

A review of and some comments on the attempts to construct an overarching theory of ecosystems plasticity

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It is generally accepted that life uses two distinct mechanisms during adaptation to the environment: evolutionary and individual. The latter is known as phenotypic plasticity. However, several decades ago, a conviction emerged and later strengthened that populations and ecological communities also tend to stabilize the essential variables (total biomass, productivity, adaptability, etc.) to a certain degree, regardless of uncertainty of environmental conditions. A response to this uncertainty is a change in the frequency of preadapted genotypes and compensatory fluctuations in population sizes. Adaptation can be regarded as a never-ending multilevel hierarchical process of individual-, population- and community-level adjustments to a changing environment. According to these concepts, adaptation is like a process during which individuals, populations and entire communities can adjust their optima to the ever-changing environmental conditions. Individual and populational rearrangements are means for a more subtle adjustment of the community optimum and the lines of defence, one following the other, on the road of stressful impacts towards the essential variables of an ecosystem. The authors of this conception, e. g. M. Conrad, V. N. Novoseltsev, H.-R. Gregorius, E. Lekevičius, also believe that these mechanisms should interact in a quite determined manner; this brings us hope that a unified theory on the plasticity of ecosystems will be developed.

In this review an attempt is made to describe these concepts which are still in development and to reveal their strong, well-founded aspects as well as weak points. It is concluded that the multifarious attempts to falsify the conception are needed.

Key words: adaptation, plasticity, hierarchical adaptability theory, homeostasis, evolutionary mechanisms, deductive reasoning

INTRODUCTION

Adaptability or plasticity is one of the fundamental characteristics of life. Basically, biologists associate the concept of adaptation with evolution and natural selection. In eco-physiology this concept is also used when dealing with individual reactions to a changing environment, such as behavioural acts, physiological adaptation or “phenotypic plasticity”. This term of adaptation is actually sometimes interchanged with other corresponding terminology, for example, acclimation, acclimatization or homeostasis.

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A new theoretical branch of biology, Hierarchical Adaptability Theory (HAT), has formed over recent decades. Its proponents (e. g. Conrad, 1975, 1983; Novoseltsev, 1978; Lekevičius, 1986, 1997; Gregorius, 1996) suggest a broader view of the adaptation phenomenon: they define adaptation as the process by which a decline in biological activity (growth, reproduction, primary production, etc.) induced by environmental changes is restored. For example, recent studies have provided strong evidence that species diversity enhances the functional stability of ecosystems (e. g. McNaughton, 1977; Yachi, Loreau, 1999; Isbell

et al., 2009; Loreau, 2010). The stabilizing effect of species diversity results from the fact that different coexisting species are complementary in their responses to environmental fluctuations. The authors maintain that no matter how environmental conditions change within usual limits there can always be found species for which these environmental conditions are favourable. The increased biological activity of these species compensates for the decreased activity or growth of other species from the same community (Gonzalez, Loreau, 2009), so that the functional stability of the aggregate community properties is achieved. In other words, species in a community are pre-adapted to a range of usual environmental changes.

Functional properties of populations can in turn be stabilized due to another component of biodiversity, i. e. genotypic diversity. An environmental change that is unfavourable to some genotypes may be favourable to others. Thus, some genotypes may compensate for a decreased activity in others. Differential genotype multiplication caused by seasonal changes in environmental conditions was first observed in insects and later in protists and planktonic crustaceans (for survey see, e. g. Lekevičius, 2007). This phenomenon was called seasonal selection. The essence of this phenomenon is that different genotypes respond differently to temperature, light, humidity and other abiotic environmental factors. Hence, under seasonal changes in the environment, the frequency of genotypes varies periodically. For instance, cold-preferring genotypes reproduce in early spring and autumn, while heat-preferring genotypes reproduce in summer. Due to this, the rate of reproduction and total biomass are stabilized in a certain degree. By analogy, we can also talk about day-to-day and year-to-year selection (Lekevičius, unpublished).

Additionally, the proponents of HAT assert that all adaptation mechanisms – individual, populational, biocenotic and evolutionary – interact with each other in a certain, rather determined manner during the process of adaptation. Thereby, these scientists hope to formulate a general theory, which would embrace each one of the aforementioned mechanisms. The basic target of HAT itself is the same as in every field of science – to organize often very plentiful and highly complicated

empirical material and extract essential information from it, converting it into cohesive theoretical outlines and generalizations, which could be both explanatory and predictive.

In this paper it is tried to review those studies which, to my mind, have contributed the most to HAT. This review is probably the first in this field. Such a circumstance might seem curious to somebody. The idea itself has emerged more than forty years ago. During this time approximately one hundred publications have been issued, including several monographs. There is one possible explanation for this. Many quite important works in this field were primarily published in Russian; therefore, they were not accessible to Western readers. According to the information available to me, no conference or symposium has ever been organized on this topic. I think that this low level of activity of the proponents of this new discipline is truly inexcusable.

WESTERN SCHOOL: ASHBY, CONRAD, FEDRA, GREGORIUS, MEYERS AND BULL

According to Ashby (1956) the organism, considering it as a functional unit, is a collection of essential and subsidiary variables. Examples of an essential variable could be the concentration of oxygen in the brain, the amount of glucose in the blood and the body temperature of a mammal. The organism must be able to stabilize these key indicators (reach homeostasis); its well-being and survival depend on this. Conversely subsidiary variables can and must alternate over a broad range in order to stabilize essential variables, regardless of the uncertainty of environmental conditions. Such alternations of variables are responses to the changes in the environment and they usually have an adaptive nature. For living systems the following scheme could be applied:

$$D \rightarrow R \rightarrow E,$$

where D is deviations in environmental conditions, R is regulator, and E is a set of essential variables; R acts in such a way that it minimizes a possible impact of D on E. Essential variables must be stable. Following this necessity, it is clear that the diversity of possible responses must be as wide as the diversity of possible environmental

conditions. In other words, homeostasis is only possible when the internal variety (of responses) fully neutralizes the variety of external conditions. Ashby termed this concept as the “law of requisite variety”.

Conrad (1972a, 1972b) was the first to further develop this idea of Ashby and applied it in order to describe all adaptation phenomena. He began to construct his own version calling it the hierarchical adaptability theory (HAT). Later he compiled his previous work into a monograph (Conrad, 1983). He utilized certain equations from the information theory seeking to improve accurateness and capacity of Ashby’s ideas. However, the remaining mathematical device was an invention of Conrad himself.

