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Simple lattice model of macroevolution

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ABSTRACT

In future astrobiology, like in modern astrophysics, the numerical simulations can be a very important tool for proving theories. In this paper, I propose a simple lattice model of a multi-species ecosystem suitable for the study of emergent properties of macroevolution. Unlike the majority of ecological models, the number of species is not fixed—they emerge by “mutation” of existing species, then survive or go extinct depending on the balance between local ecological interactions. The Monte-Carlo numerical simulations show that this model is able to qualitatively reproduce phenomena that have been empirically observed, like the dependence between size of the isolated area and the number of species inhabiting there, primary production and species-diversity. The model allows also studying the causes of mass extinctions and more generally, repeatability, and the role of pure chance in macroevolution.

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1. Introduction

As Christopher G. Langton, the godfather of the Artificial Life research paradigm,¹ said: “Biology is the scientific study of life-in principle, anyway. In practice, biology is the scientific study of life on Earth based on carbon-chain chemistry. There is nothing in its charter that restricts biology to carbon-based life; it is simply that this is the only kind of life that has been available to study.” Langton proposed that we can recreate important biological phenomena from scratch using computer models, robots or other artificial media made chemically, and we can study them in a full-controlled manner avoiding inherent limitations, inevitable when we deal with real life forms. From 1987, when Langton defined for the first time the field of Artificial Life (first at a conference, and then in his publication in 1990), this way of thinking has propagated, and now we have three main branches of AL, named for their approaches: soft, from software; hard, from hardware; and wet, from (bio)chemistry.

The “sole example problem” pointed to by Langton concerns all theoretical branches of biology, but especially astrobiology, which almost by definition has to take under consideration other examples of living systems in order to extract the most universal properties of life. But for now, in the absence of any alien life forms, astrobiology does not have any other living systems

available for studying. Therefore, astrobiological researches are currently restricted to related problems of astrophysics and astrochemistry and to very specific fields of our “non-extraterrestrial” biology, such as microbiology of extremophiles—bacteria and archaeans living in physically or geochemically extreme conditions, micropaleobiology, and biogenesis. Unfortunately, only the last one utilizes AL methods—mostly in “wet” form, rarely in “soft” form. Opposite to cosmology and astrophysics but may be similar to the main stream of biology, in the field of astrobiology, computer simulations seem to be underestimated as an equivalent way to acquire scientific knowledge.

However, it could be a very promising approach—the simulation model presented below is just one, a rather simple, but surprisingly promising example. Designed as simple as possible, it allows to attack an abstract question that is potentially important for astrobiology, and very important for evolutionary biology and paleontology: How much is *macroevolution* determined by environmental restrictions and how much does it depend on random events?

The term macroevolution refers traditionally to biological evolution that occurs at, or especially, above the level of species. The so-called Modern Evolutionary Synthesis School claims that this distinction is not important, and macroevolution could be understood as a longtime compound effect of microevolutionary processes. However, some theoreticians argue, that there may be some macro processes or system properties that are *emergent*, and cannot be derived easily from the microevolution level.

The discussion remains open, among other things, because macroevolution acts typically in very long timescales and in the context of many ecosystems and the whole biosphere. So, even

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on the Earth it is not available for experimental research—only post-factum observations are possible. Therefore, like in astrophysics, mathematical models and numerical simulations seem to be very important for study of the macro level of evolution. They may be the only possible way to deeply understand the huge body of observable facts, repeatable and recurrent processes and patterns, and still disputable consequences of such phenomena like the Red Queen principle, key-innovations, adaptive radiations, emergence or vanishing of natural barriers, climate change, local and global catastrophes, spontaneous or induced mass extinctions etc.

2. A brief view on modeling ecology and macroevolution

Unfortunately for “real” biologist and paleontologists, the models currently dominating in theoretical biology have non-biological origins, and most authors working on them have a rather limited biological background. This leads to dismissing or omitting different aspects of biological systems, which are obviously essential for the study of evolutionary processes.

Perhaps the first computer model of macroevolution was designed by (Raup and Gould, 1974; Raup et al., 1973), but probably the best known one was proposed by Bak and Sneppen (1993) as an attempt to elucidate causes of the hypothetical punctuated equilibrium dynamics (Eldredge and Gould, 1972). They showed how self-organized criticality might explain the main features of the whole fossil record (e.g. distribution of sizes of extinction events). Within a years, the model was intensely disputed (e.g. Roberts and Newman, 1996; Head and Rodgers, 1996) and is still explored by statistical physicists, bioinformatics and computer scientists (e.g. Melkemi et al., 2006). However, because of its very abstract and quite too simple understanding of adaptations and co-evolution of species, that oversimplifies the real mechanisms of speciation and extinction events, it seems to be not applicable for more detailed evolutionary questions.

