



LINEAR DISCRETE POPULATION MODELS WITH TWO TIME SCALES IN FAST CHANGING ENVIRONMENTS I: AUTONOMOUS CASE

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ABSTRACT

In this work we consider a structured population with groups and subgroups of individuals. The intra-group dynamics is assumed to be fast in comparison with the inter-group dynamics. We study linear discrete models where the slow dynamics is represented by a single matrix and the fast dynamics is described by means of the first k terms of a converging sequence of different matrices. The number k can be interpreted as the ratio between the two time scales.

The aim of this work is to extend aggregation techniques to the case of fast changing environments. The main idea of aggregation is to build up a new system, with lower dimension, that summarizes the information concerning the fast process. This “aggregated” system provides essential information on the original one. It is shown that the asymptotic behavior of the original system can be approximated by the asymptotic behavior of the aggregated system when the ratio between the two time scales is large enough.

We present an example of an age structured population in a patchy environment. The migration process is assumed to be fast in comparison with the demographic process. Numerical simulations illustrate that the asymptotic growth rate and the stable age distribution of the population in the original and the aggregated systems are getting closer as the ratio k increases.

1. INTRODUCTION

Mathematical models employed in ecology usually involve a large number of variables. For instance, in structured population models we may classify individuals regarding their age, size, activity or location (Caswell, 2001), resulting in high dimensional models which are likely to be difficult to study analytically. The only available technique for the study of these systems is computer simulation, which makes it impossible to evaluate the robustness of the results. Most of the simple models, which are mathematically tractable, do not take into account essential information about the internal structure of the population. Frequently, the simplifying assumptions, upon which the system is based, are not adequately justified.

The so-called aggregation methods describe general complex systems that can be studied approximately from simpler ones. The words complex and simple refer to

large and small number of variables, respectively. The property of these systems that allows their aggregation is the existence of two or more different time scales.

Nature offers many examples of systems where several events occur at different time scales. It is then a common practice to consider those events occurring at the fastest scale as being instantaneous with respect to the slower ones. Under some natural assumptions we will be able to describe the evolution of the population through a reduced number of variables. A subsequent issue is to determine how far the results obtained from the reduced system are from the real ones. Let us think of a hierarchically structured system divided into subsystems that are slowly coupled but exhibiting a fast internal dynamics. The idea of aggregation is to choose a global variable, sometimes also called macrovariable, for each subsystem and to build up a reduced system for these global variables. The reduced system, or aggregated system, must reflect 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 influences between the different hierarchical levels.

Aggregation methods were initially applied on very different fields such as automatic control or economy (Simon and Ando, 1961) and, later, ecology (Iwasa *et al.*, 1987). If the consistency between the dynamics of the variables in the original and the aggregated system is only approximate we refer to it as approximate aggregation (Iwasa *et al.*, 1989).

Applications of approximate aggregation to ecology have been widely studied for both linear and density dependent models in the context of continuous time systems (Auger and Roussarie, 1994; Poggiale and Auger, 1995; Auger and Poggiale, 1996a, 1996b; Auger and Bravo de la Parra, 2000) and discrete systems (Sánchez *et al.*, 1995; Bravo de la Parra and Sánchez, 1998; Sanz and Bravo de la Parra, 1998, 1999, 2000, 2001; Bravo de la Parra *et al.*, 1999).

In this work we develop aggregation methods for time dependent discrete systems continuing the work initiated by Sanz and Bravo de la Parra (1998, 2001). The study of non autonomous linear discrete systems arises in population dynamics when the time dependence of demographic or migration parameters is considered; factors of the external environment which affect survival, fecundity or dispersal may vary over time (Charlesworth, 1994; Caswell, 2001).

The time dependent discrete systems treated by Sanz and Bravo de la Parra (1998, 2001) include two processes taking place at different time scales and the environmental variation of the model parameters acts at the slow time scale, i.e. it was considered that during a slow time unit the parameters defining the fast process do not change. The aim of this work is to extend this framework in order to incorporate environmental variation of the fast process at its own time scale.

The idea of introducing two time scales in a discrete model is to establish the system time unit as the one associated with the slow process. So, in each time unit, the slow process acts once while the fast process acts a certain number of times. It roughly represents the ratio between the two time scales. Our model allows the fast process to vary each time it acts along a slow time unit. The paper is divided into two parts: the

first one is devoted to the analysis of the autonomous case and the second, to be published in a next issue of this journal, will deal with some non-autonomous cases.

In Section 2 we introduce the original model. It is a general time dependent discrete system including two processes that take place at different time scales. The slow dynamics is described by means of a general non-negative matrix. For the fast dynamics, it is necessary to make certain assumptions in order to carry out the reduction of the system. The details of the procedure are outlined in Section 3; the aggregated model is a reduced time dependent discrete system evolving at a slow time scale. In Section 5 we study the relationships between the aggregated and the original systems in the autonomous case, i.e., when the vital rates of the model are constant in time. Section 5 is devoted to the illustration of the method by an example with two age classes and two patches.

2. THE ORIGINAL MODEL

We deal with a linear discrete autonomous stage-structured model. Population is classified into stages or groups in terms of any characteristic of the life cycle. Moreover, each of these groups is divided into several subgroups that can correspond to different spatial patches, different individual activities, etc.

