

AGGREGATION AND EMERGENCE IN HIERARCHICALLY ORGANIZED SYSTEMS: POPULATION DYNAMICS

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ABSTRACT

The aim of this work is to present aggregation methods of hierarchically organized systems allowing one to replace the initial micro-system by a macro-system described by a few global variables. We also study the relations between the fast micro-dynamics and the slow macro-dynamics which can produce global properties. Emergence corresponds to a bottom-up coupling that is the result effected by a micro-level at a macro-level. As an example, we present prey-predator models with different time scales in a heterogeneous environment. A fast time scale is associated to the migration process on spatial patches and a slow time scale is associated to growth and interactions between the populations. Preys must go on spatial patches where resources are located and where predators can attack them. The efficiency of the predators to catch preys is patch dependent. Perturbation methods allow us to aggregate the initial system of differential equations for the patch sub-populations into a macro-system of two differential equations governing the total population densities. We study the case of density independent and density dependent migrations. In the latter case, we show that different functional responses can emerge in the macro prey-predator model as a result of the coupling between the slow and fast systems.

1. INTRODUCTION

Ecological systems are complicated in the sense that if one wants to describe them in details, their dynamics involve many variables and many parameters. Communities are sets of several interacting species. Individuals belong to different genotypes, phenotypes and age classes. They also can be grouped into different behavioral classes etc. As a consequence, a detailed description of ecological systems implies that we must deal with many variables and that it leads to large scale mathematical models, i.e. for example a system of many coupled Ordinary Differential Equations (ODE's). It is common to make computer simulations of these systems for very particular values of the parameters and initial conditions. However, these simulations represent only a particular situation.

Another way is to simplify the Ecological system by considering it from a global point of view. This leads to consider phenomenological macro-models involving few variables (for example the total density of a prey and its predator). The analysis of these systems can be performed by describing fixed points, their stability, existence of periodic solutions etc. These models are chosen for their simplicity. They represent the Ecological system at a macro-level as we preconceive it.

The approach from these two points of view differs. Ecological systems exhibits many facets and the mathematical models take into account particular aspects corresponding to a certain space and time window of observation. Our aim is to start with a detailed model involving many parameters and variables which describe the system at a micro-scale of observation. Then, we use aggregation and emergence methods to get a macro-model which describes the system at a macro-scale. For perfect aggregation, we refer to the works of Iwasa *et al.* (1987, 1989). Our particular method allows to derive a macro model which is an approximation of the micro-system. This aggregated macro-model corresponds to one aspect of the complex system.

We do not aim to get the real and unique model of an ecological system, rather we study the compatibility between local and global models. A particular choice of local dynamics at a micro scale leads to a global model at a macro scale. E.g., considering specific interactions between the individuals leads to a particular global prey predator model (such as a system of two ODE's for the total prey and predator densities) (as in the case of aggregative or repulsive behaviours between prey and predator individuals on different local spatial patches). Mainly, this problem is related to a change of level of observation,

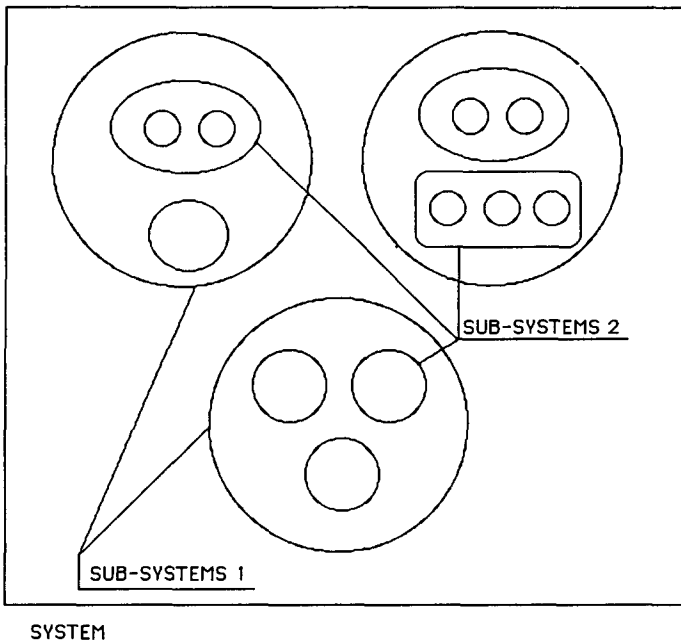


Fig. 1. Sub-division of a system into sub-systems 1 of first order, themselves sub-divided into smaller sub-systems 2 of second order etc. Individuals belongs to the sub-systems.

i.e. to a change of space and time scales. Local processes take place fast and small spatial ranges while global processes occur over longer times and longer distances.

The systems we consider are hierarchically organized in the sense that the system can be sub-divided into sub-systems. Figure 1 presents a simple representation of such a hierarchically organized systems whose importance has been recognized by many authors (Allen *et al.*, 1982; O'Neill *et al.*, 1986; Mesarovic *et al.*, 1976; Pattee, 1973; Simon, 1962, 1969; Whyte *et al.*, 1969). In our approach, the internal dynamics within each sub-systems takes place fast, it is the microdynamics (Auger, 1982, 1983, 1986, 1989, 1990). The interactions between the sub-systems which are weakly coupled correspond to the macrodynamics over longer times. The methods that we are going to recall briefly in the first section allows to aggregate the micro-system into a macro-system with few global variables. These methods also allow us to study the couplings between the different levels and, in particular, to look for emerging properties at a macro scale.

