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Aggregation and Emergence in Systems of Ordinary Differential Equations

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Abstract—The aim of this article is to present aggregation methods for a system of ordinary differential equations (ODE's) involving two time scales. The system of ODE's is composed of the sum of fast parts and a perturbation. The fast dynamics are assumed to be conservative. The corresponding first integrals define a few global variables. Aggregation corresponds to the reduction of the dimension of the dynamical system which is replaced by an aggregated system governing the global variables at the slow time scale. The centre manifold theorem is used in order to get the slow reduced model as a Taylor expansion of a small parameter. We particularly look for the conditions necessary to get emerging properties in the aggregated model with respect to the nonaggregated one. We define two different types of emergences, functional and dynamical. Functional emergence corresponds to different functions for the two dynamics, aggregated and nonaggregated. Dynamical emergence means that both dynamics are qualitatively different. We also present averaging methods for aggregation when the fast system converges towards a stable limit cycle.

Keywords—Time scales, Perturbation technics, Center manifold, Emerging dynamics, Averaging methods, Aggregation of variables.

1. INTRODUCTION

One of the major problems of modelling biological systems is that many variables seem to be involved in the evolution of the system and cannot be cancelled without an important loss of information. Many variables and parameters seem necessary to describe its dynamics. Thus, the complexity of the model partly lies in the very large number of degrees of freedom which seems necessary to consider in order to describe the system. It is difficult to know the level of details which is really relevant. To avoid missing some important details, one can build a model with a very detailed description including a large set of variables and parameters. However, such a model cannot be used easily, and in most cases only computer simulations can be performed. In some cases, one must try to simplify it. Thus, it is necessary to make a selection among the variables, but one needs a rigorous method for detecting which variables are really relevant for the description of the system and which ones can be forgotten. One wishes to delete some variables, keeping only a few which are absolutely necessary to describe the dynamics.

This problem concerns the reduction of the size of a system. This should be done rigorously and not simply by use of qualitative criteria. It seems to us that in many cases the deletion of variables is made on the basis of certain *a priori* ideas and under a certain argumentation which is not always clearly expressed and which in any case might be checked by appropriate rigorous methods. Aggregation means that from a micro-system, that is, the mathematical model for a large scale system involving a very large number of micro-variables, one can extract a macro-

model or aggregated model for a few global variables. The process consists of condensation or reduction of a big micro-system into a smaller macro-system which we hope to be much simpler to study.

Perfect aggregation corresponds to the exact replacement of the micro-system by a macro-system for an appropriate choice of global aggregated variables. Perfect aggregation means that the macro-system is not obtained by an approximation of the micro-system, but that the aggregation is perfectly done. It implies the possibility to exactly condense the initial system into an aggregated version. In such a case, the aggregation is in a certain sense trivial because the macro-system is a pure copy of the micro-system. It is simply another way to rewrite the micro-system in a new form and in a new combination. As we shall see in Section 1, the required conditions are very strong and are often biologically irrelevant.

Approximate aggregation seems more interesting. It corresponds to the replacement of the micro-system by a macro-system which is obtained by an approximation. It implies that some simplifications can be justified and some approximations can be realized. This is the case when some variables are fast with respect to others. Fast variables can rapidly reach an attractor and the approximation consists of replacing the fast variables with equilibrium values. For example, if the fast variables tend to an asymptotically stable fast equilibrium, then we can replace them with the equilibrium values. In another case, the fast variables can be periodic functions of time and one can replace them with their time averages. These methods mainly look for relaxation or averaging of fast variables. One also can neglect the variations of very slow variables which do not have time to change during the observation time of the system. This leads to an aggregated model of the complete system which is an approximation of the big system and which holds for a given space-time window in relation to the observation of the system. This approximated version is not a simple copy of the micro-system, it is another system different from it, but having certain similarities to it at some level of observation.

Mathematical theory of perturbations provides a series of results and theorems which are useful to perform approximate aggregation [1–6]. Sections 2–5 present mathematical models in a form which are suitable for applying perturbation methods for approximate aggregation. The main point is to consider models with different time scales for the processes going on at the different levels of observation of the system. As a consequence, the models that we propose are composed of two parts, a fast part describing processes going on at a fast time scale and a slow part describing processes at a slow time scale.

In order to aggregate the initial micro-model, we present a method based on a Center Manifold Theorem. The originality of our methods lies in the fact that the chosen global variables are first integrals of the fast systems which are assumed to be conservative. The method consists of replacing the fast variables with fast equilibrium values which are functions of the global variables. If the obtained aggregated system is structurally stable, then it is a good approximation of the micro-system. Otherwise, one must carry out a second step. The second step consists of calculating high order terms with respect to powers of ε. As it will be shown, the first step is generally simple and sufficient while the second step is more complicated. Note that the general method in the case of an equilibrium of the fast part can be found in [7]. We also refer to our works with applications in population dynamics [8–19] and extension to time discrete models [20].

2. THE GENERAL PROBLEM OF AGGREGATION IN A SYSTEM OF ODE'S

2.1. Perfect Aggregation

First, let us consider the micro-system, that is, a large scale dynamical system that we would like to aggregate. This micro-system is a set of nonlinear coupled ODE's involving a large

number N of micro-variables n_i:

$$\frac{dn_i}{dt} = f_i(n_1, n_2, \ldots, n_N), \tag{1}$$

f_i are nonlinear functions of the micro-variables. Perfect aggregation means that one can find a set of macro-variables Y_j which are defined from the previous set of micro-variables:

$$Y_j = g_j(n_1, n_2, \ldots, n_N), \tag{2}$$

g_j are functions of the micro-variables. Furthermore, to perform perfect aggregation, one must obtain a set of ODE's, the macro-system, governing the macro variables Y_j and only depending on them:

$$\frac{dY_j}{dt} = h_j(Y_1, Y_2, \ldots, Y_A), \qquad j = 1, 2, \ldots, A, \tag{3}$$

where h_j are functions of the macro-variables only. This method of perfect aggregation is very interesting when $A \ll N$ in which case the large micro-system has been reduced or condensed into a much smaller macro-system. If such a perfect aggregation is realizable, the big system is exactly replaced by a copy of itself written differently, but in a more synthetic way. From equations (2), one sees that the time derivatives of the macro-variables are the following:

$$\frac{dY_j}{dt} = \sum_{k=1}^{N} \frac{\partial g_k}{\partial n_k} \frac{dn_k}{dt}. \tag{3a}$$

However, in general, perfect aggregation cannot be performed because the right member of equation (3a) cannot be written as a function h_j only of the macro-variables Y_j, (see [21]) in which conditions are given to perform perfect aggregation. Methods of perfect aggregation can only be performed in very particular cases when the parameters of the micro-model take particular values. We shall see this in several simple examples in the field of population dynamics.

2.2. A Set of Growing Subpopulations

For example, one can simply consider a set of N subpopulations i, say n_i, growing linearly with a growth rate r_i:

$$\frac{dn_i}{dt} = r_i n_i. \tag{4}$$

Can we aggregate these equations into a single equation governing a single variable, the total population $Y = n_1 + n_2 + \cdots + n_N$? It is obvious that this will be possible only when all the growth rates are the same: $r_1 = r_2 = \cdots = r_i = r$ leading to the aggregated system (5):

$$\frac{dY}{dt} = rY. \tag{5}$$

Otherwise, it is impossible to reduce the set of N equations into a single equation. This example is simple and rather trivial. However, it shows in a simple case that perfect aggregation is in general impossible. When perfect aggregation is possible, it means that the parameters of the micro-model take very particular values. In this example, all the growth rates must be equal. More generally, as soon as we have linear terms, and in the case of an additive macro-variable Y, the aggregation will imply that the linear coefficients are identical.

