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The Principle of Optimal Biodiversity and Ecosystem Functioning

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Abstract We propose the principle of optimal diversity of biosystems. According to this principle, the optimal values of inner diversity of biosystems correspond to their maximum viability (minimum extinction probability). We have investigated a mathematical model of a two-level "population-community" system in a 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 of these populations. The optimality criteria correspond to the maximum effectiveness of resource utilization by the biosystems, which is possible to consider as an index of ecosystem functioning. Optimal values of diversity depend on the intensity of resource flow and the instability of the environment. optimal species diversity increases in more stable and "rich" environments, while optimal intrapopulation diversity decreases in more stable environments and is independent of the intensity of resource flow. These opposite reactions allow us to make an assumption of the different roles of intrapopulation diversity and species diversity in a fluctuating environment: intrapopulation diversity is the basis of adaptation to environmental instability, while species diversity enables a community to use resources to the maximum and effectively.

In general, the results of our modelling agree with empirical biodiversity patterns, giving us grounds to propose the principle of optimal biodiversity as a working hypothesis complementary to other ideas about interrelation between biodiversity and ecological functioning.

Keywords Optimal Diversity, Intrapopulation Diversity, Species Diversity, Ecosystem Functioning

1. Introduction

The relationship between biodiversity and ecological functioning has been a focus of ecological research for a long period of time. The results of experimental, observational and theoretical investigations demonstrate that this interrelation is a significant phenomenon and is of crucial importance in nature protection theory and practice[1 - 6]. D. Tilman[1] points out that diversity must now be added to the list of factors that influence ecosystem functioning.

In our opinion, extremal principles may lead to considerable benefits in the investigations of interconnections between ecosystem properties and diversity. According to these principles, biosystems have a tendency to reach only such states when their important characteristics associated with the survival, viability and development are extremal (maximum or minimum depending on their positive or negative values), for example, the maximum energy efficiency of an organism, the minimum mortality in the population, the maximum total biomass of the community,etc.These indicators of viability are called optimality crite ria.Optimized characteristics of biosystems are adjustedsuch as to achieve the extreme values of the optimality criteria.

The extremal principles have got wide distribution in biology. There are a lot of examples of their successful application in physiology, biochemistry, embryology, evolution theory, population dynamics, and ecology. However, in the field of biodiversity research, the capacities of this method have not been used in full measure.

2. Principle of Optimal Biodiversity

In the field of biodiversity researchesthe two following main extremalapproaches are possible.

One approach is based on the assumption that the diversity of elements of a biosystem (complexity of a biosystem) is maximized. An example of such approach is the entropy extreme principle for communities[7] which implies the maximization of community complexity at fixed volumes of resource consumption by different species.

We suggest the second approach called optimal diversity principle[8]. This principle is based on the suggestion that

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the diversity of elements of a biosystem is related to the fundamental characteristics which define its viability (survival probability). These vital characteristics have a tendency to reach their maximum given their corresponding value of diversity (Figure 1). This value of diversity is optimal (D* in Figure 1).

At each passing moment of time, the system is trying to reach a state with maximum viability and optimal diversity (V*, D*). When the environmental conditions are changed, the system adapts to those and changes its parameters so that the optimal value of its diversity also can be changed. We can assume that the diversity levels of undisturbed natural systems are the closest to the optimal values. An artificial decrease or increase of inner biosystem diversity in line with the fast environmental changes leads to a decrease of biosystem viability.

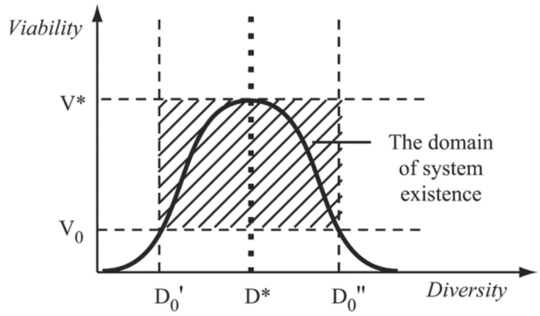

Figure 1. Optimal value of diversity (D*) corresponds to maximum biosystem viability (V*). V_0, a critical value of viability; D_0, a critical value of diversity; the shaded area is a domain of system existence

We propose to combine both population and community levels in the concept of interconnection between biodiversity and ecosystem functioning.

In the present article, we do not consider the processes of raising of biosystem organization levels and biosystem complication during the evolution. Our sphere of interest is the adaptation of biosystem with definite organization levels to different environmental conditions.

