Dispersal and Metapopulation Viability in a Heterogeneous Landscape

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Conditions of persistence or extinction of a metapopulation of a colonizing annual species are studied in a heterogeneous landscape, a mixture of two elementary landscapes. An elementary landscape is a landscape whose age-structure is described by only one transition matrix, giving the probability for a site to be disturbed, or to follow the process of succession. We first provide an analytical study of the range of dispersal rates that allow metapopulation persistence in an elementary landscape. Second, conditions for metapopulation persistence in a heterogeneous landscape are derived from results obtained in each elementary landscape. Three cases are distinguished. If the two ranges of dispersal rates defined in each elementary landscape overlap, the metapopulation persists in any mixture of the elementary landscapes. If these two dispersal rates ranges are non-overlapping, either the metapopulation goes extinct for some values of the proportion of the elementary landscapes, or two discontinuous ranges of dispersal rates allow the metapopulation persistence. The consequences of these results are discussed in terms of landscape management. In particular, it is shown that under some conditions, a rapid change in environment (from one elementary landscape to another one) might less often lead to metapopulation extinction than a slower change.

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Introduction

Ecology, evolution and conservation biology are sciences that need a proper understanding of how species persist in their habitat, why they go extinct and what the major processes at work during the course of extinction are. Many species are able to survive even though none of the local populations are able to persist in the long term. Species living in temporary habitats such as successional environments provide an example of such a situation: they continually disappear from local sites as these become unsuitable through replacement by more competitive species or through local disturbances (Huston & Smith, 1987). Each local population has thus a finite lifetime expectancy. Nonetheless, these may persist regionally if they are able to establish local populations elsewhere. Such an assemblage of extinction-prone local populations connected to each other by dispersal was called a metapopulation by Levins in 1970. The persistence of this assemblage depends on a balance between local population extinctions and the founding of new populations through dispersal. Another factor is likely to play a predominant role in determining
the founding of new populations: the metapopulation habitat that will be called hereafter a landscape (sensu Forman & Godron, 1981; Wu & Levin, 1994).

In this context, a landscape can be defined as a set of sites of various age since last disturbance. Several models based on Levins (1970) consider only favourable (colonizable) sites and assume a constant extinction rate through disturbance. Thus, the landscape is made of only two kinds of sites, empty and occupied sites. The existence of unsuitable (uncolonizable) sites is incorporated in the possible cost of dispersal for those individuals (e.g. seeds) unable to discriminate among colonizable and uncolonizable sites. Some authors explicitly consider unfavourable sites (Fahrig & Merriam, 1985; Lavorel et al., 1993; Wiens et al., 1993), but assume that these sites remain unsuitable, whether or not they are disturbed. In fact, for many colonizing species living in successional environments (Huston & Smith, 1987), disturbance may reset a late-successional site into a colonizable, thus favourable site. Permanent unsuitability of a site may still be taken into account by considering a cost of dispersal. Among potentially suitable sites, natural disturbances (Connell & Slatyer, 1977; Sousa, 1984) and relative competitive ability will determine the overall pattern for the species considered (Huston & Smith, 1987). The landscape is then a mosaic of successional sites of different ages (Begon & Harper, 1996). The temporal dynamics of the landscape sites (or the aging process of sites in the landscape) can be represented by a matrix of (disturbance/non-disturbance) transition probabilities (Olivieri & Gouyon, 1985; Horvitz & Schemske, 1986; Alvarez-Buylla & Garcia-Barrios, 1993). A landscape whose sites dynamics is defined by only one matrix will be called an elementary landscape.

However, the schematic view of the landscape, as described above, is quite simple and limited. In particular, it supposes homogeneity of the metapopulation habitat. In such a model, all sites in a given landscape undergo the same successional events. However, it is obvious that many ecological variations exist among sites of the same landscape (Holt, 1992). Variations in sites quality and distribution and shapes of sites are the main elements that are assumed to contribute to landscape heterogeneity (Wiens, 1997). The effects of sites pattern have been investigated in previous models (Hanski & Gyllenberg, 1993; Adler & Nuernberger, 1994; Wu & Levin, 1994; Lavorel et al., 1995; Hanski & Gyllenberg, 1997; Holt, 1997). The influence of the quality of sites themselves can be taken into account using the spatially implicit representation of an elementary landscape. Sites within the same landscape may have different probabilities of becoming destroyed by disturbances. Furthermore, sites may have different characteristics leading to various fecundities of the species considered and may cease to be favourable more or less rapidly over the course of time, according to the speed of the succession. In this case, the landscape can be viewed as composed of different sets of sites, each set (equal to an elementary landscape) exhibiting a specific temporal dynamics. Such a landscape, mixture of several elementary landscapes, will be referred to as a heterogeneous landscape. The temporal dynamics of its sites will be defined by several transition matrices (one of each elementary landscape). A case study which may fit roughly the heterogeneous landscape assumptions is the natural successional system of the Skeppsvik Archipelago (Sweden) studied by Giles & Goudet (1997). This area is subject to land uplift so that there is a continuous creation of new islands, which will differ in age as the process continues. The plant species considered, Silene dioica, is a component of early stages of primary succession on these islands and disappears as later successional species invade each island. In this system, colonization and successional processes are quicker in the inner archipelago than in the outer islands, subjected to stronger wind, wave and ice action. This case study system is thus composed of sites of different ages (the islands) distributed in two sets having different temporal dynamics: the set of sites in the exposed part of the archipelago and the set of sites in the protected part. Given the overall low genetic differentiation observed among islands, it is likely that the whole system function as an island model of migration (Wright, 1931; Slatkin, 1977).

Dispersal plays a key role in the cohesion of metapopulation systems from both the dynamic and the genetic perspectives (Johnson & Gaines,
1990; Hanski & Gilpin, 1991; Venable & Brown, 1993; Harrison & Hastings, 1996; Olivieri & Gouyon, 1997). The evolution of dispersal will be influenced by the heterogeneity of the landscape (Gustafson & Gardner, 1996). Since models have addressed dynamics and patterns arising in uniform environments (see Kareiva & Wenner-gren, 1995), a great challenge is now to study how habitat heterogeneity alters these patterns, and what are the critical parameters influencing the metapopulation dynamics (Wiens, 1997). In a preliminary study, using numerical iterations, Olivieri & Gouyon (1997) have analysed the equilibrium metapopulation size as a function of dispersal rate (probability of dispersal per propagule per generation) in a heterogeneous landscape, composed of two elementary landscapes. They have identified a non-trivial prediction, namely that the metapopulation may go extinct in the heterogeneous landscape, whereas the metapopulation is viable in each elementary landscape.

