What the books say

Review 2

Hot extensions of neo-Darwinism

By Peter Schuster

Darwin’s natural selection and Mendelian genetics, united in the neo-Darwinian synthetic theory of evolution, are the basis of our current understanding of biology. Neo-Darwinism, although extremely successful and accepted by most scientists, is criticized by several biologists, among them the world-famous author of this new comprehensive monograph, because of its central belief in adaptive selection as the universal and exclusive force shaping everything we see in nature. The aim of Stuart Kauffman in his own words is ‘not so much to challenge than to broaden this neo-Darwinian tradition’. In this sense he is searching for laws of form that are acting in their own right and independently of selection. These laws, as already seen from the title of his book, are subsumed under the heading ‘self-organization’. Stuart Kauffman thus presents his view on order-creating dynamics as critical to complex systems of biology. He is advocating a new kind of physical biology which uses the knowledge of complex dynamical systems in order to understand biology. In addition to an introductory chapter reviewing current evolutionary theory, the book contains three major parts dealing with ‘adaptation to the edge of chaos’, ‘the crystallization of life’ and ‘order and ontogeny’. The author is well known for his highly original contributions to research in all three areas and hence we can expect to get first hand insights into three hot topics of current biology.

In the first part of the trilogy, the author uses the catchphrase ‘the edge of chaos’, which was invented to characterize interesting behaviour of cellular automata that are neither so rigid as to converge to a constant state nor so seemingly unrepeatedly flickering as the solutions of the quasi-chaotic cases. Steve Wolfram’s class 4 automata, for example, are the best examples for this intermediate behaviour and they are traded as universal computers. Stuart Kauffman, puzzled as well as inspired by the apparent complexity of such complex systems with simple rules, concludes together with his colleagues Norman Packard and Chris Langton that ‘life exists at the edge of chaos’. A friendly critic, however, may object that, as everything being complex need not have the same complexity, existing at ‘the edge of chaos’ (taking for granted that it is actually true) might be a very weak characteristic, if not an unimportant ingredient of life. Below the cover of this catchy title, Kauffman presents the central and, at least in my eyes, most important conceptual issue of the book: the notion of ‘rugged (fitness) landscapes’ being the stage for adaptive evolution. Evolution is not the smooth walk uphill but rather is a complicated flow of entire populations on complex ‘rugged fitness landscapes’ that is shaped by the detailed properties of these landscapes and thus is structured by self-organization.

A typical rugged fitness landscape is a high-dimensional multi-peaked object with a hierarchy of local optima. Motivated by his own earlier work on random Boolean networks, Kauffman conceived a spin-glass-like model which he called the NK model of rugged fitness landscapes (N is the number of genes in a genotype and K is the number of couplings to other genes, a measure of the richness in epistatic interactions). Variation in K allows the tuning of landscapes from the ‘Fujiyama-type’ single peak landscape (K=0) to the completely irregular and random multi-peak case (K=N−1). The NK model is clearly a statistical model and all we can get out of it are statistical constructs of evolutionary processes. A complexity catastrophe is envisaged: the larger the value of K, the more local optima exist on the landscape and at the same time their relative height decreases. What eventually remains at high K values is a random collection of tiny hills, too low to be suitable for adaptive walks. The beauty of the Kauffman family of NK model landscapes lies in the fact that a fairly simple parameter (K) provides a handle on the complexity of adaptive processes. The landscape concept is applied to an incredibly wide range of diverse problems in organismic and molecular biology: Cambrian explosion in the numbers of species versus Permian quiescence, the error threshold problem of mutation versus selection, the role of recombination in adaptive evolution, protein evolution in the immune system, the design of catalytically active biopolymers by applied molecular evolution, adaptation in complex dynamical systems and dynamics of coevolution. All these problems are viewed in the light of adaptive flows on rugged landscapes, again taking for granted that landscape models are a suitable tool for describing these processes.

The second part of the trilogy deals with the origin of life problem. Here the author presents his own view which, to me, is somewhat reminiscent of the concept of autopoiesis: the origin of life is tantamount to the origin of a defined organized (cellular) metabolism. Autocatalytic sets of biopolymers, self-sustaining and proliferating, stand in the pole position for the start of life and biological evolution. Stuart Kauffman sees life emerging when a collection of processes gathered at random undergoes a phase transition to become a collective that replicates as a whole without having a replicating genome in its core. He argues that such sets of reactions of organic molecules are common and the formation of an autocatalytic set is a probable event. In contrast to the more conventional views, he advocates the start of a complex metabolism in
synchrony rather than by gradual stepwise extension of already-existing metabolic functions whenever an environmental resource dried out or when it was exhausted by too many competitors. In the core of the trilogy's second part we find a theoretical concept for dealing with functional organization which is new in biology. Kauffman calls it 'random grammars': the elements of an organization are considered as strings operating on strings producing new strings. New phenomenologies of network dynamics arise in numerical simulations, which are discussed in terms of colourful names like 'jets', 'lightning balls', 'mushrooms', 'filigreed fogs', etc. Three issues are considered in great detail: the origin of functional webs, the integration of individual elements into an organized whole and the transformation of organizations through phase-transition-like changes called 'avalanches'. This concept of autocatalytic sets of biopolymers, whether it is relevant for the origin of life problem or not, has inspired work on the origin of closed reaction networks and initiated the development of novel theories of organization by the author and by others. It may well be irrelevant for the purpose it was conceived for, but it might create some novel thinking about complex networks of coupled processes being chemical reactions or something else.

