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SPÉCIALITÉ :   BIOLOGIE DES POPULATIONS ET ÉCOLOGIE
FORMATION DOCTORALE :   Évolution et Écologie
ÉCOLE DOCTORALE :   Biologie des systèmes intégrés, Agronomie, Environnement

Démographie animale
et biologie des populations
modélisation et applications à la gestion d'espèces sauvages

par

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Soutenue le 27 octobre 1994 devant le Jury composé de :

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$$\begin{bmatrix} 0 & (1-m_1)f_1 & 0 & m_2f_2 \\ s_1 & s_1 & 0 & 0 \\ 0 & m_1f_1 & 0 & (1-m_2)f_2 \\ 0 & 0 & s_2 & s_2 \end{bmatrix}$$

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Modèle matriciel type Leslie
pour métapopulations
simulation d'un système « source–puits »

Récemment, les modèles des populations demeurant dans des habitats fragmentés ont acquis une importance biologique majeure. En effet, d'une part la fragmentation des habitats naturels à la suite des activités humaines est un processus croissant. De nombreuses populations précédemment unitaires sont devenues des ensembles de populations locales de taille plus réduite. D'autre part, les espèces sont toujours constituées en populations (sauf certaines espèces endémiques), plus ou moins ouvertes au flux de gènes de leurs semblables. Il existe donc un grand intérêt pour la phénomènologie des métapopulations (Hanski & Gilpin 1991).

On retrouve le début de cette tradition de modélisation dans le concept de « voisinage » de Wright (1931) et son « modèle en îles » –un ensemble de populations locales interchangeant de façon aléatoire des gènes entre elles. Le concept de métapopulation était déjà présent d'une certaine façon dans le modèle de la « niche » écologique habitée par des populations locales

$$\begin{bmatrix} 0 & (1-m_1)f_1 & 0 & m_2f_2 \\ s_1 & s_1 & 0 & 0 \\ 0 & m_1f_1 & 0 & (1-m_2)f_2 \\ 0 & 0 & s_2 & s_2 \end{bmatrix}$$

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constituant « dèmes », de Levene (1953). Dans cette époque, des écologues comme Kluyver et Tinbergen (1953) discutent le rôle régulateur de la territorialité sur la densité des passereaux et le généticien Kimura (1953) explique les variations de fréquences géniques à l'aide du concept de voisinage dans son modèle « stepping stone » –modèle en îles réduit au flux de migrants uniquement entre les populations directement voisines.

Un peu plus tard, ce sont les biogéographes qui ont continué à développer le concept de métapopulation avec le modèle « île–continent » de MacArthur & Wilson (1967), dans lequel la migration est unidirectionnelle, provenant d'un population continentale considérée inépuisable vers des populations isolées installées dans des îles, où l'extinction totale est évitée seulement si l'immigration est continue. D'autres écologues de populations discutent le rôle de la dispersion dans la dynamique de populations (Lidicker 1975), notamment son effet stabilisateur ou *buffer effect* (Brown 1969).

Une nouvelle version du modèle de MacArthur & Wilson est le récent modèle « source–puits » de Pulliam (1988, Pulliam & Danielson 1991), dans lequel la population « source » n'est pas nécessairement inépuisable (ni de plus grande taille, comme on le montrera au cours du présent Chapitre) et la population « puits » n'est pas nécessairement dans une île (ni de plus petite taille). Morris (1991) montre qu'il est possible d'interpréter la colonisation des habitats « puits » comme une stratégie de dispersion évolutivement stable (ESS) uniquement si la migration est bidirectionnelle.

Le terme de *métapopulation* est proposé par Levins (1970) pour décrire une « population de populations ». Le modèle de Levins suppose que le taux de migration doit être supérieur au taux d'extinction locale pour maintenir une fraction des habitats disponibles occupés. Jusqu'ici, les modèles ne tiennent pas compte des différences de taille, ni des taux de migration et d'extinction entre les dèmes, ni de leurs structures internes, ni de la qualité ou structure des habitats (*patches*) occupés. C'est alors que les chercheurs étudiant des métapopulations se sont penché à développer des modèles considérant l'une ou l'autre de ces caractéristiques (Lande 1987, Söderström 1989, Hanski 1982, 1991, Hastings 1991), ou même à introduire la stochasticité (Verboom *et al.* 1991). Cependant, la grande intégration reste à faire.

Ayant opté pour les modèles en temps discret, le concept de métapopulation nous offre l'occasion de montrer que dans ce cas ils sont aussi les plus souples, tant sur le plan théorique que pratique. Nous montrerons comment intégrer dans la matrice de Leslie plusieurs

$$\begin{bmatrix} 0 & (1-m_1)f_1 & 0 & m_2f_2 \\ s_1 & s_1 & 0 & 0 \\ 0 & m_1f_1 & 0 & (1-m_1)f_2 \\ 0 & 0 & s_2 & s_2 \end{bmatrix}$$

populations, la migration, des différents taux de multiplication pour chaque population locale, et la dépendance de la densité. Les résultats de la matrice ainsi configurée expriment l'équilibre global du système, avec le taux de multiplication de l'ensemble des populations locales, et la structure asymptotiquement stable entre populations locales et à l'intérieur de chacune d'elles. Le résultat central consiste à montrer, par simulation, l'effet stabilisateur de la migration sur un système métapopulation, malgré la situation de déséquilibre que peuvent présenter les populations locales. Il est vrai cependant que, dans un système « source–puits », si au lieu de faire intervenir l'émigration d'une population excédentaire vers une autre déficitaire on fait intervenir une mortalité indépendante de la densité plus élevée dans la population « source », le résultat, pour elle, serait le même en termes de l'équilibre démographique qu'elle atteindrait. Mais l'intérêt est d'observer le résultat du système, y compris l'équilibre atteint par les populations qui jouent le rôle de « puits ». Et bien entendu, si l'on s'intéressait à une étude évolutive, il faudrait tenir compte aussi de l'émigration des populations « puits » vers les « sources » pour pouvoir expliquer le rôle de la dispersion comme une stratégie évolutivement stable (Morris 1991).

$$\begin{bmatrix} 0 & (1-m_1)f_1 & 0 & m_2f_2 \\ s_1 & s_1 & 0 & 0 \\ 0 & m_1f_1 & 0 & (1-m_2)f_2 \\ 0 & 0 & s_2 & s_2 \end{bmatrix}$$

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$$\begin{bmatrix} 0 & (1-m_1)f_1 & 0 & m_2 f_2 \\ s_1 & s_1 & 0 & 0 \\ 0 & m_1 f_1 & 0 & (1-m_2)f_2 \\ 0 & 0 & s_2 & s_2 \end{bmatrix}$$

AN INTRODUCTION TO MODELS OF SUBDIVIDED POPULATIONS

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ABSTRACT

Models concerning populations living in fragmented habitats are of increasing biological interest. As a consequence, there is a growing interest in metapopulation models and source-sink models. In this paper we introduce elementary discrete-time matrix models for subdivided populations. We discuss the stabilizing role played by migration, in particular in the presence of strong rates of increase and of population structures (e.g., age). Although the emphasis is on demography, we expect applications in evolutionary biology. Another hope is to provide basis to graduate students, with emphasis on the philosophy of model building and use rather than on mathematical difficulties.

Keywords: Population dynamics, source-sink models, metapopulation models, matrix population models, migration, population regulation.

1. Introduction

The literature concerning population dynamics models is very large and diverse. This is in particular the case for models concerning "subdivided populations", although the biological interest in the subject has been fairly recent. The biological questions addressed with such models deal with the emergence of the metapopulation concept [55,14,52,32,69,11,33,28] and the consequences of habitat fragmentation [51,18,17,68].

From the demographical and genetical points of view, migration plays a main role in subdivided population dynamics (e.g., [2,4,21,38,6,23,29,36,31,16,1,34,13]). Models of migration embedded in a *density-independent* growth process have been particularly proposed by Lefkovitch [47], Rogers [66], Usher and Williamson [75] and Lebras [43]. Such models have been considered in a stochastic context, both in continuous [5,37] and discrete time [3,76].

On the other hand, following the classical logistic growth models (from [77], and for present state of discussion see [72,24–26,59,73]), *density-dependent* models were developed in innumerable ways (for density-dependent *matrix* models e.g., [50], and many authors for density-dependent *continuous-time* models). In particular

$$\begin{bmatrix} 0 & (1-m_1)f_1 & 0 & m_2f_2 \\ s_1 & s_1 & 0 & 0 \\ 0 & m_1f_1 & 0 & (1-m_2)f_2 \\ 0 & 0 & s_2 & s_2 \end{bmatrix}$$

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discrete-time density-dependent models have retained a lot of attention because of their diversity of behaviour (e.g. [56,70]).

Population biologists have linked very early regulation and dispersal [39,8,54]. However, most often (and this has been emphasized by e.g., [60,61]), *density-dependent* models including a *dispersal* component have rarely been considered until recently (e.g., [67]). If so, they have been treated in an *ad hoc* way, with a strong emphasis on simulation (e.g., [27]), while mathematical approaches (e.g., [42]) are technically difficult.

Our goal in this paper is to present some basic results on models for subdivided populations in a simple and progressive framework. We will try not to depart from the principle of "economy of hypotheses", which seems to us particularly important in such a pluridisciplinary endeavour, to reach conclusions based on minimal assumptions.

Our hope is to provide guidelines for a better assessment of the literature which seems to us extremely vast and confusing. Another hope is that this text could serve for lectures for graduate students, with an emphasis on the philosophy of model building and use rather than on mathematical difficulties. This is why we restrict our attention to discrete time models. Many authors have firmly underlined that discrete-time population models are worth *per se* [35,45,15,30,10]. We also include in an appendix instructions to do the calculations involved, using program ULM [46].

2. A Simple Model

2.1. *A Simple Growth Model*

We consider two populations with $N_1(t)$ and $N_2(t)$ individuals at time t. Each population is supposed to grow in a density-independent way, with respective multiplication rates a and b

$$N_1(t) = aN_1(t-1)$$
$$N_2(t) = bN_2(t-1)$$

(2.1)

These equations can be easily expressed in a matrix fashion:

$$\begin{bmatrix} N_1(t) \\ N_2(t) \end{bmatrix} = \begin{bmatrix} a & 0 \\ 0 & b \end{bmatrix} \begin{bmatrix} N_1(t-1) \\ N_2(t-1) \end{bmatrix}$$

$$\mathbf{N}(t) = \begin{bmatrix} a & 0 \\ 0 & b \end{bmatrix} \mathbf{N}(t-1)$$

(2.2)

$$\mathbf{N}(t) = \mathbf{C}\mathbf{N}(t-1)$$

This matrix formulation is clearly analogous to a multiplication by a *constant*. This underlines the absence of any regulation. One can see this model of simultaneous growth as a simplistic model for two non-connected populations, with no age-structure. Each population grows geometrically and increases to infinity if a

$$\begin{bmatrix} 0 & (1-m_1)f_1 & 0 & m_2 f_2 \\ s_1 & s_1 & 0 & 0 \\ 0 & m_1 f_1 & 0 & (1-m_2)f_2 \\ 0 & 0 & s_2 & s_2 \end{bmatrix}$$

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and $b > 1$; according to $N_1(t) = a^t N_1(0)$, $N_2(t) = b^t N_2(0)$, or in a matrix manner: $\mathbf{N}(t) = \mathbf{C}^t \mathbf{N}(0)$. We may consider also that one population increases while the other one decreases, i.e., $a > 1$ but $b < 1$. This last case constitutes a first simple model of population growth in a heterogeneous environment.