The primary idea of Conrad was that the essential variables of populations and ecological communities, not only individuals, are capable of reaching homeostasis. To achieve homeostasis life employs all types of structural and functional diversity: macromolecular and metabolic pathway varieties in an organism, genotypic diversity in a population and species diversity in a local community. The greater this structural and functional diversity, the greater is the variety of potential responses. According to the tradition of information theory, Conrad calls the latter the entropy or, to be more exact, the behavioural uncertainty of biota. Correspondingly, a diversity of environmental conditions can be considered environmental uncertainty. Further he asserts the following (Conrad, 1975):

“The adaptability of an organism or community is its ability to function in an uncertain environment <...>. All the various forms of adaptability, regardless of their outward diversity, should be amenable to a single, general characterization; for they are all adaptations to one thing, environmental uncertainty. To capitalize on this consideration we treat the biotic community and envi-

ronment as a system with sets of states and with certain (generally unknown) sets of probabilities governing the state to state transitions.”

According to Conrad, adaptability of biota may be determined by its potential behavioural uncertainty (or repertoire of possible behaviours) together with its ability to either anticipate or ignore the environment. The fundamental inequality of the theory is as follows (Conrad, 1975, 1983):

behavioural uncertainty of biota – anticipation + indifference \geq behavioural uncertainty of environment.

The interpretation by Conrad of this inequality is as follows: a community can successfully cope with the environment only in case the inequality runs. Adaptability of biota (left side of the inequality) consists of three components: behavioural uncertainty of biota, anticipation, and indifference. If a community is capable of predicting changes in the environment, its adaptation will do with less behavioural uncertainty. Besides, organisms may use some other ways to avoid consequences that are unfavourable thereto, for example, by retreating to another geographical locality or physically isolating themselves from the environment. Conrad calls such trait indifference.

According to Conrad this inequality is distinguished by a tendency to become an equation; redundant adaptability is not stimulated by selection. What is the reason for this? Conrad answers to this question as follows (Conrad, 1975):

“Basically no form of biological adaptability comes free. Gene pool diversity is costly in terms of unfit individuals; developmental plasticity means carrying extra genetic information, indeed potentially extra regimes of development; behavioral adaptability means supporting excellent information transmission and processing capabilities, or maintaining behavior patterns which are precisely patterned to the environment.”

Table 1. Modes of adaptation (Conrad, 1975, 1983)

Levels	Modes
Community	Plasticity of species composition. Inter-substitution in food chains.
Population	Fluctuations in abundance and redistribution of individuals in space.
Organism	Plasticity of ontogeny.
Phenotype	Morphological, physiological and behavioural plasticity.
Genotype	Gene pool diversity.

Responses to environmental changes may include adaptive reorganizations in a community (Conrad, 1975, 1976, 1983), such as a reversible change in species composition and reorganization of a food web, changes in population sizes and spatial location of individuals, various physiological and ontogenetic reactions and, ultimately, the emergence of new traits owing to genetic variability.

Thus an ecosystem copes with the environment by reorganizations that occur at all levels of the organizational hierarchy, starting at the molecular level and ending at the ecosystem. It is highly important to accentuate that, according to Conrad, the inequality described above runs with respect to a separate population or individual, as well as community.

Usually thousands of species coexist in one locality. Therefore, according to Conrad, it might be predicted that adaptability is similar in all of them, although the contribution of separate adaptation mechanisms might differ markedly. Microorganisms, for example, are characterized by a high evolutionary plasticity; however, they are indigent of behavioural acts. Higher forms of animal life are distinguished by low evolutionary plasticity and ability to change population size; however, they exhibit a remarkably developed individual (phenotypic) plasticity. Conrad refers to such regularity as the “principle of compensation”. It is correct to apply it exclusively to organisms dwelling in an environment that is similar by its uncertainty. In areas where the environment is more stable, the expectation may be a greater integrity of parts of biota in addition to lower adaptability. Population and community levels are distinguished by the least integrity, which is one of the reasons why the local nutrient cycle and ecosystem energy flow are the most buffered functions of life.

What was the influence of this concept on biologists? So far as known to me, the ideas of Conrad have been exploited since nowadays; however, basically by non-biologists (e. g. Creese et al., 1997; Kampfner, 2002; and Kirby, 2002; although see Salthe, 1985 as a rare example of biological application). Discussing the contribution of Conrad to theoretical biology, Pattee (2002) writes:

“None of these fundamental issues Michael [Conrad – E. L.] raised over 30 years ago has been

settled, and some of them have not yet been fully understood by most biologists.”

Kirby (2002) commented on the scientist’s legacy as follows:

“While many Conrad themes and ideas had widespread influence, the adaptability formalism itself was apparently not contagious. This may be due to the complexities of the formalism, the bewildering variety of reformulations of it, <...> and the difficulties in what he himself would call the ‘epistemological statuses of the equations’. Nevertheless, he stood by the formalism for over two decades.”

Fedra (1979), another theoretician, does not attempt to formulate an adaptability theory. However, my opinion is that several of his propositions were valuable. For example, he introduced the concept of “environmental tracking”. Its main idea is that, due to internal reorganizations, biosystems are able to change their optima to follow environmental fluctuations. Thus, in a certain sense, the process of adaptation is the optima fitting which is ensured by physiological and ecological mechanisms. Ecological mechanisms work through (Fedra, 1979) “<...> the differential success of the functionally different component species under different environmental conditions. The basic machinery of the set of component species is always available and is tuned by quantitative changes in the species composition according to the respective environmental conditions. The functional dissimilarity or diversity is therefore a basic prerequisite of community adaptability <...>. Due to the continuous adjustment of community features by enhanced dominance of the “best” adapted, environmental tracking is again a basic strategy.”

According to Fedra, due to such a mechanism, the optimum of the entire community shifts from one to another direction with respect to the environmental gradient. However, adaptation does require time; therefore, a time lag is unavoidable, particularly when the environment changes suddenly. Furthermore, environmental changes are often hardly predictable; thus, most organisms, species and communities are simply condemned to function in a suboptimal regime almost permanently.

By using the open dynamical systems theory, Gregorius (e. g. 1996, 1997, 2001) describes certain “generic principles of adaptation”. One such

principle is as follows: reorganizations of adaptive character occur at all levels, from the cell to the ecological community. Besides, regulatory adaptation (characterized by the stationarity of the system state) as a rule precedes structural adaptation (characterized by state changes). Stationarity at one level implies the stationarity of all higher level characteristics. This means that adaptation mechanisms are organized in a natural or compositional hierarchy. Responses of lower levels are quicker; they become useful in coping with sharp and hardly predictable changes. However, all mechanisms at the disposition of an ecosystem often operate simultaneously. As environmental conditions change yet another time, numerous, previously little active structures “latent features” of different ranks become activated. As Gregorius (2001) writes:

“Activation of formerly latent features is usually accompanied by a change in state, as in the case with the ‘turning on’ of a structural gene, the increase in frequency of an allele that becomes advantageous in a population under changed environmental conditions, or the multiplication of companion species [see the definition below – E. L.] following ecological disturbances.”