We consider q groups. Let N_i be the number of subgroups within group i . We define the state variables x_t^{ij} as the number of individuals in the j -th subgroup of the i -th group at time t , $i = 1, \dots, q$; $j = 1, \dots, N_i$; $t = 0, 1, 2, \dots$. Therefore, the population is described by the vector

$$x_t = (x_t^{1,1}, \dots, x_t^{1,N_1}, x_t^{2,1}, \dots, x_t^{2,N_2}, \dots, x_t^{q,1}, \dots, x_t^{q,N_q})^T \in \mathbf{R}^N \tag{1}$$

where $N = N_1 + \dots + N_q$ (the superscript T denotes transposition).

In the evolution of the population we consider two processes whose corresponding characteristic time scales, and consequently their projection intervals, are very different from each other. In order to include both time scales in our model we describe these two processes, which we call fast and slow dynamics, by means of two different matrices.

As the projection interval of our model we choose the one corresponding to the slow dynamics, i.e., the time elapsed between times t and $t + 1$, which we will call I_t (this is the projection interval of the slow process).

We make no special assumptions regarding the characteristics of the slow dynamics. Thus, the slow dynamics is represented by a nonnegative projection matrix $M \in \mathbf{R}^N$ which we consider as divided into blocks M^{ij} , $1 \leq i, j \leq q$. We then have

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

where each block $M^{ij} = [M_{ij}^{ml}]$ has dimensions $N_i \times N_j$ and characterizes the rates of transference of individuals from the subgroups of group j to those of group i . More specifically, for each $m = 1, 2, \dots, N_i$ and each $l = 1, 2, \dots, N_j$, M_{ij}^{ml} represents the rate of transference of individuals, due to the slow process, from subgroup l of group j to

subgroup m of group i in one time step. This is a generic model; in a particular case M could contain mortality and reproduction values for the different stages.

Since the projection interval of the model is that of the slow process, we assume that, during a time unit, the fast process occurs k times before the slow process (where k is an integer that can be interpreted as the ratio between the projection intervals corresponding to the slow and the fast dynamics). Our model allows the fast process to act differently in each of the k occasions. So, for a time unit, the fast process is represented by the following product of k matrices:

$$P_k \cdot P_{k-1} \cdots P_1$$

A) We assume that the fast dynamics is internal for each group.

This assumption means that the fast dynamics does not produce transference of individuals among different groups. Consequently, every matrix P_l ($l = 1, \dots, k$) is a block-diagonal matrix, whose blocks we call P_l^i ($i = 1, \dots, q$):

$$P_l = \text{diag} \{P_l^1, \dots, P_l^q\} \quad (2)$$

B) We assume that the fast dynamics conserves the number of individuals of each group.

This hypothesis is included in the model by assuming each block P_l^i to be a column stochastic matrix, i.e., a matrix whose columns are probability vectors.

Therefore the proposed model will consist of the following discrete system that we will call "microsystem" or "original system":

$$x_{t+1} = MP_k \cdots P_1 x_t \quad (3)$$

In a previous work (Sánchez *et al.*, 1995), aggregation techniques have been applied to the following model:

$$x_{t+1} = MP^k x_t \quad (4)$$

where the matrices corresponding to the fast dynamics are constant. In the next section we construct a reduced system, the so-called aggregated system.

3. AGGREGATION OF THE MODEL

Aggregation consists of defining a small number of global variables, functions of the state variables and building up a system describing their dynamics. When the aggregated dynamics are consistent with the original dynamics in the sense that the global variables behave identically both in the initial system and in the aggregated one, it is called perfect aggregation (Iwasa *et al.*, 1987). Perfect aggregation is rarely possible and methods for approximate aggregation have been developed (Iwasa *et al.*, 1989). By approximate aggregation we mean the kind of aggregation where the consistency between the dynamics of the global variables in the original and the aggregated system is only approximate.

Approximate aggregation of the original system applies when the fast dynamics make the frequencies of state variables in each group approach certain equilibrium values during a time unit. A sufficient condition for the previous property to hold is the next assumption:

C) The sequence $\{P_k^i\}$ tends, when $k \rightarrow \infty$, to a certain (necessarily stochastic) primitive matrix P^i .

Henceforth we suppose the three assumptions on fast dynamics (A, B and C) hold.

To construct the aggregated system we need to make use of the following result.

Proposition 3.1

Let $\{P_k\}$ be a sequence of column stochastic matrices that converges to a primitive matrix P . Let v be the right probability normed eigenvector of P associated with the eigenvalue 1. Then

$$\lim_{k \rightarrow \infty} P_k \cdot \dots \cdot P_1 = v \mathbf{1}^T$$

where $\mathbf{1}$ is the column vector of the appropriate dimension with all its entries equal to 1.

Proof. (See Appendix).

From assumptions A , B and C we can apply Proposition 3.1 to the blocks of the fast dynamics. Hence it follows that, for each $i = 1, \dots, q$:

$$\lim_{k \rightarrow \infty} P_k^i \cdot \dots \cdot P_1^i = v^i \mathbf{1}^T \tag{5}$$

where v^i is the right probability normed eigenvector of the matrix P^i cited in Assumption C .

Now, if we define, $\bar{P}^i = v^i \mathbf{1}^T$, $\bar{P} = \text{diag}(\bar{P}^1, \dots, \bar{P}^q)$, $U = \text{diag}\{\mathbf{1}, \dots, \mathbf{1}\}$ and $V = \text{diag}\{v^1, \dots, v^q\}$ then we have

$$\bar{P} = \lim_{k \rightarrow \infty} P_k \cdot \dots \cdot P_1 = VU^T \tag{6}$$

Hence the original system (3) can be considered as a perturbation of the following:

$$X_{t+1} = M\bar{P}X_t \tag{7}$$

This new system, called the ‘‘auxiliary system’’, can be interpreted as the microsystem when we substitute the fast process corresponding to each interval I_t by the equilibrium frequencies of the fast process in I_t . In other words, we are letting $k \rightarrow \infty$ in the expression of the microsystem, supposing that I_t is long enough with respect to the projection interval of the fast process for the fast dynamics to reach equilibrium frequencies. Note that we use capital letters when referring to variables associated with the auxiliary system.

