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On fitness in structured metapopulations

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Abstract. In this paper we derive a general expression measuring fitness in general structured metapopulation models. We apply the theory to a model structured by local population size and in which local dynamics is explicitly modelled. In particular, we calculate the evolutionarily stable dispersal strategy for individuals that can assess the local population density in the case where only dispersal is subject to evolutionary control but all other model ingredients are assumed fixed. We show that there exists a threshold size such that at ESS everyone should stay as long as the population size is below the threshold and everyone should disperse immediately as the population size reaches the threshold.

1. Introduction

During the past decade we have witnessed an increasing interest in the dynamics of metapopulations. The book edited by Hanski and Gilpin (1997) and the book by Hanski (1999) contain more than 1000 references each. At the same time the evolution of dispersal has caught the interest of many scientists (Hastings 1983; Holt and McPeek 1996; Doebeli and Ruxton 1997; Parvinen 1999). Long-term evolution is the result of invasions of mutant traits and the success of invasion attempts is determined by the fitness of the mutant. As most species have a hierarchical spatial structure with several local populations connected by dispersal comprising a metapopulation, the evolution of migration or dispersal is most conveniently modelled in the framework of metapopulation dynamics. It is the purpose of the present paper to present a mathematical definition of fitness in structured metapopulation models.

In a single population *fitness* is usually defined as the long-term exponential growth rate $r(E)$ of a phenotype in a given environment E (Metz *et al.* 1992). Here one should think of the environment as an interaction variable through which all (nonlinear) feedback takes place. If the environment is constant, $E(t) \equiv \overline{E}$, then one can alternatively and equivalently use the *basic reproduction ratio* $R(\overline{E})$ as fitness measure because it is well known that $R(\overline{E})$ is less than, equal to, or greater than 1 depending on whether $r(\overline{E})$ is less than, equal to, or greater than 0. $R(\overline{E})$ is

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the expected lifetime production of offspring. The difference between r and R is that r is the growth rate in real time, whereas R operates at the generation level.

The question concerning successful invasion is easily addressed using the basic reproduction ratio R. Assume that the resident population is in demographic equilibrium corresponding to a constant environment $\overline{E}^{\mathrm{res}}$. Since at demographic equilibrium every individual on average exactly replaces itself one has $R^{\mathrm{res}}\left(\overline{E}^{\mathrm{res}}\right) = 1$. The basic reproduction ratio R depends on both the environment and the strategy and the superscript res refers to the strategy played by the resident. A mutant playing a different strategy can invade if and only if

$$R^{\mathrm{mut}}\left(\overline{E}^{\mathrm{res}}\right) > 1. \tag{1.1}$$

This means that a mutant can invade if and only if its basic reproduction ratio in the environment set by the resident is greater than 1.

When we want to apply the procedure outlined above to metapopulations we encounter several difficulties. The most obvious one is that even if the environmental interaction variable is constant at the resident attractor, a mutant experiences different conditions in different patches, and moreover, the conditions change in the patch due to the development of the resident local population. So it is far from obvious how to define $R^{\mathrm{mut}}\left(\overline{E}^{\mathrm{res}}\right)$ in the case of metapopulation models.

In this paper we present, for a large class of structured metapopulation models including models with stochasticity at the level of local populations, a mathematical definition of a quantity that plays the same role as $R^{\mathrm{mut}}\left(\overline{E}^{\mathrm{res}}\right)$ for ordinary populations. In order not to unduly multiply notation we shall denote this new quantity by the same symbol $R^{\mathrm{mut}}\left(\overline{E}^{\mathrm{res}}\right)$ as there is no risk of ambiguity. In Section 5 we give an explicit formula for $R^{\mathrm{mut}}\left(\overline{E}^{\mathrm{res}}\right)$ for a model with deterministic growth of local populations. We also calculate the evolutionarily stable dispersal strategy assuming that the tendency to migrate depends only upon the local population size and not for instance on the age of the individual. Because of the deterministic nature of local dynamics this model assumes infinite local populations. In a companion paper (Metz and Gyllenberg 2001) we work out the details for the finite local population case and give recipes to efficiently calculate $R^{\mathrm{mut}}\left(\overline{E}^{\mathrm{res}}\right)$ using existing software. In that paper we also calculate the evolutionarily stable dispersal strategy for the case of juvenile migration and infinite local populations as opposed to the age-independent migration considered in the present paper.

2. Structured metapopulation dynamics

In this paper we model structured metapopulations in the spirit of Gyllenberg *et al.* (1997). We start by giving a brief description of that part of the theory which is essential for our present needs. As pointed out by Metz and Diekmann (1986) (see also Diekmann *et al.* 1988, 1989), the theory of structured populations can be applied to metapopulations in a rather straightforward manner if one makes the analogy between local populations and individuals and between metapopulation and population. Our approach is therefore merely an adaptation of the general structured population framework of Diekmann *et al.* (1993, 1998, 2001) to metapopulation models.

We consider a given configuration of habitat patches that can support local populations and that allow for migration between the patches. We regard a metapopulation as a population of such local populations plus the population of dispersers. Local populations and dispersers are called *local entities*. A local entity is characterized by its *state* x, which typically is a vector in a finite dimensional space. The components of x may for instance stand for the size of a local population or the quality of the patch it inhabits. Dispersers may be structured by age, etc.

