

PRZEMYSŁAW TROJAN

## UNITS OF HOMEOSTATIC ORGANIZATION IN TERRESTRIAL ECOSYSTEMS

### ABSTRACT

The requirements that should be met by the theory of homeostasis in terrestrial ecosystems are characterized. A hypothesis is suggested that the organization of the biocoenosis is the carrier of homeostatic mechanisms in the ecosystem. The organization involves four hierarchical categories of ecological units: subsystems, food chains, competitive associations, and populations (species). The definitions of the first three units are formulated. The composition and specific character of the functioning of these units as integrated systems are analysed. A complete ecosystem with efficient homeostatic mechanisms has well developed compensatory abilities, due to which the function of some components can be replaced by the function of the others, and the function of destroyed units can be compensated by the activation of other units.

### INTRODUCTION

All important theoretical and practical problems in the contemporary ecology are focused on the theory of ecological homeostasis. The purpose of this theory is to define the principles determining the structure and functioning of mechanisms controlling the ecosystem as a whole. Due to these mechanisms it can persist in a steady state; they also influence the species composition and structure of particular biocoenoses. Many important questions concerning the functioning of the biosphere, landscapes and single ecosystems can be solved only on the basis of the theory of ecological homeostasis. Applied sciences should find in it an explanation of pest outbreaks and weed invasions into crops, or the reasons for impermanency of the introduction of predators and parasites into economically exploited systems. Nature protection should find in this theory the reasons why efforts at plant and animal species protection frequently ended in failure.

The choice of methods leading towards an objective picture of the homeostasis organization of ecosystems is open to discussion at present [13]. For some ecologists (Andrewartha, Łomnicki) the only

proper way goes through reduction: construction of a biocoenosis on the basis of individual and population characteristics [1, 4]. For supporters of the holistic approach each unit functioning in nature shows specific features, different from those of its components, therefore, it should be analysed as a whole [7]. This direction, however, is "hereditary handicapped" by considering biocoenoses as "superorganisms", on the one hand, and by the view that function has priority over organization in ecological systems, on the other. Lack of methods for studying collective, multispecies systems favours this situation. Recent ecosystem analyses from the point of view of thermodynamics, and based on the information theory [3] show that the maintenance of the steady state, which corresponds to the concept of a dynamic equilibrium in ecosystems, is firstly an effect of the specificity of living matter organized in individuals, populations and biocoenoses [11]. They represent integrated ecological systems controlling the whole ecosystem. Consequently, the point of gravity in looking for homeostatic mechanisms is being shifted towards this field of ecological studies which deals with the organization of biocoenoses. Regulatory ability of these systems does not result from their existence as such but from the degree of their organization. Therefore, it can be admitted that the organization of biocoenoses should increase with their development. But this problem has not sufficiently been studied yet because it is not clear which components are involved in homeostatic mechanisms within ecosystems.

Differentiation among individuals, usually considered as a result of the evolutionary progress, has also a biocoenotic aspect. Schmalhausen has accurately emphasized that the biocoenosis is the arena where natural selection acts. Here all new characters acquired by individuals are verified [9]. This thesis can be further developed by indicating that all progress in individual organization is of importance to the species only to the extent in which it improves the homeostatic organization of an ecosystem. Various types of individual adaptations are of different importance to ecosystem organization. MacArthur pointed out the role of individuals with broad food spectrum, as compared with those having highly specialized food requirements [6]. Reichle et al. emphasize the importance of long-lived individuals to maintaining the equilibrium and organization of ecological systems [8]. Also the role of individuals with short life-cycles and high migratory abilities is extremely important to ecosystems. This group searches for any accumulation of organic matter, decomposes it and recycles in this way. Here numerous coprophages are included, as well as the species specialized in the decomposition of fermenting substances, such as *Drosophilidae*.

A dominant type of relationships among species within a biocoenosis is the exploitation of one species by another. Both energy transfer and number regulation occur through trophic relationships. These are basic forms of information transfer in the ecosystem. An additional factor regulating particular populations is represented by paratrophic relationships based on chemical interactions among species, which either stimulate their activity or limit their occurrence. The regulation processes of this type are effected through "environmental hormones" (ectocrines) and due to so-called "allelopathy". They enable to establish relationships among species not linked through trophic webs, and even very distant from one another.