The next sections will be devoted to applications to population dynamics. We are studying the relationships between the individual migration behaviours of preys and predators on a set of discrete patches and between the overall growth and dynamics of their populations.

2. SYSTEMS OF ODE'S WITH DIFFERENT TIME SCALES

Now, we will give the main guidelines for the study of aggregation and emergence in dynamical systems. We present the method in the simplest way based on perturbation methods (Hoppensteadt, 1966; Nayfeh, 1966) and our contribution (Auger & Benoît, 1993). Another approach based on the centre manifold theorem can be found in Auger and Roussarie (1994) in which the aggregated model is a Taylor expansion of the small parameter.

2.1 The Micro-System

We consider a large model which we call the micro-system. But, we assume that it is structured into a certain number N of sub-systems. We assume that the inter sub-systems interactions are weak in comparison to intra sub-systems ones. The micro-system is a set of weakly coupled sub-systems. In the context of population dynamics, these sub-systems can be different sub-populations composed of individuals going on different spatial patches. The micro-system is described by a set of ordinary differential equations governing many variables which we call the micro-variables. Let N^α be the number of micro-variables associated to sub-system α , $\alpha \in [1, N]$. N is the number of sub-systems. 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 complicated model involving a lot of micro-variables and parameters.

Let i be the index for the micro-variables belonging to sub-systems 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 sub-population i belonging to population α , $i \in [1, \dots, N^\alpha]$. Consider the next system of ODE's written in the frame of singular perturbation theory, governing the micro-variables:

$$\varepsilon \frac{dn_i^\alpha}{dt} = f_i^\alpha(n^1, n^2, \dots, n^N) + \varepsilon \sum_{\beta=1}^N f_i^{\alpha\beta}(n^1, n^2, \dots, n^N), \quad (1)$$

with

$$n^\alpha = (n_1^\alpha, n_2^\alpha, \dots, n_{N^\alpha}^\alpha),$$

where

$$f_i^\alpha (n^1, n^2, \dots, n^N) = O(n^\alpha) \text{ and } f_i^{\alpha\beta} (n^1, n^2, \dots, n^N) = O(n^\alpha),$$

and where ϵ is a small parameter. At this stage, the different functions f_i^α and $f_i^{\alpha\beta}$ are not explicit.

2.2 A Quick Derivation of the Macro-System

For each sub-system, we make the following change of variables:

$$(n_1^\alpha, n_2^\alpha, \dots, n_{N^\alpha}^\alpha) \rightarrow (n^\alpha, n_2^\alpha, \dots, n_{N^\alpha}^\alpha) \tag{2}$$

where n^α is the total density of population α , $n^\alpha = \sum_i n_i^\alpha$ that we choose as global variables associated to each sub-system α . The macro-variables are assumed to be *first integrals* for the fast dynamics which is the case of the applications of the next sections. Thus, in (2) we keep for each sub-system $N^\alpha - 1$ fast equations for the variables $(n_2^\alpha, \dots, n_{N^\alpha}^\alpha)$ and the slow equation (second (3)) for the macro-variable n^α . The new system of equations can be written in the following form:

$$\begin{aligned} \epsilon \frac{dn_i^\alpha}{dt} &= f_i^\alpha(n^1, n^2, \dots, n^N) + \epsilon f_i^{\alpha\beta} (n^1, n^2, \dots, n^N), \quad i \in [2, N^\alpha] \\ \frac{dn^\alpha}{dt} &= \sum_{\beta=1}^N \sum_{i=1}^{N^\alpha} f_i^{\alpha\beta} (n^1, n^2, \dots, n^N), \end{aligned} \tag{3}$$

in which we omit the first N^α equation for sub-system α . Now, for simplicity, we assume that each fast system (4) obtained by neglecting the small inter sub-systems terms of (3):

$$\frac{dn_i^\alpha}{d\tau} = f_i^\alpha(n^1, n^2, \dots, n^N), \text{ where } \tau = \frac{t}{\epsilon} \tag{4}$$

has at least a unique globally stable equilibrium $n^{\alpha*} = (n_1^{\alpha*}, n_2^{\alpha*}, \dots, n_{N^\alpha}^{\alpha*})$ in the positive orthant. Each system (4) is conservative and n^α is the first integral of (4). This means that we assume an asymptotically stable point for each fast system. The eigenvalues associated to the linear parts of (4) at this equilibrium have negative real parts. In general, this equilibrium point is dependent on the first integrals (n^1, n^2, \dots, n^N) . This case corresponds to density dependence studied in applied sections. Thus, we write the fast equilibrium $n^{\alpha*}(n^1, n^2, \dots, n^N)$. After a short time, the fast part (4) almost reaches the equilibrium $n^{\alpha*}(n^1, n^2, \dots, n^N)$ and the macro-variables n^α are almost (with errors of order ϵ) solutions of the following aggregated macro-system:

$$\frac{dn^\alpha}{dt} = \sum_{\beta=1}^N \sum_{i=1}^{N^\alpha} f_i^{\alpha\beta} (n^{1*}(n^1, n^2, \dots, n^N), \dots, n^{N*}(n^1, n^2, \dots, n^N)). \tag{5}$$