3. Two-level "Populations-community" Model

We have demonstrated operability of the principle of optimal diversity by the example of models of two types of biological systems - statistical and structural (in accordance with the notation of the two ways of forming of a top-level control system by A. Lyapunov[9], which can be interpreted as model of phenotypic diversity of the population[10],[11] and the optimal number of species in a community of one trophic level[11].

As a next step we have developed and investigated a mathematical model of two-level "populations-community" system in which optimal diversity is forming at both levels during their interaction.Full description and mathematical equations have been presented in previous publications[12]. Here we briefly repeat its basic properties.

Environment is characterized by the intensity of resource flow and by the environmental parameter that can be interpreted as any resource characteristic (for example, light wave length, size of the prey and so on) or as any environmental factor that supplies resource consumption (for example, temperature, humidity, etc.). At each passing moment of time, some value of this parameter is realized. The dispersion of the distribution of its values defines the degree of environmental instability.

The lower level – population – is represented as the stochastic model which was investigated by means of statistical tests (Monte Carlo method). Populations consist of various phenotypes. The death rate is set by exponential dependence with a constant mortality; reproduction is modeled by a logistic function with birth rate index, which is monotonously decreasing with the growth of population size.

Phenotype characteristic is the ability of individuals to propagate in a given environmental conditions (Figure 2). At each passing moment of time, the realized environmental factor f* corresponds with a definite phenotype, for which the given environmental conditions are the most favorable. At this moment, a group of phenotypes breeds around it. The value of dispersion of distribution of breeding at each moment according to phenotypes (black bars in Figure 2) can be interpreted as an index of the width of the zone of individual tolerance. The value of dispersion of distribution of their offspring (shaded bars) serves as an index of diversity reproduced by the population at each step of its development.

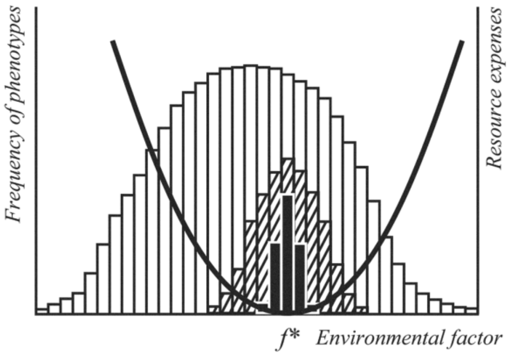

Figure 2. Phenotypic diversity in population and resource spending by phenotypes. f*, the value of environmental parameter realized at a given moment of time; white bars, existing phenotypes; black bars, phenotypes breeding at a given moment; shaded bars, offspring of the breeding phenotypes, black curve, resource spending by phenotype f* when environment deviates from the f* value

To maintain their existence and reproduction, individuals should spend some resource. The farther the realized environmental parameter is from the optimal value for a given phenotype, the greater the resource spending by this phenotype (Figure 2).

During computer experiments, populations die out or reach some stationary quantity with definite phenotype diversity (white bars in Figure 2) and with the level of resource consumption.

The optimality criterion for population is its maximum size (biomass) at a fixed volume of available resource. This task is equivalent to the minimization of resource spending per individual at a fixed population size (biomass).

The upper level – community – is represented as the analytic model which includes lower subsystems as functions which were found by means of statistical tests.

The community consists of populations which share the available resources. Therefore, we modeled a community of one trophic level. The number of populations in the community is considered as species diversity.

The optimality criterion for the community is the maximum of total quantity of individuals (total biomass) of all populations at a fixed volume of available resource (this task is equivalent to the minimization of resource spending by each population under the condition of full consumption of the available resource).

Optimal diversity is settled during iterative interaction of the two hierarchical levels by the following steps:

- each population trying to reach the maximum size (biomass) by setting its inner diversity at the optimal level;each population consumes the resource allocated to it by the community level;
- the values of population size chosen at the bottom level are transferred upward to a level of community;
- the upper level in view of these values defines the number of populations (number of species) at which the total quantity of individuals (biomass) is maximum (or specific resource spending is minimum);
- a particular part of the total resource is allocated to every population;
- recurrence of the first step: populations solve their optimization problem on the basis of resource allocated to them, etc.

As a result of multiple iterations, the final values of optimal diversity are established on the levels of populations and community.

