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## Two-Level Hierarchical Model of Optimal Biological Diversity

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**Abstract**—In order to analyze the possible mechanisms of optimization of biodiversity, the two-level hierarchical model was developed and studied. The lower level subsystems are interpreted as the populations and the upper level is considered as the community of one trophic level consisting of these populations. The indexes at the population level (phenotypic diversity) and at the community level (the number of species) were considered as the characteristics of an integrated hierarchical system. The adaptation of biosystems to environmental conditions occurs through the optimization of diversity at the population and community levels during their interaction. The criteria of optimization used in the lower and upper levels correspond to maximal efficiency of resource utilization by biosystems. The results of modeling correspond to a known empirical biodiversity pattern that allows the use of the optimal diversity principle as an additional mechanism of its formation at the population and cenosis levels.

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The study of the dependence of the ecosystem functionality on the biodiversity indexes is one of the most rapidly developing issues in ecological studies [Balvaneira et al., 2006]. Understanding of these dependences is necessary for effective environmental protective policy implementation and rational resource utilization, which is especially important in terms of the global ecological crisis [Pavlov, Bukvareva, 2007]. The results obtained in the framework of such large international projects as LTER (The Long Term Ecological Research), BIODEPTH (Biodiversity and Ecological Processes in Terrestrial Herbaceous Ecosystems), Ecotron (study artificially created ecological processes), and the DIVERSITAS international program proved that biodiversity is an important factor which determines stability and functions of ecosystems [Tilman, 2000; Hector et al., 2001; Loreau et al., 2001; Naeem et al., 2002; Symstad et al., 2003; Bulte et al., 2005; Hooper et al., 2005; Spehn et al., 2005].

### OPTIMAL DIVERSITY PRINCIPLE

The use of extreme principles for studying the relation of biosystem diversity and its stability and productivity in different environmental conditions is widely applied in practice [Fursova et al., 2003]. According to these, the system strives to the state where the key determining parameter is the optimal (maximal or minimal).

However, these principles likely were used to study biodiversity.

There are two main statements in order to evaluate extremal properties of biosystem diversity at the population and community levels. First, the principles of maximal diversity presumed that the diversity of biosystem components becomes maximal at certain limits. Second is the principle of optimal diversity, which supposes that the diversity of the biosystem might be optimized and regulate parameters that allow the maximization or minimization of other important characteristics.

Based on the first statement, the principle of maximum entropy of a community and the principle of maximal diversity in species biomass distribution in a population were suggested [Levich, 2004; Lurie et al., 1983; Wagensberg, Valls, 1987]. These principles supposed that the steady state of biosystems might be characterized by extremal properties of their structure. The first principle suggested the maximization of community complexity at a particular volume of resource consumption by various species, and the second principle emphasized the maximization of the diversity index in the distribution of species in a population according to their weight with a certain maximal biomass of the population. Some experimental and natural populations and communities comply with these principles, for instance, experimental polycultures of phytoplankton, its communities in lakes from various regions around the world, fish distribution according to their masses in catches, etc.

In our study we used the second statement, the principle of optimal biosystem diversity [Bukvareva, Aleshchenko, 2005] based on the assumption that diversity is related to some fundamental characteristics of biosystems determined by their viability. The biosystem viability is maximal at a certain level of diversity that is optimal. The reduction or increase of diversity above or below the optimal level leads to decrease in the biosystem viability. At every time moment the system strives for the statement with maximal viability and optimal diversity. In the case of influence of any external factor, the system recovers its optimal diversity. The optimum state might change to another optimum under changed environmental conditions.

The principle of auto regulation of the biosphere suggested by Levchenko and Starobogatov is most similar to this principle among others [Levchenko, Starobogatov, 2003]. Their principle explains how the biosphere strives to keep the biodiversity which corresponds to the present moment and the instability of external conditions on the planet.<sup>1</sup> The idea of optimum genetic diversity was suggested by Altukhov [Altukhov, 2003] as the concept of optimal gene diversity (the optimal levels for average heterozygosity and polymorphism) as an important condition for the normal existence of populations in a normally fluctuating environment.

