

## THE INFLUENCE OF DISPERSAL BEHAVIOUR ON METAPOPOPULATION VIABILITY

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### ABSTRACT

The dynamics of the metapopulation is described by a Markov chain with three possible states of each subpopulation: 0 (extinct), 1 (lower size), and 2 (carrying capacity). Migrations between subpopulations can depend both on the state of the source subpopulation (e.g., inversely) and the state of the target habitat. The strategies of conspecific attraction, when occupied patches receive a larger fraction of migrants, and conspecific repulsion, i.e., the preference for empty patches, are modelled. Emigration events affect the density of the source habitat. Immigration causes either a recolonisation of an empty patch or the transition from state 1 to state 2 of the target habitat. Application of queuing theory methods made it possible to obtain analytical formulas for extinction probability and persistence time.

The effect of dispersal behaviour was investigated. The influence of random dispersal and of directional dispersal depends on population parameters. It is demonstrated that, while at high growth and mortality rates, conspecific repulsion provides better metapopulation viability, there exists a threshold value for the growth rate below which aggregation becomes favourable. Biological interpretation of these results is discussed and a classification of species is suggested associating population kinetic rates and dispersal strategy.

*Keywords:* Metapopulation, extinction risk.

### 1. Introduction

The problem of assessment of the extinction risk for a single population was formulated accurately by Bartlett [6]. MacArthur and Wilson [22] considered the current

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biodiversity of a natural habitat as an equilibrium between extinctions and recolonisations. Since most endangered species are threatened by habitat fragmentation, and therefore exist in small patches, it was extremely important to link these ideas to the metapopulation concept [14].

This approach, called the extinction-centred view of metapopulations has recently become common in conservation biology and as most environments are becoming increasingly fragmented, it seems clear that much of the metapopulation research in the future will be motivated by and applied to conservation biology.

The term metapopulation has been used to refer to a set of populations with frequent local extinctions, in which the interplay of dispersal and local dynamics becomes the key to understanding the overall population dynamics in stochastic environments. Application to conservation biology raised the problem "Single Large habitat patch Or Several Small patches" (SLOSS) [14].

The aim of this paper is to investigate the influence of dispersal behaviour on metapopulation viability. Different techniques exist for this assessment. The most common approach is simulation modelling in which numerous runs are used to evaluate the metapopulation dynamics and the extinction risk. Such technique and the software of numerical risk assessment based on the concept of probability of quasi-extinction [5], i.e., the probability that population density will drop below a given preassigned level, were developed by Akçakaya and Ferson [4,13]. The underlying models consider age and space structures. Other versions of stochastic models incorporating effects of environmental variability, demographic uncertainty, and density dependence were developed by Akçakaya [1], Akçakaya and Ginzburg [2,3] and Burgman *et al.* [7]. Dombrovsky and Tyutyunov [9,10,11,12] developed a stochastic model of metapopulation dynamics, which made it possible to assess numerically the extinction risk as a function of habitat size, fragmentation level, and migration rate among local subpopulations.

These simulation techniques make it possible to consider rather complicated population models. However, this approach requires sometimes enormous computation time. Another drawback of this approach is that operating only with a restricted set of parameter combinations does not ensure the completeness of analysis of parameter influence.

The alternative approach based on occupancy models [7, 16, 21] avoids this drawback since it gives analytical expressions for the percentage of occupied patches. However, it uses a highly simplified description of the populations and, hence, may be insufficient in modelling certain effects. The Markov chain approach followed in the present paper can suggest a kind of compromise between these two approaches [8].

Migrations between populations can depend both on the density of the source population (e.g., inversely) and the density of the target habitat. In [18] Hansson gives many examples of source density dependence. There is also abundant evidence that animal dispersal may not be random with respect to the habitat patches available [23]. It is possible that dispersal is initially directed or actually instigated by

perception of conspecifics on other patches [25]. Preference to habitats occupied by conspecifics may promise certain social benefits such as mating success or defence against predation.

Analysing the situation in [23], Ray *et al.* arrive at the conclusion that "con-specific attraction results in occupied patches receiving a disproportionately large fraction of the dispersing propagules. Thus, empty patches receive fewer dispersing propagules, resulting in a lower colonisation rate. The fraction of occupied patches will decline if the lower colonisation rate is not offset by a proportionately lower extinction rate." The authors [23] demonstrated that patch occupancy is always inversely related with the level of conspecific attraction in various mathematical models. A question arises: under what conditions does conspecific attraction still provide a higher metapopulation viability? Apparently the answer depends on the species' biology, in particular, on the existence of an Allee effect [5]: aggregation may bring a population far from the dangerous threshold size, creating a kind of "rescue effect".