One may also consider a set of N logistically growing subpopulations with growth rates r_i and carrying capacities K_i as follows:

$$\frac{dn_i}{dt} = r_i n_i \left(1 - \frac{n_i}{K_i}\right). \tag{6}$$

In this case, perfect aggregation cannot be performed, even in the very particular case when all the growth rates are the same (say r) and so for all the carrying capacities (say K). The equation for the total population contains nonlinear quadratic terms which remain impossible to aggregate:

$$\frac{dY}{dt} = rY - \frac{r}{K}\left((n_1)^2 + (n_2)^2 + \cdots + (n_N)^2\right). \tag{7}$$

The sum of the squares of the subpopulations cannot be replaced by the square of the sum, that is, as a function of Y and only of Y. Now, similarly to [21], let us consider the case of two populations of prey and their predator, respectively, of densities n_1, n_2, and n_3:

$$\frac{dn_1}{dt} = r_1 n_1 \left(1 - \frac{a_{13}n_3}{K_1}\right), \tag{8a}$$

$$\frac{dn_2}{dt} = r_2 n_2 \left(1 - \frac{a_{23}n_3}{K_2}\right), \tag{8b}$$

$$\frac{dn_3}{dt} = -r_3 n_3 + (a_{31}n_1 + a_{32}n_2)n_3. \tag{8c}$$

It is possible to aggregate this system of three equations into a system of two equations for the variables $Y_1 = n_1 + n_2$ and $Y_2 = n_3$. This means that we aggregate the prey into a single compartment. This is possible when the parameters of the micro-model (8) satisfy the following set of relations:

$$r_1 = r_2 = r, \qquad K_1 = K_2 = K, \qquad a_{23} = a_{13} = a, \qquad \text{and} \quad a_{32} = a_{31} = a'. \tag{9}$$

Then, the macro-model will be the following:

$$\frac{dY_1}{dt} = rY_1 \left(1 - \frac{aY_2}{K}\right), \tag{10a}$$

$$\frac{dY_2}{dt} = -r_3 Y_2 + a' Y_1 Y_2. \tag{10b}$$

These conditions are very restrictive and suppose very particular values of the parameters. These examples are simple and many other examples in the context of population dynamics could be studied. Some of them can be found in [21] such as an age structured population. However, these simple examples show that perfect aggregation is in general impossible to realize. When perfect aggregation is possible, it corresponds to very particular conditions: the parameters of the micro-model satisfy very specific relationships.

Furthermore, it means that the micro-system is obviously not the system of interest to be studied. If it can be condensed exactly, that is, by rewriting it in a different manner, one should use immediately the macro-system and not a more complex copy. (Note that Gard [22] has also given perfect aggregation methods for stochastic models.)

2.3. Approximate Aggregation

As perfect aggregation is generally not possible, it is very useful to investigate approximate aggregation methods. The aim is, by starting with a complex differential system, to construct a simpler one for which solutions approximate the solutions of the initial system. The problem is: how to build another macro-model from an initial micro-model which is not a simple copy but different from it and requiring that the solutions of both systems remain close in a given window of observation? For example, one can define a measure or a distance between the solutions of the micro-system and the macro-system. This measure should be maintained small enough to consider that the solutions of both systems are almost the same at least during a certain time. Refer to [23] for more details.

This is a problem of *resemblance* between two systems. One tries to build a new and simpler system having a similar behaviour (or close enough) to the complex micro-system during a certain period of time. Still, there are two ways to think about this problem.

1. Two differential systems can have solutions close during a certain period of time while the two models are actually independent [23–25].
2. The structure of the micro-dynamics is such that there is an invariant manifold in the phase space which is globally attractive. In this case, by replacing the micro-system with its restriction on the invariant manifold, one obtains a macro-system approximating the micro-system.

Case 2 is the case of study in this article. Now, when we refer to approximate aggregation, we will mean Case 2. To perform approximate aggregation, one must use mathematical methods in order to approximate a big system of ODE's by a smaller one. The method, based on a Center Manifold Theorem, allows us to build an approximate model as close as necessary to the micro-model. It is possible to get the macro-model as an asymptotic expansion in terms of a small parameter ε. The calculation of higher order terms allows one to obtain a solution of the macro-model close enough to the solution of the micro-model. Case 2 relates to the reduction of a micro-model into a macro-model on the basis of the real dynamics. The macro-model is obtained from the structure of the micro-model and has strong relationships with it.

3. AGGREGATION OF SYSTEMS OF ODE'S WITH TWO TIME SCALES

Now we shall give the main guidelines for the study of aggregation in dynamical multitime scales systems.

3.1. The Micro-System

We consider a model which is called the micro-system and we assume that it is structured into a certain number N of subsystems. In this way, we can regard this system as hierarchically organized. Hierarchy has been recognized to play an important role in biological and ecological systems [26–31]. In our early works, we studied dynamics and thermodynamics of hierarchically organized systems, see [8–13]. We assumed that the intra-subsystem interactions are large in comparison to inter-subsystem ones. For example, in the context of population dynamics, these subsystems can be different subpopulations corresponding to individuals situated on different spatial patches. The micro-system is described by a set of equations governing many variables which we call the micro-variables. Let N^α be the number of micro-variables associated to subsystem α, $\alpha \in [1, N]$. The total number of micro-variables is $N^* = \sum_\alpha N^\alpha$ which is assumed to be large, $N^* \gg 1$. This means that we deal with a complex model with a lot of micro-variables and parameters.

Let i be the index for the micro-variables belonging to subsystems α of first order. In the case of population dynamics, the micro-variables $n_i^\alpha(t)$ are the numbers or densities of individuals of subpopulation i belonging to population α, $i \in [1, \ldots, N^\alpha]$. Consider the next system of ODE's, written in the frame of the perturbation theory, governing the micro-variables:

$$\frac{dn_i^\alpha}{dt} = Rf_i^\alpha\left(\mathbf{n}^1, \mathbf{n}^2, \ldots, \mathbf{n}^N\right) + F_i^\alpha\left(\mathbf{n}^1, \mathbf{n}^2, \ldots, \mathbf{n}^N\right), \tag{11}$$

with

$$\mathbf{n}^\alpha = \left(n_1^\alpha, n_2^\alpha, \ldots, n_{N^\alpha}^\alpha\right),$$

where

$$f_i^\alpha\left(\mathbf{n}^1, \mathbf{n}^2, \ldots, \mathbf{n}^N\right) = O(n^\alpha) \quad \text{and} \quad F_i^\alpha\left(\mathbf{n}^1, \mathbf{n}^2, \ldots, \mathbf{n}^N\right) = O(n^\alpha),$$

and where R is the time factor scale and is large with respect to one, $R \gg 1$. This system is the micro-system. It is assumed that it is a large scale system with many variables n_i^α. At this stage, the different functions f_i^α and F_i^α are nonlinear and not explicit. There is a possibility to rewrite the equations in a different way by considering a new time scale τ such that $\tau = tR$. With respect to this time scale, (11) becomes

$$\frac{dn_i^\alpha}{d\tau} = f_i^\alpha\left(\mathbf{n}^1, \mathbf{n}^2, \ldots, \mathbf{n}^N\right) + \varepsilon F_i^\alpha\left(\mathbf{n}^1, \mathbf{n}^2, \ldots, \mathbf{n}^N\right), \tag{12}$$

with $\varepsilon = 1/R$ a small parameter. In (11), R can be regarded as a kind of measure of the ratio of the characteristic time scales for the fast and slow process, respectively, governed by functions f_i^α and F_i^α. However, the form of equation (12) is the more familiar in perturbation theory.

Systems (11) and (12) are written in a particular form in which we consider separately interactions between subpopulations within the same population (internal fast part), and interactions between subpopulations of different populations (external slow part). f_i^α are intra-population α terms while F_i^α are inter-population terms. Both terms may depend on all the vectors $\mathbf{n}^\beta$. The interactions between the subpopulations in the same population α and between two populations can both depend in general on the subpopulations of different populations. We assume that the intra-population terms are much larger than the inter-population terms: inter-population terms are seen as perturbations with respect to intra-population ones.

3.2. Macro-Variables and Invariance

Given a micro-system (12), in general, it is not obvious how to make a good choice of macro-variables Y_i. In a particular biological context, sometimes a biologist might tell us which macro-variables would be of interest from a biological point of view and this could be an important guide for this choice. However, one must try to give a general method for realizing this choice in a rigorous way.

In our approach, macro-variables are connected to levels of organization. These levels of organization themselves correspond to levels of invariance. Macro-variables are *always* chosen as constants of motion of the fast parts of the micro-system. Consequently, this means that we assume that the fast parts of the micro-system (12) are conservative. When one neglects the perturbation terms in the micro-system, that is, when one neglects the small perturbation terms by putting $\varepsilon = 0$ in (12), the micro-system is only governed by the fast part:

$$\frac{dn_i^\alpha}{d\tau} = f_i^\alpha\left(\mathbf{n}^1, \mathbf{n}^2, \ldots, \mathbf{n}^N\right), \tag{13}$$

We assume that for any subsystem α, there exists a constant of motion Y^α. This means that system (13) is conservative and that macro-variables Y^α are first integrals of (13):

$$\frac{dY^\alpha}{d\tau} = 0, \tag{14}$$

which means that Y^α are constant along the trajectories of equations (13) for the micro-variables n_i^α. There is a family of trajectories of system (13) corresponding to different initial conditions $(n_1^\alpha(0), n_2^\alpha(0), \ldots, n_N^\alpha(0))$. The macro-variable Y^α takes a constant value for each set of initial conditions and remain constant along the trajectories of the fast system (13).

Another way to consider this point is to say that the macro-variables are not sensitive to the fast part, but only to the slow part of equation (12). This condition of invariance of the macro-variables with respect to the fast part of the equations is important for two reasons.

