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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 (Hilario 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
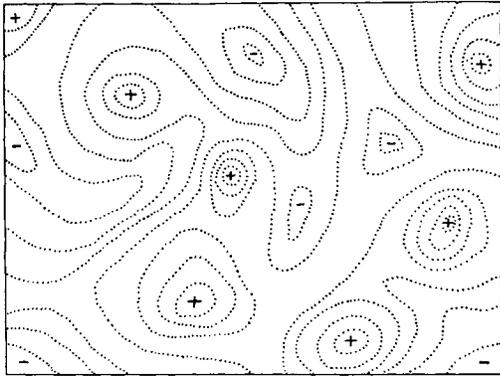
Fig. 1. Sewall Wright's original toy model "representation of the field of gene combinations", with contour lines "with respect to adaptiveness". From (Wright, 1932).

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 peaks (Gordon, 1994), which can be taken as a flaw in the fitness landscape toy model (Gavrilets and Gravner, 1997). However, others suggest that the model is still robust (Østman, 2014; Østman and Adami, 2014).

While fitness landscapes are an appealing and intuitively powerful tool for understanding fitness dynamics, the actual utility of these models thus might be limited. Pigliucci (Pigliucci, 2008a) argues that as a toy model, fitness landscapes may not always provide a faithful view of the evolutionary process. This point is also made by (Kaplan, 2008), who argues that the model also may result in conceptual difficulties with respect to an unfolding evolutionary process. This can be overcome by representing higher-order features on the fitness landscape, such as epistasis (Beerenwinkel et al., 2007). However, this additional complexity reduces conceptual clarity. Nevertheless, fitness landscapes provide both a heuristic indicator and common context for how individuals and populations adapt to a changing environment.

1.2. The Red Queen hypothesis

"Now here, you see, it takes all the running you can do, to keep in the same place. If you want to get somewhere else, you must run at least twice as fast as that!", quoting the Red Queen (Carroll, 1875).

A toy model that helps to explain co-evolutionary dynamics is the Red Queen hypothesis (Ridley, 1993; Stenseth and Smith, 1984). Adapted from a literary metaphor, the Red Queen model attempts to capture co-evolutionary arms races between competing organisms and/or populations (Dasgupta et al., 2005). Originally devised as a model to explain the evolution and stable maintenance of biparental sex (Green and Mason, 2013), the Red Queen model can more generally explain why and how adaptation accelerated over evolutionary time (Barnosky, 2001; Markov, 2000). As the Red Queen tends to outperform alternate hypotheses of co-evolution (Tobler and Schupp, 2008), we can say that the Red Queen serves as a robust and widely-applicable toy model (Benton, 2010; Lewin, 1985). As a special instance of zero-sum game theory (van Valen, 1973), the Red Queen model provides an opportunity for all plausible co-evolutionary outcomes in a biological system to be characterized (Marshall and Tokumine, 2004). The Red Queen model seems to fit the data for systems as diverse as bacterial-nematode coevolution (Morran et al., 2011), extant ecosystems

(Castrodeza, 1979), paleospecies (Benton, 1990), and digital organisms (Wilke, 2003). The Red Queen model may also allow us to better understand the rapid evolution of highly complex systems of traits (Robson, 2005).

1.3. Hardy–Weinberg equilibrium

The Hardy–Weinberg equilibrium (HWE) (Hardy, 1908; Weinberg, 1908) is a toy model that allows us to characterize evolution as a change in allele frequencies. In its basic form, HWE describes the frequency of a two-locus, monogenic trait from phenotypic observations. HWE is based on observations made at equilibrium, or when the forces of evolution are not actively changing allele frequencies and there is no intragenic recombination (Andrews, 2010). Equilibrium can also be defined as sustained allelic proportions (Mayo, 2008), which provides us with information about which allelic states contribute to a phenotype. Due to this reliance on equilibrium, the HWE model is an example of incomplete evolutionary change. While no toy model can completely encompass the entirely of an evolutionary trajectory, HWE serves as a discontinuous model of evolutionary dynamics, only providing information about distinct equilibrium points rather than temporal motifs or other explicitly dynamical components. If this is the case, how does HWE provide information about the evolutionary process? HWE is concerned with the heterogeneity of a population, which is explicitly linked to potential rather than actual evolutionary change. One example of this potential for change is the concept of a population's evolvability (Pigliucci, 2008b; Wagner, 2005), which is not explicitly captured by the other toy models presented here.

As an incomplete model of dynamics and potential model for evolvability, tests of HWE can be expanded to infinite site, infinite allele models (Kimura and Crow, 1964), which can describe the most complex traits from simple phenotypic observations. Yet at its core, the HWE model is a sparse but fairly complete representation of evolutionary equilibrium. In this way, we can capture the static properties of a population (Stark and Seneta, 2013). In genetic association studies, a departure from Hardy–Weinberg equilibrium can be used to better understand the genetic structure of common diseases (Wittke-Thompson et al., 2005). Such deviations can also allow us to make predictions about the action of selection and drift on equilibrium allele frequencies (Lachance, 2009). As we will see in the following sections, because there is no explicitly dynamic component to the HWE, it also lacks the historical information of ladder- and tree-like models.

1.4. Nonlinear avalanches and evolutionary trends

To better characterize evolutionary trends, we can turn to a toy model that incorporates nonlinearities over time. Darwin's concept that " . . . it is far more probable that each form remains for long periods unaltered, and then again undergoes modification" did not appear until the 4th edition of Origin of Species (Clark, 1984; Darwin, 1866). It was later rediscovered and named "punctuated equilibrium", i.e., stasis followed by evolutionarily rapid change (Eldredge and Gould, 1972; Gould, 2002; Gould and Eldredge, 1977; Løvtrup, 1981; Penny, 1983, 1985; Rhodes, 1983). One toy model that captures unevenly distributed changes in the evolutionary process is the sandpile model (Bak and Chen, 1991). The sandpile model of self-organized criticality (SOC) is a physical model that generically characterizes scale-free, stochastic dynamics (Bak and Sneppen, 1993). The concept is straightforward: adding sand grains to a sandpile sequentially will lead to displacements from the pile (Fig. 9A–B). The distribution of these displacements tends to be uneven over time, and is characterized by many small and a few large avalanches (Fig. 9C–D).
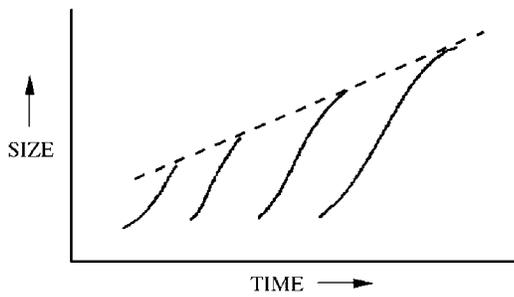
Fig. 2. "If we now compare the long-term, maximum size changes that alter very slowly over billions of years and the sizechanges within groups that follow Cope's law, there is an important message. The maximum sizes are each attained from a different, major group of organisms: for plants they are, for instance, lycopods, gymnosperms, and angiosperms; for animals they are trilobites, eurypterids, fish, amphibians, dinosaurs, and mammals. These maximum sizes were reached by progressive size increases within each group. This means that overall size change during evolution is a result of a series of rises of different successive taxons". From (Bonner, 1988) with permission of Princeton University Press [requested]. (Bonner, 1988) One of us has called this "Bonner's law" (Gordon, 1999).