As a result, all these adaptive rearrangements make the local nutrient cycle and the energy flow attending such a cycle, irrespective of environmental vagaries.

Gregorius (1996) says that the adaptive roles of species coexisting in one community differ. Some, “key species”, perform important functions in the nutrient cycle. Their population sizes vary insignificantly, and they are able to cope with easily predictable changes, usually due to physiological reactions and polymorphism. Others, “companion species”, widely use drastic changes in population sizes along with the aforementioned means for adaptation. Their participation in the nutrient cycle is not vitally important; however, they ensure its stability, particularly when unpredictable and drastic changes in the environment occur. Yet, since companion species buffer the functions of key species against disturbances, they may play an essential role in ecosystem stability and adaptability.

Two other scientists, Meyers and Bull (2002), present several valuable thoughts about the adaptation phenomenon in their brief article. They

urge biologists to create “a comprehensive theory of adaptive variation”. In their opinion, the theory should unify the data about “an enormous variety” of mechanisms to cope with environmental fluctuations into one concept. The main mechanisms distinguished by these authors are physiological and developmental plasticity, somatic mutations, “bet hedging” (e. g. diapause, dispersal), adaptation due to polymorphism and evolution. The contribution of separate mechanisms to population adaptability may vary greatly, mostly depending on the generation time incidental to the organisms: the longer the generation time, the lesser is the contribution of polymorphism and evolution to adaptation and the greater is the role of individual mechanisms. Meyers and Bull hold the opinion that, although strategies for adaptation to the environment are numerous, they have an analogous destination. Thereby there are grounds for conceptual synthesis. For unknown reasons these authors do not provide references to any publications by Ashby, Conrad, Fedra or Gregorius.

ORIGINATORS OF THE EASTERN SCHOOL VERSION: SHKORBATOV, NOVOSELTSEV, AND SHILOV

As mentioned in Introduction, certain HAT authors published most of their works in Russian and, naturally, these works are little-known among most English-speaking readers. Therefore, these will be covered in somewhat greater detail.

An unusual outlook, which was propagated by ecologists and evolutionists, formed in the countries of the former Soviet system approximately 50 years ago. Its roots can be traced to the ideas of a microbiologist, Winogradsky (1856–1953), and a biogeochemist, Vernadsky (1863–1945). This outlook consists of the following basic theses: life can exist in the form of a nutrient cycle (\approx an ecosystem) only. Ecosystems are organized systems; the emergence of life on earth was inevitably accompanied by the appearance of the first nutrient cycles. Additionally, there is one more, quite independent evolutionary lineage in addition to species evolution – the evolution of ecosystems extending via individual selection, its direction predetermined by an ecological community. Contraposing the study from the West, G. A. Zavarzin, an academician

of the Russian Academy of Sciences, termed this arrangement of views as the Russian paradigm in one of his publications (for details see Lekevičius, 2006).

The version of HAT, which the proponents of this school (e. g. Shkorbatov, 1982; Novoseltsev, 1978; Lekevičius, 1986; Shilov, 1988) had been formulating over recent decades, fits rather nicely into the conceptual frame, which is called the Russian paradigm by Zavarzin. It is clear that the development of views of these authors were strongly influenced by their intellectual environment.

Shkorbatov (1971) was probably the first to urge biologists to develop a "general adaptation theory". According to him, this theory should encompass all modes of adaptation found in nature, as well as analogous processes characteristic of inanimate nature and human society (Shkorbatov, 1982). Shkorbatov (1971, 1982, 1986) singled out biological mechanisms for adaptation as being individual responses that are possible within the bounds of individual reaction norms, populational or evolutionary responses and biocenotic rearrangements or ecological succession. In the world of life, all these interact and complement each other. The general theory needs to perform a synthesis and describe all the mechanisms and their interactions by means of a single doctrine. However, the author does not suggest any particular way for accomplishing this.

In his monograph, Novoseltsev (1978) does not urge the development of HAT but he does present some untraditional ideas, which must be mentioned here. He believes that the phenomena of homeostasis and adaptation are inseparable from the control mechanisms which are characteristic of biological systems. Control is characteristic of the ecosystem level, not only of the cell and organism levels. Ecosystems are organized systems, the same as organisms are. The only difference is that control in ecosystems is realized mainly through the interaction of components (species) which are equivalent in respect of control. Interacting individuals and species restrict behaviour of each other. In such way, restricted behaviour is directed in a manner which ensures the greatest possible productivity of the ecosystem. The fluctuations in population sizes related to alternations in environmental conditions are actually the

means which stabilize the amount of energy flowing through the ecosystem. Thus, this instability at the population level guarantees the stability of ecosystem functions. Following Ashby, such means of control and homeostasis are considered to be passive by Novoseltsev, and he differentiates them from the active means, which are characteristic of organisms.

According to Novoseltsev (1978), the functions of control mechanisms are to maintain the stationary, thermodynamically non-equilibrium state (first order or main goal), stabilize functional parameters (second order goal) and optimize functions (third order goal). The stationary state is understood as equality in the rates of the inflow and outflow of energy and materials. As conditions suddenly and uniformly worsen, the optimal state is initially lost, and then the deterioration of homeostasis follows. Under especially intensive stress, the stationary state is lost as well. Homeostasis of life is maintained by the differential activity of genes, humoral and nervous control mechanisms, differential growth of populations and changes in species composition. Homeostasis as well as the control mechanisms characteristic of lower levels of the organizational hierarchy are included into the mechanisms of higher levels as component parts. Thus, as environmental conditions gradually deteriorate, initially the cellular mechanisms, then other individual mechanisms and finally biocenotic mechanisms become activated. Only when the abilities of the latter are exhausted, the stationary state of the ecosystem is deteriorated, and a catastrophe occurs. All in all, the global parameters of an ecosystem are the most protected from the whims of the environment.

Shilov (1988) begins with the thought that long-term existence of life would not be possible without the nutrient cycle. This is only possible with the participation of all three fundamental functional groups: producers, consumers and reducers. However, species diversity within each of these groups is also important as well as the diversity of individuals in populations, diversity of enzymes, metabolic pathways and acts of behaviour characteristic of a separate individual. Due to this great diversity, the nutrient cycle of an ecosystem becomes stabilized and independent of the whims of the environment because, no matter how

much it might change, a response always appears that can make the particular environment more or less acceptable. As Shilov asserts, every species has adjusted to average parameters of the climate by evolution; meanwhile the aforementioned non-genetic (not requiring evolutionary changes) rearrangements assure adaptation to fluctuations in conditions. These restructurings become somewhat more labile than are the evolutionary mechanisms, assisting them when reciprocity of responses becomes necessary.

