LINEAR DISCRETE POPULATION MODELS WITH TWO TIME SCALES IN FAST CHANGING ENVIRONMENTS II: NON-AUTONOMOUS CASE

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ABSTRACT

As the result of the complexity inherent in nature, mathematical models employed in ecology are often governed by a large number of variables. For instance, in the study of population dynamics we often deal with models for structured populations in which individuals are classified regarding their age, size, activity or location, and this structuring of the population leads to high dimensional systems. In many instances, the dynamics of the system is controlled by processes whose time scales are very different from each other. Aggregation techniques take advantage of this situation to build a low dimensional reduced system from which behavior we can approximate the dynamics of the complex original system.

In this work we extend aggregation techniques to the case of time dependent discrete population models with two time scales where both the fast and the slow processes are allowed to change at their own characteristic time scale, generalizing the results of previous studies. We propose a non-autonomous model with two time scales, construct an aggregated model and give relationships between the variables governing the original and the reduced systems. We also explore how the properties of strong and weak ergodicity, regarding the capacity of the system to forget initial conditions, of the original system can be studied in terms of the reduced system.

KEYWORDS: Approximate aggregation, population dynamics, time scales, strong ergodicity, weak ergodicity.

1. INTRODUCTION

The present paper is a continuation of the work "Linear Discrete Population Models with Two Time Scales and Fast Changing Environments I: Autonomous Case" (Blasco *et al*., 2001).

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In Blasco *et al*. (2001), in which the reader can find a detailed exposition of the aims and scope of aggregation techniques, we developed a technique for the aggregation of an autonomous linear discrete system involving two processes taking place at different time scales. In such a context we obtained a lower dimensional system that we called "aggregated" and it was shown how essential information on the behavior of the original system could be obtained by studying the reduced system.

This second part deals with the reduction of the model proposed in the above-mentioned work to deal with the case in which the parameters of the model are functions of time. Previous works dealing with the aggregation of non-autonomous discrete models (Sanz and Bravo de la Parra, 1998, 2001) choose as the time step for the model the one corresponding to the slow process and assume that, during each of these time steps, the fast process acts a high number of times. However, the characteristics defining the fast process were supposed to be constant in each time step of the model. In our work, that restriction is removed and we deal with the general case in which the fast process can change at its own time scale, only requiring that the fast dynamics tend to an equilibrium.

There are different approaches to the study of non-autonomous models depending on the kind of environmental variation for the system. We will focus on two such types of variation. In the first place, let us contemplate the case in which the environment, though changing with time, tends to an equilibrium. Models with this property frequently exhibit the property called strong ergodicity, i.e., the structure of the population vector tends asymptotically to a fixed vector independent of initial conditions (Cohen, 1979a). In the case in which there is no specific pattern of variation for the environment, we have that under very general assumptions, the system is weakly ergodic, i.e., the structure of the population structure, although it may not converge, it does become independent of initial conditions.

In Section 2 we extend the aggregation method developed in Blasco *et al*. (2001) to the case where the original system is non-autonomous. The aggregation procedure consists of two stages: first we assume that the fast dynamics reach equilibrium in each time step corresponding to the slow process; hence, we obtain an "auxiliary" system which can be considered as an approximation of the original system. This auxiliary system is shown to be redundant in the sense that it can be reduced to a lower dimensional aggregated system, the dynamics of which is governed by a reduced set of so called "global variables".

Section 3 relates the population vector corresponding to the original system with that corresponding to the aggregated system, showing that we can approximate the former in terms of the latter. A brief summary of the theory of non-autonomous systems, detailing the different kinds of environmental variation and the corresponding behavior that those patterns of variation induce on the system is included in Section 4.

The relationships between the property of strong ergodicity for the aggregated system and for the original system in the case of an environment tending to an equilibrium are explored in Section 5. In Section 6, we carry out the study of the relationships of the weak ergodicity of the original and the reduced system under very general assumptions on the type of environmental variation.

In Section 7 the theoretical results are applied to the aggregation of a multiregional non-autonomous model in which migration is supposed to be fast with respect to demography. The study of the weak ergodicity of the multiregional model in terms of the reduced system is carried out with a simple example. Finally, some numerical simulations have been performed to illustrate the theoretical results.

2. AGGREGATION OF A NON-AUTONOMOUS SYSTEM WITH TWO TIME SCALES

We consider a population classified into q groups. In addition, each group $i = 1,...,q$ is subdivided into N_i subgroups. We define $x_t^{i,j}$ as the number of individuals in the j-th subgroup of the i-th group at time t. Therefore, the population is described by the following column vector of state variables, also called microvariables,

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

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

In the evolution of the population we will consider two processes whose corresponding characteristic time scales, and consequently their projection intervals, are very different from each other. We will refer to them as slow and fast dynamics.

We will choose as the projection interval of our model, the one corresponding to the slow dynamics. This means that the time elapsed between times t and $t + 1$ is the time interval on which the slow process acts.

We will make no special assumptions regarding the characteristics of the slow dynamics. Thus, for a certain fixed projection interval $I_t = [t,t + 1)$, the slow dynamics will be represented by a non-negative projection matrix $M_t \in \mathbf{R}^{N\times N}$ which we consider divided into blocks M_t^{ij}, $1 \le i,j \le q$. We then have

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

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

Since the projection interval of the model is that of the slow process, we will assume that, in each projection interval, the fast process acts k times before the slow process does, where k is an integer that can be interpreted as the ratio between the projection intervals corresponding to the slow and fast dynamics. Therefore, if we denote by Δt the time step of the fast process, we can consider that interval I_t is divided into k subintervals of the form $I_{t,l} = [t + (l - 1)\,\Delta t,\ t + l\Delta t)$; $l = 1,...,k$.

In our model, the parameters of the fast process are allowed to change with each of the projection intervals $I_{t,l}$. We will denote by $P_{t,l}^i \in R^{N_i \times N_i}$ the matrix determining the transferring of individuals among the subgroups within group i during the time interval $I_{t,l}$.

We make the following three assumptions on the fast process:

A) It is internal for each group, i.e., it cannot transfer individuals between different groups.

B) It is conservative with respect to the number of individuals.

From Hypotheses A and B we have that the fast dynamics for the whole population during interval $I_{t,l}$ is represented by a matrix:

$$P_{t,l} := diag\{P_{t,l}^1, ..., P_{t,l}^q\}. \quad (2)$$

where each block $P_{t,l}^i$ is a column stochastic matrix, i.e., a matrix whose columns are probability vectors.

C) For each t, the parameters of the fast dynamics during interval I_t tend to constant values, i.e., for each t and each i, the sequence $\{P_{t,l}^i\}$ tends, when $l \to \infty$, to a certain (necessarily stochastic) matrix P_t^i. In addition we suppose matrix P_t^i to be primitive.

Hypothesis C) implies that the characteristics of the fast process in each I_t tend to an equilibrium represented by matrix

$$P_t := \lim_{l \to \infty} P_{t,l} = diag\{P_t^1, ..., P_t^q\} \quad (3)$$

and is essential for our aggregation procedure in the sense that, as we will see, guarantees that the fast dynamics tend to an equilibrium in each I_t.

The evolution of the population is determined by the following discrete system that we will call “microsystem” or “original system”:

$$x_{t+1} = M_t P_{t,k} \cdots P_{t,1} x_t. \quad (4)$$

In previous works (Sanz and Bravo de la Parra, 1998, 2001), the authors have dealt with the reduction of the following model:

$$x_{t+1} = M_t P_t^k x_t \quad (5)$$

which is a particular case of (4) when the characteristics of the fast dynamics are constant within each I_t, i.e., $P_{t,k} = \cdots = P_{t,1} = P_t$.

In order to carry out the aggregation of model (4) we will approximate it by a so called “auxiliary system” that is susceptible to being perfectly aggregated, i.e., of being reduced to a simpler system without the need to make any approximation. To do so we will make use of the following proposition, extracted from Blasco *et al*. (2001).

