

Aggregation and emergence in ecological modelling: integration of ecological levels

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Abstract

Modelling ecological systems implies to take into account different ecological levels: the individual, population, community and ecosystem levels. Two large families of models can be distinguished among different approaches: (i) completely detailed models involving many variables and parameters; (ii) more simple models involving only few state variables. The first class of models are usually more realistic including many details as for example the internal structure of the population. Nevertheless, the mathematical analysis is not always possible and only computer simulations can be performed. The second class of models can mathematically be analysed, but they sometimes neglect some details and remain unrealistic. We present here a review of aggregation methods, which can be seen as a compromise between these two previous modelling approaches. They are applicable for models involving two levels of organisation and the corresponding time scales. The most detailed level of description is usually associated to a fast time scale, while the coarser one rather corresponds to a slow time scale. A detailed model is thus considered at the individual level, containing many micro-variables and consisting of two parts: a fast and a slow one. Aggregation methods allow then to reduce the dimension of the initial dynamical system to an aggregated one governing few global variables evolving at the slow time scale. We focus our attention on the emerging properties of individual behaviours at the population and community levels. © 2000 Elsevier Science B.V. All rights reserved.

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1. Modelling ecological systems: state of the art with a special emphasis on integrating the ecological levels

In ecological modelling, one must roughly con-

sider three ecological levels: the individual, the population and the community-ecosystem levels. The dynamics of an ecological system entails the co-evolution of the three levels, and it seems necessary to develop methods for integrating the different ecological levels.

This implies for example incorporating the individual behaviour in population dynamics models. A first attempt was made in the field of statistical

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physics, with the early work of Kerner (1972), who noted that Lotka–Volterra equations are conservative and can be rewritten as a Hamiltonian system. The consequence is that a set of many interacting species obeying Lotka–Volterra dynamics can be regarded as a Gibbs ensemble. Thus, it is possible to obtain functions expressing the probability that a population density belongs to a given interval ($n, n + dn$). Unfortunately, such an approach can only be used for an even number of interacting species, and the fact that the Lotka–Volterra model is not structurally stable (Arrowsmith and Place, 1992, p. 185), can cause problems.

A similar approach can be found in Demetrius (1983) for discrete time models describing the dynamics of age-structured populations by use of Leslie matrix models. The population entropy is calculated, based on the assumption that ecological systems tend to maximise it.

The physics representation to integrate the biological levels is justified and has been widely investigated. In particular, mean field theory has been used to describe random motion of individuals in space and to obtain general spatial patterns (Levin and Pacala, 1997). The moment closure method is also powerful in providing moments of different orders, for spatially distributed populations, average density, variance.... This method was applied to species competing for space (Pacala and Levin, 1997; Gandhi et al., 1998).

A rather similar point of view is considered in structural dynamical models (Jorgensen, 1986). A global index, the exergy, allows to determine the set of connections between the different compartments of a system that maximise the exergy function. The maximum of exergy corresponds to a network adapted to the actual environmental conditions.

Likewise, slow–fast models are widely used in ecological modelling. The main reason is from the presence, in ecological systems, of significantly different orders of magnitude (of the parameters as well as the variables). Slow–fast models are good tools for reducing the dimension of dynamical systems and have been used for example to

model food chains (Kooi et al., 1998) or various ecological systems (Rinaldi and Muratori, 1992a,b; Muratori and Rinaldi, 1992; Rinaldi et al., 1996; De Feo and Rinaldi, 1998).

The complexity of a system of ordinary differential equations is not easy to define. Ecological systems are considered complex systems. Indeed, an ecosystem is a set of a large number of interacting species in a fluctuating environment. Real ecosystems and communities exhibit complex graphs of interactions between the species. Cohen et al. (1990) give many real examples of community structures showing complex networks of connected interacting populations (see also Logofet, 1993). Species are also composed of individuals with different ages. Individuals do many activities such as looking for resources of different types, taking care of the juveniles and so forth. Thus, to be realistic, each population should be divided into sub-populations, corresponding to ages, behavioural strategies associated to phenotypes, individual states (ill or safe), etc.