The avalanche model of punctuated evolutionary change allows us to understand the role of critical phenomena in evolution. For example, the dynamical processes that lead to macroevolution might be characterized as critical phenomena (Sole and Bascompte, 1996). This observation is based on the concept of universality, which represents a class of dynamics between random and highly-ordered. It is universality which might explain how the quasi-randomness of evolution can be highly subject to historical constraints. The historical context of avalanches (e.g., punctuations) in evolution can also be better understood using the sandpile model. Bak and Paczuski (Bak and Paczuski, 1995) have shown that previously uncoupled events become correlated during critical periods of evolution. These types of nonlinear changes contribute to the emergence of macroevolutionary diversity, and are well within the scope of representation through such a toy model.

Likewise, there is a superficial relationship between punctuated equilibrium (Gould and Eldredge, 1977) and SOC dynamics. In this case, species undergo long periods of stasis with bursts of rapid and substantial change. The SOC model can also act as a model of bursty changes in allele frequencies (e.g., biological

variants in a population) over time. Thus, the SOC model can not only produce temporal variation, but also sensitivity for different scales of effects wrought by initial changes in variant frequencies. Mass extinction modeling includes bad luck and "bad" genes and has been examined from the point of view of SOC (Tokita and Yasutomi, 1999).

Macroevolutionary trends have often been modeled as a sequence of catastrophic events, such as asteroids hitting the earth, volcanoes, climatic heating or cooling, changes in atmospheric composition, and other factors thought to lead to mass extinctions (Prothero, 2009). Of course, catastrophes occur on all scales and thus are analogous to avalanches and can be represented by the sandpile model of evolution. For example, stochastic runs of epidemics can cause population declines ranging over orders of magnitude in effect (Gordon and Tyson, 1993), and old toy models, such as Cope's law which suggests that size increases in a group (Raia and Fortelius, 2013), have been compounded by Bonner (Bonner, 1988) into cycles of organism size increase and collapse, with the maximum size achieved in each cycle increasing (Fig. 2). While this is a rough empirical observation, the implication is that there is an underlying mechanism (Tokita and Yasutomi, 1999).

1.5. Intentionally false models to capture evolutionary transience

Toy models that are intentionally false may allow us to better characterize transient evolutionary changes. In such cases, a given toy model would prioritize functional accuracy over structural accuracy. False models (Wimsatt, 1987) have been shown to provide an understanding of highly complex systems by intentionally ignoring parts of that system which are not well understood. One example of this involves modeling the evolution of phenotypes while intentionally ignoring structure of the underlying genotype (Weissing, 1996). Paradoxically, and perhaps because the dynamics of genotype are more important than its structure, this perspective can provide a more unbiased dialogue between phenotype and genotype (Fig. 3). A form of this toy model has been proposed in Hammerstein's (Hammerstein, 1996) streetcar model in which evolving populations make a number of temporary stops that represent transient equilibria. At the end of the evolutionary process, a final stop is made that represents the
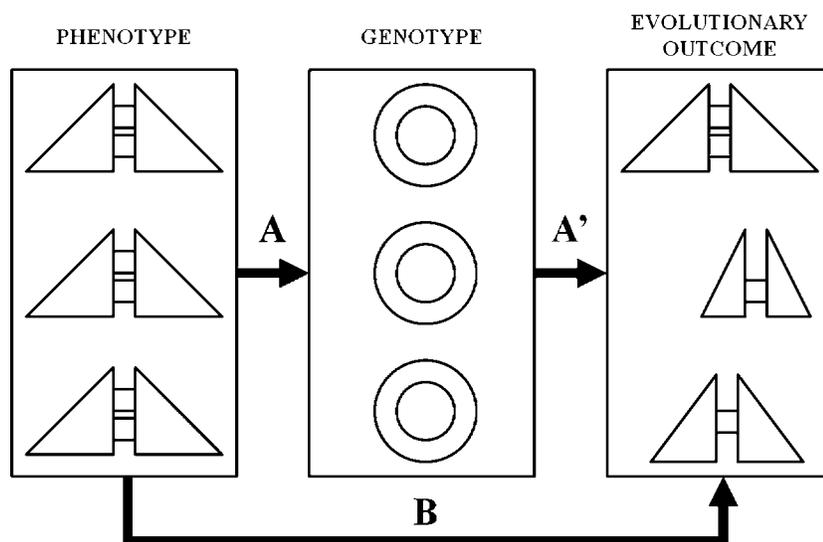
Fig. 3. Models of phenotypes without genotypes, which constitutes an intentionally incomplete or false toy model of organismal evolution. A,A′: conventional path from ancestral to derived phenotype (via genotypic change), B: exclusively phenotypic model of evolutionary change (excluding genotype).
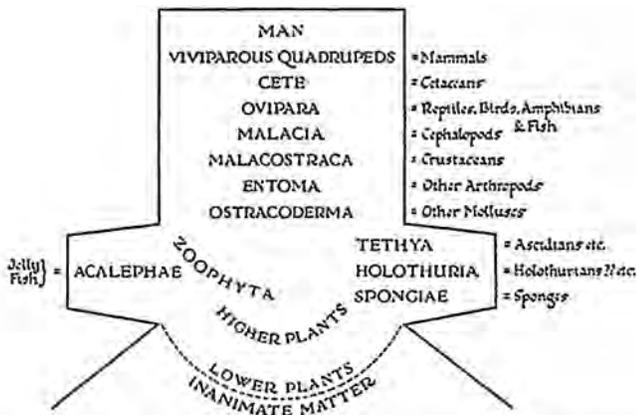
FIG. 18. The *Scala Naturae* or "Ladder of Life" according to the descriptions of Aristotle.

