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## Reduction of slow–fast discrete models coupling migration and demography

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## ABSTRACT

This work deals with a general class of two-time scales discrete nonlinear dynamical systems which are susceptible of being studied by means of a reduced system that is obtained using the so-called aggregation of variables method. This reduction process is applied to several models of population dynamics driven by demographic and migratory processes which take place at two different time scales: slow and fast. An analysis of these models exchanging the role of the slow and fast dynamics is provided: when a Leslie type demography is faster than migrations, a multi-attractor scenario appears for the reduced dynamics; on the other hand, when the migratory process is faster than demography, the reduction process gives rise to new interpretations of well known discrete models, including some Allee effect scenarios.

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## 1. Introduction

Ecological models always entail a decision on the level of detail to be included in them, and this decision should be taken on the basis of optimizing the benefit of the study. Any model is a compromise between generality and simplicity on the one hand and biological realism on the other. The more biological details are included in specifying a model the more complicated and specific it becomes.

Nature offers many examples of systems where several processes act at different time scales. It is then usual to consider those events occurring at the fast scale as being instantaneous with respect to the slower ones. This sort of decoupling implies a reduction of the number of variables or parameters needed to describe the evolution of the system. A subsequent issue is to determine conditions for these reductions to give good approximations of the real results. An example of this general framework are the so-called *aggregation methods* which study the relationship between a large class of two-time scales complex systems and their corresponding *aggregated* or reduced ones. The aim of aggregation methods is twofold. On the one hand they construct

the reduced systems that summarize the dynamics of the complex ones, thus simplifying their analytical study, and on the other hand, looking at the relationship in the opposite sense, the complex systems serve as explanations of the simple form of the aggregated ones. A review on these methods in different mathematical settings, with updated bibliography, can be found in Auger and Bravo de la Parra (2000) and Auger et al. (2008).

In this work we will apply the aggregation of variables method in the setting of discrete dynamical systems. In the construction of a discrete model with two-time scales it is essential to decide if the time unit should be associated to the slow process or to the fast one. Bravo de la Parra et al. (1995) and Bravo de la Parra et al. (1997) study models in which the time unit of the dynamical system is chosen to be that of the fast dynamics. Nevertheless, this choice is not always possible, because the action of the slow process during a fast time unit may not be describable. But if the system is expressed in the slow time unit, it is always possible to describe the action of the fast process during it by repeating a large enough number of times its action during a slow unit. From this point of view, it is interesting to extend to nonlinear cases previous work, made by some of us, that develop the methods of aggregation of variables for linear discrete systems expressed in the slow time unit (see Sanchez et al., 1995; Sanz and Bravo de la Parra, 1999).

A first attempt to do this is Bravo de la Parra et al. (1999), where the slow dynamics is assumed to be linear. An extension to a general class of nonlinear discrete models has been recently

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made by some of the authors and can be found in Sanz et al. (2008). In this work, a very general discrete system including two different processes acting at different time scales is proposed. The time unit is the one corresponding to the slow dynamics and the effect of the fast dynamics is represented assuming that the slow time unit is divided into a large number of fast time units and so that it acts a large number of times during one single slow time unit. Then some assumptions, generalizing those required in previous works, are proposed which allow the construction of a reduced model associated to the original one. Several results relating the solutions to both systems have been established: it is possible to study the existence, stability and basins of attraction of steady states and periodic solutions to the original system performing the study for the corresponding aggregated system.

The hypotheses of the general results of Sanz et al. (2008) are not easy to prove in particular cases. In Nguyen Huu et al. (2008) this is done for a particular multi-patch host–parasitoid model where migration, which is fast in comparison to demography, is considered density independent for hosts and dependent on local host population density for parasitoids. In this work we present a general class of two-time scales nonlinear discrete models as a particular case of the more abstract setting described in Sanz et al. (2008). Then we construct the corresponding reduced models and prove that the approximation results established in Sanz et al. (2008) are valid. The reduction process is applied to several models of population dynamics driven by nonlinear demographic and migration processes which take place at two different time scales, slow and fast. We provide an analysis of these models exchanging the role of the slow and fast dynamics: when a Leslie type demography is faster than migrations, a multi-attractor scenario appears for the aggregated dynamics; on the other hand, when the migratory process is faster than demography, by introducing different migration schemes we derive some well known discrete models whose analysis gives rise to some Allee effect scenarios.

The organization of the paper is as follows: in Section 2 we specify the mathematical formulation of a general class of two-time scales discrete nonlinear dynamical systems to which a reduction process can be applied, yielding the so-called *aggregated model*, whose dynamical features approximate those of the original more complex model. Section 3 is devoted to the application of these mathematical results to several specific models of population dynamics. Some conclusions are given in Section 4. To facilitate the reading, technical mathematical proofs of the results established in Section 2 are deferred to a final Appendix A.

## 2. Application of the aggregation of variables method to the reduction of a general nonlinear discrete dynamical system

The main goal of this section is to apply the aggregation of variables method to the reduction of a general class of nonlinear discrete models with two-time scales, which fit in the framework of an original formulation made by some of the authors and developed in detail in Sanz et al. (2008). To facilitate the reading, we will start describing the model and its main mathematical features, as done in Sanz et al. (2008).

First of all, let us present the so-called *complete* or *general system* to which the aggregation of variables method will be applied.

The model evolves in discrete time and is driven by two processes with different time scales, *slow* and *fast*. Such processes are defined, respectively, by two mappings

$$S, F : \Omega_N \longrightarrow \Omega_N, \quad S, F \in C^1(\Omega_N),$$

where  $\Omega_N \subset \mathbb{R}^N$  is a non-empty open set.

We choose as time step of the model that corresponding to the slow dynamics. In order to approximate the effect of the fast process over a time interval much bigger than its own, we assume that during this time step the fast process acts  $k$  times before the slow process acts, where  $k$  is a positive integer that in applications will take a big value.

Therefore, denoting by  $X_{k,n} \in \mathbb{R}^N$  the vector of state variables at time  $n$ , the *complete* or *general system* is defined by

$$X_{k,n+1} = S(F^k(X_{k,n})) =: H_k(X_{k,n}), \tag{1}$$

where  $F^k$  denotes the  $k$ -fold composition of  $F$  with itself.

In order to reduce system (1), we have to impose some conditions on the fast process, which are specified in the following hypothesis:

**Hypothesis 1.** For each initial condition  $X \in \Omega_N$ , the fast dynamics tends to an equilibrium. That is, there exists a mapping  $\bar{F} : \Omega_N \rightarrow \Omega_N$ ,  $\bar{F} \in C^1(\Omega_N)$ , such that

$$\forall X \in \Omega_N, \quad \lim_{k \rightarrow \infty} F^k(X) = \bar{F}(X).$$

Moreover, there exist a nonempty open set  $\Omega_q \subset \mathbb{R}^q$  with  $q < N$ , and two mappings

$$G : \Omega_N \longrightarrow \Omega_q, \quad E : \Omega_q \longrightarrow \Omega_N, \quad E \in C^1(\Omega_q)$$

such that  $\bar{F}$  can be expressed as  $\bar{F} = E \circ G$ .

Let us define a new set of variables, called *global variables*, by

$$Y_n := G(X_n).$$

The *reduced* or *aggregated system* which approximates system (1) is given by

$$Y_{n+1} = G \circ S \circ E(Y_n) =: \bar{H}(Y_n). \tag{2}$$

Note that through this procedure we have constructed an approximation that allows us to reduce a system with  $N$  variables to a new system with  $q$  variables. In most practical applications,  $q$  will be much smaller than  $N$ .

