Synergistic Selection: A Bioeconomic Theory of Complexity in Evolution

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Abstract. The rise of complexity in living systems over time has become a major theme in evolutionary biology, and a search is underway for a "Grand Unified Theory" (as one biologist characterized it) that can explain this important trend, including especially the major transitions in evolution. As it happens, such a theory already exists. It was first proposed more than 30 years ago and was re-discovered independently by biologists John Maynard Smith and Eörs Szathmáry in the 1990s. It is called the Synergism Hypothesis, and it is only now emerging from the shadows as evolutionary theory moves beyond the long-dominant, gene-centered paradigm known as neo-Darwinism. The Synergism Hypothesis is, in essence, an economic theory of complexity. It is focused on the costs and benefits of complexity, and on the unique creative power of synergy in the natural world. The theory proposes that the overall trajectory of the evolutionary process over the past 3.8 billion years or so has been shaped by functional synergies of various kinds and a dynamic of Synergistic Selection (in effect, a sub-category of natural selection). The synergies produced by various forms of cooperation create interdependent "units" of adaptation and evolutionary change. Cooperation may have been the vehicle, but synergy was the driver. Some highlights of a new (2018) book devoted to this theory will also be discussed.

Keywords: Synergy, cooperation, evolution

1 Introduction

Much of the work in complexity science in recent years has been focused on the physical, structural, functional, and dynamical aspects of complex phenomena. However, complex living organisms are distinctive in that they are also subject to basic economic criteria, and to economic constraints. Biological complexity is not simply an historical artifact, much less the product of some exogenous physical trend, force, or "law". Over the years, many candidate laws have been proposed that have claimed to explain complexity in evolution, going back to Jean Baptiste de Lamarck's "power of life" and Herbert Spencer's "universal law of evolution" in the nineteenth century. In the latter part of the twentieth century, the development of new mathematical tools and rise of complexity theory in various disciplines inspired a plethora of new law-like, or mechanistic explanations. This theme has continued into the new century, as documented in detail in *Synergistic Selection: How Cooperation Has Shaped Evolution and the Rise of Humankind.*[1] (This paper will provide a brief summary of the argument in this book, rather than a stand-alone theoretical monograph.)

The problem with all such deterministic theories is that they explain away the very thing that needs to be explained – namely, the contingent nature of living systems and their fundamentally functional, adaptive properties. As the biologist Theodosius Dobzhansky long ago pointed out: "No theory of evolution which leaves the phenomenon of adaptation an unexplained mystery can be satisfactory." The purveyors of these theories often seem oblivious to the inescapable challenges associated with what Darwin called the "struggle for existence" in the natural world, and they discount the economics – the costs and benefits of complexity. Nor can they explain the fact that some 99 percent of all the species that have ever evolved are now extinct. Life is phenomenon that is at all times subject to the requirement that the bioeconomic benefits (direct or indirect) of any character or trait – including complexity -- must outweigh the costs. It is subject to functional criteria and the calculus of economic costs and benefits in any given environmental context.

2 Defining Biological Complexity

The basic question, therefore, is what are the advantages of biological complexity? However, there is also a prior question: What is "complexity"? One must start by defining what the term complexity means in relation to living systems before examining how – and why – biological complexity has evolved over time.

The issue of how to define biological complexity has been much-debated over the years, and it is evident that there is no one correct way to measure it; it can be defined in different ways for different purposes. However, two alternative methodologies are relevant (at least in theory) as ways of characterizing the broad evolutionary trend toward multi-leveled complex systems over the past 3.8 billion years or so, beginning with the origins of life and culminating (temporally at least) in humankind.

One method is structural. A synthetic complexity scale can be constructed from the number of levels of organization (inclusive of social organization), the number of distinct "parts", the number of different kinds of parts, and the number of interconnections among the parts. The other method is functional. A complexity scale can be derived from the number of functionally discrete "tasks" in the division/combination of labor at all levels of organization, coupled with the quantity of "control information" that is generated and utilized by the system.[2] Control information is defined as "the capacity to control the capacity to do work" in a cybernetic process; it is equivalent to the amount of thermodynamic work that a system can perform.[3] Both of these methodologies are relevant for the theory that will be described here.

