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The optimal biodiversity–A new dimension of landscape assessment

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ABSTRACT

The principle of the optimal biodiversity suggests that diversity is an adaptation of biological systems to environmental conditions. Biosystems with the optimal values of diversity are the most effective, have the maximum viability and capacity of ecosystem functioning and services. The optimal diversity values depend on the degree of environmental stability and the amount of available resource. The optimal values of intrapopulation diversity decrease in more stable conditions, while the optimal values of species richness increase. The resource amount does not affect the optimal values of intrapopulation diversity and increases the optimal species richness.

The objective of this article is to propose possible applications of the optimal biodiversity principle to estimation of biodiversity on a landscape. A landscape can be considered as a mosaic of undisturbed natural communities with the near-optimal diversity and communities that were disturbed by people and moved away from the optimal state for different distances.

The main implications of the optimal biodiversity concept to landscape management are as follows:

- The criterion of ecological importance is the optimal biodiversity, and not high indices of species diversity. Natural ecosystems with low species richness can be no less important than the highly diverse habitats.
- Both species and intrapopulation diversity should be monitored and managed.
- Different ecosystem services require different management strategy in relation to biodiversity. Trade-off between provisioning and regulating services should take into account the reaction of biodiversity to management actions.

1. Introduction

The relationship between biodiversity and ecosystem functioning was one of the most important ecological research issues over the last decades. Hundreds of experiments demonstrated positive effects of species richness on ecosystem functioning (productivity, biomass, rate of nutrient cycling, invasion resistance, etc.) and stability (Bardgett and van der Putten, 2014; Cardinale et al., 2012; Gross et al., 2014; Handa et al., 2014). The importance of intraspecific diversity for viability and functioning of populations, communities and ecosystems was revealed in dozens of experiments that manipulated genetic and phenotypic diversity of plants, animals, and bacteria (Forsman, 2014; Forsman and Wennersten, 2016; Hughes et al., 2008). In some experiments effects of intraspecific diversity were comparable in magnitude to the effects of species diversity. (Cook-Patton et al., 2011; Hughes et al., 2008).

Surveys of real-world systems confirmed the positive relationship between species diversity and functioning of marine, freshwater and terrestrial ecosystems (Lewandowska et al., 2016). The evidence obtained for grasslands (Grace et al., 2016; Maestre et al., 2012) and forests (Baruffo et al., 2013; Cavanaugh et al., 2014; Nadrowski et al., 2010; Paquette and Messier, 2011; Thompson et al., 2009; Vilà et al., 2013; Wang et al., 2011 Wang et al., 2011) may be the most interesting for landscape research. Field observations also confirmed the importance of intraspecific genetic and phenotypic diversity for population fitness (number of adult progeny, population growth rate, distributional range size, resistance to extinction risk) and community functioning (Forsman and Wennersten, 2016; Hughes et al., 2008; Reed and Frankham, 2003).

Thus, today there is the consensus about the crucial importance of biodiversity for effectiveness and stability of ecosystem functioning (Cardinale et al., 2012; Tilman et al., 2014). The impacts of biodiversity loss on ecological processes can be comparable with effects of other global drivers of environmental changes such as climate warming, ultraviolet radiation, increase in the concentration of CO_2, nitrogen addition, droughts (Hooper et al., 2012; Tilman et al., 2012).

Optimization principles can broaden the understanding of interconnections between biodiversity and ecosystem functioning. These principles are widely used in physiology, biochemistry, evolution

