# Hierarchically Organized Populations: Interactions between Individual, Population, and Ecosystem Levels

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ABSTRACT

We consider a population of individuals which can be distributed in different equivalence classes. These classes are gathered in groups so that intragroup transformations are much more frequent than intergroup ones. We study linear systems in general, illustrated by the example of coupled individual and population levels. Then, we study nonlinear systems with the example of coupled population and ecosystem levels. We give methods to derive the dynamical equations for the different levels and to calculate interlevel coupling terms. We compare the coupling effects in the linear and in the nonlinear case.

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## 1. INTRODUCTION

In ecology, one distinguishes generally three levels of organization: the individual level, the population level, and the ecosystem level. There are different models for each level of organization. At the individual level, the chosen variables can be the number of animals in a given state: hunting, resting, hiding, and so on. At the population level, one can choose the number of animals having a certain age: Leslie's model or the thermodynamical Demetrius model [1–5]. At the ecosystem level, one usually chooses the numbers of animals of species, as in the Lotka-Volterra model or the thermodynamical Kerner model [7–9]. The purpose of this work is to try to establish connections between these different levels of organization.

The problem is double. First of all, it is necessary to use methods which permit one to obtain the equations of the population level from the knowledge of equations which have been chosen at the individual level, or similarly to obtain dynamical equations at the ecosystem level from the knowledge of equations chosen at the population level. Secondly, one can obtain coupling terms between these different levels of organization which permit one to study the interactions: the influences of one level of organization on another level.

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We believe that one should calculate the dynamical equations relative to each level and the interlevel coupling terms instead of choosing phenomenological equations at each level and phenomenological coupling terms. Indeed, the equations for a collective level are entirely determined by the equations for a more microscopic level. In choosing phenomenological equations for different levels, one may turn out to have chosen incompatible equations.

In general, the problem is rather difficult, and the separation between these three levels is not always possible. For this reason, in this paper, we have chosen to study specific systems, which can be called hierarchically organized systems, corresponding to weakly coupled levels. For instance, the probabilities per unit time for a change of state are assumed to be much larger than the probabilities for a change of age class. This assumption leads to nearly independent equations at the individual level and at the population level. Similarly, we assume that the probabilities for a change of age class are much larger than the corresponding terms associated with the prey-predator process. This assumption leads also to nearly independent equations at the population level and at the ecosystem level. In both cases, we nevertheless get interlevel coupling terms, small enough to result in nearly independent equations at each level, but giving rise to interactions between the different levels.

First of all, in Section 2, we study the general case of linear systems, illustrated by an example of the individual level coupled to the population level. In this section, we use a quite similar formalism to that of linear transformation systems [10–11]. We then study the case of nonlinear systems, particularly with the example of coupled population and ecosystem levels. The models are essentially based on the Leslie model or on the Demetrius model for the population level and on the Lotka-Volterra model for the ecosystem level. We particularly discuss the effects of the interactions between the levels of organization, and we compare the results in linear and in nonlinear models.

## 2. HIERARCHICALLY ORGANIZED LINEAR SYSTEMS

To begin with, we assume that the elements can be distributed in different equivalence classes $E_j$. Then $N_j$ is the number of elements belonging to the equivalence class $E_j$, and $n$ is the total number of classes. In linear systems of transformations, the equations for the time dependence of the populations $N_j$ are

$$\dot{N}_j = \sum_i a_{ji} N_i, \qquad \text{where} \quad \dot{N}_j = \frac{dN_j}{dt}, \quad t \text{ the time.}$$

The $a_{ji}$ are time independent and define a $n \times n$ matrix $A$. The entry $a_{ji}$

corresponds to the transformation of elements from the class $E_i$ to the class $E_j$.

The previous equations can also be written

$$\{\dot{N}\} = A\{N\},$$
$$\{\dot{N}\} = (\dot{N}_1, \dot{N}_2, \ldots, \dot{N}_n),$$
$$\{N\} = (N_1, N_2, \ldots, N_n).$$

We are going to consider a hierarchically organized system, i.e., the classes can be gathered in $\mathcal{A}$ groups. $\alpha$ is an index for the group: $\alpha = 1, \ldots, \mathcal{A}$. $\mathcal{N}_\alpha$ is the number of classes belonging to group $\alpha$. The total number of classes $n$ can be expressed as follows:

$$n = \sum_\alpha \mathcal{N}_\alpha.$$

This grouping of classes is introduced in order to reflect a hierarchy in the transformations between the elements of the system, i.e., we consider a system in which the intragroup transformations are frequent in comparison with the intergroup transformations. This means that the coefficients $a_{ij}$ for a pair of classes $i$ and $j$ belonging to the same group $\alpha$ are always much larger than the coefficients $a_{kl}$ for a pair of classes $k$ and $l$ belonging to different groups $\alpha$ and $\beta$, i.e.,

$$|a_{kl}| \ll |a_{ij}|.$$

In order to indicate to which group $\alpha$ a class belongs, we now label its population with two indices $i$ and $\alpha$: $\alpha$ is the index of the group, $i$ the index of the class belonging to this group. $N_{i\alpha}$ is thus the population of the class $E_{i\alpha}$ belonging to group $\alpha$. Thus, $i$ varies from 1 to $\mathcal{N}_\alpha$. Each group is now characterized by its own set of population numbers $\{N_\alpha\}$:

$$\{N_\alpha\} = (N_{1\alpha}, N_{2\alpha}, \ldots, N_{\mathcal{N}_\alpha \alpha}).$$

Now, let us rewrite the dynamical equations for the populations $\{N_\alpha\}$ by separating intragroup transformations and intergroup transformations:

$$\dot{N}_{i\alpha} = \underbrace{\sum_{j \in \alpha} a_{ij\alpha} N_{j\alpha}}_{\substack{\text{intragroup } (\alpha) \\ \text{transformations}}} + \underbrace{\sum_{\beta \neq \alpha} \sum_{l \in \beta} a_{il\alpha\beta} N_{l\beta}}_{\substack{\text{intergroup } (\alpha, \beta) \\ \text{transformations}}}. \tag{1}$$

