Review / Revue

Methods of aggregation of variables in population dynamics

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Abstract – In ecology, we are faced with modelling complex systems involving many variables corresponding to interacting populations structured in different compartmental classes, ages and spatial patches. Models that incorporate such a variety of aspects would lead to systems of equations with many variables and parameters. Mathematical analysis of these models would, in general, be impossible. In many real cases, the dynamics of the system corresponds to two or more time scales. For example, individual decisions can be rapid in comparison to growth of the populations. In that case, it is possible to perform aggregation methods that allow one to build a reduced model that governs the dynamics of a lower dimensional system, at a slow time scale. In this article, we present a review of aggregation methods for time continuous systems as well as for discrete models. We also present applications in population dynamics. A first example concerns a continuous time model of a single population distributed on a system of two connected patches (a logistic source and a sink), by fast migration. It is shown that under a certain condition, the total equilibrium population can be larger than the carrying capacity of the logistic source. A second example concerns a discrete model of a population distributed on two patches, still a source and a sink, connected by fast migration. The use of aggregation methods permits us to conclude that density-dependent migration can stabilize the total population. © 2000 Académie des sciences/Éditions scientifiques et médicales Elsevier SAS

approximate aggregation of variables / population dynamics / time scales / dynamical systems / source–sink models

Résumé – Méthodes d'agrégation de variables en dynamique de population. En écologie, nous sommes confrontés à la modélisation de systèmes complexes mettant en jeu un grand nombre de variables correspondant à des populations structurées en différentes classes d'âge, de comportement ou encore distribuées spatialement sur des sites. Un modèle qui prendrait en compte un tel niveau de détail dans la structure des populations serait composé d'un système d'équations comportant un grand nombre de variables et de paramètres. L'analyse mathématique d'un tel modèle serait en général impossible. Cependant, dans certains cas, la dynamique du système correspond à différentes échelles de temps. Par exemple, les décisions individuelles peuvent être rapides en comparaison de la croissance des populations. Dans ce cas, il est possible d'utiliser la méthode d'agrégation des variables qui permet de construire un modèle réduit gouvernant la dynamique d'un système de faible dimension à une échelle de temps lente. Dans cet article, nous présentons une revue des méthodes d'agrégation

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pour les modèles en temps continu et en temps discret. Nous proposons également des applications en dynamique de populations. Un premier exemple concerne un modèle en temps continu d'une population distribuée sur deux sites (une source avec croissance logistique et un puits) connectés par des migrations se déroulant à une échelle de temps rapide. Nous montrons que, sous certaines conditions, l'effectif total de la population à l'équilibre peut être supérieur à celui de la source isolée. Un second exemple concerne un modèle en temps discret d'une population encore distribuée sur un système puits–source avec des migrations rapides. La méthode d'agrégation permet de montrer que la densité dépendance des taux de migration peut stabiliser la population totale à l'équilibre. © 2000 Académie des sciences/Éditions scientifiques et médicales Elsevier SAS

agrégation de variables par approximation / dynamique de population / échelles de temps / systèmes dynamiques / modèles puits–source

Version abrégée

Dans cette contribution, nous présentons une revue des articles portant sur les méthodes d'agrégation des variables et sur leurs applications en dynamique de population. Dans le domaine de la dynamique des communautés et des populations, une tendance actuelle consiste à prendre en compte les structures internes des populations. Une communauté est un ensemble de plusieurs populations en interaction, elles-mêmes subdivisées en des sous-populations distribuées spatialement sur des sites ou encore correspondant à des classes d'âge ou de comportement. La prise en compte d'un niveau de description détaillé en dynamique de population conduit alors à des modèles mathématiques pouvant comporter de nombreuses variables d'état. L'étude analytique de tels modèles est en général impossible et bien souvent l'étude se réduit à des simulations numériques sur ordinateur.

Cependant, les systèmes écologiques sont composés de plusieurs niveaux d'organisation. En général, les niveaux de l'individu, de la population et de la communauté sont pris en compte. À ces niveaux d'organisation correspondent des échelles spatio-temporelles différentes. En effet, les décisions individuelles concernent typiquement une échelle de temps de l'ordre de la journée, les croissances des populations sont annuelles et les évolutions des structures des communautés peuvent se faire sur des durées encore beaucoup plus longues.

La prise en compte d'échelles de temps différentes dans un modèle de dynamique de population permet dans certains cas de réduire la dimension du système dynamique. Cette opération s'appelle une agrégation de variables. À partir du modèle mathématique initial comportant de nombreuses variables d'état, il est possible de tirer parti de l'existence d'échelles de temps différentes afin d'obtenir un modèle mathématique réduit gouvernant la dynamique de quelques variables globales. Ce modèle agrégé est un nouveau modèle obtenu par des méthodes d'approximation dont la

dynamique est très proche de celle du modèle complexe initial. L'approximation consiste à supposer que les processus rapides atteignent un équilibre qui doit être stable. Le modèle réduit présente parfois l'avantage de pouvoir être étudié de manière analytique, ce qui permet alors d'obtenir des résultats généraux sur la dynamique.

