LINEAR DISCRETE MODELS WITH DIFFERENT TIME SCALES

Eva Sánchez[1], Rafael Bravo de la Parra[2], Pierre Auger[3]

[1] Depto. Matemáticas, E.T.S.I. Industriales, U.P.M., c/ José Gutiérrez Abascal, 2, 28006 Madrid, Spain.
[2] Depto. Matemáticas, Univ. de Alcalá, 28871 Alcalá de Henares, Madrid, Spain.
[3] Univ. Claude Bernard-Lyon 1, 43 Boul. 11 novembre 1918, F-69622 Villeurbanne Cedex, France.

ABSTRACT

Aggregation of variables allows to approximate a large scale dynamical system (the micro-system) involving many variables into a reduced system (the macro-system) described by a few number of global variables. Approximate aggregation can be performed when different time scales are involved in the dynamics of the micro-system. Perturbation methods enable to approximate the large micro-system by a macro-system going on at a slow time scale. Aggregation has been performed for systems of ordinary differential equations in which time is a continuous variable. In this contribution, we extend aggregation methods to time-discrete models of population dynamics. Time discrete micro-models with two time scales are presented. We use perturbation methods to obtain a slow macro-model. The asymptotic behaviours of the micro and macro-systems are characterized by the main eigenvalues and the associated eigenvectors. We compare the asymptotic behaviours of both systems which are shown to be similar to a certain order.

KEYWORDS Approximate aggregation of variables, population dynamics, perturbations, time scales, eigenvalues and eigenvectors analysis.

1. INTRODUCTION

Ecological modelling deals with systems involving a large number of variables. Indeed, an ecosystem is a set of interacting populations. Populations are composed of individuals of different ages or in different physiological stages. Individuals do perform several activities. For example, they search for food of different types, they take care of youngs a.s.o. Furthermore, individuals move and can go to different sites. Thus, populations are divided into various sub-populations corresponding to ages, stages, individual states or activities, phenotypes, genotypes, spatial patches etc. When modelling ecological systems, we are faced to a complexity of structures of populations.

A first solution is to build a mathematical model describing the real system in details. This leads to a family of models involving a very large number of variables. The

Acta Biotheoretica **43**: 465–479, 1995.
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complexity of the system is included in the model. Few mathematical techniques are available for these models which are difficult to handle. Mostly, one must use computer simulations. Robustness of the solutions with respect to parameters and initial conditions is in general unknown. If one wants to take into account all aspects in the same model, this leads to a complex model involving a too large number of coupled variables.

On the contrary, many models of ecological communities only deal with a few number of variables. This means that the structure of the populations is often ignored. The populations are considered as entities and are described by a single variable, for example the total population or density. This simplification implies that the effect of the internal structure of the population is neglected. It is an assumption corresponding to an approximation of the total system by a reduced system which has to be checked. However, in most cases, simplified models are used and few arguments are given to justify these models.

Our approach is half way between these two approaches. We intend to take into account the existence of different time scales to proceed to approximations which allow to substitute to a large scale system a reduced model. Thus, we start with a large scale model but, we use methods to reduce it into a simple aggregated version. Perturbation and averaging methods allow to perform these approximations in a rigorous way and lead to a simplification of the initial system into a reduced system which is described by few global variables at a slow time scale. Moreover, these approximations not only provide a simple version but also, interaction terms between the fast and slow dynamics which have important ecological significances.

The simplified model is an approximation of the initial system and is obtained by an approximate aggregation of variables. In previous contributions (Auger, 1989; Auger & Benoit, 1993; Auger & Roussarie, 1994), we realized aggregations of systems of ordinary differential equations with different time scales. In these models, time was a continuous real variable. The aim of this work is to perform approximate aggregation in time discrete models. A first contribution can be found in Bravo *et al.* (to appear) in which we described the growth of an age and patch structured population.

Time discrete models are widely used in population dynamics and many ecological models involve a discrete time. For example, the Leslie model describes an age structured population at discrete times (Caswell, 1989; Logofet, 1993). The Nicholson-Bailey model describes the dynamics of a host-parasitoid system of insect populations (Edelstein-Keshet, 1988). Time discrete models are particulary well adapted for the study of the life cycle of different populations. When the reproduction occurs periodically each year, time discrete models can provide the density of the populations at consecutive generations.

Most of the usual time discrete models describe the dynamics of the total density of population. However, individuals migrate and go to different patches, they also perform different types of activity (such as search of parasites or preys, attack, etc.) at a fast time scale in comparison to age or stage changes or else to the overall growth of the populations to which they belong. In order to take into account the patch dynamics and the individual behaviour, it is necessary to subdivide the populations into several subpopulations associated to spatial patches or to individual states. Then, one must start with a time discrete model which describes the dynamics of many subpopulations.

In this article, we present different time discrete models with subpopulations dynamics at different time scales. We use aggregation methods to condense this large scale model into a reduced version. We prove that the asymptotic behaviours of the initial large scale system and of the reduced approximated system are close enough when the two time scales are sufficiently different. Following (Bravo *et al.*, to appear) we show that the main eigenvalues and the associated eigenvectors of initial and reduced systems are of the same order.

