Principle of biosystem optimal diversity : two-level hierarchical model "populations-community"

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Abstract

We are inclined to propose the principle of optimal diversity of biosystems. According to this principle the optimal values of biosystem diversity correspond to their maximum viability (minimum extinction probability). We have investigated a mathematical model of optimal diversity of a two-level hierarchical biosystem in fluctuating environment. The subsystems of the lower level are interpreted as populations, while those of the upper level are interpreted as a community of one trophic level made up by these populations. The optimality criteria correspond to maximum effectiveness of resource utilization by biosystems. The analysis of the two-level system shows that optimal values of diversity at different hierarchical levels depend on environmental instability in the opposite way: the optimal species diversity increases in more stable environments while the optimal intrapopulation diversity decreases. These results allow us to make an assumption about the different role of intrapopulation and species diversity in fluctuating environment: intrapopulation diversity is the base of adaptation to environmental instability, species diversity enables community to use resources maximum effectively.

Keywords: Diversity-viability relationship; Fluctuating environment; Optimal biodiversity; Phenotypic diversity; Species diversity

The principle of biosystem optimal diversity

The interrelation between diversity, stability and effectiveness of biosystems is a focus of ecological research for a period of time and is a question of crucial importance for nature protection theory and practice. We strongly believe that the usage of extremal principles will contribute to biodiversity researches. Extremal principles are extensively used in biology (in physiology, biochemistry, embryology, evolution theory, population dynamics etc.) however they are not widely spread in the field of biodiversity studies. We propose one of possible approaches.

The principle of biosystem optimal diversity is based on the assumption that diversity is linked to certain fundamental characteristics of biosystems that determine their viability (survival probability). Any biosystem tends to maximize its own viability in the course of development and adaptation. To reach this state (V^* in fig.1), the system should establish the optimal level of diversity of its elements (D^*). Any deviation of diversity from the optimal value leads to viability reduction. If viability decreases below the critical value V_0, the system destructs (turns into another system). The corresponding diversity values D_0' and D_0'' are critical values.

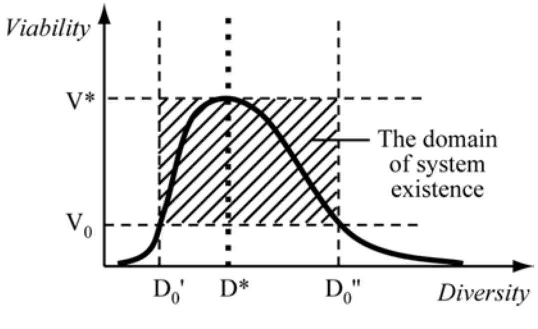

Fig. 1. Optimal and critical values of biosystem diversity.

Some applications of this approach in the fields of biodiversity evolution and biodiversity conservation were examined earlier (Bukvareva and Aleshchenko, 1994, 1997).

The two-level hierarchical model “populations-community”

Let’s consider the model of populations and community which consists of them, existing in fluctuating environment.

E*nvironment* is characterized by the intensity of resource flow R and ensemble $W=\{w_i\}$ of values of some environmental parameter, which can be the characteristic of resource (for example, light-wave length, size of prey, etc.) or the environmental factor providing its consumption (for example, temperature, humidity, etc.). At each moment of time t some value of environmental parameter is realized in accordance with the distribution of probability density of its values realization $P_w = V(w, c^V)$. Variance σ^V of this distribution reflects the degree of environmental instability.

Population consists of various phenotypes (Aleshchenko et al., 1991). Dimension of the ensemble of phenotypes $F=\{f_i\}$ is equal to dimension of the ensemble W of environmental parameter values. Number of individuals of phenotype f is equal $n(t,f)$, i.e. $N(t) = \Sigma n(t,f)$. The phenotypic feature is the ability to reproduce when certain value of the environmental parameter is realized. Each phenotype f corresponds to an element w of the ensemble W, which is optimal for reproducing this phenotype. When the favorable environmental value w* is realized a group of phenotypes reproduces around the phenotype f* (Fig. 2). Proportion of reproduced individuals of each phenotype is determined by function $A(f, w^*, c^A)$, which meets the conditions $\forall f \in F, w^* \in W : 0 \le A(f, w^*, c^A) \le 1; A(f^*, w^*, c^A) = 1$. Variance value of distribution of the reproducing phenotypes σ^A can be interpreted as an index of individual tolerance to environmental conditions. Each phenotype produces a set of phenotypes around itself in accordance with function $B(g, f^*, c^B)$, $(\forall f^* \in F)$, which meets the conditions of normalization similarly to the previous function. Variance value of distribution of the progeny σ^B can be interpreted as the level of diversity reproduced by population at each step of its development.