On the other hand, individuals can move between different spatial patches to feed or to defend territories. Physical conditions of the environment fluctuating with seasons (often randomly) also have a strong influence on the dynamics of the populations and the community. Thus, in order to take into account all these aspects in the dynamics of a community at all levels, we should consider a complicated model involving many variables, that is a great number of degrees of freedom and parameters. Such ‘big models’ are very difficult to handle, and only computer simulations can be performed. Moreover, sensitivity to initial conditions and to parameter values is in general unknown, and the model only provides computed time series for each variable that correspond to a particular set of conditions.

Nevertheless, ‘big models’ of ecosystems have been considered and studied. The book by Deanigelis (1992) shows many examples of models for ecosystems and communities. These models are already a schematic representation of the real ecosystem, although many compartments are considered for biomass. They can be numerically

simulated and they provide interesting results that can be compared to real observed time series.

A contrary approach in ecological modelling is to build models involving only few variables. The prototype of such models is the classical Lotka–Volterra model and all related models in which a few number of variables are considered, as for example the total density of preys and predators (Murray, 1989; Edelstein-Keshet, 1988). Such simple models can be analysed and results can mathematically be proved, such as the existence of equilibrium points, periodic solutions... But, they are often too simple and not realistic enough to be of interest for biologists, who consider them as a caricature of the real ecological system.

Aggregation methods are a compromise between big models and simple ones. They can be performed when the system involves different time scales, a fast one at the individual level and a slow one at the population or the community level. At the most microscopic level (for example, the individual level), one considers a complicated detailed model involving many state variables and parameters. Then, by taking advantage of the two time scales, it is possible to build up, by aggregating some variables, a reduced model involving only a few global variables, varying at a slow time scale, and describing the dynamics at the population or community level.

In this article, we present a review of aggregation methods that are devoted to the reduction of the dimension of dynamical systems. We shall also present an example of aggregation of variables in population dynamics. This example relates to a prey–predator model in a heterogeneous environment of interconnected patches. This model investigates the effect of individual decisions of preys to leave a patch where predators can attack them, on the global stability of the community in the long run. For simplicity, the model is applied to the case of two patches, but could easily be implemented for a large set of connected spatial patches organised in a complex network.

2. Aggregation and emergence in ecology

One of the major problems in modelling of ecological systems is a result of the fact that many variables are involved in the evolution of such systems and cannot be omitted without an important loss of information. Many variables and parameters seem necessary to describe the dynamics of a given system, and it is difficult to decide about the level of detail which is really relevant. However, one would need rigorous methods for detecting which variables are really relevant for the description of the system, and which ones can be neglected.

This is the problem of size reduction, usually dealt with by qualitative considerations, based on assumed properties of the system. In rare advents, reduction will be justified by mathematical reasoning and computations. Aggregation consists of extracting, from an initial micro-system, a small macro-model (or aggregated model) governing a few global variables. The main goal of such a technique is to obtain an aggregated system simpler and easier to handle analytically than the original one.

Perfect aggregation is the name given to the simplest case, when a lower dimension dynamical system can be associated to the original one, and accordingly each solution of the original system is associated—in some functional way—to a solution of the aggregated one. Examples of perfect aggregation in ecology can be found in Iwasa et al. (1987), as in the case of modelling an age-structured population. Iwasa et al. (1987) studied the conditions that are necessary to perform perfect aggregation. Perfect aggregation supposes very particular values of the parameters. Note also that Gard (1988) has given perfect aggregation methods for stochastic models.

As perfect aggregation is generally not possible, it is very useful to investigate a more general aggregation. This may be called ‘approximate aggregation’ as opposed to ‘perfect aggregation’. Starting with a complex differential system, the aim is to construct a simpler system, solutions of which approximate the solutions of the initial system. The problem is: how to build a macro-model from an initial micro-model such that the

solutions of both systems are not in functional relationship but a sort of approximate relationship can be demonstrated. For example, one might 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 Iwasa et al. (1989) for more details.

