

Aggregation methods in dynamical systems and applications in population and community dynamics

P. Auger , R. Bravo de la Parra , J.C. Poggiale , E. Sánchez , L. Sanz

IRD UR Geodes, 32 avenue Henri Varagnat, 93143 Bondy cedex, France

Departamento de Matemáticas, Universidad de Alcalá, Spain

Centre d'Océanologie de Marseille, UMR CNRS 6117, Université de la Méditerranée, France

Departamento de Matemática Aplicada, E.T.S.I. Industriales, Universidad Politécnica de Madrid, Spain

Abstract

Approximate aggregation techniques allow one to transform a complex system involving many coupled variables into a simpler reduced model with a lesser number of global variables in such a way that the dynamics of the former can be approximated by that of the latter. In ecology, as a paradigmatic example, we are faced with modelling complex systems involving many variables corresponding to various interacting organization levels. This review is devoted to approximate aggregation methods that are based on the existence of different time scales, which is the case in many real systems as ecological ones where the different organization levels (individual, population, community and ecosystem) possess a different characteristic time scale. Two main goals of variables aggregation are dealt with in this work. The first one is to reduce the dimension of the mathematical model to be handled analytically and the second one is to understand how different organization levels interact and which properties of a given level emerge at other levels. The review is organized in three sections devoted to aggregation methods associated to different mathematical formalisms: ordinary differential equations, infinite-dimensional evolution equations and difference equations.

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

1. Introduction

Mathematical ecology provided a first generation of simple models involving a small number of state variables and parameters. The time continuous Lotka–Volterra models, published in the beginning of the XXth century, as well as the discrete host-parasite Nicholson–Bailey models can be found among many other examples in many biomathematical textbooks as the book by Edelstein-Keshet and the book by Murray. In population dynamics models, the state variables are frequently chosen as the population densities and the model is a set of a few number of

nonlinear coupled ordinary differential equations (ODE's) or discrete equations. These simple models involving few variables and parameters are in general more likely to be handled analytically.

During the last decades, supported by the fast development of computers, a new generation of ecological models has appeared. Nowadays, lots of ecological models consider more and more details. Incorporating more details in models is necessary to advance toward a more realistic description of ecological systems and to understand how living organisms respond to the forcing imposed by their environment changes. The drawback of a detailed description of systems is the fact that models become more complex, involving an increasing number of variables and parameters. A mathematical study with general and robust results is then difficult to perform. For this reason, it is important to find which details are really relevant and must be incorporated in a model. An important goal of ecological modelling should thus be to describe tractable models.

In ecology, the problem of aggregation of variables may be set in this way: when considering a detailed system with various interacting organization levels, is there a way to find, at each level, a reduced set of variables describing the dynamics of this level? How to find such variables? How to find the relations between these macro variables and the micro variables associated to the detailed description? Under which assumptions these questions could be dealt with? Do these assumptions have a realistic basis? This review aims to describe some mathematical methods of aggregation of variables which have been developed in the recent years to give answers to two main goals. The first one is to reduce the dimension of the mathematical model to be handled analytically. The second one is to understand how different organization levels interact and which properties of a given level emerge at other levels.

Aggregation of variables was introduced in the field of economics and was made popular in ecology by Iwasa, Andreasen and Levin in 1987, [Iwasa et al. 1987](#). In general, the aggregation of a system consists of defining a small number of global variables, functions of all state variables, and to derive a system describing their dynamics. In this review, we focus on approximate aggregation [Iwasa et al. 1987](#) which are methods of reduction where the consistency between the dynamics of the global variables in the complete system and the aggregated system is only approximate.

This review is devoted to present approximate aggregation methods that are based on the existence of different time scales. Indeed, it is usual in ecology to consider different ecological levels of organization, [Iwasa et al. 1987](#) the individual, population, community and ecosystem levels to which different characteristic time scales are associated. For example, a fast time scale would correspond to individual processes while a slower time scale could be associated to demographic ones. It is then possible to take advantage of these time scales in order to reduce the dimension of the initial complete model and to build a simplified system describing the dynamics of a few number of global variables. Such methods originated in Auger [Auger 1994](#) and were presented in a rigorous mathematical form for ODEs in Auger and Roussarie in 1994 [Auger and Roussarie 1994](#) and in Auger and Poggiale in 1998 [Auger and Poggiale 1998](#), and were extended to discrete models in Sanchez et al. in 1995 [Sanchez et al. 1995](#) and in Bravo de la Parra et al. in 1995 [Bravo de la Parra et al. 1995](#), and also to PDEs in Arino et al. in 1999 [Arino et al. 1999](#) and to DDEs in Sánchez [Sánchez 2000](#). The review is organized in three main sections corresponding to aggregation methods and applications in ODEs, some infinite-dimensional dynamical systems and difference equations respectively.

2. Aggregation of variables for ODE's systems

2.1. Notation and position of the problem

Let us consider a population dynamics model describing the interactions between A populations and let us assume that each population is structured in subpopulations. We denote by n_i^α the abundance of subpopulation i in population α , $\alpha = 1, \dots, A$ and $i = 1, \dots, N_\alpha$ where N_α is the number of subpopulations in population α . We now assume that the dynamics of the subpopulation i in population α results from the interactions of a set of processes among which some are much faster than the other ones. The complete model reads:

$$\frac{dn_i^\alpha}{d\tau} = F_i^\alpha(\mathbf{n}) + \varepsilon f_i^\alpha(\mathbf{n}), \quad (1)$$

where \mathbf{n} is the vector $(n_1^1, n_2^1, \dots, n_{N_1}^1, n_1^2, n_2^2, \dots, n_{N_2}^2, \dots, n_1^\alpha, n_2^\alpha, \dots, n_{N_\alpha}^\alpha, \dots, n_1^A, n_2^A, \dots, n_{N_A}^A)$, F_i^α describe the fast processes affecting n_i^α and εf_i^α describes the slow processes affecting n_i^α . The parameter ε is small and means that the speed of the processes described in f_i^α are slow. This model is assumed to contain all the details that we want to include in the description. It governs the so-called micro-variables n_i^α which are those associated to a detailed level.

We denote by k the number of micro-variables, that is the dimension of \mathbf{n} . More precisely, we have:

$$k = \sum_{\alpha=1}^A N_{\alpha}.$$

We want now to build a model which describes the system at a macro level. We thus define a set of macro-variables. In this framework, a macro-variable is a variable varying slowly, that is a first integral of the fast dynamics. More precisely, let us define Y_j , $j = 1, \dots, N$, the macro-variables. Such a variable can be defined as a function of \mathbf{n} . The fact that Y_j is a slow variable means that its derivative with respect to τ is of order of ε :

$$Y_j = \Phi_j(\mathbf{n}), \quad j = 1, \dots, N, \quad (2a)$$

$$\frac{dY_j}{d\tau} = \sum_{\alpha=1}^A \sum_{i=1}^{N_{\alpha}} \frac{\partial \Phi_j(\mathbf{n})}{\partial n_i^{\alpha}} \frac{dn_i^{\alpha}}{d\tau} = O(\varepsilon). \quad (2b)$$

The second equation (2b), associated with Eq. (1), implies the following equality:

$$\sum_{\alpha=1}^A \sum_{i=1}^{N_{\alpha}} \frac{\partial \Phi_j(\mathbf{n})}{\partial n_i^{\alpha}} F_i^{\alpha}(\mathbf{n}) = 0, \quad j = 1, \dots, N. \quad (3)$$

Finally, the equations for the macro-variables read:

$$\frac{dY_j}{d\tau} = \varepsilon \sum_{\alpha=1}^A \sum_{i=1}^{N_{\alpha}} \frac{\partial \Phi_j(\mathbf{n})}{\partial n_i^{\alpha}} f_i^{\alpha}(\mathbf{n}). \quad (4)$$

Since the system is more detailed at the micro-level, we should have $N \ll k$. In order to use the macro-variables, we replace N micro-variables in the complete model (1) by some expressions depending of the macro-variables and this can be done under the following conditions. We suppose that the set of N Eqs. (2a) permits to write N variables among the micro-variables n_i^{α} , $\alpha = 1, \dots, A$, $i = 1, \dots, N_{\alpha}$, as functions of the N macro-variables Y_j , $j = 1, \dots, N$. We thus have to deal with k variables among which N are macro-variables and $k - N$ are micro-variables. This system is formed by $k - N$ equations of system (1) and the N equations of system (4). In other words, we perform a change of variables $(X, Y) \mapsto \mathbf{n}(X, Y)$ where X is a $k - N$ vector for which the coordinates are taken among the micro-variables n_i^{α} . With this change of variables, the complete system reads:

$$\frac{dX_i}{d\tau} = F_i(X, Y) + \varepsilon f_i(X, Y), \quad i = 1, \dots, k - N, \quad (5a)$$

$$\frac{dY_j}{d\tau} = \varepsilon G_j(X, Y), \quad j = 1, \dots, N, \quad (5b)$$

where

$$G_j(X, Y) = \sum_{\alpha=1}^A \sum_{i=1}^{N_{\alpha}} \frac{\partial \Phi_j(\mathbf{n}(X, Y))}{\partial n_i^{\alpha}} f_i^{\alpha}(\mathbf{n}(X, Y)).$$

In this form, the model (5) is a so-called slow-fast system of differential equations, or slow-fast vector field. The Geometrical Singular Perturbation (GSP) theory provides some results to deal with such systems and most important is that, under some conditions, we can reduce the complete model into an aggregated model governing only the macro-variables. We now first recall some important points of this theory and then explain the conditions for the reduction and their consequences.

2.2. Normally hyperbolic manifolds and GSP theory

There exist lots of results concerning the reduction of the dimension of a dynamical system in order to facilitate its study. For instance, we can find several statements of the center manifold theorem in various contexts (ordinary differential equations, partial differential equations, delay differential equations, difference equations). Carr's book

gives a detailed description of the theorem with many applications. The center manifold theorem states some conditions under which there exists a regular manifold containing the nontrivial part of the dynamics. This kind of manifolds are associated to nonhyperbolic singularities and are local ones. In 1971, Fenichel [10] stated a theorem which provides conditions under which an invariant manifold persists to small enough perturbations, in the case of vector fields. In the same time, Hirsch [11] gave some necessary conditions for the persistence and developed the normally hyperbolic manifolds theory. The perturbations of invariant manifolds theory originates from the works of Krylov and Bogoliubov [12]. Nowadays, this theory has lots of applications and some illustrations can be found in Pliss and Sell's book [13]. Furthermore, Wiggins [14] gives a complete description of the theory in finite dimension, this book is based on the Fenichel original paper. In these references, the conditions of normal hyperbolicity are based on geometrical considerations, which are not always useful in applications. In 1990, Sakamoto [15] gave similar conditions by using eigenvalues of Jacobian matrices. His proof may also be obtained by Fenichel's methods. Our reduction method is based on this approach, Auger et al. in 1999 [16], Auger et al. in 2000 [17], Auger and Poggiale in 1995, 1996 and 1998 [18]. Note that the Fenichel theorem has been extended to semi-groups on Banach spaces by Bates et al. in 1998 and in 2000 [19].

2.3. Reduction theorem

In order to perform the analysis, we add to system (5) the equation $d\varepsilon/d\tau = 0$:

$$\frac{dX_i}{d\tau} = F_i(X, Y) + \varepsilon f_i(X, Y), \quad i = 1, \dots, k - N, \quad (6a)$$

$$\frac{dY_j}{d\tau} = \varepsilon G_j(X, Y), \quad j = 1, \dots, N, \quad (6b)$$

$$\frac{d\varepsilon}{d\tau} = 0. \quad (6c)$$

The system (6) can be considered as an ε -perturbation of the system obtained with $\varepsilon = 0$. The situation where $\varepsilon = 0$ refers to the nonperturbed problem. The conditions for the reduction are:

(C1) When ε is null in system (6), then Y is a constant. We assume that, for each $Y \in \mathbb{R}^N$, there exists at least one equilibrium $(X = X^*(Y), Y, 0)$, defined by $F_i(X^*(Y), Y) = 0, i = 1, \dots, k - N$. We define the set:

$$\mathcal{M}_0 = \{(X, Y, \varepsilon); X = X^*(Y); \varepsilon = 0\}.$$

This invariant set for the nonperturbed system shall play the role of the invariant normally hyperbolic manifold mentioned in the GSP theory.

(C2) Let us denote $J(Y)$ the linear part of system (6) around the equilibrium $(X^*(Y), Y, 0)$. We assume that the Jacobian matrix $J(Y)$ has $k - N$ eigenvalues with negative real parts and $N + 1$ null eigenvalues. With this condition, the set \mathcal{M}_0 is said *normally hyperbolic* since, at each point in \mathcal{M}_0 , the restriction of the linear part to the \mathcal{M}_0 normal space has negative eigenvalues. We now give the statement of the main theorem.

Theorem 1. *Under the conditions (C1) and (C2), for each compact subset Ω in \mathbb{R}^N and for each integer $r > 1$, there exists a real number ε_0 and a C^r application Ψ ,*

$$\begin{aligned} \Psi : \Omega \times [0; \varepsilon_0] &\rightarrow \mathbb{R}^{k-N} \\ (Y, \varepsilon) &\mapsto X = \Psi(Y, \varepsilon) \end{aligned}$$

such that:

- (1) $\Psi(Y, 0) = X^*(Y)$;
- (2) the graph \mathcal{W} of Ψ is invariant under the flow defined by the vector field (6);
- (3) at each $(X^*(Y), Y, 0) \in \mathcal{M}_0$, \mathcal{W} is tangent to the central eigenspace E^c associated to the eigenvalues of $J(Y)$ with null real parts.

