



Aggregation Methods in Population Dynamics Discrete Models

R. BRAVO DE LA PARRA

Dpto. Matemáticas, Universidad de Alcalá de Henares
28871 Alcalá de Henares, Madrid, Spain
mtbravo@alcala.es

E. SÁNCHEZ

Dpto. Matemáticas, E.T.S.I. Industriales, Universidad Politécnica de Madrid
c/ José Gutiérrez Abascal, 2, 28006 Madrid, Spain
c0550005@ccupm.upm.es

Abstract—Aggregation methods try to approximate a large scale dynamical system, the general system, involving many coupled variables by a reduced system, the aggregated system, that describes the dynamics of a few global variables. Approximate aggregation can be performed when different time scales are involved in the dynamics of the general system. Aggregation methods have been developed for general continuous time systems, systems of ordinary differential equations, and for linear discrete time models, with applications in population dynamics.

In this contribution, we present aggregation methods for linear and nonlinear discrete time models. We present discrete time models with two different time scales, the fast one considered linear and the slow one, generally, nonlinear. We transform the system to make the global variables appear, and use a version of center manifold theory to build up the aggregated system in the nonlinear case. Simple forms of the aggregated system are enough for the local study of the asymptotic behaviour of the general system, provided that it has certain stability under perturbations. In linear models, the asymptotic behaviours of the general and the aggregated systems are characterized by their dominant eigenvalues, that are proved to coincide to a certain order.

The general method is applied to aggregate a multiregional Leslie model in the constant rates case (linear) and also in the density dependent case (nonlinear).

Keywords—Approximate aggregation of variables, Population dynamics, Time scales, Dynamical systems.

1. INTRODUCTION

In the modelization of biological systems, particularly ecological ones, we always find very complex systems. An ecosystem, for instance, should be considered as a set of interacting populations; these populations should be considered structured by age and/or some other types of physiological stages; moreover, we should take account of their geographical distribution and we could still go further. Anyway, we should manage to get some insights from this great complexity.

A first method to do this consists in building an abstract model describing the real system in detail. This leads to a family of models involving a very large number of variables. The complexity of the system is included in the model. So, few mathematical results are available for these models that they become analytically unmanageable. The only tool always usable in a study of this sort of system is computer simulation. But in that case, robustness of the solutions with respect to parameters and initial conditions is generally unknown.

This work has been supported by Proyecto DGCYT PB94-0396.

Typeset by $\mathcal{A}\mathcal{M}\mathcal{S}$ - $\mathcal{T}\mathcal{E}\mathcal{X}$

At the other extreme, is a very common method that uses models that avoid almost every detail in order to get mathematically tractable systems. These models of ecological communities only deal with a few variables. But the structure of the populations is often ignored, the populations are considered as entities described by a single variable, such as the total population or density. This simplification is based upon the assumption that the internal structure of the population has no important effect and can be neglected. This assumption corresponds to an approximation of the total system by means of a reduced one that should be checked. However, in most cases, simplified models are used and few arguments are given to justify them.

In between these two methods are the so-called aggregation methods. These methods describe general complex systems that could be approximately studied from simpler ones, and justify their "aggregation". The property of these systems that allows their aggregation is the existence of two or more different time scales. As a result, we can think of a hierarchically structured system with a division into subsystems that are weakly coupled but still exhibit a strong internal dynamics. The idea of aggregation is then to choose a global variable, sometimes called a macrovariable, for each subsystem and to build up a reduced system for these global variables.

The reduced system, or aggregated system, must reflect in a certain way both dynamics, the one corresponding to the fast time scale and the one corresponding to the slow time scale. The slow dynamics of the general system, the initial complex one, usually corresponds to the dynamics of the reduced system, meanwhile, the fast dynamics of the general system is reflected in the coefficients of the reduced one in such a way that it is possible to study the influences between the different hierarchical levels, which seems meaningful from an ecological point of view.

The aggregation methods have already been developed in the case of continuous time systems, systems of ordinary differential equations with different time scales, see [1–4].

The aggregation of discrete systems has also a clear interest. Discrete time models are widely used in population dynamics and many ecological models involve necessarily discrete time. For example, the classical Leslie or Leftkovich models describe an age or stage, respectively, structured population evolving in discrete time, see [5,6]. Discrete models are also very useful in addressing the population dynamics of organisms that have distinct breeding periods and life-cycle stages, notably insects and other arthropods, see [7,8]. A model that has received considerable attention from theoretical and experimental population biologists is that of the host-parasitoid system, in particular, the Nicholson-Bailey model [9,10].

The aggregation of time discrete systems has already been developed by the authors in the linear, density independent case, see [11,12]. In those works we aggregate a very general linear model and prove that the elements defining the asymptotic behaviour of the general and the aggregated systems are equal up to certain order. These results are applied to models of structured populations with subpopulations in each stage class associated to different spatial patches or individual activities, considering a fast time scale for patch or activity dynamics and a slow time scale for demographic processes.

Though there are some widely used linear models, for example the Leslie model, the nonlinear models are recognized to be more realistic, density dependence being a generally accepted characteristic of ecological systems. In this article, we develop aggregation methods in the case of nonlinear discrete models, we are considering systems with a linear fast dynamics but a general nonlinear slow dynamics. We also review the case of linear slow dynamics.

In Section 1, we present a general model that distinguishes two time scales, with a group of populations subdivided into subpopulations. The fast dynamics, apart from linear, is internal for each population and asymptotically leads each population to certain constant proportion among its subpopulations. The slow dynamics is as general as possible, being represented by a smooth mapping. The global variables used in the aggregation are the total number of individuals in each population, which are constants of motion for the fast dynamics. This general system is transformed so as to make the global variables appear, and the differences between original

variables and the fast dynamics equilibrium values. The latter tends to zero, if close enough to the equilibrium, while the global ones dominate the dynamics of the system.

In Section 2, we consider a linear model whose dynamics is governed by a strictly dominant eigenvalue and its associated eigenvector. We propose an approximated aggregated system, supposing that the fast dynamics has reached its equilibrium frequencies, and show that the dominant eigenvalues of the initial and the aggregated systems are equal to first order, and that the aggregated version of the zero order approximation of the dominant eigenvector of the initial system is a dominant eigenvector of the aggregated system.

Section 3 uses a version of center manifold theorem for an invariant manifold of attractive equilibrium points to make precise the study of the nonlinear case.

And finally, in Section 4, we propose a model of an age-structured population divided into geographical patches. At the fast time scale, we have the migration dynamics, and at the slow time scale the demographic dynamics. The aggregated system, whose variables are the total number of individuals in each age class, is a Leslie model at a slow time scale. We present density independent and density dependent versions, and apply the results of previous sections.

2. GENERAL MODEL

We suppose in discrete time, a general population classified into groups and each of these groups is divided into several subgroups. We consider a set of p populations (or groups) which are subdivided into subpopulations (or subgroups), with population i having N^i subpopulations, $i = 1, \dots, p$. Let x_n^{ij} be the density of subpopulation j of population i at time n , $j = 1, \dots, N^i$ and $i = 1, \dots, p$. N is the total number of variables, i.e., of subpopulations, $N = N^1 + \dots + N^p$. We use vector \mathbf{X}_n to describe the total population at time n . This vector is a set of population vectors \mathbf{x}_n^i describing the internal structure of each subpopulations as follows:

$$\mathbf{X}_n = (\mathbf{x}_n^1, \dots, \mathbf{x}_n^p)^\top, \quad \text{where } \mathbf{x}_n^i = (x_n^{i1}, \dots, x_n^{iN^i})^\top,$$

and $^\top$ denotes transposition.

In the evolution of this population, we distinguish between two different time scales, and so we will speak henceforth of two different dynamics, a slow one and a fast one. The fast dynamics is considered linear while the slow dynamics is generally nonlinear. We represent all this by means of the following system:

$$\mathbf{X}_{n+1} = \mathbf{P}\mathbf{X}_n + \varepsilon\mathbf{F}(\mathbf{X}_n, \varepsilon), \quad (1)$$

where \mathbf{P} is an $N \times N$ matrix and \mathbf{F} is a mapping from $\mathbf{R}^N \times (0, \varepsilon_0)$ to \mathbf{R}^N that we will describe below, (2) and (6), and ε is a small positive parameter, $0 < \varepsilon < \varepsilon_0$.

The fast dynamics, represented by the term $\mathbf{P}\mathbf{X}$, must verify some hypotheses so that the general system could be approximately aggregated. For every group i , $i = 1, \dots, p$, let fast dynamics be internal conservative of the total number of individuals and with an asymptotically stable frequency distribution among the subgroups. These hypotheses are fulfilled if we let \mathbf{P} be a block diagonal matrix

$$\mathbf{P} = \text{diag}\{\mathbf{P}_1, \dots, \mathbf{P}_p\}, \quad (2)$$

where \mathbf{P}_i is a regular stochastic matrix of dimensions $N^i \times N^i$ that is the projection matrix associated to the fast dynamics for every group i .

Every matrix \mathbf{P}_i has an asymptotically stable probability distribution $\boldsymbol{\nu}^i = (\nu^{i1}, \dots, \nu^{iN^i})^\top$ that verifies the following properties:

$$\mathbf{P}_i \boldsymbol{\nu}^i = \boldsymbol{\nu}^i, \quad \mathbf{P}_i^\top \mathbf{1}^i = \mathbf{1}^i,$$

where $\mathbf{1}^i = (1, \dots, 1^{N^i})$ and $\mathbf{1}^i \boldsymbol{\nu}^i = 1$. We define

$$\bar{\mathbf{P}}_i = \lim_{k \rightarrow \infty} \mathbf{P}_i^k = (\boldsymbol{\nu}^i | \dots | \boldsymbol{\nu}^i),$$

where \mathbf{P}_i^k is the k^{th} power of the matrix \mathbf{P}_i .

