

THE ROLE OF SYNERGY IN THE EVOLUTION OF LIVING SYSTEMS

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ABSTRACT

Living Systems Theory (LST), as well as System of Systems Processes Theory (SSP), and other theory and research in the systems sciences and complexity science have illuminated many aspects of how living systems work – their mechanisms, processes and relationships. The Synergism Hypothesis, originally proposed in 1983, addresses the evolution of “cooperation” in nature and why there has been a secular trend over time toward increased complexity in living systems. The theory highlights the role of functional synergy – adaptively significant combined effects that are interdependent and otherwise unattainable – in shaping the “progressive” emergence of complex living systems, an approach that is entirely consistent with modern evolutionary biology and natural selection theory. It is thus radically opposed to various orthogenetic/deterministic theories of complexity that have been proposed over the years. This theory has recently gained scientific support, and there is growing appreciation for the role of various kinds of synergy as an influence in the evolutionary process.

Keywords: Evolution, synergy, natural selection, systems theory, complexity theory

THE QUEST FOR A “GENERAL SYSTEMS THEORY”

It was the biologist Ludwig von Bertalanffy, more than anyone else, who inspired what came to be known as the systems sciences. His vision of a general system theory (and his advocacy for it) was a catalyst for the movement that led to the founding, in 1955, of the original Society for the Advancement of General Systems Theory. The founders included such luminaries as Anatol Rapoport, Kenneth Boulding, Margaret Mead, Ralph Gerard, and James Grier Miller, among others.¹

At the time, this was a bold and controversial step. Throughout the preceding two decades and more, scientific thinking and research had been dominated by reductionism, and by analytical approaches to scientific research. Holistic thinking was considered almost taboo, or verboten, in some quarters. The influential philosopher Bertrand Russell, for example, claimed that wholes are merely epiphenomena. He asserted that “analysis enables us to arrive at a structure such that the properties of the complex can be inferred from those of the parts” (Russell 1927, pp. 285-286). While the reductionists conceded that it was not currently possible, in many cases, for science to make such

inferences and predictions, this shortcoming was a reflection of the state of the art in science and not of some superordinate property in nature itself. In time, it was said, reductionism would be able to give a full accounting for emergent phenomena.

Von Bertalanffy rebelled against this scientific strait jacket. He reached back into an older intellectual/scientific tradition – dating back to Plato and Aristotle – which asserted the reality of “wholes” and the need for a science that studied their distinctive emergent properties -- properties that could not be accounted for in terms of the parts alone. (It was Aristotle, in fact, who coined what has become the mantra for systems thinkers. In *The Metaphysics*, he wrote “the whole is over and above its parts and not just a sum of them all” (1961, Book H, 1045:8-10).

In the inaugural edition of the annual Yearbook for the General Systems Society in 1956, von Bertalanffy spoke of a “quest for a general system theory.” (Note that both here and elsewhere he used the singular form of the term “system”.) As he explained it in his later, book-length monograph *General System Theory* (1968):

There exist models, principles and laws that apply to generalized systems, or their subclasses, irrespective of their particular kind, or the nature of their component elements, and the relations or “forces” between them. It seems legitimate to ask for a theory, not of systems of a more or less special kind, but of universal principles applying to systems in general (p. 32).

I will not recount here the ensuing debates over systems theory -- some of which remain unresolved to this day. (See especially the review by Troncale, 1988, updated in 2009, which identified some 33 major “obstacles” for the systems sciences.) Suffice it to say that these issues include such fundamental questions as how to define a system and whether or not there are any truly general, *non-trivial* principles that apply to all systems – ranging from, say, a “system” of philosophical thought (like Marxism) at one extreme to a binary star system out in the cosmos.

In any case, the idea of a single “general theory” encompassing systems of all kinds soon came under severe attack over what appeared to be its grandiose pretensions. Many of the scholars who called themselves systems scientists in the 1950s quickly backed away from von Bertalanffy’s “idealism”. (But see the detailed assessment of von Bertalanffy’s many contributions by Pouvreau and Drack 2007.) Indeed, within the first year, economist Kenneth Boulding – one of the founding fathers of the movement – famously characterized general systems theory (he used the plural form of the term), not as the search for a Holy Grail but as a “skeleton” (or a scaffolding) for the more modest aim of studying the many different kinds of systems and, hopefully, discovering some common principles and features among them. In his lead article for the first issue of the *General Systems Yearbook* (reprinted from a *Management Science* article) in 1956, Boulding spiced his argument (as always) with some colorful prose:

General Systems Theory is the skeleton of science in the sense that it aims to provide a framework or structure of systems on which to hang the flesh and blood of particular disciplines and particular subject matters in an orderly and coherent corpus of knowledge. It is also, however, something of a skeleton in a cupboard - the cupboard in this case being the unwillingness of science to admit the very low level of its successes in systematization, and its tendency to shut the door on problems and subject matters which do not fit easily into simple mechanical schemes...General Systems Theory may at times be an embarrassment in pointing out how very far we still have to go, and in debating excessive philosophical claims for overly simple systems. It also may be helpful however in pointing out to some extent where we have to go. The skeleton must come out of the cupboard before its dry bones can live (pp. 207-208).

Needless to say, the skeleton *did* come out of the cupboard, and in time it produced an impressive body of theory and research on the properties of systems of various kinds. In the process, the ideal of a general system theory faded into the background, and (significantly) the Society for the Advancement of General Systems Theory changed its name – twice. Today, of course, it is known as the International Society for the Systems Sciences (ISSS). Even von Bertalanffy acknowledged that living systems have certain unique properties that are not found (to our knowledge) in other kinds of systems – properties that are best characterized by the cybernetic concepts of “teleonomy” (goal-directedness), information, communications, control, and feedback, not to mention having a thermodynamic foundation.

