

## Original Research Article

## A review on spatial aggregation methods involving several time scales

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## ABSTRACT

This article is a review of *spatial aggregation of variables* for time continuous models. Two cases are considered. The first case corresponds to a discrete space, i.e. a set of discrete patches connected by migrations, which are assumed to be fast with respect to local interactions. The mathematical model is a set of coupled ordinary differential equations (O.D.E.). The *spatial aggregation* allows one to derive a global model governing the time variation of the total numbers of individuals of all patches in the long term. The second case considers a continuous space and is a set of partial differential equations (P.D.E.). In that case, we also assume that diffusion is fast in comparison with local interactions. The spatial aggregation allows us again to obtain an O.D.E. governing the total population density, which is obtained by integration all over the spatial domain, at the slow time scale. These *aggregations* of variables are based on time scales separation methods which have been presented largely elsewhere and we recall the main results. We illustrate the methods by examples in population dynamics and prey–predator models.

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## 1. Introduction

In ecology, several levels of organization are often considered, the individual, the population and the community levels. In order to keep realistic, most models in ecology and in population dynamics must take into account those levels of organization leading to mathematical models involving more and more variables. Therefore, the mathematical models are sets of many coupled nonlinear equations. Those models are complex, because there are in general difficulties in handling the equations and in obtaining analytical results such as existence of positive equilibria and stability properties, existence of periodic solutions, or else asymptotic behavior. As a consequence, there was interest in developing methods that allow a reduction of the complexity of dynamical systems involving many state variables. For example, an important question is how to build macro models governing a few global variables.

Early works proposed some methods to reduce complexity for a class of particular systems, which are hierarchically organized including different levels of organization (Auger, 1980, 1983, 1989). In this generic approach, one considered a system which is organized

in a hierarchical manner in the sense that processes involved in the dynamics of the complete system could be ordered into several classes of interactions, intra-group and inter-group interactions for a system with two levels of organization. Furthermore, intra-group interactions were assumed to be strong (or fast) in comparison of inter-group (or slow) interactions. An important problem is to define some global or else macro variables associated with each group and that can characterize each group as a whole. In this *hierarchical* approach, it was assumed that the intra-group dynamics was conservative and therefore, global variables were defined as first integrals of the intra-group dynamics for each group. On the one hand, conservative intra-group dynamics is an extra assumption that may not be verified for any system but, on the other hand, when this assumption is true, each group can be characterized by some global variables that are constants of motion for the intra-group dynamics and as a consequence keep constant at the fast time scale. However, those macro-variables are no more constant when one takes into account the inter-group dynamics. Such first integrals of the intra-group dynamics are of course very good candidates to characterize the dynamics of the complete system in the long term because they do not vary at the short time scale but vary slowly as a result of the inter-group dynamics. In the final step of the procedure of reduction, it was possible to derive a macro-model governing those global variables associated with each group and varying at a slow time scale. This method of reduction of the dimension could be

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extended to a hierarchically organized system involving any number of organization levels.

At the same period, some authors extended methods of aggregation of variables which are also methods for deriving a macro model from a complete detailed model. Aggregation of variables is coming from economy and has been introduced in ecology by Iwasa et al. (1987). Two types of aggregation of variables have been studied, perfect aggregation and approximate aggregation of variables. In perfect aggregation, one considers a complex dynamical model with many coupled variables, the micro-variables.

$$x_i'(t) = f_i(x_1(t), \dots, x_n(t))$$

where ' denotes the time derivative with respect to  $t$  ( $' = d/dt$ ),  $x_i(t)$  are micro-variables and  $i \in \{1, \dots, n\}$ ,  $n$  being the total number of micro-variables assumed large,  $n \gg 1$ . In the next step, one looks for existence of some global or macro-variables which are defined by some functions of the micro-variables:

$$G_j = g_j(x_1, \dots, x_n)$$

where  $G_j$  are macro-variables and  $j \in \{1, \dots, N\}$ ,  $N$  being the total number of macro-variables assumed,  $N$  is assumed to be small with respect to  $n$ . Perfect aggregation is realized when the mathematical equations of the dynamics of the global variables can finally be expressed exactly (without any approximation) in terms of those global variables.

$$G_j'(t) = \sum_{i=1}^n \frac{\partial g_j}{\partial x_i} x_i'(t) = \sum_{i=1}^n \frac{\partial g_j}{\partial x_i} f_i(x_1(t), \dots, x_n(t)) = F_j(G_1, \dots, G_N)$$

In general, such a perfect aggregation is not possible unless parameters take very particular values that allow the global variables to appear in the right hand side of the previous equations. Perfect aggregation is a very particular situation which is rarely possible since it requires drastic conditions. Consequently, methods for approximate aggregation have been developed by Iwasa et al. (1989). Approximate aggregation deals with methods of reduction where the consistency between the dynamics of the global variables in the complete system and the aggregated system is only approximate. In this frame, the previous method of reduction of hierarchically organized systems mentioned above (Auger, 1980, 1983, 1989) fell into this scope.

Methods of aggregation of variables were presented in a rigorous mathematical form for O.D.E. in Auger and Roussarie (1994), Auger and Poggiale (1996) and Poggiale and Auger (1996), extended to discrete models in Sánchez et al. (1995) and Bravo de la Parra et al. (1997), to P.D.E. in Arino et al. (1999) and to D.D.E. in Sánchez et al. (2006). For aggregation methods in time discrete models we refer to Auger et al. (2008a,b) and to Nguyen Huu et al. (2006) for spatial aggregation in this context.

This article is a short review on spatial aggregation of variables for time continuous models. We focus on spatial aggregation even if the principle of aggregation can be applied in other contexts i.e. when aggregation is based on other criteria rather than space. For example, we mention aggregation when individual behavior is taken into account in population and community models (Auger et al., 2002, 2006; Dubreuil et al., 2006). Aggregation was also useful to model the dynamics of a virus epidemics, Poggiale et al. (2009), and in eco-epidemiology to study the effects of an epidemics on the dynamics of a prey–predator system (Auger et al., 2009). A first extension of the method to non autonomous systems of ordinary differential equations has been proposed with applications to epidemiological models in patchy-environment (see Marva et al., 2012). We also refer to applications of aggregation in fishery modeling (Auger et al., 2010a,b).

Two cases are considered in this paper. The first case deals with a discrete space which is a set of patches connected by migration events. In the second case, space is assumed to be continuous. In both cases, migration (case 1) or diffusion (case 2) is assumed to be rapid in comparison with local interactions. This last assumption allows us to proceed to a *spatial aggregation* that is to derive a global model governing the total density of individuals, obtained either by summation of the local patch densities or by integration over the spatial domain of the local density.

The article is organized as follows: in Section 2 we present methods of spatial aggregation in the case of continuous time and discrete space with fast migration (O.D.E.). Section 3 studies spatial aggregation in the case of continuous time and space with fast diffusion (P.D.E.). The paper ends with a section of conclusions.

## 2. Aggregation in a patchy environment

A lot of models of biotic interactions have been proposed in ecology to understand the population dynamics by means of their interactions with other populations (see Murray, 1989 or Edelstein-Keshet, 2005 for instance). Moreover, the role of space (dispersal, spatial variability, etc.) has also been investigated to show how it can modify the properties of the biotic interaction models: stabilitization/destabilization effects, synchronization/desynchronization, spatial patterns formations, permanence properties and so on, have been discussed under the light of spatially extended models (see Murray, 1989 or Malchow et al., 2008 for instance). It is often the case that mathematical analysis is difficult, even impossible, when dealing with communities in patchy-environments and in such situations, results are obtained with numerical simulations. However, it is interesting when possible to get rather simple rules which integrate the local interactions and the spatial variability on the whole spatial domain and explain how these characteristics are combined to lead the whole population dynamics. Scale Transition Theory Chesson (1998) have been proposed for such an objective. Spatial aggregation method is another approach which also permits detailed models at local scale to be defined and simplify them to get a model at the global scale as well as relationships between these local and global scales. The Scale Transition Theory allows the relationship between the spatial distribution of the populations to be synthesized in an elegant manner, via their mean and spatial variance, and the local nonlinear dynamics under which they are submitted. This is very useful for understanding the link between local processes and global dynamics. However, it is based on a truncated Taylor expansion which may not always be sufficient. Moreover, even if the above truncation is valid, it is necessary to simulate the complete model to get the spatial variance and be able to simulate the total population dynamics. In the aggregation method, the simulation of the reduced model does not need the simulation of the complete one. The methods presented in this paper need that processes take place at different time scales, for instance that migration are fast with respect to local interactions.

The family of models used in this context is now introduced more precisely and the assumptions used for the methods are listed. We consider a community with  $A$  populations leaving in a patchy environment constituted by  $N$  patches. We denote by  $x_i^\alpha$  the density of sub-population  $\alpha$  located on patch  $i$ , where  $\alpha \in \{1, \dots, A\}$  and  $i \in \{1, \dots, N\}$ . We assume that the displacements take place on a short time scale in comparison to the demographic processes (birth, death, etc.). The general form of the models considered here is:

$$x_i^{\alpha'}(t) = \frac{1}{\varepsilon} F_i^\alpha(X(t)) + f_i^\alpha(X(t)) \tag{1}$$

where ' denotes the time derivative with respect to  $t$  ( $' = d/dt$ ),  $X^\alpha(t) = (x_1^\alpha(t), \dots, x_N^\alpha(t))$  and  $X = (X^1(t), \dots, X^A(t))$ ,  $F_i^\alpha$  represents the displacements of individuals of population  $\alpha$  related to patch  $i$  and

$f_i^\alpha$  describes the demographic processes as well as the biotic interaction effects. Finally, the parameter  $\varepsilon$  is a small dimensionless parameter (called scale parameter), which is assumed to be small and characterizes the difference of time scales:  $\varepsilon \ll 1$ . The maps  $F_i^\alpha$  and  $f_i^\alpha$  are assumed to be  $C^r$  with  $r \geq 1$ .

The function  $F_i^\alpha$  is often a function of the vector  $X^\alpha$ . It allows the changes of patches to be represented. When density-dependent effects like effects of predator densities on prey movements for instance are taken into account, the function  $F_i^\alpha$  is thus a function of the vector  $X$ .

Since the displacement of individuals is a conservative process, the total density of each population  $x^\alpha = \sum_{i=1}^N x_i^\alpha$  is not modified by the migrations and thus:

$$\sum_{i=1}^N F_i^\alpha(X) = 0$$

In the first sub-section, a brief summary of the reduction method is provided. In the second sub-section, some recent extensions and new perspectives are presented. The third and fourth sub-sections propose two examples which illustrate different aspects of the method. This method is discussed in the context of ecological complexity in the last sub-section.