The existence of steady-state solutions for multi-species community structure of one trophic level under the stipulation that the task of maximization of its capacity and the running energy is being solved was demonstrated by Svirzev and Logofet [Svirzev, Logofet, 1978].

## TWO-LEVEL MODEL OF OPTIMAL DIVERSITY

To illustrate the process mechanism of the optimal diversity principle, we created and studied a two-level hierarchical model which included populations joined to the community of one trophic level [Aleshchenko, Bukvareva, 1991, 1994, 2005]. The diversity indexes at the population level (phenotypic diversity) and cenosis levels (species amount) were considered as the characteristics of a single hierarchical system. The adaptation of biosystems to environmental conditions included optimization of diversity at the population and cenosis levels during their interaction.

Let community  $\Omega$  consists of  $M$  populations  $\omega_\mu$  ( $\mu = 1, 2, \dots, M$ ) and exist in a random environment which characterized the volume incoming into the community resource  $R$  and  $\sigma^R$  determining the level of environment instability. The populations are arranged

in the community of one trophic level and share some resource  $R$ , so every population obtained a part of the resource  $\rho_\mu$ .

At this stage of modeling, the principle of equivalence of parameters in all populations was accepted and domination and deviation of niches were not considered. Instead whole populations of the cenosis populations were considered as the parts of real populations inhabiting the present community. It is obvious that optimization of these parts was not considered as parts of the species population.

*Lowest level: population.* There are two multitudes  $S = \{s_i\}$  and  $F = \{f_i\}$  ( $i = 1, 2, \dots, I$ ), the elements of which are equal. Multitude  $S$  is the set of values for the environmental parameter, and multitude  $F$  is the set of phenotypes in the population.

The environmental parameter might be interpreted as a resource characteristic or as any other environmental factor provided its consumption by species of a population, for instance, temperature or moisture. The function of the distribution for choice probability of the  $s$  value for  $V(s, c^R)$  environmental parameter required for normalization conditions in multitude  $S$  (for the task of the  $\rho_\mu$  level is a constant and accepted equal to 1):

$$\forall s \in S : V(s, c^R) \geq 0; \quad \sum_{s \in S} V(s, c^R) = \rho_\mu. \quad (1)$$

At every moment in time, the parameter of the environment gains a new value according to the defined probability distribution law  $V(s, c^R)$ . The dispersion  $\sigma^R$  for this distribution characterizes the level of environmental instability.

The population consists of species of various phenotypes (multitude  $F$ ). The modeled phenotypic feature was the ability of reproduction under a certain environmental parameter. The element  $t$  from multitude  $F$  (phenotype), where the environmental parameters are most favorable for reproduction, exists for every realized element  $s$  (environmental parameter) of multitude  $S$  at every time moment  $t$ .

The amount of species in a population is equal to  $N(t)$  at every time moment. All species are distributed according to the  $F$  phenotypes. The amount of species of phenotype  $f$  equals  $n(t, f)$  and  $N(t) = \sum n(t, f)$  (Fig. 1,  $I$ ).

The group of phenotypes is reproduced among phenotype  $f^*$  which corresponds to the realized environmental conditions at time  $t$  for element  $s^*$  of multitude  $S$ . Supposing that close values of environmental parameters correspond to close phenotypes, it is possible to determine the part of species for each phenotype involved in reproduction at every time moment  $t$  for element  $s^*$  represented as the function  $A(f, s^*, c^A)$

<sup>1</sup> This principle is similar to Ashby's law of requisite variety [Ashby, 1959] for cybernetic systems, which says that the variety affecting variations of a complicated system requires the proper variety of the system regulator.

determined for all elements  $s^* \in S$  and adhering to the following conditions:

$$\forall f \in F, s^* \in S: 0 \leq A(f, s^*, c^A) \leq 1; \quad (2)$$

$$A(f^*, s^*, c^A) = 1.$$

The distribution  $A(f, s^*, c^A)$  may be explained in two ways. First, as the phenotype retired from  $f^*$ , either the reproductive ability of the species decreased or the amount of species involved in reproduction decreased. The value for distribution dispersion of reproducing phenotypes  $\sigma^A$  might be interpreted as the index of the zone width of individual tolerance of species in a population.