3. Emergence of global properties at the macro-level

Variable aggregation methods in dynamical systems with different time scales take advantage of the existence of these different time scales associated to the ecological levels in order to simplify a complex model. Aggregation methods have been widely performed for continuous time models (Auger and Roussarie, 1994; Auger and Poggiale, 1996, 1998), as well as for time discrete models (Bravo de la Parra et al., 1997; Bravo de la Parra and Sanchez, 1998). A special issue in Mathematical and Computer Modelling (1998) was devoted to aggregation techniques and their applications to population dynamics (Antonelli and Auger, 1998).

A micro-system is structured into a certain number N of subsystems. In this way, we can regard this system as hierarchically organised (Auger, 1989; O'Neill et al., 1986). The micro-system is described by a set of ordinary differential equations (ODE) governing many variables called the micro-variables.

Let i be the index for the micro-variables belonging to the subsystem α . 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 . The micro-system reads then as follows:

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

with $n^\alpha = (n_1^\alpha, n_2^\alpha, \dots, n_N^\alpha)$ and ε a small parameter ($\varepsilon < 1$). Functions f_i^α and F_i^α correspond respectively to fast and slow processes.

One can build up an aggregated model (refer to Auger and Benoît (1993), Poggiale (1994), Auger and Roussarie (1994) for more details) at the slow time scale t , governing a few global variables that are for example the total populations of each sub-system:

$$n^\alpha = \sum_i n_i^\alpha$$

$$\frac{dn^\alpha}{dt} = \sum_{i=1}^{N^\alpha} F_i^\alpha(v_1^{1*} n^1, v_2^{1*} n^1, \dots, v_1^{2*} n^2, \dots, v_1^{N^*} n^N, \dots) \quad (2)$$

in which $v_i^{\alpha*} = n_i^{\alpha*}/n^\alpha$ represents the individual proportions in each sub-population at the fast equilibrium (denoted by a star subscript).

The dynamics of the aggregated model (2) is a good approximation of the dynamics of the micro-model (1), as it can be proved that the error is of order ε .

The aggregation method is not only useful because it reduces the dimension and the complexity of the micro-system. It is also interesting, as it makes new global properties emerge for the dynamics at the macro-level.

We shall now discuss coupling effects between the slow dynamics corresponding to the aggregated system and the fast dynamics corresponding to the sub-population system. At the fast time scale, the frequencies tend to a stable equilibrium.

- When the fast model is linear, the frequencies tend to constant values (Auger and Poggiale, 1996). However, a change in the parameter values of the fast model modifies the equilibrium frequencies $v_i^{\alpha*}$. This in turn changes the parameters of the aggregated model, as if for example individuals select a new behaviour. Jorgensen (1999) proposes a similar process about the change of parameter sets adapted to a change of environmental conditions.
- When the fast functions f_i^α are non-linear, the equilibrium frequencies $v_i^{\alpha*}$ are generally functions of the slow variables (n^1, \dots, n^N), and are not constant any more. 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 sub-populations by $n^\alpha \times$

$v_i^{\alpha*}(n^1, \dots, n^N)$ into functions F_i^α will now lead to a new macro-system:

$$\frac{d n^\alpha}{d t} = \sum_{i=1}^{N^\alpha} F_i^\alpha(v_1^1(n^1, \dots, n^N)n^1, \dots, v_1^{N^\alpha}(n^1, \dots, n^N)n^N, \dots, v_1^{N^*}(n^1, \dots, n^N)n^N, \dots) \quad (3)$$

This new macro-system includes new terms with respect to the slow part of the micro-system, which result from the density dependence in the new equilibrium frequencies. The emergence of these new terms can be seen as a coupling between the fast and the slow dynamics. For each set of values in the slow macro-variables, the fast system reaches a different equilibrium, which differs also for each set of macro-variables. Hence, this process induces an emergence in the approximated macro-system. As a consequence, different fast models coupled to the same slow model can lead to different global dynamics.

4. Use of aggregation method to model a prey–predator system in a heterogeneous environment

When modelling host-parasite systems, it is necessary to take into account the individual behaviour of the animals. Indeed, it is observed that the parasite and its host co-evolve. For example, juvenile treespine (*Gasterosteus aculeatus*) and blackspotted sticklebacks (*Gasterosteus wheatlandi*) remain in groups when they try to lower

their risk of being parasitized by the crustacean ectoparasite *Argulus canadensis* (Poulin and Fitzgerald, 1989a,b). The trematode parasite *Dicrocoelium dendriticum* can provoke aberrant behaviour in infected ants and make them available for ingestion by grazing sheep (Romig et al., 1980, cited in Combes, 1991).

