

COMPLEX ECOLOGICAL MODELS WITH SIMPLE DYNAMICS: FROM INDIVIDUALS TO POPULATIONS

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ABSTRACT

The aim of this work is to study complex ecological models exhibiting simple dynamics. We consider large scale systems which can be decomposed into weakly coupled subsystems. Perturbation Theory is used in order to get a reduced set of differential equations governing slow time varying global variables. As examples, we study the influence of the individual behaviour of animals in competition and predator-prey models. The animals are assumed to do many activities all day long such as searching for food of different types. The degree of competition as well as the predation pressure are dependent upon these activities. Preys are more vulnerable when doing some activities during which they are very exposed to predators attacks rather than for others during which they are hidden. We study the effect of a change in the average individual behaviour of the animals on interspecific relationships. Computer simulations of the whole sets of equations are compared to simulations of the reduced sets of equations.

KEY WORDS: Aggregation methods, competition, predation, individual behaviour, perturbation theory.

1. INTRODUCTION

It has been shown that simple mathematical models can exhibit complex dynamics (May et al., 1976). Simple discrete systems can exhibit cascades of bifurcations and chaotic behaviours (Lorenz, 1963; May et al., 1976). As a consequence, recently there has been a great interest in the study of these systems in various fields. For example, chaotic behaviour has been investigated in many disciplines. Simple systems such as a discrete logistic model in population dynamics can present complex behaviour with respect to parameters values. Roughly, we can say that there is a kind of paradox between the simplicity of the equations and the unexpected complexity of their solutions.

The complexity (or the simplicity) of a system of ordinary differential equations or still of its solutions does not seem easy to define. Ecological systems often are considered as complex systems. Indeed, large numbers of species interact in ecosystems and sometimes

they can be grouped into clusters, i.e. groups of strongly interacting species (Allen and Starr, 1982; O'Neill et al., 1986). The species are sets of individuals which can be of different ages. These individuals are doing many activities all day long such as searching for food of different types, feeding the young and so on. As a consequence, the populations must be divided into subpopulations corresponding to ages, activities, phenotypes, exposure to predation. Furthermore, these individuals can move, meet and interact in a fluctuating environment. This means that we would have to consider 1000 ordinary differential equations, for instance in a homogeneous case when neglecting the motions of the animals, and if we want to study the interactions between 10 species, with 5 age classes and 20 activities. We certainly will consider this a very complex model. Anyway, it is a large scale system, or a system with many degrees of freedom and parameters. Consequently, it would be very difficult to handle so many equations and variables.

Roughly, one considers the three ecological 'levels', the individual, the population and the ecosystem. The dynamics of ecological systems is a coupled process at each of these levels which necessitates development of methods for integrating these levels. Many authors have noted the importance of hierarchical structures in biology (Allen & Starr, 1986; Ehresmann & Vanbremeersch, 1987; MacMahon et al., 1978; Pattee, 1973; Whyte et al., 1969). Methods using successive hierarchical clusters are good tools for the study of populations which are subdivided into subpopulations, themselves subdivided into further smaller sub-subpopulations and so on. These methods are mainly helpful for the integration of time scales. Another aspect concerns spatial scales. Processes occur very differently according to the level of observation, i.e. to the spatial scale (Burel & Baudry, 1990; Di Castri & Hadley, 1988; Wiens, 1989).

Aggregation methods have been widely developed in different fields and particularly in ecological modelling. Large scale systems are condensed into smaller systems by aggregation of variables. These methods investigate conditions necessary to obtain a reduced set of equations governing the aggregated variables and depending upon them (Cale et al., 1983; Gard, 1988; Gardner et al., 1982; Iwasa et al., 1987, 1989; Shaffer, 1981). Aggregation methods, such as perfect aggregation, cannot be applied in general. Perfect aggregation will be possible when parameters take particular values.

The aim of this study is to show that aggregation methods can also be applied when there are different time scales in the dynamical systems. The aggregated system is then described with the help of approximation methods based on perturbation theory. This study shows that particular complex models or large scale systems can exhibit simple dynamics. Such a reduction in the complexity can be obtained when the system can be subdivided into subsystems or groups such that the strengths of the interactions within a subsystem are much larger than those between subsystems. The important differences in the strengths of the interactions lead to different time scales, respectively associated to the intra-group and intergroup dynamics.

Then, with each subsystem is associated at least one slow time varying global variable, or aggregated variable, which must be a constant of motion, i.e. invariant for the intra-group dynamics. Consequently, the differences in the orders of magnitude of the time scales allows one to apply approximations which leads at each level to a reduced set of equations governing global variables or aggregated variables. We shall show that under certain conditions, perturbation theory enables to obtain such a reduced set of differential equations governing the global variables (Abraham & Robbin, 1967; Fenichel, 1971; Hirsch et al., 1977; Hoppensteadt, 1966; Nayfeh, 1973). This reduced set of equations can be simulated

more easily than the whole set of equations.

We can say that a hierarchical structure is the response to complexity for these systems. By taking an appropriate hierarchical organization, the complexity of the system is reduced because its elements mainly interact inside the same subsystem and very few between different subsystems. This spontaneous tendency to self-organize in a hierarchical way can be justified in the frame of thermodynamics (Auger, 1989, 1990). The existence of quasi-autonomous clusters rapidly evolving towards intra-group equilibrium leads to the decoupling between slow varying global variables and fast varying intra-group variables.

The influence of the average individual behaviour of animals on interspecific relationships, particularly in the framework of competition and prey-predator models is going to be investigated. In most mathematical models of predation, each interacting population is considered a whole i.e., all individuals are assumed to be identical and homogeneous in space and time. In this way, one has to consider two differential equations describing the time variations of the total population of preys and predators. These types of predator-prey models do not take into account the activities of the animals. Nevertheless, animals are doing many activities all day long whose sequences can also vary with seasons or else with environmental changes such as pollution or climate changes.

For example, when one considers predator-prey models in connection to activity sequences, one should consider that the prey animals may be much more vulnerable when they search for food sources than for anything else. Indeed, they can be hidden from predators attacks. As a consequence, the predation pressure on the prey would not be fixed 'a priori' but, it would be determined by the individual behaviour selected by animals with respect to surrounding environment. How a change in the individual behaviour can affect the interspecific relationships? In this study, we consider competition models and prey-predator models.

2. KINETICS OF SUBPOPULATIONS: POPULATION KINETICS

In this first section, we will briefly recall the method for the study of dynamical models of hierarchically organized populations described in more details in previous work (Auger, 1982, 1983, 1985, 1986, 1989). Here, we present the method in the framework of regular perturbation theory.

2.1. Subpopulations System of Differential Equations

Consider a set of populations which can be subdivided into subpopulations. In general, the system is composed of many subpopulations i that can vary with time, $i \in [1, N]$. Let $n_i(t)$ be the number of individuals in subpopulation i at time t . The system behaviour is described by the set of differential equations governing the subpopulation variables $n_i(t)$:

$$\frac{dn_i}{dt} = f_i(n_1, n_2, \dots, n_N). \quad (1)$$

Usually, such equations are nonlinear and the behaviour of the system can be very complex, in particular if there are many subpopulations leading to many coupled differential equations. For this reason, in our previous work Auger (1989), we have considered particular systems, i.e. hierarchically organized populations for which one can obtain a simplified description.

We consider a partition of two populations into subpopulations. Let N^α be the number of subpopulations in population α , $\alpha \in [1, 2]$. Let i_α be the index for subpopulation i of population α , $i_\alpha \in [1, N^\alpha]$. The variables are $n_{i_\alpha}^\alpha(t)$, i.e. numbers of individuals in the i_α th subpopulation of population α at time t , noted more simply $n_i^\alpha(t)$. We use an upper index to indicate the population and a lower index to indicate the subpopulation. Using these notations, equations (1) become:

$$\frac{dn_i^\alpha}{dt} = R f_i^\alpha(n^\alpha) + f_i^{\alpha\beta}(n^\alpha, n^\beta), \tag{2}$$

$$\text{with } n^\alpha = (n_1^\alpha, n_2^\alpha, \dots, n_{N^\alpha}^\alpha) \quad \text{and} \quad n^\beta = (n_1^\beta, n_2^\beta, \dots, n_{N^\beta}^\beta),$$

$$\text{where } f_i^\alpha(n^\alpha) = O(|n^\alpha|) \quad \text{and} \quad f_i^{\alpha\beta}(n^\alpha, n^\beta) = O(|n^\alpha|),$$

$$\text{and where } R \gg 1 \quad \text{or still} \quad \varepsilon = 1/R \ll 1.$$

In equations (2), if $\alpha = 1$, $\beta = 2$ and reciprocally. R is a constant, called scaling factor large with respect to one. Using eq. (2), we consider separately intra-population interactions and inter-population interactions. f_i^α are intra-population α functions only depending upon components of group α vector n^α , while $f_i^{\alpha\beta}$ are inter-population functions depending upon vectors n^α and n^β . We assume that the intra-population terms are much larger than the inter-population terms. Thus, we can regard inter-population terms as perturbations with respect to intra-population ones. If we assume that the functions f_i^α and $f_i^{\alpha\beta}$ are of the same order of strength, it implies that the scaling factor is large or else that its inverse is a small parameter. Typically $R = 50-100$ (i.e. $\varepsilon = 0.02-0.01$) is usually sufficient to apply perturbation methods. Eq. (2) may be rewritten in a more familiar way, that is in the framework of regular perturbation theory as follows:

$$\frac{dn_i^\alpha}{d\tau} = f_i^\alpha(n^\alpha) + \varepsilon f_i^{\alpha\beta}(n^\alpha, n^\beta), \tag{3}$$

where $\varepsilon = 1/R \ll 1$ and $t = \varepsilon \tau$. τ is a fast time scale with respect to t . We have put equation (3) in a form which is suitable to regular perturbation theory rather than in a form suitable to singular perturbation theory (Hoppensteadt, 1966; Nayfeh, 1973). We now use the Fenichel central manifold theorem (Abraham et al., 1967; Fenichel, 1971; Hirsch et al., 1977).