We will see that the aggregated system can be perfectly aggregated. In order to do so, we define the global variables, for each time t , in the following way:

$$y_t = (y_t^1, \dots, y_t^q) \tag{8}$$

where $y_t^i = X_t^{i,1} + \dots + X_t^{i,N_i}$, i.e. y_t^i represents the total number of individuals in group i at time t assuming that the fast dynamics reaches its equilibrium frequencies in each time unit.

Note that these global variables can be obtained from the variables of the auxiliary system as follows:

$$y_t = U^T X_t \tag{9}$$

Therefore, if we premultiply equation (7) by matrix U^T , we obtain:

$$U^T X_{t+1} = U^T M\bar{P}X_t = U^T M V U^T X_t$$

This is the aggregated system, which can be expressed in the following way:

$$y_{t+1} = \bar{M}y_t \quad (10)$$

where $\bar{M} = U^T M V$. We have reduced the dimension of the model from $N = N_1 + \dots + N_q$ to q , since, in the aggregated system, each group is represented by one single variable.

In next section we will show how this new system provides information on the asymptotic behavior of the population represented by the microsystem.

4. RELATIONSHIPS BETWEEN THE AGGREGATED AND THE ORIGINAL SYSTEMS

This section is devoted to the study of the relationships between the aggregated system (10) and the original system (3) defined in Section 3.

At this stage, let us introduce some concepts and notation that will be useful in further developments: We denote $\|*\|$ as the 1-norm in \mathbf{R}^N , i.e., given $x = (x^1, x^2, \dots, x^N)^T \in \mathbf{R}^N$, then $\|x\| = |x^1| + |x^2| + \dots + |x^N|$. If we are modelling the dynamics of a stage-structured population and x_t is the population vector at time t , then the total population is given by $\|x_t\|$ and the population structure is given by $\frac{x_t}{\|x_t\|}$. A system is said to be strongly ergodic (Cohen, 1979) if the population structure asymptotically becomes fixed and this “equilibrium structure” is independent of the initial population, i.e., a vector v exists such that for any non-negative, non-zero initial condition x_0 we have $\lim_{t \rightarrow \infty} \frac{x_t}{\|x_t\|} = v$.

We make the following assumption on the aggregated matrix:

H1: matrix \bar{M} is primitive.

Let λ be the dominant eigenvalue of matrix \bar{M} , r its corresponding positive right eigenvector such that $\|r\| = 1$ and l its corresponding positive left eigenvector normed in such a way that $l^T r = 1$. Then in the long term for every initial state we have:

- the population size grows exponentially at a rate λ .
- the population reaches a stable structure given by the vector r .
- the reproductive values (Caswell, 2001) associated with each group are given by vector l .

Relationships between the aggregated and the auxiliary systems

Theorem 4.1 (Sánchez *et al.*, 1995) relates the projection matrices of both systems.

Theorem 4.1

Matrices $M\bar{P}$ and \bar{M} verify:

1. $\det(\lambda I_N - M\bar{P}) = \lambda^{N-q} \det(\lambda I_q - \bar{M})$. Therefore the non-zero eigenvalues of matrices $M\bar{P}$ and \bar{M} coincide.

2. Let r be a right eigenvector of \bar{M} associated with the eigenvalue $\lambda \neq 0$. Then $MVr \neq 0$ is a right eigenvector of $M\bar{P}$ associated with the same eigenvalue λ .

3. Let l be a left eigenvector of \bar{M} associated with the eigenvalue $\lambda \neq 0$. Then $Ul \neq 0$ is a left eigenvector of $M\bar{P}$ associated with the same eigenvalue λ .

We also make the following assumption:

H2: matrix M is row-allowable.

A matrix is called row-allowable (Hajnal, 1976) if it has, at least, one positive entry in each row. Note that *H2* can be interpreted by saying that the slow process verifies that for all $i = 1, 2, \dots, q$ and $j = 1, 2, \dots, N_i$, at least one allowed transition towards subgroup j of group i exists.

Under assumptions *H1* and *H2* we obtain the following result:

Proposition 4.2

Let us suppose that the projection matrix of the aggregated system, \bar{M} , is primitive (*H1*). Let λ be its dominant eigenvalue, r its corresponding positive right eigenvector such that $\|r\| = 1$ and l its corresponding positive left eigenvector normed in such a way that $l^T r = 1$. Let us suppose that matrix M , which governs the slow dynamics in the original system, is row-allowable (*H2*). For the auxiliary system we then have:

1. It is strongly ergodic.
2. The population size grows exponentially at a rate λ .
3. For any initial condition X_0 the population structure tends to a limit vector given by $\frac{M^T V r}{\|M^T V r\|}$.
4. The reproductive values associated with each group are given by vector Ul .

Proof. From Theorem 4.1 we have:

- The non-zero eigenvalues of \bar{M} and $M\bar{P}$ coincide. Hence, λ is a simple and strictly dominant eigenvalue of $M\bar{P}$.
- The right and left eigenvectors of $M\bar{P}$ associated with λ are $r' = M^T V r$ and $l' = Ul$, respectively.