It is useful to define new variables, the frequencies $v_i^\alpha(t)$ having a simple meaning. They represent the proportions of individuals in the different sub-populations i of each population α :

$$v_i^\alpha(t) = \frac{n_i^\alpha(t)}{n^\alpha(t)}. \quad (6)$$

A normalization relation holds. The sum of the frequencies equals 1 for each vector α :

$$v^\alpha = (v_1^\alpha, v_2^\alpha, \dots, v_{N^\alpha}^\alpha); \sum_{i=1}^{N^\alpha} v_i^\alpha = 1 \quad (7)$$

The stable equilibrium point can be expressed in terms of equilibrium frequencies $v^{\alpha^*}(n^1, n^2, \dots, n^N)$ of the fast system and of the macro-variable n^α :

$$n^{\alpha^*}(n^1, n^2, \dots, n^N) = n^\alpha \cdot v^{\alpha^*}(n^1, n^2, \dots, n^N). \quad (8)$$

The fast part of the micro-system reaches an equilibrium and the macro-system is simply obtained by substitution of this equilibrium in the equations for the macro-variables. The macro-system is a first order approximation of the micro-system and is given by the next relation:

$$\frac{dn^\alpha}{dt} = \sum_{\beta=1}^N \sum_{i=1}^{N^\alpha} f_i^{\alpha\beta} \left(n^1 v^{1^*}(n^1, n^2, \dots, n^N), \dots, n^N v^{N^*}(n^1, n^2, \dots, n^N) \right) \quad (9)$$

This system is the aggregated macro-model which governs the dynamics of the macro-variables. It is expressed in terms of the macro-variables themselves. This system depends only on the ε -perturbation terms of the micro-system and thus it varies at a slow time scale.

3. EMERGENCE OF GLOBAL PROPERTIES AT THE MACRO-LEVEL

Now, we are interested in the relation between the micro-model and the macro-model. In particular, we want to focus on the emergence of new global properties in the macro-model as a result of the connection between fast and slow dynamics. Indeed, the aggregation is not only useful because it reduces the dimension of the micro-system. The macro-model is not simply a copy obtained by approximation of the micro-model but, it can have new qualitative properties with respect to the micro-model. First, we study a case of a linear fast system. Then, we look at the more interesting case of a non-linear fast part.

3.1 Linear Fast System: Formal Equivalence Between Micro and Macro-Systems

A case of a linear fast system is found in a density independent migration described in section 4.2. When the functions f_i^α are linear, equilibrium frequencies v^{α^*} can be independent of (n^1, n^2, \dots, n^N) . This means that the equilibrium frequencies of the fast part of the micro-system are constants $v^{\alpha^*} = \text{constant}$. As shown by the derivation method of the macro-model, the macro-system is simply obtained by replacing the sub-populations n_i^α by $n^\alpha v^{\alpha^*}$ into functions $f_i^{\alpha\beta}$ of (9). The macro-system is then given by the following equations:

$$\frac{dn^\alpha}{dt} = \sum_{\beta=1}^N \sum_{i=1}^{N^\alpha} f_i^{\alpha\beta}(n^1 v^{1*}, \dots, n^{N^\alpha} v^{N^\alpha*}) = g_0^\alpha(n^1, n^2, \dots, n^N). \quad (10)$$

If the equilibrium frequencies are constant, it is obvious that the macro-system (10) is formally identical to the slow part of the micro-system (1). The functions g_0^α are of the same form for the macro-variables n^α as the functions $f_i^{\alpha\beta}$ are for the micro-variables n_i^α , because the substitution of the sub-populations n_i^α by $n^\alpha v^{\alpha*}$ into functions $f_i^{\alpha\beta}$ simply leads to replace the sub-populations n_i^α by n^α at some proportional constant terms. Consequently, the macro-model and the slow part of the micro-model have the same form. If functions $f_i^{\alpha\beta}$ are linear (resp. quadratic etc.) for the micro-variables, functions g_0^α are also linear (resp. quadratic etc.) for the macro-variables. No new terms occur in the macro-model in comparison to the perturbation terms of the micro-model (we say that there is no emergence). However, aggregation has been successful to reduce the dimension of the micro-system.