#### ELEMENTS OF HOMEOSTATIC ORGANIZATION IN BIOCOENOSES

On the basis of the considerations presented above, the following working hypothesis can be considered on homeostatic mechanisms acting within ecosystems.

Hierarchical organization of the biocoenosis is a carrier of homeostatic mechanisms in the ecosystem. This organization consists of four categories of ecological units: a subsystem, trophic chain, competitive association, and species (population).

The subsystem involves all biological components of the ecosystem which are controlled by the same trophic substrate, although species with different trophic specialization can occur within the subsystem. Each ecosystem is composed of three subsystems.

1. The producer subsystem has a trophic input in the form of inorganic compounds dispersed in the environment (non-energetic input) and non-biological energy sources: solar radiation and inorganic compounds.

2. The saprotrophic subsystem has a trophic input, both material and energetic, in the form of dead organic matter produced within the ecosystem and, in some cases, imported from outside (e.g. aquatic ecosystems in strongly shaded forests).

3. The biotrophic subsystem has the subsystem of producers as the trophic input. In terrestrial ecosystems this subsystem includes phytophages and zoophages, which are in trophic relations with phytophages.

The trophic chain (Fig. 1) is a unit of the organization of sapro- and biotrophic subsystems and, at the same time, the main channel of energy flow. It is made up of several links corresponding to successive levels of the number pyramid. The food chains are often accompanied by a parallel side link consisted of polyphagous species and having

a regulatory effect on the whole chain. Consequently, a double regulatory system functions within the food chain. The first one takes place among particular links along the food chain. This regulation acts through the energy transfer from one link to another. The energy taken by a given link stimulates its development and, simultaneously, inhibits the development of the preceding link. Since at least all intermediate links, except for extreme, have relationships of a similar type both on the input and output, each link has a double system of feedbacks regulating numbers in a given link and the corresponding energy flow. In many cases the density-dependent factors are sufficient for number regulation. In the highest links, represented by top predators, the role of the structure-dependent factors is of greater importance; they act as a regulatory factor of population dynamics when the density-dependent regulation on the output is lacking.

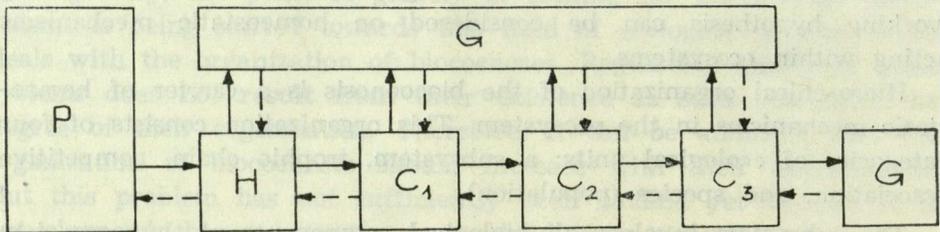


Fig. 1. Block diagram of a food chain of biotrophs.

P — producers, H — herbivores,  $C_1$ — $C_3$  — carnivores and parasites, G — general carnivores and polyphages; solid arrows denote energy flow, dotted arrows — number (biomass) regulation.

The other regulatory factor within the food chain is the side-link, which is made up of polyphagous organisms or general predators. This group exploits all links of the food chain, the highest predatory impact being exerted on the links with the highest density at a given time. The processes occurring here can be explained on the basis of density-dependent actions and learning to select the prey most abundant in the habitat.

Regulation of the energetical type has been described by Slobodkin in experimental studies on *Daphnia* food chains [10]. But the data presented by this author enable only a preliminary insight into the role of these processes in the regulation of chain systems since experimental conditions differ from natural conditions. There are many data on two-species systems of prey-predator type, but the application of these results is restricted as generally food-chains involve systems composed of a larger number of components which have not been analysed yet. The action of the side food chain is illustrated by the

results obtained for insectivorous birds, which often change their food spectrum, depending on the actual abundance of particular prey populations within a food chain. It should be noted that small insectivorous birds have a regulatory effect on other links of the food chain than, for instance, such predators as spiders and ants have.