Hypothesis *H1* says that M is a row-allowable matrix. Moreover, $V = \text{diag}\{v_1, \dots, v_q\}$ where v_i is a positive vector for all $i = 1, \dots, q$, so it is row-allowable. In Section 3 we defined U which is also row-allowable. Taking into account that the product of a row-allowable matrix and a positive vector is also a positive vector, and that r and l are positive vectors we have $r' = M^T V r$ and $l' = Ul$ are both positive vectors.

Now we make use of a theorem in Berman and Plemmons (1979, pp. 42) to deduce that $M\bar{P}$ is an irreducible matrix. Moreover, since we know that λ is a strictly dominant eigenvalue we deduce that this matrix is primitive and, therefore, the auxiliary system must be strongly ergodic.

Relationships between the auxiliary and the original systems

The original system may be considered as a perturbation of the auxiliary one:

$$MP_k \cdots P_1 = M\bar{P} + M(P_k \cdots P_1 - \bar{P}) \tag{11}$$

where the matrix $P_k \cdots P_1 - \bar{P}$ converges to zero as k tends to infinity.

Therefore, the higher the value of k , the closer the eigenvalues and eigenvectors of $MP_k \cdots P_1$ and $M\bar{P}$ are. Thus, if k is large enough we know about the asymptotic behavior of the original system from that of the auxiliary one and, therefore, indirectly, from that of the aggregated one.

In other words, from the aggregated system we approximate the elements which characterise the asymptotic behavior of the original system and the larger k is, the

more accurate these approximations become. In the remainder of this section we study how these approximations improve when k increases.

In a previous work dealing with system 4 it is proved that the projection matrix of the original system converges geometrically to that of the auxiliary system (Sánchez *et al.*, 1995, Prop. 3.2). Under some conditions on the sequence $\{P_k\}$ we obtain an analogous result:

Theorem 4.3

Let $\|\cdot\|$ be a norm in the space of real matrices $M_{N \times N}$ and suppose a value $0 < \alpha < 1$ exists such that $\|P_k - P\| = o(\alpha^k)$ (fast convergence). Then another value $\alpha \leq \delta < 1$ exists such that $\|M(P_k \dots P_1 - \bar{P})\| = o(\delta^k)$.

Proof. (See Appendix).

As previously stated the elements defining the asymptotic behavior of the original system tend to those approximations given by the aggregated system as $k \rightarrow \infty$. Now we make use of some results on perturbation theory to determine the speed of convergence of these characteristics.

Proposition 4.4

Suppose hypotheses H1 and H2 are verified, then we can conclude that, for k large enough, the original system is strongly ergodic. Moreover, if a number $0 \leq \alpha < 1$ exists such that $\|P_k - P\| = o(\alpha^k)$, then another number $\alpha < \delta < 1$ exists such that

- 1) The population size grows exponentially at a rate $\lambda_k = \lambda + o(\delta^k)$;
- 2) The population vector reaches a stable structure given by vector $r_k = \frac{MVr}{\|MVr\|} + o(\delta^k)$;
- 3) The reproductive values of each group are given by vector $l_k = Ul + o(\delta^k)$.

Proof. From Proposition 3.1 we have

$$MP_k \dots P_1 \xrightarrow[k \rightarrow \infty]{} M\bar{P}$$

Proposition 4.2 establishes that matrix $M\bar{P}$ associated with the auxiliary system is primitive. Then, for k large enough, $MP_k \dots P_1$ has, at least, the same positive entries as $M\bar{P}$ which implies that $MP_k \dots P_1$ will also be primitive.

Proposition 4.2 also established that a) the asymptotic growth rate of the auxiliary system is λ ; b) its asymptotic stable structure is given by vector $\frac{MVr}{\|MVr\|}$; and c) its reproductive values are given by vector Ul .

Since, from (11), we may consider matrix $MP_k \dots P_1$ as a perturbation of $M\bar{P}$, using (Stewart and Sun, 1990, pp. 183 and 240) we have

$$\begin{aligned} \lambda_k &= \lambda + \frac{l^T U^T M(P_k \dots P_1 - \bar{P}) MVr}{l^T U^T MVr} + O(\|M(P_k \dots P_1 - \bar{P})\|^2) \\ r_k &= \frac{MVr}{\|MVr\|} + O(\|M(P_k \dots P_1 - \bar{P})\|) \\ l_k &= Ul + O(\|M(P_k \dots P_1 - \bar{P})\|) \end{aligned} \quad (12)$$

Now, making use of Theorem 4.3, 1), 2) and 3) follow.

Note that we have used the continuity of the dot product to deduce that:

$$\frac{l^T U^T M(P_k \cdots P_1 - \bar{P}) M V r}{l^T U^T M V r} = o(\delta^k)$$

As shown, we can obtain essential information on the asymptotic behavior of the original system (growth rate, stable distribution, reproductive values) through the study of the aggregated system. Now we illustrate these results with a numerical example on an age structured population in a patchy environment.

5. AN AGE STRUCTURED POPULATION IN A PATCHY ENVIRONMENT

We consider a population divided into two age classes and distributed between two spatial patches. Then, the population vector is:

$$x_t = (x_t^{1,1}, x_t^{1,2}, x_t^{2,1}, x_t^{2,2})^T$$

where x_t^{ij} is the number of individuals of age i that live in patch j at time t .

