ELSEVIER

Mathematical Biosciences 157 (1999) 91–109

Mathematical Biosciences
an international journal

A discrete model with density dependent fast migration

Rafael Bravo de la Parra [a,*], Eva Sánchez [b,1], Ovide Arino [c,2], Pierre Auger [d,3]

[a] *Departamento de Matemáticas, Universidad de Alcalá, 28871 Alcalá de Henares, Madrid, Spain*
[b] *Departamento de Matemáticas, E.T.S.I. Industriales, Universidad Politécnica de Madrid, c/José Gutiérrez Abascal, 2, 28006 Madrid, Spain*
[c] *Department of Mathematics, I.P.R.A., University of Pau, 1 av de l'Université 64 000 Pau, France*
[d] *U.M.R. C.N.R.S. 5558, Université Claude Bernard Lyon-1, 43 Boul. 11 Novembre 1918, 69622 Villeurbanne cedex, France*

Received 31 December 1997; received in revised form 15 July 1998; accepted 9 October 1998

Abstract

The aim of this work is to develop an approximate aggregation method for certain non-linear discrete models. Approximate aggregation consists in describing the dynamics of a general system involving many coupled variables by means of the dynamics of a reduced system with a few global variables. We present discrete models with two different time scales, the slow one considered to be linear and the fast one non-linear because of its transition matrix depends on the global variables. In our discrete model the time unit is chosen to be the one associated to the slow dynamics, and then we approximate the effect of fast dynamics by using a sufficiently large power of its corresponding transition matrix. In a previous work the same system is treated in the case of fast dynamics considered to be linear, conservative in the global variables and inducing a stable frequency distribution of the state variables. A similar non-linear model has also been studied which uses as time unit the one associated to the fast dynamics and has the non-linearity in the slow part of the system. In the present work we transform the system to make the global variables explicit, and we justify the quick derivation of the aggregated system. The local asymptotic behaviour of the aggregated system entails

* Corresponding author. Tel.: +34-91 885 4903; fax: +34-91 885 4951; e-mail: mtbravo@alcala.es
[1] E-mail: esanchez@etsii.upm.es
[2] E-mail: Ovide.Arino@univ-pau.fr
[3] E-mail: pauger@biomserv.univ-lyon1.fr

PII: S 0 0 2 5 - 5 5 6 4 (9 8) 1 0 0 7 8 - 0

that of the general system under certain conditions, for instance, if the aggregated system has a stable hyperbolic fixed point then the general system has one too. The method is applied to aggregate a multiregional Leslie model with density dependent migration rates.

Keywords: Approximate aggregation of variables; Population dynamics; Time scales; Discrete dynamical systems

---

1. Introduction

When modelling ecological systems we always have to decide the level of complexity we should introduce so as to optimize the profit of the study. Any model is a compromise between generality and simplicity on the one hand and biological realism on the other. The more biological details are included in specifying a model, the more complicated and specialized it becomes. Models describing ecological systems in detail involve a very large number of coupled variables, which usually results in analytical intractability. At the other extreme, very simple models, which are mathematically tractable, do not justify the assumptions to be made in order to obtain such simplicity.

Nature offers many examples of systems where several events occur at different time scales. It is then common practice to consider those events occurring at the fastest scale as being instantaneous with respect to the slower ones which results in a lesser number of variables or parameters needed to describe the evolution of the system. A subsequent issue is to determine how far the results obtained from the reduced system are from the real ones. Several mathematical methods have been developed in relation with the two above-mentioned issues, reduction and an estimation of the discrepancy between the complete system and the systems arising from the reduction, to name the best known: averaging methods, singular perturbation methods and aggregation methods. As far as applications of these methods are concerned, by far the most important ones have been in physics, chemistry, mechanics and industrial processes. In comparison, not much has been done up to now in life sciences although there are many examples of biological systems with different time scales. The issue was mainly considered in the context of ecological systems involving several species with different developmental stages, or a single species engaged in several actions with different time scales (reproduction, aging, food intake), or both, by means of the aggregation methods. The study was initiated about 10 years ago by one of us, Auger [1], in the frame of ordinary differential equations. The main effort was spent in deriving the so-called aggregated systems and a general formal computational method, the quick derivation method, was described by Auger in a large class of systems possessing one or several invariants. The method was refined and a number of examples were investigated by Auger and his collaborators [2–4].

Aggregation methods study the relationship between a large class of complex systems and their corresponding aggregated systems. The aim of aggregation methods is twofold: on the one hand they construct the aggregated systems that summarize the dynamics of the complex ones, simplifying their analytical study, and on the other, looking at the relationship in the opposite sense, the complex systems are explanations of the simple form of the aggregated ones. The essential property of complex systems that allows their aggregation is the existence of two different time scales. As a result of that we can think of a hierarchically structured system with a division into subsystems that are weakly coupled and simultaneously exhibit a strong internal dynamics. The idea of aggregation is then to choose a global variable, sometimes called a macro-variable, for each subsystem and to build up a reduced system for these global variables. The aggregated system reflects 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, while the fast dynamics of the general system is reflected in the parameters 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.

Recently, some of the authors have extended aggregation methods to the case of discrete systems. In Refs. [5,6] the case of linear, density independent, time discrete systems is studied; a very general linear model with two time scales is aggregated and it is proved that the elements defining the asymptotic behaviour of the general and the aggregated systems are equal up to a 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 the demographic process. In Refs. [7,8] a non-linear case is developed in which the fast dynamics are still considered to be linear and the slow dynamics are non-linear. The distinction between time scales is based upon using the fast dynamics as time unit of the discrete process.

The aim of this work is to present another non-linear discrete case of aggregation method. For the time unit of the discrete process we use the one corresponding to the slow dynamics, which are considered to be linear and thus represented by a general non-negative matrix. The fast dynamics are dependent on global variables and we suppose that they act a large number of times during one single time unit of the slow dynamics. In Section 2, we present the general model of a population divided into groups which are also divided into subgroups. The fast dynamics are internal for every group and, for every fixed values of the global variables, asymptotically leads the group to certain constant proportions among its subgroups. The global variables used in the aggregation are the total number of individuals in each group: they are constants of motion for the fast dynamics. After introducing the aggregated system, the general model is rewritten to make explicit, as clearly as possible, its dependence on the global variables. That allows, in Section 3, a comparison of the asymptotic properties of both systems. Finally, in Section 4 we develop a general model for an age structured population divided into age classes and subdivided into geographical patches. The demographic process evolves at a slow time scale in comparison with the migration process, which is considered density dependent. The aggregated system, whose variables are the total number of individuals in each age class, is a non-linear matrix model. A particular case with two age classes and two geographical patches is treated and the results of Section 3 are used to yield the existence of a stable fixed point for the general system from the density dependent Leslie matrix appearing in the aggregated system.

2. The model

We suppose a general population, whose evolution is described in discrete time, divided into p groups, and each of these groups is divided into several subgroups.

The state of the population at time n is represented by a vector

$$\mathbf{X}_n = \left(\mathbf{x}_n^1, \ldots, \mathbf{x}_n^p\right)^\top \in \mathbb{R}_+^N$$

where every vector $\mathbf{x}_n^i \in \mathbb{R}_+^{N^i},\ i = 1, \ldots, p$, represents the state of the i group, $N = N^1 + \cdots + N^p$.