This means that we can consider the restriction of the vector field to the invariant manifold which allows us to reduce the dimension of the model. The reduced system, called aggregated model, is:

$$\frac{dY_j}{dt} = G_j(\Psi(Y, \varepsilon), Y),$$

where $t = \varepsilon\tau$. Usually, since ε is small, we approximate the previous system by:

$$\frac{dY_j}{dt} = G_j(\Psi(Y, 0), Y).$$

Moreover, since Ψ is C^r , we can calculate a Taylor expansion of the invariant manifold with respect to the small parameter ε in order to increase the accuracy of the reduced system. The reduction and the Taylor expansion are illustrated on the following example. In this example, the zero order term in the expansion leads to a nonstructurally stable system. It means that the ε term is important to understand the real dynamics. This term is then calculated and the dynamics of the complete and reduced models are compared.

2.3.1. Nontrivial example of application

Let us consider the following system based upon a model of a marine Bacteriophage infection by Beretta and Kuang

$$\begin{cases} \frac{dS}{dt} = rS\left(1 - \frac{S}{K}\right) - kSV, \\ \frac{dI}{dt} = kSV - \lambda I, \\ \frac{dV}{dt} = \beta\lambda I - kSV - \mu V, \end{cases}$$

where we assume that β and λ are much larger than the other parameters. We thus introduce a new dimensionless small parameter ε and let: $\alpha = \varepsilon\beta$ and $\gamma = \varepsilon\lambda$. Moreover, we introduce the new variable $H = S + I + \varepsilon\frac{V}{\alpha}$ and rescaling the time by $\tau = t/\varepsilon$, the previous system reads:

$$\begin{cases} \frac{dS}{d\tau} = \varepsilon rS\left(1 - \frac{S}{K}\right) - k\alpha S(H - S - I), \\ \frac{dI}{d\tau} = k\alpha S(H - S - I) - \gamma I, \\ \frac{dH}{d\tau} = \varepsilon rS\left(1 - \frac{S}{K}\right) - \varepsilon(\mu + kS)(H - S - I). \end{cases}$$

Now the system has the slow fast form that allows the aggregation method to be applied. We first consider the case $\varepsilon = 0$:

$$\begin{cases} \frac{dS}{d\tau} = -k\alpha S(H - S - I), \\ \frac{dI}{d\tau} = k\alpha S(H - S - I) - \gamma I, \\ \frac{dH}{d\tau} = 0. \end{cases}$$

It follows that on a short time scale, H is constant and $(0, 0)$ and $(H, 0)$ are the equilibria in the (S, I) space. The Jacobian matrices of the fast system near the equilibria are respectively:

$$J_{(0,0)} = \begin{pmatrix} -\alpha kH & 0 \\ \alpha kH & -\gamma \end{pmatrix} \quad \text{and} \quad J_{(H,0)} = \begin{pmatrix} \alpha kH & \alpha kH \\ -\alpha kH & -\alpha kH - \gamma \end{pmatrix}.$$

The eigenvalues of the first matrix are $-\alpha kH$ and $-\gamma$ while the second matrix has a negative determinant, meaning that $(0, 0)$ is a locally stable node and $(H, 0)$ is a saddle point. Thus, when $\varepsilon = 0$, there are two invariant manifolds, the first one is normally stable while the other one is normally unstable. They cross each other at $(S, I, H) = (0, 0, 0)$, where they lose their normal hyperbolicity.

According to Theorem 1 we can conclude that for each $H > 0$ the aggregation method applies. In other words, for each $H > 0$, there exists ε_0 such that we can aggregate the complete system for all $\varepsilon < \varepsilon_0$. However, ε_0 depends on H and if H is too small, then Theorem 1 does not apply anymore. In this case we must proceed as follows: since (S, I) tends to $(0, 0)$, we replace (S, I) by $(0, 0)$ in the H equation to get the aggregated model:

$$\frac{dH}{dt} = -\mu H + O(\varepsilon).$$

It follows that H goes to zero. The problem is thus that after a transient time, the value of H becomes of order of ε and thus one of the above referred eigenvalues, $-\alpha k H$, is close to zero. In other words, the invariant manifold is not normally hyperbolic. The way to solve the problem is considering more carefully the point $(0, 0, 0)$ in the phase space by performing a blow up:

$$\begin{cases} S = \varepsilon s, \\ I = \varepsilon i, \\ H = \varepsilon h. \end{cases}$$

The system reads then:

$$\begin{cases} \frac{ds}{d\tau} = r\varepsilon s \left(1 - \frac{\varepsilon s}{K}\right) - \varepsilon k\alpha s(h - s - i), \\ \frac{di}{d\tau} = \varepsilon k\alpha s(h - s - i) - \gamma i, \\ \frac{dh}{d\tau} = r\varepsilon s \left(1 - \frac{\varepsilon s}{K}\right) - \varepsilon(\mu + k\varepsilon s)(h - s - i). \end{cases}$$

Once again, it is a slow fast system on which we apply the aggregation method. When $\varepsilon = 0$, the system is:

$$\begin{cases} \frac{ds}{d\tau} = 0, \\ \frac{di}{d\tau} = -\gamma i, \\ \frac{dh}{d\tau} = 0. \end{cases}$$

Thus i is the only fast variable and it reaches 0. In fact, the GSP theory says more precisely that there exists an invariant manifold given by:

$$i = \varepsilon\omega_1(s, h) + o(\varepsilon).$$

In order to determine the function ω_1 , we calculate the ε expansion of $di/d\tau$ in two ways. From the previous expression, we get:

$$\frac{di}{d\tau} = \varepsilon \frac{\partial\omega_1}{\partial s} \frac{ds}{d\tau} + \varepsilon \frac{\partial\omega_1}{\partial h} \frac{dh}{d\tau} = O(\varepsilon^2).$$

On the other hand, from the i equation in the model, we have:

$$\frac{di}{d\tau} = \varepsilon k\alpha s(h - s) - \varepsilon\gamma\omega_1(s, h) + O(\varepsilon^2).$$

As a consequence, the term of order ε in the previous equation vanishes and we get:

$$\omega_1(s, h) = \frac{\alpha k s(h - s)}{\gamma}.$$

If we replace i by its equilibrium value 0 in the (s, h) equations of the model, we get:

$$\begin{cases} \frac{ds}{dt} = rs - k\alpha s(h - s) + O(\varepsilon), \\ \frac{dh}{dt} = rs - \mu(h - s) + O(\varepsilon). \end{cases}$$

Letting $y = h - s$, the system becomes:

$$\begin{cases} \frac{ds}{dt} = rs - k\alpha s y + O(\varepsilon), \\ \frac{dy}{dt} = -\mu y + k\alpha s y + O(\varepsilon). \end{cases}$$

This is an ε -perturbation of the Lotka–Volterra predator-prey model, which is not structurally stable. The ε term must then be made explicit. We get:

$$\begin{cases} \frac{ds}{dt} = rs - k\alpha s y - \varepsilon r \frac{s^2}{K} + \varepsilon \frac{(\alpha k)^2 s^2 y}{\gamma} + O(\varepsilon^2), \\ \frac{dy}{dt} = -\mu y + k\alpha s y + \varepsilon(\mu - \alpha k s) \frac{\alpha k s y}{\gamma} - \varepsilon k s y + O(\varepsilon^2). \end{cases}$$

In the positive quadrant, the trajectories of this system are unchanged by dividing each equation by the positive function $(s, y) \mapsto sy$. We shall thus analyze the trajectories of:

$$\begin{cases} \frac{ds}{dt} = \frac{r}{y} - k\alpha - \varepsilon r \frac{s}{Ky} + \varepsilon \frac{(\alpha k)^2 s}{\gamma} + O(\varepsilon^2), \\ \frac{dy}{dt} = -\frac{\mu}{s} + k\alpha + \varepsilon(\mu - \alpha ks) \frac{\alpha k}{\gamma} - \varepsilon k + O(\varepsilon^2). \end{cases}$$

Let $F(s, y) = \mu \ln(s) - \alpha ks + r \ln(y) - \alpha ky$. The dual differential form of the previous system is:

$$\omega = dF + \varepsilon \eta + o(\varepsilon),$$

where

$$\eta = -\left((\mu - \alpha ks) \frac{\alpha k}{\gamma} + k \right) ds + \left(r \frac{s}{Ky} - \frac{(\alpha k)^2 s}{\gamma} \right) dy.$$

In order to understand how the ε -perturbation modifies the center associated to the nonperturbed system, we consider a half-line starting at the positive equilibrium point (close to $(s, y) = (\mu/\alpha k, r/\alpha k)$) and we parameterize this line by level curves $F = f$. On this half line, there exists a Poincaré map P and we define the displacement function $\delta(f) = P(f) - f$. If this number is positive, then $P(f) > f$ meaning that the trajectory leaves the equilibrium while a negative value means that the trajectory is going closer to the equilibrium. The Poincaré lemma claims that:

$$\delta(f) = -\varepsilon \int_{\{F=f\}} \eta + o(\varepsilon).$$

Thus the sign of $\delta(f)$ is given by the sign of $-\int_{\{F=f\}} \eta$ if ε is small enough. By the Stokes theorem, we get:

$$\begin{aligned} - \int_{\{F=f\}} \eta &= - \int \int_{\{F \leq f\}} d\eta \\ &= \int \int_{\{F \leq f\}} \left(\frac{(\alpha k)^2}{\gamma} - \frac{r}{Ky} \right) ds \wedge dy \\ &= \frac{(\alpha k)^2}{\gamma} \int \int_{\{F \leq f\}} ds \wedge dy - \frac{r}{K} \int \int_{\{F \leq f\}} \frac{1}{y} ds \wedge dy \\ &= A(f) - \frac{r}{K} \int \int_{\{F \leq f\}} \frac{1}{y} ds \wedge dy, \end{aligned}$$

where $A(f)$ is the area of the domain $\{F \leq f\}$. If f is large, then the domain contains some points (s, y) for which y is very small, thus the negative term in the last expression is very large. Consequently, trajectories initiated far away from the equilibrium point are coming back to the equilibrium. Let us now consider trajectories close to the equilibrium. In this case, $y \simeq r/\alpha k$ and the sign of $-\int_{\{F=f\}} \eta$ is then the same as the sign of $(\alpha k)^2/\gamma - \alpha k/K = \alpha k(\alpha k/\gamma - 1/K)$. Thus if we consider, for instance, the carrying capacity (nutritive richness of the environment) as a bifurcation parameter, we see that a bifurcation occurs when $K \simeq \gamma/\alpha k$. If K is smaller than the bifurcation value, then $\alpha k(\alpha k/\gamma - 1/K) < 0$ and the equilibrium point is stable (see Fig. 1). However, when K is increased and becomes larger than the bifurcation value $\simeq \gamma/\alpha k$, then the equilibrium is unstable. Since trajectories far away from the equilibrium are getting closer to the equilibrium, the Poincaré–Bendixon theorem claims that at least a limit cycle exists (see Fig. 2).

2.4. How to define the slow and fast variables in a given system

An ecosystem involves a large number of variables and processes. It is largely recognized that some processes are much faster than others. However, each variable may be affected by fast and slow processes. It follows that, when we write a model, the slow and fast processes are mixed in the differential systems and it is not clear that some variables

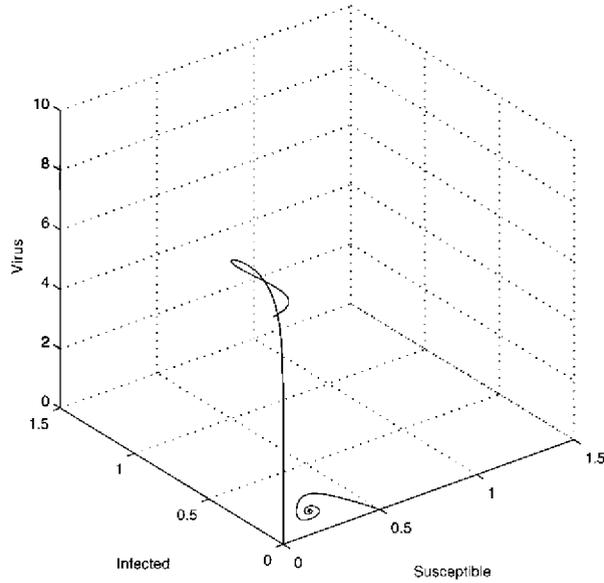


Fig. 1. This figure is obtained from the complete model simulation. The parameter values are: $r = 1$, $K = 0.5$, $k = 1$, $\alpha = 1$, $\gamma = 1$, $\mu = 0.6$ and $\varepsilon = 0.2$. The bifurcation value in this case is thus approximately 1. Since $K < 1$, the equilibrium is stable.

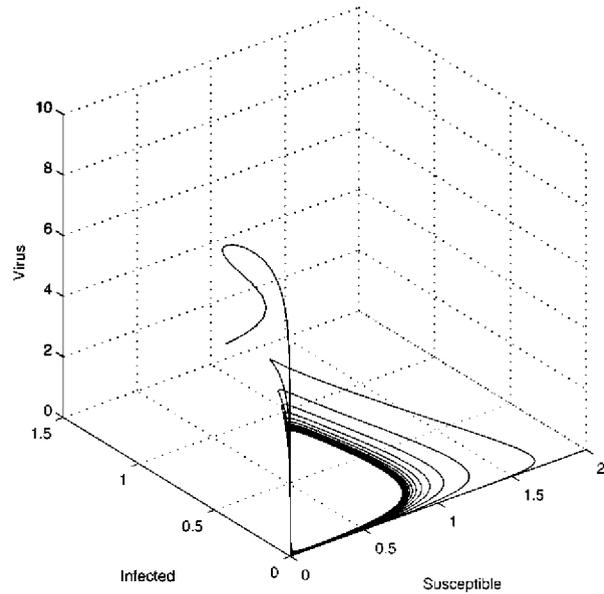


Fig. 2. This figure is obtained from the complete model simulation. The parameter values are: $r = 1$, $K = 2$, $k = 1$, $\alpha = 1$, $\gamma = 1$, $\mu = 0.6$ and $\varepsilon = 0.2$. The bifurcation value in this case is thus approximately 1. Since $K > 1$, the equilibrium is unstable and a limit cycle exists.

are faster than other ones. According to the previous notations, the problem is, given the system (1), is there an algorithm allowing to define the slow variables Y ? This is generally a crucial problem. From the mathematical point of view, such an algorithm permits to transform system (1) into system (5). Moreover, from the applied point of view, it would permit to define the variables of interest for the long time dynamics on the basis of the detailed description. In our framework, the slow variables are defined by the fact that they are first integrals of the fast processes. But it is not always easy to find such functions and this problem can limit practical applications.

