Synergy and the Bioeconomics of Complexity

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Abstract. Living systems are distinctive in that they are subject to basic economic criteria, and to economic constraints. They are obedient to the calculus of economic costs and benefits in any given environmental context. This applies to all biological traits, including complexity (which can be defined and measured in both structural and functional terms). A major theoretical challenge, therefore, is to account for the "progressive" evolution of complex living systems over time, from the origins of life itself to "superorganisms" like leaf cutter ants and humankind. Why has complexity evolved? A causal theory, called the Synergism Hypothesis, was first proposed by this author in the 1980s and was independently proposed by John Maynard Smith and Eörs Szathmáry in the 1990s. This theory is only now emerging from the shadows as a major paradigm shift is occurring in evolutionary biology away from a reductionist, individualistic, gene-centered model to a multi-level, systems perspective. The Synergism Hypothesis is, in effect, an economic (or bioeconomic) theory of complexity. It is focused on the costs and benefits of complexity, and the unique creative power of functional 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 synergies of various kinds. The synergies produced by cooperation among various elements, genes, parts, or individuals may create interdependent "units" of adaptation and evolutionary change that are favored in a dynamic that Maynard Smith termed Synergistic Selection (in effect, a sub-category of natural selection). Some methodological issues will also be discussed, and some examples will be provided.

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, as reflected in the papers for this volume. Well and good. Living systems are, after all, embedded in the physical world.

However, complex organisms are distinctive in that they are also subject to basic economic criteria, and to economic constraints. Biological complexity is not simply an end in itself, nor 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 (see the discussion in Corning 2018). In the latter part

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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. Perhaps most provocative is physiologist John Torday's (2016) claim that biological complexity is only an "epiphenomenon" of a mechanistic dynamic associated with physiological homeostasis (see also Torday and Rehan 2017).[1]

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. 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% 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

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[1] Though he is antagonistic to traditional neo-Darwinism, Torday's theory tacitly acknowledges the role of differential selection (natural selection) in evolution. His scenario posits the development of a set of highly synergistic physiological components that combined to produce homeostasis, which, he claims, has driven further physiological developments over time. But phrases like "selection advantage" and "positive selection" sneak into his discussion at various points. For example, he describes the over-engineering of lung capacity in land animals as being, very likely, the result of evolution "positively selecting for those organisms with optimal exchange capacity." It's natural selection in deep disguise.

A comment is also in order here regarding the mechanical engineer Bejan's (2016) much-hyped new theory of "everything" (his term) in physics, which he calls the "constructal law of design in nature." Bejan's claim is that there is a universal, inherent tendency for any "flow system" in nature – from rivers to living systems – to evolve over time in such a way as to provide "ever greater access to the currents that flow through it." Take, for example, the energy throughputs in living organisms. To Bejan, the increases in energy flows over the course of biological evolution accord with his physical law. It resembles similar physical trends. To a biologist, however, any increases in energy flows over time have had a strictly functional basis. An increase in efficiency, or in energy throughputs, is the end-product of natural selection – differential survival and reproduction among naturally occurring variations in energy capture/utilization capacities. Bejan's theory only accounts for the "winners". But, in reality, this is an artifact of the functional advantages involved and not of some exogenous "law". Indeed, Bejan's "flow" model cannot predict major functional variations in living systems. Consider water consumption. Filter feeders, like sponges, can process huge quantities of water in the course of a day, typically more than their own weight every few seconds. A human consumes only a small fraction of that amount, by weight. Moreover, the actual water throughput for any individual human is very much context-dependent. A marathon runner on a hot day will consume much more water (perhaps two quarts per hour) than a sedentary person of the same weight who is watching TV in an air-conditioned living room. It is the same with energy throughputs. Indeed, various specialized cells in our bodies consume vastly different amounts of energy (see below).

functional criteria and the calculus of economic costs and benefits in any given environmental context.[2]

So, the question is, what are the advantages of biological complexity? One (flippant) answer is that, if you assemble just the right "package" of attributes, you can create a human. A proper answer is much more complicated – of course. We need to start by defining what complexity means in relation to living systems and then examine how – and why – biological complexity has evolved over time.

2 Defining Biological Complexity

The question of how to define biological complexity has been much-debated over the years. 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 (see Corning and Szathmáry 2015). 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. 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 (see Corning and Kline 1998; Corning 2005, 2007). Both of these methodologies are relevant for the theoretical paradigm that will be discussed 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 of profitability 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

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[2] For example, Torday (2016) affirms that economic criteria have been operative even in the basic physiological evolution of living systems. One illustration: "…[I]t has been observed that the genome decreased by about 80%–90% after the Cambrian Extinction. The advent of endothermy may explain this phenomenon because ectotherms require complex enzymatic regulatory mechanisms in order to accommodate variable atmospheric temperatures, whereas the uniform body temperature of endotherms/homeotherms only requires one metabolic isoform to function optimally. Since metabolic genes account for 17% of the human genome, representing a fraction of the number of metabolic genes expressed by ectotherms, this reduction in metabolic enzyme heterogeneity would have contributed to the dramatic decrease in post-Cambrian genomic size." In other words, natural selection favored functional efficiencies/economies.