The notation $j \in \alpha$ means that the class $E_{j\alpha}$ belongs to the group $\alpha$. More simply, we can write the equations in the following way:

$$\{\dot{N}_\alpha\} = A_\alpha\{N_\alpha\} + \sum_{\beta \neq \alpha} A_{\alpha\beta}\{N_\beta\}. \tag{2}$$

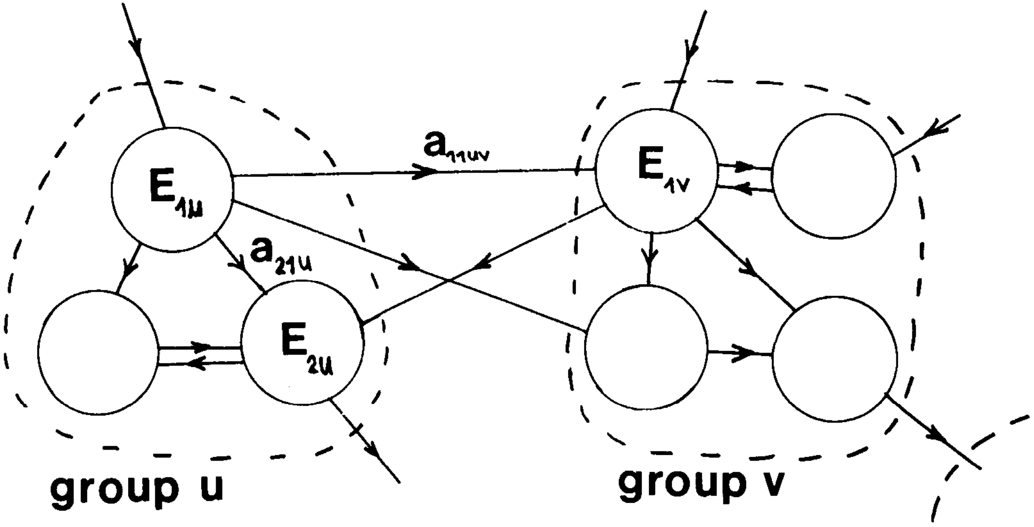

FIG. 1. The functional equivalence classes are gathered into groups of classes, in order to make intragroup transformations much more probable than intergroup ones ($|a_{ijuv}| \ll |a_{rSu}|$).

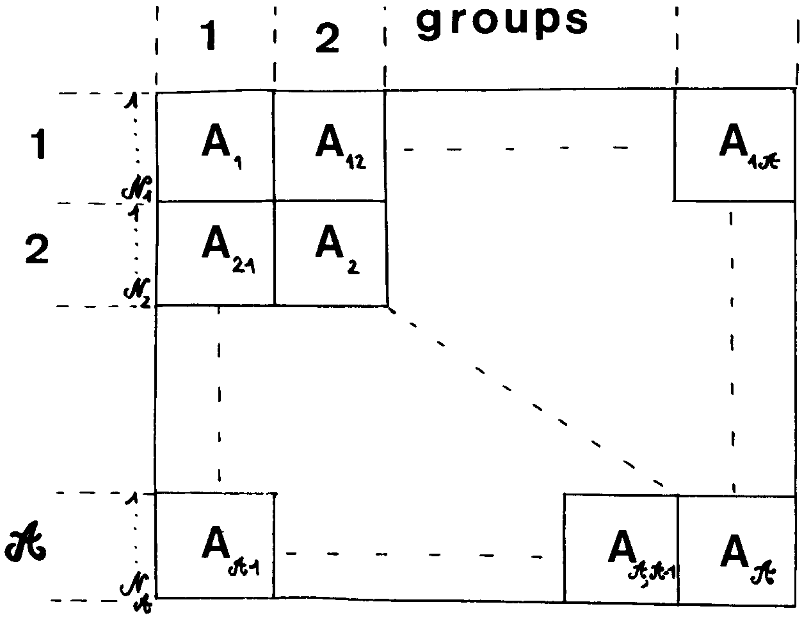

FIG. 2. The matrix $A$ is decomposed into $\mathcal{A}$ intragroup matrices $A_\alpha$ relating to intragroup ($\alpha$) transformations, and $\mathcal{A}^2 - \mathcal{A}$ intergroup matrices $A_{\alpha\beta}$ relating to intergroup ($\alpha$ and $\beta$) transformations.

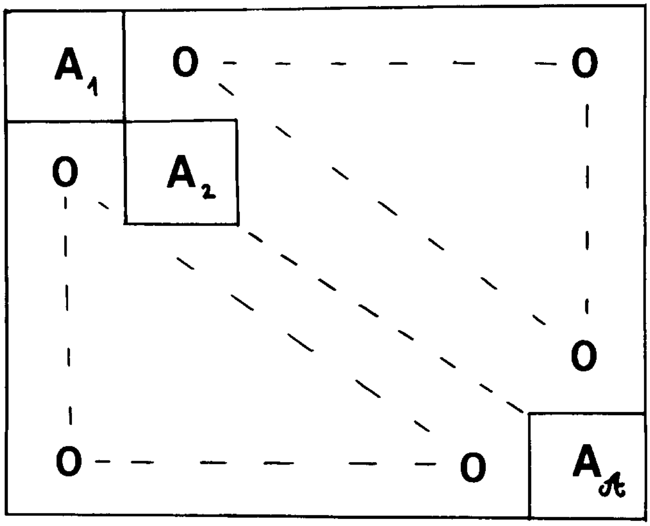

FIG. 3. For a strong hierarchy, all the intergroup matrices $A_{\alpha\beta}$ are equal to zero. All the groups are independent of each other.

$A_\alpha$ are intragroup transformation matrices, and $a_{ij\alpha}$ are the corresponding coefficients for the transformation from the class $E_{j\alpha}$ to the class $E_{i\alpha}$. $A_{\alpha\beta}$ are intergroup transformation matrices (Figures 1 and 2), and $a_{il\alpha\beta}$ are the corresponding coefficients for the transformation from the class $E_{l\beta}$ to the class $E_{i\alpha}$.

