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Interim Report IR-99-019

How Should We Define Fitness in Structured Metapopulation Models? Including an Application to the Calculation of Evolutionarily Stable Dispersal Strategies

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IIASA STUDIES IN ADAPTIVE DYNAMICS NO. 36

The Adaptive Dynamics Network at IIASA fosters the development of new mathematical and conceptual techniques for understanding the evolution of complex adaptive systems.

Focusing on these long-term implications of adaptive processes in systems of limited growth, the Adaptive Dynamics Network brings together scientists and institutions from around the world with IIASA acting as the central node.

Scientific progress within the network is reported in the IIASA Studies in Adaptive Dynamics series.

THE ADAPTIVE DYNAMICS NETWORK

The pivotal role of evolutionary theory in life sciences derives from its capability to provide causal explanations for phenomena that are highly improbable in the physicochemical sense. Yet, until recently, many facts in biology could not be accounted for in the light of evolution. Just as physicists for a long time ignored the presence of chaos, these phenomena were basically not perceived by biologists.

Two examples illustrate this assertion. Although Darwin's publication of "The Origin of Species" sparked off the whole evolutionary revolution, oddly enough, the population genetic framework underlying the modern synthesis holds no clues to speciation events. A second illustration is the more recently appreciated issue of jump increases in biological complexity that result from the aggregation of individuals into mutualistic wholes.

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Contents

Abstract

We define a fitness concept applicable to structured metapopulations consisting of infinitely many equally coupled patches, and provide means for calculating its numerical value. In addition we introduce a more easily calculated quantity R_m that relates to fitness in the same manner as R_0 relates to fitness in ordinary population dynamics: R_m of a mutant is only defined when the resident population dynamics converges to an equilibrium, and R_m is larger (smaller) than one if and only if mutant fitness is positive (negative). R_m corresponds to the average number of newborn dispersers resulting from the (on average less than one) local colony founded by a newborn disperser. As an example of the usefulness of these concepts we calculate the ES conditional dispersal strategy for individuals that can account for the local population density in their dispersal decisions.

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How Should We Define Fitness in Structured Metapopulation Models?
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J.A.J. Metz
M. Gyllenberg

1 Introduction

Classical metapopulation models are characterized by the fact that an infinite number of equally coupled patches are assumed. This poses some problems when it comes to doing ESS or Adaptive Dynamics (Metz et al., 1996; Geritz et al., 1997, 1998) calculations for these models. In particular, it is not immediately clear how we should define fitness, and what would be useful stand-ins for fitness, comparable to R_0 in the single population case. In this paper we solve these problems. To show the usefulness of the introduced concepts we calculate the ES conditional dispersal strategy if individuals can sense the local population density.

Before embarking on our program we provide a little context. In reality we have a finite, though possibly large, number of patches with different characteristics and different local population sizes, which are coupled in a complicated manner. One of the simplifying assumptions in metapopulation theory, to which we also shall adhere, is that all patches have equal characteristics, though not equal population sizes, and are equally coupled. This simplification may actually approximate reality rather well in the case of, for example, aphids, for which the dispersal distance is large relative to the intercolony distance, and where the patches correspond to single leaves in a tree.

Given the homogeneity assumption that we just introduced, we have available two overall system parameters, size of the patches ω, and number of patches Ω. When both parameters are small the metapopulation will go extinct on an ecological time scale. Therefore, if we are interested in long term evolution, at least one of these parameters should be large. We shall take the mathematician's stance and equate large with infinite, so that we may rigorously neglect process properties that at large sizes effectively disappear from sight.

In case only the patch sizes ω are infinite but there are but few patches (Ω small) the classical fitness concepts for structured populations, as expounded by Metz et al. (1992) applies. If there are no further structuring variables we just have Ω local population densities as the state variables of the metapopulation. The same holds good for a rare invader. So the local linearization of the invader dynamics, near zero invader densities, yields an Ω-dimensional linear dynamics, possibly with timevarying coefficients, depending on whether the overall environment is constant and the resident population dynamics converges to a point attractor, or some more complicated environmental and/or resident population dynamics ensues. The dominant Lyapunov exponent of this linear dynamics, which in the case of constant coefficients reduces to the dominant eigenvalue, provides the right fitness concept to be inserted into evolutionary calculations (see e.g. Parvinen, 1999). In the case of a population dynamical point equilibrium, we can use the general R_0 -concept for structured populations, introduced by Diekmann et al (1990, 1998; see also Heesterbeek, 1992), as stand-in for fitness: if and only if R_0 is larger (smaller) than one fitness will be positive (negative).

The real challenge comes when Ω is infinite, for then we are outside the standard mathematical framework for establishing the existence of an exponential growth rate and for establishing the existence of an R_0-like quantity telling in an unambiguous manner when a mutant will be able to invade. This mathematical quandary is not confined to the equal coupling case. It also applies to, say, patches coupled by nearest neighbour migration in a hexagonal grid in the plane. The only difference is that in the exceedingly symmetrical equal coupling case it can be resolved by classical analytical means whereas in the other cases there is no clear sight on a solution yet. Therefore we shall confine ourselves to the equal coupling case with Ω infinite and ω either finite or infinite.

To keep the mathematics simple we shall concentrate on the case without further structuring variables. In addition we shall assume that only newborns disperse, and that they do so by entering a dispersal pool which they leave either by dying or by entering a patch. We shall also phrase the models such that the newborns are allowed to migrate with a probability dependent on the local population density, and to choose on encountering a patch to stay or to leave again depending on the population density that they encounter. The reason for explicitly taking account of such decision rules is that this directly leads to our closing example, in which we calculate the ES conditional migration strategy. However, the arguments below are of a fully general nature, not tied to those specific model assumptions.

An excelent discussion of the litterature on life history calculations, and in particular ES dispersal strategies, in metapopulations can be found in Olivieri & Gouyon (1998; see also Ronce et al., submitted). A companion paper (Gyllenberg & Metz, 1999) dissects the abstract structure of the argument within the general framework for structured population models put forward in Diekmann et al. (1994, 1998), and calculates the ES conditional migration strategy for adult, as opposed to juvenile, dispersal.