- A consequence of condition (14) is that the macro-dynamics is partly decoupled from the micro-dynamics. There is a quasidecoupling of the fast and slow dynamics. As a

consequence, the dynamics of each subsystem is almost uncoupled to the dynamics of the other subsystems. Each subsystem of the partition acquires a relative autonomy.

- The different levels of organization correspond to levels of invariance. Levels are not defined in an arbitrary way, but correspond to conservation laws. The mathematical condition for defining macro-variables is to find first integrals of the fast parts of the micro-system.

In the other articles of this special issue, several biological and ecological examples of constants of motion for the subsystems are presented. *The existence of first integrals for biological systems is not rare. The fundamental reason is that most of the physical and biological processes are controlled by global constraints, such as a constant energy, biomass, or size, etc. There are many natural processes which are conservative.* It must be noted that we do not require that the whole system (the micro-system in its whole) be conservative, but that there exist some macro-variables which are constant of motion only for the fast parts of the micro-system.

The macro-variables Y^α correspond to the macro-system which evolves slowly with respect to the micro-system. These macro-variables characterize the whole system at a macro-scale. They correspond to a macro-level of aggregation, of organization and of observation of the system. At this macro-level, some details are not visible and the fast systems rapidly reach an attractor (equilibrium, limit cycle,...). The macro-system describes the dynamics at a more macroscopic level of observation and of aggregation or organization.

Consequently, in our approach, the level of organization is defined at least as a level of invariance. This relationship between structure and invariance is a key point. Starting from a micro-system with many variables, it is difficult to find proper macro-variables by merely aggregating some of the micro-variables. Indeed, there are many possibilities for choosing the macro-variables. This problem is the very important one of the definition of a level of organization of a system. How can we recognize a level of organization? What is the signature of a level? When can we be sure that a certain type of partition of a system into subsystems define a level of organization? Can we give rigorous definition of a level of organization? *We propose to define a level of organization as a level of invariance and of conservation.*

Jumping from a micro-level to a macro-level corresponds to a change of invariants. The micro-system is subdivided into subsystems, each one involving many micro-variables in its dynamics. Macro-variables are invariant for the fast parts which describe the interactions between the micro-variables within the subsystems. Finding a macro-level means finding new constants of motion which relate to another level of organization. In any case, the macro-variables are defined as general g-functions of the micro-variables:

$$Y^\alpha = g^\alpha(n_1^\alpha, n_2^\alpha, \ldots, n_{N^\alpha}^\alpha). \tag{15}$$

The simplest case occurs when the macro-variables are simply the total populations $Y^\alpha = \sum_{i=1}^{N^\alpha} n_i^\alpha$ or a linear combination of the micro-variables, $Y^\alpha = \sum_{i=1}^{N^\alpha} b_i^\alpha n_i^\alpha$ where b_i^α are constant parameters. However, one can imagine several examples of more complex macro-variables with various nonlinear functions g^α of the micro-variables. The condition of invariance of the macro-variables for the fast parts requires that when $\varepsilon = 0$, the next relations hold:

$$\frac{dY^\alpha}{d\tau} = \sum_{i=1}^{N^\alpha} \frac{\partial Y^\alpha}{\partial n_i^\alpha} \frac{dn_i^\alpha}{d\tau} = \sum_{i=1}^{N^\alpha} \frac{\partial Y^\alpha}{\partial n_i^\alpha} f_i^\alpha \left(\mathbf{n}^1, \mathbf{n}^2, \ldots, \mathbf{n}^N\right) = 0, \tag{16}$$

for any subsystem α. In the case of a linear macro-variable, relation (16) simply reduces to

$$\sum_{i=1}^{N^\alpha} b_i^\alpha f_i^\alpha \left(\mathbf{n}^1, \mathbf{n}^2, \ldots, \mathbf{n}^N\right) = 0. \tag{17}$$

The simplest case of the total population $Y^\alpha = \sum_{i=1}^{N^\alpha} n_i^\alpha$ leads to the next relation

$$\sum_{i=1}^{N^\alpha} f_i^\alpha \left(\mathbf{n}^1, \mathbf{n}^2, \ldots, \mathbf{n}^N\right) = 0. \tag{18}$$

Having defined the macro-variables, let us now compare the different characteristic time scales of micro- and macro-variables.

3.3. Two-Time Scales

A simple calculation shows that according to the fact that the macro-variables are constants of motion for the fast parts, the macro-system can be written in a simple form as follows:

$$\frac{dY^\alpha}{d\tau} = \varepsilon \sum_{i=1}^{N^\alpha} \frac{\partial Y^\alpha}{\partial n_i^\alpha} F_i^\alpha \left(\mathbf{n}^1, \mathbf{n}^2, \ldots, \mathbf{n}^N\right). \tag{19}$$

Macro-variables are invariant for the fast part of the micro-system, but not for the slow part. At this stage, one sees that the condition of invariance plays an important role in the sense that it leads to two different time scales for the micro-variables and the macro-variables. Indeed, *the macro-variables are only governed by the slow part while the micro-system* (20):

$$\frac{dn_i^\alpha}{d\tau} = f_i^\alpha \left(\mathbf{n}^1, \mathbf{n}^2, \ldots, \mathbf{n}^N\right) + \varepsilon F_i^\alpha \left(\mathbf{n}^1, \mathbf{n}^2, \ldots, \mathbf{n}^N\right), \tag{20}$$

is mainly governed by the fast part. When one neglects the small perturbation terms by putting $\varepsilon = 0$, (20) reduces to (21):

$$\frac{dn_i^\alpha}{d\tau} = f_i^\alpha \left(\mathbf{n}^1, \mathbf{n}^2, \ldots, \mathbf{n}^N\right). \tag{21}$$

Consequently, there exist two different time-scales associated to the internal and external parts of the dynamics. There is a time hierarchy. Macro-variables are only governed by small terms (the inter-subsystem terms), while micro-variables are mainly governed by strong terms (the intra-subsystem terms). *Macro-variables are slow variables with respect to micro-variables.* For any (α, i), we have

$$|\dot{Y}^\alpha| \ll |\dot{n}_i^\alpha|, \tag{22}$$

where the dot denotes the time derivative with respect to the time τ. The macro-variables vary at a slow time scale t and the micro-variables vary at a fast time scale τ. This time structure is a consequence of the assumption that strongly coupled micro-variables are grouped together to form a subsystem and of the condition of invariance of the macro-variables. Invariance is necessary to induce two separate time scales. Indeed, without invariance of the macro-variables for the fast parts, equation (19) would not hold because the fast parts would not vanish in the equations of the macro-variables.

The definition of a macroscopic level of organization implies having two time scales: a fast one at a microscopic level and a slow one at a macroscopic level. In this sense, invariance is an important condition for defining a level of organization.

In the following section, we present the aggregation method in the case where the fast part of system (12), obtained by putting $\varepsilon = 0$, has an equilibrium. For the sake of simplicity, we suppose the macro-variables are the global densities of population. A generalization for any macro-variables is presented in the next section.

3.4. Obtention of the Macro-System by Use of the Center Manifold Theorem

In this section, we present the general aggregation method, based on a Center Manifold Theorem. One can refer to [7], see also [17–19]. The main idea behind this method is the replacement of fast variables reaching stable equilibria by their equilibria. By doing this, we make an error of the order of the small parameter ε. As we shall see, this error can be neglected in many cases. This is the "Quick-Derivation-Method". Nevertheless, in the cases where the small error cannot be neglected, the general method allows us to reduce this error and so to neglect it.

Auger and Benoît [16] propose a quick derivation method based on another theorem [5,6]. The idea is similar as that of the center manifold theorem and consequently, we present only the theorem which permits performance of the whole of the aggregation method and not only the quick derivation part.