### 2.1. General principle of the reduction method

Let us define the frequency of population  $\alpha$  on patch  $i$  by  $v_i^\alpha = x_i^\alpha / x^\alpha$ , it follows that  $\sum_{i=1}^N v_i^\alpha = 1$ . We perform the change of variables  $x_i^\alpha \rightarrow (v_i^\alpha, x^\alpha)$ , with  $\alpha \in \{1, \dots, A\}$  and  $i \in \{1, \dots, N\}$ . System (1) becomes:

$$\dot{v}_i^\alpha(\tau) = \frac{1}{x^\alpha(\tau)} [F_i^\alpha(X(\tau)) - \varepsilon v_i^\alpha(\tau) f^\alpha(X(\tau))] \tag{2a}$$

$$\dot{x}^\alpha(\tau) = \varepsilon f^\alpha(X(\tau)) \tag{2b}$$

where  $\tau = t/\varepsilon$ ,  $\dot{x}$  denotes the time derivative of  $x$  with respect to  $\tau$  ( $\dot{x} = dx/d\tau$ ),  $\alpha \in \{1, \dots, A\}$  and  $i \in \{1, \dots, N-1\}$ ,  $f^\alpha(X) = \sum_{i=1}^N f_i^\alpha(X)$ . Under this form, it is clear that the frequencies of population on the different patches have a fast dynamics with respect to the total population densities, for which the time derivatives are very small. The new system is called a slow-fast system.

Slow-fast systems have been analyzed for a few decades, in the framework of singular perturbations theory (Hoppensteadt, 1966). A geometrical point of view is adopted here, based on the Fenichel theorem (see Fenichel, 1971 or Wiggins, 1994 for instance). This theorem provides the conditions under which we can assume that the fast variables can be replaced by asymptotic values in the equations of the slow variables, leading in this way to a lower dimension system. Let us apply the Fenichel theorem in the case of system (2.1): we first add the equation  $d\varepsilon/d\tau = 0$  and consider the case  $\varepsilon = 0$ . It follows that  $x^\alpha$  are constant and the fast variables are governed by the system:

$$v_i^\alpha(\tau) = \frac{1}{x^\alpha} F_i^\alpha(X(\tau))$$

for  $i \in \{1, \dots, N-1\}$  and  $\alpha \in \{1, \dots, A\}$ . We assume that this system has a globally asymptotically stable equilibrium and we denote by  $v_i^{\alpha*}$  the frequency equilibrium values. If the Jacobian matrix of this system at the equilibrium has only eigenvalues with strictly negative eigenvalues, then the equilibrium is called hyperbolic. In this case, the set

$$\mathcal{M}_0 = \{(v^*, x^\alpha, 0)\} \subset \mathbb{R}^{A(N-1)} \times \mathbb{R}^A \times \mathbb{R}$$

is called normally hyperbolic for the system (2.1). In this case, for all compact sets in  $\mathbb{R}^{A(N-1)} \times \mathbb{R}^A \times \mathbb{R}$ , there exists  $\varepsilon_0$  such that for all  $\varepsilon < \varepsilon_0$ , the set  $\mathcal{M}_0$  persists, that is there exists a set  $\mathcal{M}_\varepsilon$  close and diffeomorphic to  $\mathcal{M}_0$ , invariant under the flow generated by system (2.1), on which the full dynamics can be reduced. The reduced dynamics governs the total densities variables  $x^\alpha$  and an approximation of  $\mathcal{M}_\varepsilon$  by  $\mathcal{M}_0$  leads to the reduced system:

$$\dot{x}^\alpha(t) = \tilde{f}^\alpha(x^1(t), \dots, x^\alpha(t)) \tag{3}$$

where

$$\tilde{f}^\alpha(x^1, \dots, x^\alpha) = f^\alpha(v_1^* x^1, \dots, v_N^* x^1, v_1^* x^2, \dots, v_N^* x^2, \dots, v_1^* x^A, \dots, v_N^* x^A).$$

Geometrical singular perturbation theory allows us to conclude that the trajectories of the complete system (2.1) are rapidly close to the trajectories of the reduced system (3) and that, under the conditions that the trajectories remain in the compact set mentioned above, the asymptotic behavior of the complete model solutions is provided by the study of the reduced one.

### 2.2. Cautions, limits and extensions

Many papers deal with time separation techniques and do not refer to any mathematical result to apply these techniques. For instance, the so-called *quasi-steady assumption* is used in chemistry and biochemistry in order to simplify models in which two time scales are present. The fast variables are replaced by their equilibrium values in the equations governing the slow variables, exactly as the mathematical theory says. We call this the *quick derivation method* (QDM). Indeed, it is a rather intuitive idea and we could argue that it is not necessary to use the formal theorems to apply these techniques. However, there are some cases where the reduced system obtained by this way does not have a similar dynamics to the complete one. For instance, if the reduced system obtained with the QDM is not structurally stable, it must be highlighted that the mathematical theory claims that the QDM is a first approximation of the actual reduced system and even provides the tool to get a better approximation. If the actual reduced system obtained by the Fenichel theorem is approximated by the reduced QDM model and if this QDM model is not structurally stable, it is necessary to get a better approximation of the actual reduced system. Such an example is given in Poggiale and Auger (2004) where, using suitable the Fenichel theorem, it is shown that in a predator-prey system in a patchy environment, with a refuge for the prey, dispersal has a stabilizing effect. In another example where this refinement is needed, Poggiale et al. (1998) show that a ratio-dependent functional response may emerge from a local prey-dependent response and dispersal in a patchy-environment with a refuge for the prey.

Another situation where the mathematical framework is useful, concerns the bifurcation analysis of the reduced model. The Fenichel theorem allows us to guarantee that the bifurcations obtained with the reduced QDM model are the same as the bifurcations got in the analysis of the complete model. An example for which this mathematical sophistication is needed is presented in Mchich et al. (2007), where a predator-prey model in a patchy-environment, with density-dependent dispersal rates, is analyzed to understand how this density-dependence of individuals movement affects the predator-prey system stability. In this example, a non-generic Hopf bifurcation occurs.

The mathematical theorems give the formal assumptions under which the reduction is efficient. In Poggiale et al. (2009), we give examples where the fast equilibrium is always stable but the reduced model provides the correct dynamics of the complete model only during a finite time. In these examples, the invariant manifold is

normally hyperbolic except on the boundary of the biologically relevant domain. However, the trajectories periodically visit the vicinity of this region where the normal hyperbolicity is lost. Recently, some mathematical extensions in the geometrical singular perturbation theory framework have been published to get a very good description of the trajectories in this case (see Dumortier and Roussarie, 1996 or Dumortier and Roussarie, 2000 for instance).

2.3. Example 1: emergence of cycles from behavior in displacements

The model presented here, in some sense, can be related to one of the models developed in Auger et al. (2000). We aim to consider here a simple model which contains sufficient richness to illustrate various interesting properties of the method. Thus, it can be argued that some biological assumptions should not be very realistic and at least not supported by empirical evidence. Actually, the same kind of dynamics and results could be illustrated with a more realistic model, but certainly more complex and more difficult to describe in this review.

2.3.1. Assumptions, model equations and the associated slow-fast system

We consider a single population on two patches. Patch 1 is assumed to be a sink and patch 2 is assumed to be a source. We use the same notations as above but since there is only one population ( $A = 1$ ), we omit the superscript  $\alpha$ . The local densities on each patch are  $x_1(\tau)$  and  $x_2(\tau)$ . The model reads:

$$x_1'(t) = \frac{1}{\varepsilon}(m_2x_2(t) - m_1x_1(t)) - d_1x_1(t) \tag{4a}$$

$$x_2'(t) = \frac{1}{\varepsilon}(m_1x_1(t) - m_2x_2(t)) + r_2x_2(t) \tag{4b}$$

where  $m_1$  (resp.  $m_2$ ) is the displacement rate from patch 1 to patch 2 (resp. from patch 2 to patch 1),  $d_1$  is the death rate on the sink

patch and  $r_2$  is the growth rate on the source patch. We furthermore assume a particular behavior in the displacement: we assume that the displacement rate  $m_2$  is a constant while the displacement rate  $m_1$  (from the sink to the source) is a decreasing function of the local density  $x_1$ , corresponding to an aggregating behavior on this patch. This example does not aim to be very close to an actual example but it has the advantage of being rather simple and of containing the different aspects discussed in the previous sub-sections. For the sake of simplicity, let  $m_1(x_1) = \alpha/(1 + \beta x_1^2)$ . Let us introduce the aggregated variable  $x(t) = x_1(t) + x_2(t)$ , which is the total population density.

The frequencies on the different patches are  $v_1 = x_1/x$  and  $v_2 = 1 - v_1$ . The previous differential system can be written as follows:

$$\dot{v}_1(\tau) = m_2 - (m_1 + m_2)v_1(\tau) - \varepsilon v_1(\tau)(1 - v_1(\tau))(d_1 + r_2) \tag{5a}$$

$$\dot{x}(\tau) = \varepsilon(r_2 - (d_1 + r_2)v_1(\tau))x(\tau) \tag{5b}$$

$$\dot{\varepsilon}(\tau) = 0 \tag{5c}$$

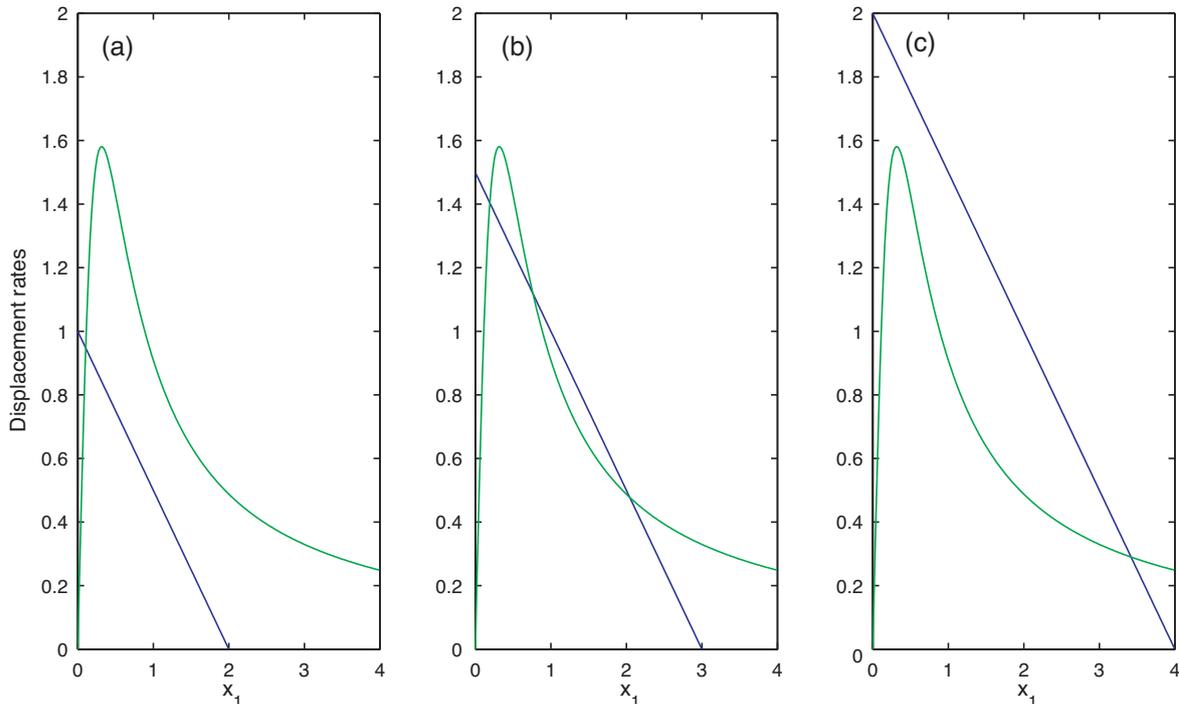
where  $\tau = t/\varepsilon$ .

