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"Synergistic selection": A Darwinian frame for the evolution of complexity

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HIGHLIGHTS

- The many non-Darwinian theories of complexity in evolution are briefly reviewed.
- We offer a Darwinian, "economic" theory that differs from gene focused approaches.
- We posit that synergy of various kinds has played a major causal role in evolution.
- This dynamic can be framed and modeled using the concept of synergistic selection.
- The growing interest in synergy and synergistic selection is briefly surveyed.

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ABSTRACT

Non-Darwinian theories of the emergence and evolution of complexity date back at least to Lamarck, and include those of Herbert Spencer and the "emergent evolution" theorists of the later nineteenth and early twentieth centuries. In recent decades, this approach has mostly been espoused by various practitioners in biophysics and complexity theory. However, there is a Darwinian alternative – in essence, an economic theory of complexity – proposing that synergistic effects of various kinds have played an important causal role in the evolution of complexity, especially in the "major transitions". We call this theory the "synergism hypothesis". We posit that otherwise unattainable functional advantages arising from various cooperative phenomena have been favored over time in a dynamic that the late John Maynard Smith characterized and modeled as "synergistic selection". The term highlights the fact that synergistic "wholes" may become interdependent "units" of selection. We provide some historical perspective on this issue, as well as a brief explication of the underlying theory and the concept of synergistic selection, and describe two relevant models.

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> "The whole is something over and above its parts, and not just the sum of them all…"
> —Aristotle, *Metaphysics* (Book H, 1045:8-10)

1. Introduction

The emergence and evolution of biological complexity over time has been a subject of speculation, theorizing, and debate for many centuries, but the predominant approach until very recently has been non-Darwinian[1]. Over the years, there have been a great variety of deterministic, orthogenetic, vitalistic, and otherwise "pre-programmed" theories. However, evolutionary biologists have recently begun to devote more attention to the problem of explaining this important aspect of the evolutionary process, with particular attention to the "major transitions" that have resulted in emergent new levels of biological organization.

Inclusive fitness, or kin selection theory, represents one pathway to solving this theoretical puzzle, but it is increasingly evident that this paradigm, while useful, is insufficient to account fully for the wide variety of cooperative phenomena in the natural world,

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[1] An anonymous reviewer reminded us of the pioneering but eccentric books on cooperation and the "bio-economics" of evolution by Reinheimer (1913, 1915).

including especially biological complexity, and the roles of both cooperation and mutualism (see Leigh, 2010a, 2010b). Here we will describe an alternative approach that could be characterized as an economic theory of cooperation and complexity, a theory that is compatible with both kin selection and multi-level selection theory.

What we call the "synergism hypothesis," and the closely related concept of "synergistic selection," involves a theoretical frame shift. The theory proposes that cooperative *functional effects* (synergies) of various kinds have provided selective advantages over time that has driven the evolution of complexity; the theory is concerned with the benefits and costs of various forms of cooperation. This theory is analogous to kin selection theory – and indeed to the concept of natural selection itself – in that it identifies an open-ended class of phenomena with common properties (functional synergies) that are said to have had causal significance in relation to an important aspect of evolution. However, there are many other influences at work as well. So kin selection, multi-level selection, mutualism, and synergistic selection are not mutually exclusive; they could well be complementary. Synergies produce combined effects that can render multi-level selection more potent. We begin with a brief review of the literature in complexity theory over the years.

2. Complexity theory, before and after Darwin

Perhaps the earliest "modern" theorist to advance the idea of an inherent evolutionary trend toward complexity was the eighteenth and early nineteenth century naturalist Lamarck (1914/1809), although the basic idea can be traced back at least to Aristotle's concept of "entelechy"[2]. A half century later, the renowned English polymath Spencer (1892/1852) elevated the idea of progress into an energy-centered "universal law of evolution" that spanned physics, biology, psychology, sociology and ethics[3].

Darwin was deeply opposed to such formulations, needless to say. He may have been directly rebutting Lamarck and Spencer, among others, when he wrote in *The Origin of Species*, "I believe in no fixed law of development" (Darwin, 1968/1859, p. 318). And again, "I believe … in no necessary law of development" (p. 348). However, Darwin never specifically addressed the evolution of complexity as such, nor even (more notoriously) the origin of species, although of course he was fascinated by the origin of complex adaptations, such as the eye, and suggested how they might evolve. Many generations of biology students have learned that Darwin was a convinced gradualist who frequently quoted the popular canon of his day, *natura non facit saltum*—nature does not make leaps. (The phrase appears no less than five times in *The Origin of Species*)[4].

2.1. Emergent evolution

Many theorists of the post-Darwinian era viewed Darwin's theory as unsatisfactory, or at least incomplete, and, in the early twentieth century, the so-called theory of emergent evolution was advanced as a way to reconcile Darwin's gradualism with the appearance of "qualitative novelties" and, equally important, with the widespread perception of a long-term trend in evolution toward new levels of organization and complexity, culminating (it was believed) in the human mind. Emergent evolution theory had several prominent adherents, but the leading figure in this school was the comparative psychologist and prolific writer, Conwy Lloyd Morgan, who ultimately published three volumes on the subject, *Emergent Evolution* (Lloyd Morgan, 1923), *Life, Mind, and Spirit* (Lloyd Morgan, 1926) and *The Emergence of Novelty* (Lloyd Morgan, 1933). (Other theorists in this vein included Samuel Alexander, Roy Wood Sellars, C.D. Broad, Arthur Lovejoy, and Jan Smuts, a one-time Prime Minister of South Africa)[5].

Emergent evolution theory represented a grand vision, but it was not an explanatory theory in the modern, scientific sense. Indeed, Lloyd Morgan, like many other theorists of his day, ultimately embraced a metaphysical teleology that portrayed the evolutionary process as an unfolding of inherent tendencies, which he associated with a creative divinity. (For a history of emergence theory, see Blitz, 1992.) But far more damaging to the concept of emergent evolution was the rise of the science of genetics in the 1920s and 1930s, along with the seminal theoretical work of Ronald Fisher, J.B.S. Haldane, Sewall Wright and others, and the triumph of the analytical, experimental method in biology[6]. Ever since the emergence of the so-called "modern synthesis" in the 1930s, evolutionary theory has been (predominantly) gene-centered and individual or kin selection-oriented. Indeed, in the wake of the discovery of the double helix and the genetic code, a gene-centered approach, generally referred to as "neo-Darwinism," came to be widely accepted as the foundation of evolutionary theory. For many years, biological complexity was mostly treated as a non-problem, or an epiphenomenon, with some important exceptions (see below).

2.2. The emergence of complexity theory

The re-emergence of emergence and complexity as mainstream theoretical concerns in the latter part of the twentieth century roughly coincided with the development of new, non-linear mathematical tools – particularly chaos theory and dynamical systems theory – which allowed theorists to model the interactions within complex, dynamic systems in new and insightful ways. Among other things, complexity theory gave mathematical legitimacy to the idea that processes involving the interactions among many parts may be at once deterministic yet for various reasons unpredictable.

However, the rise of complexity theory also spawned a new generation of non-Darwinian theorists. For instance, the computer scientist and algorithm pioneer John Holland, in his 1998 book

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[2] In his *Zoological Philosophy* (1914/1809), Lamarck spoke of an innate developmental energy in evolution – a "power of life" – which he likened to a watch spring (p. 292).

[3] "From the earliest traceable cosmical changes down to the latest results of civilization," Spencer wrote, "we shall find that the transformation of the homogeneous into the heterogeneous is that in which progress essentially consists" (Spencer, 1892/1852, I: p. 10).

[4] Indeed, Darwin rejected the very idea of sharp discontinuities in nature. In *The Origin* he emphasized what he called the "Law of Continuity," and he repeatedly stressed the incremental nature of evolutionary change, which he termed "descent with modification."

[5] The main tenets of Lloyd Morgan's paradigm will sound familiar to modern-day complexity theorists: quantitative, incremental changes can lead to qualitative changes that are different from, and irreducible to, their parts. By their very nature, moreover, the properties of such new "wholes" are unpredictable. Though higher-level, emergent phenomena may arise from lower-level parts, there may also be "return action," or what Lloyd Morgan termed "supervenience" ("downward causation" in today's parlance). But most important, Lloyd Morgan argued that the evolutionary process has an underlying "progressive" tendency, because emergent phenomena lead in due course to new levels of reality.

[6] In its most strident form, reductionism swept aside the basic claim of emergent evolutionists that wholes have irreducible properties that cannot be fully understood or predicted by examining the parts alone. Critics like Stephen C. Pepper, Charles Baylis, William McDougall, Rudolph Carnap and Bertrand Russell claimed that emergent qualities were merely epiphenomena and of no scientific significance. Russell, for instance, argued 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).

Emergence (Holland, 1998), asked: "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 in the book Holland spoke 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 (1998) illustrated with a metaphor from chess. Chess, he said, is a game in which "a small number of rules or laws can generate surprising complexity" (p. 3). He suggested that biological complexity arises from a similar body of (still hidden) simple rules.

The well-known theoretical biologist Stuart Kauffman in his early writings also aspired to the discovery of the underlying laws of evolution. In his 1995 book, *At Home in the Universe*, Kauffman (1995) asserted that "order is not accidental, that vast veins of order lie at hand. Laws of complexity spontaneously generate much of the order of the natural world….Order, vast and generative, arises naturally" (pp. 8, 25). He called it "order for free." In a later book, Kauffman (2000), p. 5, like Holland, also speculated about a possible "fourth law of thermodynamics," an inherent, energy-driven tendency in nature toward greater diversity. (It should be noted, however, that, in his more recent (Kauffman, 2008) book, his views have evolved; he now fully embraces the Darwinian paradigm.)

There have been many other variations on the non-Darwinian theme in recent years, with numerous theorists invoking inherent self-organizing tendencies in nature. Francis Heylighen et al. (1999) claimed that evolution leads to the "spontaneous emergence" of systems with higher orders of complexity. Buchanan (2000) discerned a "law of universality" in evolution – from our cosmic origins to economic societies – as a consequence of the phenomenon of "self-organized criticality" as proposed by Bak and Chen (1991). Grand (2001) viewed the emergence of networks in nature as a self-propelled, autocatalytic process. Barabási (2002) invoked "far reaching natural laws" that, he believes, govern the emergence of networks. Gregerson (2002) saw an "innate spontaneity" in the emergence of complexity. A similar argument can be found in the book by McShea, Brandon (2010). They posit a "first law' of biology—an inherent tendency in evolution for living systems to diversify and become more complex over time, unless constrained by natural selection. (See also the critical review by Bromham, 2011.)

Biophysicist Morowitz (2002) comes somewhat closer than most theorists of this school 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 (p. 55). However, Morowitz did not specify what these pruning rules are (perhaps he meant natural selection) and finds himself in sympathy with the anthropologist/priest Teilhard de Chardin (and others) in believing that there is "something deeper" in the "orderly unfolding" of the universe.