We restart with the micro-system which is written as follows:

$$\frac{dn_i^\alpha}{d\tau} = f_i^\alpha\left(\mathbf{n}^1, \mathbf{n}^2, \ldots, \mathbf{n}^N\right) + \varepsilon F_i^\alpha\left(\mathbf{n}^1, \mathbf{n}^2, \ldots, \mathbf{n}^N\right). \tag{23}$$

In this section, the macro-variables are the global densities of populations:

$$Y^\alpha = n^\alpha = \sum_{i=1}^{N^\alpha} n_i^\alpha. \tag{24}$$

Recall that we make the "invariance" assumption, that is,

$$\sum_{i=1}^{N^\alpha} f_i^\alpha\left(\mathbf{n}^1, \ldots, \mathbf{n}^N\right) = 0. \tag{25}$$

Dynamical equations of populations n^α are then obtained as follows, see (19):

$$\frac{dn^\alpha}{d\tau} = \varepsilon \sum_{i=1}^{N^\alpha} F_i^\alpha\left(\mathbf{n}^1, \mathbf{n}^2, \ldots, \mathbf{n}^N\right). \tag{26}$$

System (26) is composed of N equations while the micro-system (23) is composed of $\sum_{\alpha=1}^{N} N^\alpha$ equations. For instance, in the case of 2 populations, each one containing 10 subpopulations, we get 2 global equations (26) and 20 equations for the micro-system. This leads to an important reduction of the dimension of the micro-system. We now introduce the frequencies. With our choice of macro-variables (24), the frequencies are the proportions of subpopulations:

$$v_i^\alpha = \frac{n_i^\alpha}{n^\alpha}. \tag{27}$$

The derivatives of the frequencies with respect to the time are given by the following formula:

$$\frac{dv_i^\alpha}{d\tau} = \frac{1}{n^\alpha}\left(\frac{dn_i^\alpha}{d\tau} - v_i^\alpha \frac{dn^\alpha}{d\tau}\right). \tag{28}$$

Since the sum of the frequencies for each population is always equal to one, the sum of their derivatives is always equal to zero. Therefore, it is sufficient to know all these derivatives except one for each population. Now, the initial system (23) is equivalent to the following one:

$$\frac{dv_i^\alpha}{d\tau} = \frac{1}{n^\alpha} f_i^\alpha\left(\mathbf{n}^1, \ldots, \mathbf{n}^N\right) + \varepsilon \frac{1}{n^\alpha}\left(F_i^\alpha\left(\mathbf{n}^1, \ldots, \mathbf{n}^N\right) - v_i^\alpha \sum_{j=1}^{N^\alpha} F_j^\alpha\left(\mathbf{n}^1, \ldots, \mathbf{n}^N\right)\right), \tag{29a}$$

where $i \in \{1, \ldots, N^\alpha - 1\}$, for each α. Therefore,

$$\frac{dn^\alpha}{d\tau} = \varepsilon \sum_{i=1}^{N^\alpha} F_i^\alpha\left(\mathbf{n}^1, \mathbf{n}^2, \ldots, \mathbf{n}^N\right), \qquad \text{and} \tag{29b}$$

$$\frac{d\varepsilon}{d\tau} = 0. \tag{29c}$$

Systems (29a),(29b) contains $\sum_{\alpha=1}^{N} N^\alpha$ equations as system (23). We assume positive equilibrium frequencies $v_i^{\alpha^*}$ when ε equals zero. It means that we assume positive equilibrium for the subpopulations densities $n_i^{\alpha^*}$. The equilibrium frequencies are solutions of the next system:

$$f_i^\alpha\left(\mathbf{n}^{1^*}, \mathbf{n}^{2^*}, \ldots, \mathbf{n}^{N^*}\right) = 0, \tag{30}$$

where $\mathbf{n}^{\alpha^*} = (n_1^{\alpha^*}, \ldots, n_{N^\alpha}^{\alpha^*}) = n^\alpha(v_1^{\alpha^*}, \ldots, v_{N^\alpha}^{\alpha^*})$.

In order to apply the center manifold theorem, it is more convenient to make a translation by considering the relative frequencies as follows:

$$V_k^\alpha(t) = v_k^\alpha(t) - v_k^{\alpha^*}, \tag{31}$$

where $\sum_i V_i^\alpha = 0$.

Hence, their time derivatives are:

$$\frac{dV_i^\alpha}{d\tau} = \frac{dv_i^\alpha}{d\tau} - \frac{dv_i^{\alpha^*}}{d\tau}. \tag{32}$$

The main consequence of this change of variables is that now, the equilibrium of the fast part is the zero vector. Note that it is not necessary to make explicit the time derivatives of the frequencies or the relative frequencies to perform the quick derivation method. Indeed, we are just interested in the equilibrium frequencies which are obtained with the same equation as the fast subpopulation densities equilibrium, since the global densities are constant when $\varepsilon = 0$. The idea is to replace in (29b), the variables n_i^α with their equilibrium value $n_i^{\alpha^*} = v_i^{\alpha^*} n^\alpha$. The solutions of the initial system (23) are close to the solutions of the system obtained by replacing the fast variables with their equilibrium values only if the equilibrium is *hyperbolically stable*. This means that the equilibrium is asymptotically stable for the linearization of the fast part around the equilibrium. Therefore, at this stage, we consider the linear part of system (32) in the neighborhood of the steady state point $(\dots V_i^\alpha \dots) = (0, \dots, 0)$:

$$\frac{dV_i^\alpha}{d\tau} = \sum_{j=1}^{N^\alpha - 1} A_{ij}^\alpha V_j^\alpha, \qquad i \in \{1, \dots, N^\alpha - 1\}. \tag{33}$$

We assume that all the eigenvalues λ_i^α associated with system (33) have **negative real parts**. This is the stability condition for the fast part of the micro-system required in order to apply the Center Manifold Theorem. This theorem claims that the solutions of (23) are very soon close to the solutions of a system obtained by replacing the relative frequencies in (29b) with functions only depending on the macro-variables and on ε. In other words, one can replace the relative frequencies in (29b) with

$$V_i^\alpha \to \phi_i^\alpha \left(n^1, \dots, n^N, \varepsilon\right), \tag{34}$$

where $\phi_i^\alpha(n^1, \dots, n^N, 0) = 0$. One can make an asymptotic expansion of these functions with respect to the powers of ε which allows that $\phi(n^1, \dots, n^N, \varepsilon) = O(\varepsilon)$ is of order ε. It means that we can replace in (29b), the frequencies with

$$v_i^\alpha \to v_i^{\alpha^*} + \phi_i^\alpha \left(n^1, \dots, n^N, \varepsilon\right) = v_i^{\alpha^*} + O(\varepsilon). \tag{35}$$

Note that (35) proves that replacing the frequencies with their equilibrium values leads to an error of order ε. Note that if the model obtained by omitting the terms of order of ε is structurally stable, then from a qualitative viewpoint, its solutions are the same as the solutions obtained with the perturbation. Therefore, this perturbation can be neglected from a qualitative viewpoint. This is the quick derivation method. In Appendix A, we propose a recipe which gives the different steps that one needs in order to perform this quick derivation method.

Note that if the aggregated model is not structurally stable, one must compute the higher order ε terms in (35). The method is explained in Appendix C. In Appendix B, we present the Center Manifold Theorem in a version following the paper of Fénichel [1].

As we explained above, the quick derivation method can be obtained by using other theorems, see [5,6], since the center manifolds seem to be more complicated. However, the use of the Center Manifold Theorem is needed when the aggregated system obtained with the quick derivation method is not structurally stable. The method allows one to obtain the higher order terms of

the asymptotic expansion (35) and to obtain the real dynamics of the macro-system. Moreover, it allows one to get the desired level of approximation between the macro-system and the micro-system. Indeed, the asymptotic expansion permits us to calculate the successive terms of the series depending on the powers of ε. Each supplementary term in the series corresponds to a better approximation. Nevertheless, there is a price to pay for these different terms. The calculations can be long!

For this reason, *when the macro-system at order zero of the asymptotic expansion is structurally stable, the first term of the series is sufficient and the other terms can be neglected.* The quick derivation method is then sufficient. However, in particular cases such as centers, it is necessary to compute the first order term. We present in Appendix C, the details of the calculations of the asymptotic expansion of the center manifold.

3.5. Generalization: When the Macro-Variables Are Not the Global Densities

Generally, a macro-variable can be any function depending on the micro-variables. However, the method above cannot be applied for just any such function. Let us examine what is occurring in the general case. We propose to follow the recipe in Appendix A. Step one allows us start with the following system:

$$\frac{dn_i^\alpha}{d\tau} = f_i^\alpha\left(\mathbf{n}^1, \mathbf{n}^2, \ldots, \mathbf{n}^N\right) + \varepsilon F_i^\alpha\left(\mathbf{n}^1, \mathbf{n}^2, \ldots, \mathbf{n}^N\right), \tag{36}$$

and to add the equations:

$$\frac{dY^\alpha}{d\tau} = \varepsilon \sum_{i=1}^{N^\alpha} \frac{\partial Y^\alpha}{\partial n_i^\alpha} F_i^\alpha\left(\mathbf{n}^1, \mathbf{n}^2, \ldots, \mathbf{n}^N\right). \tag{37}$$

