AN ECOLOGICAL APPROACH TO SYSTEMS ANALYSIS BASED ON THE VOLTERRA EQUATIONS

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1. PHENOMENOLOGICAL BACKGROUND

Development processes are very often described using mathematical models based on the idea of exponential growth. One example of this is Malthus' theory of population growth, which states that a population tends to increase more rapidly than its means of subsistence and that, unless this growth is checked in some way, widespread poverty and degradation will inevitably result. This type of growth is called "uniformly proportional growth" and may be described by the equation

$$\dot{x} = Kx$$

where K is a constant.

However, exponential growth is actually observed only in isolated systems, and we should therefore try to express the real evolutionary process in a more complex way, as illustrated in Figure 1 [1,2]. In this new formulation, growth is divided into two distinct phases: an extensive stage, which may be represented by the autocatalytic expression

$$\dot{x} = Kx^k$$

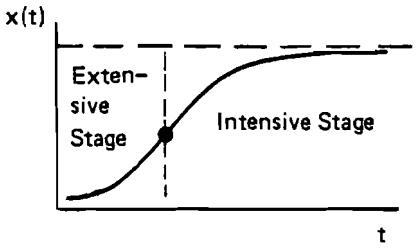

Figure 1. EVOLON - transition between two stationary states

followed by an intensive stage, given by the saturation equation

$$\dot{x} = K(B-x)^{\ell} \quad . \tag{1}$$

In the first stage, k is very often greater than 1, leading to hyperbolic growth, while in the second stage ℓ is generally less than 1, which represents parabolic growth. The above expressions can then be combined to yield

$$\dot{x} = Kx^{k}(B-x)^{\ell}$$

which is a generalization of the logistic curve ($k=\ell=1$).

This description of evolutionary processes (known as EVOLON) developed from the study of rate-coupled systems (e.g., food chains, energy chains, enzyme chains [1]), which have the general form

$$\dot{x}_i = K_i x_i x_{i+1} - L_i x_i x_{i-1} - a_i x_i \qquad i = 0,1,\ldots,N \tag{2}$$

where $L_0 = 0$ and $K_N = 0$. If we neglect the secondary effects associated with state variable x_i (the growth indicator), we obtain the exponential chain

$$\dot{x}_i = K_i x_i x_{i+1} \qquad i = 0,1,\ldots,N \tag{3}$$

which is the basis of our ecological approach.

It may be useful at this stage to compare the properties of the exponential chain with those of the Taylor series expansion of the function $x_0 = x(t)$. Table 1 provides an outline comparison of these series; a more detailed discussion is given in ref. 2.

TABLE 1. Comparison between the exponential chain and Taylor series expansion of $x_0 = x(t)$.

Taylor expansion	Exponential chain
Characteristics	
$x_0 = x(t)$	$x_0 = x(t)$
$\dot{x}_i = K_i + x_{i+1}$	$\dot{x}_i = x_i(K_i x_{i+1})$
Normalization	
$x_i(0) = 0$	$x_i(0) = 1$
$i \geq 1$	$i \geq 1$
Computation of coefficients	
$K_i = \dot{x}_i\big\|_{t=0} = x_0^{(i)}\big\|_{t=0}$	$K_i = \frac{\dot{x}_i}{x_i}\big\|_{t=0} = \frac{d}{dt} \ln x_i\big\|_{t=0}$
$K_i = F^i x_0\big\|_{t=0}$, $F = \frac{d}{dt}$	$K_i = F^i x_0\big\|_{t=0}$, $F = \frac{d}{dt} \ln$
$F^{-1} = I = \int_0^t$	$F^{-1} = e^{\int_0^t}$
Rest of expansions	
$x_R = F^{-N} F^N x_0$	$x_R = F^{-N} F^N x_0$

As an example, let us consider the function

$$x_0 = \frac{1}{(1-Kt)^{\kappa}}$$

The Taylor expansion is:

$$F^i x_0 \Big|_{t=0} = \kappa(\kappa+1) \ldots\ldots (\kappa+i-1)K^i$$

and the corresponding exponential chain is:

$$F^1 x_0 = \frac{\kappa K}{1-Kt} \qquad K_1 = \kappa K$$

$$F^i x_0 \Big|_{t=0} = K \qquad i = 2,3,\ldots$$

If $\{K_i\}$ forms a periodic sequence with period $(K_0, K_1, \ldots, K_{r-1})$, we describe it as a hypercycle of order r (see ref. 1). Figure 2 compares the basic chain structure with the structure of a hypercycle; the modes of a hypercycle of order 2 are illustrated in Figure 3.