In the case where the intergroup transformations are very rare compared to the intragroup transformations, we can neglect the matrices $A_{\alpha\beta}$ and the groups of classes are independent of each other. In this approximation to the total hierarchy, the matrix $A$ is given by the Figure 3 and the time dependence of $\{N_\alpha\}$ is obtained as follows:

$$\{\dot{N}_\alpha\} \cong A_\alpha\{N_\alpha\} \tag{3}$$

$$|a_{ij\alpha}| \ggg |a_{il\alpha\beta}|. \tag{4}$$

## 3. COLLECTIVE TRANSFORMATIONS AND INTERNAL TRANSFORMATIONS

Now, let us define a collective variable $\bar{N}_\alpha$, associated with each group $\alpha$, as the average population of the group $\alpha$:

$$\bar{N}_\alpha = \frac{1}{\mathcal{N}_\alpha} \sum_{i \in \alpha} N_{i\alpha}. \tag{5}$$

Let us define a relative or internal population $n_{i\alpha}$ as the difference between the real population $N_{i\alpha}$ and the average population $\bar{N}_\alpha$:

$$n_{i\alpha} = N_{i\alpha} - \bar{N}_\alpha. \tag{6}$$

From the previous definitions, we get the following relations:

$$N_{i\alpha} = \bar{N}_\alpha + n_{i\alpha}. \tag{7}$$

$$\sum_{i=1}^{\mathcal{N}_\alpha} n_{i\alpha} = \sum_{i=1}^{\mathcal{N}_\alpha} \dot{n}_{i\alpha} = 0. \tag{8}$$

Let us consider the time dependence of the average populations. To calculate $\dot{\bar{N}}_\alpha$, let us add the $\mathcal{N}_\alpha$ equations $\dot{N}_{i\alpha}$ of group $\alpha$:

$$\sum_{i \in \alpha} \dot{N}_{i\alpha} = \sum_{i \in \alpha} \sum_{j \in \alpha} a_{ij\alpha} N_{j\alpha} + \sum_{\beta \neq \alpha} \sum_{i \in \alpha} \sum_{l \in \beta} a_{il\alpha\beta} N_{l\beta}. \tag{9}$$

Let us replace $N_{i\alpha}$ by its expression (7) and use the relation (8):

$$\begin{aligned}\sum_{i\in\alpha} \dot{N}_{i\alpha} &= \mathcal{N}_\alpha \dot{\bar{N}}_\alpha \\ &= \sum_{i\in\alpha}\sum_{j\in\alpha} a_{ij\alpha}\left(\bar{N}_\alpha + n_{j\alpha}\right) + \sum_{\beta\neq\alpha}\sum_{i\in\alpha}\sum_{l\in\beta} a_{il\alpha\beta}\left(\bar{N}_\beta + n_{l\beta}\right). \qquad (10)\end{aligned}$$

By a suitable regrouping of terms, (10) becomes

$$\begin{aligned}\mathcal{N}_\alpha \dot{\bar{N}}_\alpha = a_\alpha^* \bar{N}_\alpha &+ \sum_{\beta\neq\alpha} a_{\alpha\beta}^* \bar{N}_\beta + \sum_{i\in\alpha}\sum_{j\in\alpha} a_{ij\alpha} n_{j\alpha} \\ &+ \sum_{\beta\neq\alpha}\sum_{i\in\alpha}\sum_{l\in\beta} a_{il\alpha\beta} n_{l\beta} \qquad (11)\end{aligned}$$

with

$$a_\alpha^* = \sum_{i\in\alpha}\sum_{j\in\alpha} a_{ij\alpha} \quad \text{and} \quad a_{\alpha\beta}^* = \sum_{i\in\alpha}\sum_{l\in\beta} a_{il\alpha\beta}.$$

## 4. SLOW-VARYING COLLECTIVE POPULATIONS AND FAST-VARYING RELATIVE POPULATIONS

In many cases, we can make a supplementary assumption (12) saying that the intragroup transformations are not responsible for the variations of the average populations $\bar{N}_\alpha$. We are going to give examples of this assumption further on.

For any group $\alpha$, let

$$\sum_i \sum_j a_{ij\alpha} N_{j\alpha} = 0. \qquad (12)$$

The internal transformations can change the distribution of the elements in the different classes $E_{i\alpha}$, but they don't modify the average populations $\bar{N}_\alpha$. Only intergroup transformations can then modify the average populations $\bar{N}_\alpha$. The assumption (12), when it can be made, is very useful because it leads to a hierarchy in time associated with the hierarchy in the transformations. Indeed (12) allows us to rewrite (11) as follows:

$$\dot{\bar{N}}_\alpha = \frac{1}{\mathcal{N}_\alpha}\sum_{\beta\neq\alpha} a_{\alpha\beta}^* \bar{N}_\beta + \frac{1}{\mathcal{N}_\alpha}\sum_{\alpha\neq\beta}\sum_{i\in\alpha}\sum_{l\in\beta} a_{il\alpha\beta} n_{l\beta}. \qquad (13)$$

On the other hand, using the hierarchy assumption (4), we can neglect the intergroup transformations in comparison with the intragroup ones in the equations (1), which can be approximated by

$$\dot{N}_{i\alpha} \cong \sum_{j \in \alpha} a_{ij\alpha} N_{j\alpha}. \tag{14}$$

Thus, the equations for the average populations (13) are entirely governed by intergroup transformations, while the equations (14) for the real populations are nearly entirely governed by intragroup transformations. Comparing (13) and (14), and using the hierarchy assumption (4), we see that $\bar{N}_\alpha$ varies very slowly in time in comparison with $N_{i\alpha}$. Only intergroup transformations are responsible for the variation in time of the average populations $\bar{N}_\alpha$, and as they are much rarer than internal transformations governing the variation of $N_{i\alpha}$, we have

$$\left|\dot{\bar{N}}_\alpha\right| \ll \left|\dot{N}_{i\alpha}\right|, \qquad \text{or} \qquad \left|\dot{\bar{N}}_\alpha\right| \ll \left|\dot{\bar{N}}_\alpha\right| \left|1 + \frac{\dot{n}_{i\alpha}}{\dot{\bar{N}}_\alpha}\right|. \tag{15}$$