Mathematical and computational ecology, in turn, classically uses Lotka–Volterra models (Lotka, 1920; Volterra, 1931) that disregard spatial differences and the discrete character of populations and do not deal with real systems, composed from more than a few nodes of the food/interaction network. Such generalizations allowed analytically achieving some interesting results, but applied in macroevolutionary studies became real drawbacks of such an approach. Some of their limitations were removed in the more generalized version of the models² (Solomon, 1998). This idea is used in recent years to solve many multi-node and even spatial problems (e.g. Louzoun and Solomon, 2001; Hariadi, 2004). In Generalized Lotka–Volterra (GLV) models, some authors start to consider also the extinctions of nodes of the interaction network (Ackleh et al., 2000). But because of the differential equation formalism such models still ignore the discreteness and highly spatial irregularities often important for describing natural populations (Shnerb et al., 2000). Moreover, such models are rather complicated and demanding even for a rough numerical solution. Also, their authors, who are mostly statistical physicists or mathematicians, concentrate rather on and questions distant from evolutionary biology (e.g. economic growth).

Ecologists, and ecology-interested physicists and mathematicians recognize the limitations of the Lotka–Volterra predator–prey models (Donaldson, 1999; Pękalski, 2004). As an alternative many kinds of microinteractive models are proposed. The first models of this kind, directly dedicated to ecology, appeared in the

late 80's, the early 90's of the 20th century (Wolff, 1988; Boccara et al., 1994), but they became more popular in first years of the 21st century as briefly reviewed by Pękalski (2004). Most of them are individual based and use a rectangular or square lattice as a substitute for the environment. In implementation they more or less resemble the cellular automata models or simple agent-based models popular in social science (Suleiman et al., 2000), whose convergence may be considered as an effect of expansion of the complex systems paradigm in science during the recent 20 years.

Contemporary works explore rather different aspects of the dynamics of predator–prey or predator–herbivore–plant systems, or optionally consider also environmental changes (e.g. Droz and Pękalski, 2001, 2002; He et al., 2003), but they rarely raise questions much more close to macroevolution like sympatric speciation (e.g.: Luz-Burgoa et al., 2003), or the causes of mass extinctions. For example, Lipowski (2005) utilizes the concept of a multi-species lattice model of an ecosystem built out of a non-fixed number of predatory species competing for one species of prey and for a space to place their offspring. Because of a mutation mechanism combined with selective pressures, which act between different predator species, some of them are able to specialize, and win the competition for a period of time. Over a long time it leads to a periodic behavior of low-medium-high level of specialization, with avalanches of extinctions occurring, when “too-well-specialized” predators evolved.

The model presented in this paper seems to be quite similar to these microinteractive models. However, there are very important differences—the number of species, both producers (“plants”) and consumers (“herbivores”, “predators” etc.) are not fixed, all populations could potentially interacting with each other and by speciation they could take every ecological niche possible in the particular moment. This feature allows the model to show properties and to achieve results similar both to stochastic models of macroevolution (Raup and Gould, 1974; Bak and Sneppen, 1993) and for “predator–prey” based microsimulations (like these ones reviewed by Pękalski, 2004).

3. Principles of the CO-EVO model

I tried to design a minimalistic individual based model of macroevolution as much as possible similar to cellular automata. I combined basic concepts used typically in classical kinds of CA and other minimalistic microsimulations, like simple entities in a partially occupied rectangular lattice, local interaction in a Moore neighborhood and Monte-Carlo (M-C) dynamics, with the most important aspects designed from a biological point of view.

Firstly, the understanding of a *community* of species living in particular ecosystem as a system of energy (or biomass) that flows from every population of producers (autotrophs) to a number of interconnected populations of consumers (heterotrophs) is a quite basic idea for modern ecology.

Secondly, there are some properties of the space of possible ecological niches. It is obviously very large, if not infinite, and includes places for any level of specialization of autotrophs, as well as omnivores, herbivores, and predators; some of them may be defenseless, some heavily armored etc. This space is searched by speciation (the emergence of new species) in a manner resembling the so-called “random walk”—a newly emerged species takes a niche adjacent to the niche of its ancestral species. It is possible to find a longer or a shorter evolutionary path from every niche to another. However, the local flow of energy in ecosystems plays a limiting role for such possibilities. Each population in the ecosystem, in order to survive and create evolutionarily new forms has to obtain efficiently enough energy from abiotic sources or from other populations. Moreover, it has to

² GLV—“Generalized Lotka–Volterra”.

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