Due to the occurrence of the two types of regulatory processes within a food chain, it can be ecologically considered as an integrated element which, together with other chains included to the subsystem, forms an ecological unit of a higher order.

The number of chains involved in a given subsystem is open to discussion (Fig. 1). The classification of trophic chains within the biotrophic subsystem can be based on differences in the relations of phytophages, i.e. the initial link, to the producer link. The starting point can be here the way of food intake and its significance for primary production processes.

The first group consist of ectotrophs — phytophages with biting mouth-parts. They include vertebrate herbivores and larvae of *Lepidoptera* and *Symphyla*, as well as the majority of *Orthoptera*. These groups feed on green plant parts, which implies that their activity leads towards the limitation of plant photosynthetic potential, and when the link of ectotrophs is abundant, it threatens the producer system as a whole.

The second group consists of endotrophs — phytophages using plant material without disturbing the assimilative apparatus. Here are included small invertebrates, mainly insects with piercing mouth-parts, e.g., *Aphidae*, *Homoptera-Auchenorrhyncha*, and phytophagous *Heteroptera*. They often take food directly from vascular bundles and in this way they become production consumers without disturbing productive abilities of plants. From the ecological point of view this is a safe and advantageous type of trophic relationships, characterized by durability and lack of threat against particular components of this system.

The third group consists of organisms consuming energy retended in plants. They use such food-stuff as wood, rhizome, tubers, and other storing organs of plants. This group also includes xylophages, some phytophagous *Elateridae*, and other animals feeding on storing organs of plants or on fruit. They do not disturb primary production, nevertheless, they may occasionally largely injure plants so that they may be dangerous to the plant as a whole (xylophages) or they may affect plant reproduction.

In critical situations when one of the trophic chains in a subsystem is limited or excluded, its function can be taken over by the parallel chain (Fig. 2).

The competitive association is a basic component of the food chain. Each link of the food chain contains not only single species, as usually shown in models of ecological relationships presented in the form of food chains, but a community of species with the same ecological niche [5]. Thus, these are species using the same food substrates and exploited by the same group of predators and parasites. The definition of the competitive association also determines its position in a particular link of the food chain. Each species in the competitive association differs from the others by its environmental adaptations that can be presented in the form of a curve of ecological tolerance. This curve characterizes ecological properties and genetic (phenotypic) structure of the species. Tolerance limits of the association forming links of a food chain are represented by a curve with a rather large range (Fig. 3). Due to this, the range of ecological variability in a competitive association is larger, than the variability range of a single species. Any shift in environmental conditions is followed by a decrease in the number of these species the ecological optima of which are beyond the zone of environmental variability, and by an increase in the

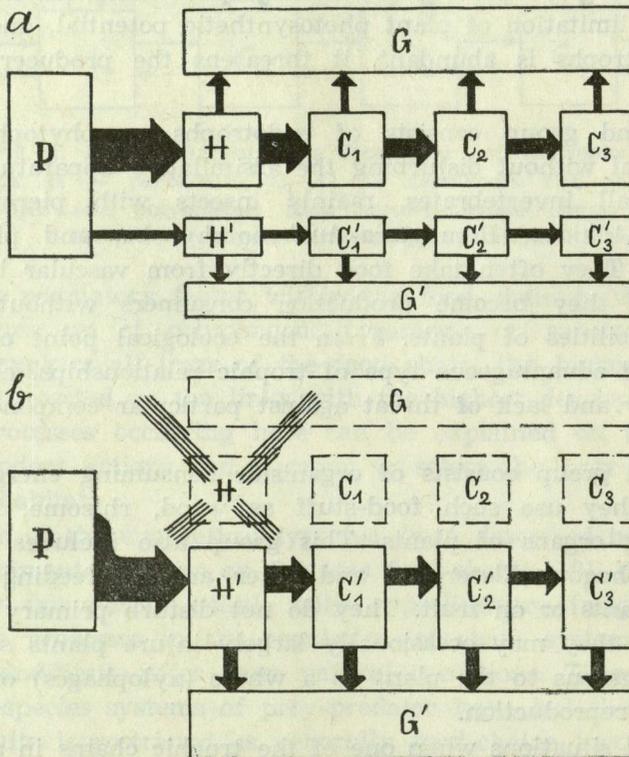


Fig. 2. Functional shift from a destroyed food chain (a) to a parallel food chain (b). Symbols as in Fig. 1.

