



Letter to the Editor

On ecological modelling problems in the context of resolving the biodiversity paradox



ARTICLE INFO

Keywords:

Individual-based models
Cellular automata
Biodiversity paradox
Competitive exclusion principle
Neutral theory
Quantum mechanics

ABSTRACT

The biodiversity paradox has been a long-standing enigma in theoretical ecology. It emerged as a contradiction between the competitive exclusion principle and the natural species richness. There are two competing ecological theories which try to explain this issue: niche theory and neutral theory. The problem is that both theories are based on nontransparent models which ignore local interactions between individuals and cannot provide an understanding of interspecific competition mechanisms. Mathematical models of complex systems may be of three general types: black-box, grey-box and white-box models. Classical ecological models – Malthusian, Verhulst and Lotka–Volterra models are of black-box type. Black-box models are nonmechanistic. They cannot help to create a mechanistic ecological theory as they do not provide a direct insight into individual-based mechanisms. Here we make some critical notes on the recent attempts to resolve the paradox by black-box and grey-box approaches. We critically discuss a contribution of the neutral theory and the attempts to solve the paradox by methods of the classical quantum mechanics. These attempts are rather ineffective due to the lack of mechanicalness and likely lead to more confusion than clarity in understanding of biodiversity mechanisms. We also discuss our solution to the biodiversity paradox through a verification of the competitive exclusion principle with using the white-box approach to mathematical modelling of competitive coexistence.

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“I can never satisfy myself until I can make a mechanical model of a thing. If I can make a mechanical model, I can understand it. As long as I cannot make a mechanical model all the way through I cannot understand”.

Lord Kelvin (Thomson, 1884)

1. On the paradox of biodiversity

Historically, the biodiversity paradox arose as a contradiction between the competitive exclusion principle and the observed richness of trophically related species – *“The apparent contradiction between competitive exclusion and the species richness found in nature has been a long-standing enigma”* (Sommer, 1999). The debate on this controversy was initiated at British Ecological Society’s symposium on *“The Ecology of Closely Allied Species”* on 21 March 1944 (Anonymous, 1944; Hardin, 1960). A brief definition of the principle was: *“Complete competitors cannot coexist”* (Hardin, 1960).

In theory, according to the competitive exclusion principle, complete competitors cannot coexist, but in practice, there are many examples of such coexistence: tropical rainforest, coral reefs, grasslands, plankton communities (Sommer, 1999). This contradiction has resulted in that *“resolving the diversity paradox became the central issue in theoretical ecology”* (Lehman and Tilman, 1997). The urgent tasks of biodiversity conservation became additional motivation of the long-standing biodiversity debates. As biodiversity of trophically related species is a fact, then the problem of solving the

paradox is reduced to verification of the eligibility of the competitive exclusion principle. Experimental verification of the validity of the competitive exclusion principle is impossible because we always will be suspicious that some experimental factor has not been taken into account – *“There are many who have supposed that the principle is one that can be proved or disproved by empirical facts, among them Gause himself. Nothing could be farther from the truth. The “truth” of the principle is and can be established only by theory, not being subject to proof or disproof by facts, as ordinarily understood”* (Hardin, 1960). Thus, verification of the competitive exclusion principle became a great theoretical challenge for mathematical modelling.

The most well-known model of interspecific competition is the Lotka–Volterra model. This model predicts stable coexistence of two similar species when, for both species, an interspecific competition is weaker than intraspecific one. This interpretation follows directly from the model. However, the further interpretation of this interpretation, known as the competitive exclusion principle has no rigorous justification under itself. Many different formulations of the principle have been offered, but the problem has still remained. The unified neutral theory of biodiversity and biogeography (neutral theory or UNTB) was proposed as an attempt to exit from this theoretical impasse (Hubbell, 2001). Hubbell offered an idea of ecological equivalence of trophically similar species and a controversial solution:

“We no longer need better theories of species coexistence; we need better theories for species presence-absence, relative abundance”

and persistence times in communities that can be confronted with real data. In short, it is long past time for us to get over our myopic preoccupation with coexistence” (Hubbell, 2001).

In fact, the neutral theory proposed to replace the mechanisms of interspecific interactions by statistical predictions of species presence-absence. This way is based on the assumptions which are clearly not true, but that allow to make some predictions. Unreality of the hypothesis of ecological equivalence is obvious and for Hubbell with colleagues, as they assert that “the real world is not neutral” (Rosindell et al., 2012). But an illusion of solving the old mystery of the biodiversity paradox in the form of UNTB has appeared. The controversial character of the neutral theory focused theoretical ecologists’s concentration away from the attention of real ecological problems towards unclear points of the neutral theory: ecological drift, a link between pattern and process, relations of simplicity and complexity in modelling, the role of stochasticity, and others. Real ecological problems, including the study of mechanisms of competitive coexistence, were put on the backburner. The long-standing debates on the biodiversity paradox as “competitive exclusion principle versus natural biodiversity” has been substituted for theoretical debates “neutrality versus the niche” (Whitfield, 2002). Recently in Cell Press Discussion the debates have been continued under the title: “Ecological neutral theory: useful model or statement of ignorance?” (Craze, 2012). The starting statement of the discussion was: “UNTB generates confusion” (Clark, 2012). We agree with Clark that “the dramatic shift in ecological research to focus on neutrality could have a cost in terms of scientific understanding and relevance to real biodiversity threats” (Clark, 2009).