2.2 *A Simple Migration Model*

Consider now two populations with constant numbers and migration between them. We denote as p and q the proportion of individuals staying in populations 1 and 2, respectively, at each time step. Thus, between $t - 1$ and t:

$$N_1(t) = pN_1(t - 1) + (1 - q)N_2(t - 1)$$
$$N_2(t) = (1 - p)N_1(t - 1) + qN_2(t - 1) \tag{2.3}$$

or, in matrix notation:

$$\begin{bmatrix} N_1(t) \\ N_2(t) \end{bmatrix} = \begin{bmatrix} p & 1 - q \\ 1 - p & q \end{bmatrix} \begin{bmatrix} N_1(t - 1) \\ N_2(t - 1) \end{bmatrix}$$

$$\mathbf{N}(t) = \begin{bmatrix} p & 1 - q \\ 1 - q & q \end{bmatrix} \mathbf{N}(t - 1) \tag{2.4}$$

$$\mathbf{N}(t) = \mathbf{M}\mathbf{N}(t - 1)$$

It is easy to check, by adding the two equations in (2.3) that the total number of individuals does not change over time.

Thus, the behaviour of the model can be summarized by the variation of the ratio $U_1(t) = N_1(t)/(N_1(t) + N_2(t))$, as a function of the original ratio $U_1(0) = N_1(0)/(N_1(0) + N_2(0))$. Matrix algebra leads to (e.g., [3] p. 53):

$$U_1(t) = \frac{1 - q}{(1 - p) + (1 - q)} - \frac{(p + q - 1)^t}{(1 - p) + (1 - q)}((1 - q)[1 - U_1(0)] - (1 - p)[U_1(0)]) , \tag{2.5}$$
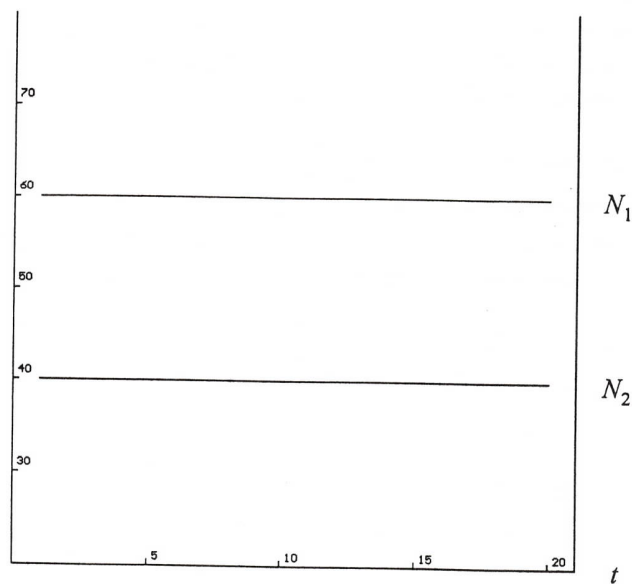
hence $\lim_{t \to \infty} U_1(t) = \frac{1-q}{(1-p)+(1-q)} = U_1(\infty)$, the convergence to this value is damped according to $m = p + q - 1$, which varies between -1 ($p = q = 0$) and 1 ($p = q = 1$). When m varies from -1 to 1, the overall proportion of individuals moving varies from 100 % to 0 %. Hence, m measures the intensity of migration in the system. Since Eq. (2.5) reduces to $U_1(t) = U_1(\infty) + m^t Z$, the sign of m determines the type of convergence to $U_1(\infty)$.

If $m < 0$ (strong migration), the equilibrium is reached by damped oscillations; if $m > 0$ (weak migration), there are no oscillations; and if $m = 0$ there is an immediate convergence to $U_1(\infty)$. Figure 1 summarizes the possible behaviours of this model.
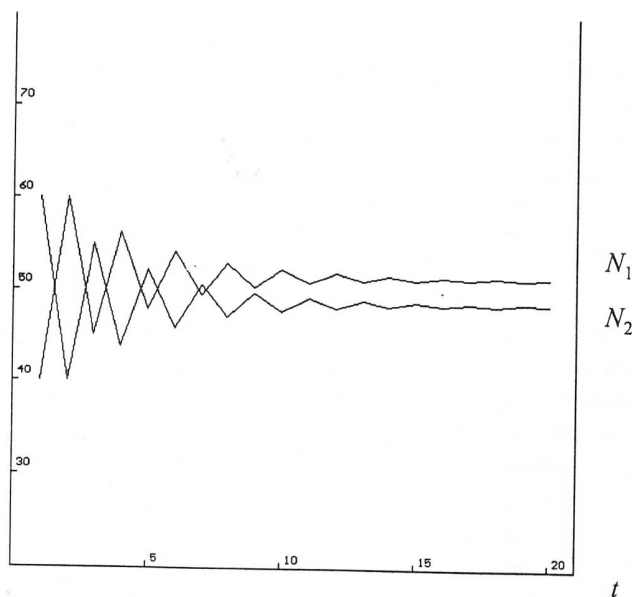
The model can be seen from the probabilistic point of view, p and q being then interpreted as probabilities of presence, $1 - p$ and $1 - q$ as probabilities of migration. It constitutes a simple Markov chain.

$$\begin{bmatrix} 0 & (1-m_1)f_1 & 0 & m_2f_2 \\ s_1 & s_1 & 0 & 0 \\ 0 & m_1f_1 & 0 & (1-m_2)f_2 \\ 0 & 0 & s_2 & s_2 \end{bmatrix}$$

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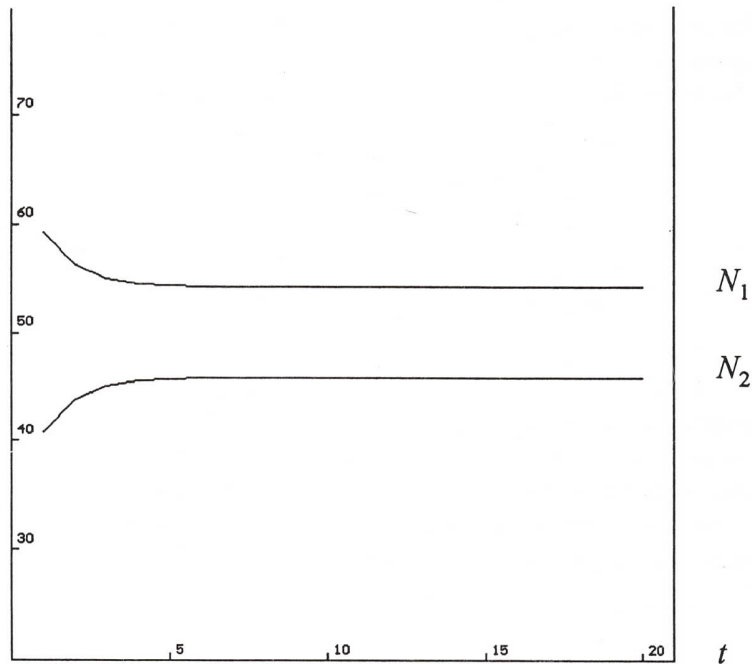**392** *Lebreton & Gonzalez-Davila*

(a)

(b)

Fig. 1. Behaviour of $N_1(t)$ and $N_2(t)$ in relation with m value; $N_1(0) = 66.67$ and $N_2(0) = 33.33$. (a) immediate stability: $p = 0.6, q = 0.4$, then $m = 0$; (b) oscillations toward stability: $p = 0.15$, $q = 0.1$, then $m < 0$; (c) no oscillations toward stability: $p = 0.725, q = 0.675$, then $m > 0$.

$$\begin{bmatrix} 0 & (1-m_1)f_1 & 0 & m_2f_2 \\ s_1 & s_1 & 0 & 0 \\ 0 & m_1f_1 & 0 & (1-m_2)f_2 \\ 0 & 0 & s_2 & s_2 \end{bmatrix}$$

(c)

Fig. 1. (*Continued*)

This model can be easily extended to n-sites. In particular, one may consider movements restricted to neighbouring sites. Mathematicians will speak of "random walk" models ([3], ch. IV, pp. 24–37,[4]), biologists of "stepping stone" models [75,63]. When such a random walk occurs on a line, the transition matrix will have elements only on the three principal diagonals, each column summing up to unity:

$$\mathbf{M}_n = \begin{bmatrix} p & (1-p)/2 & 0 & \ldots & 0 \\ 1-p & p & (1-p)/2 & 0 & \ldots \\ 0 & (1-p)/2 & p & \ldots & 0 \\ \ldots & 0 & (1-p)/2 & \ldots & 1-p \\ \ldots & \ldots & 0 & \ldots & p \end{bmatrix} \qquad (2.6)$$

Such models have been considered in population genetics [58].

$$\begin{bmatrix} 0 & (1-m_1)f_1 & 0 & m_2 f_2 \\ s_1 & s_1 & 0 & 0 \\ 0 & m_1 f_1 & 0 & (1-m_2)f_2 \\ 0 & 0 & s_2 & s_2 \end{bmatrix}$$

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2.3. *A Simple Growth and Migration Model*

2.3.1. *"Coupling" Growth and Migration*

We will now link the two previous models. We consider that, between $t-1$ and t, the two populations are submitted to growth and then to migration. By substitution of the linear equations (2.2) and (2.4), or directly by matrix calculus, one gets

$$\begin{bmatrix} N_1(t) \\ N_2(t) \end{bmatrix} = \begin{bmatrix} p & 1-q \\ 1-p & q \end{bmatrix} \begin{bmatrix} a & 0 \\ 0 & b \end{bmatrix} \begin{bmatrix} N_1(t-1) \\ N_2(t-1) \end{bmatrix}$$

$$\mathbf{N}(t) = \mathbf{MCN}(t-1)$$

$$\begin{bmatrix} N_1(t) \\ N_2(t) \end{bmatrix} = \begin{bmatrix} ap & b(1-q) \\ a(1-p) & bq \end{bmatrix} \begin{bmatrix} N_1(t-1) \\ N_2(t-1) \end{bmatrix}$$

$$\mathbf{N}(t) = \mathbf{GN}(t-1) \tag{2.7}$$

MC and **CM** have the same eigenvalues and, thus, will lead to the same results in terms of growth rate, so there is no problem in considering growth first and then migration, rather than migration first and then growth. The study of matrix **G** will allow us to understand the behaviour of a two populations system, with growth and migration. The characteristic polynomial of matrix **G** is:

$$\lambda^2 - (ap + bq)\lambda + abm = 0 \tag{2.8}$$

where $m = p + q - 1$ as before, measures the intensity of migration.

The greatest root of the characteristic polynomial is the greatest eigenvalue of matrix **G**. It measures the asymptotic multiplication rate of the system, since $\mathbf{N}(t) \to \lambda \mathbf{N}(t-1)$ if $t \to \infty$. Solving (2.8) gives:

$$\lambda = \frac{(ap + bq) \pm \sqrt{(ap + bq)^2 - 4abm}}{2} \tag{2.9}$$

where $m > 0$ or $m < 0$ determines which of the two roots of Eq. (2.9) is the greatest one.

If $a = b$, the multiplication rate λ becomes equal to a, as it can be obtained from Eq. (2.9).

$$\lambda = a\frac{(p + q) \pm \sqrt{(p + q - 2)^2}}{2} = a \tag{2.10}$$

If $p + q = 1$, m becomes equal to zero, the multiplication rate reduces to $ap + bq$. This means that the system grows at a rate intermediate between a and $b : b < \lambda < a$ if $b < a$ and $a < \lambda < b$ if $a < b$.

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$$\begin{bmatrix} 0 & (1-m_1)f_1 & 0 & m_2f_2 \\ s_1 & s_1 & 0 & 0 \\ 0 & m_1f_1 & 0 & (1-m_2)f_2 \\ 0 & 0 & s_2 & s_2 \end{bmatrix}$$

2.3.2. *A Simple Model in Heterogeneous Environment*

A relevant case is when $b < 1 < a$ and $p < q = 1$. Population 1 has a surplus ($a > 1$) and exports individuals (at rate $1-p$) to population 2. Population 2 shows a negative balance and does not contribute migrants to population 1. Although this can be irrelevant in an evolutionary perspective, it may be a reasonable approximation from the demographic point of view. Thus, $m = p$ and

$$\lambda = \frac{ap + b \pm \sqrt{(ap+b)^2 - 4abp}}{2} = \frac{ap + b \pm \sqrt{(ap-b)^2}}{2}$$

$$= \sup[ap, b] \tag{2.11}$$

The latter expresses that migrants to population 2 "acquire" the multiplication rate $b < 1$. If they are too many migrants, i.e., $p < 1/a$, then $ap < 1$; therefore, the numbers decreases globally at a rate always bigger than b. On the contrary, if there are not many migrants to population 2, i.e. $p > 1/a$, then $ap > 1$; therefore, population 2 receives an exponentially growing number of immigrants and the system increases at the same asymptotic rate in both populations notwithstanding that $b < 1$. Generally, there will be an intermediate "coupled" growth rate, between the values of the "uncoupled" growth rates.