2.5. Relation between aggregation and emergence

Aggregation not only provides a reduction of the dimension of the initial model and its simplification, but it also provides interesting information about the emergence of fast processes at a global level in the long run. Indeed, the invariant manifold on which the reduction is performed is a graph on the slow variables $X = \Psi(Y, \varepsilon)$. In other words, at a fast time scale, the fast variables reach an attractor, for instance, an equilibrium, which depends on the slow variables. From the practical point of view, the reduced model is obtained by replacing the fast variables by $\Psi(Y, \varepsilon)$ in the slow variables equations. Consequently, if the fast part of the model is changed, then Ψ is modified and the aggregated model as well. This application Ψ contains the effects of the fast part on the long term dynamics. These effects can lead to emerging properties. The concept of emergence has been widely developed in ecology. In [13], we provided two kinds of emergence concepts by using the aggregation approach.

3. Aggregation of variables in linear infinite-dimensional dynamical systems

In this section we will apply the aggregation of variables method to linear models of population dynamics formulated mathematically in an infinite-dimensional abstract setting. To be precise, we will consider two situations: an age structured model formulated as a system of linear partial differential equations (P.D.E.) and another one formulated in terms of delayed differential equations (D.D.E.). The different time scales introduce into the model a small parameter $\varepsilon > 0$ which gives rise to a singular perturbation mathematical problem. Although both contexts are mathematically very different, the underlying ideas in the construction of the aggregated model are similar in both cases, due to the structure of the fast dynamics: it is supposed that this dynamics is represented by a matrix K whose spectrum allows the decomposition of the space \mathbf{R}^N into a direct sum of the eigenspace $\ker K$ associated to the eigenvalue 0 and generated by a vector v , plus a complementary stable subspace S corresponding to the remaining part of the spectrum, which are eigenvalues with negative real part. The aggregated model is constructed by adequately projecting the global dynamics onto $\ker K$. The theory of semigroups allows a unified formulation of both situations aimed at obtaining approximation results for the solutions to the perturbed global model by the solutions to the aggregated model, using the same technique in both cases: with the help of a variation-of-constants formula, the perturbed system is transformed into a fixed point problem for the projection of the solution onto $\ker K$.

3.1. Aggregation in age structured population models

We will apply the aggregation of variables method to a linear age-structured population dynamics model with age a and time t being continuous variables. The population is distributed into N spatial patches. The evolution of the population is due to the migration process between different patches at a fast time scale and to the demographic process at a slow time scale. The impression is that of a spatially homogeneous age-dependent population governed by a Von Foerster equation with birth and death coefficients averaged from the original patch-dependent coefficients through a weighted average. The weights are computed in terms of a migration matrix and are in fact the mark of the hidden underlying spatial structure. See [16,34,35] for the details.

Let $n_i(a, t)$ be the population density in patch i ($i = 1, \dots, N$) so that $\int_{a_1}^{a_2} n_i(a, t) da$ represents the number of individuals in patch i whose age $a \in [a_1, a_2]$ at time t and

$$\mathbf{n}(a, t) := (n_1(a, t), \dots, n_N(a, t))^T.$$

Let $\mu_i(a)$ and $\beta_i(a)$ be the patch and age-specific mortality and fertility rates respectively and

$$M(a) := \text{diag}\{\mu_1(a), \dots, \mu_N(a)\}; \quad B(a) := \text{diag}\{\beta_1(a), \dots, \beta_N(a)\}.$$

Let $k_{ij}(a)$ be the age-specific migration rate from patch j to patch i , $i \neq j$, and

$$K(a) := (k_{ij}(a))_{1 \leq i, j \leq N} \quad \text{with } k_{ii}(a) := - \sum_{j=1, j \neq i}^N k_{ji}(a).$$

A crucial assumption is that the jump process is conservative with respect to the life dynamics of the population, that is to say, no death or birth is directly incurred by spatial migrations.

The model based upon the classical McKendrick–Von Foerster model for an age-structured population is as follows:

$$\begin{cases} \frac{\partial \mathbf{n}}{\partial t}(a, t) + \frac{\partial \mathbf{n}}{\partial a}(a, t) = [-M(a) + \frac{1}{\varepsilon} K(a)] \mathbf{n}(a, t) & (a > 0, t > 0), \\ \mathbf{n}(0, t) = \int_0^{+\infty} B(a) \mathbf{n}(a, t) da & (t > 0), \\ \mathbf{n}(a, 0) = \Phi(a) := (\Phi_1(a), \dots, \Phi_N(a))^T & (a > 0), \end{cases} \quad (7)$$

where $\varepsilon > 0$ is a constant small enough which takes into account the two different time scales.

For each initial age distribution $\Phi \in X := L^1(\mathbf{R}_+; \mathbf{R}^N)$, the problem (7) has a unique solution \mathbf{n}_ε that defines a strongly continuous semigroup of linear operators (C_0 -semigroup) on X , $\{T_\varepsilon(t)\}_{t \geq 0}$, such that $T_\varepsilon(t)\Phi := \mathbf{n}_\varepsilon(\cdot, t)$.

In what follows we will assume that the matrix $K(a)$ is irreducible for every $a > 0$. As a consequence 0 is a simple eigenvalue larger than the real part of any other eigenvalue. The left eigenspace of matrix $K(a)$ associated with the eigenvalue 0 is generated by vector $\mathbf{1} := (1, \dots, 1)^T \in \mathbf{R}^N$. The right eigenspace is generated by vector $\mathbf{v}(a) := (v_1(a), \dots, v_N(a))^T$ and is unique if we choose it having positive entries and verifying $\mathbf{1}^T \mathbf{v}(a) = 1$.

3.1.1. The aggregated model

We build up a model which describes the dynamics of the total population:

$$n(a, t) := \sum_{i=1}^N n_i(a, t) \quad (\text{global variable})$$

with the help of the approximation:

$$v_i(a, t) := \frac{n_i(a, t)}{n(a, t)} \approx v_i(a), \quad i = 1, \dots, N,$$

which leads to the following *aggregated model* for the density of the total population:

$$\begin{cases} \frac{\partial n}{\partial t}(a, t) + \frac{\partial n}{\partial a}(a, t) = -\mu^*(a)n(a, t) & (a, t > 0), \\ n(0, t) = \int_0^{+\infty} \beta^*(a)n(a, t) da & (t > 0), \\ n(a, 0) = \varphi(a) := \sum_{i=1}^N \Phi_i(a) & (a > 0), \end{cases} \quad (8)$$

where

$$\mu^*(a) := \sum_{i=1}^N \mu_i(a)v_i(a); \quad \beta^*(a) := \sum_{i=1}^N \beta_i(a)v_i(a).$$

It is a classical Sharpe–Lotka–McKendrick linear model to which the general theory applies. Under some technical conditions which are specified the solutions to this problem define a C_0 -semigroup on $L^1(\mathbf{R}_+)$, which has the so-called *asynchronous exponential growth property*, namely

Proposition 1. *There exists a unique $\lambda_0 \in \mathbf{R}$ (Malthusian parameter) such that $\lim_{t \rightarrow +\infty} e^{-\lambda_0 t} n(a, t) = c(\varphi)\theta_0(a)$, where $c(\varphi) > 0$ is a constant depending on the initial value $\varphi \in L^1(\mathbf{R}_+)$ and $\theta_0(a) := e^{-\lambda_0 a} e^{-\int_0^a \mu^*(\sigma) d\sigma}$ is the asymptotic distribution.*

3.1.2. Approximation result

Let us say a few words about the nature of the convergence of the solutions to the perturbed problem (7) when $\varepsilon \rightarrow 0_+$ to the solutions to the aggregated model (8).

The irreducibility of matrix $K(a)$ allows the direct sum decomposition $\mathbf{R}^N = [v(a)] \oplus S$ in which $[v(a)]$ is the one-dimensional subspace generated by the vector $v(a)$ and $S := \{\mathbf{v} \in \mathbf{R}^N; \mathbf{1}^T \cdot \mathbf{v} = 0\}$. Notice that S is the same for all a , and moreover $K_S(a)$, the restriction of $K(a)$ to S is an isomorphism on S with spectrum $\sigma(K_S(a)) \subset \{\lambda \in \mathbf{C}; \operatorname{Re} \lambda < 0\}$.

According to it, we can decompose the solutions to the perturbed problem, that is to say

$$\mathbf{n}_\varepsilon(a, t) := p_\varepsilon(a, t)v(a) + \mathbf{q}_\varepsilon(a, t); \quad \mathbf{q}_\varepsilon(a, t) \in S$$

giving

$$\frac{\partial p_\varepsilon}{\partial t}(a, t) + \frac{\partial p_\varepsilon}{\partial a}(a, t) = -\mu^*(a)p_\varepsilon(a, t) - \mathbf{1}^T M(a)\mathbf{q}_\varepsilon(a, t), \quad (9)$$

$$\frac{\partial \mathbf{q}_\varepsilon}{\partial t}(a, t) + \frac{\partial \mathbf{q}_\varepsilon}{\partial a}(a, t) = -[M_S(a)v(a) + v'(a)]p_\varepsilon(a, t) + \left[\frac{1}{\varepsilon}K_S(a) - M_S(a)\right]\mathbf{q}_\varepsilon(a, t), \quad (10)$$

$$p_\varepsilon(a, t) = \int_0^{+\infty} \beta^*(a)p_\varepsilon(a, t) da + \int_0^{+\infty} \mathbf{1}^T B(a)\mathbf{q}_\varepsilon(a, t) da, \quad (11)$$

$$\mathbf{q}_\varepsilon(0, t) = \int_0^{+\infty} B_S(a)v(a)p_\varepsilon(a, t) da + \int_0^{+\infty} B_S(a)\mathbf{q}_\varepsilon(a, t) da, \quad (12)$$

where $M_S(a)$, $B_S(a)$ are the projections of $M(a)$ and $B(a)$ respectively onto S .

The solutions to the homogeneous problem associated to \mathbf{q}_ε define a C_0 -semigroup $\{\mathcal{U}_\varepsilon(t)\}_{t \geq 0}$ which satisfies the estimation

$$\|\mathcal{U}_\varepsilon(t)\| \leq C_1 e^{(C_2 - C_3/\varepsilon)t}, \quad t \geq 0 \quad (C_1, C_2, C_3 > 0).$$

Therefore, under some technical conditions and using a variation-of-constants formula, we can express the solution to the nonhomogeneous system (10)–(12) in terms of $\mathcal{U}_\varepsilon(t)$ and p_ε . Then substituting this expression in (9)–(11), we can transform these equations into a fixed point problem for p_ε that can be solved using standard techniques, which provide the following result of approximation:

Theorem 2. *For each $\varepsilon > 0$ small enough, we have*

$$\mathbf{n}_\varepsilon(a, t) = n(a, t)v(a) + (\mathcal{U}_\varepsilon(t)\mathbf{q}_0)(a) + O(\varepsilon),$$

where $n(a, t)$ is the solution to the aggregated model corresponding to the initial age distribution p_0 and $\Phi := p_0v + \mathbf{q}_0$ ($\mathbf{q}_0 \in S$) is the initial age distribution for the perturbed system.

We point out that the above formula is of interest mainly in the case when $\lambda_0 \geq 0$. In this case, it can be concluded from the above formula that $\mathbf{n}_\varepsilon(\cdot, t) \approx n(\cdot, t)v(\cdot)$ as $t \rightarrow +\infty$ uniformly with respect to $\varepsilon > 0$ small enough. Also, if $\lambda_0 < 0$ then $\mathbf{n}_\varepsilon(\cdot, t) \rightarrow 0$ as $t \rightarrow +\infty$ and this is again uniform with respect to $\varepsilon > 0$ small enough. In this case, however, $n(\cdot, t)v(\cdot)$ does not dominate in general the terms $O(\varepsilon)$.

See [16] for the details. In this paper it is also shown that the semigroup $\{T_\varepsilon(t)\}_{t \geq 0}$ has the asynchronous exponential growth property. Roughly speaking, it is shown that for $\varepsilon > 0$ small enough, each solution $\mathbf{n}_\varepsilon(a, t)$ of the perturbed system is such that

$$\mathbf{n}_\varepsilon(a, t) \approx C(\Phi)e^{\lambda_\varepsilon t}\Psi_\varepsilon(a) \quad (t \rightarrow +\infty),$$

where $C(\Phi) > 0$ is a constant depending on the initial age distribution and $\lim_{\varepsilon \rightarrow 0^+} \lambda_\varepsilon = \lambda_0$, $\lim_{\varepsilon \rightarrow 0^+} \Psi_\varepsilon = v\theta_0$, where λ_0 and θ_0 are, respectively, the Malthus parameter and the associated asymptotic distribution of the aggregated system mentioned in Proposition 1.

3.2. Aggregation of variables in linear delayed differential equations

Let us describe in some detail the aggregation of variables method in a simple linear model with a discrete delay. On one side, this case is interesting in itself and clarifies other abstract formulations while on the other, it has its own methods for the step-by-step construction of the solution.

The model consists of the following system of linear delayed differential equations, depending on a small parameter $\varepsilon > 0$, that we call the *perturbed system*:

$$\begin{cases} dX(t)/dt = (1/\varepsilon)KX(t) + AX(t) + BX(t-r), & t > 0, \\ X(t) = \Phi(t), & t \in [-r, 0]; \Phi \in C([-r, 0]; \mathbf{R}^N), \end{cases} \quad (13)$$

where $X(t) := (\mathbf{x}_1(t), \dots, \mathbf{x}_q(t))^T$, $\mathbf{x}_j(t) := (x_j^1(t), \dots, x_j^{N_j}(t))^T$, $j = 1, \dots, q$.