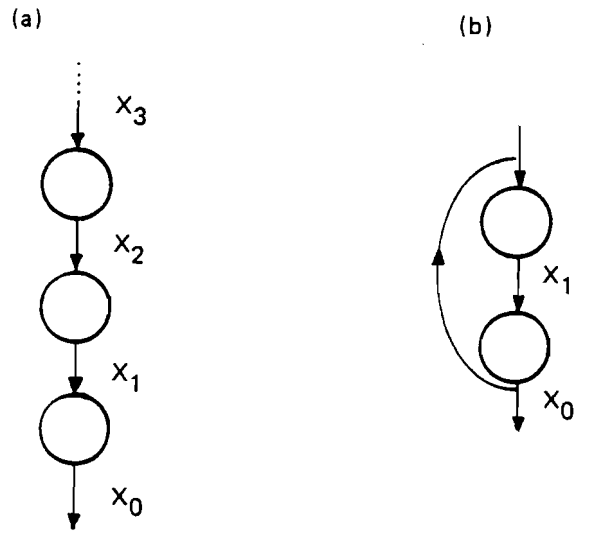

Figure 2. Illustration of the basic chain structure (a) and the Hypercycle of order r = 2 (b)

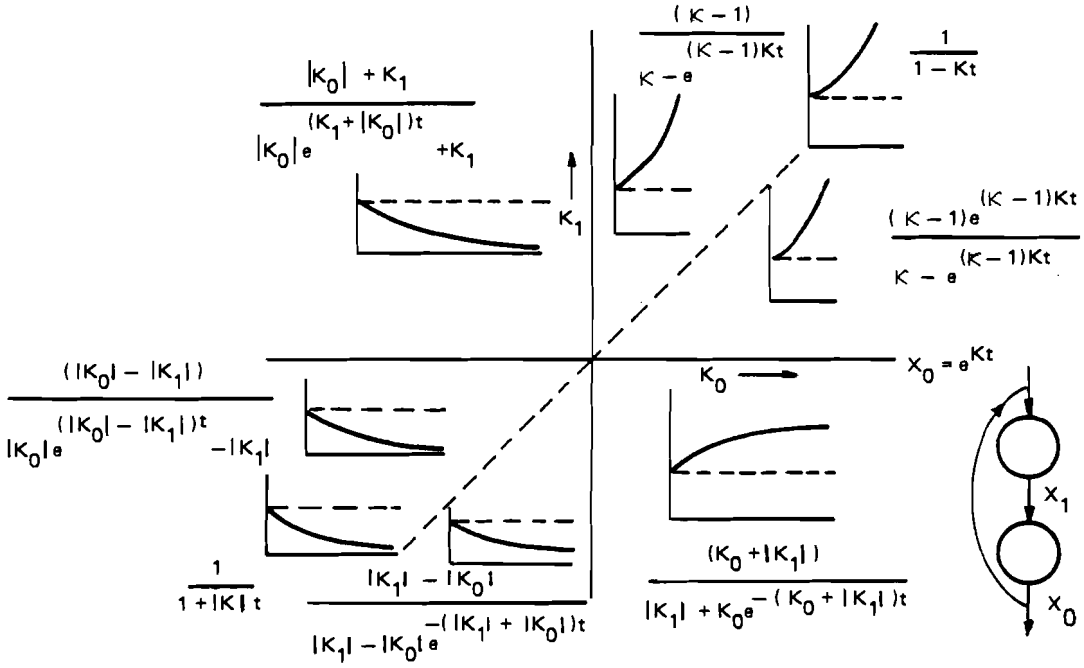

Figure 3. Behavior modes of the Hypercycle of order r = 2

The definitions given above show that the function $x_0 = 1/(1-Kt)$ can be interpreted as a hypercycle of order 1. However, long chains of homogeneous rate-coupled "exponential" systems $x_i = Kx_ix_{i+1}$ tend to display hyperbolic growth:

$$\frac{dx_0}{dt} = K x_0^2 \quad .$$

This can be interpreted as the Law of Large Numbers in ecology.

As a generalization, let us consider a homogeneous chain with the basic operator

$$F = \frac{d\phi(\cdot)}{dt} \tag{4}$$

where ϕ is a monotonic function. The general solution is:

$$x(t) = \phi^{-1}\{\phi(x(0)) + \int_0^t y\, dt\} \quad . \tag{5}$$

Let $\xi = \phi^{-1}\{\int_0^t y\, dt\}$. Then, for $\phi(\xi)\big|_{t=0} = 0$, eqn. (5) becomes:

$$x(t) = \phi^{-1}\{\phi(x(0)) + \phi(\xi)\} = x(0) + \xi \tag{6}$$

This is a generalized statement of the principle of superposition.

Using these definitions, the equation for each element (module) of the chain becomes:

$$\frac{d}{dt}\,\phi(\xi_i) = \tilde{K}_i\,\phi^{-1}\{K_i + \phi(\xi_{i+1})\} \tag{7}$$

employing the normalization $\phi(\xi_i)\big|_{t=0} = 0$.

As an illustration, we shall consider the two special cases $\phi(u) = u$ and $\phi(u) = \ell n\ u$.

$\underline{\phi(u) = u}$. In this case we have linear superposition and eqn. (7) becomes:

$$\dot{\xi}_i = \tilde{K}_i(K_i + \xi_{i+1})$$

where $\xi_i(0) = 0$. This is the Taylor expansion.

$\underline{\phi(u) = \ell n\ u}$. In this case we have the exponential chain:

$$\dot{\xi}_i/\xi_i = \tilde{K}_i\xi_{i+1}\, e^{K_i}$$

and from $\ell n\ \xi_i(0) = 0$ we can deduce $\xi_i(0) = 1$.

A more interesting example is given by $\phi(u) = u^\kappa$. In this case we have

$$\kappa\xi^{\kappa-1}\dot{\xi}_i = \tilde{K}_i(K_i + \xi_{i+1}^\kappa)^{1/\kappa}$$

and $\xi_i(0) = 0$.

The next section presents an approach to the structural design of nonlinear and nonstationary systems based on the description of growth processes outlined above.

2. STRUCTURAL DESIGN OF NONLINEAR AND NONSTATIONARY SYSTEMS

The basic operator corresponding to (4) for rate-coupled chains is

$$F = \frac{d}{dt} \ell n \quad . \tag{8}$$

There are many complex ecological systems built up from food chains; these chains are usually internally consistent with a relatively small number of linkages between them. This observation leads to certain conclusions about the structure of the overall system.

STRUCTURAL DESIGN PRINCIPLE

> Interacting coupled systems should be composed of a small number of long chains of rate-coupled systems with relatively few feedbacks within each chain and a small number of linkages between different chains.

We consider these chains or hypercycles to be the structural elements of the ecological system, just as shift registers and counter registers are the basic building blocks in automata theory.

This Principle suggests a number of flexible rules for the design of complex systems:

1. We apply the basic operator $F = \frac{d}{dt} \ell n$ successively to any explicit or implicit signal $x(t)$ (output, growth indicator, etc.) to try to build up a chain $Fx_i \sim x_{i+1}$, where $\sim$ implies proportionality. In general, $Fx_i \sim A_i$ is an expression containing both familiar signals and new signals.

2. If A_i contains signals that have already been identified, these are labeled according to the existing structure. There is some degree of freedom in labelling the unknown signals, which are then expanded as in step 1.