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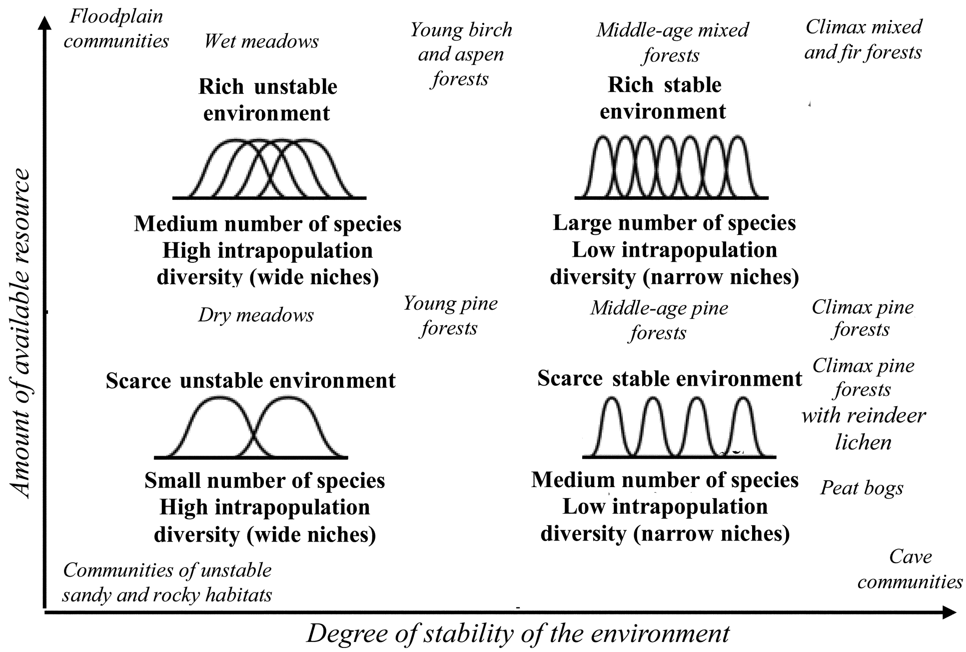

Fig. 1. The expected values of the optimal species and intrapopulation diversity in communities adapted to different environments and examples of communities of the middle part of European Russia.

theory, population dynamics and other biological sciences. However, so far they are not used in the field of biodiversity research to their full capacity. The optimal biodiversity principle (Bukvareva, 2014; Bukvareva and Aleshchenko, 2013b) was proposed as the theoretical approach to initiate research in this direction. This principle suggests that inner diversity of a biological system (i.e. diversity of its elements) is an adaptive feature and affects biosystem viability. The biosystem viability is maximal if the diversity is optimal. Biosystems tend to achieve the optimal diversity values in the course of adaptation to environmental conditions. Thus, undisturbed climax communities and their constituent populations (rather, coenopopulations) can be considered as the closest to the optimal diversity. Hereinafter, saying "the optimal diversity", we mean "the closest to the optimal". Any shift away from the optimal diversity values decreases biosystem viability.

The optimal biodiversity principle was analyzed by the following theoretical mathematical models: the model of phenotypic diversity in a population (Aleshchenko and Bukvareva, 1991); the two-level hierarchical model "population - community" without possibility of divergence of ecological niches (Aleshchenko and Bukvareva, 2010); the two-level hierarchical model "population - community" with the possibility of ecological niches divergence (Bukvareva and Aleshchenko, 2013a). The formal description of all models and short overview of modelling results were presented in the summary of the principle (Bukvareva, 2014).

The aim of the present paper is to propose possible applications of the optimal biodiversity principle to landscape assessment. The discourse considers the optimization of biosystems on the scope of ecological processes. The microevolutionary and evolutionary optimization is not considered in this article. At first, we briefly present the main theoretical predictions of previously published models about how the optimal biodiversity values depend on environmental parameters. After that, we speculatively analyze how these predictions can work at the landscape level and what main factors shift real-world populations and communities away from their optimal state. Finally, the general ideas about consideration of the optimal diversity values in landscape management are proposed and discussed.

2. The optimal values of species and intrapopulation diversity on a landscape

The above mentioned models (Bukvareva, 2014) showed that the optimal diversity values depend on parameters of the environment and characteristics of species. Theoretical predictions that may be of interest for landscape research relate primarily to the dependence of the optimal diversity values on the degree of environmental stability and the amount of resource available to organisms. The models predicted that intrapopulation phenotypic diversity and species diversity depend on environmental stability in the opposite mode. The optimal values of intrapopulation diversity decrease in more stable conditions. In other words, a population needs lower inner diversity to reach the maximum size in a more stable conditions (at the same time the maximum possible population size is higher in stable conditions than in unstable ones). In contrast to intrapopulation diversity, the optimal values of species richness increase in more stable conditions. The optimal values of intrapopulation diversity don't depend on the amount of available resource, but the amount of resource affects the optimal values of species richness that increase in more "rich" conditions.