4. Results of Modeling

4.1. Domain of Population Stability

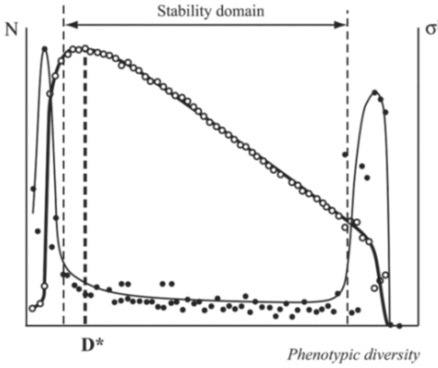

Figure 3. Dependence of population size N (white circles) and its dispersion σ N (black circles) on phenotypic diversity. Dispersion of population numbers obtained during model tests is an index of population stability (low values correspond to stable populations). D*, optimal phenotypic diversity

The level of phenotypic diversity in the population dramatically influences its stability. There is a range of diversity values at which the population is stable in a given environment. When the population leaves this range for a decrease or increase, it becomes unstable (Figure 3). The causes of population stability loss at the decrease of phenotypic diversity are obvious: when the diversity is low, the realization probability of favorable environmental conditions decreases. The stability loss at diversity growth occurs because each phenotype class has a few individuals and so the probability of population extinction increases. In less stable environments, the stability range is reduced owing to the areas with low indexes of birth rate and phenotypic diversity.

The existence of population stability limits at low intrapopulation diversity agrees with the common notions of conservation population genetics. The conclusion about the presence of such limits at a high diversity is less evident.

4.2. Existence of Optimal Phenotypic and Species Diversity

The model experiments reveal the existence of optimal values of phenotype diversity which correspond to the maximum population size/biomass (D* in Figures 1 and 3). Any case of diversity deviation from the optimal value leads to a decrease in population size or growth of resource spending.

It is interesting to note that the optimal values of diversity in the explored model are close to the bottom border of population stability. If we suppose that natural populations have phenotypic diversity close to optimal values, this result will certainly emphasize the danger of intrapopulation diversity decrease. Even a slight decrease in the level of phenotypic diversity reproduced by the population at each passing moment of time can lead to the loss of its stability.

There arise optimal values of species diversity (number of populations in a community) which correspond to the maximum total quantity/biomass of all populations.

4.3. Shift of Values of Optimal Diversity and Population Size Under Changes of Environment

Optimal values of intrapopulation and species diversity as well as population size depend on the degree of environment stability and the intensity of resource flow in the following way.

At the population level:

- the optimal values of intrapopulation diversity decrease in more stable environments and are independent of the intensity of resource flow (Figure 4a);
- the maximum values of population numbers/biomass increase in more stable and “rich” environments (Figure 4a);
- the minimum values of resource spending per individual decrease in more stable environments and are independent of the intensity of resource flow (Figure 4b).

At the community level:

- the optimal values of species diversity increase in more stable and “rich” environments;

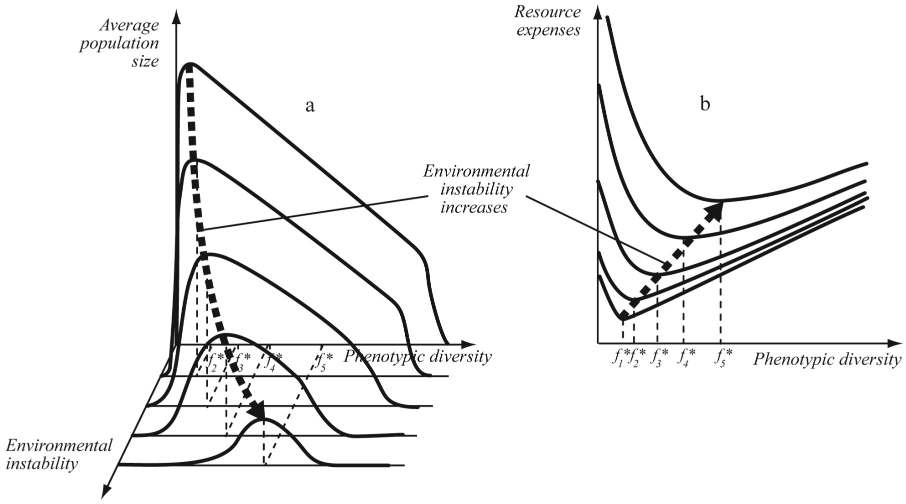

Figure 4. Optimal values of phenotypic diversity (f*), population numbers and resource spending in environments with different stability

- the maximum values of total quantity of individuals (total biomass) of all populations change in the same way.

These results suggest that populations that are adapted to less stable environments have higher intrapopulation diversity and also higher resource spending at equal population size (or lower population size at equal resource spending, depending on optimality criterion).

These results also show that optimal values of diversity at different hierarchical levels change in the opposite manner as the degree of environmental stability varies: optimal intrapopulation diversity increases in less stable environments, but optimal species diversity decreases.