To establish a relationship between the solutions to systems (1) and (2), the following assumption is crucial:

**Hypothesis 2.** The mappings  $F$  and  $\bar{F}$  satisfy that

$$\lim_{k \rightarrow \infty} F^k = \bar{F}, \quad \lim_{k \rightarrow \infty} DF^k = D\bar{F}$$

uniformly on any compact set  $K \subset \Omega_N$ .

As usual, the notation  $DF$  represents the differential of  $F$ .

Then, the following theorem, whose details can be found in Sanz et al. (2008), guarantees that the existence of an equilibrium point  $Y^*$  for the aggregated system implies, for large enough  $k$ , the existence of an equilibrium  $X_k^*$  for the original system, which can be approximated in terms of  $Y^*$ . Moreover, in the hyperbolic case, the stability of  $Y^*$  is equivalent to the stability of  $X_k^*$  and in the asymptotically stable (AS) case, the basin of attraction of  $X_k^*$  can be approximated in terms of the basin of attraction of  $Y^*$ .

**Theorem 1.** Under Hypotheses 1 and 2, let  $Y^* \in \mathbb{R}^q$  be a hyperbolic equilibrium point of system (2). Then, there exists an integer  $k_0 \geq 0$  such that for all  $k \geq k_0$  system (1) has an equilibrium point  $X_k^*$  which is hyperbolic and satisfies

$$\lim_{k \rightarrow \infty} X_k^* = X^*, \quad X^* := S \circ E(Y^*).$$

Moreover, the following holds:

- (i)  $X_k^*$  is AS (resp. unstable) if and only if  $Y^*$  is AS (resp. unstable).
- (ii) Let  $Y^*$  be AS and let  $X_0 \in \Omega_N$  be such that  $Y_0 := G(X_0)$  satisfies that  $\lim_{n \rightarrow \infty} \bar{H}^n(Y_0) = Y^*$ . Then, for all  $k \geq k_0$ ,  $\lim_{n \rightarrow \infty} H_k^n(X_0) = X^*$ .

Although it is not stated in Theorem 1, these results are also valid for  $m$ -periodic points (see Sanz et al., 2008).

Let us recall that an equilibrium point  $X^*$  of a discrete dynamical system  $X_{n+1} = T(X_n)$  is hyperbolic if none of the eigenvalues of the differential operator  $DT(X^*)$  has modulus 1. If all the eigenvalues of  $DT(X^*)$  have modulus strictly less than 1, then  $X^*$  is AS and the set of initial conditions whose corresponding solutions tend to  $X^*$  is called the basin of attraction. If any of the eigenvalues of  $DT(X^*)$  have modulus larger than 1, then  $X^*$  is unstable. See Robinson (1995) for the general theory.

### 2.1. Fast dynamics depending on global variables

As we mentioned in the Introduction, for a particular two-time scales discrete model it is difficult to prove that Hypothesis 2 in Theorem 1 is met. Here we present a class of models for which this is proved and so Theorem 1 applies.

Let us suppose a population divided into groups, and each of these groups divided into several subgroups. We can think, for instance, of an age-structured population occupying a multi-patch environment. In this case, the population can be considered divided into groups which are the age classes, and each group divided into subgroups which are the individuals inhabiting each of the different patches.

The state at time  $n$  of a population distributed into  $q$  groups is represented by a vector  $X_n := (x_n^1, \dots, x_n^q)^T \in \mathbb{R}_+^N$ , where each vector  $x_n^i := (x_n^{i1}, \dots, x_n^{iN^i})^T \in \mathbb{R}_+^{N^i}$ ,  $i = 1, \dots, q$ , represents the state of the  $i$ -group which in turn is divided into  $N^i$  subgroups with  $N = N^1 + \dots + N^q$ .

Following Sanchez et al. (1995), we will suppose that for each group  $i = 1, \dots, q$ , the fast dynamics is internal, conservative of the total number of individuals and with an AS distribution among the groups. These assumptions are met in the particular case of representing the fast dynamics for each group  $i$  by a projection matrix which is a regular stochastic matrix of dimensions  $N^i \times N^i$ . Hypothesis 2 in Theorem 1 is trivially satisfied if these projection matrices are constant. Our aim in what follows is to extend this situation to the nonlinear case in which such projection matrices depend on the total number of individuals in each group. To be precise, let us introduce some definitions.

Let  $\mathbf{1}_i := (1, \dots, 1)^T \in \mathbb{R}^{N^i}$ ,  $i = 1, \dots, q$ ,  $\mathcal{U} := \text{diag}(\mathbf{1}_1^T, \dots, \mathbf{1}_q^T)$  and  $\Omega_q := \mathcal{U}\Omega_N \subset \mathbb{R}^q$ .

For each  $i = 1, \dots, q$ , let  $P_i(\cdot) \in C^1(\Omega_q)$  be a matrix function such that for all  $Y \in \Omega_q$ ,  $P_i(Y)$  is a regular stochastic matrix of dimensions  $N^i \times N^i$ . As a consequence, 1 is an eigenvalue simple and strictly dominant in modulus for  $P_i(Y)$ , with associated right and left eigenvectors  $\mathbf{v}_i(Y)$ ,  $\mathbf{1}_i$ , respectively. The eigenvector  $\mathbf{v}_i(Y)$  is the AS probability distribution, i.e.,  $\mathbf{v}_i(Y) \geq 0$  and  $\mathbf{1}_i^T \mathbf{v}_i(Y) = 1$ .

The fast dynamics for the whole population is represented by the block diagonal matrix:

$$\forall Y \in \Omega_q, \quad \mathcal{F}(Y) := \text{diag}(P_1(Y), \dots, P_q(Y)).$$

The Perron–Frobenius theorem applies to each matrix  $P_i(Y)$ , so that we have

$$\bar{P}_i(Y) := \lim_{k \rightarrow \infty} P_i^k(Y) = (\mathbf{v}_i(Y) | \dots | \mathbf{v}_i(Y)) = \mathbf{v}_i(Y) \mathbf{1}_i^T.$$

Introducing the notations

$$\begin{aligned} \bar{\mathcal{F}}(Y) &:= \text{diag}(\bar{P}_1(Y), \dots, \bar{P}_q(Y)), \\ \mathcal{V}(Y) &:= \text{diag}(\mathbf{v}_1(Y), \dots, \mathbf{v}_q(Y)) \end{aligned}$$

we also have

$$\forall Y \in \Omega_q, \quad \overline{\mathcal{F}}(Y) = \lim_{k \rightarrow \infty} \mathcal{F}^k(Y) = \mathcal{V}(Y) \mathcal{U}.$$

Finally, the nonlinear model that we are considering is formulated as

$$X_{k,n+1} = S(\mathcal{F}^k(\mathcal{U}X_{k,n})X_{k,n}). \tag{3}$$

If we think that the ratio of slow to fast time scale tends to infinity i.e.,  $k \rightarrow \infty$ , or in other words, that the fast process is instantaneous in relation to the slow process, we can approximate system (3) by the following auxiliary system:

$$X_{n+1} = S(\overline{\mathcal{F}}(\mathcal{U}X_n)X_n) = S(\mathcal{V}(\mathcal{U}X_n)\mathcal{U}X_n).$$

We see that the evolution of this system depends on  $\mathcal{U}X_n \in \mathbb{R}^q$ , which suggests the global variables should be defined by

$$Y_n := \mathcal{U}X_n$$

and therefore the aggregated system of system (3) is

$$Y_{n+1} = \mathcal{U}S(\mathcal{V}(Y_n)Y_n). \tag{4}$$

We can now establish an approximation result between the solutions to the complete system (3) and the aggregated model (4), as a consequence of Theorem 1.