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 in behavioral ecology and bioeconomics that is focused on just such proximate issues (see especially Davies, Krebs and West 2012, as well as such journals as *Behavioral Ecology, Behavioral Ecology and Sociobiology*, and the *Journal of Bioeconomics*).

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. 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 (see for examples, Morowitz 1968; Kauffmann 1995; Holland 1998; Schneider and Sagan 2005).

A famous experiment in physics, Maxwell’s Demon, unwittingly demonstrated why this assumption is incorrect (see the detailed critique in Corning 2005, Chap. 13). 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 has never been a free good (although initially the costs may have been exogenous to the system, or “externalities” – see Corning 2018). As biological complexity has increased over time, the work required to obtain and use energy to sustain the system has increased correspondingly (see the review in Corning 2005). 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, do we 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 within mainstream evolutionary biology, and a search has been underway for “a Grand Unified Theory” – as biologist McShea (2015) characterizes it – that is consistent with Darwin’s great vision.

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. The same idea was later independently proposed in their two books on the "major transitions" in evolution. 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 create 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. I refer to it as Holistic Darwinism because it is entirely consistent with natural selection theory, *properly understood* (see the book-length elaboration in Corning 2005). 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).

Illustrates this idea with an analogy. The recipe for a biscuit/cookie is rather like the genome in living organisms. It represents a set of instructions for how to make an end-product. A shopper who buys a biscuit/cookie selects the "phenotype" – the end-product, not the recipe. So, if the recipe survives and the number of cookies multiply over time, it's only because shoppers like the end-product and are willing to purchase more of them. Although it may seem like backwards logic, the thesis is that functional synergy is the cause of cooperation and complexity in living systems, not the other way around.

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. As I argue in my 2018 book, 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. Synergistic Selection focuses our attention on the causal dynamics and selective outcomes when synergistic phenomena of various kinds arise in the natural world. For it is synergy, and Synergistic Selection, that has driven the evolution of cooperation and complexity in living systems over time, including especially the major transitions in evolution.

One example (among the many cited in my book) is the evolution of eukaryotes. Increased size and complexity can have many functional advantages in the natural world (see below), and eukaryotic cells, inclusive of their complex internal architecture, 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 novel 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. I refer to it as a "synergy of scale." (See also Lane 2017. For related work on the evolution of multicellularity, see Ratcliff et al. 2012, 2015.)

6 The Creative Role of Synergy

It should be emphasized that 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 is also important to stress 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) in the natural world. 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* (for details, see Corning 2018).

7 Quantifying Synergy

Synergistic effects can also 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. To repeat, 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 individual alone; 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 comparison between lichen partnerships and their independently-living cousins. Some of the most relevant examples can be found in comparative genomics (e.g., see Berens et al. 2015).

9 "Why Size Matters"

In his important book, *Why Size Matters,* Bonner (2006) focused on the critical role of size in evolution and, equally important, the close linkage between size and biological complexity as he defined it, namely, an internal cellular division of labor. Bonner's thesis was that increased complexity (thus defined) in living systems is driven by increases in size. "There are universal rules imposed by size," he tells us (p.x). He also asserts that "size is the supreme regulator of all matters biological" (p. 2). Indeed, "size is a prime mover in evolution…increased size requires changes in structure and function" (ibid.).

It is certainly true that there is an interplay between the physics of size and the engineering and functional challenges associated with building and maintaining a larger organism. Gravity is an obvious problem. And so is the problem of producing and diffusing greater quantities of oxygen, energy and nutrients throughout a much larger system. However, like many other monolithic theories, the truth in this case probably lies somewhere in the middle. Increased functional capabilities and efficiencies are also necessary as prerequisites for increased size, and the question of which came first might be resolved by viewing the causal dynamics from a longitudinal perspective – as a process of *reciprocal causation* over time (see especially Laland 2011, 2013). It is an argument that goes back to Darwin himself in *The Origin of Species.*

But more important, Bonner's hypothesis begs the question. Why have organisms grown larger over time? Why do we see a progression in evolutionary history from microscopic prokaryotes with their relatively simple internal division of labor to much larger, intricately organized and far more complex eukaryotes, then to multicellular organisms, and, finally, to organized societies composed of many individual organisms, sometimes numbering in the millions? The answer, in brief, is that 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, more efficient and effective reproduction, and, not least, protection from predators.

10 A Classic Example

Consider, for example, the 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 Bell (1985), and in more recent studies by Michod (1999, 2007, 2011). 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*. These algae 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 the filter feeders.

