

Distributed Self-regulation in Ecological and Economic Systems

V. V. Gafiychuk*

*Institute for Applied Problems of Mechanics and Mathematics,
National Academy of Sciences of Ukraine,
3b Naukova str., Lviv, 290601, Ukraine*

I. A. Lubashevsky†

*Institute of General Physics,
Academy of Science of Russian Federation,
Vavilova street, 38, Moscow, 117942, Russia*

R. E. Ulanowicz‡

*University of Maryland Chesapeake Biological Laboratory,
Solomons, MD, 20688, USA*

We consider an ecological system governed by Lotka–Volterra dynamics and an example of an economic system as a mesomarket with perfect competition. We propose a mechanism for cooperative self-regulation that enables the system under consideration to respond properly to changes in the environment. This mechanism is based on (1) active individual behavior of the system elements at each hierarchical level and (2) self-processing of information caused by the hierarchical organization. It is shown how the proposed mechanism suppresses nonlocal interaction of elements belonging to a particular level as mediated by higher levels.

1. Introduction

A great number of natural systems are organized hierarchically. Their hierarchical organization allows that such a system can be divided into a collection of subsystems (which will be called levels) involving many elements that are similar in their properties. The elements of the various levels differ substantially, however, in their characteristics. The subsystems can be ordered according to their mutual interactions: The behavior of an element at each level is determined by the aggregated state of a certain large group of elements belonging to the nearest lower level, while each element of a lower level is directly governed by a given element of the higher level.

*Electronic mail address: viva@iapmm.lviv.ua.

†Electronic mail address: ialub@fpl.gpi.ru.

‡Electronic mail address: ulan@cbl.umces.edu.

Such hierarchical organization is inherent in many ecological and economic systems. For example, we encounter a huge number of goods in an economic market in contrast to relatively few types of raw materials. Hence, the network of products and trade that transforms natural materials into a wide variety of goods will be a highly branching system. Suppose firms of a given type of activity that are approximately equal in power make up a certain level. The market then involves several such levels, from lower ones consisting of retailing companies up to the highest one that deals with the production of raw materials. In this case, the prices of products of firms dealing in wholesale trade are the direct averages of the prices of goods at the terminal retail points that are supplied by these firms.

Hierarchical organization is encountered frequently in ecological systems as well. Ecological systems often form trophic food chains or pyramids. Levels of such an ecosystem are made up of animals comparable in size and playing much the same role in the prey–predator relationships. Energy usually flows from smaller organisms *via* consumption to larger predators. The linkages from the small organisms generally vary over smaller scales. The larger animals that dominate these smaller organisms do so over larger scales of space and time. That is, because of their wider ambits, predators control larger regions of space for longer times. From this perspective, the hierarchical levels of most pelagic trophic networks are defined according to particle size [16]. It becomes possible to regard the populations at each level as being continuously distributed across their particular segment of space. This representation of the trophic hierarchy is depicted in Figure 1.

In a similar manner we can represent economic systems wherein firms producing raw materials are at the top of the scheme, and retail trade shops appear at the bottom.

The characteristic feature of hierarchical systems is the nonlocal interference among elements at the same level, as mediated by the higher levels. The term *nonlocal* means that the state of some elements depends on the state of some surrounding neighbors. Higher levels in their turn feel only the averaged state of the proceeding levels. Thus, local variations in the behaviors of elements belonging to lower levels reflect the states of elements at higher levels over larger scales. The larger component then changes the state of elements at the lower level in a region whose domain substantially exceeds the size of the initial perturbation. Such nonlocal interaction is not reliable, because it does not stem from the local laws of element interaction between neighboring levels that control the life of the system.