Proposition 1

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

$$\lim_{l \to \infty} A_l \cdots A_1 = v\mathbf{1}^T$$

where $\mathbf{1} = (1,1,\ldots,1)^T$. *Therefore, for any initial condition, a population whose dynamics is controlled by the sequence $\{A_l\}$ will asymptotically reach an equilibrium distribution of the individuals among the stages given by vector v.*

Let us now consider, for each t and i, the probability normed eigenvector v_t^i of P_t^i associated with eigenvalue 1. From Proposition 1 vector v_t^i can be interpreted in terms of the fast dynamics of group i in interval I_t in the following way: Let us consider a hypothetical situation in which the system is governed by the fast process exclusively. Suppose, moreover, that I_t is long enough with respect to the projection interval corresponding to the fast process for this to reach its equilibrium conditions during I_t. Then, for any "initial condition" of the system at time t, the structure of the population of group i at the end of I_t would be defined by v_t^i.

We define matrices

$$V_t := diag\{v_t^1, ..., v_t^q\};\ U := diag\{1_{N_1}, ..., 1_{N_q}\}$$

from which we immediately have

$$P_t V_t = V_t. \quad (6)$$

Let us introduce the so called "auxiliary system"

$$X_{t+1} = M_t \overline{P}_t X_t \quad (7)$$

where

$$\overline{P}_t := \lim_{k \to \infty} P_{t,k} \cdots P_{t,1}. \quad (8)$$

Making use of Proposition 1 on each block we have $\overline{P}_t = V_t U^T$.

The auxiliary system can therefore be interpreted as the limit of the original system when $k \to \infty$, i.e., as the original system under the assumption that the interval I_t is long enough with respect to the projection interval of fast process for this to reach its equilibrium. Notice the use of capital letters to denote the variables associated with the auxiliary system.

We will show that the auxiliary system can be perfectly aggregated. In order to do so, we define the vector of global variables

$$y_t = (y_t^1, ..., y_t^q) \quad (9)$$

where

$$y_t^i = X_t^{i,1} + \cdots + X_t^{i,N_i},$$

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 interval I_t. Note that these global variables can be obtained from the variables of the auxiliary system by

$$y_t = U^T X_t. \quad (10)$$

Premultiplying by U^T on both sides of (7) we obtain

$$U^T X_{t+1} = U^T M_t \overline{P}_t X_t = U^T M_t V_t U^T X_t,$$

which can be expressed as follows:

$$y_{t+1} = \overline{M}_t y_t, \quad (11)$$

where we have denoted

$$\overline{M}_t = U^T M_t V_t.$$

In the aggregated system, each group is represented by one single variable. Therefore, we have reduced the dimension of the model from $N = N_1 + \cdots + N_q$ to q. In the next sections we will see how this new simpler system provides information on the dynamics of the population represented in the original system.

The following lemma, which is a straightforward consequence of the definition of $\overline{M}_t$ and the fact of vectors v_t^i and 1_{N_i} being positive for all *i* and *t*, allows us to relate the structure of matrices M_t and $\overline{M}_t$.

Lemma 2

For all t, $\overline{M}_t$ *is a non-negative matrix in which the element of row i and column j is non-zero if and only if matrix* M_t^{ij} *is not zero.*

Note from this last result that the pattern of non-zero elements in $\overline{M}_t$ coincides with the pattern of non-zero blocks M_t^{ij} for the slow dynamics.

3. RELATIONSHIP BETWEEN MICROVARIABLES AND GLOBAL VARIABLES

Recall the original system (4)

$$x_{t+1} = M_t P_{t,k} \cdots P_{t,1} x_t,$$

and the auxiliary system (7)

$$X_{t+1} = M_t \overline{P}_t X_t,$$

where $\overline{P}_t$ is

$$\overline{P}_t = \lim_{k \to \infty} P_{t,k} \cdots P_{t,1} = V_t U^T.$$

The variables of the auxiliary system can be obtained through the knowledge of the global variables. Indeed,

$$\begin{aligned} X_t &= M_t \overline{P}_t M_{t-1} \overline{P}_{t-1} \cdots M_1 \overline{P}_1 X_0 = M_t V_t U^T M_{t-1} V_{t-1} U^T \cdots M_1 V_1 U^T X_0 \\ &= M_t V_t \overline{M}_{t-1} \cdots \overline{M}_1 y_0 = M_t V_t y_{t-1}. \end{aligned} \tag{12}$$

The next proposition shows that, for fixed *t*, the state variables x_t corresponding to the original system can be approximated by vector $M_tV_ty_{t-1}$. In addition, if the convergence of matrices $P_{t,k}$ to P_t is "geometric", then the distance between the approximation and x_t decays also geometrically.

Proposition 3

a) Given any initial condition x_0 *and any fixed value for t, the solutions of the original and the aggregated systems verify*

$$\lim_{k \to \infty} x_t = M_t V_t y_{t-1}$$

b) Moreover, let us assume that $0 < \alpha < 1$ *exists such that, for all t,* $P_{t,k} - P_t = o(\alpha^k);\ k \to \infty$. *Then,* δ *exists with* $\alpha \le \delta < 1$ *such that, for any initial condition* x_0 *and any fixed value of t, the solutions of the original and the aggregated verify*

$$x_t = M_t V_t y_{t-1} + o(\delta^k);\ k \to \infty.$$

Proof

Let us first prove b). By (12) all we have to show is that δ exists with $\alpha \leq \delta < 1$ such that

$$x_t = X_t + o(\delta^k) \tag{13}$$

for all t and any initial condition x_0.

In the proof we will make use of the following theorem, proved by the authors in Blasco *et al*. (2001):

Theorem I

Let $\{Q_k\}$ be a sequence of column stochastic matrices that converge to a primitive matrix Q and let

$$\overline{Q} := \lim_{k\to\infty} Q_k Q_{k-1} \cdots Q_1$$

Let us suppose that $0 < \alpha < 1$ exists such that $Q_k - Q = o(\alpha^k)$. Then δ exists verifying $\alpha \leq \delta < 1$ such that $Q_k \cdots Q_1 - \overline{Q} = o(\delta^k)$.

We will proceed by induction. We have that

$$x_1 = M_1 P_{1,k} \cdots P_{1,1} x_0 = M_1(\overline{P}_1 + o(\delta^k))x_0 = M_1 \overline{P}_1 x_0 + o(\delta^k) = X_1 + o(\delta^k),$$

where we have applied Proposition (8) and Theorem I in the second equality. Now assume (13) holds at time t. Then we have

$$\begin{aligned} \| x_{t+1} - X_{t+1} \| &= \| M_t P_{t,k} \cdots P_{t,1} x_t - M_t \overline{P}_t X_t \| \\ &\leq \| M_t P_{t,k} \cdots P_{t,1} x_t - M_t P_{t,k} \cdots P_{t,1} X_t \| + \\ &\quad \| M_t P_{t,k} \cdots P_{t,1} X_t - M_t \overline{P}_t X_t \| \\ &\leq \| M_t \| \ \| P_{t,k} \cdots P_{t,1} \| \ \| x_t - X_t \| + \\ &\quad \| M_t \| \ \| P_{t,k} \cdots P_{t,1} - \overline{P}_t \| \ \| X_t \| = o(\delta^k) \end{aligned}$$

as we required. In the last equality we have used the induction hypothesis and Theorem I.

The proof of a) is absolutely analogous to that of b) making $\delta = 1$ and applying (8).■

So far we have explored the relationships between the original and the aggregated systems for a given value of time. Now we will deal with some relationships between the asymptotic behavior of both systems. We begin by reviewing some general facts about non-autonomous linear discrete systems in Section 4.

4. SOME TOPICS ON NON-AUTONOMOUS LINEAR DISCRETE SYSTEMS

Let us consider the following system

$$z_{t+1} = A_t z_t \tag{14}$$

where $A_t \in \mathbf{R}^{N\times N}$. If we define $H_t = A_{t-1}A_{t-2}\cdots A_1 A_0$ then

$$z_t = H_t z_0$$

In the sequel we will denote by $\| * \|$ the 1-norm in $\mathbf{R}^N$, i.e., given $z = (z^1, z^2, \ldots, z^N)^T$ then $\| z \| = | z^1 | + | z^2 | + \ldots + | z^N |$.

If we are modelling the dynamics of a stage-structured population, z_t is the population vector at time t, the total population is given by $\| z_t \|$ and the population structure is $z_t / \| z_t \|$.

In general, the asymptotic behavior of the population structure depends on both the pattern of environmental variation, given by the sequence $\{A_t;\ t = 0,1,2,...\}$, and the initial condition z_0. However, under some conditions on the matrices A_t the population structure becomes, asymptotically, independent of the initial conditions. This "forgetting of the past" is called ergodicity.