A local entity develops (i.e., its state changes with time) as a consequence of for instance patch quality dynamics, local population growth due to births, deaths and migration; it gives rise to new local entities (e.g. local populations produce dispersers, dispersers colonize empty patches); and vanishes (e.g. when a local population goes extinct or a disperser dies). To model mechanisms at the local level, we therefore need two ingredients, one describing the production of new local entities and one describing the development and survival of local entities.

In this paper we shall only be concerned with constant environments and this makes the notation much simpler as compared with the one in (Gyllenberg *et al.* 1997). In particular we shall drop the overbar on constant environments and since the environment is always assumed to be set by the resident, the superscript res becomes superfluous. We thus write simply E instead of $\overline{E}^{\mathrm{res}}$.

We let Ω denote the local state space, that is, the set of all admissible local states. We introduce the *lifetime cumulative reproduction measure* Λ and the *local development measure* as follows: For each given constant environment E, each $x \in \Omega$ and each measurable set $\omega \subset \Omega$ we let

$\Lambda_E(x)(\omega) =$ expected number of new local entities with birth state in ω produced by a local entity with birth state x during its entire life, the expectation being taken over all possible sample functions of birth giving by local entities starting in state x,

$u_E(x;t)(\omega) =$ probability that a local entity with state x will still be alive and have state in ω, t time units later.

The measures $\Lambda_E(x)$ and $u_E(x;t)$ are not independent but satisfy certain consistency relations (Diekmann *et al.* 1998, 2001; Gyllenberg *et al.* 1997). For instance, the measures $u_E(x;t)$ are the transition probabilities of a Markov process and therefore they satisfy the Chapman-Kolmogorov relation.

The *metapopulation state* is by definition the distribution of local states and is represented by a measure $m \in M_+(\Omega)$, the set of all finite positive Borel measures in Ω. We can now lift the model to the metapopulation level by defining the *next generation operator* W and the *next state operators* $T(t),\ t \geq 0$ acting on $M_+(\Omega)$. For each given constant environment E, each $m \in M_+(\Omega)$ and each measurable set $\omega \in \Omega$ we set

$$(W_E m)(\omega) = \int_\Omega \Lambda_E(x)(\omega) m(dx), \tag{2.1}$$

$$(T_E(t)m)\,(\omega) = \int_{\Omega} u_E(x;t)(\omega)m(dx). \tag{2.2}$$

$(W_E m)\,(\omega)$ is the expected number of new local entities with birth state in ω produced by a collection of local entities distributed as m, during their entire lives. $T_E(t)m$ is the distribution at time t of a collection of local entities which at time zero were distributed as m. It follows from the fact that u_E satisfies the Chapman-Kolmogorov relation that $\{T_E(t)\}_{t\geq 0}$ is a semigroup.

Following Diekmann *et al.* (1990, 1998), Heesterbeek (1992) and Gyllenberg *et al.* (1997) we now define the basic reproduction ratio $R(E)$ as the spectral radius of the operator W_E.

In most cases of interest positivity arguments guarantee that $R(E)$ is an eigenvalue and that all other eigenvalues have absolute value less than or equal to $R(E)$. An irreducibility condition is needed to accomplish that $R(E)$ is the only positive eigenvalue and that it is simple.

Let b_E be the eigenvector corresponding to $R(E)$. b_E and $R(E)$ have important biological interpretations: b_E is the distribution of birth states at equilibrium and $R(E)$ is the expected number of new local entities produced by one "typical", that is, sampled from b_E, local entity during its entire life.

Usually the set Ω_b of admissible birth states is much smaller than the local state space Ω. It is clear that for solving the eigenvalue problem (determining $R(E)$) one only has to consider the restriction of W_E to $M_+(\Omega_b)$. In many models there are only a finite number of admissible birth states. When this is the case determining $R(E)$ boils down to finding the dominant eigenvalue of a nonnegative (finite dimensional) matrix. Without risk of confusion we shall use the same symbol for W_E and its restriction to $M_+(\Omega_b)$ or the corresponding matrix.

The steady metapopulation state corresponding to E is given by

$$m_E = \int_0^{\infty} T_E(t) b_E dt. \tag{2.3}$$

A necessary condition for equilibrium is

$$R\,(E) = 1. \tag{2.4}$$

Often, and in particular in the cases considered below, the environmental interaction variable E is connected to the metapopulation state through a linear operator A and this gives us an additional equilibrium condition:

$$E = Am_E. \tag{2.5}$$

We emphasize that at the local level the model is stochastic and that it therefore allows for finite local population sizes taking on integer values. But the way in which the model is lifted to the metapopulation level involves taking expectations and therefore the full model is deterministic and based on the tacit assumption of an infinite number of patches.

3. A class of structured metapopulation models

In this section we specify the class of models to which the general framework of Section 2 will be applied.

We assume that selection operates at the level of individuals and therefore we shall always include local population density x_1 as a component of the structuring variable x of local populations. Other components can for instance reflect patch quality and area (Hanski and Gyllenberg 1993, 1997; Gyllenberg and Hanski 1997) and they may or may not be dynamical variables. The set of all admissible x is denoted by Ω_p (p for population). The dispersers are unstructured and they do not reproduce during migration. The condition of being a disperser is symbolically represented by "d". The local state space is thus $\Omega = \Omega_p \cup \{d\}$.