These characteristics make such hierarchical systems fragile with respect to perturbations in the environment. In order for systems to remain alive, there must be some mechanism of self-regulation that can

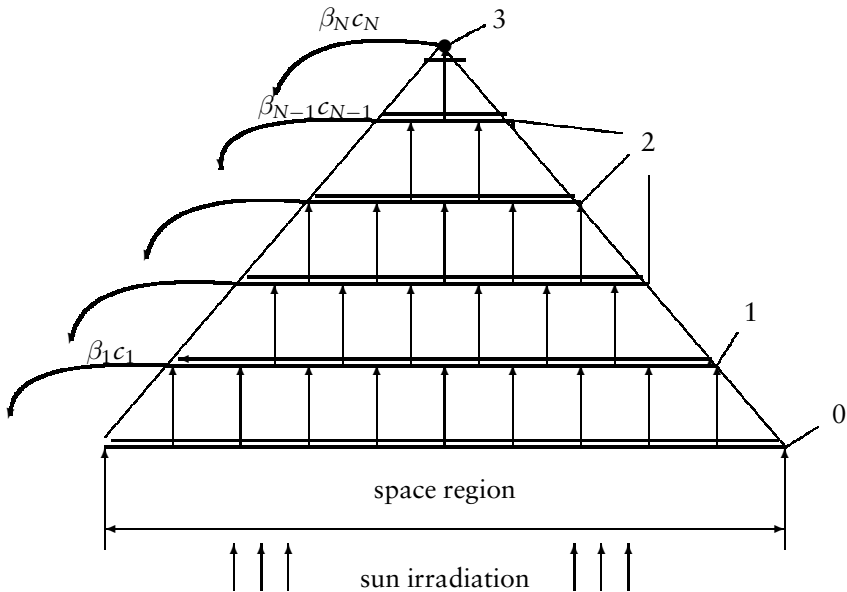


Figure 1. Trophic level representation, where: 0 phytoplankton, 1 small organisms, 2 organisms belonging to different classes, and 3 large predators.

maintain system stability and suppress (at least, to some extent) nonlocal interactions among elements at the same level.

We now briefly explain the terms we will use and the types of mechanisms we will consider. To begin, we consider the system to be distributed in space and consisting of different subsystems. These subsystems are represented by horizontal lines on Figure 1. Each subsystem will be characterized by some characteristic length in space l_i (Figure 1), and the total size L of the system will be represented as the set of the embedded diffusion lengths, l_i . Each diffusion length characterizes the domain of its corresponding distinct subsystem. Elements belonging to subsystem i can be characterized by domains which have the size of order l_i . The number of elements belonging to each subsystem can be estimated as the quotient L/l_i . The larger the characteristic length of subsystem elements, the higher is the position of that subsystem in the hierarchy of relations. All the subsystems are connected to each other by material flows, as shown in Figure 1.

The first property the system under consideration should possess is the absence of nonlocal interaction between the elements of any subsystem at the same hierarchical level. That is, if in one of the subsystems

elements (say i) there arises some perturbation, then this perturbation will not lead to a perturbation in any other element that is far removed from i . In other words, nonlocal influence of one element on another should be depressed.

In order to restrain nonlocal influence, some mechanism for self-regulation should be inherent in the organization of the systems under consideration. That is, the system should have an adaptive property that limits changes in the environment at a particular location to that region alone. But all the subsystems are connected *via* the upper hierarchical levels, so the question arises: What organization of the system will restrict changes to their region of impact?

For different elements to fulfill their individual functions independently of one another on the same level, the network connecting the different subsystems through hierarchical organization should, at least in the ideal case, have the capacity to control its bottom states at each point. This requirement is equivalent to the local control of material flow through the system. Hence, the independence of material flow at any level from flows of the same element at other points becomes a desirable property, which is referred to as *self-regulation*.

Now consider the bottom level of the system. In this type of system only the material flow at a given point determines the state of the system at that point. If the material flow at one point reacted substantially to the material flow at other points, then the elements of the same level would interfere with one another, and the system would lose its adaptive capacity. However, in trying to describe how this self-regulation might be implemented, that is, its particular mechanism, we encounter the fundamental problem that none of these subsystems can individually control the distribution of material flow through the distributed network of the system. For a large natural system it is unlikely that any one of its elements or subsystems would possess all the information required to govern the perfect response to changes in the environment, and this is true in particular of the life activities at the bottom level. This is because such control requires the processing of a great amount of information necessary to characterize the state at all spatial scales (i.e., at all levels of the supply network).