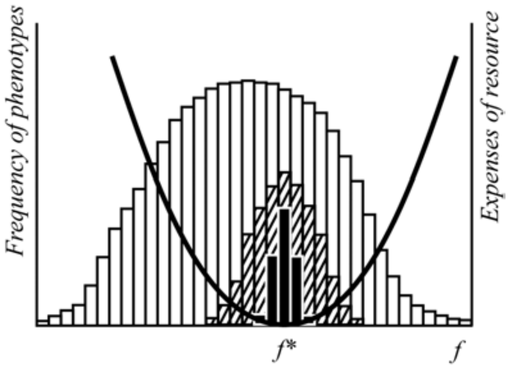

Fig.2. Phenotypic diversity in model population. f* - the phenotype fit to the realized environmental parameter value; white bars - existing phenotypes; black bars - reproducing phenotypes; dashed bars – progeny of the reproducing phenotypes; black curve - resource expenses by phenotype f*.

The death rate is set by exponential dependence with a constant mortality index *d*. Reproduction is modelled by the logistic function with birth rate index *r (t),* monotonously decreasing with growth of population size: $r(t,N) = r_{max}(1-N(t)/N_{max})$, were r_{max}, N_{max} — are constant maximum values of the birth rate and population size. Individuals reproduct in discrete moments of time. The distribution of progeny among phenotypes is calculated as follows: $r(t,N)\sum_{f\in F} A(f,w^*,c^A)B(g,f,c^B)n(t,f)(\forall g\in F)$. The distribution of dead individuals at each step *t* is defined as $n(t, g)\, d(\forall g\in F)$. At the beginnig of *t+1* step of simulation the distribution of all individuals among phenotypes is determined as follows: $n(t+1,g) = n(t,g) + r(t,N)\sum_{f\in F} A(f,w^*,c^A)B(g,f,c^B)n(t,f) - n(t,g)d$. This set of recurring equations determines population dynamics and distribution of phenotypes.

Individuals spend a resource for self-maintenance and reproducing (Aleshchenko and Bukvareva, 1994). The more the realized environmental factor value differs from the optimal one for this phenotype, the greater its resource expenses are (Fig. 2). Expenses for self-maintenance of an individual at each step of simulation are calculated as follows: $\overline{E}_e(t) = 1/N(t)\sum_{f=1}^{F}(f-f^*)^2 n(f,t)$, where $N(t) = \sum_{f=1}^{F} n(f,t)$ is total population size at the moment *t*. Expenses for reproduction are calculated as follows:

$\overline{E}_r(t) = 1/N(t)\sum_{f=1}^{F}(f - f^*)^2 n'(f,t)$, where $n'(f, t)$ is the total number of descendants born at the moment t. The total expenses per individual are $E = \overline{E}_e(t) + \overline{E}_r(t)$.

While the computing experiment is being conducted the population becomes extinct or reaches some stationary state. This state is characterized by the average population size, phenotypic diversity and certain level of the resource expenses.

The phenotypic diversity of progeny (σ^B), strongly influences stability of population. There is σ^B value area at which the population is stable in the given environment. Fig. 3 shows dependence of variance of population size σ^N (an index of population stability) on σ^B. Small values of σ^N correspond to stability range of population.

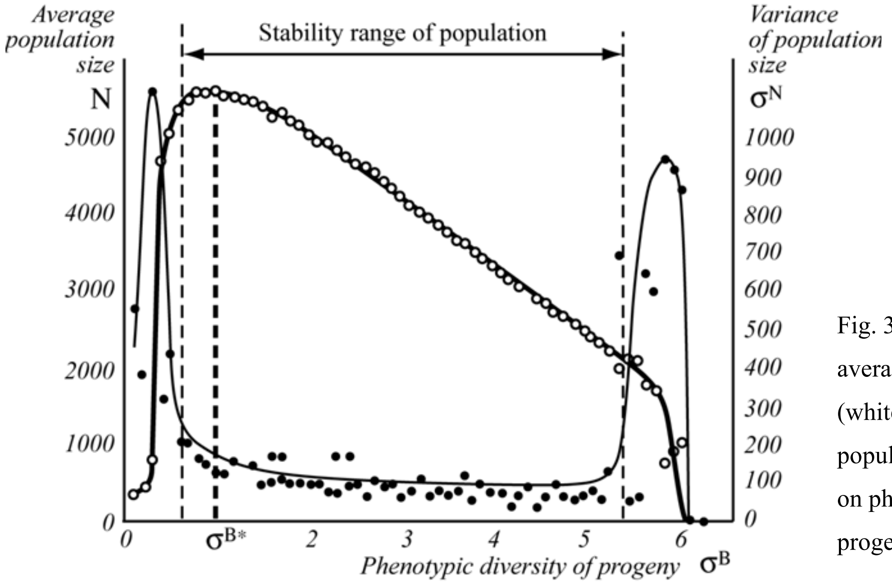

Fig. 3. The dependence of average population size (white dots) and variance of population size (black dots) on phenotypic diversity of progeny.