Although our model allows for stochastic development of local entities, it is deterministic as the reproduction measure Λ describes expectation. In order to justify the deterministic approximation we assume that both the number of patches and the patch size are very large, that is, mathematically speaking, infinite. The total patch density (that is, the number of patches per unit of area) will be scaled to 1. The disperser pool will be scaled by letting D denote the number of dispersers per patch and patch area. We shall refer to D as the *density of dispersers*. We refer to the paper by Metz and Gyllenberg (2001) for a detailed discussion of the appropriate limit as the patch size tend to infinity.

The density D of dispersers affects local dynamics through immigration. This is most conveniently modelled by taking D as one component of the environmental interaction variable (Gyllenberg and Hanski 1992). We shall do so in this paper.

We shall allow for local disasters in which all individuals of a patch die. A local disaster is considered as the simultaneous death of the old local population and the birth of a new local population with size zero. This is a valid model assumption, since in our deterministic setting there is a continuous inflow of migrants from the disperser pool: There are no empty patches.

Emigration is interpreted as a local population giving birth to a disperser. The set of population birth states is therefore $\Omega_b = \Omega_{bp} \cup \{d\}$, where Ω_{bp} is a subset of $\left\{x \in \Omega_p \mid x_1 = 0\right\}$.

We represent a measure on Ω by a 2-vector the first component of which is a measure p on Ω_p and the second component is a real number D. Because there are no empty patches in our model, p is a probability measure, that is, its total mass equals 1. Similarly a measure on Ω_b is represented by a vector with components consisting of a measure $b^{(p)}$ on Ω_{bp} and a real number $b^{(d)}$. With this notation the components of $\Lambda_E(x)$ become $\Lambda_E^{(p)}(x)$ and $\Lambda_E^{(d)}(x)$. $\Lambda_E^{(p)}(x)(\omega)$ is the expected number of new local populations with birth state in ω and $\Lambda_E^{(d)}(x)$ is the expected number of dispersers produced by a local population born in state x during its lifetime. By our model description dispersers do not produce new local entities. The next generation operator W therefore vanishes on the $b^{(d)}$ component of b and we have

$$W_E \begin{pmatrix} b^{(p)} \\ \\ b^{(d)} \end{pmatrix} = \begin{pmatrix} W_E^{(p)} & 0 \\ \\ W_E^{(d)} & 0 \end{pmatrix} \begin{pmatrix} b^{(p)} \\ \\ b^{(d)} \end{pmatrix} = \begin{pmatrix} \int_{\Omega_{bp}} \Lambda_E^{(p)}(x) b^{(p)}(dx) \\ \\ \int_{\Omega_{bp}} \Lambda_E^{(d)}(x) b^{(p)}(dx) \end{pmatrix}. \tag{3.1}$$

Because by our model assumption there is neither loss nor gain of local populations it is clear that the spectral radius of $W_E^{(p)}$ is one and hence the same is true of W_E. It follows that

$$R\,(E) = 1. \tag{3.2}$$

The eigenvector $b_E = \left(b_E^{(p)}, b_E^{(d)}\right)^T$ corresponding to $R\,(E) = 1$ (unique up to a multiplying constant) is now obtained by first solving

$$\int_{\Omega_{bp}} \Lambda_E^{(p)}(x) b_E^{(p)}(dx) = b_E^{(p)}, \tag{3.3}$$

and then defining

$$b_E^{(d)} = \int_{\Omega_{bp}} \Lambda_E^{(d)}(x) b_E^{(p)}(dx). \tag{3.4}$$

Finally the equilibrium metapopulation state is obtained from (2.3) and (2.2)

$$p_E = \int_0^\infty \int_{\Omega_{bp}} u_E(x;t) b_E^{(p)}(dx)dt, \tag{3.5}$$

$$D = \tau b_E^{(d)}, \tag{3.6}$$

where

$$\tau = \int_0^\infty u_E(d;t)dt \tag{3.7}$$

is the expected time a disperser stays (until dying or immigrating into a patch) in the disperser pool. We now determine the hidden constant in $b_E^{(p)}$ by requiring

$$\int_\Omega p_E(dx) = 1. \tag{3.8}$$

Note that in the calculations above we have pretended that the constant environment E is given. As we have pointed out E is determined by the metapopulation state and contains D as a component. Therefore (3.5) and (3.6) are not explicit formulas but equations from which E (and hence D) can be solved. An example of how this can be done is given in Section 5.

4. The fitness of a rare mutant

Assume that the resident population has reached an equilibrium m_E corresponding to a constant environment E. The fitness of a rare mutant is in principle defined in a straightforward manner along the lines outlined in the introduction and in Section 2. We thus let Λ_E^{mut} be the lifetime cumulative reproduction measure of mutants when the environment is set by the resident. The next generation operator of the mutant is then analogously to (2.1) given by

$$\left(W_E^{\mathrm{mut}} m\right)(\omega) = \int_\Omega \Lambda_E^{\mathrm{mut}}(x)(\omega) m(dx) \tag{4.1}$$

and $R^{\mathrm{mut}}(E)$ is defined as the spectral radius of W_E^{mut}.