3. This procedure comes to an end when no new signals can be identified, yielding a finite structure.

4. Finally, we introduce names x_i for the output signals of the basic modules F into the structure.

Our experience in using these rules has shown that it is possible to construct the system topology for a signal x(t) without considering the multiplicative constants. Only when the topology of the system has been completed is it necessary to determine these arbitrary coefficients.

We will now discuss two examples illustrating the use of structural design rules listed above.

The first example involves growth in which the driving force is a product of exponentials, such as $\dot{x} = Kx^k(B-x^w)^\ell$. Applying the structural design rules, we obtain

$$x_0 = x$$

$$x_1 \sim \frac{\dot{x}}{x} \sim x^{k-1}(B-x^w)^\ell$$

$$x_2 \sim x_1 + x^{w-1+k}(B-x^w)^{\ell-1}$$

On relabelling the variables, we obtain the following equations for the structure of the system (illustrated in Figure 4a):

$$\dot{x}_0 = K_0 x_0 x_1$$

$$\dot{x}_1 = x_1(K_1 x_1 + L_1 x_2)$$

$$\dot{x}_2 = x_2(K_2 x_2 + L_2 x_1)$$

This is a second-order Volterra-Lotka system driving an exponential integrator.

The second example is based on the simple pendulum, the motion of which may be represented mathematically as follows:

$$\ddot{x} + D\dot{x} + \frac{g}{\ell} \cdot \sin x = 0 \quad .$$

Applying the structural design rules, we obtain:

$$\dot{x}_0 = x_0 x_1$$

$$\dot{x}_1 = x_1(-x_1 - D - (g/\ell)x_2)$$

$$\dot{x}_2 = x_2(x_3 + D + (g/\ell)x_2)$$

$$\dot{x}_3 = x_3(-x_4 - x_3 - D - (g/\ell)x_2)$$

$$\dot{x}_4 = x_4(x_4 + x_3 - D - (g/\ell)x_2)$$

The corresponding structure is illustrated in Figure 4b.

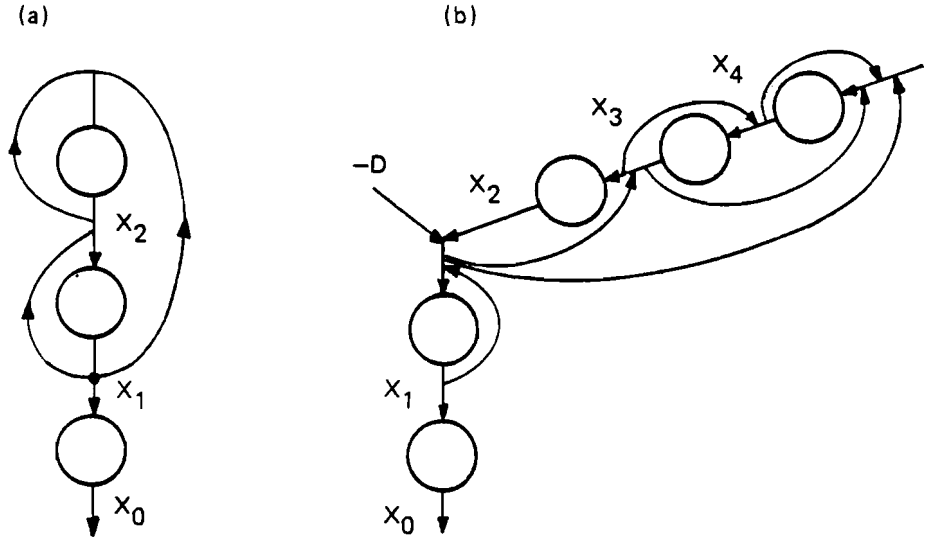

Figure 4. Structure of a system with power driving force (a) and of the simple pendulum (b)

3. SPECIAL FEATURES OF STRUCTURES PRODUCED BY A DESIGN PROCESS WITH EXPONENTIAL CHAINS

The basic elements of an analogue computer include addition of constants, multiplication by constants (amplification), integration (and its inverse) and signal multipliers $x = y_1 y_2$; our proposed approach requires only the basic module $F = \frac{d}{dt}\,\ell n$ (and its inverse $F^{-1} = e^{\int_0^t}$. Nevertheless, the following statement can be shown to be true: All structures which have a finite representation on an analogue computer have a finite description in terms of exponential chains. The reverse is also true. (It should be noted that this result holds only in the sense of the topological structure of the system, and has nothing to do with its behavior, e.g., its numerical stability).