In deterministic models we can find two kinds of ergodicity (Cohen, 1979a):

1. Strong ergodicity. In a strongly ergodic system, the population structure becomes asymptotically fixed and this "equilibrium structure" is independent of the initial population, i.e., there exists a vector v such that for any non-negative, non-zero initial condition z_0 we have $\lim_{t\to\infty} \frac{z_t}{\|z_t\|} = v$.

2. Weak ergodicity. In a weakly ergodic system, two populations with different initial conditions have structures that will become more and more alike, although neither of them will necessarily converge. In other words, for any non-zero initial conditions z_0 and z_0'

$$\lim_{t\to\infty} \left\| \frac{z_t}{\|z_t\|} - \frac{z_t'}{\|z_t'\|} \right\| = 0. \tag{15}$$

Note that strong ergodicity implies weak ergodicity.

Returning to the study of the system (14), we distinguish different patterns of environmental variation:

1. Constant environment. In this case $A_t = A$ for all t, so the system becomes autonomous. These kind of systems exhibit strong ergodicity if and only if matrix A is primitive. The aggregation of model (5) when M_t and P_t are constant with time, has been dealt with in Sánchez *et al*. (1995).

2. Cyclical variation. In these systems there exists a positive integer τ such that $A_{t+\tau} = A_t$ for all t, i.e., the environment changes periodically with a period τ. The classical approach (Skellam, 1967; Caswell, 2001) consists of considering products of matrices of length τ, which renders the system autonomous. The system cannot be expected to be strongly ergodic, but under very general assumptions there is weak ergodicity (Sanz and Bravo de la Parra, 2001).

3. "Stabilizing environment". Frequently, the sequence of environmental matrices $\{A_t\}$ tends, when $t \to \infty$, to a fixed matrix A which can be interpreted as the matrix of vital rates for the population when the environment has reached equilibrium. Under very general conditions, these kind of systems behave asymptotically similarly to autonomous systems with projection matrix A, and therefore strong ergodicity holds if and only if A is primitive. Note that, in Section 2, we assumed that the fast process in each time step of the slow process follows this pattern of variation. The reduction of the model (5) and the relationships between the original and the aggregated systems in the cases of cyclical variation and vital rates tending to an equilibrium, has been addressed in Sanz and Bravo de la Parra (1998).

4. General variation. Even in the case where there is not a particular pattern of environmental variation, given some assumptions on the set of possible environmental matrices the system is weakly ergodic. The relationships between the weak ergodicity

of system (5) and its corresponding reduced system can be found in Sanz and Bravo de la Parra (2001).

In Blasco *et al*. (2001) the authors explored the relationships between the asymptotic behavior of the aggregated system (11) and the original system (4), assuming a constant environment, i.e., the projection matrices $M_tP_{t,k}\cdots P_{t,1}$ are the same for all t. The next section is devoted to studying these relationships in the case of an environment that tends to an equilibrium when $t \to \infty$. Furthermore, Section 6 explores the relationships between the weak ergodicity of the original system and that of the aggregated system when environment does not have a particular kind of temporal variation.

Before proceeding, let us introduce some concepts that will be useful in subsequent discussions. A non-negative matrix is said to be row (column) allowable if it has, at least, one positive entry in each row (column) (Hajnal, 1976). Some properties of these matrices are: a) the product of a row-allowable matrix by a positive vector is another positive vector, b) the product of a column-allowable matrix by a non-zero vector is another non-zero vector, c) the product of two row (column) allowable matrices is another row (column) allowable matrix. A non-negative matrix is said to be allowable if it is both row and column allowable. The incidence matrix of a non-negative matrix A is a matrix of the same dimension of A containing one/zero in each position where A has a non-zero/zero element. We will write $A \sim B$ to denote that A and B have the same incidence matrix and write $A > 0$ ($A \geq 0$) to denote that A is positive (non-negative).

5. STRONG ERGODICITY IN AN ENVIRONMENT TENDING TO STABILIZATION

The original system described in Section 2 is:

$$x_{t+1} = M_tP_{t,k}\cdots P_{t,1}x_t$$

We shall study the relationships between the aggregated system and the original system under the hypothesis that the environment tends to stabilization. In Sanz and Bravo de la Parra (1998) the authors present a summary on the study of strong ergodicity for general non-autonomous systems. There we find the following result that gives very general sufficient conditions for the system to be strongly ergodic and to have a fixed asymptotic growth rate:

Theorem 4

Let A_t, $t \geq 0$ be a sequence of square non-negative and column allowable matrices that converge to a primitive matrix A with dominant eigenvalue λ and associated probability normed eigenvector v. Then, for all initial conditions $z_0 \geq 0$, $z_0 \neq 0$ we have that $\| z_t \| \neq 0$ for all t and:

a) $$\lim_{t\to\infty} \frac{z_t}{\|z_t\|} = r$$

b) $$\lim_{t\to\infty} \frac{\|z_{t+1}\|}{\|z_t\|} = \lambda.$$

The requirement A_t column allowable for all t, is a sufficient condition for the population not to become extinct in a finite time. Proposition 1, in Section 2, can be deduced from Theorem 4, taking into account that every column stochastic matrix is column allowable.

Coming back to our model with two time scales, we introduce the assumption that the population lives under environmental conditions that tend to an equilibrium.

H1. The sequence $\{M_t\}$ *tends, when* $t \to \infty$*, to a certain matrix M. Moreover, for each l, the sequences* $\{P_{t,l}\}$ *and* $\{P_t\}$ *converge, when* $t \to \infty$*, to certain matrices that we will denote* $P_{\infty,1}$ *and* P_∞*, respectively.*

Matrices M and $P_{\infty,1},\ldots,P_{\infty,k}$ can be interpreted as the vital rates for the slow and fast process respectively, when the environment has reached equilibrium.

Let us recall the aggregated system

$$y_{t+1} = \overline{M}_t y_t$$

From *H1* we have that the sequence $\{P_t\}$ tends, when $t \to \infty$, to a certain matrix P_∞. Hence, from (6) and due to the continuity of the eigenvectors on the entries of the matrix, it follows that the sequence $\{V_t\}$ converges when $t \to \infty$ to certain matrix V verifying

$$P_\infty V = V$$

and the projection matrices of the aggregated system $\overline{M}_t = U^T M_t V_t$, tend to matrix $\overline{M} = U^T M V$.

In the remaining part of this section, we will show that certain sufficient conditions for the strong ergodicity of the aggregated system are also sufficient for the ergodicity of the original system.

The following assumptions guarantee that the aggregated system meets the requirements of Theorem 4.

H2. Matrices $\overline{M}_t$ *are column allowable.*

Using Lemma 2 we have that hypothesis *H2* is equivalent to the following condition: for each group *j*, there exists *i* such that $M_t^{ij} \neq 0$, that is, the slow dynamics allows, at every instant, the transition from any group *j* to at least another group (possibly also group *j*).

H3. $\overline{M}$ *is primitive, i.e., there exists an integer h such that* $(\overline{M})^h$ *is a positive matrix. Let* λ *be the dominant eigenvalue of* $\overline{M}$*, r its corresponding positive right eigenvector such that* $\| r \|_1 = 1$ *and let l be its corresponding positive left eigenvector normed in such a way that* $l^T r = 1$.

We have then, that under hypotheses *H1*, *H2*, and *H3*, the aggregated system (11) verifies that, for each initial condition $y_0 \neq 0$:

a) $$\lim_{t\to\infty} \frac{y_t}{\| y_t \|} = r$$

i.e., the aggregated system is strongly ergodic and the asymptotic population structure is given by vector *r*.

b) $$\lim_{t\to\infty} \frac{\| y_{t+1} \|}{\| y_t \|} = \lambda$$

i.e., the aggregated system has an asymptotic growth rate given by λ.

Now we state two assumptions that, we will see, guarantee the strong ergodicity of the original system.

H4. The convergence of the products $M_t P_{t,k} \cdots P_{t,1}$ to $MP_{\infty,k} \cdots P_{\infty,1}$ is uniform in k.

Hypothesis *H1* guarantees that, for each k, the products $M_t P_{t,k} \cdots P_{t,1}$ tend, when $t \to \infty$, to matrices $MP_{\infty,k} \cdots P_{\infty,1}$. In *H4* we assume that the convergence of these products when $t \to \infty$ takes place with a similar speed for all values of k.