In this study, we shall consider a host-parasite model, incorporating individual behaviour of the hosts. The model is based on results obtained by Poulin and Fitzgerald (1989a,b), concerning blackspotted sticklebacks and their crustacean ectoparasites. Two spatial patches or habitats can be considered for fishes. A first one is near the surface and contains vegetation, the second one corresponds to deeper water and is open. The risk of being attacked by parasites is much larger in the surface habitat, but this patch provides food and resources. The second habitat is safe from parasitism but fishes cannot find resources and not enough food to remain all the time in that patch. It is observed that fishes can live in both habitats, even if parasites are found in the surface patch.

The same model can also be thought for prey–predator systems in a two patches environment. On a first patch, preys can grow but are vulnerable because of an easy attack by the predators hunting on that patch; on the second patch, preys are safe from predation (or mostly safe). Hence, preys can go on the second patch considered as a refuge, but migrate also on the first patch where food and water are available.

4.1. Presentation of the complete model

Let $n_1(t)$ and $n_2(t)$ be prey (or host) densities on both spatial patches, corresponding for example to the surface patch and the deep water patch respectively in the case of sticklebacks and their ectoparasites. Let $p_1(t)$ be the predator (or parasite) density on patch 1. Predators (or parasites) are present in patch 1 only, while preys (or hosts) can move and migrate from patch 1 to patch 2 and conversely. Preys are assumed to grow according to a logistic law on each patch characterised by a carrying capacity K_i and a growth rate r_i on patch i . We assume a Lotka–Volterra func-

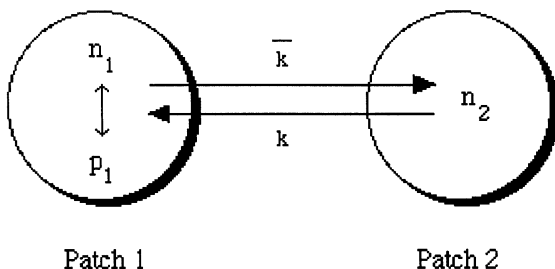


Fig. 1. Flowchart of the model of prey's patch selection induced by predators.

tional response for the predation relationship on patch 1, and we denote a the predation rate (/predator/prey/time unit). We call c the conversion rate of prey biomass into predator biomass, and μ is the natural death rate of predators. The model also takes into account the migration of preys between the two patches, according to the rule shown in Fig. 1. Finally, we make the hypothesis that migrations go faster than growth and predation processes on each patch. Two time scales are thus involved in the model, a fast one for prey migration (each day for example) and a slow one for growth and predation.

The complete model, describing both migration and reproduction processes, can then be written as a set of three ODEs:

$$\begin{cases} \varepsilon \frac{dn_1}{dt} = (kn_2 - \bar{k}n_1) + \varepsilon \left(r_1 n_1 \left(1 - \frac{n_1}{K_1} \right) - an_1 p_1 \right) \\ \varepsilon \frac{dn_2}{dt} = (\bar{k}n_1 - kn_2) + \varepsilon r_2 n_2 \left(1 - \frac{n_2}{K_2} \right) \\ \varepsilon \frac{dp_1}{dt} = \varepsilon (-\mu p_1 + can_1 p_1) \end{cases} \quad (4)$$

where ε is a small parameter, and k and \bar{k} are the prey migration rates. In a previous work (Morand et al., 1998), k and \bar{k} were assumed constant, and it was shown that model (4) can be aggregated into a macro-model with only two equations governing total prey and predator densities. The analysis of the model showed that only two cases might occur according to parameter values:

- The predator population becomes extinct, while the prey population tends to a constant density;
- The prey and the predator populations coexist at constant densities.