Apart from the above defined variables we give a prominent role to the global variables, the total number of individuals in every group, denoted

$$s_n^i = \sum_{j=1}^{N^i} x_n^{ij}, \quad i = 1, \ldots, p.$$

We denote by $\mathbf{1}$ the row vector all whose entries are equal to 1, specifying its length with a subindex if there exists any ambiguity. So, we have $s_n^i = \mathbf{1}\mathbf{x}_n^i$, and denoting $\mathbf{U}$ the matrix

$$\mathbf{U} = \operatorname{diag}\{\mathbf{1}_{N^1}, \ldots, \mathbf{1}_{N^p}\} = \begin{pmatrix} 1\overset{N^1)}{\cdots}1 & 0\cdots0 & \cdots & 0\cdots0 \\ 0\cdots0 & 1\overset{N^2)}{\cdots}1 & \cdots & 0\cdots0 \\ \vdots & \vdots & \ddots & \vdots \\ 0\cdots0 & 0\cdots0 & \cdots & 1\overset{N^p)}{\cdots}1 \end{pmatrix},$$

we obtain

$$\mathbf{s}_n = \left(s_n^1, \ldots, s_n^p\right)^\top = \left(\mathbf{1}\mathbf{x}_n^1, \ldots, \mathbf{1}\mathbf{x}_n^p\right)^\top = \mathbf{U}\mathbf{X}_n \in \mathbb{R}_+^p.$$

In the evolution of this population we distinguish between two different time scales, and so we will speak henceforth of the slow dynamic and the fast dynamic. The fast dynamic is non-linear, dependent on global variables, internal to every group and conservative of its total number of individuals. Asymptotically, the fast dynamic leads the group to certain constant proportions among its subgroups for every fixed value of $\mathbf{s}$.

These conditions are fulfilled if we introduce the density-dependent block diagonal matrix

$$\mathbf{P}\colon \mathbb{R}^p_+ \to \mathbb{R}^{N\times N}_+; \quad \mathbf{P}(\mathbf{s}) = \operatorname{diag}\{\mathbf{P}_1(\mathbf{s}), \ldots, \mathbf{P}_p(\mathbf{s})\},$$

where $\mathbf{P}_i(\mathbf{s})$ is a real matrix of dimensions $N^i \times N^i$, that is the projection matrix associated to the fast dynamics for each group $i = 1, \ldots, p$. These matrices satisfy the following hypothesis.

Hypothesis (H1).
(i) $\mathbf{P} : \mathbb{R}^p_+ \to \mathbb{R}^{N\times N}_+$ is C^1.
(ii) $\mathbf{P}_i(\mathbf{s})$ is a regular stochastic matrix for every $i = 1, \ldots, p$ and every $\mathbf{s} \in \mathbb{R}^p_+$.

A regular stochastic matrix is a primitive non-negative matrix whose columns sum up to 1. It is well known that, for each matrix $\mathbf{P}_i(\mathbf{s})$, 1 is a simple eigenvalue, larger than the real part of any other eigenvalue, with strictly positive left and right eigenvectors. To be more specific, the left eigenspace of this matrix associated to the eigenvalue 1 is generated by vector $\mathbf{1}^\top$ and the right eigenspace is generated by vector $\boldsymbol{v}^i(\mathbf{s})$, that is unique if we choose it having positive entries and verifying $\mathbf{1}\boldsymbol{v}^i(\mathbf{s}) = 1$.

We define

$$\mathbf{P}_i = \lim_{k\to+\infty} \mathbf{P}_i^k(\mathbf{s}) = (\boldsymbol{v}^i(\mathbf{s})| \ldots |\boldsymbol{v}^i(\mathbf{s})),$$

where $\mathbf{P}_i^k(\mathbf{s})$ is the kth power of the matrix $\mathbf{P}_i(\mathbf{s})$.

We use as time unit of the discrete process the one corresponding to the slow dynamics, which is considered to be linear and thus represented by a general non-negative matrix $\mathbf{M}$ of dimensions $N \times N$. Then, the general model to be studied is

$$\mathbf{X}_{n+1} = \mathbf{M}\mathbf{P}^k(\mathbf{U}\mathbf{X}_n)\mathbf{X}_n = \mathbf{M}\mathbf{P}^k(\mathbf{s}_n)\mathbf{X}_n, \tag{1}$$

where we have represented the fast dynamics by the kth power of matrix $\mathbf{P}(\mathbf{s})$, where k is large, which means that it acts a large number of times during one single time unit of the slow dynamics.

2.1. The aggregated model

We build up a model which describes the dynamics of the global variables $\mathbf{s}_n$. The exact model satisfied by these variables is obtained premultiplying in (1) by matrix $\mathbf{U}$:

$$\mathbf{s}_{n+1} = \mathbf{U}\mathbf{X}_{n+1} = \mathbf{U}\mathbf{M}\mathbf{P}^k(\mathbf{s}_n)\mathbf{X}_n.$$

In order to get a system with the global variables as the unique state variables, we propose the following approximation, which means that the fast dynamics has reached its equilibrium distribution:

$$\mathbf{U}\mathbf{M}\mathbf{P}^k(\mathbf{s}_n)\mathbf{X}_n \approx \mathbf{U}\mathbf{M}\overline{\mathbf{P}}(\mathbf{s}_n)\mathbf{X}_n = \mathbf{U}\mathbf{M}\mathbf{P}_c(\mathbf{s}_n)\mathbf{U}\mathbf{X}_n = \mathbf{U}\mathbf{M}\mathbf{P}_c(\mathbf{s}_n)\mathbf{s}_n,$$

where

$$\overline{\mathbf{P}}(\mathbf{s}) = \lim_{k\to+\infty}\mathbf{P}^k(\mathbf{s}) = \operatorname{diag}\{\overline{\mathbf{P}}_1(\mathbf{s}),\ldots,\overline{\mathbf{P}}_p(\mathbf{s})\},$$

$$\mathbf{P}_c(\mathbf{s}) = \operatorname{diag}\{\boldsymbol{v}^1(\mathbf{s}),\ldots,\boldsymbol{v}^p(\mathbf{s})\}$$

and we have used that

$$\overline{\mathbf{P}}(\mathbf{s}) = \mathbf{P}_c(\mathbf{s})\mathbf{U}.$$

The approximate model for the global variables, which we call *aggregated system*, is the following:

$$\mathbf{s}_{n+1} = \mathbf{U}\mathbf{M}\mathbf{P}_c(\mathbf{s}_n)\mathbf{s}_n. \tag{2}$$

The aim of this work is to show that, under some hypotheses of regularity, the dynamics of this aggregated system reflect that of the general system (1).

2.2. The general model in terms of global variables

For each $i = 1,\ldots,p$, let us consider the new variables

$$y^{i1} = s^i; \quad y^{ik} = x^{ik} - v^{ik}(\mathbf{s})s^i, \quad k = 2,\ldots,N^i$$

that is, y^{i1} is the global variable s^i and the other $N^i - 1$ variables in group i are changed into the difference between the old variable and the corresponding value in the fast dynamics equilibrium.

In matrix form, this change reads

$$\mathbf{y}^i = \begin{pmatrix} y^{i1} \\ y^{i2} \\ \vdots \\ y^{iN^i} \end{pmatrix} = \begin{pmatrix} 1 & 1 & \ldots & 1 \\ -v^{i2}(\mathbf{s}) & 1 - v^{i2}(\mathbf{s}) & \ldots & -v^{i2}(\mathbf{s}) \\ \vdots & \vdots & \ddots & \vdots \\ -v^{iN^i}(\mathbf{s}) & -v^{iN^i}(\mathbf{s}) & \ldots & 1 - v^{iN^i}(\mathbf{s}) \end{pmatrix} \begin{pmatrix} x^{i1} \\ x^{i2} \\ \vdots \\ x^{iN^i} \end{pmatrix}$$

$$= \mathbf{T}_i^{-1}(\mathbf{s})\mathbf{x}^i,$$

where

$$\mathbf{T}_i(\mathbf{s}) = \begin{pmatrix} v^{i1}(\mathbf{s}) & -1 & -1 & \ldots & -1 \\ v^{i2}(\mathbf{s}) & 1 & 0 & \ldots & 0 \\ v^{i3}(\mathbf{s}) & 0 & 1 & \ldots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ v^{iN^i}(\mathbf{s}) & 0 & 0 & \ldots & 1 \end{pmatrix}; \quad i = 1,\ldots,p.$$

Denoting $\mathbf{T}(\mathbf{s})$ the matrix of dimensions $N \times N$:

$$\mathbf{T}(\mathbf{s}) = \mathrm{diag}\{\mathbf{T}_1(\mathbf{s}), \dots, \mathbf{T}_p(\mathbf{s})\},$$

we can write

$$\begin{pmatrix} \mathbf{x}^1 \\ \vdots \\ \mathbf{x}^p \end{pmatrix} = \mathbf{T}(\mathbf{s}) \begin{pmatrix} \mathbf{y}^1 \\ \vdots \\ \mathbf{y}^p \end{pmatrix}.$$

We now transform system (1) by using the above change of variables:

$$\mathbf{Y}_{n+1} = \mathbf{T}^{-1}(\mathbf{s}_{n+1})\mathbf{M}\mathbf{P}^k(\mathbf{s}_n)\mathbf{T}(\mathbf{s}_n)\mathbf{Y}_n, \tag{3}$$

where we have introduced the notation $\mathbf{Y} = (\mathbf{y}^1, \dots, \mathbf{y}^p)^\top$.