In this paper we use three-state models. While the 0-state corresponds to the absence of individuals, the 1- and 2-states correspond to low and high density states, respectively. The former is supposed to be close to the lower threshold size and the latter is of the order of the local carrying capacity.

One of the basic and strong assumptions underlying our spatially structured model is that migration of individuals to another habitat affects the population density of the source habitat. For instance, a recolonisation of habitat I by individuals from habitat II reduces the density of habitat II to a lower value.

Obviously, this is not true for plants dispersing by seeds. The model applies to animal populations only and it does not take into account cases where the density is high enough that withdrawal of a substantial number of individuals from a habitat does not reduce the density considerably.

The use of methods of Markov chains and queuing theory makes it possible to analyse analytically not only random dispersal but more sophisticated migration behaviours, e.g., conspecific attraction or density-dependent dispersal [18].

Modelling the rescue effect consists in our model in a transition of a subpopulation from the low density state to the high density state when receiving immigrants. This effect can have either a demographic or a genetic nature: it reduces local extinction probability. The model also makes it possible to simulate other dispersal behaviours, that is, active dispersal or conspecific repulsion, i.e., preference for empty patches.

Another feature of the model is the possibility of recolonisation from an external source, say, from the mainland when all local subpopulations have become extinct. We incorporate into the model a parameter describing the intensity of the external flow of propagules,  $\alpha$ . Thus, when  $\alpha = 0$  we have the special case of an isolated metapopulation which is doomed to eventual extinction. With a positive  $\alpha$ , the metapopulation stays in the 0-state (i.e., extinct) for some period of time (depending

on  $\alpha$ ) until a recolonisation occurs. This turnover lasts indefinitely. It can be considered just as reiterated simulations of the extinction events.

It occurs in mathematical theories that when considering a more general situation one can efficiently analyse a particular case. This seems to be the case with the extended metapopulation model. As we will see, this approach and the application of the methods of queuing theory [20] make it possible to obtain explicit formulas of the extinction probability and average time to extinction for an isolated metapopulation and to analyse the sensitivity of the metapopulation viability in relation to exchange rates and other parameters.

## 2. Models

### 2.1. Model for One Population

The essential stochasticity of an environment makes it reasonable to concentrate on the probabilities of such events as birth, death and migration of individuals. Let us first consider a model for a local population. We will distinguish only three states of the subpopulation:

- 0 – the population is extinct,
  - 1 – the population is at a low density (close to the Allee threshold size),
  - 2 – the population is at a high density (close to the habitat’s carrying capacity)
- (Fig. 1).

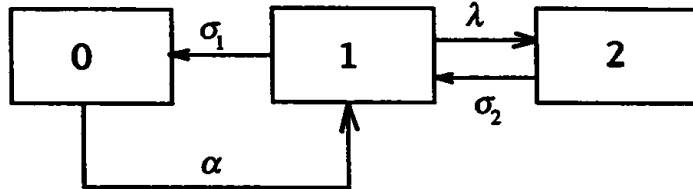


Fig. 1. Transitions in the model for an isolated population with three possible states.

The parameter  $\lambda$  will characterise the transition intensity from state 1 to state 2 (the growth rate);  $\sigma_i$  is the transition intensity from state  $i$  to state  $i - 1$  ( $i = 1, 2$ ) (death rates). We also introduce the parameter  $\alpha$ , the transition intensity from state 0 to state 1, which can be interpreted either as the recolonisation rate of extinct patches from the mainland or as the replication process of the stochastic simulations of the model.

Let  $p_i(t + \Delta t)$  be the probability for the population to be in state  $i$  at time  $t + \Delta t$  ( $i = 0, 1, 2$ ). In this case, the probability of being extinct is

$$p_0(t + \Delta t) = p_0(t)(1 - \alpha\Delta t) + p_1(t)\sigma_1\Delta t + O(\Delta t). \tag{2.1}$$

We can rewrite this in the form

$$\frac{p_0(t + \Delta t) - p_0(t)}{\Delta t} = -\alpha p_0(t) + p_1(t)\sigma_1 + \frac{O(\Delta t)}{\Delta t}. \tag{2.2}$$

