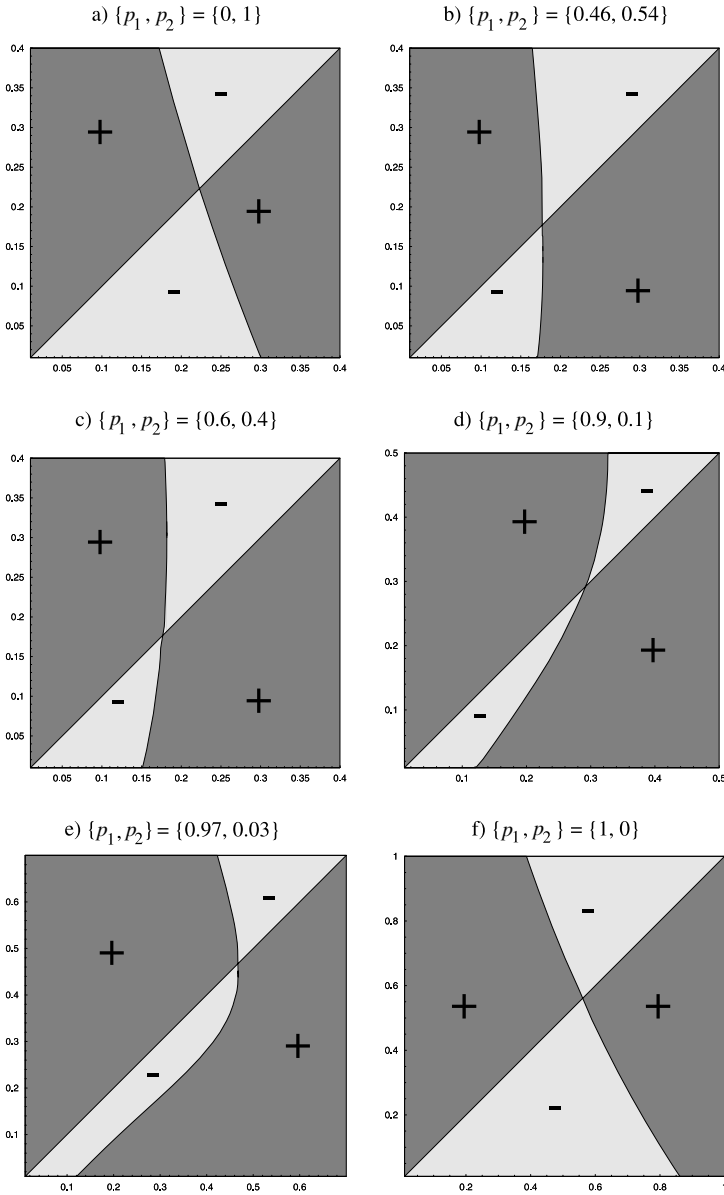


Fig. 2. Pairwise invasibility plots. Parameters: $M = 2$, $\alpha = 0.5$, $\nu = 0.1$. Patch properties: $a_1 = 1$, $K_1 = 1$, $\mu_1 = 0.5$, $a_2 = 0.7$, $K_2 = 1.5$, $\mu_2 = 0.1$.

is also evolutionarily stable (Figure 2a,f). When p_1 changes, the singular strategy changes and loses its evolutionary stability (Figure 2b,e).

With intermediate values of p_1 , the singular strategy k^* is a branching point (Figure 2c,d), see also Figure 3a. When the singular strategy k^* is a branching point, evolutionary branching occurs and the metapopulation becomes dimorphic, that is, there are two resident phenotypes k_1, k_2 . In that case the fitness of a mutant phenotype can be calculated using the method explained in Section 2.3. Because of mutations and mutant-resident replacements, the resident strategies (k_1, k_2) will change in the set of protected dimorphisms (see Geritz *et al.* 1998, 1999) until an evolutionarily stable dimorphism (k_1^*, k_2^*) is reached.