In the last system we need to separate the equations corresponding to the global variables from the rest of equations. To this end, we change the order of variables in system (3) by means of the following transformation:

$$\mathbf{s} = \begin{pmatrix} s^1 \\ \vdots \\ s^p \end{pmatrix} = \begin{pmatrix} y^{11} \\ \vdots \\ y^{p1} \end{pmatrix} = \begin{pmatrix} \mathbf{e}_1 & \dots & \mathbf{0} \\ \vdots & \ddots & \vdots \\ \mathbf{0} & \dots & \mathbf{e}_p \end{pmatrix}_{p \times N} \begin{pmatrix} \mathbf{y}^1 \\ \vdots \\ \mathbf{y}^p \end{pmatrix},$$

where $\mathbf{e}_i = (1, 0, \dots, 0)$ is a row of dimensions $1 \times N^i, \; i = 1, \dots, p$.

Also, we need the new variables, defined for each $i = 1, \dots, p$:

$$\mathbf{z}^i = \begin{pmatrix} z^{i1} \\ z^{i2} \\ \vdots \\ z^{iN^i-1} \end{pmatrix} = \begin{pmatrix} y^{i2} \\ y^{i3} \\ \vdots \\ y^{iN^i} \end{pmatrix} = \begin{pmatrix} 0 & 1 & 0 & \dots & 0 \\ 0 & 0 & 1 & \dots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & \dots & 1 \end{pmatrix}_{(N^i-1)\times N^i} \begin{pmatrix} y^{i1} \\ y^{i2} \\ \vdots \\ y^{iN^i} \end{pmatrix} = \mathbf{B}_i \mathbf{y}^i.$$

Let us introduce the following notations

$$\mathbf{A} = \mathrm{diag}\{\mathbf{e}_1, \dots, \mathbf{e}_p\}_{p \times N} \quad \text{and} \quad \mathbf{B} = \mathrm{diag}\{\mathbf{B}_1, \dots, \mathbf{B}_p\}_{(N-p)\times N},$$

which enable us to express the change of variables in matrix form

$$\mathbf{s} = \mathbf{A} \begin{pmatrix} \mathbf{y}^1 \\ \vdots \\ \mathbf{y}^p \end{pmatrix} \quad \text{and} \quad \mathbf{z} = \begin{pmatrix} \mathbf{z}^1 \\ \vdots \\ \mathbf{z}^p \end{pmatrix} = \mathbf{B}\mathbf{Y},$$

and also

$$\mathbf{Y} = \mathbf{A}^\top \mathbf{s} + \mathbf{B}^\top \mathbf{Z}.$$

Bearing Eq. (3) in mind, we obtain the following system

$$\mathbf{s}_{n+1} = \mathbf{A}\mathbf{Y}_{n+1} = \mathbf{A}\mathbf{T}^{-1}(\mathbf{s}_{n+1})\mathbf{M}\mathbf{P}^k(\mathbf{s}_n)\mathbf{T}(\mathbf{s}_n)[\mathbf{A}^\top \mathbf{s}_n + \mathbf{B}^\top \mathbf{Z}_n], \tag{4}$$

$$\mathbf{Z}_{n+1} = \mathbf{B}\mathbf{Y}_{n+1} = \mathbf{B}\mathbf{T}^{-1}(\mathbf{s}_{n+1})\mathbf{M}\mathbf{P}^k(\mathbf{s}_n)\mathbf{T}(\mathbf{s}_n)[\mathbf{A}^\top \mathbf{s}_n + \mathbf{B}^\top \mathbf{Z}_n]. \tag{5}$$

We will simplify this system applying some properties of the matrices which we summarize in the following lemma.

Lemma 1.

(a) *For each* $i = 1, \dots, p$ *and each* $\mathbf{s} \in \mathbb{R}^p_+$, *we have*

$$\mathbf{R}_i(\mathbf{s}) = \mathbf{T}_i^{-1}(\mathbf{s})\mathbf{P}_i(\mathbf{s})\mathbf{T}_i(\mathbf{s}) = \begin{pmatrix} 1 & \mathbf{0} \\ \mathbf{0} & \mathbf{Q}_i(\mathbf{s}) \end{pmatrix},$$

where $\mathbf{Q}_i(\mathbf{s})$ *is a real matrix of dimensions* $(N^i - 1) \times (N^i - 1)$.

(b) $\det(\mathbf{P}_i(\mathbf{s}) - \lambda\mathbf{I}) = (1 - \lambda)\det(\mathbf{Q}_i(\mathbf{s}) - \lambda\mathbf{I})$.

(c) $\mathbf{A}\mathbf{T}^{-1}(\mathbf{s}) = \mathbf{U}$.

(d) $\mathbf{B}\mathbf{T}^{-1}(\mathbf{s}) = \mathbf{N}(\mathbf{s}) = \mathrm{diag}\{\mathbf{N}_1(\mathbf{s}), \dots, \mathbf{N}_p(\mathbf{s})\}$, *where*

$$\mathbf{N}_i(\mathbf{s}) = (-\mathbf{B}_i\boldsymbol{v}^i(\mathbf{s}) | \mathbf{I}_{N^i-1} - \mathbf{B}_i\boldsymbol{v}^i(\mathbf{s})\mathbf{1}_i), \quad i = 1, \dots, p.$$

(e) $\mathbf{T}(\mathbf{s})\mathbf{A}^\top = \mathbf{P}_c(\mathbf{s})$.

(f) $\mathbf{H}_i^{(k)}(\mathbf{s}) = \mathbf{T}_i(\mathbf{s})\mathbf{R}_i^k(\mathbf{s})\mathbf{B}_i^\top = \begin{pmatrix} -\mathbf{1}_{N^i-1}\mathbf{Q}_i^k(\mathbf{s}) \\ \mathbf{Q}_i^k(\mathbf{s}) \end{pmatrix}, \quad i = 1, \dots, p, \ k = 1, 2, \dots,$ *where* $\mathbf{R}_i(\mathbf{s})$ *is defined in* (a).

(g) $\mathbf{R}^k(\mathbf{s})\mathbf{A}^\top = \mathbf{A}^\top, \ k = 1, 2, \dots,$ *where* $\mathbf{R}(\mathbf{s}) = \mathrm{diag}\{\mathbf{R}_1(\mathbf{s}), \dots, \mathbf{R}_p(\mathbf{s})\}$.

Proof. See Appendix A.

From (b) and hypothesis **(H1)** (b) we conclude that the eigenvalues of $\mathbf{Q}_i(\mathbf{s}), \ i = 1, \dots, p$, are, for each $s \in \mathbf{R}^p_+$, those of $\mathbf{P}_i(\mathbf{s})$ except 1. This implies that the spectral radius of $\mathbf{Q}_i(\mathbf{s})$ is less than 1, that is $\rho(\mathbf{Q}_i(\mathbf{s})) < 1$.

Lemma 2. *Let* $K \subset \mathbb{R}^p_+$ *be a compact set. Then,*

$$\lim_{k\to\infty} \mathbf{Q}^k(\mathbf{s}) = \mathbf{0} \quad \textit{uniformly for } \mathbf{s} \in K$$

where $\mathbf{Q}(\mathbf{s}) = \mathrm{diag}\{\mathbf{Q}_1(\mathbf{s}), \dots, \mathbf{Q}_p(\mathbf{s})\}$.