2.2. From Subpopulations to Populations

Now, let us recall methods allowing to obtain differential equations governing population variables n^α which are the following variables

$$n^\alpha = \sum_i n_i^\alpha, \tag{4}$$

Macro variables such as the total biomass of each population could be of interest. In this case we would also have a linear relationship between aggregated variables and subpopulations, but with parameters such as the average biomass of each subpopulation. In the following parts we limit the study to relations (4). Dynamical equations of populations n^α can be obtained as follows

$$\frac{dn^\alpha}{d\tau} = \sum_{i=1}^{N^\alpha} \frac{dn_i^\alpha}{d\tau}. \tag{5}$$

Eq. (5) is composed of 2 equations while equations (2) or (3) are composed of $N^1 + N^2$ equations. For instance, in the case of 2 populations each one containing 10 subpopulations, we get 2 global equations (5) and 20 equations (2) or (3). Of course, such a system (5) is interesting if it is autonomous. This will be possible under certain conditions. Perturbation theory and particularly the Fenichel central manifold theorem will determine these conditions. For this determination the equations have to be written in a form suitable for applying this theorem.

2.3. Slow Varying Populations, Fast Varying Subpopulations

Now, substitute time derivatives of equations (3) into equations (5)

$$\frac{dn^\alpha}{d\tau} = \sum_{i=1}^{N^\alpha} f_i^\alpha(n^\alpha) + \varepsilon \sum_{i=1}^{N^\alpha} f_i^{\alpha\beta}(n^\alpha, n^\beta) = I + E, \quad (6)$$

For notational convenience, let I represent intra-population processes and E inter-population processes which are defined as follows

$$I = \sum_{i=1}^{N^\alpha} f_i^\alpha(n^\alpha) \quad \text{and} \quad E = \varepsilon \sum_{i=1}^{N^\alpha} f_i^{\alpha\beta}(n^\alpha, n^\beta). \quad (7)$$

Thus, the dynamics in eq. (6) can be represented by the two terms I and E . It is required that the intra-population term I vanishes in equations (6). This means that the population variable n^α is a constant of motion for the intra-population dynamics leading to a simplified form for eq. (6)

$$\frac{dn^\alpha}{d\tau} = \varepsilon \sum_{i=1}^{N^\alpha} f_i^{\alpha\beta}(n^\alpha, n^\beta). \quad (8)$$

$$\text{or still in time scale } t \quad \frac{dn^\alpha}{dt} = \sum_{i=1}^{N^\alpha} f_i^{\alpha\beta}(n^\alpha, n^\beta).$$

As a consequence, there is a time hierarchy. Population variables n^α are slow time varying with respect to any subpopulation variable n_i^α

$$\left| \frac{dn^\alpha}{dt} \right| \ll \left| \frac{dn_i^\alpha}{dt} \right|. \quad (9)$$

The characteristic time scale for population variables is t while it is τ for subpopulations. Indeed, equation (6) shows that as a result of the deletion of the intra-population part I , the population variables n^α are only governed by small inter-population terms which are perturbations in equation (3). On the contrary, subpopulations are mainly governed by strong intra-population terms which are the dominant part of the equation (3).

2.4. Equations for the Population Frequencies

Let us define new variables, intra-population frequencies $v_i^\alpha(t)$ as follows

$$v_i^\alpha(t) = \frac{n_i^\alpha(t)}{n^\alpha(t)}. \quad (10)$$

These frequencies are the proportions of individuals in the different subpopulations i of each population α . Let us consider the intra-population part of the equation (3) alone, or else by

putting $\varepsilon = 0$ into equation (3)

$$\frac{dn_i^\alpha}{d\tau} = f_i^\alpha(n^\alpha), \tag{11}$$

In general, eq. (11) will be characterized by several equilibrium points. We assume eq. (11) with at least one equilibrium point. Let us consider a neighbourhood of one of these points at equilibrium. We assume positive equilibrium subpopulations $n_i^{\alpha*}$ and frequencies $v_i^{\alpha*}$ solutions of the next eq. (12)

$$f_i^\alpha(n^{\alpha*}) = 0, \tag{12}$$

In the vicinity of this point, we define relative frequencies as follows

$$V_k^\alpha(t) = v_k^\alpha(t) - v_k^{\alpha*}, \tag{13}$$

Using the previous relative frequencies, the equilibrium point is $\mathbf{0}$. Now, we consider the linear part of eq. (11) around this steady state point

$$\frac{dV_i^\alpha}{d\tau} = \sum_j A_{ij}^\alpha V_j^\alpha, \quad i \in [1, N^\alpha] \tag{14}$$

where $\sum_i V_i^\alpha = 0$ and $A_{ij}^\alpha = \frac{\partial f_i^\alpha}{\partial V_i^\alpha}$ at $\mathbf{0}$,

Moreover, for the use of the Fenichel central manifold theorem, let us rewrite this previous equation by considering $N^\alpha - 1$ variables V_i^α only

$$\frac{dV_i^\alpha}{d\tau} = \sum_{j=1}^{N^\alpha-1} \bar{A}_{ij}^\alpha V_j^\alpha + O(|V^\alpha|^2), \quad i \in [1, N^\alpha - 1], \tag{15}$$

where $|V^\alpha|^2$ is the square of the norm of the following vector $V^\alpha = (V_1^\alpha, V_2^\alpha, \dots, V_{N^\alpha-1}^\alpha)$ and where the parameters \bar{A}_{ij}^α can be easily expressed in terms of the parameters A_{ij}^α . In equation (15), $V_{N^\alpha}^\alpha$ is replaced by $[1 - \sum_{i=1}^{N^\alpha-1} V_i^\alpha]$. We assume that all the eigenvalues λ_i^α associated to eq. (15) have negative real parts. This is a stability condition for each subpopulation. This condition is required in order to apply the Fenichel central manifold theorem.

2.5. The Complete System of Equations

From definitions (10) and (13), it is easy to show that:

$$n_i^\alpha(t) = [V_i^\alpha(t) + v_i^{\alpha*}] \cdot n^\alpha(t), \tag{16}$$

into equation (8), one gets dynamical equations for populations:

$$\frac{dn^\alpha}{d\tau} = \varepsilon \sum_{i=1}^{N^\alpha} F_i^{\alpha\beta}(n^\alpha, n^\beta, V^\alpha, V^\beta, v^{\alpha*}, v^{\beta*}) = \varepsilon n^\alpha N^\alpha(n^\alpha, n^\beta, V^\alpha, V^\beta, v^{\alpha*}, v^{\beta*}), \tag{17}$$

where $F_i^{\alpha\beta}(n^\alpha, n^\beta, V^\alpha, V^\beta, v^{\alpha*}, v^{\beta*}) = f_i^{\alpha\beta}((V_i^\alpha + v_i^{\alpha*}) \cdot n^\alpha, (V_k^\beta + v_k^{\beta*}) \cdot n^\beta)$,
 and where $v^{\alpha*} = (v_1^{\alpha*}, v_2^{\alpha*}, \dots, v_{N^\alpha}^{\alpha*})$ and $v^{\beta*} = (v_1^{\beta*}, v_2^{\beta*}, \dots, v_{N^\beta}^{\beta*})$,

Thus, functions $F_i^{\alpha\beta}$ are obtained by substitution of expressions (16) into functions $f_i^{\alpha\beta}$. Moreover, due to assumptions concerning functions f_i^α and $f_i^{\alpha\beta}$ (see equations (2)), the variable n^α can be factorized defining functions N^α . Another set of equations relates to relative frequencies V_i^α . To get these equations, let us derive with respect to time τ the previous relations (16):

$$\frac{dn_i^\alpha}{d\tau} = [V_i^\alpha + v_i^{\alpha*}] \cdot \frac{dn^\alpha}{d\tau} + n^\alpha \cdot \frac{dV_i^\alpha}{d\tau}. \quad (18)$$