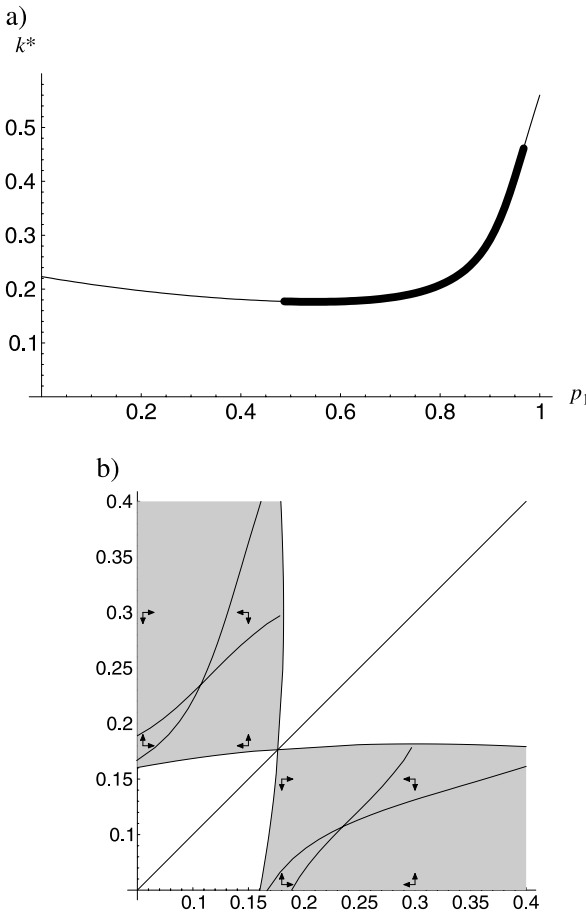
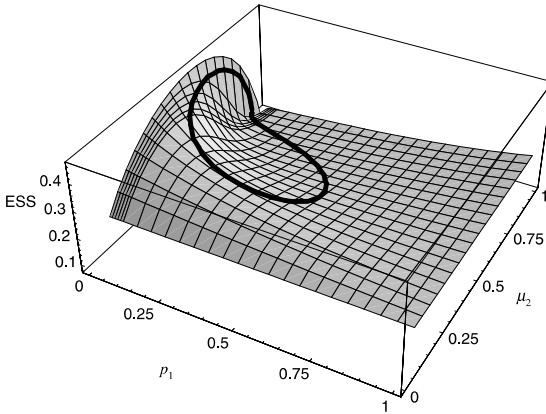


Fig. 3. a) Singular dispersal strategies k^* with respect to p_1 . The thin curve corresponds to evolutionarily stable strategies and the thick curve to branching points. b) The domain of protected dimorphisms (plotted in grey) and the direction of evolution when $\{p_1, p_2\} = \{0.6, 0.4\}$ (Corresponds to Figure 2c) Parameters: $M = 2, \alpha = 0.5, \nu = 0.1$. Patch properties: $a_1 = 1, K_1 = 1, \mu_1(x) = 0.5, a_2 = 0.7, K_2 = 1.5, \mu_2(x) = 0.1$.

In Figure 3b we have plotted one example of such a case. The singular strategy $k^* \approx 0.17$ is a branching point. Because the numbering of the strategies k_1 and k_2 is arbitrary, the domain of protected dimorphisms is symmetric across the diagonal. Let $k'_i = \frac{\partial}{\partial k_{\text{mut}}} R^{\text{mut}}|_{k_{\text{mut}}=k_i}$. The probable direction of evolution is (k'_1, k'_2) . When (k_1, k_2) is close to (k^*, k^*) , the smaller resident strategy will decrease and the larger increase. The strategies (k_1, k_2) will finally reach the evolutionarily attracting dimorphism at the point where the isoclines $k'_i = 0$ cross, which is approximately at $(0.11, 0.235)$ or $(0.235, 0.11)$. This unique convergence stable dimorphism is evolutionarily stable, and is therefore the final outcome of the evolutionary process. (In principle the convergence stable dimorphism could be also evolutionarily unstable, which would lead to further branching.)