These predictions suggested that natural undisturbed communities that are adapted to rich and stable conditions tend to consist of a large number of species with low intrapopulation diversity. It was previously theoretically justified that intrapopulation phenotypic diversity can be interpreted as an important factor affecting the width of the population ecological niche (Bukvareva and Aleshchenko, 2013b), so, in this case we can speak about specialists with narrow ecological niches. Communities that are adapted to scarce unstable conditions tend to consist of a small number of species with high intrapopulation diversity, that is, generalists with wide ecological niches (captions in bold in Fig. 1). In rich unstable and scarce stable environments, we may expect some intermediate optimal diversity values (Bukvareva and Aleshchenko, 2013b; Bukvareva, 2014). Obviously, community history is also the important factor of biodiversity patterns, but it is not discussed in this article.

At the global scale, we can speculate that tropical rain forests are located in the top right corner of our chart in rich and stable conditions and have the highest values of the optimal species richness and relatively low optimal values of intrapopulation diversity (narrow ecological niches). Polar deserts, tundra and highlands can be located in scarce and unstable conditions in the bottom left corner and have the lowest values of the optimal species richness and relatively high intrapopulation diversity (wide ecological niches). Caves are examples of communities that are adapted to extremely scarce and stable conditions (the bottom right corner) and have relatively low optimal species richness and the lowest optimal intrapopulation diversity (narrow niches). Estuaries can be located in the top left corner in rich unstable conditions and have medium optimal values of species richness and high intrapopulation diversity (wide niches). Other ecosystems occupy intermediate positions in the environmental "resource-stability" axes and have intermediate optimal values of diversity. These assumptions in general are consistent with global environmental and biodiversity patterns and this allows us to continue our reasoning.

On a landscape, an initial environmental "resource-stability" pattern is determined by natural conditions (relief, soils, water supply, etc.). Anthropogenic disturbance and succession stages transform this initial pattern. Thus, we need to include these factors in our "resource-stability" chart.

In terms of *ecological successions,* theoretical predictions consider internal diversity of serial and climax communities. In accordance with E.P. Odum (1983), in the course of a succession, biogeochemical cycles become more closed, stock volume and turnover time of nutrients increase, the whole system becomes more stable. Climax communities have the active function of regulation of their internal environment and they are more autonomous from the external environment compared with initial succession stages. During a succession, the community internal environment becomes more stable. Thus, the initial succession stages may be regarded as communities adapted to unstable conditions and the later stages may be regarded as communities adapted to more stable conditions. Within the optimal biodiversity principle, a succession can be regarded as the trajectory of a community transition from states which are optimal in unstable conditions, to states which are optimal in stable conditions (Fig. 2). It means that the optimal intrapopulation diversity (niche width) decreases and the optimal species richness increases in the course of succession. The speculative example of possible distribution of the optimal diversity values considering some of the main initial natural communities and their succession stages for a landscape of the middle part of European Russia is shown in Fig. 1.

As the result of *human impact,* the optimal biodiversity values can be broken in two main ways: a) due to anthropogenic changes of environmental conditions and b) because of the disturbance of populations and communities.

The general direction of anthropogenic changes of the environment is destabilization, which can occur in the following cases (black arrows in Fig. 3): destabilization and enrichment (e.g. fertilization, eutrophication), destabilization (e.g. human disturbance of animals), destabilization and depletion of biotic environment (removal of biomass, e.g. logging, fishing, etc.). The main direction of adaptation of populations and communities to anthropogenic destabilization of the environment is increase in intrapopulation diversity. The necessary diversity changes are marked with thin black frames in Fig. 3.

Anthropogenic impact on populations and communities is expressed primarily in reduction of species richness and intrapopulation diversity, as a result of which populations and communities leave their optimal state and move to suboptimal state (dashed arrows and frames in Fig. 3). As indicated above, adaptation of populations to anthropogenic destabilization of the environment requires increasing intrapopulation diversity, but human impact on populations reduces their size and intrapopulation diversity. Thus, disrupted populations are deprived of the opportunity to adapt to anthropogenic pressure, and, as a result, mechanisms of adaptation at the community level start to work and typical native species are replaced by other species. It is often manifested in the shift in species composition from K-strategists to r-strategists and from specialists to generalists, which corresponds to the modern proliferation of synanthropic biota. Some or all of populations and communities on an anthropogenic landscape don't have optimal