2.3.2. First step: fast dynamics and quick derivation method

The aggregation method consists first of considering the case  $\varepsilon = 0$  and determining the fast dynamics attractors (i.e. looking for the invariant manifold  $\mathcal{M}_0$ ). It follows that the total density  $x$  is a constant and in our example, only one differential equation is fast, thus  $v_1(\tau)$  is going toward an limit when  $\tau$  goes to infinity. The equilibria of this fast equation are obtained by solving the equation:

$$m_2(1 - v_1) = \frac{\alpha v_1}{1 + \beta x^2 v_1^2} \tag{6}$$

with respect to the frequency  $v_1$ , where we replaced  $v_2$  by  $1 - v_1$ . The left-hand side is a decreasing linear function of  $v_1$  and the



**Fig. 1.** Equilibria of Eq. (5a) for  $\varepsilon = 0$  in the generic situations: these equilibria are obtained by the intersection of the two curves which corresponds to the left-hand side (straight line) and right-hand side (non monotone curve) of Eq. (6). On the left panel (a), the total density is low. It follows that there is only one equilibrium  $v_{11}^*$  corresponding to a small proportion of the population on patch 1. On the central panel (b), there are three equilibria:  $v_{11}^*$  and  $v_{13}^*$  are stable while  $v_{12}^*$  is unstable.  $v_1(\tau)$  tends to  $v_{11}^*$  or  $v_{13}^*$ , according to the initial condition  $v_1(0)$ . On the right panel (c), there is again only one equilibrium  $v_{13}^*$ , which is stable and corresponds to a high proportion of the population on patch 1.

right-hand side is a non monotone function, which can cross the linear function one, two (not generic case) or three times, depending on the value of the total density  $x$ . Fig. 1 illustrates the two generic situations: 1 or 3 fast equilibria. If initially, the total population density is low, the fast dynamics leads to an equilibrium  $v_{11}^*$  which is small, that is most of the population is located on patch 2 (see Fig. 1a). If initially, the total population density is high, the fast dynamics leads to an equilibrium  $v_{13}^*$  which is large: most of the population is on patch 1 (see Fig. 1c). In the intermediate situation, there are three equilibria  $v_{11}^*$ ,  $v_{12}^*$  and  $v_{13}^*$ ,  $v_{11}^*$  and  $v_{13}^*$  are stable and  $v_{12}^*$  is unstable. The initial condition  $v_1(0)$  determines which stable equilibrium the fast variable is going to. Since there are potentially two stable equilibria for the fast part, it follows that there are two aggregated models:

$$x'(t) = (r_2 - (d_1 + r_2)v_{1,1}^*(x(t)))x(t) \tag{7}$$

and

$$x'(t) = (r_2 - (d_1 + r_2)v_{1,3}^*(x(t)))x(t) \tag{8}$$

It is rather common analysis to show that each of these models leads to the same qualitative dynamics, which is a logistic-like one. Since  $v_{11}^*(x) < v_{13}^*(x)$ , it follows that the equilibrium  $x^{1*}$  of the total density with model (7) is higher than the total density equilibrium  $x^{2*}$  obtained with the model (8):  $x^{1*} > x^{2*}$ .

### 2.3.3. Global dynamics: a heuristic explanation

Let us consider an initial condition for the complete model  $(v_1(0), x(0))$  with a very low total population density  $x(0) \ll 1$ . Very rapidly, the frequency  $v_1(\tau)$  is close to  $v_{11}$ . Thus  $x(t)$  increases slowly and will tend to  $x^{1*}$ . If this apparent carrying capacity  $x^{1*}$  is larger than the threshold which makes the fast equilibrium  $v_{11}^*$  disappear (saddle-node bifurcation when  $v_{11}^*(x)$  encounters  $v_{12}^*(x)$ ), then the above reduced model is no longer valid. It follows that  $v_1$  will suddenly jump to  $v_{13}^*$ . When  $v_1$  becomes large, the individuals are mainly on the sink patch and the population density decreases:  $x(t)$  is now decreasing to  $x^{2*}$ . The fast equilibrium  $v_{11}^*$  then appears again. The fast variable  $v_1$  will not necessarily jump to that equilibrium because it may still be in the basin of attraction of  $v_{13}^*$ . In other words, it may be necessary to wait for some time until  $x(t)$  decreases enough, which is possible if  $x^{2*}$  is lower than the threshold which makes the fast equilibrium  $v_{13}^*$  disappear (saddle-node bifurcation when  $v_{13}^*(x)$  encounters

$v_{12}^*(x)$ ). In this case,  $v_{13}^*$  disappears and then  $v_1$  jumps fast to  $v_{11}^*$ . This mechanism provokes oscillations of the total density and it is also true for the local densities, by the way (see Fig. 2). This heuristic explanation is quite simple and provides the qualitative behavior of the solutions of the complete model. However, a more precise description would need more complex tools which are given by the geometrical singular perturbation theory (GSPT) as explained at the end of Section 2.4, for instance for determining exactly when one of the aggregated model is no longer valid and when should we consider the second one.

Geometrical singular perturbation theory provides a set of tools which helps to understand exactly what is going on for this kind of situation: it allows namely the precise description of the fate of the trajectories when they leave the invariant manifold used to get the aggregated model, which occurs when the fast equilibria are becoming unstable (or at least not hyperbolically stable).

### 2.4. Example 2: a predator–prey model in a patchy environment with a refuge for the prey

Methods of aggregation of variables are useful in order to reduce the complexity of mathematical models. This occurs when one can reduce the dimension of a mathematical model involving many variables and parameters. We illustrate this in the next example: we consider a predator–prey model in a patchy-environment. We assume that the prey has a refuge. We aim to determine the minimal number of patches where predator–prey interaction takes place to allow the predator to invade. We illustrate on this example that aggregation method provides analytical results on the complete system and allow to determine this threshold value on the number of patches. This is a theoretical example just presented as an illustration of the method, it is a simplified version of the model studied in Auger et al. (2010b). However, it could get different kind of applications (Marine Protected Area, Biological control of pests, and so on).

We consider prey and predator populations interacting on a linear chain of  $N$  patches connected by dispersal. We assume that the prey population has a refuge from which it can reach any of the interaction patches. It is assumed that the prey cannot survive in the refuge where no resource are available and that they die at a rate  $\mu_R$ . Consequently, prey leave frequently the refuge at a rate  $k$  to reach a patch  $i$  where food is available. On these patches, the prey population grow logistically with growth rate  $r_i$  and carrying capacity  $K_i$ . Let  $n_R(t)$  be the density of prey in the refuge at time  $t$ ,

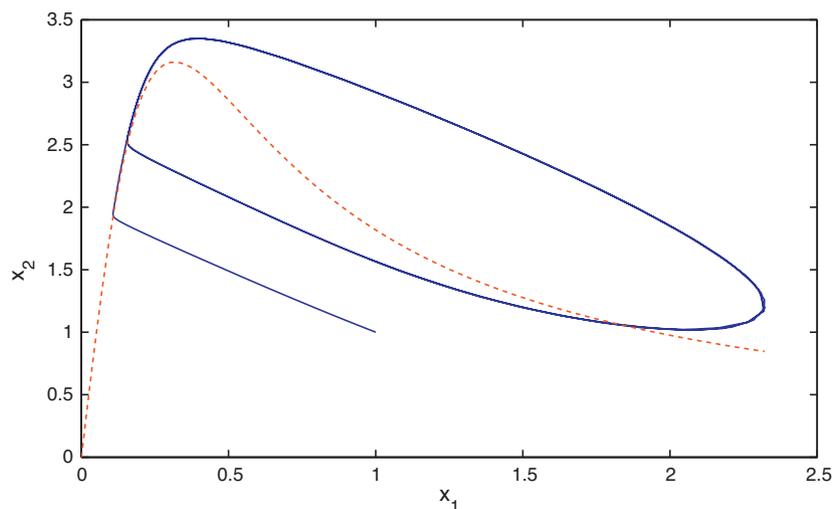


Fig. 2. A limit cycle (solid line) in the phase space of model (1). The dashed curve corresponds to the set in the phase space where the fast variable time derivative vanishes:  $\dot{v}_1 = 0$ . The parameters value used for this simulation are:  $\alpha = 10$ ;  $\beta = 10$ ;  $m_2 = 0.5$ ;  $d_1 = 2$ ;  $r_2 = 1$ ;  $\varepsilon = 0.04$ .