We perform the second step by putting $\varepsilon = 0$ in (36) and (37) and we obtain that Y^α are constant. We must solve the system:

$$f_i^\alpha\left(\mathbf{n}^1, \mathbf{n}^2, \ldots, \mathbf{n}^N\right) = 0, \qquad \alpha \in \{1, \ldots, N\},\ i \in \{1, \ldots, N^\alpha - 1\}, \tag{38a}$$

$$Y^\alpha\left(\mathbf{n}^1, \ldots, \mathbf{n}^N\right) = C^{te}, \qquad \alpha \in \{1, \ldots, N\}, \tag{38b}$$

$$\sum_{i=1}^{N^\alpha} \frac{\partial Y^\alpha}{\partial n_i^\alpha} f_i^\alpha\left(\mathbf{n}^1, \mathbf{n}^2, \ldots, \mathbf{n}^N\right) = 0, \tag{38c}$$

where (38a) is the fast equilibrium condition and (38b),(38c) are obtained by the "invariance" condition (16). Let us *assume that the following equality always holds*:

$$\frac{\partial Y^\alpha}{\partial n_{N^\alpha}^\alpha} \neq 0. \tag{39}$$

Note that we have considered in (39) the derivative of each macro-variable Y^α with respect to the *last* component of vector $\mathbf{n}^\alpha$. If (39) does not hold for this derivative but does for another component of $\mathbf{n}^\alpha$, then we clearly obtain (39) by permuting the indices. Assumption (39) added to (38) means that one can always express the variables $n_{N^\alpha}^\alpha$ as functions of the variables $n_1^\alpha, \ldots, n_{N^\alpha-1}^\alpha$. Furthermore, by using (38c), one can express $f_{N^\alpha}^\alpha(\mathbf{n}^1, \mathbf{n}^2, \ldots \mathbf{n}^N)$ as follows:

$$f_{N^\alpha}^\alpha\left(\mathbf{n}^1, \mathbf{n}^2, \ldots, \mathbf{n}^N\right) = -\left(\frac{\partial Y^\alpha}{\partial n_{N^\alpha}^\alpha}\right)^{-1} \sum_{i=1}^{N^\alpha - 1} \frac{\partial Y^\alpha}{\partial n_i^\alpha} f_i^\alpha\left(\mathbf{n}^1, \mathbf{n}^2, \ldots, \mathbf{n}^N\right). \tag{40}$$

In this case, system (38) is a system of $(\sum_{\alpha=1}^{N}(N^\alpha - 1)) = (\sum_{\alpha=1}^{N} N^\alpha) - N$ equations with the same number of variables. One can proceed as in the previous example, where the macro-variables were the global densities. If equation (39) does not hold, it is rather more complicated and is generally not possible to aggregate the initial system.

4. AVERAGING METHODS AND AGGREGATION

The simplest case that we have first investigated corresponds to an equilibrium of the fast dynamics which is asymptotically stable. The next step is to consider a fast oscillating system. For example, the fast system can be characterized by a stable limit cycle. In this case, it is necessary to average the fast variables along the limit cycle. Averaging methods are devoted to realizing this averaging process for the fast variables. We are now going to present a combination of averaging and aggregation methods to obtain a slow macro-model.

4.1. The Micro-System with Fast Oscillations

We consider a differential system of the usual form:

$$\frac{dn_i^\alpha}{d\tau} = f_i^\alpha\left(\mathbf{n}^1,\ldots,\mathbf{n}^N\right) + \varepsilon F_i^\alpha\left(\mathbf{n}^1,\ldots,\mathbf{n}^N\right), \qquad i \in [1, N^\alpha], \tag{41}$$

α is the number of subsystems $\alpha \in [1, N]$. We assume that the internal dynamics is conservative. $n^\alpha = \sum_i n_i^\alpha$ are constants of motion of the fast parts and thus are the slow macro-variables. This leads to

$$\sum_{i=1}^{N^\alpha} f_i^\alpha\left(\mathbf{n}^1,\ldots,\mathbf{n}^N\right) = 0, \tag{42}$$

and the equations for the macro-variables thus are the following:

$$\frac{dn^\alpha}{d\tau} = \varepsilon \sum_{i=1}^{N^\alpha} F_i^\alpha\left(\mathbf{n}^1,\ldots,\mathbf{n}^N\right). \tag{43}$$

It is easy to get the equations for the frequencies $v_i^\alpha = n_i^\alpha/n^\alpha$:

$$\frac{dv_i^\alpha}{d\tau} = \frac{1}{n^\alpha}\left(\frac{dn_i^\alpha}{d\tau} - v_i^\alpha \frac{dn^\alpha}{d\tau}\right). \tag{44}$$

Now, the whole system can be rewritten as follows:

$$\frac{dv_i^\alpha}{d\tau} = h_i^\alpha(\ldots v_k^\beta \ldots, \ldots n^\gamma \ldots, \varepsilon), \tag{45a}$$

$$\frac{dn^\alpha}{d\tau} = \varepsilon h^\alpha(\ldots v_k^\beta \ldots, \ldots n^\gamma \ldots, \varepsilon), \tag{45b}$$

with h-functions of $(\sum_\alpha N^\alpha) - N$ variables v_i^α and N variables n^α. We assume that for $\varepsilon = 0$, solutions of each of the fast systems tend to a stable limit cycle denoted γ^α:

$$\frac{dv_i^\alpha}{d\tau} = h_i^\alpha(\ldots v_k^\beta \ldots, \ldots n^\gamma \ldots, 0). \tag{46}$$

This means that the frequencies are periodic functions of time at a fast time scale. This limit cycle γ^α (its amplitude, period, etc.) is a function of the *constant* n^α, and thus is denoted $\gamma^\alpha(n^\alpha)$. For any initial conditions, $v_i^\alpha(0), n^\alpha(0)$, the trajectories rapidly approach the limit cycle γ^α (at the fast time scale). We shall now aggregate by averaging on this fast limit cycle.

4.2. The Averaged Macro-System

It can be shown [19] that in the neighborhood of each fast limit cycle, the following change of variables can be made:

$$v_i^\alpha \to (z_i^\alpha, \phi_i^\alpha), \tag{47}$$

where z_i^α is a modulus and ϕ_i^α is an angle. Roughly, variables $(z_i^\alpha, \phi_i^\alpha)$ are similar to polar coordinates and describe the limit cycle. Then it is possible to rewrite the micro-system in terms of the new coordinates:

$$\frac{dz_i^\alpha}{d\tau} = \mu_i^\alpha(z_i^\alpha, \phi_i^\alpha) z_i^\alpha + O\left(\|z\|^2\right) + O(\varepsilon), \tag{48a}$$

$$\frac{d\phi_i^\alpha}{d\tau} = \omega_i^\alpha(n^\alpha) + O(\|z\|) + O(\varepsilon), \tag{48b}$$

$$\frac{dn^\alpha}{d\tau} = \varepsilon h^\alpha(z_i^\alpha, \phi_i^\alpha, n^\gamma, \varepsilon), \tag{48c}$$

where μ and ω are functions not explicit here. Looking at the system at the slow time scale, we are now going to assume that the trajectories are close enough to the limit cycle $\gamma^\alpha(n^\alpha)$. Consequently, each fast system is described by its fast limit cycle γ^α. This means that for any initial condition and any subset α, there exists a time t_0^α such that for $t > t_0^\alpha$, system (48) can be written

$$\frac{dz_i^\alpha}{d\tau} = O(\varepsilon), \tag{49a}$$

$$\frac{d\phi_i^\alpha}{d\tau} = \omega_i^\alpha(n^\alpha) + \varepsilon\lambda_i^\alpha(\phi_i^\alpha, n^\alpha, 0), \tag{49b}$$

$$\frac{dn^\alpha}{d\tau} = \varepsilon h^\alpha(\phi_i^\alpha, n^\alpha, 0). \tag{49c}$$

System (49) makes the assumption that the dynamics of each fast system is reduced to the limit cycle γ^α. The last step is to average the function h^α along the fast limit cycles. First, let us define average h-functions:

$$H^\alpha(n^\alpha) = \frac{1}{2\pi}\int_0^{2\pi} h^\alpha(\phi_i^\alpha, n^\alpha, \varepsilon) d\phi_i^\alpha. \tag{50}$$

The slow aggregated macro-system is a system of N coupled differential equations and is given by the following equations:

$$\frac{dn^\alpha}{d\tau} = \varepsilon H^\alpha(n^\alpha). \tag{51}$$

This system which is homogeneous in terms of macro-variables can be rewritten at the slow time scale t and at first order:

$$\frac{dn^\alpha}{dt} = H^\alpha(n^\alpha). \tag{52}$$

This macro-system plays a similar role to that of the aggregated system in the case of fast asymptotically stable equilibrium. However, in this case the fast systems do not tend to a fixed steady state point, but oscillate at a fast time scale. The macro-system is obtained by assuming that each subset rapidly reaches its stable limit cycle, and then by taking an average of the limit cycle.

The next step would be to consider different attractors for the fast dynamics such as strange attractors. Then it would be necessary to average or to look for ergodic measures for the fast dynamics.

5. EMERGENCE OF GLOBAL PROPERTIES AT THE MACRO-LEVEL

Now, we are interested in the comparison between the micro-model and the macro-model. In particular, we focus on the emergence of global properties in the macro-model as a result of the coupling between the fast and the slow dynamics. Indeed, the aggregation is not only useful

because it reduces the dimension and the complexity of the micro-system. It is also interesting if it makes new global properties emerge at the macro-level.