We denote $\text{diag}\{\bar{\mathbf{P}}_1, \dots, \bar{\mathbf{P}}_p\}$ by $\bar{\mathbf{P}}$, and so we have

$$\lim_{k \rightarrow \infty} \mathbf{P}^k = \bar{\mathbf{P}}. \quad (3)$$

The global variables whose dynamics is going to be approximated by the aggregated system are the total number of individuals in every population, and we shall denote it by s^i

$$s^i = \sum_{j=1}^{N^i} x^{ij}, \quad i = 1, \dots, p,$$

and they form the vector $\mathbf{s} = (s^1, \dots, s^p)^\top$. Vector \mathbf{s} is obtained from vector \mathbf{X} through the so-called *aggregation matrix*

$$\mathbf{U} = \text{diag}\{\mathbf{1}^1, \dots, \mathbf{1}^p\}, \quad \mathbf{s} = \mathbf{U}\mathbf{X}. \quad (4)$$

In the following, we will also use matrix

$$\bar{\mathbf{P}}_c = \text{diag}\{\nu^1, \dots, \nu^p\},$$

which allows us to express all the equilibrium points of the fast dynamics from the global variables as

$$\bar{\mathbf{P}}_c \mathbf{s},$$

that is, $\mathbf{X} = \bar{\mathbf{P}}_c \mathbf{s}$, $\mathbf{s} \in \mathbf{R}^p$, are all the solutions of equation $\mathbf{X} = \mathbf{P}\mathbf{X}$.

We summarize the properties of matrices \mathbf{P} , $\bar{\mathbf{P}}$, $\bar{\mathbf{P}}_c$, and \mathbf{U} that we will use below. We will, henceforth, denote by \mathbf{I} the identity matrix of the required dimension

$$\begin{aligned} \bar{\mathbf{P}}\mathbf{P} &= \mathbf{P}\bar{\mathbf{P}} = \bar{\mathbf{P}}\bar{\mathbf{P}} = \bar{\mathbf{P}}, \\ \bar{\mathbf{P}}\bar{\mathbf{P}}_c &= \bar{\mathbf{P}}_c\bar{\mathbf{P}} = \bar{\mathbf{P}}_c, \\ \mathbf{U}\bar{\mathbf{P}} &= \mathbf{U}, \quad \mathbf{U}\bar{\mathbf{P}}_c = \mathbf{I}, \quad \bar{\mathbf{P}}_c\mathbf{U} = \bar{\mathbf{P}}. \end{aligned} \quad (5)$$

From (5), we find that \mathbf{s} is invariant for fast dynamics

$$\mathbf{s}_{n+1} = \mathbf{U}\mathbf{X}_{n+1} = \mathbf{U}\mathbf{P}\mathbf{X}_n = \mathbf{U}\mathbf{X}_n = \mathbf{s}_n,$$

and also the asymptotic property of fast dynamics: if we let \mathbf{X}_0 be any initial condition and we make $\mathbf{s}_0 = \mathbf{U}\mathbf{X}_0$, then we obtain from (3) by (5)

$$\lim_{k \rightarrow \infty} \mathbf{P}^k \mathbf{X}_0 = \bar{\mathbf{P}}\mathbf{X}_0 = \bar{\mathbf{P}}_c \mathbf{U}\mathbf{X}_0 = \bar{\mathbf{P}}_c \mathbf{s}_0.$$

The slow dynamics is represented by the term $\varepsilon \mathbf{F}(\mathbf{X}, \varepsilon)$, where $\mathbf{F} \in C^\infty(\mathbf{R}^N \times (0, \varepsilon_0))$, and following the same notation as for vector \mathbf{X} , we have

$$\mathbf{F}(\mathbf{X}, \varepsilon) = (\mathbf{f}^1(\mathbf{X}, \varepsilon), \dots, \mathbf{f}^p(\mathbf{X}, \varepsilon))^\top \quad \text{and} \quad \mathbf{f}^i(\mathbf{X}, \varepsilon) = (f^{i1}(\mathbf{X}, \varepsilon), \dots, f^{iN^i}(\mathbf{X}, \varepsilon))^\top. \quad (6)$$

We suppose that $\mathbf{f}^i(\mathbf{X}, \varepsilon) = O(|\mathbf{x}^i|)$, $i = 1, \dots, p$. From this we see that for nonnegative values of variables x^{ij} , we have

$$\mathbf{f}^i(\mathbf{X}, \varepsilon) = O(s^i), \quad i = 1, \dots, p,$$

which implies, in particular, that slow dynamics do not produce any variations if the total number of individuals of a population i is zero.

2.1. Change of Variables

Before proposing an aggregated model for system (1), we make a change of variables so that the global variables appear explicitly.

For every $i = 1, \dots, p$, we substitute the variable x^{iN^i} by global variable s^i and the other $N^i - 1$ variables in group i by the new variables $q^{ij} = x^{ij} - \nu^{ij}s^i$, $j = 1, \dots, N^i - 1$, that is, we change each variable, except the last in every group, by itself minus the corresponding value in the fast dynamics equilibrium, and the last ones are changed by the global variables.

We will use the following notation:

$$\mathbf{q}^i = (q^{i1}, \dots, q^{iN^i-1})^\top \quad \text{and} \quad \mathbf{q} = (\mathbf{q}^1, \dots, \mathbf{q}^p),$$

also let Π_i be the projector

$$\begin{aligned} \Pi_i : \mathbf{R}^{N^i} &\rightarrow \mathbf{R}^{N^i-1}, \\ (x^{i1}, \dots, x^{iN^i})^\top &\rightarrow \Pi_i \mathbf{x}^i = (x^{i1}, \dots, x^{iN^i-1})^\top, \end{aligned}$$

and denote its matrix representation $\Pi_i = (\mathbf{I} \mid \mathbf{0})$, where \mathbf{I} represents the identity matrix of order $(N^i - 1)$ and $\mathbf{0}$ a null column vector of dimension $(N^i - 1)$. Finally, let Π denote the matrix of dimensions $(N - p) \times N \text{ diag}\{\Pi_1, \dots, \Pi_p\}$.

We then have

$$\mathbf{q}^i = \Pi_i \mathbf{x}^i - s^i \Pi_i \boldsymbol{\nu}^i = \Pi_i (\mathbf{x}^i - s^i \boldsymbol{\nu}^i), \quad i = 1, \dots, p,$$

and

$$\mathbf{q} = \Pi (\mathbf{X} - \bar{\mathbf{P}}_c \mathbf{s}),$$

and from (4),(5)

$$\mathbf{q} = \Pi (\mathbf{I} - \mathbf{P}) \mathbf{X}. \quad (7)$$

To get \mathbf{X} from \mathbf{s} and \mathbf{q} , we have

$$x^{ij} = q^{ij} + \nu^{ij} s^i, \quad j = 1, \dots, N^i - 1,$$

and

$$x^{iN^i} = s^i - \sum_{j=1}^{N^i-1} x^{ij} = s^i - \sum_{j=1}^{N^i-1} (q^{ij} + \nu^{ij} s^i) = \nu^{iN^i} s^i - \mathbf{1} \mathbf{q}^i,$$

where $\mathbf{1}$ means a row vector with every component equal to 1 and the required dimension for the expression to make sense. Henceforth, we will use this convention unless stated otherwise.

The last equalities allow us to write

$$\mathbf{x}^i = \boldsymbol{\nu}^i s^i + (q^{i1}, \dots, q^{iN^i-1}, -\mathbf{1} \mathbf{q}^i)^\top,$$

and denoting by \mathbf{D}_i the $N^i \times (N^i - 1)$ matrix

$$\mathbf{D}_i = \begin{pmatrix} \mathbf{I} \\ -\mathbf{1} \end{pmatrix},$$

and by \mathbf{D} the $N \times (N - p)$ matrix $\mathbf{D} = \text{diag}\{\mathbf{D}_1, \dots, \mathbf{D}_p\}$, we obtain $\mathbf{x}^i = \boldsymbol{\nu}^i s^i + \mathbf{D}_i \mathbf{q}^i$ and finally,

$$\mathbf{X} = \bar{\mathbf{P}}_c \mathbf{s} + \mathbf{D} \mathbf{q}. \quad (8)$$

The reverse relationship is summarized in the following two (see (4) and (7)) identities:

$$\begin{aligned} \mathbf{s} &= \mathbf{U}\mathbf{X}, \\ \mathbf{q} &= \mathbf{\Pi}(\mathbf{I} - \mathbf{P})\mathbf{X}. \end{aligned} \tag{9}$$