3.2 Emergence of Global Properties

When the fast functions f_i^α are nonlinear, then, in general the equilibrium frequencies $v^{\alpha*}$ are functions of the slow variables (n^1, \dots, n^N) , see section 4.2 (ii). The individual migration behaviour is different when there are many individuals or few individuals on each patch. This effect can result from aggregative or repulsive effects between individuals on each spatial patch. Regarding the fast migration model, it means that the migration rates are not constant any more but are now functions of the total populations (n^1, \dots, n^N) or even of the different patch sub-population densities. When the migration rates are not constant but depend on the macro-variables, the equilibrium frequencies are in general functions of the total population sizes. Thus, we must write $v^{\alpha*}(n^1, \dots, n^N)$. This has an important consequence for the macro-model. Indeed, the substitution of the sub-populations n_i^α by $n^\alpha v^{\alpha*}(n^1, \dots, n^N)$ into functions $f_i^{\alpha\beta}$ will now lead to a new macro-system (11):

$$\frac{dn^\alpha}{dt} = \sum_{i=1}^{N^\alpha} f_i^{\alpha\beta}(n^1 v^{1*}(n^1, \dots, n^N), \dots, n^{N^\alpha} v^{N^\alpha*}(n^1, \dots, n^N)) \quad (11)$$

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. For each set of values of the slow macro-variables, the fast system reaches a new equilibrium. This equilibrium is different for each set of macro-variables. This process induces an emergence of new terms in the approximated macro-system.

We say that there is emergence when the macro-model involves new and different formal terms with respect to the perturbation of the micro-model. The coupling between the fast local and the slow global dynamics leads to emergence of global properties in the macro-model. In this case, the macro-model is not a simple copy of the micro-model. Aggregation does not only reduce the dimension of a micro-system, but, it leads to a global model with new qualitative properties different from the perturbation properties of the micro system. In the next sections we shall illustrate aggregation and emergence by applying these general methods to population dynamics.

4. A TWO-PATCH PREY-PREDATOR MODEL

In this section, we consider two populations, the prey population 1 and its predator 2. Both prey and predator individuals can go on spatial patches. For example, the spatial patches are sites on which some resources or still refuges can be found. Preys go on the patches to feed. Predators also go on these patches to capture them. $n_j^\alpha(t)$ are the sub-population densities on patch j of population α . For general prey-predator models, we refer to Murray (1989) and Edelstein-Keshet (1988).

4.1 The Micro-Model

Prey Equation

To simplify, we shall discuss the case of two spatial patches 1 and 2. Patch 2 is a refuge and patch 1 is a resource patch. We assume that predators can only capture preys on patch 1. For predators, it is the hunting patch. Patch 1 is a common patch for preys and predators and patches 2 are refuges for preys and predators respectively. Now, we choose the set of differential equations for the prey sub-populations on the two patches:

$$\begin{aligned} \varepsilon \frac{dn_1^1}{dt} &= -k_{21}^1 n_1^1 + k_{12}^1 n_2^1 + \varepsilon \left(r_1^1 n_1^1 \left(1 - \frac{n_1^1}{K_1^1} \right) - b_1^{12} n_1^1 n_1^2 \right) \\ \varepsilon \frac{dn_2^1}{dt} &= -k_{12}^1 n_2^1 + k_{21}^1 n_1^1 + \varepsilon \left(r_2^1 n_2^1 \left(1 - \frac{n_2^1}{K_2^1} \right) \right) \end{aligned} \quad (12)$$

ε is a small parameter. k_{ij}^1 is the rate of patch change or migration rate from patch j to i for preys. The prey sub-populations grow logistically on each patch. r_i^1 is the prey growth rate on patch i . One may assume that r_1^1 is larger than r_2^1 which signifies that patch 1 is better than patch 2. Important resources necessary for the diets of preys are found on patch 1. Preys must go on this patch where predators can attack them. K_i^1 is the prey carrying capacity on patch i . If the predators get extinct, preys grow logistically on each patch i and reach K_i^1 . We assume a Lotka-Volterra predation term. Thus, we assume a quadratic predation term based on *random encounters* between preys and predators on patch 1. In this way, we consider that patch 1 is homogeneous and that the law of mass action holds for the prey-predator interaction. b_1^{12} is the predation rate on patch 1.

Predator Equation

For predators, we choose the following two differential equations for the patch sub-populations which also correspond to a generalization of the classical Lotka-Volterra model with two patches:

$$\begin{aligned} \varepsilon \frac{dn_1^2}{dt} &= -k_{21}^2 n_1^2 + k_{12}^2 n_2^2 + \varepsilon (-d_1^2 + c_1^{21} n_1^1) n_1^2, \\ \varepsilon \frac{dn_2^2}{dt} &= -k_{12}^2 n_2^2 + k_{21}^2 n_1^2 + \varepsilon (-d_2^2 n_2^2). \end{aligned} \quad (13)$$

Similarly, k_{ij}^2 is the migration rate from patch j to i for predators. d_i^2 is the death rate

of the predators on patch i . When predators do not capture preys, their population progressively gets extinct. c_1^{12} is a constant and positive predation parameter on patch 1. It is assumed to be proportional to the previous parameter b_1^{12} , corresponding to a rate of conversion of prey into predator biomass.

4.2 Equilibrium of the Fast Systems

Let us consider separately the fast part which describes how individual preys and predators migrate. This fast part is obtained when one neglects the perturbation in (12) and (13):

$$\begin{aligned}\frac{dn_1^1}{d\tau} &= -k_{21}^1 n_1^1 + k_{12}^1 n_2^1, \\ \frac{dn_2^1}{d\tau} &= -k_{12}^1 n_2^1 + k_{21}^1 n_1^1, \\ \frac{dn_1^2}{d\tau} &= -k_{21}^2 n_1^2 + k_{12}^2 n_2^2, \\ \frac{dn_2^2}{d\tau} &= -k_{12}^2 n_2^2 + k_{21}^2 n_1^2.\end{aligned}\tag{14}$$

This fast system describes the preys and predators patch dynamics. One can easily check that this fast system is conservative. The total populations n^1 and n^2 are constants of motion for this fast system. Migration does not vary the total population densities.