2. TWO DISCRETE MODELS THAT DISTINGUISH TIME SCALES

We suppose a stage-structured population, then classified into groups or stages based on the structure of the life cycle. Moreover, each of these groups is divided into several subgroups, that we consider as being different spatial patches, different individual activities or any other character that could change the life cycle parameters.

Our study is general. Thus, we do not state in detail the nature of the subpopulations which can correspond to patches, individual states or any other types of subpopulations. We consider a set of q populations (or groups) which are subdivided into subpopulations (or subgroups). Let x_n^{jk} be the density of subpopulation k of population j at time n, $j = 1,...,q$ and $k = 1,...,N^j$. N^j is the number of subpopulations of population j and N is the total number of variables, i.e. of subpopulations, $N = N^1 +...+ N^q$. We use vector X_n to describe the total population at time n. This vector is a set of population vectors $\bar{x}_n^j$ describing the internal structure of each subpopulations as follows:

$$X_n = (\bar{x}_n^1,\cdots,\bar{x}_n^q)^T \quad \text{where} \quad \bar{x}_n^j = (x_n^{j1},\cdots,x_n^{jN^j})$$

and $(*,...,*)^T$ denotes transposition.

In the evolution of this population we distinguish between two different dynamics, a slow one and a fast one.

The slow dynamics, for a certain fixed projection interval, is represented by a non-negative projection matrix M, that in this context is usually called *Leftkovitch matrix*. M is divided into blocks M_{ij}, $1 \le i,j \le q$,

$$M = \begin{bmatrix} M_{11} & M_{12} & \cdots & M_{1q} \\ M_{21} & M_{22} & \cdots & M_{2q} \\ \vdots & \vdots & \ddots & \vdots \\ M_{q1} & M_{q2} & \cdots & M_{qq} \end{bmatrix}$$

being M_{ij} of dimensions $N^i \times N^j$ and representing the rates of transference of individuals from the subgroups of group j to the subgroups of group i.

The fast dynamics is, for every group $i,j = 1,...,q$, internal, conservative of the total number of individuals and with an asymptotically stable distribution among the subgroups.

For every group j, the fast dynamics, considering a fixed projection interval, small in comparison with that chosen for the slow dynamics, is represented by a projection matrix P_j, which is a regular stochastic matrix of dimensions $N^j \times N^j$. The matrix P that represents the fast dynamics for the whole population is then

$$P = \text{diag}\{P_1,...,P_q\}$$

Every matrix P_j has an asymptotically stable probability distribution $\bar{v}_j$ that verifies the following properties:

$$P_j\bar{v}_j = \bar{v}_j \quad ; \quad P_j^T\bar{1}_j = \bar{1}_j$$

where P_j^T is the transpose of P_j, $\bar{1}_j = (1,...,1)^T$, $(N^j \times 1)$ and $< \bar{v}_j, \bar{1}_j >= 1$. We define

$$\bar{P}_j = \lim_{k\to\infty} P_j^k = (\bar{v}_j|...|\bar{v}_j)$$

where P_j^k is the kth power of the matrix P_j.

We denote diag$\{\bar{P}_1,...,\bar{P}_q\}$ by $\bar{P}$, and so we have $\lim_{k\to\infty} P^k = \bar{P}$.

Though in the continuous case it is immediate to include two different time scales, (see Auger, 1989), there is not a direct way to do so in the discrete case. In our model we have to combine two projection matrices whose associated projection intervals of which one much longer than the other. To avoid this problem we propose two qualitatively similar models which can prove to be a good approximate aggregation.

In the first model we use as projection interval the one associated to the fast dynamics, that is, to the matrix P. We need, therefore, to approximate the effect of matrix M over a projection interval much shorter than its own. For that we use matrix

$$M(\varepsilon) = \varepsilon M + (1-\varepsilon)\, I_N$$

where $\varepsilon > 0$ and little enough.

We could think that $M(\varepsilon)$ makes M act in proportion ε, as little as we want, and let variables unchanged in proportion $1 - \varepsilon$. From a mathematical point of view the following property of $M(\varepsilon)$ reflects the fact that we have approximately translated the dynamics of M to the time scale of P:

If M has a dominant eigenvalue λ with an associated eigenvector $\bar{v}$, then $M(\varepsilon)$ has $\varepsilon\lambda + (1-\varepsilon)$ as strictly dominant eigenvalue and $\bar{v}$ is also its associated eigenvector.

That implies that dynamics associated to M and $M(\varepsilon)$ have the same asymptotically stable stage distribution but M has a much greater growth rate than $M(\varepsilon)$ because $\varepsilon\lambda + (1 - \varepsilon)$ is closer to 1 than λ.