Using a deterministic metapopulation model (used to study the evolution of dispersal by Olivieri et al., 1995), the aim of this paper is to understand the metapopulation dynamics in a heterogeneous landscape (e.g. a metapopulation the habitat of which is composed of two elementary landscapes) and to underline the critical features of the landscape that can influence the metapopulation dynamics. In this aim, it is necessary first to find persistence conditions of the metapopulation in an elementary landscape. Conditions that allow the persistence of a metapopulation inhabiting a heterogeneous landscape are derived from the results on elementary landscapes. The critical parameters of the elementary landscape are identified as well as the consequences of a change in the temporal dynamics of sites within the metapopulation habitat on metapopulation viability. The possible consequences of a change in agricultural practices (for example, increase of soil fertilization) for metapopulation viability of weedy species are given as a theoretical example.

**Model Description**

Our study is based on a deterministic structured model that has been described in Olivieri et al. (1995) and Ronce & Olivieri (1997). A metapopulation of an annual plant species is considered. As found in a number of plant species, each individual produces two kinds of seeds: seeds with a great ability to disperse, and seeds that do not disperse (see Olivieri et al. 1983; Olivieri & Gouyon, 1985). The dispersal rate $D$ is the fraction of seeds that, each generation, leave the site where they were produced. $D$ is assumed to be fixed and genetically based. The metapopulation is assumed to inhabit first an elementary landscape, and then a heterogeneous landscape. Two processes are modelled, first the aging process of sites, and second the local population growth. These two processes are assumed to be completely independent. No demographic stochasticity and no Allee effect are considered. Since we are concerned with the metapopulation viability (i.e. whether the metapopulation tends to grow or decline at low densities), we need not consider regulation, even if some kind of density dependence is necessary to prevent the metapopulation from demographic explosion (Hastings & Wolin, 1989).

**THE METAPOPULATION IN AN ELEMENTARY LANDSCAPE**

**Sites dynamics in the elementary landscape**

The landscape is assumed to be made of an infinite number of sites (deterministic model), each containing at most one population. Each site is the largest spatial unit for which the probability of disturbance is independent of other units (uncorrelated local disturbances). A given site is characterized by its age, equal to the time since the last disturbance, and may exist in any age states $0, 1, 2, \ldots, Z$. State $Z$ characterizes all sites whose last disturbance event occurred at least $Z$ years ago. A site becomes unsuitable when it reaches age $Z$, because the annual species is excluded by the invasion of more competitive species. $Z$ is thus the maximal population lifetime of the species considered (but the site could well be suitable for another species: $Z$ is a property of both the species and the landscape). $1 - A_i$ is the probability that a site of age $i$ is disturbed and again becomes empty. The empty sites that are
FIG. 1. Dynamics of local populations in an elementary landscape. In each occupied site, seeds are produced. A proportion \((1 - D)\) of them disperse whereas a proportion \(D\) remain in their natal site. A proportion \(q\) of dispersed seeds survive and form the migrant pool. Each site of age \(i\) can be either disturbed with probability \(A_i\) or left undisturbed with probability \(1 - A_i\), and then proceeds to the following successional state \(i + 1\). New individuals are issued from dispersed and non-dispersed seeds, except in sites of age 1, in which they are issued only from dispersed seeds.

ocal populations dynamics (Fig. 1)

At the beginning of each season, residents of occupied sites reproduce and die. Let \(N_i(t)\) be the local population size in a site of age \(i\) at time \(t\), and \(f\) be the net potential fecundity, equal to the number of seeds produced per individual that would survive to adulthood the following generation in the absence of disturbance and successional processes. The effective seed number produced on a site of age \(i\) is \(fN_i(t)\). A fraction \(D\) of these seeds disperse whereas a fraction \((1 - D)\) of them remain on their original site. The migrant pool is composed of a proportion \(q\) of dispersed seeds that survive to dispersal. In an island model of migration, each site of the landscape receives a similar amount of dispersed seeds equal to \(fDq\sum_{i=1}^{Z-1} V_iN_i(t)\). In each site of age \(i\) (\(i \geq 1\)), \(f(1 - D)N_i(t)\) resident seeds are produced. At time \((t + 1)\), on a site of age \(i + 1\), new individuals are issued from both dispersed seeds and non-dispersed seeds except on sites of age 1, in which new individuals are issued only from dispersed seeds, that arrived on empty sites. With these assumptions, variation of local population sizes of reproducing adults in sites is described by the
following (Z) equations:
\[
N_0(t) = 0,
\]
\[
N_1(t) = fDq \sum_{i=1}^{Z-1} V_i N_{i-1}(t-1),
\]
\[
N_i(t) = f(1-D)N_{i-1}(t-1) + fDq \sum_{i=1}^{Z-1} V_i N_i(t-1) \quad \text{for } i \in [2, Z-1].
\]

To summarize, the mosaic age-structure of an elementary landscape is defined by four parameters, the three probabilities of non-disturbance of sites, \(A_0\), \(A_1\), \(A_Z\) and the maximum age of a site \(Z\). The metapopulation dynamics is a function of the net potential fecundity \(f\), the dispersal rate \(D\) and the survival during dispersal \(q\).

THE METAPOPULATION IN A HETEROGENEOUS LANDSCAPE: A MIXTURE OF TWO ELEMENTARY LANDSCAPES

In this model, a heterogeneous landscape is made of two elementary landscapes with a proportion \(\alpha\) of landscape 1 and a proportion \(1 - \alpha\) of landscape 2 (Fig. 2). Each elementary landscape is a set of sites having its own temporal dynamics, and is thus characterized by the four parameters described above, resulting in the equilibrium frequencies of the sites, and by the fecundity of plants inhabiting these sites. Two transition matrices are thus defined. Local population dynamics is the same as in an elementary landscape but dispersed seeds come from all occupied sites of landscapes 1 and 2. We further assume that the seeds fall equally among all sites of the heterogeneous landscape (island model of migration).