a) Singular strategies



b) Parameter domain

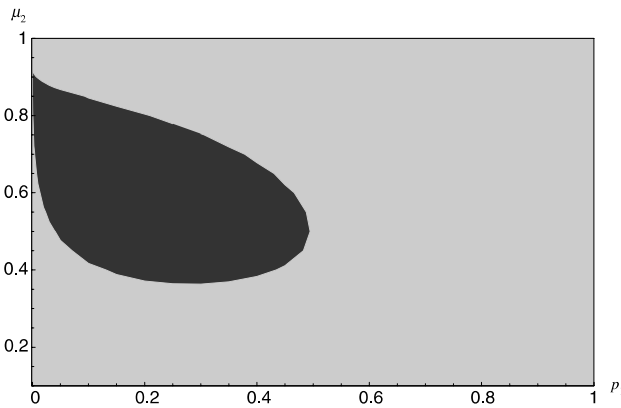


Fig. 4. a) Singular dispersal strategies k^* and b) parameter values for which branching occurs with respect to p_1 and μ_2 . The parameters domain for which branching occurs is plotted in black in (b). The boundary of the corresponding area is plotted with a thick curve in (a). Parameters: $M = 2, \alpha = 0.5, \nu = 0.15$. Patch properties: $a_{1,2} = 1, K_{1,2} = 1, \mu_1(x) = 0.1$.

We have thus found out that evolutionary branching can occur when there is enough spatial heterogeneity in the sense of different patch types with sufficient proportions, and temporal variation caused by catastrophes.

3.3. Dependence on patch properties

To further analyze the occurrence of branching, we take two equal patch types, and choose one property of the second patch type we vary. Then we see for which combinations of this parameter and the fraction of patches p_1 evolutionary branching occurs. More specifically, we vary the catastrophe rate μ_2 and carrying capacity K_2 .

The results with respect to the catastrophe rate μ_2 are plotted in Figure 4. We observe that branching occurs for intermediate values of the catastrophe rate μ_2 , where the difference between the ESS dispersal rates of the patch types alone is largest.

Next we study the effect of differences in the carrying capacity K . When there is only one patch type present and the catastrophe rate does not depend on the pop-

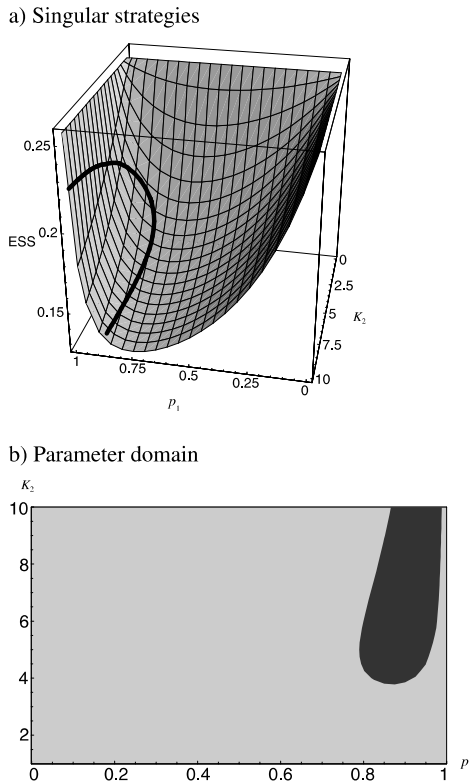


Fig. 5. Singular dispersal strategies k^* and parameter values for which branching occurs with respect to p_1 and K_2 . The parameters domain for which branching occurs is plotted in black in (b). The boundary of the corresponding area is plotted with a thick curve in (a). Parameters: $M = 2, \alpha = 0.5, \nu = 0.1$. Patch properties: $a_{1,2} = 1, K_1 = 1, \mu_{1,2}(x) = 0.1$.

ulation size, it can be shown analytically that the basic reproduction ratios do not change if both the immigration rate I and the carrying capacity K are multiplied with the same positive constant. The carrying capacity is therefore just a scaling factor of population size, and its value does not affect dispersal behaviour.