**Theorem 2.** *Let  $Y^* \in \mathbb{R}^q$  be a hyperbolic equilibrium point of system (4). Then, there exists an integer  $k_0 \geq 0$  such that for all  $k \geq k_0$  system (3) has an equilibrium point  $X_k^*$  which is hyperbolic and satisfies*

$$\lim_{k \rightarrow \infty} X_k^* = X^*, \quad X^* := S(\mathcal{V}(Y^*)Y^*).$$

Moreover, the following holds:

- (i)  $X_k^*$  is AS (resp. unstable) if, and only if,  $Y^*$  is AS (resp. unstable).
- (ii) Let  $Y^*$  be AS and let  $X_0 \in \Omega_N$  be such that the solution  $\{Y_n\}_{n=0,1,\dots}$  to (4) corresponding to the initial data  $Y_0 := \mathcal{U}X_0$  satisfies that  $\lim_{n \rightarrow \infty} Y_n = Y^*$ . Then, for all  $k \geq k_0$ , the solution to (3)  $\{X_{k,n}\}_{n=0,1,\dots}$  with  $X_{k,0} = X_0$  satisfies that  $\lim_{n \rightarrow \infty} X_{k,n} = X_k^*$ .

**Proof.** See Appendix A.

In some applications, particularly in ecology, it would be more realistic to have the fast dynamics dependent on the state variables and not just on the global variables as in Theorem 2. Nevertheless, it does not seem easy to find a proof for this more general case and specific proofs should be provided for each particular case of fast dynamics depending on state variables as it is done in Nguyen Huu et al. (2008). On the other hand, as we will see in the next section, it is possible to develop interesting applications keeping in the framework of Theorem 2.

## 3. Two-time discrete population dynamics models including demography and migrations

In this section we illustrate the previous results by means of some applications. We begin treating the case of a population inhabiting a multi-patch environment but with no further structure, thus the corresponding aggregated model is a scalar difference equation. Then we develop the reduction of a model of an age-structured population in a multi-patch habitat with the special feature of considering demography fast in comparison with migration. This last example extends slightly the framework presented in Section 2.1.

### 3.1. Multi-patch models with fast migrations

The models we are considering in this section fit in the general setting of Section 2.1 but consider a non-structured population, that is, a population constituted by just one group which is



subdivided into  $m$  sub-groups representing the local populations at the  $m$  patches making up its habitat.

As a consequence, the population vector at time  $n$  is  $X_n = (x_n^1, \dots, x_n^m)^T$ , the fast dynamics (associated in our models to the migration process) is represented by a regular stochastic matrix  $\mathcal{F}(y)$ , whose entries depend on the total population  $y := x^1 + \dots + x^m$ , and the slow dynamics is represented by a general  $C^1$ -map  $S: \Omega_m \subset \mathbb{R}_+^m \rightarrow \Omega_m$  which gives the local demography in each patch that, in general, could be influenced by the population densities in all the patches.

For the sake of simplicity in what follows we will consider a two patch environment (i.e.  $m = 2$ ), and the local dynamics depending only on the local population. That is, the slow dynamics is described by

$$S(X_n) := (s_1(x_n^1), s_2(x_n^2)), \quad X_n := (x_n^1, x_n^2),$$

where  $s_i$ ,  $i = 1, 2$ , are two non-negative  $C^1$  functions defined on  $\mathbb{R}_+$ .

The migration matrix  $\mathcal{F}(y)$  can be written in terms of two  $C^1$  real functions  $a, b: \mathbb{R}_+ \rightarrow (0, 1)$ :

$$\mathcal{F}(y) := \begin{pmatrix} 1 - a(y) & b(y) \\ a(y) & 1 - b(y) \end{pmatrix}.$$

Since  $\mathcal{F}(y)$  is a regular stochastic matrix, we have

$$\bar{\mathcal{F}}(y) := \lim_{k \rightarrow \infty} \mathcal{F}^k(y) = (\mathbf{v}(y)|\mathbf{v}(y)),$$

where

$$\mathbf{v}(y) := \begin{pmatrix} v_1(y) \\ v_2(y) \end{pmatrix} = \begin{pmatrix} \frac{b(y)}{a(y) + b(y)} \\ \frac{a(y)}{a(y) + b(y)} \end{pmatrix}.$$

A straightforward application of the results established in Section 2 leads to the aggregated system:

$$y_{n+1} = s_1(v_1(y_n)y_n) + s_2(v_2(y_n)y_n). \tag{5}$$

### 3.1.1. Malthusian local demography

We will carry out a detailed analysis of the above model assuming that a malthusian dynamics acts at each patch, that is

$$S(X_n) := (d_1 x_n^1, d_2 x_n^2). \tag{6}$$

Moreover we will assume that  $0 < d_1 < 1 < d_2$ , which means that patch 1 behaves as a sink and patch 2 as a source.

When the slow dynamics is given by (6), the aggregated model (5) reads as

$$y_{n+1} = \left( \frac{d_1 b(y_n) + d_2 a(y_n)}{a(y_n) + b(y_n)} \right) y_n := h(y_n) y_n. \tag{7}$$

It is evident that  $y_0 = 0$  is a fixed point of the above model, but we are mainly interested in the existence and stability properties of the positive fixed points  $y_*$ , which are the solutions to equation  $h(y) = 1$ .

To study the behaviour of function  $h$ , we should take into account its derivative:

$$h'(y) = (d_2 - d_1) \frac{a'(y)b(y) - a(y)b'(y)}{[a(y) + b(y)]^2}.$$

For the sake of simplicity we restrict our analysis to the case in which functions  $a(y)$ ,  $b(y)$  are monotone. When one of them is increasing and the other is decreasing, it is evident that  $h(y)$  is strictly monotone. Therefore, whether function  $h(y)$  crosses or not the line  $y = 1$  is completely determined by the values  $h(0)$  and  $h(\infty) := \lim_{y \rightarrow +\infty} h(y)$ . Moreover, in the case in which  $y_*$  exists, it is

unique and its stability is determined by the value  $h'(y_*)y_*$ . On the other hand, the stability of the fixed point  $y_0 = 0$  depends on the value of  $h(0)$ .

These results are summarized as follows:

$a(y)$	$b(y)$	$h(0)$	$h(\infty)$	$y_0 = 0$	$y_*$
$\searrow$	$\nearrow$	$> 1$	$\in (0, 1)$	U	$\exists$ , U or AS
$\searrow$	$\nearrow$	$> 1$	$> 1$	U	$\exists$
$\searrow$	$\nearrow$	$\in (0, 1)$	$\in (0, 1)$	GAS	$\exists$
$\nearrow$	$\searrow$	$\in (0, 1)$	$> 1$	AS	$\exists$ , U
$\nearrow$	$\searrow$	$\in (0, 1)$	$\in (0, 1)$	GAS	$\exists$
$\nearrow$	$\searrow$	$> 1$	$> 1$	U	$\exists$

where the arrows  $\searrow$  and  $\nearrow$  stand for a decreasing and an increasing function, respectively, and U, AS and GAS stand for unstable, asymptotically stable and globally asymptotically stable, respectively.

The fact that local dynamics are of malthusian type allows extinction and unbounded growing to be expected at a global level. Nevertheless, as we see in the first row of the previous table, certain kinds of density dependent migrations can lead to a positive AS equilibrium. Two examples are described below.