K , A and B are $N \times N$ real constant matrices with $N = N_1 + \dots + N_q$. As usual, $C([-r, 0]; \mathbf{R}^N)$ represents the Banach space of \mathbf{R}^N -valued continuous functions on $[-r, 0]$ ($r > 0$), endowed with the norm $\|\varphi\|_C := \sup_{\theta \in [-r, 0]} \|\varphi(\theta)\|$. System (13) can be solved by the classical step-by-step procedure,

Throughout this section, we suppose that matrix K is a block-diagonal matrix $K := \text{diag}\{K_1, \dots, K_q\}$ in which each diagonal block K_j has dimensions $N_j \times N_j$, $j = 1, \dots, q$, whose spectra $\sigma(K_j)$ can be written as $\sigma(K_j) = \{0\} \cup \Lambda_j$, $\Lambda_j \subset \{z \in \mathbf{C}; \text{Re } z < 0\}$ and 0 is a simple eigenvalue of K_j .

As a consequence, $\ker K_j$ is generated by an eigenvector associated to eigenvalue 0, which will be denoted \mathbf{v}_j . The corresponding left eigenspace is generated by a vector \mathbf{v}_j^* and we choose both vectors verifying the *normalization condition*: $(\mathbf{v}_j^*)^T \mathbf{v}_j = 1$.

3.2.1. The aggregated model

In order to build the *aggregated system* of system (13), we define the matrices: $\mathcal{V}^* := \text{diag}\{(\mathbf{v}_1^*)^T, \dots, (\mathbf{v}_q^*)^T\}$, $\mathcal{V} := \text{diag}\{\mathbf{v}_1, \dots, \mathbf{v}_q\}$ and consider the following direct sum decomposition of space $\mathbf{R}^N = \ker K \oplus S$, where $\ker K$ is a q -dimensional subspace generated by the columns of matrix \mathcal{V} and $S := \text{Im } K = \{\mathbf{v} \in \mathbf{R}^N; \mathcal{V}^* \mathbf{v} = \mathbf{0}\}$.

We now define the q *aggregated variables*:

$$\mathbf{s}(t) := (s_1(t), \dots, s_q(t))^T = \mathcal{V}^* X(t),$$

which satisfy a linear differential system obtained by premultiplying both sides of (13) by \mathcal{V}^* . We get the aggregated variables on the left-hand side but we fail to on the right-hand side. To avoid this difficulty, we use the above sum direct decomposition, so that $X(t) = \mathcal{V}\mathbf{s}(t) + X_S(t)$ and then

$$d\mathbf{s}(t)/dt = \mathcal{V}^* A \mathcal{V} \mathbf{s}(t) + \mathcal{V}^* B \mathcal{V} \mathbf{s}(t-r) + \mathcal{V}^* A X_S(t) + \mathcal{V}^* B X_S(t-r).$$

Therefore, we propose as *aggregated model* the following approximated system

$$d\mathbf{s}(t)/dt = \bar{A}\mathbf{s}(t) + \bar{B}\mathbf{s}(t-r), \quad t > r; \quad \bar{A} := \mathcal{V}^* A \mathcal{V}, \quad \bar{B} := \mathcal{V}^* B \mathcal{V}. \quad (14)$$

Eq. (14) is a delayed linear differential system of equations which can be solved by a standard step-by-step procedure from an initial data in $[0, r]$ which is given by:

$$\mathbf{s}(t) = e^{t\bar{A}} \left[\mathcal{V}^* \Phi(0) + \int_0^t e^{-\sigma\bar{A}} \mathcal{V}^* B \Phi(\sigma-r) d\sigma \right]. \quad (15)$$

3.2.2. Comparison between the solutions to systems (13)–(14)

Decomposing the system (13) according to the above direct sum decomposition and solving it with the help of a variation-of-constants formula in a similar way of the previous section, we can obtain a comparison between the solutions of both systems (13) and (14).

Theorem 3. *For each initial data $\Phi \in C([-r, 0]; \mathbf{R}^N)$, $\Phi = \mathcal{V}\psi + \varphi$, the corresponding solution X_ε to system (13) can be written as:*

$$\forall t \geq r, \quad X_\varepsilon(t) = \mathcal{V}\mathbf{s}_0(t) + \mathbf{r}_\varepsilon(t),$$

where \mathbf{s}_0 is the solution to the aggregated system (14) for $t \geq r$, with the initial data defined $\forall t \in [0, r]$ by (15). Moreover, there exist three constants $C > 0$, $C^* > 0$, $\gamma > 0$, such that

$$\forall t \geq r, \quad \|\mathbf{r}_\varepsilon(t)\| \leq \varepsilon(C + C^* e^{\gamma t}) \|\Phi\|_C.$$

Therefore, for each $T > r$, $\lim_{\varepsilon \rightarrow 0_+} X_\varepsilon = \mathcal{V}\mathbf{s}_0$ uniformly in the interval $[r, T]$.

This approximation result is similar to that obtained in the previous section for continuous time structured models formulated in terms of partial differential equations, but we have to point out that the delay introduces significant differences due to the influence of the initial data on the solution in the interval $[0, r]$. In fact, the approximation when $\varepsilon \rightarrow 0$ is valid only for $t \geq r$ and hence the initial data in $[0, r]$ for the aggregated system is $\mathcal{V}^* X_\varepsilon(t)$, which is the projection on $\ker K$ of the exact solution to system (13), constructed in $[0, r]$ from an initial data $\Phi \in C([-r, 0]; \mathbf{R}^N)$.

The above procedure can be generalized to the following *perturbed system* of linear delayed differential equations:

$$\begin{cases} dX(t)/dt = L(X_t) + (1/\varepsilon)KX(t), & t > 0, \\ X_0 = \Phi \in C([-r, 0]; \mathbf{R}^N), \end{cases} \quad (16)$$

where $L: C([-r, 0]; \mathbf{R}^N) \rightarrow \mathbf{R}^N$ is a bounded linear operator and X_t ($t \geq 0$), is the *section of function X at time t*, namely, $X_t(\theta) := X(t + \theta)$, $\theta \in [-r, 0]$.

The *aggregated model* is

$$ds(t)/dt = \bar{L}(s_t), \quad t \geq r; \quad \bar{L}(\psi) := \mathcal{V}^* L(\mathcal{V}\psi).$$

As in the previous case, the initial data in $[0, r]$ should be constructed, but in this abstract setting it presents higher mathematical difficulties. In particular, we should use the Riesz representation theorem of bounded linear operators on $C([-r, 0]; \mathbf{R}^N)$.

3.2.3. Application to a structured model of population dynamics with two time scales

Let us consider a continuous-time two-stage structured model of a population living in an environment divided into two different sites. Let us refer to the individuals in the two stages as juveniles and adults, so that $j_i(t)$ and $n_i(t)$ denote the juvenile and adult population respectively at site i , $i = 1, 2$. Changes in the juvenile population at site i occur through birth, maturation to the adult stage and death. Therefore, in absence of migrations, the growth rate is expressed as $\beta_i n_i(t) - e^{-\mu_i^* r_i} \beta_i n_i(t - r_i) - \mu_i^* j_i(t)$ where $\beta_i, \mu_i^*, \mu_i \geq 0$ are the fecundities and per capita death rates of juveniles and adults, respectively, and $r_i > 0$ is the juvenile-stage duration in site i . Without loss of generality, we suppose $0 < r_1 < r_2$.

In a similar way, the adult population growth rate in site i must contain recruitment and mortality terms so that in absence of migrations reads $e^{-\mu_i^* r_i} \beta_i n_i(t - r_i) - \mu_i n_i(t)$.

We consider a model which includes the demographic processes described below, together with a fast migration process between sites for the adult population defined by two parameters: $m_1 > 0$ represents the migration rate from site 1 to site 2 and $m_2 > 0$ is the migration rate from site 2 to site 1.

The difference between the two time scales: slow (demography) and fast (migration) is represented by a small parameter $\varepsilon > 0$:

$$\begin{cases} dj_1(t)/dt = \beta_1 n_1(t) - e^{-\mu_1^* r_1} \beta_1 n_1(t - r_1) - \mu_1^* j_1(t), \\ dj_2(t)/dt = \beta_2 n_2(t) - e^{-\mu_2^* r_2} \beta_2 n_2(t - r_2) - \mu_2^* j_2(t), \\ dn_1(t)/dt = (1/\varepsilon)[m_2 n_2(t) - m_1 n_1(t)] + e^{-\mu_1^* r_1} \beta_1 n_1(t - r_1) - \mu_1 n_1(t), \\ dn_2(t)/dt = (1/\varepsilon)[m_1 n_1(t) - m_2 n_2(t)] + e^{-\mu_2^* r_2} \beta_2 n_2(t - r_2) - \mu_2 n_2(t). \end{cases}$$

As we notice, the last two equations of the above system are autonomous, so we can reduce the system into them:

$$dn(t)/dt = \frac{1}{\varepsilon} K n(t) + A n(t) + B_1 n(t - r_1) + B_2 n(t - r_2), \quad (17)$$

where

$$\begin{aligned} n(t) &:= \begin{pmatrix} n_1(t) \\ n_2(t) \end{pmatrix}; & K &:= \begin{pmatrix} -m_1 & m_2 \\ m_1 & -m_2 \end{pmatrix}; & A &= \begin{pmatrix} -\mu_1 & 0 \\ 0 & -\mu_2 \end{pmatrix}; \\ B_1 &:= \begin{pmatrix} e^{-\mu_1^* r_1} \beta_1 & 0 \\ 0 & 0 \end{pmatrix}; & B_2 &:= \begin{pmatrix} 0 & 0 \\ 0 & e^{-\mu_2^* r_2} \beta_2 \end{pmatrix} \end{aligned}$$

together with an initial condition $\Phi(t) := (\Phi_1(t), \Phi_2(t))^T$, $t \in [-r_2, 0]$.

In order to build the *aggregated model* of (17) we choose the right and left eigenvectors associated to eigenvalue $\lambda = 0$ of K as $\mathbf{v} := 1/(m_1 + m_2)(m_2, m_1)^T$, $\mathbf{v}^* := (1, 1)^T$, so that we construct an aggregated model for the total adult

population:

$$\mathbf{n}(t) := (\mathbf{v}^*)^T \mathbf{n}(t) = n_1(t) + n_2(t).$$

Due to the two different delays this model does not fit in the formulation given by (13). Therefore we apply (16) so that we have

$$\forall \Phi \in C([-r_2, 0]; \mathbf{R}^2), \quad L(\Phi) := A\Phi(0) + B_1\Phi(-r_1) + B_2\Phi(-r_2)$$

and then, $\forall \psi \in C([-r_2, 0]; \mathbf{R})$:

$$\bar{L}(\psi) := -\mu^* \psi(0) + v_1^* \psi(-r_1) + v_2^* \psi(-r_2)$$

with

$$\mu^* := \frac{\mu_1 m_2 + \mu_2 m_1}{m_1 + m_2}; \quad v_1^* := \frac{e^{-\mu_1^* r_1} \beta_1 m_2}{m_1 + m_2}; \quad v_2^* := \frac{e^{-\mu_2^* r_2} \beta_2 m_1}{m_1 + m_2}.$$

The aggregated model is, for $t \geq r_2$:

$$dn(t)/dt = -\mu^* n(t) + v_1^* n(t - r_1) + v_2^* n(t - r_2) \quad (18)$$

together with the initial condition defined by:

$$\begin{aligned} n(t) &= \Phi_1(t) + \Phi_2(t), & t &\in [-r_2, 0], \\ dn(t)/dt &= -\mu^* n(t) + e^{-\mu_1^* r_1} \beta_1 \Phi_1(t - r_1) + e^{-\mu_2^* r_2} \beta_2 \Phi_2(t - r_2), & t &\in [0, r_1], \\ dn(t)/dt &= -\mu^* n(t) + v_1^* n(t - r_1) + e^{-\mu_2^* r_2} \beta_2 \Phi_2(t - r_2), & t &\in [r_1, r_2]. \end{aligned}$$

We have reduced the initial complete system of four equations to a single equation governing the total adult population. If the solution to this equation is given, then the juvenile population densities can be derived from it.

It can be shown that, for each $T > r_2$, the solution to system (17) satisfies

$$\lim_{\varepsilon \rightarrow 0^+} \begin{pmatrix} n_{1\varepsilon}(t) \\ n_{2\varepsilon}(t) \end{pmatrix} = \frac{1}{m_1 + m_2} \begin{pmatrix} m_2 \\ m_1 \end{pmatrix} n(t)$$

uniformly in $[r_2, T]$, $n(t)$ being the solution to the aggregated model (18).

4. Aggregation methods of discrete models

Let us suppose in this section a population whose evolution is described in discrete time. Apart from that, the population is generally divided into groups, and each of these groups divided into several subgroups. We will represent the state at time t of a population with q groups by a vector $\mathbf{n}(t) := (\mathbf{n}^1(t), \dots, \mathbf{n}^q(t))^T \in \mathbb{R}_+^N$ where T denotes transposition. Every vector $\mathbf{n}^i(t) := (n^{i1}(t), \dots, n^{iN^i}(t)) \in \mathbb{R}_+^{N^i}$, $i = 1, \dots, q$, represents the state of the i group which is divided into N^i subgroups, with $N = N^1 + \dots + N^q$. Following the terminology of previous sections, the n^{ij} are the micro-variables. The total population is $\|\mathbf{n}(t)\|$, where $\|\cdot\|$ denotes the 1-norm.

In the evolution of the population we will consider two processes which corresponding characteristic time scales, and consequently their projection intervals, that is their time units, are very different from each other. We will refer to them as the fast and the slow processes or, still, as the fast and the slow dynamics. We will start with the simplest case by considering both processes to be linear and autonomous and go on with the presentation of the linear nonautonomous and linear stochastic setting. Finally we will present the nonlinear case.