EASTERN SCHOOL: AN EXPANDED VERSION OF HAT

This version is described in detail elsewhere (e. g. Lekevičius, 1985, 1986, 1997, 2007). I begin formulating this version starting from the “concept of the conditionally complete causal explanation”. Further developing this concept, I conclude that the most rational way to develop a new type of evolutionary theory is to start with a pursuit for the principles describing the functioning of life, not from building evolutionary theory directly. It is particularly important to explain the nature of the relationships between the entity and its components. Later the principles of functioning should be included in an explanans of evolutionary explanations.

I describe the nature of relationships between biosystems and their subsystems as follows. Life is a hierarchy of functions (and control) extending from singular functions of macromolecules all the way to global functions – the local nutrient cycle and the energy flow that leads it (the 1st principle). The explanation is that not a single individual and not a single species is functionally independent, because none is able to “turn” the nutrient cycle on its own (e. g. Lekevičius, 2002, 2006). Just as a virus is alive only within its host, species are also alive only within the ecosystem (= a nutrient cycle). Even the so-termed autotrophs are not independent in the context of long-term functionality. Here the author remains loyal to the “Russian paradigm” of ecology (see above).

On the other hand, sensitivity thresholds are characteristic of all biological control mechanisms and usually the greatest ones are at the levels above the organism (the 2nd principle). The thresholds make the functional hierarchy more

dynamic and less inflexible. The commentaries on these assertions follow. Neither a population nor an ecosystem can be considered a super-organism. All biological structures which compose the local ecosystem, starting from separate cells and ending with species, all cooperate and compete at the same time. Only two primary forces in living nature are worth attention: “biotic attraction” or cooperation, and “biotic repulsion” or competition. These forces, although oppositely directed, are not incompatible. Actually the reverse is much more likely. They seem to balance each other; their peaceful coexistence goes right through all organizational levels. Such a situation in the biological hierarchy, which seems complicated at the first glance, is enabled by the “leaky” biological control and sensitivity thresholds of it, which are greater in cases of a population and a community and lesser in case of a separate organism. Here the same meaning is ascribed to the threshold concept as it is in the systems theory (Ashby, 1956). The same as Mesarovic et al. (1970), I consider the control threshold the freedom of components, which they can use satisfying their own needs, purposes, not necessarily coinciding with those goals that the higher level seeks.

Employing the two principles described above, I construct my own model of adaptive rearrangements (Fig. 1). At a certain moment of time, only a part (X_3) of all elementary (enzymatic) functions which are present in a community participates in the maintenance of the local nutrient cycle and the energy flow leading it. Another part includes the functions that have been little activated; they lay in wait in zones below the threshold. Thus they play a certain role in the functioning of separate populations or individuals. Still another part lays in wait in the $X\Sigma - X_1$ zone (the shaded area in Fig. 1), which is below the threshold with respect to individual control mechanisms.

As a result of routine changes in environmental conditions, some structures (and related functions) lose their optima, whereas others gain them. The former structures disintegrate or their activity is inhibited; the latter multiply and their associated functions are strengthened. For example, an elementary (enzymatic) function can be strengthened in the following ways: the enzyme concentration in a cell increases (1); the number of cells carrying this enzyme grows due to mitosis (2); the frequency

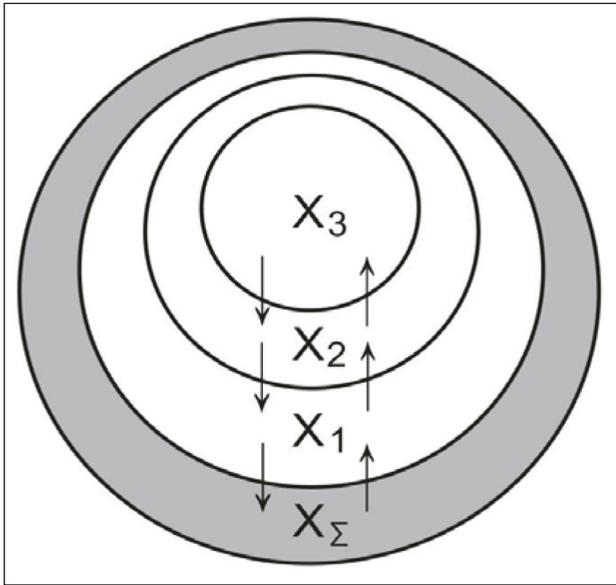


Fig. 1. Temporal section of an ecological community and adaptive transitions (arrows) caused by changing environmental conditions. $X_3 \subset X_2 \subset X_1 \subset X_\Sigma$, where \subset is the inclusion sign, and X_3 , X_2 , X_1 are sets of elementary (enzymatic) functions participating at a given moment in the maintenance of essential parameters of the community (X_3), separate populations (X_2) and individuals (X_1). The shaded area is the below-threshold zone for individual control mechanisms. Further explanations are found in the text (Lekevičius, 1986)

of genotypes producing this enzyme increases (3); or the population itself grows (4). This is how adaptive transitions take place, from one zone to another (Fig. 1). The first two ways are known as individual mechanisms (e. g. Hochachka, Somero, 1973). The third can be called populational, and the last one is a specific adaptation mechanism of ecological communities (Table 2). The third way

of adaptation is only possible in the presence of genetic polymorphism – only when genotypes that are preadapted for ever-changing conditions exist in a population.

Therefore, according to this model, adaptation (or homeostasis in this case) is like a process during which individuals, populations and entire communities can adjust their optima to ever-changing environmental conditions. Nevertheless, homeostasis (stability of essential variables) as well as optimization (maximization or minimization of certain parameters defining biological activity) are most likely permanent challenges rather than they are reached and maintained because as soon as necessary adjustments, such as reactions to certain changes have been started, frequently new changes occur and so forth.

One of the strengths of this theory is that it predicts the existence of a considerable number of reserve structures (e. g. “silent” and weakly transcribable genes, rare genotypes, and rare species) situated in below-threshold zones. These reserve structures can be viewed as a form of memory about past events, as hidden information, part of which occasionally resurfaces whenever environmental conditions require it. This model also forecasts that a considerable number of analogous functions should exist in populations and ecosystems. These are genotypes and species which do not differ with respect to their biotic roles, but their abiotic optima do not coincide. Thereby, no matter how abiotic conditions happen to change (in a routine range), genotypes and species always appear for which such changes are favourable. Due to this the biological activities of species and of the entire community are buffered.