If we choose

$$a(y) = \frac{\alpha - d_1(1 + \beta y)}{d_2 - d_1} \quad \text{and} \quad b(y) = \frac{d_2(1 + \beta y) - \alpha}{d_2 - d_1} \tag{8}$$

for positive parameters  $\alpha$  and  $\beta$ , formal calculations yield the well-known [Beverton–Holt \(1957\)](#) equation:

$$y_{n+1} = \frac{\alpha y_n}{1 + \beta y_n}$$

which always possesses a positive equilibrium which is globally AS. The formal calculations are valid provided that  $a(y), b(y) \in (0, 1)$ , which is true if

$$\frac{\alpha - d_2}{\beta} < y < \frac{\alpha - d_1}{d_2 \beta}.$$

So, if we choose  $\alpha \in (d_1, d_2)$  and  $\beta \in (0, \alpha - d_1/d_2\hat{y})$  we can easily prove that  $a(y), b(y) \in (0, 1)$  whenever  $y \in [0, \hat{y}]$ .

Similar requirements allow us to obtain the [Ricker \(1954\)](#) equation

$$y_{n+1} = \exp(r(1 - y_n/K))y_n,$$

where  $r$  and  $K$  are positive parameters, by choosing

$$a(y) = \frac{e^{r(1-y/K)} - d_1}{d_2 - d_1} \quad \text{and} \quad b(y) = \frac{d_2 - e^{r(1-y/K)}}{d_2 - d_1}. \tag{9}$$

We have illustrated how the aggregation procedure provides an explanation of two classical mono-species discrete models in terms of a sink–source environment with fast density dependent migrations coupled to simple local malthusian dynamics. Similar approaches using aggregation methods for ordinary differential equations were presented in [Auger and Poggiale \(1996\)](#) and [Auger et al. \(2000\)](#).

Some others interpretations of this kind have been recently presented by [Geritz and Kisdi \(2004\)](#). There, starting from a continuous-time resource–consumer model for the dynamics within a year, a discrete-time model for the between-year dynamics is derived. This model is analysed assuming that the within-year resource dynamics in absence of consumers takes different functional forms. Considering particular constant rates for the influx and efflux of the resource, the Beverton–Holt model, the Ricker model and many other models are recovered. Further models derived by systematically varying the within-year patterns of reproduction and aggression between individuals can be found in [Eskola and Geritz \(2007\)](#).

To go on with the study of Eq. (7), we notice that the cases in which both  $a(y)$  and  $b(y)$  are simultaneously increasing or decreasing functions yield a more complicated dynamics and Allee effect scenarios may arise.

We illustrate this fact with the next example. Let us assume that  $a(y)$  and  $b(y)$  are increasing functions given by

$$a(y) := \frac{y^2}{y^2 + \beta} \quad \text{and} \quad b(y) := \frac{y^2 + \beta}{y^2 + \delta}, \quad 0 < \beta < \delta.$$

Function  $h(y)$  in (7) becomes

$$h(y) = \frac{d_1(y^2 + \beta)^2 + d_2(y^2 + \delta)y^2}{(y^2 + \beta)^2 + (y^2 + \delta)y^2}.$$

The qualitative analysis of Eq. (7) is straightforward having in mind that positive solutions are decreasing if  $h(y) < 1$ , increasing if  $h(y) > 1$  and the positive fixed points are the roots of equation  $h(y) = 1$ . Since  $h(0) = d_1 < 1$ , the fixed point  $y_0^* = 0$  is always AS.

To find when  $h(y) < 1$  and when  $h(y) > 1$  we know that  $h(0) = d_1 < 1$  and  $\lim_{y \rightarrow \infty} h(y) = (d_1 + d_2)/2$ . Moreover, if we look at the sign of  $h'(y)$ ,

$$h'(y) = \frac{2(d_2 - d_1)y(2\beta - \delta)y^4 + 2\beta^2y^2 + \beta^2\delta}{(2y^4 + (2\beta + \delta)y^2 + \beta^2)^2},$$

we see that if  $\delta \leq 2\beta$  then  $h(y)$  is increasing in  $[0, \infty)$  while if  $\delta > 2\beta$  then  $h(y)$  is increasing in  $[0, y_M)$  and decreasing in  $(y_M, \infty)$ , where  $y_M = \sqrt{\beta\delta/(\delta - 2\beta)}$  is the only positive root of equation  $h'(y) = 0$ . Thus, we have:

- If  $\delta \leq 2\beta$  and  $(d_1 + d_2)/2 \leq 1$ , there is no positive fixed point.
- If  $\delta \leq 2\beta$  and  $(d_1 + d_2)/2 > 1$ , there is a positive fixed point which is unstable.
- If  $\delta > 2\beta$  and  $h(y_M) < 1$ , there is no positive fixed point.
- If  $\delta > 2\beta$  and  $h(y_M) = 1$ ,  $y_M$  is the only positive fixed point and it is unstable.
- If  $\delta > 2\beta$ ,  $h(y_M) > 1$  and  $(d_1 + d_2)/2 \geq 1$ , there is a positive fixed point,  $y_1^* < y_M$ , which is unstable.
- If  $\delta > 2\beta$ ,  $h(y_M) > 1$  and  $(d_1 + d_2)/2 < 1$ , there are two positive fixed points,  $y_1^* < y_M < y_2^*$ . In this case the positive solutions of Eq. (7), which are all monotone, verify the following:  
 If the initial condition  $y_0 < y_1^*$  then  $\lim_{n \rightarrow \infty} y_n = 0$  and if  $y_0 > y_1^*$  then  $\lim_{n \rightarrow \infty} y_n = y_2^*$ ,  
 i.e., at low population densities population gets extinct, while the evolution of population densities above  $y_1^*$  leads to  $y_2^*$ .

As we see in the last case, an Allee effect scenario appears out of local malthusian dynamics in a sink–source environment with fast density dependent migrations.

### 3.1.2. Beverton–Holt local demography

Our main goal in this section is to illustrate through another example, now with local dynamics different from malthusian, that nonlinear fast migrations can give rise to a variety of situations, among them Allee-type effect dynamics. Let us choose a local demography of Beverton–Holt type, together with monotone migrations. That is, in lieu of (6), we assume that the slow dynamics is given by

$$S(X_n) := \left( \frac{d_1 x_n^1}{1 + c_1 x_n^1}, \frac{d_2 x_n^2}{1 + c_2 x_n^2} \right), \quad 0 < d_1 < 1 < d_2, \quad c_i > 0, \quad i = 1, 2$$

and that functions  $a(y)$ ,  $b(y)$  defining the fast dynamics  $\mathcal{F}(y)$  are given by

$$a(y) := \frac{y}{1 + y}, \quad b(y) := \frac{1}{1 + y}.$$

In this situation, the aggregated system (5) reads

$$y_{n+1} = h(y_n)y_n, \quad h(y_n) := \frac{d_1}{1 + (1 + c_1)y_n} + \frac{d_2 y_n}{1 + y_n + c_2 y_n^2}.$$

Arguing in a similar way to the previous section, we obtain that  $y_0 = 0$  is an equilibrium point which is always AS since  $h(0) = d_1 < 1$ .

The positive equilibria, if they exist, are the positive solutions to  $h(y) = 1$ . Notice that

$$h'(y) = -\frac{d_1(1 + c_1)}{[1 + (1 + c_1)y]^2} + \frac{d_2(1 - c_2y^2)}{(1 + y + c_2y^2)^2}.$$

If  $d_2 > d_1(1 + c_1)$ , then there exists a unique value  $y_M \in (0, 1/\sqrt{c_2})$  such that  $h'(y_M) = 0$  and moreover  $h$  takes its maximum value at this point. Therefore, bearing in mind that  $h(0) = d_1 < 1$  and  $h(+\infty) = 0$ , the equation  $h(y) = 1$  will have either two positive solutions or none according to  $h(y_M) > 1$  or  $h(y_M) < 1$ , respectively. One sufficient condition for  $h(y_M) > 1$  is that  $h(1/\sqrt{c_2}) > 1$  which yields a relationship between the parameters of the model. In turn, a simple sufficient condition for this is  $d_2 > 1 + 2\sqrt{c_2}$ . Summing up, we can assure that for large enough values of  $d_2$  the aggregated model has two positive equilibria  $0 < y_* < y_{**}$  such that  $y_*$  is unstable and  $y_{**}$  can be AS or unstable.