In a further contribution (Chiorino et al., 1999), was considered the case of a prey migration rate, \bar{k} from patch 1 to patch 2, which depends on the predator density on patch 1. Hence, it was assumed that $\bar{k} = \alpha p_1$ with α , a positive constant. Preys are then supposed to leave patch 1 at a rate increasing with the number of predators on that patch. Such an assumption is equivalent to a repulsive effect exerted by predators on preys. The

mathematical analysis of the aggregated model has shown that the two previous cases may also occur, but that a new situation can arise:

- Extinction of the predator population and coexistence of preys and predators can occur at the same time. There is a separatrix in the phase portrait, and according to the initial conditions on both sides of this separatrix, either the predator goes to extinction or both the prey and the predator coexist.

In the present work, we shall assume a reinforced repulsion effect of the predator on the prey, that is $\bar{k} = \alpha p_1^2$. Instead of leaving patch 1 with a rate simply proportional to the predator density as in Chiorino et al., the rate is now proportional to the square of the predator density. With this assumption, the complete model now reads:

$$\begin{cases} \varepsilon \frac{dn_1}{dt} = (kn_2 - \alpha p_1^2 n_1) + \left[r_1 n_1 \left(1 - \frac{n_1}{K_1} \right) - an_1 p_1 \right] \\ \varepsilon \frac{dn_2}{dt} = (\alpha p_1^2 n_1 - kn_2) + \varepsilon r_2 n_2 \left(1 - \frac{n_2}{K_2} \right) \\ \varepsilon \frac{dp_1}{dt} = \varepsilon (-\mu p_1 + can_1 p_1) \end{cases} \quad (5)$$

4.2. The aggregated model

Let $N = n_1 + n_2$ and $P = p_1$ be the aggregated variables, i.e. total prey and predator densities added on both patches. The first step of aggregation consists of looking for the fast equilibrium of the model that is for the prey migrations. This fast equilibrium is obtained when the two migration flows are equal $kn_2 = \alpha P^2 n_1$.

As migration is conservative (the total prey density N is a constant of motion for migrations), one can substitute $N - n_1$ for n_2 in the previous equation. After some algebra, we obtain the prey density at the fast equilibrium in terms of the total prey and predator densities:

$$\begin{cases} n_1^* = \frac{kN}{k + \alpha P^2} \\ n_2^* = \frac{\alpha P^2 N}{k + \alpha P^2} \end{cases} \quad (6)$$

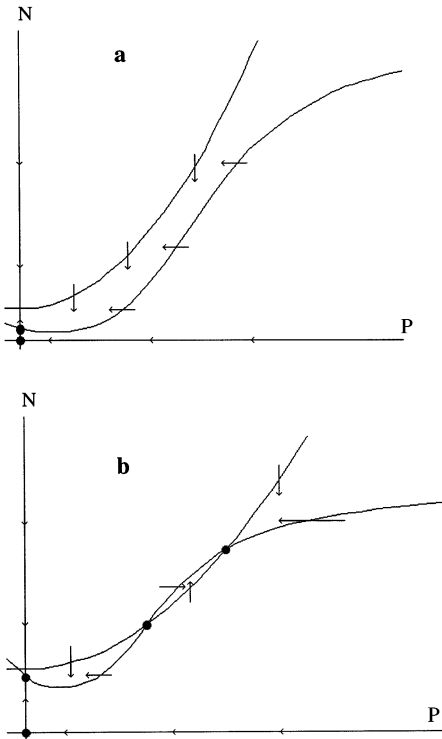


Fig. 2. Nullclines and flow directions corresponding to model (7) in the case $K_1 < \mu/ac$ in the plane (P, N) . (a) Two steady states; (b) Four steady states.

The star subscript denotes the fast equilibrium. At high density of predators, preys avoid patch 1 and concentrate on patch 2. It can be easily shown that this fast equilibrium is asymptotically stable, that is, a condition needed in order to proceed to aggregation (Auger and Roussarie, 1994; Poggiale, 1994) holds.