Regenerative species produce progeny of various phenotypes at every moment in time. The progeny of every regenerative phenotype  $f^*$  (Figs. 1, 3) distributed according to phenotypes and function  $B(q, f^*, c^B)$ ,  $\forall f^* \in F$  determined in multitude and complied to normalizing conditions similar  $F$  to (2) includes the following:

$$\forall f^*, q \in F: \sum_{q \in F} B(q, f^*, c^B) = 1; B(q, f^*, c^B) \geq 0. \quad (3)$$

Thus, the value  $B(q, f^*, c^B)$  determined the part of species with the  $q$  phenotype in the progeny reproducing phenotype  $f^*$ . Vectors  $c^R$ ,  $c^B$ , and  $c^A$  in (1), (2), and (3) were the parameters of appropriate distributions.

The value of the distribution dispersion according to phenotypes of born species  $\sigma^B$  determined by the vector  $c^B$  components is the index of progeny diversity at every step of population development. The diversity indexes of reproducing ( $\sigma^A$ ) and born ( $\sigma^B$ ) phenotypes form the total phenotypic diversity in the population during the experiment. The most variable parameter which allows the population to quickly change its diversity according to new environmental conditions is the diversity of born species at every moment of time. According to these, the parameter  $\sigma^B$  was used to explain some data obtained during experiments.

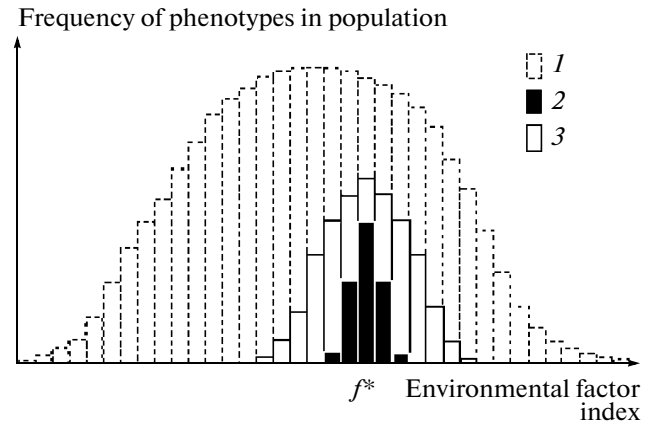
The mortality level was determined by the exponential dependence including the mortality coefficient  $d$ . The amount of species dying during time period  $\Delta t$  can be expressed as  $N(t)d\Delta t$ .

The regulatory mechanism of the birth rate was modeled by the logistic law with the reproduction constant  $b(t)$ , which constantly decreases with growth in size of the population:

$$b(t, N) = b_{\max} \left( \frac{1 - N(t)}{N_{\max}} \right) \quad (4)$$

where  $b_{\max}$ ,  $N_{\max}$  are the constants determining the maximal values for the reproduction constant and population size.

Supposed that species reproduction occurs in discrete moments and the environmental influence was the constant between consecutive moments of reproduction, then the model of a population consisting of species with different phenotypes could be represented



**Fig. 1.** The phenotype diversity in a population.  $f^*$  is the value of an environmental parameter at the present moment in time. (1) Existing phenotypes, (2) reproducing phenotypes at the present time, (3) the progeny of reproducing phenotypes.

as follows: at every step of modeling ( $t = 1, 2 \dots$ ), the realized value of environmental parameter  $s^*$  was determined using a random number generator (RNG) according to the probable value  $V(s, c^R)$  of the distribution of the environmental parameter. For the obtained element  $s^*$  according to distributions (2), (3) and dependence (4), the distribution of progeny with different phenotypes was calculated as follows:

$$b(t, N) \sum_{f \in F} A(f, s^*, c^A) B(q, f, c^B) n(t, f) (\forall q \in F).$$

The distribution of dead species at the  $t$ -step was determined by  $n(t, q)$  and  $d(\forall q \in F)$  values.