The optimality criterion for population is its maximum size (biomass) at the predetermined volume of the resource available. This task is equivalent to minimization of resource expenses per individual at the predetermined population size (biomass). Fig. 3 shows that the dependence of the average population size on phenotypic diversity of progeny (white dots) has a maximum which corresponds to the optimal diversity value (σ^{B*}).

The results which has been received for variance value of progeny distribution is true as well for the existing phenotypes distribution. The last one is the secondary index – it is formed in the course of birth and death of individuals and directly depends on diversity of progeny. Thus, we deal with population phenotypic diversity as a whole.

The community consists of the mentioned populations which consume available resource - therefore we model a community of one trophic level.

At the community level we applied the maximum of total biomass (total quantity of individuals) of all populations at a predetermined volume of available resource as an optimality criterion. This task is equivalent to minimization of expenses on population self-maintenance under the condition of full absorption of available resource.

We used in essence the same optimality criteria at the population and community levels: the maximum quantity (biomass) at a fixed amount of available resource or the minimum expenses in condition of a full absorption of available resource. These criteria are reduced to a single – the minimum expenses for the production and maintenance of an individual or unit of biomass. It is a question of the effectiveness of resources utilization by biosystem. The model populations and communities establish the optimal internal diversity at which their effectiveness is maximum. Such an optimality criterion for biosystems seems reasonable enough, because it is directly linked to biosystems viability.

Optimal diversity values in populations and in community are formed during the interaction of these two hierarchical levels. It is an iterative process.

Step 1. Each population aspires to reach the maximum size (biomass) by setting its internal diversity at the optimal level. Each population consumes the whole resource, allocated to it by the top level. It has an optimal internal diversity and maximum size $n^*(r, \sigma^V)$, which is possible in the given environment. When other populations appear in this environment, the resource is divided between them and consequently their sizes do not reach possible maximum values. At the same time specific expenses increase due to additional charges for competition and compensation of size deviation from optimal values (for example, due to the fact that individuals have to waste some extra energy looking for a sexual partner or compensating some other ways of disturbance in population structure by rarefaction).

Step 2. The values of the population size chosen at the bottom level are transferred upward - to the level of community.

Step 3. The upper level in view of these values defines number of populations G (number of species) at which the total quantity of individuals (biomass) of all populations is maximum (or resource expenses are minimum).

Step 4. A particular part of the total resource is allocated to every population.

Step 5. Recurrence of a step 1. Populations solve their optimization problem on the basis of resource allocated to them, etc.

The formalized model looks as follows.

System S (community) consists of subsystems (populations) s_g $(g=1,2,\ldots G)$. Every subsystem s_g using internal parameter p_g, maximizes its size $n_g\ (r_g, \sigma^V, p_g)$, where r_g is the resource allocated by S to s_g.

The task of system S is to minimize expenses on s_g subsystem maintenance under the condition of full consumption of the resource R. System S has two free parameters: G – the number of subsystems and N_g – the quantity of individuals in subsystem s_g (which is always lower than the maximum preferred size of population due to the resource split into G parts).

Let's define the problems of the lower and upper levels.

The system defines a number of subsystems G and divides resource R, allocating for each subsystem its part r_g $(\sum_{g=1}^{G} r_g = R)$; criterion function of system S considers "requests" of subsystems for their optimal size

$$n_g^*(r_g, \sigma^V) = max\ n_g(r_g, \sigma^V, p_g). \qquad (1)$$

This is the set of tasks of subsystem s_g.

The condition of complete processing of resource R may be presented as follows

$$\sum_{g=1}^{G} C_g N_g = R, \tag{2}$$

where C_g – resource quantity processed by an individual of population s_g.

Criterion function of the community S is as follows

$$\mathrm{E} = \sum_{g=1}^{G} b_{1g} N_g + \sum_{g=1}^{G} f_g (N_g, n_g *), \tag{3}$$

where b_{1g} – expenses for maintenance of an individual of population s_g; f_g – penalty function for a deviation from optimal size of population s_g.

Thus, the system task may be formulated as follows: to minimize the criterion function (3) complying with restriction (2).