abundance of these species the optima of which will be within the range of the actual environmental variability (Fig. 3). In this way, interactions occurring within the association as a whole have a compensatory character and secure, within a large variability range, the maintenance of a stable number level in the link. Consequently, they secure its permeability in the energetical channel such as the trophic chain.

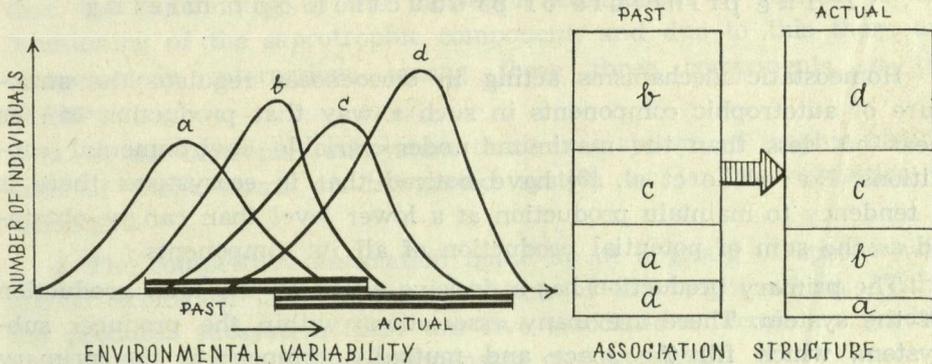


Fig. 3. Changes in the association structure as an effect of shifts in the range of environmental variability.

STRATEGY OF BIOCOENOSIS FUNCTIONING

The maintenance of ecological equilibrium is a basic function that can be expected in an efficiently functioning biocoenosis. But the concept of ecological equilibrium is equivocal, and various definitions of the equilibrium are based on completely different ecological principles [12]. The basic feature of balanced biocoenosis is an equilibrium between production and destruction of organic matter within the ecosystem. A deviation from the state of balance in these processes is followed by multidirectional developmental processes always related to instability of the system as a whole.

Ecosystems are as old as organic life, and the information contained in them reflects historical experience, firstly related to the struggle for system stabilization. The state of an ideal ecological equilibrium cannot be reached, nevertheless the stabilization of a system and the action of processes enhancing the maintenance of its actual state are possible, at least from the point of view thermodynamics. The functioning of each biocoenotic system is based on three strategical principles:

### 1. The principle of matter cycling

Without matter cycling no ecosystem can exist. The blocking of matter cycling at any ecosystem point creates a situation which threatens its ecological equilibrium, and sometimes it can also result in an ecological catastrophe. Mechanisms acting within biocoenoses are firstly adapted to the maintaining of matter cycling.

### 2. The principle of production optimizing

Homeostatic mechanisms acting in biocoenoses regulate the structure of autotrophic components in such a way that production can be near but less than the maximum under variable environmental conditions. Reichle et al. [8] have noticed that in ecosystems there is a tendency to maintain production at a lower level than can be obtained as the sum of potential production of all its components.

The primary production has a decisive effect on the total production of the system. There are many associations within the producer subsystem, which fill the space and mutually compensate the primary production. In most developed producer subsystems of the temperate zone of the Northern Hemisphere, represented by forest ecosystems, there are five associations: trees, shrubs, herbs, ground layer (mosses and lichens), algae inhabiting soil surface and tree bark, as well as epiphytes, mainly lichens. In simplified systems such as crop fields, the production of the main plant is compensated by weed communities. When the growth of potatoes is reduced, solar energy used by weeds compensates for losses in potato production [2]. In alfalfa fields, weed communities develop after the peak of alfalfa production. As a result, the period of production is prolonged, and the total production of the whole field is higher than for only one plant species.