Proof. See Appendix A.

We are now ready to simplify the systems (4) and (5). First of all, we have that

$$\mathbf{P}^k(\mathbf{s})\mathbf{T}(\mathbf{s})\mathbf{A}^\top = \mathbf{T}(\mathbf{s})\mathbf{R}^k(\mathbf{s})\mathbf{A}^\top = \mathbf{T}(\mathbf{s})\mathbf{A}^\top = \mathbf{P}_c(\mathbf{s})$$

and

$$\mathbf{P}^k(\mathbf{s})\mathbf{T}(\mathbf{s})\mathbf{B}^\top = \mathbf{T}(\mathbf{s})\mathbf{R}^k(\mathbf{s})\mathbf{B}^\top = \mathbf{H}^{(k)}(\mathbf{s}),$$

where $\mathbf{H}^{(k)}(\mathbf{s}) = \mathrm{diag}\{\mathbf{H}_1^{(k)}(\mathbf{s}), \dots, \mathbf{H}_p^{(k)}(\mathbf{s})\}$.

Therefore, the final version of the model in terms of global variables is

$$\mathbf{s}_{n+1} = \mathbf{U}\mathbf{M}\mathbf{P}_c(\mathbf{s}_n)\mathbf{s}_n + \mathbf{U}\mathbf{M}\mathbf{H}^{(k)}(\mathbf{s}_n)\mathbf{Z}_n, \tag{6}$$

$$\mathbf{Z}_{n+1} = \mathbf{N}(\mathbf{s}_{n+1})\mathbf{M}\mathbf{P}_c(\mathbf{s}_n)\mathbf{s}_n + \mathbf{N}(\mathbf{s}_{n+1})\mathbf{M}\mathbf{H}^{(k)}(\mathbf{s}_n)\mathbf{Z}_n. \tag{7}$$

3. Analysis of the relationship between the general and the aggregated model

In this section we establish the fundamental result of this paper and some of its consequences which are easily used in applications.

Let $\mathbf{F}: \mathbb{R}^p_+ \to \mathbb{R}^p_+$ be the function defined by $\mathbf{F}(\mathbf{s}) = \mathbf{UMP}_c(\mathbf{s})\mathbf{s}$, which is the map associated to the aggregated system (2).

Definition 3. An open and bounded set $A \subset \mathbb{R}^p_+$ is called F-shrinkable if there exists a positive number δ such that the compact set $\bar{A}_\delta = \{\mathbf{s} \in \mathbb{R}^p_+ : d(\mathbf{s}, A) \leqslant \delta\}$ verifies

$$\mathbf{F}(\bar{A}_\delta) \subset A.$$

Now, we solve Eq. (7) for the variables $\mathbf{Z}_n$ in terms of global variables $\mathbf{s}_n$. To this end, let us denote

$$\mathbf{R}(m,n) = \prod_{j=n}^{m-1} \mathbf{N}(\mathbf{s}_{j+1})\mathbf{MH}^{(k)}(\mathbf{s}_j), \quad m > n, \ \ \mathbf{R}(n,n) = \mathbf{I}.$$

Then, a straightforward calculation leads to

$$\mathbf{Z}_n = \mathbf{R}(n,0)\mathbf{Z}_0 + \sum_{j=0}^{n-1} \mathbf{R}(n,j+1)\mathbf{N}(\mathbf{s}_{j+1})\mathbf{MP}_c(\mathbf{s}_j)\mathbf{s}_j, \quad n \geqslant 1.$$

Substituting in Eq. (6), we obtain

$$\begin{aligned} \mathbf{s}_{n+1} &= \mathbf{UMP}_c(\mathbf{s}_n)\mathbf{s}_n \\ &\quad + \mathbf{UMH}^{(k)}(\mathbf{s}_n)\left(\mathbf{R}(n,0)\mathbf{Z}_0 + \sum_{j=0}^{n-1} \mathbf{R}(n,j+1)\mathbf{N}(\mathbf{s}_{j+1})\mathbf{MP}_c(\mathbf{s}_j)\mathbf{s}_j\right), \end{aligned} \tag{8}$$

which is an equation where variables $\mathbf{Z}$ appears just as their initial values $\mathbf{Z}_0$. The next result gives sufficient conditions for the expression

$$\mathbf{UMH}^{(k)}(\mathbf{s}_n)\left(\mathbf{R}(n,0)\mathbf{Z}_0 + \sum_{j=0}^{n-1} \mathbf{R}(n,j+1)\mathbf{N}(\mathbf{s}_{j+1})\mathbf{MP}_c(\mathbf{s}_j)\mathbf{s}_j\right)$$

to have a bound which tends to zero, uniformly for $\mathbf{s}$ in a certain compact set, when k tends to infinity.

Theorem 4. *Let $A \subset \mathbb{R}^p_+$ be a F-shrinkable set. There exist a positive integer k_0 and a compact set $K \subset \mathbb{R}^N$ of the form $\bar{A}_\delta \times K_1$, K_1 compact subset of $\mathbb{R}^{N-p}$, such that, for $k \geqslant k_0$, K is positively invariant for the system (6,7). Moreover, restricted to K, there exist positive constants C_1 and C_2, which are independent of k, such that the following inequalities hold*:

$$\|\mathbf{s}_{n+1} - \mathbf{UMP}_c(\mathbf{s}_n)\mathbf{s}_n\| \leqslant C_1 Q^{(k)},$$

$$\|\mathbf{Z}_{n+1} - \mathbf{N}(\mathbf{s}_{n+1})\mathbf{MP}_c(\mathbf{s}_n)\mathbf{s}_n\| \leqslant C_2 Q^{(k)},$$

where $Q^{(k)} = Sup\{\|\mathbf{Q}^k(\mathbf{s})\| : \mathbf{s} \in \bar{A}_\delta\}$.

Proof. See Appendix A.

If we come back to the initial state variables, $\mathbf{X}$, we can express Theorem 4 as follows in the next corollary.

Corollary 5. *Assuming the hypotheses of Theorem* 4. *There exist a positive integer k_0 and a compact set $\bar{K} \subset \mathbb{R}^N$ such that, for $k \geqslant k_0, \bar{K}$ positively invariant for the initial system* (1), $\mathbf{X}_{n+1} = \mathbf{MP}^k(\mathbf{s}_n)\mathbf{X}_n$. *Moreover, restricted to $\bar{K}$, there exists a positive constant $\bar{C}$, which is independent of k, such that the following inequality holds*:

$$\|\mathbf{X}_{n+1} - \mathbf{MP}(\mathbf{s}_n)\mathbf{X}_n\| \leqslant \bar{C}Q^{(k)}.$$

The last result yields that the initial system (1) can be considered a small perturbation of system

$$\mathbf{X}_{n+1} = \mathbf{MP}(\mathbf{s}_n)\mathbf{X}_n, \tag{9}$$

when restricted to an appropriate positively invariant compact set.