Fig. 4. Aristotle's one-dimensional scale of life. From (Singer, 1931) with permission of Oxford University Press. Supernatural beings were added above Man in the Middle Ages (Kuntz and Kuntz, 1987; Lovejoy, 1936).

action of phenotypic selection and a more persistently stable equilibrium (Marrow et al., 1996).

1.6. Ladders and spectra, toy models as scenarios

Toy models can also be used to build various scenarios of potential evolutionary schemes. As in the case of intentionally false models, such scenarios need not be epistemologically complete. The ladder of life is an ancient concept of a linear hierarchy in the universe. Beginning with Aristotle (Fig. 4) and continuing through medieval times, this worldview was overthrown by Darwinian evolution. As a metaphor, however, the ladder of life is still very much with us. Even though the notion is flawed, it still acts as an organizing principle for classification. We give two examples that come about when complexity is conceived as a scalar, resulting in a one-dimensional (1D) model for evolution.

Stephen J. Gould argued against scalar progression in evolution by suggesting that there is a "wall of complexity" against which life continues to bounce as organisms randomly mutate (Gould, 1993). That "wall" he regarded as the simplicity or minimal complexity of a bacterium (cf. "minimal genomes" (Venter, 2011)). Gould summarizes this idea in the form of what

we would call a toy model, which is equivalent to a 1D random walk on a half-line with a reflecting boundary at this minimal complexity. His conclusion is heavily dependent on two assumptions: that there is a 1D (scalar) measure of complexity and that movement along this coordinate is an unbiased random walk. Indeed, under these assumptions, in Gould's model the probability of return to the origin of minimum complexity for any lineage of creatures is 1. However, if we grant that creatures are multidimensional then this toy model fails (Gordon, 1999). In 2D the probability of return to the origin remains 1, but in 3D it drops to 35% (Feller, 1968) and keeps going down for higher dimensions (Pólya, 1921; Weisstein, 2014). In other words, for evolution that occurs in three or more parameters, there is no wall of complexity. Thus the purpose of Gould's 1D toy model, to "prove" that evolution is not progressive, fails because this particular model does not capture the essence of random walk models, let alone other factors relevant to evolution.

The failure of a single instance of 1D toy models does not necessarily condemn all 1D models of evolution to the theoretical dustbin. We have proposed a 1D model for evolution based on a specific scalar complexity measure: "the suggestion to measure genetic complexity by the length of functional and non-redundant DNA sequence" in a genome (Sharov and Gordon, 2013).

The American Museum of Natural History houses a 100-foot long installation called the Spectrum of Life (American Museum of Natural History, 2014). The Spectrum of Life is a way to model a representative sample of biodiversity from across 3.5 billion years and 1500 species. The point of such 1D representations is to provide broad generalizations about scale and process. Unlike the ladder of evolution, the spectrum provides no inherent information about direction. Unlike the tree of life, the spectrum does not organize taxa with respect to common ancestry. Much like the ladder of life, however, the Spectrum of Life thereby conveys somewhat misleading evolutionary information.

As models of potential alternative evolutionary hypotheses, ladders and spectra can define very broad trends in the evolutionary process which do not explicitly involve descent with modification. The question then becomes the extent to which these alternative hypotheses can uncover unexplained phenomena in the scope of observed biodiversity. Models such as these, organized around a single axis rather than being explicitly 1D, can uncover key relationships and unanswered questions more reliably than a more formal model.
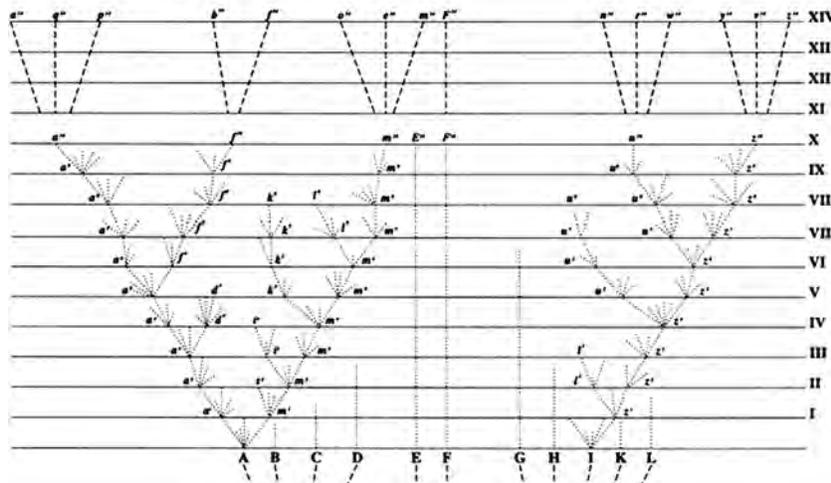

Fig. 5. Darwin's published tree of life (Darwin, 1859).

1.7. The tree of life

Toy models can also help us reconstruct evolutionary relationships from combinatorial ambiguity. While toy models such as the tree of life are better than intentionally false ones, they also require a more complete understanding of the underlying data. For example, Darwin's tree (or branching bush) of life (Fig. 5) is superior to the ladder metaphor in a number of ways. It makes explicit the hypothesis that all species descended from a common ancestor, and that common ancestry relies on the presence of a single, universal ancestor. However, Darwin saw even further than this, explicitly formulating what we now call punctuated equilibrium and recognizing what we have recently labeled as the fractal nature of the phylogenetic tree (Darwin, 1859, 1866). It is worth quoting his original language to see his prescient thinking, which did not catch on until more than a century later.

On punctuated equilibrium, or stasis alternating with rapid evolution:

"But I must here remark that I do not suppose that the process ever goes on so regularly as is represented in the diagram (Fig. 5), though in itself made somewhat irregular, nor that it goes on continuously" (Darwin, 1859) . . . "; it is far more probable that each form remains for long periods unaltered, and then again undergoes modification" (Darwin, 1866).

This may be interpreted as Darwin recognizing the multiscalar, fractal nature of the tree of life:

"I see no reason to limit the process of modification, as now explained, to the formation of genera alone" (Darwin, 1872).

The concept of self-similarity awaited the later work of Cantor (Cantor, 1883; Wikipedia, 2014a) and fractals came nearly a century later (Mandelbrot, 1977). Branching, dendritic structures have been likened to the Cantor set (Williamson and Saigal, 1996). The scale independence or fractal nature of evolution has been proposed a few times since Darwin (Chaline, 2010; Gordon, 1992, 1999; Green, 1991; Leroi, 2000; Nottale et al., 2002), albeit with different mechanisms proposed as the basis of the self-similarity.