Let \(N_{1i}(t)\) be the local population size in a site of age \(i\) of landscape 1, and \(N_{2i}(t)\) the local population size in a site of age \(i\) of landscape 2, at time \(t\). Let \(f_1\) and \(f_2\) be the net potential fecundities defined, respectively, in landscapes 1 and 2, and \(Z_1\), \(Z_2\) be the maximal population lifetimes. The fraction of dispersed seeds that is received by each site of the heterogeneous landscape, mixture of two elementary landscapes L1 (sites \(S_{1i}\)) and L2 (sites \(S_{2i}\)). L1 is in proportion \(\alpha\), L2 in proportion \((1 - \alpha)\). The sites mosaic age-structure of L1 is defined by \(A_{10}\), \(A_{11}\), \(A_{1Z}\), and \(Z_1\) and the sites mosaic age-structure of L2, by \(A_{20}\), \(A_{21}\), \(A_{2Z}\), and \(Z_2\). The migrant pool is composed of seeds coming from all occupied sites of L1 and L2.
The mosaic age structure of a heterogeneous landscape is thus defined by nine parameters, the two sets of four parameters associated, respectively, with landscapes 1 and 2 and the proportion \( \alpha \) of landscape 1. The metapopulation dynamics is a function of the two net potential fecundities \( f_1 \) and \( f_2 \) associated with landscapes 1 and 2, the dispersal rate \( D \) of the species considered and the survival during dispersal \( q \).

### Analytical Solution of Metapopulation Persistence

Using Mathematica software, we determined the range of dispersal rate allowing metapopulation persistence. A necessary condition for viability is a metapopulation growth rate above one at low densities, when density-dependence regulation does not yet operate. From the equations that describe the local variation of population sizes, a matrix \( \mathbf{M} \) is determined for each landscape (the whole mathematical analysis is given in appendix A in the case of the elementary landscape; for the heterogeneous ones, a similar analysis can be developed but is not given). \( \mathbf{M} \) is a square matrix, such that \( \mathbf{N}(t) = \mathbf{M} \cdot \mathbf{N}(t-1) \), where \( \mathbf{N}(t) \) is the vector of the local population sizes \([N_i(t) \text{ in the elementary landscape, } N_{i1}(t) \text{ and } N_{i2}(t) \text{ in the heterogeneous landscape}] \). For \( D = 0 \), the matrix \( \mathbf{M} \) is not positive and has its eigenvalues all equal to 0. For \( D \neq 0 \), \( \mathbf{M} \) is a positive matrix and has a unique positive eigenvalue (see Appendix A), which is the dominant eigenvalue and which determines the asymptotic properties of population growth (Perron–Frobenius theorem, see Caswell, 1989). From the characteristic equation of the matrix, we have derived the net replacement number \( R_0 \) (see Gyllenberg et al., 1997; Gyllenberg & Hanski, 1997). Another way to find the net replacement number \( R_0 \) is to consider the expected number of seeds, descendants of a single founder seed, which will leave the site until it goes extinct (see Section A.4 for the elementary landscape and Appendix B for the heterogeneous ones). If \( R_0 \) is greater or equal to one, then the metapopulation will persist; otherwise the metapopulation will go extinct. To find the range of dispersal rates that allow the metapopulation persistence, we thus look for the values of dispersal rate corresponding to a value of \( R_0 \) greater than or equal to one. The extreme values of the dispersal rate \( D \) that are the roots of the equation \( R_0(D) = 1 \) determine the range of dispersal rates that allow the metapopulation persistence.

### The Metapopulation in the Elementary Landscape

The complete analysis is given in Appendix A. It is shown that the equation \( R_0(D) = 1 \) has at most two roots and that the metapopulation...
persistence depends on two conditions. If $R_0(1)$ (all seeds are dispersed) is greater than one, the equation $R_0(D) = 1$ has exactly one root $D_1$ between 0 and 1. The range of dispersal rates that allow the metapopulation persistence is thus $[D_1, 1]$, and the metapopulation may persist even for high dispersal rates (Fig. 3). Conversely, when $R_0(1)$ is less than one, two cases can be distinguished. First, if the term $A_1 \times f$ is less than one, then the equation $R_0(D) = 1$ has no root on $[0, 1]$ and the metapopulation goes extinct for all dispersal rates. Second, if the term $A_1 \times f$ is greater than one, then the equation $R_0(D) = 1$ has at most two roots on $]0, 1[$, and the metapopulation will persist only when the dispersal rate belongs to the interval determined by these two roots (see Fig. 3). The influence of landscape parameters on the range of dispersal rates allowing metapopulation persistence may be studied through their influence on $R_0(D)$. Let us show in particular the influence of $A_1$, $f$ and $Z$ [Fig. 4(a)–(c)]. Figure 4(a) (cases 1 and 2) shows that $A_1$ has a strong effect on the dispersal range: as expected, the lower $A_1$ (the larger the disturbance rate), the larger the dispersal rate must be for metapopulation persistence. However, this pattern varies with $Z$ the maximal population lifetime: when $Z$ is low, the persistence range is reduced to
intermediate values of dispersal. Figure 4(b) shows that, for low values of $Z$, the threshold value of $f$ (below which the metapopulation is not viable regardless the dispersal rate) increases with $A_1$, while the persistence range of dispersal is reduced to intermediate values. Figure 4(c) shows that if $A_1 \times f < 1$, $Z$ has virtually no effect on the dispersal range. Conversely, if $A_1 \times f > 1$ (case 2), as $Z$ increases, the dispersal range is very rapidly equal to $[0, 1]$.

2. THE METAPOPULATION IN THE HETEROGENEOUS LANDSCAPE: MIXTURE OF TWO ELEMENTARY LANDSCAPES L1 AND L2

In the heterogeneous landscape (see Appendix B), the net replacement number $R_0(D)$ is a function of $x$ and of the two net replacement numbers, $R_{01}(D)$ and $R_{02}(D)$, derived respectively in each elementary landscapes L1 and L2: $R_0(D) = xR_{01}(D) + (1 - x)R_{02}(D)$ [eqn (B.1)]. This allows to determine $R_0(D)$ from $R_{01}(D)$ and $R_{02}(D)$, and thus allows to conclude about whether the metapopulation persists or goes extinct in the heterogeneous landscape. Three cases must be distinguished according to the value of dispersal rate $D$.

Case 1: $D$ is such that $R_{01}(D)$ and $R_{02}(D)$ are both greater than one. $R_0(D)$ is then always greater than one whatever the proportion of L1 ($x$), so that the metapopulation always persists for this dispersal rate whatever the mixture of the two elementary landscapes.

Case 2: $D$ is such that $R_{01}(D)$ and $R_{02}(D)$ are both below one. $R_0(D)$ is then less then one whatever $x$, and the metapopulation always goes extinct for this dispersal rate.

Case 3: $D$ is such that either $R_{01}(D)$ is greater than one and $R_{02}(D)$ is lower than one or the reverse. $R_0(D)$ may be greater than one, if $D$ is such that $(R_{01}(D) - 1)/(1 - R_{02}(D)) > (1 - x)/x$.