The latter system and the aggregated system (2), $\mathbf{s}_{n+1} = \mathbf{UMP}_c(\mathbf{s}_n)\mathbf{s}_n$, give an example of the so called perfect aggregation, see Ref. [9]. This means that the following diagram is commutative,

$$\begin{tikzcd} \mathbb{R}^N_+ \arrow[r, "\mathbf{M\bar{P}}(\mathbf{U}\cdot)"] \arrow[d, "\mathbf{U}"'] & \mathbb{R}^N_+ \arrow[d, "\mathbf{U}"] \\ \mathbb{R}^p_+ \arrow[r, "\mathbf{UM\bar{P}}_c(\cdot)"'] & \mathbb{R}^p_+ \end{tikzcd}$$

that is $\mathbf{U}[\mathbf{MP}(\mathbf{UX})\mathbf{X}] = \mathbf{UMP}_c(\mathbf{UX})\mathbf{UX}$. It is easy to derive the relationship between the solutions of both systems. If $\{\mathbf{X}_n\}_{n\in\mathbf{N}}$ is a solution of the system $\mathbf{X}_{n+1} = \mathbf{MP}(\mathbf{s}_n)\mathbf{X}_n$ then $\{\mathbf{s}_n\}_{n\in\mathbf{N}} = \{\mathbf{UX}_n\}_{n\in\mathbf{N}}$ is a solution of the system $\mathbf{s}_{n+1} = \mathbf{UMP}_c(\mathbf{s}_n)\mathbf{s}_n$. And if $\{\mathbf{s}_n\}_{n\in\mathbf{N}}$ is a solution of the system $\mathbf{s}_{n+1} = \mathbf{UMP}_c(\mathbf{s}_n)\mathbf{s}_n$ then $\{\mathbf{X}_n\}_{n\in\mathbf{N}} = \{\mathbf{MP}_c(\mathbf{s}_n)\mathbf{s}_n\}_{n\in\mathbf{N}}$ is a solution of the system $\mathbf{X}_{n+1} = \mathbf{MP}(\mathbf{s}_n)\mathbf{X}_n$. In particular, if $\mathbf{s}^*$ is a fixed (periodic) point of the aggregated system we have that $\mathbf{MP}_c(\mathbf{s}^*)\mathbf{s}^*$ is a fixed (periodic) point of system (9).

The established relationship among the systems (1), (2), (9) and the usual implicit function theorem argument give us an easy to apply consequence of the main result.

Corollary 6. *Let $\mathbf{s}^*$ be a fixed point of the aggregated system* (2), $\mathbf{s}_{n+1} = \mathbf{UMP}_c(\mathbf{s}_n)\mathbf{s}_n$, *and suppose that the eigenvalues of the associated linearized map have modulus less than one. Then, for k sufficiently large, there exist $\mathbf{X}^*$ fixed point of the initial system* (1), $\mathbf{X}_{n+1} = \mathbf{MP}^k(\mathbf{s}_n)\mathbf{X}_n$, *for which the eigenvalues of the associated linearized map have also modulus less than one. Moreover, there exists* *a positive constant* $\bar{C}$, *which is independent of k, such that the following inequality holds*:

$$\|\mathbf{X}^* - \mathbf{M}\mathbf{P}_c(\mathbf{s}^*)\mathbf{s}^*\| \leqslant \bar{C}Q^{(k)}.$$

4. Multiregional demography with two time scales

In this section we apply the above general aggregation method to the case of an age-structured population located in a multipatch environment. These kinds of models have been frequently treated in the literature, see Refs. [10,11]. In contrast with those 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 suppose migration to be density dependent.

We consider a population divided into p age-classes and living in an environment composed of m patches. We denote

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

$i = 1, \ldots, p$ and $j = 1, \ldots, m$. And using the notation of Section 2,

$$\mathbf{X}_n = \left(\mathbf{x}_n^1, \ldots, \mathbf{x}_n^p\right)^\top, \quad \text{where } \mathbf{x}_n^i = \left(x_n^{i1}, \ldots, x_n^{im}\right)^\top,$$

$$s_n^i = \sum_{j=1}^{m} x_n^{ij}, \quad i = 1, \ldots, p, \quad \text{and} \quad \mathbf{s_n} = \left(s_n^1, \ldots, s_n^p\right)^\top.$$

We suppose that the migration rates between different patches of individuals belonging to the same age class i are dependent on $\mathbf{s}$, the vector of number of individuals in every age class. Those migration rates form a regular $m \times m$ stochastic matrix $\mathbf{P}_i(\mathbf{s})$, for every value of $\mathbf{s}$. So, the matrix $\mathbf{P}(\mathbf{s}) = \mathrm{diag}\{\mathbf{P}_1(\mathbf{s}), \ldots, \mathbf{P}_p(\mathbf{s})\}$ represents the complete migration process.

The demography is considered density independent and, therefore, it is defined by means of two kinds of constant transition coefficients as in the classical Leslie model:

F_i^j = fertility rate of age class i in patch j, $i = 1, \ldots, p$ and $j = 1, \ldots, m$.

S_i^j = survival rate of age class i in patch j, $i = 1, \ldots, p-1$ and $j = 1, \ldots, m$.

The coefficients satisfy the usual constraints of Leslie models.

We define the matrices $\mathbf{F}_i = \mathrm{diag}\{F_i^1, \ldots, F_i^m\}$, $i = 1, \ldots, p$ and $\mathbf{S}_i = \mathrm{diag}\{S_i^1, \ldots, S_i^m\}$, $i = 1, \ldots, p-1$. And finally we get a generalized Leslie matrix

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

Finally, we propose the following multipatch density dependent Leslie model

$$\mathbf{X}_{n+1} = \mathbf{L}\mathbf{P}^k(\mathbf{s}_n)\mathbf{X}_n, \tag{10}$$

which has the form of the general system (1).

The corresponding aggregated system is

$$\mathbf{s}_{n+1} = \mathbf{U}\mathbf{L}\mathbf{P}_c(\mathbf{s}_n)\mathbf{s}_n, \tag{11}$$

where $\mathbf{ULP}_c(\mathbf{s}_n)$ is a general density dependent Leslie matrix of order p, that we denote $\mathbf{L}(\mathbf{s})$.We have

$$\mathbf{L}(\mathbf{s}) = \begin{pmatrix} \varphi_1(\mathbf{s}) & \varphi_2(\mathbf{s}) & \dots & \varphi_{p-1}(\mathbf{s}) & \varphi_p(\mathbf{s}) \\ \sigma_1(\mathbf{s}) & \mathbf{0} & \dots & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \sigma_2(\mathbf{s}) & \dots & \mathbf{0} & \mathbf{0} \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ \mathbf{0} & \mathbf{0} & \dots & \sigma_{p-1}(\mathbf{s}) & \mathbf{0} \end{pmatrix},$$

where

$$\varphi_i(\mathbf{s}) = \mathbf{1}\mathbf{F}_i\boldsymbol{v}^i(\mathbf{s}), \quad i = 1, \dots, p,$$

and

$$\sigma_i(\mathbf{s}) = \mathbf{1}\mathbf{S}_i\boldsymbol{v}^i(\mathbf{s}), \quad i = 1, \dots, p.$$

The aggregated system (11), finally written

$$\mathbf{s}_{n+1} = \mathbf{L}(\mathbf{s}_n)\mathbf{s}_n \tag{12}$$

is a typical non-linear matrix equation, which can exhibit a very complex behaviour even in two dimensions, see Ref. [12]. Recently, Cushing [13–16] has presented a general theory for the asymptotic dynamics of non-linear matrix equations as they apply to the dynamics of structured populations; existence and stability of equilibrium class distribution vectors are studied by means of bifurcation theory techniques using a single composite, biologically meaningful quantity as a bifurcation parameter, namely the inherent net reproductive rate.

4.1. Particular case: two ages and two patches

To illustrate the usefulness of the aggregated system to study the general system we develop a less general example where Corollary 6 applies.

We suppose a population divided in 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 migration rate in the adult class depending on the global density of adult individuals.

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

$$\mathbf{F}_i = \begin{pmatrix} F_i^1 & 0 \\ 0 & F_i^2 \end{pmatrix}, \quad i = 1, 2, \quad \text{and} \quad \mathbf{S} = \begin{pmatrix} S^1 & 0 \\ 0 & S^2 \end{pmatrix}.$$

The migration process is represented by matrix

$$\mathbf{P} = \mathrm{diag}\{\mathbf{P}_1, \mathbf{P}_2\} = \begin{pmatrix} 1-p_1 & p_2 & 0 & 0 \\ p_1 & 1-p_2 & 0 & 0 \\ 0 & 0 & \frac{a}{s^2+a} & \frac{1}{2} \\ 0 & 0 & \frac{s^2}{s^2+a} & \frac{1}{2} \end{pmatrix},$$

where we have tried to represent the existence of a good patch, the first one, and a bad patch, the second one; at low adult density individuals in patch 1 mostly stay there, while at high adult density individuals mostly migrate to patch 2.