Table 2. Classification of adaptation mechanisms (Lekevičius, 1986, with modifications). R and R_{ec} are individual and ecosystem respiration rates, respectively; B and B_{ec} are individual and ecosystem biomass, respectively; b is birth rate; d is death rate. For greater detail see further

Mechanism	Way of adaptation	Essential variables (“goal” functions in a stationary phase)
Individual	Differential activity of genes	R/B (is minimized)
Populational	Differential reproduction of preexisted genotypes	b and d (are minimized)
Biocenotic	Differential reproduction of species (ecological succession)	R_{ec}/B_{ec} (is minimized)
Genetic or evolutionary	Genetic variability and natural selection	All mentioned above (are minimized)

When the abiotic environment changes comparatively rapidly towards some particular direction (as an example a case of recent change in climate can be taken) a different situation is being created. In the beginning, individual mechanisms should compensate a fall in the degree of adaptation (= adaptedness) caused by such a change. As conditions continue to worsen, a change in the frequency of genotypes should be observed in polymorphic populations until the abilities of these mechanisms are finally exhausted. Then changes in population sizes (= ecological succession) and evolutionary processes should begin. A significant change in the essential variables of an ecosystem and the extinction of species can only be expected when evolutionary processes could not keep up with environmental changes on a timely basis.

This model anticipates that two “attraction centres” unavoidably form while adjusting to abiotic changes – the abiotic change itself, and the biotic surroundings demanding no loss of co-adaptation. The demand to be adapted and co-adapted at the same time undoubtedly lessens the adaptability of life. It seems likely that due to these circumstances control mechanisms at levels above an organism contain larger thresholds and are so “loose”. Thus, there is a weaker integration of components, and demands for their co-adaptation are not as great. It could be thought that ecosystems would convert into true super-organisms only if an entirely stable environment surrounded them.

The various levels of adaptation form a hierarchy. This means that populations have a richer repertoire of responses than do the individuals that constitute them: they can respond to environmental changes not only through phenotypic plasticity, but also through changes in genotype frequency. Ecological communities have an even richer repertoire as they can adapt to environmental changes not only through individual-level phenotypic plasticity and population-level genotypic diversity, but also through changes in species abundances made possible by species diversity. Therefore, aggregate ecosystem properties, such as total biomass, primary production, and nutrient cycling efficiency, should be most buffered.

Hierarchy means also that while the biocenotic mechanisms are working, physiological

adaptation and a change in the frequency of pre-adapted genotypes should be operating together; the opposite would not be accurate indeed. Individual and populational rearrangements are only a means for a more subtle adjustment of the community optimum and the lines of defence, one following the other, on the road of stressful impacts towards the essential variables of an ecosystem.

I also discuss the concept of adaptability itself. The ability to adapt, or adaptability, comprises two components: adaptation rate and plasticity limits or boundaries. The latter indicator describes the range of environmental conditions within which adaptation is possible at all. Adaptation rate can be viewed as the rate at which tolerance curves shift along the environment gradient. The faster the adaptation rate and the broader the plasticity limits are, the greater the adaptability of an individual, population or community is. Although the adaptation rate of individual-level mechanisms is the fastest, these mechanisms operate only within a comparatively narrow range of environmental conditions. Thus, they ensure comparatively narrow plasticity limits. In contrast, although evolutionary mechanisms operate very slowly, they make it possible to adapt to virtually all conditions. Population- and community-level mechanisms lie somewhere between these two extremes. In short, there is a trade-off between adaptation rate and plasticity limits, which arises from the fact that adaptive rearrangements are restricted by different factors at different levels of organisation (Fig. 2).

The rate of synthesis and decay of macromolecules as well as the velocity of mitosis primarily limits

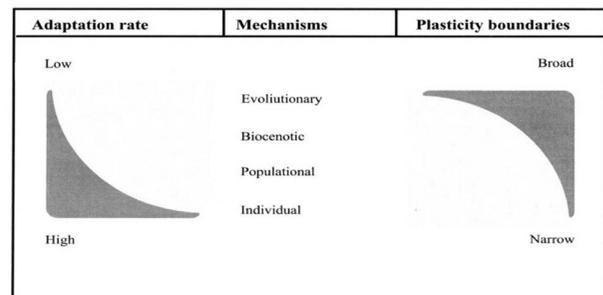


Fig. 2. Tentative ratios of adaptability components (adaptation rate and plasticity boundaries) characteristic of different adaptation mechanisms (Lekevičius, 1997)

the rate of individual adaptation. Generation time limits the rate of restructuring at the levels of the population and the community; whereas, the rate of evolution is additionally limited by population size, mutation and recombination frequencies.

MODELLING EVOLUTION: CASCADE SELECTION MODEL

How does new genetic information in the form of mutation or recombination become an attribute that changes the functioning of an individual, population and the entire ecosystem? In reply I (Lekevičius, 1986) make use of the temporal section model of a community discussed previously (Fig. 1). As soon as new genetic information appears, it literally finds itself in a neutral zone (the shaded area in the drawing). This is so because, as a rule, it appears in one of a billion of individuals comprising a community, not in many at once. Moreover, genetic material is not a kinetic part of metabolism in general; its function is informational. Thus, in and of themselves, all mutations and recombinations are neutral by their nature up to the point of their transmission into the kinetic sphere or phenotype.

New genetic information must be strengthened by the way of multiplication to be able to cross the routine threshold. This may be done by means of mechanisms, aforementioned in the discussion devoted to non-genetic rearrangements, as follows:

- (i) transcription and translation of a newly appeared gene increasing in the concentration of mutant (recombinant) macromolecules in a cell;
- (ii) mitosis of cells carrying the gene;
- (iii) growth in the frequency of mutants (recombinants) in a population;
- (iv) growth of the population carrying the evolutionary novelty and widening of the species range.

Additionally, the variation has at least one more theoretical chance to be strengthened, which is to become the property of numerous species during the course of speciation.

A community reacts to the strengthening of new genetic information similarly as it does to a gradual worsening of abiotic conditions, such as in the case of a change in climate (see above). The only difference is that it is an internal disturbance this time. In the beginning the intracellular control

(and adaptation) mechanisms respond. Later, as the new information continues strengthening, it is the organs controlling the entire organism that reacts, and so forth until the biocenotic control mechanisms are reached.