Now, two cases can occur:

- *Density independent migration*: Migration rates are constants (which is the case of a linear fast model).

- *Density dependent migration*: Migration rates are functions of the total prey and predator populations and (or) of patch sub-populations, (which is the case of a nonlinear fast model). In this case, individuals migrate in a different way when the size of the total population to which they belong is large or small. For example, individuals can have aggregative or repulsive behaviours. Preys can have a tendency to aggregate on rich patches. Predators can aggregate on a patch where preys are abundant. The two previous types of migrations will now be studied separately.

i) Density Independent Migration

This is the simplest case, at the fast equilibrium, simple relations (15) hold:

$$n_1^{1*} = \frac{k_{12}^1}{k_{21}^1} n_2^{1*} \quad \text{and} \quad n_1^{2*} = \frac{k_{12}^2}{k_{21}^2} n_2^{2*}\tag{15}$$

It is useful to consider preys and predators patch frequencies or proportions of individuals on the patches at the fast equilibrium which are the following ones:

$$\begin{aligned}
v_1^{1*} &= \frac{n_1^{1*}}{n^{1*}} = \frac{n_1^{1*}}{n_1^{1*} + n_2^{1*}} = \frac{k_{12}^1}{k_{12}^1 + k_{21}^1}, \\
v_2^{1*} &= \frac{n_2^{1*}}{n^{1*}} = \frac{n_2^{1*}}{n_1^{1*} + n_2^{1*}} = \frac{k_{21}^1}{k_{21}^1 + k_{12}^1}, \\
v_1^{2*} &= \frac{n_1^{2*}}{n^{2*}} = \frac{n_1^{2*}}{n_1^{2*} + n_2^{2*}} = \frac{k_{12}^2}{k_{12}^2 + k_{21}^2}, \\
v_2^{2*} &= \frac{n_2^{2*}}{n^{2*}} = \frac{n_2^{2*}}{n_1^{2*} + n_2^{2*}} = \frac{k_{21}^2}{k_{12}^2 + k_{21}^2}.
\end{aligned} \tag{16}$$

Consequently, when the migration rates k_{ij}^α are constants which corresponds to a density independent migration, the equilibrium frequencies are also constant. Then the macro-model is obtained by substitution of this fast equilibrium in the equations describing the dynamics of the aggregated variables (quick derivation method). In this density dependent case, the aggregated model is formally identical to the ε -perturbation of the micro-model (see section 3.3 i).

ii) Density Dependent Migration

The density dependent case is much more interesting. Still, two cases can be distinguished, a total density dependent case and a sub-population density dependent case:

- The first simple case occurs when the migration rates k_{ij}^α are only functions of the total populations n^1 and n^2 and not of the sub-populations densities.
- A second and more general case occurs when the migration rates k_{ij}^α are also functions of the sub-populations densities n_i^1 and n_i^2 .

The first case remains simple because the total populations are constants of motion for the fast system (first integrals). For the fast system, the total populations are constants. The fast equilibrium are parametrized by the constants n^1 and n^2 . As a consequence, the equilibrium frequencies are still given by equations (16) but, the k -parameters are now density dependent $k_{ij}^\alpha(n^1, n^2)$, i.e. functions of the total populations. Then, the equilibrium frequencies which are obtained by substitution of expressions $k_{ij}^\alpha(n^1, n^2)$ in equations (16) also are density dependent, i.e. are functions of the type $v_k^{\alpha*}(n^1, n^2)$. The substitution of these density dependent frequencies into the aggregated model (11) does emerge a new aggregated model.

The sub-population density dependent case is more general and complicated. It corresponds to the case when migration rates are functions not only of the total densities but also of the sub-populations, i.e. $k_{ij}^\alpha(n_1^1, n_2^1, n_1^2, n_2^2)$. As a consequence, it is then necessary to look for a fixed point of the fast system which is now composed of two equations (17):

$$\begin{aligned}
 -k_{21}^1(n_1^1, n_2^1, n_1^2, n_2^2)n_1^1 + k_{12}^1(n_1^1, n_2^1, n_1^2, n_2^2)n_2^1 &= 0, \\
 -k_{21}^2(n_1^1, n_2^1, n_1^2, n_2^2)n_1^2 + k_{12}^2(n_1^1, n_2^1, n_1^2, n_2^2)n_2^2 &= 0.
 \end{aligned}
 \tag{17}$$

System (17) is reduced into system (18) of two variables only by taking into account that n^1 and n^2 are first integrals. Thus, $(n^1 - n_1^1)$ and $(n^2 - n_2^1)$ are substituted to n_1^2 and n_2^2 respectively:

$$\begin{aligned}
 -k_{21}^1(n_1^1, n_1^2, n_1^1, n^2)n_1^1 + k_{12}^1(n_1^1, n_1^2, n_1^1, n^2)(n^1 - n_1^1) &= 0, \\
 -k_{21}^2(n_1^1, n_1^2, n_1^1, n^2)n_1^2 + k_{12}^2(n_1^1, n_1^2, n_1^1, n^2)(n^2 - n_2^1) &= 0.
 \end{aligned}
 \tag{18}$$