We now transform system (1) by using the change of variables described by (4), (8), (9), and the equalities (5)

$$\begin{aligned} \mathbf{s}_{n+1} &= \mathbf{U}\mathbf{X}_{n+1} = \mathbf{U}\mathbf{P}\mathbf{X}_n + \varepsilon\mathbf{U}\mathbf{F}(\mathbf{X}_n, \varepsilon) = \mathbf{s}_n + \varepsilon\mathbf{U}\mathbf{F}(\bar{\mathbf{P}}_c\mathbf{s}_n + \mathbf{D}\mathbf{q}_n, \varepsilon), \quad \text{and} \\ \mathbf{q}_{n+1} &= \mathbf{\Pi}(\mathbf{I} - \mathbf{P})\mathbf{X}_{n+1} = \mathbf{\Pi}(\mathbf{X}_{n+1} - \bar{\mathbf{P}}_c\mathbf{s}_{n+1}) \\ &= \mathbf{\Pi}[\mathbf{P}\mathbf{X}_n + \varepsilon\mathbf{F}(\mathbf{X}_n, \varepsilon) - \bar{\mathbf{P}}_c(\mathbf{s}_n + \varepsilon\mathbf{U}\mathbf{F}(\mathbf{X}_n, \varepsilon))] \\ &= \mathbf{\Pi}\mathbf{P}(\bar{\mathbf{P}}_c\mathbf{s}_n + \mathbf{D}\mathbf{q}_n) - \mathbf{\Pi}\bar{\mathbf{P}}_c\mathbf{s}_n + \varepsilon\mathbf{\Pi}(\mathbf{I} - \bar{\mathbf{P}}_c)\mathbf{U}\mathbf{F}(\bar{\mathbf{P}}_c\mathbf{s}_n + \mathbf{D}\mathbf{q}_n, \varepsilon) \\ &= \mathbf{\Pi}\mathbf{P}\mathbf{D}\mathbf{q}_n + \varepsilon\mathbf{\Pi}(\mathbf{I} - \bar{\mathbf{P}})\mathbf{F}(\bar{\mathbf{P}}_c\mathbf{s}_n + \mathbf{D}\mathbf{q}_n, \varepsilon). \end{aligned}$$

If we consider $\mathbf{\Pi}\mathbf{P}\mathbf{D}$ as an $(N-p) \times (N-p)$ matrix that we denote by \mathbf{Q} , we have that this matrix is block-diagonal, $\mathbf{Q} = \text{diag}\{\mathbf{Q}_1, \dots, \mathbf{Q}_p\}$, and that the eigenvalues of \mathbf{Q}_i , $i = 1, \dots, p$, are those of \mathbf{P}_i except 1, what implies that the spectral radius of \mathbf{Q} is less than one, $\rho(\mathbf{Q}) < 1$.

LEMMA 1. *Let \mathbf{Q}_i be the matrix $\mathbf{\Pi}_i\mathbf{P}_i\mathbf{D}_i$, $i = 1, \dots, p$. Then \mathbf{Q}_i is a matrix of order $N^i - 1$ whose eigenvalues are those of \mathbf{P}_i different from 1.*

PROOF. We decompose \mathbf{P}_i into blocks in the following way:

$$\left(\begin{array}{c|c} \mathbf{P}_i^{11} & \mathbf{p}_i^{12} \\ \hline \mathbf{p}_i^{21} & p_i^{22} \end{array} \right),$$

where \mathbf{P}_i^{11} is a submatrix of dimensions $(N^i - 1) \times (N^i - 1)$, \mathbf{p}_i^{12} is $(N^i - 1) \times 1$, \mathbf{p}_i^{21} is $1 \times (N^i - 1)$, and p_i^{22} is 1×1 . So, we have

$$\mathbf{Q}_i = (\mathbf{I} \mid \mathbf{0}) \left(\begin{array}{c|c} \mathbf{P}_i^{11} & \mathbf{p}_i^{12} \\ \hline \mathbf{p}_i^{21} & p_i^{22} \end{array} \right) \begin{pmatrix} \mathbf{I} \\ -\mathbf{1} \end{pmatrix} = \mathbf{P}_i^{11} - \mathbf{p}_i^{12}\mathbf{1}.$$

We can prove the relationship between the characteristic polynomials of matrices \mathbf{P}_i and \mathbf{Q}_i , $\Delta_{\mathbf{P}_i}(\lambda)$ and $\Delta_{\mathbf{Q}_i}(\lambda)$, respectively. Using that columns of \mathbf{P}_i summed up to one, we get

$$\begin{aligned} \Delta_{\mathbf{P}_i}(\lambda) &= \det \left(\begin{array}{c|c} \mathbf{P}_i^{11} - \lambda\mathbf{I} & \mathbf{p}_i^{12} \\ \hline \mathbf{p}_i^{21} & p_i^{22} - \lambda \end{array} \right) = \det \left(\begin{array}{c|c} \mathbf{P}_i^{11} - \lambda\mathbf{I} & \mathbf{p}_i^{12} \\ \hline (1-\lambda)\mathbf{1} & 1-\lambda \end{array} \right) \\ &= \det \left(\begin{array}{c|c} \mathbf{P}_i^{11} - \mathbf{p}_i^{12}\mathbf{1} - \lambda\mathbf{I} & \mathbf{p}_i^{12} \\ \hline \mathbf{0} & 1-\lambda \end{array} \right) = (1-\lambda)\Delta_{\mathbf{Q}_i}(\lambda). \quad \blacksquare \end{aligned}$$

Moreover, denoting by \mathbf{f} the mapping from $\mathbf{R}^N \times (0, \varepsilon_0)$ to \mathbf{R}^p ,

$$\mathbf{f}(\mathbf{s}, \mathbf{q}, \varepsilon) = \mathbf{U}\mathbf{F}(\bar{\mathbf{P}}_c\mathbf{s} + \mathbf{D}\mathbf{q}, \varepsilon), \tag{10}$$

and by \mathbf{g} the mapping from $\mathbf{R}^N \times (0, \varepsilon_0)$ to \mathbf{R}^{N-p} ,

$$\mathbf{g}(\mathbf{s}, \mathbf{q}, \varepsilon) = \mathbf{\Pi}(\mathbf{I} - \bar{\mathbf{P}})\mathbf{F}(\bar{\mathbf{P}}_c\mathbf{s} + \mathbf{D}\mathbf{q}, \varepsilon), \tag{11}$$

the general system (1) is transformed into the following one:

$$\begin{aligned} \mathbf{s}_{n+1} &= \mathbf{s}_n + \varepsilon\mathbf{f}(\mathbf{s}_n, \mathbf{q}_n, \varepsilon), \\ \mathbf{q}_{n+1} &= \mathbf{Q}\mathbf{q}_n + \varepsilon\mathbf{g}(\mathbf{s}_n, \mathbf{q}_n, \varepsilon), \end{aligned} \tag{12}$$

where \mathbf{f} and \mathbf{g} are C^∞ mappings that verify $\mathbf{f}(\mathbf{0}, \mathbf{0}, 0) = \mathbf{0}$ and $\mathbf{g}(\mathbf{0}, \mathbf{0}, 0) = \mathbf{0}$.

3. AGGREGATION OF THE LINEAR MODEL

We suppose that we are dealing with a linear and discrete system depending on the small parameter ε , that we call the *perturbed system*:

$$\begin{pmatrix} \mathbf{x}_{n+1}^1 \\ \vdots \\ \mathbf{x}_{n+1}^p \end{pmatrix} = \begin{pmatrix} \mathbf{A}_{11}(\varepsilon) & \dots & \mathbf{A}_{1p}(\varepsilon) \\ \vdots & \ddots & \vdots \\ \mathbf{A}_{p1}(\varepsilon) & \dots & \mathbf{A}_{pp}(\varepsilon) \end{pmatrix} \begin{pmatrix} \mathbf{x}_n^1 \\ \vdots \\ \mathbf{x}_n^p \end{pmatrix}, \quad (13)$$

or briefly

$$\mathbf{X}_{n+1} = \mathbf{A}(\varepsilon)\mathbf{X}_n,$$

where we keep the notations of the previous section. Every matrix $\mathbf{A}_{ij}(\varepsilon)$ has dimensions $(N^i) \times (N^j)$ and we will suppose analytic dependence on ε .

To be in the framework of Section 2, we need the following hypothesis.

HYPOTHESIS (H1). *The matrix $\mathbf{A}(0) = \mathbf{P}$ associated with the unperturbed system ($\varepsilon = 0$) satisfies the following conditions: $\mathbf{A}_{ij}(0) = \mathbf{0}$, whenever $i \neq j$ and $\mathbf{A}_{ii}(0) = \mathbf{P}_i$ is a regular stochastic matrix, $i = 1, \dots, p$.*

So, we could write $\mathbf{A}(\varepsilon)$ in the next form, $\mathbf{A}(\varepsilon) = \mathbf{P} + \varepsilon\mathbf{M}(\varepsilon)$, and we have $\mathbf{M}(0) = \mathbf{A}'(0)$. The linear system (13) then becomes

$$\mathbf{X}_{n+1} = \mathbf{P}\mathbf{X}_n + \varepsilon\mathbf{M}(\varepsilon)\mathbf{X}_n.$$

If we transform this system by means of the change of variables (4), (8), (9), making

$$\mathbf{F}(\mathbf{X}, \varepsilon) = \mathbf{M}(\varepsilon)\mathbf{X},$$

we obtain

$$\begin{aligned} \mathbf{s}_{n+1} &= \mathbf{s}_n + \varepsilon\mathbf{U}\mathbf{M}(\varepsilon) (\bar{\mathbf{P}}_c\mathbf{s}_n + \mathbf{D}\mathbf{q}_n), \\ \mathbf{q}_{n+1} &= \mathbf{\Pi}\mathbf{P}\mathbf{D}\mathbf{q}_n + \varepsilon\mathbf{\Pi}(\mathbf{I} - \bar{\mathbf{P}})\mathbf{M}(\varepsilon) (\bar{\mathbf{P}}_c\mathbf{s}_n + \mathbf{D}\mathbf{q}_n), \end{aligned}$$

and in the matrix form

$$\begin{pmatrix} \mathbf{s}_{n+1} \\ \mathbf{q}_{n+1} \end{pmatrix} = \begin{pmatrix} \mathbf{I} & \mathbf{0} \\ \mathbf{0} & \mathbf{\Pi}\mathbf{P}\mathbf{D} \end{pmatrix} \begin{pmatrix} \mathbf{s}_n \\ \mathbf{q}_n \end{pmatrix} + \varepsilon \begin{pmatrix} \mathbf{U}\mathbf{M}(\varepsilon)\bar{\mathbf{P}}_c & \mathbf{U}\mathbf{M}(\varepsilon)\mathbf{D} \\ \mathbf{\Pi}(\mathbf{I} - \bar{\mathbf{P}})\mathbf{M}(\varepsilon)\bar{\mathbf{P}}_c & \mathbf{\Pi}(\mathbf{I} - \bar{\mathbf{P}})\mathbf{M}(\varepsilon)\mathbf{D} \end{pmatrix} \begin{pmatrix} \mathbf{s}_n \\ \mathbf{q}_n \end{pmatrix}.$$