The third part of the book deals with the hottest current problem in the heart of all organismic biology: cell differentiation and morphogenesis in ontogeny. Here the author builds upon his own experience as an experimental and theoretical developmental biologist in the seventies and early eighties. Order emerging in genetic regulatory networks is discussed by means of random graph models that allow the discussion of statistical features like the influence of connectivity on network properties. This approach provides a means for the classification of network architectures. Network dynamics is modelled by an idealization in which the network elements are Boolean functions. Known regulatory properties of molecular genetic switches and genetic cascades are interpreted as analyzing Boolean functions. In the author's view, cell differentiation is visualized as a consequence of the ensemble properties of Boolean genetic networks: different cell types are understood as different attractors of complex network dynamics. Morphogenesis is discussed as the result of several models leading to complex dynamics with unique features: biochemical Turing-like patterns, mechanochemical models, models based on cell-cell interactions through chemical intercellular communication, models based on long-range order and positional information, models of cell sorting based on simple surface-energy considerations, and others. All these models have in common that they can provide explanations for the embryonic patterns of organismic shapes and early developmental defects actually observed. They all lead to a limited repertoire of admissible forms upon which selection is acting. No matter which of these mechanisms is truly in operation in nature, or whether there is a group of mechanisms acting in synergy, Stuart Kauffman concludes that what we see in biology is determined by these dynamical laws rather than by the constructing force of adaptive selection.

The point that Kauffman raises in his book is well taken. Only a few naturalists, I guess, would claim that natural selection has the exclusive capacity for creating form in biology. I do not, however, see as much contradiction to the neo-Darwinian view as he claims. Surely the insights into the creation of biological forms gained by molecular biology and by the dynamics of complex systems are fairly new, but even a hard-nosed Darwinian would not seriously doubt that physics and chemistry set the stage for evolution. What else then has provided these new results besides a search for patterns in physics and chemistry which were already known to exist in biology (the stripes of the zebra, after all, were known long before the discovery of Liesegang rings or Turing patterns)? Taking the role of devil's advocate, I would be even more radical concerning the role of self-organization in biology: there is one and only one concept of evolutionary dynamics, and it is tantamount to application of the concepts from self-organization to biology; selection is part of it (I would thus never speak about 'self-organization and selection'). Other laws of dynamical processes may counteract and suppress selection, not only complement it. This argument becomes particularly clear in the discussion on co-evolution. The author uses the concept of coupled 'fitness landscapes', which are continuously modified by the evolution of other species in the ecosystem. Thus he still stays in the realm of optimization through adaptive selection. In the dynamics of ecosystems, strictly speaking, there are no fitness landscapes; landscapes can only be used as a metaphor to gain some reality in the limiting case of weak (and slow) coupling between species.

Stuart Kauffman, irrespective of the problems one may have with his views in detail but in view of his enormous creativity, provides us with plenty of new ideas that can give rise to experimental tests and to new unexpected developments. As an example, I mention his idea of the 'catalytic task space' of proteins that is covered by 100 million proteins, which thus provide a universal enzymatic tool-box. Honestly, I do not believe in the number, but the concept of a finite set of catalysts doing everything is truly fascinating. He gets the idea by transferring known evidence from immunology to protein catalysis and the success of catalytic antibodies apparently shows that he is right. There is the concept of autocatalytic sets of biopolymer...
mers. It could well be verified in sets of RNA molecules and give rise to an interesting novel kind of chemical kinetics (my chemical intuition makes me hesitate to believe that it would work with proteins). And there are many other new ideas waiting to be exploited. Entering a novel area of research implies that speculation inevitably will outweigh hard facts, and in this sense the monograph presented by the author is no exception. The book certainly raises more questions than it provides (conclusive) answers to problems, but in my opinion this is its strength and not its weakness.

In summary, Kauffman presents an interesting comprehensive monograph on 'how to extend the neo-Darwinian view in order to provide a richer repertoire of mechanisms creating order and form in biology'. In the sense of the author's own suggestion, the book is provocative; it has given rise to some discussion already and, I hope and I am convinced, will create more of that in the future. I wish the book many future editions, which could be used, for example, to balance the presentation of speculations with hard facts as the knowledge in this new territory to be explored increases. I am convinced that complex evolutionary dynamics will become a central issue in future evolutionary biology and Stuart Kauffman will be among the pioneers in this field. My recommendation to biologists, biochemists, physicists or biomathematicians is: if this review made you curious or provoked your scepticism, go buy the book and read it.

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