If  $\Delta t \rightarrow 0$ , then

$$\frac{dp_0(t)}{dt} = -\alpha p_0(t) + \sigma_1 p_1, \tag{2.3}$$

and in the stationary case, putting the derivative equal to 0, we have

$$\alpha p_0 = \sigma_1 p_1. \tag{2.4}$$

In the same way, or just using the mnemonic rule “in equals out” (i.e., the probability of entering a state is equal to the probability of leaving this state), we can obtain analogous conditions for each state of the population:

$$\left. \begin{aligned} \alpha p_0 &= \sigma_1 p_1 \\ (\lambda + \sigma_1) p_1 &= \alpha p_0 + \sigma_2 p_2 \\ \sigma_2 p_2 &= \lambda p_1 \end{aligned} \right\}. \tag{2.5}$$

We can replace the third equation in this system by the trivial condition  $p_0 + p_1 + p_2 = 1$  and we define the parameter  $\rho = \lambda/\sigma_2$  (the so-called system loading factor). Besides, we can set  $\sigma_1 = 1$  by time scaling. Finally we have the system

$$\left. \begin{aligned} \alpha p_0 &= p_1 \\ \rho p_1 &= p_2 \\ [1 + \alpha(\rho + 1)] p_1 &= \alpha \end{aligned} \right\}, \tag{2.6}$$

and the solution is

$$\left. \begin{aligned} p_0 &= \frac{1}{1 + \alpha(\rho + 1)} \\ p_1 &= \frac{\alpha}{1 + \alpha(\rho + 1)} \\ p_2 &= \frac{\alpha\rho}{1 + \alpha(\rho + 1)} \end{aligned} \right\}. \tag{2.7}$$

The average time spent by the system in state 0 during the time period  $T$  is  $p_0 T$ . The average duration of an extinction event is  $1/\alpha$ . The ratio of these two values  $\alpha p_0 T$  is the average number of occurrences of the state 0 (extinction) during the time period  $T$ . Hence,  $N = \alpha p_0$  is the average number of extinctions per unit time:

$$N = \alpha p_0 = \frac{\alpha}{1 + \alpha(\rho + 1)}. \tag{2.8}$$

The average lifetime between extinctions is

$$\tau = \frac{T - p_0 T}{NT} = \frac{1 - p_0}{\alpha p_0} = \frac{1 + \alpha(\rho + 1) - 1}{\alpha} = 1 + \rho = 1 + \frac{\lambda}{\sigma}. \tag{2.9}$$

This value depends linearly on the birth rate and is inversely proportional to the mortality rate.

### 2.2. Two Subpopulations

The above technique can also be applied to a metapopulation. We first consider two subpopulations with exchange of individuals. Each state of such system can be

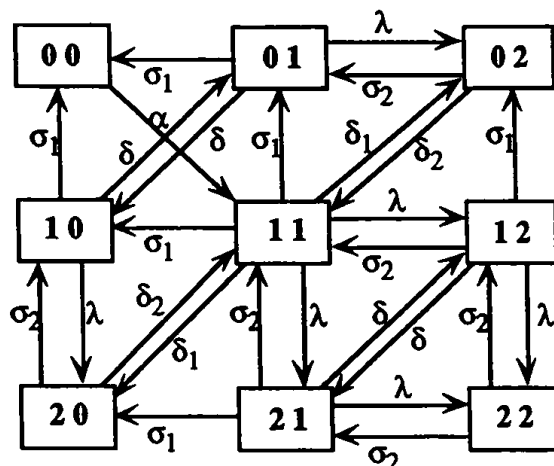


Fig. 2. Transition graph for a metapopulation consisting of two subpopulations.

described by a pair of numbers  $(i, j)$ , where  $i, j = 0, 1, 2$ . Let  $p_{ij}$  be the probability for the metapopulation to be in the state  $(i, j)$ . All possible transitions in this system are depicted in Fig. 2.

We suppose that exchanges occurring in this system affect both subpopulations and can be either independent of population density (constant diffusion rate  $\delta$ ), driving transitions like  $(1, 0) \leftrightarrow (0, 1)$  and  $(2, 1) \leftrightarrow (1, 2)$ , or be density-dependent. Transition from state  $(2, 0)$  to state  $(1, 1)$  (recolonisation of an empty patch from a densely populated one) occurs with intensity  $\delta_2$  (active dispersal or conspecific repulsion). The opposite transition from state  $(1, 1)$  to state  $(2, 0)$  has intensity  $\delta_1$  (conspecific attraction). We set  $\sigma_1 = 1$  by time scaling and instead of  $\sigma_2$  use  $\sigma = \sigma_2/\sigma_1$ .

