

# The dark side of theoretical ecology

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Dedicated to the memory of Sir John Maddox<sup>1</sup>

## Abstract

Good science must be clearly transparent in its theories, models and experiments. Earlier David Tilman drew attention to the fact that ecologists investigate interspecific competition phenomenologically, rather than mechanistically. To create a mechanistic model of a complex dynamic system we need to logically describe interactions of its subsystems which lead to emergence of new properties on the macro-level. There are black-, grey-, and white-box models of complex systems. Black-box models are completely nonmechanistic. We cannot investigate interactions of subsystems of such non-transparent model. A white-box model of a complex system has “transparent walls” and directly shows underlined mechanistic mechanisms – all events at micro-, meso- and macro- levels of the modeled dynamic system are directly visible at all stages. Grey-box models are intermediate. Basic ecological models are of black-box type, e.g. Malthusian, Verhulst, Lotka-Volterra models. These models are not individual-based and cannot show features of local interactions of individuals of competing species. That is why they principally cannot provide a mechanistic insight into interspecific competition. To create a white-box model we need a physical theory of the object domain and its intrinsic axiomatic system. On the basis of axiomatic system there is a possibility to logically generate a new knowledge by logical deterministic cellular automata. Understanding of biodiversity mechanisms is the global research priority. Only knowledge of mechanisms of interspecific interactions can allow us to efficiently operate in the field of biodiversity conservation. Obviously that such knowledge must be based on mechanistic models of species coexistence. In order to create a serviceable theory of biodiversity it is necessary to renew attempts to create a basic mechanistic model of species coexistence. But the question arises: Why ecological modelers prefer to use the heaviest black-box mathematical methods which cannot produce mechanistic models of complex dynamic systems in principle, and why they do not use simple and long-known pure logical deterministic cellular automata, which easily can produce white-box models and directly generate clear mechanistic insights into dynamics of complex systems?

Good science must be clearly transparent in its theories, models and experiments. In my research I often remember David Tilman’s great article which draws attention to the fact that ecologists investigate interspecific competition phenomenologically, rather than mechanistically<sup>2</sup>. The article is titled “The importance of the mechanisms of interspecific competition”. It was published in

1987 however it is still relevant for biodiversity science and mathematical modeling of complex systems. It tells about a problem with more than 150 field experiments designed to test for the existence of interspecific competition in natural communities. A reason of the problem was formulated by David Tilman as follows: *“The design of the experiments, though, is a memorial to the extent to which the often-criticized Lotka-Volterra competition equations still pervade ecological thought. The experiments used a nonmechanistic, Lotka-Volterra-based, phenomenological definition of competition: two species compete when an increase in the density of one species leads to a decrease in the density of the other, and vice versa. ... With a few notable exceptions, 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. ... Experiments that concentrate on the phenomenon of interspecific interactions, but ignore the underlying mechanisms, are difficult to interpret and thus are of limited usefulness.”*<sup>2</sup> To design an adequate field experiment we should have a mechanistic model based on a mechanistic definition of interspecific competition.

How to create one such model? First of all we need to know how to mechanistically model a complex dynamic system. A complex system may be considered as consisting of subsystems. Interactions between subsystems lead to emergence of new properties on the macro-level. Thus we should define these subsystems and logically describe their interactions.

Let’s describe what kind of models of complex dynamic systems are possible to create in general. There are three types: black-, grey-, and white-box models (Fig. 1).