2 The finite patch size case

2.1 Model specification

The state equations for a structured metapopulation are similar to the differential equations for the state probabilities of a continuous time Markov process. There are good reasons for this similarity. Every single patch undergoes a Markov process. Only the collective of all infinitely many patches together behaves as a determinis-

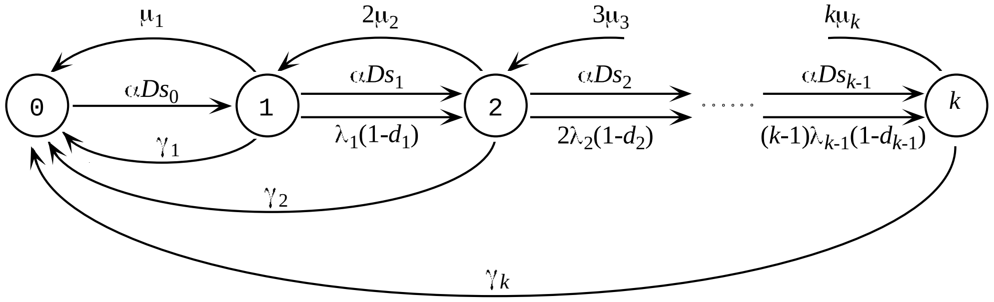

Figure 1: State transition diagram for a single patch.

tice entity. In the case of finite ω the Markovian state of a single patch (p-state) corresponds to the number of individuals present in it. To make our life easy we shall assume that there is a maximum k to the number of individuals in a patch. The state of the metapopulation (m-state) is given by the fractions p_n of patches with various numbers of individuals in them together with the disperser density D. Figure 1 shows the possible p-state transitions for the model that we have in mind. The μ_i are the per capita death rates, α is the rate constant of patch encounter for the dispersers, the s_i are the probabilities that a newly arrived immigrant decides to stay, the λ_i are the per capita birth rates, the d_i are the probabilities that a newly born individual decides to disperse, and the γ_i are the rates of externally imposed catastrophes wiping out the whole local population in one go. The strategy parameters d_i, and s_i are assumed to be heritable properties of the individuals. The other parameters α, γ_i, μ_i, and λ_i are supposed to be either constants or else to fluctuate in an ergodic manner. (In practice this means that the α, γ_i, μ_i, and λ_i should not show any systematic trends on any relevant time scale. The reason for invoking the term "ergodic" is to guarantee the truth of some of our mathematical statements below.) The m-state equations corresponding to the scheme in Figure 1 are

$$\begin{aligned}
\frac{dp_0}{dt} &= -\alpha D s_0 p_0 + \mu_1 p_1 + \sum_{j=1}^{k} \gamma_j p_j, \\
\frac{dp_i}{dt} &= [\alpha D s_{i-1} + (i-1)\lambda_{i-1}(1-d_{i-1})]p_{i-1} \\
&\quad -[i\mu_i + \alpha D s_i + i\lambda_i(1-d_i) + \gamma_i]p_i + (i+1)\mu_{i+1}p_{i+1}, \\
\frac{dD}{dt} &= -\alpha \sum_{i=0}^{k-1} p_i s_i D + \sum_{i=1}^{k} i\lambda_i d_i p_i - \mu_D D,
\end{aligned} \tag{1}$$

with μ_D the per capita death rate of the dispersers, which also is assumed to be either constant or else ergodic. In writing down (1) we used the conventions that $p_{-1} = 0$, $p_{k+1} = 0$, $s_k = 0$, and $d_k = 1$ (the first convention only becomes relevant at a later stage). The first two conventions bring the form of the equations for the p_i, with i next to the boundary of the feasible domain, in line with those for the p_i, with i in the interior of that domain. The assumptions about s_k and d_k are biological consistency conditions. We assume that the local population size never can become larger than k. Anybody born or immigrating into a population of size k therefore had better leave lest she die.

No general results about the equilibria of (1) are known. However, we know of no cases where for constant parameters (1) was found not to have a globally stable point equilibrium. For special models this equilibrium can be calculated numerically by solving $F(\widehat{D}) = 0$, e.g. using a bisection method, where F is defined by the following algorithm (if $F(D) < 0$ for all $D > 0$ the metapopulation is not viable):

- Supply a value of D.
- The next step is to calculate two sequences of numbers to be called $\widetilde{p}_{1,i}$ and $\widetilde{p}_{2,i}$, $i = 0, ..., k$. The calculation is started by setting $\widetilde{p}_{1,0} = 0$ and $\widetilde{p}_{1,1} = 1$, and $\widetilde{p}_{2,0} = 1$ and $\widetilde{p}_{2,1} = 0$.
- Successively calculate the following $\widetilde{p}_{1,i}$, $i = 2, ..., k$, using

$$\widetilde{p}_{1,i+1} = \frac{\begin{array}{r}[i\mu_i + \alpha D s_i + i\lambda_i(1-d_i) + \gamma_i]\widetilde{p}_{1,i} \\ -[\alpha D s_{i-1} + (i-1)\lambda_{i-1}(1-d_{i-1})]\widetilde{p}_{1,i-1}\end{array}}{(i+1)\mu_{i+1}}. \tag{2}$$

- Calculate the $\widetilde{p}_{2,i}$ in exactly the same manner as the $\widetilde{p}_{1,i}$.
- Calculate $P_1 = \sum_{i=0}^{k} \widetilde{p}_{1,i}$ and $P_2 = \sum_{i=0}^{k} \widetilde{p}_{2,i}$.
- Calculate $Q_1 = \sum_{i=1}^{k} \gamma_i \widetilde{p}_{1,i}$ and $Q_2 = \sum_{i=1}^{k} \gamma_i \widetilde{p}_{2,i}$.
- Calculate $W = (\mu_1 + Q_1)P_2 + (\alpha D s_0 - Q_2)P_1$.
- Calculate $u_1 = (\alpha D s_0 - Q_2)/W$ and $u_2 = (\mu_1 + Q_1)/W$.
- Calculate the numbers $\widehat{p}_i = u_1 \widetilde{p}_{1,i} + u_2 \widetilde{p}_{2,i}$.
- Calculate $F(D)$ as

$$F(D) = \sum_{i=1}^{k} i\lambda_i d_i \widehat{p}_i - \alpha \sum_{i=0}^{k-1} \widehat{p}_i s_i D - \mu_D D. \tag{3}$$

From the equilibrium $\widehat{D}$ of D, we can calculate the equilibrium values $\widehat{p}_i$ of the p_i by the same rules as before with $\widehat{D}$ substituted for D.

2.2 The linearized mutant equations

Now consider what happens when a mutant having strategy parameters d_i^* and s_i^* is introduced. In that case we have to consider an extended set of state variables for the metapopulation, for which we choose the relative frequencies of the patches filled with different resident and mutant numbers, $q_{i,j}$, i$\geq$ 0, $j \geq 0$, $i + j \leq k$, where i refers to the number of individuals of the original resident type and j refers to the number of the mutants. In addition we have equations for the resident and mutant disperser pools. The former we shall again denote as D, the latter as D^*. A schematic representation of the p-state transitions is indicated in Figure 2.