Finally, the emeritus biologist Robert G.B. Reid, in his book *Biological Emergences: Evolution by Natural Experiment* (Reid, 2007) claims that emergent complexity in evolution has been the result of an autonomous physiological experiment and that natural selection has played no significant role. In fact, Reid argues, it has often been a hindrance. He claims that freedom from ecological competition and natural selection has been an important facilitator of emergent evolution, and that the contribution of natural selection to the history of life on Earth has been confined at best to "fine-tuning" and "stabilizing" the innovations that arise from what he characterizes as an internally guided process. Once basic organismal integrity and homeostatic capabilities evolved, Reid says, evolution could go forward as an independent process subject only to the "obstructionism" of natural selection. As Reid puts it, Darwin got it "fundamentally wrong" (p. xiii)[7].
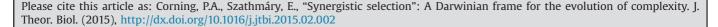
3. Darwinian approaches to complexity

All of these non-Darwinian theories can be called reductionist in the sense that they rely on some underlying, inherent force, agency, tendency, or "law" (or in Reid's case an autonomous process) that is said to determine the course of the evolution, or at least shape the evolution of complexity, independently of natural selection. In effect, these theorists explain away the very thing that needs to be explained—namely, the contingent nature of living systems and their fundamentally functional, adaptive properties. These theorists often seem oblivious to the inescapable challenges associated with what Darwin called the "struggle for existence" and they discount the bioeconomics—the costs and benefits of complexity. (For an extended discussion of this issue, see Keller, 2007.)

As Egbert Leigh (personal communication) has pointed out, Darwinian approaches to cooperation and complexity also have a deep tradition, although they have been less visible until quite recently. Darwin himself well understood the functional advantages of increased size and complexity. Indeed, the early twentieth century biologists J.B.S. Haldane and Julian Huxley, in their pioneering textbook *Animal Biology* (Haldane and Huxley, 1927), viewed an increase in size and complexity over time as the very essence of what they called "biological progress" (a characterization that is, of course, widely rejected today) and pointed out, among other things, the importance of modular organization and a "division of labour" (pp. 234–235)[8]. Also noteworthy was the early work on self-organization and the evolution of complexity by Hutchinson (1965) and especially John Tyler Bonner. In his 1988 book, *The Evolution of Complexity by Means of Natural Selection* (Bonner, 1988), Bonner explored at length the thesis that increased size and complexity were interrelated, and that these were functionally advantageous developments that had been favored over time by natural selection (see also Bonner, 2003).

In the latter part of the twentieth century, the role of cooperation in "symbiogenesis" – a term coined by the Russian theorist, Mereschkovsky (1909) – was championed by Margulis (1970, 1993), also Margulis and Fester (1991), especially in relation to the origin

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[7] How can it be that natural selection was *not* involved in what Reid concedes was an important trial-and-error dynamic—an "experiment"? Indeed, he tells us that: "Given a choice among similar individuals, those whose wholes are slightly greater than the sum of their parts will out-compete those whose wholes are slightly less" (2007, p. 197). In other words, natural selection was involved, but Reid restricts its role by assuming that basic homeostasis and organismal integrity created an internal autonomy – a protected experimental laboratory – and by re-defining natural selection so that it refers only to *external* ecological competition and predation. Natural selection really was a key player after all, but Reid hides its vital role in emergent evolution with a deeply flawed premise and a semantic segue.

[8] In Haldane and Huxley's words: "Thus we cannot say that evolution consists simply in the development of higher from lower forms of life; it consists of raising the upper level of organization reached by living matter, while still permitting the lower types of organization to survive. This general direction to be found in evolution, this gradual rise in the upper level of control and independence to be observed in living things over the passage of time, may be called evolutionary or biological progress. It is obviously of great importance, and can be seen, on reflection, to be another necessary consequence of the struggle for existence. This improvement has been brought about in two main ways, which we may call aggregation and individuation. Individuation is the improvement of the separate unit, as seen, for example, in the series Hydra–Earthworm–Frog–Man. Aggregation is the joining together of a number of separate units to form a super-unit, as when coral polyps unite to form a colony. This is often followed by division of labour among the various units, which of course is the beginning of individuation for the super-unit, the turning of a mere aggregation into an individual." (1927, pp. 234–5) We thank Egbert Leigh for providing us with this quote.

of eukaryotes but also more broadly (Margulis, 1998; Margulis and Sagan, 2002). Margulis saw symbiogenesis as a major pathway to increased complexity. Also important was Leigh (1977, 1991, 2010a, 2010b)'s work on "the common good" and on the factors allowing group selection to override within-group selection (see also Leigh, 1983). Finally, the extensive work on the role of development, and especially modularity, has further illuminated the evolution of biological complexity. (See especially Gould, 1977; Jablonka and Lamb, 1995; Raff, 1996; West-Eberhard, 2003; Kirschner and Gerhart (2006); and Wagner, 2014.) Complexity has now become a major theme in evolutionary biology (see below).

3.1. What is natural selection?

Here we will offer what is, in essence, an economic theory of complexity called the "synergism hypothesis" (Corning, 1983, 2003, 2005, 2007a, 2013), a theory that is compatible with various selection paradigms, including especially multi-level selection theory. But before we unpack this theory, it is important first to clarify the concept of natural selection, for it is often seriously misunderstood. The term is actually a metaphor for an important aspect, or property of the ongoing evolutionary process. (Darwin's inspiration for his metaphor was the "artificial selection" practiced by animal breeders.) Natural selection is really an umbrella concept that refers to whatever functionally-significant factors (as opposed to historical contingencies, fortuitous effects or physical laws and forces) are responsible in a given context for causing differential survival and reproduction. Properly conceptualized, these causal factors are always relational; they are defined both by organism(s) and their environment(s), and by the interactions between them.

Hence, we believe one cannot (technically) speak of a "mechanism" or fix on a particular "selection pressure" in explaining the workings of natural selection; these are only shorthand expressions. Clearly, natural selection can produce adaptations that are mechanisms (the cell cycle, the bacterial flagellum, the ribosome, etc.), but the "mechanism" of natural selection has a different meaning. One must instead focus on the relationships and interactions that occur within an organism, and between the organism and its environment(s), inclusive of other organisms. Natural selection does not "do" anything. As a causal agency, it refers to the functional consequences for differential survival and reproduction of adaptively significant changes in a given organism-environment relationship. In other words, it is a way of characterizing the bioeconomic consequences of any functional change. The "proximate" locus of causation is the developing organism and the fully-developed phenotype in a given environment—as many theorists have pointed out (e.g., Lande and Arnold, 1983; Grafen, 1984; Brandon, 1996; Hammerstein, 1996; Lewontin, 2000; Gould, 2002; West-Eberhard, 2003)[9]. We find useful philosopher Dennett (1995) characterization of evolution as an algorithmic process—a self-contained, step-by-step problem-solving process, albeit one that also includes a degree of randomness (see also Bäck, 1996; Maynard Smith, 1998).

Many things, at many different levels, may be responsible for bringing about changes in an organism-environment relationship and differential survival. It could be a functionally-significant mutation, a chromosomal transposition, a change in the physical environment that affects development (ontogeny), a change in one species that affects another species, or (often enough) it could be a change at the behavioral level that results in a new organism-environment relationship. (For an in-depth discussion of the role of behavior as a shaping influence in the evolutionary process, see Corning, 2014; also Bateson, 1988, 2004; Weber and Depew, 2003; Jablonka and Lamb, 2006a. See also the important work on "niche construction theory" and "ecosystem engineering" in Odling-Smee et al., 1996, 2003, 2013; Laland et al., 1999, inter alia.)

In fact, a whole sequence of changes may ripple through a pattern of relationships. For instance, a climate change might alter the local ecology, which might prompt a behavioral shift to a new habitat or niche, which might encourage an alteration in nutritional habits, which might precipitate changes in the interactions among different species, resulting ultimately in the differential survival and reproduction of alternative morphological characters and the DNA coding sequences that support them. The long-running research program among "Darwin's finches" in the Galápagos Islands, led by Peter Grant and his wife, Rosemary, provides an in vivo illustration of this causal dynamic (Grant, 1986; Grant and Grant, 2014; also Lack, 1961/1947; Weiner, 1994).

4. The synergism hypothesis

The synergism hypothesis represents an extension of this line of reasoning. The focus is on the selection of functional "wholes" of different kinds, 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 causes of differential selection. In effect, the parts (and their genes) that are responsible for producing the synergies may become interdependent "units" of evolutionary change.

Thus, 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 proximate 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 complexity, in living systems, not the other way around; proximate causes and ultimate causes are closely intertwined. So it is really, at heart, an economic theory of emergent complexity, and it applies both to biological and socio-economic evolution, most notably in humankind. (For more on this theory, see Corning, 2003, 2005.)

4.1. Synergy and the major transitions in evolution

John Maynard Smith and Eörs Szathmáry, in their two books on The Major Transitions in Evolution (Maynard Smith and Szathmáry, 1995) and The Origins of Life (Maynard Smith and Szathmáry, 1999), came to the same conclusion independently. As they put it in their later book: "Cooperation will not evolve unless it pays. Two cooperating individuals must do better than they would if each acted on its own…Behavioural examples are easy to think of, but the principle is relevant at all levels" (Maynard Smith and Szathmáry, 1999 pp. 23–24). Indeed, the primary focus of their two books is the major turning points in evolution that resulted in new levels of complexity. In every case, these transitions involved important new forms of synergistic cooperation, along with novel ways of storing, transmitting and using information. The transitions they identified included the following:

The emergence of the first replicating molecules in segregated, protective "enclosures";
The origin of chromosomes, which linked various replicating molecules together in cooperative relationships;

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[9] To use Mayr's (1961) 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 genomes of a given breeding population or species. It should also be noted that Laland et al. (2011) concur. In a reconsideration of Mayr's classic paper, they conclude that Mayr's proximate/ultimate distinction is deficient in that "it ignores the fact that proximate mechanisms contribute to the dynamics of selection." They argue that the concepts of reciprocal causation and recursion might be more useful. See also the cautionary analysis in Schulz (2014) regarding the imperfect relationship between economic "utility" and biological "fitness".

The origin of the genetic code for protein synthesis that linked RNA-based autocatalysis to that involving DNA and proteins;
The origin of eukaryotes from independent, free-living prokaryotes;
The rise of sexual reproduction;
The emergence of multi-cellular organisms and, over time, the development of an increasingly elaborate division of labor (or, more accurately, a "combination of labor");
The origin of social groups culminating in complex, highly integrated, communications-dependent species with a social division/combination of labor, like honeybees and humans.

As Queller (1997, 2000) has pointed out, these transitions involved two distinct pathways, which he characterized as "fraternal" and "egalitarian". In the former case, all of the participants were closely related, and this greatly facilitated the emergence of a reproductive division of labor (separation of the germ line), as well as the appearance of functionally differentiated tissues. A striking example is the rise of multi-cellular organisms. In the egalitarian case, the pathway was more "democratic" in the sense that each of the participants was genetically unrelated and retained the freedom to reproduce independently, while providing complementary functions for a new partnership. An obvious example here is the symbiotic mitochondria in eukaryotic cells (see also **Q4** Queller, 2004)[10] . Accordingly, the two terms "division of labor" and "combination of functions" as used by Queller (1997) refer to the origin of specialized actors in the fraternal and egalitarian scenarios, respectively. Our term "combination of labor" is functionally-oriented and includes both forms of cooperation.