Darwin's tree of life model had a major implication: that all life might be derived from a single organism, which we now call the "last universal common ancestor" (LUCA) (Wikipedia, 2014b). As we struggle to figure out the origin of life, we realize that the first protocells preceding LUCA may have been a heterogeneous lot (Adamala and Szostak, 2013), indeed making the tree of life a toy model (unless we figuratively were to add "roots"). Even this caveat was recognized by Darwin:

" . . . probably all the organic beings which have ever lived on this earth have descended from one primordial form, into which life was first breathed . . . . There is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one . . . " (Darwin, 1859).

But his toy model has had many uses and continues as the tree of life internet database (Maddison and Schulz, 2014), which can now be visualized explicitly in fractal form (Rosindell and Harmon, 2012).

Darwin unfortunately missed either knowing about or understanding Mendel's work (Galton, 2009), delaying our conceptions of the relationship between genetics and evolution. He apparently also missed the contemporary development of the concept that lichens are symbionts (Sapp, 1994), which as distinct compound organisms messed up his tree-like toy model for evolution (Fig. 5). We now understand that the "tree" of life has many anastomoses. While generally limited (Zhaxybayeva and Doolittle, 2011), the relative importance of endosymbiosis, horizontal/lateral gene transfers, and whole genome transfers are being thrashed out in the scientific literature (Bowler et al., 2008; Christin et al., 2012; Gladyshev et al., 2008; Hart and Grosberg, 2009; Keeling and Palmer, 2008; Margulis, 2006; Margulis et al., 1999; Ragan, 2009; Sapp, 2012; Sawyer, 2012; Williamson, 1992, 2003; Yu et al., 2003). Hybridization events between closely-related taxa (Koblmüller et al., 2007; Linder and Rieseberg, 2004; Xu, 2000) also create an opportunity for reticulate connections between branches. Despite their infrequency in the history and diversity of life, these horizontal connections change phylogenetic relationships from a tree of life to a graph-theoretic structure called a "reticulate" web (Makarenkov and Legendre, 2004). All of the anastomoses are represented as horizontal vectors ("reticulate events") placed on an otherwise vertically branching structure (Doolittle, 1999). It is certainly not a tree in the graph theory sense, though the term "network" (Ragan, 2009) is too general. Some later conceptions (such as Fig. 6) are accurate in depicting the reticulate events as being perpendicular to the otherwise branching, tree-like structure.

1.8. Adaptive ratchets and differentiation trees

While trees and networks are good at defining common ancestry and other genealogical relationships, toy models are also needed to describe both the adaptive and conserved features of a population in a small number of dimensions. One popular model is a ratchet (Gordon, 1999; Lukeš et al., 2011). Adaptive ratchets are models that are capture circumstances when the scope of variation is selectively constrained to a single degree of freedom (Alicea, 2013). These
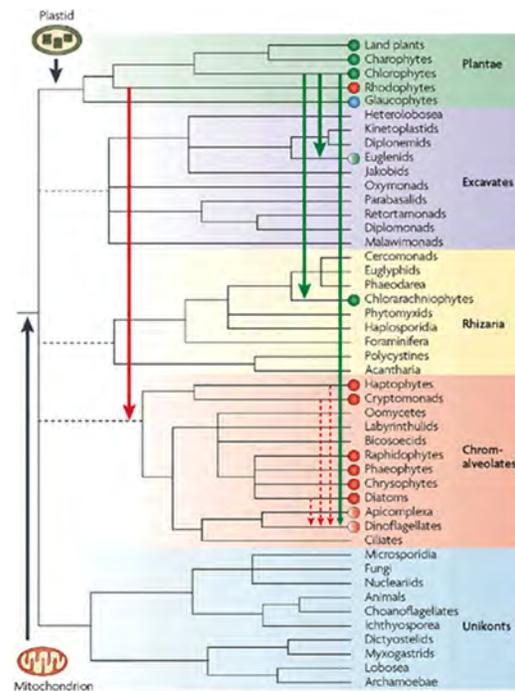
Fig. 6. The major bifurcations and reticulations in eukaryotic evolution, represented by vertical arrows placed across an otherwise tree-like representation of the phylogenetic tree. "Major endosymbiotic events that led to the origin and spread of mitochondria and plastids are shown as vertical arrows. Black [vertical] solid arrows indicate the primary endosymbioses at the origin of mitochondria and plastids. Red and green arrows indicate the movement of red or green plastids, respectively, by secondary (solid arrows) and tertiary (dashed arrows) endosymbiosis" (Keeling and Palmer, 2008), with permission of Nature Publishing Group. Events not shown include incorporation of viral and eukaryotic genes and genomes. For black and white version, red arrows are the following: diatoms to dinoflagellates, cryptomonads to dinoflagellates, and haptophytes to dinoflagellates (all dashed); rhodophytes to stem of chromalveolates clade (solid). Green arrows are the following: chlorophytes to chlorarachniophytes, chlorophytes to euglenids, chlorophytes to dinoflagellates (solid). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

constraints are not necessarily guided or supervised, but rather put in place by natural limitations such as the evolvability of a lineage (Pigliucci, 2008b; Wagner, 2005) or prior evolutionary history. Conveniently, ratchets offer a means to reduce these complex relationships to a simple conceptual mechanism.

Conceived of in this way, evolutionary variation can be constrained in specific ways. When confronted with an ever-changing environment, the ratchet generally does not provide an adaptive advantage to an organism or population. However, there is some evidence that genetic variation can be selected upon or constrained in a directional manner. For example, the rates of forward and reverse mutation may differ by an order of magnitude (Lieb, 1951). When this is coupled with a static environment, a genetic ratcheting mechanism can result in directional evolution. There is no going back to a previous evolutionary configuration (Gould, 1970). This is what makes the adaptive ratchet the ideal toy model for investigating the potential of strongly directional changes in gene frequencies and traits in a candidate population.

Can we also investigate such changes that involve developmental or even genealogical mechanisms? Differentiation trees are developmental versions of the adaptive ratchet that approximate the differentiation of tissues in organisms (Gordon, 1999). Differentiation trees also incorporate the features of a tree-based toy model, and describe variation as being sequentially constrained by evolution in the course of developmental events. Differentiation trees are built upon the assumption that differentiation is a binary event or bifurcation, in which cells in each embryonic tissue become one of two new kinds (tissues) of cells. At each step this is accomplished by a wave of cytoskeletal contraction that is transmitted through a portion of the cells, triggering them to differentiate in one direction, and a wave of cytoskeletal expansion that goes through another portion of the cells, triggering them to differentiate in another direction. Thus a group of cells of type A is split into two groups, say B and C. The whole of embryogenesis can thus be represented by a binary, or bifurcating tree of cell types. Some A cells may persist at the boundary between the B and C groups, and are presumed to be set aside as pluripotent stem cells (Gordon, 2011). B and C cells may go on to form groups of cells of new types (D,E) and (F,G), respectively, etc. (Gordon, 2014). Each edge of a differentiation tree represents all of the genes involved in a given embryonic cell type (Gordon and Gordon, 2015).