The first model consist of the following system of linear difference equations

$$X_{n+1} = M(\varepsilon)PX_n \tag{1}$$

In the second model the projection interval coincides with that of the slow dynamics, the one associated to matrix M. And so, we need to approximate the effect of matrix P over a projection interval a number times longer than its own. We suppose in that case that P has operated such a number of times, that is, we use matrix P^k, where k is a big enough integer.

In that way our second model consist in the following system of linear difference equations:

$$X_{n+1} = MP^kX_n \tag{2}$$

3. AGGREGATION OF MODEL $X_{n+1} = M(\varepsilon)PX_n$

In this and the next section we approximate a general system of N variables, those corresponding to the subgroups, by an aggregated system of q variables and those associated to the groups. We shall prove that the general and aggregated system exhibit a similar asymptotic behaviour; to be more precise, that the elements defining the asymptotic behaviour of both systems, dominant eigenvalues and eigenvectors, coincide to a certain degree.

Beginning with the general system (1) and following the notation of the former section we define the global variables

$$x_n^j = \sum_{k=1}^{N^j} x_n^{jk}, \quad j = 1,\dots,q \tag{3}$$

that indicate the total number of individuals in every group.

Those new variables could be obtained from vector X_n multiplying by matrix $U = \mathrm{diag}\{\bar{1}_1^T,\dots,\bar{1}_q^T\}$

$$(x_n^1,\dots, x_n^q)^T = UX_n \tag{4}$$

If in the general system (1) we multiply by matrix U

$$UX_{n+1} = U\,(M(\varepsilon)P)\,X_n \tag{5}$$

we get the global variables in the first member but we do not get an autonomous system on these variables.

If the system (5) were autonomous on the global variables, we would have obtained an example of what it is called *perfect aggregation*, see (Iwasa *et al.*, 1987), that is only possible in very particular cases.

To avoid this problem we consider the following system instead of system (5)

$$U\,X_{n+1} = U\,(M(\varepsilon)P)\,\bar{P}X_n \tag{6}$$

where we suppose that, before aggregating, the subgroups variables have reached the stable distributions associated to the fast dynamics.

To describe the so-called aggregated system we need to define a new matrix

$$\bar{P}_c = \mathrm{diag}\{\bar{v}_1,\dots,\bar{v}_q\}$$

If we have a vector belonging to R_+^q, that indicates the total number of individuals included in the different groups, and we multiply it by $\bar{P}_c$, we will obtain a vector belonging to R_+^N that would give how these individuals would be divided in the subgroups depending on the stable distributions of the fast dynamics.

In the following Lemma we state the properties of the matrices P, $\bar{P}$, $\bar{P}_c$, and U that we will use frequently throughout the paper.

Lemma 3.1. *The matrices P, $\bar{P}$, $\bar{P}_c$, and U verify the following identities:*

a) $\bar{P}P = P\bar{P} = \bar{P}\bar{P} = \bar{P}$

b) $P\bar{P}_c = \bar{P}\bar{P}_c = \bar{P}_c$

c) $U\bar{P} = U$; $U\bar{P}_c = I_q$; $\bar{P}_cU = \bar{P}$

The system (6) could be written as follows

$$UX_{n+1} = UM(\varepsilon)\bar{P}_c(UX_n)$$

and denoting the new variables UX_n by Y_n, we obtain

$$Y_{n+1} = UM(\varepsilon)\bar{P}_cY_n$$

where

$$UM(\varepsilon)\bar{P}_c = U(\varepsilon M + (1-\varepsilon)I_N)\bar{P}_c = \varepsilon(UM\bar{P}_c) + (1-\varepsilon)I_q$$

and making $\bar{M} = UM\bar{P}_c$ and $\bar{M}(\varepsilon) = \varepsilon\bar{M} + (1-\varepsilon)I_q$, the aggregated system presents the next simple form

$$Y_{n+1} = \bar{M}(\varepsilon)Y_n \qquad (7)$$

We point out that $\bar{M}$ and $\bar{M}(\varepsilon)$, and M and $M(\varepsilon)$ are related in the same way.

The coefficients of the matrix $\bar{M} = (\bar{m}_{ij})_{q\times q}$ are obtained using the next expression

$$\bar{m}_{ij} = \bar{1}_i^T M_{ij}\bar{v}_j$$

So $\bar{M}$ could be considered as a classical Leftkovitch matrix whose coefficients are calculated from the coefficients of M and the stable distributions of fast dynamics.

$\bar{M}(\varepsilon)$ would depict in a certain sense the effect of $\bar{M}$ over a projection interval ε times shorter than that of $\bar{M}$.

Summarizing, we have three different kinds of variables, the general variables X_n that verify (1), the exact global variables UX_n that verify (5), and finally the approximate aggregated variables that verify (7).

Below we describe the asymptotic behaviour of these variables, showing their similarities. The following results are direct consequences of those proven in Bravo *et al.* (to appear), see Appendix I. Though we could state more general results, we start from the following hypothesis:

Hypothesis (H). $\bar{M}$ is a primitive matrix.