$n_i(t)$  is the prey density on patch  $i$  at time  $t$  and  $p_i(t)$  is the predator density on patch  $i$  at time  $t$ . Prey return from patch  $i$  to their refuge at a rate  $k_{Ri} = \alpha/K_i$ , which means that prey are more likely to remain on a patch  $i$  when its carrying capacity is large. For predators, we assume that individuals can move to the two neighbouring patches  $i$  of the chain and that the dispersal rates are correlated to the distance between patches thus the migration rate from patch  $j$  to patch  $i$   $m_{ij}$  is equal to the migration rate from patch  $i$  to patch  $j$   $m_{ji}$ .  $\mu_i$  is the mortality rate for predators on patch  $i$ ,  $a_i$  and  $b_i$  are classical predation parameters that are assumed to be patch dependent. Finally, we assume that dispersal rates of prey and predators are high with respect to demographic rates (populations growth and mortality rates, predation rates). According to these assumptions, species densities vary according to the classical prey predator model as follows:

$$n'_R(t) = \frac{1}{\varepsilon} \left( \sum_{i=1}^N k_{Ri} n_i(t) - N k n_R(t) \right) - \mu_R n_R(t) \tag{9a}$$

$$n'_i(t) = \frac{1}{\varepsilon} (k n_R(t) - k_{Ri} n_i(t)) + r_i n_i(t) \left( 1 - \frac{n_i(t)}{K_i} \right) - a_i n_i(t) p_i(t) \tag{9b}$$

$$p'_i(t) = \frac{1}{\varepsilon} (m_{i,i-1} p_{i-1}(t) + m_{i,i+1} p_{i+1}(t) - (m_{i-1,i} + m_{i+1,i}) p_i(t)) + (b_i n_i(t) - \mu_i) p_i(t) \tag{9c}$$

$$p'_1(t) = \frac{1}{\varepsilon} (m_{1,2} p_2(t) - m_{2,1} p_1(t)) + (b_1 n_1(t) - \mu_1) p_1(t) \tag{9d}$$

$$p'_N(t) = \frac{1}{\varepsilon} (m_{N,N-1} p_{N-1}(t) - m_{N-1,N} p_N(t)) + (b_N n_N(t) - \mu_N) p_N(t) \tag{9e}$$

where  $i \in \{2, \dots, N-1\}$ ,  $\varepsilon$  is a small positive dimensionless parameter which traduces the time scale separation between dispersal and demography. This model, which we will call the complete model, deals with  $2N + 1$  equations, that is a high number of equations when  $N$  is large. It is then difficult to handle with and to get analytical results about its asymptotic behavior. Therefore, the aggregation method will be useful to reduce the number of equation, to build an aggregated model for which analytical results are obtained. Since the dispersal process is fast, prey and predator densities reach a fast stable equilibrium, obtained by vanishing the differential equations with  $\varepsilon = 0$ . We get:

$$n_i^* = v_i^* n \quad \text{and} \quad n_R^* = v_R^* n$$

where the total prey density  $n = \sum_{i=1}^N n_i + n_R$  is a constant when  $\varepsilon = 0$ ,  $v_i^* = k K_i / (\alpha + k \sum_{i=1}^N K_i)$  and  $v_R^* = \alpha / (\alpha + k \sum_{i=1}^N K_i)$ . Furthermore, the predator densities at fast equilibrium are:

$$p_i^* = \frac{p}{N}$$

where  $p = \sum_{i=1}^N p_i$  is the total predator density. The previous equation means that the predator population is homogeneously distributed on the spatial domain. We now derive the corresponding aggregated model by computing the time derivative of  $n(t)$  and  $p(t)$  in which  $n_i(t)$ ,  $n_R(t)$  and  $p_i(t)$  are replaced by the above mentioned equilibrium values. It reads:

$$n'(t) = R n(t) \left( 1 - \frac{n(t)}{K} \right) - A n(t) p(t) + O(\varepsilon) \tag{10a}$$

$$p'(t) = B n(t) p(t) - \mu p(t) + O(\varepsilon) \tag{10b}$$

where  $R = \sum_{i=1}^N v_i^* r_i - v_R^* \mu_R$ . We assume that this quantity is nonnegative otherwise the prey population would die out and the system would not be interesting. The total prey carrying capacity is

$K = R / (\sum_{i=1}^N (r_i (v_i^*)^2 / K_i))$ , the total predator population death rate is  $\mu = \sum_{i=1}^N v_i^* \mu_i$  and the total predation parameters are  $A = (1/N) \sum_{i=1}^N a_i v_i^*$  and  $B = (1/N) \sum_{i=1}^N b_i v_i^*$ . This system admits a positive equilibrium provided that:

$$K > \frac{\mu}{B} \tag{11}$$

When this equilibrium exists, it is globally asymptotically stable for all initial conditions in the nonnegative domain. The condition (11) can be written as follows:

$$k \left( \sum_{i=1}^N r_i K_i \right) \left( \sum_{i=1}^N (b_i K_i - \mu_i) \right) > \alpha \mu_R \sum_{i=1}^N b_i K_i \tag{12}$$

If we now assume for instance that the patches are rather similar, such that  $r_i = r$ ,  $K_i = \tilde{K}$ ,  $b_i = b$  and  $\mu_i = \mu$  for all  $i \in \{1, \dots, N\}$ , then the existence condition (12) depends explicitly on  $N$ , we get a condition on  $N$  for which the predator population can survive. In this case, condition (12) reads:

$$N > \frac{\alpha \mu_R b}{kr(b\tilde{K} - \mu)} \tag{13}$$

where  $\tilde{K}$  is assumed to be larger than  $\mu/b$  in order to allow the predator to survive on each patch separately. This is a necessary condition, but as shown in Eq. (13), it is not sufficient. Indeed, there is a minimal number of patches given by Eq. (13) under which the predator is excluded, even if on each patch separately it could invade. In this example, the threshold value for the minimal number of patches allowing predator invasion depends on the prey displacement rates  $\alpha$  and  $k$ , on the mortality rate of the prey in they refuge  $\mu_R$ , on the local predator response to predation  $b$ , on the local carrying capacity of each patch  $\tilde{K}$  and on the local (and global) mortality rate of the predator  $\mu$ .

### 2.5. Ecological complexity

Since ecosystems can be seen as a large number of entities, interacting in a non linear way, in varying environments, two different extreme approaches may be opposed (see Jorgensen, 2002 for instance for more details). The holistic approach tries to define global descriptors of ecosystems properties, omitting the details. On the contrary, the reductionist approach aims to understand the ecosystem properties on the basis of mechanisms and therefore tries to describe the processes at a detailed level and to find how they interact to get the whole dynamics. One might ask if it is really necessary to insert details in model of ecosystems and which details are important or not, the problem is still opened (see for instance Raick et al., 2006 and Poggiale et al., 2010). Of course, many approaches provide a trade off between these extremes.

In the context of this article, the complexity also occurs from the spatial description of population or communities dynamics. Space is, in this section, represented by an arbitrary large number of patches on which population are distributed. In each patch, populations grow and interact with each other in the community. Our aim is to develop a method to reduce the resulting complexity of such systems governed by a large number of variables. Two points are important in our approach. Firstly, we use a hierarchical point of view for defining different time scales: individuals are moving at a short time scale while population dynamics take place on a longer time scale. Secondly, we use a reduction method to simplify the models at long time and large space scales. Thirdly, we use this method to keep a link between the different involved organization levels. The reduction of complexity allows to determine some general rules at the global scale on the basis of detailed description, as in example 2 above. The relationships

between local and global levels allow to keep the dynamics of the complete model while dealing with the simplified ones. The emergent properties at the global spatial level, obtained by bottom-up effects, can thus be explained from local interactions, displacement behaviors and spatial variability. Furthermore, the global dynamics can lead the aggregated variables to threshold values which, in turn, lead to drastic changes at the local level, a top-down response of the complex system, as in example 1.

More precisely, example 1 has been chosen to show that the method permits to reduce the complete model to simpler ones but that different simplified (aggregated) models can result from the complete one. In the example, two aggregated models can be derived but we can easily imagine that in more complex systems, more than two aggregated models would be derived to be able to represent the dynamics of the complete model. In order to know which aggregated model should be used when several models are derived from the complete one, we need first to know the initial conditions but it is also useful to use the geometrical singular perturbation theory (GSPT) to detect the regions in the phase space where the trajectories of the complete model jump from one aggregated representation to another one. These regions are characterized by a loss of normal hyperbolicity of the perturbed invariant manifold  $\mathcal{M}_\varepsilon$  given by Fenichel's theorem. Blowing up techniques allow us to deal with this situation ((Dumortier and Roussarie, 1996, 2000)).

As said previously, the aggregation method bridges local nonlinear interactions to global population or community dynamics, this has been illustrated in the previous sub-sections. Dispersal of individuals in a patchy-environment can be random or driven by individuals density-dependent behaviors. The method can for instance be used to parameterize a model at a large scale on the basis of formulations obtained at small scales, like in laboratory experiments. For instance, in Michalski et al. (1997), we show that predator-prey models at a global scale can be parameterized from simple laws, like Mass Action law, associated to behavioral rules for individuals (displacement behavior for instance). General ecological rules can thus be derived on different community properties (predation, see Poggiale et al., 1998; Poggiale, 1998a, stability, see Poggiale and Auger, 2004, coexistence, see Poggiale, 1998b, etc.). Furthermore, the method provides some general rules to control complex systems like in Auger et al. (2010b) for instance.

There was a lot of interest to study the dynamics of prey and predators, competitors in an heterogeneous environment with many patches connected by dispersal, see for example Amarasekare (1998) and Amarasekare and Nisbet (2001). In the most general case, the complexity of such spatial models is becoming very important and only very simplified versions can be studied, either with simple density independent dispersal rules and/or with same local interactions in any patch. Spatial aggregation methods provide an important step to solve this complexity. Indeed, when one can assume that dispersal is fast with respect to local interactions, spatial aggregation allows one to derive simplified models for which analytical results may be obtained. However, even those reduced models remain often so complex that they are difficult to analyze. As a consequence, either authors concentrated in systems with 2 or few patches (Elabdloui et al., 2007; Nguyen Ngoc et al., 2010) or studied multi-patch systems with similar local interactions (Nguyen Huu et al., 2008; Auger et al., 2010b) for which some results could be obtained. Spatial aggregation methods may also be helpful to study real cases, such as multi-site fisheries with density dependent fleet movements (Moussaoui et al., 2011) as well as sardine fishery in Morocco where two fish stocks can be considered in two regions, (Charouki et al., 2011).

To conclude this section, we point out that, according to the above described mechanism, the method presented here provides a tool to analyze models of spatial self-organization. Indeed, as illustrated in Fig. 3 obtained for example 1 presented in Section 2.3, sub-populations density oscillates periodically. Under the time scale assumption, this spatial pattern can be well understood by decomposing the time in periods during which the aggregated model alternates.

### 3. Aggregation for continuous space models: a semigroup approach

There are several ways to introduce space in mathematical models of population dynamics. A first approach has been described in the previous section: it consists of considering the environment as a set of discrete patches connected by migration, the evolution processes being described by a set of O.D.E. taking into account local interactions on each patch (birth, death, trophic interactions). This section deals with another way to introduce the spatial structure in mathematical modeling that consists of

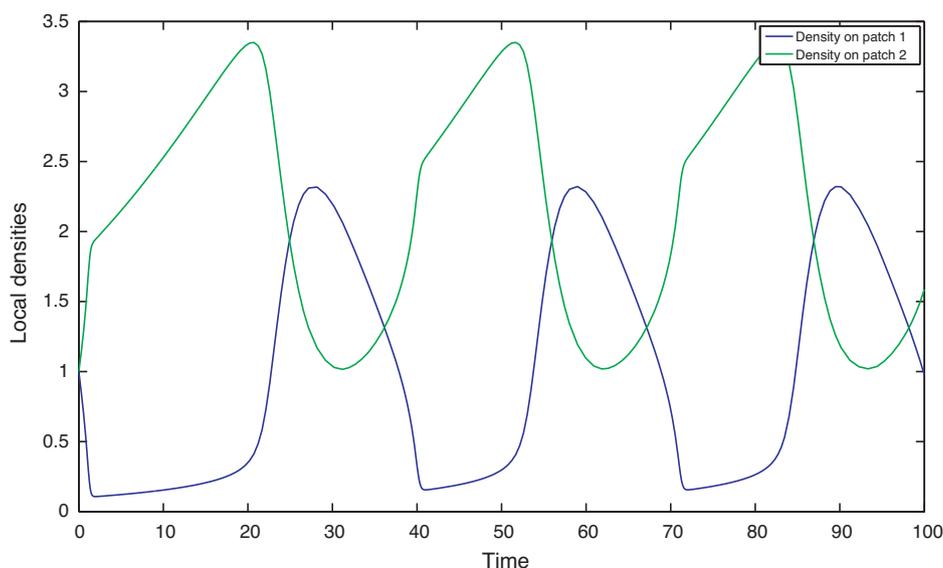


Fig. 3. Dynamics of the local densities simulated with the model (4). The parameters value used for this simulation are:  $\alpha = 10$ ;  $\beta = 10$ ;  $m_2 = 0.5$ ;  $d_1 = 2$ ;  $r_2 = 1$ ;  $\varepsilon = 0.04$ .

considering a continuous space, which usually leads to reaction-diffusion models, formulated as a set of partial differential equations (P.D.E.). Our aim is to extend aggregation methods to this setting. In particular, we will consider continuously spatially distributed populations in which the diffusion takes place at a faster time scale than local growth. Choosing the total population as a new variable, we can reduce the model to a set of O.D.E. governing the dynamics without losing the individual features. In fact, we will show that the  $C_0$ -semigroup theory provides a unified approach to the treatment of a wide class of slow-fast models, that includes both discrete and continuous spatial structures.