The foregoing leads us to assume that self-regulation can be implemented through cooperative mechanisms [13, 14]. In this scenario, each subsystem in the framework of material transfer receives a small piece of the information about the state of the bottom level of the system, and its reaction to this information gives rise to the desired redistribution of the mass flow over the distributed network. In other words, the subsystems vary in a self-consistent way that enables them to provide, for example, an additional biomass or material flow to those subsystem elements which need more, without disturbing material flow at other points of the system.

However, before the cooperative mechanism of self-regulation can come into being, a certain self-processing of the information must occur to enable the elements (hierarchically connected subsystems) to react adequately, according to where they are in the hierarchical network. Secondly, the physical properties of the network should give rise to a cooperative effect among variations in that particular branch of the material flow that will lead to its redistribution while gaining the desired results.

We now suggest a possible mechanism for such self-regulation. In section 2 we insert that mechanism into a particular set of model ecosystems governed by Lotka–Volterra dynamics. Certainly, the dynamics of real ecosystems are far more sophisticated, however, models with Lotka–Volterra dynamics typify many ecosystem characteristics and highlight the nonlocal fragility in a most pronounced way.

As already mentioned, a cooperative mechanism for self-regulation whereby the hierarchical system as a whole can react perfectly has been developed in [13, 14]. This mechanism consists in the response by each individual element to an available small piece of the information on the state of the whole system. The conservation of medium flowing through the supplying network gives rise to an ensuing processing of information that results in self-consistent behavior of the elements that culminates in perfect self-regulation.

2. An ecosystem model with distributed self-regulation

We begin by considering a simple mathematical model of a pelagic marine ecosystem involving N levels in which is found a large number of animal species. At the bottom of this system is phytoplankton (level 0) and at the top (level N) stands the population of large predatory fish. The characteristic features that distinguish each level, for example level i , are the body size of the individual organisms and the spatial size ℓ_i of the domain that is controlled by each individual fish at this level.

The flow of biomass in this trophic system is assumed to be governed by the Lotka–Volterra model, which describes hierarchical level i in terms of the spatial distribution of the biomass $c_i(\mathbf{r}, t)$ and treats the interaction between different levels as feeding relations, where the larger species play the role of predators and the smaller, those of prey. According to the discussion in section 1, we assume that the characteristic lengths $\{\ell_i\}$ of the control by individuals meet the following inequalities:

$$\ell_1 \ll \ell_2 \ll \dots \ll \ell_N. \quad (1)$$

This assumption may be justified on allometric grounds, that is, most physiological processes scale as an algebraic power of body size. Here we are extending the allometric notion to include the ambits of the organisms in question [3, 21].

The dimensionless distribution $c_i(\mathbf{r}, t)$ is governed by the equation

$$\tau_i \frac{\partial c_i}{\partial t} = (c_i c_{i-1} - c_i c_{i+1} + c_i \alpha \delta_{i1} - \beta_i c_i) - \ell_i \nabla J_i \quad (2)$$

where τ_i , β_i are given constants, and the term $\alpha \delta_{i1}$ (δ_{i1} is the Kronecker symbol) describes the input of biomass through the first level (phytoplankton). Equation (2) is an example of the standard form of the Lotka–Volterra dynamics as applied to a linear trophic chain (with the exception of the last term on the right-hand side). The final term describes the dynamics of nonuniformities in the spatial distribution of species i , where J_i is the movement of its members through space. Usually, the relationship between the J_i and nonuniformities in their distributions $c_i(\mathbf{r}, t)$ is written in the form [20]:

$$J_i = -\ell_i \nabla c_i. \quad (3)$$

Equation (3) actually corresponds to the passive behavior of animals undergoing random motion in space, independent both of other members of the same species and of their predators and prey. In this paper we account for the active behavior of animals at every hierarchical level. This means that each animal attempts (1) to avoid any region where the concentration of members of the same species is large, in order to decrease the competition for feed resources; (2) to prefer to visit domains containing high concentrations of prey; and (3) to avoid regions with many predators. Such active behavior is described by the following expression:

$$J_i = \ell_i \left[-(1 + \omega_{i,i} c_i) \nabla c_i - \omega_{i,i+1} c_i \nabla c_{i+1} + \omega_{i,i-1} c_i \nabla \langle c_{i-1} \rangle_{\ell_{i-1}} \right] \quad (4)$$