Thus, at the beginning  $t + 1$  step of modeling, the total amount of species with different phenotype distributions is expressed as follows:

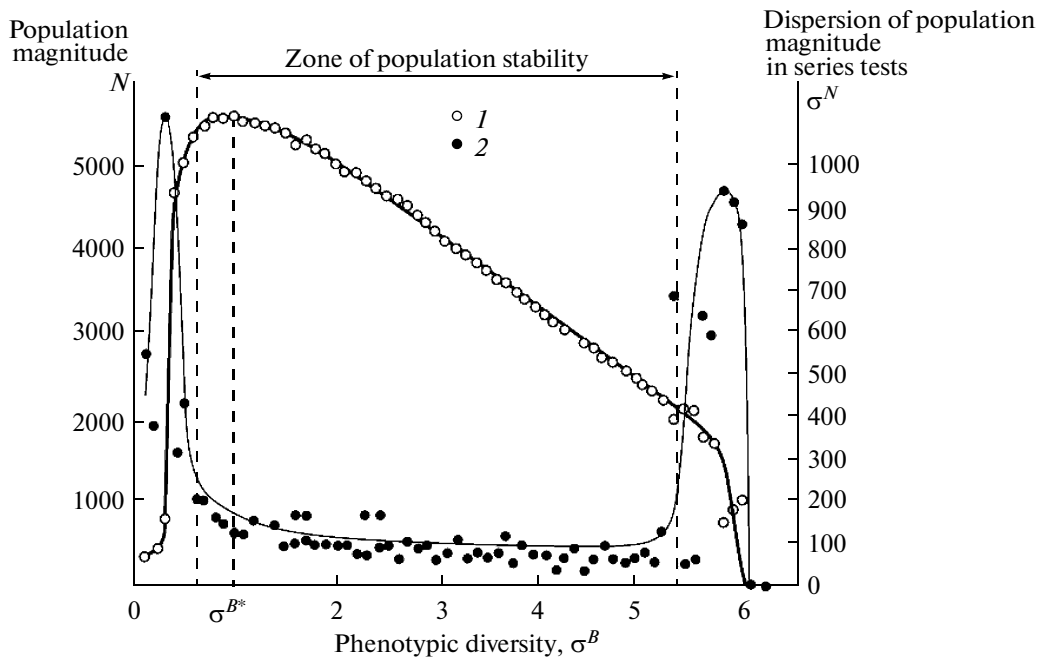
$$n(t + 1, q) = n(t, q) + b(t, N) \sum_{f \in F} A(f, s^*, c^A) B(q, f, c^B) n(t, f) - n(t, q)d. \quad (5)$$

System (5) is the main system of recurrent equations determining the dynamics of the total population size and species distribution according to phenotypes. The sequential analysis of equations (5) for specified conditions  $n(0, q)$  was carried out according to the scheme of the method of statistical testing.

The results of population size modeling  $N(t)$  at the stationary level and parameter  $\sigma^B$  variation have shown the optimal value of expectation, which means the existence of a value for parameter  $\sigma^B$  where the value of expectation  $N(t)$  reaches its maximal value  $N^*$  (Fig. 2). The value  $N^*$  and its appropriate value for parameter  $\sigma^B$  depend also on the stability of environment  $\sigma^R$  (Fig. 3). At this level the task could be expressed as

$$N^*(\sigma^R) = \max\{N(\sigma^R, \sigma^B)\}. \quad (6)$$

Obviously, the value of maximum size (6) also depends on the amount of available resources, which



**Fig. 2.** An example of the appearance of the optimal value for phenotypic diversity ( $\sigma^{B*}$ ) in tests series. (1) Average values for population magnitude, (2) dispersion of population size (the index of frequency amplitude of size in various tests series).

was accepted equal to 1 for the task at this level, and for the next level it was equal to  $\rho_\mu$ .