4.4. Demographic Compensation of Shift of Optimal Diversity Values

The decrease in mortality, as well as the increase in birth rate and the increase in individual tolerance (diversity of breeding phenotypes at each moment), produces the same effect on location of optimal diversity values as stabilization of environment (Figure 5).

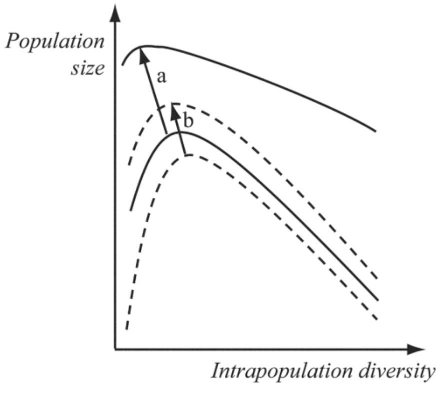

Figure 5. Changes in optimal values of intrapopulation diversity: a, at increase in fertility; b, at increase in individual's ecological tolerance

Thus, there are different ways to compensate environmental fluctuations: to increase population growth rate, to decrease mortality or to broaden the zone of individual tolerance. This mechanism can work on the level of one population inside the limits of its adaptive capability, and on the level of community due to the change in species composition; for example, shifting between K- and r-strategists or between specialists and generalists. In the last case populations with high growth rate and narrow zone of individual tolerance may be regarded as r-strategists, and populations with low growth rate and wide zone of individual tolerance may be regarded as K-strategists.

5. Discussion

5.1. Criteria of Biodiversity Optimality and Ecosystem Functioning

We used in essence the same optimality criteria at population and community levels: the maximum quantity/biomass at a fixed amount of available resource or the minimum spending of resource at a fixed total quantity/biomass. These criteria are reduced to only one – minimum spending of an individual or biomass unit can be considered an effective measure of resource utilization by the biosystem. The model populations and communities establish the optimal inner diversity at which their effectiveness is maximum. Such an optimality criterion for biosystems seems reasonable enough, because it is directly linked to biosystem viability.

The optimality criteria used can give a rough estimate of the effectiveness of ecosystem functioning. Indeed, for stationary communities which use all the resource available, the constantly supported total biomass or effectiveness of resource utilization can be an index for supporting and regulating ecosystem services. These characteristics are often applied as indices of ecosystem functioning in experiments and field observations[13 - 16]. Thus, we may suppose that if a community is in an optimal state, ecosystem functioning is maximum. If a community leaves a zone of optimal diversity values, the effectiveness of ecosystem functioning decreases.

5.2. Possible Mechanisms of Optimization of Diversity

Possible mechanisms of optimization of diversity throughout ecological, microevolutionary and evolutionary processes are considered by us in a separate publication[17]. Hereweonlybrieflylistthemain mechanisms.

Optimization of species diversity in a community is going onin the process of its "self-assembly" from the available regional species pool. The lack of species in the regional pool for any type of extreme habitats may lead to hump-backed function of species number on some environmental gradient (see Section 5.4) or can be compensated by the formation of the intraspecies ecological forms. During succession optimum values change. Climaxcommunity in the framework of our model can be considered as a community that uses every available opportunityto achieve the optimal values of diversity.

Optimization of intrapopulation diversity can occur primarily due to changes in the diversity of offspring (shaded bars in Figure 2). This parameter depends on the level of genetic diversity in the population and the average width of the reaction norm. "Tuning" diversity within the reaction norm does not require genetic changes and is the most labile mechanism ofoptimization of phenotypic diversity. When environment stabilizes necessary reduction in intrapopulation diversity can be quickly achieved by producing more homotypic offspring. In moderate destabilization of the environment phenotypic diversity increases due to epigenetic components within the reaction norm.At extreme deviations of environmental conditions offspring phenotypes may go beyond the previous norm of reaction.

Further optimization of the phenotypic diversity may also occur due to changes inintrapopulation genetic diversity, but it obviously requires more time.Other population parameters that shape phenotypic diversity - the width of the ecological tolerance of propagatingphenotypes (black bars in Figure 2), the function of the resource expenditures and the maximum rate of population growth - are species traits and their changes occur in the evolutionary time scale.

With a lack of species in a regional pool, optimization of diversity can occur through the development of intraspecific sympatric ecological forms. The formation of discrete intraspecific ecological forms fundamentally differs from the increase in diversity of continuous phenotypic distribution. If we consider the ecological structure of a community, in the first case intraspecific forms occupy different niches, in the second casethe single niche expands.Intraspecific sympatric forms can be represented as a dynamic system, constantly tuning parameters of diversity in accordance with changes of environment –when environment stabilizes the number of discrete ecological forms increases, when environment destabilizes this number decreases.