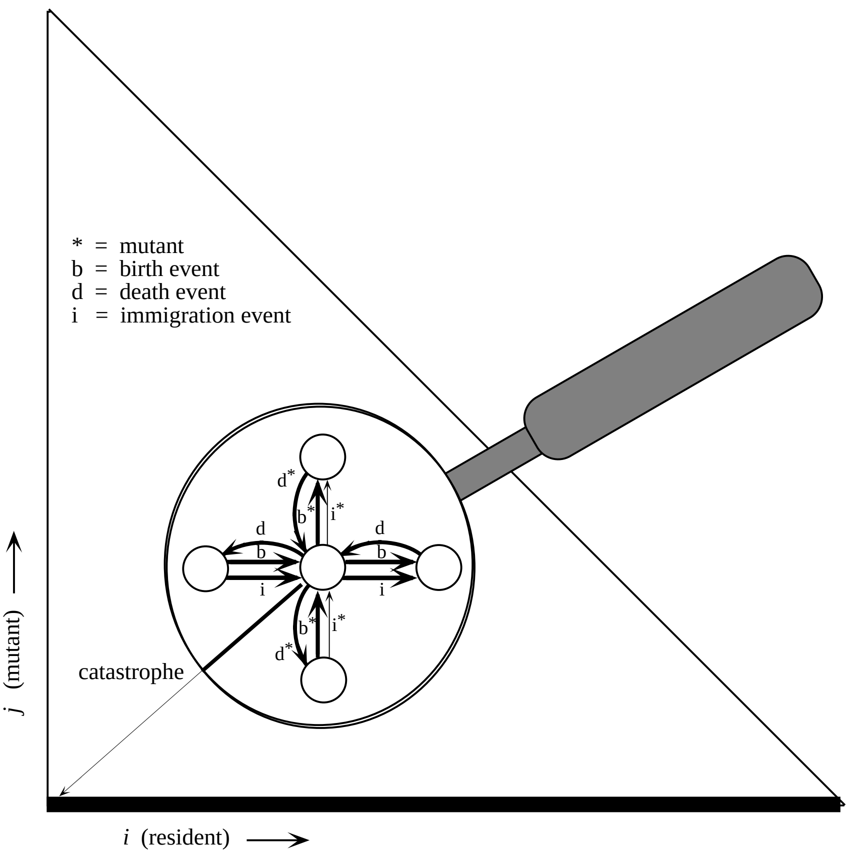

Figure 2: Schematic representation of the p-state transitions in a combined resident plus mutant patch. Thin arrows indicate transitions that are relatively rare.

We are primarily interested in the mutant population. This population is represented by those $q_{i,j}$ for which $j \neq 0$. Initially these $q_{i,j}$ may be supposed to be very small relative to the $q_{i,0}$. When the mutant population is still rare it has little influence on the resident dynamics. Therefore the $q_{i,0}$, $i = 0, ..., k$, can be approximated with the p_i calculated from (1), after we have given that resident dynamics some time to relax to an attractor. When the environment is constant we substitute $q_{i,0} = \widehat{p}_i$ and $D = \widehat{D}$.

Initially D^* also will be small. This allows us to neglect any further mutant immigration into the rare patches which already have mutants in them. To first order of approximation all mutant immigration occurs in patches which are either empty or solely occupied by residents. In Figure 2 we have visualized this relative scarcety of immigrating mutants in the width of the corresponding arrows. These observations allow us to immediately write the linearized mutant equation from first principles using the scheme in Figure 2 as a reference. We start with introducing some conventions to simplify the notation. We shall notionaly set $q_{-1,j} = 0$, $q_{i,j} = 0$ when $i + j = k + 1$, and $s_k = s_k^* = 0$, and $d_k = d_k^* = 1$. The rationale is the same as that for the similar conventions for the p_i. Moreover, we shall add stars to all parameters pertaining to mutant individuals to emphasize the generality of the calculations. For the concrete special case under consideration, where mutants and residents differ only with respect to the probabilities that newborns disperse from a patch, d, and the probabilities that dispersers stay in a patch, s, just set

$$\alpha^* = \alpha, \qquad \lambda^*_{i+j} = \lambda_{i+j}, \qquad \mu^*_{i+j} = \mu_{i+j}, \qquad \gamma^*_{i,j} = \gamma_{i+j}.$$

The differential equations for the $q_{i,1}$ have a term corresponding to the immigration of mutants into patches with only residents. In the equations for the $q_{i,j}$, $j > 1$ this term is lacking.

$$\begin{aligned}
\frac{dq_{i,1}}{dt} &= \alpha^* D^* s^*_i p_i + [\alpha D s_i + (i-1)\lambda_i(1-d_i)]q_{i-1,1} \\
&\quad -[i\mu_{i+1} + \mu^*_{i+1} + \alpha D s_{i+1} + i\lambda_{i+1}(1-d_{i+1}) + \lambda^*_{i+1}(1-d^*_{i+1}) + \gamma^*_{i,1}]q_{i,1} \\
&\quad +(i+1)\mu_{i+2}q_{i+1,1} + 2\mu^*_{i+2}q_{i,2}, \\
\frac{dq_{i,j}}{dt} &= [\alpha D s_{i+j-1} + (i-1)\lambda_{i+j-1}(1-d_{i+j-1})]q_{i-1,j} \qquad\qquad (4) \\
&\quad +(j-1)\lambda^*_{i+j-1}(1-d^*_{i+j-1})q_{i,j-1} \\
&\quad -[i\mu_{i+j} + j\mu^*_{i+j} + \alpha D s_{i+j} + i\lambda_{i+j}(1-d_{i+j}) + j\lambda^*_{i+j}(1-d^*_{i+j}) + \gamma^*_{i,j}]q_{i,j} \\
&\quad +(i+1)\mu_{i+j+1}q_{i+1,j} + (j+1)\mu^*_{i+j+1}q_{i,j+1}, \\
\frac{dD^*}{dt} &= -\alpha^* \sum_{i=0}^{k-1} p_i s^*_i D^* + \sum_{i=0}^{k-1}\sum_{j=1}^{k-i} j\lambda^*_{i+j}d^*_{i+j}q_{i,j} - \mu^*_D D^*.
\end{aligned}$$

Equation (4) forms a sufficient starting point for the discussion of invasion fitness in structured metapopulations, even in the most general case where all the individual parameters are functions of some strategy parameter S, i.e., for example, $\lambda_{i+j} = \Lambda_{i+j}(S)$, $\lambda^*_{i+j} = \Lambda_{i+j}(S^*)$, $\gamma^*_{i,j} = \Gamma_{i,j}(S, S^*)$, and $\gamma_i = \Gamma_{i,0}(S, S^*)$.