When it comes to the actual specification of the reproduction measures we observe a fundamental difference between Λ_E^{mut} and Λ_E^{res}. Recall from Section 3 that there is no reproduction event associated with a resident disperser immigrating into a patch — the local resident population already exists and immigration will only affect the growth of the local population and not its existence. For the mutant the situation is different. A mutant disperser arriving at a patch with only resident individuals will indeed initiate a new mutant local population. After that the development of the mutant local population depends only on the state of the resident local population in the same patch, because the rarity of the mutant makes its contribution to density dependent effects negligible. This means that the mutant population is structured by the state of the corresponding local resident population. Contrary to the case of the resident for which the admissible birth states of local populations were restricted to a subset Ω_{bp} of $\left\{x \in \Omega_p \mid x_1 = 0\right\}$, the mutant local populations can have any birth state in Ω_p.

Precisely as for the resident a mutant local population is considered to produce or "give birth" to mutant dispersers.

In order to derive a simple formula for the mutant fitness we make the additional assumption that dispersers choose their new patch at random. The fate of a disperser is then completely determined by the probability π of surviving migration. The value of π may of course be different for residents and mutants.

Consider now a newborn mutant. It is either a disperser or a mutant colony surrounded by residents in a patch. If it is a disperser it will survive migration with probability π^{mut} in which case it founds a new mutant colony. Because the disperser chooses its patch at random, the state at birth of the new mutant colony is distributed according to the resident metapopulation steady state p_E given by (3.5). It follows that the life-time production of new local entities produced by one mutant disperser is described by the measure

$$\Lambda_E^{(p)}(d) = \pi^{\mathrm{mut}} p_E.$$

If the mutant is born in a patch it will start to reproduce in the patch and form a local mutant colony. How many mutant dispersers this colony is expected to produce during its entire life is affected by competition with the residents. Since the mutants are rare, this expectation is determined by the state of the resident local population at time of initiation of the mutant colony. Consistently with our notation, we denote it by $\Lambda_E^{(d)\,\mathrm{mut}}(x),\ x \in \Omega_p$.

Lifting this description of local mutant behaviour to the level of the metapopulation we obtain the next generation operator:

$$W_E^{\mathrm{mut}} \begin{pmatrix} b^{(p)} \\ \\ b^{(d)} \end{pmatrix} = \begin{pmatrix} \pi^{\mathrm{mut}} b^{(d)} p_E \\ \\ \int_{\Omega_p} \Lambda_E^{(d)\,\mathrm{mut}}(x) b^{(p)}(dx) \end{pmatrix}. \tag{4.2}$$

The definition (4.2) of W_E^{mut} should be compared with the corresponding definition (3.1) for the next generation operator of the resident.

The mutant fitness is now obtained as a solution to the eigenvalue problem

$$W_E^{\mathrm{mut}} \begin{pmatrix} b^{(p)} \\ b^{(d)} \end{pmatrix} = R^{\mathrm{mut}}(E) \begin{pmatrix} b^{(p)} \\ b^{(d)} \end{pmatrix} \tag{4.3}$$

It follows from (4.2) and (4.3) that

$$R^{\mathrm{mut}}(E) = \sqrt{\pi^{\mathrm{mut}} \int_{\Omega_p} \Lambda_E^{(d)\,\mathrm{mut}}(x) p_E(dx)}. \tag{4.4}$$

Formula (4.4) calls for some comments. First of all $-R^{\mathrm{mut}}(E)$ is also an eigenvalue of W_E^{mut} so the spectral radius is not a strictly dominant eigenvalue. This is due to the fact that the mutant has alternating generations: dispersers give rise to local populations and vice versa, so at the generation level the mutant metapopulation oscillates. On the other hand, because the generations overlap, there will be convergence towards a stable metapopulation state in real time.

The invasion criterion $R^{\mathrm{mut}}(E) > 1$ is of course equivalent to the condition $\left(R^{\mathrm{mut}}(E)\right)^2 > 1$ and because the period on the generation level is two generations, the square of the basic reproduction ratio is easier to interpret biologically. The probability that the state of the local population inhabiting the patch at which a mutant disperser arrives lies in ω is $p_E(\omega)$. This mutant produces a local mutant colony. The expected number of dispersers produced by such a colony is $\int_{\Omega_p} \Lambda_E^{\mathrm{mut}\,(d)}(x) p_E(dx)$. Of these a fraction π^{mut} will reach a habitat patch where they can found a new colony. The product of these two last mentioned numbers is $\left(R^{\mathrm{mut}}(E)\right)^2$ which therefore is the expected number of new mutant colonies produced by one newly started mutant colony in an otherwise mutant free metapopulation. Thus $\left(R^{\mathrm{mut}}(E)\right)^2$ is here the direct local-entity analogue of the usual individual level concept of basic reproduction ratio.

5. An example

In the general discussion above we have assumed that Λ_E^{mut} is given beforehand. In applications the reproduction measure of mutants has, however, to be determined from the vital rates of both the resident and the mutant. In this section we shall illustrate the general theory by calculating $\left(R^{\mathrm{mut}}(E)\right)^2$ for a concrete example.