4.1. Linear discrete models

We present in detail the results concerning the basic autonomous case as developed in Sánchez and Sanz and Bravo de la Parra

We represent fast and slow processes by two different matrices F and S . The characteristic time scale of the fast process gives the projection interval associated to matrix F , that is, the state of the population, due to the fast

process, after one fast time unit is $F\mathbf{n}(t)$. Analogously, the effect of the slow process after one slow time unit is calculated multiplying by matrix S . In order to write a single discrete model combining both processes, and therefore their different time scales, we have to choose its time unit. Two possible and reasonable choices are the time units associated to each one of the two processes. We use here as time unit of the model that corresponding to the slow dynamics, i.e., the time elapsed between times t and $t + 1$ is the projection interval associated to matrix S . We then need to approximate the effect of the fast dynamics over a time interval much longer than its own. In order to do so we will suppose that during each projection interval corresponding to the slow process matrix F has operated a number k of times, where k is a big enough integer that can be interpreted as the ratio between the projection intervals corresponding to the slow and fast dynamics. Therefore, the fast dynamics will be modeled by F^k and the proposed model will consist in the following system of N linear difference equations that we will call *general system*:

$$\mathbf{n}_k(t + 1) = SF^k\mathbf{n}_k(t). \quad (19)$$

In order to reduce the system we must make some assumptions on the fast dynamics. We suppose that for each group $i = 1, \dots, q$ the fast dynamics is internal, conservative of a certain global variable, macro-variable, for the group and with an asymptotically stable distribution among the subgroups. These assumptions are met if we represent the fast dynamics for each group i by a $N^i \times N^i$ projection matrix F_i which is primitive with 1 as strictly dominant eigenvalue, for example, a regular stochastic matrix. The matrix F that represents the fast dynamics for the whole population is then $F := \text{diag}(F_1, \dots, F_q)$. Every matrix F_i has, associated to eigenvalue 1, positive right and left eigenvectors, v_i and u_i , respectively column and row vectors, verifying $F_i v_i = v_i$, $u_i F_i = u_i$ and $u_i \cdot v_i = 1$. The Perron–Frobenius theorem applies to matrix F_i and we denote $\bar{F}_i := \lim_{k \rightarrow \infty} F_i^k = v_i u_i$, where F_i^k is the k th power of matrix F_i . Denoting $\bar{F} := \text{diag}(\bar{F}_1, \dots, \bar{F}_q)$, we also have that:

$$\bar{F} = \lim_{k \rightarrow \infty} F^k = VU, \quad (20)$$

where $V := \text{diag}(v_1, \dots, v_q)_{N \times q}$ and $U := \text{diag}(u_1, \dots, u_q)_{q \times N}$.

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 (19) by the following so-called *auxiliary system*:

$$\mathbf{n}(t + 1) = S\bar{F}\mathbf{n}(t), \quad (21)$$

which using (20) can be written as

$$\mathbf{n}(t + 1) = SVU\mathbf{n}(t).$$

Here we see that the evolution of the system depends on $U\mathbf{n}(t) \in \mathbb{R}^q$, what suggests that dynamics of the system could be described in terms of a lesser number of variables, the global variables or macro variables defined by

$$Y(t) := U\mathbf{n}(t). \quad (22)$$

The auxiliary system (21) can be easily transformed into a q -dimensional system premultiplying by matrix V , giving rise to the so-called aggregated system or macro system $Y(t + 1) = USVY(t)$, where we denote $\bar{S} = USV$ and obtain

$$Y(t + 1) = \bar{S}Y(t). \quad (23)$$

The solutions to the auxiliary system can be obtained from the solutions to the aggregated system. It is straightforward that the solution $\{\mathbf{n}(t)\}_{t \in \mathbb{N}}$ of system (21) for the initial condition \mathbf{n}_0 is related to the solution $\{Y(t)\}_{t \in \mathbb{N}}$ of system (23) for the initial condition $Y_0 = U\mathbf{n}_0$ in the following way: $\mathbf{n}(t) = SVY(t - 1)$ for every $n \geq 1$. The auxiliary system is an example of perfect aggregation in the sense of Iwasa

Once the task of building up a reduced system is carried out, the important issue is to see if the dynamics of the general system (19) can also be studied by means of the aggregated system (23). In Sánchez it is proved that the asymptotic elements defining the long term behavior of system (19) can be approximated by those of the corresponding aggregated system when the matrix associated to the latter is primitive.

Hypothesis (H). \bar{S} is a primitive matrix.

Assuming Hypothesis (H), let $\lambda > 0$ be the strictly dominant eigenvalue of \bar{S} , and \bar{w}_l and \bar{w}_r its associated left and right eigenvectors, respectively. We then have that, given any nonnegative initial condition Y_0 , system (23) verifies

$$\lim_{t \rightarrow \infty} \frac{Y(t)}{\lambda^n} = \frac{\bar{w}_l \cdot Y_0}{\bar{w}_l \cdot \bar{w}_r} \bar{w}_r.$$

Concerning the asymptotic behavior of the auxiliary system (21), it is proved that the same $\lambda > 0$ is the strictly dominant eigenvalue of $S\bar{F}$, $U^T \bar{w}_l$ its associated left eigenvector and $SV \bar{w}_r$ its associated right eigenvector.

The asymptotic behavior of the general system (19) could be expressed in terms of the asymptotic elements of the aggregated system (21) by considering SF^k as a perturbation of $S\bar{F}$. To be precise, let us order the eigenvalues of F according to decreasing modulus in the following way: $\lambda_1 = \dots = \lambda_q = 1 > |\lambda_{q+1}| \geq \dots \geq |\lambda_N|$. So, if $\|*\|$ is any consistent norm in the space $\mathcal{M}_{N \times N}$ of $N \times N$ matrices, then for every $\alpha > |\lambda_{q+1}|$ we have $\|SF^k - S\bar{F}\| = o(\alpha^k)$ ($k \rightarrow \infty$). This last result implies, see [38], that matrix SF^k has a strictly dominant eigenvalue of the form $\lambda + O(\alpha^k)$, an associated left eigenvector $U^T \bar{w}_l + O(\alpha^k)$ and an associated right eigenvector $SV \bar{w}_r + O(\alpha^k)$. Having in mind that α can be chosen to be less than 1, we see that the elements defining the asymptotic behavior of the aggregated and the general systems can be related in a precise way as a function of the separation between the two time scales.

In Sanz and Bravo de la Parra these results are extended to more general linear cases where the projection matrices F_i defining the fast dynamics in each group need not be primitive.

In Blasco the fast process is still considered linear but changing at the fast time scale. The fast dynamics is described by means of the product of the first k terms of a converging sequence of different matrices. This case is called the fast changing environment case. Under certain assumptions the limit of the sequence of matrices plays the same role than matrix \bar{F} in (20) obtaining an aggregated system. Similar results to the already described relating the asymptotic properties of the complete and the aggregated systems are proved.

It is also possible to build the general system using as time unit the projection interval of the fast dynamics, see Sánchez Bravo de la Parra and Bravo de la Parra and Sánchez

4.1.1. Example: Multiregional model with fast demography and slow migrations

We consider a population with juveniles (age class 1) and adults (age class 2) in a two-patch environment. Let $n^{ij}(t)$ be the density of the subpopulation aged i on patch j at time t . On each patch, the population grows according to a Leslie model. Individuals belonging to a given age-class also move from patch to patch.

Let S_j be the survival rate of juveniles on patch j and F_j^i the fertility rate of age class i on patch j . Assuming the following order of the state variables, $\mathbf{n}(t) = (n^{11}(t), n^{21}(t), n^{12}(t), n^{22}(t))$, the matrix describing the demography of the population in both patches is the following:

$$L = \begin{pmatrix} F_1^1 & F_1^2 & 0 & 0 \\ S_1 & 0 & 0 & 0 \\ 0 & 0 & F_2^1 & F_2^2 \\ 0 & 0 & S_2 & 0 \end{pmatrix}.$$

The migration of individuals of age i is described by the following migration rates: p_i (resp., q_i) is the migration rate from patch 1 to patch 2 (resp., from patch 2 to patch 1). So the matrix describing the migration process of the population is:

$$M = \begin{pmatrix} 1 - p_1 & 0 & q_1 & 0 \\ 0 & 1 - p_2 & 0 & q_2 \\ p_1 & 0 & 1 - q_1 & 0 \\ 0 & p_2 & 0 & 1 - q_2 \end{pmatrix}.$$

The restrictions over the vital rates so that matrices

$$L_1 = \begin{pmatrix} F_1^1 & F_1^2 \\ S_1 & 0 \end{pmatrix} \quad \text{and} \quad L_2 = \begin{pmatrix} F_2^1 & F_2^2 \\ S_2 & 0 \end{pmatrix}$$

have dominant eigenvalue 1 are $F_1^1 + F_1^2 S_1 = 1$ and $F_2^1 + F_2^2 S_2 = 1$. Besides we will suppose that $F_1^1, F_1^2, F_2^1, F_2^2, S_1$ and S_2 are positive and then matrices L_1 and L_2 are primitive. Vectors v_i and u_i are given by

$$v_1 = \frac{1}{1 + S_1} (1, S_1)^T, \quad v_2 = \frac{1}{1 + S_2} (1, S_2)^T,$$

$$u_1 = \frac{1 + S_1}{1 + F_1^2 S_1} (1, F_1^2)^T, \quad u_2 = \frac{1 + S_2}{1 + F_2^2 S_2} (1, F_2^2)^T.$$

Furthermore, it is assumed that the demographic process is fast in comparison to the migration process.

The dynamics of the four state variables $\mathbf{n}(t) = (n^{11}(t), n^{21}(t), n^{12}(t), n^{22}(t))^T$ is thus described by the following system:

$$\mathbf{n}(t+1) = ML^k \mathbf{n}(t) = \begin{pmatrix} 1-p_1 & 0 & q_1 & 0 \\ 0 & 1-p_2 & 0 & q_2 \\ p_1 & 0 & 1-q_1 & 0 \\ 0 & p_2 & 0 & 1-q_2 \end{pmatrix} \begin{pmatrix} F_1^1 & F_1^2 & 0 & 0 \\ S_1 & 0 & 0 & 0 \\ 0 & 0 & F_2^1 & F_2^2 \\ 0 & 0 & S_2 & 0 \end{pmatrix}^k \mathbf{n}(t), \quad (24)$$

where k represents the ratio between the projection intervals corresponding to the slow and fast processes.

We now proceed to reduce system (24). For that we need the matrices U and V used in expression (20) which are composed of left and right eigenvectors of matrices L_i associated to eigenvalue 1. So they can be expressed in the following way:

$$U = \begin{pmatrix} \frac{1+S_1}{1+F_1^2 S_1} & \frac{(1+S_1)F_1^2}{1+F_1^2 S_1} & 0 & 0 \\ 0 & 0 & \frac{1+S_2}{1+F_2^2 S_2} & \frac{(1+S_2)F_2^2}{1+F_2^2 S_2} \end{pmatrix} \quad \text{and} \quad V = \begin{pmatrix} \frac{1}{1+S_1} & 0 \\ \frac{S_1}{1+S_1} & 0 \\ 0 & \frac{1}{1+S_2} \\ 0 & \frac{S_2}{1+S_2} \end{pmatrix}.$$

The global variables $Y(t) = (Y_1(t), Y_2(t)) = U\mathbf{n}(t)$, corresponding respectively to patches 1 and 2, are

$$Y_1(t) = \frac{1}{1 + F_1^2 S_1} n^{11}(t) + \frac{F_1^2}{1 + F_1^2 S_1} n^{12}(t),$$

$$Y_2(t) = \frac{1}{1 + F_2^2 S_2} n^{12}(t) + \frac{F_2^2}{1 + F_2^2 S_2} n^{22}(t)$$

which have a biological meaningful interpretation as they are the total population at each patch weighted by the reproductive values of each age class. The aggregated system, $Y(t+1) = ULVY(t)$, governing these weighted total populations in both patches reads as follows:

$$Y(t+1) = \begin{pmatrix} \frac{((1-p_1)+F_1^2 S_1(1-p_2))}{1+F_1^2 S_1} & \frac{(1+S_1)(q_1+F_1^2 S_1 q_2)}{(1+S_2)(1+F_1^2 S_1)} \\ \frac{(1+S_2)(p_1+F_2^2 S_2 p_2)}{(1+S_1)(1+F_2^2 S_2)} & \frac{((1-q_1)+F_2^2 S_2(1-q_2))}{1+F_2^2 S_2} \end{pmatrix} Y(t). \quad (25)$$

The results stated in the previous section allow us to approximate the asymptotic elements of system (24) in terms of the corresponding elements of system (25). Thus, we can study the influence of the fast demographic process in the reduced system, which evolves at the slow time scale corresponding to migration. Let us see an example; migration is a conservative process for the total number of individuals, so if we consider a model in which migration is the only process acting, the system will keep constant its total population. However, the matrix in system (25) does not have, in the general case, 1 as its dominant eigenvalue and therefore, if we consider also demography in the model, the system has a total population which, depending on the values of the migration and vital rates, either decays to zero or grows exponentially.

4.2. Linear nonautonomous discrete models

The approximate aggregation methods for time discrete linear models have been extended to the linear nonautonomous case, appropriate to model populations living in an environment that varies with time so that both the slow and the fast process are functions of time.

Using the slow time unit as the time step of the complete model, we can build up the model simply by generalizing the model corresponding to the autonomous case. Indeed following Sanz and Bravo de la Parra we assume that the matrices $S(t)$ and $F(t)$ that model the slow and the fast process respectively are functions of time and that, for each value of t , the hypotheses following (19) concerning the fast process hold. Therefore the nonautonomous model

reads

$$\mathbf{n}_k(t+1) = S(t)F^k(t)\mathbf{n}_k(t), \quad (26)$$

where $F(t) := \text{diag}(F_1(t), \dots, F_q(t))$ and for all $t = 0, 1, 2, \dots$ and $i = 1, \dots, q$ matrices $F_i(t)$ verify that are primitive with 1 as strictly dominant eigenvalue.

