



Toy models for macroevolutionary patterns and trends



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ABSTRACT

Many models have been used to simplify and operationalize the subtle but complex mechanisms of biological evolution. Toy models are gross simplifications that nevertheless attempt to retain major essential features of evolution, bridging the gap between empirical reality and formal theoretical understanding. In this paper, we examine thirteen models which describe evolution that also qualify as such toy models, including the tree of life, branching processes, adaptive ratchets, fitness landscapes, and the role of nonlinear avalanches in evolutionary dynamics. Such toy models are intended to capture features such as evolutionary trends, coupled evolutionary dynamics of phenotype and genotype, adaptive change, branching, and evolutionary transience. The models discussed herein are applied to specific evolutionary contexts in various ways that simplify the complexity inherent in evolving populations. While toy models are overly simplistic, they also provide sufficient dynamics for capturing the fundamental mechanism(s) of evolution. Toy models might also be used to aid in high-throughput data analysis and the understanding of cultural evolutionary trends. This paper should serve as an introductory guide to the toy modeling of evolutionary complexity.

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1. Introduction

The concept of evolution by natural selection has enabled evocative questions ever since it was introduced by Charles Darwin and Alfred Russell Wallace (Darwin and Wallace, 1858). Application of the concept has two basic aspects: 1) did evolution actually occur 2) if so, how? Creationists often conflate these two points in an attempt to deny the entire process (Seckbach and Gordon, 2008). Here we accept evolution as an established fact and focus on the second question, asking whether or not there are broad macroevolutionary trends that apply to the entire tree of life. While some people argue that there are mechanisms for increases in the complexity of life over time (Gordon, 1999; McShea and Brandon, 2010), findings from specific contexts can suggest otherwise. We demonstrate here that models which optimally balance predictive power and descriptive sparsity have the potential to uncover these overarching trends. To do this, we must go a bit beyond the normal scope of evolutionary dynamics and also consider ecological and behavioral contributions.

Any theory that attempts to encompass all 8.7×10^6 extant species (Mora et al., 2011), their ancestors, and extinct lineages must necessarily leave out many details. Nevertheless, phenomena such as convergent evolution provide clues that certain themes recur, despite the contingencies of evolution (Hengeveld, 2005; Morris, 2009). Here we consider models that greatly oversimplify phenomenology in an attempt to characterize certain motifs or themes in evolutionary change. Such themes of evolutionary change include the dynamics of state, the variety of rates, shifts in variant frequencies, and specific mechanisms (e.g., physiological, developmental). Because these models focus on components of the evolutionary process which may or may not provide grand explanations they can explicitly be called “toy models” of evolution. Calling a concept a “toy model” in no way denigrates it. There are over 1300 papers titled “toy model” in the scientific literature, some of them on various aspects of biological evolution (Aldous, 1995; Aoki, 1986; Ben-Avraham et al., 2007; Graham and Oppacher, 2007; Meszéna et al., 1997; Polanco et al., 2013; Szathmáry, 1994; Vandewalle and Ausloos, 1996; Vargas et al., 1999). We therefore hope that those authors whose models we classify this way will consider themselves in good company.

In what ways do toy models relate to broader theoretical models, and how can this help us to understand macroevolution? Toy models provide a simple and intuitive way to summarize what are often complex and subtle evolutionary dynamics. As

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with phylogenetic relationships, they may be viewed as parsimonious constructs. Like phylogenetic trees, toy models emphasize some aspects of evolution (common ancestry) over others (gene flow, hybridization, lateral gene transfer, symbiosis or convergent evolution). Toy models are meant to provide conceptual unification using a simplified context, much like animal models with unusual traits (e.g., the regenerative capabilities of *Planaria* and axolotls) are used to advance experimental science. The use of abstract models to approximate the subtleties of macroevolutionary trends is consistent with mathematical logic (Suppe, 1989), but also allows us to incorporate sets of exemplary objects into this axiomatic structure (abstraction). So, in general, models help us to realize theoretically predicted structure. In particular, toy models focus on specific equations or predicted mathematical relationships.

Models (and more specifically toy models) are also essential to acquiring and organizing knowledge (organization). Models are investigative tools that utilize surrogate reasoning (Swoyer, 1991), which is a key feature of toy models. According to the semantic view of theories, models can either be isomorphic or similar to the phenomenon at hand (Frigg, 2006). In the case of toy models, isomorphic modeling is the predominant approach. For example, brute-force modeling techniques such as those that might describe a unified process of evolution would have too many free parameters to be of much use. In addition, using a multiplicity of smaller models allows us to account for complexity and all of its contradictory demands (Levins, 1966). Thirdly, toy models allow us to build a so-called prepared description of a problem without moving to a formal set of mathematical statements or propositions (level of representation). According to Cartwright (Cartwright, 1993), part of applying an empirically based theory to data involves moving from an unprepared description of a system to a prepared description of that system. In this case, toy models provide just the right amount of description.