3.1. Aggregation of variables in an abstract two-time semilinear evolution differential equation.

To simplify the reading, we reduce the description to a scalar setting, but the reader can find a general formulation as well as a detailed description of technical details in Sánchez et al. (2011).

Let us consider the following Cauchy problem for an abstract semilinear parabolic differential equation defined on a Banach lattice  $(X, \| \cdot \|_X)$ :

$$(CP)_\varepsilon \begin{cases} n'_\varepsilon(t) = \frac{1}{\varepsilon} A n_\varepsilon(t) + \mathcal{F}(n_\varepsilon(t)), & t > 0 \\ n_\varepsilon(0) = n_0 \end{cases}$$

where  $\varepsilon > 0$  is a small parameter and we assume that operators  $A$  and  $\mathcal{F}$  satisfy the following hypotheses:

**Hypothesis 1.** The operator  $A : D(A) \subset X \rightarrow X$  is the infinitesimal generator of a  $C_0$ -semigroup  $\{T_0(t)\}_{t \geq 0}$  defined on  $X$ , which is eventually compact, positive and irreducible.

Moreover, the spectral bound of  $A$ ,  $s(A) := \sup \{ \operatorname{Re} \lambda, \lambda \in \sigma(A) \}$ , satisfies that  $s(A) = 0$ . As usual,  $\sigma(A)$  stands for the spectrum of operator  $A$ .

**Hypothesis 2.** The nonlinear operator  $\mathcal{F} : X \rightarrow X$  is locally Lipschitz continuous. That is, for each  $\gamma > 0$  there exists a constant  $L_\gamma > 0$  such that for each  $\varphi_i \in X$  with  $\|\varphi_i\|_X \leq \gamma$ ,  $i = 1, 2$ , the following holds:

$$\|\mathcal{F}(\varphi_1) - \mathcal{F}(\varphi_2)\|_X \leq L_\gamma \|\varphi_1 - \varphi_2\|_X.$$

With the help of the variation of constants formula, the differential problem  $(CP)_\varepsilon$  can be transformed into the integral equation

$$n_\varepsilon(t) = T_\varepsilon(t)n_0 + \int_0^t T_\varepsilon(t - \sigma) \mathcal{F}(n_\varepsilon(\sigma)) d\sigma, \quad t \geq 0 \tag{14}$$

where we have introduced the rescaled semigroup  $T_\varepsilon(t) := T_0((1/\varepsilon)t)$ , which takes into account the factor  $1/\varepsilon$  of the model.

As usual, the notation  $C([0, T]; X)$  ( $T > 0$ ) represents the Banach space of continuous functions  $n : [0, T] \rightarrow X$ , endowed with the norm  $\|n\|_C := \sup_{t \in [0, T]} \|n(t)\|_X$ . Then, a classical solution to  $(CP)_\varepsilon$  is a function  $n_\varepsilon \in C([0, T]; X)$  for some  $T > 0$  such that  $n_\varepsilon$  is continuously differentiable on  $(0, T)$ ,  $n_\varepsilon(t) \in D(A)$  for  $t > 0$ , and satisfies  $(CP)_\varepsilon$ . A function  $n_\varepsilon \in C([0, T]; X)$  which satisfies (14) for  $t \in [0, T]$  is called a mild solution to  $(CP)_\varepsilon$ .

The standard theory on abstract semilinear parabolic differential equations assures that, under Hypotheses 1 and 2, for each initial data  $n_0 \in X$  there exists a unique  $n_\varepsilon$  mild solution to  $(CP)_\varepsilon$  defined on a maximal interval  $[0, T_{\max})$ ,  $T_{\max} > 0$ . Moreover, if  $T_{\max} < +\infty$ , then  $\lim_{t \rightarrow T_{\max}^-} \|n_\varepsilon(t)\|_X = +\infty$ . If  $\mathcal{F}$  is continuously Fréchet-differentiable and the initial data  $n_0 \in D(A)$ , then  $n_\varepsilon$  is the classical solution to  $(CP)_\varepsilon$ .

Under Hypothesis 1, the Perron-Frobenius theory on positive  $C_0$ -semigroups can be applied, so that the following holds:

- (i) There exists  $\alpha^* > 0$  such that  $\sigma(A) = \{0\} \cup \Lambda$ , with  $\Lambda \subset \{z \in \mathbb{C} \mid \operatorname{Re} z < -\alpha^*\}$ .
- (ii)  $\dim \ker A = 1$  and there exist  $\mu \in \ker A$ ,  $\mu > 0$  and a strictly positive functional  $\mu^* \in \ker A^*$  such that  $\langle \mu^*, \mu \rangle = 1$ , where  $A^*$  is the adjoint operator of  $A$  and  $\langle \cdot, \cdot \rangle$  stands for the duality  $(X, X)$ .
- (iii) There exists a direct sum decomposition

$$X = \ker A \oplus S; \quad S := \operatorname{Im} A \tag{15}$$

which reduces  $A$  and the semigroup  $\{T_0(t)\}_{t \geq 0}$ . That is,  $\ker A$  and  $S$  are closed invariant subspaces under  $A$  and  $T_0(t)$ ,  $t \geq 0$ .

Moreover,  $\sigma(A_S) = \Lambda$  and  $\|T_S(t)\| \leq M_S e^{-\alpha^* t}$ ,  $t > 0$ , where  $A_S$  and  $T_S(t)$  represent respectively the restriction of  $A$  and  $T_0(t)$  to  $S$ .

- (iv) In the direct sum decomposition (15) we have

$$\operatorname{Im} A = \{\varphi \in X; \langle \mu^*, \varphi \rangle = 0\}$$

and the associated projection onto  $\ker A$  is given by:

$$\forall \psi \in X, \quad \Pi_A \psi := \langle \mu^*, \psi \rangle \mu.$$

The underlying idea in the construction of an aggregated model consists of projecting the dynamics of  $(CP)_\varepsilon$  onto  $\ker A$ . To this end, we choose the so-called global variable defined by:

$$N_\varepsilon(t) := \langle \mu^*, n_\varepsilon(t) \rangle \Rightarrow N'_\varepsilon(t) = \langle \mu^*, \mathcal{F}(n_\varepsilon(t)) \rangle$$

Notice that the right-hand side of this equation depends on  $n_\varepsilon(t)$ . To avoid this difficulty, we substitute it with its projection onto  $\ker A$ ,  $n_\varepsilon(t) \approx N(t)\mu$ , so that we approximate the initial perturbed model, which is a functional differential equation defined on a Banach lattice, by the aggregated model which is a nonlinear ordinary differential equation:

$$N'(t) = \langle \mu^*, \mathcal{F}(N(t)\mu) \rangle; \quad N(0) = \langle \mu^*, n_0 \rangle. \tag{16}$$

Once an aggregated model has been constructed, it is necessary to establish approximation results between the solutions to both problems, so that conclusions on the behavior of the perturbed model  $(CP)_\varepsilon$  can be deduced from an analysis of the reduced model.

To this end, let us introduce some notation. According to (15), each  $n_0 \in X$  can be written as:

$$n_0 = N_0 \mu + \rho_0; \quad N_0 := \langle \mu^*, n_0 \rangle \quad \langle \mu^*, \rho_0 \rangle = 0$$

and then, for each  $W(\mathcal{A})$  neighbourhood of the set  $\mathcal{A}$  in  $\mathbf{R}$  and for each  $\delta > 0$ , we can define a neighbourhood of  $\mathcal{A}\mu$  in  $X$  by:

$$\mathcal{N}(W(\mathcal{A}); \delta) := \{N\mu + \rho, N \in W(\mathcal{A}); \quad \rho \in S, \|\rho\|_X < \delta\}.$$

The main comparison result between the solutions to  $(CP)_\varepsilon$  and (16) is established in the following theorem, whose proof can be found in Sánchez et al. (2011):

**Theorem 1.** Under Hypotheses 1 and 2 and, assume that there exists a local compact attractor  $\mathcal{A}$  for the aggregated model (16). Then, fixing any neighbourhood  $W(\mathcal{A})$  and  $\delta > 0$ , there exist a neighbourhood  $W^*(\mathcal{A}) \subset W(\mathcal{A})$ ,  $\delta^* \in (0, \delta)$  and  $\varepsilon^* > 0$  such that for all  $\varepsilon \in (0, \varepsilon^*)$  and  $n_0 = N_0 \mu + \rho_0 \in \mathcal{N}(W^*(\mathcal{A}); \delta^*)$ , the solution to  $(CP)_\varepsilon n_\varepsilon(t) := N_\varepsilon(t)\mu + \rho_\varepsilon(t)$  such that  $n_\varepsilon(0) = n_0$  is defined for all  $t \geq 0$  and satisfies the following:

- (i)  $n_\varepsilon(t) \in \mathcal{N}(W^*(\mathcal{A}); \delta)$ .
  - (ii)  $\|\rho_\varepsilon(t)\|_X \leq C_1 e^{-\beta t/\varepsilon} \|\rho_0\|_E + C_2 \varepsilon$
- for some positive constants  $C_1, C_2 > 0$  (non dependent on  $W(\mathcal{A}), \delta$ ) and any  $\beta \in (0, \alpha^*)$ .

Roughly speaking, this theorem means that if the aggregated model has a local compact attractor  $\mathcal{A}$  (e.g. a locally asymptotically stable equilibrium or a stable limit cycle) then for  $\varepsilon > 0$  small enough, the solutions to  $(CP)_\varepsilon$  that start close to  $\mathcal{A}\mu$  remain close to  $\mathcal{A}\mu$  for all  $t \geq 0$ .