Substituting $\frac{dn_i^\alpha}{d\tau}$ by its expression (3) and $\frac{dn^\alpha}{d\tau}$ by its expression (17) into (18), derivatives $\frac{dV_i^\alpha}{d\tau}$ can be extracted and may be rewritten as follows

$$\frac{dV_i^\alpha}{d\tau} = \sum_{j=1}^{N^\alpha-1} \bar{A}_{ij}^\alpha V_j^\alpha + o(|V^\alpha|^2) + \varepsilon \phi_i^\alpha(n^\alpha, n^\beta, V^\alpha, V^\beta, v^{\alpha*}, v^{\beta*}). \quad (19)$$

$$\text{or still } \frac{dV^\alpha}{d\tau} = \bar{A}^\alpha V^\alpha + o(|V^\alpha|^2) + \varepsilon \phi^\alpha(n^\alpha, n^\beta, V^\alpha, V^\beta, v^{\alpha*}, v^{\beta*}).$$

Functions Φ_i^α can be easily written. Φ^α is the vector (Φ_i^α) . Particular functions Φ_i^α will be calculated in the framework of the examples of next sections. The last equation is the following one, $\frac{d\varepsilon}{d\tau} = 0$. Grouping equations (17), (19) and the one regarding ε , one

gets the following completed set (20)

$$\begin{aligned} \frac{dn^\alpha}{d\tau} &= \varepsilon n^\alpha N^\alpha(n^\alpha, n^\beta, V^\alpha, V^\beta, v^{\alpha*}, v^{\beta*}), \\ \frac{dV^\alpha}{d\tau} &= \bar{A}^\alpha V^\alpha + o(|V^\alpha|^2) + \varepsilon \psi^\alpha(n^\alpha, n^\beta, V^\alpha, V^\beta, v^{\alpha*}, v^{\beta*}) \text{ and } \frac{d\varepsilon}{d\tau} = 0. \end{aligned} \quad (20)$$

Written in this form, we can now apply the Fenichel central manifold theorem. First, we present this theorem in a form which is suitable for our study.

2.6. Fenichel Central Manifold Theorem

We assume the existence of a vector field X on R^N , $N = k_1 + 3$. X is C^∞ . $[(0), R^2, 0]$ is a set of zeroes for X . In our application, the variables are $V^\alpha = [V_i^\alpha] \in R^{k_1} : k_1 = (N^1 + N^2 - 2)$, $n = (n^1, n^2) \in R^2$ and $\varepsilon \in R$.

For any point n and at $(0, n, 0)$, we consider the set of eigenvalues of the linear part of X which is noticed $DX(n)$. We assume that $DX(n)$ owns k_1 eigenvalues with negative real part and that 0 is an eigenvalues with multiplicity 3. At any point $n \in R^2$, one can consider two spaces E_n^S and E_n^C respectively the stable and central spaces of $DX(n)$ such as $\dim(E_n^S) = k_1$ and $\dim(E_n^C) = 3$. All the eigenvalues of $DX(n)$ restricted to E_n^S have negative real

parts. Using these notations and assumptions, the Fenichel central manifold theorem can be expressed in the next form:

Theorem:

On any bounded part Δ included into R^2 and for $k \in N$, there exists a manifold W , graph of an application C^k , let say $V^\alpha(n, \varepsilon) : \Delta x[-\varepsilon, +\varepsilon] \rightarrow R^{kI}$, such as $V^\alpha(n, 0) = 0$, being invariant through X and being tangential to E_n^C at any point $(0, n, 0)$. W is a central manifold (of class k).

The invariability of W means that at any point $(V^\alpha, n, \varepsilon) \in W$, the field X is tangential to W . At points $(0, n, 0)$, the central manifold W is tangent to the space $(0, R^2, 0)$. At these points, E_n^C is generated by $(0, R^2, 0)$ and by the vectors $\frac{\partial V^\alpha}{\partial \varepsilon}(0, n, 0) = W_1^\alpha(n)$, see

appendix 1 for the details of calculation. In the next sections, we shall apply this central manifold theorem to examples of population dynamics with subpopulations.

2.7. Reduced Set of Equations for Populations n

The whole set of differential equations is the previous one (20). In (20), we consider the linear part of the intra-population equations in the neighbourhood of an equilibrium point such as indicated before. The central manifold V^α can be calculated as follows

$$V^\alpha(n, \varepsilon) = \varepsilon W_1^\alpha(n) + o(\varepsilon^2) \quad \text{with} \quad W_1^\alpha = -(\bar{A}^\alpha)^{-1}(\psi^\alpha(n, v^{\alpha*}, v^{\beta*})), \quad (21)$$

$$\text{where} \quad \psi^\alpha(n, v^{\alpha*}, v^{\beta*}) = \Phi^\alpha(n^\alpha, n^\beta, 0, 0, v^{\alpha*}, v^{\beta*}).$$

The details of the calculation of the central manifold are given in the appendix 1. The central manifold is a graph of a function of (n, ε) . Consequently, equation (22) is obtained by substitution of $V^\alpha(n, \varepsilon)$ into equations (20)

$$\frac{dn^\alpha}{dt} = \varepsilon g^\alpha(n^\alpha, n^\beta, v^{\alpha*}, v^{\beta*}, \varepsilon), \quad (22)$$

where $g^\alpha(n^\alpha, n^\beta, v^{\alpha*}, v^{\beta*}, \varepsilon) = n^\alpha N^\alpha(n^\alpha, n^\beta, V^\alpha(n, \varepsilon), V^\beta(n, \varepsilon), v^{\alpha*}, v^{\beta*})$,

$$\text{or still using time } t \quad \frac{dn^\alpha}{dt} = g^\alpha(n^\alpha, n^\beta, v^{\alpha*}, v^{\beta*}, \varepsilon).$$

In this way, one gets a reduced system (22) governing the slow time variation of the populations n^1 and n^2 . We can expand g^α in powers of ε .

$$\frac{dn^\alpha}{dt} = g_0^\alpha(n^\alpha, n^\beta, v^{\alpha*}, v^{\beta*}, 0) + O(\varepsilon). \quad (23)$$

Equation (23) is an ε -perturbation of equation (24) obtained for $\varepsilon = 0$.

$$\frac{dn^\alpha}{dt} = g_0^\alpha(n^\alpha, n^\beta, v^{\alpha*}, v^{\beta*}, 0). \quad (24)$$

This equation (23) remains unchanged for small values of ε , if (24) is structurally stable [3, 24, 40]. We recall this important notion in appendix 2. Now, let us study particular

examples of subpopulation dynamics where the reduced limit equation (24) will be structurally stable.

3. INFLUENCE OF ACTIVITY SEQUENCES ON COMPETITION MODELS

In most models of competition between species, the competition between two species for the same food source can lead to the extinction of one of the two competing species. Classical models of competition do not take into account the activities of the animals. Nevertheless, the animals do many different activities all day long such as searching for different food types. As a consequence, when one considers competition in connection to activity sequences, one must take into account that the animals may strongly compete in some activities and only weakly in other activities. In this section, we discuss the influence of the average individual behaviour on parameters in competition models. How can a change in the individual behaviour affect the interspecific competitive relationships? How can small changes in the individual behaviour have large effects on the population and ecosystem?

3.1. The Classical Competition Models

Let us recall a classical competition model described in May (1976) and in Murray (1989). Let n_1 and n_2 be the populations of two species 1 and 2 competing for the same food source. In a Lotka-Volterra competition model, the competition process is described by the differential equations

$$\begin{aligned}\frac{dn_1}{dt} &= r_1 n_1 [1 - n_1/K_1 - b_{12} n_2/K_1], \\ \frac{dn_2}{dt} &= r_2 n_2 [1 - n_2/K_2 - b_{21} n_1/K_2],\end{aligned}\tag{25}$$

where r_1, r_2 are the linear birth rates, K_1, K_2 are the carrying capacities respectively for species 1 and 2. b_{12} and b_{21} are parameters relative to the competition effects between the two species. These parameters are positive. Depending upon the values of the parameters and upon the initial conditions, several cases can appear but in most cases only one species will survive and supplant the other; the principle of competition exclusion.

3.2. Competition Models and Individual Activity Sequences

In a similar way, we consider two competing species 1 and 2 but with their individual activity sequences. The animals can select different activities r all day long, such as searching for food of different types, resting, hiding, reproducing and so on. We assume the existence of such a set of discrete activities. Let r be the index for the activities of the animals of species 1 or 2. N^1 and N^2 are the numbers of possible activities for an animal of species 1 and 2, respectively. For simplicity, we make the choice $N^1 = N^2 = N$. Let us divide the total populations of the two species into subpopulations corresponding to the activities. As a consequence, let $n_r^1(t)$ and $n_r^2(t)$ be the numbers of animals of the subpopulations, i.e. belonging to species 1 and 2, respectively, and doing the activity r at time t . Consider the following differential equations

$$\begin{aligned}\frac{dn_r^1}{dt} &= R \left(\sum_s k_{rs}^1 n_s^1 - \sum_s k_{sr}^1 n_r^1 \right) + r^1 n_r^1 \left[1 - n_r^1 / K^1 - \sum_s b_{rs}^{12} n_s^2 / K^1 \right], \\ \frac{dn_t^2}{dt} &= R \left(\sum_s k_{ts}^2 n_s^2 - \sum_s k_{st}^2 n_t^2 \right) + r^2 n_t^2 \left[1 - n_t^2 / K^2 - \sum_s b_{ts}^{21} n_s^1 / K^2 \right],\end{aligned}\quad (26)$$

where R is the scaling factor between intra-population and inter-population parts of the equations, typically 100 or even 1000. The matrices $A^\alpha = [k_{rs}^\alpha]$ describe the activity changes for animals of species 1 or 2. k_{rs}^α is the rate of transition from the activity s towards the activity r for animals of species α . In this example, we chose the linear functions f_i^α . r^α is the linear birth rate for animals of species α , and K^α the corresponding carrying capacity. $b_{rs}^{\alpha\beta}$ are competition parameters between animals of species α performing the activity r and animals of species β performing the activity s . We now assume that for some (couples of) activities the animals are in strong competition and that for others they are in weak competition. Then, the parameters $b_{rs}^{\alpha\beta}$ are large and small respectively.