3 Measuring the Costs and Benefits

There are also various ways of measuring the economic costs and benefits of biological complexity. The "ultimate" measure is, of course, reproductive success. Although the level of personal investment can vary widely in the natural world, an organism must sustain a minimal economic "profit" in order to be able to reproduce itself, and the more offspring it produces the more profitable it is from an ultimate evolutionary perspective.

However, there are also a many other "proximate" ways of measuring the costs and benefits involved in "earning a living" in nature, and a number of familiar economic criteria are likely to have been important from a very early stage in the history of life on Earth – capital costs, amortization, operating costs and, most especially, strict economic profitability. The returns had to outweigh the costs. There is, of course, a large research literature and various journals in behavioral ecology and bioeconomics that are focused on just such proximate issues.[4]

Consider the fundamental need for energy capture. Dating back to Erwin Schrödinger's classic lectures and small book, *What is Life?* in 1944, it has long been appreciated that thermodynamics is of central importance in understanding the nature of life, and the challenges of living.[5] Living systems must do work and are subject to thermodynamic entropy and the Second Law. This imposes significant functional requirements. However, there is also a deep tradition in biophysics that assumes away the economic challenges involved in creating "negative entropy" (Schrödinger's neologism for how living systems contradict the Second Law). Indeed, there is a school of theorists who have advanced the proposition that energy is somehow a free good and that available energy itself "drives" the process of creating order and organization in the living world.[6]

A famous experiment in physics, Maxwell's Demon, unwittingly demonstrated why this assumption is incorrect.[7] In a nutshell, there is no way the Demon could create thermodynamic order "without the expenditure of work" (to use Maxwell's own, ill-considered claim for the Demon). Living systems must adhere to the first and only law (so far) of "thermoeconomics", namely, that the energetic benefits (the energy made available to the system to do work) must outweigh the costs required for capturing and utilizing it. From the very origins of life, energy capture and metabolism has played a key role. As biological complexity has increased over time, the work required to obtain and use energy to sustain the system has increased correspondingly. Indeed, improvements in bioenergetic technologies represent a major theme in evolutionary history and, in every case, involved synergistic phenomena.

4 The Synergism Hypothesis

How, then, can one account for the evolution of biological complexity? Over the course of the past two decades, the subject of complexity has emerged as a major theme in mainstream evolutionary biology, and a search has been underway for "a Grand Unified Theory" – as biologist Daniel McShea characterizes it – that is consistent with Darwin's great vision.[8]

As it happens, such a theory already exists. It was first proposed in *The Synergism Hypothesis: A Theory of Progressive Evolution* in 1983, and it involves an economic (or perhaps bioeconomic) theory of complexity.[9] The same idea was later independently proposed by John Maynard Smith and Eörs Szathmáry in their two books on the "major transitions" in evolution.[10,11] Simply stated, cooperative interactions of various kinds, however they may occur, can produce novel combined effects – *synergies* – with functional advantages that may, in turn, become direct causes of natural selection. The focus of the Synergism Hypothesis is on the favorable selection of synergistic "wholes" and the combinations of genes that produce these wholes. The parts (and their genes) that produce these synergies may, in effect, become interdependent units of evolutionary change.

In other words, the Synergism Hypothesis is a theory about the unique combined effects produced by the relationships and interactions between things. It could also be referred to it as Holistic Darwinism because it is entirely consistent with natural selection theory, properly understood. Accordingly, it is the functional (economic) benefits associated with various kinds of synergistic effects in any given context that are the underlying cause of cooperative relationships – and of complex organization – in the natural world. The synergy produced by the whole provides the proximate functional payoffs that may differentially favor the survival and reproduction of the parts (and their genes). The well-known 20th century Behaviorist psychologist, B.F. Skinner, called it "selection by consequences."