### 3. The principle of structure preservation

Biocoenosis organization, which is the carrier of homeostatic mechanisms, is also an object of the preservative action. All biocoenoses tend to restore the state of balance. These processes, known as secondary succession, lead towards regeneration of the system destroyed in a catastrophe, for instance, as a result of human activity. Secondary succession in forest ecosystems can occur for a few decades, while the primary succession, in which a given system is formed from the beginning, takes several times longer periods.

## CONCLUSIONS

1. Mechanisms responsible for ecosystem homeostasis are incorporated into the trophic web of the biocoenosis; in addition, this system is regulated by paratrophic relationships due to which interactions occur among the components not interrelated through food.

2. The ecosystem consists of three subsystems: producers, biotrophs and saprotrophs. It is difficult to estimate general relationships among them but in relatively balanced ecosystems the ratio of saprotrophic to biotrophic transformation is variable. Thus, it may be suggested that the functioning of the biotrophic component is related to the functioning of the saprotrophic component, and due to this there are compensatory interactions among these three components of the system.

3. In the biotrophic subsystem there is a system of trophic chains; each of them forms an integrated system as far as regulation is concerned.

4. The competitive association made up of a group of species with similar ecological niche forms each link of the trophic chain. Within the producer subsystem there are five associations forming a productive system in which they compensate one another.

5. Functioning of the trophic-competitive organization system as a homeostatic mechanism consists in:

5.1. Maintenance of a stable number level in the association (link of the trophic chain) under variable environmental conditions due to compensatory effect of the number of one species on another.

5.2. Functional replacement of one species by another in the situation when the ability to transform matter of one of them will be reduced by stressing factors acting in the ecosystem.

6. Responses observed in ecosystems and related to changes in number proportions within associations, without limiting their total numbers, reflect the adaptation of the system to variable environmental conditions.

7. Elimination of any link is followed by disintegration of the whole trophic chain.

8. If the function of an eliminated chain can be taken over by a parallel trophic chain of the subsystem, an interchain compensation occurs in this subsystem, and the system maintains its stability.

9. If the function of an eliminated chain cannot be taken over by another trophic chain, organic matter is accumulated within the ecosystem and the whole system is endangered. This can often result in

an ecological catastrophe finally leading towards a destruction of the whole system.

Instytut Zoologii PAN  
ul. Wilcza 64  
00-679 Warszawa  
Polska

#### REFERENCES

1. Andrewartha, H. G. 1967. Introduction to the study of animal populations. Chicago.
2. Herbich, M. 1969. Primary production of a potato field. *Ekol. Pol.*, 17: 73—86.
3. Kowalczyk, E. 1977. Entropia a informacja. *Kosmos Ser. A*, 26: 341—348.
4. Łomnicki, A. 1978. Przygody ekologów i ewolucjonistów w krainie superorganizmów. *Wiad. Ekol.*, 24: 249—259.
5. Łuczak, J., Prot, E. 1967. Zagadnienia ekologii zwierząt. Warszawa.
6. MacArthur, R. 1955. Fluctuations in animal populations, and a measure of community stability. *Ecology*, 36: 533—536.
7. Odum, E. P., 1977. The emergence of ecology as a new integrative discipline. *Science*, 195: 1289—1291.
8. Reichle, D. E., O'Neill, R. V., Harris, W. F. 1974. Principles of energy and material exchange in ecosystems. In: *Unifying concepts in ecology* (by W. H. van Dobben and R. H. Lowe-McConnell), pp. 27—43.
9. Schmalhausen, I. I. 1968. *Kiberneticheskie voprosy biologii*. Novosybirsk.
10. Slobodkin, L. B. 1959. Energetics in *Daphnia pulex* populations. *Ecology*, 40: 232—243.
11. Stugren, B. 1976. *Zasady ekologii ogólnej*. Warszawa.
12. Trojan, P. 1978. Pojęcie równowagi ekologicznej ekosystemów. *Kosmos Ser. A*, 27: 139—149.
13. Trojan, P. 1978. Redukcjonista na poletku ekologii. *Wiad. Ekol.*, 24: 272—276.