So, $\bar{M}$ possesses a strictly dominant eigenvalue $\lambda > 0$, and associated to λ two positive eigenvectors, a left one $\bar{v}_l$ and a right one $\bar{v}_r$:

$$\bar{v}_l^T\bar{M} = \lambda\bar{v}_l^T \quad ; \quad \bar{M}\bar{v}_r = \lambda\bar{v}_r$$

3.1. Asymptotic behaviour of the aggregated system (7)

$\bar{M}(\varepsilon)$ is a primitive matrix, with $\lambda(\varepsilon) = \varepsilon\lambda + 1 - \varepsilon = 1 + \varepsilon(\lambda-1)$ as strictly dominant eigenvalue, and $\bar{v}_l$ and $\bar{v}_r$ as left and right associated eigenvectors, respectively.

So, if Y_0 is any non negative initial condition we have

$$\lim_{n\to\infty} \frac{Y_n}{(\lambda(\varepsilon))^n} = \frac{<\bar{v}_1, Y_0>}{<\bar{v}_1, \bar{v}_r>}\bar{v}_r$$

where $<*,*>$ is the usual scalar product in R^q.

3.2. Asymptotic behaviour of the general system (1)

$M(\varepsilon)P$ is a primitive matrix, with its strictly dominant eigenvalue of the form

$$\lambda(\varepsilon) + O(\varepsilon^2) \quad (\varepsilon \to 0)$$

and its left and right associated eigenvectors, respectively:

$$U^T\bar{v}_l + O(\varepsilon) \quad ; \quad \bar{P}_c\bar{v}_r + O(\varepsilon) \quad (\varepsilon\to 0)$$

Then, if X_0 is any non negative initial condition we obtain

$$\lim_{n\to\infty} \frac{X_n}{(\lambda(\varepsilon)+O(\varepsilon^2))^n} = \frac{< U^T\bar{v}_l+O(\varepsilon),X_0 >}{< U^T\bar{v}_l+O(\varepsilon),\bar{P}_c\bar{v}_r+O(\varepsilon) >}(\bar{P}_c\bar{v}_r+O(\varepsilon))$$

$$= \frac{< \bar{v}_l,UX_o >}{< \bar{v}_l,\bar{v}_R >}\bar{P}_c\bar{v}_r + O(\varepsilon)$$

3.3. Asymptotic behaviour of the exact global variables UX_n

$$\lim_{n\to\infty} \frac{UX_n}{(\lambda(\varepsilon)+O(\varepsilon^2))^n} = \frac{< \bar{v}_1,UX_0 >}{< \bar{v}_1,\bar{v}_r >}\bar{v}_r + O(\varepsilon)$$

4. AGGREGATION OF MODEL $X_{n+1} = MP^kX_n$

The results of last section that allow approximate aggregation of the system $X_{n+1} = M(\varepsilon)PX_n$ were based upon considering the matrix $M(\varepsilon)P = P + \varepsilon(M-I)P$ as an analytical perturbation of the matrix P, see Bravo *et al.* (to appear). In this section the results concerning approximation will be deduced from the identities

$$\lim_{k\to\infty} P^k = \bar{P} \quad , \quad MP^k = M\bar{P} + M(P^k-\bar{P})$$

that let us consider the matrix MP^k as a perturbation of matrix $M\bar{P}$

Starting with the general system (2), which we will call perturbed system, we define the so-called non-perturbed system

$$X_{n+1} = M\,\bar{P}\,X_n \tag{8}$$

This system admits the interpretation of being an approximation of (2) in which the last dynamics has reached its stable distributions.

In order to build an aggregated system we define the global variables x_n^j as in (3) and (4), and we verify that

$$UX_{n+1} = U\,M\,P^k\,X_n$$

is again a non-autonomous system on these global variables.

Nevertheless, if we aggregate variables in the non-perturbed system (8) we obtain

$$UX_{n+1} = U\,M\,\bar{P}\,X_n = U\,M\,\bar{P}_c\,U\,X_n$$

and making $Y_n = UX_n$ and $\bar{M} = UM\bar{P}_c$, following the notation of the last section, we get the next aggregated system:

$$Y_{n+1} = \bar{M}Y_n \tag{9}$$

We could remark that the non-perturbed system (8) is one of those few exceptional systems that are susceptible of being perfectly aggregated.

The rest of the section is devoted to the development of similar results to those proven in Section 3 about the asymptotic behaviour of the different treated systems. We start with relating the spectral properties of the matrices $M\bar{P}$ and $\bar{M}$, associated to the systems (8) and

(9), and later, using the matrix perturbation theory, we will compare the asymptotic elements of the matrices $M\bar{P}$ and MP^k, what will yield the relation between systems (8) and (2).

We summarize in the next theorem the spectral relations between matrices $M\bar{P}$ and $\bar{M}$ that we will use below.

