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Themes and Variations in Complex Systems

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Brass musical instruments have evolved dramatically over the past 200 years. This ca 1855 photograph of an American band shows now-obsolete circular, upright, bell front, and over-shoulder designs. COURTESY OF THE HAZEN COLLECTION, SMITHSONIAN INSTITUTION ARCHIVES

Complex systems display diversification in type, patterning, and behavior over time through varied selective mechanisms. Such systems are observed in numerous natural and cultural contexts, including nucleosynthesis, minerals, prebiotic organic synthesis, languages, material culture, and cellular life. These systems possess such qualitatively similar characteristics as diversification into new environments (radiation), episodic periods of innovation (punctuation), and loss of types (extinction). Comparisons among these varied systems thus point to general principles of complexification.

KEYWORDS: evolution, complexity, diversity, punctuation, extinction

EVOLUTION UNDER FIRE

Biological evolution has become a lightning rod for controversy. No other topic in science has led to such contentious debate and rancor. In no other arena is the epistemological contrast between science and religion so starkly etched. Hardliners on both sides continue to polarize the issue, while many deeply conflicted nonscientists wonder if they must make the wrenching choice between science and God.

Here we propose a new rhetorical tack in this old debate. Systems that transform from relatively simple states to those of increasing complexity are not an isolated idiosyncrasy of biology, but rather a ubiquitous and recurrent characteristic of the physical and biological world (Chaisson 2001; Morowitz 2002; Zaikowski and Friedrich 2008). Examples include the formation of isotopes through stellar nucleosynthesis (Olive 2008; Schatz 2008, 2010 this issue); the evolution of mineralogy in terrestrial planets and moons (Hazen et al. 2008, 2009); the synthesis of prebiotic organic compounds at or near Earth's surface (Morowitz 2002; Hazen 2005); the evolution of languages (Dixon 1997; Atkinson et al. 2008); and innovation, technology transfer, and competitive selection in material culture (Eldredge 2002, 2009; Temkin and Eldredge 2007). Complexification in this broader context is the process by which a wide variety of natural and engineered systems display increased diversity in type, patterning, and behavior over time. In this context, why should the evolution of life be different from all other complex systems?

Given the universal occurrence of complex systems, coupled with the special importance assigned to understanding biological evolution, it is useful to compare and contrast these varied natural and human systems. In particular, we explore the roles of such themes as selection, diversification, punctuation, and extinction, as well as such variable evolutionary aspects as mutability, heritability, and lateral transfer. These concepts, which are readily

applied to biological evolution (e.g. Futuyama 2009), may have relevance to a much broader range of complex systems as well.

WHAT IS "EVOLUTION"?

The study of themes and variations in complex systems is complicated by two familiar but subtle terms that are shared across disciplines. "Species," for example,

has been formally applied to isotopes, minerals, and organic molecules, as well as to biological populations. However, the superficial similarity of these usages (meaning a distinct type or kind) may obscure the fundamental differences between the biological and nonbiological meanings. "Species" of isotopes, minerals, and molecules are characterized by immutable, quantifiable physical and chemical properties, in sharp contrast to the variable, evolving populations that comprise biological species.

Even more problematic is the word "evolution," which has been applied to numerous so-called "complex evolving systems" (Bowen 1928; Chaisson 2001; Morowitz 2002; Hazen et al. 2008; Zaikowsky and Friedrich 2008), albeit with some objections (Rosing 2008; Eldredge 2009). "Evolution" applies to all these systems only in the most general sense of "change over time," or perhaps "change with diversification over time" (i.e. complexification). Such a broad usage of the word "evolution" fails to capture the distinct and nuanced nature of biological evolution by natural selection, which itself can be defined in several ways (Eldredge 2008). Paleontologists might prefer the idea that all species that have ever lived on Earth are descended from a single common ancestor—a concept elucidated by the fossil record. Geneticists, in contrast, focus on information transfer: evolution is any permanent change in genetic information. Neither of these linked biological definitions of evolution bears any relationship to those applied to the complexification of nonliving systems. In this context, neither individual mineral species nor Earth's mineralogy *in toto* evolves.

EXAMPLES OF COMPLEX SYSTEMS

Diversification in type, patterning, and behavior is a universal property of complex systems that experience cycles of selective pressure, for example, through changing environmental conditions. In the following section we review distinctive characteristics of six familiar complex systems.