As Maynard Smith and Szathmáry anticipated, other theorists have subsequently augmented their list of transitions, or have modified it in various ways. For instance, Jablonka and Lamb (2006b) consider the evolution of the nervous system, and the many changes that have resulted in the way information is stored and transmitted within living organisms, as another major breakthrough. There have also been various criticisms of the major transitions paradigm over the years (e.g., Calcott and Sterelny, 2011). In particular, there is a continuing debate about how to define biological complexity and exactly what a major transition in evolution means (see Szathmáry, 2015 for a thorough update of the field).

4.2. Measuring complexity

Our view is that there is no one correct way to measure complexity, or the major trends and transitions in evolution; they can be defined in different ways for different purposes. As a way of characterizing the broad evolutionary trend culminating (temporally at least) in humankind, we suggest two alternative methodologies (at least in theory). One is structural: A synthetic complexity scale compounded 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 derived from the number of functionally discrete "tasks" in the division/combination of labor at all levels, 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, 2007b.)

4.3. Defining synergy

A word is in order here about how to define synergy. As used here, the term refers to the combined, cooperative effects that arise from the relationships and interactions among various forces, particles, elements, genes, genomes, parts, individuals, or groups in a given context—*effects that are not otherwise attainable*. The term is derived from the Greek word *synergos*, meaning "working together" or, literally, "co-operating." Synergy is often associated with the cliché "The whole is greater than the sum of its parts," which dates back to Aristotle (as quoted above), but sometimes wholes are not greater than the sum of their parts, just different. A classic, much cited example is water, a versatile liquid compounded from the two elemental gases hydrogen and oxygen.

So defined, synergy is strictly a functional term, and the benefits and/or costs for the various "parts" must be separately determined. Although the term is sometimes treated as a synonym for cooperation, in fact it refers to the functional effects that are produced by cooperation. It highlights a class of causal influences with distinct functional properties (they are inherently relational and interdependent)—properties which, in the natural world, are always subject to the ultimate "verdict" of natural selection.

Some theorists may object to using such a broad definition of synergy, but it would be arbitrary to limit it only to a subset of cooperative effects and, more serious, would be unjustified if it excludes categories that are theoretically relevant. Another frequent objection is that the term should exclude additive forms of cooperation and include only those that involve "non-additive" phenomena. However, there are many forms of synergy that cannot be reduced to quantitative terms; they involve "qualitative novelties," as the emergence theorists have insisted. The criterion should be whether or not there are combined effects that are interdependent and cannot be achieved by the "parts" acting alone. Szathmáry (2002) cites the interactions between organelles in a eukaryotic cell as an example and illustrates with a steeply rising, non-linear "fitness curve."

In a similar fashion, if two hyenas can achieve success by coordinating their hunting activities but would not be successful if each one hunted independently, their combined efforts are synergistic; the two hyenas "added together" produce an interdependent, qualitatively different functional result. By the same token, if a specialization and division of labor (what we prefer to call a "combination of labor") can achieve significant economies/efficiencies with respect some overarching task or goal, this too is synergistic. In economics, the archetypical example is the description of an eighteenth century pin factory in Smith (1964/1776). Smith observed that the ten workers together were able to produce "upwards" of 48,000 pins per day, whereas, Smith opined, they probably could not independently have produced even 20 pins per man[11]. In biology, the archetypical example is, perhaps, the eukaryotic cell, and it is insufficient merely to say that the interactions among various organelles in a eukaryote are non-additive.

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[10] Since the actors that come together are functionally different to begin with, their separate functions can be combined, which provides the major advantage in egalitarian transitions. However, in the classical division/combination of labor scenario, labor is, of course, "divided" among the collaborators and then combined in a synergistic manner. It is also important to note that egalitarian transitions invariably involve a non-linear element at the outset. If the partners have complementary roles, one of them alone can do very little or nothing in the particular context. In the case of the fraternal transitions functional complementary is secondary, but does not necessarily require a long time to evolve. Cells when staying together to form primitive multicellular bodies (Schlichting, 2003) and individual insects when forming a colony (Robinson, 1992) may readily divide labor, as a result of the original individual adaptations and different thresholds for behavioral responses in different individuals. Apart from this, the initial advantage of staying together can be non-linear (hence synergistic) even among individuals of the same species. Such economies of scale may have been associated with the origin of many fraternal transitions (Queller, 1997). We will return to this issue below.

[11] See also ⟨http://www2.hn.psu.edu/faculty/jmanis/adam-smith/wealth-nations.pdf⟩ (accessed November 30, 2014), p. 11.

It is also important to note that there are many different forms of selectively-relevant synergy in the natural world, including synergies of scale (when larger numbers, or a larger size, provide an otherwise unattainable collective survival advantage), threshold effects, functional complementarities, augmentation or facilitation (as in catalysis), joint environmental conditioning, risk- and cost-sharing, information-sharing, collective intelligence, animal-tool "symbiosis" and, of course, the many examples of a division (combination) of labor at every level in living systems (see Corning, 1983, 2003, 2005; Maynard Smith and Szathmáry, 1995, 1999). Indeed, the major role of a division/combination of labor in the evolution of complexity has been highlighted by a number of theorists in recent years (e.g., Bonner, 2003; Kirk, 2005; Ratcliff et al., 2012; Simpson, 2012; Wilson, 2013)[12].

5. Facilitators and constraints

To be sure, many factors can influence the likelihood of cooperation—the ecological context, specific opportunities, competitive pressures, the risks (and costs) of cheating/parasitism, effective deterrents to "defection", genetic relatedness, genetic "preadaptations", and especially the distribution of costs and benefits. However, an essential requisite for sustainable cooperation is functional synergy. Just as natural selection is agnostic about the sources of the "variations" that can influence differential survival and reproduction, the synergism hypothesis is agnostic about how synergistic effects may 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 (see Corning, 2014).

It is also important to note that there are a great many different kinds of negative synergy (or "dysergy") in the natural world—cooperative effects that are deleterious to one or more participants, or to various "bystanders". For instance, cooperative hunting might be very beneficial for a group of predators, but the outcome would amount to negative synergy for their prey. Parasitism also provides innumerable examples. (More on negative synergy can be found in Corning, 2003.)

It should also be stressed that the synergies produced by cooperation can almost always be measured and quantified in various ways. Most often in the natural world they are related directly to survival and reproduction. Thus, hunting or foraging collaboratively – a behavior found in many bacteria, 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 defensive 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).

However, the costs and benefits of any synergistic effect are always contingent and context specific and must, on balance, provide a "profit" in terms of the 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 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 in the Antarctic to huddle together to share heat (as they do in winter) during the warm summer months, or for Mexican desert spiders to huddle against the threat of dehydration during the rainy season. And hunting as a group is not advantageous if the prey are small and easily caught by an individual hunter without assistance.

Richard Michod, in his book *Darwinian Dynamics* (Michod, 1999), observes that "cooperation is now seen as the primary creative force behind ever greater levels of complexity and organization in all of biology" (p. xi). However, it is not cooperation per se that is the "creative force." Rather, it is the functional consequences or effects produced by cooperation that are the key. And these in turn are shaped by various kinds of *functional synergy*. In other words, it is synergies of different kinds that have been the drivers for the evolution of cooperation and multi-level complex systems over time; the synergism hypothesis draws our attention to a broad class of causal influences that are found at all levels of organization throughout the living world, from genomes to empires. In a review of the current theoretical debate among proponents of inclusive fitness theory and its various opponents, Gadagkar (2010) points out that "the problem with most empirical studies inspired by [inclusive fitness theory] is that they have neglected the benefit and cost terms and focused almost exclusively on relatedness." (See also Fletcher et al., 2006; Michod and Herron, 2006; West et al., 2007a; Brown and Vincent, 2008.) The synergism hypothesis speaks to this concern.

6. Synergistic selection

One way of framing this economically-oriented causal dynamic is with the term coined by Maynard Smith (1982) paper on "The Evolution of Social Behaviour," where he identified synergistic selection as one of six different kinds of selection processes, along with individual selection, interdemic selection, kin selection, group selection, and reciprocal altruism. In his original formulation, Maynard Smith assumed that social cooperation necessarily involves altruism (as did most theorists of that era), and he defined synergistic selection as a process which involves non-relatives that interact as individuals. He compared it to Wilson's (1975) concept of "trait group selection," which also assumed an altruistic trait. (See also Leigh, 1997, 1991, 2010b's, work on the "common good.")

However, in Maynard Smith's analysis, the focus was not on the structure and composition of a "group" but rather on the functional/economic advantages (the synergies) that a group might possess as a result of their interactions. (Maynard Smith's analysis is summarized in Box 1.) In a subsequent paper, Maynard Smith (1983) also drew on Wilson's trait group selection model to illustrate how synergistic interactions might be selectively advantageous (although he viewed Wilson's term as inadequate). As Maynard Smith noted, it is the size of the "interaction term" in a synergistic selection model that is the

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[12] Bonner (2003) proposed that an increase in size has been a "prime mover" in the evolution of biological "differentiation." Kirk (2005), a student of volvocine green algae, identified what he called a "twelve-step program" leading from ancestral *Chlamydomonas* to *Volvox* (notable for its division/combination of labor) and found that it did not require a large number of genetic changes. Ratcliff et al. (2012), in a series of experiments in unicellular yeast (*Saccharomyces cerevisiae*), concluded that the benefits associated with a division/combination of labor played a key role in the emergence of multi-cellular "clusters". Finally, Simpson (2012) hypothesized that a reproductive division/combination of labor has led the way in "the majority of cases" where multi-cellularity has evolved. All of these theorists recognized the importance of a division/combination of labor but did not stress the independent causal role of the functional benefits—the synergies.

Box 1–Maynard Smith's "synergistic selection" model.

Synergistic selection is best illustrated by the simple textbook case in Maynard Smith (1998). Let W_0 be the fitness in the absence of interaction, c is the cost of help, b is the benefit that one cooperator C can provide and s is a non-additive bonus when two cooperators meet. In standard game theoretical format:

	D	C
D	W_0	$W_0 + b$
C	$W_0 - c$	$W_0 + b - c - s$

Let us consider the two cases: an additive one (left) and synergistic one:

$W_0 = 2, b = 2, c = 1, s = 0$			$W_0 = 2, b = 2, c = 1, s = 2$		
	D	C		D	C
D	2	4	D	2	4
C	1	3	C	1	5

It is apparent that for the additive case D is always the ESS, whereas for the synergistic case it pays to play D when meeting D, but it is better to play C when meeting C ($s > c$). The additive case corresponds to the Prisoner's Dilemma. When C gets somehow established (e.g., through kinship), it remains stable without punishment, or kin selection, or the like.

key factor. He likened synergistic selection to selection for "mutualism" in symbiotic relationships. Thus, Maynard Smith was shifting the theoretical focus to the functional dynamics of the phenotypes—the "vehicles" rather than the "replicators", in Dawkins' (1989/1976) terminology.

Needless to say, Maynard Smith's views about the nature of cooperation and the role of synergy evolved and expanded over time as he (and others, including Wilson) came to recognize that the term "cooperation" can refer simply to functional relationships and interactions of all kinds. In this formulation, cooperation may or may not also be considered "altruistic" or selfish, mutualistic or parasitic, positive or negative. Such attributes involve additional, post-hoc judgments about the consequences of a cooperative relationship with respect to some separately specified goals or values for the various participants. Indeed, there can even be coerced cooperation, where punishments are used as enforcers in a deeply asymmetrical relationship. An extreme example is a slave system[13].