H5: M is row-allowable.

This assumption can be interpreted by saying that, when the environment has reached equilibrium, the slow process verifies that, for any $i = 1,2,...,q$ and $j = 1,2,...,N_i$, there exists at least one allowed transition towards subgroup j of group i.

Now we obtain the following result:

Proposition 5

Under assumptions H1-H5, the original system is strongly ergodic. For any initial condition $x_0 \geq 0$, $x_0 \neq 0$ we have that $\| x_t \| \neq 0$ for all t and:

1. The population size grows exponentially at a rate λ_k given by

$$\lim_{t \to \infty} \frac{\| x_{t+1} \|}{\| x_t \|} = \lambda_k$$

where $\lambda_k \underset{k \to \infty}{\longrightarrow} \lambda$.

2. The population structure $(x_t) / \| x_t \|$ converges to a stable structure given by a vector r_k that verifies $r_k \underset{k \to \infty}{\longrightarrow} \frac{MVr}{\| MVr \|}$.

Proof

(See Appendix.) ■

6. GENERAL ENVIRONMENTAL VARIATION AND WEAK ERGODICITY

Let us consider again the generic non-autonomous system (14). As it was mentioned in Section 4, in the case in which the environment changes with time in a general fashion, see for example (Quinn, 1981), it is not possible to expect that the population grows exponentially or that population structure converges to a certain vector. However, under quite general circumstances, the system exhibits weak ergodicity, i.e., meets (15). In other words, the population structure "forgets its past" in the sense that two different initial populations, subjected to the same sequence of environmental variation, have structures that become more and more alike (even though they do not necessarily converge).

When this property holds, the population structure for sufficiently high times will be determined by the recent history of vital rates. The importance of weak ergodicity lies in the fact that, in the absence of some kind of ergodic result, the explanation of population structure at a given time would require an explanation of the initial population, i.e., we would need to know its prior age structures indefinitely into the past (Cohen, 1979a). The rest of this paper is devoted to establishing relationships between the property of weak ergodicity for the original system and for the aggregated system.

In our approach, and in other works in the field of population dynamics (López, 1961; Golubitsky *et al.*, 1975; Kim and Sykes, 1976; Cohen, 1979a) weak ergodicity has to do with the capacity of the system to become independent of conditions at time 0. Most of the mathematical approaches to weak ergodicity (Hajnal, 1976; Cohen, 1979b; Seneta, 1981) are slightly different in the sense that in them weak ergodicity means the capacity of the system to become independent of the conditions of the system at any time and not only of initial conditions.

Most of the mathematical theory involved in the study of weak ergodicity can be found in Seneta (1981). In order to study the weak ergodicity of a system, it is customary to use a mathematical tool called "projective distance" (Golubitsky *et al.*, 1975; Seneta, 1981). This is a pseudometric that measures the distance between positive vectors attending to their relative composition, i.e., it is independent of their size and only depends on the structure of the vectors under consideration. Related to the projective distance is the "ergodicity coefficient" of a non-negative matrix, that loosely speaking measures the capacity of the matrices to act contractively in this metric.

In order to study the ergodicity of a system using the projective distance and the ergodicity coefficient as a tool, it is usual to slightly modify the definition of (15). In particular, the attention is restricted to system (14) when the A_t are allowable matrices. We adopt as a definition of weak ergodicity the following one (Cohen, 1979b; Seneta, 1981):

Definition 6

Let A_t be a sequence of N×N allowable matrices. The products $H_t = [h_t^{ij}]$ are weakly ergodic or, equivalently, system (14) is weakly ergodic, when there exists a sequence of N×N positive matrices of rank one $S_t = [s_t^{ij}]$ such that

$$\lim_{t\to\infty} \frac{h_t^{ij}}{s_t^{ij}} = 1 \text{ for all } i, j = 1, 2, ..., N. \tag{16}$$

It is straightforward to check that condition (16), which can be paraphrased saying that, asymptotically, the columns of H_t become positive and proportional, implies (15). Note that a necessary condition for the weak ergodicity of system (14) to hold is that the products H_t become positive for big enough t.

Conditions on matrices A_t which are both necessary and sufficient for weak ergodicity to hold are not known.

The following theorem gives very general sufficient conditions for weak ergodicity which hold in many practical situations for populations and, moreover, are very easily checked in practice.

Theorem 7.

Assume primitive matrices B and C exist such that for all t

$$B \le A_t \le C$$

(in the sequel condition (E)). Then system (14) is weakly ergodic.

Proof

(See Appendix). ■

Note that, in particular, condition (E) implies that all matrices A_t are primitive. In addition, if condition (E) is met, then system (14) is weakly ergodic for any pattern of variation in the environment for which the resulting projection matrices belong to the set $\{A_1, A_2,...\}$, i.e., any system $z_{t+1} = R_t z_t$ with $R_t \in \{A_1, A_2,...\}$ will be weakly ergodic.

Let us now consider the particular case in which the number of different possible environments for the population is finite, i.e., the case in which matrices A_t belong to a finite set $\{E^1,E^2,...,E^\sigma\}$ (this is the most common case in practice). Then it is clear that matrices A_t will always be bounded above by a primitive matrix. Moreover, the condition $B \leq A_t$ with B primitive, will depend only on the incidence matrices of the E^i, i.e., will depend only on the pattern of non-zero elements of these matrices and not on their specific values. Precisely, condition (E) will be met if and only if $\min\{i(E^1),...,i(E^\sigma)\}$ is a primitive matrix, where $\min\{A_1,...,A_p\}$ is a matrix whose elements in position (i,j) is $\min\{a_{ij}^1,...,a_{ij}^p\}$.

We will adopt the notation $\min^+(A)$ and max (A) to denote, respectively, the smallest positive element and the largest element of A. Now we introduce two hypotheses on our system:

H6. The non-zero entries of matrices M_t and $P_{t,k}$ are bounded away from zero and infinity, i.e., there exist positive constants a, a′, b and b′ such that for all t and k we have

$$\min{}^+(M_t) \geq a;\ \min{}^+(P_{t,k}) \geq a'$$

$$\max(M_t) \leq b;\ \max(P_{t,k}) \leq b'$$

Notice that $H6$ is always met if there is only a finite number of different environments.

H7. For each t, M_t is row-allowable.

This means that, in each interval I_t the slow process verifies that, for any $i = 1,2,...,q$ and $j = 1,2,...,N_i$, there exists at least one allowed transition towards subgroup j of group i.

The following result allows one to study the weak ergodicity of the original system in terms of the aggregated system.

Proposition 8

Let us assume that H6 and H7 hold. If the aggregated system meets condition (E), i.e., there exist primitive matrices B and C such that

$$B \leq \overline{M}_t \leq C,$$

holds for all t, then the original system is weakly ergodic for big enough k.

Proof

(See Appendix) ■

The next section is devoted to illustrating the results obtained in previous Sections 3 and 6 on a multiregional age-structured model. An illustration of similar results to those obtained in Section 5, can be found in Section 5 of Blasco *et al.* (2001).

7. A NON-AUTONOMOUS MULTIREGIONAL MODEL

In this section we will illustrate the aggregation procedure proposed in Section 2 through the reduction of a multiregional non-autonomous model with fast migration. Moreover, we will show through numerical simulations the results on weak ergodicity obtained in the preceding section for the case of a "general pattern" of temporal variation. In particular, we will illustrate numerically how the weak ergodicity of the original system can be guaranteed from very simple considerations on the aggregated system.

We consider a population divided into two age classes, young and adult individuals, and distributed between two geographical patches. The population vector is

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

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

The dynamics of the population is governed by two processes, demography and migration, whose associated vital rates depend on the environmental conditions, that we will suppose are changing with time. We assume that migration is fast compared with demography and choose the projection interval I_t of the model to be the one associated with demography. We make the natural assumption that newborn individuals live in their parents patch. In this way, demography in each I_t is characterized by a matrix

$$M_t = \begin{pmatrix} f_t^{1,1} & 0 & f_t^{2,1} & 0 \\ 0 & f_t^{1,2} & 0 & f_t^{2,2} \\ s_t^{1,1} & 0 & s_t^{2,1} & 0 \\ 0 & s_t^{1,2} & 0 & s_t^{2,2} \end{pmatrix} \tag{17}$$

where $f_t^{i,j}$ and $s_t^{i,j}$ represent, respectively, the fertility rate and the survival probability of an individual of age i living in patch j at time t.