In this case it is quite difficult to solve this problem. To estimate the behaviour of the system and its subsystems quite roughly, we have simplified a task of the upper level.

So, every subsystem receives an identical part of resource $r = R/G$ and sets an optimal size $n^*(r, \sigma^V)$. In this case the restriction (2) may be presented in the following way

$$CGN = R, \tag{4}$$

Criterion function (3) will be like this: $E = G(b_1N + f(N,n^*))$, where N is a size of each population which S "wants" to set, and n^* is own optimal size for each subsystem.

The penalty function is equal to 0 if $N = n^*$ and increases as N deviates from n^*. Having assumed, that the solution will fall within a linear neighborhood n^*, we may present function $f(N,n^*)$ in the following way $f(N,n^*) = b_2(n^*-N)^2$.

So, the criterion function of the upper level is as follows

$$E = G(b_1N + b_2(N-n^*(r, \sigma^V))^2) \rightarrow min_{G,\,N} \tag{5}$$

Now the problem of function of a two-level system may be formulated in the following way: the lower level maximizes the population size

$$n^*(R/G, \sigma^V) \to \max_p n\,(R/G, \sigma^V, p) \qquad (6)$$

the upper level minimizes the expences (criterion function (5) at the restriction (4).

The function $n^*(R/G, \sigma^V)$ *is* revealed in population model and this two-level task can be solved without iterative procedures. To simplify the solution we may assume linearity of function n^* in relation to its variables,

i.e. $$n^*=a_1R/G+a_2\,\sigma^V \qquad (7)$$

On the basis of the ratio (7) and (5) we can present an optimization problem of the upper level expressed in the terms of that level only, thereafter it allows us to solve it easily.

In this case we'll have $G^* \sim R/\sigma^V$, where G^* is an optimal number of populations.

It is necessary to note, that other equivalent statements of problems both at the top, and at the bottom levels are also possible. For instance, for the upper level we may apply the restriction (2) or (4) as the criterion function, and the criterion function (3) or (5) as the restriction. The solutions of the equivalent problems will be functionally the same.

The results of modeling

The population level

1. In less stable environments the stability range of population is reduced owing to the areas with low indexes of birth rate and phenotypic diversity.

2. The optimal value of intrapopulation diversity decreases in more stable environments and does not depend on the intensity of the resource flow (Fig. 4).

3. The maximum population size (biomass) increases in more stable and "rich" environments. The minimum value of resource expenses per individual decreases in more stable environments and does not depend on the intensity of the resource flow (Fig. 4).

4. The optimal values of diversity are next to the bottom limit of population stability (Fig.3). If natural populations have phenotypic diversity close to optimal value, this result will certainly emphasize the danger of intrapopulation diversity decrease.

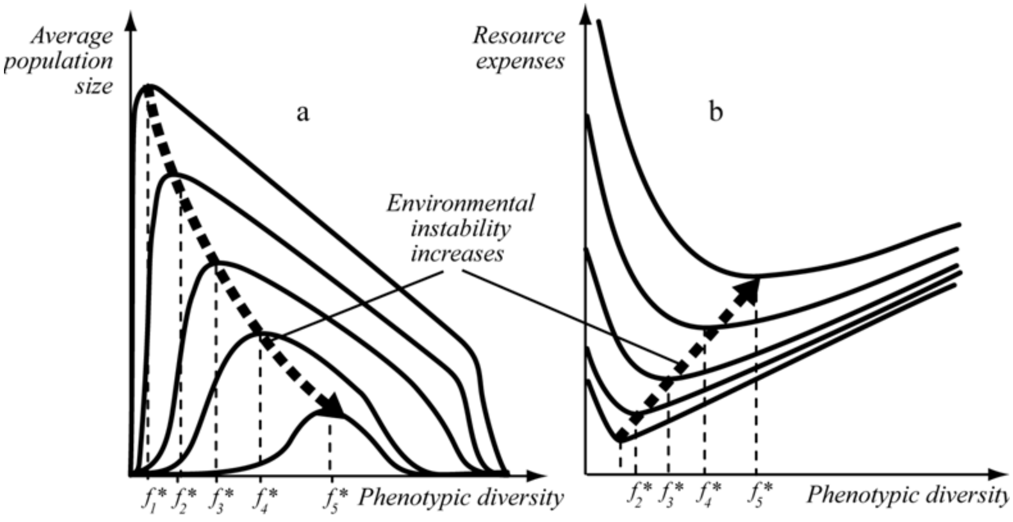

Fig.4. Dependence of average population size (a) and resource expenses per individual (b) on the phenotypic diversity in environments with different degrees of instability. f*- optimal values of diversity in different environments. Dotted arrows show changes of optimal values of diversity when environment destabilizes.