This simple growth-and-migration model is a model of the dynamics of a subdivided population in a heterogeneous environment, or in the terminology of Pulliam [60], a source-sink model.

3. Introducing Density Dependence

3.1. *Density Dependence for One Population*

A straightforward *density-dependent* model (DDM) for each population can be written as

$$N_i(t) = a_i(N_i(t-1)) \times N_i(t-1) \qquad i = 1, 2, \ldots \tag{3.1}$$

$a_i(N_i(t-1))$ is the density dependent multiplication rate of population i. For the sake of realism $a_i(x)$ must be a decreasing positive function, for example

$$\exp[r_i(1 - N_i(t)/K_i)] . \tag{3.2}$$

This model is one of the well known discrete time logistic growth models [65,57,40]. Its behaviour is close to $\exp[r_i t]N_i(0)$ for small $N_i(0)$, and, at least for small r_i, $N_i(t)$ grows in a sigmoid way up to an asymptotic level K_i.

$$\begin{bmatrix} 0 & (1-m_1)f_1 & 0 & m_2f_2 \\ s_1 & s_1 & 0 & 0 \\ 0 & m_1f_1 & 0 & (1-m_2)f_2 \\ 0 & 0 & s_2 & s_2 \end{bmatrix}$$

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3.2. *Migration and Density Dependent Growth*

A straightforward way of coupling *density-dependent* growth with migration, from Eqs. (2.7) and (3.2), is:

$$\begin{bmatrix} N_1(t) \\ N_2(t) \end{bmatrix} = \begin{bmatrix} a(N_1(t-1))p & b(N_2(t-1))(1-q) \\ a(N_1(t-1))(1-p) & b(N_2(t-1))q \end{bmatrix} \begin{bmatrix} N_1(t-1) \\ N_2(t-1) \end{bmatrix} \qquad (3.3)$$

or

$$\mathbf{N}(t) = \mathbf{D}(N_1(t-1), N_2(t-1))\mathbf{N}(t-1)$$

The four terms in the matrix become decreasing functions of one or another population size. The same type of model would be obtained with a *density-dependent* migration: q function of N_2, p function of N_1. Thus, under growth *or* growth and migration *density-dependent* functions, the behaviour of the whole system will be similar, excepting little differences in the structure of the models that will affect their second order behaviour. *Density-dependence* in migration *only*, is unable to stabilize the system (Clobert, pers.comm.).

Coming back to the subdivided-population-in-a-heterogeneous-environment model of Eq. (2.11), let us consider *density-dependence* in population 1 only. Hence, $b(N_2) = b$, i.e., no *density-dependence* in decreasing population 2, with absolute philopatry $q = 1$. This is a slightly more sophisticated source-sink model. Population 2 shows a negative balance because it inhabits an unfavourable environment. If such a sink population is small compared to the source populations, the fact that it does not send out migrants can be acceptable as long as questions about natural selection of a philopatry-dispersion equilibrium are not of concern [58]. The present condition of the Blue tit *Parus caeruleus* populations inhabiting evergreen oak forests in the south of France (Blondel unpublished, [12]), provides a good case for the application of this model.

Under the simple hypotheses above, Eq. (3.3) reduces to

$$\begin{bmatrix} N_1(t) \\ N_2(t) \end{bmatrix} = \begin{bmatrix} a[N_1(t-1)]p & 0 \\ a[N_1(t-1)](1-p) & b \end{bmatrix} \begin{bmatrix} N_1(t-1) \\ N_2(t-1) \end{bmatrix} \qquad (3.4)$$

where $a(x)$ is, for instance, $\exp[r(1 - N_1(t)/K_1]$, as in Eq. (3.2). In the uncoupled condition ($p = 1$) this model leads population 1 to the equilibrium K_1 and population 2 to $K_2 = 0$, i.e., to extinction.

3.3. *Numerical Study of the Density Dependent Source-Sink Model (DDSSM)*

We consider the source-sink system described by Eqs. (3.4) and (3.2), with $p = 0.9, q = 1, r = 0.7, b = 0.8$ and $K_1 = 100$. The conjugated effects of *density-*

$$\begin{bmatrix} 0 & (1-m_1)f_1 & 0 & m_2f_2 \\ s_1 & s_1 & 0 & 0 \\ 0 & m_1f_1 & 0 & (1-m_2)f_2 \\ 0 & 0 & s_2 & s_2 \end{bmatrix}$$

dependent-regulation and migration stabilise the size of population 1 to a level below K_1. The surplus of population 1, constantly exported, induces a stable size of population 2 in spite of its negative balance. This model perfectly reproduces the *buffer effect*, proposed by Brown in 1969, that may be considered as a landmark in the development of the source-sink population concept. We have

$$\begin{bmatrix} N_1(t) \\ N_2(t) \end{bmatrix} = \begin{bmatrix} \exp(r(1 - N_1(t-1)/K_1))p & 0 \\ \exp(r(1 - N_1(t-1)/K_1))(1-p) & b \end{bmatrix} \begin{bmatrix} N_1(t-1) \\ N_2(t-1) \end{bmatrix}$$

$$= \begin{bmatrix} \exp(0.7(1 - N_1(t-1)/100))0.9 & 0 \\ \exp(0.7(1 - N_1(t-1)/100))0.1 & 0.8 \end{bmatrix} \begin{bmatrix} N_1(t-1) \\ N_2(t-1) \end{bmatrix} \tag{3.5}$$

The numerical results of this model are given in Fig. 2. Coupling the two populations prevents extinction of population 2. Although the asymptotic value of population 1 is decreased to below 85, the total numbers at equilibrium is near to over 132.
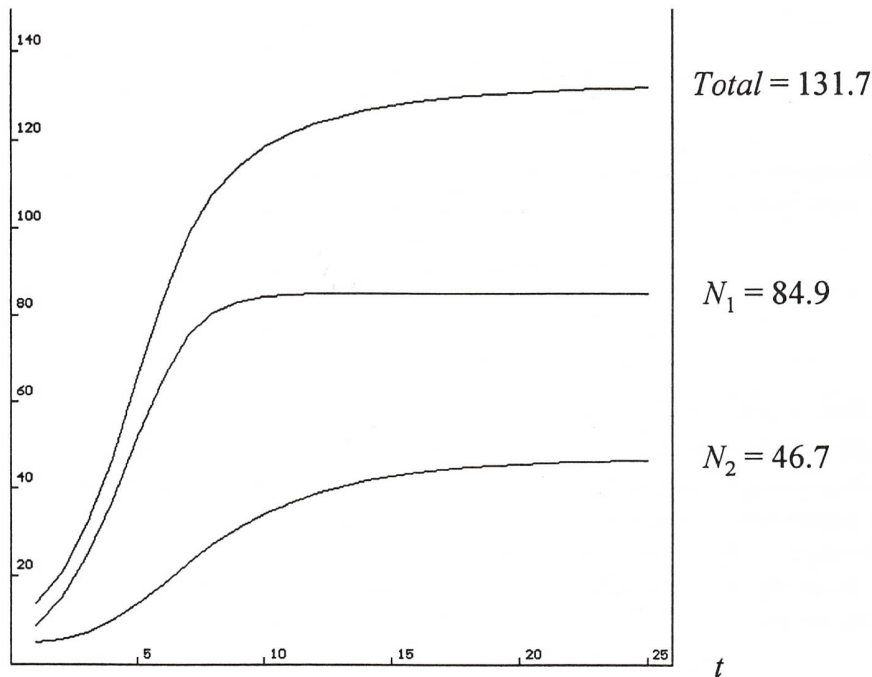

Fig. 2. Elementary behaviour of a source-sink metapopulation system, with density-dependent growth and migration values as described by Eq. (3.5) "Source" population N_1 diminishes its asymptotic limit from 100 above 80 meanwhile "sink" population N_2 saves itself of extinction, and the total metapopulation size increases up to $132 > K_1$.

$$\begin{bmatrix} 0 & (1-m_1)f_1 & 0 & m_2 f_2 \\ s_1 & s_1 & 0 & 0 \\ 0 & m_1 f_1 & 0 & (1-m_2)f_2 \\ 0 & 0 & s_2 & s_2 \end{bmatrix}$$

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3.4. *A Formal Study of DDSSM*

The uncoupled (i.e., when $p = q = 1$) equilibrium of the two populations system is simply: $[K_1, 0] = [100, 0]$. The coupled equilibrium is obtained from the system

$$N_1^* = pa(N_1^*)N_1^* \qquad \text{and}$$
$$N_2^* = bN_2^* + (1-p)a(N_1^*)N_1^* \tag{3.6}$$

in which N_1^* and N_2^* are $N_1(t^*)$ and $N_2(t^*)$ respectively, at *equilibrium time t^**, when they do not change anymore. The first equation yields:

$$1 = pa(N_1^*)$$

$$= \exp(\ln p)\exp\left(r\left(1 - \frac{N_1^*}{K_1}\right)\right)$$

$$= \exp\left(r + \ln p - N_1^*\left(\frac{r}{K_1}\right)\right)$$

$$= \exp\left((r + \ln p)\left(1 - \frac{N_1^*}{K_1\left(1 + \frac{\ln p}{r}\right)}\right)\right) \tag{3.7}$$

This expression is identical to that one of the uncoupled condition but with r and K_1 replaced respectively by r^* and K_1^* according to

$$r^* = r + \ln p \quad \text{and}$$
$$K_1^* = K_1\left(1 + \frac{\ln p}{r}\right) = N_1^* < K_1 \tag{3.8}$$

In fact, as noted by JL Gouzé (pers. comm.), population 1 behaves according to $N_1(t) = N_1(t-1)\exp\left(r^*\left(1 - \frac{N_1(t-1)}{K_1^*}\right)\right)$; $r^* = r + \ln p$ shows that the rate $\ln p < 0$ corresponding to migration and removed from r, plays the role of an extra-mortality for population 1. When $p < 1/a(0) = e^{-r}, r^* < 0$ and $K_1^* \approx 0$, so that population 1 is eaten out by its migration rate to population 2.

From the second *equilibrium* Eq. (3.6), and taking in account Eqs. (3.7) and (3.8), we get

$$(1-b)N_2^* = (1-p)a(N_1^*)N_1^*$$

$$N_2^* = \frac{(1-p)}{(1-b)}\frac{K_1^*}{p}$$

$$= \frac{1-p}{p(1-b)}\left(1 + \frac{\ln p}{r}\right)K_1 \tag{3.9}$$

which can be denoted as K_2^*.

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$$\begin{bmatrix} 0 & (1-m_1)f_1 & 0 & m_2 f_2 \\ s_1 & s_1 & 0 & 0 \\ 0 & m_1 f_1 & 0 & (1-m_2)f_2 \\ 0 & 0 & s_2 & s_2 \end{bmatrix}$$

For population 2, immigration always implies an asymptotic size K_2^* greater than under the uncoupled condition where $K_2 = 0$.

We reach thus the following **conclusions. First:** contrary to the uncoupled condition, in density regulated metapopulations, migration from good toward bad habitats induces a "buffered" *equilibrium*. It is very interesting to observe that the total population size at *equilibrium* $N_1^* + N_2^*$ varies with migration intensity $1 - p$ and may exceed K_1, notwithstanding that the "carrying capacity" $[K_1, 0]$, prevailing in the uncoupled condition, has not changed. Thus, it exists an optimal migration value in relation to the total population size. The maximum of $(N_1^* + N_2^*)$ as a function of p, is obtained explicitly locating iteratively the point where the first derivative of this function equals zero, i.e., for $p_{opt} = 0.744239\ldots$. To this p_{opt} corresponds a total *equilibrium* population size of $[N_1^* + N_2^*]_{opt} = 157.118816$ (Fig. 3).