**FIG. 5.** Net replacement number $R_0$ in a heterogeneous landscape, as a function of the dispersal rate $D$, and $x$, the proportion of the landscape 1. The hatched area corresponds to values of $x$ and $D$, such as $R_0(D) > 1$, the white area to $R_0(D) < 1$, and the curve to $R_0(D) = 1$. Two cases must be distinguished: (a) the two metapopulation persistence ranges $[D_1 - D_1']$ and $[D_2 - D_2']$ defined, respectively, in L1 and L2 overlap. (b,c) These two ranges are non-overlapping. Either there exists a range of $D$ for which the metapopulation is not viable whatever $D$ (b), or there exists a range of $D$ for which two discontinuous ranges of $D$ allow the metapopulation persistence (c). Parameters used ($q = 1$): $a = L_1$, $A_{10} = 0.4$, $A_{11} = 0.9$, $A_{1Z_1} = 0.95$, $Z_1 = 3$, $f_1 = 8$, $L_2$, $A_{20} = 0.1$, $A_{21} = 0.9$, $A_{2Z_2} = 0.999$, $Z_2 = 7$, $f_2 = 5.5$, $b_1 = L_1$, $A_{10} = 0.4$, $A_{11} = 0.8$, $A_{1Z_1} = 0.95$, $Z_1 = 3$, $f_1 = 7.5$, $L_2$, $A_{20} = 0.4$, $A_{21} = 0.9$, $A_{2Z_2} = 0.999$, $Z_2 = 7$, $f_2 = 4.5$, $b_2 = L_1$, $A_{10} = 0.3$, $A_{11} = 0.1$, $A_{1Z_1} = 0.999$, $Z_1 = 7$, $f_1 = 5.8$, $L_2$, $A_{20} = 0.3$, $A_{21} = 0.9$, $A_{2Z_2} = 0.999$, $Z_2 = 7$, $f_2 = 5$. 
From these three cases, it can be shown that (Fig. 5):

- If the two dispersal ranges that allow the metapopulation persistence in each elementary landscape respectively overlap, then the metapopulation always persists whatever \( z \) in the heterogeneous landscape [Fig. 5(a)].
- If these two ranges are discontinuous, there exists a range of \( z \) for which either the metapopulation goes extinct regardless the dispersal rate [Fig. 5(b)], or for which two different and discontinuous ranges of dispersal rate allow the metapopulation persistence [Fig. 5(c)].

**Discussion**

**THE METAPOPULATION DYNAMICS**

The analysis presented earlier allows to study the persistence and extinction of a metapopulation in an elementary landscape and in a heterogeneous landscape. As in Gyllenberg *et al.* (1997), the number \( R_0 \) plays a crucial role. In their paper, these authors define this term as “the expected number of new local entities produced in a virgin environment by a typical local entity during its lifetime”. This term is analogous to the basic reproduction ratio used in the epidemiological models which gives the expected number of secondary cases caused by one typical infected individual during its entire infectious period in a population consisting of susceptible individuals only (Diekmann *et al.*, 1990). In the case of metapopulation models, a population is analogous to the infected individual, and the new founded populations, to the secondary cases. Thus, this term can be interpreted as the expected number of new local populations produced by a local population during its lifetime. In other words, a metapopulation can be seen as a system with two demographic levels: the individual in the population and the population in the metapopulation. From this prospect, the net replacement number is the fitness of a population, e.g. the number of populations generated by a single population.

In our model, the number \( R_0 \) has been derived in a purely mathematical way from the matrix expression of the metapopulation dynamics, without distinguishing the population level from the individual level as we work on local population sizes \( N_i \). \( R_0 \) can also be calculated by considering the expected number of seeds, descendants of a single founder seed, which will leave the site until it goes extinct. Instead of counting from seeds to seeds, one can count from plants to plants. Thus, \( R_0 \) can also be derived by considering the expected number of plants, descendants of a single founder plant and issued from seeds which will leave the site until it goes extinct (see Section A.4). Dealing with number of seeds or individuals, these derivations of \( R_0 \) do not take explicitly into account the two demographic levels. They appear thus in contrast with the net replacement number of Gyllenberg *et al.* (1997). In fact, in our deterministic model, an infinite number of sites is considered. Our mathematical derivation of \( R_0 \) assumes an infinite number of individuals since it is based on the expression of the variation of \( N_i \). Indeed, if we had a finite number of individuals, the \( N_i \) would be on expectancy all equal to zero. However, the biological derivation of \( R_0 \) is true even for a finite number of individuals. In this case, the number \( R_0 \) is derived under the same conditions as Gyllenberg *et al.* (1997) (in a virgin environment). As long as the number of individuals is sufficiently low, our model behaves like one in which the fraction of dispersed seeds could be replaced by the expected number of seeds per site, which itself is equivalent to a probability of colonization when it is sufficiently less than one. In such a case, it can be treated as a model in which a finite number of seeds would fall into an infinite number of sites. Two implications arise: first, each successful dispersed seed will create a new local population, and second, a local population is settled by the progeny of a single founder seed. Thus, the new founded local populations are equivalent to the number of new individuals able to reproduce. Although the net replacement number \( R_0 \) is derived in our model from dynamics of individuals, this term can be interpreted as the expected number of new local populations produced by a local population during its lifetime.

The persistence or extinction of the metapopulation in a landscape depends only on the expected number of seeds, descendants of a single founder seed, which will leave the site until it goes extinct. This might have been predicted since local populations have a limited lifetime
and dispersed seeds are the only ones allowing the birth of new local populations. The values of dispersal rate for which $R_0$ will be equal to one will determine the range of dispersal rates that allow the metapopulation persistence in each landscape.