To have the ability to be multiplied, the variation must either increase or at least maintain an unchanged degree of structural adaptation (= adaptedness), which carries the variation. Once any of the thresholds are crossed, the corresponding system is forced to perform an act of self-organization – to evaluate anew all the structures and functions that are at the disposition of its control mechanism, including also the variant on the standpoint of compatibility (co-adaptation). Theoretically, the results of this evaluation can be the following: (1) complete elimination of the variant along with the entire system, (2) stabilization of its activity by transferring it to the below-threshold zone, or (3) further activation in the event of exceptional success, only this time by means of multiplication of the entire system. During the process of this self-organization, other structures and functions which had become entrenched earlier can cross over from one zone to another. As it multiplies, the new variation can pull an entire trail of structures that previously had been little active into the above-threshold zone after itself. This is the mobilizing reserve of evolution without which it could hardly operate at all. In case of success, such restructurings caused by the appearance and strengthening of the variant can end with the variant function crossing into zone X_3 and becoming entrenched in it for a long time.

All components can accumulate traits that are beneficial only to themselves; however, individuals and populations have the broadest opportunities at their disposal for doing so. This is because the biocenotic threshold is comparatively large, the individual control mechanisms are somewhat less “leaky” and a greater degree of integration is characteristic for organism subsystems. Therefore, two comparatively independent lineages of evolution can be expected: phylogenesis or species evolution, and ecosystem evolution. However, a selection of species or ecosystems as units is entirely unnecessary for these two lineages to reach realization. The fundamental unit of selection can only be an individual, as the most

integrated system. It is specifically individuals that perish or have fewer offspring, whereas all structures, from molecules to ecosystems, evolve in the manner described above.

I recommend to consider natural selection as constraints of a functional character, which appear as structures of the same rank interact. Mutations and recombinations generate a field of undirected potential possibilities constrained in a specific way by control mechanisms on each organizational level. This way undirected genetic variability is forced into a more or less directed evolutionary development. Differential survival and reproduction of individuals remain the most noticeable external consequence of such constraints but no more. The reasons for an embryo or individual dying or having fewer offspring can be different. For example, it can be an incompatibility of enzymes, metabolic pathways or organs, poor resistance to unfavourable climatic factors, or loss of co-adaptation with sexual partners or with other species. In other words, I suggest taking the accent off the units for selection (this issue is easily resolvable) and focusing on the sort of forces that perform selection, from what is being selected over to what selects. This outlook on selection as being the functional constraints that appear as a new evolutionary variation gradually strengthens was named the cascade selection model (Lekevičius, 1986).

The following example to demonstrate the occurrence of this kind of constraints may be presented (Lekevičius, 2002, p. 30):

“The first terrestrial plants were herbaceous, not woody. It could be supposed, however, that since the very occupation of land there was a strong selection pressure inducing the appearance of lignin, wood, bushes, and trees. Evidently (Richardson, 1992), already rhyniophytes synthesized lignin, though the first true bushes and trees appeared on land just in the middle of the Devonian. <...> There is no doubt that in the beginning lignin (a new hard to decompose compound) should have accumulated in soil and just after a certain period of evolution lignin-decomposing fungi or bacteria could have risen. They occupied the newly-established niche, and the nutrient cycle was restored.”

It is possible that the mutation providing fungi with a lignin decomposing feature was occurring

prior to the appearance of this compound. However, while there were more prohibitions than permissions (e. g. in the form of a vacant niche), this new variation might not have even stepped over the first threshold (Fig. 1). In other words, it never became a vital, mature mutant. The appearance of lignin in detritus became permission or a vacant niche; thereby, this mutation was strengthened and transmitted into the X_3 zone, possibly even more rapidly than the mutation providing plants with the feature for synthesizing this compound did. One way or another, the nutrient cycle was reinstated; however, this was reached due to great rearrangements at all levels. This hypothetical example, in my opinion, well illustrates how a community directs the evolution of species and how the conflict between the “goals” of different species and of the entire community comes to a resolution. For more examples and details see Lekevičius (2002, 2011).

My perception is that certain directedness is characteristic of evolution that is the result of selection or, more precisely, the constraints of an invariable nature. What is the physical nature of such constraints by which life is directed? One possible answer is as follows. Evolution, like all other (reversible) adaptation processes, presumably has the following trends (see also Table 2):

The major indicator is $B_{ec.} \rightarrow max$, where $B_{ec.}$ is the total biomass in an ecosystem.

The subsidiary indicators are:

$R_{ec.}/B_{ec.} \rightarrow min$, where $R_{ec.}$ is ecosystem respiration;

Efficiency of materials and energy usage $\rightarrow max$;

Reproduction efficiency ($b^{-1} = d^{-1}$, in a stationary phase; here b is birth rate and d is death rate) $\rightarrow max$.

The work of Odum and Pinkerton (1955) may be interpreted as contrary to this one in some respects. Their concept of maximum power can be defined as the maximum rate of useful energy transformation. They defined “power” in electronic terms as the rate of work, where work is understood as a “useful energy transformation”. This approach presupposed an analogical view which sees the world as an ecological-electronic-economic engine. In contrast to this, I emphasize the efficiency of functioning, not rates.

Although the evolutionary direction of any species is guided by the other species interacting

with it, the immanent characteristic of every species is to accumulate its own biomass without any restrictions, irrespective of how that might affect the entire ecological community at some time. As such, the indicated trends of ecosystem evolution are the natural consequences of trends that are characteristic of separate species. However, on the other hand, within this there is also a programmed conflict, which can turn into a huge cataclysm. The species that have accumulated an overly great amount of selfish characteristics can become super-rivals, in other words, true “consumers of biodiversity”. *Homo sapiens* and first woody plants may be mentioned as most obvious examples of super-rivals.

COMPARISON OF THE CASCADE SELECTION MODEL WITH MULTILEVEL AND HIERARCHICAL THEORIES

Several decades ago it has already been known that the characteristics of species and ecosystems can evolve the same as those of individuals do. That was when the viewpoint that evolution can only take place with the participation of “non-Darwinian” selection originated; in other words, it happens when entire families, demes, species and ecosystems/communities are selected. Wynne-Edwards (1962) and Lewontin (1970) were among the first scientists to air such views, which were further developed by Gould (1982, 1998), Wilson and Sober (Wilson, Sober, 1989; Wilson, 1980; Wilson, 1997) and quite a number of other evolutionists (see Keller, 1999). Gould (1982, 1998) uses the term “the hierarchical theory of selection” to define his views. In his opinion, Darwin mistakenly thought that natural harmony and species peculiarities are the by-products of selection at an individual level. This is sheer and unjustifiable reductionism. It would be more logical to assume that individual traits evolve via individual selection and species characters via species selection. In addition to these two units of selection, the author also distinguishes genes, demes and clades. Wilson and Sober (Wilson, Sober, 1989; Wilson, 1980; Wilson, 1997) term their conception as the multilevel selection theory. Its basic difference from the theory by Gould lies in the following: the evolution of ecosystems is impossible without a specific mechanism, the selection of communities. Those

local communities (Wilson, 1997, p. 2020, 2024) “that function well as a unit contribute differentially to the next generation. <...> Traits can therefore spread not by virtue of their advantage within local communities, but by virtue of the advantage that they bestow on their local community, relative to other local communities. <...> When natural selection operates at the community level, all of the species in a local community become part of a single interacting system that produce a common phenotype.”