Dans cet article, nous présentons une revue des modèles mathématiques pour lesquels les méthodes d'agrégation de variables ont été développées, les systèmes d'équations différentielles ordinaires et les systèmes discrets. Nous présentons également deux applications nouvelles en dynamique de population. Dans les deux cas, il s'agit d'une population distribuée sur deux sites, un puits (un site défavorable où la population ne peut survivre) et une source (un site favorable) connectés par des migrations. Le modèle initial décrit la dynamique des deux sous-populations sur les sites. Nous faisons l'hypothèse que la dynamique de migration se produit à une échelle de temps plus rapide que la dynamique de croissance des sous-populations sur chaque site. L'agrégation de variables permet d'obtenir un modèle mathématique gouvernant une seule variable, la population totale des deux sites.

Le premier exemple concerne un modèle en temps continu. Nous montrons que, sous certaines conditions, la population totale tend vers un équilibre qui peut être supérieur, c'est-à-dire avec un effectif plus élevé, que celui de la sous-population sur le site favorable. La connection d'une source avec un puits par un processus de migration rapide peut ainsi favoriser le développement global de la population totale.

Le second exemple concerne un modèle en temps discret. Dans ce cas, nous étudions la dynamique d'une population distribuée sur un système puits–source. Dans le cas de migrations à taux constants, selon les cas, la population s'éteint ou bien croît sans limites. Nous étudions ensuite l'effet d'une migration densité dépendante sur la croissance globale de la population. Dans le cas d'une migration de la source vers le puits dont le taux augmente avec l'effectif des individus sur

la source, l'effectif global de la population peut être stabilisé et tendre vers un équilibre. Cet exemple illustre ainsi comment les comportements individuels rapides peuvent émerger au niveau de la population.

1. Introduction

A first generation of mathematical models in ecology and in population dynamics has provided simple models involving a small number of state variables and parameters. The time continuous prey–predator Lotka–Volterra models as well as the discrete host–parasite Nicholson–Bailey models are classic examples, see Edelstein-Keshet [1] and Murray [2]. In such models, the state variables are often chosen as the population numbers and the model is a system of non-linear coupled ODEs or discrete equations that describe the time variation of the interacting populations. The next step in ecological modelling is to consider more and more detailed models. Populations must not be considered as homogeneous in the sense that all individuals are identical but structured in sub-groups corresponding to different ages or stages, compartmental classes, or still distributed geographically on patches connected by migrations.

Incorporating more details in the models is necessary to advance towards a more realistic description of ecological systems. Against a detailed description of systems is the fact that models become more complex, involving an increasing number of variables and parameters, and so making them impossible to study mathematically. For this reason, it is important to find which details are really relevant and must be incorporated in a model. An important goal of ecological modelling is thus to describe tractable models. Slow–fast models and perturbation methods permit some simplifications, see Muratori and Rinaldi [3] and Rinaldi and Muratori [4, 5].

In this article, we focus on a method of aggregation of variables. The main goal is to reduce the dimension of the mathematical model to be handled analytically. In general, the aggregation of a system consists in defining a small number of global variables, functions of its state variables, and a system describing their dynamics. When the aggregated dynamics are consistent with the original dynamics in the sense that the global variables behave identically both in the initial system and in the aggregated one, it is called perfect aggregation, see Iwasa et al. [6]. Perfect aggregation is rarely possible and methods for approximate aggregation have been developed, see Iwasa et al. [7], and also Levin and Pacala [8] and Pacala and Levin [9]. By approximate aggregation we mean the kind of aggregation where the consistency between the dynamics of the global variables in the original and the aggregated system is only approximate.

In this article, we consider approximate aggregation methods that are based on the existence of different time scales. This approximate aggregation is closer to the perfect aggregation as the ratio between time scales grows. It is common in ecology to consider different ecological

levels of organization, the individual, population, community and ecosystem levels. In general, different characteristic time scales are associated with these levels of organization. For example, a fast time scale corresponds to individual processes and a slow one to demographic ones. It is possible to take advantage of these two time scales in order to reduce the dimension of the initial complete model and to build a simplified system that describes the dynamics of a small number of global variables. In this article, we focus on approximate aggregation methods and we shall refer to a series of papers by P. Auger and a group of co-workers.

In section 2 we present a review of aggregation methods for time continuous models. Section 3 does the same for discrete models. Sections 4 and 5 present applications of aggregation methods for a population distributed on two spatial patches connected by fast migrations in continuous and discrete time contexts, respectively. In both examples, aggregation allows us to derive an equation that governs the time evolution of the total population at the slow time scale.

2. Review of aggregation methods for time continuous models

We study a general case of a population that can be partitioned into several classes or sub-populations. Let $n_i(t)$ be the number of individuals of class i at time t, $i = 1,... N$. We assume that different processes occur at two different time scales. A fast process corresponds to the changes of classes of individuals and a slow process corresponds to the internal dynamics of each class. Under these general assumptions, the dynamics of the state variables can be written in a general form as follows:

$$\varepsilon \frac{dn_i}{dt} = f_i(n_1,...,n_N) + \varepsilon g_i(n_i), \quad \varepsilon > 0, i = 1,...,N \quad (1)$$

where the function $f_i(n_1,...,n_N)$ relates to the fast dynamics and are functions of all state variables. Functions $g_i(n_i)$ relate to the slow dynamics and only depend on the corresponding state variable. It is usual to define a fast time scale in comparison to the slow time scale t, such as $\tau = \frac{t}{\varepsilon}$ which allows one to rewrite the previous system, called the complete system, as follows:

$$\frac{dn_i}{d\tau} = f_i(n_1,...,n_N) + \varepsilon g_i(n_i), \quad \varepsilon > 0, i = 1,...,N \quad (2)$$