First, in an elementary landscape, the existence of a metapopulation persistence range agrees with the results of Roff (1975), and Hanski & Zhang (1993), who have analysed metapopulation viability as a function of dispersal rate. However, in our model, the local carrying capacity does not influence the metapopulation persistence dispersal rate range as we studied conditions for metapopulation growth at low density only. Our model does not suppose the existence of a minimum viable population size as in Roff (1975). Two elements are crucial for the metapopulation persistence: the value of the net replacement number when all seeds are dispersed ($R_0(1)$), and the term $A_1 \times f$, which can be interpreted as the expected number of offspring produced by a seed on an occupied site if the site is not disturbed. In all cases, the dispersal rate must exceed a minimum value in order that foundations of new populations could compensate for extinctions. When all seeds are dispersed, if $R_0(1)$ is above one, the metapopulation persists even for high values of dispersal. It is the case for some parameter values corresponding particularly to habitats, for which either the frequency of empty sites is high [as in Fig. 3 (case 1), $V_0 = 0.7499$, $\sum_{i=1}^{Z-1} V_i = 0.2499$, $V_Z = 0.0002$], or the successional process is rapid. Conversely, in habitats where the unsuitable sites are the most frequent [Fig. 3 (case 2), $V_0 = 0.02$, $\sum_{i=1}^{Z-1} V_i = 0.01$, $V_Z = 0.97$, $R_0(1)$ is below one, since a majority of dispersed seeds are lost on these sites. If the term $A_1 \times f$ is below one, the number of progeny is not sufficient to allow the growth of local populations and the metapopulation goes inevitably extinct. If this term is above one, the metapopulation may persist for intermediate values of dispersal rate. Note that there is a particular value of dispersal rate for which $R_0$ is maximum. Below this value, the number of dispersed seeds produced is not sufficient for the metapopulation to have maximal growth. Over this value, the number of dispersed seeds produced is too high and some are lost into unsuitable sites. The existence of an optimal dispersal value (not necessarily evolutionarily stable) has been shown in other models as well (e.g. Roff, 1975; Comins et al., 1980; Motro, 1982).

Second, our analysis allows to predict conditions that allow the persistence of a metapopulation in the heterogeneous landscape from the results on metapopulation dynamics in an elementary landscape and thus to understand the surprising prediction shown by Olivieri & Gouyon (1997) in the heterogeneous landscape. This analysis shows that the metapopulation is always able to persist in the heterogeneous landscape (whatever the proportion of the two elementary landscapes) if the two dispersal ranges allowing the metapopulation persistence, respectively, in the two elementary landscapes overlap. Indeed, a sufficient condition for metapopulation persistence is that there exist common dispersal rates within the two persistence ranges. When these two dispersal ranges are discontinuous, two cases have been identified: either there exist values of $z$ such that the metapopulation goes extinct whatever the dispersal rate, or there exist values of $z$ such that two ranges of dispersal rate allow metapopulation persistence. The expression of the net replacement number in the heterogeneous landscape as a function of the two net replacement numbers determined, respectively, in each of the two elementary landscapes gives insight on the metapopulation dynamics. In particular, the metapopulation may behave like a source–sink metapopulation sensu Hanski & Simberloff (1997) in the heterogeneous landscape. Indeed, for some values of dispersal, in one of the elementary landscapes, the net replacement number is below one and in the other elementary landscape, it is above one [e.g. Fig. 5(a) for $z = 0.2$, $D \in [D_2, D_1]$, $R_{01}(D) < 1$ and $R_{02}(D) > 1$]. Thus, in the heterogeneous landscape one elementary landscape behaves like a sink, whereas the other behaves like a source. In this case, the metapopulation persists in the heterogeneous landscape only if the excess of dispersed seeds produced on the source elementary landscape compensates the deficit on the sink elementary landscape. If the two elementary landscapes behave like a sink [e.g. Fig. 5(b) and (c), $D \in [D_2, D_1]$, the metapopulation goes inevitably extinct. This result is in apparent contrast to the study of Jansen.
& Yoshimura (1998), who showed that a population can persist in two sink habitats, when the environmental conditions in one of them are not constant but fluctuate. In fact, a habitat in their model is a unique site. As Jansen & Yoshimura (1998) themselves recognize in their discussion, their prediction that a population can persist in two sink habitats resumes to the prediction that a metapopulation may be viable even though each population has a finite lifetime.

THE LANDSCAPE

The analytical derivation of the metapopulation dynamics in the landscape identifies the main elements of the landscape, that determine and influence the future of the metapopulation.

In the elementary landscape, as in Hanski & Zhang (1993), our model predicts that species living in unstable environments (with high turn-over of sites) should have intermediate dispersal rates, if the landscape has a low suitability [Fig. 4(a), case 2, $V_Z = 0.69$, $A_1 = 0.4$]. Because we take process of succession into account, we further predict that species should also have intermediate dispersal rates if the replacement of the species by the process of succession is rapid (low maximal population lifetime). This is because the average extinction rate of an occupied site depends both on the disturbance rate $(1 - A_1)$ and on the process of succession. Unexpectedly, as shown in Fig. 4(b), in a highly disturbed landscape (high disturbance rate of occupied sites associated with a reduced expected lifetime of populations), the threshold value of $f$ is lower than in a more stable habitat (low disturbance rate of occupied sites and same maximal population lifetime). In the first case, the frequency of colonizable sites is large ($V_0 = 0.62$) and high dispersal rates are sufficient to allow metapopulation persistence. Conversely, in the latter case, as the frequency of non-colonizable sites is very high ($V_Z = 0.94$), most dispersed seeds are lost to these sink sites and the metapopulation persists only for high values of local population growth, found only when fecundity is large. When $Z$ tends to a large value [Fig. 4(c)], the frequency of unsuitable sites is negligible. If the number $A_1 \times f$ is lower than 1, the occupied sites are frequently disturbed and the local population growth is low. Thus, the metapopulation persists for high dispersal rates if the survival rate of dispersed seeds and the colonization rate of empty sites are high enough [Fig. 4(c), case 1]. Conversely, if $A_1 \times f$ is greater than 1, the expected number of offspring produced by a seed on an occupied site is high and the metapopulation persists rapidly for all dispersal rates as $Z$ increases [Fig. 4(c), case 2].

In the heterogeneous landscape, different temporal dynamics of sites resulting from ecological variations within the same landscape can lead to complex patterns of metapopulation dynamics and especially to metapopulation extinction. Many studies have shown that the spatial pattern of the metapopulation habitat can affect dispersal and metapopulation survival. Ecosystem fragmentation (Saunders et al., 1991), increased average isolation between sites, decreased site areas (Hanski, 1994; Gustafson & Gardner, 1996) and the arrangement of sites in the habitat (Adler & Nuernberger, 1994) are the major cited factors. But in our case extinction does not result from either a decrease in the availability of suitable sites, or from an increase in the fragmentation of the landscape. The metapopulation extinction is caused by changes in the proportions of the elementary landscapes; these changes lead to situations in which no proportions of the elementary landscapes; these changes lead to situations in which no dispersal rates allow persistence.