In the last equalities, we see the system which the global variables \mathbf{s} should satisfy, but it is not uncoupled for these variables. To avoid the problem, in order to get an aggregated system, we suppose that the fast dynamics in every population i has reached the equilibrium distribution determined by the corresponding regular stochastic matrix \mathbf{P}_i . In that case, we consider the next system for variables \mathbf{X} ,

$$\mathbf{X}_{n+1} = \mathbf{A}(\varepsilon)\bar{\mathbf{P}}\mathbf{X}_n.$$

We have

$$\mathbf{X}_{n+1} = (\mathbf{P} + \varepsilon\mathbf{M}(\varepsilon))\bar{\mathbf{P}}\mathbf{X}_n = \bar{\mathbf{P}}\mathbf{X}_n + \varepsilon\mathbf{M}(\varepsilon)\bar{\mathbf{P}}\mathbf{X}_n,$$

and the change of variables (4), (8), (9) makes, using (5),

$$\begin{aligned} \mathbf{s}_{n+1} &= \mathbf{s}_n + \varepsilon\mathbf{U}\mathbf{M}(\varepsilon)\bar{\mathbf{P}} (\bar{\mathbf{P}}_c\mathbf{s}_n + \mathbf{D}\mathbf{q}_n) \\ &= \mathbf{s}_n + \varepsilon\mathbf{U}\mathbf{M}(\varepsilon)\bar{\mathbf{P}}\bar{\mathbf{P}}_c\mathbf{s}_n + \varepsilon\mathbf{U}\mathbf{M}(\varepsilon)\bar{\mathbf{P}}\mathbf{D}\mathbf{q}_n, \end{aligned}$$

which yields, noting that $\bar{\mathbf{P}}\mathbf{D} = \mathbf{0}$,

$$\mathbf{s}_{n+1} = \mathbf{s}_n + \varepsilon\mathbf{U}\mathbf{M}(\varepsilon)\bar{\mathbf{P}}_c\mathbf{s}_n.$$

Analogously,

$$\begin{aligned}\mathbf{q}_{n+1} &= \Pi \bar{\mathbf{P}} \mathbf{D} \mathbf{q}_n + \varepsilon \Pi (\mathbf{I} - \bar{\mathbf{P}}) \mathbf{M}(\varepsilon) \bar{\mathbf{P}} (\bar{\mathbf{P}}_c \mathbf{s}_n + \mathbf{D} \mathbf{q}_n) \\ &= \varepsilon \Pi (\mathbf{I} - \bar{\mathbf{P}}) \mathbf{M}(\varepsilon) \bar{\mathbf{P}} \bar{\mathbf{P}}_c \mathbf{s}_n + \varepsilon \Pi (\mathbf{I} - \bar{\mathbf{P}}) \mathbf{M}(\varepsilon) \bar{\mathbf{P}} \mathbf{D} \mathbf{q}_n,\end{aligned}$$

and finally,

$$\mathbf{q}_{n+1} = \varepsilon \Pi (\mathbf{I} - \bar{\mathbf{P}}) \mathbf{M}(\varepsilon) \bar{\mathbf{P}}_c \mathbf{D} \mathbf{q}_n,$$

or in matrix form

$$\begin{pmatrix} \mathbf{s}_{n+1} \\ \mathbf{q}_{n+1} \end{pmatrix} = \begin{pmatrix} \mathbf{I} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} \end{pmatrix} \begin{pmatrix} \mathbf{s}_n \\ \mathbf{q}_n \end{pmatrix} + \varepsilon \begin{pmatrix} \mathbf{U} \mathbf{M}(\varepsilon) \bar{\mathbf{P}}_c & \mathbf{0} \\ \Pi (\mathbf{I} - \bar{\mathbf{P}}) \mathbf{M}(\varepsilon) \bar{\mathbf{P}}_c & \mathbf{0} \end{pmatrix} \begin{pmatrix} \mathbf{s}_n \\ \mathbf{q}_n \end{pmatrix}.$$

In this system, the global variables are uncoupled. So we propose as the aggregated system the following one:

$$\mathbf{s}_{n+1} = \mathbf{s}_n + \varepsilon \mathbf{U} \mathbf{M}(\varepsilon) \bar{\mathbf{P}}_c \mathbf{s}_n. \quad (14)$$

We call $\mathbf{B}(\varepsilon)$ to the matrix $\mathbf{I} + \varepsilon \mathbf{U} \mathbf{M}(\varepsilon) \bar{\mathbf{P}}_c$.

The main object of this section is to compare the asymptotic behaviours of both systems, the general linear system (13) and the aggregated linear system (14). For that we study the relationship between the dominant eigenvalues of matrices $\mathbf{A}(\varepsilon)$ and $\mathbf{B}(\varepsilon)$. We will use for our task the general theory of analytical perturbation of matrices. The main results used below are summarized in Appendix A. We follow Baumgartel [13] and Kato [14].

LEMMA 2. *Let $\mathbf{A}(0)$ be the unperturbed matrix of the linear system (13). Then we have the following.*

- (a) *The strictly dominant eigenvalue of $\mathbf{A}(0)$ is 1 and its algebraic multiplicity is p .*
- (b) *1 is a semisimple eigenvalue of $\mathbf{A}(0)$, and a base of its eigenspace is*

$$(\nu^1, \mathbf{0}, \dots, \mathbf{0})^\top, \quad (\mathbf{0}, \nu^2, \dots, \mathbf{0})^\top, \dots, (\mathbf{0}, \mathbf{0}, \dots, \nu^p)^\top.$$

- (c) *The eigenprojection matrix of the eigenvalue 1 is $\bar{\mathbf{P}}$.*

In the aggregated system $\mathbf{B}(0) = \mathbf{I}$, and so to compare the dominant elements of $\mathbf{A}(\varepsilon)$ and $\mathbf{B}(\varepsilon)$, we should compare the 1-groups of both. For this, we need to know the structure of the eigenvalues and eigenvectors of matrices $\bar{\mathbf{P}} \mathbf{A}' \bar{\mathbf{P}}$ and $\mathbf{B}'(0)$ (see Appendix A).

LEMMA 3. *Let $\bar{\mathbf{P}}(\mathbf{R}^N)$ be the eigenspace associated to the eigenvalue 1 of the matrix $\mathbf{A}(0)$ and $\tilde{\mathbf{A}}$, the restriction of the operator $\bar{\mathbf{P}} \mathbf{A}' \bar{\mathbf{P}}$ to this subspace. Then*

- (a) $\det(\tilde{\mathbf{A}} - \lambda \mathbf{I}) = \det(\mathbf{B}'(0) - \lambda \mathbf{I})$;
- (b) *if $\mathbf{v} \in \bar{\mathbf{P}}(\mathbf{R}^N)$ is an eigenvector associated to the eigenvalue λ , then $\mathbf{U} \mathbf{v}$ is an eigenvector of $\mathbf{B}'(0)$ associated to the same eigenvalue λ ; and*
- (c) *if $\mathbf{w} \in \mathbf{R}^p$ is an eigenvector of $\mathbf{B}'(0)$ associated to the eigenvalue λ , then $\bar{\mathbf{P}}_c \mathbf{w}$ is an eigenvector of $\bar{\mathbf{P}} \mathbf{A}' \bar{\mathbf{P}}$ associated to the same eigenvalue λ .*

Notice that the next direct sum decomposition

$$\mathbf{R}^N = \bar{\mathbf{P}}(\mathbf{R}^N) \oplus (\mathbf{I} - \bar{\mathbf{P}})(\mathbf{R}^N),$$

holds true and that both spaces are invariant under the operator $\bar{\mathbf{P}} \mathbf{A}' \bar{\mathbf{P}}$; moreover, this operator vanishes identically on the subspace $(\mathbf{I} - \bar{\mathbf{P}})(\mathbf{R}^N)$. All this means that the characteristic polynomial of $\bar{\mathbf{P}} \mathbf{A}' \bar{\mathbf{P}}$ verifies

$$\det(\bar{\mathbf{P}} \mathbf{A}' \bar{\mathbf{P}} - \lambda \mathbf{I}) = \lambda^{N-p} \det(\mathbf{B}'(0) - \lambda \mathbf{I}) = \lambda^{N-p} (\lambda - \lambda_1)^{m_1} \dots (\lambda - \lambda_r)^{m_r},$$

where $\lambda_1, \dots, \lambda_r$ are the eigenvalues of $\mathbf{B}'(0)$ with multiplicities m_1, \dots, m_r .

As $\mathbf{B}(0) = \mathbf{I}$, the 1-group of $\mathbf{B}(\varepsilon)$ is formed by all its eigenvalues. We can now state in the following theorem, the main result we were looking for, and whose proof is a direct consequence of what we have just noticed.

THEOREM 1. *Let $\mathbf{A}(\varepsilon)$ be the matrix of the general system (13) and let $\lambda(\varepsilon)$ represent the eigenvalues of the 1-group. Let $\mathbf{B}(\varepsilon)$ be the matrix of the aggregated system (14) and let $\mu(\varepsilon)$ represents its eigenvalues. There exists $\delta > 0$ such that if $0 < |\varepsilon| < \delta$, then the eigenvalues $\lambda(\varepsilon)$ and $\mu(\varepsilon)$ are classified in the $1 + \varepsilon\lambda_s$ -groups, $s = 1, \dots, r$, satisfying the following.*

(a) $\lambda(\varepsilon)$ belongs to the $1 + \varepsilon\lambda_s$ -group if and only if

$$\lambda(\varepsilon) = 1 + \varepsilon\lambda_s + O\left(\varepsilon^{1+(1/p_s)}\right), \quad (\varepsilon \rightarrow 0),$$

where p_s is an integer that satisfies $1 \leq p_s \leq m_s$.