As the animals often change activities, i.e. several times per day, there is a hierarchy in the order of magnitude of the parameters of the model. As a consequence, the intra-population part is very large with respect to the inter-population part. In our notation, parameters k_{rs}^α , r^α , b_{rs}^α are of the same order of magnitude and the hierarchy is introduced by means of the large value of the scaling factor $R \gg 1$ or the small value of $\epsilon = 1/R \ll 1$.

3.3. Intra-population Dynamics

Let us study the intra-population part of the equations alone

$$\begin{aligned}\frac{dn_r^\alpha}{dt} &= I = R \left(\sum_s k_{rs}^\alpha n_s^\alpha - \sum_s k_{sr}^\alpha n_r^\alpha \right). \\ \text{or still } \frac{dn_r^\alpha}{d\tau} &= \left(\sum_s k_{rs}^\alpha n_s^\alpha - \sum_s k_{sr}^\alpha n_r^\alpha \right).\end{aligned}\quad (27)$$

Instead of treating an abstract system, we shall consider a particular system (27). Other models for activity sequences have been developed (Metz et al., 1983). Our model can be represented schematically by a transition graph shown in figure 1. Such a graph displays the activities and shows the links between them. This particular graph was described in previous work (Auger, 1989), we briefly recall it. Activity 1 is a fundamental activity, for instance hiding from predators. The only possible transitions are from 1 to another activity i and then return from i to the first activity which is a branching point. From this activity, the animals have choices for various activities. The equations (27) may be rewritten as

follows, in which $\dot{n} = \frac{dn}{d\tau}$

$$\begin{aligned}r \neq 1, \quad \dot{n}_r^\alpha &= \left(k_{r1}^\alpha n_1^\alpha - k_{1r}^\alpha n_r^\alpha \right), \\ r = 1, \quad \dot{n}_1^\alpha &= \left(\sum_s k_{1s}^\alpha n_s^\alpha - \left(\sum_t k_{t1}^\alpha \right) n_1^\alpha \right).\end{aligned}\quad (28)$$

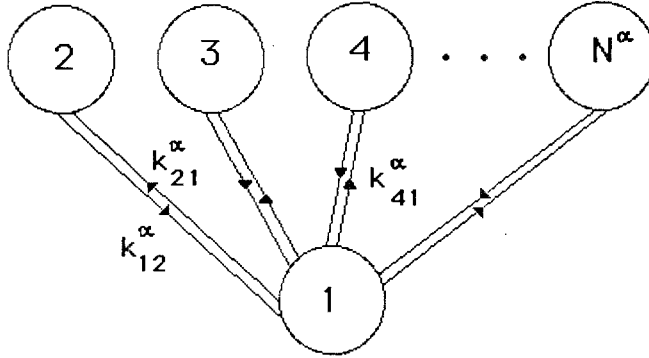


Fig.1. The branching graph is an example of activity transition graph for animals belonging to species α . The animals select new activities such as research of different types of food from a fundamental activity 1.

\dot{n}_1^α is a linear combination of the $N^\alpha - 1$ other equations. This means that $n^\alpha(t) = \sum_I n_r^\alpha(t)$ is a constant of motion for the intra-population dynamics because the activity changes are not responsible for the variations of the total numbers of animals of each species. Furthermore, the frequencies v_r^α represent the proportions of animals of species α engaged in activity r and rapidly approach equilibrium activity frequencies $v_r^{\alpha*}$ such as

$$v_r^{\alpha*} = \frac{k_{r1}^\alpha}{k_{1r}^\alpha + k_{1r}^\alpha \sum_{s=2}^{N^\alpha} \frac{k_{s1}^\alpha}{k_{1s}^\alpha}} \tag{29}$$

Indeed, returning to section 1, one can look for the dynamical equations governing the relative frequencies V_i^α which are given by

$$\frac{dV_i^\alpha}{d\tau} = \sum_j k_{ij}^\alpha V_j^\alpha + \varepsilon \phi_i^\alpha(n^\alpha, n^\beta, V_i^\alpha, V_k^\beta, \varepsilon), \tag{30}$$

In this precise case, one can get the functions ϕ_i^α as follows

$$\phi_i^\alpha = \frac{r^\alpha (v_i^{\alpha*} + V_i^\alpha) n^\beta}{K^\alpha} \left(\sum_{ij} b_{ij}^{\alpha\beta} v_i^{\alpha*} v_j^{\beta*} + \sum_{ij} b_{ij}^{\alpha\beta} V_i^\alpha (v_j^{\beta*} + V_j^\beta) - \sum_j b_{ij}^{\alpha\beta} (v_j^{\beta*} + V_j^\beta) \right). \tag{31}$$

In (31), if $\alpha = 1$, then $\beta = 2$ and reciprocally. Keeping $N^\alpha - 1$ variables, the eigenvalues of the linear part of system (30) have negative real parts. Then, the conditions required to apply the Fenichel central manifold theorem are obtained. The central manifold can be developed as an ε power. In this example, the equations for the populations equivalent to equations (23) are the following

$$\begin{aligned}\frac{dn^1}{dt} &= r^1 n^1 \left[1 - n^1/K^1 - (n^2/K^1) \left(\sum_{ij} b_{ij}^{12} v_i^{1*} v_j^{2*} + \sum_{ij} b_{ij}^{12} V_i^1 (v_j^{2*} + V_j^2) \right) \right], \\ \frac{dn^2}{dt} &= r^2 n^2 \left[1 - n^2/K^2 - (n^1/K^2) \left(\sum_{ij} b_{ij}^{21} v_i^{2*} v_j^{1*} + \sum_{ij} b_{ij}^{21} V_i^2 (v_j^{1*} + V_j^1) \right) \right].\end{aligned}\quad (32)$$

We have used the slow time t instead of the rapid time τ . These equations can be rewritten in a simpler form

$$\begin{aligned}\frac{dn^1}{dt} &= r^1 n^1 \left[1 - n^1/K^1 - (n^2/K^1) \left(\sum_{ij} b_{ij}^{12} v_i^{1*} v_j^{2*} + 0(\varepsilon) \right) \right], \\ \frac{dn^2}{dt} &= r^2 n^2 \left[1 - n^2/K^2 - (n^1/K^2) \left(\sum_{ij} b_{ij}^{21} v_i^{2*} v_j^{1*} + 0(\varepsilon) \right) \right].\end{aligned}\quad (33)$$

The non-perturbed system for $\varepsilon = 0$ is

$$\begin{aligned}\frac{dn_1}{dt} &= r_1 n_1 [1 - n_1/K_1 - b_{12} n_2/K_1], \\ \frac{dn_2}{dt} &= r_2 n_2 [1 - n_2/K_2 - b_{21} n_1/K_2],\end{aligned}\quad (34)$$

For certain conditions of the parameters r_1 , r_2 , K_1 , K_2 , b_{12} and b_{21} , system (34) is a Morse-Smale system (see appendix 2) and consequently is structurally stable. In this form, we returned to the classical competition model. But, now the global interspecific parameters b^{12} or b^{21} at first order are calculated from the equilibrium activity frequencies through the following relations

$$b^{12} = \sum_{r,s} b_{rs}^{12} v_r^{1*} v_s^{2*} \quad \text{and} \quad b^{21} = \sum_{r,s} b_{rs}^{21} v_r^{2*} v_s^{1*}.\quad (35)$$

It is interesting to notice that the global interspecific parameters depend upon the equilibrium activity frequencies for the animals of species 1 or 2. The previous relations establish links between the individual and the population level. On the other hand, system (26) is composed of $2N$ equations (for 2 species and N activities for animals in each species) while system (32) is composed of only 2 equations. Jumping from the individual to the population level generates an important reduction in the number of variables.

Parameters b_{rs}^{12} and b_{rs}^{21} can vary very much. If, for some pairs of activities, animals strongly compete, then these parameters are large. As a consequence, the value of the global parameters b^{12} and b^{21} is not fixed. It will depend upon the activity frequencies v_r^{1*} and v_s^{2*} of the animals of both species.