In general, system (18) has several solutions, corresponding to several steady states. We assume at least one particular solution which corresponds to a fixed point of system (18) in the positive orthant for a certain range of the constants n^1 and n^2 :

$$n_1^{1*}(n^1, n^2), n_2^{1*}(n^1, n^2), n_1^{2*}(n^1, n^2), n_2^{2*}(n^1, n^2).
 \tag{19}$$

Equilibrium patch frequencies are then obtained:

$$v_1^{1*}(n^1, n^2) = \frac{n_1^{1*}(n^1, n^2)}{n_1^{1*}(n^1, n^2) + n_2^{1*}(n^1, n^2)}; \quad v_1^{2*}(n^1, n^2) = \frac{n_1^{2*}(n^1, n^2)}{n_1^{2*}(n^1, n^2) + n_2^{2*}(n^1, n^2)}
 \tag{20}$$

$$v_2^{1*}(n^1, n^2) = 1 - v_1^{1*}(n^1, n^2); \quad v_2^{2*}(n^1, n^2) = 1 - v_1^{2*}(n^1, n^2).$$

It follows that the equilibrium frequencies are also functions of the total population sizes n^1 and n^2 . Equations (20) show that equilibrium frequencies are total density dependent. Moreover, according to the different types of migrations rates (that is to the different types of functions $k_{ij}^\alpha(n_1^1, n_2^1, n_1^2, n_2^2)$), one can obtain many different types of equilibrium frequencies.

4.3. Obtaining the Macro-Model and the Functional Response

i) Density Independent Case

When the migration rates are constant, the aggregated system is obtained by the quick derivation method and is given by the following set of differential equations:

$$\frac{dn^1}{dt} = r^1 n^1 \left(1 - \frac{n^1}{K^1} \right) - a^{12} n^1 n^2,
 \tag{21}$$

$$\frac{dn^2}{dt} = -d^2 n^2 + a^{21} n^1 n^2.$$

Parameters of (21) are given in terms of equilibrium prey and predator patch frequencies:

$$r^1 = r_1^1 v_1^{1*} + r_2^1 v_2^{1*} \quad \text{and} \quad \frac{r^1}{K^1} = \left(\frac{r_1^1 (v_1^{1*})^2}{K_1^1} + \frac{r_2^1 (v_2^{1*})^2}{K_2^1} \right), \quad (22)$$

$$d^2 = d_1^2 v_1^{2*} + d_2^2 v_2^{2*},$$

$$a^{12} = b_1^{12} v_1^{1*} v_1^{2*} \quad \text{and} \quad a^{21} = c_1^{21} v_1^{1*} v_1^{2*},$$

r^1 is a global growth rate for preys. K^1 is the global carrying capacity of preys. d^2 is a global death rate for predators. a^{12} and a^{21} are global prey-predator parameters which depend on the proportions of preys and predators on the different patches at equilibrium. In the density independent case, the prey and predator equations are *formally identical* to the slow part of the micro-system (12) and (13), which is the ϵ -perturbation. Local predation terms on each patch are quadratic. Global predation terms are also quadratic terms (i.e. products of the total prey and predator densities). The law of mass action which holds on each patch also holds for the total populations. The global capture term is formally identical to the capture term on patch 1 which is proportional to the product of the prey and predator densities on this patch, i.e. $n_1^1 n_1^2$. The functional response FR is defined as the number of preys eaten per predator and per unit time. In the density independent case, the corresponding global functional response in (22) is the Lotka-Volterra one, $FR = a^{12} n^1$.

The Lotka-Volterra functional response is a very simple one and can be criticized for several reasons. In particular, there is no saturation effect concerning the predator appetite. The number of preys captured per predator and per unit time is proportional to the total prey density. Thus, when the prey density n^1 is large, a single predator would be able to eat a very large number of preys without any saturation of its appetite, which is unrealistic. As a consequence, many other functional responses have been proposed. Now we shall see that in the density dependent case, some different FR can be reobtained when one assumes particular types of density dependent migrations.

ii) density dependent case

In this section, we consider density dependent migration behaviours of preys and predators. We shall discuss the influence of the type of density dependence on the functional response which is obtained in the aggregated model. For example, we can assume repulsive or aggregative behaviours between individuals on some patches. Preys can avoid to aggregate on certain patch because they would be easily detected and captured by predators. On the contrary, preys can aggregate to form groups to be better protected against attacks of predators. Predators can aggregate on rich patches where many preys are available. Different prey and predator density dependent migration processes can be considered, and as we shall see, can lead to various functional responses.