### 2.2.1. Random Dispersal

We would like to analyse how different dispersal strategies can affect the extinction probability. First, we consider the simplest case of full symmetry and assume that only random dispersal takes place, i.e.,  $\delta_2 = \delta_1 = \delta$  is the random dispersal (diffusion) intensity. It is easy to see that  $p_{ij} = p_{ji}$  ( $i, j = 0, 1, 2$ ) in this case, and the equations simplify to:

$$\left. \begin{aligned} -\alpha q_0 + 2q_1 &= 0 \\ -(1 + \lambda)q_1 + \sigma q_2 + q_3 &= 0 \\ \lambda q_1 - (\sigma + \delta)q_2 + \delta q_3 + q_4 &= 0 \\ q_0 + 2q_1 + 2q_2 + q_3 + 2q_4 + q_5 &= 1 \\ \lambda q_3 - (1 + \sigma + \lambda)q_4 + \sigma q_5 &= 0 \\ \lambda q_4 - \sigma q_5 &= 0 \end{aligned} \right\}, \tag{2.10}$$

where  $q_0 = p_{00}$ ;  $q_1 = p_{01} = p_{10}$ ;  $q_2 = p_{02} = p_{20}$ ;  $q_3 = p_{11}$ ;  $q_4 = p_{21} = p_{12}$ ;  $q_5 = p_{22}$ .

The matrix form of these equations is

$$\begin{bmatrix} -\alpha & 2 & 0 & 0 & 0 & 0 \\ 0 & -(1 + \lambda) & \sigma & 1 & 0 & 0 \\ 0 & \lambda & -(\sigma + \delta) & \delta & 1 & 0 \\ 1 & 2 & 2 & 1 & 2 & 1 \\ 0 & 0 & 0 & \lambda & -(1 + \sigma + \lambda) & \sigma \\ 0 & 0 & 0 & 0 & \lambda & -\sigma \end{bmatrix} \begin{pmatrix} q_0 \\ q_1 \\ q_2 \\ q_3 \\ q_4 \\ q_5 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \\ 1 \\ 0 \\ 0 \end{pmatrix}. \quad (2.11)$$

Using a computer software like REDUCE [19] or Mathematica [27] for analytical computations, it is not difficult to find a vector solution  $\mathbf{q}^*$  of this system. The most interesting component of this vector is the extinction probability  $q_0$ .

Now, working analogously with the case of one population, and using the obvious formula  $q_0 = 1/(\alpha\tau + 1)$  (see 2.9), we can derive the expected time to extinction:

$$\tau = \frac{\delta(\lambda^2 + \lambda^3 + 5\sigma + 5\lambda\sigma + 2\lambda^2\sigma + 7\sigma^2 + 3\lambda\sigma^2 + 2\sigma^3) + \sigma(4\lambda + 3\lambda^2 + 3\sigma + 6\lambda\sigma + 3\sigma^2)}{2\sigma[\delta(1 + 2\sigma + \sigma^2) + \sigma(1 + \lambda + \sigma)]}. \quad (2.12)$$

Thus, the queuing theory approach enables us to derive the exact formula for  $p_{00}$  and to analyse the influence of different model parameters. First, it is easy to see that, as  $q_0$  is a ratio of linear functions of the migration activity parameter  $\delta$ , it can only increase or decrease monotonously with  $\delta$ . Since

$$q_0 \Big|_{\delta=0} = \frac{1}{\frac{\alpha(4\lambda + 3\lambda^2 + 3\sigma + 6\lambda\sigma + 3\sigma^2)}{2\sigma(1 + \lambda + \sigma)} + 1}, \quad (2.13)$$

and

$$q_0 \Big|_{\delta=\infty} = \frac{1}{\frac{\alpha(\lambda^3 + \lambda^2 + 5\sigma + 5\lambda\sigma + 2\lambda^2\sigma + 7\sigma^2 + 3\lambda\sigma^2 + 2\sigma^3)}{2\sigma(1 + 2\sigma + \sigma^2)} + 1}, \quad (2.14)$$