Thus, if the animals change their activity sequences v_r^{1*} and v_s^{2*} to $v_r^{1*} + \Delta v_r^{1*}$ and $v_s^{2*} + \Delta v_s^{2*}$, where Δv_r^{1*} and Δv_s^{2*} are the variations in the activity frequencies, the global parameters of interactions between the species change, b^{12} and b^{21} become $b^{12} + \Delta b^{12}$ and $b^{21} + \Delta b^{21}$ with

$$\begin{aligned}\Delta b^{12} &= \sum_{r,s} b_{rs}^{12} [\Delta v_r^{1*} v_s^{2*} + v_r^{1*} \Delta v_s^{2*}] \\ \text{and} \\ \Delta b^{21} &= \sum_{r,s} b_{sr}^{21} [\Delta v_r^{1*} v_s^{2*} + v_r^{1*} \Delta v_s^{2*}],\end{aligned}\quad (36)$$

where Δb^{12} and Δb^{21} are variations of the global interspecific parameters at first order.

Equations (34) can be non dimensionalized by defining new variables and parameters

$$\frac{du^1}{dt'} = u^1[1 - u^1 - a^{12}u^2], \quad \frac{du^2}{dt'} = \rho u^2[1 - u^2 - a^{21}u^1], \quad (37)$$

with

$$u^i = \frac{n^i}{K^i} \quad i = 1, 2, \quad t' = r_1 t, \quad \rho = \frac{r^2}{r^1}, \quad a^{12} = b^{12} \frac{K^2}{K^1} \quad \text{and} \quad a^{21} = b^{21} \frac{K^1}{K^2}.$$

Four steady states $(0,0)$, $(1,0)$, $(0,1)$ and $(u_1^* = \frac{1-a^{12}}{1-a^{12}a^{21}}, u_2^* = \frac{1-a^{21}}{1-a^{12}a^{21}})$ exist.

Except in the case of weak competition, for which $a^{12} < 1$ and $a^{21} < 1$, the steady state point (u_1^*, u_2^*) is unstable and, depending upon the initial conditions or upon the values of the parameters, the system evolves either towards $(1,0)$ or $(0,1)$ which are stable. This means that only one species can survive. In summary, in strong competition, only one species survives. In weak competition, both can coexist. Our hierarchical approach includes an approximation which must be checked. Let us consider a particular case and compare numerical simulations of the whole set of equations for subpopulations and of the reduced set for populations.

3.4. Numerical Simulations

3.4.1 Strong competition case

Consider the example of two populations and three activities

$$\begin{aligned} \frac{dn_1^1}{dt} &= 100 \left(-3.2n_1^1 + 0.2n_2^1 + 0.3n_3^1 \right) + n_1^1[1 - n^1], \\ \frac{dn_2^1}{dt} &= 100 \left(-0.2n_2^1 + 1.5n_1^1 \right) + n_2^1[1 - n^1] - 4.2n_2^1 n_2^2, \\ \frac{dn_3^1}{dt} &= 100 \left(-0.3n_3^1 + 1.7n_1^1 \right) + n_3^1[1 - n^1] - 4.5n_3^1 n_3^2, \\ \frac{dn_1^2}{dt} &= 100 \left(-2.2n_1^2 + 0.3n_2^2 + 0.45n_3^2 \right) + n_1^2[1 - n^2], \\ \frac{dn_2^2}{dt} &= 100 \left(-0.3n_2^2 + 0.9n_1^2 \right) + n_2^2[1 - n^2] - 4.1n_2^1 n_2^2, \\ \frac{dn_3^2}{dt} &= 100 \left(-0.45n_3^2 + 1.3n_1^2 \right) + n_3^2[1 - n^2] - 4.5n_3^1 n_3^2, \end{aligned} \quad (38)$$

For simplicity, we have chosen the canonical form with $r^1 = r^2 = 1$. For each species, we have a branching activity graph, branching from activity 1 towards 2 and 3. In this case, we have chosen a scaling factor equal to 100. Figure 2 (a) presents a computer simulation of the above equations. Instead of presenting the six subpopulations, we present the result

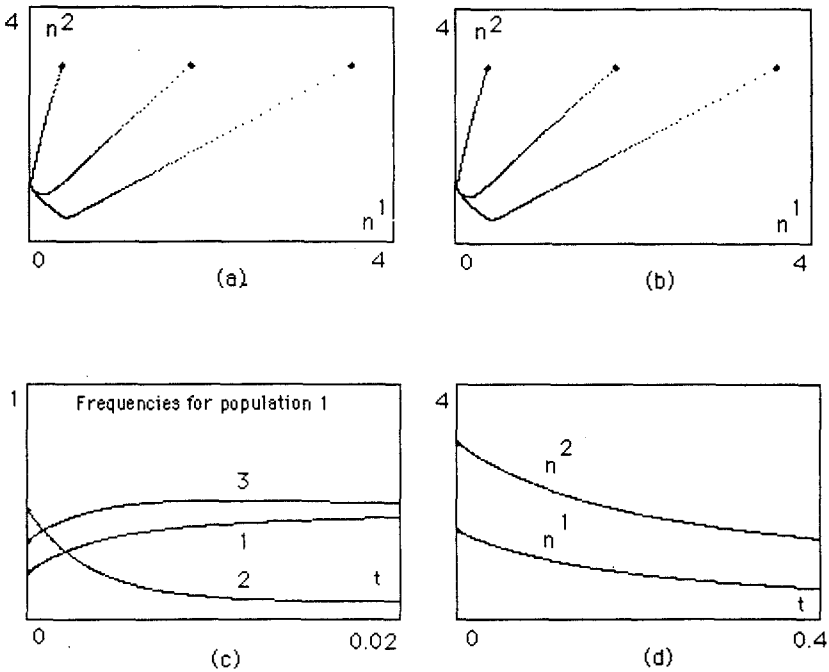


Fig.2. Strong competition case. (a) $R = 100$ that is $\epsilon = 0.01$. Simulation of the whole set of equations showing that for various initial conditions, the trajectories are converging towards (0,1). (b) Simulation of the reduced set of equations with similar trajectories. (c) time variation of the activity frequencies of population 1. (d): time variation of the total populations 1 and 2. The comparison between (c) and (d) shows two very different time scales for subpopulations and populations variables.

for the two population variables n^1 and n^2 obtained by summation over the three subpopulations corresponding to activity classes. Figure 2 (a) shows that trajectories with various initial conditions are converging towards (0,1) which is the sign of strong competition. Using equations (29) let us calculate the equilibrium activity frequencies

$$\begin{aligned} v_1^{1*} &= 0.0706, & v_2^{1*} &= 0.529, & v_3^{1*} &= 0.4, \\ v_1^{2*} &= 0.145, & v_2^{2*} &= 0.435, & v_3^{2*} &= 0.419. \end{aligned} \quad (39)$$

Then, using equations (35), one gets the global competition parameters

$$\begin{aligned} a^{12} &= b_{22}^{12} v_2^{1*} v_2^{2*} + b_{33}^{12} v_3^{1*} v_3^{2*} = 1.723, \\ a^{21} &= b_{22}^{21} v_2^{1*} v_2^{2*} + b_{33}^{21} v_3^{1*} v_3^{2*} = 1.683. \end{aligned} \quad (40)$$

These parameters are larger than unity which is in agreement with the strong competition case. Figure 2 (b) shows the result of the numerical simulation of the global competition equations which are

$$\frac{dn^1}{dt} = n^1[1 - n^1 - 1.723 n^2], \quad \frac{dn^2}{dt} = n^2[1 - n^2 - 1.683 n^1]. \quad (41)$$

The simulation shows that the trajectories of the global equations are nearly identical to the trajectories obtained in figure 2 (a). It is a Morse-Smale system (see appendix 2) and our approximation at first order is then valid. Figures 2 (c) and (d) respectively present the time variations of the activity frequencies for species 1 and the time variation of the population variables for the same initial conditions (0.3, 0.7, 0.5, 1., 1., 1.) obtained from the whole set of equations. Their comparison shows that as a result of a choice of a large scaling factor $R = 100$, that is $\epsilon = 0.01$, the characteristic time scales for intra-population frequencies and for population variables are very different. Typically, for ϵ equal to about 0.01, the approximation is valid.

In order to test the validity, one can define measures of the differences between the population trajectories calculated from the reduced set and from the whole set of equations. Such methods are used to characterize the success of aggregation processes such as Iwasa et al. (1989). In our study, the theorem proves that there exists a central manifold and that for enough small values of ϵ , the trajectories tend to the approximate ones at an exponential rate. In this application, the time scales are really very different and ϵ should probably be smaller than 0.01.

It is interesting to note that ϵ does not need to be known because finally it does not appear in the approximated population equations. All is needed is to apply the theorem, i.e. to have some stability conditions verified for the intra-population part of the equations (real parts of all the eigenvalues being negative for the intra-population terms). Then, there exists a central manifold with required properties and, for ϵ sufficiently small, one can use the global population equations instead of the whole set of equations.