Accordingly, we believe that the concept of synergistic selection can legitimately be expanded to include all the circumstances, at all levels of biological organization, in which synergistic effects exert a significant causal influence in evolutionary continuity and change. (We should note that the role of synergistic selection was also stressed by Maynard Smith in his 1998 textbook and, of course, in *The Major*

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[13] It should be noted that some theorists continue to define cooperation in such a way that it is theoretically problematical: altruism is treated as the default state. Thus, Sachs et al. (2004), claim that "Cooperation by definition involves an interaction between individuals that benefits the recipient but not necessarily the donor." See also Lehmann and Keller (2006), West et al. (2007a, 2007b, 2011). We disagree with this definition. One problem is that it conflates the functional properties of cooperation with the costs and benefits for the participants, and even perhaps with their psychological motivations. It also blurs the still-relevant distinction between proximate and ultimate explanations. These should be kept distinct from one another. The framework proposed by Sachs and his colleagues also obscures the phenomenon of "teamwork," joint efforts toward a common goal where there are no "donors" and "recipients".

Transitions.) As Maynard Smith and Szathmáry (1995) observed in *The Major Transitions* (p. 261), "if an individual can produce two offspring on its own but by cooperating in a group consisting of 'n' individuals can produce '3n' offspring, it pays to cooperate."

(It should be pointed out that this approach also has the effect of shifting the focus from "synchronic" treatments of group selection to a "diachronic" approach. Thus, what could be called multilevel selection type 1, where groups do not reproduce and group fitness is the average fitness of individuals in that group, can give rise through evolution to multilevel selection type 2, where groups reproduce as units and group fitness is neither defined in terms of, nor proportional to, average individual fitness, as Okasha, 2005, has noted.)

Thus, synergistic selection can be observed in processes as diverse as symbiosis, social selection, kin selection, group selection, altruism, mutualism, and, arguably, even in some cases characterized as manipulation or parasitism. Whenever synergies are in fact the functional drivers in any of these well-known theoretical categories, they also provide examples of synergistic selection. In other words, synergistic selection highlights a major functional/causal influence in selectively relevant biological processes when two or more genes, genomes, parts, individuals, groups, or even species are involved. (One route for achieving a favorable synergistic selection regime is represented in the theoretical work on so-called n-person public goods games with non-linear synergistic benefits. See Archetti and Scheuring, 2012. A different model, involving what we refer to as "corporate goods," can be found in Box 2. See also Frank, 1995 on the role of synergy in symbiosis.)

7. The problem of "control"

Synergy may be necessary for cooperation and complex organization, but it is obviously not sufficient. There are many challenges and obstacles associated with achieving and sustaining cooperative relationships, and these can be viewed as different aspects of the broad, many-faceted problem of control.

Perhaps most important is the problem of establishing and coordinating the relationships among the "parts"—that is, the cybernetic problem of communications and control in any teleonomic ("purposeful") dynamic system. The evolution of informational processes is addressed in some detail in *The Major Transitions* and *The Origins if Life*, where it is shown that new forms of information have played a key role in the emergence of complexity at every level, from DNA coding sequences in the genome to pheromone "signals" in social insects, the evolution of language in humankind, and (now) the binary/digital code of the internet age. (For a critique of traditional information theory and a functional alternative, see Corning and Kline, 1998; also Corning, 2007b. For a perspective on the synergistic nature of human language and its integration with other cognitive abilities, see Szathmáry and Számadó, 2008.)

Another critical set of challenges to achieving and sustaining synergistic cooperation are the many different problems related to the integrity and stability of various physical, biological and chemical processes, especially the potential for errors or mistakes, wear and tear, and environmental threats and depredations of varying kinds. Over time, living systems have evolved a great many mechanisms for dealing with these problems, from regulatory and repair capabilities at the molecular level to morphological redundancies, sensory/feedback capacities, developmental flexibilities, and, indeed, the opportunities for renewal and change associated with reproduction itself. Innumerable examples can be found in any introductory biology textbook.

There is also a major class of control issues related to the ever-present problems of reproductive competition, "cheating," and free-riding in the natural world, as evolutionary theorists ever since Darwin have stressed, and there is a vast and ever-increasing body of theory and research on various aspects of this challenge, with hundreds of analytical models. These constraints and facilitators are

Box 2–The "corporate goods" model of cooperation and synergy.

Corporate goods are benefits that are jointly produced by two or more participants but, unlike public goods, can be divided up in different ways among the actors—for example, the distribution of meat from a large game animal procured by a group of hunters, or the sales receipts for the pins produced in Adam Smith's pin factory. (We note that the term "public goods" is often misused in the evolutionary literature, because one of the defining features of public goods is that they are non-rivalrous. This is not true for corporate goods.)

In order for a corporate goods relationship to be favorably selected (synergistic selection) and be "sustainable" (or evolutionarily stable), the following conditions apply:

  i. There must be an overall "profit" (the benefits must outweigh the costs).
  ii. The benefits to each participant (direct, indirect, or both) net of the costs must be positive.
  iii. The relationship is supported/sustained by one or more of the following:
      a. There is a functional interdependence, such that the relationship is self-enforcing (as in the "rowing model");
      b. There is no better alternative (i.e., a more favorable benefit-cost ratio) available to any participant by "defecting" to some other relationship (a Nash equilibrium);
      c. The benefits may be reduced or denied to any defector;
      d. There is some other punishment/sanction for defecting (e.g., ostracism, denial of other benefits in a multi-faceted cooperative relationship, etc.).

Several models in the evolutionary literature utilize a corporate goods paradigm. One example is the stochastic corrector model (Szathmáry and Demeter, 1987; Grey et al., 1995; Maynard Smith and Szathmáry, 1995). In this model, different replicating genes (assumed to be ribozymes) co-operate in order to drive the metabolism of a protocell. Replication rates of the genes differ, so there is within-compartment competition (an early form of intra-genomic conflict), which translates to differential sharing of the corporate good (the raw materials for reproduction). Fast-replicating genes have a within-compartment advantage. It can be shown that, without a "corrective" population structure, such a model is unstable, despite the tight functional coupling among the genes for metabolism. It is important to add that, since here protocells are also units of evolution, variation among them, generated by stochasticity in growth and assortment, is a "target" on which natural selection "acts" among the protocells. (The stochastic corrector is also one of the earliest models of multi-level selection.)

addressed in such familiar structural categories as kin selection, group selection, indirect reciprocity, the extensive work on the role of "policing" and "sanctions" in cooperative relationships, and much more. (For an up-to-date overview, see the fiftieth anniversary issue of the *Journal of Theoretical Biology* in 2012 with some 20 articles devoted to various aspects of cooperation. For a critical review of the work on sanctions, see Frederickson, 2013.)

7.1. Rowing *versus "sculling"*

It should also be noted that there is another "structural" category of cooperative relationships that is often underrated or even overlooked, namely the many contexts in which there is a functional interdependence, and when the participants are dependent upon the benefits (the synergies) in such a way that cheating or free-riding would undermine those benefits and become self-defeating. Whenever such interdependencies exist, and they are more common than is often appreciated, a cooperative relationship is, in effect, self-enforcing. (Many mutualisms fit this model, as Leigh, 2010a has pointed out.) Or, alternatively, it may involve a situation where any "policing" costs are offset by enhanced benefits. These are examples of what Maynard Smith termed an evolutionarily stable strategy (ESS).

A hypothetical example is provided in *The Major Transitions*. It involves a game theory model in which two oarsmen in a rowboat are seeking a common objective, like crossing a river. If the two oarsmen utilize a "sculling" arrangement, each one would have a pair of oars and they would row in tandem. In this situation, it is easy (in theory at least) for one oarsman to slack off and let the other one do the heavy work. This corresponds to the classical two-person game. However, in a two-person "rowing" model, each oarsman has only one opposing oar. Now their relationship to the performance of the boat is interdependent. If one oarsman slacks off, the boat will go in circles.

An obvious biological example can be found in chromosomes. If a "selfish gene," in Dawkins' (1989/1976) metaphor, "defects" (and there are numerous well-known examples—see Crow, 1979), it undermines the ability of the genome to reproduce the organism successfully. Indeed, thanks to the human genome sequencing project, we now know that reproduction requires close collaboration (and synergy) among our 20,000 plus genes. One well-documented example is the homeobox (or Hox) cluster, a remarkably conserved gene set (with variations in number, from 8 to more than 40) that collectively determines the basic body plans of *Drosophila* flies, human embryos, and everything in between (Hunt, 1998). It is also relevant to mention the "parliament of genes" metaphor in this context, introduced by Leigh (1971). An individual selfish gene may be suppressed by an appropriate mutant of any other gene if all other genes are behaving in an orderly Mendelian manner: the latter in effect "vote the selfish member down." It is an objective of major transitions research to explain how "institutions" suppressing within-unit competition/conflict may have originated at various levels of organization in the first place.

The interdependent "rowing" scenario is especially relevant whenever a cooperative relationship involves a division (combination) of labor or a functional complementarity. In such cases, a defection or default could be fatal to a synergistic relationship. Imagine, as a thought experiment, a hemoglobin molecule without its heme group, or a eukaryotic cell without its mitochondria, or, for that matter, an automobile without a wheel. The synergies would vanish.

It is also important to emphasize that, *in theory*, the synergies in any given situation may be independent of how the costs and benefits are distributed among the participants (see Box 2). However, the distribution of costs and benefits matters greatly. Indeed, it is central to the distinctions theorists make between positive symbiosis and parasitism, mutualism and altruistic "sacrifices", reciprocity and free-riding, etc. This is the reason why the outcome in any game theory model is always dependent upon how the "payoff matrix" is constructed. And this is also why the ideal distribution of costs and benefits in any voluntaristic relationship is represented by a "Nash equilibrium" in which none of the participants can improve on their lot by defecting. (For more extensive discussion of this issue see especially Steven Frank's "The Origin of Synergistic Symbiosis," 1995, and Binmore, 2005) Of course, measuring the benefits and costs in any real world situation is often a challenge.

8. A technical note on the levels of selection debate

Finally, we wish to emphasize that the causal dynamics underlying the concept of synergistic selection are fully compatible with both kin selection theory and multi-level, or group selection theory. Here is our view of the matter.

In order to appreciate the relevant subtleties of a sometimes arcane debate, we will use the example of primordial evolution, since the issues relating to the first major transitions, involving molecules and protocells, are behaviorally simpler than in more complex organisms. As Eigen (1971) recognized, inaccurate replicators must somehow combine to form a genome. But there is a problem. If chromosomes are too long to be maintained by selection, the genome must consist of unlinked genes, which in turn gives rise to an early version of "intragenomic conflict" in that the genes can compete with each other. This conflict must somehow be mediated. Eigen (1971) proposed the hypercycle as a solution in which (in its two-member form) molecule A catalyses the replication of molecule B, and vice versa. There is synergy, because there can be no coherent growth of the whole system unless both partners are present; the effect is non-additive and synergistic. When both molecules are present, the system is ecologically stable.