This is true for any class $E_{i\alpha}$ of any group $\alpha$. It can also be written

$$\left|\dot{n}_{i\alpha}\right| \gg \left|\dot{\bar{N}}_\alpha\right|. \tag{16}$$

The internal motion $|\dot{n}_{i\alpha}|$ is large compared to the average population motion $|\dot{\bar{N}}_\alpha|$. The average populations $\bar{N}_\alpha$ are slow-varying variables compared to the internal fast-varying populations $n_{i\alpha}$. The internal distribution of the elements in the classes $E_{i\alpha}$ belonging to the same group $\alpha$ fluctuates rapidly, while the average populations $\bar{N}_\alpha$ vary relatively slowly. Finally, we get the coupled equations for the average population dynamics and for the relative population dynamics:

$$\dot{\bar{N}}_\alpha = \frac{1}{\mathfrak{N}_\alpha} \sum_{\beta \neq \alpha} a^*_{\alpha\beta} \bar{N}_\beta + \frac{1}{\mathfrak{N}_\alpha} \sum_{\alpha \neq \beta} \sum_{i \in \alpha} \sum_{l \in \beta} a_{il\alpha\beta} n_{l\beta} \tag{17}$$

$$\dot{n}_{i\alpha} \cong a^*_\alpha \bar{N}_\alpha + \sum_{j \in \alpha} a_{ij\alpha} n_{j\alpha}. \tag{18}$$

In the equations (18), we neglect the intragroup transformations and also the term $-\bar{N}_\alpha$, which can be called the inertia term.

## 5. THERMODYNAMICAL TREATMENT OF RELATIVE VARIABLES

The hierarchy in time can be used in order to reduce the number of variables considerably by carrying out a thermodynamical treatment of the internal variables $n_{i\alpha}$ in each group $\alpha$. The internal fast-varying variables $n_{i\alpha}$ vary so rapidly with respect to the average populations $\bar{N}_\alpha$ that for each interval $\Delta t$ corresponding to a small variation of the average populations, we can assume statistical equilibrium for all the internal variables $n_{i\alpha}$.

Such thermodynamical treatments can be carried out [4,7,8]. In particular, one can obtain probability densities for linear systems [4,7,8]. In the case where there exists constants of the motion, one can use the Gibbs distribution for a canonical ensemble (see Appendix).

The thermodynamical treatment of the relative variables allows us to forget the internal dynamic and to replace the relative variables $n_{i\alpha}$ directly by their time averages $\langle n_{i\alpha}\rangle$ in the equations (17) for the average populations:

$$\dot{\bar{N}}_\alpha = \frac{1}{\mathcal{N}_\alpha}\sum_{\beta\neq\alpha} a^*_{\alpha\beta}\bar{N}_\beta + \frac{1}{\mathcal{N}_\alpha}\sum_{\alpha\neq\beta}\sum_{i\in\alpha}\sum_{l\in\beta} a_{il\alpha\beta}\langle n_{l\beta}\rangle. \tag{19}$$

To get the previous equations, one must multiply (17) by the densities $\rho$ and integrate over the whole space of the relative populations $n_{i\alpha}$.

The purpose of such a thermodynamical treatment of the internal variables $n_{i\alpha}$ is to reduce considerably the number of calculations. From $n$ equations (1), we only obtain $\mathcal{A}$ equations (19). The distribution of the elements in the classes $E_{i\alpha}$ fluctuates rapidly, but for long enough intervals $\Delta t$, we are not interested in each instantaneous distribution but only in the average distribution in time. In the equations (19), $\langle n_{l\beta}\rangle$ is calculated for each interval lasting $\Delta t$, and the densities $\rho$ must be renormalized for new values of $\bar{N}_\alpha$.

## 6. COUPLED INDIVIDUAL AND POPULATION LEVELS

The elements are animals belonging to the same species. These animals have different ages $i$ and can be in different states $S$. These states correspond to hunting, hiding, sleeping, searching for food, sexual activity, and so on. $\mathcal{N}_i$ is the number of possible states $S$ for an animal with age $i$. Let us denote by $N_{Si}$ the number of animals which are in a state $S$ with the age $i$, and $E_{Si}$ the corresponding equivalence class. The $\mathcal{N}_i$ classes $E_{Si}$ constitute a group of classes, which we call age class $i$. The total number of classes $E_{i\alpha}$ is given by the relation

$$n = \sum_{i=1}^{\mathcal{A}} \mathcal{N}_i, \tag{20}$$

where $\mathcal{A}$ is the number of age-classes.

Let us choose the following dynamical equations for $\dot{N}_{Si}$:

$$\dot{N}_{Si} = \underbrace{\sum_{r} a_{Sri} N_{ri}}_{\substack{\text{intragroup}\\ \text{transformations}}} + \underbrace{\sum_{j \neq i} \sum_{t} a_{Stij} N_{tj}}_{\substack{\text{intergroup}\\ \text{transformations}}}. \tag{21}$$

$a_{Sri}$ relates to a transformation from state $r$ to state $S$ for an animal with age $i$. $a_{Stij}$ relates to a transformation from state $t$ with age $j$ to state $r$ with age $i$.

The hierarchy in the transformation signifies that the animals often change state ($r \to S$ in $i$), while they relatively rarely change age class ($i \to j$). The corresponding relation to (4) is

$$|a_{Sri}| \gg |a_{Stij}|. \tag{22}$$

In the present case, the hierarchy in the transformations leads to a hierarchy in time. Indeed, we must have a supplementary relation saying that when an animal changes state in the same age class $i$, it does not increase the number of animals with age $i$:

$$\sum_{S} \sum_{r} a_{Sri} N_{ri} = 0. \tag{23}$$

Let us define average populations $\bar{N}_i$ and relative population $n_{si}$ as in (5) and (6). The general results obtained for linear systems give us the time dependence of the population number of age class $i$, $u_i$:

$$u_i = \sum_{S} N_{Si} = \mathcal{N}_i \bar{N}_i \tag{24}$$

and

$$\dot{u}_i = \mathcal{N}_i \dot{\bar{N}}_i = \frac{1}{\mathcal{N}_j} \sum_{j \neq i} a^*_{ij} u_j + \underbrace{\sum_{j \neq i} \sum_{S} \sum_{t} a_{Stij} n_{tj}}_{= C_i}. \tag{25}$$