then, the inequality

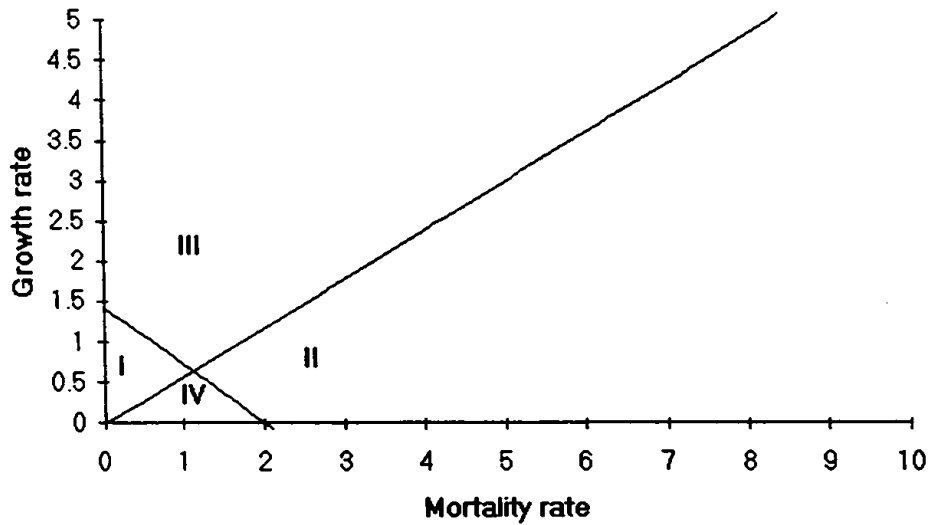
$$q_0 \Big|_{\delta=0} > q_0 \Big|_{\delta=\infty} \quad (2.15)$$

gives the condition  $\lambda^4 + 2\lambda^3 - 2\lambda^2 - 4\lambda - \sigma^4 + 3\sigma^2 + 2\sigma + 3\lambda^3\sigma + 2\lambda^2\sigma^2 + 2\lambda^2\sigma - \lambda\sigma^3 - \lambda\sigma^2 - 4\lambda\sigma > 0$ , which is equivalent to the condition

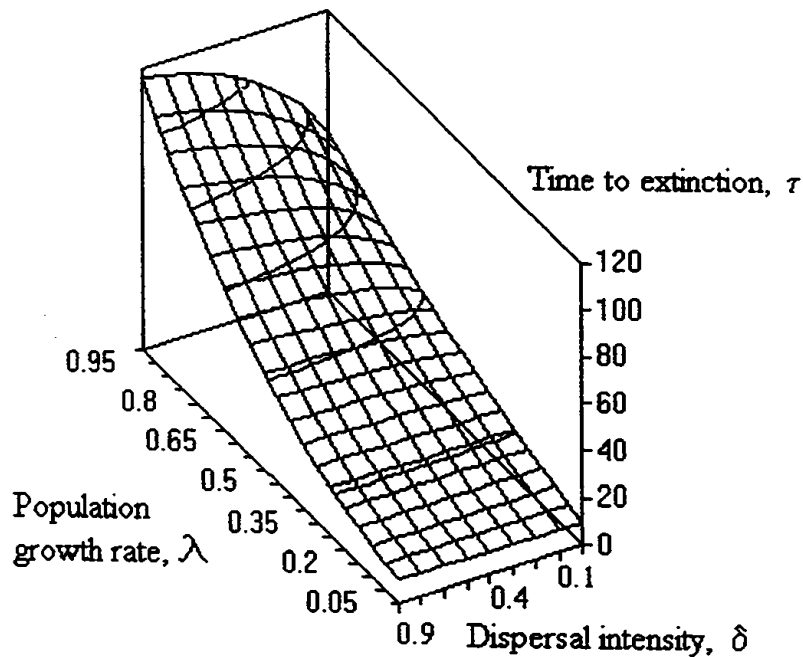
$$\left[ \lambda + \frac{1}{2} \left( 2 + \sigma - \sqrt{4 + 8\sigma + 5\sigma^2} \right) \right] (\lambda + \sigma - \sqrt{2 + \sigma}) > 0. \quad (2.16)$$

This condition is realized in regions III and IV of Fig. 3.

Thus, it has been proved analytically that random dispersal between two populations can reduce the extinction probability, if the patch conditions are favourable for population growth (e.g., if the birth rate is much higher than mortality



**Fig. 3.** Qualitative analysis of the model in the plane of parameters  $\lambda$  and  $\sigma$ . Density-independent migrations (diffusion) increase persistence of the metapopulation in regions I and II. Density-dependent migrations show different patterns: conspecific attraction increases persistence in regions I and IV, while it is conspecific repulsion (active dispersal) that increases it in regions II and III.



**Fig. 4.** Population lifetime (2.12) versus dispersal intensity  $\delta$  and population growth rate  $\lambda$ . The mortality rate is fixed ( $\sigma_1 = \sigma_2 = 0.1$ ).

(region III in Fig. 3)). This fact has been shown many times both by simulation [4, 7, 9, 10, 12, 24] and by analysing field data [14, 22, 26]. The meaning of region IV will appear more clearly when  $\delta_1 \neq \delta_2$ .