Toy models provide us with a number of advantages over formal predictive models or biological laws. For one, toy models offer a tool for quantitative reasoning. According to Gunawardena (Gunawardena, 2014), this is an often missing piece of modern biological empiricism. Like theories, toy models give us a logical, quantitative structure upon which to organize conceptual advances. Yet toy models also fill the gap between the phenomenology of data and predictive models so important to revealing structure and trends in the data (Gunawardena, 2014). This is particularly true when the phenomenon at hand is poorly understood. In this sense, toy models can give us a perspective which is greater than mere reductionism but also without the formality of a theoretical framework. In an ideal context, toy models provide a set of first principles for understanding the underlying features of macroevolution.

A toy model is supposed to represent and structurally or functionally capture some aspect of the biological process, with no presumptions about how it maps to empirical observation. This allows us to base the structure of any given toy model on biological trends, mathematical consistency, or a combination of both. Ideally, this should allow for a logical structure to be inferred without encountering the problem of overfitting. Toy models are intentionally overly simplistic, as even the simplest toy models should be able to describe major features of the evolutionary process. Whether or not these models fit every case study is beside the point. The goal is to potentially uncover broad trends in the macroevolutionary process. Thirteen distinct kinds of toy model will be considered:

1. The fitness landscape
2. The Red Queen hypothesis
3. Hardy–Weinberg equilibrium
4. Nonlinear avalanches and evolutionary trends
5. Intentionally false models to capture evolutionary transience
6. Ladders and spectra, toy models as scenarios

7. The tree of life
8. Adaptive ratchets and differentiation trees
9. Bio-phenomenological–mathematical hybrid models
10. Coupled avalanches and evolutionary dynamics
11. Self-organized adaptive change
12. Grounded branching processes
13. Daisyworld and predator/prey models

These models were selected to incorporate various aspects of macroevolution. We decided to be as inclusive as possible, presenting toy models that approximate and explain evolutionary dynamics, ecological and behavioral dynamics, adaptive change, the role of phylogeny, branching and development, and the distinction between evanescent and longer-lasting changes. Some of our candidate toy models have been previously introduced as ecological and evolutionary hypotheses, while others are introduced by us de novo through synthesis of the existing literature. With this breadth of potential toy models, we also explore several subthemes, including the role of evolutionary constraint, common ancestry, relationships between genotype and phenotype, and mathematically-inspired biological hypotheses. This allows us to not only explore the breadth of possible models, but to address their biological plausibility as well.

1.1. The fitness landscape

A toy model often used to assess the relative fitness of individuals and populations over time is the fitness landscape. Fitness landscapes were first proposed by Wright (Wright, 1932) as a quasi-geographical approach called “surfaces of selective value” (Pigliucci, 2008c). The landscape metaphor was chosen to represent changes along a gradient. Fitness landscape models were later advanced to include more explicit information about the population’s location in genotype/phenotype space (Østman and Adami, 2014). The goal of a fitness landscape is to map variations in fitness across all possible genotypic/phenotypic configurations to a low-dimensional (e.g., three-dimensional (3D)) topology. Fitness landscapes are toy models in the sense that all possible contributions to fitness are represented on a finite topology in a reduced number of dimensions. While fitness landscapes do not precisely represent adaptive outcomes, such highly simplified models are still useful for understanding when a given population has reached a fitness valley or optimum. Increasing the resolution of these spaces (e.g., adding dimensions) can help to clarify the location and true constraints on a given adaptive path (Gavrilets, 2004).

The overall ruggedness of a fitness landscape also determines the challenges posed to a population as it adapts to environmental challenges. Kauffman (Kauffman, 1993) suggests that the more rugged a fitness landscape is, the harder it is for a population to adapt to new equilibria. On the other hand, a rugged fitness landscape might also force a population to make large-scale adaptations in a manner not possible under smooth landscapes. Fitness valleys can also provide a challenge as well as an opportunity. For example, work on the evolution of Batesian mimicry (Hilaro and Gogarten, 1993) suggests change (e.g., punctuated evolutionary processes) may be the mechanism by which entire populations cross these fitness valleys (Leimar et al., 2012). However, fitness valleys pose a challenge to stepwise mutation models of evolution, instead lending support to more complex mechanisms such as epistasis (Weissman et al., 2009).

Sewall Wright deliberately grouped all “gene combinations in two dimensions instead of many thousands”, with fitness as a third dimension (Fig. 1) (Wright, 1932), fully realizing: “The two dimensions . . . are a very inadequate representation of such a field”. Increasing the number of gene dimensions, as via gene duplication, can permit evolution to avoid the valleys between

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