Second: there is a paradox, similar to those of seasonal environment models [19,44], in the sense that the *equilibrium* levels of populations cannot be simply interpreted as "carrying capacities" of the environment [59,24–26,73].
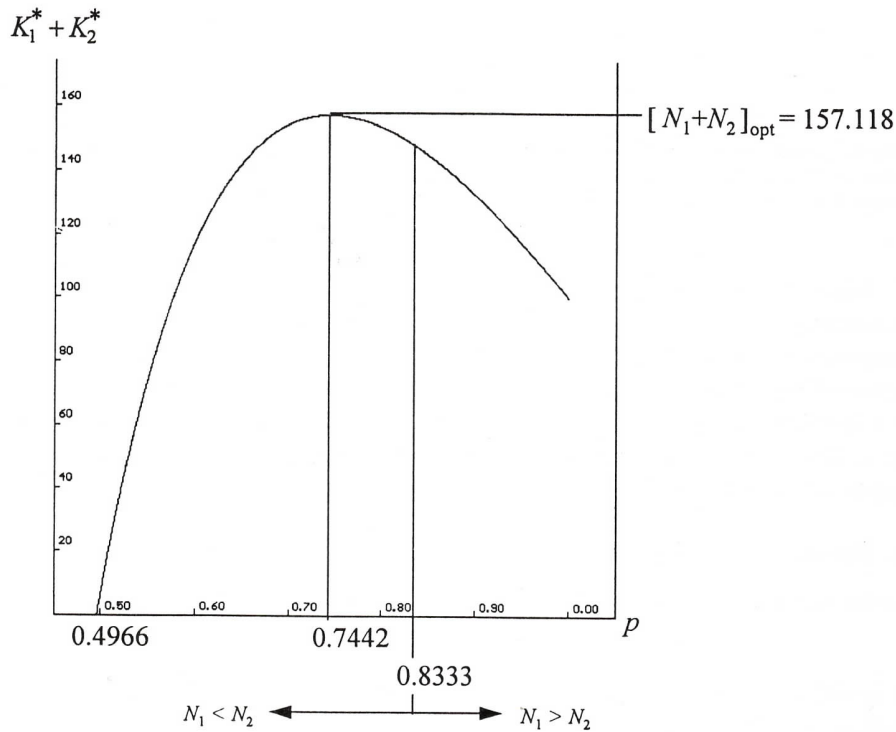

Fig. 3. Variation of total asymptotic limit metapopulation size in function of fidelity rate p. $N_1^* > N_2^*$ whenever $0.8333 < p \leq 1$, $N_1^* < N_2^*$ whenever $0.4966 < p < 0.8333$, $N_1^* + N_2^*$ reaches its maximum when $p = 0.7422$, extinction occurs whenever $p \leq 0.4966$.
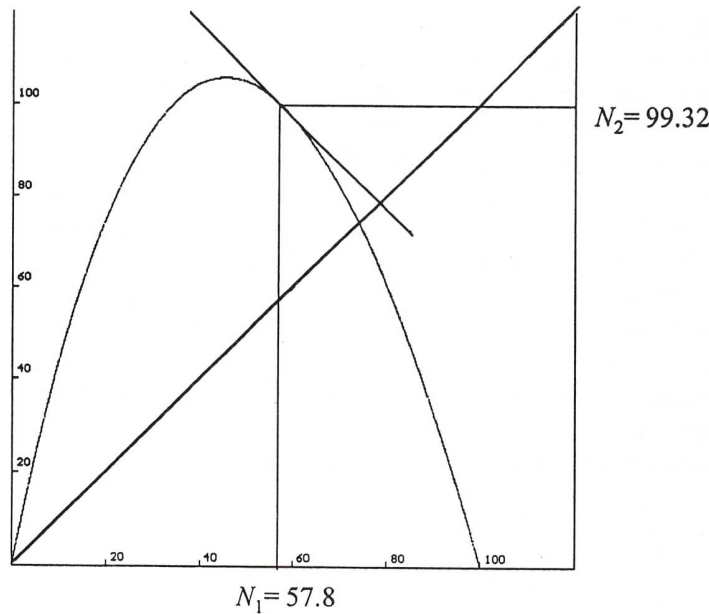
$$\begin{bmatrix} 0 & (1-m_1)f_1 & 0 & m_2 f_2 \\ s_1 & s_1 & 0 & 0 \\ 0 & m_1 f_1 & 0 & (1-m_2)f_2 \\ 0 & 0 & s_2 & s_2 \end{bmatrix}$$

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$N_2 = 99.32$

$N_1 = 57.8$

Fig. 4. Coördinates $\{N_1^*, N_2^*\}$ in function of population 1 fidelity rate $0 \le p \le 1$. The maximum value of $N_1^* + N_2^* = 157.12$ is reached in the point where the orthogonal projection to the first diagonal is tangent to the curve. Then $N_1^* = 57.8$ and $N_2^* = 99.32$.

Figure 4 shows the variation of $\{N_1^*, N_2^*\}$ coördinates for $0 < p \le 1$. $[N_1^* + N_2^*]_{\text{opt}}$ is reached in the point where the orthogonal projection to the first diagonal is tangent to the curve. Computing Eqs. (3.8) and (3.9) for p_{opt} — always considering figures of Eq. (3.5) —, N_1^* is then equal to 57.800992 and N_2^* to 99.318111. Between $p = 0.496585$ and $p = 0.833333$, $N_2^* > N_1^*$. Hence, **a third conclusion:** there is no a direct link between the population size, at *equilibrium*, and the demographic regime of the population.

4. Effects of Strong Rates of Increase

Under *uncoupled* condition, the dynamics of population 1 is described by:

$$N_1(t) = \exp(r(1 - N_1(t-1)/K_1))N_1(t-1) \tag{4.1}$$

It is well known that stability of *equilibrium* K_1 may be studied by linear approximation of $N_1(t)$, in the neighbourhood of K_1.

$$N_1(t) \approx K_1 - (1 - r)(K_1 - N_1(t-1))$$
$$= N_1(t-1) + r(K_1 - N_1(t-1)) \tag{4.2}$$

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$$\begin{bmatrix} 0 & (1-m_1)f_1 & 0 & m_2f_2 \\ s_1 & s_1 & 0 & 0 \\ 0 & m_1f_1 & 0 & (1-m_2)f_2 \\ 0 & 0 & s_2 & s_2 \end{bmatrix}$$

For $0 < r < 2$, there is a local stability: after a deviation of magnitude $(K_1 - N_1(t-1))$, the next deviation $(K_1 - N_1(t))$ is smaller than the former one in absolute value, and the system reaches gradually K_1. The *equilibrium* begins to be unstable when $r > 2$, then it appears a non-periodical oscillatory regime, passing by growing oscillatory periods as long as r value increases up to $2.6924\ldots$ For $r > 2.6924\ldots$ a chaotic regime appears, non-periodical, whose value points never pass more than one time through the same real number. Figure 5 illustrates the successive bifurcations in the asymptotic values of N_1 when r increases.

Under *coupled* condition, the dynamics of the system, described by Eqs. (3.2) and (3.4), is buffered because r is replaced by $r^* = r + \ln p$, (Eq. 3.8). It is easy to observe that as long as $0 < p < 1, \ln p < 0$, and $r^* < r$; this buffers strong rates of increase. Hence, **fourth conclusion**: migration has a stabilizing effect over the population trajectories (Fig. 6).

When r increases, the probability of extinction — in stochastic counterparts of this model (e.g., [20]) — increases (Fig. 7), just because N_1 is more often close to zero (Fig. 5). To keep relatively low values of r buffers the extinction risks. Thus, **fifth conclusion**: migration has well then a cushioning effect over extinction probabilities, including local ones.
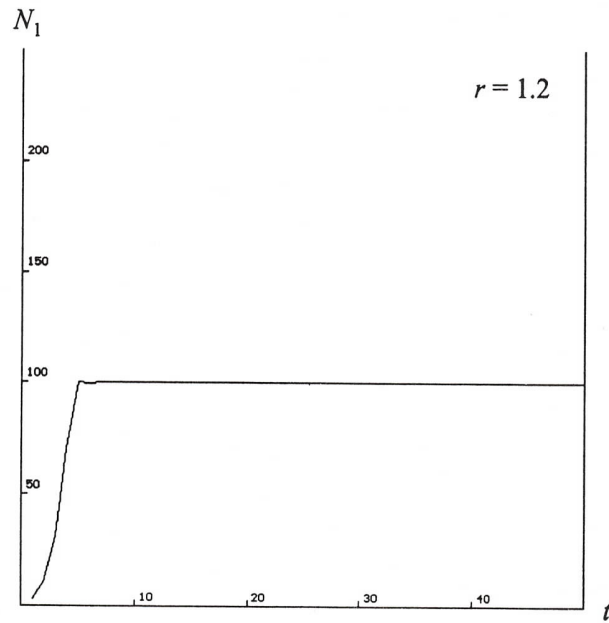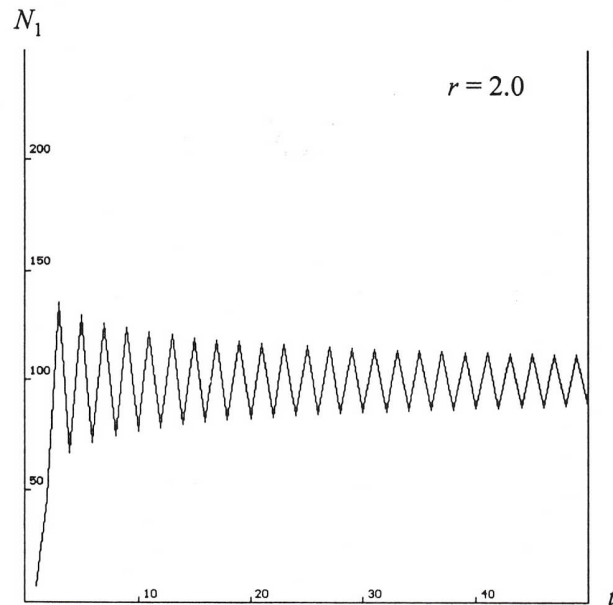

$r = 0.2, \quad p = 1, \quad b = 0.8$

$a(x) = \exp\left(r\left(1 - \frac{N_1(t)}{K_1}\right)\right)$

$N_1(0) = 1, \quad K_1 = 100$
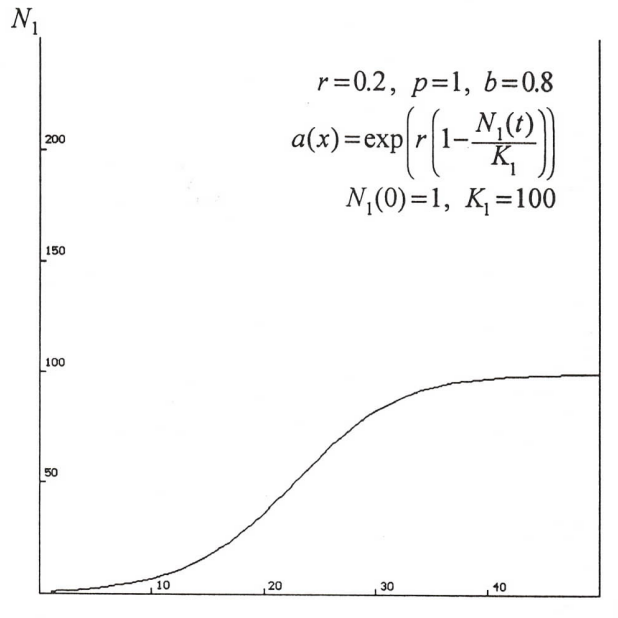
(a)

Fig. 5. Non-oscillating, oscillating, and chaotic regimes of a DDSS system in function of the value of $r; p = 1, a(x) = \exp(r(1 - N_1(t)/K_1)), b = 0.8, N_1(0) = 1,$ and $K_1 = 100$. (a) Typical value of a growing population $r = 0.2$; (b) reaching fast the asymptote $r = 1.2$; (c) incipient oscillations $r = 2.0$; (d) convergent oscillatory regime $r = 2.3$; (e) chaos $r = 2.7$; (f) chaos and greater risk of extinction $r = 3.1$.