Holling function

In this subsection, we shall obtain the Holling functional response (Murray, 1989). For this, we assume constant migration rates for preys leading to constant prey equilibrium frequencies. In contrast, we assume that predators have a migration behaviour which is prey density dependent. We assume that predators leave patch 1 (on which preys can be

captured) when the prey density is large. At large prey densities, predators easily capture preys and consequently do not spend a long time on this patch. Predators bring back captured preys to their own refuge 2 for example to feed and to take care of the juveniles. One can also assume that they capture and eat preys on patch 1 and that they come back to the refuge when their appetite is satisfied. We make the following choice of migration rates of predators depending on the prey density:

$$k_{21}^2 = a_{21}^2 n_1^1 \text{ and } k_{12}^2 = \text{constant}, \tag{23}$$

in which a_{21}^2 is a constant positive parameter. k_{21}^2 is the migration rate from patch 1 to the refuge and is proportional to the prey sub-population on patch 1. When preys are abundant on the hunting patch, predators easily capture them. Thus, they leave this patch rapidly to go back to the refuge. A constant migration rate from the refuge to the hunting patch is also assumed. Under these assumptions, the equilibrium patch frequencies are the following ones:

$$\text{Preys: } v_1^{1*} = \frac{k_{12}^1}{k_{12}^1 + k_{21}^1} = \text{constant}; v_2^{1*} = \frac{k_{21}^1}{k_{12}^1 + k_{21}^1} = \text{constant} \tag{24}$$

$$\text{Predators: } v_1^{2*} = \frac{k_{12}^2}{k_{12}^2 + a_{21}^2 v_1^{1*} n^1}; v_2^{2*} = \frac{a_{21}^2 v_1^{1*} n^1}{k_{12}^2 + a_{21}^2 v_1^{1*} n^1}$$

As a consequence, we obtain total density dependent equilibrium patch frequencies of predators. When n^1 is close to zero, v_1^{2*} is nearly equal to 1, i.e. predators spend most of their time to find preys which are rare and need a long time for capture. When $n^1 \gg 1$, v_1^{2*} tends to 0. Predators spend a short time on the hunting patch because preys are very many and thus easy to capture. Similarly, when n^1 is close to 0, v_2^{2*} is almost 0 and when $n^1 \gg 1$, v_2^{2*} is close to 1. In this particular case, the substitution of the previous density dependent frequencies in the aggregated model (21) with parameters (22) leads to the following prey equation:

$$\frac{dn^1}{dt} = r^1 n^1 \left(1 - \frac{n^1}{K^1} \right) - b_1^{12} v_1^{1*} \frac{k_{12}^2 n^1 n^2}{k_{12}^2 + a_{21}^2 v_1^{1*} n^1}, \tag{25}$$

or else
$$\frac{dn^1}{dt} = r^1 n^1 \left(1 - \frac{n^1}{K^1} \right) - \frac{kn^1 n^2}{D + n^1}.$$

This equation exhibits a saturation effect described by Holling. The functional response FR is given by the next relation and the parameters of the model are given by (26):

$$FR = \frac{kn^1}{D + n^1} \tag{26}$$

$$D = \frac{k_{12}^2}{a_{21}^2 v_1^{1*}} \text{ and } k = \frac{b_1^{12} k_{12}^2}{a_{21}^2}.$$

This functional response of the aggregated prey equation exhibits a saturation effect and is *formally different* from the functional response on patch 1 which is a Lotka-Volterra

quadratic one. The saturation effect is the result of the particular density-dependent migration process of predators. Predators adapt their density on the hunting patch with respect to the available density of preys. The global functional response is not a Lotka-Volterra one but a Holling one. Relationships (26) are also of interest because they establish links between the individual and the population levels.

Ratio-dependent functional responses

The main result of the ratio dependent theory is that functional responses not only depend on the prey density, but also on the predator density and their ratio (Arditi & Ginzburg, 1989; Arditi *et al.*, 1991; Hanski, 1991). This means that the functional response must be a function g of the general form:

$$FR = g(n^1/n^2) \quad \text{or else} \quad FR = g(n^1/(n^2)^m), \quad (27)$$

where m is a positive parameter in the interval $[0,1]$. When $m = 1$, it is a pure ratio dependent FR . When $m = 0$, the FR is not ratio-dependent. Intermediate values of m correspond to different degrees of ratio-dependence. Now, let us propose a density dependent migration model which allows a ratio dependent FR . Assume the following prey migration rates:

$$k_{12}^1 = \alpha \frac{n_1^1}{n_2^1} \quad \text{and} \quad k_{21}^1 = \beta n_1^1, \quad (28)$$

α and β are positive parameters. k_{12}^1 is the migration rate from the refuge to the resource patch which depends on the ratio of prey densities at the resource patch and at the refuge. The interpretation can be the following. Preys have a tendency to aggregate on patch 1 where some food source has been found by some preys. When the proportion of preys on patch 1 is becoming larger, more preys get the information of available food and migrate to this patch. When food is available on patch 1, preys detect it and go more frequently to this patch to exploit it.

k_{21}^1 is the migration rate in the inverse direction assumed proportional to n_1^1 . On the contrary, this is a repulsive effect between preys on the resource patch. When the density of preys is large on the vulnerable patch, more preys leave this patch and return to the refuge. One can assume that large densities of preys are easily detected by searching predators and that preys tend to decrease their density on the dangerous patch to avoid predators.