Natural biosystems exist in a changing environment. They must continually "tune" their parameters, including diversity, in accordance with the changes taking place. We can assume that natural undisturbed communities and populations existing in historically typical environment are closest to the optimal diversity values. Anysignificant and rapid (exceeding the speed of biosystems adaptation time) environmental changing and disturbance of the biosystems will make them deviate from their optimal state, and their effectiveness and viability will be reduced.

5.3. Opposite Reaction of Optimal Values and Different Role of Intrapopulation and Species Diversity

The opposite reaction of optimal diversity values on environmental destabilization at population and community levels allows us to make an assumption about their different role in a fluctuating environment: intrapopulation diversity is the basis for adaptation to environmental instability, while species diversity due to niche differentiation enables the community to use resources effectively. Some experiments show that higher species diversity stabilizes and increases the ecosystem processes but destabilizes and decreases the population level[18], and that species diversity increases biomass production but decreases community resistance to drought perturbations[19]. These results indirectly confirm the different role of intrapopulation and species diversity and can be interpreted as a reflection of the fact that the adaptation to environmental fluctuations is carried out primarily at the population level.

J. Norberg and coauthors[20] have found out a similar behaviour of model system: in a fast changing environment, phenotype variance increases and total system's biomass decreases. However, these authors interpret phenotypes as generalized phenotypes of separate species inside a functional group and make up a conclusion about the growth of interspecies differences inside a functional group when the rate of environmental variability increases.

The opposite behaviour of optimal values and the probable different role of intrapopulation and species diversity in a fluctuating environment allow us to expand some recent ideas about biodiversity functioning. For instance, a large number of species is considered a kind of community preadaptation and “insurance” against unpredictable environmental shifts[21],[22]. But we hypothesize that the adaptation of communities to a high level of stationary environmental fluctuations increases intrapopulation diversity and decreases species diversity.

Our results also allow us to change the angle of view on the question “does functional redundancy exist[23]?” The principle of optimal biodiversity assumes that functional redundancy is the optimized parameter of a community as well as intrapopulation and species diversity as a whole. The degree in which the ecological niches overlap is a result of optimization of diversity parameters at population and community levels. Functional redundancy is not only a “safety factor” similar to engineered redundancy[24], and a reservoir of variations allowing to ad-just to changing conditions[25], but also the optimized property that allows the maximum effectiveness of community in the given environment.

5.4. Does the Optimal Biodiversity Principle Agree to

Empirical Data?

The optimal biodiversity principle predicts that natural communities which are adapted to “rich” and stable environments consist of a large number of species with low intrapopulation diversity (specialists), while communities which are adapted to “poor” unstable environments consist 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 (Figure 6). We emphasize that these conclusions are made for undisturbed natural systems which exist in a typical historical environment.

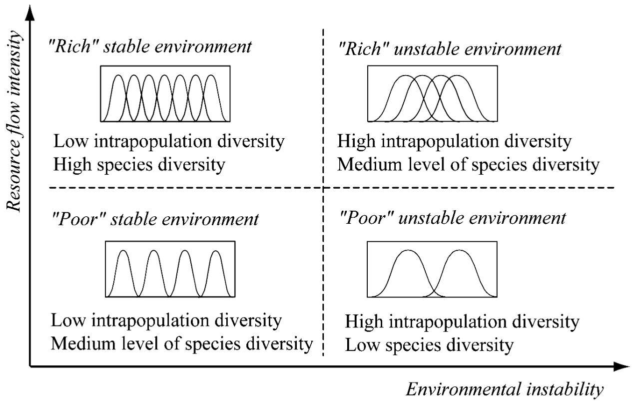

Figure 6. Assumed levels of species and intrapopulation diversity in communities which are adapted to different environments

Such a pattern of diversity corresponds to general common ideas about diversity distribution across natural regions and climatic zones, giving grounds to regard the principle of optimal biodiversity as a working hypothesis.

The inference about increase in optimal intrapopulation diversity in unstable environment corresponds to the conception of R. MacArthur about widening of ecological niche in more variable conditions which underlies the “latitude-niche breadth hypothesis”[26].

It is difficult to compare directly our results with empirical evidence because the overwhelming majority of investigations contains inseparable data about stability and intensity of the resource flow. Nevertheless some parallels may be found, for example, negative relationship between species richness and habitat variability in small rock pools in Jamaica[27].