This provides us with a model for development that has consequences for macroevolution (Fig. 7). Like adaptive ratchets, differentiation trees provide us with a logical structure for how variation is operated upon during evolution. In their own right, however, differentiation trees allow for a toy model of evolutionary development. While differentiation trees serve as a toy model for understanding the effect of development on evolution, they might also provide a window into other evolutionary phenomena. For example, differentiation tree models could employ developmental and plasticity-related mechanisms to describe so-called "open-ended evolution" (Bedau et al., 2001; Damer et al., 2012; Ikegami and Hanczyc, 2009; Rasmussen et al., 2003) in which evolution proceeds according to the changing needs of an organism or population constantly exposed to ever-changing environments and/or novelty generation.

Differentiation trees may also be used to visualize phylogenetic trees. In this case, the nodes of a phylogenetic tree represent distinct differentiation trees, which stand for individual species. This may allow us to examine the question of cell differentiation in somatic evolution (Pepper et al., 2007) in a comparative manner. As a toy model of phylogeny, there are two major ways a differentiation tree can mutate: 1) changes in the genes expressed in a given cell type ranging from allelic changes to timing changes (microevolution), or 2) changes in the topology of the tree (macroevolution). Differentiation trees thus suggest new definitions for micro- and
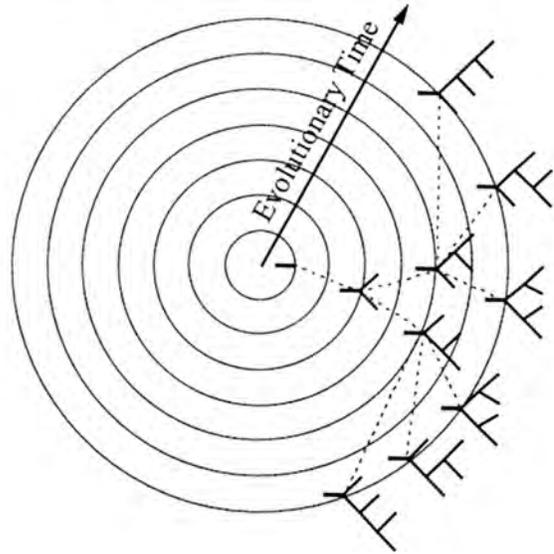
Fig. 7. An example of how the differentiation tree can serve as a toy model for evolutionary development in visualized (top) and schematic (bottom) form. Evolution is depicted here as a phylogenetic tree whose nodes are differentiation trees. Each differentiation tree represents a distinct genome, and each macroevolutionary change involves a change in the topology of the differentiation tree. Note that two trees with the same topology can nevertheless be quite different in the origin of their branches, and in the genes that are expressed in each branch. In this example, growth of the differentiation tree exceeds that of pruning, providing a ratcheting mechanism and thus progress in evolution. Sketch from (Gordon and Gordon, 2015) with permission of World Scientific Press.

macroevolution. In particular, the second mutational mode may introduce new cell types. This could occur within ancestral cell types via some combination of transposable mutagenesis and the reduction of molecular signaling crosstalk (Gordon, 1999). In this toy model, it is then plausible to predict a progressive increase in the number of cell types over time. Whether this assumption is borne out by the data, particularly in comparisons across lineages, is another question entirely. But this is where toy models provide an advantage over formal theories. In the toy model, it would be relatively easy to incorporate a mechanism such as pruning or a branching threshold that might incorporate results that are anomalous to overall trends.

1.9. Bio-phenomenological–mathematical hybrid models

Aside from acting as a middle-ground between data and formal theory, toy models may also provide a bridge between macroevolutionary dynamics and mathematical regularities. In this way, the logical rules of math and physics are used to guide but not to directly interpret biological phenomena. For example, differentiation trees may be an example of "combinatorial explosions" inherent in graph transformation rules (Andersen et al., 2013; Hanczyc and Merkle, 2014). Gregory Chaitin (Chaitin, 2013) has proposed a mathematical model of evolution that emphasizes the creative role of natural selection. In this case, evolution by natural selection is formulated as a provable proposition. While incomplete, these propositions set up a toy model that resembles the

Turing-complete artificial life platform AVIDA (Adami et al., 2000). One interesting outcome of this work is how much the evolutionary process is dominated by creative mechanisms, with natural selection often rewarding the most creative variants. In this case, a rigorous system of propositions allows us to critically examine the plausibility of novelty due to natural variation.

By imbuing toy models with this additional property, they may also bring us closer to understanding whether or not evolution is computationally universal (Bennett, 1995). As the enabling factor of creative evolutionary scenarios, computational universality is a dynamical process that utilizes a program (e.g., genome and protein-making machinery) to produce all possible outputs. Differentiation trees as combinatorial explosions may fit this mold. If the generation of variation can be understood as a computationally universal process, it would go a long way towards our understanding of how cellular processes give rise to macroevolutionary change.

1.10. Coupled avalanches and evolutionary dynamics

While the SOC model is a general model for evolutionary dynamics, there is a missing piece. That missing piece involves non-random mechanisms that mitigate a population's reaction to environmental changes. While this issue might be solved by simply introducing genomic diversity into the sandpile model, a more comprehensive accounting of genomic structure can also be useful. Carlson and Doyle (Carlson and Doyle, 1999) propose that a mechanism called highly-optimized tolerance (HOT) might explain the tendency towards robustness in complex, networked systems. HOT dynamics are essentially a directed version of SOC dynamics. However, these directed dynamics are based on multiple, interconnected stochastic processes, thus making HOT suitable as an evolutionary model. Interconnected dynamics are important features of evolutionary change. Kauffman and Johnsen (Kauffman and Johnsen, 1991) used fitness landscapes to represent epistatic effects between coevolving species. It is these epistatic effects (as opposed to additive genetic effects) which result in nonlinear evolutionary avalanches such as rapidly occurring phenotypic changes or speciation events.