The concept of emergence is not simple to define in a rigorous way. In our case each micro-variable n_i^α is mainly governed by a fast dynamics, and each macro-variable n^α is only governed by the slow part of the dynamics of the micro-variables n_i^α. One could imagine that it is sufficient to know the slow part of the micro-dynamics in order to know the macro-dynamics, but it is *not* the case. Indeed, it is necessary to take into account the way in which the micro-variables reach their fast attractor, because this makes new properties emerge in the macro-dynamics. If we consider two micro-models with the same slow part, we can obtain two different macro-models according to the differences between the fast parts. This is true in spite of the fact that the macro-variables are only governed by the slow part, as shown by formula (19). This is why we speak about emergence from the micro-level to the macro-level.

More rigorously, we shall give two mathematical definitions of emergence: the *functional* emergence and the *dynamical* emergence. Then we will study the links between them.

5.1. Definitions: Functional and Dynamical Emergence

In order to give a simple and clear definition of *functional emergence*, we assume that the function F_i^α depends only on the micro-variables $(n_i^1, \ldots, n_i^N)$ and macro-variables $Y^\alpha = n^\alpha$. For example, this is the case if we consider some populations subdivided into subpopulations according to a spatial distribution: on patch i, each subpopulation interacts only with the subpopulations living in the same patch i. Furthermore, let us assume that for each α, all the functions F_i^α are the same function with different parameters values. As we have shown in Section 4, one can write the macro-models as

$$\frac{dn^\alpha}{d\tau} = \varepsilon \sum_{i=1}^{N^\alpha} F_i^\alpha \left(n_i^1, \ldots, n_i^N\right) = \varepsilon F^\alpha \left(n^1, \ldots, n^N\right). \tag{53}$$

DEFINITION. *We say that there is a functional emergence from the micro-dynamics to the macro-dynamics if the function F^α, defined by formula (53), is not the same function as the functions F_i^α.*

First, let us look at the case of a linear fast part. When the functions f_i^α which are the fast parts of the micro-model are linear functions, frequencies at equilibrium v^{α^*} are independent of n^α. This means that the equilibrium frequencies of the fast part of the micro-system are constant numbers or else that the equilibrium micro-variables of the fast part are proportional to the macro-variable.

This can be checked on particular fast models. For example, in population dynamics, animals can go on different spatial patches and the subpopulations correspond to animals on the different patches. Let us study an example of a fast part which describes the fast migration process of individuals on different spatial patches. The micro-variables are thus n_i^α and represent the subpopulations on patch i of population α. The fast system is described by equation (54):

$$\frac{dn_r^\alpha}{dt} = R\left(\sum_s k_{rs}^\alpha n_s^\alpha - \sum_s k_{sr}^\alpha n_r^\alpha\right), \tag{54}$$

or still

$$\frac{dn_r^\alpha}{d\tau} = \left(\sum_s k_{rs}^\alpha n_s^\alpha - \sum_s k_{sr}^\alpha n_r^\alpha\right).$$

Parameter k_{rs}^α is the migration rate between patch r to patch s assumed constant to have a linear migration model. Instead of treating an abstract system, we shall consider a particular

fast migration model. This particular migration process was described in a previous work [12] and we briefly recall it. Patch 1 is a fundamental patch, the refuge, for instance, being hidden from any predator. Possible patch-to-patch transitions are from the refuge to another patch i and then return from patch i to the refuge. To go to a new patch j from patch i, individuals must come back to the refuge. From the refuge, individuals can go on any patch i to perform various activities and exploit various resources associated with the different patches. This particular patch dynamics can be described by the following set of differential equations:

$$\dot{n}_r^\alpha = (k_{r1}^\alpha n_1^\alpha - k_{1r}^\alpha n_r^\alpha), \qquad r \neq 1, \tag{55a}$$

$$\dot{n}_1^\alpha = \left(\sum_s k_{1s}^\alpha n_s^\alpha - \left(\sum_t k_{t1}^\alpha \right) n_1^\alpha \right), \qquad r = 1. \tag{55b}$$

The last equation $\dot{n}_1^\alpha$ is a linear combination of the $N^\alpha - 1$ remaining equations. The fast system is conservative. This means that $n^\alpha(t) = \sum_r n_r^\alpha(t)$ is a constant of motion for the intra-population dynamics because the patch changes are not responsible for the variations of the total number of animals. In this example, it is very easy to calculate the equilibrium patch frequencies. Indeed, at equilibrium, the $N^\alpha - 1$ first equations allow one to calculate the ratio between the equilibrium subpopulations of any patch and of the refuge. Then, a simple calculation leads to the equilibrium patch frequencies $v_r^{\alpha^*}$, which represent the proportions of individuals of population α in patch r:

$$v_r^{\alpha^*} = \frac{k_{r1}^\alpha}{k_{1r}^\alpha + k_{1r}^\alpha \sum_{s=2}^{N^\alpha} (k_{s1}^\alpha / k_{1s}^\alpha)}, \qquad r \neq 1, \tag{56a}$$

$$v_1^{\alpha^*} = 1 - \sum_{r=2}^{N^\alpha} v_r^{\alpha^*}. \tag{56b}$$

This equilibrium point of the fast migration process is asymptotically stable. Consequently, when the functions f_i^α are linear and due to the fact that the total population is invariant through the fast part of the micro-model, equations (56) show that the components of the vector v^{α^*} are independent of n^α. The equilibrium subpopulations of the fast part are homothetic, i.e., proportional to the total population $n_i^{\alpha^*} = v_i^{\alpha^*} n^\alpha$.

This has an important consequence. In the case of the quick derivation method of the macro-model, the approximated macro-system is simply obtained by replacing all the subpopulations $n_i^{\beta^*}$ with $n^\beta v_i^{\beta^*}$ into functions F_i^α. As a consequence, the function F^α is the sum of functions depending on all the n^β and all these functions are formally the same. If they are additive, then their sum has the same form. For instance, if the F_i^α are quadratic polynomials, then their sum is a quadratic polynomial: in this case, the function F^α is of the same form with respect to the macro-variables n^α, as the functions F_i^α are with respect to the micro-variables. Therefore, nothing new occurs in the macro-model with respect to the ε-perturbation of the micro-system. There is no functional emergence.

Now, we are going to discuss coupling effects between the slow dynamics corresponding to the aggregated system and the fast dynamics corresponding to the subpopulations system. In the previous case, the subpopulation frequencies rapidly tended toward constant values. This is the case when the fast part of the equations are simply linear. The equilibrium frequencies of the subpopulations v_r^α remain constant along the slow trajectory on the slow manifold.

On the contrary, generally when the fast functions f_i^α are nonlinear, the equilibrium frequencies $v_i^{\alpha^*}$ are functions of the slow variables $(n^1, \ldots, n^N)$. For example, in the previous migration process, one can imagine that the migration rates k_{rs}^α are density dependent. This corresponds, for instance, to the case when the migration process depends on the total number of individuals of the different populations on the patches. The individual migration behaviour may be different when there are many individuals or few individuals on each patch. This is due to aggregative or

repulsive effects between individuals on each spatial patch. Regarding the fast migration model, it means that the migration rates are no longer constant, but are now functions of the total populations $(n^1,\dots,n^N)$, that is, of the macro-variables.

Consequently, when the migration rates are not constant parameters, but depend on the macro-variables, the equilibrium frequencies are also no longer constant numbers. They are now functions of the total population sizes and we must write them $v_i^{\alpha^*}(n^1,\dots,n^N)$. This has an important consequence for the macro-model. Indeed, the substitution of the subpopulations by $n^\alpha v_i^{\alpha^*}(n^1,\dots,n^N)$ into functions F_i^α will now lead to a macro-system:

$$\frac{dn^\alpha}{dt} = \sum_{i=1}^{N^\alpha} F_i^\alpha\left(n^1 v_i^{1^*}\left(n^1,\dots,n^N\right),\dots,n^N v_i^{N^*}\left(n^1,\dots,n^N\right)\right). \tag{57}$$

This macro-system includes new and different terms with respect to the slow part of the micro-system. This is the result of the density dependence of the equilibrium frequencies leading to new terms in the macro-model. This can be seen as a coupling between the fast and the slow dynamics. For each set of values of the slow macro-variables, the fast system reaches an equilibrium. But this equilibrium is different for each set of macro-variables. This process induces a functional emergence in the approximated macro-system.

We will now define the *dynamical emergence*. Let us assume that the dynamics for each patch is the same, modulo a topological equivalence. For example, in each patch, without migration, the dynamics is given by the existence of a globally attractive equilibrium between all the subpopulation's densities living on the patch.

DEFINITION. *We say that there is a dynamical emergence from the micro-dynamics to the macro-dynamics, if the dynamics given by the macro-model is not topologically equivalent to the dynamics on each patch.*

Thus, dynamical emergence relates to qualitative differences between local dynamics (on each patch) and global dynamics (the total population). For example, it means that the total population grows in a different way than does its parts. Some examples of dynamical emergence in population dynamics are given in the following articles of this special issue.