But there is also a problem, as Maynard Smith (1979) observed. Imagine a parasite A' that replicates faster than A by accepting the help given by B but in return gives back little or nothing. Accordingly, without some population structure the system will go extinct. This teaches us that synergy provides great opportunities, but its origin and maintenance may require some form of multilevel selection. A simple way of taming the parasites is to put the hypercycles into compartments, in which case protocells with fewer parasites enjoy a reproductive advantage at the protocell level.

Now consider this case in light of the sculling game. The hypercycle resembles this model, and a parasite in the hypercycle is comparable to the oarsman who is not pulling on his (or her) oar. The boat corresponds to biological compartmentalization: literally, if the cooperators are in the same boat, it does not pay to rock it. In the sculling game there are two evolutionarily stable strategies (ESSs) and the spread of a cooperative equilibrium requires some grouping and selection at that level. The question is what might be the nature of this grouping, in addition to (and temporally before) reproductive compartmentalization? Here we must address some general questions relating to altruism, kin, and group selection.

Let us assume, as in the network of the stochastic corrector model, that two replicators A and B both contribute to a common metabolism M, which is a "corporate good" (Box 2). Assume M cannot work unless both genes are present. In other words, there is a clear synergy between A and B through complementary functions. Despite this synergy, however, the system is ecologically unstable *even in the absence of parasites*, provided A or B can drain metabolites (the corporate good) differentially for their own replication. The stochastic corrector model shows that reproductive compartments also save this system. Is it possible to have a simpler, but still effective, population structure ensuring cooperative coexistence? The answer is yes. It can be achieved in the surface-bound metabolic replicator model (Czárán and Szathmáry, 2000). Here a purely random formation of local groups is sufficient to maintain the coexistence of the cooperators in a basically D.S. Wilson-type (Wilson, 1975) MLS1 model. This is so because A relative to a faster replicating parasitic mutant A' is a weak altruist (Wilson, 1990) that pays only a relative cost; it helps itself as well, but it helps others even more.

Imagine, in contrast, a "one-member" hypercycle, i.e., a replicase enzyme R that is helping the replication of other copies of itself. R' is a parasite that is enzymatically inefficient but replicates when helped by R faster than R itself (Szabó et al., 2002). This system cannot be saved from the spread of R' by random grouping because R pays an absolute cost. In other words, one copy of R cannot help itself, because it needs another R acting as a template. Limited dispersal, and consequent kin selection, is necessary for survival. The same is true for hypercycles in general. Of course, the previously mentioned reproductive compartmentalization in protocells can also solve the problem via group selection.

The moral is that, when fitness costs are absolute, kin or group selection must operate. So we cannot escape considering the relation between the two. Hamilton (1975) cast Wilson (1975)'s model into a kin selection framework, showing that the Price formalism can express group (multilevel) selection as well (see also Crow and Aoki, 1982). Without going into the details here, there is a general feeling that, after all, it is a matter of taste, a secondary criterion, which type of modeling one can use. Others, however (e.g., Nowak, E.O. Wilson), argue that inclusive fitness calculations can give wrong answers. We call attention here to the important overview of Birch and Okasha (2015), who analyzed the various claims about inclusive fitness in detail. First, they point out that it pays to distinguish between three different versions of Hamilton's rule: (i) the general rule based on the use of regression, (ii) the special case, where costs and benefits are payoffs from an evolutionary model, and (iii) the approximate case where costs and benefits are first-order, marginal approximations of the regression coefficients. The conclusion is that (i) is always true, has explanatory but no predictive power. Case (ii) works well without synergy, but, when synergy is present, modifications of the original rule are needed on a case by case basis (van Veelen, 2009). Case (iii) is by definition approximate[14].

It would seem, therefore, that inclusive fitness works generally, but only in a loose sense, and in the various "stretched" situations it loses elegance and power. In the general case (i), inclusive fitness depends on the whole population state, and the assertion that the goal of an evolutionary agent is to "maximize its inclusive fitness" is not very helpful. Many actors in this debate nevertheless seem to believe that in principle kin and group selection models can always be translated into each other. This is not so. Especially in relation to the discussion about the major transitions, consider again the stochastic corrector model (Box 2). It is a continuous-time, fully dynamic model with reproducing and dying-out groups. Szathmáry (2012) suspected that a kin selection version of this model would be impossible, and Simon (2014) has shown that this is indeed the case. Kin selection versions of such group selection models are dynamically insufficient. Once you solve the group selection model you can always post hoc make up one using inclusive fitness, but this produces no additional information. Note that the stochastic corrector model (Szathmáry and Demeter, 1987) was preceded by the application of the same model to the origin of eukaryotic cells (Szathmáry, 1986), where protocells and cells provide strict group selection conditions.

Where does this leave us in relation to synergy? Synergistic interactions provide many opportunities for an increase in complexity. If these interactions are cooperative in the evolutionary sense, some appropriate selective influence is needed to stabilize the interaction. Sometimes there is a synergy between a synergistic interaction and selection. This happens in cases where the interaction allows for a cooperative equilibrium—when cooperators have an interdependent common interest (as in the rowing game). In these cases, the "work" needed from multilevel/kin selection is modest. When synergy does not lead to a stable synergistic equilibrium, it is harder to stabilize. But in all cases the complex interaction structure that gets selected is based on synergy among the components, and these synergies translate into considerable fitness advantages under the appropriate selection scenario.

9. Synergistic selection in recent publications

In recent years there has been a steadily increasing appreciation for the role of synergy in evolution. As West et al. (2008) point out (paraphrasing a comment in Maynard Smith, 1983): "A greater understanding in evolutionary biology is often obtained by looking

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[14] As Leigh (personal communication) points out, the so-called "egalitarian syndrome" in humankind (Boehm, 1997), including our monogamous propensities, represent a clear cut example of social behaviors that have served to reduce within-group reproductive variance.

at the same problem in different ways." Below is a brief survey of the rapidly growing number of synergy-oriented publications.

Some early efforts to find a theoretical basis for non-kin cooperation, though still constrained by the altruism assumption, included papers by Matessi and Jayakar (1976), Cohen and Eshel (1976) and Uyenoyama (1979), as well as the papers and a book by Wilson (1975, 1977, 1978, 1980) regarding his trait group selection model. (An early paper by Leigh, 1983, showed that within-group variance in reproductive success must be far lower than between-group variance in order for group selection to overcome strong within-group selection.) Following the publication of Maynard Smith's synergistic selection paper, other theorists began to move toward a more explicitly functional/synergism approach (often characterized as "non-additive" effects), notably including Queller (1985), Nee (1989) and Mesterton-Gibbons and Dugatkin (1992). Synergy was also invoked in the book-length thesis by Buss (1987), mentioned earlier, about the evolution of metazoans, and in a paper by Avilés (1999) that incorporated synergistic effects into a model of cooperative behaviors that utilized non-linear dynamics (see also Avilés et al., 2002).

Also notable were the papers by Frank (1995, 1997, 2006) on the role of synergy in the evolution of symbioses. Frank (1995) concluded: "A dominant theme in the history of life has been the evolutionary innovations of cooperative symbiosis." Elsewhere, Frank (2006) elaborated: "The first genomes near the origin of life probably evolved by biochemical synergism between different replicating molecules; eukaryotic cells arose by symbioses between different species; and lichens, mycorrhizal-plant systems, and many other symbioses have contributed greatly to the complexity of modern life." Indeed, there is a growing appreciation among biologists for the fact that symbiotic relationships are ubiquitous in nature and provide an important source of evolutionary innovations. (For more on symbiogenesis, see Sapp, 2004, 2009; Gontier, 2007; Carrapiço, 2010; Leigh, 2010a, 2010b; Gilbert et al., 2012; Pereira et al., 2012.)

A growing number of theorists over time have also explicitly adopted the term synergistic selection with regard to various biological phenomena. For instance, Guilford and Cuthill (1991) referred to it in their explanation for the evolution of warning coloration in marine gastropods. Toumi and Augner (1993) used it in relation to the evolution in plants of traits for unpalatability to predators. And Leimar and Toumi (1998) extended their work on the evolution of plant defenses to a consideration of how synergistic selection might work with "graded traits"[15].

It should be noted that David Sloan Wilson's views on the evolution of cooperation and complexity have also evolved over time. He adopted a more functionally-focused approach to defining "groups" in two papers with Elliott Sober (Wilson and Sober, 1989, 1994) and in their co-authored book, *Unto Others* (Sober and Wilson, 1998), where they provided numerous examples and case-studies of functional (synergistic) group selection. They also promoted the idea that an organized group may have properties that are analogous to those of an individual organism—a "superorganism". (A history and critical analysis of this term can be found in Corning, 2005; see also Wilson, 2006; Wilson and Sober, 1989; Hölldobler and Wilson, 2009)[16].

Also notable is Richard Michod's extensive work on the major transitions in evolution and the challenge of attaining new levels of "individuality" (functional interdependence) (Michod, 1999, 2005, 2007, 2011; see also Ghiselin, 1997). Michod's particular focus is the rise of multi-cellularity, as well as the origins of sexual reproduction, and he rightly emphasizes the cardinal importance of a division/combination of labor. He uses as his models the diverse colonies of volvocine green algae, which can range in size from a handful of cells to several thousand specialized cells arrayed in a large hollow sphere. As Bell (1985) first documented many years ago, the much larger, more complex *Volvox* species enjoy significant functional advantages over the smaller *Gonium*. Indeed, the rudimentary division/combination of labor in *Volvox* colonies has long been considered a "transitional" example pointing toward one of the most distinctive characteristics of multi-cellular organisms[17].

Among the many more recent examples of synergy-oriented publications, the theoretical paper by Nowak et al. (2010) on "The Evolution of Eusociality" – which challenges kin selection theory – is particularly relevant[18]. With regard to the emergence of eusocial insects in particular, the major causal factors singled out by these theorists were collaboration in building collectively defensible nests and an internal division/combination of labor, both synergistic behavioral. (But see also the sharp criticisms of this paper in Abbot et al., 2011 et. seq., and the authors' reply.)

Other recent theoretical support for the role of synergy includes a paper by Nowak (2006), where he identifies five "rules" for cooperation (kin selection, direct reciprocity, indirect reciprocity, network reciprocity and group selection) and points out that each depends upon the benefit-cost ratios—in other words, the synergies. (See also Nowak, 2011, 2012.) Traulsen and Nowak (2006) also stress the role of multilevel selection in the evolution of cooperation. Hauert et al. (2006) examine the effect of discounting in synergistically enhanced benefits based on the number of cooperators. Calcott (2008) invokes synergies in relation to the all-important benefit side of the cost-benefit calculus in cooperative behaviors, while Wilson and Wilson (2008) highlight the synergistic potential of social information. Referring to a phenomenon characterized as "the group mind," Wilson and Wilson observe that "the collective benefits of making a wise decision can be great and the within group costs can be low." (See also Seeley, 1995 for an example in honeybees.)

van Veelen (2009) also argues that group selection models are required where synergies are involved. Citing examples, he observes

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[15] However, the term has not always been used correctly, in our view. Tim Caro, in his book on *Anti-predator Defenses in Birds and Mammals* (2005) equates Synergistic Selection with what Dawkins (1989/1976), following Hamilton, called the "green beard effect"—preferential treatment toward an unrelated individual who happens to share a similar trait. This circumstance may be a facilitator, but we believe the term synergistic selection should be confined to the *consequences* of synergistic functional interactions – say, collective defense of a nest or coordinated hunting – where selectively-relevant synergies are jointly produced by the participants.