We suppose that in each time interval I_t, migration acts k times before demography does, where k is a big integer that can be considered as the ratio between the projection intervals of demography and migration. Therefore, if we denote by Δt the time step of the fast process, we can consider each time interval $I_t = [t,t+1)$ divided into k subintervals (migration periods) of the form $I_{t,l} = [t+(l-1)\Delta t, t+l\Delta t)$; $l = 1,...,k$. We will denote by $P_{t,l} \in \mathbf{R}^{4\times 4}$ the matrix that defines migration in interval $I_{t,1}$. In this way, the set of matrices characterizing migration during interval I_t is

$$P_{t,l} = \begin{pmatrix} 1-p_{t,l}^1 & q_{t,l}^1 & 0 & 0 \\ p_{t,l}^1 & 1-q_{t,l}^1 & 0 & 0 \\ 0 & 0 & 1-p_{t,l}^2 & q_{t,l}^2 \\ 0 & 0 & p_{t,l}^2 & 1-q_{t,l}^2 \end{pmatrix};\ l = 1,..,k \tag{18}$$

where $p_{t,l}^i$ represents the probability of an i-aged individual living in patch 1 at the l-th migration period of interval I_t, to migrate to patch 2. Analogously, $q_{t,l}^i$ represents the probability of an i-aged individual living in patch 2 at the l-th migration period of time t, to migrate to patch 1.

Then our multiregional model (original system with the nomenclature of Section 2) reads

$$x_{t+1} = M_t P_{t,k} \cdots P_{t,1} x_t. \tag{19}$$

In order to aggregate the system, we assume that, for each t, the sequence $\{P_{t,k}\}$ converges when $k \to \infty$ to a certain matrix P_t

$$P_t = \begin{pmatrix} 1-p_t^1 & q_t^1 & 0 & 0 \\ p_t^1 & 1-q_t^1 & 0 & 0 \\ 0 & 0 & 1-p_t^2 & q_t^2 \\ 0 & 0 & p_t^2 & 1-q_t^2 \end{pmatrix},$$

with the parameters p_t^1, p_t^2, q_t^1 and q_t^2 belonging to interval (0,1).

Following the aggregation procedure in Section 2, we have that the vectors v_t^1 and v_t^2 that define the equilibrium proportions of migration in each interval I_t are given by

$$v_t^1 \begin{pmatrix} \frac{q_t^1}{p_t^1+q_t^1} \\ \frac{p_t^1}{p_t^1+q_t^1} \end{pmatrix}; \; v_t^2 \begin{pmatrix} \frac{q_t^2}{p_t^2+q_t^2} \\ \frac{p_t^2}{p_t^2+q_t^2} \end{pmatrix}$$

We define the global variables y_t^i (i = 1,2) as the total population with age i, i.e.,

$$y_t^1 := x_t^{1,1} + x_t^{1,2}; \; y_t^2 := x_t^{2,1} + x_t^{2,2}$$

and then the aggregated system reads

$$\begin{pmatrix} y_{t+1}^1 \\ y_{t+1}^2 \end{pmatrix} = \overline{M}_t \begin{pmatrix} y_t^1 \\ y_t^2 \end{pmatrix} \tag{20}$$

where

$$\overline{M}_t = \begin{pmatrix} \frac{f_t^{1,1} q_t^1 + f_t^{1,2} p_t^1}{p_t^1+q_t^1} & \frac{f_t^{2,1} q_t^2 + f_t^{2,2} p_t^2}{p_t^2+q_t^2} \\ \frac{s_t^{1,1} q_t^1 + s_t^{1,2} p_t^1}{p_t^1+q_t^1} & \frac{s_t^{2,1} q_t^2 + s_t^{2,2} p_t^2}{p_t^2+q_t^2} \end{pmatrix}$$

Let us now illustrate how we can study the weak ergodicity of system (19) through the study of system (20). For the sake of simplicity of exposition, let us consider a model with two possible environmental conditions that we denote 1 and 2. In accordance with this consideration let A^i be the projection matrix which defines demography in environment i and B_l^i; $l = 1,2,..$, the sequence of matrices which characterizes migration in environment i (i = 1,2). These matrices have the form

$$A^i = \begin{pmatrix} f^{1,1}(i) & 0 & f^{2,1}(i) & 0 \\ 0 & f^{1,2}(i) & 0 & f^{2,2}(i) \\ s^{1,1}(i) & 0 & s^{2,1}(i) & 0 \\ 0 & s^{1,2}(i) & 0 & s^{2,2}(i) \end{pmatrix}$$

$$B_l^i = \begin{pmatrix} 1-p_l^1(i) & q_l^1(i) & 0 & 0 \\ p_l^1(i) & 1-q_l^1(i) & 0 & 0 \\ 0 & 0 & 1-p_l^2(i) & q_l^2(i) \\ 0 & 0 & p_l^2(i) & 1-q_l^2(i) \end{pmatrix},$$

where the meaning of the vital rates is clear from (17) and (18).

Therefore, the matrices $M_t P_{t,k} \cdots P_{t,1}$ of vital rates for our multiregional system (19) take values in the set $\{E^1, E^2\}$, where

$$E^1 = A^1 B_k^1 \cdots B_1^1;\ E^2 = A^2 B_k^2 \cdots B_1^1$$

In accordance with the discussion above, assume that the sequences $\{B_l^1\}$ and $\{B_l^2\}$ converge to matrices B_l^1 and B_l^2 given by

$$B^i = \begin{pmatrix} 1-p^1(i) & q^1(i) & 0 & 0 \\ p^1(i) & 1-q^1(i) & 0 & 0 \\ 0 & 0 & 1-p^2(i) & q^2(i) \\ 0 & 0 & p^2(i) & 1-q^2(i) \end{pmatrix};\ i = 1, 2.$$

with the parameters $p^1(i)$, $p^2(i)$, $q^1(i)$ and $q^2(i)$ belonging to interval (0,1). Then, the matrix $\overline{E}^i$ associated with the aggregated system in environment i is

$$\overline{E}^i = \begin{pmatrix} \frac{f^{1,1}(i)q^1(i)+f^{1,2}(i)p^1(i)}{p^1(i)+q^1(i)} & \frac{f^{2,1}(i)q^2(i)+f^{2,2}(i)p^2(i)}{p^2(i)+q^2(i)} \\ \frac{s^{1,1}(i)q^1(i)+s^{1,2}(i)p^1(i)}{p^1(i)+q^1(i)} & \frac{s^{2,1}(i)q^2(i)+s^{2,2}(i)p^2(i)}{p^2(i)+q^2(i)} \end{pmatrix};\ i = 1, 2.$$

so matrices $\overline{M}_t$ in (20) belong to the set $\{\overline{E}^1, \overline{E}^2\}$.

If the conditions of Proposition 8 hold, then for any pattern of environmental variation, i.e., for any specific choice of environment in each interval I_t, the multiregional system (19) is weakly ergodic. In other words, any two different populations subjected to the same sequence of environmental conditions will asymptotically have a common structure.

According to Section 6, since the number of different environmental conditions is finite, in order to guarantee that the hypothesis of Proposition 8 is met, we only need to pay attention to the incidence matrices of A_1 and A_2. We consider, for example, the case

$$i(A^1) = \begin{pmatrix} + & 0 & + & 0 \\ 0 & 0 & 0 & + \\ + & 0 & + & 0 \\ 0 & + & 0 & 0 \end{pmatrix};\ i(A^2) = \begin{pmatrix} 0 & 0 & + & 0 \\ 0 & 0 & 0 & + \\ 0 & 0 & + & 0 \\ 0 & + & 0 & 0 \end{pmatrix}$$

where + denotes a non-zero element. Then, Lemma 2 guarantees that the incidence matrices of $\overline{E}^1$ and $\overline{E}^2$ are

$$i(\overline{E}^1) = \begin{pmatrix} + & + \\ + & + \end{pmatrix};\ i(\overline{E}^2) = \begin{pmatrix} 0 & + \\ + & + \end{pmatrix}$$

and therefore the aggregated system verifies condition (E) and is weakly ergodic. Since matrices $i(A^1)$ and $i(A^2)$ meet conditions *H6* and *H7*, we can assure that the multiregional model (19) is weakly ergodic.