where $\omega_{i,i}$, $\omega_{i,i+1}$, and $\omega_{i,i-1}$ are positive constants and $\langle c_{i-1} \rangle_{\ell_{i-1}}$ is the concentration of prey averaged over the domain of their individual life-spans. We specify the value of $\langle c_i \rangle_{\ell_i}$ by the expression

$$\langle c_i \rangle_{\ell_i}(\mathbf{r}) = \int d\mathbf{r}' A \exp \left\{ \frac{(\mathbf{r} - \mathbf{r}')^2}{2\pi\ell_i^2} \right\} c_i(\mathbf{r}') \quad (5)$$

where A is a normalization constant. The nonlinear terms in equation (4) are those responsible for the self-regulation. It should be noted that a similar expression for J_i has been used in [1] and [12] to describe the active behavior of zooplankton.

Let us justify the assumptions on active behavior by analyzing a steady-state small perturbation in the uniform distribution $\{c_i^0\}$ of the given species in space under the constraints. For this purpose let us consider, for simplicity, that the number of trophic levels is even ($N = 2n$). This allows us to assume that sources in equation (2) are stipulated solely by the biomasses that transfer medium through the network and to write the solution in the very simple form:

$$c_{i-1}^0 - c_{i+1}^0 + \alpha \delta_{i1} - \beta_i = 0.$$

If the number of levels is odd ($N = 2n + 1$), we must include Verhulst terms in equation (1) (see [6]). This complicates the homogeneous solutions slightly, but does not change our overall conclusions.

Linearizing equations (2) and (4) with respect to steady-state perturbation $\delta c_i \propto \exp(ikr)$, we get for $i \geq 2$

$$-k^2 \ell_i^2 [(1 + \omega_{i,i} c_i^0) \delta c_i / c_i^0 + \omega_{i,i+1} \delta c_{i+1} - F(k\ell_{i-1}) \omega_{i,i-1} \delta c_{i-1}] + \delta c_{i-1} - \delta c_{i+1} = 0 \tag{6}$$

where $F(k\ell_i) = \exp\{-\frac{1}{2}k^2 \ell_i^2\}$ is the Fourier transform of the kernel of integral operator (5).

We now analyze how a perturbation occurring initially at a lower level propagates through the trophic system to its highest levels and the opposite case, that is, a perturbation moving from top to bottom. In the first case it is useful to introduce the quantities [7]

$$f_i = \frac{\delta c_i / c_i^0}{\delta c_{i-1} / c_{i-1}^0}$$

that relate the relative values of perturbation at one level with those at the nearest neighboring levels. This allows us to rewrite equation (6) in the form

$$k^2 \ell_i^2 (1 + \omega_{i,i} c_i^0) + (1 + k^2 \ell_i^2 \omega_{i,i+1}) c_{i+1}^0 f_{i+1} = (1 + k^2 \ell_i^2 F(k\ell_{i-1}) \omega_{i,i-1}) c_{i-1}^0 f_i^{-1} \tag{7}$$

In order to analyze the propagation of the perturbation in the chosen direction we may set $\delta c_{2n} = 0$ [7], that is, $f_{2n} = 0$. So for $i = 2n - 1$

$$f_{2n-1} = \left. \frac{(1 + k^2 \ell_i^2 F(k\ell_{i-1}) \omega_{i,i-1}) c_{i-1}^0}{k^2 \ell_i^2 (1 + \omega_{i,i} c_i^0)} \right|_{i=2N-1} \tag{8}$$

and for $1 < i < 2n - 1$

$$f_i = \frac{(1 + k^2 \ell_i^2 F(k\ell_{i-1}) \omega_{i,i-1}) c_{i-1}^0}{k^2 \ell_i^2 (1 + \omega_{i,i} c_i^0) + (1 + k^2 \ell_i^2 \omega_{i,i+1}) c_{i+1}^0 f_{i+1}} \tag{9}$$