The system (10) in this particular case reads as follows

$$\begin{pmatrix} x_{n+1}^{11} \\ x_{n+1}^{12} \\ x_{n+1}^{21} \\ x_{n+1}^{22} \end{pmatrix} = \begin{pmatrix} F_1^1 & 0 & F_2^1 & 0 \\ 0 & F_1^2 & 0 & F_2^2 \\ S^1 & 0 & 0 & 0 \\ 0 & S^2 & 0 & 0 \end{pmatrix} \begin{pmatrix} 1-p_1 & p_2 & 0 & 0 \\ p_1 & 1-p_2 & 0 & 0 \\ 0 & 0 & \frac{a}{s_n^2+a} & \frac{1}{2} \\ 0 & 0 & \frac{s_n^2}{s_n^2+a} & \frac{1}{2} \end{pmatrix}^k \begin{pmatrix} x_n^{11} \\ x_n^{12} \\ x_n^{21} \\ x_n^{22} \end{pmatrix}. \tag{13}$$

The equilibrium frequencies of fast dynamics are included in matrix $\mathbf{P}_c(s^2)$,

$$\mathbf{P}_c(s^2) = \mathrm{diag}\{\boldsymbol{v}^1, \boldsymbol{v}^2(s^2)\} = \begin{pmatrix} \frac{p_2}{p_1+p_2} & 0 \\ \frac{p_1}{p_1+p_2} & 0 \\ 0 & \frac{s^2+a}{3s^2+a} \\ 0 & \frac{2s^2}{3s^2+a} \end{pmatrix},$$

The aggregated system (12) is then constructed as follows:

$$\begin{pmatrix} s_{n+1}^1 \\ s_{n+1}^2 \end{pmatrix} = \begin{pmatrix} 1 & 1 & 0 & 0 \\ 0 & 0 & 1 & 1 \end{pmatrix} \begin{pmatrix} F_1^1 & 0 & F_2^1 & 0 \\ 0 & F_1^2 & 0 & F_2^2 \\ S^1 & 0 & 0 & 0 \\ 0 & S^2 & 0 & 0 \end{pmatrix} \begin{pmatrix} \frac{p_2}{p_1+p_2} & 0 \\ \frac{p_1}{p_1+p_2} & 0 \\ 0 & \frac{s_n^2+a}{3s_n^2+a} \\ 0 & \frac{2s_n^2}{3s_n^2+a} \end{pmatrix} \begin{pmatrix} s_n^1 \\ s_n^2 \end{pmatrix}$$

and so, we have

$$\begin{pmatrix} s^1_{n+1} \\ s^2_{n+1} \end{pmatrix} = \begin{pmatrix} \varphi & \frac{aF^1_2+(F^1_2+2F^2_2)s^2_n}{a+3s^2_n} \\ \sigma & 0 \end{pmatrix} \begin{pmatrix} s^1_n \\ s^2_n \end{pmatrix}, \tag{14}$$

where

$$\varphi = \frac{F^1_1 p_2 + F^2_1 p_1}{p_1 + p_2} \quad \text{and} \quad \sigma = \frac{S^1 p_2 + S^2 p_1}{p_1 + p_2}.$$

We now try to find under which conditions system (13) has an asymptotically stable equilibrium. We start studying the same problem for the aggregated system (14) and then we will apply Corollary 6.

We assume that $F^1_2 > F^2_2$, that is, the adult fertility rate is larger in the good patch than in the bad patch.

The system (14) has an equilibrium $\mathbf{s}^* = (s^{1*}, s^{2*})^\top$ if s^{2*} satisfies the equation

$$\det \begin{pmatrix} \varphi - 1 & \frac{aF^1_2+(F^1_2+2F^2_2)s^2}{a+3s^2} \\ \sigma & -1 \end{pmatrix} = 0, \tag{15}$$

that is

$$1 - \varphi - \sigma\left(\frac{aF^1_2 + (F^1_2 + 2F^2_2)s^2}{a + 3s^2}\right) = 0.$$

That happens, for $s^{2*} > 0$, if and only if

$$\frac{1}{3}F^1_2 + \frac{2}{3}F^2_2 < \frac{1-\varphi}{\sigma} < F^1_2. \tag{16}$$

In particular, last conditions implies that $(1-\varphi)/\sigma > 0$ or $\varphi < 1$, which is a natural assumption because otherwise if the young fertility rate is larger than one the evolution of the population always exhibits exponential growth.

To simplify the writing of some coming expressions we denote $b = (1 - \varphi)/\sigma$.

Assuming conditions (16) the only value s^{2*} satisfying Eq. (15) is

$$s^{2*} = \frac{a(b - F^1_2)}{F^1_2 + 2F^2_2 - 3b}$$

and the corresponding s^{1*} is s^{2*}/σ.

We are proving that $\mathbf{s}^*$ verifies the hypotheses of Corollary 6. For that, if we call $\mathbf{G}$ the map associated to system (14), $\mathbf{G}(\mathbf{s}) = \mathbf{L}(s^2)\mathbf{s}$, we need to prove that the eigenvalues of its jacobian matrix at $\mathbf{s}^*$ have modulus less than one.

Some straightforward calculations yield

$$J\mathbf{G}(\mathbf{s}^*) = \begin{pmatrix} \varphi & \frac{ba+(F^1_2+2F^2_2)s^{2*}}{a+3s^{2*}} \\ \sigma & 0 \end{pmatrix}.$$

An equivalent condition to that of the eigenvalues being inside the unit disk is

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

which means in our particular case

$$\varphi < 1 - \sigma \frac{ba + (F_2^1 + 2F_2^2)s^{2*}}{a + 3s^{2*}} < 2.$$

The rightmost inequality obviously holds and the first one is equivalent to

$$\frac{1}{3}F_2^1 + \frac{2}{3}F_2^2 < b,$$

which is already included in conditions (16).

Summarizing the conclusions of Corollary 6:

If

$$\frac{1}{3}F_2^1 + \frac{2}{3}F_2^2 < \frac{1 - \frac{F_1^1 p_2 + F_1^2 p_1}{p_1 + p_2}}{\frac{S^1 p_2 + S^2 p_1}{p_1 + p_2}} < F_2^1$$

and k is sufficiently large then the system (13) possesses an asymptotically stable fixed point $\mathbf{X}^* = (x^{11*}, x^{12*}, x^{21*}, x^{22*})^\top$ which can be written as

$$\begin{pmatrix} F_1^1 & 0 & F_2^1 & 0 \\ 0 & F_1^2 & 0 & F_2^2 \\ S^1 & 0 & 0 & 0 \\ 0 & S^2 & 0 & 0 \end{pmatrix} \begin{pmatrix} \frac{p_2}{p_1+p_2} & 0 \\ \frac{p_1}{p_1+p_2} & 0 \\ 0 & \frac{s^{2*}+a}{3s^{2*}+a} \\ 0 & \frac{2s^{2*}}{3s^{2*}+a} \end{pmatrix} \begin{pmatrix} s^{1*} \\ s^{2*} \end{pmatrix}$$

$$= \begin{pmatrix} F_1^1 \frac{p_2}{p_1+p_2} s^{1*} + F_2^1 \frac{s^{2*}+a}{3s^{2*}+a} s^{2*} \\ F_1^2 \frac{p_1}{p_1+p_2} s^{1*} + F_2^2 \frac{2s^{2*}}{3s^{2*}+a} s^{2*} \\ S^1 \frac{p_2}{p_1+p_2} s^{1*} \\ S^2 \frac{p_1}{p_1+p_2} s^{1*} \end{pmatrix}$$

plus another term which tends to zero as k tends to infinity.

5. Conclusion

In the present work we have introduced a model of an age structured population in a multipatch environment where we have distinguished between two different time scales. We have reduced the initial complex model to a non-linear matrix equation, whose coefficients reflect the asymptotic information of the fast dynamics (the migration process). This is an example of how a simpler model admits an explanation given by a more complex model. The study of the simpler model, the aggregated model, give us information of the initial model via the general results of Section 3.