The aggregated system is obtained by adding the two prey equations and by substituting the previous fast equilibrium (6) in the prey and predator equations:

$$\begin{cases} \frac{dN}{dt} = \frac{N}{k + \alpha P^2} \left[r_1 k \left(1 - \frac{N}{K_1} \frac{k}{k + \alpha P^2} \right) + r_2 \alpha P^2 \left(1 - \frac{N}{K_2} \frac{k}{k + \alpha P^2} \right) - akP \right] \\ \frac{dP}{dt} = P \left(ca \frac{k}{k + \alpha P^2} N - \mu \right) \end{cases} \quad (7)$$

This aggregated system is an approximation of

the complete system. It is valid when ε is small enough (typically 0.1 or less) and when the aggregated model is structurally stable. This model is very different from the local model on each patch, which assumes a logistic growth of the prey, a constant mortality of the predator and a Lotka–Volterra functional response. It shows how the density-dependent fast migrations, at the individual level, emerge at the population level. The form of the model is not only modified, but as we shall see in the next section, new dynamical properties are also emerging.

4.3. Dynamics of the aggregated model

In this section, we shall consider the phase portrait in the (P, N) plane. Equilibrium points of the aggregated model can be obtained by looking to the nullclines of the system.

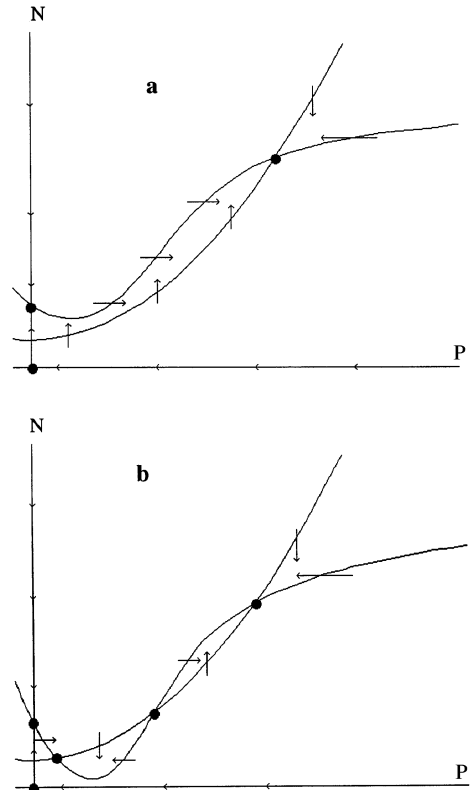


Fig. 3. Nullclines and flow directions corresponding to model (7) in the case $K_1 > \mu/ac$ in the plane (P, N) . (a) Three steady states; (b) Five steady states.

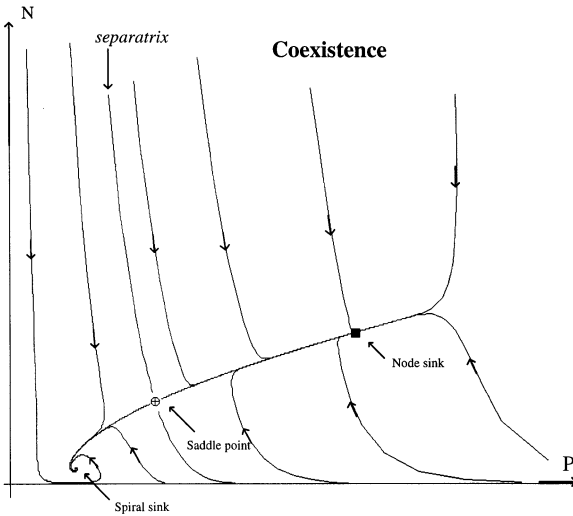


Fig. 4. Phase portrait corresponding to the case of Fig. 3b.

- The $dP/dt = 0$ nullclines are given by the next two functions:

$$\begin{cases} P = 0 \\ (A): N = \frac{\mu\alpha}{cak}P^2 + \frac{\mu}{ca} \end{cases} \quad (8)$$

- The $dN/dt = 0$ nullclines are given by the next two functions:

$$\begin{cases} N = 0 \\ (B): N = \frac{K_1K_2(k + \alpha P^2)(r_2\alpha P^2 - akP + r_1k)}{K_1r_2\alpha^2P^4 + K_2r_1k^2} \end{cases} \quad (9)$$

The positive quadrant is positively invariant, and the equilibrium points are found at the intersection of both types of nullclines (A) and (B). Four possibilities can be observed according to parameter values, that is to relative positions of the nullclines (Figs. 2 and 3). $(0, 0)$ and $(0, K_1)$ are equilibrium points in the four cases, and if $K_1 < \mu/ac$, situations of Fig. 2 can occur, while those of Fig. 3 are possible when $K_1 > \mu/ac$.