Gould, Wilson and Sober resort to various empirical data to ground their ideas, but most evolutionists still seem to doubt the reality of supra-individual selection or believe it to perform only an episodic role in evolution. Whatever the case, these ideas are widely discussed in the contemporary scientific and even non-scientific press and they receive more attention than, for instance, co-evolution.

The primary difference between the cascade selection model, on one side, and the hierarchical and multilevel theories, on the other side, is such: as follows from the propositions given above, I, differently than Gould, Sober and Wilson, do not believe that selection at a corresponding level is necessary for genes, genotypes, demes, clades, populations and communities to evolve. Individuals are selected, whereas all these structures evolve by means of genetic variability and constraints. Meanwhile, it had to be a different attention on the nature of the relationship between the entity and its parts that caused the difference in the views on evolution in this case. None of these authors, to my knowledge, has sought an answer to the issues of concern to them in the systems theory. Naturally, the differences in methodology and initial premises also caused the differences in results.

HOW CAN HAT BE FALSIFIED?

The designation of every truly scientific theory is to explain the already known phenomena or facts and foresee new ones. If such explanations and predictions remain steadfast against an empirical test, they are accepted for use. Can the correctness of HAT be similarly verified? Most likely, to a greater extent, this depends on the strictness of the theory and the concreteness of the explanations

and predictions. A portion of predictions which according to the understanding herein unambiguously follow from various HAT versions are presented. It will probably be possible to prove or disprove them empirically very soon. Unquestionably, this list is quite incomplete, particularly in the field of evolution:

1. When environmental conditions do not change in time and / or space, the naturally occurring diversity of genotypes within populations and species diversity within guilds should decrease after some time. (A note: Abiotic environmental conditions in the tropics are generally considered to be comparatively stable and homogenous, but species diversity is extraordinarily high. I think this diversity may be considered mainly biotic rather than abiotic specialization of species).
2. By means of differential multiplication, this diversity (see Prediction 1) should stabilize the functional parameters / essential variables of corresponding biosystems relevant to time and space.
3. Due to the ability of all subsystems to accumulate traits that are beneficial only to themselves, in all below-threshold zones (Fig. 1) there should exist structures which are unconditionally harmful to the adjacent upper level, not only the structures “designated” for maintaining the essential variables of an ecosystem although, by definition, in comparatively less activated states. The existence of selfish games, selfish individuals and selfish species is the most likely. Here “selfishness” means existence of features that are harmful for the adjacent upper level – see the text above.
4. Such selfish features have a tendency to accumulate within populations during the course of evolution, and sometimes this should have called forth the appearance and expansion of strong competitors and super-rivals (such as woody plants in Devonian and humans in Quaternary). For greater detail see Lekevičius (2002).
5. A guild composed of organisms with a generation time that does not exceed 2–3 weeks should adapt to seasonal changes in environmental conditions by employing all non-genetic mechanisms of adaptation. See Lekevičius (1997) for explanations and practical tests.

6. A year for small organisms with generation time that does not exceed 2–3 weeks is equivalent to a millennium for trees. Therefore, the forest tree communities are expected to adjust to recurring multi-year climate oscillations as easily as microorganisms to seasonal variability (by increased expression or proliferation of pre-adapted genes, genotypes, and species). This subject will be discussed in detail elsewhere (Lekevičius, unpublished).

7. When external conditions are uniformly worsening so suddenly that evolutionary mechanisms are unable to keep up with them (probably what is currently being observed in the case of climate change), the most probable chain of events is as follows. After individual responses, a rise in the frequency of preadapted genotypes should be observed in polymorphic populations. Later, there should be changes initiated in the spectrum of predominating species. Finally, and only when the latter mechanisms have exhausted their possibilities, a significant change in the essential variables of an ecosystem should be observed.

8. The first nutrient or biogeochemical cycles should have appeared with the appearance of life on Earth. It is most likely that wherever life is found in the future it will have taken on the form of a nutrient cycle.

9. The functional convergence of the Earth's ecosystems, in other words a resemblance between local nutrient cycles and production (energy) pyramids, should be observed. It can be explained by the existence of the above-mentioned invariability in biocenotic constraints which appear as self-organization (evolution and succession) is occurring. This subject was discussed in detail elsewhere (Lekevičius, 2002).

DISCUSSION AND CONCLUSIONS

In one scope or another, probably all the HAT founders used deductive logic. Thus, a question naturally arises: should this feature of HAT be considered positive or negative? What pluses and minuses do generally characterize the deductive method? There are the most various opinions regarding this issue. It is likely that one sort of answer would be heard from a physicist and an entirely different one from most biologists. As Murray

(2001) writes, deduction holds no authority among biologists, which essentially separates them from physicists. In his discussion of current theories in biology, Murray notes that they are inductive generalizations but not deductive theories. The explanation, in the opinion of Murray, does not lie in the weakness of the deductive method and not in the peculiarities of the object under study but rather in a lack of imagination and courage.

I leave it for the reader to decide if this point of view is acceptable; apparently, there can also be a different sort of explanation. For example, it is possible that nobody ever trained future biologists in deductive argumentation nor demonstrated its potential benefits to them either in general education schools or universities. In the countries of the former Soviet camp, at any rate, such indifference to methodological issues was very widespread before now.

On the other hand, there are not that many examples to follow in using the deductive method for constructing theories in biology as it is in physics (models of population genetics may be mentioned as an exception). Thus, the situation of a teacher can be understood as well. Clearly, Darwinism would also fit here. However, hardly anyone heard a biologist stating that Darwinism was formulated as a theory by making use of deductive logic, thus those who believe that the theory has aged and is no longer suitable for current viewpoints need to make a critical review of the very core of the theory, particularly the propositions of a universal nature that Darwin made. A more thorough and in-depth theory can be constructed by amending or supplementing the propositions with new ones. Perhaps a physicist might speak in such a manner – such is the traditional practice of working with deductive theories in the “hard” sciences.

Specifically, deductive theory operating not only by real facts but also by theoretically imaginable possibilities can explain why this and not some other event came into being. Physicists might validly consider that the explanations gained in this manner are more in-depth than are those gained by what is called inductive reasoning. This is because the researcher using inductive methods alone is not interested in unrealized possibilities.