[16] In *Unto Others* and elsewhere, Wilson has also championed the idea of multi-level selection and has argued for viewing human evolution as a process that has involved human groups as "adaptive units." (See especially Wilson, 2006; also Wilson and Wilson, 2007, 2008). Wilson also drew our attention to the paradox –

(*footnote continued*)

first pointed out by Maynard Smith's revered and feared mentor, Haldane (1932) – that within-group altruism may serve to increase an altruist's absolute reproductive fitness even as it might reduce its fitness relative to other group members.

[17] However, we do have some disagreements with his interpretation of the role of synergy. Michod assumes synergistic relationships are cost free. We believe this is seldom the case; a favorable cost-benefit ratio is far more common. He also assumes that synergistic selection can occur only if there are heritable variants available, but in many situations the selective differences in fitness are binary—between cooperators and non-cooperators. Lichen symbioses, which can sometimes be facultative, provide an example. By the same token, a selective difference might be measured in relation to the bioeconomic payoffs—say, the interactions between a group of predators and their prey. Michod also assumes that there must be specialization among the members of any "higher level" group. This is very often the case (certainly in the major transitions), but it is not universally true. For instance, collective behaviors such as mobbing or joint defense of a nest-site may produce a "synergy of scale" with "public goods." *Volvox* provide a striking example. In nature, these planktonic green algae are subject to predation from filter feeders like the ubiquitous copepods, but there is an upper limit to the prey size these organisms can consume. So the largest, multicellular *Volvox* colonies are virtually immune from copepod predation (Bell, 1985). (Queller, 1997, referred to it as an "economy of scale.")

[18] Nowak and his colleagues argue that "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." In his 2013 book, E.O. Wilson elaborates on this point at some length.

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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) addresses the issue of cooperation among non-kin and sees mutual benefits (synergies) as more important than strict reciprocities. He notes, "In some cases, cooperation generates immediate synergistic benefits shared by cooperators that exceed the costs of providing assistance." He also cites several examples. Synergy also figures in the comparative economics framework of Vermeij (2009), while Bonsall (2010) discusses synergism in various host-plant pathogen interactions. Social scientists Price and Johnson (2011) highlight the role of synergistic cooperation in human groups. Ohtsuki (2012) examines the role of synergies in various Prisoners' Dilemma games. Purcell et al. (2012) argue that synergistic benefits can expand the conditions for the occurrence of sociality. And Taylor (2013) analyzes synergistic effects in graph-structured populations.

Especially significant is the accumulating evidence for synergistic effects at the molecular and cellular levels. For instance, microbiologist Shapiro (2012), in his book, *Evolution: A View from the 21st Century,* focuses on what he characterizes as "natural genetic engineering " and 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 [in the genome]…(p. 31). Later on Shapiro stresses again 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). (It is also important to stress that synergies within individuals may or may not elicit such effects between individuals. In other words, there may or may not be a correlation of synergistic effects within and between interactors.)

Synergy is also invoked by the neurobiologist/anthropologist Terrence Deacon in his *Incomplete Nature: How Mind Emerged from Matter* (Deacon, 2012). He assigns a key role to synergistic effects in the origin of life and the emergence of purposeful, teleonomic systems, culminating in the human mind. Deacon concludes, "On reflection, we can now see that 'life's several powers' [a quote from Darwin] include and depend on the underlying morphogenetic processes that synergistically support and generate one another" (p. 462). Deacon uses variations on the term "synergy" no less than 51 times in his volume.

Finally, it is noteworthy that David Sumpter deployed the concept of synergy extensively as an explanatory concept (and model) in his comprehensive study, *Collective Animal Behavior* (Sumpter, 2010). Sumpter addresses collective behaviors across a broad range of species and behaviors, from migration to food acquisition, information sharing, decision making, collective defense, and risk sharing, and he focuses especially on the relationship between mechanisms and their functions. Equally important, he utilizes his own and others' game theory models to analyze in detail the relationship between costs and benefits, and the functional consequences of cooperation or defection.

10. Conclusion

We think it fair to say that synergy is an idea whose time has come. Perhaps, therefore, the synergism hypothesis will come to be recognized as a plausible Darwinian theory of complexity in evolution, while the concept of synergistic selection may serve to help build a bridge between a selectionist theoretical framework and the many-faceted causal role that functional synergy has played in the rise of cooperation and complexity in living systems over time.

Ratnieks (2006), p. 1413, commenting on a "target" theoretical article about cooperation in the *Journal of Evolutionary Biology* (Lehmann and Keller, 2006) in which the authors alluded in passing to the role of synergy, summed it up as follows:

The condition under which cooperative helping is favoured by natural selection is simply the condition under which most traits are favoured by natural selection: greater reproductive success… However, this does not mean that there are no biological puzzles in understanding cooperation, or that the problems to be solved are trivial. For example, we still need to know how synergisms occur when individuals help each other. That is, how does cooperation enlarge the cake and how does it get shared…rather than monopolized? In my opinion, the answer to this problem will not be an all-encompassing condition arising out of a theoretical breakthrough, but a multitude of biological situations and idiosyncrasies that lead to the necessary synergy and sharing.

There is a story attributed to the famed twentieth century philosopher Bertrand Russell about a public lecture in which he discussed various properties of the Solar System. At the end of his lecture, an elderly woman in the audience approached him and told him he was wrong. The sun is held up on a turtle's back, she said. A startled Russell responded by asking her, so what holds up the turtle? "You think you're so clever," she replied. "It's turtles all the way down."

So what explains the rise of complexity in evolution? From the perspective of the synergism hypothesis and synergistic selection, it's synergies all the way up.

Uncited references Q2

Caro (2005), Law (1991), West et al. (2011).

Acknowledgements

References

Abbot, P., Abe, J., Alcock, J., Alizon, S., Alpedrinha, C., Andersson, M., et al., 2011. Inclusive fitness theory and eusociality ("Brief Communications Arising"). Nature 471, E1–E10.

Archetti, M., Scheuring, I., 2012. Review: game theory of public goods in one-shot social dilemmas without assortment. J. Theor. Biol. 299, 9–20.

Avilés, L., 1999. Cooperation and non-linear dynamics: an ecological perspective on the evolution of sociality. Evol. Ecol. Res. 1, 459–477.

Avilés, L., Abbot, P., Cutter, A.D., 2002. Population ecology, nonlinear dynamics, and social evolution. I. Associations among nonrelatives. Am. Nat. 159 (2), 115–127.

Bäck, T., 1996. Evolutionary Algorithms in Theory and Practice: Evolution Strategies, Evolutionary Programming, Genetic Algorithms. Oxford University Press, Oxford.

Bak, P., Chen, K., 1991. Self-organized criticality. Sci. Am. 261 (1), 46–53.

Barabási, A-L., 2002. Linked: The New Science of Networks. Perseus Books, Cambridge, MA.

Bateson, PPG, 1988. The active role of behavior in evolution. In: Ho, M.-W., Fox, S.F. (Eds.), Evolutionary Processes and Metaphors. Wiley, New York, NY, pp. 191–207.

Bateson, PPG, 2004. The active role of behaviour in evolution. Biol. Philos., 19; , pp. 283–298.

Bell, G., 1985. Origin and early evolution of germ cells as illustrated by the Volvocales. In: Halvorson, H.O., Monrony, A. (Eds.), Origin and Evolution of Sex. Alan R. Liss Inc., New York, NY, pp. 221–256.

Birch, J., Okasha, S., 2015. Kin selection and its critics. BioScience 65, 22–32.

Binmore, K., 2005. Natural Justice. MIT Press, Cambridge, MA.

Blitz, D, 1992. Emergent Evolution: Qualitative Novelty and the Levels of Reality. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Boehm, C., 1997. Impact of the human egalitarian syndrome on Darwinian selection mechanics. Am. Nat. 150, 5100–5120.

Bonner, J.T., 1988. The Evolution of Complexity by Means of Natural Selection. Princeton University Press, Princeton, NJ.

Bonner, J.T., 2003. On the origin of differentiation. J. Biosci. 28, 523–528.

Bonsall, M.B., 2010. The impact of non-lethal synergists on the population and evolutionary dynamics of host-pathogen interactions. J. Theor. Biol. 262, 567–575.

Brandon, R.N., 1996. Concepts and Methods in Evolutionary Biology. Cambridge University Press, New York.

Bromham, L, 2011. Wandering drunks and general lawlessness in biology: does diversity and complexity tend to increase in evolutionary systems? Biol. Philos. 26, 915–933.

Brown, J.S., Vincent, T.L, 2008. Evolution of cooperation with shared costs and benefits. Proc. R. Soc. B 275, 1985–1994.

Buchanan, M., 2000. Ubiquity: Why the World is Simpler Than We Think. Weidenfeld & Nicolson, London.

Buss, L.W., 1987. The Evolution of Individuality. Princeton University Press, Princeton, NJ..

Calcott, B., 2008. The *other* cooperation problem: generating benefit. Biol. Philos. 23, 179–203.

Calcott, B., Sterelny, K., 2011. The Major Transitions in Evolution Revisited. MIT Press, Cambridge, MA.

Caro, T., 2005. Antipredator Defenses in Birds and Mammals. University of Chicago Press, Chicago.

Carrapiço, F., 2010. How symbiogenic is evolution? Theor. Biosci. 129, 135–139.

Clutton-Brock, T., 2009. Cooperation between non-kin in animal societies. Nature 462, 51–57.

Cohen, D., Eshel, I., 1976. On the founder effect and the evolution of altruistic traits. Theor. Popul. Biol. 10, 276–302.

Corning, P.A., 1983. The Synergism Hypothesis: A Theory of Progressive Evolution. McGraw-Hill, New York.

Corning, P.A., 2003. Nature's Magic: Synergy in Evolution and the Fate of Humankind. Cambridge University Press, New York, NY.

Corning, P.A., 2005. Holistic Darwinism: Synergy, Cybernetics and the Bioeconomics of Evolution. University of Chicago Press, Chicago.

Corning, P.A., 2007a. Synergy goes to war: a bioeconomic theory of collective violence. J. Bioecon. 9, 104–144.

Corning, P.A., 2007b. Control information theory: the 'missing link' in the science of cybernetics. Syst. Res. Behav. Sci. 24, 297–311.

Corning, P.A., 2013. Rotating the Necker cube: a bioconomic approach to cooperation and the causal role of synergy in evolution. J. Bioecon. 15, 171–193.

Corning, P.A., 2014. Evolution 'on purpose': how behaviour has shaped the evolutionary process. Biol. J. Linn. Soc. 112, 242–260. http://dx.doi.org/10.1111/bij.12061.

Corning, P.A., Kline, S.J., 1998. Thermodyanmics, information and life revisited, Part II: Thermoeconomics and control information. Syst. Res. Behav. Sci. 15, 453–482.

Crow, J.F., 1979. Genes that violate Mendel's rules. Sci. Am. 240 (2), 134–146.

Crow, J.F., Aoki, K., 1982. Group selection for a polygenic behavioral trait: a differential proliferation model. Proc. Natl. Acad. Sci. U.S.A. 79, 2628–2631.