During the experiment the population died out or reached a statistically constant level with a certain final size and phenotype distribution. The width of this distribution is the index of realized intrapopulation phenotypic diversity for certain environmental conditions. This width might be compared with the width of its ecological niche and the diversity of reproducing phenotypes with an intraphenotypic niche component [Pianka, 1981].

*Upper level: community.* Consider community  $\Omega$  consisting of set  $M$  of populations  $\omega_\mu$  ( $\mu = 1, 2, \dots, M$ ). Every subsystem  $\omega_\mu$  using the internal parameter  $\sigma_\mu^B$  maximized its magnitude (6)

$$N_\mu^*(\rho_\mu, \sigma^R) = (N_\mu(\rho_\mu, \sigma^R, \sigma_\mu^B)) \quad (7)$$

where  $\rho_\mu$  is the resource evolving by  $\Omega$  for  $\omega_\mu$ .

The task of cost minimization by system  $\Omega$  in order to keep its subsystems  $\omega_\mu$  under the condition of consumption of whole resource  $R$  was considered for the upper level, which is equal to the task of minimization of the total community biomass for a certain volume of the resource. Suppose that system  $\Omega$  has two free parameters  $M$ , the amount of subsystems (populations), and  $N_\mu$ , the magnitude of population  $\omega_\mu$  which is always less than the maximum possible size  $N_\mu^*$  because the population has been obtained by only part of the available resource.

The system of the upper level (community) determined the amount of subsystems  $M$  and divides

resource  $R$  of every subsystem into part  $\rho_\mu$  ( $\sum_{\mu=1}^M \rho_\mu = R$ ). The target function of system  $\Omega$  took into account the demands of the subsystems on the optimal size (7).

The term of total processing of resource  $R$  might be expressed as

$$\sum_{\mu=1}^M \rho_{1\mu} N_\mu = R, \quad (8)$$

where  $\rho_{1\mu}$  is the amount of the resource processed by a species of  $\mu$  populations.

The target function of the upper level system  $\Omega$  might be expressed as

$$E = \sum_{\mu=1}^M \beta_{1\mu} N_\mu + \sum_{\mu=1}^M \varphi_\mu(N_\mu, N_\mu^*), \quad (9)$$

where  $\beta_{1\mu}$  is the cost spent on maintenance of one species of the  $\mu$  population,  $\varphi_\mu$  is the "fine" function due to deviation of the  $\mu$  population from the optimal size ( $N_\mu$  always lower than  $N_\mu^*$ ), which might be interpreted as the growth of additional costs to interspecies competition or compensation of population density deviations from optimal values.

Thus, the task for the upper level was formulated as the minimization of target function (9) on implementation of restrictions (8).

*Hierarchical task formulation and solution.* The common appearance of a two-level hierarchical model is

$$L_2(U_2, U_1) \xrightarrow{U_2} \text{extr} L_1(U_1, U_2) \xrightarrow{U_1} \text{extr}$$

$$\omega_2(U_2, U_1) \leq 0 \quad \omega_1(U_1, U_2) \leq 0,$$

where  $L_2$  is the target function of upper level (9),  $\omega_2$  is the restriction for upper level (8),  $U_2$  is the amount of subsystems of the lower level ( $M$ ),  $L_1$  is the target function of the lower level (6),  $\omega_1$  is the restriction of the lower level (amount of resource provided to the population by the upper level), and  $U_1$  is the value of phenotypic diversity of born or reproducing species ( $\sigma^B, \sigma^A$ ).

Such formulation of the task differs from the few approaches mentioned above to analysis of extreme principles of biodiversity organization, which consider tasks at only one level.

In our research the target function of whole system differed from the target functions of its subsystems [Germeyer, 1976]. At present, the analysis of such a model is possible only using the principle of "strict subordination" [Fatkin, 1972]. According to this principle, the subsystems with the target functions must push its parameters to extreme values in conditions determined by the upper level, the task of which is the task of the whole system and the tasks of the lower level of which are solved by its subsystems.