We consider two processes involved in this model: a demographic one, that determines the number of births and deaths in each time interval, and a migratory one, that determines the transference of individuals between the two spatial patches. We assume that migration is fast compared with demography and we choose the projection interval of the model to be the one associated with demography. We suppose that migration acts k times before demography does. So, denoting Δt as the time step of the migration process, we can consider that each projection interval of the demographic process, $I_t = [t, t+1)$, is divided into k subintervals of the form $I_{t,l} = [t + (l - 1)\Delta t, t + l\Delta t)$; $l = 1, \dots, k$.

We suppose that migration acts once in each interval $I_{t,l}$ and that it depends on l but not on t . The demographic rates are constant in time. For each patch, demography is described by matrices:

$$M_1 = \begin{pmatrix} 0 & f^{2,1} \\ s^{1,1} & s^{2,1} \end{pmatrix}; \quad M_2 = \begin{pmatrix} 0 & f^{2,2} \\ s^{1,2} & s^{2,2} \end{pmatrix}$$

where f^{ij} is the mean number of offspring produced by an individual of age i living at patch j (there is a single reproductive age) and s^{ij} is the survival rate for the individuals of age i living at patch j .

Migration between patches 1 and 2 is depicted by the matrices

$$P_l^1 = \begin{pmatrix} 1 - p_l^1 & q_l^1 \\ p_l^1 & 1 - q_l^1 \end{pmatrix}; \quad P_l^2 = \begin{pmatrix} 1 - p_l^2 & q_l^2 \\ p_l^2 & 1 - q_l^2 \end{pmatrix}; \quad l = 1, \dots, k$$

where p_l^i represents the proportion of individuals of age i that migrate from patch 1 to patch 2 during the l -th migratory period ($I_{t,l}$). Analogously, q_l^i represents the proportion of individuals of age i that migrate from patch 2 to patch 1 during $I_{t,l}$.

Matrix P_l is block-diagonal because the migration process is considered internal, in the sense that individuals do not change their age class while moving from one patch to another. Moreover, the blocks of P_l are column stochastic matrices. This is due to the fact that the migration process is conservative of the total number of individuals.

Then, the matrices that describe the demographic and the migration processes for the whole population are, respectively:

$$M = \begin{pmatrix} 0 & 0 & f^{2,1} & 0 \\ 0 & 0 & 0 & f^{2,2} \\ s^{1,1} & 0 & s^{2,1} & 0 \\ 0 & s^{1,2} & 0 & s^{2,2} \end{pmatrix} \text{ and } P_l = \begin{pmatrix} 1-p_l^1 & q_l^1 & 0 & 0 \\ p_l^1 & 1-q_l^1 & 0 & 0 \\ 0 & 0 & 1-p_l^2 & q_l^2 \\ 0 & 0 & p_l^2 & 1-q_l^2 \end{pmatrix}; \quad l=1, \dots, k$$

The complete original system reads as follows:

$$x_{t+1} = MP_k \dots P_1 x_t.$$

We assume that the sequence of migration matrices converge to the following matrix:

$$P = \begin{pmatrix} 1-p^1 & q^1 & 0 & 0 \\ p^1 & 1-q^1 & 0 & 0 \\ 0 & 0 & 1-p^2 & q^2 \\ 0 & 0 & p^2 & 1-q^2 \end{pmatrix}$$

If the intervals $I_{t,l}$ are small in comparison to I_t (i.e., if k is large), the spatial distribution of the i -aged individuals between the patches, can be approximated by the probability normed right Perron-Frobenius eigenvector of block i in P , i.e.:

$$v_i = \left(\frac{q^i}{p^i + q^i}, \frac{p^i}{p^i + q^i} \right)^T$$

To aggregate the system we denote the global variables in the following way:

$$y_t = (y_t^1, y_t^2)$$

where y_t^i represents the total number of individuals in group i at time t .

In the aggregated system we are assuming that the migration process reaches its equilibrium frequencies within each projection interval of the original system and, so, the spatial distribution of i -aged individuals is given by vector v_i .

The aggregated system reads:

$$y_{t+1} = \bar{M} y_t \text{ where } \bar{M} = \begin{pmatrix} 0 & \frac{f^{2,1}q^2 + f^{2,2}p^2}{p^2 + q^2} \\ \frac{s^{1,1}q^1 + s^{1,2}p^1}{p^1 + q^1} & \frac{s^{2,1}q^2 + s^{2,2}p^2}{p^2 + q^2} \end{pmatrix}$$

Note that we averaged over the spatial structure, so we obtain a matrix with global fertility and survival rates for each age class. The global fertility and survival rates are weighted means of the fertility and survival rates in each patch where the weights are the equilibrium frequencies of the migration process.

We gave some numerical values to the parameters of the model and computed some of its main characteristics, such as growth rate or asymptotic population structure. We also built the aggregated system and obtained the corresponding approximations. We were particularly interested in illustrating the accuracy of these approximations in relation to the value of k .

First, we supposed that the proportion of i -aged individuals migrating from patch 2 to patch 1 changes in each migratory period $I_{t,l}$ and tends, when $l \rightarrow \infty$, to 0.75:

$$q_l^1 = 0.75 - 1/(1 + l)$$

Figure 1 shows how the growth rate of the original system (o) converges to that of the aggregated system (+) when k increases.