We assume that the local populations are only structured by size and that the density D of dispersers is the only component of the environmental interaction variable. We thus write $D = E$. The local population state space is $\Omega_p = [0, \infty)$. The space of admissible local population birth states of the resident is a single point: $\Omega_{bp} = \{0\}$. The birth state measure can therefore be represented by a vector $\left(b^{(p)}, b^{(d)}\right)^T \in \mathbf{R}^2$ and the next generation operator W_D becomes a 2×2 matrix.

Our model is specified by the following ingredients:

$g(x)$	density dependent per capita growth rate due to local births and deaths,
$k(x)$	density dependent per capita emigration rate,
α	immigration rate per disperser,
ν	death rate per disperser,
$\mu(x)$	density dependent local disaster rate.

The first four of these rates describe individual behaviour. Therefore they depend on the strategy and will be equipped with superscripts res and mut whenever it is needed. The disaster rate μ operates at the level of local populations and is therefore independent of the strategy (recall that we assume that selection occurs at the individual level).

When two types are simultaneously present it is conceivable that they affect the local environment in different ways and therefore the functions g, k and μ are in general functions of both the resident and mutant densities. However, below we shall only consider the invasion problem in the case of infinite local populations and there the mutant is present only in infinitesimal quantities so its influence on these functions can be neglected.

Local dynamics are deterministic and are governed by the ordinary differential equation

$$\frac{dx}{dt} = g(x)x - k(x)x + \alpha D. \tag{5.1}$$

For constant D the local population size can never exceed the least positive x for which the right hand side of (5.1) is zero. We denote this value by $x_{\max}(D)$. If the right hand side of (5.1) is positive for all $x \in [0, \infty)$, then $x_{\max}(D) = \infty$.

For constant D, let $X_D(y; t)$ be the solution of (5.1) with initial condition $x(0) = y$. Then

$$u_D(x;t) = \begin{cases} \exp\left(-\int_0^t \mu(X_D(x;s)ds)\right) \delta_{X_D(x;t)} & \text{if } x \in [0, \infty), \\ \exp\left(-(\alpha + \nu)t\right) \delta_d & \text{if } x = d. \end{cases} \tag{5.2}$$

Here δ_x denotes the point mass concentrated at x. The expected time a disperser spends migrating is

$$\tau = \frac{1}{\alpha + \nu} \tag{5.3}$$

and the probability of surviving dispersal is

$$\pi = \frac{\alpha}{\alpha + \nu}. \tag{5.4}$$

Next we derive the equilibrium of the resident metapopulation following the procedure described in Section 3. We therefore have to compute the next generation operator, which, as noted above, in the present case reduces to a 2 × 2 matrix. We know that the the element in the upper left corner has spectral radius 1, but because it is now a scalar the element itself equals one: $W_D^{(p)} = 1$. This reflects the fact that when a local population goes extinct, the patch is immediately recolonized by immigrants from other patches. We therefore only have to compute the other nonzero element $W_D^{(d)} = \Lambda_D^{\mathrm{res}\,(d)}(0)$ which is the expected number of dispersers produced by a newly initiated local population during its entire life.

Consider a local population. The probability that it is still extant when it has size x is

$$\exp\left(-\int_0^x \frac{\mu(\xi)}{g^{\mathrm{res}}(\xi)\xi - k^{\mathrm{res}}(\xi)\xi + \alpha^{\mathrm{res}} D} d\xi\right). \tag{5.5}$$

A local population produces

$$\frac{k^{\mathrm{res}}(x)x\,dx}{g^{\mathrm{res}}(x)x - k^{\mathrm{res}}(x)x + \alpha^{\mathrm{res}} D} \tag{5.6}$$

dispersers while its size is in the infinitesimal interval $[x, x+dx]$. The denominator in (5.5) and (5.6) is of course nothing but the conversion factor between growth and aging of a population as defined by equation (5.1). Summing up over all sizes at which a local population produces dispersers one obtains

$$\begin{aligned}\Lambda_D^{\mathrm{res}\,(d)}(0) = \int_0^{x_{\max}(D)} & \frac{k^{\mathrm{res}}(x)x}{g^{\mathrm{res}}(x)x - k^{\mathrm{res}}(x)x + \alpha^{\mathrm{res}} D} \cdot \\ & \times \exp\left(-\int_0^x \frac{\mu(\xi)}{g^{\mathrm{res}}(\xi)\xi - k^{\mathrm{res}}(\xi)\xi + \alpha^{\mathrm{res}} D} d\xi\right) dx. \end{aligned} \tag{5.7}$$

The eigenvector $\left(b^{(p)}, b^{(d)}\right)^T$ corresponding to the eigenvalue 1 of the matrix W_D is now obtained from the equation

$$W_D \begin{pmatrix} b^{(p)} \\ b^{(d)} \end{pmatrix} = \begin{pmatrix} 1 & 0 \\ \Lambda_D^{\mathrm{res}\,(d)}(0) & 0 \end{pmatrix} \begin{pmatrix} b^{(p)} \\ b^{(d)} \end{pmatrix} = \begin{pmatrix} b^{(p)} \\ b^{(d)} \end{pmatrix}. \tag{5.8}$$