2.3 Invasion fitness

Before we get to the definition of fitness we rewrite (4) in a slightly more accessible form. To this end we define the vector V as

$$V = [(q_{i,j})_{i=0,..k-1,j=1,..,k-i}, D^*]^{\mathrm{T}},$$

where the pairs (i,j), are supposed to be lexicographically ordered, i.e., put in the order $(0,1)$,$(0,2)$,...,$(0,k)$,$(1,1)$,$(1,2)$,...,$(1,k-1)$,...,$(k-1,1)$, so that $v_1 = q_{0,1}$, $v_2 = q_{0,2}$, ... , $v_{k(k+1)/2} = q_{k-1,1}$, $v_{1+k(k+1)/2} = D^*$. The map transforming a pair (i,j), $i = 0$, .. , $k-1$, $j = 1$, .. , $k-i$, into its position n in the lexicografic order we shall call L. With this notation we can write

$$\frac{dV}{dt} = BV, \qquad (5)$$

where the matrix B contains the various coefficients from (4) ordered in the appropriate manner. If, as we supposed, the coefficients in (4) fluctuate in an ergodic manner, there exists a dominant Lyapunov exponent ρ associated with (5). In biological terms: the total mutant population size will overall grow or decline exponentially at a per capita rate ρ. Generalizing from the case of ordinary population

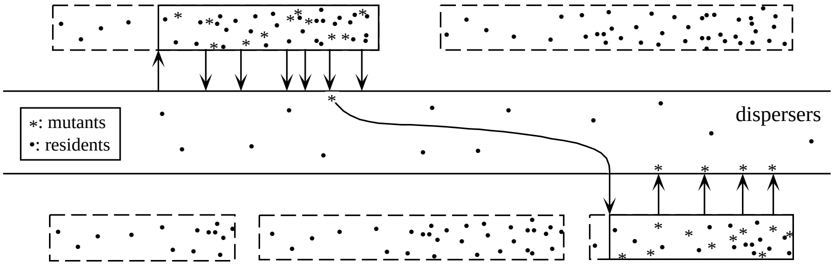

Figure 3: Schematic representation of the rationale behind the definition of R_m

dynamics we shall call ρ the *fitness* of the strategy $S^* = (d^*, s^*)$ in the environment set by an $S = (d, s)$ resident.

In the general case we can only calculate ρ by (i) numerically solving (1) till some time t_1 which should be sufficient to let the resident population relax to its attractor, then (ii) in parallel with (1) numerically solving (5), or equivalently (4), starting from some positive initial condition at t_1, and finally (iii) estimating ρ from the average linear increase rate of $\ln(D^*)$ with time.

When the resident dynamics converges to a point equilibrium we can calculate ρ as the dominant eigenvalue of the corresponding constant matrix B. However, this is a hard task, and in this case there is a more easy solution to the invasion problem which we shall discuss in the next section.

2.4 A stand-in for fitness in the case of population dynamical point equilibria

In order to remove clutter we shall below adhere to the convention that "individual" and "disperser", refers to mutant individuals, dispersing mutants, etc.

In the model as formulated individuals may live in very many different environments: They are either dispersing, or they are in an (i, j)-patch and therefore have i residents and $j - 1$ mutants impinging on them. This makes calculating the usual R_0, i.e., the mean lifetime number of children of a randomly chosen individual, a very difficult task. The way out is to proceed not on an idividual but on a colony basis, i.e., to work not from birth to births, but from emigration event to emigration events (see Figure 3), on the rationale that in the usual structured metapopulation model all dispersers are taken to be equivalent.

We shall call the average number of dispersers produced by the (0 or 1) colonies founded by a newly born disperser R_m, m from metapopulation. We shall calculate R_m in a number of steps: First we observe that a newborn migrant has probability

$$\pi_i = \frac{\alpha^* s_i^* \widehat{p}_i}{\alpha^* \sum_{j=0}^{k-1} s_j^* \widehat{p}_j + \mu_D^*} \tag{6}$$

to end up in an $(i, 0)$-patch, turning it into a $(i, 1)$-patch. The newly founded colony then undergoes a Markovian stochastic population process till it dies out. The states of this continuous time Markov chain are the pairs (i, j), $j > 0$, $i \geq 0$, $(i + j) \leq k$.

We shall number these states according to the same scheme that we used in the previous subsection. The corresponding probability vector $X(a)$, a the age of the colony, satisfies

$$\begin{aligned} \frac{dX}{da} &= \widetilde{B}X, \qquad X(0) = Y, && (7) \\ \text{with} \quad y_n &= \pi_i \qquad \text{for } n = L(i,1),\ i = 0, .., k-1, \text{ and } j = 1, \\ &= 0 \qquad \text{for all other } n, \end{aligned}$$

with $\widetilde{B}$ constructed from B by removing the last row and column. (i,j)-patches produce dispersers at a rate $j\lambda^*_{i+j}d^*_{i+j}$. We collect those rates in a vector A in the now usual manner, i.e., we set $j\lambda^*_{i+j}d^*_{i+j} = a_{L(i,j)}$ for $i = 0, .., k-1$, $j = 1, .., k-i$. Then the general theory of continuous time Markov chains tells us that

$$R_m = -A^{\mathrm{T}}\widetilde{B}^{-1}Y, \tag{8}$$

or equivalently,

$$R_m = -A^{\mathrm{T}}Z, \tag{9}$$

with Z the solution of

$$\widetilde{B}Z = Y. \tag{10}$$

In principle (10) corresponds to $k(k+1)/2$ equations in as many unknowns. In appendix A we indicate how solving (10) can effectively be reduced to solving k linear equations in k unknowns, so that treatment of cases with k smaller than, say, 70 becomes numerically feasible. Taken together (9) and (10) provide a quick way for numerically calculating R_m for concrete models. In the next section we shall derive an approximation for R_m applicable for large patch sizes.

R_m is a function of two variables, the resident strategy S and the mutant strategy S^*, which we can express by writing $R_m(S, S^*)$. Consistency requires that $R_m(S, S) = 1$. This property was born out by numerical work on various special models, but we have not been able to prove it in general.

3 The infinite patch size case

3.1 Taking the limit for patch size going to infinity

There exists a large body of theory for structured metapopulations in which the local population density x is treated as a continous variable (see e.g. Gyllenberg et al., 1997). Biologically these models can be seen as useful limits for large patch sizes of models with discrete local population sizes. We shall proceed in this spirit. We shall argue heuristically in what manner our results simplify when we let the size of the patches ω move towards infinity; in a companion paper (Gyllenberg & Metz, 1999) we give a direct treatment of the invasion problem for structured metapopulations including continuous ones. Moreover, we shall immediately concentrate on situations where population dynamical equilibrium obtains, as these are the only cases where we can arrive at analytical results. For fluctuating environments, we have to go numeric, which comes close to using the model with a discrete structuring variable from which we started. (Actually this last statement is bit facetious as there are now efficient numerial techniques for handling deterministic structured population models with continuous structuring variables (De Roos et al., 1992; De Roos & Metz, 1991).)