Czárán, T., Szathmáry, E., 2000. Coexistence of replicators in prebiotic evolution. In: Dieckmann, U., Law, R., Metz, J.A.J. (Eds.), The Geometry of Ecological Interactions: Simplifying Spatial Complexity. IIASA and Cambridge University, Cambridge, UK, pp. 116–134.

Darwin, C.R., 1968/1859. On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life. Penguin, Baltimore, MD.

Dawkins, R., 1989/1976. The Selfish Gene, second ed. Oxford University Press, Oxford UK.

Deacon, T.W., 2012. Incomplete Nature: How Mind Emerged from Matter. W.W. Norton & Co., New York, NY.

Dennett, D., 1995. Darwin's Dangerous Idea: Evolution and the Meaning of Life. Simon & Schuster, New York.

Eigen, M., 1971. Self-organization of matter and the evolution of macromolecules. Naturwiss 58, 465–523.

Fletcher, J.A., Zwick, M., Doebeli, M., Wilson, D.S., 2006. What's wrong with inclusive fitness? Trends Ecol. Evol. 21 (11), 597–598.

Frank, S.A., 1995. The origin of synergistic symbiosis. J. Theor. Biol. 176, 403–410.

Frank, S.A., 1997. Models of symbiosis. Am. Nat. 150 (S80-S99).

Frank, S.A., 2006. Social selection. In: Fox, C.W., Wolf, J.B. (Eds.), Evolutionary Genetics: Concepts and Case Studies. Oxford University Press, New York, NY, pp. 350–363.

Frederickson, M.E., 2013. Rethinking mutualism stability: cheaters and the evolution of sanctions. Q. Rev. Biol. 88, 269–295.

Gadagkar, R., 2010. Sociobiology in turmoil again. Curr. Sci. 99, 1036–1041.

Ghiselin, M., 1997. Metaphysics and the Origin of Species. State University of New York Press, Albany, NY.

Gilbert, S.F., Sapp, J., Tauber, A.I., 2012. A symbiotic view of life: we have never been individuals. Q. Rev. Biol. 87, 325–341.

Gontier, N., 2007. Universal symbiosis: an alternative to universal selectionist accounts of evolution. Symbiosis 44, 167–181.

Gould, S.J., 1977. Ontogeny and Phylogeny. Harvard University Press, Cambridge, MA.

Gould, S.J., 2002. The Structure of Evolutionary Theory. Belknap. Harvard University Press, Cambridge, MA.

Grafen, A., 1984. Natural selection, kin selection and group selection. In: Krebs, J.R., Davies, N.B. (Eds.), Behavioural Ecology. Blackwell Scientific Publications, Oxford, UK, pp. 62–84.

Grand, S., 2001. Creation: Life and How to Make It. Harvard University Press, Cambridge, MA.

Grant, P.R. 1986. Ecology and Evolution of Darwin's Finches. Princeton University Press, Princeton, NJ.

Grant, P.R., Grant, B.R., 2014. 40 Years of Evolution: Darwin's Finches on Daphne Major Island. Princeton University Press, Princeton, NJ.

Gregerson, N.H. (Ed.), 2002. From Complexity to Life: Explaining the Emergence of Life and Meaning. Oxford University Press, New York, NY.

Grey, D., Hutson, V., Szathmáry, E., 1995. A re-examination of the stochastic corrector model. Proc. R. Soc. B 262, 29–35.

Guilford, T., Cuthill, I., 1991. The evolution of aposematism in marine gastropods. Evolution 45, 449–451.

Haldane, J.B.S., 1932. The Causes of Evolution. Harper & Row, New York, NY.

Haldane, J.B.S., Huxley, J., 1927. Animal Biology. Oxford University Press, Oxford, UK.

Hamilton, W.D., 1975. Innate social aptitudes of man: an approach from evolutionary genetics. In: Fox, R. (Ed.), Biosocial Anthropology. Malaby Press, London, pp. 133–153.

Hammerstein, P., 1996. Darwinian adaptation, population genetics and the streetcar theory of evolution. J. Math. Biol. 34, 511–532.

Hauert, C., Michor, F., Nowak, M.A., Doebeli, M., 2006. Synergy and the discounting of cooperation in social dilemmas. J. Theor. Biol. 239, 195–202.

Heylighen, F., Bollen, J., Riegler, A. (Eds.), 1999. The Evolution of Complexity: The Violet Book of 'Einstein Meets Magritte'. Kluwer Academic Press, Dordrecht, The Netherlands.

Holland, J.H., 1998. Emergence: From Chaos to Order. Addison-Wesley (Helix Books), Reading, MA.

Hölldobler, B., Wilson, E.O., 2009. The Superorganism: The Beauty, Elegance and Strangeness of Insect Societies. W.W. Norton, New York, NY.

Hunt, P., 1998. The function of the Hox genes. In: Bittar, E.E., Bittar, N. (Eds.), Developmental Biology. Elsevier, London, pp. 261–291.

Hutchinson, G.E., 1965. The Ecological Theater and the Evolutionary Play. Yale University Press, New Haven, CT.

Jablonka, E., Lamb, M.J., 1995. Epigenetic Inheritance and Evolution: The Lamarckian Dimension. Oxford University Press, New York, Oxford.

Jablonka, E., Lamb, M.J., 2006a. Evolution in Four Dimensions: Genetic, Epigenetic, Behavioral, and Symbolic Variation in the History of Life. MIT Press, Cambridge, MA.

Jablonka, E., Lamb, M.J., 2006b. The evolution of information in the major transitions. J. Theor. Biol. 239, 236–246.

Kauffman, S.A., 1995. At Home in the Universe: The Search for the Laws of Self-Organization and Complexity. Oxford University Press, New York, NY.

Kauffman, S.A., 2000. Investigations. Oxford University Press, New York.

Kauffman, S.A., 2008. Reinventing the Sacred: A New View of Science, Reason, and the Sacred. Basic Books, New York, NY.

Keller, E.F., 2007. The disappearance of function from 'self-organizing systems'. In: Boogard, F.C., Bruggman, F.T., Hoffmeyr, J.-H.S., Westerhoff, H.V. (Eds.), Systems Biology. Elsevier, Amsterdam, pp. 303–317.

Kirk, D.L., 2005. A twelve-step program for evolving multicellularity and a division of labor. BioEssays 27, 299–310.

Kirschner, M.W., Gerhart, J.C., 2006. The Plausibility of Life: Resolving Darwin's Dilemma. Yale University Press, New Haven, CT.

Lack, D.L., 1961/1947. Darwin's Finches. Harper & Row, New York, NY.

Laland, K.N., Odling-Smee, F.J., Feldman, M.W., 1999. Evolutionary consequences of niche construction and their implications for ecology. Proc. Natl. Acad. Sci. U.S.A. 96, 10242–10247.

Laland, K.N., Sterelny, K., Odling-Smee, J., Hoppitt, W., Uller, T., 2011. Cause and effect in biology revisited: is Mayr's proximate-ultimate dichotomy still useful? Science 334, 1512–1516.

Lamarck, J.B., 1914/1809. Zoological Philosophy (Trans. H. Elliot.). Macmillan & Co., Ltd., London.

Lande, R., Arnold, S.J., 1983. Measurement of selection on correlated characters. Evolution 37, 1210–1226.

Law, R., 1991. The symbiotic phenotype: origins and evolution. In: Margulis, L., Fester, R. (Eds.), Symbiosis as a Source of Evolutionary Innovation. MIT Press, Cambridge, MA, pp. 57–71.

Lehmann, L., Keller, L., 2006. The evolution of cooperation and altruism—a general framework and a classification of models. J. Evol. Biol. 19, 1365–1376.

Leigh Jr., E.G., 1971. Adaptation and Diversity. Freeman, Cooper and Co., San Francisco.

Leigh Jr., E.G., 1977. How does selection reconcile individual advantage with the good of the group? Proc. Natl. Acad. Sci. U.S.A. 74, 4542–4546.

Leigh Jr., E.G., 1983. When does the good of the group override the advantage of the individual? Proc. Natl. Acad. Sci. U.S.A. 80, 2985–2989.

Leigh Jr., E.G., 1991. Genes, bees and ecosystems: the evolution of a common interest among individuals. Trends Ecol. Evol. 6, 257–262.

Leigh Jr., E.G., 2010a. The evolution of mutualism. J. Evol. Biol. 23, 2507–2528.

Leigh Jr., E.G., 2010b. The group selection controversy. J. Evol. Biol. 23, 6–19.

Leimar, O., Toumi, J., 1998. Synergistic selection in graded traits. Evol. Ecol. 12, 59–71.

Lewontin, R., 2000. The Triple Helix: Gene, Organism and Environment. Harvard University Press, Cambridge, MA.

Lloyd Morgan, C., 1923. Emergent Evolution. Williams and Norgate, London.

Lloyd Morgan, C., 1926. Life, Mind and Spirit. Williams and Norgate, London.

Lloyd Morgan, C., 1933. The Emergence of Novelty. Henry Holt and Co., New York, NY.

Margulis, L., 1970. Origin of Eukaryotic Cells. Yale University Press, New Haven, CT.

Margulis, L., 1993. Symbiosis in Cell Evolution. W.H. Freeman, New York.

Margulis, L., 1998. Symbiotic Planet: A New Look at Evolution. Basic Books, New York, NY.

Margulis, L., Fester, R (Eds.), 1991. Symbiosis as a Source of Evolutionary Innovation: Speciation and Morphogenesis. MIT Press, Cambridge, MA.

Margulis, L., Sagan, D., 2002. Acquiring Genomes: A Theory of the Origins of Species. Basic Books, New York, NY.

Matessi, C., Jayakar, S.D., 1976. Conditions for the evolution of altruism under Darwinian selection. Theor. Popul. Biol. 9, 360–387.

Maynard Smith, J., 1979. Hypercycles and the origin of life. Nature 280, 445–446.

Maynard Smith, J., 1982. The evolution of social behavior—a classification of models. In: The King's College Sociobiology Group (Eds.), Current Problems in Sociobiology. Cambridge University Press, Cambridge, UK, pp. 28–44.

Maynard Smith, J., 1983. Models of evolution. Proc. R. Soc. B 219, 315–325.

Maynard Smith, J., 1998. Evolutionary Genetics, second ed. Oxford University Press, Oxford, UK.

Maynard Smith, J., Szathmáry, E., 1995. The Major Transitions in Evolution. Freeman Press, Oxford, UK.

Maynard Smith, J., Szathmáry, E., 1999. The Origins of Life: From the Birth of Life to the Origin of Language. Oxford University Press, Oxford, UK.

Mayr, E., 1961. Cause and effect in biology. Science 134, 1501–1506.

McShea, D.W., Brandon, R.N., 2010. Biology's First Law: The Tendency for Diversity and Complexity to Increase in Evolutionary Systems. University of Chicago Press, Chicago, IL.

Mereschkovsky, K.C., 1909. The Theory of Two Plasms as the Basis of Symbiogenesis. New Studies About the Origins of Organisms (in Russian), Kazan, USSR.

Mesterton-Gibbons, M., Dugatkin, L.A., 1992. Cooperation among unrelated individuals: evolutionary factors. Q. Rev. Biol. 67, 267–281.