11 Toward a Post-modern Evolutionary Synthesis

Many theorists these days are calling for a new post-modern, post-neo-Darwinian synthesis. Some advocate the adoption of a more elaborate "multilevel selection" model. Others speak of an "Extended Evolutionary Synthesis" that would include developmental processes and Lamarckian inheritance mechanisms, among other things (see Pigliucci and Müller 2010; Jablonka 2013). Noble (2013) has proposed what he calls an "Integrative Synthesis" that would include the role of physiology in the causal matrix.

Whatever the label, it is clear that a much more inclusive framework is needed, one that captures the full dynamics, and the 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.

In the heyday of the Modern Synthesis in the twentieth century, the explanatory framework in evolutionary biology was often truncated to focus on genetic mutations, sexual recombination, and the mathematics of differential selection (changes in gene frequencies) in an interbreeding population. This mathematical framework, albeit with many refinements, remains the theoretical backbone of the discipline to this day. The fundamental problem is that it explains very little. Natural selection (properly understood) is not an external causal agency or a "mechanism". It is a metaphor – an umbrella term for a wide-open framework that encompasses whatever specific factors may influence biological continuity and change in any given environment. Equally important, it is no longer tenable to view genetic mutations as the primary source of creativity in evolution. There are many different sources of innovation. In the words of Noble 2014) and his co-authors: “DNA does not have a privileged place in the chain of causality.”[3] (See also Woese 2004.)

12 An Inclusive Synthesis

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,

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[3] Over the past few decades the fundamental tenets of neo-Darwinism have been convincingly challenged. It seems that organisms are active participants in shaping the evolutionary process. There is now a paradigm shift under way from an atomistic, reductionist, gene-oriented, mechanistic (robotic) model to a systems perspective in which “purposeful” actions and informational processes are recognized as fundamental properties of living organisms at all levels. In his important book, *Evolution: A View from the 21st Century,* the leading microbiologist Shapiro (2011, 2009) argues that cells must be viewed as complex systems that control their own growth, reproduction and even shape their own evolution over time. He refers to it as a “systems engineering” perspective. Indeed, there is no discreet DNA unit that fits the neo-Darwinian model of a one-way, deterministic gene. Instead, the DNA in a cell represents a two-way, “read-write system” wherein various “coding sequences” are mobilized, aggregated, manipulated and even modified by other genomic control and regulatory molecules in ways that can influence the course of evolution itself. “We need to develop a new lexicon of terms based on a view of the cell as an active, sentient entity,” Shapiro stresses. Echoing the views of a number of other theorists recently, he calls for “a deep rethinking of basic evolutionary concepts.” Indeed, Shapiro cites some 32 different examples of what he refers to as “natural genetic engineering,” including immune system responses, chromosomal rearrangements, diversity generating retroelements, the actions of mobile genetic elements called transposons, genome restructuring, whole genome duplication, and symbiotic DNA integration. As Shapiro emphasizes, ``The capacity of living organisms to alter their own heredity is undeniable. Our current ideas about evolution have to incorporate this basic fact of life.'

The well-known senior physiologist Noble (2012, 2013), in a recent paper, argues that all the basic assumptions underlying the Modern Synthesis and neo-Darwinism have been proven wrong. Specifically, (1) genetic changes are often very far from random and in many cases are directed by “epigenetic” (developmental) and environmental influences; (2) genetic changes are often not gradual and incremental (Noble cites, among other things, the radical effects of DNA transposons, which have been found in more than two-thirds of the human genome); (3) an accumulation of evidence for a Lamarckian inheritance of epigenetic influences that has now reached the flood stage; and (4) natural selection, rather than being gene focused, is in fact a complex multi-leveled process with many different levels and categories of causation. Woese and Goldenfeld (2009) in their critique of the modern synthesis characterize life as a “collective phenomenon.” And evolutionary theorist Eva Jablonka and her colleagues (Jablonka et al. 1998; Jablonka and Raz 2009; Jablonka and Lamb 2014) identify four distinct “Lamarckian” modes of inheritance: (1) directed adaptive mutations, (2) the inheritance of characters acquired during development and the lifetime of the individual, (3) behavioral inheritance through social learning, and (4) language-based information transmission. It could be called the extended genome. In a recent review of the mounting evidence for this Lamarckian view, Jablonka (2013) concludes: “The existing knowledge of epigenetic systems leaves little doubt that non-genetic information can be transmitted through the germ line to the next generation, and that internal and external conditions influence what is transmitted and for how long.” The developmental biologist West-Eberhard (2003) goes even further: “Genes are followers, not leaders, in adaptive evolution.”

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. Nor would it seek to reduce natural selection ultimately to some simple formula or "mechanism". No single discipline (or model) can capture such a complex, multi-faceted narrative. In the longer run, our theoretical enterprise will require a synthesis and integration of the many different specialized and rapidly growing areas of knowledge (see Love 2010).

In the meantime, the historical process through which these 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. The arc of evolution bends toward synergy.

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