Figure 4 presents the dependence of the persistence time (2.12) graphically. Concerning  $\lambda$ , one can see a parabolic increase of  $\tau$  with increasing growth rate.



Regarding the influence of the dispersal intensity,  $\delta$ , it depends on the value of  $\lambda$ . The larger the population growth rate, the stronger is this influence. With  $\lambda = 1$  the persistence time can more than double for sufficiently high  $\delta$ .

2.2.2. Density-Dependent Migration

The case of density-dependent migrations is more complicated. In general, with different values of  $\sigma_1, \sigma_2, \delta_1$  and  $\delta_2$ , (see transition graph on Fig. 2) the same technique gives the following formula for the extinction probability (here too  $\sigma_1 = 1$  and  $\sigma_2 = \sigma$ ):

$$p_{00} = \frac{A\delta_2 + B\delta_1 + C}{D\delta_2 + F\delta_1 + E}, \tag{2.17}$$

where

$$\begin{aligned} A &= 2\sigma(1 + \sigma); \\ B &= 2\sigma^2(1 + \sigma); \\ C &= 2\sigma^2(1 + \sigma + \lambda); \\ D &= A + \alpha(3\sigma(\sigma + \lambda) + \lambda^2 + \sigma\lambda^2 + 2\sigma\lambda^2 + \lambda^3); \\ F &= B + 2\alpha(\sigma + 2\sigma^2 + \sigma\lambda + \sigma^3 + \sigma^2\lambda); \\ E &= C + \alpha(3\sigma^2 + 4\sigma\lambda + 3\sigma^3 + 6\sigma^2\lambda). \end{aligned}$$

Hence,  $p_{00}$  depends monotonously on parameters  $\alpha, \lambda, \delta_1$ , and  $\delta_2$ . The probability for the metapopulation to be in the state (0, 0) decreases with increasing values of parameters  $\alpha$  and  $\lambda$ , but the form of the response to changes of aggregation,  $\delta_1$ , and active dispersal,  $\delta_2$ , depends on the values of the parameters  $\sigma$  and  $\lambda$ .

As  $p_{00}$  is a monotonous function of  $\delta_i$ , we can find the influence of each dispersal strategy (i.e., active dispersal or aggregation) on the extinction probability. For active dispersal this condition is

$$p_{00} \Big|_{\delta_2=0} > p_{00} \Big|_{\delta_2=\infty}, \tag{2.18}$$

and for aggregation

$$p_{00} \Big|_{\delta_1=0} > p_{00} \Big|_{\delta_1=\infty}. \tag{2.19}$$

In other terms:

$$\frac{B\delta_1 + C}{F\delta_1 + E} > \frac{A}{D} \tag{2.20}$$

and

$$\frac{A\delta_2 + C}{D\delta_2 + E} > \frac{B}{F}. \tag{2.21}$$

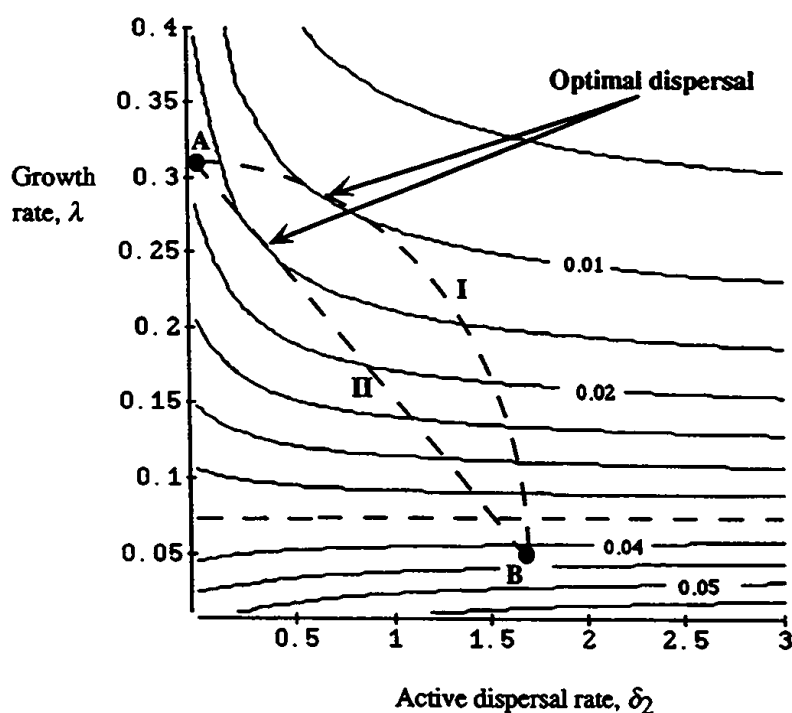
Therefore, an increase of active dispersal decreases the extinction probability if

$$DC - AE + \delta_1(DB - AF) > 0; \tag{2.22}$$

and an increase of aggregation reduces the extinction probability if

$$FC - BE + \delta_2(FA - DB) > 0. \quad (2.23)$$

As we might have presumed, the relative effect of migration activity on the extinction probability does not depend on the recolonisation parameter  $\alpha$ .