(b) $\mu(\varepsilon)$ belongs to the $1 + \varepsilon\lambda_s$ -group if and only if

$$\mu(\varepsilon) = 1 + \varepsilon\lambda_s + O\left(\varepsilon^{1+(1/q_s)}\right), \quad (\varepsilon \rightarrow 0),$$

where q_s is an integer that satisfies $1 \leq q_s \leq m_s$. The dimension of the $1 + \varepsilon\lambda_s$ -group is m_s in both cases.

(c) If $\mathbf{v}(\varepsilon)$ is an eigenvector of $\mathbf{A}(\varepsilon)$ associated to the eigenvalue $\lambda(\varepsilon)$ of the $1 + \varepsilon\lambda_s$ -group, continuous at $\varepsilon = 0$ and such that $\mathbf{v}(0) \neq 0$, then

$$\bar{\mathbf{P}}\mathbf{A}'\bar{\mathbf{P}}\mathbf{v}(0) = \lambda_s\mathbf{v}(0), \quad \mathbf{B}'(0)(\mathbf{U}\mathbf{v}(0)) = \lambda_s(\mathbf{U}\mathbf{v}(0)).$$

(d) If $\mathbf{w}(\varepsilon)$ is an eigenvector of $\mathbf{B}(\varepsilon)$ associated to the eigenvalue $\mu(\varepsilon)$ of the $1 + \varepsilon\lambda_s$ -group continuous at $\varepsilon = 0$ and such that $\mathbf{w}(0) \neq 0$, then

$$\mathbf{B}'(0)\mathbf{w}(0) = \lambda_s\mathbf{w}(0), \quad \bar{\mathbf{P}}\mathbf{A}'\bar{\mathbf{P}}(\bar{\mathbf{P}}_c\mathbf{w}(0)) = \lambda_s(\bar{\mathbf{P}}_c\mathbf{w}(0)).$$

Finally, we make an additional hypothesis in order to get the systems (13) and (14) having an asymptotic behaviour governed by a strictly dominant eigenvalue.

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

Let $\mathbf{v} = (v_1, \dots, v_N)^\top$ be an eigenvector of $\bar{\mathbf{P}}\mathbf{A}'\bar{\mathbf{P}}$ associated to μ .

THEOREM 2. *If $\varepsilon \geq 0$, $|\varepsilon| < \delta$, then matrix $\mathbf{A}(\varepsilon)$ has a simple eigenvalue $\lambda_{\max}(\varepsilon)$ modulus strictly dominant that admits the following expansion:*

$$\lambda_{\max}(\varepsilon) = 1 + \varepsilon\mu + \varepsilon f(\varepsilon), \quad \lim_{\varepsilon \rightarrow 0^+} f(\varepsilon) = 0.$$

Associated to this eigenvalue there exists a unique eigenvector of $\mathbf{A}(\varepsilon)$ that can be written in the following way:

$$\mathbf{x}(\varepsilon) = \mathbf{v} + O(\varepsilon), \quad (\varepsilon \rightarrow 0).$$

Moreover, $\mathbf{B}(\varepsilon)$ has a simple eigenvalue $\mu_{\max}(\varepsilon)$ modulus strictly dominant that admits the following expansion:

$$\mu_{\max}(\varepsilon) = 1 + \varepsilon\mu + \varepsilon g(\varepsilon), \quad \lim_{\varepsilon \rightarrow 0^+} g(\varepsilon) = 0,$$

and an associated eigenvector

$$\mathbf{y}(\varepsilon) = \mathbf{U}\mathbf{v} + O(\varepsilon), \quad (\varepsilon \rightarrow 0).$$

So, the asymptotic behaviour of system (13) is

$$\lim_{n \rightarrow +\infty} \frac{\mathbf{X}_n}{(1 + \varepsilon\mu + \varepsilon f(\varepsilon))^n} = C_0(\mathbf{v} + O(\varepsilon)), \quad (\varepsilon \rightarrow 0),$$

and, therefore, the aggregated variables behave as

$$\lim_{n \rightarrow +\infty} \frac{\mathbf{UX}_n}{(1 + \varepsilon\mu + \varepsilon f(\varepsilon))^n} = C_0(\mathbf{Uv} + O(\varepsilon)), \quad (\varepsilon \rightarrow 0).$$

Being that the asymptotic behaviour of the aggregated system (14) is

$$\lim_{n \rightarrow +\infty} \frac{\mathbf{s}_n}{(1 + \varepsilon\mu + \varepsilon g(\varepsilon))^n} = C_0(\mathbf{Uv} + O(\varepsilon)), \quad (\varepsilon \rightarrow 0),$$

we have the similarity of asymptotic behaviours for which we were looking.

3. AGGREGATION OF THE NONLINEAR MODEL

In this section, we propose an aggregated system for the general system (1)

$$\mathbf{X}_{n+1} = \mathbf{PX}_n + \varepsilon \mathbf{F}(\mathbf{X}_n, \varepsilon),$$

that was transformed, in Section 1, into the following one:

$$\begin{aligned} \mathbf{s}_{n+1} &= \mathbf{s}_n + \varepsilon \mathbf{f}(\mathbf{s}_n, \mathbf{q}_n, \varepsilon), \\ \mathbf{q}_{n+1} &= \mathbf{Qq}_n + \varepsilon \mathbf{g}(\mathbf{s}_n, \mathbf{q}_n, \varepsilon), \end{aligned} \quad (15)$$

where \mathbf{f} and \mathbf{g} are C^∞ mappings that verify $\mathbf{f}(\mathbf{0}, \mathbf{0}, 0) = \mathbf{0}$ and $\mathbf{g}(\mathbf{0}, \mathbf{0}, 0) = \mathbf{0}$.

The system (15) verifies the hypothesis of the center manifold theorem developed in Appendix B. So, for every $M > 0$, there exists $\delta > 0$ and a mapping $\mathbf{q} = \mathbf{h}(\mathbf{s}, \varepsilon)$ defined for $|\mathbf{s}| < M$ and $|\varepsilon| < \delta$, whose graph, W_ε , for a fixed ε is a locally attractive invariant manifold that allows us to study the dynamics of system (15) by means of its restriction to W_ε .

The system restricted to W_ε is what we call the *aggregated system*, and from (27) has the form

$$\mathbf{s}_{n+1} = \mathbf{s}_n + \varepsilon \mathbf{f}(\mathbf{s}_n, \mathbf{h}(\mathbf{s}_n, \varepsilon), \varepsilon),$$

or using (28) (in Appendix B)

$$\mathbf{s}_{n+1} = \mathbf{s}_n + \varepsilon \mathbf{f}(\mathbf{s}_n, \varepsilon (\mathbf{I} - \mathbf{Q})^{-1} \mathbf{g}(\mathbf{s}_n, \mathbf{0}, 0) + O(\varepsilon^2), \varepsilon),$$

where (11) implies that $\mathbf{g}(\mathbf{s}, \mathbf{0}, 0) = \mathbf{A}(\mathbf{I} - \bar{\mathbf{P}})\mathbf{F}(\bar{\mathbf{P}}_c \mathbf{s}, 0)$. It is also possible to express the aggregated system in the simpler form

$$\mathbf{s}_{n+1} = \mathbf{s}_n + \varepsilon \mathbf{f}(\mathbf{s}_n, \mathbf{0}, 0) + O(\varepsilon^2),$$

that yields, using (10),

$$\mathbf{s}_{n+1} = \mathbf{s}_n + \varepsilon \mathbf{UF}(\bar{\mathbf{P}}_c \mathbf{s}_n, 0) + O(\varepsilon^2). \quad (16)$$

4. MULTIREGIONAL DENSITY DEPENDENT LESLIE MODEL WITH DIFFERENT TIME SCALES

In this section, we are going to apply the above general aggregation method to the case of an age-structured population located in a multipatch environment. These kind of models have been frequently treated in the literature (for an introduction and a list of references, see [15,16]). In contrast with these two references, we propose a model where the migration and the demographic processes develop at different time scales, migration being a fast process in comparison with demography. We will also allow demography to be density dependent.

We suppose a population divided into p age-classes and living in an environment composed of m patches. We follow the notation of Section 1, being

$$x_n^{ij} = \text{number of individuals of age } i \text{ in patch } j \text{ at time } n,$$

$$i = 1, \dots, p, j = 1, \dots, m,$$

$$\begin{aligned} \mathbf{X}_n &= (\mathbf{x}_n^1, \dots, \mathbf{x}_n^p)^\top, \quad \text{where } \mathbf{x}_n^i = (x_n^{i1}, \dots, x_n^{im})^\top, \\ s_n^i &= \sum_{j=1}^m x_n^{ij}, \quad i = 1, \dots, p, \quad \text{and } \mathbf{s}_n = (s_n^1, \dots, s_n^p)^\top. \end{aligned}$$

We suppose that the changes between different patches of individuals of age i are represented by a regular stochastic matrix \mathbf{P}_i of order $m \times m$. So matrix $\mathbf{P} = \text{diag}\{\mathbf{P}_1, \dots, \mathbf{P}_p\}$ represents the migration process of whole population.

The demography is defined by means of two kinds of transference coefficients as in the classical Leslie model.