5.2. Functional and Dynamical Emergence: Are They Linked?

Let us compare both definitions of emergence. We want to answer to the following question:

Does functional emergence imply dynamical emergence?

The answer to this question is no! Indeed, *two formally different systems can lead to the same dynamics*. It is the case if both dynamics are topologically equivalent [32,33]. Let us consider, for example, a predator-prey system in a multipatch environment. We assume in this example that in each patch, the prey has a logistic growth and predation is given by an attack rate of the Holling-type 2 form as follows:

$$\frac{dn_1^1}{d\tau} = k_{12}^1 n_2^1 - k_{21}^1 n_1^1 + \varepsilon n_1^1\left(r_1\left(1-\frac{n_1^1}{K_1}\right) - \frac{a_1 n_1^2}{1+b_1 n_1^1}\right), \tag{58a}$$

$$\frac{dn_2^1}{d\tau} = k_{21}^1 n_1^1 - k_{12}^1 n_2^1 + \varepsilon n_2^1\left(r_2\left(1-\frac{n_2^1}{K_2}\right) - \frac{a_2 n_2^2}{1+b_2 n_2^1}\right), \tag{58b}$$

$$\frac{dn_1^2}{d\tau} = k_{12}^2 n_2^2 - k_{21}^2 n_1^2 - \varepsilon n_1^2\left(\mu_1 - \frac{e_1 a_1 n_1^1}{1+b_1 n_1^1}\right), \tag{58c}$$

$$\frac{dn_2^2}{d\tau} = k_{21}^2 n_1^2 - k_{12}^2 n_2^2 - \varepsilon n_2^2\left(\mu_2 - \frac{e_2 a_2 n_2^1}{1+b_2 n_2^1}\right), \tag{58d}$$

where n^1 and n^2 are, respectively, the prey and the predator densities. The predator mortality in the absence of the prey in each patch is assumed to be exponential. Let us suppose that the

migration process is linear, that is, the migration rates are constant. In this example, there is a functional emergence because the functions F_i^α are the same for a given α and they are not additive. However, the global dynamics is the same as the dynamics on each patch without migration. Thus, this model does not give dynamical emergence.

We can conclude that functional *emergence does not imply dynamical emergence.* However, generally, when we have functional emergence, we have dynamical emergence as will be shown in several examples in the following articles of this special issue.

6. DISCUSSION AND CONCLUSION

When starting with initial conditions, rapidly the trajectory of the fast parts of the micro-system "jumps" onto the center manifold. The fast part of the equations tends to equilibrium, which is assumed asymptotically stable. If this equilibrium depends on the position of the point on the slow manifold, i.e., $v_i^{\alpha^*}(n^1, \ldots, n^N)$, we have an effect of the slow dynamics on the fast dynamics. This effect can be called a *top-down effect* or also **immergence.**

The slow global variables "force" the fast system to reach different equilibrium points. The fast equilibrium is depending on global constraints. The term immergence relates to global effects which affect local processes. We call it "immergence" because the direction of this effect is from the top to the internal structures of the system, in comparison to "emergence" which is a *bottom-up effect.*

A particularly interesting situation may occur when several equilibrium points exist for the fast systems. In this case, several aggregated systems exist according to the initial conditions driving the fast system to a particular fast equilibrium. As a consequence, global constraints may provoke local bifurcations. The global variables which are constants of motion for the fast parts can be regarded as bifurcation parameters for these fast dynamics. For example, some asymptotically stable point (for some values of the global variables) may become unstable (in another range of values). At bifurcation, the fast system can jump into another attractor. The slow system exerts immerging effects in the sense that it forces its internal structures to change. In a second step, the slow system may also bifurcate.

Indeed, the slow macro-system depends at each instant on the equilibrium frequencies of the fast system. As a consequence, any change in the equilibrium point of the fast part has an effect on the slow dynamics. It can provoke in turn the emergence of another aggregated system corresponding to another fast equilibrium. We can regard this effect as a bottom-up effect or **emergence.** The term emergence relates to the effects of local changes which affects the global dynamics. We call it emergence because the direction of this effect is from the internal structures to the top and to global levels of organization of the system.

In reality, both effects occur simultaneously. The whole process can be regarded as an **emergence/immergence** process with emergence of nonlinear terms in the slow system because different functions $v_i^{\alpha^*}(n^1, \ldots, n^N)$ give birth to different nonlinear terms in the macro-model The coupling between the two dynamics, i.e., between the fast and the slow dynamics, works by making nonlinear terms emerge in the slow system and by "forcing" the fast systems to obey and to adapt to global constraints.

This general method of approximate aggregation can be used to study complex systems composed of a large number of elements and presenting a hierarchical structure. These systems cannot be studied very easily in some other way. Indeed, if the system contains a lot of variables, it corresponds to a very large number of coupled differential equations. The computer simulation of such a system would need a lot of computer time and the results would be very difficult to use because of the complexity of the information obtained. On the contrary, if the hierarchical partition corresponds to few subsystems with many micro-variables associated with each of them, one obtains a set with only a few differential equations for the macro-model. Thus, one obtains an important reduction in the number of variables needed to describe, with a good approximation,

the behavior of the system. Aggregation is a method which actually utilizes the complexity of large scale systems in reduced form. One way to reduce this complexity is to find a hierarchical structure which permits aggregation of the system.

But these methods are not only useful for reducing the complexity. Another important point is that multilevel systems change and evolve as the result of coupled dynamical processes going on at the different levels of organization in the hierarchical system. This evolution is due to the coupling between the fast and slow parts. The dynamics must not be considered simply at one level, but as a coordinated process of dynamics in each level. As we noted, the coupling between the fast and slow processes can cause emergence of global properties in the slow macro-model. In this case, the macro-model is not simply a copy of the micro-model, but it contains more structure. The fast part does not occur in the macro-model, because the macro-variables are constants of motion for the fast dynamics. However, the fast dynamics strongly influences the macro-model through the equilibrium frequencies which can be *nonlinear* functions of the macro-variables. These nonlinear functions substituted into the macro-model cause emergence of new nonlinear terms at the macro-level. Thus, the macro-model contains more information than the slow part of the micro-model. Aggregation does not only reduce the complexity of the micro-system, but realizes a process of emergence/immergence. Global properties emerge at a macro-level and global constraints immerge in the system.

It is interesting that this process of emergence is connected to nonlinearity of the fast part of the micro-system. This makes sense within the framework of *nonequilibrium thermodynamics*. The process of emergence that we have described above can be regarded as a process of *self-organization* in the macro-system. Different fast parts lead to different macro-models with different nonlinear terms and properties. Similar to the thermodynamical approach of Prigogine's group, self-organization occurs here when the system is far from equilibrium. To self-organize, it is necessary to reach a region of state-space lying in the domain of nonlinear thermodynamics where thermodynamical flows and forces are nonlinear functions. Thermodynamical nonlinearity also seems to play an important role in emergence because nonlinear fast systems are also required.

Finally, we state a few facts about *successive aggregation in multilevel systems*: namely, when the system is composed of subsystems, which themselves are decomposed into smaller subsystems, or *subsystems of second order*. The corresponding micro-variables are $n_j^{a\alpha}(t)$, i.e., numbers of individuals in compartment j of subsystem of second order α belonging to subsystem of first order a. In a *three level system*, there is a *double hierarchical structure*. Intra-subsystem interactions are strong with respect to inter-subsystem interactions and this holds, generally, for subsystems of first and second order. The same methods as above can be applied twice. There are *three characteristic time scales*, one for *global variables*, rapid with respect to *global variables*, themselves fast with respect to *super global variables*. The generalization of aggregation methods is, of course, possible for more than two or three levels.

APPENDIX A
THE QUICK DERIVATION METHOD: A RECIPE

(1) Write the initial model in the form (23) and add the equations of the macro-variables by using (19).

(2) Put $\varepsilon = 0$ and find the equilibria of the subpopulation's densities. Check that the Jacobian matrix associated with the part of the model at the equilibrium has only eigenvalues with negative real parts.

(3) If (2) is satisfied, replace the subpopulation's densities with their equilibrium value in the equations of the macro-variables. You obtain a model with only N equations, which is the aggregated model.

(4) Check that this model is structurally stable (see Appendix C for the case where $N = 2$). If it is structurally stable, then it approximates the initial model: the quick derivation method ends here.