Very different applications can be undertaken by writing different situations in the general form of system (1) and applying Theorem 4 to the required particular case. For instance, it is possible to study 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.

In the future, we intend to extend our methods to more general fast and slow dynamics, as well as to aggregated systems whose global variables are obtained more generally than by adding up state variables. 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].

Acknowledgements

This work has been partly supported by the grants *Acción Integrada HF1996-0211* and *PICASSO 96/001*, and exchange program between France and Spain, and *Proyecto DGCYT PB95-0233-A*.

Appendix A

Proof of Lemma 1. We only provide a proof of (a) and (b). Straightforward calculations yield the rest of statements.

(a) We multiply the matrices using the following decomposition:

$$\mathbf{P}_i(\mathbf{s}) = \begin{pmatrix} p_{11}(\mathbf{s}) & \mathbf{p}_{12}^{\top}(\mathbf{s}) \\ \mathbf{p}_{21}(\mathbf{s}) & \mathbf{P}_{22}(\mathbf{s}) \end{pmatrix},$$

where $p_{11}(\mathbf{s}) \in \mathbb{R},\ \mathbf{p}_{12}(\mathbf{s}),\ \mathbf{p}_{21}(\mathbf{s}) \in \mathbb{R}^{N^i-1},\ \mathbf{P}_{22}(\mathbf{s}) \in \mathbb{R}^{(N^i-1)\times(N^i-1)}$,

$$\mathbf{T}_i(\mathbf{s}) = \begin{pmatrix} v^{i1}(\mathbf{s}) & -\mathbf{1}_{N^i-1} \\ \mathbf{B}_i \boldsymbol{v}^i(\mathbf{s}) & \mathbf{I}_{N^i-1} \end{pmatrix} \quad \text{and}$$

$$\mathbf{T}_i^{-1}(\mathbf{s}) = \begin{pmatrix} 1 & \mathbf{1}_{N^i-1} \\ -\mathbf{B}_i \boldsymbol{v}^i(\mathbf{s}) & \mathbf{I}_{N^i-1} - \mathbf{B}_i \boldsymbol{v}^i(\mathbf{s}) \mathbf{1}_{N^i-1} \end{pmatrix}$$

Then,

$$\mathbf{T}_i^{-1}(\mathbf{s}) \mathbf{P}_i(\mathbf{s}) = \begin{pmatrix} 1 & \mathbf{1}_{N^i-1} \\ -\mathbf{B}_i \boldsymbol{v}^i(\mathbf{s}) + \mathbf{p}_{21}(\mathbf{s}) & -\mathbf{B}_i \boldsymbol{v}^i(\mathbf{s}) \mathbf{1}_{i-1} + \mathbf{P}_{22}(\mathbf{s}) \end{pmatrix},$$

$$\mathbf{T}_i^{-1}(\mathbf{s}) \mathbf{P}_i(\mathbf{s}) \mathbf{T}_i(\mathbf{s}) = \begin{pmatrix} 1 & \mathbf{0} \\ \mathbf{0} & \mathbf{P}_{22}(\mathbf{s}) - \mathbf{p}_{21}(\mathbf{s}) \mathbf{1}_{N^i-1} \end{pmatrix} = \begin{pmatrix} 1 & \mathbf{0} \\ \mathbf{0} & \mathbf{Q}_i(\mathbf{s}) \end{pmatrix},$$

where we have used the notation

$$\mathbf{Q}_i(\mathbf{s}) = \mathbf{P}_{22}(\mathbf{s}) - \mathbf{p}_{21}(\mathbf{s})\mathbf{1}_{N^i-1}.$$

(b) Using (a) we have

$$\begin{aligned}\det(\mathbf{P}_i(\mathbf{s}) - \lambda I) &= \det(\mathbf{T}_i^{-1}(\mathbf{s})\mathbf{P}_i(\mathbf{s})\mathbf{T}_i(\mathbf{s}) - \lambda I)\\ &= (1-\lambda)\det(\mathbf{Q}_i(\mathbf{s}) - \lambda I). \qquad \Box\end{aligned}$$

Proof of Lemma 2. We are proving that, for each $\varepsilon > 0$, there if a $k_0 \in \mathbf{N}$ such that is $k \geqslant k_0$, then

$$\text{for every } \mathbf{s} \in K, \quad \|\mathbf{Q}^k(\mathbf{s})\| < \varepsilon.$$

Since $\rho(\mathbf{Q}(\mathbf{s})) < 1$, given an $\varepsilon > 0$, for each $\mathbf{s} \in K$ there exists a natural number $k_0(\mathbf{s})$ such that, for $k \geqslant k_0(\mathbf{s})$,

$$\|\mathbf{Q}^k(\mathbf{s})\| < \frac{\varepsilon}{2}.$$

From Hypothesis $(\mathbf{H1})(a)$, we deduce that $\mathbf{Q}$ is a continuous function of $\mathbf{s}$ so that there exists an open neighborhood of $\mathbf{s}$, $W(\mathbf{s})$, such that

$$\text{for every } \mathbf{t} \in W(\mathbf{s}), \quad \|\mathbf{Q}^k(\mathbf{t})\| < \varepsilon.$$

The family $\{W(\mathbf{s}) : \mathbf{s} \in K\}$ is an open covering of the compact set K. Then there exists a finite subfamily such that

$$K \subset W(\mathbf{s}_1) \cup \cdots \cup W(\mathbf{s}_r).$$

If we choose $k_0 = \max\{k_0(\mathbf{s}_1), \ldots, k_0(\mathbf{s}_r)\}$, we have, for $k \geqslant k_0$:

$$\text{for every } \mathbf{s} \in K, \quad \|\mathbf{Q}^k(\mathbf{s})\| < \varepsilon$$

and the Lemma follows. $\Box$

Proof of Theorem 4. We have $\delta > 0$ such that $\bar{A}_\delta = \{\mathbf{s} \in \mathbb{R}^p_+ : \mathrm{d}(\mathbf{s}, A) \leqslant \delta\}$ verifies that $\mathbf{F}(\bar{A}_\delta) \subset A$, and we begin by establishing the following assertion (A1): There exists $k_0 \in \mathbb{N}$ such that for $k \geqslant k_0$ and $\mathbf{s}_0 \in \bar{A}_\delta$ it is implied that $\mathbf{s}_n \in \bar{A}_\delta$ for every $n = 1, 2, \ldots$

Reasoning by induction, let us suppose that $\mathbf{s}_0, \mathbf{s}_1, \ldots, \mathbf{s}_n \in \bar{A}_\delta$ and prove that $\mathbf{s}_{n+1} \in \bar{A}_\delta$, that is, $\|\mathbf{s}_{n+1} - \mathbf{F}(\mathbf{s}_n)\| \leqslant \delta$.

With the purpose of finding a bound for $\|\mathbf{R}(m, n)\|$ we define the following constants:

$$a = \sup_{\mathbf{s}\in\bar{A}_\delta}\|\mathbf{s}\|, \quad b = \sup_{\mathbf{s}\in\bar{A}_\delta}\|\mathbf{N}(\mathbf{s})\|, \quad c = \sup_{\mathbf{s}\in\bar{A}_\delta}\|\mathbf{P}_c(\mathbf{s})\|.$$

The existence of b and c yields from the special structures of matrices $\mathbf{N}(\mathbf{s})$ and $\mathbf{P}_c(\mathbf{s})$ whose columns are vectors of 1-norm smaller than 2 and equal to 1 respectively.