5 Synergistic Selection

Maynard Smith also proposed the concept of Synergistic Selection in a 1982 paper as (in effect) a sub-category of natural selection. Synergistic Selection refers to the many contexts in nature where two or more genes/genomes/parts/individuals have a shared fate; they are functionally interdependent. Maynard Smith illustrated with a formal mathematical model that included a term for "non-additive" benefits. However, Synergistic Selection is an evolutionary dynamic with much wider scope even than Maynard Smith envisioned. It includes, among other things, many additive phenomena with combined threshold effects and, more important, many "qualitative novelties" that cannot even be expressed in quantitative terms. There are, in fact, many different kinds of synergy.[1] Synergistic Selection focuses our attention on the causal dynamics and selective outcomes when synergistic effects of various kinds arise in the natural world. The claim is that synergy, and Synergistic Selection, has driven the evolution of cooperation and complexity in living systems over time, including especially the major transitions in evolution.

One example (among many cited in the book) is the evolution of eukaryotes. Increased size and complexity can have many functional advantages in the natural world, and eukaryotic cells, inclusive of their complex internal architecture, are on average some 10-15,000 times larger than the typical prokaryote. However, this huge size difference requires many orders of magnitude more energy, and the key to solving this functional imperative was a symbiotic (synergistic) union between an ancestral prokaryote and an ancestor of the specialized, energy producing mitochondria in modern eukaryotic cells. Not only was this potent new combination of labor mutually beneficial for each of the two partners but it created a pathway for expanding and multiplying those benefits many times over. Some specialized cells in complex organisms like humans may contain hundreds, or even thousands, of mitochondria. Liver cells, for instance, have some 2,500 mitochondria and muscle cells may have several times that number. It could be referred to as a "synergy of scale."

6 The Creative Role of Synergy

Many things can influence the likelihood of cooperation and synergy in the natural world – the ecological context, specific opportunities, competitive pressures, the risks (and costs) of cheating or parasitism, effective policing, genetic relatedness, biological "pre-adaptations", and especially the distribution of costs and benefits. However, an essential requisite for cooperation (and complexity) – is functional synergy. Just as natural selection is agnostic about the sources of the functional variations that can influence differential survival and reproduction, so the Synergism Hypothesis is agnostic about how synergistic effects can arise in nature. They could be self-organized; they could be a product of some chance variation; they could arise from a happenstance symbiotic relationship; or they could be the result of a purpose-driven behavioral innovation by some living organism.

It should also be stressed that there are many different kinds of synergy in the natural world, including (as noted above) synergies of scale (when larger numbers provide an otherwise unattainable collective advantage), threshold effects, functional complementarities, augmentation or facilitation (as with catalysts), joint environmental conditioning, risk- and cost-sharing, information-sharing, collective intelligence, animal-tool "symbiosis" and, of course, the many examples of a division of labor (or more accurately, a "combination of labor"). Indeed, many different synergies may be bundled together (a synergy of synergies) in a complex socially organized "superorganism" like leaf cutter ants or *Homo sapiens.*

It should also be noted that size has played a critically important role in evolution, and that there is a close linkage between size and biological complexity, as discussed in depth by biologist John Tyler Bonner in his book, *Why Size Matters*.[12] However, size is not an end in itself. It arises because it confers various functional advantages – various synergies of scale. These may include such things as improved mobility, more effective food acquisition, efficiencies in energy consumption, more efficient and effective reproduction, and, not least, protection from predators.

Consider the example of volvocines, a primitive order of aquatic green algae that form into tight-knit colonies resembling integrated organisms. One of the smallest of these colonies (*Gonium*) has only a handful of cells arranged in a disk, while the *Volvox* that give the volvocine line its name may have some 50-60,000 cells arranged in the shape of a hollow sphere that is visible to the naked eye. Each *Volvox* cell is independent, yet the colony-members collaborate closely. For instance, the entire colony is propelled by a thick outer coat of flagella that coordinate their exertions to keep the sphere moving and slowly spinning in the water – in other words, a synergy of scale.