Nucleosynthesis Earth today hosts approximately 2000 different natural and anthropogenic isotopes, each representing a different combination of protons and neutrons. All of these isotopes emerged from reactions of the original four types of nuclei (H, D, He-4, and Li-6) that formed in

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nuclear condensation events within the first million years of the Big Bang (Olive 2008; Schatz 2008, 2010 this issue). Isotopic diversification began quickly with the formation of stars and the initiation of fusion reactions, which produced dozens of new isotopes of elements up to Fe in the periodic table (element 26). The first supernovae generated hundreds of new isotopes in dramatic punctuation events that seeded the cosmos with the raw materials of the first planets. Radioactive decay led to even greater isotopic diversity, while human engineering in the past 70 years has resulted in small-scale production of the heaviest-known elements and isotopes.

Mineral “Evolution” The mineralogy of the terrestrial planets has diversified over time as a consequence of a range of physical, chemical, and biological processes, as outlined in previous articles in this issue. In prestellar, dense, molecular clouds, widely dispersed microscopic dust particles contain approximately a dozen refractory minerals that represent the starting point of planetary mineralogy. Subsequent stages of mineral complexification, which led to the >4400 species known today, arose from three primary mechanisms. The first mechanism entailed progressive separation and concentration of elements by partial melting, crystal settling, phase separation, and other physicochemical processes. These various processes produced element concentrations in relatively small volumes compared to their original homogeneous distribution in the presolar nebula. New minerals also appeared as a result of an increase in the range of intensive variables, such as pressure, temperature, and the activities (effective concentrations) of H₂O, CO₂ and O₂ (i.e. new mineralogical environments). Finally, thousands of new minerals formed on Earth as a result of biological activity, which notably generated far-from-equilibrium conditions such as increased concentrations of atmospheric oxygen.

Prebiotic Organic Synthesis A prerequisite for the origin of life was the synthesis and selection of organic, molecular building blocks, including amino acids, sugars, lipids, and bases—a process commonly referred to as “molecular evolution” or “chemical evolution.” Numerous experiments employing a variety of energy sources and environmental conditions have demonstrated the facile synthesis of these and many other prebiotic organic compounds (Hazen 2005). Organic synthesis is governed by equilibrium thermodynamics (Helgeson and Amend 1994), yet the stereochemical and isomeric plasticity of organic compounds, coupled with the similarities in free energy of numerous varied states, leads to a kind of mutability in organic chemical species not seen in isotopes or minerals. For example, in many organic molecular species –SH may substitute for –OH, or –CH₃ for –H, with little change in the free energy of the system. Consequently, millions of different, plausible, small organic molecules may have populated Earth’s “prebiotic soup” (in contrast to the thousands of known isotopes and minerals).

Languages The evolution of languages provides an important example of a complex system with a form of heritable (and mutable) information. As language is passed from one generation to the next, it undergoes many gradual as well as relatively sudden changes, for example, in vocabulary, syntax, and idiom (Dixon 1997; Atkinson et al. 2008; Gray et al. 2009). Languages also display lateral transfer of vocabulary, and, especially when isolated in a small population, individual words and even entire languages may eventually become extinct.

Material Culture The rapid advance of material culture, especially in the realm of complex technologies, provides many of the most familiar and dramatic everyday examples of evolution, albeit evolution by design (Eldredge 2002, 2009; Temkin and Eldredge 2007). Computers, cars,

cornets, and countless other familiar objects change rapidly in competitive commercial environments, where personal choices by numerous individuals collectively apply selective pressure. Consider the case of cornets, a group of soprano brasswind musical instruments (Hazen and Hazen 1987; Eldredge 2002) that first appeared in 19th-century France as orchestral instruments and were most prominently employed at the Paris Opera (Fig. 1). By the mid-19th century, cornets had diversified, with numerous specialized models: over-shoulder designs for marching, higher- and lower-pitched versions for brass bands, tightly coiled “pocket” cornets for travel, and even jewel-encrusted cornets for popular soloists. Additional new styles of cornets were introduced as the instrument became a mainstay in American jazz, while older inferior versions, or designs that simply fell out of fashion, gradually became extinct (Eldredge 2002).



FIGURE 1 Cornets are members of the family of soprano brasswind musical instruments. They have displayed significant evolution during almost two centuries of development. PARISIAN CORNET, CA 1850, COURTESY NILE ELDRIDGE COLLECTION

Cellular Life Cellular life provides the quintessential example of an evolving complex system (e.g. Futuyma 2009). Biological evolution by natural selection shares some characteristics with complexification in other systems, but life’s evolution is fundamentally distinct in terms of its two intertwined defining characteristics: (1) common descent from a common ancestral cell or consortium of cells (Woese 1998) and (2) information transfer with genetic mutability as manifest in the variability of individual traits within populations.