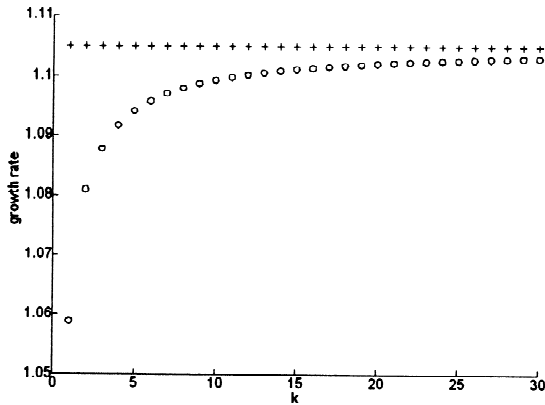


Figure 1. Convergence of the growth rate. Parameter values are: $f^{21} = 0.5$, $f^{22} = 2$, $s^{11} = 0.9$, $s^{12} = 0.6$, $s^{21} = 0.5$, $s^{22} = 0.1$, $p^1 = 0.7$, $q_1^1 = 0.75 - 1 / (1 + l)$, $p^2 = 0.4$, $q^2 = 0.55$. The symbols employed are '+' for the growth rate given by the aggregated system and 'o' for that corresponding to the original system for each value of k .

Secondly, we consider the case where:

$$q_1^1 = 0.75 - 1/2^l$$

for which, q_1^1 tends to 0.75 much faster than in the previous case. Figure 2 shows that we achieve good approximations even for low values of k . Theorem 4.3 provides a theoretical explanation of this fact.

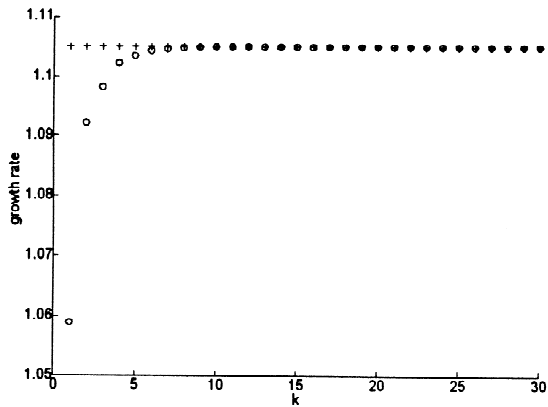


Figure 2. Convergence of the growth rate. Symbols '+' and 'o' are used as in Figure 1.

Figure 3 depicts, in this latter case, the evolution of the population structure over time. It shows that the asymptotic proportions of individuals in the different groups, computed by use of the original system (o) become closer and closer to the ones of the aggregated system (+) as k increases.

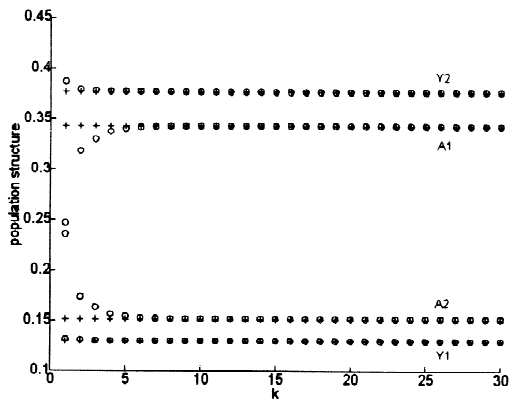


Figure 3. Convergence of the population structure. The numerical values are those of Figure 1. We can see the proportion of young in patch 1 (Y1), young in patch 2 (Y2), adult in patch 1 (A1) and adult in patch 2 (A2). The symbols employed are '+' for the aggregated system and 'o' for the original one.

6. CONCLUSIONS

The aggregation method presented here allows one to reduce a complex system with two processes acting at different time scales to a system with a lower dimension.

The variables which govern the aggregated system summarize the information contained in the state variables of the original system. The parameters of the aggregated system can easily be expressed as functions of the parameters of the slow dynamics and the equilibrium frequencies of the fast process.

The main point of interest of this technique is to obtain good approximations of the elements governing the asymptotic behavior of the original system, such as the asymptotic growth rate or the stable population structure, from the study of the aggregated system. The accuracy of the approximations depends on the ratio between the characteristic time scales of the slow and the fast processes.

Our contribution is a generalization of previous works (Sánchez *et al.*, 1995) to the case where fast dynamics is allowed to vary each time it occurs. To aggregate these models we have made the parameters defining the fast process tend to some equilibrium values, i.e., we need environmental conditions related to the fast process that become stable in the long-term. We studied the relationships between the aggregated and the original systems in the autonomous case, where population parameters do not depend on time, and we analyzed a numerical example of a multiregional age-structured model. In general, if the migration process is sufficiently fast in comparison to the demographic process, the aggregated system gives good approximations of the asymptotic behaviour of the microsystem, the accuracy of the approach being dependent on the speed with which the fast process reaches its equilibrium.

In the second part of this paper we will deal with the non-autonomous case where both, the slow dynamics and the fast dynamics, are allowed to vary with time. In the first place, we present a non-autonomous model with two time scales and proceed at this reduction. Moreover, we study the relationships between the original system and the aggregated system in two cases regarding the kind of environmental variation: in the first one we shall assume that population is affected by a variable environment that

tends to an equilibrium and study the relationships between the property of strong ergodicity for the original and that property for the reduced system. In the second one, we shall consider the case of a general temporal variation and undertake the study of the relationships between the weak ergodicity of both systems.

APPENDIX

Proof of Proposition 3.1

Let us consider the following system:

$$x_k = P_k x_{k-1}$$

The sequence $\{P_k\}$ converges to a primitive matrix and each matrix is column-allowable (it has, at least, one positive entry in each column). From (Seneta, 1981, pp. 96) we deduce that the system is strongly ergodic. Then we have for any initial vector x_0 :

$$\lim_{k \rightarrow \infty} \frac{x_k}{\|x_k\|} = v$$

where $\|v\| \equiv 1^T v = I$.