If we choose all the $a^*_{ij}/\mathcal{N}_j$ equal to zero except the terms in $a^*_{1j}$ (or $m_j$) and in $a^*_{i+1,i}$ (or $b_i$), we get finally the well-known form

$$\{\dot{u}\} = A^*\{u\} + \{C\}, \tag{26}$$

where

$$\begin{aligned} \{\dot{u}\} &\equiv (\dot{u}_1, \dot{u}_2, \ldots, \dot{u}_{\mathcal{A}}), \\ \{u\} &\equiv (u_1, u_2, \ldots, u_{\mathcal{A}}), \\ \{C\} &\equiv (C_1, C_2, \ldots, C_{\mathcal{A}}). \end{aligned} \tag{27}$$

$A^*$ is the transition matrix, like the one in the discrete Lotka model due to Leslie [4] (see Figure 4):

$$A^* = \begin{bmatrix} m_1 & m_2 & \cdot & \cdot & \cdot & \cdot & m_{\mathfrak{A}} \\ b_1 & 0 & & & & & 0 \\ 0 & \cdot & \cdot & & & & \cdot \\ \cdot & \cdot & \cdot & \cdot & & & \cdot \\ \cdot & & \cdot & \cdot & \cdot & & \cdot \\ \cdot & & & \cdot & \cdot & \cdot & \cdot \\ 0 & \cdot & \cdot & \cdot & 0 & b_{\mathfrak{A}-1} & 0 \end{bmatrix}.$$

The terms $m_i$ relate to the birth process, and the terms $b_j$ to the age process. We have supplementary terms $C_i$. A term $a_{St1i}$ signifies that an animal with age $i$ in a state $t$ which corresponds to sexual activity gives birth to a young animal with age 1 in a state $S$, and could be taken independent of $S$. A term $a_{Sti(i-1)}$ corresponds to the aging process and signifies that animals with age $i-1$ become older and move to the following age class $i$. These last terms can be assumed independent of $S$ and $t$, because the aging process is regular.

In these conditions, we get similar equations to (19):

$$\{\dot{u}\} = A^*\{u\} + \{\langle C\rangle\}. \tag{28}$$

Here $\langle C_i\rangle$ are time averages corresponding to the terms $C_i$ obtained by replacing $n_{tj}$ with their time average relative populations $\langle n_{tj}\rangle$. The terms $\langle C_i\rangle$ in the relations (28) couple the population dynamics and the individual dynamics. Let us now study particularly these coupling effects in the linear case.

## 7. COUPLING BETWEEN POPULATION AND INDIVIDUAL LEVELS IN THE LINEAR CASE

Let us imagine a variation of the average values $\langle C_i\rangle$. For instance, the coefficients $a_{Sri}$ governing the changes of state in the same age class $i$ can depend on external parameters or environmental parameters $\phi_k$, $k = 1, \ldots, K$, where $K$ is the number of external parameters. The equation (18) for the relative population numbers $n_{Si}$ can be written

$$\dot{n}_{Si} \cong \sum_r a_{Sri}(\phi_k)\cdot(\bar{N}_i + n_{ri}). \tag{29}$$

Over the year, the environment varies. The environmental parameters $\phi_k$ are time dependent. The time averages $\langle n_{ri}\rangle$ and the coefficients $\langle C_i\rangle$ vary slowly with the coefficients $\phi_k(t)$. The variation of the $\phi_k$ is very slow compared to the time of internal equilibration in each age class $i$, i.e., we

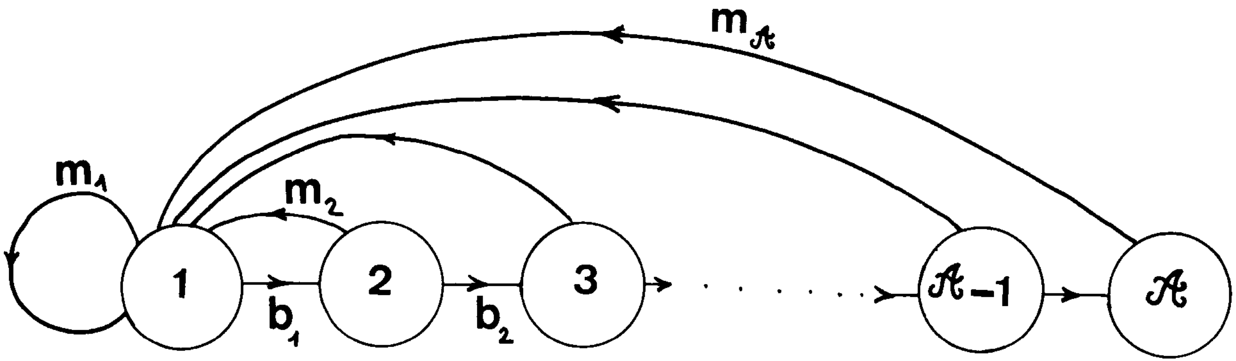

FIG. 4. In Leslie's model of population, the terms $m_i$ are relative to the birth process and the terms $b_i$ to the aging process. Each circle represents an age class $i$; the arrows, the transformations between classes.

have for any $(S, i)$ and $k$

$$|\dot{\phi}_k| \ll |\dot{n}_{Si}|. \tag{30}$$

Let us look at the effects of this slow variation of the coefficients $\langle C_i \rangle$ on the level of the population. We return to the equations (28):

$$\{\dot{u}\} = A^*\{u\} + \{\langle C \rangle\}. \tag{28}$$

Let us eliminate the terms $\langle C_i \rangle$ and find a new basis in which we simply have

$$\{\dot{u}^*\} = A^*\{u^*\}, \tag{31}$$

$$\{u^*\} = \{u\} + \{v\}. \tag{32}$$

Here $\{v\}$ is a vector which is simply given by

$$\{v\} = (A^*)^{-1}\{\langle C \rangle\}. \tag{33}$$

Thus, the effect of a modification of the constant $\{\langle C \rangle\}$ is a change of origin (a translation) for the vector $\{u\}$, but no change in the matrix elements $A^*$. For instance, if we use a statistical model at the level of the population, such as the Demetrius model, we get no change in the matrix $A^*$. The free energy is unchanged, but we must translate the equilibrium population numbers $u_j$.