### 3.2. An age-structured population model with fast demography

This section can be considered as an extension of some results in Sanz and Bravo de la Parra (1999), where a linear case is discussed. The theory developed in Section 2 does not exactly match with the setting here, but it can be easily adapted: everything works if the fast dynamics is given by a non-negative  $C^1$  matrix function whose dominant eigenvalue is 1 and the corresponding associated normalized left eigenvector is constant.

To be precise, let us consider an age-structured population distributed between two spatial patches. We will distinguish two age classes: juvenile (class 1, non-reproductive) and adult (class 2, reproductive), so that the state of the population at time  $n$  is represented by a vector:

$$X_n := (x_n^1, x_n^2)^T \in \mathbb{R}_+^4, \quad x_n^i := (x_n^{i1}, x_n^{i2})^T, \quad i = 1, 2,$$

where  $x_n^j$  stands for the individuals of class  $j$  inhabitant patch  $i$ .

Let us set demography as a local process driven by a Leslie  $C^1$  matrix function:

$$\forall y \in \mathbb{R}_+, \quad L_i(y) := \begin{pmatrix} 0 & f_{12}^i(y) \\ t_{21}^i(y) & t_{22}^i(y) \end{pmatrix}, \quad i = 1, 2,$$

where, as usual,  $f_{12}^i(\cdot)$  stands for the fertility rate of the adults and  $t_{2j}^i(\cdot)$ ,  $j = 1, 2$ , stand for the survival rate of each age class. In order to fit in the framework of Section 2.1, let us impose that 1 is the strictly dominant in modulus eigenvalue of matrix  $L_i(\cdot)$ , which yields

$$\forall y \in \mathbb{R}_+, \quad t_{22}^i(y) + f_{21}^i(y)t_{21}^i(y) = 1, \quad i = 1, 2. \quad (10)$$

As a consequence, we can find associate positive right and left eigenvectors  $\mathbf{v}_i(y)$ ,  $\mathbf{u}_i(y)$ , which can be chosen normalized by the condition  $\mathbf{u}_i^T(y)\mathbf{v}_i(y) = 1$ . In fact, these vectors are given by

$$\mathbf{u}_i(y) = \begin{pmatrix} 1 \\ \frac{1}{t_{12}^i(y)} \end{pmatrix} := \begin{pmatrix} u_1^i(y) \\ u_2^i(y) \end{pmatrix},$$

$$\mathbf{v}_i(\mathbf{y}) = \begin{pmatrix} \frac{f_{12}^i(\mathbf{y})t_{21}^i(\mathbf{y})}{1 + f_{12}^i(\mathbf{y})t_{21}^i(\mathbf{y})} \\ \frac{t_{21}^i(\mathbf{y})}{1 + f_{12}^i(\mathbf{y})t_{21}^i(\mathbf{y})} \end{pmatrix} := \begin{pmatrix} v_1^i(\mathbf{y}) \\ v_2^i(\mathbf{y}) \end{pmatrix}.$$

The general theory of non-negative matrices applies, so that there exists the limit:

$$\forall \mathbf{y} \in \mathbb{R}_+, \quad \bar{L}_i(\mathbf{y}) := \lim_{k \rightarrow \infty} L_i^k(\mathbf{y}) = \mathbf{v}_i(\mathbf{y})\mathbf{u}_i^T(\mathbf{y}), \quad i = 1, 2.$$

The fast dynamics for the whole population will be represented by the block diagonal matrix:

$$\forall Y := \begin{pmatrix} y_1 \\ y_2 \end{pmatrix} \in \mathbb{R}_+, \quad L(Y) := \begin{pmatrix} L_1(y_1) & 0 \\ 0 & L_2(y_2) \end{pmatrix}.$$

Bearing in mind the above considerations, it is evident that the following limit exists:

$$\bar{L}(Y) := \lim_{k \rightarrow \infty} L^k(Y) = \begin{pmatrix} \bar{L}_1(y_1) & 0 \\ 0 & \bar{L}_2(y_2) \end{pmatrix} = \mathcal{V}(Y)\mathcal{U}(Y),$$

whereas in Section 2 we have introduced the notations:

$$\mathcal{V}(Y) := \text{diag}(\mathbf{v}_1(y_1), \mathbf{v}_2(y_2)), \quad \mathcal{U}(Y) := \text{diag}(\mathbf{u}_1^T(y_1), \mathbf{u}_2^T(y_2)).$$

In addition, we consider migrations between patches. To simplify, we will consider a linear process represented by a constant stochastic matrix:

$$M := \begin{pmatrix} 1 - a_1 & 0 & a_2 & 0 \\ 0 & 1 - b_1 & 0 & b_2 \\ a_1 & 0 & 1 - a_2 & 0 \\ 0 & b_1 & 0 & 1 - b_2 \end{pmatrix}, \quad a_i, b_i \in (0, 1),$$

$i = 1, 2,$

where  $a_i$  and  $b_i$  stand for the fraction of juvenile and adult individuals which move from patch  $i$ , respectively.

In this section we are assuming that demography is much faster than migrations and spatially internal, that is, only dependent on the population on each patch. In order to be able to retain the smoothness results established in Section 2, we will assume that matrix  $\mathcal{U}(\cdot)$  is constant. To meet this assumption we only need to suppose that  $t_{21}^i(\cdot)$  is constant, what we do in the sequel.

Then, the global variables are defined by

$$Y_n := \mathcal{U}X_n = \begin{pmatrix} x_n^{11} + (1/t_{12}^1)x_n^{12} \\ x_n^{21} + (1/t_{12}^2)x_n^{22} \end{pmatrix} := \begin{pmatrix} y_n^1 \\ y_n^2 \end{pmatrix}$$

which have a biological meaningful interpretation as they are the population at each patch weighted by its reproductive values. Therefore it makes sense to consider the fertility rates of the reproductive class as a function of the global variables, and then the coefficients  $t_{22}^i(\cdot)$ ,  $i = 1, 2$  are also dependent on the global variables because of relation (10).

Finally, the slow–fast model that we are considering is

$$X_{k,n+1} = ML^k(\mathcal{U}X_{k,n})X_{k,n}$$

which, arguing as in Section 2 can be reduced to the following system expressed in terms of the global variables:

$$Y_n = \mathcal{U}M\mathcal{V}(Y_n)Y_n.$$

Direct substitutions lead to the following nonlinear aggregated system:

$$\begin{cases} y_{n+1}^1 = [u_1^1(1 - a_1)v_1^1(y_n^1) + u_2^1(1 - b_1)v_2^1(y_n^1)]y_n^1 \\ \quad + [u_1^1a_2v_1^2(y_n^2) + u_2^1b_2v_2^2(y_n^2)]y_n^2, \\ y_{n+1}^2 = [u_1^2a_1v_1^1(y_n^1) + u_2^2b_1v_2^1(y_n^1)]y_n^1 \\ \quad + [u_1^2(1 - a_2)v_1^2(y_n^2) + u_2^2(1 - b_2)v_2^2(y_n^2)]y_n^2 \end{cases}$$

to which the general results on stability of equilibria established in Section 2 apply.