The first component of Equation (5.8) is $b_D^{(p)} = b_D^{(p)}$ and gives no information. The other component yields

$$b_D^{(d)} = \Lambda_D^{\mathrm{res}\,(d)}(0) b_D^{(p)}. \tag{5.9}$$

It follows from (3.5) and (5.2) that

$$\begin{aligned} p_D(dx) = & \frac{b_D^{(p)}}{g^{\mathrm{res}}(x)x - k^{\mathrm{res}}(x)x + \alpha^{\mathrm{res}} D} \\ & \times \exp\left(-\int_0^x \frac{\mu(\xi)}{g^{\mathrm{res}}(\xi)\xi - k^{\mathrm{res}}(\xi)\xi + \alpha^{\mathrm{res}} D} d\xi\right) dx. \end{aligned} \tag{5.10}$$

The expression (5.10) for p_D still contains the unknown quantity $b_D^{(p)}$. But because p_D is a probability measure, $b_D^{(p)}$ is determined by the requirement

$$\int_0^{x_{\max}(D)} p_D(dx) = 1.$$

Hence

$$b_D^{(p)} = \frac{1}{\ell_D^{\mathrm{res}}}, \tag{5.11}$$

where

$$\begin{aligned}\ell_D^{\mathrm{res}} = \int_0^{x_{\max}(D)} & \frac{1}{g^{\mathrm{res}}(x)x - k^{\mathrm{res}}(x)x + \alpha^{\mathrm{res}} D} \\ & \times \exp\left(-\int_0^x \frac{\mu(\xi)}{g^{\mathrm{res}}(\xi)\xi - k^{\mathrm{res}}(\xi)\xi + \alpha^{\mathrm{res}} D} d\xi\right) dx.\end{aligned} \tag{5.12}$$

Notice that ℓ_D^{res} is the expected life-time of a resident local population.

From (3.6), (5.3), (5.4), (5.9) and (5.11) we now deduce the equation

$$\alpha^{\mathrm{res}} D = \pi^{\mathrm{res}} \frac{\Lambda_D^{\mathrm{res}\,(d)}(0)}{\ell_D^{\mathrm{res}}} \tag{5.13}$$

from which the equilibrium number D of dispersers per patch can be solved. Note that equation (5.13) is a balance equation. It says that at equilibrium the immigration rate equals the emigration rate times the probability of surviving dispersal. Once D has been solved from (5.13), the equilibrium metapopulation state p_D is obtained from (5.10).

Next we derive the expression for the mutant fitness. In order to apply formula (4.4) we still have to calculate $\Lambda_D^{\mathrm{mut}\,(d)}(x)$. To do so, recall that since the mutant is rare it does not affect the local population dynamics. The structuring variable x (the size of the local resident population) will still grow according to (5.2). If the mutation happened in a local population of size x the mutant colony will therefore grow thereafter (as long as the mutants remain rare) according to the time dependent linear ordinary differential equation

$$\frac{dy}{dt} = \Big(g^{\mathrm{mut}}(X_D(x;t)) - k^{\mathrm{mut}}(X_D(x;t))\Big) y. \tag{5.14}$$

Solving equation (5.14) we find that the mutant colony initiated when the resident local population had size x has size

$$\exp\left(\int_0^t \Big(g^{\mathrm{mut}}(X_D(x;\tau)) - k^{\mathrm{mut}}(X_D(x;\tau))\Big)\right) d\tau$$

t time units later. Shifting back to size of the resident population as book-keeping variable we find that a mutant colony that was initiated when the resident population had size x has size

$$\exp\left(\int_x^y \frac{g^{\mathrm{mut}}(\xi) - k^{\mathrm{mut}}(\xi)}{g^{\mathrm{res}}(\xi)\xi - k^{\mathrm{res}}(\xi)\xi + \alpha^{\mathrm{res}} D} d\xi\right)$$

when the resident population has reached size y. Arguing precisely as when deriving formula (5.7) we conclude that the expected number of mutant dispersers produced by a mutant local population that was initiated when the corresponding resident local population had size x is

$$\Lambda_D^{\mathrm{mut}\,(d)}(x) = \int_x^{x_{\max}(D)} \frac{k^{\mathrm{mut}}(y)}{g^{\mathrm{res}}(y)y - k^{\mathrm{res}}(y)y + \alpha^{\mathrm{res}}D} \times \exp\left(\int_x^y \frac{g^{\mathrm{mut}}(\xi) - k^{\mathrm{mut}}(\xi) - \mu(\xi)}{g^{\mathrm{res}}(\xi)\xi - k^{\mathrm{res}}(\xi)\xi + \alpha^{\mathrm{res}}D} d\xi\right) dy. \tag{5.15}$$