Theorem 4.1. *The matrices $M\bar{P}$ and $\bar{M}$ verify:*

a) $\det(\lambda I_N - M\bar{P}) = \lambda^{N-q}\det(\lambda I_q - \bar{M})$.

b) *If $\bar{u}_r \neq 0$ is a right eigenvector of $M\bar{P}$ associated to the eigenvalue $\lambda \neq 0$, then $U\bar{u}_r \neq 0$ is a right eigenvector of $\bar{M}$ associated also to λ.*

c) *If $\bar{v}_r \neq 0$ is a right eigenvector of $\bar{M}$ associated to the eigenvalue $\lambda \neq 0$, then $M\bar{P}_c\,\bar{v}_r \neq 0$ is a right eigenvector associated to the same eigenvalue λ.*

d) *If $\bar{u}_l \neq 0$ is a left eigenvector of $M\bar{P}$ associated to the eigenvalue $\lambda \neq 0$, then there exists $\bar{v}_l \in R^q - \{0\}$ such that $\bar{u}_l = U^T\bar{v}_l$, and $\bar{v}_l$ is a left eigenvector of $\bar{M}$ associated to λ too.*

e) *If $\bar{v}_l \neq 0$ is a left eigenvector of $\bar{M}$ associated to the eigenvalue $\lambda \neq 0$, then $U^T\bar{v}_l \neq 0$ is a left eigenvector of $M\bar{P}$ associated also to λ.*

Proof. a) $\bar{P}$ is a projector and so we could write

$$R^N = \ker\bar{P} \oplus \operatorname{Im}\bar{P}$$

Then we build a basis of R^N starting with any basis of $\ker\bar{P}$ and adding the column vectors of matrix $\bar{P}_c$, that form a basis of $\operatorname{Im}\bar{P}$. Let K be the matrix of dimensions $N \times (N-q)$ whose columns are the vectors in the basis of $\ker\bar{P}$. We now find the matrix representation, K, of the operator $M\bar{P}$ respect to the basis first defined. K should verify the following identity:

$$M\bar{P}(K|\bar{P}_c) = (K|\bar{P}_c)X$$

as $M\bar{P}K = 0$, decomposing K into appropriate blocks, we have

$$(0|M\bar{P}\bar{P}_c) = (K|\bar{P}_c)\begin{pmatrix}0 & A\\ 0 & B\end{pmatrix}$$

and

$$(0|M\bar{P}_c) = (0|KA+\bar{P}_cB)$$

So

$$M\bar{P}_c = KA+\bar{P}_cB$$

and multiplying on the left by U:

$$UM\bar{P}_c = UKA+U\bar{P}_cB$$

we obtain

$$\bar{M} = U\bar{P}KA+I_qB = B$$

what yields

$$K = \begin{pmatrix} 0 & A \\ 0 & \bar{M} \end{pmatrix}$$

and then follows that

$$\det(\lambda I_N - M\bar{P}) = \det(\lambda I_N - K) = \lambda^{N-q}\det(\lambda I_q - \bar{M})$$

b) $\bar{u}_r \neq 0$ verifies $M\bar{P}\bar{u}_r = \lambda\bar{u}_r \neq 0$.
As $M\bar{P}\bar{u}_r = M\bar{P}_c U\bar{u}_r \neq 0$, then $U\bar{u}_r \neq 0$. Moreover

$$\bar{M}U\bar{u}_r = UM\bar{P}_c U\bar{u}_r = UM\bar{P}\bar{u}_r = \lambda U\bar{u}_r$$

c) $\bar{v}_r \neq 0$ verifies $\bar{M}\bar{v}_r = \lambda\bar{v}_r \neq 0$.
As $UM\bar{P}_c\bar{v}_r \neq 0$, then $M\bar{P}_c\bar{v}_r \neq 0$. Also

$$M\bar{P}M\bar{P}_c\bar{v}_r = M\bar{P}_c UM\bar{P}_c\bar{v}_r = M\bar{P}_c\bar{M}\bar{v}_r = \lambda M\bar{P}_c\bar{v}_r$$

d) $\bar{u}_l \neq 0$ verifies $\bar{u}_l^T M\bar{P} = \lambda\bar{u}_l^T$.

As the first N^1 columns of $\bar{P}$ are identical, and so happen to the next N^2 columns, and so on, we have the same identities among the columns of $\bar{u}_l^T M\bar{P}$ and therefore among the components of $\bar{u}_l^T$.
From that we deduce that there exists a vector $\bar{v}_l \in R^q - \{0\}$ such that

$$\bar{v}_l^T U = \bar{u}_l^T \quad \text{and also} \quad \bar{v}_l^T = \bar{u}_l^T\bar{P}_c$$

Moreover

$$\bar{v}_l^T\bar{M} = \bar{v}_l^T UM\bar{P}_c = \bar{u}_l^T M\bar{P}\bar{P}_c = \lambda\bar{u}_l^T\bar{P}_c = \lambda\bar{v}_l^T$$

e) $\bar{v}_l \neq 0$ verifies $\bar{v}_l^T\bar{M} = \lambda\bar{v}_l^T \neq 0$.
So $U^T\bar{v}_l \neq 0$ and

$$(U^T\bar{v}_l)^T M\bar{P} = \bar{v}_l^T UM\bar{P}_c U = \lambda\bar{v}_l^T U = \lambda(U^T\bar{v}_l)^T.$$