In order to illustrate this result, we will consider a deterministic sequence of environments in which there is not a particular pattern of variation. More in particular, we will consider a temporal variation without any cyclic pattern nor a tendency to equilibrium. Notice that in any of these two cases the problem becomes trivial and weak ergodicity follows almost directly (Section 4). In order to meet our requirements, we generate a sequence of environments using the equation

$$\phi_{t+1} = 4\phi_t\,(1 - \phi_t). \tag{21}$$

The projection matrix for the original system corresponding to time t, was generated according to the following criteria:

$$E_t = \begin{cases} E^1 \text{ if } \phi_t \in (0, 0.5) \\ E^2 \text{ if } \phi_t \in [0.5, 1) \end{cases}, \; t = 1, 2, ...$$

Given an initial value $\phi_0 \in (0,1)$, equation (21) yields a chaotic sequence of numbers in the real interval (0,1) and, therefore, the pattern of environmental variation satisfies the above conditions, i.e., it does not exhibit any cyclic pattern nor a tendency to equilibrium.

In our simulation we have assigned an initial value $\phi_0 = 0.1$. In addition we have given acceptable numerical values to the vital rates associated with each environment:

$$A^1 = \begin{pmatrix} 0.2 & 0 & 1.5 & 0 \\ 0 & 0 & 0 & 0.5 \\ 0.9 & 0 & 0.8 & 0 \\ 0 & 0.6 & 0 & 0 \end{pmatrix}; \; A^2 = \begin{pmatrix} 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 2 \\ 0 & 0 & 0.3 & 0 \\ 0 & 0.4 & 0 & 0 \end{pmatrix}$$

$$B_l^1 = \begin{pmatrix} 0.5 & 0.5 & 0 & 0 \\ 0.5 & 0.5 & 0 & 0 \\ 0 & 0 & 0.6 & 0.9 - \frac{1}{2^l} \\ 0 & 0 & 0.4 & 0.1 + \frac{1}{2^l} \end{pmatrix}; \; B_l^2 = \begin{pmatrix} 0.4 & 0.3 & 0 & 0 \\ 0.6 & 0.7 & 0 & 0 \\ 0 & 0 & 0.4 & 0.9 - \frac{1}{2^l} \\ 0 & 0 & 0.6 & 0.1 + \frac{1}{2^l} \end{pmatrix}; \; l = 1, 2, ..., k.$$

With these vital rates, the matrices associated with each environment in the aggregated system are

$$\overline{E}^1 = \begin{pmatrix} 0.1 & 1.1923 \\ 0.75 & 0.5538 \end{pmatrix}; \; \overline{E}^2 = \begin{pmatrix} 0 & 1.4 \\ 0.1333 & 0.12 \end{pmatrix}$$

Proposition 3 claims that the population vector at a given time t can be approximated through that of the aggregated system. Figure 1 shows the evolution of both systems, for $k = 6$. Note that the discrepancy between the approximations and the real values obtained on the original system are insignificant for $t \leq 60$.

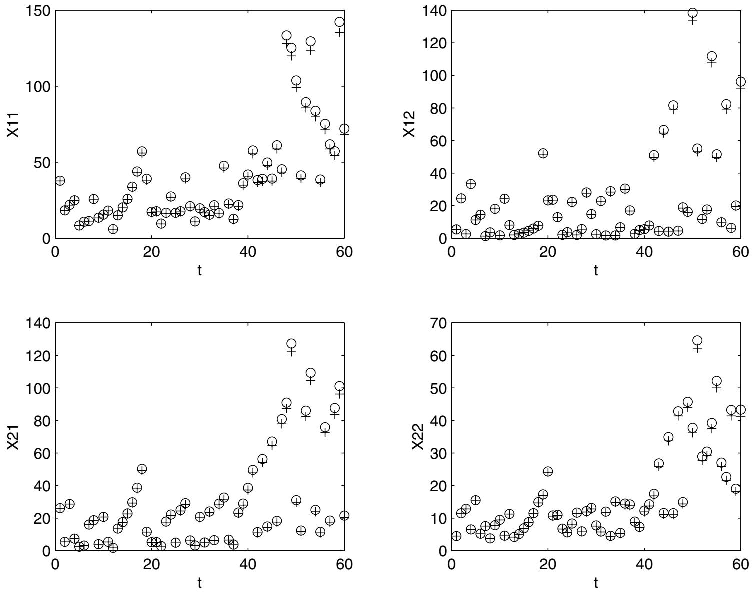

Figure 1. Evolution of the solutions of the original and the aggregated systems as t grows. The symbols employed are '+' for the population numbers given by the aggregated system and 'o' for those given by the original system with $k = 6$.

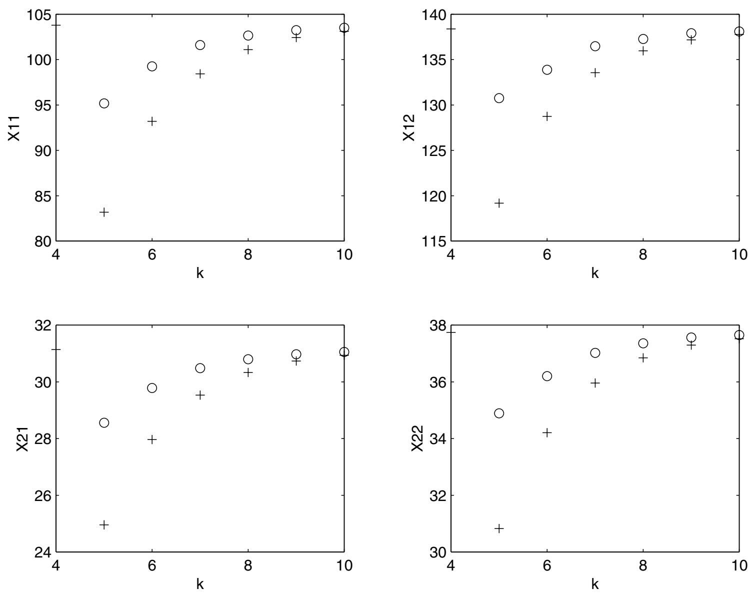

Figure 2. Convergence of the population vectors provided by the aggregated (o) and the original (+) systems when k grows.

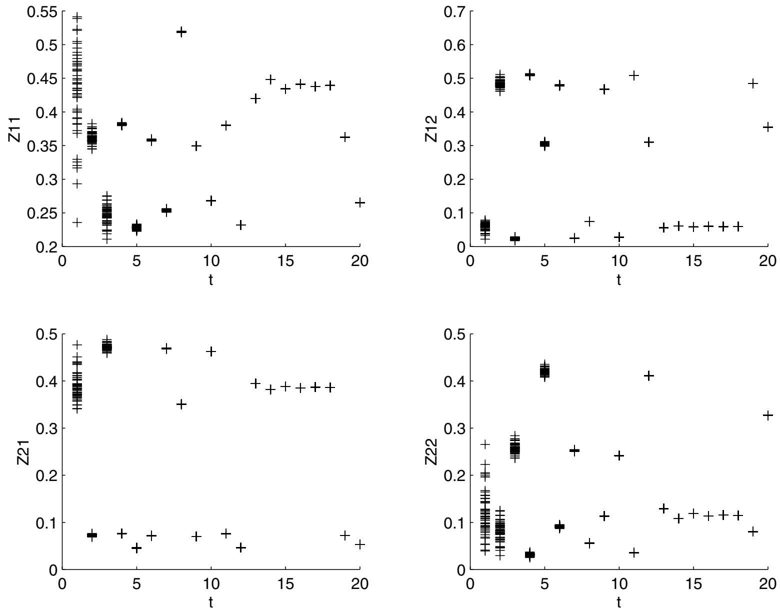

Figure 3. Convergence of the population structure for different initial conditions. *Zij* represents the proportion of *i*-aged individuals living in patch *j*. This behavior is due to the weak ergodicity of the original system, predicted through the analysis of the aggregated one.

Figure 2 compares the population vector at time $t = 50$ for values of k growing from 4 to 10 and shows how the approximation given by the aggregated system for the population vector at a fixed time t, is sharper the higher k is. As one can see the differences between the vectors obtained through both the original and the aggregated systems become negligible for k close to 10.

In order to show the weak ergodicity in the original system, we have run the model for fifty different initial conditions and for the first twenty time steps. Figure 3 shows the structure of the population for all those initial conditions. We can see that, for small values of t, there are differences in the population structures corresponding to different initial conditions, but for higher values of t population structure becomes independent of initial conditions.