To perform a numerical analysis of this system, set

$$f_{12}^i(y^i) := \frac{\alpha_i}{1 + y^i}, \quad \alpha_i \geq 0, \quad i = 1, 2$$

which provides the aggregated system:

$$\begin{cases} y_{n+1}^1 = \left[ \frac{(1 - a_1)\alpha_1 t_{21}^1 + (1 - b_1)(1 + y_n^1)}{1 + \alpha_1 t_{21}^1 + y_n^1} \right] y_n^1 \\ \quad + \left[ \frac{t_{21}^2(a_2\alpha_2 + b_2(1 + y_n^2)/t_{21}^2)}{1 + \alpha_2 t_{21}^2 + y_n^2} \right] y_n^2, \\ y_{n+1}^2 = \left[ \frac{t_{21}^1(a_1\alpha_1 + b_1(1 + y_n^1)/t_{21}^1)}{1 + \alpha_1 t_{21}^1 + y_n^1} \right] y_n^1 \\ \quad + \left[ \frac{(1 - a_2)\alpha_2 t_{21}^2 + (1 - b_2)(1 + y_n^2)}{1 + \alpha_2 t_{21}^2 + y_n^2} \right] y_n^2 \end{cases}$$

whose fixed points are the solutions to

$$\begin{cases} 0 = \frac{a_1\alpha_1 t_{21}^1 + b_1(1 + y^1)}{1 + \alpha_1 t_{21}^1 + y^1} y^1 \\ \quad + \frac{t_{21}^2(a_2\alpha_2 + b_2(1 + y^2)/t_{21}^2)}{1 + \alpha_2 t_{21}^2 + y^2} y^2, \\ 0 = \frac{t_{21}^1(a_1\alpha_1 + b_1(1 + y^1)/t_{21}^1)}{1 + \alpha_1 t_{21}^1 + y^1} y^1 \\ \quad - \frac{a_2\alpha_2 t_{21}^2 + b_2(1 + y^2)}{1 + \alpha_2 t_{21}^2 + y^2} y^2. \end{cases} \quad (11)$$

Obviously,  $(y_0^1, y_0^2) := (0, 0)$  is a fixed point to Eq. (11). Moreover, there are no fixed points of the form  $(y^1, 0)$  or  $(0, y^2)$  with  $y^1 > 0$  or  $y^2 > 0$ . Further calculations give rise to

$$y^2 = \frac{a_2 b_1 \alpha_2 (y^1 + 1)}{a_1 b_2 \alpha_1} - 1,$$

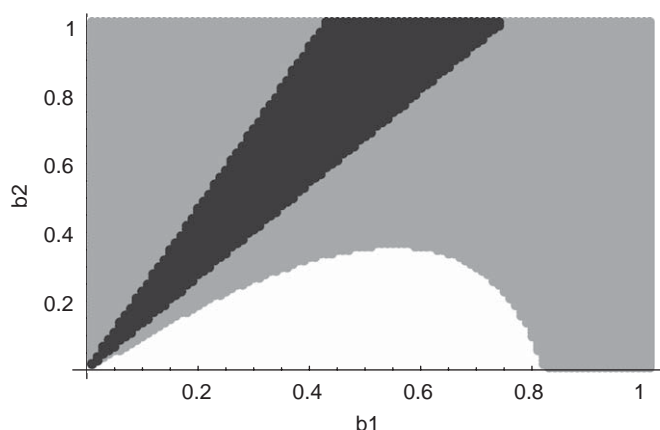
where  $y^1$  is any solution to equation

$$\frac{a_1\alpha_1 t_{21}^1 + b_1(1 + y^1)}{1 + \alpha_1 t_{21}^1 + y^1} y^1 = \frac{t_{21}^2 \left( a_2\alpha_2 + \frac{a_2 b_1 \alpha_2 (1 + y^2)}{a_1\alpha_1 t_{21}^1} \right)}{\alpha_2 t_{21}^2 + \frac{a_2 b_1 \alpha_2 (1 + y^1)}{a_1 b_2 \alpha_1}} \times \left[ \frac{a_2 b_1 \alpha_2 (y^1 + 1)}{a_1 b_2 \alpha_1} - 1 \right].$$

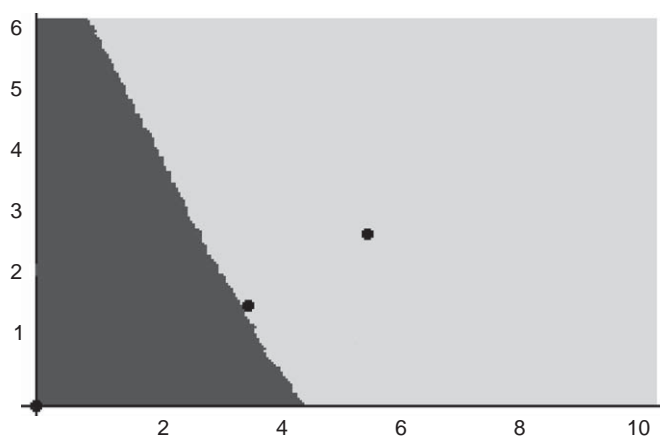
Numerical experiments carried out using a large range for the parameters show that there are several scenarios for which there exists a positive AS fixed point, as well as several scenarios for which there exist two positive AS fixed points. This is shown for particular values of the parameters in Figs. 1 and 2.

#### 4. Conclusions

In this paper we have presented a general class of nonlinear two-time scales discrete dynamical systems susceptible to be reduced by the so-called aggregation of variables method. These systems can serve as models for population dynamics that combine both migratory and demographic processes taking place



**Fig. 1.** From white to black, zones with none, one or two positive asymptotically stable fixed points. Parameter values:  $a_1 = 0.1$ ,  $a_2 = 0.3$ ,  $\alpha_1 = 100$ ,  $\alpha_2 = 45$ ,  $t_{21}^1 = 0.3$ ,  $t_{21}^2 = 0.1$ , and  $b_1, b_2$  range from 0.01 to 1.0, step 0.005.



**Fig. 2.** Basins of attraction of the asymptotically stable fixed points (0,0), (3.44, 1.57) (too small to be plotted in this picture) and (5.36, 2.68). Parameter values:  $a_1 = 0.1$ ,  $a_2 = 0.3$ ,  $b_1 = 0.3$ ,  $b_2 = 0.7$ ,  $\alpha_1 = 100$ ,  $\alpha_2 = 45$ ,  $t_{21}^1 = 0.3$ ,  $t_{21}^2 = 0.1$ .

at different time scales. In the applications proposed in this paper we have considered situations in which demography can be considered fast with respect to migration and others in which the opposite holds.

We have shown that our formulations enter in the more abstract framework described in Sanz et al. (2008), so that it is possible to study the hyperbolic fixed points of the slow–fast complex system, as well as their basins of attraction in the case they are stable, by performing the corresponding study in the aggregated system.

In Section 3.1 we consider that migration, which is dependent on the total population, is fast when compared with demography. In the simplest case that migrations depend monotonically on the total population, and the local demography is of malthusian type, we have derived the classical Beverton–Holt and Ricker models in terms of source–sink systems linked by migrations, which constitutes a possible interpretation for these models.

In the same setting, with more complex situations corresponding to monotone migrations, the Allee effect can appear. Our analysis can be related with the results in Boukal and Berec (2007) concerning the Allee effect. These authors critically review and classify deterministic non-spatial models of single species population dynamics subject to the demographic Allee effect. The outcome of all models studied in the above-mentioned work is either unconditional extinction, extinction-survival scenario or

unconditional survival. The same kinds of results have been established in Section 3.1 for the aggregated model. As the general slow–fast spatially structured model miss its spatial features when its aggregation is performed, our method allows us to study spatially distributed populations by means of non-spatial models.