Michod, R.E., 1999. Darwinian Dynamics, Evolutionary Transitions in Fitness and Individuality. Princeton University Press, Princeton, NJ.

Michod, R.E., 2005. On the transfer of fitness from the cell to the mutlicellular organism. Biol. Philos. 20, 967–987.

Michod, R.E., 2007. Evolution of individuality during the transition from unicellular to multicellular life. Proc. Natl. Acad. Sci. U.S.A. 104, 8613–8618.

Michod, R.E., 2011. Evolutionary transitions in individuality: multicellularity and sex. In: Calcott, B., Sterelny, K. (Eds.), The Major Transitions in Evolution Revisited. MIT Press, Cambridge, MA, pp. 169–197.

Michod, R.E., Herron, M.D., 2006. Cooperation and conflict during evolutionary transitions in individuality. J. Evol. Biol. 19, 1406–1409.

Morowitz, H.J., 2002. The Emergence of Everything. Oxford University Press, Oxford, UK.

Nee, S., 1989. Does Hamilton's rule describe the evolution of reciprocal altruism? J. Theor. Biol. 141, 81–91.

Nowak, M.A., 2006. Five rules for the evolution of cooperation. Science 314, 1560–1563.

Nowak, M.A., 2011. Super Cooperators: Altruism, Evolution and Why We Need Each Other to Succeed (with R. Highfield). Free Press, New York, NY.

Nowak, M.A., 2012. Evolving cooperation. J. Theor. Biol. 299, 1–8.

Nowak, M.A., Tarnita, C.E., Wilson, E.O., 2010. The evolution of eusociality. Nature 446, 1057–1062.

Odling-Smee, F.J., Laland, K.N., Feldman, M.W., 1996. Niche construction. Am. Nat. 147, 641–648.

Odling-Smee, F.J., Laland, K.N., Feldman, M.W., 2003. Niche Construction: The Neglected Process in Evolution. Princeton University Press, Princeton, NJ.

Odling-Smee, J., Erwin, D.H., Palkovacs, E.P., Feldman, M.W., Laland, K.N., 2013. Niche construction theory: a practical guide for ecologists. Q. Rev. Biol. 88, 3–28.

Ohtsuki, H., 2012. Does synergy rescue the evolution of cooperation? An analysis for homogeneous populations with non-overlapping generations. J. Theor. Biol. 307, 20–28.

Okasha, S., 2005. Multilevel selection and the major transitions in evolution. Philos. Sci. 72, 1013–1025.

Pereira, L., Rodrigues, T., Carrapiço, F., 2012. A symbiogenic way in the origin of life. In: Seckbach, J. (Ed.), Genesis—In the Beginning: Precursors of Life, Chemical Models and Early Biological Evolution. Springer Science+Business Media, Dordrecht, The Netherlands, pp. 723–742.

Price, M.E., Johnson, D.D.P., 2011. The adaptationist theory of cooperation in groups: evolutionary predictions for organizational cooperation. In: Saad, G. (Ed.), Evolutionary Psychology in the Business Sciences. Springer-Verlag, Berlin-Heidelberg, pp. 95–133.

Purcell, J., Brelsford, A., Avilés, L., 2012. Co-evolution between sociality and dispersal: the role of synergistic cooperative benefits. J. Theor. Biol. 312, 44–54.

Queller, D C, 1985. Kinship, reciprocity, and synergism in the evolution of social behavior. Nature 318, 366–367.

Queller, D.C., 1997. Cooperators since life began. (Review of the major transitions in evolution, by John Maynard Smith and Eörs Szathmáry.). Q. Rev. Biol. 72, 184–188.

Queller, D.C., 2000. Relatedness and the fraternal major transitions. Philos. Trans. R. Soc. B 355, 1647–1655.

Queller, D.C, 2004. Kinship is relative. Nature 430, 975–976.

Raff, R.A., 1996. The Shape of Life: Genes, Development, and the Evolution of Animal Form. University of Chicago Press, Chicago, IL.

Ratcliff, W.C., Denison, R.F., Borrello, M., Travisano, M., 2012. Experimental evolution of multicellularity. Proc. Natl. Acad. Sci. U.S.A. 109 (5), 1595–1600.

Ratnieks, F.L.W., 2006. The evolution of cooperation and altruism: the basic conditions are simple and well known. J. Evol. Biol. 19, 1413–1414.

Reid, R.G.B., 2007. Biological Emergences: Evolution by Natural Experiment. MIT Press, Cambridge, MA.

Reinheimer, H., 1913. Evolution by Co-operation: A Study in Bioeconomics. Kegan, Paul, Trench, Trubner, London.

Reinheimer, H., 1915. Symbiogenesis: The Universal Law of Progressive Evolution. Knapp Dewett and Sons, London.

Robinson, G.E., 1992. Regulation of division of labor in insect societies. Annu. Rev. Entomol. 37, 637–665.

Russell, B., 1927. The Analysis of Matter. Allen and Unwin, London.

Sachs, J.L., Mueller, U.G., Wilcox, T.P., Bull, J.J., 2004. The evolution of cooperation. Q. Rev. Biol. 79, 135–160.

Sapp, J., 2004. The dynamics of symbiosis: an historical overview. Can. J. Bot. 82, 1046–1056.

Sapp, J., 2009. The New Foundations of Evolution, on the Tree of Life. Oxford University Press, Oxford, UK.

Schlichting, C.D., 2003. Origins of differentiation via phenotypic plasticity. Evol. Dev. 5, 98–105.

Schulz, A., 2014. Niche construction, adaptive preferences, and the differences between fitness and utility. Biol. Philos. 29, 315–335.

Seeley, T.D., 1995. The Wisdom of the Hive: The Social Physiology of Honey Bee Colonies. MIT Press, Cambridge, MA.

Shapiro, J.A., 2012. Evolution: A View from the 21st Century. FT Press Science, Upper Saddle River, NJ.

Simon, B., 2014. Continuous-time models of group selection, and the dynamical insufficiency of kin selection models. J. Theor. Biol. 349, 22–31.

Simpson, C., 2012. The evolutionary history of the division of labour. Proc. R. Soc. B 279, 116–121.

Sober, E., Wilson, D.S., 1998. Unto Others: The Evolution and Psychology of Unselfish Behavior. Harvard University Press, Cambridge, MA.

Smith, A., 1964/1776. The Wealth of Nations (2 vols.). J.M. Dent, London.

Spencer, H., 1892/1852. The development hypothesis. Reprinted in Essays: Scientific, Political and Speculative, vol. I. Appleton, New York, NY, pp. 1–7.

Sumpter, D.J.T., 2010. Collective Animal Behavior. Princeton University Press, Princeton, NJ.

Szabó, P., Scheuring, I., Czárán, T., Szathmáry, E., 2002. In silico simulations reveal that replicators with limited dispersal evolve towards higher efficiency and fidelity. Nature 420, 360–363.

Szathmáry, E., 1986. The eukaryotic cell as an information integrator. Endocytobiol. Cell Res. 3, 113–132.

Szathmáry, E., 2002. Cultural processes: the latest major transition in evolution. In: Nadel, L. (Ed.), Encyclopedia of Cognitive Science. Nature Publishing Group, Macmillan, London http://dx.doi.org/10.1002/0470018860.s00716.

Szathmáry, E., 2012. Transitions and social evolution. A review of principles of social evolution, by Andrew F.G. Bourke. Philos. Theor. Biol. 4, e302.

Szathmáry, E., 2015. Towards major transitions theory 2.0. Proc. Natl. Acad. Sci. U.S.A. (accepted).

Szathmáry, E., Demeter, L., 1987. Group selection of early replicators and the origin of life. J. Theor. Biol. 128, 463–486.

Szathmáry, E., Számadó, S., 2008. Language: a social history of words. Nature 456 (6), 40–41.

Taylor, P., 2013. Inclusive and personal fitness in synergistic evolutionary games on graphs. J. Theor. Biol. 325, 76–82.

Toumi, J., Augner, M., 1993. Synergistic selection of unpalatability in plants. Evolution 47, 668–672.

Traulsen, A., Nowak, M.A., 2006. Evolution of cooperation by multilevel selection. Proc. Natl. Acad. Sci. U.S.A. 103, 10952–10955.

Uyenoyama, M.K., 1979. Evolution of altruism under group selection in large and small populations in fluctuating environments. Theor. Popul. Biol. 15, 58–85.

van Veelen, M., 2009. Group selection, kin selection, altruism and cooperation: when inclusive fitness is right and when it can be wrong. J. Theor. Biol. 259, 589–600.

Vermeij, G.J., 2009. Comparative economics: evolution and the modern economy. J. Bioecon. 11, 105–134.

Wagner, G.P., 2014. Homology, Genes and Evolutionary Innovation. Princeton University Press, Princeton, NJ.

Weber, B.H., Depew, D.J., 2003. Evolution and Learning: The Baldwin Effect Reconsidered. MIT Press, Cambridge, MA.

Weiner, J., 1994. The Beak of the Finch. Vintage Books, New York, NY.

West, S.A., Griffin, A.S., Gardner, A., 2007a. Evolutionary explanations for cooperation (review). Curr. Biol. 17, R661–R672.

West, S.A., Griffin, A.S., Gardner, A., 2007b. Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. J. Evol. Biol. 20, 415–432.

West, S.A., Griffin, A.S., Gardner, A., 2008. Social semantics: how useful has group selection been? J. Evol. Biol. 21, 374–385.

West, S.A., El Mouden, C., Gardner, A., 2011. Sixteen common misconceptions about the evolution of cooperation in humans. Evol. Hum. Behav. 32, 231–262.

West-Eberhard, M.J., 2003. Developmental Plasticity and Evolution. Oxford University Press, Oxford, UK.

Wilson, D.S., 1975. A theory of group selection. Proc. Natl. Acad. Sci. U.S.A. 72, 143–146.

Wilson, D.S., 1977. Structured demes and the evolution of group advantageous traits. Am. Nat. 111, 157–185.

Wilson, D.S., 1978. Structured demes and trait-group variation. Am. Nat. 113, 606–610.

Wilson, D.S., 1980. The Natural Selection of Populations and Communities. Benjamin Cummings, Menlo Park, CA.

Wilson, D.S., 1990. Weak altruism, strong group selection. Oikos 59, 135–140.

Wilson, D.S., 2006. Human groups as adaptive units: toward a permanent consensus. In: Carruthers, P., Laurence, S., Stich, S. (Eds.), The Innate Mind: Culture and Cognition. Oxford University Press, Oxford, UK, pp. 88–90.

Wilson, D.S., Sober, E., 1989. Reviving the superorganism. J. Theor. Biol. 136, 337–356.

Wilson, D.S., Sober, E., 1994. Reintroducing group selection to the human behavioral sciences. Behav. Brain Sci. 17, 585–608.

Wilson, D.S., Wilson, E.O., 2007. Rethinking the theoretical foundation of sociobiology. Q. Rev. Biol. 82, 327–348.

Wilson, D.S., Wilson, E.O., 2008. Evolution 'for the good of the group'. Am. Sci. 96, 380–389.

Wilson, E.O, 2013. The Social Conquest of Earth. Liveright Publishing Corp, New York, NY.