Some of the synergies in the *Volvox* were documented in a study many years ago by Graham Bell,[13] and in more recent studies by Richard Michod.[14] The largest of the *Volvox* colonies have a division of labor between a multi-cellular body and segregated reproductive cells. Bell's analyses suggested some of the benefits. A division of labor and specialization facilitates growth, resulting in a much larger overall size. It also results in more efficient reproductive machinery (namely, a larger number of smaller germ cells). The large hollow enclosure in *Volvox* also allows a colony to provide a protective envelope for its daughter colonies; the offspring disperse only when the parental colony finally bursts apart.

But there is one other vitally important synergy of scale in *Volvox*. It turns out that their larger overall size results in a much greater survival rate than in the smaller *Gonium*. The volvocines are subject to predation from filter feeders like the ubiquitous copepods, but there is an upper limit to the prey size that their predators can consume. The larger, integrated, multi-cellular *Volvox* colonies are virtually immune to predation from these filter feeders.

7 Quantifying Synergy

It should also be stressed that synergistic effects can be measured and quantified in various ways. In the biological world, they are predominantly related to survival and reproduction. Thus, hunting or foraging collaboratively – a behavior found in many insects, birds, fish and mammals – may increase the size of the prey that can be pursued, the likelihood of success in capturing prey or the collective probability of finding a "food patch." Collective action against potential predators – herding, communal nesting, synchronized reproduction, alarm calling, coordinated defensive measures, and more – may greatly reduce an individual animal's risk of becoming a meal for some other creature.

Likewise, shared defense of food resources – a practice common among social insects, birds, and social carnivores alike – may provide greater food security for all. Cooperation in nest-building, and in the nurturing and protection of the young, may significantly improve the collective odds of reproductive success. Coordinated movement and migration, including the use of formations to increase aerodynamic or hydrodynamic efficiency, may reduce individual energy expenditures and/or aid in navigation. Forming a coalition against competitors may improve the chances of acquiring a mate, or a nest-site, or access to needed resources (such as a watering-hole, a food patch, or potential prey). In all of these situations, it is the synergies that are responsible for achieving greater efficiencies and enhancing profitability.

8 Testing for Synergy

There are also various ways of testing for synergy. One method involves experiments, or "thought experiments" in which a major part is removed from the whole. In many cases (not all), a single deletion, subtraction or omission will be sufficient to eliminate the synergy. Take away the heme group from a hemoglobin molecule, or the mitochondria from a eukaryotic cell, or the all-important choanocytes from sponges, or, for that matter, remove a wheel from an automobile. The synergies will vanish.

Another method of testing for synergy derives from the fact that many adaptations, including those that are synergistic, are contingent and context specific, and that virtually all adaptations incur costs as well as benefits. Again, the benefits of any trait must, on balance, outweigh the costs; it must be profitable in terms of its impact on survival and reproduction. Thus, it may not make sense to form a herd, or a shoal, or a communal nest if there are no threatening predators in the neighborhood, especially if proximity encourages the spread of parasites or concentrates the competition for scarce resources. Nor does it make sense for emperor penguins in the Antarctic to huddle together for warmth at high-noon during the warm summer months, or for Mexican desert spiders to huddle against the threat of dehydration during the wet rainy season. And hunting as a group may not be advantageous if the prey is small and easily caught by an individual hunter without assistance.

Another way of testing for synergy involves the use of a standard research methodology in the life sciences and behavioral sciences alike – comparative studies. Often a direct comparison will allow for the precise measurement of a synergistic effect. Some of the many documented examples in the research literature include flatworms that can collectively detoxify a silver colloid solution that would otherwise be fatal to any one individual; nest construction efficiencies that can be achieved by social wasps compared to individuals; lower predation rates in larger meerkat groups with more sentinels; higher pup survival rates in social groups of sea lions compared to isolated mating pairs; the hunting success of cooperating hyenas in contrast with those that fail to cooperate; the productivity of choanocytes in sponges compared to their very similar, free-swimming relatives called choanoflagellates, and the difference in nutrient uptake between lichen partnerships and their independent-living cousins.