As a consequence, under additional smoothness conditions for the operator  $A$ , it can be shown that, for each  $\varepsilon > 0$  small enough, there exists a local compact attractor  $\mathcal{A}_\varepsilon$  of the perturbed problem which is close to  $\mathcal{A}\mu$ . This can be done by proving that there exists a set  $\mathcal{N}^*$  of initial conditions whose omega-limit set is a compact attractor for  $(CP)_\varepsilon$ .

Recall that a local compact attractor  $\mathcal{A}$  is an invariant compact set for which there exists a neighbourhood  $U$  such that the omega-limit set of  $U$  is  $\mathcal{A}$ .

Recall also (see Hale, 1988, Lemma 3.1.2) that if  $B \subset X$  is such that the set of positive orbits  $\gamma_+(B)$  is precompact, then the omega-limit set of  $B$ ,  $\omega(B)$ , is nonempty, compact, invariant and  $\omega(B)$  attracts  $B$ .

If  $n_0 \in X$  is an initial condition such that the corresponding solution to  $(CP)_\varepsilon$   $n_\varepsilon(t; n_0)$  exists for all  $t \geq 0$ , the positive orbit is defined as the set  $\gamma_+^{(\varepsilon)}(n_0) := \{n_\varepsilon(t; n_0); t \geq 0\}$  and also, for a set  $B \subset X$  of such initial conditions,  $\gamma_+^{(\varepsilon)}(B) := \cup_{n_0 \in B} \gamma_+^{(\varepsilon)}(n_0)$ .

A standard way to prove the precompactness of a subset  $M$  of a Banach space  $X$  consists of showing that  $M$  is a bounded subset of some Banach space  $F$  such that  $F \subset X$  and the embedding is compact. In our setting we will proceed by imposing supplementary smoothness conditions to the semigroup  $\{T_0(t)\}_{t \geq 0}$ , so that the general theory on sectorial operators could be applied. To be precise, we assume the following:

**Hypothesis 3.** The semigroup  $\{T_0(t)\}_{t \geq 0}$  is an analytic semigroup on  $X$ . Moreover, the infinitesimal generator  $A$  has compact resolvent.

Then, the direct sum decomposition (15) allows us to assure that for each  $\beta \geq 0$ , the fractional power operator  $(-A_S)^\beta$  can be defined on a domain  $X_S^\beta \subset X$  which is a Banach space with respect to the norm  $\|\varphi_S\|_\beta := \|(-A_S)^\beta \varphi\|_X$ . Moreover, for  $\beta \in (0, 1)$ , the embedding  $X_S^\beta \subset S$  is compact and therefore it can be shown that for  $\varepsilon \in (0, \varepsilon^*)$ ,  $\gamma_+^{(\varepsilon)}(\mathcal{N}^*)$  is a precompact set, where

$$\mathcal{N}^* := \{n_0 = N_0\mu + \rho_0; N_0 \in W^*(A), \rho_0 \in X_S^\beta, \|\rho_0\|_\beta < \delta^*\} \subset \mathcal{N}(W^*(A); \delta^*).$$

The above considerations provide an outline of the proof of the following result, which improves the comparison result established in Theorem 1.

**Theorem 2.** Under Hypotheses 1–3, assume that there exists a compact attractor  $\mathcal{A}$  for the aggregated model (16). Then, there exists  $\varepsilon_0^* > 0$  such that  $\forall \varepsilon \in (0, \varepsilon_0^*)$ , there exists a compact attractor  $\mathcal{A}_\varepsilon$  for the perturbed model  $(CP)_\varepsilon$ . Moreover we have  $\mathcal{A}_\varepsilon \subset \mathcal{N}(W(A); \delta)$  for each neighbourhood of  $\mathcal{A}\mu$  in  $X$  and  $\varepsilon > 0$  small enough. Also  $\text{diam}(S \cap \mathcal{A}_\varepsilon) \rightarrow 0(\varepsilon \rightarrow 0^+)$ .

In the particular case in which  $\ker A$  is invariant under operator  $\mathcal{F}$ , we have the following:

**Corollary 1.** Under the hypotheses of Theorem 2, let us assume that  $\mathcal{F}(\ker A) \subset \ker A$ . Then, for all  $\varepsilon \in (0, \varepsilon_0^*)$ ,  $\mathcal{A}\mu$  is a compact attractor for the perturbed model  $(CP)_\varepsilon$ .

Another kind of approximation results consists of comparing directly the solutions to  $(CP)_\varepsilon$  and (16). This can be done by establishing previously some global existence and boundedness results for the solutions to both models, like the following:

- There exist a subset  $\mathcal{D} \subset X$  and  $\varepsilon_0 > 0$  such that for each initial data  $n_0 \in \mathcal{D}$  and for all  $\varepsilon \in (0, \varepsilon_0)$ , the following holds:

- (i) The corresponding solution to  $(CP)_\varepsilon$   $n_\varepsilon(t) := N_\varepsilon(t)\mu + \rho_\varepsilon(t)$ , is defined on  $[0, +\infty)$ .
- (ii) There exists a constant  $K(n_0) > 0$  such that  $\sup_{t \geq 0} \|n_\varepsilon(t)\|_X \leq K(n_0), \forall \varepsilon \in (0, \varepsilon_0)$ .
- The solutions to the aggregated model (16) satisfy the following:
  - (i) For each initial data  $N_0$  such that  $n_0 = N_0\mu + \rho_0 \in \mathcal{D}$ , the corresponding solution  $N(t)$  is defined on  $[0, +\infty)$ .
  - (ii) There exists a constant  $K(N_0) > 0$  such that  $\sup_{t \geq 0} \|N(t)\| \leq K(N_0)$ .

Then,  $y_\varepsilon(t) := N_\varepsilon(t) - N(t)$  satisfies for  $t \geq 0$ :

$$y'_\varepsilon(t) = \langle \mu^*, \mathcal{F}(N_\varepsilon(t)\mu + \rho_\varepsilon(t)) - \mathcal{F}(N(t)\mu) \rangle, \quad y_\varepsilon(0) = 0$$

from which, bearing in mind the global boundedness of solutions and the local Lipschitz continuity of operator  $\mathcal{F}$ , we deduce:

$$|y_\varepsilon(t)| \leq C_1 \int_0^t |y_\varepsilon(\sigma)| d\sigma + C_2 \varepsilon \|\rho_0\|_X (1+t)$$

and applying the Gronwall inequality:

$$|y_\varepsilon(t)| \leq C_1 \varepsilon \|\rho_0\|_X (1+t) e^{C_2 t} \leq C_1 \varepsilon \|\rho_0\|_X e^{a^* t}, \quad a^* > 0.$$

Summing up, we have the following approximation result for the solutions to the perturbed and the aggregated models:

**Proposition 1.** For each initial data  $n_0 := N_0\mu + \rho_0 \in \mathcal{D}$  and  $\varepsilon \in (0, \varepsilon_0)$ , the corresponding solution to  $(CP)_\varepsilon$  can be written as:

$$n_\varepsilon(t) = N(t)\mu + \mathcal{Q}_\varepsilon(t), \quad t \geq 0$$

where  $N(t)$  is the solution to the aggregated model (16) corresponding to the initial data  $N(0) = N_0$ .

Moreover, there exist three constants  $M_1 > 0, M_2 > 0, a^* > 0$  such that, for all  $\varepsilon \in (0, \varepsilon_0)$ :

$$\forall t \geq 0, \quad \|\mathcal{Q}_\varepsilon(t)\|_X \leq [M_1 \varepsilon e^{a^* t} + M_2 e^{-\alpha^* t/\varepsilon}] \|\rho_0\|_X.$$

We point out that the above formula shows that  $\lim_{\varepsilon \rightarrow 0^+} \|n_\varepsilon(t) - N(t)\mu\|_X = 0$  for each  $t > 0$ . This convergence is not uniform on  $[0, +\infty)$ , but it is on each compact interval  $[t_0, T]$  with  $0 < t_0 < T < +\infty$ .

The same underlying ideas for the reduction of two-time abstract semilinear evolution equations defined on Banach spaces have been developed in Ei and Mimura (1984), where an aggregated model is constructed and analyzed without using the general tools provided by the Perron-Frobenius theory of positive  $C_0$ -semigroups. Assuming that the aggregated model has a hyperbolic locally asymptotically stable equilibrium, similar results to ours in Theorems 1, 2 and Corollary 1 are established.

### 3.2. Two time scales in reaction-diffusion models of population dynamics

We are illustrating the general aggregation of variables method described in the previous section by applying it to a reaction-diffusion system which represents the dynamics of several continuously spatially distributed populations whose evolution processes occur at two different time scales: a slow one for the demography and a fast one for migrations. A general introduction to reaction-diffusion models in population dynamics

can be found in Murray (2002, 2003) and in Cantrell and Cosner (2003).

Let us consider  $q$  ( $q \geq 1$ ) populations living in a spatial region  $\Omega \subset \mathbf{R}^p$ , ( $p \geq 1$ ), where  $\Omega$  is a non-empty bounded, open and connected set with smooth boundary  $\partial\Omega \in C^k$ ,  $k \geq 1$ . Let  $n_i(x, t)$   $i = 1, \dots, q$  be their spatially structured population densities i.e.,  $\int_{\Omega_0} n_i(x, t) dx$  represents the number of individuals of population  $i$  that at time  $t$  are occupying the region  $\Omega_0 \subset \Omega$  and set  $n(x, t) := (n_1(x, t), \dots, n_q(x, t))^T$ .