LIVING SYSTEMS THEORY

Boulding’s skeleton metaphor was apropos in another sense as well. Much of the systems science work done in that era was anatomical in nature – the focus was descriptive. Systems theorists were more concerned with *how* systems worked, and with finding “isomorphies” among them, than with how they came to be -- an explanation for *why* they evolved. The apotheosis of this orientation was James Grier Miller’s Living Systems Theory (LST) and his monumental 1978 book entitled *Living Systems*. Miller’s book amounted to a kind of Gray’s Anatomy of living systems in that it sought to identify and describe in detail what he postulated to be the 20 “critical subsystems” associated with each of what he saw as eight distinct levels of organization in the natural world, inclusive of our uniquely human social organizations. Miller also posited some 173 cross-level hypotheses about the properties, relationships and interactions within living systems. (For a retrospective on Miller’s many contributions to the systems sciences, see Hammond, with Wilby, 2006.)

Miller’s model also included many of the features that are now widely recognized to be distinctive aspects of living systems: their open thermodynamic properties; their self-organizing capabilities; their goal-directedness; the important role of information and cybernetic processes; and the complex structural and functional relationships and interactions that characterize their dynamics. Miller’s living systems hierarchy included

cells, organs, tissues, organisms, groups, organizations, societies and the supra-national system. He recognized, though, that the real world does not always neatly fit into his hierarchy like “nested Chinese boxes,” as he put it. Indeed, we now know that ancient bacteria formed into tissues, groups, organizations (complete with a division of labor) and societies, literally billions of years before the emergence of eukaryotic cells, much less complex multi-cellular organisms.

One concern is that the nomenclature for Miller’s 20 subsystems has a somewhat abstract and mechanistic character. It includes such things as ingestors, transducers, decoders, timers, deciders, distributors, motors, and extruders, etc. In his later years, Miller conceded that his subsystems were “metaphorical” categories, but he continued to believe that there were functional commonalities between all of his system levels. Thus, he saw functional analogies between cilia (or undulopodia) at the cellular level and the United Nations’ motor pool, and between ribosomes in eukaryotic cells and the Office of Public Information at the U.N. and the drafters of U.N. treaties.

A more serious concern is that Miller’s model did not fully capture some aspects of the evolutionary process. He claimed, for instance, that a functional dynamic of “fray-out,” or a functional elaboration, was associated with the emergence of more inclusive systems. In fact, symbiogenesis – mergers of previously independent entities -- have come to be recognized as a major factor in the evolution of new levels of complexity and organization over time (among others, see Margulis 1970, 1993; Margulis and Fester 1991; Margulis and Sagan 1995, 2002; Maynard Smith and Szathmáry 1995; Corning 2003, 2005).

By the same token, many of the major discontinuities in evolution, such as the emergence of birds, are now well understood to be the result of incremental adaptations over time for one global purpose that were later recruited for a very different purpose through behavioral innovations. As bird evolution specialists Kevin Padian and Luis M. Chiappe (1998, p. 44), observed in a review article: "In summary, a great many skeletal features that were once thought of as uniquely avian innovations...were already present in theropods before the evolution of birds. Those features generally served different uses than they did in birds and were only later co-opted for flight and other characteristically avian functions, eventually including life in the trees." (See also Ostrom 1975.) The concept of “fray-out,” as an elaboration of the division of labor, might be more applicable to the evolution of complex human societies.

Another concern about Miller’s schema is that there are well-defined systems below the cellular level in living organisms, including organelles like the mitochondria and the chloroplasts (plastids) in eukaryotic cells that were originally free-living bacteria. Indeed, in many forms of symbiosis, the various system “partners” retain their individuality. Bacterial symbionts are vitally important partners in many complex organisms, including humans. Miller also may have underrated the role of what has come to be known as “downward causation” (or supervenience), the influence of more inclusive system levels in shaping the properties, the behavior, and the evolution of the parts over time (see Corning 2005).

Finally, there is now much evidence for the fact that each level of biological organization has unique “emergent” properties. Two landmark articles in *Science* many years ago advanced this argument. In “Life’s Irreducible Structure” (1968), chemist Michael Polanyi pointed out that each level in the hierarchy of nature involves “boundary conditions” that impose more or less stringent constraints on lower-level phenomena, and that each level operates under its own, irreducible principles and laws.

Likewise, the Nobel physicist Philip Anderson, in “More is Different”(1972), noted that one cannot start from reductionist laws of physics and reconstruct the universe. “The constructionist hypothesis breaks down when confronted with the twin difficulties of scale and complexity...At each level of complexity entirely new properties appear.” To illustrate, size matters – a lot. As the distinguished biologist John Tyler Bonner (2012) points out in his engaging new book on the subject, this is why a fly can walk up a wall much more easily than a human can.

In short, Miller’s model of living systems involved a somewhat static construct that was designed mainly to support the architecture of his framework. However, he was also insistent that modifications and refinements could be expected over time with the advancement of the biological and human sciences. (For an updated treatment of Living Systems Theory, with many elaborations, see the important contribution of Simms 1999. For a recent critique, see Troncale 2006.)

In any case, the focus of Miller’s *Living Systems* was on the mechanics of how complex living systems are constructed and on a search for functional isomorphies among various sub-systems, not on why living systems have evolved over time – in other words, a theory that could account for the “progressive” evolution of emergent complexity as a highly contingent phenomenon in the context of a challenging and ever-changing environment.

