Dynamic landscapes: A model of context and contingency in evolution

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HIGHLIGHTS

- Model combines evolution in high-dimension genotype space with ecological interaction.
- Results are qualitatively similar to empirically observed patterns of extinction.
- Model results also show a realistic exploration of genotype space.
- The model is highly abstract, and thus, applicable also to RNA or protein evolution.

GRAPHICAL ABSTRACT
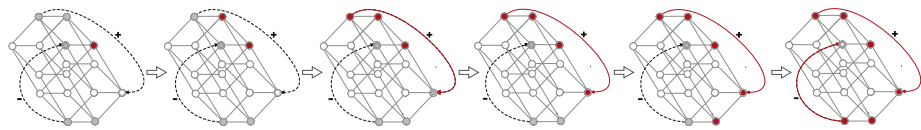
ABSTRACT

Although the basic mechanics of evolution have been understood since Darwin, debate continues over whether macroevolutionary phenomena are driven by the fitness structure of genotype space or by ecological interaction. In this paper we propose a simple model capturing key features of fitness-landscape and ecological models of evolution. Our model describes evolutionary dynamics in a high-dimensional, structured genotype space with interspecies interaction. We find promising qualitative similarity with the empirical facts about macroevolution, including broadly distributed extinction sizes and realistic exploration of the genotype space. The abstraction of our model permits numerous applications beyond macroevolution, including protein and RNA evolution.

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1. Introduction

What drives evolution? Since the days of Darwin, the prevailing explanation has emphasized heritable variation and selection. But while the mechanism of heredity and the importance of random mutation for generating variation have been thoroughly explicated, the nature and causal agents of selection remain mysterious. We still struggle to explain the most striking events in the drama of life: the mass extinctions, adaptive radiations, and local speciations that generated the millions of species alive today and the hundredfold greater number that have become extinct (Gavrilets, 2003).

Theories addressing these macroevolutionary questions fall into two categories, each with a distinct orientation. The first approach builds on the fitness landscape introduced by Wright (1932). Selection cannot directly influence genotype frequencies; it only acts on the associated phenotypes. This approach therefore focuses on the map between genotype and fitness, as mediated by phenotype. This map (the fitness landscape) assigns a scalar fitness value to every point in genotype space. Random mutants with higher fitness are favored by selection, on average, while those with lower fitness are eliminated.

The second approach, coming from ecology and dynamical systems theory, emphasizes the role of interactions between species. The genotype space is essentially ignored, and the fate of species is determined by interacting population dynamics (Hofbauer and Sigmund, 1998) in a given ecology. For example, abundant prey may drive the growth of a predator population, which drives another prey species to extinction.

Both approaches capture important features of macroevolution. The interaction between genotype and phenotype is of central importance to phenomena like speciation, adaptive radiation (Gould, 1989), and punctuation in the rate of evolution (Sneppen et al., 1995; Stadler et al., 2001). Likewise, empirical studies suggest that ecological interactions play an important role in determining speciation rates (Wagner et al., 2012; Losos and Mahler, 2010), while theoretical work indicates an important role for interspecies dynamics in generating extinctions (Bak and Sneppen, 1993; Solé et al., 1996). Each approach captures important aspects of context (e.g., particular ecological configurations rendering some genotypes unfit) or contingency (e.g., particular mutational histories limiting accessible genotypes) in evolution.

Our model integrates these two approaches into a simple, unified model of evolutionary dynamics. We extract the "stylized facts" captured in these two approaches and reflect them in an abstract model that combines mutation, selection (represented as percolation on a high-dimensional n-cube), and interspecies interactions (represented as a random graph). These abstractions allow the model to potentially support a range of interpretations, from molecular evolution to technological innovation. Here, the model is shown to capture qualitative features of macroevolutionary processes that have been observed empirically: We find broad distributions of extinction sizes and evidence that evolution traces out an "advancing front" through genotype space. Our model thus describes evolution on a richly structured, dynamic fitness landscape, where context and contingency determine the subsequent evolution of the simulated biosphere.

Section 2 summarizes the fitness landscape and ecological models above and gathers the stylized facts guiding our model. Section 3 describes our model and its implementation. Section 4 reviews the results. In Section 5 we discuss the results and offer our conclusions as well as an outline of future work.