First we consider the dynamics of the local resident densities $x = i/\omega$, i the number of residents, and of the correspondingly scaled disperser pool $M = D/\omega$, without any mutants present. To arrive at a continuum limit we have to make the biologically reasonable assumption that our individuals, be they mutants or residents, only react to the local densities. Therefore we may write

$$\lambda_i = \lambda(i/\omega), \quad \mu_i = \mu(i/\omega), \quad \gamma_i = \gamma(i/\omega), \quad d_i = d(i/\omega), \quad s_i = s(i/\omega). \tag{11}$$

After ω has gone to infinity, and in between catastrophes, the resident dynamics satisfies

$$\frac{dx}{d\tau} = g(x, M) := [\lambda(x)(1 - d(x)) - \mu(x)]x + \alpha s(x)M, \tag{12}$$

with τ the time since the last catastrophe, and

$$\frac{dM}{dt} = \int_0^\infty \lambda(x)d(x)xp(x)dx - \alpha \int_0^\infty s(x)p(x)dx\; M - \mu_D M, \tag{13}$$

with p the current probability density of the local population densities. This probability density can be calculated from a partial differential equation, as discussed by Metz & Diekmann (1986) and Gyllenberg& Hanski (1992), or using the integral equation approach discussed in Gyllenberg et al. (1997; also compare Diekmann et al., 1998), using g from (12) as one of their ingredients.

Mutants start their career as single individuals. Therefore, if we want to consider how a mutant population takes off we have to deal with infinitesimally small values of M^*. This means that in contrast to the resident case there is no continuous stream of mutant immigrants into the patches, at least during the initial phase of the invasion process. We have to consider single immigration events. The resulting infinitesimally small local mutant population densities never grow out to appreciable size since (i) they are swamped by the immigration of residents, and (ii) local populations have only a finite time to go before they are wiped out by a catastrophe. Therefore even for infinite ω, we have to treat the local mutant population dynamics as a stochastic process. (The reason why we did not have this discrepancy between mutant and resident dynamics in the case of finite ω is that the small patch size guarantees that also the local residents behave stochastically. In the case of finite ω it is only D^* which is very small relative to D. This means that the relative density of patches with also mutants in them is very small. But when we concentrate on what happens in those patches, mutant and resident population sizes are of the same order of magnitude.)

The smallness of the local mutant populations also has a helpful side. The presence of mutants leaves the local resident population unaffected. In the same vein the population dynamical characteristics of the mutant individuals are unaffected by the local mutant density. It is only the local value of x that determines the local show. Therefore the local mutant numbers j develop according to a linear birth and death process with x-dependent time-varying parameters.

3.2 Calculating R_m

The procedure for calculating R_m proceeds along similar lines as in the finite patch size case. Our closing example has been chosen such that it is possible to skip most of the calculations. Yet, we shall outline the full procedure as it is both conceptually relevant and a necessary ingredient in some other applications.

First we have to calculate the equilibrium values $\widehat{p}$ for p, the probability density of the local resident population densities:

- To this end we first calculate the function $\widetilde{p}$ of the two variables x and M as

$$\begin{aligned} \widetilde{p}(x,M) &= \frac{C}{g(x,M)} \exp\left[-\int_0^x \frac{\gamma(\xi)}{g(\xi,M)} d\xi\right] && \text{for } 0 \le x < \widehat{x}(M) \\ &= 0 && \text{for } \widehat{x}(M) < x, \\ \text{with} \qquad C &= \left(\int_0^\infty \frac{1}{g(x,M)} \exp\left[-\int_0^x \frac{\gamma(\xi)}{g(\xi,M)} d\xi\right] dx\right)^{-1}, && (14) \end{aligned}$$

  with $\widehat{x}(M)$ the positive solution of

$$g(\widehat{x}, M) = 0, \tag{15}$$

  provided such a solution exists (in which case it is unique), else $\widehat{x}(M) = \infty$. In practice it will usually be necessary to evaluate the integrals numerically, i.e., one has to write a procedure which takes M as its input and returns a table with values of $\widetilde{p}$ for different well chosen values of x. This is not easy as $1/g(\xi, M)$ becomes unmanageably large when ξ gets near $\widehat{x}(M)$. Appendix B describes a simple procedure to calculate the various integrals using existing packages for solving differential equations.

- The next step is to calculate $\widehat{M}$ by (numerically) solving the equation (if $G(M) < 0$ for all $M > 0$ the metapopulation is not viable)

$$\int_0^\infty \lambda(x) d(x) x \widetilde{p}(x, \widehat{M}) dx - \alpha \int_0^\infty s(x) \widetilde{p}(x, \widehat{M}) dx \widehat{M} - \mu_D \widehat{M} := G(\widehat{M}) = 0. \tag{16}$$

- Finally we calculate $\widehat{p}$ as

$$\widehat{p}(x) = \widetilde{p}(x, \widehat{M}). \tag{17}$$

From $\widehat{p}$ we calculate the probability density π for the patches in which a newly immigrating mutant migrant will find itself:

$$\pi(x) = \frac{\alpha^* \widehat{p}(x) s^*(x)}{\alpha^* \int_0^\infty \widehat{p}(\xi) s^*(\xi) d\xi + \mu_D^*}. \tag{18}$$

The resident density $y_x(a)$ surrounding a mutant colony for which the resident density at the moment of founding was x, can be calculated from

$$\frac{dy_x}{da} = g(y_x, \widehat{M}), \qquad y_x(0) = x. \tag{19}$$

The independence of the individuals in the mutant colony has as consequence that the average size m_x of that mutant colony satisfies the differential equation

$$\frac{dm_x}{da} = [\lambda^*(y_x)(1-d^*(y_x)) - \mu^*(y_x) - \gamma(y_x)]m_x, \qquad m_x(0) = 1, \tag{20}$$

where we now include the possibility that the colony has been eradicated by a catastrophe. The expected reproductive output at age a from such a colony equals $\lambda^*(y_x(a))d^*(y_x(a))m_x(a)$. Therefore, the expected number of dispersers produced by a colony founded by a mutant immigrant entering at resident density x equals

$$R(x) = \int_0^\infty \lambda^*(y_x(a))d^*(y_x(a))m_x(a)da, \tag{21}$$

and

$$R_m = \int_0^\infty R(x)\pi(x)dx. \tag{22}$$

Appendix C describes a simple procedure to calculate R_m using existing packages for solving differential equations.