**Fig. 5.** Isopleth diagram of extinction probability versus birth rate  $\lambda$  and dispersal intensity parameter  $\delta_2$  for the two-population model ( $\sigma_1 = \sigma_2 = 0.1$ ). I and II are two possible trade-off lines with the points of highest potential growth rate (A) and highest potential dispersal rate (B) (see Sec. 3).

If both migration strategies are not present together (i.e.,  $\delta_1 = 0$  in (2.22) and  $\delta_2 = 0$  in (2.23)), conditions (2.22) and (2.23) can be simplified and it is not difficult to show that in this case they are simply mutually exclusive. If

$$\lambda > -\sigma + \sqrt{2 + \sigma}, \quad (2.24)$$

(regions II and III in Fig. 3), then it is the active dispersal strategy that minimizes the extinction probability (see Fig. 5). Otherwise (in regions I and IV), it is aggregation that increases population viability. This means that, for any mortality rate  $\sigma_2$  in the interval  $[0, 2\sigma_1)$ , there exists a threshold of the growth rate  $\lambda$  below which aggregation has a positive effect. The use of two-state occupancy models with empty and occupied patches (see [3,7]) does not lead to such result about a threshold value of local reproduction because, in these models, exchanges do not

affect the density of extant subpopulations. In two-state models, aggregation always has a negative effect on population persistence [23].

### 2.3. Three Subpopulations

Can the addition of a third subpopulation change the qualitative properties of the model? Working analogously, we consider now three subpopulations and the state of the whole metapopulation is described by three numbers  $(i, j, k)$ , where  $i, j, k = 0, 1, 2$ .

One can imagine a three-dimensional cube in which possible transitions occur. All model parameters  $\alpha, \lambda, \sigma_1, \sigma_2, \delta_1$ , and  $\delta_2$  have the same meaning as in the previous case of two subpopulations. If the system is symmetrical, all patches are connected by migration flows, and if  $p_{000} = q_0, p_{100} = p_{010} = p_{001} = q_1, p_{110} = p_{011} = p_{101} = q_2, p_{200} = p_{020} = p_{002} = q_3, p_{111} = q_4, p_{210} = p_{120} = p_{102} = p_{201} = p_{021} = p_{012} = q_5, p_{112} = p_{121} = p_{211} = q_6, p_{221} = p_{212} = p_{122} = q_7, p_{222} = q_8, p_{022} = p_{202} = p_{220} = q_9$ , we can write for the stationary condition the system of linear equations  $[\mathbf{A}]\mathbf{q} = \mathbf{e}_6$ , where  $\mathbf{e}_6 = (0, 0, 0, 0, 0, 1, 0, 0, 0, 0)^T \in R^{10}$ , and  $[\mathbf{A}]$  is the matrix

$$\begin{bmatrix} -\alpha & 3 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & -(1+\lambda) & 2 & \sigma & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & -(2+2\lambda+3\delta_1) & 3\delta_2 & 1 & 2\sigma & 0 & 0 & 0 & 0 & 0 \\ 0 & \lambda & 3\delta_1 & -(\sigma+3\delta_2) & 0 & 2 & 0 & 0 & 0 & 0 & 0 \\ \frac{\sigma}{3} & 0 & 0 & 0 & -(\lambda+1+\delta_1) & 2\delta_2 & \sigma & 0 & 0 & 0 & 0 \\ 1 & 3 & 3 & 3 & 1 & 6 & 3 & 3 & 1 & 3 & 3 \\ 0 & 0 & 0 & 0 & \lambda & 0 & -2(\lambda+1+\delta_1)-\sigma & 2\sigma & 0 & 2\delta_2 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 2\lambda & -(\lambda+2\sigma+1) & \sigma & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & \lambda & -\sigma & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 2\lambda & 2\delta_1 & 1 & 0 & -2(\sigma+\delta_2) & 0 \end{bmatrix}$$

and calculate the extinction probability  $q_0$  as a function of model parameters. This formula is too long to be presented here (the ratio of two polynomial functions of model parameters). The only difference with the two-population case above is a lower value for the extinction probability, i.e., a higher value of the persistence time  $\tau$  (see Table 1 in Sec. 3). With the same set of model parameters as in the case of two populations, we obtained numerically the switching condition between aggregation and active dispersal corresponding to the value of the population growth rate  $\lambda > -\sigma + \sqrt{2 + \sigma}$ .