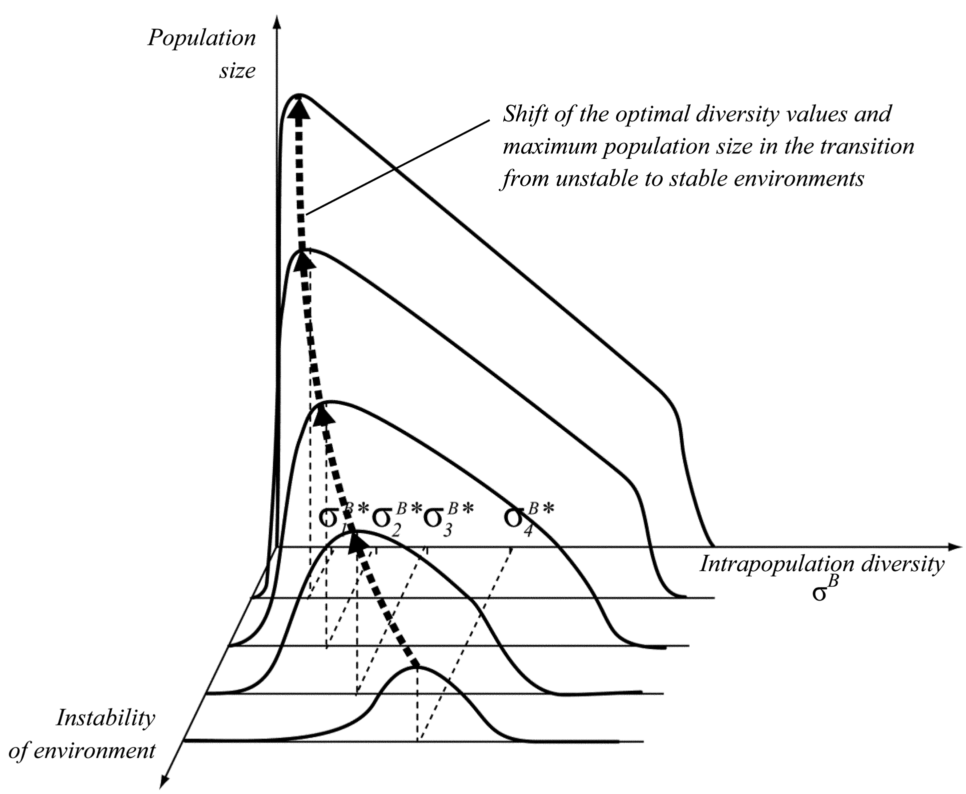

Fig. 2. The population size and the optimum values of phenotypic diversity (σ^{B*}) in environments with different degree of instability (Bukvareva, 2014).

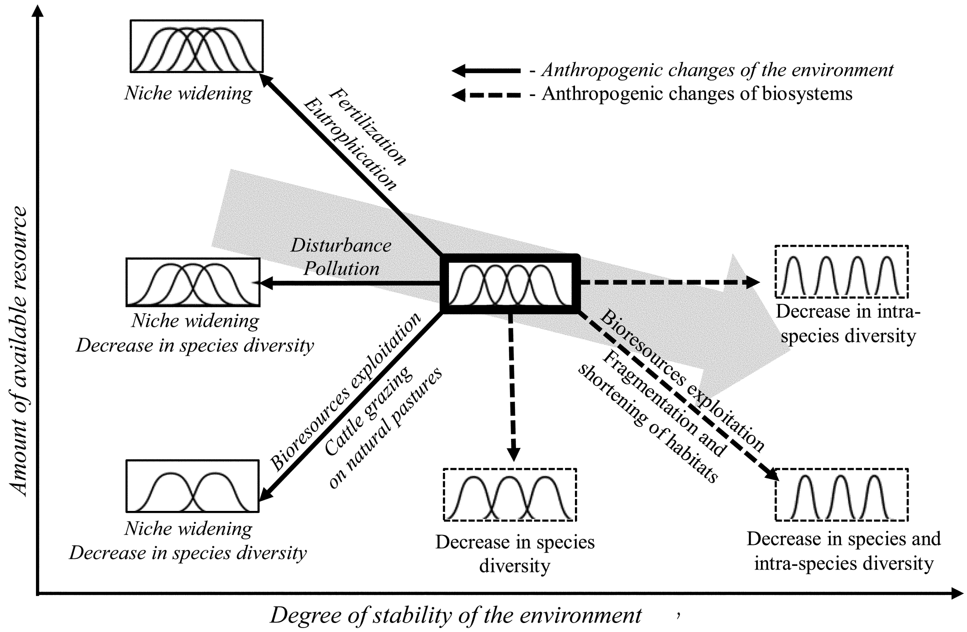

Fig. 3. The directions of anthropogenic changes of the environment, populations and communities and corresponding shifts of diversity values.

diversity values and are moved away from the optimal states to different distances in the general direction to the shortening of intrapopulation diversity (gray arrow in Fig. 3).