$$\begin{bmatrix} 0 & (1-m_1)f_1 & 0 & m_2f_2 \\ s_1 & s_1 & 0 & 0 \\ 0 & m_1f_1 & 0 & (1-m_2)f_2 \\ 0 & 0 & s_2 & s_2 \end{bmatrix}$$

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(b)

(c)

Fig. 5 (*Continued*)

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$$\begin{bmatrix} 0 & (1-m_1)f_1 & 0 & m_2f_2 \\ s_1 & s_1 & 0 & 0 \\ 0 & m_1f_1 & 0 & (1-m_2)f_2 \\ 0 & 0 & s_2 & s_2 \end{bmatrix}$$

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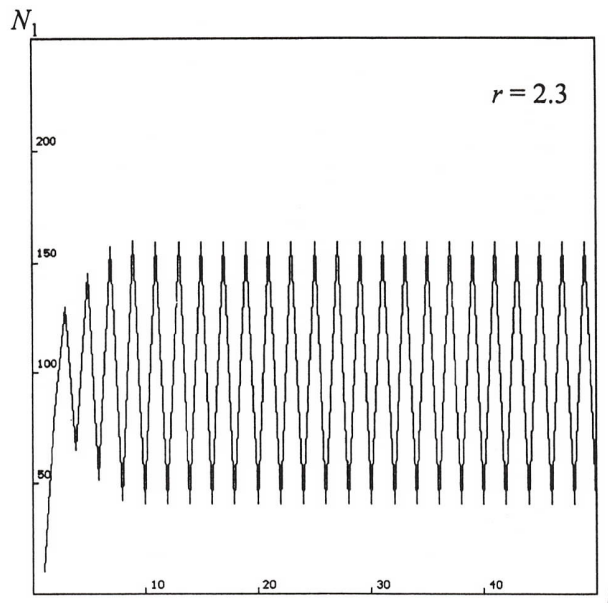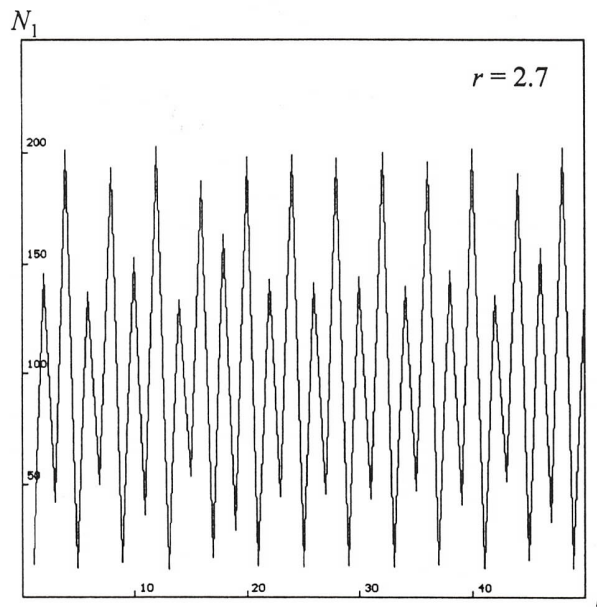N_1

$r = 2.3$

(d)

N_1

$r = 2.7$

(e)

Fig. 5 (*Continued*)

$$\begin{bmatrix} 0 & (1-m_1)f_1 & 0 & m_2f_2 \\ s_1 & s_1 & 0 & 0 \\ 0 & m_1f_1 & 0 & (1-m_2)f_2 \\ 0 & 0 & s_2 & s_2 \end{bmatrix}$$
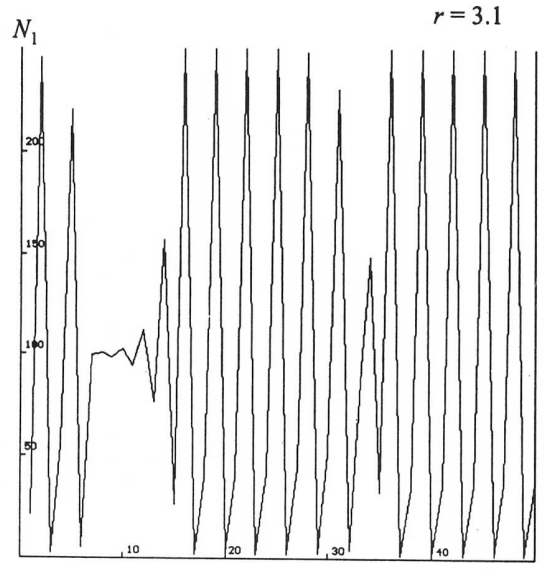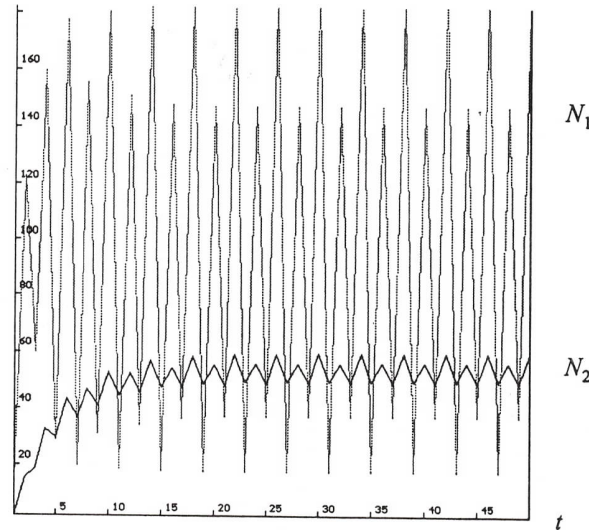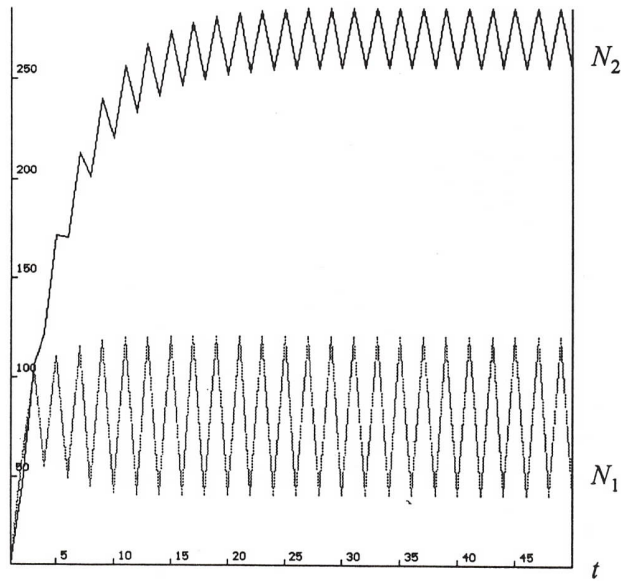
(f)

Fig. 5 (*Continued*)

(a)

Fig. 6. Moving from a chaotic to a stable regime thanks to migration's *buffer effect*. $r = 2.7, q = 1, a(x) = \exp(r(1 - N_1(t)/K_1)), b = 0.8, N_1(0) = 1 = N_2(0)$, and $K_1 = 100$. (a) $p = 0.9$ then $r^* = 2.6$; (b) $p = 0.6$ then $r^* = 2.2$; (c) $p = 0.3$ then $r^* = 1.5$, – observe the great size of "sink" population $N_2(t)$.

$$\begin{bmatrix} 0 & (1-m_1)f_1 & 0 & m_2f_2 \\ s_1 & s_1 & 0 & 0 \\ 0 & m_1f_1 & 0 & (1-m_2)f_2 \\ 0 & 0 & s_2 & s_2 \end{bmatrix}$$

$$r = 2.7 \quad p = 0.6 \quad \text{then} \quad r^* = 2.2$$

(b)

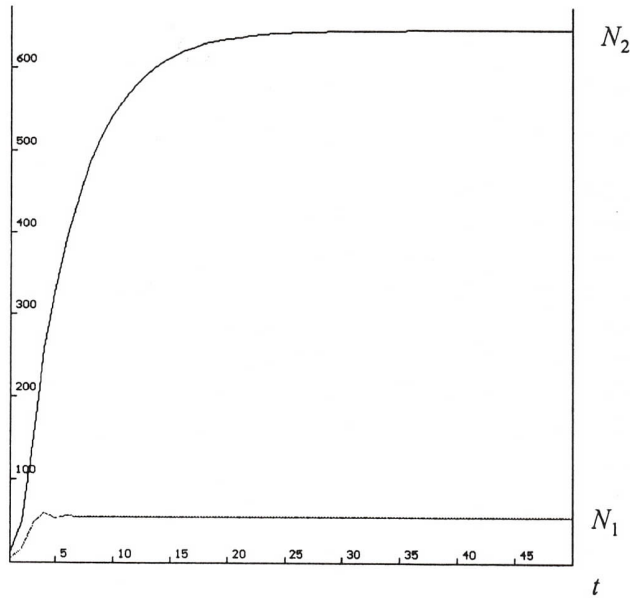$$r = 2.7 \quad p = 0.3 \quad \text{then} \quad r^* = 1.5$$

(c)

Fig. 6 (*Continued*)

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$$\begin{bmatrix} 0 & (1-m_1)f_1 & 0 & m_2f_2 \\ s_1 & s_1 & 0 & 0 \\ 0 & m_1f_1 & 0 & (1-m_2)f_2 \\ 0 & 0 & s_2 & s_2 \end{bmatrix}$$

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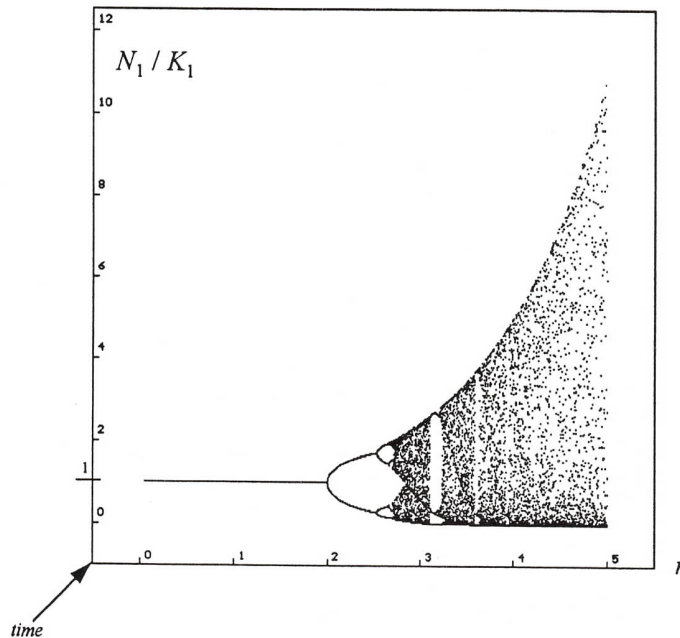
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Fig. 7. Bifurcations of N_1/K_1 occurring at $r = 2, 2.53, 2.66, 2.69$, and chaos from $r = 2.7$.

5. Effect of the Structure of the Population

5.1. *A Structured DDSSM*

A *structured* DDSSM in its simplest case contains only two "populations", each one having a structure, e.g., in age. Formally, modeling does not pose major problems. N_1 and N_2 are now column vectors reflecting the structure of each population. We consider here the simplest case of only two age-classes, one of immatures and one of adults: n_{11} and n_{12} for population **1**, n_{21} and n_{22} for population **2**. Possible applications of this model are frequently found in nature, e.g., the Peregrine *Falcon Falco peregrinus anatum* in California [78]. Consider first, in a fashion similar to Eqs. (2.1)–(2.4) and particularly in Eqs. (2.7) and (3.1), density-dependent growth and migration

$$\begin{aligned} \mathbf{N}_1(t) &= \mathbf{PAN}_1(t-1) + [\mathbf{I} - \mathbf{Q}]\mathbf{BN}_2(t-1) \\ \mathbf{N}_2(t) &= [\mathbf{I} - \mathbf{P}]\mathbf{AN}_1(t-1) + \mathbf{QBN}_2(t-1) \end{aligned} \tag{5.1}$$

P and **Q** are now phylopatry *matrices*, $[\mathbf{I} - \mathbf{P}]$ and $[\mathbf{I} - \mathbf{Q}]$ migration *matrices*.