### 3. Discussion

In this paper, we investigated the influence of dispersal behaviour, that is, of dispersal intensity and direction, on metapopulation dynamics. A three-state model for local populations was used. It seems to provide a suitable compromise between a two-state patch occupancy model and a continuous density model. The application of queuing theory methods made it possible to obtain analytical formulas for extinction probabilities and persistence time.

**Table 1.** Time to extinction for different parameter values and migration strategies for models for two subpopulations and for three subpopulations. Mortality parameters are fixed at  $\sigma_1 = \sigma_2 = 0.1$ .

Comment	Strategy	$\delta_1$	$\delta_2$	Two pops	Three pops
High population growth ( $\lambda = 0.5$ );	No migration	0.0	0.0	93.57	116.34
Active dispersal is favourable.	Diffusion	0.1	0.1	175.00	628.23
	Active dispersal	0.0	0.1	198.33	883.69
	Aggregation	0.1	0.0	88.00	106.60
Low population growth ( $\lambda = 0.01$ );	No migration	0.0	0.0	16.74	20.66
Aggregation is favourable.	Diffusion	0.1	0.1	17.92	22.02
	Active dispersal	0.0	0.1	16.42	19.95
	Aggregation	0.1	0.0	18.82	24.23

The analytical formulas greatly facilitate the analysis of parameter influence. For instance, in [12] the authors, using simulation experiments only, failed to find the conditions for which conspecific attraction increases metapopulation viability, while this was obtained in the present paper. This result differs from patch occupancy model in which emigration does not affect the density of the source patch.

The conclusion that, due to the rescue effect, dispersal can increase metapopulation viability in a stochastic environment, agrees with experimental and field data [14]. However, this is trivial unless we take into account that dispersal should be “paid for” either by increased mortality or by reduced growth. Incorporating into the model a trade-off between mobility and local kinetics should provide an optimal dispersal value minimising the extinction probability. Two possible trade-offs between the active dispersal intensity,  $\delta_2$ , and the growth rate,  $\lambda$ , are superimposed on Fig. 5 over the isopleths of constant extinction probability. Unfortunately, we have not been able to find observed data about these relationships, either within a species or within a taxon. The simplest relationship is the linear one (broken line II). A more realistic case is the convex curve I. Convexity implies an accelerating decrease of the growth rate with an increasing dispersal rate, since individuals must apply the trade-off for increasing their mobility. In both cases I and II, one can see that viability increases when moving along the trade-off line away from the extreme points A and B. It reaches its maximum at the point where an extinction probability isopleth is tangent to the trade-off curve I or II.

The analysis of directional dispersals gives more complicated results. The influences of both active dispersal and conspecific attraction are ambiguous. While with high values of growth and mortality, active dispersal (i.e., the tendency to occupy empty patches) increases viability, it becomes harmful in a population with slow kinetics. The situation with conspecific attraction is the reverse. Formula (2.24) defines a curve separating the two cases (Fig. 3): on one side of the curve, it is conspecific attraction that maximizes viability, while it is active dispersal on the opposite side.

The biological interpretation of this result may be a differentiation of species into two categories: one with fast kinetics and tendency to active dispersal, and a second one with low growth and mortality rates and with a tendency to conspecific attraction, and hence with a lower capability of occupying new habitats. Species of the first type should be abundant and ubiquitous. Following the classification of Hanski [17], they are referred to as “core species”, while species of the second type are termed as “satellite species”.

In the case of three subpopulations, these results do not change qualitatively, but an increase in the number of subpopulations increases the persistence time of the metapopulation. Some figures are given in Table 1. They confirm the ambiguity of the role of aggregation: while at high growth and mortality rates  $\lambda$  and  $\sigma$  (regions II and III in Fig. 3) conspecific attraction reduces persistence time  $\tau$  considerably, it increases  $\tau$  at low  $\lambda$  and  $\sigma$  (regions I and IV in Fig. 3).

In this paper, we did not consider the evolutionary stability of dispersal behaviour patterns, i.e., how could certain patterns, say, conspecific attraction or density-dependent dispersal, evolve and be fixed evolutionary. It is possible that an evolutionary stable dispersal strategy will not minimize the extinction risk.

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