The results obtained in the heterogeneous landscape show that a modification of the proportion of one elementary landscape can have various consequences for several different causes. This can be critical for metapopulation viability. Indeed, imagine that the metapopulation habitat is at first equivalent to landscape 2, that sites dynamics is modified so that the metapopulation habitat becomes progressively a heterogeneous landscape, made of landscapes 2 and 1, and eventually becomes equivalent only to landscape 1. Assuming the cases of Fig. 5, two different scenarios can be envisaged:

Scenario 1: the metapopulation is able to persist whatever the mixture of the two elementary landscapes [see Fig. 5(a)]. If the initial dispersal rate lies between $D_1$ and $D_2$, the metapopulation will be viable whatever $x$. But, assume now that the initial genetic variability was reduced by natural selection acting on dispersal. If the initial
dispersal rate lies between $D_2$ and $D_1$, the metapopulation will persist only if the change in the proportion of the landscape 1 is slow enough to allow the evolution of a dispersal rate within the persistence range of the metapopulation in the new landscape ($[D_1, D_1']$).

Scenario 2: let us assume that, as in Fig. 5(b), there exists a large range of the proportion of the landscape 1 for which no dispersal rates allow metapopulation persistence. Only if landscape proportions change drastically and variability in dispersal rate is already present in the metapopulation will persistence be allowed.

In summary, if there exists a dispersal range allowing metapopulation persistence whatever $z$, the modification of the habitat should be slow. Conversely, if there exist some values of $z$ for which no dispersal rates allow metapopulation persistence, the metapopulation will persist if the landscape proportions change rapidly. However, with an abrupt change there will be a transitory period during which the landscape itself will not be in equilibrium, with respect to frequencies of patches in different states. This was not taken into account in our model. During this transitory period, local populations may drop dangerously low, even though the long-term deterministic expectation is a positive growth rate in the new landscape at its equilibrium.

The present results can give insight into consequences of different management practices. Indeed a change in a part of a landscape that modifies the landscape sites dynamics may lead to metapopulation extinction, in particular if only the disturbance rate of occupied sites is modified (results not shown). Thus, if in a local region, agricultural practices or particular land management pattern [like fire, grazing or flood water management (Noble & Gitay, 1996)] increase the disturbance rate of some sites, this could lead to the species extinction if the metapopulation habitat is initially equivalent to an elementary landscape with low probability of disturbance. This extinction can occur also if the disturbance rate is decreased, for example by management decisions such as protecting some sites of the metapopulation habitat against disturbing influences, if the habitat is initially equivalent to an elementary landscape with high probability of disturbance. Moreover, extinction may result also from change in the maximal population lifetime and fecundity. For instance, if fertilizers are applied to some sites, fecundity in these sites may be increased, but the successional process may also be accelerated, thereby decreasing the population lifetime ($Z$). This action may lead to the metapopulation extinction, because no dispersal rate allowing metapopulation persistence may exist. The same process may arise if initially all landscape sites receive fertilizers and if progressively application of fertilizers is stopped.

**Conclusion**

A better understanding of metapopulation dynamics is of fundamental interest in evolution and in ecology (Olivieri et al., 1990; Bascompte & Solé, 1995; Hanski & Gilpin, 1997) as well as in landscape ecology (Wiens, 1997) and conservation biology (Doak & Mills, 1994, McCullough, 1996). This study points out how the landscape structure can have complex effects on metapopulation dynamics. As landscape features change, the evolution of dispersal is a critical characteristic of the metapopulation. If the evolution of dispersal towards new values adapted to the novel landscape features is not possible, the metapopulation can be doomed to extinction. But, even if it is possible, the existence of sufficient variation with regard to the speed of landscape change is a critical parameter for the future of the species.

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**REFERENCES**


### APPENDIX A

#### $R_0(D)$ in the Elementary Landscape

**A.1. Equilibrium Frequencies of Sites in an Elementary Landscape**

It has been shown in Olivieri *et al.* (1995) that

$$V_0 = \frac{1}{1 + A_0[(1 - A_1 Z^{-1})(1 - A_1) + A_1 Z^{-1}(1 - A_Z)]},$$

$$V_i = A_0 V_0 A_1^{-1}, \quad \forall i \in [1, Z - 1],$$

$$V_Z = \frac{A_0 V_0 A_1^{-1}}{1 - A_Z}.$$

**A.2. Matrix Expression of the Metapopulation Dynamics**

$M$ is the matrix such that $N(t) = M \cdot N(t - 1)$, where $N(t)$ is the vector of local population sizes ($N_i(t)$, $i \in [1, Z - 1]$). Let $b_i = f \cdot D \cdot q \cdot V_i$ and $x = f(1 - D)$. From the equations of the model,

$$M = \begin{bmatrix}
  b_1 & b_2 & \cdots & \cdots & \cdots & b_{Z-1} \\
  b_1 + x & b_2 & \cdots & \cdots & \cdots & b_{Z-1} \\
  b_1 & b_2 + x & \cdots & \cdots & \cdots & b_{Z-1} \\
  \vdots & \vdots & \ddots & \ddots & \ddots & \vdots \\
  b_1 & \cdots & \cdots & b_{Z-2} + x & b_{Z-1} 
\end{bmatrix}.$$

**A.3. Mathematical Derivation of $R_0(D)$**

The characteristic equation of $M$ is

$$\det[M - \lambda I] = 0,$$  

(A.1)

$$\det[M - \lambda I] = 0 \iff \exists X \neq 0 \text{ such that } (M - \lambda I)X = 0 \text{ where } X \text{ is the vector of } X_i's.$$ Denote $Y = b_1 X_1 + \cdots + b_{Z-1} X_{Z-1}$,

$$\begin{pmatrix}
  X_1 = \frac{Y}{\lambda}, \\
  \vdots \\
  X_k = \frac{Y}{\lambda} \left[ 1 + x/\lambda + \cdots + x^{k-1}/\lambda^{k-1} \right], \\
  \vdots \\
  X_{Z-1} = \frac{Y}{\lambda} \left[ 1 + x/\lambda + \cdots + x^{Z-2}/\lambda^{Z-2} \right],
\end{pmatrix}$$

therefore

$$Y = b_1 \frac{Y}{\lambda} + b_2 \frac{Y}{\lambda} \left[ 1 + x/\lambda \right] + \cdots + b_{Z-1} \frac{Y}{\lambda} \left[ 1 + x/\lambda + \cdots + x^{Z-2}/\lambda^{Z-2} \right].$$  

(A.2)