The stability of the system is associated with the various feedbacks. If positive feedback is sufficiently large, the system will become unstable, and a different set of self-organizational dynamics will come to dominate the system. Negative feedback is responsible for the recovery of the system back to the stable state. Diffusion processes usually increase system stability, but if cross diffusion is inherent in the system the situation could become more complex. It is commonly assumed that cross diffusion serves to destabilize Lotka–Volterra systems [15]. In this case, depending on the sign and magnitude of the terms, cross diffusion can play the role of either positive or negative feedback. But the existence

of positive feedback leads to instability only when the value of positive feedback is sufficiently large. In equation (9) the terms $k^2 \ell_i^2 (1 + \omega_{i,i} c_i^0)$ and $(k^2 \ell_i^2 \omega_{i,i+1}) c_{i+1}^0$, induced by diffusion, are responsible for the negative feedback, while the term $k^2 \ell_i^2 F(k \ell_{i-1}) \omega_{i,i-1} c_{i-1}^0$ generates positive feedback. We will show that the introduced cross diffusional terms responsible for positive feedback are never so great as to lead to system instability. It should be noted that the cross diffusion terms in the equations were proposed in 1959 by Kerner [11] and Jorne in 1977 [10] and are still being intensively studied [4, 18].

Consider the situation when $k = 0$ [7]. Then

$$f_{i+1} = \frac{c_{i-1}^0}{c_{i+1}^0 f_i}. \tag{10}$$

If a small perturbation were applied to level i^* of the system and if $f_{i^*} \ll 1$, this perturbation would spread to the top of the system organization. Therefore, in the case corresponding to the passive behavior of animals, the quantities $f_{i^*+1}, f_{i^*+3}, \dots$ are large. This last condition means that the relative variations of the concentrations $\delta c_2/c_2, \delta c_4/c_4, \dots$, can be large in comparison with the perturbation $\delta c_1/c_1$ occurring at the bottom of the trophic system. In other words, the passive ecosystem is fragile.

In order to analyze the behavior of the quantities f_i as the level i changes and $k \neq 0$, we fix the wave number k such that $k \ell_{i^*} \ll 1$, whereas $k \ell_{i^*+1} \gg 1$ for a particular level i^* (e.g., $k = (\ell_{i^*} \ell_{i^*+1})^{-1/2}$).

As follows from equation (9), for $i < i^*$ the values f_i and f_{i+1} are related by equation (10) and the value f_i has behavior similar to that considered previously.

If $\omega_{i^*+1,i^*}, \omega_{i^*-1,i^*} = 0$, for $i > i^*$, and $k = (\ell_{i^*} \ell_{i^*+1})^{-1/2}$ the value of f_i

$$f_i = \frac{c_{i-1}^0}{\ell_i^2 / \ell_{i^*} \ell_{i^*+1} + c_{i+1}^0 f_{i+1}} \ll 1$$

for any level $i > i^*$. So because of diffusion (negative feedback) the perturbation will decrease in amplitude as it spreads to the top of the system.

For $\omega_{i+1,i} c_{i+1}^0, \omega_{i-1,i} c_{i-1}^0 \leq 1$, and $k = (\ell_{i^*} \ell_{i^*+1})^{-1/2}$ we see that the magnitude of the quantity f_i depends substantially on the parameters $\omega_{i+1,i}, \omega_{i-1,i}$:

$$f_i = \frac{F(k \ell_{i-1}) \omega_{i,i-1} c_{i-1}^0}{(1 + \omega_{i,i} c_i^0) + \omega_{i,i+1} c_{i+1}^0 f_{i+1}}, \tag{11}$$

with $f_i \leq 1$. When the animals exhibit active behavior, however, all the values f_i for $i > i^*$ are of order unity, so that a small perturbation at the bottom of the ecosystem cannot lead to substantial perturbations

at other levels. The perturbations of each level are comparable to the perturbation at the initial level. This is the essence of the proposed mechanism for self-regulation.

It should be noted that perturbations of lower levels lead to responses with consistently the same signs going up the food chain toward top carnivores (big animals). This agrees with the results obtained in [7]. Indeed, stock changes in the ecosystems under consideration can be represented as $([+], s, s, \dots, s)$, signifying that changes in stocks of the producer (the bracketed term) lead to stock changes at successively higher levels that have the same sign as that of the perturbed lower compartment (here s means the perturbation has the same sign).