5. The increase in mortality, as well as the decrease in birth rate and the decrease in individual tolerance σ^A produce the same effect, that is the destabilization of environment. Thus, there are different ways to compensate for increase in environmental fluctuations: to increase in population growth rate or to increase in ecological valence (tolerance). At the level of community it stands for a shift of species structure from K- to r-strategists and from specialists to generalists.

The community level

6. Optimal number of populations G* (optimal species diversity) increases in more stable environments and at the growth of resource flow intensity: $G^* \sim R/\sigma$.

7. Maximum possible value of the total quantity (biomass) of individuals of all populations in a community (which corresponds to an optimal species diversity) increases in more stable and “rich” environments.

8. Behaviour of one trophic level is qualitatively true for a community as a whole (within the limits of simulated mechanisms). In more stable environment the maximum biomass at each level increases. It corresponds to reduction of energy losses at the transmission from one level to another, that leads to the increase in number of trophic levels. Thus, the structure of a multilevel community tends to become more hierarchical in more stable environments.

These results show that optimal values of diversity at different hierarchical levels change in the opposite manner as degree of environmental stability varies: the optimal intrapopulation diversity increases in less stable environments, but optimal species diversity decreases. These results allow us to make an assumption about the different role of intrapopulation and species diversity when a community exists in fluctuating environment: intrapopulation diversity is the base for adaptation to environmental instability, species diversity enables community to use resources maximum effectively.

On the basis of the obtained dependencies we may assume that natural communities existing in "rich" and stable environments will consist of a large number of species with low intrapopulation diversity (specialists), in the "poor" unstable environments – of a small number of species with high intrapopulation diversity (generalists), in "rich" unstable and "poor"stable environments we expect the medium level of species and, consequently, high and low intrapopulation diversity (Fig.5).

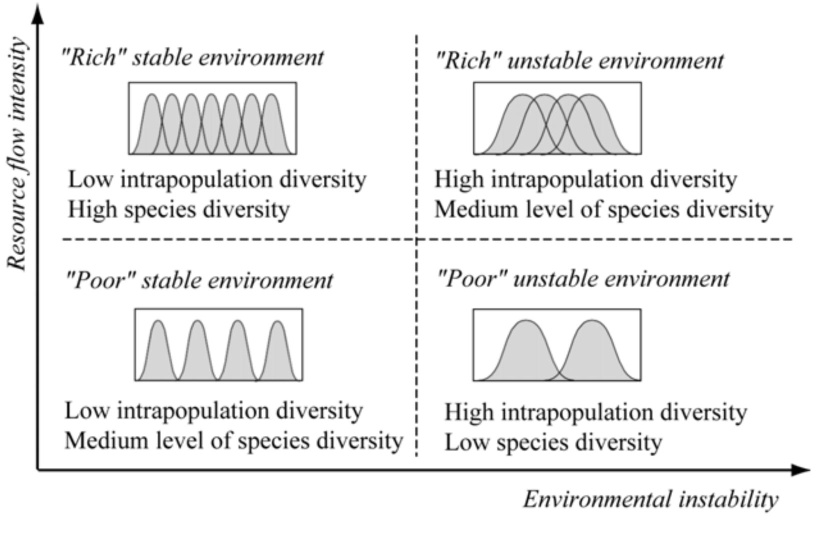

Fig. 5. Assumed levels of species and intrapopulation diversity in the communities adapted to different environments.

These conclusions are made for natural systems which exist in historically typical environment and have optimal diversity levels.

As far as diversity levels of undisturbed natural systems are concerned, they are mostly close to optimal values. Artificial decrease or increase in biosystem internal diversity as well as fast environment changes leads to the decrease in its vitality.

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References

Aleshchenko, G.M., Bel’chanskii, G.N., Bukvareva, Ye.N. 1991. Use of computer experiment for the study of biodiversity on population level. Reports of the Academy of Sciences of the USSR 316, 759-763.

Aleshchenko, G.M, Bukvareva, E.N. 1994. The variant of integration of models of diversity at population and biocenotic levels. Zhurnal obshchei biologii (Journal of General Biology) 55, 70-77 (in Russian).

Bukvareva, E.N., Aleshchenko, G.M. 1994. The problem of optimization of man - nature interaction and the strategy of biodiversity conservation.Uspechi sovremennoi biologii 114, 133-143 (in Russian).

Bukvareva, E.N., Aleshchenko, G.M. 1997. The scheme of complication of biological hierarchy in the fluctuating environment. Uspechi sovremennoi biologii 117, 18-32 (in Russian).