We begin now the study of the spectral relations between the matrices $M\bar{P}$ and MP^k, having in mind that MP^k could be considered a perturbation of $M\bar{P}$:

$$MP^k = M\bar{P} + M(P^k - \bar{P}) = M\bar{P} + M(P - \bar{P})^k$$

As every matrix P_i, $i = 1,\ldots,q$ is a regular stochastic matrix of dimensions $N^i \times N^i$, we could order their eigenvalues according to decreasing modulus in the following way:

$$\lambda_i^1 = 1 > |\lambda_i^2| \geq \ldots \geq |\lambda_i^{N^i}|$$

If we do the same with the matrix P we should obtain

$$\lambda_1 = \ldots = \lambda_q = 1 > |\lambda_{q+1}| \geq \ldots \geq |\lambda_N|$$

where

$$|\lambda_{q+1}| = \max|\lambda_i^2| \; ; \quad i = 1,\ldots,q$$

The next proposition allows to find a bound of the perturbation.

Proposition 3.2. *If $\| * \|$ is any consistent norm in the space $\mathcal{M}_{N\times N}$ of $N \times N$ matrices, then for every $\alpha > |\lambda_{q+1}|$ it is verified that*

$$\|MP^k - M\bar{P}\| = o(\alpha^k) \quad (k \to \infty)$$

Proof. See Appendix II.

Before stating the asymptotic behaviours of the different mentioned systems, we make the same hypothesis proposed in Section 3.

Hypothesis (H). *$\bar{M}$ is a primitive matrix.*

Let $\lambda > 0$ be the strictly dominant eigenvalue of $\bar{M}$, and $\bar{v}_l$ and $\bar{v}_r$ its associated left and right eigenvectors, respectively. We then have that, given any non-negative initial condition Y_0, the aggregated system (9) verifies

$$\lim_{n \to \infty} \frac{Y_n}{\lambda^n} = \frac{<\bar{v}_1, Y_0>}{<\bar{v}_1, \bar{v}_r>} \bar{v}_r$$

Proposition 4.3. *The non perturbed system (8), given any non-negative initial condition X_0 verifies that*

$$\lim_{n \to \infty} \frac{X_n}{\lambda^n} = \frac{<\bar{v}_l, UX_0>}{\bar{v}_l, \bar{v}_r>} \frac{1}{\lambda} M\bar{P}_c\bar{v}_r \tag{10}$$

Proof. From Theorem 4.1 we deduce that

$$\begin{aligned}\lim_{n \to \infty} \frac{X_n}{\lambda^n} &= \frac{<U^T\bar{v}_l, X_0>}{<U^T\bar{v}_1, M\bar{P}_c\bar{v}_r>} M\bar{P}_c\bar{v}_r \\ &= \frac{<\bar{v}_l, UX_0>}{<\bar{v}_l, UM\bar{P}_c\bar{v}_r>} M\bar{P}_c\bar{v}_r \\ &= \frac{<\bar{v}_l, UX_0>}{<\bar{v}_l, \lambda\bar{v}_r>} M\bar{P}_c\bar{v}_r\end{aligned}$$

and that yields (10).

Proposition 4.4. *The matrix MP^k has a strictly dominant eigenvalue*

$$\begin{aligned}\mu_k &= \lambda + \frac{<U^T\bar{v}_l, M(P-\bar{P})^k M\bar{P}_c\bar{v}_r>}{<U^T\bar{v}_l, M\bar{P}_c\bar{v}_r>} + o(\alpha^{2k}) \\ &= \lambda + O(\alpha^k)\end{aligned}$$

and associated to μ_k there exist a left and a right eigenvectors that could be written in the following form, respectively

$$U^T\bar{v}_l + O(\alpha^k) \quad (positive)$$

and

$$M\bar{P}_c\bar{v}_d + O(\alpha^k) \quad (non\text{-}negative)$$

Proof. Immediate consequence of the Theorem in Appendix II.

Theorem 4.5. *Let system (2) verify (H). Then, given any non negative initial condition X_0 the system (2) verifies*

$$\lim_{n\to\infty} \frac{X_n}{(\mu_k)^n} = \frac{<\bar{v}_l, UX_0>}{<\bar{v}_l, \bar{v}_r>} \frac{1}{\lambda} M\bar{P}_c\bar{v}_r + O(\alpha^k) \tag{11}$$

Proof. From Proposition 4.4 we have

$$\lim_{n\to\infty} \frac{X_n}{(\mu_k)^n} = \frac{<U^T\bar{v}_l + O(\alpha^k), X_0>}{<U^T\bar{v}_l + O(\alpha^k), M\bar{P}_c\bar{v}_r + O(A^k)>} \left(M\bar{P}_c\bar{v}_r + O(\alpha^k)\right)$$

$$= \frac{<\bar{v}_l, UX_0> + O(\alpha^k)}{<\bar{v}_l, M\bar{v}_r> + O(\alpha^k)} \left(M\bar{P}_c\bar{v}_r + O(\alpha^k)\right)$$

$$= \left(\frac{<\bar{v}_l, UX_0>}{<\bar{v}_l, \bar{v}_r>} \frac{1}{\lambda} + O(\alpha^k)\right) \left((M\bar{P}_c\bar{v}_r + O(\alpha^k)\right)$$

and that yields (11).