When there are two patch types with different carrying capacities the situation changes completely. The different scales create spatial heterogeneity. Dispersing individuals may now enter a patch of different size, which changes dispersal behaviour. The evolutionarily singular dispersal rates decrease, as can be seen in Figure 5a. Branching happens when the difference of the carrying capacities is large enough. (Starting from $K_2 \approx 4$).

In Figure 3 the parameter values of p_1 for which branching occurs are not in the center of the parameter region. The same phenomenon occurs in Figure 4, and also in Figure 5. When the only difference in the patch types is the catastrophe rate μ , the average population size in the patches is higher in the patch type 1 with lower μ . Therefore the patch type 1 dominates and branching cannot happen if p_1 is too high. The biggest level of spatial heterogeneity from the point of view of an individual occurs thus for relatively small values of p_1 . Correspondingly, when patches differ only in the carrying capacity K , the bigger patch type 2 dominates, and branching happens for high values of p_1 .

We conclude that spatial heterogeneity can lead to a polymorphic population through evolutionary branching. The necessary level of spatial heterogeneity can be obtained with differences in growth conditions alone, as well as with differences in catastrophe rates alone, and should be measured from the point of view of an individual.

4. Conclusion

We have presented a generalisation of the metapopulation model presented by Gyllenberg and Metz (2001) and Metz and Gyllenberg (2001). We then gave a method for analyzing resident and mutant behaviour in a metapopulation with many different patch types. The method covers also the polymorphic situation with several resident phenotypes. This was, in fact, mentioned as an open research task in Metz and Gyllenberg (2001). Using these methods we studied the evolution of dispersal in the generalized model. We found that evolutionary branching can occur when there is enough spatial heterogeneity in the sense of different patch types with sufficient proportions, and temporal variation caused by catastrophes. The level of spatial heterogeneity should be measured from the point of view of an individual.

Evolutionary branching of dispersal strategies has been found before (Holt and McPeck 1996; Doebeli and Ruxton 1997; Parvinen 1999; Johst *et al.* 1999; Mathias *et al.* 2001; Kisdi 2002). More precisely, Holt and McPeck (1996), Doebeli and Ruxton (1997), and Parvinen (1999) studied discrete-time metapopulation models. Holt and McPeck (1996) found polymorphisms and branching in a model with two patches when local dynamics is chaotic and patches are unequal. Doebeli and Ruxton (1997) and Parvinen (1999) studied the difference of equilibrium and two-cyclic population orbit cases. Parvinen (1999) proved analytically that in the

case of fixed point equilibria, the strategy not to migrate is evolutionarily stable and convergence stable. Therefore no branching occurs in fixed point equilibrium cases. If the resident attractor is a two-cyclic orbit, then evolutionary branching can occur. Johst *et al.* (1999) studied evolution of dispersal and complexity of dynamics in a discrete-time metapopulation model with spatial lattice structure. They also found branching of dispersal strategies in the case of temporal variation. McPeck and Holt (1992) found dispersal polymorphisms in a model with temporally and spatially varying carrying capacities. In a similar setting, Mathias *et al.* (2001) found evolutionary branching. Kisdi (2002) studied evolution of dispersal and local adaptation in a stochastic metapopulation model with two patches, and found evolutionary branching of the dispersal strategy, as well as of the local adaptation strategy. See also Meszéna *et al.* (1997) Our work is to our knowledge therefore the first one to show that evolutionary branching of dispersal strategies can occur also in the case of spatial heterogeneity and temporal variation caused by catastrophes. Without catastrophes evolutionary branching cannot occur in our model.

Geritz *et al.* (1998) studied a model where the strategy describes local adaptation in patches. In different patches different strategies are optimal. If all patches are equal, the strategy which is optimal is naturally evolutionarily stable and convergence stable. If the difference of the optimal local strategies is large enough, in other words there is enough spatial heterogeneity, then evolutionarily branching occurs. In our model the situation is a little bit different. When all patches are equal, changing the carrying capacity of all of them does not have an effect on the evolutionarily stable dispersal rate. However, adding another patch type with a different carrying capacity does change the dispersal behaviour, and evolutionary branching can occur. Evolutionary branching is thus possible even though the evolutionarily stable strategies in the different patch types alone would be equal.