Fertility rates:

$$F_i^j = \text{fertility rate of age class } i \text{ in patch } j, \quad i = 1, \dots, p, \quad j = 1, \dots, m.$$

Survival rates:

$$S_i^j = \text{survival rate of age class } i \text{ in patch } j, \quad i = 1, \dots, p-1, \quad j = 1, \dots, m.$$

These coefficients satisfy the usual constraints of Leslie model.

We define matrices $\mathbf{F}_i = \text{diag}\{F_i^1, \dots, F_i^m\}$, $i = 1, \dots, p$, $\mathbf{S}_i = \text{diag}\{S_i^1, \dots, S_i^m\}$, $i = 1, \dots, p-1$. Finally, we get a generalized Leslie matrix

$$\mathbf{L} = \begin{pmatrix} \mathbf{F}_1 & \mathbf{F}_2 & \dots & \mathbf{F}_{p-1} & \mathbf{F}_p \\ \mathbf{S}_1 & \mathbf{0} & \dots & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{S}_2 & \dots & \mathbf{0} & \mathbf{0} \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ \mathbf{0} & \mathbf{0} & \dots & \mathbf{S}_{p-1} & \mathbf{0} \end{pmatrix},$$

where \mathbf{L} is considered density dependent, so $\mathbf{L} = \mathbf{L}(\mathbf{X})$ in a general way.

In order to distinguish between the two different time scales, those associated to \mathbf{P} and \mathbf{L} , respectively, we chose as unit time, the projection interval corresponding to \mathbf{P} and approximate the effect of \mathbf{L} over that interval, which is much shorter than its own projection interval, using the following matrix:

$$\mathbf{L}_\varepsilon = \varepsilon \mathbf{L} + (1 - \varepsilon) \mathbf{I}, \quad 0 < \varepsilon \ll 1.$$

Finally, we propose the following multipatch density dependent Leslie model:

$$\mathbf{X}_{n+1} = \mathbf{L}_\varepsilon(\mathbf{X}_n) \mathbf{P} \mathbf{X}_n,$$

or in the form of general system (1)

$$\mathbf{X}_{n+1} = \mathbf{P}\mathbf{X}_n + \varepsilon(\mathbf{L}(\mathbf{X}_n) - \mathbf{I})\mathbf{P}\mathbf{X}_n. \quad (17)$$

4.1. Density Independent Case

We let matrix \mathbf{L} be constant so we can apply the results in Section 2, where $\mathbf{M}(\varepsilon) = (\mathbf{L} - \mathbf{I})\mathbf{P}$. The aggregated system (14) becomes

$$\mathbf{s}_{n+1} = \mathbf{s}_n + \varepsilon\mathbf{U}(\mathbf{L} - \mathbf{I})\mathbf{P}\bar{\mathbf{P}}_c\mathbf{s}_n = \mathbf{s}_n + \varepsilon\mathbf{U}(\mathbf{L} - \mathbf{I})\bar{\mathbf{P}}_c\mathbf{s}_n = \mathbf{s}_n + \varepsilon(\mathbf{UL}\bar{\mathbf{P}}_c - \mathbf{I})\mathbf{s}_n, \quad (18)$$

where $\bar{\mathbf{L}} = \mathbf{UL}\bar{\mathbf{P}}_c$ is a classical Leslie matrix of order p whose coefficients are

$$\begin{aligned} f_i &= \mathbf{1F}_i\nu^i, & i &= 1, \dots, p, & (\text{fertility rates}), \\ s_i &= \mathbf{1S}_i\nu^i, & i &= 1, \dots, p-1, & (\text{survival rates}). \end{aligned}$$

If we denote by $\bar{\lambda}$ and $\bar{\mathbf{v}}$ the dominant eigenvalue and eigenvector of positive components of $\bar{\mathbf{L}}$, after Theorem 2, we have that

$$\lim_{n \rightarrow +\infty} \frac{\mathbf{s}_n(\varepsilon)}{(\varepsilon\bar{\lambda} + (1 - \varepsilon))^n} = C\bar{\mathbf{v}}.$$

And for the general system, we have the asymptotic behaviour:

$$\lim_{n \rightarrow +\infty} \frac{\mathbf{X}_n(\varepsilon)}{(\varepsilon\bar{\lambda} + (1 - \varepsilon) + O(\varepsilon^2))^n} = C(\bar{\mathbf{P}}_c\bar{\mathbf{v}} + O(\varepsilon)), \quad (\varepsilon \rightarrow 0),$$

and so it is clear that the asymptotic behaviour of the general system is mostly defined by the asymptotic properties of the classical Leslie matrix $\bar{\mathbf{L}}$, whose entries summarize the effect of fast dynamics on slow dynamics.

4.2. Density Dependent Case

In this case, we suppose $\mathbf{L} = \mathbf{L}(\mathbf{X})$ in a general way and we can aggregate system (17) using the method of Section 3. We have $\mathbf{F}(\mathbf{X}) = (\mathbf{L}(\mathbf{X}) - \mathbf{I})\mathbf{P}\mathbf{X}$ and equation (16) becomes

$$\mathbf{s}_{n+1} = \mathbf{s}_n + \varepsilon\mathbf{U}(\mathbf{L}(\bar{\mathbf{P}}_c\mathbf{s}_n) - \mathbf{I})\mathbf{P}\bar{\mathbf{P}}_c\mathbf{s}_n + O(\varepsilon^2),$$

and using (5), we obtain

$$\mathbf{s}_{n+1} = \mathbf{s}_n + \varepsilon\mathbf{U}(\mathbf{L}(\bar{\mathbf{P}}_c\mathbf{s}_n) - \mathbf{I})\mathbf{P}\bar{\mathbf{P}}_c\mathbf{s}_n + O(\varepsilon^2) = \mathbf{s}_n + \varepsilon(\mathbf{UL}(\bar{\mathbf{P}}_c\mathbf{s}_n)\bar{\mathbf{P}}_c - \mathbf{I})\mathbf{s}_n + O(\varepsilon^2), \quad (19)$$

where $\mathbf{UL}(\bar{\mathbf{P}}_c\mathbf{s})\bar{\mathbf{P}}_c$ is a general density dependent Leslie matrix of order p , denoted by $\bar{\mathbf{L}}(\bar{\mathbf{P}}_c\mathbf{s})$, whose entries are obtained as in the linear case.

To illustrate the usefulness of the aggregated system to study the general system we develop a less general example.

We suppose a population divided into two age-classes and living in an environment composed of two patches, with the migration changes performed in a much faster time scale than the demography changes, and with a survival rate in the young class, depending on the density of young individuals.

The migration process is represented by matrix

$$\mathbf{P} = \text{diag}\{\mathbf{P}_1, \mathbf{P}_2\} = \begin{pmatrix} 1 - p_1 & q_1 & 0 & 0 \\ p_1 & 1 - q_1 & 0 & 0 \\ 0 & 0 & 1 - p_2 & q_2 \\ 0 & 0 & p_2 & 1 - q_2 \end{pmatrix},$$

and so the equilibrium frequencies of fast dynamics are included in

$$\bar{\mathbf{P}}_c = \text{diag}\{\nu^1, \nu^2\} = \begin{pmatrix} \frac{q_1}{p_1 + q_1} & 0 \\ \frac{p_1}{p_1 + q_1} & 0 \\ 0 & \frac{q_2}{p_2 + q_2} \\ 0 & \frac{p_2}{p_2 + q_2} \end{pmatrix}.$$

The demography is defined by means of the matrix

$$\mathbf{L} = \begin{pmatrix} \mathbf{F}_1 & \mathbf{F}_2 \\ \mathbf{S} & \mathbf{0} \end{pmatrix},$$

where

$$\mathbf{F}_i = \begin{pmatrix} f^{i1} & 0 \\ 0 & f^{i2} \end{pmatrix}, \quad i = 1, 2 \quad \text{and} \quad \mathbf{S} = \begin{pmatrix} \mu_1 \exp(-\alpha_1 x^{11}) & 0 \\ 0 & \mu_2 \exp(-\alpha_2 x^{12}) \end{pmatrix},$$

where μ_i and α_i are positive parameters.

The general system (17) is then

$$\mathbf{X}_{n+1} = \mathbf{P}\mathbf{X}_n + \varepsilon \begin{pmatrix} f^{11} - 1 & 0 & f^{21} & 0 \\ 0 & f^{12} - 1 & 0 & f^{22} \\ \mu_1 \exp(-\alpha_1 x_n^{11}) & 0 & -1 & 0 \\ 0 & \mu_2 \exp(-\alpha_2 x_n^{12}) & 0 & -1 \end{pmatrix} \mathbf{P}\mathbf{X}_n. \quad (20)$$

The aggregated system (19) can be expressed in the form

$$\begin{pmatrix} s_{n+1}^1 \\ s_{n+1}^2 \end{pmatrix} = \begin{pmatrix} s_n^1 \\ s_n^2 \end{pmatrix} + \varepsilon \left[\begin{pmatrix} f^1 & f^2 \\ S(s_n^1) & 0 \end{pmatrix} - \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix} \right] \begin{pmatrix} s_n^1 \\ s_n^2 \end{pmatrix} + O(\varepsilon^2), \quad (21)$$

where

$$f^i = \frac{f^{i1}q_i + f^{i2}p_i}{p_i + q_i}, \quad i = 1, 2, \quad \text{and} \\ S(s^1) = \frac{q_1}{p_1 + q_1} \mu_1 \exp\left(-\alpha_1 \frac{q_1}{p_1 + q_1} s^1\right) + \frac{p_1}{p_1 + q_1} \mu_2 \exp\left(-\alpha_2 \frac{p_1}{p_1 + q_1} s^1\right) \\ = a_1 \exp(-b_1 s^1) + a_2 \exp(-b_2 s^1).$$