We now consider characteristics of the propagation of perturbations from the top to the bottom. In this case it makes sense to consider only perturbations characterized by a spatial scale comparable to the size ℓ_{2n} of the domain controlled by the largest predators. That is, we may assume that $k\ell_i \ll 1$ for practically all levels. Under such conditions we may set $\delta c_1 = 0$ [7], and it is useful to introduce the quantities $\{f_i\}$ specified by the expression

$$f_i = \frac{\delta c_i / c_i^0}{\delta c_{i+1} / c_{i+1}^0},$$

which allows us to rewrite equation (6) as

$$k^2 \ell_i^2 (1 + \omega_{i,i} c_i^0) + c_{i+1}^0 f_i^{-1} = c_{i-1}^0 f_{i-1}. \tag{12}$$

In a similar way we get

$$f_1 = 0, \tag{13}$$

$$f_2 = - \left. \frac{c_{i+1}^0}{k^2 \ell_i^2 (1 + \omega_{i,i} c_i^0)} \right|_{i=2},$$

and for $i > 2$,

$$f_i = \frac{c_{i+1}^0}{c_{i-1}^0 f_{i-1} - k^2 \ell_i^2 (1 + \omega_{i,i} c_i^0)}. \tag{14}$$

Whence it follows that the changes in stocks can be represented as $(\dots, o, s, o, [+])$, where an increase in the stocks of the top carnivores alternates the sign of the perturbations going down the chain. (0 means that the perturbation has the opposite sign.) In addition, the values f_i alternate between small and large as we pass through the levels. In other words, ecosystems configured as trophic chains cannot effectively regulate themselves with respect to perturbations in populations of the large predators. This difficulty does not pertain, however, to our postulated mechanism of self-regulation, which suppresses nonlocal interaction of lower level elements as mediated by the higher levels. In general,

our results accord with the consensus among ecologists that bottom-up control tends to be stabilizing, whereas top-down influences are usually destabilizing.

It should be noted that different mechanisms have been proposed recently that serve to increase the stability of ecosystems distributed heterogeneously in space. For example, in [17] a mechanism was proposed whereby prey can find refuge from predation, which dampens oscillations in the populations, smooths the distribution in body sizes (*via* the relative magnitudes of trophic interactive strengths), augments the resilience, and increases the probability of local stability in the linear chain model [9].

Of course, in nature there could exist an active flow from larger organisms to smaller organisms *via* the coexistence of competing parasites [8], and, more generally, passive flows through the microbial loop. While these circumstances influence the behavior of systems, clearly in nature there are no storehouses of top-predator carcasses. Top predator biomass gets recycled as does all the rest. None of this, however, changes the essential mechanism considered in the framework of this paper. Our ideas are similar to Cousins' ecosystem trophic module concept [3]. The assumptions made in the framework of this article serve not only to enhance the stability of the system, but also to perfect its functioning whenever local changes at the bottom lead (in such a way that no nonlocal interaction occurs there) to observable changes at the top.

3. Self-regulation in a market with perfect competition

In this section we create a simple, distributed model of a market in which the price of each type of goods does not depend on the demand for goods of other types. In other words, in such a market there is no nonlocal interaction of the flows of different goods, which is due to the mechanism of self-regulation to be considered. In this context it is reasonable to confine ourselves to a mesomarket of goods made primarily from the same raw material. Hence, this market will involve a single network that joins the ultimate consumers with all types of producers, including the firms producing the raw material, those producing particular types of goods, and the wholesale sellers. That is, this market supplies consumers in different districts with practically the same set of goods.

The latter assumption allows us to treat the given market as a collection of levels made up of firms with similar activities. Furthermore, we can specify the density of each level of identical firms (e.g., level i) by $\rho_i(\mathbf{r})$ and the material flow through one firm by $x_i(\mathbf{r})$. The levels are ordered according to the power of the firms and the higher the level, the fewer the total number of firms at that level. Each firm buys the product of firms at the level just above it and sells its own product to firms in the next lower level. The highest level consists of the firm that

extracts the raw material, and the lowest one is made up of retail sellers. Therefore, each level i also contains micromarkets of products made by those firms and, thus, should be characterized by a spatial distribution of prices $p_i(\mathbf{r})$.