3.4.2. From strong to weak competition

Usually, in order to go from strong to weak competition, one considers smaller values of the competition parameters. Now, we consider a case which is still derived from the previous case but in which the parameters of the activity transition graph have been changed. The equations are

$$\begin{aligned}
 \frac{dn_1^1}{dt} &= 100(-0.032n_1^1 + 0.2n_2^1 + 0.3n_3^1) + n_1^1[1 - n^1], \\
 \frac{dn_2^1}{dt} &= 100(-0.2n_2^1 + 0.015n_1^1) + n_2^1[1 - n^1] - 4.2n_2^1n_2^2, \\
 \frac{dn_3^1}{dt} &= 100(-0.3n_3^1 + 0.017n_1^1) + n_3^1[1 - n^1] - 4.5n_3^1n_3^2, \\
 \frac{dn_1^2}{dt} &= 100(-2.2n_1^2 + 0.3n_2^2 + 0.45n_3^2) + n_1^2[1 - n^2], \\
 \frac{dn_2^2}{dt} &= 100(-0.3n_2^2 + 0.9n_1^2) + n_2^2[1 - n^2] - 4.1n_2^1n_2^2, \\
 \frac{dn_3^2}{dt} &= 100(-0.45n_3^2 + 1.3n_1^2) + n_3^2[1 - n^2] - 4.5n_3^1n_3^2,
 \end{aligned} \tag{42}$$

The inter-population part is the same as in the previous model, i.e. we have large values for the competition parameters. Thus, we remain in a case of large competition parameters. But, a new sequence of activities for animals of species 1 is now chosen. Figure 3 shows the

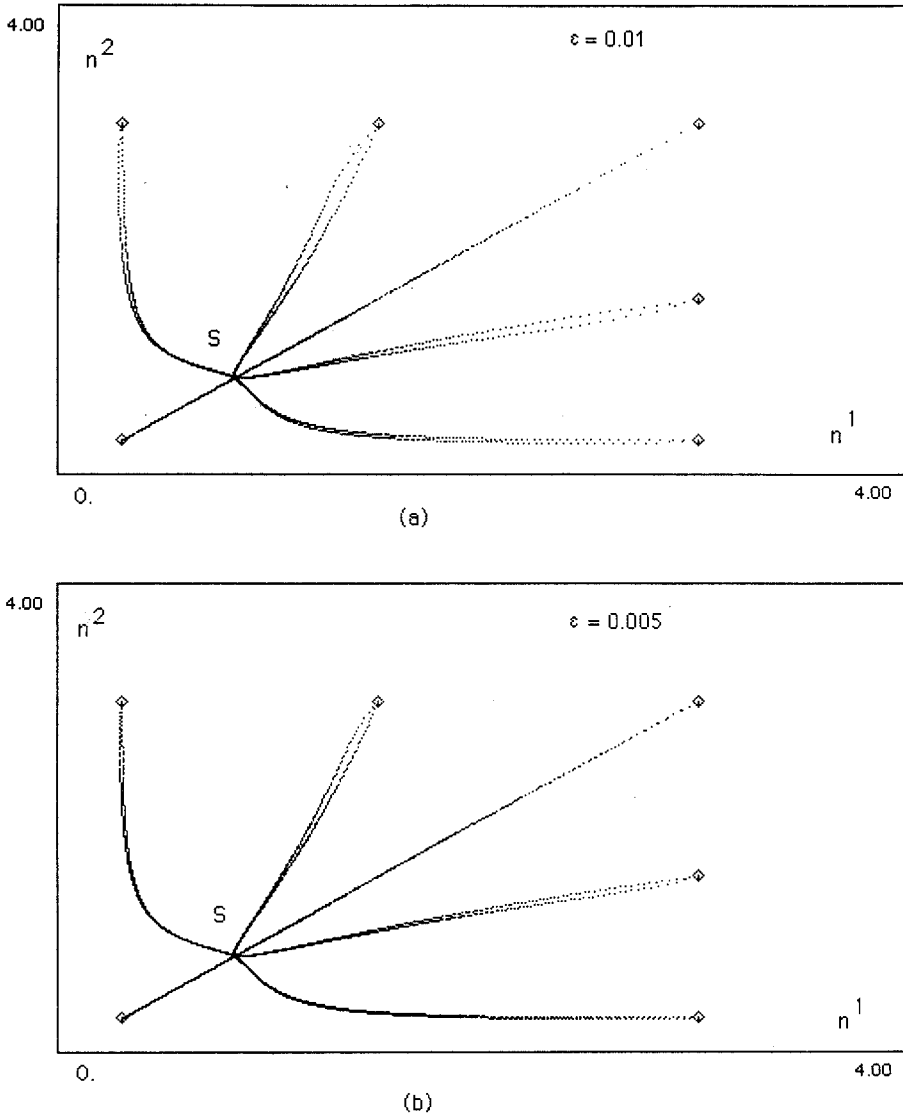


Fig. 3. Weak competition case. $R = 100$ that is $\epsilon = 0.01$. Simulation of the whole set of equations and of the global equations for different values of ϵ : (a) $\epsilon = 0.01$ and (b) $\epsilon = 0.005$. This figure shows that the phase portrait is kept. For $\epsilon = 0.005$, both trajectories are nearly confounded. For various initial conditions, the trajectories are now converging towards a stable node $S(n^{1*}, n^{2*})$. The change in the activity sequence of animals of species 1 has an important consequence, that is the two species can now coexist. The numerical of the reduced set of equations is not shown because it exhibits similar trajectories.

variations of the population variables n^1 and n^2 obtained by numerical simulations of the whole set of equations (42). This figure shows that all the trajectories are now converging towards the steady state point (n^{1*}, n^{2*}) . This means that we are in a case of weak competition with coexistence of the two species. Indeed, using equations (29), let us calculate the new values of the equilibrium activity frequencies for species 1 (unchanged for species 2)

$$v_1^{1*} = 0.884, \quad v_2^{1*} = 0.0662, \quad v_3^{1*} = 0.0500, \quad (43)$$

Contrary to the previous case, the animals of species 1 are doing activity 1 for most of their time (about 88%), only few of them are doing activities 2 and 3 for which they are in strong competition with animals of species 2. Consequently, we expect the global competition parameters to be much smaller than in the previous case. Indeed, this is the case and we get

$$\begin{aligned} a^{12} &= b_{22}^{12} v_2^{1*} v_2^{2*} + b_{33}^{12} v_3^{1*} v_3^{2*} = 0.2157, \\ a^{21} &= b_{22}^{21} v_2^{1*} v_2^{2*} + b_{33}^{21} v_3^{1*} v_3^{2*} = 0.2107. \end{aligned} \quad (44)$$

These parameters are smaller than unity which is in agreement with the weak competition case. Then, we get global competition equations

$$\begin{aligned} \frac{dn^1}{dt} &= n^1 [1 - n^1 - 0.2157 n^2], \\ \frac{dn^2}{dt} &= n^2 [1 - n^2 - 0.2107 n^1]. \end{aligned} \quad (45)$$

The trajectories of the global equations and of the total system of equations are presented on the same figure 3. For $\epsilon = 0.005$, they are nearly identical. Phase portraits are globally unchanged. Similar to the previous case, time variations of the activity frequencies and of the population variables obtained from the whole set of equations show very different time scales which are not shown.

4. PREY-PREDATOR MODELS AND ACTIVITY SEQUENCES

4.1. Classical Prey-Predator Model

The earliest predator-prey model is the Lotka-Volterra model which exhibits trajectories of various amplitudes and time periodicity with respect to initial conditions. These trajectories are centers. This model assumes exponential growth of the preys in absence of predators. It also requires a non bounded predation pressure for preys. More realistic classical predator-prey models have been developed (see May, 1976; Murray, 1989; Volterra, 1931). Let us recall a classical prey-predator model. The following differential equations describe the predator-prey interaction

$$\begin{aligned}\frac{dn^1}{dt} &= rn^1 \left(1 - \frac{n^1}{K} - \frac{kn^2}{(n^1+D)} \right), \\ \frac{dn^2}{dt} &= sn^2 \left(1 - \frac{hn^2}{n^1} \right),\end{aligned}\tag{46}$$

where r, s, K, k, D and h are positive constants. r and s are, respectively, linear growth rates for the preys and the predators. K is the carrying capacity of the prey. In absence of predators, the prey population obeys a logistic growth equation. k and h are predator-prey coefficients of interactions. The predation term shows a saturation effect for large prey densities. It is very useful to rewrite the system in a non-dimensional form with new variables u and v and only three parameters a, b and d

$$\begin{aligned}\frac{du}{d\tau} &= u(1-u) - \frac{auv}{(u+d)}, \\ \frac{dv}{d\tau} &= bv\left(1 - \frac{v}{u}\right),\end{aligned}\tag{47}$$

where

$$u(\tau) = \frac{n^1(t)}{K}, \quad v(\tau) = \frac{hn^2(t)}{K}, \quad \tau = rt, \quad a = \frac{k}{hr}, \quad b = \frac{s}{r} \quad \text{and} \quad d = \frac{D}{K}.$$

There exists a steady state point with positive populations (u^*, v^*) such as

$$u^* = v^* \quad \text{and} \quad u^* = \frac{(1-a-d) + [(1-a-d)^2 + 4d]^{1/2}}{2}.\tag{48}$$

A stability analysis around this steady state point can be performed. For a detailed analysis, we refer to [35]. Roughly, for some values of the parameters in the tri-dimensional phase plane (a, b, d) , there is a stable domain, for which all the eigenvalues of the community matrix are negative. In this case, the steady state point is a stable point. For other parameter values, the steady state point is unstable for which limit cyclic oscillations of the two populations occur. Consequently, there is a bifurcation surface of Hopf-Andronov in the tri-dimensional parameter plane separating stable and unstable domains.