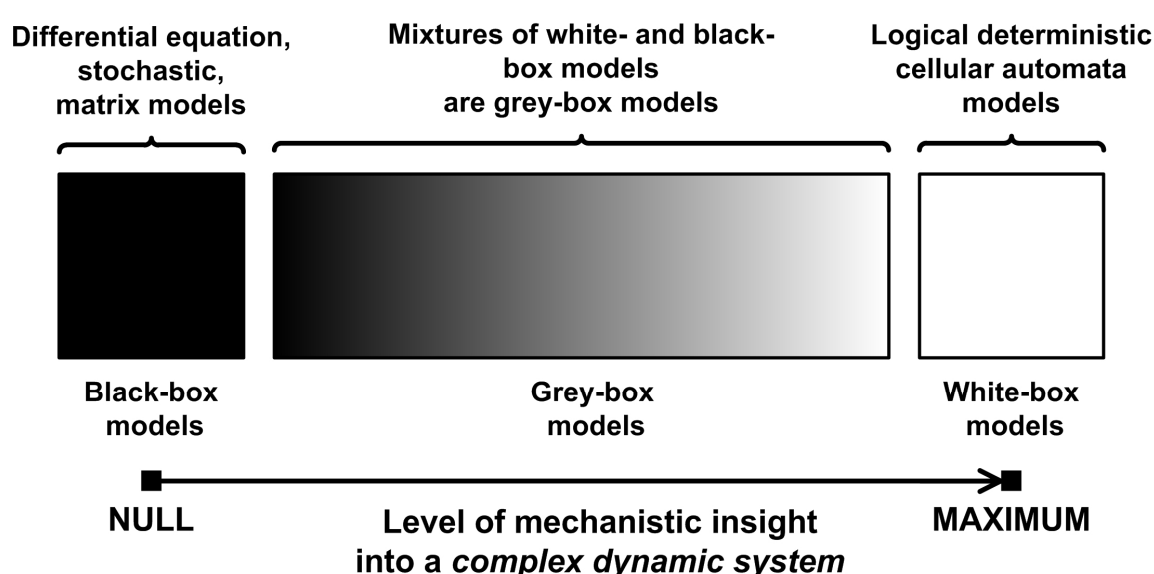


Figure 1. **Three types of mathematical models of complex dynamic systems.**

Black-box models are completely nonmechanistic. We cannot investigate interactions of subsystems of such non-transparent model. A white-box model of

complex dynamic systems has “transparent walls” and directly shows underlined mechanistic mechanisms – all events at micro-, meso- and macro- levels of the modeled dynamic system are directly visible at all stages<sup>3</sup>. Grey-box models are intermediate. Basic ecological models are of black-box type, e.g. Malthusian, Verhulst, Lotka-Volterra models. These models are not individual-based and cannot show features of local interactions of individuals of competing species. That is why they principally cannot provide a mechanistic insight into interspecific competition.

To create a white-box model we need a physical theory of the object domain. A core of a scientific theory is axiomatic system. It is a system of ideal objects of the domain under study. The most familiar axiomatic system is Euclidean geometry that investigates the relations between ideal spatial figures. If a scientist physically understands how a complex dynamic system works then he can try to formulate an axiomatic system. When scientists verify a theory first of all they should verify its axioms. On the basis of axiomatic system there is a possibility to logically generate a new knowledge by logical deterministic cellular automata. However, if at least one axiom is inadequate then the theory and corresponding models are inadequate. I question whether theoretical ecology has such physical theories and mechanistic models.

Stephen Hubbell in his Unified Neutral Theory of Biodiversity (UNTB) in fact refuses a mechanistic understanding of interspecific competition: “*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*”<sup>4</sup>. However, he admits that “*the real world is not neutral*”<sup>5</sup>. It means that the UNTB has wrong axiomatic system. But an illusion of a new knowledge has appeared. I agree with James 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*”<sup>6</sup>. The neutral theory looks like explanation of the obscure by the more obscure.

Understanding of biodiversity mechanisms is the global research priority. Only knowledge of mechanisms of interspecific interactions can allow us to efficiently operate in the field of biodiversity conservation. Obviously that such knowledge must be based on mechanistic models of species coexistence. Also I agree with James Clark that as the UNTB is not based on really mechanistic models, - “*it is just a statement of ignorance about which species can succeed and why*”<sup>6,7</sup>.

In order to create a serviceable theory of biodiversity it is necessary to renew attempts to create a basic mechanistic model of species coexistence. But the question arises: Why ecological modelers prefer to use the heaviest black-box mathematical methods which cannot produce mechanistic models of complex dynamic systems in principle, and why they do not use simple and long-known pure

logical deterministic cellular automata, which easily can produce white-box models and directly obtain clear mechanistic insights into dynamics of complex systems?

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## References

- 1 Maddox, J. The dark side of molecular biology. *Nature* **363**, 13-13, doi: <http://dx.doi.org/10.1038/363013a0> (1993).
- 2 Tilman, D. The importance of the mechanisms of interspecific competition. *The American Naturalist* **129**, 769-774, doi: <http://dx.doi.org/10.1086/284672> (1987).
- 3 Kalmykov, L. V. & Kalmykov, V. L. Verification and reformulation of the competitive exclusion principle. *Chaos, Solitons & Fractals* **56**, 124-131, doi: <http://dx.doi.org/10.1016/j.chaos.2013.07.006> (2013).
- 4 Hubbell, S. P. *The unified neutral theory of biodiversity and biogeography*. (Princeton University Press, 2001).
- 5 Rosindell, J., Hubbell, S. P., He, F., Harmon, L. J. & Etienne, R. S. The case for ecological neutral theory. *Trends in Ecology & Evolution* **27**, 203-208, doi: <http://dx.doi.org/10.1016/j.tree.2012.01.004> (2012).
- 6 Clark, J. S. Beyond neutral science. *Trends in Ecology & Evolution* **24**, 8-15, doi: <http://dx.doi.org/10.1016/j.tree.2008.09.004> (2009).
- 7 Clark, J. S. The coherence problem with the Unified Neutral Theory of Biodiversity. *Trends Ecol Evol* **27**, 198-202, doi: <http://dx.doi.org/10.1016/j.tree.2012.02.001> (2012).