Experiments manipulating species numbers and answering a question how ecosystem functioning depends on diversity show overall mean positive effect[14 - 16]. At first it seems that this statement contradicts the optimal biodiversity principle, according to which this dependence should have a unimodal (“humpbacked”) form. However, we believe that no contradictions may be found here. As mentioned earlier, optimal values of diversity most likely correspond to undisturbed natural communities in a typical environment. An overwhelming majority of manipulating experiments use fewer number of species than is typical for nature communities and therefore reflect only the left ascending arm of optimal dependence (in other words experimental communities are in suboptimal state because of lack of species diversity).

The other group of experiments and field observations is aimed at an inverse function: how diversity depends on productivity or, rather, fertility of a site. Field observations most often show humpbacked and positive dependence of diversity on productivity[13],[22],[28]. Our results predict an increase in optimal diversity values and total community biomass in more “rich” conditions, which contradict the humpbacked form. We propose a few possible explanations. All of them imply a difference between productivity and fertility: the first one is a property of the community, the second a property of the site. So the question is: how diversity and productivity depend on fertility[29]?

1. We may suppose that the enrichment of environment is often accompanied by its destabilization (anthropogenic or natural), and a community adjusts simultaneously to these two factors. According to our results, these adjustments will have opposite directions: optimal diversity increases in more “rich” environments but decreases in unstable environments. The sum of these processes may give a humpbacked dependence under certain conditions (Figure 7). Simultaneous enrichment and destabilization of the environment can lead not only to the reduction of species diversity but also to the shift of species structure from K- to r-strategists and from specialists to generalists. We see something like this in ruderal and anthropogenic communities.

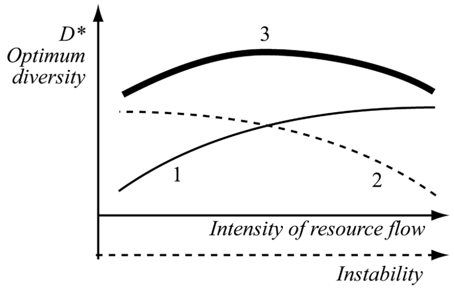

Figure 7. Changes in optimal diversity values at simultaneous enrichment and destabilization of the environment: 1 - in-crease in diversity at enrichment; 2 - decrease in diversity at destabilization; 3 - the sum curve

2. One more explanation may be the species pool hypothesis[30 - 34], which supposes that high-fertile habitats are less typical than low- and medium-fertile ones within the investigated biomes/regions, and so there are not enough species well adapted to such habitats in regional pools.

M. Partel and coauthors[31] have showed that the unimodal relationship is common for temperate regions, where high-fertile habitats have historically been rare, and species pools which are adapted for such conditions are relatively small, but a positive relationship is common for tropics, where high-fertile habitats have been relatively common and specifically species pools are quite rich. W. Cornwell and P. Crubb[35] have demonstrated that the peak in species richness for the grasslands of Central Europe (the most popular community type in diversity-productivity researches) occurs on nutrient-poor soils, while the peak for forests is on nutrientrich soils. Thus, species pool hypothesis supposes that regions with historically typical high-fertile habitats demonstrate a positive diversity-fertility relationship which corresponds to our results.

Most experiments with fertilization show a reduction of species diversity[13],[36],[37], which is similar to community changes at eutrophication. These cases may be interpreted as extreme variants of atypical conditions and environmental destabilization; thus a decrease in species diversity is predictable in the context of the principle of optimal biodiversity.

7. "Diversity - Ecosystem Functioning - Environment" Relationship

Many authors[17],[22],[38] have pointed at bidirectional interrelations between diversity and the main characteristics of ecosystem functioning (stability, magnitude, productivity). Moreover, this is under the influence of environmental conditions – the intensity of available resource flow and the degree of environmental stability (Figure 8a). So we have quite an inoperable scheme where all things are interconnected with each other.

The optimal biodiversity principle changes this scheme (Figure 8b) to a two-lewel self-optimizing hierarchical system (populations-community) which adjusts its parameters to the given environmental conditions. Diversity at both hierarchical levels is the optimized parameter, in which optimal values provide maximum resource effectiveness and biosystem viability. Environment parameters (instability and richness) govern optimal diversity values and extreme values of ecosystem functioning indexes. Such a notion may help overcome some obstacles in the practical application of "biodiversity-ecosystem functioning" hypothesis in nature conservation; for example to shift the formulation of biodiversity conservation aims from maximum diversity and maximum ecosystem functioning[39] to optimal ones

8. Biodiversity and the Purpose of Management of Ecosystem Services

Ecosystem functions may be grouped into three main categories: the formation and maintenance of environmental parameters suitable for human life – environment-forming functions; the biomass taken by humans from nature (seafoods, timber, fodders, fuel, raw materials for pharmaceutics and industry, etc.) – productive functions(so-called ecosystem goods); information present in natural systems and their cultural, scientific, and educational significance – informationfunctions.