THEMES IN COMPLEX EVOLVING SYSTEMS

The six varied examples of complex systems cited above share several traits that collectively help to characterize such systems.

Agents An intriguing similarity among all complex systems is that each type or kind (i.e. “species” in its most generic usage) can be described in terms of an arrangement of smaller building blocks, or “agents,” which can be combined in large numbers of configurations (Morowitz 2002; Hazen 2005). For example, all isotopes form from combinations of protons and neutrons; all minerals from arrangements of the 83 geochemically stable elements; and all cornets from standard components like mouthpieces, tubing, valves, and bells. Similarly, 26 different letters form words in English, whereas four different nucleotides encode genetic information in biological systems. The key to complexity is thus not a great diversity of agents, but rather a large number of potential configurations of those agents (Hazen 2009).

Selection In complex systems, new types or kinds arise through a selective process. Agents in these systems have the potential to adopt combinatorially large numbers of different configurations, such as combinations of protons and neutrons in isotopes, arrangements of atoms in minerals, and topologies of mechanical components in cornets. However, only a small fraction of all possible

configurations is observed owing to selection rules (e.g. Morowitz 2002; Szostak 2003; Hazen et al. 2007; Hazen 2009). Thus, neutrons and protons assemble into only a few hundred stable isotopes, while 83 chemical elements combine to form only a few thousand minerals. Similarly, while brass tubing and valves can be arranged into a vast range of intricate topologies, the laws of acoustics and human anatomy impose selective limits on the range of functional cornet designs. In all evolving systems, stochastic processes may influence specific outcomes of some selective events, but selection is ultimately guided by physical and chemical principles and thus, by definition, is not random.

Environments and Radiation Radiation into new environments is another common, if not universal, aspect of complex systems. New “species” (again in its most generic meaning) often populate new environments as they are created: new isotopes are formed in stellar cores, new evaporite minerals precipitate in dry lakes, and new amino acids are synthesized in Miller-Urey-type environments. One key to successful product marketing is the creation of new niches through clever advertising—a phenomenon seen repeatedly in the evolution of material culture (Eldredge 2009).

Punctuation and Stasis The proposal by Eldredge and Gould (1972)—that biological evolution may at times occur in rapid spurts of innovation between long intervals of relative stasis, or “punctuated equilibria”—reflects a common theme in a variety of complex systems. Punctuation is most often cited in a biological context (e.g. Pagel et al. 2006). Nevertheless, the near-instantaneous synthesis of hundreds of new isotopes in supernovae (Olive 2008; Schatz 2008), the diversification of near-surface minerals during the Great Oxidation Event (Hazen et al. 2008, 2009; Sverjensky and Lee 2010 this issue), the invention and introduction of technological innovations such as variants of the piston valve in brass musical instruments (Eldredge 2002, 2009; Temkin and Eldredge 2007), the publication of Noah Webster’s *American Dictionary of the English Language* (Atkinson et al. 2008), and geographical patterns of language change (Dixon 1997; Gray et al. 2009) can all be viewed in the context of punctuational events. Consequently, the introduction of new types or kinds in complex systems is not a steady process through time.

Extinction Extinction, the disappearance of some types or kinds, is a recurrent feature of complex systems. Short-lived radionuclides, such as ^{26}Al (half-life = 0.73 Ma), played an important role early in the development of the solar system but are no longer found naturally on Earth. Some near-surface mineral species, for example, some hydrous minerals on Venus following the runaway greenhouse effect, become unstable and disappear permanently from a terrestrial planet (Donahue and Pollack 1983; Johnson and Fegley 2003). Extinction is also familiar in complex systems associated with life: new technological innovations inevitably replace the old (Fig. 2), some words become obsolete, and more than 99% of biological species have become extinct.

VARIATIONS: NECESSITY VERSUS CHANCE

In spite of their many similarities, the diverse complex systems described above differ fundamentally in the extent to which changes result from necessity, chance, or design. The physicochemical processes of nucleosynthesis, mineral diversification, and prebiotic organic synthesis (at least in their initial stages) all appear to be largely deterministic: the same elements, isotopes, rock-forming minerals, and simple organic molecules are likely to be present on any Earth-like planet. These systems complexify according to principles of equilibrium thermodynamics, and thus diver-