Acknowledgements. The author wishes to thank Stefan Geritz, Mats Gyllenberg, and Éva Kisdi for discussions. This work has been supported by the Graduate School in Computational Biology, Bioinformatics, and Biometry, the Academy of Finland and Turku University Foundation.

A. Cumulative formulation

In the modelling approach of Diekmann *et al.* (2001) individual development, survival, and reproduction are assumed to depend on the environmental condition or environmental interaction variable, which we denote by I . The key point is that the variable I should be chosen such that for given $I = I(t)$ the population model becomes a nonautonomous linear model. In this sense the variable I acts as an input to the system. Individuals affect their own environment. This is modelled by specifying an individual output. The total population output is then obtained by adding up all the individual outputs. In mathematical terms the population output is thus a linear functional of the population state. Finally the full nonlinear problem is obtained by closing the feedback-loop by declaring input equal to output. In this model the immigration rate I works as an input to the patch dynamics.

The nonlinear theory of general structured population models was presented by Diekmann *et al.* (2001) and adapted to structured metapopulation models by Gyllenberg *et al.* (1997). The model with one patch type was presented by Gyllenberg and Metz (2001).

Local population growth is modelled as a Markov process with local extinction as an absorbing state by specifying the transition probabilities $u_I(t, x, j)$, that is, $u_I(t, x, j)(\omega)$ is the probability that a local population which had size x in a patch of type j at time 0 is still extant at time t and has size in the set ω .

Let $X_I(t, x, j)$ be the solution of

$$\begin{cases} \frac{d}{dt} X(t) = g_j(X(t))X(t) - k(X(t))X(t) + I(t) \\ X(0) = x. \end{cases} \quad (25)$$

A local population, which at time 0 had size x , will at time t have size $X_I(t, x, j)$, provided it has not been wiped out by a local catastrophe.

The probability \mathcal{F} that a catastrophe has not occurred before time t , and thus the population is still extant, has to satisfy the differential equation $\frac{d}{dt} \mathcal{F}_I(t, x, j) = -\mu_j(X_I(s, x, j))\mathcal{F}_I(t, x, j)$. The solution is

$$\mathcal{F}_I(t, x, j) = \exp \left[- \int_0^t \mu_j(X_I(s, x, j)) ds \right]. \quad (26)$$

The transition probability of the local population size in a patch of type j is given by the measure

$$u_I(t, x, j) = \mathcal{F}_I(t, x, j) \delta_{X_I(t, x, j)}, \quad (27)$$

where $\delta_{X_I(t, x, j)}$ is a measure concentrated on a single point $X_I(t, x, j)$. $u_I(t, x, j)(\omega)$ is the probability that a local population which had size x at time 0 is still extant at time t and has size in the set ω .

When a local population is wiped out by a catastrophe, the patch it inhabited will immediately be recolonized by migrants arriving from the dispersal pool provided $I > 0$. We consider this event as the simultaneous death of the local population and the birth of a new local population with size 0. The expected number of new local populations produced in the time interval $[0, t)$ by a local population having size x at time 0 and subject to the input $I > 0$ is therefore

$$1 - \mathcal{F}_I(t, x, j). \quad (28)$$

If $I = 0$, there are no dispersers and there will still be death but no birth of a new population.

Reproduction (the formation of new local populations) is modelled by specifying the reproduction kernel Λ : $\Lambda_I(t, x, j)(\omega)$ is the expected number of new local populations with “size-at-birth” in the set ω , produced in the time interval $[0, t)$ by a local population which had size x at time 0. As all new populations are born with size zero, the reproduction kernel is

$$\Lambda_I(t, x, j) = \begin{cases} (1 - \mathcal{F}_I(t, x, j))\delta_0 & \text{if } I > 0 \\ 0 & \text{if } I = 0. \end{cases} \quad (29)$$

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