Conceptual models are customary tools in the work of biologists (e. g. Miller, 1996). Such models

can have various forms: block schemes, diagrams or graphics without precise scales on axes, or the like. They differ from ordinary verbal write-ups by that as well as by somewhat more strictly defined terminology. Experts in the general systems theory legitimized this type of modelling as a full-fledged means (Gigch, 1981). Of course, these models must lack contradiction, they must be complete (no unprovable statements).

The major objective for such means is investigations of super complex systems. However, these experts generally emphasized another matter as well. It is accurate to begin with conceptual models; though afterwards a more accurate mathematical picture should be sought. The HAT founders including myself, as I am aware, do not discuss the future perspectives for the work themselves. Apparently they leave future generations to resolve the matter. In my opinion, during the first stages of an investigation, when a hypothesis is raised, it is risky to become attached to one mathematical approach only, especially in areas like HAT, since it can lead the researcher rather far off track from the predetermined goals.

It is important to highlight one, possibly rather untraditional feature, which probably characterizes all the reported authors of HAT, without a single exception. Despite that they do not employ a strict axiomatic method; it is still rather evident that this does not interfere with their conviction that valuable conclusions can be deduced even from hypotheses which have taken the form of a conceptual model. It seems to me that they have to think so: if it was possible to deduce so many important conclusions from Darwin's theory, which could hardly be considered a conceptual model from a modern standpoint, then it should be possible to deduce something valuable from HAT versions, which are somewhat more strictly formulated.

Retrospectively, we, biologists, probably could have borrowed the means for constructing theories based on deductive reasoning along with the habit of verifying theoretical predictions experimentally from physicists, not only the strictness and exactness linked with mathematical methods. Have we, biologists, not made a huge mistake by selecting only the latter instrument of those available for constructing science, thereby having a tremendous impact on the course of the biological sciences?

In his famous article on “strong inference”, Platt, a biophysicist, wrote about the habit specific to biologists to make a fetish about mathematical models (Platt, 1964):

“Today we preach that science is not science unless it is quantitative. We substitute correlations for causal studies, and physical equations for organic reasoning. Measurements and equations are supposed to sharpen thinking, but, in my observation, they more often tend to make the thinking noncausal and fuzzy. They tend to become the object of scientific manipulation instead of auxiliary tests of crucial inferences. Many – perhaps most – of the great issues of science are qualitative, not quantitative, even in physics and chemistry. Equations and measurements are useful when and only when they are related to proof; but proof or disproof comes first and is in fact strongest when it is absolutely convincing without any quantitative measurement. Or to say it another way, you can catch phenomena in a logical box or in a mathematical box. The logical box is coarse but strong. The mathematical box is fine-grained but flimsy. The mathematical box is a beautiful way of wrapping up a problem, but it will not hold the phenomena unless they have been caught in a logical box to begin with.”

The fundamental requirement for hypotheses from which valuable conclusions can be deduced is that they must be unambiguous – formulated strictly and accurately – so they can be proved or disproved. The language of mathematics is most appropriate for that. A look through such a prism shows that not a single one of the HAT versions reported above is as strict and unambiguous as a physicist-theoretician would like. All of the versions can be termed qualitative or conceptual models, or hypotheses of the same sort, but not quantitative or mathematical models/hypotheses. Although to name one, there are quite a few mathematical formulations found in the works by Conrad. Despite this, all of them have a qualitative nature; in other words, they define the relationships and connections among parameters which are usually very difficult or impossible to measure. The author highlights this in nearly each of his articles himself. The models of other representatives of HAT can be similarly assessed. Such a situation can be partially explained: all these researchers do not become attached to specific ecosystems, popu-

lations or individuals in their HAT versions. They are only interested in the attributes that are common to all ecosystems and all organisms. In this way they are developing universal hypotheses. So, these hypotheses cannot be anything but rough, and the derived results can only be tentative. On the other hand, a complete mathematical model of all adaptive transformations, from biochemical changes to species sorting, will be difficult to build because these transformations occur at multiple hierarchical levels.

In summary, it should be emphasized that the system of views, named as the hierarchical adaptation theory in this publication, today still cannot be considered a completed construction suitable for employment without thorough critical analysis. The ideal situation for a broad circle of experts – physiologists, ecologists, evolutionists and systems theoreticians – would be to highlight its advantages and disadvantages.

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BANDYMAI SUKURTI VISAAPIMANČIĄ EKOSISTEMŲ PLASTIŠKUMO TEORIJĄ: APŽVALGA IR VIENAS KITAS KOMENTARAS

S a n t r a u k a

Žinoma, kad gyvybė prie aplinkos gali prisitaikyti dviem skirtingais būdais: evoliucijos būdu ir panaudodama individo reakcijas, kurios dar vadinamos fenotipiniu plastiškumu. Tačiau pastaraisiais dešimtmečiais atsirado ir išgalėjo įsitikinimas, kad populiacijos ir ekologinės bendrijos taip pat geba kažkiek stabilizuoti savo esminius kintamuosius (bendrą biomasę, produktyvumą ir pan.) nepaisant neapibrėžtų aplinkos sąlygų. Kaip atsakas į šį neapibrėžtumą keičiasi preadaptuotų genotipų dažnis, atsiranda kompensaciniai populiacijų dydžio svyravimai. Adaptaciją galima traktuoti kaip niekada nesibaigiantį daugialygį hierarchinį procesą, kurio metu vyksta individo, populiacijos ir bendrijos prisiderinimas prie besikeičiančios aplinkos. Pagal šią sampratą, adaptacija yra procesas, kurio metu individai, populiacijos ir bendrijos gali priderinti savo optimumus prie besikeičiančių aplinkos sąlygų. Individualūs ir populiaciniai persitvarkymai yra subtilesnės bendrijos optimumo priderinimo priemonės, kartu einančios viena po kitos „gynybos linijos“ stresinio poveikio keliu link ekosistemos esminių kintamųjų. Šios sampratos autoriai (pvz., M. Conrad, V. N. Novoseltsev, H.-R. Gregorius, E. Lekevičius) taip pat mano, kad šie mechanizmai sąveikauja gana determinuotai, todėl galima tikėtis, kad bus sukurta bendra ekosistemų plastiškumo teorija.

Šioje apžvalgoje bandoma aprašyti šias iki šiol nenusistovėjusias sampratas bei išryškinti stipriąsias, gerai pagrįstas, ir silpnąsias jų puses. Daroma išvada, kad reikalingos įvairiapusės pastangos falsifikuoti šias sampratas.

Raktažodžiai: adaptacija, plastiškumas, hierarchinė adaptyvumo teorija, homeostazė, evoliuciniai mechanizmai, deduktyvi logika