2. Background

Our model builds on two important traditions in the mathematical modeling of evolution. In both cases, researchers have sought to translate key features of the evolutionary process into mathematics. We draw from these models "stylized facts" to inform a more realistic abstraction of the evolutionary process.

2.1. Fitness landscapes

Since their introduction by Wright (1932), fitness landscapes have played a dominant role in evolutionary theory (Gavrilets, 2003). This dominance follows from their conceptual simplicity: the genetic code of the organism defines a space of genetic configurations or "genotype space" (denoted $\mathcal{G}$). A fitness function Φ is defined on the genotype space. This fitness function is a map $\Phi : \mathcal{G} \to \mathbb{R}^+$ from the genotype to some scalar measure of fitness. A population of individuals is defined over $\mathcal{G}$, and the population dynamics is shaped by $\Phi(\mathcal{G})$.

Following Wright, the fitness landscape is metaphorically described and often mathematically modeled as a geographical landscape. These "rugged landscapes" have many adaptive peaks, separated by adaptive valleys (Gavrilets, 2003). This oversimplification of Wright's picture has several flaws when used as

an explicit model for fitness landscapes (Pigliucci, 2010; Pigliucci and Kaplan, 2006). First, low-dimensional models (of the sort suggested by the geographic landscape metaphor) fail to generate speciation events with any reasonable probability. Selection pushes the population up adaptive peaks; crossing a valley to a new peak is hence unlikely. Neither shifting balance (in which a population is subdivided so that a stochastic shift across a valley is more likely) nor founder effect speciation (in which a small number of individuals found a new population more likely to cross a valley) can explain the observed fecundity of the biosphere (Gavrilets, 2003).

The second flaw also follows directly from the oversimplified landscape picture. $\mathcal{G}$ is very high dimensional; most organisms have thousands of genes and millions of base-pairs (dim $\mathcal{G}$ ~10^6–10^9) (Gavrilets, 2003). Fisher observed that high dimensionality converts "adaptive peaks" into saddle points, and makes a single peaked landscape, albeit in enormously high dimensions, more likely (Gavrilets, 2008).

Third, Kimura's claim that most evolutionary change is neutral, or indifferent with respect to fitness (Kimura, 1983), has been supported by extensive experimental evidence. For example, the genotype-phenotype map for RNA and proteins is now known to be many-to-one, implying that many mutations are selectively neutral (Stadler et al., 2001).

An important compromise embracing ruggedness, high dimensions, and neutrality was suggested by John Maynard Smith. He noted that functional phenotypes must "form a continuous network which can be traversed by unit mutational steps without passing through nonfunctional intermediaries" (Maynard Smith, 1970). This suggestion—that genotype space is percolated by networks of more-or-less equally fit genotypes, which nevertheless represent a small fraction of all possible genotypes—forms the core of the neutral network or holey landscape approach pioneered by Gavrilets (2003, 2008), Gavrilets and Gravner (1997), Gravner et al. (2007). Selection plays a role in this approach, defining the neutral network(s) and preventing populations from mutating into the "holes" of the landscape. Neutrality also plays its part, since most evolution takes place neutrally along interweaving networks. Maynard Smith and Gavrilets' compromise position suggests that continuous, rugged landscapes misrepresent the actual structure of genotype space. This critique must be taken seriously; the holey landscape picture is supported by both theoretical arguments and by empirical evidence from studies of RNA and proteins (Gavrilets, 2003; Gavrilets and Gravner, 1997; Gravner et al., 2007; Bornberg-Bauer, 2002; Breen et al., 2012). Indeed, some advocates claim that the structuring of genotype space by neutral networks is the *primary* factor in speciation, adaptive radiation, and punctuated equilibrium (Stadler et al., 2001).

Summarizing the stylized facts, we want:

- selection to matter, while ignoring small differences in fitness;
- very few genotypes to be fit;
- the genotype space to be suitably high dimensional;
- neutrality to play a substantial role; and
- neutral *networks* to exist in the genotype space.

2.2. Ecological models

Fitness landscape models focus on genotype space, highlighting the macroevolutionary phenomenon of speciation. Ecological models focus on interspecies interaction, highlighting the phenomenon of extinction (Sneppen et al., 1995; Solé et al., 1996). Evidence for extinction played an important role in overturning static pre-Darwinian biology. More recently, the discovery of mass