We assume that the demography is given by a nonlinear reaction term  $f(x, n)$  that satisfies the following regularity conditions:

**Hypothesis 4.** The function  $f: \overline{\Omega} \times \mathbf{R}^q \rightarrow \mathbf{R}^q$ ,  $f := (f_1, \dots, f_q)$ , is continuous and there exists a real-valued continuous positive function  $h$  defined on  $\overline{\Omega} \times \mathbf{R}^q \times \mathbf{R}^q$  such that  $\forall x \in \overline{\Omega}$  and  $\forall u, v \in \mathbf{R}^q$ :

$$|f(x, u) - f(x, v)| \leq h(x, u, v)|u - v|.$$

We also assume a linear diffusion process in  $\Omega$  for each population, with coefficient  $D_i \in C^2(\overline{\Omega})$ ,  $D_i(x) \geq d_i^* > 0$ ,  $i = 1, \dots, q$ , that occurs at a fast time scale determined by a parameter  $\varepsilon > 0$  small enough. A standard application of the balance law leads to the following two-time reaction-diffusion system for the population densities, where the Neumann boundary conditions indicate that the spatial domain is isolated from the external environment, and  $i = 1, \dots, q$ :

$$\begin{cases} \frac{\partial n_i}{\partial t}(x, t) = \frac{1}{\varepsilon} \operatorname{div}(D_i(x) \operatorname{grad} n_i(x, t)) + f_i(x, n(x, t)), & x \in \Omega, t > 0 \\ \frac{\partial n_i}{\partial \nu}(x, t) = 0, & x \in \partial\Omega, t > 0 \\ n(x, 0) = n_0(x), & x \in \Omega, n_0(x) := (n_1^0(x), \dots, n_q^0(x))^T. \end{cases} \quad (17)$$

Rescaling the time as  $t = \varepsilon\tau$  in Eq. (17) and making  $\varepsilon \rightarrow 0_+$ , we obtain the dynamics at a fast time scale:

$$\frac{\partial n_i}{\partial \tau}(x, \tau) = \operatorname{div}(D_i(x) \operatorname{grad} n_i(x, \tau)), \quad i = 1, \dots, q$$

At this fast time scale the total population  $N_i(\tau) := \int_{\Omega} n_i(x, \tau) dx$  satisfies that

$$N_i'(\tau) = \int_{\Omega} \operatorname{div}(D_i(x) \operatorname{grad} n_i(x, \tau)) dx = \int_{\partial\Omega} D_i(x) \frac{\partial n_i}{\partial \nu}(x, \tau) d\sigma = 0$$

which reflects the obvious result that the total population is conserved under the migration process, without taking into account the demographic evolution. This simple idea suggests constructing a reduced model to approximate the model (17), taking as *global variables* the total populations:

$$N_i(t) := \int_{\Omega} n_i(x, t) dx; \quad N(t) := (N_1(t), \dots, N_q(t))^T.$$

Integrating with respect to the space variable  $x$  on both sides of Eq. (17), applying the Gauss Theorem and bearing in mind the Neumann boundary conditions, we have:

$$N_i'(t) = \int_{\Omega} f_i(x, n(x, t)) dx, \quad i = 1, \dots, q. \quad (18)$$

Notice that the right-hand side of Eq. (18) is expressed in terms of the density  $n(x, t)$ . To avoid this difficulty, we will look for an

approximation of  $n(x, t)$  in terms of the total populations. To this end, we assume that the fast dynamics reach an equilibrium. Recall that the only equilibria of the fast dynamics are the constants and since the total population is conserved under the fast dynamics, the initial conditions in (17) fix the values of the stationary states for the fast dynamics:

$$\int_{\Omega} n_i^0(x) dx = n_i^* \operatorname{vol}(\Omega) \Rightarrow n_i^* = \frac{1}{\operatorname{vol}(\Omega)} \int_{\Omega} n_i^0(x) dx, \quad i = 1, \dots, q$$

where  $\operatorname{vol}(\Omega)$  is the Lebesgue measure of the domain  $\Omega$ . That is, in absence of demography, the stationary state of the population is a homogeneous distribution on the spatial region.

Then, coming back to the construction of an approximated model for the dynamics of the total population, the above considerations suggest the following approximation:

$$n_i(x, t) \approx \frac{N_i(t)}{\operatorname{vol}(\Omega)}, \quad i = 1, \dots, q$$

which yields the *aggregated model* of (17):

$$N'(t) = F(N(t)), \quad N(0) = N_0 := \int_{\Omega} n_0(x) dx \quad (19)$$

where  $F: \mathbf{R}^q \rightarrow \mathbf{R}^q$   $F := (F_1, \dots, F_q)$  is the function defined by:

$$\forall u \in \mathbf{R}^q, \quad F(u) := \int_{\Omega} f\left(x, \frac{u}{\operatorname{vol}(\Omega)}\right) dx.$$

The comparison between the solutions to both models can be made by applying the general theory described in the previous section. To this end we choose as state space  $X := [C(\overline{\Omega})]^q$ , where  $C(\overline{\Omega})$  is the Banach space of continuous real-valued functions defined on  $\overline{\Omega}$ , endowed with the sup norm. Making the usual identification  $n_{\varepsilon}(t)(\cdot) := n_{\varepsilon}(\cdot, t)$ , we can formulate (17) as an abstract evolution equation on  $X$ , the main point consisting of proving that the linear diffusion operator together with Neumann boundary conditions is the infinitesimal generator of a  $C_0$ -semigroup on  $X$  which satisfies Hypotheses 1 and 3. It is so when the diffusion is defined by a strongly elliptic operator, and the technical details can be found in Sánchez et al. (2011).

Therefore Theorem 2 applies, allowing us to conclude that if the aggregated model (19) has a compact attractor  $\mathcal{A} \subset \mathbf{R}^q$ , then the model (17) has, for  $\varepsilon > 0$  small enough a compact attractor  $\mathcal{A}_{\varepsilon}$  close to  $\mathcal{A}$ .

The particular case where the reaction term does not depend on the space variable corresponds with the situation  $\mathcal{F}(\ker A) \subset \ker A$  and recovers the formulation given in Conway et al. (1978) and Hale (1986) for reaction-diffusion equations with large diffusivity. These authors show that the solutions to a semilinear parabolic system including a big enough diffusion term can be approximated by the solutions to an O.D.E. determined by the reaction term, which coincides with our aggregated model. A more general situation can be found in Hale and Sakamoto (1989), where the dynamics of a class of reaction-diffusion models with large diffusivity is described by a so-called *shadow system*, whose underlying ideas are close to the construction of an aggregated model.

As a simple illustration, we apply the above ideas to a spatial interspecific competition model with fast constant diffusion and population growth given by a logistic law. To be precise, we are considering the model, for  $x \in \Omega$ ,  $t > 0$ :

$$\begin{cases} \frac{\partial n_1}{\partial t}(x, t) = \frac{D_1}{\varepsilon} \Delta n_1(x, t) + r_1(x)n_1(x, t) \left(1 - \frac{n_1(x, t)}{K_1(x)} - \frac{a_1(x)}{K_1(x)} n_2(x, t)\right) \\ \frac{\partial n_2}{\partial t}(x, t) = \frac{D_2}{\varepsilon} \Delta n_2(x, t) + r_2(x)n_2(x, t) \left(1 - \frac{n_2(x, t)}{K_2(x)} - \frac{a_2(x)}{K_2(x)} n_1(x, t)\right) \\ \frac{\partial n_i}{\partial \nu}(x, t) = 0, \quad x \in \partial\Omega, \quad t > 0, \quad i = 1, 2 \\ n_i(x, 0) = n_i^0(x), \quad x \in \Omega, \quad i = 1, 2 \end{cases} \quad (20)$$

where  $n_i(x, t)$   $i = 1, 2$  are the population densities of the two competing species and  $D_i > 0$   $i = 1, 2$  are the respective constant diffusion coefficients.

The global variables are the total populations of both competing species:

$$N_i(t) := \int_{\Omega} n_i(x, t) dx; \quad i = 1, 2$$

Integrating on  $\Omega$  on both sides of system (20) and making the approximation:

$$n_i(x, t) \approx \frac{N_i(t)}{\text{vol}(\Omega)}; \quad i = 1, 2$$

we arrive to the aggregated model:

$$\begin{cases} N'_1(t) = r_1^* N_1(t) \left(1 - \frac{N_1(t)}{K_1^*} - a_1^* N_2(t)\right) \\ N'_2(t) = r_2^* N_2(t) \left(1 - \frac{N_2(t)}{K_2^*} - a_2^* N_1(t)\right) \end{cases}$$

where, for  $i = 1, 2$ :

$$r_i^* := \frac{1}{\text{vol}(\Omega)} \int_{\Omega} r_i(x) dx; \quad K_i^* := \frac{\text{vol}(\Omega) \int_{\Omega} r_i(x) dx}{\int_{\Omega} (r_i(x)/K_i(x)) dx}$$

$$a_i^* := \frac{1}{\text{vol}(\Omega)} \frac{\int_{\Omega} (a_i(x)r_i(x)/K_i(x)) dx}{\int_{\Omega} r_i(x) dx}.$$

This aggregated model is a classical competition model with logistic growth for both species, in which the spatial structure has been taken into account in the parameters.

Regarding the asymptotic behavior of this model, we know that if  $a_2^* K_1^* < 1$  and  $a_1^* K_2^* < 1$ , the two species coexist at some positive equilibrium which is globally asymptotically stable. According to Theorem 2, coexistence of both species in model (20) also holds for  $\varepsilon > 0$  small enough. For the rest of the values of the parameters  $a_i^* K_j^* > 1$  and  $a_j^* K_i^* > 1$ ,  $i, j = 1, 2, i \neq j$ , one of the two species in the aggregated model goes to extinction while the other goes to its carrying capacity. In these cases, Theorem 2 assures that the solutions to model (20) are asymptotically close to the solutions to the aggregated model, so that for  $\varepsilon > 0$  small enough, one of the two species is close to extinction while the other survives. See Ei and Mimura (1984) for a detailed analysis of conditions for extinction in the perturbed model.

Similar approximation results for two-time reaction-diffusion models have been established by applying the so-called two-timing method, as introduced by Shigesada (1984) in spatially structured population dynamics models. See Ei (1988) for an interesting development of these methods applied to slow-fast population dynamics in heterogeneous environments. For related work see also Ei (1987), Fang (1990) and Ni et al. (2001).

The general aggregation method described in this section has been illustrated by an application to reaction-diffusion models

with large diffusivity, which leads to reduced models corresponding to populations spatially homogeneously distributed. Nevertheless, the abstract formulation can also be applied to spatially heterogeneous distributions of species. This setting introduces additional mathematical difficulties, since the existence of spatial patterns i.e., spatially heterogeneous stable steady-states must be analyzed, and constitutes for us a perspective of future work. An interesting overview can be found in Cantrell and Cosner (2003). A seminal paper on spatial pattern formation for reaction-diffusion two species competition models is Matano and Mimura (1983), and further analysis can be found in Mimura et al. (1991) and Ikeda and Mimura (1993).

### 3.3. An approximation result for nonnegative solutions to two-time reaction-diffusion models

In this section we proceed to apply the approximation result established in Proposition 1, that is, we will compare the solutions to (17) with the solutions to the aggregated model (19) when  $\varepsilon \rightarrow 0_+$ , without assuming the existence of equilibria for the aggregated model. The analysis is restricted to the comparison of positive solutions, but the global existence of these solutions as well as the existence of suitable bounds needs some additional smoothness assumption on the reaction term. To simplify, we consider a scalar setting; then, a sufficient standard condition to eliminate blow-up of nonnegative solutions can be:

**Hypothesis 5.** The function  $f : \bar{\Omega} \times \mathbf{R} \rightarrow \mathbf{R}$  satisfies the following:

- (i)  $f(x, 0) = 0, \forall x \in \bar{\Omega}$ .
- (ii) There exists a constant  $C > 0$  such that  $\forall x \in \bar{\Omega}$  and  $\forall u \in \mathbf{R}$  with  $|u| \geq C$ , we have  $f(x, u) \leq 0$ .