OTHER SYSTEMS THEORIES

In addition to Miller’s influential work, there have been many other important theoretical (and organizational) foci in the systems sciences over the years, from various cybernetic models to dynamical systems theory, control theory, systems dynamics, systems engineering, network theory and soft systems methodology, along with more specialized systems theories in specific disciplines, ranging from psychology to engineering, sociology, health care, and the management sciences. The many prominent systems theorists who have made book-length contributions over the years include (among others) Timothy Allen (1982; also Allen and Ahl 1996), H. Ross Ashby (1956, 1960), Kenneth Bailey (1990), Béla Bánáthy (1996), Stafford Beer (1959, 1972), Kenneth Boulding (1978), Peter Checkland (1981; also Checkland and Scholes 1990), C. West Churchman (1968, 1979), John Dillon (1982), Heinz von Foerster (1949), Michael Jackson (1991, 2000), George Klir (1969, 1972), George Lasker (1981), Ervin László (1996a), Humberto Maturana and Francisco Varela (1980), Mijahlo Mesarovic (1964, 1968), Howard Odum (1983), Talcott Parsons (1951, 1971), Howard Pattee (1973),

Robert Rosen (1970, 1991), and Paul Weiss (1971), along with the many contributors to the General Systems yearbooks and the Proceedings of the annual meetings of the ISSS over the years.

Especially notable is the work of Len Troncale, a former ISSS president, along with his colleagues on what he calls a System of Systems Processes (SSP) framework that is focused on identifying and mapping isomorphies among systems nodes and processes of all kinds, including some 100 that have been identified so far. (See especially Troncale 2006, where there are also comparisons with Miller's LST.)

Another notable contribution is the mathematical work in "Relational Biology" by biophysicist Robert Rosen (1970, 1978, 1991) and his followers. Rosen did path-breaking work in defining complexity and complex systems in dynamic terms and developed a sophisticated mathematics of organizational and functional relationships. (For recent work that builds on Rosen's foundation, see Kineman 2008, 2009, 2011; and Louie 2009.) Especially significant was Rosen's pioneering exploration of the phenomenon of "anticipation", which has added an important new dimension to cybernetics, control theory, artificial intelligence, and information theory (see especially Rosen 1985, Louie 2009, 2012; Nadin 2010a,b, 2012; Heylighen 2012).² Special note should also be made of the prolific and important work of physicist Herman Haken in synergetics, the science of cooperative phenomena (see Haken 1973, 1974, 1977, 1983, 1988, 1990).

However, the "ghost in the machine" -- to borrow the term popularized by the novelist/polymath Arthur Koestler (1967) -- is that much of the work in the systems sciences over the years, especially with regard to *living systems*, has lacked an evolutionary perspective. For instance, it is well understood in evolutionary biology that the interactions between an organism and its environment(s) shape the very character of the "system" over time, including its development, its viability, its longevity and its reproductive success, and that biological causation is inescapably interactional. Indeed, historical contingencies have greatly influenced the evolution of living systems, including the fate of human-designed systems. (Some theorists who did adopt an evolutionary perspective include Boulding, László, Maturana and Varela, Mesarovic, and Weiss. It should also be noted that Kineman has recently been striving to add a "contextual" domain to Rosen's framework. See Kineman 2011.)

Another concern is that systems scientists on the whole seem to have had a bias that takes cooperative relationships for granted and often assumes away or downgrades the ubiquitous influence of competitive interactions and their equally profound influence in the evolution of living systems. Both competition and cooperation have played major roles in shaping the evolutionary process, and one can only make sense of all this by introducing "bioeconomic" criteria and applying economic analyses to the problem of "earning a living" in the context of an unavoidably challenging environment. A more balanced perspective is central to the modern evolutionary paradigm and to a realistic understanding of the natural world (what could be referred to as "Darwin's Darwinism" as opposed to the "selfish gene" model of "neo-Darwinism").

NON-DARWINIAN THEORIES OF EVOLUTION

Of course, non-Darwinian orthogenetic and vitalistic theories of evolution also have an ancient pedigree (dating back at least to Aristotle) and have had a continuing presence in the theoretical dialogue over the centuries. There was Lamarck's "power of life," Herbert Spencer's energy-centered "law of evolution," Henri Bergson's *élan vital*, Hans Driesch's *entelechy*, Jean Piaget's *savoir faire*, Pierre Tielhard de Chardin's *omega point*, Ilya Prigogine's thermodynamic "dissipative structures," and many others. More recently, the rise of complexity theory has seen a new generation of orthogenetic theorists, many of them supported by the Santa Fe Institute, who have been inspired by new developments in non-linear mathematics and computer modeling.

For instance, John Holland, in his important 1998 book *Emergence*, asks: "How do living systems emerge from the laws of physics and chemistry...Can we explain consciousness as an emergent property of certain kinds of physical systems?"(p. 2). Elsewhere he speaks of his quest for what amounts to the antithesis of the entropy law (the Second Law of Thermodynamics) — namely, an inherent tendency of matter to organize itself. Holland illustrates with a metaphor. Chess, he says, is a game in which "a small number of rules or laws can generate surprising complexity." He believes that biological complexity arises from a similar body of simple rules.

There have been many variations on this basic theme in recent years, with numerous theorists invoking inherent self-organizing tendencies in nature. Francis Heylighen and his colleagues (1999) have claimed that evolution leads to the "spontaneous emergence" of systems with higher orders of complexity. Mark Buchanan (2000) discerns a "law of universality" in evolution — from our cosmic origins to economic societies — as a consequence of "self-organized criticality" as proposed by Per Bak and his colleagues (Bak and Chen 1991).