Since populations and communities can be moved away from the optimal state in two above mentioned ways, the optimal biodiversity can be restored in the same ways: by reduction of anthropogenic changes of the environment, and by regeneration of the typical structure and diversity of populations and communities.

3. Discussion: what may be ways of application of the optimal biodiversity principle on landscape scale

What empirical reasons do we have for application of the optimal biodiversity principle for landscape assessment? The task of investigating the biodiversity optimality has not been posed so far, therefore we can use only indirect evidence. Most of experiments and field surveys, as noted in the introduction, found the monotonic positive relationship between indicators of ecosystem functioning and indicators of species and intrapopulation diversity. Experiments usually explore diversity values that are lower than the typical values of natural communities and populations. Comparative surveys analyze sets of natural undisturbed communities with near-optimal diversity and disturbed communities which have diversity less than optimal. Thus, both experiments and field surveys usually investigate the ascending branch of the optimal dependence. However, some experiments that manipulated genetic diversity found the optimal relationship (Burls et al., 2014; Caesar et al., 2010; Forsman and Wennersten, 2016). The author of the optimal genetic diversity concept Yu. Altukhov (2003) detected the optimal dependence of offspring fitness on the degree of parental heterozygosity (the average proportion of genes that carry two different alleles) in natural populations of spruce and salmon. With regard to species diversity, the unimodal humpbacked dependence of community functioning indices on species richness was found in microalgae freshwater communities (Passy and Legendre, 2006). It showed that community functioning is maximal at the medium species richness, which can be considered as optimal. The general qualitative verification of the optimal diversity models based on available literature data demonstrated that published results of biodiversity experiments and field surveys of populations and communities generally do not contradict the main predictions of the optimal biodiversity principle and confirm them in some cases (Bukvareva and Aleshchenko, 2013b). This allowed us to consider the principle as a working hypothesis.

The optimal biodiversity principle has a number of consequences for landscape conservation and management.

The first consequence is the necessity to take into account both species and intraspecific/intrapopulation diversity. The concept of the optimal biodiversity (Bukvareva and Aleshchenko, 2013b; Bukvareva, 2014) assumes that intrapopulation and species diversity presents two inseparable aspects of the whole process of biological adaptation to the environmental conditions. The opposite reaction of these two biodiversity hierarchical levels to environment destabilization suggests that adaptation mechanisms are divided between them. Intrapopulation diversity provides adaptation to environmental fluctuations, while species diversity allows the maximal effectiveness of use of available resources due to species complementarity and portfolio effects. The optimal intrapopulation diversity is adaptation of populations to a given degree of environmental instability, which allows them to exist in a steady-state (stationary) mode in normally fluctuating conditions. This adaptation can be considered as basis of dynamic resistance of populations. Along with resilience (i.e. capacity to recover quickly after disturbance) it is a key component of the general sustainability of populations, and therefore, of communities and ecosystems that include them. Relationship between the optimal values of species and intrapopulation diversity are especially important just on a landscape scale because of close interaction of population and community processes.

The second consequence concerns the choice of conservation priorities. The concept of biodiversity optimality questioned the well-known conservation strategies that are based on the priority of high species richness. They are used mainly for global choice of conservation priorities (Mittermeier et al., 2011; Myers et al., 2000; Trebilco et al., 2011), but also are discussed on large landscape scale (Flather et al., 2008). These strategies give priority to areas with the highest diversity indices (biodiversity hotspots, megadiversity countries, etc.). In contrast, the optimal biodiversity principle justifies the other priorities, namely, the need to maintain the optimal diversity, that can be quite low under certain conditions, but no less valuable. For example, in the northern biomes in severe and unstable conditions the small values of species richness are optimal and provide the maximal effectiveness of ecosystem functioning. Northern ecosystems have much less species diversity than tropical ecosystems, but play a key role in the biosphere regulation. On a landscape, communities with low species diversity that are adapted to unstable or scarce conditions and communities with high diversity that are adapted to rich and stable conditions are equally important. For example, species richness of peat bogs or dry rocky communities is significantly lower than diversity of mixed forests, but their ecosystem functions and services are no less important. In other words, the most valuable objects are undisturbed populations and communities with typical (near-optimal) diversity regardless of whether high or low are formal biodiversity indices.