Lemma 2 and the structure of matrix $\mathbf{H}^{(k)}(\mathbf{s})$ allow us to find a number $k_1 \in \mathbb{N}$ such that

$$\|\mathbf{H}^{(k)}(\mathbf{s})\| < \frac{1}{2b\|\mathbf{M}\|} \text{ for every } k \geqslant k_1 \text{ and } \mathbf{s} \in \bar{A}_\delta. \tag{17}$$

Now it is straightforward to find a bound for $\|\mathbf{R}(m,n)\|$,

$$\|\mathbf{R}(m,n)\| \leqslant \prod_{j=n}^{m-1} \|\mathbf{N}(\mathbf{s}_{j+1})\| \, \|\mathbf{M}\| \, \|\mathbf{H}^{(k)}(\mathbf{s}_j)\| \leqslant \prod_{j=n}^{m-1} b\|\mathbf{M}\| \frac{1}{2b\|\mathbf{M}\|} = 2^{n-m}. \tag{18}$$

Using Eq. (8) and bound (18) we can deduce

$$\begin{aligned}\|\mathbf{s}_{n+1} - \mathbf{F}(\mathbf{s}_n)\| &\leqslant \|\mathbf{U}\|\|\mathbf{M}\|\|\mathbf{H}^{(k)}(\mathbf{s}_n)\| \\ &\quad \times \left(\|\mathbf{R}(n,0)\|\|\mathbf{Z}_0\| + \sum_{j=0}^{n-1} \|\mathbf{R}(n,j+1)\| \, \|\mathbf{N}(\mathbf{s}_{j+1})\|\|\mathbf{M}\|\|\mathbf{P}_c(\mathbf{s}_j)\|\|\mathbf{s}_j\| \right) \\ &\leqslant \|\mathbf{U}\|\|\mathbf{M}\|\|\mathbf{H}^{(k)}(\mathbf{s}_n)\|(2^{-n}\|\mathbf{Z}_0\| + \sum_{j=0}^{n-1} 2^{j+1-n} b\|\mathbf{M}\|ca) \\ &\leqslant \|\mathbf{U}\|\|\mathbf{M}\|(2^{-n}\|\mathbf{Z}_0\| + 2abc\|\mathbf{M}\|)\|\mathbf{H}^{(k)}(\mathbf{s}_n)\|.\end{aligned}$$

Before finding k_0 let us define $K_1 = \{\mathbf{Z} \in \mathbb{R}^{N-p}: \|\mathbf{Z}\| \leqslant d\}$, where d can be chosen to be any number verifying $d \geqslant 2abc\|\mathbf{M}\|$.

Supposing, without any loss of generality, that $\mathbf{Z}_0 \in K_1$ we yield from Lemma 2 the existence of $k_0 \geqslant k_1$ such that inequality

$$\|\mathbf{H}^{(k)}(\mathbf{s})\| \leqslant \frac{\delta}{\|\mathbf{U}\| \, \|\mathbf{M}\|(d + 2abc\|\mathbf{M}\|)}$$

holds for every $k \geqslant k_0$ and $s \in \bar{A}_\delta$, and so assertion (A1) is an immediate consequence.

To prove the positive invariance of the compact set $\bar{A}_\delta \times K_1$ we only need to prove, using Eq. (7), that if $\mathbf{s}_n \in \bar{A}_\delta$ and $\mathbf{Z}_n \in K_1$ then

$$\mathbf{N}(\mathbf{s}_{n+1})\mathbf{M}\mathbf{P}_c(\mathbf{s}_n)\mathbf{s}_n + \mathbf{N}(\mathbf{s}_{n+1})\mathbf{M}\mathbf{H}^{(k)}(\mathbf{s}_n)\mathbf{Z}_n \in K_1 \quad \text{for } k \geqslant k_0$$

and that is straightforward using bound (17) and the fact that $d \geqslant 2abc\|\mathbf{M}\|$,

$$\begin{aligned}\mathbf{N}(\mathbf{s}_{n+1})\mathbf{M}\mathbf{P}_c(\mathbf{s}_n)\mathbf{s}_n + \mathbf{N}(\mathbf{s}_{n+1})\mathbf{M}\mathbf{H}^{(k)}(\mathbf{s}_n)\mathbf{Z}_n\| &\leqslant b\|\mathbf{M}\|ca + b\|\mathbf{M}\| \frac{1}{2b\|\mathbf{M}\|} d \\ &\leqslant \frac{d}{2} + \frac{d}{2} = d.\end{aligned}$$

To finish the proof we have just to deduce the two stated inequalities. The structure of matrix $\mathbf{H}^{(k)}(\mathbf{s})$ allow us to find a constant h, independent of k, such that

$$\|\mathbf{H}^{(k)}(\mathbf{s})\| \leqslant h\|\mathbf{Q}^k(\mathbf{s})\|.$$

And now from systems (6) and (7) we have

$$\|\mathbf{s}_{n+1} - \mathbf{UMP}_c(\mathbf{s}_n)\mathbf{s}_n\| = \|\mathbf{UMH}^{(k)}(\mathbf{s}_n)\mathbf{Z}_n\| \leqslant \|\mathbf{U}\|\,\|\mathbf{M}\|\,\|\mathbf{H}^{(k)}(\mathbf{s})\|d$$
$$\leqslant \|\mathbf{U}\|\,\|\mathbf{M}\|h\|\mathbf{Q}^k(\mathbf{s})\|d \leqslant (dh\|\mathbf{U}\|\,\|\mathbf{M}\|)Q^{(k)}$$

and analogously

$$\|\mathbf{Z}_{n+1} - \mathbf{N}(\mathbf{s}_{n+1})\mathbf{MP}_c(\mathbf{s}_n)\mathbf{s}_n\| \leqslant (bdh\|\mathbf{M}\|)Q^{(k)}. \qquad \square$$

References

[1] P. Auger, Dynamics and Thermodynamics in Hierarchically Organized Systems. Applications in Physics, Biology and Economics, Pergamon, Oxford, 1989.
[2] P. Auger, J.C. Poggiale, Emergence of population growth models: Fast migrations and slow growth, J. Theoretical Biol. 182 (1996) 99.
[3] P. Auger, R. Roussarie, Complex ecological models with simple dynamics: From individuals to populations, Acta Biotheoretica 42 (1994) 111.
[4] P. Auger, E. Sánchez, R. Bravo de la Parra, Influence of individual aggressiveness on the dynamics of competitive populations, Acta Biotheoretica 45 (1997) 321.
[5] R. Bravo de la Parra, E. Sánchez, P. Auger, Aggregation methods in discrete models, J. Biol. Systems 3 (1995) 603.
[6] E. Sánchez, R. Bravo de la Parra, P. Auger, Linear discrete models with different time scales, Acta Biotheoretica 43 (1995) 465.
[7] R. Bravo de la Parra, E. Sánchez, Aggregation methods in population dynamics discrete models, Math. Comput. Model. 27 (4) (1998) 23.
[8] R. Bravo de la Parra, E. Sánchez, P. Auger, Time scales in density dependent discrete models, J. Biol. Systems 5 (1997) 111.
[9] Y. Iwasa, V. Andreasen, S.A. Levin, Aggregation in Model Ecosystems. (I) Perfect Aggregation, Ecol. Model. 37 (1987) 287.
[10] H. Caswell, Matrix Population Models, Sinauer Associates, Sunderland, 1989.
[11] D.O. Logofet, Matrices and Graphs. Stability Problems in Mathematical Ecology, CRC, Boca Ratón, FL, 1993.
[12] J. Guckenheimer, G.F. Oster, A. Ipaktchi, The dynamics of density dependent population models, J. Math. Biol. 4 (1976) 101.
[13] J.M. Cushing, Non-linear matrix models and population dynamics, Natural Resource Modeling 2 (1988) 539.
[14] J.M. Cushing, Non-linear matrix models for structured populations, in: O. Arino, D. Axelrod, M. Kimmel, M. Langlais (Eds.), Mathematical Population Dynamics III: Mathematical Methods and Modelling of Data, ch. 26, Wuerz, Winnipeg, 1995.
[15] J.M. Cushing, Non-linear matrix equations and population dynamics, in: S. Tuljapurkar, H. Caswell (Eds.), Structured-Population Models in Marine, Terrestrial, and Freshwater Systems, ch. 6, Chapman and Hall, New York, 1997.
[16] J.M. Cushing, Y. Zhou, The net reproductive number and stability in linear structured population models, Natural Resource Modeling 8 (1995) 297.
[17] M.P. Hassell, H.N. Comins, R.M. May, Spatial structure and chaos in insect population dynamics, Nature 353 (1991) 255.