Understanding biodiversity mechanisms is the global research priority. Only a deep knowledge of coexistence mechanisms can allow us to efficiently operate in the field of biodiversity conservation. Such knowledge should be based on mechanistic models. The UNTB is not based on a mechanistic model, – “it is just a statement of ignorance about which species can succeed and why” (Clark, 2009; Clark, 2012). Tilman considered that “Experiments that concentrate on the phenomenon of interspecific interactions, but ignore the underlying mechanisms, are difficult to interpret and thus are of limited usefulness” (Tilman, 1987). Thus, the neutral theory could not solve the biodiversity paradox and in order to solve this problem, it is necessary to create a mechanistic model of species coexistence.

2. Methodological problems

To solve this issue we should have a model based on a mechanistic definition of interspecific competition (Tilman, 1987). Otherwise, we will not be able to overcome limitations of phenomenological approach which hides from us internal functional mechanisms of ecosystems. Only a mechanistic approach will allow us not only to restrain the loss of biodiversity, but to understand what needs to be done to conserve it. And only a mechanistic approach will allow us to verify the competitive exclusion principle and to solve the biodiversity paradox. How to create such a mechanistic model? First, we need to know how to mechanistically model a complex dynamic system. A complex dynamic system may be considered as consisting of subsystems that interact. Interactions between subsystems lead to emergence of new properties, e.g. new pattern formations. Therefore, we should define these subsystems and logically describe their interactions. If we want to understand how a complex dynamic system works, we should understand cause–effect relations and part–whole relations in this system. The causes should be sufficient to understand their effects and the parts should be sufficient to understand the whole. In population studies, the “whole” is an ecosystem with populations of

Table 1
Three general types of mathematical models of complex dynamical systems.

Type of the model	Methods of implementation of the model	Level of mechanistic insight into a complex dynamic system under study
Black-box	Differential equations, matrices, stochasticity	Null
Grey-box	A mix of elements of white-box and black-box approaches	In proportion to a degree of transparency of a model
White-box	Logical deterministic cellular automata	Maximum

competing species and the “parts” are individuals, their intrinsic environment, and interactions between individuals and their immediate environment.

There are three general types of possible models of complex dynamic systems: black-box, grey-box, and white-box models (Kalmykov and Kalmykov, 2015a,b). These three general types of mathematical models of complex dynamical systems we have presented in Table 1.

A level of mechanistic insight into a complex system correlates with a degree of its model’s transparency. Black-box models are completely nonmechanistic and nontransparent because we cannot investigate interactions of their subsystems. We cannot investigate interactions of subsystems of nontransparent models. A white-box model of a complex dynamic system has ‘transparent walls’ and directly shows underlying mechanisms – all events at micro-, meso- and macro-levels of a modelled dynamic system are directly visible at all stages. Logical deterministic cellular automata allow to create white-box models of complex dynamic systems (Kalmykov and Kalmykov, 2015b). A micro-level is modelled by a cellular automata cell. A meso-level of local interactions of micro-objects is modelled by a cellular automata neighbourhood. A macro-level is modelled by the entire cellular automata field. Unfortunately, this simple cellular automata approach is commonly used in the overloaded form, which makes it less transparent. This is achieved by mixing cellular automata with differential equations, matrices and stochasticity. In result we will have a grey-box model of a complex system. A grey-box model is a result of mixing black-box and white-box approaches (Table 1). Grey-box models are diverse and have varying degrees of transparency. We consider that the greater the uncertainty in the model, the less its clarity and its transparency. Stochastic cellular automata models and cellular automata models with embedded differential equations are examples of grey-box models. Differential equations do not allow to model individual-based mechanisms. The degree of transparency of a complex system model depends on how we define space, basic elements of the model and their changes. A model may have a cellular automata field with cells, however, if a change of a parameter of a cell is mediated by differential equations or stochasticity we will get only partially transparent grey-box approach.

Tilman draws attention to the fact that ecologists investigate interspecific competition phenomenologically, rather than mechanistically – “most ecologists have studied competition by asking if an increase in the density of one species leads to a decrease in the density of another, without asking how this might occur” (Tilman, 1987). Phenomenological models and phenomenological mechanisms show what happens with the modelled object on a macro-level but does not show how it happens on a micro-level of individuals. They describe some empirical observations, but have no foundations in mechanisms or first principles. It makes difficult a prediction, generation of new knowledge and creation of new technologies. Basic ecological models are of black-box type, e.g. Malthusian, Verhulst, Lotka–Volterra models (Kalmykov and Kalmykov, 2015b).

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