Substituting (5.4), (5.15), and (5.10) into (4.4) we obtain the following formula for the fitness of the mutant:

$$\begin{aligned} R^{\mathrm{mut}}(D)^2 = {} & \frac{\alpha^{\mathrm{mut}}}{\alpha^{\mathrm{mut}} + \nu^{\mathrm{mut}}} \frac{1}{\ell_D^{\mathrm{res}}} \int_0^\infty \int_x^{x_{\max}(D)} \frac{k^{\mathrm{mut}}(y)}{g^{\mathrm{res}}(y)y - k^{\mathrm{res}}(y)y + \alpha^{\mathrm{res}}D} \\ & \times \exp\left(\int_x^y \frac{g^{\mathrm{mut}}(\xi) - k^{\mathrm{mut}}(\xi) - \mu(\xi)}{g^{\mathrm{res}}(\xi)\xi - k^{\mathrm{res}}(\xi)\xi + \alpha^{\mathrm{res}}D} d\xi\right) dy \\ & \times \frac{1}{g^{\mathrm{res}}(x)x - k^{\mathrm{res}}(x)x + \alpha^{\mathrm{res}}D} \\ & \times \exp\left(-\int_0^x \frac{\mu(\xi)}{g^{\mathrm{res}}(\xi)\xi - k^{\mathrm{res}}(\xi)\xi + \alpha^{\mathrm{res}}D} d\xi\right) dx. \end{aligned} \tag{5.16}$$

Here D is a solution of (5.13) representing the equilibrium value of the environmental interaction set by the resident.

We close this section by calculating the evolutionarily stable dispersal strategy, when only k is under evolutionary control but all other vital rates are the same for the resident and the mutant. We therefore drop the superscripts res and mut from all other ingredients than k and consider R^{mut} given by (5.16) as a function of k^{res} and k^{mut}. The ESS is obtained by maximising R^{mut} in k^{mut} and then putting mutant equal to resident.

We assume that g and μ are continuous, that $g - \mu$ is decreasing and that the equation

$$g(x) - \mu(x) = 0 \tag{5.17}$$

has a unique positive solution, which we denote by $\tilde{x}$.

It follows from (4.4) that maximising R^{mut} amounts to maximising $\Lambda_D^{\mathrm{mut}\,(d)}(x)$ for all x. It follows from our assumptions that for all x one has

$$\Lambda_D^{\mathrm{mut}\,(d)}(x) \le \int_x^{x_{\max}(D)} \frac{k^{\mathrm{mut}}(y)}{g(y)y - k^{\mathrm{res}}(y)y + \alpha D} \times \exp\left(\int_x^y \frac{g(x) - k^{\mathrm{mut}}(\xi) - \mu(x)}{g(\xi)\xi - k^{\mathrm{res}}(\xi)\xi + \alpha D} d\xi\right) dy. \tag{5.18}$$

If the mutant local population is initiated when the resident local population has size $x > \tilde{x}$, then

$$\Lambda_D^{\mathrm{mut}\,(d)}(x) < \int_x^{x_{\max}(D)} \frac{k^{\mathrm{mut}}(y)}{g(y)y - k^{\mathrm{res}}(y)y + \alpha D} \times \exp\left(-\int_x^y \frac{k^{\mathrm{mut}}(\xi)}{g(\xi)\xi - k^{\mathrm{res}}(\xi)\xi + \alpha D} d\xi\right) dy = 1. \tag{5.19}$$

A mutant disperser arriving at a local population with size $x > \tilde{x}$ will therefore on average produce less than one new mutant disperser. It follows that it does not pay to stay in such a population; the mutant should leave immediately. In our formulation this requires the per capita emigration rate to be infinite for $x > \tilde{x}$.

It is easily seen that if $x < \tilde{x}$, then the number of mutant dispersers produced is maximised by not producing any dispersers until x reaches $\tilde{x}$ at which time all mutants in the local population should leave. In other words, the per capita emigration rate should be zero for $x < \tilde{x}$ (Metz and Gyllenberg 2001, Appendix).

What happens at the critical size $x = \tilde{x}$? Because all individuals leave for $x > \tilde{x}$ one must have $x_{\max}(D) = \tilde{x}$. $k(\tilde{x})$ can now be solved from the equation $g(x)x - k(x) + \alpha D = 0$. We have thus shown that the evolutionarily stable dispersal strategy is

$$k(x) = \begin{cases} 0 & \text{if } x < \tilde{x}, \\ g(\tilde{x}) - \frac{\alpha D}{\tilde{x}} & \text{if } x = \tilde{x}, \\ \infty & \text{if } x > \tilde{x}. \end{cases} \tag{5.20}$$

Strictly speaking it does not make sense to model population dynamics with rates that take on infinite values on intervals of positive measure. But turning to the cumulative framework (now at the level of *individuals* as opposed to local entities as previously in this paper) this is easily remedied. Let us first note that our model is memoryless in the sense that an individual born in a patch with local population size x is indistinguishable from a disperser arriving at a patch with local population size x. In the cumulative framework the individual dispersal strategy is most conveniently described in the context of a thought experiment in which the individual in question is equipped with a guardian angel who eliminates all causes of death (both individual death and catastrophes). The cumulative ingredient is thus

$\lambda_D(x;t)$	the probability that an individual born in (or arriving at) a patch with local population size x has not migrated t time-units later, given that the individual is not subject to any risk of death.