4 Example: Calculating evolutionarily stable dispersal strategies

We already included in our basic model formulation two explicit strategy vectors, $(d_i)_{i=1,..,k-1}$, the probabilities that a newborn disperses when born in a patch with population size i, and $(s_j)_{j=0,..,k-1}$, the probabilities that a disperser stays on encountering a patch with population size j. We shall only consider the simpler infinite patch size case here. In that case the strategy consists of two functions d and s of the continuous variable x. In order to simplify calculating the ESS, denoted as $(\widehat{d}, \widehat{s})$, we introduce some biologically reasonable asumptions on the other model ingredients: We shall assume that the birth rate λ, the death rate μ, and the catastrophe rate γ are continuous functions of x, that $\lambda - (\mu + \gamma)$ does not increase with the local population density x, that $\lambda(0) > \mu(0) + \gamma(0)$, and that there exists a unique positive $\widetilde{x}$ such that

$$\lambda(\widetilde{x}) = \mu(\widetilde{x}) + \gamma(\widetilde{x}). \tag{23}$$

We get the ESS by maximising $R_m[(d, s), (d^*, s^*)]$ in (d^*, s^*) and then setting mutant equal to resident (so that $R_m = 1$).

Due to the lack of memory of the disperser state a just arriving immigrant in a patch with resident density x has a future indistinguishable from a newly born individual at the same value of x. Therefore $\widehat{d}(x) = 1 - \widehat{s}(x)$ for all x where $(\widehat{d}(x), \widehat{s}(x))$ is the unique maximizer of R_m in the $(d^*(x), s^*(x))$-direction. It will turn out later that at such x either $\widehat{d}(x) = 1 - \widehat{s}(x) = 1$ or $\widehat{d}(x) = 1 - \widehat{s}(x) = 0$. Where uniqueness fails there is a one-dimensional continuum of maximizing values $0 \leq \widehat{s}(x) \leq 1$ and $0 \leq \widehat{d}(x) \leq 1$; we shall see below that this happens only at a single special value of x.

Since mutant individuals reproduce and die independently, for a newborn stayer the expected number of dispersing descendants produced by all its within patch descendants also equals $R(x)$. A newborn had better disperse whenever staying would lead to an expected number of dispersing descendants from its within patch descendants that would be smaller than one. More precisely: At population dynamical equilibrium a resident disperser has $R_m = 1$. A mutant who at some point produces more future dispersers than the resident and everywhere else doesn't do worse than the resident will invade. So a strategy which has stayers at local densities where staying results in a net loss ($R(x) < 1$) can always be invaded, and therefore cannot be an ESS. The same argument applies to a strategy which has leavers at local densities where staying would result in a net gain ($R(x) > 1$): A newborn should always stay at densities for which the expected number of dispersing descendants produced by all its within patch descendants together is above one.

$R(x)$ can be calculated from (21) and (20):

$$\begin{aligned} R(x) \;&=\; \int_0^\infty \lambda(y_x(a))d^*(y_x(a)) \quad \times \\ &\qquad \exp[\int_0^a [\lambda(y_x(\tau))(1 - d^*(y_x(\tau)) - \mu(y_x(\tau)) - \gamma(y_x(\tau))]d\tau] \quad da, \end{aligned} \tag{24}$$

where y_x should be calculated from (19).

The general theory of structured population models tells that for our model $\widehat{p}(x) \geq 0$ if and only if $g(x, \widehat{M}) \geq 0$. There is no way in which a local population can ever reach values of x for which $g < 0$. Therefore we can safely assume that in (24) $y_x \geq x$. Therefore always $R(x) \leq H(x, x)$ with H defined by

$$\begin{aligned} H(z, x) \;&:=\; \int_0^\infty \lambda(z)d^*(y_x(a)) \quad \times \\ &\qquad \exp[\int_0^a [\lambda(z)(1 - d^*(y_x(\tau)) - \mu(z) - \gamma(z)]d\tau] \quad da. \end{aligned} \tag{25}$$

Our assumptions about λ, μ, an γ together with the definition (23) of $\widetilde{x}$ guarantee that at values of $x > \widetilde{x}$

$$R(x) \leq H(x, x) < H(\widetilde{x}, x) = 1. \tag{26}$$

Thereforefore everybody should disperse whenever $x > \widetilde{x}$.

The previous result implies that at the ESS $\widehat{p}(x) = 0$ for all $x > \widetilde{x}$. Now consider what happens at values of $x < \widetilde{x}$. Using the fact that x never grows beyond $\widetilde{x}$ we can conclude that here $R(x) > H(\widetilde{x}, x) = 1$. So in the ESS everybody should stay as long as $x < \widetilde{x}$. Therefore

$$g(x, \widehat{M}) > g_-(\widetilde{x}, \widehat{M}) := \lim_{x \nearrow \widetilde{x}} g(x, \widehat{M}) = [\lambda(\widetilde{x}) - \mu(\widetilde{x})]\widetilde{x} + \alpha\widehat{M} > 0 \tag{27}$$

for $x < \widetilde{x}$. This means that at the ESS $0 < \widehat{p}(x) < \infty$ for $0 \leq x < \widetilde{x}$.

Next we consider what happens at $\widetilde{x}$. From $g(x, \widehat{M}) > g_-(\widetilde{x}, \widehat{M}) > 0$ for $x < \widetilde{x}$ we conclude that $\widetilde{x}$ is reachable from zero in finite time. Therefore at the ESS $\widehat{p}$ contains a delta function component at $\widetilde{x}$ representing a concentrated probability mass. Moreover, consistency requires that the local population growth rate of the resident precisely at $\widetilde{x}$

$$g(\widetilde{x},\widehat{M}) = [\lambda(\widetilde{x})(1-\widehat{d}(\widetilde{x})) - \mu(\widetilde{x})]\widetilde{x} + \alpha\widehat{s}(\widetilde{x})\widehat{M} = 0. \tag{28}$$

If $g(\widetilde{x},\widehat{M})$ were larger than 0 at the ESS, the local population density would grow beyond $\widetilde{x}$, at which point it would immediately start to decrease to $\widetilde{x}$, since beyond $\widetilde{x}$ all newborns leave. The same argument applies at the other side of $\widetilde{x}$. If $g(\widetilde{x},\widehat{M})$ were smaller than 0 at the ESS, the local population density would decrease below $\widetilde{x}$, at which point it would immediately start to increase to $\widetilde{x}$, since below $\widetilde{x}$ all newborns stay. Averaging over the resulting dither would precisely amount to $g(\widetilde{x},\widehat{M}) = 0$. The biological counterpart of this consistency argument runs as follows. Below $\widetilde{x}$ individuals should stay, above $\widetilde{x}$ they should leave. At $\widetilde{x}$ it is unclear what they should do. In practice they will perceive the surrounding population density with some small error. So some of them will leave a little too early and some a little too late. If by chance many were to err on the late side the local population density would increase further beyond $\widetilde{x}$ forcing them to leave anyway. This natural feedback loop would (i) produce a very steep hump in $\widehat{p}$ around $\widetilde{x}$, with $\widehat{p} = 0$ somewhat further beyond $\widetilde{x}$, and (ii) produce a pattern of leaving over the small x-interval under the hump, which when looked at through foggy glasses would be indistinguishable from (28). (Notice that $\widehat{M}$ in (28) is not a constant: the algorithm for calculating $\widehat{p}$ returns different values of $\widehat{M}$ for different pairs $(s(\widetilde{x}), d(\widetilde{x}))$.)