We now try to find under which conditions system (20) has an asymptotically stable equilibrium. For this, we start studying the same problem for system

$$\mathbf{s}_{n+1} = \mathbf{s}_n + \varepsilon (\bar{\mathbf{L}}(s_n^1) - \mathbf{I}) \mathbf{s}_n, \quad (22)$$

that is, the aggregated system neglecting the $O(\varepsilon^2)$ term. The system (22) has an equilibrium $\mathbf{s}^* = (s^{1*}, s^{2*})^\top$ if s^{1*} satisfies

$$0 = \det(\bar{\mathbf{L}}(s^1) - \mathbf{I}) = 1 - f^1 - f^2 (a_1 \exp(-b_1 s^1) + a_2 \exp(-b_2 s^1)). \quad (23)$$

That happens, for $s^{1*} > 0$, if and only if $f^1 < 1 < f^1 + f^2(a_1 + a_2)$, that is,

$$\frac{f^{11}q_1 + f^{12}p_1}{p_1 + q_1} < 1 < \frac{f^{11}q_1 + f^{12}p_1}{p_1 + q_1} + \left(\frac{f^{21}q_2 + f^{22}p_2}{p_2 + q_2} \right) \left(\frac{\mu_1 q_1 + \mu_2 p_1}{p_1 + q_1} \right). \quad (24)$$

In that case, there is only one value s^{1*} that satisfies (23) and the corresponding s^{2*} is $((1 - f_1)/f_2)s^{1*}$. We are proving that \mathbf{s}^* is always asymptotically stable for small ε .

If we call \mathbf{F} to the map associated to system (22)

$$\mathbf{F}(\mathbf{s}) = \mathbf{s} + \varepsilon (\tilde{\mathbf{L}}(s^1) - \mathbf{I}) \mathbf{s},$$

its Jacobian matrix at \mathbf{s}^* is

$$J\mathbf{F}(\mathbf{s}^*) = \begin{pmatrix} 1 - \varepsilon + \varepsilon f^1 & \varepsilon f^2 \\ \varepsilon c(\mathbf{s}^*) & 1 - \varepsilon \end{pmatrix},$$

where

$$c(\mathbf{s}^*) = a_1 (1 - b_1 s^{1*}) \exp(-b_1 s^{1*}) + a_2 (1 - b_2 s^{1*}) \exp(-b_2 s^{1*}).$$

Using that s^{1*} satisfies (23)

$$c(\mathbf{s}^*) = \frac{1 - f_1}{f_2} - s^{1*} (a_1 b_1 \exp(-b_1 s^{1*}) + a_2 b_2 \exp(-b_2 s^{1*})),$$

which implies that

$$\text{Tr}(J\mathbf{F}(\mathbf{s}^*)) = 2(1 - \varepsilon) + \varepsilon f_1 = 2 + \varepsilon(f_1 - 2)$$

and

$$\begin{aligned} \det(J\mathbf{F}(\mathbf{s}^*)) &= (1 - \varepsilon + \varepsilon f_1)(1 - \varepsilon) - \varepsilon^2 f_2 c(\mathbf{s}^*) \\ &= 1 + \varepsilon(f_1 - 2) + \varepsilon^2 f_2 s^{1*} (a_1 b_1 \exp(-b_1 s^{1*}) + a_2 b_2 \exp(-b_2 s^{1*})). \end{aligned}$$

For small ε , we have

$$|\text{Tr}(J\mathbf{F}(\mathbf{s}^*))| < 1 + \det(J\mathbf{F}(\mathbf{s}^*)) < 2,$$

and this yields $\rho(J\mathbf{F}(\mathbf{s}^*)) < 1$.

The previous study of system (22) gives the following information about systems (21) and (20). If condition (24) is verified, then there exists a unique equilibrium that is asymptotically stable for small ε , of the form $\mathbf{s}^* + O(\varepsilon)$ for system (21), and of the form $\bar{\mathbf{P}}_c \mathbf{s}^* + O(\varepsilon)$ for system (20), \mathbf{s}^* being the unique equilibrium of system (22).

5. CONCLUSION

Our general results have different applications. In the present work, we have introduced a model of an age structured population in a multipatch environment, but it is possible to study, for example, the influence of spatial heterogeneity on the stability of ecological communities.

Spatial heterogeneity can play a very important role in the stability of ecological communities [17]. 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 on the dynamics and stability of the community.

Our method yields the simplified aggregated model and also, 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 the density dependent Leslie model where the fecundity and survival 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 that can be calculated.

In the future, we intend to use our general methods given here for the study of patch structured communities. We plan to model a patch structured host-parasitoid community and try to obtain similar results to those for the cellular automaton spatial model based upon Nicholson-Bailey model [17].

In another direction, we will develop more general aggregation methods in the discrete case, including more general fast dynamics.

APPENDIX A

GENERAL RESULTS OF THE THEORY OF ANALYTICAL PERTURBATION OF MATRICES

Let X be a complex linear space of finite dimension N and let $\mathbf{T}(\varepsilon)$ be a linear operator defined on X , that admits the following expansion:

$$\mathbf{T}(\varepsilon) = \mathbf{T}_0 + \varepsilon\mathbf{T}_1 + \varepsilon^2\mathbf{T}_2 + \dots, \quad |\varepsilon| < R.$$

Let λ_0 be an eigenvalue of \mathbf{T}_0 (unperturbed operator) and \mathbf{P}_0 its associated eigenprojection with $\dim(\mathbf{P}_0) = n \leq N$. The dependence of the eigenvalues $\lambda(\varepsilon)$ of $\mathbf{Y}(\varepsilon)$ is continuous in ε and the subset of eigenvalues of $\mathbf{T}(\varepsilon)$ that verify $\lambda(\varepsilon) \rightarrow \lambda_0$ when $\varepsilon \rightarrow 0$ is called λ_0 -group.

The spectrum of operator $\tilde{\mathbf{T}}_1 = \mathbf{P}_0\mathbf{T}_1\mathbf{P}_0$ gives a partition of the λ_0 -group. Without loss of generality, we can suppose that all the eigenvalues of $\tilde{\mathbf{T}}_1$ on \mathbf{P}_0X are different from zero and as this operator vanishes identically on $(\mathbf{I} - \mathbf{P}_0)X$, we can write

$$\det(\tilde{\mathbf{T}}_1 - \mu\mathbf{I}) = \mu^{N-n}(\mu - \mu_1)^{m_1} \dots (\mu - \mu_r)^{m_r},$$

with $\mu_i \neq \mu_j$ if $i \neq j$, $\mu_j \neq 0$, $j = 1, \dots, r$, $m_1 + \dots + m_r = n$.

The λ_0 -group admits a partition in r subgroups corresponding to the r different eigenvalues μ_1, \dots, μ_r , called $\lambda_0 + \varepsilon\mu_j$ -groups, $j = 1, \dots, r$.

THEOREM 3. *Let $\mathbf{T}(\varepsilon)$ be an holomorphic perturbation of $\mathbf{T}(0) = \mathbf{T}_0$ and let λ_0 be a semisimple unperturbed eigenvalue. It exists $\delta > 0$ such that if $|\varepsilon| < \delta$ and $\lambda(\varepsilon)$ is a perturbed eigenvalue of the λ_0 -group of $\mathbf{T}(\varepsilon)$, we have that $\lambda(\varepsilon)$ belongs to the $\lambda_0 + \varepsilon\mu_j$ -group if and only if*

$$\lambda(\varepsilon) = \lambda_0 + \varepsilon\mu_j + O\left(\varepsilon^{1+(1/p)}\right),$$

where p is an integer verifying $1 \leq p \leq m_j$.

Also, if $\mathbf{x}(\varepsilon)$ is a perturbed eigenvector associated to the eigenvalue $\lambda(\varepsilon)$ of the $\lambda_0 + \varepsilon\mu_j$ -group continuous at $\varepsilon = 0$ and with $\mathbf{x}(0) = \mathbf{x}_0 \neq \mathbf{0}$, then it follows that

$$\tilde{\mathbf{T}}_1\mathbf{x}_0 = \mu_j\mathbf{x}_0.$$

It is simple to prove the following result about dominant eigenvalues.

LEMMA 4. *Let λ_0 be a semisimple unperturbed eigenvalue of \mathbf{T}_0 and modulus strictly dominant. Suppose that μ_1 is the eigenvalue of $\tilde{\mathbf{T}}_1$ with the largest real part. Then the eigenvalues of the $\lambda_0 + \varepsilon\mu_1$ -group are modulus strictly dominant for $\mathbf{T}(\varepsilon)$ when $\varepsilon \geq 0$, $\varepsilon \rightarrow 0$.*

In particular, if μ_1 is simple, the eigenvalue of $\mathbf{T}(\varepsilon)$ that admits the following expansion

$$\lambda(\varepsilon) = \lambda_0 + \varepsilon\mu_1 + O(\varepsilon^2), \quad (\varepsilon \rightarrow 0)$$

is modulus strictly dominant when $\varepsilon \geq 0$, $\varepsilon \rightarrow 0$.

APPENDIX B

CENTRAL MANIFOLD THEOREM

To obtain the aggregated system in Section 3, we use a center manifold theorem. The classical center manifold theorem is valid in a neighbourhood of an equilibrium point of a dynamical system and tells us that it is possible to study the general dynamics of the system by means of its restriction to a certain invariant manifold, the center manifold, that corresponds to the nonhyperbolic part of the equilibrium, see [18]. There are much more general settings where this kind of result applies, see for instance [19], where the equilibrium point is allowed to be a general invariant manifold.

In this work, we need a center manifold that is not just for an equilibrium point, but rather, for a simple manifold of equilibrium points, which represents a small generalization of the classical result. To be specific, let us state the theorem.