Since the matrices are stochastic we have $\|x_k\| = \|x_0\|$ for each k , so:

$$\lim_{k \rightarrow \infty} P_k \cdot \dots \cdot P_1 x_0 = \lim_{k \rightarrow \infty} x_k = v \|x_0\|$$

whatever x_0 is.

Finally, note that:

$$\lim_{k \rightarrow \infty} P_k \cdot \dots \cdot P_1 = (\lim_{k \rightarrow \infty} P_k \cdot \dots \cdot P_1 e_1 \mid \dots \mid \lim_{k \rightarrow \infty} P_k \cdot \dots \cdot P_1 e_p)$$

where $\{e_1, \dots, e_p\}$ are the vectors of the canonical base of \mathbf{R}^p . Now:

$$\lim_{k \rightarrow \infty} P_k \cdot \dots \cdot P_1 = (v \|e_1\| \mid \dots \mid v \|e_p\|) = (v \mid \dots \mid v) = v \mathbf{1}^T.$$

Proof of Theorem 4.3

Since all matrix norms are equivalent we can use any of them. We will use the 1-matrix norm, i.e., $\|A\| = \max_{j=1, \dots, n} \sum_{i=1}^n |a_{ij}|$. We have that $\|M(P_k \cdot \dots \cdot P_1 - \bar{P})\| \leq \|M\| \|P_k \cdot \dots \cdot P_1 - \bar{P}\|$ and $\|P_k \cdot \dots \cdot P_1 - \bar{P}\| \leq \|(P_k \cdot \dots \cdot P_1 - P^k)\| + \|P^k - \bar{P}\|$.

In Sánchez *et al.*, (1995) the authors proved that if $\lambda_2 < \gamma < 1$, where λ_2 is the subdominant eigenvalue of the matrix P , $\|P^k - \bar{P}\| = o(\gamma^k)$ so we only need demonstrate geometric convergence $\|P_k \cdot \dots \cdot P_1 - P^k\|$.

Since all the matrices are block diagonal and the dimension of the i -th block is always $N_i \times N_i$, we can restrict our study to the convergence of a single block. Let Q and Q_1 be the i -th blocks of P and P_1 , respectively. We want to study the convergence of $\|Q_k \cdot \dots \cdot Q_1 - Q^k\|$.

We have that Q is primitive, so the ergodicity coefficient (Birkhoff's contraction coefficient, see (Seneta, 1981)) of its powers verifies $\tau_B(Q^k) \rightarrow 0$. Therefore we can choose a number k_0 such that

$$\tau_B(Q^{k_0}) = \beta < \alpha \tag{13}$$

This happens for all blocks of P so we can choose k_0 such that (13) is verified by every block. We define $\varepsilon_k \equiv \|Q_k - Q\|$. Clearly $\varepsilon_k = o(\alpha^k)$, since $\|P_k - P\| = o(\alpha^k)$.

Now, taking into account that $\|Q\| = 1$ (since P is column stochastic):

$$\begin{aligned} d_k &\equiv \|Q_k \cdot \dots \cdot Q_1 - Q^k\| \leq \|Q_k \cdot \dots \cdot Q_1 - QQ_{k-1} \cdot \dots \cdot Q_1\| + \\ &\quad \|QQ_{k-1} \cdot \dots \cdot Q_1 - Q^k\| \\ &= \|Q_k - Q\| \|Q_{k-1} \cdot \dots \cdot Q_1\| + \|Q(Q_{k-1} \cdot \dots \cdot Q_1 - Q^{k-1})\| \\ &\leq \varepsilon_k + \|Q(Q_{k-1} \cdot \dots \cdot Q_1 - QQ_{k-2} \cdot \dots \cdot Q_1)\| + \|Q(QQ_{k-2} \cdot \dots \cdot Q_1 - Q^{k-1})\| \tag{14} \\ &= \varepsilon_k + \|Q\| \|Q_{k-1} - Q\| \|Q_{k-2} \cdot \dots \cdot Q_1\| + \\ &\quad \|Q^2(Q_{k-2} \cdot \dots \cdot Q_1 - Q^{k-2})\| \\ &\leq \dots \leq \varepsilon_k + \varepsilon_{k-1} + \dots + \varepsilon_{k-k_0+1} + \|Q^{k_0}(Q_{k-k_0} \cdot \dots \cdot Q_1 - Q^{k-k_0})\|. \end{aligned}$$

Let x and y be probability vectors. In Seneta (1981) it is proven that, if Q is a column stochastic matrix, then $\|Q(x - y)\| \leq \tau_B(Q) \|x - y\|$. Now, if A and B are both stochastic matrices:

$$\|Q(A - B)\| \leq \max_{i=1, \dots, p} \|Q(a_i - b_i)\|$$

where a_i and b_i are the i -th columns of A and B , respectively. Then:

$$\|Q(A - B)\| \leq \tau_B(Q) \max_{i=1, \dots, p} \|a_i - b_i\| = \tau_B(Q) \|A - B\|$$

As a product of column stochastic matrices is another column stochastic matrix, $Q_{k-k_0} \cdot \dots \cdot Q_1$ and Q^{k-k_0} are both column stochastic matrices. Then:

$$\|Q^{k_0}(Q_{k-k_0} \cdot \dots \cdot Q_1 - Q^{k-k_0})\| \leq \tau_B(Q^{k_0}) \|Q_{k-k_0} \cdot \dots \cdot Q_1 - Q^{k-k_0}\| = \beta d_{k-k_0}$$

Moreover:

$$\sum_{l=k-k_0+1}^k \varepsilon_l \leq k_0 \cdot \varepsilon_k^*$$

where $\varepsilon_k^* = \max\{\varepsilon_l : l = k - k_0 + 1, \dots, k\}$, so we have, from (14):

$$d_k \leq k_0 \cdot \varepsilon_k^* + \beta d_{k-k_0} \tag{15}$$

We can express k in the following form: $k = pk_0 + q$ where p is an even number and $1 \leq q \leq 2k_0$ (actually q can be considered as k modulus $2k_0$).