In order to proceed to aggregation, we need to define a global variable. The global variable depends on the N state variables. Furthermore, we need this global variable

to be constant of motion for the fast dynamics. In this section, we choose the most usual global variable, the sum of all state variables:

$$n(t) = \sum_{i=1}^{N} n_i(t) \qquad (3)$$

In that case, the condition for the global variable to be constant at the fast time scale is the following one:

$$\sum_{i=1}^{N} f_i(n_1,...,n_N) = 0 \qquad (4)$$

The next step consists in calculating the fast equilibrium. The fast equilibrium is obtained by neglecting the small terms of the order of ε of the previous complete system and by looking for solutions for which the velocity is equal to zero:

$$\begin{cases} f_i(n_1,...,n_N) = 0, \ i = 1,...,N \\ \sum_{i=1}^{N} n_i = n \end{cases} \qquad (5)$$

The previous system may have several different solutions or no solution. Let us assume that there exists one solution which is an asymptotically stable equilibrium of system

$$\frac{dn_i}{d\tau} = f_i(n_1,...,n_N), \ i = 1,...,N$$

when considered on the manifold

$$\sum_{i=1}^{N} n_i = n$$

This asymptotic stability condition is necessary to perform aggregation. The fast equilibrium is noted by an upper star and obviously verifies

$$f_i\left(n_1^*,...,n_{N-1}^*, n - \sum_{i=1}^{N-1} n_i^*\right) = 0, \quad i = 1,..., N$$

As a consequence, the fast equilibrium is a function of the global variable n and we denote its co-ordinates $(n_1^*(n),...,n_N^*(n))$.

The next step consists in adding the N equations of the initial complete system (1) and substituting the previously calculated fast equilibrium as a function of n for the variables n_i in equation (1) to arrive at (6):

$$\frac{dn}{dt} = \sum_{i=1}^{N} g_i(n_1^*(n),...,n_N^*(n)) + O(\varepsilon) \qquad (6)$$

This equation governs the global variable n and is the so-called aggregated model. This aggregated model is an approximation of the initial complete model. It is obtained as a Taylor expansion with respect to the powers of the small parameter $\varepsilon > 0$. The first term of the series is a good approximation of the real dynamics of the complete system when the two following conditions hold:

- system $\frac{dn}{dt} = \sum_{i=1}^{N} g_i(n_1^*(n),...,n_N^*(n))$ is structurally stable, see Auger and Roussarie [10], and Poggiale [11];
- the small parameter $\varepsilon > 0$ is small enough.

In the case of an aggregated equation that is not structurally stable, it is necessary to calculate the next term of the Taylor expansion with respect to the small parameter ε in order to approximate the real dynamics. We refer to Auger and Poggiale [12] where the calculation of further terms of the series is made and applied to the study of a concrete example. Here, we assume that the aggregated model is structurally stable, and thus the first term of the series is a good approximation of the real dynamics of the global variable.

By aggregating, we have reduced the dimension of the model from N to 1. Indeed, the dimension of the initial complete model is N which is the number of initial state variables while the dimension of the aggregated model is 1 because we have considered a single global variable. In general, the mathematical analysis of the initial complete model is impossible because it involves too many variables and equations. But, the mathematical analysis of the aggregated equation may be possible by studying only the first term of the series, higher order terms being neglected.

Aggregation not only provides a reduction of the dimension of the initial model and its simplification, but it also provides interesting information about the emergence of fast processes at a global level in the long run. Indeed, although the aggregated equation does not depend explicitly on the functions $f_i(n_1,...,n_N)$, $i = 1,...,N$, of the fast dynamics, the fast equilibrium points depend on the choice of these functions. Different functions f_i have different fast equilibrium points $(n_1^*(n),...,n_N^*(n))$. Remember that to aggregate, the fast equilibrium is substituted into the equations of the complete system. Consequently, in general, different fast models lead to different aggregated equations. Thus, the aggregation method provides a tool for studying the effects of different types of fast dynamics on the slow dynamics of a global variable.

It is also important to note that in general there is not uniqueness of the aggregated model. In the case of different asymptotically stable fast equilibrium points, each one having its own basin of attraction, we obtain a different aggregated equation for each of them. Thus, in general, we do not have a single aggregated model but a family of aggregated models, each of them associated to a different fast equilibrium point. The aggregated model describing approximately the dynamics of the general system finally depends on the initial conditions which are attracted to only one of the fast equilibrium points.

Aggregation methods have been developed in more general contexts than the one presented in this article.

- Aggregation methods can be performed for more than a single global variable and we refer to Auger [13] for general methods and applications.

- Aggregation can be used for global variables that are not just the sum of initial state variables but that can be non-linear combinations of them (Auger and Poggiale [14]).
- Aggregation methods can be used in cases of fast cyclic variations of initial state variables, for example for a fast limit cycle (Poggiale and Auger [15]).
- Aggregation can be used in some cases of infinite dimensional dynamical systems, for example PDEs (Arino et al. [16, 17], Bravo et al. [18]).