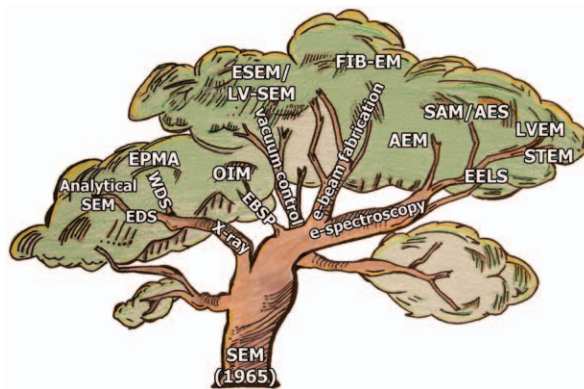


FIGURE 2 Scientific instruments display aspects of complex, evolving systems. The origin and evolution of scanning electron microscopes is represented in this tree diagram. ILLUSTRATION COURTESY OF JAMES D. SCHIFFBAUER, UPDATED AND ADAPTED FROM BALL (1996)

sify principally in response to the emergence of new physical and chemical environments in nebular, stellar, and planetary systems.

By contrast, chance genetic variations introduced through such mechanisms as mutations, sexual reproduction, and lateral gene transfer play a central role in biological evolution by Darwinian natural selection. Yet, while biology is unique among complex systems in the extent to which such variations facilitate change over time, some other complex systems, including language and material culture, also display information transfer with stochastic attributes (Dixon 1997; Eldredge 2002, 2009; Gray et al. 2009). It is important to recognize, however, that while genetic variations may be random, subsequent selective processes are not. Thus, biological systems display a significant degree of determinism, as reflected in the convergent evolution of such traits as eyes for seeing, wings for flying, legs for walking, and fins for swimming. Similarly, all languages require words that serve as nouns, verbs, or adjectives and that are phonetically consistent with oral anatomy, while evolution in material culture is bounded by such constraints as the desired function and human physiology.

The fundamentally deterministic characteristic of cycles of random mutation followed by selection serves as the basis for a number of modern technologies. For example, the experimental evolution of RNA aptamers (RNA oligomers that selectively bind to target molecules) is accomplished by first generating a solution with $>10^{14}$ random RNA sequences (Ellington and Szostak 1990; Bartel and Szostak 1993). This RNA-rich solution is poured into a container with glass beads that have been coated with target molecules. Most RNA oligomers do not interact, but a few sequences bind weakly to the target molecule and thus remain attached to the glass. These binding RNA strands are recovered and replicated with mutations to produce a new population of approximate copies, some of which display enhanced binding. After several cycles of recovery, mutation, and selective binding, optimal RNA aptamers are achieved. This elegant evolutionary process is now used to produce RNA sequences with a wide range of specialized functions, including locking onto target viruses.

Genetic algorithms (Holland 1992; Goldberg 1989; Koza et al. 1997) provide a computational approach that mimics Darwinian evolution to optimize solutions for problems that are too complex to solve with traditional design strategies. Exceptionally difficult problems in such fields as fluid dynamics, materials science, and electronic circuit design are now routinely solved with this evolutionary approach. Of special interest in the context of minerals are genetic

algorithms designed to predict crystal structures, for example, of minerals under extreme pressure and temperature conditions (Glass et al. 2006; Oganov and Glass 2006). One strategy is to sample a wide range of structure space by first identifying relatively stable structural subunits and then shearing, stacking, or otherwise shuffling these subunits to converge on optimally stable structures. In some respects this computational process may mimic the actual physical shuffling of atoms and molecules in three dimensions during crystal growth.

A FINAL COMMENT ON DESIGN

Engineering by design, which stands in sharp contrast to engineering by computational evolutionary algorithms, can act as a powerful mechanism for complexification (Eldredge 2008, 2009). Obvious examples arise in material culture, where innovation drives the evolution of new products. Many other systems are also subject to evolution by design: dozens of human-made isotopes are produced in high-energy accelerators, thousands of new mineral-like compounds find technological applications, and millions of organic molecules have been synthesized in laboratories.

Genetic engineering has resulted in numerous new varieties of single-celled and multicelled organisms, and holds the prospect of creating new species by design.

Nevertheless, the idea that life is “irreducibly complex” and, consequently, that the origin of life required an intelligent designer has been soundly refuted on both scientific and philosophical grounds (Pennock 2002; Forrest and Gross 2004). Indeed, in terms of generating systems of high complexity, evolution by the cyclic Darwinian process of mutation and selection has proven to be far more effective than design. Darwinian evolution thus emerges as the most dramatic example of the cosmic imperative of complexification, which leads inexorably from atoms, to stars, to mineral-rich planets, and perhaps ultimately to life that is learning to know itself.

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