We should notice that the exact global variables verifies

$$\lim_{n\to\infty} \frac{UX_n}{(\lambda + O(\alpha^k))^n} = \frac{<\bar{v}_l, UX_0>}{<\bar{v}_l, \bar{v}_r>} \frac{1}{\lambda} UM\bar{P}_c\bar{v}_r + O(\alpha^k)$$

$$= \frac{<\bar{v}_l, UX_0>}{<\bar{v}_l, \bar{v}_r>} \bar{v}_r + O(\alpha^k)$$

5. CONCLUSION

Our general results allow for different applications. For example, it is possible to model a patch and age structured population, or else a patch structured community. Age structured populations are commonly described by a Leslie matrix. When individuals go to different spatial patches, one must also consider the spatial distributions of individuals among the different sites. If patch migration takes place at a fast time scale with respect to age changes, one can describe a patch and age structured population (see Bravo *et al.*, to appear).

It has been shown that spatial heterogeneity can play a very important role regarding the stability of ecological communities (Hassel *et al.*, 1991). This was shown in a time and space discrete version of the host-parasitoid Nicholson-Bailey model. Although the one patch model is always unstable, computer simulations have shown that the spatial version becomes stable when the size n of the $2D$ array of $(n \times n)$ patches is large enough. This result shows that the spatial dynamics can have important consequences for the dynamics and stability of the community.

Our method allows to get the simplified aggregated model and also, to obtain the relationships between the parameters of the aggregated model and the parameters which control the fast dynamics. For example, in the patch and age structured population, the aggregated model is a classical Leslie matrix in which the overall fecundities and aging rates are expressed in terms of the spatial distributions of individuals on the different patches. Thus, a change in the spatial distribution has an effect on the aggregated Leslie matrix which can be calculated.

Facing local unfavourable situations and in order to avoid extinction, two main strategies can be developed, either migration to find a better site or prolonged diapause to wait for a better context in the future. There are two alternate strategies. The Leslie model with fast patch dynamics is a good tool for estimating the advantages of these two different strategies. We are now on the point to confront our model to experimental data relating to an insect population (the chestnut weevil) (Menu, 1993; Debouzie *et al.*, 1993).

In the future we also intend to use our general methods given here for the study of patch structured communities. For example, we plan to model a patch structured host-parasitoid community. An interesting problem is to check if one can obtain similar results than in the cell automaton spatial model of a Nicholson-Bailey model (Hassel *et al.*, 1991).

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APPENDIX I

We present in this appendix a general result developed in Bravo *et al.* (to appear), that implies the asymptotic results of Section 3. (See Baumgartel, 1985; Horn & Johnson, 1985; Kato, 1980).

We follow the notation of Sections 2 and 3.

We have the following general difference equations system depending on the little parameter ε:

$$\begin{bmatrix} \bar{x}^1_{n+1}(\varepsilon) \\ \vdots \\ \bar{x}^q_{n+1}(\varepsilon) \end{bmatrix} = \begin{bmatrix} A_{11}(\varepsilon) & \cdots & A_{1q}(\varepsilon) \\ \vdots & & \vdots \\ A_{q1}(\varepsilon) & \cdots & A_{qq}(\varepsilon) \end{bmatrix} \begin{bmatrix} \bar{x}^1_n(\varepsilon) \\ \vdots \\ \bar{x}^q_n(\varepsilon) \end{bmatrix}$$

or shortly

$$X_{n+1}(\varepsilon) = A(\varepsilon)X_n(\varepsilon) \tag{12}$$

Every matrix $A_{jk}(\varepsilon)$ has dimensions $N^j \times N^k$ and depends holomorphically on ε. So

$$A(\varepsilon) = A(0) + \varepsilon A'(0) + \ldots$$

We make the next two hypothesis on $A(\varepsilon)$:

Hypothesis (H1). *$A(0)$ has the same structure of matrix P, that is, $A_{jk}(0) = 0$ whenever $j \neq k$, and $A_{jj}(0)$ is a regular stochastic matrix, $j,k = 1,\ldots,q$.*

Hypothesis (H2). *Matrix $\bar{P}\,A'(0)\,\bar{P}$ has a simple nonzero eigenvalue μ whose real part is strictly greater than the real parts of the rest of eigenvalues.*