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

- modelling a trout fish population in an arborescent river network composed of patches connected by fast migrations (Charles et al. [19, 20]);
- studying the effects of different individual decisions on the global dynamics of a prey–predator system in an heterogeneous environment composed of patches connected by fast migrations (Auger and Benoît [21], Auger and Poggiale [12], Auger et al. [22], Bernstein et al. [23], Chiorino et al. [24], Morand et al. [25], Michalski et al. [26], Poggiale et al. [27]);
- modelling a sole larvae population with a continuous age with fast migration between different spatial patches (Arino et al. [17], Bravo et al. [18]);
- modelling the influence of different individual strategies on the dynamics of a population or of two competing populations using fast game dynamics (Auger and Pontier [28], Sánchez et al. [29], Auger et al. [30]);
- modelling food chain structures (Kooi et al. [31]).

3. Review of aggregation methods for discrete models

We now suppose a population, whose evolution is described in discrete time, which is classified into groups according to any characteristic of its life cycle or its environment. We consider the population subdivided into N sub-populations (or groups). We will denote by $n_i(t)$ the density of sub-population i at time t, with $i = 1, 2,..., N$ and $t = 0,1,2,...$ In order to describe the population at time t we will use the vector $\mathbf{n}(t) = (n_1(t),...,n_N(t))^T \in \mathbb{R}^N$, where T denotes transposition.

In the evolution of the population we will consider two processes whose corresponding characteristic time scales, and consequently their projection intervals, that is their time units, are very different from each other. In order to take account of both time scales we will model these two processes, to which we will refer as the fast and the slow dynamics, by two different matrices. We will choose as the projection interval for our model that corresponding to the slow dynamics, i.e. the time elapsed between times t and $t + 1$ is the projection interval of the slow dynamics.

In principle, we will make no special assumptions regarding the characteristic features of the slow dynamics.

Thus, for a certain fixed projection interval the slow dynamics will be represented by a non-negative projection matrix $\mathbf{L} = (l_{ij})_{1 \le i,j \le N} \in \mathbb{R}^{N \times N}$, which in this context is usually referred to as a Leftkovitch matrix. Each entry l_{ij} represents the average number of individuals transferred to sub-population i per individual in sub-population j per unit of time.

As far as the fast dynamics is concerned, we will make the following assumptions.

a) The fast dynamics will be represented by a non-negative matrix $\mathbf{P} = (p_{ij})_{1 \le i,j \le N} \in \mathbb{R}^{N \times N}$.

b) There exists a fixed and sufficiently large time span which makes possible the transference of individuals from every sub-population to any other including itself. This is a common feature in the modelling of biological systems (see Caswell [36]). In technical terms, this is equivalent to the condition that matrix $\mathbf{P}$ is primitive.

c) The total population does not, by means of the fast dynamics, asymptotically decay to zero or grow to infinity, i.e. the dominant eigenvalue of $\mathbf{P}$ is equal to one. This assumption has a clear biological justification. Indeed, if the dominant eigenvalue of $\mathbf{P}$ were smaller or greater than one then, if the separation between the two time scales is sufficiently high, the fast process would lead the total population of this group to zero or infinity, respectively, before the slow process has time to act. In that case, the dynamics of the general system would be controlled by the fast process alone, and the distinction of two processes in the evolution of the system would be unnecessary.

As mentioned above , the projection interval of the model is that corresponding to matrix $\mathbf{L}$. We then need to approximate the effect of the fast dynamics over a time interval much longer than its projection interval. In order to do so we will suppose that during each projection interval corresponding to the slow process matrix $\mathbf{P}$ has operated a number k of times, where k is an integer large enough that can be interpreted as the ratio between the projection intervals corresponding to the slow and fast dynamics. Therefore, the fast dynamics is included in the system as $\mathbf{P}^k$ and the proposed model reads as follows:

$$\mathbf{n}(t + 1) = \mathbf{L}\mathbf{P}^k \mathbf{n}(t) \tag{7}$$

The fact that $\mathbf{P}$ is primitive implies that 1 is its strictly dominant eigenvalue. Let us choose $\mathbf{v} = (v_1,...,v_N)$ and $\mathbf{u} = (u,...,u_N)$ right and left eigenvectors of $\mathbf{P}$ associated to eigenvalue 1, which verify that they are both positive, the components of $\mathbf{v}$ add up to one, $v_1 +...+v_N = 1$ and the scalar product of $\mathbf{v}$ and $\mathbf{u}$ is 1,

$$\mathbf{u}^T \mathbf{v} = u_1 v_1 + \cdots + u_N v_N = 1$$

If the fast dynamics was the only one acting on the population, a stable distribution among the sub-populations would be attained. This stable structure is represented by $\mathbf{v}$. The entries of vector $\mathbf{u}$ are interpreted as the relative reproductive values of the sub-populations and we use them to define the global variable of the

aggregated system. We denote $n(t)$ this global variable which is defined as follows:

$$n(t) = \mathbf{u}^T \mathbf{n}(t) = \sum_{i=1}^{N} u_i n_i(t)$$

it can be interpreted as a total reproductive value of the entire population. It is straightforward that $n(t)$ is an invariant for the fast dynamics, $\mathbf{u}^T \mathbf{Pn}(t) = \mathbf{u}^T \mathbf{n}(t)$.