- When $K_1 < \mu/ac$, two or four equilibrium points can exist in the phase portrait:
 - In the case of Fig. 2a, $(0, 0)$ and $(0, K_1)$ are the only equilibrium points. As indicated by the flow directions on the nullclines, the

origin is unstable, and the prey population tends to its carrying capacity of patch 1, while the predator is excluded.

- In the case of Fig. 2b, two more equilibrium points exist in the positive quadrant. Flow directions show that $(0, 0)$ is unstable and $(0, K_1)$ is stable. Among the two other equilibrium points, the one at high density is stable and the one at low density is a saddle point. Thus, there is a separatrix and according to the initial condition, either the predator population goes to extinction or the prey and predator population coexist.
 - When $K_1 > \mu/ac$, three or five equilibrium points can exist in the phase portrait, and $(0, 0)$ and $(0, K_1)$ are always unstable (saddle points). Two types of situations can occur:
 - Fig. 3a: There is only one stable equilibrium point in the positive quadrant, which corresponds to preys and predators coexisting at constant densities.
 - Fig. 3b: There are three equilibrium points in the positive quadrant, two stable ones and a saddle point between them. According to the initial densities and with respect to the separatrix shown on Fig. 4, the prey and the predator coexist either at low densities or at high densities.
- Fig. 4 presents a Runge–Kutta simulation of the aggregated model in the case corresponding to Fig. 3b. The phase portrait of Fig. 4 is completely new compared to those obtained in previous works (Morand et al., 1998; Chiorino et al., 1999). The dynamics is very interesting on a biological point of view:
- If the system is initially at the high-density equilibrium, capture of prey (by hunting for example) can push the population state through the separatrix and then to the low-density equilibrium.
 - If the system is initially at the low-density equilibrium, a flow of migrants, coming from outside, can again push the population state through the separatrix and switch to the high-density equilibrium.

This situation of switching between two stable equilibrium points has interesting consequences in terms of management of the populations. In the case of host-parasite systems, where both population coexist at high density, a treatment of the parasitism (by a chemical substance for example) might lead to a less high prevalence of the infection in the total population.

5. Conclusion

The model presented here was detailed as an illustrative example in the simple case of two patches. It shows how the individual behaviour can lead to complex dynamics for the total population. However, aggregation methods can also be used for complex networks of interconnected patches involving many sub-populations. Such a model was developed in the case of discrete time models (Leslie type) for a fish population (the brown trout) in an arborescent river network (Charles et al., 1998a,b). In this work, the model describes the global population dynamics in a river network of 15 patches: demographic process takes place in each patch and individuals are supposed to migrate many times per year between patches. The model then allows the quantification of the effects of some changes in the structure of the network (because of dams or channels) on the global dynamics.

The aggregation method is a convenient tool to study complex systems composed of a large number of elements and presenting a hierarchical structure. This method was applied to prey–predator models in a heterogeneous environment. In particular, the effect of density-dependent migration decisions of preys and predators on the structure of the global prey–predator model was studied (Auger and Poggiale, 1996; Michalski et al., 1997; Bernstein et al., 1999). The method was also used to study the effects of different individual tactics, hawk, and dove at the fast time scale, on the global growth of a cat population (Auger and Pontier, 1998). And it is possible to implement aggregation methods in order to simplify community graphs (Kooi et al., 1998). Finally, the

method was developed in the case of discrete models (Bravo de la Parra et al., 1995).

Future developments are necessary to incorporate individual behaviour into population dynamics as well as the structure of the community. This could be carried out by considering three time scales or more. Stochastic processes should also be added in the models. Recent developments have been carried out along this line in stochastic discrete time models (Sanz Lorenzo, 1998).

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