Biophysicist Stuart Kauffman in his most recent book, *Investigations* (2000), speaks of a new "fourth law of thermodynamics" — an inherent organizing tendency in the cosmos that counteracts the entropic influence of the Second Law. "A few deep and beautiful laws may govern the emergence of life and the population of the biosphere." Steve Grand (2001) views the emergence of networks as a self-propelled, autocatalytic process. Albert-László Barabási (2002) invokes "far reaching natural laws" that, he believes, govern the emergence of networks. And Niels Gregersen and his contributors (2002) see an "innate spontaneity" in the emergence of complexity.

Biophysicist Harold Morowitz (2002) comes closer than most theorists of this genre to a view that is compatible with the Darwinian paradigm. Recognizing that variability is inherent in the living world at every level, Morowitz posits that there are "pruning rules" that shape the forms that arise out of the many possibilities in evolution. However, Morowitz cannot specify what these pruning rules are and finds himself in sympathy with Tielhard de Chardin (and others) in believing that there is "something deeper" in the "orderly unfolding" of the universe.

A similar vision has been developed within the systems sciences community by the former ISSS president, futurist, and prolific theorist Ervin László. László and his many followers have advanced what he has called a General Evolution Theory (1996a,b; see also A. Laszlo 2009). GET, as it is sometimes called, postulates an inherent “cosmic process” in the universe – a universal evolutionary trend toward ever increasing complexity that is driven by “throughputs” of energy and information. László tells us “Evolution is not an accident but occurs necessarily whenever certain parametric preconditions are fulfilled” (1996b, p. 31). Thus, “biological evolution unfolds in a law-like manner...” (p. 89). And again, “The arrow of time in biological evolution points toward increasingly dynamic and autonomous species” (p. 91).

The “parametric preconditions” that László was referring to are thermodynamic in character. His theory was influenced by the nonequilibrium thermodynamics of physicist Ilya Prigogine and his theory about self-organizing “dissipative structures” (see Prigogine 1978, 1980, Prigogine and Nicolis 1971, Prigogine et al. 1972a,b; also see the critique of Prigogine in Corning and Kline 1998a,b). Thus, László tells us that “Periodic destabilizations of systems far from equilibrium coupled with an organizing effect of concomitant energy flow, push bifurcating systems up the ladder of the evolutionary hierarchy” (p. 50).³ (It should also be noted that, in his recent work, László has moved far beyond the confines of evolutionary biology and even the traditional physical sciences into the realm of a highly speculative panpsychic cosmology that invokes the influence of a cosmic information field – see e.g., László 2004.)

The key issue in László’s theory and others of a similar character is whether or not some intrinsic or external agency independently “drives” the process of biological evolution. Where is the locus of causation? From a Darwinian perspective, the problem with various orthogenetic theories is that they invoke overriding deterministic influences, rather than recognizing that biological evolution is at once shaped by the laws of physics (and thermodynamics) and yet is also historically determined, context-specific, and highly contingent. Biological evolution involves an open-ended, cumulative, opportunistic “trial-and-success” (or failure) process – an “economic” process in which local conditions play a key part. In fact, it is estimated that close to 99 percent of all the species that have ever evolved are now extinct.⁴

Thus, the many grand orthogenetic visions that have been advanced over the years can be called reductionist in the sense that they posit some underlying, inherent force, agency, tendency or “law” that is said to determine the course of the evolutionary process and the emergence of complexity in nature independently of the ongoing challenges of survival and reproduction. In effect, they explain away the problem that needs to be explained and deny the contingency of the (biological) evolutionary process.⁵

THE SYNERGISM HYPOTHESIS

One alternative to these non-Darwinian theories of complexity is known as the “Synergism Hypothesis,” which was proposed almost 30 years ago in the first of three books on the subject called *The Synergism Hypothesis: A Theory of Progressive*

Evolution (1983). The Synergism Hypothesis will be unpacked below, but it is worth noting that in 1983 very few scholars recognized it for what it was – a theory about living systems that is fundamentally “economic” in nature and yet is fully consistent with modern evolutionary biology. The theory was mostly ignored. One notable exception was Kenneth Boulding, a leading economist as well as a founding father of the ISSS. In a review for *Science Digest*, Boulding wrote:

This is a remarkable work, first of scholarship, and also of ideas. The scholarship is almost overwhelming. There are eighty pages of footnotes, almost all of them references...Furthermore, the works cited cover a great variety of disciplines, through the biological to the social sciences. It certainly stands out as a remarkable achievement, even though it is one that is almost impossible to review because of its richness and complexity....My own view... is that evolution consists of the filling of empty niches in ecosystems through mutations of different kinds... This view, however, supplements rather than contradicts the Corning hypothesis, with which I find myself in substantial agreement.

The Synergism Hypothesis also received a positive review from the well-known biologist Michael Ghiselin: “The basic thesis is sound...and Corning’s erudition lends great solidity to the work.”

Why is it that this theory was so poorly received (overall) back in 1983? There were in fact several interrelated reasons -- what could be called a “negative synergy,” or perhaps a “perfect storm.” These are discussed in some detail in a recently published retrospective article on the history of the theory (Corning 2011). However, bad timing was a major factor in an era dominated by the “selfish gene” model of evolution.