At the ESS, $R(\widetilde{x}) = 1$ independent of the value of $\widehat{d}(\widetilde{x})$. Apart from (28) there is no further constraint on $\widehat{d}(\widetilde{x})$ and $\widehat{s}(\widetilde{x})$. If we arbitrarily decide that also $\widehat{d}(\widetilde{x}) = \widehat{s}(\widetilde{x})$, we can uniquely solve $\widehat{d}(\widetilde{x}) = \widehat{s}(\widetilde{x})$ from (28). But there is no good biological or mathematical argument for making such a choice.

The final conclusion is that the ESS overall has the pattern of a bang bang control: $\widehat{s}(x) = 1$, $\widehat{d}(x) = 0$ for all $x < \widetilde{x}$, $\widehat{s}(x) = 0$, $\widehat{d}(x) = 1$ for all $x > \widetilde{x}$. Only for $x = \widetilde{x}$ the decisions are no longer deterministic. At this value of x the ESS is also nonunique: there is a one dimensional continuum of ESSes characterized by the pairs $(\widehat{s}(\widetilde{x}), \widehat{d}(\widetilde{x}))$, $0 \leq \widehat{s}(\widetilde{x}) \leq 1$, $0 \leq \widehat{d}(\widetilde{x}) \leq 1$, satisfying $\lambda(\widetilde{x})(1-\widehat{d}(\widetilde{x})) - \mu(\widetilde{x}) + \alpha\widehat{M}\widehat{s}(\widetilde{x}) = 0$ together with $G(\widehat{M}) = 0$.

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A How to calculate R_m when ω is finite

The renumbering scheme L used in subsections 2.3 and 2.4 had as only purpose to bring out the classical vector-matrix structure of the procedures. To calculate Z from (10) it is actually easier to go back to the original numbering scheme in terms of i and j (the numbers of residents respectively mutants in the patch). This we do by setting $u_{i,j} = z_{L(i,j)}$. The components of the matrix $\widetilde{B}$ we shall denote as:

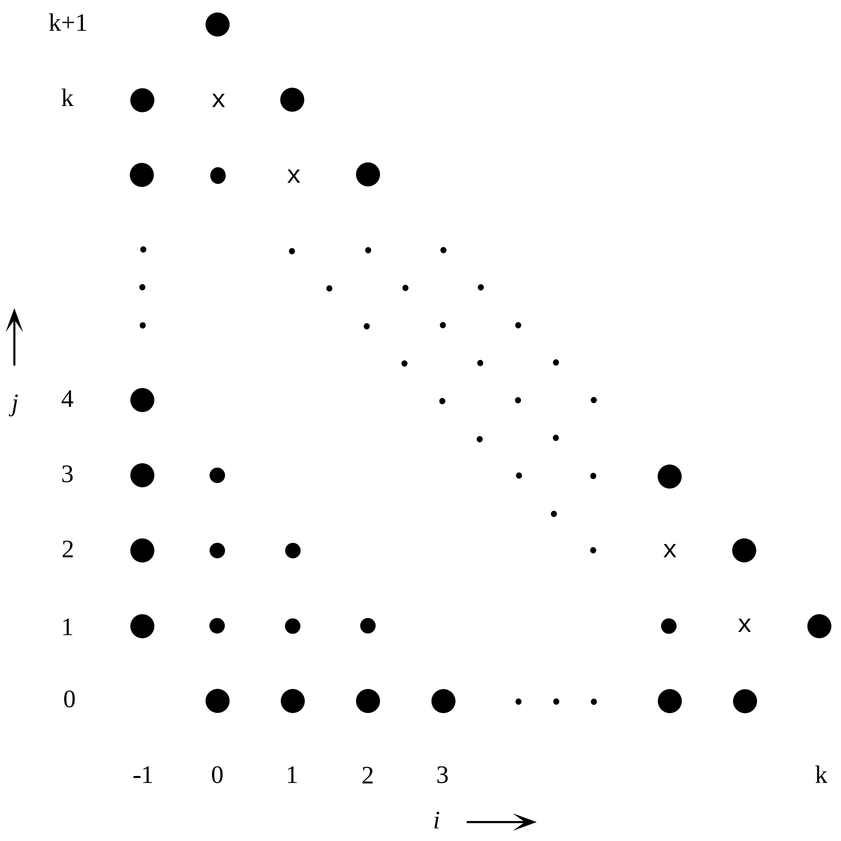

Figure 4: Calculating the $u_{i,j}$ from a boundary value problem. The values at the fat dots are prescribed, those at the x-es and smaller dots have to be calculated. The idea is first to take the values at the x-es as parameters, then to calculate the remaining $u_{i,j}$ working downwards using a simple recurrence along the anti-diagonals, and then to adjust the values at the x-es to satisfy the remaining boundary conditions.

$$
\begin{aligned}
c^a_{i,j} &= (j+1)\mu^*_{i+j+1}, \\
c^l_{i,j} &= \alpha\widehat{D}s_{i+j-1} + (i-1)\lambda_{i+j-1}(1-d_{i+j-1}), \\
c^c_{i,j} &= -[i\mu_{i+j} + j\mu^*_{i+j} + \alpha\widehat{D}s_{i+j} + i\lambda_{i+j}(1-d_{i+j}) + j\lambda^*_{i+j}(1-d^*_{i+j}) + \gamma^*_{i,j}], \\
c^r_{i,j} &= (i+1)\mu_{i+j+1}q_{i+1,j}, \\
c^b_{i,j} &= (j-1)\lambda^*_{i+j-1}(1-d^*_{i+j-1}), \qquad \text{for } j>1.
\end{aligned}
$$

(The indices a, l, c, r, and b stand for above, respectively left, center, right, and below.) In addition we define

$$c^b_{i,1} = -1.$$

With these conventions we can write, for $i \geq 0$, $j \geq 1$, $i + j \leq k$,

$$0 = c^a_{i,j} u_{i,j+1} + c^l_{i,j} u_{i-1,j} + c^c_{i,j} u_{i,j} + c^r_{i,j} u_{i+1,j} + c^b_{i,j} u_{i,j-1},$$

together with the boundary conditions (see figure 4)

$$u_{-1,j} = 0, \qquad u_{i,0} = \pi_i, \qquad u_{i,j} = 0 \quad \text{for } i + j = k + 1.$$

One way to solve this boundary value problem is indicated in figure 4. The procedure suggested there leads to the following algortihm.