We now build a nonautonomous model for a population with juveniles and adults in a two-patch environment, as it is done in the previous section except that we consider migration fast with respect to demography, by allowing the fecundity, survival and migration rates to be dependent on t , so we would obtain a model

$$\begin{aligned} \mathbf{n}(t+1) &= L(t)P(t)^k\mathbf{n}(t) \\ &= \begin{pmatrix} f_{11}(t) & 0 & f_{21}(t) & 0 \\ 0 & f_{12}(t) & 0 & f_{22}(t) \\ s_1(t) & 0 & 0 & 0 \\ 0 & s_2(t) & 0 & 0 \end{pmatrix} \begin{pmatrix} 1-p_1(t) & q_1(t) & 0 & 0 \\ p_1(t) & 1-q_1(t) & 0 & 0 \\ 0 & 0 & 1-p_2(t) & q_2(t) \\ 0 & 0 & p_2(t) & 1-q_2(t) \end{pmatrix}^k \mathbf{n}(t). \end{aligned}$$

Coming back to system (26) and its reduction, and reasoning along the lines of the autonomous case, we define $v_i(t)$ and $u_i(t)$ through the relationships $F_i(t)v_i(t) = v_i(t)$, $u_i(t)F_i(t) = u_i(t)$ and $u_i(t) \cdot v_i(t) = 1$ and then consider matrices $\bar{F}_i(t) := \lim_{k \rightarrow \infty} F_i^k(t) = v_i(t)u_i(t)$ and $\bar{F}(t) := \text{diag}(\bar{F}_1(t), \dots, \bar{F}_q(t))$. Therefore letting $k \rightarrow \infty$ in (26) we obtain the auxiliary system

$$\mathbf{n}_k(t+1) = S(t)\bar{F}(t)\mathbf{n}_k(t) \quad (27)$$

that we can express in the form

$$\mathbf{n}_k(t+1) = S(t)V(t)U(t)\mathbf{n}_k(t), \quad (28)$$

where $V(t) := \text{diag}(v_1(t), \dots, v_q(t))_{N \times q}$ and $U(t) := \text{diag}(u_1(t), \dots, u_q(t))_{q \times N}$. Now premultiplying both sides of (28) by $U(t+1)$ and defining the vector of q global variables through

$$Y(t) := U(t)\mathbf{n}(t),$$

we obtain the reduced system

$$Y(t+1) = \bar{S}(t)Y(t), \quad (29)$$

where

$$\bar{S}(t) = U(t+1)S(t)V(t).$$

For any finite value of t , the population vector of the original system can be approximated through the knowledge of the population vector for the reduced system. Indeed in Sanz and Bravo de la Parra [42] it is shown that for each $t \geq 0$

$$\mathbf{n}(t) = S(t)V(t)Y(t) + \mathbf{o}(\alpha^k), \quad (30)$$

where α verifies $0 < \alpha < 1$ and can be determined in a way that is analogous to the one described in the autonomous case. The term $\mathbf{o}(\alpha^k)$ depends on t .

In order to examine the relationships between the original system (26) and the reduced one (29) we consider three different patterns of temporal variation. In the first case, following Sanz and Bravo de la Parra we deal with the case in which the environment is periodic and therefore we have $S(t+m) = S(t)$ and $F(t+m) = F(t)$ for a certain positive integer m . Let $\bar{A} := \bar{S}(m-1) \cdots \bar{S}(1)\bar{S}(0)$ and let us assume this matrix is primitive and has dominant eigenvalue μ and dominant right eigenvector \mathbf{s} . Then, being a particular case of a linear periodic model

the population of the reduced system (29) grows asymptotically with an asymptotic growth rate per time step given by $\mu^{1/m}$ and, when $t \rightarrow \infty$, $Y(tm)/\|Y(tm)\|$ tends to $\mathbf{s}/\|\mathbf{s}\|$, i.e., for large values of t the structure of the population vector at time tm is defined by vector $\mathbf{s}/\|\mathbf{s}\|$. Then Sanz and Bravo de la Parra show that if k is large enough, for any initial condition the original system (26) grows asymptotically with an asymptotic growth rate per time step given by $\mu^{1/m} + \mathbf{o}(\alpha^k)$ and $\lim_{t \rightarrow \infty} \mathbf{n}_k(tm)/\|\mathbf{n}_k(tm)\| = BV(0)\mathbf{s} + \mathbf{o}(\alpha^k)$ where matrix B is given by

$$B := S(m-1)\bar{F}(m-1) \cdots S(1)\bar{F}(1)S(0).$$

In the second situation, contemplated in Sanz and Bravo de la Parra [19] we consider that the environment, although changing with time, tends to stabilization, i.e., matrices $S(t)$ and $F(t)$ converge when $t \rightarrow \infty$ to certain matrices S_* and $F_* = \text{diag}(F_{1*}, \dots, F_{q*})$ that model the slow and the fast process in equilibrium. It can be shown that the matrices $\bar{S}(t)$ corresponding to the reduced system converge to a certain matrix \bar{S}_* that represents the equilibrium vital rates for the reduced system.

Let us consider the asymptotic behavior of general linear nonautonomous models in which the environment tends to stabilize, i.e., models of the form

$$\mathbf{z}(t+1) = A(t)\mathbf{z}(t), \quad (31)$$

where matrices $A(t)$ are nonnegative for all $t \geq 0$ and such that there exists the limit $A_* := \lim_{t \rightarrow \infty} A(t)$. If for all $t \geq 0$ matrices $A(t)$ have no zero columns (so that if $\mathbf{z}(0) \neq 0$ then one has $\mathbf{z}(t) \neq 0$ for all $t \geq 0$) and matrix A_* is primitive then, roughly speaking, system (31) behaves qualitatively like an autonomous system with matrix A_* .

More precisely, one can assure that $\lim_{t \rightarrow \infty} \|\mathbf{z}(t+1)\|/\|\mathbf{z}(t)\| = \gamma$ and $\lim_{t \rightarrow \infty} \mathbf{z}(t)/\|\mathbf{z}(t)\| = \mathbf{d}$ where γ is the dominant eigenvalue of matrix A_* and \mathbf{d} is its associated right eigenvector normalized so that $\|\mathbf{d}\| = 1$.

Coming back to the reduced system (29), let us assume that for all $t \geq 0$ matrices $\bar{S}(t)$ have no zero columns and that matrix \bar{S}_* is primitive with dominant eigenvalue γ and associated right eigenvector \mathbf{d} normalized so that $\|\mathbf{d}\| = 1$. Then using the result above we can write

$$\lim_{t \rightarrow \infty} \|Y(t+1)\|/\|Y(t)\| = \gamma; \quad \lim_{t \rightarrow \infty} Y(t)/\|Y(t)\| = \mathbf{d}.$$

In Sanz and Bravo de la Parra [19] it is proved that under the mild assumption of matrix S_* having no zero rows, then for k large enough the matrices $S(t)F^k(t)$ have no zero columns for all $t \geq 0$. Moreover matrix $S_*F_*^k$ is primitive, and its dominant eigenvalue γ_k verifies $\gamma_k = \gamma + o(\beta^k)$ where $0 < \beta < 1$, whilst an associated right eigenvector can be written $S_*V_*\mathbf{d} + o(\beta^k)$ where V_* is a certain matrix that can be obtained in terms of F_* . Therefore we can write

$$\lim_{t \rightarrow \infty} \|\mathbf{n}_k(t+1)\|/\|\mathbf{n}_k(t)\| = \gamma + o(\beta^k); \quad \lim_{t \rightarrow \infty} \mathbf{n}_k(t)/\|\mathbf{n}_k(t)\| = S_*V_*\mathbf{d} + o(\beta^k)$$

and one can approximate the asymptotic behavior of the original system in terms of magnitudes calculated for the reduced system.

Finally let us consider the study of the relationships between the original and the aggregated system in the case the environment changes with time in a general fashion. First let us describe some features of the asymptotic behavior of models of this kind, i.e., of models

$$\mathbf{z}(t+1) = A(t)\mathbf{z}(t),$$

where matrices $A(t)$ are nonnegative for all $t \geq 0$. Obviously, in that case 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 population structure $\mathbf{z}(t)/\|\mathbf{z}(t)\|$ “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), i.e., for any nonzero initial conditions $\mathbf{z}(0)$ and $\mathbf{z}'(0)$ we have

$$\lim_{n \rightarrow \infty} \left\| \frac{A(n) \cdots A(1)A(0)\mathbf{z}(0)}{\|A(n) \cdots A(1)A(0)\mathbf{z}(0)\|} - \frac{A(n) \cdots A(1)A(0)\mathbf{z}'(0)}{\|A(n) \cdots A(1)A(0)\mathbf{z}'(0)\|} \right\| = 0, \quad (32)$$

and in that case we say that the system is weakly ergodic. Actually the precise mathematical definition of weak ergodicity is more elaborated and implies (32). We refer the reader to [45] for details.

The study of the property of weak ergodicity for the original and for the reduced system is carried out in Sanz and Bravo de la Parra [19]. It is shown that under quite general conditions, if k is large enough then very general sufficient conditions for weak ergodicity, that have to do with the positivity of the product of a consecutive number of matrices in the system, is satisfied simultaneously for both systems.

In the works considered so far the relationship between the variables of the original system and the variables of the reduced system is given by (30). However this expression is only useful in the limit when k tends to infinity. However, in practice one can be interested in knowing the error we incur in when we approximate the variables $\mathbf{n}(t)$ through $S(t)V(t)Y(t)$ for finite values of k . In Sanz and Bravo de la Parra [19] different bounds are obtained for this error.

Observe that the model (26) implicitly assumes that the fast process, modeled through $F(t)$, can only change its characteristics with the time step of the slow process. A more realistic model should allow the fast process to change with its associated time step. Therefore within each time interval $[t, t + 1)$ the fast process acts k times but each time its characteristics can be different. In this way the model reads

$$\mathbf{n}_k(t + 1) = S(t)F(t, k) \cdots F(t, 2)F(t, 1)\mathbf{n}_k(t),$$

where for each $t \geq 0$ and $s = 1, \dots, k$ matrix $F(t, s)$ models the fast process during the s th subinterval of the time interval $[t, t + 1)$. Of course, for one to be able to reduce the system the fast process must reach equilibrium, which can be shown to hold if we assume that for all $t \geq 0$, matrices $F(t, k)$ tend when $k \rightarrow \infty$ to certain appropriate matrices. The aggregation of this kind of models and the study of the relationships between the original and the corresponding reduced system is carried out in Blasco

4.3. Stochastic discrete models

Let us now consider the reduction of time discrete linear models incorporating the so-called environmental stochasticity, i.e., the randomness introduced when we consider random fluctuations in the environment and, consequently, in the vital rates which affect the population.

First let us examine the general form of linear models that incorporate environmental stochasticity. Let us consider a population living in an habitat in which there are l different environmental conditions $\{1, \dots, l\}$. Let $\mathbf{z}(t)$ be the population vector and let τ_t be the random variable that defines the environment under which the population lives in the time step $[t - 1, t)$. Now let matrix $A(\sigma)$ be the matrix of vital rates for the population in environment σ , $\sigma = 1, \dots, l$. Then the model for the population reads

$$\mathbf{z}(t + 1) = A(\tau_{t+1})\mathbf{z}(t). \quad (33)$$

In order to formulate a model with two time scales that incorporates the effect of environmental stochasticity, we can consider (26) as a starting point and to allow the temporal variation to be random. Indeed, let us assume that there are l different environmental conditions $\{1, \dots, l\}$ and let τ_t be the random variable that defines the environment under which the population lives in the time step $[t - 1, t)$. Now let $S(\sigma)$ and $F(\sigma)$ denote the matrices of vital rates for the slow and the fast process respectively, in environment σ , $\sigma = 1, \dots, l$. Therefore, the model with two time scales reads

$$\mathbf{n}_k(t + 1) = S(\tau_{t+1})F^k(\tau_{t+1})\mathbf{n}_k(t). \quad (34)$$

The reduction of these kind of models is dealt with in Sanz and Bravo de la Parra under quite general conditions that basically imply that each one of the matrices $F_i(\sigma)$ is primitive and with dominant eigenvalue equal to one. In order to simplify this exposition we will deal with the particular case in which the $F_i(\sigma)$ are primitive stochastic matrices. For each $i = 1, \dots, l$, we define vectors $v_i(\sigma) > 0$ through the relationships $F_i(\sigma)v_i(\sigma) = v_i(\sigma)$ and $\|v_i(\sigma)\| = 1$ and then consider matrices $\bar{F}_i(\sigma) := \lim_{k \rightarrow \infty} F_i^k(\sigma) = v_i(\sigma)1$, where 1 denotes a row vector with all its components equal to 1, and $\bar{F}(\sigma) := \text{diag}(\bar{F}_1(\sigma), \dots, \bar{F}_q(\sigma))$. Reasoning along the lines of the nonautonomous case, we let $k \rightarrow \infty$ in (34) and we obtain the auxiliary system

$$\mathbf{n}_k(t + 1) = S(\tau_{t+1})\bar{F}(\tau_{t+1})\mathbf{n}_k(t)$$

that we can express in the form

$$\mathbf{n}_k(t + 1) = S(\tau_{t+1})V(\tau_{t+1})U\mathbf{n}_k(t), \quad (35)$$

where $V(\sigma) := \text{diag}(v_1(\sigma), \dots, v_q(\sigma))_{N \times q}$ and $U(t) := \text{diag}(1, \dots, 1)_{q \times N}$. Now premultiplying both sides of (35) by U and defining the vector of q global variables through

$$Y(t) = (y^1(t), \dots, y^q(t)) := U\mathbf{n}(t) = (n^{11}(t) + \dots + n^{1N^1}(t), \dots, n^{q1}(t) + \dots + n^{qN^q}(t))$$

so that $y^i(t)$ corresponds to the total population in group i , we obtain the reduced system

$$Y(t + 1) = \bar{S}(\tau_{t+1})Y(t), \quad (36)$$

where

$$\bar{S}(\sigma) = US(\sigma)V(\sigma), \quad \sigma = 1, \dots, l.$$

Let us examine the relationships between the original system (34) and the reduced one (36). As it was the case in the nonautonomous setting, for any finite value of t the population vector of the original system can be approximated through the knowledge of the aggregated system

$$\mathbf{n}_k(t) = S(\tau_t)V(\tau_t)Y(t-1) + \mathbf{o}(\delta^k), \quad k \rightarrow \infty,$$

where δ verifies $0 < \delta < 1$ and $\mathbf{o}(\delta^k)$ depends on t . In Sanz and Bravo de la Parra bounds are obtained for the “error” we incur in when we approximate $\mathbf{n}_k(t)$ by $S(\tau_t)V(\tau_t)Y(t-1)$ for finite values of t .