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$$\begin{bmatrix} 0 & (1-m_1)f_1 & 0 & m_2f_2 \\ s_1 & s_1 & 0 & 0 \\ 0 & m_1f_1 & 0 & (1-m_2)f_2 \\ 0 & 0 & s_2 & s_2 \end{bmatrix}$$

Thus, one may rewrite Eq. (5.1) as

$$\mathbf{N}(t) = \begin{bmatrix} \mathbf{N}_1(t) \\ \mathbf{N}_2(t) \end{bmatrix} = \begin{bmatrix} \mathbf{PA} & [\mathbf{I} - \mathbf{Q}]\mathbf{B} \\ [\mathbf{I} - \mathbf{P}]\mathbf{B} & \mathbf{QB} \end{bmatrix} \begin{bmatrix} \mathbf{N}_1(t-1) \\ \mathbf{N}_2(t-1) \end{bmatrix} = \mathbf{G}_s\mathbf{N}(t-1) \quad (5.2)$$

where $\mathbf{G}_s$ is equivalent to matrix $\mathbf{G}$ in Eq. (2.7), but for *structured* populations.

To model *density-dependence* $\mathbf{A}$ and $\mathbf{B}$ transform to functions of the numbers in each population

$$\begin{bmatrix} \mathbf{N}_1(t) \\ \mathbf{N}_2(t) \end{bmatrix} = \begin{bmatrix} \mathbf{PA}(\mathbf{N}_1(t-1)) & [\mathbf{I} - \mathbf{Q}]\mathbf{B}(\mathbf{N}_2(t-1)) \\ [\mathbf{I} - \mathbf{P}]\mathbf{A}(\mathbf{N}_1(t-1)) & \mathbf{QB}(\mathbf{N}_2(t-1)) \end{bmatrix} \begin{bmatrix} \mathbf{N}_1(t-1) \\ \mathbf{N}_2(t-1) \end{bmatrix} \quad (5.3)$$
$$\mathbf{N}(t) = \mathbf{D}_s(\mathbf{N}_1(t-1), \mathbf{N}_2(t-1))\mathbf{N}(t-1)$$

where $\mathbf{D}_s$, for structured populations, is equivalent to matrix $\mathbf{D}$ in Eq. (3.3).

5.2. *Numerical Study of the Structured DDSSM*

Such a model for two populations each one with two age-classes, can be studied like that of Eq. (3.4). Hence, population **1** is *density-dependent*, increases and yields migrants to population **2**; population **2** is not density-dependent, decreases and does not yield migrants. Then $\mathbf{A}(\mathbf{N}_1(t))$ is a function, $\mathbf{B}(\mathbf{N}_2(t))$ is a constant, and $\mathbf{Q} = \mathbf{I}$. Equation (5.3) becomes:

$$\begin{bmatrix} \mathbf{N}_1(t) \\ \mathbf{N}_2(t) \end{bmatrix} = \begin{bmatrix} \mathbf{PA}(\mathbf{N}_1(t-1)) & 0 \\ [\mathbf{I} - \mathbf{P}]\mathbf{A}(\mathbf{N}_1(t-1)) & \mathbf{B} \end{bmatrix} \begin{bmatrix} \mathbf{N}_1(t-1) \\ \mathbf{N}_2(t-1) \end{bmatrix}$$
$$\begin{bmatrix} n_{1,1} \\ n_{1,2} \\ n_{2,1} \\ n_{2,2} \end{bmatrix}_t = \begin{bmatrix} 0 & pf_1(t-1) & 0 & 0 \\ s & s & 0 & 0 \\ 0 & (1-p)f_1(t-1) & 0 & f_2 \\ 0 & 0 & s & s \end{bmatrix} \begin{bmatrix} n_{1,1} \\ n_{1,2} \\ n_{2,1} \\ n_{2,2} \end{bmatrix}_{t-1} \quad (5.4)$$

where, as in a typical Leslie matrix [7,53,48,49], there are fecundities f_1 and f_2, and survival s. Fecundity f_1 is a *density-dependent* function as described by Eq. (3.2), i.e., $f_1 = \exp[r(1-n_{12}/K_1)]$, and $f_2 = 0.8$ is constant as is the case for b in Eq. (3.5). Survival is $s = 0.5$, it appears also in the lower right corner of $\mathbf{A}$ and $\mathbf{B}$, as proposed by Usher [74] to include in a single group all older individuals. Obviously, survival rates differing across populations could be considered in case of need. We consider $K_1 = 100$ and $r = 3.1$.

The maximal rate of increase for population **1** is obtained for $n_{12} = 0$ and $p = 1$. Then $\mathbf{PA}(\mathbf{N}_1(t))$ equals

$$\begin{bmatrix} 0 & \exp[r] \\ s & s \end{bmatrix} \quad (5.5)$$

with dominant eigenvalue $\lambda = 3.5909$. Then the log-growth rate $\ln \lambda = 1.2784$. It is analogous to $r^* = r + \ln p$ of the *non-structured* DDSSM (Eq. (3.8)). Without and with migration, i.e., $p = 1$ or $p < 1$, the general behaviour of these age-structured populations is similar to that of the non-structured ones (see Fig. 8 and cfr. Fig. 5).

$$\begin{bmatrix} 0 & (1-m_1)f_1 & 0 & m_2f_2 \\ s_1 & s_1 & 0 & 0 \\ 0 & m_1f_1 & 0 & (1-m_2)f_2 \\ 0 & 0 & s_2 & s_2 \end{bmatrix}$$
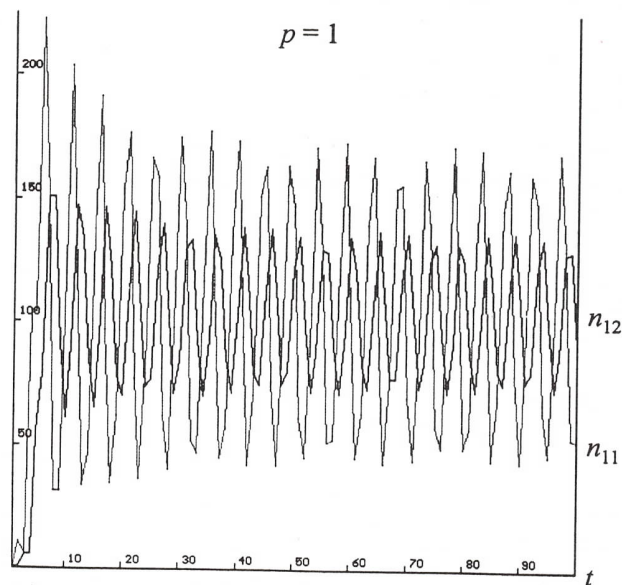
(a)
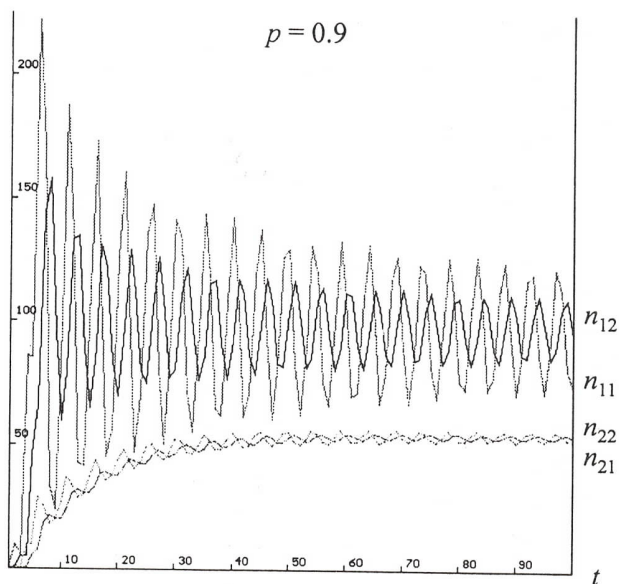
(b)

Fig. 8. General behaviour of two coupled age-structured populations. $n_{11}(0) = 1, n_{12}(0) = n_{21}(0) = n_{22}(0) = 0, f_1 = \exp(r(1 - n_{12}(t)/K_1)), f_2 = 0.8, s = 0.5, K_1 = 100$, and $r = 3.1$. (a) Without migration: $p = 1$; (b) with migration: $p = 0.9$.

$$\begin{bmatrix} 0 & (1-m_1)f_1 & 0 & m_2f_2 \\ s_1 & s_1 & 0 & 0 \\ 0 & m_1f_1 & 0 & (1-m_2)f_2 \\ 0 & 0 & s_2 & s_2 \end{bmatrix}$$

To observe more precisely this behaviour (Fig. 9), the numbers of adults n_{12} may be plotted as a function of the numbers of immatures n_{11}, in population **1**. Considering first the *uncoupled* condition, i.e., no migration $p = 1$, then $\mathbf{N}_2^* = \mathbf{0}$. The result illustrates the displacement of the successive $\{n_{11}, n_{12}\}$ values, turning around a starting point, but never getting back to the same pair of values, going over close but always different cycles, i.e., an *attractor*.

Consider now the *coupled* condition. In this case, the dominant eigenvalue if $p = 0.9$ is $\lambda = 3.4204$, then $\ln \lambda = 1.2298$. This time the result is a stable limit point reached very slowly.

The same, divergent and convergent, *attractors* can be attained notwithstanding the initial values of n_{11}, n_{12}, n_{21} and n_{22} were different. So, **sixth conclusion:** migration has also a stabilizing effect over structured populations; not enough anyway to totally buffer the destabilizing effect of age-structures and of partial density-dependences.
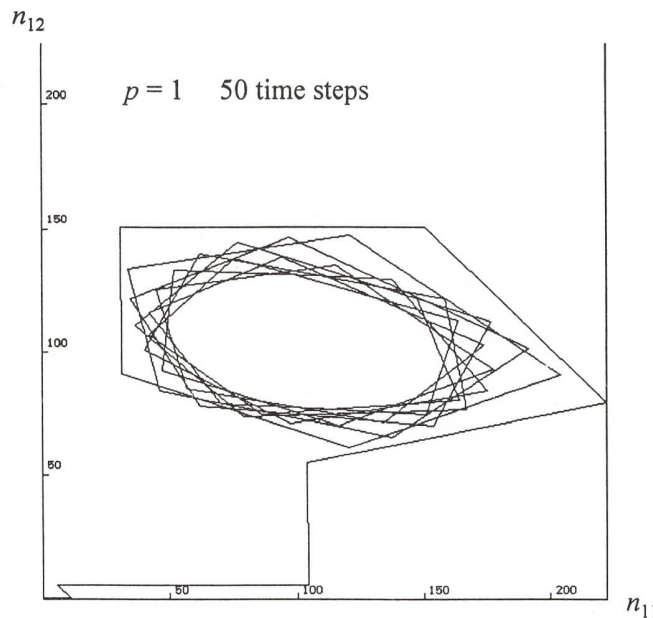
(a)

Fig. 9. Different asymptotic limits of successive pairs of $\{n_{11}, n_{12}\}$ values in time, as a function of fidelity rate p. (a,b,c) $p = 1$, so no convergence to a stable age-structure of population **1**. (d,e) $p = 0.9$, so convergence to a stable age-structure of population **1**, whatever the starting numbers of individuals n_{ij}: (d) $n_{11} = 1, n_{12} = n_{2j} = 0$; (e) $n_{11} = 0, n_{12} = 7, n_{21} = 13$, and $n_{22} = 1$.

$$\begin{bmatrix} 0 & (1-m_1)f_1 & 0 & m_2f_2 \\ s_1 & s_1 & 0 & 0 \\ 0 & m_1f_1 & 0 & (1-m_2)f_2 \\ 0 & 0 & s_2 & s_2 \end{bmatrix}$$