To proceed to aggregate system (7) we suppose that fast dynamics has acted for a long enough time to be at the equilibrium structure described by vector $\mathbf{v}$. This is equivalent to substituting in system (7) variables $n_i(t)$ for $v_i n(t)$, i.e. $\mathbf{n}(t)$ for $\mathbf{v}n(t)$. Using this substitution and multiplying both sides of system by $\mathbf{u}^T$ yields the aggregated system

$$n(t+1) = \mathbf{u}^T \mathbf{Lv}n(t) \qquad (8)$$

which is a scalar difference equation.

If $\mathbf{L}$ and $\mathbf{P}$ are constant matrices both the general and the aggregated systems are linear. The aggregated system is a scalar linear difference equation whose solutions are of the form $n(t) = (\mathbf{u}^T \mathbf{Lv})^t n_0$, n_0 being any initial condition. If the positive number $\lambda = \mathbf{u}^T \mathbf{Lv}$ is > 1 then solutions grow geometrically while if $\lambda < 1$ they decay exponentially to 0. In Sanz and Bravo de la Parra [39], see also Sánchez et al. [42], it is proved that the dominant eigenvalue of matrix $\mathbf{LP}^k$ can be expressed as $\lambda + o(\alpha^k)$, for $\alpha < 1$, which means that the larger k is, the more alike the full system and the aggregated one behave asymptotically. With the same meaning it is also proved that the right eigenvector of matrix $\mathbf{LP}^k$ can be expressed as $\mathbf{Lv} + o(\alpha^k)$ and the left eigenvector as $\mathbf{u} + o(\alpha^k)$.

In Bravo de la Parra et al. [35] the case is developed where the fast dynamics is dependent on the global variable. To be specific, the fast dynamics is represented by a stochastic matrix, $\mathbf{P}(n)$, dependent upon the population global density. A stochastic matrix is a positive matrix whose columns add up to 1, and it is the appropriate kind of matrix to represent a migration process, where the total number of individuals in the population is kept constant. In that case we have

$$n(t) = \sum_{i=1}^{N} n_i(t)$$

as the global variable, vector $\mathbf{u}$ is constant; in fact we could choose it to be $(1,...,1) \in \mathbb{R}^N$, and then vector $\mathbf{v}(n)$ represents the equilibrium proportions established by the fast process for a population of global size n. The general system, $\mathbf{n}(t+1) = \mathbf{LP}^k(\mathbf{n}(t))\mathbf{n}(t)$, is non-linear as well as the aggregated system, $n(t+1) = \mathbf{u}^T \mathbf{Lv}(\mathbf{n}(t))\mathbf{n}(t)$, which becomes a non-linear scalar difference equation. If there exists a fixed point, n^*, of the aggregated system and the absolute value of $\left| \frac{d}{dn}(\mathbf{u}^T \mathbf{Lv}(n)n) \right|_{n=n^*}$ is less than 1, then, for k sufficiently large, there exists an asymptotically stable fixed point, $\mathbf{n}^*$, of the general system which can be expressed as $\mathbf{Lv}n^* + o(\alpha^k)$, $o(\alpha^k)$ having the same meaning as before.
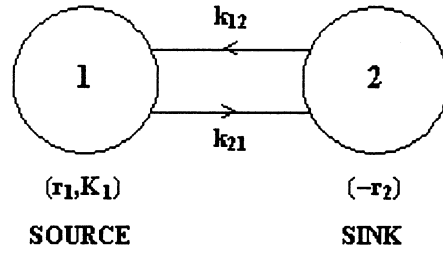

Figure 1. Schema of a system of two spatial patches connected by migrations.

The previous results, presented in the case of one population divided into sub-populations, are easily extended, see [35, 39, 42], to the case of p populations each one divided into N_i, $i = 1,..., p$, sub-populations. Thus, the general system has $N = N_1 + \cdots + N_p$ variables while the corresponding aggregated system has p only. The linear case has been extended to non-autonomous and stochastic systems in Sanz [37] and Sanz and Bravo de la Parra [38, 40, 41].

It is also possible to build the general system using as time unit the projection interval of the fast dynamics, see Sánchez et al. [42], Bravo de la Parra et al. [32, 33] and Bravo de la Parra and Sánchez [34]. In that case the general system becomes $\mathbf{n}(t+1) = (\mathbf{I} - \varepsilon(\mathbf{L} - \mathbf{I}))\mathbf{Pn}(t)$, where $\mathbf{I}$ is the identity matrix and ε a positive small number reflecting the ratio between slow and fast time scales. The associated aggregated system is still (8).

4. A time continuous model for the study of the global growth of a population distributed on two patches with fast migration

We consider a population of individuals that can live on two spatial patches, a sink and a logistic source. Let $n_1(t)$ and $n_2(t)$ be the numbers of individuals on patch 1 (the source) and patch 2 (the sink), respectively. We assume that individuals can migrate from patch 1 to patch 2 and that migration is faster than demography on each patch. k_{12} (resp. k_{21}) is the migration rate from patch 2 (resp. 1) to patch 1 (resp. 2). *Figure 1* shows a schematic representation of a system of two connected patches.