The toy models of SOC and HOT are used to characterize non-gradualist, sudden evolutionary change in a very general way. However, they do not distinguish between genotype and phenotype, nor account for the connections between them. Can we use these toy models to understand a complex organism embedded in an evolving system? To represent the genotype–phenotype map (Atallah and Larsen, 2009; Hill and Zhang, 2012; Wagner and Altenberg, 1996; Wagner and Zhang, 2011), we require a variant of the SOC model called the coupled avalanche model (Fig. 8). The coupled avalanche model consists of two SOC processes operating in parallel (Fig. 8A–D). These avalanches are partially overlapping, representing the overlapping (but not linear) relationship between genotype and phenotype (Fig. 8E–F).

The coupled avalanche model can also operate both in and out of phase. For example, while large-scale displacements of one sandpile are likely to trigger a sizable displacement in the other, small displacements in each pile will often occur independently. In the parlance of evolving organisms, genotypic change does not always necessitate phenotypic change, and vice versa. In addition, let us recall that the ultimate mechanism for large-scale avalanches is the cumulative stochastic activity of small-scale displacements. When this process occurs in two different sandpiles that are also partially linked, changes at one level of the organism (e.g., phenotype) put quasi-selective pressure on the other level (e.g., genotype). This is another way to look at the inherent robustness (or adaptive potential) of a given evolutionary system without complete replication of context and/or complexity.
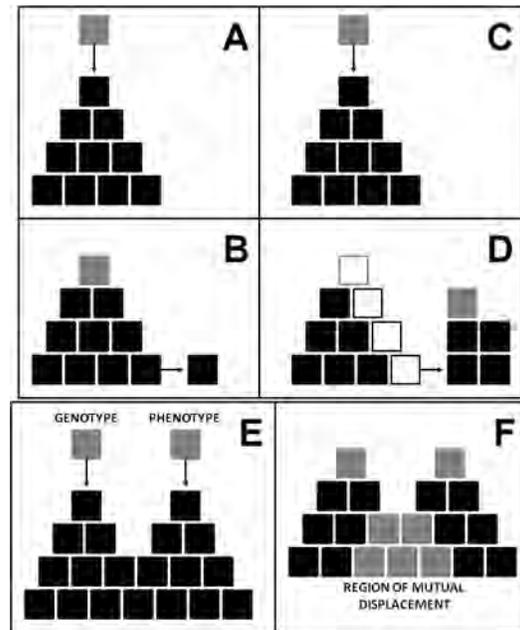

Fig. 8. Characterization of the coupled avalanche model using a sandpile of blocks. A–B: a sandpile with small-scale displacement (A: one block added, B: one block displaced). C–D: a sandpile with large-scale displacement (C: one block added, D: many blocks displaced, i.e., an avalanche). E–F: a coupled sandpile with one pile representing genotype and the other representing phenotype (E: one block each added to the genotype and phenotype, F: addition of blocks can result in an avalanche in the region of mutual displacement shown in red). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

1.11. Self-organized adaptive change

Toy models can also be used to emphasize certain features of a macroevolutionary set of relationships. In this sense, a selected branch on the tree of life (e.g., vertebrates) can be treated as a system. Whereas some phenomena can hold true across the tree of life (e.g., non-linearity of evolutionary change), other phenomena explain evolution in some clades much more so than in other clades. For example, despite its stochastic nature and generative tendencies, the SOC model cannot account for historical contingencies. Historical contingencies represent the memory of an evolutionary system. Such contingencies restrict the possibilities for subsequent evolutionary change and act as a form of recursive information. A toy model that might be used for characterizing historical contingencies and the bootstrapping aspect of evolutionary change is based on existing models of self-organized learning (French and Sougne, 2001). While there are many different ways to model this phenomenon, we will only consider a connectionist model of selection based on connectivity between genotype and phenotype governed by a threshold (e.g., learning) function (Fig. 9A). In this case, evolution by natural selection can be modeled as a form of combinatorial learning based on the idea of learning by artificial neural networks (Zou et al., 2008).

Modeling evolution as learning relies on another aspect of toy models: the use of analogies that potentially fit the data. For example, using a well understood process like learning as an analogy can help us understand how a fitness function might govern the relationship between genotype and phenotype. (This need not imply that evolution by natural selection is a formal mode of learning.) We can even map the technical details of the connectionist model to problems of organismal evolution. For example, the transfer function (Duch and Jankowski, 1999) often used to govern a connection threshold between two nodes (Fig. 9A)
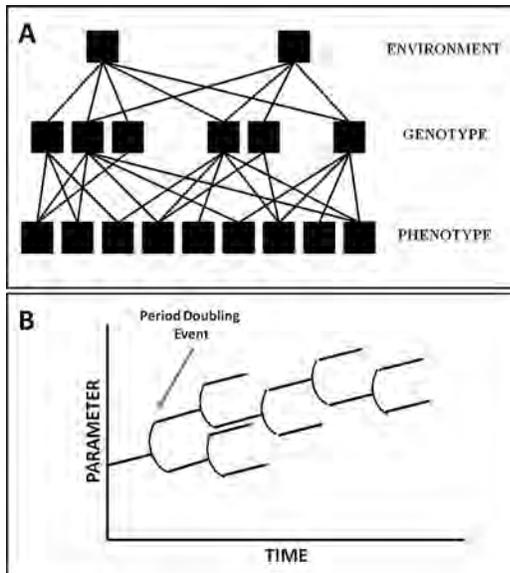
Fig. 9. Connectionist- and period doubling-inspired toy models of evolution. A: connectionist (e.g., self-organizing) models for evolution. Input layer: environment, hidden layer: genotype, output layer: phenotype. B: period doubling in evolution using a version of the logistic map.

can resemble a fitness function, and might be used in a similar manner when applied to a combinatorial evolution model.

While this type of model application may seem like an exercise in provocative overfitting, it actually suggests that some evolutionary outcomes are more plausible than others. To explore this idea, Conrad (Conrad, 1990) proposed that certain phenotypic outcomes are favored over others on the basis of their geometric configuration. A combinatorial model can draw out these biases in a manner that is sensitive to genotypic variation and genotype–phenotype relationships. As a matter of preferred genotypic configuration, plausibility also appears to be related to maintaining fitness in the face of evolutionary change (Conrad, 1990). Thus, bias among all possible combinations of genotype and phenotype is related to the evolvability of a species. With a self-organized adaptive change model, we can model both the bias towards plausible evolutionary configurations and account for diversity across a species or populations.