Existence and boundedness of global positive solutions to both problems can be proved (see Sánchez et al. (2011) for the technical details), so that the following approximation result is a direct consequence of Proposition 1:

**Proposition 2.** For each nonnegative initial data  $n_0 \in C(\bar{\Omega})$ , the two time scales reaction-diffusion model (17) has a unique classical nonnegative global solution  $n_\varepsilon(x, t)$  which can be written as:

$$\forall x \in \Omega, \forall t > 0, \quad n_\varepsilon(x, t) = \frac{1}{\text{vol}(\Omega)} N(t) + r_\varepsilon(x, t)$$

where  $N(t)$  is the solution to the aggregated model (19) corresponding to the initial data  $N(0) = \int_{\Omega} n_0(x) dx$  and

$$\sup_{x \in \Omega} |r_\varepsilon(x, t)| \leq a_1^* \varepsilon e^{a_2^* t} + a_3^* e^{-(\alpha^*/\varepsilon)t}, \quad t > 0, \quad \varepsilon > 0$$

where  $a_i^*, i = 1, 2, 3$  are positive constants depending on the initial value  $n_0$ .

Notice that this approximation result means that  $n_\varepsilon(x, t)$  tends when  $\varepsilon \rightarrow 0_+$  and  $t > 0$  fixed, to an homogeneous spatial distribution given by the solution to the aggregated model. Moreover, this convergence is uniform with respect to  $x$  in  $\bar{\Omega}$  and with respect to  $t$  on each compact interval  $[t_0, T]$  with  $0 < t_0 < T < +\infty$ .

### 3.4. Slow-fast population models with discrete spatial structure.

The aim of this section is to illustrate the fact that the abstract setting also includes simpler situations in which the state space is

finite-dimensional. In this case, the operator  $A$  is a matrix whose spectrum  $\sigma(A)$  must satisfy some conditions that assure the essential point in our development, namely decomposition (15) of the state space in invariant *conservative* and *stable* parts. Despite the fact that this situation can be studied directly using tools from classical analysis, it is interesting from the point of view of modelling in population dynamics, as it is a suitable formulation to represent discrete spatial structure.

To be precise, let us consider  $q$  populations ( $q \geq 1$ ) living in a region divided into discrete spatial patches. The evolution processes are described by an ordinary differential system taking into account nonlinear local interactions on each patch that occur at a slow time scale and linear migration terms describing patch changes that are assumed to occur at a fast time scale. The model we are considering reads as:

$$X'_\varepsilon(t) = \frac{1}{\varepsilon}AX_\varepsilon(t) + f(X_\varepsilon(t)) \quad X_\varepsilon(t) := (\mathbf{x}_{j\varepsilon}(t))_{j=1,\dots,q}^T;$$

$$\mathbf{x}_{j\varepsilon}(t) := (x_{j\varepsilon}^i(t))_{i=1,\dots,N_j}^T$$

where  $x_{j\varepsilon}^i(t)$  is the number of individuals of population  $j$  living in the spatial patch  $i$  at time  $t$ , with  $j = 1, \dots, q$ , and  $N = N_1 + \dots + N_q$  is the total number of spatial patches.

We also assume that  $f: \mathbf{R}^N \rightarrow \mathbf{R}^N$  is a locally Lipschitz continuous function and that matrix  $A$  is a block-diagonal matrix  $A := \text{diag}(A_1, \dots, A_q)$  in which each diagonal block  $A_j$  has dimensions  $N_j \times N_j$ , and satisfies the following hypothesis:

**Hypothesis 6.** For each  $j = 1, \dots, q$ ,  $\sigma(A_j) = \{0\} \cup A_j$  with  $A_j \subset \{z \in \mathbf{C} \mid \text{Re } z < 0\}$ . Furthermore  $0$  is a simple eigenvalue of matrix  $A_j$ .

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

**Remark 1.** Hypothesis 6 holds for a matrix  $A$  if each diagonal block  $A_j$  is an irreducible matrix with non-negative elements outside the diagonal and in addition satisfies that  $\mathbf{v}_j^* := \mathbf{1}_j^T := (1, \dots, 1)^T \in \mathbf{R}^{N_j}$ . In this case,  $A$  is a suitable matrix to represent conservative migrations between patches.

In order to simplify the calculations, we introduce the following matrices

$$\mathcal{U} := \text{diag}((\mathbf{v}_1^*)^T \dots (\mathbf{v}_q^*)^T); \quad \mathcal{V} := \text{diag}(\mathbf{v}_1 \dots \mathbf{v}_q)$$

which satisfy  $\mathcal{U}A = 0$ ,  $A\mathcal{V} = 0$  and  $\mathcal{U}\mathcal{V} = I_q$ ,  $I_q$  being the  $q \times q$  identity matrix.

The above considerations assure the existence of the decomposition (15) of the space  $X := \mathbf{R}^N$  where  $\ker A$  is a  $q$ -dimensional subspace generated by the columns of the matrix  $\mathcal{V}$  and  $S := \{v \in \mathbf{R}^N \mid \mathcal{U}v = \mathbf{0}\}$ .

The *global variables* are defined by:

$$\mathbf{s}(t) := (s_1(t), \dots, s_q(t))^T = \mathcal{U}X(t); \quad s_j(t) := (\mathbf{v}_j^*)^T \mathbf{x}_j(t).$$

Notice that in the case  $\mathbf{v}_j^* = \mathbf{1}_j$ , this set of variables represents the total number of individuals of each population. Finally, the aggregated model is given by:

$$\mathbf{s}'(t) = \mathcal{U}f(\mathcal{V}\mathbf{s}(t)). \tag{21}$$

In this finite-dimensional setting it is straightforward to check the assumptions needed to apply Theorem 2 and therefore the

approximation result between the asymptotic behavior of solutions to both models holds. Also, a direct comparison result when  $\varepsilon \rightarrow 0_+$  between the solutions similar to Proposition 2 can be established without major difficulties. The main point in this case is to assume supplementary smoothness conditions on function  $f$  so that global existence and boundedness of solutions to the perturbed and aggregated models can be assured.

Finally, let us illustrate the method with the following example, which is a discrete-space version of the classical predator–prey model. The model consists of two populations of predators and preys living in a spatial region divided into two patches, connected by fast migrations:

$$\begin{cases} n'_1(t) = \frac{1}{\varepsilon}(k_{12}n_2(t) - k_{21}n_1(t)) + r_1n_1(t)\left(1 - \frac{n_1(t)}{K_1}\right) - a_1n_1(t)p_1(t) \\ n'_2(t) = \frac{1}{\varepsilon}(k_{21}n_1(t) - k_{12}n_2(t)) + r_2n_2(t)\left(1 - \frac{n_2(t)}{K_2}\right) - a_2n_2(t)p_2(t) \\ p'_1(t) = \frac{1}{\varepsilon}(m_{12}p_2(t) - m_{21}p_1(t)) - \mu_1p_1(t) + b_1n_1(t)p_1(t) \\ p'_2(t) = \frac{1}{\varepsilon}(m_{21}p_1(t) - m_{12}p_2(t)) - \mu_2p_2(t) + b_2n_2(t)p_2(t) \end{cases}$$

where  $n_i(t)$ ,  $p_i(t)$ , represent the populations of preys and predators respectively at time  $t$  in patch  $i$  ( $i = 1, 2$ ), the positive constants  $k_{12}$ ,  $k_{21}$  are the prey migration rates and the positive constants  $m_{12}$ ,  $m_{21}$  are the predator dispersal rates.

Simple calculations show that the global variables are the total populations of preys and predators:

$$N(t) := n_1(t) + n_2(t); \quad P(t) := p_1(t) + p_2(t)$$

and the aggregated model (21) is the classical predator–prey model:

$$\begin{cases} N'(t) = r^*N(t)\left(1 - \frac{N(t)}{K^*}\right) - a^*N(t)P(t) \\ P'(t) = b^*N(t)P(t) - \mu^*P(t) \end{cases}$$

in which:

$$r^* := \frac{r_1k_{12} + r_2k_{21}}{k_{12} + k_{21}}; \quad K^* := \frac{r^*}{(r_1/K_1)\tilde{k}_1^2 + (r_2/K_2)\tilde{k}_2^2}$$

$$a^* := a_1\tilde{k}_1\tilde{m}_1 + a_2\tilde{k}_2\tilde{m}_2; \quad b^* := b_1\tilde{k}_1\tilde{m}_1 + b_2\tilde{k}_2\tilde{m}_2;$$

$$\mu^* := \mu_1\tilde{m}_1 + \mu_2\tilde{m}_2$$

where

$$\tilde{k}_1 := \frac{k_{12}}{k_{12} + k_{21}}; \quad \tilde{k}_2 := \frac{k_{21}}{k_{12} + k_{21}}; \quad \tilde{m}_1 := \frac{m_{12}}{m_{12} + m_{21}};$$

$$\tilde{m}_2 := \frac{m_{21}}{m_{12} + m_{21}}.$$

#### 4. Discussion and conclusions

In this work we have shown that spatial aggregation methods can be useful to derive from an initial spatial complete model involving many variables associated with many patches a reduced model governing few variables at a slow time scale. We extended as well the method to continuous space, allowing us to obtain an aggregated O.D.E. model from the complete P.D.E. model. The method is

particularly useful when one cannot get analytical results from the complete model while the analysis can be done for the aggregated model which in turn can be used to understand the dynamics of the complete model. The method presented in previous sections can be applied to several examples in population dynamics and some concrete examples are presented in other articles of this issue.

Aggregation methods may also be applied to reduce complex models in which complexity is not the result of a spatial extension but for instance, results from individuals properties (behavior, physiology, etc.) in problems where these properties are of importance for populations or communities dynamics. Ecology has nowadays to face new challenges since important perturbations (climate change, human activities like harvesting, etc.) modify ecosystem functioning and the services associated. To address these problems, approaches integrating different organization levels and various spatial and time scales are needed. It is non sense to expect to get a general approach or a theory which unifies the various concepts from those associated to individuals properties (metabolism modifications in varying environment, individuals responses to these modifications, changes of behavior, etc.) to those concerning ecosystem functioning (matter fluxes like CO<sub>2</sub> production/consumption, etc.). However, it is important to propose methods which allows to get some bridges between these organization levels and the associated concepts. Aggregation methods, with indeed some assumptions like characteristic time scales, are developed in this perspective.

To conclude with perspectives in a spatial context, we think that it would be interesting to consider chemotactic terms as well as convective terms in continuous spatially structured models. Indeed, this would allow us to obtain at the fast equilibrium spatial distributions which are not spatially homogeneous, but depending on the spatial variables. In that case, the aggregated model would pilot at the slow time scale a succession of spatial patterns associated with different fast equilibria, modeling thus pattern formation and morphogenesis processes. Our approach would also include particular cases like situations where one population (predator) moves faster than another one (its prey), which is known to produce spatial structures (see for instance de Roos et al., 1998 and references therein).

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