The following system of differential equations describes the dynamics of the two variables:

$$\varepsilon \frac{dn_1}{ddt} = (k_{12} n_2 - k_{21} n_1) + \varepsilon r_1 n_1 \left(1 - \frac{n_1}{K_1}\right)$$

$$\varepsilon \frac{dn_2}{dt} = (k_{21} n_1 - k_{12} n_2) - \varepsilon r_2 n_2 \qquad (9)$$

where r_1 is the growth rate and K_1 the carrying capacity on patch 1. r_2 is the mortality rate on patch 2. $0 < \varepsilon < 1$ is a

small parameter. Using the fast time scale $\tau = \frac{t}{\varepsilon}$ allows one to rewrite the previous system as follows:

$$\frac{dn_1}{d\tau} = (k_{12} n_2 - k_{21} n_1) + \varepsilon r_1 n_1 \left(1 - \frac{n_1}{K_1}\right)$$

$$\frac{dn_2}{d\tau} = (k_{21} n_1 - k_{12} n_2) + \varepsilon r_2 n_2$$

In that form, it is clear that migration is going on at the fast time scale τ and that demography corresponds to comparatively small terms that are of the order of the small parameter ε. The aggregation method will now be used in order to obtain an equation that governs a global variable which is the total population $n(t) = n_1(t) + n_2(t)$. At first, we must look for the fast equilibrium of the previous system, which can be calculated by neglecting the small terms of the order of ε and by considering that the velocity is equal to zero. This leads to the following system of two equations:

$$\begin{cases} k_{12} n_2 = k_{21} n_1 \\ n = n_1 + n_2 \end{cases}$$

which can be solved with respect to the variable n. We denote the fast equilibrium with a upper star as follows:

$$n_1^* = \frac{k_{12}}{k_{12} + k_{21}} n \quad \text{and} \quad n_2^* = \frac{k_{21}}{k_{12} + k_{21}} n$$

It can be easily shown that this fast equilibrium is asymptotically stable. The next step consists in obtaining the aggregated equation that governs the total population. For this, we insert the previous fast equilibrium in the full system (9) and then add up both equations. The aggregated model reads as follows:

$$\frac{dn}{dt} = \left(r_1 \frac{k_{12}}{k_{12} + k_{21}} - r_2 \frac{k_{21}}{k_{12} + k_{21}}\right) n - \frac{r_1}{K_1}$$
$$\left(\frac{k_{12}}{k_{12} + k_{21}}\right)^2 n^2 + O(\varepsilon) \qquad (10)$$

The last equation (10) for $\varepsilon = 0$ is structurally stable except in the case $r_1 k_{12} = r_2 k_{21}$. So, for small enough $\varepsilon > 0$, it is a good approximation of the real dynamics of the global variable n. Two cases must be considered.

4.1. Extinction of the total population

First, let us assume that the following condition holds: $r_1 k_{12} < r_2 k_{21}$.

In that case, it is obvious that the two terms of the sum occurring in the aggregated equation are negative for $n > 0$. Consequently, any solution with initial condition $n(0) > 0$ is decreasing tending to 0, which means that the population is always becoming extinct.

4.2. Logistic growth of the total population

Now, let us assume that the unequal sign is reversed: $r_1 k_{12} > r_2 k_{21}$.

The aggregated equation, for $\varepsilon = 0$, can be rewritten in a logistic form as follows:

$$\frac{dn}{dt} = rn\left(1 - \frac{n}{K}\right)$$

where the total growth rate r is:

$$r = \left(\frac{1}{k_{12} + k_{21}}\right)(r_1 k_{12} - r_2 k_{21})$$

and the total carrying capacity K is:

$$K = K_1 \left(\frac{k_{12} + k_{21}}{k_{12}}\right)\left(1 - \frac{r_2}{r_1}\frac{k_{21}}{k_{12}}\right)$$

Both the total growth rate r and the total carrying capacity K are positive. Thus, the aggregated equation is a classical logistic equation. 0 and K are the two equilibrium points. 0 is unstable and K is globally asymptotically stable for positive initial conditions. An interesting situation can occur when the total carrying capacity K is larger than the local carrying capacity K_1 of patch 1, the source. A simple calculation shows that this is possible when

$$\left(\frac{k_{12} + k_{21}}{k_{12}}\right)\left(1 - \frac{r_2}{r_1}\frac{k_{21}}{k_{12}}\right) > 1$$

holds.

By defining two parameters $\alpha = \frac{k_{21}}{k_{12}}$ and $\beta = \frac{r_2}{r_1}$, the previous condition becomes $\beta(1 + \alpha) < 1$, and the conditions for extinction and logistic growth, respectively, $1 < \alpha\beta$ and $\alpha\beta < 1$.

Figure 2 shows the domain of the parameter plane (α, β) within which these conditions hold. From a biological point of view, the case of logistic growth with $K > K_1$ is an interesting situation. Indeed, the patch with logistic growth is coupled to a sink on which individuals die. However, the total carrying capacity for the system of two patches is larger than the carrying capacity of patch 1. At first, one may think that the connection of the source patch with a sink patch would maintain the total population at a lower equilibrium than in the case of an isolated source uncoupled to the sink. Our study demonstrates that it is not always the case. Indeed, two processes act at the same time:

• the migration flow from the source to the sink provokes an extra mortality of individuals on the sink;

• the migration flow from the source to the sink also provokes a decrease in the number of individuals on the source leaving the source for the sink but in turn it favours the growth of the population on the source.