In Section 3.2 we change the point of view and consider demographic processes depending on population densities as fast dynamics driven by Leslie-type matrices. We may think, for instance, of a parasitoid population being the guest in a species that migrates. After building up a general aggregated system for this setting, numerical experiments considering migration, survival and fertility rates as parameters give rise to multi-attractor scenarios.

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### Appendix A

#### A.1. Proof of Theorem 2

The result is a consequence of Theorem 1, since model (3) fits in the general formulation given by (1) if we choose

$$\forall X \in \Omega_N, \quad F(X) := \mathcal{F}(\mathcal{U}X)X. \quad (12)$$

Therefore, bearing in mind that for all  $Y \in \mathbb{R}^q$  we have  $\mathcal{U}\mathcal{F}(Y) = \mathcal{U}$ , the following holds for all  $X \in \Omega_N$ :

$$\lim_{k \rightarrow \infty} F^k(X) = \lim_{k \rightarrow \infty} \mathcal{F}^k(\mathcal{U}X)X = \overline{\mathcal{F}}(\mathcal{U}X)X = \mathcal{V}(\mathcal{U}X)\mathcal{U}X.$$

Then,

$$\forall X \in \Omega_N, \quad \bar{F}(X) := \mathcal{V}(\mathcal{U}X)\mathcal{U}X \quad (13)$$

and since the global variables are defined by  $G(X) := \mathcal{U}X$ , finally we choose

$$\forall Y \in \mathbb{R}^q, \quad E(Y) := \mathcal{V}(Y)Y.$$

Now we will check that Hypotheses 1 and 2 are satisfied in the above setting.

The regularity conditions imposed in Hypothesis 1 hold immediately from the  $C^1$  regularity of eigenvectors  $\mathbf{v}_i(\cdot)$ ,  $i = 1, \dots, q$ , as established in Lemma 1.

**Lemma 1.** Let  $P(\cdot)$  be a  $C^1$  matrix function defined on  $\Omega_q$ , such that for each  $Y \in \Omega_q$ ,  $P(Y)$  is a  $n \times n$  regular stochastic matrix.

Let us consider the function  $\mathbf{v} : \Omega_q \rightarrow \mathbb{R}^n$  where  $\mathbf{v}(Y)$  is the unique eigenvector associated to eigenvalue 1, normalized by the condition  $\mathbf{1}_n^T \mathbf{v}(Y) = 1$ .

Then,  $\mathbf{v} \in C^1(\Omega_q)$ .

**Proof.** For each  $Y \in \Omega_q$ , the normalized eigenvector  $\mathbf{v}(Y)$  associated to the eigenvalue 1 is the unique solution to the system:

$$(EV) \quad \begin{cases} (P(Y) - I_n)\mathbf{v} &= \mathbf{0}, \\ \mathbf{1}_n^T \mathbf{v} &= 1. \end{cases}$$

Set  $Y_0 \in \Omega_q$  and let  $\mathbf{v}(Y_0)$  be the corresponding solution to (EV). Since  $\mathbf{1}_n^T(P(Y) - I_n) = \mathbf{0}_n^T$ , an elementary application of the Rank Theorem (see Zeidler, 1986, problem 4.4d, p. 199) allows to solve system (EV) in a neighbourhood of  $(Y_0, \mathbf{v}(Y_0))$ ,  $N(Y_0) \subset \Omega_q \times \mathbb{R}^n$ , by eliminating the last row of the matrix  $P(Y) - I_n$ . As an immediate consequence, this theorem assures that the function  $\mathbf{v}(\cdot)$  defined implicitly by system (EV) is  $C^1$  in a neighbourhood of  $Y_0$ , as we wanted to prove.  $\square$



Let us observe that the application of the Rank Theorem to system (EV) is based on the following elementary result:

For each  $n \times n$  regular stochastic matrix  $P_0$ , we have

$$\text{Rank} \begin{pmatrix} P_0 - I_n \\ \mathbf{1}_n^T \end{pmatrix} = n.$$

Regarding Hypothesis 2, let us notice that for each  $Y \in \Omega_q$ , matrix  $\mathcal{F}(Y)$  can be written as

$$\begin{aligned} \mathcal{F}(Y) &= (\mathcal{V}(Y)|R(Y)) \begin{pmatrix} I_q & O \\ O & H(Y) \end{pmatrix} \begin{pmatrix} \mathcal{U} \\ S(Y) \end{pmatrix} \\ &= \mathcal{V}(Y)\mathcal{U} + Q(Y) \end{aligned}$$

with  $Q(Y) := R(Y)H(Y)S(Y)$ ,  $R(Y)$ ,  $S(Y)$  are suitable matrices and  $H(Y)$  corresponds to the Jordan blocks of  $\mathcal{F}(Y)$  associated to eigenvalues of modulus strictly less than 1. Therefore

$$\forall Y \in \Omega_q, \quad \rho(Q(Y)) < 1, \tag{14}$$

where  $\rho$  denotes the spectral radius.

Moreover, straightforward calculations lead to

$$\mathcal{F}^k(Y) = \mathcal{V}(Y)\mathcal{U} + Q^k(Y), \quad k = 1, 2, \dots \quad \square \tag{15}$$

Bearing in mind Lemma 1, and since  $\mathcal{F} \in C^1(\Omega_q)$ , let us observe that we also have  $Q \in C^1(\Omega_q)$ .

We are now able to prove the following:

**Proposition 1.** *The functions  $F$  and  $\bar{F}$  defined in (12) and (13) satisfy that:*

- (i)  $\lim_{k \rightarrow \infty} F^k = \bar{F}$ ,
- (ii)  $\lim_{k \rightarrow \infty} DF^k = D\bar{F}$

uniformly on each compact set  $K_N \subset \Omega_N$ .

**Proof.** From (15) we have, for each  $X \in \Omega_N$ :

$$\begin{aligned} \|F^k(X) - \bar{F}(X)\| &= \|\mathcal{F}^k(\mathcal{U}X)X - \mathcal{V}(\mathcal{U}X)\mathcal{U}X\| \\ &\leq \|Q^k(\mathcal{U}X)\| \|X\|. \end{aligned}$$

Therefore, as  $\mathcal{U}$  is a constant matrix, to prove (i) it is enough to prove that, for each compact set  $K_q \subset \Omega_q$  we have

$$\sup_{Y \in K_q} \|Q^k(Y)\| \rightarrow 0 \quad (k \rightarrow \infty)$$

which, in turn, will be a consequence of the existence of two constants  $C > 0$  and  $\beta \in (0, 1)$  such that

$$\forall Y \in K_q, \quad \|Q^k(Y)\| \leq C\beta^k, \quad k = 1, 2, \dots \tag{16}$$

Since  $Q(\cdot)$  is continuous, the spectral radius  $\rho(Q(\cdot))$  is also continuous on  $\Omega_q$  and then, bearing in mind (14), we can assure the existence of a constant  $\alpha$  with  $0 < \alpha < 1$  such that  $\sup_{Y \in W} \rho(Q(Y)) \leq \alpha$ , where  $W$  is some bounded open set with  $K_q \subset W$  and  $\bar{W} \subset \Omega_q$ .

Let  $\beta$  be fixed with  $\alpha < \beta < 1$  and set  $Y \in W$ . It is a well known fact that there exists a matrix norm  $\|\cdot\|_Y$  (depending on  $Y$ ) for which  $\|Q(Y)\|_Y < \beta$ .

The continuity of  $Q(\cdot)$  and of the norm allow us to assure the existence of an open neighbourhood of  $Y$ ,  $B(Y) \subset W$ , such that  $\sup_{Z \in B(Y)} \|Q(Z)\|_Y \leq \beta$ .