Let us now concentrate in the case, of great practical importance, in which the environmental process τ_t is Markovian. In this case one has that under some hypotheses each realization of the system grows (or decays) exponentially with the same rate. More specifically, let us consider system (33) and let us assume the following hypothesis:

Hypothesis (H1). τ_t is an homogeneous Markov chain such that its matrix of transition probabilities is primitive. Moreover, the set $\{A(1), \dots, A(l)\}$ is “ergodic”, i.e., there exists a positive integer r such that the product of any r matrices drawn from this set is a positive matrix.

Under Hypothesis (H1) (see Tuljapurkar [50]) there exists the following limit with probability one

$$a := \lim_{t \rightarrow \infty} \frac{\log \|\mathbf{z}(t)\|}{t}, \quad (37)$$

where a , the so-called stochastic growth rate (s.g.r.) of the system, is a fixed (nonrandom) number independent of the initial probabilities of the chain and of the initial (nonzero) population vector $\mathbf{z}(0) \geq \mathbf{0}$. The s.g.r. is the most important parameter in order to characterize the behavior of models of the kind (33). Therefore, and coming back to the study of the relationships between the systems (34) and (36), it is important to study the conditions for the existence of a s.g.r. for these systems and the relationship between them.

Let us assume that τ_t is an homogeneous Markov chain with a primitive matrix of transition probabilities, and let us assume that set of matrices $\{\bar{S}(1), \dots, \bar{S}(l)\}$ is an ergodic set. Therefore the reduced system (36) verifies the sufficient conditions (H1) for the existence of a s.g.r. $a := \lim_{t \rightarrow \infty} \log \|Y(t)\|/t$, where the limit is with probability one. Sanz and Bravo de la Parra show that if matrices $S(1), \dots, S(l)$ have no zero rows, then for large enough k the set $\{S(1)F^k(1), \dots, S(l)F^k(l)\}$ is ergodic and therefore the original system (34) verifies that there exists a s.g.r. $a_k := \lim_{t \rightarrow \infty} \log \|\mathbf{n}_k(t)\|/t$. Besides, it is proved that $\lim_{k \rightarrow \infty} a_k = a$ and therefore, if k is large enough, we can approximate the s.g.r. a_k of the original system through that of the reduced system. Moreover, [49] derives bounds for $|a_k - a|$ for finite values of k , so we can estimate the error we incur in when we approximate the study of (34) through that of (36). Finally, shows that for all positive integer m , the asymptotic behavior when $t \rightarrow \infty$ of the moments of order m of system (34) can be approximated through the behavior of the corresponding moments for the reduced system (36).

4.4. Nonlinear discrete models

The previous framework can be extended to include general nonlinear fast and slow processes. We present the complete model which will be susceptible of being reduced. Both processes, fast and slow, are defined, respectively, by two mappings

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

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

We first choose as time step of the model that corresponding to the slow dynamics as we did in the linear case, see Sanz et al. [51]. We still assume that during this time step the fast process acts k times before the slow process acts. Therefore, denoting by $\mathbf{n}_k(t) \in \mathbb{R}^N$ the vector of state variables at time t , the complete system is defined by

$$\mathbf{n}_k(t+1) = S(F^k(\mathbf{n}_k(t))), \quad (38)$$

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

In order to reduce the system (38), we have to impose some conditions to the fast process. In what follows we suppose that the following hypotheses are met. 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 for each $X \in \Omega_N$, $\lim_{k \rightarrow \infty} F^k(X) = \bar{F}(X)$. This equilibrium depends on a lesser number of variables in the following form: there exists a nonempty open set $\Omega_q \subset \mathbb{R}^q$ with $q < N$ and two mappings $G: \Omega_N \rightarrow \Omega_q$, $G \in C^1(\Omega_N)$, and $E: \Omega_q \rightarrow \Omega_N$, $E \in C^1(\Omega_q)$, such that $\bar{F} = E \circ G$.

Now, we proceed to define the so-called *auxiliary system* which approximates (38) when $k \rightarrow \infty$, i.e., when the fast process has reached an equilibrium. Keeping the same notation as in the linear case, this auxiliary system is

$$\mathbf{n}(t+1) = S(\bar{F}(\mathbf{n}(t))) \quad (39)$$

which can be also written as $\mathbf{n}(t+1) = S \circ E \circ G(\mathbf{n}(t))$.

The *global variables* in this case are defined through

$$Y(t) := G(\mathbf{n}(t)) \in \mathbb{R}^q. \quad (40)$$

Applying G to both sides of (39) we have $Y(t+1) = G(\mathbf{n}(t+1)) = G \circ S \circ E \circ G(\mathbf{n}(t)) = G \circ S \circ E(Y(t))$ which is an autonomous system in the global variables $Y(t)$. Summing up, we have approximated system (38) by the *reduced* or *aggregated* system defined by

$$Y(t+1) = \bar{S}(Y(t)), \quad (41)$$

where we denote $\bar{S} = G \circ S \circ E$.

Now we present some results relating the behavior of systems (38) and (41), for big enough values of parameter k . All the results in this section are presented in a more general setting. First we compare the solutions of both systems for a fixed value of t . The next theorem states that the dynamics of the auxiliary system is completely determined by the dynamics of the reduced system and that the solution to the complete system, given mild extra assumptions, for each t fixed can be approximated by the solution to the aggregated model.

Theorem 4. *Let $\mathbf{n}_0 \in \Omega_N$ and let $Y_0 = G(\mathbf{n}_0) \in \Omega_q$. Then:*

- (i) *The solution $\{\mathbf{n}(t)\}_{t=1,2,\dots}$ to (39) corresponding to the initial condition \mathbf{n}_0 and the solution $\{Y(t)\}_{t=1,2,\dots}$ to (41) corresponding to the initial condition $Y_0 = G(\mathbf{n}_0)$ are related by the following expressions*

$$Y(t) = G(\mathbf{n}(t)) \quad \text{and} \quad \mathbf{n}(t) = S \circ E(Y(t-1)), \quad n = 1, 2, \dots \quad (42)$$

- (ii) *Let t be a fixed positive integer and let us assume that there exists a nonempty bounded open set Ω such that $\bar{\Omega} \subset \Omega_N$, $\bar{\Omega}$ contains the points $\mathbf{n}(0)$, $\mathbf{n}(i+1) = S \circ E(Y_i)$ ($i = 0, \dots, n-1$), and such that $\lim_{k \rightarrow \infty} F^k = \bar{F}$ uniformly in Ω . Then the solution $\mathbf{n}_k(t)$ to (38) corresponding to the initial condition $\mathbf{n}(0)$ and the solution $Y(t)$ to (41) corresponding to the initial condition Y_0 are related by the following expressions*

$$Y(t) = \lim_{k \rightarrow \infty} G(\mathbf{n}_k(t)) \quad \text{and} \quad \lim_{k \rightarrow \infty} \mathbf{n}_k(t) = S \circ E(Y(t-1)).$$

Now we turn our attention to the study of some relationships between the fixed points of the original and reduced systems. Concerning the auxiliary system, relations (42) in Theorem 4 yield straightforward relationships between the fixed points of the auxiliary and reduced systems: if $\mathbf{n}^* \in \Omega_N$ is a fixed point of (39) then $Y^* = G(\mathbf{n}^*) \in \Omega_q$ is a fixed point of (41); conversely, if Y^* is a fixed point of (41) then $\mathbf{n}^* = S \circ E(Y^*)$ is a fixed point of (39). The corresponding fixed points in the auxiliary and aggregated systems are together asymptotically stable or unstable.

In the following result, it is guaranteed that, under certain assumptions, the existence of a fixed point Y^* for the aggregated system implies, for big enough values of k , the existence of a fixed point \mathbf{n}_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 \mathbf{n}_k^* and in the asymptotically stable case, the basin of attraction of \mathbf{n}_k^* can be approximated in terms of the basin of attraction of Y^* .

Theorem 5. Let us assume that $\bar{F} \in C^1(\Omega_N)$ and that $\lim_{k \rightarrow \infty} F^k = \bar{F}$, $\lim_{k \rightarrow \infty} DF^k = D\bar{F}$ uniformly on any compact set $K \subset \Omega_N$, where D denotes the differential of the transformation.

Let $Y^* \in \mathbb{R}^q$ be a hyperbolic fixed point of (41) which is asymptotically stable (resp. unstable). Then there exists $k_0 \in \mathbb{N}$ such that for each $k \geq k_0$, $k \in \mathbb{N}$, there exists a hyperbolic fixed point \mathbf{n}_k^* of (38) which is asymptotically stable (resp. unstable) and that satisfies $\lim_{k \rightarrow \infty} \mathbf{n}_k^* = S \circ E(Y^*)$.

Moreover, let $\mathbf{n}_0 \in \Omega_N$. If the solution $Y(t)$ to (41) corresponding to the initial condition $Y_0 = G(\mathbf{n}_0)$ is such that $\lim_{t \rightarrow \infty} Y(t) = Y^*$ then for each $k \geq k_0$, $k \in \mathbb{N}$, the solution $\mathbf{n}_k(t)$ to (38) corresponding to \mathbf{n}_0 verifies $\lim_{t \rightarrow \infty} \mathbf{n}_k(t) = \mathbf{n}_k^*$.

Particular models where this last result applies are presented in Bravo de la Parra and the review paper Auger and Bravo de la Parra

As in the linear case we can build the general system using as time unit the one of fast dynamics. In Bravo de la Parra et al. and Bravo de la Parra and Sánchez a system with linear fast dynamics and general nonlinear slow dynamics is reduced by means of a center manifold theorem.

4.4.1. Example: Multiregional model with fast migrations and slow demography

We are considering a simple model of a nonstructured population, that is, a population constituted by just one group which is subdivided into 2 subgroups representing the local populations at the 2 patches making up its habitat. The population vector at time t is represented by $\mathbf{n}(t) = (n_1(t), n_2(t))$. We suppose that local demographic dynamics is slow with respect to migrations between patches and depending only on local population. Thus, the slow dynamics can be described by

$$S(\mathbf{n}(t)) := (s_1(n_1(t)), s_2(n_2(t)))$$

with s_i , $i = 1, 2$, being two nonnegative C^1 functions defined on \mathbb{R}_+ . The fast dynamics associated to the migrations is represented by a regular stochastic matrix $\mathcal{F}(y)$, whose entries depend on total population $y(t) := n_1(t) + n_2(t)$,

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

where $a, b : \mathbb{R}_+ \rightarrow (0, 1)$ are C^1 functions. We define then

$$F(\mathbf{n}(t)) = \mathcal{F}(y(t))\mathbf{n}(t)$$

and the complete model reads

$$\mathbf{n}(t+1) = S(\mathcal{F}^k(y(t))\mathbf{n}(t)). \quad (43)$$

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 results established in the previous section leads to the aggregated system:

$$y(t+1) = s_1(v_1(y(t))y(t)) + s_2(v_2(y(t))y(t)). \quad (44)$$

We could now carry out a certain qualitative analysis of system (43) by performing it in system (44) with the help of Theorem 5.

We will just stress the power of aggregation methods by making some remarks in the particular case of local Malthusian dynamics, that is,

$$S(\mathbf{n}(t)) := (d_1 n_1(t), d_2 n_2(t)).$$

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

The fact that local dynamics are of Malthusian type allows extinction and blow-up to be expected at a global level. To show that density dependent migrations can stabilize the system we present in the following two examples migrations which yield aggregated systems that are well-known models. If we choose

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

then we recover as aggregated system the Beverton–Holt equation

$$y(t + 1) = \frac{\alpha y(t)}{1 + \beta y(t)},$$

where α and β are positive constants, and if we choose

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

the aggregated system is the Ricker equation

$$y(t + 1) = e^{r(1-y(t)/K)} y(t)$$

with r and K also positive constants.

This 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.

5. Perspectives and conclusions

Regarding applications to population dynamics, aggregation methods have also been used in the following cases:

- Modelling the effect of migrations processes on the population dynamics in continuous time
- Modelling the effect of individual behavior on the population dynamics
- Modelling the effect of migrations processes on host-parasitoid systems
- Modelling a trout fish population in an arborescent river network composed of patches connected by fast migrations
- Modelling fisheries dynamics
- Modelling a sole larvae population with a continuous age with fast migration between different spatial patches
- Modelling food chain structures

In this review, we have presented aggregation methods in several contexts, ODE's, Discrete models, PDE's and DDE's. However, there is still work to be done to show that a complete detailed mathematical model can be replaced by a reduced aggregated model. For example, there is no doubt that more work should be devoted to the case of stochastic models.

In our opinion, a major problem relates to the understanding of mechanisms which are responsible for the emergence of individual behavior at the population and community level. In many cases, biologists prefer to use an Individual Based Model (IBM) to take into account many features of each individual to model how they interact. The IBM is then simulated with a computer and it is used to look for global emerging properties at the level of the population and of the community. However, it can be difficult to obtain robust and general results from a complete and detailed IBM.