9 A "Grand Unified Theory"?

Albert Einstein long ago observed that "a theory is all the more impressive the greater is the simplicity of its premises, the more different are the kinds of things it relates and the more extended its range of applicability." I believe it is both possible and appropriate to reduce a fundamental aspect of the evolutionary process, in nature and human societies alike, to a unifying theoretical framework. Like the concept of natural selection itself, the Synergism Hypothesis involves an "umbrella term" (an open-ended category) that identifies a common causal principle across a very diverse array of phenomena. Synergistic Selection focuses our attention on the causal role that functional synergies have had at every step in the evolution of biological complexity, beginning with the origins of life itself, and especially including the major transitions in evolution; the "economic" benefits have always been the key.[1]

The Synergism Hypothesis can also account for the unique trajectory of human evolution, including the transformative influence of cultural evolution. Synergistic behavioral and cultural innovations played a key role at every stage. (There are three chapters in *Synergistic Selection* related to this thesis.)[1] It can also help to explain warfare in human societies, as elsewhere in the natural world. Among other things, warfare is a highly synergistic phenomenon.

The Synergism Hypothesis also encompasses the role of both "positive" and "negative" synergies and their selective consequences for a given organism, group, or species. One obvious example is how organized, cooperative predation may be viewed very differently by a group of predators and their prey. Another example is how individuals and corporations in human societies may benefit in various ways from burning fossil fuels, yet their combined actions also produce global warming (a negative synergy of scale).

It should also be noted that Synergistic Selection is a dynamic that occurs at both the "proximate" (functional) level and at the "ultimate" evolutionary level. Indeed, proximate synergies are in many cases the direct cause of differential survival and reproduction over time. Some predator-prey interactions are, again, a canonical example.

The Synergism Hypothesis also offers an explanation for the ubiquitous role of cybernetic "control" processes in living systems at all levels. (In humankind, we refer to it, variously, as "management", "politics", and "governance".) As Maynard Smith and Szathmáry detail in their two books on the major transitions in evolution, every new form of organization in the natural world represents a distinct "combination of labor" that requires integration, coordination, and regulation/policing.[10,11] From eukaryotic protists to Adam Smith's pin factory and the emerging global society in humankind, cybernetic governance is a central challenge and a necessary concomitant.

Finally, it should be stressed that Synergistic Selection can also be formally modeled. Two alternative models can be found in a 2015 paper in the *Journal of Theoretical Biology* co-authored with Eörs Szathmáry.[2]

10 Conclusion

Many theorists these days are calling for a new post-modern, post-neo-Darwinian evolutionary synthesis. Some theorists advocate the adoption of a more elaborate "multilevel selection" model.[15] Others speak of an "Extended Evolutionary Synthesis" that would include developmental processes and Lamarckian inheritance mechanisms, among other things.[16] Denis Noble has proposed what he calls an "Integrative Synthesis" that would include the role of physiology in the causal matrix.[17]

Whatever the label, it is clear that a much more inclusive framework is needed, one that captures the full dynamics and interactions among the many different causal influences at work in the natural world. We also need to view the evolutionary process in terms of multi-leveled systems – functional organizations of matter, energy, and information, from genomes to ecosystems. And we must recognize that the level of selection – of differential survival and reproduction – in this hierarchy of system levels is determined in each instance by a synergistic configuration, or network of causes. Indeed, the outcome in any given context may be a kind of vector sum of the causal forces that are at work at several different levels at once.

What is needed going forward is a broadly ecumenical paradigm that would provide more of a work plan than a finished product. Perhaps it could be characterized as an "Inclusive Synthesis." It would be an open-ended framework for explaining how, precisely, natural selection "does its work" in any given context (what causal factors influence adaptive changes). It would also represent an ongoing work-in-progress rather than a completed theoretical edifice.

However, the historical process through which multilevel biological systems have evolved over time can be framed as a sequence of major transitions in complexity – from the very origins of life itself to the emerging global society that humankind is now engaged in creating (for better or worse). And, at every level in this hierarchy, we can see the driving influence of synergy and Synergistic Selection. From an evolutionary/biological perspective, complexity has a purpose – or perhaps even many. In any case, biological complexity must ultimately pass the test of being useful for survival and reproduction. Cooperation may have been the vehicle, but synergy was the driver.

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