In order to get a change in the matrix elements, it is necessary to consider nonlinear terms in the dynamical equations (21).

## 8. COUPLING BETWEEN POPULATION AND INDIVIDUAL LEVELS IN THE NONLINEAR CASE

Let us choose the following nonlinear equations for $\dot{N}_{Si}$ instead of (21):

$$\dot{N}_{Si} = \underbrace{k_{Si}N_{Si} + \sum_j \sum_r \sum_t k^{Si}_{rtj} N_{ri} N_{tj}}_{\substack{\text{I = changes of states in the} \\ \text{same age class } i}} \underbrace{+\, a_{i-1}u_{i-1} + \sum_{j,k} \sum_{r,t} a^{Si}_{rtjk} N_{rj} N_{tk}}_{\text{II = changes of age class}}. \tag{34}$$

The changes of states of an animal (nonlinear term I) result here from meetings between animals. An animal in state $r$ belonging to age class $i$ meets another animal in state $t$ belonging to age class $j$. The result of this meeting is a change of state of the animals, putting the first animal in

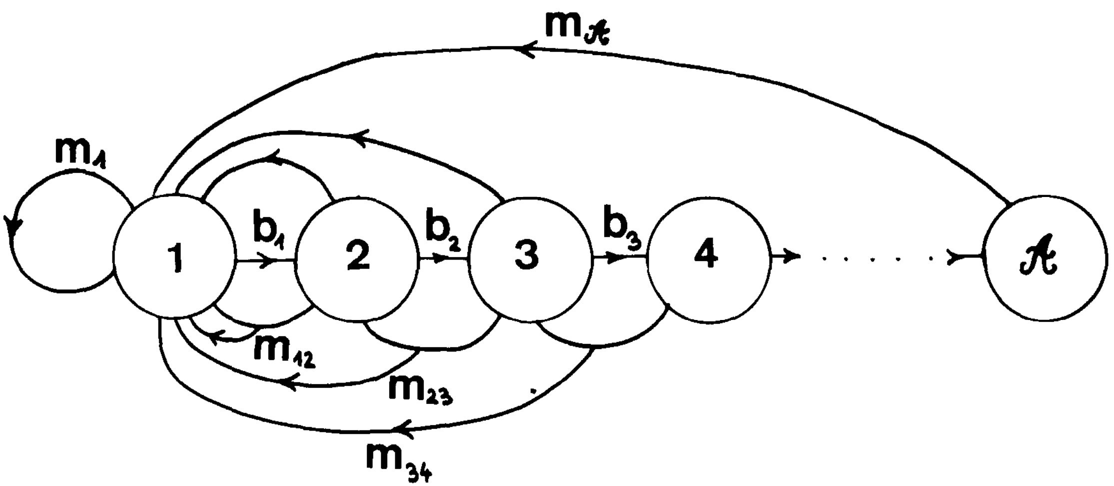

FIG. 5. In the nonlinear model, the birth process results from the meeting between a male (female) of age class $i$ with a female (male) of age class $j$. The terms $m_{ij}$ are the corresponding transformation coefficients.

state $S$ (but always in age class $i$) and the second one in state $S'$ (but always in age class $j$). The linear term $k_{Si}N_{Si}$ indicates that in absence of meetings, the animal spontaneously chooses some states rather than others. We have a kind of chemistry of changes of states. Term II corresponds to exchange between the age classes. The terms $a_{i-1}u_{i-1}$ correspond to the aging process. The last term corresponds to the birth process. A male (a female) in state $r$ belonging to age class $j$ meets a female (a male) in state $t$ belonging to age class $k$, and the female gives birth to young animals in age class 1: $a^{Si}_{rtjk} = 0$ except for $i = 1$.

We assume here that the population is always composed of half males and half females. In the last term, relating to the birth process, we must use the populations $N_{rj}/2$ and $N_{tk}/2$. The coefficient $\frac{1}{4}$ is already contained in $a^{S1}_{rtjk}$. States $r$ and $t$ must correspond to sexual activity.

We can choose the convention that at birth the young animals are equally distributed in the states $S$ of the age class 1, i.e., the coefficients $a^{S1}_{rtjk}$ are independent of $S$ and become $a_{rtjk}$. The relation saying that changes of states in the same age class $i$ do not increase the number of animals with age $i$, similar to (23), is

$$\sum_S \left( k_{Si}N_{Si} + \sum_j \sum_{r,t} k^{Si}_{rtj} N_{ri} N_{tj} \right) = 0. \tag{35}$$

Now, the equations for the population dynamics $(\dot{u}_i)$ are

$$\begin{aligned} &\dot{u}_i = b_{i-1}u_{i-1} \quad \text{for } i \neq 1, \qquad b_i = \mathcal{N}_i a_i, \\ &\dot{u}_1 = \sum_{j,k} \sum_{r,t} a_{rtjk} N_{rj} N_{tk}. \end{aligned} \tag{36}$$

Let us replace $N_{rj}$ and $N_{tk}$ by their functions of $u_j$ and $u_k$:

$$\begin{aligned} &\dot{u}_i = b_{i-1}u_{i-1} \qquad \text{for} \quad i \neq 1, \\ &\dot{u}_1 = \sum_{j,k} m_{jk} u_j u_k + \sum_j m_j u_j + \sum_k m_k u_k + C_1. \end{aligned} \tag{37}$$

The previous equations can be more simply written

$$\begin{aligned} &\{\dot{u}\} = A^*_{\text{n.l.}}\{u\} + \{u\}\cdot M\{u\} + \{C\}_{\text{n.l.}}, \\ &\{C\}_{\text{n.l.}} \equiv (C_1, 0, 0, \ldots, 0). \end{aligned} \tag{38}$$

$M$ is the matrix of the $m_{jk}$, and $\{u\}\cdot M\{u\}$ is the product of the vector $\{u\}$ and the vector $M\{u\}$. The subscript n.l. indicates that it corresponds to the nonlinear case (see Figure 5).