These two effects play in opposite directions. The second one favours the growth of the total population contrary to the first one. As a consequence, one can find a domain of the parameters (α, β) in which the total equilibrium number of individuals is larger than the source carrying capacity.
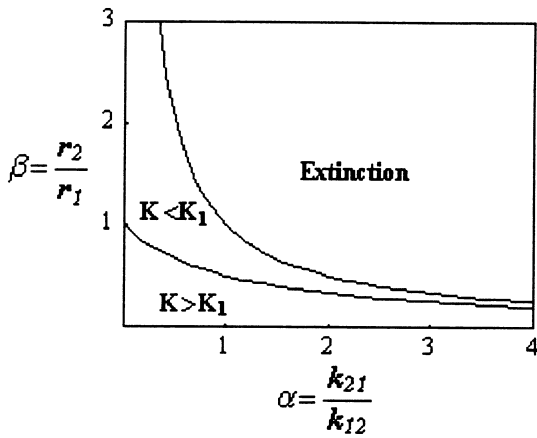
Figure 2. Domain of the parameters plane (α, β) corresponding to three cases: extinction, logistic growth ($K < K_1$) and ($K > K_1$).

5. A discrete model for the study of the influence of density-dependent migration on the growth of a population distributed on two patches

In this section, we consider a population that can be distributed on two spatial patches, a source (patch 1) and a sink (patch 2). In a discrete model, growth rates are positive but larger than 1 for the source, $r_1 > 1$, and smaller than 1 for the sink, $0 < r_2 < 1$. We assume that a proportion f_1 of individuals (resp. f_2) can migrate from patch 1 to patch 2 (resp. from patch 2 to patch 1) in the time interval $[t, t+1]$. Migration is assumed to be fast in comparison to demography. *Figure 3* shows a schema of the processes involved in the model.

Let $n_1(t)$ and $n_2(t)$ be population densities on the two patches at time t. According to these assumptions, the model reads:

$$\begin{pmatrix} n_1(t+1) \\ n_2(t+1) \end{pmatrix} = \begin{pmatrix} r_1 & 0 \\ 0 & r_2 \end{pmatrix} \begin{pmatrix} 1-f_1 & f_2 \\ f_1 & 1-f_2 \end{pmatrix}^k \begin{pmatrix} n_1(t) \\ n_2(t) \end{pmatrix}$$
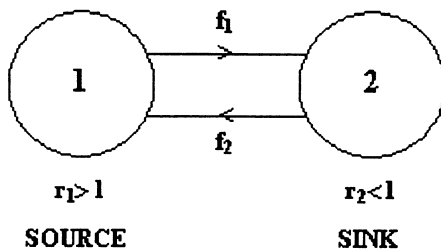
(11)

Figure 3. Schema of a system of two spatial patches connected by migrations.

where k is an integer assumed to be high, $k \gg 1$. Between two time steps, migration acts k times while growth only once. This discrete model can be rewritten in a more condensed form as described in section (3), $\mathbf{n}(t+1) = \mathbf{LP}^k \mathbf{n}(t)$, where

$$\mathbf{L} = \begin{pmatrix} r_1 & 0 \\ 0 & r_2 \end{pmatrix} \quad \text{and} \quad \mathbf{P} = \begin{pmatrix} 1-f_1 & f_2 \\ f_1 & 1-f_2 \end{pmatrix}$$

$\mathbf{L}$ is the growth matrix and $\mathbf{P}$ the migration matrix. We shall consider two cases.

5.1. Constant proportions of migrants

In that case, the stable structure vector $\mathbf{v} = (v_1, v_2)$ must verify

$$-f_1 v_1 + f_2 v_2 = 0 \quad \text{and} \quad v_1 + v_2 = 1$$

so $\mathbf{v} = \left(\dfrac{f_2}{f_1 + f_2}, \dfrac{f_1}{f_1 + f_2} \right)$. As $\mathbf{P}$ is a stochastic matrix we have $\mathbf{u} = (1,1)$, the global variable $n(t)$ is $n_1(t) + n_2(t)$, that is, the total population, and the aggregated linear equation is:

$$n(t+1) = \left(\frac{r_1 f_2 + r_2 f_1}{f_1 + f_2} \right) n(t) = r n(t) \qquad (12)$$

The total growth rate r is positive and is always smaller than r_1. This means that the total growth rate of the system of a source coupled to a sink cannot have a growth rate larger than the one of the source. Furthermore, the total growth rate r can be either larger than 1 (the total population grows) or smaller than 1 (the total population decays). The result depends on the comparison of two ratios, the migration rates ratio, $\dfrac{f_1}{f_2}$, and the ratio of the positive differences between growth rates and 1, $\dfrac{r_1 - 1}{1 - r_2}$. The condition to have a growing total population is the following:

$$\frac{f_1}{f_2} < \frac{r_1 - 1}{1 - r_2}$$

5.2. Density-dependent proportion of migrants

In this section, we assume that the proportion of migrants from the source to the sink is an increasing function of the total density, $f_1(n) = \dfrac{n}{n + \alpha}$, where α is a positive constant. Then, we can calculate

$$\mathbf{v}(n) = \left(\frac{f_2(n+\alpha)n}{n + f_2(n+\alpha)}, \frac{n^2}{n + f_2(n+\alpha)} \right)$$