- Define new variables $v^{(h)}_{i,j}$, $h = 0, ..., k-1$, and $i = -1, ..., k$, $j = 0, \dots , k+1$, $i + j \leq k + 1$.
- For $h = 0, \dots , k-1$ set

$$\begin{aligned} v^{(h)}_{-1,j} &= 0 && \text{for all j}, \\ v^{(h)}_{0,k+1} &= 0,\ v^{(h)}_{1,k} = 0, \dots , v^{(h)}_{k,1} = 0, \\ v^{(h)}_{0,k} &= 0, .. , v^{(h)}_{h-1,k-h+1} = 0,\ v^{(h)}_{h,k-h} = 1,\ v^{(h)}_{h+1,k-h-1} = 0, .. , v^{(h)}_{k-1,1} = 0. \end{aligned}$$

- For each h succesively calculate the $v^{(h)}_{i,j}$ for $i = 0$, $j = k-1$; ... ; $i = k-2$, $j = 1$; $i = 0$, $j = k-2$; ... ; $i = k-3$, $j = 1$; ... ... ; $i = 0$, $j = 2$; $i = 1$, $j = 1$; $i = 0$, $j = 1$, using

$$v^{(h)}_{i,j} = -\frac{(c^a_{i,j+1} v^{(h)}_{i,j+2} + c^l_{i,j+1} v^{(h)}_{i-1,j+1} + c^c_{i,j+1} v^{(h)}_{i,j+1} + c^r_{i,j+1} v^{(h)}_{i+1,j+1})}{c^b_{i,j+1}}.$$

- Solve the set of k linear equations in the k unknowns x_h, $h = 0, \dots , k-1$

$$\sum_{h=0}^{k-1} (c^a_{i,1} v^{(h)}_{i,2} + c^l_{i,1} v^{(h)}_{i-1,1} + c^c_{i,1} v^{(h)}_{i,1} + c^r_{i,1} v^{(h)}_{i+1,1}) x_h = \pi_i.$$

- Finally calculate the $u_{i,j}$ as

$$u_{i,j} = \sum_{h=0}^{k-1} v^{(h)}_{i,j} x_h.$$

A computationally slightly cheaper alternative for the last step is to calculate the $u_{i,j}$ using the same rule that is used for calulating the $v^{(h)}_{i,j}$, but with $u_{0,k} = x_0$, $u_{1,k-1} = x_1$, $\dots$, $u_{k-1,1} = x_{k-1}$.

R_m then can be calculated as

$$R_m = -\sum_{i=0}^{k-1} \sum_{j=1}^{k-i} j \lambda^*_{i+j} d^*_{i+j} u_{i,j}.$$

B How to calculate $\widetilde{p}(x, M)$

An efficient way to calculate $\widetilde{p}(x, M)$ makes use of the fact that for a given fixed M there exists a monotone relation (to be called X) between the age of the local resident population, τ, defined as the time since a patch underwent its last catastrophe, and the present resident population density x. The integrals can be calculated using a standard package for solving differential equations. The differential equations to be solved are (with the two arguments τ and M suppressed; the X, Y, Z, V and W below bear no relation to the same symbols from the main text)

$$\begin{aligned}
\frac{dX}{d\tau} &= g(X, M), & X(0) &= 0, \\
\frac{dY}{d\tau} &= -\gamma(X)Y, & Y(0) &= 1, \\
\frac{dZ}{d\tau} &= Y, & Z(0) &= 0, \\
\frac{dV}{d\tau} &= \lambda(X)d(X)XY, & V(0) &= 0, \\
\frac{dW}{d\tau} &= s(X)Y, & W(0) &= 0.
\end{aligned}$$

X describes the development of the local population size, Y the survival of the colony. The other three quantities are calculated only to find their values for large τ which are needed as a normalization factor and in the equation for $\widehat{M}$. Given the solution of these differential equations G from (16) can be calculated as

$$G(M) = V(\infty)/Z(\infty) - [\alpha W(\infty)/Z(\infty) + \mu_D]M.$$

In practice one can take τ to be ∞ as soon as Y has decreased to a sufficiently low value, say 10^{-5}. $\widehat{x}(M)$ corresponds to $X(\infty)$. The equilibrium colony age distribution $\widehat{q}$ corresponds to

$$\widehat{q}(\tau) = \widehat{Y}(\tau)/\widehat{Z}(\infty),$$

where a $\widehat{\ }$ means that the quantity has been evaluated at $M = \widehat{M}$. The stationary colony size distribution is calculated by transforming from population age to size:

$$\widehat{p}(\widehat{X}(\tau)) = \frac{\widehat{q}(\tau)}{g(\widehat{X}(\tau), \widehat{M})}.$$

C How to calculate R_m when ω is infinite

To calculate R_m in practice, it is again easier to revert to a representation in terms of local population ages. We start calculating a quantity related to the $m_x(a)$:

$$\frac{dU}{d\tau} = [\lambda^*(\widehat{X})(1 - d^*(\widehat{X})) - \mu^*(\widehat{X}) - \gamma(\widehat{X})]U, \qquad U(0) = 1,$$

with $\widehat{X}(\tau)$ the quantities already calculated in appendix B (so that $m_{\widehat{X}(\tau)}(a) = U(\tau + a)/U(\tau)$). In parallel we calculate a quantity related to the $R(x)$:

$$\frac{dQ}{d\tau} = \lambda^*(\widehat{X})d^*(\widehat{X})U, \qquad Q(0) = 0$$

(so that $R(\widehat{X}(\tau)) = [Q(\infty) - Q(\tau)]/U(\tau))$, as well as three helper quantities

$$\begin{aligned}
\frac{dA}{d\tau} &= \frac{s^*(\widehat{X})\widehat{Y}}{U}, & A(0) &= 0,\\
\frac{dB}{d\tau} &= \frac{Qs^*(\widehat{X})\widehat{Y}}{U}, & B(0) &= 0,\\
\frac{dC}{d\tau} &= s^*(\widehat{X})\widehat{Y}, & C(0) &= 0,
\end{aligned}$$

with $\widehat{Y}(\tau)$ the quantities calculated in appendix B. R_m can then be calculated as

$$R_m = \frac{\alpha^*[Q(\infty)A(\infty) - B(\infty)]}{\alpha^* C(\infty) + \mu_D^* \widehat{Z}(\infty)},$$

with $\widehat{Z}(\infty)$ the quantity calculated in appendix B.