The firms are linked with one another by selling-buying processes; the output of firms belonging to higher ranks is input to firms of lower rank. The direction of the flows of material is opposite to that of the biomass flows considered in the previous section. At the bottom level (level 1) the firms are connected directly with consumers (level 0) supplying them with goods of various types. In other words, inputs and outputs of different firms form a schema of material flows x_i going from the top (raw material) trunk to the consumer medium.

It should be noted that the selling-buying interaction engenders a certain type of economic system that, on one hand, involves a large number of participants, and exhibits a behavior typical of all markets, while, on the other, is but a small part of the whole market society producing goods of a certain type. For example, the steel, food, and clothing industries may be regarded as such a microeconomic market.

Particular interconnections between different firms can come and go during the formation and evolution of the market under consideration, where interaction is governed by trade. This latter process stimulates money flow in the market network in the direction opposite to the material flow, that is, in the direction from the consumers to the producers of raw materials. The arrows in Figure 1 identify these selling-buying interactions and indicate the flow of money from the bottom to the top. The conservation of money as it passes between the firms at different levels enables the firms to play the role of aggregated information on the state of the consumer medium as well as the status of the firms' activities. In fact, for a particular firm i to be able to supply firms of lower rank, with which they are directly linked with the inputs they require, it is necessary and sufficient that the supplying firm possess information that characterizes the state of the consumer in the whole region controlled by the given firms. Such information is embedded in the price of its output [5].

Under the framework of a market with perfect competition we show that a certain hierarchical distribution in spatial structures may arise spontaneously to supply consumers with the needed goods. This implies that, to a first approximation, change in the demand at one point of the consumer medium does not directly cause variations in the flow of goods at other points, even though the material flowing along various branches visits all the hierarchical levels.

The conservation of materials at each level allows us to write

$$x_i(\mathbf{r})\rho_i(\mathbf{r}) = \int_Q d\mathbf{r}' G_{\mathbf{r},\mathbf{r}'}^{i,i-1} x_{i-1}(\mathbf{r}')\rho_{i-1}(\mathbf{r}'). \quad (15)$$

Here $G_{\mathbf{r},\mathbf{r}'}^{i,i-1}$ is the function that specifies the trade interaction between firms at levels i and $i-1$ that is localized in the domain controlled by the individual firms at level i , and Q is the domain of size L . In particular,

$$\int_Q d\mathbf{r}' G_{\mathbf{r},\mathbf{r}'}^{i,i-1} = 1.$$

It should be noted that equation (15) reflects the fact that the higher the level, the larger the domain of control exerted on firms below it. At the lowest level (level 1, the retail sellers) the flow of goods obeys the equality

$$x_1(\mathbf{r})\rho_1(\mathbf{r}) = S(p_1(\mathbf{r}) | \mathbf{r}), \quad (16)$$

where $S(p_1(\mathbf{r}) | \mathbf{r})$ is a given function of the consumer demands. Change in consumer demand leads to variation in the material flow through the market network. The latter in turn causes the firm's profit to vary and, thus, induces these firms either to increase or decrease their activities.

The activity of each firm results in the profit [19]

$$\pi_i(\mathbf{r}) = [p_i(\mathbf{r}) - p_{i+1}(\mathbf{r})] x_i(\mathbf{r}) - t_i(\mathbf{r} | x_i(\mathbf{r})), \quad (17)$$

where the function $t_i(\mathbf{r} | x_i)$ quantifies the total cost of the production activity of firms at level i that are localized in the region \mathbf{r} . For the highest level (N), $p_{N+1}(\mathbf{r}) = 0$. The cost $t_i(\mathbf{r} | x)$ is a convex function of its argument x , that is, the curve $t_i(\mathbf{r} | x_i)$ slopes upward, and

$$\frac{\partial t_i}{\partial x} > 0, \quad \frac{\partial^2 t_i}{\partial x^2} > 0. \quad (18)$$

The function also takes into account the fixed cost, that is

$$t_i(\mathbf{r} | 0) > 0. \quad (19)$$

The interaction of trade between different levels will be specified by an equilibrium in the supply-demand relations such that each firm maximizes its own profit,

$$\frac{\partial \pi_i}{\partial x_i} = 0, \quad (20)$$

and the market is assumed to be characterized by perfect competition,

$$\pi_i = 0. \quad (21)$$

Equation (21) implies that there is no barrier to any firm entering or leaving the market. In particular, there are no barriers to the entry of new firms. With respect to the short-run profits being made in the given market, competition gravitates to the industry where the profits are occurring, and some existing firms will expand or contract accordingly.