In that case, the aggregated equation reads:

$$n(t+1) = \left(\frac{(r_1 f_2 + r_2)n(t) + \alpha r_1 f_2}{(1+f_2)n(t) + \alpha f_2} \right) n(t) = f(n(t))$$
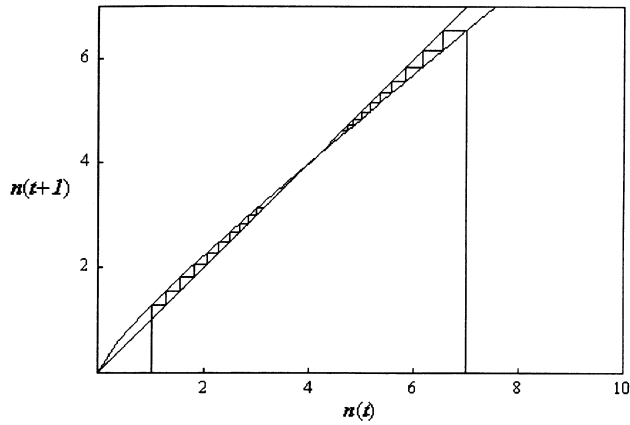
(13)

Figure 4. Cobweb graph of equation (13) with particular values: $r_1 = 1.8$, $r_2 = 0.64$, $f_2 = 0.2$ and $\alpha = 5$.

The aggregated equation is non-linear. This equation has two fixed points, the origin and a non-trivial fixed point:

$$n^* = \frac{\alpha f_2 (r_1 - 1)}{f_2 (1 - r_1) + 1 - r_2}$$

The origin is always unstable, $f'(0) = r_1 > 1$. The relevant case for the non-trivial fixed point is when it becomes positive. The condition on the parameter values for $n^* > 0$ to hold is

$$\frac{1}{f_2} > \frac{r_1 - 1}{1 - r_2}$$

and in that case n^* is globally asymptotically stable. From the results in section (3) we can conclude that the general system possesses an asymptotically stable equilibrium n^* very close (depending on k) to

$$\mathbf{Lv}(n^*)\, n^*$$

Figure 4 shows a numerical simulation, a cobweb graph, of the last case.

6. Conclusion

In this article, we have presented a review of methods of aggregation of variables for continuous and discrete systems. We have also given two original examples in population dynamics corresponding to both kinds of models. These simple examples clearly show how aggregation methods can be used in concrete applications. The first example of section 4 has shown that even in the case of a linear fast model, aggregation can lead to non-trivial results. Indeed, aggregating a system of two spatial patches, a source and a sink, with fast migration, we have obtained a system that can have a global carrying capacity which can be larger than the one of the source patch. This result is in a certain sense unexpected a priori because the

source patch is coupled to a sink patch which induces an extra mortality for the population. Thus, one may expect that the global system reaches a lower equilibrium than in the case of an isolated source patch. This work has demonstrated that under certain conditions, the opposite conclusion can be obtained. The second example of section 5 has shown that density-dependent migrations can make emerge different global dynamics where the total population stabilizes.

Incorporation of different types of internal structures of populations, such as for example age, behaviour and spatial distribution, leads to more and more complex models involving an increasing number of variables and parameters. Aggregation methods are useful tools for simplifying the kind of complex systems we are faced with in ecological modelling. Aggregating a complex system allows one to obtain a reduced version of the model which is a good approximation of the real system. This reduced system can in general be more easily studied than the initial complete model because it involves a lower number of global variables and parameters.

Until now, aggregation methods have been used for deterministic models. In the future, an important problem to be studied will be to demonstrate that aggregation methods can also be performed for stochastic models. Interesting applications arise when considering models including demographic or environmental stochasticity.

Several new applications must also be developed in the future. The aggregation method is particularly suited for the study of spatially distributed populations in a network of patches connected by migrations. Aggregation allows one to obtain a system of equations governing the dynamics of the total population. The method was applied to a trout fish population in a river network represented as an arborescent set of patches. Aggregation could also be applied to other concrete cases, such as fish population dynamics in a lake that could be represented as a set of connected patches of different types, with gravel, sand, or still rocks. According to the age and the period of the year, fishes distribute differently among the patches. Aggregation could provide information about the global population dynamics in the long term according to different types of environments which would correspond to different patches and connections between them.

Aggregation methods are also very useful for the study of the influence of different behaviours on the global dynamics of populations. We had studied the effects of aggressive behaviour of individuals on the global equilibrium of a domestic cat population [28]. An interesting work that we intend to carry out in the future will be to study the effects of aggressive or co-operative behaviour of predators on the stability of a global prey–predator system. An important goal of ecology is to understand how the individual behaviour can influence the dynamics of the population and the structure of the community. In that matter, methods of aggregation of variables are useful tools because they allow us to simplify a full model involving individual and population dynamics, and to obtain a

reduced model that can be sometimes solved analytically. As different fast dynamics in general lead to different aggregated models, it is possible to understand how a change of individual behaviour emerges at the population and community levels.

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