CENTER MANIFOLD THEOREM. *Let the system*

$$\begin{aligned} \mathbf{x}_{n+1} &= \mathbf{B}\mathbf{x}_n + \varepsilon\mathbf{F}(\mathbf{x}_n, \mathbf{y}_n, \varepsilon), \\ \mathbf{y}_{n+1} &= \mathbf{C}\mathbf{y}_n + \varepsilon\mathbf{G}(\mathbf{x}_n, \mathbf{y}_n, \varepsilon), \end{aligned} \quad (25)$$

be such that $\mathbf{x} \in \mathbf{R}^k$, $\mathbf{y} \in \mathbf{R}^m$, and $\varepsilon \in \mathbf{R}$, \mathbf{B} is an $k \times k$ matrix whose eigenvalues have modulus equal to 1 and \mathbf{C} is an $m \times m$ matrix of eigenvalues lying in the open unit disk, and \mathbf{F} and \mathbf{G} are C^∞ mappings from \mathbf{R}^{k+m+1} to \mathbf{R}^k and \mathbf{R}^m , respectively, with $\mathbf{F}(\mathbf{0}, \mathbf{0}, 0) = \mathbf{0}$ and $\mathbf{G}(\mathbf{0}, \mathbf{0}, 0) = \mathbf{0}$. For every $M > 0$, there exists $\delta > 0$ and a C^∞ mapping $\mathbf{h}(\mathbf{x}, \varepsilon)$ defined for every $|\mathbf{x}| < M$ and $|\varepsilon| < \delta$ with range in \mathbf{R}^m that satisfies the following.

- (i) $|\mathbf{h}(\mathbf{x}, \varepsilon)| < K|\varepsilon|$, with K constant.
- (ii) For every ε , $|\varepsilon| < \delta$, the graph of $\mathbf{h}(\cdot, \varepsilon)$, W_ε , is a locally invariant manifold, that is, for $|\mathbf{x}| < M$

$$\mathbf{h}(\mathbf{x} + \varepsilon\mathbf{F}(\mathbf{x}, \mathbf{h}(\mathbf{x}, \varepsilon), \varepsilon)) = \mathbf{C}\mathbf{h}(\mathbf{x}, \varepsilon) + \varepsilon\mathbf{G}(\mathbf{x}, \mathbf{h}(\mathbf{x}, \varepsilon), \varepsilon). \quad (26)$$

- (iii) The dynamics of system (25) restricted to W_ε is defined by the equation,

$$\mathbf{u}_{n+1} = \mathbf{B}\mathbf{u}_n + \varepsilon\mathbf{F}(\mathbf{u}_n, \mathbf{h}(\mathbf{u}_n, \varepsilon), \varepsilon), \quad \mathbf{u} \in \mathbf{R}^k. \quad (27)$$

- (iv) W_ε is locally attractive, that is, if $\{(\mathbf{x}_k, \mathbf{y}_k)\}$ is a solution of system (25) with $|\mathbf{x}_0| < M$ and \mathbf{y}_0 small enough, then there exists $\{\mathbf{u}_k\}$ solution of equation (27) such that

$$|\mathbf{x}_k - \mathbf{u}_k| \leq K\beta^k \quad \text{and} \quad |\mathbf{y}_k - \mathbf{h}(\mathbf{u}_k, \varepsilon)| \leq K\beta^k,$$

where K and β are positive constants, with $\beta < 1$.

PROOF. We follow the proof of Center Manifold Theorem in [20, pp. 146–153] using the functional space

$$\mathbf{A}_0 = \{\varphi : \mathbf{R}^k \times \mathbf{R} \rightarrow \mathbf{R}^m : \varphi \in C^0, |\varphi|_\infty \leq 1, \varphi(\mathbf{x}, 0) = \mathbf{0} \text{ and } |\varphi(\mathbf{x}, \varepsilon) - \varphi(\mathbf{x}', \varepsilon)| \leq |\mathbf{x} - \mathbf{x}'|\},$$

and the mapping \mathcal{F} from \mathbf{A}_0 to \mathbf{A}_0 defined by

$$(\mathcal{F}\varphi)(\tilde{\mathbf{x}}, \varepsilon) = \mathbf{C}\varphi(\mathbf{x}, \varepsilon) + \varepsilon\mathbf{G}(\mathbf{x}, \varphi(\mathbf{x}, \varepsilon), \varepsilon),$$

where $\tilde{\mathbf{x}} = \Phi_{\varphi, \varepsilon}(\mathbf{x}) = \mathbf{x} + \varepsilon\mathbf{F}(\mathbf{x}, \varphi(\mathbf{x}, \varepsilon), \varepsilon)$.

In system (12), we have $\mathbf{B} = \mathbf{I}$, and the points of the form $(\mathbf{s}, 0)$ represent the manifold of equilibrium points for $\varepsilon = 0$. Though, in general, it is not possible to find out explicitly $\mathbf{h}(\mathbf{x}, \varepsilon)$, and even the center manifold is not unique, we know that the coefficients of its Taylor series are unique, and therefore, we could use the equality (26) to calculate its expansion in ε powers. If we make $\mathbf{h}(\mathbf{x}, \varepsilon) = \varepsilon\mathbf{h}_1(\mathbf{x}) + O(\varepsilon^2)$, then (26) yields

$$\begin{aligned} \varepsilon\mathbf{h}_1[\mathbf{x} + \varepsilon\mathbf{F}(\mathbf{x}, \varepsilon\mathbf{h}_1(\mathbf{x}) + O(\varepsilon^2), \varepsilon)] + O(\varepsilon^2) \\ = \mathbf{C}(\varepsilon\mathbf{h}_1(\mathbf{x}) + O(\varepsilon^2)) + \varepsilon\mathbf{G}(\mathbf{x}, \varepsilon\mathbf{h}_1(\mathbf{x}) + O(\varepsilon^2), \varepsilon), \end{aligned}$$

and identifying the terms in ε , we obtain

$$\mathbf{h}_1(\mathbf{x}) = \mathbf{C}\mathbf{h}_1(\mathbf{x}) + \mathbf{G}(\mathbf{x}, \mathbf{0}, 0) \quad \text{and} \quad \mathbf{h}_1(\mathbf{x}) = (\mathbf{I} - \mathbf{C})^{-1}\mathbf{G}(\mathbf{x}, \mathbf{0}, 0),$$

and so

$$\mathbf{h}(\mathbf{x}, \varepsilon) = \varepsilon(\mathbf{I} - \mathbf{C})^{-1}\mathbf{G}(\mathbf{x}, \mathbf{0}, 0) + O(\varepsilon^2),$$

and equation (27) admits the form

$$\mathbf{u}_{n+1} = \mathbf{u}_n + \varepsilon\mathbf{F}(\mathbf{u}_n, \varepsilon(\mathbf{I} - \mathbf{C})^{-1}\mathbf{G}(\mathbf{u}_n, \mathbf{0}, 0) + O(\varepsilon^2), \varepsilon). \quad (28)$$

REFERENCES

1. P. Auger, *Dynamics and Thermodynamics in Hierarchically Organized Systems. Applications in Physics, Biology and Economics*, Pergamon Press, Oxford, (1989).
2. P. Auger and E. Benoit, A prey-predator model in a multipatch environment with different time scales, *Jour. Biol. Systems* **1**, 187–197 (1993).
3. P. Auger and R. Roussarie, Complex ecological models with simple dynamics: From individuals to populations, *Acta Biotheoretica* **42**, 111–136 (1994).
4. P. Auger and J.C. Poggiale, Emerging properties in population dynamics with different time scales, *Jour. Biol. System* **3**, 591–602 (1995).
5. P.H. Leslie, On the use of matrices in certain population mathematics, *Biometrika* **33**, 183–212 (1945).
6. L.P. Leftkovich, The study of population growth in organisms grouped by stages, *Biometrics* **21**, 1–18 (1965).
7. L. Edelstein-Keshet, *Mathematical Models in Biology*, Random-House, New York, (1988).
8. J.D. Murray, *Mathematical Biology*, Springer-Verlag, Berlin, (1989).
9. A.J. Nicholson and V.A. Bailey, The balance of animal populations. Part I, *Proc. Zool. Soc. Lond.* **3**, 551–598 (1935).
10. M.P. Hassel, *The Dynamics of Arthropod Predator-Prey Systems*, Princeton University Press, Princeton, (1978).
11. R. Bravo de la Parra, P. Auger and E. Sánchez, Aggregation methods in discrete models, *Jour. Biol. Systems* **3**, 603–612 (1995).
12. E. Sánchez, R. Bravo de la Parra and P. Auger, Linear discrete models with different time scales, *Acta Biotheoretica* **43**, 465–479 (1995).
13. H. Baumgartel, *Analytic Perturbation Theory for Matrices and Operators*, Birkhäuser Verlag, Basel, (1985).
14. T. Kato, *Perturbation Theory for Linear Operators*, Springer-Verlag, Berlin, (1980).
15. H. Caswell, *Matrix Population Models*, Sinauer Associates Inc., Sunderland, (1989).
16. D.O. Logofet, *Matrices and Graphs*, CRC Press, Boca Ratón, FL, (1993).
17. M.P. Hassel, H.N. Comins and R.M. May, Spatial structure and chaos in insect population dynamics, *Nature* **353**, 255–258 (1991).
18. J. Carr, *Applications of Center Manifold Theory*, Springer-Verlag, New York, (1981).
19. M.W. Hirsch, C.C. Pugh and M. Shub, *Invariant Manifolds*, Springer-Verlag, Berlin, (1977).
20. G. Iooss, *Bifurcation of Maps and Applications*, North-Holland, Amsterdam, (1979).