Complex systems theory and evolution

Melanie Mitchell and Mark Newman
Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, NM 87501

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A "complex system" is a group or organization which is made up of many interacting parts. Archetypal complex systems include the global climate, economies, ant colonies, and immune systems. In such systems the individual parts—called "components" or "agents"—and the interactions between them often lead to large-scale behaviors which are not easily predicted from a knowledge only of the behavior of the individual agents. Such collective effects are called "emergent" behaviors. Examples of emergent behaviors include short and long-term climate changes, price fluctuations in markets, foraging and building by ants, and the ability of immune systems to distinguish "self" from "other" and to protect the former and eradicate the latter.

Another important example of a complex system is an ecosystem. Depending on one's point of view, one may regard either individual organisms, or entire species, as being the agents from which an ecosystem is built. Interactions among these agents take a variety of forms. Much interest has traditionally focused on predator-prey and host-parasite interactions. These interactions are asymmetric, the two agents involved playing different roles. There are also symmetric interactions, such as competition among agents for resources like food or space. Such competition may be among members of different species or among members of the same species. Other competition, such as competition for mates, is only among members of the same species. Symbiotic relationships between individuals or species are another form of symmetric interaction, in this case beneficial to both partners.

And what is the emergent behavior of an ecosystem? There are many emergent behaviors, in fact. The very structure of an ecosystem is itself an emergent property. For example, the fact that we have many competing species rather than only a single one is a result of species interactions. Competition and cooperation between species makes it advantageous for species to inhabit restricted "niches," feeding on specific resources, or living in particular environments. The many different forms of life seen on the Earth today are as much the result of interactions between organisms as they are the result of the influence of the external physical environment. Animal and plant behaviors are also substantially the result of interactions. However, perhaps the classic emergent behavior of an ecosystem is evolution, and in fact the other behaviors above can themselves be regarded as merely one aspect of evolution.

Evolution, the compounded result over long time periods of variation and selection, is responsible for every feature of ecosystem diversity that we see today. But conversely, ecosystem diversity is itself responsible for evolution. The selection pressures which make one variant of a species more successful, on average, than another, come in large part from interactions with other individuals or species. Textbook examples of the effects of such selection pressures include the trees of the rainforest canopy, which have evolved to great height in order to reach the sunlight—the tallest tree will receive the light while shading others from it. Thus some species of trees have become far taller than they should be for optimum structural soundness. The coevolution of predators and prey, such as cheetahs and antelope, can similarly drive each to run faster, the one to catch its dinner and the other to avoid becoming dinner.

A principal result to which evolution gives rise is sophisticated organismal forms that are highly adapted to their particular niches. If we agree to call unexpected collective behaviors of complex systems "emergent," then surely the evolution of current organismal forms is an extraordinary example of emergence.

What can the study of complex systems contribute to evolutionary theory? There are at least two major ways in which it can help. The first is in the contribution of novel methods of mathematical and computational modeling that aid our understanding of emergent behaviors. The second is in the identification and elaboration of ideas from other complex systems that are relevant to ecologies and evolution.

Agent-based modeling is one modeling method relevant for evolutionary theory that has been developed in the complex systems research community. The term "agent-based modeling" (sometimes called "individual-based modeling") refers to a collection of computational techniques in which individual agents and their interactions are explicitly simulated, and emergent properties observed. This contrasts with more traditional differential-equation modeling methods in which much larger-scale properties of a system—population densities of species, densities of resources, and the like—are the atomic elements of the model, rather than individual agents. The goal of agent-based modeling is to design models that are sufficiently simple that the mechanisms of emergence can be understood and yet elaborate enough to show interesting behavior.

Genetic algorithms (GAs) are one class of agent-based modeling techniques that were designed to capture the essence of evolution and adaptation and yet be simple enough to be mathematically tractable [7]. In GA methods one studies the evolution of simple strings of symbols on a computer, or fragments of computer code, rather than attempting to simulate the behavior of real organisms. An early result from research on GAs was the mathematical characterization of adaptation as a near-optimal trade off between exploitation of traits that have already been found to be useful and exploration for new useful traits [7]. GA research has also led to mathematical characterizations of the roles of mutation, sexual recombination, diploidy, and other genetic processes and characteristics. In addition, GAs have a practical use as computational search and learning methods inspired by evolution. Textbooks on GAs discussing these various results include Refs. [1, 5, 6, 11].

Artificial life simulations are another class of agent-based models, in which organisms and interactions are explicitly simulated. These models tend to include more complex interactions than do typical GAs, and attempt to represent the conditions of the evolution of real organisms to a greater extent. Some well-known examples of artificial life simulations are Ray's Tierra system [14], which demonstrated that increasingly efficient methods of self-reproduction can emerge in a simple ecological model; Holland's Echo system [7, 8] which attempted to demonstrate the emergence of multicellularity via cooperative and competitive interactions among agents; and Bedau and Packard's Bugs model [3] in which the "evolutionary activity" of the system—the rate at which the system generates novel adaptations—is quantified and measured. This measurement has also been applied to other simulations and evolutionary data [4]. In each of these simulations, an emergent behavior of the system is identified and quantified, and proposals are made for identifying and quantifying similar behaviors in more realistic systems.

The simulation of macroevolutionary processes is a further class of agent-based modeling relevant to evolutionary theory. Macroevolutionary theory describes evolution at the level of higher taxa—species, genera, families, and so forth—and concerns itself with such large-scale phenomena as species extinction and origination and long-term patterns of biodiversity. Probably the best-known example of a macroevolutionary model is the coevolution model of Bak and Sneppen [2], which attempts to explain mass extinction as a result of species interactions. Other examples include the extinction model of Newman [12], which models extinction instead as the result of environmental influences on species, and the "reset" model of Sibani and co-workers [16], which models evolution and extinction as a non-equilibrium process and makes predictions about patterns of change on very long time-scales.

In addition to simulation and modeling methods, the other major contribution to evolutionary theory from complex systems research is the appropriation of concepts and results from other complex systems for the purposes of explaining evolution. A good example of this is the recent adoption of ideas from statistical physics in the field of evolution. One such idea is that of "energy landscape." Building on Sewell Wright's original proposal that evolution could be characterized as movement on a "fitness landscape" [20], some complex systems researchers have modeled evolutionary dynamics as many-body dynamics on appropriate energy landscapes, similar to the physics concept of spin glasses. Kauffman, for example, has characterized evolutionary dynamics as adaptive walks on tunably rugged fitness landscapes, and correlated the statistics of these landscapes (in terms of quantities such as average numbers of local peaks, average distance between peaks, and correlations between fitnesses at fixed distances on the landscape) with the effectiveness of evolution on these landscapes [9]. Other researchers have built on Kimura's idea of selective neutrality [10] and applied statistical physics concepts such as percolation to characterize evolutionary dynamics on neutral networks [15]. Others still have adapted concepts and methods from statistical mechanics and advanced statistics to describe population dynamics in simple evolutionary systems at a coarse-grained level [13, 18]. For example, van Nimwegen and co-workers have used such methods to demonstrate that metastable behavior in evolutionary systems can be the result of finite-population effects and can in some simple simulated cases be predicted in detail [18, 19], and have proposed that these and related results may explain emergent behaviors seen in molecular evolution [17].

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