The content of formula (5.20) can now more appropriately be formulated by saying that the evolutionarily stable dispersal strategy is given by

$$\lambda_D(x;t) = \begin{cases} 1 & \text{if } x < \tilde{x} \text{ and } t < T_D(x,\tilde{x}), \\ \exp\left(-\left(g(\tilde{x}) - \frac{\alpha D}{\tilde{x}}\right)(t - T_D(x,\tilde{x}))\right) & \text{if } x < \tilde{x} \text{ and } t \geq T_D(x,\tilde{x}), \\ \exp\left(-\left(g(\tilde{x}) - \frac{\alpha D}{\tilde{x}}\right)t\right) & \text{if } x = \tilde{x}, \quad t > 0, \\ 0 & \text{if } x > \tilde{x}, \quad t > 0. \end{cases} \tag{5.21}$$

Here $T_D(x, y)$ is the time it takes for a population to grow from size x to size y. In words, at ESS an individual born in or arriving at a patch with local population size less than $\tilde{x}$ should stay until the population reaches the size $\tilde{x}$. An individual born in or arriving at a patch with local population size precisely $\tilde{x}$ should stay for an exponentially distributed time. Nobody should stay if the local population size exceeds $\tilde{x}$.

We mention in passing that the cumulative formulation of the full problem including death is quite complicated because we have to deal with a so-called competing risk problem with dependent risks. But these complications are of no importance for the ESS problem and they are therefore omitted.

Finally we observe that at the ESS the equilibrium distribution of local population sizes is a measure p concentrated on $[0, \tilde{x}]$. It has an absolutely continuous part with density

$$\phi(x) = \frac{b^{(p)}}{g(x)x + \alpha D} \exp\left(-\int_0^x \frac{\mu(\xi)}{g(\xi)\xi + \alpha D} d\xi\right) \tag{5.22}$$

and an atom at $\tilde{x}$ containing the rest of the mass of p.

We close by pointing out that adding physiological structure of the individuals leaves most of the arguments in the above example intact. Only the rank of the reproduction operator becomes larger since we have to take the individual state of dispersers into account. But the fitness and ESS can be calculated as above *mutatis mutandis*.

6. Concluding remarks

In this paper we have introduced a fitness measure for structured metapopulations that play the same role as the familiar basic reproduction ratio for ordinary unstructured populations. The derivation was done at an abstract level in order to assure the greatest possible generality. The example in Section 5 should show how the calculations can be done in practice. In addition the example is of interest in its own right.

It remains to consider the generality of the framework from a biological perspective. The generality of our presentation is limited by three essential assumptions only. First of all we assume that the size of the local patches is sufficiently large that we can apply a deterministic approximation of the local dynamics. A companion paper (Metz and Gyllenberg 2001) indicates in what manner this assumption can be relaxed. That paper also gives algorithms for how to proceed in the cases where there are no further structuring variables than local population densities.

The second essential assumption is that the catastrophes are (i) independent and (ii) fully eradicate the local population. If (i) is relaxed, no population dynamical point equilibrium will be reached and we cannot expect to find any fitness measure resembling the basic reproduction ratio. For a further discussion of this general case we refer to (Metz and Gyllenberg 2001). If the catastrophes do not set the local populations back to zero, then the cardinality of Ω_b is enlarged in one go from 2 to that of the continuum. The same arguments as in this paper still apply, but the inherent simplicity of the calculations is lost. We now have to solve a complicated eigenvalue problem for which no simple solution exists.

The third assumption is that all patches are coupled through dispersal with all other patches in precisely the same manner. Though obviously far from being realistic, this assumption is actually quite harmless. The theory of spatial population waves as discussed for instance by Metz *et al.* (2000) shows that in a more realistic spatial setting, as long as (i) dispersers from a single patch are spread over a sufficiently large number of patches to make a deterministic approximation feasible, (ii) patches are distributed homogeneously over space at the resolution set by the dispersal scale, and (iii) dispersal behaviour is invariant under translation of the spatial coordinates, a small initial mutant introduction will result in an invasion if and only if $R^{\text{mut}}\left(E^{\text{res}}\right) > 1$.

A final point is how the condition $R^{\text{mut}}\left(E^{\text{res}}\right) > 1$ is related to the probability of the mutant type going to fixation. Mutants arise as single individuals. So initially the deterministic theory developed in this paper does not apply as such. However, the general theory of branching processes (Jagers 1975) applied to local mutant colonies as generalized individuals tells us that a mutant has a positive probability of invading if and only if $R^{\text{mut}}\left(E^{\text{res}}\right) > 1$. For ESS considerations this is all that matters. An ESS (denoted by res*) should be protected against invasion by alternative variants, which is guaranteed by the condition $R^{\text{mut}}\left(E^{\text{res}^*}\right) < 1$ for all mut $\neq$ res*. One cannot give a general answer to what happens after invasion. In the case $R^{\text{mut}}\left(E^{\text{res}}\right) > 1, \quad R^{\text{res}}\left(E^{\text{mut}}\right) < 1$ we may expect a substitution, but even this is not guaranteed as all depends on the fine details of the dynamics when the mutant is not rare any longer. Moreover, there is a possibility of protected polymorphisms in the case $R^{\text{mut}}\left(E^{\text{res}}\right) > 1, \quad R^{\text{res}}\left(E^{\text{mut}}\right) > 1$. An example of such a case is given by Parvinen (2001). He also discussed how further evolution in the resulting dimorphic population can be treated along the lines laid down in the present paper.

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