All finite structures employing $F = \frac{d}{dt}\,\ell n$ do not require signal multipliers -- this means that the structural design approach uses more complex basic elements than the analogue computer and yields a unified system description.

If we introduce the output signals of the basic modules as state variables x_i, the system will always be described by a set of Volterra equations [3-7]:

$$\dot{x}_i = x_i(\varepsilon_i - \sum_{j=0}^{m} \gamma_{ij}; x_j) \qquad i = 0,1,\ldots,n \quad . \tag{9}$$

The resource parameters ε_i and the interaction coefficients γ_{ij} are constant, where the ε_i can also be used as a parameter for manipulating the system.

However, it would be more general to consider nonautonomous Volterra equations ("Volterra networks") of the type:

$$\frac{dx_i}{dt} = x_i\Big(\sum_{r=0}^{n} b_{ir} y_r - \sum_{j=0}^{m} \gamma_{ij} x_j\Big) \qquad i = 0,1,\ldots,n \tag{10}$$

This would make it possible to use optimal control approaches in conjunction with the Volterra-type models, in view of the fact that:

1. The representation of a given system by Volterra equations is not unique -- there may be a large number of equivalent Volterra representations.

2. There is already a well-established theory of bilinear systems

$$\dot{x} = Ax + \sum_{k=0}^{m} y_k B_k x \qquad (11)$$

in control theory, where A and B_k are constant matrices and y_k are scalar controls.

The relationship between the theory of bilinear systems and Volterra equations is discussed in more detail in ref. 8. Here we shall just state the main result: - there exists a finite Volterra structure for every bilinear system, but every Volterra system does not necessarily have an equivalent bilinear structure.

4. RELATED PROBLEMS

1. When a given signal x(t) or a given differential equation for x(t) is put through the topological structural design process it yields a structure with a set of free parameters. This suggests the inverse problem: that of identifying the differential equations embedded in a given topological structure. In the case $\dot{x} = Kx^k(B-x^w)^\ell$ the inverse problem can be solved (assuming normalization with $x_i(0) = 1$) to give the original differential equation and the following forms:

$$\dot{x} = Kx^k(B-\ell nx)^\ell$$

$$\dot{x} = Kx^k e^{wx^\ell}$$

2. The degrees of freedom associated with a given signal x(t) or differential equation during the design process can result in a set of equivalent Volterra representations. This

suggests the second problem: what are the transformation rules between equivalent Volterra representations? The set of all equivalence transformations is obviously a semigroup, but what are the generators of this group?

3. Can we establish rules for structure simplification through approximation? Are there dominated and non-dominated structures?

4. Can we develop a general approach that stabilizes the numerical behavior of Volterra representations sufficiently to perform reliable simulation experiments on the computer?

5. Is it possible to develop general parameter estimation procedures for Volterra representations, and methods for studying their robustness?

6. Can we use qualitative analysis to find the parameter configurations in a given Volterra structure that result in singularities, catastrophes (in the sense of catastrophe theory), or that produce strange attractors and chaotic phenomena?

7. The following principle may be deduced from the design procedure outlined above: the order of the Volterra representation, i.e., that of the equivalent representation of lowest order, is higher than the original order of the differential equation. This suggests the following problem: how is the original state space related to the full state space of the Volterra representation?

8. When we randomize the Volterra representation by substituting independent stochastic variables for the parameters, how are the corresponding stochastic phenomena related to the behavior of the real system under uncertainty?

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