4.2. Activity Dependent Predator-Prey Models

We consider two interacting species 1 and 2 with activity sequences. Animals can still select different activities i all day long. Consider the following dynamical differential equations

$$\begin{aligned}\frac{dn_i^1}{dt} &= R \left(\sum_s k_{is}^1 n_s^1 - \sum_s k_{si}^1 n_i^1 \right) + n_i^1 \left(r \left[1 - \frac{n^1}{K} \right] - \sum_k \frac{k_{ik}^{12} n_k^2}{(n^1+D)} \right), \\ \frac{dn_i^2}{dt} &= R \left(\sum_s k_{is}^2 n_s^2 - \sum_s k_{si}^2 n_i^2 \right) + sn_i^2 \left(1 - \frac{n^2}{\sum_k P_{ik}^{21} n_k^1} \right).\end{aligned}\tag{49}$$

R is the scaling factor between intra-population and inter-population terms. The terms k_{rs}^α

still describe activity changes for animals of species 1 or 2. Other terms describe growth of the populations and their interactions. r and s are linear growth rates for preys and predators, respectively. K is the carrying capacity for the prey. k_{ik}^{12} are predator-prey parameters between preys 1 doing activity i (for instance search of food of type i) and predators 2 doing activity k (hunting preys 1). Similarly, p_{ik}^{21} are predator-prey parameters between prey 1 doing activity k and predator 2 doing activity i .

Various other choices of equations could be made. Here, we have chosen that the predation term in the equation for the predator is proportional to the subpopulations of the preys which are vulnerable. For some couples of activities (i,k) , the preys are vulnerable. For others, they are hidden from predators. In the vulnerable case, the coefficients k_{ik}^{12} and p_{ik}^{21} will be large and in the other case, the coefficients will be small and even equal to zero. As a consequence, the strength of the predation is not fixed *a priori* but will be fixed by the individual behaviour of the animals.

All conditions required to apply the central manifold theorem are realized. Thus, there exists a central manifold which can be calculated. At first order, one can obtain two differential equations governing population variables of the preys and of the predators $n^1(t)$ and $n^2(t)$

$$\begin{aligned}\frac{dn^1(t)}{dt} &= rn^1 \left[1 - \frac{n^1}{K} \right] - \frac{k^{12}n^1n^2}{(n^1+D)}, \\ \frac{dn^2(t)}{dt} &= sn^2 \left[1 - \frac{h^{21}n^2}{n^1} \right].\end{aligned}\quad (50)$$

The global interspecific parameters k^{12} and h^{21} are given by

$$k^{12} = \sum_{r,s} k_{rs}^{12} v_r^{1*} v_s^{2*} \quad \text{and} \quad h^{21} = \sum_r \left(\frac{v_r^{2*}}{\sum_s p_{rs}^{21} v_s^{1*}} \right). \quad (51)$$

Parameters k_{rs}^{12} and p_{rs}^{21} determine the values of the global predation parameters k^{12} and h^{21} of the animals.

4.3. Numerical Simulations

Consider an example with one prey population doing three possible activities. For simplicity, we assume that the predators only are engaged in one activity: hunting preys. This system is described by

$$\begin{aligned}\frac{dn_1^1}{dt} &= 100(-3.2n_1^1 + 0.2n_2^1 + 0.3n_3^1) + n_1^1[1 - n^1], \\ \frac{dn_2^1}{dt} &= 100(-0.2n_2^1 + 1.5n_1^1) + n_2^1[1 - n^1] - \frac{6.n_2^1n^2}{[n^1 + 0.2]}, \\ \frac{dn_3^1}{dt} &= 100(-0.3n_3^1 + 1.7n_1^1) + n_3^1[1 - n^1] - \frac{1.n_3^1n^2}{[n^1 + 0.2]}, \\ \frac{dn^2}{dt} &= 0.1n^2 \left(1 - \frac{n^2}{[1.2n_2^1 + 0.2n_3^1]} \right).\end{aligned}\quad (52)$$

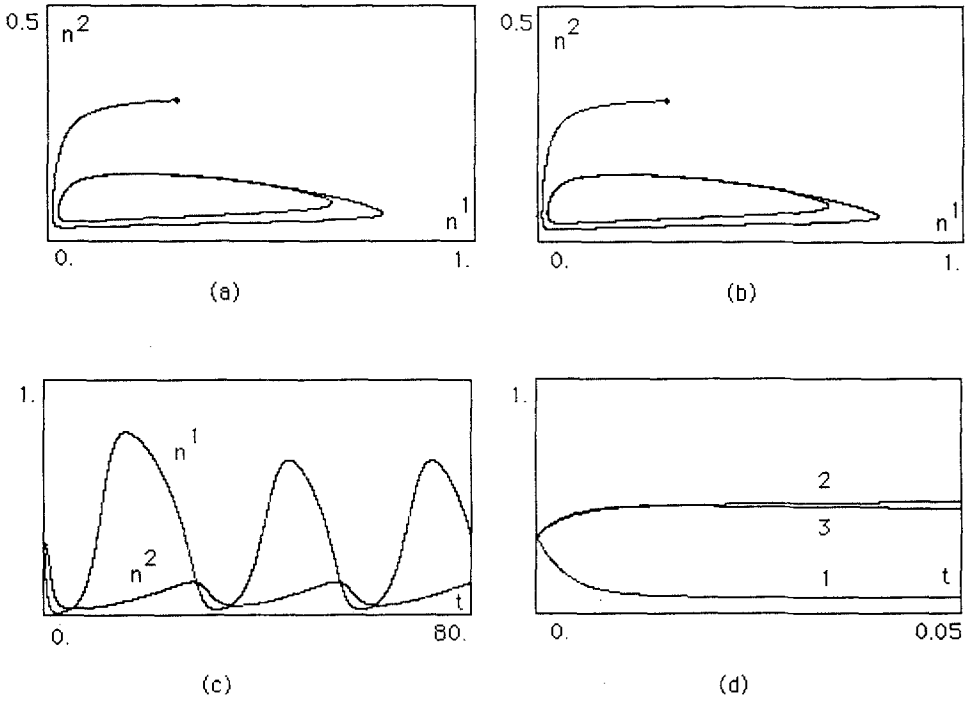


Fig. 4. Prey-predator models with activity sequences (a) $R = 100$. Simulation of the whole set of equations showing a stable limit cycle. (b) Simulation of the reduced set of equations with similar trajectories. (c): time variation of the total populations of preys 1 and predators 2. (d) time variation of the activity frequencies of preys population 1. The comparison between (c) and (d) shows two very different time scales for subpopulations and global variables explaining the agreement between (a) and (b).

We see that the prey is hidden from its predator in activity 1 and is 6 times more exposed to the predator attacks in activity 2 than in activity 3. Figure 4 (a) presents a computer simulation of the four previous equations with the initial conditions $(0.1, 0.1, 0.1, 0.3)$. We present the result for the two global populations n^1 and n^2 with summation of the three subpopulations of the prey. Figure 4 (a) shows that there exists a stable limit cycle for the prey and predator total populations. The equilibrium activity frequencies are

$$v_1^{1*} = 0.0706, \quad v_2^{1*} = 0.529, \quad v_3^{1*} = 0.400. \tag{53}$$

Then, one can calculate the values of the global parameters

$$k^{12} = k_2^{12} v_2^{1*} + k_3^{12} v_3^{1*} = 6 v_2^{1*} + 1 v_3^{1*} = 3.58, \tag{54}$$

$$h^{21} = \frac{1}{p_2^{21} v_2^{1*} + p_3^{21} v_3^{1*}} = \frac{1}{1.2 v_2^{1*} + 0.2 v_3^{1*}} = 1.40.$$

Then, the global approximated prey-predator equations are at first order

$$\begin{aligned}\frac{dn^1}{dt} &= n^1 \left[1 - n^1 - \frac{3.58n^2}{[n^1 + 0.2]} \right], \\ \frac{dn^2}{dt} &= 0.1n^2 \left[1 - \frac{1.40n^2}{n^1} \right].\end{aligned}\tag{55}$$

The simulation is presented on figure 4 (b) with the initial condition (0.3,0.3). The simulation shows that the trajectory of the global variables are nearly identical to the trajectory obtained previously for the whole set of four equations. This shows that the approximation of using equilibrium frequencies for the intra-group part is correct. Figures 4 (c) and (d) respectively present the time variations of the global variables and of the activity frequencies for the preys for the same initial condition obtained from the whole set of equations. Their comparison shows that as a result of a choice of a large scaling factor $R = 100$, that is $\epsilon = 0.01$, the characteristic time scales for intra-population frequencies and for population variables are very different. As soon as the scaling factor R is large enough, the central manifold theorem can be applied. Instead of simulating $2N$ equations (with N activities for each interacting population), a reduced set of two global equations only can be simulated.