Suffice it to say here that a sea change is currently underway in evolutionary biology that has created a more favorable climate for the theory and that the Synergism Hypothesis has recently gained significant support. As the distinguished microbiologist James Shapiro observes in his new book, *Evolution: A View from the 21st Century* (2012), we are currently in the midst of “a deep rethinking of basic evolutionary concepts” (p xvii). There is a paradigm shift underway from an atomistic, reductionist, gene-centered, mechanical model to a systems perspective in which “purposeful” actions and cybernetic (information and control) processes are recognized as fundamental properties of living systems at all levels.

For instance, Shapiro points out that synergy plays a significant role even at the molecular and cellular level. He notes that “Most of the interactions between biomolecules tend to be relatively weak and need multiple synergistic attachments to produce stable functional complexes....the synergistic nature of most molecular complexes provides dynamism and flexibility to the transcriptional machinery... (p. 31) Later on he emphasizes “the importance of cooperative synergistic interactions... The need for cooperativity arises because many biomechanical interactions are either weak or

transitory, and multiple synergistic events stabilize the formation of functional complexes for carrying out cellular tasks...”(p 131)

Shapiro is not alone in recognizing the significance of synergy in evolution. Especially important was the endorsement of this idea by the distinguished biologists John Maynard Smith and Eörs Szathmáry in their 1999 book, *The Origins of Life*, where they arrived independently at the same theoretical conclusion while acknowledging the priority of the Synergism Hypothesis. Biologist Ernst Mayr also endorsed the theory when he read portions of *Nature's Magic: Synergy in Evolution and the Fate of Humankind* (2003). *Nature's Magic* also received very favorable reviews, overall, with one exception. Biologist David Sloan Wilson (2004), in an influential on-line review, headlined a dismissive critique with the title “Beware of Theories of Everything.” He was unresponsive to the author’s rejoinder, “Beware of Caricatures,” which was posted at www.synergy-live.blogspot.com. Wilson has since become more supportive.

More recently, the 2005 book, *Holistic Darwinism: Synergy, Cybernetics and the Bioeconomics of Evolution*, has gained additional visibility for the theory. It too received several favorable reviews. The recent surge of interest in “emergence” has also expanded interest the theory, and a paper on “The Causal Role of Synergy in Emergent Evolution,” presented at a European conference on emergence in 2008, was published in a special issue of the journal *Synthese* devoted to emergent evolution (Corning 2010).

Equally significant, there has also been a growing appreciation for the role of synergy recently among other theorists and researchers in the biological sciences. One important example is the theoretical paper on “The Evolution of Eusociality” by Martin A. Nowak, Corina Tarnita and Edward O. Wilson (2010) in *Nature*. Nowak and his colleagues point out that, in the inclusive fitness model of cooperative relationships, “all interactions must be additive and pairwise. This limitation excludes most evolutionary [situations] that have synergistic effects....A group can be pulled together [whenever] cooperation among unrelated members proves beneficial to them, whether by simple reciprocity or by mutualistic synergism, or manipulation.... Relatedness is better explained as a consequence rather than a cause of sociality.” (See also the sharp criticisms and the authors’ reply in “Brief Communications Arising,” *Nature*, 471: E1-E10, especially Abbot et al. 2011)

Other recent theoretical support for the role of synergy in evolution includes a paper by E.O. Wilson and Hölldobler (2005) arguing that the evolution of eusociality in insects and termites is a product of group selection in relation to the ecological advantages – the synergies. In addition, Nowak (2006) identified five “rules” for cooperation (kin selection, direct reciprocity, indirect reciprocity, network reciprocity and group selection) and pointed out that each depends upon the benefit-cost ratios – in other words, the synergies. Traulsen and Nowak (2006) also stressed the role of group selection in the evolution of cooperation, while D.S. Wilson and E.O. Wilson (2008) highlighted certain kinds of synergistic phenomena (such as information) that may benefit a group as a whole. Van Veelen (2009) also argued that group selection models are required where synergies are involved. He observed that “there is a more general, but still very realistic

class of models with synergies, for which it is *not* possible to summarize their predictions on the basis of an evaluation of inclusive fitness.” And Clutton-Brock (2009) addressed the issue of cooperation among non-kin and saw mutual benefits (synergies) as more important than strict reciprocities. He noted “In some cases, cooperation generates immediate synergistic benefits shared by cooperators that exceed the costs of providing assistance.” He cited several examples. Synergy also figures in the comparative economics framework of Vermeij (2009).

Finally, neuroscientist/anthropologist Terrence Deacon’s *Incomplete Nature: How Mind Emerged from Matter* (2012) assigns a key role to synergistic effects in the emergence of purposeful, teleonomic systems in biological evolution, global effects that transcend the actions (and interactions) of the material “parts”. As Deacon concludes, “In effect, the new higher-order synergistic relationship that results is an expression of the morphodynamic processes that are implicit in the teleodynamics of the whole....On reflection, we can now see that ‘life’s several powers’ [quoting Darwin] include and depend on the underlying morphogenetic processes that synergistically support and generate one another” (p. 462).

Indeed, Deacon identifies many synergistic phenomena associated with the emergence of living systems. (Variations on the term are used some 51 times in his book.) For example, he proposes that the first step in producing self-organized, self-repairing, self-replicating “autogens” (as he calls them) involved a reciprocal complementarity -- a “source of synergy” -- between the two distinct processes of autocatalysis and self-assembling enclosures (p. 304). (For a different perspective on the origins of life, see Szathmáry 1999, 2005; also Periera et al. 2012.)