This division of ecosystem functions differs from that adopted for ecosystem services in the international documents (e.g.[40]), but we propose to use it, because it is more convenient for understanding the biological and other natural processes.

The basic characteristics of the biosystems – theirbiomassand levels ofthe internal diversity – used in our model, can act as the indicators of effectiveness. The effectiveness of ecosystemservicesisinextricablyconnectedwith indicators ofbiological diversity, therefore it is necessary to consider the status andpossible changes inbiodiversity for developmentof themethodsand strategies ofthe ecosystem servicesassessment and using. Hence, while determiningthe objectives for management of the ecosystems functions as a single complex,itisnecessarytotakeintoaccountthe changes in biodiversity andbiomass, which will take place if using any given functions (Table 1).

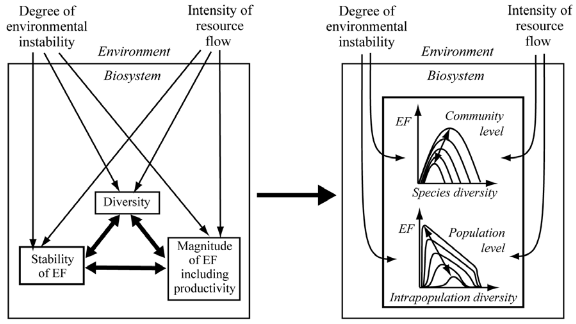

Figure 8. Relationship between diversity and general characteristics of ecosystem functioning and environment in the context of optimal biodiversity principle

Table 1. Management objectivesforthe use ofdifferentecosystem functions andbiodiversity changes in this respect

Functions of biodiversity	Purposes of management	Changes of biodiversity	Changes of continuously supported biomass
Productive	The maximum of biomass being steadily retrieved	Decrease in diversity	Decreaseincontiniously supported biomass
Environment - -forming	Effective and sustainablee-cosystemfunctioning	Preservation of the naturallevel of biodiversity	Preservation of the naturallevel of biomass
Information	Getting information from-natural systems	Preservation of the naturallevel of biodiversity	Preservation of the naturallevel of biomass

Theuseofdifferentbiodiversityfunctionsrequiresdifferentstrategies.It is showedinthereport "Millennium Ecosystem Assessment"[40], thatmeaningfulimprovement inone functionoften leadsto decline inanother. Theoretically,this is whatyou might expect,since it is impossibleto optimize the systemat onceby many criteria, especially if they contradict each other.And suchcontradictions do arisein the management ofbiodiversity.

When using theenvironment-formingand information functionsthemanagement objectivescoincidewith the maintenance ofnatural levelsof biodiversity andbiomass, and when usinga productivefunctionsmanagement objectivescontradict this.Environment-forming functions are most effectively andsustainablyimplemented byundisturbedclimaxnaturalbiosystems, and any of theirdisruptions leadto a weakening ofthe naturalenvironment regulation.Thus, the management objective for using of the environment-forming functions is to minimize the disturbances ofnaturalsystems.And using of production function, on the contrary, requires retrieving of biomass from the ecosystems, which would be optimal on early and middlestages of succession, characterized by the highest productivity. If we down to the level of exploitedpopulationsthe maximization ofbiomasswithdrawnmeansthe maximum ofincreased mortality allowableunder thedemographicsustainability.This corresponds toa strongdestabilization of theenvironmentwith its simultaneousdepletion.Under suchinfluencesadaptivebiosystemstrendsare as follows:increase inintrapopulationdiversity, reducingin species diversity, reduction intotalcontinuously supported biomass.If we consider thatthe commercialpressure onpopulations almost eliminates thepossibility ofthe first mechanism, onlythe second andthird leaving,which are contrary tothe objectives ofmanagementwhen usingenvironment-formingfunctionsand information.Minimization of thepopulation biomassreducesitsecosystem functions.

Increasing of the bioresources use (increase in biomass retrieving) leads to different alterations in different ecosystemservices (Figure 9):

- environment-formingand information services monotonically decrease;
- productive functions (volume of biomass retrieved) grow at first and then decrease.