Then, applying (15) recursively we obtain:

$$d_k \leq k_0(\varepsilon_k^* + \varepsilon_{k-k_0}^* \beta + \varepsilon_{k-2k_0}^* \beta^2 + \dots + \varepsilon_{k-(p-1)k_0}^* \beta^{p-1}) + \beta^p d_q \tag{16}$$

We have $d_q \leq d^* \equiv \max\{d_l : l = 1, 2, \dots, 2k_0 - 1\}$ and $p = \frac{k-q}{k_0}$. Then:

$$\frac{\beta^p d_q}{\alpha^{\frac{k}{k_0}}} = \left(\frac{\beta}{\alpha}\right)^{\frac{k}{k_0}} \beta^{\frac{-q}{k_0}} d_q \xrightarrow{k \rightarrow \infty} 0$$

so the last term of (16) is $(\alpha^{\frac{k}{k_0}})$.

Now we focus on the first term. It can be expressed in the following way:

$$k_0(\varepsilon_{pk_0+q}^* + \varepsilon_{(p-1)k_0+q}^* \beta + \varepsilon_{(p-2)k_0+q}^* \beta^2 + \dots + \varepsilon_{k_0+q}^* \beta^{p-1}) \tag{17}$$

We have, by hypothesis, $\varepsilon_k = o(\alpha^k)$. Then, using Lemma 6.1, $\varepsilon_k^* \equiv \sup_{i \geq k} \varepsilon_i = o(\alpha^k)$ and this is a monotone non-increasing sequence so any subsequence $\varepsilon_{k_l}^*$ verifies $\varepsilon_{k_l}^* = o(\alpha^{k_l})$. Then, for simplicity we will denote $\eta_l = \varepsilon_{lk_0+q}^*$ and we know that $\eta_l = o(\alpha^{k_l})$. Now (17) can be expressed as $k_0(\eta_p + \eta_{p-1}\beta + \eta_{p-2}\beta^2 + \dots + \eta_1\beta^{p-1})$ which can be split into two terms:

$$\begin{aligned} & k_0(\eta_p + \eta_{p-1}\beta + \dots + \eta_{\frac{p}{2}+1}\beta^{\frac{p}{2}-1} + \eta_{\frac{p}{2}}\beta^{\frac{p}{2}} + \dots + \eta_1\beta^{p-1}) \\ \leq & k_0(\eta_{\frac{p}{2}+1} \frac{1-\beta^{\frac{p}{2}}}{1-\beta} + \eta_1\beta^{\frac{p}{2}} \frac{1-\beta^{\frac{p}{2}}}{1-\beta}) \\ = & k_0(\eta_{\frac{k-q}{2k_0}+1} \frac{1-\beta^{\frac{k-q}{2k_0}}}{1-\beta} + \eta_1\beta^{\frac{k-q}{2k_0}} \frac{1-\beta^{\frac{k-q}{2k_0}}}{1-\beta}) = o(\alpha^{\frac{k}{2k_0}}) \end{aligned}$$

So we conclude: $d_k = o(\alpha^{\frac{k}{2k_0}})$. Since this is true for the i -th block, whatever i is, we deduce that $\|P_k \cdot \dots \cdot P_1 - P^k\| = o(\alpha^{\frac{k}{2k_0}})$. Finally, if δ is a number such that $\max\{\alpha^{\frac{1}{2k_0}}, \lambda_2\} \leq \delta < 1$, then:

$$\frac{\|M(P_k \cdot \dots \cdot P_1 - \bar{P})\|}{\delta^k} \leq \frac{\|P_k \cdot \dots \cdot P_1 - P^k\|}{\delta^k} + \frac{\|P^k - \bar{P}\|}{\delta^k} \xrightarrow{k \rightarrow \infty} 0$$

So it has been proven that $\|M(P_k \cdot \dots \cdot P_1 - \bar{P})\| = o(\delta^k)$.

Lemma 6.1

Let a_k be a sequence of nonnegative numbers and $0 < \gamma < 1$. Then:

$$\frac{a_k}{\gamma^k} \xrightarrow{k \rightarrow \infty} 0 \Rightarrow \frac{\sup_{l \geq k} a_l}{\gamma^k} \rightarrow 0$$

Proof.

For all $\varepsilon > 0$, k_0 exists such that, if $k \geq k_0$, $\frac{a_k}{\gamma^k} < \varepsilon$. Therefore, if $k \geq k_0$:

$$\frac{\sup_{l \geq k} a_l}{\gamma^k} = \frac{\sup\{a_k, a_{k+1}, a_{k+2}, \dots\}}{\gamma^k} \leq \frac{\sup\{\varepsilon\gamma^k, \varepsilon\gamma^{k+1}, \varepsilon\gamma^{k+2}, \dots\}}{\gamma^k} = \sup\{\varepsilon, \varepsilon\gamma, \varepsilon\gamma^2, \dots\} = \varepsilon.$$

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