A simple calculation shows that the equilibrium patch frequencies for the preys are density dependent and are given by the following relations:

$$v_1^{1*} = \frac{\alpha}{\beta n^1} \quad \text{and} \quad v_2^{1*} = 1 - v_1^{1*}, \quad n^1 > \frac{\alpha}{\beta}. \quad (29)$$

The last inequality in (29) describes that a frequency larger than 1 is never reached. We assume that n^1 is larger than this minimum density. In our model of migration, the prey density is maintained at a constant level $n_1^{1*} = v_1^{1*} n^1 = \frac{\alpha}{\beta}$ on patch 1. Thus, this fast migration model corresponds to a process of regulation of the prey density on the patch where they can be captured. It can be regarded as a protective effect against predators mostly sensible to large prey densities.

The global functional response is given by the following expression:

$$FR(n^1, n^2) = b_1^{12} v_1^{1*} v_1^{2*} n^1 = k v_1^{2*} (n^1, n^2), \text{ where } k = \frac{\alpha}{\beta} b_1^{12}. \tag{30}$$

The global functional response FR is proportional to v_1^{2*} . Consequently, in order to obtain a ratio dependent FR , patch 1 predator frequency at equilibrium also must be ratio dependent such as:

$$v_1^{2*} (n^1, n^2) = \frac{\gamma n^1}{(n^2)^m}, \text{ where } \gamma \text{ is a positive constant.} \tag{31}$$

Relation (31) can be obtained with appropriate total density dependent migration rates for predators:

$$k_{12}^2 = B n^1, \quad k_{21}^2 = C (n^2)^m, \tag{32}$$

where B and C are positive constant parameters. We can give the following interpretation. Predators are attracted by preys and go more frequently on patch 1 when the prey density is large. At the same time, the migration rate from the hunting patch to the refuge is proportional to $(n^2)^m$. Predators leave more frequently patch 1 when their density is large. Predators do not aggregate on the hunting patch to avoid overcrowding by negative interactions between them. Under these assumptions, one gets the following equilibrium patch frequencies for predators:

$$v_1^{2*} = \frac{\delta \cdot n^1}{(n^2)^m} \quad \text{and} \quad v_2^{2*} = \frac{1}{1 + \frac{\delta \cdot n^1}{(n^2)^m}}, \tag{33}$$

with $\delta = \frac{B}{C}$. Then, one obtains the following ratio dependent FR:

$$FR = k' \frac{\frac{n^1}{(n^2)^m}}{1 + \frac{\delta \cdot n^1}{(n^2)^m}}, \tag{34}$$

where $k' = k \delta$. One can summarize the whole process as follows. Preys maintain a constant density on patch 1. Predators go more on patch 1 when the prey density is large and leave it more frequently when the predator density is large. When $m = 1$, one obtains a pure ratio dependent FR:

$$FR = k' \frac{\frac{n^1}{n^2}}{1 + \frac{\delta \cdot n^1}{n^2}}, \tag{35}$$

However, we can criticize the particular choice of migration rates (32) because we have considered functions of the total densities and not of the patch densities. Nevertheless, migration is assumed to take place fast and thus it is acceptable to imagine that preys and

predators which frequently change patches can make an estimate of the total densities of the populations. Another choice also leading to the pure ratio dependent FR can be made:

$$k_{12}^2 = B \left(\frac{n_1}{n_2} \right), \quad k_{21}^2 = C, \quad (36)$$

In this case, predators leave the hunting patch at a constant rate. But, the proportion of preys per predator in the refuge determines the rate at which predators go to patch 1. $\left(\frac{n_1}{n_2} \right)$ represents the number of preys available per predator which can leave the refuge to patch 1. It is an estimate of the potential gain for a predator leaving its refuge to go on a patch to catch preys. Model (36) assumes that predators can make such an estimate. As they frequently move from one patch to another, they experience captures and would have the ability to estimate potential gains for moving.

Thus, several choices of migration rates can lead to the same type of *FR*. The choice of the migration strategy in order to obtain a particular *FR* is not unique. However, aggregation determines the *FR* associated to a particular individual behaviour for migration in a unique way.

5. CONCLUSION

The last section 3 of this article constitutes an interpretation of some functional responses on the basis of a scenario of fast migration of predators. A large variety of attack rates have been proposed in many prey-predator models. This work shows that it may be possible to give interpretations of this "zoology" of different models in terms of the individual behaviour of preys and predators. However, our method may be useful in the inverse way, that is assuming a particular individual migration behaviour and use the aggregation method to derive the global corresponding prey predator model and its associated functional response.

In this contribution, we have focused our attention on the functional response. However, equations (21) and (22) show that emerging properties occur not only in the prey equation but also in the predator equation. Even more, not only the predation part but also the growth part of the prey equation can be changed accordingly to the different types of density dependent migrations. Consequently, there is no doubt that the use of realistic migration rules for preys and predators can lead to many different types of aggregated prey-predator models. Most of these models may be different from the classical phenomenological models that are commonly used. Thus, we can imagine that a new generation of global prey predator models can be developed from the study of aggregation.

To conclude, we mention that this general method of modelling aggregation and emergence phenomena can be applied for several other cases of population dynamics. For example, it can be used in the fast game dynamics. It can also be used to study hierarchically organized communities.

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