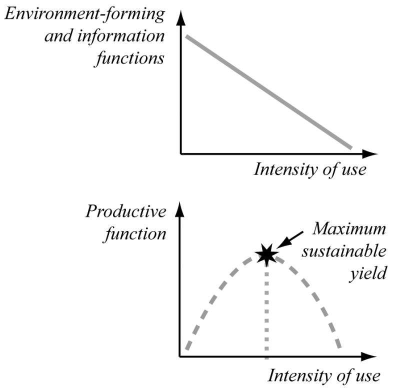

Figure 9. Alterations of variousbiodiversity functionsunder theintensification ofthe biological resources exploitation

The important issue in determining of the strategy ofmaximizing of ecosystem servicesis to determine theoptimalintensity of naturalbiosystems exploitation.The valueof ecosystem servicesand the formof its dependence onthe intensity ofexploitation of biological resourcesare defined by"benefits" derivedfrom the differentfunctionsof biodiversity (Figure10).

Wecan't yet determine the exactquantitative relationships between valuesof different ecosystemservices. Methods ofeconomic evaluationare sufficientlydevelopedforproductiveservices only (timber, seafood, furs, etc.). Forother functions,there are onlyrough estimates.

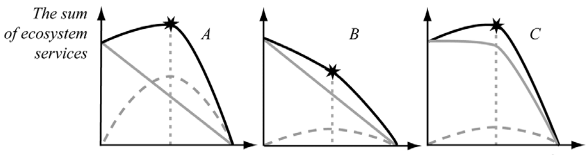

Figure 10. The value of ecosystem services (S)for different ratiosof productionand theenvironment-formingservices.Graydashed lines-productiveservices; solidgray line-environment-formingservices; solid black line- the total value ofservices;an asterisk-the maximum sustainableyield (explanation in text)

Commercialexploitationofnaturalsystemsisadvisableonlyifthevalueoftheirenvironment-formingservicesdoesnotexceed thevaluesofderivedbioproduction(Figure10A), butthiscaseisnottypical.It is obvious thatin most casesthe value ofenvironment-forming functionsgreatly exceeds all the benefits could be gained, getting bioproductionfrom naturalecosystems (e.g., according to[41]), the costof productivefunctions of biodiversityis only about6%of the total value of ecosystemservices).The valueof productiveservices, as a rule, will be significantlyless than value of environment-formingother services(Figure10B).In these cases,the implementation of "maximum sustainable yield" strategy significantly reducesthe total"benefit" of biodiversity.But todaywe can'trefuse the use ofbioproductionfrom natural ecosystems(althoughin the long runsuch a goalis likely tobeset).How to combine exploitation of bioresources and maintenance of environment-forming ecosystem functions?The only way is -the "ecosystem approach". Volumes andforms of removal of bioresourcesshould be tightlylimited according tothe requirement ofconservation ofstructure andenvironment-forming ecosystems functions, speciesand populations.It is necessary to develop the methods toget biomass from natural ecosystems without disturbance of their structure and diversity(Figure10C).If we could gettheseforms of natural ecosystemsexploitation, not deterioratingtheirown ecologicalfunctions, it would be possible to provide the integral optimization ofallecosystem services.

For thousands of years productive functions of natural ecosystems were the main for humankind, but nowadays, the prioritiesare changing and environment-forming functions(maintenance ofthe atmospheric parametersandstable climate, smoothing of the extreme natural events, formation and protectionof soils from erosion, water purification andstabilization ofhydrological regime, etc.)are more essential for human.This understanding should be the basis for a new environmental strategy[42].

9. Conclusions

1. The proposed principle of optimal biodiversity supposes that the optimal values of inner diversity of the biosystems (intrapopulation diversity and species diversity) correspond to their maximum viability.

2. The results of mathematical modeling have showed the

existence of optimal values which obtain maximum effectiveness of resource utilization at the population and community levels. Maximum effectiveness of resource utilization is possible to consider as an index of effectiveness of the ecosystem functioning.

3.The optimal values of diversity at the population and community levels depend on environmental instability in an opposite manner: optimal species diversity increases in more stable environments, but optimal intrapopulation diversity decreases. These results speak about the different role of intrapopulation and species diversity: intrapopulation diversity is the basis for adaptation to environmental instability, while species diversity enables a community to use the resource to the maximum and effectively. Thus, the principle of optimal biodiversity integrates population and community levels in the concept of interconnection between biodiversity, ecosystem functioning and environmental conditions.

4.The predictions of optimal biodiversity principle agree to general biodiversity patterns and empirical data of experiments and field observations. Seeming contradiction between unimodal (humpbacked) dependence of diversity on productivity and our predictions of its positive form may be explained by species pool hypothesis or by simultaneous enrichment and destabilization of the environment which shift optimal diversity values in the opposite directions. Thus, the optimal biodiversity principle may be proposed as a working hypothesis complementary to other ideas about interrelation between biodiversity and ecological functioning.

5.The optimization concept of the “diversity - ecosystem functioning - environment” relationship may be used as a complementary approach in new strategyof nature management.

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