Let $\bar{v}$ be an eigenvector of $\bar{P}A'(0)\bar{P}$ associated to μ. Let

$$B(\varepsilon) = U\,A(\varepsilon)\bar{P}_c = I_q + \varepsilon U\,A'(0)\bar{P}_c + \ldots$$

and so the aggregated system is

$$Y_{n+1}(\varepsilon) = B(\varepsilon)Y_n(\varepsilon)$$

Theorem. *Let system* (12) *verify* (H1) *and* (H2). *Then, there exist* $\delta > 0$ *such that for every* $\varepsilon > 0$, $\varepsilon < \delta$, *we have:*

a) *$A(\varepsilon)$ has a simple eigenvalue whose modulus is strictly dominant and that admits the following expression:*

$$\lambda_{\max}(\varepsilon) = 1 + \varepsilon\mu + o(\varepsilon^2)\ ,\ (\varepsilon \to 0)$$

Associated to this eigenvalue there exist a unique eigenvector of $A(\varepsilon)$ that could be written as follows:

$$\bar{x}(\varepsilon) = \bar{v} + O(\varepsilon)\ ,\ (\varepsilon \to 0)$$

b) *$B(\varepsilon)$ has a simple eigenvalue whose modulus is strictly dominant and that admits the following expansion:*

$$\mu_{\max}(\varepsilon) = 1 + \varepsilon\mu + O(\varepsilon^2)\ ,\ (\varepsilon \to 0)$$

Associated to this eigenvalue there exist the next eigenvector of $B(\varepsilon)$:

$$\bar{y}(\varepsilon) = U\bar{v} + O(\varepsilon)\ ,\ (\varepsilon \to 0)$$

APPENDIX II

Proof of Proposition 3.2.

As $\bar{P}$ is the projector over the eigenspace of P associated to the eigenvalue 1 we have

$$R^N = \mathrm{Im}\bar{P} \oplus \ker \bar{P}$$

and also the restriction of P to $\mathrm{Im}\bar{P}$ is the identity, and so

$$(P - \bar{P})_{\mathrm{Im}\bar{P}} = 0 \; ; \; (P - \bar{P})_{\ker\bar{P}} = P$$

We then conclude that the eigenvalues of $P-\bar{P}$ ordered by decreasing modulus could be written as follows:

$$|\lambda_{q+1}| \geq \ldots \geq |\lambda_N| \geq 0 = \ldots(q)\ldots = 0 \tag{13}$$

Next, we apply the following known result relating the norms and the spectral radius of a matrix:

For every A belonging to the space $\mathcal{M}_{nxn}$ of $n \times n$ matrices and every $\varepsilon > 0$ there exists a consistent norm $\|*\|_\varepsilon$ in $\mathcal{M}_{nxn}$ such that $\rho(A) \leq \|A\|_\varepsilon < \varepsilon + \rho(A)$, being $\rho(A)$ the spectral radius of A.

From (13) we have $\rho(P-\bar{P}) = |\lambda_{q+1}|$ and from the last result we deduce that for every $\alpha > |\lambda_{q+1}|$ we could find a consistent norm $\|*\|_\alpha$ such that

$$\|P - \bar{P}\|_\alpha < \alpha$$

As any two norms in $\mathcal{M}_{nxn}$ are equivalents we have for any norm $\|*\|$ in M_{nxn} and any $k = 1,2,\ldots$ that there exists $C > 0$ such that

$$\|P^k - \bar{P}\| \leq \|P^k - \bar{P}\|_\alpha$$

Finally, for any consistent norm $\|*\|$ we have

$$\lim_{k \to \infty} \frac{\|MP^k - M\bar{P}\|}{\alpha^k} \leq \|M\| C \lim_{k \to \infty} \frac{\|P^k - \bar{P}\|_\alpha}{\alpha^k}$$

$$= \|M\| C \lim_{k \to \infty} \left(\frac{\|P - \bar{P}\|_\alpha}{\alpha} \right)^k = 0$$

Below we state the main result about matrix perturbation that it is applied in Section 4, see (Stewart, 1990).

Theorem. *Let λ be a simple eigenvalue of $n \times n$ matrix A, with left and right eigenvectors $\bar{x}_l$ and $\bar{x}_r$, respectively. Let $\tilde{A} = A + E$ be a perturbation of matrix A, and $\|*\|$ any consistent norm in $\mathcal{M}_{nxn}$. Then there exists a unique eigenvalue $\tilde{\lambda}$ of $\tilde{A}$ such that*

$$\tilde{\lambda} = \lambda + \frac{\bar{x}_l^T E \bar{x}_r}{\bar{x}_l^T \bar{x}_r} + O(\|E\|^2)$$

Moreover, associated to $\tilde{\lambda}$ there exist left and right eigenvectors $\tilde{\bar{x}}_l$ and $\tilde{\bar{x}}_r$, respectively, such that

$$\tilde{\bar{x}}_l = \bar{x}_l + O(\|E\|) \quad ; \quad \tilde{\bar{x}}_r = \bar{x}_r + O(\|E\|)$$

The eigenvalue $\tilde{\lambda}$ is the unique eigenvalue of $\tilde{A}$ close to λ whenever $\|E\|$ is little enough. In our application of that result we will use that if λ is strictly dominant so will be $\tilde{\lambda}$ for little $\|E\|$.