1.12. Grounded branching processes

Grounding connectionist models in an evolutionary context involves treating each connectionist topology as a distinct set of branching processes. While directed networks called phylogenies (trees of life) are often used to represent evolutionary relationships, there are other implications of branching (or Galton–Watson) processes (Kimmel and Axelrod, 2002). Branching processes are often used to characterize discrete generations (Geritz et al., 1997). However, they can also be used to represent how the SOC model generates diversity. Branching processes also allow us to characterize the role of period doubling in evolutionary dynamics (Fig. 9B). Period doubling can be compared to the branching processes that accompany the adaptive growth of a phylogenetic tree structure (Geritz et al., 1998). From a purely chaotic systems standpoint, period doubling can be characterized through the construction of a logistic map (Feigenbaum, 1978). In this case, we can use a logistic map to represent period doubling (e.g., the origins of new lineages) in an initial population. The chaotic aspect of this approach is the stochastic nature of multiple variables (e.g., mutation, selective breeding) that contribute to the establishment of new lineages.

Aside from genealogical and phylogenetic relationships, how do toy models based on branching relationships help us understand evolution? One way is by combining phenomena into a hybrid toy model (based on so-called hybrid models). While we will not present a formal example here, two papers suggest that models of critical events and period doubling (e.g., fractal phenomena) might be useful for understanding the complexity of phenotypes (Gordon, 1992). In Fussy, Grössing and Schwabl (Fussy et al., 1997), punctuated equilibrium is shown to be part of a larger set of processes encompassing fractal and hierarchical phenomena. While fractal processes and punctuated equilibria can be represented using a logistic map, fractal processes in evolution (Burlando, 1993) are a promising frontier of evolutionary and toy modeling, as we saw above in considering the tree of life.

1.13. Daisyworld and predator/prey models

Finally, toy models should be able to bridge between macroevolution and the more general features of biocomplexity. This includes providing a broader ecological context for macro-evolutionary change in addition to accounting for behavioral dynamics. As an extension of its original form, the Daisyworld model (Watson and Lovelock, 1983) for Gaia (Ruse, 2013) fits our criteria for considering the potential for toy models. It is a population dynamics model in which black daisies reflect 25% of the sun's light, white daisies reflect 75%, and the bare ground reflects 50% (Fig. 10). The contribution of ecological factors to macroevolution is apparent when considering the role of solar luminosity on the biosphere of early earth (Fig. 10). This toy model ignores mutation and hybridization, and supposes only two kinds of organisms. In a way it is a zero dimensional (0D) model for evolution, characterized by a single variable (temperature, a scalar quantity) and what "evolves" is the thermal homeostasis of the Earth and biosphere. It has been both widely criticized (Ruse, 2013) and modified, partly lifting these restrictions (reviewed in: (Wood et al., 2008)). Higher dimensional versions add one dimension (latitude) (Biton and Gildor, 2012) or use cellular automata or networks to let the daisies spread in two dimensions (Punithan et al., 2011, 2012). Recent additions to modeling include symbiosis (Boyle et al., 2011), greenhouse gases (Viola et al., 2013), and time
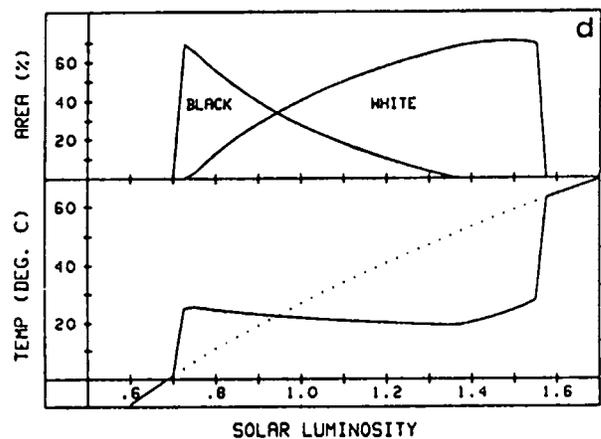
Fig. 10. The Daisyworld model for thermoregulation of the Earth presumes that the Earth is covered by two colors of daisies with equal growth and death rates, with low (black) and high (white) albedos. Both have the same optimum growth temperature of 22.5 °C, but black daisies warm the Earth and white daisies cool it. As the sun's luminosity increases over geological time, the daisies regulate the temperature over a long time period, compared to an uninhabited Earth with just bare ground (dotted line). From (Watson and Lovelock, 1983) under a Creative Commons Attribution 4.0 International (CC-BY 4.0) License per http://www.tellusb.net/index.php/tellusb, reproduced as modified by James Lovelock from http://www.jameslovelock.org/page31.html.

scale analysis (Weaver and Dyke, 2012). A Daisyworld approach to terraforming of uninhabited planets has even been proposed (Lenton and Watson, 2011).

The effect of cloud albedo on habitable zones around stars (Yang et al., 2013) has apparently not yet included the effects of life on albedo and thermoregulation, which might extend the habitable zone and therefore candidates for extrasolar planets with life, taking advantage of the essence of the Gaia hypothesis: that life modifies climate and can even regulate it within broad limits. Gaia thus has a major impact on how seriously we need to worry about global warming (Johnston, 2012; Ruse, 2013; Watson, 2009). The effect of life on the atmosphere (Margulis and Lovelock, 1974) and vice versa is obvious with the great oxidation event caused by cyanobacteria (Schirrmeister et al., 2013). The model in Fig. 10 avoids the question of where the daisies came from, as Earth is barren up until their sudden appearance. The effects of early atmosphere on the origin of life have long been considered (Miller and Urey, 1959; Tuck, 2002), but maybe even then (on Earth or elsewhere: (Sharov and Gordon, 2013)) it was a reciprocal relationship. Daisyworld and a variant called DaisyBall are available to run online (Booth, 2010) with user controlled parameters.

Like Daisyworld the original predator/prey models also started with just two interacting species that don't themselves evolve, and were 0D (Wikipedia, 2014c). Additions of spatial components and genetic change came later (Abrams, 2000; Briggs and Hoopes, 2004). While the long time scale of Daisyworld has not been considered, predator/prey models invoking seasonal and climate change have been entertained (Schmidt et al., 2008). Predator/prey toy models can be applied even more broadly than organismal evolution. Cycles of overshoot and collapse that occur in predator/prey models have been generalized to human societies in attempts to model the rise and fall of civilizations (Motesharrei et al., 2014). Toy models can effectively deal with determining the proper scale of these phenomena. While in the past these dynamics might have been seen exclusively on the local scale, globalization might result in these cycles becoming worldwide phenomena. As Motesharrei et al. (Motesharrei et al., 2014) point out: "We can think of the human population as the 'predator', while nature (the natural resources of the surrounding environment) can be taken as the 'prey', depleted by humans". As one could imagine these models, as those of global warming, resulting in policy changes, how seriously we take our toy models of evolution may no longer be just fun and games.