As $Y \neq 0$, dividing both sides of eqn (A.2) by $Y$, one obtains

$$1 = (b_1 + \cdots + b_{Z-1}) \lambda^{-1} + x(b_2 + \cdots + b_{Z-1})$$

$$+ \lambda^{-2} + \cdots + x^{k-1}(b_k + \cdots + b_{Z-1}) \lambda^{-k} + \cdots$$

$$+ x^{Z-2} b_{Z-1} \lambda^{-Z+1}.$$  

(A.3)

Let the right-hand side of eqn (A.3) be $S(\lambda, x, b_i)$. $S(\lambda, x, b_i)$ is a strictly decreasing function of $\lambda$ tending to $+\infty$ as $\lambda \to 0^+$ and to 0 as $\lambda \to +\infty$. This proves that the characteristic equation has a unique positive root $\lambda$ which is the dominant root according to the Perron–Frobenius theorem (see Caswell, 1989). Denote $S(\lambda, x, b_i)$ evaluated at $\lambda = 1$ by $R_0$. The expression of $R_0$ is

$$R_0 = \sum_{i=0}^{Z-2} x^i \sum_{j=i+1}^{Z-1} b_j.$$
or

\[
R_0(D) = f D q \sum_{i=0}^{Z-2} f^i (1 - D)^j \sum_{j=i+1}^{Z-1} V_j.
\]

A.4. BIOLOGICAL DERIVATION OF \(R_0(D)\)

Consider the sites of the landscape almost empty and a dispersed seed which arrives on a site of the landscape just before the period of disturbance. The aim is to calculate the expected number of seeds, descendants of this founder, which will leave the site.

- With probability \(V_Z\), the dispersed seed falls in an unsuitable site and has no progeny.
- With probability \(V_i (i \in [1, Z - 1])\), the dispersed seed arrives on a suitable site of age \(i\).

With probability \(A_1\) (the site is not disturbed), the founder seed will produce \(fD\) dispersed seeds and \(f(1 - D)\) non-dispersed seeds.

If the site is not disturbed the following generation, each of the \(f(1 - D)\) non-dispersed seeds will produce \(fD\) dispersed seeds. Thus, the founder seed will have produced \(fD[f(1 - D)]\) dispersed seeds.

By recurrence, in the \(j\)th time after the dispersed seed entered the site of age \(i\), its expected production of dispersed seeds is

\[
A_1 [A_1 f(1 - D)]^{j-i-1} f D.
\]

- With probability \(V_0\), the dispersed seed falls in a suitable site of age 0.

The same reasoning applies except that the initial probability of non-disturbance is \(A_0\).

The expected production of dispersed seeds by the founder seed is thus \(A_0 [A_1 f(1 - D)]^{j-i-1} f D\).

Each of all these dispersed seeds will survive with probability \(q\).

Therefore, the expected production of dispersed seeds produced by the founder seed is

\[
Q(D) = f D q \left[ V_0 \sum_{j=1}^{Z-1} A_0 [A_1 f(1 - D)]^{j-1} + \sum_{i=1}^{Z-2} \sum_{j=i+1}^{Z-1} V_i A_1 [A_1 f(1 - D)]^{j-i-1} \right].
\]

Since \(V_i = A_0 V_0 A_1^{i-1}, \forall i \in [1, Z - 1]\),

\[
Q(D) = f D q \left[ \sum_{j=1}^{Z-1} V_j [f(1 - D)]^{j-1} + \sum_{i=1}^{Z-2} \sum_{j=i+1}^{Z-1} V_j [f(1 - D)]^{j-i-1} \right],
\]

This quantity is equal to \(R_0(D)\).

Each dispersed seed will generate a plant able to reproduce (i.e. the seed finds a suitable site and this site is not disturbed) with probability

\[
V_0 A_0 + \sum_{i=1}^{Z-2} (V_i A_1) = 1 - V_0 - V_Z.
\]

This is true for the founder seed as well as its progeny.

Therefore, a dispersed seed will produce, on expectation:

- \(1 - V_0 - V_Z\) plants able to reproduce.
- \(R_0\) dispersed seeds and \(R_0(1 - V_0 - V_Z)\) plants able to reproduce.

Thus, \(R_0\) is also equal to the expected number of plants, descendants of a founder plant and issued from seeds which will leave the site until it goes extinct.

A.5. NUMBER OF ROOTS OF THE EQUATION \(R_0(D) = 1\)

To show that \(R_0(D) = 1\) has at most two roots on \([0, 1]\), it is sufficient to show that \(R_0(D)\) has a unique extremum. Since \(R_0(0) = 0\) and \(R_0(D) \geq 0 \forall D \in [0, 1]\), this extremum is a maximum. By the change of variable \(x = f(1 - D)\), one gets

\[
R_0(x) = q(f - x) \sum_{i=0}^{Z-2} x^i \sum_{j=i+1}^{Z-1} V_j.
\]

\(R_0(x) = q(f - x) P(x)\), where \(P(x)\) is a polynomial of degree \((Z - 2)\).

From now on, as \(D\) varies from 0 to 1, \(R_0(x)\) will be studied only for \(x \in [0, f]\). We now demonstrate that \(R_0(x)\) has a unique extremum on \([0, f]\).
One can write $R_0(x)$ as a polynomial
$$R_0(x) = \sum_{k=0}^{z-1} r_k x^k$$
with $r_k$, the coefficients of the polynomial $R_0(x)$:
$$r_0 = q f, \quad r_k = q \left[ -V_k + (f-1) \sum_{j=k+1}^{z-1} V_j \right], \quad \forall k \in [1, Z-2],$$
$$r_{Z-1} = -qV_{Z-1},$$
$$r_0 > 0 \quad \text{and} \quad r_{Z-1} < 0,$$
$$R_0(0) = r_0 \quad \text{and} \quad R_0(f) = 0.$$

The function $R_0(x)$ depends on the sign of $R_0'(x)$ (the derivative of $R_0$ with respect to $x$), which itself depends on the sign of $R_0^{(2)}(x)$, and so on until $R_0^{(Z-1)}(x)$. We now study the successive derivatives of $R_0(x)$.

$$R_0^{(Z-1)}(x) = (Z-1)! \cdot r_{Z-1}$$
and is always negative,
$$R_0^{(k)}(x) = q(f-x)P^{(k)}(x) - qkP^{(k-1)}(x)$$
$$\forall k \in [1, Z-2].$$

In particular,
$$R_0^{(0)}(0) = k! r_k,$$
$$R_0^{(k)}(f) = -qkP^{(k-1)}(f).$$

$R_0^{(k)}(0)$ has the sign of $r_k$, and $R_0^{(k)}(f)$ is always negative,
$$r_k = q \left[ -V_k + (f-1) \sum_{i=k+1}^{Z-1} V_i \right], \forall k \in [1, Z-2].$$