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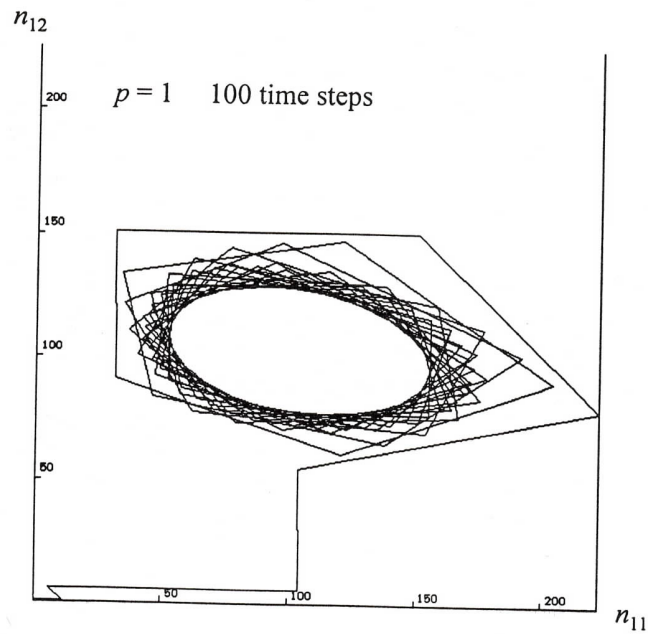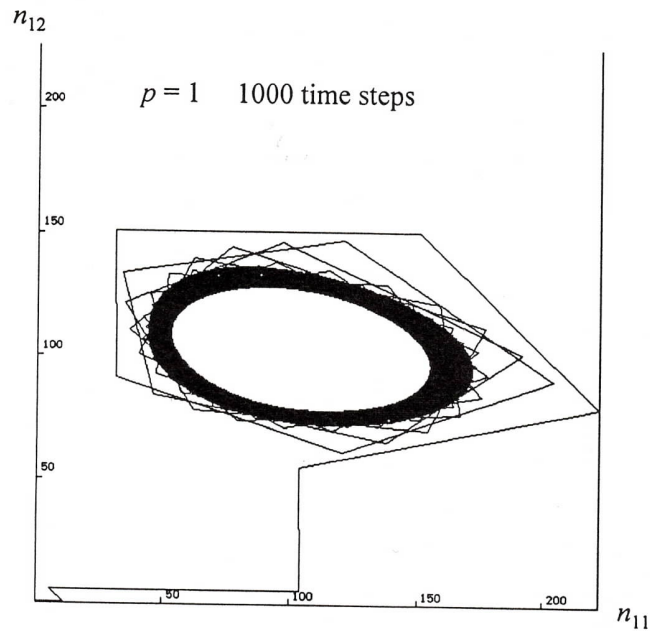
(b)

(c)

Fig. 9 (*Continued*)

$$\begin{bmatrix} 0 & (1-m_1)f_1 & 0 & m_2 f_2 \\ s_1 & s_1 & 0 & 0 \\ 0 & m_1 f_1 & 0 & (1-m_2)f_2 \\ 0 & 0 & s_2 & s_2 \end{bmatrix}$$

n_{12}

$p = 0.9$ 1500 time steps

n_{11}

(d)

Fig. 9 (*Continued*)

n_{12}

$p = 0.9$ 1500 time steps
and new original n_{ij} values

n_{11}

(e)

Fig. 9 (*Continued*)

$$\begin{bmatrix} 0 & (1-m_1)f_1 & 0 & m_2f_2 \\ s_1 & s_1 & 0 & 0 \\ 0 & m_1f_1 & 0 & (1-m_2)f_2 \\ 0 & 0 & s_2 & s_2 \end{bmatrix}$$

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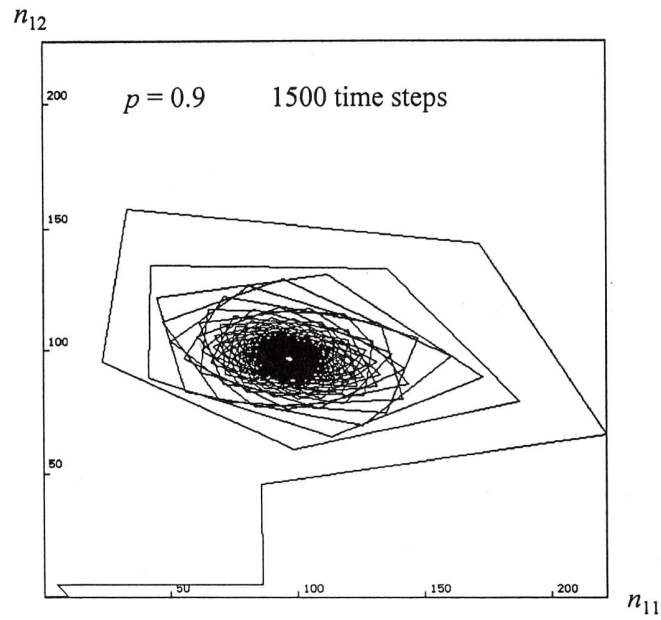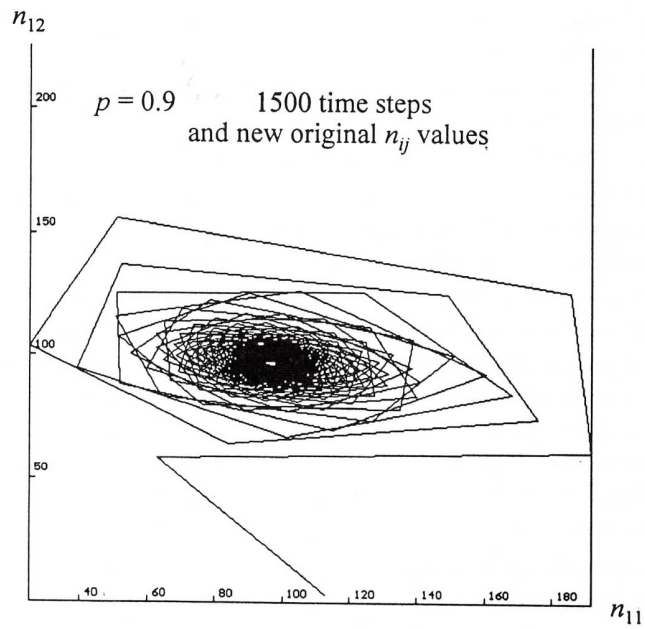
6. Discussion and Conclusions

The DDSSM studied here allows us to demonstrate, to a certain extent, some effects of migration on population numbers, in particular its strong stabilising role. Migration from high towards low quality habitats leads to more stability. The resulting equilibrium levels are buffered when compared to a situations without migration, and are linked in a complex way to demographic parameters. As a consequence, the concept of *carrying capacity* appears as extremely misleading. Migration makes less frequent the occurrence of periodicities and chaotic regimes, and reduces local and global extinction probabilities. However, this stabilising role is not always sufficient to counteract totally the destabilising effects of age (or others) structures, of partial density-dependence, etc. Other main demographic and evolutionary consequences of dispersal remain to be studied in the same DDSSM context, particularly consequences on survival patterns, age at first reproduction and fecundity.

Concerning the modelling process itself we emphasize the need of a detailed mathematical study. Simulations must always be strongly based on a sound mathematical framework. This is the only way to provide correct responses to questions concerning equilibrium, periodicity, or chaotic behaviour. There is always the risk of estimating by simulation quantities that do not exist, such as an average age-structure when there is no convergence.

To run the model presented herein we have used a powerful tool especially designed for discrete time dynamic models: program ULM (Unified Life Models [46]). The Appendix contains a brief description to use it to obtain the results and figures in this paper. However, many pieces of software can be used to run this kind of simulations, such as S.PLUS, MATHLAB, CALMAT [62] and DERIVE [64]. In all cases, attention must be paid to rounding errors and to the quality of pseudo-random numbers generators.

It is fairly clear that our understanding of the dynamics of subdivided populations is far from adequate. Evolution is more rapid in small, at least partially isolated, populations [41]. Management and conservation of populations depends strongly on the degree of resilience of the populations under concern: the stabilising role of migration makes it a key process among the mechanisms which have led to the present level of biological diversity. Strong losses of biological diversity are expected as a direct and indirect consequence of human activity [71]. Among impacts of human activity, the fragmentation of natural habitats [22] e.g., by deforestation, is an issue directly related to the topic of this paper. It is clear the tools presented here are adequate for gaining general knowledge in a fairly theoretical context. However, we have recalled that standard demographic models, such as Leslie matrices, can be used in the context of subdivided populations.

Our understanding on the dynamics of subdivided populations might be strongly improved by using such tools in an empirical context, i.e., with survival, reproduction and migration rates, and their relation to density and to environmental variations, estimated from field data. Practical applications concern the dynamics of

$$\begin{bmatrix} 0 & (1-m_1)f_1 & 0 & m_2f_2 \\ s_1 & s_1 & 0 & 0 \\ 0 & m_1f_1 & 0 & (1-m_2)f_2 \\ 0 & 0 & s_2 & s_2 \end{bmatrix}$$

populations inhabiting growing fragmented landscapes, which increase everywhere in the world, with consequences on the environment and resource management. The population geneticists could make better use of these models, and of the first demographical conclusions presented here, to improve the knowledge concerning the evolution of dispersal and the micro evolution of small populations and/or metapopulations, for example the equilibrium between migration and philopatry, and differences in fitness between movers and stayers.

7. Acknowledgements

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$$\begin{bmatrix} 0 & (1-m_1)f_1 & 0 & m_2f_2 \\ s_1 & s_1 & 0 & 0 \\ 0 & m_1f_1 & 0 & (1-m_2)f_2 \\ 0 & 0 & s_2 & s_2 \end{bmatrix}$$

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$$\begin{bmatrix} 0 & (1-m_1)f_1 & 0 & m_2f_2 \\ s_1 & s_1 & 0 & 0 \\ 0 & m_1f_1 & 0 & (1-m_2)f_2 \\ 0 & 0 & s_2 & s_2 \end{bmatrix}$$

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$$\begin{bmatrix} 0 & (1-m_1)f_1 & 0 & m_2f_2 \\ s_1 & s_1 & 0 & 0 \\ 0 & m_1f_1 & 0 & (1-m_2)f_2 \\ 0 & 0 & s_2 & s_2 \end{bmatrix}$$

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APPENDIX: Running the Models with ULM

Introduction

There are many programming languages with good matrix manipulation abilities, but few to perform simulations in matricial demography. Among the best known softwares, we may cite for instance CALMAT, DYNAMAC, GAUSS, MATHLAB, SAS, SPLUS, etc. They allow to perform more or less easily the computations associated with matrix models. Nevertheless, none of those is *specially* designed for handling demographic matrix models, and more generally, dynamic models defined by recurrence equations. ULM (Unified Life Models) fills a gap by providing a very powerful and subtle tool designed for demographical simulation incorporating modern graphic abilities.

ULM is available, for PC/MS-DOS and for SUN/UNIX systems, from S. Legendre at the ENS, CNRS-URA 258, 46 Rue d'Ulm, 75230 Paris Cedex 05 [46]. Models representing the dynamics of populations are defined symbolically and can be studied interactively by means of simple commands and graphics displays.

General Features

ULM allows to consider
>deterministic, age or stage classified, Leslie models,
>stochastic environments and random vital rates,
>density-dependent models, and
>metapopulation models,
>competition, dispersal and migration.

Among the main available features are:
>matrix properties: primitivity, irreducibility, eigenvalues, left and right eigenvectors, mean generation time,
>sensitivity analysis: matrix entries, lower level parameters (through formal derivative computation), constant fitness curves,
>mathematical random functions, statistical estimators, growth rate, stochastic sensitivities, extinction probability,
>lyapunov exponent computation, spectrum, correlation,
>multi-model capabilities, and user defined input and output data files.

In all cases ULM starts by reading a file defining the model to be used. There are many commands available, but here we refer only those to run the models herein. Our aim is to help using these models in practice, e.g., for graduate teaching.