The constants $m_{jk}$ and $m_j$ are given as follows:

$$m_{jk} = \frac{1}{\mathcal{N}_j \mathcal{N}_k} \sum_{r,t} a_{rtjk},$$
$$m_j = \frac{1}{\mathcal{N}_j} \sum_{r,t} a_{rtjk} n_{tk} \quad \text{and} \quad C_1 = \sum_{r,t} a_{rtjk} n_{rj} n_{tk}. \tag{39}$$

In the case of a strong hierarchy, the variables $n_{tk}$ can be treated statistically and replaced by the time averages $\langle n_{tk} \rangle$. Indeed, in the hierarchical system, we must have the following relation saying that the coefficients $k_{Si}$ or $k^{Si}_{rtj}$ are very large compared to the other parameters $a_i$ and $a_{rtjk}$, so that we obtain

$$\dot{N}_{Si} \cong k_{Si} N_{Si} + \sum_j \sum_{rt} k^{Si}_{rtj} N_{ri} N_{tj}. \tag{40}$$

Systems of this kind have well been studied [7,8]. It is possible to define a density $\rho$ for these nonlinear systems; see E. H. Kerner [7, pp. 151–167]. Then, considering times of observation long enough compared to times necessary to reach thermodynamical equilibrium for relative populations $n_{ri}$, we can replace them by their time averages $\langle n_{ri} \rangle$ in the equations (38).

In the nonlinear case, we can see that a change in the values $\langle n_{Si} \rangle$ modifies not only the constant $C_1$ but also the terms $m_j$, and $m_k$ [see (39)]. The effect is not only a change of origin in the space of the populations $u_i$, but also in the probabilities of birth and the matrix $A^*_{\text{n.l.}}$. For instance, if we use a thermodynamical model at the level of the population, like L. Demetrius', it affects the free energy. In nonlinear cases, we have changes of the matrix and not only of the constant terms $\langle C \rangle$ or $\langle C \rangle_{\text{n.l.}}$.

## 9. COUPLING BETWEEN POPULATION AND ECOSYSTEM LEVELS IN THE NONLINEAR CASE

We can imagine similar methods to couple the population level and the ecosystem level. Let us denote by $u_{ir}$ the number of animals in age class $i$ belonging to species $r$. Here, we forget the individual levels. The dynamical equation for $u_{ir}$ can be written

$$i \neq 1: \quad \dot{u}_{ir} = \underbrace{b_{i-1,r} u_{i-1,r}}_{\text{age process}} + \underbrace{\sum_{S \neq r} \sum_j \alpha_{irjS} u_{ir} u_{jS}}_{\text{prey-predator process}},$$
$$i = 1: \quad \dot{u}_{1r} = \underbrace{\sum_{S \neq r} \sum_j \alpha_{1rjS} u_{1r} u_{jS}}_{\substack{\text{prey-predator}\\ \text{process}}} + \underbrace{\sum_i m_{ir} u_{ir}}_{\substack{\text{birth}\\ \text{process}}}. \tag{41}$$

The terms $b_{j_r}$ relate to age-process for species $r$; the terms $m_{i_r}$, to the birth process coming from age class $i$ of species $r$. The last terms relate to the prey-predator process. $\alpha_{i_r j_S}$ represents the action of the predators of species $r$ with age $i$ on the prey of species $S$ with age $j$ (positive case, $\alpha_{i_r j_S} > 0$) or the action of the predators of species $S$ with age $j$ on the prey of species $r$ with age $i$ (negative case, $\alpha_{i_r j_S} < 0$). To get the collective equations for the ecosystem, one must add all the equations over the age classes $i$ for a given species $r$:

$$N_r = \sum_i u_{i_r}. \tag{42}$$

$N_r$ is the number of animals in species $r$:

$$\sum_i \dot{u}_{i_r} = \dot{N}_r = \sum_i b_i u_{i_r} + \sum_i m_{i_r} u_{i_r} + \sum_{r \neq S} \sum_{ij} \alpha_{i_r j_S} u_{i_r} u_{i_S}. \tag{43}$$

The hierarchy in the interactions assumes here that the prey-predator coefficients are very small compared to the aging-process coefficients, i.e. that we have the relations

$$|\alpha_{i_r j_S}| \ll |m_{i_r}|, |b_{i_r}|. \tag{44}$$

It is clear that this is not the case for all ecosystems. Here, we study one ecosystem which corresponds to this assumption. In these conditions, we can write $\dot{u}_{i_r}$ and $\dot{u}_{1_r}$ as follows:

$$\begin{aligned} i \neq 1: &\quad \dot{u}_{i_r} \cong b_{i-1,r} u_{i-1,r}, \\ i = 1: &\quad \dot{u}_{1_r} \cong \sum_i m_{i_r} u_{i_r}. \end{aligned} \tag{45}$$

The relation equivalent to (23) or (35) is:

$$\dot{u}_{1_r} + \sum_{i \neq 1} \dot{u}_{i_r} \cong 0,$$

i.e., in the absence of the prey-predator process the populations $N_r$ do not vary. Similar methods to the ones presented in Section 8 would give $\dot{N}_r$ and $\dot{n}_{i_r}$, with the usual definition $u_{i_r} = N_r / \mathcal{N}_r + n_{i_r}$.

## 10. MULTILEVEL SYSTEMS

We can imagine describing a hierarchically organized three level system. For this, we might define the populations $N_{S i_r}$ of animals of species $r$ with age $i$ in state $S$. Then, we might choose dynamical equations for $\dot{N}_{S i_r}$ which might be decomposed into three contributions: a first term would correspond to changes of states in the same age class, a second term to changes of age in the same species, and a third term to the prey-predator process. The hierarchy would be introduced in the probabilities of transformations, i.e., the changes of state would be assumed very frequent compared to age changes, themselves very frequent compared to prey-predator coefficients. The methods to get the equations on a more collective level are identical to those presented previously. We are not going to give the results.