8. CONCLUSION

Aggregation methods allow one to reduce, under certain conditions, the dimension of a system of difference equations involving two time scales. In population models (Sanz and Bravo de la Parra, 1998, 2001), these scales correspond to two different processes affecting the evolution of the population.

So far aggregation techniques had been applied to autonomous and non-autonomous systems under the simplifying assumption that the vital rates associated with the fast dynamics remain constant in each time interval of the slow dynamics. This work, together with Blasco *et al*. (2001), is a generalization of those methods in the sense that we allow the fast process to vary with its own time scale. Blasco *et al*.

(2001) deals with the autonomous case while this work explores the case in which the environment varies with time.

We aggregate a very general system with two time scales and show that we can obtain good approximations to the population vector of the original system through the knowledge of that of the reduced model. Moreover, the capacity of the original system to become independent of initial conditions can be studied in terms of the aggregated system.

As a future contribution, it would be interesting to study whether this work can be generalized by taking into account more general behaviors in the fast process; in this way, one might be able to obtain an aggregated system even if the fast process does not reach an equilibrium in each projection interval of the model and only shows some kind of long term independence with respect to initial conditions. Analogously, the authors would like to generalize the aggregation procedure to cover the case of stochastically varying environments, continuing the work of Sanz and Bravo de la Parra (2000).

APPENDIX

Proof of Proposition 5

In the first place we will prove that the auxiliary System (7) is strongly ergodic. We know that the sequence $\{V_t\}$ converges to a certain matrix V. Then it follows that $\overline{P}_t \equiv V_t U^T \to \overline{P} \equiv VU^T$ and, so, we have $M_t\overline{P}_t \to M\overline{P}$.

1) Let us prove that $M\overline{P}$ is primitive. Using Theorem 4.1. in Blasco *et al*. (2001) the non-zero eigenvalues of $M\overline{P} \equiv MVU^T$ including multiplicities, are those of $\overline{M}$. Therefore, since $\overline{M}$ is primitive by hypothesis, λ is simple and the strictly dominant eigenvalue for $M\overline{P}$. Moreover, from the same theorem we obtain that MVr and Ul are dominant eigenvectors for $M\overline{P}$. Since M is row allowable, U and V are allowable and r and l are positive, it follows that MVr and Ul are both positive. Now we apply the following theorem (Berman and Plemmons, 1979, page 42); A non-negative square matrix A is irreducible if and only if the spectral radius of A is simple and is associated with positive right and left eigenvectors. Therefore, matrix $M\overline{P}$ is irreducible and moreover, since λ is strictly dominant, it is primitive.

2) Now, let us prove that $M_t\overline{P}_t$ is column-allowable for all t. Let t be fixed and recall that

$$\overline{P}_t = diag(\overline{P}_t^1, \overline{P}_t^2, ..., \overline{P}_t^q)$$

where the diagonal blocks $\overline{P}_t^i$ verify $\overline{P}_t^1 = v_t^1 \mathbf{1}^T > 0$. Now, matrix $M_t\overline{P}_t$ has the form

$$M_t\overline{P}_t = \begin{pmatrix} M_t^{11}\overline{P}_t^1 & M_t^{12}\overline{P}_t^2 & \cdots & M_t^{1q}\overline{P}_t^q \\ M_t^{21}\overline{P}_t^1 & M_t^{22}\overline{P}_t^2 & \cdots & M_t^{2q}\overline{P}_t^q \\ \vdots & \vdots & \ddots & \vdots \\ M_t^{q1}\overline{P}_t^1 & M_t^{q2}\overline{P}_t^2 & \cdots & M_t^{qq}\overline{P}_t^q \end{pmatrix}$$

Hypothesis $H2$ together with Lemma 2 implies that, for each $j = 1,...,q$ and each t, $i = i(j,t)$ exists such that $M_t^{ij} \neq 0$ and, since the $\overline{P}_t^i$ are positive matrices, then $M_t^{ij}\overline{P}_t^j$ has at least a positive row, which proves that $M_t\overline{P}_t$ is column-allowable.

Therefore Theorem 4 guarantees that the auxiliary system is strongly ergodic: the asymptotic stable structure of the population is

$$\lim_{t\to\infty}\frac{X_t}{\| X_t \|} = \frac{MVr}{\| MVr \|},$$

meanwhile the asymptotic growth rate of the total population size is:

$$\lim_{t\to\infty}\frac{\| X_{t+1} \|}{\| X_t \|} = \lambda .$$

Let us now prove that the original system satisfies the hypotheses of Theorem 4. For each k we have

$$M_t P_{t,k} \cdots P_{t,1} \underset{t\to\infty}{\to} MP_{\infty,k} \cdots P_{\infty,1} .$$

Then we need to prove that the matrices $M_t P_{t,k} \cdots P_{t,1}$ are column-allowable for each t, and that matrix $MP_k \cdots P_1$ is primitive.

If a sequence of matrices $\{A_k\}$ converges to a matrix A, then for large enough values of k, the positive entries of A_k will be, at least, those of A. Hence, if A is column-allowable, for large enough values of k, A_k will be too. The same can be said regarding irreducibility and primitivity that cause these properties to depend exclusively on the pattern of positive entries of the matrix (*).

We know that, for all t, $M_t P_{t,k} \cdots P_{t,1} \underset{k\to\infty}{\to} M_t\overline{P}_t$ and that matrices $M_t\overline{P}_t$ are column-allowable and so it follows that matrices $M_t P_{t,k} \cdots P_{t,1}$ are column-allowable for all t.

Due to the uniform convergence of the products $M_t P_{t,k} \cdots P_{t,1}$ given by Assumption $H4$, we have that:

$$\lim_{k\to\infty} MP_{\infty,k} \cdots P_{\infty,1} = \lim_{k\to\infty}\lim_{t\to\infty} M_t P_{t,k} \cdots P_{t,1} =$$
$$\lim_{t\to\infty}\lim_{k\to\infty} M_t P_{t,k} \cdots P_{t,1} = \lim_{t\to\infty} M_t\overline{P}_t = M\overline{P}.$$

Above we saw that matrix $M\overline{P}$ is primitive. Using (*) we have that $MP_{\infty,k} \cdots P_{\infty,1}$ is primitive, so we conclude that the original system satisfies the hypotheses of Theorem 4 and is strongly ergodic.

Finally, let λ_k be the dominant eigenvalue of $MP_{\infty,k} \cdots P_{\infty,1}$ and r_k its corresponding positive right eigenvector such that $\| r_k \|_1 = 1$. Due to the continuity of the eigenvalues and eigenvectors on the entries of the matrix we have

$$\lim_{k\to\infty}\lambda_k = \lambda; \quad \lim_{k\to\infty} r_k = \frac{MVr}{\| MVr \|}$$

and so the desired result follows.

Proof of Theorem 7

Definition 6 corresponds to Seneta's definition of a weakly ergodic product (Seneta, 1981) in the case where the first matrix in the product is A_0. As shown in this reference, a characterization of weak ergodicity can be stated in terms of the contraction coefficient in the following way: Let A_t be a sequence of allowable matrices (which in our case for the A_t are primitive). System (14) is weakly ergodic if and only if $\lim_{t\to\infty} \tau_B(A_t A_{t-1} \cdots A_0) = 0$.

Since matrix B is primitive there exists a positive integer h such that $B^h > 0$. Therefore, from condition (E) we have $0 < B^h \leq A_{p+h-1}A_{p+h-2}\cdots A_p \leq C^h$ for all p. Let $a = \min B^h > 0$ and $b = \max C^h$. Therefore we have $0 < a\mathbf{1}\mathbf{1}^T \leq A_{p+h-1}A_{p+h-2}\cdots A_p \leq b\mathbf{1}\mathbf{1}^T$ (*). From (Seneta, 1981, pp. 84) we have that, for any positive matrix $A = [a_{ij}] > 0$, $\tau_B(A) = \frac{1-\sqrt{\phi(A)}}{1+\sqrt{\phi(A)}}$ where $\phi(A) = \min_{i,j,k,l} \frac{a_{ik}a_{jl}}{a_{jk}a_{il}}$. Therefore we have that, for all p, $\phi\ (A_{p+h-1}A_{p+h-2}\cdots A_p) \geq (a/b)^2$. So, for all p, we obtain $\tau_B(A_{p+h-1}A_{p+h-2}\cdots A_p) \leq 1-(a/b) = \delta$, say. Moreover, decomposing the previous products into factors with h matrices in each, using $\tau_B(AB) \leq \tau_B(A)\tau_B(B)$ for any two matrices, and taking into account that $\tau_B(A) \leq 1$, we obtain $0 \leq \lim_{t\to\infty} \tau_B(A_t A_{t-1} \ldots A_0) \leq \lim_{t\to\infty} \delta^{\left[\frac{t}{h}\right]} = 0$ ([*] denotes integer part) that we wanted to show.