The realization of the "strict subordination" principle is possible in the following ways:

(1) Every population consumes all resources provided by the upper level and strives to reach the maximal magnitude  $N_\mu^*$  ( $\rho_\mu, \sigma^R$ ), establishing proper internal diversity at the optimal level ( $\sigma^{B^*}$ ).

(2) The values of population size exhausted at the lower level are moved to the upper level (communities).

(3) The upper level according to the values of population size at the lower level determines the amount of populations  $M$  for which the costs of their maintenance are minimal.

(4) According to the chosen amount of populations  $M$ , the upper level provides part of common resource  $\rho_\mu$  to each population.

(5) Return to step 1.

However, such a formulation of the task would not provide a solution. Therefore, it was suggested to simplify the task for the upper level as follows.

Let every subsystem obtain a similar amount of resource  $\rho = R/M$  and establish the optimal size  $N^*(\rho, \sigma^R)$ . The restriction (8) looks like

$$\rho MN = R. \quad (10)$$

Then the target function (9) becomes

$$E = M(\beta_1 N + \varphi(N, N^*)),$$

where  $N$  is the magnitude of every population, which is determined by system  $\Omega$ , and  $N^*$  is the optimal magnitude for every subsystem.

The "fine" function was equal 0 at  $N = N^*$  and increased upon deviation of value  $N$  from  $N^*$ . Therefore, the solution would be located in quadratic region  $N^*$  and the function  $\varphi(N, N^*)$  could appear as follows:

$$\varphi(N, N^*) = \beta_2(N^* - N)^2.$$

Thus, the target function of the upper level might be expressed as

$$E = M(\beta_1 N + \beta_2(N - N^*(\rho, \sigma^R))^2) \rightarrow \min_{M, N}. \quad (11)$$

Then, the task of two-level system functionality formulated as the lower level maximized the magnitude:

$$N^*(R/M, \sigma^R) \rightarrow \max_{\sigma^B} N(R/M, \sigma^R, \sigma^B). \quad (12)$$

Thus, the upper level minimized the target function  $E$  (11) at the restriction (10) and the lower level maximized the magnitude (12). The optimum criteria were further defined as the "efficiency," i.e., the maximal efficiency of resource utilization by biosystems.

The solution for the two-level task without use of iteration procedures that can received only function  $N^*(R/M, \sigma^R)$  is known. These data were received from preliminary studies [Aleshchenko, Bukhareva, 1991]. However, the linear function  $N^*$  as regards its variables was suggested in order to simplify the solution

$$N^* = \alpha_1 R/M - \alpha_2 \sigma^R. \quad (13)$$

Using (13) and (11), we received the task of upper level optimization. In this case we received

$$M^* \sim R/\sigma^R,$$

where  $M^*$  is the optimal amount of populations.

The analysis of the two-level model was carried out using the combination data on the stochastic model of the population received using the Monte Carlo method and analytical solution of the optimization task for the upper level (community level).

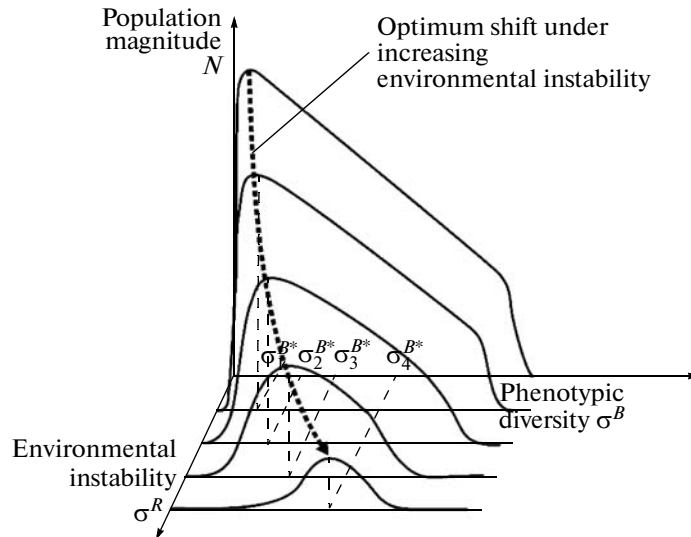
## RESULTS OF MODELING

The optimal values for intrapopulation phenotypic and species diversity in the community and their dependence on environmental conditions and biosystem properties were considered in this study.