Finally, the optimal biodiversity concept may be an additional approach to resolve the conflict of management goals when using different ecosystem services (trade-off between ecosystem services). It was shown that intensive use of certain provisioning services, especially food, fiber and biofuel production, greatly simplified ecosystem structure. This simplification enhanced certain provisioning services, but reduced others, particularly regulating services (Cardinale et al., 2012). One of the reasons for this trade-off is the different response of biodiversity to ecosystem service management. The optimal biodiversity principle predicts that populations and communities with the optimal diversity provide regulating services in the best way. That is, the management goal for regulating services is to maintain the natural biodiversity values, which are close to the optimal ones. However, the management goal for provisioning services is to maximize sustainable biomass yield. Removal of biomass from natural communities and populations inevitably disrupts their structure and increases mortality in populations. Such impact is similar to the destabilization of the environment. In this case, adaptive trends of biodiversity are as follows: increase in intrapopulation diversity; reduction in species diversity; reduction of total biomass. Exploitative pressure on populations eliminates the first possibility, leaving only the second and third, which are contrary to the management goal for regulating services. Thus, there is a contradiction between biodiversity reaction to management for provisioning and regulating services. This conflict of management goals should be considered in biodiversity valuation and use. If the management priority is to maintain regulating services, the use of provisioning services should be limited in order to preserve the typical (near-optimal) biodiversity.

What indicators may be useful in order to take into consideration both species diversity within communities and intrapopulation diversity? Diversity within communities is measured by widely used indexes of species richness, species diversity and functional species diversity. Intrapopulation diversity can be evaluated as genetic and phenotypic diversity. Modern technologies have generated a wide range of indicators of genetic diversity that includes allelic diversity, allelic and genotypic richness, heterozygosity, nucleotide diversity, percentage of polymorphic loci, genetic variance, heritability (Forsman and Wennersten, 2016; Hughes et al., 2008). However, the most environmentally significant factor is phenotypic diversity. Relationship between genetic and phenotypic diversity is complex and ambiguous. This is in itself requires special investigations. Therefore, in some cases, indicators of phenotypic diversity may be more useful. These include measures of color polymorphism, morphological variability (e.g. body mass or length), reproductive variability (litter sizes, age of sexual maturity), variability of ecological traits, the number ecological (life-history, trophic, seasonal) morphs within a population (Forsman and Wennersten, 2016).

4. Conclusion

1 The initial pattern of the optimal biodiversity values on a landscape is determined by environmental stability and the amount of available resource. Anthropogenic and successional disturbances of the environment, populations and communities push biodiversity away from the optimal state. The general direction of the anthropogenic changes of the environment is destabilization, while disturbance of populations is expressed in reduction of intrapopulation diversity and thus reduces the possibility of populations to adapt to the environmental destabilization. Restoring of near-optimal biodiversity is possible by reduction of anthropogenic changes of the environment, and by regeneration of the typical structure of populations and communities.

2 Species diversity and intraspecific/intrapopulation diversity are inseparable adaptations of communities and species to environmental conditions. Adaptation mechanisms are divided between them. The optimal species diversity allows the most efficient use of available resources. The optimal intrapopulation diversity ensures adaptation of populations to environmental fluctuations and, thus, steady-state (stationary) existence of community as a whole in normally fluctuating conditions. Thus, both species and intrapopulation diversity should be monitored and preserved (restored).

3 The optimal species diversity can be relatively low in unstable or scarce conditions. Despite this, it provides the maximal effectiveness of a community under these conditions. Thus, the criterion for the choice of conservation priorities should be the distance of anthropogenic shift away from the optimal diversity, but not high formal diversity indexes (e.g. species richness).

4 The biodiversity reaction on management for regulating and provisioning services is different. While the first requires conservation of the optimal diversity values, the latter push populations and communities away from the optimal state. Thus, landscape planning should consider the conflict between goals of biodiversity management for different ecosystem services.

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