It must be noticed that in this case the number of indices can become important. For instance, we might consider coefficients $\alpha_{riStjS'}$ related to the action of predator $r$ with age $i$ in a state $S$ on prey $t$ with age $j$ in a state $S'$, or reciprocally. The model could be simplified by only considering interactions between consecutive levels, i.e. ecosystem-population couplings and population-individual couplings. The chosen time of observation, $\mathfrak{T}_0$, must permit one to treat the individual level thermodynamically if $\mathfrak{T}_0$ is large compared to the characteristic time scale for individual interactions. If $\mathfrak{T}_0$ is also large compared to the characteristic time scale for the aging process, we can realize a thermodynamical treatment of the population level. The hierarchy in the transformations leads to a hierarchy in time, and it permits one to reduce considerably the number of variables by thermodynamical treatments, by the choice of a suitable time of observation $\mathfrak{T}_0$.

## 11. CONCLUSION

The systems studied here are special systems, i.e. hierarchically organized systems. The interest in studying them is double. Firstly, these systems are complex systems, but nevertheless one can study them in a rather detailed way. Indeed, the hierarchical properties lead to separations between collective slow-varying variables and internal fast-varying ones. The system is divided into many subsystems corresponding to sets of variables associated to very different scales of parameters and of time. This allows, for instance, an important reduction of the calculations. By replacing internal fast-varying variables with their time averages, one can forget the internal dynamics, which is replaced by a Gibbs ensemble, and get a few equations governing the collective dynamics relative to the smallest possible number of collective variables. Secondly, many authors have noticed the fact that many complex systems in nature are hierarchically structured [12–19]. J. Bok and G. Toulouse explain this spontaneous hierarchical organization in many systems by a principle of least difficulty [16]. Complex systems spontaneously self-organize in a hierarchical way to minimize the number of individual interactions (because the intergroup interactions can be neglected). This paper gives a supplementary contribution to the study of these not so complex, and fairly common, systems.

## APPENDIX. GIBBS DISTRIBUTION AND CONSTANTS OF MOTION

In some cases, there exists a constant of motion $G_\alpha$ associated with each group $\alpha$. For linear systems, we assume that $G_\alpha$ is linear in the population numbers $N_{i\alpha}$:

$$G_\alpha = \sum_{i \in \alpha} b_{i\alpha} N_{i\alpha} = \text{constant}.$$

The $b_{i\alpha}$ are time independent parameters. The existence of such constants of the motion is very interesting in linear systems because it permits us to define a Gibbs distribution $\rho_\alpha$ for a subspace of each group $\alpha$ defined by a set $s_\alpha$ of only $n_\alpha$ classes $E_{i\alpha}$ ($n_\alpha < \mathcal{N}_\alpha$) which create a canonical ensemble. $\rho_\alpha$ is a function of the populations $N_{i\alpha}$, $i$ corresponds to the $n_\alpha$ classes [7], and

$$\rho_\alpha = \rho_{0\alpha} e^{-G_\alpha/\theta_\alpha},$$

where $\theta_\alpha$ is the "temperature" for the group $\alpha$, and $\rho_{0\alpha}$ is a constant of normalization:

$$\rho_{0\alpha} = \oint \rho_\alpha \prod_i dN_{i\alpha} \Big/ \oint e^{-G_\alpha/\theta_\alpha} \prod_i dN_{i\alpha}, \qquad i \in s_\alpha.$$

The integral is calculated by integrating over each $N_{i\alpha}$ from 0 to $+\infty$. The product $\rho_\alpha \prod dN_{i\alpha}$ gives the probability of finding the classes $E_{i\alpha}$ with their population numbers between $N_{i\alpha}$ and $N_{i\alpha} + dN_{i\alpha}$, $i \in s_\alpha$.

In the case of slow-varying average populations, we can cut up the time into intervals $\Delta t$, corresponding to small variations of the average populations (i.e., $\dot{\bar{N}}_\alpha \Delta t \cong 0$), but large compared to the time variation of the internal variables (i.e., $\dot{n}_{i\alpha} \Delta t \neq 0$). In this case, the Gibbs distribution can be expressed in terms of with the relative or internal variables $n_{i\alpha}$ alone, for times between $t$ and $t + \Delta t$:

$$\rho_\alpha = \rho'_{0\alpha} \exp\left[ -\frac{\sum_i b_{i\alpha} n_{i\alpha}}{\theta_\alpha} \right]$$

with

$$\rho'_{0\alpha} = \rho_{0\alpha} \exp\left[ -\frac{b^*_\alpha \bar{N}_\alpha}{\theta_\alpha} \right], \qquad b^*_\alpha = \sum_i b_{i\alpha}.$$

The probability of finding the relative variable $n_{i\alpha}$ between $n_{i\alpha}$ and $n_{i\alpha} + dn_{i\alpha}$ is thus given by $\rho_\alpha \prod_i dn_{i\alpha}$. The average value of the relative variable $n_{i\alpha}$, denoted $\langle n_{i\alpha}\rangle$, is given by

$$\langle n_{i\alpha}\rangle = \frac{\oint \rho_\alpha n_{i\alpha} \prod_i dn_{i\alpha}}{\oint \rho_\alpha \prod_i dn_{i\alpha}}.$$

The integration is done for each relative population from $-\overline{N}_\alpha$ to $+\infty$.

For instance, in the example of coupled individual population levels, treated in Section 6, one can get a constant of the motion. If we assume that for each kind of activity associated with each state $S$, the animal spends a certain energy per unit time $b_{Si}$, then we can calculate the average energy $\overline{E}_i$ spent per unit time by an animal in age class $i$ at time $t$ as follows:

$$\overline{E}_i = \frac{1}{\overline{N}_i} \sum_S b_{Si} N_{Si},$$

$$G_i = \overline{N}_i \overline{E}_i.$$

$G_i$ can be assumed to stay quite constant over long enough intervals $\Delta t$, corresponding nevertheless to negligible variation of the average populations $\overline{N}_i$ ($\dot{\overline{N}}_i \Delta t \cong 0$).

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