The optimal diversity values exist on the population biocenosis levels. An example of the optimal diversity appearing in the modeled population is shown in Fig. 2.

It should be mentioned that there are some other mechanisms of the appearance of the optimal diversity level. For instance, the formation of the optimal value of the amount of species maximizes the efficiency of ecosystem functionality and might occur due to the balance of positive and negative effects and growth diversity [Bond, Chase, 2002].

The optimal diversity values depend on the environmental properties such as stability level and resource flow intensity. The reactions of population and cenosis levels to changes in environment stability are different. Thus, the optimal values of intrapopula-



**Fig. 3.** Increasing of optimal values for intrapopulation diversity and decreasing of maximal population magnitude under rising environmental instability.

tion diversity grow during decrease of the environment stability level, whereas the optimal species amount and biosystem efficiency decrease. In contrast this, the optimal intrapopulation diversity decreases, the optimal species amount grows, and biosystem efficiency increase under increasing environmental stability. At the same time, the increasing of the intensity of the resource flow does not affect the optimal values of intrapopulation diversity or increase the optimal amount of species in the community.

The conclusions on increasing intrapopulation diversity in a nonstable environment agree with the ideas of MacArthur [MacArthur, 1955], who stated that the width of the ecological niche is related to the level of population stability and more stable populations might have narrower niches. Similar conclusions were made by Dlusskii [Dlusskii, 1981], who added the index of environmental variability to the model of May and MacArthur [May, MacArthur, 1972]. His study explained that the species amount consuming the same resource depends not only on the amount of this resource but also on the level of environmental variability. The first idea of MacArthur [MacArthur, 1955] was developed into a hypothesis on the relation of ecological niche width with geographic latitude. According to this hypothesis, in higher latitudes characterized by less stable conditions, species have to have wider niches [MacArthur, 1972]. A negative correlation between the diapason of average monthly temperatures and the species diversity was found among birds, mammals, and mollusks [MacArthur, 1975]. However, this hypothesis was not supported by any evidence [Vasquez, Stevens, 2004].

Norberg et al., in studying the model where the group of phenotypes follows environmental shifts, have found that increasing the speed of the environmental parameter changes leads to the growth of phenotype diversity and decrease of the total biomass [Norberg et al., 2001]. However, the interpretation of these results is contradictory because the authors considered phenotypes as generalized characteristics of various species competing for the same resource.

An inverse relation of niche width to the amount of species in the community is observed in real communities especially in extreme conditions [Giller, 1988; Chernov, 2005].

On the basis of the reaction of optimal diversity values at the population and biocenosis levels in the case of changes in the environmental stability level, it is possible to suppose a different role of diversity at these two levels. The intrapopulation diversity is the main adaptation mechanism of populations and communities to environmental instability, and species diversity allows the community more effective resource utilization due to niche differentiation. This conclusion was made for isolated systems, existing in a typical environment with an optimal diversity level. Some data obtained using experimental herbal communities might serve as indirect confirmation for this assumption. For instance, the results of experiments of Pfisterer and Schmid have shown that the modeled communities consisting of multiple species are characterized by greater biomass but less resistance to droughts than the communities with fewer species. Thus, the species diversity allows efficiency of resource utilization but does not provide resistance to environmental changes.

The optimal values for diversity depend on the parameters of model populations and the diversity of reproducing phenotypes at every moment in time, maximal growth speed, and mortality coefficient.<sup>2</sup> The progressive changes of any of these parameters at other constants may be interpreted as an increase in the evolutionary level of organisms. Such changes lead to the decreasing indexes for optimal intrapopulation diversity, increasing efficiency of populations (Fig. 4), and growth of optimal values of species diversity. Thus, it was supposed that increase in the evolutionary level of organisms might provide for the growth of species diversity in communities.

