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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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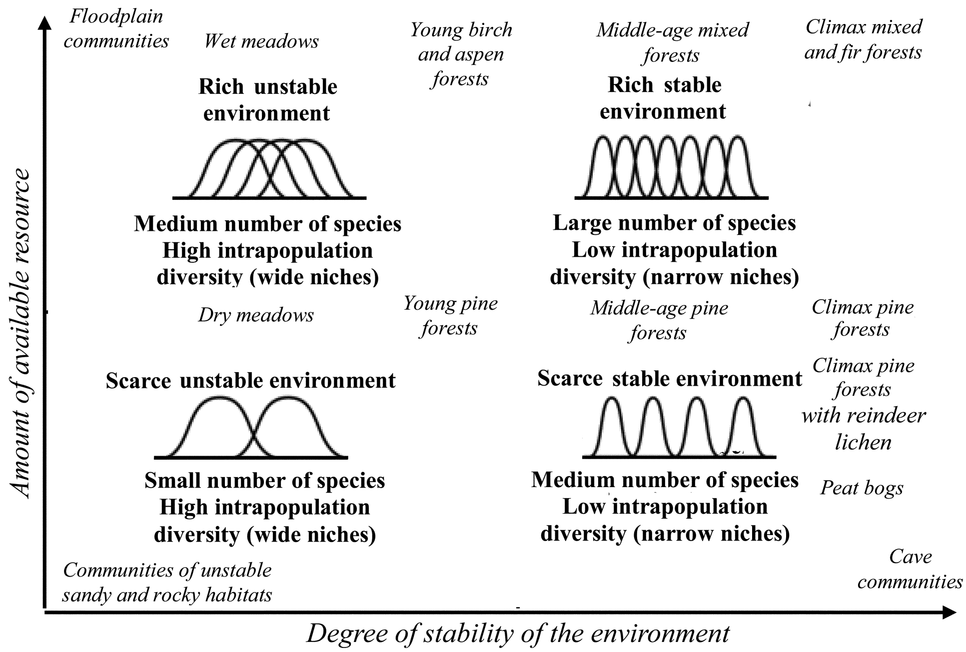

Fig. 1. The expected values of the optimal species and intrapopulation diversity in communities adapted to different environments and examples of communities of the middle part of European Russia.

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