3. Discussion and conclusion

As bridges between reductionist oriented empirical observation and formal theory, toy models serve a heuristically useful role in understanding evolutionary dynamics. They allow us to representationally approximate the complexity of macroevolution, while still providing an output that is sufficiently complex enough to (we hope) approximate an evolving biological system. The toy models presented here have broad themes that span evolutionary transitions, macroevolution, and the relationship between phenotype and genotype. As such, toy models can also serve as interdisciplinary templates which facilitate cross-subfield understanding. In an ideal situation, concepts implicit to an evolutionary molecular biologist can be made salient to an evolutionary ecologist in just a few toy models. The three philosophical aspects of toy models (abstraction, organization, and level of representation) demonstrate the validity of the toy models in describing macroevolutionary processes as a series of modular models. While toy models are not comprehensive models of evolution, they boil essential components of evolutionary systems to a useful set of scalable relationships, analogies, and compact representations of subtlety and uncertainty.

We have not covered all models that might describe overarching trends and mechanisms in macroevolution. There is a huge literature on the thermodynamics of evolution (Gatenby and Frieden, 2013; Weber et al., 1988; Wicken, 1987), and the role of biosemiotics in evolution is also being tackled (Barbieri, 2008; Martin and Gordon, 2001). In terms of the potential for complexity related evolutionary change, the theory of facilitated variation (FV – see (Gerhart and Kirschner, 2007; Kirschner and Gerhart, 2005)) suggests that evolutionary constraints and the subsequent expansion of variation play a role in providing a directional mechanism to the evolutionary process. While this may be somewhat controversial, characterizing FV as a type of adaptive ratchet model might serve to strengthen its usefulness as a toy model. In turn, characterizing FV as a single or series of toy models might ultimately strengthen its predictive power. As this example emphasizes, we are far from achieving a single "grand toy model" of evolution. However, the toy model template might enable such a grand theoretical model.

Toy models can also address an underlying emerging theme in the evolutionary literature. This involves whether or not evolution even produces long-term, macroevolutionary trends. On the one hand, many empirical results fail to reveal either progress or directionality in evolution. This includes the evolution of wings in stick insects (Whiting et al., 2003) and mammalian cheek tooth evolution (Harjunmaa et al., 2012). In the case of the latter study, an experimental result shows that increased complexity can be had by modifying the developmental program, something that is not observed phylogenetically. As a counter to the ad hoc school, two theorists (McShea and Brandon, 2010) have identified something called the zero-force evolutionary law (ZFEL) by taking a broad look at macroevolution. The ZFEL states that evolutionary change (as opposed to stasis) is constant. Unless evolutionary forces (e.g., strong selection or genetic drift) intervene, complexity will generally increase over time. Barrett et al. (Barrett et al., 2012) suggest that the ZFEL should be inverted, but still agree with the notion of increasing complexity given the proper conditions. We have shown here some examples of how toy models can capture general trends and perhaps even progressive evolution without the biases of a single dataset or the strictures of a formal theory.

Toy models also contribute to several meta-theoretical issues in evolutionary science. One area in which toy models can be very useful is in creating representations for evolutionary simulations. Whether one is interested in using a genetic algorithm, an artificial life model, or an agent-based simulation, toy models can help to organize the major features of this architecture. Particularly with respect to reducing the phenomenology of a particular study area down to its essential components, toy models can aid in reducing Type III error (Schwartz and Carpenter, 1999) in the representational structure of both experimental evolution and evolutionary simulations. As errors in understanding the ultimate causes of a given outcome, Type III errors can serve to distort the inference of mechanisms that underlie evolutionary dynamics. Given one or a series of toy models, such interpretive problems can be reduced.

As toy models can contribute to our understanding of evolution, they cannot serve as a replacement for experimentation and data. Toy models can only serve to understand or simulate trends in the data, and perhaps allowing us to distinguish meaningful trends and outliers from extraneous noise in an inherently stochastic system. This ability to potentially isolate intrinsic stochasticity (biological noise) from extrinsic stochasticity (technical or environmental noise) is limited, however, as a toy model is only as useful as its supporting data will allow. While some toy models (e.g., phylogenetic trees and Hardy–Weinberg model) are well-characterized by data, other toy models (such as the hybrid and self-organized models) are less well-characterized with respect to the data. This means that such toy models can lead to a greater number of Type II

classification errors, where the model combines with the data to lead to a false conclusion about the evolutionary process. Overall though, using a toy model based on approximating the evolutionary process to a reasonable degree is superior to using no toy model at all.

Additionally, the toy model can serve a number of more practical uses in the analysis of biological data. One of these is as an antidote to high throughput datasets. While it is fashionable to leverage as much data as possible to address a problem, toy models can be informative in cases where the data's structure is sparse but the volume of data is great. In cases where the data are messier than the formal theoretical models at hand, toy models might be particularly suited to finding structure in the data much more effectively and with fewer false positives than a correlative analysis. In cases such as metagenomics (Eren et al., 2011) where we have large volumes of next generation sequence data, multiple toy models might be used in parallel to model dynamical, ecological, and adaptive processes all in the same context. Toy models may also serve as a guide to data integration, or as a model of consensus in cases of datasets from different processes and levels of organization (e.g., phenotype, genotype, proteome). Overall, toy models can serve as a complement to data from specific sources in addition to serving as more subtle models for scientific communication and theory building.

Another practical application of toy models is in the cross-validation of evolutionary simulations. As an increasingly necessary component of the scientific enterprise, evolutionary simulations can provide significant "what if" information to a potential evolutionary hypothesis. As ready made abstractions, toy models can provide a basis for a compact but predictive *in silico* analogue to specific features of the evolutionary process. However, it is important to realize that some toy models (such as the self-organized adaptive change, high dimensional fitness landscapes, and even large scale phylogenetic instances of the tree of life) require intense computation and may not provide exact answers to the problems at hand. Nevertheless, the use of toy models as a low dimensional conceptual heuristic is essential for any application to the broader empirical or theoretical domain. Short of formal statistical tests or a unified theory, we can still use a comparison (via simulation) of toy models to understand what makes a good toy model given the structure of available and future data. Therefore, future work should focus on developing a more rigorous comparison of candidate toy models for specific problems.

More details regarding the toy models introduced in this paper can be found in the toy model repository, located at the Github repository (Alicea, 2014). This repository will provide the latest information on toy model methods and development.

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