Since $V_k = A_0 V_0 A_1^{k-1}$, we have
$$r_k = q A_0 V_0 A_1^{k-1} \left[ -1 + A_1 (f-1) \frac{1 - A_1^{Z-1-k}}{1 - A_1} \right].$$

$r_k$ has thus the sign of $A_1 f - 1 - A_1^{Z-1-k} (f-1)$. We may distinguish two cases:

**Case 1**: $A_1 \times f \leq 1$. \quad \forall k \in [0, Z-1], r_k < 0. Therefore, $R_0^{(0)}(0) < 0$ and $R_0^{(k)}(f) < 0$. Since $\forall x \in [0, f]$, $R_0^{(Z-1)}(x) < 0$, $R_0^{(Z-2)}(x)$ is a strictly decreasing, negative function of $x$. So is $R_0^{(Z-3)}(x)$, ... and so is $R_0^{(0)}(x)$. Therefore, $R_0(x)$ is a decreasing function of $x$, with a maximum at $x = 0$ and a minimum at $x = f$. We may further distinguish two cases:

- if $R_0(0) < 1$, then $\forall x \in [0, f]$, $R_0(x) < 1$, the metapopulation is not viable $\forall D \in [0, 1]$
- if $R_0(0) > 1$, then $\exists! x_1 / R_0(x_1) = 1$. Therefore, $\exists! D_1 = 1 - x_1 / f$ such that $R_0(D_1) = 1$, and the metapopulation persists for $D \in [D_1, 1]$.

**Case 2**: $A_1 \times f > 1$. In this case, $r_k$ may be positive for some values of $k$. Let us study the sign of $r_{k+1} - r_k$.
$$\forall k \in [1, Z-2], \quad r_{k+1} - r_k$$
$$= q (V_k - fV_{k+1})$$
$$= q A_0 V_0 A_1^{k-1} (1 - A_1 f),$$

and thus $r_{k+1} - r_k < 0$.

Therefore, we have
$$r_0 > 0,$$
$$r_{Z-1} < \cdots < r_k < \cdots < r_1,$$
$$r_{Z-1} < 0.$$

If $\forall k \in [1, Z-1]$, $r_k < 0$, then the demonstration of case 1 applies.

If $\exists j / r_{Z-1} < r_{Z-2} < \cdots < r_{j+1} < 0 < r_j < \cdots < r_1$, then $\forall k \in [f+1, Z-1]$, $\forall x \in [0, f]$, $R_0^{(j)}(x) < 0$. In particular, $\forall x \in [0, f]$, $R_0^{(j+1)}(x) < 0$, $R_0^{(j)}(x)$ is thus a strictly decreasing function of $x$, with $R_0^{(j)}(0) = j! r_j > 0$ and $R_0^{(j)}(f) < 0$. Therefore, $\exists! m_j \in [0, f] / R_0^{(j)}(m_j) = 0$. Thus, for $x \in [0, m_j]$, $R_0^{(j)}(x) \geq 0$ and for $x \in [m_j, f]$, $R_0^{(j)}(x) \leq 0$. $R_0^{(j-1)}(x)$ is an increasing function of $x$ on $[0, m_j]$ and a decreasing function on $[m_j, f]$, with $R_0^{(j-1)}(0) = (j-1)! r_{j-1} > 0$ and $R_0^{(j-1)}(f) < 0$.

Therefore, $\exists! m_{j-1} \in [m_j, f] / R_0^{(j-1)}(m_{j-1}) = 0$.

By continuing the recurrence, it follows that $R_0(x)$ is an increasing function of $x$ on $[0, m_2]$ and a decreasing function on $[m_2, f]$, with $R_0(0) = r_1 > 0$ and $R_0(f) < 0$. Therefore, $\exists! m_1 \in [m_2, f] / R_0(m_1) = 0$.

Thus, for $x \in [0, m_1]$, $R_0(x) \geq 0$ and for $x \in [m_1, f]$, $R_0(x) \leq 0$. Therefore, $R_0(x)$ is an increasing function on $[0, m_1]$, and a decreasing function on $[m_1, f]$, and $R_0(x)$ has a unique maximum on $[0, f]$. 


• if $R_0(0) < 1$, then the equation $R_0(D) = 1$ has at most two roots on [0, 1], which define the persistence range of the metapopulation,
• if $R_0(0) > 1$, then there exists $x_1 \in [0, f]/R_0(x_1) = 1$, therefore $\exists! D_1 = 1 - x_1/f$ such that $R_0(D_1) = 1$, and the metapopulation persists for $D \in [D_1, 1]$.

To sum up these results for $R_0$ as a function of $D$, $D \in [0, 1]$:
• if $R_0(1) > 1$, the metapopulation persists for $D \in [D_1, 1]$.
• if $R_0(1) < 1$,
  if $A_1 f \leq 1$, the metapopulation is not viable \( \forall D \in [0, 1] \),
  if $A_1 f > 1$, the metapopulation can persist for $D \in [D_1, D_2]$.

APPENDIX B

$R_0(D)$ in the Heterogeneous Landscape

The metapopulation habitat is a heterogeneous landscape, mixture of the two elementary landscapes L1 and L2. L1 is in proportion $\alpha$, which varies from 0 to 1. Let $V_{1i}$ be the frequencies of sites $S_{1i}$ of the elementary landscape L1. $V_{2i}$ the frequencies of sites $S_{2i}$ of the elementary landscape L2. $f_1$ and $f_2$ are the net potential fecundities, and $Z_1$ and $Z_2$ the maximal population lifetimes, in L1 and L2, respectively.

We use the biological interpretation of the $R_0$ in the elementary landscape (see Section A.4). A dispersed seed arrives in L1 with probability $\alpha$, and in L2 with probability $(1 - \alpha)$. In each elementary landscape, its expected production of dispersed seeds is:

- in L1 $R_{01}(D) = f_1 D q \sum_{i=0}^{Z_1-2} f_1^i (1 - D)^i \sum_{j=i+1}^{Z_1-1} V_{1j}$,
- in L2 $R_{02}(D) = f_2 D q \sum_{i=0}^{Z_2-2} f_2^i (1 - D)^i \sum_{j=i+1}^{Z_2-1} V_{2j}$.

Thus, in the heterogeneous landscape, the expected number of dispersed seeds produced by a dispersed seed is

$$R_0(D) = \alpha R_{01}(D) + (1 - \alpha) R_{02}(D). \quad (B.1)$$