RE-INTRODUCING THE SYNERGISM HYPOTHESIS

Let us begin an overview of this theory by revisiting the concept of natural selection. It is important to keep in mind that natural selection is not (technically) a “mechanism”. It is an umbrella term that applies to whatever factors are responsible in a given context for causing differential survival and reproduction. Natural selection as a *causal agency* refers to the functional consequences that result from adaptively significant changes in a given organism-environment relationship. One must focus on the interactions that occur within an organism and between the organism and its environment(s), inclusive of other organisms. In other words natural selection is a consequence of the bioeconomic Apayoffs@ in various organism-environment interactions.

Another way of putting it is that natural selection does not Aselect@ genes; it differentially rewards, or disfavors, the functional effects produced by genes in a given context (the phenotype). As biologists Russell Lande and Stevan J. Arnold observed in an important overview article in the journal *Evolution* (1983, p. 1210): ANatural selection acts on phenotypes, regardless of their genetic basis, and produces immediate phenotypic effects within a generation that can be measured without recourse to principles of heredity or evolution.@ Alan Grafen (1991) calls it the Aphenotypic gambit.@ (See also

Brandon 1996; Hammerstein 1996; West-Eberhard 2003.) The phenotype is where the “payoffs” occur that lead to differential survival and reproduction.

One illustration is the English land snail (*Cepaea nemoralis*). These snails are subject to predation from thrushes, which have developed the clever habit of capturing the snails and then breaking open their shells with stones. In other words, a synergistic behavioral innovation (tool use) in one species has become a cause of natural selection in another species.

However, the impact of natural selection in the snails is also shaped by two additional factors, one genetic and the other ecological. It happens that *C. nemoralis* exhibit genetically-determined variations in shell banding patterns, which in turn provide varying degrees of camouflage. The result is that the more "cryptic" genotypes are less intensively preyed upon than those that are more visible to predators. However, the pattern of predation by thrushes (and the frequencies of the different snail genotypes) also varies greatly from one location to the next. The reason is that the thrush populations, being subject themselves to predators (like hawks), display a strong preference for well-sheltered localities. Paradoxically, the snails are much less subject to predation in more open areas (Clarke 1975). So it is a combination of genetic, ecological, and behavioral factors that has shaped the course of natural selection in *C. nemoralis*.

A further illustration of this causal dynamic can be found in the long-running research program among "Darwin's finches" in the Galápagos Islands, led by Peter Grant and his wife, Rosemary. Over the years, the Grants have documented many evolutionary changes in these closely-related bird species, particularly in the mix of beak sizes and shapes, in response to pronounced environmental fluctuations. During drought periods, for instance, the larger ground finches with bigger beaks survive better than their smaller cousins. Small seeds become scarce during the lean years, so the only alternative food source for a seed-eater is much larger, tougher seeds that must be cracked open to get at their kernels. Birds with bigger, stronger beaks have an obvious functional advantage, and this is the proximate cause of their differential survival (Grant 1986, 1991; Grant and Grant 1979, 1989, 1993, 2002; also Lack 1961/1947; Weiner 1994).

In both of these examples, the "causes" of natural selection were the functional effects of various organism-environment interactions, insofar as they impacted on differential survival and reproduction. Another way of putting it is that causation in evolution also runs backwards from our conventional view of things; in evolutionary change, effects are also causes. To use Ernst Mayr's (1965) well-known distinction, it is the "proximate" functional effects arising from any change in the organism-environment relationship that are the causes of the "ultimate" (transgenerational) changes in the genes, and the gene pool, of a species.

The Synergism Hypothesis represents an extension of this line of reasoning. It has also been referred to as "Holistic Darwinism," because the focus is on the selection of “wholes” and the combinations of genes that produce those wholes. Simply stated, cooperative interactions of various kinds, however they may occur, can produce novel

combined effects -- synergies -- that in turn become the causes of differential selection. The "parts" (and their genes) that are responsible for producing the synergies then become interdependent "units" of evolutionary change. Maynard Smith (1982, 1983) called it "synergistic selection," while David Sloan Wilson (1975, 1980; also Wilson and Sober 1994) speaks of "trait group selection."

In other words, it is the "payoffs" associated with various synergistic effects in a given context that constitute the underlying cause of cooperative relationships -- and complex organization -- in nature. The synergy produced by the "whole" provides the functional benefits that may differentially favor the survival and reproduction of the "parts". Although it may seem like backwards logic, the thesis is that functional synergy is the underlying cause of cooperation (and functional organization) in living systems, not the other way around. To repeat, it is really, at heart, a "bioeconomic" theory of cooperation and complexity in evolution.

Because this may be an unfamiliar idea, I will restate it in a slightly different way. The functional effects produced by cooperation (and organization) are the very cause of complexity in evolution. The "mechanism" (so to speak) underlying the evolution of complex systems is none other than the combined functional effects that these systems produce. It is the synergies that are the proximate causes of natural selection (or synergistic selection/trait group selection). Synergistic effects represent a distinct "class" of the "variations" that may be "favored" by natural selection. (It should be stressed that the Synergism Hypothesis is not a theory about the mechanics of how cooperative relationships and living systems work. Like natural selection, it is a theory about "why" these relationships and systems exist.)

It should also be emphasized that the Synergism Hypothesis is agnostic about how a selectively relevant synergy may arise, just as natural selection is agnostic about the sources of the "variations" that can influence differential survival and reproduction. A synergistic effect could be self-organized; it could be a product of some chance variation; it could arise from a happenstance symbiotic partnership, or it could entail a purpose-driven behavioral innovation by some living organism.