Now, let us assume that during the year, due to climate changes, the preys may modify their activity sequences. For instance, some food sources may become rare and the animals may have to search for other food. This will modify their activities sequences. As a consequence, the activity frequencies of the preys may vary and this will induce in turn a variation in the global parameters. For instance, with frequencies of the preys now equal to

$$v_1^{1*} = 0.884, \quad v_2^{1*} = 0.0663, \quad v_3^{1*} = 0.0501,\tag{56}$$

one obtains new values of the predator-prey parameters, which are $k^{12} = 0.448$ and $h^{21} = 11.2$ and two global competition equations

$$\begin{aligned}\frac{dn^1}{dt} &= n^1 \left[1 - n^1 - \frac{0.448n^2}{[n^1 + 0.2]} \right], \\ \frac{dn^2}{dt} &= 0.1n^2 \left[1 - \frac{11.2n^2}{n^1} \right].\end{aligned}\tag{57}$$

The numerical simulation of this reduced set of equations is presented in figure 5. The simulation shows that with various initial conditions, the trajectories of the global variables are now converging towards a stable point S . With $R = 100$, that is $\epsilon = 0.01$, computer simulations of the whole set of four equations exhibit similar trajectories. This example shows that a change in the average individual behaviour of the animals may strongly modify the stability and the structure of the dynamical solutions of the interacting species. It also shows that some stable configurations may appear during certain parts of the year. By selecting new activities better adapted to environment changes, a bifurcation in the (n^1, n^2) plane may occur. This example is a typical case of what can be called an interaction between the individual and the population levels, i.e. the effect of a change at the individual level on the populations.

It seems that the problem of the dynamics or of the stability of the ecosystem cannot

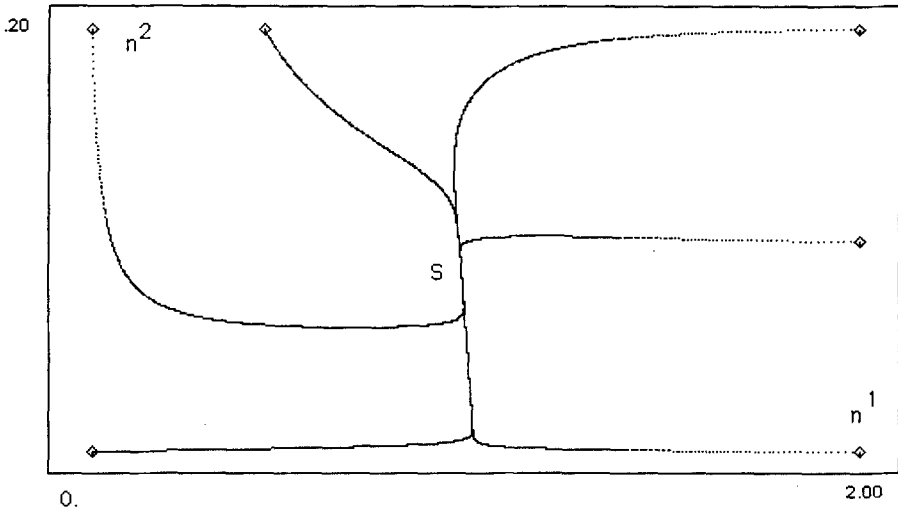


Fig. 5. Prey-predator models with activity sequences with a scaling factor $R = 100$. Simulation of the whole set of equations showing that the trajectories now evolve towards a stable steady state point S .

be considered from a global point of view alone, but that interactions between the individual, population and ecosystem levels have to be taken into account. A change in each of these levels has an impact on the other levels. The whole dynamics is governed by these coupled dynamics.

5. DISCUSSION AND CONCLUSION

In the future, we would like to apply these competition and prey-predator models to the case of two sibling bird species, *Hippolais polyglotta* and *H. icterina*, coexisting near Dijon (France) which are studied by the Laboratory of Ecology of our University. The two species are morphologically indistinguishable, there is only a difference in their songs and probably a slight one in their behaviours. One of the species occurs in northern Europe the other in southern Europe. There is a band-like area in Europe (passing over Burgundy) where the two species coexist. It was observed that one of the two species is gradually replaced by the other. We plan to use activity dependent competition or prey-predator models to answer the following questions: can the observed differences in the food sources of the two species explain the disappearance of one of them? Does a predator attack more often the young of one species than those of the other species, due to differences in the average individual behaviour? We hope that this class of hierarchical prey-predator and competition models coupling the activity sequences to the interspecific interactions will help in confirming or suppressing assumptions made to understand the extinction of one of these species. Right now, some of us are collecting data.

The general method that we have mentioned in section 1 can be used to study complex

systems composed of a large number of elements and presenting a hierarchical structure. These systems cannot be studied very easily in another manner. Indeed, if the system contains many possible states, it asks for the description of a set of a very large number of coupled differential equations. The computer simulation of such a system will need very much computer time and the results (if obtained) will be very difficult to interpret due to the complexity of the information obtained. On the contrary, if the hierarchical partition corresponds to few groups with many states in each of them, one obtains a set of a few number of differential equations and an important reduction in the number of variables. It also signifies that separating the levels, then the complexity of the system is much reduced.

One of the aspects of this article is to stress the point that multi-level systems evolve as a result of coupled dynamical processes at the different levels of organization of the hierarchical system. The dynamics must not be considered in one level alone but as a coordinated process of dynamics in each level of the hierarchically organized system (Jean, 1982). More complete models should include interspecific interactions for animals of different ages, doing various activities and belonging to different phenotypes in interactions with the environment. Many problems are also linked to the spatial hierarchies and scales which have not been treated here. Our models concern hierarchical systems with successive clusters in population dynamics, i.e. populations subdivided into subpopulations, and again subdivided into sub-subpopulations and so on. All the equations are homogeneous and the spatial hierarchies are not taken into account. In this way, possibilities of migration at different spatial scales should also be considered. Here, we have limited our study to the limits of this method in connection with classical ecological models before considering to investigate the method for multi-level and very large scale systems in space.

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APPENDIX 1

Calculation of the Central Manifold

In order to simplify the calculations, assuming that the f_i^α are linear, the equations (20) can be rewritten in the next form

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

where N^α and Φ^α are functions of $\mathbf{n} = (n^1, n^2), V^\alpha, V^\beta, v^{\alpha*}, v^{\beta*}$ which can be easily explained. V^α, Φ^α have values in $\mathbb{R}^{N^\alpha-1}$ and $\bar{A}^\alpha = (\bar{A}_{ij}^\alpha)$ i and $j \in [1, N^\alpha-1]$. Let us look for the central manifold according to the following form

$$V^\alpha(\mathbf{n}, \varepsilon) = \varepsilon W^\alpha(\mathbf{n}, \varepsilon) \quad \text{with} \quad W^\alpha(\mathbf{n}, \varepsilon) = W_1^\alpha + \varepsilon W_2^\alpha + o(\varepsilon).\tag{A-2}$$

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

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

Substitute of (A-2) into (A-3). Then, identify term of order ε

$$\bar{A}^\alpha W_1^\alpha + \Phi^\alpha(\mathbf{n}, v^{\alpha*}, v^{\beta*}) = 0.\tag{A-4}$$

where $\Phi^\alpha(\mathbf{n}, v^{\alpha*}, v^{\beta*}) = \Phi^\alpha(\mathbf{n}, \mathbf{0}, \mathbf{0}, v^{\alpha*}, v^{\beta*})$. Finally, because \bar{A}^α is inversible, one obtains the result given in equation (21)

$$W_1^\alpha = -(\bar{A}^\alpha)^{-1}(\Phi^\alpha(\mathbf{n}, v^{\alpha*}, v^{\beta*})),\tag{A-5}$$

Identifying terms of different order ε in (A-3), we have an iterative process which allows to obtain the functions W_i^α for any i .

APPENDIX 2

Structural Stability: The Andronov-Pontryagin Theorem

Definition: Let X be a vector field defined in a neighbourhood of a disk D of \mathbb{R}^2 . X is said structurally stable if on D there exists a neighbourhood N of X in the space of vector fields defined in a neighbourhood of D , in the C^1 -topology on D , such that for each $Y \in N$, there exists an homeomorphism h_Y on a neighbourhood of D ($h_Y: V \rightarrow W$, V and W are neighbourhoods of D) sending orbits of X in V into orbits of Y in W . One says that h_Y is a topological equivalence between X and Y on D . The structural stability of a system is characterized by the following Andronov-Pontryagin (Andronov & Pontryagin, 1937).

Theorem: Let X be a vector field defined on a neighbourhood of D such that:

1) All singular points and all periodic orbits of X are hyperbolic, (there is only a finite number of such critical orbits).

2) There are no connections between saddle points of X (i.e. there is no point q whose α and ω -limit are saddle points).

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