APPENDIX B
THE FENICHEL CENTER MANIFOLD THEOREM

The Center Manifold Theorem is mainly a reduction theorem. It is first a tool which determines the local structure of the flow near a fixed point $\mathbf{0}$ at which the Jacobian matrix corresponding to the linear part has at least a zero and negative eigenvalues. The simplest case occurs for a system with two variables $x(t)$ and $y(t)$ such as (B.1) with 0 and -1 as eigenvalues of the linear part, see [34] for more details. One can also refer to many books treating ODE's, such as [33], where, for example,

$$\begin{aligned} \frac{dx}{dt} &= f(x,y), \\ \frac{dy}{dt} &= -y + g(x,y), \end{aligned} \tag{B.1}$$

where f and g are the nonlinear parts. The center manifold is a graph $y = h(x)$ which satisfies $h(0) = 0$ and which is tangent to the x-axis at 0. These two previous conditions are used in practice to calculate the center manifold. The center manifold is invariant under the flow. This means that the trajectory corresponding to an initial point on the center manifold remains on this manifold. The main result is that the dynamics in the neighborhood of 0 can be reduced to

$$\frac{dx}{dt} = f(x, h(x)). \tag{B.2}$$

In this case, system (B.1) of dimension 2 can be reduced to system (B.2) of dimension 1 in the neighborhood of the origin. As a consequence, the Center Manifold Theorem can be useful for aggregation methods.

Now, we are going to give the Fenichel version of the Center Manifold Theorem which is used in our applications. The theorem above is a local version. However, the following is a global version used when the equilibrium is not isolated as in our applications: indeed, for each fixed macro-variable, there exists an equilibrium for the micro-variables. It follows that the set of equilibria, when $\varepsilon = 0$, is the space of the macro-variables, since they are first integrals.

We assume the existence of a vector field $\mathbf{X}$ on R^Z, $Z = k_1 + N + 1$. $\mathbf{X}$ is C^∞. $[(\mathbf{0}), R^N, 0]$ is a set of zeroes for $\mathbf{X}$. In our application, the variables are $\mathbf{V}^\alpha = [V_i^\alpha] \in R^{k_1} : k_1 = (\sum_{\alpha=1}^N N^\alpha - N)$, $\mathbf{n} = (n^1, n^2, \ldots, n^N) \in R^N$ and $\varepsilon \in R$.

For any point $\mathbf{n}$ and at $(\mathbf{0}, \mathbf{n}, 0)$, we consider the set of eigenvalues of the linear part of $\mathbf{X}$ which is noticed $D\mathbf{X}(\mathbf{n})$. We assume that $D\mathbf{X}(\mathbf{n})$ possesses k_1 eigenvalues with negative real part and that $\mathbf{0}$ is an eigenvalue with multiplicity $N + 1$. At any point $\mathbf{n} \in R^N$, one can consider two spaces E_n^S and E_n^C, respectively, the stable and central spaces of $D\mathbf{X}(\mathbf{n})$ such as $\dim(E_n^S) = k_1$ and $\dim(E_n^C) = N + 1$. All the eigenvalues of $D\mathbf{X}(\mathbf{n})$ restricted to E_n^S have negative real parts. Using these notations and assumptions, the Fenichel Center Manifold Theorem can be expressed in the following form.

THEOREM. *On any bounded set Δ contained in R^N and for any integer k, there exists a manifold $\mathbf{W}$, graph of a C^k map, say $\mathbf{V}^\alpha(\mathbf{n}, \varepsilon) : \Delta x[-\varepsilon, +\varepsilon] \to R^{k_1}$, such that $\mathbf{V}^\alpha(\mathbf{n}, \mathbf{0}) = \mathbf{0}$, being invariant under $\mathbf{X}$ and being tangential to E_n^C, at any point $(\mathbf{0}, \mathbf{n}, 0)$. $\mathbf{W}$ is a center manifold (of class k).*

The invariance of $\mathbf{W}$ implies that at any point $(\mathbf{v}^\alpha, \mathbf{n}, \varepsilon) \in \mathbf{W}$, the vector field $\mathbf{X}$ is tangential to $\mathbf{W}$. At points $(\mathbf{0}, \mathbf{n}, 0)$, the center manifold $\mathbf{W}$ is tangent to the space $(\mathbf{0}, R^N, 0)$. At these points, E_n^C is generated by $(\mathbf{0}, R^N, 0)$ and by the vectors $\frac{\partial \mathbf{V}^\alpha}{\partial \varepsilon}(\mathbf{0}, \mathbf{n}, 0) = \mathbf{W}_1^\alpha(\mathbf{n})$, see Appendix C for the details of calculation.

APPENDIX C
CALCULATION OF THE CENTER MANIFOLD

The full system of equations is as follows:

$$\begin{aligned} \frac{dn^\alpha}{d\tau} &= \varepsilon n^\alpha N^\alpha, \\ \frac{d\mathbf{V}^\alpha}{d\tau} &= \bar{A}^\alpha \mathbf{V}^\alpha + \varepsilon \Phi^\alpha, \\ \frac{d\varepsilon}{d\tau} &= 0, \end{aligned} \tag{C.1}$$

where N^α and Φ^α are functions of $\mathbf{n} = (n^1, \ldots, n^N), (V^1, \ldots, V^N), (v^{1^*}, \ldots, v^{N^*})$, which can be easily explained. V^α, Φ^α have values in $R^{N^\alpha - 1}$ and $\bar{A}^\alpha = (\bar{A}^\alpha_{ij})$, i and $j \in [1, N^\alpha - 1]$. Let us look for the center manifold in the following form:

$$\mathbf{V}^\alpha(\mathbf{n}, \varepsilon) = \varepsilon \mathbf{W}^\alpha(\mathbf{n}, \varepsilon), \qquad \text{with } \mathbf{W}^\alpha(\mathbf{n}, \varepsilon) = \mathbf{W}^\alpha_1 + \varepsilon \mathbf{W}^\alpha_2 + o(\varepsilon). \tag{C.2}$$

The center manifold $V^\alpha(\mathbf{n}, \varepsilon)$ is the solution of the next equation:

$$\bar{A}^\alpha \mathbf{V}^\alpha + \varepsilon \Phi^\alpha = \sum_\beta \frac{\partial V^\alpha}{\partial n^\beta} \frac{dn^\beta}{d\tau} = \varepsilon^2 \sum_\beta \frac{\partial W^\alpha}{\partial n^\beta} n^\beta N^\beta. \tag{C.3}$$

Substitute (C.2) into (C.3). Then, identify terms of order ε:

$$\bar{A}^\alpha \mathbf{W}^\alpha_1 + \Phi^\alpha \left(\mathbf{n}, v^{1^*}, \ldots, v^{N^*}\right) = 0, \tag{C.4}$$

where $\Phi^\alpha(\mathbf{n}, v^{1^*}, \ldots, v^{N^*}) = \Phi^\alpha(\mathbf{n}, 0, \ldots, 0, v^{1^*}, \ldots, v^{N^*})$. Finally, because $\bar{A}^\alpha$ is invertible, one obtains the result given in equation (45):

$$\mathbf{W}^\alpha_1 = -\left(\bar{A}^\alpha\right)^{-1} \Phi^\alpha \left(\mathbf{n}, v^{1^*}, \ldots, v^{N^*}\right). \tag{C.5}$$

Identifying terms of different order ε in (C.3), we have an iterative process which allows one to obtain the functions W^α_i for any i.

APPENDIX D
STRUCTURAL STABILITY: THE ANDRONOV-PONTRYAGIN THEOREM

Intuitively, structural stability means that the dynamical system is not sensitive to small perturbations. For example, this is *not* the case for a system with a linear part in the neighborhood of a fixed point, which is stable (neutral stability), for example, centers. Let us give a definition and a theorem on structural stability.

DEFINITION. *Let X be a vector field defined in a neighborhood of a disk D in R^2. X is called structurally stable if on D there exists a neighborhood U of X in the space of vector fields defined in a neighborhood of D, in the C^1-topology on D, such that for each $Y \in U$, there exists a homeomorphism h_Y in a neighborhood of D($h_Y : V \to W$, V and W are neighborhoods of D) sending orbits of X in V into orbits of Y in W. One says that h_Y is a local topological equivalence between X and Y on D. The structural stability of a system is characterized by the following Andronov and Pontryagin theorem [35].*

THEOREM. *Let X be a vector field defined on a neighborhood of D such that:*

1. *all singular points and all periodic orbits of X are hyperbolic, (there is only a finite number of such critical orbits), and*
2. *there are no connections between saddle points of X (i.e., there is no point q whose α and ω-limit are saddle points).*

Then, X is structurally stable. Moreover, one can find a continuous map $Y \in U \to h_Y$, such that $h_X = Id$. A vector field X in the previous theorem is called a Morse-Smale vector field. Thus, if X_ε is a one-parameter family of vector fields with $X_0 = X$, a Morse-Smale vector field, it follows that a *continuous* one-parameter family of homeomorphisms h_ε exists on some neighborhood V on D, such that $h_\varepsilon(V)$ contains D for any value of ε, $h_0(x) = x$, and h_ε is a topological equivalence between X_0 and X_ε for any $\varepsilon \in [0, \varepsilon_0]$, ε_0 sufficiently small.

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