TAKING THE MEASURE OF SYNERGY

As the foregoing suggests, there are many different forms of selectively-relevant synergy in the natural world, including synergies of scale (when larger numbers provide an otherwise unattainable survival advantage), threshold effects, functional complementarities, augmentation or facilitation, joint environmental conditioning, risk- and cost-sharing, information-sharing, collective intelligence, animal-tool Asymbiosis@ and, of course, the many examples of a division of labor (although it should perhaps be called a "combination of labor") at every level in complex living systems (see Corning 2003, 2005). Moreover, the synergies can almost always be measured and quantified in various ways. Most often they are related directly 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". Joint action against potential predators -- alarm calling, herding, communal nesting, synchronized reproduction, coordinated defensive measures, and more -- may greatly reduce the individual's risk of becoming a meal for some other creature. Likewise, shared defense of food resources -- a practice common to 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 facilitate 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 water-hole, a food patch, or potential prey. (Many other examples are described in Corning 1983, 2003, 2005.)

Just as synergy comes in many different forms, 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 energy-producing mitochondria from a complex eukaryotic cell, 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 most adaptations, including those that are synergistic, are contingent and context-specific and that virtually all adaptations incur costs as well as benefits. The benefits of any adaptation must, on balance, outweigh the costs (it must be "profitable" in terms of its impact on the survival and reproduction). Thus, it may not make sense to form a herd, or a shoal, or a communal nest if there are no predators about, especially if proximity encourages the spread of parasites or concentrates the competition for locally scarce resources. Nor does it make sense for emperor penguins to huddle together for warmth at high-noon during the summer months in the Antarctic, or for Mexican desert spiders to huddle to prevent dehydration during the rainy season. And group-hunting is not advantageous if the potential prey are small and easily caught by an individual hunter without assistance. Orthogenetic approaches to complexity, like those described earlier, are blind to such functional contingencies, while the Synergism Hypothesis predicts that cooperation, and complexity, are ultimately dependent upon these bioeconomic criteria. Such contingencies are the rule.

A further 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 comparative study will allow for the precise measurement of a synergistic effect. Some examples (detailed in Corning 2005) include Planaria (flatworms) that can collectively detoxify a silver colloid solution; emperor penguins that can reduce their energy expenditures by up to 50 percent when they huddle together in winter; wasp

colonies with multiple queens that can out-compete colonies with single queens; 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 versus isolated mating pairs; the hunting success of cooperating hyenas in contrast with those that fail to cooperate; and the comparison between the choanocytes in sponges and the very similar free-swimming choanoflagellates.

A classic experiment in ecology provides a textbook illustration of how the effects of synergistic combinations can be measured and compared to the available alternatives. The experiment was designed to study the effects of sunlight and two different fertilizers (nitrate and phosphorus) on the growth of a small woodlands flower (*Impatiens parviflora*). One significant finding was that varying amounts of increased sunlight made little difference during the five-week test period without the addition of fertilizers. Furthermore, the use of only nitrate or phosphorous (essential ingredients for amino acids and proteins) made only an incremental difference. But when the plants were treated with the two fertilizers together, they weighed 50% more at the end of the test period than either of the two single-fertilizer groups and almost twice as much as the non-fertilized "controls". The results were clear cut. The separate contributions of sunlight, nitrogen and phosphorus in plant growth are synergistic, and the consequences are measurable -- as any skilled gardener already knows (Peace and Grubb 1982).

SYNERGY AND THE EVOLUTION OF COMPLEX SYSTEMS

An illustration of the role of synergy in the evolution of complex systems can be found in sponges, one of the simplest multi-cellular organisms in the natural world. (The following discussion is drawn from Bergquist 1978, George and George 1979, Ricketts, et al. 1985, and Curtis and Barnes 1989.) Although sponges come in many different sizes and shapes, the "model" sponge looks more like an urn or a vase than your typical kitchen sponge. Sponges are also the most rudimentary of all animals in terms of complexity. Indeed, they are often confused with plants because they are immobile and have no internal organs, no mouth, no gut, no sensory apparatus nor even a nervous system. They are more like a colony of cooperating independent cells. Sponges even have their own separate classification (Porifera, or "pore-bearers"), and they may have evolved separately from other animals.

Sponges also earn their living in one of the simplest possible ways, as filter feeders. They pull water into an internal cavity through large pores in their "skin", which consists of an outer layer of epithelial cells and a gelatinous inner layer with a skeleton of thin, bony "spicules"). The sponge's internal cavity is in turn lined with a layer of specialized "collar cells" (choanocytes) that are equipped with a whip-like flagellum and numerous filaments. These collar cells combine forces to move the water through the sponge and then push it out through a large opening at the top called an osculum. As the water passes through the sponge, the collar cell filaments extract oxygen and food particles (microbes and organic debris of various kinds). These vital nutrients are then distributed to the non-feeding cells via another specialized set of mobile transporter cells

called amoebocytes. The amoebocytes are also responsible for carrying wastes and for manufacturing and distributing various kinds of skeletal materials -- calcium carbonate, silica, spongin (a tough protein-like substance) or some combination of these, depending upon the type of sponge.

Reproduction in sponges is also (typically) a cooperative effort. Although the freshwater forms frequently reproduce asexually (often by casting off "gemmules" that are somewhat like seed pods), most sponges are hermaphrodites, meaning that they produce both sperm cells and eggs. The sperm cells are launched into the sponge's cavity and are ejected through the osculum in the hope that they will find their way to another sponge's cavity. When a sperm is lucky enough to enter a recipient sponge, it may be captured by one of the collar cells and then transferred to an amoebocyte, which in turn carries it to an awaiting egg. Eventually, the fertilized egg will become a free-swimming larva and will venture out on its own to find an appropriate site for developing into a new adult. It is really a unique reproductive system.