Proof of Proposition 8

The proof will follow the following scheme. We will prove that given condition (E) on the aggregated system and *H7*, there exists an integer m such that any product of m consecutive matrices in the original system is positive. In addition to using *H6* we will show that the non-zero elements of the matrices of the original system are bounded away from zero and infinity. Then the result will follow using the same reasoning as that of Theorem 7.

For notational convenience let us denote $P_t(k) = P_{t,k}\ldots P_{t,1}$.

It is straightforward to check the validity of the following result: if $A \in \mathbf{R}^{t\times r}$ and $B \in \mathbf{R}^{r\times l}$ are non-negative and $AB \neq 0$, then $\min^+(AB) \geq \min^+(A)\min^+(B)$ and $\max(\mathrm{AB}) \leq r\cdot\max(A)\max(B)$. So, if matrices A and B belong to a set $\mathbf{T}$ for which there exist positive constants a and b such that $\min^+(A) \geq a$ and $\max(A) \leq b$ for $A \in \mathbf{T}$ then $\min^+(AB) \geq a^2$ and $\max(A) \leq rb^2$, for all $A,B \in \mathbf{T}$. Then, as a consequence of *H6* we have, for fixed k, the non-zero elements of matrices $M_t P_{t,k}\ldots P_{t,1}$ are bounded away from zero and infinity, i.e., there exist positive constants α and β such that for all t, $\min^+(M_t P_t(k)) \geq \alpha$ and $\max(M_t P_t(k)) \leq \beta(1)$.

Now, let us denote, for each $p \geq 0$ and each $t > p$ the following matrix products:

$$\Pi_{t,p}(k) = M_{t-1}P_{t-1}(k)\ldots M_{p+1}P_{p+1}(k)M_p P_p(k);$$

$$\Pi'_{t,p} = M_{t-1}\overline{P}_{t-1}\ldots M_{p+1}\overline{P}_{p+1}M_p\overline{P}_p;$$

$$\overline{\Pi}_{t,p} = \overline{M}_{t-1}\ldots\overline{M}_{p+1}\overline{M}_{p.}$$

Note that the products $\overline{\Pi}_{t,p}$ and $\Pi'_{t,p}$ can be related by $\Pi'_{t+1,p} = M_t V_t \overline{\Pi}_{t,p} U^T$ (**). Indeed,

$$M_t V_t \overline{\Pi}_{t,p} U^T = M_t V_t \overline{M}_{t-1} \cdots \overline{M}_p U^T = M_t V_t U^T M_{t-1} V_{t-1} \cdots U^T M_p V_p U^T$$
$$= M_t \overline{P}_t M_{t-1} \overline{P}_{t-1} \cdots M_t \overline{P}_t = \Pi'_{t+1,p},$$

where we have used $\overline{P}_t = V_t U^T$.

Since matrix B is primitive there exists a positive integer h such that $B^h > 0$. Therefore, from condition (E) on the aggregated system we have, for all p, that the product $\overline{\Pi}_{p+h,p}$ is positive. Now, we will prove that, for all p, $\Pi_{p+h+1,p}(k) > 0$ for k big enough (2). Indeed, from (**) above, we have $\Pi'_{p+t+1,p} = M_{p+t} V_{p+t} \overline{\Pi}_{p+t,p} U^T$. Since the M_t and the V_t are row allowable, so is their product. Therefore $M_{p+t} V_{p+t} \overline{\Pi}_{p+t,p} > 0$ and since U^T is allowable then $\Pi'_{p+t+1,p} > 0$. The desired result (2) now follows taking into account Lemma 9.

Since $\Pi_{p+h+1,p}(k) > 0$ for all p and for k big enough, we obtain, setting $m = h + 1$ and using the bounds (1), that for fixed k, $\alpha^m \mathbf{1}\mathbf{1}^T \le \Pi_{p+m,p}(k) \le N^{m-1} \beta^m \mathbf{1}\mathbf{1}^T$, and therefore we are in the same situation as in (*) in the proof of Theorem 7, with $a = \alpha^m$ and $b = N^{m-1}\beta^m$. Using the same reasoning as we did there we obtain $\lim_{t\to\infty} \tau(\Pi_{t,0}(k)) = 0$ and therefore the original system is weakly ergodic.

Lemma 9

There exists a positive integer k_0 such that for all $k \ge k_0$ we have $\overline{P}_t \sim P_{t,k} \cdots P_{t,1}$ (and therefore $M_t \overline{P}_t \sim M_t P_{t,k} \cdots P_{t,1}$) for all t.

Proof

Let i be fixed. From Proposition 1, we have $\lim_{k\to\infty} P^i_{t,k} \cdots P^i_{t,1} = v^i_t \mathbf{1}^T = \overline{P}^i_t > 0$ and, therefore, for k greater than a certain $k_0(i)$ the product $P^i_{t,k} \cdots P^i_{t,1}$ is positive. Since matrix $\overline{P}^i = v^i \mathbf{1}^T$ is also positive then the result follows for $k \ge \max\{k_0(1),...,k_0(q)\}$. ■

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REFERENCES

Berman, A. and R.J. Plemmons (1979). Nonnegative matrices in the mathematical sciences. Academic Press, San Diego.

Blasco, A., L. Sanz, P. Auger and R. Bravo de la Parra (2001). Linear Discrete Population Models with Two Time Scales in Fast Changing Environments I: Autonomous Case. Acta Biotheoretica 49: 261-276.

Caswell, H. (2001). Matrix population models. Sinauer Associates Inc., Sunderland, Massachusetts.

Charlesworth, B. (1994). Evolution in age-structured populations. Cambridge University Press, Cambridge. 306pp.

Cohen, J.E. (1979a). Ergodic theorems in demography. Bulletin of the American Mathematical Society 1: 275-295.

Cohen, J.E. (1979b). Contractive inhomogeneous products of non-negative matrices. Mathematical Proceedings of the Cambridge Philosophical Society 86: 351-364.

Golubitsky, M., E.B. Keeler and M. Rothschild (1975). Convergence of the age structure: applications of the projective metric. Theoretical Population Biology 7: 84-93.

Hajnal, J. (1976). On products of non-negative matrices. Mathematical Proceedings of the Cambridge Philosophical Society 79: 521-530.

Kim, Y.J. and Z. M. Sykes (1976). An experimental study of weak ergodicity in human populations. Theoretical Population Biology 10: 150-172.

López, A. (1961). Problems in Stable Population Theory. Princeton University Press, Princeton, NJ.

Quinn, T.J. (1981). The use of Leslie type age-structured models for the pacific halibut population. Quantitative Population Dynamics, D.G. Chapman and F. Galluci (eds), 217-242.

Sánchez, E., R. Bravo and P. Auger (1995). Linear discrete models with different time scales. Acta Biotheoretica 43: 465-479.

Sanz, L. and R. Bravo de la Parra (1998). Variables aggregation in time varying discrete systems. Acta Biotheoretica 46: 273-297.

Sanz, L. and R. Bravo de la Parra (1999). Variables aggregation in a time discrete linear model. Mathematical Biosciences 157: 111-146.

Sanz, L. and R. Bravo de la Parra (2000). Time scales in stochastic multiregional models. Nonlinear Analysis: Real World Applications 1: 89-122.

Sanz, L. and R. Bravo de la Parra (2001). Time scales in a non autonomous linear discrete model. Mathematical Models and Methods in Applied Sciences (accepted).

Seneta, E. (1981). Non-negative matrices and Markov chains. Springer Verlag, New York. 279pp.

Skellam, J.G. (1967). Seasonal periodicity in theoretical population ecology. Proceedings of the 5th Berkeley Symposium in Mathematical Statistics and Probability Vol. 4: 179-205, Univ. of California Press, Berkeley.