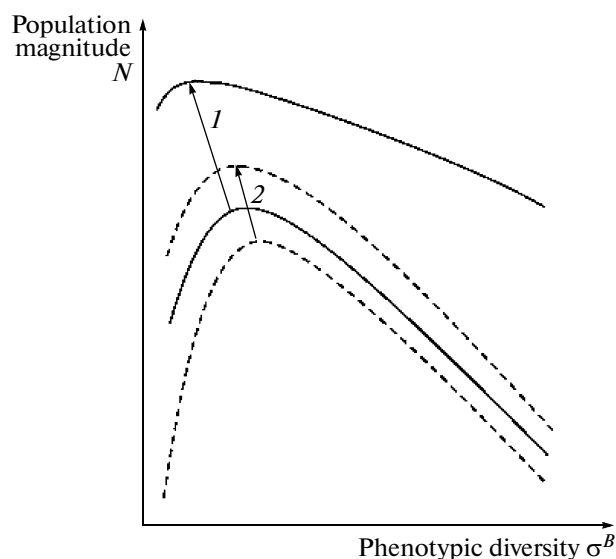
The simultaneous multidirectional changes of parameters of a population when improvement of one parameter leads to a decline in another, for instance increasing of population speed growth, are limited by changes in the optimal values for diversity.

The rising of optimal values of intrapopulation and species diversity in the studied model which did not include the diversity of niches and competition allowed the assumption that diversity optimization might be another mechanism additional to these factors which are the base for species and community diversity.<sup>3</sup> For instance, the fast speciation on islands and other isolated ecotopes with depleted biotic environment are often interpreted as the result of lack of competition. Another group of communities with a variety of intraspecific ecological forms is usually formed under extreme conditions. The intensive speciation in these conditions occurs due to lack of species diversity [Chernov, 2005]. The principle of optimal diversity allows these processes to be interpreted as the shift of community to the optimal diversity level in the absence of species and might serve as an explanation of the appearance of sympatric double species. First of all, it is impossible to recognize ecologically close species at the biocenosis level due to dividing first the amount and width of niches and then their location according to environmental conditions [Severtsov, 2001]. The results obtained in our research allow the supposition that first of all the parameters of diversity are optimizing without considering the niche location on the resource gradient.

According to the modeling results, the nature communities located in a wealthy and stable environment must consist of a great amount of species at the low intrapopulation diversity. At the same time, in a

<sup>2</sup> The diversity index of born progeny at every moment was considered as the degree of freedom which is used by population with different parameters for adaptation to environmental conditions.

<sup>3</sup> The hypothesis of neutrality (or functional equivalence) proposed by Hubbel [Hubbel, 2001, 2005] has been used more in recent years, where the main mechanism of species diversity formation is the balance of speciation, mortality, and settling speeds.



**Fig. 4.** Alterations of optimal level of intrapopulation diversity and efficiency of a population: (1) increasing of maximal growth speed of the population; (2) the extending of zone ecological species tolerance.

“poor” and unstable environment the community includes fewer species but with high intrapopulation diversity. This conclusion corresponds to some empirical patterns of diversity distribution in different types of ecosystems and climate conditions<sup>4</sup> that allow us to accept the principle of optimal diversity in biosystems as the working hypothesis [Pianka, 1981; Odum, 1986; Giller, 1988; Bigone et al., 1989].

## CONCLUSIONS

The hierarchical two-level optimized model (population–community) allows evaluation of possible alterations of optimal diversity levels at the population (intrapopulation phenotype diversity) and cenosis levels (amount of species) according to species properties and environmental parameters (intensity of resource flow and its stability). The diversity indexes at the population and cenosis levels were considered as characteristics of the single hierarchical system. The adaptation of biosystems to environmental conditions includes the optimization of diversity at both levels during their interaction. The similarity of modeling results to some empirical regularity of diversity distribution allows the principle of optimal diversity of biosystems to be accepted as the working hypothesis.

<sup>4</sup> The problem of the dependence of biodiversity on environmental parameters is still not clear.

## ACKNOWLEDGMENTS

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