Competition eventually causes the average profit at each branch to be maintained at zero. Of course this requirement is not mandatory in our case. The results do not essentially change if we take constant profits into account (i.e., $\pi_i = \pi_i^0 = \text{const}$ for each hierarchical level). This circumstance merely complicates our formula slightly.

Equations (20) and (21) constitute the essence of the proposed model for self-regulation of such an hierarchically organized market. We now show that, under the given assumptions, the price of any one type of goods does not depend on the demand for other goods.

As follows from equations (17) through (19), there is a unique solution of the system of equations (20) and (21): $x_i^*(\mathbf{r})$, $\Delta p_i(\mathbf{r}) \stackrel{\text{def}}{=} [p_i(\mathbf{r}) - p_{i+1}(\mathbf{r})]$ meeting the conditions [5]

$$\left. \frac{\partial \ln [t_i(\mathbf{r} | x)]}{\partial \ln x} \right|_{x=x_i^*(\mathbf{r})} = 1, \tag{22}$$

$$\Delta p_i(\mathbf{r}) = \left. \frac{\partial t_i(\mathbf{r} | x)}{\partial x} \right|_{x=x_i^*(\mathbf{r})}. \tag{23}$$

The value $x_i^*(\mathbf{r})$ and the corresponding value $\Delta p_i(\mathbf{r})$ depend solely on the properties of the function $t_i(\mathbf{r} | x_i)$, which reflects the efficiency of production. Therefore, because firms at the highest level extract the raw material rather than buy it ($p_{N+1}(\mathbf{r}) = 0$), all prices at each level in such a perfect market are specified by the efficiencies of their technological processes and not by their demands. The demand by ultimate consumers for goods at the lowest level determines the total flow of products through the levels. It follows in this case from equations (15) and (16) that the demand alone determines the density of firms at each level. Therefore, variations in consumer demand for one type of goods has no effect on the price and flow of goods of another type.

4. Closing remarks

We realize that the models for ecological and economic systems that we have considered are quite simplistic and cannot be applied directly to real systems. Rather, our goal here has been to elaborate the mechanism of self-regulation, which, we believe, is inherent in every natural system. Such a mechanism is required by all natural living systems because of their complex organization and the necessity that at each level they adapt to changes in the environment. Indeed, the very complex organization of ecological or economic systems implies that none of their elements can possess all the necessary information on how the system must adapt to changes in the environment. Indeed, if each element were to interact with every other one, it either would take an infinite time for the system to adapt or the system as a whole would be unstable. One of the ways available for such a system to avoid this problem is to organize

itself in hierarchical fashion. Unfortunately, such organization might also cause the system to acquire undesirable nonlocal interactions that are mediated through higher levels. To suppress such interaction there must be some cooperative mechanism for system self-regulation. In our opinion, this self-regulation is implemented by the active behavior of elements at each level. Each element acts according to only its own goal, responding to only the small amount of information it receives. However, the law of material conservation acting across the hierarchical organization leads to the self-processing of information. Thus, the small amount of information available to each element informs it in an aggregated and implicit way about the state of the system as a whole. Through such a cooperative way the individual behavior of different elements is made consistent across levels and enables the system to respond properly to changes in the environment [13, 14].

We hypothesize that this mechanism for self-regulation arises in ecosystems from the preference of animals to move in the direction of increasing prey density and to avoid regions with an increasing number of predators. The latter response dampens variations in the species population which otherwise could become critical, because the higher the population of one prey, the greater the extent its predators will specialize in hunting them to the exclusion of others.

In economic systems, each firm attempts to maximize its own profit, so if the total profit increases in the neighboring region (either of space or type of goods), firms will tend to relocate (or retool) into this region. Such active behavior gives rise to variations in the density of firms. We have related this active behavior to the condition that the total profit be zero, due to the presence of perfect competition.

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