In this review we have shown that, in some cases, interactions between individuals can also be taken into account by classical models with differential or difference equations. When two time scales are involved in the model, aggregation methods allow to proceed to a significant reduction of the dimension of the model and sometimes to a complete analysis of the aggregated model. This reduced model is useful to understand how the individual behavior can influence the dynamics of the total population and its community. Therefore, aggregation methods can be considered as a new and promising tool for the study of emergence of global properties in complex systems with many potential applications in ecological dynamics.

Acknowledgements

P. Auger, R. Bravo de la Parra, E. Sánchez and L. Sanz were supported by Ministerio de Educación y Ciencia (Spain), proyecto MTM2005-00423 and FEDER.

References

- Lotka AJ. Undamped oscillations derived from the Mass Action law. *Journal of the American Chemical Society* 1920;42:1595–9.
- Lotka AJ. *Elements of physical biology*. Baltimore: William and Wilkins; 1925.
- Volterra V. Variazioni e fluttuazioni del numero d'individui in specie animali conviventi. *Mem R Accad Naz dei Lincei Ser. VI* 1926;2.
- Nicholson AJ. The balance of animal populations. *Journal of Animal Ecology* 1933;2:132–78.
- Nicholson AJ, Bailey VA. The balance of animal populations, Part I. In: *Proceedings of the Zoological Society*, vol. 3. London; 1935. p. 551–98.
- Edelstein-Keshet L. *Mathematical models in biology*. New York: Random House; 1989.
- Murray JD. *Mathematical biology*. *Biomathematics text*, vol. 19. Berlin: Springer-Verlag; 1989.
- Iwasa Y, Andreasen V, Levin S. Aggregation in model ecosystems I: Perfect aggregation. *Ecological Modelling* 1987;37:287–302.
- Iwasa Y, Levin S, Andreasen V. Aggregation in model ecosystems II: Approximate aggregation. *Journal of Mathematics Applied in Medicine and Biology* 1989;6:1–23.
- Auger P, Lett C. Integrative biology: Linking levels of organization. *Comptes Rendus de l'Académie des Sciences Biologies* 2003;326:517–22.
- Auger P. *Dynamics and thermodynamics in hierarchically organized systems*. Oxford: Pergamon Press; 1989.
- Auger P, Roussarie R. Complex ecological models with simple dynamics: from individuals to populations. *Acta Biotheoretica* 1994;42:111–36.
- Auger P, Poggiale JC. Aggregation and emergence in systems of ordinary differential equations. *Mathematical Computer Modelling* 1998;27:1–22.
- Sánchez E, Bravo de la Parra R, Auger P. Discrete models with different time-scales. *Acta Biotheoretica* 1995;43:465–79.
- Bravo de la Parra R, Auger P, Sánchez E. Aggregation methods in discrete models. *Journal of Biological Systems* 1995;3:603–12.
- Arino O, Sánchez E, Bravo de la Parra R, Auger P. A singular perturbation in an age-structured population model. *SIAM J Appl Math* 1999;60:408–36.
- Sánchez E, Bravo de la Parra R, Auger P, Gómez-Mourelto P. Time scales in linear delayed differential equations. *J Math Anal Appl* 2006;323:680–99.
- Carr J. *Applications of centre manifold theory*. New York: Springer-Verlag; 1981.
- Fenichel N. Persistence and smoothness of invariant manifolds for flows. *Indiana University Mathematics Journal* 1971;21:193–226.
- Hirsch MW, Pugh CC, Shub M. *Invariant manifolds*. *Lectures notes in mathematics*, vol. 583. Springer-Verlag: Berlin; 1977.
- Krylov N, Bogoliubov N. The application of methods of nonlinear mechanics to the theory of stationary oscillations, Publication 8 of the Ukrainian Academy of Science, Kiev; 1934.
- Pliss VA, Sell GR. Perturbations of normally hyperbolic manifolds with applications to the Navier–Stokes equations. *Journal of Differential Equations* 2001;169:396–492.
- Wiggins S. *Normally hyperbolic invariant manifolds in dynamical systems*. AMS, vol. 105. New York: Springer-Verlag; 1994.
- Sakamoto K. Invariant manifolds in singular perturbations problems for ordinary differential equations. *Proc Roy Soc Ed* 1990;116:45–78.
- Auger P, Chiorino G, Poggiale JC. Aggregation, emergence and immersion in hierarchically organized systems. *Int J General Systems* 1999;27:349–71.
- Auger P, Charles S, Viala M, Poggiale JC. Aggregation and emergence in ecological modelling: integration of the ecological levels. *Ecological Modelling* 2000;127:11–20.
- Auger P, Poggiale JC. Aggregation and emergence in hierarchically organized systems: population dynamics. *Acta Biotheoretica* 1996;44:301–16.
- Auger P, Poggiale JC. Emergence of population growth models: Fast migration and slow growth. *Journal of Theoretical Biology* 1996;182:99–108.
- Auger P, Poggiale JC. Emerging properties in population dynamics with different time scales. *Journal of Biological Systems* 1995;3:591–602.
- Bates PW, Lu K, Zeng C. Invariant foliations near normally hyperbolic invariant manifolds for semiflows. *Transactions of the American Mathematical Society* 2000;352:4641–76.
- Bates PW, Lu K, Zeng C. Existence and persistence of invariant manifolds for semiflow in Banach space. *Memoirs of the American Mathematical Society* 1998;135:645.
- Beretta E, Kuang Y. Modeling and analysis of a marine Bacteriophage infection. *Mathematical Biosciences* 1998;149:57–76.
- Auger P, Bravo de la Parra R, Poggiale JC, Sánchez E, Nguyen-Huu T. Aggregation of variables and applications to population dynamics. In: Magal P, Ruan S, editors. *Structured population models in biology and epidemiology*. *Lecture notes in mathematics*, vol. 1936. Berlin: Springer-Verlag; 2008. p. 209–63 [Mathematical biosciences subseries].
- Arino O, Sánchez E, Bravo de la Parra R. A model of an age-structured population in a multipatch environment. *Math Comp Modelling* 1998;27:137–50.
- Bravo de la Parra R, Arino O, Sánchez E, Auger P. A model of an age-structured population with two time scales. *Math Comp Modelling* 2000;31:17–26.
- Arino O, Hbid ML, Ait Dads E, editors. *Delay, differential equations and applications*. NATO sciences series. Berlin: Springer; 2006.

Sanz L, Bravo de la Parra R. Variables aggregation in a time discrete linear model. *Mathematical Biosciences* 1999;157:111–46.

Stewart GW, Guang Sun JI. *Matrix perturbation theory*. Boston: Academic Press; 1990.

Blasco A, Sanz L, Auger P, Bravo de la Parra R. Linear discrete population models with two time scales in fast changing environments II: Non autonomous case. *Acta Biotheoretica* 2002;1:15–38.

Bravo de la Parra R, Sánchez E, Auger P. Time scales in density dependent discrete models. *Journal of Biological Systems* 1997;5:111–29.

Bravo de la Parra R, Sánchez E. Aggregation methods in population dynamics discrete models. *Mathematical and Computer Modelling* 1998;27:23–39.

Sanz L, Bravo de la Parra R. Time scales in a non autonomous linear discrete model. *Mathematical Models and Methods in Applied Sciences* 2001;11:1203–35.

Sanz L, Bravo de la Parra R. Variables aggregation in time varying discrete systems. *Acta Biotheoretica* 1998;46:273–97.

Skellam JG. Seasonal periodicity in theoretical population ecology. In: *Proceedings of the 5th Berkeley symposium in mathematical statistics and probability*, vol. 4. Berkeley: Univ. of California Press; 1967. p. 179–205.

Seneta E. *Non-negative matrices and Markov chains*. New York: Springer-Verlag; 1981.

Sanz L, Bravo de la Parra R. Approximate reduction techniques in population models with two time scales: Study of the approximation. *Acta Biotheoretica* 2002;50:297–322.

Blasco A, Sanz L, Auger P, Bravo de la Parra R. Linear discrete population models with two time scales in fast changing environments I: Autonomous case. *Acta Biotheoretica* 2001;49:261–76.

Sanz L, Bravo de la Parra R. Time scales in stochastic multiregional models. *Nonlinear Analysis: Real World Applications* 2000;1:89–122.

Sanz L, Bravo de la Parra R. Approximate reduction of multiregional models with environmental stochasticity. *Mathematical Biosciences* 2007;206:134–54.

Tuljapurkar S. *Population dynamics in variable environments*. Springer-Verlag; 1990.

Sanz L, Bravo de la Parra R, Sánchez E. Approximate reduction of nonlinear discrete models with two time scales. *Journal of Difference Equations and Applications* (2008);

Bravo de la Parra R, Sánchez E, Arino O, Auger P. A discrete model with density dependent fast migration. *Mathematical Biosciences* 1999;157:91–110.

Auger P, Bravo de la Parra R. Methods of aggregation of variables in population dynamics. *C R Acad Sci Paris Sciences de la vie* 2000;323:665–74.

Auger P, Benoit E. A prey-predator model in a multi-patch environment with different time scales. *Journal of Biological Systems* 1993;1:187–97.

Bernstein C, Auger P, Poggiale JC. Predator migration decisions, the ideal free distribution and predator-prey dynamics. *The American Naturalist* 1999;153:267–81.

Chiorino G, Auger P, Chasse JL, Charles S. Behavioral choices based on patch selection: a model using aggregation methods. *Mathematical Biosciences* 1999;157:189–216.

Michalski J, Poggiale JC, Arditi R, Auger P. Effects of migrations modes on patchy predator-prey systems. *Journal of Theoretical Biology* 1997;185:459–74.

Mchich R, Auger P, Poggiale JC. Effect of predator density dependent dispersal of prey on stability of a predator-prey system. *Mathematical Biosciences* 2007;206:343–56.

Poggiale JC. Lotka–Volterra’s model and migrations: breaking of the well-known center. *Mathematical Computer Modelling* 1998;27:51–62.

Poggiale JC. From behavioural to population level: growth and competition. *Mathematical Computer Modelling* 1998;27:41–50.

Poggiale JC. Predator-prey models in heterogeneous environment: emergence of functional response. *Mathematical Computer Modelling* 1998;27:63–71.

Poggiale JC, Auger P. Impact of spatial heterogeneity on a predator-prey system dynamics. *C R Biologies* 2004;327:1058–63.

Poggiale JC, Michalski J, Arditi R. Emergence of donor control in patchy predator-prey systems. *Bulletin of Mathematical Biology* 1998;60:1149–66.

Auger P, Kooi B, Bravo de la Parra R, Poggiale JC. Bifurcation analysis of a predator-prey model with predators using Hawk and Dove tactics. *Journal of Theoretical Biology* 2006;238:597–607.

Auger P, Bravo de la Parra R, Morand S, Sánchez E. A predator-prey model with predators using hawk and dove tactics. *Mathematical Biosciences* 2002;177–178:185–200.

Auger P, Pontier D. Fast game theory coupled to slow population dynamics: the case of domestic cat populations. *Mathematical Biosciences* 1998;148:65–82.

Auger P, Bravo de la Parra R, Sánchez E. Hawk–Dove game and competition dynamics. *Math Computer Modelling* 1998;274:89–98.

Sánchez E, Auger P, Bravo de la Parra R. Influence of individual aggressiveness on the dynamics of competitive populations. *Acta Biotheoretica* 1997;45:321–33.

Lett C, Auger P, Bravo de la Parra R. Migration frequency and the persistence of host-parasitoid interactions. *Journal of Theoretical Biology* 2003;221:639–54.

Lett C, Auger P, Fleury F. Effects of asymmetric dispersal and environmental gradients on the stability of host-parasitoid systems. *Oikos* 2005;109:603–13.

Nguyen-Huu T, Lett C, Poggiale JC, Auger P. Effects of migration frequency on global host-parasitoid spatial dynamics with unstable local dynamics. *Ecological Modelling* 2006;197:290–5.

Nguyen-Huu T, Lett C, Auger P, Poggiale JC. Spatial synchrony in host-parasitoid models using aggregation of variables. *Mathematical Biosciences* 2006;203:204–21.

Nguyen-Huu T, Auger P, Lett C, Marvá M. Emergence of global behaviour in a host-parasitoid model with density-dependent dispersal in a chain of patches. *Ecological Complexity* 2008;5:9–21.

Charles S, Bravo de la Parra R, Mallet JP, Persat H, Auger P. Population dynamics modelling in an hierarchical arborescent river network: an attempt with *Salmo trutta*. *Acta Biotheoretica* 1998;46:223–34.

Charles S, Bravo de la Parra R, Mallet JP, Persat H, Auger P. A density dependent model describing *Salmo trutta* population dynamics in an arborescent river network: effects of dams and channelling. *C R Acad Sci Paris Sciences de la vie* 1998;321:979–90.

Charles S, Bravo de la Parra R, Mallet JP, Persat H, Auger P. Annual spawning migrations in modeling brown trout population dynamics inside an arborescent river network. *Ecological Modelling* 2000;133:15–31.

Chaumot A, Charles S, Flammarion P, Garric P, Auger P. Using aggregation methods to assess toxicant effects on population dynamics in spatial systems. *Ecological Applications* 2002;126:1771–84.

Chaumot A, Charles S, Flammarion P, Auger P. Ecotoxicology and spatial modeling in population dynamics: an attempt with brown trout. *Environmental Toxicology and Chemistry* 2003;225:958–69.

Chaumot A, Charles S, Flammarion P, Auger P. Do migratory or demographic disruptions rule the population impact of pollution in spatial networks? *Theoretical Population Biology* 2003;64:473–80.

Mchich R, Auger P, Raïssi N. The stabilizability of a controlled system describing the dynamics of a fishery. *Comptes Rendus de l'Académie des Sciences, Biologies* 2005;329:337–50.

Mchich R, Auger P, Bravo de la Parra R, Raïssi N. Dynamics of a fishery on two fishing zones with fish stock dependent migrations: Aggregation and control. *Ecological Modelling* 2002;158:51–62.

Kooi BW, Poggiale JC, Auger PM. Aggregation methods in food chains. *Mathematical Computer Modelling* 1998;27:109–20.