#### JEDNOSTKI ORGANIZACJI HOMEOSTATYCZNEJ EKOSYSTEMÓW LĄDOWYCH

##### STRESZCZENIE

W pracy przedstawiono warunki, jakie powinna spełniać teoria homeostazy ekosystemów oraz metodologiczne przesłanki pozwalające na przedstawienie obiektywnego obrazu homeostazy. Punkt ciężkości poszukiwań nad mechanizmami homeostatycznymi powinien spoczywać na organizacji biocenoz. Odmienną w niej rolę odgrywają różne gatunki, zależnie od specyfiki bionomicznej, trwania życia, zakresu specjalizacji pokarmowej itp.

Postawiono hipotezę roboczą, w myśl której nośnikiem mechanizmów homeostatycznych w biocenozie jest hierarchiczna organizacja biocenozy. Wyróżniono cztery kategorie jednostek ekologicznych składających się na tę organizację: podsystem, łańcuch troficzny, zespół konkurencyjny i gatunek (populacja). Podano definicję trzech pierwszych z tych jednostek i omówiono ich właściwości jako

układów ekologicznych zintegrowanych. Szczegółowiej omówiono strukturę podsystemu biotrofów, gdzie można podać wstępną klasyfikację typów łańcuchów pokarmowych wchodzących w skład podsystemu.

Łańcuch pokarmowy jako jednostka zintegrowana w większości przypadków wykazuje złożoną budowę. Obok szeregu ogniwi ustawionych jedno za drugim wzdłuż kanału energetycznego, jakim jest w ekosystemie dany łańcuch, znajduje się z reguły ogniwo oboczne. W jego skład wchodzi organizmy polifagiczne lub drapieżcy niewyspecjalizowani. Podano charakterystykę regulacyjną takich układów, która powoduje, że łańcuch troficzny zachowuje się jak układ zintegrowany.

W normalnych warunkach w obrębie każdego ogniwa troficznego znajduje się nie pojedynczy gatunek a szereg gatunków tworzących zespół konkurencyjny. Opisano właściwości zespołu decydujące o kompensacyjnym oddziaływaniu tego układu w obrębie ogniwa. Zabezpiecza to drożność łańcucha troficznego jako kanału energetycznego.

Działanie mechanizmów homeostatycznych w obrębie ekosystemu prowadzi do zachowania jego równowagi wewnętrznej, tj. równowagi między produkcją a destrukcją materii w układzie. Trzy zasady strategiczne określają działanie układów biocenotycznych. Są to: zasada zachowania obiegu materii, zasada optymalizacji produkcji, zasada zachowania struktury.

System jednostek tworzących strukturę troficzną w obrębie ekosystemu, regulowany dodatkowo związkami paratrophicznymi, stanowi mechanizm homeostatyczny biocenozy. Posiada on wysoko rozwinięte zdolności kompensowania działania jednych komponentów przez inne a w niektórych przypadkach obserwujemy zastępowanie jednych łańcuchów pokarmowych przez drugie.

## ЕДИНИЦЫ ГОМЕОСТАТИЧЕСКОЙ ОРГАНИЗАЦИИ НАЗЕМНЫХ ЭКОСИСТЕМ

### РЕЗЮМЕ

В статье обсуждены условия, которым должна отвечать теория гомеостаза наземных экосистем. Ставится гипотеза о том, что организация биоценозов включает гомеостатические механизмы экосистемы. В ее состав входят четыре иерархических категории экологических единиц: подсистема, цепь питания, конкурентное сообщество и популяция (вид). Приведена дефиниция трех первых единиц, обсужден их состав и специфика функционирования как интегрированных систем. Целостная экосистема с эффективно действующими гомеостатическими механизмами обладает высоко развитой способностью компенсации функционирования одних компонентов другими, а также замещения функции уничтоженных единиц путем развития активности других.