Obviously, the family  $\mathcal{B} := \{B(Y); Y \in W\}$  is an open covering of  $K_q$  and since  $K_q$  is a compact set, there exist a finite collection of points  $Y_j \in W, j = 1, \dots, r$  such that  $K_q \subset \bigcup_{j=1}^r B(Y_j)$ .

Then, for each  $Y \in K_q$  there exists  $j \in \{1, \dots, r\}$  such that  $\|Q(Y)\|_Y \leq \beta$ , and therefore  $\|Q^k(Y)\|_Y \leq \beta^k, k = 1, 2, \dots$

As a consequence, bearing in mind that all the matrix norms are equivalent, we have that  $\|Q^k(Y)\| \leq C_j \beta^k$ , for some constant  $C_j > 0$ . Choosing  $C := \max(C_1, \dots, C_r)$ , the estimation (16) holds.

To prove the assertion (ii) let us notice that (15) implies that

$$\forall X \in \Omega_N, \quad DF^k(X) = D\bar{F}(X) + D[Q^k(\mathcal{U}X)X].$$

Therefore, we have to prove that, for each compact set  $K_N \subset \Omega_N$  we have

$$\sup_{X \in K_N} \|D[Q^k(\mathcal{U}X)X]\| \rightarrow 0 \quad (k \rightarrow \infty).$$

Let us start with some straightforward calculations. Let  $A(\cdot) := (a_{ij}(\cdot))_{i,j=1,\dots,N}$  be a  $C^1$  matrix function defined on  $\Omega_N$  and set  $R$  the scalar function defined on  $\Omega_N$  by  $R(X) := A(X)X, X := (x_1, \dots, x_N)^T \in \Omega_N$ .

A direct calculation of the partial derivatives leads to the following expression:

$$DR(X) = A(X) + \begin{pmatrix} \sum_{j=1}^N x_j \text{grad } a_{1j}(X) \\ \vdots \\ \sum_{j=1}^N x_j \text{grad } a_{Nj}(X) \end{pmatrix}.$$

Choosing  $A(X) := Q^k(\mathcal{U}X)$  in the above expression, with the help of the chain rule we have

$$D[Q^k(\mathcal{U}X)X] = Q^k(\mathcal{U}X) + \begin{pmatrix} \sum_{j=1}^N x_j \text{grad } q_{1j}^{(k)}(\mathcal{U}X) \\ \vdots \\ \sum_{j=1}^N x_j \text{grad } q_{Nj}^{(k)}(\mathcal{U}X) \end{pmatrix} \mathcal{U},$$

where we have denoted by  $q_{ij}^{(k)}(Y)$  the entries of matrix  $Q^k(Y)$ .

Let  $K_N \subset \Omega_N$  be a compact set and set  $K_q := \mathcal{U}K_N \subset \Omega_q$ , which is also a compact set. Bearing in mind (16), the above expression leads to the following estimation:

$$\begin{aligned} \|D[Q^k(\mathcal{U}X)X]\| &\leq C_1 \beta^k + C_2 \|\mathcal{U}\| \|X\| \\ &\times \max_{i,j=1,\dots,N} \left( \sup_{Y \in K_q} \left| \frac{\partial q_{ij}^{(k)}}{\partial y_s}(Y) \right|, s = 1, \dots, q \right), \end{aligned}$$

where  $C_1 > 0, C_2 > 0$  are two constants whose specific values are not relevant.

For each  $Y := (y_1, \dots, y_q)^T \in \Omega_q$  and  $k = 1, 2, \dots$  we have

$$\begin{aligned} \frac{\partial Q^k}{\partial y_s}(Y) &= \frac{\partial Q}{\partial y_s}(Y)Q(Y)^{(k-1)} + Q(Y) \frac{\partial Q}{\partial y_s}(Y)Q(Y)^{(k-2)} \\ &+ \dots + Q(Y)^{(k-1)} \frac{\partial Q}{\partial y_s}(Y) \end{aligned}$$

and since  $Q(\cdot)$  has continuous partial derivatives, then bounded on each compact set, we can conclude that

$$\sup_{X \in K_N} \|D[Q^k(\mathcal{U}X)X]\| \leq C_1 \beta^k + C_3 k \beta^{k-1} \rightarrow 0 \quad (k \rightarrow \infty)$$

as we wanted to prove.  $\square$

This finishes the proof of Theorem 2.

## References

- Auger, P., Bravo de la Parra, R., 2000. Methods of aggregation of variables in population dynamics. *C. R. Acad. Sci. Paris* 323, 665–674.
- Auger, P., Poggiale, J.C., 1996. Emergence of population growth models: fast migration and slow growth. *J. Theor. Biol.* 182, 99–108.
- Auger, P., Poggiale, J.C., Charles, S., 2000. Emergence of individual behaviour at the population level: effects of density dependent migrations on population growth. *C. R. Acad. Sci. Paris* 323, 119–127.
- Auger, P., Bravo de la Parra, R., Poggiale, J.C., Sanchez, E., Nguyen Huu, T., 2008. Aggregation of variables and applications to population dynamics. In: Magal, P., Ruan, S. (Eds.), *Structured Population Models in Biology and Epidemiology*. Lecture Notes in Mathematics, vol. 1936. Mathematical Biosciences Subseries. Springer, Berlin, pp. 209–263.
- Beverton, R., Holt, S., 1957. On the dynamics of exploited fish populations. *Fisheries Investigations, Series 2*, vol. 19. H.M. Stationary Office, London.
- Boukal, D.S., Berec, L., 2007. Single-species models of the Allee effect: extinction boundaries, sex ratios and mate encounters. *Theor. Popul. Biol.* 72, 41–51.
- Bravo de la Parra, R., Auger, P., Sanchez, E., 1995. Aggregation methods in discrete models. *J. Biol. Syst.* 3, 603–612.
- Bravo de la Parra, R., Sanchez, E., Auger, P., 1997. Time scales in density dependent discrete models. *J. Biol. Syst.* 5, 111–129.
- Bravo de la Parra, R., Sanchez, E., Arino, O., Auger, P., 1999. A discrete model with density dependent fast migration. *Math. Biosci.* 157, 91–110.
- Eskola, H.T.M., Geritz, S.A.H., 2007. On the mechanistic derivation of various discrete-time population models. *Bull. Math. Biol.* 69, 329–346.
- Geritz, S.A.H., Kisdi, E., 2004. On the mechanistic underpinning of discrete-time population models with complex dynamics. *J. Theor. Biol.* 228, 261–269.
- Nguyen Huu, T., Auger, P., Lett, C., Marva, M., 2008. Emergence of global behaviour in a host-parasitoid model with density-dependent dispersal in a chain of patches. *Ecol. Complexity* 5, 9–21.
- Ricker, W.E., 1954. Stock and recruitment. *J. Fish. Res. Bd. Can.* 11, 559–623.
- Robinson, R.C., 1995. *Dynamical Systems: Stability, Symbolic Dynamics and Chaos*. CRC Press, London.
- Sanchez, E., Bravo de la Parra, R., Auger, P., 1995. Discrete models with different time scales. *Acta Biotheor.* 43, 465–479.
- Sanz, L., Bravo de la Parra, R., 1999. Variables aggregation in a time discrete linear model. *Math. Biosci.* 157, 111–146.
- Sanz, L., Bravo de la Parra, R., Sanchez, E., 2008. Approximate reduction of non-linear discrete models with two time scales. *J. Difference Equat. Appl.* 14, 607–627.
- Zeidler, E., 1986. *Nonlinear Functional Analysis and its Applications I: Fixed-Point Theorems*. Springer, Berlin.