And that is about all there is to how sponges work, except for the chemicals they produce to repel potential predators. A division (combination) of labor is the key to the system, even though it involves only six cell-types -- namely, epithelial cells, pore cells, collar cells (choanocytes), amoebocytes and two kinds of sex cells. (Some larger sponges also have specialized cells that aid in opening and closing their oscula.) The point is that even the minimal level of complexity found in sponges is tied directly to the functional effects that the parts produce together -- the synergies. Each part is specialized for the role it plays in the "system." Each part is also completely dependent upon the other parts; no part could exist without the services of the others, and only together can they survive and reproduce successfully. Furthermore, the properties and capabilities of each part cannot be understood without reference to its role in the operation of the system as a whole. Nor can we understand the whole without an appreciation of how the parts work together.

In fact, sponges display several different kinds of synergy -- functional complementarities, a "combination" of labor, synergies of scale, and even structural (gestalt) synergies. For instance, the shape of the (classic) sponge, with its exit opening located at the top, utilizes physics to help pull water through its cavity, rather like the updraft in a chimney. As a result, a sponge can typically process a quantity of water equal to its own volume in less than ten seconds. Likewise, in the larger sponges -- some taller than a human -- the internal walls may be elaborately folded. This has the effect of greatly increasing the surface area available for filtering and feeding, in order to meet the increased nutritional needs of a larger organism.

How do we know this is a synergistic system? Just take away a major part -- say the amoebocytes, or the collar cells, or the epithelial cells, or skeletal spicules. Sponges would not exist without the synergy that their parts produce together. By the same token, imagine what would happen if one were to change its accustomed environment, say by putting a sponge into a nutrient-free swimming pool, or into an ice pack. Any theory of complexity based on the operation of deterministic laws cannot deal with the effects of

different contexts, or a contingent process, but a functional (bioeconomic) theory focused on synergistic relationships can. It was the functional synergies (the economic benefits, broadly defined) that were responsible for the evolution of sponges, not some hidden law of complexity. (Indeed, sponges lack several of Miller's 20 subsystems.)

SYNERGY AND THE FUTURE OF THE SYSTEMS SCIENCES

The systems sciences will no doubt continue to be pluralistic going forward, with a variety of interests and theoretical approaches. However, the time has come, it would seem, to acknowledge that synergies of various kinds have played an important role in the evolution of biological complexity over the past three billion years. Accordingly, one of the systems science "streams" in the years ahead should be focused on the dynamics, the biology, the ecology, and the *bioeconomics* of living systems (and their artifacts). In so doing, the systems sciences will also further the vision of its founding fathers. Within the science of living systems we also have an explanatory theory to account for the *evolution* of living systems over time that is fully consistent with modern evolutionary biology and Darwin's theory of natural selection.

FOOTNOTES

1. Debora Hammond (2002), in an article based on her dissertation research, stressed that there were many tangled roots for the systems science movement and that it was a "gargantuan task" to find and trace them all.
2. The importance of anticipation was underscored by the recent research report in *Nature* by Mitchell et al. (2009), which documented that even bacteria are capable of making predictions about future events and acting accordingly.
3. A provocative variation on the energy-centered theme in evolutionary theory is the proposal by Eric D. Schneider, as described in his 2006 book with Dorion Sagan, that our "higher purpose" is to serve as a sink for degrading energy and that our evolutionary trajectory has been oriented to becoming ever more efficient at doing so. We are, in a sense, like the Bénard convection cells that self-organize while dissipating energy – an analogy that Ilya Prigogine and other theorists use ad nauseum as a physical model of self-organization in non-equilibrium thermodynamics. This is a theory that involves what could be called the fallacy of misplaced purposiveness, a kind of bootleg teleology that thoroughly muddles the causal dynamics in evolution. It would make just as much sense to say that the universe and its available energy exists in order to create life. In fact, the relationship between energy and living systems is far too complicated to support a deterministic theory, much less a teleological explanation. The energy gradient thesis breaks down when confronted with a number of inconvenient facts, including the many other "sufficient conditions" that are also necessary to sustain life. Indeed, life is a "package deal," and a basic problem for living systems is energy capture, not energy dissipation.

4. Indeed, László seems to want to have it both ways. At various places in his book on the GET he acknowledges that evolution involves a “gamble”. He tells us that “life is continuously exploring novel combinations of structures and functions” (1996a, p. 89) that are always “vulnerable”. He is also well aware of the long odds against long-term survival for any species. It is not at all clear how his biology squares with his overarching theory.
5. There is one notable exception to the orthogenetic genre that should be mentioned, namely, the quixotic anti-Darwinian theory of biological “emergence” proposed by the emeritus physiologist Robert Reid (2007). Reid posits a self-contained experimental, “trial-and-error” process that was “sheltered” from natural selection by an internal “autonomy”, once homeostatic living systems had evolved. The problems with this formulation are two-fold. One is that living systems are never autonomous – that is, independent of their environment and its vicissitudes; they are embedded in, and deeply dependent upon, the ecological context. The other problem is that Reid in effect re-defined and truncated the concept of natural selection so that it applies only to ecological sources of selection. This is not how Darwin and the overwhelming majority of biologists understand the term. Differential survival and reproduction from whatever functionally-significant causes are examples of natural selection. (For a more extended critique of Reid’s theory, see Corning 2008.)

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