GENERAL COMMANDS

COMMAND	ACTION
view	displays the current model
view *variable_name*	displays the current *variable* value
change *variable_name new_value*	changes the value of a current variable
run *number*	runs a *number* of time steps
graph *x_variable y1_variable ... yn_variable*	declares variables to plot

$$\begin{bmatrix} 0 & (1-m_1)f_1 & 0 & m_2f_2 \\ s_1 & s_1 & 0 & 0 \\ 0 & m_1f_1 & 0 & (1-m_2)f_2 \\ 0 & 0 & s_2 & s_2 \end{bmatrix}$$

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A.1 File and ULM-Commands for Section 2.2

The next equation (Eq. (2.4)), expressing the Simple Migration Model,

$$\begin{bmatrix} N_1(t) \\ N_2(t) \end{bmatrix} = \begin{bmatrix} p & 1-q \\ 1-p & q \end{bmatrix} \begin{bmatrix} N_1(t-1) \\ N_2(t-1) \end{bmatrix}$$

is declared in the file hereinafter. The file defines (under Pascal Language syntax) the name and size (*defmod*), the vector (*defvec*), the matrix (*defmat*), and the variables (*defvar*) of the model. The original values of variables p and q will be changed during the simulation.

FILE FOR THE SIMPLE MIGRATION MODEL

```
{ SPLMGMD.ulm = ASCCI file to run equations of section 2.2 and Figure 1
{ The model is the "SIMPLE MIGRATION MODEL"
{
defmod SPLMGMD(2)
vec : v
mat : m

defvec v(2)
n1 , n2

defmat m(2)
p    , 1-q
1-p , q

defvar n1 = 66.666666

defvar n2 = 33.333333

defvar n = n1 + n2

defvar p = 0.6

defvar q = 0.4
```

After ULM has read the file, the simulations may go on with the following commands:

COMMANDS FOR THE SIMPLE MIGRATION MODEL

COMMAND	ACTION	RESULT
yscale 0 100	dimensions y co-ordinate	
F1	to graph mode	
run	runs 20 time steps by default	FIGURE 1a
change p 0.15	changes p value	
change q 0.1	changes q value	
run	runs last defined number of time steps	FIGURE 1b
change p 0.725	changes p value	
change q 0.675	changes q value	
run	run	FIGURE 1c

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$$\begin{bmatrix} 0 & (1-m_1)f_1 & 0 & m_2f_2 \\ s_1 & s_1 & 0 & 0 \\ 0 & m_1f_1 & 0 & (1-m_2)f_2 \\ 0 & 0 & s_2 & s_2 \end{bmatrix}$$

A.2 File and ULM-Commands for Sections 3 and 4

To run and to perform the simulations of the model developed in Secs. 3 and 4

$$\begin{bmatrix} N_1(t) \\ N_2(t) \end{bmatrix} = \begin{bmatrix} a[N_1(t-1)]p & 0 \\ a[N_1(t-1)](1-p) & b \end{bmatrix} \begin{bmatrix} N_1(t-1) \\ N_2(t-1) \end{bmatrix}$$

where $a(x)$ is $\exp[r(1 - N_1(t)/K_1]$, one needs the following file, which defines size and name, vector, matrix, and variables of the model. Variable M equals the sum of the asymptotic growth limits under migration $(K_1^* + K_2^*)$. A number of variable values will change crossing over the simulation. One may notice that the matrix m is re'evaluated at each time step since it depends on the current value of ν.

FILE FOR THE MODEL OF SECTIONS 3 and 4 (Figs. 2, 3, 4, 5, 6, and 7)

```
{ DDSSM.ulm = ASCII file to run equations of Sections 3.3 to 4 and Figures 2 to 7
{ This model is the "DENSITY DEPENDENT SOURCE-SINK MODEL" (DDSSM)
{
defmod DDSSM(2)
mat : d
vec : v

defvec v(2)
n1 , n2

defmat d(2)
f1*p        , 0
f1*(1-p) , b

defvar n1 = 5

defvar n2 = 5

defvar n = n1 + n2

defvar f1 = exp(r*(1- n1/K1))

defvar p = 0.9

defvar b = 0.8

defvar r = 0.7

defvar K1 = 100

defvar M =(K1*(1+(ln(p)/r))) + ((1-p)/(1-b))*K1*(1+(ln(p)/r))/p))
```

After ULM has read the file, the simulations may go on with the following commands:

$$\begin{bmatrix} 0 & (1-m_1)f_1 & 0 & m_2f_2 \\ s_1 & s_1 & 0 & 0 \\ 0 & m_1f_1 & 0 & (1-m_2)f_2 \\ 0 & 0 & s_2 & s_2 \end{bmatrix}$$

COMMANDS FOR THE DDSSM (Figures 2, 3, 4, 5, 6, and 7)

COMMAND	ACTION	RESULT
graph t n1 n2 n	declares variables to plot	
xscale 0 25	range & scale of x–graph	
yscale 0 150	range & scale or y–graph	
F1	to graph mode	
run 25	runs 25 time steps	FIGURE 2
F1	move to text mode	
xscale 0.45 1.05	dimensions x co-ordinate	
ysacale 0 170	dimensions y co-ordinate	
change n 157.1188	changes n value	
graph t n	declares variables to plot	
F9	addgraph on	
F1	move to graph mode	
F2	runs 25 time steps	straight line $y = 157.1188$
change n 0.7442	changes n value	
graph n t	declares variables to plot	
F2 (several times)	run (several times)	straight line $x = 0.7442$
graph p m	declares variables to plot	
parameter p 0.496 1 0.001	p variates from 0.0496 to 1 step 0.001	
F2	runs the number of steps defined by the *parameter* command	FIGURE 3
F1	move to text mode	
run 100	runs 100 time steps	
change n1 1	changes first value of n1 to unity	
change n2 1	changes first value of n2 to unity	
xscale 0 120	dimensions x coördinate	
yscale 0 120	dimensions y coördinate	
graph t t	declares variables to plot	
F1	move to graph mode	
F2	runs 100 time steps	diagonal in Figure 4
change n 157.1188−n1	changes n value	
graph n1 n	declares variables to plot	
F3	initialises time	
F2	runs 100 time steps	orthogonal to the diagonal
graph n1 n2	declares variables to plot	
parameter p 0.496 1 0.001	p variates from 0.0496 to 1 step 0.001	
skip 95	computes all time steps skiping 95 to plot in the graph mode	
F7	graph *line_off*	
F2	runs the number of steps defined by the *parameter* command	FIGURE 4

$$\begin{bmatrix} 0 & (1-m_1)f_1 & 0 & m_2f_2 \\ s_1 & s_1 & 0 & 0 \\ 0 & m_1f_1 & 0 & (1-m_2)f_2 \\ 0 & 0 & s_2 & s_2 \end{bmatrix}$$

F1	move to text mode	
skip	skip off	
F7	graph *line_on*	
F9	*addgraph* off	
graph t n1	declares variables to plot	
xscale 0 50	dimensions x co-ordinate	
yscale 0 250	dimensions y co-ordinate	
change p 1	changes p value to unity	
change r 0.2	changes r value	
F1	move to graph mode	
run 50	runs 50 time steps	FIGURE 5a
change r 1.2	changes r value	
F2	runs 50 time steps	FIGURE 5b
change r 2	changes r value	
F2	runs 50 time steps	FIGURE 5c
change r 2.3	changes r value	
F2	runs 50 time steps	FIGURE 5d
change r 2.7	changes r value	
F2	runs 50 time steps	FIGURE 5e
change r 3.1	changes r value	
F2	runs 50 time steps	FIGURE 5f
change r 2.7	changes r value	
change p 0.9	changes p value	
run 50	runs 50 time steps	FIGURE 6a
change p 0.6	changes p value	
F2	runs 50 time steps	FIGURE 6b
change p 0.3	changes p value	
F2	runs 50 time steps	FIGURE 6c
F1	move to text mode	
r 1000	runs 1000 time steps	
F7	graph *line_off*	
F9	*addgraph* on	
c p 1	changes p value to unity	
c n n1/k1	changes n value to $n1/k1$	
g r n	declares variables to plot	
xscale −0.5 5.5	dimensions x co-ordinate	
yscale −1 12.5	dimensions y co-ordinate	
parameter r 0.05 5 0.01	p value variates from 0.05 to 5 step 0.01	
skip 995	computes all time steps skiping 995 in the graph mode plotting	
F1	move to graph mode	
F2	runs the number of steps defined by the *parameter* command	FIGURE 7

$$\begin{bmatrix} 0 & (1-m_1)f_1 & 0 & m_2f_2 \\ s_1 & s_1 & 0 & 0 \\ 0 & m_1f_1 & 0 & (1-m_2)f_2 \\ 0 & 0 & s_2 & s_2 \end{bmatrix}$$

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A.3 File and ULM-Commands for Section 5

To perform the simulations developped in section 5, on the effect of the structure of the population over the Density-Dependent Source-Sink Model, the file hereafter defines name and size, vector, matrix, and variables of the Structured-DDSSM, grounded on the next equation (Eq. (5.4))

$$\begin{bmatrix} n_{1,1} \\ n_{1,2} \\ n_{2,1} \\ n_{2,2} \end{bmatrix}_t = \begin{bmatrix} 0 & pf_1(t-1) & 0 & 0 \\ s & s & 0 & 0 \\ 0 & (1-p)f_1(t-1) & 0 & f_2 \\ 0 & 0 & s & s \end{bmatrix} \begin{bmatrix} n_{1,1} \\ n_{1,2} \\ n_{2,1} \\ n_{2,2} \end{bmatrix}_{t-1}$$

where $f_1 = \exp[r(1 - n_{12}/K_1)], f_2 = 0.8, s = 0.5$, and p value is formerly 1 (no migration) and secondly 0.9 (migration).

FILE FOR STRUCTURED DDSSM (Figs. 8 and 9)

```
{ STRDDSSM.ulm = ASCII file to run equation of Section 5 and Figures 8 & 9
{ This is the "STRUCTURED DENSITY DEPENDENT SOURCE-SINK MODEL"

defmod STRDDSSM(4)
mat : G
vec : v

defvec v(4)
n11 , n12 , n21 , n22

defmat G(4)
0 ,          p*f1 ,      0 ,     0
s ,          s ,         0 ,     0
0 ,          (1-p)*f1 ,  0 ,     f2
0 ,          0 ,         s ,     s

defvar n11 = 1

defvar n12 = 0

defvar n1 = n11 + n12

defvar n21 = 0

defvar n22 = 0

defvar n2 = n21 + n22

defvar p = 0.9

defvar f1 = exp(r1*(1-(n12/K1)))

defvar f2 = 0.8

defvar s = 0.5

defvar r1 = 3.1

defvar K1 = 100
```

$$\begin{bmatrix} 0 & (1-m_1)f_1 & 0 & m_2 f_2 \\ s_1 & s_1 & 0 & 0 \\ 0 & m_1 f_1 & 0 & (1-m_2)f_2 \\ 0 & 0 & s_2 & s_2 \end{bmatrix}$$

Simulations of Sec. 5 turn following the next commands

COMMANDS FOR THE STRUCTURED DDSSM (Figs. 8 and 9)

COMMAND	ACTION	RESULT
run 100	runs 100 time steps	
init	initiates time	
F1	pass to graph mode	
F2	runs 100 time steps	FIGURE 8a
change p 1	changes p value to unity	
F2	runs 100 time steps	FIGURE 8b
F1	pass to text mode	
graph n11 n12	declares variables to plot	
xscale 0 225	dimensions x co-ordinate	
yscale 0 225	dimensions y co-ordinate	
run 50	runs 50 time steps	FIGURE 9a
init	initiates time	
run 100	runs 100 time steps	FIGURE 9b
init	initiates time	
run 1000	runs 1000 time steps	FIGURE 9c
change p 0.9	changes p value	
run 1500	runs 1500 time steps	FIGURE 9d
change n11 0	changes $n11$ value to zero	
change n12 7	changes $n12$ value to 7	
change n21 13	changes $n21$ value to 13	
change n22 1	changes $n22$ value to unity	
F2	runs 1500 time steps	FIGURE 9e